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A species-level phylogenetic supertree of marsupials

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Abstract

Comparative studies require information on phylogenetic relationships, but complete species-level phylogenetic trees of large clades are difficult to produce. One solution is to combine algorithmically many small trees into a single, larger supertree. Here we present a virtually complete, species-level phylogeny of the marsupials (Mammalia: Metatheria), built by combining 158 phylogenetic estimates published since 1980, using matrix representation with parsimony. The supertree is well resolved overall (73.7%), although resolution varies across the tree, indicating variation both in the amount of phylogenetic information available for different taxa, and the degree of conflict among phylogenetic estimates. In particular, the supertree shows poor resolution within the American marsupial taxa, reflecting a relative lack of systematic effort compared to the Australasian taxa. There are also important differences in supertrees based on source phylogenies published before 1995 and those published more recently. The supertree can be viewed as a meta-analysis of marsupial phylogenetic studies, and should be useful as a framework for phylogenetically explicit comparative studies of marsupial evolution and ecology.

Key words: comparative studies, matrix representation with parsimony, Metatheria, *QS* support

INTRODUCTION

Large, species-level phylogenetic trees are extremely valuable to researchers in evolution and ecology, both as a framework for comparative analyses (Felsenstein, 1985; Harvey & Pagel, 1991), and as tools for studying patterns of macroevolution (Nee, Mooers & Harvey, 1992; Purvis, Nee & Harvey, 1995; Sanderson & Donoghue, 1996; Gittleman, Jones & Price, in press). However, producing complete phylogenies of large clades from primary character data still presents a major challenge, both because of the difficulty in obtaining sufficient homologous data for many different species (Sanderson *et al*., 2003), and because of analytical limitations in reconstructing large phylogenies (Sanderson & Shaffer, 2002). For this reason, researchers using comparative methods are frequently compelled to build composite phylogenies by combining multiple smaller trees. This has often been done in an informal fashion by choosing one estimate of higher-level relationships for the clade of interest, then grafting selected species-level trees on to the terminal branches (e.g. Kennedy, Spencer & Gray, 1996; Badyaev, 1997; Johnson, 1998; Ortolani, 1999; Cardillo & Bromham, 2001; Fisher, Owens & Johnson, 2001). A problem with this approach is that the basis for choosing trees from which to build the composite phylogeny can be quite arbitrary; for example, the trees chosen may simply be the most comprehensive or the most recent that are available (e.g. Cardillo & Bromham, 2001). Where alternative, conflicting phylogenetic estimates for the same group of taxa exist, this approach unavoidably ignores most of the available information about the phylogeny of that group in favour of a single hypothesis only. Furthermore, because of differences in opinion about how phylogenies are best constructed, disagreements about the choice of trees are inevitable. One solution to this is to construct supertrees. Supertrees use formal, algorithmic methods such as matrix representation with parsimony (MRP; Baum, 1992; Ragan, 1992) to combine multiple trees with non-identical taxon sets. In supertree construction, the topologies of original phylogenies ('source trees'), as opposed to the data underlying those phylogenies, are combined. As such, a supertree can be thought of as a summary or meta-analysis of original phylogenetic studies. Supertrees are becoming widely used in comparative studies, with complete species-level supertrees already published for primates (Purvis, 1995), carnivores (Bininda-Emonds, Gittleman & Purvis, 1999),

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bats (Jones *et al*., 2002), insectivores (Grenyer & Purvis, 2003), lagomorphs (Stoner, Bininda-Emonds & Caro, 2003) and tubenose seabirds (Kennedy & Page, 2002), and higher level supertrees published for mammals (Liu *et al*., 2001), platyhelminths (Wilkinson *et al*., 2001), grasses (Salamin, Hodkinson & Savolainen, 2002) and dinosaurs (Pisani *et al*., 2002).

A recent critique of the supertree approach (Springer & de Jong, 2001) pointed out the potential for non-independence of source trees through pseudoreplication in the data matrices from which supertrees are built. Such problems can be minimized by critical selection of the source trees before constructing the supertree matrix (Bininda-Emonds, Jones, Price, Grenyer *et al*., 2003; Bininda-Emonds, Jones, Price, Cardillo *et al*., in press). Such selection was done in a recent supertree of seabirds, in which the authors aimed to maximize the extent to which each source tree represented an independent piece of evidence for the phylogeny of the clade (Kennedy & Page, 2002). A newly devised protocol for the selection of source trees (Bininda-Emonds, Jones, Price, Cardillo *et al*., in press) emphasizes the principle of independence of data even more explicitly by defining a set of sequential rules for the inclusion or rejection of source trees, or for the combination of several non-independent source trees before inclusion in the supertree matrix. This is an important advance in supertree methodology because it allows the source tree selection criteria to be presented in a transparent manner, thereby promoting repeatability of selection, reducing author bias in source tree selection, and minimizing non-independence among source trees.

Here the first application of this selection protocol to yield a virtually complete species-level supertree of the marsupials (Mammalia: Metatheria) is presented. Marsupials include 272 extant species under the classification of Wilson & Reeder (1993), distributed in Australasia and the Americas. Marsupials have been the focus of phylogenetic comparative studies in a range of fields, including conservation biology (e.g. Cardillo & Bromham, 2001), macroecology (e.g. Johnson, 1998) and life-history evolution (e.g. Fisher *et al*., 2001). The results of all such studies are contingent on the use of an accurate marsupial phylogeny as a framework for analyses. However, marsupial systematics has been subject to several pervasive controversies over recent decades, and debate continues even over relationships among the seven marsupial orders and other higher-level groupings. For example, the position of the root of the marsupial tree is still not settled. Division of marsupials into the two suborders Australidelphia and Ameridelphia was first proposed by Szalay (1982), and although Australidelphia (all Australasian taxa plus the South American microbiotheriid *Dromiciops gliroides*) is well supported (e.g. Phillips *et al*., 2001), support for the monophyly of Ameridelphia has always been poor (e.g. Amrine-Madsen *et al*., 2003). The position of *Dromiciops* within the Australidelphia, either as a sister taxon to the Australasian marsupials (e.g. Amrine-Madsen *et al*., 2003) or nested within the Australasian taxa (e.g. Kirsch *et al*., 1997; Springer, Westerman *et al*., 1998), remains a subject of debate. Likewise, the positions of the marsupial moles (*Notoryctes*) and the bandicoots (Peramelimorphia) also remain uncertain. Much of this uncertainty stems from the different phylogenetic signals given by different types of data, or by the incomplete taxonomic representation of phylogenetic studies (Kirsch, Lapointe & Springer, 1997; Lapointe & Kirsch, 2001).

There have been several phylogenetic syntheses of the marsupials in recent years. Aplin & Archer (1987) combined estimates of marsupial relationships available at that time into what they referred to as ‘a syncretic consensus of current phylogenetic understanding’. Their combination of phylogenies was carried out in an informal, non-algorithmic fashion, though guided by what they called ‘cladistic principles’. Springer, Kirsch & Case (1997) presented a family-level consensus using moderately well-supported nodes from trees from various molecular datasets (DNA hybridization, P1 and 12S). Other syntheses have combined smaller datasets into supermatrices that were analysed using conventional methods: Luckett (1994) simultaneously analysed a variety of morphological and molecular characters, while Kirsch, Lapointe *et al*. (1997) produced the largest marsupial phylogeny to date from a single data type (101 species from almost all genera) by combining separate matrices of DNA hybridization distances (verified by Lapointe & Kirsch, 2001). But, to date, no complete species-level phylogeny of the marsupials has been produced. Here we present the first attempt to do so, combining systematically the majority of estimates of marsupial phylogeny published in recent decades. This is similar in principle to Aplin & Archer’s (1987) ‘syncretic consensus’, but using modern, algorithmic supertree methods. Our aims in producing a virtually complete, species-level supertree of extant marsupials are threefold. First, to provide a framework for robust comparative analyses of marsupial evolution and ecology. Second, to examine how estimates of marsupial phylogeny have changed in recent years with the rapid increase in availability of molecular data and better computing power, which together have enabled the routine use of large datasets and complex tree reconstruction algorithms. Finally, supertrees can be a useful means of taking a broad view of a group’s systematics and identifying areas in which systematic study is sparse or conflict among studies is greatest.

METHODS

Source tree collection

Published estimates of marsupial phylogeny were collected from the literature by searching *Zoological Record* and *Web of Science*, using the following search terms: phylog*, system*, classif*, taxonom*, relationships and cladistic*, together with marsupial*, metatheria* and the truncated name of each marsupial order and family. Additional relevant studies were obtained by examining the reference lists of studies collected. Because we wished to build a supertree that summarized recent thinking in marsupial systematics, yet incorporated a large number of source trees, the search for source trees was restricted to studies published since January 1980. The protocol for inclusion or rejection of source trees is described fully elsewhere (Bininda-Emonds, Jones, Price, Cardillo *et al.*, in press), but the general principle was to minimize data redundancy to ensure as far as possible that each source tree chosen represented an independent 'datapoint' in the supertree analysis. The following 3 examples from the protocol illustrate this principle: (1) trees were not accepted that had been superseded by more recent, more taxonomically inclusive trees using the same dataset; (2) where 2 or more trees with identical taxon sets, built using the same dataset but with different methods (e.g. parsimony and maximum likelihood), were presented in a study, these trees were first combined using MRP into a 'mini-supertree', which was coded as the single source tree for that study; (3) trees were not accepted that were simply reproductions of phylogenies published elsewhere, or composite phylogenies built by grafting together several smaller, previously published trees. The topology implied by the marsupial classification of Wilson & Reeder (1993) was included as a source tree. The inclusion of a classification as a 'seed' tree in MRP analyses was recommended by Bininda-Emonds & Sanderson (2001) to ensure sufficient overlap among the set of source trees, thereby improving resolution. Wilson & Reeder (1993) was chosen as the taxonomy for the seed tree because it is currently widely accepted as a taxonomic reference for mammals, and because its low resolution means it can easily be overruled by more resolved phylogenies, minimizing its influence on the final supertree. Each source tree topology was reconstructed in TreeView (Page, 1996), taxa defined as outgroups by the authors were collapsed to a single tip, and the tree saved in Nexus file format for use in analyses. Because the source trees were collected from literature spanning 3 decades, synonymies and differences in species designations were inevitable. All synonymies were therefore converted to a common nomenclature (that of Wilson & Reeder, 1993) before analysis. Where a species could not be synonymized to the Wilson & Reeder nomenclature, it was excluded.

Construction of supertrees

To construct supertrees using MRP, the nodes in each source tree were first represented as a series of partial binary 'pseudocharacters' indicating the inclusion of each terminal taxon below that node. For each pseudocharacter, descendants of that node were scored as '1', non-descendants as '0', and taxa missing from that source tree as '?' (Baum, 1992; Ragan, 1992). Matrices of MRP pseudocharacters were constructed using RadCon (Thorley & Page, 2000) and analysed with parsimony using PAUP* v.4b10 (Swofford, 2002) to reconstruct the supertree. In most large supertrees published to date, assumed monophyletic subclades have been analysed separately, then grafted together based on a higher-level supertree, to reduce computational times. We avoided any assumptions of monophyly by performing a single analysis of all marsupial species. To speed the search for most parsimonious trees the Parsimony Ratchet, a heuristic search method that searches treespace more broadly than conventional heuristic algorithms (Nixon, 1999), was applied. Our implementation of the ratchet consisted of 10 separate runs, each with 500 iterations. Within each iteration, 25% of the characters were selected randomly and upweighted by a factor of 2. The trees from all runs were used as the starting trees for a final 'brute force' search using TBR branch swapping. We saved 10 000 of the most parsimonious trees and combined them as a strict consensus, to give a conservative estimate of phylogeny showing only nodes that appeared among all the most parsimonious trees.

In MRP supertrees, as in other parsimony analyses, loss of resolution can occur due to the presence of 'floating' species (Wilkinson, 1995), species for which so little information on their phylogenetic associations exists that they can be grouped equally parsimoniously with numerous other species. Such species were identified using the program PerlEq (Jeffery & Wilkinson, 2003) to apply safe taxonomic reduction (Wilkinson, 1995), a strategy for reducing the number of most parsimonious trees by eliminating species with non-unique combinations of character states. These species were removed from the matrix, which was then re-analysed to reveal the hidden resolution.

Support measures

To assess the level of support for supertree clades and for entire supertrees, we used the *QS* measures of Bininda-Emonds (2003). These measures categorize the support for supertree clades into: (1) hard support, where the clade is specified exactly by at least 1 source tree; (2) hard conflict, where the clade is contradicted by every source tree; (3) soft support, where the clade is uncontradicted among the set of source trees; (4) soft conflict, where the clade is contradicted by some, but not all the source trees. The *QS* index for a supertree clade varies between -1 (where all source trees conflict with the clade) and 1 (where all source trees support the clade directly), and the *QS* index for an entire supertree is the average of all clades in the tree. Because *QS* samples at the level of source trees, the measures are not affected by the inherent non-independence of the MRP coding method, as are other support measures such as the bootstrap and Bremer support (Bininda-Emonds, 2003). The *QS* indices correlate broadly with bootstrap values, although they are more informative (Bininda-Emonds, 2003).

Weighting schemes

The decision about whether or not to apply differential weighting to pseudocharacters before constructing a supertree has been much debated and discussed in previous supertree papers (Purvis, 1995; Bininda-Emonds, Gittleman *et al*., 1999; Jones *et al*., 2002; Pisani *et al*., 2002; Grenyer & Purvis, 2003; Stoner *et al*., 2003). Source trees vary widely in the data used and the methods employed to estimate phylogeny, and some types of data and analysis are considered more reliable indicators of phylogeny than others. Comparisons of supertrees based on weighted and unweighted characters, however, have found that weighting has only minor effects on topology (Bininda-Emonds, Gittleman *et al*., 1999; Jones *et al*., 2002; Grenyer & Purvis, 2003). Therefore, the supertree presented here is based on unweighted characters. Nevertheless, we were interested in investigating the influence of different types of source trees. To investigate the influence of the increasing use of larger datasets, faster computers and more efficient search algorithms in recent years, the supertree analysis was repeated for trees published before the median source tree date of 1995 ('old' trees) and for trees published from 1995 to February 2003 ('new' trees). The analysis was also repeated under 2 differential weighting schemes. First, pseudocharacters were weighted according to method: trees built using algorithmic methods of tree reconstruction (distance methods, parsimony, maximum likelihood and Bayesian methods) were given 4 times the weight of trees constructed by informal, non-algorithmic procedures, following Purvis (1995). Second, pseudocharacters were weighted according to data quantity: trees based on 1–10, 11–50, and > 50 morphological characters, or on 1–100, 101–500, and > 500 base pairs, were given weights of 1, 2 and 4, respectively. Trees based on DNA hybridization and other distance-based molecular methods were given a weight of 4. No attempt was made to weight pseudocharacters by the level of node support because many trees, particularly those > 10 years old or based on morphological characters, did not include support measures. We emphasize that our weighting factors are arbitrary – we were interested in comparisons of weighted *vs* non-weighted analyses, rather than effects of the weighting factors themselves.

RESULTS AND DISCUSSION

Source trees

A total of 158 source trees from 107 published studies was suitable for use in the supertree analysis under the protocol of Bininda-Emonds, Jones, Price, Cardillo *et al*. (in press). The source trees were based on a wide range of data types, including molecular sequences, DNA hybridization, karyotypes, and immunological, morphological and behavioural data. There has been a rapid increase in work on marsupial systematics in recent years: > 80% of the studies from which source trees were taken were published in 1990 or later, and the median publication date of studies was 1995. In particular, the number of studies using molecular data increased sharply after 1990, while the number of studies using morphological data has remained low since 1980 (Fig. 1).

Supertrees: resolution and support

Five supertrees were produced:

(1) *unweighted tree*: pseudocharacters weighted equally;

(2) *method tree*: pseudocharacters weighted by phylogenetic construction method;

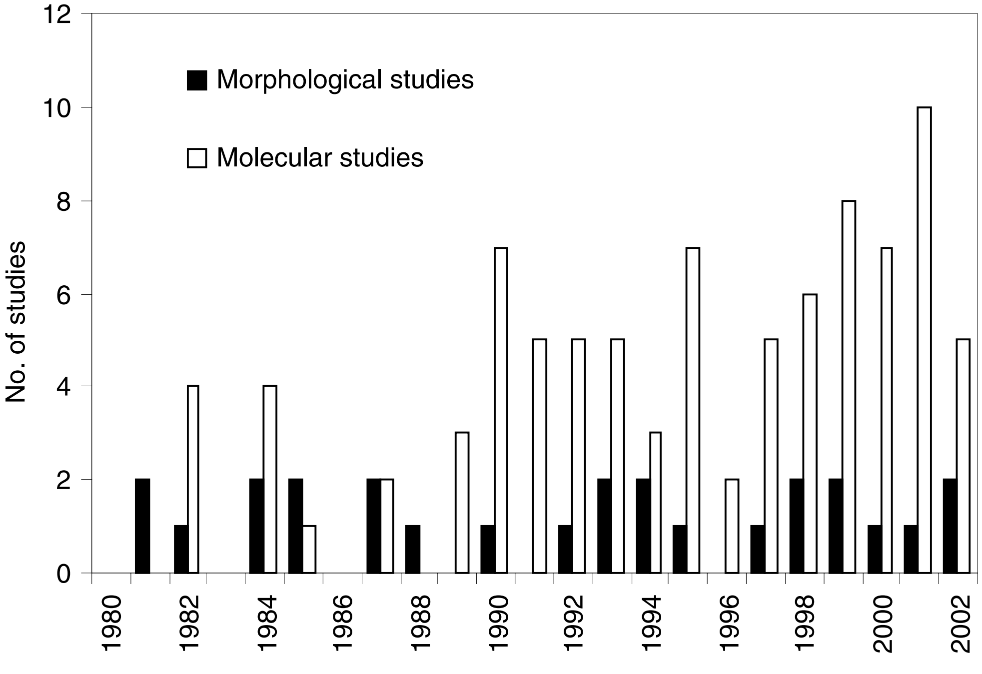

Fig. 1. Number of studies per year since 1980 contributing source trees included in the marsupial supertree.

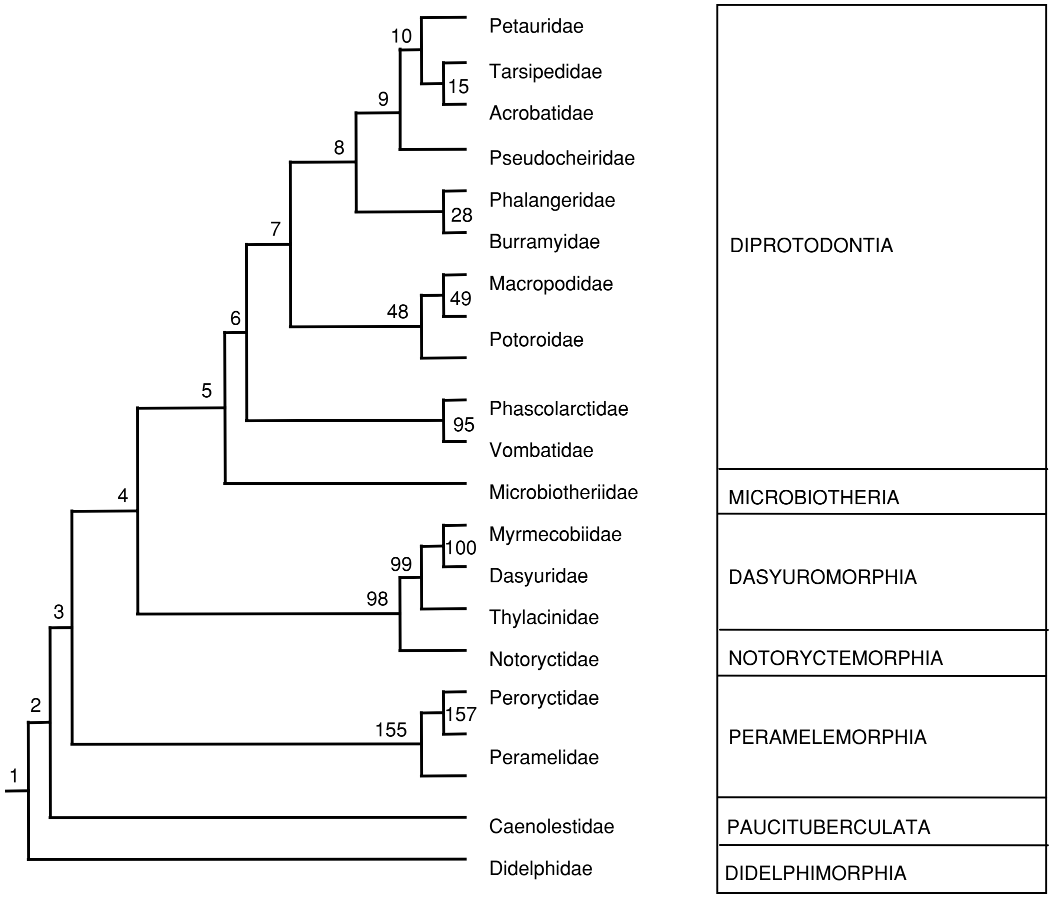

Fig. 2. Unweighted supertree relationships among the families and orders of marsupials recognized by Wilson & Reeder (1993). Note that Potoroidae and Peramelidae are paraphyletic. Branch lengths are arbitrary. Nodes are numbered sequentially.

(3) *data tree*: pseudocharacters weighted by data quantity;
(4) *old tree*: studies published before 1995;
(5) *new tree*: studies published in 1995 or later.

Using PerlEq to implement safe taxonomic reduction, five floating species which contributed to substantial loss of resolution were identified and removed: *Pseudocheirus schlegeli, Sminthopsis fuliginosus, Phalanger rothschildi, Thylamys velutinus* and *Perameles eremiana*. Removal of these species improved the resolution of the trees considerably. A strict consensus of the 10 000 most parsimonious trees found with all pseudocharacters weighted equally is presented in Figs 2 & 4–10. Family-level topologies of the four variant supertrees are shown in Fig. 3. All supertrees in Nexus file format, the MRP data matrices, and an EndNote file of the source trees used are available from the first author. The unweighted supertree and its MRP data matrix have been deposited on TreeBASE (www.treebase.org).

Table 1. Summary statistics for the five marsupial supertrees

Tree	No. of source trees	No. of pseudo-characters	No. of clades	% resolution	*QS* index
Unweighted	158	1775	196	73.7	– 0.09
Method	158	1775	190	71.2	– 0.088
Data	158	1775	204	76.4	– 0.089
Old	76	691	127	47.6	– 0.098
New	83	1151	132	49.4	– 0.093

Summary statistics for each of the five supertrees are given in Table 1. None of the supertrees contain any unsupported ‘novel clades’ (clades which are contradicted by all source trees; Bininda-Emonds & Bryant 1998). Resolution of the unweighted tree (73.7%) compares well with other published species-level mammalian supertrees: 78.1% for carnivores, 79.2% for primates, 46.4% for bats, and 69.9% for insectivores. Resolution is slightly lower for the method tree (71.2%), but higher for the data tree (76.4%), implying greater agreement among trees produced from larger datasets. On the other hand, both old and new trees are considerably less well-resolved (47.6% and 49.4%, respectively), most probably reflecting the smaller number of source trees (or more accurately, the smaller number of nodes) contributing to each.

Resolution also varies among taxa. Although this is partly the result of variation in the degree of conflict among source trees (e.g. relationships within the wombat + koala clade (Vombatidae + Phascolarctidae)

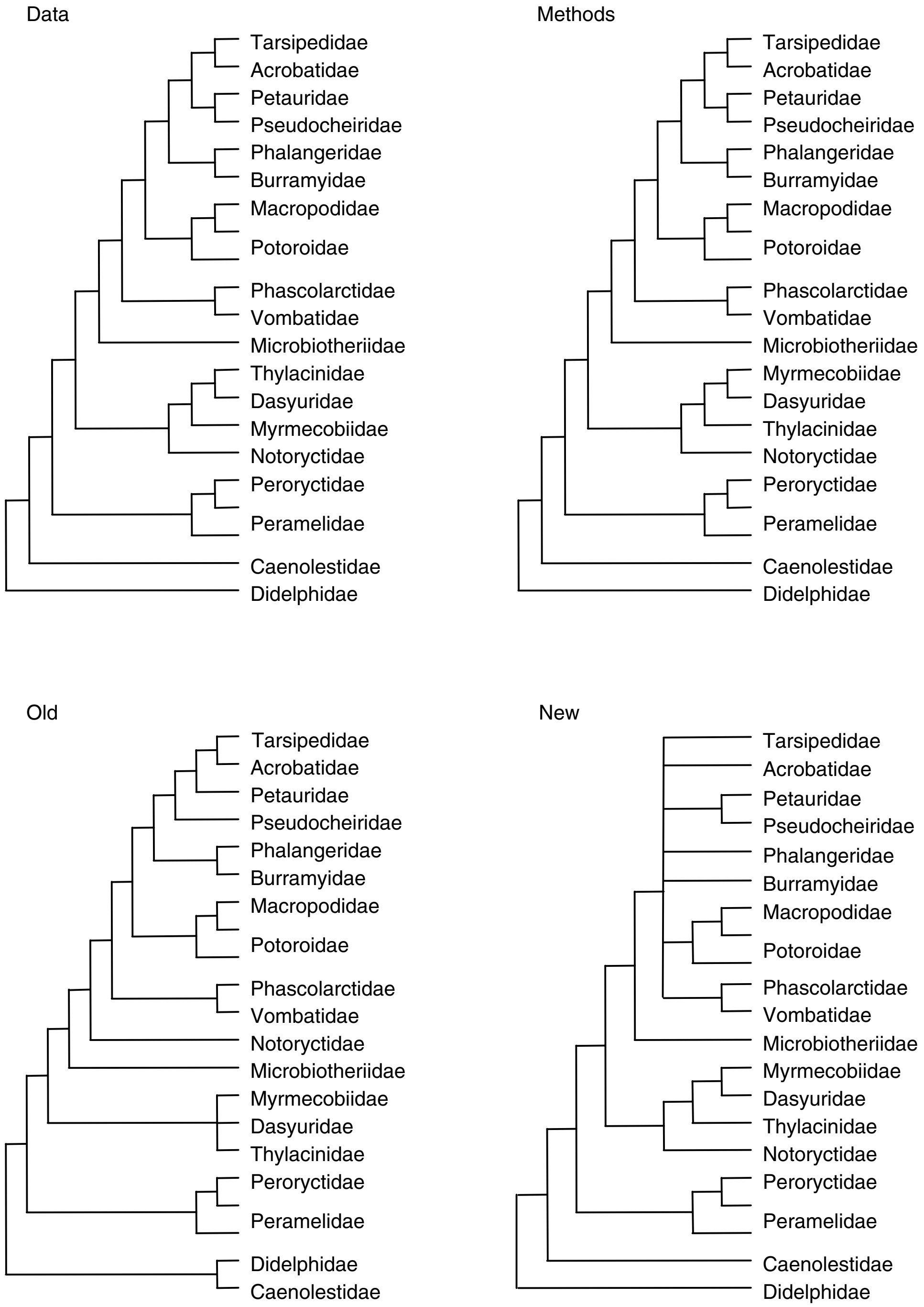

Fig. 3. Family-level topologies for the marsupial supertrees weighted by method and data quantity, and for 'old' (source trees pre-1995) and 'new' (source trees 1995–2003) supertrees.

are uncontroversial), it is also the result of variation in the amount of phylogenetic information available. This is made clear in Table 2, which shows the per cent resolution in the unweighted tree, together with the mean number of pseudocharacters in the matrix, the number of source trees and the *QS* index, for each of the marsupial families. The most poorly-resolved of the families (47.5%) is the Didelphidae. This reflects a relative lack of systematic effort: there are an average of 133.9 pseudocharacters per species for the didelphids, compared to an average of 243 across all marsupial species. Although relationships among the didelphid genera are fully resolved, there is a near-complete lack of resolution within each of the three largest genera (*Monodelphis*, *Marmosa* and *Marmosops*): mean numbers of pseudocharacters per species for these genera are 117.2, 102.1 and 105.1, respectively. In *Monodelphis*, for example, only one source tree (Kirsch *et al.*, 1997) resolves relationships among more than two species, and because this tree does not include all *Monodelphis* species, these relationships are not recovered by the supertree. In contrast, the Dasyuridae, with the same number of species as the didelphids,

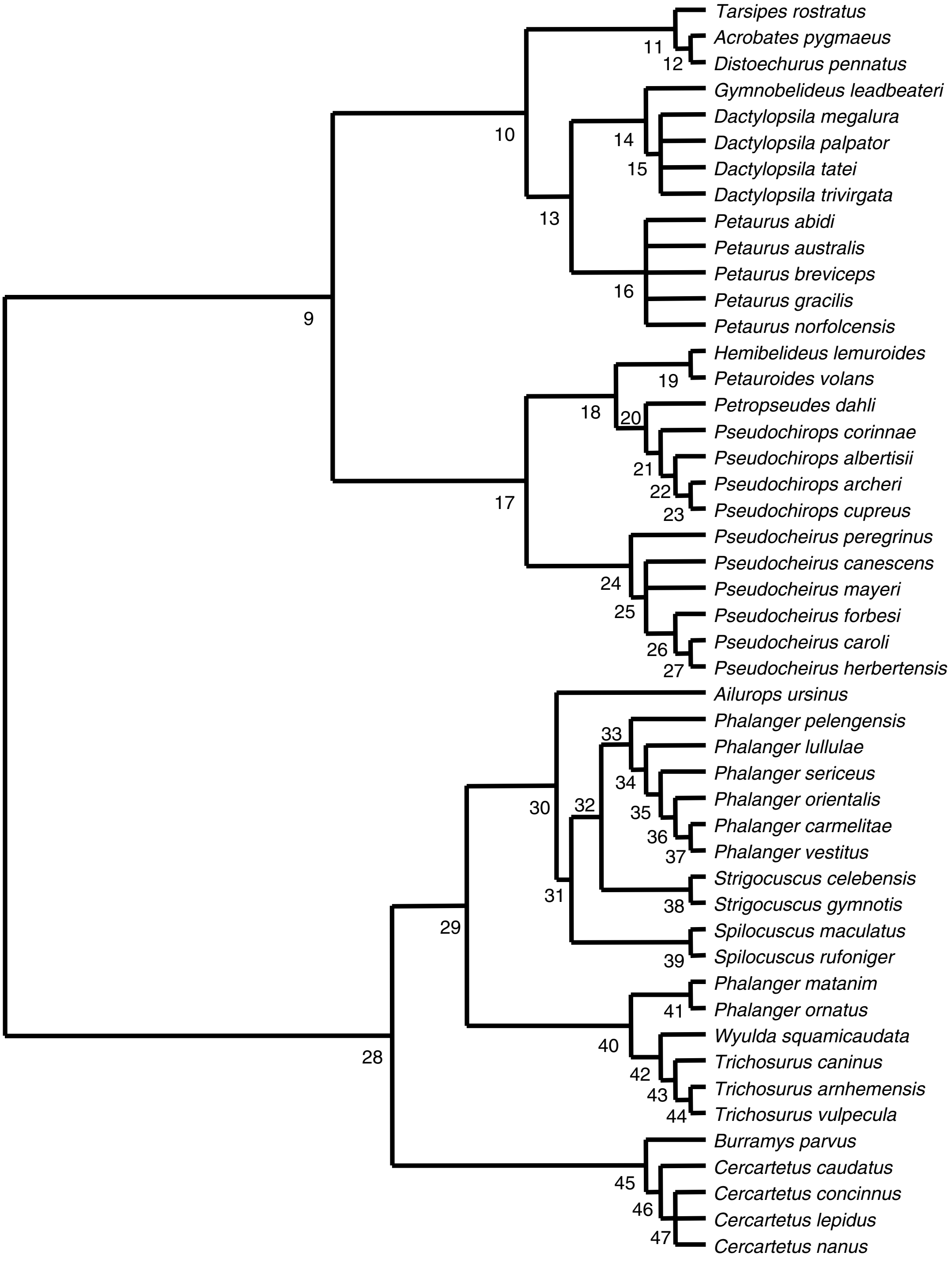

Fig. 4. Unweighted supertree relationships for the possum families Pseudocheiridae, Petauridae, Acrobatidae, Tarsipedidae, Phalangeridae and Burramyidae. Two species (*Pseudocheirus schlegeli* and *Phalanger rothschildi*) have been omitted from this part of the supertree under safe taxonomic reduction.

have 428.3 pseudocharacters per species, and are 85.7% resolved.

Values for the support measure *QS* varied little among the five supertrees (Table 1). Support was slightly higher for the two weighted trees, and slightly lower for both old and new trees, although there is not yet a method available for significance testing of differences in *QS* values. The negative *QS* values indicate that, overall, there were more mismatches than matches between source trees and supertree clades, with 67.9% of clades showing a hard mismatch (i.e. contradicted by at least one source tree), and 99.5% showing either a soft or hard mismatch. This should not be interpreted as poor overall support for the supertrees, as a large number of non-overlapping source trees will increase the probability of conflict (Bininda-Emonds & Sanderson, 2001; Bininda-Emonds,

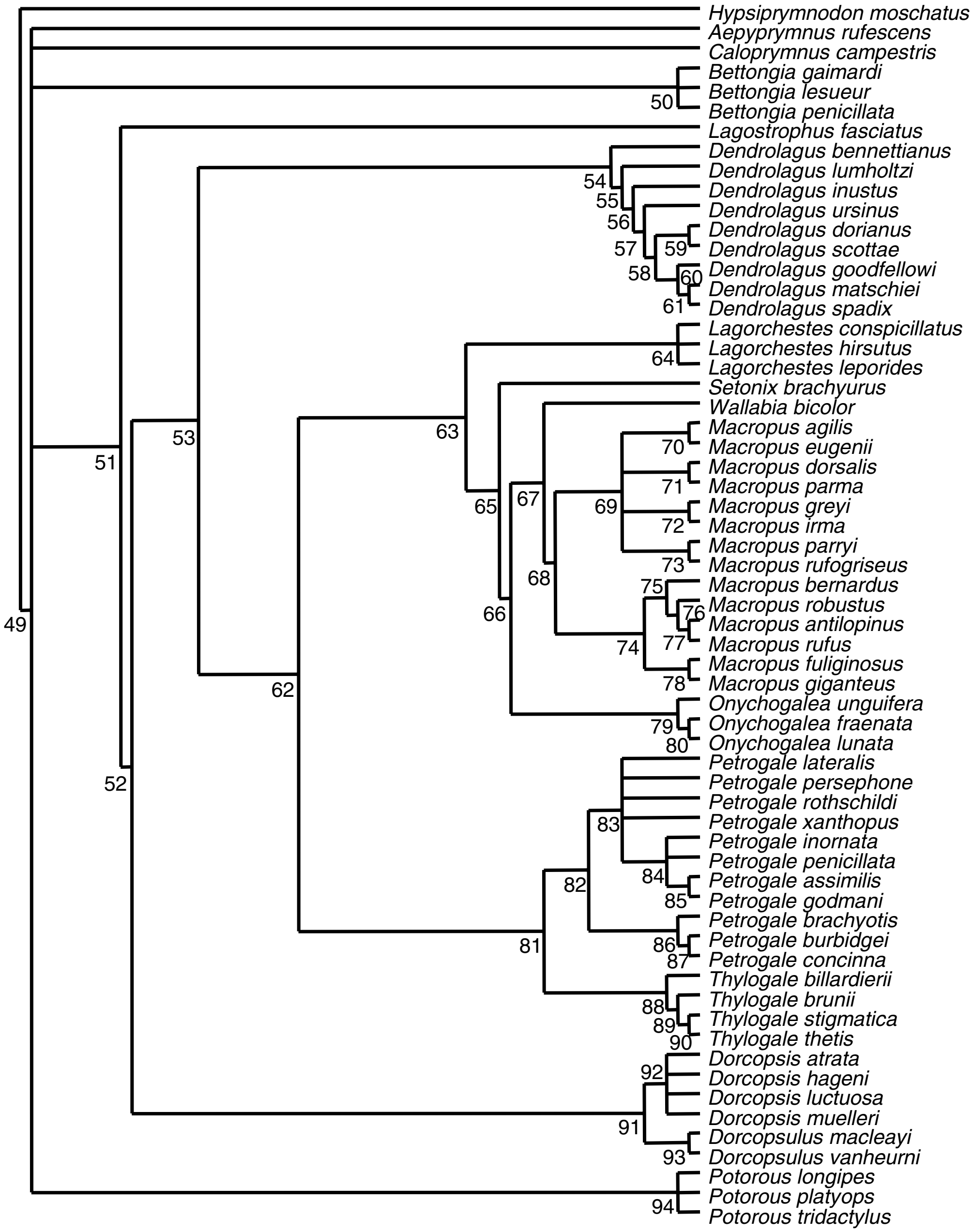

Fig. 5. Unweighted supertree relationships for the families Macropodidae and Potoroidae.

2003). Simulated supertrees had *QS* values between zero and -0.1 where source trees were highly overlapping, and around -0.3 where there was little overlap (Bininda-Emonds, 2003). In this context, values of around -0.09 for the marsupial supertrees, for which there were a large number of source trees with relatively little overlap, seem to indicate a good overall level of support. This is not very different from the carnivore supertree (Bininda-Emonds, Gittleman *et al.*, 1999), for which *QS* was -0.029, and 74.7% of clades showed a hard mismatch, while 95.5% showed either a soft or hard mismatch. All except the smallest of the separate supertrees making up the overall carnivore supertree had negative *QS* values (Bininda-Emonds, 2003).

Effects of differential weighting

Differences in the family-level topology of the five supertrees are shown in Fig. 3. Table 3 shows topological distances among all pairs of trees using the partition metric (Robinson & Foulds, 1981), which reveals the number of clades present in either tree in a pair, but not both. Weighting pseudocharacters, either by method or by data quantity, had only minor effects on the higher-level topology of the supertrees: distances from the unweighted tree are 14.3% and 7.9%, respectively (Table 3). In the unweighted tree, the possum family Pseudocheiridae is the sister to a clade formed by the families Petauridae, Acrobatidae and Tarsipedidae, but in both the methods

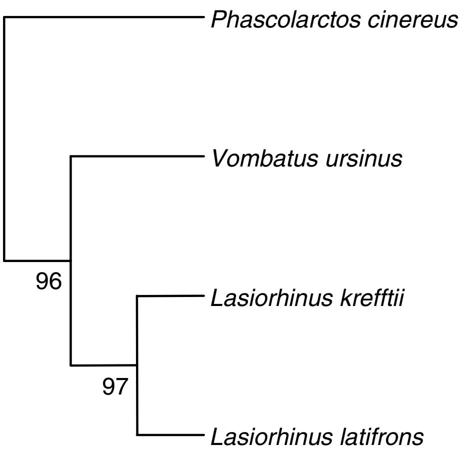

Fig. 6. Unweighted supertree relationships for the families Phascolarctidae and Vombatidae.

and data trees, the Petauridae and Pseudocheiridae are grouped as sister clades, supporting Aplin & Archer's (1987) superfamily Petauroidea. Additionally, the data tree groups *Thylacinus* (Thylacinidae) with Dasyuridae to the exclusion of *Myrmecobius* (Myrmecobiidae), whereas unweighted and methods trees group *Myrmecobius* with Dasyuridae.

There were, however, important differences in topology between the old and new trees, including the placement of the marsupial root and the position of *Notoryctes* (discussed in more detail below). In general, the topology of the new tree more closely resembled that of the unweighted tree than did the old tree (28.3% and 40.6% difference, respectively). This can be explained by the fact that newer trees tend to be larger: although the number of source trees contributing to the old and new supertrees was similar (76 and 83, respectively), the old source trees contributed only about half the number of pseudocharacters as the new source trees (691 and 1151, respectively). Hence, the newer source trees had a greater influence in the overall MRP analysis. However, any temptation to present the new tree as a more representative and up-to-date summary of marsupial systematic understanding is countered by the low resolution. The older source trees are needed to improve taxonomic representation and supertree resolution, although they clearly do not overwhelm the topology of the supertree.

Marsupial systematics

Although the taxonomic rank of major marsupial clades has been re-assessed periodically over the past few decades, there is little debate over the monophyly of the seven orders first proposed by Aplin & Archer (1987), and which are currently widely accepted. The monophyly of the families recognized by Wilson & Reeder (1993), the classification followed in this study, is also accepted widely, although there remains some controversy. The unweighted supertree supports monophyly of all Wilson & Reeder families with the exceptions of Peramelidae (Fig. 8) and Potoroidae (Fig. 5). The division of bandicoots (order Peramelemorphia) into two families, Peramelidae and Peroryctidae, was suggested by Groves & Flannery (1990) and is followed by Wilson & Reeder (1993), but other authors (e.g. Springer, Kirsch *et al.*, 1997) have continued to support the division of bandicoots into Peramelidae and Thylacomyidae, as suggested by Kirsch (1977). The supertree reflects this uncertainty, indicating that Peramelidae is paraphyletic with respect

Table 2. Summary statistics for each of the families of marsupials within the unweighted supertree

Family	Species	Pseudocharacters per species	Source trees	% resolution	*QS*
Microbiotheriidae	1	437			
Pseudocheiridae	13	221.46	39	100	– 0.13
Petauridae	10	192.2	28	50	– 0.095
Tarsipedidae	1	281			
Acrobatidae	2	264	24		– 0.05
Phalangeridae	18	222.83	56	100	– 0.187
Burramyidae	5	199.8	22	80	– 0.073
Potoroidae	9	153.44		[a]	[a]
Macropodidae	54	177.59	53	83.3	– 0.18
Phascolarctidae	1	594			
Vombatidae	3	258	21	100	– 0.066
Notoryctidae	2	332	22		– 0.063
Thylacinidae	1	364			
Myrmecobiidae	1	425			
Dasyuridae	63	428.32	79	85.7	– 0.266
Peramelidae	10	232.7		[a]	[a]
Peroryctidae	11	157.45	19	30	– 0.07
Caenolestidae	5	187.2	19	50	– 0.06
Didelphidae	63	133.92	35	47.5	– 0.127

[a] Paraphyletic families.

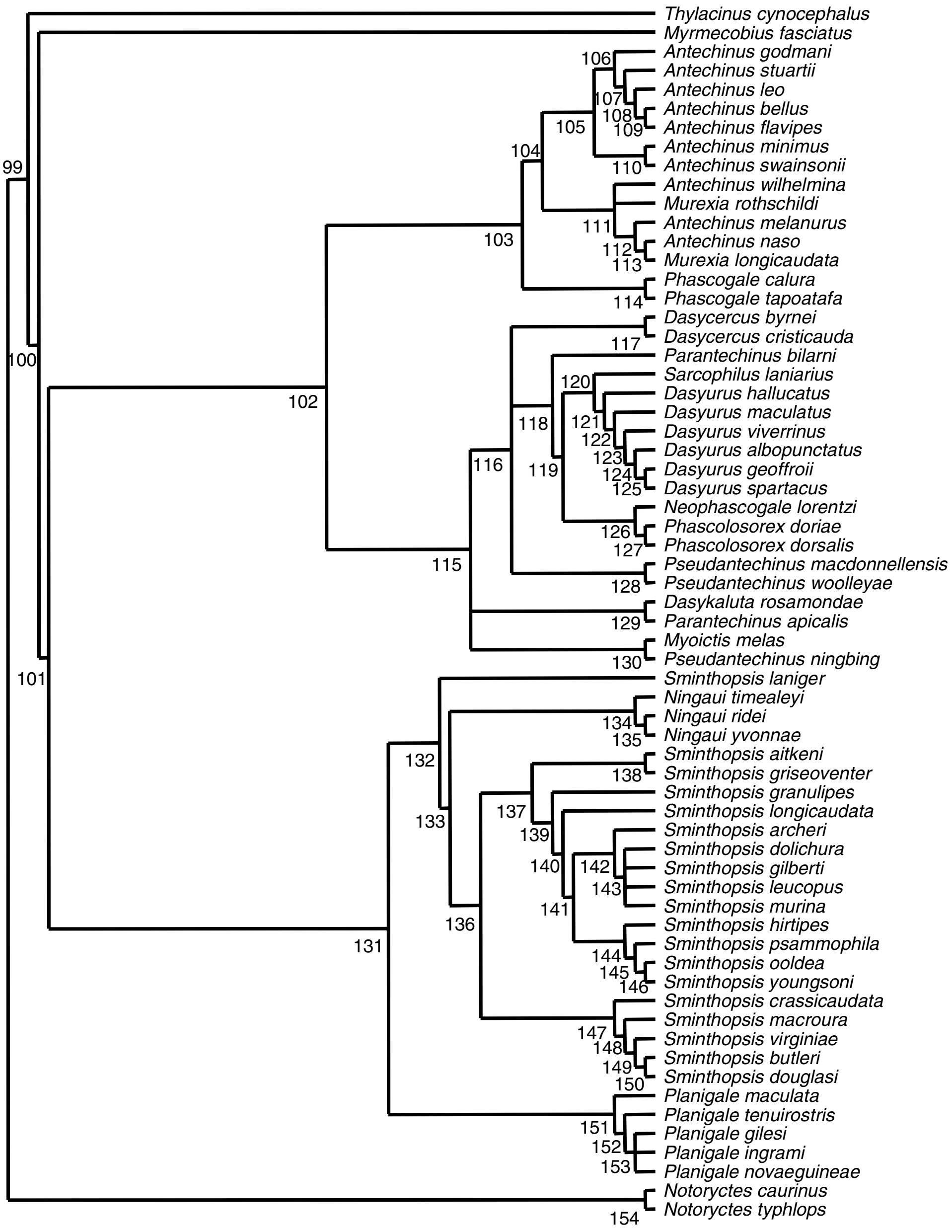

Fig. 7. Unweighted supertree relationships for the families Thylacinidae, Myrmecobiidae, Dasyuridae and Notoryctidae. One species (*Sminthopsis fuliginosus*) has been omitted from this part of the supertree under safe taxonomic reduction.

to both a monophyletic Peroryctidae and a monophyletic Thylacomyidae. The uncertainty is also reflected in the low *QS* value of -0.158 (compared to the average value of -0.09 of all clades in the unweighted supertree) for the clade containing the Peroryctidae and several of the Peramelidae species (Appendix 2). The supertree also indicates a paraphyletic Potoroidae with respect to a monophyletic Macropodidae. Again, the *QS* value of the clade containing Macropodidae and several of the Potoroidae is relatively low (-0.177), indicating disagreement among source trees.

Table 3. Percentage differences in topology between all pairwise combinations of the five marsupial supertrees, based on the partition metric

	Unweighted	Data	Method	New
Unweighted				
Data	7.9			
Method	14.3	18.9		
New	28.3	32.8	27.2	
Old	40.6	42.1	42.5	39.4

All supertrees support the monophyly of Australidelphia, the clade formed by the grouping of the South American microbiotheriid *Dromiciops gliroides* with the Australasian marsupial taxa. This grouping was first proposed by Szalay (1982) based on shared possession of a continuous lower ankle joint pattern, and has subsequently been supported by molecular data, including

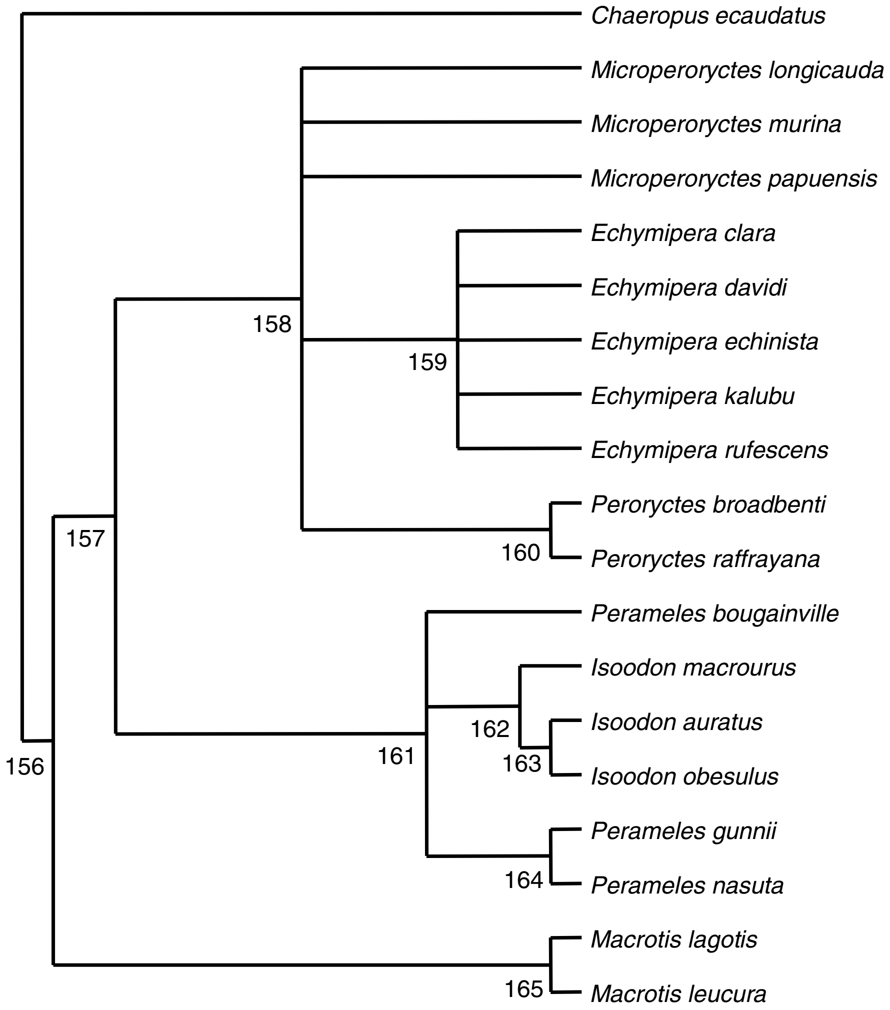

Fig. 8. Unweighted supertree relationships for the families Peramelidae and Peroryctidae. One species (*Perameles eremiana*) has been omitted from this part of the supertree under safe taxonomic reduction.

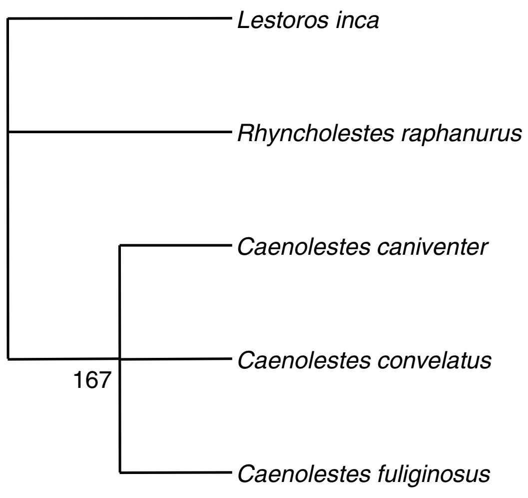

Fig. 9. Unweighted supertree relationships for the family Caenolestidae.

DNA hybridization (e.g. Kirsch, Dickerman *et al*., 1991; Kirsch, Lapointe *et al*., 1997), and both mitochondrial (e.g. Phillips *et al*., 2001; Springer, Westerman & Kirsch, 1994) and nuclear (e.g. Retief *et al*., 1995; Amrine-Madsen *et al*., 2003) genes. Although Australidelphian monophyly has been disputed by several studies (e.g. Reig, Kirsch & Marshall, 1987; Hershkovitz, 1992) and was equivocal in others (e.g. Westerman & Edwards, 1991; Springer, Kirsch *et al*., 1997), the majority of recent studies support it. The general support for the Australidelphia since Szalay (1982) is reflected in all five supertrees, regardless of weighting or age.

Monophyly of Ameridelphia (the clade formed by the American orders Didelphimorphia and Paucituberculata), however, is supported only by the old supertree (Fig. 3). All other supertrees indicate that the marsupial root lies between the Didelphimorphia and other marsupials, with the Paucituberculata as the sister clade to Australidelphia. Although the old supertree indicates a monophyletic Ameridelphia, this finding derives from only six studies published before 1995 that contain information relevant to the grouping of the two American orders. In general,

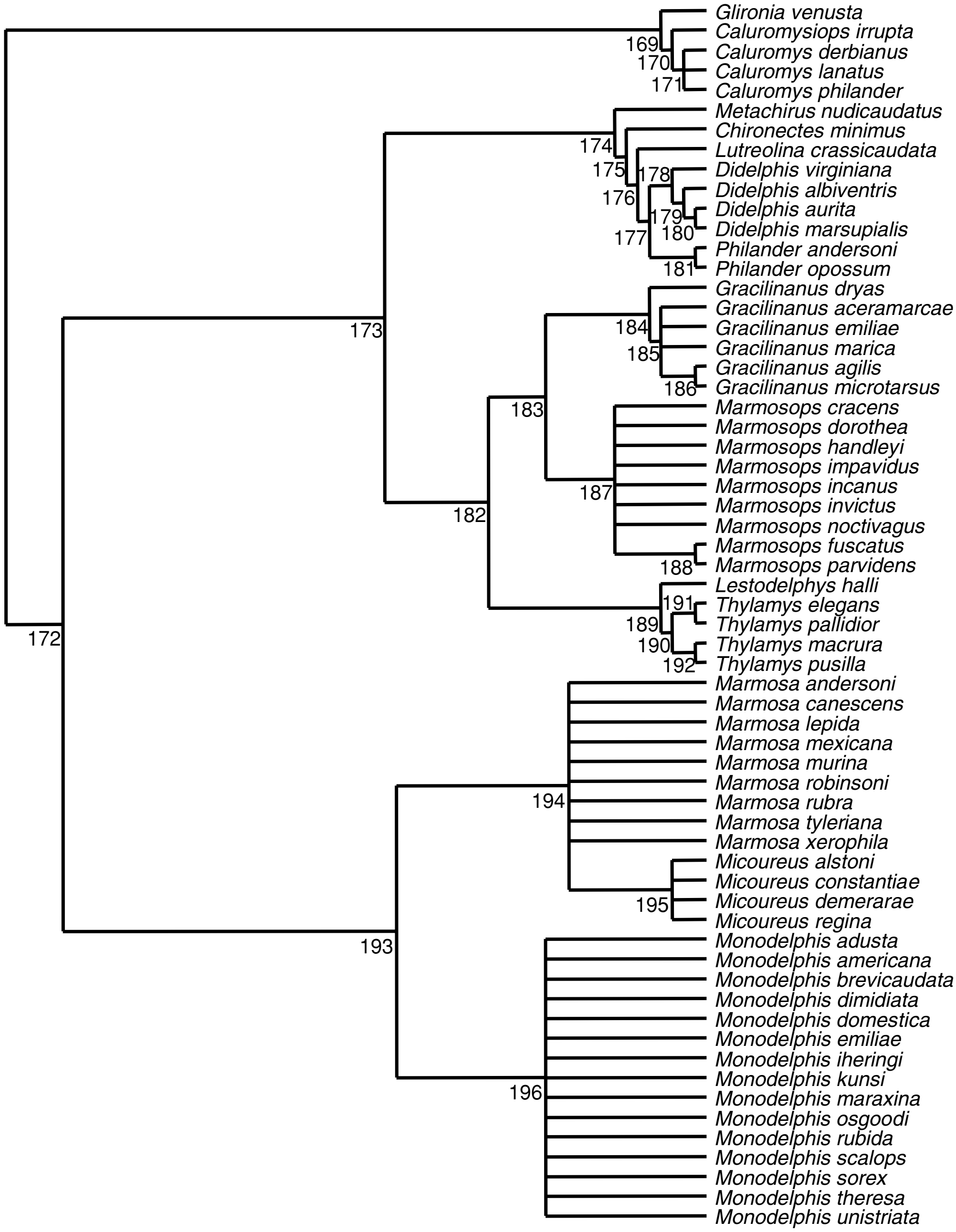

Fig. 10. Unweighted supertree relationships for the family Didelphidae. One species (*Thylamys velutinus*) has been omitted from this part of the supertree under safe taxonomic reduction.

the grouping of Didelphimorphia and Paucituberculata is not supported strongly by morphological studies as most of their shared characters are considered to be retained ancestral traits (Luckett, 1994). However, two of the pre-1995 studies support Ameridelphian monophyly (Marshall, Case & Woodburne, 1990; Luckett, 1994) based on analysis of a wide range of morphological characters. Most other pre-1995 studies fail to resolve the monophyly of Ameridelphia and only one (Sharman, 1982) does not support it. Since our supertree was completed, the placement of the marsupial root between Didelphimorphia and other marsupials has been corroborated by a new study based on maximum likelihood and Bayesian analyses of a concatenation of five nuclear genes (Amrine-Madsen *et al*., 2003).

Since Szalay (1982) first proposed grouping *Dromiciops gliroides* with the Australasian taxa, the position of *Dromiciops* within the Australidelphia has been a source of debate, and one with important implications for the biogeographic history of marsupials (Clemens, Richardson & Baverstock, 1989). The supertrees indicate *Dromiciops* as the sister clade to the Diprotodontia, with the exception of the old tree which indicates *Dromiciops* as the sister to the clade formed by Diprotodontia and Notoryctemorphia. Again, however, only a small number of source trees published before 1995 have information relevant to this issue, and all of them either place the Notoryctemorphia between *Dromiciops* and Diprotodontia (e.g. Archer, 1984; Marshall *et al*., 1990; Sharman, 1982; Szalay, 1982) or fail to resolve the grouping (e.g. Luckett, 1994). Since 1995, however, the grouping of *Dromiciops* with Diprotodontia has been the most commonly supported, mostly by DNA hybridization studies (e.g. Kirsch, Lapointe *et al*., 1997; Lapointe & Kirsch, 2001), although there is also some morphological evidence (Springer, Kirsch *et al*., 1997). However, a variety of other positions for *Dromiciops* are suggested by other data types. For example, Amrine-Madsen *et al*. (2003), using a concatenation of nuclear genes, place *Dromiciops* at the base of Australidelphia; Springer, Westerman *et al*. (1998), using mitochondrial and nuclear genes, place *Dromiciops* as sister to a clade formed of Diprotodontia, Dasyuromorphia and Notoryctemorphia; and Palma & Spotorno (1999), using 12S rDNA sequences, place *Dromiciops* in a clade with Notoryctemorphia and Dasyuromorphia.

All supertrees place the bandicoots (Peramelemorphia) at the base of the Australidelphia. The position of bandicoots has been another of the major uncertainties in the higher-level relationships of marsupials. The hitherto largest phylogenies of marsupials, the DNA hybridization study of Kirsch, Lapointe *et al*. (1997) and the supertree of Lapointe & Kirsch (2001), placed bandicoots between the Paucituberculata and all other marsupials, but such a grouping has rarely been supported by other studies. Some studies, notably those based on mitochondrial genes, have placed bandicoots with American taxa (e.g. Springer *et al*., 1994; Palma & Spotorno 1999) although Phillips *et al*. (2001) put them in Australidelphia using mitochondrial sequences. Studies based on nuclear genes usually include the bandicoots within the Australidelphia, but in varying positions: for example, Retief *et al*. (1995) placed bandicoots at the base of the Australidelphia, while Amrine-Madsen *et al*. (2003) placed them as sister to a clade formed of Dasyuromorphia and Notoryctemorphia.

CONCLUSIONS

The marsupial supertree presented here continues in the tradition of such studies as Aplin & Archer (1987), Kirsch, Lapointe *et al*. (1997) and Springer, Kirsch *et al*. (1997) in combining and synthesizing the results of many smaller studies into a broader phylogeny. It represents the first virtually complete species-level phylogeny of extant marsupials built using modern, algorithmic supertree methods. We hope that it will encourage comparative studies of marsupial evolution and ecology by providing a framework for phylogenetically explicit analyses across the whole marsupial clade, as well as stimulating further debate about marsupial relationships. The supertree also highlights the great discrepancy in systematic effort between the Australasian and American marsupial taxa: the American genera *Monodelphis*, *Marmosa* and *Marmosops* are particularly lacking in systematic knowledge. We hope that the supertree will inspire further systematic work on these clades.

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Appendix 1. Nodal support values for the unweighted supertree. Node numbers refer to Figs 2–9. Derivation of the *QS* index is described fully in Bininda-Emonds, Jones, Price, Cardillo *et al.* (in press)

				No. of source trees				
Node	Number of Species	Status	*QS* index	Hard match	Hard mismatch	Equivocal	Soft match	Soft mismatch
1	267	equivocal	– 0.5	0	0	0	0	158
2	205	softConflict	– 0.503	0	16	15	0	127
3	200	softConflict	– 0.5	0	14	14	0	130
4	180	softConflict	– 0.494	0	18	20	0	120
5	116	softConflict	– 0.37	0	17	58	0	83
6	115	softConflict	– 0.335	0	8	60	0	90
7	111	softConflict	– 0.345	0	11	60	0	87
8	48	softConflict	– 0.278	0	10	80	0	68
9	26	softConflict	– 0.165	0	6	112	0	40
10	13	softConflict	– 0.13	0	13	130	0	15
11	3	softConflict	– 0.089	0	6	134	1	17
12	2	softSupport	– 0.051	0	0	134	4	20
13	10	softConflict	– 0.095	0	2	130	0	26
14	5	softConflict	– 0.079	0	4	137	0	17
15	4	softSupport	– 0.051	0	0	140	1	17
16	5	softSupport	– 0.082	0	0	130	1	27
17	13	softConflict	– 0.13	0	2	119	0	37
18	7	softConflict	– 0.117	0	8	129	0	21
19	2	softSupport	0.022	0	0	137	14	7
20	5	softConflict	– 0.063	0	1	139	0	18
21	4	softConflict	– 0.063	0	2	138	1	17
22	3	softConflict	– 0.073	0	4	137	1	16
23	2	softConflict	– 0.019	0	4	134	11	9
24	6	softConflict	– 0.111	0	5	126	1	26
25	5	softConflict	– 0.035	0	1	144	2	11
26	3	softConflict	– 0.032	0	2	146	2	8
27	2	softConflict	– 0.022	0	1	146	3	8
28	22	softConflict	– 0.222	0	12	100	0	46
29	17	softConflict	– 0.187	0	3	102	0	53
30	11	softConflict	– 0.133	0	7	123	0	28
31	10	softConflict	– 0.133	0	7	123	0	28
32	8	softConflict	– 0.133	0	7	123	0	28
33	6	softConflict	– 0.127	0	7	123	1	27
34	5	softConflict	– 0.114	0	5	125	1	27
35	4	softConflict	– 0.114	0	6	126	1	25
36	3	softConflict	– 0.092	0	5	130	2	21
37	2	softConflict	– 0.016	0	4	143	7	4
38	2	softConflict	– 0.051	0	2	142	1	13
39	2	softSupport	0.041	0	0	143	14	1
40	6	softConflict	– 0.142	0	2	115	0	41
41	2	softSupport	– 0.016	0	0	151	1	6
42	4	equivocal	– 0.111	0	0	123	0	35
43	3	softSupport	– 0.108	0	0	122	1	35
44	2	softSupport	– 0.101	0	0	116	5	37
45	5	softConflict	– 0.073	0	1	136	0	21
46	4	softSupport	– 0.044	0	0	142	1	15
47	3	softSupport	– 0.009	0	0	149	3	6
48	63	equivocal	– 0.168	0	0	105	0	53

Appendix 1. Continued

				No. of source trees				
Node	Number of Species	Status	*QS* index	Hard match	Hard mismatch	Equivocal	Soft match	Soft mismatch
49	62	softConflict	– 0.177	0	3	105	0	50
50	3	softSupport	– 0.022	0	0	149	1	8
51	54	softConflict	– 0.18	0	4	105	0	49
52	53	softConflict	– 0.184	0	5	105	0	48
53	47	softConflict	– 0.19	0	7	105	0	46
54	9	softSupport	– 0.06	0	0	137	1	20
55	8	softConflict	– 0.063	0	1	137	1	19
56	7	softConflict	– 0.06	0	1	138	1	18
57	6	softConflict	– 0.054	0	1	140	1	16
58	5	softConflict	– 0.041	0	1	144	1	12
59	2	softSupport	– 0.016	0	0	147	3	8
60	3	softSupport	– 0.022	0	0	149	1	8
61	2	softSupport	– 0.006	0	0	150	3	5
62	38	softConflict	– 0.177	0	9	111	0	38
63	23	softConflict	– 0.171	0	11	115	0	32
64	4	softConflict	– 0.022	0	1	148	2	7
65	19	softConflict	– 0.165	0	9	115	0	34
66	18	softConflict	– 0.158	0	8	116	0	34
67	15	softConflict	– 0.146	0	4	116	0	38
68	14	softConflict	– 0.155	0	8	115	1	34
69	8	softConflict	– 0.079	0	4	133	2	19
70	2	softConflict	– 0.022	0	1	136	8	13
71	2	softSupport	0.009	0	0	153	4	1
72	2	softSupport	0	0	0	152	3	3
73	2	softSupport	0.013	0	0	146	8	4
74	6	softConflict	– 0.123	0	5	122	1	30
75	4	softSupport	– 0.082	0	0	130	1	27
76	3	softSupport	– 0.073	0	0	131	2	25
77	2	softSupport	– 0.054	0	0	133	4	21
78	2	softSupport	– 0.038	0	0	136	5	17
79	3	softSupport	– 0.022	0	0	149	1	8
80	2	softSupport	0	0	0	154	2	2
81	15	softConflict	– 0.066	0	5	142	0	11
82	11	softConflict	– 0.047	0	1	142	1	14
83	8	softSupport	– 0.041	0	0	143	1	14
84	4	softSupport	– 0.013	0	0	152	1	5
85	2	softSupport	0.003	0	0	153	3	2
86	3	softSupport	– 0.006	0	0	154	1	3
87	2	softSupport	– 0.003	0	0	153	2	3
88	4	softSupport	– 0.028	0	0	147	1	10
89	3	softSupport	– 0.028	0	0	147	1	10
90	2	softSupport	– 0.009	0	0	147	4	7
91	6	softConflict	– 0.038	0	1	147	0	10
92	4	softSupport	– 0.003	0	0	153	2	3
93	2	softSupport	– 0.028	0	0	145	2	11
94	3	softSupport	– 0.038	0	0	144	1	13
95	4	softConflict	– 0.089	0	1	131	0	26
96	3	equivocal	– 0.066	0	0	137	0	21
97	2	softSupport	– 0.022	0	0	149	1	8
98	64	softConflict	– 0.291	0	12	78	0	68
99	62	softConflict	– 0.259	0	3	79	0	76
100	61	softConflict	– 0.272	0	7	79	0	72
101	60	softConflict	– 0.266	0	5	79	0	74
102	33	softConflict	– 0.209	0	6	98	0	54
103	14	softConflict	– 0.142	0	3	116	0	39
104	12	softConflict	– 0.146	0	9	121	0	28
105	7	softConflict	– 0.073	0	2	135	1	20
106	5	softConflict	– 0.082	0	5	135	1	17
107	4	softConflict	– 0.095	0	7	133	1	17
108	3	softConflict	– 0.044	0	3	143	2	10
109	2	softConflict	– 0.019	0	2	140	7	9
110	2	softSupport	– 0.019	0	0	134	9	15
111	5	softConflict	– 0.114	0	3	125	0	30

Appendix 1. Continued

Node	Number of Species	Status	*QS* index	No. of source trees				
				Hard match	Hard mismatch	Equivocal	Soft match	Soft mismatch
112	3	softConflict	– 0.07	0	4	134	3	17
113	2	softConflict	– 0.073	0	6	129	6	17
114	2	softSupport	– 0.066	0	0	119	9	30
115	19	softConflict	– 0.19	0	5	103	0	50
116	15	softConflict	– 0.225	0	17	104	0	37
117	2	softConflict	– 0.06	0	10	141	4	3
118	11	softConflict	– 0.206	0	12	105	0	41
119	10	softConflict	– 0.193	0	10	107	0	41
120	7	softConflict	– 0.155	0	5	114	0	39
121	6	softConflict	– 0.161	0	7	112	1	38
122	5	softConflict	– 0.13	0	6	121	1	30
123	4	softConflict	– 0.076	0	2	134	1	21
124	3	softConflict	– 0.025	0	2	150	1	5
125	2	softConflict	0.006	0	1	147	7	3
126	3	softConflict	– 0.066	0	3	140	0	15
127	2	softSupport	– 0.054	0	0	139	1	18
128	2	softConflict	– 0.038	0	5	141	5	7
129	2	softConflict	– 0.032	0	7	133	11	7
130	2	softConflict	– 0.025	0	2	146	3	7
131	27	softConflict	– 0.139	0	4	118	0	36
132	22	softConflict	– 0.142	0	6	119	0	33
133	21	softConflict	– 0.165	0	11	117	0	30
134	3	softConflict	– 0.022	0	1	146	3	8
135	2	softConflict	0.038	0	1	135	18	4
136	18	softConflict	– 0.171	0	14	116	1	27
137	13	softConflict	– 0.07	0	5	139	1	13
138	2	softSupport	0.038	0	0	146	12	0
139	11	softConflict	– 0.07	0	5	139	1	13
140	10	softConflict	– 0.076	0	6	138	1	13
141	9	softConflict	– 0.057	0	3	141	1	13
142	5	softConflict	– 0.038	0	1	143	2	12
143	4	softConflict	– 0.051	0	3	141	2	12
144	4	softConflict	– 0.044	0	6	148	1	3
145	3	softConflict	– 0.038	0	5	149	1	3
146	2	softConflict	– 0.009	0	4	143	8	3
147	5	softConflict	– 0.136	0	5	118	1	34
148	4	softConflict	– 0.063	0	1	137	1	19
149	3	softConflict	– 0.057	0	4	142	1	11
150	2	softSupport	– 0.028	0	0	145	2	11
151	5	softConflict	– 0.104	0	3	126	1	28
152	4	softConflict	– 0.076	0	1	133	1	23
153	3	softConflict	– 0.082	0	1	131	1	25
154	2	softSupport	– 0.063	0	0	136	1	21
155	20	softConflict	– 0.149	0	2	113	0	43
156	19	softConflict	– 0.155	0	3	112	0	43
157	17	softConflict	– 0.158	0	4	112	0	42
158	11	softConflict	– 0.07	0	3	139	0	16
159	5	softConflict	– 0.057	0	2	140	1	15
160	2	softSupport	– 0.025	0	0	148	1	9
161	6	equivocal	– 0.117	0	0	121	0	37
162	3	softSupport	– 0.073	0	0	131	2	25
163	2	softConflict	– 0.006	0	1	147	5	5
164	2	softSupport	– 0.032	0	0	136	6	16
165	2	softSupport	– 0.016	0	0	151	1	6
166	5	equivocal	– 0.06	0	0	139	0	19
167	3	softSupport	– 0.06	0	0	137	1	20
168	62	softConflict	– 0.127	0	5	123	0	30
169	5	softConflict	– 0.032	0	2	150	0	6
170	4	equivocal	– 0.025	0	0	150	0	8
171	3	softSupport	– 0.022	0	0	149	1	8
172	57	softConflict	– 0.13	0	6	123	0	29
173	29	softConflict	– 0.136	0	7	122	0	29
174	9	softConflict	– 0.092	0	2	131	0	25

Appendix 1. Continued

Node	Number of Species	Status	*QS* index	No. of source trees				
				Hard match	Hard mismatch	Equivocal	Soft match	Soft mismatch
175	8	softConflict	– 0.089	0	1	131	0	26
176	7	softConflict	– 0.089	0	1	131	0	26
177	6	softConflict	– 0.089	0	1	131	0	26
178	4	softConflict	– 0.082	0	1	131	1	25
179	3	softConflict	– 0.028	0	1	148	1	8
180	2	softSupport	– 0.016	0	0	147	3	8
181	2	softSupport	– 0.019	0	0	150	1	7
182	20	softConflict	– 0.054	0	3	144	0	11
183	15	softConflict	– 0.051	0	4	146	0	8
184	6	softSupport	– 0.013	0	0	148	3	7
185	5	softSupport	– 0.013	0	0	148	3	7
186	2	softSupport	– 0.006	0	0	148	4	6
187	9	softConflict	– 0.025	0	1	147	2	8
188	2	softSupport	0	0	0	152	3	3
189	5	softConflict	– 0.035	0	2	149	0	7
190	4	softConflict	– 0.016	0	2	149	3	4
191	2	softConflict	0.003	0	1	148	6	3
192	2	softConflict	– 0.003	0	3	148	6	1
193	28	softConflict	– 0.057	0	3	143	0	12
194	13	softConflict	– 0.032	0	1	149	0	8
195	4	softSupport	– 0.016	0	0	149	2	7
196	15	softSupport	– 0.038	0	0	142	2	14

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