Towards comprehensive phylogenies: examples within the Carnivora (Mammalia)

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Abstract

Using case studies from the mammalian order Carnivora, I investigate some of the issues, implications, methodologies, and uses within systematic biology of more complete phylogenies. Chapter 1 reviews the benefits (increased phylogenetic accuracy; more powerful tests of a wider range of hypotheses) and costs (increased analysis times) of larger phylogenies and ways to construct them by combining existing phylogenetic information.

Chapter 2 examines the implications of one shortcut used for phylogenetic analysis at higher taxonomic levels, that of representing supraspecific groups as single terminal taxa. Using hypothetical examples and a complete phylogeny of the true seals (family Phocidae), I show that representing a monophyletic group by the states of its common ancestor minimizes errors compared to two other techniques. For paraphyletic taxa, no technique was satisfactory.

Chapter 3 investigates the mechanics and biases of matrix representation with parsimony analysis (MRP), a new method of combining phylogenetic information that appears to combine the benefits of more established techniques. This is done as a prelude to Chapter 4, where I use MRP to combine 274 partial estimates of carnivore phylogeny into the first fully dated composite tree of all extant carnivore species.

In Chapter 5, I divide the 274 carnivore source trees according to 1) data source, 2) study size, 3) study age, and 4) the tree selection criteria used to generate them to investigate the impact of these factors on inferences of carnivore phylogeny. Composite trees derived using MRP did not differ significantly within or among factors, or between families, indicating that all methodologies provide the same estimate of carnivore phylogeny.

In Chapter 6, I use the method of independent contrasts together with my carnivore tree to test the widely held, but poorly justified, claim that adaptations to the aquatic habitat functionally separate aquatic from non-aquatic carnivores in general and pinnipeds from the remaining species (fissipeds) in particular. My analysis of 22 morphological, life history, and physiological variables revealed that the differences have been overstated: only limited differences exist between aquatic and non-aquatic carnivores and none between pinnipeds and fissipeds.

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Table of contents

Chapter 1

General Introduction

Larger phylogenies — benefits and problems

An area of recent interest in evolutionary biology is the push towards producing larger and more comprehensive phylogenies. This drive has been fueled by advances in computer technology, which are allowing the accumulation and analysis of increasing amounts of data. Perhaps for the first time, we are in a position to produce large, comprehensive phylogenies using robust and rigorous methodologies (e.g., Chase *et al*., 1993; Purvis, 1995a; Soltis *et al*., 1997).

The size of a phylogenetic study can refer to either the number of characters or taxa it contains, and the drive towards larger phylogenies has seen increases in both parameters. Increases in character number are not problematic. Given that the additional characters are not misleading and that the phylogenetic estimation procedure used is "consistent" under the given conditions (i.e., converges on the right answer as characters are added; *sensu* Felsenstein, 1978a), it is widely agreed that more characters improve estimates of phylogeny, even if only slightly so (e.g., Wheeler, 1992; Kesner, 1994; Cummings *et al*., 1995; Graybeal, 1998; Soltis *et al*., 1998). The computational cost of adding characters to an analysis is also usually small.

Instead, the more important issue in evolutionary biology, and the one that underlies this thesis, concerns increases in taxon number. Again, the phylogenetic benefits of doing so are clear and largely agreed upon (although see Graur *et al*., 1996; Kim, 1996). Adding taxa can improve the accuracy of phylogenetic estimates by minimizing the deleterious effects of high rates of evolution (Hillis, 1996), taxon sampling (see Arnold, 1981; Donoghue *et al*., 1989; Lecointre *et al*., 1993), and especially long branch attraction (Felsenstein, 1978a; Hendy & Penny, 1989), a phenomenon that leads most tree selection criteria astray to various degrees (see Huelsenbeck & Hillis, 1993; Huelsenbeck, 1995). The benefits of including more taxa

also extend to the increasing number of fields that use evolutionary information: biogeography, conservation biology, comparative biology, and studies of character evolution to name a few. The scope of the problems examined in these latter fields depends on the sizes of the phylogenies they employ: larger, more complete phylogenies allow more powerful tests of a wider range of hypotheses.

Despite these advantages, increasing the number of taxa in a phylogenetic analysis faces two problems. First, large numbers of taxa present severe analytical problems for optimization-based tree reconstruction techniques (e.g., parsimony or likelihood methods) because the number of possible fully bifurcating rooted trees to choose from increases super-exponentially (as [2n – 3]!!; Felsenstein, 1978b) as the number of taxa (n) is increased. With current computer technology, the use of "NP-complete" tree building criteria such as parsimony, which are thought unlikely to have an efficient solution (Garey & Johnson, 1979; Graham & Foulds, 1982; Day, 1983), can guarantee optimal solutions in a reasonable amount of time for up to 20-30 taxa only. Beyond this, heuristic approaches must be used (see Swofford *et al*., 1996). However, the nature of the problem means that an upper limit to the number of taxa in an analysis of raw data will always exist, even with tremendous advances in computer technology. For example, one of the largest matrices so far analyzed was for a phylogeny of seed plants based on 500 nucleotide sequences of the chloroplast gene *rbc*L; the initial analysis lasted about four weeks (Chase *et al*., 1993). When Rice et al. (1997) re-analyzed the data, it required 11.6 months of CPU time to derive a solution that was trivially shorter (five steps or 0.03%).

A second problem concerns collecting sufficient character data for the additional taxa. Although technological advances have reduced the time, effort, and cost of generating molecular data, it remains that many species are poorly known (both morphologically and molecularly), that only relatively few genes have been sequenced, and that, with the possible exception of the botanical community (see Rice *et al*., 1997; W. J. Hahn, pers. comm.), data collection has been largely uneven and unsynchronized. Thus, we know comparatively little about a few species only and almost nothing about the remaining ones.

Possible solutions

Fortunately, some workarounds exist to ameliorate the problems inherent to having large numbers of taxa in an analysis. As regards searching through the vastness of "tree space," continued advances in computer technology will allow ever larger problems to be tractable. Aiding this process is the use of search strategies such as compartmentalization (Mishler, 1994), and algorithmic shortcuts such as branch and bound (Hendy & Penny, 1982) or heuristic search algorithms (see Swofford *et al*., 1996) and parsimony jackknifing (Farris *et al*., 1996). In some instances, additional taxa (and characters) may increase signal strength and therefore actually improve the performance of search algorithms (see Soltis *et al*., 1998).

A more promising avenue concerns the problems surrounding data collection. While initiatives like Systematics Agenda 2000 (Anonymous, 1991) seek increased funding for basic systematic research to identify new species in poorly known groups and poorly researched habitats, a more economical approach for phylogeneticists currently is to combine the vast amounts of data already collected. Numerous repositories of raw data and data matrices now exist and are easily accessible through the World Wide Web: GenBank and HOVERGEN (Duret *et al*., 1994) for gene sequences, PIR for protein sequences (George *et al*., 1997), TreeBASE (Sanderson *et al*., 1994) for source trees, and archives of journals or individual researchers. The only requirement for combining data is that a partition (i.e., each data matrix) shares at least two taxa with another partition, something that can be determined by heuristic devices such as "tree-graphs" (see Sanderson *et al*., 1998).

Together, these solutions provide exciting prospects for producing larger, more complete estimates of phylogeny. Before outlining the structure of this thesis, I describe the two main methods of combining phylogenetic data so as to provide the necessary background against which to compare the relatively new technique of matrix representation with parsimony analyses (MRP; Baum, 1992; Ragan, 1992b) that I examine and use in this thesis.

Combining phylogenetic information

Historically, two approaches to combining existing phylogenetic information have dominated, both of which were devised initially to assess the degree of congruence between independent data sets. "Character congruence" (*sensu* Kluge, 1989) combines and re-analyzes the raw (primary) data to derive the most consistent, unified statement regarding relationships among a set of taxa (Swofford, 1991). With "taxonomic congruence" (*sensu* Mickevich, 1978), the data sets are analyzed individually and the resultant trees are combined using consensus techniques to indicate those clades supported by the most independent lines of evidence (Swofford, 1991). I discuss the advantages and limitations of each approach in turn before introducing a recently developed technique: constructing "phylogenetic supertrees" (*sensu* Sanderson *et al.*, 1998).

Character congruence has been promoted on the principle of "total evidence" (*sensu* Kluge, 1989): the best phylogenetic hypothesis is that which uses all the available data and as much information within those data as possible. For many, its appeal derives from the advantages of combining raw data. First, signals and subsignals within the data can interact to support one another, yielding relationships that need not be indicated by any single source study ("signal enhancement;" de Queiroz *et al.*, 1995; also Nixon & Carpenter, 1996). Second, studies are easily differentially weighted to reflect confidence levels and sample sizes. Finally, using the raw data maximizes the descriptive and explanatory power of the solution (Kluge & Wolf, 1993; Nixon & Carpenter, 1996). For instance, the solution can be used to infer processes such as character evolution and can be summarized using standard support measures such as goodness-of-fit indices (Swofford, 1991), bootstrapping (Felsenstein, 1985a), or Bremer decay indices (Källersjö *et al.*, 1992).

Disadvantages of character congruence include the necessity of a single tree-building technique (typically parsimony), which limits its use to compatible data types only. Another potential problem is whether data pointing to vastly different solutions

should be combined. This statistical argument takes its lead from ecology where one routinely tests for data heterogeneity prior to prospective pooling. Many have argued against combining phylogenetic data lacking a single underlying distribution (e.g., Bull *et al*., 1993; de Queiroz *et al*., 1995), but some remain unconvinced (e.g., Nixon & Carpenter, 1996).

Taxonomic congruence instead combines trees and thus is one step removed from the primary data. To many, this is less desirable, so that taxonomic congruence is advocated more as a fall-back option when character congruence cannot be applied (e.g., when there is data heterogeneity or incompatibility) (Bull *et al*., 1993; Rodrigo *et al*., 1993; de Queiroz *et al*., 1995). This dual strategy has been referred to as either "prior agreement" (Chippindale & Wiens, 1994) or the "conditional combination approach" (Huelsenbeck *et al*., 1996). Taxonomic congruence has also been criticized on the basis that the choice of consensus technique used to combine the source trees is essentially arbitrary (Kluge, 1989).

However, the strategy of combining trees presents certain advantages. Methodologically, consensus techniques find solutions in polynomial time as opposed to the less efficient exponential ("non-deterministic polynomial") time of optimization-based tree-building techniques (Graham & Foulds, 1982; see above). Therefore, taxonomic congruence is less prone to size limitations than character congruence. Data sets are also combined equally, preventing smaller ones from being "swamped." Concerns about swamping have been strongest for combining morphological and molecular data sets as the latter tend to be much larger (Kluge, 1983; Miyamoto, 1985; Barrett *et al*., 1991). However, swamping may be less of a problem than formerly thought: most molecular characters are not phylogenetically informative (i.e., they are invariant or the changes do not cluster taxa) and so the two sources are often more equal in information content ("size") than they might first appear. Finally, it is easier to visualize conflict between data sets using taxonomic congruence because conflicts are presented as polytomies (although this depends to some degree on the consensus technique used). This becomes important philosophically because many hold the best

hypothesis as that which has the most independent lines of evidence supporting it (Mickevich, 1978; Farris, 1983; Penny & Hendy, 1986; Novacek, 1992b).

A new solution for combining phylogenetic information is to construct a phylogenetic supertree. Building supertrees, for which MRP is one method, resembles taxonomic congruence methodologically in that trees are combined rather than raw data. Thus, supertrees can combine heterogeneous or incompatible data. However, the algorithms do not rely on (conventional) consensus techniques to do so, and the supertree method is distinguished by being able to combine source trees with different sets of terminal taxa. (Except for Lanyon's [1993] modified semi-strict consensus algorithm, all consensus techniques require source trees to have the same set of taxa.) Other than MRP, the description of which I defer until Chapter 3, the only formal procedure for building supertrees is the "strict supertree" algorithm (*sensu* Sanderson *et al*., 1998), which constructs one or more supertrees that are consistent with all the source trees, if such a set of supertrees exists (see Gordon, 1986; Steel, 1992). At first glance, supertrees, and MRP in particular, appear to combine the benefits of both the character and taxonomic congruence approaches. I raise this topic again in Chapter 3.

Mammalian carnivores as a case study

In this thesis, I use examples involving the mammalian order Carnivora to illustrate some representative problems in evolutionary biology to which comprehensive phylogenies can provide answers. Carnivores constitute a diverse assemblage of 271 extant species grouped into 11 families (following Wozencraft, 1993) of varying size. The largest is Mustelidae (weasels, otters, skunks, and badgers) with 65 species, followed by Canidae (dogs), Felidae (cats), Herpestidae (mongooses), and Viverridae (civets and genets) with around 35 each. At the other end of the scale are Hyaenidae (hyaenas; four species) and the monotypic Odobenidae (walruses), the current distributions of which belie earlier, more successful radiations in the fossil record (see Werdelin & Solounias, 1991; Repenning & Tedford, 1977, respectively).

Beyond this taxonomic diversity, carnivores also possess a remarkable degree of morphological, physiological, and ecological diversity. Carnivores span the largest range in size of any mammalian order, from the 100g least weasel (*Mustela nivalis*) to the 3 600kg male southern elephant seal (*Mirounga leonina*). Ecologically, carnivores cross all habitat and, despite their ordinal name, dietary classes. Physiologically, carnivores possess adaptations to such extreme conditions as deep sea diving (pinnipeds) and polar climates (e.g., Arctic fox, true seals) among others.

Carnivores are also well-studied, both phylogenetically and ecologically. Reasonable amounts of phylogenetic information exist for most families (with the exception of herpestids, procyonids [raccoons], and possibly viverrids; see Chapter 4) and a large amount of life history data is also known for many species (e.g., Harrison, 1969; Stirling, 1983; Gittleman, 1986b, 1993; Bygrave & Cooke, 1994). However, both phylogenetic and ecological research effort in carnivores tends to be divided along aquatic-terrestrial lines, thus hindering us from understanding carnivore biology as a whole and serving as a major impetus behind Chapter 6 (see below).

Structure of this thesis

Using carnivores as a source of case studies, this thesis examines many diverse topics. As I noted above, generating large phylogenies is desirable, but not always feasible, particularly at higher taxonomic levels. A common shortcut is to represent supraspecific taxa as single terminal taxa, a procedure that involves implicit assumptions of the monophyly of the taxa and of how they are to be represented. In Chapter 2, I examine the implications of this shortcut and its attendant assumptions on the accuracy of our phylogenetic estimates using the restricted example of the Phocidae (true seals). I pose and answer the following questions: 1) how severe are the alterations in topology (if any) and, more pragmatically, 2) are there procedures for representing supraspecific taxa that limit any negative effects?

In describing the two dominant methods of combining phylogenetic information to produce more expansive phylogenies, it is apparent that both possess shortcomings.

Supertree construction appears to address these shortcomings, but the method has not been examined in much detail. In Chapter 3, I focus on the mechanics, limitations, and biases of MRP, a promising supertree procedure that has attracted some preliminary and oft-times conflicting methodological consideration (e.g., e.g., Rodrigo, 1993, 1996; Williams, 1994; Purvis, 1995b; Ronquist, 1996). This is done as a prelude to Chapter 4, where I use MRP to combine 274 independent phylogenetic estimates to derive a fully dated composite tree of all extant species of carnivore. I also address the systematic implications of the composite tree (e.g., identify paraphyletic taxa, compare the tree to previous opinion) and compare fossil versus molecular estimates of divergence times.

The source trees used to derive the carnivore composite tree differed in terms of 1) the tree selection criteria used to generate them, 2) the data source used, 3) the size of the study (i.e., number of included taxa), and 4) the age of the study. These four variables, and the implementations thereof, are believed to affect the accuracy of our phylogenetic estimates. Therefore, in Chapter 5, I recombined the source trees to generate composite trees for each variable in order to answer three questions: 1) do the different implementations within each variable produce trees that are significantly different from one another, 2) do all variables show the same levels of internal conflict or do some have a greater impact on our phylogenetic estimates, and 3) are the phylogenetic inferences among the carnivore groups differentially affected by a given methodology?

While the carnivore (and specifically arctoid) affinities of pinnipeds have been acknowledged for over 100 years (e.g., Turner, 1848; Flower, 1869), their largely aquatic existence (and concomitant adaptations thereto) is frequently used to justify separating them from the rest of the order taxonomically and ecologically. However, this conclusion is highly intuitive, lacks empirical evidence, and has not been analyzed within a rigorous phylogenetic or statistical framework. In Chapter 6, I examine the related questions of what differences exist between aquatic and terrestrial carnivores in general, and between pinnipeds and the remaining “fissiped” carnivores in particular, with respect to 22 morphological, life history, physiological, and ecological variables. My use of the method of independent contrasts (Felsenstein, 1985b) as implemented in the CAIC package

(Purvis & Rambaut, 1995) in combination with my carnivore composite tree to control for phylogenetic effects provides the first rigorous examination of these two questions and an excellent example of the utility of large, complete phylogenies outside of phylogenetic biology.

I conclude the thesis with a short discussion on the importance of distinguishing between large and complete phylogenies and how it is the latter we should be striving towards in phylogenetic analysis.

Chapter 2

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

(Note: this chapter appears in press as Bininda-Emonds, O. R. P., H. N. Bryant, and A. P. Russell. 1998. Supraspecific taxa as terminals in cladistic analysis: implicit assumptions of monophyly and a comparison of methods. Biological Journal of the Linnean Society 64: 101–133.)

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Synopsis

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. I examine the effects of using supraspecific terminal taxa using a parallel analysis of hypothetical examples and an actual data matrix for the true seals (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 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.

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 *et al*., 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 I 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 *et al*., 1991), mustelids (Wayne *et al*., 1989a; 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 carnivores in Chapter 4), 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 *et al*., 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 *et al*., 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). I refer to these three methods as the ancestral, exemplar (Mishler, 1994; Yeates, 1995:344), and democratic methods, respectively.

I 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 allows me to isolate some of the factors that impinge on the use of supraspecific taxa. I 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 (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 analysis 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 tree selection criterion) 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 taxa, 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 and 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, 1988b). 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). I 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. I 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 I 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 paleontological criterion for character state polarization — see Eldredge and 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 programs (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 *et al.*, 1994a; Kuma & Miyata, 1994; Schreiber *et al*., 1994; Cummings *et al*., 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 *et al.*, 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. I therefore focus my 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 I 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

I 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 me 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," I 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 (Figures 2.1–2.6) 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 to determine the effect on the inferred topology. Although I 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) (Figure 2.1) 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

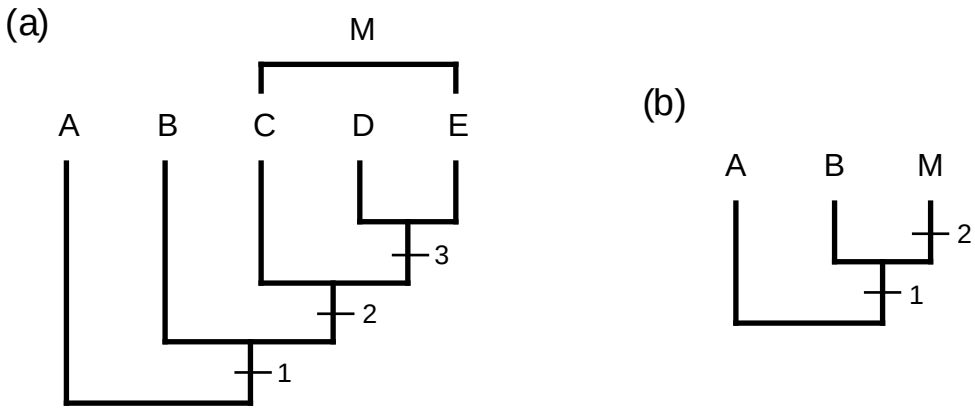


Figure 2.1: Representation of a monophyletic group (C,D,E) as a single terminal taxon (M) and the effect on topology in the absence of homoplasy. a) The original tree including C, D, and E. b) The simplified tree in which (C,D,E) is replaced by M. Characters supporting the nodes are indicated with bars. See text for explanation.

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 2.2a, 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) (Figure 2.2b). Characters 2 and 3, that together with character 1 outweighed characters 4 and 5 in the original matrix, are no longer informative in the condensed matrix. In Figure 2.2c, 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 (Figure 2.2b). 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.

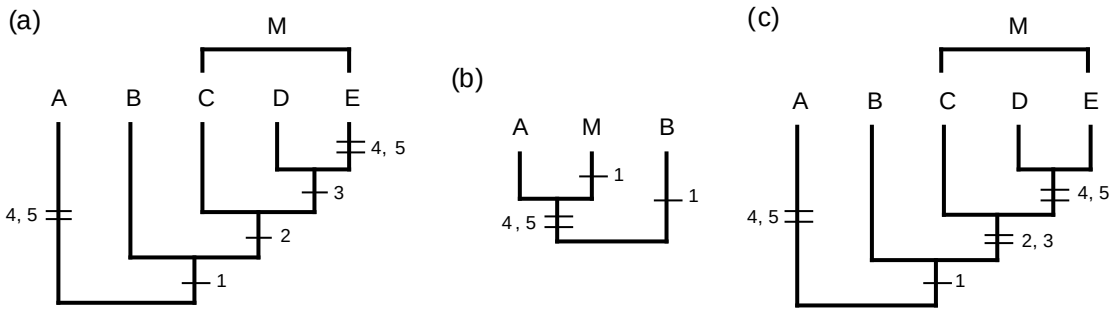


Figure 2.2: Representation of a monophyletic group (C,D,E) as a single terminal taxon (M) and the effect on topology in the presence of homoplasy. a) and c) Two original trees including C, D, and E with different distributions of characters 1–5. b) Simplified tree in which M groups with A rather than 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.

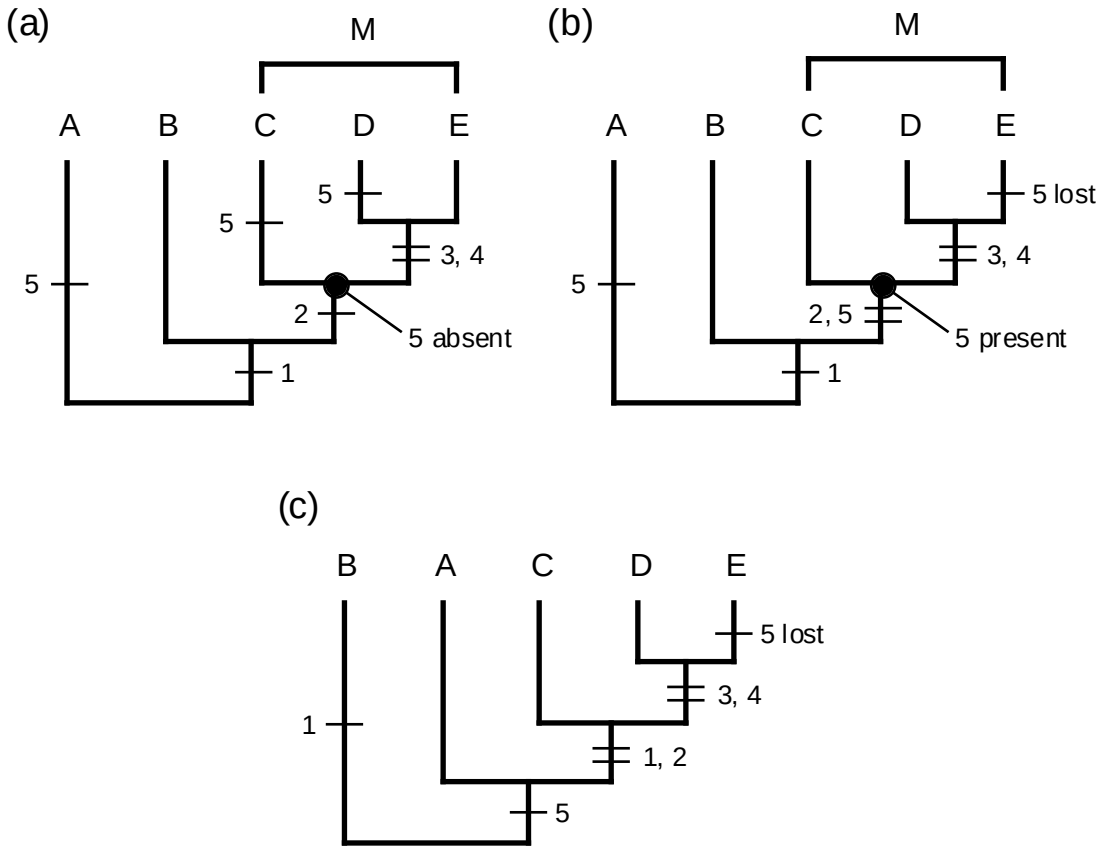


Figure 2.3: Equivocal inference of the character states of a hypothetical ancestor due to equally parsimonious optimizations at the ancestral node (indicated by a solid circle). a) Absence of character 5 using DELTRAN (delayed transformation). b) Presence of character 5 using ACCTRAN (accelerated transformation). c) Equally parsimonious tree to those in (a) and (b) in which the positions of A and B are reversed.

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 (Figure 2.2), 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 Figures 2.3a 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 (Figure 2.3a), 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

(Figure 2.3b), 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 (Figure 2.3c) in which A is more closely related to (C,D,E) than B is. I have 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 2.4a is replaced by M, the relationships among the remaining taxa are unchanged (Figure 2.4b); however, Figure 2.4b suggests that M and F are sister 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 2.5a is replaced by M, each method produces a different character distribution for M (Figure 2.5b) and the relationship of M to the remaining taxa is different in each instance (Figures 2.5c–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 Figure 2.2), 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 2.6a, 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 (Figure 2.6b). On the

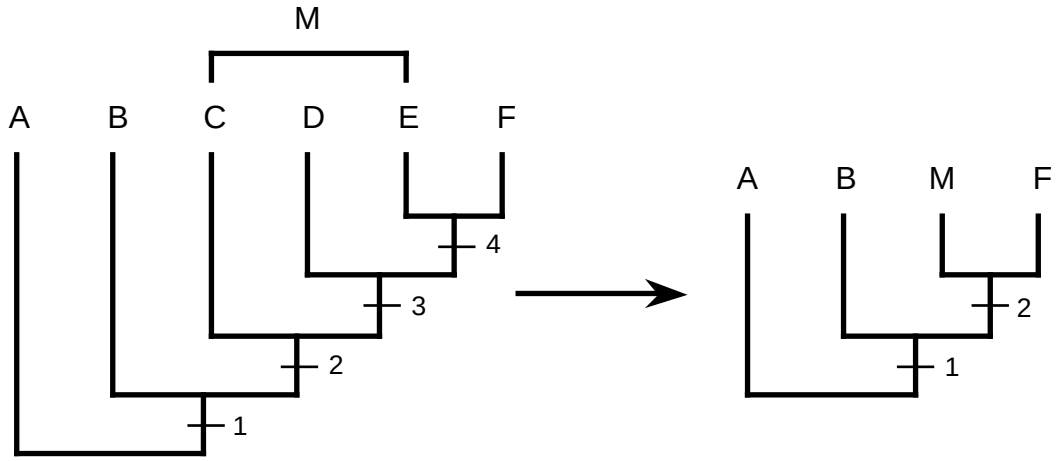


Figure 2.4: Representation of a paraphyletic group — C,D,E — as a single terminal taxon (M) and the effect on topology in the absence of homoplasy. a) Original tree. b) Simplified tree generated by all three representation methods on which F is the sister taxon of M, rather than its actual sister taxon, E.

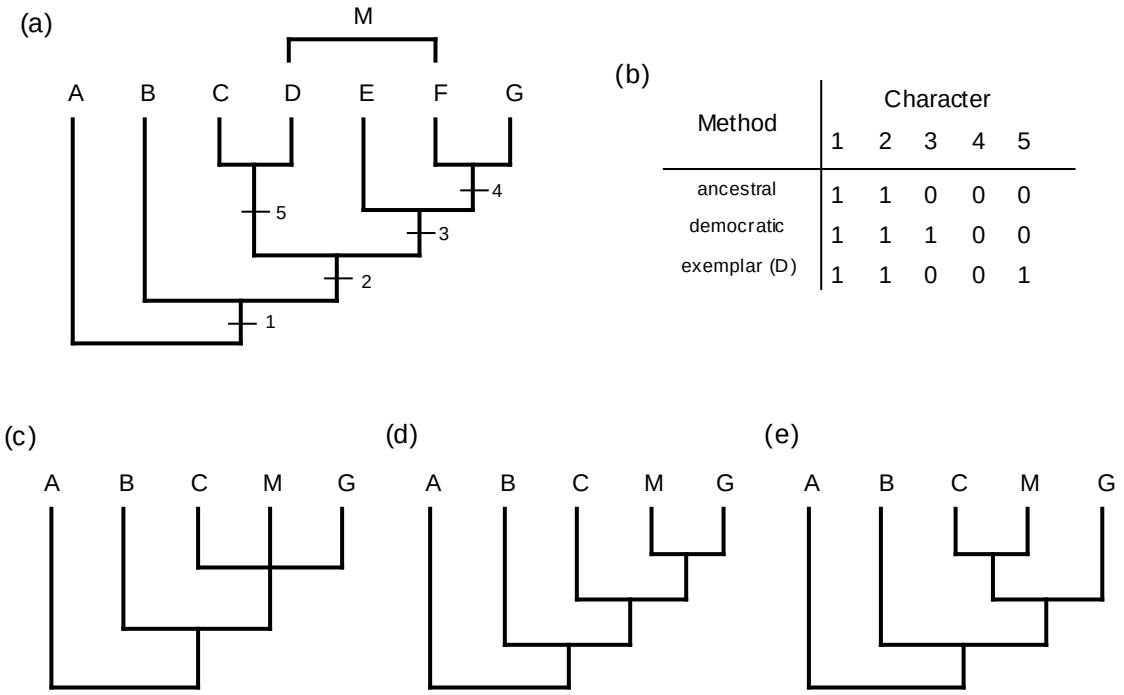


Figure 2.5: Representation of a paraphyletic group — D,E,F — as a single terminal taxon (M) and the effect on topology in the absence of homoplasy. a) Original tree. b) Character matrix illustrating the different character states of M using the three representation methods. c) Simplified tree using the ancestral method. d) Simplified tree using the democratic method. e) Simplified tree using D as the exemplar.

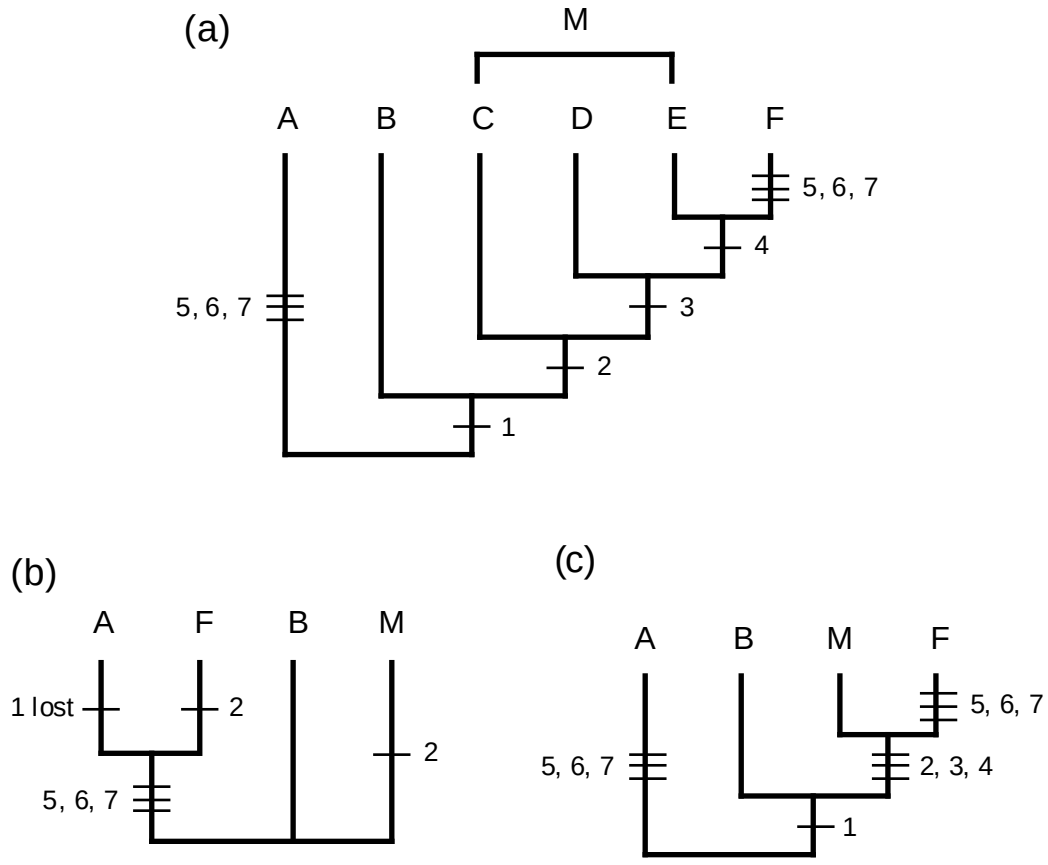


Figure 2.6: Representation of a paraphyletic group — C,D,E — as a single terminal taxon (M) and the effect on topology in the presence of homoplasy. a) Original tree. b) Consensus of three equally parsimonious simplified trees using the ancestral method or using C as the exemplar. c) Simplified tree using E as the exemplar.

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 2.6b 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 (Figure 2.6c). 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 Figure 2.6). 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, 1988b; not demonstrated, but endorsed by Berta & Wyss [1994]), *Phoca* (Chapskii, 1955; de Muizon, 1982b; Wyss, 1988b; Arnason *et al*., 1993, 1995; Mouchaty *et al*., 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 my knowledge, the non-monophyly of only *Mirounga* has never been suggested.

I 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 (see Appendix A) 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 weddellii* for the Lobodontini, and *Mirounga leonina*, *Monachus schauinslandi*, and *Phoca vitulina* for their respective genera. I 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 A 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 analyzed 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 analyzed 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) (Figure 2.7), which, for the purposes of this study, was considered to be correct. I

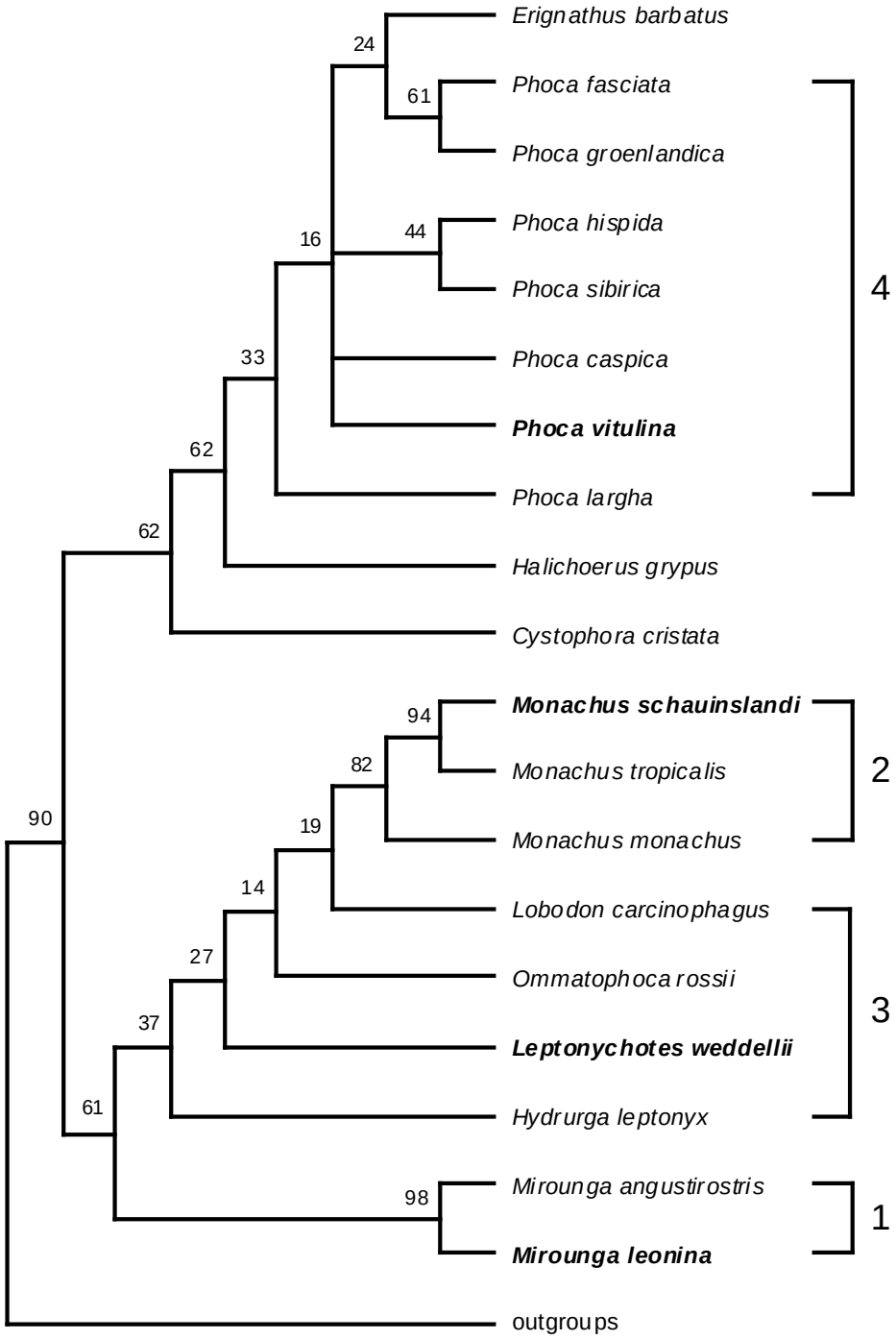


Figure 2.7: Majority rule consensus solution with bootstrap frequencies (1 000 replications) of all extant species of phocid seals (plus *Monachus tropicalis*) and outgroup taxa from Bininda-Emonds & Russell (1996). All nodes were found in both of the two equally most parsimonious solutions. Supraspecific 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.

focus primarily on changes in topology; however, I 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, 1985a) were calculated for each matrix based on 1 000 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* (Figures 2.8 and 2.9, 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 (Figure 2.8c) or both (Figure 2.8b) 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 (Figure 2.9b). Other changes include the creation of a monophyletic Lobodontini due to the exclusion of *Monachus*, and numerous alterations within the phocines (most notably a basal shift for

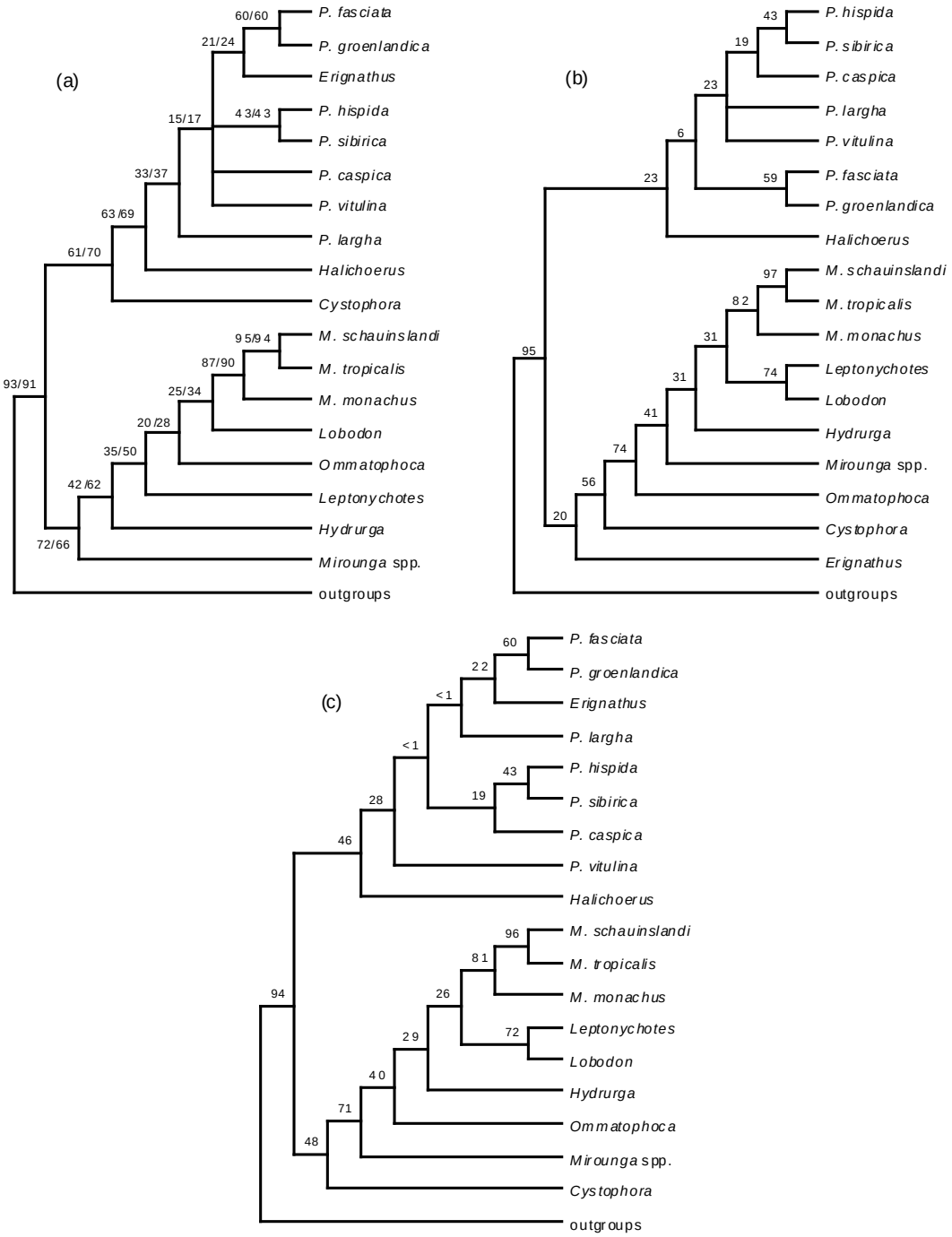


Figure 2.8: Ingroup topologies with bootstrap frequencies (1 000 replications) resulting from assuming a monophyletic *Mirounga* as represented using the following methods: a) ancestral (both ACCTRAN and DELTRAN optimization — bootstrap frequencies in that order), b) democratic, and c) exemplar (using *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 are given in Figure 2.7.

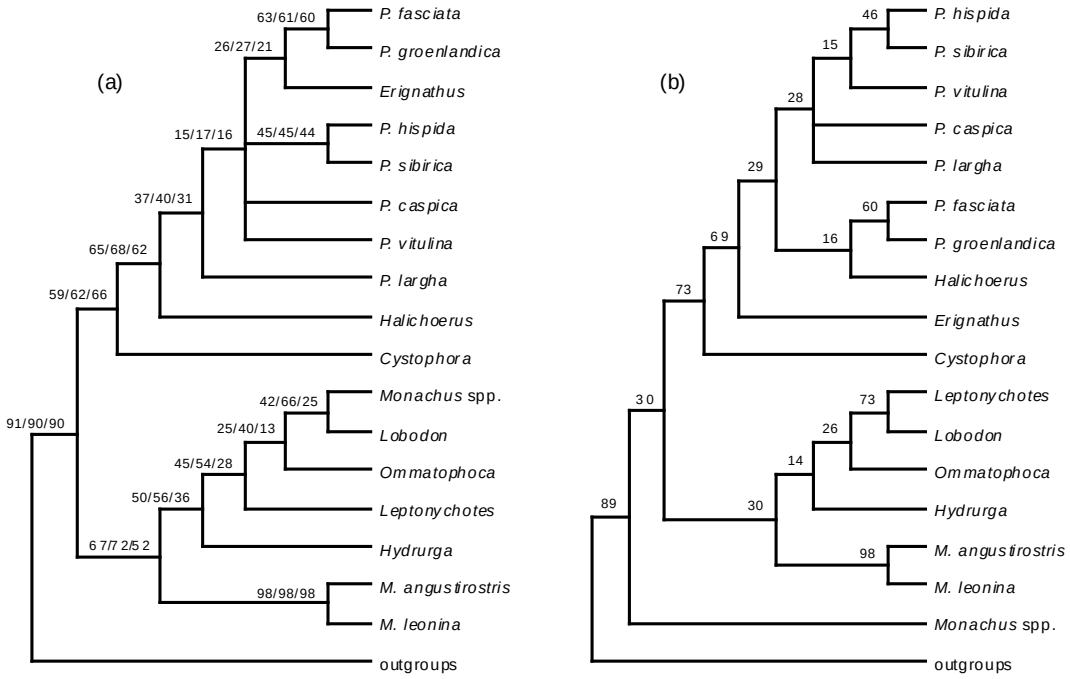


Figure 2.9: Ingroup topologies with bootstrap frequencies (1 000 replications) resulting from assuming a monophyletic *Monachus* as represented using the following methods: a) ancestral (both ACCTRAN and DELTRAN optimization) and democratic (bootstrap frequencies in that order) and b) exemplar (using *M. schauinslandi*). All trees are majority rule consensus solutions with all nodes occurring in 100% of the equally most parsimonious solutions. Full species names are given in Figure 2.7.

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, 1988b), 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 (Figures 2.10d and 2.11c, 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 Figure 2.11b).

The only other correct answer for the paraphyletic taxa was obtained using the democratic method for *Phoca* (Figure 2.11c), while the ancestral method failed in both instances, even generating different answers for each optimization (compare Figures 2.10a and b, and 2.11a 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 2.1) 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.

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 2.1); differences in these values were independent of the representation method, the accuracy

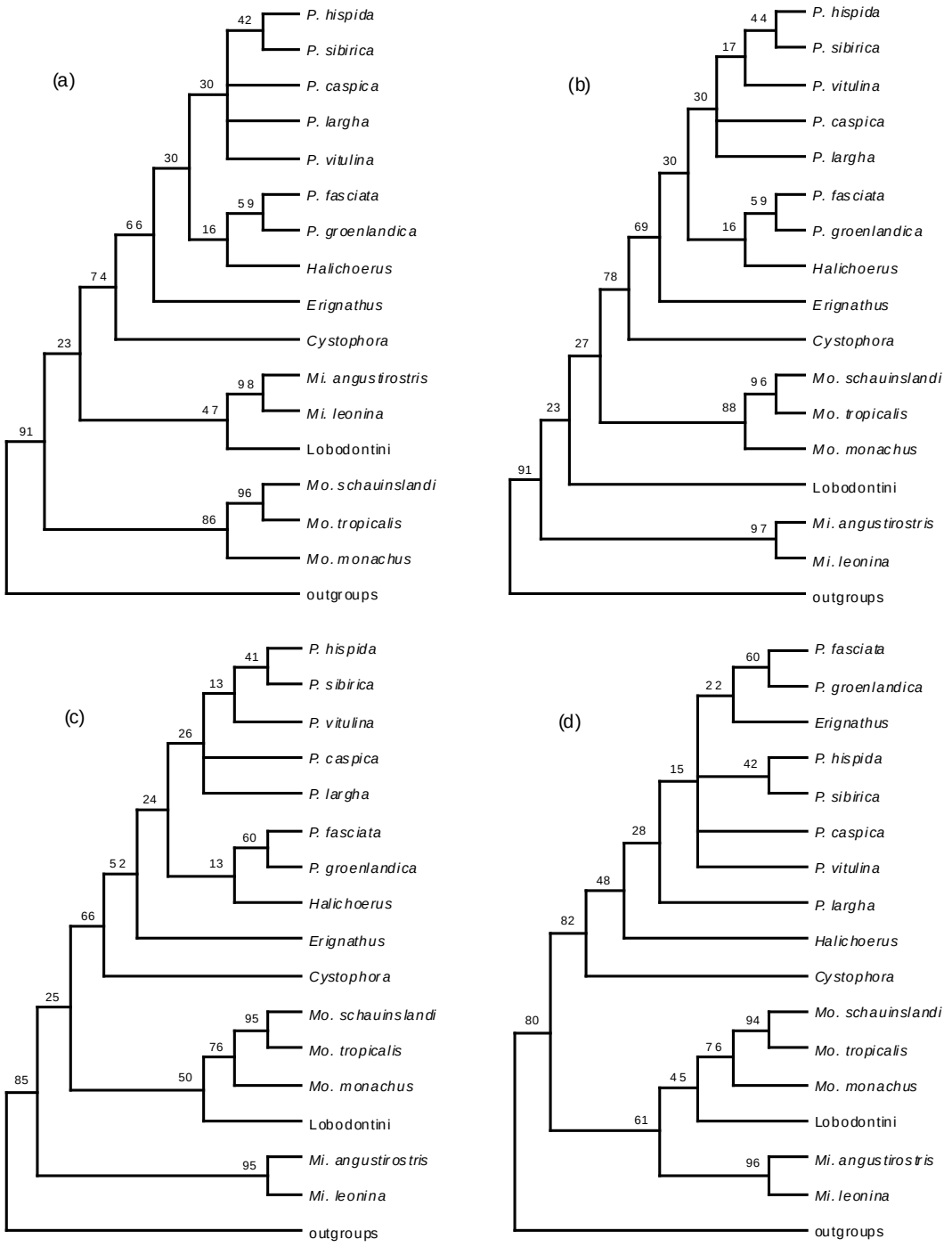


Figure 2.10: Ingroup topologies with bootstrap frequencies (1 000 replications) resulting from assuming a monophyletic Lobodontini as represented using the following methods: a) ancestral (ACCTRAN optimization), b) ancestral (DELTRAN optimization), c) democratic, and d) exemplar (using *Leptonychotes weddellii*). All trees are majority rule consensus solutions with all nodes occurring in 100% of the equally most parsimonious solutions. Full species names are given in Figure 2.7.

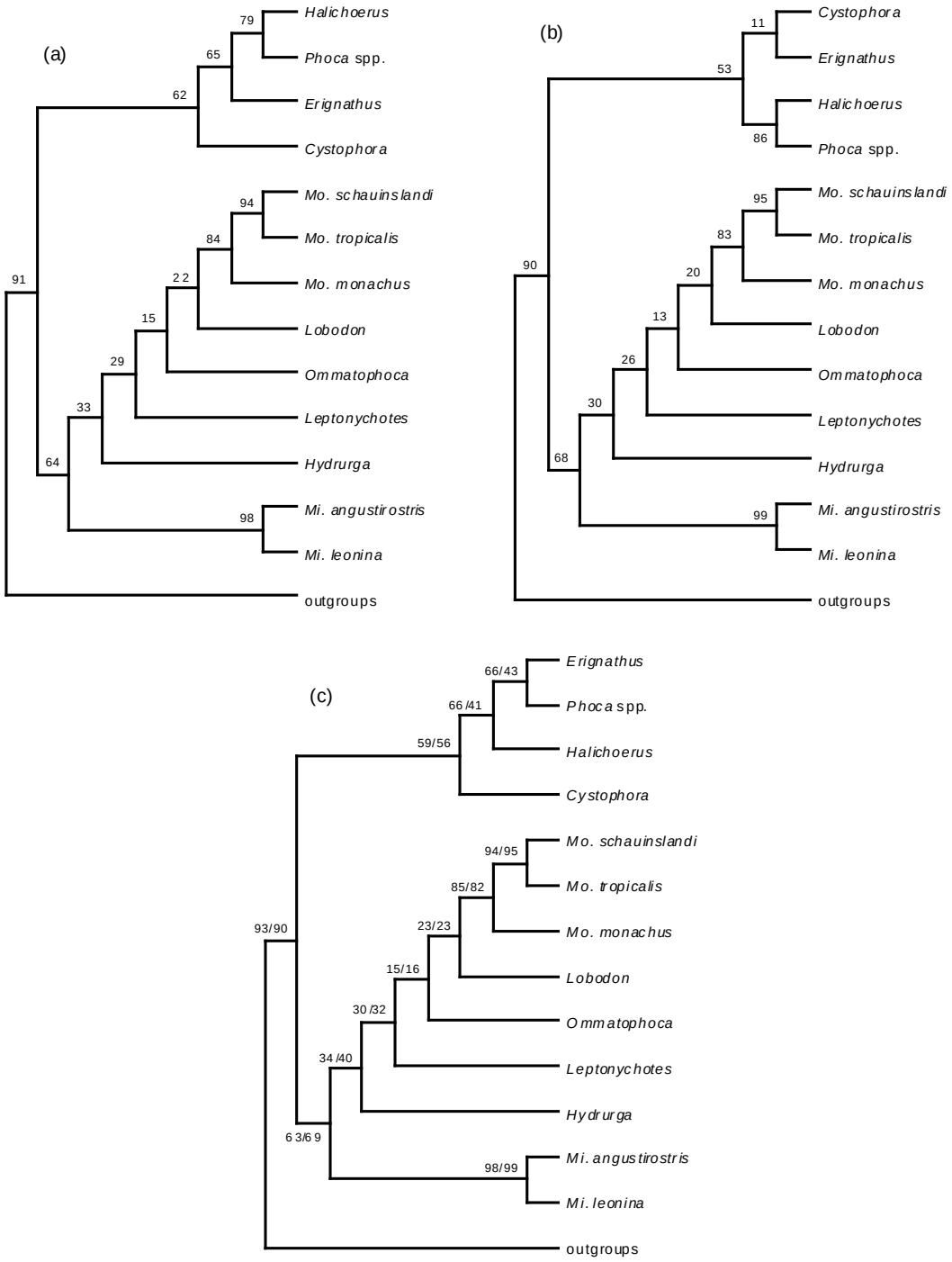


Figure 2.11: Ingroup topologies with bootstrap frequencies (1 000 replications) resulting from assuming a monophyletic *Phoca* (*sensu* Burns & Fay, 1970) as represented using the following methods: a) ancestral (ACCTRAN optimization), b) ancestral (DELTRAN optimization), and c) democratic and exemplar (using *P. vitulina*) (bootstrap frequencies in that order). All trees are the single most parsimonious solution. Full species names are given in Figure 2.7.

Table 2.1: 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.

Table 2.2: 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 analyzed using a Kruskal-Wallis test (value given is H corrected for ties with $n = 4$ for each sample), while the latter two were analyzed using a Mann-Whitney test (value given is U_S with $n = n' = 8$). Significant results ($p \leq 0.05$) 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

of the topology, or the cladistic status of the supraspecific taxon (Table 2.2). 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 2.2), 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, I 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 2.1; 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 2.4; 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 Figure 2.7 with Figures 2.8–2.12). 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 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 (Figures 2.8–2.12), 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 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 Figure 2.9b) can be tied largely to three of them: characters 17, 41, and 69 (see Appendix A). 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, I quantified the similarity in character states ("character identity") between the various phocid terminals (representing either supraspecific taxa or species) (Tables 2.3 and 2.4). Due to the large amount of polymorphism, I 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.

The character identity among a supraspecific taxon, as represented using any method, and its constituent species (Table 2.3) closely matched the identity between the species themselves (Table 2.4). However, identities between the representation methods (Table 2.3) 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

Table 2.3: 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. **(Presented overleaf)**

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	–

Table 2.4: 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

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 2.3). 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 partition 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 ancestral (ACCTRAN optimization) and exemplar methods show 100% identity (Table 2.3), but produce strikingly different solutions (compare Figures 2.9a and b). Similarly, the two species of *Mirounga* share 87.5% character identity (Table 2.3), 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* (Figures 2.10a, b and 2.11a, b), the differences in topology arise, at most, due to 10 and four characters, respectively (Table 2.3).

Multiple taxa and interactive effects

Thus far, I 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, I simultaneously condensed all possible combinations of the four higher level phocid taxa. Clear trends were evident, so I will restrict the detailed presentation of results to instances where all four taxa were condensed.

The inclusion of four supraspecific terminal taxa (Figure 2.12) produced similar results to analyses involving only one such taxon. Again, the ancestral method arguably

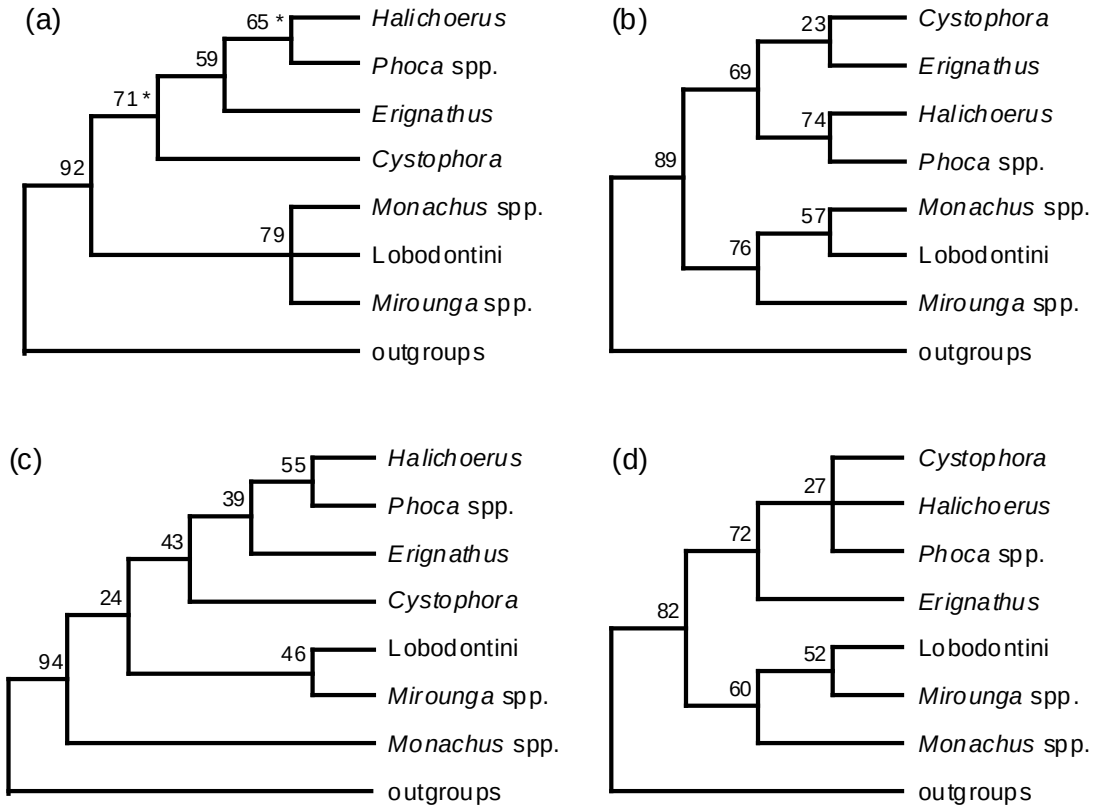


Figure 2.12: Ingroup topologies with bootstrap frequencies (1 000 replications) resulting from assuming the monophyly of the four higher level phocid taxa Lobodontini, *Mirounga*, *Monachus*, and *Phoca* (*sensu* Burns & Fay, 1970) as represented using the following methods: a) ancestral (ACCTRAN optimization), 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 (b) marked with an asterisk which were found in 75%. Full species names are given in Figure 2.7.

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 Figure 2.7), only the ancestral method either preserved the topology for the monachines (Figure 2.12b) or did not contradict it (Figure 2.12a). 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 (Figure 2.12c).

Table 2.5: 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).

	Representation method			
Collapsed taxa	ancestral (ACCTRAN)	ancestral (DELTRAN)	democratic	exemplar
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

Figure 2.12 also includes some novel topologies, presumably due to interactive effects. The tree obtained using the democratic method (Figure 2.12c) 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 (Figure 2.10a). Similarly for the exemplar method (Figure 2.12d), 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* (Figure 2.9b). 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 2.5) 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 myself 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 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 2.5 and 2.6), 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

Table 2.6: 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		Paraphyletic taxa	
	Mirounga	*Monachus*	Lobodontini	*Phoca*
ancestral (ACCTRAN)	+	+	–	–
ancestral (DELTRAN)	+	+	–	–
democratic	–	+	–	+
exemplar	–	–	+	+

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 2.6), 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 Figure 2.6c). 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 2.6); 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, I 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 my ancestral method should improve its performance in comparison with intuitive groundplan analysis.

The distinction among my three methods is often not as clear-cut as I 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 effect 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 branch 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. My 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, 1993b; Logan *et al*., 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*., 1994b; 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 *et al*., 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*., 1994b). Although these factors are frequently important, my 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), I suggest that molecular studies containing only a few representatives of the relevant species be treated with some reservation. As I 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 1 800 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*., 1994b; Freye & Hedges, 1995). Given my 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, I 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, I 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 my 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, I suggest that the use of the exemplar method must be included in this list.

In conclusion, I 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 requires more research. In addition, I 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.

Chapter 3

Properties of matrix representation with parsimony analyses

(Note: this chapter appears in press as Bininda-Emonds, O. R. P. and H. N. Bryant. 1998. Properties of matrix representation with parsimony analyses. Systematic Biology 47: 507–518.)

Acknowledgements:

I thank Andy Purvis for introducing me to MRP, for many fruitful initial discussions regarding the technique, and for pointing out the counterexample in Figure 3.2. Fredrik Ronquist kindly supplied me with a preprint copy of his manuscript. David Cannatella, Paul Harvey, Andy Purvis, Alan Rodrigo, and Fredrik Ronquist made constructive comments on an earlier version of this paper.

Synopsis

Matrix representation with parsimony analysis (MRP) is a relatively new technique for constructing phylogenetic supertrees from existing information that appears to combine some of the positive features of character congruence and taxonomic congruence. I investigate the mechanics, limitations, and biases of MRP to assess its suitability for phylogenetic inference. Much of the previous criticism against MRP can be resolved by acknowledging that there are two very different viewpoints as to how phylogenetic information (in the form of trees) should be combined. I call these viewpoints the "node-based" and "tree-based" perspectives. Although MRP appears to be combining trees, it does so in a node-based fashion (i.e., where source trees are "weighted" according to the amount of hierarchical information they contain) and thus can behave very differently from the conventional consensus techniques it is often compared to, which operate in a tree-based fashion (i.e., where source trees are combined equally). Unlike most consensus techniques, MRP can also infer components on the composite tree that were not present on any source tree ("novel clades") and can weight source trees according to some measure of evidential support, although the latter should be done with caution. Together, these characteristics clearly set MRP apart from consensus techniques as used in taxonomic congruence and cause it to resemble character congruence techniques in a number of ways.

Introduction

Baum (1992) and Ragan (1992b) independently devised a method that uses additive binary coding and parsimony to combine trees derived from different data sets, a procedure Ragan termed matrix representation with parsimony analysis (MRP). Because the method utilizes the topology of source trees rather than the original data, 1) trees derived from different data types (e.g., molecular sequences, morphological characters, pairwise distances) and analyzed using different clustering techniques (e.g., maximum parsimony, maximum likelihood, neighbor joining) can be combined, and 2) the source patterns are evaluated on a more-or-less equal basis, so that the phylogenetic signal from data matrices with a smaller number of characters is not swamped by those with a larger number (see Miyamoto, 1985; Hillis, 1987). The method is also unusual in that 1) trees with different terminal taxa can be combined, a feature that among consensus methods characterizes only the supertree method (Gordon, 1986; Steel, 1992) and the semi-strict algorithm as modified by Lanyon (1993), and 2) it is less sensitive to conflict among source trees than are most conventional consensus techniques so that resolution is not necessarily lost as increasing numbers of conflicting trees are analyzed (see also Purvis, 1995b).

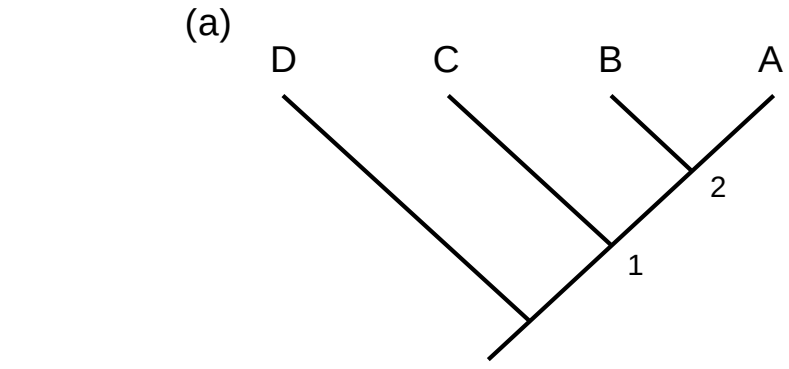
Although the appropriateness of MRP to phylogenetic inference has been discussed (Baum & Ragan, 1993; Rodrigo, 1993, 1996; Bruneau *et al*., 1995) and modifications to the method have been proposed (e.g., Purvis, 1995b; Ronquist, 1996), its properties, mechanics, and biases have not been considered in sufficient depth. I discuss some of the properties of MRP, show how MRP differs from standard consensus techniques, and explore some modifications to the method. Although other clustering methods, such as compatibility (Ragan, 1992a; Purvis, 1995b; Rodrigo, 1996), have also been suggested as methods for generating composite trees by using matrix representation, I will not discuss them.

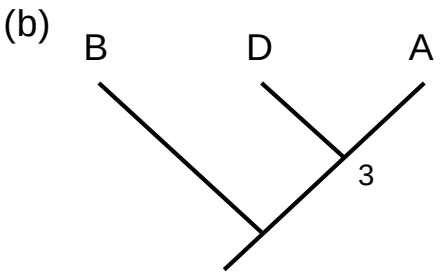
The Basic Procedure and Suggested Modifications

MRP uses additive binary coding (Farris *et al*., 1970) to represent the hierarchical structure of trees as a series of "matrix elements" (Baum & Ragan, 1993:637). Each node (= component; *sensu* Wilkinson, 1994) on each source tree is represented by a binary matrix element, with terminal taxa in the clade delimited by that node scored as 1 and all other taxa scored as 0. Taxa that are missing from an individual source tree are coded as missing for elements that represent that tree. Trees are rooted either by an all-zero outgroup (Ragan, 1992b; Purvis, 1995b) or by using a taxon common to all source trees (Baum, 1992). Parsimony analysis of the element matrix produces a tree or trees (hereinafter, the composite tree[s]; Purvis, 1995a) that most parsimoniously synthesize(s) the hierarchical information in the source trees (for details, see Baum, 1992; Ragan, 1992b). Analyses that generate multiple most-parsimonious composite trees (MPCTs) are summarized by using strict consensus to generate a consensus composite tree (CCT).

Purvis (1995b) argued that the topology of particular source trees can unduly influence that of the composite tree (Figure 3.1). He attributed this to the lack of independence among elements derived from a source tree, which adds redundant information to the matrix. He removed this apparent redundancy by coding taxa that are not in either the clade delimited by the node or its sister taxon as ? rather than 0. As with unmodified MRP (Ragan, 1992b), parsimony analysis of the elements derived from one source tree recovers the correct topology (Purvis, 1995b).

Ronquist (1996) demonstrated that this modification to the coding procedure is flawed. He showed that the information content of matrices generated with Purvis's (1995b) method is less than that generated by standard additive binary coding and demonstrated that Purvis's method does not always achieve its goals. Also, because of the specific manner by which Purvis's coding adds missing data to the matrix, the relative positional stability of taxa is altered (Ronquist, 1996: his Figure 3) so that the position of a taxon on the composite tree is influenced more by source trees on which it is further from the base. I would add that although the zeros replaced under Purvis's method are not





(c)

Taxon	Components 1	2	3
A	1	1	1
B	1	1	0
C	1	0	?
D	0	0	1

Figure 3.1: Purvis's (1995b) conflicting source trees (a, b) (with components numbered), and the combined element matrix (c). MRP analysis of the matrix results in tree a. Purvis's method results in an unresolved CCT.

strictly informative because they denote the lack of membership of taxa in components, they provide essential, *restrictive* information regarding the position of a taxon on its source tree that might become important when its elements are combined with those from other source trees.

Ronquist (1996) concluded that the bias described by Purvis (1995b) was associated, not with redundant information, but with the relative sizes of the source trees. Purvis's method proportionately reduces the influence of larger trees because they contribute a proportionately larger number of missing data points to the element matrix. Ronquist argued that the difference in the amount of information contributed by each source tree could be removed by inversely weighting each tree according to its number of internal branches (= nodes). However, Ronquist favored weighting based on the support for nodes as measured by Bremer's decay index (Bremer, 1988) or the bootstrap (Felsenstein, 1985a), both of which he implied would also compensate for any size bias.

Ronquist's (1996) analyses focused largely on the ability of various coding and weighting options to represent the information in a single source tree (and the original data set), rather than the ability of MRP to appropriately combine the information provided by multiple source trees in a single topology. My discussion focuses more on the latter.

Properties of MRP

Matrix elements versus characters

I have referred to the coded components of source trees as "matrix elements" rather than as "characters" because the two are not equivalent (Baum & Ragan, 1993). Characters are attributes of organisms. In contrast, a matrix element refers to a component of a tree and is a membership criterion. Matrix elements also differ from characters in that groups of elements representing a single source tree are necessarily congruent, forming a clique of elements. Conflicts between matrix elements from different source trees often involve other elements from their respective source trees, with members of each clique of elements supporting one another.

Although characters are also occasionally derived by using additive binary coding, its requisite use in MRP results in non-independence among matrix elements. This non-independence implies that, compared to standard character matrices, goodness-of-fit indices should be interpreted differently (e.g., the CI would have a higher minimum value and would presumably measure the agreement among source trees) and some statistical methods may be inappropriate (e.g., bootstrap analysis; see Felsenstein, 1985b; Purvis, 1995b).

Does MRP combine nodes or trees?

Although MRP is described as a method for combining trees (Baum, 1992; Ragan, 1992b; Purvis, 1995b; Ronquist, 1996), matrix elements represent the nodes on those source trees. As a result, source trees can contribute different amounts of information; trees with more nodes (due to having more taxa and/or greater resolution) contribute more

elements to the matrix and therefore generally have a greater influence on the topology of the composite tree. Thus, the claim that MRP eliminates the effect of data matrix size (Baum, 1992; Ragan, 1992b) applies to the number of characters, but not to the number of taxa.

However, the claim that MRP favors larger source trees (Ronquist, 1996) is inaccurate. Despite the difference in size of the two source trees in Figure 3.2, clade (A,B,C) is unresolved in the CCT (Figure 3.2c) because each source tree provides one (conflicting) piece of information regarding its resolution. The relative number of matrix elements provided by the source trees determines the resolution of regions of conflict ([A,B,C] in this example). The placement of taxa D–H is determined by the larger tree, which provides the only information concerning their positions. In other words, a size bias occurs only when the "missing nodes" (missing taxa or polytomies) are located

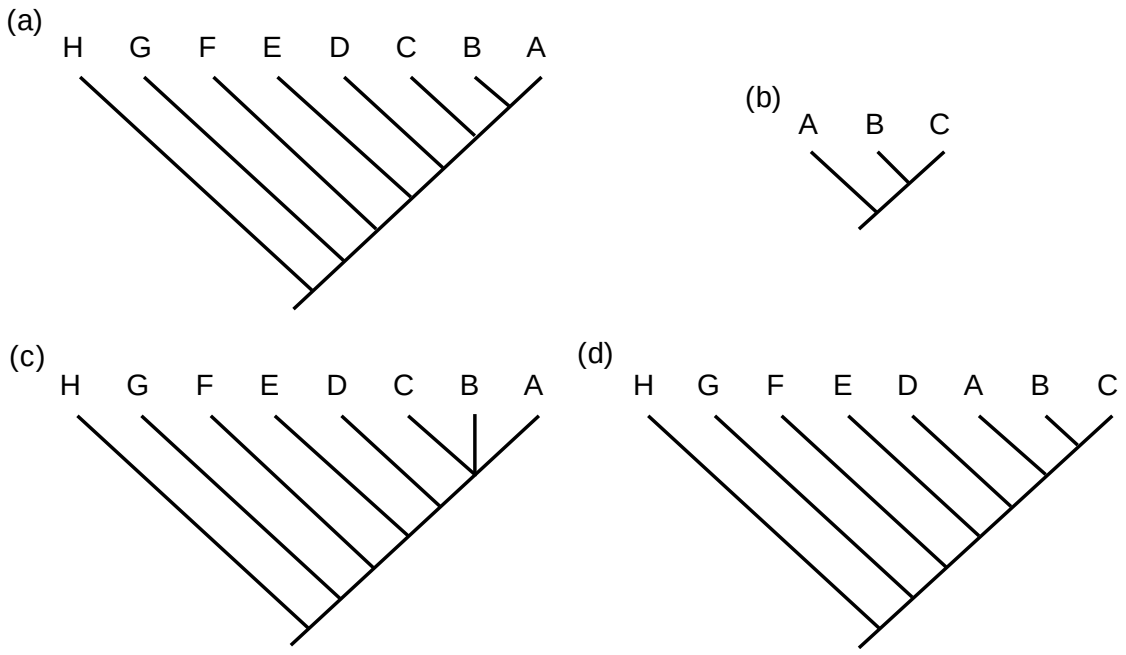


Figure 3.2: Demonstration of the localized nature of the size bias in MRP. Although tree a is much larger than tree b, the CCT (c) is unresolved in the region they share (A,B,C), reflecting the equal information content of the two trees in this region. d) The intuitively erroneous result that results from inversely weighting the source trees according to their number of nodes.

within the region of conflict among the source trees. In Purvis's (1995b) example (Figure 3.1), the region of conflict coincides with the entire tree.

This bias towards trees with more information (nodes) in regions of conflict may or may not be perceived as a problem. Trees with more nodes possess more hierarchical clustering information; this provides the basis for the argument that these trees should have a greater contribution to that region of the composite tree. In Figure 3.1, MRP results in the topology of the larger tree because both elements from Figure 3.1a support (A,B)D and therefore overrule the single conflicting element from Figure 3.1b. From this node-based perspective, whereby trees are viewed as solely the sum of their nodes, any size bias associated with MRP is appropriate.

From a tree-based perspective, however, each source tree is seen as a holistic entity that should have equal input into the topology of the composite tree. Purvis (1995b) noted that no placement of C on Figure 3.1b yields agreement with Figure 3.1a; as a result, he argued that the composite tree should be unresolved and that MRP's bias toward the larger tree was inappropriate. Purvis's (1995b) argument, and this perspective as a whole, tacitly assumes that the addition of C to Figure 3.1b will not alter other relationships on that tree (see also Arnold, 1981; Donoghue *et al.*, 1989; Lecointre *et al.*, 1993), possibly to a pattern more similar to that on Figure 3.1a.

The use of MRP under a tree-based perspective requires that the bias toward trees with more nodes in regions of conflict be corrected for. Inversely weighting elements based on the number of nodes on the source tree so that the total weight of each tree is equal (Ronquist, 1996) fails when the region of conflict forms only part of one or more of the source trees because it ignores the local nature of the size bias. For example, if the nodes on the trees in Figure 3.2 are inversely weighted, the composite tree includes A(B,C) (Figure 3.2d); in contrast, unweighted MRP leaves (A,B,C) unresolved on the CCT, the intuitively correct result. Thus, weighting must be applied only to the conflicting regions between source trees, which becomes increasingly complex as more source trees are combined.

Differentiation between node- and tree-based perspectives is relevant methodologically only when the source trees have different terminal taxa or distributions of resolved nodes. Until recently, techniques that summarized multiple trees on a single topology dealt with multiple equally most parsimonious trees (MPTs) derived from a single data set, among which differences in the number of nodes arose only from differences in resolution. With the development of MRP and other methods that combine trees with different terminal taxa, the question of whether a tree is equal solely to the sum of its nodes (see Adams [1986] for a discussion of this issue within a different context) has become an issue.

Novel components

In the discussion of his composite tree synthesizing previous phylogenetic hypotheses concerning extant primates, Purvis (1995a:414) claimed that "because all of the information on which it is based has been published previously, the composite tree cannot contain any clades that have not been implied by any previous study." Although this statement was intended to apply only to his modified coding method (A. Purvis, pers. comm.), it is also true of most consensus methods, which simply accept or reject components based on the agreement among source trees. One exception is Adams consensus (Adams, 1972), which resolves disagreement among source trees by placing taxa of uncertain position as part of a polytomy at the least inclusive common node (Wilkinson, 1994). In contrast, MRP's use of parsimony to produce the composite tree provides the potential that the incongruence among the matrix elements may generate novel clades. This potential may be increased by MRP's ability to combine trees with different terminal taxa.

In Figure 3.3, the CCT (Figure 3.3c) includes a clade (marked with a solid circle) that is not present in either source tree (Figure 3.3a and b). The CCT resembles Figure 3.3a except that *Pteronura* clusters with *Lutrogale*, as on Figure 3.3b. *Pteronura*'s membership in three components on Figure 3.3b appears to outweigh the evidence for a

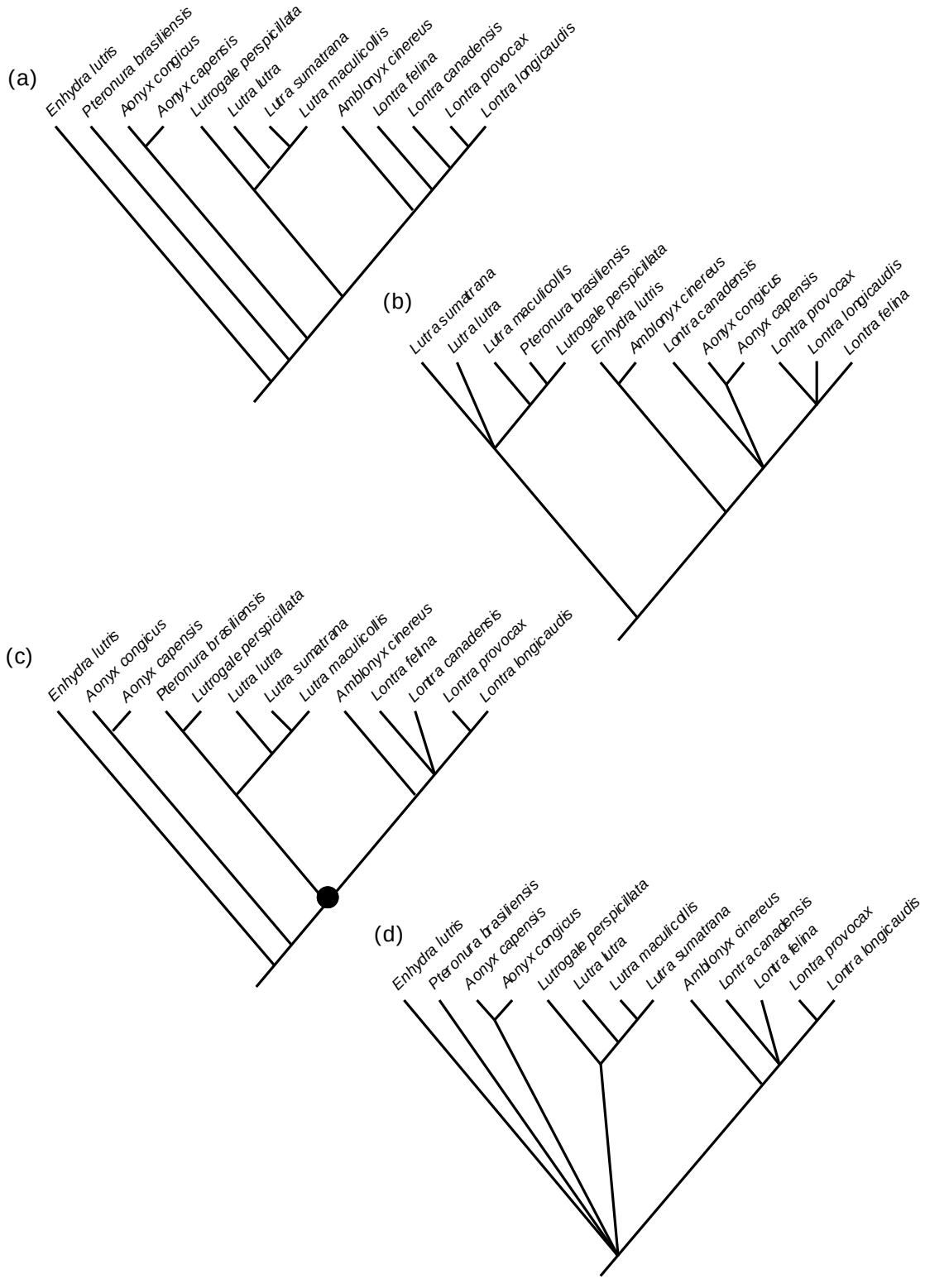


Figure 3.3: Creation of novel components using MRP (lutrine data from van Zyll de Jong, 1987). a, b) Two source trees. c) CCT with a component (●) that is not found in either tree a or tree b. d) CCT generated when reversals are prohibited. The topology is reminiscent of that of an Adams consensus tree.

more basal position (Figure 3.3a). The overall resemblance of the CCT to Figure 3.3a reflects the polytomies (lower information content) in Figure 3.3b.

The creation of novel clades appears to be uncommon. In the carnivore composite tree from Chapter 4, only 8 of the 198 nodes (= 4.0%) on the 13 composite trees occurred on none of the 274 source trees. The apparent rarity of novel clades may be related to the congruence among the matrix elements derived from each source tree, which may reduce the ability of individual elements from different source trees to interact in new combinations to form novel components. Most novel clades found in my analyses occur on only a fraction of a set of MPCTs and therefore are subsumed within a polytomy when the MPCTs are summarized using a strict CCT.

Is MRP a consensus technique?

Although both conventional consensus techniques and MRP combine source trees based on their nodes, there are fundamental differences between them. Most consensus techniques look for the common occurrence of (agreement among) constituent nodes among source trees; conflict usually results in a polytomy (exceptions: majority rule and other consensus trees of the M_l family [McMorris & Neumann, 1983], which retain components found on a certain percentage of the trees). Within source trees, nodes are treated in isolation; individual components are either accepted or rejected (based on information from other source trees) and support for less inclusive nodes by more inclusive ones consists only of allowing those nodes with which they are congruent to occur on the consensus tree. Thus, although standard consensus techniques look for agreement among components, they are tree-based, in that source trees are combined equally, regardless of their size.

In contrast, in MRP, elements representing more inclusive nodes directly support those of less inclusive ones. For example, in Figure 3.1a the grouping of A and B to the exclusion of D is supported by both nodes on the tree: (A,B,C)D and (A,B)C,D. When that tree is combined with the smaller tree, (A,D)B, the composite tree includes (A,B). Using standard consensus techniques the contradiction of (A,B) by the second tree results

in A and B forming part of a polytomy. The latter also occurs using Lanyon's (1993) modified semi-strict consensus algorithm, which can handle trees with different terminal taxa. This feature of MRP results from it being node-based, and arises through the use of additive binary coding to produce the element matrix and parsimony to resolve the incongruence among elements from different source trees.

MRP has often been considered a consensus technique for combining the information in multiple data sets (e.g., DeSalle, 1994; Williams, 1994; Bruneau *et al*., 1995; de Queiroz *et al*., 1995), particularly because it eliminates the effect of differences in character number. Although both MRP and consensus techniques appear superficially to combine trees, clustering them on this basis conceals their different mechanics. Also, the ability of MRP to incorporate information about signal strength in the source matrix (see below) sets it still further apart from consensus techniques. Given the fundamental differences in how MRP combines source trees, I argue that MRP is not a consensus technique.

Other Possible Modifications to MRP

Prohibiting reversals

The use of parsimony algorithms that allow reversals entails that clades in the composite tree can be supported in whole or in part by 0s in the element matrix. Again, in the carnivore composite tree in Chapter 4, between 39 (19.7%) and 81 (40.9%) of the 198 nodes (DELTRAN vs. ACCTRAN optimization respectively) were supported by one or more 0s. A few nodes were supported by more 0s than 1s, particularly under ACCTRAN optimization (Figure 3.4).

Clustering on the basis of 0s seems inappropriate in MRP because support for a clade is based in part on taxa sharing a lack of membership in the components on the source trees. Unlike conventional character data, in which transformation in either direction between character states can be considered potential evidence for clustering taxa, in MRP only the 1s in the element matrix represent membership in components and

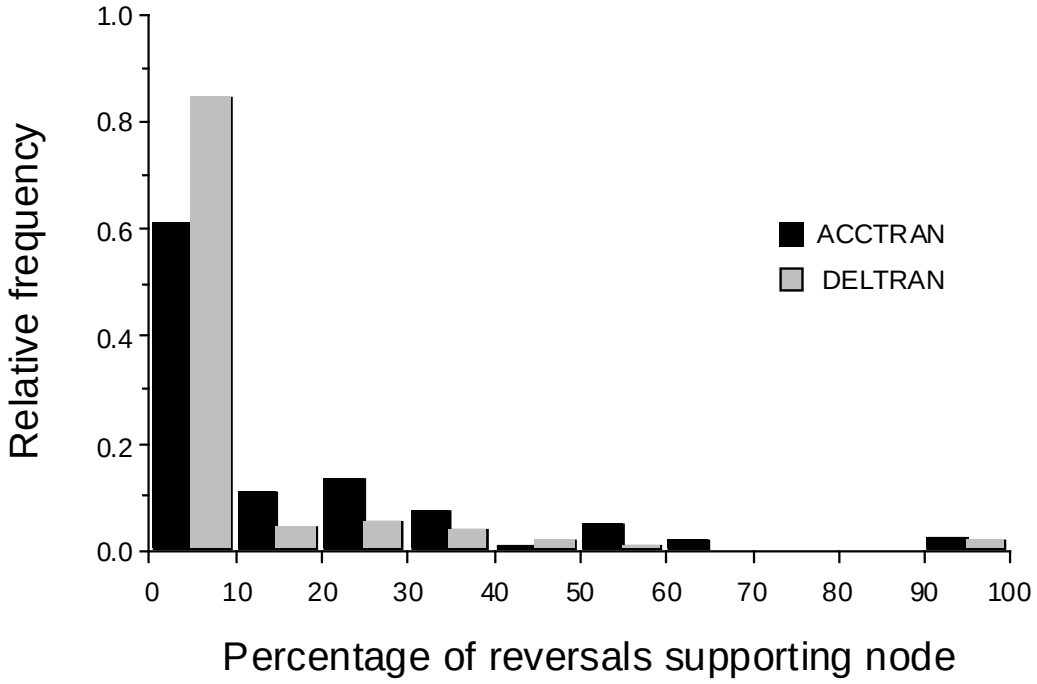


Figure 3.4: Frequency histogram showing the percentage of reversals supporting each of the 198 nodes of the carnivore composite tree in Chapter 4 under both ACCTRAN and DELTRAN optimizations. Most nodes were not supported by any 0s.

therefore seem appropriate for grouping taxa. This suggests that the parsimony algorithm used in MRP should not allow reversals.

To test the effect of prohibiting reversals, I reanalyzed 19 recent "total evidence" studies (*sensu* Kluge, 1989; Table 3.1), using MRP to combine the topologies of the process partitions. Analyses were conducted with and without reversals and differences in topology between the (consensus) composite trees and the total evidence tree were quantified by using the partition metric (Penny & Hendy, 1985). Despite the variation among the 19 studies in partition size, number of taxa, and disagreement among the partition trees, the effect of prohibiting reversals was usually minor. In eight cases, MRP with and without reversals produced the same CCT; in five cases prohibiting reversals yielded a CCT that was more similar to the total evidence tree, whereas in six cases allowing reversals produced a CCT that was closer to the total evidence tree. The topologies with and without reversals were markedly different from each other in only

Table 3.1: Comparison of MRP with and without reversals in 19 total evidence studies. The CCTs obtained from the respective MRP analyses of the partitions were compared with the total evidence topology and each other using the partition metric.

Study	Number of taxa	Number of partitions	With reversals vs. total evidence	Without reversals vs. total evidence	With vs. without reversals
Kluge (1989)	11	2	3	3	0
Vane-Wright *et al*. (1992)	10	2	1	3	2
Cundall *et al.* (1993)	18	3	13	13	0
Eernisse & Kluge (1993)	5	7	1	0	1
Wheeler *et al.* (1993)	26	3	15	17	12
Kim & Jansen (1994)	7	4	2	0	2
Lundrigan & Tucker (1994)	12	3	0	0	0
Omland (1994)	9	2	1	1	0
Vrana *et al.* (1994)	31	2	9	7	4
Yoder (1994)	13	2	7	5	2
Littlewood & Smith (1995)	45	3	9	10	1
Paterson *et al.* (1995)	18	3	6	7	1
Tehler (1995)	5	2	2	1	1
Zhang (1995)	8	2	0	0	0
Bininda-Emonds & Russell (1996)	27	7	22	32	20
Bremer (1996)	33	2	12	16	8
Friesen *et al.* (1996)	25	2	14	14	0
Sites *et al.* (1996) (*Enyalioides* outgroup)	14	3	4	4	0
Sites *et al.* (1996) (*Oplurus* outgroup)	14	3	0	0	0

three instances; two of these (Bininda-Emonds & Russell, 1996; Bremer, 1996) were the only cases where the source trees conflict strongly.

The example in Figure 3.5 may suggest why prohibiting reversals does not necessarily produce the better result. Although allowing reversals produces the intuitively correct result in this example, the reversal (Figure 3.5c) involves only taxon B (i.e., it does not support a clade) and simply represents the incongruence of the position of B on the CCT with that on one of the source trees (Figure 3.5a). This example suggests that

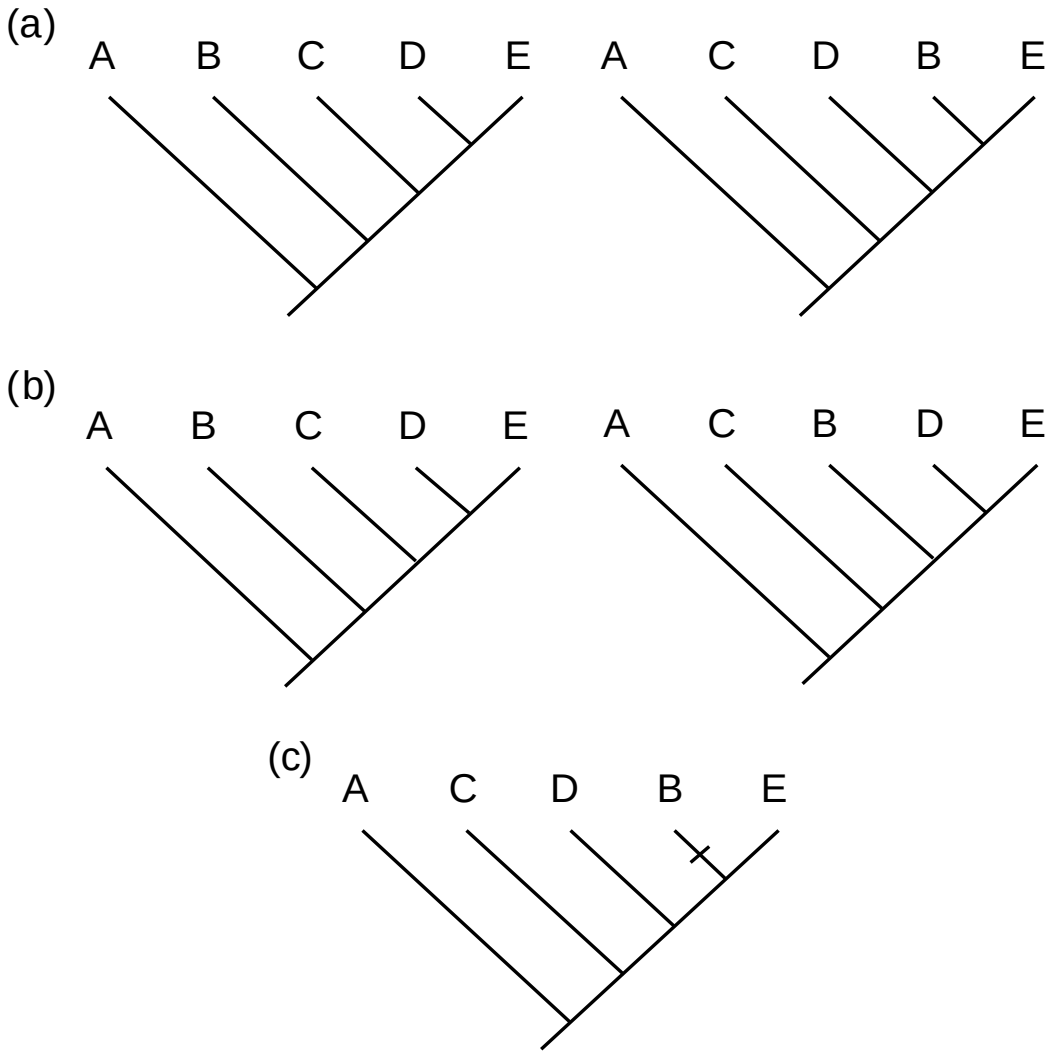


Figure 3.5: Comparison of standard MRP and MRP without reversals. a) Source trees. b) Two equally parsimonious composite trees generated by MRP without reversals. c) Additional tree produced with reversals (location marked with a bar). The three MPCTs based on standard MRP seem to better cover the range of possible positions of taxon B on the source trees.

MRP might perform better if it were based on an algorithm that prohibited reversals on internal branches but allowed them on terminal ones.

The question of whether to allow reversals in MRP analyses requires further study. My sample shows that prohibiting reversals usually produces only minor differences in topology. Prohibiting reversals does not markedly alter the number of novel clades (which may be supported largely by 0s). Reanalysis of the source trees in Chapter 4 with reversals prohibited increased the number of novel clades from 8 to 10. These reanalyses also suggest that MRP without reversals is somewhat conservative, frequently producing a CCT that, like Adams consensus trees, places incongruent components (e.g., Figure 3.3d) or particular members of those components (e.g., taxon B in Figure 3.5) in basal positions.

Increasing the informativeness of source tree polytomies

The number of nodes on a source tree, and consequently the number of matrix elements associated with it, is reduced by polytomies. Thus, for a given number of terminal taxa, trees with more polytomies have relatively less influence on the pattern of the composite tree in regions of conflict than completely dichotomous trees. MRP's use of additive binary coding makes it unable to distinguish between polytomies that are considered "hard" (representing putative multiple speciation events) and those that are considered "soft" (representing either a lack of resolution or conflicting resolutions) (Maddison, 1989); all polytomies are considered unresolved. While this is appropriate for soft polytomies that do represent a lack of resolution, it is inappropriate for polytomies that are purported to be hard, and therefore fully resolved, and for soft polytomies that represent conflicting solutions such as those on a strict consensus tree.

I have no suggestions for counteracting any perceived bias this causes against hard polytomies. Nonetheless, the problems in identifying hard polytomies makes this largely a non-issue. For soft polytomies that represent conflicting resolutions, the goal is to retrieve those resolutions of the polytomy that occur among the MPTs. Although a case can be made for using the consensus solution on practical grounds when there are large

numbers of MPTs (Ragan, 1992b), ideally, the more resolved topologies of the MPTs and not that of the less resolved consensus should contribute to the element matrix.

This can be accomplished by coding each unique component on any one or more trees in a set of MPTs as an element in the combined matrix (see Figure 3.6). These elements can be handled in at least two ways. Weighting each component according to its frequency among the MPTs is the equivalent of Ragan's (1992b) suggestion of individually coding and including each MPT in the element matrix. Using this procedure, the influence of a clade on the pattern of the composite tree depends on its frequency among the MPTs: clades that occur on more of the MPTs will have a greater influence, and any clade occurring on only some MPTs will have less weight in the analysis than clades supported by data sets producing only one MPT. Alternatively, some view the above weighting as inappropriate (H. N. Bryant, pers. comm.). Because each of the shortest trees obtained from a single data set is equally parsimonious, overall evidence in the data set for each clade on any one or more of the MPTs is equal and so they should all receive equal weight.

In either instance, weighting of these elements relative to those based on other source trees is not necessary. Although the number of elements derived from data sets that produce more than one MPT will usually be larger than that associated with a single MPT with the same number of taxa, either the frequency-dependent weighting of, or the incongruence among, elements representing alternative resolutions of polytomies on consensus trees negates the increased influence their increased number might have on the topology of the composite tree (see Figure 3.6).

Weighting elements based on evidential support

Because MRP generates composite trees based solely on the topologies of the source trees, there is no inherent consideration of either the overall support for the topology of a source tree or for the differential support for the nodes on that tree (Rodrigo, 1993; Galtier & Gouy, 1994; Bandelt, 1995; Bruneau *et al*., 1995). Although bypassing the original data is necessary in some instances, it has been argued that the

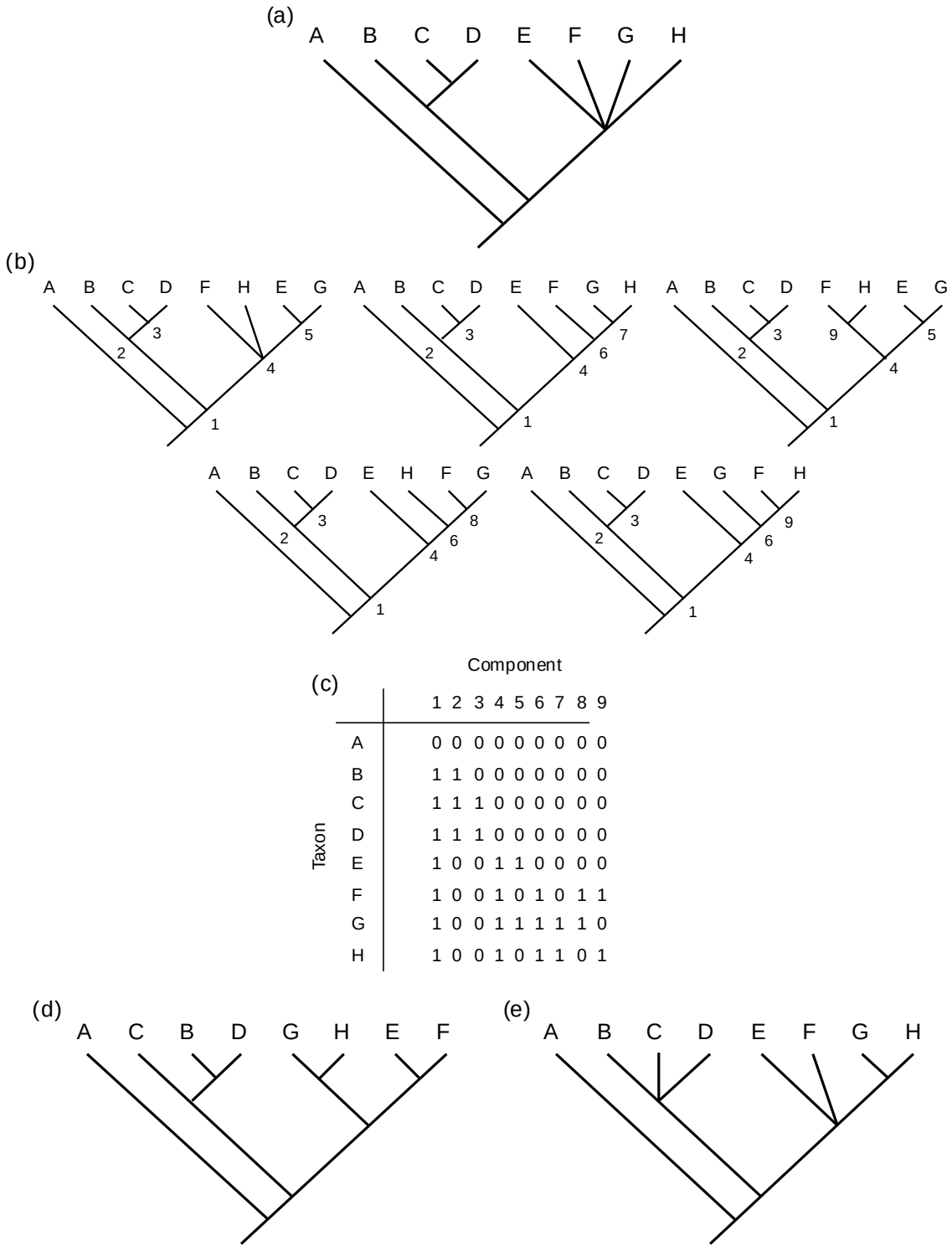


Figure 3.6: One method of coding source trees with polytomies. a) Consensus tree. b) Five MPTs (the nine unique components are numbered). c) Matrix consisting of one element for each of the numbered unique components. d) Conflicting source tree. e) CCT resulting from unweighted MRP analysis of the matrix c and the elements derived from the conflicting source tree d.

differential support for the overall topologies of, or different nodes on, the source trees could or should be used in deriving the composite tree whenever possible (Purvis, 1995b; Ronquist, 1996).

Potential measures of support for entire source trees include goodness-of-fit indices (Farris, 1989; Baum, 1992), PTP values (Faith & Cranston, 1991), or total support (Källersjö et al., 1992). Potential means of weighting based on differential support for individual clades on source trees include bootstrap frequencies (Felsenstein, 1985a), Bremer support (Bremer, 1988), the number of unique synapomorphies (Kluge, 1989), or T-PTP probabilities (Faith, 1991). Ronquist (1996) showed that weighting elements from single source trees based on either Bremer support or bootstrap values improves the correlation between tree lengths obtained from the element matrix and those obtained from the original character data. Weighting by Bremer support also causes the decay values to be reproduced exactly (Ronquist, 1996). Thus, these methods apparently solve a major criticism of MRP, namely, that it fails to incorporate relative support for nodes into the analysis.

The use of any of these measures of support requires that two conditions be met. First, the chosen metric must be available for all source trees. Because source trees lacking the metric should not be ignored, this requirement may preclude the use of weighting based on evidential support in some instances. The use of multiple metrics might be feasible in some of these cases; however, the necessity that they all yield equivalent, standardized information will probably prevent this. Second, the values of the chosen metric must provide a comparable measure of the relative support for a given node across studies, regardless of the characteristics of the original data and the algorithm that produced the source tree. Bremer support, total support, and the number of unique synapomorphies are influenced by the number of characters in the original data matrices and need to be standardized across data sets. Bremer support cannot be used when components on multiple MPTs, rather than those on their consensus, are coded because the Bremer support values for components that do not occur on all MPTs are zero and so their associated elements would have a weight of zero. The bootstrap may be less

influenced by the differential characteristics of data sets (i.e., values are probably more standardized), but this issue requires further study.

Because all these weighting schemes based on support for entire trees or individual nodes operate on the elements in the matrix, they do not offset the inherent size bias of MRP (contra Ronquist, 1996). The problems associated with weighting the element matrix to make MRP tree-based are only compounded if weighting based on evidential support in the original data is also desired.

Closing Statements

MRP is unique in that it combines source trees by using additive binary coding to convert the hierarchical information within them into an element matrix and parsimony to derive the composite tree; these mechanics clearly differentiate MRP from standard consensus techniques despite being associated with them by many authors. MRP is inherently node-based. The influence of individual source trees on the composite tree depends on their size and resolution, and the matrix elements derived from a single source tree directly support one another. As a result, source trees are not combined equally. In contrast, consensus techniques are tree-based. Although they also operate at the node level, components are treated in isolation and are simply accepted or rejected based on the agreement among the source trees. Therefore, all trees have an equal vote regarding the topology of the consensus tree. This difference is fundamental, and is the basis for my conclusion that MRP is not a consensus technique. The difference in both the mechanics and results of MRP, as compared to those of consensus techniques, may require a shift in current thinking as to appropriate methods for combining source trees. At the very least, MRP is providing a different synthesis than consensus techniques of the information in a set of source trees.

MRP has been promoted as a “total evidence approach” (Purvis, 1995b:253) for data sets that are not amenable to standard character congruence methods (e.g., Kluge, 1989). The data in Table 3.1 suggest that MRP often falls short of this goal. In only 3 of 19 cases does the topology produced using MRP match the total evidence tree, and in

several instances the differences between the results of the two methods are marked. MRP tends to collapse clades found on the total evidence tree, producing more polytomies, but taxa are also occasionally placed in different positions. There is no obvious relationship between the number of partitions and the ability of MRP to match the total evidence tree.

The use of parsimony allows for weighting of the matrix elements to adjust for inherent biases in the method or to incorporate additional information. To date, attempts to adjust for any perceived bias toward more informative (i.e., larger and/or more resolved) regions of source trees (e.g., Purvis, 1995b; Ronquist, 1996) to make the method tree-based have been unsuccessful. The appropriateness of correcting for this bias is arguable; however, without this correction, MRP should not be used if a tree-based result is desired. With certain limitations, weighting provides a means of incorporating the differential support for entire trees or individual clades present in the original data into the analysis, while still allowing the composite tree to be based primarily on the hierarchical information in the source trees. These modifications might allow MRP to more closely approximate a “total evidence” result.

Baum (1992) noted that detailed study of the properties of MRP, empirical testing of its results, and comparisons with standard consensus techniques had not yet been conducted. Subsequent analyses (Baum & Ragan, 1993; Rodrigo, 1993; Purvis, 1995b; Ronquist, 1996; this chapter) have considered some of these issues. Issues requiring further study include the appropriateness of allowing reversals within matrix elements (on either all or only terminal branches) and the ability of MRP to replace total evidence analyses when the data are not suitable for the latter. These studies are essential to assess the potential contribution of MRP and its variants to phylogenetic inference.

Chapter 4

A complete phylogeny of the extant Carnivora

(Note: a version of this chapter is in review with Biological Reviews as Bininda-Emonds, O. R. P., J. L. Gittleman, and A. Purvis. Building large phylogenies by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia).)

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Synopsis

I demonstrate the utility of the supertree technique matrix representation using parsimony analysis (MRP) for building larger, more complete phylogenies by deriving a complete phylogeny for all 271 extant species of Carnivora from 177 literature sources. Beyond providing a "consensus" estimate of carnivore phylogeny, the tree also indicates taxa for which the relationships remain controversial (e.g., the red panda; within canids, felids, and hyaenids) or have not been studied in any great detail (e.g., herpestids, viverrids, and intrageneric relationships in procyonids). Times of divergence throughout the tree were also estimated from 74 literature sources based on both fossil and molecular data. The tree will provide a useful foundation for comparative and conservational studies involving carnivores.

Introduction

The benefits of a complete phylogeny for a given taxon (beyond the systematic ones) are clear. Phylogenies underpin comparative biology (Felsenstein, 1985b; Harvey *et al.*, 1996), and trees that are well-resolved, complete, and include estimates of divergence dates allow more powerful tests of a wider range of hypotheses (Harvey & Pagel, 1991). In addition to facilitating general studies of adaptation, complete phylogenies are critical for testing macroevolutionary hypotheses (Purvis, 1996; Mooers & Heard, 1997). For instance, have rates of diversification varied over time or among lineages? Are there any recurring correlates of diversity (e.g., key innovations, environmental or ecological factors, biogeographic events)? Finally, complete phylogenies may have implications for conservation efforts (Humphries *et al*., 1995; Vazquez & Gittleman, 1998).

Attempts to generate complete phylogenies from primary data face two size-related limitations: 1) obtaining sufficient data that are informative for all sets of relationships spanning the history of the group in question and 2) the inability of current computer algorithms to find optimal trees for more than about 20 taxa (Swofford, 1993). The first limitation is perhaps the more serious. Although optimal solutions cannot be guaranteed for analyses with large numbers of taxa, heuristic search algorithms appear to be remarkably powerful (Swofford, 1993), particularly when prefaced by the combination of compartmentalization (Mishler, 1994) whereby large data sets are broken down into more manageable nested subsets, and parsimony jackknifing (Farris *et al*., 1996), which is a fast procedure for detecting well-supported clades.

Despite the recent explosion in phylogenetic studies, the uneven distribution of research effort across taxa and of the resulting phylogenetic information into many individual studies means that homologous data (e.g., the same gene sequences or morphological characters) for all members of a group often do not exist. Furthermore, when such data exist, they frequently cannot resolve relationships throughout the tree, particularly for groups with long evolutionary histories. One solution is a coordinated effort to fill in the missing information. A simpler and more cost effective solution might

be to combine the vast amount of phylogenetic information that already exists, and this is the strategy I employ herein for the carnivores.

The mammalian order Carnivora is a diverse collection of 271 extant species (following Wozencraft, 1993) found on every continent and occupying habitats ranging from oceans to rain forest and deserts. Carnivores range in body size over four orders of magnitude — more than any other mammalian order — and are also notably diverse in their physiology, social structure, and, despite their ordinal name, their feeding ecology. Furthermore, there are marked differences in the current species richness among high-level taxa (e.g., there are 65 mustelids and only four hyaenids).

Recent comparative studies of adaptation in the Carnivora include the evolution of life histories (Gittleman, 1994a); colour patterns (e.g., Ortolani & Caro, 1996); body, brain, and skull size (e.g., Gittleman, 1994b; Gittleman & Van Valkenburgh, 1997); home range size (e.g., Garland *et al*., 1993); energetics and physiology (e.g., Lee *et al*., 1991; McNab, 1995); and social structure (Creel & Macdonald, 1995; Geffen *et al*., 1996). Yet, despite its utility for studying carnivore evolution, no complete species-level phylogeny has ever been assembled for this diverse and varied order. All the above studies were limited by having only a partial or poorly resolved phylogeny of carnivores available that included only a number of key taxa (rarely more than 30) spread throughout the order (e.g., Wayne *et al*., 1989a; Garland *et al*., 1993; Wyss & Flynn, 1993; Vrana *et al*., 1994; Ledje & Arnason, 1996).

I illustrate the utility of matrix representation with parsimony analysis (MRP; Baum, 1992; Ragan, 1992b) for building larger, more comprehensive phylogenies by deriving the first complete species-level phylogeny of extant carnivores based on a thorough survey of the systematic literature from the past 25 years. I also date the nodes in the resulting cladogram as fully as possible, following methods in Purvis (1995a). Although the carnivore "supertree" will facilitate tests of comparative hypotheses, I stress that it is not intended to be the final word in carnivoran phylogeny, but more to provide a working hypothesis, to provoke alternative hypotheses, and to direct more systematic attention to groups that have so far received little or none.

Methodology

Mechanics and limitations of matrix representation

In addition to its potential shortcomings mentioned in Chapter 3, MRP as applied here also has some historically-based limitations. To some degree, the method amounts to a majority rule summary of past and present systematic opinion, and so will be heavily biased against new, non-traditional hypotheses, even if they are now widely accepted. A case in point is the recent contention by Wyss (1987) of a walrus-phocid pairing to the exclusion of otariids. Although currently accepted by many pinniped systematists (e.g., Flynn, 1988; Berta, 1991; Cozzuol, 1992; Wyss & Flynn, 1993; Berta & Wyss, 1994; Vrana *et al*., 1994; but see Arnason *et al*., 1995; Bininda-Emonds & Russell, 1996), this hypothesis has not yet accumulated sufficient support to outweigh the more traditional view of a walrus-otariid pairing. Results from molecular studies would be expected to suffer the most from this bias due to the relatively recent origin of the field.

Additionally, the analyses do not provide a strong test of the monophyly of some taxa because many sources tacitly assume the monophyly of taxa above the species level. I minimized this problem whenever possible by identifying the species being referred to; however, this was often not possible with older references, particularly the more taxonomic ones.

Determination of the composite phylogeny

Potential source trees were identified from on-line searches of the Science Citation Index (1981–1995; via Bath Information and Data Services), Biological Abstracts (1990–1995), and Zoological Record (1978–1995) for any of the keywords cladistic*, clado*, classif*, phylogen*, systematic*, or taxonom* in combination with any major carnivoran taxon name (scientific or common). Additional sources were obtained from references within previously found articles. I restricted the search to between the years 1970 and 1995 inclusive. Exceptions were made only for “landmark” articles (e.g., Gregory & Hellman, 1939; Leone & Wiens, 1956), “in press” articles of which I was aware of by the

end of 1995, and articles for groups (notably herpestids and viverrids) that otherwise yielded too few source trees. Species assignments followed Wozencraft (1993).

My phylogeny explicitly details relationships among extant carnivorans; however, recognizing that fossil information can overturn phylogenetic hypotheses based on extant forms alone (Gauthier *et al*., 1988; Donoghue *et al*., 1989; Novacek, 1992a), I included source trees with fossil and extant species whenever possible.

Source trees were obtained from a total of 177 publications (see Table 4.1 for a breakdown according to family). Only that information which the author(s) indicated to have phylogenetic relevance was used. Where a researcher or group has published a series of papers using virtually the same methodology and data source, only the most recent and complete study was used. However, when different researchers analyzed the same data source, I used each tree because differences in the analyses (e.g., assumptions, use of different segments of the same gene) might change the results between the studies. Finally, when a source contained multiple analyses of a given data set, I combined the results of these analyses into a single source tree using MRP.

Unlike Purvis (1995a), I drew no distinction between source trees based on the type of analysis used to obtain them (but see Chapter 5). Hence, all elements from all source trees received equal weight in the final analysis. Because any choice of weights, including equal weighting, is inevitably subjective (Barrett *et al*., 1991), I also examine the effects of a differential weighting scheme (see Purvis, 1995a).

The size of the problem precluded an efficient single analysis of all species, so composite estimates were made for the following taxa: Canidae, Felidae, Herpestidae, Hyaenidae, Mustelidae (and Lutrinae and Mephitinae therein), Otariidae, Phocidae, Procyonidae, Ursidae (including the giant panda, *Ailuropoda melanoleuca*), and Viverridae, and one linking these taxa plus the monotypic walrus (*Odobenus rosmarus*) and red panda (*Ailurus fulgens*) together ("higher groups"). The nested estimates were combined into a single tree in a process akin to compartmentalization. Most of these groups are widely, if not universally, accepted as monophyletic. The only substantive objections that might be raised lie with grouping *Ailuropoda* with ursids, and the assumed

monophyly of procyonids, mustelids, and viverrids. Despite the historical controversy surrounding the relationships of *Ailuropoda*, the clear majority now hold it to be a primitive ursid (O'Brien *et al*., 1985; see Mayr, 1986 for a summary). Among recent studies, only Peters (1982) and Tagle *et al*. (1986; but see Czelusniak *et al*., 1991) dissent from this view. Support for a monophyletic Procyonidae comes from Seal *et al*. (1970), Baskin (1982, 1989), Wozencraft (1989), and Decker & Wozencraft (1991). While growing evidence exists that mephitines are only distantly related to the remaining mustelids (Arnason & Widegren, 1986; Wayne *et al*., 1989a; Arnason & Ledje, 1993; Vrana *et al*., 1994; Ledje & Arnason, 1996), this claim still requires further substantiation. There is also speculation that the African palm civet (*Nandinia binotata*) may be a primitive feloid, and not a viverrid, based on the primitive morphology of its auditory bulla (Hunt, 1974; Wiig, 1985; Flynn *et al*., 1988; Hunt & Tedford, 1993; Flynn, 1996), but I could not adequately test this hypothesis because the topological disparity of the two hypotheses was difficult to accommodate under the constraints of the nested analysis. Therefore, I constrained *Nandinia* to be a viverrid.

Matrices were constructed using the data editor of MacClade 3.05 (Maddison & Maddison, 1992). A hypothetical all-zero outgroup was added to each to polarize the elements. All matrices were analyzed with PAUP 3.1.1 (Swofford, 1993). The exact branch-and-bound algorithm was used for matrices with fewer than 20 taxa. For larger matrices, I used the approximate heuristic algorithm with a random addition sequence (25 repetitions), TBR branch swapping on minimal trees only (steepest descent on), collapsed zero length branches, and unlimited MAXTREES. Equally most parsimonious solutions were summarized using strict consensus.

Only one search could not be completed due to memory limitations. Initial results for herpestids were highly unresolved (see Figure 4.11a), with at least 30 000 most parsimonious solutions, because many herpestid species have scarcely been investigated systematically. Because the phylogenetic position of many species is unknown beyond a certain level (e.g., subfamilial or generic assessment), MRP indicates all placements within that clade to be equally parsimonious, collapsing the clade to a bush under strict

consensus. To improve resolution within this family, I applied "safe taxonomic reduction" (Wilkinson, 1995) to identify poorly known taxa whose (few) matrix elements were identical with those of one or more of the more completely known species and provided no novel clustering information. Twelve species were identified in this manner and removed from the analysis. However, contra Wilkinson (1995), these species were reinserted into the tree at the most basal position indicated for them in the literature (dashed branches in Figure 4.11b). For example, both *Dologale dybowskii* and *Rhynchogale melleri* are known to be herpestines, but no study has placed them any more precisely, so both taxa were added to the basal node of this subfamily. Such placements do not strictly reflect phylogeny (although weak membership statements can be made from them), but rather identify poorly studied taxa, much like Adams consensus (Adams, 1972) identifies "rogue" taxa among many competing source trees. Although the same lack of information applied to the intrageneric relationships of procyonids (see Figure 4.5), safe taxonomic reduction could not improve the resolution there.

I use Bremer support (Bremer, 1988; Källersjö *et al*., 1992) to estimate the robustness of each node in the composite tree. Bremer support indicates how much less parsimonious the tree would have to be before the clade in question disappears. Bremer support depends on how many characters or elements there are (Novacek, 1991) and how well they agree, so values may be low because of small numbers of source trees or conflict among them (see Results and Discussion).

Establishing times of divergence

Following Purvis (1995a), a combination of absolute (fossil and point molecular estimates) and relative (molecular) dates from the literature were used to date the composite tree. Both kinds of data present inherent difficulties.

No clear guidelines have emerged for estimating times of divergence from the fossil record. I followed Wayne *et al*. (1991) in using the time of first occurrence of either descendant lineage, unless there was good phylogenetic or biogeographic evidence to the contrary. One problem with fossil information is the greater instability of fossil

systematics. This reflects 1) changes in phylogenetic opinion caused by the discovery of new species or of additional material for poorly known species, and 2) that fossil species are frequently grouped taxonomically rather than phylogenetically. (Similar problems affect analyses of extant forms, but are generally less severe.) Taxonomic groupings tend to be unstable at many levels (e.g., tribe, subfamily), something also arising from shifts in phylogenetic opinion. Thus, the context of a taxon might have changed since a fossil species was assigned to it. For example, Viverridae long included mongooses and kin as the subfamily Herpestinae. Recently, however, mongooses have been accorded sister status to viverrids (as Herpestidae). Thus, when using fossil information that predates this taxonomic change, one must ensure that the fossil "viverrid" is what we would recognize as a viverrid today.

Furthermore, not all fossil information is usable in the current context. The absence of fossil species in the phylogeny means the divergence estimated by many fossils will not be present, particularly those that predate the most recent common ancestry of the extant taxa. For example, *Hesperocyon* is widely regarded as the oldest known canid, but since it is not a member of the clade including extant forms (Savage & Russell, 1983; Wang, 1994), its time of first occurrence cannot be used to date their radiation. Information from *Hesperocyon* would, however, be appropriate for dating the divergence of all canids from the remaining caniforms.

Altogether, these problems necessitate care to be exercised when using fossil dates. My general strategy was to use information from relatively well known and stable fossil species only and then to use it to establish divergence times for nodes equivalent to the more robust taxonomic levels (generally families and genera).

The use of molecular data to derive times of divergence is hampered by different lineages evolving at different rates (Gillespie, 1991; Wayne *et al*., 1991; Flynn, 1996) and evidence of a decrease in the rate of change with increasing divergence times (Wayne *et al*., 1991; Gittleman *et al*., 1996). As such, calibrating molecular information to a few widely spaced nodes of known age will likely lead to correlated errors (and typically underestimates; Wayne *et al*., 1991) throughout the tree. As in Purvis (1995a), the concept

of a local molecular clock (Bailey *et al*., 1991) was employed to minimize potential errors. Briefly, this method estimates the date of a node relative to some (not necessarily immediately) ancestral node based on relative branch lengths (see Purvis, 1995a for more detail and a worked example). Whenever possible, the branch lengths I used for this were derived from the original pairwise matrices in the source paper.

A total of 74 studies yielded 545 point estimates (293 fossil, 236 molecular, and 16 from a study assimilating both types) for 150 nodes throughout the tree. To minimize the effect of outliers, the divergence time for a node was calculated as the median of available estimates. Whatever their source, estimates of divergence time are likely to be underestimates. Fossil dates will consistently be so because the first appearance in the fossil record need not correspond with the origin of a taxon (Marshall, 1990; Flynn, 1996). This bias will, in turn, affect the relative molecular estimates, as I calibrated such estimates against fossil dates. The negative correlation between divergence time and the rate of molecular change further compounds this problem for molecular estimates, particularly when calibrations are based on only a few nodes. I therefore incorporated fossil dates throughout the tree (unlike Purvis, 1995a).

Finally, dates for those nodes that did not possess an estimate in the literature were interpolated using a pure birth model, under which a clade's age is proportional to the logarithm of the number of species it contains (see Purvis, 1995a:416). Estimates were calibrated relative to dated ancestral and, unlike Purvis (1995a), from dated descendent nodes whenever possible. The use of more than one calibration point should reduce errors associated with erroneous dating of calibration points. My interpolations are intended more to accommodate those comparative methods requiring a complete set of branch lengths than as precise estimates of divergence times.

Results and discussion

Distribution of taxonomic coverage

Prior systematic effort has not been distributed evenly throughout carnivores (Table 4.1). The groups for which there are most source trees include canids, felids,

Table 4.1. Indices relating to the distribution of taxonomic coverage for and the resolution on the composite tree of various carnivoran taxa. The parenthetical value of percent resolution for the herpestids refers to when "safe taxonomic reduction" (Wilkinson 1995) was used to improve the resolution of this family (see Figure 4.11b). I refer to the index elements per source tree per taxon as the "coverage index" in the text.

Taxon	Number of source trees	Number of elements	Percent resolution	Elements per taxon	Elements per source tree per taxon
"higher groups"	62	202	100.0	16.8	0.27
Mustelidae	30	155	72.7	3.4	0.11
Lutrinae	6	37	75.0	2.8	0.47
Mephitinae	5	18	87.5	2.0	0.40
Procyonidae	7	27	52.9	1.5	0.21
Otariidae	15	46	69.2	3.3	0.22
Phocidae	21	120	94.4	6.3	0.30
Ursidae	28	50	85.7	6.2	0.22
Canidae	36	180	69.7	5.3	0.15
Felidae	40	282	97.1	7.8	0.20
Hyaenidae	6	8	66.7	2.0	0.33
Herpestidae	9	53	27.8 (55.6)	1.4	0.16
Viverridae	9	90	97.0	2.6	0.29

mustelids, phocids, ursids, and the interfamilial relationships of carnivores. This uneven distribution of effort has many causes. Geographic distribution (largely Africa and southern Asia) and a low profile both count against herpestids and viverrids, whereas some families have been targeted by particular research groups (e.g., U. Arnason & colleagues for phocids, S. J. O'Brien & colleagues for felids, R. K. Wayne & colleagues for canids), often with conservation in mind. Additionally, researchers have been attracted to groups whose relationships are controversial. Finally, many species that are poorly known systematically are also unstudied with respect to other biological characteristics. It is unsurprising that most of these species are nocturnal, solitary, fast, and have large home ranges, often in poorly inhabited or remote regions (see Gittleman, 1989a, 1996).

The groups that have been studied the most often also tend to have the most binary elements per taxon. However, this latter measure does distinguish among the more poorly studied groups, with herpestids and procyonids lagging behind the rest.

A final measure, the "coverage index" (i.e., elements per source tree per taxon), reveals how thoroughly a group has been investigated in each study. High values indicate that individual studies have on average examined a large proportion of the constituent taxa (although the number of elements is also determined by the resolution of the source tree). Hyaenids, lutrines, mephitines, and phocids have high coverage indices. Except for phocids, these groups did not have many source trees. Groups with low coverage indices include canids, felids, herpestids, and mustelids. Note that a low coverage index does not necessarily imply that only the same few taxa have been examined in each tree (although this is true of herpestids). Given the inherent difficulties in examining a larger number of taxa, it is unsurprising that smaller taxa tend to have higher coverage indices than larger ones ($r^2 = 0.43$, $p = 0.01$).

The numbers for viverrids are deceptive. This family has been poorly studied, except for one complete species-level phylogeny (Wozencraft, 1984). Without this study, the number of elements for viverrids would drop by over a third and the two ratios would fall to the levels found in other poorly studied taxa. The exclusion would also improve the correlation between the coverage index and the size of the group ($r^2 = 0.51$, $p = 0.006$).

Resolution and robustness

The composite tree (divided among Figures 4.1–4.12; presented as a whole in Figure 4.13) contains 211 nodes, making it 78.1% resolved compared to a fully bifurcating solution. Resolution varies among groups, ranging between 27.8% (herpestids) and 100% (higher groups) (Table 4.1). Removing the poorly known herpestid species (see Methodology) improves the resolution for this family to 55.6%. Apart from herpestids, the poorest resolution was for Procyonidae (52.9%). Most groups were at least 70% resolved, and three (felids, phocids, and viverrids) were more than 90% resolved. However, for

viverrids, this resolution is again due to Wozencraft's (1984) full species-level analysis. If this study were excluded, resolution for the family would fall to 69.7%.

The poor resolution for procyonids is restricted to within the genera *Bassaricyon* and *Procyon* and arises not from conflict between the source trees but from a complete lack of information. This may reflect suggestions that there are fewer legitimate species than are currently recognized (e.g., Poglayen-Neuwall & Poglayen-Neuwall, 1965; Lotze & Anderson, 1979; Hall, 1981; Olson & Pregill, 1982).

Bremer support values differed significantly among groups (Kruskal-Wallis H = 48.4, $p < 0.0001$). Taxa with large values are the higher groups, hyaenids, phocids, and ursids; only herpestids display low values. Older nodes tend to show higher Bremer support values ($r^2 = 0.17$, $p < 0.0001$) because relationships at these levels are more agreed upon and better studied. Many phylogenies, particularly molecular ones, detail relationships among somewhat distantly related species. This provides information at the older, higher levels, but none for the more closely related sister species that are missing from the analysis.

The differential weighting of source trees according to the data and/or methodology used to obtain them had little impact on the composite tree (Tables 4.2–4.13). When more robust source trees (following Purvis, 1995a) were weighted four times as heavily, only 10 of the 198 nodes of the composite tree that could be contradicted were, most often due to a slightly altered position for a single clade (which automatically results in two, non-independent contradictions). Differential weighting also resolved six polytomies within the composite tree. This extra resolution is not surprising given that weighting certain elements essentially amounts to increasing their number within the matrix, which has been demonstrated to increase resolution (Hillis & Huelsenbeck, 1992; Wheeler, 1992). However, three nodes within herpestids collapsed under the differential weighting scheme, including the basal node for *Herpestes* (Table 4.12). To summarize, it seems that most source trees are giving the same general pattern of carnivore phylogeny, regardless of the data or methodology used to generate them.

Similarly, using MRP with reversals prohibited (see Chapter 3) did not alter the topology of the composite tree substantially: only 16 nodes were contradicted, 20 were collapsed, and 5 were resolved (Tables 4.2–4.13). Many of the contradictions (5) occurred along the backbone of the felid tree, a region of the tree that was not well supported in the original analysis (Table 4.11; Figure 4.10; see below); the topology within the major felid groups was otherwise unaltered. These findings reiterate the claim I made in Chapter 3 that prohibiting reversals in MRP has minor effects only, most of which are to collapse regions of weak support into basal polytomies.

Times of divergence

Date estimates were obtained from the literature for 150 nodes on the composite tree, 73 of which had at least one estimate from both fossil and molecular sources. Four families plus the higher level relationships had date estimates for every node, with all remaining families except herpestids and viverrids having at least 66% coverage. For these latter two families, date estimates were only available for 8 out of 20 (40.0%) and 7 out of 32 (21.9%) nodes respectively.

Errors in median dates were reasonable, with "coefficients of variation" (calculated relative to the median and not the mean) exceeding 100% for only 12 nodes of the 105 that possessed two or more date estimates. Using a one-way analysis of variance of log transformed dates with node number as the grouping factor (see Purvis, 1995a for more detail), the error for the 45 nodes with only a single date estimate was calculated as ±80%. Fortunately, the effect of all these errors on comparative studies should be minimal, given that all estimates are likely to be underestimates and that comparative methods are fairly robust in such cases (Purvis *et al.*, 1994; Purvis, 1995a).

Generally, nodes with higher "coefficients of variation" were 1) relatively recent, making any error proportionately larger or 2) those whose dates were derived from very few estimates, allowing a single discrepant estimate to inflate the standard deviation (and hence my reason for using medians rather than means). Naturally, there are exceptions. For example, despite the nodes for ursine bears (node 3 on Figure 4.8), the genus

Panthera (node 11 on Figure 4.10), and that uniting *Alopex* with *Vulpes velox* (node 20 on Figure 4.9) being strongly supported and having dates estimated from a relatively large number of sources (e.g., 17 in the case of ursine bears), the "coefficients of variation" in each case exceeded 100%.

Eleven of the 236 molecular estimates were single point estimates and so could not be re-calibrated. The remaining molecular estimates were calibrated against a total of 56 nodes. The nodes used most often for calibration include the basal node for the Arctoidea (20 estimates), the canid-arctoid divergence (17), the caniform-feliform divergence (15), and the basal nodes for many families (e.g., mustelids, phocids, ursids). Nodes with only a single date estimate (either fossil or molecular) were used as calibration points on only five occasions and none was used to calibrate more than two nodes.

Twenty-two nodes were estimated to be older than an ancestral one (resulting in a negative branch length). In most (15), the difference was less than 100% of the age of the ancestral node. The largest discrepancy was 770% (nodes 21 and 22 in Mustelidae [Figure 4.2; Table 4.3]). Felids and mustelids had the largest number of negative branch lengths with six apiece. The basal nodes for felids, herpestids, and phocids, upon which molecular estimates within these families largely depend, were indicated to be more recent than a descendent node. The consistency of dates within herpestids and viverrids probably arises from there being very few date estimates for either family.

Negative branch lengths normally arose in one of two ways. First, they were more likely if at least one of the dates was based on three or fewer estimates or was derived from the pure birth model. Such dates tend to have larger confidence intervals, so many of the negative branch lengths are simply overlapping regions of uncertainty. The second way applies only to dates derived from fossil information and occurs when a well-recognized clade, believed to be relatively ancient, is in a fairly terminal position within the phylogeny. Some taxa with good fossil records were indicated to have (frequently monotypic) sister groups with a poor one. Therefore, the time of divergence may be a vast underestimate when taken to be the time of first occurrence of the apparently much younger sister group. This problem is exacerbated if the crown clade of an ancient lineage

has diversified only recently. Dates obtained solely from molecular sources frequently resolved the inconsistency; however, such estimates were not always available.

Fossil versus molecular dates

Are fossil and molecular estimates of divergence times similar? Wayne *et al.* (1991) showed that molecular distance data are highly correlated with fossil estimates of divergence time within carnivores and primates. However, fossil and molecular estimates could be highly correlated and yet still differ systematically. I examined this possibility by considering the 73 nodes that possessed at least one estimate from both fossil and molecular sources.

Initial results gave a weakly significant difference (paired *t* of log-transformed dates = -2.21, $p = 0.03$). However, this finding depends upon how the molecular estimates are calibrated. In the above case, I used two (absolute) molecular estimates of the time of the caniform-feliform divergence. One estimate (52.0 million years before present [MYBP]; Sarich, 1969b) was derived from an albumin clock calibrated with primate data while the other (40.6 MYBP; Goodman *et al.*, 1982) used a molecular clock of many different proteins calibrated using an estimate of 90 MYBP for the common ancestor of all extant eutherian mammals. Thus, the average calibration point (46.3 MYBP) was independent of the carnivore fossil record. This does not seem appropriate given that different lineages evolve at different rates (Gillespie, 1991; Wayne *et al.*, 1991; Flynn, 1996) and any rate anomalies peculiar to carnivores would therefore likely be missed.

When the molecular estimates are calibrated against the carnivore fossil record (using the median estimate of 55.0 MYBP obtained from the fossil sources), they now clearly provide significantly older estimates (paired *t* of log-transformed dates = -3.71, $p = 0.0004$). This seems reasonable given that fossil estimates will nearly always be underestimates of the true time of divergence (Marshall, 1990; Flynn, 1996). I add that although both differences are significant, they are small. Back-transforming shows the mean difference in dates between the two sources to be either 1.3 or 1.5 million years, depending on the calibration point used. In a majority of cases, these values are smaller

than the standard errors associated with either data source for a given node (results not shown).

The discrepancy between the two tests stems from Goodman *et al.*'s (1982) date for the divergence of (extant) carnivores being substantially more recent than both Sarich's (1969b) and the fossil estimate. This arises from their use of a calibration point of 90 MYBP for the origin of extant eutherians, a figure now held to be at least 30 million years too recent (Graur, 1993; U. Arnason, pers. comm.). Although I used the original date estimate for the divergence of carnivores advocated by Goodman *et al.*, it is interesting that using the currently held value of 120 MYBP for the calibration point shifts Goodman *et al.*'s value to 54.1 MYBP in agreement with the other estimates. At the very least, this highlights the importance of using an accurate calibration point to derive divergence times using molecular data.

Systematic implications

Detailed comments concerning all proposed relationships specified by the composite tree are beyond the scope of this paper. Instead, I highlight some results in areas of particular historical interest. The composite tree is merely a (most parsimonious) synthesis of a number of source trees; therefore, direct evidence supporting (or refuting) particular relationships on the composite tree should be sought from the original references.

Among higher groups (Figure 4.1), two long-standing areas of contention concern the relationships of the red panda (*Ailurus fulgens*) and those of pinnipeds. The composite tree places *Ailurus* as the sister group to the clade of mustelids plus procyonids, a relationship advocated directly by only Braunitzer & Hofmann (1987). In part, this unusual placement reflects the support for an *Ailurus*-procyonid clade (four source trees), but one that is outweighed by ten source trees linking mustelids and procyonids with no statement regarding *Ailurus.* Interestingly, more source trees (11) advocate allying *Ailurus* with ursids, but this solution is not globally most parsimonious. It should be noted

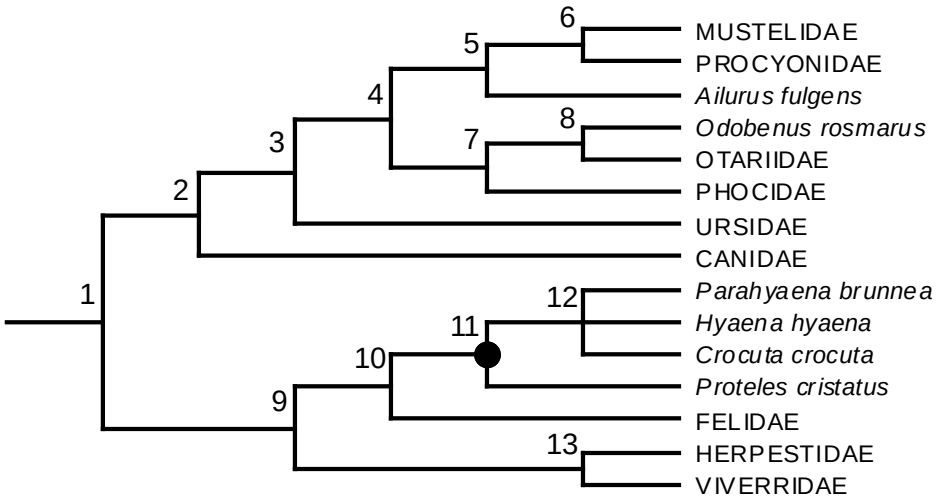

Figure 4.1: The composite tree for the higher groups of carnivores plus Hyaenidae (which was assumed to be monophyletic as denoted by the solid circle, ●). Node numbers refer to Table 4.2. In this and Figures 4.2–4.12, branch lengths are not proportional to time.

that support for the placement of the red panda in the composite tree is exceptionally weak compared to the remaining nodes at this level (Table 4.2). Pinnipeds are held to be monophyletic in agreement with current opinion, but with an unusual sister group: Musteloidea (plus *Ailurus*) in place of the more commonly suggested ursids. The composite tree also shows strong support for the traditional Otarioidea (odobenids plus otariids), in contrast to Wyss's (1987) recent assertion of an odobenid-phocid pairing.

Within mustelids (Figure 4.2), the monophyly of the classic Simpsonian subfamilies (Lutrinae, Melinae, Mellivorinae, Mephitinae, Mustelinae; Simpson, 1945) are upheld with the possible exception of badgers (Melinae) and ignoring the monotypic Mellivorinae. Although no definite statement can be made regarding the cladistic status of the former subfamily, the position of the meline taxa at the base of the tree suggest that it might have been originally erected on the basis of shared primitive features (symplesiomorphies). In the analyses, mephitines (skunks) were constrained to be mustelids; however, the large negative branch length around this region (Tables 4.3 and 4.5) suggests a more ancient origin of this group and may support the paraphyly of Mustelidae (e.g., Arnason & Widegren, 1986; Wayne *et al*., 1989a; Arnason & Ledje,

Table 4.2. Statistics relating to the times of divergence of and support for the nodes of the composite tree for the "higher groups" of carnivores plus the Hyaenidae (assumed to be monophyletic) (see Figure 4.1). All divergence times are in millions of years before present. Both median and mean estimates for a number of date estimates from the literature (*n*) are presented as is the standard error of the mean (SE). Dates proportional to the logarithm of the number of species in the clade ("birth model"; see text) are given for nodes without a literature estimate. The best estimate for a node is the literature estimate or, secondarily, the birth model estimate corrected for negative branch lengths. Results for "differential weighting" or "reversals prohbited" refer to whether or not a node was retained when the weighting scheme of Purvis (1995a) was applied or reversals were prohibited, respectively. Unless otherwise indicated, the node was retained unaltered under these alternative weighting schemes.

	Literature estimates				Birth	Best	Bremer	Differential	Reversals
Node	*n*	median	mean	SE	model	estimate	support	weighting	prohibited
1	6	53.8	53.6	3.1		53.8	n/a		
2	16	41.5	41.1	2.2		41.5	24		
3	14	36.0	37.1	1.7		36.0	13		
4	2	35.5	35.5	0.5		35.5	1	no	no
5	9	29.3	27.9	2.5		29.3	1	no	no
6	6	28.1	29.4	2.1		28.1	4		
7	11	24.0	23.7	2.1		24.0	14		
8	5	14.2	18.2	4.8		14.2	9		
9	12	37.6	35.4	2.1		37.6	20		
10	13	35.0	32.7	2.5		35.0	2		
11	3	17.5	17.5	0.0		17.5	n/a		
12	5	10.0	9.2	1.3		10.0	4		
13	9	32.5	33.8	1.4		32.5	4		

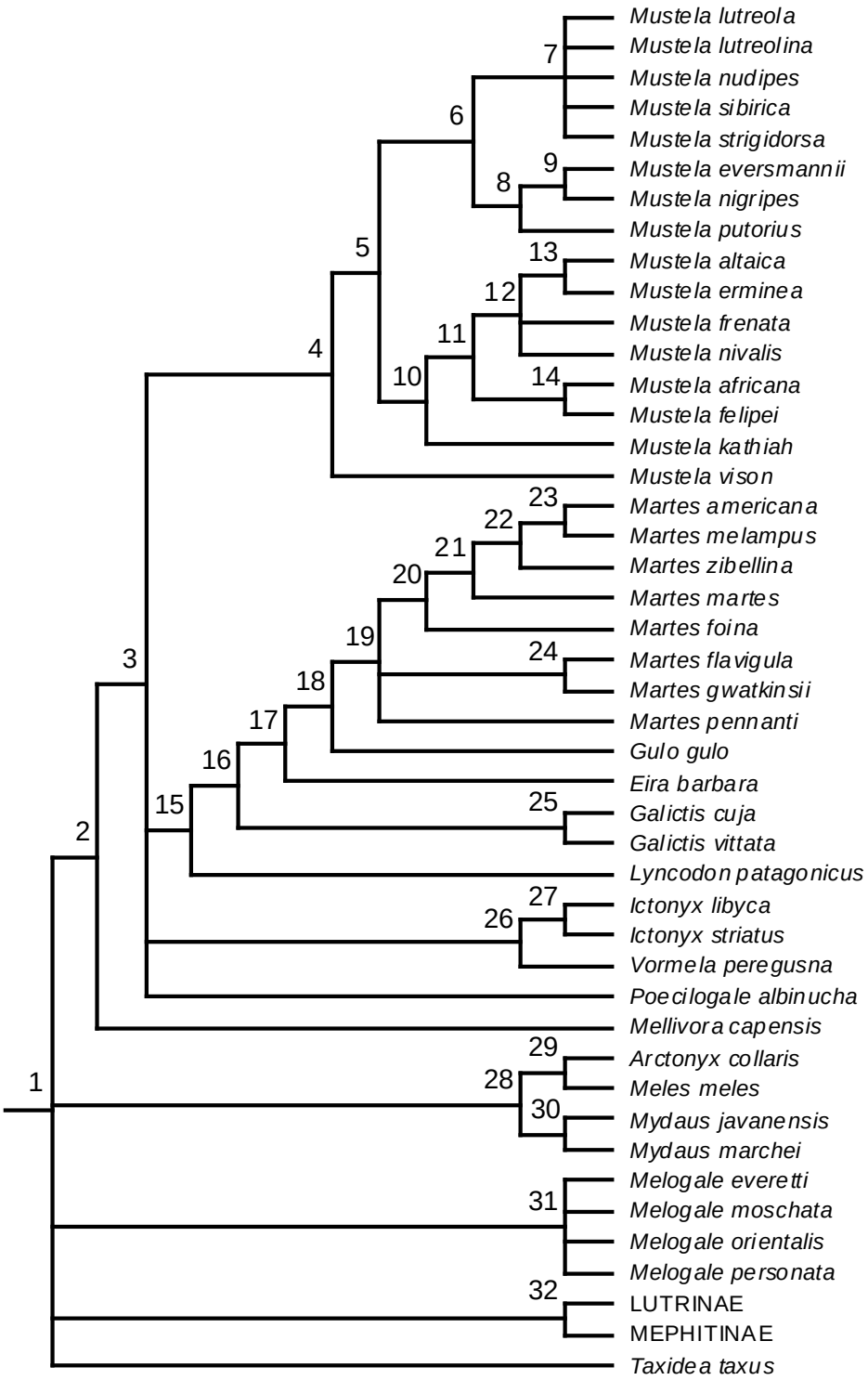

Figure 4.2: The composite tree for the Mustelidae (exclusive of the Lutrinae and Mephitinae). Node numbers refer to Table 4.3.

Table 4.3. Statistics relating to the times of divergence of and support for the nodes of the composite tree for the Mustelidae (exclusive of the Lutrinae and Mephitinae) (see Figure 4.2).

Node	Literature estimates				Birth	Best	Bremer	Differential	Reversals
	n	median	mean	SE	model	estimate	support	weighting	prohibited
1	10	20.8	20.8	1.5		20.8	n/a	resolved	
2	2	8.2	8.2	0.0		11.4	2		collapsed
3	6	14.6	13.6	1.8		11.4	2		collapsed
4	3	10.4	10.7	2.0		10.4	3		
5	5	4.4	5.5	1.4		4.4	3		
6	2	2.8	2.8	0.7		2.8	1		
7	1	0.2	0.2	–		0.2	1		
8	4	2.8	3.0	1.3		2.8	4		
9	3	0.2	0.5	0.3		0.2	3		
10	0	–	–	–	3.4	3.4	1		
11	0	–	–	–	3.1	3.1	1		
12	4	2.6	2.5	0.6		2.6	1	no	
13	1	1.2	1.2	–		1.2	1		
14	0	–	–	–	1.1	1.1	2		
15	0	–	–	–	6.9	8.2	3		collapsed
16	0	–	–	–	6.7	8.2	1		no
17	0	–	–	–	6.2	8.2	1		no
18	1	2.6	2.6	–		8.2	1		collapsed
19	2	18.7	18.7	4.2		8.2	6		
20	3	0.2	0.5	0.4		1.8	1		
21	2	0.6	0.6	0.4		1.8	1		
22	2	4.8	4.8	4.1		1.8	1		
23	1	0.3	0.3	–		0.3	1		
24	1	0.9	0.9	–		0.9	1		
25	1	1.8	1.8	–		1.8	4		

Table 4.3. Continued.

Node	Literature estimates				Birth model	Best estimate	Bremer support	Differential weighting	Reversals prohibited
	n	median	mean	SE					
26	1	4.2	4.2	–		4.2	1		
27	1	0.3	0.3	–		0.3	1		
28	0	–	–	–	13.7	13.7	1		
29	2	10.2	10.2	2.1		10.2	3		
30	0	–	–	–	3.5	3.5	6		
31	0	–	–	–	6.9	6.9	3		
32	2	14.9	14.9	3.6		17.1	4		

1993; Vrana *et al*., 1994; Ledje & Arnason, 1996). Relationships within mustelids are generally not strongly supported (Tables 4.3–4.5). All subgenera of *Mustela* (see Youngman, 1982; Nowak, 1991) are indicated to be monophyletic except the nominal subgenus (species *altaica*, *erminea*, *frenata*, *kathiah*, and *nivalis*) (Figure 4.2). Within otters (Figure 4.3), *Lutra* is polyphyletic and there is much uncertainty regarding the relationships among the major lineages. Among mephitines (Figure 4.4), the South American species of *Conepatus* (*chinga*, *humboldtii*, and *semistriatus*) do not form a single clade.

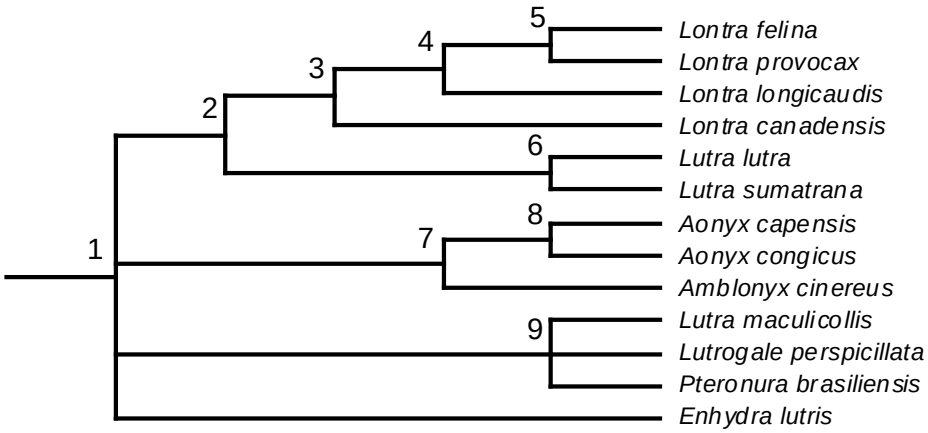

Figure 4.3: The composite tree for the Lutrinae. Node numbers refer to Table 4.4.

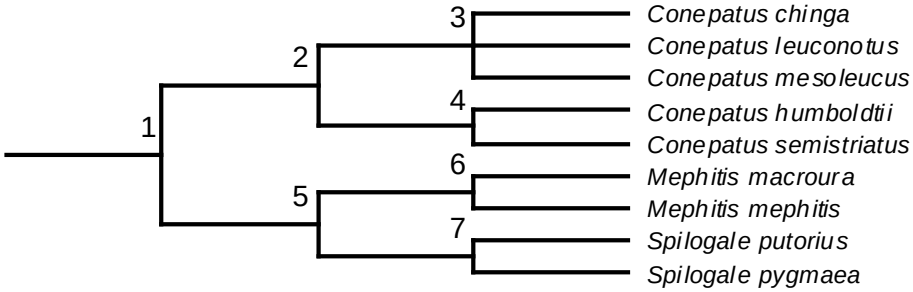

Figure 4.4: The composite tree for the Mephitinae. Node numbers refer to Table 4.5.

Procyonids are divided into their two recognized subfamilies with all relationships receiving intermediate support (Figure 4.5; Table 4.6). The lack of resolution within *Bassaricyon* and *Procyon* reflects a complete lack of information as noted previously.

Table 4.4. Statistics relating to the times of divergence of and support for the nodes of the composite tree for the Lutrinae (see Figure 4.3).

	Literature estimates				Birth	Best	Bremer	Differential	Reversals
Node	*n*	median	mean	SE	model	estimate	support	weighting	prohibited
1	2	9.9	9.9	1.7		9.9	n/a	resolved	resolved
2	1	7.0	7.0	–		7.0	1		
3	1	1.2	1.2	–		1.2	6		
4	0	–	–	–	1.0	1.0	1		collapsed
5	0	–	–	–	0.6	0.6	1		collapsed
6	1	0.2	0.2	–		0.2	2		
7	0	–	–	–	4.2	4.2	3		
8	1	2.6	2.6	–		2.6	4		
9	1	0.3	0.3	–		0.3	1	resolved	resolved

Table 4.5. Statistics relating to the times of divergence of and support for the nodes of the composite tree for the Mephitinae (see Figure 4.4).

	Literature estimates				Birth	Best	Bremer	Differential	Reversals
Node	*n*	median	mean	SE	model	estimate	support	weighting	prohibited
1	3	19.2	17.6	1.8		17.1	n/a		
2	1	2.6	2.6	–		4.0	2		
3	3	5.5	4.7	1.8		4.0	1		
4	0	–	–	–	1.1	1.1	1		
5	5	12.8	11.4	3.0		12.8	1		
6	4	5.0	5.5	2.0		5.0	4		
7	2	2.1	2.1	0.9		2.1	2		

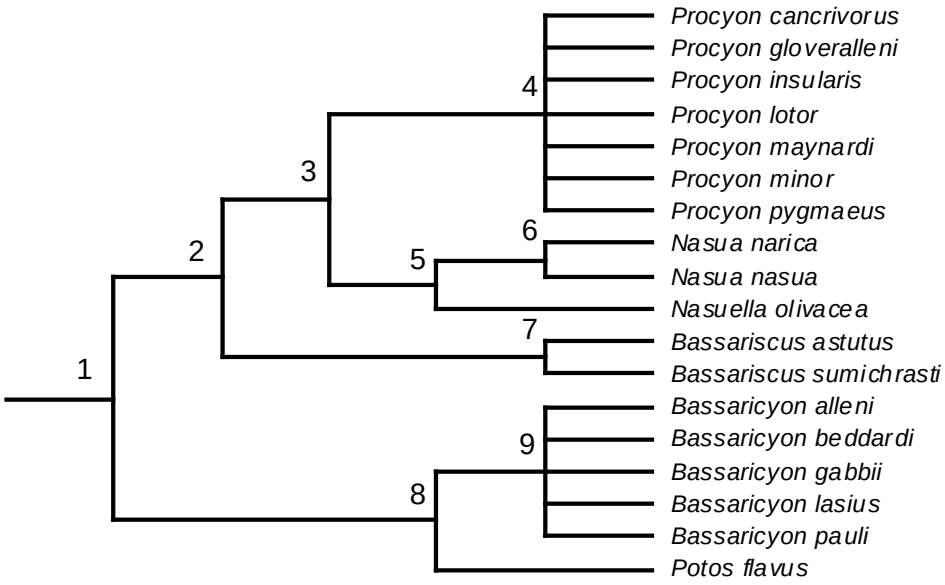

Figure 4.5: The composite tree for the Procyonidae. Node numbers refer to Table 4.6.

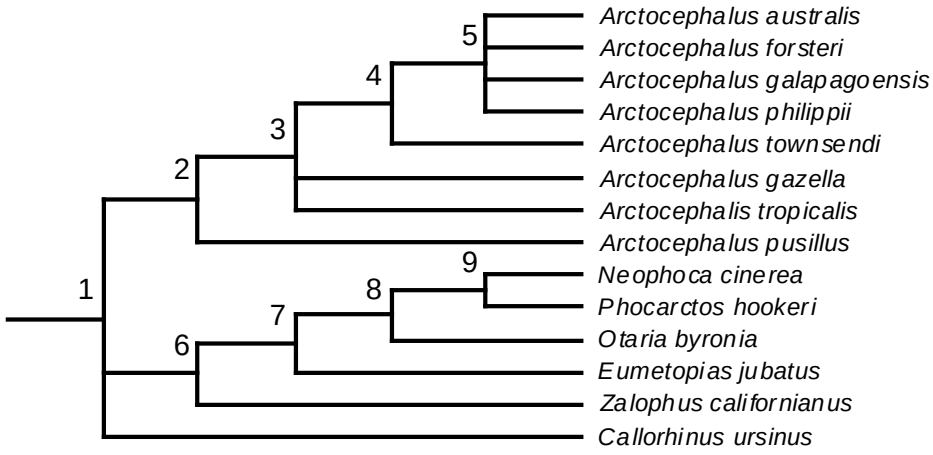

Figure 4.6: The composite tree for the Otariidae. Node numbers refer to Table 4.7.

The composite tree bears on two issues within pinnipeds. Within otariids (Figure 4.6), there is much uncertainty concerning the fur seals (genera *Arctocephalus* and *Callorhinus*). Monophyly of this subfamily cannot be assured, supporting the view that subfamilial distinction within otariids is unnecessary (Tedford, 1976; Repenning & Tedford, 1977). Relationships within *Arctocephalus* are largely unresolved due to both a general lack of research effort and conflicting source trees, the latter possibly owing to the high degree of convergence among species (Berta & Deméré, 1986). In contrast, the

Table 4.6. Statistics relating to the times of divergence of and support for the nodes of the composite tree for the Procyonidae (Figure 4.5).

	Literature estimates				Birth	Best	Bremer	Differential	Reversals
Node	*n*	median	mean	SE	model	estimate	support	weighting	prohibited
1	2	22.1	22.1	0.8		22.1	n/a		
2	4	17.6	17.1	1.0		17.6	2		
3	3	6.5	6.0	0.5		6.5	2		
4	1	1.2	1.2	–		1.2	3		
5	1	3.7	3.7	–		3.7	1		
6	0	–	–	–	2.3	2.3	2		
7	1	0.3	0.3	–		0.3	3		
8	1	19.0	19.0	–		19.0	1		
9	0	–	–	–	17.1	17.1	5		

Table 4.7. Statistics relating to the times of divergence of and support for the nodes of the composite tree for the Otariidae (see Figure 4.6).

	Literature estimates				Birth	Best	Bremer	Differential	Reversals
Node	*n*	median	mean	SE	model	estimate	support	weighting	prohibited
1	7	11.5	11.5	1.1		11.5	n/a		
2	3	3.4	3.8	0.6		6.1	5		
3	1	8.1	8.1	–		6.1	1		
4	0	–	–	–	6.7	6.1	1		collapsed
5	0	–	–	–	5.8	5.8	1		collapsed
6	6	3.2	4.7	1.1		3.2	8		
7	3	3.0	3.0	0.3		3.0	5		
8	2	1.6	1.6	0.2		1.6	3		
9	2	0.9	0.9	0.4		0.9	1	no	

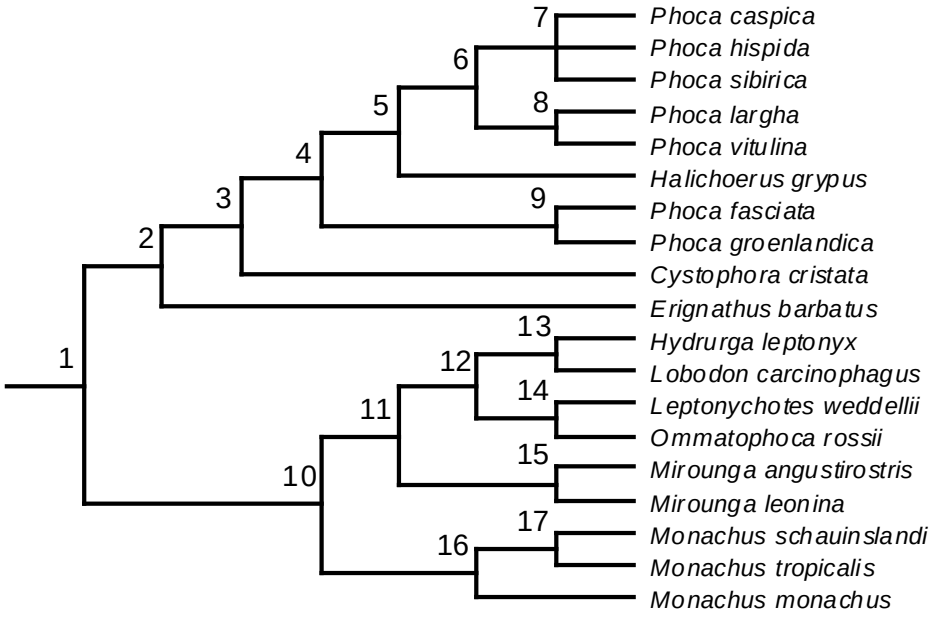

Figure 4.7: The composite tree for the Phocidae. Node numbers refer to Table 4.8.

phocid tree (Figure 4.7) is more resolved and addresses four hypotheses of paraphyly within the family. The genus *Phoca* is indicated to be paraphyletic (although its subgenera [see Burns & Fay, 1970] are monophyletic) with respect to *Halichoerus*, a point often raised in the literature (e.g., Chapskii, 1955; McLaren, 1975; de Muizon, 1982b; Wyss, 1988b; Arnason *et al*., 1993, 1995; Mouchaty *et al*., 1995; Perry *et al*., 1995). Other hypotheses of paraphyly within phocids are not supported here: the subfamily Monachinae (Wyss, 1988b), the tribe Lobodontini (Bininda-Emonds & Russell, 1996), and the genus *Monachus* (Wyss, 1988b) are all monophyletic in the composite tree. Finally, Arnason *et al.* (1996) have used the divergence of *Phoca* (but actually equivalent to node 5 on Figure 4.7) as a standard reference for calibrating recent mammalian divergence events (the "*Phoca* standard"); however, Table 4.8 indicates their estimate of 2.7 MYBP to be too recent.

The giant panda (*Ailuropoda melanoleuca*), which was constrained to be an ursid (see "Methodology"), is very clearly the sister group to the other bears in the composite tree (Figure 4.8; Table 4.9). The position of the American black bear (*Ursus americanus*) remains contentious and merits further investigation; the polytomy in this region agrees

Table 4.8. Statistics relating to the times of divergence of and support for the nodes of the composite tree for the Phocidae (see Figure 4.7).

Node	Literature estimates				Birth model	Best estimate	Bremer support	Differential weighting	Reversals prohibited
	n	median	mean	SE					
1	11	15.0	14.4	0.7		16.0	n/a		
2	4	17.0	17.7	2.2		16.0	6		
3	2	12.9	12.9	0.1		12.9	3		
4	3	12.4	11.8	0.7		12.4	6		
5	4	5.6	5.8	0.3		7.1	3		
6	4	8.6	8.0	2.6		7.1	1		
7	1	2.8	2.8	–		2.8	4	resolved	
8	2	3.9	3.9	0.5		3.9	4		
9	1	9.9	9.9	–		9.9	9		
10	5	14.7	14.7	0.1		14.7	4		
11	7	8.8	8.7	1.6		8.8	1		
12	5	6.7	7.2	1.3		6.7	7		
13	1	4.9	4.9	–		4.9	1		
14	2	3.8	3.8	0.7		3.8	2		
15	3	3.1	3.0	0.3		3.1	8		
16	1	4.8	4.8	–		4.8	8		
17	1	2.8	2.8	–		2.8	2		

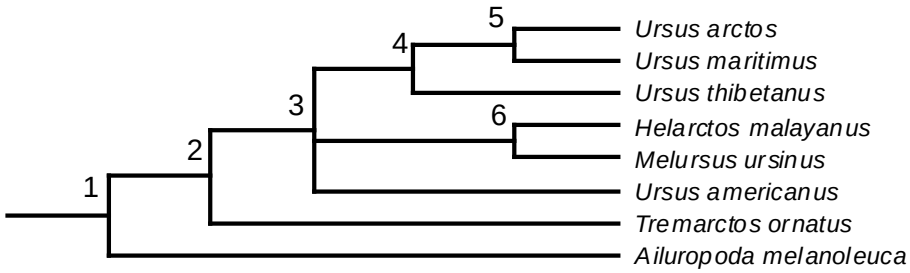

Figure 4.8: The composite tree for the Ursidae. Node numbers refer to Table 4.9.

with recent, independent molecular findings (L. Waits, pers. comm.). At present, the monophyly of *Ursus* is not assured, which supports continuing calls for a revision of the genus-level taxonomy of ursids (see Goldman *et al*., 1989; Zhang & Ryder, 1994). The close association between the brown and polar bears (*U. arctos* and *U. maritimus*, respectively) is upheld, reflecting suggestions that the two might be conspecific (e.g., Cronin *et al*., 1991; Talbot & Shields, 1996). The elevation of the polar bear to its own genus (*Thalarctos*; Corbet & Hill, 1991) is clearly not appropriate without additional taxonomic alterations.

Canids are divided into two main clades (Figure 4.9), corresponding roughly to the "dog-like" and "fox-like" forms of many authors (= Canini and Vulpini, respectively, of Tedford *et al*. [1995]). The problematic genera *Nyctereutes* and *Otocyon* cluster with the dog-like and fox-like clades respectively, although *Nyctereutes* could almost equally well be placed with *Otocyon* (results not shown). Of the monotypic dog-like genera, only the Falkland Island wolf (*Dusicyon*) is placed unambiguously, forming the sister group to the South American "foxes" (*Pseudalopex* spp.), which have frequently been considered to belong in the same genus as it. *Canis* forms a well-defined clade divided into "wolf-like" and "jackal-like" forms. The Simien jackal (*C. simensis*) clearly clusters with wolf-like forms and so justifies its less frequently used common name of the Ethiopian wolf (see Gottelli *et al*., 1994; Geffen *et al*., 1996). The red wolf (*C. rufus*) forms the sister taxon to the grey wolf (*C. lupus*), although this placement is not as strongly supported as indicated in Table 4.10. Several authors (e.g., Wayne & Jenks, 1991; Roy *et al*., 1994; possibly Lawrence & Bossert, 1967) hold *C. rufus* to be a hybrid between the coyote and

Table 4.9. Statistics relating to the times of divergence of and support for the nodes of the composite tree for the Ursidae (see Figure 4.8).

Node	Literature estimates				Birth model	Best estimate	Bremer support	Differential weighting	Reversals prohibited
	n	median	mean	SE					
1	13	21.8	21.5	2.5		21.8	n/a	resolved	resolved
2	17	14.5	13.1	1.1		14.5	13		
3	17	5.7	8.6	1.7		5.7	9		
4	6	3.3	3.4	0.7		3.3	2		
5	12	1.0	1.2	0.3		1.0	3		
6	3	1.0	4.7	3.8		1.0	1		

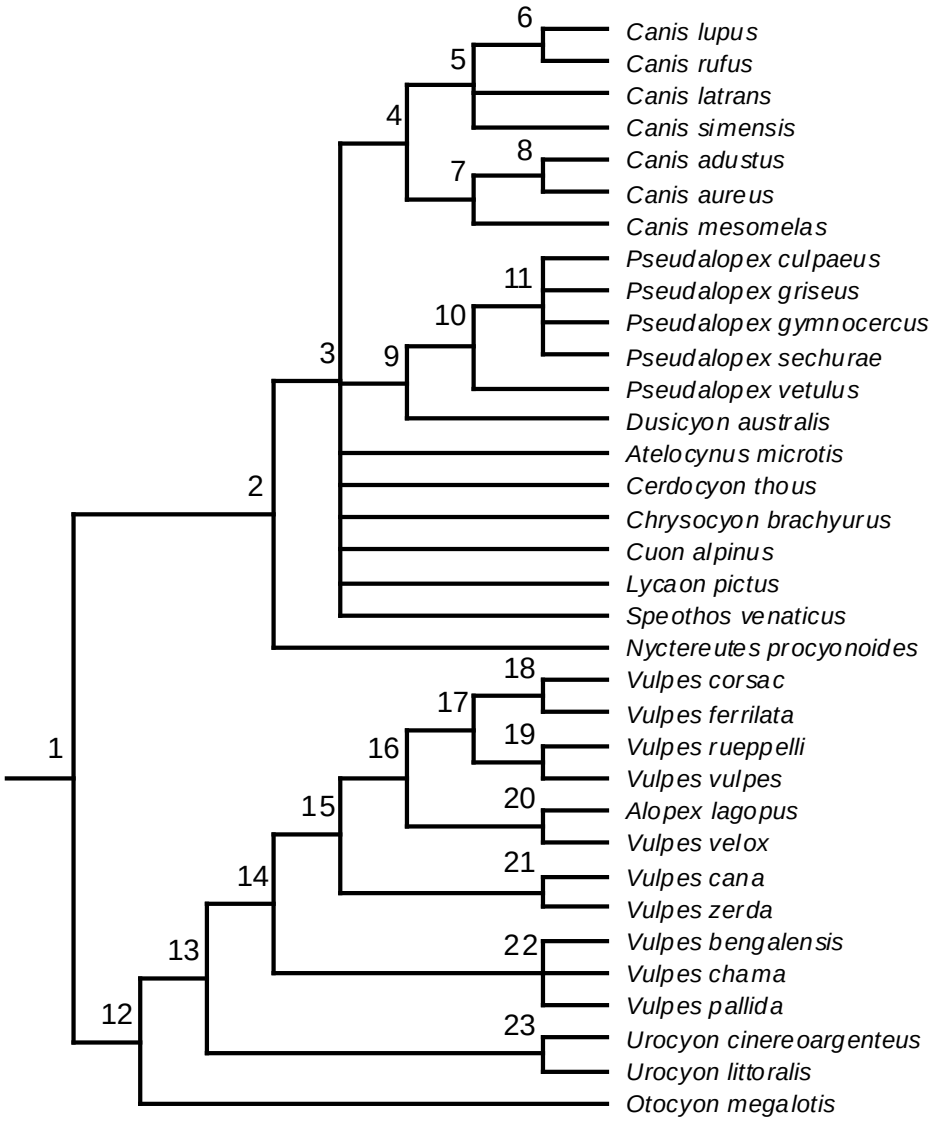

Figure 4.9: The composite tree for the Canidae. Node numbers refer to Table 4.10.

grey wolf, which I coded as a polytomy between the three species. However, in the analyses, a polytomy is always outweighed by any fully resolved answer. Two studies advocated a hybrid origin while four clustered *C. rufus* with *C. lupus* as on the composite tree. With the exception of the South American "foxes", fox-like canids form a distinct cluster with *Otocyon* and *Urocyon* in basal positions. *Vulpes* is indicated to be paraphyletic with respect to the Arctic fox (*Alopex*), an outcome supporting those arguing against the generic distinction of the latter (e.g., Tedford *et al*., 1995).

Table 4.10. Statistics relating to the times of divergence of and support for the nodes of the composite tree for the Canidae (see Figure 4.9).

Node	Literature estimates				Birth model	Best estimate	Bremer support	Differential weighting	Reversals prohibited
	n	median	mean	SE					
1	5	12.5	15.1	3.5		12.5	n/a		
2	2	9.3	9.3	2.3		9.3	1		collapsed
3	6	7.6	7.3	0.6		7.6	3		partly resolved
4	8	6.1	6.5	0.9		6.1	10		
5	11	2.5	2.5	0.3		2.5	2		
6	4	1.1	1.0	0.3		1.1	2		
7	3	2.5	2.6	0.4		2.5	2		
8	3	2.5	2.2	1.0		2.5	1		
9	3	2.5	2.1	0.4		2.5	1		
10	1	2.5	2.5	–		2.5	1		
11	2	0.8	0.8	0.4		0.8	1		
12	2	7.0	7.0	4.4		8.4	3		collapsed
13	1	8.2	8.2	–		8.4	1		collapsed
14	2	10.1	10.1	0.2		8.4	6		
15	3	6.8	6.8	2.3		6.8	1		collapsed
16	3	2.0	3.2	1.6		2.0	1		
17	1	1.9	1.9	–		1.9	1		
18	1	0.2	0.2	–		0.2	1		
19	4	1.1	2.4	1.7		1.1	1		
20	6	1.1	1.8	0.7		1.1	1		
21	4	2.9	3.4	1.7		2.9	1		
22	2	1.5	1.5	0.0		1.5	1		
23	4	4.7	4.5	1.3		4.7	7		

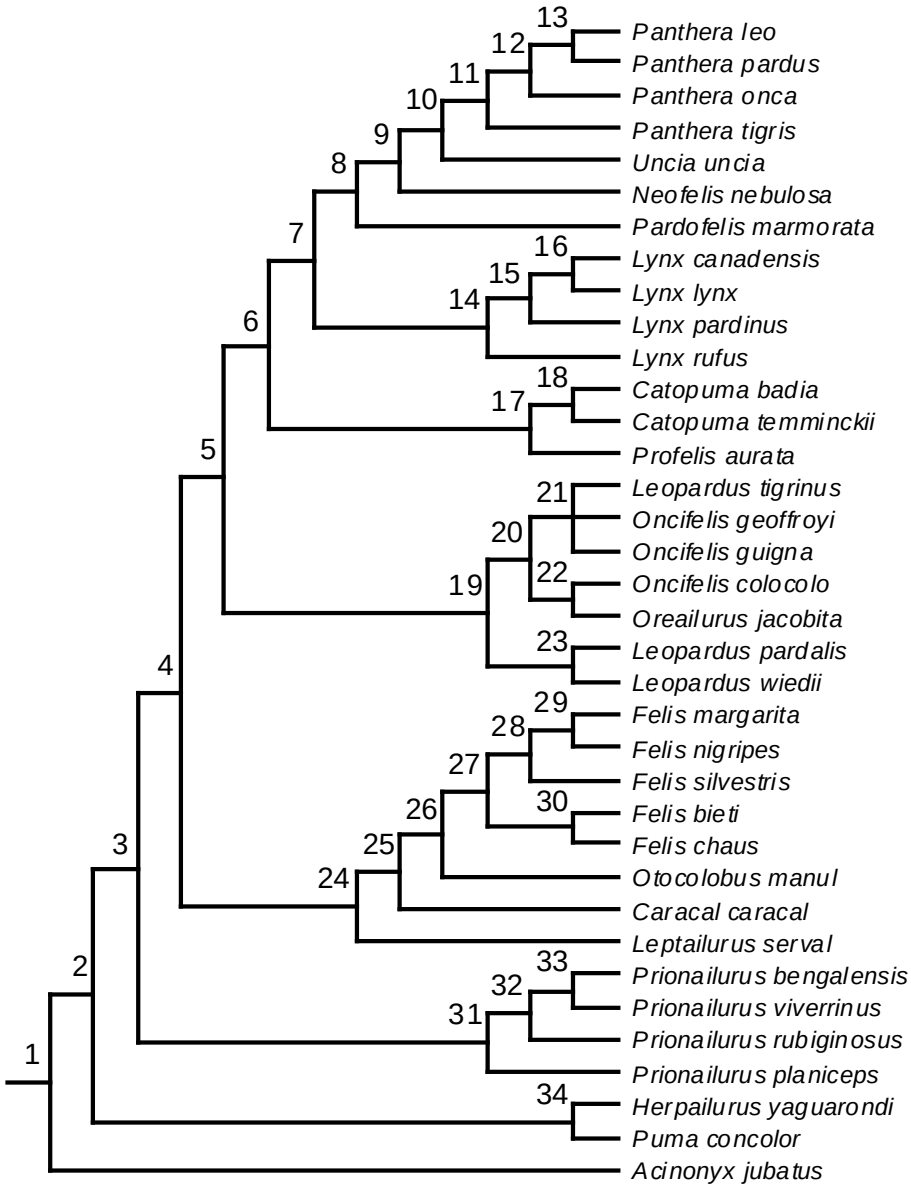

Figure 4.10: The composite tree for the Felidae. Node numbers refer to Table 4.11.

The composite tree for felids is largely resolved (Figure 4.10), but the backbone is weakly supported (Table 4.11), reflecting the historical controversy over felid phylogeny. Three of the better supported clades (nodes 7, 19, and 26) correspond to major clades in recent molecular phylogenies from O'Brien's research group: the *Panthera* group, the ocelot lineage, and the domestic cat lineage respectively (see O'Brien *et al*., 1996). Most of the extant species within the ocelot lineage radiated between 3.7 and 3.0 MYBP (Table 4.11). Although this time scale accords with some estimates of the earliest formation of

Table 4.11. Statistics relating to the times of divergence of and support for the nodes of the composite tree for the Felidae (see Figure 4.10).

Node	Literature estimates				Birth model	Best estimate	Bremer support	Differential weighting	Reversals prohibited
	n	median	mean	SE					
1	8	12.5	14.1	2.4		16.2	n/a		
2	0	–	–	–	15.4	16.2	2	no	no
3	0	–	–	–	16.6	16.2	1	no	no
4	3	20.2	20.9	7.6		16.2	1		no
5	2	12.8	12.8	1.2		12.8	1		no
6	1	7.3	7.3	–		8.5	1		no
7	2	5.4	5.4	1.1		8.5	7		
8	1	10.6	10.6	–		8.5	2	no	no
9	2	10.6	10.6	1.7		8.5	3		
10	2	4.2	4.2	0.0		4.2	8		
11	8	2.2	3.8	1.7		2.2	4		
12	5	1.5	1.8	0.3		2.1	3		no
13	7	2.6	2.5	0.7		2.1	2		
14	5	3.1	3.1	0.3		3.1	14		
15	1	2.2	2.2	–		2.2	1		
16	3	0.2	0.2	0.0		0.2	1		
17	1	5.0	5.0	–		5.0	2		
18	0	–	–	–	3.2	3.2	4		
19	6	3.7	4.9	1.4		3.7	7		
20	2	3.5	3.5	0.1		3.5	5		
21	1	3.2	3.2	–		3.2	3	resolved	resolved
22	2	1.9	1.9	0.1		1.9	1		
23	3	0.3	0.6	0.4		0.3	9		
24	1	16.5	16.5	–		16.2	3	no	
25	2	3.3	3.3	0.8		8.8	1		no
26	3	14.4	13.6	1.9		8.8	3		

Table 4.11. Continued.

Node	Literature estimates				Birth model	Best estimate	Bremer support	Differential weighting	Reversals prohibited
	n	median	mean	SE					
27	4	5.4	6.3	1.8		5.4	1		
28	4	2.3	2.5	0.5		2.3	1		no
29	0	–	–	–	1.5	1.5	2		
30	2	0.2	0.2	0.1		0.2	1		no
31	0	–	–	–	4.8	4.8	3		
32	0	–	–	–	3.8	3.8	2		
33	0	–	–	–	2.4	2.4	2		
34	4	3.1	2.7	0.5		3.1	4		

the Panamanian land bridge (e.g., White, 1986; Martin, 1989), it predates others (e.g., Stehli & Webb, 1985; Wayne *et al*., 1991) as well as the first appearance of fossil felids in South America (1.9–2.4 MYBP; Hunt, 1996) and the time of the greatest faunal exchange between North and South America (Plio-Pleistocene; Hunt, 1996). If my dates are accurate, they suggest that much of the diversification within the ocelot lineage may have occurred before it reached South America (contra Pecon Slattery *et al*., 1994) or shortly thereafter. The pantherine lineage of O'Brien *et al*. (1996) is not monophyletic in my tree, being split into a major terminal clade (node 6) and numerous smaller lineages in the basal portion of the composite tree. The cheetah (*Acinonyx*) occupies its traditional position as sister taxon to the remaining felids (Král & Zima, 1980; Martin, 1980) rather than to *Puma* (contra O'Brien *et al*., 1996). Within the terminal clade, golden cats (*Catopuma temminckii* and *Profelis aurata*) are paraphyletic with respect to the bay cat (*Catopuma badia*), rather than polyphyletic as found by O'Brien *et al*. Despite the lack of robustness of many nodes, all but two of the genera recognized by Wozencraft (1993), *Leopardus* and *Oncifelis*, are monophyletic. Altogether, the pattern I found of well supported groups of uncertain interrelationships (i.e., the weak backbone) reflects current opinion of felid phylogeny (S. J. O'Brien, pers. comm.).

In hyaenids (Figure 4.1), the only point of consensus is the sister group status of the aardwolf (*Proteles*) to the remaining species. The traditional view that *Crocuta* was the sister group to the previously congeneric *Hyaena* and *Parahyaena* has fallen out of favour recently (see Werdelin & Solounias, 1991), but no dominant opinion has replaced it: all three possible resolutions of the polytomy were represented at least once among the five relevant source trees.

The initial analysis of all herpestid species supported only the monophyly of the two subfamilies and the genera within them (Figure 4.11a). However, removing the poorly known species from the analysis (see "Methodology") revealed a surprising amount of structure within herpestines, although resolution within genera is still poor (Figure 4.11b). The positions of two genera, *Dologale* and *Rhynchogale*, within herpestines are completely unknown and their positions in Figure 4.11b should be treated

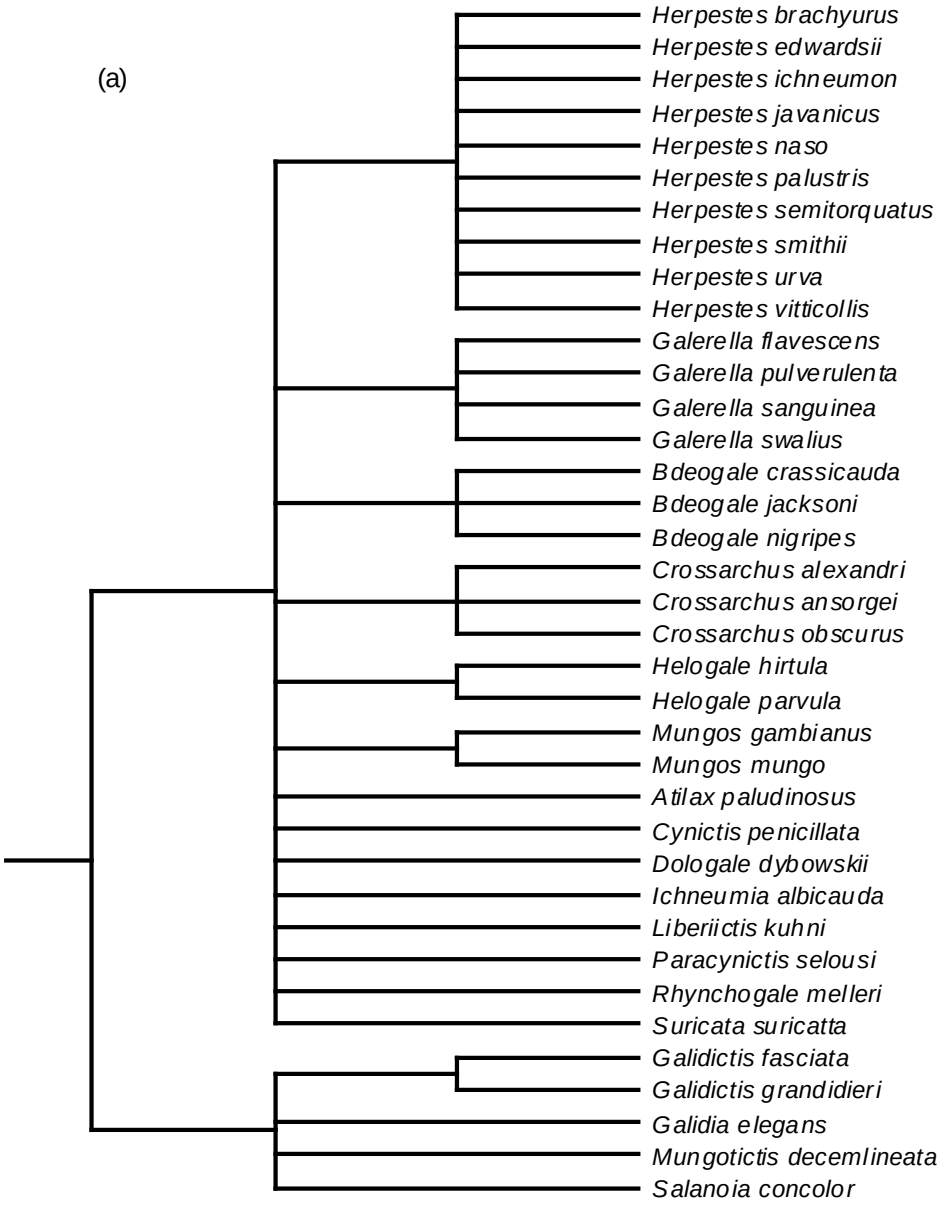

Figure 4.11: The composite tree for the Herpestidae. a) Initial analysis of all species. b) Subsequent analysis in which poorly known species (indicated by a dashed branch) displaying taxonomic equivalence with better known species were excluded from the analysis (following Wilkinson 1995) and subsequently re-included at the least inclusive level indicated for them. Node numbers in (b) refer to Table 4.12.

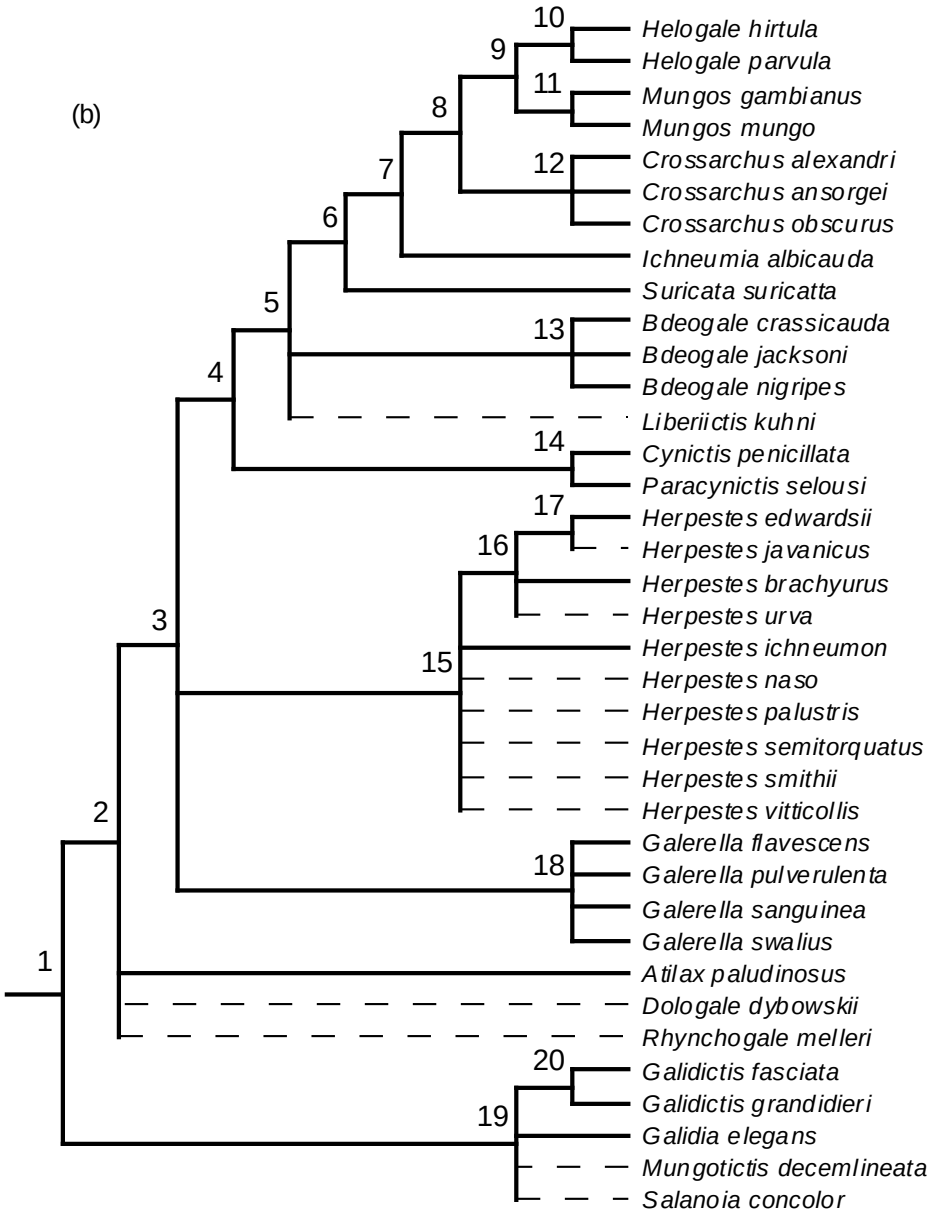

Figure 4.11: Continued.

as highly suspect. This family in general and the poorly known species in particular (whose indicated positions are more statements of membership than hypotheses of relationship) need further systematic research.

Viverrids (Figure 4.12) cluster into their commonly recognized subfamilies (see Wozencraft, 1993). *Nandinia* forms the sister group to paradoxurines in this analysis, but my assumption of viverrid monophyly precluded a test of the suggestion that it may be a primitive feliform (Hunt, 1974; Wiig, 1985; Flynn *et al*., 1988; Hunt & Tedford, 1993;

Table 4.12. Statistics relating to the times of divergence of and support for the nodes of the composite tree for the Herpestidae (see Figure 4.11b).

Node	Literature estimates				Birth model	Best estimate	Bremer support	Differential weighting	Reversals prohibited
	n	median	mean	SE					
1	1	18.5	18.5	–		19.0	n/a		
2	1	19.6	19.6	–		19.0	2		
3	2	17.6	17.6	0.1		17.7	0	collapsed	collapsed
4	0	–	–	–	17.8	17.7	0	collapsed	collapsed
5	0	–	–	–	16.9	16.9	0		
6	0	–	–	–	14.5	15.5	0		no
7	1	16.5	16.5	–		15.5	0		
8	1	2.6	2.6	–		2.6	0		collapsed
9	1	2.6	2.6	–		2.6	0		
10	0	–	–	–	1.3	1.3	1		
11	0	–	–	–	1.3	1.3	1		
12	0	–	–	–	1.5	1.5	1		
13	0	–	–	–	5.8	5.8	1		
14	1	2.6	2.6	–		2.6	0		
15	0	–	–	–	12.1	12.1	1		
16	0	–	–	–	7.3	7.3	0	collapsed	
17	0	–	–	–	3.6	3.6	0		
18	1	11.4	11.4	–		11.4	1		
19	0	–	–	–	8.2	8.2	2		
20	0	–	–	–	3.6	3.6	1		

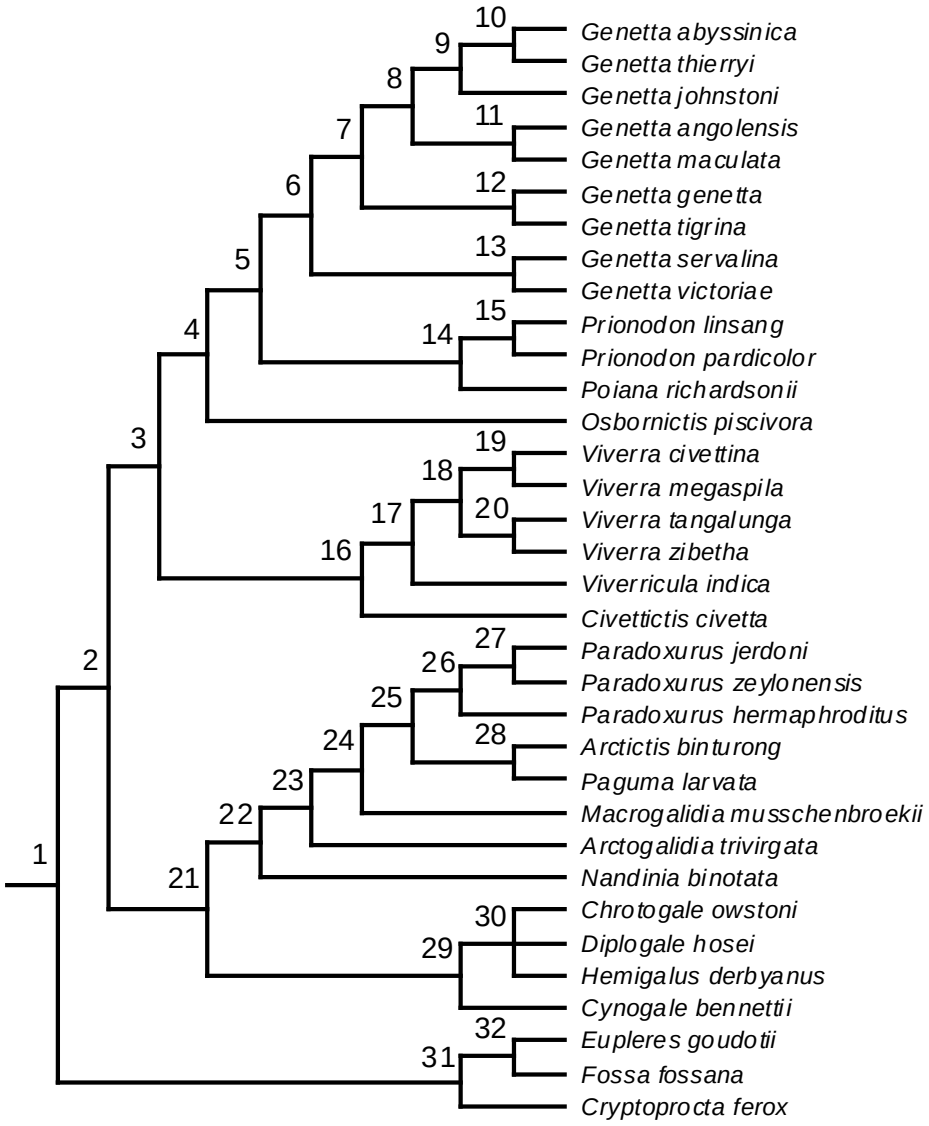

Figure 4.12: The composite tree for the Viverridae. Node numbers refer to Table 4.13.

Flynn, 1996; but see Radinsky, 1975). Evidence for the latter placement relies largely on the morphology of the auditory bulla. An equal number of studies based on wider selection of data place *Nandinia* within viverrids (e.g., Gregory & Hellman, 1939; Petter, 1974; Stains, 1983; Wozencraft, 1984; Taylor, 1988); however, these studies may not have directly tested this question. Removal of the unusually comprehensive (and possibly dominating) study of Wozencraft (1984) did not alter the basic topology, but decreases resolution within paradoxurines and *Genetta* (results not shown). Table 4.13 shows three

Table 4.13. Statistics relating to the times of divergence of and support for the nodes of the composite tree for the Viverridae (see Figure 4.12).

Node	Literature estimates				Birth model	Best estimate	Bremer support	Differential weighting	Reversals prohibited
	n	median	mean	SE					
1	0	–	–	–	27.5	27.5	n/a		
2	1	27.2	27.2	–		27.2	5		
3	3	27.2	26.4	3.2		27.2	6		
4	0	–	–	–	14.5	14.5	1		collapsed
5	0	–	–	–	14.0	14.0	1		no
6	3	4.5	7.4	3.5		4.5	4		
7	0	–	–	–	4.0	4.0	1		collapsed
8	0	–	–	–	3.3	3.3	1		collapsed
9	0	–	–	–	2.2	2.2	1		collapsed
10	0	–	–	–	1.4	1.4	2		
11	0	–	–	–	1.4	1.4	1		
12	1	2.6	2.6	–		2.6	1		
13	0	–	–	–	1.4	1.4	2		
14	0	–	–	–	10.2	10.2	2		
15	0	–	–	–	6.4	6.4	3		
16	1	2.6	2.6	–		10.3	1		
17	2	15.2	15.2	1.4		10.3	1		
18	0	–	–	–	13.0	10.3	2		
19	0	–	–	–	6.5	6.5	2		
20	0	–	–	–	6.5	6.5	1		
21	0	–	–	–	27.2	27.2	3		
22	0	–	–	–	22.7	22.7	1		
23	0	–	–	–	21.3	21.3	3		
24	0	–	–	–	19.6	21.0	1		
25	1	22.4	22.4	–		21.0	1		
26	0	–	–	–	15.3	15.3	3		

Table 4.13. Continued.

Node	Literature estimates				Birth model	Best estimate	Bremer support	Differential weighting	Reversals prohibited
	n	median	mean	SE					
27	0	–	–	–	9.7	9.7	1		
28	0	–	–	–	9.7	9.7	1		collapsed
29	0	–	–	–	11.0	11.0	6		
30	0	–	–	–	8.7	8.7	1		
31	0	–	–	–	8.4	8.4	2		
32	0	–	–	–	5.3	5.3	4		

viverrid lineages are long-lived, diversifying before those in other families, if not before the diversification of (the extant members of) the families themselves.

In summary, instances of non-monophyly were rare, occurring only for the genera *Lutra* (lutrines), *Phoca* (phocids), *Vulpes* (canids), *Leopardus* (felids), *Oncifelis* (felids), and possibly *Ursus* (ursids); the nominal subgenus of *Mustela* (mustelids); and some other felid groups. This low level of non-monophyly reflects both tacit assumptions of monophyly of higher level taxa (see "Methodology"), but probably also the general consensus over current carnivoran taxonomy.

Conclusions

Supertree construction is a powerful new tool for building larger and more comprehensive phylogenies. MRP in particular combines positive aspects of both character and taxonomic congruence approaches. By using MRP, I have constructed the first full species-level phylogeny for all extant species of Carnivora from a wide variety of data sources spanning 25 years of systematic research into this mammalian order. The incompatibility and potential heterogeneity in signal among some of these data sets would preclude obtaining an answer using character congruence, and taxonomic congruence's reliance on consensus techniques would result in a much less resolved answer.

The composite tree shows that disparate studies of carnivoran phylogeny agree to a surprising extent: poorly resolved taxa are generally those that have been studied least. More research is clearly merited for herpestids and viverrids as a whole and within the procyonid genera *Bassaricyon* and *Procyon*. For some other questions (e.g., relationships among felid genera and among hyaenines, and the positions of the red panda and of the monotypic "dog-like" canid genera), no clear answers have emerged despite considerable effort. Additional data may help resolve these issues; however, it may be that they are inherently difficult because they involve successive splitting events that were close together in time, and long ago.

The tree I present (summarized in Figure 13) is the largest complete species-level phylogeny for any group. It will provide a touchstone for many kinds of comparative

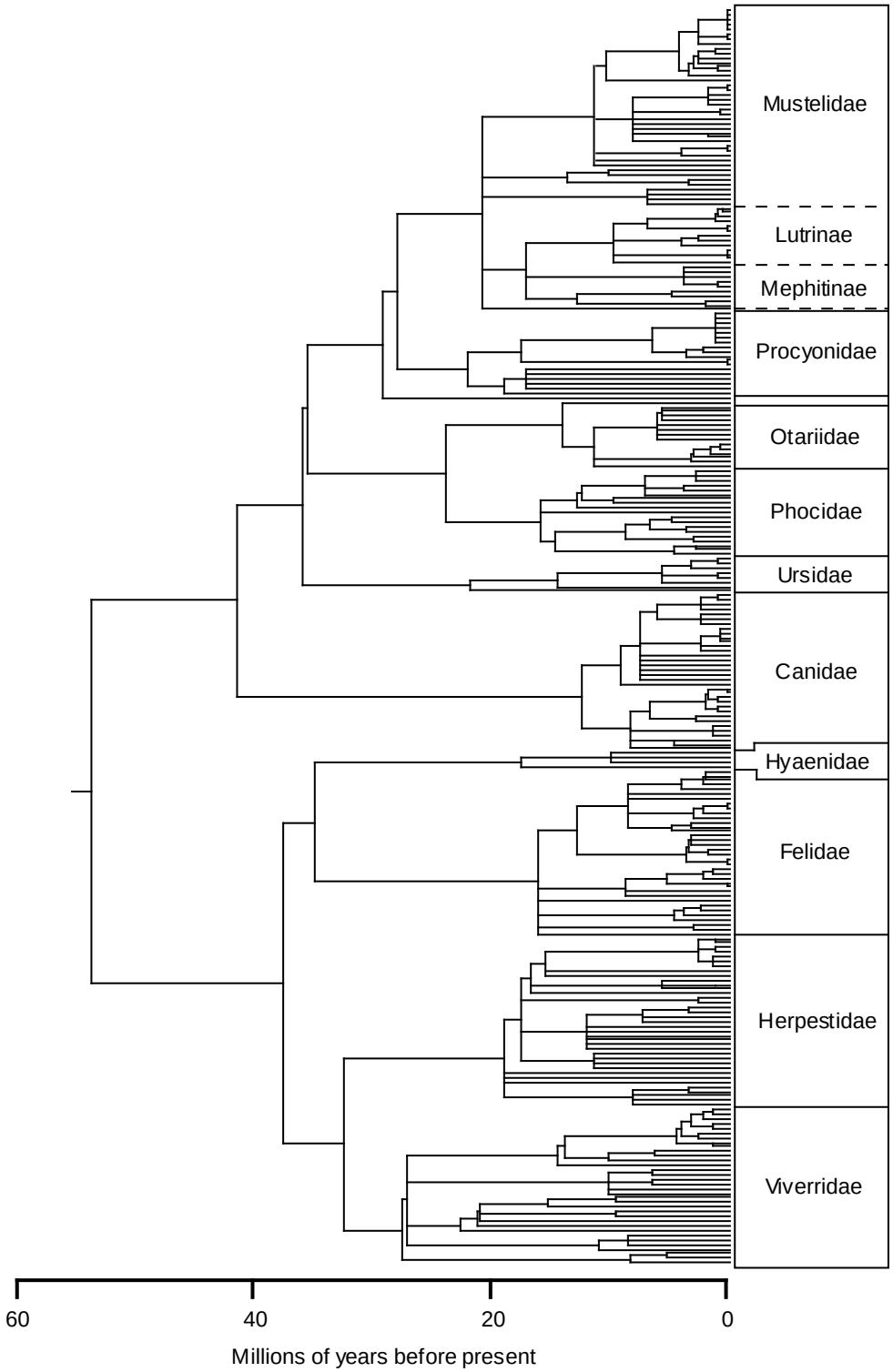

Figure 4.13: The composite tree for all 271 species of carnivore, including estimated times of divergence Within major taxa, species are presented in the same order as in Figures 4.1–4.12. Dates were estimated either from the literature (see Tables 4.2–4.13) or via a pure birth model. Negative branch lengths are drawn as having zero length. See text for further details.

study within carnivores (e.g., character evolution, macroevolutionary studies, conservation studies) and has already been used to test for correlations between population size and geographic range in British mammals (Blackburn *et al*., 1997) and between body size and species richness in all carnivores (Gittleman & Purvis, 1998), and to examine for edge effects with respect to the conservation biology of large carnivores (Woodroffe & Ginsberg, 1998). The tree also serves as a strawman for further systematic research into this fascinating order.

Chapter 5

Factors influencing phylogenetic inference in carnivores

Acknowledgements:

I thank Andy Purvis for initially suggesting this project to me and for many stimulating early discussions. Paul Harvey, Colleen Kelly, and especially Mike Charleston provided many helpful suggestions on how to improve this chapter.

Synopsis

Phylogenetic reconstruction has undergone numerous developments in the areas of tree selection criteria (e.g., cladistics, phenetics, maximum likelihood), available data sources (morphology versus molecules and subsets of each), and practical limits on study size. Together with the age of the study, I examined the effects of these factors (variables) on inferences of phylogeny for the mammalian carnivores. The raw data comprised 274 source trees spread among 13 carnivoran taxa (generally families), which I divided into categories for each of the variables above and then combined using matrix representation with parsimony analysis. Incongruence was assessed between both the resultant tree topologies and the underlying data using four comparison measures, each with slightly different properties: the triplet measures "do not conflict" and "explicitly agree," the partition metric, and the Mickevich-Farris index. Generally, no significant differences in incongruence levels were found — either among the different categories within each variable, between the variables themselves, or between the various taxa — indicating that most estimates of carnivore phylogeny point towards the same solution regardless of the methodology or data source employed. This conclusion held regardless of the comparison measure used, although the measures differed slightly depending on the amount of resolution in the competing data.

Introduction

Phylogenetic inference has undergone numerous developments. In the early days, systematists generally clustered taxa based on their (overall) morphological similarity. Since then, and particularly in the last 40 years or so, phylogenetic analysis has seen three important advances: 1) the development of more rigorous clustering techniques, 2) the discovery of additional, molecular data sources, and 3) changes in the number of taxa that could be analyzed.

Of these three advances, the most attention has been focused on the accuracy of different clustering techniques and, more recently, of different data sources. Much has been written about the clash between proponents of two early rigorous tree selection criteria: phenetics and cladistics (see Hull, 1980 for an overview). Despite its eventual "victory," cladistics and parsimony now face a new challenge from more complex model-based or theoretical algorithms (e.g., maximum likelihood, neighbour joining). Recent examinations of the relative efficacy of these techniques under various simulated conditions have generally concluded that most techniques possess shortcomings under certain specific sets of conditions, but are generally similar (Nei, 1991; Hillis & Huelsenbeck, 1993; Charleston *et al*., 1994; Hillis *et al*., 1994; Tateno *et al*., 1994; Huelsenbeck, 1995).

Development of the many newer tree selection criteria is tied to the recent rise of molecular information as a data source. Although in use for only about 30 years, molecular data has surpassed morphological data as the data source of choice and has shown its own rapid development from initial karyological and immunological studies to karyotypic banding studies to amino acid sequences and finally to DNA sequence data of various forms. Despite the perception of a conflict between morphological and molecular data, numerous studies and reviews indicate that the two data sources do not produce substantively different answers on the whole (e.g., Hillis, 1987; Sanderson & Donoghue, 1989; Patterson *et al*., 1993; although see Goodman, 1989; Graur, 1993). A recent twist concerning which data source to employ is character congruence or the "total evidence"

approach (*sensu* Kluge, 1989), which holds that the best answers are obtained when all the available data, morphological and molecular, are combined and analyzed simultaneously.

Study size can also affect the accuracy of phylogenetic inference. As I stated in Chapter 1, "size" can refer to both the number of characters and taxa in an analysis; however, I will again restrict myself to discussing the latter. Recently, it has been asserted that larger, more complete analyses yield more reliable results (see Hillis, 1998 and references therein) because the *judicious* inclusion of as many taxa as possible minimizes the number of long branches (Swofford *et al*., 1996) and avoids assumptions of monophyly or selection of exemplar taxa (Arnold, 1981; Donoghue *et al*., 1989; Lecointre *et al*., 1993; see Chapter 2 also). Study size shows an interesting history. In early systematic studies, the simple, roughly intuitive clustering techniques allowed the inclusion of large numbers of taxa (e.g., Gregory & Hellman, 1939). Somewhat ironically, the advent of more rigorous clustering techniques initially decreased study sizes because the more complicated calculations limited the number of taxa that could be worked with, either by hand or early computers. It is only relatively recently that advances in computer technology combined with algorithmic shortcuts (e.g., the branch and bound algorithm: Hendy & Penny, 1982; heuristic tree search strategies: see Swofford *et al*., 1996; parsimony jackknifing: Farris *et al*., 1996; matrix representation with parsimony analysis [MRP]: Baum, 1992; Ragan, 1992b; compartmentalization: Mishler, 1994) have allowed systematic studies to become larger and more inclusive than ever before (e.g., Chase *et al*., 1993; Purvis, 1995a; Soltis *et al*., 1997).

Have the advances listed above (which I refer to as "variables" hereafter) changed our phylogenetic inferences? Certainly, differences have been advocated by proponents of a specific methodology, but their impact has rarely been examined in a large-scale comparative or statistical framework. The question remains whether these variables have changed our phylogenetic estimates to any substantial degree, or in a consistent manner. The 274 source trees I used to derive the composite phylogeny in Chapter 4 are ideal for testing this question given that they span from 1970 to 1995 and reflect the changes in

methodology over this period. I therefore used the source trees to test the effect of various factors, including the three variables above, on estimates of carnivore phylogeny.

Methods and materials

Variables under examination

I subdivided the 274 source trees used in Chapter 4 (see Appendix B) into the following categories for each of five variables:

1) Tree selection criteria — discrete character, distance data, and "intuitive parsimony."

I followed Nei (1991) in dividing the many (formal) clustering techniques into two broad classes: those for discrete character data (e.g., parsimony and maximum likelihood) and those for distance data (e.g., phenetics, UPGMA, neighbour joining, minimum evolution, and morphometrics). I added a third category for studies that did not appear to use a formal methodology, but rather derived a phylogeny from a set of data using a form of "intuitive parsimony."

2) Data source — morphological, molecular, and total evidence.

I classified studies according to whether they were purely morphological, purely molecular, or whether both data types were used together (total evidence).

3) Molecular source — sequence, karyology, and "other."

This variable is a subclass of the previous one. Despite the relative youth of molecular systematics, advances in the field (see above) have led to many distinct classes of molecular data. "Sequence" includes DNA and amino acid sequence studies, restriction site analyses (e.g., restriction-fragment length polymorphisms or RFLPs), and microsatellite studies. Any form of chromosomal analysis falls under "karyology." "Other" is a catch-all category for techniques that were not common enough in my sample to merit their own category: allozymes, hybridization, serology, and immunology.

4) Size and resolution — low and high.

I took the size of a study to be the amount of hierarchical information (i.e., nodes) it contains. Using the number of terminal taxa as a measure of study size is unsuitable because studies that (implicitly) include all species can still provide limited phylogenetic information (e.g., taxonomies). Instead, the number of nodes in a study is a fairer representation of its "size," although this measure is somewhat biased against studies with large numbers of polytomies. "Low" resolution studies had < 50% of the maximum number of informative nodes for the taxonomic group. The only exception was Hyaenidae, which with four extant species (and therefore two informative nodes at most) could not be < 50% resolved. Therefore, "low" resolution for hyaenids was ≤ 50%.

5) Date of study — 1970s (and before), 1980s, and 1990s.

This variable essentially examines the effects of the remaining variables acting in concert. In many ways, it is reminiscent of Benton and Storrs (1994), who asked whether our increased knowledge and surveying of the fossil record with time have changed the interpretations derived from it. In the present case, some correlations are apparent. Studies from the 1970s tend to be morphological, relatively small, and analyzed using parsimony, phenetics, or "intuitive parsimony." By the 1990s, studies are predominantly molecular, larger, and analyzed using parsimony, maximum likelihood, or some algorithm for distance data. Although the 1990s encompasses only six years in the sample (to the end of 1995), the recent explosion in systematic effort means that sample sizes for the 1990s were roughly the same as for each of the 1970s and 1980s.

As in Chapter 4, I determined composite trees for the various carnivoran taxa for each category using MRP. Parsimony analysis followed the procedure in Chapter 4 and was conducted using PAUP 3.1.1 (Swofford, 1993). I did not account for differential signal strength among source trees as this information was often not provided and, when it was, it was summarized by different metrics, which may not yield equivalent

information (see Chapter 3). Strict consensus was used to summarize equally most parsimonious solutions.

Although MRP is remarkable in maintaining resolution even when source trees conflict strongly (Purvis, 1995b), the subdivision I employed in this chapter often rendered the category sample sizes too small for good resolution. Frequently, a species lacked any information for a given category, thereby clustering equally parsimoniously with every other species and reducing the composite tree to a bush under strict consensus. I counteracted this by using Wozencraft's (1993) taxonomy to provide a backbone of limited clustering information for most species. Only analyses of interfamilial relationships ("higher groups") could not be seeded in this manner because the taxonomy did not extend beyond the family level. In more extreme cases, I used "safe taxonomic reduction" (Wilkinson, 1995) to identify and remove taxa that limited resolution (see Chapter 4 also). This was only done on very poorly resolved trees within a variable. Since most tree comparison metrics (see below) can compare trees with identical sets of terminal taxa only, I created a set of agreement subtrees (see Page, 1993) for each variable by pruning the same taxon (or taxa) from the composite trees of the remaining categories. The contrasting approaches of safe taxonomic reduction versus pruning to form agreement subtrees reflects the differing strategies for obtaining the best inference depending on the amount of information in the matrix. For poorly resolved trees, the best inference is when problematic taxa that contain no unique clustering information are removed and the analysis is rerun. Such is not the case with well resolved trees within the same variable. Here, safe taxonomic reduction removes non-trivial information and may alter the inferred relationships. Instead, the best inference is when all taxa are analyzed and the required taxa subsequently pruned from the composite tree. Analyses involving Herpestidae always excluded at least the 12 poorly known species identified in Chapter 4.

Comparison of composite trees within each variable

One problem with the current exercise is the lack of an obvious reference tree to which to make the comparisons. The composite tree from Chapter 4 is unsuitable due to

non-independence: the source trees in each category all contributed to this tree. Categories with more source trees had greater input into the topology of the overall composite tree and so will tend to resemble it more closely than smaller categories. To avoid this problem, I instead compared all combinations of composite trees within a variable to one another.

With this approach, it is not possible to state whether one category yields a "better" answer than another, but only whether it gives a significantly different answer from the remaining categories. The corresponding hypotheses for this question are:

H_O: The different categories within a variable are all equally different from one another.

H_A: One or more categories is/are significantly different from the remaining categories.

Note that the construction of these hypotheses is such that categories may produce trees that are very different from one another, but still not produce a significant result so long as all trees are *equally* different from one another.

Two subsidiary questions examine how any differences are distributed among the major higher carnivoran taxa (generally families and the subfamilies Lutrinae and Mephitinae within Mustelidae) and the variables themselves. Are differences among the categories larger or smaller in some taxonomic groups (within each variable) or some variables? For instance, the choice of tree selection criterion may produce trees that are more different from one another than does the data source that was employed. Again, the corresponding hypotheses are:

H_O: The differences between the categories are equal among all taxonomic groups (within each variable) or among all variables.

H_A: One or more taxonomic groups / variables have significantly different values from the remaining ones.

Because the data often were not normally distributed, nor possessing equal variances, I tested each of the three sets of hypotheses using the non-parametric Kruskal-Wallis test. The critical value to reject each null hypothesis was 0.05, corrected for multiple comparisons (i.e., the different metrics; see below) within each variable using a sequential Bonferroni technique (Rice, 1989).

Comparison metrics

Differences between all composite trees within each variable were quantified using four metrics of slightly different properties. The first three metrics compared tree topologies only: the partition metric (Penny & Hendy, 1985) and two metrics from triplet analysis (Estabrook *et al*., 1985; Day, 1986). The partition metric describes the number of clades found in one tree or the other, but not both. As such, it treats polytomies as being "hard" (see Maddison, 1989) and can indicate a large difference between two trees even if they differ in the placement of only a single taxon (Page, 1993).

Triplet analysis avoids some of these limitations by breaking rooted trees down into their smallest possible informative subtrees (sets of three taxa or "triplets") and determining whether each possible pair of triplets between the two trees have the same topology, different topologies, or whether either one or both are unresolved. Of the many metrics available to summarize triplet analysis (see Day, 1986), I only used the dissimilarity metrics "do not conflict" (DC), which gives the proportion of resolved triplets that are different, and "explicitly agree" (EA), which adds triplets that are unresolved in either or both trees to this value (Estabrook *et al*., 1985).

A potential shortcoming of the previous tree comparison metrics is their independence from the data underlying the topologies. Thus, what appear to be two categories yielding similar solutions might still be highly incongruent at the level of the raw data. I tested for data incongruence using the Mickevich-Farris index (I_{MF}; Mickevich & Farris, 1981; *sensu* Kluge, 1989), which determines the amount of incongruence in a combined analysis of two test matrices that is over and above ("extra to") the summed level of incongruence within each test matrix. In all cases, incongruence

is defined as the length of the most parsimonious solution(s) yielded by a matrix minus the number of synapomorphies in the matrix (i.e., the number of additional steps over the ideal, minimal length). The I_{MF} is then the "extra" incongruence present in the combined matrix divided by the total incongruence of the combined matrix (see Kluge, 1989 for a worked example).

An advantage of the I_{MF} in the current context is that it can compare solutions where safe taxonomic reduction has resulted in different sets of terminal taxa. This is because the removed taxa are "redundant" with other taxa in the matrix and so do not affect tree length, numbers of synapomorphies, or consistency index, the latter being a measure of incongruence (Wilkinson, 1995). However, taxa were still removed from the combined analysis if they were removed from both individual analyses.

I used COMPONENT (Page, 1993) to obtain values of the partition and triplet analysis metrics and PAUP to obtain most parsimonious lengths and numbers of synapomorphies for calculating the I_{MF}. For all metrics, higher values indicate increasingly different solutions. Both triplet metrics and the I_{MF} are bounded by 0 and 1. I standardized the partition metric by dividing it by twice the maximum number of informative nodes (= number of taxa – 2), which is the maximum distance between any two fully resolved trees. My use of Wozencraft's (1993) taxonomy to seed each analysis will cause all measures of incongruence to be slightly lower than they should be. However, because this is true for all analyses and because I am making comparative rather than absolute statements, this should not be a problem.

Sliding window analysis

In addition to the preceding statistical framework, I examined how opinions regarding two long-standing carnivoran systematic questions have changed over time. These questions are the affinity of pinnipeds (including the associated question of whether they are mono- or diphyletic) and of the red panda (*Ailurus fulgens*). Although the giant panda (*Ailuropoda melanoleuca*) historically was a subject of similar uncertainty, its status as a primitive ursid (see O'Brien *et al*., 1985) is now largely

unquestioned. Also, since I previously constrained the giant panda to be an ursid (see Chapter 4), any examination of its historical status here is moot.

The methodology I used was a "sliding window analysis" in which I ordered the 62 source trees that provided clustering information about the carnivoran families in ascending chronological order (and secondarily by ascending alphabetical order by author name). Composite trees were determined for contiguous, overlapping sets of 15 trees (e.g., for source trees 1–15, 2–16, 3–17, and so on). This number of source trees provided sufficient clustering information for each terminal taxon to avoid the use of safe taxonomic reduction.

For each "window" of 15 source trees, the sister groups for pinnipeds (ursid, mustelid, both, neither, or not applicable) and red panda (ursid, procyonid, both, or neither) were determined, as well as the cladistic status of pinnipeds. I also compared the composite tree from each window to the composite tree in Figure 4.1 using the metrics above. Although the issue of non-independence remains, I felt it to be less problematic here because all windows were about equal in size and therefore non-independent to roughly the same degree. The I_{MF} could not be applied because the matrix for the overall composite tree contains all the source trees (and their incongruences) for a given window and no extra incongruence is possible (i.e., the I_{MF} would always be 0). In its place, I quantified data incongruence by using PAUP to constrain the solution for each window to the topology of Figure 4.1. I then divided the number of extra steps this required by the length of the most parsimonious solution for that window to derive a simple "incongruence metric." Note that this metric does not have an upper bound of 1 as do the other metrics.

Results

Distribution of previous research effort

Numbers of source trees and matrix elements (a proxy for tree size) for each taxon are presented in Table 5.1. Most taxa had at least one source tree in every category. Two

Table 5.1: Distribution of research effort among the different variables and their categories. Entries are given as the number of source trees / number of matrix elements. Numbers within a variable need not add up to the totals in the first column because of the inclusion of Wozencraft (1993) to seed each analysis and because the same source tree may appear in more than one category.

Taxon	Total	Date			Resolution		Tree selection criterion		
		1970s	1980s	1990s	low	high	discrete	distance	intuitive
Higher groups	62 / 202	15 / 51	21 / 80	26 / 81	44 / 82	18 / 130	37 / 138	19 / 51	12 / 37
Canidae	36 / 180	15 / 76	7 / 34	16 / 80	34 / 146	3 / 40	16 / 86	7 / 34	12 / 58
Felidae	40 / 282	5 / 41	22 / 179	15 / 85	36 / 182	5 / 114	19 / 187	20 / 131	6 / 34
Herpestidae	9 / 53	4 / 35	4 / 14	3 / 20	9 / 51	—	3 / 20	2 / 13	7 / 40
Hyaenidae	6 / 8	3 / 3	3 / 4	2 / 3	4 / 4	3 / 5	5 / 7	—	2 / 2
Lutrinae	6 / 37	2 / 13	4 / 25	2 / 6	3 / 7	4 / 34	5 / 28	—	3 / 23
Mephitinae	5 / 18	—	2 / 9	4 / 12	3 / 8	3 / 13	4 / 15	2 / 6	—
Mustelidae	30 / 155	5 / 26	18 / 105	7 / 43	27 / 121	2 / 45	10 / 84	11 / 47	10 / 47
Otariidae	15 / 46	7 / 19	4 / 15	6 / 14	13 / 33	3 / 14	6 / 17	5 / 8	7 / 25
Phocidae	21 / 120	8 / 39	5 / 32	10 / 55	17 / 71	5 / 52	11 / 78	8 / 22	7 / 34
Procyonidae	7 / 27	—	3 / 15	5 / 18	6 / 19	2 / 14	6 / 25	2 / 8	2 / 8
Ursidae	28 / 50	6 / 9	8 / 20	16 / 26	24 / 34	5 / 19	15 / 30	11 / 19	7 / 11
Viverridae	9 / 90	3 / 35	6 / 61	2 / 11	7 / 43	3 / 56	2 / 40	3 / 16	6 / 51

Table 5.1: Continued.

Taxon	Data source			Molecular source		
	morphology	molecular	both	sequence	karyology	other
Higher groups	20 / 85	36 / 109	6 / 18	19 / 58	9 / 27	17 / 46
Canidae	15 / 86	19 / 85	4 / 19	16 / 64	4 / 27	4 / 17
Felidae	13 / 94	24 / 152	5 / 59	11 / 44	9 / 112	10 / 64
Herpestidae	5 / 29	5 / 31	—	2 / 16	3 / 20	2 / 13
Hyaenidae	6 / 8	—	—	—	—	—
Lutrinae	5 / 27	—	2 / 14	—	—	—
Mephitinae	2 / 5	3 / 10	2 / 9	2 / 7	2 / 9	3 / 12
Mustelidae	12 / 75	15 / 51	3 / 48	5 / 21	7 / 62	8 / 61
Otariidae	10 / 36	5 / 8	2 / 4	3 / 5	2 / 4	4 / 7
Phocidae	9 / 68	12 / 44	2 / 14	7 / 31	4 / 18	5 / 23
Procyonidae	3 / 21	5 / 12	—	4 / 10	2 / 8	—
Ursidae	4 / 6	21 / 42	5 / 7	13 / 24	5 / 8	10 / 21
Viverridae	7 / 86	3 / 13	—	—	2 / 10	2 / 11

notable exceptions were hyaenids and lutrines, which lacked any purely molecular source trees.

The amount of phylogenetic effort directed among carnivoran taxa was discussed in Chapter 4: interfamilial relationships of carnivores ("higher groups"), canids, felids, mustelids, phocids, and ursids are comparatively well studied (i.e., high numbers of source trees), while herpestids, hyaenids, lutrines, mephitines, procyonids, and viverrids are rather poorly researched.

Trends are also apparent within each variable. For tree selection criteria, studies using discrete characters were normally the most common for each taxon. This largely reflects both the longevity of parsimony and its simplicity. Parsimony is the only criterion to span all 25 years examined in this study and was largely unchallenged for a considerable stretch after the demise of phenetics. Despite the large number of techniques currently available, parsimony remains popular, reflecting perhaps its ease of calculation compared to the newer, more computationally-intensive techniques. The distribution of research effort among the remaining categories depended on how well known a taxon is. Well known taxa tended to be analyzed by the more rigorous distance data criteria, while "intuitive parsimony" tended to predominate in studies of poorly known taxa.

Molecular data generally yielded more source trees for each taxon than morphological data, but produced fewer matrix elements. Thus, although molecular data are more popular, they are available for fewer species. This appears to have two root causes. First, the greater molecular research effort is replicated among the different data types for the same small group of well known species. Second, molecular data has until recently been relatively expensive and difficult to obtain, again limiting its accumulation for different species. Of the different molecular data sources, sequence data tended to be the most numerous, although all are about equally represented. Total evidence studies employing both morphological and molecular data were generally few in number and small in size.

There were fewer trees of "high" resolution, but their larger size compared to trees of "low" resolution meant that the number of matrix elements was about equal in each.

Finally, study date showed increased numbers of trees and matrix elements with time. In fact, the 1990s was often the largest category, despite not including any source trees from after 1996.

Statistical comparisons

Except for resolution where no comparison was possible, no significant differences were found for within variable comparisons (Table 5.2), indicating that the raw data or resultant trees within each variable were all equally different among the categories. This was true for all variables and comparison metrics. In only one case (molecular technique measured by I_{MF}) did the *p* value drop below 0.10. In general, the metrics showed good agreement with one another as indicated by their similar *p* values. (As the metrics measure incongruence slightly differently [see "Discussion"], their average values need not be comparable or mean the same thing.)

Nor did the variables differ significantly amongst themselves with respect to the level of discordance exhibited by their respective categories (Table 5.3). However, the metrics were less harmonious on this point. Both EA and the I_{MF} clearly failed to reject the null hypothesis of no differences between the variables, while DC and the partition metric indicated results approaching significance (uncorrected $p < 0.10$).

Similarly, essentially no significant differences existed between the carnivoran taxa (Table 5.4). Although all variables except resolution had one or more metrics indicating results bordering on significance — *p* values were generally below 0.15 and often below 0.10 — the only significant difference obtained when correcting for multiple comparisons was for study date as measured by EA. For this one case, examining the mean ranks from the Kruskal-Wallis test revealed that the value for felids was noticeably higher than those of the remaining taxa, hinting that inferences of felid phylogeny have differed more over time than those of other carnivoran taxa. In contrast, "higher groups" and hyaenids had noticeably lower values, which indicate more stable phylogenetic inferences over time.

Table 5.2: Examination of whether categories within a variable are producing significantly different inferences of phylogeny: mean values for four different comparison metrics, range of standard errors, and results of a Kruskal-Wallis test (*H* corrected for ties; *df* = degress of freedom). None of the differences were significant at the 0.05 level (corrected for multiple comparisons).

	Comparison metric			
Comparison	DC	EA	Partition	I_{MF}
Tree selection criterion				
discrete-distance	0.056	0.470	0.273	0.136
discrete-intuitive	0.072	0.304	0.232	0.110
distance-intuitive	0.022	0.475	0.203	0.103
SE	0.012–0.036	0.060–0.090	0.028–0.043	0.029–0.044
H (*df* = 2)	2.196	2.957	2.826	0.210
p value	0.3335	0.2280	0.2434	0.9002
Data source				
morphology-molecular	0.057	0.423	0.289	0.130
morphology-both	0.071	0.386	0.267	0.158
molecular-both	0.058	0.389	0.252	0.143
SE	0.029–0.031	0.059–0.078	0.034–0.039	0.030–0.058
H (*df* = 2)	0.320	0.168	0.500	0.039
p value	0.8628	0.9194	0.7788	0.9805
Molecular source				
sequence-karyology	0.035	0.494	0.252	0.225
sequence-other	0.007	0.429	0.211	0.223
karyology-other	0.013	0.384	0.152	0.082
SE	0.007–0.024	0.058–0.094	0.040–0.053	0.043–0.059
H (*df* = 2)	1.662	1.569	2.177	4.819
p value	0.4356	0.4563	0.3367	0.0899
Resolution				
low-high	0.063	0.328	0.286	0.119
SE	0.032	0.032	0.040	0.031
H (*df* = 1)	n/a: insufficient comparisons			
Date				
1970s-1980s	0.061	0.441	0.307	0.190
1970s-1990s	0.069	0.374	0.242	0.178
1980s-1990s	0.104	0.418	0.326	0.164
SE	0.026–0.042	0.049–0.084	0.037–0.045	0.031–0.041
H (*df* = 2)	0.286	0.600	1.839	0.287
p value	0.8668	0.7407	0.3987	0.8663

Table 5.3: Examination of whether differences between categories are the same across all variables: mean values for four different tree comparison metrics, range of standard errors, and results of a Kruskal-Wallis test (*H* corrected for ties; *df* = degress of freedom). There was no significant difference among variables at the 0.05 level (corrected for multiple comparisons).

Variable	Comparison metric			
	DC	EA	Partition	I_{MF}
Tree selection criterion	0.051	0.416	0.238	0.117
Data source	0.062	0.402	0.271	0.143
Molecular source	0.019	0.436	0.204	0.175
Resolution	0.063	0.328	0.286	0.119
Date	0.079	0.411	0.294	0.176
SE	0.009–0.032	0.035–0.044	0.021–0.040	0.021–0.031
H (*df* = 4)	9.966	1.821	8.580	4.696
p value	0.0410	0.7686	0.0725	0.3200

For Tables 5.2–5.4, EA generally had the highest values and DC the lowest. The partition metric and I_{MF} were intermediate between these two extremes, with the former often having slightly higher values.

Sliding window analysis

Both portions of the sliding window analysis revealed changes over time in our inferences of family-level relationships among the carnivores. The different metrics (Figure 5.1) show that inferences from the 1980s resembled that of the overall composite tree for the whole period to the greatest degree. Adding studies from either the 1970s or 1990s increased incongruence with the overall tree to about equal levels, although it is not possible to discern whether the corresponding changes in topology are similar (but see below). It is also not possible to qualify the importance of these differences from Figure 5.1; however, the previous section showed that, for study date, “higher groups” possessed a similar and possibly slightly lower level of conflict compared to other carnivoran taxa (Table 5.4) and that there were no significant differences over all taxa (Table 5.2).

Table 5.4: Examination of whether differences between categories are the same across all carnivoran taxa for a given variable: mean values for four different tree comparison metrics, range of standard errors, and results of a Kruskal-Wallis test (*H* corrected for ties; *df* = degress of freedom). An asterisk indicates a significant difference among taxa at the 0.05 level (corrected for multiple comparisons).

	Comparison metric			
Taxon	DC	EA	Partition	I_{MF}
Tree selection criterion				
Canidae	0.008	0.566	0.281	0.320
Felidae	0.144	0.708	0.314	0.087
Herpestidae	0.000	0.508	0.048	0.074
Higher groups	0.048	0.097	0.300	0.049
Hyaenidae	0.000	0.250	0.000	0.000
Lutrinae	0.381	0.399	0.500	0.167
Mephitinae	0.000	0.357	0.214	0.000
Mustelidae	0.179	0.447	0.240	0.190
Otariidae	0.009	0.742	0.278	0.067
Phocidae	0.001	0.390	0.235	0.052
Procyonidae	0.000	0.340	0.062	0.037
Ursidae	0.024	0.178	0.278	0.093
Viverridae	0.022	0.265	0.344	0.263
SE	0.000–0.092	0.000–0.258	0.018–0.055	0.012–0.131
H (*df* = 12)	19.994	22.729	20.834	18.336
p value	0.0672	0.0301	0.0529	0.1059
Date source				
Canidae	0.082	0.481	0.250	0.236
Felidae	0.082	0.690	0.382	0.148
Herpestidae	0.082	0.257	0.186	0.278
Higher groups	0.077	0.093	0.300	0.069
Hyaenidae	n/a	n/a	n/a	n/a
Lutrinae	0.000	0.350	0.136	0.517
Mephitinae	0.079	0.357	0.190	0.111
Mustelidae	0.177	0.568	0.372	0.251
Otariidae	0.037	0.434	0.222	0.147
Phocidae	0.000	0.142	0.157	0.033
Procyonidae	0.000	0.518	0.125	0.125
Ursidae	0.012	0.488	0.389	0.033
Viverridae	0.000	0.361	0.359	0.000
SE	0.000–0.101	0.000–0.121	0.015–0.076	0.002–0.111
H (*df* = 11)	14.135	22.387	19.104	18.535
p value	0.2160	0.0215	0.0592	0.0700

Table 5.4: Continued.

Taxon	Comparison metric			
	DC	EA	Partition	I_{MF}
Molecular source				
Canidae	0.001	0.298	0.219	0.308
Felidae	0.046	0.767	0.363	0.240
Herpestidae	0.000	0.520	0.057	0.229
Higher groups	0.052	0.512	0.467	0.210
Hyaenidae	n/a	n/a	n/a	n/a
Lutrinae	n/a	n/a	n/a	n/a
Mephitinae	0.079	0.321	0.190	0.111
Mustelidae	0.004	0.706	0.264	0.208
Otariidae	0.000	0.419	0.056	0.333
Phocidae	0.000	0.229	0.118	0.056
Procyonidae	0.000	0.266	0.062	0.000
Ursidae	0.000	0.232	0.222	0.000
Viverridae	0.000	0.361	0.000	0.000
SE	0.000–0.079	0.006–0.197	0.028–0.086	0.000–0.167
H (*df* = 10)	19.308	15.893	21.545	12.380
p value	0.0365	0.1027	0.0176	0.2604
Resolution				
Canidae	0.095	0.229	0.453	0.155
Felidae	0.393	0.413	0.456	0.118
Herpestidae	n/a	n/a	n/a	n/a
Higher groups	0.023	0.118	0.300	0.104
Hyaenidae	0.000	0.250	0.000	0.000
Lutrinae	0.064	0.432	0.318	0.053
Mephitinae	0.000	0.357	0.214	0.000
Mustelidae	0.098	0.495	0.395	0.232
Otariidae	0.003	0.266	0.167	0.250
Phocidae	0.011	0.315	0.265	0.083
Procyonidae	0.000	0.518	0.125	0.000
Ursidae	0.036	0.214	0.333	0.100
Viverridae	0.029	0.333	0.406	0.333
SE	n/a	n/a	n/a	n/a
H (*df* = 11)	11.000	11.000	11.000	11.000
p value	0.4433	0.4433	0.4433	0.4433

Table 5.4: Continued.

Taxon	Comparison metric			
	DC	EA	Partition	I_{MF}
Date				
Canidae	0.019	0.574	0.344	0.218
Felidae	0.041	0.784	0.461	0.191
Herpestidae	0.000	0.559	0.067	0.247
Higher groups	0.087	0.116	0.317	0.080
Hyaenidae	0.167	0.167	0.333	0.222
Lutrinae	0.155	0.530	0.364	0.269
Mephitinae	0.238	0.357	0.286	0.333
Mustelidae	0.291	0.583	0.333	0.305
Otariidae	0.037	0.275	0.167	0.120
Phocidae	0.023	0.261	0.333	0.146
Procyonidae	0.000	0.518	0.094	0.000
Ursidae	0.012	0.309	0.278	0.097
Viverridae	0.015	0.347	0.302	0.051
SE	0.000–0.124	0.000–0.153	0.000–0.167	0.016–0.111
H (*df* = 12)	21.520	26.097	16.444	17.239
p value	0.0433	0.0104 *	0.1717	0.1408

As in the previous section, the metrics were in good agreement and track each other closely throughout Figure 5.1. This is true despite the partition metric being on a different scale from the remaining metrics. It consistently possessed the highest values (unlike the previous section), rarely dropping below the maximum of 0.170 obtained by DC, EA, and the simple incongruence metric (despite the latter being unbounded above). Values for DC were always less than or equal to those of EA, while the incongruence metric could be higher or lower than either.

Some detail behind the apparent changes in topology are present in Figure 5.2, which displays the inferred sister groups of pinnipeds and the red panda. Again, a clear time effect is evident. Both taxa are inferred to have ursid affinities in the 1990s, but mustelid affinities in the 1980s. No pattern emerges from the 1970s, but, due to the distribution of studies, there is no extended period when studies from this decade dominate.

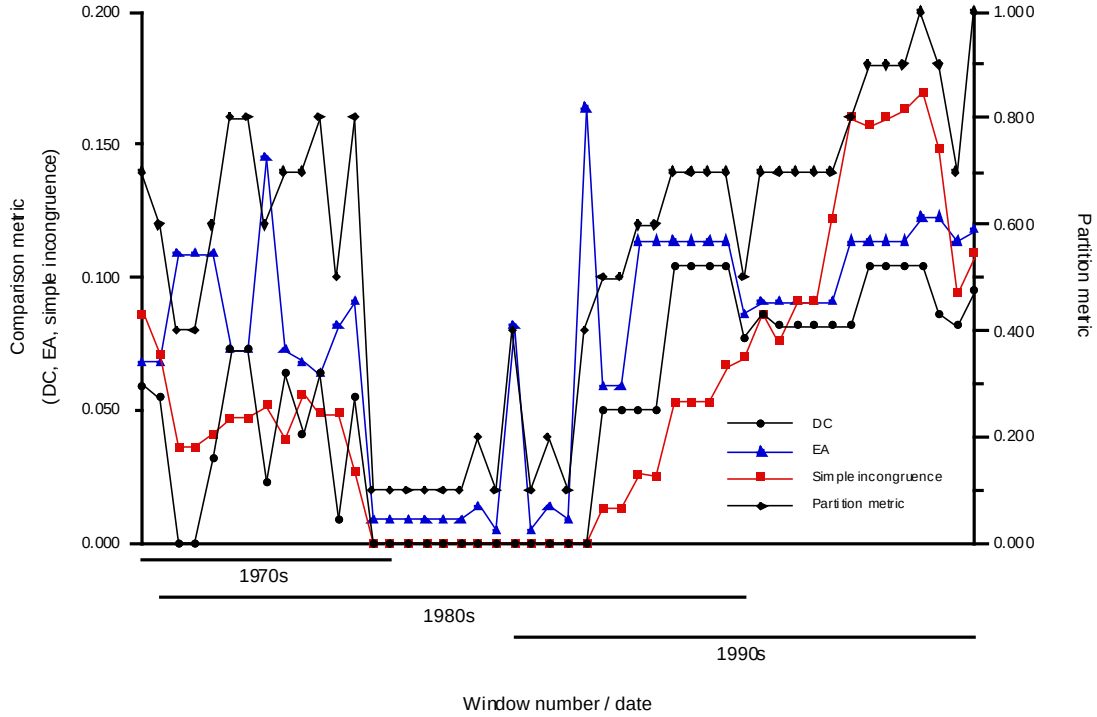

Figure 5.1: Sliding window analysis examining the changes in higher level carnivoran phylogeny over time for four tree comparison metrics. For each window of 15 source trees, composite trees were determined and compared to the composite tree for "higher groups" in Chapter 4 (Figure 4.1).

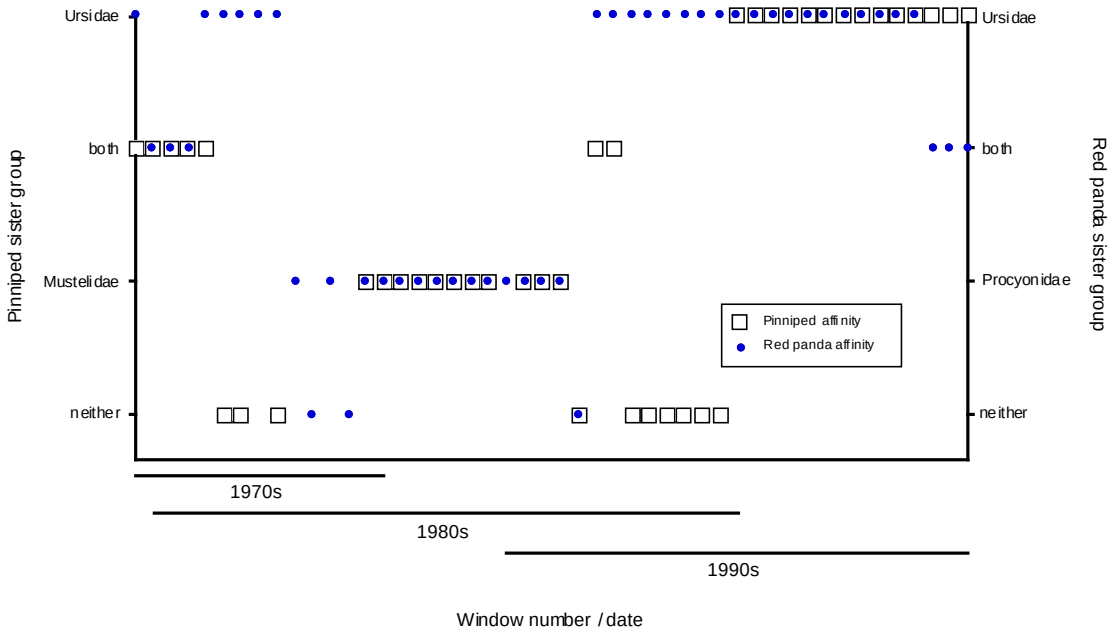

Figure 5.2: Sliding window analysis examining the changes in the inferred phylogenetic affinities of the pinnipeds and red panda (*Ailurus fulgens*) over time. Each window represents a composite tree of 15 source trees.

Interestingly, a majority of windows (24 versus 14 for the next largest group) inferred the red panda to have an ursid sister group, despite the overall composite tree placing it as the sister group to the musteloids (mustelids and procyonids). A similar discrepancy was noted in Chapter 4: although more studies indicated a red panda-ursid pairing, such a topology was not globally most parsimonious. However, the windows promoting procyonid affinity (1980s) spanned the same period wherein the resemblance to the composite tree is the greatest (Figure 5.1). The inferred sister group of pinnipeds was split about equally between mustelids and ursids. Most windows indicated a monophyletic Pinnipedia, with only six windows at the interchange of the 1970s and 1980s indicating paraphyly. This accords well with the time of greatest popularity of the diphyly hypothesis.

Discussion

One limitation of this study was that not all source trees from the period 1970 to 1995 inclusive were sampled; those appearing in smaller or less publicized journals were more likely to be overlooked or unobtainable. However, other than a deliberate tendency on my part to underrepresent taxonomies (as they are summaries of primary sources rather than primary sources themselves), I don’t feel there is any systematic bias among taxa or categories. Therefore, the results and trends noted above are likely to still be valid.

Overall, a consistent picture emerged whereby no large-scale differences were found between the different categories within a variable, nor in the level of discordance between categories for the variables themselves or between different taxa within each variable. This lack of significant differences suggests that most estimates of carnivoran phylogeny are pointing at the same solution or, minimally, that we cannot distinguish between them. Any absolute differences that do exist could therefore be interpreted as random variation around some measure of central tendency (which is hopefully the true tree). Similarly, no single advancement in phylogenetic methodology (i.e., the variables) stood out as having had more influence than the rest on our phylogenetic inferences. Although these results are strictly applicable to carnivores only, they are still

encouraging, particularly for "total evidence" and supertree reconstruction (*sensu* Sanderson *et al*., 1998) approaches to combining phylogenetic information. Both approaches appear able to give larger and/or more robust phylogenies, but implicitly depend on homogeneity among the different data sets or source trees (see Bull *et al*., 1993; Huelsenbeck *et al*., 1996).

Much has been written concerning the relative merits or deficiencies of different tree selection criteria (in particular, cladistics versus any other) or data sources. For the former, evidence has been marshaled based on philosophical discussions of methodological validity (e.g., Cracraft & Helm-Bychowski, 1991; Kluge & Wolf, 1993) or on outcomes of experimental studies involving a known phylogeny or simulations (e.g., Nei, 1991; Hillis *et al*., 1992, 1994; Hillis & Huelsenbeck, 1993; Tateno *et al*., 1994; Huelsenbeck, 1995). Although all the conclusions may be valid under the specific sets of conditions they were obtained from, their practical manifestations appear to be insignificant on the whole, matching the results obtained by Charleston (1994) and Charleston *et al*. (1994). For the latter "conflict" between molecules and morphology, my results reinforce the underpublicized statement that morphological and molecular data give largely concordant results, or at least not any more incongruent than studies within each data type (compare also metric values between data source and molecular source; Table 5.3), and are often complementary, each providing answers where the other is unable to (Hillis, 1987; Patterson *et al*., 1993; Smith & Littlewood, 1994). Differences, when they do occur, are often the result of different sets of assumptions or methods of analysis (Hillis, 1987). Even the celebrated example of this conflict within carnivores, that of pinniped monophyly or diphyly, has recently come to a similar conclusion. Historically, most morphological and paleontological studies of pinniped evolution favour a diphyletic origin of the group (e.g., Flower, 1869; McLaren, 1960; Tedford, 1976; de Muizon, 1982b), whereas most molecular studies indicate a monophyletic origin (e.g., Sarich, 1969a, 1969b; Arnason, 1974, 1977; de Jong, 1982; Wayne *et al*., 1989a). However, much of the conflict rested not on the different data types *per se*, but on questions about character applicability and inclusion for the morphological data (see

Wyss, 1988a, 1989; and the exchange between Repenning [1990] and Berta and Wyss [1990] in particular). The resolution of this issue has seen numerous morphological studies supporting a monophyletic Pinnipedia (e.g., Wyss, 1987; Flynn *et al*., 1988; Wyss & Flynn, 1993; Berta & Wyss, 1994; Bininda-Emonds & Russell, 1996).

The lack of an absolute reference tree tempers any statement as to whether a given category is "better" than another; however, there are indications that such statements can also be rejected by this analysis. For variables with three categories, arguments can be constructed as to why one category might be better or worse at estimating the one true tree. For instance, some might argue that the more rigorous discrete and distance data tree selection criteria should yield better estimates of the true tree than "intuitive parsimony." The same might be said of source trees from the 1990s given the advancements in phylogenetic methodology and theory. Therefore, solutions for discrete and distance data criteria should resemble each other more closely than either does with that from "intuitive parsimony" and those from the 1970s and 1980s should be more dissimilar than either would be with that of the 1990s (as each would contain at least some signal and thus resemble the more accurate 1990s tree to a greater extent). However, Table 5.2 reveals that these hypotheses are not borne out: the discrete-distance comparison was never the lowest of the three for any metric and the 1970s-1980s comparison showed no consistent pattern.

The comparison metrics used in this study showed a remarkable degree of concordance despite their different properties. Methodologically, the metrics could be grouped in one of two ways: the level at which they measure incongruence (raw data or tree topologies) and how they account for poor resolution (polytomies) among the source trees.

In the first case, one might expect data comparison metrics (I_{MF} and the simple incongruence metric) to produce different answers from tree comparison metrics (DC, EA, and the partition metric), given that no linear correspondence has been established between patterns of incongruence between data sets and of differences in the associated topologies. Highly congruent data sets should produce similar trees, but the reverse does

not automatically follow. Depending on the amount, direction, and distribution of the conflict, incongruent data sets could still yield similar trees (e.g., if the incongruence was relatively rare, randomly distributed, or confined to homoplastic characters). Even large amounts of incongruence could be tolerated so long as the signal-producing characters within the data sets were congruent.

Although this study does not examine the point rigorously, it appears that incongruence among data sets does translate monotonically to differences in tree topologies. Both I_{MF} and the simple incongruence metric track the results of the tree comparison metrics relatively closely through a wide range of apparent incongruence (Tables 5.2–5.4; Figure 5.1). However, this conclusion is tempered by the directionless aspect of all four metrics: they merely indicate a difference of a certain magnitude, not in which direction the difference is. Thus, two solutions can be equally different compared to some reference point, but very different from one another (within the limits of the triangle inequality). Similarly, it does not follow that two data sets that are incongruent in a certain manner will each produce a tree that differs from the other along an analogous direction. Unfortunately, the directionless nature of both tree space and the incongruence between data sets make it unlikely that a comparison metric will ever be developed that incorporates directional information.

Instead, the important distinction between the metrics is how they are affected by differences in resolution. DC tabulates differences between resolved nodes only, whereas EA measures polytomies as differences between trees. The partition metric holds polytomies to be different from resolved solutions only, not from other identical polytomies. The behaviour of the I_{MF} depends on the nature of the polytomy. Polytomies arising because of a lack of clustering information in the data are simply ignored as there can be no incongruence between the data sets. However, polytomies that summarize conflicting resolutions are evaluated as if they were resolved since they essentially represent two or more resolved clades with their underlying incongruent characters. Thus, the metrics could give different answers if the taxa or variables (“classes”) display differing propensities for producing poorly resolved solutions. EA would be the most

likely to yield significant differences as classes producing poorly resolved trees would yield high values of the metric, while those producing well resolved (and congruent) solutions would have low values. DC and to a lesser extent the partition metric should be largely unaffected by differences in resolution, although classes with poorly resolved trees will have fewer resolved nodes to provide differences and thus may produce lower values. The behaviour of I_{MF} is difficult to predict because of the two ways in which it can respond to differences in resolution.

These arguments form the basis of testable hypotheses since the taxa and variables examined herein do differ in the resolution of their composite trees (see Chapter 4). Poorly resolved composite trees stemming from conflicting information are characteristic of felids, canids, and mustelids. Poor resolution, but from a lack of information (generally a small number of source trees), is typical of herpestids, otariids, procyonids, possibly viverrids, and the variable molecular source. “Higher groups,” phocids, ursids, and the remaining variables tend to possess well resolved solutions.

As expected, EA is the most likely of the metrics to reject the null hypothesis of no difference between trees derived from different classes and the classes fall out as hypothesized: those identified above that tend to yield poorly resolved trees generally have lower values for EA than those generating well resolved trees (Tables 5.3 and 5.4).

The partition metric and DC show a weak tendency to reject the null hypothesis, suggesting that they too are affected by the amount of resolution in the trees because it limits the number of resolved nodes to be compared. However, the classes do not fall out exactly as expected for either metric. Felids, “higher groups,” and mustelids yield high values for each metric, while herpestids, phocids, procyonids, and molecular technique give low values. The largest discrepancy from our expectations is for the taxa, but this might be because both metrics are giving an accurate indication of the incongruence among the different categories for a given taxon. Phylogenetic inferences for the taxa above with high metric values are historically contentious, while those for taxa with low values are largely agreed upon, even if only poorly known (see Chapter 4 also).

Finally, the I_{MF} is the least likely to reject the null hypothesis of no differences, with canids, mustelids, and possibly hyaenids and lutrines having high values of the metric and "higher groups," phocids, procyonids, ursids, and viverrids having low values. Barring "higher groups," this distribution of taxa resembles that produced by DC and the partition metric, likewise suggesting that the I_{MF} is giving an accurate estimate of the incongruence among the different categories. Some differences in the distributions of taxa do exist, however, and may stem from each set of metrics passing the raw data through different "filters": parsimony only for I_{MF}, but parsimony and consensus techniques for DC and the partition metric. It could also be argued that the behaviour of the I_{MF} is not typical in the current context since the "data" are really cleaned up representations of the source trees for the MRP analysis, rather than the raw data yielding the source trees. Although it is difficult to determine the exact consequences of this, the effect is likely minimal or even beneficial: assuming that noise in the raw data is randomly distributed, using representations of the source trees removes this potential incongruence, improving the signal to noise ratio and thereby giving a clearer picture of the incongruence among source trees.

Conclusions

All the factors examined in this chapter have previously been proposed to (strongly) influence phylogenetic reconstruction. However, my results demonstrate that the differential impact of 1) tree selection criterion, 2) data source, 3) study size, and 4) study age on inferences of carnivore phylogeny have been minimal. The general lack of significant differences either within or among these factors or between taxonomic groups (generally families) suggests that all estimates of carnivore phylogeny are pointing to the same solution (with some error, naturally) and that the inferences for any carnivore group are no more susceptible to the methodology used than for any other group.

The findings were consistent across the four comparison metrics I used, although the different properties of the metrics caused them to vary in their propensity to indicate significant differences between contrasting solutions. Surprisingly perhaps, the most

important property in this regard was not whether the metrics measured incongruence at the level of the raw data (I_{MF}) or of the resultant trees (DC, EA, and the partition metric), but in how they responded to a lack of resolution in the data. Thus, tree comparison metrics may provide a quick estimate of the incongruence between partitions of raw data, a finding with important practical implications given that they are generally more accessible than data comparison metrics. However, this inference requires confirmation. More detailed investigation of the behaviour of the different comparison metrics is also warranted.

Chapter 6

Flippers versus feet: is there a difference between aquatic and non-aquatic carnivores?

Acknowledgements:

I am indebted to John Gittleman for providing me with his carnivore data set for my analyses, including many updates and revisions that have not yet been published. Jonathan Cooper of the IFAW and Robert Barclay (somewhat unbeknownst to him; thanks Dorothy Hill) kindly let me sift through journals in their possession. I thank Paula Jenkins and the many assistants at the Natural History Museum for again allowing me access to pinniped specimens in their care. David Bininda tracked down a longevity record for an Asiatic black bear. John Gittleman, Paul Harvey, Rob McCall, Mark Pagel, and Andy Purvis provided much helpful discussion and valuable comments during the writing of this chapter.

Synopsis

It is largely accepted that numerous adaptations characterize carnivores that have shifted to an aquatic lifestyle, and that the extreme expression of these characters in pinnipeds (seals, sea lions and fur seals, and walruses) serves as the basis for distinguishing them from the remaining terrestrial carnivores ("fissipeds") ecologically, if not taxonomically. However, these claims have never been strongly tested and the frequent exclusion of pinnipeds from comparative studies of carnivores may render the results of the latter invalid. Therefore, I tested numerous hypotheses that purport to distinguish aquatic and terrestrial carnivores by examining 22 morphological, life history, physiological, and ecological variables. Unlike previous work in this area, I corrected for phylogenetic effects using the method of independent contrasts based on my complete species level phylogeny of the extant carnivores. My results indicate that differences between aquatic and terrestrial carnivores are more restricted than previously thought. Compared to their terrestrial sister taxa, aquatic carnivores are larger, have larger brains, decreased litter sizes and interbirth intervals, a decreased red blood cell count, and increased heart rates. However, these same differences do not distinguish pinnipeds from fissiped taxa of an equivalent rank. Pinnipeds displayed the same rate of evolution as the fissiped taxa for all variables and putative grade shifts were limited to only three variables: litter weight (vs. gestation length), birth weight, and age of eyes opening (both vs. size). I conclude that the potential differences between aquatic and terrestrial carnivores, and especially between pinnipeds and fissipeds, have been overstated, thus overshadowing important differences that occur within each of these groups. It is hoped that recognition of this fact will lead to a more complete understanding of carnivore biology as a whole through more unified comparative analyses.

Introduction

The carnivoran (and arctoid) affinities of pinnipeds have been recognized and largely unquestioned since the middle of the last century (Turner, 1848; Flower, 1869). Despite this, there is a strong tendency to acknowledge a fundamental division within carnivores between pinnipeds (literally, “fin-foot”) and the remaining primarily terrestrial forms, the fissipeds (literally “claw-foot”). This is reflected in many taxonomies, which have the pinnipeds as a separate suborder within carnivores (e.g., Turner, 1848; Flower, 1869; Mivart, 1885; Simpson, 1945; King, 1983b) or even an order unto themselves (e.g., Scheffer, 1958; Ewer, 1973; Corbet & Hill, 1991).

The justification given for this non-phylogenetic distinction is that pinnipeds are very different due to their aquatic habits. An eloquent summary of the argument is provided by Gittleman (1989a:ix), who, despite acknowledging precedents for both including and excluding pinnipeds from carnivores, writes:

> “I have thus excluded the pinnipeds from discussion; the behavioral, ecological, and evolutionary features of adaptations for aquatic living set this group apart from the other terrestrial carnivores. A further, more practical reason is that other volumes nicely synthesize recent advances on research on the pinnipeds.”

The final sentence illustrates that the pinniped-fissiped distinction is also upheld by pinniped biologists.

The pinniped-fissiped distinction is likely aided because, unlike the similarly highly aquatic, but mustelid-like otters, pinnipeds do not strongly resemble another fissiped lineage either morphologically, behaviourally, or reproductively. The distinct status for pinnipeds persisted even while they were widely held to have arisen independently from two arctoid ancestors (roughly the period between the publications of McLaren [1960] and Wyss [1987]). In fact, the “diphyly hypothesis” may have paradoxically enhanced the distinctiveness of pinnipeds by emphasizing their (convergent) aquatic adaptations.

The existence of this distinction is unproductive, obscuring both similarities among all carnivores and differences within pinnipeds. Estes (1989) noted the lack of any

clear and unambiguous differences between aquatic and terrestrial carnivores, adding that most carnivores are good swimmers. Within pinnipeds, there are obvious differences in reproductive strategies, hematological parameters, and diving ability between otariids and phocids (see King, 1983b for a review). The pinniped-fissiped distinction is also suspect considering that the most aquatic of all carnivores, the sea otter (Estes, 1980; Kenyon, 1981b), is unfailingly included with fissipeds.

More importantly, the distinction has important methodological consequences. With 35 species, pinnipeds constitute a fair proportion of extant carnivores (12.9%), and their habitual exclusion from comparative analyses of "carnivores" (actually only fissipeds; e.g., Gittleman, 1986b, 1991, 1993, 1994b) could be giving misleading results (see Gittleman, 1989c for a discussion of taxon sampling in comparative analyses).

The arguments and observations supporting this division within carnivores are largely intuitive, lack empirical evidence, and have not been tested within a solid methodological framework. My strategy for testing its existence is two-fold, examining first for differences between aquatic and non-aquatic carnivores in general before specifically contrasting pinnipeds to the remaining carnivores. I focus on features held to be necessary for aquatic adaptation (following Repenning, 1976; Estes, 1989), which is where any important differences should lie. A large data set of morphological, life history, physiological, and ecological variables was constructed based on the work of Gittleman (1984, 1985, 1986a, 1986b, 1991, 1993, unpubl. data) and supplemented with observations for pinnipeds as well as other carnivores to provide at least some information for most of the 271 extant carnivoran species. Using the complete species-level phylogeny in Chapter 4, I analyzed the data using the method of independent contrasts (Felsenstein, 1985b) to control for the effects of phylogeny.

Methods and materials

Definitions

For this study, I take aquatic carnivores to be those species with strong aquatic tendencies or largely aquatic habits: pinnipeds, otters, the mustelids *Mustela lutreola* and

M. vison, the herpestid *Atilax paludinosus*, and the viverrids *Cynogale bennettii* and *Osbornictis piscivora*. This is a less stringent definition than has been used previously (e.g., those species with an obligate link to water; Estes, 1989); however, as noted by Estes (1989) the definition of "aquatic" for carnivores is highly arbitrary. Except possibly for the sea otter (*Enhydra lutris*), all carnivores are dependent on land at some point in their life cycle, usually during reproduction and parturition. It would perhaps be more accurate to speak of "amphibious" carnivores.

My definition is motivated largely by practical necessity. More standard definitions of aquatic tend to include only pinnipeds and otters; however, this would not yield enough independent contrasts to test in a statistical fashion. Although some might view the additional species included here as not being truly aquatic, if the adaptations for an aquatic lifestyle are real and strong, they should still be visible, albeit more weakly perhaps, when these "semi-aquatic" species are compared to their non-aquatic sister taxa.

Hypotheses and the data set

Expanding on Repenning (1976), Estes (1989) divided the many putative adaptations between aquatic and non-aquatic carnivores into 10 broad, interdependent categories. Although all categories yield testable hypotheses, sufficient data for testing was only available for three — heat conservation, oxygen conservation, and life history traits — plus some miscellaneous traits. These categories are listed below together with their attendant hypotheses (summarized in Table 6.1) and variables (described fully in Appendix C). Unless otherwise noted, all hypotheses are from Estes (1989). Where directionality for a hypothesis is given, it always refers to the value in aquatic forms (or pinnipeds) as compared to non-aquatic forms (or fissipeds).

1) Heat conservation

Due to its greater thermal conductivity, water is a much colder environment than air. Other than decreasing their thermal conductance (for which data are scanty) by being

better insulated via blubber or a thicker coat, aquatic carnivores could conserve or generate additional body heat in one of three main ways.

a) increasing basal metabolic rate (BMR)

Although supported by older experimental studies, the assertion that aquatic mammals in general have proportionately higher BMRs for their mass was recently cast into doubt (see Lavigne *et al*., 1986 and references therein). Because of their larger size, many physiological studies of marine mammals are performed on juveniles, whereas those of most terrestrial mammals are performed on adults in accordance with Kleiber's (1975) criteria for measuring BMR (adults that are postabsorptive, non-reproductive, at rest, and in thermoneutral conditions), and juveniles have elevated BMRs compared to adults (Ashwell-Erickson *et al*., 1979; Little, 1995). Metabolic data for marine mammals meeting Kleiber's criteria apparently do not show elevated BMRs (Lavigne *et al*., 1986). Complicating this issue, previous studies did not account for phylogenetic effects. Elgar and Harvey (1987) detected increased BMRs for aquatic mammals using cross-species regression only; the effect disappeared when taxonomic information was included in the analysis.

Economos (1979) and Platt and Silvert (1981) argued on theoretical grounds that BMR should scale differently with body mass in aquatic versus terrestrial animals. Because aquatic organisms are not exposed to as much of a gravitational load, they argue that these forms are not similar geometrically to terrestrial organisms such that their BMRs scale only to the two-thirds power and not three-fourths as in terrestrial forms. Thus, for a given increase in weight, BMR would increase proportionately less in aquatic organisms.

I examined both mass-specific BMR (measured in mL O_2 / g / min) and total BMR (in mL O_2 / min) to eliminate possible autocorrelative effects (Elgar & Harvey, 1987).

b) decreasing surface area to volume ratio

A decreased ratio, which minimizes the radiative surface to the environment, can be achieved by increasing body size and by becoming more spherical in shape. Thus aquatic carnivores should be larger and less elongate than their non-aquatic sister taxa. Although there are exceptions, the trend to increased size is found in many aquatic forms (see Estes, 1989) and there is fossil evidence indicating an increase in size along aquatic lineages (Estes, 1989; Wyss, 1994). Otters are less elongate than most other mustelids (Estes, 1989), but this may be due to selection in weasels for an extremely elongate body plan; other less elongate mustelids also exist (see Brown & Lasiewski, 1972; Knudsen & Kilgore, 1990). The relevant variables are body mass and head and body length.

c) decreasing body temperature (Morrison, 1962; Hubbard, 1968)

Morrison (1962) observed a slight trend for decreased body temperatures in marine mammals, which he tentatively attributed to their larger body sizes. Hubbard (1968) later suggested the trend may be connected with diving ability, as better, deeper divers tend to have lower temperatures. The relation between temperature and body size is unclear. Although Morrison and Ryser (1952) found temperature to be independent of weight across mammals, they allowed that some relationship might occur within "homogeneous subgroups" like carnivores (also Folk *et al*., 1977); White *et al*. (1996) reported a negative relationship between mass and body temperature in black bears. McNab (1984) suggests that a complex interaction may exist between size, temperature, and BMR.

2) Oxygen conservation

This category applies mostly to the subset of aquatic carnivores that dive, where the associated pressure changes and extended periods of apnea require a suite of physiological and morphological adaptations (see Scholander, 1940). These changes, particularly in hematological variables, are more pronounced in deeper diving forms

(Lenfant *et al*., 1970; Ridgway, 1972; Wickham *et al*., 1990; Melrose *et al*., 1995). The paucity of data, especially for terrestrial species, limits the variables to a few blood parameters. The parameters below are not exhaustive. Others such as mean cell volume exist, but are derivable from the ones I have included. Also, the parameters I use might not be where strong differences lie because they are interdependent and vary within narrow limits to maintain optimal oxygen transport (Hawkey, 1977). A critical adaptation for diving forms appears to be increased oxygen stores (but not affinity), through either increased blood volume or increased oxygen capacity, both of the blood and hemoglobin (Lenfant, 1969; Lapennas & Reeves, 1982; Hochachka, 1992). With more data for terrestrial species, investigations along these lines might be more productive.

Relative to terrestrial forms, aquatic species are characterized by the following:

a) increased hematocrit (Hct) levels

Hematocrit (or packed cell volume) is the proportion of blood composed of red blood cells (Brannon, 1985). Like most hematological variables, Hct is a dynamic parameter that can be (rapidly) altered in response to apnea, stress, development, molting, and captivity, and will also vary according to the measuring technique (Castellini *et al*., 1996).

b) increased hemoglobin concentration

Together with (a), these hypotheses might be true of phocid seals only, which are the best divers among aquatic carnivores; the sea otter and otarioids (sea lions, fur seals, and walruses) have similar values to terrestrial species (Lenfant *et al*., 1970, but see Lane *et al*., 1972). Increasing either Hct or hemoglobin levels would increase oxygen stores; however, Hawkey (1977) indicates both variables to be constant throughout mammals.

c) decreased red blood cell (RBC) count (Hawkey, 1977)

This hypothesis derives from an inverse relationship between RBC size and number to maintain constant Hct. Larger RBCs are thought to be beneficial for all diving

mammals because the decreased surface area to volume ratio ensures a constant, slower release of oxygen (Hawkey, 1977; also Wickham *et al*., 1989).

d) possible changes in resting heart rate (pers. interpretation)

Apart from hibernators, diving forms are distinguished from other mammals by the ability to tremendously slow their heart rates (while diving). Even on land, heart rates can vary (King, 1983b), ignoring compounding factors such as sleep bradycardia and sleep apnea in northern elephant and Weddell seals (Bartholomew, 1954; Kooyman, 1981d, 1985). Yet, correlates of heart rate are poorly known beyond a negative relationship with size (Stahl, 1967) and correlates thereof. I propose no specific hypothesis, but will examine if heart rates differ systematically between the groups of interest herein.

3) Life history traits

Life history traits are well studied in carnivores. Within fissipeds, most traits vary among the major lineages (families), correlate positively with size (by being dependent on general physiology) and each other, and are largely independent of many ecological factors (e.g., diet, zonation, habitat vegetation, and activity pattern) (Gittleman, 1986b, 1993). Life history traits are as well known for pinnipeds (e.g., Harrison, 1969; Stirling, 1983); however, as noted by Estes (1989), the changes in these traits necessary for adapting to an aquatic environment, if any, are comparatively unknown.

The variables I examined were gestation length (not including any period of delayed implantation; i.e., active gestation), birth (neonate) weight, litter size, litter weight, age at which the eyes open, age of weaning, age of independence from parental care, age of sexual maturity (male and female), interbirth interval, and longevity. Of these, all correlate positively with size and each other except litter size (which correlates negatively with some variables) and eye opening; correcting the variables for size reduces the number of intercorrelations (Gittleman, 1986b; also Clutton-Brock & Harvey, 1983 and references in both). Because aquatic carnivores are putatively larger than non-aquatic

ones (see above), their life history traits, except litter size (decreased) and age of eye opening (no change), should be increased as well, so long as size is not corrected for.

Beyond the allometric relationships of life history traits, several other testable hypotheses arise based on previous findings (e.g., Laws, 1959; Stirling, 1983; Gittleman, 1986b, 1994b), which are an attempt to target key differences accruing from the lifetime reproductive strategy of pinnipeds, which unlike most other carnivores shows several K-selected traits: a single, large precocial neonate; delayed sexual maturity; and a long absolute and reproductive lifespan (McLaren, 1967; Hennemann, 1983; Stirling, 1983; Schmitz & Lavigne, 1984). These hypotheses comprise most of the "miscellany" category in Table 6.1.

4) Miscellaneous characters

a) (overall) brain weight

Relative brain size in aquatic mammals has been the subject of much conjecture and debate. Early hypotheses held that aquatic mammals have proportionately smaller brains for their weight because the high metabolic and energetic demands of neural tissue conflicts with the need to conserve oxygen while diving (Robin, 1973; Hofman, 1983) or because large animals have proportionately smaller brains, and diving forms are large to maximize their oxygen storage capabilities (Worthy & Hickie, 1986; see above). In contrast, Estes (1989) mentioned, but didn't advocate that the need to interpret their more complex three dimensional environment might select for larger brains in aquatic forms. Some empirical evidence describes pinnipeds as having among the largest indices for various brain regions for carnivores (Wirz, 1950; Stephan, 1972), except for the olfactory lobes which are reduced, particularly in phocids (Fish, 1898; Harrison & Kooyman, 1968). However, other evidence indicates no difference in overall brain size between aquatic and terrestrial mammals (Gittleman, 1986a; Worthy & Hickie, 1986).

I examine overall brain weight only because the sizes of different brain components tend to be poorly reported, especially for pinnipeds. Fortunately, overall brain size correlates strongly with the sizes of most brain components (Jerison, 1973).

One notable exception is the olfactory lobes, which are also very much reduced or absent in aquatic mammals, reflecting the diminished role of olfactory information in such environments (Fish, 1898; Harrison & Kooyman, 1968; Jerison, 1973; Gittleman, 1991).

b) degree of sexual dimorphism

Estes (1989) raised this character for otters, but his preliminary analysis revealed no trends and no hypothesis was proposed. Among carnivores, only two groups show strong dimorphism in body size: mustelids and pinnipeds. Phocids may be monomorphic or dimorphic in either direction, while otarioids are the most dimorphic of mammals (Weckerly, 1998). Factors influencing the degree of sexual dimorphism are breeding system and body size, with sexual dimorphism being greater in larger animals (Bartholomew, 1970; Ralls, 1977; Weckerly, 1998).

The degree of sexual dimorphism was calculated for body weight, brain weight, head and body length, and age of sexual maturity.

c) (decreased) population density

Estes (1989) suggested population density to be a function of food availability (also Gittleman, 1984, 1989c), with both being lower in marine versus freshwater environments for otters. If differences in food availability extend to terrestrial versus aquatic environments in general then a distinction in population density might also occur. Differences may also exist within aquatic carnivores since pinnipeds are almost exclusively marine while the remaining forms are almost exclusively freshwater.

Gittleman and Harvey (1982) noted a positive correlation between home range size and metabolism (and therefore body size). Thus, aquatic carnivores could be expected to exist at smaller densities due to their presumed larger body size and increased metabolisms (see above). However, this argument assumes a negative relationship between home range size and population density (see Gittleman, 1984, 1989c), which relies on the exclusivity of home ranges among other factors. I did not examine home range size because no such data exist for pinnipeds.

Table 6.1: Summary of the hypotheses under study and the variables used to test them. Predictions refer to the value expected in aquatic forms (or pinnipeds) as compared to non-aquatic forms (or fissiped taxa) (+ = increased, – = decreased, 0 = no change) and are given for when the variables have and have not been corrected for size (body or brain weight). Full names for all variables are found in Appendix C.

Category	Dependent variable	Independent variable	Raw hypothesis	Size-corrected hypothesis
Allometry	SWt		+	+
	SHB		+	+
	SBr		conflicting	conflicting
	LS		–	none
	GL		+	none
	BWt		+	none
	LWt		+	none
	WA		+	none
	AI	body	+	none
	MMat	weight	+	none
	FMat	or	+	none
	IB	brain	+	none
	EO	weight	0	none
	LO		+	none
	mBMR		+	+
	tBMR		+	+
	T_B		–	–
	Hct		not –	not –
	Hb		+	+
	RBC		–	–
	HR		none	none
	PD		–	–
Dimorphism	MWt	FWt	none	none
	MHB	FHB	none	none
	MBr	FBr	none	none
	MMat	FMat	none	none
Miscellany	SBr	GL	none	none
	SBr	EO	none	none
	LWt	GL	none	none
	AI	WA	none	none
	MMat	LO	none	none
	FMat	LO	none	none
	WA	EO	none	none
	PD	mBMR	none	none
	PD	tBMR	none	none

The data set used to test these hypotheses consists of 22 morphological, life history, physiological, and ecological variables (see Table 6.1). Most of the fissiped data are from Gittleman (1984, 1985, 1986a, 1986b, 1991, 1993, unpubl. data), although I supplemented data from the literature for missing values where possible. I obtained pinniped data from numerous literature sources, except for brain weight which I estimated from the cranial capacities of specimens measured at Natural History Museum, London. I followed the protocol of Gittleman (1986a) for this, although time constraints meant that I could only measure two specimens (generally one male, one female) for each species. Complete descriptions of all variables and the procedure used to compile the data set are found in Appendix C.

Analysis

Correcting for phylogenetic effects

A problem with comparative analysis is that species values are not independent due to hierarchical descent with modifications through evolution: species sharing a common ancestor are likely to be more similar than species that do not, rendering simple cross-species regression invalid (Harvey & Pagel, 1991; Pagel, 1993; Purvis *et al*., 1994). I corrected for the effects of phylogeny using the method of independent contrasts (Felsenstein, 1985b) as implemented in the CAIC package (Purvis & Rambaut, 1995). Based on a phylogeny, branch length information (= model of evolution; e.g., gradual vs. punctuational), and some specified predictor variable, CAIC generates "contrasts" between nodes calculated from values of the variables in each node's descendent taxa. The predictor variable can be dichotomous or continuous (for what are referred to in CAIC as BRUNCH or CRUNCH analyses, respectively). Unless otherwise noted, analyses were based on the carnivore phylogeny and associated "best estimate" branch lengths from Chapter 4 (see Figure 4.13, Tables 4.2–4.13). I did not include any data for the herpestids *Dologale dybowskii* and *Rhynchogale melleri*, effectively excluding them from the analyses, because of the extreme uncertainty in their phylogenetic position (see Chapter 4). Variables were log-transformed (base e) to better conform to CAIC's

underlying random walk model of evolution (Felsenstein, 1985b; Purvis & Rambaut, 1995), to equalize variances and improve normality, and to change the many allometric power relationships into linear ones. For age of eyes opening, it was necessary to add one to the raw values before the transformation.

I tested whether the variables under examination displayed phylogenetic effects, and if so then at what level, using the Moran's *I* statistic (a form of nested ANOVA) as implemented in the Phylogenetic Autocorrelation package (Gittleman & Kot, 1990; Purvis *et al*., 1994). Groups are typically delineated for this procedure using taxonomic information. However, because this obscures phylogenetic information, I used my carnivore tree to produce a "phylogenetic taxonomy." I divided the tree into five intervals of 13.45 million years to yield an equivalent number of ranks as found in most carnivore taxonomies. I refer to these ranks as "time slices" (TS) and number them from 0 (highest; equivalent to the entire order) to 4 (lowest; equivalent to species). The taxa were simply those monophyletic lineages occurring at each time slice.

Allometric effects

Most of the variables, particularly the life history traits, are reported to show some relationship with size (see above). Therefore, I performed a series of CRUNCH analyses in CAIC with size as the independent, predictor variable to determine which do and to produce size-corrected variables. I used species values of size in all cases except for life history traits where I used female values (or male values for age of male sexual maturity) (following Gittleman, 1986b).

Typically, body weight is taken to estimate size; however, it is highly variable, changing with season, reproductive condition, and physical condition among other factors (Gittleman, 1986b). Thus, body length is frequently used to estimate size in pinnipeds (Lavigne *et al*., 1982; McLaren, 1993). Some also argue that brain weight is a better estimator of size because neural tissue growth constrains somatic cell proliferation and thus determines development (Sacher & Staffeldt, 1974) or, in terms of life history traits, because it may be more closely tied with maternal metabolic rate (Gittleman, 1986b).

Brain weight often accounts for a greater proportion of the variance in numerous variables than body weight (Sacher & Staffeldt, 1974; Gittleman, 1986b) because it is less variable intraspecifically, thus reducing the amount of noise (Economos, 1980). As my goal was simply to correct for size, I tested all variables against both body and brain weight and used the one that showed the stronger relationship based on *p* values, followed by the one with the higher coefficient of determination (r^2). This less rigorous procedure was used instead of multiple regression because the strong collinearity of body and brain weight renders the latter invalid.

Aquatic versus non-aquatic comparisons

To test whether a distinction between aquatic and non-aquatic carnivores exists in general, I conducted a BRUNCH analysis in CAIC using a dichotomous habitat variable (aquatic vs. terrestrial) as the predictor variable. Size correction, when necessary, followed the procedure in the CAIC manual: an initial CRUNCH analysis with size as the (continuous) predictor variable, with the least squares regression equation (determined through the origin) from this fitted to the species (not contrast) data points to generate a set of residuals for the BRUNCH analysis (Purvis & Rambaut, 1995).

Analyses of sexual dimorphism used ratios calculated as ln(male value / female value), which, so long as the source variables (body weight, head and body length, brain weight, and age of sexual maturity) are normally distributed, yields another normally distributed variable. I did not correct the ratios for allometric effects.

If a distinction between aquatic and non-aquatic carnivores does exist, all the contrasts will be in the same direction. Therefore, results were tested with a sign test (one- or two-tailed depending if a hypothesis was ventured). I did not correct for multiple comparisons because the limited number of contrasts (= number of aquatic-terrestrial sister taxa; eight maximum) often could not yield a low enough *p* value (derived from Zar, 1984) to indicate significance under such circumstances, even if all contrasts were in the same direction.

The limited number of contrasts also meant that the still contentious issue of the placement of pinnipeds within arctoids could affect the outcome. Therefore, I performed the analyses using three different tree topologies incorporating the major competing hypotheses of pinniped relationships: 1) a monophyletic Pinnipedia with mustelid affinities, 2) a monophyletic Pinnipedia with ursid affinities, or 3) a diphyletic Pinnipedia with phocids having a mustelid affinity and otarioids having an ursid affinity (Figure 6.1; see Bininda-Emonds and Russell [1996] for a review). Note that Tree 3 yields an extra contrast relative to Trees 1 and 2 as phocids and otarioids each possess a non-aquatic sister taxon.

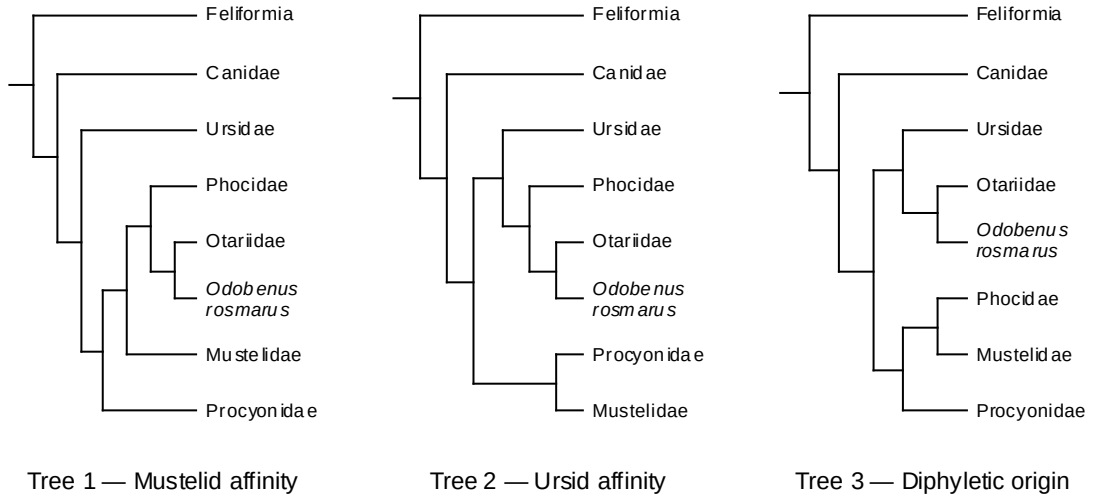

Figure 6.1: The major competing hypotheses for the placement of the pinnipeds within the arctoids as tested herein. Numbers are relevant divergence times in millions of years. I consider the composite phylogeny in Chapter 4 (see Figure 4.1) to be a variant of Tree 1 (mustelid affinity).

Pinniped versus fissiped comparisons

Having thus established the characters that distinguish aquatic from non-aquatic carnivores, I then examined whether these same characters separate pinnipeds from fissipeds. Straight comparisons between pinnipeds and fissipeds are invalid because the latter are an unnatural clustering of diverse taxa, some of which are more closely related

to pinnipeds than to other fissipeds. I therefore derived a set of fissiped taxa comparable to pinnipeds using the time slice of my "phylogenetic taxonomy" at which pinnipeds formed a single taxon (TS2) (Table 6.2).

I measured sexual dimorphism by regressing the male value for a variable on the female one. All variables for all hypotheses were corrected for size if necessary. I accomplished this for the dimorphism and miscellany hypotheses (see Table 6.1) using a CRUNCH analysis with size as the predictor variable to determine contrasts for both variables of interest. I then used these latter contrasts for the least squares regression analysis. I again used both body and brain weight to estimate size and used the one that yielded the stronger relationship based on *p* values and then r^2 values.

Any differences between pinnipeds and the fissiped taxa could arise in three ways: 1) different rates of evolution, 2) different patterns of evolution, or 3) different "starting points" between groups (i.e., grade effects). The latter two are normally determined by comparing the slopes and intercepts of the regression equations, respectively, for each group. With independent contrasts, however, regressions must pass through the origin. Therefore, grade effects are visualized instead by the relevant contrast (e.g., the pinniped-

Table 6.2: Taxa occurring at the level of time slice 2 (= 26.9 million years before present). Names follow Wozencraft (1993) with Pinnipedia comprised of Phocidae, Otariidae, and *Odobenus rosmarus*.

Mustelidae
Procyonidae
Ailurus fulgens
Pinnipedia
Ursidae (excluding *Ailurus*)
Canidae
Hyaenidae
Felidae
Herpestidae
Genetta spp. + *Osbornictis piscivora* + *Poiana richarsdsonii* + *Prionodon* spp.
Civettictis civetta + *Viverra* spp. + *Viverricula indica*
Nandiniinae + Paradoxurinae
Hemigalinae
Cryptoproctinae + Euplerinae

ursid node in Tree 1) being a significant outlier from the other contrasts (Purvis & Rambaut, 1995). Rates of evolution are estimated directly by CAIC's standardized contrasts (Purvis & Rambaut, 1995).

Although many variables were significantly related to the predictor variable over the entire order, the relationships often disappeared at the TS2 level (results not shown), meaning that patterns of evolution could not be compared (or can be considered to be identical). Therefore, for the remaining tests, corrections for the independent variable (typically size), when necessary, used residuals from the regression for the entire order.

I tested for differences in evolutionary rates using a Kruskal-Wallis analysis of the standardized contrasts or (size-corrected) residuals thereof for each variable. Multiple comparisons were corrected for using a sequential Bonferroni technique (Rice, 1989). Differences between groups were localized using a non-parametric Student-Newman-Keuls test with pinnipeds as the control taxon (Zar, 1984). I identified putative grade shifts on the part of pinnipeds by determining whether the standardized contrast (or residual thereof) for the node connecting pinnipeds to the fissipeds was greater than 1.96 standard deviations away from the mean of the remaining points using *Z*-scores (i.e., whether it fell into either 2.5% tail of the distribution).

All analyses comparing pinnipeds and fissipeds were based on Tree 1 only (see Figure 6.1). Because each node in the carnivore tree could supply a contrast for these comparisons, the greater number of contrasts (usually > 75) made the results less sensitive to different phylogenetic placements of pinnipeds, which would only affect a handful of contrasts. All contrasts were used to determine regression equations, but I tested for differences in evolutionary rates among TS2 taxa using only the contrasts within each taxon and I tested for grade effects using the contrasts linking TS2 taxa.

Results

Presence and location of phylogenetic autocorrelation

Dividing the phylogeny in Figure 4.13 into five time slices at intervals of 13.45 million years produced taxa with 1, 3, 14, 57, and 271 members (for TS0 to TS4),

compared to one order, two suborders, 12 families, 123 genera, and 271 species of a standard taxonomy (Wozencraft, 1993). The rate of increase between time slices was more uniform than that of the Linnaean taxonomy. There was roughly a four-fold increase between each slice compared to a range of two to ten-fold between Linnaean ranks. This steady rate of increase does not appear to be an artifact of the pure birth model used in Chapter 4 to establish divergence times for nodes when literature estimates were lacking. Only 35 nodes (= 16.6% of the 211 nodes in the phylogeny) had dates derived in this manner from nodes older than 13.45 million years, of which only 15 (= 7.1%) were older than this value. This should not affect taxon numbers in the lower time slices to any great extent.

All variables displayed both criteria indicating significant phylogenetic correlation under the Moran's *I* test: 1) the *Z*-value (standardized relative to values sampled from the n! permutations of the raw data) for at least one time slice was greater than 1.96 (= $p \leq 0.05$) and 2) *Z*-values were positive and large at the lower slices (i.e., TS2 or 3) before decaying to negative values at the higher slices (Table 6.3; Gittleman & Kot, 1990). The transition point from positive to negative values, which indicates where most of the variation is occurring, was at the TS2 level for most variables. Only weaning age (TS1) and age of independence, interbirth interval, age of eyes opening, Hct, and hemoglobin concentration (all TS3) did not follow this pattern. This reinforced my decision to examine for differences among groups at the TS2 level (see Table 6.2). Generally, TS2 taxa equate to the carnivoran families, except for the red panda (*Ailurus fulgens*) and the subdivision of viverrids into five lineages, roughly along subfamilial lines.

Correlations with size (Table 6.4)

All variables displayed a significant relationship with size (body or brain weight) except age of independence, age of eyes opening, body temperature, Hct, and hemoglobin concentration. Brain weight usually explained the variation in a variable slightly better; only total BMR and RBC count were slightly more closely related to body weight.

Table 6.3: Moran's *I* statistics demonstrating phylogenetic autocorrelation between all variables and time slice ranks. *Z*-values greater than 1.96 are significant at $p \leq 0.05$. Full names for all variables are found in Appendix C.

Variable	Time slice	Moran's *I*	Normalized Moran *I*	*Z*-value
MWt	3	0.819	0.832	15.745
	2	0.820	0.780	24.833
	1	-0.346	-0.464	-27.485
	0	-0.063	-0.290	-9.575
FWt	3	0.809	0.825	15.817
	2	0.795	0.758	23.927
	1	-0.376	-0.532	-29.773
	0	-0.045	-0.243	-6.406
SWt	3	0.797	0.846	18.538
	2	0.827	0.775	32.555
	1	-0.332	-0.423	-34.960
	0	-0.050	-0.257	-9.983
MHB	3	0.828	0.812	13.225
	2	0.748	0.831	11.086
	1	-0.537	-0.768	-21.659
	0	-0.061	-0.271	-4.000
FHB	3	0.823	0.817	12.819
	2	0.747	0.788	11.323
	1	-0.568	-0.800	-21.651
	0	-0.049	-0.243	-2.899
SHB	3	0.796	0.846	19.106
	2	0.843	0.784	33.490
	1	-0.341	-0.475	-37.345
	0	-0.038	-0.224	-7.641
MBr	3	0.860	0.851	13.682
	2	0.839	0.795	18.495
	1	-0.323	-0.439	-20.022
	0	-0.105	-0.367	-12.230
FBr	3	0.835	0.830	13.184
	2	0.827	0.783	17.901
	1	-0.357	-0.486	-21.833
	0	-0.085	-0.331	-9.644
SBr	3	0.834	0.871	18.951
	2	0.882	0.811	32.084
	1	-0.267	-0.367	-28.109
	0	-0.072	-0.307	-14.183
LS	3	0.765	0.821	16.039
	2	0.510	0.602	17.994
	1	-0.283	-0.484	-25.948
	0	-0.048	-0.343	-8.140
GL	3	0.863	0.870	16.246
	2	0.929	0.842	26.974
	1	-0.508	-0.668	-35.748
	0	-0.041	-0.252	-5.454

Table 6.3: Continued.

Variable	Time slice	Moran's *I*	Normalized Moran *I*	*Z*-value
BWt	3	0.902	0.872	15.576
	2	0.929	0.835	21.154
	1	-0.492	-0.698	-30.118
	0	-0.045	-0.248	-4.995
LWt	3	0.818	0.827	14.141
	2	0.872	0.797	19.839
	1	-0.456	-0.665	-27.883
	0	-0.034	-0.212	-3.528
WA	3	0.721	0.741	12.257
	2	-0.140	-0.213	-3.072
	1	-0.062	-0.328	-3.531
	0	-0.003	-0.100	0.481
AI	3	0.745	0.733	9.375
	2	0.429	0.541	6.441
	1	0.060	0.109	2.610
	0	-0.138	-0.436	-10.382
MMat	3	0.736	0.727	10.690
	2	0.734	0.756	13.953
	1	-0.296	-0.444	-12.858
	0	-0.135	-0.434	-12.586
FMat	3	0.681	0.738	11.156
	2	0.629	0.661	14.748
	1	-0.273	-0.495	-16.316
	0	-0.065	-0.341	-7.891
IB	3	0.385	0.478	6.361
	2	0.296	0.406	6.835
	1	0.114	0.204	7.505
	0	-0.099	-0.366	-12.125
EO	3	0.876	0.848	13.408
	2	1.009	0.886	22.495
	1	-0.580	-0.880	-35.966
	0	-0.013	-0.134	-0.692
LY	3	0.601	0.659	9.674
	2	0.503	0.567	13.485
	1	-0.215	-0.391	-15.724
	0	-0.039	-0.238	-4.976
mBMR	3	0.663	0.639	6.191
	2	0.206	0.316	2.229
	1	-0.207	-0.571	-5.441
	0	-0.018	-0.170	-0.112
tBMR	3	0.626	0.635	5.764
	2	0.717	0.664	7.268
	1	-0.266	-0.488	-7.037
	0	-0.015	-0.142	0.051
T_B	3	0.508	0.532	4.251
	2	0.064	0.092	0.907
	1	-0.161	-0.496	-3.803
	0	-0.024	-0.223	-0.321

Table 6.3: Continued.

Variable	Time slice	Moran's *I*	Normalized Moran *I*	*Z*-value
Hct	3	0.644	0.670	6.960
	2	0.382	0.406	4.612
	1	0.209	0.368	6.065
	0	-0.256	-0.587	-15.733
Hb	3	0.735	0.728	8.570
	2	0.372	0.373	4.579
	1	0.146	0.231	4.380
	0	-0.245	-0.571	-15.269
RBC	3	0.593	0.645	6.838
	2	0.718	0.714	8.371
	1	-0.145	-0.229	-3.301
	0	-0.159	-0.458	-8.934
HR	3	0.638	0.661	4.665
	2	0.364	0.451	3.232
	1	-0.235	-0.576	-2.456
	0	-0.020	-0.187	0.218
PD	3	0.284	0.409	3.447
	2	0.500	0.548	6.403
	1	-0.177	-0.509	-5.073
	0	-0.018	-0.168	-0.337

Variables that regressed significantly on only one size measure were litter size, age of weaning, interbirth interval (all with brain size), and heart rate (with body weight). This discrepancy usually arose from differences in the correction for multiple comparisons. Except for litter size, uncorrected *p* values were less than 0.05 for these variables when they were regressed on the other size estimator.

Aquatic versus non-aquatic comparisons

Few significant differences existed between aquatic and non-aquatic carnivores, and most would disappear if multiple comparisons were corrected for. However, distinct trends were still discernible (Table 6.5; full results in Appendix E). I hold "weak" trends to be those where a clear majority of contrasts are in one direction and "strong" trends to be those where all contrasts are in the same direction. Strong trends need not imply a

Table 6.4: Results of least squares regression analyses of independent contrasts with size (body or brain weight) as the independent variable. An asterisk indicates slopes significantly different than zero at the 0.05 level (corrected for multiple comparisons using a sequential Bonferroni correction). Where both body weight and brain weight yielded significant relationships, preference was given to the one that was more significant, followed by the one with larger coefficient of determination (indicated in bold face). Full names for all variables are found in Appendix C.

Variable	Versus body weight			Versus brain weight		
	n	slope	r^2	*n*	slope	r^2
SW	n/a	n/a	n/a	**187**	**1.479 ***	**0.718**
SHB	198	0.204 *	0.533	**189**	**0.481 ***	**0.726**
SBr	**187**	**0.462 ***	**0.714**	n/a	n/a	n/a
LS	151	0.010	0.001	**118**	**-0.131 ***	**0.075**
GL	133	0.062 *	0.060	**109**	**0.205 ***	**0.176**
BWt	117	0.531 *	0.440	**97**	**1.245 ***	**0.747**
LWt	117	0.550 *	0.480	**97**	**1.172 ***	**0.736**
WA	118	0.118	0.044	**101**	**0.283 ***	**0.070**
AI	78	0.160	0.075	70	0.195	0.043
MMat	95	0.153 *	0.163	**85**	**0.385 ***	**0.322**
FMat	116	0.106 *	0.069	**98**	**0.405 ***	**0.324**
IB	117	0.082	0.052	**101**	**0.249 ***	**0.139**
EO	114	-0.063	0.020	96	-0.184	0.045
LO	145	0.148 *	0.121	**142**	**0.356 ***	**0.216**
mBMR	55	-0.123 *	0.147	**55**	**-0.231 ***	**0.171**
tBMR	**56**	**0.941 ***	**0.926**	56	1.409 *	0.819
T_B	51	0.001	0.000	51	0.010	0.047
Hct	65	-0.018	0.020	65	-0.019	0.007
Hb	66	0.019	0.016	66	0.041	0.024
RBC	**63**	**-0.076 ***	**0.120**	63	-0.132 *	0.117
HR	**35**	**-0.166 ***	**0.237**	36	-0.212	0.128
PD	68	-0.733 *	0.197	**66**	**-1.597 ***	**0.290**

significant difference (e.g., insufficient contrasts for a test), nor does a significant difference necessarily require a strong trend.

The underlying topology did not affect the results much, merely occasionally shifting the findings one step along in the no trends to weak trends to strong trends continuum. In contrast, inferred differences between aquatic and non-aquatic carnivores were strongly affected by whether the variables were corrected for size and then by the size estimator that was used.

When no size correction was undertaken, most variables showed no clear trend or a weak to occasionally strong tendency to increased values in aquatic species. Head and body length and brain weight in particular were significantly larger in aquatic species. When size was corrected for using body weight, most of the relevant variables retained their slight to strong tendencies to increased values. Only one reversal was seen, that of a weak negative trend in population density to a weak positive trend, although total BMR does go from a strong positive trend to no clear trend when corrected for body size. When brain weight was used to correct for size, most trends were "muted" to show no clear patterns whatsoever. Only birth weight and population density displayed trends to larger values in aquatic species, the latter again being a reversal from the case where no size correction was used.

I will base further discussion on the "best estimate" for each variable (Table 6.5), which follows the outcome of the allometric portion of the study (i.e., the set of contrasts chosen accorded with whether a variable was size-independent or regressed more strongly with body or brain weight). Most variables did not display a clear trend and there were no significant differences. Morphologically, aquatic species showed weak tendencies to be relatively smaller in body size (compared to brain weight) than non-aquatic forms and, equivalently, to have relatively larger brains for their body weight. Generally, there was no difference in morphological sexual dimorphism, although aquatic forms may be less dimorphic in head and body length. In life history terms, aquatic species showed strong

Table 6.5: Summary of differences in aquatic carnivores as compared to terrestrial carnivores. A question mark indicates no clear trend, whereas a plus or minus sign indicates a trend to increased or decreased values, respectively, for that variable in aquatic forms. Single signs correspond to a clear majority of the contrasts being in the indicated direction, double signs to all contrasts being in the same direction, and triple signs to the trend being significant at the 0.05 level (uncorrected for multiple comparisons) using a sign test. The "best estimate" gives the best estimate for each variable based on the outcome of the allometric analysis. Full names for all variables are found in Appendix C. **(Presented overleaf)**

	Uncorrected for size				Size-corrected using body weight			
Variable	Tree 1	Tree 2	Tree 3	Summary	Tree 1	Tree 2	Tree 3	Summary
SW	+	+	+++	+				
SHB	+++	+++	+++	+++	+++	+++	+++	+++
SBr	+++	+++	+++	+++	+	+	+	+
LS	-	-	-	-				
GL	+	+	+	+	+	+	+	+
BWt	+	+	+	+	++	++	+++	++
LWt	+	+	+	+	++	++	+++	++
WA	?	?	+	?				
AI	+	+	?	+				
MMat	+	+	+	+	+	?	+	+
FMat	+	?	+	+	+	+	+	+
IB	-	?	?	?				
EO	?	?	-	?				
LO	+	?	?	?	-	-	?	-
mBMR	?	?	?	?	?	?	+	?
tBMR	++	++	+	++	?	?	?	?
T_B	?	?	?	?				
Hct	?	?	?	?				
Hb	?	?	-	?				
RBC	--	--	--	--	--	--	--	--
HR	?	?	?	?	++	++	++	++
PD	--	-	-	-	+	+	+	+
SDWt	+	?	?	?				
SDHB	-	-	-	-				
SDBr	+	?	?	?				
SDMat	+	+	?	+				

Table 6.5: Continued.

	Size-corrected using brain weight				Best estimate			
Variable	Tree 1	Tree 2	Tree 3	Summary	Tree 1	Tree 2	Tree 3	Summary
SW	-	-	-	-	-	-	-	-
SHB	?	?	?	?	?	?	?	?
SBr					+	+	+	+
LS	--	--	-	--	--	--	-	--
GL	?	?	?	?	?	?	?	?
BWt	+	+	+	+	+	+	+	+
LWt	?	?	-	?	?	?	-	?
WA	?	?	+	?	?	?	+	?
AI					+	+	?	+
MMat	?	?	+	?	?	?	+	?
FMat	+	?	?	?	+	?	?	?
IB	--	--	---	--	--	--	---	--
EO					?	?	-	?
LO	-	-	-	-	-	-	-	-
mBMR	?	?	+	?	?	?	+	?
tBMR	?	?	-	?	?	?	?	?
T_B					?	?	?	?
Hct					?	?	?	?
Hb					?	?	-	?
RBC	--	--	--	--	--	--	--	--
HR					++	++	++	++
PD	+	+	+	+	+	+	+	+
SDWt					+	?	?	?
SDHB					-	-	-	-
SDBr					+	?	?	?
SDMat					+	+	?	+

tendencies to reduced litter sizes and interbirth intervals, and weak trends to higher birth weights, older ages of independence, and decreased longevity with respect to non-aquatic species. They may also be more dimorphic in terms of age of sexual maturity. Finally, aquatic species showed strong tendencies towards lower RBC counts (a consistent result regardless of the methodology) and higher heart rates, and a weak tendency to higher population densities than terrestrial forms. Many of these results run contrary to the hypothesized trends (see Table 6.1). This was the case for body weight, interbirth interval, longevity, and population density.

The mink (*Mustela viso*n) was the taxon that most frequently displayed a trend opposite to the hypothesized direction or, when no hypothesis was presented, to the clear majority of the remaining forms for each tree topology (Table 6.6; Appendix E). The marsh mongoose (*Atilax*) was usually the next most frequent "discrepant taxon," followed by pinnipeds and otters. Data for both the otter civet (*Cynogale*) and the aquatic genet (*Osbornictis*) were too scanty to render any judgement in this regard.

Table 6.6: Frequency of each taxon to be the "discrepant taxon" for the best estimate of each variable (see text). Presented as the number of variables the taxon was discrepant / total number of variables it supplied a contrast for. "Within viverrids" refers to a contrast at the root of the viverrid tree that could not be assigned to either *Cynogale* or *Osbornictis*.

Taxon	Tree 1	Tree 2	Tree 3
Atilax	4 / 15	3 / 15	6 / 15
Cynogale	2 / 4	2 / 4	2 / 4
Mustela lutreola	4 / 21	3 / 21	3 / 21
Mustela vison	8 / 25	7 / 25	10 / 25
Osbornictis	1 / 1	0 / 1	0 / 1
otters	5 / 26	4 / 26	5 / 26
pinnipeds	4 / 26	5 / 26	n/a
otarioids	n/a	n/a	5 / 26
phocids	n/a	n/a	5 / 26
"within viverrids"	0 / 1	0 / 1	0 / 1

Pinniped versus fissiped comparisons

Dimorphism and miscellany

In addition to those variables displaying allometric effects (Table 6.4; see above), significant relationships with other independent variables were observed (Table 6.7). All four male variables (body weight, head and body length, brain weight, and age of sexual maturity) showed strong relationships with their female analogs. Only two of the nine miscellaneous hypotheses did not display significant regressions. Weaning age was independent of the age of eye opening and population density was independent of mass-specific BMR despite showing a significant relationship with total BMR.

Rates of evolution

Only three sets of relationships exhibited significant differences among the TS2 taxa — body weight, weaning age, and interbirth interval (all vs. size) — but all three were non-significant when multiple comparisons were corrected for (Table 6.8). A non-parametric Student-Newman-Keuls test with pinnipeds as the control revealed that pinnipeds were not significantly different from the other TS2 taxa for each of these three variables (results not shown).

Comparisons between pinnipeds and fissipeds as a whole revealed the same pattern of few significant differences (five), none of which remained when multiple comparisons were corrected for (Table 6.8). Four relationships tended to be different between taxa (i.e., $p \leq 0.10$) for both sets of comparisons: weaning age, interbirth interval, age of eye opening (all vs. size), and age of male sexual maturity (vs. longevity). However, there was quite a bit of variation between the comparisons. Twelve sets of relationships fell into the same "bin" of probability ranges, but 13 were placed in a bin with a lower *p* value and 10 in a bin with a higher value by the pinniped-fissiped comparisons with respect to the TS2 taxa comparisons.

Table 6.7: Results of least squares (LS) regression analyses of independent contrasts testing hypotheses from the dimorphism or miscellany categories. All variables were corrected for size and the size estimator yielding the best regression is shown. An asterisk indicates LS slopes significantly different than zero at the 0.05 level (corrected for multiple comparisons using a sequential Bonferroni correction). Values for slopes determined by reduced major-axis regression (RMA) are also given. Full names for all variables are found in Appendix C.

Category	Dependent	Independent	n	LS slope	r^2	Size estimator	RMA slope
Dimorphism	MWt	FWt	143	0.930 *	0.886	brain	0.958
	MHB	FHB	78	0.870 *	0.809	body	0.930
	MBr	FBr	118	0.945 *	0.902	body	0.945
	MMat	FMat	95	0.463 *	0.244	body	0.936
Miscellany	SBr	GL	142	0.603 *	0.074	body	1.728
	SBr	EO	115	-0.258 *	0.044	body	-0.888
	LWt	GL	95	1.141 *	0.177	brain	2.064
	AI	WA	69	0.614 *	0.321	brain	1.107
	MMat	LO	89	0.433 *	0.091	brain	1.343
	FMat	LO	115	0.645 *	0.190	brain	1.461
	WA	EO	92	0.024	0.000	brain	n/a
	PD	mBMR	36	1.464	0.129	brain	n/a
	PD	tBMR	36	-1.194 *	0.323	brain	-3.384

Table 6.8: Results of non-parametric tests (corrected for ties) examining for differences in rates of evolution between time slice 2 groups (Kruskal-Wallis) or between pinnipeds and fissipeds (Mann-Whitney U). Independent variables, if not size, are listed in parentheses. No differences were significant when a sequential Bonferroni correction for multiple comparisons was used. Full names for all variables are found in Appendix C.

Comparison	$p \leq 0.05$	$0.05 < p \leq 0.10$	$0.10 < p \leq 0.50$	$p > 0.50$
Between TS2 taxa	IB SW WA	EO Hb MMat (LO) PD (mBMR) RBC SBr (EO) SDHB	BWt FMat GL Hct LS LWt LO mBMR SBr SDMat SHB tBMR T_B WA (EO)	AI AI (WA) FMat (LO) HR LWt (GL) MMat PD PD (tBMR) SBr (GL) SDBr SDWt
Pinnipeds versus fissipeds	EO IB MMat (LO) WA WA (EO)	AI BWt FMat (LO) LWt SBr SDBr SDMat	FMat GL Hb Hct HR MMat PD (mBMR) RBC SBr (EO) SBr (GL) SW tBMR T_B	AI (WA) LS LWt (GL) LO mBMR PD PD (tBMR) SDHB SDWt SHB

Grade shifts

The contrast representing the node linking pinnipeds to musteloids plus *Ailurus* was a significant outlier for three of the 35 sets of relationships: litter weight (vs. gestation), birth weight, and age of eyes opening (both vs. size). Inferred grade effects

were as rare for other higher level contrasts. Of all possible contrasts bearing on the origin of the 14 TS2 taxa, only two produced values that were outliers for at least one variable: ursid origin — birth and litter weights (both vs. size), and phocid origin — weaning age (vs. size and age of eyes opening) and age of independence (vs. size). These represent outlier frequencies of 8.6% (pinnipeds), 9.1% (phocids), and 5.7% (ursids).

Discussion

Cross-species regression versus independent contrasts

When comparing the results of this study to previous ones, it must be remembered that they were often derived using different methodologies. Most studies in this area have employed simple cross-species regression and thus may overstate the strength of a relationship by failing to distinguish similarity due to common ancestry from that due to similar selection pressures (Harvey & Pagel, 1991). Such was the case here when I re-examined the allometric relationships using cross-species regression (see below also). Except for age of independence and possibly hematocrit, all variables displayed a significant relationship with size (either body or brain weight), with uncorrected *p* values often less than 0.0001. Throughout the discussion, I assume that my use of independent contrasts is at least a partial explanation for any different findings compared to the literature and will instead concentrate my attention on other, more case specific causes.

That being said, the limited results from carnivore data analyzed using both cross-species regression and some form of analysis correcting for phylogeny (e.g., Gittleman, 1986b, 1993, 1994b; Elgar & Harvey, 1987; Ferguson *et al*., 1996) are not that different from one another. (However, many of the early corrections resemble cross-species techniques more than current ones, which account more effectively for phylogenetic effects.) Thus, although cross-species regression is theoretically invalid (Purvis *et al*., 1994), it may still give approximately correct answers, especially when the relationship is strong (Pagel, 1993) and largely independent of phylogeny as appears might be the case in carnivores.

Allometric effects and other correlations

All but five variables showed some relationship with size, agreeing with previous observations that most morphological, life history, physiological, and behavioural characters display allometric effects (Clutton-Brock & Harvey, 1983; Gittleman, 1986b and references in both). Only the negative result for age of independence conflicts strongly with previous findings (Gittleman, 1986b, 1993). However, Gittleman did not correct for multiple comparisons (J. L. Gittleman, pers. comm.); if such a correction was not undertaken here, age of independence would regress significantly on body size (uncorrected $p = 0.0145$), indicating that it may be on the borderline. Gittleman (1994b) found no link between female brain size and age of eye opening, a result matched here, but one that again hinges on correcting for multiple comparisons (uncorrected $p = 0.0371$). Equivalent statements for the remaining variables are difficult to make. Brannon (1985) suggested that hemoglobin concentration may correlate with size, which was not upheld here, and no statement exists for hematocrit beyond Hawkey's (1977) assertion that it is constant among mammals. There is no clear consensus whether body temperature shows an allometric relationship (see above and compare Morrison & Ryser, 1952 with Folk *et al*., 1977; White *et al*., 1996).

The directions of the relationships for variables displaying allometric effects were consistent with those in the literature (see Umminger, 1977; Gittleman & Harvey, 1982; Clutton-Brock & Harvey, 1983; Gittleman, 1986b), although the presence of a (negative) relationship for litter size is unclear (compare Gittleman, 1986b and Clutton-Brock & Harvey, 1983). A minor discrepancy concerned whether life history traits correlated more strongly with body or brain weight. Of the seven traits mentioned by Gittleman (1986b), the only agreement is for birth and litter weights (both with brain weight). In three cases — age of independence, weaning age, and interbirth interval — my results indicated no significant regression with the size indicator listed by Gittleman. However, it is probably meaningless to search for causative explanations for this discrepancy. Body and brain weight correlate strongly with one another (uncorrected $p < 0.0001$; also Gittleman, 1986b), so the one displaying the stronger relationship with a life history trait may simply

be the less noisy one in that case. Brain weight is less variable intraspecifically than body weight (e.g., Economos, 1980; Gittleman, 1986b) and it often showed the slightly stronger relationship with the variables in this study. Also, differences in strength between the "competing" regressions were very small in this study; this appears true of Gittleman's (1986b) results as well. Thus, the different conclusions may be a consequence of the two different data sets that were used (i.e., sampling error).

Instead, the largest discrepancy with previous results concerns the values of the allometric exponents. Most of the exponents determined herein underestimate previous findings (Table 6.9). Although this is not as important for life history exponents, which are comparatively poorly reported (see Gittleman, 1986b for carnivoran values), several other exponents are widely agreed upon and used to explain many phenomena: 0.75 for brain size (Martin, 1981; Hofman, 1983; although older studies place it as 0.67 [see Jerison, 1973 and references therein] and the exact value may depend on the taxonomic rank examined [see Jerison, 1973; Eisenberg, 1981; Pagel & Harvey, 1989]), -0.25 for mass-specific BMR and 0.75 for total BMR (Schmidt-Nielsen, 1984 and references therein), and -0.25 for heart rate (Stahl, 1967).

Three possible explanations exist for the discrepancy in exponent values. First, I determined slopes using least squares regression, which will underestimate their values when there is error associated with the independent variable, as was the case here. Second, the values of the contrasts are based on the branch lengths in Tables 4.2–4.13. Although these represent the best estimates of divergence times within carnivores, using them in CAIC assumes a gradualistic model of evolution, which may not be the correct model (although CAIC's diagnostic tests indicated that analyses using these branch lengths did not violate any assumptions of the method). Third, previous exponent values were determined using cross-species regression. Although Pagel (1993) indicates that both cross-species regression and independent contrasts should theoretically give unbiased estimates of an allometric exponent, some differences might still result. To determine the effect of these various factors, I recalculated the allometric exponents using 1) reduced major-axis regression (which provides an upper bound to the estimate of the

exponent), 2) CAIC to recalculate contrast values based on equal branch lengths, thereby assuming a punctuational model of evolution, and 3) simple cross species-regression.

Each of these three "corrections" generally increased the magnitude of the slope over that determined by least squares regression, particularly when body weight was used to estimate size (Table 6.9). However, these increases did not necessarily improve

Table 6.9: Effects of different techniques on the values of the slopes for allometric relationships. Techniques include least squares regression (LS) and reduced major-axis regression (RMA) of contrasts determined using the carnivore phylogeny and associated branch length from Chapter 4, least squares regression of contrasts determined using the same topology but with equal branch lengths (EQ), and simple cross species regression (CS). ns = not significant at the 0.05 level corrected for multiple comparisons. Expected values of slopes are included where available and the value most closely approaching this is presented in bold face. Full names for all variables are found in Appendix C.

Size estimator	Variable	Expected value [1]	LS	RMA	EQ	CS
Body weight	SW	n/a	n/a	n/a	n/a	n/a
	SHB	0.33	0.20	**0.31**	0.28	**0.31**
	SBr	0.75	0.46	0.60	0.53	**0.66**
	LS		ns	ns	ns	-0.17
	GL	0.11	0.06	0.36	**0.10**	0.26
	BWt	0.81	0.53	1.07	**0.73**	1.07
	LWt	0.86	0.55	**0.98**	0.73	0.90
	WA	0.23	ns	ns	0.17	0.10
	AI	0.41	ns	ns	0.20	ns
	MMat		0.15	0.58	0.22	0.28
	FMat	0.58	0.11	**0.82**	0.17	0.26
	IB	0.10	ns	ns	0.11	0.10
	EO		ns	ns	ns	-0.45
	LO	0.12	**0.15**	0.60	0.17	0.18
	mBMR	-0.25	-0.12	-0.39	ns	**-0.21**
	tBMR	0.75	0.94	1.06	0.93	**0.79**
	T_B		ns	ns	ns	-0.01
	Hct		ns	ns	ns	ns
	Hb		ns	ns	ns	0.06
	RBC		-0.08	-0.38	-0.08	-0.12
	HR	-0.25	**-0.17**	-0.62	-0.14	-0.14
	PD	-0.75	**-0.73**	-2.34	-0.83	-0.51

Table 6.9: Continued.

Size estimator	Variable	Expected value [1]	LS	RMA	EQ	CS
Brain weight	SW		1.48	1.96	1.45	1.44
	SHB		0.48	0.59	0.48	0.46
	SBr	n/a	n/a	n/a	n/a	n/a
	LS		-0.13	-0.79	ns	-0.27
	GL	0.14	**0.21**	0.69	0.22	0.38
	BWt	1.35	1.25	1.64	**1.30**	1.58
	LWt	1.63	1.17	**1.53**	1.23	1.31
	WA	0.37	**0.28**	1.59	0.27	0.18
	AI	0.76	ns	ns	ns	ns
	MMat		0.39	1.05	0.41	0.43
	FMat	0.58	**0.41**	1.02	0.36	0.40
	IB	0.13	0.25	0.99	0.22	**0.14**
	EO		-0.18	-1.25	-0.38	-0.67
	LO	0.22	0.36	1.08	0.31	**0.27**
	mBMR		-0.23	-0.75	-0.23	-0.31
	tBMR		1.41	1.79	1.31	1.13
	T_B		ns	ns	ns	-0.01
	Hct		ns	ns	ns	0.04
	Hb		ns	ns	ns	0.09
	RBC		-0.13	-0.62	-0.14	-0.19
	HR		ns	ns	-0.22	-0.22
	PD		-1.60	-4.20	-1.30	-0.71

[1] Expected values for head and body length taken from Schmidt-Nielsen (1984), for life history traits from Gittleman (1986b), and for population density from Gittleman (1989c). Sources for the remaining values are found in the text.

estimates of the allometric exponents as they now frequently overestimated the expected value. No one technique consistently provided the best estimates either. It is difficult to determine the importance of the differences between the techniques. The coefficients of determination (Table 6.4) reveal that many of the relationships are not very strong, despite being significant; standard errors of the slopes were correspondingly large (results not shown). Large confidence intervals are also implied by comparing the slopes obtained with least squares and reduced major-axis regression, which provide approximate lower and upper bounds, respectively, on values for the allometric exponents. It would appear

that the differences between techniques represent natural variation around some weak trends.

Except for ages of sexual maturity, slopes for the dimorphism variables were slightly under unity, especially when estimated using major-axis regression. This suggests there to be little or possibly slight reverse sexual dimorphism in carnivores, at least for rates of change. To my knowledge, no one has examined dimorphism in rates of change; however, the suggestion of reverse dimorphism is surprising considering how rarely it occurs among mammals. Within carnivores, only hyaenids and scattered herpestids and phocids display this phenomenon (Ralls, 1976). Instead, most carnivores are monomorphic, with weasels, otarioids, and some phocids displaying significant sexual dimorphism (Weckerly, 1998).

The presence of significant relationships among most of the miscellany variables agrees with the results of Gittleman (1986b), who indicated that most life history traits correlate positively with one another. Because these relationships were designed primarily to distinguish pinnipeds from the remaining carnivores, the values of the slopes are not important. However, both the r^2 values and the large difference in value of the slopes as estimated using least squares and reduced major-axis regression (Table 6.7) reveal these relationships to be the weakest in the entire study.

Aquatic versus non-aquatic carnivores

Differences between aquatic and non-aquatic carnivores are few. At best, only strong trends for decreased litter sizes, decreased interbirth intervals, decreased RBC counts, and increased heart rates in aquatic carnivores can be discerned; none of these trends are significant. Only the result for RBC count agrees with previous opinion. (Smaller litter sizes in aquatic species were predicted, but only when size was not accounted for.)

The advantage of a reduced RBC count was discussed earlier. Reduced litter size is one character diagnostic of K-selected species, which include otters and pinnipeds (McLaren, 1967; Hennemann, 1983; Stirling, 1983; Schmitz & Lavigne, 1984). There

may be a tendency towards precocial young as well given the weak trend towards larger neonates. Together, these two characters provide numerous advantages for both the mother and offspring in dealing with their amphibious lifestyle. Given that dens or rookeries must be close to the water, suitable sites might be at a premium, thus limiting the number of offspring that can be raised. Precocial young would be advantageous because of the greater risks the aquatic environment places on newborns (e.g., risk of drowning, problems with flotation) and the increased complexity of dealing with both terrestrial and aquatic habitats (only sea otter offspring will potentially never set foot on land; Kenyon, 1981b). However, this "advanced development" does not require an extended active gestation period and also offsets the smaller litter sizes so that aquatic and terrestrial carnivores have litters of equal weight.

It is difficult to postulate biological explanations for the remaining strong trends. The result for interbirth interval may be an artifact. With few exceptions, carnivores have interbirth intervals of 12 months. Many viverrids have shorter interbirth intervals than this and many large carnivores have longer intervals; together, these two "exceptions" are sufficient to produce a positive correlation between interbirth interval and brain weight. Thus, although most aquatic species have 12 month interbirth intervals like their sister taxa, they appear shorter when scaled to their relatively large brain size; comparisons uncorrected for size showed no trend (Table 6.5). Gittleman (1989c) also noted that comparative statements regarding interbirth interval are often suspect due to rounding errors in the raw data. The trend to increased heart rates in aquatic species should be regarded with some suspicion. Data were available for 39 species only and although I attempted to include resting heart rates only, this could not always be guaranteed. Also, the strong trend derives from only two contrasts (the third contrast was zero and excluded; see Appendix E) and obviously needs to be confirmed with more data.

It is unclear why Estes (1989; also Repenning, 1976) mentioned sexual dimorphism as a distinguishing character of aquatic carnivores. To my knowledge, no justification for this claim has been provided beyond the observation that pinnipeds, and otarioids in particular, are the most dimorphic of mammals (see Weckerly, 1998). The

extreme dimorphism arises due to the polygynous breeding system of most pinnipeds, which admittedly has been hypothesized in turn to be a consequence of the dichotomy between marine feeding and the limited number of terrestrial breeding sites (Bartholomew, 1970; Repenning, 1976). However, analogous circumstances for the foraging and breeding sites of terrestrial carnivores, many of which are polygynous (Gittleman and Bininda-Emonds, unpubl. data) could apply equally well. Among carnivores, the only other strongly dimorphic group, at least for size, are mustelids, exclusive of otters (Estes, 1989; Weckerly, 1998), further diminishing any aquatic association for this character.

A more interesting outcome of this portion of the study was the difference between using body versus brain weight as the estimator of size. Analyses uncorrected for size demonstrated that aquatic carnivores are absolutely larger than terrestrial ones for both these size measures (and also a third, head and body length), as hypothesized for thermoregulatory reasons. But, it appears aquatic carnivores have proportionately large brains for their size, despite having reduced olfactory lobes (Fish, 1898; Gittleman, 1991). When corrected for body weight, brain weight showed a weak trend to increased values in aquatic forms whereas correcting for brain weight indicated a weak trend to decreased body weight. This was unexpected given that no one has strongly advocated that aquatic carnivores have larger brains, despite some empirical evidence in support of it (Wirz, 1950; Stephan, 1972), and also because the magnitude of the contrasts in the analysis uncorrected for size were generally larger for body weight than for brain weight (Appendix E). However, my interpretation that aquatic carnivores do possess proportionately larger brains for their body weight does explain the opposing patterns in the size-corrected analyses. Correcting for body weight revealed the same trends as the uncorrected analysis, but correcting for the proportionately larger brain weight caused most of the positive trends to disappear or occasionally reverse. In other words, using brain weight as a size estimator makes aquatic carnivores appear larger than they really are (in terms of body size), thereby causing variables displaying allometric effects to appear smaller in aquatic carnivores.

The adaptive explanation for relatively larger brains in aquatic carnivores relates to Estes's (1989) conjecture of the need for such species to interpret what is a complex three dimensional environment, a form of the perceptual complexity hypothesis (see Eisenberg & Wilson, 1978; Eisenberg, 1981). Adding to this is the reality that aquatic carnivores are really amphibious. Larger brains may thus also be an adaptation to properly interpret two very different environments, each with very different demands and effects on the sensory apparati. The amphibious nature of aquatic carnivores also explains why they retain small olfactory lobes (Fish, 1898; Hubbard, 1968; Gittleman, 1991), structures that are absent or nearly so in cetaceans (Jerison, 1973). For example, in pinnipeds, and otariids in particular, identification of newborns and pups by their mothers is based primarily on smell (King, 1983b).

A key shortcoming for this portion of the study is the paucity of contrasts. At most, there were only eight (seven otherwise) aquatic-terrestrial sister taxa, and only with a currently discredited phylogenetic hypothesis (see Wyss, 1987; Flynn *et al.*, 1988; Chapter 4 among others). Furthermore, the seven to eight contrasts were achieved only by including carnivores (the non-otters and non-pinnipeds) that some would consider "semi-aquatic" at best. But, by being at least semi-aquatic, these species should still follow the expected trends, albeit possibly to a lesser degree. My results suggest otherwise: the semi-aquatic species are more likely to be the discrepant taxon. However, the virtual lack of information for the semi-aquatic viverrids *Cynogale* and *Osbornictis* currently prevents any definitive judgement.

The small sample size meant that a significant result for most variables required that the maximum number of contrasts were available and all in the same direction. Again, the lack of information for *Cynogale* and *Osbornictis* meant that most reproductive and hematological variables could not be examined statistically. Despite this, it was clear in many cases that no trend existed. More data should be obtained for the few variables where it appears that a trend might be present: litter size, interbirth interval, RBC count, and heart rate.

Increases in sample size within carnivores are not possible; however, these analyses should be expanded to test how well the "aquatic adaptation" hypotheses apply across mammals. There are many aquatic mammals, notably cetaceans, sirenians, hippopotamuses, the platypus, some shrews, and numerous rodents. Unfortunately, the identity of their non-aquatic sister taxa is often unknown or contentious, particularly for rodents where there is much uncertainty about relationships within the group (see Parker, 1990; Nowak, 1991) or even if it is monophyletic (see Chapter 2). The sister taxa for cetaceans (possibly including hippos; Arnason & Gullberg, 1996) and sirenians are reasonably well agreed upon (artiodactyls and proboscideans, respectively; Irwin *et al*., 1991; Novacek, 1992b; Arnason & Gullberg, 1996; Stanhope *et al*., 1996), but the age of both groups (≥ 60 million years; Novacek, 1992b; Arnason & Gullberg, 1996; Lavergne *et al*., 1996) presents special problems. For either taxon pair, extensive species data and well-resolved phylogenies for both sister groups will be needed to provide an accurate value for the resulting contrast. As well, the long divergence times means that any differences might have accrued for selective forces other than the adaptations to an aquatic environment.

Pinnipeds versus fissipeds

Although the previous section demonstrated that aquatic carnivores in general differ from their terrestrial sister taxa in a few, key traits, these same characteristics did not distinguish pinnipeds from the remaining carnivoran taxa. Any differences in the latter case could have arisen in three ways, but in no case were any systemic differences indicated.

First, pinnipeds may differ from fissipeds in their pattern or direction of evolution. Unfortunately, this could not be examined. Although most variables showed a significant relationship with the independent variable (typically size) over the entire order, this was not the case at the TS2 level (contrary to the findings of Gittleman [1986b] for several life history variables). Of the many sets of relationships I examined, only five displayed significant regressions for six or more of the TS2 taxa: the allometric relationships for

body weight, head and body length, brain weight, and the dimorphic relationships for body weight and brain weight (results not shown). This general loss of significance is not a true "taxon-level effect" (*sensu* Pagel & Harvey, 1989; see their Figure 1): although there is a clear size gradient within carnivores (Figure 6.2a), it breaks down when contrasts of the size estimator rather than its raw values are examined (Figure 6.2b; although this is not necessarily a property of independent contrasts), and further breaks down when some variable is plotted against the size estimator (Figure 6.2c). In the latter two cases, except for mustelids which display a wide range of size contrasts, there are no clear differences between the TS2 taxa as required for a taxon-level effect. Instead, the emergent nature of the relationships at the ordinal level seems to arise from most of the indicated relationships being quite weak. Coefficients of determination were low, usually below 0.5 and often less than 0.2. The smaller sample sizes at the TS2 level thus made it difficult to detect a significant trend amongst this scatter. Supporting evidence for this conjecture is that the five sets of relationships mentioned above that remained at the TS2 level possessed some of the highest coefficients of determination (all greater than 0.7) and some of the largest overall sample sizes (see Table 6.4).

Second, pinnipeds could be distinguished by having a different rate of evolution; however, no such differences existed among any of the 35 sets of relationships I examined. Admittedly, three allometric relationships (for body weight, age of weaning, and interbirth interval) showed differences among the TS2 taxa at the 0.05 level, but this number can be expected by chance alone and the differences were not significant when I accounted for multiple comparisons. Also, further statistical analyses confirmed that the differences, if any, were not due to the pinnipeds. An important lesson from this portion of the study is that comparisons should be made between sister, or at least equivalent, taxa. In the past, pinnipeds were usually contrasted to fissipeds as a whole, an invalid comparison that may falsely indicate differences between the groups. When I performed the comparisons in this way, the results clearly bore no relation to those when I compared among TS2 taxa. The variables in Table 6.8 changed probability bins largely at random between the two comparison types and weak differences (i.e., variables in bins of $p \leq$

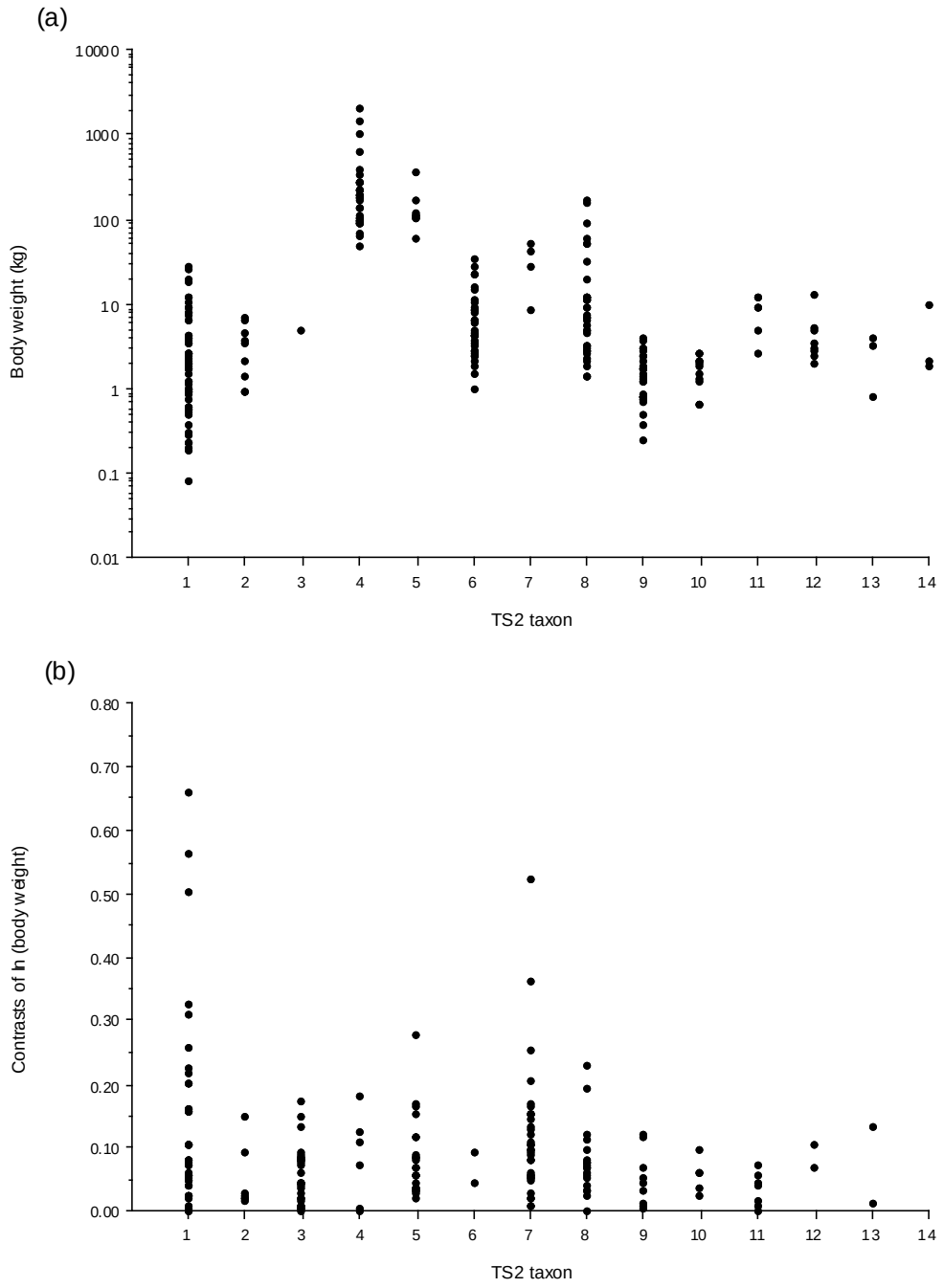

Figure 6.2: Demonstration of the lack of a taxon-level effect to explain why significant regressions among the entire order do not appear among the TS2 taxa. The size gradient among carnivores (a) disappears when contrasts of the size estimator are used (b). c) An allometric plot of contrasts of some variable (litter weight) versus contrasts of size shows no differences among taxa. Taxa are listed in the same order as presented in Table 6.2.

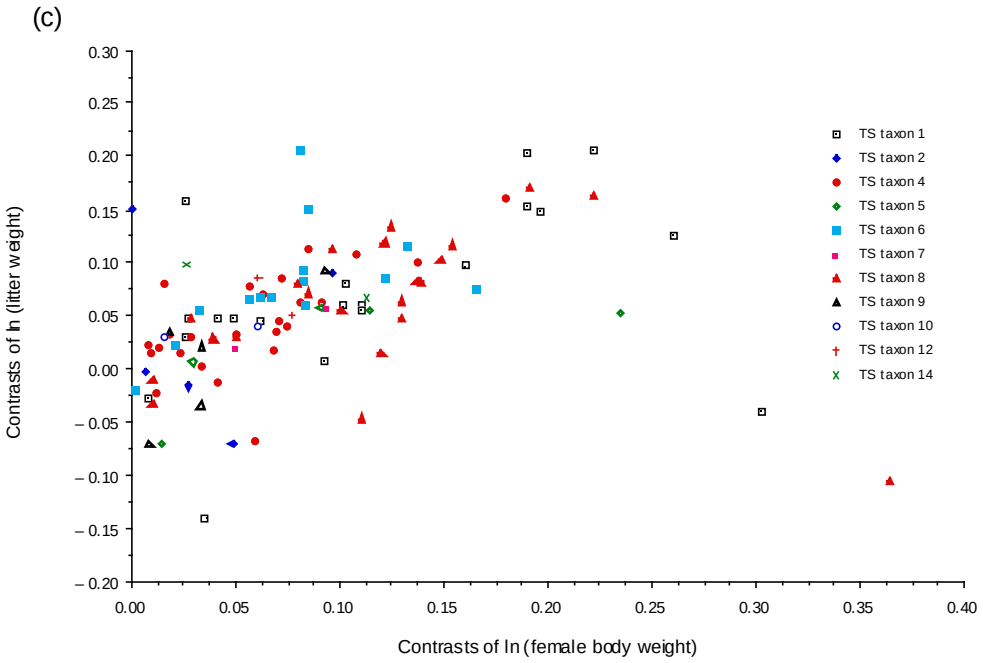

Figure 6.2: Continued.

0.10) between pinnipeds and fissipeds were indicated where analogous comparisons among TS2 taxa revealed that pinnipeds were not different from the remaining taxa. This inconsistency arises because pinnipeds, while not displaying the most extreme values for a variable, rarely possess median values either. For example, pinnipeds have relatively short ages of weaning. Pooling fissipeds together accentuates this (as most have relatively longer weaning ages) and makes pinnipeds appear different.

Third, pinnipeds may differ because of grade effects, due to either a sudden, punctuational change or a series of smaller, gradual changes followed by extinction of the more basal forms. Again, this is not supported as only a few grade effects were indicated that merely substantiate a few distinctive features in some taxa: high birth and litter weights in pinnipeds (compared to fissipeds) and short periods of lactation and ages of independence in phocids (compared to otarioids). The observed frequencies of the grade shifts could also be accounted for by chance alone. Thus, contrary to Gittleman's (1986b) findings, widespread and prevalent grade effects have not directed carnivore evolution. Instead, carnivore evolution seems to have proceeded at a steady and gradual rate, a finding supported by the steady rate of increase in taxa numbers between time slices.

It appears that too much has been made historically of distinctive pinniped features, but not enough of the characteristics distinguishing fissiped taxa from one another. Pinnipeds undoubtedly display several adaptations to the aquatic environment (e.g., bullar morphology, flippers, hematology). But, do these features justify a distinct status for pinnipeds more than those present for arboreality in viverrids, hypercarnivory in most hyaenids and several fossil groups, or a largely solitary and nocturnal hunting style in felids, to name but a few, do? The blanket grouping of pinnipeds as aquatic forms also conceals important differences between the major groups. For example, otariids and phocids possess different reproductive strategies. Otariids are invariably polygynous and the young are dependent on the mother for long periods, often upwards of a year or more. In contrast, phocids are polygynous, monogamous, or even promiscuous and display some of the shortest times of lactation and dependency for their size and among mammals in general (Harrison, 1969; Stirling, 1983; Bowen *et al*., 1985). Differences in hematological parameters are also present between pinniped families (see above).

Conclusions

It has been argued that certain key changes are required by aquatic members of the Carnivora to adapt to the their environment (see Repenning, 1976; Estes, 1989; Gittleman, 1989a). The purported extreme expression of these changes in pinnipeds, the most aquatically-adapted carnivores, has been used by many to justify the historical splitting of carnivores into pinnipeds and the remaining terrestrial forms (fissipeds). Yet, despite the widespread acceptance of this division, the justification behind it and evidence for it have never been tested adequately.

The adaptations for an aquatic lifestyle in carnivores and the distinctiveness of pinnipeds have been overstated. My examination of 22 morphological, life history, ecological, and physiological variables using independent contrasts to correct for phylogenetic effects revealed that while some trends do characterize carnivores that have switched to an aquatic habitat, they are much fewer than has been supposed and none demarcate pinnipeds from fissipeds. In fact, pinnipeds are indistinguishable from fissiped

taxa of equivalent status (roughly the carnivore families). Therefore, carnivores as a whole appear to be a remarkably homogeneous group as mentioned for fissipeds alone by Morrison and Ryser (1952) and Pagel and Harvey (1989).

The invocation of the aquatic environment as a general selective force is often an extreme simplification and conceals that there are important differences within terrestrial (e.g., cursorial vs. arboreal species) and aquatic forms. Pinnipeds show distinct differences between otariids and phocids in their reproductive strategies and, to a lesser degree, their hematology. While these differences are recognized by pinniped biologists, they appear to be less well known, or at least less acknowledged, outside this community.

Previous support for the pinniped-fissiped split appears largely intuitive or based on questionable methodology. Presupposing the split by comparing pinnipeds to (the paraphyletic) fissipeds only increasing the likelihood of finding differences between the two. I demonstrated the importance of taking phylogeny into account and comparing either sister taxa or taxa of equivalent rank: comparisons between pinnipeds and fissipeds as a whole revealed differences that were not supported when pinnipeds were compared to individual fissiped groups of an equivalent rank. My use of independent contrasts to correct for phylogenetic effects explains many of the differences with previous findings, possibly even differences in the value of several allometric exponents.

Fortunately, the growing tendency to produce classifications that reflect considerations of monophyly means that pinnipeds are now being properly placed in a taxonomic context (e.g., Wozencraft, 1993; McKenna & Bell, 1997). I hope that the results of this study will show that there is no reason to view pinnipeds as being distinct from the remaining carnivores on the basis of their morphology, life history traits, or physiology. This recognition will only lead to a better understanding of the entire, diverse order of carnivores.

Chapter 7

General Conclusions

Phylogenetic reconstruction has seen a recent drive towards generating ever larger phylogenies (e.g., Chase *et al*., 1993; Purvis, 1995a; Soltis *et al*., 1997). But, while larger phylogenies present many benefits throughout evolutionary biology (see Chapter 1), I would suggest the goal of deriving larger phylogenies as it is currently pursued is slightly misdirected.

The number of taxa in an analysis is only one facet of producing larger phylogenies. A less appreciated, but more important, issue is to which of two general locations of an existing phylogeny the extra taxa are added: 1) outside of the current ingroup or 2) within the ingroup to fill in gaps (Kim, 1996; Hillis, 1998). Both strategies of taxon addition lead to larger phylogenies, but only the second produces more complete ones. Like Kim (1996), I suggest the second strategy to be the more desirable. Adding taxa outside the current ingroup accrues all the disadvantages inherent to larger analyses (e.g., longer analysis times) without necessarily improving the accuracy of the reconstruction by eliminating long branches or the effects of taxon sampling. Adopting this strategy, while allowing more sweeping statements about a wider variety of taxa to be made, only makes the problem larger and the solution possibly less accurate. Adding taxa within the ingroup similarly increases the size of the problem, but the judicious selection of taxa in this instance potentially ameliorates errors associated with taxon sampling and long branch attraction (Arnold, 1981; Huelsenbeck & Hillis, 1993; Lecointre *et al*., 1993; Kim, 1996; Graybeal, 1998; see Chapter 2 also). The resulting denser trees are likely to be more accurate and also permit more comprehensive statements about the evolution of the group of interest, both in a systematic sense and in those fields using such information (e.g., character evolution, comparative studies, rates of evolution). Comparative analyses in particular require data to be evenly distributed among taxa; the omission of a taxonomic group can yield misleading results (Gittleman, 1989c).

Therefore, the drive in phylogenetics should be to produce more complete phylogenies. However, "complete" need not necessarily imply "large," as is often assumed. The phylogeny of extant phocid seals I used in Chapter 2 is complete, at least for the ingroup of 19 species, but with only 26 species total, it is not especially large. Many of the large phylogenies listed above straddle the gray area between "large" and "complete" as defined by the two taxon addition strategies in the previous paragraph. For the plant phylogenies in particular, the sheer scope of producing a phylogeny of all seed plants combined with the early stage of the data accumulation means that taxon addition has largely followed the first strategy above (i.e., adding taxa to merely make the problem bigger). Only recently has the breadth of the ingroup been covered such that the tree is beginning to be filled in.

Realistically, however, the goal of building complete phylogenies is unfeasible given that all the relevant species can never be included. For a variety of reasons, only a minute fraction of the total species diversity is known for most groups. Problematic groups include those with small, secretive, or cryptic members, those with members in environments that are inaccessible or thought to be "hostile" to life (e.g., marine trenches or volcanic calderas), those where species differentiation is disputed or unclear or species concepts are difficult to apply (e.g., bacteria and viruses), those with many members (e.g., how certain are we that we know every species of beetle?), those with members that aren't "attractive" enough to generate much scientific interest, or any combination of the above. It is tempting to think that intensively-studied groups like mammals (and certain orders within mammals in particular) have few undescribed species, but such is not the case. A quick on-line search of the Science Citation Index (via Bath Information and Data Services) revealed the discovery of 16 new mammal species since 1990: seven rodents (Musser & Holden, 1991; Leo & Gardner, 1993; Hutterer, 1994; Patton & da Silva, 1995; Ruedas, 1995; Lavrenchenko *et al*., 1998), three shrews (Ruedi, 1995; Ivanitskaya *et al*., 1996), three bats (Kalko & Handley, 1994; Handley, 1996), two bovids (Dung *et al*., 1993; Peter & Feiler, 1994a, 1994b), and one viverrid (*Viverra tainguensis*; Sokolov *et al*., 1997). Many more undiscovered papers and species undoubtedly exist. Although

most of these new species have yet to be verified under rigorous taxonomic examination and several result from the vagaries of taxonomic splitting, many, including the bovids (the first large mammals discovered since 1937; Dung *et al*., 1993), are descriptions of species formerly unknown to western science due to being located in remote areas of southeast Asia and South America.

Generating truly complete phylogenies is also unfeasible because extant species comprise only a very small fraction of all the species that have ever existed (<< 1%; Novacek & Wheeler, 1992). Most extinct species are undiscovered (and likely to remain so due to the incompleteness of the fossil record) and beyond the reach of molecular analysis in any case. However, the inclusion of fossil evidence is another facet of taxon sampling: including fossil information can drastically alter relationships determined from an analysis of extant forms only (Gauthier *et al*., 1988; Donoghue *et al*., 1989; Novacek, 1992a). Given the serious ramifications of excluding fossil evidence and our goal of generating complete phylogenies, a priority in future research should be deriving phylogenetic estimates from both paleontological and neontological data. This can now be easily accomplished using character congruence, taxonomic congruence, or supertree construction.

With all these points in mind, I endeavoured to base the results in this thesis on two phylogenies that were as complete as possible. Unfortunately, neither contains any direct information about fossil species; however, I noted the limitations of this in each case (see Bininda-Emonds & Russell, 1996 and Chapter 4, respectively) and some source trees for the carnivore phylogeny did include fossil information. The carnivore tree also lacks two putative species, the Iriomote cat, *Felis iriomotensis,* and the newly described viverrid, *Viverra tainguensis.* However, the Iriomote cat was held to be an island subspecies of the leopard cat, *Felis bengalensis*, by Wozencraft (1993) and the taxonomic status of *Viverra tainguensis*, which was first described after construction of the carnivore tree, still needs verification.

My use of complete phylogenies allowed me to ask questions that could not be properly answered without one, and to find answers that would not be as robust without

one. Chapter 2 directly demonstrates the effects of taxon sampling for higher level analyses and methods of representing supraspecific taxa. Because the carnivore tree in Chapter 4 is complete, I could make statements regarding the cladistic status of carnivoran taxa with confidence. The findings from Chapter 5, which show that different methods of phylogenetic inference have little impact on our estimates of carnivore phylogeny, would not be as compelling had they been ascertained for a selection of carnivoran species only. Just as I could not extrapolate the results of this chapter to other taxonomic groups, it would be as invalid to do so for any carnivore species (or families) that might have been excluded. Finally, Chapter 6 illustrates the power of a large, complete phylogeny for fields that use phylogenetic information. For the first time, statements regarding the distinct status of aquatic carnivores and pinnipeds were examined rigorously, revealing an answer perhaps very much contrary to prevailing opinion: there are few significant differences among all carnivores. I hope that this result will spur more integrated research of all carnivores, something which can only be regarded as an extension of the “complete perspective” I advance for phylogenetic inference.

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Appendix A

Phocid character matrix

The following character matrix is derived from that found in Bininda-Emonds & Russell (1996). I list only the 168 characters included by Bininda-Emonds & Russell (1996) in their analyses and divide the matrix into 1) outgroup taxa, 2) phocid species, and 3) the states I determined for the higher level phocid taxa Lobodontini, *Mirounga*, *Monachus*, and *Phoca*. A brief desciption of each character and its associated states follows the matrix.

Character states for the higher level phocid taxa were derived from the species states according to the following representation methods (see Chapter 2): ancestral (ACCTRAN and DELTRAN optimization), democratic, and exemplar. Democratic character states were determined using an algorithm devised by Bininda-Emonds & Russell (1996:19–20) 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, I 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.

In the matrix, missing data are represented by a question mark and polymorphic data are represented as follows: A = (01), B = (012), C = (0123), D = (013), E = (019), F = (02), G = (023), H = (0234), J = (029), K = (03), L = (09), M = (12), N = (123), P = (129), Q = (13), R = (14), S = (19), T = (23), U = (234), V = (24), W = (29), and X = (34). Character numbers correspond to those in Bininda-Emonds & Russell (1996), which contains detailed descriptions of all characters.

Taxon	Characters 3–103
	111
	11111111222222233334444444444555555556666666666777777778888888899999999000
	34567890123456790124689018901234567890123468901234567890234568901234568912345678912 3
Outgroups	
Canis lupus	10000002211000111 00LM10102010290000121220192210110119901900022212011?00220000999999
Procyon lotor	100000A22110001001090001020102 90A000112201910101A01199111001M1M022011?F021A0101A2010
Enhydra lutris	1A0A011F21100010L111000A0M0100900000MA22009121011AB199019A002LA00200009010 00A0112A10
Lutra canadensis	A00000M221100A10A11A1A0102000F91A000202200922100001099019 1001M00020000L01AA0001A2010
Martes americana	100000AF211000000100A1000100029010101022019A0101101A990ME01019112211 1?90201099000000
Ursus americanus	1A0000002112011010 00M1111201020A0001F12M01920101101199019000121001011?M1221010002000
Odobenus rosmarus	100A1111210901109 1011S000S0010922001201M009A2000A0209902AA001W1000A101011010101A2000
Zalophus californianus	1000000021090100B10129002210101221112122009001000010SS0ML00010100A010021221010002000
Phocid species	
Cystophora cristata	00009009001W00110101L90012000M010000B021002001010 0M0991M112111122200 01M0110010101010
Erignathus barbatus	0000001B211000119100990001900010210001121101111020110990111 01MAM2220001A0111099100110
Halichoerus grypus	0000011001110001 01A999001W00A0A1000010220002210 10A109900S1012B0222000190201010100010
Hydrurga leptonyx	1001000201100011A10M9900ME0010022000201100 1M21A00A10SW11111029021 0A101A0120000112110
Leptonychotes weddellii	1011000F211000009100990 0M1001A012000101110101 1A00A009900A110M0A022A101A01A0000102A10
Lobodon carcinophagus	A01100A201120000910099002FA0101M2000211000001100A1001010911020122201 01001M0000101110
Mirounga angustirostris	1001900900190011210M990011101001000020MM00199910011012121110 0M00220101902A00001A2010
Mirounga leonina	1009909900190001210299002100 1A1200001021001LES101011991211A0000B2201019010 0000A02010
Monachus monachus	A0110002B11900000101990021 00AA1121101022001A1110A010111191212AA22A000120110AA0102010
Monachus schauinslandi	01A1000221110010L1099900M000001A100010110019991A001012009120ML1111100120M20000102111
Monachus tropicalis	01A0000221101000L10L990029001A1B210000100021M10A0100200091M0ML11201A0120M20A00102110
Ommatophoca rossii	0010900900100 00A91019900M2000011100010100A1AF101A010991AA1A11000210101A01A0000102110
Phoca caspica	00000012211A0001011999001P0001100000A0220021M101A1109901011A10122200019009991 1100010
Phoca fasciata	000A000F211A000191009900110000000000002M00B111010120A00A1101M21B220001902M1010101010
Phoca groenlandica	00000000211100A191A9990002000B900000A0MM00AM1100002099111101M210220001L0211010101010
Phoca hispida	0000000B211A000101A999001M0001A00000A0M20011M10101A09901A101M1122200019020101 1000010
Phoca largha	0000000221100001A1A999001100AAA00000002M0012210A0A00990A0101M112220001902010 1010A010
Phoca sibirica	000000A12110000191199900120000A0000010M20001M1011110SL01010A1A1222000190FLSL11100010
Phoca vitulina	00000002A110000101A99900M2000M000000A02M00A121000000SE0191012MAA220001L0201010100010

Taxon	Characters 3–103
	111
	1111111112222222333344444444445555555566666666667777777788888888999999999000
	3456789012345679012468901890123456789012346890123456789023456890123456891234567891 23
Higher level phocid taxa	
Lobodontini	
democratic	A01100020110000A910B9900MB0010AM2000M01A001AB1000AA0SJ1AA110M0AF2B0101A01B0000102110
ancestral (ACCTRAN)	1001000201100011010199002100100120001011001021000010991111102000220101001100000102110
ancestral (DELTRAN)	1001000201100011010199002100100120002011001021000010991111101200220101001000000102110
exemplar	1011000F2110000091009900M1001A012000101110101 1A00A009900A110M0A022A101A01A0000102A10
Mirounga	
democratic	100S90L9001900A1210M9900M1A01AAM0000M0MM001LES10AA1ASW1211A00B0B22010190MA0000AA2010
ancestral (ACCTRAN)	1001900900190011210299002100100100001021001999100010991211100000220101901000000102010
ancestral (DELTRAN)	1001900900190011210199002100100100002021001091100010991211100200220101901000000102010
exemplar	1009909900190001210299002100 1A1200001021001LES101011991211A0000B22010190100000A02010
Monachus	
democratic	0AAA0002211EA0A0L10E99002E00AA1AMAA0A0MB00MEPSAA0AA0MBAA912AML1MMAA00120M20A00102A1A
ancestral (ACCTRAN)	0011000221100000010199002000101121001010001111100010101091202012210001201100000102110
ancestral (DELTRAN)	0011000201100000910199002100101120001010001011000010101091202012200001201100000102110
exemplar	01A1000221110010L1099900M000001A100010110019991A001012009120ML1111100120M20000102111
Phoca	
democratic	0000000221100001L1A999001M000AA00000A02200A1M10101B09901A101MM122200019020101A100010
ancestral (ACCTRAN)	0000000221100001011999001200010000001022001221010110990101011112220001902010101000 10
ancestral (DELTRAN)	0000000221100001010999001200000000001022001221010010990101011112220001902010101000 10
exemplar	00000002A110000101A99900M2000M000000A02M00A121000000SE0191012MAA220001L0201010100010

Taxon	Characters 104-196
	11111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111
	00000111111111112222223333333333444444444455555555666666666677777777888888889999999
	46789012345678901236780123456789012345678901234579012345678902345678012346789012345 6
Outgroups	
Canis lupus	9109911200101110 01A33301000342999990091000110200900001121221002101102100009010000010
Procyon lotor	0009911200101192000033000003329999900910001102002001A1121211012A011A2100109010100010
Enhydra lutris	00A99012001001S2AA1132210A012299999009100111020 0MA011010111110201111210010910A100010
Lutra canadensis	00A990120010010220?933A1A1022299999009100F110210M101111112110L20111A1100A09011100010
Martes americana	00099112M0101192001S3321A00232999990091000M10200099110121211012011112101109010100010
Ursus americanus	1109901B201011120101330100 02U2999991A9100M11021A1100111211111A2A01102100A09110100010
Odobenus rosmarus	0209901B201011A2201L1009999000099999119000101A100110000A2000009111110910 0A09T02100000
Zalophus californianus	0209901000100112200332F1000T2ALSL99119000V110M0AA100A0100000911110A0102A092AM1A0010
Phocid species	
Cystophora cristata	0200200A22001000102021B190022ALSL001A100042002A000111A1F1001MMM11001M002A13312100110
Erignathus barbatus	0001200A220010AA2A293201A0022101011002000010121 1M01110121111A92A1A01000211T3121A0011
Halichoerus grypus	00A020002200100110GF3221A00221010QQ112000F210210M011101211012221100120A2113T12100110
Hydrurga leptonyx	0000200222001000 20A1222A10022100100001000210 00AAL000000F000009210110901211F301000112
Leptonychotes weddellii	0M1120022M00100020B12M11S01220999330020A02M000A0A11000020001102AAAAA001211K30M100111
Lobodon carcinophagus	00112000210010A020292201001222991110010012 0010A0010000A00001102A001A101A11C302A00111
Mirounga angustirostris	090000002200101A2029210A9002N0999V3111001401 0100LA0000AF0001AL2A01009012A103011??100
Mirounga leonina	A9000000220010A020M0210190022ALLL4H11100040A0AA0LA0000A10001A02A0100900F11D30M110100
Monachus monachus	000020001000 1000M0F122011A0221010KA001110410A010010000000AA119200100001A11030210000M
Monachus schauinslandi	0100200000011000101L2201AA02211003100M1103100000910000000000 10900A10AL000010302A00001
Monachus tropicalis	0001200000011000201E220110022ASEL330010103000A0A910000A20001A9100101900A01F3021A0001
Ommatophoca rossii	A201F000020010A0T0ML221110122ALSL00001000TB000A0LA000000000019210A00901M11N302A00112
Phoca caspica	00A0200F2200100A10?0322AA00221110110020002111211101111101111222110 0M2002A1M2121??110
Phoca fasciata	0000200022001011T03032M11002210100R002000F11121A201110121101222A10012002113212100111
Phoca groenlandica	0000200222001 00A203032201002210 10Q10010002111211201 11A1F1AA122211002M002A1C312100111
Phoca hispida	001A2000220010A020103221A002211A01100100021112 1A20111A1011012M201001200M111312100111
Phoca largha	00002000220010A0202L3221100221110Q100M000211021A20111?1211112M2110022001011312 1??110
Phoca sibirica	0011000122001 00A10M932M10002211003100200021112102011101M10012120100210010 1N312AAA111
Phoca vitulina	0000200222001 0A020M03211?002T11101100211021112112011101011012M201001200211A3121A0110

Taxon	Characters 104-196
	1111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111
	0000011111111111222222333333333344444444445555555566666666667777777788888888899999999
	4678901234567890123678012345678901234567890123457901234567890234567801234678901234567
Higher level phocid taxa	
Lobodontini	
democratic	0BA1200F2M00100020BS22B110122BLLEDD0010002B000A00A00000F000A1L210AA0E01M11C30MA0011M
ancestral (ACCTRAN)	0200200222001000202122211002219990000100021000000000000200010921010090121103011001111
ancestral (DELTRAN)	0000200022001000202122011002219990000100021000000000000200010021010090121103021001110
exemplar	0M1120022M00100020B12M11S01220999330020A02M000A0A11000020001102AAAAA001211K30M100111
Mirounga	
democratic	A9000000220010AA20ML210A9002NALLLVH11100A40A0AA0LA0000AB0001AL2A010090AFA1D30M110100
ancestral (ACCTRAN)	0900000022001010202021019002209994311100040101000000000200010021010090121103011101000
ancestral (DELTRAN)	0900000022001000202021019002219994011100040101000000000120001002101009002110302100100
exemplar	A9000000220010A020M0210190022ALLL4H11100040A0AA0LA0000A10001A02A0100900F11D30M110100
Monachus	
democratic	0A0A2000A00A1000M0BS22011A0221AA03D001A10XA000A0L100000F0001A9B0010AL0AAA10302100001
ancestral (ACCTRAN)	0000200000001000202922011002210003100111031000000100000000001192001009010110302100001
ancestral (DELTRAN)	0001200020001000202922011002219900100101021000000100000000001192001009010110302100001
exemplar	0100200000011000101L2201AA02211003100M1103100000910000000000010900A10AL000010302A00001
Phoca	
democratic	0000200F2200100020N0322110022111011002000211121120111011F1101222A100M2002A1131210011A
ancestral (ACCTRAN)	0000200022001000202032211002211101100200021102112011101211012221100120021113121001100
ancestral (DELTRAN)	0000200022001000202032211002211101100200021102102011101211012221100120021113121001100
exemplar	00002002220010A020M03211?002T11101100211021112112011101011012M201001200211A3121A0110

List of Characters

Snout (18 characters)

3) shape of anterior margin of premaxilla in dorsal view: 0 = flat, square, or bi-lobed; 1 = tapered and/or rounded.

4) triangular lateral extensions of premaxilla into maxilla in dorsal view: 0 = absent; 1 = rudimentary or present.

5) visibility of ventral portion of nasal processes of premaxilla along maxilla in lateral view: 0 = always visible; 1 = not always visible.

6) visibility of middle portion of nasal processes of premaxilla along maxilla in lateral view: 0 = always visible; 1 = not always visible; 9 = n/a — middle portion not present.

7) visibility of dorsal portion of nasal processes of premaxilla along maxilla in lateral view: 0 = always visible; 1 = not always visible; 9 = n/a — dorsal portion not present.

8) shape of ventral portion of nasal processes of premaxilla along maxilla: 0 = concave; 1 = straight; 2 = convex.

9) shape of middle portion of nasal processes of premaxilla along maxilla: 0 = concave; 1 = straight; 2 = convex; 9 = n/a — middle portion not present.

10) shape of dorsal portion of nasal processes of premaxilla along maxilla: 0 = concave; 1 = straight; 2 = convex; 9 = n/a — dorsal portion not present.

11) contact between nasal processes of premaxilla and nasals: 0 = none; 1 = little (less than width of nasal processes); 2 = broad (greater than or equal to width of nasal processes).

12) length of nasal processes of premaxilla along maxilla: 0 = extend only part way to nasals; 1 = extend fully or virtually fully to nasals.

13) shape of anterior margin of nasals (ignoring contribution of nasal suture): 0 = flat or broadly indented; 1 = lobular (uni-, bi-, or tri-lobed).

14) relative lengths of anterior prongs of nasal bones with a trident-shaped (= tri-lobular) morphology: 0 = lateral prongs greater than medial prong; 1 = lateral prongs subequal with medial prong; 2 = lateral prongs less than medial prong; 9 = n/a — nasal bones not trident-shaped.

15) visibility of nasal septum in dorsal view: 0 = does not extend beyond nasals (not visible); 1 = extends beyond nasals (visible).

16) shape of posterior edge of nasals, I: 0 = v-shaped (convergent); 1 = w-shaped (divergent).

17) shape of posterior edge of nasals, II: 0 = pointed; 1 = rounded.

19) distinct caninus fossa: 0 = absent; 1 = present.

20) depth of unnamed fossa on ventrolateral side of premaxilla: 0 = shallow; 1 = medium; 2 = deep; 9 = absent.

21) anterior opening of infraorbital canal relative to nasolacrimal foramen: 0 = anterior; 1 = ventral (or posterior).

Orbit and zygomatic arch (25 characters)

22) swelling of maxilla anterior to zygomatic arch: 0 = absent; 1 = present.

24) size of preorbital process of maxilla: 0 = small; 1 = medium; 2 = large; 9 = absent.

26) size of postorbital process of maxilla: 0 = small; 1 = medium; 2 = large; 9 = absent.

28) size of nasolacrimal foramen: 0 = small; 1 = medium or greater; 9 = absent.

29) location of inferior oblique muscle origin relative to nasolacrimal foramen: 0 = widely separate; 1 = closely adjacent.

30) lacrimal: 0 = absent / not visible; 1 = visible.

31) amount of bone reduction along maxillo-frontal suture in interorbital region: 0 = none / irregular perforations; 1 = little — small foramen or narrow fissure; 2 = great — large foramen and/or greatly widened suture.

38) degree of anterior extension of orbitosphenoid: 0 = extends to distinctly less than one-half length of palatine; 1 = extends to about one-half length of palatine; 2 = extends to distinctly greater than one-half length of palatine; 9 = absent / barely extends onto palatine.

39) ethmoid / turbinal bones in wall of interorbital region: 0 = absent; 1 = present.

40) approach of palatine to lacrimal region: 0 = does not reach lacrimal region; 1 = reaches or almost reaches lacrimal region.

41) location of sphenopalatine vacuity: 0 = enclosed in palatine; 1 = not enclosed in palatine.

42) relationship of sphenopalatine foramen and pterygopalatine canal: 0 = totally confluent, only single foramen visible; 1 = confluent, but individually distinguishable; 2 = separate.

43) continuity of sphenopalatine vacuity and widened maxillo-frontal suture: 0 = separate; 1 = confluent; 9 = n/a — widened maxillo-frontal suture absent.

44) relative vertical position of optic foramina: 0 = in lower third of interorbital region; 1 = between lower third and upper two-thirds of interorbital region; 2 = in upper two-thirds of interorbital region.

45) intracranial openings of optic foramina of orbitosphenoid: 0 = separate; 1 = converging / intermediate; 2 = confluent.

46) interorbital septum anterior to optic foramina: 0 = absent; 1 = present.

47) continuity of bilateral optic foramina in interorbital region: 0 = not continuous, no common passage; 1 = continuous, form passage through interorbital region.

48) alisphenoid canal: 0 = absent; 1 = present.

49) location of least interorbital width: 0 = distinctly anterior to middle of interorbital region; 1 = approximately in the middle of interorbital region; 2 = distinctly posterior to middle of interorbital region.

50) location of greatest zygomatic width: 0 = anterior to glenoid fossa (i.e., within zygomatic arch proper); 1 = at level of glenoid fossa (i.e., at squamosal).

51) relative position of zygomatic arches: 0 = lower than tooth row; 1 = level with tooth row; 2 = higher than tooth row.

52) direction of arch of anterior portion of jugal: 0 = downwards; 1 = flat, no distinct arch; 2 = upwards.

53) degree of overlap of maxillary and squamosal processes of zygomatic arch, on medial surface of zygomatic arch: 0 = little or none; 1 = approach closely — maxilla and squamosal almost or in contact.

54) approach of jugal to lacrimal region: 0 = does not approach lacrimal region; 1 = reaches lacrimal region / almost touches or does touch anterior wall of orbit.

56) degree of interlock between jugal and dorsal process of squamosal process of zygomatic arch: 0 = weak; 1 = medium; 2 = strong; 9 = dorsal process of squamosal absent.

Palate and ventral side of snout (16 characters)

58) size of incisive foramina: 0 = small; 1 = medium; 2 = large; 9 = absent.

59) posterior extension of incisive foramina: 0 = enclosed within premaxilla; 1 = contact premaxillary-maxilla suture; 2 = extend into maxilla; 9 = incisive foramina absent.

60) number of incisive foramina: 0 = one; 1 = two; 9 = absent.

61) reduction of incisive foramina: 0 = absent; 1 = present.

62) position of major palatine foramen relative to maxillo-palatine suture: 0 = anterior; 1 = on; 2 = posterior.

63) shape of maxillo-palatine suture: 0 = flat / square; 1 = rounded / triangular.

64) outline of palatine bones in ventral view: 0 = square; 1 = “butterfly-shaped”.

65) shape of posterior edge of palatine: 0 = (roughly) triangular; 1 = arched; 2 = straight.

66) presence of posteriorly directed process in midline of posterior edge of palatine: 0 = absent; 1 = present.

67) morphology of notching in posterior edge of palatine: 0 = rounded; 1 = triangular; 2 = incision; 9 = none.

68) size of notching in posterior edge of palatine: 0 = small; 1 = medium; 2 = large; 9 = absent.

69) relationship of bony nasal septum to posterior edge of palate: 0 = does not reach posterior edge of palate; 1 = closely approaches / reaches posterior edge of palate.

70) orientation of pterygoid hamuli: 0 = directed laterally; 1 = in midline; 2 = directed medially.

72) degree of contact between ethmoid and pterygoid process of basisphenoid: 0 = narrow; 1 = greater than or equal to medium breadth; 9 = none.

73) relationship between pterygoid process of basisphenoid and auditory bulla: 0 = does not extend to auditory bulla; 1 = extends to auditory bulla.

74) bony constituents of wall of foramen ovale with respect to alisphenoid and squamosal: 0 = alisphenoid only; 1 = both alisphenoid and squamosal; 2 = squamosal only.

Basicranial region (38 characters)

75) visibility of the mastoid process in dorsal view: 0 = not visible; 1 = visible.

76) relative shape of basioccipital-basisphenoid region: 0 = concave; 1 = flat; 2 = convex.

78) size of postglenoid (= glenoid) foramen in squamosal: 0 = small; 1 = medium; 2 = large; 9 = absent.

79) shape of anterior edge of auditory bulla: 0 = concave; 1 = flat; 2 = convex.

80) inflation of ectotympanic: 0 = not inflated; 1 = slightly / moderately inflated; 2 = inflated.

81) inflation of caudal entotympanic along anteroposterior axis: 0 = not inflated; 1 = slight / moderate inflation; 2 = inflated.

82) inflation of medial portion of caudal entotympanic: 0 = not inflated; 1 = slight / moderate inflation; 2 = inflated.

83) distinct sulcus dividing ectotympanic and entotympanic portions of auditory bulla: 0 = absent; 1 = present.

84) relationship between auditory bulla and petrosal: 0 = does not cover petrosal; 1 = covers petrosal.

85) relationship between auditory bulla and paroccipital process: 0 = does not reach process; 1 = reaches (or very closely approaches) process.

86) groove separating mastoid bulla and petrosal: 0 = absent; 1 = present.

88) depth of hypomastoid fossa: 0 = shallow; 1 = medium; 2 = deep; 9 = absent.

89) distinct petromastoid ridge connecting paroccipital and mastoid processes: 0 = absent; 1 = present.

91) morphology of paroccipital processes: 0 = absent; 1 = elongated ridges; 2 = bumps / pillars.

92) size of paroccipital processes: 0 = small / not prominent; 1 = intermediate; 2 = large / prominent; 9 = processes absent.

93) relationship between paroccipital processes and mastoid bone: 0 = separate; 1 = adjacent / continuous; 9 = n/a — paroccipital processes absent.

94) relationship between paroccipital processes and nuchal (= lambdoidal) crest: 0 = separate; 1 = adjacent / continuous; 9 = n/a — paroccipital processes absent.

95) relative size and shape of posterior lacerate foramen: 0 = not confluent with petrobasilar fissure; 1 = confluent with petrobasilar fissure; 9 = petrobasilar fissure absent.

96) relationship between petrobasilar fissure and basioccipital-basisphenoid suture: 0 = in contact, suture unexpanded; 1 = in contact, suture greatly expanded and confluent with fissure; 9 = petrobasilar fissure absent.

97) visibility of posterior opening of carotid canal in ventral view: 0 = not visible; 1 = visible; 9 = carotid canal absent.

98) visibility of foramen of posterior opening of carotid canal in ventral view: 0 = not visible; 1 = visible; 9 = carotid canal absent.

99) direction of posterior opening of carotid canal, I: 0 = distinctly greater than 45° medially (i.e., roughly medially); 1 = roughly 45° medially; 2 = distinctly less than 45° medially (i.e., roughly posteriorly); 9 = absent.

101) posteromedial bony shelf of auditory bulla extending from aperture of carotid canal to posterior lacerate foramen: 0 = absent; 1 = rudimentary or present; 9 = carotid canal absent.

102) dorsal wall of carotid canal: 0 = open; 1 = closed; 9 = carotid canal absent.

103) unidentified bone encircling posterior opening of carotid canal: 0 = absent; 1 = present; 9 = carotid canal absent.

104) opening of carotid canal in auditory bulla: 0 = anterior or anteroventral to posterior lacerate foramen; 1 = adjacent to posterior lacerate foramen; 9 = carotid canal absent.

106) size of median lacerate foramen: 0 = small; 1 = medium; 2 = large; 9 = absent.

107) mastoid lip in region of external cochlear foramen: 0 = absent; 1 = rudimentary or present.

108) external cochlear foramen: 0 = open; 1 = closed; 9 = absent.

109) relationship between stylomastoid and auricular foramen: 0 = confluent / common; 1 = intermediate; 2 = separate; 9 = auricular foramen absent.

110) relationship of tympanohyal and stylomastoid foramen: 0 = separated; 1 = closely associated.

111) location of tympanohyal relative to stylomastoid foramen: 0 = anterior; 1 = posterior.

112) position of petrosal relative to intracranial ridges of basioccipital continuous anteriorly with the dorsum sellae: 0 = widely separate; 1 = intermediate; 2 = closely adjacent.

113) relative size of dorsal region of petrosal: 0 = unexpanded; 1 = intermediate; 2 = expanded.

114) relative size and shape of petrosal apex: 0 = absent / unexpanded and pointed; 1 = intermediate; 2 = dorsoventrally thickened and bulbous.

115) roof of internal auditory meatus: 0 = reduced; 1 = full internal auditory meatus.

116) bony spur of roof of internal auditory meatus: 0 = absent; 1 = present.

117) inflation of bullar chamber: 0 = not inflated; 1 = inflated.

Bony tentorium and bony falx (5 characters)

118) contribution of parietal to bony tentorium: 0 = none / processus tentoricus absent; 1 = contributes.

119) contribution of parietal to bony falx: 0 = none; 1 = contributes; 9 = bony falx absent.

120) ventral extension of bony tentorium: 0 = does not approach floor of braincase; 1 = approaches dorsal region of petrosal; 2 = approaches or contacts floor of braincase.

121) morphology of bony falx proper: 0 = absent; 1 = sail-shaped; 2 = vertical; 3 = inverse sail.

122) partial bony falx: 0 = absent; 1 = present.

Dorsal braincase (2 characters)

123) shape of fronto-parietal suture: 0 = flat; 1 = unilobe; 2 = bi-lobed; 3 = tri-lobed or greater.

126) size of sagittal crest: 0 = absent, but separate temporal ridges present; 1 = small; 2 = medium; 3 = large; 9 = absent.

Teeth (22 characters)

127) number of upper incisors in one-half of jaw: 0 = zero; 1 = one; 2 = two; 3 = three.

128) number of lower incisors in one-half of jaw: 0 = zero; 1 = one; 2 = two; 3 = three.

130) shape of upper incisors in cross-section: 0 = round; 1 = intermediate; 2 = (strongly) laterally compressed; 9 = absent.

131) relative size of upper incisors: 0 = outermost incisor about equal in size to remaining incisor(s); 1 = outermost incisor of much greater size than remaining incisor(s); 9 = n/a — only one upper incisor present per quadrant.

132) relative size of lower incisors: 0 = outermost incisor about equal in size to remaining incisor(s); 1 = outermost incisor of much greater size than remaining incisor(s); 9 = n/a — one or fewer lower incisors present per quadrant.

133) displacement of incisors (upper or lower): 0 = absent — all in line with one another; 1 = present — incisor series slanted; 9 = n/a — incisors absent or singular.

134) procumbency of incisors (upper or lower): 0 = absent; 1 = present; 9 = n/a — upper or lower incisors absent.

135) number of upper postcanines: 0 = three; 1 = four; 2 = five; 3 = six.

136) number of lower postcanines: 0 = three; 1 = four; 2 = five; 3 = six; 4 = seven.

137) morphology of postcanines: 0 = peg-like / unicuspate; 1 = triconodont; 2 = multicuspate.

138) tendency to form additional cusps in triconodont postcanines: 0 = absent; 1 = present; 9 = n/a — postcanines not triconodont.

139) tendency to lose accessory cusps in triconodont postcanines: 0 = absent; 1 = present; 9 = n/a — postcanines not triconodont.

140) size of accessory cusps in triconodont or multicuspate postcanines: 0 = small, continuous with major cusp; 1 = larger, distinct from major cusp; 9 = n/a — postcanines not triconodont or multicuspate.

141) relative size of upper postcanines: 0 = all subequal; 1 = #1 (PM^1) noticeably smaller than rest, which are subequal; 2 = #5 (M^1) noticeably smaller than rest, which are subequal; 3 = #1 and #5 noticeably smaller than rest, which are subequal; 4 = #1 and/or #5 noticeably larger than rest, which are subequal; 9 = n/a — postcanine homology uncertain.

142) relative size of lower postcanines: 0 = all subequal; 1 = #1 (PM_1) noticeably smaller than rest, which are subequal; 2 = #5 (M_1) noticeably smaller than rest, which are subequal; 3 = #1 and #5 noticeably smaller than rest, which are subequal; 4 = #1 and/or #5 noticeably larger than rest, which are subequal; 9 = n/a — postcanine homology uncertain.

143) tendency to single-rooting of upper postcanines: 0 = absent; 1 = present.

144) tendency to single-rooting of lower postcanines: 0 = absent; 1 = present.

145) relative size of gap between upper postcanines 4 and 5: 0 = smaller than other gaps; 1 = subequal to other gaps; 2 = larger than other gaps; 9 = n/a — postcanine homology uncertain.

146) crowding of postcanines (upper and/or lower): 0 = not touching / overlapping; 1 = touching or overlapping.

147) obliqueness of postcanine implantation relative to long axis of tooth row (upper and lower): 0 = straight; 1 = anterior / posterior end of postcanine directed laterally.

148) obliqueness of postcanine implantation (upper and lower) relative to vertical: 0 = straight; 1 = slanted.

149) curvature of upper tooth row (postcanines only): 0 = sigmoidal; 1 = arched; 2 = straight; 3 = kinked between $PC^{1,2}$, otherwise straight; 4 = reverse arch.

Mandible (3 characters)

150) shape of lingual face of mandible at middle postcanines: 0 = concave; 1 = flat; 2 = convex.

151) shape of posteroventral edge of mandible: 0 = rounded; 1 = jagged.

152) distinct medially directed flange along ventral edge of jaw located posterior to mandibular symphysis and ventral to posterior postcanines: 0 = absent; 1 = present.

Forelimb (15 characters)

153) relative size of scapular spine: 0 = reduced to prominent acromion; 1 = medium; 2 = prominent.

154) relative shape of axillary (= caudal) border of scapula: 0 = straight; 1 = curved.

155) distinct hook-like teres major process on scapula: 0 = absent; 1 = present.

157) relative degree of development of supinator (= lateral epicondylar) ridge on humerus: 0 = weak; 1 = medium; 2 = strong; 9 = absent.

159) relative length of deltopectoral crest on humerus: 0 = less than or equal to one-half length of humerus; 1 = greater than one-half length of humerus; 9 = absent.

160) merging of deltopectoral crest to shaft of humerus: 0 = smooth; 1 = abrupt; 9 = absent.

161) entepicondylar foramen of humerus: 0 = absent; 1 = present.

162) distally projecting ledge (palmar process) on cuneiform of carpus: 0 = absent; 1 = present.

163) general morphology of metacarpal shaft: 0 = no lateral shaft ridges; 1 = lateral shaft ridges.

164) general morphology of metacarpal head: 0 = smooth; 1 = “palmar” ridges present.

165) cross-sectional shape of phalanges: 0 = flat; 1 = intermediate; 2 = round.

166) morphology of proximal phalangeal articular surface: 0 = hinge-like; 1 = trochleated.

167) comparative length of metacarpals I and II: 0 = I > II; 1 = I subequal to II; 2 = I < II.

168) comparative overall diameter of metacarpals I and II: 0 = I > II; 1 = I subequal to II; 2 = I < II.

169) relative degree of development of foreflipper claws: 0 = not well developed or absent; 1 = well developed, prominent.

Pelvis (7 characters)

170) eversion of wing of ilium: 0 = distinctly less than 45°; 1 = roughly 45°; 2 = distinctly greater than 45°.

172) depth of gluteal fossa on ilium: 0 = shallow; 1 = medium; 2 = deep; 9 = absent.

173) relationship of obturator nerve foramen to obturator foramen: 0 = distinctly separate, at least unilaterally; 1 = intermediate — foramina confluent, but individually recognizable; 2 = confluent — obturator nerve foramen not apparent.

174) ridges in anterior portion of obturator foramen: 0 = absent; 1 = present.

175) relative length of post-acetabular region of the pelvis: 0 = shortened (and rounded); 1 = elongated (and narrow).

176) general curvature of pelvis around long axis: 0 = relatively straight; 1 = distinctly twisted.

177) relative location of ischiatic spine (= tuber ischiad): 0 = roughly midway along the post-acetabular region; 1 = located in posterior post-acetabular region.

Hind Limb (10 characters)

178) position of greater trochanter on femur: 0 = lower than head; 1 = equal with head; 2 = higher than head.

180) depth of trochanteric fossa on femur: 0 = shallow; 1 = medium; 2 = deep; 9 = absent.

181) lesser trochanter: 0 = absent; 1 = present.

182) relative width of femur distally: 0 = gracile (less than medium breath); 1 = robust.

183) proximal fusion of tibia and fibula: 0 = unfused; 1 = rudimentary — not fused all the way around; 2 = totally fused.

184) relative degree of development of the post-tibial (= intercondyloid) fossa of tibia: 0 = weak; 1 = strong.

186) posterior process on plantar aspect of astragalus: 0 = absent; 1 = present.

187) depth of groove on plantar aspect of posterior process of astragalus: 0 = groove absent; 1 = shallow; 2 = moderate; 3 = deep; 9 = posterior process absent.

188) length of metatarsal III relative to remaining metatarsals (shape of posterior flipper margin): 0 = metatarsal III longest; 1 = metatarsal III intermediate; 2 = metatarsal III subequal or slightly shorter; 3 = metatarsal III distinctly shorter.

189) relative degree of development of hind flipper claws: 0 = not well developed or absent; 1 = well developed, prominent.

Miscellaneous (7 characters)

190) location of posterior end of cribriform plate: 0 = within interorbital region; 1 = posterior portion of interorbital region; 2 = anterior end of braincase.

191) relative position of vertebrarterial (= intervertebral) foramen of atlas: 0 = visible in dorsal view; 1 = visible in posterior view.

192) claw morphology in cross-section, I: 0 = semicircular; 1 = triangular.

193) claw morphology in cross-section, II: 0 = dorsal ridge or annuli absent; 1 = dorsal ridge or annuli present.

194) mystacial whiskers: 0 = smooth; 1 = beaded.

195) secondary hairs: 0 = (largely) absent; 1 = present.

196) relative overall size of males and females: 0 = females smaller than males; 1 = females subequal to males; 2 = females larger than males.

Appendix B

Carnivore phylogeny sources

The following references were used as source trees and/or to provide date estimates for the composite phylogeny. References are divided according to the various matrices they contributed to and so may appear more than once.

Higher groups (excluding Hyaenidae) (Fig. 4.1, Table 4.2)

Source trees: Gregory & Hellman (1939); Leone & Wiens (1956); Wurster (1969); Hunt (1974); Sarich (1975); Tedford (1976); Arnason (1977); Bugge (1978); Hendey (1978); Ling (1978); Schmidt-Kittler (1981); Dutrillaux *et al*. (1982); Flynn & Galiano (1982); Ginsburg (1982); Wozencraft (1984, 1989); Couturier & Dutrillaux (1985); de Jong (1986); Braunitzer & Hofmann (1987); Wyss (1987); Flynn *et al*. (1988); Holmes (1988); Rodewald *et al*. (1988); Ahmed *et al*. (1990); Czelusniak *et al*. (1990, 1991); Nojima (1990); McKenna (1991); Arnason & Ledje (1993); Wolsan (1993); Wyss & Flynn (1993); Berta & Wyss (1994); Hunt & Barnes (1994); Vrana *et al*. (1994); Lento *et al*. (1995); Austin (1996); Bininda-Emonds & Russell (1996); Werdelin (1996)

Date estimates: Repenning *et al*. (1979); Martin (1980); Radinsky (1982); Savage & Russell (1983); Barnes *et al*. (1985); Gittleman (1986a); Anderson (1989); Jinchu (1990); Wayne *et al*. (1991); Werdelin & Solounias (1991); Janczewski *et al*. (1995); Hunt (1996)

Both: Sarich (1969a, 1969b, 1976); Seal *et al*. (1970); Radinsky (1975); Thenius (1979); Goodman *et al*. (1982); O'Brien *et al*. (1985); Goldman *et al*. (1989); Wayne *et al*. (1989a); Janczewski *et al*. (1992); Garland *et al*. (1993); Hashimoto *et al*. (1993); Hunt & Tedford (1993); Veron & Catzeflis (1993); Masuda & Yoshida (1994a); Slade *et al*. (1994); Arnason *et al*. (1995); Pecon Slattery & O'Brien (1995)

Mustelidae (excluding Lutrinae and Mephitinae) (Fig. 4.2, Table 4.3)

Source trees: Petter (1971); Graphodatsky *et al*. (1976, 1989); Stains (1976); Long (1981); Schmidt-Kittler (1981); de Muizon (1982a); Youngman (1982); Belyaev *et al*. (1984); Wozencraft (1984, 1989, 1993); Couturier &

Dutrillaux (1985); Arnason & Widegren (1986); Holmes (1988); Lushnikova *et al*. (1989); Obara (1991); Vrana *et al*. (1994)

Date estimates: Sarich (1976); Savage & Russell (1983); Anderson *et al*. (1986); Wayne *et al*. (1991); Garland *et al*. (1993); Masuda & Yoshida (1994b); Hunt (1996)

Both: Anderson (1970, 1989); Simonsen (1982); Hartl *et al*. (1988); O'Brien *et al*. (1989); Wayne *et al*. (1989a); Bryant *et al*. (1993); Hashimoto *et al*. (1993); Hosoda *et al*. (1993); Masuda & Yoshida (1994a)

Lutrinae (Fig. 4.3, Table 4.4)

Source trees: Davis (1978); de Muizon (1982a); van Zyll de Jong (1987); Holmes (1988); Bryant *et al*. (1993); Wozencraft (1993)

Date estimates: Savage & Russell (1983); Wayne *et al*. (1991); Masuda & Yoshida (1994a)

Mephitinae (Fig. 4.4, Table 4.5)

Source trees: Holmes (1988); Bryant *et al*. (1993); Wozencraft (1993)

Date estimates: Savage & Russell (1983); O'Brien *et al*. (1989); Wayne *et al*. (1989a, 1991)

Both: Dragoo *et al*. (1993)

Procyonidae (Fig. 4.5, Table 4.6)

Source trees: Couturier & Dutrillaux (1985); Decker & Wozencraft (1991); Wozencraft (1993)

Date estimates: Sarich (1976); Savage & Russell (1983); Wayne *et al*. (1989a); Garland *et al*. (1993); Hunt (1996)

Both: Baskin (1982); Zhang & Ryder (1993); Pecon Slattery & O'Brien (1995)

Otariidae (Fig. 4.6, Table 4.7)

Source trees: Sarich (1969b, 1975); Stirling & Warneke (1971); Morejohn (1975); Ling (1978); Trillmich & Majluf (1981); Berta & Deméré (1986); Beentjes

(1990); Wozencraft (1993); Berta & Wyss (1994); Hirota (1994); Lento *et al.* (1995)

Date estimates: Repenning *et al*. (1979); Bogdanov & Pastukhov (1982); Savage & Russell (1983); Hoberg & Adams (1992)

Both: Kim *et al*. (1975); Sarich (1976); Barnes *et al*. (1985); Arnason *et al.* (1995)

Phocidae (Fig. 4.7, Table 4.8)

Source trees: Chapskii (1955); Burns & Fay (1970); Anbinder (1971); Sarich (1975); Ling (1978); de Muizon (1982b); Couturier & Dutrillaux (1985); Wyss (1988b); Nojima (1990); Wozencraft (1993); Berta & Wyss (1994); Lento *et al.* (1995); Mouchaty *et al*. (1995); Bininda-Emonds & Russell (1996)

Date estimates: Repenning *et al*. (1979); Savage & Russell (1983); Hoberg & Adams (1992); Arnason *et al*. (1993)

Both: Sarich (1969b, 1976); Hendey (1972); Bogdanov & Pastukhov (1982); Slade *et al.* (1994); Arnason *et al*. (1995); Perry *et al*. (1995)

Ursidae (Fig. 4.8, Table 4.9)

Source trees: Wurster (1969); Seal *et al*. (1970); Nash & O'Brien (1987); Czelusniak *et al.* (1990, 1991); Zhang & Shi (1991); Taberlet & Bouvet (1992); Wozencraft (1993); Mazza & Rustioni (1994); Trajano & Ferrarezzi (1994); Vrana *et al*. (1994)

Date estimates: Sarich (1976); Savage & Russell (1983); Jinchu (1990); Wayne *et al.* (1991); Janczewski *et al*. (1992, 1995); Zhang & Ryder (1993); Hunt (1996)

Both: Thenius (1976, 1979); Ficcarelli (1979); O'Brien *et al*. (1985); Hofmann & Braunitzer (1987); Goldman *et al*. (1989); Wayne *et al*. (1989a); Cronin *et al.* (1991); Shields & Kocher (1991); Garland *et al*. (1993); Hashimoto *et al.* (1993); Zhang & Ryder (1994); Arnason *et al*. (1995); Pecon Slattery & O'Brien (1995)

Canidae (Fig. 4.9, Table 4.10)

Source trees: Kleiman (1967, 1969, 1975); Todd (1970); Atkins & Dillon (1971); Fox (1971); Chiarelli (1975); Stains (1975); Clutton-Brock *et al*. (1976); Darbre & Lehmann (1976); Atkins (1978); Nowak (1978); Van Gelder (1978);

Tagle *et al*. (1986); Braunitzer & Hofmann (1987); Czelusniak *et al*. (1990); Wayne *et al*. (1990); Wayne & Jenks (1991); Phillips & Henry (1992); Girman *et al*. (1993); Wozencraft (1993); Roy *et al*. (1994); Vrana *et al*. (1994); Tedford *et al*. (1995)

Date estimates: Savage & Russell (1983); Wayne *et al*. (1989b, 1991); Lehman *et al*. (1991); Janczewski *et al*. (1992); Hunt (1996)

Both: Nowak (1979); Berta (1987); Wayne *et al*. (1987a, 1987b, 1989a); Wayne & O'Brien (1987); Geffen *et al*. (1992, 1996); Garland *et al*. (1993); Hosoda *et al*. (1993); Gottelli *et al*. (1994)

Hyaenidae (Fig. 4.1, Table 4.2)

Source trees: Gregory & Hellman (1939); Galiano & Frailey (1977); Howell & Petter (1980); Qui (1987); Wozencraft (1993)

Date estimates: Savage & Russell (1983); Wayne *et al*. (1989a, 1991); Garland *et al*. (1993); Veron & Catzeflis (1993)

Both: Werdelin & Solounias (1991)

Felidae (Fig. 4.10, Table 4.11)

Source trees: Kratochvíl (1976, 1982); Glass & Martin (1978); Hemmer (1978, 1981); Robinson (1979); Král & Zima (1980); Grove (1982); Wurster-Hill & Centerwall (1982); Herrington (1983, 1986); Werdelin (1983); Tumlison & McDaniel (1984); Couturier & Dutrillaux (1985); Tagle *et al*. (1986); Peters (1987); Modi & O'Brien (1988); Czelusniak *et al*. (1990); Ahmed *et al*. (1992); Salles (1992); Schreiber *et al*. (1993); Wozencraft (1993); Masuda *et al*. (1994); Vrana *et al*. (1994); Russell *et al*. (1995); Decker (1996)

Date estimates: Savage & Russell (1983); Centerwall *et al*. (1985); Kitchener (1991); Randi & Ragni (1991); Wayne *et al*. (1991); Arnason *et al*. (1995); Hunt (1996)

Both: Martin (1980); Werdelin (1981); Benveniste (1985); Collier & O'Brien (1985); O'Brien *et al*. (1987); Essop *et al*. (1988); Wayne *et al*. (1989a); Janczewski *et al*. (1992, 1995); Garland *et al*. (1993); Veron & Catzeflis (1993); Pecon Slattery *et al*. (1994)

Herpestidae (Fig. 4.11, Table 4.12)

Source trees: Gregory & Hellman (1939); Fredga (1972); Petter (1974); Stains (1983); Couturier & Dutrillaux (1985); Taylor (1988); Wozencraft (1993); Austin (1996)

Date estimates: Savage & Russell (1983); Wayne *et al*. (1991); Veron & Catzeflis (1993)

Both: Taylor *et al*. (1991)

Viverridae (Fig. 4.12, Table 4.13)

Source trees: Gregory & Hellman (1939); Petter (1974); Crawford-Cabral (1982); Stains (1983); Wozencraft (1984, 1993); Couturier & Dutrillaux (1985); Taylor (1988)

Date estimates: Savage & Russell (1983); Wayne *et al*. (1989a); Hunt (1996)

Both: Veron & Catzeflis (1993)

Appendix C

Carnivore data set and sources

The data set used in Chapter 6 is built on one compiled by Gittleman (1984, 1985, 1986a, 1986b, 1991, 1993, unpubl. data) detailing morphological and life history characteristics of numerous fissipeds. As such, I have attempted to follow his definitions and procedures. Except for most pinniped brain weights (see below), values were gleaned from the literature (sources listed following the tables). I used original publications whenever possible; if these were unavailable, I used review articles or encyclopedic sources (e.g., Mammalian Species Accounts; Parker, 1990; Nowak, 1991). Unless otherwise noted, species values for a variable are medians of what I deemed to be independent estimates of it. Therefore, an article could contain more than one independent estimate (e.g., widely separated populations or subspecies with different expressions of a character). In the case of large discrepancies between sources (including Gittleman's numbers), preference was given to those articles with larger sample sizes or employing a more robust methodology.

I supplemented the meager information available on pinniped brain sizes by measuring specimens housed in the Natural History Museum, London (specimen list in Appendix D). I followed the procedure of Gittleman (1986a): the volume of cleaned, undamaged skulls was determined using 2.0 mm plastic beads and this value was used to directly estimate brain weight (i.e., assuming 1 mL = 1 g).

I have arbitrarily divided the variables into three categories — morphology, life history, and physiology / miscellany — for presentation purposes.

Morphological variables

1) Body weight (SWt, MWt, and FWt): average weight of the body (in kg). I attempted to exclude estimates for individuals that were pregnant, preparing to begin or end hibernation, or were in exceptionally good or poor condition. The species value (SWt) was calculated as the median of weight estimates that did not specify a gender and the average of male (MWt) and female weight (FWt).

2) Head and body length (SHB, MHB, and FHB): distance from the tip of the snout to the base of the tail (in cm). Head and body length is not typically recorded for pinnipeds. Instead, I used standard length, which is the distance from the snout to the tail tip, measured with the animal on its back (American Society of Mammalogists, 1967). Despite including the tail, standard length is a roughly equivalent measure since pinniped tails are negligible in length compared to the head and body. In all cases, the species value (SHB) was calculated as the average of male (MHB) and female (FHB) values.

3) Brain weight (SBr, MBR, FBr): weight of the brain (in g). When only the brain volume or cranial capacity was given, I assumed that 1 mL of brain tissue weighed 1 g (J. L. Gittleman, pers. comm.). The species value (SBr) was calculated as the median of estimates that did not specify a gender and the average of male (MBr) and female brain weight (FBr).

Table C.1: Values of selected morphological characters for all extant species of carnivore. See text for identity and descriptions of variables. Sources follow the table.

	MWt	FWt	SWt	MHB	FHB	SHB	MBr	FBr	SBr
CANIDAE									
Alopex lagopus	3.50	2.90	3.20			56.65	34.00	37.00	35.50
Atelocynus microtis			9.03			83.35			62.18
Canis adustus	12.00	10.60	11.30			74.75	50.10	53.50	51.80
Canis aureus	8.79	8.32	8.55			83.00			56.26
Canis latrans	11.50	9.70	10.60			87.50	92.10	84.50	88.30
Canis lupus	35.10	31.10	33.10	105.50	104.50	105.00	134.60	130.00	132.30
Canis mesomelas	8.20	7.20	7.70			70.94	61.60	52.00	56.80
Canis rufus	27.68	25.69	26.69			110.43			101.49
Canis simensis	16.20	12.80	14.50	96.30	91.90	94.10			100.27
Cerdocyon thous	6.00	6.00	5.74			65.00	43.10	40.50	41.80
Chrysocyon brachyurus	23.80	22.85	23.33			124.94	124.00	116.00	120.00
Cuon alpinus	17.80	13.80	15.80	100.50	100.50	97.50	95.00	95.00	95.00
Dusicyon australis						96.00			
Lycaon pictus	21.80	22.20	22.00	94.00	94.00	91.43	130.00	128.00	129.00
Nyctereutes procyonoides	3.75	4.69	4.22	46.71	43.04	44.87			28.50
Otocyon megalotis	4.12	4.07	4.10			53.92	29.10	24.50	26.80
Pseudalopex culpaeus	9.72	7.52	8.62	73.80	70.70	72.25	52.00	51.00	51.50
Pseudalopex griseus			6.34			51.80			37.71
Pseudalopex gymnocercus	4.60	4.20	4.40			62.10	40.00	40.00	40.00
Pseudalopex sechurae			4.48			56.06			30.88
Pseudalopex vetulus			3.35			60.18			
Speothos venaticus	5.33	8.00	6.67			66.38	39.50	41.50	40.50
Urocyon cinereoargenteus	4.10	3.30	3.70			60.35	42.10	39.50	40.80
Urocyon littoralis	1.95	1.90	1.92	48.45	46.08	47.26			27.66
Vulpes bengalensis	3.00	1.80	2.40			52.32	27.10	24.50	25.80

Table C.1: Continued.

	MWt	FWt	SWt	MHB	FHB	SHB	MBr	FBr	SBr
Vulpes cana	1.04	0.94	0.99	42.39	43.05	42.72			
Vulpes chama	2.87	2.90	2.89			53.38	34.00	33.00	33.50
Vulpes corsac			2.85			58.00			29.96
Vulpes ferrilata	7.00		5.00			60.18			43.82
Vulpes pallida			2.50			43.05			25.03
Vulpes rueppelli			2.38			46.00			24.29
Vulpes velox	2.20	1.98	2.09	51.52	49.54	50.53			32.14
Vulpes vulpes	4.30	3.90	4.10	64.70	61.10	62.90	44.00	43.00	43.50
Vulpes zerda	1.50	1.50	1.50			37.54	17.10	17.50	17.30
FELIDAE									
Acinonyx jubatus	57.60	60.00	58.80			148.49	114.00	106.00	110.00
Caracal caracal	13.50	9.68	11.59			74.15	57.10	53.50	55.30
Catopuma badia			4.70			55.00			43.82
Catopuma temminckii		4.20	11.50			89.00			68.03
Felis bieti			5.47			78.63			
Felis chaus	8.07	5.85	6.96			70.63	41.60	37.00	39.30
Felis margarita	3.13	2.69	2.91			51.29			24.53
Felis nigripes	1.50	1.32	1.41			40.13			20.09
Felis silvestris	4.88	4.09	4.49	52.20	47.80	50.00	39.30	34.50	36.90
Herpailurus yaguarondi	7.00		6.88			66.05			40.04
Leopardus pardalis	13.01	10.75	11.88	79.84	67.32	73.58	67.60	60.00	63.80
Leopardus tigrinus	2.60	1.75	2.18			49.91			32.14
Leopardus wiedii			3.28			63.20			33.78
Leptailurus serval	13.00	10.40	11.70			83.50	56.60	57.00	56.80
Lynx canadensis	10.01	8.59	9.30	72.52	68.36	70.44			69.41
Lynx lynx	20.80	17.80	19.30			85.37	71.50	68.50	70.00
Lynx pardinus	12.80	9.30	11.05			96.29			78.26

Table C.1: Continued.

	MWt	FWt	SWt	MHB	FHB	SHB	MBr	FBr	SBr
Lynx rufus	7.20	5.20	6.20	73.05	65.33	69.19	58.10	58.50	58.30
Neofelis nebulosa	12.00	9.45	10.73			84.10			68.72
Oncifelis colocolo			4.92			61.50			33.12
Oncifelis geoffroyi	2.20	2.20	2.20	59.00	56.05	57.53	32.50	35.50	34.00
Oncifelis guigna			2.51			43.07			24.05
Oreailurus jacobita			7.21			60.09			
Otocolobus manul	3.05		3.05			57.50			34.47
Panthera leo	176.10	135.50	155.80	195.00	157.50	176.25	228.00	219.00	223.50
Panthera onca	94.80	77.60	86.20	145.40	121.72	133.56	154.00	149.00	151.50
Panthera pardus	65.50	39.30	52.40			135.50	139.00	112.00	125.50
Panthera tigris	191.00	131.00	161.00	191.53	163.31	177.42	311.60	247.00	279.30
Pardofelis marmorata			3.25			51.80			30.88
Prionailurus bengalensis	3.30	2.25	2.78			68.53	30.10	28.50	29.30
Prionailurus planiceps			1.85			47.64			21.98
Prionailurus rubiginosus	1.61	1.25	1.43			40.72	19.00	19.00	19.00
Prionailurus viverrinus	11.30	6.30	8.80			78.00	47.50	45.50	46.50
Profelis aurata			11.94			80.00			57.97
Puma concolor	64.00	39.60	51.80	151.63	128.48	140.05	132.00	119.00	125.50
Uncia uncia	32.50	32.50	32.50			115.00	106.00	98.00	102.00
HERPESTIDAE									
Atilax paludinosus	4.10	3.30	3.70	51.38	48.72	50.05	30.00	27.00	28.50
Bdeogale crassicauda	1.93	1.57	1.75	45.00	45.00	44.59			16.95
Bdeogale jacksoni									21.98
Bdeogale nigripes			2.75			61.32			21.98
Crossarchus alexandri			1.51			45.03			11.25
Crossarchus ansorgei	0.70		0.85	34.20	31.10	32.65			
Crossarchus obscurus	1.55	1.31	1.43			34.00	10.10	9.50	9.80

Table C.1: Continued.

	MWt	FWt	SWt	MHB	FHB	SHB	MBr	FBr	SBr
Cynictis penicillata	0.75	0.64	0.69	28.60		30.40	11.00	10.00	10.50
Dologale dybowskii			0.37			29.00			5.99
Galerella flavescens									
Galerella pulverulenta	0.89	0.69	0.79			35.04			11.02
Galerella sanguinea	0.54	0.44	0.49	34.50	31.50	33.00	8.50	9.00	8.75
Galerella swalius									
Galidia elegans	0.81	0.81	0.81			35.32	11.60	10.00	10.80
Galidictis fasciata						30.80			11.94
Galidictis grandidieri									
Helogale hirtula			0.81			23.04			5.00
Helogale parvula	0.25	0.25	0.25			20.22	4.50	5.00	4.75
Herpestes brachyurus	1.59	0.79	1.19			41.57	14.00	11.00	12.50
Herpestes edwardsii	1.52	1.04	1.28			39.94	11.00	10.00	10.50
Herpestes ichneumon	3.20	2.90	3.05			57.50	23.60	23.00	23.30
Herpestes javanicus	1.03	0.53	0.78	29.78	23.98	26.88	7.50	7.00	7.25
Herpestes naso			3.00			55.44			25.53
Herpestes palustris			0.74			30.80			7.24
Herpestes semitorquatus									
Herpestes smithii	2.15	1.25	1.70			40.75	14.10	13.50	13.80
Herpestes urva	2.72	2.04	2.38			50.78	22.00	20.00	21.00
Herpestes vitticollis	3.06	1.70	2.38			47.82	25.60	26.00	25.80
Ichneumia albicauda	4.25	3.53	3.89			57.34	26.10	22.50	24.30
Liberiictis kuhni	2.30	1.00	1.65	42.30	47.80	45.05			16.97
Mungos gambianus			1.80			35.07			9.97
Mungos mungo	1.29	1.23	1.26			36.35	11.00	10.00	10.50
Mungotictis decemlineata			0.80			32.38			
Paracynictis selousi	1.76	1.64	1.70			42.92	16.10	15.50	15.80
Rhynchogale melleri	2.31	1.92	2.12			46.10			16.95
Salanoia concolor			0.78			32.00			11.02

Table C.1: Continued.

	MWt	FWt	SWt	MHB	FHB	SHB	MBr	FBr	SBr
Suricata suricatta	0.74	0.72	0.73			28.66	10.60	10.00	10.93
HYAENIDAE									
Crocuta crocuta	48.70	55.30	52.00	124.40	136.40	130.40	134.00	153.00	143.50
Hyaena hyaena	27.00	26.60	26.80	110.80	110.80	110.80	97.60	98.00	97.80
Parahyaena brunnea	42.70	43.90	43.30			120.00	104.00	110.00	107.00
Proteles cristatus	8.32	8.36	8.34	70.00	70.00	70.00	34.10	36.50	35.30
MUSTELIDAE									
Amblonyx cinereus			3.53			51.80			38.09
Aonyx capensis	20.00	18.00	19.00			80.00	97.00	93.00	95.00
Aonyx congicus			19.65			83.57			
Arctonyx collaris			10.49			69.23			49.40
Conepatus chinga	2.37	1.47	1.92			41.99			
Conepatus humboldtii	1.25	0.83				35.42			11.02
Conepatus leuconotus			3.39			42.27			14.44
Conepatus mesoleucus	1.89	2.67	7.46						
Conepatus semistriatus			2.26						18.92
Eira barbara	4.32	3.95	4.14			62.00	36.60	35.00	35.80
Enhydra lutris	32.20	24.40	28.30	148.00	140.00	144.00	132.00	119.00	125.50
Galictis cuja			1.00			42.46			15.03
Galictis vittata	3.40	1.80	2.60			51.29	25.10	23.50	24.30
Gulo gulo	12.85	10.35	11.60	83.08	74.28	78.68	84.50	72.50	78.50
Ictonyx libyca	0.23		0.23			24.25			4.48
Ictonyx striatus	0.91	0.63	0.77			33.50	11.10	8.50	9.80
Lontra canadensis	8.60	7.80	8.20			68.51	55.10	50.50	52.80
Lontra felina			4.10			67.86			38.86

Table C.1: Continued.

	MWt	FWt	SWt	MHB	FHB	SHB	MBr	FBr	SBr
Lontra longicaudis	9.25	3.86	6.56			60.18			
Lontra provocax						58.99			
Lutra lutra	10.70	7.10	8.90			69.00	45.00	39.00	42.00
Lutra maculicollis	4.58	3.50	4.04			59.59	47.00	33.00	40.00
Lutra sumatrana			6.48			76.51			
Lutrogale perspicillata	10.26	7.30	8.78			88.89	69.00	61.00	65.00
Lyncodon patagonicus			0.23			32.44			
Martes americana	0.97	0.77	0.87	40.50	36.00	38.25	17.10	14.50	15.80
Martes flavigula		3.40	2.51			55.00			34.12
Martes foina	2.05	1.30	1.68	51.00	42.50	46.00			20.91
Martes gwatkinsii			2.03			51.29			
Martes martes	1.36	1.02	1.19	46.50	41.00	51.39	22.00	18.00	20.00
Martes melampus			1.00			44.18			18.73
Martes pennanti	5.25	2.25	3.75	83.55	66.80	75.18	34.60	29.00	31.80
Martes zibellina	1.33	1.03	1.18	47.50	42.75	45.13	20.00	17.00	18.50
Meles meles	12.30	10.90	11.60			70.80	55.50	45.50	50.50
Mellivora capensis	8.57	7.59	8.08			68.50	81.60	64.00	72.80
Melogale everetti									
Melogale moschata			1.99			38.50			14.73
Melogale orientalis									12.81
Melogale personata			2.00			39.94			15.18
Mephitis macroura	1.19	1.11	1.15			30.80			9.49
Mephitis mephitis	2.80	2.00	2.40			40.08	10.60	10.00	10.30
Mustela africana						31.00			7.03
Mustela altaica	0.25	0.13	0.19	25.55	23.30	24.43	4.50	4.50	4.50
Mustela erminea	1.28	0.62	0.95	23.37	19.89	21.63	5.00	3.00	4.00
Mustela eversmannii	2.05	1.35	1.70	46.35	40.50	43.43			
Mustela felipei				21.70		21.70			
Mustela frenata	0.26	0.15	0.20	24.45	21.55	23.00	4.00	4.00	4.00

Table C.1: Continued.

	MWt	FWt	SWt	MHB	FHB	SHB	MBr	FBr	SBr
Mustela kathiah	0.36	0.20	0.28			25.99			4.01
Mustela lutreola	0.74	0.44	0.59	35.50	36.00	35.75	9.00	8.00	8.50
Mustela lutreolina	0.47		0.47	30.90		30.90			
Mustela nigripes	1.03	0.80	0.91	41.81	37.62	39.71			8.50
Mustela nivalis	0.10	0.06	0.08	19.75	18.00	18.88	1.50	1.50	1.50
Mustela nudipes	0.65	0.50	0.57			32.69			
Mustela putorius	1.26	0.80	1.03	40.50	31.50	36.00	9.60	7.00	8.30
Mustela sibirica	0.74	0.40	0.57	33.50	27.88	30.69	7.50	6.00	6.75
Mustela strigidorsa			1.50			28.73			
Mustela vison	1.21	0.61	0.91	38.00	35.00	36.50	10.00	7.00	8.50
Mydaus javanensis			2.50			44.25			19.49
Mydaus marchei			2.50			39.08			14.44
Poecilogale albinucha	0.35	0.25	0.30			30.50	5.10	4.50	4.80
Pteronura brasiliensis	28.00	24.00	26.00			114.14			85.63
Spilogale putorius	0.67	0.43	0.55	31.78	28.30	30.04	5.00	5.00	5.00
Spilogale pygmaea		0.37	0.37						
Taxidea taxus	8.60	5.62	4.05			56.00	49.50	48.50	49.00
Vormela peregusna	0.67	0.53	0.60	31.00	31.50	33.03	5.60	4.00	4.80
Odobenus rosmarus	1232.95	811.50	1022.23	315.75	260.00	287.88	1303.00	1340.50	1160.88
OTARIIDAE									
Arctocephalus australis	159.00	48.50	103.75	189.25	141.25	165.25	350.00	265.00	307.50
Arctocephalus forsteri	164.38	55.00	109.69	199.38	141.88	170.63	340.00	300.00	320.00
Arctocephalus galapagoensis	64.50	27.40	45.95	151.25	120.00	135.63	302.50	280.00	291.25
Arctocephalus gazella	155.00	38.20	96.60	185.90	128.75	157.33	360.00	322.00	341.00
Arctocephalus philippii	140.00	50.00	95.00	200.00	140.00	170.00	415.00		415.00
Arctocephalus pusillus	279.50	78.00	178.75	220.00	161.00	190.50	401.25	337.50	369.38

Table C.1: Continued.

	MWt	FWt	SWt	MHB	FHB	SHB	MBr	FBr	SBr
Arctocephalus townsendi	145.00	49.55	97.28	200.30	141.60	170.95			
Arctocephalus tropicalis	152.50	50.00	101.25	180.00	145.00	162.50	322.50	330.00	326.25
Callorhinus ursinus	227.00	44.75	135.88	213.00	135.00	174.00	355.00	302.50	328.75
Eumetopias jubatus	1000.00	287.55	643.78	300.00	240.15	270.08	747.50	575.00	661.25
Neophoca cinerea	300.00	78.55	189.28	212.50	148.20	180.35	440.00	337.50	388.75
Otaria byronia	300.00	144.00	222.00	234.88	188.86	211.87	546.25	470.00	508.13
Phocarctos hookeri	364.00	183.00	273.50	225.00	180.00	202.50	417.50	370.00	393.75
Zalophus californianus	300.00	91.00	195.50	225.00	180.00	202.50	405.00	361.50	379.13
PHOCIDAE									
Cystophora cristata	343.18	222.50	282.84	260.00	206.00	233.00	480.00	430.00	455.00
Erignathus barbatus	265.00	276.36	270.68	230.00	230.00	230.00		460.00	417.50
Halichoerus grypus	233.00	155.00	194.00	216.35	180.00	198.18	342.50	272.50	307.50
Hydrurga leptonyx	324.00	367.00	345.50	287.00	322.48	304.74	765.00	660.00	712.50
Leptonychotes weddellii	360.00	376.00	368.00	250.00	259.50	254.75	501.50	563.15	526.16
Lobodon carcinophagus	220.50	224.00	222.25	226.00	228.50	227.25	578.17	538.75	558.46
Mirounga angustirostris	2275.00	700.00	1487.50	450.00	295.00	372.50	700.00	640.00	670.00
Mirounga leonina	3510.00	503.00	2006.50	467.00	270.00	368.50	1431.25	898.75	1165.00
Monachus monachus	260.00	301.00	280.50	254.75	264.60	259.68	480.00	480.00	480.00
Monachus schauinslandi	173.00	265.00	219.00	214.20	233.70	223.95	370.00		370.00
Monachus tropicalis		160.00	160.00	233.00	225.63	229.31	460.00		460.00
Ommatophoca rossii	173.80	185.00	179.40	199.00	214.60	206.80	425.00	530.00	477.50
Phoca caspica	70.50	55.00	62.75	150.00	136.40	143.20	165.00	160.00	149.65
Phoca fasciata	94.80	80.36	87.58	153.00	154.70	153.85	257.50	240.00	248.75
Phoca groenlandica	135.00	129.50	132.25	176.00	169.30	172.65	297.50	252.50	276.50
Phoca hispida	71.67	66.50	69.08	129.30	128.90	129.10	229.25	220.00	189.31
Phoca largha	97.00	86.00	91.50	168.95	159.00	163.98	257.50	250.00	253.75
Phoca sibirica	89.50	89.50	89.50	130.00	125.35	127.68	185.00	190.00	187.50

Table C.1: Continued.

	MWt	FWt	SWt	MHB	FHB	SHB	MBr	FBr	SBr
Phoca vitulina	97.13	77.50	87.32	171.51	151.80	161.66	362.25	265.00	275.00
Ailurus fulgens	5.00	4.90	4.95	59.25	59.25	58.00	41.68	41.68	41.68
PROCYONIDAE									
Bassaricyon alleni									
Bassaricyon beddardi									
Bassaricyon gabbii			1.44			41.25			19.30
Bassaricyon lasius									
Bassaricyon pauli									
Bassariscus astutus	1.03	0.87	0.95			34.00	17.00	16.00	16.50
Bassariscus sumichrasti	1.28	0.53	0.91			42.50			19.30
Nasua narica	4.78	4.14	4.46	60.70	51.50	56.10	37.00	37.00	37.00
Nasua nasua	3.97	3.45	3.71			54.90			29.96
Nasuella olivacea				38.30	39.40	38.85			27.94
Potos flavus	2.20	2.00	2.10	61.25	47.30	54.28	27.00	24.00	25.50
Procyon cancrivorus	7.63	6.27	6.95			60.18			61.56
Procyon gloveralleni									36.60
Procyon insularis						57.82			39.65
Procyon lotor	6.43	6.32	6.37	48.95	49.00	48.98	41.00	39.00	40.00
Procyon maynardi						47.34			36.23
Procyon minor									38.86
Procyon pygmaeus			3.50			42.84			32.14
URSIDAE									
Ailuropoda melanoleuca	139.00	97.00	118.00			135.00	263.60	205.00	234.30
Helarctos malayanus	65.00	50.00	57.50			122.44			354.25

Table C.1: Continued.

	MWt	FWt	SWt	MHB	FHB	SHB	MBr	FBr	SBr
Melursus ursinus			100.75			160.00			304.90
Tremarctos ornatus	161.25	55.50	108.38	190.00		167.62			219.20
Ursus americanus	124.00	97.00	110.50	148.50	128.50	138.50	290.00	228.00	259.00
Ursus arctos	213.00	111.86	162.43	158.15	139.55	148.85	337.60	339.00	338.30
Ursus maritimus	410.00	320.00	365.00	219.85	179.85	199.85	554.00	365.00	459.50
Ursus thibetanus	130.10	77.50	103.80			151.02	327.00	298.00	312.50
VIVERRIDAE									
Arctictis binturong	13.00	13.00	13.00			78.75	42.00	38.00	40.00
Arctogalidia trivirgata	2.40	2.40	2.40			52.85	23.00	21.00	22.00
Chrotogale owstoni			3.29			57.20			25.53
Civettictis civetta	12.38	11.92	12.15			79.25	35.00	39.00	37.00
Cryptoprocta ferox		7.00	9.50			74.99			32.14
Cynogale bennettii			4.01			62.64			29.96
Diplogale hosei						60.09			15.49
Eupleres goudotii	2.10	2.10	2.10			56.25	17.00	17.00	17.00
Fossa fossana	2.00	1.60	1.80			49.26	21.60	18.00	19.80
Genetta abyssinica			1.20			42.41			11.94
Genetta angolensis			2.10			47.34			15.49
Genetta genetta	2.00	1.80	1.90			55.41	14.00	14.00	14.00
Genetta johnstoni									
Genetta maculata	1.40		1.95						7.39
Genetta servalina			1.31			48.78			15.03
Genetta thierryi						41.99			11.70
Genetta tigrina	2.10	2.02	2.06			54.50	15.10	15.50	15.30
Genetta victoriae			2.51			57.25			20.91
Hemigalus derbyanus	0.80	0.86	0.83			46.00	22.00	16.00	19.00
Macrogalidia musschenbroekii	6.10	4.18	5.14	71.50	66.50	69.00			38.86

Table C.1: Continued.

	MWt	FWt	SWt	MHB	FHB	SHB	MBr	FBr	SBr
Nandinia binotata	2.05	1.90	1.97			50.00	17.60	17.00	17.30
Osbornictis piscivora	1.43	1.50	1.47	47.00	44.50	45.75			
Paguma larvata	4.40	5.00	4.70			63.50	32.10	29.50	30.80
Paradoxurus hermaphroditus	3.30	2.70	3.00			53.39	18.50	18.50	18.50
Paradoxurus jerdoni			3.58			58.99			24.05
Paradoxurus zeylonensis	3.30	2.30	2.80			48.89	18.10	17.50	17.80
Poiana richardsonii			0.65			38.00			9.03
Prionodon linsang	0.62	0.72	0.67			40.04	9.00	8.00	8.50
Prionodon pardicolor			2.55			35.42			9.03
Viverra civettina			12.06			84.56			36.97
Viverra megaspila			8.87			84.56			36.60
Viverra tangalunga			4.71			65.77			24.05
Viverra zibetha	9.60	9.00	9.30			81.92	37.50	36.50	37.00
Viverricula indica	2.83	2.49	2.66			54.00	16.60	17.00	16.80

Sources by family:

Canidae: Paradiso & Nowak (1972); Mech (1974); Storm *et al*. (1976); Cohen (1978); Egoscue (1979); McGrew (1979); Eisenberg (1981); Berta (1982, 1986); Fritzell & Haroldson (1982); Gittleman (1984, 1985, 1986a, 1991, unpubl. data); Fritzell (1987); O'Farrell (1987); Scott-Brown *et al*. (1987); Voigt (1987); Voigt & Berg (1987); Parker (1990); Ward & Wurster-Hill (1990); Nowak (1991); Geffen (1994); Sillero-Zubiri & Gottelli (1994); Moore & Collins (1995); Silva & Downing (1995); Ferguson *et al*. (1996); Larivière & Pasitschniak-Arts (1996); Novaro (1997)

Felidae: Hemmer (1972); Ximenez (1975); Groves (1980); Eisenberg (1981); Mazák (1981); Currier (1983); Gittleman (1984), 1985, 1986a, 1991, unpubl. data); Quinn & Parker (1987); Rolley (1987); Tewes & Schmidly (1987); Seymour (1989); Parker (1990); Nowak (1991); Silva & Downing (1995); Ferguson *et al*. (1996); Larivière & Walton (1997); Murray & Gardner (1997)

Herpestidae: Baldwin *et al*. (1952); Taylor (1972, 1975, 1987); Lin & Kobayashi (1976); Eisenberg (1981); Gittleman (1984, 1985, 1986a, 1991, unpubl. data); Goldman (1987); Goldman & Taylor (1990); Parker (1990); Nowak (1991); Baker (1992); Cavallini (1992); Van Rompaey & Colyn (1992); Taylor & Meester (1993); van Staaden (1994); Silva & Downing (1995)

Hyaenidae: Eisenberg (1981); Rieger (1981); Mills (1982); Gittleman (1984, 1985, 1986a, 1991, unpubl. data); Koehler & Richardson (1990); Parker (1990); Nowak (1991)

Mustelidae: Van Gelder (1968); Long (1973); Hillman & Clark (1980); Eisenberg (1981); Kenyon (1981b); Powell (1981); Wade-Smith & Verts (1982); Gittleman (1984, 1985, 1986a, 1991, unpubl. data); Anderson *et al*. (1986); Clark *et al*. (1987); Eagle & Whitman (1987); Fagerstone (1987); Hash (1987); Melquist & Dronkert (1987); Messick (1987); Rosatte (1987); Parker (1990); Williams (1990); Youngman (1990); Nowak (1991); Kinlaw (1995); Pasitschniak-Arts & Larivière (1995); Silva & Downing (1995); Ferguson *et al*. (1996); Vargas & Anderson (1996); Sheffield & Thomas (1997)

Odobenus rosmarus: Crile & Quiring (1940); Laws (1959); Bryden (1972); Brenton (1979b); Eisenberg (1981); Fay (1981, 1982, 1985); King (1983b); Dierauf (1990); Walsh *et al*. (1990); Nowak (1991); McLaren (1993); Silva & Downing (1995); Ferguson *et al*. (1996)

Otariidae: Laws (1959); Scheffer (1960); Keyes (1968); Bryden (1972); Sacher & Staffeldt (1974); Sobolevskij (1977); Aguayo (1979); Bonner (1979a, 1979e, 1981b, 1982); Crawley & Warneke (1979); King & Marlow (1979); Lander (1979); Marlow & King (1979); Mate (1979); Mate & Gentry (1979); Shaughnessy (1979); Vaz-Ferreira (1979a, 1979b, 1981, 1982a, 1982b); Warneke (1979); Walker & Ling (1980, 1981a, 1981b); Trillmich & Arnold (1980); Eisenberg (1981); Odell (1981); Schusterman (1981); Shaughnessy (1982a, 1982b); Thurman *et al*. (1982); King (1983b); Trillmich (1984); Gentry *et al*. (1986); Gentry & Kooyman (1986); Croxall & Gentry

(1987); Loughlin *et al*. (1987); Costa & Trillmich (1988); Costa *et al*. (1988, 1989); Boyd & McCann (1989); Dierauf (1990); Boyd & Duck (1991); Nowak (1991); Ling (1992); McLaren (1993); Chabot (1994); Silva & Downing (1995); Ferguson *et al*. (1996); Gallo-Reynoso & Figueroa-Carranza (1996); Ono & Boness (1996)

Phocidae: Lindsey (1937); Crile & Quiring (1940); Laws (1959); Usher & Churcher (1969); Bryden (1972); Robin (1973); Sacher & Staffeldt (1974); Kooyman (1975, 1981a, 1981b, 1981c); Leshko & Nikitenko (1975); Bryden & Erickson (1976); Hofman *et al*. (1977); Sobolevskij (1977); Sergeant *et al*. (1978); Bonner (1979b, 1979c, 1979d, 1981a); Boulva (1979a, 1979b); Boulva & McLaren (1979); Brenton (1979a); Ferren & Elsner (1979); Helle (1979); Hofman (1979); Laws & Hofman (1979); Le Boeuf (1979); Sergeant (1979); Bigg (1981); Burns (1981a, 1981b); Eisenberg (1981); Frost & Lowry (1981); Kenyon (1981a); Ling & Bryden (1981, 1992); McGinnis & Schusterman (1981); Ray (1981); Reeves & Ling (1981); Ronald & Healey (1981, 1982); Lavigne *et al*. (1982); Naito (1982); Popov (1982); Ronald *et al*. (1982); Finley *et al*. (1983); King (1983b); Bryden *et al.* (1984); Stewart & Yochem (1984); Bowen *et al.* (1985); Kovacs & Lavigne (1985, 1986a); Lydersen & Gjertz (1987); Costa *et al.* (1988); McCann *et al*. (1989); Testa *et al.* (1989); Dierauf (1990); Hammill *et al*. (1991); Nowak (1991); Smith *et al*. (1991); Hindell *et al.* (1992, 1994); Le Boeuf *et al*. (1992); Slip *et al.* (1992); McLaren (1993); Stewart & Huber (1993); Skinner & Klages (1994); Silva & Downing (1995); Ferguson *et al.* (1996)

Ailurus fulgens: Gittleman (1984, 1985, 1986a, 1991, unpubl. data); Roberts & Gittleman (1984); Parker (1990)

Procyonidae: Lotze & Anderson (1979); Eisenberg (1981); Gittleman (1984, 1985, 1986a, 1991, unpubl. data); Chevalier (1987); Ford & Hoffman (1988); Poglayen-Neuwall & Toweill (1988); Parker (1990); Nowak (1991); Gompper (1995); Silva & Downing (1995)

Ursidae: Chorn & Hoffman (1978); DeMaster & Stirling (1981); Eisenberg (1981); Gittleman (1984, 1985, 1986a, 1991, unpubl. data); Kolenosky (1987); Kolenosky & Strathearn (1987); Parker (1990); Nowak (1991); Pasitschniak-Arts (1993); Silva & Downing (1995)

Viverridae: Eisenberg (1981); Gittleman (1984, 1985, 1986a, 1991, unpubl. data); Köhncke & Leonhardt (1986); Van Rompaey (1988); Parker (1990); Nowak (1991); Ray (1995); Silva & Downing (1995)

Life history traits

1) Litter size: average number of offspring at birth.

2) (Active) gestation length (GL): average time from conception to birth (in days), minus any period of delayed implantation.

3) Birth weight (BWt): average weight of a single neonate at birth (in g).

4) Litter weight (LWt): litter size multiplied by birth weight (in g).

5) Weaning age (WA): time from birth of the young to independence from maternal milk (in days). In cases where weaning occurs over a protracted period, I followed Gittleman (1984, 1986b) in using the largest value to reflect complete nutritional independence from the mother.

6) Age of independence (AI): age when the juvenile disperses from the natal territory or is independent of parental care in group-living species (in days).

7) Age of sexual maturity (MMat and FMat): age at first conception (in days). Unlike Gittleman (1984, 1986b), I determined separate estimates for males (MMat) and females (FMat).

8) Interbirth interval (IB): time between successive births (in months).

9) Age of eyes opening (EO): age when the eyes of the neonate first open (in days).

10) Longevity (LY): age of the oldest recorded individual (in months). Preference was given to records from captive individuals, reflecting the greater reliability and accuracy of such estimates. However, I also used what I felt to be reliable estimates determined from natural populations (e.g., mark-recapture studies).

Table C.2: Values of selected life history characters for all extant species of carnivore. See text for identity and descriptions of variables. Sources follow the table.

	LS	GL	BWt	LWt	WA	AI	MMat	FMat	IB	EO	LY
CANIDAE											
Alopex lagopus	7.10	53.30	66.00	468.60	67.00	165.00	327.86	300.00	12.00	15.03	180.00
Atelocynus microtis											132.00
Canis adustus	4.30	63.30			67.00	330.00	270.00	210.00			137.00
Canis aureus	4.01	62.25	216.25	867.40	63.00		414.38	408.75	12.00	7.50	192.00
Canis latrans	6.20	61.50	225.00	1395.00	98.00	255.00	435.00	365.00	12.00	11.94	262.00
Canis lupus	5.50	63.00	425.00	2337.50	67.00	180.00	656.25	1020.00	12.00	14.01	240.00
Canis mesomelas	3.80	60.00	197.50	750.50	61.00	270.00	255.00	392.00	9.00		168.00
Canis rufus	5.50	61.00						697.50	12.00		194.80
Canis simensis		61.00			70.00	180.00	730.00	730.00	12.00		
Cerdocyon thous	3.10	56.00	140.00	434.00	90.00	195.00	270.00	270.00	8.00	14.00	138.00
Chrysocyon brachyurus	1.80	63.30	360.00	648.00	105.00			365.00		9.03	162.00
Cuon alpinus	4.30	62.00	275.00	1182.50	57.00	210.00	365.00	365.00	12.00	14.01	186.00
Dusicyon australis											
Lycaon pictus	8.80	70.50	365.00	3212.00	77.00	390.00	944.25	660.00	13.00	11.94	132.00
Nyctereutes procyonoides	6.00	61.50	83.75	502.50	53.50	150.00	327.86	313.93	12.00	9.50	168.00
Otocyon megalotis	3.50	62.50	120.50	421.75	105.00	255.00		365.00	6.00		165.00
Pseudalopex culpaeus	5.00	57.50	168.00	840.00	48.50		365.00	365.00	12.00		
Pseudalopex griseus											
Pseudalopex gymnocercus	4.00	58.00							12.00		164.00
Pseudalopex sechurae											
Pseudalopex vetulus	3.00								12.00		
Speothos venaticus	3.50	65.00	157.50	551.25	169.50		365.00	365.00	8.12	14.00	124.00
Urocyon cinereoargenteus	3.80	63.00	107.50	408.50	60.00	210.00	365.00	300.00	12.00	9.75	180.00
Urocyon littoralis	2.17	51.50	100.00	217.00		150.00		313.50	12.00	10.50	96.00
Vulpes bengalensis	3.50	52.00	58.50	204.75							120.00

Table C.2: Continued.

	LS	GL	BWt	LWt	WA	AI	MMat	FMat	IB	EO	LY
Vulpes cana	2.00	55.00	29.00	58.00	45.00	150.00		330.00			72.00
Vulpes chama	4.00	51.50						270.00			
Vulpes corsac	5.62	52.88	63.75	358.28				888.75	12.00		
Vulpes ferrilata	3.50	52.00	90.00	315.00	56.00			365.00			
Vulpes pallida	4.00										
Vulpes rueppelli	2.25										
Vulpes velox	4.50	51.50	39.95	179.78	49.00	150.00	313.50	660.00	12.00	12.50	240.00
Vulpes vulpes	4.80	54.50	105.00	504.00	56.00	225.00	304.17	300.00	12.00	14.01	180.00
Vulpes zerda	2.80	54.30	34.80	97.44	66.00		315.00	255.00	12.00	16.95	175.00
FELIDAE											
Acinonyx jubatus	3.80	91.00	388.42	1476.00	109.00	465.00	645.00	645.00	18.00	9.03	228.00
Caracal caracal	3.00	73.50	232.50	697.50	123.00	365.00	397.50	450.00	12.00	9.97	204.00
Catopuma badia											
Catopuma temminckii	1.50	95.00	250.00	375.00							216.00
Felis bieti											
Felis chaus	2.90	65.00	135.50	392.95	102.00			330.00	4.87	11.94	144.00
Felis margarita	4.13	61.00	39.00	160.88					6.50	14.00	
Felis nigripes	1.73	66.25	72.00	124.56	160.00			585.00	7.50	7.00	132.00
Felis silvestris	3.05	62.00	106.59	325.09	84.00	140.00	616.75	296.50	6.00	10.96	336.00
Herpailurus yaguarondi	2.75	73.42						912.50	6.00		127.83
Leopardus pardalis	1.50	80.00	250.00	375.00	270.00	759.00	742.50	653.00	18.00	9.97	243.00
Leopardus tigrinus	1.50	75.00	60.00	90.00	90.00			821.25		17.00	240.00
Leopardus wiedii	1.50	80.00	125.25	187.88	84.00			912.50		13.50	240.00
Leptailurus serval	2.40	71.00	254.00	631.20	145.00		510.00	770.00	6.00	9.03	276.00
Lynx canadensis	3.75	63.00	204.00	765.00	112.00		730.00	660.00	12.00	14.00	321.00
Lynx lynx	2.30	67.80	269.50	619.85	113.00	240.00	860.00	690.00	12.00	11.94	262.00
Lynx pardinus	2.50	68.00									

Table C.2: Continued.

	LS	GL	BWt	LWt	WA	AI	MMat	FMat	IB	EO	LY
Lynx rufus	3.20	63.00	311.50	996.80	60.00	365.00	730.00	593.00	12.00	8.00	388.00
Neofelis nebulosa	2.54	89.75	166.50	422.91	145.00		765.00	721.50		9.25	204.00
Oncifelis colocolo	2.00										
Oncifelis geoffroyi	2.00	69.50	65.00	130.00	63.00		720.00	480.00	8.00	14.00	
Oncifelis guigna											
Oreailurus jacobita											
Otocolobus manul	4.67	74.50	89.00	415.33							
Panthera leo	2.60	105.50	1650.00	4290.00	256.88	1080.00	1422.06	1620.00	25.00	3.00	360.00
Panthera onca	2.50	104.50	816.60	2041.50	157.50	638.75	1277.50	1110.00	12.00	8.00	276.00
Panthera pardus	2.60	98.00	549.30	1428.18	124.25	600.00	600.00	1187.00	19.32	9.03	276.00
Panthera tigris	2.50	104.10	1255.00	3137.50	165.00	570.00	1642.50	1463.34	28.32	9.03	315.00
Pardofelis marmorata	2.00		85.00	170.00							
Prionailurus bengalensis	2.50	67.30	83.00	207.50	25.00		912.50	750.00	5.44	9.97	162.00
Prionailurus planiceps											
Prionailurus rubiginosus	2.50										
Prionailurus viverrinus	2.50	68.50	170.00	425.00	180.00					16.00	120.00
Profelis aurata	2.25	78.00	211.25	475.31	120.00		600.00	660.00			
Puma concolor	2.50	90.00	400.00	1000.00	75.00	420.00	885.00	913.00	19.00	8.00	240.00
Uncia uncia	2.12	96.80	442.60	939.79	102.00			730.00	12.00	7.03	216.00
HERPESTIDAE											
Atilax paludinosus	2.50	74.10	100.00	250.00	38.00		255.50		6.00	11.50	209.00
Bdeogale crassicauda	1.00										
Bdeogale jacksoni											
Bdeogale nigripes	1.00										190.00
Crossarchus alexandri	4.00										
Crossarchus ansorgei											
Crossarchus obscurus	4.00	70.00	9.78	39.12	21.00		270.00	270.00	4.00	12.00	108.00

Table C.2: Continued.

	LS	GL	BWt	LWt	WA	AI	MMat	FMat	IB	EO	LY
Cynictis penicillata	2.50	54.50			42.00	365.00	315.00	365.00	12.00		182.00
Dologale dybowskii	4.00										
Galerella flavescens											
Galerella pulverulenta	2.25		20.20	45.45							104.50
Galerella sanguinea	2.50	60.00			54.75			463.75	6.00	20.00	72.00
Galerella swalius											
Galidia elegans	1.00	69.87	47.50	47.50	56.00			730.00	12.00	5.00	158.00
Galidictis fasciata	1.00								12.00		
Galidictis grandidieri	1.00								12.00		
Helogale hirtula											
Helogale parvula	3.60	51.00			21.00			300.00	4.67		131.00
Herpestes brachyurus	3.50										
Herpestes edwardsii	2.58	60.50			35.00			270.00	3.60	16.50	
Herpestes ichneumon	3.30	72.75			60.00	365.00	730.00	730.00	12.00		240.00
Herpestes javanicus	2.68	46.00	21.00	56.18	45.50	84.00	180.00	200.00	6.00	18.50	120.00
Herpestes naso											
Herpestes palustris											
Herpestes semitorquatus											
Herpestes smithii	2.50										
Herpestes urva	3.00	63.00									160.00
Herpestes vitticollis	3.00										
Ichneumia albicauda	2.50					270.00	730.00	730.00			144.00
Liberiictis kuhni											
Mungos gambianus											
Mungos mungo	3.29	59.00	20.00	65.71				323.00	12.00	9.97	144.00
Mungotictis decemlineata	1.00	97.50	50.00	50.00	60.00	730.00		730.00		0.00	
Paracynictis selousi	1.92										
Rhynchogale melleri	2.00										
Salanoia concolor											57.00

Table C.2: Continued.

	LS	GL	BWt	LWt	WA	AI	MMat	FMat	IB	EO	LY
Suricata suricatta	3.00	77.00	30.50	91.50	56.00		365.00	365.00	12.00	12.94	150.00
HYAENIDAE											
Crocuta crocuta	2.00	110.00	1500.00	3000.00	390.00	913.00	638.75	913.00	14.50	0.00	493.00
Hyaena hyaena	2.50	87.00	700.00	1750.00	120.00		912.50	821.00		7.03	288.00
Parahyaena brunnea	2.30	97.00	693.00	1593.90	360.00	900.00		700.00	17.50	14.00	156.00
Proteles cristatus	2.80	90.00	275.00	770.00	120.00	365.00		547.50			300.00
MUSTELIDAE											
Amblonyx cinereus	1.75	62.00	57.00	99.75	80.00				6.00	40.00	121.00
Aonyx capensis	2.63	63.00				365.00				27.11	132.00
Aonyx congicus	2.50	60.00					365.00	365.00			
Arctonyx collaris	3.00	42.00	58.00	174.00							167.00
Conepatus chinga	3.50										79.00
Conepatus humboldtii	3.50										
Conepatus leuconotus	3.00	60.00			60.00			365.00		25.00	84.00
Conepatus mesoleucus	3.25	60.00					315.00	315.00	6.00	25.00	
Conepatus semistriatus	3.50										
Eira barbara	2.63	64.00	83.00	217.88	95.00			664.38		41.50	216.00
Enhydra lutris	1.00	120.00	1894.38	1894.38	180.00	182.00	2007.50	1095.00	12.00	0.00	360.00
Galictis cuja											87.00
Galictis vittata	2.00										126.00
Gulo gulo	2.80	35.00	99.20	277.76	70.00	639.00	702.92	668.59	27.00	27.94	216.00
Ictonyx libyca	2.00	37.00									60.00
Ictonyx striatus	2.30	36.00	15.00	34.50	56.00		660.00	285.00	12.00	35.16	160.00
Lontra canadensis	3.00	56.00	140.00	420.00	106.50	225.00	730.00	730.00	12.00	33.12	300.00
Lontra felina	3.25	61.50							12.00		

Table C.2: Continued.

	LS	GL	BWt	LWt	WA	AI	MMat	FMat	IB	EO	LY
Lontra longicaudis											
Lontra provocax											
Lutra lutra	2.07	62.88	285.00	589.54	112.00	238.00	756.00	720.00	12.00	35.87	144.00
Lutra maculicollis	2.00	56.00						730.00	12.00		
Lutra sumatrana											
Lutrogale perspicillata	3.25	62.00			126.00						180.00
Lyncodon patagonicus											
Martes americana	2.60	26.50	28.00	72.80	46.00		450.00	486.67	12.00	36.97	228.00
Martes flavigula	2.50	143.50	57.50	143.75	90.00			1095.00	6.00	32.50	168.00
Martes foina	3.79	29.50	30.00	113.57	67.50		730.00	693.75	12.00		217.00
Martes gwatkinsii											
Martes martes	3.30	30.00	30.00	99.00	54.50	157.50	710.00	730.00	12.00	29.96	204.00
Martes melampus											
Martes pennanti	2.70	30.00	28.00	75.60	84.67	150.00	730.00	565.75	12.00	53.00	121.77
Martes zibellina	3.00	28.00	32.50	97.50	49.00		465.00	600.00		35.16	180.00
Meles meles	3.00	42.00	93.06	279.19	91.88	210.00	441.04	488.57	12.00	35.16	194.00
Mellivora capensis	2.21	174.00	210.00	465.00					6.00	33.12	317.00
Melogale everetti	2.00										
Melogale moschata	2.00										126.00
Melogale orientalis	2.00										
Melogale personata	2.50										
Mephitis macroura	4.75	58.00									
Mephitis mephitis	4.87	63.00	33.00	160.82	46.00	84.00	332.50	308.00	12.00	21.98	155.00
Mustela africana											
Mustela altaica	5.40	40.00			56.00	56.00			12.00		
Mustela erminea	6.75	30.00	1.70	11.47	70.00	105.00	365.00	72.64	12.00	35.10	85.23
Mustela eversmannii	6.50	39.50	5.00	32.50	45.00	90.00	307.50	315.00	12.00	30.00	
Mustela felipei											
Mustela frenata	6.60	23.50	3.10	20.46	30.00	84.00	450.00	105.00	12.00	35.87	85.23

Table C.2: Continued.

	LS	GL	BWt	LWt	WA	AI	MMat	FMat	IB	EO	LY
Mustela kathiah											
Mustela lutreola	4.50	38.50	7.25	32.63	70.00	97.50	330.00	341.88	12.00	33.00	102.00
Mustela lutreolina											
Mustela nigripes	3.40	43.50	7.40	25.16	60.00	120.00	343.25	343.25	12.00	35.00	144.00
Mustela nivalis	5.30	39.50	2.00	10.60	51.86	135.00	218.50	135.00	6.00	29.08	120.00
Mustela nudipes	4.00										
Mustela putorius	8.48	41.00	9.50	80.55	43.00	70.00	318.00	365.00	12.00	29.08	168.00
Mustela sibirica	6.00	29.00			56.00	90.00				27.94	106.00
Mustela strigidorsa											
Mustela vison	5.00	29.00	9.00	45.00	54.75	120.00	408.75	420.00	12.00	35.16	120.00
Mydaus javanensis											
Mydaus marchei											
Poecilogale albinucha	2.00	32.00	4.00	8.00	77.00		990.00	335.50	8.00	32.14	62.00
Pteronura brasiliensis	2.25	67.50	204.25	459.56	120.00				12.00	28.00	154.00
Spilogale putorius	4.85	30.00	15.90	77.12	56.00		150.00	217.50	8.00	30.07	120.00
Spilogale pygmaea	4.00	48.00	6.90	27.60						28.00	
Taxidea taxus	3.13	42.00	93.20	291.25	42.00	365.00	448.13	317.50	12.00	35.00	312.00
Vormela peregusna	6.00	61.50							12.00		107.00
Odobenus rosmarus	1.00	330.00	59090.91	59090.91	720.00	730.00	3285.00	2372.50	24.00	0.00	480.00
OTARIIDAE											
Arctocephalus australis	1.00	236.25	4400.00	4400.00	540.00		2555.00	1095.00	12.00	0.00	252.00
Arctocephalus forsteri	1.00	232.50	3875.00	3875.00	330.00		3650.00	1825.00	12.00	0.00	180.00
Arctocephalus galapagoensis	1.00	210.00	3500.00	3500.00	1080.00	1095.00	2920.00	1460.00	36.00	0.00	264.00
Arctocephalus gazella	1.00	233.25	5433.33	5433.33	118.50		1825.00	1277.50	12.00	0.00	276.00
Arctocephalus philippii	1.00								12.00		
Arctocephalus pusillus	1.00	240.00	6000.00	6000.00	365.00		1460.00	1231.88	12.00	0.00	252.00

Table C.2: Continued.

	LS	GL	BWt	LWt	WA	AI	MMat	FMat	IB	EO	LY
Arctocephalus townsendi	1.00				330.00				12.00	0.00	288.00
Arctocephalus tropicalis	1.00	231.75	4900.00	4900.00	330.00		1277.50	1733.75	12.00	0.00	276.00
Callorhinus ursinus	1.00	240.00	5000.00	5000.00	120.00	120.00	1825.00	1460.00	12.00	0.00	420.00
Eumetopias jubatus	1.00	240.00	19500.00	19500.00	365.00		1916.25	1825.00	12.00	0.00	360.00
Neophoca cinerea	1.00	255.00	7000.00	7000.00	540.00		2190.00	1095.00	18.00	0.00	192.00
Otaria byronia	1.00	255.00	12820.00	12820.00	365.00		2007.50	1460.00	12.00	0.00	274.00
Phocarctos hookeri	1.00				300.00	365.00	2190.00		12.00	0.00	
Zalophus californianus	1.00	240.00	6000.00	6000.00	365.00		3285.00	2099.00	12.00	0.00	360.00
PHOCIDAE											
Cystophora cristata	1.00	234.00	22000.00	22000.00	11.00	7.50	1825.00	1095.00	12.00	0.00	420.00
Erignathus barbatus	1.00	270.00	35500.00	35500.00	18.00	18.00	2372.50	2007.75	18.00	0.00	377.43
Halichoerus grypus	1.00	242.00	14468.75	14468.75	19.54	21.00	2190.00	1642.50	12.00	0.00	560.07
Hydrurga leptonyx	1.00	276.00	30000.00	30000.00	28.00	28.00	1460.00	1204.50	12.00	0.00	312.00
Leptonychotes weddellii	1.00	262.75	29000.00	29000.00	45.00	50.00	1642.50	1095.00	12.00	0.00	300.00
Lobodon carcinophagus	1.00	255.00	22000.00	22000.00	31.50	29.75	1460.00	1277.50	12.00	0.00	468.00
Mirounga angustirostris	1.00	229.50	37500.00	37500.00	28.00	27.20	1733.75	1186.25	12.00	0.00	243.50
Mirounga leonina	1.00	225.00	41000.00	41000.00	23.00	24.00	1733.75	1171.04	12.00	0.00	276.00
Monachus monachus	1.00	330.00	20000.00	20000.00	43.00	569.00	1460.00	1460.00	24.00	0.00	284.00
Monachus schauinslandi	1.00	330.00	16250.00	16250.00	38.00	38.00	1460.00	1825.00	15.37	0.00	360.00
Monachus tropicalis	1.00								18.00		
Ommatophoca rossii	1.00	247.50	17000.00	17000.00	28.00	28.00	1277.50	1323.13	12.00	0.00	252.00
Phoca caspica	1.00	330.00	5000.00	5000.00	31.50	31.50	2372.50	1825.00	12.00	0.00	600.00
Phoca fasciata	1.00	234.00	10000.00	10000.00	28.00	28.00	1642.50	1277.75	12.00	0.00	365.26
Phoca groenlandica	1.00	232.50	10150.00	10150.00	12.00	16.50	2463.75	1825.00	12.00	0.00	504.00
Phoca hispida	1.00	225.00	4500.00	4500.00	49.00	49.00	2528.93	2190.00	12.00	0.00	552.00
Phoca largha	1.00	248.00	8300.00	8300.00	28.00	28.00	1642.50	1460.00	12.00	0.00	426.13
Phoca sibirica	1.00	270.00	3050.00	3050.00	70.00	72.50	2007.50	1642.50	12.00	0.00	672.00

Table C.2: Continued.

	LS	GL	BWt	LWt	WA	AI	MMat	FMat	IB	EO	LY
Phoca vitulina	1.00	247.75	10150.00	10150.00	38.50	38.50	1916.25	1277.50	12.00	0.00	480.00
Ailurus fulgens	2.00	134.20	120.00	240.00	90.00	270.00	555.00	540.00	12.00	18.00	168.00
PROCYONIDAE											
Bassaricyon alleni											
Bassaricyon beddardi											
Bassaricyon gabbii	1.00	73.50	55.00	55.00	90.00		547.50	630.00		18.50	300.00
Bassaricyon lasius											
Bassaricyon pauli											
Bassariscus astutus	3.00	52.00	28.00	84.00	120.00	180.00	300.00	300.00	12.00	33.12	198.00
Bassariscus sumichrasti	2.00				120.00			730.00			276.00
Nasua narica	4.00	73.50	140.00	560.00	130.00	365.00	1186.25	875.00	12.00	5.00	212.00
Nasua nasua	4.19	73.50	150.00	628.13	135.00			730.00	12.00	8.00	168.00
Nasuella olivacea											
Potos flavus	1.25	112.00	170.50	213.13	120.00	160.00	547.50	860.63	12.00	16.95	348.00
Procyon cancrivorus	2.75	66.50	70.00	192.50	112.00	365.00		547.50		21.00	168.00
Procyon gloveralleni											
Procyon insularis											
Procyon lotor	3.80	64.70	105.90	402.42	119.00	317.50	365.00	540.00	12.00	20.91	247.00
Procyon maynardi											
Procyon minor											
Procyon pygmaeus											
URSIDAE											
Ailuropoda melanoleuca	1.70	50.00	104.80	178.16	180.00	540.00	2372.50	2160.00	18.00	44.00	360.00
Helarctos malayanus	1.50	96.10	325.00	487.50	90.00					14.00	297.00

Table C.2: Continued.

	LS	GL	BWt	LWt	WA	AI	MMat	FMat	IB	EO	LY
Melursus ursinus	1.61	195.00			501.25	914.25		1095.00	36.00	21.00	480.00
Tremarctos ornatus	2.00	225.00	320.00	640.00							437.00
Ursus americanus	2.50	91.00	285.00	712.50	168.00	483.00	1642.50	1452.55	27.00	38.86	360.00
Ursus arctos	2.00	63.00	482.14	964.29	730.00	912.50	1432.63	1544.48	30.00	31.82	600.00
Ursus maritimus	1.90	62.00	641.60	1219.04	776.00	821.00	2190.00	1604.48	24.69	34.12	458.00
Ursus thibetanus	2.00	210.00	357.50	715.00	119.00	912.50	1095.00	1186.00	12.00	7.03	422.00
VIVERRIDAE											
Arctictis binturong	2.64	90.30	317.35	838.51	150.00		831.00	912.00	8.00	3.00	272.00
Arctogalidia trivirgata	2.80	45.00			60.00			730.00	6.00	11.02	190.00
Chrotogale owstoni											
Civettictis civetta	2.23	68.50	600.00	1337.14	140.00		210.00	453.00	6.68	1.50	336.00
Cryptoprocta ferox	3.00	90.00	100.00	300.00	123.50	525.00		1095.00		17.50	240.00
Cynogale bennettii	2.50										60.00
Diplogale hosei											
Eupleres goudotii	1.50	90.00	150.00	225.00	63.00					1.00	
Fossa fossana	1.00	85.00	82.50	82.50	63.50	365.00		730.00	12.00	2.50	132.00
Genetta abyssinica											
Genetta angolensis											
Genetta genetta	2.22	71.80	77.75	172.80	175.00			1095.00	6.00	8.00	258.00
Genetta johnstoni											
Genetta maculata	2.25										
Genetta servalina	1.50										
Genetta thierryi											
Genetta tigrina	2.50	70.00	85.50	213.75	56.00			730.00	10.00	11.94	180.00
Genetta victoriae											
Hemigalus derbyanus	1.50		125.00	187.50	70.00					9.75	144.00
Macrogalidia musschenbroekii											

Table C.2: Continued.

	LS	GL	BWt	LWt	WA	AI	MMat	FMat	IB	EO	LY
Nandinia binotata	1.80	64.00	56.00	100.80	64.00		1095.00	907.50	6.00		222.00
Osbornictis piscivora	1.00										
Paguma larvata	2.34								6.00	9.03	185.00
Paradoxurus hermaphroditus	3.30	60.00	92.08	303.85				345.00	6.00		269.00
Paradoxurus jerdoni											
Paradoxurus zeylonensis	2.50										
Poiana richardsonii	2.50										64.00
Prionodon linsang	2.50		40.00	100.00					6.00		128.00
Prionodon pardicolor	2.00								6.00		
Viverra civettina											
Viverra megaspila											
Viverra tangalunga	2.00										144.00
Viverra zibetha	2.80	77.00							6.00	9.97	240.00
Viverricula indica	3.80										102.00

Sources by family:

Canidae: Altman & Dittmer (1972); Paradiso & Nowak (1972); Storm *et al*. (1976); Egoscue (1979); McGrew (1979); Eisenberg (1981); Fritzell & Haroldson (1982); Jones (1982); Gittleman (1984, 1986b, 1989b, 1993, unpubl. data); Carbyn (1987); Fritzell (1987); O'Farrell (1987); Scott-Brown *et al*. (1987); Parker (1990); Ward & Wurster-Hill (1990); Nowak (1991); Hayssen *et al*. (1993); Geffen (1994); Sillero-Zubiri & Gottelli (1994); Moore & Collins (1995); Ferguson *et al*. (1996); Novaro (1997)

Felidae: Altman & Dittmer (1972); Hemmer (1972); Eisenberg (1981); Mazák (1981); Jones (1982); Currier (1983); Gittleman (1984, 1986b, 1993, unpubl. data); Quinn & Parker (1987); Rolley (1987); Tewes & Schmidly (1987); Seymour (1989); Parker (1990); Nowak (1991); Hayssen *et al*. (1993); Ferguson *et al*. (1996); Murray & Gardner (1997)

Herpestidae: Eisenberg (1981); Jones (1982); Gittleman (1984, 1986b, 1993, unpubl. data); Goldman (1987); Parker (1990); Nowak (1991); Baker (1992); Cavallini (1992); Hayssen *et al*. (1993); Taylor & Meester (1993); van Staaden (1994)

Hyaenidae: Eisenberg (1981); Rieger (1981); Jones (1982); Mills (1982); Gittleman (1984, 1986b, 1993, unpubl. data); Parker (1990); Nowak (1991); Hayssen *et al*. (1993)

Mustelidae: Mead (1968, 1989); Altman & Dittmer (1972); Long (1973); Rowe-Rowe (1978); Estes (1980); Hillman & Clark (1980); Eisenberg (1981); Kenyon (1981b); Powell (1981); Jones (1982); King (1983a); Gittleman (1984, 1986b, 1993, unpubl. data); Anderson *et al*. (1986); Clark *et al*. (1987); Douglas & Strickland (1987); Eagle & Whitman (1987); Fagerstone (1987); Garshelis (1987); Melquist & Dronkert (1987); Messick (1987); Rosatte (1987); Strickland & Douglas (1987); Parker (1990); Williams (1990); Youngman (1990); Nowak (1991); Hayssen *et al*. (1993); Sheffield & King (1994); Pasitschniak-Arts & Larivière (1995); Ferguson *et al*. (1996); Vargas & Anderson (1996); Sheffield & Thomas (1997)

Odobenus rosmarus: Laws (1959); Harrison & Kooyman (1968); Harrison (1969); Bryden (1972); Brenton (1979b); Fay (1981, 1982, 1985); King (1983b); Schmitz & Lavigne (1984); Oftedal *et al*. (1987); Riedman (1990); Walsh *et al*. (1990); Boyd (1991); Nowak (1991); Hayssen *et al*. (1993); Ferguson *et al*. (1996)

Otariidae: Laws (1959); McLaren (1967); Harrison & Kooyman (1968); Harrison (1969); Bryden (1972); Sacher & Staffeldt (1974); Bonner (1979a, 1979e, 1981b, 1982); Crawley & Warneke (1979); King & Marlow (1979); Lander (1979); Marlow & King (1979); Mate (1979); Mate & Gentry (1979); Shaughnessy (1979); Vaz-Ferreira (1979a, 1979b, 1981, 1982a, 1982b); Warneke (1979, 1982); York (1979); Jouventin & Cornet (1980); Trillmich & Arnold (1980); Gentry (1981); Odell (1981); Schusterman (1981); Jones (1982); Shaughnessy (1982a, 1982b); King (1983b); Eibl-Eibesfeldt (1984); Schmitz & Lavigne (1984); Trillmich (1984, 1986); Trillmich &

Limberger (1985); Gentry *et al*. (1986); Croxall & Gentry (1987); Loughlin *et al*. (1987); Oftedal *et al*. (1987); Costa & Trillmich (1988); Costa *et al*. (1988, 1989); Higgins *et al*. (1988); Boyd & McCann (1989); Mead (1989); Dierauf (1990); Fowler (1990); Riedman (1990); Trites (1990); Boyd (1991); Nowak (1991); Ling (1992); Lunn (1992); Hayssen *et al*. (1993); Higgins & Gass (1993); Lunn *et al.* (1993); Trites & York (1993); Wickens (1993); Ferguson *et al*. (1996)

Phocidae: Lindsey (1937); Laws (1959, 1977, 1979a, 1979b); Smith (1965); McLaren (1967); Harrison & Kooyman (1968); Harrison (1969); Stirling (1969, 1971, 1977, 1979); Bryden (1972); Bigg & Fisher (1974); Sacher & Staffeldt (1974); Potelov (1975); Elsner *et al*. (1977); Reiter *et al*. (1978); Sergeant *et al*. (1978); Bonner (1979b, 1979c, 1979d, 1981a); Boulva (1979a, 1979b); Boulva & McLaren (1979); Brenton (1979a); DeMaster (1979); Helle (1979); Hofman (1979); Lavigne (1979); Laws & Hofman (1979); Le Boeuf (1979); Popov (1979a, 1979b, 1979c, 1982); Sergeant (1979); Stirling & Archibald (1979); Stirling & Calvert (1979); Jouventin & Cornet (1980); Stewart & Lavigne (1980); Bigg (1981); Bowen *et al*. (1981); Burns (1981a, 1981b); Frost & Lowry (1981); Kenyon (1981a); Kooyman (1981a, 1981b, 1981c, 1981d); Ling & Bryden (1981, 1992); McGinnis & Schusterman (1981); Ray (1981); Reeves & Ling (1981); Ronald & Healey (1981, 1982); Capstick & Ronald (1982); Jones (1982); Lavigne *et al.* (1982); Naito (1982); Ronald *et al*. (1982); Thomas *et al*. (1982); Warneke (1982); Hennemann (1983); King (1983b); Thomas & DeMaster (1983); Worthy & Lavigne (1983); Bryden *et al*. (1984); Schmitz & Lavigne (1984); Stewart & Yochem (1984); Bowen *et al*. (1985); Kovacs & Lavigne (1985, 1986a, 1986b, 1986c); Huber (1987); Little *et al*. (1987); Lydersen & Gjertz (1987); Oftedal *et al*. (1987, 1993); Costa *et al*. (1988); Heide-Jørgensen & Härkönen (1988); Hindell & Little (1988); Le Boeuf *et al*. (1989); McCann *et al.* (1989); Mead (1989); Shaughnessy & Kerry (1989); Riedman (1990); Boyd (1991); Guinet (1991); Hammill *et al.* (1991); Nowak (1991); Reiter & Le Boeuf (1991); Smith *et al*. (1991); Sydeman *et al*. (1991); Rea & Costa (1992); Arnbom *et al*. (1993); Campagna *et al*. (1993); Hayssen *et al*. (1993); Iverson *et al*. (1993); Muelbert & Bowen (1993); Stewart & Huber (1993); Skinner & Klages (1994); Teilmann & Dietz (1994); Stirling & Øritsland (1995); Ferguson *et al*. (1996); Haller *et al*. (1996)

Ailurus fulgens: Gittleman (1984, 1986b, 1993, unpubl. data); Roberts & Gittleman (1984); Parker (1990); Nowak (1991); Hayssen *et al*. (1993)

Procyonidae: Lotze & Anderson (1979); Eisenberg (1981); Jones (1982); Gittleman (1984, 1986b, 1993, unpubl. data); Kaufmann (1987); Sanderson (1987); Ford & Hoffman (1988); Poglayen-Neuwall & Toweill (1988); Parker (1990); Nowak (1991); Hayssen *et al*. (1993); Gompper (1995); Ferguson *et al*. (1996)

Ursidae: Altman & Dittmer (1972); DeMaster & Stirling (1981); Eisenberg (1981); Jones (1982); Gittleman (1984, 1986b, 1989b, 1993, unpubl. data); Kolenosky (1987); Mead (1989); Parker (1990); Nowak (1991); Hayssen *et al*. (1993); Pasitschniak-Arts (1993); Ferguson *et al*. (1996); D. Bininda (pers. comm.)

Viverridae: Altman & Dittmer (1972); Eisenberg (1981); Jones (1982); Gittleman (1984, 1986b, 1993, unpubl. data); Köhncke & Leonhardt (1986); Parker (1990); Nowak (1991); Hayssen *et al*. (1993); Ray (1995)

Physiological and miscellaneous variables

Whenever possible, I only used physiological data taken from healthy adult individuals that were at rest and not anaesthetized.

1) Basal metabolic rate (mBMR and tBMR): metabolic rate for adult individuals fulfilling Kleiber's (1975) conditions of being postabsorptive, at rest, and in a thermoneutral environment. Total metabolic rates (tBMR; in mL O_2 min^{-1}) were derived from mass-specific metabolic rates (mBMR; in mL O_2 kg^{-1} min^{-1}) by multiplying by species body weight.

2) Body temperature (T_B): resting body temperature determined by any method (e.g., rectal thermometers, thermotelemetry) (in °C).

3) Hematocrit (Hct): proportion of blood composed of red blood cells (%). Hematocrit is rapidly influenced by numerous factors including physiological condition, activity, and stress levels (see Chapter 6; Castellini *et al*., 1996). Therefore, I only used estimates for animals that were in normal health (e.g., not pregnant) and resting.

4) Hemoglobin concentration (Hb): grams of hemoglobin per 100 mL of blood (in g / 100 mL or g%).

5) Red blood cell count (RBC): millions of red blood cells per milliliter of blood (in 10^6 RBC / mL).

6) Heart rate (HR): resting heart rate (in beats min^{-1}).

7) Population density (PD): average number of individuals of all ages found in a given area (in number of individuals / km^2).

Table C.3: Values of selected physiological and miscellaneous characters for all extant species of carnivore. See text for identity and descriptions of variables. Sources follow the table.

	mBMR	tBMR	T_B	Hct	Hb	RBC	HR	PD
CANIDAE								
Alopex lagopus	8.48	27.12	38.60	48.00	15.10	8.00	103.05	
Atelocynus microtis								
Canis adustus								
Canis aureus				40.50	13.70	5.20		
Canis latrans	4.54	48.11		49.00	15.40	7.70		0.49
Canis lupus	5.67	187.57	38.00	43.50	14.80	6.20	84.00	0.02
Canis mesomelas								0.37
Canis rufus								
Canis simensis								1.22
Cerdocyon thous	4.61	26.48	38.20					
Chrysocyon brachyurus								
Cuon alpinus								0.63
Dusicyon australis								
Lycaon pictus	11.10	244.28	38.50	46.00	16.87	8.16		0.01
Nyctereutes procyonoides	6.88	28.99					122.00	12.02
Otocyon megalotis				46.00	13.00	6.60		0.85
Pseudalopex culpaeus								1.01
Pseudalopex griseus								
Pseudalopex gymnocercus								
Pseudalopex sechurae								
Pseudalopex vetulus								
Speothos venaticus				48.00	13.80	5.63		
Urocyon cinereoargenteus				36.50	10.90	5.73		2.39
Urocyon littoralis								3.95
Vulpes bengalensis								

Table C.3: Continued.

	mBMR	tBMR	T_B	Hct	Hb	RBC	HR	PD
Vulpes cana								1.25
Vulpes chama								
Vulpes corsac								
Vulpes ferrilata								
Vulpes pallida								
Vulpes rueppelli								
Vulpes velox	8.90	18.57	39.00	46.90	14.90	8.40	140.00	0.45
Vulpes vulpes	8.75	35.88	39.31	48.10	13.63	9.02	124.80	5.94
Vulpes zerda	6.00	9.00	37.95	42.30	14.50		88.05	
FELIDAE								
Acinonyx jubatus	5.83	343.00		36.47	13.98	7.36		0.01
Caracal caracal				39.50	13.00	9.05		
Catopuma badia								
Catopuma temminckii								
Felis bieti								
Felis chaus					12.20	5.60		
Felis margarita								
Felis nigripes								
Felis silvestris	11.83	53.07		36.91	11.52	7.64	175.00	
Herpailurus yaguarondi								0.53
Leopardus pardalis	5.17	61.38	37.75	41.50	13.10	8.08		0.40
Leopardus tigrinus								
Leopardus wiedii	4.67	15.31						
Leptailurus serval				37.75	13.40	6.23		
Lynx canadensis								0.04
Lynx lynx				35.85	13.10	7.56		0.03
Lynx pardinus								

Table C.3: Continued.

	mBMR	tBMR	T_B	Hct	Hb	RBC	HR	PD
Lynx rufus	7.16	44.42		45.00	14.40	9.26		0.10
Neofelis nebulosa				40.90	12.85	7.26		
Oncifelis colocolo								
Oncifelis geoffroyi								
Oncifelis guigna								
Oreailurus jacobita								
Otocolobus manul								
Panthera leo	2.93	457.01		37.65	13.50	8.05	40.00	0.10
Panthera onca	3.07	264.35		37.00	13.01	7.49		0.06
Panthera pardus				38.90	12.80	7.67	60.00	0.04
Panthera tigris	2.95	474.95		40.54	13.59	7.09	64.00	0.03
Pardofelis marmorata								
Prionailurus bengalensis				39.00	13.70	7.90		
Prionailurus planiceps								
Prionailurus rubiginosus								
Prionailurus viverrinus								
Profelis aurata								
Puma concolor	4.28	221.68		41.50	15.40	10.25	60.00	0.02
Uncia uncia				34.00	11.10	9.06		0.08
HERPESTIDAE								
Atilax paludinosus								
Bdeogale crassicauda								
Bdeogale jacksoni								
Bdeogale nigripes								
Crossarchus alexandri								
Crossarchus ansorgei								
Crossarchus obscurus								

Table C.3: Continued.

	mBMR	tBMR	T_B	Hct	Hb	RBC	HR	PD
Cynictis penicillata								
Dologale dybowskii								
Galerella flavescens								
Galerella pulverulenta								10.00
Galerella sanguinea	12.67	6.21	38.70	43.00	14.00	9.80		
Galerella swalius								
Galidia elegans								
Galidictis fasciata								
Galidictis grandidieri								
Helogale hirtula								
Helogale parvula								
Herpestes brachyurus								
Herpestes edwardsii								
Herpestes ichneumon								
Herpestes javanicus	12.50	9.75	38.94	49.60	11.20			
Herpestes naso								
Herpestes palustris								
Herpestes semitorquatus								
Herpestes smithii								
Herpestes urva				48.50	15.30	11.60		
Herpestes vitticollis								
Ichneumia albicauda								4.30
Liberiictis kuhni								
Mungos gambianus								
Mungos mungo								18.00
Mungotictis decemlineata								7.33
Paracynictis selousi								
Rhynchogale melleri								
Salanoia concolor								

Table C.3: Continued.

	mBMR	tBMR	T_B	Hct	Hb	RBC	HR	PD
Suricata suricatta	6.17	4.50	36.80				109.60	
HYAENIDAE								
Crocuta crocuta				28.00	9.00	5.65		0.16
Hyaena hyaena	2.85	76.38		44.50	15.60	7.76		
Parahyaena brunnea				40.00	13.20	7.00		0.15
Proteles cristatus	4.23	35.31	37.00					1.00
MUSTELIDAE								
Amblonyx cinereus								
Aonyx capensis								0.35
Aonyx congicus								
Arctonyx collaris								
Conepatus chinga								
Conepatus humboldtii								
Conepatus leuconotus								
Conepatus mesoleucus								
Conepatus semistriatus								
Eira barbara	6.90	28.53	38.40	40.50	12.50	6.40		
Enhydra lutris	11.99	339.20	37.85	50.28	17.85	4.42	151.50	6.47
Galictis cuja								
Galictis vittata				44.00	14.40	6.25		
Gulo gulo	7.05	81.78	38.00					0.01
Ictonyx libyca								
Ictonyx striatus								
Lontra canadensis							153.50	1.13
Lontra felina								

Table C.3: Continued.

	mBMR	tBMR	T_B	Hct	Hb	RBC	HR	PD
Lontra longicaudis								
Lontra provocax								
Lutra lutra	7.50	66.75						0.85
Lutra maculicollis								
Lutra sumatrana								
Lutrogale perspicillata								
Lyncodon patagonicus								
Martes americana	11.01	9.58		64.00	18.40	14.90		0.90
Martes flavigula								
Martes foina								
Martes gwatkinsii								
Martes martes	13.33	15.81						
Martes melampus								
Martes pennanti								0.02
Martes zibellina								0.08
Meles meles	4.80	55.68		35.60	12.25	7.75		
Mellivora capensis								
Melogale everetti								
Melogale moschata								
Melogale orientalis								
Melogale personata								
Mephitis macroura								
Mephitis mephitis	4.43	10.64	36.45	51.40	15.10	10.00	166.00	8.84
Mustela africana								
Mustela altaica								
Mustela erminea	28.00	26.60	39.75				357.00	6.25
Mustela eversmannii								
Mustela felipei								
Mustela frenata	16.84	3.44	39.50				182.00	0.76

Table C.3: Continued.

	mBMR	tBMR	T_B	Hct	Hb	RBC	HR	PD
Mustela kathiah								
Mustela lutreola			37.30				255.00	0.08
Mustela lutreolina								
Mustela nigripes								2.00
Mustela nivalis	44.65	3.41	36.60					18.36
Mustela nudipes								
Mustela putorius	13.72	14.13	38.74	51.00	15.20	9.98	231.00	0.10
Mustela sibirica								
Mustela strigidorsa								
Mustela vison	13.06	11.88	40.00	48.00	13.87	8.97		2.50
Mydaus javanensis								
Mydaus marchei								
Poecilogale albinucha								
Pteronura brasiliensis								
Spilogale putorius	7.92	4.35	36.50					5.00
Spilogale pygmaea								
Taxidea taxus	5.33	21.60	37.80	43.10	15.60		101.50	2.45
Vormela peregusna								
Odobenus rosmarus			36.60	46.00	16.48	3.27	55.00	1.27
OTARIIDAE								
Arctocephalus australis				49.30	16.80			
Arctocephalus forsteri				47.60	16.90	5.41		
Arctocephalus galapagoensis	4.51	207.23	37.70					
Arctocephalus gazella								22.01
Arctocephalus philippii								
Arctocephalus pusillus			37.50	39.00	13.60	4.04	85.00	

Table C.3: Continued.

	mBMR	tBMR	T_B	Hct	Hb	RBC	HR	PD
Arctocephalus townsendi								
Arctocephalus tropicalis								
Callorhinus ursinus			37.70	46.58	15.64	4.58	100.00	18.00
Eumetopias jubatus			38.50	40.20	14.68	3.95		
Neophoca cinerea				56.29	19.00	5.53	120.00	
Otaria byronia								
Phocarctos hookeri								
Zalophus californianus			37.50	45.00	15.30	4.40	95.00	0.50
PHOCIDAE								
Cystophora cristata	3.71	1049.85	36.50	63.00	26.40	4.80	100.00	0.00
Erignathus barbatus			37.13	56.40				0.02
Halichoerus grypus	3.32	643.43	36.50	56.00	19.03	5.13	127.50	
Hydrurga leptonyx					19.60	4.40		0.12
Leptonychotes weddellii	5.15	1895.20	36.70	58.72	23.70	3.73	60.00	0.13
Lobodon carcinophagus					18.20	4.41		1.01
Mirounga angustirostris			34.90	57.00	24.33	3.25	59.63	
Mirounga leonina			36.30	60.60	22.85	2.85	39.60	
Monachus monachus								
Monachus schauinslandi			36.20	54.70				
Monachus tropicalis								
Ommatophoca rossii			37.80				151.00	0.17
Phoca caspica								1.47
Phoca fasciata				66.80	24.48	4.49		
Phoca groenlandica	3.10	410.02	36.00	59.00	22.10	5.11	116.75	0.10
Phoca hispida	3.09	213.55	38.25	61.80	24.45	5.24	85.00	0.95
Phoca largha	6.53	597.42		54.45	18.00	4.70		
Phoca sibirica				62.93	18.00	5.50		1.59

Table C.3: Continued.

	mBMR	tBMR	T_B	Hct	Hb	RBC	HR	PD
Phoca vitulina	6.18	539.18	37.50	53.00	18.35	5.36	98.75	5.68
Ailurus fulgens	2.59	12.83	37.60					
PROCYONIDAE								
Bassaricyon alleni								
Bassaricyon beddardi								
Bassaricyon gabbii								
Bassaricyon lasius								
Bassaricyon pauli								
Bassariscus astutus			37.60					6.58
Bassariscus sumichrasti	8.25	7.47	38.80					
Nasua narica	8.62	38.43	38.85					26.00
Nasua nasua	4.93	18.29	38.71	39.50	11.90	6.70	70.00	17.80
Nasuella olivacea								
Potos flavus	5.67	11.90	36.20	47.00	15.80	7.10	77.45	41.18
Procyon cancrivorus	6.67	46.33						
Procyon gloveralleni								
Procyon insularis								
Procyon lotor	5.25	33.46	38.50	39.50	11.48	10.00		4.17
Procyon maynardi								
Procyon minor								
Procyon pygmaeus								
URSIDAE								
Ailuropoda melanoleuca								0.12
Helarctos malayanus								

Table C.3: Continued.

	mBMR	tBMR	T_B	Hct	Hb	RBC	HR	PD
Melursus ursinus	2.10	211.57		49.00	17.50	6.31		0.08
Tremarctos ornatus				38.00	11.00	7.70		
Ursus americanus	3.68	406.09	38.18	50.15	16.23	7.97	75.00	0.45
Ursus arctos	2.13	346.51	37.40	49.00	17.10	7.05	45.00	0.02
Ursus maritimus	2.02	739.10	37.20	54.50	19.70	8.34	52.25	0.01
Ursus thibetanus				43.50	14.95	6.21		
VIVERRIDAE								
Arctictis binturong	1.96	25.46	36.70					
Arctogalidia trivirgata	4.79	11.50	36.20					
Chrotogale owstoni								
Civettictis civetta								
Cryptoprocta ferox								
Cynogale bennettii								
Diplogale hosei								
Eupleres goudotii								
Fossa fossana	6.68	12.02	37.90					
Genetta abyssinica								
Genetta angolensis								
Genetta genetta								
Genetta johnstoni								
Genetta maculata								
Genetta servalina								
Genetta thierryi								
Genetta tigrina	7.33	15.11	38.50					
Genetta victoriae								
Hemigalus derbyanus								
Macrogalidia musschenbroekii								

Table C.3: Continued.

	mBMR	tBMR	T_B	Hct	Hb	RBC	HR	PD
Nandinia binotata	*3.93*	*7.76*	*37.40*					*5.00*
Osbornictis piscivora								
Paguma larvata								
Paradoxurus hermaphroditus	3.75	11.26	36.45	40.00	12.30	10.30		
Paradoxurus jerdoni								
Paradoxurus zeylonensis								
Poiana richardsonii								1.00
Prionodon linsang								
Prionodon pardicolor								
Viverra civettina								
Viverra megaspila								
Viverra tangalunga								
Viverra zibetha								
Viverricula indica								

Sources by family:

Canidae: Taylor *et al*. (1971); Altman & Dittmer (1974); Mech (1974); Hawkey (1975); Gates & Goering (1976); Bekoff (1977); Folk *et al*. (1977); McGrew (1979); Noll-Banholzer (1979); McNab (1980, 1989); Fritzell & Haroldson (1982); Maloiy *et al*. (1982); Golightly & Ohmart (1983); Hennemann (1983); Hennemann *et al*. (1983); Korhonen *et al*. (1983, 1985); Seal & Mech (1983); Jain (1986); Carbyn (1987); Elgar & Harvey (1987); Fritzell (1987); O'Farrell (1987); Okarma & Koteja (1987); Pospísil *et al*. (1987a); Voigt (1987); Voigt & Berg (1987); Kreeger *et al*. (1989, 1990a, 1990b, 1990c); Wickham *et al*. (1989); Ward & Wurster-Hill (1990); Womer & Richards (1990); DelGiudice *et al*. (1991); Nowak (1991); White *et al*. (1991); Klir & Heath (1992); Geffen (1994); Sillero-Zubiri & Gottelli (1994); Moore & Collins (1995); Larivière & Pasitschniak-Arts (1996); Novaro (1997)

Felidae: Altman & Dittmer (1974); Hawkey (1975); Currier & Russell (1982); Currier (1983); Corts & Lindzey (1984); Jain (1986); Elgar & Harvey (1987); Lindzey (1987); Pospísil *et al*. (1987b); Quinn & Parker (1987); Rolley (1987); Tewes & Schmidly (1987); Mautz & Pekins (1989); McNab (1989); Sandell (1989); Seymour (1989); Knick (1990); Nowak (1991); Larivière & Walton (1997); Murray & Gardner (1997)

Herpestidae: Baldwin *et al*. (1952); Nellis & McManus (1974); Hawkey (1975); Ebisu & Whittow (1976); Lin & Kobayashi (1976); Folk *et al*. (1977); Kamau *et al*. (1979); Müller & Lojewski (1986); Elgar & Harvey (1987); Sandell (1989); Nowak (1991); Cavallini (1992); van Staaden (1994)

Hyaenidae: Hawkey (1975); McNab (1984, 1989); Jain (1986); Pospísil *et al*. (1987a); Koehler & Richardson (1990); Nowak (1991)

Mustelidae: Lenfant *et al*. (1970); Brown & Lasiewski (1972); Long (1973); Altman & Dittmer (1974); Morrison *et al*. (1974); Hawkey (1975); Folk *et al.* (1977); McNab (1978, 1989, 1995); Casey & Casey (1979); Harlow (1981); Harlow & Seal (1981); Powell (1981); Worthen & Kilgore (1981); Wade-Smith & Verts (1982); Hennemann (1983); King (1983a); Korhonen *et al*. (1983); Anderson *et al*. (1986); Jain (1986); Williams (1986); Clark *et al*. (1987); Douglas & Strickland (1987); Eagle & Whitman (1987); Elgar & Harvey (1987); Fagerstone (1987); Garshelis (1987); Hash (1987); Kästner & Apfelbach (1987); Melquist & Dronkert (1987); Messick (1987); Rosatte (1987); Strickland & Douglas (1987); Mahmood *et al*. (1988); Sandell (1989); Knudsen & Kilgore (1990); Parker (1990); Wickham *et al*. (1990); Williams (1990); Youngman (1990); Nowak (1991); Sheffield & King (1994); Kinlaw (1995); Pasitschniak-Arts & Larivière (1995); Sheffield & Thomas (1997)

Odobenus rosmarus: Harrison & Kooyman (1968); Lenfant *et al*. (1970); Irving (1973); Estes & Gilbert (1978); King (1983b); Fedoseev (1984); Fay (1985); Gilbert (1989); Bossart & Dierauf (1990); Dierauf (1990); Walsh *et al*. (1990); Little (1995)

Otariidae: Bartholomew & Wilke (1956); Harrison & Kooyman (1968); Hubbard (1968); Irving (1969, 1973); Lenfant (1969); Ronald *et al*. (1969); Lenfant *et al*. (1970); Lane *et al*. (1972); Ridgway (1972); Sobolevskij (1977); Wells (1978); Needham *et al*. (1980); Gentry (1981); Odell (1981); Kooyman & Sinnett (1982); Thurman *et al*. (1982); King (1983b); Hunt *et al.* (1986); Limberger *et al*. (1986);

Trillmich *et al*. (1986); Bonnell & Ford (1987); Jablonski *et al*. (1987); Costa & Trillmich (1988); Bossart & Dierauf (1990); Dierauf (1990); Williams *et al*. (1990); Hedrick & Duffield (1991); Nowak (1991); Butler *et al*. (1992); Hunt *et al.* (1992); Little (1995); Castellini *et al.* (1996)

Phocidae: Bartholomew (1954); Pugh (1959); Tyler (1960); Morrison (1962); Harrison & Kooyman (1968); Hubbard (1968); Bryden & Lim (1969); Irving (1969, 1973); Lenfant (1969); Ronald *et al*. (1969, 1977, 1982); Lenfant *et al*. (1970); Geraci (1971); Stirling (1971); Lane *et al*. (1972); Ridgway (1972); Kerem & Elsner (1973); Altman & Dittmer (1974); Geraci & Smith (1975); Hawkey (1975); Kooyman (1975, 1981a, 1981c, 1981d, 1985); Øritsland & Ronald (1975); Folk *et al.* (1977); Gilbert & Erickson (1977); Laws (1977); Sobolevskij (1977); Stirling *et al*. (1977, 1982); St. Audin *et al*. (1978); Ashwell-Erickson *et al*. (1979, 1986); Ferren & Elsner (1979); Finley (1979); Gallivan & Ronald (1979); Kenny (1979); Popov (1979a, 1979b, 1982); Stirling & Calvert (1979); Kooyman *et al.* (1980); Needham *et al*. (1980); Bigg (1981); Burns (1981b); Eisenberg (1981); Frost & Lowry (1981); Kenyon (1981a); Ray (1981); Reeves & Ling (1981); Ronald & Healey (1981); Sinnett *et al*. (1981); Kooyman & Sinnett (1982); Lapennas & Reeves (1982); Lavigne *et al*. (1982); Worthy & Lavigne (1982); Erickson *et al*. (1983, 1989); Finley *et al*. (1983); Hennemann (1983); King (1983b); Erickson (1984); Schmitz & Lavigne (1984); Davis *et al*. (1985); Kingsley *et al*. (1985); Fedak (1986); Hedrick *et al*. (1986); Kovacs & Lavigne (1986a); Keiver *et al*. (1987); Castellini *et al*. (1988, 1996); Wickham *et al*. (1989, 1990); Bossart & Dierauf (1990); Dierauf (1990); Erickson & Hanson (1990); Hammill & Smith (1990); Härkönen & Heide-Jørgensen (1990); Olesiuk *et al*. (1990); Williams *et al*. (1990); Hedrick & Duffield (1991); Nowak (1991); Harwood & Stirling (1992); Ling & Bryden (1992); Lydersen *et al*. (1992); Castellini & Castellini (1993); Gales & Renouf (1993); Ponganis *et al.* (1993); Stewart & Huber (1993); Gelatt *et al*. (1994); Renouf & Gales (1994); Stenson & Kavanagh (1994); Bester *et al.* (1995); Boily & Lavigne (1995); Little (1995); Melrose *et al*. (1995); Stirling & Øritsland (1995); Mathews & Kelly (1996)

Ailurus fulgens: McNab (1988, 1989)

Procyonidae: Hoff *et al*. (1974); Hawkey (1975); McNab (1978, 1989, 1995); Lotze & Anderson (1979); Chevillard-Hugot *et al*. (1980); Müller & Rost (1983); Jain (1986); Chevalier (1987); Kaufmann (1987); Sanderson (1987); Ford & Hoffman (1988); Poglayen-Neuwall & Toweill (1988); Sandell (1989); Parker (1990); Nowak (1991); Gompper (1995)

Ursidae: Hawkey (1975); Øritsland *et al*. (1977); Chorn & Hoffman (1978); Follman *et al.* (1979); DeMaster & Stirling (1981); Brannon (1985); Jain (1986); Elgar & Harvey (1987); Jonkel (1987); Kolenosky (1987); Kolenosky & Strathearn (1987); Pospísil *et al*. (1987a); Watts *et al*. (1987); McNab (1989, 1992); Sandell (1989); Parker (1990); Torgerson (1990); Nowak (1991); Hissa *et al*. (1992); Pasitschniak-Arts (1993); White *et al*. (1996)

Viverridae: Hawkey (1975); Hennemann & Konecny (1980); McNab (1989, 1995); Sandell (1989); Nowak (1991)

Appendix D

Specimen list for pinniped brain sizes

I measured the volumes of the brain cavities (see Chapter 6) for the following pinniped specimens from the Natural History Museum, London. Sexes, where known, are indicated as M for male and F for female.

Otariidae

Arctocephalus australis — 1879.8.21.5 (F); 1984.973 (M)

Arctocephalus forsteri — 1968.9.26.5 (F); 1968.9.26.6 (M)

Arctocephalus galapagoensis — 1991.1 (M); 1991.2 (F)

Arctocephalus gazella — 1960.8.10.5 (F); 1960.8.10.51 (M)

Arctocephalus philippii — 1883.11.8.1 (M?)

Arctocephalus pusillus doriferus — 1960.1.29.4 (M); 1968.9.26.1 (F)

Arctocephalus pusillus pusillus — 1925.1.2.68 (M); 1927.7.2.6 (F)

Arctocephalus townsendi — none available

Arctocephalus tropicalis — 1955.3.14.5 (F); 1957.4.23.11 (M)

Callorhinus ursinus — 1950.3.29.8 (M); 1960.5.2.2 (F)

Eumetopias jubatus — 1950.3.29.10 (F); 1950.3.29.12 (M)

Neophoca cinerea — 1968.9.26.25 (M); 1968.9.26.27 (F)

Otaria byronia — 1939.1.21.112 (F); 1939.1.21.169 (M)

Phocarctos hookeri — 336.b (M); 1908.2.20.52 (F)

Zalophus californianus — 1951.3.6.2 (F); 1968.6.10.1 (M)

Odobenidae

Odobenus rosmarus — 1926.12.2.1 (F); 1926.12.2.4 (M)

Phocidae

Cystophora cristata — 332.h (M); 1844.6.23.1 (F)

Erignathus barbatus — 1896.9.23.6 (?); 1938.11.26.1 (?)

Halichoerus grypus — 1951.11.28.1 (F); 1956.9.26.4 (M)

Hydrurga leptonyx — 1901.1.4.15 (M); 1959.12.17.4 (F)

Leptonychotes weddellii — 1908.2.20.26 (M); 1908.2.20.63 (F)

Lobodon carcinophagus — 1939.2.4.5 (F); 1959.12.8.7 (M)

Mirounga angustirostris — none available

Mirounga leonina — 1954.5.20.21 (F); 1954.5.20.34 (M)

Monachus monachus — 1863.4.1.1 (M); 1894.7.27.2 (F)

Monachus schauinslandi — 1958.11.26.1 (M)

Monachus tropicalis — 1889.11.5.1 (M)

Ommatophoca rossii — 1908.2.20.48 (M); 1951.4.21.1 (F?)

Phoca caspica — 1965.7.19.1 (M); 1965.7.19.2 (F)

Phoca fasciata — 1965.7.19.8 (M); 1965.7.19.9 (F)

Phoca groenlandica — 1938.12.10.3 (F); 1951.11.28.2 (M)

Phoca hispida — 1938.11.26.6 (M); 1938.12.10.5 (F)

Phoca largha — 1965.7.19.12 (F); 1965.7.19.14 (M)

Phoca sibirica — 1963.7.19.8 (F); 1963.7.19.9 (M)

Phoca vitulina — 329.i (M); 1928.9.1.2 (?)

Appendix E

Standardized contrasts for aquatic versus non-aquatic comparisons

This appendix gives the values of the standardized contrasts for the aquatic / non-aquatic comparisons, for which the general trends are summarized in Table 6.5. I hold "discrepant species" (or taxa) to be those displaying a trend opposite to the hypothesized direction (see Table 6.1) or, when no hypothesis was presented, to the clear majority of the remaining forms for each tree topology.

Table E.1: Standardized contrasts for aquatic / non-aquatic sister taxa comparisons based on the topology of Tree 1: a) corrected for size using body weight, b) corrected for size using brain weight, and c) uncorrected for size. Contrasts of "discrepant species" are in bold face.

	Contrast involving								
Variable	*Atilax*	*Cynogale*	*Osbornictis*	within viverrids	*Mustela lutreola*	*Mustela vison*	otters	pinnipeds	*p*
a) Corrected using body weight									
SWt									
SHB	0.001	0.001	0.003	0.098	0.008	0.034	0.032		0.0078
SBr	0.017	**-0.008**		0.105	0.014	0.075	0.044		0.2188
LS									
GL	0.006			0.140	**-0.019**	0.013	0.061		0.3750
BWt	0.051			0.053	0.054	0.107	0.182		0.0625
LWt	0.041			0.004	0.037	0.040	0.126		0.0625
WA									
AI									
MMat	**-0.035**			0.019	0.000	0.083	0.039		0.3750
FMat				0.010	0.093	0.068	0.038		0.1250
IB									
EO									
LY	**0.014**	-0.075		-0.025	-0.007	**0.021**	-0.004		0.6875
mBMR					**-0.029**	0.052	0.012		0.5000
tBMR					**-0.033**	0.041	**0.000**		0.8750
T_B									
Hct									
Hb									
RBC					-0.008	-0.034	-0.015		0.1250
HR				0.000		0.013	0.032		0.2500
PD				-0.322	**0.028**	**0.015**	**0.097**		0.9375

Table E.1: Continued.

	Contrast involving								
Variable	*Atilax*	*Cynogale*	*Osbornictis*	within viverrids	*Mustela lutreola*	*Mustela vison*	otters	pinnipeds	*p*
b) Corrected using brain weight									
SWt	**-0.004**	0.032		**-0.150**	**-0.002**	**-0.062**	0.018		0.6563
SHB	**-0.009**	**-0.005**		0.020	0.000	**-0.006**	0.007		0.3438
SBr									
LS	0.000			-0.125	-0.017	-0.040	-0.032		0.0625
GL	-0.001			0.110	-0.022	0.002	0.044		1.0000
BWt	0.011			**-0.058**	0.013	0.019	0.111		0.3750
LWt	0.003			-0.139	0.004	-0.039	0.071		1.0000
WA	-0.026			0.070	0.001	0.022	-0.051		1.0000
AI									
MMat	-0.046			0.008	-0.017	0.047	0.016		1.0000
FMat				**-0.016**	0.074	0.022	0.002		0.6250
IB	-0.034			-0.004	-0.001	-0.021	-0.025		0.0625
EO									
LY	**0.007**	-0.070		-0.060	-0.015	-0.012	-0.023		0.2188
mBMR					**-0.025**	0.066	0.017		0.5000
tBMR					**-0.051**	**-0.011**	0.006		0.8750
T_B									
Hct									
Hb									
RBC					-0.007	-0.026	-0.014		0.1250
HR									
PD				-0.263	**0.083**	**0.145**	**0.153**		0.9375

Table E.1: Continued.

Variable	Contrast involving *Atilax*	*Cynogale*	*Osbornictis*	within viverrids	*Mustela lutreola*	*Mustela vison*	otters	pinnipeds	*p*
c) Uncorrected									
SWt	0.068	0.067	0.010		**-0.090**	0.057	0.159	0.262	0.0625
SHB	0.014	0.012	0.005		0.086	0.019	0.069	0.086	0.0078
SBr	0.047	0.034			0.115	0.037	0.152	0.165	0.0313
LS	**0.003**	**0.034**	-0.056		-0.048	-0.015	-0.056	-0.046	0.2266
GL	0.012				0.140	**-0.016**	0.023	0.076	0.1875
BWt	0.101				**-0.007**	0.103	0.185	0.309	0.1875
LWt	0.092				**-0.056**	0.087	0.120	0.262	0.1875
WA	**-0.007**				0.110	0.011	0.061	**-0.006**	0.5000
AI					0.040	0.022	0.065	**-0.054**	0.3125
MMat	**-0.025**				0.004	0.015	0.089	0.078	0.1875
FMat					**-0.003**	0.103	0.068	0.063	0.3125
IB	**-0.019**				0.000	0.015	0.019	0.013	0.3125
EO	-0.016				0.080	0.007	-0.039	-0.185	1.0000
LY	0.025	**-0.059**			**-0.020**	0.001	0.045	0.034	0.3438
mBMR						**-0.037**	0.031	**-0.011**	0.8750
tBMR						0.021	0.204	0.180	0.1250
T_B					-0.005	**0.003**	**0.002**	-0.001	0.6875
Hct						**-0.004**	**-0.001**	0.012	0.8750
Hb						**-0.006**	0.009	0.018	0.5000
RBC						-0.008	-0.044	-0.033	0.1250
HR					0.013		-0.005	-0.013	1.0000
PD					-0.266	-0.041	-0.116	-0.078	0.0625
SDWt	**-0.005**		**-0.001**		0.045	0.013	0.003	0.019	0.6875
SDHB	-0.001			-0.001	-0.095	-0.005	-0.003	**0.004**	0.2188
SDBr	0.004				**-0.050**	0.013	0.006	0.000	0.3750
SDMat					0.005	**-0.088**	0.021	0.011	0.6250

Table E.2: Standardized contrasts for aquatic / non-aquatic sister taxa comparisons based on the topology of Tree 2: a) corrected for size using body weight, b) corrected for size using brain weight, and c) uncorrected for size. Contrasts of "discrepant species" are in bold face.

	Contrast involving								
Variable	*Atilax*	*Cynogale*	*Osbornictis*	within viverrids	*Mustela lutreola*	*Mustela vison*	otters	pinnipeds	*p*
a) Corrected using body weight									
SWt									
SHB	0.001	0.001	0.003	0.098	0.008	0.034	0.011		0.0078
SBr	0.017	**-0.008**		0.105	0.014	0.075	0.011		0.2188
LS									
GL	0.006			0.140	**-0.019**	0.013	0.049		0.3750
BWt	0.051			0.053	0.054	0.107	0.193		0.0625
LWt	0.042			0.004	0.037	0.041	0.161		0.0625
WA									
AI									
MMat	-0.035			0.019	0.000	0.083	0.000		1.0000
FMat				0.010	0.093	0.068	**-0.007**		0.6250
IB									
EO									
LY	**0.014**	-0.075		-0.025	-0.007	**0.021**	-0.010		0.6875
mBMR					**-0.029**	0.052	0.022		0.5000
tBMR					**-0.033**	0.041	0.023		0.5000
T_B									
Hct									
Hb									
RBC					-0.008	-0.034	-0.022		0.1250
HR				0.000		0.013	0.020		0.2500
PD				-0.322	**0.028**	**0.015**	**0.102**		0.9375

Table E.2: Continued.

	Contrast involving								
Variable	*Atilax*	*Cynogale*	*Osbornictis*	within viverrids	*Mustela lutreola*	*Mustela vison*	otters	pinnipeds	*p*
b) Corrected using brain weight									
SWt	**-0.003**	0.032		**-0.155**	**-0.002**	**-0.062**	**-0.004**		0.8906
SHB	**-0.009**	**-0.005**		0.020	0.000	**-0.006**	0.005		0.3438
SBr									
LS	-0.001			-0.125	-0.017	-0.040	-0.029		0.0625
GL	-0.001			0.110	-0.022	0.002	0.056		1.0000
BWt	0.011			**-0.058**	0.014	0.019	0.174		0.3750
LWt	0.003			-0.139	0.004	-0.039	0.144		1.0000
WA	-0.026			0.070	0.001	0.022	-0.057		1.0000
AI									
MMat	-0.045			0.009	-0.017	0.048	-0.005		1.0000
FMat				-0.016	0.074	0.022	-0.017		1.0000
IB	-0.034			-0.004	-0.001	-0.021	-0.022		0.0625
EO									
LY	**0.007**	-0.070		-0.060	-0.015	-0.012	-0.014		0.2188
mBMR					**-0.025**	0.066	0.024		0.5000
tBMR					**-0.051**	**-0.011**	0.012		0.8750
T_B									
Hct									
Hb									
RBC					-0.007	-0.026	-0.022		0.1250
HR									
PD				-0.265	**0.084**	**0.145**	**0.119**		0.9375

Table E.2: Continued.

	Contrast involving								
Variable	*Atilax*	*Cynogale*	*Osbornictis*	within viverrids	*Mustela lutreola*	*Mustela vison*	otters	pinnipeds	*p*
c) Uncorrected									
SWt	0.068	0.067	0.010		**-0.090**	0.057	0.159	0.038	0.0625
SHB	0.014	0.012	0.005		0.086	0.019	0.069	0.019	0.0078
SBr	0.047	0.034			0.115	0.037	0.152	0.028	0.0313
LS	**0.003**	**0.034**	-0.056		-0.048	-0.015	-0.056	-0.031	0.2266
GL	0.012				0.140	**-0.016**	0.023	0.049	0.1875
BWt	0.101				**-0.007**	0.103	0.185	0.213	0.1875
LWt	0.092				**-0.056**	0.087	0.120	0.182	0.1875
WA	**-0.007**				0.110	0.011	0.061	**-0.048**	0.5000
AI					0.040	0.022	0.065	**-0.094**	0.3125
MMat	**-0.025**				0.004	0.015	0.089	0.005	0.1875
FMat					**-0.003**	0.103	0.068	**-0.002**	0.6875
IB	**-0.019**				0.000	0.015	0.019	**-0.020**	0.6875
EO	-0.016				0.080	0.007	-0.039	-0.169	1.0000
LY	0.025	**-0.059**			**-0.020**	0.001	0.045	**-0.005**	0.6563
mBMR						**-0.037**	0.031	0.023	0.5000
tBMR						0.021	0.204	0.015	0.1250
T_B					**-0.005**	0.003	0.002	**-0.001**	0.6875
Hct						**-0.004**	**-0.001**	0.008	0.8750
Hb						**-0.006**	0.009	0.014	0.5000
RBC						-0.008	-0.044	-0.025	0.1250
HR					0.013		-0.005	0.016	1.0000
PD					-0.266	-0.041	-0.116	**0.083**	0.3125
SDWt	-0.005		-0.001		0.045	0.013	0.003	0.000	1.0000
SDHB	-0.001			-0.001	-0.095	-0.005	-0.003	**0.001**	0.2188
SDBr	0.004				-0.050	0.013	0.006	-0.006	1.0000
SDMat					0.005	**-0.088**	0.021	0.009	0.6250

Table E.3: Standardized contrasts for aquatic / non-aquatic sister taxa comparisons based on the topology of Tree 3: a) corrected for size using body weight, b) corrected for size using brain weight, and c) uncorrected for size. Contrasts of "discrepant species" are in bold face.

	Contrast involving									
Variable	*Atilax*	*Cynogale*	*Osbornictis*	within viverrids	*Mustela lutreola*	*Mustela vison*	otters	otarioids	phocids	*p*
a) Corrected using body weight										
SWt										
SHB	0.000	0.001	0.002		0.105	0.008	0.033	0.011	0.045	0.0039
SBr	0.016	**-0.008**			0.110	0.014	0.075	0.020	0.058	0.0625
LS										
GL	0.005				0.135	**-0.020**	0.010	0.063	0.099	0.2188
BWt	0.046				0.058	0.049	0.097	0.236	0.247	0.0313
LWt	0.038				0.008	0.034	0.034	0.196	0.174	0.0313
WA										
AI										
MMat	**-0.036**				0.020	**-0.000**	0.081	0.006	0.037	0.6875
FMat					0.011	0.093	0.067	**-0.002**	0.055	0.3750
IB										
EO										
LY	0.014	-0.075			-0.025	-0.007	0.021	-0.017	0.011	1.0000
mBMR						**-0.029**	0.053	0.021	0.003	0.3125
tBMR						**-0.033**	0.042	0.024	**-0.012**	0.6875
T_B										
Hct										
Hb										
RBC						-0.008	-0.033	-0.028	-0.017	0.0625
HR					0.001		0.011	0.021	0.013	1.0000
PD					-0.320	**0.027**	**0.013**	**0.254**	**0.140**	0.9688

Table E.3: Continued.

Variable	Contrast involving *Atilax*	*Cynogale*	*Osbornictis*	within viverrids	*Mustela lutreola*	*Mustela vison*	otters	otarioids	phocids	*p*
b) Corrected using brain weight										
SWt	**-0.003**	0.032			**-0.155**	**-0.002**	**-0.063**	**-0.013**	0.016	0.7734
SHB	**-0.008**	**-0.004**			0.020	0.000	**-0.007**	0.000	0.011	0.5000
SBr										
LS	**0.001**				-0.120	-0.016	-0.036	-0.034	-0.046	0.2188
GL	-0.003				0.105	-0.024	-0.003	0.068	0.079	1.0000
BWt	0.004				**-0.059**	0.007	0.005	0.189	0.169	0.2188
LWt	-0.001				-0.141	-0.001	-0.049	**0.152**	**0.116**	0.6875
WA	**-0.027**				0.070	0.001	0.020	0.019	**-0.127**	0.6875
AI										
MMat	**-0.046**				0.008	**-0.017**	0.047	0.001	0.008	0.6875
FMat					-0.016	0.075	0.023	-0.018	0.012	1.0000
IB	-0.033				-0.004	0.000	-0.019	-0.026	-0.027	0.0313
EO										
LY	**0.007**	-0.070			-0.060	-0.015	-0.012	-0.025	-0.012	0.1250
mBMR						**-0.025**	0.066	0.027	0.005	0.3125
tBMR						**-0.051**	**-0.010**	**-0.020**	0.017	0.6875
T_B										
Hct										
Hb										
RBC						-0.007	-0.024	-0.027	-0.015	0.0625
HR										
PD					-0.263	**0.079**	**0.134**	**0.281**	**0.178**	0.9688

Table E.3: Continued.

	Contrast involving									
Variable	*Atilax*	*Cynogale*	*Osbornictis*	within viverrids	*Mustela lutreola*	*Mustela vison*	otters	otarioids	phocids	*p*
c) Uncorrected										
SWt	0.068	0.067	0.010		**-0.090**	0.057	0.159	0.052	0.334	0.0352
SHB	0.014	0.012	0.005		0.086	0.019	0.069	0.022	0.114	0.0039
SBr	0.047	0.034			0.115	0.037	0.152	0.044	0.214	0.0078
LS	**0.003**	**0.034**	-0.056		-0.048	-0.015	-0.056	-0.040	-0.073	0.1445
GL	0.012				0.140	**-0.016**	0.023	0.062	0.123	0.1094
BWt	0.101				**-0.007**	0.103	0.185	0.255	0.422	0.1094
LWt	0.092				**-0.056**	0.087	0.120	0.215	0.348	0.1094
WA	**-0.007**				0.110	0.011	0.061	0.034	**-0.071**	0.3438
AI					0.040	0.022	0.065	**-0.023**	**-0.153**	0.5000
MMat	**-0.025**				0.004	0.015	0.089	0.015	0.084	0.1094
FMat					**-0.003**	0.103	0.068	0.002	0.089	0.1875
IB	**-0.019**				0.000	0.015	0.019	**-0.022**	0.018	0.5000
EO	-0.016				**0.080**	**0.007**	-0.039	-0.213	-0.257	0.6875
LY	0.025	**-0.059**			**-0.020**	0.001	0.045	**-0.009**	0.059	0.5000
mBMR						**-0.037**	0.031	0.028	**-0.027**	0.6875
tBMR						0.021	0.204	**-0.026**	0.214	0.3125
T_B					-0.005	**0.003**	**0.002**	0.000	-0.003	0.5000
Hct						**-0.004**	**-0.001**	0.002	0.023	0.6875
Hb						**-0.006**	0.009	0.007	0.030	0.3125
RBC						-0.008	-0.044	-0.033	-0.039	0.0625
HR					0.013		-0.005	0.017	-0.038	1.0000
PD					-0.266	-0.041	-0.116	**0.223**	-0.045	0.1875
SDWt	-0.005		-0.001		0.045	0.013	0.003	0.030	-0.009	1.0000
SDHB	-0.001			-0.001	-0.095	-0.005	-0.003	**0.007**	-0.001	0.0625
SDBr	0.004				-0.050	0.013	0.006	-0.007	-0.004	1.0000
SDMat					0.005	-0.088	0.021	0.016	-0.008	1.0000