doi:10.1111/j.1420-9101.2009.01843.x

Strong morphological support for the molecular evolutionary tree of placental mammals

M. S. Y. LEE*† & A. B. CAMENS*

*School of Earth and Environmental Sciences, University of Adelaide, Adelaide, Australia
†Earth Sciences Section, The South Australian Museum, Adelaide, Australia

Keywords:

Bayesian;
cladistics;
eutheria;
hidden branch support;
homoplasy;
mammalia;
molecular phylogenetics;
morphological phylogenetics;
partitioned branch support;
placentalia.

Abstract

The emerging molecular evolutionary tree for placental mammals differs greatly from morphological trees, leading to repeated suggestions that morphology is uninformative at this level. This view is here refuted empirically, using an extensive morphological and molecular dataset totalling 17 431 characters. When analysed alone, morphology indeed is highly misleading, contradicting nearly every clade in the preferred tree (obtained from the molecular or the combined data). Widespread homoplasy overrides historical signal. However, when added to the molecular data, morphology surprisingly *increases* support for most clades in the preferred tree. The homoplasy in the morphology is incongruent with all aspects of the molecular signal, while the historical signal in the morphology is congruent with (and amplifies) the historical signal in the molecular data. Thus, morphology remains relevant in the genomic age, providing vital independent corroboration of the molecular tree of mammals.

Introduction

The advent of large datasets of molecular sequences has greatly improved our understanding of placental mammal phylogeny (e.g. Madsen *et al.*, 2001; Murphy *et al.*, 2001; Springer *et al.*, 2004; see Bininda-Emonds *et al.*, 2007). The new data have robustly resolved most of the earliest divergences among placentals, and retrieved several clades that until the mid-1990s were either contentious (e.g. Paenungulata, Glires) or unexpected (e.g. Afrotheria, Whippomorpha). Conversely, the molecular data have largely upheld other long-accepted morphological groupings, such as most mammalian 'orders' (e.g. Gregory, 1910; Simpson, 1945; McKenna, 1975; see Asher *et al.*, 2009). Like many sources of potential phylogenetic information, morphological data such as osteology, soft anatomy, or dentition contain a mixture of informative and misleading traits that are able to resolve some clades but unable to retrieve others.

Morphological data are often misleading, although this perception might be amplified by publication bias that emphasizes cases where long-held morphological ideas are overturned using molecular data (see Lee *et al.*, 2004). The general utility of morphological data for phylogenetic reconstruction has been questioned (e.g. Hedges & Maxson, 1996; Scotland *et al.*, 2003) and defended (e.g. Jenner, 2004; Wiens, 2004). This debate remains prominent in mammal phylogeny. One early molecular study (Graur, 1993, p. 142) discussed problems with morphological analysis in placental mammals and suggested the field represented a 'dead end'. Other studies have questioned the utility of dental characters, due to high developmental correlation (e.g. Kangas *et al.*, 2004), and soft anatomy, due to ecological constraints (Jiang & Takatsuki, 1999). A further study (Springer *et al.*, 2007) demonstrated that the osteological and morphological signals deviated greatly from well-supported molecular trees. That study used heuristic pseudoextinction (Asher & Hofreiter, 2006) to evaluate the osteological signal: a focal extant (living) taxon is artificially treated as extinct (fossil) by exclusion of all of its molecular and soft anatomical data. In many instances, the osteological data alone failed to accurately resolve the affinities of the 'pseudoextinct' taxon. Furthermore, the morphological data were demonstrated to be highly incongruent with the molecular data, leading to the conclusion that the two sources of data were 'not readily miscible' (Springer *et al.*,

Correspondence: Michael Lee, Earth Sciences Section, The South Australian Museum, North Terrace, Adelaide, SA 5000, Australia.
Tel.: 61 8 8207 7568; fax: 61 8 8207 7222;
e-mail: michael.s.lee@adelaide.edu.au

2007). These results led to the conclusion that morphology was largely uninformative for higher-level placental mammal phylogeny. The validity of this approach and conclusions were subsequently discussed (Asher *et al.*, 2008; Springer *et al.*, 2008).

None of the above studies, however, empirically evaluated whether adding morphological data increases or decreases clade support, or the overall contribution of morphological or molecular data to the placental mammal tree. Such an evaluation is best achieved in the context of a combined analysis, due to the potential interaction of datasets. It would also be appropriate given that morphology is increasingly analysed in combination with other (usually molecular) data. Importantly, theoretical expectations and empirical data have shown that adding apparently incongruent datasets to a combined analysis can still improve support and/or resolution of the resultant trees (e.g. Kluge, 1989; Barrett *et al.*, 1991; Baker & DeSalle, 1997; Gatesy *et al.*, 1999, 2003; Gatesy & Arctander, 2000; Wahlberg *et al.*, 2005; Lee, 2009). Thus, although morphological data are often highly incongruent with the molecular data (Graur, 1993; Springer *et al.*, 2007), it does not automatically follow that morphology lacks phylogenetic utility. A recent evaluation of a broad cross-section of datasets indicates that adding morphology to molecular analyses generally increases resolution, but not necessarily support (Wortley & Scotland, 2006).

Using one of the most recent and extensive morphological datasets available for placental mammals (Asher, 2007), we here demonstrate that morphology contributes strong positive phylogenetic signal, but only when analysed in combination with molecular data. When analysed in isolation, morphology contradicts nearly every clade in the 'preferred' tree (retrieved by the molecular data alone and by the combined morphological and molecular data). However, when morphology is combined with extensive molecular data, morphology increases branch (Bremer) support for every clade in the preferred tree. These results demonstrate the utility of morphological data: not in spite of, *but because of*, extensive molecular data. Furthermore, many of the molecular datasets examined (e.g. mtDNA and several nuclear loci) behave in a similar fashion, being highly incongruent with the preferred tree when analysed in isolation, but boosting support for most clades when incorporated into a combined analysis. Finally, identification of a latent signal in the morphology that is highly congruent with the molecular data greatly increases confidence in the molecular tree itself.

Methods

Data matrix

The matrix of Asher (2007) includes one of the most comprehensive morphological datasets for placental mammals, combined with indel data and a large molecular alignment (Roca *et al.*, 2004). That matrix was here augmented with the addition of one new trait (Sánchez-Villagra *et al.*, 2007); unalignable regions identified previously (Roca *et al.*, 2004; Asher, 2007) were also slightly altered based on reading frame. These minor changes did not influence the optimal trees retrieved, which were the same as those in Asher (2007) when the same models were employed. The number of alignable characters (total, variable, parsimony informative) in each data partition are as follows : morphology (197, 196, 189), indels (221, 214, 74), mtRNA (1624, 717, 510), adora2 exon (330, 218, 177), adrb2 exon (833, 378, 281), atp7a exon (690, 460, 343), bdnf exon (561, 236, 157), cnr1 exon (1002, 367, 284), edg1 exon (978, 440, 318), pnoc exon (315, 199, 151), rag1 exon (773, 340, 283), rag2 exon (444, 255, 195), tyr exon (426, 252, 201), zfx exon (204, 70, 55), vwf exon (1251, 907, 692), brca1 exon (2923, 2555, 2130), irbp exon (1176, 822, 634), a2ab exon (1086, 646, 512), app intron (678, 404, 254), bmi1 intron (340, 136, 60), crem intron (408, 258, 183) and plcb4 intron (337, 281, 225).

Online Appendices S1–S3 contain the follow items discussed below: the updated matrix in both PAUP* (Appendix S1) and MrBayes (Appendix S2) formats with annotations listing modifications, a sample nexus batch command (Appendix S3) for calculating BS_{sep}.

Parsimony analyses

Parsimony analyses were performed using PAUP* (Swofford, 2002). The data were analysed with and without fossil taxa, and with and without third codon positions. Inclusion or exclusion of fossil taxa did not greatly change relationships among extant (living) taxa (see the Results section). However, the best trees with and without third codon positions differed substantially (as noted by Asher, 2007); hence all branch support analyses were performed on both these topologies (hereafter termed 'All Data Tree' and 'Thirds Deleted Tree') using the appropriate datasets (all data or third codons deleted). Branch supports and partitioned branch supports (PBS) were found in PAUP* using commands modified from TreeRot output (Sorenson & Franzosa, 2007). Most searches employed 1000 random addition replicates with no limit on maximum number of trees held; however, searches with small datasets that returned huge numbers of trees (i.e. short nuclear loci minus third positions) were performed with 100 random addition replicates each saving no more than 20 000 trees.

Branch support in combined analysis

Branch (=Bremer) support is the length difference between the best trees with and without a clade (Bremer, 1988); large positive values mean data strongly support a clade (best tree with clade is much shorter than best tree without clade), large negative values mean the reverse.

As this study is evaluating the influence of morphology and fossils on inferred relationships among *extant* (living) taxa, branch support was calculated for clades of extant taxa on the 'All Data' and 'Thirds Deleted' trees. In analyses without extinct (fossil) taxa, finding the lengths of the best trees with and without a particular clade is straightforward (using constraints and reverse constraints in PAUP*). In analyses including extinct taxa, these same constraints among extant taxa were enforced as backbone constraints, with extinct taxa allowed to 'float' and thus influence tree searches and tree length calculations (e.g. Wilkinson *et al.*, 2000; Gatesy *et al.*, 2003; Lee, 2009). Branch support analyses were performed for all clades within the ingroup (Placentalia); supports were not calculated for outgroup clades and for the ingroup node, as morphological characters for these clades were not explicitly sampled.

Partitioned branch support

Partitioned branch support (Baker & DeSalle, 1997) was calculated for each data partition in the combined analysis. PBS is the support a data partition contributes to a focal clade *in the context of a combined analysis*: it represents how strongly that data partition arbitrates between the best trees (*found for the combined data*) with and without a focal clade, and can either be positive (improves support for the focal clade) or negative (reduces support).

Five data partitions were initially implemented: mtDNA, nuclear exon, nuclear intron, indels and morphology. Although any partitioning scheme is inevitably somewhat subjective, these data partitions are widely recognized to differ in evolutionary dynamics and/or nature of character states. Because the nuclear exon and nuclear intron datasets contain multiple independently segregating loci, further PBS analyses were performed using individual loci as partitions. Four exons (adora3, adrb2, atp7a and bdnf) and two introns (app, plcb4) had sequences for all ingroup taxa and were thus analysed. PBS was not calculated for the other nuclear loci due to missing data, which causes artefacts in PBS analyis (zero support for most clades). This could not be easily ameliorated by reducing the data matrix to only taxa with sequences for all loci, as this would have dramatically reduced taxon sampling. The alternative solution of using backbone constraints comprising only taxa with no missing loci (e.g. Gatesy *et al.*, 2003; Lee, 2009) was impractical as the resultant 'backbone' would again be very taxon-poor; in addition, two different backbone constraints would need to have been simultaneously enforced in analyses with fossil taxa (see above).

Branch support in separate analysis

The branch support (Bremer, 1988) for each of the above data partitions for each clade, *when each data partition was analysed alone*, was also calculated. BS_{sep} is the support a data partition contributes to a clade *when analysed alone*. It represents how strongly a data partition arbitrates between the best trees *found for that data partition alone* with and without a clade, and can either be positive (improves support for the clade) or negative (reduces support for the clade).

Hidden branch support

Hidden branch support (HS: Gatesy *et al.*, 1999) was calculated for each of the above data partitions for each clade. HS is the difference between PBS and BS_{sep} – the *extra* support a dataset contributes to a node, emerging in the context of a combined analysis due to interaction between datasets. A positive number indicates that a data partition is more consistent with a clade in a combined analysis than in a separate analysis: for example, it can support the clade even more strongly (e.g. PBS = 10 vs. $BS_{sep} = 4$, HS = 6) or contradict it more weakly (e.g. PBS = −3 vs. $BS_{sep} = -8$, HS = 5).

Bootstrapping

Nonparametric bootstrapping (1000 replicates) was performed with all (extant and extinct) taxa and all (morphological and molecular) data partitions; analyses were performed with and without third codons. Bootstrap frequencies for each node in the relevant tree ('All Data tree' and 'Thirds deleted tree') was then ascertained. The analyses were repeated with the fossils deleted and then with morphological characters deleted; these reduced analyses revealed the effect of fossils and the effect of morphology. Reduced consensus approaches (Wilkinson *et al.*, 2000) allowed direct comparison of support for clades of extant (living) taxa, with and without fossils. In the analyses with the full taxon set, fossil taxa were included each bootstrap replicate (and thus allowed to influence relationships among extant taxa), the fossil taxa were subsequently deleted so that a reduced consensus was constructed of extant taxa alone. All PAUP* bootstrap trees were saved to a file (with tree weights, so that each bootstrap replicate rather than each tree was weighted equally); the tree file was then loaded into PAUP* (with tree weights retained) and fossil taxa deleted from the working data file, which automatically prunes these taxa from the trees held in memory.

Model-based (Bayesian) analyses

The combined morphological and molecular data, and the molecular data alone, were analysed in MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) using the following partitions: mtDNA, nuclear exons codon1, nuclear exons codon2, nuclear exons codon3, nuclear introns, indels, morphology). Bayes factors (>> 100) supported this partitioning scheme over simpler tested schemes (e.g. nuclear exons not split into codons). More complex partitioning schemes (e.g. by locus) could not be evaluated as they failed to reach stationarity even after very long runs (10 million generations). All analyses were

performed without fossils, as their inclusion caused analyses to fail to reach stationarity even after extremely long runs (as noted by Asher, 2007). The indels were analysed using the restriction site model (Ronquist *et al.*, 2005; Asher, 2007) and morphology using the standard stochastic model. Branch lengths were allowed to vary according to a rate scalar across the five nucleotide partitions, and fully unlinked across the remaining partitions. AIC tests selected the GTRig model for the nucleotide partitions, whereas Bayes factors indicated that the gamma parameter (rate variability) was required for the morphological, but not indel, partitions. Scoring bias (against invariant characters) was accommodated using the 'coding=noabsence' and 'coding=variable' commands for the indel and morphological datasets respectively. Two independent MCMC analyses were used, each with 10 chains and 6 million generations, sampling every 1000 generations. Stationarity was reached well before the burn-in of 3 million generations, as indicated (Ronquist *et al.*, 2005) by low (< 0.01) split frequencies across runs, with potential scale reduction factors for all parameters approaching 1 (< 1.01). The MrBayes data file with relevant commands is given in Appendix S2.

Partitioned Bayesian support for each dataset for each node cannot yet be calculated as MrBayes 3.1.2 does not implement reverse constraints, and even if possible (as planned for the forthcoming MrBayes 3.2), would not be feasible for the current datasets due to excessive computation time. Partitioned likelihood support (Lee & Hugall, 2003) also could not be performed as current likelihood programs (e.g. PAUP*, Garli) do not accommodate morphology or indel data, and again (even if possible) would be unfeasibly slow.

Results

Parsimony analyses

Phylogenetic relationships

The optimal (shortest) trees retrieved were identical to those in Asher *et al.* (2008). Branch support and bootstrap values for clades of extant (living) taxa are shown in Figs 1 and 2. When all characters, and extant and extinct taxa, were analysed, the four shortest trees [length (L) = 47 670, consistency index (CI) = 0.5] all had the same arrangement of living taxa (Fig. 1; see also Fig. S1). This was largely consistent with many well-supported placental mammal groupings (e.g. Xenarthra, Laurasiatheria, Euarchontoglires) but had an unorthodox rooting within Afrotheria, with *Echinops* being sister to all other ingroup taxa (Fig. 1). Interestingly, this rooting did not appear on the bootstrap consensus tree. When the analysis was repeated with extinct taxa deleted, the resultant shortest tree (L = 47 503, CI = 0.5) preserved identical relationships among extant taxa. Again, the unorthodox rooting within Afrotheria did not appear on the bootstrap consensus tree. Analysis of the molecular (including indel) data alone retrieved largely the same unrooted network, but with an even

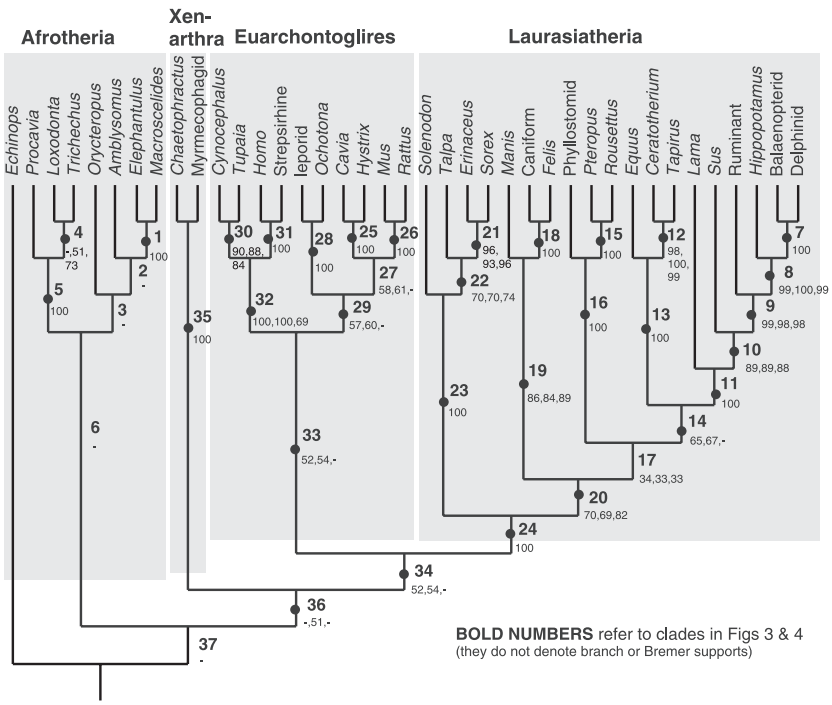

Fig. 1 Phylogenetic relationships among extant (living) placental mammals found in analyses combining all molecular data (third codons included) and morphological data. This same topology for extant (i.e. living) taxa was found in analyses including all (extant and extinct) taxa, and only extant taxa. Large (bold) font numbers refer to clades in Figs 3 and 4. Small font numbers refer to bootstrap support in analysis with all taxa/extant taxa only/molecular data only; dash indicates a particular clade was not found in majority-rule bootstrap consensus tree for the relevant analysis. A single small font number (e.g. 100) indicates the same result was found in all three analyses. Dots indicate clades found in Bayesian analyses (Fig. 7). For position of fossil taxa, see also Fig. S1.

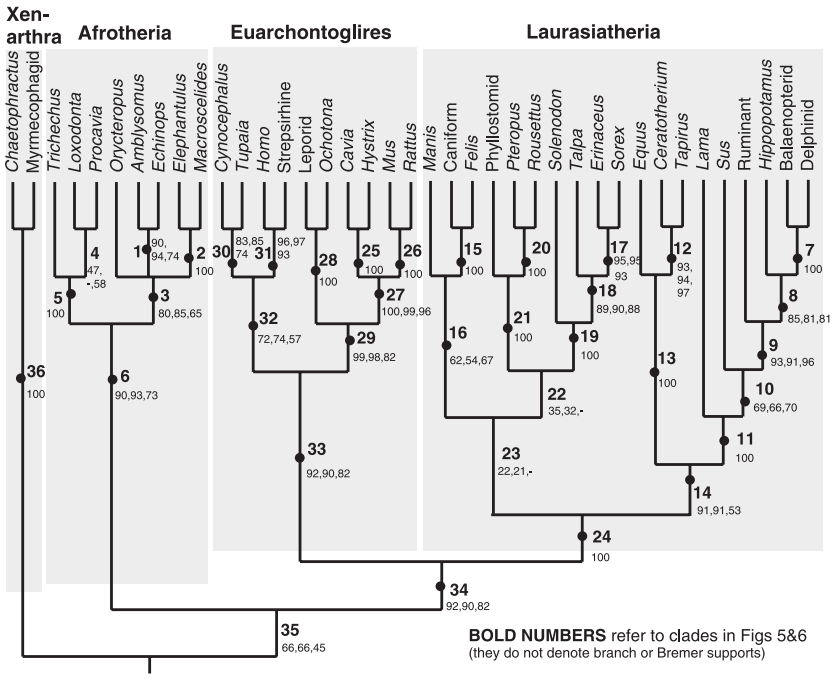

Fig. 2 Phylogenetic relationships among extant (living) placental mammals found in phylogenetic analyses combining molecular data (minus third codons) and morphological data. This topology for extant taxa was found in the analysis including all (extant and extinct) taxa; the analysis including only extant taxa retrieved all clades except for clade 4. Large (bold) font numbers refer to clades in Figs 5 and 6. Small font numbers refer to bootstrap support in analysis with all taxa/extant taxa only/molecular data only; dash indicates a particular clade was not found in majority-rule bootstrap consensus tree for the relevant analysis. A single small font number indicates the same result was found in all three analyses. Dots indicate clades found in Bayesian analyses (Fig. 7).

more unorthodox rooting within rodents (see Asher, 2007).

The combined morphology and molecular data, when third codon positions were deleted, produced eight trees (L = 26 716, CI = 0.54) with largely the same clades of extant taxa as previously retrieved (Fig. 2; see also Fig. S1B), but with a more orthodox rooting (between xenarthrans and all other placentals; e.g. Kriegs *et al.*, 2006) resulting in a monophyletic Afrotheria. Fossil taxa again had very minor influence: when they were excluded, the resultant tree (L = 26 548, CI = 0.54) had a minor rearrangement within living Afrotheria, with all other extant groupings remaining unchanged. Analysis of the molecular (including indel) data alone retrieved an almost identical tree, with only minor differences within Afrotheria.

The combined-data trees (with and without third codons, and with and without fossil taxa) are very similar to each other and highly consistent with trees found in other recent comprehensive studies, including model-based analyses of exclusively molecular data (Springer *et al.*, 2004; Kriegs *et al.*, 2006; Asher, 2007; Nikolaev *et al.*, 2007; Wildman *et al.*, 2007). They are also highly consistent with the Bayesian analyses here, which retrieved very similar trees using either the molecular data alone or using the combined data (see below). The position of *Echinops* as basal to all other placentals rather than nested within Afrotheria in the 'all data' trees results in disagreement within Afrotheria between the present phylogeny and many model-based molecular phylogenies (and other combined parsimony analyses; Seiffert, 2007); however, exclusion of third codons largely removes this disagreement. The general congruence across data and methods suggests reasonable confidence in these topologies, making them suitable benchmarks for evaluating the contribution of morphology and other datasets to clade support. Notably, the results below hold qualitatively whether one uses the 'all data' tree and analyses (with an unusual rooting within Afrotheria) and 'thirds deleted' tree and analyses (with a rooting between Xenarthra and Epitheria, and a monophyletic Afrotheria).

Partitioned branch support and hidden branch support

There were high levels of HS in the analysis, from all datasets. Notably, many datasets (including most nuclear loci when analysed individually) contradicted the combined-data phylogeny when analysed in isolation, but boosted support for this phylogeny when analysed in combination with the rest of the data. Inclusion or exclusion of third codon positions, and inclusion or exclusion of fossil taxa, did not qualitatively change the behaviour of PBS and HS. The following discussion therefore focuses on the most complete analysis (third codons included and fossil taxa included; Figs 3 and 4, upper figure in each cell); the results for the other three analyses are qualitatively similar (Figs 3 to 6).

When all characters and fossil taxa are included, and a combined analysis is performed with the data partitioned into mtDNA, nuclear exon, nuclear intron, indels and morphology, the bulk of the support for the phylogeny comes from the combined nuclear exon dataset (Fig. 3). Branch support from all datasets (over all nodes) totals

2923 with the nuclear exon partition contributing a total PBS of 1887. However, nuclear introns (total PBS = 625), indels (41) and morphology (449) also contribute strong overall support, with only the mtDNA (−79) being in overall conflict. When these numbers are divided by the number of parsimony-informative characters in each data partition, to give average branch support per (informative) character, the figures are: overall +0.36, morphology +2.37, indels +0.55, mtDNA −0.15, nuclear exons +0.29 and nuclear introns +0.87. These numbers and ratios vary across the different analyses (including or excluding third codons and extinct taxa), but the same general patttern is consistent. It is notable that the nuclear intron, indel and morphology datasets show very high levels of hidden support (HS). For instance, when analysed alone, the morphological dataset contradicts most clades in the phylogeny (BS_{sep} values are negative for most clades, and total $BS_{sep} = -277$). But in a combined analysis, the morphology adds support for most nodes (36/37 PBS values are positive, and total PBS = +449; HS is therefore 726). This dramatic difference is explained in the discussion.

Interestingly, even though the combined nuclear exon (1887) and combined nuclear intron (625) datasets each contribute high levels of support, much of this is due to HS that only emerges when all the nuclear exons, or all the nuclear introns, are combined (and idiosyncratic behaviour of each locus is therefore 'averaged out' to improve phylogenetic signal). When the six well-sampled nuclear loci (4 exons and 2 introns) are analysed simultaneously with all other data, they contribute substantial branch support (497), but when analysed in isolation, they offer little net support (24) (Fig. 4). Considered in isolation, two loci strongly contradict the phylogeny (total BS_{sep} of adrb2 = −96 and bdnf = −34), one locus very weakly contradicts the phylogeny (adora3 = −1), one locus offers very weak net support (app = 13) and two loci offer strong support (atp7a = 62, plcb4 = 80). However, all six loci offer much stronger support for the phylogeny when analysed in combination with the rest of the full dataset: five of the six loci have greatly increased (and high positive) PBS values, and the 'worst' locus is now nearly neutral instead of strong conflicting (adrb2: PBS = −7, up from $BS_{sep} = -96$).

Model-based (Bayesian) analyses

The Bayesian analyses, with all data and with molecules only, returned almost identical topologies, with posteriors of 1.0 for nearly all clades. The sole topological difference between these two Bayesian analyses consisted of rearrangement around a single node within Afrotheria (Fig. 7 and caption). The Bayesian trees were highly consistent with both the All-Data MP tree, and the Thirds-Deleted MP tree, in nearly all clades (Figs 1 and 2; concordant clades indicated by dots). They are also highly consistent with the Bayesian trees of Asher (2007), which used a simpler (three-way) partitioning scheme. The only difference concerns relationships within Laurasiatheria: here, a more orthodox arrangement is retrieved, with bats and carnivorans excluded from a monophyletic Cetartiodactyla (e.g. Springer *et al.*, 2004).

Discussion

This evaluation of a comprehensive morphological dataset for placental mammals (Asher, 2007) reveals that it contains surprisingly strong support for the molecular tree, but *only* when analysed with molecular data. When analysed in isolation, morphology fails to retrieve high-level placental mammal clades recently established using largely molecular data (e.g. see Springer *et al.*, 2008). Morphology instead strongly supports many conflicting clades, resulting in high incongruence that is reflected in a large overall negative BS_{sep} (−277; Fig. 3). However, when combined with molecular data, morphology behaves very differently, and strongly boosts support for nearly every clade. Notably, the morphological dataset is not the only dataset exhibiting such behaviour. When analysed in isolation, the indel, nuclear BDNF and nuclear adora3 datasets also fail to retrieve most clades in the 'combined data tree' (Fig. 1); thus, for each dataset, BS_{sep} is negative for most clades and negative overall (Figs 4 and 5). But it does not follow that these datasets lack (or contain misleading) phylogenetic signal. When analysed in combination with all other datasets, each of these datasets bolsters support for the combined-data phylogeny: each dataset increases branch support for most clades (PBS is positive for most clades and positive overall). This is most extreme for the morphological data,

Fig. 3 Phylogenetic utility of mtDNA, nuclear exons, nuclear introns, indels and morphology, in analyses incorporating all molecular (including 3rd codons) and morphological data. Clades are shown in the left column and are numbered as in Fig 1. For each clade support found in analyses with all taxa are shown in the upper row, support found in analyses excluding extinct taxa are shown in the lower row. For each data partition, left column (highlighted in blue online) shows Partitioned Branch Support (i.e. phylogenetic signal a data partition provides when analysed with all other data); centre column (highlighted in pink online) shows Branch Support in a separate analysis (i.e. phylogenetic signal a data partition provides when analysed in isolation); right column (highlighted in yellow online)shows Hidden Support (i.e. additional support that emerges in the combined analysis). Note that morphology (the Morph data partition) offers positive support for nearly all nodes when combined with the molecular data (left/blue column), but contradicts most nodes when analysed in isolation (centre/pink column), and thus has a high amount of hidden support (right/yellow column). Totals (summed over partitions) for each clade are shown in the rightmost three columns; totals (summed over clades) for each data partition are shown in the bottom rows.

which contradicts most nodes when analysed in isolation, but supports nearly all nodes when analysed in combination. Similar results are obtained whether third codon positions, and fossil taxa, are included or excluded.

The reasons for the radically different behaviour of datasets in isolation and in combination have been much discussed (e.g. Kluge, 1989; Barrett *et al.*, 1991; Bull *et al.*, 1993; Gatesy *et al.*, 1999, 2003; Wiens, 2004;

CLADE		MtDNA			NucExon			NucIntron			Indels			Morph			TOTAL		
(Fig. 1)		PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS
1	all taxa	12	23	-11	236	246	-10	61	54	7	2	1	1	13	9	4	**324**	**333**	**-9**
	no fossils	8.5	"	-14.5	235	"	-11	61	"	7	2	"	1	20.5	7	13.5	**327**	**331**	**-4**
2	all taxa	-19	-10	-9	-22	-5	-17	25	-2	27	0	0	0	19	-12	31	**3**	**-29**	**32**
	no fossils	-16	"	-6	-6	"	-1	19	"	21	0	"	0	6	-10	16	**3**	**-27**	**30**
3	all taxa	6	-5	11	-2	-5	3	0	-5	5	0	-1	1	-2	-23	21	**2**	**-39**	**41**
	no fossils	-16	"	-11	-6	"	-1	19	"	24	0	"	1	6	-23	29	**3**	**-39**	**42**
4	all taxa	-9	-2	-7	-9	-8	-1	2	-2	4	0	-1	1	17	1	16	**1**	**-12**	**13**
	no fossils	-15.4	"	-13.4	-13.8	"	-5.8	14.6	"	16.6	0	"	1	18.6	7	11.6	**4**	**-6**	**10**
5	all taxa	17.06	10	7.06	47.87	49	-1.13	9.1	5	4.1	0	0	0	5.97	-3	8.97	**80**	**61**	**19**
	no fossils	17	"	7	48	"	-1	9	"	4	0	"	0	6	2	4	**80**	**66**	**14**
6	all taxa	-19	-7	-12	-22	-5	-17	25	-5	30	0	-1	1	19	-34	53	**3**	**-52**	**55**
	no fossils	-16	"	-9	-6	"	-1	19	"	24	0	"	1	6	-34	40	**3**	**-52**	**55**
7	all taxa	13	13	0	107	117	-10	28	24	4	3	2	1	46	24	22	**197**	**180**	**17**
	no fossils	22	"	9	119	"	2	25	"	1	3	"	1	29	19	10	**198**	**175**	**23**
8	all taxa	0	-2	2	16.75	20	-3.25	6	2	4	0.25	0	0.25	7	-6	13	**30**	**14**	**16**
	no fossils	2	"	4	21	"	1	5	"	3	0	"	0	1	-7	8	**29**	**13**	**16**
9	all taxa	-2.5	-8	5.5	15	20	-5	9.4	4	5.4	0.1	0	0.1	5	-9	14	**27**	**7**	**20**
	no fossils	-3	"	5	21	"	1	7	"	3	0	"	0	1	-12	13	**26**	**4**	**22**
10	all taxa	-13	-11	-2	9	13	-4	5	0	5	0	0	0	13	-10	23	**14**	**-8**	**22**
	no fossils	-8	"	3	20	"	7	3	"	3	0	"	0	1	-12	13	**16**	**-10**	**26**
11	all taxa	7	3	4	135	136	-1	23	18	5	6	1	5	13	-5	18	**184**	**153**	**31**
	no fossils	-4	"	-7	144	"	8	29	"	11	5	"	4	5	-6	11	**179**	**152**	**27**
12	all taxa	6	7	-1	18	17	1	-1	0	-1	0	0	0	-2	-1	-1	**21**	**23**	**-2**
	no fossils	6	"	-1	18	"	1	-1	"	-1	0	"	0	-2	1	-3	**21**	**25**	**-4**
13	all taxa	13	8	5	108	115	-7	9	7	2	0	0	0	6	-1	7	**136**	**129**	**7**
	no fossils	13	"	5	108	"	-7	9	"	2	0	"	0	6	2	4	**136**	**132**	**4**
14	all taxa	-9	0	-9	-9	0	-9	2	0	2	0	-2	2	17	-6	23	**1**	**-8**	**9**
	no fossils	-6	"	-6	0	"	0	0	"	0	0	"	2	9	-4	13	**3**	**-6**	**9**
15	all taxa	20	16	4	264	259	5	20	19	1	4	4	0	6	7	-1	**314**	**305**	**9**
	no fossils	20	"	4	264	"	5	20	"	1	4	"	0	6	6	0	**314**	**304**	**10**
16	all taxa	-14	3	-17	74	71	3	15	7	8	1	1	0	22	9	13	**98**	**91**	**7**
	no fossils	-12	"	-15	79	"	8	13.5	"	6.5	1	"	0	19.5	12	7.5	**101**	**94**	**7**
17	all taxa	3	0	3	-5	-3	-2	3	0	3	0	-2	2	0	-16	16	**1**	**-21**	**22**
	no fossils	3.33	"	3.33	-4	"	-1	2	"	2	0	"	2	1.67	-13	14.67	**3**	**-18**	**21**
18	all taxa	13	9	4	131	138	-7	12	8	4	0	0	0	3	4	-1	**159**	**159**	**0**
	no fossils	13	"	4	131	"	-7	12	"	4	0	"	0	4	5	-1	**160**	**160**	**0**
19	all taxa	0.5	-4	4.5	-0.5	6	-6.5	6	1	5	1	1	0	7	-11	18	**14**	**-7**	**21**
	no fossils	2	"	6	3	"	-3	5	"	4	1	"	0	2	-13	15	**13**	**-9**	**22**
20	all taxa	-1	-4	3	-8	6	-14	3	-2	5	1	-1	2	7	-25	32	**2**	**-26**	**28**
	no fossils	3	"	7	-1	"	-7	1	"	3	1	"	2	-1	-26	25	**3**	**-27**	**30**
21	all taxa	-8.33	-9	0.67	19.33	27	-7.67	14.67	8	6.67	0.67	0	0.67	2.67	-7	9.67	**29**	**19**	**10**
	no fossils	-6	"	3	25	"	-2	13	"	5	1	"	1	-2	-7	5	**31**	**19**	**12**
22	all taxa	1.8	-7	8.8	-12.4	0	-12.4	10.6	2	8.6	0	0	0	8	-10	18	**8**	**-15**	**23**
	no fossils	-7.33	"	-0.33	-12.33	"	-12.33	18.33	"	16.33	0	"	0	12.33	-10	22.33	**11**	**-15**	**26**
23	all taxa	-4	-9	5	38	40	-2	8	1	7	2	-1	3	14	-7	21	**58**	**24**	**34**
	no fossils	-2	"	7	46	"	6	6	"	5	2	"	3	6	-9	15	**58**	**22**	**36**
24	all taxa	6	-12	18	53	64	-11	0	2	-2	0	-2	2	-3	-39	36	**56**	**13**	**43**
	no fossils	6	"	18	53	"	-11	0	"	-2	0	"	2	1	-39	40	**60**	**13**	**47**
25	all taxa	-11	8	-19	196	216	-20	43	27	16	2	0	2	25	5	20	**255**	**256**	**-1**
	no fossils	-9	"	-17	212	"	-4	37	"	10	2	"	2	12	5	7	**254**	**256**	**-2**
26	all taxa	8	28	-20	419	440	-21	89	64	25	14	4	10	22	3	19	**552**	**539**	**13**
	no fossils	11	"	-17	434	"	-6	83	"	19	14	"	10	8	2	6	**550**	**538**	**12**
27	all taxa	-19	0	-19	-22	-5	-17	25	8	17	0	0	0	19	3	16	**3**	**6**	**-3**
	no fossils	-16	"	-16	-6	"	-1	19	"	11	0	"	0	6	1	5	**3**	**4**	**-1**
28	all taxa	-1	6	-7	80	99	-19	26	16	10	5	2	3	27	-2	29	**137**	**121**	**16**
	no fossils	2	"	-4	96	"	-3	20	"	4	5	"	3	14	-1	15	**137**	**122**	**15**
29	all taxa	-19	-9	-10	-22	-5	-17	25	-8	33	0	-1	1	19	10	9	**3**	**-13**	**16**
	no fossils	-16	"	-7	-6	"	-1	19	"	27	0	"	1	6	7	-1	**3**	**-16**	**19**
30	all taxa	17.06	4	13.06	-2.21	3	-5.21	0.63	-9	9.63	1	-1	2	0.52	-8	8.52	**17**	**-11**	**28**
	no fossils	18	"	14	0	"	-3	0	"	9	1	"	2	0	-5	5	**19**	**-8**	**27**
31	all taxa	6	2	4	33	31	2	12	5	7	0	-3	3	6	4	2	**57**	**39**	**18**
	no fossils	3	"	1	33	"	2	12	"	7	0	"	3	8	2	6	**56**	**37**	**19**
32	all taxa	3	0	3	4	3	1	0	-9	9	0	-3	3	2	-8	10	**9**	**-17**	**26**
	no fossils	3	"	3	4	"	1	0	"	9	0	"	3	2	-4	6	**9**	**-13**	**22**
33	all taxa	-19	-10	-9	-22	-5	-17	25	2	23	0	-1	1	19	-11	30	**3**	**-25**	**28**
	no fossils	-16	"	-6	-6	"	-1	19	"	17	0	"	1	6	-8	14	**3**	**-22**	**25**
34	all taxa	-19	-7	-12	-22	-5	-17	25	6	19	0	0	0	19	-42	61	**3**	**-48**	**51**
	no fossils	-16	"	-9	-6	"	-1	19	"	13	0	"	0	6	-44	50	**3**	**-50**	**53**
35	all taxa	-6.93	11	-17.93	107.2	118	-10.8	8.6	8	0.6	-1.93	0	-1.93	9.05	-8	17.05	**116**	**129**	**-13**
	no fossils	-3	"	-14	113	"	-5	7.5	"	-0.5	-2	"	-2	-0.5	-9	8.5	**115**	**128**	**-13**
36	all taxa	-19	-7	-12	-22	-5	-17	25	2	23	0	0	0	19	-38	57	**3**	**-48**	**51**
	no fossils	-16	"	-9	-6	"	-1	19	"	17	0	"	0	6	-42	48	**3**	**-52**	**55**
37	all taxa	-19	-8	-11	-22	-5	-17	25	-5	30	0	-3	3	19	-14	33	**3**	**-35**	**38**
	no fossils	-16	"	-8	-6	"	-1	19	"	24	0	"	3	6	-17	23	**3**	**-38**	**41**
TOTAL	**all taxa**	**-79**	**20**	**-99**	**1887**	**2198**	**-311**	**625**	**253**	**372**	**41**	**-7**	**48**	**449**	**-277**	**726**	**2923**	**2187**	**736**
	no fossils	**-67**	"	**-87**	**2142**	"	**-56**	**583**	"	**330**	**40**	"	**47**	**242**	**-277**	**519**	**2940**	**2187**	**753**

Gatesy & Baker, 2005; Wahlberg *et al.*, 2005; Springer *et al.*, 2008; Lee, 2009). There is a widespread view that synergism should occur when datasets are combined: idiosyncratic homoplasy in independent datasets will cancel out, but shared historical signal will amplify. This is reflected here by the combined analysis revealing much HS from all datasets, a pattern commonly observed (see previous references). In the four analyses here, between 25% and 44% of branch support emerges due to the interaction of the five primary data partitions (mtDNA, nuclear exons, introns, indel and morphology).

CLADE		adora3			adrb2			atp7a			bdnf			app-intron			plcb4-intron			TOTAL		
(Fig 1)		PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS
1	all taxa	12	15	-3	5	0	5	30	37	-7	8	5	3	15	12	3	26	18	8	**96**	**87**	**9**
	no fossils	12	"	-3	4	"	4	29	"	-8	10	"	5	15	"	3	25.5	"	7.5	**95.5**	"	**8.5**
2	all taxa	-4	-2	-2	-7	-3	-4	-7	-5	-2	-1	-2	1	-1	-4	3	11	-1	12	**-9**	**-17**	**8**
	no fossils	-7	"	-5	-9	"	-6	-7	"	-2	0	"	2	-1	"	3	8	"	9	**-16**	"	**1**
3	all taxa	0	-3	3	-3	-6	3	0	-5	5	-1	-7	6	1	-3	4	0	-2	2	**-3**	**-26**	**23**
	no fossils	-7	"	-4	-9	"	-3	-7	"	-2	0	"	7	-1	"	2	8	"	10	**-16**	"	**10**
4	all taxa	4	3	1	-1	0	-1	-2	-2	0	4	-1	5	0	0	0	0	0	0	**5**	**0**	**5**
	no fossils	-0.8	"	-3.8	-5	"	-5	-5	"	-3	1	"	2	-0.6	"	-0.6	5.8	"	5.8	**-4.6**	"	**-4.6**
5	all taxa	2	1	1	0.03	0	0.03	7	5	2	-4.03	-5	0.97	4	0	4	4.06	1	3.06	**13.06**	**2**	**11.06**
	no fossils	2	"	1	0	"	0	7	"	2	-4	"	1	4	"	4	4	"	3	**13**	"	**11**
6	all taxa	-4	-5	1	-7	-3	-4	-7	-4	-3	-1	-3	2	-1	-3	2	11	-3	14	**-9**	**-21**	**12**
	no fossils	-7	"	-2	-9	"	-6	-7	"	-3	0	"	3	-1	"	2	8	"	11	**-16**	"	**5**
7	all taxa	5	1	4	3	0	3	1	2	-1	10	6	4	5	4	1	6	4	2	**30**	**17**	**13**
	no fossils	1	"	0	4	"	4	3	"	1	7	"	1	5	"	1	5	"	1	**25**	"	**8**
8	all taxa	1.67	1	0.67	-0.78	-2	1.22	-0.56	-1	0.44	-0.22	-1	0.78	0.78	0	0.78	0.11	-1	1.11	**1**	**-4**	**5**
	no fossils	0	"	-1	-1	"	1	-1	"	0	0	"	1	1	"	1	0	"	1	**-1**	"	**3**
9	all taxa	-0.58	-2	1.42	-0.38	0	-0.38	4.31	3	1.31	4.5	0	4.5	4	2	2	4.15	2	2.15	**16**	**5**	**11**
	no fossils	-3	"	-1	-2	"	-2	3	"	0	6	"	6	4	"	2	3	"	1	**11**	"	**6**
10	all taxa	5	-1	6	-3	-6	3	-1	0	-1	3	0	3	0	0	0	3	2	1	**7**	**-5**	**12**
	no fossils	1	"	2	-2.5	"	3.5	0	"	0	1.5	"	1.5	0	"	0	2.5	"	0.5	**2.5**	"	**7.5**
11	all taxa	4	-2	6	5	-3	8	10	7	3	5	-1	6	3	2	1	16	9	7	**43**	**12**	**31**
	no fossils	5	"	7	-10	"	-7	11	"	4	10	"	11	2	"	0	19	"	10	**37**	"	**25**
12	all taxa	-1	0	-1	0	0	0	-1	-1	0	1	0	1	1	0	1	-1	-1	0	**-1**	**-2**	**1**
	no fossils	-1	"	-1	0	"	0	-1	"	0	1	"	1	1	"	1	-1	"	0	**-1**	"	**1**
13	all taxa	2	-1	3	6	0	6	5	1	4	4	6	-2	6	4	2	1	2	-1	**24**	**12**	**12**
	no fossils	2	"	3	6	"	6	5	"	4	4	"	-2	6	"	2	1	"	-1	**24**	"	**12**
14	all taxa	4	-3	7	-1	-6	5	-2	0	-2	4	-3	7	0	0	0	0	-1	1	**5**	**-13**	**18**
	no fossils	0	"	3	-2	"	4	-2	"	-2	4	"	7	0	"	0	-1	"	0	**-1**	"	**12**
15	all taxa	3	4	-1	13	0	13	18	17	1	6	5	1	8	8	0	4	3	1	**52**	**37**	**15**
	no fossils	3	"	-1	13	"	13	18	"	1	6	"	1	8	"	0	4	"	1	**52**	"	**15**
16	all taxa	6	3	3	6	0	6	-5	-1	-4	2	1	1	-5	-4	-1	14	4	10	**18**	**3**	**15**
	no fossils	4.5	"	1.5	5.5	"	5.5	-5	"	-4	2.5	"	1.5	-5	"	-1	13.5	"	9.5	**16**	"	**13**
17	all taxa	0	-5	5	1	-5	6	0	-1	1	-1	-6	5	0	-6	6	2	1	1	**2**	**-22**	**24**
	no fossils	-1	"	4	-0.33	"	4.67	0.67	"	1.67	-0.67	"	5.33	-0.33	"	5.67	1.33	"	0.33	**-0.33**	"	**21.67**
18	all taxa	7	6	1	4	0	4	3	4	-1	-2	-3	1	1	-3	4	8	3	5	**21**	**7**	**14**
	no fossils	7	"	1	4	"	4	3	"	-1	-2	"	1	1	"	4	8	"	5	**21**	"	**14**
19	all taxa	4	2	2	1.5	-6	7.5	-1	-1	0	1	-4	5	-1	-6	5	5.5	0	5.5	**10**	**-15**	**25**
	no fossils	2	"	0	1	"	7	-1	"	0	1	"	5	-1	"	5	5	"	5	**7**	"	**22**
20	all taxa	3	-4	7	2	-7	9	2	1	1	-2	-7	5	0	-6	6	1	0	1	**6**	**-23**	**29**
	no fossils	-1	"	3	1	"	8	2	"	1	-2	"	5	0	"	6	0	"	0	**0**	"	**23**
21	all taxa	5.86	-1	6.86	-3.29	-2	-1.29	2.43	3	-0.57	-6.71	0	-6.71	5	2	3	2	-1	3	**5.29**	**1**	**4.29**
	no fossils	3	"	4	-4	"	-2	3	"	0	-7	"	-7	5	"	3	1	"	2	**1**	"	**0**
22	all taxa	2	1	1	-2.5	-3	0.5	-2	-2	0	-5	-4	-1	2.86	-1	3.86	4.93	1	3.93	**0.29**	**-8**	**8.29**
	no fossils	-2.67	"	-3.67	-8	"	-5	-5.67	"	-3.67	-4.67	"	-0.67	2.33	"	3.33	7.67	"	6.67	**-11.01**	"	**-3.01**
23	all taxa	8	-1	9	-1	0	-1	4	4	0	-2	-6	4	-1	-2	1	5	0	5	**13**	**-5**	**18**
	no fossils	5	"	6	-2	"	-2	3.5	"	-0.5	-2	"	4	-1	"	1	4	"	4	**7.5**	"	**12.5**
24	all taxa	3	-3	6	-2	0	-2	3	1	2	2	-1	3	1	-3	4	1	0	1	**8**	**-6**	**14**
	no fossils	3	"	6	-2	"	-2	3	"	2	2	"	3	1	"	4	1	"	1	**8**	"	**14**
25	all taxa	6	7	-1	-3	0	-3	7	15	-8	17	22	-5	0	4	-4	14	4	10	**41**	**52**	**-11**
	no fossils	3	"	-4	-5	"	-5	7	"	-8	18	"	-4	0	"	-4	11	"	7	**34**	"	**-18**
26	all taxa	17	16	1	11	0	11	9	20	-11	13	15	-2	20	22	-2	27	20	7	**97**	**93**	**4**
	no fossils	14	"	-2	9	"	9	9	"	-11	14	"	-1	20	"	-2	24	"	4	**90**	"	**-3**
27	all taxa	-4	2	-6	-7	-4	-3	-7	-1	-6	-1	-3	2	-1	1	-2	11	2	9	**-9**	**-3**	**-6**
	no fossils	-7	"	-9	-9	"	-5	-7	"	-6	0	"	3	-1	"	-2	8	"	6	**-16**	"	**-13**
28	all taxa	10	6	4	2	0	2	-2	8	-10	-4	-1	-3	3	7	-4	13	7	6	**22**	**27**	**-5**
	no fossils	7	"	1	0	"	0	-2	"	-10	-3	"	-2	3	"	-4	10	"	3	**15**	"	**-12**
29	all taxa	-4	-5	1	-7	-4	-3	-7	-1	-6	-1	-9	8	-1	-4	3	11	0	11	**-9**	**-23**	**14**
	no fossils	-7	"	-2	-9	"	-5	-7	"	-6	0	"	9	-1	"	3	8	"	8	**-16**	"	**7**
30	all taxa	0.33	-10	10.33	-0.33	-4	3.67	1	-2	3	1	-4	5	0	-5	5	2.33	0	2.33	**4.33**	**-25**	**29.33**
	no fossils	-1	"	9	-1	"	3	1	"	3	1	"	5	0	"	5	2	"	2	**2**	"	**27**
31	all taxa	0	-3	3	3	0	3	0	-2	2	5	-4	9	4	2	2	3	1	2	**15**	**-6**	**21**
	no fossils	0	"	3	3	"	3	0	"	2	5	"	9	4	"	2	3	"	2	**15**	"	**21**
32	all taxa	0	-5	5	4	-2	6	-1	-4	3	0	-8	8	0	-6	6	1	0	1	**4**	**-25**	**29**
	no fossils	0	"	5	4	"	6	-1	"	3	0	"	8	0	"	6	1	"	1	**4**	"	**29**
33	all taxa	-4	-7	3	-7	-5	-2	-7	-5	-2	-1	-6	5	-1	-4	3	11	1	10	**-9**	**-26**	**17**
	no fossils	-7	"	0	-9	"	-4	-7	"	-2	0	"	6	-1	"	3	8	"	7	**-16**	"	**10**
34	all taxa	-4	-6	2	-7	-8	1	-7	-10	3	-1	-3	2	-1	0	-1	11	2	9	**-9**	**-25**	**16**
	no fossils	-7	"	-1	-9	"	-1	-7	"	3	0	"	3	-1	"	-1	8	"	6	**-16**	"	**9**
35	all taxa	6.93	4	2.93	3.28	0	3.28	3.35	9	-5.65	-3.48	0	-3.48	-1	3	-4	4.6	1	3.6	**13.68**	**17**	**-3.32**
	no fossils	5.5	"	1.5	4	"	4	4	"	-5	-4.5	"	-4.5	-1	"	-4	4.5	"	3.5	**12.5**	"	**-4.5**
36	all taxa	-4	-4	0	-7	-8	1	-7	-12	5	-1	-2	1	-1	0	-1	11	1	10	**-9**	**-25**	**16**
	no fossils	-7	"	-3	-9	"	-1	-7	"	5	0	"	2	-1	"	-1	8	"	7	**-16**	"	**9**
37	all taxa	-4	0	-4	-7	-9	2	-7	-15	8	-1	0	-1	-1	0	-1	11	1	10	**-9**	**-23**	**14**
	no fossils	-7	"	-7	-9	"	0	-7	"	8	0	"	0	-1	"	-1	8	"	7	**-16**	"	**7**
TOTAL	**all taxa**	**88**	**-1**	**89**	**-7**	**-96**	**89**	**37**	**62**	**-25**	**51**	**-34**	**85**	**69**	**13**	**56**	**260**	**80**	**180**	**497**	**24**	**473**
	no fossils	**7**	"	**8**	**-67**	"	**29**	**26**	"	**-37**	**64**	"	**98**	**64**	"	**51**	**237**	"	**157**	**330**	"	**306**

Fig. 4 Phylogenetic utility of six well-sampled nuclear loci in analyses incorporating all molecular (including third codons) and morphological data. Clades are shown in the left column and are numbered as in Fig. 1. The loci include four exons (adora3, adrb2, atp7a, bdnf) and two introns (app, plcb4). Information in rows and columns is structured as in Fig. 3; see that caption for details.

CLADE (Fig 2)		MtDNA			NucExon			NucIntron			Indels			Morph			TOTAL		
		PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS
1	all taxa	7.13	1	6.13	0.88	-1	1.88	0.63	-4	4.63	1	-1	2	8.38	-3	11.38	**18.0**	**-8**	**26**
	no fossils	9.5	"	8.5	-8	"	-7	1	"	5	0.5	"	1.5	26	-2	28	**29.0**	**-7**	**36**
2	all taxa	30.13	23	7.13	105.9	106	-0.12	58.63	54	4.63	1	1	0	8.38	9	-0.62	**204.0**	**193**	**11**
	no fossils	33.5	"	10.5	101	"	-5	58	"	4	0.5	"	-0.5	14	7	7	**207.0**	**191**	**16**
3	all taxa	2.84	0	2.84	3.02	-1	4.02	2.91	3	-0.09	0	0	0	0.23	-22	22.23	**9.0**	**-20**	**29**
	no fossils	12	"	12	-1	"	0	-2	"	-5	-2	"	-2	4	-22	26	**11.0**	**-20**	**31**
4	all taxa	-4.88	-5	0.12	9.88	2	7.88	1.63	2	-0.37	1	1	0	-6.63	-7	0.37	**1.0**	**-7**	**8**
	no fossils*	-11	"	-6	9	"	7	6	"	4	1	"	0	-8	-9	1	**-3.0**	**-9**	**6** *
5	all taxa	9.46	10	-0.54	34.94	36	-1.06	4.09	5	-0.91	1	0	1	-0.49	-3	2.51	**49.0**	**48**	**1**
	no fossils	19	"	9	25	"	-11	-3	"	-8	0	"	0	5	2	3	**46.0**	**53**	**-7**
6	all taxa	7.13	7	0.13	0.88	-1	1.88	0.63	5	-4.37	1	-1	2	8.38	-34	42.38	**18.0**	**-24**	**42**
	no fossils	9.5	"	2.5	-8	"	-7	1	"	-4	0.5	"	1.5	26	-38	64	**29.0**	**-28**	**57**
7	all taxa	13.13	13	0.13	58.88	57	1.88	31.63	24	7.63	5	2	3	24.38	23	1.38	**133.0**	**119**	**14**
	no fossils	16.5	"	3.5	60	"	3	28.5	"	4.5	4	"	2	25	19	6	**134.0**	**115**	**19**
8	all taxa	0.38	-2	2.38	0.63	1	-0.37	6.88	2	4.88	0.67	0	0.67	0.46	-6	6.46	**9.0**	**-5**	**14**
	no fossils	2	"	4	1	"	0	5	"	3	0	"	0	1	-7	8	**9.0**	**-6**	**15**
9	all taxa	-19.88	-8	-11.88	25.88	14	11.88	13.63	4	9.63	2	0	2	-5.63	-9	3.37	**16.0**	**1**	**15**
	no fossils	-19	"	-11	27	"	13	13	"	9	2	"	2	-8	-12	4	**15.0**	**-2**	**17**
10	all taxa	-11.73	-11	-0.73	12.73	4	8.73	8.63	0	8.63	2	0	2	-4.63	-10	5.37	**7.0**	**-17**	**24**
	no fossils	-12	"	-1	15	"	11	8	"	8	2	"	2	-6	-12	6	**7.0**	**-19**	**26**
11	all taxa	4.5	3	1.5	66.26	57	9.26	19.63	18	1.63	3.54	1	2.54	-4.93	-5	0.07	**89.0**	**74**	**15**
	no fossils	8	"	5	61	"	4	18	"	0	3	"	2	-1	-6	5	**89.0**	**73**	**16**
12	all taxa	6.9	7	-0.1	4.99	4	0.99	0.07	0	0.07	0	0	0	0.04	-1	1.04	**12.0**	**10**	**2**
	no fossils	6	"	-1	7.5	"	3.5	0.5	"	0.5	-0.5	"	-0.5	-1.5	1	-2.5	**12.0**	**12**	**0**
13	all taxa	8.13	8	0.13	48.88	47	1.88	10.63	7	3.63	0	0	0	1.38	-1	2.38	**69.0**	**61**	**8**
	no fossils	8	"	0	52	"	5	8	"	1	-1	"	-1	2	2	0	**69.0**	**64**	**5**
14	all taxa	-7.38	0	-7.38	7.88	0	7.88	3.63	0	3.63	0.5	-2	2.5	5.38	-6	11.38	**10.0**	**-8**	**18**
	no fossils	-6	"	-6	8	"	8	1	"	1	-1	"	1	8	-4	12	**10.0**	**-6**	**16**
15	all taxa	9.13	9	0.13	53.88	55	-1.12	12.63	8	4.63	0	0	0	2.38	4	-1.62	**78.0**	**76**	**2**
	no fossils	10	"	1	54	"	-1	12	"	4	0	"	0	1	5	-4	**77.0**	**77**	**0**
16	all taxa	-4.88	-4	-0.88	-0.13	0	-0.13	5.63	1	4.63	2	1	1	-1.63	-11	9.37	**1.0**	**-13**	**14**
	no fossils	-5	"	-1	2.5	"	2.5	5	"	4	2	"	1	-2.5	-13	10.5	**2.0**	**-15**	**17**
17	all taxa	-8.88	-9	21.02	21.02	13	8.02	13.91	8	5.91	0	0	0	-4.05	-7	2.95	**22.0**	**5**	**17**
	no fossils	-9	"	0	21	"	8	14	"	6	0	"	0	-3	-7	4	**23.0**	**5**	**18**
18	all taxa	2.41	-7	9.41	6.59	1	5.59	5.63	2	3.63	-0.86	0	-0.86	-0.77	-10	9.23	**13.0**	**-14**	**27**
	no fossils	4	"	11	7	"	6	5	"	3	-1	"	-1	-2	-10	8	**13.0**	**-14**	**27**
19	all taxa	-3.88	-9	5.12	19.88	21	-1.12	8.63	1	7.63	1	-1	2	5.38	-7	12.38	**31.0**	**5**	**26**
	no fossils	-3	"	6	20	"	-1	8	"	7	1	"	2	4	-9	13	**30.0**	**3**	**27**
20	all taxa	21.66	16	5.66	115.3	112	3.26	22.32	19	3.32	4	4	0	1.76	7	-5.24	**165.0**	**158**	**7**
	no fossils	19.5	"	3.5	114.5	"	2.5	24.5	"	5.5	4	"	0	3.5	6	-2.5	**166.0**	**157**	**9**
21	all taxa	-7.48	3	-10.48	32.78	28	4.78	15.63	7	8.63	2.9	1	1.9	13.18	9	4.18	**57.0**	**48**	**9**
	no fossils	1	"	-2	24	"	-4	12	"	5	2	"	1	24	12	12	**63.0**	**51**	**12**
22	all taxa	-4.88	-11	6.12	-0.13	-1	0.87	5.63	0	5.63	2	-3	5	-1.63	-15	13.37	**1.0**	**-30**	**31**
	no fossils	-5	"	6	2.5	"	3.5	5	"	5	2	"	5	-2.5	-16	13.5	**2.0**	**-31**	**33**
23	all taxa	-3.54	-16	12.46	0.21	-2	2.21	4.63	0	4.63	1.33	-2	3.33	-1.63	-29	27.37	**1.0**	**-49**	**50**
	no fossils	0	"	16	1	"	3	2	"	2	0	"	2	-2	-33	31	**1.0**	**-53**	**54**
24	all taxa	3.63	-12	15.63	30.38	28	2.38	2.13	2	0.13	0	-2	2	-4.13	-39	34.87	**32.0**	**-23**	**55**
	no fossils	-0.5	"	11.5	32.5	"	4.5	3	"	1	-0.5	"	1.5	-1.5	-39	37.5	**33.0**	**-23**	**56**
25	all taxa	7.9	8	-0.1	124	118	5.99	25.29	27	-1.71	0	0	0	3.82	5	-1.18	**161.0**	**158**	**3**
	no fossils	8	"	0	124	"	6	26	"	-1	0	"	0	3	5	-2	**161.0**	**158**	**3**
26	all taxa	13.13	28	-14.87	244.9	234	10.88	86.63	64	22.63	16	4	12	12.38	3	9.38	**373.0**	**333**	**40**
	no fossils	22	"	-6	235	"	1	83	"	19	15	"	11	18	2	16	**373.0**	**332**	**41**
27	all taxa	-13.88	0	-13.88	23.88	11	12.88	22.63	8	14.63	2	0	2	10.38	3	7.38	**45.0**	**22**	**23**
	no fossils	-4	"	-4	13	"	2	19.5	"	11.5	1.5	"	1.5	15	1	14	**45.0**	**20**	**25**
28	all taxa	5.54	6	-0.46	89	77	12	23.63	16	7.63	6.65	2	4.65	19.2	-2	21.2	**144.0**	**99**	**45**
	no fossils	14	"	8	82	"	5	20.5	"	4.5	6.5	"	4.5	23	-1	24	**146.0**	**100**	**46**
29	all taxa	0.13	-9	9.13	11.88	1	10.88	3.63	-8	11.63	0	-1	1	15.38	10	5.38	**31.0**	**-7**	**38**
	no fossils	1	"	10	13	"	12	4	"	12	0	"	1	14	7	7	**32.0**	**-10**	**42**
30	all taxa	15.13	4	11.13	0.88	-1	1.88	0.91	-9	9.91	0	-1	1	-1.91	-8	6.09	**15.0**	**-15**	**30**
	no fossils	16	"	12	1	"	2	2	"	11	0	"	1	-1	-5	4	**18.0**	**-12**	**30**
31	all taxa	11.92	2	9.92	10.43	11	-0.57	3.13	5	-1.87	-0.29	-3	2.71	1.82	4	-2.18	**27.0**	**19**	**8**
	no fossils	13	"	11	11	"	0	3	"	-2	-1	"	2	3	2	1	**29.0**	**17**	**12**
32	all taxa	-1.99	0	-1.99	6.15	-1	7.15	2.18	-9	11.18	0.53	-3	3.53	-1.88	-8	6.12	**5.0**	**-21**	**26**
	no fossils	1	"	1	1	"	2	2	"	11	0	"	3	0	-4	4	**4.0**	**-17**	**21**
33	all taxa	5.13	-10	15.13	13.88	1	12.88	-1.38	2	-3.38	0	-1	1	0.38	-11	11.38	**18.0**	**-19**	**37**
	no fossils	5.5	"	15.5	8.5	"	7.5	0	"	-2	-0.5	"	0.5	5.5	-8	13.5	**19.0**	**-16**	**35**
34	all taxa	3.13	-7	10.13	8.88	1	7.88	9.63	6	3.63	0	0	0	1.37	-42	43.37	**23.0**	**-42**	**65**
	no fossils	8.86	"	15.86	9.43	"	8.43	6.29	"	0.29	0.57	"	0.57	0.86	-44	44.86	**26.0**	**-44**	**70**
35	all taxa	-6.16	-8	1.84	11.02	-4	15.02	1.48	-2	3.48	1.14	0	1.14	-1.48	-15	13.52	**6.0**	**-29**	**35**
	no fossils	-6	"	2	11	"	15	2	"	4	1	"	1	-1	-15	14	**7.0**	**-29**	**36**
36	all taxa	3.63	11	-7.37	51.46	50	1.46	11.38	8	3.38	0.33	0	0.33	2.21	-8	10.21	**69.0**	**61**	**8**
	no fossils	7	"	-4	50	"	0	7	"	-1	0	"	0	5	-9	14	**69.0**	**60**	**9**
TOTAL	**all taxa**	**92**	**31**	**83**	**1258**	**1078**	**180**	**449**	**276**	**173**	**57**	**-4**	**61**	**105**	**-256**	**347**	**1962**	**1125**	**823**
	no fossils	**174**	"	**143**	**1187**	"	**109**	**409**	"	**133**	**42**	"	**46**	**191**	**-254**	**445**	**2003**	**1127**	**876**

*NOTE: Clade 4 is absent in the most parsimonious tree when fossils are excluded, hence total PBS is negative (-3)

Fig. 5 Phylogenetic utility of mtDNA, nuclear exons, nuclear introns, indels and morphology, in analyses incorporating molecular data (*excluding* third codons) and morphological data. Clades are shown in the left column and are numbered as in Fig. 2. Information in rows and columns is structured as in Fig. 3; see that caption for details.

CLADE (Fig 2)		adora3			adrb2			atp7a			bdnf			app-intron			plcb4-intron			TOTAL		
		PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS	PBS	BS-Sep	HS
1	all taxa	2	-1	3	0.13	0	0.13	0.75	4	-3.25	1.13	1	0.13	2.75	2	0.75	-5.63	-5	-0.63	**1.13**	**1**	**0.13**
	no fossils	4.5	"	5.5	0	"	0	0	"	-4	2	"	1	2	"	0	-5	"	0	**3.5**	"	**2.5**
2	all taxa	6	4	2	0.13	0	0.13	26.75	23	3.75	-0.88	0	-0.88	19.75	12	7.75	25.38	18	7.38	**77.13**	**57**	**20.13**
	no fossils	8	"	4	0	"	0	25.5	"	2.5	-0.5	"	-0.5	19	"	7	25.5	"	7.5	**77.5**	"	**20.5**
3	all taxa	0	-3	3	0.13	0	0.13	-2.11	-2	-0.11	-0.16	-2	1.84	0.75	0	0.75	0.52	-1	1.52	**-0.87**	**-8**	**7.13**
	no fossils	3	"	6	-1	"	-1	-1	"	1	1	"	3	1	"	1	-1	"	0	**2**	"	**10**
4	all taxa	-3	-3	0	0.13	0	0.13	2.75	2	0.75	-0.88	-3	2.12	1.75	0	1.75	-0.63	0	-0.63	**0.12**	**-4**	**4.12**
	no fossils	-3	"	0	1	"	1	1	"	-1	0	"	3	0	"	0	2	"	2	**1**	"	**5**
5	all taxa	-3	-1	-2	-0.88	0	-0.88	6.56	3	3.56	-1.16	-3	1.84	1.42	0	1.42	-0.53	1	-1.53	**2.41**	**0**	**2.41**
	no fossils	0	"	1	-1	"	-1	3	"	0	0	"	3	-2	"	-2	-2	"	-3	**-2**	"	**-2**
6	all taxa	2	-3	5	0.13	-1	1.13	0.75	4	-3.25	1.13	-4	5.13	2.75	2	0.75	-5.63	-1	-4.63	**1.13**	**-3**	**4.13**
	no fossils	4.5	"	7.5	0	"	1	0	"	-4	2	"	6	2	"	0	-5	"	-4	**3.5**	"	**6.5**
7	all taxa	2	0	2	-0.88	0	-0.88	-0.25	1	-1.25	3.13	3	0.13	2.75	4	-1.25	9.38	4	5.38	**16.13**	**12**	**4.13**
	no fossils	1	"	1	-1	"	-1	0.5	"	-0.5	2.5	"	-0.5	3.5	"	-0.5	6.5	"	2.5	**13**	"	**1**
8	all taxa	0.67	-1	1.67	0.04	-1	1.04	-1.42	-1	-0.42	0.38	0	0.38	0.58	0	0.58	1.79	-1	2.79	**2.04**	**-4**	**6.04**
	no fossils	0	"	1	0	"	1	-1	"	0	0	"	0	1	"	1	0	"	1	**0**	"	**4**
9	all taxa	-1	-5	4	2.13	0	2.13	0.75	0	0.75	2.13	0	2.13	0.75	2	-1.25	9.38	2	7.38	**14.14**	**-1**	**15.14**
	no fossils	-1	"	4	2	"	2	1	"	1	2	"	2	1	"	-1	9	"	7	**14**	"	**15**
10	all taxa	1.57	-4	5.57	1.13	-1	2.13	-0.82	-1	0.18	1.13	0	1.13	-1.25	0	-1.25	8.38	2	6.38	**10.14**	**-4**	**14.14**
	no fossils	1	"	5	1	"	2	0	"	1	1	"	1	-1	"	-1	8	"	6	**10**	"	**14**
11	all taxa	-1.62	-7	5.38	1.13	1	0.13	8.37	0	8.37	-2.41	0	-2.41	3.83	2	1.83	8.84	9	-0.16	**18.14**	**5**	**13.14**
	no fossils	0	"	7	1	"	0	7	"	7	-2	"	-2	3	"	1	9	"	0	**18**	"	**13**
12	all taxa	-1	-1	0	-1	-1	0	-1	-1	0	0	-1	1	1	0	1	0	-1	1	**-2**	**-5**	**3**
	no fossils	-0.5	"	0.5	-1	"	0	-0.5	"	0.5	0.5	"	1.5	1	"	1	0	"	1	**-0.5**	"	**4.5**
13	all taxa	2	2	0	1.13	0	1.13	4.75	1	3.75	-0.88	-2	1.12	3.75	4	-0.25	3.38	2	1.38	**14.13**	**7**	**7.13**
	no fossils	3	"	1	1	"	1	5	"	4	0	"	2	4	"	0	1	"	-1	**14**	"	**7**
14	all taxa	2	-7	9	0.13	-1	1.13	-1.25	0	-1.25	1.13	-3	4.13	-0.25	0	-0.25	1.88	-1	2.88	**3.64**	**-12**	**15.64**
	no fossils	1	"	8	0	"	1	0	"	0	1	"	4	0	"	0	0	"	1	**2**	"	**14**
15	all taxa	2	2	0	1.13	-1	2.13	1.75	0	1.75	-1.87	-3	1.13	0.75	-3	3.75	7.38	3	4.38	**11.14**	**-2**	**13.14**
	no fossils	2	"	0	1	"	2	2	"	2	-2	"	1	1	"	4	7	"	4	**11**	"	**13**
16	all taxa	2	0	2	0.13	-1	1.13	-1.25	-1	-0.25	1.13	-2	3.13	-1.25	-6	4.75	5.38	0	5.38	**6.14**	**-10**	**16.14**
	no fossils	2	"	2	0	"	1	-0.5	"	0.5	1	"	3	-1	"	5	5	"	5	**6.5**	"	**16.5**
17	all taxa	6	1	5	-3.02	-4	0.98	0.04	-1	1.04	-5.02	-2	-3.02	5.04	2	3.04	1.95	-1	2.95	**4.99**	**-5**	**9.99**
	no fossils	6	"	5	-3	"	1	0	"	1	-5	"	-3	5	"	3	2	"	3	**5**	"	**10**
18	all taxa	1	1	0	-0.88	-6	5.12	0.75	-2	2.75	-0.28	-3	2.72	2.75	-1	3.75	2.51	1	1.51	**5.85**	**-10**	**15.85**
	no fossils	1	"	0	-1	"	5	1	"	3	0	"	3	3	"	4	2	"	1	**6**	"	**16**
19	all taxa	4	0	4	0.13	-5	5.13	-1.25	0	-1.25	1.13	-1	2.13	-1.25	-2	0.75	5.38	0	5.38	**8.14**	**-8**	**16.14**
	no fossils	4	"	4	0	"	5	-1	"	-1	1	"	2	-1	"	1	5	"	5	**8**	"	**16**
20	all taxa	0.23	2	-1.77	2.51	0	2.51	11.29	8	3.29	-0.34	1	-1.34	10.83	8	2.83	4.14	3	1.14	**28.66**	**22**	**6.66**
	no fossils	0	"	-2	3	"	3	10.5	"	2.5	0	"	-1	10	"	2	5.5	"	2.5	**29**	"	**7**
21	all taxa	-1.65	-1	-0.65	-1.88	1	-2.88	1.49	-2	3.49	1.13	1	0.13	0.58	-4	4.58	7.46	4	3.46	**7.13**	**-1**	**8.13**
	no fossils	1.5	"	2.5	-2.5	"	-3.5	0	"	2	1.5	"	0.5	0	"	4	6.5	"	2.5	**7**	"	**8**
22	all taxa	2	-2	4	0.13	-7	7.13	-1.25	-2	0.75	1.13	-1	2.13	-1.25	-4	2.75	5.38	-1	6.38	**6.14**	**-17**	**23.14**
	no fossils	2	"	4	0	"	7	-0.5	"	1.5	1	"	2	-1	"	3	5	"	6	**6.5**	"	**23.5**
23	all taxa	1.33	-4	5.33	0.13	-5	5.13	-0.58	-2	1.42	0.13	-3	3.13	-0.92	-5	4.08	4.04	-1	5.04	**4.13**	**-20**	**24.13**
	no fossils	0	"	4	0	"	5	1	"	3	-2	"	1	0	"	5	1	"	2	**0**	"	**20**
24	all taxa	-1	-12	11	-0.59	-7	6.41	3.46	-2	5.46	-2.59	-4	1.41	1.18	-3	4.18	0.23	0	0.23	**0.69**	**-28**	**28.69**
	no fossils	0	"	12	-0.5	"	6.5	3	"	5	-0.5	"	3.5	0	"	3	3	"	3	**5**	"	**33**
25	all taxa	3	2	1	3.01	-1	4.01	13.97	10	3.97	8.79	5	3.79	5.97	4	1.97	5.15	4	1.15	**39.89**	**24**	**15.89**
	no fossils	3	"	1	3	"	4	14	"	4	8	"	3	6	"	2	5.5	"	1.5	**39.5**	"	**15.5**
26	all taxa	6	9	-3	-0.88	0	-0.88	9.75	8	1.75	6.13	5	1.13	25.75	22	3.75	18.38	20	-1.62	**65.13**	**64**	**1.13**
	no fossils	9.5	"	0.5	-1.5	"	-1.5	8	"	0	6.5	"	1.5	25	"	3	17.5	"	-2.5	**65**	"	**1**
27	all taxa	-6	0	-6	-3.88	-3	-0.88	2.75	-2	4.75	1.13	-1	2.13	4.75	1	3.75	2.38	2	0.38	**1.13**	**-3**	**4.13**
	no fossils	-3	"	-3	-4.5	"	-1.5	1	"	3	0	"	1	4	"	3	1.5	"	-0.5	**-1**	"	**2**
28	all taxa	0.71	1	-0.29	0.13	-1	1.13	5.46	2	3.46	1.13	0	1.13	7.89	7	0.89	4.8	7	-2.2	**20.12**	**16**	**4.12**
	no fossils	2	"	1	-0.5	"	0.5	5	"	3	0	"	0	8	"	1	3.5	"	-3.5	**18**	"	**2**
29	all taxa	1	-1	2	-0.87	-4	3.13	0.75	-1	1.75	0.13	-2	2.13	-0.25	-4	3.75	1.38	0	1.38	**2.14**	**-12**	**14.14**
	no fossils	1	"	2	-1	"	3	1	"	2	-1	"	1	0	"	4	2	"	2	**2**	"	**14**
30	all taxa	0	-4	4	0.13	-4	4.13	-1.25	-4	2.75	0.98	-1	1.98	-0.25	-5	4.75	2.52	0	2.52	**2.13**	**-18**	**20.13**
	no fossils	0	"	4	0	"	4	-1	"	3	0	"	1	0	"	5	3	"	3	**2**	"	**20**
31	all taxa	-1.29	-1	-0.29	1.92	1	0.92	-0.01	-3	2.99	2.15	-1	3.15	-0.19	2	-2.19	4.58	1	3.58	**7.16**	**-1**	**8.16**
	no fossils	-2	"	-1	2	"	1	0.5	"	3.5	1	"	2	0	"	-2	3.5	"	2.5	**5**	"	**6**
32	all taxa	-2.04	-3	0.96	0.13	-6	6.13	2.79	-5	7.79	-0.76	-3	2.24	1.11	-6	7.11	0.9	0	0.9	**2.13**	**-23**	**25.13**
	no fossils	0	"	3	0	"	6	1	"	6	-1	"	2	0	"	6	2	"	2	**2**	"	**25**
33	all taxa	0	-2	2	0.13	-4	4.13	3.75	0	3.75	-1.88	-6	4.12	2.75	-4	6.75	-0.63	1	-1.63	**4.12**	**-15**	**19.12**
	no fossils	1.5	"	3.5	0.5	"	4.5	0.5	"	0.5	-1	"	5	1	"	5	1	"	0	**3.5**	"	**18.5**
34	all taxa	1	-4	5	-3.88	-6	2.12	-0.25	-2	1.75	0.13	-4	4.13	-0.25	0	-0.25	1.38	2	-0.62	**-1.87**	**-14**	**12.13**
	no fossils	0.71	"	4.71	-4.43	"	1.57	0.86	"	2.86	-0.57	"	3.43	0.86	"	0.86	-0.42	"	-2.42	**-2.99**	"	**11.01**
35	all taxa	1.6	-5	6.6	0.06	-5	5.06	0.15	-2	2.15	0.73	-4	4.73	-0.92	0	-0.92	4.24	-1	5.24	**5.86**	**-17**	**22.86**
	no fossils	1	"	6	0	"	5	-0.5	"	1.5	0.5	"	4.5	-0.5	"	-0.5	2.5	"	3.5	**3**	"	**20**
36	all taxa	3	3	0	1.13	0	1.13	5.75	3	2.75	-1.37	-1	-0.37	3.87	3	0.87	-0.88	1	-1.88	**11.5**	**9**	**2.5**
	no fossils	4	"	1	1	"	1	4.5	"	1.5	0	"	1	3	"	0	-1.5	"	-2.5	**11**	"	**2**
TOTAL	**all taxa**	**32**	**-48**	**80**	**-2**	**-72**	**71**	**103**	**33**	**70**	**16**	**-44**	**60**	**107**	**30**	**77**	**145**	**73**	**72**	**400**	**-28**	**428**
	no fossils	**58**	"	**106**	**-6**	"	**66**	**91**	"	**58**	**17**	"	**61**	**98**	"	**68**	**130**	"	**57**	**387**	"	**415**

Fig. 6 Phylogenetic utility of six well-sampled nuclear loci in analyses incorporating molecular data (*excluding* third codons) and morphological data. Clades are shown in the left column and are numbered as in Fig. 2. The loci include four exons (adora3, adrb2, atp7a, bdnf) and two introns (app, plcb4). Information in rows and columns is structured as in Fig. 3; see that caption for details.

A specific example will focus on the morphological evidence for Euarchontoglires (rodents, lagomorphs, tree-shrews, colugos and primates), a clade supported by multiple diverse molecular datasets (e.g. Murphy *et al.*, 2001; Springer *et al.*, 2004; Kriegs *et al.*, 2006; Bininda-Emonds *et al.*, 2007) and the combined analyses here (Figs 1 and 2, clade 33). Analysis of the current morphological dataset in isolation, with or without fossil taxa, fails to retrieve Euarchontoglires: colugos group with bats due to shared traits partly connected with aerial locomotion, while tree-shrews group with other insectivorans, rodents and lagomorphs due partly to shared similarities in the vertebrae and lower limbs. This is consistent with a similar result from another morphological dataset (Springer *et al.*, 2007). Thus, considered in isolation, morphology strongly contradicts

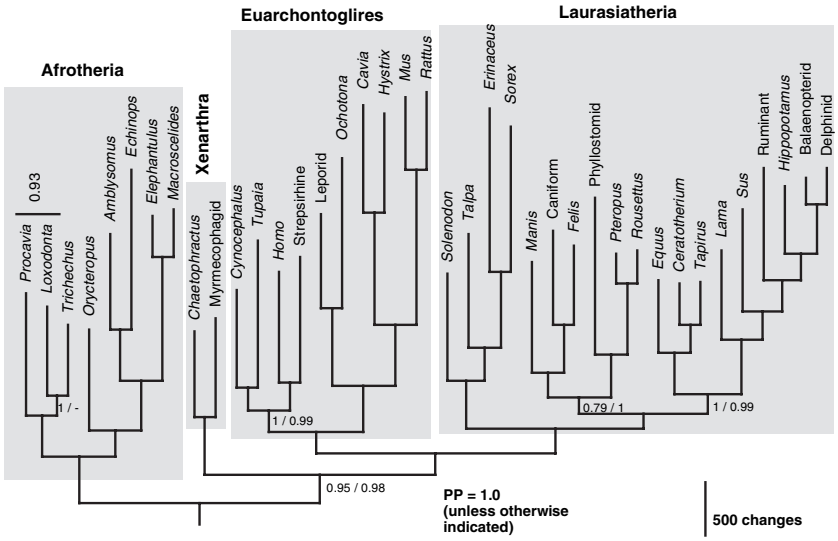

Fig. 7 Bayesian majority-rule consensus tree for living placental mammals: topology shown is retrieved using the combined morphological and molecular data, the topology retrieved using only the molecular (including indel) data is identical except for a Loxondonta/Procavia clade (PP = 0.93). For nearly all clades, posterior probabilities are 1.0 in both analyses. For clades with lower support in one or both analyses, the posteriors are listed in this order: combined data/molecules only.

Euarchontoglires (BS_{sep} = −11). However, in the combined analysis, the bulk of the data (mainly molecular) firmly rejects the colugo-bat and insectivore-glires groupings. Morphology is largely constrained by the weight of other data to arbitrate between the best combined-data tree (which contains Euarchontoglires; Fig. 1), and the best combined-data tree which breaks up Euarchontoglires (Fig. 8); the latter has a paraphyletic Euarchontoglires, placing rodents basal to all other placentals. That tree is retrieved in the molecules-only (parsimony) analysis (see Asher, 2007) and is probably driven by unusual molecular evolution in rodents (e.g. Springer *et al.*, 2008). In a combined analysis, therefore, morphology is constrained to arbitrate only the two best trees generated by the combined data (monophyletic vs. paraphyletic Euarchontoglires), and strongly supports first tree over the second, thus increasing branch support for Euarchontoglires (PBS = +19). The fact that morphology acting alone prefers a totally different tree (with a highly polyphyletic Euarchontoglires) is no longer relevant in the context of a combined analysis, where this idiosyncratic morphology-only topology is excluded from consideration by the molecular influence in the combined data. Thus, beneath the evident widespread homoplasy, there is a deep signal in the morphological data that is congruent with, and boosts support for, the molecular tree.

The results also highlight the dangers of generalizing about the phylogenetic utility of classes of data, when there can be heterogeneity within these perceived classes. Morphology has been suggested to be of limited phylogenetic utility in general (e.g. Scotland *et al.*, 2003), and in mammals in particular (Graur, 1993; Kangas *et al.*, 2004; Springer *et al.*, 2007, 2008), based on failure to retrieve trees generated from large molecular datasets, and/or high incongruence with molecular data. However, in terms of topological similarity, morphology is no

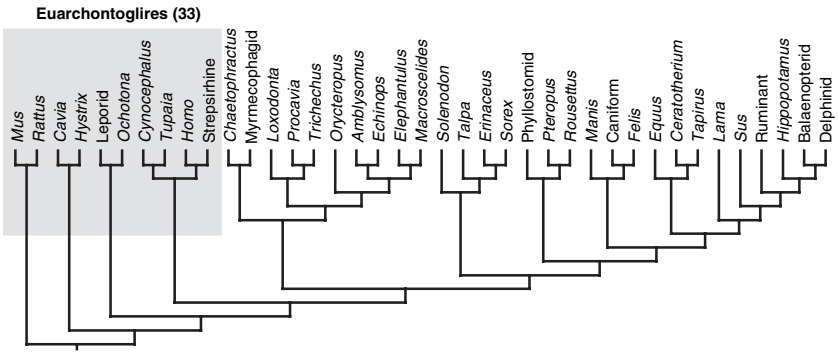

Fig. 8 The shortest tree violating Euarchontoglire monophyly, in the context of a phylogenetic analyses of all data (molecular and morphological), and all taxa (extant and extinct). Note the basal position of rodents, largely due to information in the molecular partitions. The best tree in this analysis (which retrieves Euarchontoglire monophyly) is shown in Fig. 1. For ease of comparison with Fig. 1, only relationships among extant taxa are shown (i.e. extinct taxa have been pruned). Morphology strongly supports the phylogeny in Fig. 1 over the phylogeny in this figure (see Fig. 3, clade 33), thus boosting support for Euarchontoglire monophyly in combined analyses.

worse than many individual molecular partitions: when analysed in isolation, the mtDNA (Fig. 3) and three of the six well-sampled nuclear loci (Fig. 4) each fail to retrieve *most* nodes in the combined data phylogeny. In terms of incongruence, two of the nuclear loci have high overall negative branch support (BS_{sep}) values (adrb2 = −96, bdnf = −34). This is still much less than the morphological incongruence (−277), supporting previous observations (e.g. Springer *et al.*, 2008). Nevertheless, based on either topology or incongruence, some molecular loci would likely be rejected as phylogenetically uninformative. Yet, these molecular datasets generally contribute much positive phylogenetic signal when combined with the rest of the data (e.g. Springer *et al.*, 2008). Morphology is merely a more extreme example of this pattern. Finally, even if one wishes to use the problematic approach of assessing phylogenetic utility based on topological similarity or congruence, it is difficult to rigorously apply this criterion (Kluge, 1989). If all the nuclear exons are treated as a single combined partition, then this dataset would retrieve most clades in the combined-data trees and has an overall positive BS_{sep} (Fig. 3), suggesting phylogenetic informativeness. But if the nuclear exons are partitioned and analysed as individual loci, many (e.g. bdnf, adrb2, adora3) fail to retrieve most clades in the combined-data trees and also have an overall negative BS_{sep} (Fig. 4); these loci would be rejected as phylogenetically uninformative. The presumed utility of the nuclear bdnf locus (for instance) therefore depends entirely on whether it is treated as part of a larger character set, or by itself.

Although the general pattern is highly stable across analyses, there are substantial variations in the exact values of PBS and HS, depending on the inclusion of fossil taxa and third codons. For instance, there is strong hidden conflict (negative HS) in the nuclear exon partition when third codons and fossil taxa are included (HS = −311; Fig. 3), but this situation is reversed when third codons and fossil taxa are excluded (HS = +180; Fig. 5). Much of this pattern can be attributed to taxa (in this case, rodents) that shift across several nodes with little change in tree length; such taxa determine support across several branches simultaneously, and thus greatly affect the total amount of branch support, PBS and HS (linked branch support: Gatesy, 2000). In the analysis including third codons and fossil taxa, a tree only three steps longer than the optimal tree (Fig. 1) places two rodents (*Mus*, *Rattus*) as a basal to all other placentals (Fig. 8). These two are the relevant trees for computing support for several nodes in Fig. 1, namely 27 (Rodentia), 29 (Glires), 33 (Euarchontoglires), 34 (Boreotheria), 36 and 37: all these nodes accordingly have linked (and identical) PBS values. The nuclear exon data strongly favour the tree in Fig. 8 when third codons positions are included, leading to large negative PBS values at all of the linked nodes (PBS = −22; Fig. 3). When third codons are deleted, the nuclear exon data no longer favour a basal position of rodents, the negative PBS disappears at all these linked nodes and the nuclear exon data instead contribute positive PBS to Rodentia, Glires, Euarchontoglires and Boreotheria (Fig. 6).

The bootstrap results generally reveal a positive influence for morphological data, with support for certain clades falling if morphology is excluded: Euarchontoglires, Glires, Rodentia, Cetartiodactyla + Perissodactyla (Figs 1 and 2). However, the contribution of morphology is less obvious because bootstrap frequencies for many clades remain at the maximum 100%, despite support being reduced after the removal of morphology. No pattern is evident in the Bayesian analysis as nearly all clades have posterior probabilities of 1.0, whether morphology is included or excluded (Fig. 3).

The above results do not contradict studies demonstrating that osteology (and presumably morphology) alone will often be unable to accurately resolve affinities, especially when molecular data are missing for entire supraordinal clades (e.g. Springer *et al.*, 2007). However, even small suites of morphological characters can perform well in the context of a well-sampled molecular backbone (e.g. Asher & Hofreiter, 2006). This is consistent with the inituitive expectation that morphology will more accurately place a particular taxon if a close relative (sharing many morphological synapomorphies) is already robustly resolved based on extensive molecular data (see Wiens, 2009). Finally, although many supraordinal clades cannot be retrieved if constituent taxa are scored only for morphology (Springer *et al.*, 2007), the same analyses have not been performed for each molecular locus. Thus, it has not yet been confirmed that the molecular loci perform better than morphology in such analyses. The higher congruence of the genetic partitions with the preferred tree leads to such an expectation (Springer *et al.*, 2008), but direct analysis is still required.

Given the recency of a well-resolved placental mammal tree, research on the morphological evidence for novel clades is only beginning (e.g. Asher *et al.*, 2009). Yet, new anatomical features have already been identified as potential synapomorphies for many clades (Tabuce *et al.*, 2008); notable examples include striking aquatic adaptations shared by whales and hippos (Gatesy *et al.*, 1999), and patterns of tooth eruption (Asher & Lehmann, 2008), vertebral counts (Sánchez-Villagra *et al.*, 2007; Seiffert, 2007), tooth cusp and reproductive anatomy (Seiffert, 2007) in afrotherians. In addition, certain morphological characters here optimize as novel synapomorphies of clades recently corroborated by molecular data, e.g. absence of an exposed lacrimal foramen in Whippomorpha (Asher, 2007; character 71), and anterior opening of the alisphenoid canal in Laurasiatheria (Asher, 2007; character 31). Although these synapomorphies occur in a few taxa outside these respective clades, those taxa are clearly distantly related based on the combined molecular and morphological evidence. Thus, in the combined analyses, these mor-

phological characters boost support for Whippomorpha and Laurasiatheria. Indeed, most nucleotide substitutions that corroborate higher clades are similarly homoplasious. Identification of new morphological characters, and reciprocal illumination between 'older' characters and molecular data, contradicts the suggestion that morphology is largely uninformative or misleading at supraordinal levels. Morphological datasets are undoubtedly riddled with homoplasy, and separating signal from noise can be difficult (Graur, 1993; Kangas *et al.*, 2004; Wortley & Scotland, 2006; Springer *et al.*, 2007). However, the same applies to molecular sequence datasets (Kriegs *et al.*, 2006; Willerslev *et al.*, 2009): noise can swamp signal even in datasets containing dozens of genes (e.g. see Phillips *et al.*, 2004; Rheede *et al.*, 2006; Regier *et al.*, 2008). Yet molecular sequences rightly remain fundamental to modern phylogenetics.

The current analysis strongly demonstrates the continuing relevance of morphology in placental mammal phylogeny. Previous studies (Graur, 1993; Springer *et al.*, 2008) have shown that morphology is highly incongruent with molecular data, thus concluding that morphological data are of limited utility. The current analysis simultaneously supports their results, but contradicts their main conclusions. Morphological data that appear phylogenetically uninformative when analysed alone becomes highly informative when combined with molecular data, when it arbitrates (generally correctly) between plausible molecular trees. Although one should be wary of extrapolating from one dataset for one clade (see Asher *et al.*, 2008; Springer *et al.*, 2008), broader surveys have suggested that morphology generally increases either support (e.g. Baker & Gatesy, 2002) or resolution (e.g. Wortley & Scotland, 2006). The molecular results for mammals have also guided the successful search for novel new phylogenetically informative characters that are highly congruent with the molecular signal, which can help resolve the affinities of extinct and extant taxa. Perhaps even more importantly, these positive results from morphology also increase our confidence in the molecular tree itself (Jenner, 2004; Wiens, 2004). Trees based on even genome-scale datasets can be incorrect and should not be uncritically accepted if incongruent with diverse lines of evidence (e.g. Regier *et al.*, 2008). The possibility of genome-wide biases (e.g. rate heterogeneity causing rodents to be misplaced; Springer *et al.*, 2008) emphasizes the need for corroboration from independent data such as morphology. If the emerging molecular tree of placental mammals correctly reflects evolutionary history, this history should be tracked by at least some characters from other phylogenetic datasets (although these characters might be overwhelmed by noise in those same datasets). Recognition of a hidden signal in existing morphological data congruent with the molecular signal, and discovery of additional congruent morphological traits, therefore greatly increases confidence in the emerging tree of placental mammals driven largely by molecular sequence data.

Acknowledgments

We thank the Australian Research Council for funding (to ML), the University of Adelaide for a Postgraduate Scholarship (to AC), and Robert Asher, John Gatesy and Michel Laurin for constructive comments, although all errors remain ours alone.

References

Asher, R.J. 2007. A web-database of mammalian morphology and a reanalysis of placental phylogeny. *BMC Evol. Biol.* **7**: 108; doi: 10.1186/1471-2148-7-108.

Asher, R.J. & Hofreiter, M. 2006. Tenrecid phylogeny and the noninvasive extraction of nuclear DNA. *Syst. Biol.* **55**: 181–194.

Asher, R.J. & Lehmann, T. 2008. Dental eruption in afrotherian mammals. *BMC Biol.* **6**: 14; doi: 10.1186/1741-7007-6-14.

Asher, R.J., Geisler, J. & Sánchez-Villagra, M.R. 2008. Morphology, paleontology, and placental mammal phylogeny. *Syst. Biol.* **57**: 311–317.

Asher, R.J., Bennett, N. & Lehmann, T. 2009. The new framework for understanding placental mammal evolution. *BioEssays* **31**: 853–864.

Baker, R.H. & DeSalle, R. 1997. Multiple sources of character information and the phylogeny of Hawaiian drosophilids. *Syst. Biol.* **46**: 654–673.

Baker, R.H. & Gatesy, J. 2002. Is morphology still relevant? In: *Molecular Systematics and Evolution: Theory and Practice* (R. DeSalle, G. Giribet & W. Wheeler, eds), pp. 163–174. Birkhauser Verlag, Basel, Switzerland.

Barrett, M., Donoghue, M.J. & Sober, E. 1991. Against consensus. *Syst. Zool.* **40**: 486–493.

Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L. & Purvis, A. 2007. The delayed rise of present-day mammals. *Nature* **446**: 507–512.

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* **42**: 795–803.

Bull, J.J., Huelsenbeck, J.P., Cunningham, C.W., Swofford, D.L. & Waddell, P.J. 1993. Partitioning and combining data in phylogenetic analysis. *Syst. Biol.* **42**: 384–397.

Gatesy, J. 2000. Linked branch support and tree stability. *Syst. Biol.* **49**: 800–807.

Gatesy, J. & Arctander, P. 2000. Hidden morphological support for the phylogenetic placement of *Pseudoryx nghetinhensis* with bovine bovids: a combined analysis of gross anatomical evidence and DNA sequences from five genes. *Syst. Biol.* **49**: 515–538.

Gatesy, J. & Baker, R. 2005. Hidden likelihood support in genomic data: can forty-five wrongs make a right? *Syst. Biol.* **54**: 483–492.

Gatesy, J., O'Grady, P. & Baker, R.H. 1999. Corroboration among data sets in simultaneous analysis: hidden support for phylogenetic relationships among higher level artiodactyl taxa. *Cladistics* **15**: 271–313.

Gatesy, J., Amato, G., Norell, M., DeSalle, R. & Hayashi, C. 2003. Combined support for wholesale taxic atavism in gavialine crocodylians. *Syst. Biol.* **52**: 403–422.

Graur, D. 1993. Molecular phylogeny and the higher classification of eutherian mammals. *Trends Ecol. Evol.* **8**: 141–147.

Gregory, W.K. 1910. The orders of mammals. *Bull. Amer. Mus. Nat. Hist.* **27**: 1–524.

Hedges, S.B. & Maxson, L.R. 1996. Re: molecules and morphology in amniote phylogeny. *Mol. Phylogenet. Evol.* **6**: 312–319.

Jenner, R.A. 2004. Accepting partnership by submission? Morphological phylogenetics in a molecular millennium. *Syst. Biol.* **53**: 333–342.

Jiang, Z. & Takatsuki, S. 1999. Constraints on feeding type in ruminants: a case of morphology over phylogeny. *Mammal Study* **24**: 79–89.

Kangas, A.T., Evans, A.R., Thesleff, I. & Jernvall, J. 2004. Nonindependence of mammalian dental characters. *Nature* **432**: 211–214.

Kluge, A.G. 1989. A concern for the evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Syst. Zool.* **38**: 7–25.

Kriegs, J.O., Churakov, G., Kiefmann, M., Jordan, U., Brosius, J. & Schmitz, J. 2006. Retroposed elements as archives for the evolutionary history of placental mammals. *PLoS Biol.* **4**: e91; doi: 10.1371/journal.pbio.0040091.

Lee, M.S.Y. 2009. Hidden support from unpromising datasets strongly unites snakes and anguimorph lizards. *J. Evol. Biol.* **22**: 1308–1316.

Lee, M.S.Y. & Hugall, A.F. 2003. Partitioned likelihood support and the evaluation of data set conflict. *Syst. Biol.* **52**: 11–22.

Lee, M.S.Y., Reeder, T.W., Lawson, R. & Slowinski, J. 2004. Resolving reptilian relationships: morphological and molecular markers. In: *Assembling the Tree of Life* (J. Cracraft & M. Donoghue, eds), pp. 451–467. Oxford University Press, New York.

Madsen, O., Scally, M., Douady, C.J., Kao, D.J., DeBry, R.W., Adkins, R., Amrine, H.M., Stanhope, M.J., de Jong, W.W. & Springer, M.S. 2001. Parallel adaptive radiations in two major clades of placental mammals. *Nature* **409**: 610–614.

McKenna, M.C. 1975. Toward a phylogeny and classification of the Mammalia. In: *Phylogeny of the Primates: A Multidisciplinary Approach* (W.P. Luckett & F.S. Szalay, eds), pp. 21–46. Plenum, New York.

Murphy, W.J., Eizirik, E., O'Brien, S.J., Madsen, O., Scally, M., Douady, C.J., Teeling, E., Ryder, O.A., Stanhope, M.J., de Jong, W.W. & Springer, M.S. 2001. Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science* **294**: 2348–2351.

Nikolaev, S., Montoya-Burgos, J.I., Margulies, E.H., Rougemont, J., Nyffeler, B., Antonarakis, S.E. & NISC Comparative Sequencing Program 2007. Early history of mammals is elucidated with the ENCODE multiple species sequencing data. *PLoS Genet.* **3**: e2; doi: 10.1371/journal.pgen.0030002.

Phillips, M.J., Delsuc, F.D. & Penny, D. 2004. Genome-scale phylogeny and the detection of systematic biases. *Mol. Biol. Evol.* **21**: 1455–1458.

Regier, J.C., Shultz, J.W., Ganley, A.R., Hussey, A., Shi, D., Ball, B., Zwick, A., Stajich, J.E., Cummings, M.P., Martin, J.W. & Cunningham, C.W. 2008. Resolving arthropod phylogeny: exploring phylogenetic signal within 41 kb of protein-coding nuclear gene sequence. *Syst. Biol.* **57**: 920–938.

Rheede, T., Bastiaans, T., Boone, D.N., Hedges, S.B., de Jong, W.W. & Madsen, O. 2006. The platypus is in its place: Nuclear genes and indels confirm the sister group relation of monotremes and therians. *Mol. Biol. Evol.* **23**: 587–597.

Roca, A.L., Bar-Gal, G.K., Eizirik, E., Helgen, K.M., Maria, R., Springer, M.S., O'Brien, S.J. & Murphy, W.J. 2004. Mesozoic origin for West Indian insectivores. *Nature* **429**: 649–651.

Ronquist, F. & Huelsenbeck, J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.

Ronquist, F., Huelsenbeck, J.P. & van der Mark, P. 2005. *MrBayes 3.1*. Available at: http://mrbayes.csit.fsu.edu/index.php (Accessed 10 September 2009).

Sánchez-Villagra, M.R., Narita, Y. & Kuratani, S. 2007. Thoracolumbar vertebral number: the first skeletal synapomorphy for afrotherian mammals. *Syst. Biodiv.* **5**: 1–7.

Scotland, R.W., Olmstead, R.G. & Bennett, J.R. 2003. Phylogeny reconstruction: the role of morphology. *Syst. Biol.* **52**: 539–548.

Seiffert, E. 2007. A new estimate of afrotherian phylogeny based on simultaneous analysis of genomic, morphological, and fossil evidence. *BMC Evol. Biol.* **7**: 13; doi: 10.1186/1471-2148-7-224.

Simpson, G.G. 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* **85**: 1–350.

Sorenson, M.D. & Franzosa, E.A. 2007. *TreeRot*, version 3. Boston University, Boston, MA. Available at: http://people.bu.edu/MSOREN/TreeRot.html (accessed 30 June 2009).

Springer, M.S., Stanhope, M.J., Madsen, O. & de Jong, W.W. 2004. Molecules consolidate the placental mammal tree. *Trends Ecol. Evol.* **19**: 430–438.

Springer, M.S., Burk-Herrick, A., Meredith, R., Eizirik, E., Teeling, E., O'Brien, S.J. & Murphy, W.J. 2007. The adequacy of morphology for reconstructing the early history of placental mammals. *Syst. Biol.* **56**: 673–684.

Springer, M.S., Meredith, R.W., Eizirik, E., Teeling, E. & Murphy, W.J. 2008. Morphology and placental mammal phylogeny. *Syst. Biol.* **57**: 499–503.

Swofford, D.L. 2002. *PAUP*: Phylogenetic Analysis Using Parsimony (and Other Methods) 4.0 Beta*. Computer program and documentation. Sinauer Associates, Sunderland, MA.

Tabuce, R., Asher, R.J. & Lehmann, T. 2008. Afrotherian mammals: a review of current data. *Mammalia* **72**: 2–14.

Wahlberg, N., Braby, M.F., Brower, A.V.Z., de Jong, R., Lee, M.-M., Nylin, S., Pierce, N., Sperling, F.A., Vila, R., Warren, A.D. & Zakharov, E. 2005. Synergistic effects of combining morphological and molecular data in resolving the phylogeny of butterflies and skippers. *Proc. R. Soc. Lond. B Biol. Sci.* **272**: 1577–1586.

Wiens, J.J. 2004. The role of morphological data in phylogeny reconstruction. *Syst. Biol.* **53**: 653–661.

Wiens, J.J. 2009. Paleontology, genomics, and combined-data phylogenetics: can molecular data improve phylogenetic estimation for fossil taxa? *Syst. Biol.* **58**: 87–99.

Wildman, D.E., Uddin, M., Opazo, J.C., Liu, G., Lefort, V., Guindon, S., Gascuel, O., Grossman, L.I., Romero, R. & Goodman, M. 2007. Genomics, biogeography, and the diversification of placental mammals. *Proc. Natl. Acad. Sci. USA* **104**: 14395–14400.

Wilkinson, M., Thorley, J.L. & Upchurch, P. 2000. A chain is no stronger than its weakest link: double decay analysis of phylogenetic hypotheses. *Syst. Biol.* **49**: 754–776.

Willerslev, E., Gilbert, M.T.P., Binladen, J., Ho, S.Y.W., Campos, P.F., Ratan, A., Tomsho, L.P., da Fonseca, R.R., Sher, A., Kuznetsova, T.V., Nowak-Kemp, M., Roth, T.L., Miller, W. & Schuster, S.C. 2009. Analysis of complete mitochondrial genomes from extinct and extant rhinoceroses reveals lack of phylogenetic resolution. *BMC Evol. Biol.* **9**: 95; doi: 10.1186/1471-2148-9-95).

Wortley, A.H. & Scotland, R.W. 2006. The effect of combining molecular and morphological data in published phylogenetic analyses. *Syst. Biol.* **55**: 677–685.

Supporting information

Additional supporting information may be found in the online version of this article:

Appendix S1 Data matrix in PAUP* format.

Appendix S2 Data matrix in MrBayes format.

Appendix S3 PAUP commands for calculating branch support.

Appendix S4 References for S1–S3.

Figure S1 Strict consensus trees of parsimony analyses of the full taxon set.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Received 6 July 2009; revised 17 August 2009; accepted 26 August 2009