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A complete phylogeny of the whales, dolphins and even-toed hoofed mammals (Cetartiodactyla)

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ABSTRACT

Despite the biological and economic importance of the Cetartiodactyla, the phylogeny of this clade remains controversial. Using the supertree approach of matrix representation with parsimony, we present the first phylogeny to include all 290 extant species of the Cetacea (whales and dolphins) and Artiodactyla (even-toed hoofed mammals). At the family-level, the supertree is fully resolved. For example, the relationships among the Ruminantia appear as (((Cervidae, Moschidae) Bovidae) (Giraffidae, Antilocapridae) Tragulidae). However, due to either lack of phylogenetic study or contradictory information, polytomies occur within the clades *Sus*, *Muntiacus*, *Cervus*, Delphinidae, Ziphiidae and Bovidae. Complete species-level phylogenies are necessary for both illustrating and analysing biological, geographical and ecological patterns in an evolutionary framework. The present species-level tree of the Cetartiodactyla provides the first opportunity to examine comparative hypotheses across entirely aquatic and terrestrial species within a single mammalian order.

Key words: Cetacea, Artiodactyla, Cetartiodactyla, supertree, matrix representation with parsimony (MRP), comparative methods.

CONTENTS

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I. INTRODUCTION

Taxonomically complete phylogenies are needed to conduct rigorous comparative analyses of evolutionary patterns and processes. Comparative methods are now inherently statistical in nature (Harvey & Pagel, 1991) and require sufficient statistical power to be done properly. This power is ultimately derived from the number of sister-group relationships that are resolved in a given phylogeny. Larger phylogenies enhance the potential number of sister pairings and therefore allow for more statistical power and a greater confidence in the results. An immediate approach for constructing a complete phylogeny is the supertree method, which quickly provides rigorous and comprehensive phylogenies (Bininda-Emonds & Bryant, 1998; Bininda-Emonds *et al.*, 2002). To provide an independent assessment of the phylogenetic relationships resolved in the supertree, the topology is compared to the most comprehensive character-based tree available for the Cetartiodactyla, that of Gatesy *et al.* (2002).

Here, we present the first synthesis of cetacean and artiodactyl phylogeny into an inclusive species-level phylogenetic hypothesis using supertree methodology. Aside from its systematic value, the phylogeny of the Cetartiodactyla is also of general interest because the phylogeography of domesticated artiodactyls might illuminate certain aspects of human evolution.

Throughout human history, cetaceans and artiodactyls have been of both cultural and economic importance. For example, recent discovery of rock carvings in South Korea provides evidence that whaling existed in prehistoric times (somewhere between 6000 and 1000 B.C.) (Lee & Robineau, 2004) and in the 18th and 19th century whaling briefly became a commercial industry to provide oil for lamps and heating. Since the moratorium on commercial whaling in 1986 the most immediately obvious value of cetaceans stems from their aesthetic appeal to all cultures as illustrated by the popularity of whale-watching trips and by the rich mythology associated with these animals. One of the earliest records is from the 5th century B.C., where Herodotus chronicles the myth of the musician Arion who is saved from the sea and carried to shore by a dolphin.

The importance of the artiodactyls stems from their utility; the earliest known art, circa 28000 B.C., is cave paintings (Chauvet Cave, Vallon-Pont-d'Arc, France) depicting large hoofed mammals some of which have been wounded by arrows. Between 8000 and 2500 B.C. artiodactyls were domesticated, providing a variety of products and services such as meat, transportation, draft power, fertiliser, wool, leather and dairy. It is this utility that has led to the assertion that animal domestication was crucial to the development of human civilisation (Diamond, 1996). Worldwide, the Artiodactyla is the most valuable source of domesticated species, including pigs (*Sus scrofa*), sheep (*Ovis aries*), goats (*Capra hircus*), cows (*Bos taurus*), bactrian camels (*Camelus bactrianus*), dromedary camels (*Camelus dromedarius*), water buffalo (*Bubalus bubalis*), llamas (*Lama glama*) and alpacas (*Lama pacos*). Domesticated artiodactyls are of global economic value far beyond the native range of their ancestors. For example, the revenue from meat of *B. taurus*, which is thought to have originated in the Middle East, totalled $36 322 million dollars in the USA in 1997 (USDA, 1997). In Australia, 7 % of gross agricultural production and A$3.8 billion in export income is obtained from the wool industry alone (Shafron *et al.* 2002).

Despite the interest shown in cetaceans and artiodactyls, their precise phylogenetic relationships remain controversial. As early as 1891, Flower observed a close affinity between the superficially very different Artiodactyla and Cetacea. Flower emphasised the resemblances of the larynx, stomach, liver, reproductive organs, and foetal membrane between pigs and whales (as summarised in Gregory, 1910). Until recently, it was generally believed that although artiodactyls and cetaceans both shared a condylarthran ancestry, the whales were the sister-taxon of the extinct mesonychids (e.g. Van Valen, 1966), whereas artiodactyls descended from arctocyonid condylarths (Van Valen, 1971; Rose, 1996). This view was supported by modern morphological evidence (O'Leary, 1999; Gatesy & O'Leary, 2001). By contrast the majority of post-1994 molecular studies resolved a paraphyletic Artiodactyla with Cetacea nested within the artiodactyls as sister to hippopotamids (Irwin & Arnason, 1994; Gatesy *et al.*, 1996; Shimamura *et al.*, 1997), forming a clade known as the Cetartiodactyla. The recent description of two archaic whales that revealed clear morphological homology between cetaceans and artiodactyls to the exclusion of mesonychids (Gingerich *et al.*, 2001; Thewissen *et al.*, 2001) has more or less reconciled the morphological and molecular view of cetacean and artiodactyl phylogeny. However, little morphological evidence exists to support the sister-taxon relationship between Hippopotamidae and Cetacea.

Relationships within, as opposed to between, the cetaceans and artiodactyls have been no less controversial. The higher-level phylogeny of the artiodactyls remains highly unstable. The only consensus is that six families cluster to form the Ruminantia (Tragulidae, Moschidae, Antilocapridae, Cervidae, Bovidae and Giraffidae) with the tragulids at the base (e.g. Randi *et al.*, 1996; Montgelard *et al.*, 1997; Matthee *et al.*, 2001). Relationships both within the Pecora (Ruminantia minus Tragulidae) (e.g. Gatesy *et al.*, 1996; Hassanin & Douzery, 1999*b*; Su *et al.*, 1999; Hassanin & Douzery, 2003) and among non-ruminants (e.g. Cronin *et al.*, 1996; Geisler, 2001; Madsen *et al.*, 2001) remain controversial.

There have been several proposals that cetaceans are polyphyletic in origin (e.g. Yablokov, 1964), with toothed and baleen whales having evolved independently from different ancestors. Although upholding cetacean monophyly, Milinkovitch *et al.* (1993) questioned the monophyly of each of these two groups, suggesting that Physeteridae are more closely related to Mysticeti (baleen whales) than they are to the other Odonotoceti (toothed-whales). Both suggestions were debated, with the current consensus favouring the traditional view of a monophyletic Cetacea (e.g. Van Valen, 1968) composed of the two traditional monophyletic suborders (e.g. Arnason & Gullberg, 1994; Cerchio & Tucker, 1998; Messenger & McGuire, 1998).

Here, we address these phylogenetic controversies within the Cetartiodactyla using supertree construction to produce the first complete species-level phylogeny of this clade based on a robust methodology. Supertrees combine previously published phylogenetic estimates, as compared to the more conventional method of combining raw character data (DNA sequences, morphological characters). Supertree approaches currently represent the best possibility for building a complete cetartiodactyl phylogeny. At present, building a complete tree from a single molecular or morphological dataset is not possible because not all the species have been sampled for the same character(s). Even the combination of these single raw datasets in a total-evidence framework (*sensu* Kluge, 1989) is hindered by the lack of compatible overlapping datasets. Currently, the largest published cetartiodactyl total-evidence tree based on a broad selection of data sources contains only 51 out of the 290 extant species (Gatesy *et al.*, 2002), although a virtually complete tree could be constructed from the mitochondrial genes cytochrome *b* and 12S rDNA (John Gatesy, personal communication). By contrast, supertrees can combine all available phylogenetic hypotheses to yield a complete cetartiodactyl tree that may serve as a foundation for phylogenetic comparative analyses and will highlight poorly known or controversial areas that are especially in need of additional data collection.

II. METHODOLOGY

(1) Data collection

Sources of phylogenetic information were collected from the literature by searching Web of Science and BioAbstracts using the keywords Artiodactyl* and Cetace* and extracting articles that were likely to contain phylogenetic information. Additional information was found by searching BIOSIS using the terms Artiodactyl* or Cetace* with any of phylogen*, fossil*, systematic*, cladistic*, cladogram*, phenogram* and taxonom*. Finally, bibliographies of all collected papers were searched to find any additional papers.

All methods of phylogenetic estimation (including informal techniques with no algorithm) were accepted from sources dating from 1960 onwards. However, the only taxonomies to be included were those from Grubb (1993) and Mead & Brownell (1993), which include all 212 extant artiodactyl species and all 78 extant cetacean species. Together, these two taxonomies act as a 'seed tree' (Bininda-Emonds & Sanderson, 2001) that overlaps with all source trees to produce a backbone for the analysis. The seed tree will provide minimal phylogenetic information for taxa that are little studied but can be easily overruled by more robust source trees where more phylogenetic information is available. No other taxonomy was included because there is no way of accounting for duplication of information among taxonomies. The source trees were stored by drawing the tree exactly as presented in the original paper into the tree view window of MacClade (Maddison & Maddison, 2003) and saving them in a single nexus-formatted treefile (Maddison, 1997).

(2) Tree building

There are an increasing number of methods of supertree construction (Bininda-Emonds, 2004). We employ the most commonly used approach, matrix representation with parsimony (MRP) (Baum, 1992; Ragan, 1992). MRP converts all source-tree topologies into a matrix based on simple graph theoretic principles. For every source tree, the informative nodes are represented as a series of partial binary 'pseudocharacters'. Taxa descended from a given node are coded as '1', taxa that are not descended from that node are coded as '0', and taxa that do not appear on a given source tree are represented by a '?'. Both rooted and unrooted source trees were used. For rooted source trees, an all-zero hypothetical ancestor is added to the matrix to preserve this rooting information. For unrooted source trees, this hypothetical ancestor is coded entirely using '?' (Bininda-Emonds, Beck & Purvis, in press). The final matrix is then analysed using conventional parsimony analysis to generate the supertree topology. Like all methods of phylogenetic inference, critical selection of the source data in a supertree analysis is key. Without quality control, duplicated datasets and phylogenies derived using less robust inference methods can bias the resultant supertree (Springer & de Jong, 2001; Gatesy *et al.*, 2002). To reduce the occurrence of dataset duplication, the protocol of Bininda-Emonds *et al.* (2004) was followed. It establishes a set of rules that lead to the rejection of all source trees that duplicate character data in other studies without adding a substantial amount of new data/species. The addition of new data/species can lead to very different phylogenetic results and hence were such studies considered 'independent' phylogenetic estimates.

Another issue with particular importance for the cetartiodactyl clade is the inherent historical dimension of supertree analyses (see Bininda-Emonds *et al.*, 1999). For example, the hippo-whale clade was first proposed by Irwin and Arnason (1994) and is supported by the vast majority of molecular data. However, this relationship is likely to be swamped in the matrix by traditional hypotheses that have a longer history in the literature. In this study, neither the Artiodactyla nor the Cetacea were assumed to be monophyletic because such assumptions are inadvisable (Springer & de Jong, 2001; Gatesy *et al.*, 2002), particularly when there is conflicting evidence, as seen in the Cetartiodactyla.

To account for differences in species definitions and taxonomy, species names were standardised using the synonymy list in Grubb (1993) and Mead & Brownell (1993) implemented in the Perl script synonoTree.pl (Bininda-Emonds *et al.*, 2004). All species discovered post-1993 (e.g. *Pseudoryx nghetinhensis*) were necessarily excluded because they could not be placed with respect to the reference taxonomy (Grubb, 1993; Mead & Brownell, 1993). Genus-level tips in the source trees were assigned the type species for that taxon (following Jones *et al.*, 2002; Bininda-Emonds *et al.*, 2004). Any taxon that could not be unambiguously assigned to a species was pruned from the source tree. All mammalian species in the source trees that were not members of the cetartiodactyl clade were reduced to a single terminal taxon (outgroup) that was used to root the supertree: source studies consisting of cetartiodactyl species only were purposely unrooted and encoded as such (following Bininda-Emonds *et al.*, in press). All other taxa in the source trees that were not extant mammals were deleted from the source tree. After standardization of species names, the source trees were converted to MRP additive binary coding (Ragan, 1992; Baum & Ragan, 1993) using the Perl script SuperMRP.pl. (Matrix available at www.treebase.org/treebase study accession number S1188, matrix accession number M2055).

The full MRP matrix was analysed without topological constraints (i.e. without assumptions on sub-ordinal monophyly). A parsimony ratchet was used to analyse the matrix as it searches a greater proportion of tree space more effectively than other heuristic searches (Nixon, 1999; Quicke *et al.*, 2001). Briefly, the ratchet operates through a series of fast searches coupled with differential character weighting. From an initial starting tree, a random proportion of the characters are upweighted and further searches on the tree are continued. The characters are then returned to their original weights and the search is continued. The single tree resulting from this iteration is then saved and a new iteration of re-weighting is initiated. Specifically, the form of the ratchet was 100 batches of 1000 reweighting iterations each (i.e. a '100.1000' ratchet). The initial tree was found using a single random addition sequence followed by Tree Bisection Reconnection (TBR) branch swapping. For each iteration, a randomly chosen 25% of the pseudocharacters were upweighted by a factor of two; TBR branch swapping was used in all cases to return a single tree at each step. All saved trees were then taken as the starting points for a final brute-force TBR search with all pseudocharacters given equal weight. For quicker processing, the ratchet search was split into 10 batches each running 10 000 replicates (i.e. 10 10.1000 ratchets) and submitted to the University of Virginia Aspen Linux cluster running the Linux version of PAUP* v4b10 (Swofford, 2003). The outputs from the 10 batches were combined and the final brute-force search was run on a single node of the cluster saving 100 000 equally most parsimonious trees. These were combined as a strict consensus tree to give the full species-level supertrees presented in Figs 1–4. The instructions for the ratchet were written using the Perl script perlRat.pl and implemented in PAUP*.

(3) Assessing support

We employed two different techniques to assess the support for our inferred supertree topology in relation to the set of source trees. First, we examined the impact of poorer quality source trees on the supertree. The inclusion of such source trees in a supertree analysis remains a point of contention. Despite strong empirical evidence that poor-quality source trees generally do not impact the supertree analysis negatively (Purvis, 1995; Bininda-Emonds *et al.*, 1999; Jones *et al.*, 2002; Stoner, Bininda-Emonds & Caro, 2003), the inclusion of such data remains sharply criticized (Gatesy *et al.*, 2002, 2003; Gatesy *et al.*, 2004; Gatesy & Springer, 2004). The conventional method to assess the effect of source tree quality has been to downweight poorer quality source trees by a factor of 4:1. However, we employed the more stringent criterion advocated by Gatesy *et al.* (2004) of excluding all source trees derived from informal or less rigorous phylogenetic techniques (e.g. chromosome banding, parsimony by eye, best phylogenetic guesses, UPGMA) altogether. This resulted in the removal of 396 (of 2068 total) pseudocharacters from the full matrix as well as 38 species, the positions of which were known only from the

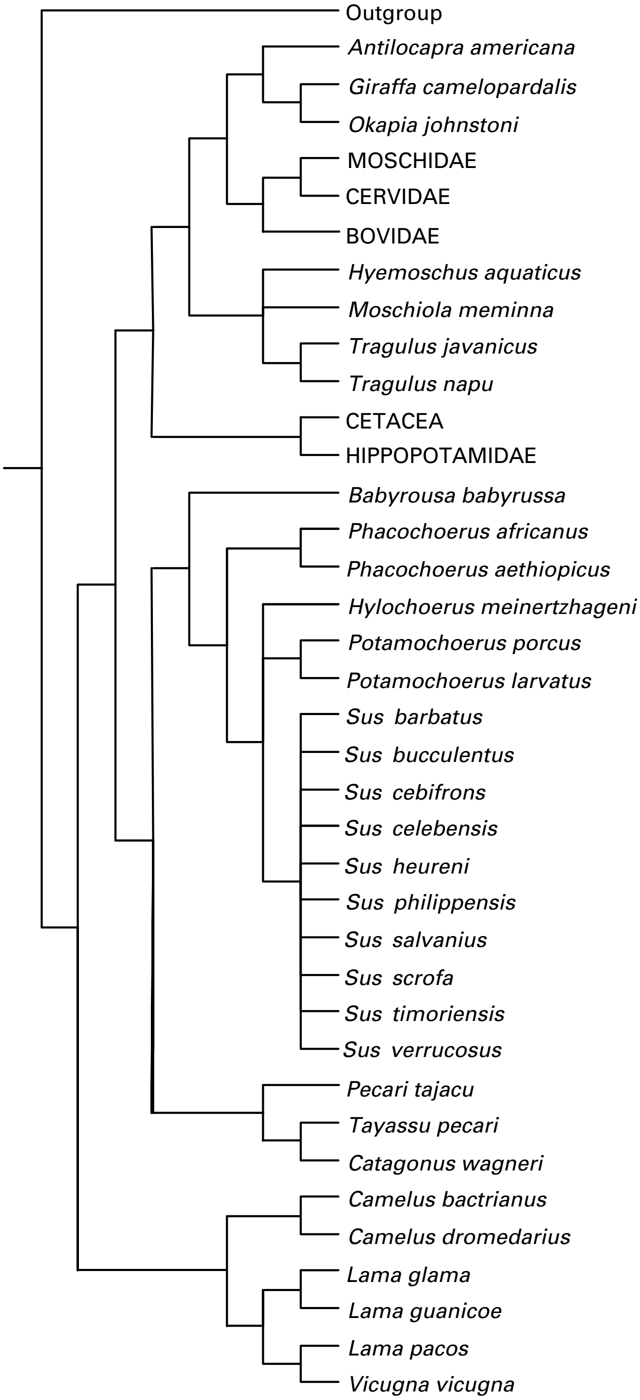


Fig. 1. Complete higher-level cetartiodactyl supertree. The Bovidae, Cervidae and Cetacea have been collapsed down to the family level; the species-level phylogenies of these families are presented in Figs 2–4.

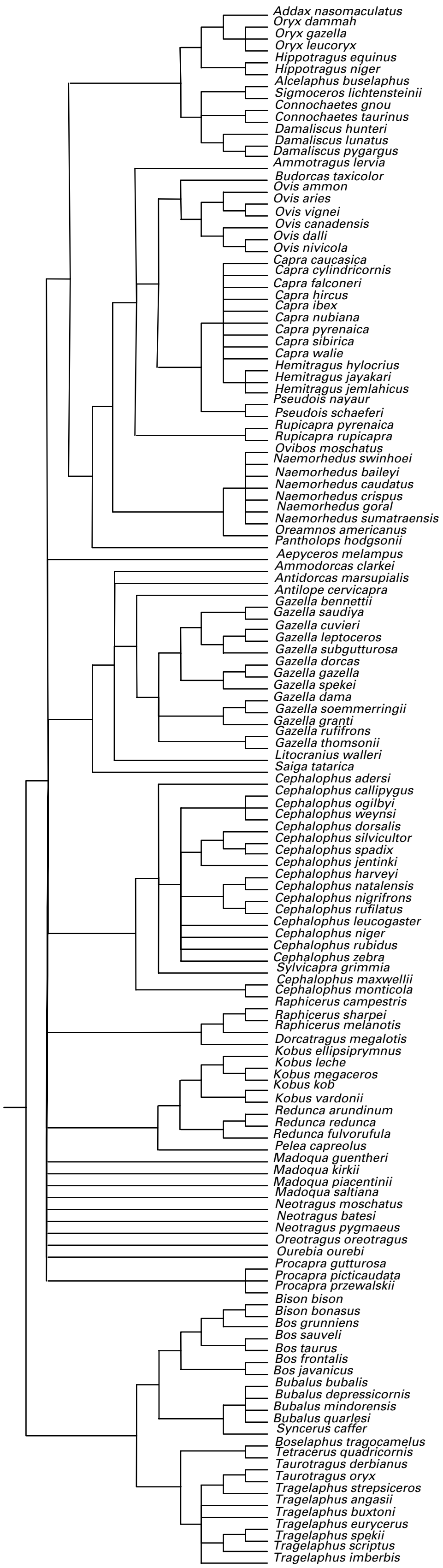


Fig. 2. Complete species-level phylogeny of the Bovidae.

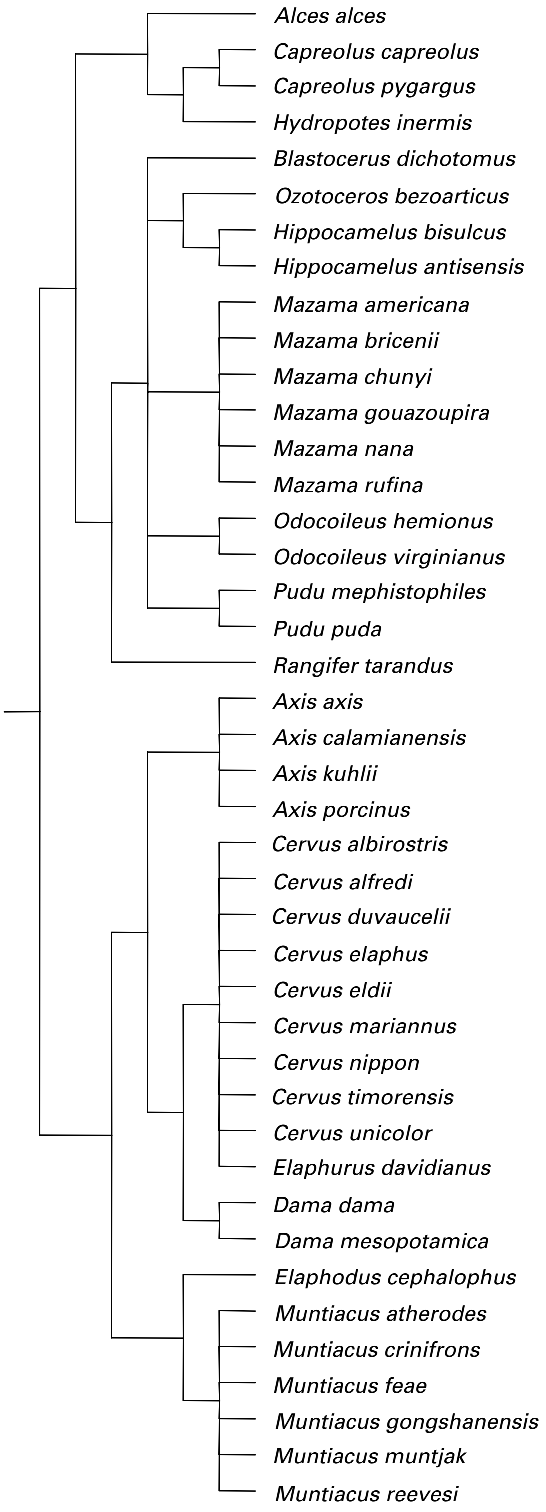


Fig. 3. Complete species-level phylogeny of the Cervidae.

two taxonomic sources. The reduced matrix was analysed in the same manner as for the full matrix to yield a second, reduced supertree.

Second, we assessed the amount of support for individual nodes of the supertree among the set of source trees

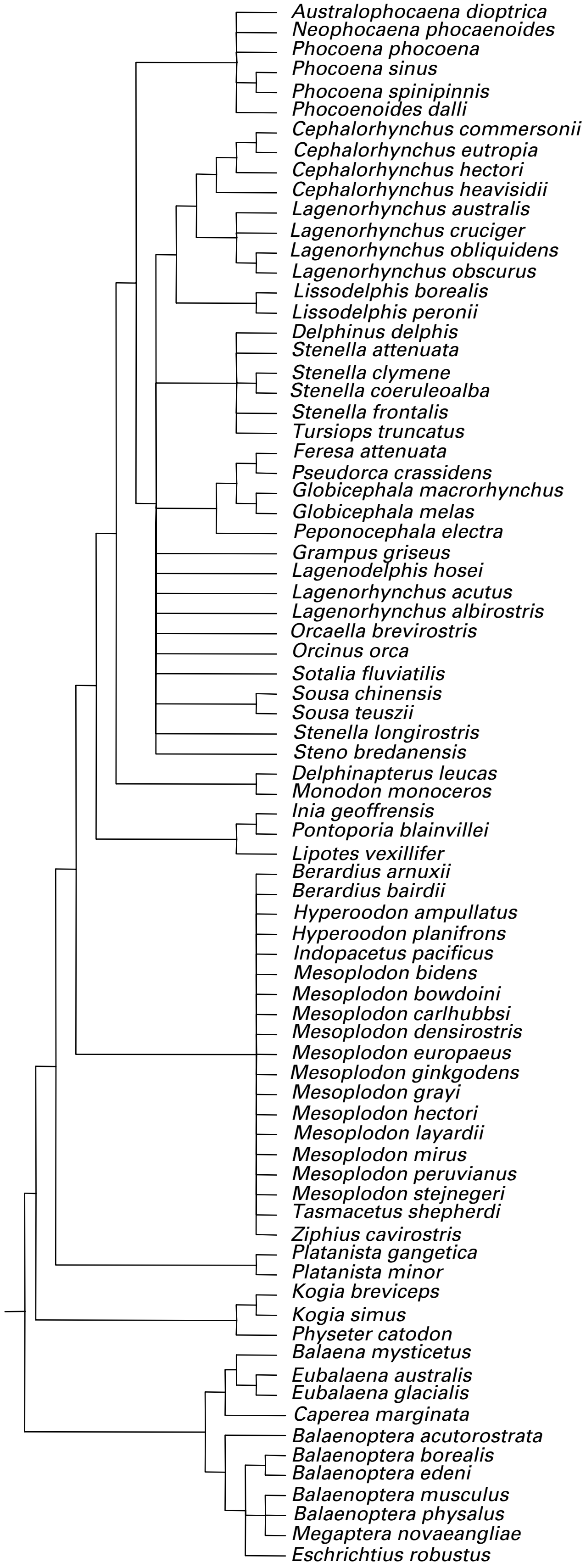


Fig. 4. Complete species-level phylogeny of the Cetacea.

using the qualitative support (QS) index (Bininda-Emonds, 2003). Unlike traditional character-based phylogenetic support measures (e.g. Bremer support or the bootstrap), the QS index was specifically designed for (MRP) supertree analyses and accounts for the inherent non-independence among MRP-encoded 'pseudocharacters'. Briefly, the QS index quantifies the relative degree of support among the set of source trees for each node in the supertree. Specifically, it determines whether a given source tree supports, conflicts, or is equivocal with respect to a given node. The results are then summed across the set of source trees and normalized to fall between +1 and −1, with the two values indicating that all source trees directly support (+1) or conflict (−1) with the supertree clade in question. Intermediate values indicate the relative amount of support *versus* conflict among the set of source trees. Note that the QS index is purely descriptive, such that factors that increase the likelihood that the supertree clade will be contradicted (e.g. a clade of large size and/or a high number of source trees) will result in increasingly negative values (for more information, see Bininda-Emonds, 2003).

We used two variants of the QS index. In the first (the full QS index, QS), the supertree as given was compared to the source trees. In this case, some taxa present on the supertree might be missing from the source tree, such that it must be determined whether the source tree can potentially support or conflict with a given supertree clade, leading to hard and soft concepts of support and conflict. In the second variant (the reduced QS index, rQS), the supertree was pruned to the same taxon set as the source tree it is being compared to and support *versus* conflict can be determined absolutely.

(4) Tree comparison

Calculations of congruence between tree topologies were performed in PAUP* (Swofford, 2003) using two different tests: the symmetric difference metric (d_S, Robinson & Foulds, 1979, 1981) and the consensus fork index (*sensu* Colless, 1981). The symmetric difference distance calculates the number of groups that appear on one tree or the other but not on both. The consensus fork index (CFI) quantifies the amount of resolution in the consensus tree (of the trees being compared) by dividing the number of non-trivial clusters (two or more taxa) by the maximum possible (number of terminal taxa minus 2) number of non-trivial clusters. If one or more of the trees being compared contains polytomies, the CFI will be lower as polytomies are treated as incorrect. Three comparisons were made: full supertree *versus* reduced supertree, full supertree *versus* most comprehensive total-evidence tree (Gatesy *et al.*, 2002) and reduced supertree *versus* most comprehensive total-evidence tree (Gatesy *et al.*, 2002). Because the trees contained different taxon sets, the more inclusive supertrees were pruned in MacClade (Maddison & Maddison, 2003) until the taxon sets were matching. In cases where higher taxon names were used, the supertree species names were converted to the appropriate genus/tribe and collapsed to a single terminal branch.

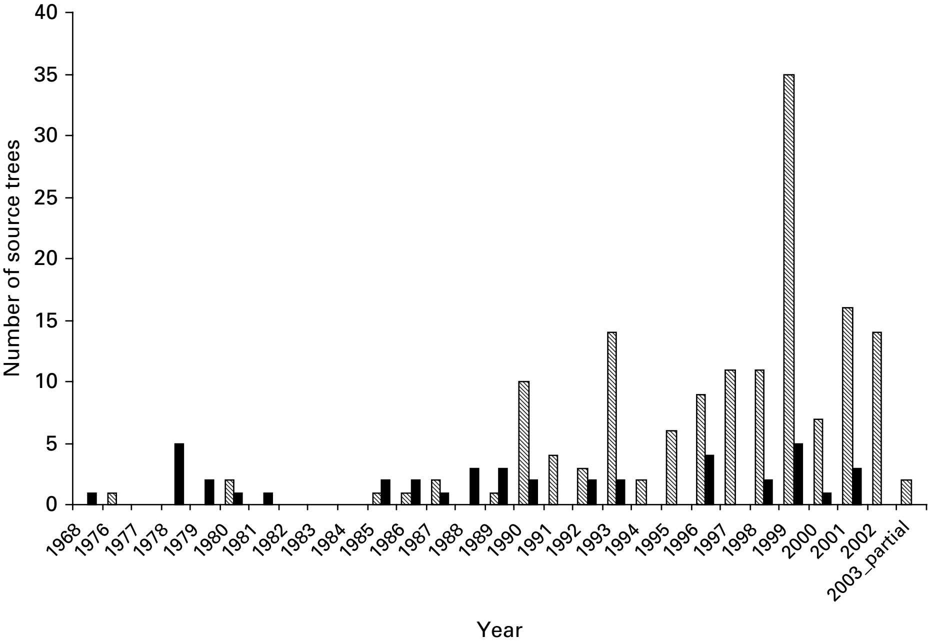


Fig. 5. Number of studies per year since 1960 to halfway through 2003 (2003_partial) contributing source trees to the unweighted cetartiodactyl supertree. Cross-hatched bars represent molecular data and black bars represent purely non-molecular data e.g. morphological, behavioural. Trees that combined datasets from different publishing years were not included.

III. RESULTS AND DISCUSSION

The full supertree (see Fig. 1 for higher-level supertree and Figs 2–4 for the expansion of Bovidae, Cervidae and Cetacea to the species level) was obtained from 201 source trees derived from 141 published articles (denoted by a * in the References), representing 0.69 source trees per species. This latter value is comparable to that in previous large-scale supertrees of well-studied mammalian orders; 0.6 in primates (Purvis, 1995) and 0.7 in carnivores (Bininda-Emonds *et al.*, 1999). Thirty-nine source trees were derived from purely morphological data, with the number of morphological studies being relatively constant over time see Fig. 5. By contrast, 65 % of the 147 purely molecular source trees were from 1997 onwards.

(1) Resolution, robustness and support

The resolution of the full tree was 59.9 %, which is lower than in the primate (79.2 %: Purvis, 1995), carnivore (78.1 %: Bininda-Emonds *et al.*, 1999), insectivore (69.9 %: Grenyer & Purvis, 2003) and marsupial supertrees (73.7 %: Cardillo *et al.*, 2004). The low resolution stems largely from a lack of information. In particular, many species are poorly known such that they can cluster equally parsimoniously with several other species, thereby reducing resolution locally. Although it is possible to identify such 'floating' species using safe taxonomic reduction (Wilkinson, 1995), the application of this approach in order to unambiguously re-include the removed species produced negligible gains in resolution (data not shown). The least resolved areas of the tree are within the families Ziphiidae, Cervidae, Suidae and Bovidae. The genera *Sus*, *Muntiacus* and *Cervus*, and the family Ziphiidae are each completely unresolved owing to a lack of phylogenetic information. For example, excluding the seed trees, only five source trees included two or more of the 10 species in *Sus*. The largest *Sus* source tree included six species (Groves, 1997), the next largest three species (Randi *et al.*, 2002), and rest included only two species apiece. In sharp contrast, the polytomy at the base of the Bovidae is caused by conflicting phylogenetic information among the 35 source trees providing information for this node.

The full and reduced supertrees are highly congruent (CFI = 0.56, which means 56 % clades are shared; d_S = 0.114, which means 11.4 % clades were not shared), the differences between the indices are due to the CFI index being adversely affected by the lower resolution in the full supertree. The only difference at the family level between the two trees is the collapsing of the ((Phocoenidae + Delphinidae) Monodontidae) clade in the full supertree to a polytomy in the reduced tree. This suggests that the majority of the higher-level relationships are robust to the effects of poorly known species and 'poor' quality methods of phylogenetic reconstruction. However, the reduced version has noticeably higher resolution within the Bovidae, probably due to the removal of many floating species. As a result, the resolution of the entire reduced tree (68.5 %) is noticeably higher than for the full supertree (59.9 %).

The full and reduced QS index (QS and rQS, respectively) for the clades in the full and the reduced tree are presented in Appendices 2 and 3 (available at www.faculty.virginia.edu/gittleman/CetartiodactylSupertreeAppendix.zip). Most of the nodes have negative QS index values indicating that there are more mismatches than matches between the source trees and the supertree clade. By contrast the rQS index shows support for the majority of clades, with only nine negative nodes and eight equivocal nodes. It is therefore not surprising that the rQS index for the supertree as a whole (rQS_{Tree}) shows weak support for the supertree topology (0.034) and that the QS_{Tree} shows little or no support for the supertree topology (−0.087). The sharp differences between the QS and the rQS index are due to the way taxa missing from the source tree but within the supertree clade are treated. The QS index is highly conservative; it takes into account every missing species that can potentially contradict the supertree clade, creating many soft mismatches. By contrast the rQS index prunes the supertree to contain only the taxa in the source tree so there can be no soft matches or mismatches, which allows for many more matches between source tree and supertree. 60.7 % of nodes are contradicted by at least one tree and in the QS index 98.3 % of all nodes have at least one hard or soft mismatch. However, a negative QS index does not necessarily indicate poor support for the clade as it is known to become more negative when the tree is built using a large number of poorly overlapping sources (Bininda-Emonds, 2003). The QS_{Tree} value of −0.087 compares well to that of the marsupial supertree −0.09 (Cardillo *et al.*, 2004) and the lagomorph supertree −0.109 (Bininda-Emonds, 2003). Most family-level relationships have a highly negative QS index, with less negative values occurring towards the tips of the tree where the clade sizes are smaller. This trend is consistent with the results of simulation tests and is again due to the greater possibility of conflict in large *versus* small clades (Bininda-Emonds, 2003).

(2) Higher-level relationships

(*a*) *Placement of Cetacea*

The supertree (see Fig. 1) supports the hypothesis that cetaceans are the sister taxon to hippopotamids as upheld by the majority of molecular source trees (e.g. Arnason & Gullberg, 1994; Gatesy *et al.*, 1999). Support for the Cetacea-Hippopotamidae clade is strong, with 31 source trees supporting it and 13 directly contradicting it (rQS = 0.09). The traditional morphological view that cetaceans and mesonychids are sister taxa (e.g. O'Leary, 1999) could not be examined directly as only extant taxa were added to the matrix. However, it is indirectly refuted by our data because of the nesting of Cetacea within Artiodactyla.

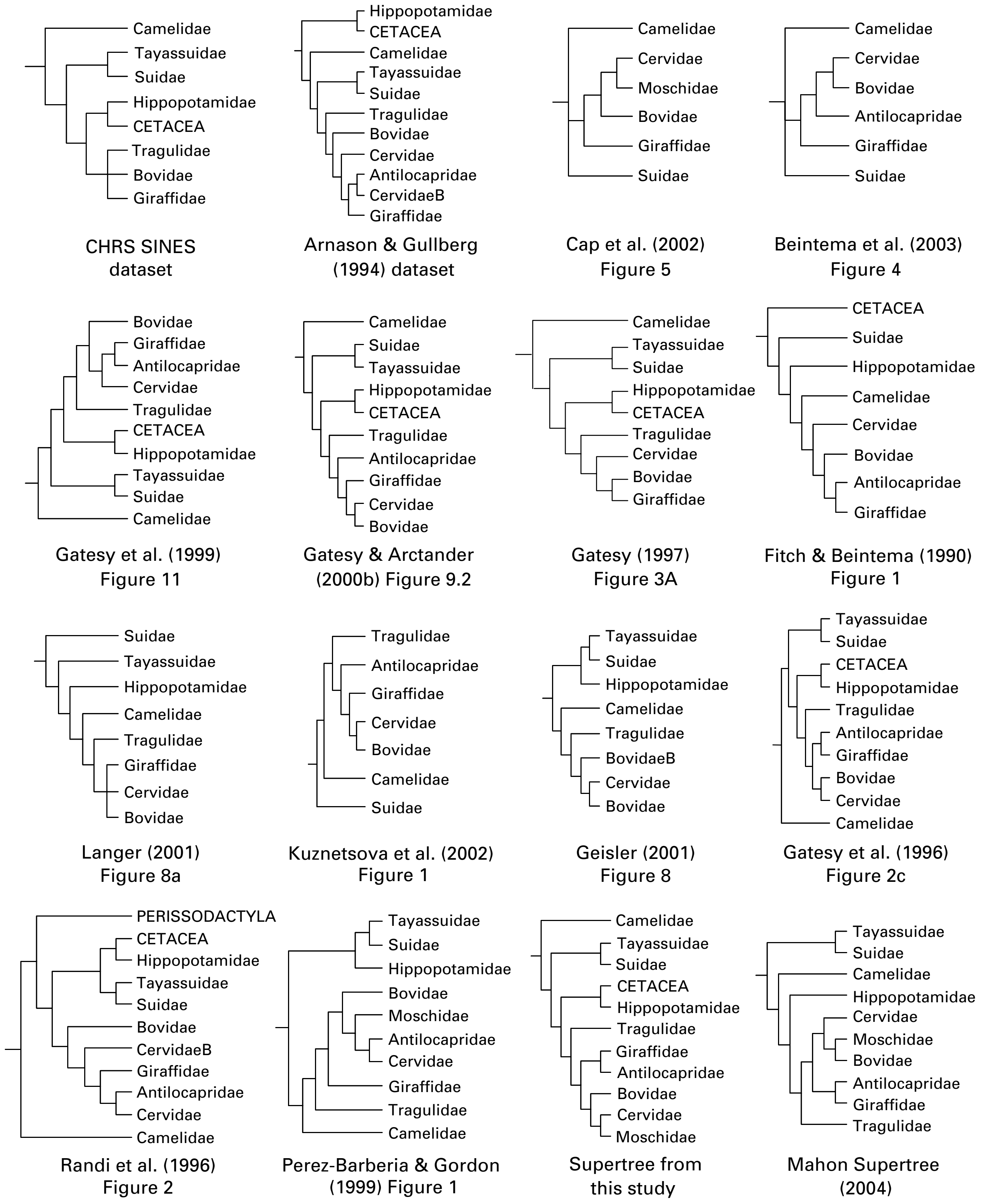
(*b*) *Basal clades*

The placement of hippopotamids as sister taxon to cetaceans contradicts the traditional view that hippopotamids cluster with the suids (pigs) and tayassuids (peccaries) (Langer, 2001) to form the Suiformes. The supertree supports the hypothesis that suids and tayassuids are sister taxa and together they form the sister group to all remaining cetartiodactyls excluding camelids. The uncertainty regarding basal relationships in the Cetartiodactyla is illustrated by the rQS index value of −0.005, with 23 hard matches to 24 hard mismatches and by the sample of 15 source trees and the recent artiodactyl supertree (Mahon, 2004) presented in Fig. 6. Four trees in Fig. 6 support the topology found here of the camelids being the most basal clade followed by the suid-tayassuid clade. Nine contradict this set of relationships, whereas the remaining topologies are equivocal. The nine contradictory trees instead propose many different clades as being basal within Cetartiodactyla: a hippopotamid-cetacean clade (Arnason & Gullberg, 1994 minisupertree; Beintema *et al.*, 2003), a suid-tayassuid clade (Gatesy *et al.*, 1996; Mahon, 2004) or the traditional Suiformes (Perez-Barberia & Gordon, 1999; Geisler, 2001).

(*c*) *Family-level relationships within Artiodactyla*

The six families of the suborder Ruminantia (Tragulidae, Moschidae, Giraffidae, Cervidae, Bovidae and Antilocapridae) form a monophyletic clade. Support for ruminant monophyly is strong; only seven source trees present contradictory topologies (e.g. Cronin *et al.*, 1996; Gatesy *et al.*, 1999) whereas 47 are in agreement. Relationships among the ruminant families were fully resolved in the supertree to give (((Bovidae (Cervidae, Moschidae)) (Antilocapridae, Giraffidae)) Tragulidae). Support for the tragulids as the basal ruminant family is strong (rQS = 0.199) and derives from all data types and tree construction methods (e.g. Chikuni *et al.*, 1995; Gatesy & Arctander, 2000*a*). Support for the supertree topology among the five remaining ruminant families (the Pecora) is mixed, particularly as only three source trees include all six families (Perez-Barberia & Gordon, 1999; Su *et al.*, 1999; Hassanin & Douzery, 2003). The sister-taxon relationship between Cervidae and Moschidae is also well supported (rQS = 0.109) but the sample size is very small; only three source trees support the relationship and one source contradicts it. The sister-taxon relationship between the cervid and moschid clade and Bovidae has weaker support; 36 source trees are in agreement with the placement and 25 contradict it (rQS = 0.055). The sister-taxon relationship between Giraffidae and Antilocapridae is equivocal (rQS = −0.005) with 11 source trees contradicting the relationship and 10 supporting it. Of the three source trees that include all five pecoran families and the partial artiodactyl supertree of Mahon (2004), only Su *et al.* (1999) resolve the same relationships as the supertree. The Mahon (2004) and the Hassanin & Douzery (2003) trees differ by placing the moschids as sister taxa to the bovids. The tree of Hassanin and Douzery (2003) is also equivocal in its support for the sister-taxon relationship between giraffids and antilocaprids. The Perez-Barberia & Gordon (1999) tree disagrees entirely with the supertree topology for the Pecora.

Moschidae (musk deer) and the monotypic Antilocapridae (pronghorn) account for most of the instability within Pecora. Historically, these two clades have always been difficult to place. It was not until fairly recently that moschids were even recognised as a separate family distinct from Cervidae (Corbert & Hill, 1980; Leinders & Heintz, 1980); they are now typically held to cluster with the cervids (e.g. Fig. 5 in Cap *et al.*, 2002) and/or the bovids (Hassanin & Douzery, 2003). Antilocapridae has floated around the tree, with proposed sister-taxon relationships with Cervidae



CHRS SINES dataset

Arnason & Gullberg (1994) dataset

Cap et al. (2002) Figure 5

Beintema et al. (2003) Figure 4

Gatesy et al. (1999) Figure 11

Gatesy & Arctander (2000b) Figure 9.2

Gatesy (1997) Figure 3A

Fitch & Beintema (1990) Figure 1

Langer (2001) Figure 8a

Kuznetsova et al. (2002) Figure 1

Geisler (2001) Figure 8

Gatesy et al. (1996) Figure 2c

Randi et al. (1996) Figure 2

Perez-Barberia & Gordon (1999) Figure 1

Supertree from this study

Mahon Supertree (2004)

Fig. 6. A sample of previous phylogenetic hypotheses concerning the higher-level cetartiodactyl phylogeny. The Cetacea are reduced to a single terminal taxon. CHRS SINES dataset is the mini-supertree that combines all source trees built using CHRS SINES (denoted by Ψ in the References).

(e.g. Arnason & Gullberg, 1994 minisupertree), Giraffidae (e.g. Douzery & Catzeflis, 1995) and the clade comprising Bovidae, Cervidae and Giraffidae (e.g. Gatesy & Arctander, 2000*b*). It is therefore not surprising that the QS index for the inter-family nodes in the Pecora are more negative than for any other family-level cluster within the supertree.

(*d*) *Family-level relationships within Cetacea*

The traditional odontocete and mysticete suborders are both monophyletic in the supertree. However, support for a monophyletic Odontoceti is weak; 17 source trees support monophyly and 16 oppose it (rQS = 0.005). The poor support is due to a proliferation of studies supporting the claims of Milinkovitch *et al.* (1993) that the odontocete family Physeteridae (sperm whales) clusters with the Mysticeti (e.g. Milinkovitch *et al.*, 1996; Montgelard *et al.*, 1997; Yang & Zhou, 1999). This hypothesis has since been rejected by the majority of researchers due to the lack of morphological support and the sensitivity of the result on outgroup choice and sequence alignment (Messenger & McGuire, 1998). It is therefore not surprising that the support for the placement of the Physteridae at the base of the odontocetes is also weak; 15 studies support its placement and 10 contradict it (rQS = 0.025). The basal position of the Physeteridae is the preferred placement of the majority of studies that reconstruct the traditional Odontoceti (e.g. Messenger & McGuire, 1998; Nikaido *et al.*, 2001). The Platanistidae (river dolphins) are paraphyletic in agreement with current molecular phylogenies (e.g. Hamilton *et al.*, 2001; Nikaido *et al.*, 2001). The positions of the Platanistidae genera within the supertree receive no support: *Platanista* is placed as next basal clade to the Physeteridae (rQS = 0), whereas the remaining three genera cluster together further up the tree in the clade (*Lipotes* (*Inia* + *Pontoporia*)) (rQS = −0.01).

The remaining relationships in the supertree among odontocete families largely agree with the current literature. The close relationship between Phocoenidae, Delphinidae and Monodontidae is well supported; 25 source trees support it whereas only two contradict it (rQS = 0.114). The full supertree also supports a Delphinidae + Phocoenidae pairing, which is the most frequently resolved sister-taxon relationship among these three families; 16 sources uphold this pairing while only four provide topologies that go against it (rQS = 0.045). It is difficult to assess support for the position of the Ziphiidae because its position in the source trees is highly dependent on whether a paraphyletic Odontoceti and/or Platanistidae are reconstructed; however, the rQS index shows weak support for its placement within the supertree (rQS = 0.085).

Mysticete relationships within the supertree contradict most traditional taxonomic groupings; however, this is not surprising given that most of the source trees also challenge the traditional views. The nesting of Eschrichtiidae within the Balaenopteridae is supported by 11 source trees and also the total evidence tree of Gatesy *et al.* (2003). Support for a monophyletic clade comprising the Eschrichtiidae and Balaenopteridae is even higher, with 18 source trees supporting this relationship and only one contradicting it; the majority of the support is due to source trees reconstructing a Balaenopteridae-Eschrichtiidae polytomy (e.g. Hasegawa *et al.*, 1997). The sister-taxon relationship between Neobalaenidae and Balaenidae is equivocal (rQS = 0) with four source trees supporting the relationship (e.g. Randi *et al.*, 1996; Gatesy & Arctander, 2000*b*), and four contradicting it (e.g. Adegoke *et al.*, 1993; Arnason *et al.*, 1993).

(3) Tree comparison: supertree *versus* supermatrix

The full and reduced supertree topologies were highly congruent with the most comprehensive published tree of the Cetartiodactyla, namely the supermatrix of Gatesy *et al.* (2002) see Fig. 7. There was between 72 % and 79 % congruence between the supertrees and the supermatrix (full CFI = 0.729, $d_S = 0.213$; reduced CFI = 0.75, $d_S = 0.213$). At higher taxonomic levels, the differences between the supertree and the supermatrix topologies are minimal. In the supermatrix tree, the sister-taxon relationship between Giraffidae and Antilocapridae is not resolved but they appear in the same position within the Pecora (((Bovidae, Cervidae) Giraffidae) Antilocapridae) as apposed to ((Bovidae, Cervidae) (Giraffidae, Antilocapridae)). The supermatrix also resolves a sister-taxon relationship between Monodontidae and Phocoenidae rather than the supertree grouping of Delphinidae and Phocoenidae. This is not surprising because there is contradictory evidence concerning the sister-taxon relationship among these three families as illustrated by the polytomy in the reduced supertree. The last difference is the appearance of the novel, but unstable clade ((Suidae, Tayassuidae) Camelidae) in the supermatrix analysis at the base of the cetartiodactyl tree, whereas the supertree decomposes this clade into the more traditional (Suidae, Tayassuidae) followed by Camelidae at the very base of the tree. This degree of congruence between the supertrees and the supermatrix tree suggests independent support for the phylogenetic hypothesis proposed by the supertree. Altogether, this result implies that with careful source tree selection, supertree methods can give valid topologies that agree with other methods of tree construction (*contra* Gatesy *et al.*, 2002).

IV. CONCLUSIONS

(1) We present the first phylogeny to include all 290 extant species of artiodactyls and cetaceans recognised in Wilson and Reeder (1993). The supertree topology is fully resolved at the family level and is highly congruent (72–79 %) with the largest total-evidence cetartiodactyl tree. It supports the current consensus that Cetacea are nested within Artiodactyla as sister taxa to Hippopotamidae rather than to Artiodactyla as a whole and that the sub-order Ruminantia is a valid monophyletic clade. The other relationships within the tree are more controversial because no consensus exists within the literature and support is often inconclusive due to inadequate taxon sampling.

(2) The complete tree is provided as a guide for further phylogenetic research while simultaneously facilitating

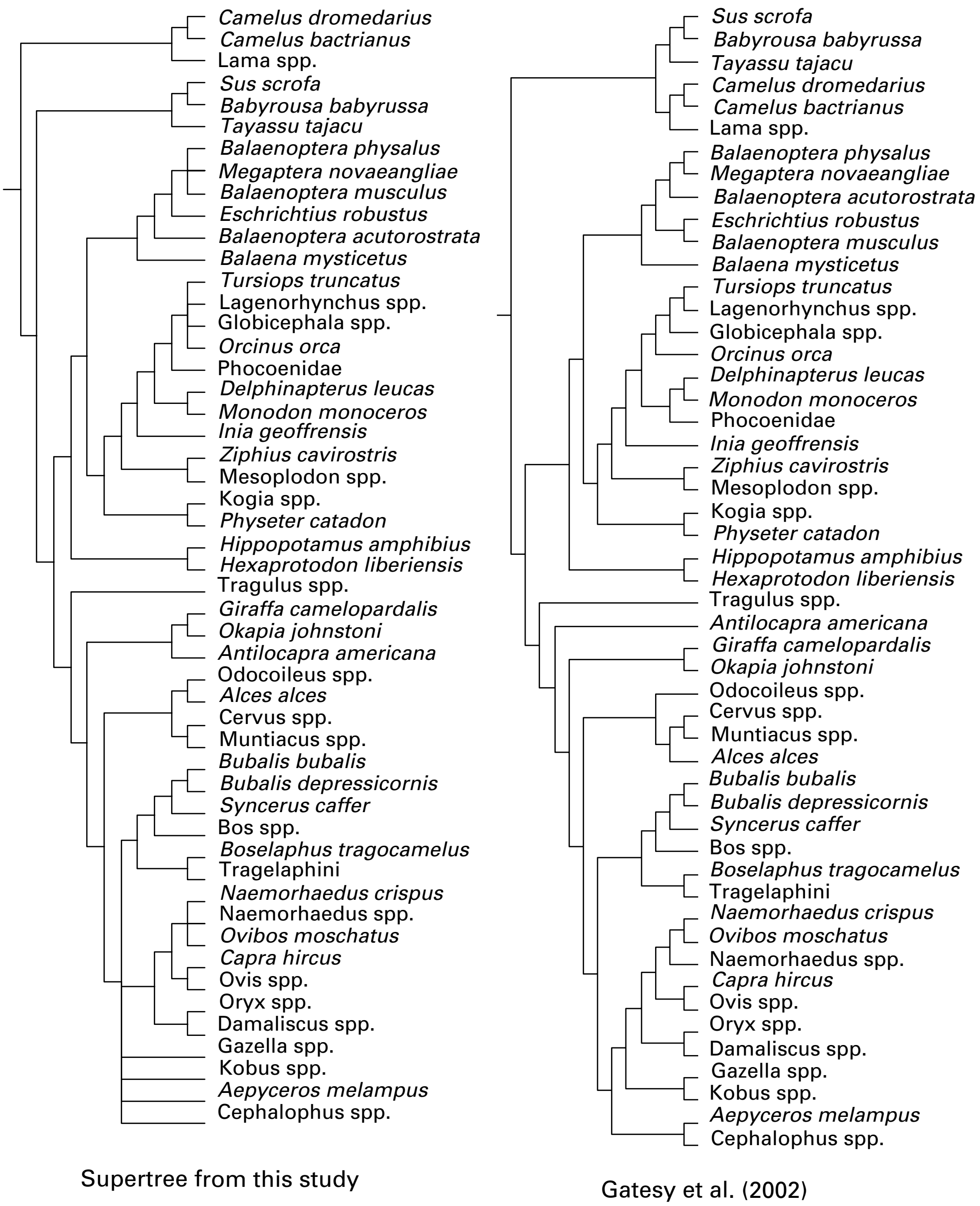


Fig. 7. The full supertree from this study reduced to the cetartiodactyl taxon set of Gatesy *et al.* (2002) and the Gatesy *et al.* (2002) supermatrix tree pruned to contain only cetartiodactyl species.

large-scale comparative analyses. In particular, a complete species-level tree of the Cetartiodactyla provides the first opportunity to study functional and behavioural ecology hypotheses across obligate aquatic and terrestrial species in the same clade. Representative questions include: (i) whether changes in the rate of morphological or life history evolution exist that are associated with the terrestrial–aquatic boundary; (ii) whether the social evolution hypotheses in the terrestrial hoofed mammals linking group size and structure to body size, predation and life-history (Estes, 1974; Geist, 1974; Jarman, 1974) can be extrapolated to the aquatic species; and (iii) to what degree the factors that correlate with extinction risk (*sensu* Purvis *et al.*, 2000) are ecologically determined in that the same traits do not predict extinction risk in the ecologically diverse Artiodactyla and Cetacea. The supertree topology can be used to control for phylogenetic relationships with a degree of confidence due to the independent support for many of the relationships given by the supermatrix of Gatesy *et al.* (2002).

(3) The supertree highlights areas in need of further phylogenetic research and data collection. Work needs to be focussed especially on Suidae, Ziphiidae, Cervidae and Delphinidae, where very little phylogenetic information is

currently available. However, since the completion of the major search for source trees in 2001, several much-needed, nearly complete, molecular trees of the Ziphiidae have been published (Dalebout *et al.*, 2002, 2003).

(4) In Cetacea, the lack of phylogenetic information also mirrors the deficiency of data in other aspects of their biology. This is illustrated by the fact that 56 % of delphinids and 75 % of ziphiids are categorised as data deficient in the IUCN Red List of threatened species (www.redlist.org). In the genera *Sus* and *Cervus*, the polytomies have more immediate and serious conservation implications as approximately 40 % of species in these genera are categorised as threatened by the Red List.

(5) The polytomy at the tribal level within Bovidae also highlights this as an area in need of further research. In contrast to the Suidae, Ziphiidae, Cervidae and Delphinidae, the loss of resolution stems from a lack of consensus among studies. However, consensus might be difficult to achieve if, as the fossil record suggests, there was rapid radiation around 15 million years ago when all the tribes first appeared. As such, the short branch lengths in this region of the tree may represent a genuinely difficult phylogenetic problem that might not be solvable simply by sequencing additional genes. Instead, a more profitable strategy may be to identify rare genomic changes (see Rokas & Holland, 2000) that resolve the relationships in question because such changes are less prone to convergent evolution.

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$^{\lambda}$ Source trees combined in a mini-supertree to represent the Arnason and Gullberg (1994) dataset.

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VII. APPENDIX

Full QS index (QS) and reduced QS (rQS) index for full cetartiodactyl supertree. Nodes are numbered from the base of the tree along the left-hand backbone of the tree until the first tip is reached then each clade is coded in the same way always starting at the most basal clade and going to the left first.

Node	Clade size	Status	Mean QS index	Number of sources with hard matches	Number of sources with hard mismatches	Number of sources with equivocal trees	Number of sources with soft matches	Number of sources with soft mismatches
1	284	softConflict	−0.527	0	24	7	3	167
2	265	softConflict	−0.527	0	26	13	1	161
3	185	softConflict	−0.413	0	7	42	0	152
4	181	softConflict	−0.413	0	7	42	0	152
5	178	softConflict	−0.458	0	25	42	0	134
6	132	softConflict	−0.368	0	15	68	0	118
7	109	softConflict	−0.289	0	17	102	0	82
8	46	softConflict	−0.249	0	14	115	0	72
9	13	softConflict	−0.112	0	6	162	0	33
10	6	softConflict	−0.07	0	1	174	0	26
11	4	equivocal	−0.04	0	0	185	0	16
12	3	softSupport	−0.032	0	0	184	2	15
13	2	softConflict	−0.015	0	1	180	8	12
14	7	equivocal	−0.09	0	0	165	0	36
15	2	softConflict	−0.035	0	3	182	4	12
16	2	softSupport	−0.027	0	0	180	5	16
17	3	softConflict	−0.087	0	4	168	1	28
18	2	softSupport	−0.06	0	0	167	5	29
19	33	softConflict	−0.201	0	7	127	0	67
20	32	softConflict	−0.204	0	9	128	0	64
21	24	softConflict	−0.229	0	19	128	0	54
22	21	softConflict	−0.224	0	18	129	0	54
23	7	softConflict	−0.167	0	2	136	0	63
24	6	softConflict	−0.157	0	1	137	1	62
25	3	softConflict	−0.137	0	1	143	2	55
26	2	softConflict	−0.127	0	1	143	4	53
27	3	softSupport	−0.03	0	0	187	1	13
28	2	softSupport	−0.022	0	0	188	2	11
29	14	softConflict	−0.124	0	3	154	0	44
30	12	softConflict	−0.127	0	3	153	0	45
31	3	softSupport	−0.015	0	0	193	1	7
32	2	softSupport	−0.012	0	0	192	2	7
33	2	softSupport	−0.015	0	0	189	3	9
34	8	softConflict	−0.082	0	5	173	0	23
35	7	softConflict	−0.07	0	2	175	0	24
36	18	softConflict	−0.122	0	4	156	0	41
37	17	softConflict	−0.117	0	4	158	0	39
38	14	softConflict	−0.109	0	4	161	0	36
39	13	softConflict	−0.102	0	4	162	1	34
40	8	softConflict	−0.037	0	1	185	1	14
41	5	softConflict	−0.022	0	2	192	1	6
42	2	softConflict	0	0	1	194	4	2
43	3	softSupport	−0.01	0	0	193	2	6
44	2	softSupport	0.005	0	0	195	4	2
45	3	softSupport	−0.015	0	0	187	4	10
46	2	softSupport	0.002	0	0	188	7	6
47	3	softSupport	−0.05	0	0	177	2	22
48	2	softSupport	−0.007	0	0	188	5	8
49	2	softSupport	−0.02	0	0	183	5	13
50	19	equivocal	−0.067	0	0	174	0	27
51	17	softConflict	−0.062	0	2	178	0	21
52	15	softConflict	−0.04	0	1	184	1	15
53	3	softConflict	−0.002	0	1	197	2	1
54	4	softSupport	−0.025	0	0	189	1	11

Appendix (*cont.*)

Node	Clade size	Status	Mean QS index	Number of sources with hard matches	Number of sources with hard mismatches	Number of sources with equivocal trees	Number of sources with soft matches	Number of sources with soft mismatches
55	3	softSupport	−0.02	0	0	189	2	10
56	2	softSupport	0.007	0	0	194	5	2
57	4	softSupport	−0.01	0	0	195	1	5
58	2	softSupport	−0.002	0	0	192	4	5
59	2	softSupport	0.01	0	0	197	4	0
60	2	softSupport	−0.025	0	0	181	5	15
61	4	equivocal	−0.03	0	0	189	0	12
62	3	softSupport	−0.012	0	0	192	2	7
63	2	softConflict	−0.01	0	2	189	5	5
64	9	softConflict	−0.067	0	1	175	0	25
65	8	softConflict	−0.065	0	2	177	0	22
66	5	softConflict	−0.045	0	2	183	1	15
67	3	softConflict	−0.047	0	3	183	1	14
68	2	softSupport	−0.012	0	0	188	4	9
69	2	softSupport	0.002	0	0	194	4	3
70	3	softConflict	−0.04	0	2	185	1	13
71	2	softConflict	−0.007	0	1	189	5	6
72	3	softSupport	−0.012	0	0	194	1	6
73	23	softConflict	−0.256	0	7	105	0	89
74	12	softConflict	−0.244	0	7	110	0	84
75	7	softConflict	−0.221	0	3	115	0	83
76	5	softConflict	−0.244	0	12	115	0	74
77	3	softConflict	−0.097	0	8	170	0	23
78	2	softConflict	−0.052	0	3	169	7	22
79	2	softSupport	−0.197	0	0	114	4	83
80	2	softConflict	−0.032	0	4	178	7	12
81	5	softConflict	−0.114	0	3	158	0	40
82	4	softConflict	−0.095	0	2	165	0	34
83	11	softConflict	−0.124	0	11	162	0	28
84	2	softConflict	−0.027	0	1	169	11	20
85	9	equivocal	−0.082	0	0	168	0	33
86	3	softConflict	−0.075	0	5	176	0	20
87	2	softSupport	−0.052	0	0	176	2	23
88	3	softConflict	−0.02	0	2	187	4	8
89	2	softConflict	0.005	0	1	190	7	3
90	46	softConflict	−0.236	0	9	115	0	77
91	42	softConflict	−0.234	0	9	116	0	76
92	19	softConflict	−0.192	0	12	136	0	53
93	4	softConflict	−0.137	0	9	155	0	37
94	3	softConflict	−0.075	0	5	176	0	20
95	2	softConflict	−0.025	0	1	182	5	13
96	15	softConflict	−0.124	0	7	158	0	36
97	14	softConflict	−0.109	0	3	160	0	38
98	3	softConflict	−0.02	0	2	195	0	4
99	2	softSupport	−0.01	0	0	195	1	5
100	6	softConflict	−0.032	0	1	187	1	12
101	2	softConflict	−0.07	0	1	160	7	33
102	2	softSupport	−0.005	0	0	197	1	3
103	23	softConflict	−0.189	0	7	132	0	62
104	16	softConflict	−0.164	0	5	140	0	56
105	4	softSupport	−0.017	0	0	192	1	8
106	12	softConflict	−0.157	0	6	144	0	51
107	10	softConflict	−0.147	0	3	145	0	53
108	2	softSupport	−0.03	0	0	185	2	14
109	7	softConflict	−0.06	0	1	178	0	22
110	6	softSupport	−0.052	0	0	178	1	22
111	4	softSupport	−0.015	0	0	193	1	7
112	3	softSupport	0.002	0	0	200	1	0
113	2	softSupport	0.005	0	0	199	2	0
114	3	softConflict	−0.144	0	11	154	0	36

Appendix (*cont.*)

Node	Clade size	Status	Mean QS index	Number of sources with hard matches	Number of sources with hard mismatches	Number of sources with equivocal trees	Number of sources with soft matches	Number of sources with soft mismatches
115	2	softSupport	−0.085	0	0	159	4	38
116	4	equivocal	−0.085	0	0	167	0	34
117	2	softSupport	−0.025	0	0	165	13	23
118	80	softConflict	−0.209	0	13	128	1	59
119	78	softConflict	−0.179	0	2	131	0	68
120	67	softConflict	−0.204	0	16	135	0	50
121	64	softConflict	−0.182	0	10	138	0	53
122	62	softConflict	−0.189	0	13	138	0	50
123	43	softConflict	−0.164	0	4	139	0	58
124	40	softConflict	−0.159	0	2	139	0	60
125	38	softConflict	−0.152	0	7	147	0	47
126	6	softConflict	−0.07	0	1	174	0	26
127	2	softSupport	−0.002	0	0	192	4	5
128	32	softConflict	−0.124	0	2	153	0	46
129	10	softConflict	−0.057	0	3	181	0	17
130	8	softConflict	−0.05	0	2	183	0	16
131	4	softConflict	−0.022	0	1	191	1	8
132	3	softConflict	−0.015	0	1	194	1	5
133	2	softSupport	−0.007	0	0	194	2	5
134	4	softSupport	−0.032	0	0	186	1	14
135	2	softSupport	−0.027	0	0	184	3	14
136	2	softSupport	−0.007	0	0	192	3	6
137	6	softConflict	−0.087	0	2	168	0	31
138	2	softSupport	−0.01	0	0	193	2	6
139	5	softConflict	−0.06	0	2	179	0	20
140	4	softConflict	−0.057	0	1	179	0	21
141	2	softConflict	−0.007	0	1	193	3	4
142	2	softSupport	−0.04	0	0	179	3	19
143	2	softSupport	−0.017	0	0	192	1	8
144	2	softConflict	−0.015	0	1	172	12	16
145	3	softConflict	−0.047	0	7	187	1	6
146	2	softConflict	−0.007	0	5	185	9	2
147	19	equivocal	−0.067	0	0	174	0	27
148	2	softSupport	−0.01	0	0	191	3	7
149	3	softConflict	−0.075	0	1	172	0	28
150	2	softSupport	−0.007	0	0	186	6	9
151	11	softConflict	−0.134	0	2	149	0	50
152	4	softConflict	−0.045	0	4	187	0	10
153	3	equivocal	−0.022	0	0	192	0	9
154	2	softSupport	−0.015	0	0	193	1	7
155	7	softConflict	−0.112	0	1	157	0	43
156	6	softConflict	−0.102	0	5	165	0	31
157	2	softSupport	0.02	0	0	191	9	1
158	3	softConflict	−0.097	0	4	164	1	32
159	2	softSupport	−0.042	0	0	164	10	27
160	19	softConflict	−0.119	0	1	154	0	46
161	16	softConflict	−0.119	0	1	154	0	46
162	15	equivocal	−0.117	0	0	154	0	47
163	13	equivocal	−0.117	0	0	154	0	47
164	2	softSupport	−0.002	0	0	198	1	2
165	10	softSupport	−0.114	0	0	153	1	47
166	2	softSupport	−0.007	0	0	192	3	6
167	3	softConflict	−0.017	0	1	193	1	6
168	2	softSupport	0.005	0	0	195	4	2
169	6	equivocal	−0.09	0	0	165	0	36
170	2	softSupport	−0.05	0	0	167	7	27
171	4	equivocal	−0.04	0	0	185	0	16
172	2	softConflict	−0.025	0	1	182	5	13
173	2	softConflict	−0.01	0	2	191	4	4

Node	Clade size	Mean rQS index	Number of sources with hard matches	Number of sources with hard mismatches	Number of sources with equivocal trees
1	284	−0.005	23	24	154
2	265	0.045	35	26	140
3	185	0.199	47	7	147
4	181	0.229	53	7	141
5	178	0.055	36	25	140
6	132	0.09	33	15	153
7	109	0.055	28	17	156
8	46	0.085	31	14	156
9	13	0.065	19	6	176
10	6	0.055	12	1	188
11	4	0.035	7	0	194
12	3	0.04	8	0	193
13	2	0.04	9	1	191
14	7	0.075	15	0	186
15	2	0	3	3	195
16	2	0.025	5	0	196
17	3	0.01	6	4	191
18	2	0.02	4	0	197
19	33	0.129	33	7	161
20	32	0.109	31	9	161
21	24	0.01	21	19	161
22	21	0.01	20	18	163
23	7	0.06	14	2	185
24	6	0.045	10	1	190
25	3	0.01	3	1	197
26	2	0.005	2	1	198
27	3	0.02	4	0	197
28	2	0.005	1	0	200
29	14	0.045	12	3	186
30	12	0.045	12	3	186
31	3	0.005	1	0	200
32	2	0.01	2	0	199
33	2	0.015	3	0	198
34	8	0.01	7	5	189
35	7	0.03	8	2	191
36	18	0.06	16	4	181
37	17	0.035	11	4	186
38	14	0.005	5	4	192
39	13	0.01	6	4	191
40	8	0.02	5	1	195
41	5	0.005	3	2	196
42	2	0.01	3	1	197
43	3	0.015	3	0	198
44	2	0.01	2	0	199
45	3	0.01	2	0	199
46	2	0.01	2	0	199
47	3	0.025	5	0	196
48	2	0.015	3	0	198
49	2	0.02	4	0	197
50	19	0.075	15	0	186
51	17	0.01	4	2	195
52	15	0.01	3	1	197
53	3	0.005	2	1	198
54	4	0.02	4	0	197
55	3	0.02	4	0	197
56	2	0.015	3	0	198
57	4	0.015	3	0	198
58	2	0.01	2	0	199
59	2	0.015	3	0	198
60	2	0.02	4	0	197
61	4	0.045	9	0	192

Appendix (*cont.*)

Node	Clade size	Mean rQS index	Number of sources with hard matches	Number of sources with hard mismatches	Number of sources with equivocal trees
62	3	0.045	9	0	192
63	2	0.005	3	2	196
64	9	0.065	14	1	186
65	8	0.05	12	2	187
66	5	0.04	10	2	189
67	3	0.025	8	3	190
68	2	0.015	3	0	198
69	2	0.015	3	0	198
70	3	0.04	10	2	189
71	2	0.015	4	1	196
72	3	0.01	2	0	199
73	23	0.159	39	7	155
74	12	0.119	31	7	163
75	7	0.144	32	3	166
76	5	0.03	18	12	171
77	3	0.015	11	8	182
78	2	0.015	6	3	192
79	2	0.005	1	0	200
80	2	0	4	4	193
81	5	0.1	23	3	175
82	4	0.075	17	2	182
83	11	0.005	12	11	178
84	2	0.045	10	1	190
85	9	0.1	20	0	181
86	3	0	5	5	191
87	2	0.01	2	0	199
88	3	0.01	4	2	195
89	2	0.01	3	1	197
90	46	0.109	31	9	161
91	42	0.114	32	9	160
92	19	−0.01	10	12	179
93	4	−0.03	3	9	189
94	3	−0.01	3	5	193
95	2	0.02	5	1	195
96	15	0.01	9	7	185
97	14	0.035	10	3	188
98	3	−0.005	1	2	198
99	2	0.005	1	0	200
100	6	0.005	2	1	198
101	2	0.03	7	1	193
102	2	0.005	1	0	200
103	23	0.055	18	7	176
104	16	0.055	16	5	180
105	4	0.005	1	0	200
106	12	0.035	13	6	182
107	10	0.055	14	3	184
108	2	0.01	2	0	199
109	7	0.02	5	1	195
110	6	0.04	8	0	193
111	4	0.01	2	0	199
112	3	0.005	1	0	200
113	2	0.005	1	0	200
114	3	−0.005	10	11	180
115	2	0.02	4	0	197
116	4	0.055	11	0	190
117	2	0.05	10	0	191
118	80	0.09	31	13	157
119	78	0.184	39	2	160
120	67	0.005	17	16	168
121	64	0.025	15	10	176

Appendix (*cont.*)

Node	Clade size	Mean rQS index	Number of sources with hard matches	Number of sources with hard mismatches	Number of sources with equivocal trees
122	62	0	13	13	175
123	43	0.085	21	4	176
124	40	0.114	25	2	174
125	38	0.045	16	7	178
126	6	0.07	15	1	185
127	2	0.005	1	0	200
128	32	0.1	22	2	177
129	10	−0.005	2	3	196
130	8	0	2	2	197
131	4	0.005	2	1	198
132	3	0	1	1	199
133	2	0.005	1	0	200
134	4	0.005	1	0	200
135	2	0.01	2	0	199
136	2	0.015	3	0	198
137	6	0.045	11	2	188
138	2	0.005	1	0	200
139	5	−0.005	1	2	198
140	4	0.005	2	1	198
141	2	0	1	1	199
142	2	0.015	3	0	198
143	2	0.005	1	0	200
144	2	0.055	12	1	188
145	3	−0.01	5	7	189
146	2	0.015	8	5	188
147	19	0.075	15	0	186
148	2	0.01	2	0	199
149	3	0.055	12	1	188
150	2	0.03	6	0	195
151	11	0.065	15	2	184
152	4	0	4	4	193
153	3	0.04	8	0	193
154	2	0.005	1	0	200
155	7	0.085	18	1	182
156	6	0.03	11	5	185
157	2	0.025	5	0	196
158	3	0.025	9	4	188
159	2	0.05	10	0	191
160	19	0.045	10	1	190
161	16	0.045	10	1	190
162	15	0.035	7	0	194
163	13	0.035	7	0	194
164	2	0.005	1	0	200
165	10	0.035	7	0	194
166	2	0.015	3	0	198
167	3	0.015	4	1	196
168	2	0.015	3	0	198
169	6	0.065	13	0	188
170	2	0.035	7	0	194
171	4	0.025	5	0	196
172	2	0.02	5	1	195
173	2	0.01	4	2	195

Full QS (QS) index and reduced QS (rQS) index for reduced cetartiodactyl supertree. Nodes are numbered from the base of the tree along the left-hand backbone of the tree until the first tip is reached then each clade is coded in the same way always starting at the most basal clade and going to the left first.

Node	Clade size	Status	Mean QS index	Number of sources with hard matches	Number of sources with hard mismatches	Number of sources with equivocal trees	Number of sources with soft matches	Number of sources with soft mismatches
1	246	softConflict	−0.536	0	23	6	3	120
2	236	softConflict	−0.53	0	23	12	1	116
3	162	softConflict	−0.424	0	5	28	0	119
4	158	softConflict	−0.424	0	5	28	0	119
5	155	softConflict	−0.477	0	21	28	0	103
6	121	softConflict	−0.398	0	14	45	0	93
7	100	softConflict	−0.303	0	13	73	0	66
8	42	softConflict	−0.263	0	8	80	0	64
9	13	softConflict	−0.115	0	4	121	0	27
10	6	softConflict	−0.076	0	1	130	0	21
11	4	equivocal	−0.046	0	0	138	0	14
12	3	softSupport	−0.036	0	0	137	2	13
13	2	softConflict	−0.026	0	1	133	6	12
14	7	equivocal	−0.099	0	0	122	0	30
15	4	softConflict	−0.062	0	5	138	0	9
16	2	softSupport	−0.016	0	0	139	4	9
17	2	softSupport	−0.03	0	0	137	3	12
18	3	softConflict	−0.099	0	3	123	1	25
19	2	softSupport	−0.079	0	0	122	3	27
20	29	softConflict	−0.227	0	5	88	0	59
21	28	softConflict	−0.23	0	7	89	0	56
22	7	softConflict	−0.197	0	1	93	0	58
23	6	softConflict	−0.194	0	1	92	1	58
24	3	softSupport	−0.161	0	0	99	2	51
25	2	softSupport	−0.151	0	0	98	4	50
26	11	softConflict	−0.128	0	1	114	0	37
27	9	softConflict	−0.132	0	1	113	0	38
28	7	softConflict	−0.138	0	4	112	1	35
29	6	softConflict	−0.138	0	4	112	1	35
30	4	softConflict	−0.128	0	4	113	2	33
31	2	softSupport	0	0	0	148	2	2
32	2	softSupport	−0.01	0	0	145	2	5
33	6	softConflict	−0.079	0	2	130	0	20
34	2	softSupport	−0.023	0	0	141	2	9
35	4	softConflict	−0.086	0	3	129	0	20
36	3	softSupport	−0.023	0	0	143	1	8
37	2	softSupport	0.01	0	0	149	3	0
38	2	softSupport	−0.003	0	0	145	3	4
39	2	softConflict	−0.039	0	5	125	10	12
40	56	softConflict	−0.188	0	14	109	0	29
41	47	softConflict	−0.188	0	14	109	0	29
42	27	softConflict	−0.128	0	1	114	0	37
43	13	softConflict	−0.112	0	2	118	1	31
44	8	softConflict	−0.036	0	1	140	1	10
45	5	softConflict	−0.023	0	2	145	1	4
46	2	softConflict	0	0	1	145	4	2
47	3	softSupport	−0.007	0	0	146	2	4
48	2	softSupport	0.013	0	0	148	4	0
49	5	softSupport	−0.079	0	0	126	1	25
50	3	softSupport	−0.056	0	0	133	1	18
51	2	softSupport	−0.003	0	0	143	4	5
52	2	softSupport	−0.016	0	0	139	4	9
53	3	softSupport	−0.013	0	0	144	2	6
54	2	softConflict	−0.016	0	2	141	4	5
55	20	softConflict	−0.118	0	7	123	0	22
56	19	equivocal	−0.076	0	0	129	0	23
57	17	softConflict	−0.066	0	1	133	0	18
58	15	softSupport	−0.036	0	0	139	1	12

Appendix (*cont.*)

Node	Clade size	Status	Mean QS index	Number of sources with hard matches	Number of sources with hard mismatches	Number of sources with equivocal trees	Number of sources with soft matches	Number of sources with soft mismatches
59	3	softConflict	0	0	1	149	2	0
60	4	softSupport	−0.023	0	0	143	1	8
61	3	softSupport	−0.023	0	0	143	1	8
62	2	softSupport	0.013	0	0	148	4	0
63	4	softSupport	−0.007	0	0	148	1	3
64	2	softSupport	0.003	0	0	145	4	3
65	2	softSupport	0.013	0	0	148	4	0
66	2	softSupport	−0.033	0	0	134	4	14
67	9	softConflict	−0.069	0	1	132	0	19
68	8	softConflict	−0.066	0	2	134	0	16
69	5	softConflict	−0.046	0	2	138	1	11
70	2	softSupport	0.007	0	0	148	3	1
71	2	softSupport	−0.01	0	0	143	3	6
72	3	softConflict	−0.049	0	2	137	1	12
73	2	softSupport	−0.007	0	0	144	3	5
74	21	softConflict	−0.296	0	6	68	0	78
75	12	softConflict	−0.293	0	7	70	0	75
76	7	softConflict	−0.263	0	2	74	0	76
77	3	softConflict	−0.105	0	7	127	0	18
78	2	softConflict	−0.066	0	3	125	5	19
79	2	softConflict	−0.033	0	3	133	6	10
80	2	softSupport	−0.234	0	0	73	4	75
81	5	softConflict	−0.128	0	3	116	0	33
82	4	softConflict	−0.105	0	2	122	0	28
83	9	softConflict	−0.112	0	8	126	0	18
84	2	softConflict	−0.03	0	1	124	10	17
85	7	equivocal	−0.069	0	0	131	0	21
86	6	softConflict	−0.066	0	3	135	0	14
87	5	softConflict	−0.053	0	2	138	0	12
88	3	softSupport	0	0	0	144	4	4
89	2	softSupport	0.016	0	0	143	7	2
90	34	softConflict	−0.263	0	6	78	0	68
91	30	softConflict	−0.266	0	8	79	0	65
92	13	softConflict	−0.217	0	9	95	0	48
93	4	softConflict	−0.151	0	6	112	0	34
94	3	softConflict	−0.072	0	3	133	0	16
95	2	softSupport	−0.016	0	0	137	5	10
96	9	softConflict	−0.132	0	4	116	0	32
97	8	softConflict	−0.132	0	4	116	0	32
98	7	softConflict	−0.118	0	2	118	0	32
99	4	softConflict	−0.112	0	1	119	0	32
100	3	softConflict	−0.036	0	1	142	0	9
101	2	softSupport	−0.03	0	0	141	1	10
102	17	softConflict	−0.224	0	6	90	0	56
103	11	softConflict	−0.201	0	5	96	0	51
104	2	softSupport	−0.016	0	0	145	1	6
105	6	softConflict	−0.062	0	1	134	0	17
106	5	softSupport	−0.049	0	0	135	1	16
107	4	softConflict	−0.026	0	1	143	1	7
108	3	softSupport	−0.007	0	0	148	1	3
109	2	softSupport	0.007	0	0	146	4	2
110	4	softSupport	−0.013	0	0	146	1	5
111	3	softSupport	0.003	0	0	151	1	0
112	2	softSupport	0.007	0	0	150	2	0
113	3	softConflict	−0.181	0	10	107	0	35
114	2	softSupport	−0.115	0	0	111	3	38
115	4	equivocal	−0.109	0	0	119	0	33
116	2	softSupport	−0.036	0	0	117	12	23
117	74	softConflict	−0.23	0	13	93	1	45
118	72	softConflict	−0.194	0	2	95	0	55

Appendix (*cont.*)

Node	Clade size	Status	Mean QS index	Number of sources with hard matches	Number of sources with hard mismatches	Number of sources with equivocal trees	Number of sources with soft matches	Number of sources with soft mismatches
119	62	softConflict	−0.23	0	16	98	0	38
120	59	softConflict	−0.201	0	10	101	0	41
121	57	softConflict	−0.207	0	12	101	0	39
122	42	softConflict	−0.178	0	2	100	0	50
123	39	equivocal	−0.171	0	0	100	0	52
124	6	softConflict	−0.066	0	1	133	0	18
125	3	softConflict	−0.02	0	1	145	1	5
126	2	softSupport	−0.007	0	0	144	3	5
127	31	softConflict	−0.138	0	2	112	0	38
128	10	softConflict	−0.066	0	2	134	0	16
129	8	softConflict	−0.062	0	2	135	0	15
130	4	softConflict	−0.03	0	1	142	1	8
131	3	softConflict	−0.02	0	1	145	1	5
132	2	softSupport	−0.01	0	0	145	2	5
133	4	softSupport	−0.039	0	0	138	1	13
134	2	softSupport	−0.033	0	0	136	3	13
135	2	softSupport	−0.007	0	0	144	3	5
136	5	softConflict	−0.089	0	1	126	0	25
137	2	softSupport	−0.01	0	0	145	2	5
138	5	equivocal	−0.043	0	0	139	0	13
139	4	equivocal	−0.039	0	0	140	0	12
140	3	equivocal	−0.039	0	0	140	0	12
141	2	softSupport	−0.03	0	0	137	3	12
142	2	softConflict	−0.026	0	1	127	9	15
143	3	softConflict	−0.03	0	2	143	1	6
144	2	softSupport	0.02	0	0	142	8	2
145	15	equivocal	−0.076	0	0	129	0	23
146	14	softConflict	−0.076	0	2	131	0	19
147	12	softConflict	−0.053	0	1	137	0	14
148	2	softSupport	−0.007	0	0	144	3	5
149	3	softConflict	−0.095	0	1	124	0	27
150	2	softSupport	−0.003	0	0	139	6	7
151	10	softConflict	−0.161	0	2	105	0	45
152	3	softConflict	−0.043	0	3	142	0	7
153	2	softSupport	0.013	0	0	142	7	3
154	7	softConflict	−0.148	0	1	108	0	43
155	6	softConflict	−0.125	0	4	118	0	30
156	2	softSupport	0.023	0	0	143	8	1
157	3	softConflict	−0.118	0	3	117	1	31
158	2	softSupport	−0.053	0	0	116	10	26
159	10	softConflict	−0.148	0	1	108	0	43
160	7	softConflict	−0.148	0	1	108	0	43
161	6	equivocal	−0.145	0	0	108	0	44
162	2	softSupport	−0.007	0	0	144	3	5
163	4	equivocal	−0.145	0	0	108	0	44
164	3	softSupport	−0.135	0	0	109	1	42
165	2	softSupport	0	0	0	146	3	3
166	3	softConflict	−0.02	0	1	145	1	5
167	2	softSupport	0.01	0	0	147	4	1
168	6	equivocal	−0.115	0	0	117	0	35
169	2	softSupport	−0.062	0	0	119	7	26
170	4	equivocal	−0.049	0	0	137	0	15
171	2	softConflict	−0.03	0	1	134	5	12
172	2	softConflict	−0.013	0	2	142	4	4

Node	Clade size	Mean rQS index	Number of sources with hard matches	Number of sources with hard mismatches	Number of sources with equivocal trees
1	246	−0.026	19	23	110
2	236	0.046	30	23	99
3	162	0.243	42	5	105
4	158	0.283	48	5	99
5	155	0.072	32	21	99
6	121	0.099	29	14	109
7	100	0.072	24	13	115
8	42	0.138	29	8	115
9	13	0.092	18	4	130
10	6	0.053	9	1	142
11	4	0.039	6	0	146
12	3	0.053	8	0	144
13	2	0.033	6	1	145
14	7	0.079	12	0	140
15	4	0	5	5	142
16	2	0.02	3	0	149
17	2	0.02	3	0	149
18	3	0.013	5	3	144
19	2	0.013	2	0	150
20	29	0.158	29	5	118
21	28	0.132	27	7	118
22	7	0.072	12	1	139
23	6	0.046	8	1	143
24	3	0.02	3	0	149
25	2	0.013	2	0	150
26	11	0.059	10	1	141
27	9	0.053	9	1	142
28	7	−0.007	3	4	145
29	6	−0.013	2	4	146
30	4	−0.013	2	4	146
31	2	0.007	1	0	151
32	2	0.013	2	0	150
33	6	0.033	7	2	143
34	2	0.007	1	0	151
35	4	0.013	5	3	144
36	3	0.013	2	0	150
37	2	0.013	2	0	150
38	2	0.02	3	0	149
39	2	0	5	5	142
40	56	−0.066	4	14	134
41	47	−0.053	6	14	132
42	27	0.079	13	1	138
43	13	0.013	4	2	146
44	8	0.02	4	1	147
45	5	0.007	3	2	147
46	2	0.013	3	1	148
47	3	0.02	3	0	149
48	2	0.013	2	0	150
49	5	0.026	4	0	148
50	3	0.02	3	0	149
51	2	0.02	3	0	149
52	2	0.02	3	0	149
53	3	0.053	8	0	144
54	2	0	2	2	148
55	20	−0.02	4	7	141
56	19	0.079	12	0	140
57	17	0.013	3	1	148
58	15	0.013	2	0	150
59	3	0.007	2	1	149
60	4	0.02	3	0	149
61	3	0.02	3	0	149

Appendix (*cont.*)

Node	Clade size	Mean rQS index	Number of sources with hard matches	Number of sources with hard mismatches	Number of sources with equivocal trees
62	2	0.02	3	0	149
63	4	0.02	3	0	149
64	2	0.013	2	0	150
65	2	0.02	3	0	149
66	2	0.02	3	0	149
67	9	0.066	11	1	140
68	8	0.046	9	2	141
69	5	0.026	6	2	144
70	2	0.013	2	0	150
71	2	0.013	2	0	150
72	3	0.026	6	2	144
73	2	0.013	2	0	150
74	21	0.178	33	6	113
75	12	0.112	24	7	121
76	7	0.164	27	2	123
77	3	0.013	9	7	136
78	2	0.007	4	3	145
79	2	0	3	3	146
80	2	0.007	1	0	151
81	5	0.099	18	3	131
82	4	0.092	16	2	134
83	9	0.013	10	8	134
84	2	0.053	9	1	142
85	7	0.105	16	0	136
86	6	0.033	8	3	141
87	5	0.033	7	2	143
88	3	0.026	4	0	148
89	2	0.02	3	0	149
90	34	0.145	28	6	118
91	30	0.132	28	8	116
92	13	−0.007	8	9	135
93	4	−0.02	3	6	143
94	3	0	3	3	146
95	2	0.033	5	0	147
96	9	0.02	7	4	141
97	8	0.02	7	4	141
98	7	0.026	6	2	144
99	4	0.02	4	1	147
100	3	0	1	1	150
101	2	0.007	1	0	151
102	17	0.072	17	6	129
103	11	0.059	14	5	133
104	2	0.007	1	0	151
105	6	0.02	4	1	147
106	5	0.039	6	0	146
107	4	0.007	2	1	149
108	3	0.026	4	0	148
109	2	0.02	3	0	149
110	4	0.013	2	0	150
111	3	0.007	1	0	151
112	2	0.007	1	0	151
113	3	0	10	10	132
114	2	0.02	3	0	149
115	4	0.066	10	0	142
116	2	0.059	9	0	143
117	74	0.112	30	13	109
118	72	0.237	38	2	112
119	62	−0.007	15	16	121
120	59	0.013	12	10	130

Appendix (*cont.*)

Node	Clade size	Mean rQS index	Number of sources with hard matches	Number of sources with hard mismatches	Number of sources with equivocal trees
121	57	−0.013	10	12	130
122	42	0.112	19	2	131
123	39	0.132	20	0	132
124	6	0.053	9	1	142
125	3	0	1	1	150
126	2	0.007	1	0	151
127	31	0.099	17	2	133
128	10	0	2	2	148
129	8	0	2	2	148
130	4	0.007	2	1	149
131	3	0	1	1	150
132	2	0.007	1	0	151
133	4	0.007	1	0	151
134	2	0.013	2	0	150
135	2	0.02	3	0	149
136	5	0.026	5	1	146
137	2	0.007	1	0	151
138	5	0.013	2	0	150
139	4	0.007	1	0	151
140	3	0.007	1	0	151
141	2	0.02	3	0	149
142	2	0.053	9	1	142
143	3	0.02	5	2	145
144	2	0.046	7	0	145
145	15	0.086	13	0	139
146	14	0.039	8	2	142
147	12	0.039	7	1	144
148	2	0.013	2	0	150
149	3	0.059	10	1	141
150	2	0.039	6	0	146
151	10	0.079	14	2	136
152	3	0.007	4	3	145
153	2	0.053	8	0	144
154	7	0.099	16	1	135
155	6	0.046	11	4	137
156	2	0.033	5	0	147
157	3	0.039	9	3	140
158	2	0.066	10	0	142
159	10	0.053	9	1	142
160	7	0.053	9	1	142
161	6	0.046	7	0	145
162	2	0.02	3	0	149
163	4	0.046	7	0	145
164	3	0.046	7	0	145
165	2	0.013	2	0	150
166	3	0.02	4	1	147
167	2	0.02	3	0	149
168	6	0.079	12	0	140
169	2	0.046	7	0	145
170	4	0.033	5	0	147
171	2	0.026	5	1	146
172	2	0.013	4	2	146