Marine Mammals of the World

Systematics and Distribution

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INTRODUCTION

The unprecedented growth of interest in living marine mammals over the last two decades has triggered a resurgence in studies of their systematics and distribution. Increasing paleontological activity is also leading to finds of some remarkable fossil marine mammals that are filling the gaps in the evolutionary trees of these animals (Repenning 1976*a,* Berta and Deméré 1994). During this period systematic biology has undergone major transformations in both theory and practice (Minelli 1993, Quicke 1993). Because of these developments, *A List of the Marine Mammals of the World (Third Edition)* (Rice 1977) became so outdated that a complete rewriting was necessary (the first two editions were published by Scheffer and Rice 1963, and by Rice and Scheffer 1968). I have taken this opportunity to expand the coverage of the taxonomic literature and to provide more detailed accounts of geographical ranges.

One of the fundamental changes in systematic biology is that phylogenetic systematics, or cladistics, developed by the German entomologist Willi Hennig (1966), has been embraced by almost all systematists. For reconstructing phylogenetic trees, cladistics provides an objective procedure that has a sound theoretical basis (Wiley 1981, Ax 1987). Along with it has come the insistence on strictly phylogenetic classifications, instead of the so-called "evolutionary" or syncretistic principles espoused by Mayr (1942, 1969) and Simpson (1945, 1961). Phylogenetic systematists insist that each taxon be monophyletic—meaning, in practice, that it must be diagnosed by derived character-states, or evolutionary novelties (apomorphies), not by primitive ones (plesiomorphies). This has necessitated the elimination of many familiar, traditional groups that were paraphyletic—such as "suborder Archaeoceti" among the Cetacea. It has also generated some inconveniences, such as "lopsided" classifications with a proliferation in the number of ranks. Paleontologists have yet to settle upon suitable conventions for including fossil taxa in a classification of living members, without making it overly complex and cumbersome. One method is to forego the conventional designations of rank, and to indicate relative rank by subordination—shown by indentation, numeration, or a cladogram.

The other significant advance is the rapid proliferation and growing sophistication of molecular techniques. These are leading to breakthroughs in our understanding of the life histories, ecology, and demography of a wide variety of species, as well as their phylogeny and systematics. In the latter fields, molecular assays can establish the identity and genealogy of individual plants and animals, and at the other end of the evolutionary hierarchy they can resolve the phylogenetic relationships between the primary divisions of living organisms.

Besides the older methods of cytogenetics and enzyme electrophoresis, we can now sequence the amino-acids of proteins, and the nucleotides of nuclear and mitochondrial DNA and RNA (Hillis and Moritz 1990, Li and Graur 1991, Miyamoto and Cracraft 1991, Avise 1994, Ferraris and Palumbi 1996, Hillis *et al.* 1996, Li 1997). A procedure with coarser resolution is restriction-site mapping of DNA. These techniques have opened a trove of new data for cladistic analyses. One of the oldest molecular techniques is immunologic cross-reactions, which provides only quantitative distance data (*i.e.,* relative magnitude of differences between taxa); even though such data are not suitable for cladistic analyses, they have been shown to be fairly reliable for estimating phylogenies (Prager 1993, Sarich 1993). DNA hybridization is another "distance" method that is being used to reconstruct phylogenies (Sibley and Ahlquist 1990).

Initial faith in the near-infallibility of these molecular studies has now been tempered by a more sober appraisal of their strengths and weaknesses. Molecular techniques are not free of many of the difficulties—such as homoplasy—that beset morphological techniques, and they have some all their own—such as paralogy and correct sequence alignment. Unlike morphological data, nucleotide sequence data generate only gene-phylogenies, not species-phylogenies. In any given clade, gene-phylogenies are not necessarily congruent with the species-phylogeny or with each other, so that cladograms derived from different kinds of molecular data are frequently contradictory. Even cladograms derived from a single data set may differ in accordance with the particular method used to reconstruct the phylogeny. Also, the polarity of character-state changes cannot be inferred *a priori,* so that only unrooted cladograms can be produced; even when outgroups are included in the analysis, placement of the root still depends ultimately on morphological evidence. In any given cladistic analysis, the consistency index[1] of the most parsimonious cladogram is often quite low, especially when the number of taxa is high, and there are usually a number of alternate cladograms with consistency indices almost as great.

Perhaps the most serious deficiency that has compromised the credibility of many molecular phylogenetic studies is that each higher taxon is usually represented by only one or a few of its species; such incomplete analyses frequently yield incorrect results, especially for phylogenies in which the internal, ancestral branches are short relative to the terminal branches (Philippe and Douzery 1994; Adachi and Hasegawa 1995, 1996).

Another serious deficiency has been the routine use of only one or at most a few specimens to represent each species, so that no cognizance is taken of individual or geographic variation (Smouse *et al.* 1991). For example, in a cladogram based on the amino acid sequences of myoglobin, one specimen of *Delphinus delphis* formed a clade with *Tursiops truncatus* and *Stenella frontalis,* but another specimen formed a clade with *Globicephala melas* and *Orcinus orca* (Goodman *et al.* 1982).

[1] The consistency index (C.I.) is a measure of the relative number of homoplasies (parallel, convergent, or reverse changes in character-states) in a cladogram. In simple terms, 1.00 minus the C.I. is equal to the proportion of character-state changes (or steps) that are homoplastic. If, for example, the C.I. is 0.75, it means that one quarter of all changes are homoplastic. A perfectly consistent cladogram with no inferred homoplasies, in which each character-state change takes place only once, has a C.I. of 1.00.

Molecular studies have almost always corroborated previous classifications that were strongly supported by morphological evidence. It is in those groups where the morphological analyses have been ambivalent or poorly-resolved that molecular studies are proving most useful. When molecular conclusions contradict a well-supported morphological classification, the fault likely lies with the model used in the molecular analysis—for a cautionary tale see Sullivan and Swofford (1997).

Format of list—This list includes all Recent species of seals, sea-lions, and walruses (order Carnivora: taxon Pinnipedia), whales, dolphins, and porpoises (order Cetacea), and sea-cows (order Sirenia). Almost all of them depend on the marine habitat for their survival, but for completeness I have listed all species of these three taxa, even though 2 of the 36 species of pinnipeds, 3 of the 83 species of cetaceans, and 1 of the 5 species of sirenians inhabit inland waters exclusively—in all cases freshwater rivers and lakes, except for one pinniped endemic to the landlocked saline Caspian Sea. One other order of marine mammals, the Desmostylia, has been extinct since the early Pliocene (see discussion under order Sirenia). Yet another order of mammals, the Xenarthra (sloths, anteaters, armadillos, and the extinct glyptodonts), was lately added to the list of orders with marine species when bones of an apparently amphibious ground sloth *Thalassocnus natans* (family Megalonychidae) were discovered in the Pliocene of Peru (Muizon and McDonald 1995).

Several other species that are sometimes regarded as marine mammals are listed in Appendix 1. These include three fissiped (non-pinniped) carnivores that are dependent on the marine environment—the polar bear and two otters. In addition, some local populations of several other kinds of otters and the arctic fox also live in marine environments, but those species are not dependent on marine habitats so they are not formally regarded as marine mammals. Finally, among the bats, order Chiroptera, a few species have taken to preying on fishes and other small aquatic animals, including two species that regularly fish in marine waters.

In this list the sequence of orders, families, genera, *etc.,* generally follows the customary guidelines (paraphrased from Mayr and Greenway 1956): (1) to follow as closely as possible the traditional arrangements, except where subsequent work has shown conclusively that a change is advisable; (2) to place near each other taxa which are presumably closely related; and (3) to place the more primitive taxa near the beginning and the more derived taxa near the end. In taxa for which published cladograms are available, I have used the "phyletic sequencing" convention (Nelson 1973) where feasible, but no linear list can reflect a branching phylogeny, so one should not read too much into the sequence.

The entry for each species includes its scientific name, any English names, a brief review and assessment of published studies on geographical variation, and a delineation of its geographical distribution.

This list of the world's marine mammals, like any such list, is only a progress report—a synopsis of our knowledge and uncertainties at the time it was written. No list of scientific names can ever be considered the "correct" list. Taxonomists sometimes disagree with each other, and classifications are changed continually as new facts are brought to light and new interpretations emerge. Even in such well-studied groups as the rorquals (*Balaenoptera*), the bottlenose dolphins (*Tursiops*), and the saddleback, or "common," dolphins (*Delphinus*), major taxonomic problems at the species level are just now beginning to be unraveled. All researchers, whatever their specialty, must stay aware of the current taxonomic literature.

Scientific names—The formal zoological names are sometimes called Latin names, although most generic names are derived from the Greek—either transliterated into the Roman alphabet, or Latinized. In practice, any names are accepted, even barbarous ones. Native vernacular names have given us *Pusa* (Inuit of Greenland), *Mirounga* (Australian aboriginal), *Inia* (Guarayu of Bolivia), *Sousa* (Hindi), *Grampus* (English), *Feresa* (French), and *Dugong* (Malay). A few others, such as *Sotalia,* were arbitrarily made up.

Names from the rank of superfamily down to subspecies are governed by the International Code of Zoological Nomenclature (hereinafter ICZN Code), published by the International Commission on Zoological Nomenclature (ICZN 1985). Genus-group (genus and subgenus) names are singular nouns. Species-group (species and subspecies) names may be adjectives, nouns in apposition, attributive nouns, or possessive nouns. If they are Latin adjectives, they must agree in gender with the generic name. With each generic and specific name, I have included the name of the author and the date (separated by a comma, as recommended by the ICZN Code, Article 22), but have not included the original publications in the Literature Cited. If the author and date of a species-group name are in parentheses, the name has been transferred to a genus other than the one in which it was originally described, as prescribed by Article 51(c) of the ICZN Code. The author's name and the date are not part of the scientific name (Article 51(a) of the ICZN Code), and are unnecessary in the text or title of a scientific publication, unless it deals specifically with matters of nomenclature.

For full citations to the original descriptions of generic names, living and fossil, along with their etymology and type species, see *Index generum mammalium* by Palmer (1904); its supplements by Conisbee (1953, 1960, 1964, 1970, 1975) include only living genera. These references include all genus-group names—synonyms as well as valid names—of Recent marine mammals except for *Australophocoena,* which was proposed later by Barnes (1985*a*). For most species and subspecies, the type localities, synonyms, and bibliographic details for the original publications may be found in the *Catalog of living whales* by Hershkovitz (1966), in the monographs on pinnipeds by Allen (1880) and Scheffer (1958), and in the bibliography of sirenians by Domning (1996). The pre-1841 literature on cetaceans and sirenians was compiled and abstracted by Allen (1881). Other useful sources are the world list of mammals by Wilson and Reeder (1993), and regional checklists, particularly those by Anderson (1946), Miller and Kellogg (1955), and Hall (1981) for North

America, Central America, and the West Indies; by Cabrera (1957, 1961) for South America; by Ellerman and Morrison-Scott (1951) and Corbet (1978) for the Palearctic and Indian regions; by Corbet and Hill (1992) for the Indomalayan region; by Chasen (1940; supplement by Ellerman and Morrison-Scott 1955) for the Malay Peninsula and Greater Sundas; by Allen (1939; supplement by Ansell 1989), Ellerman *et al.* (1953), and Meester *et al.* (1986) for Africa; and by Bannister *et al.* (1988) and Iredale and Troughton (1934) for Australia. In the accounts that follow, I have included those generic and specific synonyms that are frequently encountered in mid to late 20th century references.

The basic principle of the ICZN Code is priority (Melville 1995), but Article 23(b) of the Code dictates that if the application of the Principle of Priority would disturb stability or universality, existing usage should be maintained, and the case should be referred to the Commission for a ruling. The Commission renders Opinions on individual cases, and, as appropriate, names may be entered in the Official Lists of Names in Zoology, which ensures their availability (but not necessarily their priority), or in the Official Indexes of Rejected and Invalid Names. Several names in this list have been conserved by Opinions of the Commission, and one case is currently pending before the Commission (Appendix 2). In this list I have also retained one generic and two family-group names that are junior synonyms, but which have enjoyed near-universal usage for many decades, in anticipation that the ICZN will be petitioned to conserve them.

The names of family-group taxa, which includes all categories from superfamily down to subtribe, were not subject to the law of priority until publication of the third edition of the Code in 1985 (ICZN 1985). Each family-group name is formed from the grammatical stem of the name of an included genus, with the addition of an appropriate suffix (see Appendix 3). The prescribed Latin plural suffixes are: superfamily, -oidea; family, -idae; subfamily, -inae; tribe, -ini; and subtribe, -ina. These names are treated as plural nouns, notwithstanding the adjectival origin of their suffixes. Names at all ranks in the family-group are nomenclaturally equivalent, so precedence is given to the earliest name, regardless of its original rank (and suffix). Even if its rank and suffix are changed, its author and date remain the same (ICZN Code Article 36(a)). Prior to 1985, there was little consistency in the way that authorship was attributed to family-group names. Therefore I have cited in full the original publication of the names of all Recent family-group taxa—including unused synonyms as well as names that are currently recognized as valid taxa. I have included any emended spellings of the stem of each name, but I have not cited alterations in the suffixes that denote rank, because the formal rank, *per se,* conveys no phylogenetic information. The names of family-group taxa based upon fossil genera (Appendix 3) have the same status under the ICZN Code as any other family-group names, but none happens to have priority over any of the names used in this list for Recent family-group taxa.

Names above the family-group—Phylum, Class, Order, Suborder, Infraorder, *etc.*—are not covered by the ICZN Code; rather their usage is governed

Table 1. Number of genera and species in the major taxa of marine mammals.

Taxon	Number of genera	Number of species	Mean number of species per genus	Number (and percent) of monotypic genera[a]
Pinnipedia[b]	21	36	1.71	19 (90%)
Cetacea[c]	39	83	2.13	30 (77%)
Sirenia	3	5	1.67	3 (100%)
All three	63	124	1.97	52 (83%)

[a] Includes quasimonotypic as well as strictly monotypic genera.
[b] *Arctocephalus* and *Monachus* are the only genera of pinnipeds here considered polytypic, and the status of both is debatable.
[c] Cetacean genera here considered polytypic are *Balaena, Balaenoptera, Phocoena, Cephalorhynchus, Lagenorhynchus, Stenella, Delphinus, Mesoplodon,* and *Kogia.*

by tradition and consensus. There are no generally accepted suffixes for them. Although many formal zoological names are formed with Latin plural adjectival endings, usually neuter, such as *-acea* and *-ia,* all are treated as plural nouns.

In the present classification, the three major taxa of marine mammals—Pinnipedia, Cetacea, and Sirenia—include 124 species arranged into 63 genera, an average of only 1.97 species per genus (Table 1). By contrast, the ungulates (orders Perissodactyla, Artiodactyla, and Proboscidea), a comparable assemblage of large terrestrial mammals, include 240 species divided among 89 genera, an average of 2.70 species per genus (Wilson and Reeder 1993). Eighty-three percent of marine mammal genera are monotypic—either strictly so (containing only one species) or quasimonotypic (containing one superspecies) (*cf.* Amadon 1968). Only 11 of the 89 genera are polytypic, and, ironically, at least two of these—*Lagenorhynchus* and *Stenella*—may be polyphyletic or paraphyletic assemblages of species. It is clear that in the classification of the marine mammals, the generic category is not being used in a very effective way. The information content of the classification would be significantly increased if future taxonomic studies lead to fewer, more broadly-construed genera—particularly among the Otariidae, Phocidae, and Delphinidae.

English names—A distinction must be recognized between vernacular names and literary names. Vernacular, colloquial, or common names are the "names used by people who are sympatric with" the animals in question (Parkes 1975). For marine mammals, this most often means the names used by fishermen and other mariners who encounter them in their day-to-day work, and especially the whalers and sealers—both commercial and subsistence—who have customarily hunted them. Unfortunately, the majority of marine mammal species have no specific vernacular names. Other species—especially those that are widely distributed, as are many marine mammals—may be known by different vernacular names in different regions, even where the same language is spoken; a good example is *Phoca vitulina,* which Americans call the "harbor seal," but which the British call the "common seal" (despite its being the rarer of the two resident species of seals in the British Isles). Conversely, the same vernacular name may be used for different species in different areas; for instance, when they said "bottlenose whale," whalers in California and British Columbia meant *Berardius bairdii,* but whalers in Newfoundland meant *Hyperoodon ampullatus.* I have not listed vernacular names in foreign languages, except for those in use by English-speaking people, and those that have been adopted by English-language writers. Hershkovitz (1966) and Ridgway and Harrison (1981–1994) provided comprehensive lists of foreign names for cetaceans.

Literary names, or "book names," are the names that appear only in published works, popular or scientific. Fortunately, in some instances—such as "fin whale"—the vernacular and literary names are the same. For the many species of marine mammals that have no specific vernacular names, cetologists have contrived at least one literary name. Many distinctive English names have been formed by adding a modifier (often geographic) to the vernacular name. In the example of the bottlenose whales mentioned above, the two species may be called the "North Pacific bottlenose whale" and the "North Atlantic bottlenose whale," respectively.

Depending on the audience, either the vernacular name or the literary name may be more appropriate. If the readers are familiar with cetaceans, they will understand that the vernacular "susu" means *Platanista gangetica,* but for a general audience, "susu" is meaningless, whereas the book name "Ganges river-dolphin" would be comprehensible.

In the formation of compound group names, I have adopted the convention proposed by Parkes (1978) for English names of bird species. If its second component is a misnomer, the name should be spelled as a closed compound, or as a hyphened compound if a single word might imply an incorrect pronunciation. Thus I use the hyphened compound "sea-lion" instead of "sea lion," because sea-lions are not lions. Likewise "sea-cow" rather than "sea cow," "sea-elephant" rather than "sea elephant," and "fur-seal" rather than "fur seal" (the term "seal" is better restricted to the "true," or earless, seals of the family Phocidae). On the other hand, "elephant seal" is written as an open compound because it is a true seal.

In the use of possessives *versus* attributives for patronyms, I have ignored consistency in favor of euphony and common sense. "Ross seal" is obviously better than "Ross's seal," while "True's beaked whale" and "Gray's beaked whale" avoid the ambiguity that could arise from "True beaked whale" and "Gray beaked whale." Geographical modifiers may be adjectives (Japanese sea-lion; Antillean manatee) or attributive nouns (California sea-lion, Florida manatee), depending on conventional usage. Similarly, compound modifiers may be adjectives (white-beaked dolphin, longfinned blackfish), nouns in apposition (humpback whale, bottlenose dolphin), or a combination (shortsnouted spinner dolphin; longbeaked saddleback dolphin). Following standard grammatical practice, compound modifiers are always hyphened or closed (bottlenose dolphin, *not* bottle nose dolphin; right-whale dolphin, *not* right whale dolphin).

The listings of common names are intended to be informative, not prescrip-

Table 2. Number of species currently considered polytypic in the major taxa of marine mammals.

Taxon	Total number of species	Number (and percent) of polytypic species
Pinnipedia	36	6 (17%)
Cetacea	83	17 (20%)
Sirenia	5	2 (40%)
All three	124	25 (20%)

tive. I have tried to put the most suitable ones, or those most widely used, first. Vernacular names are given preference over book names. Guidelines for choosing between alternate names have been drafted by the American Fisheries Society (AFS) (Robins *et al.* 1991) and the American Ornithologists' Union (AOU 1973). For example, the AFS rejects the use of patronyms, and both reject the use of the modifier "common," as meaningless to most people. Thus "grampus" is preferable to "Risso's dolphin," and "harbor seal" is preferable to "common seal." Such rules should not be blindly obeyed, however. "Bryde's whale," for example, is a true vernacular name, and has no contending synonyms. Others such as "Weddell seal" and "Dall's porpoise," are so well-entrenched among researchers that it would be silly to try to change them to something more "appropriate." Especially in the large and confusing genus *Mesoplodon,* patronyms, such as "Stejneger's beaked whale" for *M. stegnegeri,* can serve as mnemonic devices.

The term "porpoise" has often been used for dolphins of the family Delphinidae, especially by Americans; the term "dolphin," however, is never used for the true porpoises of the family Phocoenidae. The etymology of these names and other English vernacular generic names is explained in *The Oxford English Dictionary, second edition,* and in Partridge's (1983) *Origins.*

Finally, I urge anyone who has a serious interest in marine mammals to learn their scientific names. Amateur gardeners have no difficulty with names such as *Delphinium, Philodendron,* and *Zinnia,* so no one should have trouble learning *Delphinus, Phocoenoides,* and *Ziphius.*

Geographical variation—For most of the widespread species of marine mammals, the number of specimens in collections is far too few to provide even a vague picture of their geographic variation. Vast areas of the world's oceans are still unrepresented by any cetacean specimens. Until museums acquire many more specimens from all over the globe, the full extent of the biodiversity represented by the world's marine mammal fauna will remain unknown. This may explain why marine mammals largely escaped the orgiastic naming of new subspecies that afflicted the study of terrestrial mammals in the late 19th and much of the 20th centuries. However, recent studies reveal that most of the widespread species of cetaceans and other marine mammals do show geographic variation. At the present time only 22% of the species of marine mammals are considered polytypic (Table 2), but future studies will doubtless increase the number that have formally recognized subspecies. By comparison, among the 240 species of ungulates listed by Wilson and Reeder (1993), 147 (61%) are currently considered polytypic, according to the latest taxonomic literature on the various taxa.

Populations of large whales isolated in major ocean basins tend to differ; a common pattern among species with an antitropical (bipolar) distribution is morphological divergence between Northern and Southern hemisphere populations (Tomilin 1946). Small cetaceans, which are generally less migratory than the great whales, may vary sharply over sometimes relatively short distances; two major patterns are divergence between inshore and offshore populations, and between populations on the open ocean and those in enclosed seas (Perrin 1984). Among the river-dolphins, populations in different drainage basins have differentiated, and most landlocked seals differ from their nearest marine relatives.

The strongest geographical differentiation tends to develop between isolated populations. However, contiguous populations may also differ just as much—such as in the spinner dolphins of the eastern tropical Pacific. Intergradation between adjacent subspecies may be clinal over a wide zone (often correlated with ecological gradients), as in the polar bear and bearded seal, or it may be abrupt, as in the spinner dolphins. In the former situation, termed primary intergradation, the boundary line—if one must be drawn—is rather arbitrarily positioned along the midline of the character-gradient (Mengel and Jackson 1977). Many of the abrupt subspecies boundaries—often with a narrow "hybrid zone"—are thought to result from secondary intergradation, or contact between previously disjunct populations. This may be the case with the "whitebelly" spinner dolphins in the eastern tropical Pacific, which appear to be a *Stenella longirostris longirostris* × *S. l. orientalis* hybrid swarm (Dizon *et al.* 1994).

A comparison of almost any two natural populations will reveal statistically significant differences in the means of at least some parameters, but it would serve no purpose to name each slightly-differentiated population as a subspecies. Each taxonomist has his own opinion on the amount of morphological overlap that is allowable for subspecies (Rand and Traylor 1950). The criterion most often cited is the 75 percent rule, which states that "75 per cent of a population must be separable from all (99+ per cent) of the members of overlapping populations to qualify as a subspecies. An equivalent statement is that 97 per cent of one of two overlapping populations must be separable from 97 per cent of the other" (Amadon 1949). In the past, subspecies were often based on univariate, or at most bivariate (ratios), metrics. More recently the development of multivariate statistical procedures has allowed more discriminating analyses based on multiple parameters.

Molecular genetics has now opened an additional perspective, termed phylogeography, on the process of subspeciation (Avise *et al.* 1987, Avise and Ball 1990, O'Brien and Mayr 1990, Avise 1994). Within a species, alternate alleles differ in their geographical distribution. If the phylogeny of the alleles at each of several loci are reconstructed, the resulting "gene trees" can be compared between loci and across the various regional populations of the species. The matrilineally-inherited, haploid mitochondrial genome is particularly informative, because it evolves rapidly and does not undergo recombination. The "geneological concordance," or geographical congruence among the gene trees, reveals much of the historical pattern of dispersal and vicariance of the populations, and—in concert with morphological data—permits the recognition of more realistic boundaries between subspecies. So far this approach has been applied to humpback whale (Baker *et al.* 1994), minke whale (Wada *et al.* 1991), Bryde's whale (Pastene *et al.* 1997), and bottlenose dolphin (Curry 1997,[2] Curry and Smith 1998) populations around the globe, to populations of dolphins (*Stenella attenuata, S. longirostris, S. coeruleoalba,* and *Delphinus delphis*) in the eastern tropical Pacific (Dizon *et al.* 1994), and to sea otter populations in the North Pacific (Cronin *et al.* 1996).

Biological species are, by definition, separated by intrinsic reproductive isolation (Dobzhansky 1937, Mayr 1942). The evolution of complete reproductive isolation is a gradual, continuing process, a side-effect of genetic divergence between disjunct populations. However, reproductive isolation is not necessarily closely correlated with the magnitude of overall genetic or phenotypic differences. For example, the two kinds of spotted dolphins (*S. attenuata* and *S. frontalis*) are so similar that cetologists did not properly differentiate them until a few years ago, yet they are clearly good species, because they coexist throughout the tropical Atlantic; such similar species are called *sibling species*—a term of convenience with no particular biological significance. At the other extreme, the three kinds of spinner dolphins in the eastern Pacific (*S. l. longirostris, S. l. orientalis,* and *S. l. centroamericana*) differ so much that cetologists never suspected that they were conspecific, until it was found that they intergraded where their ranges come together.

Since speciation is a recurrent and gradual process, it is to be expected that at any given time in the earth's history there will be many borderline situations in which it will be difficult to say whether two geographically isolated populations have become separate species, or remain subspecies of a single polytypic species. There are a number of these debatable cases among the marine mammals, in *Arctocephalus, Zalophus, Platanista, Sousa, Lissodelphis, Berardius,* and other genera. Evidence of reproductive incompatibility between these allopatric populations can rarely be established empirically. When it cannot, the usual practice is to compare the magnitude of the differences between the taxa in question with the magnitude of the differences that separate intergrading subspecies, and those that separate noninterbreeding sympatric species, preferably in the same genus. In addition to morphology, factors such as mating behavior and timing of the breeding season should be weighed. To rank questionable allopatric populations, an operational criterion is to assume that two populations are reproductively compatible, and therefore members of the same

[2] Curry, B. E. 1997. Phylogenetic relationships among bottlenose dolphins (genus *Tursiops*) in a worldwide context. Ph.D. dissertation, Texas A&M University, College Station, TX. 138 pp.

species, unless they are 100% separable on morphological features—in at least one sex or age group. It is not very important—either theoretically or practically—whether these borderline taxa are ranked as species or subspecies.

Closely-related taxa that are allopatric or parapatric, yet which have attained full species status, are said to comprise a superspecies, or Artenkreis. Examples are the Caspian, Baikal, and ringed seals in the genus *Pusa,* and the longfin and shortfin pilot whales in the genus *Globicephala.* The accepted formal notation for superspecies (optional) is to include the name of the first-described species in square brackets between the generic and specific names (Amadon 1966); for example the seals mentioned above could be listed as *Pusa [hispida] caspica, Pusa [hispida] sibirica,* and *Pusa [hispida] hispida,* with the latter species further divisible into subspecies such as *Pusa [hispida] hispida hispida, Pusa [hispida] hispida botnica, etc.*

Distribution—Marine mammals inhabit all oceans and peripheral seas, which cover 71% of the earth's surface. Ringed seals and polar bears have been sighted at the North Pole; Weddell and crabeater seals, fin and blue whales, and several other pinnipeds and cetaceans have been seen at the front of the the Ross and Filchner ice shelves at 78°S—the farthest south where open water can be found. Some species, such as the killer whale and the sperm whale, are virtually cosmopolitan. At the other extreme are a few species, such as the New Zealand sea-lion, the vaquita porpoise, and the vanished Steller's sea-cow, which are endemic to very limited regions. Many species are circum-global, but are restricted to particular climatic zones; examples are the many pantropical dolphins and the bipolar, or antitropical, ranges of many baleen whales that live in the temperate or subpolar zones. Some pinnipeds, cetaceans, and sirenians also range many hundreds of kilometers up the great rivers of Siberia, Alaska, southeastern Asia, South America, and Africa—either seasonally or permanently.

In this list, the limits of the geographical distribution of each species are described from north to south, and from west to east, for the Atlantic, Indian, and Pacific oceans sequentially. If there are generally-accepted or well-defined subspecies, the range of each is described separately. Otherwise, the range of the species as a whole is described, followed by reference to any studies that dealt with geographical variation. The described ranges are those that have been occupied during historical times; some species have since been extirpated from parts of their original ranges (Bertram and Bertram 1973, IUCN 1973, FAO 1979, Foster-Turley *et al.* 1990, Klinowska 1991, Reijnders *et al.* 1993, Reeves and Leatherwood 1994). Three known species have already been exterminated by man—*Zalophus japonicus* (Nishiwaki 1973, Nakamura 1997), *Monachus tropicalis* (LeBoeuf *et al.* 1986), and *Hydrodamalis stelleri* (Stejneger 1887)—and an unknown species of pinniped disappeared from the Chagos Archipelago soon after 1786 and from the Seychelles after 1808 (Stoddart 1972). All specific sites of occurrence in this list are based on published records, but I have documented only fossil, subfossil, and archeological locality records of living species, corrections to erroneous locality records that have been repeated in the literature, and records of artificial range extensions.

Place names follow *The Times Atlas of the World: Comprehensive Edition,* 7th and 8th editions. Geographical features that fall entirely within the territorial boundaries of one nation are given the names by which they are known in the official language of that nation. Features that fall, at least in part, on the high seas, or within the territorial boundaries of more than one nation, are given their traditional English names. Where a city bears the same name as the surrounding province or equivalent political division (for example Buenos Aires), the latter is meant unless otherwise specified. Foreign geographical terms used herein are listed in Appendix 4.

Order CARNIVORA

This group was first named Carnivori by Vicq d'Azyr (1792). The name is the plural of the masculine Latin noun *carnivorus,* compounded from the noun *caro,* genitive *carnis* 'flesh,' and the verb *vorare* 'to devour.' Bowdich (1821) gave it a neuter plural ending, Carnivora—a spelling that has been universally adopted.

The dozen or so families of living carnivores are classified into two primary taxa which are usually ranked as suborders (Wayne *et al.* 1989, Wozencraft 1993, Wyss and Flynn 1993). Suborder Feliformia contains the families Viverridae (civets, *etc.*), Herpestidae (mongooses), Hyaenidae (hyenas), and Felidae (cats). Suborder Caniformia includes the Canidae (dogs), Ursidae (bears and giant panda), Ailuridae (red panda), Procyonidae (raccoons, *etc.*), and Mustelidae (weasels, otters, and allies), along with the three families of pinnipeds (sea-lions, walruses, and seals)—Otariidae, Odobenidae, and Phocidae. A phylogenetic classification of the living and fossil Carnivora is outlined in Tables 3 and 4.

The principal marine carnivores, and the ones most highly adapted for an aquatic lifestyle, are the seals, sea-lions, and walruses. In the past they were usually classified as a separate order—the Pinnipedia, or as a suborder of the order Carnivora, all the terrestrial carnivores being included in a suborder Fissipedia. The name Pinnipedia, bestowed by Illiger (1811), is the plural of the Modern Latin noun *pinnipes,* meaning one who is 'wing-footed,' such as Hermes (Mercury) and Perseus of Greco-Roman mythology, but here taken to mean 'fin-footed.' *Pinnipes,* in turn, was compounded from the Classical Latin *pinna* 'feather' or 'wing,' and *pes* (genitive *pedis*) 'foot.'

Recently, virtually all morphological and molecular studies have revealed that the affinities of the Pinnipedia lie within the suborder Caniformia of the order Carnivora. The only contradictory evidence was an immunological study which separated *Phoca vitulina* as the out-group to 17 other species representing 8 orders of placental mammals (Schreiber *et al.* 1994).

The long-recognized distinction between the eared seals and the earless seals was first given formal taxonomic expression by Péron (1816), who called them Phocacea auriculata and Phocacea inauriculata, respectively. Gill (1866) divided the living pinnipeds into three families, Phocidae for the earless seals, Otariidae for the eared seals, and Rosmaridae [=Odobenidae] for the walruses—a family-level division accepted to this day. Allen (1880) classified his suborder Pinnipedia into two primary groups of undesignated rank: Gressigrada containing the families Otariidae and Odobenidae, and Reptigrada containing the family Phocidae. Smirnov (1908) recognized Allen's groups as superfamilies Otarioidea and Phocoidea, respectively, and his terminology has been generally accepted.

The monophyly of the Pinnipedia was not questioned until Mivart (1885) argued that the otarioids were most closely related to the Ursidae, while the phocoids were related to the Mustelidae. This debate was rekindled by McLaren (1960*a*). Following Tedford's (1976) publication of what was ostensibly

Table 3. Classification of the living and fossil Carnivora.[a] Extinct taxa are marked with a dagger (†). For a more detailed division of the taxon Pinnipedia (2.2.1.2.2.2.) see Table 4.

Carnivora
1. Feliformia
1.1. Feloidea
1.1.1. unnamed clade
1.1.1.1. Felidae (cats)
1.1.1.2. Hyaenidae (hyenas, aardwolf)
1.1.2. Viverridae (civets, etc.)
1.1.3. Herpestidae (mongooses)
1.2. †Nimravidae
2. Caniformia
2.1. Canidae (dogs)
2.2. Arctoidea
2.2.1. unnamed clade
2.2.1.1. Procyonidae (raccoons, etc.
2.2.1.2. unnamed clade
2.2.1.2.1. Ailurus [=Ailuridae] (red panda)
2.2.1.2.2. Ursida
2.2.1.2.2.1. Ursoidea
2.2.1.2.2.1.1. †Amphicyonidae
2.2.1.2.2.1.2. Ursidae (hears, giant panda)
2.2.1.2.2.2. Pinnipedia
2.2.1.2.2.2.1. unnamed clade
2.2.1.2.2.2.1.1. Odobenidae (walruses)
2.2.1.2.2.2.1.2. Phocoidea
2.2.1.2.2.2.1.2.1. †Desmatophocidae
2.2.1.2.2.2.1.2.2. Phocidae (earless seals)
2.2.1.2.2.2.2. Otariidae (sea-lions, fur-seals)
2.2.2. Mustelidae
2.2.2.1. unnamed clade
2.2.2.1.1. Lutrinae (otters)
2.2.2.1.2. Mephitinae (skunks)
2.2.2.2. Mustelinae (weasels, etc.)
2.2.2.3. Melinae (badgers)

[a] Derived from Wyss and Flynn (1993, fig. 4.3). Taxa are not given formal designations of rank, and weakly-supported clades are left unnamed. The authors presented the classification as a cladogram; here subordination is indicated by numeration. Some family-group names commonly used by other authors have been added in brackets.

a cladistic analysis of the Recent Carnivora, most mammalogists accepted his conclusion that the Otariidae plus the Odobenidae comprised the sister-taxon of the Ursidae, while the Phocidae were the sister-group of the Mustelidae, or more specifically the Lutrinae. Tedford's analysis was flawed (Wiig 1983), however, and later cladistic analyses, based upon the totality of morphological characters, show the living pinnipeds as a monophyletic group (Wyss 1987, Flynn *et al.* 1988, Wyss and Flynn 1993). Wozencraft (1989*a*) also made a cladistic analysis of living pinnipeds based on morphology, but he disregarded all characters that were obvious aquatic adaptations, because he believed that

Table 4. Classification of the living and fossil Pinnipedia.[a] Extinct taxa are marked with a dagger (†).

1. †*Kolponomos*
2. Pinnipedimorpha
2.1. †*Enaliarctos* [=Enaliarctidae]
2.2. Pinnipediformes
2.2.1. †*Pteronarctos*
2.2.2. Pinnipedia
2.2.2.1. Otariidae
2.2.2.1.1. *Callorhinus*
2.2.2.1.2. unnamed clade
2.2.2.1.2.1. *Arctocephalus*
2.2.2.1.2.2. Otariinae
2.2.2.2. Phocomorpha
2.2.2.2.1. Phocoidea
2.2.2.2.1.1. †*Allodesmus* [=Allodesminae]
2.2.2.2.1.2. †*Pinnarctidion*
2.2.2.2.1.3. †*Desmatophoca* [=Desmatophocinae]
2.2.2.2.1.4. Phocidae
2.2.2.2.1.4.1. unnamed clade [=Monachinae]
2.2.2.2.1.4.1.1. †unnamed clade
2.2.2.2.1.4.1.1.1. †*Acrophoca*
2.2.2.2.1.4.1.1.2. †unnamed clade
2.2.2.2.1.4.1.1.2.1. †*Homiphoca*
2.2.2.2.1.4.1.1.2.2. †*Piscophoca*
2.2.2.2.1.4.1.2. *Monachus*
2.2.2.2.1.4.1.3. *Mirounga*
2.2.2.2.1.4.1.4. Lobodontini
2.2.2.2.1.4.2. Phocinae
2.2.2.2.1.4.2.1. *Erignathus*
2.2.2.2.1.4.2.2. unnamed clade
2.2.2.2.1.4.2.2.1. *Cystophora*
2.2.2.2.1.4.2.2.2. Phocini
2.2.2.2.2. Odobenidae
2.2.2.2.2.1. †*Neotherium*
2.2.2.2.2.2. unnamed clade
2.2.2.2.2.2.1. †*Imagotaria* [=Imagotariinae]
2.2.2.2.2.2.2. unnamed clade
2.2.2.2.2.2.2.1. †Dusignathinae[b]
2.2.2.2.2.2.2.2. Odobeninae[c]

[a] Derived from Berta and Wyss (1994: fig. 2), except that the genus *Kolponomos* has been added from Tedford *et al.* (1994), and the subtaxa of the Odobenidae follow Déméré (1994). Taxa are not given formal designations of rank, and weakly-supported clades are left unnamed. The authors presented the classification as a cladogram; here subordination is indicated by numeration. Some family-group names commonly used by other authors have been added in brackets.

[b] Includes †*Pontolis*, †*Dusignathus*, and †*Gomphotaria*.

[c] Includes †*Aivukus*, †*Pliopedia*, †*Alachtherium*, †*Prorosmarus*, *Odobenus*, and †*Valenictis*.

there was a high probability that such characters could have evolved convergently in the two groups of pinnipeds. His results supported the hypothesis of diphyly as proposed by Tedford. Until recently, most paleontologists (Mitchell and Tedford 1973, Muizon 1982*a*) also favored the diphyletic hypothesis, but the latest cladistic analyses of both fossil and living forms support a monophyletic Pinnipedia (Wyss 1987, 1988*b*; Berta 1991; Berta and Wyss 1994).

Data other than the traditional morphological characters are almost unanimous in showing that pinnipeds comprise a monophyletic group. These include karyotypes (Fay *et al.* 1967, Kulu 1972, Árnason 1977, Anbinder 1980, Couturier and Dutrillaux 1986); immunological distances (Sarich 1969*a, b*; Seal *et al.* 1971); amino acid sequences of myoglobin (Goodman *et al.* 1982, McKenna 1987), α-crystallin A (De Jong 1982, McKenna 1987), and combined protein sequences (Czelusniak *et al.* 1990); nucleotide sequences of single-copy nuclear DNA (Slade *et al.* 1994), the mitochondrial cytochrome *b* gene (Vrana *et al.* 1994, Árnason *et al.* 1995, Lento *et al.* 1995), and the 12S ribosomal RNA (rRNA) gene (Lento *et al.* 1995); and molecular hybridization of unique DNA (Wayne *et al.* 1989) and of highly repetitive DNA (Árnason and Widegren 1986).

Although evidence corroborating the monophyly of pinnipeds is now overwhelming, their relationship within the suborder Caniformia remains problematical. Morphological analyses placed them as a sister-group to the Ursidae (Wyss and Flynn 1993, Hunt and Barnes 1994), as did a study of the nucleotide sequences of the cytochrome *b* gene (Vrana *et al.* 1994). Another study of the nucleotide sequences of the mitochondrial cytochrome *b* gene and the 12S rRNA gene placed them close to the ursid-ailurid-procyonid radiation (Lento *et al.* 1995). A cladistic analysis of certain Oligocene and early Neogene carnivores by Wolsan (1993) showed the taxon Mustelida (Pinnipedia, Mustelidae, Procyonidae, and *Ailurus*) as a monophyletic sister-group to the Ursida (Ursidae and related fossil taxa). Karyotypes suggested that the pinnipeds form a clade with the Mustelidae and Procyonidae, and are distant from the Ursidae (Couturier and Dutrillaux 1986). Hybridization of highly-repetitive DNA indicated that the Pinnipedia were the sister-group to the Mustelidae (Árnason and Widegren 1986), and the amino acid sequences of several proteins indicated that they were the sister-group to a clade that includes all the terrestrial arctoids—*i.e.,* the Ursidae, Procyonidae, and Mustelidae (Czelusniak *et al.* 1990). Studies of other characters resulted in an unresolved polychotomy between the pinnipeds, ursids, and mustelids (and the procyonids pairing with either the ursids or mustelids); these characters include immunology (Sarich 1969*a,* Seal *et al.* 1971), amino acid sequences of myoglobin and α-crystallin A (McKenna 1987), and hybridization of unique DNA (Wayne *et al.* 1989). Berta (1991) and Berta and Wyss (1994) recognize Pinnipedia as an unranked taxon under suborder Caniformia.

For a new "total-evidence" analysis of the caniform carnivores, Dragoo and Honeycutt (1997) utilized the 12S rRNA, the 16S rRNA, and the cytochrome *b* genes, along with morphological data. Their most parsimonious cladogram showed the following phyletic sequence (*Ailurus* is included in the Procyonidae, and the skunks are separated from the traditional Mustelidae as family Mephitidae): (Canidae (Ursidae (Pinnipedia (Mephitidae (Procyonidae + Mustelidae))))).

Until quite recently, almost all mammalogists accepted Allen's (1880) opinion that the Odobenidae belonged in the superfamily Otarioidea. This view seemed to be well-supported by cytogenetics (Árnason 1977, Couturier and Dutrillaux 1986), immunogenetics (Sarich 1969*b*), and nucleotide sequences of the cytochrome *b* gene (Vrana *et al.* 1994, Árnason *et al.* 1995). Mitchell (1966*a*, 1968, and 1975), followed in the main by Barnes (1979, 1989), even put the walruses in the family Otariidae, which they divided into seven subfamilies: Odobeninae for the walruses, Otariinae for the fur-seals and sea-lions, and five extinct subfamilies—Imagotariinae, Dusignathinae, Desmatophocinae, Allodesminae, and Enaliarctinae. Repenning (1975) and Repenning and Tedford (1977) split these seven subfamilies into four families: Odobenidae (including Imagotariinae and Dusignathinae), Desmatophocidae (including Allodesminae), Otariidae, and Enaliarctidae, but still included all of them within the superfamily Otarioidea.

Lately the belief that these four families comprise a monophyletic superfamily has been challenged by cladistic analyses of the morphology of both Recent (Wyss 1987, Flynn *et al.* 1988, Vrana *et al.* 1994) and fossil species (Berta 1991, 1994*b*; Berta and Wyss 1994; Wyss and Flynn 1993), which show walruses as being more closely related to the phocids than to the otariids. In the analyses by Wyss and Flynn (1993), Berta (1994*b*), and Berta and Wyss (1994), Odobenidae is revealed as the sister-group to the superfamily Phocoidea. Within the latter taxon, the genus *Pinnarctidion*—originally described as an enaliarctine (Barnes 1979)—turns out instead to be the sister-group to all the other phocoids, and among the latter, the Desmatophocidae are the sister-group to the family Phocidae. The family Enaliarctidae is revealed as a paraphyletic group, with *Enaliarctos, Pacificotaria,* and *Pteronarctos* as three separate and successive branches from the basal stem of the Pinnipedia (Berta *et al.* 1989; Berta 1991, 1994*a*; Barnes 1992). (Another "enaliarctid" from the Miocene of Kamchatka, *Kamtschatarctos sinelnikovae,* for which Dubrovo (1981) erected the new subfamily Kamtschatarctinae, was reallocated to the Imagotariidae by Barnes 1989.) Berta *et al.* (1989) designated Pinnipedia as an unranked taxon that includes the Otariidae, Odobenidae, and Phocoidea; and named Pinnipedimorpha as an unranked taxon that includes the Pinnipedia, *Enaliarctos,* and *Pteronarctos* (*Pacificotaria* had not yet been described).

A different arrangement of the Pinnipedia resulted from the "total evidence" analysis by Dragoo and Honeycutt (1997), mentioned above. Their cladogram agrees with the traditional arrangement in that the Odobenidae are paired with the Otariidae (*Zalophus*) rather than with the Phocidae (*Phoca* and *Halichoerus*). Also, the Desmatophocidae fit as a basal branch of the pinniped radiation, rather than as the sister-group to the family Phocidae.

The genera *Enaliarctos* (4 spp.), *Pacificotaria* (1 sp.), and *Pteronarctos* (1 sp.) from the late Oligocene to the middle Miocene of Oregon are the most archaic pinnipeds known, and they were probably close to the ancestor of all other Pinnipeds. *Enaliarctos mealsi* had all four limbs transformed into flippers, and was capable of quadrupedal locomotion on land, much like sea-lions, but it was smaller than any living pinniped, and its teeth still resembled those of land carnivores in that the premolars and molars were well-differentiated, and one cheek-tooth in each quadrant was modified into a carnassial tooth (Mitchell and Tedford 1973, Berta *et al.* 1989, Berta and Ray 1990).

Another putative relative of the pinnipeds is the enigmatic genus *Kolponomos,* represented by two species, *K. clallamensis* and *K. newportensis,* which lived along the coasts of Washington and Oregon during the early Miocene. These strange bear-like creatures appear to have been amphibious mammals that foraged in shallow inshore waters but were still capable of terrestrial locomotion. Their sea-otter-like cheek teeth suggest that they fed on hard-shelled invertebrates from rocky bottoms (Tedford *et al.* 1994). At first Stirton (1960) thought that the genus *Kolponomos* had most likely branched from the stem-lineage of the Procyonidae in the Oligocene. Ray (1976*b*) concluded that they were not procyonids, but were probably closest to the ursid-enaliarctid lineage, and later (*in* Barnes *et al.* 1985) he believed them to be members of the Enaliarctidae. Finally, a cladistic analysis by Tedford *et al.* (1994) placed the genus as the sister-taxon to the clade containing *Enaliarctos* plus all the other pinnipeds.

Lastly, much speculation has been engendered by several enigmatic carnivores that have been described as seal-like otters or otter-like seals. These are *Potamotherium valetoni* and *P. miocenicum* from the late Oligocene to late Miocene of Europe and North America (Savage 1957), *Semantor macrurus* from the late Miocene or early Pliocene of Kazakhstan (Orlov 1931, 1933), and *Necromites nestoris* from the late Pliocene of Azerbaijan (Bogachev 1940, Akhundov 1960). The first genus is known from abundant remains, including entire skeletons, but each of the latter two is known only from a single specimen consisting of several elements of the rear half of the skeleton (except for a disputed humerus thought to go with the *Semantor* specimen—Kirpichnikov 1955). These animals resembled otters, but their tails were shorter (that of *Necromites* not known), and their pelvic bones, femora, and tibiae showed several of the derived features found in seals, particularly phocid seals. *Necromites* came from coastal marine deposits, whereas *Potamotherium* and *Semantor* were found in continental deposits, so the latter must have been inhabitants of freshwater lakes and streams.

Potamotherium has been considered a close relative of the phocids by several authors (Kellogg 1922, Kirpichnikov 1955, McLaren 1960*a*), and Wolsan's (1993) cladistic analysis of Oligocene and early Neogene carnivores placed *Potamotherium* as the sister-taxon of the Phocidae. On the other hand, Viret (1955) and Piveteau (1961) regarded it as a specialized otter with no close relationship to the Pinnipedia. However, *Potamotherium* lacks the cranial synapomorphies that characterize the Mustelidae, so it is more likely that it is an early branch of the musteloid lineage, and that its aquatic adaptations were independently evolved (Flynn *et al.* 1988, Bryant *et al.* 1993). Schmidt-Kittler

(1981) even excluded *Potamotherium* from the Musteloidea, and thought that it was more closely related to the Procyonidae.

Semantor was likewise regarded as a pinniped by Orlov (1931), who put it in a new family, Semantoridae. Tedford (1976) included both *Semantor* and *Potamotherium* in Semantorinae, a subfamily of the Phocidae. He, along with McLaren (1960*a*) and Muizon (1982*b*), thought that the phocids descended from a mustelid or lutrine ancestor, and they interpreted *Semantor* and *Potamotherium* as early branches of the lineage leading from the (paraphyletic) Mustelidae or Lutrinae to the Phocidae; Muizon (1982*b*) also placed the sea otter *Enhydra* and its extinct relative *Enhydriodon* as the sister-group to the Semantoridae plus Phocidae. Thenius (1949) and Chapskii (1961) denied any phocid affinities for *Semantor*; they thought it was probably an otter, or at least an amphibious mustelid, and that its resemblance to seals is due to convergent evolution.

Necromites was also referred to the family Semantoridae by Bogachev (1940), but Akhundov (1963) denied any such relationship, and in 1967 he placed it in Necromitinae, a new subfamily of Phocidae (Gromov and Baranova 1981).

The phylogenetic relationship of these three enigmatic genera to each other and to other carnivores will not be resolved until more complete specimens of *Semantor* and *Necromites* become available.

Aside from the pinnipeds, three other families of the order Carnivora also include species that are members of the marine ecosystem (Appendix 1). The otters (family Mustelidae, subfamily Lutrinae) include only two species, *Lutra felina* and *Enhydra lutris,* that forage exclusively in marine waters. The other eight species inhabit mainly freshwater streams and lakes, but some local populations of at least six of them have been found to feed regularly or wholly in marine waters.

Among the remaining Carnivora, only the polar bear (family Ursidae) is dependent on the marine habitat. Although they have no manifest anatomical or physiological adaptations for an aquatic life, polar bears spend prolonged periods on the drifting pack ice far from land. Polar bears are accomplished swimmers, and they play a significant role in the marine ecosystem as predators of seals. Arctic foxes, *Vulpes lagopus* Linnaeus, 1758 [=*Alopex lagopus*], are another species that makes extended forays onto the sea ice, where they have been sighted as far as 89°11′N—only 91 km from the North Pole. They regularly scavenge on polar bear kills, and often prey on ringed seal pups in their subnivean lairs (Freuchen 1935, Riewe 1977, Stirling and Smith 1975, Smith 1976).

Family OTARIIDAE Gray, 1825

Otariina Gray 1825:340 (Type genus: *Otaria*)
Arctocephalina Gray 1837:582 (Type genus: *Arctocephalus*)
Otariarina Gray 1843:xxiii (Type genus: *Otaria*)
Callorhinina Gray 1869*a*:269 (Type genus: *Callorhinus*)
Eumetopiina Gray 1869*a*:269 (Type genus: *Eumetopias*)

Zalophina Gray 1869*a*:269 (Type genus: *Zalophus*)
Gypsophocina Gray 1874:27 (Type genus: *Gypsophoca* Gray, 1866 [=*Arctocephalus*])
Trichiphocinæ Allen 1870:23 (Included genera: *Otaria, Eumetopias,* and *Zalophus*; not available because it is not based on the stem of a generic name)
Ouliphocinæ Allen 1870:23 (Included genera: *Callorhinus* and *Arctocephalus*; not available because it is not based on the stem of a generic name)
Trichophocacæ Allen 1880:208 (=Trichiphocinæ; emended spelling)
Ouliphocacæ Allen 1880:210 (=Ouliphocinæ; emended spelling)
Phocarctinae von Boetticher 1934:359 (Type genus: *Phocarctos*)
Callorhinae [*sic*] Muizon 1978:182 (Type genus: *Callorhinus*; proposed as new subfamily, but improperly formed, and synonymous with Callorhinina Gray, 1869, above)
Otaridae *auctorum* (incorrect subsequent spelling)

Only the fur-seals and sea-lions remain in this family, their supposed fossil allies having been reclassified, as noted above. The taxonomy of the living otariids was treated by King (1954, 1960), Sivertsen (1954), and Scheffer (1958). Morejohn (1975) proposed a phylogeny of the living genera, based on the morphology of the baculum, and Berta and Deméré (1986) provided a cladogram of all the living and some of the fossil species; these studies showed that all the living species fall into two monophyletic groups which many authors recognize as subfamilies: Arctocephalinae for the fur-seals, and Otariinae for the sea-lions. Von Boettiger (1934) recognized a third subfamily, Phocarctinae, for Hooker's sea-lion, because he thought that it was intermediate between the fur-seals and sea-lions, but it is a typical sea-lion. One cladistic analysis (Berta and Wyss 1994) suggested that the southern fur-seals *Arctocephalus* are more closely related to the sea-lions than to the northern fur-seal *Callorhinus.* All of the living otariids are, in fact, so closely related that subfamily designations are best avoided. Some earlier authors (Mivart 1885, Flower and Lydekker 1891) even included all of them in the one genus *Otaria.* Peters (1877) recognized three genera—*Otaria* for the South American sea-lion, *Eumetopias* for all other sea lions, and *Arctocephalus* for the fur seals. Beddard (1890), followed by Winge (1924, 1941) and Wood Jones (1925*a, b*), placed only the South American sea-lion in the genus *Otaria,* and included all of the other sea-lions and all of the fur-seals in the genus *Arctocephalus,* but later Beddard (1902) put all the living species of otariids in *Otaria.*

The genera of sea-lions are widely allopatric, except for *Eumetopias* and *Zalophus,* which occur together in the coastal waters from Vancouver Island south to southern California, and (formerly) in the southern Ostrova Kuril'skiye and northern Hokkaido.

The close relationship between fur-seals and sea-lions is revealed by a number of intergeneric hybrids. In the wild *Zalophus californianus* has hybridized with *Eumetopias jubatus* (Gorodezky 1995) and with *Callorhinus ursinus* (DeLong 1990, Duffield 1990), and a possible hybrid between *Arctocephalus townsendi* and *Callorhinus ursinus* was observed (Repenning and Tedford 1977). A lone *Arctocephalus townsendi* male was seen copulating with *Zalophus californianus* females (Stewart *et al.* 1987). In captivity *Zalophus californianus* has crossed with *Arctocephalus pusillus* (Jennison 1914, Schliemann 1968) and with *Otaria flavescens* (Kirchshofer 1968). The report of a cross between *Callorhinus ursinus* and *Otaria flavescens* (Ackermann 1898) is almost certainly erroneous (Van Gelder 1977).

Genus ARCTOCEPHALUS E. Geoffroy Saint-Hilaire and F. Cuvier, 1826

Iredale and Troughton (1934) and Troughton (1941) used the generic name *Gypsophoca* Gray, 1866, for the Australian species, and Sivertsen (1954) split off *Arctocephalus philippii* and *A. townsendi* as genus *Arctophoca,* Peters, 1866, but subsequent workers have not upheld these divisions. Eight species are currently recognized in *Arctocephalus* (Repenning *et al.* 1971). There have been dissenting opinions regarding the taxonomic status of several forms. Sivertsen (1954) and Scheffer (1958) thought that *A. tropicalis* was the same as *A. gazella,* but King (1959*a, b*) pointed out their differences and recognized *A. gazella* as a subspecies of *A. tropicalis.* King (1954) believed that *A. townsendi* was identical with *A. philippii,* and Scheffer (1958) classified it as a subspecies of the latter. King (1954) likewise thought that *A. galapagoensis* was conspecific with *A. australis,* whereas Scheffer (1958) ranked it as a subspecies of the latter, and Sivertsen (1954) considered it a full species. For a long time, the systematics of the fur-seals of the Australian and New Zealand regions were perplexing, until King (1968, 1969) worked out their identity, distribution, and nomenclature. Cladistic relationships among all the fur-seals were analysed by Berta and Deméré (1986).

All eight species of *Arctocephalus* are distributed almost entirely allopatrically, but there are five sites where two species regularly occur in the same or nearby rookeries. As a result of intense exploitation during the late 18th and the 19th centuries, fur-seal populations were severely depleted or even extirpated on virtually all of their breeding grounds. Most of these areas of overlap have come about recently, as the various populations have increased and spread. The social and genetic interactions between species in these areas of overlap are as follows:

(1) Prince Edward Islands—*A. gazella* has recently colonized Marion Island, where it is greatly outnumbered by *A. tropicalis,* the original inhabitant. The two species generally occupy separate rookeries, but a limited amount of hybridization is taking place (Condy 1978, Kerley 1983, 1984, Kerley and Robinson 1987). Hybrids constitute about 0.02% of the total fur seal population, and their number appears to be dropping as the populations of both species rise (Hofmeyr *et al.* 1997).

(2) Îles Crozet—Prior to exploitation, *A. gazella* was the only species on the islands. At present on Île de la Possession, the recently-arrived *A. tropicalis* is more numerous than *A. gazella.* The two species usually occupy separate rookeries, but a few females of each species have been found in the mating

territories of males of the other species; nonetheless no hybrids have been identified (Jouventin *et al.* 1982, Roux 1987, Guinet *et al.* 1994).

(3) Heard Island—*A. gazella* was the original inhabitant, but lately a few *A. tropicalis* have begun to visit this island frequently, and one female gave birth to a pup in the mating territory of an *A. gazella* bull (Goldsworthy and Shaughnessy 1989).

(4) Bass Strait—19th century sealers claimed that both *A. pusillus* and *A. forsteri* occurred on islands in Bass Strait, between Tasmania and the mainland of Australia (Warneke 1982), but we have no information on interactions between the two species.

(5) Macquarie Island—*A. tropicalis* is believed to have been the original inhabitant of this island; it was nearly, if not entirely, extirpated in the last century. During this century, fur-seals have reoccupied the island. Now *A. tropicalis* is the most numerous species. Some females of *A. gazella* are found in the mating territories of male *A. tropicalis,* and very few male *A. gazella* are present, but no hybrid adults have been found (Shaughnessy and Fletcher 1987, Shaughnessy *et al.* 1988) (One skull of *A. gazella* dating from the 1870s or 1880s was unearthed—Townrow and Shaughnessy 1991). Large numbers of *A. forsteri* are also present seasonally; they are almost entirely non-breeding individuals, although a few females occasionally bear their pups on Macquarie Island.

Individuals of most species of *Arctocephalus* have a propensity to wander and frequently show up within the range of other species of the genus.

Arctocephalus pusillus (Schreber, 1775) (Tasmanian and Cape fur-seals; giant fur-seal; brown fur-seal).

There has been some confusion about the publication dates of names in Schreber's *Die Säugethiere...*; the name *Phoca pusilla* first appeared in Theil 2, Heft 13, Plate 85, which was published in 1775 (Sherborn 1891).

There are two widely disjunct but weakly differentiated subspecies (Repenning *et al.* 1971, Warneke and Shaughnessy 1985).

A. p. pusillus—Ranges along the west coast of southern Africa, with rookeries located from Cape Cross (21°47′S), Namibia, south to the Cape of Good Hope, thence east to Black Rocks, Cape Province (26°16′E). Vagrant north to Baia do Quicombo (11°19′S) in Angola, and southeast to Marion Island.

A. p. doriferus Wood Jones, 1925—Ranges in the coastal waters of southeastern Australia, with rookeries located from Lady Julia Percy Island (38°25′S, 142°00′E) in Victoria, east through Bass Strait, and to Pedra Blanca (43°52′S, 146°58′E) in southern Tasmania, thence north to Seal Rocks (32°28′S, 152°33′E) in New South Wales. Vagrant north to Port Stephens (32°44′S), New South Wales (see note under *Neophoca cinerea*).

In Classical Latin, *dorifer* is the correct masculine spelling of the subspecies name; masculine forms with *-ferus* endings "are found only in late, decadent Latin" (Steyskal 1980). However, under the ICZN Code, this is insufficient justification for emending the original spelling of *doriferus* (*contra* Steyskal 1980). Linnaeus (1758) himself used the *-ferus* ending for the musk-deer *Moschus moschiferus.*

Arctocephalus gazella (Peters, 1875) (Antarctic fur-seal; Kerguelen fur-seal).

Primarily Antarctic Zone of South Atlantic, Indian, and western South Pacific sectors of Southern Ocean. Rookeries, historical or present, on islands mainly south of the Antarctic Convergence—South Georgia, South Sandwich Islands, South Orkney Islands, South Shetland Islands, Bouvetøy, Marion Island, Îles Crozet, Îles Kerguelen, Heard Island, McDonald Island, and Macquarie Island. Vagrant to Tierra del Fuego, Mar del Plata in Argentina, and the Islas Juan Fernández. A fur-seal at Mawson Station (62°52′E), Antarctica, was most likely of this species.

Arctocephalus tropicalis (Gray, 1872) (Subantarctic fur-seal; Amsterdam fur-seal).

This form went under the name *A. elegans* (Peters, 1876) until King (1959*b*) determined that Gray's earlier name applied to it.

Primarily Subantarctic Zone of South Atlantic, Indian, and western South Pacific sectors of Southern Ocean. Rookeries, historical or present, on islands mainly north of the Antarctic Convergence—Tristan da Cunha, Gough Island, Prince Edward Island, Marion Island, Îles Crozet, Heard Island, Île Amsterdam, Île St. Paul, and Macquarie Island. Vagrant to South Georgia and adjacent Bird Island; Rio Grande do Sul, Santa Catarina, and Alagoas in Brazil; Luanda in Angola; coast of South Africa from Cape Town east to Richards Bay in Natal; Manakara (22°08′S) on the east coast of Madagascar; Comoros; southern coasts of Australia from Kalbarri (27°43′S) in Western Australia east to Evans Head (29°06′S) in New South Wales; South Island of New Zealand; Snares Islands; Antipodes Islands; and the Islas Juan Fernández.

Bester and Van Jaarsveld (1994) found a latitudinal gradient in mean adult body size, with the largest animals on Amsterdam Island (37°55′S), intermediate ones on Gough Island (40°20′S), and the smallest on Marion Island (46°55′S).

Arctocephalus townsendi Merriam, 1897 (Guadalupe fur-seal).

Now breeds only on Isla Guadalupe off Baja California. Wanders north along the coast of California as far as the Farallon Islands and Sonoma County (38°26′N), and south around Cabo San Lucas into the Golfo de California as far north as Bahía de Bacochibampo (27°55′N).

The former breeding range is impossible to delineate because earlier observers failed to distinguish between Guadalupe and northern fur-seals. The fur-seals that occupied the populous rookeries on the Islas San Benito and

Isla Cedros in the early 1800s were most likely *A. townsendi,* as were all of those on Isla Guadalupe, because these islands lie well to the south of the usual migratory range of *Callorhinus ursinus.* In the 1800s, Scammon (1874) reported that fur-seals (species?) hauled out on "many beaches" on the coast of California, and there are also records of fur-seals (species?) on Richardson's Rock near San Miguel Island, on Santa Cruz Island, and on Santa Barbara Island in the 1800s. Starks (1922) and others have speculated that the fur-seals that bred on the Farallon Islands in the early 1800s were Guadalupe fur-seals, but all fur-seal bones unearthed there have been those of northern fur-seals (Repenning *et al.* 1971).

Bones of *A. townsendi* have been recovered from aboriginal middens that date mostly from the late 1700s and 1800s. These remains attest to the probable presence of rookeries or hauling grounds on Catalina Island (Bickford and Martz 1980), on San Miguel Island (Walker and Craig 1979), and on the southern California mainland at Newport Bay (Lagenwalter 1981) and Point Mugu (Lyon 1937, Repenning *et al.* 1971). Bones from an Indian midden on Monterey Bay, California (Repenning, personal communication, 1977), and a partial skull found in an aboriginal shell-mound at Yachats (44°19′N), Oregon (Lyon 1937), were more likely from vagrant individuals.

Morrell (1832), a sealing captain, claimed to have seen fur-seals on Isla Socorro (18°47′N, 110°58′W) and Île Clipperton (10°17′N, 109°13′W) in 1825, but his narratives are notoriously untrustworthy (Bertrand 1971, Best and Shaughnessy 1979).

Arctocephalus philippii (Peters, 1866) (Juan Fernández fur-seal).

Rookery sites on Isla Alejandro Selkirk [=Isla Más Afuera], Isla Robinson Crusoe [=Isla Más á Tierra], and Isla Santa Clara in the Islas Juan Fernández; and Isla San Félix and Isla San Ambrosio in the Islas de los Desventurados. Vagrant to Punta San Juan, Peru.

Arctocephalus forsteri (Lesson, 1828) (South Australian and New Zealand fur-seals; Australasian fur-seal; Antipodean fur-seal; black fur-seal).

Two disjunct populations—one along the southern coast of Australia, the other around New Zealand.

In Australia there are rookeries from Eclipse Island, Western Australia, east to Maatsuyker Island off the south end of Tasmania, and formerly east through Bass Strait to Cape Barren Island (40°25′S, 148°50′E) in the Furneaux Group, Tasmania.

In New Zealand there are rookeries on Cape Palliser at the southern tip of North Island, along the west coast of South Island from Farewell Spit (40°30′S) south around to Ruapuke Island on the south coast, and on Stewart Island, Solander Island, the Snares, Auckland Islands, Campbell Island, Antipodes Islands, Bounty Island, and Chatham Island. Disperses northward around both coasts of North Island north to the Three Kings Islands, and south to Macquarie Island (where pups are occasionally born). Vagrant to Nouvelle Calédonie. In pre-European times, there were rookeries on northern North Island—at Tairua on the Coromandel Peninsula (Smith 1978), and at Mount Camel in Northland (Shawcross 1972).

The Australian and New Zealand populations differ somewhat in the frequency of several alleles of the transferrin gene (Shaughnessy 1970), but there are no morphological differences between the two groups (King 1969, Repenning *et al.* 1971).

Arctocephalus australis (Zimmermann, 1783) (South American fur-seal).

Coastal waters of South America. Animals from the Falkland Islands [=Islas Malvinas] are larger than those from the mainland and have been regarded as subspecifically distinct (King 1954, Scheffer 1958).

A. a. gracilis Nehring, 1887—Rookeries located from Isla Lobos de Tierra (6°30′S), Peru, south to Rocas Abtao (23°05′S), Chile; from Isla Chiloë (42°00′S), Chile, south to Isla de Los Estados (54°45′S), Argentina; Isla Arce (45°00′S) north to Isla Escondido (43°43′S), Argentina; Isla de Lobos (35°02′S), Uruguay, north to Recife dos Tôrres (29°21′S), Brazil. Vagrant to Pacific coast of Colombia and to Islas Juan Fernández.

A. a. australis—Throughout the Falkland Islands [=Islas Malvinas].

Arctocephalus galapagoensis Heller, 1904 (Galapagos fur-seal).

Endemic to the the Archipiélago de Colon [=Galapagos Islands]. Rookeries on Culpepper, Wenman, Fernandina, Isabela, Santiago [=San Salvador], Rabida, Pinzón, Santa Cruz, Baltra, Seymour, Pinta, Marchena, Genovesa, San Cristóbal, and Floreana islands. (The old familiar English names for these islands are Darwin, Wolf, Narborough, Albemarle, James, Jervis, Duncan, Indefatigable, Baltra, Seymour, Abingdon, Bindloe, Tower, Chatham, and Charles, respectively).

Genus CALLORHINUS Gray, 1859

Although it contains only one living species, this genus was represented in the late Pliocene of southern California by *Callorhinus gilmorei* Berta and Deméré, 1986.

Callorhinus ursinus (Linnaeus, 1758) (northern fur-seal).

A pelagic species which ranges from the southeastern Sea of Okhotsk, the southern Bering Sea, and the northern Gulf of Alaska south to about 35°N in the Sea of Japan [=East Sea], 40°N off the Sanriku coast of Honshu, 42°N in the central Pacific, and 32°N off northern Baja California. Vagrant northeast along arctic coast to Amundsen Gulf, and southwest to Shandong, China.

Rookeries are or were located at the following sites (**—historical site, still used; *—historical site, but now used only as hauling ground; †—historical site, no longer occupied; ‡—pre-Columbian site, inferred from archeological or subfossil remains (C. A. Repenning, personal communication, 1977; Lyman 1995); §—new site, established since 1950):

**Ostrov Tyuleniy [=Robben Island] off Sakhalin; *Ostrov Iony in the northern Sea of Okhotsk; †Urup, †Broutona, †Simushir, †Ketoy, **Srednego, †Matua, †Raykoke, **Kamennyy Lovushski, and †Shiashkotan in the Ostrova Kuril'skiye; **Ostrov Beringa and **Ostrov Mednyy in the Komandorskiye Ostrova [=Commander Islands]; †Buldir Island(?) and §Bogoslof Island in the Aleutians; **St. Paul Island, **Sea-lion Rock, †Otter Island, and **St. George Island in the Pribilof Islands; ‡Bella Bella (52°07′N, 128°05′W) and ‡Hesquiat Harbor (49°25′N, 126°25′W) in British Columbia; ‡Whale Cove (44°48′N) and ‡Seal Rock (44°30′N) in Oregon; and the †Farallon Islands, ‡Año Nuevo Point, ‡Monterey, §Castle Rock, and §San Miguel Island in California. A small rookery on "Queen Charlotte Island," British Columbia, in the 1860s or 1870s was reported by a sealer, but was never verified (Bryant *in* Allen 1880). (In 1996, a northern fur-seal gave birth to a pup on the Farallon Islands, the first such event there since the local breeding population was extirpated in the early 1800s.)

At one time it was thought that there were three species (Jordan and Clark 1899)—or at least subspecies (Stejneger 1936)—of northern fur-seals: *C. mimicus* (Tilesius, 1835) [=*C. u. niger* (Pallas, 1811), preoccupied; =*C. curilensis* Jordan and Clark, 1898] breeding on Robben Island and the Kuril Islands; *C. ursinus* breeding on the Commander Islands, and *C. cynocephala* (Walbaum, 1792) [=*C. alascanus* Jordan and Clark, 1898] breeding on the Pribilof Islands. However, subsequent research has shown that the various populations are morphologically indistinguishable (Taylor *et al.* 1955). Although most fur seals return to breed on the same island where they were born, and adults of both sexes almost always return to the same rookery each year, there is a small but steady exchange of individuals between distant breeding colonies (Taylor *et al.* 1955, Lander and Kajimura 1982). The new colony on San Miguel in the California Channel Islands was founded by animals that had been tagged on Robben Island, the Commander Islands, and the Pribilof Islands (Peterson *et al.* 1968, Lander and Kajimura 1982); Bogoslof Island in the Aleutian chain was likewise colonized by seals from both the Commander and Pribilof islands (Loughlin and Miller 1989). Gene flow thus appears sufficient to preclude the differentiation of subspecies.

Genus ZALOPHUS Gill, 1866

This genus includes three similar but widely allopatric taxa, which Scheffer (1958) and many following authors have arbitrarily regarded as conspecific. The taxonomic status of the Japanese population long remained in limbo because of inadequate specimens in museums. Itoo (1985), on the basis of new cranial material recovered at an archeological site, concluded that the differences between the Japanese and California populations would have been sufficient to inhibit or preclude their interbreeding. The morphological differences between the Galapagos sea-lions and those in California are equally great. Sivertsen (1953, 1954), the original describer, judged that the Galapagos sea-lion was specifically distinct from the California species—a decision bolstered by dissimilarities in their social behavior (Eibl-Eibesfeldt 1984) and vocalizations (Cenami Spada *et al.* 1991[3]).

Zalophus japonicus (Peters, 1866) (Japanese sea-lion).

Probably EXTINCT; last credible report was 50 to 60 individuals on Take-shima in 1951; individual sightings reported as recently as 1974 and 1975, but confusion with escaped *Z. californianus* cannot be ruled out. Original range included Ullung do (37°30′N, 130°52′E) and Take-shima [=Tok-do, =Liancourt Rocks] (37°15′N, 131°52′E) in the southern Sea of Japan [=East Sea], and coastal waters of Japan, from Okushiri-shima off southwestern Hokkaido south along the west coast to Okino-shima in Korea Strait, and from Shimokita-hantō at the northern end of Honshu south along the Pacific coast to Kyushu, including the Seto-naikai. Historical and archeological records (Nakamura 1991, 1997) point to former rookeries on Ullung-do and Take-shima in the Sea of Japan; Henashi-zaki (40°36′N, 139°52′E) and Nanatsu-jima (37°35′N, 136°53′E) on the west coast of Honshu; Inubō-saki (35°41′N, 140°52′E) on the east coast of Honshu; and To-shima (34°32′N, 139°16′E), Ombase-jima (34°10′N, 135°03E), Inambo-Jima (33°37′N, 139°18′E), and Ōnohara-jima (34°03N, 139°22E) in the Izu-shotō. Vagrant to east coast of South Korea, southwestern Sakhalin, Ostrova Kuril'skiye (Urup, Chernyye Brat'ya, and Shiashkotan), and Mys Lopatka on Kamchatka. Recounting his observations in the Ostrova Kuril'skiye, Captain Snow (1910), a seal and otter hunter, said that in addition to "*Otaria stelleri*" [=*Eumetopias jubatus*], "The black sea lion (*Otaria gillespii*) also frequents the islands, but in small numbers" (The name *O. gillespii* is now considered a synonym of *Z. californianus*).

Zalophus californianus (Lesson, 1828) (California sea-lion).

Range includes two geographical divisions, one on the Pacific coast and one in the Golfo de California. The Pacific population ranges mainly in near-shore waters, with hauling grounds located on coastal islands from Solander Island (49°57′N) on the west coast of Vancouver Island, and Denman Island (49°50′N) in the Strait of Georgia, south to Cabo San Lucas, Baja California

[3] Cenami Spada, E., E. B. Hanggi and R. J. Schusterman. 1991. Variation in vocalizations and individual recognition in two subspecies of California sea lions. Abstracts, Ninth Biennial Conference on the Biology of Marine Mammals, 5–9 December 1991, Chicago, IL. The Society for Marine Mammalogy. p. 12.

Sur; there are also two hauling grounds far offshore on oceanic islands—Islote Zapato (28°50'N, 118°20W') off the southern tip of Isla Guadalupe, and Rocas Alijos (24°57'N, 115°45'W). The hauling grounds north of southern California are occupied only by males, which migrate north for the winter; at that season, some individuals regularly enter the lower reaches of coastal rivers in northern California, Oregon, and Washington, including Lake Washington in the latter state. A few females have given birth on the Farallon Islands (37°42'N), but regular rookeries are sited only from Point Piedras Blancas (35°39'N), California, south to Punta Lobos (23°25'N), Baja California Sur. Bones from archeological sites are evidence of a rookery at Seal Rock (44°30'N), Oregon, some time between 3,000 and 300 years ago (Lyman 1995). The Golfo de California population ranges throughout the gulf, with rookeries located from Roca Consag (31°03'N, 114°28'W) south to Los Islotes (24°33'N, 110°26'W). Vagrant north to Prince William Sound, Alaska, and south to Chiapas (14°42'N), Mexico. Morrell's report of large numbers of "hair-seals" (an old name for sea-lions), as well as "sea leopards" (*Phoca vitulina*) and fur-seals on Isla Socorro (18°47'N, 110°58'W) in 1825 cannot be taken seriously (see comments above under *Arctocephalus townsendi*).

(In the western North Atlantic, free-ranging California sea-lions have been seen once in Newfoundland and more often along the eastern seaboard from Virginia to Louisiana (Gunter 1968, Schmidly 1981); in the eastern North Atlantic, there are at least two records from the North Sea coast of Great Britain (Hewer 1974). All of these individuals are doubtless former captives that escaped or were freed. No evidence of their breeding has come to light.)

Longtime genetic isolation between the Pacific population and the Golfo de California population is evident from an analysis of the control region of the mtDNA (Maldonado *et al.* 1995), but no cranial differences could be found between animals from the two regions (Orr *et al.* 1970).

Zalophus wollebaeki Sivertsen, 1953 (Galapagos sea-lion).

Originally confined to the Archipiélago de Colon [=Galapagos Islands], where there are rookeries or hauling grounds on every island; since 1986, a small rookery has been establshed on Isla de La Plata (01°16'S, 81°06,W) off the coast of Ecuador. Vagrant to Isla del Coco (05°32'N, 87°04'W), Isla Gorgona (02°58'N, 78°11'W) in Colombia, and the mainland coast of Ecuador.

Genus EUMETOPIAS Gill, 1866

Eumetopias jubatus (Schreber, 1776) (northern sea-lion; Steller's sea-lion).

There has been some confusion about the publication dates of names in Schreber's *Die Säugethiere...*; the name *Phoca jubata* first appeared in Theil 3, Heft 17, Plate 83*b*, which was published in 1776 (Sherborn 1891).

Coastal and immediate offshore waters of the cool-temperate North Pacific, from Bering Strait south to Hokkaido, Japan, and the Channel Islands off southern California. Rookeries or hauling grounds (past or present) located on Kamen' Opasnostiy and Ostrov Moneron in southern Tatarskiy Proliv, Ostrov Tyuleniy, northern Sakhalin, Ostrov Iony, the northeastern Sea of Okhotsk from Ostrov Zavyalova east to Ostrov Iamskiy, Ostrova Kuril'skiye, the coast of Kamchatka north to Mys Navarin, Komandorskiye Ostrova, the Aleutian Islands, the Pribilof Islands, and islands on the continental shelf along the coast of North America from the southern side of the Alaska Peninsula south to San Miguel Island. This is the only otariid that habitually hauls out on sea ice. Rarely enters lower reaches of coastal rivers in Washington and Oregon. Vagrant to Herschel Island (69°35′N, 139°05′W) in the Beaufort Sea, and to Jiangsu, China. (A lone female of unknown origin has been hauling-out on the Brisons, off Cape Cornwall, England, since at least 1984—Westcott 1997.)

Genus NEOPHOCA Gray, 1866

The taxonomy of the sea-lions of Australia and New Zealand (genera *Neophoca* and *Phocarctos*) was much confused by earlier authorities (Wood Jones 1925*a*, 1925*b*; Sivertsen 1954; Scheffer 1958) and remained so until King (1960) clarified the situation. The only living species of *Neophoca* is endemic to Australia, but King (1983*b*) described an extinct species, *N. palatina,* from the middle Pleistocene of New Zealand.

Neophoca cinerea (Péron, 1816) (Australian sea-lion; white-capped sea-lion).

Coastal waters of western and southern Australia; rookeries on islands from Houtman Abrolhos (28°00′S, 116°00′E), Western Australia, south and east to The Pages Islands (35°46′S, 138°18′E), South Australia. Formerly ranged east to King Island, Waterhouse Island off northern Tasmania, and Battery and Clarke islands in the Furneaux Group. Vagrant north to Shark Bay (25°00′S), Western Australia. An alleged record from Port Stephens (32°44′S), New South Wales, was based on a misidentified skull of *Arctocephalus pusillus* (Walker and Ling 1981).

Genus PHOCARCTOS Peters, 1866

Phocarctos hookeri (Gray, 1844) (Auckland sea-lion; New Zealand sea-lion; Hooker's sea-lion).

Coastal waters of New Zealand and nearby subantarctic islands. Main rookeries on Enderby, Dundas, and Figure-of-Eight islands in the Auckland group; small rookeries on Point Pegasus on Stewart Island (extirpated), the Snares, and Campbell Island. Regularly disperses south to Macquarie Island and north to Stewart Island, to about 46°S on the west coast of South Island,

and to the Otago Peninsula on the east coast; in prehistoric times ranged north along the west coast of North Island to Kaupokonui (39°35′S) (Cassels 1984), and along the east coast of North Island to Cape Kidnappers (39°39′N) (Weston *et al.* 1973) and Houhora (34°48′S) (Crawley 1990).

Genus OTARIA Péron, 1816

Otaria flavescens (Shaw, 1800) (South American sea-lion).

For use of the name *O. flavescens* instead of *O. byronia* Blainville, 1820, see Rodriguez and Bastida (1993; *cf.* Cabrera 1940, Osgood 1943, Rice 1977, King 1978, Oliva 1988).

Coastal waters of South America; rookeries located from Zorritos (03°40′S), Peru, south to Tierra del Fuego and Isla de los Estados (54°45′S), Argentina, thence north to Recife dos Tôrres (29°21′S), Brazil; also throughout the Falkland Islands [=Islas Malvinas]. Vagrant on the Atlantic side to Bahia, Brazil, and on the Pacific side to Colombia, Panama, the Archipiélago de Colon [=Galapagos Islands], and allegedly "South Pacific atolls as far west as Tahiti" (Reeves *et al.* 1992). Old reports of this species being the resident sea-lion in the Galapagos Islands were based on misidentification of *Zalophus wollebaeki.* The type specimen of Blainville's *Phoca byronia* was said to have been collected on the island of Tinian in the Marianas; while it is not inconceivable that a South American sea-lion strayed that far, more plausible is the supposition by Flower (1884*b*) and all subsequent authors that the collector, Commodore John Byron, mislabeled the specimen, and that it really came from the Falkland Islands or South America, which Byron also visited on the same voyage.

Family ODOBENIDAE Allen, 1880

Trichecidæ [*sic*] Gray 1821:302 (The type genus *Trichechus* Linnaeus, 1766 [=*Odobenus*], is preoccupied by *Trichechus* Linnaeus, 1758, given to the manatee, so the family name is not available for the walrus)

Trichechidæ Gray 1825:340 (Type genus: *Trichechus* Linnaeus, 1766; see above)

Trichisina Gray 1837:582 (Type genus: *Trichechus* Linnaeus, 1766; see above)

Rosmaridæ Gill 1866:7 (The type genus *Rosmarus* Brünnich, 1772, is a junior synonym of *Odobenus,* so the family name is invalid because it was replaced prior to 1961 (Article 40(b) of the ICZN Code))

Thalattailurina Albrecht 1879:22 (in part; included "die Phocinen oder Seehunde und die Trichechinen oder Walrosse"; not available because it is not based on the stem of a generic name)

Odobænidæ Allen 1880:5 (Type genus: *Odobaenus* Fée, 1830, an incorrect subsequent spelling of *Odobenus*; spelling suppressed by ICZN—see Appendix 2)

Odobenidæ Palmer 1904:833 (Correction of Odobænidæ Allen 1880; spelling conserved by ICZN—see Appendix 2)

The living walrus is the sole survivor of a diverse array of odobenids that lived from the early Miocene to the end of the Pliocene. A cladistic analysis by Deméré (1994) shows that most genera of the Odobenidae fall into one of two monophyletic subfamilies, Dusignathinae and Odobeninae, while two remaining genera, *Neotherium* and *Imagotaria,* comprise successive branches from the basal stem of the Odobenidae.

Genus ODOBENUS Brisson, 1762

Hall (1981), who ignored all Opinions of the ICZN, called this genus *Rosmarus* Brünnich, "1772" [=1771], because he regarded Brisson's names as non-Linnaean (see Appendix 2).

Odobenus rosmarus (Linnaeus, 1758) (walrus).

Shallow waters of the Arctic Ocean and adjoining seas. Largely restricted, at least in winter, to pack-ice zones. Two well-marked subspecies have long been recognized (Allen 1880, Degerbøl 1935), and Chapskii (1940) described the population in the Laptev Sea as a third subspecies. The latter race is weakly differentiated and somewhat intermediate between the Atlantic and Pacific races, although closer to the latter (Fay 1981), but it was admitted as a valid race by Heptner *et al.* (1976) and Gromov and Baranova (1981).

O. r. rosmarus—In the Atlantic-Arctic from eastern Canada to the Kara Sea. There are four geographically disjunct populations: (1) The eastern Canadian Arctic from Lancaster Sound, Jones Sound, and the Kane Basin, south to the Belcher Islands in Hudson Bay, Ungava Bay, and Godthåb on the west coast of Greenland; formerly found south to Miscou Island, Prince Edward Island, and the Magdalen Islands in the Gulf of St. Lawrence, and to Sable Island off Nova Scotia. (2) The east coast of Greenland from Kronprins Christian Land south to Angmagssalik; vagrant to Iceland. (3) The Svalbard archipelago and Zemlya Frantsa Iosifa. (4) Eastern Barents Sea and western Kara Sea bordering Novaya Zemlya; vagrant along coasts of Europe south to the Netherlands, Belgium, the British Isles, and the Bay of Biscay.

O. r. laptevi Chapskii, 1940—Eastern part of the Kara Sea, the Laptev Sea, and the western part of the East Siberian Sea.

O. r. divergens (Illiger, 1815)—In the Pacific-Arctic, including the Chukchi Sea from Mys Shelagskiy in Siberia east to Point Barrow in Alaska, and the Bering Sea south to Karaginskiy Zaliv in Kamchatka and Bristol Bay in Alaska. Vagrant east to the Beaufort Sea and Bathurst Inlet; southwest to southern Kamchatka, the northern Sea of Okhotsk, and Honshu; and southeast to Unalaska Island, the south side of the Alaska Peninsula, Kodiak Island, Cook Inlet, and Yakutat Bay.

Family PHOCIDAE Gray, 1821

Phocadæ [*sic*] Gray 1821:302 (Type genus: *Phoca*)

Stenorhyncina [*sic*] Gray 1825:340 (The type genus, "le Sténorhinque" F. Cuvier, 1824 [=*Stenorhinchus* E. Geoffroy St. Hilaire and F. Cuvier, 1826] is an unused senior synonym of *Hydrurga*)

Stemmotopina [*sic*] Gray 1825:340 (Type genus: "le Stemmatope" F. Cuvier, 1824 [=*Stemmatopus* E. Geoffroy St. Hilaire and F. Cuvier, 1826; =*Cystophora*])

Cystophorina Gray 1837:582 (Type genus: *Cystophora*)

Stenorynchina [*sic*] Gray 1843:xxiii, 102 (Type genus: *Stenorhynchus* F. Cuvier, 1824 [nec *Stenorhynchus* Lamarck, 1819, in Crustacea], =*Stenorhinchus* E. Geoffroy St. Hilaire and F. Cuvier, 1826)

Stenorhynchina Gray 1844:2 (Type genus: *Stenorhynchus* F. Cuvier, 1824; see preceding entry)

Halichœrina Gray 1869*b*:345 (Type genus: *Halichœrus*)

Monachina Gray 1869*b*:345 (Type genus: *Monachus*)

Lobodontina Gray 1869*b*:345 (Type genus: *Lobodon*)

Thalattailurina Albrecht 1879:22 (in part; included "die Phocinen oder Seehunde und die Trichechinen oder Walrosse"; not available because it is not based on the stem of a generic name)

Ogmorhininae Turner 1888 (Type genus: *Ogmorhinus* Peters, 1875 [=*Hydrurga*])

Hydrurginæ Trouessart 1907:7 (Type genus: *Hydrurga*)

Lobodoninae Kellogg 1922:27 (=Lobodontina; incorrect subsequent spelling)

Sibiricopusidae (p.412), Sibirico-Baicalo-Pusidae (p. 413), or Sibirico-bicuspidato-baicalopusidae (p. 414) Dybowski 1929:412–414 (Type genus: "*Baicalopusa*" Dybowski, 1929; Dybowski's names are not available because he did not consistently apply the Principle of Binomial Nomenclature—ICZN Code Articles 4(a) and 11(c))

Europäopusidae (p. 412), Europäo-Caspio-Pusidae (p. 413), or Europäo-tricuspidato-caspiopusidae (p. 414) Dybowski 1929:412–414 (Type genus: "*Caspiopusa*" Dybowski, 1929; not available—see note above)

Erignathini Chapskii 1955*a*:164 (Type genus: *Erignathus*)

Histriophocina Chapskii 1955*a*:164 (Type genus: *Histriophoca*)

Miroungini Muizon 1982*a*:199 (Type genus: *Mirounga*)

A phenetic division of the Phocidae into four subfamilies was long accepted (Kellogg 1922, Simpson 1945): Phocinae for most of the northern seals, Monachinae for the monk seals, Lobodontinae for the four genera of antarctic seals, and Cystophorinae for the elephant seals (*Mirounga*) and the hooded seal (*Cystophora*). The latter three subfamilies were reduced to tribes of an expanded subfamily Monachinae by Scheffer (1958). King (1966) concluded that the two genera in which the males possess an inflatable proboscis do not comprise a monophyletic group, and that *Cystophora* is really a member of the northern Phocinae, while *Mirounga* belongs with the southern Monachinae. Chapskii (1974) dissented, and defended a division into three subfamilies, Phocinae, Monachinae (including Lobodontinae), and Cystophorinae (including *Cysto-*

phora and *Mirounga*). However, recent cladistic analyses largely corroborate King's division into two subfamilies (Muizon 1982*a*, Wyss 1988*a*, Berta and Wyss 1994).

Subfamily PHOCINAE Gray, 1821

Within this subfamily the five genera (or subgenera) *Phoca, Pusa, Halichoerus, Histriophoca,* and *Pagophilus,* constitute a well-marked clade designated as tribe Phocini, which is distinguished from all other phocid seals by two synapomorphies—a unique karyotype and a white lanugo, or natal pelage (molted *in utero* in some members of *Phoca*) (Chapskii 1955*a*, Burns and Fay 1970, McLaren 1975). Their karyotype with 2n=32 chromosomes was derived from the 2n=34 karyotype of all other phocids by the fusion of two pairs (Árnason 1974*a*, *c*; Anbinder 1980).

Cystophora, on the other hand, retains the plesiomorphic complement of 2n=34 chromosomes, and it has a gray fetal pelage (which is shed *in utero*; the pups—called "bluebacks"—are born in their second pelage, a trait correlated with their extraordinarily short 4-d nursing period—Bowen *et al.* 1985; Oftedal *et al.*, 1991). Unexpectedly, cladistic analyses of morphological features by Muizon (1982*a*), and of the nucleotide sequences of the mitochondrial cytochrome *b* gene by Perry *et al.* (1995) and Carr and Perry (1997), would also include *Cystophora* in the Phocini. Other cladistic analyses based on morphology (Wyss 1988*a*, Berta and Wyss 1994) and on the cytochrome *b* gene (Árnason *et al.* 1995), which make *Cystophora* the sister-group to the Phocini, are more believable.

The bearded seal *Erignathus* is the most plesiomorphic phocine, and is the sister-group to the Phocini plus *Cystophora.*

For a long time the conventional phenetic classification of the Phocini recognized *Halichoerus* as a separate genus but included in *Phoca* [*sensu lato*] the subgenera *Phoca, Pusa, Histriophoca,* and *Pagophilus* (Doutt 1942; Anderson 1943, 1946; Simpson 1945; Ellerman and Morrison-Scott 1951; Miller and Kellogg 1955; Bobrinskii 1965*b*; King 1966, 1983*a*; Peterson 1966; Burns and Fay 1970; Banfield 1974; Heptner *et al.* 1976; Gromov and Baranova 1981; Pavlinov and Rossolimo 1987; Corbet and Hill 1991; Duguy and Robineau 1992; Wozencraft 1993).

Ognev (1935), followed by Chapskii (1955*a*) and Corbet (1978), continued to include *Pusa* as a subgenus of *Phoca,* but recognized *Histriophoca* and *Pagophilus* [or *Pagophoca*] as full genera. Scheffer (1958) subsequently raised *Pusa* to full generic rank, too, making a total of five genera in the Phocini; he was followed by Gromov *et al.* (1963), Hall (1981), and Jones *et al.* (1986, 1992). Repenning (*in* Bonner 1989:97) thought that the long fossil histories of *Phoca, Pusa,* and *Pagophilus,* justified ranking them (and by implication *Histriophoca*) as separate genera.

Chapskii (1955*a*) divided the tribe Phocini into two subtribes: Phocina, which contained *Halichoerus* and *Phoca* (including *Pusa* as a subgenus), and Histriophocina, which contained *Histriophoca* and *Pagophoca* [=*Pagophilus*]; he placed *Cystophora* in another tribe, Cystophorini. His arrangement has been mostly corroborated by cladistic analyses based on morphology (Muizon 1982*a*) and on mtDNA (Mouchaty *et al.* 1995, Perry *et al.* 1995, Carr and Perry 1997). These studies reveal a primary split into two clades, one including *Phoca, Pusa,* and *Halichoerus,* the other containing *Pagophilus* and *Histriophoca* (with *Cystophora* a basal member of one or the other of these two clades—but see above).

The conventional division of the Phocini into only two genera—*Halichoerus* and *Phoca*—is clearly not admissible, because the exclusion of *Halichoerus* from *Phoca* [*sensu lato*] leaves the latter as a paraphyletic grouping. On the other hand, the classification proposed by Scheffer (1958), who ranked all five taxa as full genera, and the one proposed by Chapskii (1955*a*), who recognized four full genera while merging *Pusa* with *Phoca,* are both consistent with the cladistic results. Any other allowable generic classification would necessitate including the gray seal in *Phoca,* but the gray seal has been universally known as *Halichoerus* for so long that many authors would be reluctant to adopt such a change.

One wild-born *Pagophilus groenlandicus* ♂ × *Cystophora cristata* ♀ hybrid survived at least until weaning (Kovacs *et al.* 1997). A male *Halichoerus grypus* and a female *Pusa hispida* hybridized in captivity, but their pup was stillborn (Lönnberg 1929). There is no credible basis for the claim by Troitzky (1953) that a pregnant seal collected at Corsica was a *Pagophilus groenlandicus* × *Monachus monachus* hybrid.

Genus ERIGNATHUS Gill, 1866

Erignathus barbatus (Erxleben, 1777) (bearded seal; squareflipper; ugruk).

Circumpolar at ice edge along all coasts of northern Eurasia and northern North America. Two intergrading subspecies are recognizeable (Manning 1974; *cf.* Kosygin and Potelov 1971), one in the Atlantic sector, the other in the Pacific sector.

E. b. barbatus—Central Canadian Arctic east to central arctic coast of Eurasia. Ranges north to Jones Sound in Canadian Arctic Archipelago, Kap York in western Greenland, Nordostrundingen in eastern Greenland, Svalbard, Zemlya Frantsa Iosifa, and Novaya Zemlya; ranges south to James Bay, northern Newfoundland, Kap Farvel in Greenland, Iceland, Jan Mayen, Bjørnøya, and Vesterålen in northern Norway. Vagrant to Saint Lawrence estuary, Cape Cod, British Isles, France, Spain, and Portugal.

E. b. nauticus (Pallas, 1811)—Laptev Sea east to central Canadian Arctic. Ranges north to Paluostrov Taymyr, Severnaya Zemlya, Novosibirskiye Ostrova, Ostrov Vrangelya, Banks Island, and Victoria Island; ranges south to Karaginskiy Zaliv in Kamchatka and Bristol Bay in Alaska. A disjunct population in the northern and western Sea of Okhotsk south to Tatarskiy Proliv and northern Hokkaido. Vagrant to Zhejiang, China, and Honshu, Japan.

Genus PHOCA Linnaeus, 1758

This genus contains two sibling species, the relationships of which were disentangled by Mohr (1941, 1965), Inukai (1942*a, b*), Wilke (1954), Chapskii (1960, 1967, 1969), Belkin (1964), McLaren (1966), Belkin *et al.* (1969), Naito and Nishiwaki (1975), Shaughnessy and Fay (1977), and Burns *et al.* (1984). Spotted seals *P. largha* are pagophilic and haul out on sea ice floes in pairs to whelp and mate from March to May. Harbor seals *P. vitulina* are pagophobic and whelp in groups on beaches, sandbars, and rocky reefs—or locally on bergy bits (*cf.* Armstrong and Roberts 1956) from tidewater glaciers; in areas where they are sympatric with spotted seals, they whelp and mate later, in June and July (Bigg 1969, Shaughnessy and Fay 1977). Spotted seals are born with a white lanugo, whereas most harbor seals shed it *in utero* (Stutz 1966). Harbor seals are dimorphic for pelage pattern, with dark and light phases, the ratio of which varies geographically (Stutz 1967, Kelly 1981). Larga seals are monomorphic with a pattern somewhat like the light phase of harbor seals. One obvious substantive morphological difference between the two species is in their hyoid bones (Naito 1974, 1982). Except for one possible hybrid, the complete genetic isolation of the two taxa was confirmed by a study of their mtDNA (O'Corry-Crowe and Westlake 1997). Otherwise no wild hybrids between them have been identified, even though viable hybrids have been produced in captivity (Duffield 1990).

Phoca vitulina Linnaeus, 1758 (harbor seal; common seal; Kuril seal; island seal).

Five named subspecies are recognizeable (Doutt 1942, Shaughnessy and Fay 1977, Burns *et al.* 1984, Smith *et al.* 1994):

P. v. concolor DeKay 1842—Coasts of the western North Atlantic from James Bay, Hudson Bay, Hudson Strait, Admiralty Inlet on northern Baffin Island, south to Massachusetts; southern Greenland north to Thule on the west coast and Scoresby Sund on the east coast; Iceland. Regularly enters freshwater rivers and lakes on western side of Hudson Bay and the Ungava Peninsula, and ascends the St. Lawrence River, vagrants having reached Lake Champlain, the mouth of the Gatineau River at Ottawa, Lake Ontario, and Lake Onondaga at Syracuse, New York. Vagrant south to Daytona Beach, Florida.

P. v. mellonae Doutt, 1942—Permanently resident in certain freshwater rivers and connecting lakes that flow into southeastern Hudson Bay and James Bay: Rivière Nastapoca, Petite Rivière de la Baleine, Grande Rivière de la Baleine, and La Grande Rivière. Although the validity of this subspecies has been questioned (Mansfield 1967), its distinctiveness has since been confirmed (Smith *et al.* 1994).

P. v. vitulina—Coasts of the eastern North Atlantic from the Barents Sea south to Portugal, including the British Isles and the southwestern Baltic Sea (but absent from the Faroes). Occasionally enters freshwater in the rivers of Scotland and eastern England, and in some of the larger Scottish lochs (Hope, Maree, Ness, Shiel, and Awe). There is an isolated population on Prins Karls Forland in Svalbard which is somewhat differentiated morphologically from animals in more southerly waters of the North Atlantic (Wiig 1989). Vagrant to Madeira.

P. v. stejnegeri Allen, 1902—This race has also gone under the names *P. kurilensis* Inukai, 1942, and *P. insularis* Belkin, 1964. Coasts of the western North Pacific from southeastern Kamchatka, Komandorskiye Ostrova, and the western Aleutian Islands, southwest around the Sea of Okhotsk and through the Ostrova Kuril'skiye to the Pacific coast of Hokkaido. Intergrades with the next race in the Aleutian Islands.

P. v. richardii (Gray, 1864)—Coasts of the eastern North Pacific from the eastern Aleutian Islands, the Pribilof Islands, and Kuskokwim Bay in Alaska, south to Isla Asuncion in northern Baja California Sur. Present year-round in freshwater Iliamna Lake in Alaska (which can be reached from Bristol Bay *via* the 95-km Kvichak River). Seasonally enters rivers in Alaska, British Columbia, Washington, Oregon, and Northern California, and sometimes enters Lake Washington in Seattle. Formerly ascended the lower Columbia River as far as The Dalles, 270 km above the mouth. Vagrant to Isla Guadalupe, Laguna San Ignacio, and the southern Golfo de California (Los Frailes and Los Islotes). Morrell's report of several hundred "sea leopards" (as *P. vitulina* was often known in those days) on Isla Socorro (18°47′N, 110°58′W) in 1825 cannot be taken seriously (see comments above under *Arctocephalus townsendi*).

The population of harbor seals in southern California and Baja California is somewhat distinctive, and has been called *P. v. geronimensis* Allen, 1902. Doutt (1942) provisionally accepted it as a valid subspecies on the basis of its pelage color, and Huey (1964) also thought that it was a recognizable race, but Burns *et al.* (1984) found that it is not sufficiently differentiated to warrant subspecific separation from *P. v. richardii.*

Gray (1864*a*) named this seal in honor of "Capt. Richard, the Hydrographer to the Admiralty." The captain's name, in fact, was "Richards," so P. L. Sclatèr (footnote *in* Clark 1873) and other authors, most recently Shaughnessy and Fay (1977), have argued that the name of this race should be "corrected" to *richardsi.* However, that spelling is an "unjustified emendation" because there is not "in the original publication itself, without recourse to any external source of information, clear evidence of an inadvertent error, such as a lapsus calami or a copyist's or printer's error" (Article 32(c)(ii) of the ICZN Code), so Gray's original spelling must stand (Article 31(a)(iii)).

Phoca largha Pallas, 1811 (spotted seal; larga seal).

Mohr (1941) named this species *Phoca petersi* before she realized (Mohr 1965) that it had already been named. "Larga," spelled ларга in Russian, is the name of this seal in the Tungus language of eastern Siberia; "g" rather than "gh" is now the standard transliteration of the Russian letter "Г."

Pack-ice zone of North Pacific. There are eight mostly discrete whelping and mating areas: the Liaodong Wan [=Gulf of Laotung] in the Bo Hai [=Gulf of Chihli]; Zaliv Petra Velikogo [=Peter the Great Bay]; Tatarskiy Proliv; east side of Ostrov Sakhalin to northern Hokkaido; northern Sea of Okhotsk; around Ostrov Karaginskiy in Kamchatka; northwestern Bering Sea; and southeastern Bering Sea. In spring ranges south as far as Fujian in China, Shikoku in Japan, and the eastern Aleutian Islands; in summer north into the Chukchi Sea as far as Chaunskaya Guba, Siberia, and Herschel Island, Yukon Territory.

Genus PUSA Scopoli, 1771.

This genus includes three widely allopatric species—the ringed seal, which is widespread in arctic marine waters (with two races in coastal freshwater lakes), and two strongly-differentiated species, the Caspian and Baikal seals, which are landlocked in central Asia. The three species differ in cranial features, color pattern, and reproductive behavior. The pelage of ringed seals is profusely marked with pale spots and rings on a darker background, that of Caspian seals is pale and marked with scattered dark spots (less so in females), and that of Baikal seals is uniform except for countershading. Baikal seals resemble arctic ringed seals in that the near-term females remain solitary and resort to shorefast ice, where they excavate birth lairs in the snow. Late-pregnant Caspian seals, on the other hand, congregate in sizable herds on large floes in hummocking pack ice, where the pups are born exposed.

The origins of the three species are still being debated (Chapskii 1955*b,* Davies 1958, McLaren 1960*b,* Timoshenko 1975, Grigorescu 1976, Ray 1976*a,* Repenning *et al.* 1979). Some authors have postulated that the Caspian and Baikal seals are direct offshoots of the Arctic ringed seal, which dispersed southward into an inland lake that formed during the Würm glaciation when the West Siberian ice sheet turned the flow of the Ob and Yenisey rivers southward. Other writers believe that the Caspian seal, and perhaps the Baikal seal also, are more likely descended from "*Phoca*" [=*Pusa*] *pontica* or one of the other seals that lived in the Paratethys Sea during the Miocene and Pliocene. The Paratethys was a vast, brackish, inland sea which extended from the Danube River basin in eastern Austria, Slovakia, Hungary, and Romania, east to western Kazakhstan, Uzbekistan, and Turkmenistan, encompassing the area now occupied by the Black, Azov, Caspian, and Aral seas; it had intermittent connections to the Mediterranean Sea in the region of the present Bosporus, and perhaps to the Arctic Ocean *via* northward-flowing rivers. A variant of the latter hypothesis has the genus *Pusa* originating in the Paratethys Sea, from whence one branch dispersed northward into the Arctic Ocean where it gave rise to the modern *P. hispida.*

Several 18th century explorers (Steller 1751, 1774; Krasheninnikov 1755; Pallas 1811) said that there were seals in Ozero Oron, a freshwater lake about

420 km northeast of Ozero Baykal, but on the upper Lena drainage about 3,000 km from the Arctic Ocean. None of their accounts were first-hand, and none cited any sources. Nevertheless, their claims were uncritically repeated by many authors (Schreber 1778; Pennant 1781; Gmelin 1788; Allen 1880; Trouessart 1897, 1904; Weber 1928) as late as the early 20th century. Later explorers never found any seals in Lake Oron (Ognev 1935, Scheffer 1958, McLaren 1960*b*, Heptner *in* Heptner *et al.* 1976). Nonetheless Dybowski (1922) went so far as to bestow the name *Phoca oronensis* on these mythic animals. Even more far-fetched is the statement by Grevé (1896), under the heading "*Phoca* sp.?," that unnamed "Russische und englische Reisende sahan Seehunde im Kuku-nuur. Erbeutet und bestimmt wurder sie nicht." Kuku-nuur, or Koko Nor [now Qinghai Hu], is a landlocked brackish lake 3,266 m above sea level in northeastern Xizang [=Tibet].

Surely the most outlandish sidebar to the history of pinniped taxonomy was the complex nomenclature for the landlocked Eurasian seals proposed by the Russian naturalist Dybowski (1929) when he was 95 yr old. Fifty-six years earlier Dybowski (1873) had published the first comprehensive account of the physical characteristics and habits of the Baikal seal, and he was the first to recognize it as a species separate from the arctic ringed seal. In his 1929 classification he separated the members of the ringed-seal group into two families: family "Europäo-tricuspidato-caspiopusidae" for the ringed seal and the Caspian seal, and family "Sibirico-bicuspidato-baicalopusidae" for the Baikal seal and the (mythical!) seal of Lake Oron. He named separate genera for the seals of the Caspian Sea ("*Caspiopusa*," "*Europäocaspiopusa*," or "*Europäo-tricuspidato-caspiopusa*"), Lake Baikal ("*Baicalopusa*," "*Sibirico-baicalopusa*," or "*Sibirico-bicuspidato-baicalopusa*"), and Lake Oron ("*Oronopusa*" or "*Sibirico-oron-opusa*"). At the species level he split the seals of the Caspian into three species, which he named *Caspiopusa behningi*, *C. kisielewitschi*, and *C. dierzawini*, and those of Lake Baikal into two, *Baicalopusa dorohostaiskii* and *B. wereschtschagini*. Furthermore, he elevated the landlocked races of the ringed seal to full species status, and even proposed separate generic names for the populations in the Arctic Ocean and the Baltic Sea ("*Europäoannellatopusa*"), Lake Saimaa ("*Europäosaimopusa*"), Lake Ladoga ("*Europäoladogopusa*"). Miller (1932) asserted that Dybowski's "technical terms appear to lie beyond the scope of the International Rules of Zoological Nomenclature"; Conisbee (1953) refused even to list Dybowski's generic names because "his method of nomenclature departs entirely from the Linnaean system."

Pusa hispida (Schreber, 1775) (ringed seal; fjord seal; jar seal; natchik; netsik; floe-rat).

There has been some confusion about the publication dates of names in Schreber's *Die Säugethiere...*; the name *Phoca hispida* first appeared in Theil 2, Heft 13, Plate 86, which was published in 1775 (Sherborn 1891).

Geographical variation in ringed seals has been discussed by Nordquist (1899), Smirnov (1927, 1929*a*, *b*, 1935), Naumov and Smirnov (1936), Naumov (1941), Anderson (1943), Bobrinskii (1944), Mohr (1952), Müller-Wille (1969), Fedoseev and Nazarenko (1970), and Hyvärinen and Nieminen (1990). Of the many named forms, only three geographically disjunct subspecies can be upheld in marine waters, plus two local endemic subspecies in freshwater lakes. Bobrinskii (1944) presaged this classification when he arranged the then-recognized Eurasian subspecies into three groups: (1) the Baltic group of medium-sized, dark races (*botnica, saimensis, ladogensis*); (2) the northern group of large, light-colored races (*pomororum, birulai,* and *krascheninnikovi* [*sic*]); and the far-eastern group of small, very light-colored races (*ochotensis*).

All authors agree that the populations in the Baltic Sea and in the Sea of Okhotsk, which are geographically isolated, are fairly well-differentiated morphologically from populations farther north (Ognev 1935, Bobrinskii 1944, Müller-Wille 1969). Within the Arctic Ocean, however, some authors (Heptner *et al.* 1976, Gromov and Baranova 1981) still list about a half dozen races in various sectors, including *P. h. soperi* (Anderson, 1943) from Foxe Basin and Nettilling Lake on Baffin Island, *P. h. hispida* from the coasts of Greenland and Labrador, *P. h. pomororum* (Smirnov, 1929) from the White Sea, *P. h. birulai* (Smirnov, 1929) from Novosibirskiye Ostrova, *P. h. beaufortiana* (Anderson, 1943) from the Beaufort Sea, and *P. h. krascheninikovi* (Naumov and Smirnov, 1936) from the Bering Sea [the spelling *krascheninnikovi,* used by Bobrinskii (1944), Heptner *et al.* (1976), Gromov and Baranova (1981), and Pavlinov and Rossolimo (1987), is an unjustified emendation (Article 32(c)(ii) of the ICZN Code)].

Scheffer (1958), King (1964, 1983*a*), and Corbet (1978) rather arbitrarily reduced all of these nominal subspecies to two, *P. h. hispida* in the Arctic Ocean and *P. h. krascheninikovi* in the Bering Sea. Later, Bobrinskii (1965*b*) revised his 1944 classification by lumping all populations in the Russian Arctic, from Murmanskaya to Chukotskiy (and presumably including the Bering Sea), under the name *P. h. pomororum.* Youngman (1975) could find no significant geographical variation among ringed seals from Alaska and the western and eastern Canadian Arctic, and Fedoseev and Nazarenko (1970) could find no differences between specimens from the Barents and Bering seas, so all these authors concluded that all populations in the Arctic basin and the Bering Sea should be considered as belonging to the nominate subspecies—an arrangement endorsed by Chapskii (*in* Heptner *et al.* 1976) and by Frost and Lowry (1981). The situation now appears more complex, however, with Fedoseev's (1975) discovery of slight morphological differences between the ringed seals that live in drifting pack ice and those that live in adjacent shorefast ice in the Chukchi, Bering, and Okhotsk seas. Finley *et. al.* (1983) likewise discovered a population of ringed seals inhabiting the pack ice of Baffin Bay that are morphologically distinguishable from adjacent coastal animals and appear to be reproductively isolated from them. The relationship of these offshore animals to the coastal ones remains unresolved.

In the eastern Baltic region, the freshwater populations in Lake Ladoga, Russia, and Lake Saimaa, Finland (which became separated from the Baltic Sea 8,000–9,000 yr ago), differ significantly from each other and from the nearby marine population (Müller-Wille 1969, Hyvärinen and Nieminen 1990). Bobrinskii (1965*b*), in his key to the pinnipeds of the USSR, included the Ladoga seals in the Baltic subspecies, and Corbet (1978) thought that both the Ladoga and Saimaa populations are best considered the same as the Baltic race. However, a discriminant analysis of cranial measurements showed that adults of the Baltic, Ladoga, and Saimaa populations are 100% separable (Hyvärinen and Nieminen 1990).

P. h. hispida—Mainly in shore-fast ice, but also in close, stable pack ice, throughout the Arctic Ocean and the confluent Bering Sea. Individuals have been seen within 2 km of the North Pole. Ranges south to James Bay, the Strait of Belle Isle, Kap Farvel in Greenland, coast of the Barents Sea in northern Norway, the White Sea, Karaginskiy Zaliv in Kamchatka, and northern Bristol Bay in Alaska. Also inhabits freshwater Nettilling Lake (31 m above sea level) and the 85 km-long Koukdjuak River, its outlet into Foxe Basin, on the west side of Baffin Island. Vagrant to Açôres, Germany, Portugal, New Jersey, and southern California.

P. h. botnica (Gmelin, 1788)—Throughout the northern Baltic Sea, including the gulfs of Bothnia and Finland, south to Stockholm, Sweden, and Riga, Latvia.

P. h. ladogensis (Nordquist, 1899)—Almost entirely confined to freshwater Ladozhskoye Ozero [=Lake Ladoga] (4 m above sea level) in Russia, although seals are said to occasionally transit the Neva Reka between this lake and the Gulf of Finland. Lilljeborg (1874) and Mela (1882) said that there were seals in Ozero Onezhskoye [=Lake Onega], Russia, but Nordquist (1899) could find no credible records; Onega is only 125 km from Ladoga, but it drains north into the White Sea.

P. h. saimensis (Nordquist, 1899)—Landlocked in a series of interconnected lakes in Finland: Saimaa, Haukivesi, Orivesi, Puruvesi, and Pyhäselkä; these lakes are 76 m above sea level and drain into Ladozhskoye Ozero by a stream too swift for seals to navigate.

P. h. ochotensis (Pallas, 1811)—Inhabits the western, northern, and northeastern parts of the Sea of Okhotsk, ranging south to the northern coast of Hokkaido on the west, and to Mys Lopatka, Kamchatka, on the east. Vagrant to Jiangsu in China, and Shikoku and Kyushu in Japan.

Pusa caspica (Gmelin, 1788) (Caspian seal).

Endemic to the Caspian Sea—a landlocked saline lake 28 m below sea level. Sometimes enters river mouths, and has ascended the Volga as far as Astrakhan 80 km upstream.

Pennant (1781) and Pallas (1811), followed by a few later authors, stated that this seal also inhabited the Aral Sea, another landlocked brackish lake about 370 km east of the Caspian Sea. However, as pointed out by Grimm (1883), "The notion that seals are found in the Aral is. . .incorrect."

Pusa sibirica (Gmelin, 1788) (Baikal seal).

Endemic to Ozero Baykal in Siberia; the lake is 455 m above sea level and drains 3,500 km *via* the Nizhnyaya [Lower] Angara and Yenisey rivers into the Kara Sea. On rare occasions seals have ascended the lower reaches of some of the rivers that drain into the lake: the Barguzin as far as Ust' Barguzin a few kilometers upstream, and the Selenga as far as Ust' Kyakhta 400 km upstream; they have also descended the Nizhnyaya Angara as far as Olonki 150 km downstream. (Rumors of seals in Ozero Oron are discussed above under genus *Pusa*.)

Genus HALICHOERUS Nilsson, 1820

Halichoerus grypus (Fabricius, 1791) (gray seal; horsehead; Atlantic seal; Atlantic gray seal; Baltic gray seal).

Temperate coasts of the North Atlantic. There are disjunct populations on the western and eastern sides of the North Atlantic and in the Baltic Sea. Nehring (1886) differentiated eastern Atlantic and Baltic gray seals as *H. g.* var. *atlantica* [*sic*] and *H. g.* var. *baltica* [*sic*], respectively. Subsequent authors disregarded Nehring's division until Chapskii (1975) showed that there were marked cranial differences between the eastern Atlantic (Murmanskaya and the British Isles) and Baltic populations. Chapskii recognized Nehring's "varieties" as subspecies, tacitly restricting the nominate subspecies to the western Atlantic populations (the type locality is "Greenland"; the only place in Greenland where gray seals have been found is around Disko on the west coast, so they must have come from one of the western Atlantic whelping colonies). Heptner *et al.* (1976) and Gromov and Baranova (1981) considered the eastern Atlantic population the same as the nominate race and used the prior name *H. g. macrorhynchus* Hornschuch and Schilling, 1851, for the Baltic race. Mansfield (1977)[4] found that Canadian gray seals attain a somewhat greater body size than British ones do. The various local populations of gray seals have diverged markedly in certain life-history and behavioral traits. Gray seals in the Gulf of Saint Lawrence and in the Baltic Sea whelp on shorefast sea ice, whereas those east of Nova Scotia and those on the Atlantic coast of Europe whelp on ice-free islands (Davies 1957, Mansfield and Beck 1977). In Canada their peak whelping season comes in mid-January, at various eastern Atlantic colonies some time between late September and mid-November, and in the Baltic Sea in early March.

H. g. grypus—Western Atlantic from Cape Chidley in Labrador south to Nantucket Island in Massachusetts, including Newfoundland and the Gulf of St. Lawrence. Eastern Atlantic from the Murman coast of Russia south-

[4] Mansfield, A. W. 1977. Growth and longevity of the grey seal *Halichoerus grypus* in eastern Canada. International Council for the Exploration of the Sea, Marine Mammals Committee. Document C.M.1977/N:6. 12 pp.

west along the coast to Stavanger in Norway, in Iceland, the Faroes, the Shetland Islands, the Orkney Islands, western Great Britain, Ireland, the Netherlands, and the coast of Bretagne, France. Vagrant north to Disko Bugt in Greenland, and south as far as New Jersey and Portugal.

H. g. macrorhynchus Hornschuch and Schilling, 1851—Baltic Sea from the gulfs of Bothnia and Finland south to Denmark.

Genus HISTRIOPHOCA Gill, 1873

Histriophoca fasciata (Zimmermann, 1783) (ribbon seal).

Pacific-Arctic, from the East Siberian Sea and Chukchi Sea southeast to Bristol Bay and Unalaska Island, and southwest along the coast of Kamchatka and the Ostrova Kuril'skiye as far as northern Hokkaido, including the Sea of Okhotsk south to Tatarskiy Proliv. They inhabit the pack-ice zone except during the summer, when they become pelagic. Vagrant to Cordova, Alaska, and Morro Bay, California.

Fedoseev (1984) found only weak morphological differences between populations in the western and eastern parts of the Bering Sea.

Genus PAGOPHILUS Gray, 1844

Some authors have called this genus *Pagophoca* Trouessart, 1904, in the mistaken belief that *Pagophilus* Gray, 1844, was preoccupied.

Pagophilus groenlandicus (Erxleben, 1777) (harp seal).

Pack-ice zone of the North Atlantic. Whelping and mating take place on the pack ice in three circumscribed areas: around Newfoundland, around Jan Mayen, and in the White Sea. Seals from the three whelping areas differ in size, cranial features, and pelage coloration (Khuzin 1963, 1967; Yablokov and Sergeant 1963; Yablokov and Etin 1965). There are only slight differences between the Newfoundland and Jan Mayen populations, but the White Sea population is sufficiently distinct to be treated as a separate subspecies by Russian taxonomists (Bobrinskii 1944, Heptner *et al.* 1976, Gromov and Baranova 1981).

P. g. groenlandicus—Breeds around Newfoundland (including the "Front" north of the island, and the "Gulf" west of it) and Jan Mayen. Ranges north in summer to Foxe Basin, Lancaster Sound, Jones Sound, Baffin Bay, the Greenland Sea, and Svalbard, and south in winter to Nova Scotia, Newfoundland, southern Greenland, Iceland, Jan Mayen, and northern Norway. Vagrant south to Virginia, Scotland, Germany, and France.

P. g. oceanicus (Lepechin, 1778)—Breeds in White Sea; ranges into Barents Sea as far as Zemlya Frantsa Iosifa and Severnaya Zemlya. In some years great numbers have emigrated from the Barents Sea south to the coast of Finnmark in winter and spring.

Genus CYSTOPHORA Nilsson, 1820

Cystophora cristata (Erxleben, 1777) (hooded seal; bladdernose seal).

Pack-ice zone of the North Atlantic from Baffin Bay, Denmark Strait, the northern Greenland Sea, and the Barents Sea, south to the Gulf of St. Lawrence, Newfoundland, southern Greenland, Iceland, and Jan Mayen. Whelping takes place on drifting ice in three discrete areas: (1) off southeastern Labrador, northeastern Newfoundland, and in the Gulf of Saint Lawrence; (2) in Davis Strait; and (3) around Jan Mayen. This species shows a great propensity to wander; a number of vagrants have moved west through the Canadian Arctic to the Beaufort Sea, and thence south through the Bering Strait to southeastern Alaska, and even to southern California! To the south they have wandered along the Atlantic seaboard of the United States as far as Florida, Puerto Rico, and the Virgin Islands, and down the European side as far as Denmark, the British Isles, the Bay of Biscay, Portugal, and southwestern Spain.

A multivariate analysis of skull features failed to detect any differences between specimens from Newfoundland, Davis Strait, and Jan Mayen (Wiig 1984).

Subfamily MONACHINAE Gray, 1869

Technically, the subfamily name Stenorhinchinae Gray, 1825, should take priority over Monachinae, but the latter name has been in use since at least 1897 (Trouessart 1897), whereas, as far as I can tell, Stenorhynchinae [*sic*] was last used in 1907 (Wilson 1907) [and then for a taxon that excluded *Monachus*]. For spelling see discussion below under genus *Hydrurga*. Muizon (1982*a*) divided this subfamily into three tribes: Monachini for the monk seals, Miroungini for the elephant seals, and Lobodontini for the four Antarctic genera. Among the latter, the genera *Lobodon* and *Hydrurga* are sister-taxa, and both possess trenchantly-lobed postcanine teeth, a trait associated with their feeding on krill.

Genus MONACHUS Fleming, 1822

The monk seals are the most plesiomorphic members of the subfamily, and they appear to be relict species (one is already extinct) (King 1956). Although quite similar externally, the three species are well-differentiated by cranial features; the Hawaiian species has diverged more from the Caribbean and Mediterranean populations than the latter two have from each other (Rice unpublished data). Repenning and Ray (1977) noted several characters in which the Hawaiian monk seal is more primitive than any other living phocid. Wyss (1988*a*) raised the possibility that *Monachus* may not be a monophyletic group.

Monachus tropicalis (Gray, 1850) (Caribbean monk seal; West Indian monk seal).

EXTINCT; last reliable report from Serranilla Bank in 1952. Formerly small islets and cays in the Caribbean region; known localities of occurrence were an islet (Isla de Lobos?) off northern Veracruz, Arrecifé Triangulos off Campeche, Arrecifé Alacran off Yucatan, the Dry Tortugas, Key West, Cay Sal Bank in the Strait of Florida, Cape Canaveral in Florida, the Bahamas (said to be common "throughout the islands" in the 18th century, but specific locality records are lacking), Isla de Providencia, Isla de Juventud [=Isla de Pinos], Rosalind Bank, Serranilla Bank, Pedro Cays south of Jamaica, Isla Alto Velo (near Isla Beata) south of Hispaniola, and Guadeloupe. Bones recovered from Indian middens in Pinellas, Lee, Dade, and Brevard counties in Florida; Cumberland Island in Georgia; Puerto Rico; St. Eustatius; and Nevis (Wing 1992). "Fossil" remains found near Charleston, South Carolina (Ray 1961). Specimens from archeological sites in Texas were probably traded from elsewhere (Raun 1964), and none of the alleged sight records from Texas is credible (Rice 1973). (In 1915, six monk seals from Arrecifé Triangulos were released at Pensacola, Florida, "where they remained in the bay for a while thereafter"—Allen 1942).

Monachus monachus (Hermann, 1779) (Mediterranean monk seal).

Madeira and Ilhas Desertas; Islas Canarias; the northwestern coast of Africa from the Strait of Gibraltar south to Cap Blanc, Mauritania; the coasts and islands throughout the Mediterranean Sea, and the western and southern coasts of the Black Sea. Vagrant north along the coast of Portugal (Setúbal, Peniche, and Buarcos) and the Atlantic coast of France (mouth of Rivière Gironde, La Rochelle, and near mouth of Rivière Loire), and south to the islands of Cape Verde, Cap Vert in Senegal, and The Gambia. None of the reports of monk seals in the Açôres are credible (Marchessaux 1989). There are slight morphological differences between animals of the Atlantic and Mediterranean populations (van Bree 1979).

Monachus schauinslandi Matschie, 1905 (Hawaiian monk seal).

Islands and atolls of the Leeward [=Northwestern] Chain of the Hawaiian Islands; pupping occurs on Kure Atoll, Midway Atoll, Pearl and Hermes Reef, Lisianski Island, Laysan Island, French Frigate Shoals, Necker Island, and Nihoa Island. Wanders to Maro Reef and Gardner Pinnacles. Vagrant to Niihau, Lehua, Kauai, Oahu, and Hawaii in the main Hawaiian Islands, and to Wake Island, Johnston Island, and Palmyra Island.

Genus MIROUNGA Gray, 1827

The differences between the northern and southern elephant seals were described by Davidson (1929) and Briggs and Morejohn (1976).

Mirounga leonina (Linnaeus, 1758) (southern elephant seal; southern sea-elephant).

Circumpolar in Southern Hemisphere, mainly in the subantarctic zone. Rookeries and hauling grounds mostly on oceanic islands in three general sectors of the Southern Ocean:

In the South Atlantic sector, there are, or were, rookeries on Peninsula Valdez in Argentina, the Falkland Islands [=Islas Malvinas], South Georgia, the South Sandwich Islands, the South Orkney Islands, the South Shetland Islands, Tristan da Cunha, Gough Island and Bouvetøy; also recently found breeding on Peterson Island (66°27'S, 11°30'E) on the coast of Antarctica.

In the Indian Ocean sector, rookeries are located on Prince Edward Island, Marion Island, Îles Crozet, Îles Kerguelen, Heard Island, and McDonald Island.

In the western South Pacific sector, past or present rookery sites are on King Island in Bass Strait, Macquarie Island, Campbell Island, and Antipodes Islands.

Vagrant north to Uruguay, Rio Grande do Sul (29°58'S) in Brazil, St. Helena, southern Africa from the Skeleton Coast (17°58'S) of Namibia around the Cape to Ilha Bazaruto (21°30'S) in Mozambique, Đawquirah (18°07'N) in Oman (!), Mauritius, Rodriguez, Île Amsterdam, the coast of Australia from Encounter Bay (138°43'E) in South Australia east and north to Coff's Harbour (30°19'S) in New South Wales, the Auckland Islands, the Snares Islands, Chatham Island, the eastern shores of New Zealand from Stewart Island north to Bay of Islands on South Island, Isla de Pascua, and Chañaral (26°23'S) in Atacama, Chile.

Disperses south to Wilkes Station (64°40'S, 64°03'W) on the Antarctic Peninsula, the pack ice in the Weddell Sea (77°05'S, 35°04'W), and the coast of Greater [=East] Antarctica from Mawson Station (62°52'E) east to Scott Island (67°24'S, 180°00').

The southern elephant seals were divided into four allopatric species by Peters (1875), into four subspecies by Lydekker (1909), and into five subspecies by Rothschild (1910), but Lönnberg (1910) found that the supposed distinguishing features of the regional populations all fell within the range of variation present in a series of skulls from South Georgia. Carrick *et al.* (1962) determined that the seals at Macquarie Island were significantly smaller at all ages than those at South Georgia.

Mirounga angustirostris (Gill, 1866) (northern elephant seal; northern sea-elephant).

A pelagic species which ranges throughout the northeastern Pacific from 40°N, north to the Aleutian Islands and Gulf of Alaska, and west to 173°W. Rookeries, either present-day or within historical times, on Point Reyes, the Farallon Islands, Año Nuevo Island, Cape San Martin, San Miguel Island, Santa Rosa Island, Anacapa Island, Santa Barbara Island, San Nicolas

Island, and San Clemente Island in California; Islas Los Coronados, Isla San Martín, Isla Guadalupe, Islas San Benito, Isla Cedros, Isla Natividad, Bahía San Cristobal, Isla San Roque, Isla Asuncion, Bahía San Hipolito, and Cabo San Lazaro in Baja California. Vagrant to Nii-jima in the Izu-shotō of Japan, Midway Atoll in the northwestern Hawaiian Islands, and the Golfo de California as far north as Isla Angel de la Guarda (29°30′N). Morrell's (1832) reports of elephant seals on Lisianski Island, Pearl and Hermes Reef, Midway Atoll ("Byer's Island"), and Kure Atoll ("a small low island") in the Northwestern Hawaiian Islands in July 1825 were doubtless based on misidentified monk seals; likewise no credence can be given to his report of elephant seals on Île Clipperton (10°17′N, 109°13′W) in August 1825 (see comments above under *Arctocephalus townsendi*).

Genus LEPTONYCHOTES Gill, 1872

Leptonychotes weddellii (Lesson, 1826) (Weddell seal).

The species-group name was misspelled *weddelli* in earlier editions of this list (Bonner 1988).

Circumpolar in fast ice around the coast of Antarctica, ranging as far south as the Bay of Whales and the Filchner Ice Shelf at 78°S; a disjunct resident population at South Georgia. Vagrant to Santa Cruz in Argentina, Uruguay, Falkland Islands [=Islas Malvinas], Bouvetøy, Marion Island, Îles Kerguelen, Heard Island, South Australia, Victoria, Macquarie Island, Auckland Islands, North Island in New Zealand, Islas Juan Fernández, and Isla Mocha in central Chile.

Genus OMMATOPHOCA Gray, 1844

Ommatophoca rossii Gray, 1844 (Ross seal; bigeyed seal).

The species-group name was misspelled *rossi* in earlier editions of this list (Bonner 1988).

Circumpolar in pack-ice zone of the Antarctic Ocean, south to Ross and Filchner ice shelves at 78°S. Vagrant to Îles Kerguelen, Heard Island, and South Australia.

Genus LOBODON Gray, 1844

Lobodon carcinophaga (Hombron and Jacquinot, 1842) (crabeater seal).

This species was originally named *Phoca carcinophaga.* Doubt about the authorship and date of this name was cleared up by Scheffer (1958). The specific name *carcinophaga* is a noun in apposition, not an adjective, compounded from the Scientific Latin noun *phaga* 'eater,' plus *carcino-,* the combining form of *carcinus* 'crab.' As a noun the name must retain its original feminine ending, even though it has been transferred to genus *Lobodon,* which is masculine (Article 31(b)(ii) of the ICZN Code). Most earlier authors got it right (*e.g.,* Gill 1866; Gray 1866, 1874; Allen 1880, 1905; Flower and Lydekker 1891; Andersson 1905; Kellogg 1922; Iredale and Troughton 1934; Von Boettiger 1934; Lindsey 1938; Troughton 1941), but Berg (1898), followed by Barrett-Hamilton (1902, 1903), Wilson (1902, 1907), Trouessart (1907), Bertram (1940), Scheffer (1958), and almost all recent authors, have used the improperly altered spelling with a masculine ending, *carcinophagus* (Rice 1994).

Circumpolar throughout the pack-ice zone of the Southern Ocean, south to the shores of Antarctica, including the Ross and Filchner ice shelves at 78°S. Vagrant north to provinces of Santa Cruz, Chubut, and Buenos Aires in Argentina, Uruguay, Rio de Janeiro in Brazil, Falkland Islands [=Islas Malvinas], South Georgia, Bouvetøy, Cape Province and Natal in South Africa, Heard Island, South Australia, Victoria, New South Wales, and Tasmania in Australia, and North Island and South Island of New Zealand.

Genus HYDRURGA Gistel, 1848

This generic name is a junior synonym of *Stenorhinchus* E. Geoffroy St. Hilaire and F. Cuvier, 1826; the latter has long remained unused under the mistaken belief that it was preoccupied by *Stenorhynchus* Lamarck, 1819, given to a crab. Since *Hydrurga* has been in universal use for well over half a century, I retain it under Article 23(b) of the Code, in anticipation that the ICZN will be petitioned to conserve it.

Hydrurga leptonyx (Blainville, 1820) (leopard seal).

Pack-ice zone around the Southern Ocean, south to the shores of Antarctica including the Ross and Filchner ice shelves at 78°S; year-round populations at Palmer Peninsula, South Shetland Islands, South Orkney Islands, South Sandwich Islands, South Georgia, Bouvetøy, Heard Island, and Macquarie Island. Although most leopard seals remain associated with sea ice and glacial ice throughout the year, some individuals disperse widely in winter northward to coasts of southern South America from Tierra del Fuego in Chile to Santa Catarina in Brazil, Falkland Islands [=Islas Malvinas], Tristan da Cunha, Cape Province from Cape Town to East London, Prince Edward Island, Îles Crozet, Îles Kerguelen, Heard Island, Île Amsterdam, Île St. Paul, coasts of southern Australia from Gairdner River in West Australia to Heron Island off Queensland, Lord Howe Island, Auckland Islands, Snares Islands, Campbell Island, the shores around North Island and South Island in New Zealand, Rarotonga in the Cook Islands, and Islas Juan Fernández.

Order CETACEA

In the 10th edition of *Systema Naturae,* Linnaeus (1758) called this order Cete. The name is the plural of the Classical Latin noun *cetos,* meaning any large sea creature. (The word *cetos* is a straight transliteration of the Greek κητος, plural κητε[5] [*kētos, kētē*]; the ancient Latins also used a Latinized rendering of this word, *cetus,* plural *ceti.*) Brisson (1762) altered the name to Cetacea by adding the ending *-acea,* neuter plural of the Latin adjectival suffix *-aceum,* which means 'belonging to' or 'resembling.' In the 12th edition of his book, Linnaeus (1766) included the order Cete as the sole member of a group he named Mutica—one of his three primary subdivisions of placental mammals. Gray (1821) called the cetaceans order Carnivoræ under the class Cetaceæ, in which he also included the Sirenians as order Herbivoræ.

Significant milestones in our understanding of the systematics of cetaceans are the successive contributions of Flower (1867), Gill (1871*a*), Winge (1918), Miller (1923), Kellogg (1928), Slijper (1936), and Fraser and Purves (1960). Reviews of higher-level systematics were published by Rice (1984*a*), Barnes *et al.* (1985), Fordyce and Barnes (1994), and Fordyce *et al.* (1995). A cladogram for all living and extinct cetacean families (except the mysticetes, which were combined) was constructed by Barnes (1990), and Heyning (1989, 1997) produced similar cladograms for the living forms. A complete classification, down to subfamilies, of all living and fossil cetaceans was prepared by Fordyce and Barnes (1994) and Fordyce *et al.* (1995). Muizon (1988*a, b*; 1991; 1993) expressed somewhat variant conclusions on odontocete classification, supported by cladograms down to the generic level. His classification differs from that of Fordyce and Barnes mainly in the position of some families of river-dolphins. Subsequently, Fordyce (1994) erected the new family Waipatiidae for a fossil species from the Oligocene of New Zealand, which is most closely related to the Squalodelphinidae and Platanistidae. Muizon (1993) also described a supposed new family of odontocete cetacean, Odobenocetopsidae, for *Odobenocetops peruvianus,* from the Pliocene of Peru, but Heyning (1997) noted that this bizarre creature has none of the synapomorphies of the Cetacea. A phylogenetic classification of the living and fossil Cetacea is outlined in Table 5.

The monophyly of the Cetacea was long questioned by many cetologists (Kukenthal 1922, Kleinenberg 1958, Yablokov *et al.* 1972, Mchedlidze 1976), but none of them ever proposed an explicit hypothesis of diphyly, so some authors considered the relationship between the Mysticeti (baleen whales) and the Odontoceti (toothed whales) as unresolved (Rice 1984*a*). Recently, however, overwhelming evidence has accumulated that corroborates the monophyly of a taxon Cetacea. This includes evidence from morphology (Barnes 1984*a*, 1990), karyology (Kulu 1972, Árnason 1974*b*), immunology (Boyden and Gemeroy 1950, Borisov 1969), amino acid sequences of the myoglobin (Goodman *et al.* 1982, McKenna 1987) and cytochrome *b* (Árnason *et al.* 1991),

[5] Here and elsewhere I have omitted the customary accent marks on Greek words because the ancient Greek writers never used them, and they are irrelevant in the present context (Stearn 1992).

Table 5. Classification of the living and fossil Cetacea.[a] Extinct taxa are marked with a dagger (†), and taxa that appear to be paraphyletic are marked with an asterisk(*). For authorship of family-group names see Appendix 3. For subfamilies and for geologic ranges of all taxa see Fordyce and Barnes (1994).

- Order Cetacea
  - †Suborder Archaeoceti*
    - †Superfamily Protocetoidea*
      - †Family Pakicetidae*
      - †Family Ambulocetidae*
      - †Family Protocetidae*
    - †Superfamily Remingtonocetoidea
      - †Family Remingtonocetidae
    - †Superfamily Basilosauroidea*
      - †Family Dorudontidae*
      - †Family Basilosauridae
  - Suborder Mysticeti
    - †Infraorder Crenataceti
      - †Family Llanocetidae
    - †Infraorder *incertae sedis*
      - †Family Aetiocetidae
      - †Family Mammalodontidae
      - †Family Kekenodontidae
    - Infraorder Chaeomysticeti
      - †Family Cetotheriidae*
      - Family Balaenidae
      - Family Neobalaenidae
      - Family Eschrichtiidae
      - Family Balaenopteridae
  - Suborder Odontoceti
    - †Superfamily *incertae sedis*
      - †Family *incertae sedis*[b]
      - †Family Agorophiidae[c]
    - Superfamily Physeteroidea
      - Family Physeteridae
      - Family Kogiidae
    - Superfamily Ziphioidea
      - Family Ziphiidae
    - Superfamily Platanistoidea
      - Family Platanistidae
      - †Family Waipatiidae
      - †Family Squalodelphinidae[d]
      - †Family Dalpiazinidae
      - †Family Squalodontidae
    - †Superfamily Eurhinodelphinoidea[d]
      - †Family Eurhinodelphinidae[d]
      - †Family Eoplatanistidae
    - Superfamily *incertae sedis*
      - Family Iniidae
      - Family Lipotidae
      - Family Pontoporiidae

Table 5. Continued.

Superfamily Delphinoidea[e]
†Family Kentriodontidae*
†Family Albireonidae
Family Monodontidae
Family Delphinidae
Family Phocoenidae

[a] This classification primarily follows that of Fordyce and Barnes (1994; *cf.* Fordyce *et al.* 1995), with the following alterations: (1) Mitchell's (1989) superfamilies have been inserted in the suborder Archaeoceti; (2) families Pakicetidae and Ambulocetidae have been added from Thewissen *et al.* (1996); (3) Dorudontidae and Basilosauridae are retained as families, following Kellogg (1936) and other authors, rather than being reduced to subfamilies under an expanded concept of family Basilosauridae; (4) Mitchell's (1989) infraorders have been inserted in the suborder Mysticeti; (5) the recently described family Waipatiidae has been added from Fordyce (1994); (6) Lipotidae is ranked as a family rather than as a subfamily of Pontoporiidae, following Muizon (1988*b*); and (7) the sequence has been altered somewhat. Mitchell (1989) put the Kekenodontidae as a subfamily (family *incertae sedis*) in the suborder Archaeoceti rather than in the Mysticeti; he also divided the infraorder Chaeomysticeti into three superfamilies: Balaenoidea (for the families Balaenidae and Neobalaenidae), Eschrichtloidea (for Eschrichtiidae), and Balaenopteroidea (for Cetotheriidae and Balaenopteridae). Muizon (1984, 1988*b*, 1991) recognized two additional superfamilies: Lipotoidea (for Lipotidae) and Inioidea (for Iniidae and Pontoporiidae).

[b] Includes *Archaeodelphis, Atropatenocetus, Microzeuglodon, Xenorophus,* and other unallocated Oligocene genera.

[c] Includes *Agorophius* only (Fordyce 1981).

[d] For correct spelling of Squalodelphinidae (based on *Squalodelphis*), Eurhinodelphinoidea, and Eurhinodelphinidae (based on *Eurhinodelphis*) see Appendix 3.

[e] Family Odobenocetopsidae, ostensibly closely related to the Monodontidae, was proposed by Muizon (1993) for *Odobenocetops* from the Pliocene of Peru, but Heyning (1997) concluded that it is not a cetacean.

hybridization of the highly repetitive DNA (Árnason *et al.* 1984), and nucleotide sequences in the mitochondrial ribosomal DNA sequences (Milinkovitch *et al.* 1993).

The taxon Cetacea has been ranked as an order by almost all mammalogists. One exception was Gregory (1910), who ranked it as a superorder—one of seven into which he divided all placental mammals—and elevated the traditional suborders Archaeoceti, Odontoceti, and Mysticeti to the rank of orders. Simpson (1945) ranked Cetacea as an order, but made it the sole member of "cohort" Mutica, one of his four cohorts of placental mammals. Both of these classifications implied that the Cetacea had no close affinity with any of the other orders of mammals. However, recent studies have led to a consensus that the order Cetacea is a member of a clade that includes the hoofed mammals (McKenna 1975, Szalay 1977, Novacek 1982, Miyamoto and Goodman 1986, Saccone *et al.* 1991). McKenna (1975) grouped the orders Cetacea and Acreodi (the extinct terrestrial mesonychians) together in "mirorder" Cete, which he included in "grandorder" Ungulata, along with the orders Tubulidentata (aardvarks), Artiodactyla (the even-toed hoofed mammals), Perissodactyla (the odd-toed hoofed mammals), Hyracoidea (hyraxes), Proboscidea (elephants), Sirenia (sea-cows), and 12 extinct orders. Similarly, Novacek's (1986) classification of Recent placental mammals groups the Cetacea in superorder Ungulata, along with the Artiodactyla, Perissodactyla, Hyracoidea, Proboscidea, and Sirenia. Morphological studies by Prothero *et al.* (1988) and by Thewissen (1994) confirmed the monophyly of McKenna's concept of the taxon Cete (mesonychians plus cetaceans). The analysis by Prothero *et al.* placed the Cete as the sister-group of a clade comprised of the Perissodactyla, Hyracoidea, and Tethytheria (the latter including the Proboscidea, Sirenia, and the extinct marine Desmostylia). Because of contradictory evidence, however, the branching order of these four taxa must be considered unresolved. The recent discovery of vestigial hind limb bones in certain Eocene cetaceans revealed a paraxonic arrangement similar to that in the Artiodactyla and the extinct Mesonychia (Gingerich *et al.* 1990, Wyss 1990).

Most molecular studies have produced comparable results. A sister-group relationship between the Cetacea and Perissodactyla (but not the Tethytheria) is supported by the amino acid sequences in the myoglobin (Goodman *et al.* 1982, McKenna 1987) and the pancreatic ribonucleases (Beintema and Lenstra 1982). On the other hand, sequences from α-crystallin A (McKenna 1987), cytochrome *b* (Irwin *et al.* 1991, Árnason *et al.* 1991, Irwin and Árnason 1994), cytochrome *c* (Baba *et al.* 1981, Goodman *et al.* 1982), and combined protein sequences (Czelusniak *et al.* 1990), as well as immunological comparisons (Boyden and Gemeroy 1950, Borisov 1969), all indicate that Cetacea and Artiodactyla are sister-taxa, or that cetaceans are one branch of a clade that includes the artiodactyls. A sister-group relationship of the Cetacea and Hippopotamidae was proposed by Lowenstein (1986) and Sarich (1993) on the basis of immunological distance, by Irwin and Árnason (1994) on the basis of cytochrome *b* gene sequences, and by Gatesy (1997) on the basis of γ-fibrinogen gene sequences. A sister-group relationship to the Camelidae was proposed by Irwin *et al.* (1991) on the basis of cytochrome *c* gene sequences and by Goodman *et al.* (1985) on the basis of amino acid sequences of several proteins and nucleotide sequences of DNA. More inclusive analyses imply a sister-group relationship between the Cetacea and a clade comprised of the artiodactyl subgroups Ruminantia (ruminants) and Ancodonta (hippopotamuses), but excluding the Tylopoda (camels) and Suina (pigs). This arrangement was proposed by Graur and Higgins (1994) on the basis of 5 mtDNA sequences and 11 protein sequences, and it has been supported by Shimamura *et al.* (1997) on the basis of specific short interspersed elements (SINEs), or retrosequences, in the genomes.

The orders Cetacea and Artiodactyla were joined into a supraordinal taxon Cetartiodactyla by Montgelard *et al.* (1997) on the basis of nucleotide sequences of the cytochrome *b* and 12S rRNA genes. Following an analysis of amino-acid sequences, Graur *et al.* (1997) classified Perissodactyla as the sister-group of the Cetartiodactyla, and concluded that this entire clade was closest to the order Carnivora.

The immediate ancestor of the Cetacea is conceded to have been one of the mesonychids—a primitive clade of the cohort Ungulata that is customarily designated as order Mesonychia or Acreodi. Mesonychids first appeared in the early Paleocene in North America and then dispersed over the Holarctic, where they survived as late as the early Oligocene. Most of them appear to have been cursorial hyaena-like carrion-feeders, with large heads, powerful jaws, and feet with five toes that bore hoof-like claws (Zhou *et al.* 1992). Several authorities first suggested that the cetacean ancestor was close to the genus *Hapalodectes,* which ranged in North America and Eurasia during the Late Paleocene and Eocene (Van Valen 1966, 1968; Szalay 1969; McKenna 1975; Gingerich and Russell 1981). Subsequently a cladistic analysis by Prothero *et al.* (1988) placed the Cetacea as the sister-group to the genus *Andrewsarchus.* The latter was a genus of giant, long-jawed, hyena-like or bear-like mesonychids which stood 1.9 m high at the shoulders; two species, *A. mongoliensis* and *A. crassus* lived in China and Mongolia during the Late Eocene (Osborn 1924, Ding *et al.* 1977). More recently, Thewissen (1994) proposed that the sister-group of the Cetacea is a clade composed of the families Andrewsarchidae and Mesonychidae, with the Hapalodectidae and other mesonychids more distantly related.

The oldest species that showed some of the derived cranial features of the cetaceans, such as the characteristic ear-bones, appeared in the middle of the Eocene epoch, about 50 million yr ago, near the shores of the ancient Tethys Sea (Gingerich *et al.* 1983) and the adjacent North Atlantic. The Tethys Sea stretched from the present-day Mediterranean Sea east to the Arabian Sea and the Bay of Bengal, thus separating Africa and India (which was still an island) from Eurasia. These putative cetaceans are known mainly from skulls and mandibles unearthed in northwestern India, Pakistan, Egypt, Nigeria, and Georgia in the southeastern United States. Some of them are so similar to mesonychids that it is difficult to decide whether to call them mesonychids or cetaceans. Their skull was not yet telescoped, as it is in the post-Eocene cetaceans; their nostrils were still near the tip of the snout; and they retained a primitive eutherian dentition of 44 teeth, differentiated into 3 incisors, 1 canine, 4 premolars, and 3 molars on each side of each jaw (Gingerich and Russell 1990). On most specimens, the postcranial skeleton is either missing or so incomplete that we cannot tell whether the animals were terrestrial, amphibious, or aquatic. All of these middle Eocene cetaceans were formerly grouped into the paraphyletic family Protocetidae, for which Mitchell (1989) erected the superfamily Protocetoidea. Recently, however, Thewissen *et al.* (1996) have provisionally allocated them to three families: Pakicetidae, Ambulocetidae, and Protocetidae.

The most primitive cetaceans are the Pakicetidae, which include *Pakicetus inachus, P. attocki,* and *Ichthyolestes pinfoldi* (Gingerich and Russell 1981, 1990). They are known only from cranial material, but recently some intriguing limb bones—conceivably from these animals—were found in intermittent fluvial deposits from the early-to-middle Eocene in Kashmir (Gingerich and Russell 1994). Thewissen *et al.* (1996) postulate that the pakicetids were predominantly terrestrial wolflike or hyenalike creatures. One of them probably gave rise to all later cetaceans.

Family Ambulocetidae includes *Ambulocetus natans* and probably *Gandakasia potens.* The former species, recently discovered in Pakistan, is the only species that has yielded enough of its postcranial skeleton to allow a reconstruction of the animal's appearance in life (Thewissen *et al.* 1994, 1996). An amphibious inhabitant of coastal marine waters, it had a long tail and flipper-like hind limbs which it could extend horizontally behind its body. This enabled it to propel itself through the water by means of dorso-ventral undulations of its body, much as otters do. Its forelimbs were similar to those of a sea-lion, and on land its locomotion was probably similar to that of the otariid seals.

The family Protocetidae proper currently comprises eight monotypic genera. At least two species, *Rodhocetus kasrani* and *Indocetus ramani,* still retained hind limbs, but they evidently propelled themselves solely by undulations of their tails, as did all later cetaceans (Gingerich *et al.* 1993, 1994).

Sharing the Tethys Sea with these early protocetoids were the remingtonocetoids, a short-lived side-branch of cetacean evolution. It was represented by two species of *Remingtonocetus,* two of *Andrewsiphius,* and one of *Dalanistes* (Kumar and Sahni 1986, Gingerich *et al.* 1995). They differed from the other mid-Eocene cetaceans in a number of features, most notably in having an extremely long compressed rostrum with a long mandibular symphysis—a trait convergent upon the living river-dolphins. A large, stiff sacrum suggests that well-developed hind limbs were their primary means of propulsion in the water.

By the late Eocene, the earlier cetaceans were completely supplanted by the zeuglodonts, superfamily Basilosauroidea. They evidently arose as the sister-group to the Egyptian protocetid *Eocetus schweinfurthi* (Hulbert 1994). Their remains have been unearthed in Egypt, in England, and in the southeastern United States from South Carolina to Louisiana (Kellogg 1936). The name "zeuglodont" ("yoke-toothed") alludes to their distinctive molar teeth, each of which has two long well-separated roots so it looks as if it were two teeth yoked together at the crowns. The second, third, and fourth premolars in each dental quadrant, as well as the two upper molars (they had lost the third), each bore a series of three or four accessory denticles, or serrations, along its front and rear edges; the lower molars had similar denticles along the rear edge only. The basilosauroids appear to have been exclusively aquatic. Their forelimbs were modified into flippers, and their long tail presumably terminated in horizontal flukes. At least one species, *Basilosaurus isis,* had vestigial hind limbs, which may have functioned as claspers during copulation (Gingerich et al 1990). There were two families of basilosauroids: The Basilosauridae contained four species—*Basiloteras hussaini* from Pakistan, *Basilosaurus isis* from Egypt, *B. drazindai* from Pakistan, and *B. cetoides* from the southeastern United States—which attained the length of a fin whale (17 to 20 m), but had extremely slender bodies, shortened necks, and elongated vertebral centra. The Dorudontidae, which included eight known species in four genera, were smaller and more normally proportioned. It is most likely that one of the dorudontids was the ancestor of the more advanced cetaceans with "telescoped" skulls and blowholes on the tops of their heads (Barnes and Mitchell 1978); all the other basilosauroids went extinct by the close of the Eocene.

It has long been traditional to group all of these primitive Eocene cetaceans into a separate suborder, usually called Archaeoceti—a name proposed by Flower (1883); Gill's (1871*a*) earlier name Zeuglodontia fell into disuse. Although such a paraphyletic assemblage is inadmissible in a phylogenetic system, "archeocete" and "zeuglodont" remain useful as informal terms for these cetaceans.

The advanced, post-Eocene cetaceans comprise two markedly dissimilar clades, customarily ranked as suborders: the Mysticeti, or baleen whales, and the Odontoceti, or toothed whales. Each of these taxa possesses a complex suite of synapomorphies which overwhelmingly corroborate its monophyly (notwithstanding certain molecular studies discussed below)—Heyning (1997) called the Odontoceti "one of the best supported higher-level groupings among mammals." An extensive fossil record demonstrates that the two suborders have been separate since the Oligocene. The Mysticeti and the Odontoceti differ fundamentally in the way that the bones of their skull became telescoped (Miller 1923). The baleen whales are characterized by their specialized filter-feeding mechanisms, while the odontocetes are characterized by their sophisticated echolocation system, which entails many anatomical specializations. The latter include unique mechanisms for the generation of sounds (Cranford *et al.* 1996) and for hearing (Fraser and Purves 1960, Norris 1968). Also unique are their complex narial passages which (at least in modern odontocetes) possess a slight to pronounced bilateral asymmetry that involves the surrounding structures of the head—usually including the skull (Schenkken 1973, Schenkkan and Purves 1973, Heyning 1989, Heyning and Mead 1990).

Molecular studies have been disappointingly inconsistent in resolving the interrelationships of the major divisions of Cetacea. However, four such studies do corroborate the primary dichotomy between the Mysticeti and Odontoceti: immunogenetics (Borisov 1969), restriction-site mapping of mtDNA (Ohland *et al.* 1995), sequencing of the cytochrome *b* gene (Árnason and Gullberg 1996), and sequencing of the "common cetacean DNA satellite," which is present in multiple copies in the genome (Grétarsdóttir and Árnason 1993). The latter study revealed that the genome of the giant sperm whale (*Physeter macrocephalus*) uniquely possesses two different sequences of the common cetacean satellite; one sequence ("type B") places the sperm whale as sister-group to the Ziphioidea plus Delphinoidea, with the pygmy sperm whale (*Kogia breviceps*) as an outgroup to all three; the other sequence (Type B) pairs the giant sperm whale with the pygmy sperm whale.

On the other hand, several contradictory hypotheses of paraphyly for the Odontoceti have been suggested on the basis of other molecular studies. The one that has received the most publicity recently is the contention of Milinkovitch *et al.* (1993, 1995; Milinkovitch 1995, 1997) that the sperm whales are more closely related to the baleen whales than they are to the other toothed whales, and that the Ziphioidea are the sister-taxon to all other cetaceans.

Those authors derived this hypothesis solely from an analysis of the 12S and 16S mitochondrial ribosomal DNA, ignoring all of the contradictory morphological and paleontological evidence, as well as other kinds of molecular data. Their material included 16 species—2 mysticetes and 14 odontocetes. Their cladogram had 461 steps with a consistency index of only 0.54 (see Introduction), and there were many other solutions that were almost equally parsimonious. When the topology was constrained to hold the Odontoceti monophyletic, the most parsimonious solution was only eight steps longer. Milinkovitch (1995) subsequently attempted to rationalize a complex evolutionary scenario that would bring the morphological data, as well as some of the other molecular data, into compliance with his own molecular conclusions. Klima (1995) thought that certain features of the embryogenesis of the nasal region of the skull in *Physeter* resembled those in the Mysticeti more than that in the Delphinoidea, but he made no cladistic analysis. Milinkovitch's hypothesis would require morphological convergences and reversals of a magnitude that defies credibility.

The only study that concurs with Milinkovitch's hypothesis is an analysis of partial 16S mitochondrial rRNA by Árnason *et al.* (1993*a*). An unrooted cladogram based on non-coding nuclear DNA (Douzery 1993, based on data from Schlötterer *et al.* 1991) would support either Milinkovitch's hypothesis or the traditional hypothesis of a monophyletic Odontoceti, depending on to which of two possible internodes the root is attached. One study of the amino-acid sequences of the myoglobin showed the Delphinoidea + *Inia* as the sister-group of the Mysticeti (Gurd and Jones 1979), but another such study indicated that the Physeteroidea plus the Ziphioidea comprised the sister-group of the mysticetes (Goodman *et al.* 1982). Two other sets of molecular data also show the Delphinoidea, not the Physeteroidea, as the sister-group of the Mysticeti: the 12S mitochondrial rRNA (Douzery 1993), and the cytochrome *b* gene (Árnason and Gullberg 1994). Finally, a review by Milinkovitch in collaboration with Hasegawa *et al.* (1997) based on "total molecular evidence" (12S and 16S rRNA genes, the cytochrome *b*, and myoglobin sequences) placed the Physeteroids plus the Ziphioids as the sister-group to the Mysticeti, with the Delphinoidea as the sister-taxon to all other cetaceans. Why have these molecular analyses failed consistently to resolve the branching sequence of the Mysticeti, Delphinoidea, Ziphioidea, and Physeteroidea? One problem, at least, appears to be simply the misplacement of the root on the cladogram (Heyning 1997).

Since the preceding commentary was written, Messenger and McGuire (1998) have published a thorough cladistic analysis of 67 extant species of cetaceans representing 33 genera and all families except Neobalaenidae, plus five species of artiodactyls as outgroups. They used 207 morphological characters (both osteological and soft-tissue) and nucleotide sequences of three mitochondrial genes (12S rRNA, 16S rRNA, and cytochrome *b*). Both the morphological and the molecular data strongly corroborate the traditional taxonomic arrangement of the Cetacea, including the monophyly of the Odontoceti (including Physeteroidea) and the monophyly of the Balaenopteridae (with *Eschrichtius* as its sister-taxon). Previous contradictory conclusions were based on flawed molecular analyses.

Suborder MYSTICETI

Gray (1864*b*) first proposed the formal name Mysticete for the baleen whales, but the spelling Mysticeti, introduced by Cope (1869), has become the accepted term. These words are the plurals of the Modern Latin nouns *mysticetos* and *mysticetus,* respectively (the Classical Latin *cetus,* plural *ceti,* 'sea-monster,' has the alternate spelling *cetos,* plural *cete*; see above under order Cetacea). Their use dates back at least to the time of Gesner (1558). They are Latinized forms of the Classical Greek noun μυστοκητος [*mustokētos*], which was compounded from the phrase ὁ μυς το κητος [*ho mus to kētos*], used by Aristotle (Aristoteles *ca.* 345–342 B.C.) for baleen whales. The Greek word ὁ [*ho*] is the masculine definite article; μυς [*mus*] means 'mouse' but also has the transferred meaning of 'muscle'; το [*to*] means 'is'; and κητος [*kētos*] means 'sea-monster.' In English, this phrase has been rendered as "the mouse, the whale so-called," or, more idiomatically, as "the mouse-whale." Some scholars surmise that the phrase was a mistranscription of μυστακοκητος [*mustako-kētos*], or 'mustache-whale,' compounded with the Greek μυσταξ, genitive μυστακος [*mustax, mustakos*], meaning 'upper lip,' hence 'mustache.' Flower (1867), in fact, substituted the name Mystacoceti for this suborder. Compare the word *musculus* discussed below under the blue whale. Another variant spelling is Mysticeta (De Blase 1982).

The oldest known cetacean that appears to belong to the mysticete clade was *Llanocetus denticrenatus,* recently discovered in late Eocene rocks on the Antarctic Peninsula (Mitchell 1989). It had a set of widely-spaced lobed teeth, somewhat like those of zeuglodonts, with which it could have caught krill in the manner of the crabeater seal—making it a plausible precursor for more advanced filter-feeding whales.

Around the late Oligocene there appeared three families of tooth-bearing "baleen" whales: Kekenodontidae, containing *Kekenodon onamata* from New Zealand (Fordyce 1992), and perhaps also *Phococetus vasconum* from France; Mammalodontidae, containing *Mammalodon colliveri* from Australia (Fordyce *et al.* 1995, Pritchard 1939); and Aetiocetidae, containing eight species grouped in four genera—*Aetiocetus, Chonecetus, Ashorocetus,* and *Morawanocetus*—from around the North Pacific (Emlong 1966, Russell 1968, Barnes 1995,[6] Barnes *et al.* 1995). Mchedlidze (1976) referred two other genera to the Aetiocetidae—*Mirocetus* and *Ferecetotherium* from Azerbaijan—but Barnes (1984*a*) questions the former and thinks that the latter is probably a physeteroid.

The earliest baleen-bearing mysticetes were four species of the genus *Mauicetus,* which lived in the seas around New Zealand during the late Oligocene

[6] Barnes, L. G. 1995. The Aetiocetidae: Primitive Oligocene toothed mysticetes. Abstracts, Eleventh Biennial Conference on the Biology of Marine Mammals, 14–18 December 1995, Orlando FL. The Society for Marine Mammalogy. p. 8.

(Marples 1956). Their blowhole was only about half way back from the tip of the rostrum, and their nasal bones were exceptionally long; another primitive feature was the presence of a short sagittal crest. *Mauicetus* is usually assigned to the paraphyletic family Cetotheriidae. In the Miocene the cetotheres radiated into about two dozen genera in which the blowhole had moved about as far back as it is on the living mysticetes. By the early Miocene, two kinds of cetotheres could already be distinguished by the arrangement of their nasals, premaxillae, maxillae, and frontals (Cabrera 1926; Kellogg 1928, 1943). One of these groups, the Cetotheriidae proper, probably gave rise to the gray whale (family Eschrichtiidae) and the rorquals (family Balaenopteridae); the right whales (family Balaenidae) probably arose from the other group of cetotheres, for which the name Cetotheriopsidae Brandt, 1872, is available if they should be separated from the typical cetotheres.

Most 20th century authors recognized only the three preceding families of living baleen whales. Miller (1923) and Kellogg (1928), however, separated the pygmy right whale from the larger right whales as a fourth family, Neobalaenidae. The work of Barnes and McLeod (1984) strongly supported the allocation of the pygmy right whale to its own family.

Mitchell (1989) proposed dividing the Mysticeti into several infraorders, one or more for the extinct tooth-bearing forms, and one, Chaeomysticeti, for the baleen-bearing forms. The latter he divided into three superfamilies: Balaenoidea for the Balaenidae and Neobalaenidae; Balaenopteroidea for the Balaenopteridae and the extinct Cetotheriidae; and Eschrichtioidea with only one family. The only cladistic analysis of morphological features of living baleen whales was consistent with Mitchell's classification, in that it showed Balaenidae and Neobalaenidae as sister-taxa, with Eschrichtiidae slightly more distant, and Balaenopteridae as an out-group to all three (McLeod *et al.* 1993).

Karyological data are uninformative at this level. The Eschrichtiidae and the Balaenopteridae have the plesiomorphic "general cetacean karyotype" of 2n=44, whereas the Balaenidae have a 2n=42 karyotype that was derived from the 2n=44 karyotype by fusion of two pairs of chromosomes (the chromosomes of Neobalaenidae have not been studied).

An initial analysis of the mtDNA control region agreed with the morphological evidence in placing Neobalaenidae as the sister-taxon of the Balaenidae (Baker and Palumbi 1994), but later analyses placed Neobalaenidae as an early branch of a clade comprised of Eschrichtiidae plus Balaenopteridae, with Balaenidae as an out-group to all three (Árnason *et al.* 1993*b*; Baker and Palumbi 1996). The latter arrangement is also supported by studies of the cytochrome *b* gene (Árnason and Gullberg 1994) and several repetitive sequences of nuclear DNA (Árnason and Best 1991, Adegoke *et al.* 1993, Árnason *et al.* 1992).

Molecular studies have failed consistently to resolve the branching patterns among the species of rorquals, Balaenopteridae, and the gray whale, Eschrichtiidae. An analysis of the amino-acid sequences of the myoglobin paired the gray whale with the sei whale (Goodman *et al.* 1982). Satellite DNA paired the gray whale with the genus *Balaenoptera,* with a fin whale/blue whale clade, or with the humpback whale, depending on the method of analysis (Adegoke *et al.* 1993, Árnason *et al.* 1992). Cytochrome *b* gene sequences paired the gray whale with a clade comprised of the humpback, Bryde's, sei, fin, and blue whales (Árnason and Gullberg 1994). Analyses of nucleotide sequences of the mtDNA control region first paired the gray whale with the family Balaenopteridae (Baker *et al.* 1993), then with the humpback whale (Baker and Palumbi 1994), and finally with the blue whale (Baker and Palumbi 1996). An independent analysis of the control region paired the gray whale with a humpback/fin/blue whale clade. Some of these investigators suggested that the gray whale should be included within the genus *Balaenoptera,* but the morphological and embryological evidence decisively refutes such an intimate relationship of the gray whale to the rorquals. The highly-specialized feeding technique of the rorquals depends on the unique structure and mechanics of their skull, mandibles, musculature, tongue, *cavum ventrale,* and grooved ventral pouch (Rice 1984*a*). Within the Balaenopteridae, the species of *Balaenoptera* are a closely-knit group, differing only in size, in superficial features that are allometrically related to size, and in pigmentation pattern; *Megaptera* is also much alike, differing mainly in autopomorphies of the flipper and scapula. Strikingly different is the cranial morphology, soft anatomy, and feeding technique of the gray whale (Rice 1984*a*). Despite their gross dissimilarities, the Eschrichtiidae and the Balaenopteridae do share two derived features which support a sister-group relationship between them (Rice 1984*a*): One is the unique pattern of interdigitation of the nasals, premaxillae, maxillae, and frontals. The other is the presence of throat grooves—if the two or three short creases on the throat of *Eschrichtius* are homologous to the 25–90 pleats that extend along the venter from the mandibular symphysis nearly to or beyond the umbilicus of the balaenopterids.

If superfamilies were needed in the Mysticeti, the Eschrichtiidae and the Balaenopteridae should be combined in one, while the Balaenidae and Neobalaenidae would probably each require their own superfamily. At present, neither the evidence nor the need for superfamilies is compelling.

Family BALAENIDAE Gray, 1821

Balanadæ [*sic*] Gray 1821:310 (Type genus: *Balaena*; with the incorrect spelling of its stem, the name is a homonym of the currently-used family name Balanidae Leach 1817:68, based on *Balanus* Da Costa, 1778, a genus of barnacles [Cirripedia])

Balaenidae Gray 1825:340 (Corrected spelling of Balanadæ Gray, 1821)

Eubalaenida or Liobalaenae Haeckel 1895:566 (Included *Balaena* and *Balaenotus*; neither name is available because they are not based on the stem of an included generic name)

Genus BALAENA Linnaeus, 1758

Like the species of rorquals, the two species of *Balaena* were long confused. Although whalers distinguished between the bowhead whale and the right whale as early as the 1590s or early 1600s (Allen 1908), scientists failed to recognize them for many years. The Russian naturalist Lepekhin (1805) and the French anatomist Camper (1820) were the first scientists who gave good descriptions of the differences between the "Nordkaper" (*B. glacialis*) and the "Greenland whale" (*B. mysticetus*), but it was not until Eschricht and Reinhardt (1861, 1866) published their detailed comparison between the two species that cetologists generally acknowledged the distinction.

Some authors separate the black right whale into its own genus, *Eubalaena* Gray, 1864*b*. However, according to Beddard (1902), *B. mysticetus* and *B. glacialis* "are so close that they cannot possibly be placed but in the same genus, *Balaena*." They differ from each other no more than the species of *Balaenoptera* differ among themselves (Turner 1913). McLeod *et al.* (1993) provisionally admitted four or five valid fossil species of *Balaena* [*sensu lato*]—*B. affinis, B. etrusca, B. montalionis, B. primigenius,* and *B. prisca* [=*B. mysticetus*?]—all from the Pliocene or Pleistocene of Europe. They noted that "In almost all cases, the evidence is insufficient to demonstrate that a named fossil species is actually more closely related to *Balaena* [*sensu stricto*] than it is to *Eubalaena*. . . ." Finally, Árnason and Gullberg (1994) also concluded that the two species should be placed in the same genus, because they sequenced the mitochondrial cytochrome *b* gene and found that the molecular difference between the bowhead whale and the right whale is less than that between some species of *Balaenoptera*. The distribution of the two species is essentially parapatric, with *B. mysticetus* restricted to the pack ice, and *B. glacialis* (despite its name) avoiding the ice. Most populations of both species are now greatly depleted and no longer occupy their entire historic ranges.

Balaena glacialis Müller, 1776 (right whale; black right whale; black whale).

There are three geographically disjunct populations, in the North Atlantic, the North Pacific, and the Southern Hemisphere. The practice of listing two to four separate subspecies (or even species) in various parts of the world is based more on tradition than on scientific evidence. Flower (1885; Flower and Lydekker 1891) noted that the purported differences between the various nominal species were trifling, and he combined all of the Northern and Southern hemisphere black right whales under the name *B. australis* Desmoulins, 1822. Beddard (1900) came to the same conclusion, later (Beddard 1902) noting that the name *glacialis* has priority over *australis.* Racovitza (1903) thought that any differences that had been ascribed to the several populations were likely due to individual rather than geographic variation. Turner (1913, 1914) again reviewed the evidence, and concluded that there was no reason why the right whales of the North Atlantic and Southern Hemisphere should not be regarded as conspecific, so he combined them under the name *B. biscayensis* Eschricht, 1860. Fraser (1937) noted that their "chief claim to differentiation into species appears to be that they occur in different geographical areas," and that it was preferable to regard them "not as so many distinct species, but rather as local races of one species which is widely distributed." Since then, all right whale populations around the world have been regarded as conspecific by the majority of systematists (Tomilin 1957, Klumov 1962, Bobrinskii 1965*c*, Hershkovitz 1966, Best 1971, Gromov and Baranova 1981, Meester *et al.* 1986, Sokolov and Arsen'ev 1994).

Few recent authors have actually compared specimens of right whales from different oceans. Omura (1958) and Omura *et al.* (1969) examined 13 North Pacific right whales, including the complete skeletons of four, and compared them with all published information on North Atlantic specimens, including skeletal data on 16; they could find no consistent external or skeletal differences between the Atlantic and Pacific specimens. Lönnberg (1923) compared a skeleton from South Georgia with several from the North Atlantic, and thought that they differed in some proportional measurements, but with additional data the alleged differences did not hold up (Tomilin 1957, Klumov 1962). Muller (1954) compared the skulls of four "northern" right whales with those of four "southern" animals—all eight of unstated provenance—and noted a difference in the shape of their alisphenoid bones. Best (1970) noticed a possible geographical difference in the frequency of callosities on the margin of the lower lip—1/11 (9%) in North Pacific animals, 6/7 (86%) in South African animals. A comparison of restriction-fragment length polymorphisms of the mtDNA among 10 western North Atlantic animals and 10 western South Atlantic animals showed that none of the seven identified morphs was present in both regional samples (Schaef *et al.* 1991). There is thus only a tenuous claim for subspecific differentiation between the Northern and Southern hemisphere populations. The validity of any subspecies will remain dubious until adequate series of specimens from both sides of the North Atlantic and North Pacific and from different sectors of the Southern Hemisphere, have been critically compared. The earliest available species-group names given to various regional populations are, in order of priority, *B. glacialis* Müller, 1776, in the eastern North Atlantic (Nordkapp, Norway); *B. japonica* Lacépède, 1818, in the western North Pacific (Japan); *B. australis,* Desmoulins, 1822, in the southwestern Indian Ocean (Algoa Bay, Cape Province); *B. antipodarum* Gray, 1843, in the western South Pacific (New Zealand), and *B. cisarctica* Cope, 1865, in the western North Atlantic (New Jersey).

B. g. glacialis—In the North Atlantic, occurs during the summer from Davis Strait, Denmark Strait, and the Norwegian Sea south to Massachusetts and the Bay of Biscay; during the winter ranges south to Florida and the Golfo de Cintra (23°N), Western Sahara; vagrant to the Gulf of Mexico; populations on the American and European sides of the Atlantic are probably at least partially discrete.

In the North Pacific, occurs during the summer from the Sea of Okhotsk, the southern Bering Sea, and the northern Gulf of Alaska, south to the Sea of Japan [=East Sea], the Pacific coast of northern Honshu, and the coast of central California; during the winter ranges south to Taiwan, the Ogasawara Gunto, and Baja California Sur; populations on the Asian and American sides of the Pacific are probably at least partially discrete; vagrant to the main Hawaiian Islands.

Subjective synonyms include *B. biscayensis* Eschricht, 1860, from the eastern North Atlantic, and *B. g. japonica* Lacépède, 1818, and *B. g. sieboldii* Gray, 1864*b*, from the western North Pacific.

B. g. australis Desmoulins, 1822—Occurs during the summer throughout most of the subantarctic zone, between 35°–40°S and 55°–60°S; there appear to be several more or less discrete populations in different sectors, with winter grounds centered around southern Brazil to northern Argentina, Tristan da Cunha, Namibia, southern Mozambique to Cape Province, Île St. Paul, southwestern Australia, southeastern Australia, the Kermadec Islands, and central Chile.

The name *B. antipodum* or *antipodarum* Gray, 1843, from New Zealand, is arbitrarily regarded as a synonym of *B. g. australis.*

Balaena mysticetus Linnaeus, 1758 (bowhead whale; Arctic right whale; Greenland right whale; great polar whale; ahvik).

Restricted to pack-ice zone of the Arctic Ocean and its peripheral seas. There are four or five disjunct populations:

(1) Northern Hudson Bay, western Hudson Strait, and Foxe Basin. Vagrant to Churchill, Manitoba. (May not be separable from the Davis Strait population.)

(2) Baffin Bay and Davis Strait, from Prince Regent Inlet, Lancaster Sound, and Smith Sound (78°N), south to Hopedale (55°N) in Labrador, and 65°N on the west coast of Greenland. Vagrant south through Strait of Belle Isle to Gulf of St. Lawrence.

(3) East coast of Greenland east across the Greenland Sea, the Barents Sea, and the Kara Sea to Severnaya Zemlya, going north as far as 82°30′N in the Greenland Sea and about 80°N north of Svalbard and Zemlya Frantsa-Iosifa, and going south as far as the ice front—exceptionally reaching Iceland and Finnmark in northern Norway.

(4) Northern Sea of Okhotsk from Shantarskiye Zaliv east to Zaliv Shelikhova, Gizhiginskaya Guba, and Penzhinskaya Guba.

(5) Chukchi and Beaufort seas from Chaunskaya Guba in Siberia east to Amundsen Gulf in Canada, ranging to about 74°N, and northern Bering Sea south to Karaginskiy Zaliv, St. Matthew Island, and Norton Sound; infrequently reaching Mys Kronotskiy in Kamchatka, and the Pribilof Islands. Vagrant to Osaka Bay, Japan.

The type locality of *B. mysticetus* is the Greenland Sea, between Greenland and Svalbard (Linnaeus 1758, True 1899). Cope (1869) concluded that the bowhead whale of the Pacific-Arctic was the same as the Greenland right whale. Scammon (1874) thought that bowheads in the Sea of Okhotsk—which he called "Roys' bunchback whale"—differed from bowheads in the Chukchi and Bering seas, so Dall (1874) named them *B. m. roysii,* but questioned the distinction. Malm (1883) proposed the subspecific name *B.*

m. pitlekajensis for a bowhead skeleton collected on the northern shore of the Chukotskiy Paluostrov at Pitlekay (67°07′N, 173°24′W). No adequate interpopulational comparisons were ever made, and no subsequent cetologists have recognized any subspecies. There was a long-standing controversy over the identity of certain whales called "ingotok" by the Alaskan Eskimoes, and "poggy" by 19th century American whalers, but these whales are simply small, fat bowheads, usually female (Braham *et al.* 1980).

Family NEOBALAENIDAE Gray, 1873

Neobalænidæ Gray 1873:108 (The type genus *Neobalaena* Gray, 1870, is a junior synonym of *Caperea,* but the family name remains valid because, in spite of the generic synonymy, it was not replaced before 1961 (Article 40(a) of the ICZN Code)).

Genus CAPEREA Gray, 1864

This genus long went under the name *Neobalaena* Gray, 1870. Even though Gray (1873) accepted Hector's (1873) discovery that *Neobalaena* is a junior synonym of *Caperea,* Gray and subsequent authors continued to use *Neobalaena.* Iredale and Troughton (1934) were the first to use the correct combination *Caperea marginata.*

Caperea marginata (Gray, 1846) (Pygmy right whale).

Probably circumpolar in temperate waters of the Southern Hemisphere. Individuals have stranded at Buenos Aires in Argentina, the Falkland Islands [=Islas Malvinas], Cape Province in South Africa, Western Australia north to 32°07′S, South Australia, Victoria, New South Wales north to 34°54′S, Tasmania, and both main islands of New Zealand. In addition, two specimens were collected on the high seas in the South Atlantic at 33°40′S, 00°56′E, and at 32°56′S, 12°42′E. There are very few credible sightings of live animals at sea, although a school of about 80 was recently observed and photographed at 42°S, 116°E, about 780 km south of Cape Leeuwin, Western Australia.

Family ESCHRICHTIIDAE Ellerman and Morrison-Scott, 1951

Agaphelidæ Gray 1870*a*:391 (in part) (Type genus: *Agaphelus* Cope, 1868. This genus included two species: (1) "*A. gibbosus* (Erxleben, 1777)," the designated type species, which Cope thought was the same as the "scrag whale" of Dudley, but Cope's specimen was later identified as *Balaenoptera acutorostrata*; and (2) *A. glaucus* Cope, 1868, the gray whale of the Pacific. In cases where the type species is misidentified, the ICZN must decide whether the nominal or the actual species is to be regarded as the type, according to Article 70(b)).

Rhachianectidae Weber 1904:575 (The type genus *Rhachianectes* Cope, 1869, is a junior synonym of *Eschrichtius,* so the family name is invalid because it was replaced prior to 1961 (Article 40(b) of the ICZN Code))
Eschrichtiidae Ellerman and Morrison-Scott 1951:317 (Type genus: *Eschrichtius*)
Eschrichtidae Miller and Kellogg 1955:665 (=Eschrichtiidae; incorrect subsequent spelling)

Genus ESCHRICHTIUS Gray, 1864

Eschrichtius robustus (Lilljeborg, 1861) (Gray whale).

For many years the Pacific gray whale was called *Rhachianectes glaucus* (Cope, 1868), until van Deinse and Junge (1937) discovered that it was the same as a subfossil Swedish whale that had been described earlier by Lilljeborg. Those authors then resurrected the name *E. gibbosus* (Erxleben, 1777) for the species, in the mistaken belief that Erxleben's name was based on the New England "scrag whale" of Dudley (1725), which has been identified with the gray whale; Erxleben (1777) in fact makes no mention of Dudley, and the name *E. gibbosus* must be regarded as a *nomen dubium.* This was pointed out by Cederlund (1939), who concluded that Lilljeborg's name was the correct one for the species (*cf.* Schevill 1952, Rice and Wolman 1971, Mead and Mitchell 1984).

The gray whale became extinct in the North Atlantic in early historical times but survives in the North Pacific, where there are two geographically separated populations.

The extinct North Atlantic populations are known mainly from subfossil skeletal parts unearthed in the western Atlantic from New Jersey to Florida, the most recent of which dates from about A.D. 1675 (Mead and Mitchell 1984), and in the eastern Atlantic from the Baltic coast of Sweden, the Netherlands, Belgium, and the Channel coast of England, the most recent dated from about A.D. 1650 (Bryant 1995). There were also convincing historical accounts of living gray whales from New England in the early 1700s (Dudley 1725) and from Iceland in the early 1600s (Fraser 1970).

The western North Pacific, or "Korean," population summers in the shallow northern part of the Sea of Okhotsk, from Akademii Zaliv to Zaliv Shelikhova, south on the west side to Sakhalinskiy Zaliv, and on the east side to the mouth of the Kikhchik Reka (53°57′N). In the autumn it migrates through Tatarskiy Zaliv, and travels south along the coasts of Primorskiy Kray, the east side of the Korean Peninsula, and China, to winter grounds along the mainland in Guangdong province and around the nearby Hainan Dao (but specific calving sites have never been documented). Formerly another migration corridor ran along the east coast of Japan to postulated calving grounds in the Seto-naikai. The long-held belief that the western Pacific gray whales spent the winter on the south coast of Korea was based on unsupported conjecture. Deraniyagala's (1948) secondhand account—repeated with reservation by Phillips (1984)—of a supposed gray whale that stranded in Sri Lanka, lacks even minimal documentation.

The eastern North Pacific, or "California," population summers in the shallow waters of the Chukchi and Beaufort seas, from 174°E east to 130°W, and the northwestern Bering Sea south to Mys Olyutorskiy and the waters around St. Lawrence Island; a few also summer along the Pacific coast from Vancouver Island south to central California. In the autumn the arctic population migrates southeast through Unimak Pass, and follows the shoreline south to winter grounds on the west coast of Baja California and the southeastern Golfo de California. Some calves are born along the coast of California south of San Francisco during the southward migration, but most are born in certain shallow, protected waters on the Pacific coast of Baja California—Laguna Guerrero Negro, Laguna Ojo de Liebre [=Scammon's Lagoon], Laguna San Ignacio, Bahía San Juanico, Estero de Soledad, Bahía Magdalena with Bahía Almejas, and Bahía Santa Marina; a few calves are also born on the mainland coast at Yavaros in Sonora, and Bahía Reforma in Sinaloa. The northward migration in spring follows the same route as the fall migration.

Van Deinse and Junge (1937), Cederlund (1939), and Mead and Mitchell (1984) could detect no skeletal differences between the extinct Atlantic and the living Pacific gray whales, and Andrews (1914) found that skulls from the Korean and California populations were essentially identical.

Family BALAENOPTERIDAE Gray, 1864

Balænopteridæ Gray 1864*b*:203 (Type genus: *Balaenoptera*)
Megapterina Gray 1864*b*: 205 (Type genus: *Megaptera*)
Physalina Gray, 1864*b*: 211 (Type genus: *Physalus* Gray, 1846 [=*Balaenoptera*])
Physalinidæ Gray, 1868:2 (=Physalina; incorrect subsequent spelling)
Agaphelidæ Gray 1870*a*:391 (in part) (Type genus: *Agaphelus* Cope, 1868 [?=*Balaenoptera*]; see above under family Eschrichtiidae)

The humpback whale differs so much from the "short-flippered" rorquals that most taxonomists allocate it to its own subfamily.

Subfamily MEGAPTERINAE Gray, 1864

Genus MEGAPTERA Gray, 1846

Megaptera novaeangliae (Borowski, 1781) (humpback whale).

The humpback long went under the name *Megaptera nodosa* Bonnaterre, 1789, but Kellogg (1932) showed that Borowski's name has priority.

All oceans of the world. They spend the summer on high-latitude feeding grounds, and migrate to winter grounds below the tropics in shallow waters around islands, over banks, and along continental coasts.

In the North Atlantic, they range during the summer from Disko in western Greenland, Iceland, and the White Sea, south to Massachusetts and Ireland. The North Atlantic humpbacks migrate to two wintering areas: (1) the West Indian grounds around Hispaniola and the Lesser Antilles; and (2) the Cape Verde grounds around the islands of Cape Verde. Rare vagrant into Mediterranean Sea.

In the northern Indian Ocean, humpbacks have been found from the Gulf of Aden, the Persian Gulf [=Arab Gulf], the Gulf of Oman, and the Arabian Sea, eastward around India and Sri Lanka and into the Bay of Bengal. They are present in all months of the year, and calves have been seen during the northern winter, so these animals must represent a population discrete from any in the Southern Hemisphere.

In the North Pacific, humpback whales occur during the summer from the southern Chukchi Sea south to the Sanriku coast of Honshu, the Subarctic Boundary, and southern California. They migrate to three discrete wintering grounds: (1) the Bonin Islands grounds from southern China, Taiwan, and the Philippines east through the Ryukyu Retto, Ogasawara Gunto [=Bonin Islands], Mariana Islands, and Marshall Islands; (2) the Hawaiian grounds around the Main Hawaiian Islands; and (3) the Mexican grounds around the Islas Revilla Gigedo and along the coast of Mexico from Baja California to Jalisco.

In the Southern Hemisphere the summer range comprises the entire Antarctic Zone from the Antarctic Convergence south to the pack-ice zone around the Antarctic continent. The winter grounds may be grouped into seven disjunct geographical areas: (1) Mozambique grounds—bordering the Mozambique Channel including the coast of Mozambique and the coasts around Madagascar; (2) West Australian grounds—along the northwestern coast of Western Australia; (3) Coral Sea grounds—mainly along the edge of the Great Barrier Reef in Queensland, Australia, and around the Îles Chesterfield; (4) Tonga grounds—around Nouvelle Calédonie, Îles Loyaute [=Loyalty Islands], Vanuatu, Fiji Islands and the Lau Group, the Tonga Islands, Niue, and the Cook Islands; (5) Ecuador grounds—along the northwestern coast of South America from the Golfo de Panama south to the Golfo de Guayaquil, and also the Archipiélago de Colon [=Galapagos Islands]; (6) Brazil grounds—along the coast of Brazil from Costinha (06°58′S) in Paraíba south to Cabo Frio (22°51′S) in Rio de Janeiro, including the Abrolhos Archipelago and the islands of Fernando de Noronha and Trindade; (7) Gabon grounds—in the Gulf of Guinea from eastern Nigeria south to about Lobito, Angola, including the islands of Pagalu (Annobón), São Tomé, and Fernando Pó [=Bioko]; also Saint Helena.

Southern Hemisphere humpback whales were alleged by Tomilin (1946) to represent a separate subspecies, *M. n. lalandii* (Fischer, 1829), distinguishable from the nominate Northern Hemisphere form by its greater body length. Ivashin (1958), followed by Sokolov and Arsen'ev (1994), further claimed that the populations in the Australian and New Zealand sectors of the Southern Hemisphere represented another subspecies, *M. n. novaezelan-*

diae Gray, 1864, distinguishable from populations in the Atlantic and African sectors by a slightly shorter body length and by color differences. A review of growth curves and body lengths at sexual maturity in humpback whale populations from all around the world fails to substantiate any significant geographical variation in body length. There is, however, conspicuous geographical variation in the frequency of different color morphs (Matthews 1937, Chittleborough 1965). The populations that winter in Western Australia, the Coral Sea, and the Tonga Islands and vicinity, include a high proportion of animals with a great extent of white coloration; the great majority of these animals fall into into phases 1 to 3 of Lillie (1915). The populations of humpbacks that inhabit the rest of the world consist almost entirely of mostly black individuals, phase 4 and intermediates between phases 3 and 4. An argument could thus be made for recognizing each of these regional groupings as a subspecies, *M. n. novaezelandiae* and *M. n. novaeangliae,* respectively. However the percent separability between them is not quite as high as is customarily required for division into subspecies. Furthermore, a phylogeographic analysis of restriction-fragment length polymorphisms is not congruent with such a regional division (Baker *et al.* 1994). Therefore the species is better regarded as monotypic.

Subfamily BALAENOPTERINAE Gray, 1864

Genus BALAENOPTERA Lacépède, 1804

Since at least the time of Flower (1885), all cetologists have recognized the unity of the genus *Balaenoptera,* with the conspicuous exception of Miller (1923, 1924), Kellogg (1928), and Miller and Kellogg (1955), who separated the blue whale into the monotypic genus *Sibbaldus* Gray, 1864. For a while these authors were followed by many North American authors such as Simpson (1945) and Anderson (1946). Lately, Barnes and McCleod (1984) tried to resuscitate *Sibbaldus,* but they used the unjustified emendation *Sibbaldius* Flower, 1865. Such splitting is phylogenetically indefensible and furthermore is nomenclaturally wrong, because the type species of *Sibbaldus* is the sei whale, not the blue whale (Flower 1865; Hershkovitz 1966; Jones *et al.* 1986; Rice, unpublished manuscript; *contra* Miller 1924, Miller and Kellogg 1955).

Up through the the middle of the 19th century, scientists named many supposed species of rorquals, mostly based on fragmentary skeletal parts. When harpoon-cannon whaling was initiated in 1864, the whalers were the first to differentiate the actual species. A few cetologists soon visited the whaling stations, first in Norway and later elsewhere, where many fresh carcasses could be examined. The earliest cetologists to correctly diagnose and describe the currently recognized species of this genus were: Sars (1869)—northern minke, fin, and blue whales; Guldberg (1884)—sei whale; Olsen (1913)—Brydes' whale; and Williamson (1959)—Antarctic minke whale; and finally, it was the molecular studies of Wada and Numachi (1991) which led to the realization that *B. edeni* was probably not the same as Bryde's whale.

P.-J. van Bénéden (1887) was the first to suggest that most of the species of rorquals were cosmopolitan in distribution. True (1904) demonstrated that the humpback, minke, fin, and blue whales in the western North Atlantic and the eastern North Pacific were conspecific with those in the eastern North Atlantic, and he also (True 1899; *cf.* Thomas 1911) resolved the proper application of Linnaeus' (1758) species-group names. About the same time, Racovitza (1903), who was the first biologist to make a critical first-hand study of rorquals in the Antarctic Ocean, similarly concluded that the humpback, sei, fin, and blue whales of the Antarctic could not be separated specifically from the populations in the North Atlantic.

Hybrids between *B. physalus* and *B. musculus* were reported by Doroshenko (1970) and Spilliaert *et al.* (1991).

Balaenoptera acutorostrata Lacépède, 1804 (northern minke whale; little piked whale; lesser rorqual; (?)dwarf minke whale; (?)diminutive minke whale).

In the Northern Hemisphere there are two distinguishable subspecies, one each in the Atlantic and in the Pacific (Omura 1975). In the Southern Hemisphere there is a distinctive population of "dwarf" minke whales which bear a closer morphological resemblance to the northern minke whale than they do to the Antarctic species (Best 1985, Arnold *et al.* 1987); their mtDNA also reveals a closer relationship to the North Pacific population than to the sympatric Antarctic minke whale (Wada *et al.* 1991). They may provisionally be regarded as a race of the northern species, but they have not yet received a scientific name. Another alleged subspecies, *B. a. thalmaha* Deraniyagala, 1963, which was described from an animal that stranded in Sri Lanka, remains enigmatic; the unique color pattern of its baleen plates (Deraniyagala 1963), if not aberrant, leaves doubt whether it is really a minke whale.

B. a. acutorostrata—In the North Atlantic, minke whales may be found during the summer as far north as Ungava Bay (with vagrants entering Hudson Bay and James Bay), Baffin Bay, Davis Strait, Denmark Strait, Jan Mayen, Svalbard, and the Barents Sea. Their known southern limits at that season are New Jersey, Portugal, and the western Mediterranean Sea; rare vagrant in Black Sea. The winter grounds are poorly documented, but minke whales have been sighted during the winter in the western North Atlantic from 38°N off the coast of Virginia, south to the Gulf of Mexico, Cuba, Hispaniola, Puerto Rico, the Virgin Islands, Anguilla, and Dominica; and in the eastern North Atlantic from the North Sea south at least as far as the Strait of Gibraltar.

B. a. scammoni Deméré, 1986—The name *B. a. davidsoni* Scammon, 1872, was long used for the North Pacific race, but it is preoccupied by the name for a fossil whale (Deméré 1986). In the North Pacific, the summer range of the minke whale encompasses all waters from the southern Chukchi Sea south to the East China Sea, the 30th parallel in the central Pacific, and the coast of central Baja California. Their distribution in winter is much less well known, but it extends at least from the East China Sea and central California, south to within two degrees of the equator.

B. a. subsp.—The "dwarf" minke whale appears to be distributed mainly in lower latitudes of the Southern Hemisphere, but specimens have been taken as far south as 65°04′S, 178°12′E, during the summer. Its most northerly winter localities are Costinha (06°58′S) in Paraíba, Brazil; Durban, South Africa; northern Queensland, Australia; and Nouvelle Calédonie.

Balaenoptera bonaerensis Burmeister, 1867 (Antarctic minke whale).

Many osteological and external features distinguish the Antarctic minke whale from the "dwarf" minke whale as well as from the North Pacific and North Atlantic minke whales (Williamson 1959, van Utrecht and van der Spoel 1962, Zemsky and Tormosov 1964, Kasuya and Ichihara 1965, Ohsumi *et al.* 1970, Omura 1975, Best 1985, Bushuev and Ivashin 1986). Allozyme analyses by Wada and Numachi (1991) showed that Nei's standard genetic distance between Antarctic and North Pacific minke whales is even greater than that between sei and Bryde's whales. Similarly, Árnason *et al.* (1993*b*) determined the nucleotide sequence of the control region of the mtDNA and found that the difference between Antarctic and North Atlantic minke whales was likewise greater than that between any other two species of *Balaenoptera.* Restriction-fragment length polymorphisms of the mtDNA revealed a similarly wide divergence between Antarctic and "dwarf" minke whales (Pastene *et al.* 1994). These differences, along with the sympatric distribution (Kato 1992), confirm that the Antarctic species is reproductively isolated from other minke whales.

This species summers to a great extent in the Antarctic zone. Winter records extend north to within seven degrees of the equator and south at least as far as the 35th parallel, with one record north of the equator in Surinam. To the south they have been sighted in the Ross Sea at 78°30′S and 78°10′S in January and February, respectively (Lillie 1915). In October they are concentrated between 10° and 20°S. The distribution is not entirely clear because of past confusion with the "dwarf" minke whale discussed above under *B. acutorostrata.* Deraniyagala's (1960) use of the name *B. a. bonaerensis* for a whale (which he did not examine) that stranded in Sri Lanka was arbitrary and unwarranted.

Balaenoptera edeni Anderson, 1879. (Eden's whale; Sittang whale; (?) "small-type Bryde's whale").
Balaenoptera brydei Olsen, 1913 (Bryde's whale).

In the tropical and subtropical oceans around the world there are various populations of small rorquals that have gone under the names *B. edeni* and *B. brydei.* The taxonomic relationships among these populations have long remained unresolved. In recent years most authors have followed Junge (1950), who thought that *B. brydei* was a synonym of *B. edeni.* Soot-Ryen

(1961), however, believed that Junge's proposal was premature, given the cranial differences between the two, so he kept them as separate species. The substantial size difference, as well as recent molecular studies, also support the opinion that at least two taxa are involved, but the details of their morphology, distribution, and geographical variation have only begun to be disentangled.

The confusing taxonomic history of these whales began in 1871 when a small rorqual stranded near the mouth of the Sittang River, at the northern end of the Andaman Sea in the Tenasserim District of Burma [now Myanmar]. The skeleton and six baleen plates were sent to the Indian Museum in Calcutta. Although the animal (sex unknown) was only 11.3 m long, all vertebral epiphyses except some on dorsal vertebrae 2, 4, and 5 were ankylosed, so the animal had virtually attained maximum length. Anderson (1879) gave the name *B. edeni* to this specimen, and he also referred to this new species the skull of another whale of the same size from Arakan, Burma, on the Bay of Bengal. (The date of Anderson's description of *B. edeni* is usually, but incorrectly, cited as 1878. The date 1878 does appear on the title page [~p. ix], but in the Corrigenda on the following unnumbered recto page [~p. xi] is a note explaining that the volume was not published until 1879.)

When Norwegian whalers began working out of Saldanha Bay, Cape Province, South Africa, in 1910 they encountered a previously unrecognized kind of rorqual. Olsen (1913) concluded that it was a new species, and named it *B. brydei.* These South African whales are larger than *B. edeni,* attaining sexual and physical maturity, respectively, at average lengths of 12.0–13.0 and 13.0–13.7 m in males, 12.5–12.8 and 13.9–14.5 m in females (Best 1977). (The name *B. brydei* is usually dated 1912, when it first appeared in the Kristiania [now Oslo] newspaper *Tidens Tegn,* but the latter was not "issued. . .for the purpose of providing a permanent scientific record," as required by Article 8(a)(1) of the ICZN Code).

Although *B. brydei* was then known only from external characters, Andrews (1916, 1918), after examining Anderson's two skulls of *B. edeni,* plus a third skull from Sidhi Island in the Noakhali District of eastern Bengal [now Bangladesh], broached the possibility that *B. edeni* was conspecific with *B. brydei.* Lönnberg (1931) published the first description of a skeleton of *B. brydei* from South Africa; he compared it with specimens of minke, sei, fin, and blue whales, but not with Anderson's *B. edeni.* Junge (1950) studied the skeleton of a physically mature whale "slightly over" 12 m long that stranded on Pulu Sugi in the Kepulauan Riau [=Rhio Archipelago], between Singapore and Sumatra. He compared it with the Sittang and Arakan specimens of *B. edeni* and with two *B. brydei* skeletons from South Africa, and, despite the size differences, thought that all five specimens were so much alike that they must belong to the same species. Omura (1959, 1966) compared skeletons of Bryde's whales from the Japanese North Pacific fishery with those of *B. edeni,* and accepted Junge's conclusion that *B. edeni* and *B. brydei* were conspecific. These western North Pacific animals are about the same size as South African ones, attaining sexual and physical maturity, respectively, at average lengths of 11.2 and 13.0 m in males, 11.7 and 13.5 m in females (Ohsumi 1977, Kato and Yoshioka 1996). Soot-Ryen (1961) identified another "full-grown" rorqual, "about 13.5 m" long, from Curaçao as *B. brydei,* which, as noted above, he maintained was not conspecific with the Burmese *B.edeni.* Pilleri and Gihr (1974) pointed out differences in relative skull measurements between four "*B. edeni*" from Burma, the Rhio Archipelago, and the Gulf of Thailand, and three "*B. brydei*" from South Africa.

In 1958, three unusually small "*Balaenoptera brydei*" were landed at the whaling station at Shark Bay, Western Australia (Chittleborough 1959); a male and a female were sexually mature when only 11.2 m and 11.7 m long, respectively, while the third animal, a 10.6-m female, was immature. Ohsumi (1978, 1979, 1980) found that several "Bryde's whales" collected under special scientific permits in the Solomon Sea had all attained sexual maturity even though the males were only 9.6–10.0 m long, and the females 9.2–11.5 m. Andersen and Kinze (1993[7]) examined eight rorquals that stranded in the Gulf of Thailand and the Andaman Sea; all five that were over 9 m long already had fused vertebral epiphyses. Perrin *et al.* (1996) found that 17 skulls of various ages from the subsistence fishery in the Bohol Sea in the southern Philippines were smaller than 10 skulls from other regions (Venezuela, Curaçao, South Africa, the Rhio Archipelago, Japan, the central South Pacific, and southern California); the largest Philippine skull equaled the holotype of *B. edeni.* Two similarly small skulls from the fishery on Solor in the Lesser Sundas were called *Balaenoptera borealis* by Weber (1923), but the shape of their nasal bones resembles that of Bryde's whales, so their identity should be reevaluated.

Bryde's whales from the coastal waters of western Kyushu, Japan, were found to be somewhat shorter in body length and to have relatively narrower baleen plates than those taken on the high seas in the North Pacific, and they also differed in other respects (Kawamura and Satake 1976). Subsequently Best (1977) discovered that the Bryde's whales in the waters off western Cape Province could similarly be separated on the basis of ecological and life history traits, as well as slight morphological differences, into two groups—a migratory offshore population of larger individuals with broader baleen plates, and a sedentary coastal population of slightly smaller individuals with narrower baleen plates. Omura *et al.* (1981) examined the skeletons of Bryde's whales from the southeastern Indian Ocean and the central South Pacific, and identified them as the offshore form.

An allozyme study of many samples of *Balaenoptera* spp. from all over the world was undertaken by Wada and Numachi (1991). Their material

[7] Andersen, M., and C. C. Kinze. 1993. The Brydes [*sic*] whale *Balaenoptera edeni* Anderson, 1878: its distribution in Thai waters with remarks on osteology. Abstracts, Tenth Biennial Conference on the Biology of Marine Mammals; 11–15 November 1993, Galveston, TX. The Society for Marine Mammalogy. p. 22.

included "ordinary" Bryde's whales from several localities in the Indian Ocean (Madagascar, Java) and Pacific Ocean (North Pacific, Fiji, Peru), and also two samples of smaller rorquals (which they called "small form Bryde's")—two specimens from south of Java in the southeastern Indian Ocean (in the same general area where normal-sized Bryde's whales were taken), and six specimens from the Solomon Sea, where Ohsumi had previously reported them. In a phenogram from Nei's coefficient of genetic distance, all the ordinary Bryde's whales clustered as a close sister-group to the sei whale, but the "small form Bryde's whales" clustered as a distant sister-group to the sei whale/Bryde's whale branch. Like the larger Bryde's whales, these lesser whales had a pair of lateral ridges on the rostrum, but they had two-tone baleen plates, intermediate between those of Bryde's whales and minke whales (the length of the throat grooves was not recorded). The genetic data ruled out the possibility that they were hybrids, so the authors concluded that they must represent a species other than Bryde's whale. Dizon *et al.* (1995,[8] 1996, 1998) sequenced the hypervariable region I in the control region of the mtDNA of blue, fin, sei, and Bryde's whales. Their analyses also showed that several "pygmy Bryde's whales" from Hong Kong and the Philippines clustered well outside the sei whale/Bryde's whale clade, so they likewise concluded that there are probably two species of Bryde's whales, a larger one to which the name *B. brydei* probably applies, and a smaller one which may be the same as the Burmese *B. edeni.* Pastene *et al.* (1996, 1998) analyzed restriction-fragment length polymorphisms of the D-loop in the mtDNA from Bryde's whales collected in the southeastern Indian Ocean (south of Java) and the northwestern, southwestern, and southeastern Pacific Ocean. They found the genetic distances between the Pacific samples were small, while the distance between the latter and the 99 Indian Ocean specimens was much greater.

In summary, the animals that have been called Bryde's whales seem to fall into two size-groups which are at least marginally sympatric: (1) smaller animals that may attain physical maturity as short as 9.0 m, and rarely grow much longer than about 11.5 m; and (2) larger animals that do not even become sexually mature until they attain a length of at least 11.2 m in males, 11.7 m in females, and sometimes reach a maximum length of 14.6 m in males and 15.6 m in females.

The smaller animals, as noted above, all came from the coastal and shelf waters of the eastern Indian Ocean, the Sunda Shelf, and the western Pacific. The name *B. edeni* was based on one of these small animals from the Gulf of Martaban, but, pending additional data, that name may with assurance be applied only to the holotype.

The larger animals have been found in the tropical and warm temperate

[8] Dizon, A., C. Lux, S. Costa, R. LeDuc and R. Brownell Jr. 1995. Phylogenetic relationships of the closely related sei and Bryde's whales: A possible third species? Abstracts, Eleventh Biennial Conference on the biology of marine mammals, 14–18 December 1995, Orlando FL. The Society for Marine Mammalogy. p. 31.

waters around the world. The offshore populations fit Olsen's (1913) description of *B. brydei.* The taxonomic status of the inshore animals found in Japan, South Africa, and perhaps elsewhere is uncertain; Best (1977) suggested that they represent *B. edeni,* but that is unlikely because they are not nearly as small, and the baleen plates of *B. edeni* are broader, more like those of the offshore form of Bryde's whale. In the Atlantic Ocean, where only the larger kind has been certainly identified, Bryde's whales range north to Chesapeake Bay and the Strait of Gibraltar, and south to Buenos Aires in Argentina and Cape Province in South Africa. In the Indian Ocean animals 12.5 m long or longer have been found as far north as the Red Sea (Robineau 1981), the Persian Gulf [=Arab Gulf] (Mahdi 1967, Al-Robaae 1969), the Arabian Sea (USSR 1968[9]), the Malabar Coast of India and the Gulf of Mannar (Mohan 1992), and the Strait of Malacca (Berry *et al.* 1973), and as far south as Mossel Bay in Cape Province (34°S) (Olsen 1913), 32°S, 47°E, in the western part of the Indian Ocean (Ohsumi 1978), and 32°S, 98°E, in the eastern part (USSR 1971[10]). In the Pacific Ocean, larger Bryde's whales range north to the East China Sea, Honshu, 45°N in the central North Pacific, and southern California, and to the south they go as far as North Island in New Zealand (Gaskin 1968), 29°S, 180°, in the central South Pacific, and Arauco (38°S) in Chile.

Balaenoptera borealis Lesson, 1828 (sei whale).

Found in all oceans, but tends to remain in more temperate waters than the other rorquals. Although sei whales migrate considerable distances between higher latitude summer grounds and lower latitude winter grounds, they infrequently venture into cold polar waters and the pack-ice zone, or into hot tropical waters. Their winter grounds remain poorly known, not only because of the paucity of surveys by cetologists in lower latitudes, but also because of their frequent confusion with Bryde's whales, especially in the past. The North Atlantic, North Pacific, and Southern Hemisphere populations of sei whales are disjunct. Tomilin (1946) distinguished two subspecies, one in the Northern Hemisphere, the other in the Southern Hemisphere.

B. b. borealis—In the North Atlantic, their summer range extends from Labrador, southern Greenland, Iceland, and Nordkapp, Norway, south to about North Carolina and the Bay of Biscay; rare vagrant in northwestern Mediterranean Sea. In the winter, sei whales have been reliably identified in the western Atlantic from South Carolina southward into the Gulf of Mexico as far as the Bay of Campeche, and the northern Caribbean Sea off

[9] USSR. 1968. USSR: Information on whale research in 1967 and 1967/68. Document IWC/20/SC/ProgRep submitted to Scientific Committee, International Whaling Commission, at 20th Meeting. 6 pp.

[10] USSR. 1971. USSR: Information on whale research in 1970 and 1970/71. Document IWC/23/SC/22 submitted to Scientific Committee, International Whaling Commission, at 23rd Meeting. 7 pp.

the southeast coast of Cuba and near the island of Anguilla; in the eastern Atlantic they have been found from Benzu, Ceuta (Spanish Morocco), south to Cap Blanc, Mauritania.

From the northern Indian Ocean there are a few published reports of strandings of whales alleged to be sei whales, but none is convincing. Sei whales have routinely been confounded with smaller fin whales or, more often, with Bryde's whales, by observers who were not thoroughly familiar with all three species.

In the North Pacific, the summer range of the sei whale extends north of the Aleutian Islands into the Bering Sea only in the southeastern corner of its deep southwestern basin. From the south side of the Aleutian chain and the northern Gulf of Alaska, sei whales range south to the Sanriku coast of Honshu on the west, the Subarctic Boundary across the central Pacific, and southern California on the east. Indisputably identified winter records have been noted only from the Ogasawara Gunto [=Bonin Islands] in the western Pacific, and between southern Baja California and the Islas Revilla Gigedo in the eastern Pacific.

B. b. schlegellii Flower, 1865—In the Southern Hemisphere, during the summer the majority of sei whales are to be found in the Subantarctic Zone, between the Subtropical Convergence and the Antarctic Convergence. Substantial numbers of them do move into the Antarctic Zone, however, but they rarely if ever enter the pack ice around Antarctica. In the winter, sei whales have been positively identified in catches as far north as Costinha (06°58′S) in Paraíba, Brazil; the coast of Angola; Durban, South Africa; Carnarvon, Western Australia; Cook Straits, New Zealand; and Paita, Peru. One or two have stranded on the north coast of Java.

Balaenoptera physalus (Linnaeus, 1758) (fin whale; finback whale).

Until the work of True (1899), cetologists used the name *B. musculus* (Linnaeus, 1758) for the fin whale rather than for the blue whale.

Nearly worldwide in distribution. Lönnberg (1931) separated the fin whale into two subspecies, one each in the northern and southern hemispheres, on the basis of apparent differences in their vertebrae. These differences were never confirmed, but Tomilin (1946) found that the two populations could be distinguished by body size.

B. p. physalus—In the North Atlantic, fin whales have been found during summer from 75°N in Baffin Bay, 80°N near Spitsbergen, and the Barents Sea, south to about Cape Hatteras in North Carolina, 39°N off the coast of Portugal, and the Cantabrian Sea off the northern coast of Spain. Their winter range is poorly defined, but they have been found in the western North Atlantic from the Grand Banks off Newfoundland south to the Gulf of Mexico and the Greater Antilles. In the eastern North Atlantic, their known winter range extends from the Faroes and southwestern Norway south as far as the Islas Canarias. A disjunct population occurs year-round in the northwestern Mediterranean.

From the northern Indian Ocean there are several published reports of alleged fin whales, but only one—from the Persian Gulf [=Arab Gulf]—has been well-documented. (The name *B. blythii* Anderson, 1879, was given to a set of five vertebrae in the Medical College at Calcutta. Although they lacked provenance, Anderson (1879) presumed that they came from the Bay of Bengal. He calculated that they were from an animal at least 60 ft (18.3 m) long, and believed that they represented a species intermediate in size between *B. indica* [=*B. musculus*] and *B. edeni.* Blanford (1891) noted that they were about the same size as vertebrae of the fin whale, and Allen (1939), without further ado, listed *B. blythii* in the synonymy of *B. physalus.* Subsequent authors have uncritically followed suit, but the name is best ignored as a *nomen dubium.*)

In the North Pacific, fin whales spend the summer from the southern Sea of Okhotsk, the Ostrova Kuril'skiye, the Bering Sea north into the Chukchi Sea, and the northern Gulf of Alaska, south to the Sea of Japan [=East Sea], the Sanriku coast of Honshu, and central California. In winter, fin whales range in the western North Pacific from Korea, the Sea of Japan [=East Sea], and southern Honshu south to Taiwan and the Ogasawara Gunto [=Bonin Islands]; in the central Pacific they sometimes reach the Hawaiian Islands; and on the eastern side they occur from the Big Sur coast of California south to Cabo San Lucas at the southern tip of the Baja California peninsula. There is a year-round resident population in the Golfo de California.

B. b. quoyi (Fischer, 1829)—In the Southern Ocean, fin whales are widely distributed during the summer, all the way from the Subtropical Convergence (approximately 40°S) southward, reaching as far as the Ross Ice Shelf at 78°S. At this season they are concentrated in the Antarctic Zone, above the Antarctic Convergence (about 55°S), but they rarely enter the pack ice. The population shifts to lower latitudes for the winter, but the range at that season is poorly defined, and the whales are believed to be rather widely dispersed. Fin whales have been found in the winter as far north as Cabo Frio in Brazil, Gabon, Angola, Namibia], Cape Province and Natal in South Africa, Madagascar, Carnarvon and Albany in Western Australia, both main islands of New Zealand, Colombia, Peru, and Chile.

Balaenoptera musculus (Linnaeus, 1758) (blue whale; sulphurbottom whale [obsolete]).

Historians should be aware that prior to True's (1899) evaluation of Linnaeus' sources, the name *B. musculus* was applied to the fin whale, while the blue whale was usually called *B. sibbaldii* (Gray, 1847).

Found almost everywhere in the world's oceans at one time or another. Blue whales range from the tropics north and south into the pack ice of the Arctic and Antarctic oceans. They have been encountered north of Svalbard at 80°N and at the front of the Ross Ice Shelf at 78°S. There are disjunct populations in the North Atlantic, the northern Indian, and the

North Pacific oceans. Three diagnosable subspecific names are currently accepted: *B. m. musculus* for the North Atlantic and North Pacific populations, *B. m. brevicauda* for the "pygmy" blue whales in the Subantarctic Zone, and *B. m. intermedia* for the population that summers in the Antarctic Zone (Tomilin 1946, Ichihara 1966). Another name, *B. m. indica* Blyth, 1859, has been given to the northern Indian Ocean population; its distinguishing features, if any, remain poorly known. The type specimen of *indica* was 84 ft (25.6 m) long, and another individual 90 ft (27.4 m) long was reported, whereas the largest *brevicauda* ever taken was only 79 ft (24.1 m) long. The name *indica* would take nomenclatural priority over *intermedia* or *brevicauda* if it were synonymized with either.

The specific name of the blue whale is the Classical Latin noun *musculus.* It is the diminutive of *mus,* genitive *muris,* 'mouse,' hence literally 'little mouse,' but it also carried the transferred meanings of 'muscle,' '[saltwater] mussel,' and sometimes other sea-creatures. Its oldest known use for a baleen whale was by Pliny the Elder (Plinius A.D. 77). The similarity between Pliny's description of the *musculus* and Aristotle's description of the *mustoketos* (see above under Mysticeti) suggests that the former name may have been derived from the latter.

B. m. musculus—In the North Atlantic, the summer range extends from Davis Strait, Denmark Strait, the waters north of Svalbard (Spitsbergen) as far as 80°N, and the Barents Sea south to the Gulf of St. Lawrence, Labrador, and the Bay of Biscay. The winter range remains almost unknown. Some occur at that season around the islands of Cape Verde and along the African mainland from Ras Nouadhibou [=Cape Blanc], Mauritania, south to Cap Vert, Senegal.

In the North Pacific, blue whales range during the summer in the immediate offshore waters from the Sanriku coast of Honshu, northward and eastward along the Kurilskiye Ostrova (but not into the Sea of Okhotsk) and the southern side of the Aleutian Islands, around the Gulf of Alaska, and southeastward as far as central Baja California. They do not go north of the Aleutian Islands, except rarely in the far southeastern corner of the Bering Sea. In the winter they are found regularly from southern Honshu south to the Ogasawara Gunto [=Bonin Islands], Ryukyu Retto, and Taiwan, in the western Pacific, and south at least to Nayarit, Mexico, on the eastern side; there are a few records at that season in the tropical mid-ocean waters. The population in California and Mexican waters is separate from that which spends the summer in more northerly waters. Another apparently discrete group also lives year-round in the tropical eastern Pacific, in the area from 06° to 13° N, and 85° to 100°W.

B. m. indica Blyth, 1859—In the northern Indian Ocean, the "great Indian rorqual" occurs year-round in the Gulf of Aden and the northwestern Arabian Sea, in the Persian Gulf [=Arab Gulf], along the Makran and Sind coasts of Pakistan and the Gujarat and Malabar coasts of India, and around Sri Lanka; there are no records from the Coromandel coast, but they have been reported in the northern Bay of Bengal and in the Strait of Malacca.

For almost 60 yr, authors have been perpetuating an error in the type locality of *B. indica.* In the original description, Blyth (1859) stated that the type specimen came from Juggoo or Amherst Islet, which lies off the south end of Ramree Island (18°47′N, 93°58′E) in the Arakan District of Burma [now Myanmar]. Recent authors have erroneously cited the type locality as "Sondip, Bay of Bengal"—misspelled "Sordip" by Hershkovitz (1966) and most subsequent writers, who obviously copied from him. This island—now called Sandwip Island (22°30′N, 91°25′E)—lies on the eastern side of the Mouths of the Ganges, 30 km northwest of of the port of Chittagong, Bangladesh, and 475 km north-northwest of the actual type locality in Burma. As far as I have been able to trace it, this mistake appears to have originated with Allen (1939), because all earlier authors cite the correct type locality. Allen's error must have arisen as a result of confusion with a whale, identified by Anderson (1879) as an immature *B. indica,* that stranded on Sandwip Island about November 1874—15 yr after Blyth described *B. indica.*

B. m. brevicauda Ichihara, 1966—A population of "pygmy" blue whales ranges mainly in the Subantarctic Zone of the Indian Ocean sector, between 0° and 80°E—especially in the waters around Prince Edward Island, Îles Crozet, and Îles Kerguelen. A few range west into the southeastern South Atlantic as far as 20°W, east through the waters south of the Great Australian Bight and into the Tasman Sea as far as 175°E. A population that inhabits the Peru Current along the coasts of Peru and Chile may also be pygmy blue whales. The winter range of pygmy blue whales is undefined, but a few have been taken off Saldanha Bay in Cape Province, off Durban in Natal, and off Carnarvon and Albany in Western Australia.

The name *B. m. brevicauda* was first proposed by Ichihara in a paper that he presented orally at the First International Symposium on Cetacean Research, Washington, DC, in 1963. Zemsky and Boronin (1964) subsequently used this name before the formal description by Ichihara (1966) appeared in print; they designated no type specimen, and they did not claim to be proposing a new species-group name, so the name *brevicauda* as published by them is a *nomen nudum.*

B. m. intermedia Burmeister, 1871—Most individuals spend the summer in the Antarctic Zone, above the Antarctic Convergence, and many enter the pack-ice zone that surrounds the Antarctic continent. The winter range of the Antarctic animals is virtually unknown, but there are a few records from Buenos Aires in Argentina, in Brazil at Rio Grande do Sul, Cabo Frio (22°51′S), and Costinha (6°58′S), in Gabon, Angola, Namibia, Cape Province, Natal, Madagascar, Lomblen, Moreton Island in Queensland, North Island and South Island in New Zealand, Colombia, Peru, and Chile.

Suborder ODONTOCETI

Flower (1865) named this group Odontocete, but later (Flower 1867) he changed it to Odontoceti, a spelling that has since been universally accepted (see above under suborder Mysticeti). Other permutations that never caught on were Denticete (Gray 1864*b*), Denticeti (Cope 1869), Cetodontes (van Bénéden and Gervais 1868–1879), and Odontoceta (De Blase 1982). The name Odontoceti derives from the Greek ὀδους, genitive ὀδοντος [*odous, odontos*] 'tooth,' and κητος [*kētos*] 'sea-monster,' hence 'toothed sea-monster.'

Our present concept of the Odontoceti has been recognized by virtually all authors, with the notable exception of Abel (1913*b*), who was followed by Zittel and Schlosser (1923), Weber (1928), and van Deinse (1931). Abel split the odontocetes into two newly-proposed taxa: Delphinoceti for the dolphins and porpoises, and Squaloceti for the sperm whales, beaked whales, river-dolphins, monodontids, and the extinct squalodonts and eurhinodelphids.

Odontocetes first appeared in the fossil record in the late Oligocene (not late Eocene as sometimes stated). From the late Oligocene through the early Miocene, there was a variety of archaic odontocetes (Whitmore and Sanders 1976, Fordyce 1981). One of the most primitive was *Xenorophus sloanii,* which retained a vertical supraoccipital, a sagittal crest, and a lambdoid crest, as in the archeocetes and in many terrestrial mammals.

The most prominent cetaceans in the late Oligocene and early Miocene seas were the shark-toothed dolphins of the family Squalodontidae and the long-snouted dolphins of the family Eurhinodelphinidae. The former got their name from their triangular serrate teeth (Kellogg 1923, Rothausen 1968, Muizon 1994). The latter had extraordinarily long beaks in which the toothless tip of the upper jaw projected well beyond the lower jaw (Kellogg 1925). These two families represented the now-relict superfamily Platanistoidea and the extinct superfamily Eurhinodelphinoidea, respectively. Odontocetes referable to the three major groups now living—the dolphins, the beaked whales, and the sperm whales—did not appear until the late Oligocene or early Miocene, some 12 million years after the split between the odontocetes and the mysticetes.

The primary clades of living odontocetes (if we leave aside for the moment the enigmatic river-dolphins) are usually designated as the superfamilies Delphinoidea (dolphins, blackfish, porpoises, *etc.*), Ziphioidea (beaked whales), and Physeteroidea (sperm whales). Each of the three is distinguishable by a suite of synapomorphic characters, and, as far as has been determined, each has a different karyotype (Kulu 1972, Árnason 1974*b* [and other papers]). The delphinoids have the plesiomorphic "general cetacean karyotype" of 2n=44, which is similar to that of two families of baleen whales, Eschrichtiidae and Balaenopteridae. In the Ziphioidea, only *Ziphius cavirostris* and three species of *Mesoplodon* have been examined, and they have a 2n=42 karyotype, which is obviously derived from the 2n=44 karyotype by fusion of two pairs of chromosomes (but it is not homologous with the 2n=42 karyotype of the Balaenidae). The Physeteroidea also possess a 2n=42 karyotype, but it cannot be homologized with the karyotype of any other cetacean.

The delphinoid-ziphioid-physeteroid trichotomy has not been consistently resolved by morphological or molecular studies. Cladistic analyses of skeletal features of both living and fossil species by Muizon (1984, 1985, 1991) and Fordyce (1994) and placed the ziphioids as the sister group to the physeteroids, whereas a similar study by Barnes (1985*b,* 1990) paired the ziphioids with the delphinoids. The latter view was supported by cladistic analyses of morphological features of living species by Heyning (1989, 1997). Four molecular studies also paired the ziphioids with the delphinoids rather than the Physeteroids: cytochrome *b* gene sequences (Árnason and Gullberg 1996), 12S mitochondrial rRNA sequences (Douzery 1993), satellite DNA sequences (Grétarsdóttir and Árnason 1993), and restriction-site mapping of mtDNA (Ohland *et al.* 1995).

Within the superfamily Delphinoidea, the family Monodontidae is the sister-taxon to a clade comprising the families Delphinidae and Phocoenidae (Arnold and Heinsohn 1996, Heyning 1997).

Turning now to the peculiar long-snouted cetaceans called river-dolphins (genera *Platanista, Lipotes, Inia,* and *Pontoporia*), we find the most anomalous living cetaceans. The first three genera are the only living cetaceans that are restricted to freshwater. *Pontoporia* is exclusively marine (but has earned the complimentary title of river-dolphin by virtue of inhabiting the "Río" de la Plata—a saltwater estuary). *Inia* and *Lipotes* have the "general cetacean" karyotype; the chromosomes of the other two genera have not been looked at. In all of the river-dolphins, the postero-lateral expansion of the maxilla does not roof over the temporal fossa, the zygomatic process of the squamosal is large and robust, and the jaws are long and narrow with a long mandibular symphysis. The first two of these characters, at least, are undoubtedly plesiomorphic. Otherwise the four genera differ substantially. Many authors used to lump all of them into a single family, Platanistidae, but as long ago as 1871, Flower (1874) pointed out that ". . .this family can scarcely be retained. . ..The only alternative seems to be to make each of these three genera a distinct family" (*Lipotes* had not yet been discovered). A year later Gill (1872) placed *Pontoporia* in a monotypic subfamily of the family Delphinidae, and placed *Platanista* and *Inia* each in a monotypic family under the superfamily Delphinoidea. Miller (1923) and Kellogg (1928) likewise included "*Stenodelphis*" [=*Pontoporia*] (along with the phocoenids and monodontids) in the Delphinidae, while placing *Inia* and *Lipotes* in the Iniidae, and *Platanista* in its own family. Simpson (1945) put the four genera in three subfamilies under one family, for which he proposed the separate superfamily Platanistoidea.

No two phylogenetic analyses have produced identical cladograms of river-dolphin relationships. Zhou (1982) placed each of the four genera in a monotypic family—all under superfamily Platanistoidea—with Pontoporiidae and Platanistidae the most closely related, and Iniidae the most distant. Barnes (1985*b*) still included all four genera in superfamily Platanistoidea, but he combined *Lipotes* and *Pontoporia* in family Pontoporiidae, while leaving *Inia* and *Platanista* each in its own family. Kasuya (1973) also included all four genera in superfamily Platanistoidea, but he combined *Lipotes* and *Inia* in family Iniidae, and left *Platanista* and *Pontoria* each in its own family. Muizon (1984, 1985, 1988*b*), besides regarding *Platanista* as only distantly related to the other three, segregated *Lipotes* in superfamily Lipotoidea, and placed *Inia* and *Pontoporia* each in their own family within superfamily Inioidea. Heyning

(1989) also restricted Platanistoidea to *Platanista,* but combined the other three genera in family Iniidae under superfamily Inioidea; the nucleotide sequence of the cytochrome *b* gene is consistent with the latter arrangement, with the reservation that *Lipotes* has not yet been examined (Árnason and Gullberg 1996).

The Indian river dolphin, *Platanista,* in particular, has several primitive features which hint that it may be the sister-taxon to all of the other living toothed whales; for example, it is the only odontocete that has an intestinal cecum. Such an arrangement is supported at least weakly by the nucleotide sequence of the cytochrome *b* gene (Árnason and Gullberg 1996). Most recent cladistic analyses, however (Heyning 1989, 1997; Barnes 1990; Muizon 1991, 1994) have placed *Platanista* alone as the sister-group to a clade that includes the delphinoidea plus the other river-dolphins. It is now recognized as the only extant member of the superfamily Platanistoidea.

The other three genera of river-dolphins appear to represent one or more early offshoots of the stem leading to the Delphinoidea, rather than being close relatives of the Platanistoidea. *Pontoporia,* especially, may be close to the Delphinoidea because it shares with the latter the functional asymmetry of its ovaries—a character otherwise unique among cetaceans. These three river-dolphins could be included in an expanded concept of the superfamily Delphinoidea, or they could be placed in one or more superfamilies of their own (Muizon 1991), but are best considered *incertae sedis* pending further inquiry (Fordyce and Barnes 1994).

Family PHYSETERIDAE Gray, 1821

Physeteridæ Gray 1821:310 (Type genus: *Physeter*)
Catodontidæ F. Cuvier 1836:564 (Type genus: *Catodon* Linnaeus, 1761 [=*Physeter*])
Hypognathodontidæ Brandt 1873*a*:575 (In part; includes Ziphiinae and Physeterinae; not available because it is not based on the stem of a generic name)

The giant sperm whale is the single survivor of a diverse array of some 20 or so genera of physeterids that ranged the world's oceans throughout the Miocene and Pliocene. The family is customarily divided into two subfamilies, the extinct (and probably paraphyletic) Hoplocetinae, which had functional teeth in both their upper and lower jaws, and the Physeterinae in which the upper dentition is rudimentary.

Genus PHYSETER Linnaeus, 1758

Physeter macrocephalus Linnaeus, 1758 (sperm whale; giant sperm whale; cachalot [obsolete in English]).

The name *P. macrocephalus* Linnaeus, 1758, takes precedence over *P. catodon* Linnaeus, 1758, because of the Principle of the First Reviser, as decreed in the ICZN Code Article 24 (Husson and Holthuis 1974, Holthuis 1987, Rice 1989*a*; *cf.* Schevill 1986, Mead and Brownell 1993).

The sperm whale occurs throughout the deep waters of all the world's oceans and confluent seas, including the Mediterranean, from the equator to the edges of the polar pack ice. In the North Atlantic ranges north to 68°N in Davis Strait, and 71°N in the Greenland and Norwegian seas. Vagrant north to 78°N east of Svalbard, and east through the Barents Sea as far as the Paluostrov Kanin. In the Indian Ocean ranges north into the Gulf of Aden, the Arabian Sea (but not the Persian Gulf), the Bay of Bengal, and the Andaman Sea; of only two alleged sightings in the Red Sea, one by Baschieri (1956) is self-evidently a misidentification, and the other reported by Slijper *et al.* (1964) is inadequately documented. In the Pacific ranges north to 50°N in the Sea of Okhotsk, 62°N in the western Bering Sea, and 59°N in the Gulf of Alaska. In the Southern Ocean ranges to 65°–70°S around Antarctica. Females and immature males do not go to such high latitudes as the adult males, mostly remaining below the Subpolar Convergence (about 45°N) in the North Atlantic, the Subarctic Boundary (about 42°N) in the North Pacific, and the Subtropical Convergence (about 40°S) in the Southern Hemisphere. Periodically some sperm whales make excursions into shallow shelf waters, such as the Barents Sea, the Baltic Sea, the Gulf of Thailand, and the Java Sea.

Although interchange between the populations in the Atlantic, Indian, and Pacific oceans is hindered by the African continent, the Sunda and Sahul shelves, and the Americas, geographical variation is slight (Ivanova 1955, Berzin 1971, Machin 1974), and no subspecies can be recognized.

Family KOGIIDAE Gill, 1871

Kogiinæ Gill 1871*b*:732 (Type genus: *Kogia*)

The pygmy, or short-headed, sperm whales were often included as a subfamily in the Physeteridae, but now most authors rank them as a family. Muizon (1988*a,* 1991) recognized two subfamilies, Scaphokogiinae for one Miocene species from Peru, and Kogiinae for the living genus and one fossil genus from the Miocene of Mexico.

Genus KOGIA Gray, 1846

Until quite recently, most authors followed Hector's (1878) conclusion that all pygmy sperm whales were conspecific, even though Gill (1871*b*) long ago recognized the differences between the two kinds, and had even proposed a separate genus, *Callignathus* [preoccupied by *Callignathus* Agassiz, 1846, an insect; replaced by *Callignathula* Strand, 1926], for the smaller species. The existence of two well-differentiated and broadly sympatric species was not generally admitted until it was confirmed by the work of Ogawa (1936, 1937*a*), Yamada (1954*a*), Handley (1966), and Ross (1979).

Gray (1846) gave no clue to the derivation of the word *Kogia.* Wall (1851) called it "a barbarous and unmeaning word," and proposed, rather in jest, to "call this whale [*Euphysetes Grayii* = *Kogia breviceps*] 'the new codger,' and thus distinguish it from *'the old codger,'* which is Mr. Gray's *Kogia breviceps.*" Gray (1866) retorted that "Mr. [W. S.] MacLeay [to whom Gray attributed authorship of Wall's publication; *cf.* Gill 1871*b*:739, footnote] objects to the 'barbarous' name of *Kogia*; but there is no generic name that cannot be objected to when a person wants to give a new one of his own." Beddard (1900) speculated that *Kogia* is "said to be a Latinised form of 'codger'! But it might be a tribute to a Turk of the past surnamed Cogia Effendi, who observed whales in the Mediterranean!" ('effendi' is an old Turkish title of respect).

A generic name that is neither Greek, Latin, nor modern Indo-European, "takes the gender expressly attributed to it by its author, or implied by an originally associated species-group name. If no gender was attributed or implied, the name is to be treated as masculine, except that, if the ending is clearly a natural Latin feminine or neuter one, the gender is that appropriate to the ending" (ICZN Code Article 30(d)). Gray (1846) used the name *Kogia* only in combination with the species-group name *breviceps*; since the latter name is a noun, it implies nothing about the gender of *Kogia.* Thus, by default, *Kogia* must be treated as feminine because it has a Latin feminine ending (Article 30(b)).

The species name *simus* was originally bestowed in combination with a masculine generic name, *Physeter simus.* The recent authors who resurrected the name in the combination *Kogia simus* for the dwarf sperm whale overlooked the fact that *simus, -a, -um,* is a Latin adjective, and therefore it must agree in gender with the generic name with which it is at any time combined (Article 31(b)). Thus the correct spelling of the scientific name of the dwarf sperm whale is *Kogia sima.*

Kogia breviceps (Blainville, 1838) (pygmy sperm whale).

Evidently an oceanic species that lives mostly beyond the edge of the continental shelf in tropical and temperate waters around the world. Ranges north to Nova Scotia, the Açôres, the Netherlands, Miyagi on the east coast of Honshu, Hawaii, and northern Washington State. Ranges south to Uruguay, Cape Province, the Tasman Sea, Islas Juan Fernández, and Arica, Chile.

Kogia sima (Owen, 1866) (dwarf sperm whale).

Evidently lives mainly over the continental shelf and slope off tropical and temperate coasts of all oceans. Range includes the western Atlantic from Virginia south to Rio Grande do Sul in Brazil, including the Antilles; the eastern Atlantic from the Mediterranean Sea south to Cape Province; The Indian Ocean from Cape Province north to Oman, east at least as far as Lomblen in Indonesia, and south to South Australia; the western Pacific from Chiba prefecture on the east coast of Honshu, and the Mariana Islands, south to Hauraki Gulf in New Zealand; and the eastern Pacific from Vancouver Island south to Valparaiso in Chile.

Family ZIPHIIDAE Gray, 1850

Hyperoodontina Gray 1846:245 (Type genus: *Hyperoodon*)
Ziphiina Gray 1850:59 (Type genus: *Ziphius*)
Heterodontidæ Girard 1852:319 (Type genus: *Heterodon* Blainville, 1817 [preoccupied by *Heterodon* Latreille, 1801, a reptile], =*Hyperoodon*)
Epiodontina Gray 1865:528 (Type genus: *Epiodon* Rafinesque, 1814. The type species of *Epiodon, E. urganantus* Rafinesque, 1814, has been considered a possible synonym of *Ziphius cavirostris* by some authors (Ellerman and Morrison-Scott 1951), but according to Hershkovitz (1961, 1966) it is "unidentifiable and possibly mythical.")
Ananarcinæ Gill 1871*a*:124 (Misspelling of Anarnacinae)
Anarnacinæ Gill 1871*a*:126 (Type genus: *Anarnacus* Gill, 1871*a*, an incorrect subsequent spelling of *Anarnak* Lacépède, 1804], [=*Hyperoodon*])
Hypognathodontidæ Brandt 1873*a*:575 (In part; includes Ziphiinae and Physeterinae; not available because it is not based on the stem of a generic name).
Xiphidæ Ameghino 1889:895 (=Ziphiina; incorrect subsequent spelling)
Xiphiini Winge 1918:[p. 11 of 1921 English edition] (Type genus: *Xiphius* Agassiz, 1846, an unjustified emendation of *Ziphius*)
Berardiina Moore 1968:276 (Type genus: *Berardius*)
Tasmacetina Moore 1968:276 (Type genus: *Tasmacetus*)
Indopacetina Moore 1968:277 (Type genus: *Indopacetus*)

Technically, the family name Hyperoodontidae should take priority over Ziphiidae (*contra* van Bree and Kristensen 1974). However, except for Iredale and Troughton (1934), Hershkovitz (1966), and Moore (1968), the name Ziphiidae has been in universal use for over a century, so I follow Mead and Brownell (1993) and other authors who retain it under Article 23(b) of the Code, in anticipation that the ICZN will be petitioned to conserve it. However, Hyperoodontinae is gaining currency as a subfamily name under Ziphiidae; this should be no problem, though, because the ICZN has in the past given a junior name nomenclatural priority over an earlier name without suppressing the earlier name.

Among the marine mammals, the ziphiids, with 20 living species, rank second only to the delphinids, yet they remain the most poorly-known family. Important early students of the systematics of the Ziphiidae were Flower (1874, 1878), True (1910), and Harmer (1924). The genera of living beaked whales are all well-marked, and each is readily recognizable by the general facies of the skull and, in life, by the countenance of the head (except *Indopacetus,* which is unknown in the flesh). Moore (1968) arranged the genera into two tribes: Ziphiini (which included *Ziphius* and *Berardius*) and Hyperoodontini (*Tasmacetus, Indopacetus, Hyperoodon,* and *Mesoplodon*); Muizon (1991) raised Moore's tribes to subfamily rank and transferred *Tasmacetus* to the Ziphiinae. The fact that it is the only extant ziphiid with a full set of upper and lower teeth suggests that *Tasmacetus* may be the sister-group to all other living ziphiids; so for the moment its subfamily allocation is best left unresolved. Muizon (1991) also named a third subfamily, Squaloziphiinae, for *Squaloziphius emlongi* from the Miocene of Washington State, but Fordyce and Barnes (1994) note that it lacks convincing ziphiid features and appears more reminiscent of eurhinodelphinids.

Subfamily ZIPHIINAE Gray, 1850

Genus ZIPHIUS G. Cuvier, 1823

The goosebeak whale, like the false killer whale, was first made known to science as a subfossil skull, which had been unearthed in Provence, France, in 1803. The densely ossified rostrum misled Cuvier (1823) into thinking that the specimen was petrified and therefore ancient, but it was actually of fairly recent date. During the following decades, zoologists found a number of stranded individuals of *Ziphius cavirostris,* but they failed to recognize them as such—so garbled was the understanding of beaked whale taxonomy at the time. It took almost 50 yr for cetologists, led by Turner (1872), to realize that these recently stranded whales were the same as Cuvier's "extinct" species.

Ziphius cavirostris G. Cuvier, 1823 (goosebeak whale; Cuvier's beaked whale).

All temperate and tropical waters around the world, north to Massachusetts, the Shetland Islands, the Mediterranean, Honshu, the Aleutian Islands, and the northern Gulf of Alaska; south to Tierra del Fuego, Cape Province in South Africa, Tasmania, South Island of New Zealand, and the Chatham Islands.

Geographical variation has not been analyzed, and Deraniyagala's (1945, 1964) recognition of *Z. c. indicus* P.-J. van Bénéden, 1863, as an Indo-Pacific subspecies lacks any credible basis.

Genus BERARDIUS Duvernoy, 1851

The only known difference between the two allopatric taxa in this genus appears to be the substantially smaller size of *B. arnuxii* (Pike 1953, Slipp and Wilke 1953, McCann 1975, McLachlan *et al.* 1966). More specimens of the latter form are needed to determine whether the difference is sufficient to warrant their status as separate species, or whether *B. bairdii* should be reduced to a subspecies of *arnuxii.* Hershkovitz (1966) listed the two taxa as *Berardius* [*bairdi*] *arnuxi* and *Berardius* [*bairdi*] *bairdi.*

Berardius arnuxii Duvernoy, 1851 (Arnoux's beaked whale).

The species name has frequently been misspelled *arnouxi* or *arnuxi.*

Subantarctic and antarctic waters, from São Paulo in Brazil, Cape Province in South Africa, South Australia, Hauraki Gulf in New Zealand, and the Chatham Islands, south to the waters around the Antarctic continent, including the Ross Sea at 78°S.

Berardius bairdii Stejneger, 1883 (North Pacific bottlenose whale; Baird's beaked whale; giant bottlenose whale).

Temperate North Pacific, mainly in waters over the continental slope. Ranges from the Shantarskiye Ostrova and Ostrov Iony in the Sea of Okhotsk, the Komandorskiye Ostrova, Olyutorskiy Zaliv, St. Matthew Island, and the Pribilof Islands in the Bering Sea, and the northern Gulf of Alaska. Ranges south on the Asian side as far as Zaliv Petra Velikogo [=Peter the Great Bay], and to Kyoto on the Sea of Japan [=East Sea] side of Honshu, and Chiba on the Pacific side. On the American side ranges south as far as San Clemente Island. Vagrant to southwestern Golfo de California. Alleged sightings of *Berardius bairdii* across the central Pacific south as far as 25°N have not been verified by examination of specimens (they might be *Hyperoodon* sp. or *Indopacetus* sp.—see below under *Hyperoodon*).

Subfamily *incertae sedis*

Genus TASMACETUS Oliver, 1937

This singular ziphiid was not discovered until 1933 (Oliver 1937). It is still known only from a few stranded specimens, and its external appearance has never been adequately depicted.

Tasmacetus shepherdi Oliver, 1937 (Tasman beaked whale; Shepherd's beaked whale).

Probably circumglobal in temperate waters of Southern Hemisphere, but specimens have been collected only in Tierra del Fuego and Penisula Valdez in Argentina; Tristan da Cunha; South Africa; Port McDonnell in South Australia; North Island, South Island, Stewart Island, and Chatham Island in New Zealand; and Isla Mas Afuera in the Islas Juan Fernández. Putative sightings of live individuals in western South Atlantic (53°45′S, 42°30′W) and off Christchurch on the east coast of South Island, New Zealand.

Subfamily HYPEROODONTINAE Gray, 1846

Genus INDOPACETUS Moore, 1968

Originally described as a species of *Mesoplodon,* this distinctive but poorly-known whale has erroneously been thought to be a race of *Mesoplodon mirus* (Raven 1937) or a synonym of *Hyperoodon planifrons* (McCann 1962*b*). Both Moore (1968, 1972) and Muizon (1991) classified *Indopacetus* as the sister-taxon of the *Hyperoodon-Mesoplodon* clade.

Indopacetus pacificus (Longman, 1926) (Indo-Pacific beaked whale; Longman's beaked whale).

Known only from the skulls of two animals which stranded at Danane (01°50′N, 45°03′E), Somalia, in 1955, and at Mackay (21°10S, 149°10′E), Queensland, Australia, in 1882. (It is possible that the large unidentified "tropical bottlenose whales" observed in the Indian and Pacific oceans belong to this species—see below under *Hyperoodon.*)

Genus HYPEROODON Lacépède, 1804

This genus includes two well-marked allopatric species (Fraser 1945). Moore (1968), in fact, separated *H. planifrons* into subgenus *Frasercetus* Moore, 1968. However, in a genus with only two species, subgenera are redundant.

Large "bottlenose" whales that look much like *Hyperoodon* sp. have been observed and photographed on many occasions in the tropical Pacific and Indian oceans (Mörzer Bruyns 1971, Miyashita and Balcomb 1989, Urbán *et al.* 1994). Most authors have provisionally called them *H. planifrons,* but none of the photographs that I have seen show any animals with the prominent bulbous forehead and whitish coloration that are such conspicuous field-marks of the larger adult (male?) individuals of *H. planifrons.* Conceivably they represent *Indopacetus,* but their identity will remain unknown until specimens have been collected.

Hyperoodon ampullatus (Forster, 1770) (North Atlantic bottlenose whale).

For many years some authors called this species *H. rostratus* (Müller, 1776), even though Rhoads (1902) and True (1910) had shown that Forster's name had priority.

Subarctic North Atlantic from Davis Strait, Jan Mayen, west coast of Spitsbergen, and Bjørnøya, south to Nova Scotia and the western side of the British Isles; vagrant to Rhode Island, the western Mediterranean, and the North Sea.

Most if not all past reports of *Hyperoodon ampullatus* in the temperate and subarctic North Pacific seem to have been due to confusion with *Berardius bairdii,* because both species are known colloquially as "bottlenose whales."

Hyperoodon planifrons Flower, 1882 (southern bottlenose whale; flatheaded bottlenose whale).

Southern Hemisphere, from Rio Grande do Sul in Brazil, Cape Province in South Africa, 31°S in the western Indian Ocean, Dampier Archipelago in Western Australia, Ulladulla in New South Wales, North Island in New Zealand, and Valparaiso in Chile, south to the Antarctic continent. Deraniyagala (1960) reported an alleged example from Sri Lanka; later (Deraniyagala 1964) he correctly identified it as *Ziphius cavirostris,* but his original error was perpetuated by Hershkovitz (1966) and Phillips (1984).

Genus MESOPLODON Gervais, 1850

Hershkovitz (1961) resurrected the senior synonym *Nodus* Wagler, 1830, for this genus, but subsequently he regarded *Nodus* as a *nomen oblitum,* and reverted to *Mesoplodon* (Hershkovitz 1966). Hall (1981) called it *Micropteron* Eschricht, 1849. Otherwise, the name *Mesoplodon* has been in universal use, and a petition to conserve it (Rice and Kinman 1980) was approved by the ICZN (see Appendix 2).

Thirteen described species make this the largest genus of living cetaceans. Two new species, *M. peruvianus* and *M. bahamondi,* have been discovered since the last edition of this list (Reyes *et al.* 1991, 1996), and beaked whales that appear to represent an undescribed species of *Mesoplodon* have been sighted in the eastern tropical Pacific (Pitman *et al.* 1987). All of the species are quite distinct (Nishiwaki and Kamiya 1958*a*; Moore 1963, 1966; Mead 1989), except that *M. carlhubbsi* might be a subspecies of *M. bowdoini* (Mead 1989), and more specimens of *M. bahamondi* are needed to fully reveal its characters. Beaked whales of the genus *Mesoplodon* are infrequently spotted at sea, and even then they can seldom be identified to species. Almost all museum specimens were stranded animals. Their dentition differs markedly from species to species—indeed some are the most bizarre of living cetaceans.

All 20th century systematists have recognized the unity of *Mesoplodon,* with two exceptions. Oliver (1922) erected a new genus, *Paikea,* for the two species with terminal or near-terminal teeth, *hectori* and *mirus,* but Harmer (1924) synonymized it with *Mesoplodon.* Iredale and Troughton (1934) recognized *Dioplodon* Gervais, 1850, as a separate genus for the species *densirostris.* Moore (1968) included all in *Mesoplodon,* but separated *M. layardii* and *M. densirostris,* which have the most specialized dentition, into monotypic subgenera, *Dolichodon* Gray, 1871, and *Dioplodon,* respectively. However, his arrangement would almost certainly leave the nominate subgenus—with the remaining 11 species—as a paraphyletic group, so subgenera are best ignored for now.

Mesoplodon hectori (Gray, 1871) (Hector's beaked whale).

Circumglobal in temperate waters of Southern Hemisphere. Specimens recorded from Tierra del Fuego and Chubut in Argentina, the Falkland Islands [=Islas Malvinas], Rio Grande do Sul in Brazil, Cape Province in South Africa, Tasmania, North Island and South Island in New Zealand, and Isla Navarino in Chile; also (vagrant?) in Southern California, where there were several strandings and sightings from 1975 to 1979.

McCann's (1962*a*) novel contention that *M. hectori* was simply the young of *Berardius arnuxii* was discredited by Moore (1968).

Mesoplodon mirus True, 1913 (True's beaked whale).

North Atlantic from Nova Scotia and Ireland south to Florida, San Salvador Island in the Bahamas, and Islas Canarias (an oft-repeated record from the

Outer Hebrides Islands in Scotland was based on a misidentified *Ziphius cavirostris*—Herman 1992). In the Southern Hemisphere known from Cape Province in South Africa, Western Australia, and Victoria.

Mesoplodon europaeus (Gervais, 1855) (Gervais' beaked whale: Antillean beaked whale; Gulf Stream beaked whale).

Many authors have called this species by the replacement name *M. gervaisi* (Deslongchamps, 1866), because *M. europaeus* (Gervais, 1852) is a *nomen nudum* (Ellerman and Morrison-Scott 1951). However, *M. europaeus* (Gervais, 1855) was found to be available (Hershkovitz 1961).

Mainly North Atlantic including the Gulf of Mexico, from Texas and Florida to New York, Ireland, the English Channel, and Islas Canarias, south to Jamaica, Curaçao, Trinidad, Ascension Island, Mauritania, and Guinea-Bissau.

Mesoplodon bidens (Sowerby, 1804) (Sowerby's beaked whale; North Atlantic beaked whale; North Sea beaked whale).

Temperate North Atlantic from Wild Bight (49°48'N, 55°56 'W) in Newfoundland, 71°30'N, 04°00'E in the Norwegian Sea, and Smøla (63°25'N) on the west coast of Norway, south to Nantucket Island in Massachusetts, the Açôres, and Madeira. Vagrant to Port St. Joe (29°49'W, 85°19'W) on the gulf coast of Florida.

Mesoplodon grayi von Haast, 1876 (Gray's beaked whale; Haast's beaked whale; scamperdown whale; small-toothed beaked whale)

Circumglobal in temperate waters of Southern Hemisphere, with specimen records from Argentina (Tierra del Fuego, Chubut, and Buenos Aires), Falkland Islands [=Islas Malvinas], Cape Province in South Africa, 31°S, 47°E, in the Indian Ocean, Western Australia, South Australia, Victoria, New South Wales, Tasmania, New Zealand, Chatham Islands, Paracas in Peru, and the Estrecho de Magallanes in Chile. Also (vagrant?) in North Atlantic, where there was one stranding in the Netherlands.

Mesoplodon peruvianus Reyes, Mead, and Van Waerebeek, 1991 (pygmy beaked whale; Peruvian beaked whale; lesser beaked whale).

This newly-discovered species is known only from Bahiá de la Paz in the southwestern Golfo de California, and from the coast of Peru between Playa Paraíso (11°12'S) and San Juan de Marcona (15°19'S).

Mesoplodon bowdoini Andrews, 1908 (Andrews' beaked whale; deepcrest beaked whale).

Southern Indo-Pacific; known only from Western Australia, Victoria, Tasmania, New South Wales, and North, South, Stewart, and Campbell islands in New Zealand. A purported specimen from Îles Kerguelen (Robineau 1973) was found to be misidentified (Mead 1989), and was later determined to be *M. layardii* (Robineau 1989).

Mesoplodon bahamondi Reyes, Van Waerebeek, Cárdenas, and Yáñez, 1996. (Bahamonde's beaked whale).

Isla Robinson Crusoe [=Isla Más á Tierra] in the Islas Juan Fernández, Chile. The type and only known specimen is an incomplete skull.

Mesoplodon carlhubbsi Moore, 1963 (Hubbs' beaked whale; archbeaked whale).

Temperate waters of the North Pacific. In the west recorded from the northeastern coast of Honshu; in the east found from Prince Rupert in British Columbia south to San Diego in California.

Mesoplodon ginkgodens Nishiwaki and Kamiya, 1958 (ginkgo-toothed whale).

M. ginkgodens was described as a "new species" almost simultaneously in three periodicals (Nishiwaki and Kamiya 1958*a, b, c*). *M. hotaula,* which Deraniyagala (1963) described from Sri Lanka, is a synonym (Moore and Gilmore 1965).

Tropical and warm temperate waters of the Indopacific; recorded from Sri Lanka, the Strait of Malacca, Taiwan, Kyushu, the Pacific coast of Honshu, New South Wales, the Chatham Islands, southern California, the west coast of northern Baja California Sur, and the Archipiélago de Colon [=Galapagos Islands].

Mesoplodon stejnegeri True, 1885 (Stejneger's beaked whale; Bering Sea beaked whale; saber-toothed whale).

Subarctic waters of the North Pacific from the Bering Sea south to Japan and central California.

Mesoplodon layardii (Gray, 1865) (Layard's beaked whale; strap-toothed whale; long-toothed beaked whale).

Southern Ocean; recorded from Tierra del Fuego and Chubut in Argentina, Uruguay, the Falkland Islands [=Islas Malvinas], Namibia, Cape Province, Îles Kerguelen, Western Australia, South Australia, Victoria, New South Wales, Queensland, Tasmania, New Zealand, and Isla Navarino and the Estrecho de Magallanes in Chile.

Mesoplodon densirostris (Blainville, 1817) (Blainville's beaked whale; densebeak whale).

Tropical and warm temperate waters around the world, north to Nova Scotia, Wales, Scotland, Portugal, the western Mediterranean, Japan, Midway Islands, and central California; and south to Rio Grande do Sul in Brazil, South Africa, Tasmania, and central Chile.

Family PLATANISTIDAE Gray, 1846

Platanistina Gray 1846:24 (Type genus: *Platanista*)
Susuoidea Gray 1868:4 (Implicitly based on *Susu* Lesson, 1828, a rejected senior synonym of *Platanista*; only included family and genus is Platanistidae with *Platanista*)
Holoodontidæ Brandt 1873*a*:575 (In part; includes Platanistinae, Phocaeninae, Delphininae, and Orcinae; not available because it is not based on the stem of a generic name)

Genus PLATANISTA Wagler, 1830

Hershkovitz (1961, 1966) resurrected the senior synonym *Susu* Lesson, 1828, for this genus, but a petition to conserve *Platanista* because of its long usage (Rice 1987) was approved by the ICZN (see Appendix 2).

The Indus and Ganges populations were long regarded as identical until Pilleri and Gihr (1971) divided them into two species, but Kasuya (1972; *cf.* Reeves and Brownell 1989) reduced the two taxa to subspecies of a single species. Shrestha (1995) even questioned the reality of the alleged differences between the two populations. Until the late Pliocene, the present-day Indus, Ganges, and Brahmaputra (except for its upper reach, the Yarlung Zangpo Jiang) rivers constituted a single westward-flowing river called the Indobrahm (Hora 1950, 1953). Even up until historical times there was probably sporadic faunal exchange between the Indus and Ganges drainages by way of headstream capture on the low Indo-Gangetic plains, between the Sutlej (Indus) and Yamuna (Ganges) rivers (Dey 1968).

Platanista gangetica (Roxburgh, 1801) (Indian river-dolphin; blind river-dolphin; susu [Hindi]; bhulan [Punjabi and Sindhi]; Indus and Ganges river-dolphins)

Authors cited the original description as *Delphinus gangeticus* Lebeck, 1801, until Pilleri (1971) showed that *Delphinus gangeticus* Roxburgh, 1801, took priority.

Exclusively freshwater. There are two disjunct races:

P. g. minor Owen, 1853—Indus River and its tributaries, the Jhelum, Chenab, Ravi, and Sutlej rivers, of Pakistan and India, from tidal limits to the foothills.

Pilleri and Gihr (1971) incorrectly called this taxon by its junior synonym *P. indi* Blyth 1859, but van Bree (1976*a*) showed that the name *P. g. minor* has priority. Pilleri and Gihr (1977*b*) then tried to dismiss the latter name on the grounds that it was originally designated a "variety" rather than a subspecies; however such designation does not preclude the availability of any name published before 1961 (ICZN Code Articles 16 and 45(g)). The type specimen of *P. indi,* originally in the Asiatic Society Museum, Calcutta, has disappeared, so Pilleri and Gihr (1977*b*) designated a neotype (No. 623 in the collection of G. Pilleri). However, this case does not satisfy the conditions under which the designation of a neotype is permissible, so Pilleri and Gihr's designation has no standing in nomenclature (ICZN Code Article 75).

P. g. gangetica—Throughout the Ganges-Brahmaputra river system of India, Bangladesh, Nepal, and possibly Sikkim and Bhutan, below an elevation of about 250 m. In the Ganges valley it ranges into most of the major affluents, including some of their tributaries: the Son, Yamuna, Sind, Chambal, Ramganga, Gumti, Ghaghara, Rapti, Gandak, Bagmati, Ghugri, Kosi, Kankai, and Atrai rivers. In the Brahmaputra valley it also ranges into many of the major tributaries: the Tista, Gadadhar, Champamat, Manas, Bhareli, Ranga, Dihang, Dibang, Lohit, Disang, Dikho, and Kapili rivers. Downstream it ranges through most of the larger distributaries between the Hugli and Meghna rivers, as far as the tidal limits at the mouths of the Ganges. Also reported from the Fenny, Karnafuli, and perhaps the Sangu, rivers to the southeast of the mouths of the Ganges.

Family INIIDAE Gray, 1846

Iniina Gray 1846:25 (Type genus: *Inia*)

Genus INIA d'Orbigny, 1834

Pilleri and Gihr (1977*a*) regarded *I. boliviensis* as specifically distinct from *I. geoffrensis* (and its subspecies *I. g. humboldtiana*), but van Bree and Robineau (1973), Casinos and Ocaña (1979), and most other authors regard the two as conspecific.

Inia geoffrensis (Blainville, 1817) (Amazon river-dolphin; boto; inia).

Exclusively freshwater; regularly enters flooded *várzea* forest during the high-water season. There are three morphologically distinguishable populations, which are best recognized at the subspecific level (van Bree and Robineau 1973, Casinos and Ocaña 1979, Pilleri and Gihr 1977*a,* Best and da Silva 1993).

I. g. humboldtiana Pilleri and Gihr, 1978—Orinoco River system, including the Apure and Meta rivers, upstream as far as the rapids at Puerto Ayacucho. Contact between this race and the next is restricted, at least during low water, by waterfalls from Puerto Ayacucho upstream to San Fernando de Atabapo.

I. g. geoffrensis—Throughout most of the Amazon River and its tributary rivers (below an elevation of about 100 m), including the Tocantins, the Araguaia, the lower Xingu up to the rapids at Altamira, the lower Tapajós up to the rapids at São Luis, the Madeira as far as the rapids at Pôrto Velho, the Purús, the Juruá, the Içá, the Japurá, the Branco, and up the Negro through the Canal Casiquiare into the headwaters of the Orinoco, from whence it ranges as far downstream as San Fernando de Atabapo, including its tributary the Guaviare.

I. g. boliviensis d'Orbigny, 1834.—Upper Rio Madeira drainage in Bolivia, where it is confined to the Río Mamoré and its main branch the Río Iténez [=Rio Guaporé], including lower reaches of their larger tributaries (at an elevation of 100–300 m). There are no credible reports from the Río Beni or any of its tributaries above Riberalta (Anderson 1997). This subspecies appears to be isolated from the previous one by 400 km of rapids from Pôrto Velho on the Rio Madeira in Brazil upstream to Riberalta on the Río Beni in Bolivia. However, inias of undetermined subspecies live in the Río Abuña and its tributary the Río Negro, which enters the Madeira/Beni at the border between Brazil and Bolivia (Anderson 1997).

Family LIPOTIDAE Zhou, Qian, and Li, 1978

Lipotidae Zhou, Qian, and Li 1978:11 (Type genus: *Lipotes*)

Genus LIPOTES Miller, 1918

Lipotes vexillifer Miller, 1918 (Yangtse river-dolphin; baiji; pei c'hi; whitefin dolphin).

Exclusively freshwater. Lower and middle reaches of the Chang Jiang [=Yangtse River], from its estuary upstream for 1,600 km as far as the gorges above Yichang (200 m above sea level). These dolphins entered Poyang Hu and Dongting Hu during the period of high water in summer, when they were said to "make their way up the small, clear rivers" that drain into Dongting Hu. At least one record from the lower Fuchun Jiang at Tonglu. (The older English name "whiteflag dolphin" was based on an erroneous translation of the Chinese name.)

Family PONTOPORIIDAE Gray, 1870

Pontoporiadæ [*sic*] Gray 1870*a*:393 [November 1870] (Type genus: *Pontoporia*; I have not been able to find out whether this reference or the next was published first; Palmer 1905 cites the name from Gray 1870*a,* where it simply appears in a geographical list, whereas Gray 1870*b* includes a taxonomic discussion)

Pontoporiidæ Gray 1870*b*:773 [15 November 1870]

Stenodelphininae Miller 1923:34 (Type genus: *Stenodelphis* d'Orbigny and Gervais, 1847 [=*Pontoporia*])

Stenodelphidae Pilleri and Gihr 1981:34 (=Stenodelphininae; incorrect subsequent spelling. Only included genus: *Pontoporia.* Not available because it is not based on the stem of a valid generic name)

Genus PONTOPORIA Gray, 1846

Ameghino (1891*b*) claimed that this generic name was preoccupied by *Pontoporeia* Krøyer, 1842, an amphipod (class Crustacea: order Amphipoda), so for many years most authors called this genus *Stenodelphis* d'Orbigny and Gervais, 1847. Not until Hershkovitz (1961) pointed out that there was no strict homonymy did cetologists revert to the name *Pontoporia* for the dolphin.

Pontoporia blainvillei (Gervais and d'Orbigny, 1844) (La Plata dolphin; Franciscana).

Coastal waters and estuaries of eastern South America, from Regência (19°S), Espíritu Santo, Brazil, south to Golfo San Matías (42°S), Río Negro, Argentina.

Family MONODONTIDAE Gray, 1821

Monodontidæ Gray 1821:310 (Type genus: *Monodon*)

Tachynicidae Brookes 1828:40 (Type genus *Tachynices* Brookes, 1828 [=*Monodon*])

Narvallidae Burnett 1830:360 (Type genus *Narvallus* Burnett, 1830 [=*Monodon*])

Monoceratina Gray 1846:25 (Type genus: *Monodon*)

Narwalina Reichenbach 1855:5 (Type genus: *Monodon*; not available because it is not based on the stem of an included generic name)

Beluginæ Flower 1867:115 (The type genus, *Beluga* Rafinesque, 1815, is a junior synonym of *Delphinapterus,* so the subfamily name is invalid because it was replaced prior to 1961 (Article 40(b) of the ICZN Code. Flower's paper was "Read November 22nd, 1866"; although the title page of volume 6 of the Transactions of the Zoological Society of London is dated 1869, part 3 was actually issued in 1867 (Duncan *et al.* 1937))

Belugidæ Gray 1868:9 (See Beluginæ above)

Delphinapterinæ Gill 1871*a*:124 (Type genus: *Delphinapterus*)

The unity of this group, as a subdivision of the family Delphinidae, was recognized by Flower (1867) under the name Beluginae, and by Gill (1871) under the name Delphinapterinae. Miller (1923) and Kellogg (1928) classified *Delphinapterus* and *Monodon* each in its own subfamily under the family Delphinidae—Delphinapterinae and Monodontinae, respectively, but later (Miller and Kellogg 1955) they sequestered these two subfamilies into the family Monodontidae. Earlier, Slijper (1936) had included the two genera in one family, which he called Delphinapteridae. Fraser and Purves (1960) went so far as to put the family Monodontidae into its own superfamily, Monodontoidea. All recent authorities have included the monodontids as a single family in the superfamily Delphinoidea, except for Kasuya (1973), who placed the beluga in a separate family, Delphinapteridae, along with *Orcaella* (see below under family Delphinidae). Some authors still recognize separate subfamilies for *Delphinapterus* and *Monodon,* but such an arrangement is redundant (Arnold and Heinsohn 1996). *Denebola brachycephala* from the late Miocene of Baja California, the only known fossil monodontid, was referred to the subfamily Delphinapterinae by Barnes (1984*b*), but Muizon (1988*b*) queried its subfamily allocation.

An apparent *Monodon monoceros* × *Delphinapterus leucas* hybrid was caught in West Greenland (Heide-Jørgensen and Reeves 1993).

Genus DELPHINAPTERUS Lacépède, 1804

Delphinapterus leucas (Pallas, 1776) (beluga; white whale).

The English common name "beluga" is derived from the Russian name; recently some pedantic writers have argued that it should be "belukha," but the vernacular names белуха [belukha] and белуга [beluga] are equally correct in Russian (Chapskii 1937, Tomilin 1957 Kleinenberg *et al.* 1964)—notwithstanding the fact that Russians also use the latter name for the great sturgeon (*Huso huso*). The term "beluga" has been used in English since at least 1817 (*The Oxford English Dictionary, second edition*), and it has become assimilated as a true English vernacular name for the species.

Distributed discontinuously around Arctic Ocean and adjacent seas, mainly in shallow shelf waters. Range includes Hudson and James Bay; Somerset Island, Devon Island, east coast of Baffin Island, and Ungava Bay; northwest coast of Greenland from Inglefield Bredning south to Julianehab; vicinity of Scoresby Sund on the east-central coast of Greenland; Arctic coast of western and central Eurasia from the Barents and White seas east to the Laptev Sea, including Svalbard, Zemlya Frantsa Iosifa, Novaya Zemlya, Severnaya Zemlya, and Novosibirskiye Ostrova; Arctic coast of eastern Siberia from Ostrov Vrangelya to Bering Strait; Bering Sea south to Anadyrskiy Zaliv and Bristol Bay; Arctic coast of Alaska and northwestern Canada from the Chukchi Sea and Kotzebue Sound east to the Beaufort Sea. There are widely disjunct populations in the Saint Lawrence estuary, in the northern and western Sea of Okhotsk including Tatarskiy Zaliv, and in Cook Inlet and the northern Gulf of Alaska.

In the summer, belugas may ascend rivers, sometimes for several hundred kilometers. These rivers include the Severnaya Dvina, Mezen', Pechora, Ob', Yenisey, Khatanga, Anabar, Olenëk, Lena, Kolyma, Anadyr, and Uda rivers in Asia; the Yukon and Kuskokwim rivers in Alaska; and the St. Lawrence River in eastern Canada.

Vagrant to New Jersey, Iceland, the Faroes, Ireland, Scotland, the Atlantic coast of France, the Netherlands, Denmark, Japan, and Washington State.

Some Russian authors split the belugas into three species (Barabash 1937, Klumov and Barabash 1937) or subspecies (Tomilin 1957, Bobrinskii 1965*c*, Heptner *et al.* 1976, Gromov and Baranova 1981) based on slight cranial differences but primarily on size: *D. l. marisalbi* Ostroumov, 1935 [=*D. l. freimani* Klumov, 1935] for the population of small individuals in the White Sea, *D. l. dorofeevi* Klumov and Barabash, 1935, for the disjunct population of large individuals in the Sea of Okhotsk, and *D. l. leucas* for all the animals in the remainder of the Russian Arctic. However, this tripartite division does not adequately reflect the complex pattern of regional variation in body size in this species (Kleinenberg *et al.* 1964, Sergeant and Brodie 1969, Doidge 1990), so the use of trinomials is unwarranted (Kleinenberg *et al.* 1964). Ognetev (1981) has, in fact, shown that the apparent small size of the belugas in the White Sea was due to a sampling artefact.

Genus MONODON Linnaeus, 1758

Monodon monoceros Linnaeus, 1758 (narwhal).

In the eastern Canadian Arctic and west Greenland, from Lancaster Sound, Jones Sound, and Kane Basin, south through Baffin Bay and Davis Strait as far as Cumberland Sound on Baffin Island and Disko off Greenland; a possibly isolated population lives in Foxe Basin and northern Hudson Bay. Vagrant south to coast of Labrador.

In the Eurasian Arctic, along the east coast of Greenland from Nordostrundingen (81°N) south to Umiivik (64°N), thence eastwards in the high arctic pack ice through the Greenland, Barents, Kara, Laptev, and East Siberian seas east to about 165°E, and from about 85°N southwards to Svalbard, Zemlya Frantsa Iosifa, Novaya Zemlya, Severnaya Zemlya, Novosibirskiye Ostrova, and Ostrova De-Longa (157°E). Rare or accidental south to Iceland, the Norwegian Sea, the North Sea (south to the British Isles, The Netherlands and Germany), the White Sea, and the arctic coast of mainland Eurasia; and east into the Chukchi Sea and the Bering Sea as far south as Komandorskiye Ostrova and the north side of the Alaska Peninsula.

Family DELPHINIDAE Gray, 1821

Delphinidæ Gray 1821:310 (Type genus: *Delphinus*)

Delphinusideæ Lesson 1842:197 (=Delphinidae; incorrect subsequent spelling)

Orcadina Gray, 1846:24 (Implicitly based on *Orca* Gray, 1846 [=*Orcinus*], which is preoccupied by *Orca* Wagler, 1830 [=*Hyperoodon*]. Gray included section Orcadina under family Delphinidae in a table on p. 24, but on p. 25, "since the above table was in type," he changed his mind and followed a new classification in which the genus *Orca* was included in the Delphinina. Later (Gray 1850, 1868) he resurrected the name as tribe Orcadina, containing only the genus *Orca* [in which he included *Feresa intermedia* as well as the killer whale], under the Delphinidae)

Orcini Wagner 1846:292 (Type genus *Orca* Gray, 1846 [=*Orcinus*]; unavailable because the type genus is a junior homonym (Article 39 of the ICZN Code))

Globiocephalidæ Gray, 1850:86 (Type genus: *Globiocephalus* Gray, 1843, an incorrect subsequent spelling of *Globicephala*)

Stenonina Gray 1868:5 (Type genus: *Steno*)

Lagenorhynchina Gray 1868:7 (Type genus: *Lagenorhynchus*)

Pseudorcaina Gray 1871:79 (Type genus: *Pseudorca*)

Grampidæ Gray 1871:82 (Type genus: *Grampus*)

Orcadæ Gray 1871:85 (Type genus: *Orca* Gray, 1846 [=*Orcinus*]; unavailable because the type genus is a junior homonym (Article 39 of the ICZN Code))

Holoodontidæ Brandt 1873*a*:575 (In part; includes Platanistinae, Phocaeninae, Delphininae, and Orcinae; not available because it is not based on the stem of a generic name)

Delphinoidæ Guérin, 1874:62 (Includes *Lagenorhynchus, Delphinorhynchus, Tursio,* and "Dauphins divers"; not available because it is not based on the stem of an included generic name)

Delphinorhynchidæ Sclater 1887:60 (Implicitly based on *Delphinorhynchus* Blainville, 1817, which is a *nomen dubium* according to Hershkovitz 1966)

Globicipites Winge 1918:[p. 36 of 1921 English edition] (Type genus: *Globiceps* Flower, 1884, an unjustified emendation of *Globicephala*)

Stenidae Fraser and Purves 1960:59 (=Stenonina; incorrect subsequent spelling; see Steyskal 1980; because of the incorrect spelling of its stem, the name becomes a homonym of the currently-used subfamily name Steninae [=Stenides Rey 1883:175], based on *Stenus* Latreille, 1796, a genus of rove beetles [Coleoptera: Staphylinidae])

Orcinae Fraser and Purves 1960:94, 107, 108, and Figure 26 following p. 108 (Type genus: *Orcinus* on p. 95, 107, and 108, and on Plate 31, but *Orca* on Figure 26; if *Orcinus* is considered the type, this is an "incorrect original spelling" because the grammatical stem of *orcinus* is *orcin-*; if *Orca* is considered the type, the name is unavailable because the type genus is a junior homonym (Article 39 of the ICZN Code); see discussion below under genus *Orcinus*)

Cephalorhynchinae Fraser and Purves 1960:108 (Type genus: *Cephalorhynchus*)

Lissodelphinae Fraser and Purves 1960:108 (Type genus: *Lissodelphis*; an "incorrect original spelling" under Article 32(c)(3) of the ICZN Code, because the grammatical stem of δελφις [delphis] is δελφιν- [delphin-])

Orcaellidae Nishiwaki 1963:98 (Type genus: *Orcaella*)

Globicephalidae Nishiwaki 1963:98 (=Globiocephalidae; justified emendation)

Globidelphinidae Nishiwaki 1963:98 (Only included genus: *Grampidelphis* Iredale and Troughton, 1933 [=*Grampus*]; not available because it is not based on the stem of a generic name)

Orcininae Rice 1967:324 (=Orcinae Fraser and Purves, 1960; justified emendation, in accordance with Articles 29, 32(c)(iii), and 32(d) of the ICZN Code)

Orcaelidae Nishiwaki 1972:111 (=Orcaellidae; incorrect subsequent spelling)

Sotaliinae Kasuya 1973:32 (Type genus: *Sotalia*)

Lissodelphininae Rice 1984*a*:481 (=Lissodelphinae; justified emendation, in accordance with Articles 29, 32(c)(iii), and 32(d) of the ICZN Code)

With about 36 species, the Delphinidae are the largest and most diverse family of marine mammals, and they have radiated to fill many ecological roles. Their morphological adaptations for different niches involve mainly body size and the structures for capturing prey—rostral length and width, and the number, size, and form of the teeth.

The most influential pioneering studies on the classification of the family Delphinidae were done by Flower (1884*a*) and True (1889). Most earlier authors included the Phocoenidae and Monodontidae in the Delphinidae, but the former two taxa are now universally granted family rank. Iredale and Troughton (1934) transferred "*Grampus*" [=*Orcinus*], *Pseudorca, Globicephalus* [*sic*], and "*Grampidelphis*" [=*Grampus*] to the family Phocoenidae. Lately a few authors such as Gaskin (1968) have split the delphinids into two families: Delphinidae for the smaller, mostly beaked, forms with many small teeth ("dolphins"), and the Globicephalidae for the larger forms without prominent beaks, and mostly with a few large teeth ("blackfish," "grampuses", *etc.*). Nishiwaki (1963) went even further and, besides recognizing Globicephalidae, split off *Grampidelphis* [=*Grampus*] and *Orcaella* each in their own monotypic family. Fraser and Purves (1960), on the other hand, separated *Steno, Sousa,* and *Sotalia* into a family Stenidae [*sic*; =Stenonidae], and left the remainder in Delphinidae. Kasuya (1973) left the Delphinidae intact, except for transferring *Orcaella* to the Delphinapteridae.

None of these sunderings of the Delphinidae can be justified. Despite the marked superficial differences between species, their genetic similarity is revealed by a number of intergeneric hybrids. Wild hybrids between *Tursiops truncatus* and *Grampus griseus,* including putative back-crosses, have been collected (Fraser 1940). In captivity, *Tursiops truncatus* has hybridized repeatedly with *Grampus griseus* (Hirosaki *et al.* 1981, Shimura *et al.* 1986, Sylvestre and Tasaka 1985), several times with *Pseudorca crassidens* (Nishiwaki and Tobayama 1982, Sylvestre and Tasaka 1985), at least twice with *Delphinus capensis* (W. F. Perrin, personal communication), and once each with *Steno bredanensis* (Dohl *et al.* 1974) and *Globicephala macrorhynchus* (Antrim 1981[11]). In the crosses with the rough-toothed dolphin and the pilot whale, the male of each pair was the bottlenose dolphin; in the crosses with the grampuses, the false killer whale, and the long-beaked common dolphin, the bottlenose dolphin was the female. In most cases, the hybrid offspring were aborted near term, were stillborn, or survived less than a year; exceptions were the *Tursiops* × *Steno* cross, which lived 4.0 yr, one of the *Grampus* × *Tursiops* crosses, which lived 6.6 yr, and one of the *Delphinus* × *Tursiops* crosses. An apparent hybrid between *Delphinus capensis* and *Lagenorhynchus obscurus* was caught off Peru (Reyes 1996).

At the subfamily level, several variant classifications of the Delphinidae have appeared (Slijper 1936; Fraser and Purves 1960; Rice 1967, 1984*a*; Kasuya 1973; Mead 1975; Barnes *et al.* 1985; Fordyce and Barnes 1994). Each includes two major subfamilies—Delphininae and Globicephalinae (or Orcininae)—but ranks different small splinter-groups as additional subfamilies.

A recent cladistic analysis of morphological features by Muizon (1988*b*) revealed a primary split into three clades, which he ranked as subfamilies: Delphininae (containing all of the small beaked dolphins, plus *Grampus*), Cephalorhynchinae (for *Cephalorhynchus* only), and Globicephalinae (containing the blackfishes and grampuses: *Orcaella, Peponocephala, Orcinus, Globicephala, Feresa,* and *Pseudorca*). Restriction-site mapping of mtDNA of a limited number of genera (Ohland *et al.* 1995) confirmed the isolated position of *Cephalorhynchus,* and largely supported the monophyly of Muizon's Delphininae (*Tursiops, Delphinus,* and *Stenella*) and Globicephalinae (*Globicephala* and *Feresa*)—except that *Grampus* was included in the globicephaline clade. However, a phenogram based on Nei's genetic distances between seven genera showed a monophyletic Globicephalinae (*Peponocephala, Pseudorca,* and *Globicephala*), but a paraphyletic Delphininae (*Steno, Tursiops, Stenella,* and *Lagenorhynchus*) (Shimura and Numachi 1987). The most comprehensive molecular study to date is LeDuc's (1997)[12] analysis of cytochrome *b* sequences of all species of Delphinidae except *Sousa teuszi* and *Cephalorhynchus heavisidii.* In his cladogram the 10 species customarily assigned to the genera *Tursiops, Stenella, Delphinus,* and *Lagenodelphis* comprise a closely-related, incompletely-resolved clade in which neither *Tursiops* nor *Stenella* is monophyletic. Also, the genus *Lagenorhynchus* (*q.v.*) appears polyphyletic. He also tentatively offered the following emended subfamily arrangement of the Delphinidae: Delphininae (*Delphinus, Lagenodelphis, Sousa, Stenella, Tursiops*), Globicephalinae (*Feresa, Grampus, Globicephala, Pseudorca, Peponocephala*), Lissodelphinae [*sic*; =Lissodelphininae] (*Cephalorhynchus, Lissodelphis, "Sagmatias"* [=*Lagenorhynchus* in part]), Orcininae (*Orcinus, Orcaella*), Stenoninae (*Sotalia, Steno*); *Lagenorhynchus albirostris* and "*Leucopleurus*" *acutus* [=*Lagenorhynchus acutus*] were not allocated. However,

[11] Antrim, J. E. 1981. *Globicephala-Tursiops* hybrid. Marine Mammal Information, December 1981:4.

[12] LeDuc, R. G. 1997. A systematic study of the Delphinidae (Mammalia: Cetacea) using cytochrome *b* sequences. Ph.D. dissertation, University of California, San Diego, CA. 104 pp.

pending the outcome of ongoing studies, subfamily designations in the family Delphinidae are best held in abeyance.

Genus CEPHALORHYNCHUS Gray, 1846

This peculiar genus includes four well-marked species, mostly widely allopatric in temperate coastal waters of the Southern Hemisphere (Harmer 1922), except for a minor overlap of *C. eutropia* and *C. commersonii* in the Estrecho de Magallanes and Canal Beagle.

Cephalorhynchus commersonii (Lacépède, 1804) (Commerson's dolphin; piebald dolphin; Jacobite).

There are two populations separated by 130° of longitude. The animals at Kerguelen differ markedly from those in South America (Robineau 1984, Robineau and de Buffrenil 1985) and merit designation as a separate subspecies, but they have not yet been named.

C. c. commersonii—Falkland Islands [=Islas Malvinas] and the coastal waters of southern South America between Rio Negro, Argentina, and Cabo de Hornos, and ranges south into Drake Passage as far as the South Shetland Islands. Vagrant north to Buenos Aires, Argentina, and Isla Chiloë, Chile (42°45′S), well within the range of *C. eutropia.* (An old report from South Georgia is almost certainly erroneous, as no subsequent observers have encountered the species there—Brown 1988.)

C. c. subsp.—Shallow coastal waters around all of the Îles Kerguelen in the southern Indian Ocean.

Cephalorhynchus eutropia (Gray, 1846) (Chilean dolphin; black dolphin; Eutropia dolphin).

Coastal waters of southern South America from Valparaiso, Chile, south to Isla Navarino. This is the species that Fraser (1937) called *C. albiventris* (Perez Canto, 1893).

Cephalorhynchus heavisidii (Gray, 1828) (Haviside's dolphin; hastate dolphin).

Close inshore waters of southwestern Africa, from northern Namibia (17°09′S) south to Cape Point in Cape Province (34°21′S).

Commonly called "Heaviside's dolphin," but the type specimen of this dolphin, in the Royal College of Surgeons, was brought to England by Captain Haviside, commander of an East Indiaman. Unfortunately, when naming this species, Gray confused Captain Haviside with Captain Heaviside, a surgeon who sold a collection of anatomical specimens (but no cetacean material) to the Royal College at about the same time that Haviside's dolphin specimen arrived there (Fraser 1966).

Cephalorhynchus hectori (P.-J. van Bénéden, 1881) (Hector's dolphin; Pied dolphin; whitefronted dolphin).

Endemic to inshore waters of the main islands of New Zealand. Range includes west coast of North Island from Kaipara (36°21′S) south to Palliser Bay (41°26′S), and all coasts around South Island except for Fiordland, between Milford Sound (45°00′S) on the west coast and Te Waewae Bay (167°31′E) on the south coast (not recorded from Stewart Island). Harrisson's (1960) listing of this species as an inhabitant of Sarawak waters is surely a misidentification (van Bree 1972).

Several "pied" or "white" dolphins seen in Cook Strait were described by Oliver (1946) as a new subspecies, *C. h. bicolor,* but they were simply individuals with a variant pigmentation pattern (van Bree 1972).

Genus STENO Gray, 1846

Steno bredanensis (G. Cuvier *in* Lesson, 1828) (rough-toothed dolphin).

W. E. Schevill (footnote *in* Watkins *et al.* 1987) explained why the specific name should be attributed to G. Cuvier *in* Lesson, 1828, rather than to Lesson. For a long time the species was called *S. rostratus* (G. Cuvier, 1817), but that name was preoccupied (Ellerman and Morrison-Scott 1951).

Tropical and warm temperate waters around the world. Ranges north to the Gulf of Mexico, Virginia, the Netherlands, Mediterranean Sea, Gulf of Aden, Arabian Sea, Bay of Bengal, East China Sea, Pacific coast of central Honshu, Hawaiian Islands, and Baja California Sur; vagrant north to Oregon and Washington. Ranges south to Rio Grande do Sul in Brazil, about 32°S in the eastern Atlantic, Natal, Timor Sea, Coral Sea, New Zealand, and Botija (24°30′S) in northern Chile.

Genus SOUSA Gray, 1866

Sousa was formerly included in *Sotalia,* but Fraser (1966), Fraser and Purves (1960), and Iredale and Troughton (1934) thought that the humpbacked dolphins were distinct enough to be included in a separate genus. These dolphins are largely confined to close inshore waters, tidal creeks, and estuaries in the Old World tropics and subtropics; some populations ascend the larger coastal rivers. The number of species of humpback dolphins has long remained unsettled (Ross 1984). Although five species names have been given to members of this genus (True 1889; Hershkovitz 1966; Pilleri and Gihr 1972, 1980), most recent authors have admitted only two, *S. teuszii* in West Africa, and *S. chinensis* in the Indopacific portion of the range. Zhou *et al.* (1980) thought that the differences between the populations in the Indian and Pacific oceans warranted treating them as separate species, *S. plumbea* and *S. chinensis,* respectively. Ross *et al.* (1994) provisionally admitted three species, *S. teuszii, S.*

plumbea, and *S. chinensis*; but ongoing studies (Ross *et al.* 1995[13]) suggest that there may be only one species with two subspecies—one east and one west of the Bay of Bengal. Gaskin (1972) suggested that the white dolphins of Queensland "may be a species or subspecies new to science, for which perhaps the name *Sousa queenslandensis* might be considered"; such conditional names proposed after 1960 have no standing under the ICZN Code (Article 15). A dolphin skull received from "Zambezi" [presumably the province of Zambezia in Mozambique] was described as a new genus and species, *Stenopontistes zambezicus,* by Miranda-Ribeiro (1936), but it is actually a specimen of *Sousa plumbea,* according to Brownell (1975) (not of *Steno bredanensis,* as indicated by Allen 1939 and other authors).

Sousa teuszi (Kükenthal, 1892) (Atlantic humpback dolphin; Teusz's dolphin)

Coast of West Africa from Dakhla (23°54'N) in Western Sahara south to the Arquipélago dos Bijagós (11°13'N) in Guinea-Bissau, and also in Nigeria and Cameroon (published assertions that it ranges to Angola are purely conjectural).

Sousa plumbea (G. Cuvier, 1829) (Indian humpback dolphin; plumbeous dolphin; speckled dolphin; freckled dolphin)

Coastal waters of the Indian Ocean from False Bay (18°30'E) in Cape Province north along the coast of eastern Africa, including Madagascar, to the Red Sea as far north as Gulf of Suez, the Arabian Sea, and the Persian Gulf [=Arab Gulf], thence east along the coasts of southern Asia at least as far as Vishakhapatam on the western Bay of Bengal; vagrant in the Ganges River 250 km from the sea. (Has also strayed into the Mediterranean Sea *via* the man-made Suez Canal—Beaubrun 1995.) The type locality is the Malabar Coast of India; includes *Sousa lentiginosa* (Gray, 1866) from Vishakhapatam, India.

Sousa chinensis (Osbeck, 1765) (Pacific humpback dolphin; Chinese white dolphin; Bornean white dolphin)

Almost all authors called the Chinese white dolphin by the name *S. sinensis* (Desmarest, 1822) or *S. sinensis* (F. Cuvier, 1836) until Hershkovitz (1961) showed that Osbeck was the first author to give it a name. Pilleri and Gihr (1972) attributed the original description to "Osbeck, 1751"; the first (Swedish) edition of Osbeck's book was actually published in 1757, not

[13] Ross, G. J. B., G. E. Heinsohn, V. G. Cockcroft, E. C. M. Parsons and L. J. Porter. 1995. Revision of the taxonomy of humpback dolphins, genus *Sousa.* Abstract, Proceedings of the Symposium on the Biology and Conservation of Small Cetaceans in Southeast Asia, 26–30 June 1995, Dumaguete, Philippines. 25 pp. (Working Document UNEP/SEA 95/WP19).

1751, but in any event it is pre-Linnaean. However the name is available from the 1765 German translation of Osbeck's work (Hershkovitz 1961).

Discontinuously distributed in coastal waters of the western Pacific. Known areas of occurrence include the coast of southern China, including Taiwan, from Gulf of Tonkin to Jiangsu—entering the lower reaches of the Zhu Jiang [=Canton River], the Jiulong Jiang [=Amoy River], and the Min Jiang [=Foochow River], and ascending 1,200 km up the Chang Jiang [=Yangtse River] as far as Wuhan; the Gulf of Thailand; the Strait of Malacca; the northwestern coast of Borneo from Sematan in Sarawak to Sandakan in Sabah; northwestern coast of Western Australia between North West Cape and Larrey Point; coast of eastern Australia from Cairns in Queenland to Wollonggong in New South Wales. Includes *Sousa borneensis* (Lydekker, 1901).

Genus SOTALIA Gray, 1866

Five species names have been given to members of this genus—three to freshwater animals, two to saltwater ones—but their validity has long been questioned (True 1889). Several authors (Beddard 1900, Layne 1958) expressed the opinion that the freshwater populations comprised only one species. Cabrera (1961) recognized only two species in the genus—one freshwater, one coastal. Hershkovitz (1966) listed one freshwater species, and two coastal ones—*S. guianensis* from Venezuela and the Guianas, and *S. brasiliensis* from Rio de Janeiro, Brazil. Recent analyses have shown overlap in cranial measurements between freshwater and coastal populations, so all are now considered conspecific (van Wezel 1985, Casinos *et al.* 1990[14]).

Sotalia fluviatilis (Gervais and Deville, 1853) (tucuxi or tookashee; gray river dolphin).

The freshwater Amazonian populations and the coastal marine populations are separable as subspecies; the population in Lago de Maracaibo, Venezuela, also differs somewhat from either (Casinos *et al.* 1990;[14] da Silva and Best 1994, 1996).

S. f. guianensis (P.-J. van Bénéden, 1864)—Inshore coastal waters, estuaries, and the lower reaches of rivers, along the western Atlantic from eastern Panama south to Floreanópolis, Santa Catarina, Brazil, with a (disjunct?) population on the coast of Honduras and the Costa de Mosquitos of northern Nicaragua. One specimen in the U. S. National Museum (no. 21499) "is said to have come from Florida, but the evidence is not entirely satisfactory" (True 1889). Also "A taxidermist in Florida asserts that a *Sotalia* skull in his posession was taken off the Florida coast" (R. Kellogg in letter to D.

[14] Casinos, A., C. Viladiu and F. Bisbal. 1990. A multivariate analysis of the skull of the genus *Sotalia*. Abstract, European Research on Cetaceans 4:26.

W. Rice, 4 December 1962). Includes *Sotalia brasiliensis* E. van Bénéden, 1875.

S. f. fluviatilis—Exclusively freshwater; Amazon River and most of its tributaries below an elevation of about 100 m. Includes *Sotalia pallida* (Gervais, 1855) and *S. tucuxi* (Gray, 1856).

Genus TURSIOPS Gervais, 1855

Despite the wide distribution, abundance, and popularity of bottlenose dolphins, their taxonomy remains muddled. The overall range of the genus includes tropical and temperate zones of all oceans and peripheral seas, including the Black Sea. These dolphins live in coastal areas of all continents, around most oceanic islands and atolls, and over shallow offshore banks and shoals, but in the Gulf Stream of the northwestern Atlantic, in the tropical eastern Pacific, and elsewhere there are pelagic populations that range far from land. Whether the distinctive bottlenose dolphins of the tropical Indian Ocean, *T. aduncus,* are reproductively isolated from the widespread *T. truncatus* remains undecided. Hershkovitz (1966) considered *aduncus* (which he called *T. nesarnack catalania* Gray, 1862) a subspecies of what is now called *T. truncatus,* while Van Bree (1966) and Ross (1977, 1984) thought that *T. aduncus* was a separate species. Later Ross and Cockcroft (1990) noted apparent morphological intergradation between the two forms in Australia. However, a recent phylogenetic analysis of the mtDNA revealed that specimens of *T. aduncus* (represented by specimens from South Africa, the Timor Sea, and Taiwan Strait) comprise a clade with several species of *Stenella,* well separated from *T. truncatus* proper (Curry *et al.* 1995,[15] Curry 1997,[2] Curry and Smith 1997, LeDuc 1997,[12] LeDuc and Curry 1998). The evidence is thus equivocal, but for the interim it is more useful to list *T. truncatus* and *T. aduncus* as separate species, even though the specific allocation of some populations remains in question.

Tursiops truncatus (Montagu, 1821) (bottlenose dolphin; common bottlenose dolphin).

Hershkovitz (1961, 1963) resurrected the senior synonym *T. nesarnack* (Lacépède, 1804) for this species, but was followed only by Hall (1981); subsequently he reverted to *T. truncatus* as a "*nomen conservandum*" (Hershkovitz 1966). Later, a petition to conserve *T. truncatus* because of its long usage (Rice 1984*b*) was approved by the ICZN (see Appendix 2).

In the Atlantic occurs north to the Gulf of Mexico, Georges Bank off Massachusetts, the Açôres, the British Isles, the Baltic Sea including the

[15] Curry, B. E., M. Milinkovitch, J. Smith and A. E. Dizon. 1995. Stock structure of bottlenose dolphins, *Tursiops truncatus.* Abstracts, Eleventh Biennial Conference on the Biology of Marine Mammals, 14–18 December 1995, Orlando FL. The Society for Marine Mammalogy. p. 27.

Gulf of Finland, the Mediterranean and Black seas; vagrant to Newfoundland and Norway. In the Pacific ranges north to the Bo Hai [=Gulf of Chihli], East China Sea, central Honshu, Kure Atoll, Hawaii, Isla Guadalupe, and Monterey Bay in California; vagrant north as far as Puget Sound in Washington State. In the Southern Hemisphere occurs south to Golfo San Matias in Argentina, 18°S in northern Namibia, Port Elizabeth in Cape Province, Walters Shoal (33°20'S, 43°30'E) in the southwestern Indian Ocean, the southern coast of Australia including Tasmania, South Island in New Zealand, and Concepción, Chile.

Geographical variation in bottlenose dolphins is only vaguely comprehended, and in most parts of the world subspecific designations are best avoided. The name *T. t. truncatus* (type locality: Great Britain) may be applied to the offshore populations on both sides of the North Atlantic, and some authors have used it for similar animals that live in the temperate waters of the western North Pacific, South Africa, Walters Shoal, southern Australia, and New Zealand. The dolphins that live in the Black Sea (named *T. t. ponticus* Barabash-Nikiforov, 1940) are smaller than those in the North Atlantic, while those in the Mediterranean are intermediate in size (Barabash-Nikiforov 1940, 1960; Kleinenberg 1956; Perrin 1984). In some parts of the world, sharply differentiated inshore and offshore populations live in close proximity. One such region is the western North Atlantic, where differences have been found between populations living close inshore and those living offshore in the Gulf Stream (Hersh and Duffield 1990, Mead and Potter 1995, Curry 1997[2]). In the North Pacific, bottlenose dolphins from Kyushu, and along the coast of eastern China from the Bo Hai south to Zhejiang, are larger than those to the south (Zhou and Qian 1985, Gao *et al.* 1995)—but the latter may be *T. aduncus.* The dolphins that range along the coast of southern California and Baja California (named *T. t. gillii* Dall, 1873) appear to be a population distinct from more offshore and southerly animals (Walker 1981). (Some authors have indiscriminately applied the name *T. t. gillii* to all North Pacific bottlenose dolphins.) Results of mtDNA analyses do not indicate genetic isolation among offshore populations from different ocean basins, but do show that there are differing coastal or inshore populations which are genetically isolated from offshore populations (Curry *et al.* 1995,[15] Curry 1997,[2] Curry and Smith 1997, LeDuc and Curry 1998). Electrophoretic studies revealed significant genetic differentiation between neighboring inshore populations along the coast of South Africa (Goodwin *et al.* 1996).

Tursiops aduncus (Ehrenberg, 1833) (Indian Ocean bottlenose dolphin; Red Sea bottlenose dolphin; gadamu [Telugu language of southern India])

Hershkovitz (1966) and a few other authors dated the name *aduncus* from 1832, while van Bree (1966), Fraser (*in* Ellerman and Morrison-Scott 1951), and most others dated it from 1833. Ehrenberg first published the name *Delphinus aduncus* in decas II, folio k, of the *Mammalia* section of Hemprich and Ehrenberg's *Symbolæ Physicæ...* Although folio k is imprinted September 1832, all parts of decas II were actually issued in 1833, according to Woodward (1903).

The type locality is in the Red Sea. Other names that have been used for this taxon are *T. abusalam* (Ruppell, 1842) from the Red Sea, *T. catalania* Gray, 1862, from Queensland, Australia, and *T. gadamu* (Gray, 1866) from Vishakhapatam on the Bay of Bengal.

Ranges along the coast of eastern Africa from Cape Province north to the Red Sea, thence eastward through the Persian Gulf [=Arab Gulf], Arabian Sea, and Bay of Bengal, as far as Taiwan, thence southeast to northern Australia, according to Ross and Cockcroft (1990), who restricted the name *aduncus* to populations with a spotted venter. Dolphins from Amami Gunto, between Kyushu and the Ryukyus, also agree with *aduncus* in their spotted underparts and other features (Miyazaki and Nakayama 1989). Dolphins from the Hawaiian Islands lack the ventral spotting (Rice 1960), as do all but a few old females from the eastern tropical Pacific between southern California and Peru (Leatherwood *et al.* 1982). The latter population has been named *T. nuuanu* Andrews, 1911. Hershkovitz (1963, 1966), studying mainly skulls, greatly extended the concept of *T. aduncus* to encompass not only *T. nuuanu* but also *T. gephyreus* Lahille, 1908, from the coast of Uruguay and Argentina.

Genus STENELLA Gray, 1866

The present assemblage of species was first recognized as a genus by Flower (1884*a*) under the name *Clymenia* Gray, 1868 (type species: *Delphinus euphrosyne* Gray, 1846 [=*Stenella coeruleoalba*]). A year later (Flower 1985) he changed its name to *Prodelphinus* Gervais, 1880, which had been proposed as a replacement because *Clymenia* turned out to be preoccupied. Oliver (1922) later showed that *Stenella* (type species: *Steno attenuatus* Gray, 1846 [=*Stenella attenuata*]) was the earliest available name for this group of species. Regardless, for many years some authors (*e.g.,* Simpson 1945) continued to call this genus *Prodelphinus.* The only attempt to dismember the prevailing concept of *Stenella* was made by Iredale and Troughton (1934), who erected a new genus *Fretidelphis* for *S. roseiventris* (but left *longirostris* in *Stenella*)–see below under the the latter species.

At least superficially, the five species fall into three groups: the spotted dolphins *S. attenuata* and *S. frontalis,* the spinner dolphins *S. longirostris* and *S. clymene,* and the striped dolphin *S. coeruleoalba.* Until recently there was much confusion concerning the relationships of the many nominal species of *Stenella,* but the taxonomy of the spotted dolphins and spinner dolphins was clarified by the work of Perrin (1975*b*) and Perrin *et al.* (1981, 1987), and that of the striped dolphin by Fraser and Noble (1970). There appear to be no plausible synapomorphies that would unite all of the species included herein, and *Stenella* as currently recognized is probably paraphyletic, a conclusion also apparent from cytochrome *b* sequences (LeDuc 1997[12]). *Stenella longirostris,* *S. clymene,* and *S. coeruleoalba* agree with *Delphinus* and *Lagenodelphis* in the possession of palatal grooves, albeit incipient in the last (Perrin *et al.* 1981); *S. attenuatus* and *S. frontalis,* on the other hand, are phenetically closer to *Tursiops* (Perrin *et al.* 1987). A case could thus be made for splitting *Stenella* into two or three genera, or for merging its constituent species into other genera. As noted by Corbet and Hill (1992), "Some other genera, e. g. *Tursiops* and *Stenella,* are very similar and doubtfully justify exclusion from *Delphinus.*" However, for the interim nothing would be gained by upsetting current usage before cladistic analyses—both morphological and molecular—of all the delphinids have been completed.

Stenella attenuata (Gray, 1846) (pantropical spotted dolphin).

In the past a few authors used the name *Stenella dubia* (G. Cuvier, 1812), of unknown provenance, for a species of spotted dolphin, but it is a *nomen dubium* (Perrin *et al.* 1987). The name *S. pernettensis* (Blainville, 1817) [=*S. pernettyi* (Desmarest, 1822), incorrect subsequent spelling], applied to one of the species of spotted dolphins from Cape Verde, was suppressed by the ICZN (van Bree 1971*a,* 1974; see Appendix 2).

Tropical and warm temperate waters around the world. Ranges north to Massachusetts, the islands of Cape Verde, northern Red Sea, Persian Gulf [=Arab Gulf], Arabian Sea, Bay of Bengal, South China Sea, East China Sea, Pacific coast of northern Honshu, Hawaiian Islands, and Baja California Sur; vagrant to Santa Cruz County in California, and Cold Bay on the Alaska Peninsula. Ranges south to Uruguay, Saint Helena, Cape Province, Timor Sea, New South Wales, New Zealand, and about 35°S off Talca, Chile.

This species varies geographically in cranial and postcranial measurements, and in body size and coloration (Perrin 1970, 1975*a, b*; Douglas *et al.* 1984; Schnell *et al.* 1986; Perrin *et al.* 1987), but in most of its range division into subspecies has not been attempted because too few specimens are available. However, in parts of the central and eastern Pacific, Perrin (1975*b*) was able to distinguish Hawaiian, offshore, and coastal subspecies—the first two not yet named (the type locality of *S. attenuata* is unknown).

S. a. subspecies B of Perrin (1975*b*)—Inshore waters around the Hawaiian Islands. This is the "Hawaiian spotted porpoise" of Perrin (1975*b*).

S. a. subspecies A of Perrin (1975*b*)—Eastern tropical Pacific from about 145°W. eastward to the immediate offshore waters between Baja California Sur and Colombia. This is the "Eastern Pacific offshore spotted porpoise" of Perrin (1975*b*).

S. a. graffmani (Lönnberg, 1934)—Inshore waters within about 25 km from land, between the Golfo de California and Colombia. This is the "Eastern Pacific coastal spotted porpoise" of Perrin (1975*b*) and the "coastal spotted dolphin" of Dizon *et al.* (1994).

Stenella frontalis (G. Cuvier, 1829) (Atlantic spotted dolphin; bridled dolphin).

A synonym is *Stenella froenata* (F. Cuvier, 1829).

Tropical and warm temperate Atlantic, north to the Gulf of Mexico, Cape Cod, the Açôres, and the Islas Canarias, and south to Rio Grande do Sul in Brazil, Saint Helena, and Gabon.

There is marked regional variation in the size and shape of the skull, and in adult body size (Perrin *et al.* 1987). The largest individuals inhabit the coastal waters of the southeastern United States; these are the animals that long went under the name *S. plagiodon* (Cope, 1866), and they may yet be recognized as a valid subspecies once a range-wide study has been completed.

Stenella longirostris (Gray, 1828) (spinner dolphin; longsnouted spinner dolphin).

Other names that have been used for spinner dolphins are *S. microps* (Gray, 1846) and *S. alope* (Gray, 1846), both of unknown provenance. Miller and Kellogg's (1955) identification of a specimen from the Islas Tres Marias, Nayarit, Mexico, as well as Handley's (*in* Hester *et al.* 1963) identification of specimens from the eastern tropical Pacific, as *S. microps* have not been upheld (Perrin 1990). Also Ellerman and Morrison-Scott's (1951) identification of specimens from Sri Lanka as *S. alope* is untenable.

Geographical variation in body configuration and color pattern is more pronounced in spinner dolphins than in any other species of cetacean (Perrin 1972, 1975*a, b*; Perrin *et. al.* 1981). Perrin (1990) expressed this variation by naming three subspecies.

S. l. longirostris—Mainly around oceanic islands in the tropical Atlantic, Indian, and western and central Pacific east to about 145°W. Ranges north to New Jersey, Senegal, Red Sea, Gulf of Oman, Arabian Sea, Sri Lanka, Andaman Sea, Gulf of Thailand, southern Honshu, and Hawaiian Islands. Ranges south to Paraná in Brazil, Saint Helena, Cape Province, Timor Sea, Queensland, and Tonga Islands; Vagrant to New Zealand. The many regional populations currently subsumed under this subspecies name differ somewhat in size and other features, and further study may indicate that it would be useful to recognize additional subspecies. Particularly well-marked are the "dwarf" spinner dolphins in the Gulf of Thailand and northern Australia, which may be the same as the small dolphins from the Molucca Sea and Torres Strait that were previously called *S. roseiventris* (Wagner, 1846) (Perrin *et al.* 1989; Perrin and Dolar 1995). Fraser (*in* Brown *et al.* 1966, *in* Morris and Mowbray 1966, *in* Scheffer and Rice 1968) mistakenly applied the name *roseiventris* to Hawaiian specimens. The name *S. l. hawaiiensis,* which McGinnis *et al.* (1972) used for Hawaiian animals, is a *nomen nudum.* Robineau and Rose (1983) claimed that the spinner dolphins in the northwestern Indian Ocean are smaller and have a slightly different color pattern. Perrin (1990) proposed the name "Gray's spinner dolphin" for this race; the "Hawaiian spinner porpoise" of Perrin (1975*b*) is included here. The "Whitebelly spinner porpoise" of Perrin (1975*b*) and the "southern spinner dolphin" of Perrin *et al.* (1979) are intergrades or hybrids between this race and the next.

S. l. orientalis Perrin, 1990—Pelagic waters of the tropical Pacific east of about 145°W, from 24°N off Baja California south to 10°S off Peru—exclusive of the range of the following race. This is the "eastern spinner porpoise" of Perrin (1975*b*) and the "eastern spinner dolphin" of Perrin (1990).

S. l. centroamericana Perrin, 1990—Coastal waters over the continental shelf from the Gulf of Tehuantepec in southern Mexico southeast to Costa Rica. This is the "Costa Rican spinner porpoise" of Perrin (1975*b*) and the "Central American spinner dolphin" of Perrin (1990).

Stenella clymene (Gray, 1850) (Clymene dolphin; shortsnouted spinner dolphin).

Tropical Atlantic, north to Gulf of Mexico, New Jersey, and Senegal, and south to Santa Catarina in Brazil, and the Gulf of Guinea. Also allegedly sighted in the Red Sea recently.

Stenella coeruleoalba (Meyen, 1833) (striped dolphin; Euphrosyne dolphin; blue dolphin; blue-white dolphin; Meyen's dolphin).

This species has also gone under the names *Stenella euphrosyne* (Gray, 1846) and *Stenella styx* (Gray, 1846).

Worldwide in tropical and temperate waters. Ranges north in the Atlantic to Newfoundland, southern Greenland, Iceland, the Faroes, and Denmark, including the Mediterranean Sea; and in the Pacific to the Sea of Japan [=East Sea], Hokkaido, about 40°N across the western and central Pacific, and Washington State; vagrant to Komandorskiye Ostrova. Ranges south to Buenos Aires in Argentina, Cape Province, Western Australia, New Zealand, and Peru.

Striped dolphins show only moderate geographical variation in skeletal morphometrics (Archer and Perrin 1993[16]), and little if any geographical variation in pigmentation pattern (Fraser and Noble 1970). Sylvestre (1985), Calzada and Aguilar (1995), and Di-Meglio *et al.* (1996) found slight but significant differences in body size between local populations in the eastern North Atlantic, the northwestern Mediterranean, and the southwestern Mediterranean.

[16] Archer, F. I., and W. F. Perrin. 1993. Geographical variation of striped dolphins, *Stenella coeruleoalba* from skeletal morphometrics and meristics. Abstracts, Tenth Biennial Conference on the Biology of Marine Mammals, 11–15 November 1993, Galveston TX. The Society for Marine Mammalogy. p. 23.

Genus DELPHINUS Linnaeus, 1758

A long controversy over the number of species in the genus *Delphinus* (True 1889, Miller 1936, Banks and Brownell 1969, van Bree and Purves 1972) has been substantially resolved by recent studies of their morphology (Heyning and Perrin 1994) and mtDNA sequences (Rosel *et al.* 1994), which revealed that the genus consists of at least two species: a short-beaked offshore form (*D. delphis*) and a long-beaked coastal form (*D. capensis*). Each of these species has a wide, but disjunct, distribution in tropical and warm temperate waters; their ranges are mostly parapatric, with some local marginal overlap. In the northern Indian Ocean, an even longer-beaked form with a higher tooth count, *D. tropicalis,* largely replaces *D. capensis.* On a bivariate plot of zygomatic width *versus* rostrum length, samples of *D. delphis* from the eastern Pacific, *D. capensis* from the northeastern Pacific, and *D. tropicalis* from the northern Indian Ocean form three discrete, equidistant clusters (Evans 1994). Van Bree and Gallagher (1978) and Gallagher (1991) tentatively concluded that *D. tropicalis* and *D. capensis* (which they called *D. delphis*) are sympatric in the western Arabian Sea and Gulf of Oman, but with more specimens available Smeenk *et al.* (1996) could find no clear-cut division between the two taxa in that area. *D. tropicalis* and *D. capensis* may yet be shown to intergrade along the coast of East Africa or Arabia, and perhaps also the coast of southern China. Casinos and Jaervinen (1984) found that the range of tooth counts (but not beak length) in *D. capensis* (called *D. delphis*) from Brazil overlapped that in *D. tropicalis.*

Delphinus delphis Linnaeus, 1758 (shortbeaked common, or saddleback, dolphin; offshore common, or saddleback, dolphin; whitebelly dolphin).

Widely but discontinuously distributed in warm temperate and tropical waters of the Atlantic, Pacific, and probably Indian oceans. Its total distribution is uncertain because of past taxonomic confusion. The confirmed range includes the western North Atlantic from Newfoundland to Florida (all reports of specimens and sightings of *Delphinus* sp. from the Gulf of Mexico are erroneous or unacceptable—Jefferson 1997); the eastern North Atlantic from the North Sea south to Gabon, including the Mediterranean and Black seas; the southwestern Pacific around Nouvelle Calédonie, Tasmania, and New Zealand; the western North Pacific from Honshu to Taiwan, thence east in the Kuroshio Extension, between 28° and 43°N, as far as 160°W (absent from Hawaiian waters); and the tropical and warm temperate eastern Pacific from southern California south to central Chile, and west to about 135°W. Unidentified *Delphinus* spp. have been observed in many parts of the tropical Indian and western Pacific oceans.

The population in the Black Sea is separable from those in the Mediterranean and the eastern North Atlantic (Barabash 1935, Barabash-Nikiforov 1938, Kleinenberg 1956, Heptner *et al.* 1976), and has been described as an endemic subspecies *D. d. ponticus* Barabash, 1935. In the northeastern Pacific, three populations separated by latitude can be distinguished by body length and cranial features (Evans 1982). A rare morph with a deviant pigmentation pattern has been found in several areas of the Atlantic and Pacific oceans (Perrin *et al.* 1995).

Delphinus capensis Gray, 1828 (longbeaked common, or saddleback, dolphin; neritic common, or saddleback, dolphin; Cape dolphin; Baird's dolphin).

Disjunct populations are found in warm temperate and tropical coastal waters around the world. The overall distribution remains imperfectly known because of past confusion with *D. delphis,* but specimens have been identified from the following regions: coast of eastern South America from Venezuela to northern Argentina; west Africa from Western Sahara to Gabon; coast of South Africa from western Cape Province to Natal; coastal waters around Madagascar; the Jaza'ir al Hallaniyat [=Kuria Muria Islands] off Oman; Korea and southern Honshu south to Taiwan; New Zealand; southern California south along coast of Baja California and throughout the Golfo de California; and the coast of Peru.

Individuals from the eastern North Pacific population—*D. bairdii* Dall, 1873, of past authors—and the southern African population differ from each other in vertebral count and perhaps other characters (Heyning and Perrin 1994); further study of all populations is needed to ascertain whether recognition of subspecies would be worthwhile. (Beware that some authors have haphazardly applied the name *D. bairdii* or *D. delphis bairdii* to all Pacific Ocean *Delphinus*).

Delphinus tropicalis van Bree, 1971 (Arabian common, or saddleback, dolphin; Malabar common, or saddleback, dolphin).

Coastal waters of the Arabian Sea, from the Gulf of Aden and the Persian Gulf [=Arab Gulf] to the Malabar Coast of India; South China Sea. This taxon was formerly called *D. longirostris* Cuvier, 1829, and *D. dussumieri* Blanford, 1891, but both names are preoccupied (van Bree 1971*c*).

Genus LAGENODELPHIS Fraser, 1956

The one species in this genus was not recognized until 1956, when it was described from a single skull which had been picked up on a beach in Sarawak in 1895 (Fraser 1956). It remained unknown to science as a living animal until 1971, when the species was "rediscovered" (Perrin *et al.* 1973). Once its external features became known, it turned out that tuna fishermen in the eastern tropical Pacific were already familiar with it.

Lagenodelphis hosei Fraser, 1956 (Fraser's dolphin; shortsnouted whitebelly dolphin; Hose's dolphin; Sarawak dolphin).

Pantropical. Ranges north to the Gulf of Mexico, Islas Canarias, Sri Lanka, Taiwan, southern Honshu, and Jalisco in Mexico; vagrant to France. Ranges south to Uruguay, Natal, Queensland, and Peru.

Genus LAGENORHYNCHUS Gray, 1846

This genus traditionally includes six species of cold-water dolphins that share short but trenchant beaks, strongly falcate dorsal fins, and complex pigmentation patterns. *L. albirostris* (the type species of the genus) of the North Atlantic stands somewhat apart from the other five species with its lower tooth count. LeDuc's (1997[12]) cladistic analysis of the cytochrome *b* gene of the Delphinidae shows *Lagenorhynchus* as a polyphyletic group. He tentatively proposes to divide it into three genera: *Lagenorhynchus* (for *L. albirostris* only), *Leucopleurus* Gray, 1866 (for *L. acutus*), and *Sagmatias* Cope, 1866 (for the other four species listed below), but he admonishes that formal adoption of his revised taxonomy should be deferred pending corroboration from other lines of evidence.

The Southern Hemisphere species of *Lagenorhynchus* were for a long time confused, with some authors listing as many as six nominal species. Bierman and Slijper (1947, 1948) lumped all of the Southern Hemisphere populations under the name *L. cruciger*—a hasty and ill-conceived action that only increased the confusion. Later a careful comparison by Fraser (1966) demonstrated that the southern populations represent three sympatric species that are well-defined by color pattern and cranial features. However, the North Pacific *L. obliquidens* is so similar to the Southern Hemisphere *L. obscurus* that it could almost equally well be regarded as a subspecies of the latter. The distinctiveness of all six currently-recognized species has lately been confirmed by a multivariate analysis of cranial morphology and vertebral formulae (Miyazaki and Shikano 1997*b*).

Lagenorhynchus albirostris (Gray, 1846) (whitebeaked dolphin).

Immediate offshore waters of the North Atlantic. Off the American coast from Cape Chidley, Labrador, to Cape Cod, Massachusetts; southwest coast of Greenland north to Godthab; off the European coast from Nordkapp in Norway south through the North Sea to the British Isles, Belgium, the Netherlands, Denmark, and the southwestern Baltic Sea. Vagrant to France, the north coast of Spain, the Strait of Gibraltar, and the Mediterranean Sea.

Populations in the eastern and western North Atlantic are separable on the basis of skull characters (Hill Mikkelsen and Lund 1994), but no subspecies have been named. The type locality is Great Yarmouth, England.

Lagenorhynchus acutus (Gray, 1828) (Atlantic whitesided dolphin).

A deepwater species which ranges across the North Atlantic, from southeastern Labrador (52°N) east to Trøndheimsfjord in Norway, south to Long Island in New York, the Açôres, and the Strait of Gibraltar. Vagrant to Virginia and to southwestern Greenland. Populations in the eastern and western North Atlantic are indistinguishable on the basis of skull characters (Hill Mikkelsen and Lund 1994).

Lagenorhynchus obliquidens Gill, 1865 (Pacific whitesided dolphin; Pacific striped dolphin).

Cool temperate waters of the North Pacific. Ranges on the Asian side from Komandorskiye Ostrova south to Taiwan, thence across the central Pacific between 37° and 47°N to the American side, where it ranges from the northern Gulf of Alaska south to 24°N on the Pacific side of Baja California Sur. Vagrant to Bahía de La Paz in the southwestern Golfo de California.

The populations in the western North Pacific were described as a new species, *L. ognevi,* by Sleptsov (1955), but Tomilin (1957) showed that the alleged diagnostic features all fell within the range of individual and age variation of the eastern North Pacific populations. Among the latter populations, Walker *et al.* (1986) found that the animals off Baja California had consistently larger crania than the ones from northern California northward, with intergrading populations occupying the intervening area off southern and central California. Miyazaki and Shikano (1997*a*) likewise found that specimens from Korea Strait averaged larger than those from far offshore in the western North Pacific (35°–46°N, 158°–180°E). A tiny proportion of individuals exhibit an alternate color phase (Walker *et al.* 1986, Brownell 1965, Mizroch and Rice 1998).

Lagenorhynchus obscurus (Gray, 1828) (dusky dolphin).

Populations in the South American, African, and New Zealand sectors of the range are sufficiently distinct to be regarded as subspecies, according to Van Waerebeek (1993*b*), although he did not apply scientific names to them.

L. o. fitzroyi (Waterhouse, 1838)—Coastal waters of South America from Isla Mazorca, Peru, and Mar del Plata, Argentina, south to the Estrecho de Magallanes; Falkland Islands [=Islas Malvinas]; animals of undetermined subspecies occur around Gough Island.

L. o. obscurus—coastal waters of southern Africa from Lobito in Angola south to Cape Agulhas in Cape Province; Prince Edward Islands (subspecies?); Île Amsterdam (subspecies?). *L. "superciliosus"* (Schlegel, 1841) [not *L. superciliosus* (Lesson and Garnot, 1826)] from South Africa is a synonym. *Prodelphinus petersii* Lütken, 1889, from Île Amsterdam is also conspecific with *L. obscurus* (Van Waerebeek *et al.* 1995).

L. o. subsp.—East coast of New Zealand from Whitianga on North Island south to Stewart Island; Campbell Island; Auckland Islands; Chatham Islands. Purported sightings and specimens from Îles Crozet and Îles Kerguelen (Paulian 1953, Stahl 1982) are erroneous or unverified (Robineau 1989). Likewise, reports from southern Australia, including Tasmania, have never been verified; a skull from Tasmania allegedly of this species (Pearson 1936) is actually a *Lissodelphis peronii* (Van Waerebeek 1993*a*).

Lagenorhynchus australis (Peale, 1848) (blackchinned dolphin; Peale's dolphin).

Coastal waters of southern South America from Isla Chiloé, Chile, and Comodoro Rivadavia, Argentina, south to Canal Beagle; Falkland Islands [=Islas Malvinas]. A group of dolphins closely observed and photographed near Palmerston Atoll (18°S, 163°W) in the Cook Islands also appear to be this species (Leatherwood *et al.* 1991).

Lagenorhynchus cruciger (Quoy and Gaimard, 1824) (hourglass dolphin).

Probably circumpolar in pelagic waters of the Subantarctic and Antarctic zones, south of the Subtropical Convergence; most records fall between 45°S and 65°S. Although the type specimens were not saved, the original descriptions of *L. superciliosus* (Lesson and Garnot, 1826) [but not *L. superciliosus* (Schlegel, 1841)] and *L. wilsoni* Lillie, 1915, are sufficient to identify them as synonyms of *L. cruciger.*

Genus LISSODELPHIS Gloger, 1841

A conspicuous difference in their pigmentation pattern is the most obvious feature that distinguishes the two allopatric taxa in this genus. Some taxonomists have suggested that *L. borealis* might well be regarded as only a subspecies of *L. peronii* (Honacki *et al.* 1982). Hershkovitz (1966) listed the two taxa as *Lissodelphis* [*peroni*] *peroni* and *Lissodelphis* [*peroni*] *borealis.*

Lissodelphis borealis Peale, 1848 (northern right-whale dolphin).

Temperate and subarctic waters of the North Pacific, from the Ostrova Kuril'skiye south to the Sanriku coast of Honshu, thence eastward across the Pacific between 34° and 47°N, extending north to 55°N, 145°W, in the Gulf of Alaska, to the west coast of North America from Washington State south to southern California.

A few individuals possess an alternate color pattern with a more extensive white area on the venter. These animals were referred to the Southern Hemisphere *L. peronii* by Ogawa (1937*b*) and by Tobayama *et al.* (1969). Later Nishiwaki (1972) decided that they represented a new race of the northern species, *L. b. albiventris.* However, such individuals occur sporadically in schools of normally-patterned *L. borealis* throughout the species' range, and they do not constitute a taxonomically recognizeable population (Mizroch and Rice 1998).

Lissodelphis peronii (Lacépède, 1804) (southern right-whale dolphin).

Circumpolar in the Subantarctic Zone, mainly between 40°S and 55°S, ranging north to 25°S off São Paulo in Brazil, 23°S in the Benguela Current off

Walvis Bay in Namibia, the Great Australian Bight, the Tasman Sea, the Chatham Islands, and 12°30′S in the Humboldt Current off Pucusana in Peru. The oft-cited claim by Quoy and Gaimard (1824) that they saw this species north of New Guinea at 2°S is unacceptable (Fraser 1955).

Genus GRAMPUS Gray, 1828

Many American authors, including Anderson (1946), Miller and Kellogg (1955), and Hall and Kelson (1959), followed Iredale and Troughton (1933), who established the name *Grampidelphis* for this genus in the erroneous belief that *Grampus* really belonged to the killer whale (see discussion below under genus *Orcinus.*)

Grampus griseus (G. Cuvier, 1812) (grampus; Risso's dolphin; gray grampus; whiteheaded grampus; mottled grampus).

Worldwide in temperate and tropical waters. Ranges north to Newfoundland, the Shetland Islands, the North Sea, the Mediterranean Sea, Ostrov Iturup in the Ostrova Kuril'skiye, Komandorskiye Ostrova, 56°N, 146°W in the northern Gulf of Alaska, and Stuart Island (50°N) in British Columbia; and south down eastern South America as far as Cabo de Hornos in Chile, to Cape Province in South Africa, Geographe Bay (33°S) in Western Australia, Sydney in New South Wales, North Island in New Zealand, and Valparaiso in Chile.

Genus PEPONOCEPHALA Nishiwaki and Norris, 1966

The one species was for many years regarded as a member of the genus *Lagenorhynchus,* but once it became better known, it was obvious that its affinities lie with *Feresa* and *Pseudorca* (Nakajima and Nishiwaki 1965, Nishiwaki and Norris 1966). The generic name *Electra* Gray, 1866, was briefly revived for this species, until it was realized that the name was preoccupied. According to its authors, the name *Peponocephala* is derived from the Latin *pepo,* which they say means 'melon'—hence the English name; however, *pepo* (genitive *peponis*) actually refers to the pumpkin (*Cucurbita pepo*), whereas *melo* (genitive *melonis*) is the Latin word for the melon (*Cucumis melo*) (Bailey 1949, Simpson 1968). "Punkinhead whale" would be a more correct Anglicization of the generic name.

Peponocephala electra (Gray, 1846) (melonheaded whale; many-toothed blackfish; little blackfish; Electra dolphin).

Pantropical. Ranges north to the Gulf of Mexico, Senegal, Arabian Sea, Bay of Bengal, South China Sea, Taiwan, southern Honshu, Hawaiian Islands, and Baja California Sur; ranges south to Espiritu Santo in Brazil, Timor Sea, northern New South Wales, and Peru. Vagrant to Maryland, Cornwall in England, and Cape Province in South Africa.

Genus FERESA Gray, 1870

First known from two skulls received at the British Museum—one from an unknown locality sometime before 1828, the other from the "South Seas" in 1874—the pygmy killer whale then dropped from sight for 78 yr, until one was taken in the small-whale fishery in Japan (Yamada 1954*b*). Since its appearance in life became known, it has been found in many parts of the tropics.

Feresa attenuata Gray, 1874 (pygmy killer whale).

The original description is usually cited from Gray, 1875, but see Caldwell and Caldwell (1971). The prior name *F. intermedia* (Gray, 1827) turned out to be preoccupied; the replacement name *F. occulta* Packard and Jones, 1956, was proposed before it was realized that *F. intermedia* and *F. attenuata* were the same.

Pantropical. Ranges north to Gulf of Mexico, east coast of Florida, Senegal, Arabian Sea, Sri Lanka, Honshu, Hawaii, and Gulf of Tehuantepec. Ranges south to Buenos Aires, Cape Province, Queensland, and Peru.

Genus PSEUDORCA Reinhardt, 1862

The false killer whale was assumed to be an extinct species when it was first discovered as a subfossil in the great fen of Lincolnshire, England, in 1846 (Owen 1846). Not until 1861, when a school stranded at Kiel, Germany, was it realized that it was a still-living species.

Pseudorca crassidens (Owen, 1846) (false killer whale).

Worldwide in tropical and temperate waters. Ranges north to Maryland, Scotland, southern Japan, Hawaii, and British Columbia (an oft-repeated report from Davis Strait was an error—Miller 1920). Ranges south to Chubut in Argentina, Cape Province, Western Australia, South Australia, Tasmania, South Island of New Zealand, Chatham Islands, and Concepción, Chile.

Kitchener *et al.* (1990) found substantial differences in cranial characters between false killers from Australia, Scotland, and South Africa. Deraniyagala (1945) recognized *P. c. meridionalis* (Flower, 1864) as the false killer whale of the Indo-Pacific, but provided no supporting data for its alleged diagnostic features. Recognition of any subspecies would be premature.

Genus ORCINUS Fitzinger, 1860

Until recently some authors (Slijper 1936, Fraser and Purves 1960) still used the generic name *Orca* Gray, 1846, for the killer whale, even though

Palmer (1899) had long before pointed out that Gray's name is preoccupied by *Orca* Wagler, 1830, which is a synonym of *Hyperoodon.* Iredale and Troughton (1933) argued that the generic name *Grampus* Gray, 1828, was based on the killer whale, not the gray grampus, and should therefore replace *Orcinus.* In this they were followed by many American writers, such as Miller and Kellogg (1955) and Hall and Kelson (1959), but Ellerman and Morrison-Scott (1951), Schevill (1954), and Hershkovitz (1961) exposed the flaws in their argument.

Orcinus orca (Linnaeus, 1758) (killer whale; orca).

Throughout all oceans and contiguous seas, from equatorial regions to the polar pack-ice zones, but most numerous in coastal waters and cooler regions where productivity is high. In the Atlantic ranges north to Hudson Strait, Lancaster Sound, Baffin Bay, Iceland, Svalbard, Zemlya Frantsa Iosifa, and Novaya Zemlya; range includes Mediterranean Sea. In the Pacific ranges north to Ostrov Vrangelya, the Chukchi Sea, and the Beaufort Sea. In the Southern Ocean ranges south to the shores of Antarctica, including the Ross Sea at 78°S.

Scheffer (1942), followed by Miller and Kellogg (1955) and by Hall and Kelson (1959), called the North Pacific killer whales "*Grampus*" *rectipinna* (Cope, 1869), because he thought that they differed from "*Grampus*" *orca* of the North Atlantic, but the alleged distinguishing features were simply sex- and age-related. Zemsky and Budylenko (1970) could find no consistent differences between northern and southern hemisphere populations. Each pod of killer whales, or local group of pods, is largely endogamous and differs in minor ways from neighboring groups in both morphology and genetics, as well as in traditions such as migratory behavior, prey choice, and dialects (Bigg *et al.* 1990, Hoelzel and Dover 1991, Ford *et al.* 1994). Berzin and Vladimirov (1982, 1983) described a supposed new species of "dwarf" or "yellow" killer whale, *Orcinus glacialis,* from the ice edge in the Indian Ocean sector of the Antarctic from 60°E to 141°E. The skulls—especially the teeth—of the six specimens that were collected differ noticeably from those of most other killer whales. During the summer, at least, these small animals are said to range in the same waters as typical *O. orca* but not to mix in the same schools with the latter. The two kinds are also said to select different prey—fish *vs.* mammals, respectively. Further studies are needed to ascertain whether these small whales deserve recognition as a separate species or subspecies. Earlier, Mikhalev and Ivashin (*in* Mikhalev *et al.* 1981) rather perfunctorily proposed the name *O. nanus* for some killer whales, collected at about 120°W in the Antarctic Ocean, that had attained sexual maturity at an abnormally small body size. Aside from their small size, none of the other diagnostic features claimed for *O. glacialis* were attributed to these animals. No type specimen was designated, and apparently no specimens were preserved, so *O. nanus* is best regarded as a *nomen nudum.*

Genus GLOBICEPHALA Lesson, 1828

Although they were long confused, the two species in this genus are well-defined (Weber 1923, Fraser 1950, van Bree 1971*b*). External differences between them in the North Atlantic were described by Sergeant (1962). They are largely parapatric—one circumglobal in tropical and subtropical waters, the other bipolar in temperate waters. Their known ranges overlap marginally, without intergradation, off the mid-Atlantic coast of the United States (Paradiso 1958), off southern Europe (Nores and Pérez 1988), off southern Brazil (Schmiegelow and Filha 1989), off South Africa (van Bree *et al.* 1978), around Tasmania (Guiler 1978), and probably elsewhere, but they may be seasonally segregated in these areas.

Globicephala melas (Traill, 1809) (longfinned pilot whale; longfinned blackfish; caa'ing whale).

For a long time the emended species name *melaena* was used, but *melas* is a (transliterated) Greek word and therefore must retain its original ending as decreed by Article 31(b) of the ICZN Code (Jones *et al.* 1986; Rice 1989*b*, 1990).

There are two widely disjunct populations, one in the North Atlantic, the other in the Southern Hemisphere. The latter were described as a separate species, *G. leucosagmaphora,* by Rayner (1939), on the basis of some differences in color pattern. Ellerman *et al.* (1953) pointed out that the name *G. edwardii* (A. Smith, 1834) took priority over Rayner's name. Davies (1960) found that the distinguishing features of the southern animals were slight and inconsistent, and he reduced them to subspecific rank.

G. m. melas—North Atlantic from Ungava Bay, Disko in western Greenland, 68°N in eastern Greenland, Iceland, the Faroes, and Nordland in Norway, south to North Carolina, the Açôres, Madeira, and Mauritania, including the western Mediterranean. Pilot whales on the western (Newfoundland) and eastern (Faroes) sides of the North Atlantic are distinguishable by minor external morphometric characters and may be geographically isolated from each other (Bloch and Lastein 1993).

G. melas subsp.—In the North Pacific, there are no historical records of longfinned pilot whales. However, skulls of this species have been recovered at two archeological sites in Japan, one on Rebun-tō in the northern Sea of Japan {=East Sea}, which dates from somewhere between the 8th and 12th centuries A.D., the other in Tateyama at the entrance to Tōkyō-wan, which dates from about 6,400 yr ago (Kasuya 1975). The waters around these sites are presently inhabited by shortfinned pilot whales.

G. m. edwardii (A. Smith, 1834)—Circumglobal in Southern Hemisphere, ranging north to São Paulo in Brazil, Cape Province in South Africa, Îles Crozet, Heard Island, the southern coast of Australia, Great Barrier Island in New Zealand, and Arica (19°S) in Chile (a sight record from off Ecuador cannot be accredited). Southward it extends at least as far as the

Antarctic Convergence (47° to 62°S), and has been recorded near Scott Island (67°S, 179°W) and in the central Pacific sector at 68°S, 120°W.

Globicephala macrorhynchus Gray, 1846 (shortfinned pilot whale; shortfinned blackfish).

For use of the name *G. macrorhynchus* Gray, 1846, rather than *G. sieboldii* Gray, 1846, see van Bree (1976*b*). Until recently, the specific name was usually spelled *macrorhyncha,* but, being a noun, its ending cannot be changed to agree with the gender of the generic name (ICZN Code Article 31(b)).

Probably circumglobal in tropical and warm temperate waters. In the Atlantic ranges north to New Jersey and to Charente-Maritime in France (not present in Mediterranean); in the Pacific extends north into cooler temperate waters as far as Hokkaido, Ocean Station Papa (50°N, 145°W), and Vancouver Island. Vagrant to Alaska Peninsula (57°N, 156°W). Southern limits not fully determined due to past confusion with the previous species, but known to range south to São Paulo, Cape Province, Western Australia, Tasmania, and Cape Farewell on North Island in New Zealand.

This species appears to vary geographically, but no comprehensive study has been undertaken. Off the Pacific coast of Japan, a northern and a southern population differ sharply in color pattern and in body size and shape (Kasuya *et al.* 1988) and also in cranial features (Miyazaki and Amano 1994); their taxonomic status remains unsettled.

Genus ORCAELLA Gray, 1866

This genus has frequently been called *Orcella* Anderson, 1871, "which is better etymology but incorrect zoological nomenclature" (Simpson 1945).

For a long time cetologists were unanimous in allocating this peculiar cetacean to the family Delphinidae. Kasuya (1973) dissented and placed it with *Delphinapterus* in a family Delphinapteridae. Barnes (1984*b*) then placed it with *Delphinapterus* and *Monodon* in the family Monodontidae. Fordyce (1984), Rice (1984*a*), and Heyning (1989), however, pointed out that it shares more morphological similarities with the other Delphinidae than with the Monodontidae, an opinion which was subsequently corroborated by a cladistic analysis of morphological features (Arnold and Heinsohn 1996), by isozyme and immunological distance studies (Lint *et al.* 1990), by studies of satellite DNA (Grétarsdóttir and Árnason 1992), and by sequencing the cytochrome *b* gene (Árnason and Gullberg 1996; LeDuc 1997[12]).

Orcaella brevirostris (Owen *in* Gray, 1866) (Irrawaddy dolphin; pesut).

The species name is usually attributed to Gray (1866), but Gray cites the name as "Phocæna (Orca) brevirostris, *Owen, Zool. Trans.* v., ined." and he quotes the entire description from Owen. Owen's (1866) paper was read before the Zoological Society of London on 20 June 1865; the published volume in which it appeared was dated 1869, but Owen's paper was actually published on 15 August 1866 (Arnold and Heinsohn 1996).

Discontinuously distributed mostly in the shallow, brackish, turbid waters at the mouths of rivers in southeastern Asia and Australasia. Around the Asian mainland, ranges from Vishakhapatnam, Andhra Pradesh, India, around the Bay of Bengal to the Strait of Malacca and the Gulf of Thailand; there are freshwater populations in the distributaries at the mouths of the Ganges, in the Irrawaddy as far as 2,300 km upstream to Bhamo, and in the Mekong River. On the Sunda and Sahul shelves known from the Sungai Belawan Deli in northeastern Sumatra; Belitung; north coast of Jawa Timur [East Java]; south coast of Jawa Tengah [=Central Java]; Kepulauan Bunguran [=Natuna Islands]; river mouths along the coast of Sarawak, Brunei, and Sabah; the Seruyan and Mahakam river systems, including Semayang, Melintang, and Jempang lakes, in Kalimantan Timur [=East Kalimantan]; Sungai Kumai in Kalimantan Tengah [Central Kalimantan]; southwestern Sulawesi; Teluk Cenderawasih [=Geelvink Bay] in northwestern New Guinea; southern New Guinea from coast of Merauke east to the Gulf of Papua, thence south to northern Australia where it ranges from Point Cloates in Western Australia around to Gladstone in Queensland.

Anderson (1879) alleged that the freshwater population in the Irrawaddy was morphologically distinct from the coastal populations, and it was long regarded as a separate species or race, *O. b. fluminalis* Gray, 1871. However, subsequent authors could find no differences among populations in the Irrawaddy, in the Mekong, and in marine waters (Thomas 1892, Weber 1923, Pilleri and Gihr 1974, Lloze *in* Marsh *et al.* 1989).

Family PHOCOENIDAE Gray, 1825

Phocænina [*sic*] Gray 1825:340 (Type genus: *Phocæna,* an incorrect subsequent spelling of *Phocoœna*)

Holoodontidæ Brandt 1873*a*:575 (In part; includes Platanistinae, Phocaeninae, Delphininae, and Orcinae; not available because it is not based on the stem of a generic name)

Phocoenidae Fraser 1966 (Type genus: *Phocoena*; corrected spelling of Phocænina)

Phocoenoidinae Barnes 1984*b*:17 (Type genus: *Phocoenoides*)

Miller (1923) and Kellogg (1928) included the true porpoises in the family Delphinidae and did not even grant them subfamily status. However, Slijper (1936) and Fraser and Purves (1960) recognized them as a separate family, an arrangement that has been accepted by almost all subsequent authors. The phocoenids have traditionally been divided into three well-defined genera, *Neophocaena, Phocoena,* and *Phocoenoides.* Fraser (1937), followed by Ellerman and Morrison-Scott (1951) and Simpson (1945), included *Phocoenoides* in *Pho-*

coena, but the two genera are strongly differentiated. *Phocoena dioptrica* is remarkable for its conspicuous sexual dimorphism (Fraser 1968), and Barnes (1984*b,* 1985*a*) noted morphological and behavioral similarities between it and *Phocoenoides dalli,* so he erected the new genus *Australophocaena* for *P. dioptrica,* and recognized two subfamilies, Phocoeninae for *Neophocaena* and *Phocoena,* and Phocoenoidinae for *Australophocoena* and *Phocoenoides.* However, his arrangement was not corroborated by studies of the cytochrome *b* gene and the displacement loop of the mtDNA (Rosel *et al.* 1995), which instead indicated that *Neophocoena phocoenoides* is the most basal member of the family, while all the other species fall into an unresolved trichotomy between *Phocoenoides dalli, Phocoena phocoena,* and a southern clade consisting of *P. dioptrica, P. sinus,* and *P. spinipinnis.*

Genus NEOPHOCAENA Palmer, 1899

The bewildering nomenclatural history of this genus began when Gray (1846) first named it *Neomeris.* Flower and Lydekker (1891) pointed out that Gray's name was a junior homonym of *Neomeris* Lamoureaux, 1816, given to an organism thought to be a coral polyp (class Anthozoa), so Palmer (1899) proposed *Neophocaena* as a replacement name. Later Thomas (1922) and Allen (1923) discovered that there were two earlier names, *Meomeris,* which had appeared as a misprint for *Neomeris* in a publication by Gray (1847), and *Nomeris,* another misprint, published by Coues (1890), so they resurrected *Meomeris* as the valid name for the porpoise. Shortly thereafter, Thomas (1925) learned that *Neomeris* Lamoureaux, 1816, was really a calciferous green alga (class Chlorophyceae: order Dasycladales), not a coral; since botanical nomenclature is outside the province of the ICZN Code, the name of the porpoise reverted to *Neomeris* Gray, 1846, for the next 36 years. Then Hershkovitz (1961) discovered that Gray's name was also a junior homonym of *Neomeris* Costa, 1844, a genus of annelid worms (class Polychaeta: order Opheliida), so he reinstated *Meomeris* as the correct name. About the same time, however, a new edition of the Code (ICZN 1961) decreed (Article 33(c)) that misspelled names have no status in nomenclature and cannot be used as replacement names, so Scheffer and Rice (1963) reinstated Palmer's *Neophocaena* as the earliest available name for the finless porpoise.

Neophocaena phocaenoides (G. Cuvier, 1829) (finless porpoise; little Indian porpoise).

There are three well-marked regional populations which were treated as separate species by Pilleri and Gihr (1972, 1975) and Pilleri and Chen (1980), but most other investigators believe that they warrant only subspecific rank (Fraser 1966; van Bree 1973; Amano *et al.* 1992; Wang 1992*a, b*; Gao and Zhou 1993, 1995*a, b, c*; Zhou *et al.* 1993). Even within subspecies, significant differences in skull morphology have been found among local populations (Yoshida *et al.* 1995).

N. p. phocaenoides—Coastal waters along the mainland of southern Asia from the Persian Gulf [=Arab Gulf] east to the South China Sea and southern part of the East China Sea; also coasts of southeastern Sumatra, Bangka, Belitung, Sarawak, Palawan, the Turtle Islands in the Sulu Sea, the Visayan islands and northern Mindanao, and northern Java. The allegation that the type specimen of *N. phocaenoides* came from the Cape of Good Hope is almost certainly erroneous, because the species has not been found since in South African waters, or anywhere else in Africa, despite much cetological research there (Allen 1923, 1939; Best 1971; Meester *et al.* 1986)—Gibson-Hill's (1950) alleged sighting "off the coast of South Africa" notwithstanding.

N. p. sunameri Pilleri and Gihr, 1975—Coastal waters from the southern East China Sea north to the Liaodong Wan in China, Korea, and Kyushu in Japan, thence along the Pacific coast of Japan from the Seto-naikai north to Sendai-wan in northern Honshu.

N. p. asiaeorientalis (Pilleri and Gihr, 1972)—Lower and middle reaches of the Chang Jiang [=Yangtse River], where it ranges 1,600 km upstream as far as the gorges above Yichang (200 m above sea level), and including Poyang Hu and Dongting Hu and their tributaries the Gan Jiang and the Xiang Jiang.

Genus PHOCOENA G. Cuvier, 1816

This generic name was misspelled *Phocaena* and was dated from 1817 until Hershkovitz (1961) established that *Phocoena* was the correct original spelling, and Roux (1976) proved that Cuvier's "Le Règne Animal" was published in 1816, not 1817.

Cranial features of the four species in this genus were compared by Norris and McFarland (1958) and Noble and Fraser (1971). Brownell *et al.* (1987) described the external appearance of the recently-discovered *P. sinus* and compared it with *P. phocoena* and *P. spinipinnis.*

Phocoena phocoena (Linnaeus, 1758) (harbor porpoise; common porpoise).

Restricted to shallow coastal waters. Miyazaki *et al.* (1987) and Amano and Miyazaki (1992*a*) described significant differences in the skulls of harbor porpoises from the North Atlantic, the western North Pacific, and the eastern North Pacific (*cf.* Yurick and Gaskin 1987). They recognized only two subspecies, one in the Atlantic and one in the Pacific, although they noted that western Pacific animals differ sufficiently from those in the eastern Pacific to warrant subspecific separation; no species-group name has ever been based on a western Pacific specimen. Separation of the disjunct Black Sea population as an endemic subspecies, *P. p. relicta* Abel, 1905, cannot be upheld (Kleinenberg 1956), although that population does differ somewhat from the North Atlantic population (Miyazaki *et al.* 1987). Gao and Gaskin (1996) found significant differences in skull measurements among local populations in the western North Atlantic, and Börjesson and Berggren (1997) found comparable differences between populations in the Baltic Sea and those in the Kattegat and Skagerrak. Geographical variations in pigmentation patterns were analyzed by Koopman and Gaskin (1994).

P. p. phocoena—North Atlantic Ocean. Ranges on the western side from Cumberland Sound on the east coast of Baffin Island, southeast along the eastern coast of Labrador to Newfoundland and the Gulf of St. Lawrence, thence southwest to about 34°N on the coast of North Carolina; also southern Greenland, north to Upernavik on the west coast and Angmagssalik on the east coast. In the eastern Atlantic, its range includes the coasts around Iceland; the Faroes; and the coasts of Europe from Mys Kanin and the White Sea in northern Russia, west and south as far as Cabo de Espichel, Portugal (38°24′N), including the Baltic Sea, the Gulf of Bosnia, the Gulf of Finland, and the British Isles; vagrant along arctic coast east to Novaya Zemlya and Mys Bolvanskiy; absent from the Mediterranean, except for former, or sporadic, occurrences in the western part (Strait of Gibraltar, Islas Baleares, Barcelona, and Tunisia). An apparently isolated population ranges along the coast of West Africa from Agadir (30°30′N), Morocco, south to Dakar (14°38′N), Senegal; its members appear to attain a greater body length than the European individuals do (Fraser 1958, Smeenk *et al.* 1992). Another geographically disjunct population inhabits the Black Sea, the Sea of Azov, the Bosporus, and the Sea of Marmara, with at least one individual reported in the northern Aegean Sea.

P. p. subsp.—Western North Pacific Ocean. Ranges from Olyutorskiy Zaliv south along the east coast of Kamchatka, including Komandorskiye Ostrova and the Near Islands in the western Aleutian Islands, throughout the Ostrova Kuril'skiye, and all around the shores of the Sea of Okhotsk, including Zaliv Shelikhova, Hokkaido, and Honshu as far as Nishiyama on the west coast and Taiji on the east (an alleged stranding of 109 individuals on Taiwan needs verification); vagrant north through Bering Strait as far as Ostrov Vrangelya. A distributional gap in the Aleutian Islands between Shemya and Unimak separates this race from the next.

P. p. vomerina Gill, 1865—Eastern North Pacific Ocean. Ranges from the Pribilof Islands, Unimak Island, and the southeastern shore of Bristol Bay south to San Luis Obispo Bay, California; vagrant north to Point Barrow in Alaska, and the mouth of the Mackenzie River in the Northwest Territories of Canada, and south to San Pedro in Southern California.

Phocoena sinus Norris and McFarland, 1958 (Golfo de California porpoise; pygmy porpoise; vaquita; cochito).

Endemic to the head of the Golfo de California, from Puertecitos, Baja California Norte, north and east to Puerto Peñasco, Sonora. (Reports from farther south have never been confirmed.)

Phocoena spinipinnis Burmeister, 1865 (black porpoise; Burmeister's porpoise).

West coast of South America from Paita (05°11′S), Peru, south to Valdivia (39°46′S), Chile; east coast of South America from Santa Catarina (28°48′S), Brazil, south to Chubut (42°25'), Argentina; coastal waters around Tierra del Fuego. (A specimen from Heard Island alleged to be *P. spinipinnis* was reidentified as *P. dioptrica*—Brownell *et al.* 1989.)

Phocoena dioptrica Lahille, 1912 (spectacled porpoise).

Coastal waters of southeastern South America, from Santa Catarina in Brazil, south to Tierra del Fuego; the Falkland Islands [=Islas Malvinas]; South Georgia; Îles Kerguelen; Heard Island; Tasmania; Macquarie Island; Auckland Islands; Antipodes Islands.

Genus PHOCOENOIDES Andrews, 1911

Phocoenoides dalli (True, 1885) (Dall's porpoise; True's porpoise; whitesided porpoise; whitefin porpoise).

The species-group name was misspelled *dallii* in the third edition of this list (Rice 1977).

Dall's porpoises are polymorphic for pigmentation pattern. There are two predominant morphs, or color phases, the Dalli-phase and the Truei-phase, which differ most obviously in the anterior extent of the white patch on the flanks and belly (Houck 1976,[17] Kasuya 1982, Miyazaki *et al.* 1984, Miyashita and Kasuya 1988). Formerly these color phases were thought to be separate species. Much rarer are all-black, all-gray, all-white, and intermediate Dalli-Truei phases (Morejohn *et al.* 1973, Morejohn 1979, Joyce *et al.* 1982, Rice unpublished field notes). Geographical variation in the color-phase ratio is sufficient to permit the recognition of two subspecies (Tomilin 1957, Nishiwaki 1972, Morejohn 1979). There is minor geographical variation in the color pattern of Dalli-phase animals, with the most distinctive individuals in the Sea of Japan [East Sea] (Amano and Miyazaki 1996). Skull size also varies geographically, averaging smaller in animals from the open ocean than in animals from the Sea of Japan, the Sea of Okhotsk, the Bering Sea, and the coast of California (Amano and Miyazaki 1992*b*).

P. d. dalli—These populations consist of >99% Dalli-phase and <1% Truei-phase animals (Kasuya 1982). They range in subarctic waters from the southeastern Sea of Okhotsk, the southern Bering Sea, and the northern Gulf of Alaska, south to the Sea of Japan [=East Sea], the Subarctic Boundary at about 42°N across the North Pacific, and in the California Current to about 32°N off Baja California Norte, except in the area occupied by the next subspecies. Mainly an offshore deepwater inhabitant, but occurs in narrow channels and fjords where the water is clear and relatively deep, such as those in Prince William Sound and around the Alexander Archipelago in Alaska.

[17] Houck, W. J. 1976. The taxonomic status of the species of the porpoise genus *Phocoenoides*. FAO Scientific Consultation on Marine Mammals, Bergen, Norway. Document ACMRR/MM/SC/114. 13 pp.

P. d. truei Andrews, 1911—This population consists of <5% Dalli-phase and >95% Truei-phase animals (Kasuya 1982). It ranges in a limited area of the western North Pacific immediately east of the southern Ostrova Kuril'skiye, Hokkaido, and the Sanriku coast of Honshu.

Order SIRENIA

Illiger (1811) erected the family Sirenia in the order Natantia to embrace the sea-cows. Subsequent authors raised Illiger's family name to ordinal rank. The noun Sirenia derives from the Latin *Siren,* plus *-ia,* neuter plural of the Latin adjectival suffix *-ium,* which means 'characteristic of' or 'resembling.' The Sirens of Classical Greek and Roman mythology were creatures half-woman, half-bird, who lived on an island where their dulcet songs lured mariners onto the reefs. In the Middle Ages, some authors confused the Sirens with mermaids, who were half-woman, half-fish. European explorers who first encountered manatees and dugongs imagined that they were mermaids because of their pectoral breasts and fish-like tail.

Through the middle of the 19th century, most naturalists referred to the sirenians as the "herbivorous cetacea." Gray (1821) classified them as order Herbivoræ under the class Cetaceæ, while Cuvier (1836) classified them as tribe Phytophaga under the order Cetacea, and Burmeister (1837) classified them as family Sireniformia under the order Cetacea. Other names bestowed on the group were Anthropocephala and Manatides by Billberg (1827), and Trichechiformes by Hay (1923).

The Sirenia are now recognized as members of a clade called Tethytheria, which also includes the Proboscidea and the Desmostylia (McKenna 1975, Domning *et al.* 1986, Kleinschmidt *et al.* 1986, Tassy and Shoshani 1988, Irwin and Wilson 1993, Fischer and Tassy 1993, Fischer 1996, Lavergne *et al.* 1996, Lowenstein and Shoshani 1996). The order Proboscidea includes the living elephants along with their extinct relatives—all terrestrial, the moeritheres, numidotheres, barytheres, deinotheres, gomphotheres, mastodons, and mammoths (Shoshani 1996, Tassy 1996).

Their morphology places the Tethytheria as the sister-group to the Perissodactyla, or odd-toed ungulates (Prothero *et al.* 1988, Prothero and Schoch 1989), although the cytochrome *b* gene failed to support this relationship (Irwin *et al.* 1991). Another group, the still-living hyraxes of Africa, order Hyracoidea, is a much-contested relative of the Tethytheria, with which it is sometimes grouped in a higher taxon called Paenungulata. Placement next to the tethytheres is corroborated by studies of their morphology (Novacek *et al.* 1988), myology (Shoshani 1993), the 12S rRNA gene in the mtDNA (Springer and Kirsch 1993, Lavergne *et al.* 1996), and hemoglobin (Kleinschmidt *et al.* 1986), and appears to be the more strongly-supported hypothesis (Shoshani 1992), although it is contradicted by other morphological studies which place hyraxes in the Perissodactyla (Fischer 1989, Prothero and Schoch 1989, Fischer and Tassy 1993). A recent analysis of nucleotide sequences of two nuclear and three mitochondrial genes placed the Tethytheria within in a larger "African" clade that includes not only the hyraxes but also the aardvarks (order Tubulidentata), elephant-shrews (order Macroscelidea), and golden-moles (family Chrysochloridae of order Insectivora) (Springer *et al.* 1997).

The Desmostylia were one of the two orders of marine tethytheres. Long known only from skulls, their systematic position was disputed; some taxonomists (VanderHoof 1937, Simpson 1945) placed them as a suborder of the Sirenia; Now, with more specimens—including complete skeletons—available, authorities are unanimous in ranking them as a separate order. Five genera have been described, but their family-level classification remains in abeyance (Domning 1996). Desmostylians were hippo-like amphibious creatures that were confined to shallow coastal waters around the North Pacific from the middle or late Oligocene to the early Pliocene (Domning *et al.* 1986, Reinhart 1959, Ray *et al.* 1994); specimens purported to be from Florida (Reinhart 1976) almost certainly came from California (Morgan 1994). Their distinctive teeth indicate that the desmostylians fed on seagrasses and perhaps algae.

The Sirenia are the only surviving tethytheres that live in the sea, although manatees inhabit fresh water as well. They are also the only herbivorous marine mammals. The sirenians appear to have arisen as the sister-group to *Moeritherium,* a terrestrial beast that inhabited freshwater swamps in North Africa during the Eocene and Oligocene (Savage *et al.* 1994). The most archaic known sirenians are the Eocene *Prorastomus sirenoides* (Family Prorastomidae) from the West Indies and three species of *Protosiren* (Family Protosirenidae) from Europe, Pakistan, and North Africa; bones from the Eocene of North Carolina and Florida that were formerly attributed to *Protosiren* sp. (Domning *et al.* 1982) are now thought to be from primitive dugongids (Domning and Gingerich 1994). *Prorastomus* and *Protosiren* are believed to have been quadrupedal amphibious creatures that lived along the seacoasts (Domning and Gingerich 1994; Savage *et al.* 1994).

The more advanced sirenians, including the living manatees and dugongs, lost the hind limbs and acquired horizontal tail flukes—paddle-shaped in the manatees, lunate like those of cetaceans in the dugongids. The earliest of these were seven species assigned to the genera *Eotheroides, Eosiren,* and *Prototherium,* which lived in North Africa and Europe from the middle Eocene to the early Oligocene. Although Domning (1994) left them in the family Dugongidae, his cladogram places them as basal branches of the lineage that gave rise to the post-Eocene Dugongidae and Trichechidae. The trichechids remained confined to inshore waters on both sides of the Atlantic Ocean, while the dugongids dispersed widely in coastal waters around the Atlantic, Indian, and Pacific oceans.

Important earlier works on systematics of the Sirenia were published by Simpson (1932, 1945), Sickenberg (1934), and Reinhart (1959). Cladistic analyses of all genera—living and fossil—were done by Domning (1994) and Savage (1976), and an analysis of the genera of the subfamily Dugonginae was made by Bajpai and Domning (1997). Domning (1994, 1996) provided an updated but provisional classification; however it is not entirely congruent with his cladogram, in that his "Dugongidae" are a paraphyletic assemblage. Immunological distances among the five Recent species of sirenians agree with their conventional taxonomy (Rainey *et al.* 1984).

Family TRICHECHIDAE Gill, 1872

Manatidae Gray 1821:309 (The type genus *Manatus* Brünnich, 1772, is a junior synonym of *Trichechus*, so the family name is invalid because it was replaced prior to 1961 (Article 40(b) of the ICZN Code))

Trichechidae Gill 1872:14 (Type genus: *Trichechus* Linnaeus, 1758, not *Trichechus* Linnaeus, 1766 [=*Odobenus* Brisson, 1762]; not Trichecidae [*sic*] Gray, 1821:302 [=Odobenidae])

Genus TRICHECHUS Linnaeus, 1758

The living manatees are included in the subfamily Trichechinae (Domning 1994). There are three allopatric species (Domning and Hayek 1986, Hatt 1934). The range of *Trichechus senegalensis* is widely separated, but the freshwater *T. inunguis* and the marine *T. manatus* are parapatric at the mouths of the Amazon, with no evidence of hybridization (Domning 1981). A possible reproductive isolating mechanism is the difference in chromosome numbers—2n=48 in *T. manatus*, 2n=56 in *T. inunguis* (Loughman *et al.* 1970, White *et al.* 1976).

The English name "manatee" is ultimately derived from *manati*, which is not, as often stated, the Arawak name for the animal, but rather the Arawak word for a woman's breast; the allusion is presumably to the animal's single pair of pectoral mammae. The manatee itself was called by variants of the word *kuyumuru* in most of the Arawak and Carib languages (Simpson 1941).

Trichechus manatus Linnaeus, 1758 (Caribbean manatee; West Indian manatee; Florida and Antillean manatees).

There are two well-defined subspecies (Domning and Hayek 1986, Hatt 1934). They are geographically separated by the cold northern coast of the Gulf of Mexico and by the wide, deep Gulf Stream between Florida and Cuba (although occasional sightings of manatees along the northern and northwestern coasts of the Gulf of Mexico, and near the Dry Tortugas, suggest that there may be some interchange between the two populations).

T. m. latirostris (Harlan, 1824)—Lagoons, bays, estuaries, and the lower reaches of coastal waterways (including man-made canals) around the entire Florida peninsula, from Florida Bay north to the mouth of the Suwannee River on the west coast, and to Jekyll Island, Georgia, on the east coast; also the Suwannee River upstream to its confluence with the Santa Fe River, the St. Johns River upstream to Blue Springs, and the Caloosahatchee River upstream into Lake Okeechobee. In summer disperses west to Alabama, Mississippi, and Louisiana, and north to the Carolinas, Virginia, Maryland, New Jersey, Connecticut, and Rhode Island; the manatees that have occasionally been found in the Bahamas (Grand Bahama and the Bimini Islands) appear to be vagrants from Florida, rather than residents. A dead manatee (most likely from Florida) washed ashore in the Firth of Forth, Scotland, in 1785 (Stewart 1817).

T. m. manatus—Coastal waters all along the mainland coast, including the lower reaches of rivers, from Soto la Marina in Tamaulipas, Mexico, south to Lago de Maracaibo, Venezuela, including the lower and middle reaches of the Río Atrato and Río Magdalena in Colombia (absent from Venezuelan coast east of Lago de Maracaibo as far as Golfo de Paria); the Greater Antilles (Cuba, Jamaica, Hispaniola, and Puerto Rico), the Lesser Antilles (at least the Virgin Islands, St. Kitts, Barbuda, Antigua, Marie-Galante, Martinique, St. Lucia, and Grenada), and Trinidad, thence along the mainland coast from the mouth of the Río Orinoco southeast to Cabo Norte, just north of the Amazon, in Amapa, Brazil, and including the lower and middle reaches of the Río Orinoco system. There are, or were, disjunct populations south of the Amazon, along the Rio Mearim in Maranhão, and from the Rio Sao Francisco in Alagoas south to the Rio Doce in Espirito Santo, Brazil. (The intervening area at the mouths of the Amazon is inhabited by *T. inunguis*). Vagrant north to Texas and Louisiana. (The manatees in the Panama Canal, including Gatún Lake, and occasionally in adjacent Pacific waters, are descended from individuals that were introduced into the Río Chagres in 1963, and are not the result of unassisted natural dispersal—Montgomery *et al.* 1982.)

Trichechus senegalensis Link, 1795 (African manatee; West African manatee).

The lower and middle reaches of the major river systems of West Africa: the Senegal, Gambia, Bandama, Volta, Niger-Benue, Sanaga, Ogoué, lower Congo, and Cuanza; also along the coast, including many small coastal rivers, from Senegal south to Angola. There is an isolated population in the upper Niger from Timbuktu to Ségou, Mali (2000 km upstream from the mouth), and another in the Benue from at least Numan, Nigeria, upstream to its tributary the Kebbi, and thence as far as Lac Léré in Chad (1,500 km from the sea). In the Congo River, the cataracts below Kinshasa are an obstacle to their movement farther upstream, but in the past specimens were captured at least occasionally in the Sangha and its major tributary the Likouala aux Herbes, which are a branch of the middle Congo; they presumably reached the Sangha through a link between its headwaters and the upper tributaries of the Sanaga in Cameroon. Manatees were also said to occur in the Uele and Mbomou rivers, branches of the upper Ubangi, which is another branch of the middle Congo River upstream from its junction with the Sangha. Formerly they allegedly occurred in the Chari and its tributaries the Bahr Keita and the Bamingui—a part of the endorheic Lake Chad drainage, which they could have reached during the frequent inundations of the low-lying divide between the headwaters of the Benue and Chari systems. The alleged presence of manatees at the island of St. Helena in the 17th century was based on the misidentification of elephant seals (Fraser 1934; Mortenson 1934).

Derscheid (1926), followed by Kleinschmidt (1982), listed the freshwater populations as a separate subspecies, *T. s. vogelii* (Owen, 1857), but there is no empirical support for such a taxonomic split (Domning and Hayek 1986).

Trichechus inunguis (Natterer, 1883) (Amazon manatee).

Exclusively freshwater. Throughout almost the entire Amazon River drainage (below an elevation of about 200 m). At the mouths of the Amazon, *T. inunguis* comes in contact with *T. manatus,* which occurs along the coast to the north and south. A disjunct population inhabits the upper Essequibo River and its tributary the Rupununi River in Guyana; only 10 km of flat lowland separates the upper Rupununi from a tributary of the Takatu River, which drains through the Rio Branco and the Rio Negro into the Amazon. (Reports of *T. inunguis* from the Río Orinoco are erroneous; the manatees in the Orinoco are *T. manatus*—Mondolfi 1974).

Family DUGONGIDAE Gray, 1821

Dugongidæ Gray 1821:309 (Type genus: *Dugongidus* Gray, 1821, an incorrect subsequent spelling of *Dugong*)
Halicoridæ Gray 1825:341 (Type genus: *Halicore* Illiger, 1811 [=*Dugong*])
Rhytineae Brandt 1833:115 (Type genus "*Rhytina*" [=*Rytina*] Illiger, 1811; incorrect original spelling; the type genus is a junior synonym of *Hydrodamalis* Retzius, 1794, so the family name is invalid because it was replaced prior to 1961 (Article 40(b) of the ICZN Code))
Rytinadae Gray 1843:xxiii (not p. 107, *contra* Simpson 1945) (=Rhytineae; justified emendation)
Hydrodamalidae Palmer 1895:450 (Type genus: *Hydrodamalis* Retzius, 1794)

The two Recent genera are assigned to different subfamilies (Domning 1994).

Subfamily DUGONGINAE Gray, 1821

Genus DUGONG Lacépède, 1799

Dugong dugon (Müller, 1776) (dugong).

Gohar (1957) found that the dugongs of the Red Sea are smaller and differ in other respects from those of the Indo-Australian region, and he considered them a separate subspecies. Some authors have also separated the dugongs of the Australian region as *D. d. australis* Owen, 1847. Dollman (1933) did find that the dugongs from Australia have larger and more massive skulls than do the animals from Tanzania, but recognition of an additional subspecies cannot be justified until more specimens from other parts of the dugong's range have been measured. Spain and Marsh (1981) found statistically significant differences in skull measurements between dugongs from Wellesley Island in the Gulf of Carpentaria and those from Townsville on the east coast of Queensland.

D. d. hemprichii (Ehrenberg, 1833)—Gohar (1957) called this race *D. d. tabernaculi* (Rüppell, 1834), but Ehrenberg's name has priority, as pointed out by Yalden *et al.* (1986). Ranges throughout the Red Sea from the gulfs of Suez and Aqaba south to the Bāb al Mandab. (On at least one occasion a dugong has transited the man-made Suez Canal and reached the coast of Palestine [now Israel] (Anonymous 1945); there was an earlier report (Aharoni 1930) of a dugong captured "in a shore cave, but the possibility of this having been a monk seal should not be overlooked" (Allen 1942)).

D. d. dugon—Widespread but discontinuous along the continental coasts and among the islands of the Indian and western Pacific oceans. Its mainland range includes the east coast of Africa from the Gulf of Aden south to Maputo (25°58′S) in Mozambique; Persian Gulf [=Arab Gulf]; coast of Pakistan and western India south around Cape Comorin to Point Calimere on the east coast; coast of Myanmar [=Burma] southward around the Malay Peninsula and north into the Gulf of Thailand; southeastern coast of Vietnam; and the Gulf of Tonkin. Its insular range includes the Comoros; Madagascar; Mauritius; Rodriguez; Socotra; Laccadive Islands; Sri Lanka; Andaman Islands; Nicobar Islands; Mergui Archipelago; Ryukyu Retto north to Amami O-shima (28°30′N); Taiwan; Philippines; and all the islands on and east of the Sunda Shelf as far as Guam, Yap, Palau, Pohnpei [=Ponape], New Guinea, the Bismarcks, the Solomon Islands, Vanuatu [=New Hebrides], Nouvelle Calédonie, and northern Australia south on the west coast to Shark Bay (26°00′S) and on the east coast to Moreton Bay (27°30′S). Vagrant south to Umhlali (29°30′S) in Natal, Albany (34°57′S) in Western Australia, Tathra (36°44′S) in New South Wales, and east to the Fiji Islands. There are no credible records from the Seychelles, the Chagos Archipelago, the Maldives, the Marshall Islands, Kiribati [=Gilbert Islands], or Tuvalu [=Ellice Islands].

Subfamily HYDRODAMALINAE Palmer, 1895

Evolution of this subfamily was expounded by Domning (1978).

Genus HYDRODAMALIS Retzius, 1794

Hydrodamalis gigas (Zimmermann, 1780) (Steller's sea-cow; great northern sea-cow; kapustnik; morskaya korova; rhytina).

The vernacular names *kapustnik,* or 'cabbage-eater'—which alludes to the sea-cow's diet of seaweed, locally called *morskaya kapusta* ('sea cabbage')—and *morskaya korova,* or 'sea cow,' were used by the Russian-speaking Kamchadals. Georg Wilhelm Steller, a German who accompanied Vitus Bering's second expedition, was the only scientist who ever saw the species in life; he simply called it the *manati,* or sometimes *vacca marina* (Latin: 'sea cow'), *seekuh* (German: 'seacow'), or *krautfresser* (German: 'cabbage-eater'). *Rhytina* is a Modern Latin name coined from the Greek noun ῥυτις, genitive ῥυτιδος (*rhutis, rhutidos*) 'wrinkle,' and the Latin suffix *-ina* 'like,' in allusion to the animal's wrinkled hide.

EXTINCT since 1768. As a living animal, known only from shallow waters surrounding Ostrov Beringa and Ostrov Mednyy in Komandorskiye Ostrova (which never had an aboriginal human population). Discovered by Europeans in 1741, the species was extirpated on Ostrov Mednyy by 1754, and on Ostrov Beringa by 1768. Natives of Kamchatka sometimes found dead individuals washed ashore between Kronotskiy Paluostrov and Avachinskaya Guba (Steller 1751), and a rib was found on Attu, the westernmost island of the Aleutians, in 1842 or 1843 (Brandt 1861–1868). Late Pleistocene remains were unearthed on Amchitka Island in the Aleutians (135,000 B.P.) (Gard *et al.* 1972, Whitmore and Gard 1977) and in Monterey Bay, California (19,000 B.P.) (Jones 1967). An alleged sighting of six sea-cows off Mys Navarin in the northwestern Bering Sea in July 1962 (Berzin *et al.* 1963) has been discredited (Heptner 1965).

APPENDIX 1

Bats and Fissiped Carnivores in Marine Waters

Besides the members of the three primarily marine groups of mammals listed above, several species of bats and fissiped carnivores have taken to living in marine waters—either facultatively of obligatorily.

Order CHIROPTERA

Bats fall into two suborders. The Megachiroptera include the one family of flying-foxes, or "megabats," most of which are fruit-eaters. The Microchiroptera include 16 families of "microbats." The majority of the latter are insectivores, but many others occupy a broad spectrum of ecological niches, where they may feed on fruit, nectar, and pollen, prey on lizards, birds, and rodents, or even take blood from birds and mammals. A few species have taken to preying on fishes and other small aquatic animals, but of those that do, only two forage in marine waters—one opportunistically, the other exclusively. Both have greatly enlarged feet and claws—an adaptation for gaffing fish (Bloedel 1955).

One other species of bat that enters the marine food web in a small way is *Desmodus rotundus* (E. Geoffroy, 1810), one of the three vampire bats of the subfamily Desmodontinae (family Phyllostomidae). On the beaches of northern Chile, sea-lions are the preferred victims of these bats (Mann 1950, 1955). As documented in the BBC-TV television program *Flight of the Condor,* 1982, the vampires feed on blood which they lap from lesions that they inflict on the hind flippers of the sea-lions (Andrews 1982).

Family NOCTILIONIDAE Gray, 1821

Noctilionidæ Gray 1821:299 (Type genus: *Noctilio*)

This family contains one genus.

Genus NOCTILIO Linnaeus, 1766

The greater bulldog bat feeds almost exclusively on fishes, frogs, and other aquatic organisms, from both fresh and salt water (Schnitzler *et al.* 1994). Coastal populations regularly forage over inshore marine waters, often in company with mixed flocks of sea birds (Benedict 1926, Goodwin 1928, Gudger 1945). The only other species of this genus, *N. albiventris* Desmarest, 1818, is mainly insectivorous.

Noctilio leporinus (Linnaeus, 1758) (greater bulldog bat)

Davis (1973) recognized three subspecies:

N. l. mastivus (Vahl, 1797)—From Sinaloa and Veracruz in Mexico south through Central America to northern Ecuador, Colombia, and Venezuela; Cuba; Jamaica; Hispaniola; Puerto Rico; many islands in the Lesser Antilles.

N. l. leporinus—Eastern Ecuador, northern Peru, northern Brazil, and the Guianas, south throughout the Amazon Basin.

N. l. rufescens Olfers, 1818—from eastern Bolivia, Paraguay, and southern Brazil, south to northeastern Argentina.

Family VESPERTILIONIDAE Rafinesque, 1815

Vespertilia Rafinesque 1815:54 (Type genus: *Vespertilio* Linnaeus, 1758)

Vespertilionidæ Gray 1821:299 (Type genus: *Vespertilio* Linnaeus, 1758)

This is the largest family of bats, containing about 318 species arranged in 35 genera.

Genus MYOTIS Kaup, 1829.

With about 84 species distributed on all the world's landmasses except for Micronesia, Polynesia, and Antarctica, *Myotis* is one of the largest genera of bats. Three or four species catch fish in freshwater, but *M. vivesi* is the only one which fishes at sea, where it has been seen following trawlers as far as 7.8 km from land (Reeder and Norris 1954, Patten and Findley 1970).

M. vivesi was long maintained in its own genus, *Pizonyx* Miller, 1906, because of its enormously enlarged feet (Miller and Allen 1928). Patten and L. T. Findley (1970) reduced *Pizonyx* to a subgenus of *Myotis,* and J. S. Findley (1972) synonymized it with subgenus *Leuconoe* Boie, 1830, which contains 29 other species (Koopman 1993), all with relatively large feet.

Myotis vivesi Menegaux, 1901 (fishing bat)

West coast of Baja California from Punta Malarrimo to Puerto San Bartolomé; coasts and islands in the Golfo de California from Isla Encantada and Isla San Jorge south to Bahía Rosario (24°15′N) and Guaymas.

Order CARNIVORA

All members of the Carnivora other than the pinnipeds were formerly included in suborder Fissipeda (or Fissipedia), a paraphyletic grouping no longer recognized formally, but "fissiped" remains a handy adjective. Listed below are those species of fissiped carnivores that are dependent on the marine environment (polar bear and two otters) or are facultative inhabitants of marine waters.

In addition to the listed species, at least eleven other species of terrestrial carnivores now and then prey on marine mammals, and thus become a direct link in the marine food chain; some of them are also noted for scavenging marine mammal carcasses on beaches. Pinnipeds usually remain out of reach of these terrestrial carnivores because they haul out mostly on sea ice, oceanic islands, offshore rocks, or beaches at the foot of steep cliffs; however they do become vulnerable when they haul out on mainland beaches or on shorefast ice. Under such circumstances, these predators sometimes exert noticeable influence on local pinniped populations. There are published accounts of predation by cougars *Puma concolor* on South American sea-lions (Brandenburg 1938); by jaguars *Panthera onca* on Amazon manatees (Pereira 1944) and Amazon river-dolphins (Hoogesteijn and Mondolfi 1993); by lions *Panthera leo* (Bridgeford 1985), brown hyenas *Parahyaena brunnea* (David 1987), and black-backed jackals *Canis mesomelas* (David 1987) on Cape fur-seals; by gray wolves *Canis lupus* on bearded seals (Popov 1982); by coyotes *Canis latrans* on harbor seals (Steiger *et al.* 1989) and sea otters (Riedman and Estes 1990); by red foxes *Vulpes vulpes* on ringed seals (Andriashek and Spencer 1989); by the extinct Falkland Islands "wolf" *Dusicyon australis* on fur-seals and sea-lions (Allen 1942); by brown and grizzly bears *Ursus arctos* on bearded seals (Popov 1982), ringed seals (Stirling 1988), and sea otters (Riedman and Estes 1990); and by wolverines *Gulo gulo* on ringed seals (Burns 1970).

Family CANIDAE Fischer, 1817

Canini Fischer 1817:372 (Type genus: *Canis* Linnaeus, 1758)

Vulpini Ehrenberg 1833:decas II, folio ff (Type genus: *Vulpes*)

There are 36 species of living or recently extinct dogs, wolves, and foxes, classified in 14 genera, but the arctic fox is the only one that exploits the marine ecosystem. All of the living species of canids fall into the subfamily Caninae, which may be divided into two tribes, Vulpini for the foxes, and Canini for the more wolf-like species, including all the South American genera (Tedford *et al.* 1995).

Genus VULPES Frisch, 1775

Mainly because most populations acquire white pelage in winter, the arctic fox has customarily been segregated in the monotypic genus *Alopex* Kaup, 1829, except by Bobrinskii (1965*a*) and Youngman (1975), who included it in *Vulpes* with most of the other foxes. A cladistic analysis of morphological features of living canids by Tedford *et al.* (1995) placed the arctic fox within the *Vulpes* clade; if it were excluded from the genus *Vulpes,* the latter would be rendered paraphyletic. The fossil record of the arctic fox goes back only as far as the Riss glaciation in Europe and the Wisconsin glaciation in the Yukon; it is obviously descended from a species of *Vulpes,* most likely the early Pleistocene *Vulpes alopecoides* (Kurtén 1968, Kurtén and Anderson 1980). Isozyme genetic distances (Wayne and O'Brien 1987), mtDNA sequences (Geffen *et al.* 1992, Mercure *et al.* 1993), and karyotypes (Mäkinen and Gustavsson 1982, Yoshida *et al.* 1983, Wayne *et al.* 1987) reveal that the arctic fox is the nearest relative of two of the species of *Vulpes,* the swift fox *V. velox* and the kit fox *V. macrotis,* which inhabit the plains and deserts of western North America. Hybridization between arctic foxes and red foxes *Vulpes vulpes* has frequently taken place in captivity, despite a difference in chromosome number; hybrids average 2n=43 chromosomes, *versus* 34 to 38 in the red fox and 48 to 52 in the arctic fox (Wipf and Shackleford 1949, Chiarelli 1975, Geffen *et al.* 1992). Some workers report that the hybrids are sterile in both sexes, others report that they are fertile among themselves and in backcrosses to the parental species (Gray 1954).

Vulpes lagopus (Linnaeus, 1758) (arctic fox; white fox; blue fox; polar fox; ice fox)

This species occurs in two color phases, or morphs, "white" foxes, which are brownish-gray with lighter underparts in summer and turn white in winter, and "blue" foxes, which are more uniformly grayish year-round. Color phase is controlled by a single autosomal gene incompletely dominant for blue, so that heterozygous blue foxes are slightly paler than homozygous ones (Boitsov 1937, Slagsvold 1949, Johansson 1960). The proportion of the two phases varies geographically (Fetherston 1947, Chesemore 1970).

Ecologically, these foxes fall into two groups (Braestrup 1941, Vibe 1967): "Tundra foxes," or "lemming foxes," almost all of which are in the white phase, depend on lemmings (*Lemmus* spp. and *Dicrostonyx* spp.) or other arvicoline rodents as their primary food while on land, but also take hares (*Lepus* spp.), ptarmigan (*Lagopus* spp.), ground squirrels (*Spermophilus* spp.) and other birds and mammals, and scavenge caribou (*Rangifer tarandus*) killed by wolves; while on the pack ice they scavenge polar bear kills (Chesemore 1968), and prey on ringed seal pups in their subnivean lairs (Freuchen 1935, Stirling and Smith 1975, Smith 1976, Riewe 1977). "Coast foxes," the majority of which are blue, prey mainly on colonial sea birds and their eggs during the summer; during winter and spring marine mammal carrion is their most important food (West 1987, Fay and Stephenson 1989); they also consume other carrion, fish, and marine invertebrates.

The tundra foxes that live throughout the mainland of northern Eurasia and North

America and on the arctic islands, are medium-sized, with a slight tendency for cranial size to decrease with increasing latitude, but all are sufficiently similar to include in one subspecies, *V. l. lagopus* (Ognev 1931, Rausch 1953, Novikov 1956, Heptner *et al.* 1967, Gromov and Baranova 1981, Frafjord 1993, Tsalkin 1944, Vibe 1967, Youngman 1975). The coast foxes that live on islands in the Bering Sea are substantially larger than tundra foxes, whereas those that live on the shores of the North Atlantic are generally smaller. Genetic introgression occurs when drifting ice carries tundra foxes into the ranges of coast foxes, so the most sharply differentiated coast foxes live on islands beyond the normal limits of the winter pack ice.

In North America, only two subspecies of arctic fox are recognizeable, *V. l. lagopus* for the tundra foxes, and *V. l. pribilofensis* Merriam, 1902, for the blue foxes on the Pribilof Islands (Rausch 1953, Pengilly *in* Frafjord 1993). In the old world, most Russian authorities recognize only three races: the nominate tundra race, *V. l. spitzbergenensis* (Barrett-Hamilton and Bonhote, 1898) for the small blue foxes in the Atlantic-Arctic, and *V. l. beringensis* Merriam, 1902, for the large blue foxes on the Komandorskiye Ostrova (Gromov *et al.* 1963, Gromov and Baranova 1981), but some further distinguish *V. l. semenovi* (Ognev, 1931) of Ostrov Mednyy from *V. l. beringensis* of Ostrov Beringa (Ognev 1931, Heptner et *al.* 1967). The genetic constitution of the foxes on Ostrov Beringa may have been compromised when "Arctic foxes of alien subspecies were introduced to Bering Island earlier this century" (Goltsman *et al.* 1996). Adequate series of specimens of blue foxes from the Komandorskiye and Pribilof populations have not been critically compared with each other since Merriam (1902) described each population as an endemic species; the differences between *V. l. beringensis* and *V. l. pribilofensis* are slight (Vibe 1967), and they may well be synonymous. For the North Atlantic coastal foxes, it should be noted that the name *V. l. fuliginosus* (Bechstein, 1799), applied to Icelandic specimens, has priority over *V. l. spitzbergenensis.* A dissenting taxonomic opinion was expressed by Stroganov (1962), who treated *V. lagopus* as monotypic.

V. l. lagopus—Throughout the circumpolar arctic tundra. On the Eurasian mainland from the mountains of Scandinavia east to the Chukotskiy Poluostrov and Kamchatka, and on the mainland of North America from western Alaska east to Labrador. Also Novaya Zemlya, Severnaya Zemlya, Novosibirskiye Ostrova, Ostrov Vrangelya, Hall Island, St. Matthew Island, St. Lawrence Island, the Diomede Islands, throughout the Canadian Arctic Archipelago, and northern and northeastern Greenland from Washington Land east and south to Scoresby Sund. In winter and spring, many of the arctic coastal animals make extended forays onto the sea ice; they have been sighted as far as 89°11'N—only 91 km from the North Pole. During years when lemming populations crash, tundra foxes emigrate far south into the taiga zone. This race or one of the Bering Sea races has been introduced by man to many of the small islands in Zaliv Petra Velikogo [=Peter the Great Bay], Shantarskiye Ostrova, Ostrova Kuril'skiye, Aleutian Islands, Shumagin Islands, the vicinity of Kodiak Island, Prince William Sound, and the Alexander Archipelago.

V. l. fuliginosus (Bechstein, 1799)—Western, southern, and southeastern Greenland north to Thule on the west coast and Knud Rasmussens Land on the east coast; Iceland; Jan Mayen; Svalbard; Zemlya Frantsa Iosifa; and the coast of northern Scandinavia. (All of these areas lack lemming populations.)

V. l. beringensis Merriam, 1902—Ostrov Beringa and Ostrov Mednyy in Komandorskiye Ostrova.

V. l. pribilofensis Merriam, 1902—St. Paul Island and St. George Island in the Pribilofs. Perhaps inseparable from *V. l. beringensis* (see above).

Family URSIDAE Fischer, 1817

Ursini Fischer 1817:372 (Type genus: *Ursus*)

The living ursids are the giant panda (*Ailuropoda melanoleuca*) and seven species of bears. In the past, a monotypic genus was recognized for each species of bear, the polar bear being separated into genus *Thalarctos* Gray, 1825 (or *Thalassarctos* Gray, 1825). However, it has been found that the polar bear and the brown, or grizzly, bear *Ursus arctos* are more closely related to each other than either is to any other species of bear. The polar bear does not appear in the fossil record until the beginning of the Würm glaciation, and the split between the brown and polar bears probably occurred no earlier than the middle Pleistocene (Thenius 1953, Kurtén 1964, Vereshchagin 1969, Hendey 1972). Allozymes (Goldman *et al.* 1989), mtDNA (Shields and Kocher 1991, Zhang and Ryder 1994, Talbot and Shields 1996*b*) and karyotypes (Nash and O'Brien 1987) are also consistent with a very recent divergence between the two species. Cladograms based on the mtDNA show that *Ursus arctos* is paraphyletic with respect to *U. maritimus,* with the polar bear being most closely related to the populations of brown bears on the islands of southeastern Alaska, rather than to the inland forest and tundra populations of Alaska and eastern Siberia (Cronin *et al.* 1991, Talbot and Shields 1996*a*). These facts lead to the conclusion that the polar bear evolved rapidly from a small peripheral isolate of the brown bear population; Stanley (1979) cited it as an example of "quantum speciation." Hybrids between brown and polar bears have never been found in the wild, but in zoos male polar bears have crossbred with female brown bears; matings between their hybrid offspring, and backcrosses to both parental species, have produced vigorous young (Davis 1950; Gray 1954; Kowalska 1969, 1973). Because of its close relationship to the brown bear, the polar bear is now included in the genus *Ursus* by all authors. Most taxonomists, in fact, now follow Erdbrink (1953), Hall (1981), Goldman *et al.* (1989), and O'Brien (1993) and include all of the living bears in one genus, *Ursus,* of the subfamily Ursinae, except for the distantly-related spectacled bear *Tremarctos ornatus* of South America, which is usually allocated to a separate subfamily, Tremarctinae; however a few workers (Hendey 1972; Wozencraft 1989*b,* 1993) still recognize separate genera for the sun bear (*Helarctos*) and the sloth bear (*Melursus*).

Genus URSUS Linnaeus, 1758

Ursus maritimus Phipps, 1774 (polar bear).

Pack-ice regions of the Arctic Ocean and contiguous seas, and adjacent coastal areas. Ranges across the entire Arctic basin as far as 1300 km from land, and has even been observed at the North Pole. Knottnerus-Meyer (1908) recognized six species and one additional subspecies of polar bears; Birulya (1932) reduced these seven forms to a single species with three subspecies, but now authorities agree that the living polar bears can be divided into only two, if any, subspecies. There is a circumpolar cline in skull size, with the smallest animals in East Greenland, the largest in the Chukchi and Bering seas (Chernyavskii 1969, Manning 1971, Wilson 1976, Uspenskii 1989). Ognev (1931), Novikov (1956), Stroganov (1962), Gromov *et al.* (1963), Heptner *et al.* (1967), Gromov and Baranova (1981) gave subspecific names to the two size extremes. Manning (1971) did not recognize any living subspecies, but suggested that the recently extinct population of large bears in the Bering Sea may merit subspecific status. Even larger bears, named *U. m. tyrannus* inhabited the British Isles at the end of the Pleistocene (Kurtén, 1964). Stirling (1988) suggested that the apparent geographical variation in size was an artefact caused by sampling bias, but he provided no supporting evidence for this idea.

U. m. maritimus—Maternity denning is concentrated in certain circumscribed localities, mostly on shore. These include the Simpson Peninsula in the Northwest Territories, eastern Southampton Island, eastern Baffin Island, northwestern Greenland, northeastern Greenland, eastern Svalbard, Zemlya Frantsa Iosifa, Novaya Zemlya, and Severnaya Zemlya. Range extends south to southern Labrador, southern Greenland, Bjørnøya, and Mys Kanin, Russia. Vagrant to Newfoundland, Anticosti Island, Saguenay River in Quebec, Iceland, and northern Norway.

U. m. marinus Pallas, 1776—Main denning areas are the Poluostrov Taymyr, Novosibirskiye Ostrova, Ostrova Medvezhi, Ostrov Vrangelya, Chukotskiy Poluostrov, the pack ice of the Beaufort Sea, northeastern Alaska and northern Yukon, and southern Banks Island. Range extends south into the Bering Sea as far as central Kamchatka, Komandorskiye Ostrova, St. Matthew Island, and Norton Sound. Vagrant to Pribilof Islands, Ostrova Kuril'skiye, northern Sea of Okhotsk, Sakhalin, and Hokkaido. Rarely wanders several hundred kilometers inland across tundra and even into taiga.

Family MUSTELIDAE Fischer, 1817

Mustelini Fischer 1817:372 (Type genus: *Mustela* Linnaeus, 1758)
Enhydrina Gray 1825:340 (Type genus: *Enhydra*; name suppressed by ICZN—see Appendix 2)
Lutrina Bonaparte 1838*a*:111 (Type genus: *Lutra*)
Latacina Bonaparte 1838*b*:213 (Type genus: *Latax* Gloger, 1827 [=*Enhydra*])
Lutridæ De Kay 1842:xv and 39 (Type genus: *Lutra*)
Enhydridæ H. Smith 1842:248 (Type genus: *Enhydra*)
Lataxinae Burmeister 1850:13 (Type genus: *Latax*)
Lutrinae Baird 1857:xxx, 148, and 183 (Type genus: *Lutra*)
Enhydrinae Gill, 1872:6 and 65 (Correction of Enhydrina Gray, 1825; spelling conserved by ICZN—see Appendix 2)
Mionictini Ginsburg 1968:232 (Type genus: *Mionictis* Matthew, 1924)
Aonyxina Sokolov 1973:51 (Type genus: *Aonyx*; incorrect original spelling)
Enhydriodonina Sokolov 1973:51 (Type genus: *Enhydriodon* Falconer, 1868; incorrect original spelling)
Aonychini Davis 1978:20 (Type genus: *Aonyx*)
Hydrictini Davis 1978:20 (Type genus: *Hydrictis*)
(Other family-group names based on terrestrial genera of mustelids are not listed)

Besides the amphibious otters, this family embraces a morphologically and ecologically diverse assemblage of small terrestrial carnivores, including the weasels, minks, ferrets, martens, wolverines, tayras, grisons, skunks, badgers, and ratels. The living mustelids have traditionally been classified in about five subfamilies (Simpson 1945). Some of these subfamilies are paraphyletic or polyphyletic, but monophyly of the otters, subfamily Lutrinae, is strongly supported by a number of synapomorphies (Berta and Morgan 1985, Bryant *et al.* 1993; Dragoo and Honeycutt 1997).

Pocock (1922), who split the living mustelids into 15 subfamilies, separated the sea otter and the other otters as subfamilies Lataxinae and Lutrinae, respectively; he was followed by Miller (1924), Anderson (1946), and Miller and Kellogg (1955), who called them subfamilies Enhydrinae and Lutrinae. Simpson (1945) merged the two subfamilies into one, which he called Lutrinae, evidently basing priority on the first use of each name at the rank of subfamily—Lutrinae Baird (1857) and Enhydrinae Gill (1872). Most subsequent authors followed Simpson's nomenclature, but Enhydrinae Gray, 1825, would have priority over Lutrinae Bonaparte, 1838, according to Article 23(c) of the present ICZN Code. Enhydrinae cannot be rejected as an "unused name" under the provisions of Article 23(b), because Miller (1924), Anderson (1946), Miller and Kellogg (1955) and Corbet (1978) all used it as a valid subfamily name, and more recently Gromov and Baranova (1981) and Pavlinov and Rossolimo (1987) used it as a valid tribal name, Enhydrini, under subfamily Lutrinae, despite its seniority over the latter name. Use of the name Enhydrinae instead of Lutrinae would upset prevailing usage, because for over a century, all otters other than the sea otter have always been included in subfamily Lutrinae, while the name Enhydrinae has never been used for any genus other than the sea otter. In 1956, the ICZN issued Direction 53 which placed Enhydrina Gray, 1825, on the Official Index of Rejected and Invalid Family-group Names in Zoology, because it was an "incorrect original spelling," but validated the name Enhydrinae Gill, 1872, "for use by those who consider that *Enhydra* Fleming and *Lutra* Brisson, 1762, belong to different family-group taxa" (see Appendix 2). Such action by the ICZN would have been superfluous had Article 36(a) of the current 1985 edition of the Code been in effect at that time, so the present status of ICZN Direction 53 is not clear. Also now pertinent is the fact that the name Enhydridae H. Smith, 1842—overlooked by the ICZN—is senior to Gill's Enhydrinae. Whether the name Enhydrinae is dated from Smith (1842) or from Gill (1872), it falls as a junior subjective synonym of Lutrinae Bonaparte, 1838.

Subfamily LUTRINAE Bonaparte, 1828

The earliest unquestioned otter was *Paralutra lorteti,* which appeared in the early Miocene of Europe (Savage 1967). Most of the dozen or so genera of extinct otters were a lot like their living descendants; the relationships of *Potamotherium* and other possible allies have already been discussed.

The living otters include only two species, *Lutra felina* and *Enhydra lutris,* that forage exclusively in marine waters. The other eight species inhabit mainly freshwater streams and lakes, but some local populations of at least six of them have been found to feed regularly or wholly in marine waters—from rocky subarctic shores to tropical beaches and mangrove coasts. However, they never wander far from land, and despite the fact that otters have dispersed to all continental land masses except Meganesia and Antarctica, they have failed to colonize the Antilles, Macaronesia, Madagascar, Wallacea, or any oceanic islands. (No hard evidence has ever been found that would lend credence to the long-persistent rumors of an otter in New Zealand—Harris 1968, King 1990).

Taxonomy of the living otters of the world was reviewed by Pohle (1920) and Harris (1968). Thirteen or 14 species have usually been recognized, but the number of recognizable genera has varied from 3 to 8. Davis (1978, Davis *et al.* 1979) concluded that the living forms appear to represent only nine valid species, arranged into six genera; a tenth species has since been distinguished by Imaizumi and Yoshiyuki (1989). Davis (1978) presented a tentative phylogeny based on his first-hand experience with the anatomy, behavior, vocalizations, and karyotypes of all species. He divided the otters into three tribes: Hydrictini for *Hydrictis,* Lutrini for *Lutra,* and Aonychini for the remaining four genera (but the name Enhydrini H. Smith, 1842, should take priority over Aonychini Davis, 1978). For alternative classifications—also phenetic—see Van Zyll de Jong (1972, 1987) and Wozencraft (1989*b,* 1993).

The infraspecific taxonomy of most species of otters was developed piecemeal through the years by a succession of mammalogists. Of the myriad nominal subspecies, I have listed below those that are still "on the books," primarily according to the reviews by Ellerman and Morrison-Scott (1951), Cabrera (1957), Heptner *et al.* (1967), Harris (1968), Coetzee (1971), Gromov and Baranova (1981). Even some of these races probably would not survive the scrutiny of a modern systematic revision. The subspecies of the sea otter and the New World species of *Lutra* are more solidly founded, due to the works of Wilson *et al.* (1991) and Van Zyll de Jong (1972), respectively. No one since Harris (1968) has compiled a list of all the world's subspecies of otters, so for sake of completeness, I include all species and subspecies below, even though two species—*Hydrictis macullicollis* and *Pteronura brasiliensis*—have never been found living in marine waters.

Genus HYDRICTIS Pocock, 1921

Its anatomy, karyotype, and behavior indicate that the spot-necked otter is the most primitive living species of otter, and is probably the sister-taxon to all the other species (Davis 1978, Davis *et al.* 1979). Some authors have included it in *Lutra.*

Hydrictis maculicollis (Lichtenstein, 1835) (Spot-necked otter; speckle-throated otter).

Throughout sub-Saharan Africa, except in the rain forests of west and central Africa, and arid deserts of the northeast and southwest. Five races are recognized:

H. m. matschiei (Cabrera, 1903)—Southern Niger, Nigeria, Cameroon, and Gabon.

H. m. nilotica (Thomas, 1911)—Southern Sudan and Ethiopia.

H. m. chobiensis (Roberts, 1932)—Basin of the Congo River south through Angola and Zambia to the Caprivi Strip in northeastern Namibia, northern Botswana, and northwestern Zimbabwe.

H. m. kivuana (Pohle, 1920)—Eastern Congo, Uganda, southwestern Kenya, Rwanda, Burundi, and northwestern Tanzania.

H. m. maculicollis—From southern Zimbabwe, Malawi, and Mozambique, south to Cape Province.

Genus LUTRA Brisson, 1762.

The generic name *Lutra* is provisionally cited from Brisson (1762), until the International Commission on Zoological Nomenclature issues its Opinion on an application for conservation of certain names published in the 1762 edition of Brisson's *Regnum Animale...* (Gentry 1994). If Brisson's name is rejected, *Lutra* can be dated from Brünnich (1771).

When Davis (1978) published his review, there appeared to be only three valid species in this genus—*L. canadensis* (including *longicaudis* and *provocax*) in North and South America; *L. felina* on the Pacific coast of South America; and *L. lutra* (including *sumatrana*) in the Palearctic and Oriental regions. The subsequently-described *L. nippon* constitutes a fourth species. *L. felina* is the only species which is almost exclusively marine and which is customarily regarded as a marine mammal. Van Zyll de Jong (1972, 1987) separated the American species as genus *Lontra* Gray, 1843.

Lutra lutra Linnaeus, 1758 (Eurasian river otter)

Subarctic zone across Eurasia south to northwestern Africa, Iran, India, Sri Lanka, Indochina, the Malay Peninsula, Sumatra, and Borneo. Eleven subspecies are now generally admitted:

L. l. lutra—Ireland; Great Britain; the Maghrib; continental Eurasia from Scandinavia and the Iberian Peninsula east to Kamchatka and Manchuria; Sakhalin; Ostrova Kuril'skiye. *L. l. angustifrons* Lataste, 1885, from the Maghrib, still listed by some recent authors, is indistinguishable from the nominate race (Lataste 1887, van Bree 1968).

L. l. meridionalis Ognev, 1931—Turkey, southern Caucasus, Israel, Syria, Iraq, and western Iran.

L. l. seistanica Birula, 1912—Southwestern Turkmeniya and eastern Iran east through Uzbekistan, Afghanistan, and southern Kazakhstan as far as Xinjiang [=Sinkiang].

L. l. kutab Schinz, 1844—Northern Pakistan, Kashmir and bordering region of Xizang [=Tibet].

L. l. monticola Hodgson, 1839—Uttar Pradesh, Nepal, Sikkim, and Assam.

L. l. aurobrunnea Hodgson, 1839—Higher elevations of northern Uttar Pradesh and Nepal.

L. l. chinensis Gray, 1837—Central and southern China and Indochina, south to peninsular Thailand, Pulau Langkawi off the west coast of peninsular Malaysia, and central Vietnam; Ryukyu Retto; Taiwan.

L. l. nair F. Cuvier, 1823—Isolated in southern India and Sri Lanka. Includes *L. l. ceylonica* Pohle, 1920, from Sri Lanka (Pocock 1941).

L. l. hainana Xu and Liu, 1983—Hainan. Imaizumi and Yoshiyuki (1989) regarded this insular form as a valid subspecies.

L. l. whiteleyi (Gray, 1867)—Hokkaido. Most previous authors listed this name in the synonymy of the nominate subspecies, but Imaizumi (1975) and Imaizumi and Yoshiyuki (1989) regarded it as a valid subspecies of *L. lutra.*

L. l. sumatrana (Gray, 1865)—Southern Vietnam; peninsular Malaysia; Singapore; Sumatra; Bangka; northwestern Borneo (reports from Java are erroneous). This form, the "hairy-nosed otter," was formerly considered a separate species, but sympatry between *L. l. chinensis* and *L. l. sumatrana* has not been demonstrated, and some specimens are intermediate between the two taxa (Foster-Turley *et al.* 1990). *L. l. sumatrana* appears to be "a previously isolated race of *lutra* now in secondary contact with the Asian mainland populations of that species and interbreeding with them" (Davis 1978). The name *Lutra l. barang* F. Cuvier, 1823, from "Java," has sometimes been used for a fancied Sumatran (or Sumatran and Javan) race of *L. lutra* that was thought to be sympatric with *L. sumatrana.* Its asserted type locality has been questioned because there are no credible reports of otters of the genus *Lutra* on Java—notwithstanding the appearance of both *L. lutra* and *L. sumatrana* on the most recent, but uncritical, checklist of Javan mammals (Melisch 1992). Sumatra is usually conjectured as the most likely provenance of *L. barang* (Chasen 1940). However, its original description was so inadequate that it is impossible to say whether the name is a senior synonym of *L. l. sumatrana,* or of *Lutrogale perspicillata,* the smooth-coated otter (Pohle 1920, Chasen 1940), so the name must be rejected as a *nomen dubium.*

Lutra nippon Imaizumi and Yoshiyuki, 1989. (Japanese river otter)

Japan south of Blakiston's line, including Honshu, Shikoku, and Kyushu. Imaizumi and Yoshiyuki (1989) described this well-marked taxon as a full species. Wozencraft (1993), without explanation, listed it in the synonymy of *L. lutra,* but a comparison of the nucleotide sequence of its mitochondrial cytochrome *b* gene with that of *L. lutra* specimens from Europe, China, and Hokkaido, supported the view that *L. nippon* and *L. lutra* are distinct enough to be regarded as separate species (Suzuki *et al.* 1996).

Lutra canadensis (Schreber, 1777) (American river otter)

There has been some confusion about the publication dates of names in Schreber's *Die Säugethiere...*; the name *Mustela lutra canadensis* first appeared in Theil 3, Heft 26, page 457 (Wozencraft 1993), which was published in 1777 (Sherborn 1891).

There are three geographically isolated populations: (1) Subarctic zone of Alaska and Canada, from Norton Sound, the Alaska Peninsula, and the Shumagin Islands east to Labrador, Newfoundland, Cape Breton Island, and Nova Scotia, and south to southern California, southern Texas, and southern Florida; (2) central Mexico south to Peru, northeastern Argentina and Uruguay; and (3) southern Chile and southern Argentina south to Tierra del Fuego. Van Zyll de Jong (1972) regarded the North American, neotropical, and Patagonian populations as three separate species: *Lutra* *canadensis, L. longicaudis* (Olfers, 1818), and *L. provocax* (Thomas, 1908), respectively. These populations differ mainly in the shape and extent of the bare area of the rhinarium. There is a cline in the extent of the bare area, with the most reduced rhinaria on animals living within 10° of the equator, and larger ones on the otters that live at higher latitudes to the north and south, so Davis (1978) regards all populations as conspecific, as did Hershkovitz (1969). The situation parallels that of *L. lutra* in southeastern Asia (see above). Eleven subspecies are definable on the basis of a multivariate analysis of cranial features (Van Zyll de Jong 1972):

L. c. kodiacensis Goldman, 1935—Kodiak Island, Alaska.

L. c. periclyzomae Elliot, 1905—The Queen Charlotte Islands, British Columbia.

L. c. mira Goldman, 1935—Southeastern Alaska including the Alexander Archipelago, the mainland coast of British Columbia, and Vancouver Island.

L. c. pacifica Rhoads, 1898—From Alaska, western Canada, and the northern United States west of the Rocky Mountains south to central California, northern Nevada, and northeastern Utah.

L. c. canadensis—Eastern Canada and immediately adjacent parts of the United States; Newfoundland.

L. c. sonora Rhoads, 1898—In the Colorado River system in southern Nevada, southeastern Utah, southwestern Colorado, southeastern California, northern and western Arizona, and northwestern New Mexico.

L. c. lataxina F. Cuvier, 1823—Throughout most of the United States east of the Rocky Mountains.

L. c. annectens Major, 1897—From Durango and Veracruz, Mexico, south through Central America and South America west of the Andes as far as Peru.

L. c. enudris F. Cuvier, 1823—Northern South America east of the Andes, throughout the Amazon basin and the rivers of eastern Brazil, as far south as Buenos Aires, Argentina; also the island of Trinidad.

L. c. longicaudis Olfers, 1818—Paraná River system in Paraguay, southern Brazil, northeastern Argentina, and Uruguay.

L. c. provocax Thomas, 1908—Southern tip of South America from Arauco, Chile, and Río Negro, Argentina, south to Tierra del Fuego.

Lutra felina (Molina, 1782) (marine otter; chungungo).

Marine coastal waters of western South America from Bahiá de Chimbote, Peru, south to Estrecho de Le Maire, Argentina; sometimes enters estuaries and rarely freshwater habitats, where it is marginally sympatric with *L. canadensis provocax.* Two subspecies were recognized by Mann (1945): *L. f. peruviensis* Gervais, 1841, from Peru and northern Chile, and *L. f. felina* from southern Chile to Argentina; their validity is dubious, however (Brownell 1978), and the species was considered monotypic by Cabrera (1957), Osgood (1943), and Van Zyll de Jong (1972).

Genus LUTROGALE Gray, 1865

Some authors have included the one species in *Lutra.*

Lutrogale perspicillata (I. Geoffroy Saint-Hilaire, 1826) (smooth-coated otter; sea otter [Sumatra and Java])

Ranges throughout tropical southeastern Asia from India to Indochina and the Greater Sundas, with disjunct populations in Iraq and Pakistan. Three subspecies are recognized:

L. p. maxwelli Hayman, 1957—Tigris-Euphrates valley in Iraq.

L. p. sindica Pocock, 1940—Indus valley of Pakistan.

L. p. perspicillata—India (except northwestern part), Yunnan, Indochina, and the Malay Peninsula; Sumatra; Banka; northeastern Borneo; western Java. (The name *Lutra barang* F. Cuvier, 1823, may be a senior synonym of *Lutrogale perspicillata*—see discussion above under *Lutra lutra.*)

Genus PTERONURA Gray, 1837

Pteronura brasiliensis (Gmelin, 1788) (giant otter)

Husson (1978) presented reasons why this name should be attributed to Zimmermann (1780) rather than to Gmelin (1788); while he was correct in stating that Zimmermann's 1780 work was placed on the Official List of Works Approved as Available for Zoological Nomenclature (ICZN 1954*c*), he overlooked the fact that the name *Lutra brasiliensis* Zimmermann, 1780, was subsequently placed on the Official Index of Rejected and Invalid Specific Names, while at the same time *Mustela lutris* var. *brasiliensis* Gmelin, 1788, was placed on the Official List of Specific Names (Direction 79; see Appendix 2).

Ranges throughout tropical South America east of the Andes, and south to northern Argentina and Uruguay. There are two races:

P. b. brasiliensis—Northern South America from Venezuela and the Guyanas south to Alagoas, Brazil.

P. b. paranensis (Rengger, 1830)—Drainages of the Río Paraná and Río Uruguay in Paraguay, southern Brazil, northeastern Argentina, and Uruguay.

Genus AONYX Lesson, 1827

There are two well-marked species of small-clawed, or "clawless," otters. The small Asian species is sometimes separated generically from the large African one as *Amblonyx* Rafinesque, 1832, but Davis (1978) and many other workers regard them as congeneric. Some authors have also separated certain African forms as genus *Paraonyx* Hinton, 1921 (see comments below under *Aonyx capensis*).

Aonyx capensis (Schinz, 1821) (African small-clawed otter; swamp otter)

Throughout subsaharan Africa, except in the arid northeast and southwest desert zones. Six or seven subspecies may be distinguishable. The three subspecies (*microdon, congica,* and *philippsi*) from the central African rainforest block were long thought to comprise one or more separate species, which some authors even placed in a different genus because of their small teeth (see above), but they have been shown to intergrade with the larger-toothed races in the savanna regions to the north, east, and south (Davis 1978).

A. c. meneleki (Thomas, 1903)—Isolated in northern and central Ethiopia.

A. c. subsp.—West Africa from Senegal and Guinea east to Nigeria. The West African population is often referred to the nominate race, but such allocation is unproven (Rosevear 1974, Meester *et al.* 1986), and it seems unlikely because its range is not contiguous with that of the latter. The earliest available name based on a West African specimen would appear to be *A. c. calabaricus* (Murray, 1860), should the population prove to be distinguishable.

A. c. hindei (Thomas, 1905)—From Uganda and central Kenya south to northern Zambia.

A. c. capensis—Southern Africa from Angola and Zambia southward to Cape Province.

A. c. microdon Pohle, 1920—Tributaries of the Sanaga River in Cameroon. Perret and Aellen (1956) used the name *Aonyx (Paraonyx) poensis* (Waterhouse, 1838) for small-clawed otters from Cameroon; the latter name is based on a defective skin taken on the island of Fernando Póo [=Bioko], and most authorities (Harris 1968, Coetzee 1971, Rosevear 1974) have found it unidentifiable.

A. c. congica Lönnberg, 1910—Throughout the basin of the Congo River.

A. c. philippsi (Hinton, 1921)—Highlands of northeastern Congo, southwestern Uganda, Rwanda, and Burundi.

Aonyx cinerea (Illiger, 1815) (Oriental small-clawed otter)

Found throughout tropical southeastern Asia from northern India and southern China south to Indochina and the Greater Sundas. Three subspecies are recognized (but the boundary between the first two is not satisfactorily documented) (Yoshiyuki 1971):

A. c. concolor (Rafinesque, 1832)—Northern India, Yunnan, and Myanmar [=Burma].

A. c. cinerea—Thailand, Laos, Vietnam, and Malay Peninsula; ?Taiwan; Singapore; Kepulauan Riau; Kepulauan Lingga; Sumatra; Java; Karimunjawa; Borneo; Pulau Laut; and Palawan. (Hoogerwerf 1970—surely in error—includes the "Lesser Sundas," but gives no particulars.)

A. c. nirnai (Pocock, 1940)—Isolated in southern India.

Genus ENHYDRA Fleming, 1822

In the late Pleistocene, a larger sea otter called *Enhydra macrodonta* lived in northern California, where it may have coexisted with *E. lutris* (Mitchell 1966*b,* Kilmer 1972). From the late Miocene to the early Pliocene, the closely-related genus *Enhydritherium* was represented by two species, *E. terraenovae* on the coasts of California and Florida, and *E. lluecai* on the coast of Spain; throughout the Pliocene another close relative, *Enhydriodon,* with at least three species, lived in India and Africa—probably in freshwater habitats (Repenning 1976*b,* Berta and Morgan 1985).

Enhydra lutris (Linnaeus, 1758) (sea otter).

Three subspecies are recognizable (Wilson *et al.* 1991. *cf.* Barabash-Nikiforov 1947; Scheffer and Wilke 1950; Stroganov 1962; Roest 1973, 1976; Davis and Lidicker 1975); they probably intergraded before the species dipped to near-extinction in the 1800s and early 1900s.

E. l. lutris—From Komandorskiye Ostrova southwest along the southeast coast of Kamchatka, and through Ostrova Kuril'skiye as far as northern Hokkaido. (Animals transplanted to the coast of Murmanskaya in the Atlantic-Arctic failed to become established—Barabash-Nikiforov 1961).

E. l. kenyoni Wilson, 1991—From the Aleutian and Pribilof islands, east along the south shore of the Alaska Peninsula, northeast to Prince William Sound, and thence southeast to Washington State. (Sea otters were extirpated from the Pribilof Islands and the Alexander Archipelago in Alaska, and from the coasts of British Columbia, Washington, and Oregon in the 19th century; the populations now in those areas are descended from animals that were translocated from Amchitka Island and Prince William Sound, Alaska, between 1965 and 1972—Jameson *et al.* 1982.) Alleged sight records of sea otters at Atigaru Point (151°50′W) and Cape Halkett (142°16′W) on the arctic coast of Alaska (Bee and Hall 1956) are of doubtful authenticity (Kenyon 1969).

E. l. nereis (Merriam, 1904)—Coast and nearby islands from northern California south to Morro Hermoso in Baja California Norte, including the Farallon Islands, the Channel Islands, Isla San Martín, Isla San Geronimo, Islas San Benitos, Isla Cedros, and Isla Natividad; also Isla Guadalupe, an oceanic island 260 km offshore. Vagrant south to Isla Magdalena in Baja California Sur.

APPENDIX 2

Opinions and Directions of the International Commission on Zoological Nomenclature

An Opinion is a ruling by the ICZN that applies, interprets, or suspends the provisions of the ICZN Code in a case affecting one or more stated publications, names, or nomenclatural acts. A Direction is a statement that completes or corrects a ruling in an Opinion. An Opinion may conserve a name by placing it on the Official List of Specific Names in Zoology, or on the corresponding Official Lists for Generic and Family-Group names (such placement ensures the availability of a name, but not its priority over earlier names unless specifically stated). An Opinion may also suppress a name by placing it on the Official Index of Rejected and Invalid Specific Names in Zoology, or on the corresponding Official Indexes for Generic and Family-Group names. The ICZN has issued the following 15 Opinions and 6 Directions that affect certain names used in this list, and one additional Case is pending before the ICZN:

Opinion 75 (31 January 1922)—*Balaena, Delphinus, Monodon, Phoca,* and *Ursus,* all of Linnaeus, 1758, placed on Official List of Generic Names.
Smithsonian Miscellaneous Collections 73(1):35–37

Opinion 90 (16 December 1925)—A request for suspension of the Rules for "*Rhytina*" [=*Rytina*] Illiger, 1811, failed to receive the required two-thirds majority vote, so the Law of Priority is to be applied.
Smithsonian Miscellaneous Collections 73(3):34–40.

Opinion 91 (8 October 1926)—*Cystophora* Nilsson, 1820, and *Halichoerus* Nilsson, 1820, placed on the Official List of Generic Names.
Smithsonian Miscellaneous Collections 73(4):1–2.

Opinion 112 (8 June 1929)—*Trichechus* Linnaeus, 1758, placed on Official List of Generic Names.
Smithsonian Miscellaneous Collections 73(6):19

Direction 13 (19 May 1955)—*Trichechus manatus* Linnaeus, 1758, placed on Official List of Specific Names; *Manatus* Brünnich, 1771, and *Manatus* Storr, 1780, placed on Official Index of Rejected and Invalid Generic Names.
Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature 1(Section C):57–66

Direction 22 (4 November 1955)—*Ursus arctos* Linnaeus, 1758, *Phoca cristata* Erxleben, 1777 [=*Cystophora cristata*], *Delphinus delphis* Linnaeus, 1758, *Phoca grypus* Fabricius, 1791 [=*Halichoerus grypus*], *Monodon monoceros* Linnaeus, 1758, *Balaena mysticetus* Linnaeus, 1758, and *Phoca vitulina* Linnaeus, 1758, placed on Official List of Specific Names.
Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature 1(Section C):179–200.

Direction 24 (4 November 1955)—*Trichechus* Linnaeus, 1766 [=*Odobenus* Brisson, 1762; NOT *Trichechus* Linnaeus, 1758] placed on Official Index of Rejected and Invalid Generic Names. Entries relating to the names *Cystophora* and *Halichoerus* completed [*cf.* Opinion 91 and Direction 22].
Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature 1(Section C):219–246.

Opinion 384 (20 April 1956)—*Alopex* Kaup, 1829, *Amblonyx* Rafinesque, 1832, *Enhydra* Fleming, 1822, *Pteronura* Gray, 1837, and *Thalarctos* Gray, 1825, placed on Official List of Generic Names; Canis *lagopus* Linnaeus, 1758 [=*Vulpes lagopus*], *Lutra cinerea* Illiger, 1815 [=*Aonyx cinerea*], *Amblonyx concolor* Rafinesque, 1832 [=*Aonyx cinerea concolor*], *Mustela lutris* Linnaeus, 1758 [=*Enhydra lutris*], and *Ursus maritimus* "Linnaeus, 1758" [=Phipps, 1774] placed on Official List of Specific Names.
Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature 12:71–190.

Direction 53 (1 September 1956)—Enhydrinae Gill, 1872, placed on Official List of Family-Group Names, and Enhydrina Gray, 1825, placed on Official Index of Rejected and Invalid Family-Group Names.
Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature 12:441–456.

Opinion 467 (31 May 1957)—*Odobenus* Brisson, 1762, placed on Official List of Generic Names, and *Rosmarus* Brünnich, 1871, placed on Official Index of Rejected and Invalid Generic Names; *Phoca rosmarus* Linnaeus, 1758 [=*Odobenus rosmarus*] placed on Official List of Specific Names.
Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature 16(6):73–88.

Direction 79 (10 October 1957)—*Mustela lutris* var. *brasiliensis* Gmelin, 1788 [=*Pteronura brasiliensis*] placed on Official List of Specific Names, and *Lutra brasiliensis* Brisson, 1762, and *Lutra brasiliensis* Zimmermann, 1780, placed on Official Index of Rejected and Invalid Specific Names.
Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature 16:455–464.

Direction 98 (16 May 1958)—Vespertilionidae (correction of Vespertilia) Rafinesque, 1815, placed on Official List of Family-Group Names; *Myotis* Kaup, 1829, placed on Official List of Generic Names.
Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature 1(Section F):127–160.

Opinion 544 (20 March 1959)—Odobenidae (correction of Odobaenidae) Allen, 1880, placed on Official List of Family-Group Names.
Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature 20:119–128.

Opinion 1067 (31 March 1977)—*Delphinus pernettensis* Blainville, 1817 [=*Stenella pernettensis*] placed on Official Index of Rejected and Invalid Specific Names.
Bulletin of Zoological Nomenclature 33:157–158.

Opinion 1129 (1 August 1979)—*Vulpes* Frisch, 1775, placed on Official List of Generic Names.
Bulletin of Zoological Nomenclature 36:76–78.

Opinion 1289 (2 April 1985)—*Mesoplodon* Gervais, 1850, placed on Official List of Generic Names, and *Nodus* Wagler, 1830, *Micropteron* Eschricht, 1849, and *Mikropteron* Eschricht, 1849, placed on Official Index of Rejected and Invalid Generic Names; *Physeter bidens* Sowerby, 1804 [=*Mesoplodon bidens*] placed on Official List of Specific Names.
Bulletin of Zoological Nomenclature 42:19–20.

Opinion 1320 (27 June 1985)—*Hydrodamalis* Retzius, 1794, placed on Official List of Generic Names, and *Manati* Steller, 1774, placed on Official Index of Rejected and Invalid Generic Names; *Manatus inunguis* Natterer *in* Pelzeln, 1883 [=*Trichechus inunguis*] placed on Official List of Specific Names, and *Manatus exunguis* Natterer in Diesing, 1839, placed on Official Index of Rejected and Invalid Specific Names; *Manati gigas* Zimmermann, 1780 [=*Hydrodamalis gigas*] placed on Official List of Specific Names.
Bulletin of Zoological Nomenclature 42:175–176.

Opinion 1413 (October 1986)—*Delphinus truncatus* Montagu, 1821 [=*Tursiops truncatus*] placed on Official List of Specific Names, and *Delphinus nesarnack* Lacépède, 1804, placed on Official Index of Rejected and Invalid Specific Names.
Bulletin of Zoological Nomenclature 43:256–257.

Opinion 1535 (March 1989)—*Halitherium* Kaup, 1838, with type species *Pugmeodon schinzii* Kaup, 1838, placed on Official List of Generic Names; *Pugmeodon schinzii* Kaup, 1838 [=*Halitherium schinzii*] placed on Official List of Specific Names; *Halianassa* Meyer, 1838, placed on Official Index of Rejected and Invalid Generic

Names; *Halianassa studeri* Meyer, 1838, placed on Official Index of Rejected and Invalid Specific Names.
Bulletin of Zoological Nomenclature 46(1):83–84.

Opinion 1565 (September 1989)—*Platanista* Wagler, 1830, placed on Official List of Generic Names, and *Susu* Lesson, 1828, placed on Official Index of Rejected and Invalid Generic Names; *Delphinus gangeticus* Roxburgh, 1801 [=*Platanista gangetica*] placed on Official List of Specific Names.
Bulletin of Zoological Nomenclature 46:217–218.

Opinion 1660 (September 1991)—*Steno attenuatus* Gray, 1846 [=*Stenella attenuata*] placed on Official List of Specific Names, and *Delphinus velox* Cuvier, 1829, *Delphinus pseudodelphis* Schlegel, 1841, and *Delphinus brevimanus* Wagner, 1846, placed on Official Index of Rejected and Invalid Specific Names.
Bulletin of Zoological Nomenclature 48:277–278.

Case 2998 (1994)—Application for the conservation of *Lutra* Brisson, 1762.
Bulletin of Zoological Nomenclature 51:135–146.

In this list I have also retained the following three junior synonyms that have enjoyed near-universal usage for many decades, in anticipation that the ICZN will be petitioned to conserve them:

(1) Genus *Hydrurga* Gistel, 1848, instead of *Stenorhinchus* E. Geoffroy St. Hilaire and F. Cuvier, 1826.
(2) Subfamily Monachinae (Monachina Gray, 1869) instead of Stenorhinchinae (Stenorhyncina Gray, 1825).
(3) Family Ziphiidae (Ziphiina Gray, 1850) instead of Hyperoodontidae (Hyperoodontina Gray, 1846).

APPENDIX 3

Family-group Names Based on Fossil Genera

The names of family-group taxa based upon fossil genera have the same status under the ICZN Code as any other family-group names. Although none happens to have priority over any of the names used in this list for Recent family-group taxa, for sake of completeness all proposed family-group names based on fossil genera of pinnipeds, cetaceans, and sirenians are listed below.

The ICZN Code, Article 29, dictates that each family-group name be formed by adding the appropriate rank-suffix (-oidea, -idae, -inae, -ini, or -ina) to the grammatical stem of the name of its type-genus. The stem may be found by deleting the case-ending from the genitive singular of the word, or of the final element of compound names (most Latin and Greek dictionaries give the genitive singular of each word). Neo-Latin names not found in classical dictionaries, such as *Grampus, Kogia,* and *Manatus,* are declined by analogy with classical names with the same endings. For any barbarous generic name, such as *Dugong,* that does not have a Latin or Greek ending, the grammatical stem is that used by the first author who proposes a family-group name based on that generic name.

Some family-group names were incorrectly formed, or were based on an incorrect spelling of the type genus, when first proposed. The ICZN Code, Articles 29, 32(c)(iii), 32(d), and 35(d), calls these "incorrect original spellings" and requires that their spelling be corrected (but formal authorship is still attributed to the original author). As with names based on living genera cited in the main text, I have included any emended spellings or changes in the stem of each name, but I have not cited alterations in the suffixes that denote rank. Among marine mammal family-group names, the following cases have been particularly troublesome:

Names ending in -delphidae *versus* -delphinidae:

Acrodelphis, Argyrodelphis, Brachydelphis, Champsodelphis, Eurhinodelphis, Lissodelphis, Pithanodelphis, Squalodelphis, Stenodelphis, and *Zignodelphis* are compounded from the Greek noun δελφις, genitive δελφινος [*delphis, delphinos*] 'dolphin.' The grammatical stem is δελφιν- [*delphin-*], so all family-group names formed from generic names ending in *-delphis* must end in -delphinoidea, -delphinidae, -delphininae, *etc.*

Prorastomidae *versus* Prorastomatidae:

Prorastomus—like other generic names compounded with *-stomus,* derived from the Greek στομα, genitive στοματος [*stoma, stomatos*] 'mouth'—is a Latinized word because its ending has been changed to *-us.* Taxonomists treat *stomus* as a third declension masculine noun, with *stomis* as its genitive singular. Therefore the stem of *Prorastomus* is *Prorastom-,* not the Greek *Prorastomat-,* and the correct spelling of the family name is Prorastomidae. The same situation pertains to the family name Phyllostomidae (order Chiroptera), based on *Phyllostomus* Lacépède, 1799 (Handley 1980).

Rytiodinae *versus* Rytiodontinae:

Rytiodus—like other generic names compounded with *-odus,* from the Attic Greek ὀδους, genitive ὀδοντος [*odous, odontos*] 'tooth'—looks like a Latinized word because of its *-us* ending, and has been erroneously treated as such by some authors, who thus deemed its stem to be *Rytiod-.* However, the Latin cognate (from the Ionic Greek spelling ὀδων, ὀδοντος [*odōn, odontos*]) is *dens, dentis,* whereas *odus* is the classical transliteration of ὀδούς. Therefore the name must be treated as Greek, with *Rytiodont-* as its stem, and the correct spelling of the subfamily name is Rytiodontinae. The same situation pertains to the subfamily name Desmodontinae (order Chiroptera), based on *Desmodus* Wied, 1826 (Handley 1980).

List of Names

Under each higher taxon, family-group names are listed in alphabetical order, except that any emended spellings follow the original spelling in chronological order.

PINNIPEDIA

Allodesmidae Kellogg 1931:227 (Type genus: *Allodesmus* Kellogg, 1922)
Archiphocida Haeckel 1895:579 (Hypothetical ancestral group of Pinnipedia; not available because it is not based on the stem of a generic name)
Desmatophocidae Hay 1930:557 (Type genus: *Desmatophoca* Condon, 1906)
Dusignathinae Mitchell 1968:1894 (Type genus: *Dusignathus* Kellogg, 1927)
Enaliarctinae Mitchell and Tedford 1973:218 (Type genus: *Enaliarctos* Mitchell and Tedford 1973)
Imagotariinae Mitchell 1968:1895 (Type genus: *Imagotaria* Mitchell, 1968)
Kamtschatarctinae Dubrovo 1981:970 (Type genus: *Kamtschatarctos* Dubrovo, 1981)
Necromitinae Akhundov 1967:[page ?][18] (Type genus: *Necromites* Akhundov, 1960)
Potamotherini Sokolov 1973:71 (Type genus: *Potamotherium* Geoffroy, 1833; incorrect original spelling; taxonomic position uncertain)
Semantoridae Orlov 1931:69 (Type genus: *Semantor* Orlov, 1931)

CETACEA

Acrodelphidae Abel 1905:41 (Type genus: *Acrodelphis* Abel, 1900; an incorrect original spelling because of improperly formed stem)
Acrodelphinidae Rice 1984*a*:466 (=Acrodelphidae; justified emendation)
Aetiocetidae Emlong 1966:3 (Type genus: *Aetiocetus* Emlong, 1966)
Agorophiidae Abel 1913*a*:720 (Type genus: *Agorophius* Cope, 1895)
Albireonidae Barnes 1984*b*:29 (Type genus: *Albireo* Barnes, 1984)
Ambulocetidae Thewissen *et al.* 1996:9 (Type genus: *Ambulocetus* Thewissen, Hussain, and Arif, 1994)
Archibalaenae Haeckel, 1895:566 (Alternate name for Protobalaenida; not available because it is not based on the stem of a generic name)
Argyrodelphini Winge 1918:[page 38 of 1921 English edition] (Type genus: *Argyrodelphis* Lydekker, April 1894 [=*Notocetus* Moreno, 1892, =*Diochoticus* Ameghino, February 1894])
Basilosauridae Cope 1867:144 (Type genus: *Basilosaurus* Harlan, 1834)
Brachydelphinae Muizon 1988*a*:82 (Type genus: *Brachydelphis* Muizon, 1988; an incorrect original spelling because of improperly formed stem)
Brachydelphininae *nobis* (=Brachydelphinae; justified emendation)
Cetotherinae Brandt 1872*a*:116 (Type genus: *Cetotherium* Brandt, 1841[*sic*]; an incorrect original spelling because of improperly formed stem)
Cetotheriidae Miller 1923:21 (=Cetotherinae; justified emendation)
Cetotheriopsinae Brandt 1872*a*:116 (Type genus: *Cetotheriopsis* Brandt, 1871)

[18] Akhundov, F. M. 1967. [Reference untraceable; cited from Gromov and Baranova 1981]

Champsodelphidae Scott, 1873:67 (Type genus: *Champsodelphis* Gervais, 1878; incorrect original spelling; family name overlooked by Palmer 1904)
Cynorcidae Cope 1867:144 (Type genus: *Cynorca* Cope, 1867; the type species *C. proterva*–described from a single tooth–was originally allocated to the Cetacea, but was later reidentified as a peccary, order Artiodactyla.)
Dalpiazinidae Muizon 1988*c*:66 (Type genus: *Dalpiazina* Muizon, 1988)
Dalpiaziniidae Muizon 1994:136, Figure 1 (=Dalpiazinidae; incorrect spelling)
Diaphorodontina Brandt 1873*a*:575 (Includes Squalodontidae and Zeuglodontidae; not available because it is not based on the stem of a generic name)
Dorudontidae Miller 1923:40 (Type genus: *Dorudon* Miller, 1923)
Eoplatanistinae Muizon 1988*c*:61 (Type genus: *Eoplatanista* Dal Piaz, 1916)
Eurhinodelphidae Abel 1901:60 (Type genus: *Eurhinodelphis* Du Bus, 1867; an incorrect original spelling because of improperly formed stem)
Eurhinodelphininae Miller 1923:34 (=Eurhinodelphidae; justified emendation)
Gymnorhinidae Brandt 1873*b*:313 (Alternate name for Squalodontidae; a junior homonym of Gymnorhina Wagner 1840:24 [=Gymnorhinidae Fatio 1869:39] in the order Chiroptera, but neither name is available because neither is based on the stem of a generic name)
Hemisyntrachelidae Slijper 1936:550 ((Type genus: *Hemisyntrachelus* Brandt, 1873)
Heterodontina Brandt 1873*a*:575 (Alternate name for Diaphorodontina; not available because it is not based on the stem of an included generic name, and because it is a junior homonym of Heterodontidae Girard, 1852—see main text under family Ziphiidae)
Hoplocetinae Cabrera 1926:408 (Type genus: *Hoplocetus* Gervais, 1848)
Hydrarchidae Bonaparte 1850:1 (Type genus: *Hydrarchos* Koch, 1845 [=*Basilosaurus* Harlan, 1834])
Indocetinae Gingerich *et al.* 1993:414 (Type genus: *Indocetus* Sahni and Mishra, 1975)
Kampholophinae Barnes 1978:4 (Type genus: *Kampholophos* Rensberger, 1969)
Kekenodontinae Mitchell 1989:2231 (Type genus: *Kekenodon* Hector, 1881)
Kentriodontinae Slijper 1936:556 (Type genus: *Kentriodon* Kellogg, 1927)
Llanocetidae Mitchell 1989:2220 (Type genus: *Llanocetus* Mitchell, 1989)
Lophocetinae Barnes 1978:11 (Type genus: *Lophocetus* Cope, 1868)
Mammalodontidae Mitchell 1989:2231 (Type genus: *Mammalodon* Pritchard, 1939)
Microzeuglodontidae Abel 1913*b*:220 (Type genus: *Microzeuglodon* Stromer, 1903)
Odobenocetopsidae Muizon 1993:746 (Type genus: *Odobenocetops* Muizon, 1993; originally allocated to Cetacea, but relationship is disputed)
Pachyacanthinae Brandt 1872*b*:262 (Type genus: *Pachyacanthus* Brandt, 1871)
Pakicetinae Gingerich and Russell 1990:17 (Type genus: *Pakicetus* Gingerich and Russell, 1981)
Palaeocetidae Gray, 1866:106 (suggested but not used; Type genus: *Palaeocetus* Seeley, 1865)
Parabalaenopterinae Zeigler *et al.* 1997:117 (Type genus: *Parabalaenoptera* Zeigler, Chan, and Barnes, 1997)
Parapontoporiinae Barnes 1984*b*:6 (Type genus: *Parapontoporia* Barnes, 1984)
Patriocetinae Abel 1913*b*:160 (Type genus: *Patriocetus* Abel, 1912[*sic*])
Physodontidae Lydekker 1894:4 (Type genus: *Physodon* Gervais, 1872)
Pithanodelphinae Barnes 1985*c*:1 (Type genus: *Pithanodelphis* Abel, 1905; an incorrect original spelling because of improperly formed stem)
Pithanodelphininae *nobis* (=Pithanodelphinae; justified emendation)
Pontoplanodidae Ameghino 1894:181 (Type genus: *Pontoplanodes* Ameghino, 1891)
Praemegapteridae Behrmann 1995:125 (Type genus: *Praemegaptera* Behrmann, 1995; designated as subfamily of Balaenopteridae despite family-rank ending)
Proterocetidae Ameghino, 1899:8 (Type genus: *Proterocetus* Ameghino, 1899)
Protobalaenida Haeckel 1895:566 (Type genus: the hypothetical *Protobalaena* Haeck-

el, 1895 [not *Protobalaena* Du Bus, 1869, or *Protobalaena* Leidy, 1869]; not available because it is not based on the stem of a valid generic name)

Protocetidae Stromer 1908:148 (Type genus: *Protocetus* Fraas, 1904)

Prozeuglodontidae Moustafa 1954:87 (Type genus: *Prozeuglodon* Andrews, 1906)

Remingtonocetidae Kumar and Sahni 1986:329 (Type genus: *Remingtonocetus* Kumar and Sahni, 1986)

Rhabdosteidae Gill 1871*a*:123 (Type genus: *Rhabdosteus* Cope, 1867)

Rhabdostoidea Muizon 1984:68 (=Rhabdosteidae; unjustified emendation with improperly formed stem)

Saurocetidae Ameghino 1891*a*:163 (Type genus: *Saurocetes* Burmeister 1871)

Scaphokogiinae Muizon 1988*a*:66 (Type genus: *Scaphokogia* Muizon, 1988)

Squalodelphidae Dal Piaz, 1916:32 (Type genus: *Squalodelphis* Dal Piaz, 1916; an incorrect original spelling because of improperly formed stem)

Squalodelphinidae *nobis* (=Squalodelphidae; justified emendation)

Squalodontidae Brandt 1873*a*:576 (Type genus: *Squalodon* Grateloup, 1840)

Squaloziphiinae Muizon 1991:282 (Type genus: *Squaloziphius* Muizon, 1991)

Stegorhinidae Brandt 1873*b*:334 (=Zeuglodontidae; not available because it is not based on the stem of a generic name)

Waipatiidae Fordyce 1994:147 (Type genus *Waipatia* Fordyce, 1994)

Zeuglodontidae Bonaparte 1849:618 (Type genus: *Zeuglodon* Owen, 1839 [=*Basilosaurus* Harlan, 1834])

Zignodelphidae Pilleri 1989:384 (Type genus: *Zignodelphis* Pilleri, 1989; an incorrect original spelling because of improperly formed stem)

Zignodelphinidae *nobis* (=Zignodelphidae; justified emendation)

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Archaeosireninae Abel 1914:217 (Type genus: *Archaeosiren* Abel, 1913, *nomen nudum* [=*Eosiren* Andrews, 1902])

Eotherioidinae Kretzoi 1941:154 (Type genus: "*Eotherioides*" [=*Eotheroides*] Palmer, 1899; an incorrect original spelling because of unjustified emendation of the spelling of the type genus)

Eotheroidinae Domning 1996:154 (=Eotherioidinae; justified emendation)

Halianassinae Reinhart 1959:8 (Type genus: *Halianassa* Meyer, 1838, suppressed by ICZN Opinion 1531—see Appendix 2)

Halianaissinae Reinhart 1959:23 (=Halianassinae; incorrect spelling)

Halitherida Carus 1868:168 (Type genus: *Halitherium* Kaup, 1838; an incorrect original spelling because of improperly formed stem)

Halitheriidae Gill 1872:13 (=Halitherida; justified emendation)

Metaxytheriinae Kretzoi 1941:155 (Type genus: *Metaxytherium* Christol, 1840)

Miosireninae Abel 1919:835 (Type genus: *Miosiren* Dollo, 1890)

Prorastomidae Cope 1889:876 (Type genus: *Prorastomus* Owen, 1855)

Prorastomatidae Flower and Lydekker 1891:224 (=Prorastomidae; unjustified emendation with improperly formed stem)

Protosirenidae Sickenberg 1934:193 (Type genus: *Protosiren* Abel, 1904)

Rhytiodinae Abel 1928:503 (Type genus: "*Rhytiodus*" [=*Rytiodus*] Lartet, 1866; an incorrect original spelling because of unjustified emendation of the spelling of the type genus and because of improperly formed stem)

Rytiodinae Simpson 1932:424 (=Rhytiodinae; emendation).

Rytiodontinae Kretzoi 1941:155 (=Rytiodinae; justified emendation)

Rhytiodiinae Pilleri 1987:65 (=Rytiodinae; incorrect subsequent spelling because of improperly formed stem)

Thelriopiinae Pilleri 1987:65 (Type genus: *Thelriope* Pilleri, 1987 [an unnecessary replacement name for *Rytiodus* Lartet, 1866]; an incorrect original spelling because of improperly formed stem)

APPENDIX 4

Foreign Equivalents for Geographical Terms

Ar=Arabic; Ch=Chinese; Dan=Danish; Fin=Finnish; Fr=French; Indo=Indonesian; Japn=Japanese; Kor=Korean; Mal=Malay; Mon=Mongolian; Nor=Norwegian; Por=Portuguese; Rus=Russian; Sp=Spanish.

Arrecifé (Sp) Reef
Bāb (Ar) Strait
Bahía (Sp) Bay
Baia (Por) Bay
Bredning (Dan) Bay
Bugt (Dan) Bay
Cabo (Sp) Cape
Canal (Sp) Channel
Cap (Fr) Cape
Costa (Sp) Coast
Dao (Ch) Island
-do (Kor) Island
Estero (Sp) Lagoon, Inlet
Estrecho (Sp) Strait
Golfo (Sp) Gulf
Guba (Rus) Bay
Gunto (Japn) Island group
Hai (Ch) Sea, Gulf
-hantō (Japn) Peninsula
Hu (Ch) Lake
Île (Fr) Island
Ilha (Por) Island
Isla (Sp) Island
Islote (Sp) Islet
Jiang (Ch) River
Jazirat, Jaza'ir (Ar) Island, Islands
-jima (Japn) Island
Kamennyy (Rus) Rocks
Kap (Dan) Cape
Kepulauan (Mal) Archipelago
Kray (Rus) Region
Lago (Sp) Lake
Lagoa (Por) Lagoon
Laguna (Sp) Lagoon
Morro (Sp) Cliff
Mys (Rus) Cape
-naikai (Japn) Inland sea
Nor (Mon) Lake
-ø (Dan) Island
Ostrov, Ostrova (Rus) Island, Islands
-øy, -øya (Nor) Island
Ozero (Rus) Lake
Poluostrov (Rus) Peninsula
Proliv (Rus) Strait
Puerto (Sp) Port
Pulau (Mal) Island
Recife (Por) Reef
Reka (Rus) River
Retto (Japn) Island group
Rio, Río (Por, Sp) River
Rivière (Fr) River
Roca (Sp) Rock
-saki (Japn) Cape
-selkä (Fin) Lake
Shima (Japn) Island
-shio (Japn) Current
-shotō (Japn) Island group
Sund (Dan) Sound
Sungai (Mal, Indo) River
-tō (Japn) Island
-vesi (Fin) Lake
Wan (Ch) Bay
-wan (Japn) Bay
-zaki (Japn) Cape
Zaliv (Rus) Gulf
Zemlya (Rus) Land

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INDEX TO SCIENTIFIC NAMES

This index includes all genus-group and species-group names—both valid and synonymous—of Recent marine mammals that are included in this account. Page numbers refer only to the formal entries in the main text and in Appendix 1; any passing mention elsewhere is not indexed. References to fossil, terrestrial, and other taxa are not included.

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