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Are the Fossil Data Really at Odds with the Molecular Data? Morphological Evidence for Cetartiodactyla Phylogeny Reexamined

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The phylogenetic position of Cetacea within the mammalian tree has long been a subject of debate. The traditional paleontological view is that an extinct order of mammals, the Mesonychia, is the sister taxon to Cetacea (e.g., Van Valen, 1966; Prothero et al., 1988). This view has recently been supported by morphological studies that examined both fossil and extant material (Geisler and Luo, 1998; O'Leary and Geisler, 1999). The molecular evidence, by contrast, supports a phylogenetic hypothesis in which Cetacea is nested deeply within the Artiodactyla, implying that Artiodactyla is paraphyletic with respect to Cetacea (Sarich, 1985; Milinkovitch et al., 1993; Gatesy et al., 1999, and references therein). Furthermore, several molecular studies have suggested that hippopotamids are the sister taxon to Cetacea (e.g., Irwin and Arnason, 1994; Gatesy et al., 1996; Gatesy, 1997, 1998; Montgelard et al., 1997; Nikaido et al., 1999). Although the "return to water" aspect of this phylogenetic hypothesis has a certain intuitive appeal, it has met with resistance from those who work primarily with morphology (e.g., Geisler and Luo, 1998; O'Leary and Geisler, 1999; O'Leary, 1999). Despite the resurgent interest in the problem, no consensus reconciling the different signals has yet been reached.

Obviously, a serious limitation of molecular data is that this information cannot be gathered from the fossil remains of extinct taxa. In contrast, fossils can play an important role in recovering phylogeny in morphological studies, often providing information about character states of stem lineages that

are not present in extant taxa. In some cases, the inclusion of fossils can even overturn inferences based solely on extant character distributions (e.g., Gauthier et al., 1988; Eernisse and Kluge, 1993). Because molecular data sets, by their very nature, can include only extant taxa, biased taxon sampling could possibly lead to incorrect phylogenetic inferences.

Recently, O'Leary and Geisler (1999) presented a phylogenetic analysis of morphological data from both fossil and extant mammals. Using a combined data set of characters from basicranial, cranial, dental, postcranial, and soft tissue regions, they found evidence supporting the monophyly of Cetacea, Mesonychia, Artiodactyla, and Perissodactyla. Their data also supported a sister-group relationship between Mesonychia and Cetacea, affirming the traditional paleontological view (Fig. 1). Interestingly, when fossils were excluded from the data, O'Leary and Geisler found that the phylogenetic signal present in the extant taxa was similar to that seen for the molecular data, that is, with Cetacea deeply nested within Artiodactyla. This pattern led them to propose that phylogenies based on extant data alone might be predisposed to recover inconsistent branches as a result of sparse taxon sampling. If true, this could explain why phylogenetic inferences based on molecular data (derived exclusively from extant taxa) are frequently at odds with inferences from skeletal and dental data derived from both fossil and extant forms. This is an interesting hypothesis and one that, if borne out, would have sobering implications for molecular systematics—a discipline almost

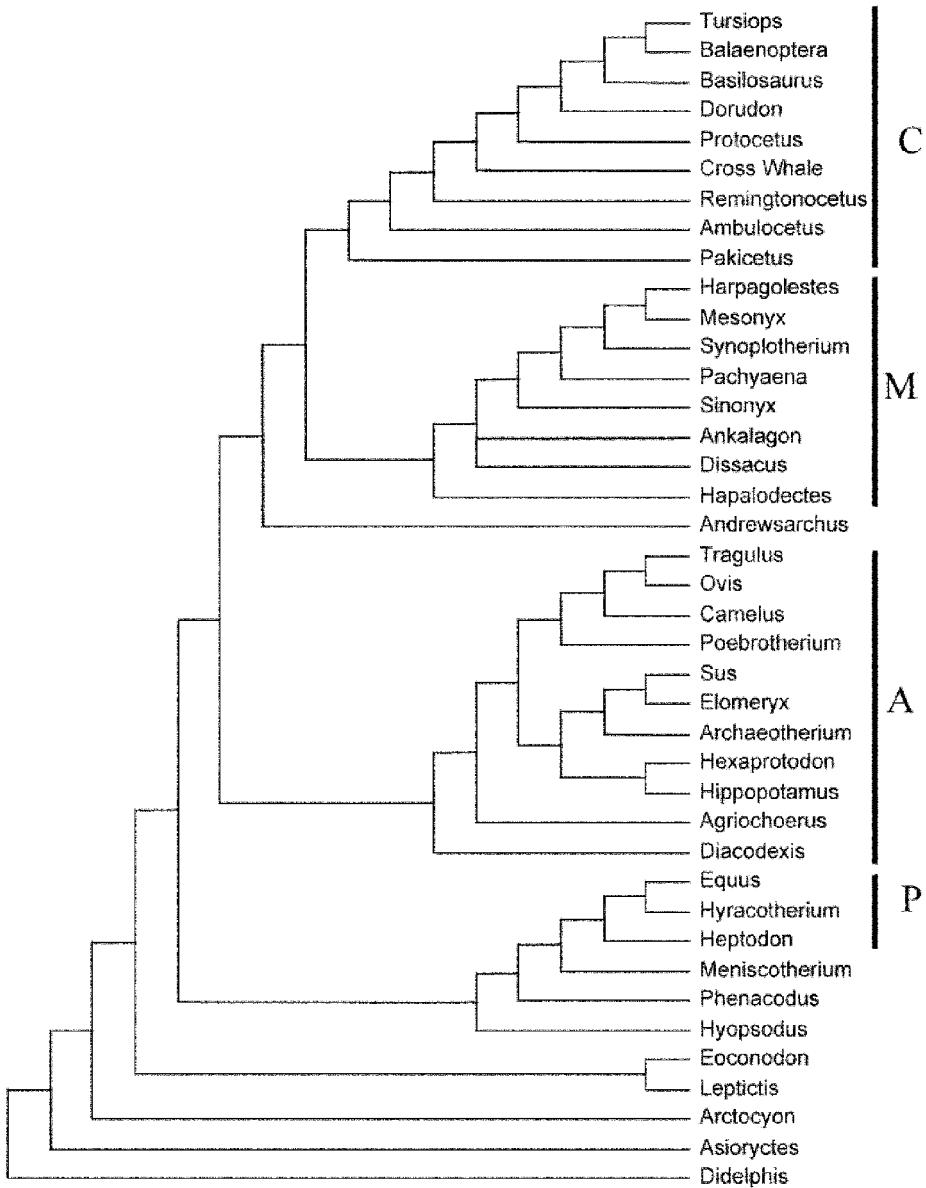


FIGURE 1. Phylogenetic hypothesis of O'Leary and Geisler (1999) proposing the monophyly of the major mammalian clades. Clades are denoted Artiodactyla (A), Cetacea (C), Mesonychia (M), and Perissodactyla (P).

exclusively restricted to the study of extant forms.

In another study, O'Leary (1999) examined the cetartiodactyla phylogeny through a combined analysis of osteological data and a class of characters consisting of retrotransposons, soft tissue, and molecular data, referred to by O'Leary as "neontological data". This distinction was set up by O'Leary to explore differences in phylogenetic signal between characters restricted to extant forms

and those that can be collected for both extant and extinct forms. A partition homogeneity test (Farris et al., 1994) carried out by O'Leary suggested significant heterogeneity between these two data partitions (osteological vs. neontological) across a variety of different weighting schemes (O'Leary, 1999: her Table 3). Although a strict consensus tree of the combined data sets yielded a tree that was unresolved for the relationships of interest, the Adams consensus tree was similar

to that seen for the neontological data alone. Nevertheless, O'Leary cautioned against accepting the results from these analyses as conclusive because the neontological partition had the most missing information, reflecting the lack of sequence data from fossils. She argued (O'Leary, 1999:328):

... the most convincing resolution of a conflict such as this one may come from two other angles: (i) skeletal evidence, particularly for fossils, may emerge to support the insertion of Cetacea into an otherwise monophyletic Artiodactyla, or (ii) increased gene sequencing and collection of data on retroposons and soft tissue, as well as increased sampling of extant taxa, may introduce heterogeneity into the neontological signal that will allow the present osteological signal to prevail

Thus, when all of the currently available evidence is brought to bear in a total evidence parsimony analysis (Kluge, 1989), the conflict between morphology and molecules with respect to the phylogenetic position of Cetacea might appear to remain unresolved.

Given the potential importance of O'Leary and Geisler's (1999) claim, we re-analyzed their data set in an effort to better understand both the nature and the magnitude of the signal conflicts among their data partitions. We first examined the homogeneity of the phylogenetic signal across the five different morphological data partitions presented in their paper (O'Leary and Geisler, 1999). We then pooled the data partitions for which the hierarchical signals were mutually compatible and subjected the resulting data set to parsimony analysis. Finally, we compared trees resulting from this analysis against competing phylogenetic hypotheses from the literature.

HOMOGENEITY AMONG DATA PARTITIONS

The character matrix of O'Leary and Geisler (1999) was obtained from TreeBASE (http://www.herbaria.harvard.edu/treebase:accession_number/S387). The data contained 40 taxa and 123 morphological characters, divided into five data partitions: basicranial, cranial, dental, postcranial, and soft tissue characters. Although O'Leary and Geisler (1999) explicitly described these partitions, they did not investigate the distribution of phylogenetic signal among them. Their partitions represent either distinct tissue types (dental, soft tissue, or skeletal) or classes based on relative position within the organism (basicranial, postcranial, or

cranial). Because O'Leary (1999) found significant heterogeneous signal between osteological and neontological characters for mammals, we felt it was of interest to examine the homogeneity of phylogenetic signals among the different data partitions in their data set. Following O'Leary (1999), we used the Incongruence Length Difference (ILD) test (Farris et al., 1994) to determine whether the phylogenetic signal was consistent among partitions. This test measures the degree of incongruence in phylogenetic signals among two or more data partitions as the difference between the lengths of the individual and combined data analyses (Mickey and Farris, 1981; Farris et al., 1994). The $(ILD) = 0$ if at least one most-parsimonious tree from each data partition is the same, and is >0 if there phylogenetic signal is somewhat heterogeneous among partitions. The significance of the observed ILD is assessed by comparing it with a distribution of ILD values obtained through random partitions of the data matrix (Farris et al., 1994; Cunningham, 1997).

We performed several homogeneity tests of the five data partitions in the data set. First, we calculated the ILD for all five data partitions simultaneously, to determine if there were overall differences in the data partitions (this is similar to an ANOVA for multiple groups). Next, we compared the phylogenetic signal in each partition relative to the aggregate signal in the remaining data to determine which, if any, of the data partitions contained a distinct signal. This yielded five "multiple comparison" tests. We then performed all pairwise comparisons to determine which individual data partitions contained signals that differed from one another (10 total comparisons). By combining the results from these a posteriori tests, we could determine which data partitions contained aberrant hierarchical signals. We used 1,000 iterations of the randomization procedure to assess the significance of ILD for all tests. Observed significance values were compared with Bonferonni-adjusted α -values. All tests were performed by using PAUP* 4.0b2 (Swofford, 1999).

We found the phylogenetic signals for the five data partitions were significantly different ($P = 0.001$). Comparing each data partition with the combined data from the remaining four partitions revealed that both

TABLE 1. Probability values from partition homogeneity tests (Farris et al., 1994) using 1,000 iterations (significant comparisons are boldface). The significance of pairwise comparisons is compared with a Bonferroni-adjusted $\alpha = 0.005$ (0.05/10), and the significance of each data partition to the remaining data found from pairwise comparisons is compared with a Bonferroni-adjusted $\alpha = 0.01$ (0.05/5).

	Basicrania1	Cranial	Dental	Postcranial	Soft tissue	Versus all
Basic rania1	—					0.001
Cranial	0.470	—				.0338
Dental	0.001	0.117	—			0.001
Postcranial	0.004	0.338	0.001	—		0.107
Soft tissue	0.999	0.998	0.975	0.951	—	0.965

the basicranial and the dental partitions contained significantly heterogeneous signal relative to the rest of the data (Table 1). Further, when all the pairwise comparisons of data partitions were performed, the dental characters emerged as the most different from the other partitions, followed by the basicranial characters (Table 1).

PHYLOGENETIC SIGNAL

We performed a series of parsimony analyses to determine the nature of the phylogenetic signal differences among data partitions found to be distinct by the ILD tests described above. We ran three analyses: (1) the combined data for all but the dental partition, (2) the combined data for all but the basicranial partition, and (3) the combined data for all but the dental and basicranial partitions combined. All phylogenetic analyses were performed in PAUP* 4.0b2 (Swofford, 1999).

When the dental partition was excluded, the resulting phylogeny was similar to that of the molecular data only. Specifically, Artiodactyla was paraphyletic with respect to Cetacea (Fig. 2a), and the Hippopotamidae were found to be the closest living relatives to Cetacea, a result seen in molecular studies (e.g., Gatesy et al., 1996; Nikaido et al., 1999). Thus, when the dental data were excluded from analysis, the remaining morphological data, both extant and fossil, supported a paraphyletic Artiodactyla and a sister-group relationship between whales and hippopotamids.

When the basicranial partition was excluded, the relationships among the major clades were nearly identical to those found by O'Leary and Geisler (1999). Artiodactyla, Cetacea, Mesonychia, and Perissodactyla were all found to be monophyletic, and

Mesonychia was the sister-group to Cetacea. This implies that the basicranial partition has little influence on the topology obtained by O'Leary and Geisler (1999).

When both the dental and basicranial partitions were excluded, Artiodactyla was found to be paraphyletic with respect to Cetacea (Fig. 2b), reflecting the same phylogenetic pattern seen in most molecular studies. However, not too much should be made of this result because excluding the dental and basicranial partition removed 65% of the characters from the O'Leary and Geisler's data matrix. Although the remaining signal supports Artiodactyl paraphyly, it does so only weakly.

The tests described above identify the dental data partition as the one exerting the most influence on topology for O'Leary and Geisler's (1999) data set. When the dental data are included in the analysis, the resulting tree corresponds to that of the traditional, morphological view. When the dental data are removed, the remaining morphological characters (extant and fossil combined) yield a tree corresponding to that obtained from an analysis of the molecular data alone. In fact, a phylogenetic analysis of the dental data alone supports a close relationship between Cetacea and Mesonychia, confirming this finding.

INSPECTION OF DENTAL CHARACTERS

Our analyses provide an interesting twist to the already intriguing story presented by O'Leary and Geisler (1999). On the one hand, O'Leary and Geisler's decomposition of the data into neontological and paleontological provides a potential explanation (inadequate taxon sampling) to reconcile the discrepancy between molecular and morphological signals. Consistent with this, they

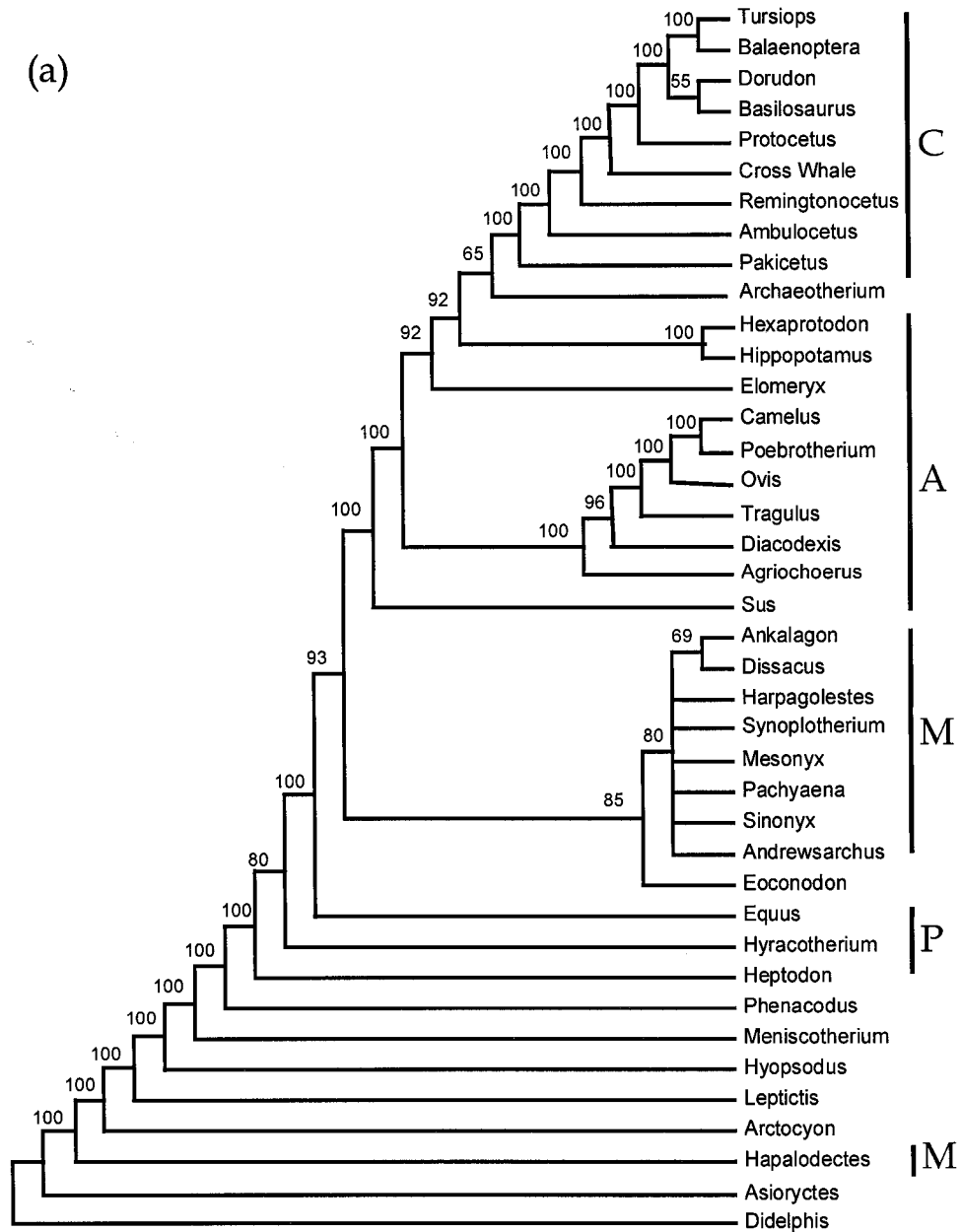


FIGURE 2. Phylogenetic hypotheses derived from majority-rule consensus trees of (a) 46,209 most-parsimonious trees from all characters except the dental characters, and (*continued*)

find that when fossils are excluded from the data set, the phylogenetic signal in the remaining extant taxa is similar to that seen for the molecular data. Accordingly, they conclude that the axis of the conflict is best characterized as “fossil versus extant” rather than “molecular versus morphological”. In contrast, our decomposition of characters

into dental and nondental provides an alternative explanation (anomalous hierarchical signal in one character partition of the data). Our phylogenetic analysis of all morphological data excluding dental characters results in a topology entirely consistent with that of the molecular data. We emphasize that this occurs when both extant and fossil taxa are

included in the analysis. Thus, one might hypothesize that perhaps the dental characters are distorting an otherwise consistent signal between the molecules and the rest of the morphology.

How can these two apparently incompatible hypotheses be reconciled? More explicitly, how can the hypothesis of a distorted dental signal explain O'Leary and Geisler's observation that when fossils are excluded from the data set, the phylogenetic signal present in the morphological data is similar to that seen for the molecular data? There is a simple explanation. A large proportion of the fossil data are in the form of dental character information. When fossil data are excluded, much of the dental signal is removed with it.

In an effort to understand how and why dental characters might be misleading, we turned to developmental genetics, a field that is playing an increasingly important role in our understanding of individuation, modularity, and covariation of morphological characters. To re-quote Owen Lovejoy, "Without knowledge from developmental studies morphologists can mistakenly assume they are dealing with independent characters—and so bias their analysis" (Gura, 2000:232). Recent studies of tooth development have shown that teeth in similar tooth groups (e.g., molars) are derived from the same tissue, and that shared developmental pathways influence these features (Jernvall and Thesleff, 2000). Additionally, knockout experiments have shown that impeding the effect of one gene does not arrest development of individual teeth but rather the entire set of teeth of that tooth type (Tucker et al, 1998; Tucker and Sharpe, 1999). Apparently, therefore, teeth of similar types (e.g., molars) are generated through the same genetic pathway.

Because the same underlying genetic architecture generates teeth in a particular tooth group, similar structures on different teeth (e.g., the hypocone) are de facto serially homologous. Therefore, measuring the same feature on multiple teeth in a tooth group represents a redundant and nonindependent sampling. We examined O'Leary and Geisler's (1999) data set, and identified a priori six sets of characters measured on multiple teeth that were presumed to exhibit such redundancy:

metaconids on lower premolars (characters 65, 66); metaconids on lower molars (74, 75, 76); paraconids on lower molars (68, 70, 72); paraconid/paracristid position on lower molars (69, 71, 73); hypoconulids on lower molars (77, 85); and the presence or absence of both the metaloph and metalophid (80, 81).

We then generated a matrix of pairwise differences among the 45 dental characters from O'Leary and Geisler's data set and performed a principal coordinates analysis. We explored the hypothesis that the six character sets identified a priori should fall out as six distinct clusters in the dental principal coordinates analysis. We fully acknowledge that shared-derived history can cause character states to covary over a tree or a principal coordinates ordination in the same way as developmental nonindependence does. However, because we described the six character sets as potentially redundant a priori, in consideration of independent criteria (i.e., developmental genetics), we think similarities in their distributions in a principal coordinates analysis, or across taxa in a tree, are more likely a consequence of functional nonindependence than shared evolutionary history.

Four of the six character sets identified a priori formed distinct clusters in the principal coordinates analysis (Fig. 3). Individual characters in close proximity were metaconids on lower molars (74, 75, 76), paraconids on lower molars (68, 70, 72), paraconid/paracristid position on lower molars (69, 71, 73), and the presence or absence of both the metaloph and metalophid (80, 81). In addition, the metacone on the upper molar M² fell close to the metaconid cluster, which may represent an additional instance of functional and developmental nonindependence (metacone and metaconids are similar structures on upper and lower teeth). This analysis suggests that the characters within each of these four sets are not independent but rather represent the same biological information (derived from the same developmental mechanisms) coded multiple times in the data set. We conclude that 11 characters in the dental data partition exhibit nonindependence and pseudoreplication reflecting multiple coding of the same features.

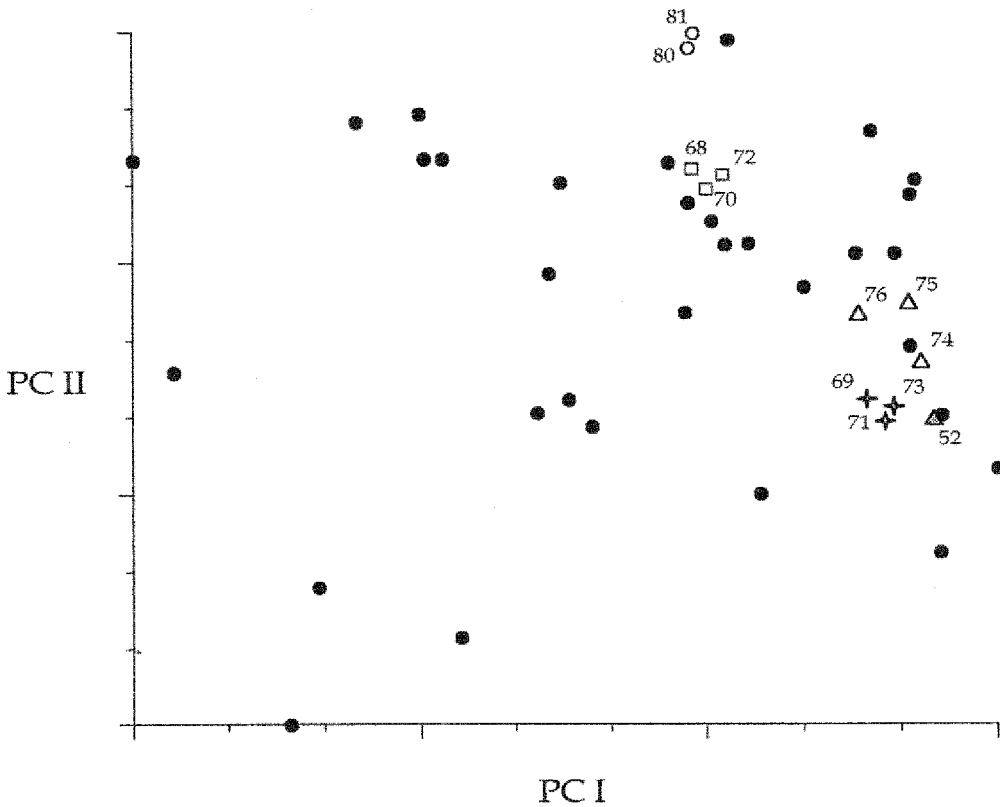


FIGURE 3. Plot of the first two dimensions of a principal coordinates analysis of the dental characters (character numbers according to O'Leary and Geisler, 1999). Character sets identified a priori as potentially redundant (from developmental genetic evidence) and then found to be redundant are as follows: open stars: paraconid /paracristid position (lower molars), open triangles: metaconid (lower molars), open squares: paraconid (lower molars), open circles: metaloph /metalophid. The gray triangle denotes the M^2 metacone, which is similar to the lower metaconids.

DISCUSSION

Determining the correct placement of Cetacea within the mammalian phylogeny is important for our understanding of the radical morphological changes that took place in that lineage with its return to water. Although there has been considerable debate as to whether Cetacea are highly derived artiodactyls or the sister group to mesonychids, much of this debate unfortunately has been couched in terms of molecules versus morphology. Molecular systematists have argued that the sequence data are more reliable markers of historical diversification on the basis of the sheer weight of evidence (potentially thousands of independent molecular characters). On the other hand, paleontologists have argued that the lack of molecular data from fossils has led to erroneous topologies because of limited taxon sampling. We have attempted to find some common ground between the two views

by investigating the hierarchical signal contained in the morphological data from both fossil and extant taxa. In this way we could examine whether the phylogenetic signal present in the morphological data was homogeneous, and if not, could determine which characters were predominantly responsible for the signal conflict observed with the molecular evidence.

Our results suggest that the dental characters contain a signal markedly different from the rest of the morphological data. When these characters were removed, the remaining data strongly supported a phylogeny identical to that found for the molecular data, namely, that Artiodactyla is paraphyletic with respect to Cetacea and that hippopotamus is the closest living relative to Cetacea. Because this analysis was carried out with both fossil and extant taxa, the claim is obviated that the signal in the molecular data is erroneous because of sparse taxon

sampling given the lack of fossil data. To put it another way, if the molecular data are truly misleading, it is curious that they should yield a phylogenetic signal identical to that found from an analysis of fossil and extant morphological data from which only the dental characters have been excluded. We believe that corroboration of results from various data sets is the strongest evidence supporting a particular hypothesis, and thus prefer to ask the question: "Why is it that teeth show a distinctly different signal from all other data sets, both molecular AND morphological?"

Although we do not have conclusive answers, we offer two hypotheses. The first is that the teeth per se do not provide a misleading signal but that the repeated measurement of nonindependent aspects of dental morphology generates a covariation among characters that is misinterpreted as a phylogenetic signal. The fact that 11 of 15 dental characters, identified a priori as potentially nonindependent, cluster closely in a correspondence analysis lends weight to this interpretation. Removing these pseudoreplicated characters from the analysis, however, yields a topology that remains consistent with that of O'Leary and Geisler (1999). Thus, the phylogenetic signal present in the dental data is still in conflict with the signal found in molecular data as well as that in the remaining morphological data.

The second more speculative hypothesis is that mammalian teeth are more evolutionarily plastic than was originally believed, and that any phylogenetic signal initially present in the dental data has been eroded because of convergent evolution (Thewissen et al., 1998). Several lines of evidence are consistent with this hypothesis. In a recent phylogenetic analysis, Luo et al. (2001) suggested that tribosphenic molars, traditionally considered to be a definitive mammalian apomorphy, may have evolved multiple times, undermining their primacy as diagnostic characters for early mammals. Further evidence of evolutionary plasticity comes from development. Developmental models of enamel knot signaling pathways provide a mechanism consistent with the frequent evolution of new tooth cusps in mammals, a genetic architectural feature that would predispose molars to evolutionary convergence (Jernvall et al., 1998; Jernvall and Thesleff, 2000). Evidently these signaling pathways are so plastic that they generate variation

in cusp size and cusp number at the population level (Jernvall, 2000). On the basis of these data, Jernvall (2000) concluded, "In phylogenetic studies, small cusps may be unreliable as phylogenetic signals." Finally, there is every reason to suspect that the more proximate and demanding dietary selection pressures associated with ecological conditions would override any phylogenetic signal originally present in an evolutionarily malleable tooth morphology (Jernvall et al., 1996). Although we acknowledge that the scenario of a phylogenetically eroded dental signal is speculative, mounting evidence suggests this may in fact be the case.

Teeth are abundant and well-preserved features of fossil vertebrates, and many of them are also highly distinctive for particular taxa. Not surprisingly, therefore, paleontologists have relied heavily on teeth to document evolutionary change and biodiversity in the fossil record. This reliance has led to the establishment of a phylogenetic orthodoxy that is strongly influenced by the characteristics of teeth found at different horizons in the fossil record. For many taxa, fossil teeth are all that we have. For other groups, however, we must be careful to consider different sources of evidence even-handedly. Over-reliance on any form of data should be viewed with caution.

The fact that all other aspects of morphology (from both fossils and extant forms), retrotransposons, and some 16 molecular studies all place Cetacea within Artiodactyla (and most place whales and hippopotamids together) suggests this is not an aberrant signal, but rather the correct one. That certainly does not mean, however, that molecular data are always to be believed over paleontological data. Molecular data can often be misleading, and we applaud O'Leary and Geisler's initial skepticism; indeed, we wish it were more widespread. Artifacts from taxon sampling can certainly lead to misleading inferences, and the inclusion of fossil taxa can sometimes rectify these difficulties. In this particular case, however, we are faced with two alternatives: The first is that the signal in the sequence data sets, retrotransposons, SINES, and nondental morphological characters truly reflects phylogeny, whereas the signal present in the dental data is anomalous. The second alternative implies that the signal in the dental

characters correctly reflects phylogeny, whereas for some as yet unidentified reason, the signals in the sequence data sets, retrotransposons, SINES, and the nondental morphological data have all converged on the same wrong answer. We claim that the most-parsimonious reconciliation is that the dental signal is suspect. Thus, we conclude that a paraphyletic Artiodactyla with respect to Cetacea is a viable, well-supported phylogenetic hypothesis for the group.

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