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Review

Cetaceans as Exemplars of Evolution and Evolutionary Ecology: A Glossary

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Abstract: Extant cetaceans (whales, dolphins, and porpoises) and their extinct ancestors offer some of the strongest and best-known examples of macroevolutionary transition as well as microevolutionary adaptation. Unlike most reviews of cetacean evolution, which are intended to chronicle the timeline of cetacean ancestry, document the current knowledge of cetacean adaptations, or simply validate the brute fact of evolution, this review is instead intended to demonstrate how cetaceans fittingly illustrate hundreds of specific, detailed terms and concepts within evolutionary biology and evolutionary ecology. This review, arrayed in alphabetical glossary format, is not meant to offer an exhaustive listing of case studies or scholarly sources, but aims to show the breadth and depth of cetacean research studies supporting and investigating numerous evolutionary themes.

Keywords: Cetacea; whales; dolphins; porpoise; evolution; macroevolution; paleontology; genetics

1. Introduction

Perhaps no story within the field of evolutionary biology has attracted more popular attention over the past half century as the evolution of whales. This is undoubtedly due to the steady stream of striking, significant, and substantial fossil finds, and to the general appeal of whales and dolphins to scientists and non-scientists alike. No general textbook of modern biology is complete without at least a minor section or box feature outlining the reversion of early cetaceans to the watery habitat of their pre-mammalian tetrapod ancestors, and the many consequent anatomical and ecological changes that followed this major shift [1–5]. This is a story well and broadly told in print, online, and in superb, instructive video documentaries. Where textbooks of the preceding century could reliably be counted on to depict evolution with the history of horses from *Eohippus* to *Equus*, cetaceans are now justifiably cited as prime exemplars of biological evolution. Given this ubiquity, Thewissen and Bajpai [6] crowned cetaceans as the current "poster child for macroevolution".

This paper is intended neither to reiterate the utility of cetaceans in validating the brute fact of evolution—a point well made in numerous popular books [7–10], magazines [11–13], and websites [14–18], and underscored by many excellent museum exhibits and other public resources—nor to review the current knowledge of cetacean ancestry, a timeline chronicled by a growing array of scholarly and popular works [19–33]. Instead, the aim is more narrowly targeted: To show how cetaceans aptly demonstrate specific evolutionary topics. I outline numerous examples of ways in which cetaceans fittingly illustrate detailed terms and concepts within evolutionary biology and evolutionary ecology. These are presented in alphabetical glossary form. They can be used by teachers or scholars searching for examples, or they can simply raise awareness about cetacean research. Neither the examples nor the cited references are meant to offer an exhaustive listing of case studies and illustrations. Rather, the aim is to provide readers, specialists, and non-specialists alike, with an appreciation for the breadth and depth of cetacean research studies.

Given their relatively rapid return to the sea, and hence major change in environment, it is instructive to examine all features of Cetacea within light of the terrestrial-to-aquatic transition.

For example, the multi-chambered cetacean stomach is well known. Is this a legacy of cetacean ancestry (specifically their close relation to—indeed, their classification within—Artiodactyla, many of which have stomachs with multiple compartments), or does this instead represent a functional adaptation: A mill for gastric breakdown of ingested food items in the absence of cusped teeth and mastication typical of mammals?

Like the compartmentalized stomach, many aspects of cetacean bodies and life history offer prime examples for explicating and elucidating evolution. The following list of examples runs the gamut from anatomical, behavioral, genetic, and physiological traits, all intended to demonstrate the ease and effectiveness with which Cetacea provides a deep, rich well of exemplars for teaching and studying evolution.

2. Examples of Evolutionary Terms and Concepts

Adaptation: There are dozens of excellent articles and books in both the classic and contemporary literature explaining numerous examples of cetacean adaptations. Chief among these are explanations of skull telescoping [34], the origins of echolocation and related changes to the ear [35–38], thermoregulation [39], different visual pigments in the eye [40], and different types of myoglobin and other respiratory pigments that bind oxygen [41,42].

Adaptive radiation: Adaptive radiations have been important in cetacean evolutionary history, both in the initial appearance of cetaceans from (presumed) raoellid ancestors as well as in other periods, such as the origin of Odontoceti and Mysticeti (for example, with the evolution of filter feeding) as well as smaller subgroups such as individual genera (e.g., *Stenella* dolphins) or families (e.g., beaked whales, Ziphiidae), or superfamilies (e.g., Delphinoidea) [31,43–46].

Aging/lifespan: The discovery of an old stone point embedded in a bowhead whale, *Balaena mysticetus*, launched a thriving subfield of cetacean studies focused on the remarkably long lifespan (100+ years) of mysticetes, with obvious ramifications for cetacean evolution [47,48]. Such research includes examination of the wax "glove finger" of the mysticete ear, isotopic studies of baleen, or racemization of eyeball amino acids.

Albinism: Albinism has been observed in many cetacean species including sperm, humpback, and killer whales and bottlenose dolphins [49]. This trait is normally governed by a simple genetic mutation, and demonstrates the impact of body coloration and social organization on survival.

Allen's rule: One of several so-called bioclimatic "rules", Allen's rule explains that organisms living at higher latitudes (with cooler climates) tend to have smaller extremities and appendages and thus have less relative surface area over which heat can be lost to the environment. This can be seen with bowhead whale flukes and flippers.

Alloparenting: Alloparenting behavior has been documented in several cetacean species, such as sperm whales that "babysit" juveniles while parents dive deep to forage, or bottlenose dolphin "aunts" (which may or may not be genetically related to true mothers) which help to rear young animals [50–52].

Allopatry: Although it is difficult for some people to see how marine species can be fully isolated geographically (i.e., in disparate and non-contiguous distributions) and thus open to allopatric speciation, demographic studies of whale and dolphin populations support cetacean allopatry [53].

Altruism (intraspecific): Altruistic behavior, which benefits another individual at potential cost to the animal performing the behavior, has been documented in many cetacean species, raising important evolutionary questions about the social circumstances that underlie the possible roots of moral behavior. Dolphins in particular have attracted attention for their apparent altruism to conspecifics, suggesting they may be reciprocal altruists [54].

Altruism (interspecific): Many examples of possible or probable altruistic behavior have also been documented in which a whale or dolphin comes to the aid of individuals of another species (as in epimeletic or care-giving behavior, listed below). This includes many anecdotes from both contemporary and ancient, classical times of whales or dolphins protecting smaller, vulnerable animals, such as seals or human swimmers, from drowning or from predators such as sharks [55]. The extent to which such behaviors might be instinctive, and to which cetaceans performing such behaviors recognize that the animals they are aiding are not members of their own species, is the object of much speculation.

Anagenesis: The possibility of cetacean taxa evolving via connected "straight-line" evolution (i.e., without cladogenesis) has been discussed [56].

Analogy/analogous features: Apart from examples of convergent evolution within Cetacea (see below), there are many obvious examples of cetaceans sharing analogous features (i.e., bearing similar form or function yet without a common evolutionary basis) with other taxa. Classic examples include the general fusiform body shape and stabilizing dorsal and pectoral plus propulsive caudal fins in sharks, ichthyosaurs, and dolphins [1–3].

Ancestral state reconstruction: Given their striking evolutionary history and increasingly well-known fossil record, reconstruction of ancestral states of cetaceans have been involved in many projects, often focused on body size (and in particular gigantism; see below) [57] but also involving changes in feeding mode over time [58,59].

Apomorphy: Examples of novel, derived traits that distinguish taxa, such as Cetacea or Mysticeti, include many detailed studies of ear bones [35–38,60,61], as well as analyses of dental and baleen morphology [62], plus highly derived bones or other cranial features related to feeding.

Atavism: The "reappearance" of "lost" hindlimbs or rudimentary yet enlarged pelvic elements are among the most notable and distinct examples of atavisms in any living animals [63].

Bergmann's rule: Like Allen's rule (see above), this bioclimatic "rule" holds that body size and shape vary by latitude, in this case with larger animals being found at higher latitudes, such that they have a relatively lower surface-to-volume ratio and correspondingly less heat loss from the body to cold ambient waters. The stout bowhead whale—which is not only more rotund than whales of other families but also of closely related right whales—is a prime example of this finding.

Biogeographical distribution: There are several good examples of cetacean distribution relating to evolution, such as the antitropical distribution of corresponding northern and southern species (such as right whale dolphins) [64], as well as the riverine and estuarine distribution of closely related or convergent taxa (such as river dolphins) [65].

Biological magnification: Cetaceans offer prime examples of biomagnification due to accumulation in tissues of neurotoxins from "red tides" as well as many types of anthropogenic pollutants including methylmercury and organochlorines [66–69].

Biostratigraphy: As is typical throughout paleontology, the fossil layers (geologic strata) in which cetacean fossils are found offer numerous clues to aid in dating the fossils as well as establish paleoecological or climatological information, making biostratigraphy a common and essential element of any fossil study [70].

Bone bed formation: Although some whale fossils, including whole skeletons, may be found isolated from bones of other individuals, the bones are frequently found in mixed "bone beds" containing fossils of multiple individuals, and sometimes multiple species. This is true of some of the oldest known archaeocetes as well as more recent whales and dolphins in many rich fossil localities, such as the Sharktooth Hill bonebed from the middle Miocene of California [71].

Capital breeding: As opposed to income breeders that use exogenous energy sources to "finance" reproduction, capital breeders build up and maintain internal energy stores before reproducing, a state that has been characterized for many mysticete species [72,73].

Carbon pump: The "fertilization" of primary production in epipelagic seas by the return of carbon, nitrogen, and other nutrients to surface waters via whale feces, has been documented and much discussed in recent years [74,75], with major implications not only for global nutrient cycles but also the key role of pre- and post-whaling cetacean populations in modulating and regulating oceanic ecosystems.

Character displacement: Basic studies of resource partitioning in cetacean taxa include studies of body size, skull telescoping and migration of external nares through evolution, and head shape and dental loss in many odontocete species [76,77].

Chronospecies: The idea that a single species might evolve directly (without divergence) into a morphologically distinct form, yielding a single species (or closely related sister species) connected over time in the fossil record (see entry for anagenesis), has been discussed for mysticetes such as minke whales [78].

Circumpolar: The bowhead whale is a good example of a single cetacean species with multiple breeding stocks in circumpolar distribution (e.g., from the Arctic Ocean to North Atlantic or North Pacific), which has clear implications for speciation, as the now-extinct population of Atlantic gray whales attests [79].

Coevolution: The contemporary and linked evolution of cetaceans with ectoparasitic whale "lice" provide a clear and strong example of host–parasite coevolution [80].

Coloration patterns: There have been several analyses of pigmentation and its relation to character displacement and species recognition, as well as to confusing or startling prey (as by the bright white flippers of humpback whales or asymmetrically colored jaws of fin whales); see countershading entry below [81].

Competition: Competition plays a major role in ecology and evolution, whether intraspecific, such as sperm competition between conspecific males [82], or interspecific, such as between whales and penguins and other species for krill and other food [83].

Constraints: Evolutionary outcomes depend on raw materials but also intrinsic (genetic) and extrinsic (environmental) constraints, which may explain why suspension feeding evolved in cetaceans but not marine reptiles [84], although a plesiosaur has recently been described that possibly was a filter feeder [85].

Convergence: There are many examples of convergent evolution within Cetacea but perhaps none more striking than the tusked, walrus-convergent *Odobenocetops* of the Miocene and Pliocene, whose skull, dentition, and presumed lifestyle appear to have closely mirrored that of the living walrus, *Odobenus* [86,87]. Another fine example of convergence involves a beaked whale-like Pliocene dolphin excavated from Antarctica [88].

Cooperation: Many cooperative behaviors, ranging from cooperative foraging to defense against predators, have been documented in cetaceans [89]. Some of these involve complex and instinctive or possibly learned traits. There also appears to be cooperative fishing with humans by some dolphins.

Countershading: A common coloration pattern in aquatic as well as terrestrial and aerial species, especially large predators, leads to light coloration on the animal's underside (so that it blends in with light from above) and dark coloration on the dorsal surface (so that an animal is hard to detect when viewed from above), and this countershading is prevalent in many cetacean species [81,90].

Culture: Several aspects of distinct cultural transmission of behaviors have been described in odontocete and mysticete species [91,92].

Death and dying behavior: There have been numerous documented instances of dolphins or other cetaceans carrying bodies of dead offspring, or of close attention paid to dead animals by various related and unrelated individuals in many cetacean species [93].

Degeneracy/"devolution": The loss of complex enamel structure (typical of nearly all non-cetacean mammals) is likely linked to the loss of dental function (typical mammalian mastication) in odontocetes; this loss of complexity appears to be an example of "devolution" [94,95]. Because such losses represent potential decline of reversal of evolution, they are often referred to as degeneracy.

Demography: The possible role of post-menopausal females in cetacean populations has spurred demographic studies focused on population breakdowns and genetics [96].

Disjunction distribution: The majority of whales, dolphins, and porpoises have disjointed (noncontinuous) geographic distributions, also known as range fragmentation. This is significant for demographic, genetic, and evolutionary reasons as well as ecological conditions [97,98].

Disruptive selection: An example of disruptive natural selection in cetaceans, apart from the obvious cases of ecological divergence based on foraging or biogeographic distribution, may involve a natural "knockout" of a basic cytokine protein that acts as an immune signal [99].

Dwarfism: The pygmy blue whale and dwarf and pygmy sperm whales are examples of subspecies and related species, respectively, that demonstrate evolutionary changes in body size (see also gigantism).

Ecotypes: One of the best examples of evolutionary divergence and resource-based character displacement involves the diversity of ecotypes among killer whales, long thought to represent a single species (*Orcinus orca*) but which may represent distinct species or subspecies in addition to clear ecotypes, such as stocks that feed mainly on salmon or other bony fish, those that prey largely on large sharks, and those that feed mainly on other marine mammals, including small porpoises and seals as well as huge whales [100,101].

Embryology: Although some morphologists studied cetacean embryos and fetuses hundreds of years ago, there is now a much more systematic study of the development of cetacean species, and particularly by using modern molecular and histological methods [102,103].

Encephalization and brain evolution: The story of cetacean brain evolution has attracted much attention in recent years, especially with regard to comparisons with the evolution of large, complex brains in hominins and other primates [104]. This promises to be fertile ground for evolutionary studies.

Endangered/vulnerable species: Several cetacean species have, for various reasons (largely whaling, ship strikes, fishing gear entanglement, and habitat destruction), been and in some cases continue to be highly endangered, including the North Atlantic right whale and the vaquita (a porpoise endemic to the Sea of Cortez which is nearly extinct).

Endemic: Like many organisms, cetaceans demonstrate endemicity, being confined to particular regions. In Cetacea this most commonly occurs in riverine or coastal dolphins [105].

Epigenetics: Apart from various means used to age individual whales and dolphins, such as accumulation of layers of dental tissues or clock-based degradation of molecules [106], epigenetic explanations (i.e., beyond genes) have been proposed to explain how cetaceans may fight cancer [107].

Epimeletic behavior: Care-giving behavior may include the altruistic behaviors described above (such as saving people or other animals from drowning or protecting them from predators) or simply devoting much care and attention to unrelated individuals [108,109].

Evolution of complexity: Just as the loss of odontocete enamel relates to loss of complex structure and function, the evolution of echolocation and vocalizing structures and behaviors in various cetaceans relates to the gain of complexity [33,36,95,110,111], as does the origin and evolution of baleen.

Evolutionarily stable strategy (ESS): Unlike an evolutionarily stable state, an ESS is a behavioral strategy that is fixed or cannot be "invaded" by an alternative gene-based behavior. Various altruistic and other cultural behaviors of dolphins or other cetaceans may qualify [54].

Evolutionary turnover: According to the turnover-pulse hypothesis, major environmental changes often spur major turnover and adaptive radiation of taxa, as is presumed to have occurred during the spread of Neoceti (crown cetaceans) due to Oligocene oceanographic changes [44,112].

Evolutionary-developmental biology ("evo-devo"): The role of regulatory genes leading to morphological changes in dentition and hindlimbs has been the subject of several studies [30,113,114].

Evolvability: The capacity of cetaceans for adaptive evolution due to their molecular and morphogenetic changes after leaving behind their terrestrial ancestry has attracted attention, often involving osteological changes related to ears and hearing or other parts of the cranium [115].

Exaptation: Much speculation about exaptation ("preadaptation") in cetaceans focuses on the hearing capabilities of the first cetaceans, which were amphibious and had water-adapted hearing that "exapted" them to evolve further into more fully aquatic habitats, and which led to diverse vocalizations (with corresponding brain and anatomical specialization) that ultimately led to echolocatory abilities [116,117].

Extinction: There have, of course, been many cetacean taxa that went extinct and are now known solely from fossil material, but there has also been a recent instance of a living species (the baiji or Yangtze River dolphin, *Lipotes vexillifer*) which was recently declared extinct [118].

Finite element analysis (FEA): Bite strength in living and extinct cetacean taxa has been analyzed by FEA [119].

Fission–fusion structure: Although more commonly studied in primates, this social structure (in which individuals of a species temporarily join, then go separate ways) has also been documented in various cetacean taxa [120].

Fitness: Among the many examples of evolutionary fitness in cetaceans, the role of the narwhal tusk stands out as an interesting and good example [121,122].

Food fall: There have been many studies investigating the trophic and other ecological roles of cetacean carcasses that decompose over many years on the seafloor (see entry on whalefall communities). These involve observations, experiments, and even analyses of fossil material [123,124].

Fossil dating: Fossils have been used to date divergence ages of extant lineages [125], and multiple methods have been employed to determine the age of cetacean fossils, ranging from traditional isotopic analysis and other molecular methods to geologic formation analysis and use of index fossils [126,127].

Fossil lagerstätte: A lagerstätte is a fossil locality with high diversity, often with numerous complete skeletons (such as the "valley of whales" bearing many basilosaurids and protocetids in Fayum, Egypt), and excellent quality of preservation, such as the Pisco Basin of Peru, where conditions led to preservation of baleen and even digestive tract contents [128,129].

Fossil reconstruction: Many aspects of cetacean form have been reconstructed in extinct taxa, ranging from body size and shape to the curvature and proportions of the spine and their role in locomotion [56,57,130,131].

Genetic drift—bottleneck: The effects of severe population size decrease, namely seemingly random fluctuations in allele and genotype frequencies, have been studied in populations of mysticetes and odontocetes [132,133].

Genetic drift—founder effect: Similar to bottlenecks, small groups can also have random genetic effects when new populations are founded by a very few individuals; this has been studied in various dolphin species [134,135].

Genomics: Several studies have looked at the evolution of the whole genome in particular cetacean species plus higher-level taxa [136–138].

Gigantism: Multiple recent studies have looked at the evolution of extreme body size in Cetacea with relation to various factors such as trophic ecology or biomechanics and morphology [139–141]. This includes not only the obvious mysticetes but also gigantic toothed whales [142].

Group selection: The concept of group selection (and levels of selection in general) is controversial in evolutionary biology, but studies of whale and dolphin sociality relate directly or indirectly to this topic [92,143].

Habitat loss: Sadly, there are many examples of the evolutionary effects of habitat loss affecting diverse cetaceans in prehistoric and modern times—with the latter obviously involving human impact [144].

Homology: Among the many obvious examples of homologous morphological structures in cetaceans are varied bones [145] and teeth [146]; there are of course homologous chromosomes and genes too.

Host–parasite interactions: There are many records of endo- and ectoparasites on and within different cetaceans, but also interesting evolutionary stories of "switching" of hosts inferred by DNA [147]. See entries below on parasitism and phoresis.

Human impact: Humans have played and continue to play a large role in influencing the evolution of cetaceans through such acts as whaling, driving climate change, and destroying habitats (see habitat loss) [148].

Human impact-anthropophily: A fascinating story of dolphins adapting to, and working cooperatively with, human fishing (in multiple locations around the world) reflects the roles of genes, instincts, and learning in driving cetacean social and behavioral evolution [149,150].

Hybridization: There have been widely reported instances of interspecific hybrid "wholphins" in captivity, but also numerous documented cases of hybrid dolphins and large whales (e.g., blue/fin whales) in natural habitats, spurring speculation as to speciation and genetic divergence [151].

Infectious disease evolution: Changes over time in frequency or at least documentation of various diseases in wild cetacean populations has focused not only on the diseases but also the role of human impact (from pollution and poor sanitation, etc.) in altering the evolution of these diseases and the way they infect whales and dolphins [152].

Irreducible complexity: Critics of evolution often argue that many traits are too complex to have evolved. Traits such as the large brains and echolocatory abilities have been mentioned among cetaceans. Darwin himself speculated, in the first edition of the *Origin of Species*, about the evolution of baleen and complex filtering form, function, and behavior from swimming bears catching aquatic insects that he presumed might someday evolve into whale-like creatures [153].

Iteroparity: Unlike semelparous organisms that reproduce just once before dying, iteroparous organisms have multiple reproductive events over their lifespan; in cetaceans the timing of this often depends on energy state and accumulation of nutrients [73].

Key innovation: There are many obvious examples of key innovations that ushered in major changes in the ecology and evolution of cetaceans, including the origins of baleen, echolocation, large brains, and structures associated with producing and receiving sound waves (such as the melon, mandibular "pan bone," and inner ear). The axial skeleton has also been offered as an example of a key innovation important to cetacean evolution [154].

Keystone predators: Killer whales have been proposed as a classic example of a keystone predator whose action helps to regulate the population dynamics and ecology of multiple species (from fish and sea otters to seals, sea lions, and other odontocetes) in marine ecosystems [155].

Kin selection: Alloparenting and related caregiving behaviors by sperm whales and post-menopausal "grandmother" killer whales has been posited as potentially being related to kin selection [96,156].

K strategy: Whales, dolphins, and porpoises are often presented as classic examples of the K-selected life history strategy favoring large bodies with slow growth and maturity, long lifespan, great devotion of resources to few offspring, and so on.

Life history: Analysis of the ways in which various life history factors (such as body size, lifespan, age of maturity, number of offspring, and so on) relate to cetacean evolution has been conducted [157].

Living fossil: The pygmy right whale, *Caperea*, has been proposed as a remnant of an otherwise ancient and extinct family of early mysticetes, the cetotheriids [158], although it appears that cetotheres persisted into the Pleistocene [159]. The Ganges river dolphin, *Platanista*, is similarly a remnant of a formerly diversified clade (Platanistoidea).

"Lumpers vs. splitters": These colloquial terms refer to the preferences among systematists to classify taxa into as few or as many species (or other taxonomic ranks) as possible. Depending on one's view, there may be 75–120 different extant cetacean species, with much of the disagreement involving dolphins, beaked whales, and rorquals of the genus *Balaenoptera*.

Mating and social systems: The intricacies of mating systems among diverse whale and dolphin species are often complex (befitting their social complexity) and interesting, as with the intense sperm competition of right whales, and have attracted much scrutiny [160,161].

Metonym (taxonomic synonym): There have been several instances of systematists taking names of extant or extinct cetacean taxa and reusing them to apply to a new taxon [162].

Migration: The relation of long migrations undertaken by whales and dolphins for mating, feeding, and other important activities related to survival and reproduction has been studied not only for specific taxa but in general terms [163].

Mimicry: A frequently cited instance of likely mimicry in Cetacea involves the shark-like appearance (with underslung jaws bearing sharp teeth, plus pigmented false gill slits) of dwarf and pygmy sperm whales, *Kogia*, although there are also many mentions of possible vocal mimicry.

Modularity: The concept of modularity, in which a structural or functional system can be subdivided into sets of autonomous yet interacting elements (which are altered and interrelated via "evo-devo" changes), has received much recent attention within evolutionary biology. This includes examples within Cetacea [164].

Molecular clock: Many estimates of the origins, divergences, and lifespans of various cetacean taxa have been derived from molecular data by many researchers [136,165–167].

Morphological disparity/phenotypic diversity: Many cetaceans display remarkable disparity (e.g., members of the beaked whale genus *Mesoplodon*), which has been used to study the evolution of Cetacea [44].

Morphological vs. molecular data: The long-standing issue of agreement between anatomical (often osteological) and molecular findings in resolving phylogenetic issues also includes several thorough analyses of cetaceans [117,140,168,169].

Morphometrics: Detailed morphometric studies of nearly every conceivable aspect of cetacean form have been carried out, ranging from overall body size and shape (as relates to locomotion or thermoregulation) as well as teeth, skin, brains, and varied skull structures; several such studies relate directly to phylogenetics and evolution [170].

Mosaic evolution: The extent to which cetacean form and function represents a blend of ancestral and derived characters has been considered in multiple studies involving various organs such as the brain [171]. The gradual loss of hindlimbs in archaeocetes and transition of the forelimb into the flipper also involve mosaic evolution.

Mutation: Along with general exploration of mutations involved in the terrestrial-to-aquatic transition of early cetaceans [1–3], many specific studies have examined specific gene mutations and their consequences in cetaceans, most notably involving key events in cetacean evolution (such the loss of body hair) and mutations related to olfaction, gustation, vision, and other senses [172–174].

Mutualism: Among the many described instances of mutualism in Cetacea are cases involving whales and non-cetacean taxa (such as seabirds, where the interaction may involve cleaning of parasites from whales as well as location of food sources), as well as discussions of mutualistic interactions (for example, for feeding or defense against predators) involving different cetacean species including interactions between dolphins and large whales [175,176].

Natural vs. artificial selection: The extent to which large-scale twentieth century industrial whaling may have inadvertently altered whale behavior, size, ecology, distribution, and so on, affords an excellent opportunity to compare the effects of human versus natural influences on evolution.

Neoteny and pedomorphosis: Among the many recent investigations focused on changes in developmental timing (see "evo-devo"), and in particular the retention of juvenile features, are comparative studies that closely examined the skulls of extant and extinct whales, dolphins, and porpoises [177,178].

Neuroscience: Outside of Primates, Cetacea is one of the most actively studied groups within the burgeoning field of evolutionary neuroscience, with many projects and publications looking at absolute and relative brain size, the organization of neural networks and brain regions, and the relationship between brain and behavior, including vocalization, sensation, and sociality.

Neutral theory: Many mutations within Cetacea are presumed to have had little to no effect on fitness, yet may elucidate phylogenetics or demographics [179].

Niche separation: The partitioning of food and other resources by contemporaneous humpback and minke whales in Antarctic waters offers a prime example of niche separation and competitive exclusion in Cetacea [180].

Nomenclature: The Latin binomials of many cetaceans—such as the beluga (*Delphinapterus leucas*, or "white dolphin without a fin"), narwhal (*Monodon monoceros*, or "one tooth, one tusk"), and humpback whale (*Megaptera novaeangliae*, or "big-winged New Englander")—offer good lessons in the principles and practice of naming taxa for experts and beginners alike, as do the common names of these species, along with others (killer whale vs. orca, rorqual, etc.).

Nutrient distribution/trophic connections: In addition to several recent studies that have looked at the role of whales in distributing nutrients throughout marine ecosystems, other investigations have explored trophic interactions between cetaceans and other marine predators (e.g., sharks and penguins) for food [83].

Opportunism: Whereas some cetaceans appear to be highly specialized, others, such as the bottlenose dolphin, *Tursiops* spp., are successful ecological opportunists, with obvious evolutionary ramifications.

Organ systems: All cetaceans offer prime examples of organs and organ systems highly modified by evolution, such as kidneys that adapted to the switch from a terrestrial to marine environment (with corresponding lack of fresh drinking water), or the lungs and diaphragm modified for greater tidal volume and more efficient pulmonary ventilation, etc. Vascular (often retial) adaptations for diving and thermoregulation are also excellent examples of fundamental evolutionary changes.

Orthogenesis: Studies of cetacean evolution and diversity have not provided evidence for the claim of progressive, directed (i.e., non-random) evolution, although the concept has been discussed [181].

Osteological correlates: The study of bony landmarks and their significance in denoting major functional changes important during cetacean evolution (such as palatal sulci relating to vasculature for baleen, or muscle scars relating to origin/insertion attachment points) has proven invaluable in cetacean paleontology and morphology.

Outgroup comparison: Numerous studies have affirmed the relationship of Cetacea within Artiodactyla (or Cetartiodactyla), with hippopotamuses as the outgroup [182]; other studies have examined outgroups within Cetacea, such as the placement of porpoises within Delphinoidea.

Pair bonding: The tucuxi (*Sotalia* spp.) is sometimes offered as an example of a cetacean with a pair-bonded mating system [183].

Paleoecology: Among the many studies of cetacean paleoecology are fascinating stories of the likely predation by the extinct giant shark *Carcharocles megalodon* on baleen whales of all sizes [184].

Parallel evolution: Comparisons between bats and odontocetes as a good example of parallel evolution of echolocation are common [185].

Paraphyly: Paraphyletic groups have been noted in cetacean systematics, especially with older classifications of river dolphins, and more recently with genetic analyses of delphinine dolphins including *Stenella* and *Tursiops* [186].

Parasitism: Cetaceans are definitive hosts for numerous ecto- and endoparasites, including *Anisakis* worms, which easily spread to humans who eat raw or undercooked fish.

Phenetic vs. cladistic systematics: Just as there have been comparisons of molecular and morphological findings in resolving systematic and phylogenetic debates about cetacean taxonomy, so too differing results of phenetics (systematics based on similarity of form) and cladistics have yielded different conclusions, and debate [170].

Phoresis: Cetaceans are well known to "carry" (in a sort of commensal mutualism) many species of ectoparasitic barnacles, worms, and whale lice, along with remoras [187]. This is related to parasitism (see entry above).

Play behavior: Play, considered an important element and indicator of complex social interaction and cognitive ability, has been documented within numerous wild and captive cetaceans [188].

Pleiotropy: The reproductive tracts of some cetaceans may demonstrate pleiotropic genetic interactions [189].

Plesiomorphy: Enamel patterns [190] within cetaceans have been cited as an example of ancestral (plesiomorphic) traits persisting in modern taxa; to a lesser extent, ear bones, although highly modified in Cetacea, also demonstrate some plesiomorphic features [60,61].

Polydactyly vs. polyphalangy: Whales largely retain the plesiomorphic condition of five digits in the forelimb (flipper), although there are instances of digit reduction in cetaceans [191]. Cetaceans, like many other aquatic tetrapods, also are unusual in having an abnormally large number of phalangeal bones within each digit, such that flipper osteology offers a good example of mosaic evolution.

Polygyny: Polygynous mating systems, in which one male has access to a "harem" of several reproductively receptive females, can be found in many cetacean species ranging from sperm to humpback whales [192].

Polymorphism: There are many examples on (and many published papers on) diverse morphological, behavioral, and molecular traits within Cetacea [193].

Polyphyly: The diverse dolphin genus *Lagenorhynchus* is sometimes offered as an example of a potentially polyphyletic taxonomic grouping within Cetacea [132,193].

Rate of evolution: The extent to which evolution occurs via incremental gradualism or sudden leaps plays a role in studies of neutral mutations, molecular clocks, and regulatory gene interactions (see entries for all items in this list), and cetaceans have provided fodder for interpretations of both slow and rapid evolutionary change, often dependent on environmental factors and the origin of key innovations [194].

Red Queen hypothesis: A spiraling evolutionary "arms race" between cetacean immune systems and pathogens, possibly including neurotoxins from paralytic shellfish poisoning, has been cited as an example of Van Valen's famous "Red Queen hypothesis," in which taxa must "keep moving just to stay in one place" [56,195].

Regulatory genes: Homeobox and other regulatory genes (like *sonic hedgehog* and *Hox*) have been cited as important in major evolutionary transformations throughout the history of Cetacea involving form and function, such as limb and dental loss and the origins of baleen and echolocation [137].

Relict populations: Diverse river dolphin taxa as well as some oceanic dolphins, notably the rough-toothed dolphin (*Steno*), have been proposed as ancestral relict populations throughout their distribution or in some locales [196].

Reproductive isolation: Reproductive isolation between cetacean populations and subpopulations have been cited as important steps toward speciation or other genetic and cultural divergence [60,64,197].

Reproductive senescence: Like some higher primates, several cetacean species have been noted as having frequent and important post-reproductive phases, including "grandmother" killer whales that potentially pass along cultural knowledge [198,199].

Resource partitioning: There have been several published examples of resource partitioning within Cetacea (e.g., of different Antarctic whale species partitioning prey or feeding habitat) as well as of cetaceans partitioning resources with other marine species including sharks and seabirds [200].

Ring species: Although there is no definitive example of a cetacean ring species, the presence of numerous subspecies, interspecific hybrids, and intergraded populations of widely dispersed species (often with circumpolar distributions, as in killer whales) makes the prospect of the ring species concept within Cetacea a distinct possibility.

Scaling (isometry vs. allometry): Dozens of publications demonstrate the roles of linear and nonlinear scaling effects in the evolution of cetacean structures ranging from bones, limbs, organs, tissues (such as skin thickness), and other features. These indicate that scaling has played a prominent role in cetacean polymorphism and phenotypic disparity [201].

Selective sweep: Studies of genetic diversity within various cetacean taxa, including some (like sperm whales) with less diversity than expected, demonstrate the likely role that strong selective sweeps play in fixing alleles within a population [202].

Sensory biology: Although studies of cetacean ears and hearing have long attracted research interest, many recent studies have demonstrated that other sensory modalities (vision, olfaction, etc.) are far more complicated and important in cetacean ecomorphology and evolution than generally appreciated [172–174].

Sexual conflict: The likelihood of diverging male and female reproductive strategies (and counterstrategies) in mating behavior and anatomy has led to a greater recognition of and research interest in applications of sexual conflict theory within Cetacea [203].

Sexual dimorphism: Sexual dimorphism is common in many cetaceans. In mysticetes, females are generally larger than males, but in odontocetes males are typically larger, often dramatically so (e.g., sperm and killer whales).

Sexual selection: The large tusk of narwhals and prominent mandibular teeth of ziphiids (which in many taxa erupt solely in males) are commonly cited examples of sexual selection in Cetacea. These teeth are often considered to play a role in competition for females, either via display or direct male-to-male fighting [56,204].

Speciation: Antitropical distributions have been cited as a means of enabling allopatric speciation in Cetacea, although other rapid genetic changes or morphological and behavioral disparity (leading to reproductive isolation) might in turn lead to sympatric or parapatric speciation [56,64].

Stabilizing selection: Several genes have been described as having been "purified" or fixed and stabilized at high levels within cetacean populations [42].

Stable isotope analysis: For several decades stable isotopes isolated from various tissues (bones, baleen, etc.) have been widely used to indicate many parameters including distinct populations, ecological states (e.g., trophic levels), and physiological condition (e.g., stress, reproductive condition, age, etc.) [205,206].

Subspecies: Genetically and morphologically distinct subspecies have been described for many species of dolphins and whales, including, for example, humpback and fin whales [207].

Symbiosis: Among the many symbiotic interactions involving cetaceans, familiar examples include multiple species of barnacles that depend exclusively on whales or dolphins for dispersal.

Sympatry: Many cetacean species have been described as sympatric, including river dolphins sharing isolated habitats as well as oceanic whales and dolphins with neritic or pelagic habitats [208,209].

Taphonomy: The condition and potential taphonomic alteration of many fossil cetacean materials has been well described [71,210–212].

Tool use: Researchers have described the use of natural sponges or similar materials by dolphins searching for prey in benthic sediments, a behavior that appears to be culturally transmitted [213].

Top-down vs. bottom-up trophic cascades: Researchers have described examples of differing trophic cascades involving whales, dolphins, and porpoises, where either the cetacean (as a large predator) heavily influences the presence and abundance of primary producers and consumers, in a so-called top-down cascade [214], as well as cases of bottom-up cascades where species lower in a trophic pyramid influence the abundance of cetaceans and other large predators [83], such that both types of trophic cascades apply to cetaceans [215,216].

Transitional fossils: Considering the remarkable evolutionary transitions that have occurred throughout cetacean history, such as wholly living, locomoting, and hearing in water instead of air, or capturing prey by filtering with baleen instead of grasping with teeth, there have been many taxa described as classic transitional fossils, indicating forms intermediate between other known forms [1–12].

Vestigial features: Cetaceans are among the best-known and frequently cited examples of organisms displaying vestigial features. These include pelvic and limb bones, and hairs and hair follicles.

Vicariance: Extant river dolphins and extinct cetotheres are among the notable taxa whose vicariance (geographic separation into discontinuously distributed groups) has been studied [217,218].

Whalefall community: As previously noted in the entry on food falls, cetacean carcasses often remain on the seafloor as an important contributor to benthic trophic webs. These dead bodies, which may take years to be fully digested and decomposed, form the basis for distinctly unique benthic "whalefall" communities [123,124].

3. Conclusions

Every group of organisms can be used to highlight specific facets of evolution and evolutionary ecology, but extant and extinct whales, dolphins, and porpoises perhaps demonstrate the breadth of evolutionary topics better than any other taxon. The items listed in this glossary are intended to demonstrate the wide range of topics studied by cetacean scientists (they are not meant to provide a complete, exhaustive listing), and this list will undoubtedly grow as new methods yield new insights and discoveries. As surely as cetaceans continue to evolve, so too the fields of study involving them continue to evolve as well.

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