

A composite species-level phylogeny of the ‘Insectivora’ (Mammalia: Order Lipotyphla Haeckel, 1866)

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Abstract

The first MRP (matrix representation with parsimony) supertree phylogeny of the Lipotyphla is presented, covering all the families that were considered to make up the traditional mammalian order Insectivora. The phylogeny does not examine relationships within the shrew subfamily Crocidurinae, but all other taxa are considered at the species level, drawing upon 41 years of systematic literature and combining information from 47 published sources. The MRP technique is also critically discussed. This study will be of use to comparative biology studies of the Lipotyphla (or of mammals as a whole) and is a rigorous review of past systematic work, as well as clearly demonstrating our current level of knowledge. The supertree clearly details a strong imbalance in phylogenetic understanding across the taxon: a great deal is known about the hedgehogs and gymnures (Erinaceidae), the New World moles (Talpidae), Palearctic species of *Sorex* (subgenus *Sorex*) and the relationships between genera of red-toothed shrews (Soricinae). The supertree, however, clearly shows areas where our knowledge is conflicting or non-existent, and these gaps do not always correspond to obscure species: nothing is known about the systematics of Old World mole genera. Also very little is known about golden moles (Chrysochloridae) and the shrew-tenrec genus *Microgale*, some of the most threatened mammals on Earth.

Key words: Lipotyphla, Insectivora, phylogeny, supertree, MRP

INTRODUCTION

Insectivore systematics

The order Insectivora (here called Lipotyphla *sensu* Butler, 1988), has perhaps the most turbulent systematic history of any mammalian order; 300 years of study have not yielded a consensus of opinion, and in some groups have not resulted even in a stable alpha taxonomy. Even the family composition has not been stable until relatively recently, despite the very familiar nature of many of the species involved. The order Lipotyphla currently contains the shrews (Soricidae), the moles and desmans (Talpidae), the hedgehogs and gymnures (Erinaceidae), the tenrecs (Tenrecidae), the golden moles (Chrysochloridae) and the enigmatic solenodons (Solenodontidae), together with the only family of mammals to reach extinction in recent history, the West Indian shrews (Nesophontidae). This composition was reached following the removal of the elephant shrews and tree shrews to the monofamilial orders Macroscelidea and Scandentia, respectively (Butler, 1972).

Compared to most other Eutherian orders, estimates of phylogeny are rare, and usually limited to a small clade or geographic assemblage. Species are very often characterized by reductions or hypothesized losses of morphological characters. This has led to poor resolution in morphological studies (MacPhee & Novacek, 1995), and conflict between morphological and molecular estimates of phylogeny. Although sequence analyses are beginning to bear fruit (e.g. interordinal relationships in Stanhope, Wadell *et al.*, 1998; Fumagalli, Taberlet *et al.*, 1999; large-scale species-level relationships) there is a pressing need for a consensus of present opinion. This study produces the first such estimate generated from a formal analysis. The estimate is produced by matrix representation with parsimony (MRP), a recently developed phylogenetic technique ideally suited to combining disparate estimates of phylogeny (Baum, 1992; Ragan, 1992; Baum & Ragan, 1993; Sanderson, Purvis & Henze, 1998).

Why is this phylogeny important? Huxley (1880) first suggested that the Lipotyphla bore a close resemblance to his putative ‘*ur-eutherian*’ ancestors. Huxley made no systematic assertions beyond this, but Matthew (1909) established the pervasive idea that the Lipotyphla were the closest living relatives of a single eutherian ancestor. Whilst the legitimacy of the statement is now doubtful

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for the order as a whole (Stanhope, Madsen *et al.*, 1998; Stanhope, Wadell *et al.*, 1998), the notion that the Lipotyphla exhibit a 'mammalian central tendency', or are useful as a baseline for comparative studies, is still widespread (MacPhee & Novacek, 1995; Stephan, Baron & Frahm, 1991).

Lipotyphlan phylogenetics is not only valuable *per se*, but also important for testing evolutionary hypotheses across the Mammalia: the province of comparative methodologies. Lipotyphlan taxa often show idiosyncratic features and extremes of morphology, life-history parameters and speciation rate. Failure to include the Lipotyphla in comparative mammalian analyses would ignore much of the variation across the Mammalia, but comparative analyses require large-scale estimates of phylogeny.

Supertrees and MRP

MRP is an algorithmic technique for combining data from phylogenetic estimates, which can be inconsistent either in taxon content or branching pattern (Baum & Ragan, 1993; Bininda-Emonds & Bryant, 1998; Sanderson *et al.*, 1998; Bininda-Emonds & Sanderson, 2001; Pisani & Wilkinson, 2002), and as such it is unique amongst current consensus techniques (Thorley & Page, 2000; Pisani & Wilkinson, 2002). MRP can be viewed as a philosophical derivative of the 'total evidence' approach in which the conclusions of multiple studies upon disparate data are combined, rather than the data themselves (*sensu* Kluge, 1989). Pisani & Wilkinson (2002) demonstrate that MRP is not a mechanistic derivative of total evidence approaches. MRP species-level phylogenies exist for three mammalian orders: Primates (Purvis, 1995), Carnivora (Bininda-Emonds, Gittleman & Purvis, 1999), Chiroptera (Jones *et al.*, 2002). A family-level composite (Liu *et al.*, 2001) exists for all extant placental mammals.

MRP is best conceptualized as a two step process: individual phylogenetic estimates (henceforth source trees) are reduced to a near-minimal set of statements of relationship; subsequently these statements are combined into a single set which is then analysed to produce a consensus which disagrees least with the complete statement set. Reduction involves the additive binary coding of each source tree (after Farris, Kluge & Eckhardt, 1970) into a data matrix in which each node in the source tree contributes a matrix element analogous to a character in a conventional cladistic data matrix. These elements are referred to here as pseudocharacters (after Bininda-Emonds & Bryant, 1998). Each terminal in *every* source tree is scored for each pseudocharacter (i.e. each node in *every* source tree) as follows: '1' if the terminal is subtended from the node in question, '0' if not, and '?' should the terminal not be included in the source tree (see further discussion in Bininda-Emonds & Bryant, 1998).

The result, for each source tree, is a subset of the data matrix that if analysed under a parsimony criterion will result in a perfect reconstruction of the original source tree. Analysis of the entire data matrix under parsimony

is intended to find a consensus that does least violence to the suggestions of relationship in all the source trees and in which no source tree has absolute power of veto over relationships (Purvis, 1995; Sanderson *et al.*, 1998). In the same way that conventional parsimony analysis discards non-parsimonious evidence of relationships as homoplasy, MRP discards disagreement between source trees where a more harmonious solution can be found. The process is conceptually similar to compatibility or clique analysis, with the practical benefit that missing data (from taxa not shared between source trees) can be included in the matrix. Areas of disagreement between source trees or poor phylogenetic knowledge are reflected in areas of poor resolution or low robustness in the resulting composite tree. MRP is therefore an extremely effective way of demonstrating where future phylogenetic effort should be concentrated.

As with any consensus technique, MRP has desirable and undesirable properties. Known problems centre either around the mechanics of conflict resolution between source trees (reviewed in Pisani & Wilkinson, 2002) or with the effect of pseudocharacter contribution by source trees scaling with both terminal number and resolution confounding attempts to regulate source tree weighting schemes (Bininda-Emonds & Bryant, 1998). This study follows the conclusions of Bininda-Emonds and Sanderson's (2001) simulations in that an MRP analysis is expected to 'reasonably approximate' a total evidence approach, whilst welcoming the conclusions of Wilkinson *et al.* (2001) that 'applicability in practice should not be confused with acceptance in principle'. Readers are drawn to the conclusions of these authors to inform their interpretation of the phylogenies presented here. In particular, care has been taken to note in discussion, nodes with which no source tree is compatible (after Pisani & Wilkinson, 2002). Most recently, the MRP supertree of Liu *et al.* (2001) has been criticized by Gatesy *et al.* (2002) for incorporating redundant pseudocharacters stemming from multiple source trees being derived from the same dataset, and for often assuming monophyly of higher taxa. Neither criticism applies to this study as noted in the Methods below.

Crocidae

Relationships within the subfamily Crocidae are not analysed in this study. The Crocidae are not amenable to analysis via MRP, and demonstrate some of the limits of the technique. There are few relevant source trees, most systematic effort having been invested in karyotyping (Maddalena & Ruedi, 1994, use karyotypic variation to infer a subgeneric division into afrotropical and palaearctic groups) and stabilizing species definitions (see McLelland, 1994). Intergeneric relationships within the Crocidae are very poorly understood; estimates of phylogeny have tended to follow the morphological hypotheses of Heim de Balsac & Lamotte (1956, 1957) and Meester (1963) in suggesting a reticulated relationship

between the genera *Suncus* and *Sylvisorex*, rendering *Crociodura* polyphyletic. Such topologies are not amenable to binary additive coding, as inclusion of any source suggesting generic monophyly will inevitably result in complete loss of resolution. Where species-level phylogenies exist, there is a low level of overlap and topological agreement between species-level source trees. Whilst the information content maybe high (e.g. Ruedi, Maddelena *et al.*, 1993; Heaney & Ruedi, 1994; Ruedi, 1996; Ruedi, Auberson *et al.*, 1998), such low levels of taxonomic overlap are found that missing data proliferate across an MRP matrix. Suggested relationships are often utterly conflicting: compare the positions of *Crociodura lamottei*, *C. luna* and *C. poensis* in Butler, Thorpe & Greenwood (1989), Maddelena (1990) and McLelland (1994). Given these problems, the subfamily were reluctantly excluded from the study. Refer to Querouil *et al.* (2001), which fell outside the time period for this study, if a phylogeny of the Crocidurinae is required for use with this MRP phylogeny of the remaining Lipotyphla.

Weighting pseudocharacters: a rationale

Some previous supertree constructions (Purvis, 1995; Jones *et al.*, 2002) have attempted to use differential weighting based upon source tree methodology. However, such weighting schemes represent unresolved problems for users of MRP. Intuitively, pseudocharacters should be differentially weighted in some way to reflect the fact that the source trees from which they are derived differ in their probability of being 'correct' or 'truthful'. MRP allows the sampling of literature from a comparatively long historical period; methodology and rigour will differ throughout that period, and this could be taken into account in the resulting composite. It is impossible to create a weighting scheme that quantitatively reflects the differing correctness of source trees; any scheme must be subjective to a degree.

One option for the MRP user is to abandon all consideration of truth as applied to source trees, and present an equally weighted analysis that must be interpreted as a measure of phylogenetic 'central tendency' resulting from the interaction of a model of pseudocharacter behaviour (parsimony) with a set of pseudocharacters: in essence a formalized literature review. Such an analysis is useful, particularly as a tool for finding areas of poor systematic understanding. A second option for the MRP user is to attempt to improve the correctness of the resulting MRP phylogeny by incorporating an *a priori* weighting scheme, and both accept the subjective nature of any weighting scheme and be prepared to justify the magnitude of weighting chosen. The dilemma faced by users of MRP is a choice between slavish rigour on one hand (an equally-weighted tree with strong limitations on its interpretation) and dangerous flexibility on the other (a tree that attempts to reconstruct phylogeny more accurately but incorporates subjective elements that are open to criticism). In light of this, we present an unweighted analysis, and refer to the effects on topology of variant weighting schemes in

passing, although a more correct phylogeny undoubtedly lies down this latter route.

METHODS

Published estimates of phylogeny were collected from a search of the literature. Initial sources were compiled using a search of BIDS, Web of Science, BIOSIS, and Zoological Record, using all combinations of the search terms Insecti*, Lipotyphl*, family names (Tenrecidae, Chrysochloridae, Talpidae, Erinaceidae, Soricidae, Solenodontidae), phylogen*, systemati*, taxonom* and relation*. A database of shrew references (Haberl, 1995) was also consulted. Relevant publications referenced within any initial sources were collected. Studies with publication dates between January 1960 and February 2001 inclusive were accepted into the study. MRP allows the combination of phylogenetic information from a wide variety of sources. This study includes source trees derived from maximum parsimony, maximum likelihood and distance criterion searches, phenetic and morphometric analyses where phylogeny was inferred by the author, taxonomies and idiosyncratic sources including manually derived trees and non-algorithmic parsimony analyses.

Following suggestions in Bininda-Emonds & Sander-son (2001), each data matrix (except *Sorex*) included a classification (McKenna & Bell, 1997) coded in an identical manner to the other source trees (a 'seed' tree, after Bininda-Emonds & Sanderson, 2001). Low taxonomic overlap between source trees leads to a high proportion of missing data, and hence a longer computation time and many equally parsimonious trees. Seeding a matrix with a classification including all terminal taxa greatly reduces the number of putative topologies by contributing a minimally informative underlying arrangement with elements common to all taxa.

No source tree contested the monophyly of any family within the Lipotyphla. As a result, separate data matrices could be compiled for each family without any loss of rigour (cf. Gatesy *et al.*, 2002). A basal matrix, comprising source trees dealing explicitly with interfamilial relationships was also assembled, onto which the resulting trees from the family matrices were attached. A similar consensus on the monophyly of *Sorex* within the Soricidae allowed a separate matrix to be constructed for the genus and attached to the relevant terminal in the Soricidae tree. Legitimate blocking of this sort reduces computational time, and greatly reduces the possibility that resolution is lost as a result of 'floating taxa' (Wilkinson, 1995).

The taxonomy of Hutterer (1993) was taken to be the complete extent of valid species, and sources were modified to reflect this using the synonym lists contained in the taxonomy. No species were added to source trees on the basis of synonymy. Species that could not be synonymized by reference to Hutterer (1993) were excluded from the study. Sources presenting higher taxa as terminals were only taken as referring to all constituents

Table 1. Source trees and tree search statistics for each of the MRP compartments

Compartment	Source trees	Resulting trees and resolution (MPTs for weighting schemes of 2, 4 and 8 magnitude, respectively, given in parentheses)
Basal	Allard & Miyamoto (1992), Butler (1988), Eisenberg (1981), Emerson <i>et al.</i> (1999), MacPhee & Novacek (1995), McKenna & Bell (1997), Stanhope, Madsen <i>et al.</i> (1998), Stanhope, Wadell <i>et al.</i> (1998), van Valen (1967), Murphy <i>et al.</i> (2001), Madsen <i>et al.</i> (2001)	Single MPT (1, 1, 1) 6 terminals ^a 100 % resolution
Chrysochloridae	Bronner (1991, 1995)	4 MPTs (n/a) 9 terminals 62.5 % resolution
Tenrecidae	Asher (1999), Eisenberg (1981), McKenna & Bell (1997), van Valen (1967)	10 MPTs (1, 1, 1) 24 terminals 34.8 % resolution
Erinaceidae	Bannikova, Fedorova <i>et al.</i> (1995), Corbet (1988), Frost <i>et al.</i> (1991), Gould (1995), McKenna & Bell (1997), Surin <i>et al.</i> (1997), van Valen (1967)	2 MPTs (1, 1, 1) 20 terminals 94.7 % resolution
Talpidae	Corti & Loy (1987), Filipucci <i>et al.</i> (1987), Hutchison (1968, 1974), Kratochvil & Král (1972), McKenna & Bell (1997), Okhamoto (1998), Okhotina (1966), Rohlf, Loy & Corti (1996), van Valen (1967), Yates & Greenbaum (1982), Yates & Moore (1990)	11340 MPTs (n/a) 29 terminals ^a 71.4 % resolution
Soricidae	Choate (1970), George (1986), McKenna & Bell (1997), Ohdachi <i>et al.</i> (1997), Reumer (1997, 1998), Ruedi (1998), van Valen (1967)	9756 MPTs (9756, 9756, 9756) 28 terminals ^a 41.1 % resolution
<i>Sorex</i>	Bannikova, Dolgov <i>et al.</i> (1996), Catzefflis (1984) Fumagalli, Hausser <i>et al.</i> (1996), Fumagalli, Taberlet <i>et al.</i> (1999), George (1986), George (1988), Hausser <i>et al.</i> (1998), Ivanitskaya (1992), Ohdachi <i>et al.</i> (1997), Ruedi (1998), Sergejev and Iljashenko (1991), Stewart & Baker (1997), Taberlet, Fumagalli & Hausser (1991), van de Zyll Jong (1982)	844 MPTs (3420, 285, 285) 36 terminals ^a 65.7 % resolution

^a Species counts and resolutions refer to the data matrix as analysed. Taxa removed due to STR or identical character states have been reinserted in Figs 1–7 and therefore the figures may differ from the values indicated.

where such was the intention of the author (e.g. McKenna & Bell, 1997); the monophyly of higher taxa was not assumed for sources using exemplar species as terminals. These decisions minimize inclusion of ‘unintentional’ statements of relationship (after Bininda-Emonds & Sanderson, 2001; see also Gatesy *et al.*, 2002).

Sometimes several sources produced phylogenetic estimates based upon a single data matrix (see Table 1). Untreated, these sources would proportionally increase the pseudocharacter contribution of the underlying datasets (this behaviour was noted as far back as Purvis (1995a), but repeated recently by Gatesy *et al.* (2002)). In these cases, each source tree was coded separately and an MRP analysis conducted on them. The strict consensus of the resulting trees was added as a single source to the overall analysis. Sources that extracted different sequences or character sets from the same specimens were included separately.

Source trees were digitized on a desktop scanner, imported into TreeThief (Rambaut, 2000) and converted to Newick format tree files. Newick files were visualized in TreeView (Page, 2000), and exported as NEXUS files, having been checked for the correct inclusion of polytomies. NEXUS files for all source trees considering a given family were imported into RadCon (Thorley & Page, 2000), and a NEXUS MRP matrix produced using Baum & Ragan’s (1993) additive binary coding scheme (Baum & Ragan, 1993; Sanderson *et al.*, 1998). Matrices were inspected for groups of taxa that shared identical character states; all but 1 of each group were removed and added by hand to the node subtending the remaining ‘exemplar’ taxon.

Each MRP matrix was subjected to a parsimony analysis in PAUP* (v.4b8; Swofford, 1998). Analyses were carried out on a cluster of 1GHz LINUX PCs running the portable version of PAUP*. Matrices were analysed using

Table 2. Details of source trees presenting multiple conclusions from a single data set that were combined into individual MRP matrices. Strict consensus trees resulting from branch-and-bound parsimony searches were included in the final MRP matrices

Source tree	Components and MRP regimes
Asher (1999)	8 MPTs under various parsimony search criteria were combined
Bannikova, Dolgov <i>et al.</i> (1996)	3 trees with different treatments of restriction site data set combined
Catzefflis (1984), Ruedi (1998)	Ruedi reanalyses Catzefflis' data; both trees combined
Fumagalli, Hausser <i>et al.</i> (1996)	2 trees from different searches on a single sequence set combined
Ohdachi <i>et al.</i> (1997)	Neighbour-joining and maximum-likelihood trees combined
Sergejev & Iljashenko (1991)	All 4 non-cladistic trees combined
van Zyll de Jong (1982)	Both presented trees combined
Volobouev & Dutrillaux (1991)	Both presented trees combined

a branch-and-bound algorithm to collect all maximally parsimonious trees from which strict consensus trees were compiled in PAUP*. The *Sorex* matrix was subjected to safe taxonomic reduction via the TAXEQ3 program (Wilkinson, 2001) to reduce runtimes, with taxa being reinserted into the consensus tree as advised by TAXEQ3. In addition, *Sorex camtschatica* was removed from the analysis and not reintroduced. Because of an unfortunate conjunction of two source tree statements, *S. camtschatica* destroyed all resolution from the *Sorex* compartment (see Wilkinson, 1995); the species was removed and not reinserted, following Bininda-Emonds *et al.* (1999).

All matrices were re-analysed under 3 different pseudocharacter weighting schemes: pseudocharacters were partitioned according to whether the methodology used to generate it relied wholly upon an explicit model of evolution. The partition consisting of pseudocharacters derived solely from computation under parsimony or maximum-likelihood algorithms were given relative weights of 2, 4 and 8 in 3 separate analyses. This allows statements of relationship that owe their existence solely to other methodologies, considered suspect in the present day, to be clearly marked on the unweighted consensus tree.

Bremer support statistics (Bremer, 1994) were compiled for each consensus tree using PAUP* batch files created by TreeRot (Sorenson, 1999), except that for Soricidae, which failed to complete because of RAM limitations. Note that in conventional parsimony analyses, Bremer indices are only meaningful across the tree for which they were calculated as the indices are expressed as units of tree length, which vary between analyses. In an MRP analysis, if pseudocharacter equality of weight is assumed, such a limitation does not apply and Bremer indices can be compared meaningfully across analyses.

RESULTS

Table 1 details the source trees, tree-searching regimes and search statistics for each subset of the Lipotyphla analysed. Table 2 details those source trees which derive from the same data, and from which source trees created by small MRP analyses have been created. Strict consensus trees for each subset are presented as follows: Fig. 1

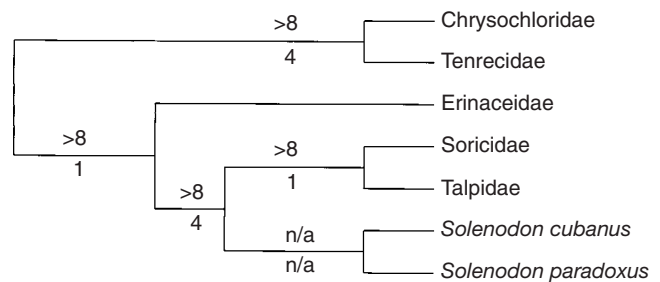


Fig. 1. Single MPT for the interfamilial compartment. Branch lengths are arbitrary. Weighting magnitude required to dissolve node listed above branches. Bremer support indices listed under branches.

(interfamilial relationships), Fig. 2 (Chrysochloridae), Fig. 3 (Tenrecidae), Fig. 4 (Erinaceidae), Fig. 5 (Talpidae), Fig. 6 (Soricidae save *Sorex*), Fig. 7 (*Sorex*). The magnitude of weighting required to dissolve each node is presented above the subtending branch on each figure. Bremer support indices for each node are presented beneath the branch subtending the node; nodes marked 'n/a' are those created by post-consensus reinsertion of taxa with identical character states (see methodology, above). NEXUS tree files for unweighted and weighted analyses, original data matrices and TAXEQ3 output are available from <http://www.bio.ic.ac.uk/evolve>.

DISCUSSION

Interfamilial relationships (Fig. 1)

The basal consensus shows complete resolution and comparatively strong Bremer support across most of the tree. The Afrosoricida grouping of Tenrecidae and Chrysochloridae (Stanhope, Madsen *et al.*, 1998, and congruent with their Afrotheria) is strongly supported and this clade falls as sister group to the remaining Lipotyphla (a 'Eulipotyphla' *sensu* Waddell, Okada & Hasegawa, 1999) in which the Erinaceidae fall basal to a strongly supported series comprising the remaining families. This Afrosoricida grouping is only contradicted by the morphological hypotheses of MacPhee & Novacek

(1995), and the seed taxonomy of McKenna & Bell (1997). Such is the support for the Afrosoricida that the most parsimonious placement of the Erinaceidae is basal to the remaining Eulipotyphla. This arrangement is not explicitly suggested in any source tree, and congruent with only three (MacPhee & Novacek, 1995; Stanhope, Madsen *et al.*, 1998; Stanhope, Wadell *et al.*, 1998). Source trees suggesting a polyphyletic Lipotyphla vary in their placement of the Erinaceidae outside the core Eulipotyphla (Emerson *et al.*, 1999, for example, disperse the Eulipotyphla families across the Eutherian tree) and the resulting most parsimonious position reflects a lack of information on the relationship of the Erinaceidae to the Afrosoricida rather than strong support for a non-basal Erinaceidae. Some recent publications support the 'traditional' monophyletic Lipotyphla (MacPhee & Novacek, 1995; Shoshani & McKenna, 1998), as well as more venerable sources (van Valen, 1967; Eisenberg, 1981; Butler, 1988). All such hypotheses are based on morphological evidence; the Afrotheria have yet to receive any morphological support, although evidence for a unique protein signature has been recently reported (van Dijk *et al.*, 2001).

Note that in this context MRP is incapable of arguing for or against the monophyly of the Lipotyphla. No non-Lipotyphla families have been included: the composite phylogeny by definition will suggest monophyly. Importantly, the composite tree is compatible with the Afrotheria hypothesis, but this analysis contains no information about whether large sections of the mammalian tree should be attached to internal nodes within the presented composite phylogeny.

Chrysochloridae (Fig. 2)

Chrysochloridae typify the problems encountered in systematic studies of the Lipotyphla: published phylogenetic studies are scarce, fragmentary and conflicting. Idiosyncratic morphology has led to inconclusive interpretations of relationship (see conclusions in von Mayer, O'Brien & Sarmiento, 1995 as an excellent example) and no comprehensive studies of sequence data have been completed. Close relationships between Chrysochloridae and Tenrecidae have been regularly suggested (van Valen, 1967; Butler, 1969; Eisenberg, 1981) and discounted over the last five decades (see discussion in Hickman, 1990), although the hypothesis was first discounted by Simpson (1945).

Source trees stem from two publications by a single author (Bronner, 1991; Bronner, 1995), and cover only nine of the 18 species of Chrysochloridae; the seed taxonomy contains no intergeneric structure. The MRP consensus contains little information beyond maintaining the interspecific relationships within *Amblysomus* (Bronner, 1995). Relationships between the genera are congruent between two source trees, with the exception of the placement of *Chrysochloris asiatica*. This single incidence of inconsistency has resulted in MRP rejecting

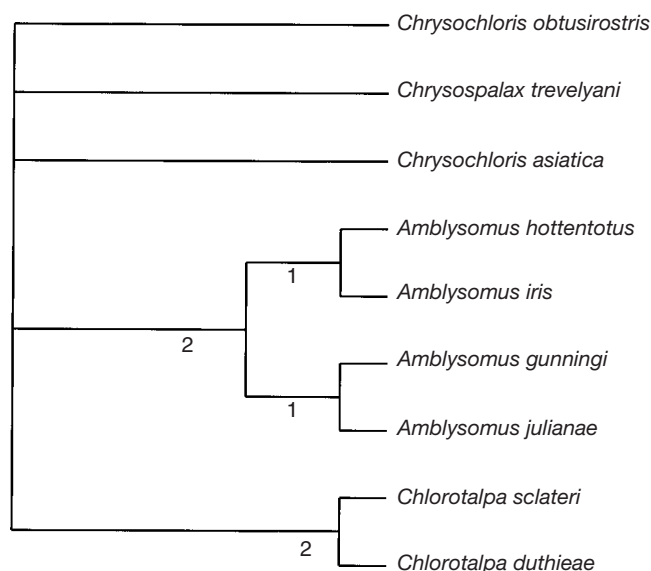


Fig. 2. Strict consensus of four MPTs for the Chrysochloridae. Branch lengths are arbitrary. No alternative weighting schemes needed to be applied to this compartment. Bremer support indices listed under branches.

the congruent placing of *Chlorotalpa* and *Calcochloris* between the two source trees, in favour of a basal polytomy. Such an occurrence serves to illustrate the limitations of MRP when faced with limited data and incongruent signal. It also demonstrates its effectiveness in indicating taxa upon which phylogenetic effort needs to be focused, such as Chrysochloridae.

Tenrecidae (Fig. 3)

Relationships between and within tenrec genera have only recently been analysed formally. As a result, the MRP analysis presented here was conducted with only two data sources apart from taxonomies: cladistic analyses of cranial and post-cranial osteology (Asher, 1999) and the informal phylogeny of Eisenberg (1981). Resolved regions of the consensus show relatively high Bremer support values; uncontroversial groupings include the subfamilies Tenrecinae (*Hemicentetes*, *Tenrec*, *Setifer* and *Echinops*) and the Potamogalinae (*Potamogale* and *Micropotamogale*) from the African mainland. The sister grouping of *Setifer* and *Echinops* is uncontested, whilst disagreement between Asher (1999) and Eisenberg (1981) over the relationship of *Tenrec* to *Hemicentetes* is reflected in a polytomy. Asher (1999) concludes that an association of *Limnogale* with the Potamogalinae is justified. Such an arrangement is not supported in the MRP tree because of disagreement between Asher (1999) and the remaining source trees, in which *Limnogale* is a member of the Oryzorictinae (*Oryzorictes* and *Microgale*, rendered paraphyletic in the MRP consensus of Asher's trees). *Limnogale* instead subtends from the basal polytomy in the final consensus. This disagreement

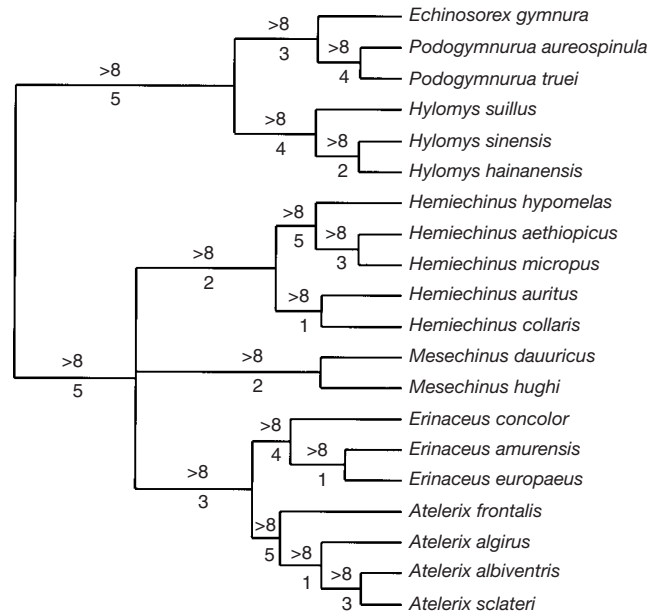


Fig. 4. Strict consensus of two MPTs for the Erinaceidae. Branch lengths are arbitrary. Weighting magnitude required to dissolve node listed above branches. Bremer support indices listed under branches.

directly and from the rigid species definitions that must underlie it (for an example see Stephenson, 1995).

Erinaceidae (Fig. 4)

Whilst the Erinaceidae have benefited from more phylogenetic study than many of the Lipotyphla, this effort has often been focused on fossil taxa (e.g. Rich, 1981; Novacek, Brown & Shankler, 1985). Formal analyses of extant Erinaceidae are rare (see discussion and references in Gould, 1995) and require some recourse to the literature of the former Soviet Union. Note that there may be more estimates in this literature than are considered here, because of poor abstract availability and translation difficulties.

Only some intergeneric relationships within the Erinaceinae genera remain unresolved; the consensus is otherwise well resolved and shows high Bremer support indices throughout. The division of the clade into the hedgehog and gymnure groups (Erinaceinae and Galericinae, respectively) is not contested in any source tree.

Relationships within the Galericinae are uncontroversial: the presented relationship is congruent across all source trees, although Frost, Wozencraft & Hoffmann (1991) refer to some possible alternative arrangements within *Hylomys*. Within the Erinaceinae, disagreement amongst sources over the placement of *Mesechinus* leads to a polytomy at the base of the Erinaceinae. *Mesechinus*, the desert-living hedgehogs of China and the Gobi Desert, is considered by Surin *et al.* (1997) and Bannikova *et al.* (1995) as sister to several members of the 'traditional'

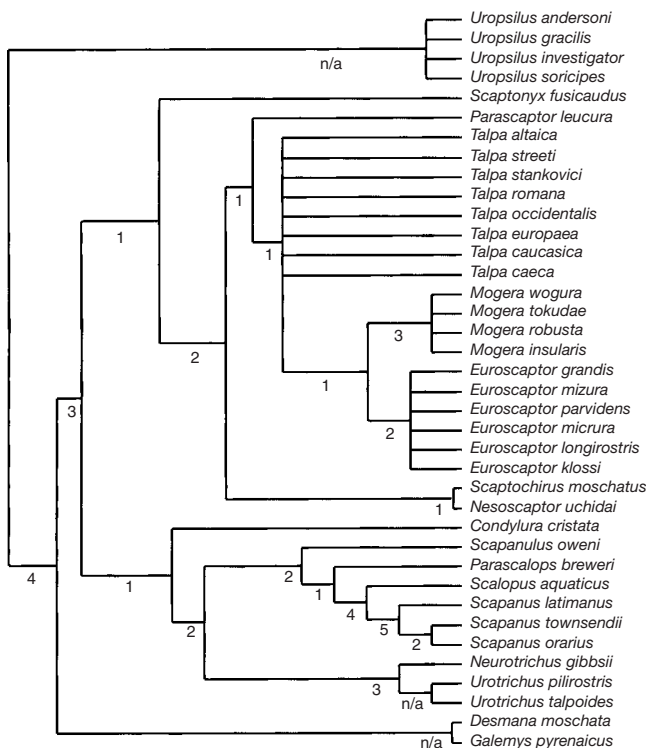


Fig. 5. Strict consensus of 11340 MPTs for the Talpidae. Branch lengths are arbitrary. No alternative weighting schemes needed to be applied to this compartment. Bremer support indices listed under branches.

desert hedgehog genus *Hemiechinus*, whilst Corbet (1988) considers *Mesechinus* as rendering *Hemiechinus* paraphyletic. Such an arrangement is explicitly discounted by Frost *et al.* (1991) and Gould (1995), who favour *Mesechinus* as a sister group to the Eurasian and African hedgehog genera *Erinaceus* and *Atelerix*. This instability is reflected both in the MRP placement of *Mesechinus*, and the low Bremer support evidence for the node subtending *Hemiechinus auritus* and *H. collaris*. Generally, the relationships between the remaining Erinaceidae are uncontroversial, and this is reflected in the high Bremer indices presented. Two poorly supported nodes deserve mention. The MRP analysis recovers the arrangement of species within the European hedgehog genus *Erinaceus* supported by Bannikova *et al.* (1995) and Surin *et al.* (1997) as a more parsimonious arrangement than the alternative proposed by Corbet (1988); other source trees are ambivalent on the matter. An identical situation occurs in the African genus *Atelerix*, where the conclusions of the cladistic analyses of Frost *et al.* (1991) and Gould (1995) are favoured over those of Corbet (1988).

Talpidae (Fig. 5)

The MRP composite for the Talpidae shows good resolution, except for within the three genera of old world moles (*Talpa*, *Euroscaptor* and *Mogera*). No source tree contains information about the interspecific relationships within the Uropsilinae (the monogeneric *Uropsilus*), but

the placement of this less-fossorial genus as sister group to the rest of Talpidae is uncontested in any source tree. Sufficient support exists for the semi-aquatic desman genera *Desmana* and *Galemys* to be recovered as a monophyletic sister group to the Talpinae, in disagreement with several source trees (van Valen, 1967; Hutchison, 1968; McKenna & Bell, 1997).

The Talpinae are recovered with a basal split delimiting two clades of Old World and New World genera, and the MRP composite broadly supports the tribal arrangements first suggested by Hutchison (1968). The Old World species group comprises the Talpini (the speciose genera *Talpa*, *Mogera* and *Euroscaptor*, together with *Parascaptor*, *Scaptochirus* and the recently erected *Nesoscaptor*), with the monotypic Scaptonychini (*Scaptonyx*) as a sister taxon. The New World group comprises the sister groups Scalopini (*Scapanus*, *Scalopus*, *Parascalops* and *Scapanulus*) and Neurotrichini (*Urotrichus* and *Neurotrichus*) along with the basal monotypic Condylurini (the star-nosed mole *Condylura cristata*).

Relationships among the members of the Old World genera have been contentious for many years. By 1968, Hutchinson was noting that 'there have been almost as many generic names applied as there are living species' (Hutchison, 1968: 6). Much confusion has arisen as a result of poor congruence between the phylogenetic signal obtained from different sets of morphological characters (for discussion and example involving the placement of fossil Talpinae, see Hutchison, 1974). In particular, the composition of the genus *Talpa* has varied, having at times contained members of the genera *Euroscaptor* and *Mogera*, as well as the monotypic genera *Parascaptor* and *Scaptochirus*. The MRP consensus shows no resolution for these taxa beyond the sister grouping of *Euroscaptor* and *Mogera*, with *Talpa* as sister to the pair. Poor resolution was exacerbated by low taxonomic overlap and high incongruity (in particular within *Talpa*) between the source trees dealing with relationships within the major genera. Whilst unsupported in a number of major taxonomic works (McKenna & Bell, 1997), the sister grouping of *Euroscaptor* and *Mogera* with respect to *Talpa* has been suggested for 25 years, and is supported by Hutchison (1974), Okamoto (1998) and Yates & Moore (1990).

The New World talpid clade recovers a sister clade relationship between the Scalopini and the Neurotrichini; such a relationship is supported by all source trees save Okhotina (1966) and Hutchison (1968), although Hutchison (1974) later supports it. The relationships of the genera within the Scalopini are congruent with Hutchison (1974), and favours the pectinate intergeneric arrangement of Yates & Moore (1990) over the twin-pair arrangement of McKenna & Bell (1997).

Soricidae (Fig. 6)

Extant shrews fall into one of two very speciose subfamilies: the Crocidurinae (white-toothed shrews) and the Soricinae (red-toothed shrews). Whilst this distinction

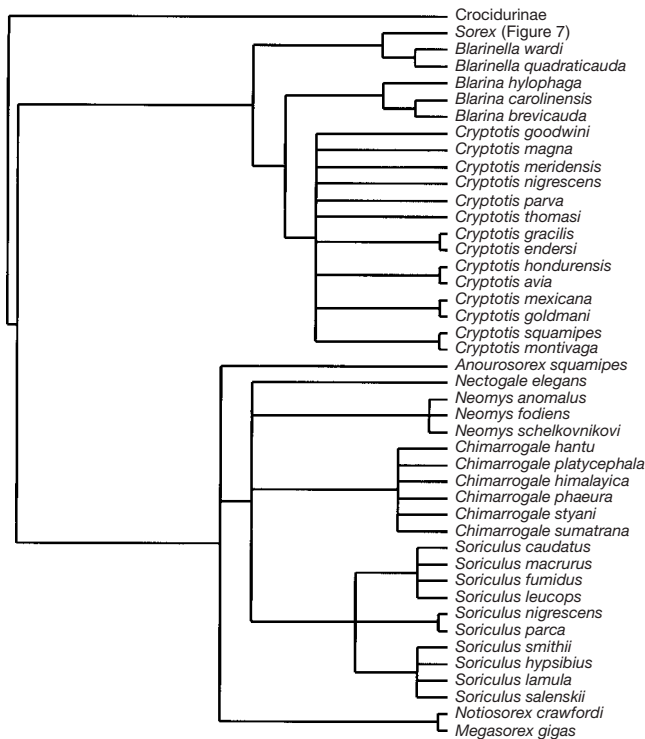


Fig. 6. Strict consensus of 9756 MPTs for the Soricinae. Branch lengths are arbitrary. All nodes supported under a eight-fold differential weighting scheme. Bremer support indices not calculated for this tree (see text).

is quite clear and uncontroversial, divisions below the subfamily level have been highly contentious. Shrews in general show very conservative post-cranial osteology, non-skeletal morphology (see discussion and conclusions of Ducommun, Jeanmaire-Besançon & Vogel, 1994 and Ventura & López-Fuster, 1997) and dentition (discussed in Reumer, 1998). Until the examination of karyotypes (e.g. George *et al.*, 1982), protein structure (see review in Ruedi, 1998) and sequence data, very little information was available on which to base solid systematic decisions.

The MRP phylogeny shows good resolution at the generic level, but poor resolution within most genera; this is unsurprising, as the amount of source information concerning such relationships is low except in *Cryptotis*, and in *Sorex*, which is considered separately below. Higher level classification of the Soricinae has been remarkably congruent since the revision of Repenning (1967). This source is identical in arrangement to the seed classification (McKenna & Bell, 1997), although higher taxon names differ, and the tribal divisions within these sources are supported in the MRP composite (Soricini: *Sorex* + *Blarinella*; Blarinini: *Blarina* + *Cryptotis*; Nectogalini (Repenning's Neomyini): *Anourosorex* + *Nectogale* + *Neomys* + *Chimarrogale* + *Soriculus* + *Notiosorex* + *Megasorex*). The grouping of Soricini and Blarinini as sister taxa to Nectogalini is congruent with George (1986); other source trees suggest a polytomy at this point.

The Soricini are uncontroversial. Within the Blarini, relationships between the species of *Cryptotis* are

covered only by Choate (1970), and resolution in the composite is lacking here because of missing data resulting from low taxonomic overlap. Relationships within the Mexican and Central American *Cryptotis mexicana/goodwini/goldmani* group have undergone recent revision, including elucidating a paraphyletic relationship involving subspecies within *Cryptotis mexicana* (Woodman & Timm, 1999). When Woodman & Timm's (1999) phylogeny is converted to the taxonomy of Hutterer (1993), this paraphyly removes all resolution from the resulting source tree. The reader is directed to this publication as a potential alternative to the arrangements presented here. Relationships within *Blarina* are those of Ruedi (1998), other source trees being equivocal.

The situation within the remaining tribe, Nectogalini, is more complex. The MRP composite shows a basal polytomy subtending the genus *Anourosorex* and a sister grouping of *Notiosorex* and *Megasorex*, together with a clade containing the remaining Nectogalini. The grouping of *Notiosorex* and *Megasorex* is only contradicted in two source trees (van Valen, 1967; George, 1986) that do not differentiate these species from the basal polytomy of the Nectogalini. The placement of *Anourosorex* within the Soricinae is problematic. The genus is not regarded as part of the Nectogalini by two source trees, but rather as basal to the Blarinini and Soricini (Reumer, 1997), or as a separate tribe subtending from the base of the subfamily (the Anourosoricini of Reumer, 1998). The parsimonious placement of *Anourosorex* in the composite phylogeny is that of McKenna & Bell (1997) and van Valen (1967). Within the remaining clade, the divisions within the Asiatic shrew genus *Soriculus* are uncontroversial and the composite phylogeny supports the division of *Soriculus* into the subgenera *Soriculus*, *Episoriculus* and *Chodsigoa* as detailed in Reumer (1997), although with the grouping of *Soriculus parca* (which Reumer did not recognize) with *Soriculus nigrescens*. The remaining Nectogalini are uncontroversial, although it should be noted that subgeneric relationships within *Chimarrogale* and *Neomys* are yet to be studied.

Genus *Sorex* (Fig. 7)

The genus *Sorex* has received more systematic attention than any other group within the Lipotyphla, although much effort has been invested in the maintenance of a stable set of species definitions and sub-generic divisions; as a result the number of source trees is less than could be expected, and the level of taxonomic overlap shown is low.

Sorex is often recognized as having three valid subgenera: *Sorex*, *Otisorex* and *Microsorex*. However, the consensus follows George (1988) in placing the pygmy shrew *Sorex hoyi* within *Otisorex*. *Sorex* is Holarctic in distribution, although multiple reinvasions between the Nearctic and Palaearctic mean that these subgenera are not restricted to either realm; indeed these successive colonization events are thought to be one of the main causative factors for the deep structure within each

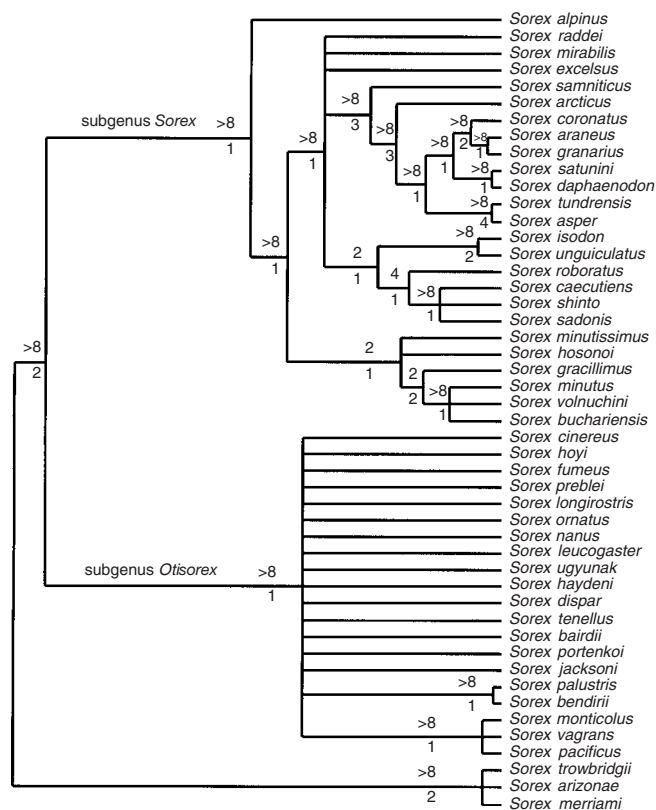


Fig. 7. Strict consensus of 844 MPTs for *Sorex*. Branch lengths are arbitrary. Weighting magnitude required to dissolve node listed above branches. Bremer support indices listed under branches.

subgenus (Fumagalli, Taberlet *et al.*, 1999). In addition there are some species that do not fit neatly into this classification scheme (see Dannelid, 1991).

Resolution in the composite tree differs greatly between the two subgenera, *Sorex* being far more resolved than *Otisorex*. This poor resolution results not from poor coverage but from inconsistency within the source trees, and demonstrates the ability of MRP to highlight areas of conflicting evidence. The MRP phylogeny suggests that a group of three species (*Sorex merriami*, *S. trowbridgii* and *S. arizonae*) occupies a position which is basal to the rest of the genus. This positioning is largely uncontested, although Fumagalli, Taberlet *et al.* (1999) and George & Sarich (1994) place the group as sister to *Otisorex* rather than the entire genus, and Ivanitskaya (1992) placed *S. trowbridgii* as a basal member of the *Sorex* subgenus without recognizing the *merriami*–*trowbridgii* group.

Several groupings are often recognized within both the major subgenera: Dannelid (1991) contains a useful, if aged, summary. Within *Sorex*, the *araneus*–*arcticus* group of Palearctic shrews is supported in the composite phylogeny (with relatively high Bremer indices), as are two groups defined on chromosome complement by Dannelid (1991), the ‘42-group’ and the ‘*S. minutus* group’.

Within the *araneus*–*arcticus* group only the MRP consensus of Volobouev (1989) and Volobouev & Dutrillaux (1991) disagrees with the composite tree to

any extent. The inclusion of *S. samniticus* as sister taxon to the *araneus*–*arcticus* group is more controversial as Dannelid (1991) and Ivanitskaya (1992) favour basal positions within the *Sorex* subgenus for this taxon. The 42-group is not recognized by Sergejev & Iljashenko (1991), who suggest that they form a paraphyletic succession of sister taxa to the *araneus*–*arcticus* group and some of the *S. minutus* group; the monophyly of the 42-group is also questioned by Ohdachi *et al.* (1997). Fumagalli, Taberlet *et al.* (1999) suggests the 42-group is rendered paraphyletic by *S. minutissimus*. The *S. minutus* group of Dannelid (1991) is supported in the composite tree, with the addition of *S. gracillimus*, although Bremer support is low, and the nodes are not supported under any non-parity weighting scheme.

The arrangement of these groups in the composite tree is controversial, with the *araneus*–*arcticus* group and the 42-group plus several other species as sister pairing to the *S. minutus* group. In particular, note that several of the nodes relating the arrangements of the three groups dissolve under weighting schemes favouring source tree methodologies that are model-based. It is clear that even in the most well-understood subset of the genus, there is a great need for modern inclusive studies of interspecific relationship.

Resolution within *Otisorex* is low, reflecting a low level of agreement between source trees and exacerbated by low taxonomic overlap. Very few consistent groupings occur, and even the few groupings supported in the composite tree are not in agreement with several sources and are controversial. The grouping of *S. fumeus* and *S. dispar*, and of *S. palustris* and *S. bendirii* after George (1988) are retained despite disagreement from Fumagalli, Taberlet *et al.* (1999). Groupings of *S. cinereus* with either *S. haydeni* or *S. fumeus* as suggested by several authors (Ohdachi *et al.*, 1997; Stewart & Baker, 1997; Fumagalli, Taberlet *et al.*, 1999) are confounded by source trees that do not consider *S. cinereus*. The composite phylogeny strongly indicates that future work within *Otisorex* must consider more species.

CONCLUSIONS

The composite phylogeny presented in this paper is the first formal consensus of lipotyphlan systematics, and democratically incorporates information derived from 50 years of systematic and evolutionary study. As such, it is both a valid working estimate of phylogeny, and, in detailing areas of poor coverage or conflicting signals, it acts as a route map for our evolutionary understanding of the group (cf. Gatesy *et al.*, 2002). The Lipotyphla have lacked a inclusive species-level phylogeny; this analysis should remedy this situation. As a tool, it is hoped that the phylogeny will further expand our understanding of this enigmatic group of mammals. As a review of the phylogenetic literature, the phylogeny is also unique and timely. It highlights, for example, the complete lack of model-based phylogenetic estimates of the Talpidae: an

entire family of mammals with a strong European and North American presence, familiar to almost everyone.

The composite tree supports the Afrotheria hypothesis, and remains congruent with a Eulipotyphla clade including the Erinaceidae. Taxa for which we have good understanding, literature coverage and consistent signals are the Erinaceidae in general, the New World Talpidae, the intergeneric arrangement of the Soricinae, and the Eurasian *Sorex* subgenus *Sorex*. However, the composite phylogeny clearly demonstrates where our knowledge is poor or conflicting. Established genera for which we have no interspecific information are the Palaearctic moles *Talpa*, *Mogera* and *Euroscaptor*, the tenrec genus *Microgale* (for which we have no estimates at all) and the Soricidae genera *Cryptotis*, for which we have little resolution, and *Chimarrogale*, for which we have none. Perhaps the most serious gaps in our knowledge concern the Chrysochloridae and the *Sorex* subgenus *Otisorex*. Phylogenetic information concerning many of the Chrysochloridae genera is not available; this situation must be recognized and remedied, especially given the threatened nature of many of these species (Hilton-Taylor, 2000). Within *Otisorex*, low resolution is caused by conflicting signals rather than poor coverage. The only remedy for this is more rigorous, more taxonomically inclusive analyses with a synthetic approach to the signal derived from different datasets. The Crocidurinae are a prime candidate for further work to support the study of Querouil *et al.* (2001).

This phylogeny is not intended to be the final word in the systematics of the Lipotyphla, and like any large phylogeny is probably wrong in many details. In particular, as for any MRP phylogeny, the composite can only reflect and summarize the work that has already been done, and it is important that structure within the composite tree is interpreted as being the product of a consensus technique. Obviously, the study of evolutionary history is not a static science, and new hypotheses of relationships need to be made encompassing the Lipotyphla: it is hoped this supertree help catalyse and guide these efforts.

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