Syst. Biol. 48(1):6–20, 1999

Stability of Cladistic Relationships between Cetacea and Higher-Level Artiodactyl Taxa

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Abstract.—Over the past 10 years, the phylogenetic relationships among higher-level artiodactyl taxa have been examined with multiple data sets. Many of these data sets suggest that Artiodactyla (even-toed ungulates) is paraphyletic and that Cetacea (whales) represents a highly derived "artiodactyl" subgroup. In this report, phylogenetic relationships between Cetacea and artiodactyls are tested with a combination of 15 published data sets plus new DNA sequence data from two nuclear loci, interphotoreceptor retinoid-binding protein (IRBP) and von Willebrand factor (vWF). The addition of the IRBP and vWF character sets disrupts none of the relationships supported by recent cladistic analyses of the other 15 data sets. Simultaneous analyses support three critical clades: (Cetacea + Hippopotamidae), (Cetacea + Hippopotamidae + Ruminantia), and (Cetacea + Hippopotamidae + Ruminantia + Suina). Perturbations of the combined matrix show that the above clades are stable to a variety of disturbances. A chronicle of phylogenetic results over the past 3 years suggests that cladistic relationships between Cetacea and artiodactyls have been stable to increased taxonomic sampling and to the addition of more than 1,400 informative characters from 15 data sets. [Artiodactyla, Cetacea, cladogram, stability.]

Stable can be defined as "resistant to sudden change or fluctuation" (Stein, 1978). If stability is desirable in cladistic analysis (see Felsenstein, 1985; Kluge, 1989, 1997; Davis, 1993; Bremer, 1994; Siddall, 1995; Nixon and Carpenter, 1996, for recent discussions), an important issue is how stability should be measured. What sort of change or fluctuation is relevant in assessments of cladistic stability? Many perturbations can be imagined (Siddall, 1995).

Davis (1993) noted that perturbations have been of two sorts: adjustments in the optimality criterion, and alterations to the original data matrix. The stability of a particular clade can be defined as robustness to relaxation of the parsimony criterion (Bremer, 1988, 1994), to alternative sequence alignments (Lake, 1991; Wheeler, 1995), to resampling of characters (Felsenstein, 1985), to different character-weighting schemes (Wheeler et al., 1993; Milinkovitch et al., 1996), to alternative taxonomic exemplars (Philippe and Douzery, 1994), or to the removal of data (Lanyon, 1985; Penny and Hendy, 1985, 1986; Davis, 1993; Siddall, 1995; Farris et al., 1996; Gatesy et al., in press). However, cladistic stability may be best defined as a resistance to change with the addition of new data. For example, if the addition of a single character or taxon to a data matrix is capable of collapsing all nodes supported by the original matrix, then those nodes are poorly supported and unstable. Conversely, if a topology is resistant to the repeated addition of new data over time, that topology is stable and predictive (Nixon and Carpenter, 1996).

The phylogenetic classification of Artiodactyla (even-toed ungulates) has fluctuated over the past 100 years and remains controversial (e.g., Simpson, 1945, and references therein; Gentry and Hooker, 1988; Graur and Higgins, 1994). Morphological characters support the monophyly of Artiodactyla (Theodor, 1996; Geisler and O'Leary, 1997), but molecular evidence contradicts this traditional clade. Sarich (1985) used as-yet unpublished immunological distances to suggest that hippopotamid artiodactyls are more closely related to Cetacea than to other artiodactyl taxa (Fig. 1). The first clear character evidence for a specific relationship between hippos and whales was reported

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by Irwin and Arnason in 1994. That same year, Graur and Higgins (1994) reanalyzed numerous published molecular data sets for Cetacea and Artiodactyla. Hippopotamidae was not included in their analyses. However, ((((Ruminantia + Cetacea) Suina) Camelidae) outgroup) was supported by amino acid sequences from five loci, and (((Ruminantia + Cetacea) Suina) outgroup) was favored by a larger data set that included five mitochondrial (mt) genes and 11 nuclear (nu) proteins (Fig. 1).

A combined $\beta + \kappa$-casein matrix (Gatesy et al., 1996) was the first data set to simultaneously corroborate the results of both Sarich (1985) and Graur and Higgins (1994). The minimum-length topology for the caseins suggests that Cetacea is nested three nodes within a paraphyletic Artiodactyla (referred to hereinafter as clades A, B, and C, Fig. 1). Since 1996, numerous data sets (de Jong et al., 1977, 1993; Baba et al., 1981; Beintema et al., 1986; Miyamoto and Goodman, 1986; Gentry and Hooker, 1988; Irwin et al., 1991; Milinkovitch et al., 1993; Irwin and Arnason, 1994; Queralt et al., 1995; Smith et al., 1996; Stanhope et al., 1996; Montgelard et al., 1997; Shimamura et al., 1997) have been added to the casein matrix, but clades A, B, and C have remained intact with the addition of these data (Gatesy, 1997, 1998; Gatesy and Arctander, in press; Gatesy et al., in press).

Here, we summarize the stability of cladistic relationships between Cetacea and higher-level artiodactyl taxa. This is done in several ways. First, new DNA sequence data for interphotoreceptor retinoid-binding protein (IRBP) exon 1, von Willebrand factor (vWF) exon 28, and recently published data for α-lactalbumin (Milinkovitch et al., 1998) are added to 14 previously published data sets for Artiodactyla + Cetacea. A chronicle of phylogenetic results over the past 3 years is used to characterize the robustness of clades A, B, and C to the addition of a variety of data sets. Second, the stability of the combined matrix of 17 data sets to various disturbances is recorded. These perturbations include (1) relaxation of the parsimony criterion, (2) successive approximations weighting, (3) bootstrap (BP) resampling of characters, (4) jackknife (JK) resampling of characters, (5) successive data set removal, (6) first-order jackknifing of taxa, and (7) increased taxonomic sampling for 10 of the DNA data sets.

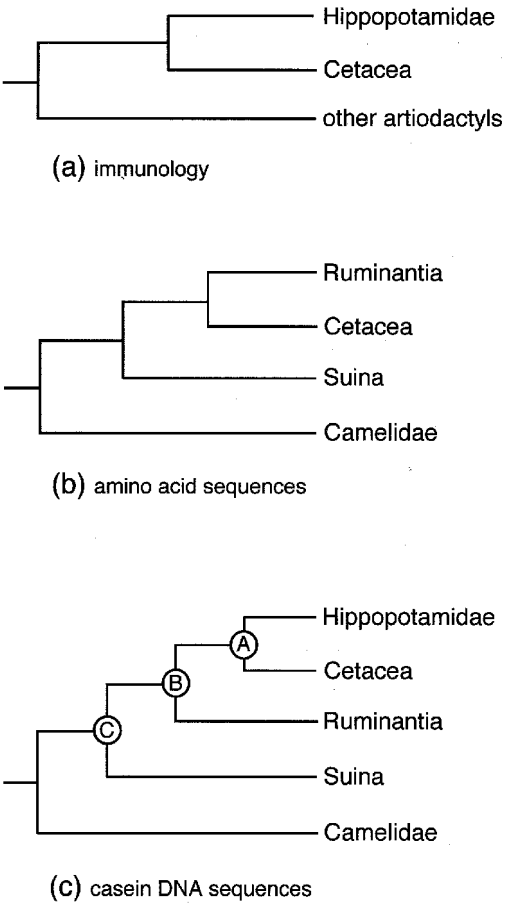


FIGURE 1. Molecular hypotheses of relationships between Cetacea and higher-level artiodactyl taxa. Clades referred to in the text are labeled A, B, and C. (a) Sarich, 1985; (b) Graur and Higgins, 1994; (c) Gatesy et al., 1996. Ruminantia = antelopes, deer, giraffes, and chevrotains; Cetacea = dolphins, porpoises, and whales; Hippopotamidae = hippos; Suina = pigs and peccaries; Camelidae = camels and llamas.

MATERIALS AND METHODS

Data

A concatenated matrix of 17 data sets (WHIPPO-1) was compiled. Representatives from 13 taxa were sampled in this

combined matrix: 8 artiodactyl taxa—Bovidae (antelopes), Cervidae (deer), Giraffidae (giraffes), Tragulidae (chevrotains), Hippopotamidae (hippos), Camelidae (camels and llamas), Tayassuidae (peccaries), and Suidae (pigs); 4 cetacean taxa—Physeteridae (sperm whales), Delphinoidea (dolphins and porpoises), Ziphiidae (beaked whales), and Mysticeti (baleen whales); and 1 outgroup taxon. At least 6 of the above taxa were sampled for each of the 17 component data sets in the WHIPPO-1 matrix.

Fifteen of the character sets in the WHIPPO-1 matrix were taken from the literature. Nuclear (nu) amino acid sequences were α-hemoglobin, β-hemoglobin, pancreatic ribonuclease, α-crystallin A, and cytochrome *c*. Mitochondrial (mt) DNA sequences were cytochrome *b*, 12S ribosomal (r) DNA, and 16S rDNA. Nu DNA sequences were β-casein exon 7 + intron 7, κ-casein exon 4, γ-fibrinogen exons 2–4 + introns 2–3, protamine P1 exons 1–2 + intron 1 + 5′–3′-noncoding regions, and α-lactalbumin exons 1–3 + introns 1–2. Skeletal/dental characters for Artiodactyla were from Gentry and Hooker (1988), and short interspersed elements (SINES) were from Shimamura et al. (1997). All amino acid sequences were downloaded from the National Center for Biotechnology Information (NCBI), and DNA sequences were from NCBI, Queralt et al. (1995), and Gatesy (1998).

The two remaining character sets in the WHIPPO-1 matrix were composed of published data plus new DNA sequences from the nu loci, IRBP and vWF. New sequences for IRBP exon 1 were *Hippopotamus amphibius* (Hippopotamidae) and *Lama glama* (Camelidae). New sequences for vWF exon 28 were *Hippopotamus amphibius* (Hippopotamidae), *Lama glama* (Camelidae), *Physeter catadon* (Physeteridae), and *Eschrichtius robustus* (Mysticeti). The genes that encode IRBP and vWF were amplified by the polymerase chain reaction and sequenced as in Stanhope et al. (1996) and Porter et al. (1996). These sequences (Genbank numbers AF108832–AF108837) were added to the data sets compiled by Stanhope et al. (1996, 1998), Smith et al. (1996), and Porter et al. (1996).

All 17 data sets in WHIPPO-1 included at least one exemplar from each of the four major clades of extant artiodactyls—Ruminantia (Bovidae + Cervidae + Giraffidae + Tragulidae), Camelidae, Hippopotamidae, and Suina (Suidae + Tayassuidae)—and 16 of the data sets had at least one representative of Cetacea. For 15 of the data sets, outgroup taxa were members of Perissodactyla (odd-toed ungulates). Because α-lactalbumin has not been sequenced from a representative of Perissodactyla, cladograms derived from the α-lactalbumin matrix were rooted with *Cavia cutleri*. The morphological data were rooted with the hypothetical ancestor of Gentry and Hooker (1988).

Most sequence alignments for the WHIPPO-1 matrix were from Gatesy et al. (in press). Exceptions were alignments for α-lactalbumin, IRBP, and vWF. The alignment for α-lactalbumin was from Milinkovitch et al. (1998). The alignments for IRBP and vWF were slight variations of alignments from Stanhope et al. (1996) and Porter et al. (1996), respectively. To incorporate new sequences, minor adjustments in these alignments were made by eye and using SeqApp 1.9a (Gilbert, 1992). Taxa that were not sequenced or scored for different data sets were coded as missing data.

A more-comprehensive, concatenated alignment of 79 taxa (WHIPPO-2) was organized for the 10 DNA sequence data sets. Alignments were from Gatesy (1998) for β-casein, κ-casein, γ-fibrinogen, mt cytochrome *b*, protamine P1, 12S mt rDNA, and 16S mt rDNA. Given the greater diversity of sequences in the 79-taxon matrix, sequence alignment was more ambiguous than in the 13-taxon matrix. Therefore, protamine P1 intron 1 and ambiguous regions in alignments for the mt rDNAs were excised as in Gatesy (1998). The α-lactalbumin alignment was from Milinkovitch et al. (1998), and the alignments for IRBP and vWF were as above. Again, taxa that were not sequenced for particular loci were coded as missing data for those loci. The combined data sets, WHIPPO-1 and

WHIPPO-2, are available at the home page for the Society of Systematic Biologists, www.utexas.edu/ftp/depts/systbiol/. Taxonomic exemplars for each of the 17 data sets in WHIPPO-1 and for each of the 10 data sets in WHIPPO-2 are attached to these matrices.

Phylogenetic Analyses

The 17 data sets in WHIPPO-1 were analyzed separately and simultaneously. The 10 data sets in WHIPPO-2 were analyzed simultaneously. Ambiguities in DNA and amino acid sequences were coded as in Gatesy et al. (in press). Transformations between any two character states were assigned unit cost, all characters were unordered, and gaps in sequence alignments were treated as missing data. Parsimony searches with PAUP 3.1.1 and PAUP* 4.0d64 (Swofford, 1993, and in press) were branch and bound or heuristic with at least 100 random taxon-addition replicates and TBR branch swapping. Branches with a maximum length of zero were collapsed. PAUP results for the WHIPPO-2 matrix were checked with NONA 1.16 (Goloboff, 1993). Search options in NONA were hold*, hold/1000, pack, amb-, and mult*100. Character coding and weighting were as above for the PAUP searches. In contrast to PAUP, however, the amb- option in NONA collapses nodes that are ambiguously supported.

For the WHIPPO-1 matrix, cladograms were rooted with the outgroups specified above. Optimal cladograms derived from the more-comprehensive WHIPPO-2 matrix were rooted with Xenarthra, the putative sister group of all other extant eutherians (e.g., Miyamoto and Goodman, 1986; Novacek, 1992; but see Arnason et al., 1997).

Stability to Relaxation of the Parsimony Criterion

The stability of nodes to relaxation of the parsimony criterion was summarized with branch support (BS). BS is the number of extra steps beyond minimum length required to collapse a given node (Bremer, 1988, 1994). For each clade of interest, the constraints command of PAUP was used to force the nonmonophyly of that group. Minimum length–constrained topologies were derived from branch and bound searches or heuristic searches with 50–1,000 random taxon-addition replicates and TBR branch swapping. Tree lengths from unconstrained searches were subtracted from tree lengths for constrained searches to determine BS for each node.

Distribution of Support among Data Sets in the Simultaneous Analysis

The influence of different data sets was assessed in two ways. First, for the optimal topology derived from the WHIPPO-1 matrix, the numbers of unambiguous synapomorphies for clades A, B, and C (Fig. 1) were noted. The distribution of these synapomorphies among the 17 component data sets of WHIPPO-1 was recorded by using the list of apomorphies option of PAUP* (Swofford, in press). Second, nodal data set influence (NDI; Gatesy et al., in press) for clades A, B, and C was calculated for each of the 17 data sets in the WHIPPO-1 matrix. NDI summarizes the influence of the removal of a specific data set on the level of BS for a given node. For a particular combined character set, a particular data partition in that combined character set, and a particular node, the NDI is the BS score at that node for the combined character set minus the BS score at that node for the combined character set without that data partition. NDI scores can be positive, negative, or zero. A positive NDI shows that removal of a given data partition reduces BS for the node of interest (i.e., the data partition has a positive influence at that node); a negative NDI shows that the removal of a particular data set increases BS (i.e., the data partition has a negative influence at that node); and an NDI of zero demonstrates that the removal of a given data partition has no influence on the BS score for a particular node (Gatesy et al., in press).

NDI was calculated as follows. For the combined WHIPPO-1 matrix of 17 data sets, each individual data set was successively removed from the original matrix. This resulted in 17 combined data sets that each lacked 1 of the 17 original data partitions. BS

scores for the 17 perturbed matrices were determined as above by using PAUP. BS scores for each of the perturbed matrices were subtracted from BS scores for the original, complete matrix to give the NDI for each data partition at nodes A, B, and C.

Stability to Differential Character Weighting

Characters in the WHIPPO-1 matrix were weighted by successive approximations (Farris, 1969; Carpenter, 1988). In the initial search, all characters were assigned equal weight. For each subsequent search, the unit-rescaled consistency index (Farris, 1989) from the previous analysis was used to weight characters differentially until a stable phylogenetic result was obtained. Parsimony searches with PAUP were heuristic with 100 random taxon-addition replicates and TBR branch swapping.

Stability to BP Resampling of Characters

Given certain assumptions, BP resampling of characters offers "confidence limits on phylogenies" (Felsenstein, 1985). The BP also provides an indication of the stability of groupings to "data reweighting or revision" (Bremer, 1994). Characters in the WHIPPO-1 matrix were subjected to BP resampling (Felsenstein, 1985). Informative characters were resampled with replacement from the original data set, and 1,000 data sets of equal size to the original were assembled. Each BP replicate involved a heuristic parsimony search with simple taxon addition and TBR branch swapping using PAUP (Swofford, 1993, and in press). BP percentages were recorded for each node supported by the WHIPPO-1 matrix.

Stability to the Removal of Characters

Characters in the WHIPPO-1 matrix were subjected to JK resampling (Penny and Hendy, 1986; Farris et al., 1996). In each JK analysis, 1,000 replicate data sets were assembled by resampling informative characters from the original matrix with PAUP* 4.0d64 (Swofford, in press.). Two JK analyses were done. In the first, each perturbed data set contained 50% of the characters from the original matrix of 1,650 informative characters. In the second, each perturbed data set contained only 25% of the characters from the original matrix. Each JK replicate involved a heuristic parsimony search with simple taxon addition and TBR branch swapping. The percentages of JK replicates that favored groups supported by the original matrix were recorded by using PAUP* 4.0d64 (Swofford, in press).

Stability to the Removal of Data Sets

The WHIPPO-1 matrix of 17 data sets was subjected to successive data set removal (Olmstead and Sweere, 1994; Gatesy et al., in press). Each individual data set and each combination of two data sets were sequentially removed from the combined matrix. These removals produced (*a*) 17 derivative data sets that each lacked 1 data set and (*b*) 136 derivative data sets that each lacked 2 data sets. The perturbed matrices were analyzed cladistically as above. PAUP searches were branch and bound. The collapse of clades that had been supported by the original matrix was noted.

Stability to the Addition of Data Sets

The stability of the casein data set compiled by Gatesy et al. (1996) to the addition of other character evidence was tracked. Since the publication of the $\beta + \kappa$-casein data set, 15 other character sets have been added to the caseins in various publications (Gatesy, 1997, 1998; Gatesy and Arctander, in press; Gatesy et al., in press). The support for nodes favored by the casein data set was recorded in a roughly chronological sequence that follows the addition of characters over the past 3 years. BS scores were calculated as above for various subsets of the WHIPPO-1 matrix.

Stability to the Removal of Taxa

Individual in-group taxa were successively removed from the WHIPPO-1 matrix (Lanyon, 1985). This resulted in 12 perturbed matrices, each of which lacked 1 of the original 12 in-group taxa. These data sets were analyzed cladistically as described above. PAUP searches were branch and bound. The JK monophyly index of Siddall (1995) was calculated for each node that had been favored by the original combined data set. This index summarizes the percentage of

JK replicates that support each clade (see Lanyon, 1985; Siddall, 1995).

Stability to the Addition of Taxa

The stability of relationships to the addition of taxa was examined by comparing minimum-length topologies for the WHIPPO-1 matrix of 13 taxa to minimum-length topologies for the WHIPPO-2 matrix of 79 taxa.

Stability to Different Sequence Alignment Parameters

The stability of phylogenetic results to different hypotheses of positional homology (Lake, 1991; Wheeler, 1995) will be addressed in a separate paper (Gatesy and O'Grady, unpubl.).

Results

Individual Data Sets

Results for separate analyses of the individual data sets are shown in Figure 2. Only 1 of the 17 separate analyses supports the monophyly of Artiodactyla. Five individual data sets favor clade A (maximum BS of 7 for IRBP), eight data sets favor clade B (maximum BS of 10 for β-casein), and six data sets favor clade C (maximum BS of 14 for β-casein). Simultaneous analysis of the WHIPPO-1 matrix yielded one most-parsimonious topology that also supports clades A, B, and C. No extra character steps are required to fit the SINE retroposon, β-casein, and α-lactalbumin data sets to the total data topology (Fig. 2).

Stability to Relaxation of the Parsimony Criterion

The traditional artiodactyl clades, Suina (Suidae + Tayassuidae), Pecora (Bovidae + Cervidae + Giraffidae), and Ruminantia (Pecora + Tragulidae), as well as Cetacea (Delphinoidea + Ziphiidae + Physeteridae + Mysticeti), are solidly supported by the WHIPPO-1 matrix. BS scores for these groups range from 82 to 108. The more controversial clades A, B, and C have BS scores from 25 to 30 (Fig. 3). A substantial relaxation in the parsimony criterion is necessary for artiodactyl monophyly to be considered a viable hypothesis. The shortest topology that supports Artiodactyla is 125 character steps longer than the minimum-length solution.

Distribution of Support among Data Sets in the Simultaneous Analysis

The numbers of unambiguous synapomorphies for clades A, B, and C are listed in Figure 4. Of the 17 data sets in the WHIPPO-1 matrix, 13 contain unambiguous synapomorphies for clade A, 13 data sets contain unambiguous synapomorphies for clade B, and 14 data sets contain unambiguous synapomorphies for clade C (Fig. 4).

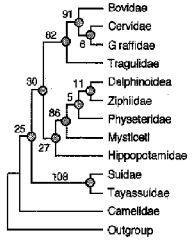
NDI scores for all 17 data sets in the WHIPPO-1 matrix are also shown in Figure 4. According to NDI, 10 data partitions have a positive influence at node A, 10 partitions have a positive influence at node B, and 9 partitions have a positive influence at node C. Many of the 17 data sets in the WHIPPO-1 matrix do not favor clades A, B, and C in separate analyses (Fig. 2); however, some of these apparently contradictory data sets provide positive character support within the context of the combined matrix. For example, α-hemoglobin does not support (Hippopotamidae + Cetacea) in separate analysis (Fig. 2), but because of hidden support, α-hemoglobin has a positive influence on BS at this node in the simultaneous analysis of the WHIPPO-1 matrix (NDI = +2, Fig. 4).

Stability to Differential Character Weighting

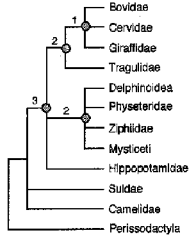
Successive approximations-weighting of the WHIPPO-1 matrix yielded a single minimum-cost cladogram. This cladogram was identical to the shortest topology, given an equal weighting of all characters (Fig. 3).

Stability to BP and JK Resampling of Characters

Clades A, B, and C are stable to BP and JK resampling of characters. BP support for these nodes ranges from 98 to 100 (Fig. 3). Deletion of 50% of the characters in each JK replicate yielded JK percentages that also ranged from 98 to 100 for clades A, B, and C. These clades were also fairly stable to removal of 75% of characters in each JK replicate (JK percentages from 89 to 93, Fig. 3).



all data
1650 inf. chars.
1 tree, 6,498 steps
CI=0.559, RI=0.501



SINE retroposons
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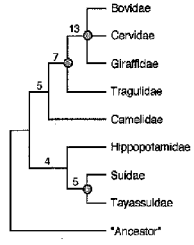
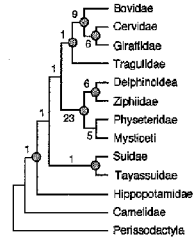
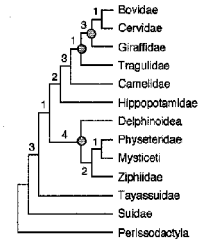
CI=1.000, RI=1.000



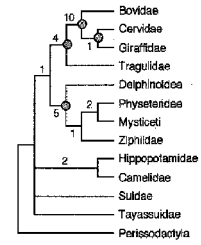
skeletal/dental
62 inf. chars.
1 tree, 137 (10) steps
CI=0.733, RI=0.796



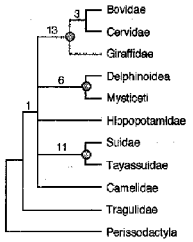
cytochrome *b*
994 inf. chars.
1 tree, 1,584 (12) steps
CI=0.451, RI=0.318



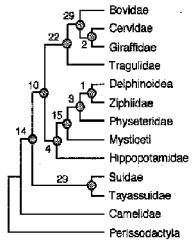
12S rDNA
87 inf. chars.
1 tree, 335 (22) steps
CI=0.494, RI=0.436



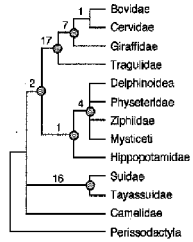
16S rDNA
103 inf. chars.
3 trees, 365 (13) steps
CI=0.484, RI=0.469



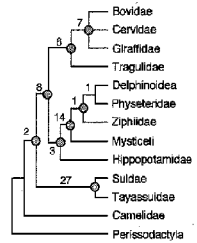
protamine P1
99 inf. chars.
7 trees, 357 (10) steps
CI=0.599, RI=0.579



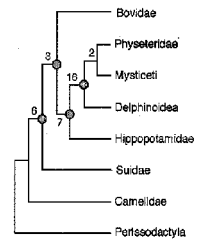
β-casein
236 inf. chars.
1 tree, 837 (0) steps
CI=0.696, RI=0.740



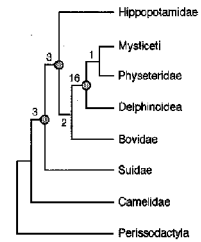
κ-casein
97 inf. chars.
28 trees, 362 (1) steps
CI=0.684, RI=0.699



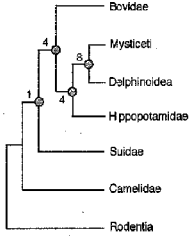
γ-fibrinogen
125 inf. chars.
2 trees, 410 (2) steps
CI=0.684, RI=0.713



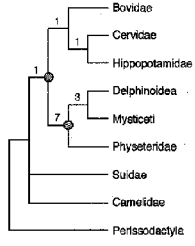
IRBP
108 inf. chars.
1 tree, 541 (2) steps
CI=0.650, RI=0.579



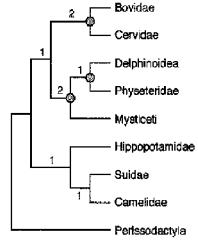
vWF
157 Inf. chars.
1 tree, 535 (2) steps
CI=0.622, RI=0.481



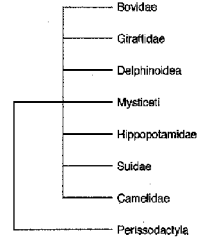
α-lactalbumin
94 inf. chars.
1 tree, 496 (0) steps
CI=0.698, RI=0.557



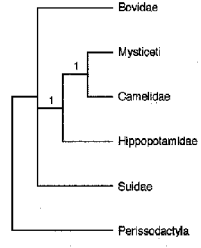
α-hemoglobin
26 inf. chars.
2 trees, 97 (5) steps
CI=0.742, RI=0.673



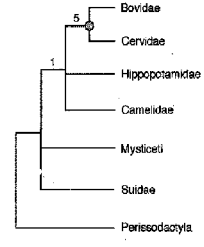
β-hemoglobin
24 Inf. chars.
1 tree, 99 (5) steps
CI=0.717, RI=0.605



α-crystallin A
5 inf. chars.
2 trees, 12 (2) steps
CI=0.625, RI=0.571



cytochrome *c*
2 inf. chars.
1 tree, 7 (2) steps
CI=1.000, RI=1.000



pancreatic ribonuclease
23 inf. chars.
2 trees, 102 (5) steps
CI=0.740, RI=0.561

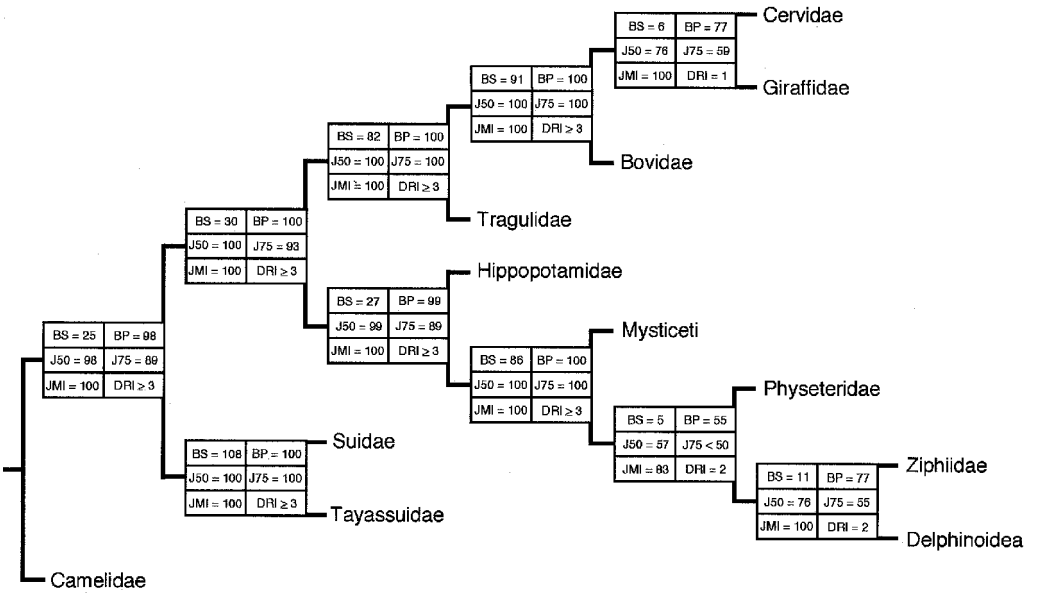


FIGURE 3. The shortest topology for the 13-taxon WHIPPO-1 matrix. At each node, the following information is given: branch support (BS), BP percentage, character JK percentage for 50% deletion of characters (J50), character JK percentage for 75% deletion of characters (J75), JK monophyly index (JMI), and the data set removal index (DRI = the minimum number of data set removals necessary to collapse that clade; Gatesy et al., in press).

Stability to the Removal of Data Sets

Clades A, B, and C are resistant to collapse after the removal of any single data set or any combination of two data sets. This shows that phylogenetic results for the combined matrix are not dependent on any single data set, gene, or gene product (in contrast to Gatesy et al., in press). At least three data sets must be removed from the WHIPPO-1 matrix to disrupt any of the controversial clades that group Cetacea within Artiodactyla (Fig. 3).

Stability to the Addition of Data Sets

Clades A, B, and C have been stable to the addition of 15 data sets and more than 1,400 informative characters over the past 3 years (Figs. 5, 6). BS for each of these clades has increased over time, but with dips in support on the addition of some character sets. In contrast, very well supported groups such as Pecora and Suina show a greater increase in BS with the addition of new data. The cost in extra steps for a monophyletic Artiodactyla also has skyrocketed with the growth of the data base (Figs. 5, 6).

Stability to the Removal of Taxa

Clades A, B, and C are stable to the removal of any single in-group taxon in the WHIPPO-1 matrix. JK monophyly indices are 100% for these clades and for six other nodes supported by the combined character set (Fig. 3).

FIGURE 2. Strict consensus trees of minimum length topologies for each of the 17 data sets and for the simultaneous analysis of all 17 data sets (WHIPPO-1 matrix). For each topology, the following information is given: number of informative characters (inf. chars.), number of equally parsimonious trees, tree length (and the number of extra steps required to fit the data set onto the total data topology), consistency index disregarding uninformative characters (CI; Kluge and Farris, 1969), and retention index (RI; Farris, 1989). Branch support (BS) is shown at internodes, and nodes consistent with the total data tree are marked by shaded circles.

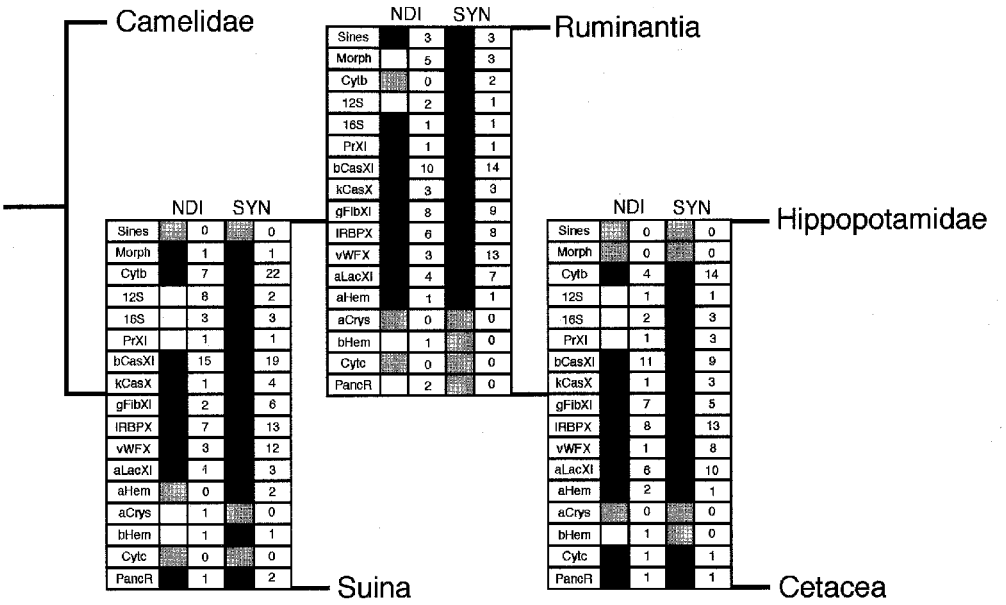


FIGURE 4. Nodal data set influence (NDI) and the numbers of unambiguous synapomorphies (SYN) for clade A (Cetacea + Hippopotamidae), clade B (Cetacea + Hippopotamidae + Ruminantia), and clade C (Cetacea + Hippopotamidae + Ruminantia + Suina). Values are shown for each of the 17 data partitions that compose the WHIPPO-1 matrix. Data sets are abbreviated as: Sines = SINE retroposons, Morph = morphological characters, Cytb = mt cytochrome *b*, 12S = 12S mt rDNA, 16S = 16S mt rDNA, PrXI = protamine P1 exons and intron, bCasXI = β-casein exon 7 and intron 7, kCasX = κ-casein exon 4, gFibXI = γ-fibrinogen exons and introns, IRBPX = IRBP exon 1, vWFX = vWF exon 28, aLacXI = α-lactalbumin exons and introns, aHem = α-hemoglobin, aCrys = α-crystallin A, bHem = β-hemoglobin, Cytc = cytochrome *c*, and PancR = pancreatic ribonuclease. Positive values are marked by black boxes to the left, negative values are marked by white boxes to the left, and values of zero are marked by gray boxes to the left.

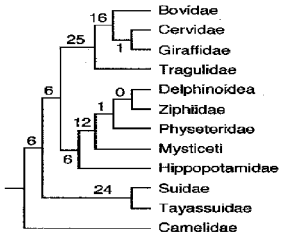
Stability to the Addition of Taxa

Relationships based on a limited taxonomic sample may be overturned by the addition of new taxa into the analysis (e.g., Philippe and Douzery, 1994; Halanych, 1998). However, the addition of 66 taxa to the 10 DNA data sets does not upset clades A, B, and C (Fig. 7). In the combined analysis of the 79-taxon matrix (WHIPPO-2), BS for these clades ranges from 17 to 29. The cost of a monophyletic Artiodactyla is 108 extra character steps beyond minimum length.

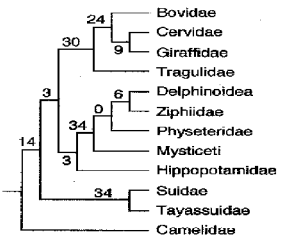
DISCUSSION

By all measures used in this study, clades A, B, and C are stable. There is corroboration from multiple data sets for each of these clades, BS ranges from 17 to 30, successive approximations weighting does not upset these groups, BP percentages range from 98 to 100, character JK percentages with 50% character removal range from 98 to 100, character JK percentages with 75% character removal range from 89 to 93, JK monophyly indices are 100%, at least three data sets must be removed from the combined matrix to collapse these clades, BS has increased with the addition of data sets over the past 3 years, and a denser sampling of taxa does not overturn the results that are based on a smaller sample of taxa (Figs. 2–7).

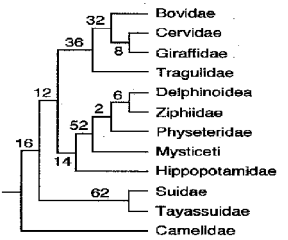
This is not to say that clades A, B, and C are true, statistically significant, or incapable of being disrupted with the addition of new data. However, the combined data set is robust to a wide variety of



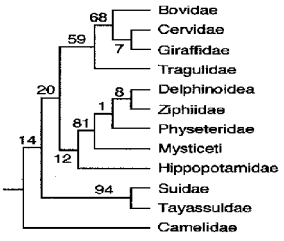
(a)
κ-casein exon 4
+ β-casein exon 7
inf. chars. = 188
3 trees, 723 steps
CI = 0.686, RI= 0.705
total inf. chars.= 188



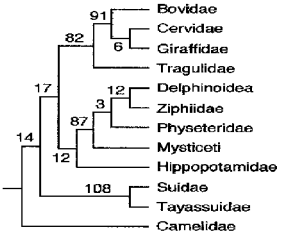
(b)
add mt cytochrome *b*
inf. chars. = 394
2 trees, 2,319 steps
CI = 0.499, RI= 0.416
total inf. chars.= 582



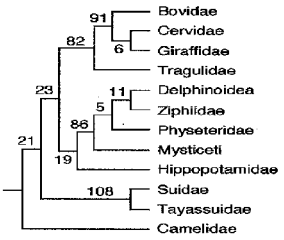
(c)
add γ-fibrinogen exons 2-4
+ γ-fibrinogen introns 2, 3
inf. chars. = 125
1 tree, 2,731 steps
CI = 0.521, RI= 0.459
total inf. chars.= 707



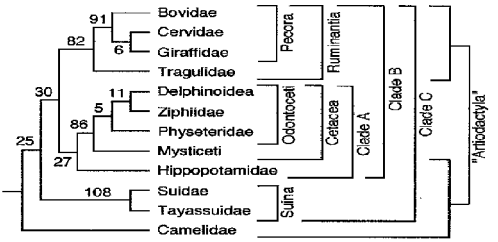
(d)
add 12S mt rDNA
+ 16S mt rDNA
+ protamine P1 exons 1, 2
+ protamine P1 5', 3' noncoding
+ β-casein intron 7
inf. chars. = 397
1 tree, 4,202 steps
CI = 0.527, RI= 0.482
total inf. chars.= 1,104



(e)
add SINE retroposons
+ morphology
+ protamine P1 intron 1
+ cytochrome *c*
+ α-crystallin A
+ pancreatic ribonuclease
+ α-hemoglobin
+ β-hemoglobin
inf. chars. = 187
1 tree, 4,822 steps
CI = 0.542, RI= 0.498
total inf. chars.= 1,291



(f)
add IRBP exon 1
inf. chars. = 108
1 tree, 5,365 steps
CI = 0.547, RI= 0.501
total inf. chars.= 1,399



(g)
add vWF exon 28
+ α-lactalbumin exons 1-3
+ α-lactalbumin introns 1, 2
inf. chars. = 251
1 tree, 6,498 steps
CI = 0.559, RI= 0.501
total inf. chars.= 1,650

FIGURE 5. A chronological summary of the addition of data sets to the κ + β-casein data compiled by Gatesy et al. (1996). Combined data sets a–g roughly follow Gatesy et al., 1996 (a and b); Gatesy, 1997 (c); Gatesy, 1998 (d); Gatesy et al., in press (e); Gatesy and Arctander, in press and this paper (f); and this paper (g). Taxonomic exemplars are as in the WHIPPO-1 matrix. For each combined data set, one of the minimum-length topologies, data sets that were added, the number of informative characters added (inf. chars.), the number of minimum-length trees, minimum tree length, consistency index disregarding uninformative characters (CI), retention index (RI), the total number of informative characters in the data set (total inf. chars.), and branch support (BS) at internodes are shown. Higher-level taxa are delimited by brackets on the topology for g.

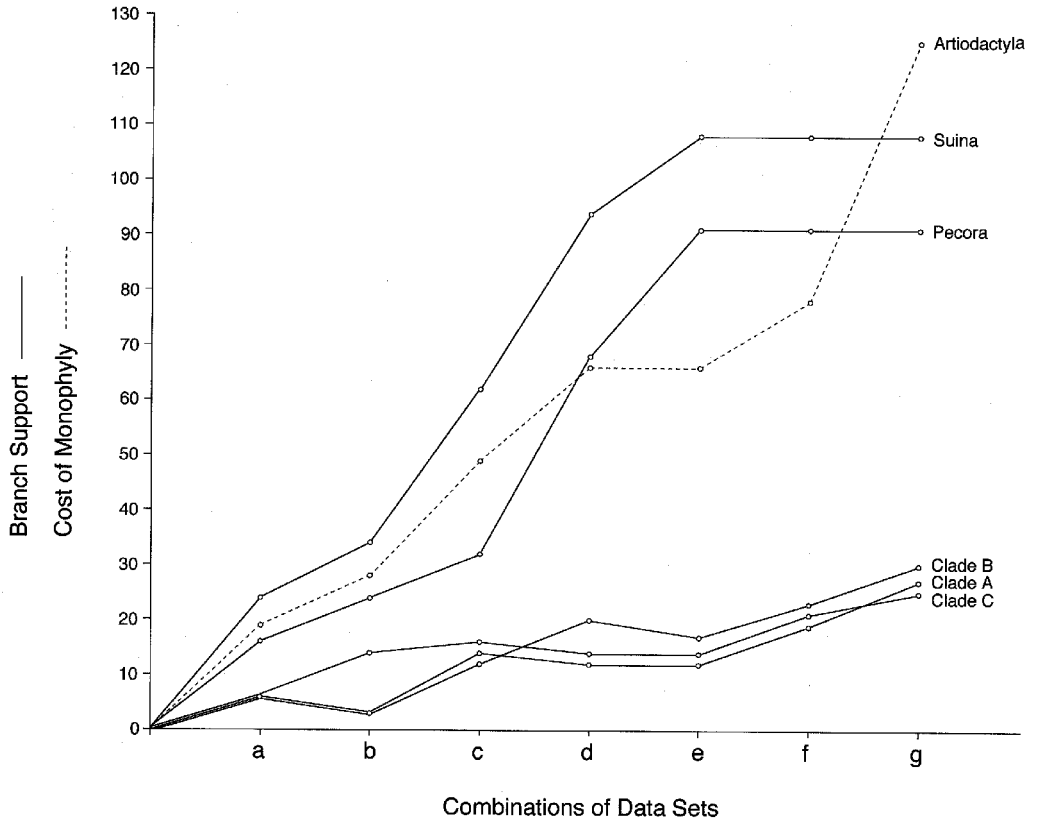


FIGURE 6. Branch support (BS) for selected nodes is plotted for data sets a–g from Figure 5 (solid lines). The cost, in extra character steps, for a monophyletic Artiodactyla also is plotted for data sets a–g (dotted line).

perturbations, and the shortest topologies that support artiodactyl monophyly are more than 100 steps longer than minimum length. This shows that, in a parsimony framework with all character transformations given equal weight (see Kluge, 1997), the insertion of Cetacea within Artiodactyla will not be overturned unless numerous contradictory characters are added to the present data base. The unwavering increase of evidence that counters artiodactyl monophyly (Figs. 5, 6) hints that there is little precedence for the discovery of 100 artiodactyl synapomorphies in the near future.

Nixon and Carpenter (1996) suggested that topologies that are stable to the addition of new data are predictive, and they argued that predictivity, stability, and repeatability are interrelated, desirable attributes in phylogenetic analysis (for related arguments see Penny and Hendy, 1985, 1986; for a different viewpoint see Kluge, 1989, 1997; Siddall and Kluge, 1997). Given this characterization of stability, clades A, B, and C are highly predictive. These groups have withstood a battery of critical cladistic tests over the past 3 years. The addition of hundreds of informative characters did not upset the basic structure of the artiodactyl cladogram (Figs. 5, 6). Likewise, the addition of 66 taxa did not overturn the conclusions that were based on a smaller sample of taxa (Fig. 7).

Stability is no guarantee of accuracy (Felsenstein, 1978; Hendy and Penny, 1989); unlike accuracy, however, stability

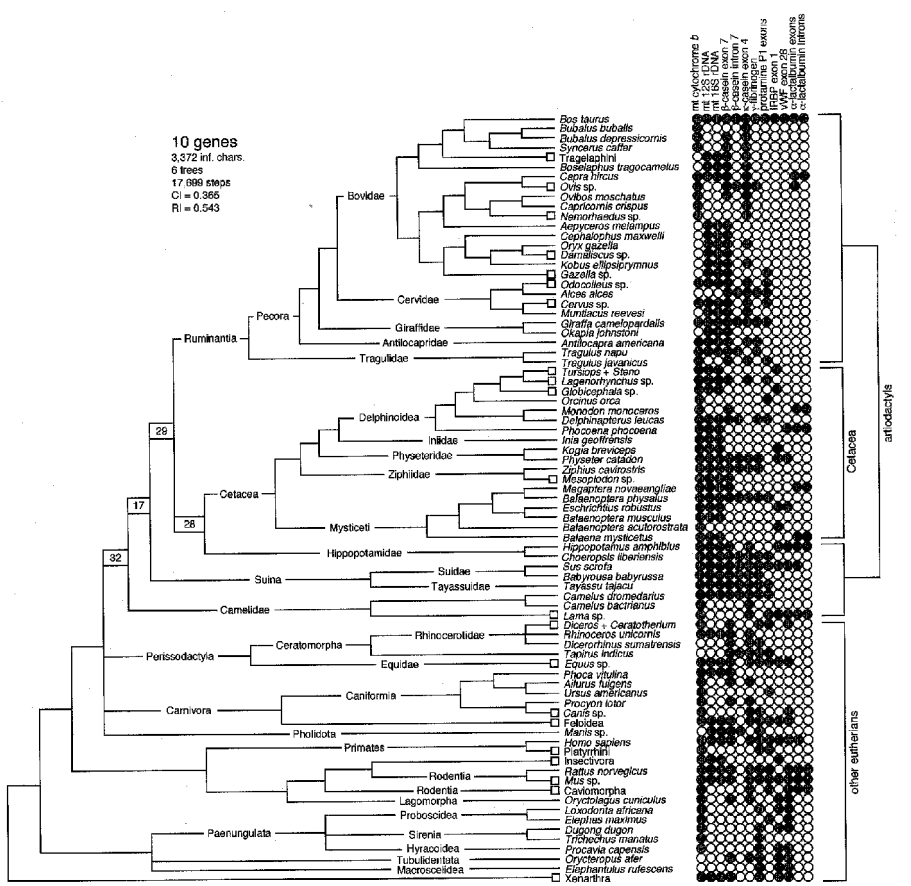


FIGURE 7. Strict consensus of minimum-length topologies for the simultaneous analysis of the 79-taxon matrix (WHIPPO-2). Six minimum-length trees were found with both PAUP (Swofford, 1993, and in press) and NONA (Goloboff, 1993). The number of informative characters (inf. chars.), the number of minimum-length trees, tree length, consistency index disregarding uninformative characters (CI), and retention index (RI) are stated (upper left). Higher- level taxa are shown at internodes or are delimited by brackets to the right of the tree. Branch support (BS) for selected clades is shown at internodes inside rectangles. Given that the combined matrix is characterized by extensive missing data and several local optima (Maddison, 1991), BS may be lower than indicated. DNA sequences sampled for each taxon are marked by shaded circles to the right of each taxon. Hybrid terminals composed of sequences from different species are marked by open boxes, as follows (abbreviations for genes are c = mt cytochrome *b*, 12 = mt 12S rDNA, 16 = mt 16S rDNA, bx = β-casein exon 7, bi = β-casein intron 7, k = κ-casein exon 4, g = γ-fibrinogen exons 2–4/introns 2–3, p = protamine P1 exons 1–2/5′, 3′-noncoding regions, ir = IRBP exon 1, vWF = vWF exon 28, alx = α-lactalbumin exons 1–3, ali = α-lactalbumin introns 1–2): Tragelaphini: 12/16 = *Tragelaphus imberbis*, bx/kx = *Taurotragus oryx*; *Ovis* sp.: c/bx/bi/k/alx = *O. aries*, g = *O. dalli*; *Nemorhaedus* sp.: c = *N. caudatus*, k = *N. goral*; *Damaliscus* sp.: 12/16 = *D. dorcas*, bx = *D. lunatus*; *Gazella* sp.: 12/16 = *G. thomsoni*, bx = *G. granti*, p = *G. dorcas*; *Odocoileus* sp.: c = *O. hemionus*, 12/16/bx/k/p = *O. virginianus*; *Cervus* sp.: c/bx/k = *C. nippon*, 12/16 = *C. unicolor*, p = *C. elaphus*; *Tursiops* + *Steno*: c/12/16 = *Tursiops truncatus*, ir = *Steno bredanensis*; *Lagenorhynchus* sp.: c = *L. albirostris*, 12/16/bx/k/p = *L. obscurus*; *Globicephala* sp.: c/12/16 = *G. melas*, ir = *G. macrorhynchus*; *Mesoplodon* sp.: c/12/16 = *M. europaeus*, bx = *M. peruvianus*; *Lama* sp.: c/k/p/alx/ali = *L. guanicoe*, ir/vWF = *L. glama*; *Diceros* + *Ceratotherium*: c/bx/g/p = *Diceros bicornis*, vWF = *Ceratotherium simum*; *Equus* sp.: c/bx/k = *E. grevyi*, 12/16/vWF = *E. asinus*, g = *E. przewalskii*, p/ir = *E. caballus*; *Canis* sp.: c/vWF = *C. familiaris*, g/k = *C. latrans*; Feloidea: c/12/16/p/ir/vWF = *Felis catus*, bx/k = *Panthera uncia*, g = *Crocuta crocuta*; Platyrrhini: c = *Saimiri sciureus*, g = *Saguinus oedipus*, p = *Alouatta seniculus*; Insectivora: c/12/16 = *Erinaceus europaeus*, ir = *Sorex palustris*; *Mus* sp.: ir/vWF = *M. domesticus*, c/12/16/bx/k/g/p/alx/ali = *M. musculus*; Caviomorpha: c/p = *Cavia porcellus*, k/alx/ali = *C. cutleri*, vWF = *Dasyprocta agouti*; Xenarthra: c = *Dasypus novemcinctus*, 12/16 = *Choloepus didactylus*, bx/g = *Cyclopes didactylus*, ir/vWF = *Bradypus tridactylus*.

can actually be measured for a given, empirical data set. Methods that attempt to improve the accuracy of phylogenetic estimation are often justified by simulations (e.g., Bull et al., 1993; Huelsenbeck and Hillis, 1993), experimental genealogies (e.g., Hillis et al., 1992; Hillis and Bull, 1993), or "known" phylogenies (e.g., Cunningham, 1997; Naylor and Brown, 1998). In contrast, inductive extrapolations are not necessary to rationalize measures of stability. A clade supported by a particular character matrix simply *is* or *is not* stable to the perturbation of interest. Stability may not be the primary goal of systematics, but many systematists would agree that internal consistency, repeatability, decisiveness, predictivity, and corroboration from multiple data sets are positive qualities.

From a practical perspective, stability may be most important for classification. Siddall (1995:34) pointed out, "Inasmuch as the systematic community needs phylogenetic classifications, it also needs to avoid the continual renaming of higher categories but also avoid reverting to appeal to subjective authority for stability." Therefore, the robustness of clades to a variety of perturbations may be critical information for taxonomic purposes. The stability of relationships among extant artiodactyl taxa suggests that a radical reordering of artiodactyl taxonomy may be warranted. However, most of the characters used in our analysis were molecular (Fig. 2). Evidence from the dense artiodactyl fossil record also needs to be considered (Simpson, 1945; Gentry and Hooker, 1988; Theodor, 1996, 1997; Geisler and O'Leary, 1997). Therefore, it would be premature to restructure the classification of Artiodactyla until the paleontological/morphological data are properly integrated with the molecular data.

The stability of groups to perturbation is also helpful for determining where more systematic work should be directed. For example, seeking disconfirming evidence for a monophyletic Cetacea would seem to be a waste of time and money at this point. Cetacea is supported by numerous morphological synapomorphies; in the present analysis it has BS of 86, a BP percentage of 100, JK percentages of 100, and is corroborated by 13 data sets (Figs. 2, 3). In contrast, relationships within Pecora are highly unstable. Cervidae + Giraffidae is weakly supported (BS = 6, BP percentage = 77) and is not stable to data set removal, jackknifing, or increased taxonomic sampling (Figs. 3, 7). The present data base does not robustly demarcate relationships among Cervidae, Giraffidae, and Bovidae. This instability indicates that more systematic work within Pecora is needed.

Conclusion

We once again assessed the stability of cladistic relationships between Cetacea and higher-level artiodactyl taxa. Combined analyses of 17 data sets, including new information from IRBP and vWF, robustly support (((((Cetacea + Hippopotamidae) Ruminantia) Suina) Camelidae) outgroup) (Figs. 3, 7). These relationships are stable to a variety of perturbations (Figs. 3–7). The molecular data strongly contradict the traditional view, in which Artiodactyla is considered monophyletic (Simpson, 1945; Gentry and Hooker, 1988; Theodor, 1996; Geisler and O'Leary, 1997). This may lead some to question the validity of the molecular results. However, within a cladistic framework, the nesting of Cetacea within Artiodactyla is perhaps the most solidly supported link between eutherian orders. Given the stability of our results, we predict that the phylogenetic grouping of Cetacea within Artiodactyla will not be overturned by either revision of the present data base or the addition of new character evidence.

Acknowledgments

A. deQueiroz, C. Hayashi, P. Waddell, J. D. Archibald, and M. Hasegawa provided constructive comments on various stages of the manuscript. This work was funded by NSF Systematics grant DEB-9509551 (J.G.), the National Fund for Scientific Research–Belgium (M.M.), the Free University of Brussels (M.M.), and the European Commission under the TMR Network Programme: ERB-FMRX-CT98-0221 (M.S).

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Received 18 July 1998; accepted 28 September 1998
Associate Editor: Peter Waddell