Biol. Rev. (2002), **77**, pp. 223–259 © *Cambridge Philosophical Society*
DOI: 10.1017/S1464793101005899 *Printed in the United Kingdom*

A phylogenetic supertree of the bats (Mammalia: Chiroptera)

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(*Received* 28 *June* 2001; *revised* 21 *November* 2001; *accepted* 12 *December* 2001)

ABSTRACT

We present the first estimate of the phylogenetic relationships among all 916 extant and nine recently extinct species of bats (Mammalia: Chiroptera), a group that accounts for almost one-quarter of extant mammalian diversity. This phylogeny was derived by combining 105 estimates of bat phylogenetic relationships published since 1970 using the supertree construction technique of Matrix Representation with Parsimony (MRP). Despite the explosive growth in the number of phylogenetic studies of bats since 1990, phylogenetic relationships in the order have been studied non-randomly. For example, over one-third of all bat systematic studies to date have focused on relationships within Phyllostomidae, whereas relationships within clades such as Kerivoulinae and Murinae have never been studied using cladistic methods. Resolution in the supertree similarly differs among clades: overall resolution is poor (46.4% of a fully bifurcating solution) but reaches 100% in some groups (e.g. relationships within Mormoopidae). The supertree analysis does not support a recent proposal that Microchiroptera is paraphyletic with respect to Megachiroptera, as the majority of source topologies support microbat monophyly. Although it is not a substitute for comprehensive phylogenetic analyses of primary molecular and morphological data, the bat supertree provides a useful tool for future phylogenetic comparative and macroevolutionary studies. Additionally, it identifies clades that have been little studied, highlights groups within which relationships are controversial, and like all phylogenetic studies, provides preliminary hypotheses that can form starting points for future phylogenetic studies of bats.

Key words: bats, evolution, matrix representation, parsimony, phylogeny, supertree construction.

CONTENTS

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I. INTRODUCTION

The order Chiroptera includes almost one quarter of all known extant mammalian species diversity (916 species; Wilson & Reeder, 1993). Despite the importance of this radiation of mammals, their evolutionary relationships have remained poorly understood until fairly recently (see reviews in Simmons 1998, 2000). As a consequence, most comparative studies seeking to identify evolutionary patterns within Chiroptera have been carried out without reference to explicit phylogenetic frameworks. For example, studies of flight morphological adaptation (Norberg & Rayner, 1987) and constraints on reproductive traits (Kurta & Kunz, 1987; Barclay, 1994; Hayssen & Kunz, 1996) that have been influential in shaping subsequent ecological and physiological research on bats were completed without an explicit phylogenetic context.

The importance of accounting for the evolutionary history of a clade when conducting comparative analyses is well documented (Felsenstein, 1985; Brooks and McLennan 1991; Harvey & Pagel, 1991; Harvey, 2000). As recently as 1996, Hayssen and Kunz (1996, p. 478) suggested that phylogenetic comparative studies of bats were 'difficult or impossible' to carry out at that time because of a lack of understanding of bat phylogenetic relationships. More recently, there has been a substantial improvement in our understanding of bat phylogeny at both the higher and lower taxonomic levels (e.g. Bogdanowicz & Owen, 1998; Kirsch *et al*., 1998; Simmons & Geisler, 1998; Teeling *et al*., 2000; Van Den Bussche & Hoofer, 2001). However, as yet there is no single bat phylogeny that covers all extant species and was derived using a robust methodology. The few previous comparative studies within Chiroptera that have used a phylogenetic approach have estimated relationships only for the species under investigation in their particular study, often using only some of the phylogenetic information available for those taxa (e.g. Barton, Purvis & Harvey, 1995; Lewis, 1995; Ferrarezzi & Gimenez, 1996; Hosken, 1997, 1998; Jones & Purvis, 1997; Jones *et al*., 2001; Jones & MacLarnon, 2001; Speakman, 2000; Barclay & Harder, in press) or conducting repeated analyses with multiple and often conflicting phylogenetic hypotheses (Kirsch & Lapointe, 1997).

II. CHIROPTERAN PHYLOGENY: A GENERAL REVIEW

Two suborders of bats have long been recognised: Megachiroptera (megabats = Old World fruit bats) and Microchiroptera (microbats = echolocating bats). Dobson (1875) was the first to provide a comprehensive classification of extant bats, but their phylogenetic relationships remained largely unstudied until the 1970s. Koopman and Jones' (1970) taxonomy coincided with the advent of the application of cladistic methods (initially intuitive, later manual, and finally computer-assisted) to bat systematic relationships [detailed reviews can be found in Simmons and Geisler (1998) and Simmons (2000)]. Chiropteran diphyly was first proposed over 30 years ago: Megachiroptera were suggested to be more closely related to primates than to Microchiroptera (Jones & Genoways, 1970; Smith,

1976; Pettigrew, 1986, reviewed in Simmons, 1994). The majority of recent morphological, biochemical, and molecular phylogenetic studies have strongly supported bat monophyly (e.g. Ammerman & Hillis, 1992; Sarich, 1993; Novacek, 1994; Simmons, 1994, 1995; Simmons & Quinn, 1994; Allard, McNiff & Miyamoto, 1996; Porter, Goodman & Stanhope, 1996; Hutcheon, Kirsch & Pettigrew, 1998; Kirsch & Pettigrew, 1998; Simmons & Geisler, 1998; Van Den Bussche *et al*., 1998*a*; Miyamoto, Porter & Goodman, 2000; Nikaido *et al*., 2000; Madsen *et al*., 2001; Murphy *et al*., 2001; Teeling *et al*., 2000). However, the results from these studies were and are contested by Pettigrew (1986, 1991, 1994, 1995) and his colleagues on three grounds.

Firstly, they argue that cladistic studies using morphological characters may be misleading in resolving bat relationships because many of the characters supporting monophyly are highly correlated with flight and hence with each other. Pettigrew (1986) suggested that these flight-adaptational characters are diametrically opposed to other characters that argue for a closer relationship of Megachiroptera to primates rather than Microchiroptera (e.g. neural pathway structure: Johnson *et al*., 1994). However, morphological characters supporting bat monophyly represent data from many additional anatomical systems, with over 33 synapomorphies diagnosing the Chiroptera (reviewed in Simmons & Geisler, 1998).

A second criticism is that although biochemical and molecular phylogenetic studies do mostly support monophyly, the power of these studies for resolving the monophyly/diphyly issue may be low. Compared to most mammals, Megachiroptera and some microchiropteran families share an inordinately high proportion of adenine (A) and thymine (T) in their DNA (Pettigrew, 1994, 1995). This 'AT bias' may effectively result in underestimating the differences between the suborders in biochemical and molecular studies, thus providing artificial support for monophyly. How AT bias affects analysis of bat phylogenetic relationships remains largely unknown but recent studies have found little evidence that base compositional bias has significantly affected hypotheses of bat monophyly (i.e. Van Den Bussche *et al*., 1998*a*; Teeling *et al*., 2000). Moreover, DNA-hybridization experiments attempting to compensate for the AT bias (Kirsch & Pettigrew, 1998) and nucleotide sequence analyses compensating for the small amount of base composition bias (Van Den Bussche *et al*., 1998*a*; Teeling *et al*., 2000) have strongly supported bat monophyly.

A third criticism has been that the level of taxonomic sampling in biochemical and molecular phylogenetic studies may have been inadequate to reject bat monophyly, and that long-branch attraction (Swofford & Olsen, 1990) may have been responsible for joining the mega- and microchiropteran clades (Kirsch & Pettigrew, 1998; Pettigrew & Kirsch, 1998). However, monophyly of Chiroptera was indirectly supported by Hutcheon *et al*.'s (1998) DNA-hybridisation analysis using a much larger and more representative taxonomic sample to attempt to ameliorate long-branch attraction. Similarly, Teeling *et al*.'s (2000) analysis of nucleotide sequence data in a wide range of bat species supported bat monophyly, as have more recent molecular studies using sequences from a wide range of mammals (Miyamoto *et al*., 2000; Nikaido *et al*., 2000; Madsen *et al*., 2001; Murphy *et al*., 2001). In summary, the available evidence suggests that despite the analytical criticisms described above, the monophyly of bats is strongly supported by the majority of molecular and morphological studies to date.

Although many early workers discussed higher-level relationships within Chiroptera (e.g. Dobson, 1875), Smith (1976) was the first to propose an explicitly cladistic arrangement. He suggested that family Pteropodidae (suborder Megachiroptera) was the sister group to the suborder Microchiroptera, and divided Microchiroptera into four superfamilies: Emballonuroidea (consisting of families Rhinopomatidae, Craseonycteridae and Emballonuridae), Rhinolophoidea (Nycteridae, Megadermatidae, Rhinolophidae and Hipposideridae), Phyllostomoidea (= Noctilionoidea) (Phyllostomidae, Mormoopidae and Noctilionidae) and Vespertilionoidea (Molossidae, Mystacinidae, Natalidae, Thyropteridae, Furipteridae, Vespertilionidae and Myzopodidae). Koopman (1985) further proposed that these superfamilies fell into two infraorders Yinochiroptera (Emballonuroidea and Rhinolophoidea) and Yangochiroptera (Noctilionoidea and Vespertilionoidea). A number of more recent phylogenetic studies have challenged this arrangement (Novacek, 1991; Pierson *et al*., 1986; Robbins & Sarich, 1988; Griffiths, Truckenbrod & Sponholtz, 1992; Luckett, 1993; Stanhope *et al*., 1993; Koopman, 1994; Porter *et al*., 1996; Hutcheon *et al*., 1998; Simmons, 1998; Teeling *et al*., 2000; Van Den Bussche & Hoofer, 2000; summarised in Simmons, 2000). The most comprehensive analysis to date has been that of Simmons and Geisler (1998) who analysed family-level relationships of bats based

on 195 morphological and 13 molecular characters. This study was unique in that it included all the relevant morphological data (Van Valen, 1979; Novacek, 1980, 1991; Barkley, 1984; Griffiths & Smith, 1991; Griffiths *et al*., 1992; Luckett, 1993) and some of the molecular data presented in previous studies (i.e. Baker, Honeycutt & Van Den Bussche, 1991; Wilkinson *et al*., 1997). Simmons and Geisler's (1998) phylogeny supported the monophyly of Microchiroptera, and suggested that the superfamily Emballonuroidea is not monophyletic because one of its consistent families (Emballonuridae) occupies a basal branch relative to all other microchiropterans. Simmons & Geisler (1998) also proposed that the superfamily Vespertilionoidea should be restricted to Vespertilionidae, and that two additional superfamilies (Molossoidea and Nataloidea) should be recognized for the other families formerly contained within it.

More recent molecular studies have produced trees that conflict with some of the interfamilial relationships proposed by Simmons & Geisler (1998) (e.g. Hutcheon *et al*., 1998; Kirsch *et al*., 1998; Kennedy *et al*., 1999; Teeling *et al*., 2000; Van Den Bussche & Hoofer, 2000; Van Den Bussche & Hoofer, 2001). Most controversial is the suggestion that the microbat superfamily Rhinolophoidea is more closely associated to Pteropodidae (Megachiroptera) than to any other microchiropteran clades, thereby rendering the Microchiroptera polyphyletic (Pettigrew and Kirsch, 1998; Kirsch and Pettigrew, 1998; Hutcheon *et al*., 1998; Kirsch *et al*., 1998; Teeling *et al*., 2000; Madsen *et al*., 2001; Springer *et al*., 2001). This rearrangement is controversial for two reasons. First, it contradicts more than 50 synapomorphies, including echolocation, from a diverse range of morphological and behavioural systems that unite the Microchiroptera (Pettigrew, 1995; Hutcheon *et al*., 1998). Instead, numerous reversals or independent acquisitions would be required at the branch joining Rhinolophoidea and Pteropodidae. However, many of the putative morphological synapomorphies are associated with flight and ventilation and thus may not be independent, and so do not provide independent assessments of phylogeny (Teeling *et al*., 2000). Second, it has been suggested that an AT bias in the DNA of both megachiropteran and rhinolophoid bats may have influenced the resulting phylogenies underestimating the differences between these two clades (Kirsch & Pettigrew, 1998). However, Teeling *et al*. (2000) found little evidence for a high AT bias in the four nuclear and three mitochondrial genes that they sequenced, suggesting that the close association of the megachiropteran and rhinolophoid clades was not a result of differences in overall base composition. The question of microchiropteran paraphyly thus remains open.

III. STUDY GOALS

The aim of the present study was to construct a hypothesis of phylogenetic relationships among all extant 916 and nine recently extinct bats based on all available recent published hypotheses. We combined estimates of bat relationships into a single 'phylogenetic supertree' (Sanderson, Purvis & Henze, 1998) using Matrix Representation using Parsimony (MRP). This method, developed by Baum (1992) and Ragan (1992), is the technique most widely used to construct supertrees (Bininda-Emonds & Sanderson, 2001). In this method, the phylogenetic structure (tree topology) of each hypothesis of bat relationships is recoded as a series of binary characters describing each node (branching point in a phylogeny) in turn. One character is used to describe each clade in a tree such that descendants of a node are scored as '1', all others as '0' except for missing taxa, which are scored '?'. An all-zero hypothetical outgroup is used to 'polarize' the characters. The resultant matrix is then analysed using parsimony to produce a consensus estimate based on the source trees (Baum, 1992; Ragan, 1992). As only source tree structure is coded into the matrix, MRP can be used to combine phylogenetic information from different types of studies that otherwise could not be analysed simultaneously (e.g. discrete character data and distance data, such as morphology and DNA-hybridisation data; Sanderson *et al*., 1998). Like other supertree techniques and unlike most traditional consensus techniques, MRP requires only that the source trees being combined have overlap in their taxon sets rather than the same sets of taxa.

Although MRP has been used to produce complete supertrees of other mammalian orders [Primates: 203 species (Purvis, 1995*a*); Carnivora: 271 species (Bininda-Emonds, Gittleman & Purvis, 1999)], and more recently a family-level supertree for placental mammals (Liu *et al*., 2001), the general supertree approach has received criticism because it only considers the topology of the source trees, effectively discarding primary data (see Springer & de Jong, 2001; Bininda-Emonds & Sanderson, 2001). However, simulations have indicated that, under most source topology input scenarios, MRP provides as accurate an estimate of a known model

topology as does analysing the 'primary data' using a total-evidence approach (Bininda-Emonds & Sanderson, 2001). These simulation results, coupled with the advantage that (unlike total-evidence approaches) all types of information can be analysed simultaneously, makes the supertree methodology a reasonable and important method for combining phylogenetic information to produce comprehensive and accurate phylogenetic estimates of entire clades. Although the supertree we present should only be viewed as a working hypothesis of bat phylogenetic relationships (not an alternative to data-based phylogenetic studies), it provides a reasonable hypothesis until more taxonomically comprehensive phylogenetic analyses are completed and some level of consensus arises among studies based on different data (e.g. morphology, mtDNA and nuclear DNA). The primate and carnivore supertrees have already been shown to be extremely useful tools in a range of research areas including analyses of trait evolution (e.g. Carbone *et al*., 1999; Nunn, Gittleman & Antonovics, 2000), macroevolution (e.g. Gittleman & Purvis, 1998; Pybus & Harvey, 2000) and conservation biology (e.g. Purvis *et al*., 2000*a*, *b*). We anticipate that the same will be true of the bat supertree.

IV. MATERIALS AND METHODS

(1) Data

Phylogenetic information was collated from all sources where phylogenetic structure could be inferred from the information presented. Source studies employed methods as diverse as informal character analyses (phylogenetic structure derived without using formal clustering algorithms, e.g. taxonomies), discrete character clustering methods (e.g. parsimony, maximum likelihood) and distance data clustering methods (e.g. neighbour-joining, morphometrics) using molecular and/or morphological data. Although some methods of phylogenetic estimation are more likely to yield more robust results than others, evaluating the relative merits of methods employed in different studies and determining what weight each type of study should have in the supertree analyses is more difficult. In Purvis' (1995*a*) primate supertree analysis, an attempt at addressing this problem was made by down-weighting phylogenetic estimates derived from less analytically robust methodologies (e.g. informal character analyses, taxonomies). This approach was subsequently dropped in Bininda-Emonds *et al*.'s (1999) analysis of Carnivora where equal weighting of all source topologies was adopted (although the effects of differential weighting were examined). Here we also adopt equal weighting of source trees, as the available evidence suggests that supertree topologies are relatively insensitive to weighting schemes: a high degree of congruency was found between the topologies resulting from differentially *versus* equally weighted (= 'unweighted') analyses of both the primate and carnivore supertrees (Bininda-Emonds *et al*., 1999; Purvis, 1995*a*). More detailed analyses of the carnivores also supported the relative robustness of supertree structures to the type of data (e.g. molecular, morphological) or analytical methodology (e.g. parsimony, phenetic) used by the original authors in developing the source topologies (Bininda-Emonds, 2000); regardless of the methodology or data source employed, most estimates of carnivore phylogenetic relationships point towards the same solution. However, we do recognise that an uncritical acceptance of all bat phylogenetic estimates that have ever been published (beginning with Dobson, 1875) may bias the sample of source topologies in favour of older, less analytically robust estimates. We attempted to deal with this problem by considering only those phylogenetic estimates published (or known to be in press) between 1970 and the end of 2000. Additionally, we investigated the relative effect of a differential weighting scheme and year of study on the relationships presented by repeating the analyses several ways, firstly by weighting the source trees *sensu* Purvis (1995*a*), and secondly by comparing the topologies obtained using source trees from the 1970s and above to those obtained using only those sources from the 1980s and above and 1990s and above.

In addition to phylogenetic data known to us from our previous work on bats, sources were also located by searching through the bibliographic databases BIOSIS and Web of Science on the search parameters Chiroptera and any of the following; phylogen*, phenogram*, cladogram*, cladistic*, taxonom* and fossil* (following Bininda-Emonds *et al*., 1999; Purvis, 1995*a*). Further sources were located from bibliographies within the articles found. In total, we identified 105 useable source trees from the 1970–2000 literature (Appendix 1). Species' Latin binomials as presented here follow those in Koopman (1993), giving a total of 925 extant and recently extinct species. Koopman's (1993) data set is the most recent widely accepted species list for Chiroptera that also includes species synonyms. Tracing synonyms is essential for establishing con-

gruence among different studies that have often used different names for the same species. Synonyms that could not be traced in the source trees were excluded from our analyses.

Assembly rules used to construct the data set were as follows: (1) where the same authors or series of authors used the same methodology and data source, the most recent or most complete study was used in our data set; (2) when different authors analysed the same data source, the most recent reanalysis was used; (3) where more than one tree based on the same or overlapping data were presented in a single source, these trees were combined into one estimate using MRP before inclusion into the main analysis; (4) trees that were secondary replications of primary phylogenetic hypotheses were not used. For example, Novacek's (1991) presentations of Koopman's (1984) taxonomy were not used, nor were previous 'supertree' estimates of phylogenetic relationships compiled from primary sources (Barton *et al*., 1995; Jones & Purvis, 1997; Liu *et al*., 2001).

(2) Matrix construction

Ideally, all 925 species would be analysed simultaneously by MRP so that *a priori* assumptions of clade monophyly (except at the species level) would not have to be made. However, current cladistic search algorithms become prohibitively slow for greater numbers of taxa and less likely to identify the optimal solution; performance of the MRP method has also been shown to decrease with increasing matrix size (Bininda-Emonds & Sanderson, 2001). In an attempt to ameliorate these size problems but to minimize monophyly assumptions, a single matrix was constructed with 186 species and 22 higher-level (supraspecific) clades as terminal taxa. For higher-level clades with greater than three taxa (15 matrices), species-level relationships were analysed in separate matrices. The monotypic taxa and clades with only two or three species were as follows: Antrozoidae (*Antrozous dubiaquercus* and *A. pallidus*), Craseonycteridae (*Craseonycteris thonglongyai*), Furipteridae (*Amorphochilus schnablii* and *Furipterus horrens*), Mystacinidae (*Mystacina tuberculata* and *M. robusta*), Myzopodidae (*Myzopoda aurita*), Noctilionidae (*Noctilio albiventris* and *N. leporinus*), Rhinopomatidae (*Rhinopoma hardwickei*, *R. microphyllum* and *R. muscatellum*), Thyropteridae (*Thyroptera discifera* and *T. tricolor*) and Tomopeatinae (*Tomopeas ravus*). Where it was not possible to assign identities to the terminal tips from the information presented in the source phylogenies, the information was excluded from the analysis. However, in sources where genera names were given with no other information, the type species for that genus was assigned as the terminal taxon, e.g. for McKenna and Bell's (1997) generic-level taxonomy. Following data presented in Simmons (1998) and Simmons & Geisler (1998), the following clades were assumed to be monophyletic: Pteropodidae (Megachiroptera) and the microchiropteran families Craseonycteridae, Emballonuridae, Furipteridae, Hipposideridae, Megadermatidae, Molossidae, Mormoopidae, Mystacinidae, Myzopodidae, Natalidae, Noctilionidae, Nycteridae, Phyllostomidae, Rhinolophidae, and Thyropteridae [all clade definitions *sensu stricto* Koopman (1994)].

Hipposideridae has been considered as a subfamily of Rhinolophidae (Koopman, 1994; Simmons, 1998; Simmons & Geisler, 1998) but we treated it as a separate monophyletic family here following Hand and Kirsch (1998) and Bogdanowicz and Owen (1998). Support for Mormoopidae monophyly has been questioned in a recent molecular study (Kennedy *et al*., 1999) in conflict with all other molecular and morphological studies to date (e.g. see recent papers by Simmons & Conway, 2001; Van Den Bussche & Hoofer, 2001). Here, we follow the majority of recent opinion and assume monophyly for this family. Monophyly was also assumed for the genus *Pteropus* in the Pteropodidae MRP clade matrix, and species-level relationships were analysed separately within this genus. Vespertilionidae is a problematic family, widely recognised as being potentially paraphyletic (Barkley, 1984; Sudman, Barkley & Hafner, 1994; Simmons, 1998; Simmons & Geisler, 1998) and consequently monophyly was not assumed for this family. For example, traditional vespertilionid genera such as *Tomopeas* and *Antrozous* have separately been considered as sister-taxa to Molossidae (Sudman *et al*., 1994; Simmons & Geisler, 1998). For this analysis we only assume monophyly for the following clades within the traditional vespertilionid assemblage: 'Antrozoidae', Tomopeatinae, Kerivoulinae, Miniopterinae, Murininae, and *Myotis*. The species-level relationships for the later four taxa were analysed in separate matrices.

(3) Analysis

Alternative topologies of clades were coded using MRP in the data editor of MacClade (version 3.08) (Maddison & Maddison, 1992). A modification to the basic coding method proposed by Purvis (1995*b*) was not applied, as this method has been criticised on its approach to weighting missing data (Ronquist,

1996), although simulation studies have shown that supertrees constructed with and without this modification are highly congruent (Bininda-Emonds & Bryant, 1998; Bininda-Emonds & Sanderson, 2001). All matrices were analysed using PAUP* 4.0b8 for Unix, (Swofford, 2001) and the matrices are available from the senior author on request and have been deposited in TreeBASE (study accession number, S688 and matrix accession numbers, M1080 through to M1095, http://www.treebase.org).

For small matrices (under 25 taxa, i.e. for Megadermatidae, Nycteridae, Natalidae, Mormoopidae, Miniopterinae, Kerivoulinae, and Murininae) the most parsimonious trees were found using the branch-and-bound algorithm (Hendy & Penny, 1982). For larger matrices (Top matrix, Pteropodidae, *Pteropus*, Emballonuridae, Rhinolophidae, Hipposideridae, Phyllostomidae, Molossidae, and *Myotis*) a strict consensus was computed of 10000 most parsimonious trees found using the parsimony ratchet (Nixon, 1999) as a heuristic search algorithm. For larger matrices, the parsimony ratchet has been demonstrated often to find increasingly optimal solutions and in a shorter amount of time than traditional 'brute force' solutions (Nixon, 1999; Quicke, Taylor & Purvis, 2001). The ratchet search strategy used was as follows: a single tree was initially found from a heuristic search using a random addition sequence with Tree-Bisection-Reconnection (TBR) branch swapping on minimal trees only, zero length branches collapsed. A random sample of 25% of the characters was then doubled in weight and a further heuristic search with TBR branch swapping was performed saving one tree of the equally most parsimonious trees found. The weights were then restored to their original values and TBR branch swapping was performed, again saving one of the equally most parsimonious trees. This ended one replicate of 1000. The 1001 trees produced (1000 replicates plus the initial start tree) were then used as a starting point for TBR branch swapping, saving up to a limit of 10000 of the equally most parsimonious trees. Through its reweighting strategy, the parsimony ratchet essentially performs numerous local mini-searches throughout 'tree space'. As such, even with only 10000 trees saved, the parsimony ratchet covers the entirety of tree space more effectively than a traditional, 'brute force' search strategy that begins at only a single location and is more likely to be trapped in that region of tree space.

Support for individual nodes within the supertrees were calculated using the Bremer decay index (Bremer, 1988; Källersjo *et al*., 1992) to determine how much less parsimonious a solution must be before the clade of interest was contradicted. Clades that are uncontradicted in increasingly less parsimonious solutions are inferred to have greater support. Bremer supports were determined using converse constraints in PAUP* to determine the shortest length at which a node was contradicted. For the large matrices, the parsimony ratchet was used to determine the Bremer support of each individual node. The strategy followed that described above except that the final round of TBR branch swapping was not used because examination of the data for the full supertree analyses revealed that the most parsimonious length was always found among the initial 1001 ratchet trees. The additional branch swapping therefore only provided a more accurate coverage of tree space, which was not necessary in this case. MacClade version 3.08 (Maddison & Maddison, 1992) and TreeView version 1.6.1 (Page, 2000) were used to represent graphically the generated topologies.

V. RESULTS AND DISCUSSION

(1) Taxonomic coverage and resolution

Compared with some other mammalian clades, bat phylogenetic relationships have been poorly studied.

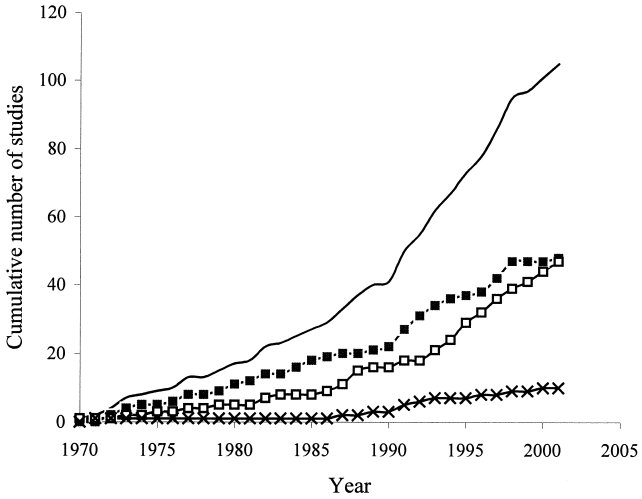

Fig. 1. Cumulative numbers of useable sources published since 1970 ($N = 105$). The solid line represents the total number of sources; solid boxes represent cumulative number of sources based on analyses of morphological data only; open boxes represent sources based on analyses of molecular data only; and crosses represent sources based on analyses combining both morphological and molecular data in a total evidence approach.

We found 105 useable sources, representing 0.1 sources per species (Appendix 1). This compares to 112 sources for 203 species of primates (0.6 sources per species) and 177 sources for 271 species of carnivores (0.7 sources per species) for similar phylogenetic compilations (Purvis 1995*a*; Bininda-Emonds *et al*., 1999). The differences are likely to be even greater as the primate supertree was based on pre-1993 literature and the carnivore supertree on pre-1996 literature. The majority of phylogenetic studies of bats have been published since 1990, with a rapid increase in the number of molecular or 'total evidence' studies from the late 1980s onwards (Fig. 1).

Not surprisingly, systematic studies have not been distributed evenly across Chiroptera (Table 1). For example, relationships within Phyllostomidae have been investigated in over one-third of the total bat systematic studies to date while at the other extreme several clades have never been investigated using cladistic methodology (e.g. Kerivoulinae, Miniopterinae, Murininae, Natalidae, and Rhinopomatidae). The number of characters in each matrix per taxon highlights the lack of information available for the poorly studied groups. These clades are often species-rich so the amount of information per taxon in the clade is low (e.g. *Pteropus* and *Myotis*, Table 1). The number of characters per source tree per taxa (Table 1) gives an indication of how thoroughly a clade has been investigated in each study: smaller clades exhibit higher values (e.g. Natalidae, Mormoopidae and Megadermatidae) compared with larger clades (e.g. Phyllostomidae, *Pteropus*). Interestingly, the lack of information about Kerivoulinae again stands out; despite being a relatively small clade, it is among the poorest covered.

The composite bat supertree of the extant taxa (Fig. 2) contains 424 nodes, which is 46.4% of a fully bifurcating solution (the position of the nine recently extinct species is indicated in Table 2). In comparison to the resolution of other supertrees for primates (79.1%) and carnivores (78.1%), the resolution for bats is low. It is likely that the lack of resolution found in bats is due to a lack of information for many clades rather than conflict among source trees leading to a loss of resolution. For example, the carnivore supertree is based on over twice as many characters per taxa (4.68) than the bat estimate (2.01). Additionally, the bat supertree shows great heterogeneity in the resolution for different clades (Table 3). The larger clades are typically less resolved but Emballonuridae, Phyllostomidae and Molossidae stand out as being large clades that are also well resolved, reflecting both the amount of agreement between source trees and the number of sources.

(2) Higher-level relationships

The MRP topology calculated from the Top matrix for the higher-level relationships is shown in Fig. 3 (source details and nodal support statistics are given in Appendix 1 and 2 and Table 3). The consensus retains Pteropodidae as a sister group to the other bats, which is consistent with numerous sources that place it in such a position, either in a clade by itself (Smith, 1976; Van Valen, 1979; Novacek, 1980; Pierson *et al*., 1986; Arnold *et al*., 1982; Koopman, 1994; Simmons & Geisler, 1998; Kennedy *et al*., 1999; Van Den Bussche & Hoofer, 2001), or clustering with the Rhinolophoidea (Kirsch *et al*., 1998; Teeling *et al*., 2000). There is strong support for this relationship (Appendix 2). The supertree does not support the diphyly of Microchiroptera as suggested by the molecular studies of Teeling *et al*. (2000) and Kirsch and colleagues (Hutcheon *et al*., 1998; Kirsch *et al*., 1998; Kirsch & Pettigrew, 1998; Pettigrew & Kirsch, 1998). Microchiropteran monophyly is supported by the majority of the morphological studies to date and some molecular studies (e.g. Pierson *et al*., 1986; Simmons & Geisler, 1998; Kennedy *et al*., 1999), and this is strongly reflected in the structure of the supertree.

The supertree supports the division of Microchiroptera into the two infraorders Yinochiroptera and Yangochiroptera, but offers mixed support for the four superfamilies Emballonuroidea, Rhinolophoidea, Noctilionoidea and Vespertilionoidea. Within the Yinochiroptera, the monophyly of Rhinolophoidea is supported, but Emballonuroidea is paraphyletic. Two of Emballonuroidea's constituent families [Rhinopomatidae and Craseonycteridae, Simmons & Geisler's (1998) Rhinopomatoidea] are found to cluster together. Rhinolophoidea and Rhinopomatoidea appear as sister taxa, and Emballonuridae appears basal to Yinochiroptera. However, Bremer support values for these nodes are low and unsurprisingly there are disagreements as to the placement of Emballonuridae in the source trees. For example, Simmons & Geisler (1998), Pierson (1986) and Griffiths *et al*. (1992) placed Emballonuridae as the sister group to all other microbat families. The switch in position of this family to a more nested position in the supertree is probably due to the closer association found in some

Table 1. *Details of the 16 matrices used to construct the bat supertree. N_{taxa}, represents number of taxa in each matrix; N_{sour}, number of different source trees in each matrix; and N_{char}, number of characters in each matrix*

Matrix	N_{taxa}	N_{sour}	N_{char}	$N_{\text{char}}/N_{\text{taxa}}$	$N_{\text{char}}/N_{\text{sour}}$ /N_{taxa}
Top	208	50	461	2.22	0.04
Pteropodidae	109	14	243	2.23	0.16
Pteropus	58	4	22	0.38	0.09
Emballonuridae	47	11	113	2.40	0.22
Megadermatidae	5	4	8	1.60	0.40
Nycteridae	12	3	14	1.17	0.39
Rhinolophidae	64	5	58	0.91	0.18
Hipposideridae	66	6	85	1.29	0.21
Natalidae	5	2	4	0.80	0.40
Mormoopidae	8	7	23	2.88	0.41
Phyllostomidae	141	39	630	4.47	0.11
Molossidae	80	12	125	1.56	0.13
Miniopterinae	10	2	5	0.50	0.25
Kerivoulinae	22	2	4	0.18	0.09
Murininae	16	2	8	0.50	0.25
Myotis	84	5	55	0.65	0.13

of the source trees between Pteropodidae and the clade containing Rhinolophoidea and Rhinopomatoidea (see above).

The relationships among the superfamilies and families in the infraorder Yangochiroptera are generally poorly supported in the supertree, although there are some strongly supported clades. For example, Noctilionoidea (Phyllostomidae, Mormoopidae, Noctilionidae) is monophyletic in the supertree due to being supported in the majority of the source topologies. The addition of Mystacinidae to this clade in the supertree receives support from recent molecular (Pierson *et al*., 1986; Kirsch *et al*., 1998; Kennedy *et al*., 1999; Van Den Bussche & Hoofer, 2001) and other morphological studies (Novacek, 1980; Simmons & Conway, 2001). Monophyly of the superfamily Vespertilionoidea is not supported in the supertree. Disagreements among the sources about the relationship of Myzopodidae to other families led to its relationship being unresolved. For example, Simmons and Geisler (1998) placed it within the Nataloidea clade (together with Thyropteridae, Furipteridae and Natalidae), while a recent molecular study placed it more basally within the microbats (Van Den Bussche & Hoofer, 2001). The monophyly of Vespertilionidae (*sensu* Koopman, 1994) is supported in the supertree with the exception of subfamily Tomopeatinae, which is placed as the sister group of Molossidae (not Vespertilionidae) in the supertree. The result reflects recent molecular and morphological findings (Sudman *et al*., 1994; Simmons & Geisler, 1998; Kennedy *et al*., 1999).

Differential weighting among source trees according to their analytical rigour increases the resolution in the higher-level relationships, but produced comparatively few changes in topology (Table 3). For example, although the relationships between microbats and Pteropodidae, and among Rhinolophoidea, remain stable when differential weighting is applied [effectively down-weighting the taxonomies of Corbet and Hill (1991), Koopman (1994) and McKenna and Bell (1997)], other relationships do change. Emballonuridae is no longer sister to the clade containing Rhinolophoidea and Rhinopomatoidea, but sister to the other microchiropteran families (Yangochiroptera). Greater resolution is also found in the relationships among the remaining microbat families. Noctilionoidea and Nataloidea form sister clades that are in turn sister to Molossidae and Tomopeatinae and then Vespertilionidae. When the higher-level analyses were split by decade of source study (1980s and 1990s and above), the topological structures were similar to the weighted analysis: only Myzopodidae shows a change in position, switching from within the Nataloidea to the sister clade Yangochiroptera plus Emballonuridae.

The unweighted supertree disagrees with a recent supertree that analysed the family-level relationships of all mammals (Liu *et al*., 2001). Their analysis placed Emballonuridae as the sister group to all

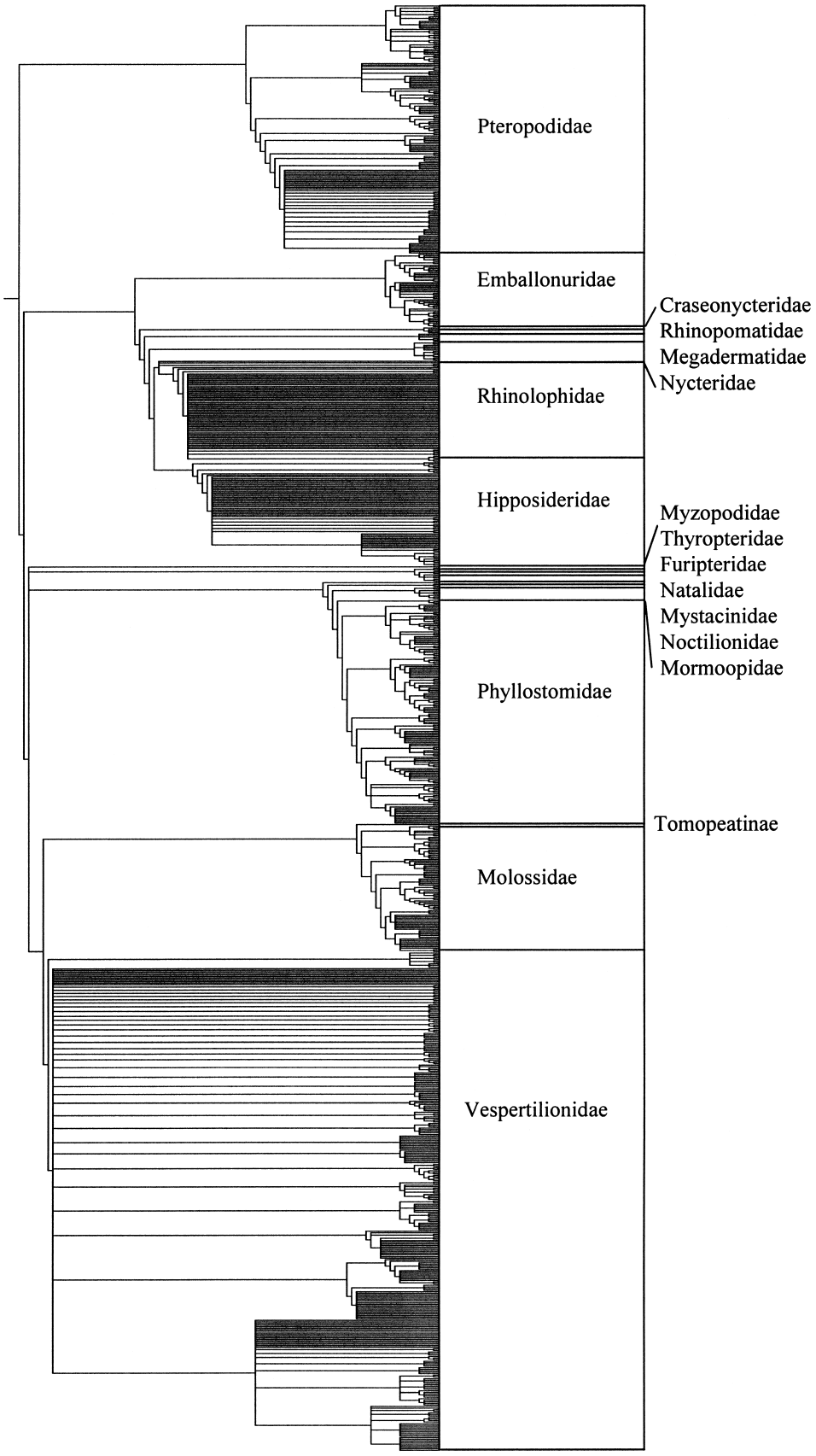

Fig. 2. The supertree for extant bat species. Branch lengths are not proportional to time and are arbitrary.

Table 2. *Node number of the position of the nine recently extinct species (sensu Koopman, 1993) on the bat supertree in Figs 3–15*

Family	Extinct species	Node
Pteropodidae	*Acerodon lucifer*	2.62
Pteropodidae	*Dobsonia chapmani*	2.55
Pteropodidae	*Nyctimene sanctacrucis*	2.07
Pteropodidae	*Pteropus brunneus*	3.01
Pteropodidae	*Pteropus pilosus*	3.14
Pteropodidae	*Pteropus subniger*	3.01
Pteropodidae	*Pteropus tokudae*	3.14
Mystacinidae	*Mystacina robusta*	1.13
Vespertilionidae	*Pipistrellus sturdeei*	1.91

other microchiropterans, and found different relationships among families within Rhinolophoidea and Yangochiroptera compared to our study. For example, although their analysis supported Noctilionoidea, relationships found among the constituent families were different and results did not support the addition of Mystacinidae to this clade, although many source trees used here support this relationship (see above). We feel that our supertree better reflects the available evidence because (1) more elements were included (especially from more recently published sources); (2) assumptions of monophyly were not made for problematic families such as for Vespertilionidae; and (3) and the sources used in our study were more independent of each other, i.e. trees using the same data from the same authors but published in different papers were treated as independent in the Liu *et al.* (2001) analysis (see critique in Springer & de Jong, 2001); and (4) our focus on Chiroptera allowed us to address specific problem areas within the order in our analyses. Additionally, our unweighted topology receives support from and is completely congruent with an independent total evidence study (Lapointe, Kirsch & Hutcheon, 1999) that combined data from three sources based on serology, DNA-hybridization and morphology.

(3) Pteropodidae

The Pteropodidae supertree (Fig. 4) finds Andersen's (1912) two subfamilies Pteropodinae (fruit feeders) and Macroglossinae (containing specialised pollen and nectar feeders) to be paraphyletic, a result in line with recent morphological and molecular studies (Hood, 1989; Colgan & Flannery, 1995; Kirsch *et al.*, 1995; Springer, Hollar & Kirsch, 1995; Alvarez *et al.*, 1999; Juste *et al.*, 1999). Pteropodidae is split instead into two different clades: one containing species traditionally classified in the tribe Cynopterini *sensu* Koopman (1994): cynopterines: *Cynopterus*, *Megaerops* (not including *Myonycteris*), and nyctimenes: *Nyctimene* and *Paranyctimene*), and a second clade that contains the rest of the family. The association of cynopterines and nyctimenes and their more distant relationship to the rest of the family is supported in a number of studies (Koopman, 1994; Colgan & Flannery, 1995; Kirsch *et al.*, 1995; Springer *et al.*, 1995; Juste *et al.*, 1999; Teeling *et al.*, 2000) and this node has comparatively high Bremer support (Appendix 2).

The non-cynopterine clade is split into two groups in the consensus: one clade containing the macroglossine species *Megaloglossus woermanni*, the rousettine bats (*Rousettus*, *Eidolon*, *Myonycteris*, *Boneia*) and epomophorine bats (*Plerotes*, *Hypsignathus*, *Epomops*, *Epomophorous*, *Micropteropus*, *Nanonycteris*, *Scotonycteris* and *Casinycteris*) and the other containing the majority of the macroglossine bats, dobsoniine, pteropodine and harpyionycterine bats. These clades have low Bremer supports although support for relationships within these groups is much higher. Within the rousettine/epomophorine clade, the monophyly of the rousettine bats (*sensu* Koopman, 1994 – see above) is not supported in the supertree (a result in line with evidence from Hood, 1989; Kirsch *et al.*, 1995; Hollar & Springer, 1997; Juste *et al.*, 1999; Teeling *et al.*, 2000). The affinities of *Rousettus*, *Myonycteris*, *Eidolon*, *Megaloglossus* and *Boneia* to the rest of the species in the rousettine/epomophorine clade in the supertree were uncertain. Additionally, the monophyly of *Rousettus* was not supported as *R. angolensis* clustered separately from the rest of the genus, a result congruent with recent molecular studies (Juste, Ibanez & Machordom, 1997). The monophyly of the exclusively African epomophorine bats (*sensu* Koopman, 1994) was supported in the consensus. Within the second clade within the non-cynopterine group, the genera typically placed in Macroglossinae (*Eonycteris*, *Macroglossus*, *Syconycteris*, *Notopteris* and *Melonycteris*) were placed as a sister group to dobsoniine bats (*Dobsonia*, *Aproteles*), pteropodine bats (*Styloctenium*, *Neopteryx*, *Pteralopex*, *Pteropus*, *Acerodon*) and harpyionycterine (*Harpyionycteris*) bats. The monophyly of Macroglossinae (*sensu* Koopman, 1994) was not supported as *Megaloglossus* (traditionally placed within this subfamily) did not cluster with the other macroglossine taxa [a result supported by evidence from Hood (1989) and Kirsch *et al.* (1995)].

Table 3. *Summary statistics for the topologies produced from the 16 supertree data matrices (unweighted and weighted results are on the first and second line, respectively). r represents where tree searches were conducted using a parsimony ratchet; h, tree searches conducted using a heuristic parsimony search; b&b, searches conducted using a branch and bound parsimony search; N_{MPT}, number of maximally parsimonious trees produced from each analysis; TL, length of the tree produced from each analysis; CI, tree consistency index; RI, tree retention index; %Res, resolution of the topology as a percentage of a fully bifurcating solution; %Dif, number of nodes that are different in the weighted (Wt), 1980s and above (1980s) and 1990s and above (1990s) trees compared to the unweighted tree as a percentage of the total number of nodes in each matrix.*

Matrix	Search type	N_{MPT}	TL	CI	RI	% *Res*	% *Dif* Wt	% *Dif* 1980s	% *Dif* 1990s
Top	r	10000	669	0.69	0.91	47.6	7.6	7.6	9.3
		10000	1808	0.68	0.88	50.0			
Pteropodidae	r	10000	361	0.67	0.91	57.0	17.0	·	3.8
		10000	947	0.66	0.88	53.3			
Pteropus	r	10000	23	0.96	0.98	23.2	0.9	·	·
		10000	48	0.96	0.98	21.4			
Emballonuridae	h	24	144	0.79	0.93	68.9	3.4	2.3	3.4
		12	439	0.78	0.93	71.1			
Megadermatidae	b&b	2	11	0.73	0.70	33.3	0.0	·	50.0
		1	38	0.68	0.65	33.3			
Nycteridae	b&b	14	15	0.93	0.96	60.0	5.6	·	·
		1	30	0.97	0.98	70.0			
Rhinolophidae	r	10000	90	0.64	0.90	17.7	1.6	·	1.6
		10000	291	0.73	0.93	14.5			
Hipposideridae	r	10000	130	0.65	0.88	35.9	4.8	·	0.0
		10000	352	0.69	0.91	29.7			
Natalidae	b&b	1	4	1.00	1.00	66.7	·	·	·
		·	·	·	·	·			
Mormoopidae	b&b	2	29	0.79	0.84	83.3	30.0	·	10.0
		1	84	0.74	0.79	100			
Phyllostomidae	r	10000	869	0.73	0.93	66.2	4.7	10.5	10.5
		10000	2866	0.71	0.92	71.2			
Molossidae	r	5299	151	0.83	0.97	56.4	5.8	3.9	14.9
		2130	422	0.82	0.97	52.6			
Miniopterinae	b&b	1	5	1.00	1.00	50.0	·	·	0.0
		·	·	·	·	·			
Kerivoulinae	h	1	4	1.00	1.00	10.0	·	·	·
		·	·	·	·	·			
Murininae	b&b	1	8	1.00	1.00	35.7	·	·	·
		·	·	·	·	·			
Myotis	r	10000	77	0.71	0.93	25.6	19.1	6.8	6.8
		10000	94	0.75	0.93	61.0			

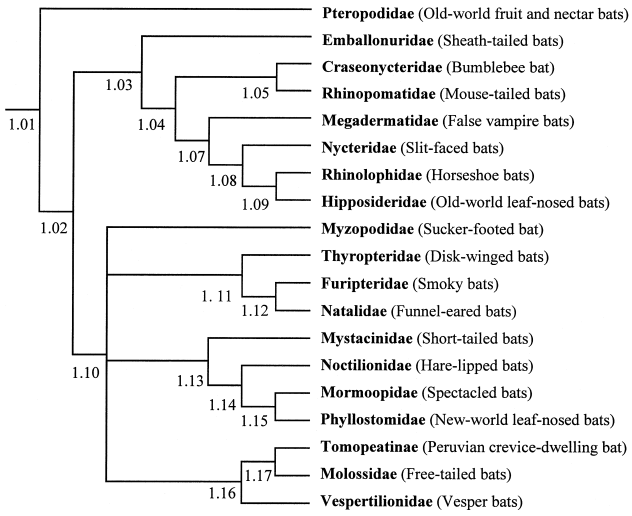

Fig. 3. The supertree for higher-level relationships. The number below each node represents the node number.

Differential weighting results in a slight decrease in overall resolution (Table 3). For example, the resolution among genera in the Cynopterini group decreases dramatically although resolution in other parts of the tree increases. The most significant change is in tree topology: 17% of the nodes in the unweighted tree were different to those in the weighted analysis (Table 3). The weighted supertree splits the family into two main clades consisting of Macroglossinae (without *Eonycteris* and *Megaloglossus*) and the Pteropodinae. Pteropodinae is further split into two clades: one containing the exclusively African genera (epomophorines and myonycterines) plus the rousettine genus *Rousettus*, and the other containing the rest of the rousettine genera as a sister group to the Cynopterini. When the analyses were split by year of study (using only studies from 1990 onwards) there was a large decrease in resolution in the relationships among the higher clades although relationships at the lower levels are broadly congruent with the unweighted topology.

(4) Emballonuridae

The MRP tree for emballonurids represents the strict consensus of 24 equally most parsimonious trees (Fig. 5, Table 3). The MRP supertree concurs with the majority of the source trees dividing the family into two groups, the subfamilies Taphozoinae (*Taphozous* and *Saccolaimus*) and Emballonurinae (other emballonurid genera) (Barghoorn, 1977; Griffiths & Smith, 1991; Robbins & Sarich, 1988; Kirsch *et al*., 1998; Dunlop, 1998). Within Emballonurinae, the supertree supports the monophyly of the tribes Emballonurini (*Emballonura*, *Mosia* and *Coleura*) and the New World tribe Diclidurini (*Cyttarops*, *Diclidurus*, *Rhynchonycteris*, *Cormura*, *Saccopteryx*, *Balantiopteryx*, *Pteropteryx* and *Centronycteris*). Following Griffiths, Koopman and Starrett (1991) and Dunlop (1998), the monophyly of *Emballonura* was not supported because *Coleura* nests within Emballonura. However, the monophyly of all other genera was supported in the supertree. Relationships within Diclidurini were largely unresolved reflecting disagreement among the sources. However, a consistent pattern of two sister clades emerged although with low Bremer support values: one consisting of *Cyttarops*, *Diclidurus* and *Rhynchonycteris* (supported by Griffiths & Smith, 1991; Dunlop, 1998) and the other of *Cormura*, *Saccopteryx*, *Balantiopteryx*, *Pteropteryx* and *Centronycteris* (Dunlop, 1998).

The supertree topology was relatively insensitive to different analytical schemes (Table 3), although the relationships within *Emballonura* and *Taphozous* were better resolved in the weighted analysis (*E. flaviventris* and *E. mixtus* as sister taxa, and *T. hamiltoni* and *T. nudiventris* as successively more basal to the other taphozoids) increasing the overall resolution in the tree. Considering successive decades of studies also did not greatly affect the tree topology although consistency and retention indices of the trees increased (1970s and above: tree consistency index $CI = 0.78$, tree retention index $RI = 0.93$; 1980s and above: $CI = 0.78$, $RI = 0.93$; 1990s and above: $CI = 0.79$, $RI = 0.93$). Relationships within the clade consisting of *Cormura*, *Saccopteryx*, *Balantiopteryx*, *Peropteryx* and *Centronycteris* were better resolved, reflecting the influence of a recent, well-resolved cladistic study on the MRP estimate (i.e. Dunlop, 1998).

(5) Rhinopomatidae

The Rhinopomatidae supertree is presented in Fig. 6. The relationships among the species in this family are unresolved due to the lack of information in the source topologies. Neither source topology year nor differential weighing had any effect on the supertree estimate.

(6) Megadermatidae

The two current cladistic hypotheses (Hand, 1985; Griffiths *et al*., 1992) of the species relationships within Megadermatidae (five species) are entirely incongruent. The MRP Megadermatidae tree

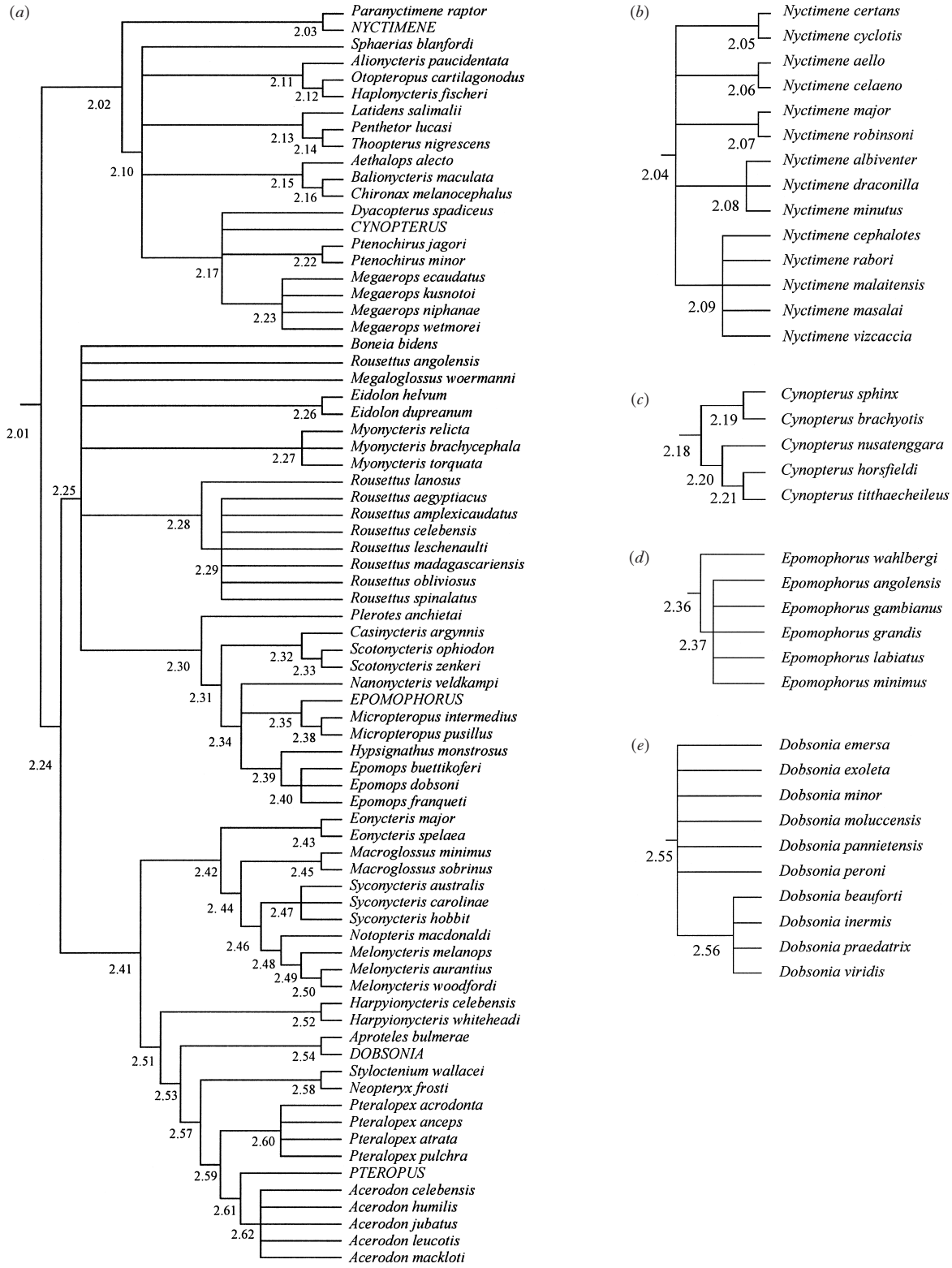

Fig. 4A. The supertree for Pteropodidae excluding *Nyctimene*, *Cynopterus*, *Epomophorous*, *Dobsonia* and *Pteropus*. Relationships within these excluded clades are shown in B, C, D, E and F, respectively.

(Fig. 7) represents a strict consensus of two equally most parsimonious trees and reflects these disagreements. Species relationships are unresolved except for a close relationship between *Megaderma lyra* and *M. spasma* that is supported by informal character analysis (Griffiths *et al.*, 1992; Koopman, 1994).

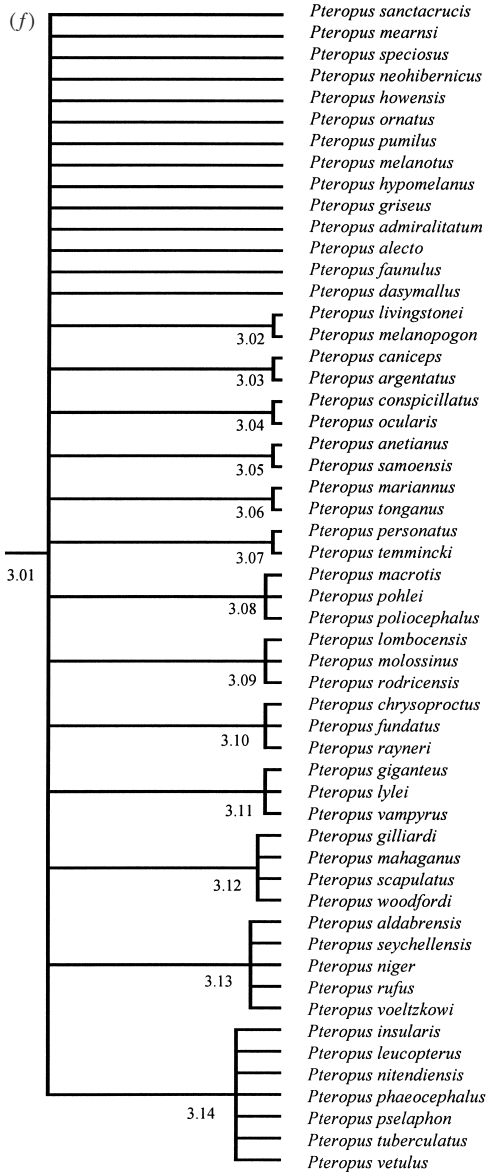

Fig. 4. For legend see facing page.

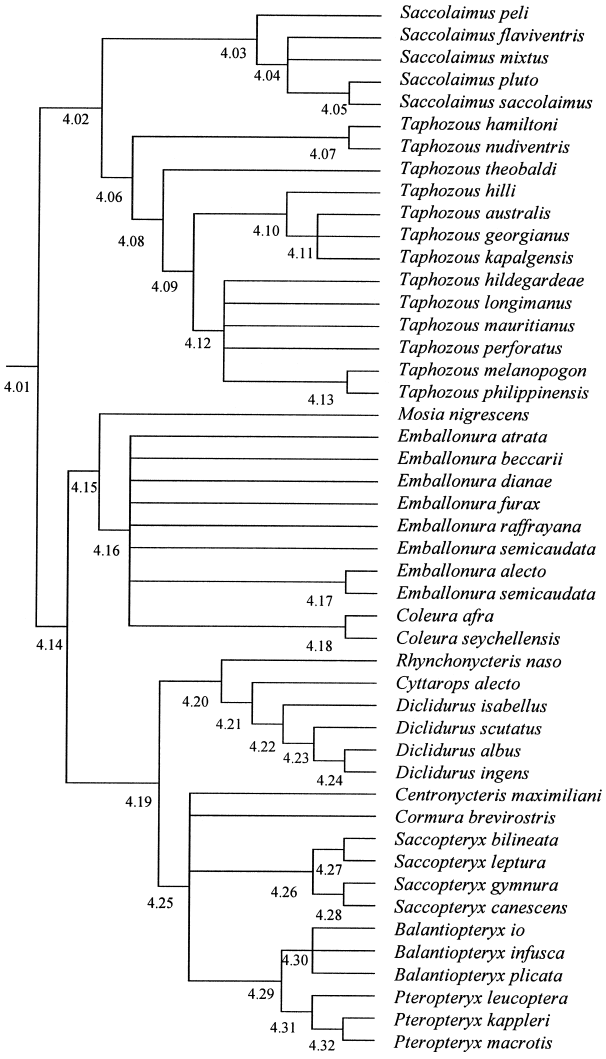

Fig. 5. Emballonuridae supertree.

Weighting sources differentially did not change the supertree topology or resolution (Table 3). However, when only sources from the 1990s and above were considered, the MRP estimate reflected Griffiths *et al.*'s (1992) proposal that *Lavia frons*, *Cardioderma cor* and *Macroderma gigas* are successive sister taxa to *M. lyra* and *M. spasma*.

(7) Nycteridae

The MRP supertree of Nycteridae (Fig. 8) represents the strict consensus of 14 equally most parsimonious trees. This tree is fairly well resolved, reflecting general agreement among the source trees. The MRP follows Van Cakenberghe and De Vree (1985, 1993*a*, *b*, 1998) and Griffiths (1997) in grouping nycterids into five species groups (*javanica*, *arge*, *hispida*, *macrotis* and *thebaica*). Disagreements concerning the relationships between *javanica* and *arge* species groups as portrayed in Koopman (1994) and Griffiths (1997) led to these relationships being unresolved in the MRP tree. If the trees are reweighted *sensu* Purvis (1995*a*) (effectively upweighting the cladistic analysis of Griffiths, 1997), additional resolution is seen (Table 3) and follows Griffiths (1997) in placing the *arge* group (*Nycteris arge*, *N. intermedia*, *N. nana*, and *N. major*) as sister to the other nycterids, and supports the grouping of the exclusively Asian *javanica* group (*N. javanica* and *N. tragata*) as sister to *hispida*, *macrotis* and *thebaica* species groups.

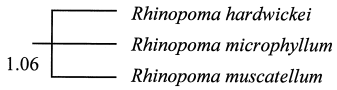

Fig. 6. Rhinopomatidae supertree.

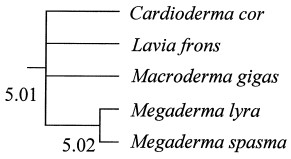

Fig. 7. Megadermatidae supertree.

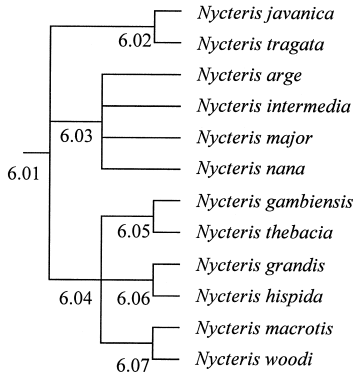

Fig. 8. Nycteridae supertree.

(8) Rhinolophidae

The Rhinolophidae MRP tree (Fig. 9) place *Rhinolophus monoceros*, *R. pusillus*, and the clade of *R. cornutus* plus *R. osgoodi* as sister groups to the rest of the rhinolophids (agreeing with Bogdanowicz & Owen, 1992), albeit with uncertain placements to one another. Similarly, the supertree supports the more basal placement of *R. imaizumii*, *R. lepidus*, *R. subbadius* and *R. cognatus* to the remaining rhinolophids (again following Bogdanowicz & Owen, 1992). However, with respect to the remaining species, there was virtually no agreement between sources (traditional taxonomies and cladistic analyses) and relationships were poorly resolved. The MRP supertree topology was largely unchanged with differential source tree weightings and source topology year (Table 3).

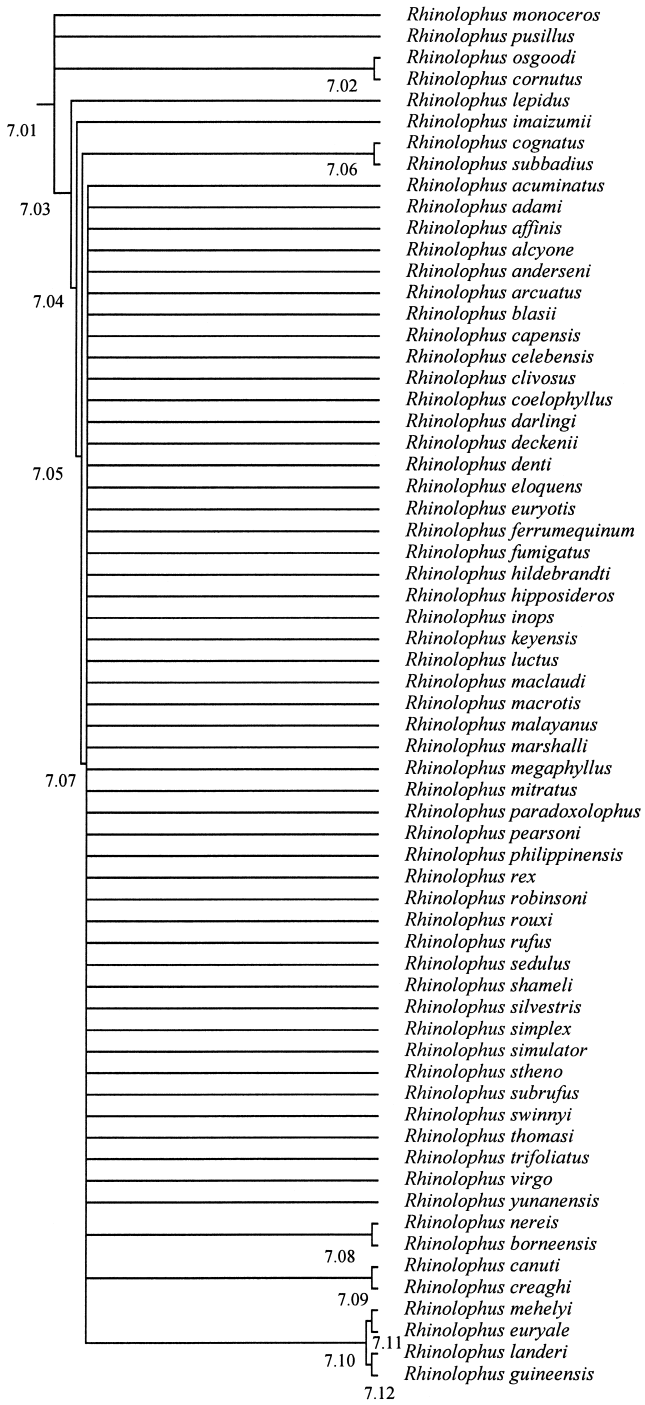

Fig. 9. Rhinolophidae supertree.

(9) Hipposideridae

The MRP supertree of Hipposideridae (Fig. 10) is poorly resolved reflecting disagreement among the source trees. The traditional split of this family into the tribes Coelopsini (containing genera *Coelops* and *Paracoelops*) and Hipposiderini (containing the remaining genera: *Anthops*, *Asellia*, *Aselliscus*, *Cloeotis*, *Rhinonicteris*, *Triaenops*, and *Hipposideros*) is supported in the supertree. *Rhinonicteris* and *Triaenops* form a clade that is the sister group to the rest of the species in Hipposiderini, with *Aselliscus tricuspidatus* and *Anthops* as successive sister taxa to this clade. The monophyly of *Hipposideros* and *Aselliscus* was not

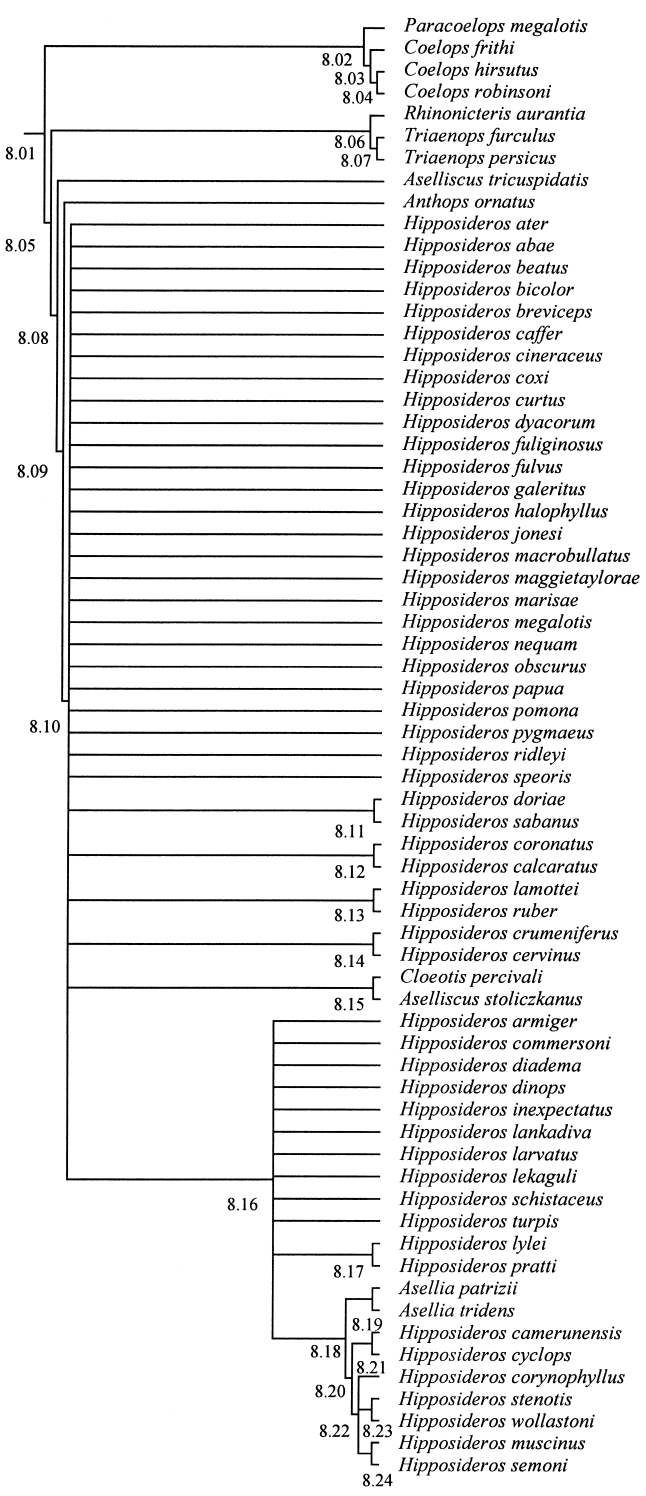

Fig. 10. Hipposideridae supertree.

supported. Relationships among the remaining taxa were largely unresolved, and there was no support for the seven taxonomic species groups of *Hipposideros* proposed by Hill (1963). A clade consisting of the *cyclops*, *pratti*, *armiger* and *diadema* species groups of *Hipposideros* plus *Asellia* was found in the consensus,

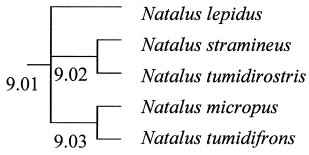

Fig. 11. Natalidae supertree.

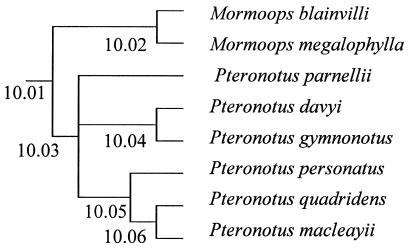

Fig. 12. Mormoopidae supertree.

supported by the majority of the source trees including more recent cladistic studies (although Bremer support values for this node are low). Relationships among the species in this clade were largely unresolved due to conflict among the source trees.

Although the supertree topology was insensitive to source year, differentially weighting the sources [effectively down-weighting the taxonomies of Corbet and Hill (1991) and Koopman (1994)] decreased resolution from 36% to 30% (Table 3) because the two recent cladistic estimates are largely incongruent (i.e. Bogdanowicz & Owen, 1998; Hand & Kirsch, 1998). Except for *Aselliscus tricuspidatus* being the sister group the remainder of the family, most higher-level relationships were unresolved. In general, the MRP supertree reflects the lack of signal in the present sources and the current confusion concerning their interrelationships.

(10) Natalidae

The MRP tree of Natalidae (Fig. 11) is the single most parsimonious tree and is congruent with the source trees. The MRP estimate follows Koopman (1994) and Corbet and Hill (1991) grouping natalid species into three species groups (*natalus*, *chilonatalus* and *nyctiellus* species groups). Relationships among these groups were not resolved in the MRP tree. Analyses examining the effect of source year or quality were not applicable.

(11) Mormoopidae

The MRP estimate (Fig. 12) represents the strict consensus two equally most parsimonious trees of the

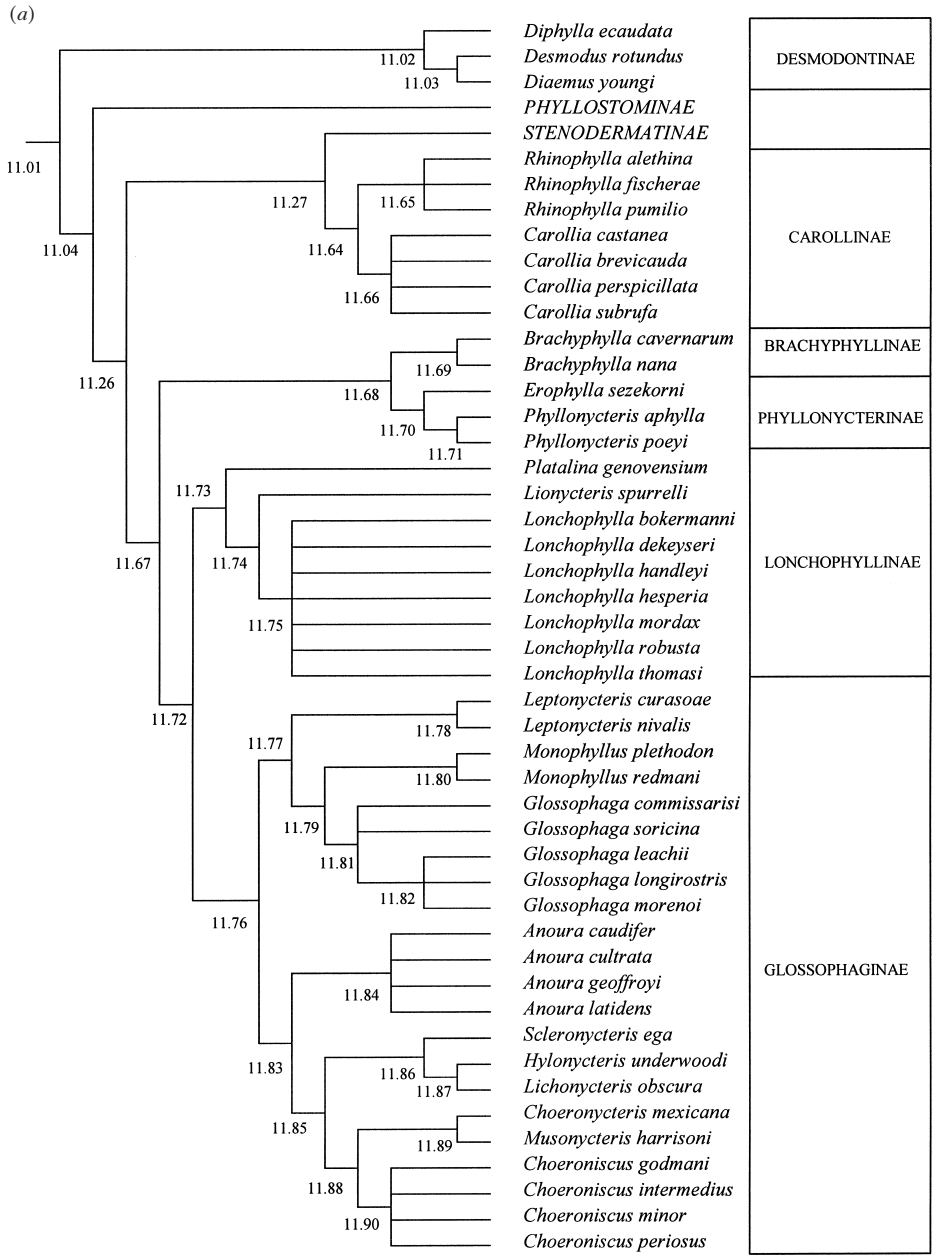

Fig. 13. A. The supertree for Phyllostomidae excluding Phyllostominae and Stenodermatinae. Relationships within these excluded clades are shown in B and C, respectively.

eight species within this family. The MRP tree is well resolved and strongly places the genus *Mormoops* as the sister taxon to *Pteronotus* (in agreement with all source trees). The MRP estimate supports the division of *Pteronotus* into three subgenera (*Pteronotus*, *Chilonycteris* and *Phyllodia*). Disagreements concerning relationships among these subgenera in the source trees led to a loss of resolution in the MRP estimate. Differentially weighting the source trees resolved the relationships among the subgenera (Table 3). The weighted analysis did not support the monophyly of subgenus *Pteronotus* (*P. davyi and P. gymnonotus*) but placed *P. davyi*, *P. parnelli* and *P. gymnonotus* as successive sister taxa to other *Pteronotus* species. When only source topologies from the 1990s were considered, the MRP supertree estimate reflected that of Simmons & Conway (2001).

(12) Phyllostomidae

The phylogenetic signal in the Phyllostomidae supertree is strong and the topology well resolved (Fig. 13,

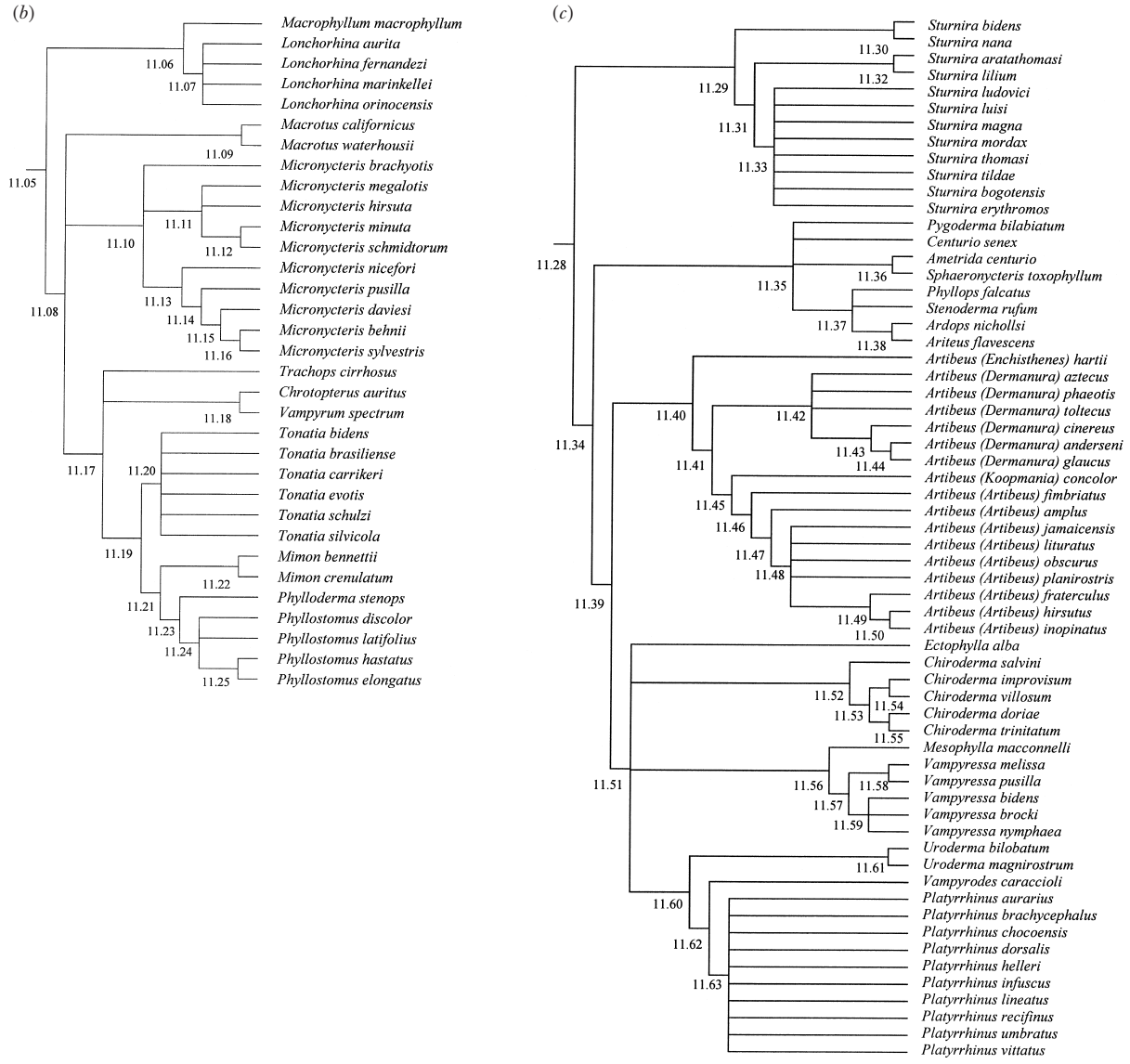

Fig. 13 For legend see facing page.

Table 3). The supertree supports the monophyly of the eight traditionally recognised subfamilies (Desmodontinae, Phyllostominae, Brachyphyllinae, Phyllonycterinae, Glossphaginae, Lonchophyllinae, Carollinae and Stenodermatinae). Desmodontinae is placed as the sister taxon to the other phyllostomid clades (supported by Hood & Smith, 1982; Wetterer, Rockman & Simmons, 2000). Among the remaining taxa, Phyllostominae is sister to the other six subfamilies (Phyllonycterinae, Brachyphyllinae, Lonchophyllinae, Glossphaginae, Stenodermatinae and Carollinae), concordant with evidence presented in Hood & Smith (1982), Baker, Hood & Honeycutt (1989), Van Den Bussche (1991), Baker *et al*. (2000). However, this arrangement is relatively poorly supported and disagrees with an influential source tree in the estimate (Wetterer *et al*., 2000) that identified a clade containing Phyllostominae, Stenodermatinae and Carollinae. However, relevant nodes in the Wetterer *et al*. (2000) tree were also poorly supported in bootstrap and decay analyses. Taken on balance the arrangement of Phyllostominae as indicated in the supertree seems more likely.

The supertree identified Stenodermatinae + Carollinae as the sister clade of Phyllonycterinae, Brachyphyllinae, Lonchophyllinae and Glossophaginae. Within Stenodermatinae (Fig. 13C), the supertree supports the sister-group placement of *Sturnira* and monophyly of two sister clades, Ectophyllina and Stenodermatina (Smith, 1976; Baker *et al*., 1989; Lim, 1993; Wetterer *et al*., 2000). The placement of the *Artibeus* complex (*Enchisthenes*,

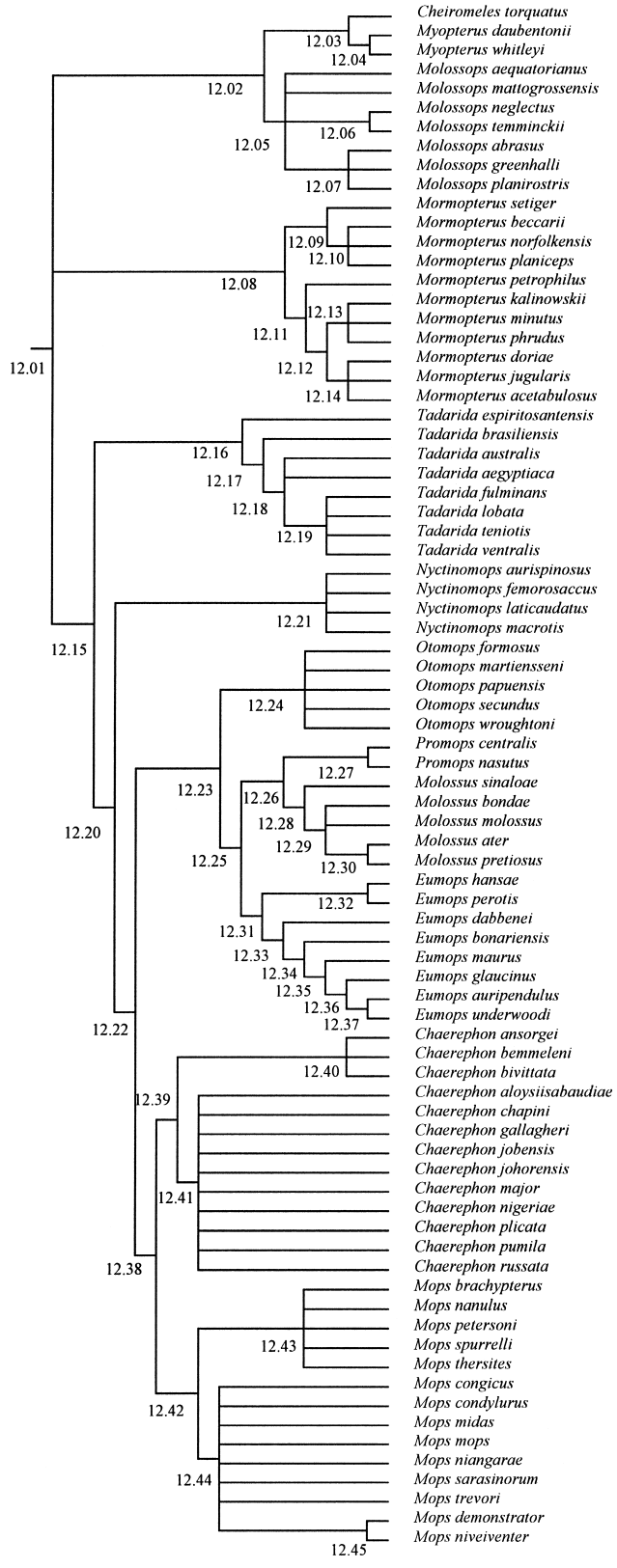

Fig. 14. Molossidae supertree.

Dermanura, *Artibeus*, and *Koopmania*) agrees with more recent studies placing *Enchisthenes* and *Dermanura*, as successive sister taxa to the clade of *Artibeus* and *Koopmania* (Pumo *et al*., 1996; Van Den Bussche, Hudgeons & Baker, 1998*b*; Wetterer *et al*., 2000). Although the monophyly of several phyllostomid genera has been questioned (Wetterer *et al*., 2000; Baker *et al*. 2000), all generic groupings (*sensu* Koopman, 1994) were supported in this analysis.

Although the resolution of the supertree increased when source studies were differentially weighted, only a small percentage of the nodes in the topology were changed (Table 3). The increase in resolution was concentrated within generic relationships within Stenodermatinae and Phyllostominae; higher-level relationships did not change. Greater topology differences were found when the analysis was split by source decade. Using data from the 1980s and above did not support the monophyly of Phyllostominae. Clades within Phyllostominae formed successive sister taxa to the clade containing Stenodermatinae + Carollinae and Brachyphyllinae + Phyllonycterinae + Lonchophyllinae + Glossophaginae. The topology using sources from the 1990s and above was congruent with the unweighted analysis. Monophyly of all subfamilies was supported, although there was some loss of resolution between subfamilies, e.g. relationships between Phyllostominae, Stenodermatinae + Carollinae and Brachyphyllinae + Phyllonycterinae + Lonchophyllinae + Glossophaginae clades were unresolved.

(13) Molossidae

The Molossidae MRP tree (Fig. 14) represents the strict consensus of 5299 trees (Table 3). The monophyly of Legendre's (1984*b*) three subfamilies (Tadaridinae, Molossinae and Chieromelinae) is not supported in the consensus. Instead, there is more support for Freeman's (1981) two proposed molossid clades (*Tadarida*-like and *Mormopterus*-like bats), although the *Mormopterus*-like clade is confined to *Molossops*, *Myopterus* and *Cheiromeles* (i.e. excluding *Mormopterus*) in our supertree. This reflects disagreements as to the affinities of *Mormopterus* from both molecular and morphological studies (Freeman, 1981; Legendre, 1984*b*; Hand, 1990; Sudman *et al*., 1994; Pierson, 1986). The monophyly of the *Tadarida*-like group was supported in the supertree, with *Tadarida* and *Nyctinomops* forming successive sister taxa to the rest of the *Tadarida*-like bats, although the Bremer support values for this

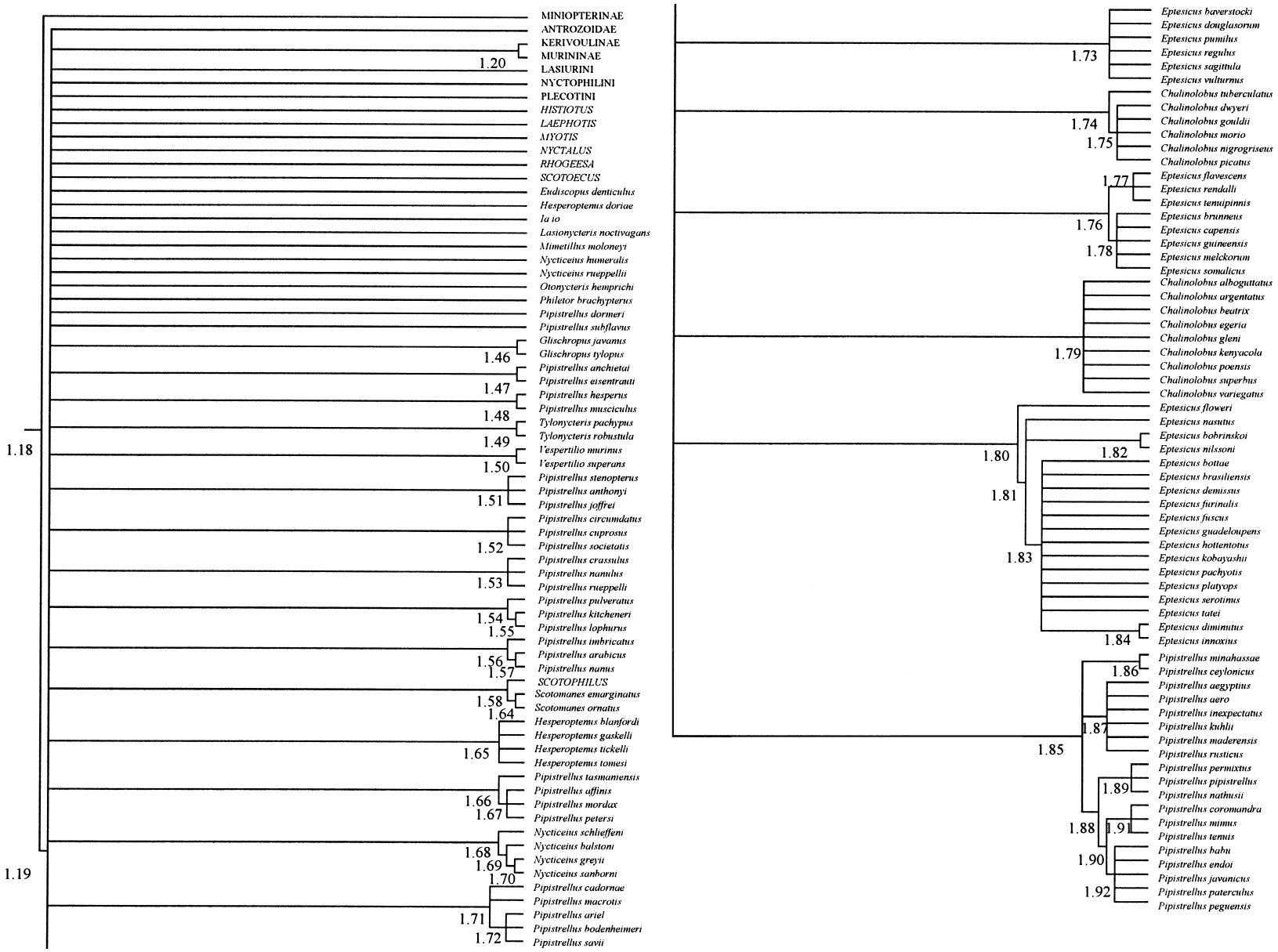

Fig. 15. The supertree for Vespertilionidae excluding Miniopterinae, Kerivoulinae, Murininae, Plecotini, Lasiurini, Nyctophilini, *Histiotus*, *Laephotis*, *Nyctalus*, *Rhogeesa*, *Scotoecus*, *Scotophilus*, *Myotis* and Antrozoidae. Relationships within these excluded clades are shown in B, C, D, E, F, G, H, I, J, K, L, M and N, respectively except for relationships within Antrozoidae where the two species (*Antrozous dubiaquercus* and *A. pallidus*) are represented by a single bifurcating node.

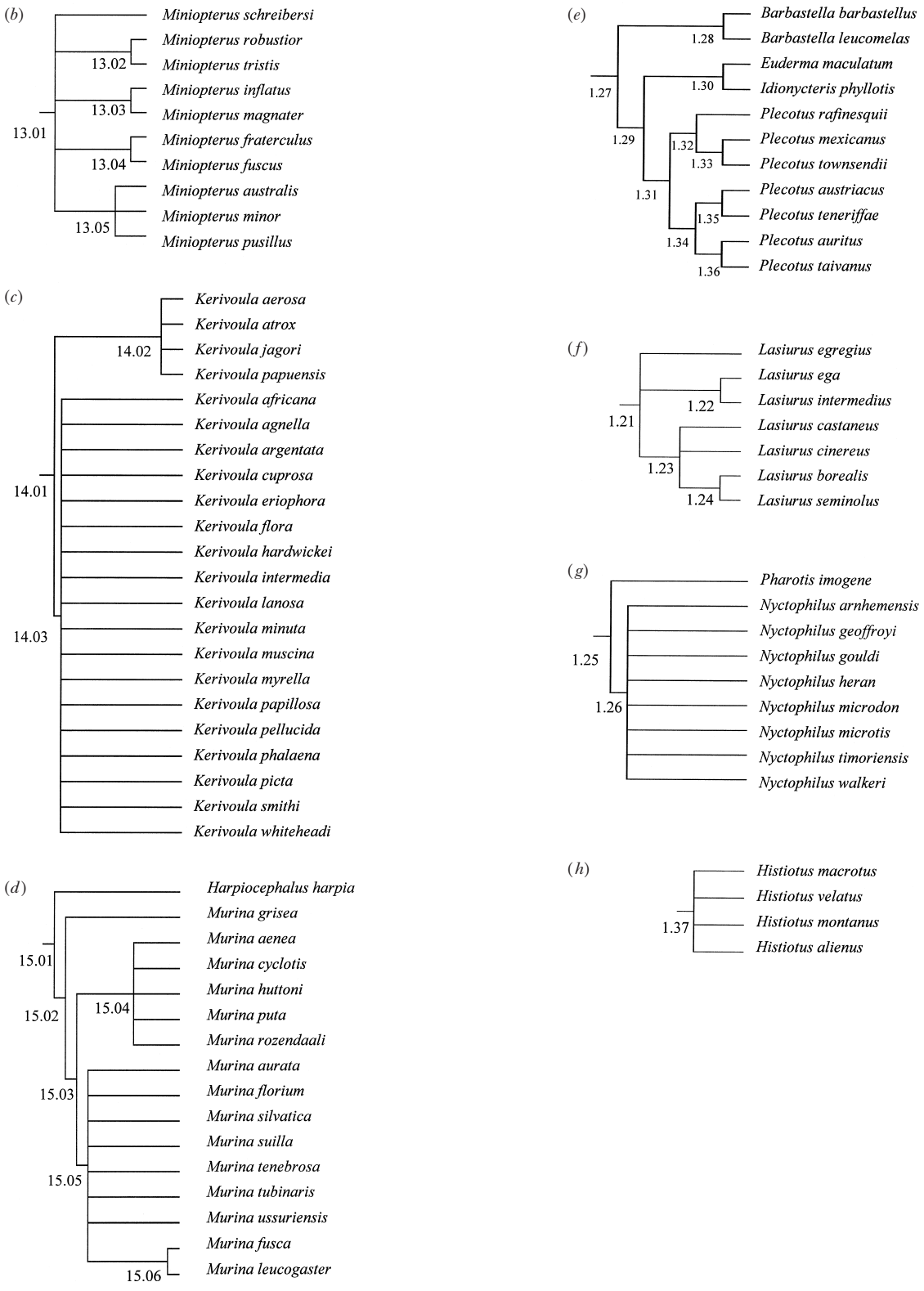

Fig. 15. For legend see page 243.

node are low. The remaining *Tadarida*-like bats were clustered into two sister clades, one containing *Otomops*, *Eumops*, *Promops* and *Molossus* and the other containing *Chaerephon* and *Mops*.

Differentially weighting the source trees did not change the lower-level topology but did result in changes in higher-level tree structure and some loss of resolution (Table 3). For example, the weighted

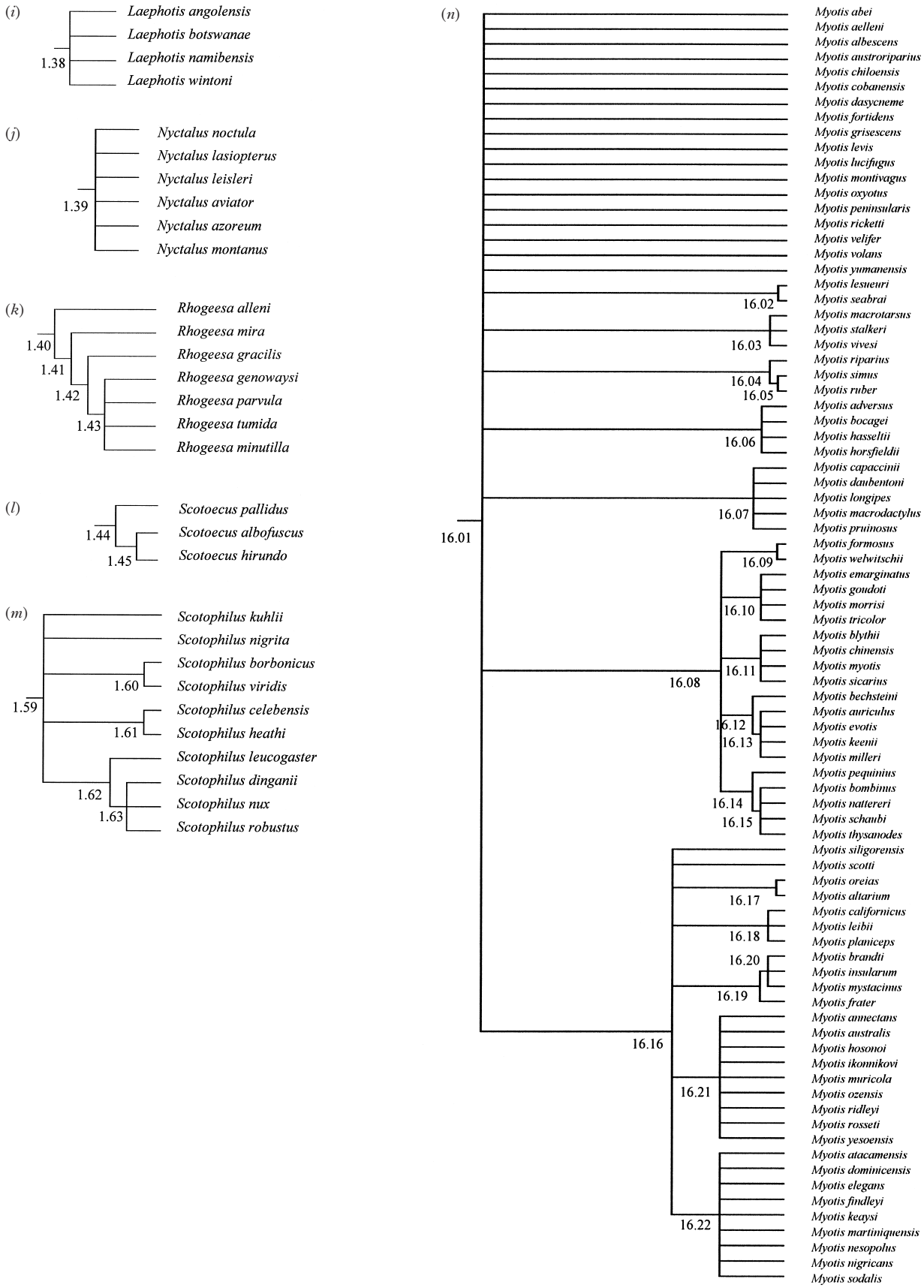

Fig. 15. For legend see page 243.

MRP tree topology does not support the monophyly of *Tadarida* (*sensu* Koopman, 1994), with *Tadarida brasiliensis* and *T. espiritosantensis* being separated from the rest of the *Tadarida* clade. The relationships within the major clades identified in the unweighted analysis (i.e. *Molossops Myopterus* + *Cheiromeles* and *Otomops* + *Eumops* + *Promops* + *Molossus* and *Chaerephon* + *Mops*) did not change, although their interrelationships are unresolved. Using sources from the 1980s and above had little effect on topology although some intrageneric relationships became unresolved because certain clades are only examined in earlier studies (e.g. *Eumops*: Eger, 1977; *Molossus*: Dolan, 1989). Using only sources from the 1990s and above resulted in a greater loss of resolution among the higher-level relationships (Table 3) with the majority of the genera being of uncertain placement relative to each other.

(14) Vespertilionidae

The monophyly of Vespertilionidae (*sensu* Koopman, 1994) is supported in the supertree with the exception that the subfamily Tomopeatinae is removed. The monophyly of the clade reflects traditional and more recent analyses (e.g. Koopman, 1994; Van den Bussche & Hoofer, 2001) although it is disputed by others (i.e. Pierson, 1986; Simmons & Geisler, 1998). For example, Simmons and Geisler (1998) found 'Antrozoidae' to be much more distantly related to the rest of the vespertilionids, whereas Hoofer and Van Den Bussche (2001) found no evidence to support this arrangement in a later molecular analysis. The relationships in the supertree (Fig. 15) are poorly resolved, reflecting a lack of agreement between the few sources that have investigated this part of the bat phylogeny. With the exception of the sister-group status of Miniopterinae to the rest of the vespertilionids and the clade formed by Murinae and Kerivoulinae, the higher-level relationships among the subfamilies were unresolved in the supertree. This conservative arrangement is caused by substantial historical disagreements in the placement of these clades and the lack of any current consensus.

Relationships within Miniopterinae (Fig. 15B) follow Koopman's (1994) grouping of miniopterid species into five subgenera (*Australis*, *Fuscus*, *Schreibersi*, *Inflatus*, *Tristis*). The supertree of the subfamily Kerivoulinae (Fig. 15C) splits *Kerivoula* into two subgenera (*Kerivoula* and *Phoniscus*) consistent with all the source trees. The species relationships within these subgenera are unresolved due to lack of information. The species relationships in subfamily Murininae (Fig. 15D) follow Koopman (1994) by splitting the clade into two subgenera (*Murina* and *Harpiola*) and further splitting the subgenus *Murina* into two groups (*suilla* and *cyclotis* species groups). Again, species relationships within these subgeneric groupings are not resolved due to lack of information. Differential weighting and decade did not have any effect on topology structure for any of these subfamily topologies (Table 3).

As the monophyly of the subfamilies Miniopterinae, Murininae, Kerivoulinae and 'Antrozoidae' were assumed *a priori*, the supertree analysis did not test these assumptions. However, the subfamily Vespertilioninae (*sensu* Koopman, 1994) was not assumed to be monophyletic and indeed it is found to be paraphyletic in the supertree (Fig. 15). There is support for monophyly of some of the tribes Koopman (1994) identified within Vespertilioninae. For example, the monophyly of tribe Plecotini (Koopman, 1994; Volleth & Heller, 1994) was supported without the addition of *Otonycteris* [as suggested by Horacek (1991) and Qumsiyeh and Bickham (1993)]. Within Plecotini, a close relationship between *Euderma* and *Idionycteris*, and *Plecotus* (*Plecotus*) and *Plecotus* (*Corynorhinus*), with *Barbastella* as their sister group, appears in the supertree (Fig. 15E). Monophyly of two of Koopman's (1994) other tribes in Vespertilioninae was also supported: Lasiurini (Fig. 15F) and Nyctophilini (Fig. 15G). In Lasiurini, the subgenus *Dasypterus* (*sensu* Koopman, 1994) appears monophyletic, but a second subgeneric grouping of *Lasiurus* (*Lasiurus*) is not. The position of *L. egregius* was unresolved because this species was not included in several well-resolved source trees (i.e. Baker *et al.*, 1988*b*; Morales & Bickham, 1995).

The other tribes within Vespertilioninae were found to be paraphyletic (i.e. Myotini, Vespertilionini, and Nycticeini) as were several genera (*Chalinolobus*, *Eptesicus*, *Nycticeius* and *Pipistrellus* as defined by Koopman, 1993). Additionally, neither of the two putative sister clades within Vespertilioninae proposed by Hill and Harrison (1987) – one containing *Eudiscopus*, *Pipistrellus*, *Nyctalus*, *Glischropus*, *Laephotis*, *Philetor*, *Hesperoptenus* and *Chalinolobus* and the other containing *Ia*, *Vespertilio*, *Histiotus*, *Tylonycteris*, *Mimetillus* and *Eptesicus* – were monophyletic (Fig. 15A). Relationships within *Scotophilus* follow Koopman (1994), who assigned subspecific status to some taxa later recognised as full species by other authors (Fig. 15M). Neither the

monophyly of *Pipistrellus* or the subgenus *Pipistrellus* (as defined by Koopman, 1993) was supported in the supertree, although several related subgeneric clades appeared monophyletic in the supertree (*Arielulus*, *Falsistrellus*, *Neoromicia*, *Scotozous*, *Vansonia* and *Vespadelus*). Relationships among *Myotis* species (Fig. 15N) were poorly resolved reflecting the sparse amount of phylogenetic information available for these taxa, and disagreements between traditional taxonomies (Findley, 1972; Koopman, 1994) and less taxonomically complete molecular sequence analyses (Hoofer & Van Den Bussche, 2001). The MRP tree supports the monophyly of three subgenera traditionally recognised within *Myotis* (*Myotis*, *Selysius* and *Cistugo*). However, the subgenus *Leuconoe* was found to be paraphyletic although some clades traditionally recognised within *Leuconoe* were supported (*macrotarsus*, *ruber*, *adversus* and *daubentoni* species groups).

Differentially weighting the source trees increased the resolution among higher-level relationships (Table 3). Miniopterinae remained the sister taxon to the rest of the vespertilionids and Myotis, Murinae, Kerivoulinae and Lasiurini, and *Scotophilus* + *Scotomanes* formed clades which were successive sister taxa to the rest of the species in the family. The suprageneric level relationships among the rest of the vespertilionids were unresolved, although Nyctophilini, Antrozoidae, *Rhogessa*, *Otonycteris* and Plecotini together formed a clade in the supertree. Using sources from different decades produced a similar topology to the weighted analysis, although in the topology produced using sources from the 1990s and above a clade consisting of Antrozoidae, Nycticeini and Plecotini was found to be sister taxa to the rest of the vespertilionids.

VI. CONCLUSIONS

(1) The bat supertree that we present here should not be viewed as the definitive work on phylogenetic relationships of bats, but rather as a substantive working hypothesis. It is not intended as a substitute for comprehensive phylogenetic analyses of primary molecular and morphological data, which are ultimately the most appropriate means of developing robust phylogenies. In an ideal world, we would already have at hand a complete phylogeny of bats based on numerous congruent morphological and molecular data sets. Unfortunately, the state of chiropteran systematics today is such that evolutionary relationships of many species have never been formally investigated, and disagreements among results of alternative studies (almost always confused by different taxonomic samples, data sources and analytical methods) further complicate the picture.

(2) In the absence of comprehensive phylogenetic analyses of primary data, the bat supertree, derived using principles of taxonomic congruence, provides an alternative to *ad hoc* hypotheses and 'cut and paste' phylogenies as we await future character congruence (total evidence) studies of bat relationships. The bat supertree provides a conservative phylogenetic hypothesis that can serve many purposes. Because the supertree method depends on congruence of source trees to support clades, lack of information and significant disagreements among studies tend to be reflected as loss of resolution in the consensus supertree. Our experiments with differential weighting of different source trees and sorting the data by decade of source publication provide further tests of clade stability, and the Bremer support values given in Appendix 2 are indicative of the amount of overall support for various groupings. In this context, the bat supertree provides a relatively conservative phylogenetic framework for future comparative studies. The latter point is especially important. Bats are unique among mammals in their ability for powered flight and often depart from the mammalian 'norm' in several other characteristics (e.g. high relative longevity; Jones & MacLarnon, 2001). Our supertree provides the means to analyse numerous comparative questions within the Chiroptera at a much broader scale than was previously possible.

(3) The bat supertree is also useful for workers interested in systematics *per se*, as it identifies groups that are desperately in need of further study and provides a starting point for future systematic studies (e.g. by suggesting appropriate outgroups for intensive studies of particular clades). This analysis highlights several ways of identifying priorities for further phylogenetic studies in order of decreasing priority; (1) poorly studied groups (e.g. Kerivoulinae, Vespertilionidae, Natalidae, Rhinolophidae, Nycteridae); (2) poorly resolved groups (e.g. Kerivoulinae, Rhinolophidae, Vespertilionidae, Hipposideridae); and (3) poorly supported groups (low Bremer supports) (e.g. Vespertilionidae, Rhinolophidae, Hipposideridae, Pteropodidae). Additionally, it serves to highlight those groups that are relatively well studied (e.g. Phyllostomidae, Mormoopidae).

(4) It is to be expected that our ideas of bat relationships will change over time as new data sets

are developed and more comprehensive analyses completed. The supertree presented here is based on studies published (or known by us to be in press) prior to the end of the year 2000. Every year will bring new studies, and incorporation of these into future supertree analyses will doubtless somewhat change the tree topology and perceived support for some clades. For example, results of Springer *et al.*'s (2001) analyses of numerous mitochondrial and nuclear DNA sequences supported monophyly of a new group they named Yinpterochiroptera (consisting of Pteropodidae + Rhinolophoidea), a group previously recovered in some molecular studies but which did not appear in our supertree. Inclusion of additional studies such as this one may ultimately serve to 'shift the balance' in favour of novel hypotheses in future iterations of the bat supertree. However, it is also interesting to note that even as major changes are being proposed, new studies frequently simply offer increased support for old ideas of relationships. For example, the same tree that supported monophyly of Yinpterochiroptera also supported a close relationship between Vespertilionidae and Molossidae, monophyly of Rhinolophoidea, and monophyly of Megachiroptera (Springer *et al.*, 2001). Thus, even as some systematic hypotheses become controversial or require modification, others are becoming even more deeply entrenched.

(5) With luck, 20 years from now we will have a complete phylogeny of bats based on simultaneous analysis of hundreds of gene sequences and morphological data from all organ systems, all of which converge (hopefully!) on a single well-supported topology. In the meantime, the bat supertree presented here offers an iterative summary of previous work, a working hypothesis that we hope will stimulate additional research in many areas of bat ecology, evolution and systematics.

VII. ACKNOWLEDGEMENTS

We thank the many people that have offered their invaluable advice and support over the course of this seemingly endless project, especially M. Charleston, G. Cowlishaw, J. Dunlop, J. Gittleman, R. Greyner, D. Hosken, J. Hutcheon, N. Isaac, P. Jenkins, G. Jones, C. Nunn, P. Racey, C. Ross, M. Sanderson, N. Thomas and J. Worthington-Wilmer. We also would like to thank two anonymous referees and W. Foster for enthusiastic comments on the manuscript. Financial support was from University of Surrey Roehampton, UK (K. E. J. and A. M.), NERC grants GR3/11526 and GR8/04371 (A. P. and K. E. J.), University of Virginia (K. E. J.) and NSF Research Grant DEB-9873663 (N. B. S).

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IX. APPENDICES

Appendix 1. Sources for supertree compilation

Top matrix: Williams *et al.* (1970); La Val (1973*b*); Hill (1974); Smith (1976); Bickham (1979); Van Valen (1979); Novacek (1980); Arnold *et al.* (1982); Hood and Smith (1982); Smith (1972, reanalysed by Arnold *et al.*, 1982); Kitchener and Caputi (1985); Kitchener *et al.* (1986); Pierson (1986); Hill and Harrison (1987); Baker *et al.* (1988*b*); Robbins and Sarich (1988); Corbet and Hill (1991); Horacek (1991); Morales *et al.* (1991); Van Den Bussche (1991); Frost and Timm (1992); Griffiths *et al.* (1992); Tumlison and Douglas (1992); Luckett (1993); Qumsiyeh and Bickham (1993); Stanhope *et al.* (1993); Koopman (1994); Sudman *et al.* (1994); Volleth and Heller (1994); Barratt *et al.* (1995); Morales and Bickham (1995); Cypher (1996); Genoways and Baker (1996); Porter *et al.* (1996); Barratt *et al.* (1997); Hollar and Springer (1997); McKenna and Bell (1997); Bogdanowicz, Kaspar and Owen (1998); Kirsch *et al.* (1998); Simmons and Geisler (1998); Juste *et al.* (1999); Kennedy *et al.* (1999); Baker *et al.* (2000); Ditchfield (2000); Teeling *et al.* (2000); Wetterer *et al.* (2000); Hoofer & Van Den Bussche (2001); Murphy *et al.* (2001); Simmons and Conway (2001); Van Den Bussche & Hoofer (2001).

Emballonuridae: Barghoorn (1977); Pierson (1986); Robbins and Sarich (1988); Corbet and Hill (1991); Griffiths and Smith (1991); Griffiths *et al.* (1991); Chimimba and Kitchener (1991); Koopman (1994); McKenna and Bell (1997); Dunlop (1998); Kirsch *et al.* (1998).

Hipposideridae: Pierson (1986); Corbet and Hill (1991); Koopman (1994); McKenna and Bell (1997); Bogdanowicz and Owen (1998); Hand and Kirsch (1998).

Kerivoulinae: Corbet and Hill (1991); Koopman (1994).

Megadermatidae: Hand (1985); Corbet and Hill (1991); Griffiths *et al.* (1992); Koopman (1994).

Miniopterinae: Maeda (1982); Koopman (1994).

Molossidae: Eger (1977); Freeman (1981); Legendre (1984*a*); Hand (1985); Pierson (1986); Dolan (1989); Corbet and Hill (1991); Koopman (1994); Sudman *et al.* (1994); Kirsch *et al.* (1998); Kennedy *et al.* (1999); Van Den Bussche & Hoofer (2001).

Mormoopidae: Smith (1972, reanalysed by Arnold *et al.*, 1982); Arnold *et al.* (1982); Hood and Smith (1982); Pierson (1986); Corbet and Hill (1991); Koopman (1994); Simmons & Conway (2001).

Murininae: Corbet and Hill (1991); Koopman (1994).

Myotis: Findley (1972); La Val (1973a); Corbet and Hill (1991); Koopman (1994); Topal (1997); Hoofer & Van Den Bussche (2001).

Natalidae: Corbet and Hill (1991); Koopman (1994).

Nycteridae: Koopman (1994); Griffiths (1997); Van Cakenberghe & De Vree (1985, 1993*a*, *b*, 1998).

Phyllostomidae: Phillips (1971); Pine (1972); Greenbaum *et al.* (1975); Gardner (1977); Straney *et al.* (1979, reanalysed by Smith and Hood, 1984); Griffiths (1982); Haiduk and Baker (1982); Koop and Baker (1983); Pierson (1986); Honeycutt and Sarich (1987*a*, *b*); Owen (1987); Baker *et al.* (1988*a*, 1989); Corbet and Hill (1991); Owen (1991); Pacheco and Patterson (1991); Van Den Bussche (1991); Gimenez (1993); Lim (1993); Van Den Bussche & Baker (1993); Webster (1993); Baker *et al.* (1994); Koopman (1994); Marques-Aguiar (1994); Pumo *et al.* (1996); Simmons (1996); McKenna and Bell (1997); Kirsch *et al.* (1998); Lim and Engstrom (1998); Van Den Bussche *et al.* (1998*b*); Kennedy *et al.* (1999); Baker *et al.* (2000); Ditchfield (2000); Wetterer *et al.* (2000); Simmons and Conway (2001); Van Den Bussche and Hoofer (2001).

Pteropodidae: Hood (1989); Hill (1992); Koopman (1994); Colgan and Flannery (1995); Springer *et al.* (1995); Bergmans (1997); Hollar and Springer (1997); Juste *et al.* (1997); McKenna and Bell (1997); Juste *et al.* (1999); Kennedy *et al.* (1999); Kirsch *et al.* (1995); Schmitt *et al.* (1995); Teeling *et al.* (2000). *Pteropus*: Koopman (1994); Colgan and Flannery (1995); Kirsch *et al.* (1995); Juste *et al.* (1999).

Rhinolophidae: Pierson (1986); Qumsiyeh *et al.* (1988); Bogdanowicz and Owen (1992); Koopman (1994); Maree and Grant (1997).

Appendix 2. Nodal summary statistics in Figs 3–15. Bremer support values for each node are given and whether the node was present in the differentially weighted (Wt), 1980s and above (1980s) and 1990s and above (1990s) analyses. p, the node was present in the other topologies; ab, absent; c, node was collapsed; r, resolved; pr, partially resolved; n/a, not applicable.

Node	Bremer Support	Wt	1980s	1990s	Node	Bremer Support	Wt	1980s	1990s
1.01	n/a	p	p	p	7.05	1	p	n/a	p
1.02	11	p	p	p	7.06	1	c	n/a	c
1.03	2	ab	ab	ab	7.07	1	c	n/a	c
1.04	1	ab	p	p	7.08	1	p	n/a	p
1.05	1	ab	p	p	7.09	1	p	n/a	p
1.06	2	p	p	p	7.10	1	p	n/a	p
1.07	3	p	p	p	7.11	1	p	n/a	p
1.08	3	p	p	ab	7.12	1	p	n/a	p
1.09	5	p	p	p	8.01	n/a	p	n/a	p
1.10	3	r	r	r	8.02	2	p	n/a	p
1.11	3	p	p	p	8.03	2	p	n/a	p
1.12	1	ab	p	p	8.04	1	p	n/a	p
1.13	5	p	p	p	8.05	1	c	n/a	p
1.14	7	p	p	p	8.06	3	p	n/a	p
1.15	2	p	p	c	8.07	3	p	n/a	p
1.16	2	p	p	p	8.08	2	c	n/a	p
1.17	2	p	p	p	8.09	2	c	n/a	p
1.18	4	p	p	p	8.10	2	p	n/a	p
1.19	3	pr	pr	c and pr	8.11	1	p	n/a	p
1.20	2	p	p	p	8.12	1	p	n/a	p
1.21	2	p	p	p	8.13	1	p	n/a	p
1.22	1	p	p	p	8.14	1	p	n/a	p
1.23	1	p	p	p	8.15	1	p	n/a	p
1.24	1	p	p	p	8.16	1	p	n/a	p
1.25	4	p	p	p	8.17	1	p	n/a	p
1.26	2	p	p	p	8.18	1	p	n/a	p
1.27	3	p	p	p	8.19	3	p	n/a	p
1.28	5	p	p	p	8.20	1	p	n/a	p
1.29	2	p	p	p	8.21	1	p	n/a	p
1.30	6	p	p	p	8.22	1	p	n/a	p
1.31	2	p	p	p	8.23	1	p	n/a	p
1.32	7	p	p	p	8.24	1	p	n/a	p
1.33	1	p	p	p	9.01	n/a	n/a	n/a	n/a
1.34	3	p	p	p	9.02	2	n/a	n/a	n/a
1.35	1	p	p	p	9.03	2	n/a	n/a	n/a
1.36	1	p	p	p	10.01	n/a	p	n/a	p
1.37	2	p	p	p	10.02	3	p	n/a	p
1.38	2	p	p	p	10.03	4	r	n/a	r
1.39	3	p	p	p	10.04	1	ab	n/a	p
1.40	4	p	p	p	10.05	3	p	n/a	p
1.41	3	p	p	p	10.06	1	p	n/a	p
1.42	1	p	c	c	11.01	n/a	p	p	p
1.43	1	p	p	p	11.02	15	p	p	p
1.44	3	p	p	p	11.03	5	p	p	p
1.45	1	p	c	c	11.04	3	p	p	p
1.46	2	p	p	p	11.05	3	p	ab	p

Appendix 2 (*cont.*)

Node	Bremer Support	Wt	1980s	1990s	Node	Bremer Support	Wt	1980s	1990s
1.47	2	p	p	p	11.06	5	p	p	p
1.48	1	p	p	p	11.07	5	p	p	p
1.49	3	p	p	p	11.08	1	r	ab	r
1.50	2	p	p	p	11.09	9	p	p	p
1.51	4	p	p	p	11.10	2	r	r	r
1.52	3	p	p	p	11.11	4	r	p	p
1.53	2	p	p	p	11.12	1	p	p	p
1.54	1	p	p	p	11.13	2	p	p	p
1.55	1	p	p	c	11.14	1	p	p	p
1.56	1	p	p	c	11.15	1	p	p	p
1.57	1	p	p	c	11.16	2	p	p	p
1.58	4	p	p	c	11.17	3	p	ab	ab
1.59	1	p	p	p	11.18	2	p	p	p
1.60	1	p	p	p	11.19	3	p	p	p
1.61	1	p	p	p	11.20	5	p	p	p
1.62	1	p	p	p	11.21	2	p	ab	p
1.63	1	p	p	p	11.22	7	p	p	p
1.64	2	p	p	p	11.23	4	p	p	p
1.65	2	p	p	p	11.24	5	p	p	p
1.66	2	p	p	p	11.25	3	p	p	p
1.67	2	p	p	p	11.26	2	p	p	c
1.68	1	p	p	ab	11.27	6	p	p	p
1.69	1	p	p	p	11.28	9	p	p	p
1.70	1	p	p	c	11.29	10	p	p	p
1.71	1	p	p	p	11.30	3	p	p	p
1.72	1	p	p	c	11.31	3	p	p	c
1.73	2	p	p	p	11.32	1	p	p	c
1.74	3	p	p	p	11.33	1	p	p	c
1.75	1	p	p	p	11.34	3	p	p	p
1.76	3	p	p	p	11.35	6	pr	r	r
1.77	2	p	p	p	11.36	1	p	p	p
1.78	2	p	p	p	11.37	2	r	r	r
1.79	2	p	p	p	11.38	1	p	p	p
1.80	3	p	p	p	11.39	1	p	c	p
1.81	3	p	p	p	11.40	5	p	p	p
1.82	2	p	p	p	11.41	10	p	p	p
1.83	1	p	p	ab	11.42	8	p	p	pr
1.84	1	p	p	p	11.43	1	p	p	p
1.85	1	ab	ab	c	11.44	1	p	p	p
1.86	1	p	p	c	11.45	4	p	p	p
1.87	2	p	p	p	11.46	4	p	p	p
1.88	1	ab	ab	c	11.47	1	p	p	p
1.89	1	c	p	c	11.48	1	p	p	p
1.90	1	ab	ab	c	11.49	2	p	p	p
1.91	1	p	p	c	11.50	1	p	p	p
1.92	1	p	p	c	11.51	2	r	p	r
2.01	n/a	p	n/a	p	11.52	9	p	p	p
2.02	3	p	n/a	p	11.53	1	p	p	p
2.03	4	p	n/a	p	11.54	1	p	p	p
2.04	2	p	n/a	p	11.55	1	p	p	p
2.05	1	p	n/a	p	11.56	2	ab	c	c
2.06	1	p	n/a	p	11.57	2	p	c	p
2.07	1	p	n/a	p	11.58	2	c	p	p

Appendix 2 (*cont.*)

Node	Bremer Support	Wt	1980s	1990s	Node	Bremer Support	Wt	1980s	1990s
2.08	1	p	n/a	p	11.59	2	c	c	r
2.09	1	p	n/a	p	11.60	1	p	p	p
2.10	4	c	n/a	p	11.61	11	p	p	p
2.11	2	p	n/a	p	11.62	5	p	p	p
2.12	1	p	n/a	p	11.63	5	p	p	p
2.13	1	c	n/a	p	11.64	7	p	p	p
2.14	1	c	n/a	p	11.65	6	p	p	p
2.15	1	c	n/a	p	11.66	8	r	r	r
2.16	1	ab	n/a	p	11.67	6	p	p	p
2.17	1	c	n/a	p	11.68	7	p	p	c
2.18	3	p	n/a	p	11.69	5	p	p	p
2.19	1	p	n/a	p	11.70	8	p	p	p
2.20	1	p	n/a	p	11.71	6	p	p	p
2.21	1	p	n/a	p	11.72	4	p	p	c
2.22	1	p	n/a	p	11.73	6	p	p	p
2.23	2	c	n/a	p	11.74	3	p	c	c
2.24	1	ab	n/a	c	11.75	6	p	p	p
2.25	1	ab	n/a	c	11.76	6	p	p	p
2.26	2	p	n/a	p	11.77	3	p	c	c
2.27	4	r	n/a	p	11.78	8	p	p	p
2.28	2	ab	n/a	p	11.79	5	p	p	p
2.29	1	p	n/a	p	11.80	9	p	p	p
2.30	4	p	n/a	p	11.81	8	p	p	p
2.31	2	p	n/a	p	11.82	1	p	p	p
2.32	3	p	n/a	p	11.83	2	p	c	c
2.33	3	p	n/a	p	11.84	9	p	p	p
2.34	1	p	n/a	p	11.85	4	p	c	c
2.35	1	ab	n/a	p	11.86	4	p	c	c
2.36	4	p	n/a	p	11.87	3	p	c	c
2.37	1	p	n/a	p	11.88	8	p	p	p
2.38	3	p	n/a	p	11.89	3	p	p	c
2.39	2	ab	n/a	p	11.90	7	p	p	p
2.40	4	p	n/a	p	12.01	n/a	p	p	p
2.41	1	ab	n/a	c	12.02	1	p	p	c
2.42	2	ab	n/a	c	12.03	1	p	p	c
2.43	3	p	n/a	p	12.04	5	p	p	p
2.44	1	ab	n/a	c	12.05	2	pr	p	pr
2.45	4	p	n/a	p	12.06	2	p	p	p
2.46	1	ab	n/a	ab	12.07	4	p	p	p
2.47	2	p	n/a	p	12.08	3	p	p	p
2.48	6	p	n/a	p	12.09	1	p	p	c
2.49	3	p	n/a	p	12.10	4	p	p	p
2.50	2	p	n/a	p	12.11	1	p	p	c
2.51	1	p	n/a	c	12.12	1	p	p	p
2.52	1	p	n/a	p	12.13	1	p	p	p
2.53	3	ab	n/a	p	12.14	1	p	p	p
2.54	3	p	n/a	p	12.15	1	c	p	c
2.55	1	p	n/a	p	12.16	1	c	p	ab
2.56	1	p	n/a	p	12.17	1	c	p	c
2.57	3	c	n/a	p	12.18	1	p	p	p
2.58	1	p	n/a	p	12.19	1	p	p	p
2.59	2	c	n/a	p	12.20	1	c	p	ab

Appendix 2 (*cont.*)

Node	Bremer Support	Wt	1980s	1990s	Node	Bremer Support	Wt	1980s	1990s
2.60	1	c	n/a	p	12.21	5	p	p	ab
2.61	1	p	n/a	p	12.22	1	ab	p	c
2.62	2	p	n/a	p	12.23	1	ab	p	c
3.01	n/a	p	n/a	n/a	12.24	4	p	p	p
3.02	1	p	n/a	n/a	12.25	5	p	p	p
3.03	1	p	n/a	n/a	12.26	4	p	p	c
3.04	1	p	n/a	n/a	12.27	4	p	p	p
3.05	1	p	n/a	n/a	12.28	1	p	p	p
3.06	1	p	n/a	n/a	12.29	1	p	p	c
3.07	1	c	n/a	n/a	12.30	1	p	p	c
3.08	1	p	n/a	n/a	12.31	5	p	p	p
3.09	1	p	n/a	n/a	12.32	1	p	c	c
3.10	1	p	n/a	n/a	12.33	1	p	c	c
3.11	1	p	n/a	n/a	12.34	1	p	c	c
3.12	1	p	n/a	n/a	12.35	1	p	c	c
3.13	1	p	n/a	n/a	12.36	1	p	c	c
3.14	1	p	n/a	n/a	12.37	1	p	c	c
4.01	n/a	p	p	p	12.38	2	p	p	p
4.02	6	p	p	p	12.39	4	p	p	p
4.03	3	p	p	p	12.40	1	p	p	p
4.04	1	r	p	p	12.41	1	p	p	p
4.05	2	p	p	p	12.42	4	p	p	p
4.06	3	p	p	p	12.43	2	p	p	p
4.07	1	ab	p	p	12.44	2	p	p	p
4.08	3	p	p	p	12.45	1	p	p	p
4.09	1	p	p	p	13.01	n/a	n/a	n/a	p
4.10	1	p	p	p	13.02	2	n/a	n/a	p
4.11	1	p	p	p	13.03	1	n/a	n/a	p
4.12	1	p	p	p	13.04	1	n/a	n/a	p
4.13	1	p	p	p	13.05	1	n/a	n/a	p
4.14	2	p	p	p	14.01	n/a	n/a	n/a	n/a
4.15	2	p	p	p	14.02	2	n/a	n/a	n/a
4.16	2	p	p	p	14.03	2	n/a	n/a	n/a
4.17	1	p	p	p	15.01	n/a	n/a	n/a	n/a
4.18	2	p	p	p	15.02	2	n/a	n/a	n/a
4.19	2	p	p	p	15.03	2	n/a	n/a	n/a
4.20	1	p	p	p	15.04	1	n/a	n/a	n/a
4.21	3	p	p	p	15.05	2	n/a	n/a	n/a
4.22	2	p	p	p	15.06	1	n/a	n/a	n/a
4.23	4	p	p	p	16.01	n/a	pr	p	p
4.24	1	p	p	p	16.02	2	p	p	p
4.25	1	p	p	r	16.03	2	p	p	p
4.26	4	p	p	p	16.04	1	p	c	c
4.27	1	p	p	p	16.05	1	p	c	c
4.28	1	p	p	p	16.06	2	p	c	c
4.29	2	p	ab	ab	16.07	1	r	p	p
4.30	2	p	p	p	16.08	1	c	c	c
4.31	4	p	p	p	16.09	3	p	p	p
4.32	3	p	p	p	16.10	1	pr	p	p
5.01	n/a	p	n/a	r	16.11	2	p	p	p
5.02	3	p	n/a	p	16.12	1	p	p	p
6.01	n/a	r	n/a	n/a	16.13	1	pr	p	p

Appendix 2 (*cont.*)

Node	Bremer Support	Wt	1980s	1990s	Node	Bremer Support	Wt	1980s	1990s
6.02	2	p	n/a	n/a	16.14	1	p	c	c
6.03	1	p	n/a	n/a	16.15	1	p	p	p
6.04	1	p	n/a	n/a	16.16	1	p	c	c
6.05	3	p	n/a	n/a	16.17	1	p	c	c
6.06	3	p	n/a	n/a	16.18	1	r	p	p
6.07	2	p	n/a	n/a	16.19	1	p	c	c
7.01	n/a	p	n/a	p	16.20	1	p	p	p
7.02	1	p	n/a	p	16.21	1	r	p	p
7.03	1	p	n/a	p	16.22	1	r	p	p
7.04	1	p	n/a	p					