Biological Journal of the Linnean Society (1998), *64:* 101–133 With 12 figures
Article ID: bj980215

Supraspecific taxa as terminals in cladistic analysis: implicit assumptions of monophyly and a comparison of methods

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Received 10 April 1997; accepted for publication 5 February 1998

The use of supraspecific terminal taxa to represent groups of species in phylogenetic analyses can result in changes to inferred relationships as compared to a complete species level analysis. These changes in topology result from interactions among (1) the cladistic status of the supraspecific taxa; (2) the method used to represent the taxa as single terminals, and (3) incongruence in the data set. We examine the effects of using supraspecific terminal taxa using a parallel analysis of hypothetical examples and an actual data matrix for the true seals (Mammalia: Phocidae). Incongruence among characters can produce changes in topology by shifting the 'balance of power' among groups of characters when supraspecific taxa are represented as single terminals. In the absence of homoplasy, the correct topology is maintained. Of the three methods for representing supraspecific taxa, the 'ancestral' method, which explicitly infers the common ancestor of the group corresponding to the taxon, performed the best, always maintaining the correct topology when monophyletic taxa were represented. This agrees with theoretical predictions. The 'democratic' and 'exemplar' methods, which represent the higher level taxon through a survey of all or one of its extant constituent species, respectively, were not as effective in maintaining the correct topology. Although both occasionally provided correct answers, their occurrences were largely unpredictable. The success of the exemplar method varies with the species selected. The simultaneous representation of two or more higher level taxa produced interactive effects where the resultant topology included different clades than when the taxa were collapsed individually. Interactive effects occurred with all three methods, albeit to a lesser degree for the ancestral method. Changes in topology were observed regardless of whether the higher

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0024–4066/98/050101+33 $25.00/0

group was monophyletic or not, but were more prevalent when it was paraphyletic. Unfortunately, there does not seem to be a reliable way to determine when a paraphyletic group has been included in the analysis (e.g. through bootstrap values or indices measuring homoplasy). The implications of these findings for phylogenetic analyses of molecular data are also discussed.

ADDITIONAL KEY WORDS:—phylogenetic inference – species – groundplan – paraphyly – homoplasy – ancestor – exemplar – Phocidae – consistency indices – molecular systematics.

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INTRODUCTION

Although the species is the fundamental unit of our taxonomic system, our systematic questions often involve more inclusive levels, necessitating that at least some of the terminal branches be represented by supraspecific taxa. Despite the advantages of including as many taxa as possible within an analysis (see Arnold, 1981; Donoghue *et al.*, 1989; Hendy & Penny, 1989; Lecointre *et al.*, 1993), including all or many of the constituent species in analyses that attempt to resolve relationships at higher levels (i.e. higher taxonomic levels in the Linnaean hierarchy or more inclusive levels in cladistic hierarchies) is impractical. The inclusion of large numbers of terminal taxa entails more complex analyses that require heuristic searches that cannot guarantee optimal solutions, or, in extreme cases, are simply not tractable using current computer technology (see Soltis & Soltis, 1996; Rice, Donoghue & Olmstead, 1997). The judicious use of supraspecific terminal taxa in higher level analyses allows for the use of exact searches or, for more expansive studies, heuristic searches that obtain results in a reasonable length of time.

The correct use of supraspecific taxa in phylogenetic analysis, however, has two requirements: (1) the taxa are monophyletic (*sensu* Hennig, 1966; but note that we use 'taxon' in the traditional Linnaean sense and not necessarily as the equivalent of 'clade') and (2) we can represent them as single terminals in a way that maintains their positions on a cladogram with respect to a solution including all species. In many instances, the monophyletic status of taxa is assumed without being strongly tested, often because of the long taxonomic history of the group. However, because our current taxonomic and classificatory schemes predate cladistics (and even the acceptance of evolution via natural selection), monophyly was not a criterion in the establishment of many older taxa. Even reasonably 'safe' (or at least commonly accepted) assumptions of monophyly may be erroneous, as has been argued recently for various taxa including rodents (Graur, Hide & Li, 1991), mustelids (Wayne *et al.*, 1989; Vrana *et al.*, 1994; Ledje & Arnason, 1996), the blackbird genus *Agelaius* (Lanyon, 1994), and numerous supraspecific seed plant taxa (Chase *et al.*, 1993). Although the cladistic status of many long-standing taxa is continually being tested, it should be realized that in many other cases their status is best regarded as uncertain. A related issue is the prevalence of including taxa whose monophyly is known to be questionable in phylogenetic analyses (e.g. as noted for Carnivora by Bininda-Emonds, Gittleman & Purvis [in review]), with the apparent assumption that any associated errors will be minimal.

The second requirement involves identifying a suitable method to generate the character states for the single terminals that represent the supraspecific taxa in the higher level analysis. Methods used to date include (1) estimating the primitive states of the taxon (e.g. Bryant, Russell & Fitch, 1993; Wyss & Flynn, 1993), using either fossil or ontogenetic evidence and/or by reconstructing a hypothetical ancestor on the basis of previous phylogenetic analyses (e.g. compartmentalization; Mishler, 1994); (2) choosing an extant member of the clade to represent the taxon as a whole (e.g. Chase *et al.*, 1993; Krettek, Gullberg & Arnason, 1995); or (3) generating character states for the taxon from a sample of its constituent species, much as species traits are delimited from a sample of individual specimens (e.g. Bininda-Emonds & Russell, 1996). We refer to these three methods as the ancestral, exemplar (Mishler, 1994; Yeates, 1995: 344), and democratic methods, respectively.

We herein explore the effects of assumptions of monophyly and methods of representing higher level taxa, two factors which may confound the use of supraspecific terminal taxa in phylogenetic analysis. The problem is addressed initially using simple hypothetical examples, which allow us to isolate some of the factors that impinge on the use of supraspecific taxa. We follow this with a more complex real life example to illustrate the interactions of these effects in larger data sets. The group chosen here is the family of true seals (Mammalia: Carnivora: Phocidae), a manageably sized group for which the first complete species-level phylogeny has recently been estimated (Bininda-Emonds & Russell, 1996). Use of the data matrix from this study provides examples of historically accepted supraspecific taxa that are monophyletic and non-monophyletic.

THE ISSUES

A subtheme throughout this study is the importance of the assumptions we make in phylogenetic analyses where our analyses largely take the form of 'if–then' statements. Given a set of raw character data, the assumptions we make in the analysis (e.g. character coding, choice of computer algorithm) will have a marked effect on the topology of the resulting trees. The danger is that the assumptions we are making may result in incorrect phylogenies, something that becomes crucial due to the increasing role that phylogenetics plays within biology today. Numerous fields of study, ranging from biogeography to conservation biology to comparative biology and character evolution now routinely incorporate systematic information. Given that assumptions must be made in our analyses and that those concerning the use of supraspecific taxa are only one of many, can we identify a set of assumptions and methods in this one case that will minimize potential errors?

Assumptions of monophyly

Cladistic theory implicitly assumes that the terminal taxa in any analysis are monophyletic (Gaffney, 1977). Collapsing a non-monophyletic assemblage to a single terminal must alter the implied relationships of its members (see Representing paraphyletic groups, below), but the broader implications of incorrect assumptions of monophyly on the outcome of an analysis has not been thoroughly examined. However, there are indications that these assumptions are important. A cogent example is found in Berta & Wyss (1994). In this study, which examined relationships among all fossil and extant pinniped genera or tribes, the genus of monk seals, *Monachus*, was reluctantly taken to be monophyletic (or at least entered as a single terminal taxon), contrary to previous accepted findings (Wyss, 1988). Several anomalous inferred relationships within the subfamily containing *Monachus* were traced to this assumption of monophyly, with the authors going so far as to question the validity of all the observed relationships within this subfamily, including its apparent monophyletic status (Berta & Wyss, 1994: 43). We show that the errors introduced by improper assumptions of monophyly may occasionally reach wider than was suspected to be the case in Berta & Wyss (1994).

Representing supraspecific taxa

Yeates (1995) recently examined two methods of representing supraspecific taxa as terminals (the exemplar method and 'intuitive groundplan analysis') and the assumptions behind them. As he noted, the character states that best represent a supraspecific taxon (i.e. maintain its position in a cladogram compared to a complete species-level solution) are those that are primitive for the group corresponding to it; in other words, those of the common ancestor. Yeates referred to these states as the 'groundplan' of the higher taxon. We add that the superiority of the groundplan approach follows from first principles: the common ancestor possesses all the apomorphies necessary to correctly infer the position of the group it represents, but lacks those that have subsequently evolved among only some of its descendants and are either uninformative at the higher level (autapomorphies) or suggest an erroneous placement for the group when taken to be representative of it (homoplasies). In theory, a greater proportion of characters remain phylogenetically informative and accurate, thus allowing the correct position of the supraspecific taxon to be determined.

Of the methods we mentioned above, only the 'ancestral method,' which attempts to directly estimate the ancestral states of the supraspecific taxon, accords with this theoretical ideal. But, although theoretically sound, use of the method is often problematic. For example, Yeates (1995) rightly criticizes the often *ad hoc* nature of 'intuitive groundplan analysis', whereby the reasons behind the assignment of the states to the groundplan are never clearly articulated. The following criteria make the ancestral method more rigorous: (1) fossil information, (2) ontogenetic evidence, and/or (3) previous phylogenetic studies. However, these criteria require assumptions that are often problematic. The use of fossil evidence has assumptions regarding both the affinity of the fossil species and the resemblance of its character states to those of the common ancestor (i.e. that they are primitive; as in the palaeontological criterion for character state polarization—see Eldredge & Novacek [1985], Bryant [1991]). Fossil evidence is largely restricted to morphological data and the often large proportion of missing data limits how completely the common ancestor can be estimated. The applicability of ontogenetic evidence remains controversial and may hinge on the version of the ontogenetic criterion employed (see and compare Patterson [1996] with Mabee [1996] and references therein). The use of one or more previous phylogenetic studies to derive a hypothetical ancestor relies on the assumptions made in those studies (e.g. choice of outgroups) and character reconstruction methods. Misrepresentation of the groundplan can also occur in this instance given that parsimonious reconstructions of a common ancestor possess only a finite probability of accurately representing the true common ancestor (Maddison, 1995) and may differ between different phylogeny reconstruction programmes (e.g. MacClade and PAUP; Maddison & Maddison, 1992).

The second option, that of representing a supraspecific taxon by the character states of a sample of its constituent species (Yeates, 1995: 344), seems to be used largely because of practical considerations, especially in molecular systematics. The 'exemplar method' is common in this field because both the time required and the expense of the procedures involved have prevented all species from being sampled to date. The underlying assumption of this method, as it is commonly used, appears to be that the selected species is/are roughly representative of the supraspecific taxon, be it on morphological or molecular grounds, and not of the states of the groundplan. However, this assumption is not always valid as species are often chosen simply because they are the only one for which data exist or may be obtained. An example is the harbour seal, *Phoca vitulina*. Since it was among the first of the mammalian carnivores to have its mitochondrial DNA fully sequenced and freely available on GenBank (Arnason & Johnsson, 1992), it is often included in phylogenetic analyses as the 'exemplar' carnivore (e.g. Cao, Adachi & Hasegawa, 1994; Kuma & Miyata, 1994; Schreiber, Erker & Bauer, 1994; Cummings, Otto & Wakeley, 1995; Freye & Hedges, 1995; Krettek *et al.*, 1995), something belying its obvious morphological (and possibly molecular; Schreiber *et al.*, 1994) distinctiveness.

The numerous derived characters possessed by most extant species reduce their ability to accurately estimate the groundplan. As a result, our choice of exemplar may seriously affect the outcome of our phylogenetic analyses (Doyle, Donoghue & Zimmer, 1994; Galtier & Gouy, 1994; Adachi & Hasegawa, 1995; Soltis & Soltis, 1996), with the added difficulty that the correct choice, if there is one, is often not ascertainable *a priori*. Yeates (1995) argued that including multiple exemplars in the analysis can improve the estimation of the groundplan; however, this does not appear to be common practice. We therefore focus our analyses on the implications of the extreme case where only a single exemplar is used.

A third method, the 'democratic method,' derives from the technique of generating character state values for a species by taking observations from a number of individual specimens. This method might also prove useful for supraspecific taxa with species being sampled in the place of specimens. Implementations of the democratic method are hardly ever formalized, either for species or higher level taxa. In its simplest form, the democratic state is the most frequent state in the sample, although some form of frequency-dependent coding might be envisaged (see Wiens, 1995). Although the democratic method avoids the oft-times arbitrariness of the exemplar method, it possesses theoretical and practical liabilities. Given that we ideally want to estimate the primitive states for the higher level taxon, the method is equivalent to the 'common equals primitive' criterion for determining character state polarity. This criterion is unreliable (Watrous & Wheeler, 1981); however, it is still used infrequently and was one mechanism cited by Yeates (1995) as having been used to estimate the groundplan via 'intuitive groundplan analysis' (although, as with the exemplar method, the presence of derived features reduces the ability of the democratic method in this regard). Also, the common equals primitive criterion has been shown so far to be incompatible with only one class of tree topology (the Hennigian comb; Watrous & Wheeler, 1981); thus, it has the potential to give correct answers in many instances, something we wanted to test in the current context. Methodological shortcomings include the necessity of a mechanism to resolve the expected high levels of polymorphism in character state values as supraspecific taxa are less likely to be phenotypically or genetically homogeneous than species, particularly at increasingly inclusive levels. The method is also labour intensive. Given that a reasonable number of the constituent species need to be sampled, it would be simpler, albeit more computationally intensive, to merely include the sampled species directly in the analysis or select a limited number as exemplars.

ANALYSIS

We explore the problems associated with the use of supraspecific terminal taxa in phylogenetic analyses through a parallel analysis of hypothetical examples and a real data set for the phocid seals (from Bininda-Emonds & Russell, 1996). This dual approach has many advantages. The hypothetical examples permit us to identify the interactions between assumptions of monophyly and the choice of the method used to represent higher level taxa. An additional important factor, incongruence in the data, is also introduced here. The examples involving the phocid seals illustrate the magnitude of the errors these factors may contribute to under 'actual' and more complex conditions, and also how they can interact to engender additional errors. As well, by virtue of this 'real life example,' we hope that the practical consequences of using supraspecific terminal taxa will be more apparent. In the end, the use of both types of examples permits a determination of the strengths and weaknesses of the various representation methods.

Hypothetical examples

The hypothetical examples (Figs 1–6) involve clades of five to seven terminal taxa (*a* through *g*). Relationships within the clade are based on the presence/absence of characters as indicated by bars on the cladograms; in all instances, absence of a character is plesiomorphic for the entire clade (i.e. trees are rooted using an outgroup [not shown] that lacks all characters). In each example, three terminal taxa are collapsed into a single terminal (*m*) using the representation methods described above

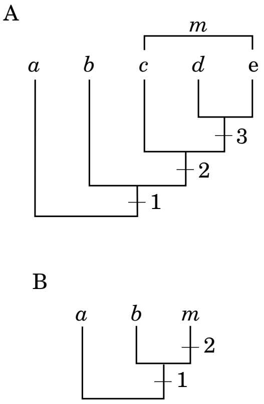


Figure 1. Representation of a monophyletic group (*c*,*d*,*e*) as a single terminal taxon (*m*) and the effect on topology in the absence of homoplasy. A, the original tree including *c*, *d*, and *e*. B, the simplified tree in which (*c*,*d*,*e*) is replaced by *m*. Characters supporting the nodes are indicated with bars. See text for explanation.

to determine the effect on the inferred topology. Although we implicitly use prior phylogenetic analyses to derive states for the ancestral method, the ancestor can also be inferred using fossil or ontogenetic information. Ancestral states for collapsed groups were derived from the least inclusive node that subsumes all members of the group. Because the character coding for *m* may differ depending on which method is used, the relationships between *m* and the other taxa within the clade may also differ. In addition, the relationships of *m* are influenced by the monophyletic or paraphyletic status of the collapsed group and the presence of homoplasy in the data matrix.

Representing monophyletic groups

In the absence of homoplasy, the replacement of a monophyletic group by a terminal taxon using any of the representation methods does not alter the inferred relationships. Nonetheless, when the clade (*c*,*d*,*e*) (Fig. 1) is replaced by a single terminal taxon, *m*, its characters differ depending on which representation method is used. Taxon *m* lacks character 3 using both the ancestral method and using *c* as the exemplar; in contrast, *m* has character 3 using either *d* or *e* as the exemplar, or using the democratic method. In all instances *m* has characters 1 and 2. Despite the differences in coding for character 3, the relationships among *a*, *b*, and *m* are not affected because character 3 occurs only within clade (*c*,*d*,*e*) and is therefore not relevant to relationships with *a* and *b*. Regardless of which method is used, *m* has character 1 and therefore is inferred correctly as more closely related to *b* than to *a*.

The exemplar and democratic methods of representing clades as terminal taxa can result in incorrect inferences of relationship when particular members of the clade share apomorphies (i.e. have homoplasies) with taxa outside the clade. In Figure 2A, if *e* is chosen as the exemplar of (*c*,*d*,*e*), *m* (= *e*) clusters with *a* rather than *b* because characters 4 and 5, which are shared by *a* and *e*, outweigh character 1 which supports the correct relationship, *a*(*b*,*m*) (Fig. 2B). Characters 2 and 3, that together with character 1 outweighed characters 4 and 5 in the original matrix, are

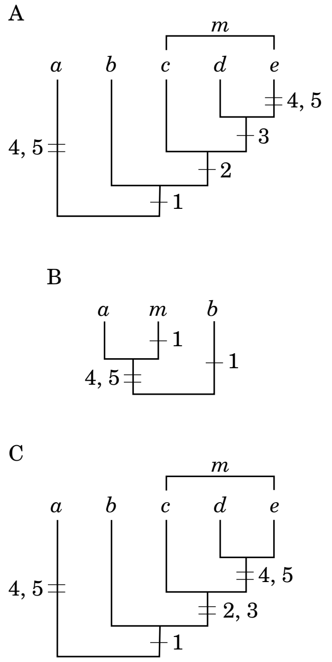


Figure 2. Representation of a monophyletic group (*c*,*d*,*e*) as a single terminal taxon (*m*) and the effect on topology in the presence of homoplasy. A, C, two original trees including *c*, *d*, and *e* with different distributions of characters 1–5. B, simplified tree in which *m* groups with *a* rather than *b*; this pattern results from using *e* as the exemplar in A, and using the democratic method with C. In both instances the homoplasy in characters 4 and 5 results in a simplified tree with an incorrect topology. The ancestral method results in the correct topology in both cases.

no longer informative in the condensed matrix. In Figure 2C, if (*c*,*d*,*e*) is represented by *m* using the democratic method, *m* has characters 4 and 5 because these characters occur in two of the three constituent taxa. As a result, *m* clusters with *a*, where these two characters also occur, rather than *b* (Fig. 2B). As in the previous example, characters 2 and 3, which supported the tree based on the original matrix, are no longer informative when (*c*,*d*,*e*) is considered a single terminal taxon.

The ancestral method is immune to homoplasy in the data because it ignores apomorphies shared by some members of the clade and outside taxa. Using the ancestral method in both of the above examples (Fig. 2), *m* would have only characters 1 and 2, and would therefore cluster with *b*, as in the original cladogram. Character state inferences at the ancestral node are equivocal when more than one character optimization is equally parsimonious. On the tree in Figure 3A and B, two optimizations for character 5 at the ancestral node of (*c*,*d*,*e*) are equally parsimonious. If character 5 evolved independently in *a*, *c*, and *d* (Fig. 3A), the ancestral node lacks character 5; as a result, *m* clusters correctly with *b*. If the ancestor of (*c*,*d*,*e*) had character 5, which was then lost in *e* (Fig. 3B), the relationships among *a*, *b*, and *m* will be unresolved; character 1 supports *a*(*b*,*m*), whereas character 5 supports *b*(*a*,*m*). However, this ambiguity regarding the relationships between *a*, *b*, and *m* is present in the original matrix which is equally congruent with a second shortest tree (Fig. 3C) in which *a* is more closely related to (*c*,*d*,*e*) than *b* is. We have

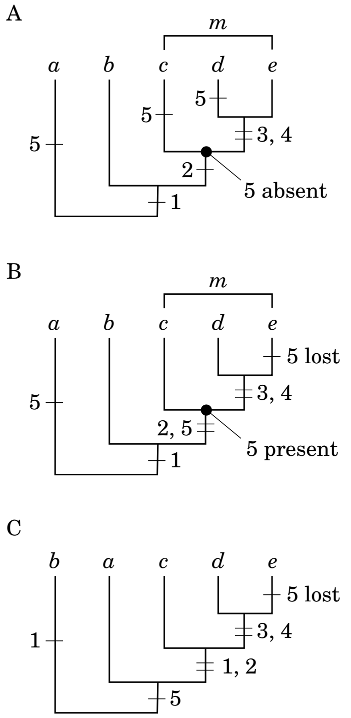


Figure 3. Equivocal inference of the character states of a hypothetical ancestor due to equally parsimonious optimizations at the ancestral node (indicated by a solid circle). A, absence of character 5 using DELTRAN (delayed transformation). B, presence of character 5 using ACCTRAN (accelerated transformation). C, equally parsimonious tree to those in A and B in which the positions of *a* and *b* are reversed.

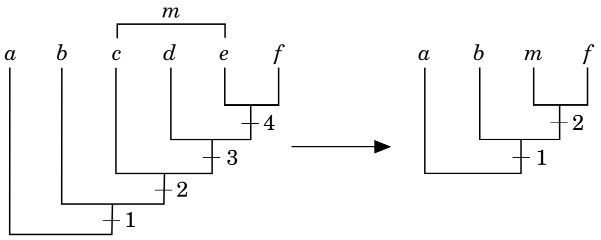
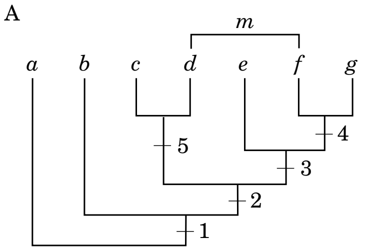


Figure 4. Representation of a paraphyletic group—*c,d,e*—as a single terminal taxon (*m*) and the effect on topology in the absence of homoplasy. A, original tree. B, simplified tree generated by all three representation methods on which *f* is the sister taxon of *m*, rather than its actual sister taxon, *e*.

been unable to find an example in which the ancestral method generates ambiguity regarding relationships that is not already present in the original data matrix.

Representing paraphyletic groups

Even in the absence of homoplasy, the replacement of a taxon that is not monophyletic by a single terminal taxon must misrepresent relationships because of the implicit assumption that terminal taxa are monophyletic. If the paraphyletic assemblage *c,d,e* in Figure 4A is replaced by *m*, the relationships among the remaining taxa are unchanged (Fig. 4B); however, Figure 4B suggests that *m* and *f* are sister



B

Method	Character 1	2	3	4	5
ancestral	1	1	0	0	0
democratic	1	1	1	0	0
exemplar (*d*)	1	1	0	0	1

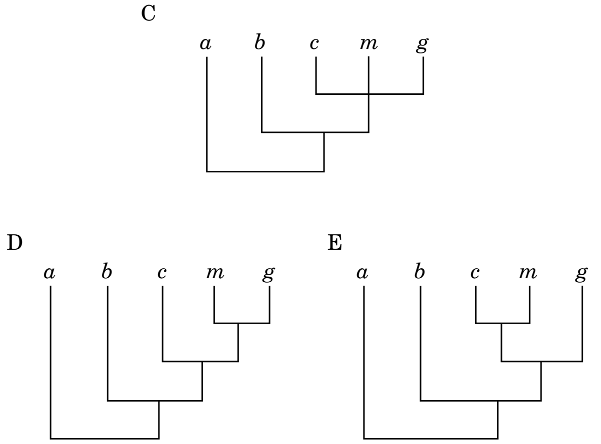


Figure 5. Representation of a paraphyletic group—*d,e,f*—as a single terminal taxon (*m*) and the effect on topology in the absence of homoplasy. A, original tree. B, character matrix illustrating the different character states of *m* using the three representation methods. C, simplified tree using the ancestral method. D, simplified tree using the democratic method. E, simplified tree using *d* as the exemplar.

taxa when, in fact, *f* is the sister taxon of only a portion of *m*, taxon *e*. In this example all three representation methods produce the 'correct' result. However, this is not always the case in more complex examples. If the assemblage *d,e,f* in Figure 5A is replaced by *m*, each method produces a different character distribution for *m* (Fig. 5B) and the relationship of *m* to the remaining taxa is different in each instance (Fig. 5C–E). Nonetheless, in the absence of homoplasy, *m* always clusters with one or both of *c* and *g*, the taxa with which the members of the paraphyletic assemblage share closest common ancestry.

When homoplasy is present, the representation of paraphyletic assemblages using the democratic and exemplar methods can result in the same errors in inferred relationships that occur with monophyletic groups (see Fig. 2), but now the ancestral method is affected as well because of homoplasies shared by taxa outside of the paraphyletic assemblage. Given the relationships and character distribution in Figure

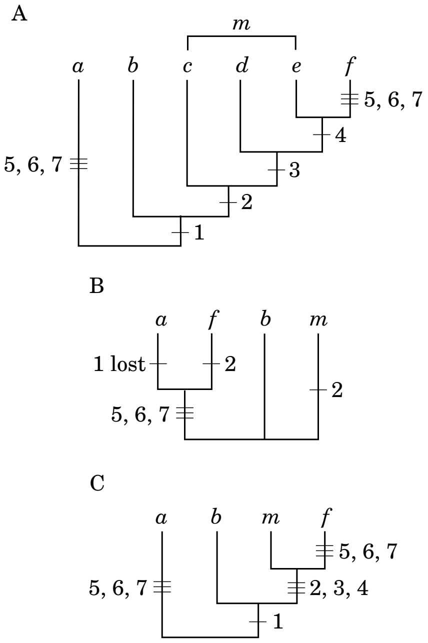


Figure 6. Representation of a paraphyletic group—*c,d,e*—as a single terminal taxon (*m*) and the effect on topology in the presence of homoplasy. A, original tree. B, consensus of three equally parsimonious simplified trees using the ancestral method or using *c* as the exemplar. C, simplified tree using *e* as the exemplar.

6A, replacement of the paraphyletic assemblage *c,d,e* by *m* using either the ancestral method or using *c* as the exemplar changes the inferred relationship of *f* (Fig. 6B). On the original tree the three characters shared by *a* and *f* are interpreted as homoplasies because characters 1–4 determine the topology of the tree. On Figure 6B characters 3 and 4 are not informative and characters 5–7 outweigh characters 1 and 2, causing *f* to cluster with *a* on all three equally parsimonious trees. In contrast, if *e* is chosen as the exemplar, characters 3 and 4 are still informative and the correct pattern is inferred (Fig. 6C). Using either *d* as the exemplar or the democratic method produces equivocal results.

Overview

These hypothetical examples demonstrate that incorrect assumptions of monophyly, the method used to represent a group of taxa as single terminals, and homoplasy in the data all contribute to errors in inferred relationships. With monophyletic groups, homoplasy can result in errors using the democratic and exemplar methods. With paraphyletic assemblages errors can occur with all representation methods. By representing clades or other assemblages of taxa as single terminals, some characters become uninformative; this can change the ‘balance of power’ among incongruent groups of characters, resulting in changes to the relationships on the tree. The ancestral method is immune to this phenomenon with monophyletic groups because it ignores derived characters (potential homoplasies) that occur in only some members of the clade. However, with paraphyletic groups the loss of derived characters can result in errors in inferred relationships; these characters contribute to the support for the relationship between the paraphyletic group and taxa that share the same most recent common ancestry, but have been excluded from the group (e.g. taxon *f* in Fig. 6). In summary, these examples suggest that with real data matrices (which almost invariably contain homoplasy) the inclusion of supraspecific terminal taxa can compromise the outcome of the analysis if (1) the groups being represented are not monophyletic, and/or (2) the democratic or exemplar methods are used. Errors using the ancestral method can occur if the inferences at the ancestral node are incorrect, a situation that was not addressed in the examples considered here.

Phocid examples

Background and methodology

Eighteen extant and one presumably extinct species of true seal are recognized and included in this study. This number includes the larga seal (*Phoca largha*), for which species status is debatable, and the Caribbean monk seal (*Monachus tropicalis*), which is believed to have gone extinct in the early 1950s (Kenyon, 1977). The family is typically divided into two presumably monophyletic subfamilies (following King, 1966) corresponding roughly to seals of the northern hemisphere (the Phocinae) and to those of the southern hemisphere plus the sub-tropical northern monk seals (the Monachinae).

Despite its long history in the systematic literature, the first cladistic analysis of all the extant species of the family was performed only recently (Bininda-Emonds & Russell, 1996) and the monophyly of most higher level phocid taxa has not been strongly tested to date. The monophyly of four such taxa below the subfamily level has been assumed historically: the genera *Mirounga* (elephant seals), *Monachus* (monk seals), and *Phoca* (*sensu* Burns & Fay, 1970; harbour seals and close relatives), and the tribe Lobodontini (Antarctic seals). Of these taxa, suggestions of non-monophyly have been raised for *Monachus* (Wyss, 1988; not demonstrated, but endorsed by Berta & Wyss [1994]), *Phoca* (Chapskii, 1955; de Muizon, 1982; Wyss, 1988; Arnason *et al.*, 1993, 1995; Mouchaty, Cook & Shields, 1995; Perry *et al.*, 1995; Bininda-Emonds & Russell, 1996), and the Lobodontini (Bininda-Emonds & Russell, 1996). The evidence against the monophyly of *Phoca* is overwhelming and virtually universally accepted; however, this taxon, like the other two, continues to be recognized. To our knowledge, the non-monophyly of only *Mirounga* has never been suggested.

We demonstrate the effects of imposed monophyly of higher taxa on phocid phylogeny by representing the above four taxa (*Mirounga*, *Monachus*, *Phoca*, and the Lobodontini) individually and collectively as single terminals in an analysis with all remaining phocid species and eight outgroup taxa representing all major caniform lineages. Character states for all taxa were taken from (or derived from in the case of higher taxa) the 168 morphological characters used by Bininda-Emonds & Russell (1996). Use of this matrix ensured that both monophyletic (*Mirounga* and *Monachus*) and paraphyletic (Lobodontini and *Phoca*) taxa were collapsed.

The exemplars for the four higher level taxa were *Leptonychotes weddelli* for the Lobodontini, and *Mirounga leonina*, *Monachus schauinslandi*, and *Phoca vitulina* for their respective genera. We selected these species because they are the best studied within their respective taxa, and therefore the most likely to be chosen as exemplars. Both fossil information and ontogenetic evidence for phocids is largely lacking; therefore, ancestral traits were reconstructed solely from the species-level solution of Bininda-Emonds & Russell (1996) using both accelerated (ACCTRAN) and delayed transformation (DELTRAN) optimizations in PAUP 3.1.1 (Swofford, 1993). Ancestral states for paraphyletic taxa were determined in the same manner as in the hypothetical examples. Democratic character states were determined according to an algorithm taken from Bininda-Emonds and Russell (1996) that attempts to preserve the most frequent state(s). Less frequent states were retained (creating a polymorphic taxon) if they occurred with a frequency of one count less than the most frequent one (see Appendix for a complete description of the algorithm, particularly its handling of polymorphic source species). Of these three representation methods, only the ancestral method did not create polymorphic higher taxa because PAUP will not generate polymorphic ancestral character states (Swofford, 1993).

The condensed matrices were analysed using PAUP's heuristic search option, with taxa added according to the RANDOM algorithm (with 25 repetitions), TBR branch swapping on minimal trees only (with steepest descent on), collapsed zero length branches, and unlimited MAXTREES. When all four supraspecific taxa were condensed simultaneously, it was possible to employ PAUP's branch-and-bound search option (with collapsed zero length branches), thereby guaranteeing an optimal solution. Characters were inversely weighted (base weight = 100) according to the number of character states each possessed and polymorphic taxa were analysed using the 'polymorphism' option. All characters were unordered, with inapplicable character states coded as a discrete state (state 9) rather than as missing. The reasoning behind this choice of options can be found in Bininda-Emonds & Russell (1996); however, because all trees, including the full species tree, were generated using the same assumptions, the appropriateness of the methods used should be irrelevant to the effects of cladistic status and representation method on topology.

Results were compared to the species-level solution of Bininda-Emonds & Russell (1996) (Fig. 7), which, for the purposes of this study, was considered to be correct. We focus primarily on changes in topology; however, we also examined three goodness-of-fit statistics (CI, RI, and RC) to ascertain changes in the level of homoplasy. As CI is known to vary with the size of the data set (Farris, 1989; Sanderson & Donoghue, 1989), CI values were compared to the values expected for a matrix of the same size (as calculated from Sanderson & Donoghue [1989]). Comparisons of RI and RC were made to their values in the complete species solution because possible relationships between these indices and the size of the data matrix have not been investigated (RC) or appear to be insignificant (RI; Hauser & Boyajian, 1997). Autapomorphies were ignored in the calculation of CI and RC. Bootstrap frequencies (Felsenstein, 1985) were calculated for each matrix based on 1000 bootstrap replicates using a heuristic search with taxa added according to the CLOSE algorithm (with HOLD = 10), TBR branch swapping on minimal trees only (with steepest descent off), collapsed zero length branches, and MAXTREES = 100. Characters were sampled with equal probability, with their weights applied subsequently.

Monophyly examples

As in the hypothetical examples, the ancestral method performed demonstrably better with monophyletic taxa, giving correct answers for both *Mirounga* and *Monachus*

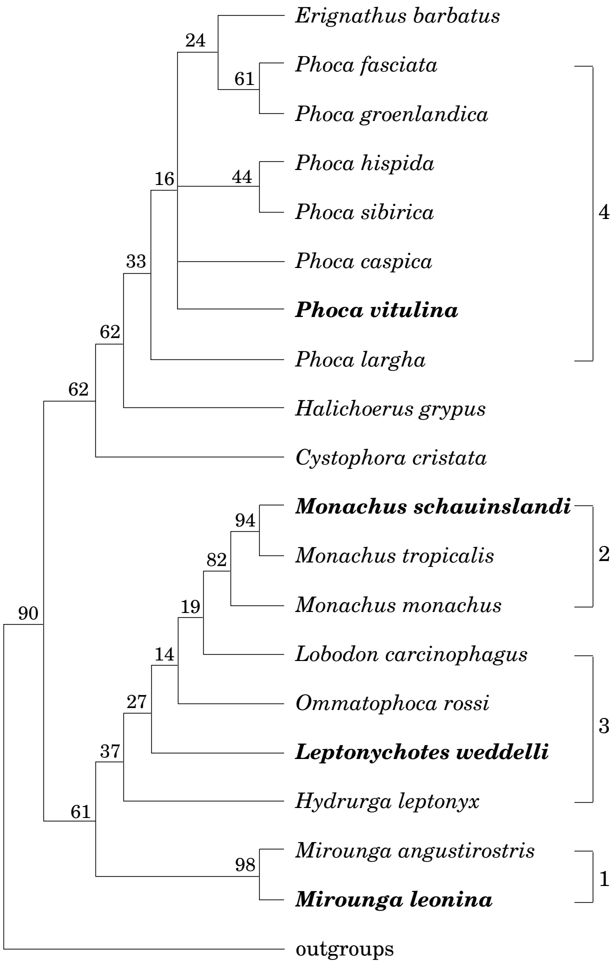


Figure 7. Majority rule consensus solution with bootstrap frequencies (1000 replications) of all extant species of phocid seals (plus *Monachus tropicalis*) and outgroup taxa from Bininda-Emonds & Russell (1996). All nodes were found in both of the two equally most parsimonious solutions. Supraspecific taxa of interest here indicated as follows: (1) *Mirounga*, (2) *Monachus*, (3) Lobodontini, and (4) *Phoca* (*sensu* Burns & Fay, 1970). Exemplars for these taxa are in bold face.

(Figs 8 and 9, respectively), regardless of character optimization. The only other correct result was obtained using the democratic method with *Monachus*. On the incorrect topologies, widespread changes were evident, with one subfamily always being rendered paraphyletic. For *Mirounga*, one (Fig. 8C) or both (Fig. 8B) of the phocines *Cystophora* and *Erignathus* became sister taxa to the monachines, with further changes within this latter subfamily arising from *Ommatophoca* being pulled to a more basal position. With *Monachus*, only the exemplar method generated a wrong answer, creating a paraphyletic Monachinae with the movement of *Monachus* from its terminal position within the monachines to become the sister taxon to all remaining phocids (Fig. 9B). Other changes include the creation of a monophyletic Lobodontini due to the exclusion of *Monachus*, and numerous alterations within the phocines (most

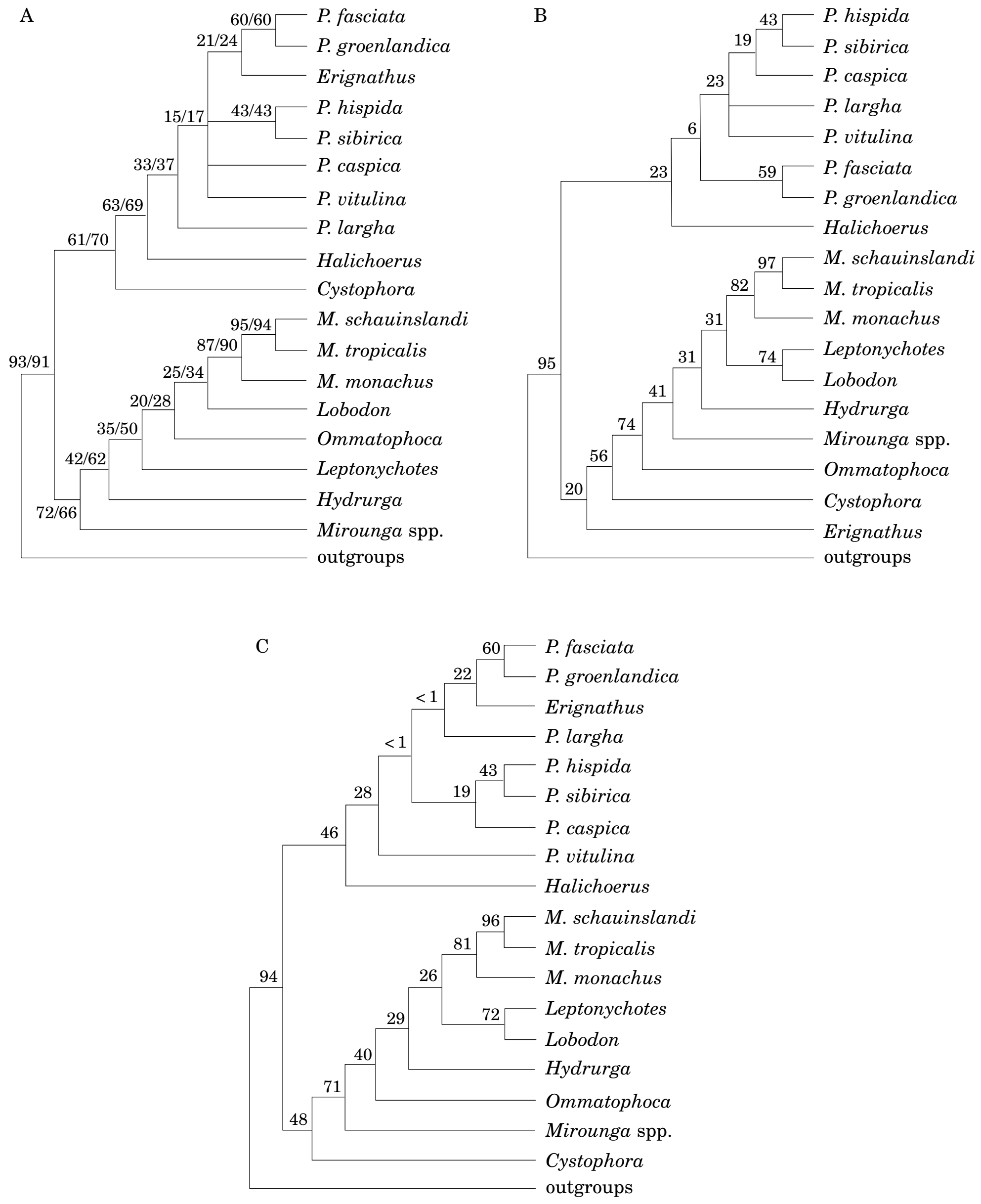


Figure 8. Ingroup topologies with bootstrap frequencies (1000 replications) resulting from assuming a monophyletic *Mirounga* as represented using the following methods: (A) ancestral (both ACCTRAN and DELTRAN optimization—bootstrap frequencies in that order), (B) democratic, and (C) exemplar (using *M. angustirostris*). All trees are majority rule consensus solutions, except (C) which was the single most parsimonious solution. All nodes occurred in 100% of the equally most parsimonious solutions. Full species names can be found in Figure 7.

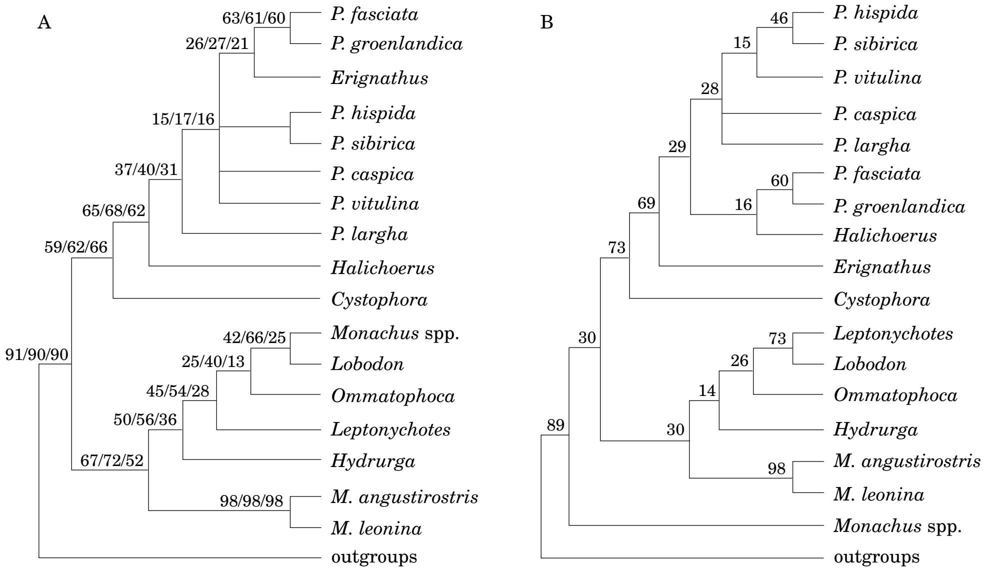


Figure 9. Ingroup topologies with bootstrap frequencies (1000 replications) resulting from assuming a monophyletic *Monachus* as represented using the following methods: (A) ancestral (both ACCTRAN and DELTRAN optimization) and democratic (bootstrap frequencies in that order) and (B) exemplar (using *M. schauinslandi*). All trees are majority rule consensus solutions with all nodes occurring in 100% of the equally most parsimonious solutions. Full species names can be found in Figure 7.

notably a basal shift for *Erignathus*). However, this distinctive topology results from the choice of *Monachus schauinslandi* as the exemplar. *M. schauinslandi* possesses a number of undoubtedly primitive phocid features that are absent in other monk seals (see Wyss, 1988), which with their removal are sufficient to drag *M. schauinslandi* to a more basal position relative to the remaining phocids (see below also). Use of either of the other two monk seals as the exemplar yields the correct or a nearly correct topology (results not shown). Clearly, the choice of exemplar for representing a supraspecific taxon is critical.

Paraphyly examples

Unlike the situation for the monophyletic taxa, the exemplar method appears to be most proficient at maintaining the topology of the full species solution when paraphyletic taxa are collapsed (within the constraints of collapsing such taxa). Although this method obtained the correct answer when either the Lobodontini or *Phoca* was collapsed (Figs 10D and 11C, respectively), the dependence of the resultant topology on the choice of exemplar for *Monachus* (see above) suggests that these choices might simply have been fortuitous. This is true for the Lobodontini in which the choice of any other species resulted in disruptions within the phocines and often a paraphyletic Monachinae as well (results not shown). However, this was not the case for *Phoca*, in which six of the seven species retained the correct answer; only *Phoca largha* generated an altered topology (identical to Fig. 11B).

The only other correct answer for the paraphyletic taxa was obtained using the democratic method for *Phoca* (Fig. 11C), while the ancestral method failed in both instances, even generating different answers for each optimization (compare Figs

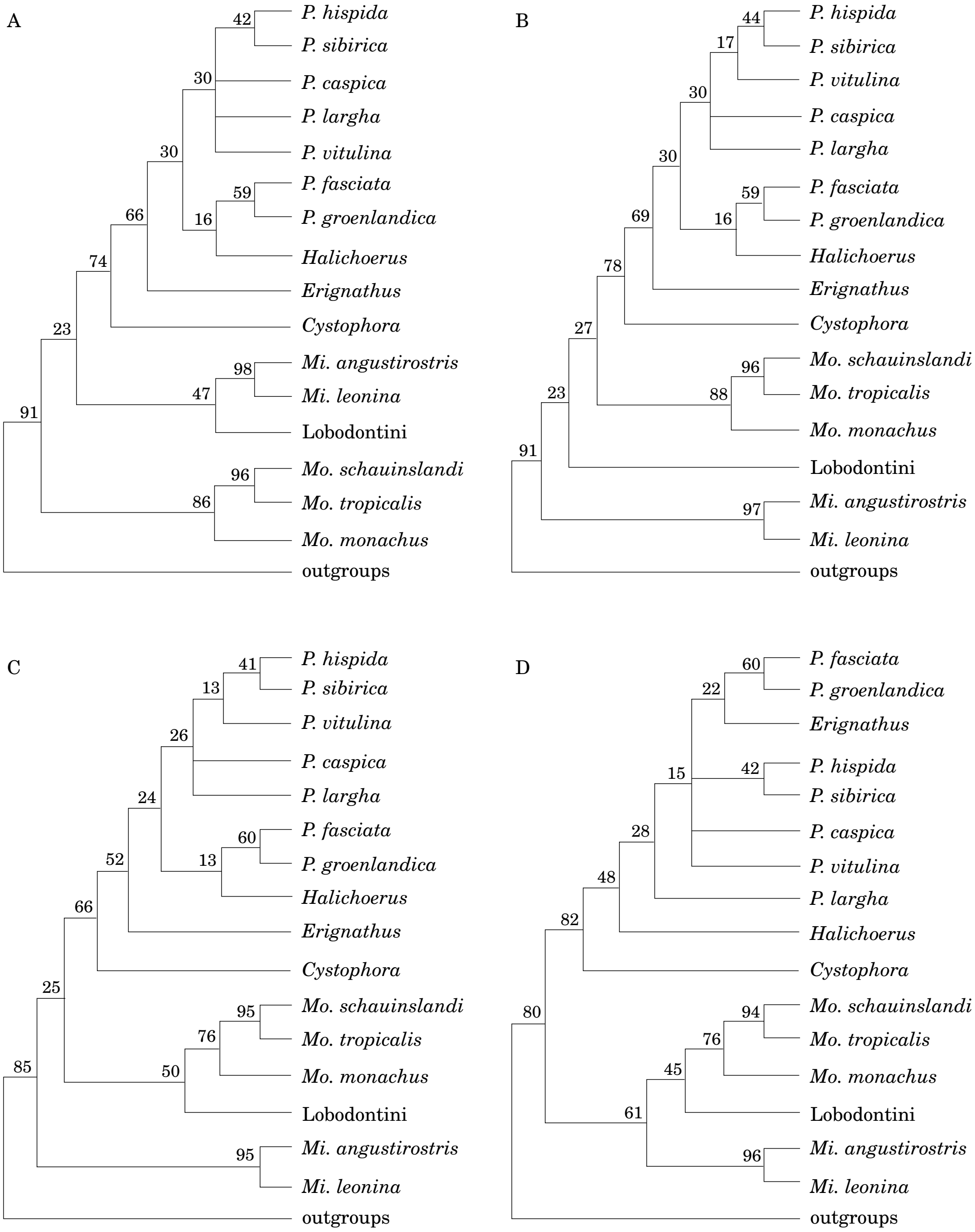


Figure 10. Ingroup topologies with bootstrap frequencies (1000 replications) resulting from assuming a monophyletic Lobodontini as represented using the following methods: (A) ancestral (ACCTRAN optimization), (B) ancestral (DELTRAN optimization), (C) democratic, and (D) exemplar (using *Leptonychotes weddelli*). All trees are majority rule consensus solutions with all nodes occurring in 100% of the equally most parsimonious solutions. Full species names can be found in Figure 7.

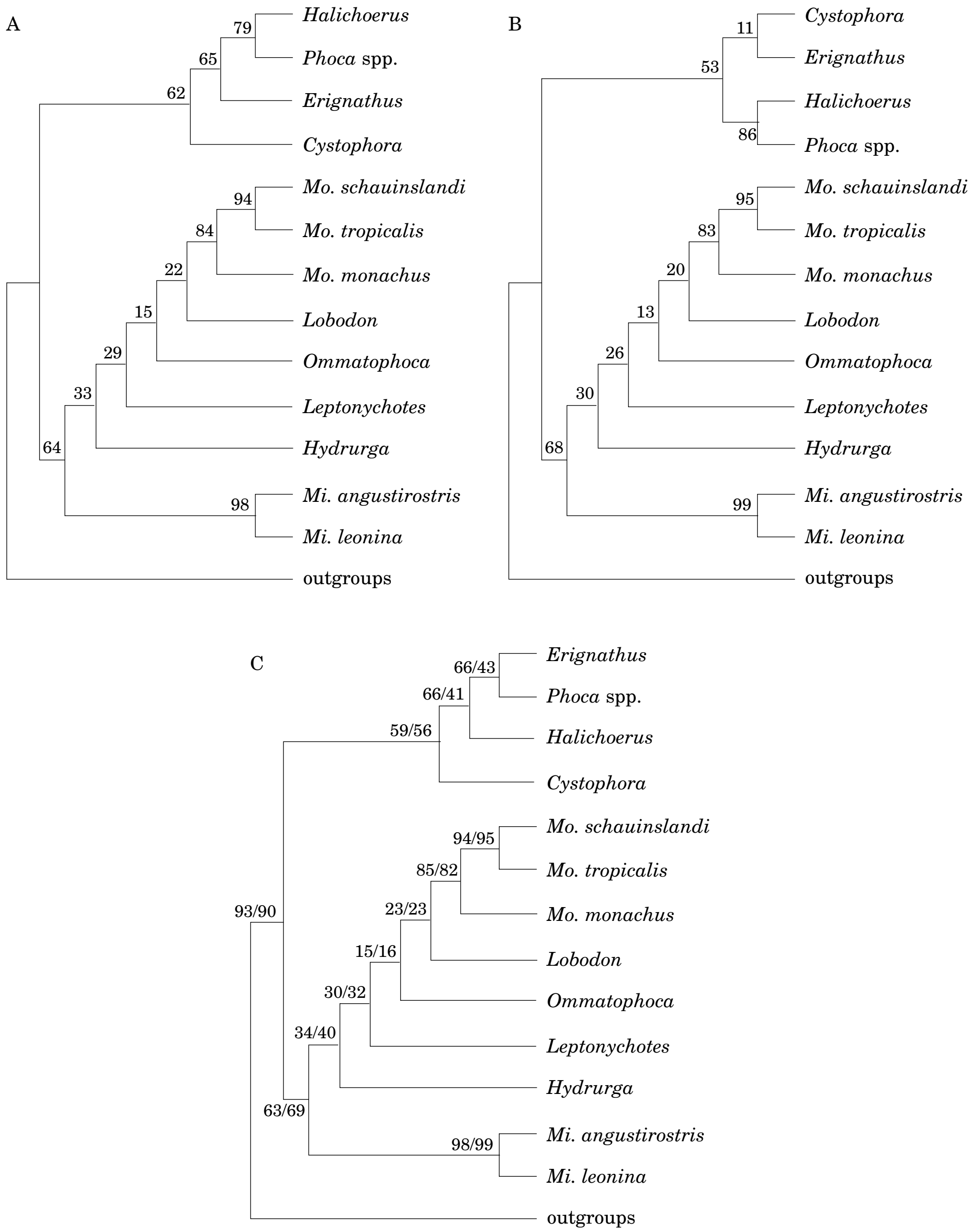


Figure 11. Ingroup topologies with bootstrap frequencies (1000 replications) resulting from assuming a monophyletic *Phoca* (*sensu* Burns & Fay, 1970) as represented using the following methods: (A) ancestral (ACCTRAN optimization), (B) ancestral (DELTRAN optimization), and (C) democratic and exemplar (using *P. vitulina*) (bootstrap frequencies in that order). All trees are the single most parsimonious solution. Full species names can be found in Figure 7.

TABLE 1. Selected parameters describing the species-level phocid tree and trees resulting from the representation of four supraspecific phocid taxa as single terminals. Goodness-of-fit indices refer to the most parsimonious solution(s) and not a consensus tree. MPT = number of most parsimonious trees. Expected CI refers to the value expected for a study of *n* taxa (includes eight outgroup taxa) as calculated from Sanderson & Donoghue (1989)

Matrix	Length	MPT	CI[1]	Expected CI	RI	RC
Full species solution ($n = 27$)	69 834	2	0.456	0.461	0.629	0.287
Lobodontini ($n = 24$)				0.495		
ancestral (ACCTRAN)	60 214	4	0.472		0.642	0.303
ancestral (DELTRAN)	59 998	4	0.473		0.644	0.305
democratic	62 810	2	0.475		0.638	0.303
exemplar	62 228	2	0.472		0.633	0.299
Mirounga ($n = 26$)				0.472		
ancestral (ACCTRAN)	66 757	2	0.459		0.627	0.288
ancestral (DELTRAN)	66 366	2	0.458		0.629	0.288
democratic	68 996	2	0.464		0.630	0.292
exemplar	67 880	1	0.460		0.623	0.287
Monachus ($n = 25$)				0.483		
ancestral (ACCTRAN)	63 186	2	0.467		0.637	0.297
ancestral (DELTRAN)	62 525	2	0.469		0.646	0.303
democratic	66 550	2	0.470		0.634	0.298
exemplar	65 036	2	0.463		0.619	0.287
Phoca ($n = 21$)				0.532		
ancestral (ACCTRAN)	59 878	1	0.469		0.609	0.286
ancestral (DELTRAN)	59 618	1	0.471		0.612	0.255
democratic	60 309	1	0.470		0.610	0.287
exemplar	61 259	1	0.467		0.601	0.281
All groups ($n = 15$)				0.618		
ancestal (ACCTRAN)	40 331	4	0.509		0.616	0.314
ancestral (DELTRAN)	39 602	1	0.514		0.630	0.324
democratic	49 058	1	0.518		0.634	0.328
exemplar	46 293	2	0.507		0.584	0.296

[1] Note that the 'polymorphism' option in PAUP inflates CI values compared to the conditions under which the expected values were derived. Therefore, the relative decreases in CI are actually greater than indicated.

10A and B, and 11A and B). For the Lobodontini, the incorrect phylogenies all produced a paraphyletic Monachinae (with varying relationships among the monachine taxa) and shifted *Erignathus* basally within the Phocinae. Changes in topology with *Phoca* were restricted to the four phocine taxa.

Levels of homoplasy and support

Concomitant with the topological changes noted above, the use of supraspecific taxa also affected the amount of homoplasy found in the condensed solutions. The slight absolute rise in the CIs of the condensed solutions (Table 1) points to an overall decrease in homoplasy associated with collapsing a number of species (which can conflict with one another and share homoplasies with species outside of the group, thereby lowering the CI) into a single terminal. However, this decrease is localized and does not translate to the remainder of the tree in any amount to raise the CIs to the levels expected for the decreased number of terminals.

TABLE 2. Results of nonparametric tests examining the influence of the representation method employed ('method'), the taxon collapsed ('taxon'), the accuracy of the topology ('accuracy'), and the cladistic status of the collapsed taxa ('status') on the values of selected goodness-of-fit indices. The former two factors were analysed using a Kruskal–Wallis test (value given is H corrected for ties with $n=4$ for each sample), while the latter two were analysed using a Mann–Whitney test (value given is U_s with $n=n'=8$). Significant results ($P<0.05$) are indicated with an asterisk

	Factor			
	Method	Taxon	Accuracy	Status
CI	0.821	13.386*	33.5	63.5*
RI	2.537	11.206*	32.0	38.0
RC	0.821	11.333*	34.0	33.0

Compared to the levels found in the full species solution, only the taxon that was collapsed significantly influenced the amount of change in RI and RC (Table 1); differences in these values were independent of the representation method, the accuracy of the topology, or the cladistic status of the supraspecific taxon (Table 2). Differences in CI (relative to the expected value given the number of taxa) were influenced not only by the taxon but also by its cladistic status (Table 2), with paraphyletic taxa showing a greater relative decrease. Although this result could mean that higher level studies with lower than expected CIs might have included terminals that represent paraphyletic taxa, we believe that the significant result observed here is a size effect. Data matrices with fewer terminals had CIs that were proportionately smaller than expected (Table 1; note especially when all four taxa are simultaneously condensed). As it happens, collapsing the two paraphyletic taxa yields the smallest matrices.

Analyses in which *Phoca* was represented by a single terminal resulted in the largest decrease in CI and the only decreases in RI and RC (ignoring that taxon number might also influence these two indices). This suggests that *Phoca*, despite showing a reasonably low level of character identity among its constituent species (Table 4; see below), contains relatively few homoplasies, either within the group or with the other phocid species. The fact that all but one species of *Phoca* yield the same result when used as the exemplar supports this suggestion. Thus, collapsing this genus to a single terminal removes this consistent region from the tree, causing the RI and RC to decrease because of those relatively more homoplastic groups that remain. Similarly, the Lobodontini and *Monachus* probably contain relatively more homoplasies (which reduction to a single terminal eliminates, thereby raising the RI and RC), whereas *Mirounga* possesses an average amount of homoplasy (reduction to a single terminal has no effect on RI or RC). In contrast, Bininda-Emonds & Russell (1996) argued that the relationships among monachines were more stable and robust than for those among phocines.

Bootstrap values were roughly similar between the nodes of the full species and the various condensed solutions (compare Fig. 7 with Figs 8–12). Despite this general consistency in bootstrap values, some clades with bootstrap support above 60% are missing from one or more of the condensed solutions. The bootstrap cannot recognize erroneous clades because it can only indicate the support for a particular clade in

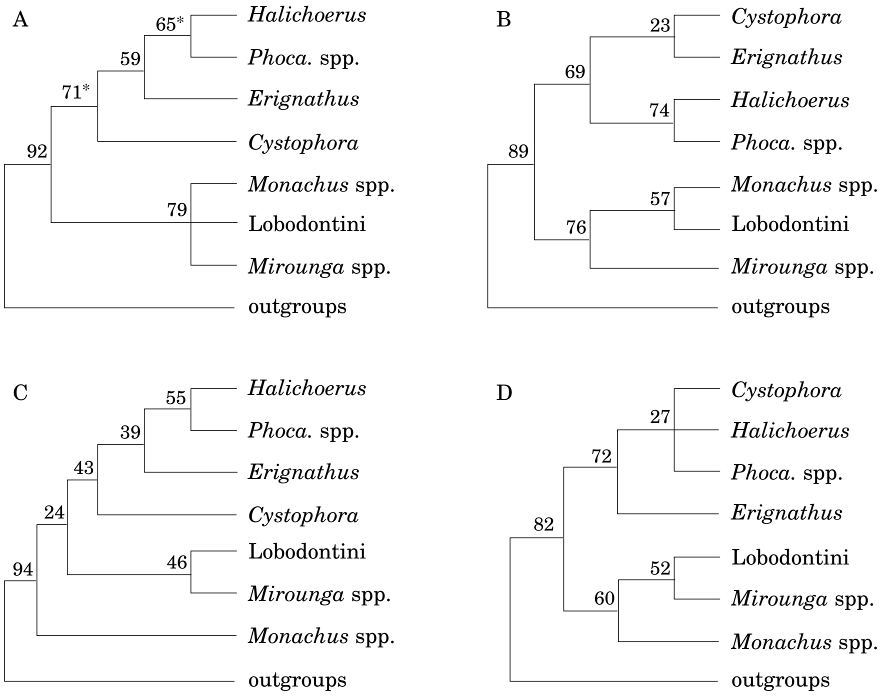


Figure 12. Ingroup topologies with bootstrap frequencies (1000 replications) resulting from assuming the monophyly of the four higher level phocid taxa Lobodontini, *Mirounga*, *Monachus*, and *Phoca* (*sensu* Burns & Fay, 1970) as represented using the following methods: (A) ancestral (ACCTRAN optimization), (B) ancestral (DELTRAN optimization), (C) democratic, and (D) exemplar. A and D are majority rule consensus solutions. All nodes were found in 100% of the equally most parsimonious solutions except those in A marked with an asterisk which were found in 75%. Full species names can be found in Figure 7.

a given data set and cannot, as is commonly believed, determine its historical reality (as pointed out by Hillis & Bull [1993]). In the condensed trees (Figs 8–12), the reduced number of terminals alters the levels of support due to a decreased number of possible alternative groupings and possibly an increased number of characters per node. For instance, reducing the Phocinae to four terminals when *Phoca* is collapsed dramatically reduces the number of alternative groupings, inflating the support for those possibilities that remain. This is another manifestation of the bootstrap only being able to assess support for relationships allowed by the data matrix (see Bininda-Emonds & Russell, 1996). Thus, bootstrap support for groups on smaller trees may be relatively high even if levels of homoplasy in the data are also relatively high.

DISCUSSION

Underlying causes: character identities

The hypothetical examples showed that homoplasy in the data can produce changes in topology when supraspecific taxa are replaced by single terminals because

Table 3. Pairwise matrices of character identities between the different representations of a given higher level phocid taxon and between each and the constituent species of the taxon. Presented as number of characters (out of 168) with at least one state in common (liberal identity; above the diagonal) and with all states in common (conservative identity; below the diagonal). Asterisks indicate pairs of methods that produced the same (correct) topology

Lobodontini	ancestral (ACCTRAN)	ancestral (DELTRAN)	democratic	exemplar	all species
ancestral (ACCTRAN)	—	158	160	163	91
ancestral (DELTRAN)	158	—	158	144	91
democratic	112	111	—	140	91
exemplar	112	116	113	—	91
all species	66	65	65	66	—

Mirounga	ancestral (ACCTRAN)	ancestral (DELTRAN)	democratic	exemplar	all species
ancestral (ACCTRAN)	—	156*	168	168	147
ancestral (DELTRAN)	156*	—	167	159	147
democratic	112	111	—	156	140
exemplar	137	133	130	—	147
all species	115	110	110	115	—

Monachus	ancestral (ACCTRAN)	ancestral (DELTRAN)	democratic	exemplar	all species
ancestral (ACCTRAN)	—	154*	167*	168	113
ancestral (DELTRAN)	154*	—	161*	140	113
democratic	102*	100*	—	131	110
exemplar	108*	124*	115	—	113
all species	78	78	78	78	—

Phoca	ancestral (ACCTRAN)	ancestral (DELTRAN)	democratic	exemplar	all species
ancestral (ACCTRAN)	—	164	166	159	98
ancestral (DELTRAN)	164	—	164	152	98
democratic	146	144	—	151*	98
exemplar	133	135	135*	—	98
all species	85	85	85	85	—

of shifts in the 'balance of power' among characters. In the more complex phocid examples, such changes can often be linked to a small number of key characters. The best example for this is when *Monachus schauinslandi* was used as the exemplar for *Monachus*. *M. schauinslandi* is characterized by numerous primitive phocid features and the basal movement of *Monachus* in this example to become the sister taxon to all other phocids (see Fig. 9B) can be tied largely to three of them: characters 17, 41, and 69 (see Appendix B in Bininda-Emonds & Russell [1996]). In a re-analysis with these characters either excluded or coded as missing for *Monachus*, *Monachus* clusters among the lobodontines, albeit as the sister taxon to *Ommatophoca*, and the Monachinae is monophyletic. Although this topology is not entirely correct, it is much closer to the full species tree and illustrates the large effect that only three characters out of 168 can produce.

To provide a more general overview, we quantified the similarity in character states ('character identity') between the various phocid terminals (representing either supraspecific taxa or species) (Tables 3 and 4). Due to the large amount of polymorphism, we measured character identities as either 'liberal,' where the taxa in question share at least one state for a given character, or 'conservative,' where all taxa must possess the identical character state(s) for that character.

Table 4. Numbers of characters (out of 168) among the constituent species of four higher level phocid taxa with at least one state in common (liberal identity) and with all states in common (conservative identity)

Taxon	Liberal identity	Conservative identity
Lobodontini	91	66
Mirounga	147	115
Monachus	113	78
Phoca	98	85

The character identity among a supraspecific taxon, as represented using any method, and its constituent species (Table 3) closely matched the identity between the species themselves (Table 4). However, identities between the representation methods (Table 3) were generally higher than either of these other two sets of identities (although this may relate to the numbers of taxa being compared in each instance). Therefore, the various representation methods provide similar approximations of a given supraspecific taxon, but ones that cannot account for the diversity of information present among all the constituent species. The latter observation explains why changes in topology occur (i.e. by retaining only some information, we run the risk of discarding phylogenetically informative characters and retaining homoplasies, thereby misrepresenting the groundplan states), while the former provides further evidence that changes in a few key characters can result in large changes in topology. Marked diversity among members of a supraspecific taxon (as observed here) can be problematic for the exemplar method because the resulting terminal taxon is more likely to include character states that misrepresent the phylogenetic position of the group for a greater number of characters. The democratic method, in constructing the 'average' of the constituent members, and especially the ancestral method, in attempting to reconstruct the hypothetical ancestor, are more immune to this problem.

Beyond this, however, the explanatory power of the character identities is limited; only a few trends are evident in the data. Between representation methods, liberal identities were typically around 95%, whereas conservative identities ranged from 60 to 80% (Table 3). Liberal identities tend to be very similar except those between the exemplar and either of the ancestral (DELTRAN optimization only) or democratic methods, which are noticeably lower. For conservative identities, there was strong similarity (over 90%) between the ACCTRAN and DELTRAN variants of the ancestral method. The democratic method may also resemble the exemplar method more than it does the ancestral method, but only for monophyletic taxa. Finally, there is no apparent relationship between character identity and changes in topology (as quantified by the symmetric-difference metric; Penny & Hendy, 1985), as only *Mirounga* demonstrated a significant (negative) regression (results not shown). This also illustrates the large effect that a few key characters can have on topology.

Given the large amount of polymorphism in the phocid data matrix, it is unsurprising that different representations of a supraspecific taxon with high liberal character identities can yield different topologies. *Monachus* provides an example: the democratic and exemplar methods show 100% identity (Table 3), but produce strikingly different solutions (compare Figs 9A and B). Similarly, the two species of

Mirounga share 87.5% character identity (Table 3), but produce very different solutions when each is used as the exemplar of the genus (*M. angustirostris* obtains a solution reasonably close to the full species tree; results not shown). Large topological differences can occur despite high conservative identities as well. In the two variants of the ancestral method for either the Lobodontini or *Phoca* (Figs 10A,B and 11A, B), the differences in topology arise, at most, due to 10 and four characters, respectively (Table 3).

Multiple taxa and interactive effects

Thus far, we have only examined the outcome when a single supraspecific taxon is collapsed to a single terminal. However, it is likely that more than one such taxon will be condensed at once, especially in studies aimed at elucidating relationships at higher taxonomic levels. Therefore, to determine the topological changes that the use of multiple supraspecific terminal taxa might induce, we simultaneously condensed all possible combinations of the four higher level phocid taxa. Clear trends were evident, so we will restrict the detailed presentation of results to instances where all four taxa were condensed.

The inclusion of four supraspecific terminal taxa (Fig. 12) produced similar results to analyses involving only one such taxon. Again, the ancestral method arguably performed the best. Although no method generated a tree with *Erignathus* and *Phoca* as sister taxa (the topology among phocines that would most closely match that in Fig. 7), only the ancestral method either preserved the topology for the monachines (Fig. 12B) or did not contradict it (Fig. 12A). Overall, changes were less extreme than when individual taxa were collapsed (possibly due to there being fewer taxa in the analysis to be affected), as the only instance of a subfamily being rendered paraphyletic was the monachines using the democratic method (Fig. 12C).

Figure 12 also includes some novel topologies, presumably due to interactive effects. The tree obtained using the democratic method (Fig. 12C) contains a topology for the monachines that was not generated when any of the four taxa were condensed individually using this method. The closest topology is that produced when the Lobodontini alone was condensed (Fig. 10A). Similarly for the exemplar method (Fig. 12D), the topologies of neither the monachines nor the phocines were found in the results when single supraspecific taxa were included as terminals. In both cases, the closest topology involves the representation of *Monachus* (Fig. 9B). The ancestral method did not display any novel topologies from interactive effects in this example.

The 10 other combinations of collapsing the four supraspecific taxa (Table 5) produced similar results to those described above. The correct topology was rarely maintained, occurring most often using the ancestral method when at least one of the taxa is monophyletic. The democratic method retained the correct topology only once and the exemplar method not at all. The frequency of novel topologies created through interactive effects differed among the representation methods, ranging from rare for the ancestral method (either optimization criterion) to ubiquitous for the democratic and exemplar methods. The exemplar method, in particular, often produced novel topologies that were very different from both the full species solution and those solutions obtained when only one supraspecific taxon was included in the analysis.

The novel topologies and probable interactive effects highlight the potential complexity of the problem when, as is commonly done, two or more supraspecific terminal taxa are included in phylogenetic analyses. Clearly, this practice increases the probability of obtaining a wrong result (although it did lead to a more correct answer in the case of the democratic method with the Lobodontini and *Mirounga* collapsed) and it is extremely difficult to identify specific causes for altered topologies.

Problems with paraphyly

In both the hypothetical and phocid examples, topologies consistent with those of complete species-level trees were obtained more often when monophyletic, rather than paraphyletic, supraspecific taxa were replaced with single terminals. The problems with collapsing paraphyletic taxa are emphasized by considering the phocid examples using the ancestral method, in which the ancestral states were derived from the same data as the topology with which the condensed trees were compared. As a result of this somewhat circular methodology, the ancestral method might be expected to generate the correct answer. Nonetheless, incorrect topologies were obtained when paraphyletic supraspecific taxa were collapsed. These results indicate that the representation of paraphyletic groups is the cause of the incorrect topologies. As the hypothetical examples show, the combination of paraphyletic groups and homoplasy provides the only situation when correct application of the ancestral method goes astray. These examples also demonstrate that the use of paraphyletic supraspecific taxa contributes to changes in topology using the democratic and exemplar methods; thus, it is clear that the use of such taxa will likely lead to errors in our analyses.

These results highlight the dangers of including supraspecific taxa of uncertain cladistic status as terminals in phylogenetic analyses. If these taxa are paraphyletic, the resultant cladogram is likely to be wrong. On the other hand, a correct result is probable when the supraspecific taxa are monophyletic and represented as terminals using the ancestral method. However, because we cannot know from the analysis itself whether the taxa included are monophyletic or not, a key objective of systematic analysis should be the elimination of paraphyletic taxa. This emphasizes the importance of species level analyses: monophyletic taxa at the lower levels need to be identified so that these taxa can be collapsed to allow relationships at a higher level to be resolved. This approach contrasts slightly with the viewpoint of Yeates (1995), who stated that neither higher nor lower level analyses should have priority because both interact and depend on one another. Although this reciprocal illumination is necessary at least to provide outgroups, especially when higher level relationships are poorly known, Yeates did not examine the issue of paraphyly. For groups where higher level relationships are more resolved, this problem provides a strong argument for giving priority to a 'species-up' approach.

Assessment of representation methods

Both Yeates (1995) and ourselves have argued from first principles that the correct way to represent a monophyletic supraspecific taxon is to infer the character states of its most recent common ancestor. Of the methods used herein, the ancestral

Table 5. Summary of analyses in which more than one supraspecific phocid taxon (1 = *Mirounga*, 2 = *Monachus*, 3 = Lobodontini, and 4 = *Phoca*) was collapsed at once. Table entries are efficacy at maintaining the topology of the species-level solution (+ = maintained, − = altered, ? = uncertain due to polytomy)/ summary of interactive effects giving rise to clades not found when only a single taxon was collapsed (M = in Monachinae only, P = in Phocinae only, B = in both subfamilies, N = in neither subfamily, ? = uncertain due to polytomy)

Collapsed taxa	Representation method ancestral (ACCTRAN)	ancestral (DELTRAN)	democratic	examplar
1+2	+/N	+/N	−/M	−/M
1+2+3	+/N	+/N	−/M	−/N
1+2+4	?/P?	−/N	−/P?	−/M
1+3	−/N	−/M	−/P	−/N
1+3+4	−/N	−/M	−/M?	−/B
1+4	?/P?	−/N	−/P?	−/B
2+3	+/N	+/N	−/M?	−/B
2+3+4	−/N	−/N	−/M?	−/B
2+4	?/P?	−/N	+/N	−/N
3+4	−/N	−/N	−/N	−/P
1+2+3+4	−/M?	−/N	−/M	−/B

Table 6. Efficacy of the various representation methods in maintaining the topology of the species-level solution when particular supraspecific terminal taxa are present. Concurrence is indicated by a plus sign and discordance by a minus sign

Reconstruction method	Monophyletic taxa *Mirounga*	 *Monachus*	Paraphyletic taxa Lobodontini	 *Phoca*
ancestral (ACCTRAN)	+	+	−	−
ancestral (DELTRAN)	+	+	−	−
democratic	−	+	−	+
exemplar	−	−	+	+

method most closely achieves this goal and should produce trees that best match the topology of the full species solution. This was borne out in the phocid results (Tables 5 and 6), where the representation of the different supraspecific taxa using this method generated topologies that were often the same, or very similar to, that of the complete species solution. The hypothetical examples showed that the ancestral method is particularly sensitive to the cladistic status of the taxa it is representing. Given that the ancestral states are inferred correctly, the ancestral method is extremely robust at representing monophyletic taxa. With paraphyletic taxa, however, homoplastic characters in the excluded members of the corresponding clade can cause this method to err. These findings were confirmed using the phocid examples.

Although the (single) exemplar method occasionally produced correct answers (particularly with the paraphyletic phocid taxa; Table 6), these instances were more often the result of good luck. Success using this method often depends on which species is chosen as the exemplar. Unfortunately, we usually lack the knowledge to make an informed decision and species are often chosen instead on practical grounds. Exemplars for paraphyletic taxa that are more closely related to excluded members of the least inclusive clade may be more likely to produce more correct topologies because these exemplars share more apomorphies with the excluded taxa (e.g. taxa *e* and *f* in Fig. 6C). However, this result will not necessarily occur in a particular instance (e.g. different exemplars for the Lobodontini) because the topology also depends on the amount and distribution of homoplasy.

The democratic method performed about on a par with the exemplar method (and arguably surpassed it when more than one taxon was condensed at a time; Table 6); by sampling from a wider range of species the democratic method should be less susceptible to errors due to the character states of a single aberrant species. Use of the democratic method might be justified when there is no rationale for choosing an exemplar or the ancestral method cannot be invoked (e.g. no fossil or ontogenetic information or previous analyses). Undesirable aspects of using both the democratic and exemplar methods include their unpredictability in obtaining the correct answer and their susceptibility to the presence of homoplasy regardless of the cladistic status of the taxon (see hypothetical examples).

These conclusions differ from those of Yeates (1995), who advocated the use of exemplars over what he called ‘intuitive groundplan analysis’ (Yeates did not examine the democratic method). However, Yeates took a largely theoretical approach to the problem that included only a limited number of empirical examples. He also argued for the use of multiple exemplars, which can improve the performance of this method, albeit at the cost of extra taxa in the analysis. The exemplar method can give correct answers; however, we have shown that, on the whole, the common use of single exemplars does not and that the circumstances under which it does (e.g. choice of taxon, amount and distribution of homoplasy, cladistic status of the taxon) are largely unpredictable. Finally, the more rigorous nature of our ancestral method should improve its performance in comparison with intuitive groundplan analysis.

The distinction among our three methods is often not as clear-cut as we have made it out to be, particularly between the ancestral and exemplar methods. The use of a fossil taxon as a surrogate for the common ancestor could be considered a special case of the exemplar method and evokes similar difficulties. Fossil taxa are unlikely to fall directly on the stem line and therefore represent the character states of the common ancestor only to an unknown degree. Thus, as with any extant exemplar, the apomorphic traits possessed by a fossil taxon allow for erroneous relationships to be formed based on homoplasies shared with other taxa in the tree. Whether this is as seriously problematic as with extant taxa requires further investigation.

The exemplar method might be improved by adopting aspects of the ancestral method. When phylogenetic evidence is available, it might prove advantageous to select one or more of the species closest to the ancestral node as the exemplar (as argued by Yeates, 1995) because they often resemble the common ancestor to the greatest extent. This need not always be true, however. For example, descendants of a very ancient basal lineage will have acquired numerous apomorphies to diverge from the groundplan. As well, it has been shown that, depending on the rate of character evolution, erroneous topologies can still occur when basal taxa are selected as the exemplar (M. McMahon, pers. comm.). It is evident that this approach requires further examination.

A factor not examined here that may affect the propensity for all the representation methods to generate erroneous topologies is how distantly related the higher taxa are phylogenetically. With more remote higher taxa, the large differences between their character states may compensate somewhat for any misrepresentation of their groundplans, although long edge attraction (see Hendy & Penny, 1989; Soltis & Soltis, 1996) remains a potential problem for molecular data. Situations in which the taxa are more closely related, or part of a rapid adaptive radiation in which fewer phylogenetically informative characters evolve, are of greater concern. In such cases, it is critical that the character states of supraspecific terminal taxa accurately reflect their groundplans. Our evidence suggests that the ancestral method is best able to achieve this.

Implications for molecular studies

Although the present study is relevant to all types of phylogenetic analysis, the implications are perhaps the most serious for analyses of molecular data, where the exemplar method is commonly used both for practical reasons and because of the nature of the data themselves. The relatively few species that have been sampled to date for a limited number of biomolecules not only rules out the democratic method, but often the ancestral method as well because there have not been enough studies to posit a hypothetical common ancestor with any degree of confidence. Estimation of the common ancestor is also hindered by the rapid degeneration of many phylogenetically useful sources of molecular data, DNA in particular (Lindahl, 1993a, b; Logan, Boon & Eglinton, 1993). Thus, we are unlikely to discover fossil molecular data of sufficient quantity to be useful.

The literature contains numerous molecular studies that include results that most would consider incorrect (e.g. Simonsen, 1982; Schreiber *et al.*, 1994; Allard & Carpenter, 1996). Typically, such results are explained away by citing any of a number of factors: the use of an insufficient amount of data (e.g. Cao *et al.*, 1994; D’Erchia *et al.*, 1996; see also Cummings *et al.*, 1995); a period of anomalous molecular evolution in one or more of the species and/or rate heterogeneity in general (e.g. Schreiber *et al.*, 1994; Freye & Hedges, 1995); implications of inferior data (e.g. Ledje & Arnason, 1996); the use of different analytical procedures (e.g. D’Erchia *et al.*, 1996; see also Hillis, Huelsenbeck & Cunningham, 1994); the use of different genes (e.g. Cummings *et al.*, 1995; Allard & Carpenter, 1996); or the use of an inappropriate or overly simplistic model of molecular evolution (e.g. Cao *et al.*, 1994). Although these factors are frequently important, our results suggest that the use of the exemplar method is another, not necessarily mutually exclusive, factor which might be causing errors in analyses.

Although the number of exemplars needed in an analysis depends on many factors (e.g. size of the group, rate of evolution), we suggest that molecular studies containing only a few representatives of the relevant species be treated with some reservation. As we have demonstrated, the single exemplar method is liable to produce erroneous topologies. Although this is true of the other representation methods as well, the exemplar method is unpredictable because it is dependent on the choice of the taxon. The selection of a different set of species may produce markedly different results (Lecointre *et al.*, 1993). A recent example is the debate concerning rodent monophyly (specifically, the phylogenetic placement of the guinea pig, *Cavia porcellus*, and other caviomorphs with respect to the remaining rodents). Numerous studies typically using, at most, four of the approximately 1800 rodent species, and often different sets of species, are divided between opposite conclusions (e.g. compare Graur *et al.*, 1991; Ma *et al.*, 1993; D’Erchia *et al.*, 1996 with Martignetti

& Brosius, 1993; Cao *et al.*, 1994; Freye & Hedges, 1995). Given our findings, the lack of agreement on this issue is not surprising. Although the factors mentioned above have all been cited as reasons for the lack of consensus, and no doubt contribute to the problem, we suggest that any errors are likely exacerbated through the use of the exemplar method.

CONCLUSIONS

This study clearly demonstrates the potential dangers of including supraspecific terminal taxa in phylogenetic analyses. However, we do not decry the value of higher level analyses in general. Species-level analyses are impractical when attempting to elucidate higher level relationships. But, before conducting such analyses, the monophyly of any higher taxa that will be represented by terminals should be corroborated; we cannot otherwise confidently detect when monophyly has been forced on non-monophyletic taxa. Likewise, no representation method is able to consistently produce correct topologies when non-monophyletic supraspecific taxa are represented by single terminals.

Of the three methods discussed herein, the ancestral method is the most likely to maintain the correct topology because it attempts to infer the character states of the groundplan (the ideal scenario from first principles). This was reflected in our examples where the ancestral method was demonstrably superior at maintaining the general topology of the full species solutions, particularly when monophyletic taxa were collapsed. In contrast, reconstructing the groundplan does not appear to be the explicit aim of either the democratic or (single) exemplar methods and both produced a larger proportion of incorrect answers, with little obvious pattern as to the conditions under which these methods failed. When more than one supraspecific taxon was represented simultaneously, all three methods, albeit to a lesser extent for the ancestral method, displayed undesirable interactive effects where the resultant topology included different clades than when the taxa were collapsed individually. The ancestral and exemplar methods are not always completely separable (e.g. a specific fossil taxon that is used as a surrogate ancestor could also be considered as an exemplar) and the ancestral method can influence the choice of exemplars (e.g. the use of basal exemplars that are expected to more closely resemble the ancestor). The exemplar method might also be improved through the use of multiple exemplars (see Yeates, 1995). One factor that causes representation methods to fail is homoplasy in the data; the ancestral method is affected less often because, by inferring the groundplan of the taxon, it ignores homoplasy in individual members of the group.

The superiority of the ancestral method for representing supraspecific taxa has serious implications for molecular analyses where this method is rarely, if ever, employed. Instead, the predominant use of the exemplar method, together with an often limited selection of all the potential species, can lead to erroneous topologies and a lack of agreement among studies. Although numerous other factors have been cited as reasons for these disagreements, we suggest that the use of the exemplar method must be included in this list.

In conclusion, we advocate general caution whenever supraspecific taxa are replaced by terminals in an analysis. Although the ancestral method performed the best in this study, the issue of how the ancestral states are arrived at (e.g. through fossil data, ontogenetic evidence, or based on previous phylogenetic analyses) might affect the outcome of the analysis, requiring more research. In addition, we stress the errors that might accrue by tacitly assuming the monophyly of higher level taxa. Such assumptions may be causing us to include paraphyletic taxa in our analyses, thus increasing the probability of generating an erroneous topology (beyond the necessary exclusion of one or more constituent taxa). Supraspecific terminal taxa imply hypotheses of monophyly, but these hypotheses must be tested beforehand because they can never be falsified by higher level analyses in which they are tacitly assumed. Therefore, it is vital that we verify the cladistic status of all supraspecific taxa that are included in an analysis.

ACKNOWLEDGEMENTS

This paper grew from the Master's research of the first author. For their assistance throughout that process, the efforts of Marc Ereshefsky, Gordon Pritchard, and Herb Rosenberg are gratefully acknowledged. Valuable comments and other help on later, continually expanding instars of the manuscript were provided by Alan Cooper, Paul Harvey, Colleen Kelly, Michelle McMahon, Sean Nee, Rod Page, Andy Purvis, and two anonymous reviewers. Financial support was provided by Alberta Heritage, the United Kingdom's Overseas Research Scholarship plan, and an NSERC postgraduate scholarship (OBE) and an NSERC operating grant (APR).

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APPENDIX

The following is a complete description of the algorithm (taken from Bininda-Emonds & Russell, 1996: 19–20) used to determine the democratic character states in the phocid examples. It was used by Bininda-Emonds & Russell (1996) to account for the high level of variation among phocid specimens when generating species' states. Since higher taxa are even less likely to be morphologically homogeneous, we similarly applied it when reconstructing the supraspecific phocid taxa.

For a given supraspecific taxon, the democratic state for each character was ordinarily the most frequent state among all the constituent species. Polymorphic data, such as when a species possessed both states 0 and 1, were treated as a discrete state (the state '01'), rather than independent occurrences of the singular states. If the next most frequent state(s) possessed the same frequency or the same frequency minus one observation, then the democratic state was a combination of these 'equally' most frequent states and the taxon was polymorphic for that character.

An exception to the above formula occurred when at least one of the 'equally' most frequent states was polymorphic. In such cases, the species' polymorphisms were 'broken,' the frequencies for each singular state were counted, and the above algorithm was reapplied. This was necessary because the democratic state of the 'equally' most frequent states 0 and 01, for instance, is meaningless (i.e. the state '001'), and probably reflects a greater preponderance of state 0 in that particular taxon. Polymorphic democratic states could still result if two or more singular states happened to be 'equally' frequent.