



Short Communication

Resolution of the laurasiatherian phylogeny: Evidence from genomic data

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ABSTRACT

Despite great progress over the past decade, some portions of the mammalian tree of life remain unresolved. In particular, relationships among the different orders included within the supraordinal group Laurasiatheria have been proven difficult to determine, and have received poor support in the vast majority of phylogenomic studies of mammalian systematics. We estimated interordinal relationships within Laurasiatheria using sequence data from 3733 protein-coding genes. Our study included data from 11 placental mammals, corresponding to five of the six orders of Laurasiatheria, plus five outgroup species. Ingroup and outgroup species were chosen to maximize the number single-copy ortholog genes for which sequence data was available for all species in our study. Phylogenetic analyses of the concatenated dataset using maximum likelihood and Bayesian methods resulted on an identical and well supported topology in all alignment strategies compared. Our analyses provide high support for the sister relationship between Chiroptera and Cetartiodactyla and also provide support for placing Perissodactyla as sister to Carnivora. We obtained maximal estimates of bootstrap support (100%) and posterior probability (1.00) for all nodes within Laurasiatheria. Our study provides a further demonstration of the utility of very large and conserved genomic dataset to clarify our understanding of the evolutionary relationships among mammals.

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1. Introduction

Advances in large-scale DNA sequencing have led to great improvement in the resolution of phylogenetic relationships among mammals. Nevertheless there are still areas of disagreement and many branches of the mammalian tree of life remain poorly supported or difficult to resolve, even with the analysis of large amounts of sequence data. Because the use of genomic-scale sequence data has the potential to resolve challenging phylogenetic questions, a number of phylogenomic studies have attempted to establish the relationships among mammalian lineages at different divergence levels (e.g. Nikolaev et al., 2007; Hallström et al., 2007, 2011; Wildman et al., 2007; Arnason et al., 2008; Hallström and Janke, 2008, 2010; Hou et al., 2009; Campbell and Lapointe, 2011). However, even the largest and most complete mammalian dataset analyzed to date, which was based on sequences from 3364 protein-coding genes and a 2,863,797 nucleotide-long alignment, failed to resolve some branches of the mammalian tree (Hallström and Janke, 2010).

One of the unsolved issues concerns the relationships among orders within the supraordinal group Laurasiatheria, which

includes six different orders: Eulipotyphla (hedgehogs, shrews and moles), Perissodactyla (equids, rhinoceroses, tapirs), Chiroptera (bats), Carnivora (carnivores), Cetartiodactyla (artiodactyls and cetaceans) and Pholidota (pangolins) (Lin et al., 2002). Although the monophyly of Laurasiatheria and the orders included therein has been well established (Murphy et al., 2001; Nishihara et al., 2006; Kjer and Honeycutt, 2007; Prasad et al., 2008; Hallström and Janke, 2008, 2010), the arrangement of orders within Laurasiatheria has remained controversial. Several recent studies have led to different conclusions, probably due to the use of different datasets and analytical approaches (e.g. Murphy et al., 2001; Arnason et al., 2002; Nishihara et al., 2006; Prasad et al., 2008; Zhou et al., 2011a,b). In addition, the fact that these orders appear to have diverged rapidly, around 1–4 million years of one another, plus other processes such as incomplete lineage sorting and hybridization have made the resolution of this problem very difficult.

Within Laurasiatheria, the placement of the order Perissodactyla is probably the most controversial issue. The first comprehensive studies of mammalian phylogeny based on molecular data placed Perissodactyla as sister to Carnivora (Murphy et al., 2001; Arnason et al., 2002, 2008; Lin et al., 2002; Kjer and Honeycutt, 2007; Hallström and Janke, 2010; Hallström et al., 2011; McCormack et al., 2012), whereas other studies placed it as sister

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to Cetartiodactyla (Kitazoe et al., 2007; Prasad et al., 2008; Hou et al., 2009), or as sister to Chiroptera (Murphy et al., 2007). The placement of Chiroptera has also been difficult to resolve. Mitogenomic and nuclear gene data generally place Chiroptera as the sister group to Fereuungulata, a supraordinal group that includes the orders Carnivora, Pholidota, Cetartiodactyla, and Perissodactyla (Murphy et al., 2001, 2007; Reyes et al., 2004; Kjer and Honeycutt, 2007; Nikolaev et al., 2007; Kitazoe et al., 2007; Arnason et al., 2008), but a genome wide analysis of retroposon insertions found support for a sister group relationship of Chiroptera to Perissodactyla + Carnivora (Nishihara et al., 2006). Interestingly, two recent phylogenomic studies recovered the highly unconventional phylogenetic position of bats as sister group to Cetartiodactyla (Hallström and Janke, 2008, 2010), but support for this node was relatively low, and the authors did not consider this phylogenetic arrangement as supported by their data. By contrast, the sister relationship between Pholidota and Carnivora has been supported in all studies that included molecular sequence data from these two orders (e.g. Reyes et al., 2004; Murphy et al., 2001, 2007; Arnason et al., 2002, 2008).

Despite all the controversies noted above, few phylogenomic studies had specifically focused on the group Laurasiatheria (see Hou et al., 2009 for an exception). Thus, the purpose of this study was to maximize the use of genome sequence data to resolve interordinal relationship within Laurasiatheria. Our analyses included sequence data from 3733 coding genes from representatives of all laurasiatherian orders other than Pholidota, plus five outgroup species. In order to minimize spurious comparisons, we restricted our data to single-copy ortholog genes for which sequence data was available for all species in our study. Our analyses yielded a highly resolved tree where all nodes within Laurasiatheria received maximal support, and where Chiroptera was placed sister to Cetartiodactyla, and Perissodactyla was placed sister to Carnivora, whereas Eulipotyphla was placed as sister to all other orders in the group.

2. Materials and methods

2.1. Genomic data

We included sequence data from eleven different species in our study, six species of Laurasiatheria and five species used as outgroup. We included representatives of five of the six laurasiatherian orders (cow, *Bos taurus*; dolphin, *Tursiops truncatus*; horse, *Equus caballus*; dog, *Canis familiaris*; flying fox, *Pteropus vampyrus*; hedgehog, *Erinaceus europaeus*). We also included four species of the supraordinal group Euarchontoglires as outgroup (human, *Homo sapiens*; chimpanzee, *Pan troglodytes*; mouse, *Mus musculus*; rat, *Rattus norvegicus*) and in addition to a representative of the supraordinal group Afrotheria (African elephant, *Loxodonta africana*). The choice of the taxa included in this study was established in order to maximize the number of orthologs recovered as determined by the orthologs matrix (OMA) project (Dessimoz et al., 2005; Schneider et al., 2007). The OMA project is a large-scale effort to identify groups of orthologous genes in publicly available genomes in order to define groups of single-copy 1:1 orthologs that are used to define the different OMA groups. The criteria used to establish the membership of the different OMA groups are very conservative since a careful search for possibly paralogy discards all suspicious matches (Schneider et al., 2007; Roth et al., 2008), and as a result, the OMA project has proved to be more accurate and have the best performance in phylogenetic tests when compared to other methods of large-scale ortholog determination (Altenhoff and Dessimoz, 2009).

2.2. Sequence alignment and phylogeny reconstruction

All data analyses describe were carried out in the High Performance Computing Cluster from the Universidad Austral de Chile. To explore the sensitivity of our analyses to changes in the alignment method, nucleotide translated sequences were aligned using MUSCLE (Edgar, 2004), the G-INS-i strategy from MAFFT (Katoh et al., 2005), and T-COFFEE (Notedrame et al., 2000). Nucleotide alignments were generated using the amino acid alignments as a template with the software PAL2NAL (Suyama et al., 2006). In all alignments third codon positions were excluded. Best-fitting nucleotide substitution model for first and second codon positions were estimated separately using the “propose model” routine from Treefinder version March 2011 (Jobb et al., 2004). Model selection was based on the Akaike information criterion with correction for small sample size. We also explored the potential role of compositional biases among species that could potentially affect our results.

We implemented two alternative strategies for phylogeny reconstruction. We first analyzed the concatenated alignments of first and second codon positions using Bayesian and maximum likelihood approaches, as implemented in Mr.Bayes v3.1.2 (Ronquist and Huelsenbeck, 2003) and Treefinder version March 2011 (Jobb et al., 2004), respectively. For the Bayesian analyses, two simultaneous independent runs were performed for 1,000,000 iterations of a Markov Chain Monte Carlo algorithm, with four simultaneous chains, sampling every 1000 generations. Support for the nodes and parameter estimates were derived from a majority rule consensus of the last 50% of the trees sampled after convergence. In maximum likelihood, we estimated the best trees, and support for the nodes was estimated with 1000 bootstrap pseudoreplicates. Alternative tree topologies were compared using the conservative Shimodaira–Hasegawa test (Shimodaira and Hasegawa, 1999) as implemented in Treefinder version March 2011. In our second analytical strategy we analyzed each individual ortholog gene separately, and used the resulting single-gene phylogenies to construct a majority-rule consensus. In this case, support for the nodes was derived from the percentage of single-gene trees that support a given node.

3. Results and discussion

3.1. Phylogenomic data

A total of 3733 1:1 ortholog genes for six laurasiatherian and five outgroup species were included. All genes were obtained for all species, our alignment did not contain “gene gaps”. The total length of the concatenated dataset for each alignment strategy are summarized in Table 1. Once the third codon positions were excluded, the alignments ranged from 5,154,748 to 5,162,886 characters, and the total size of the matrix ranged from 56,702,228 to 56,791,746 bases, depending on the alignment strategy (Table 1).

For the concatenated analyses, we selected independent GTR + Γ_5 substitution models for the first and second codon positions. For each of the 3733 1:1 orthologs, Treefinder selected a GTR + Γ_5 model for the largest proportion of individual genes (21.62%) for the first codon position, a J1 + Γ_5 (22.89%) model for the second codon position. Other models such as J3 + Γ_5 , HKY + Γ_5 , J2 + Γ_5 and TVM + Γ_5 , were also common (Supplementary Fig. 1).

Base composition seems not to be a factor affecting our phylogenetic analyses since no significant differences among species were found. The GC nucleotide composition ranged between 49.81% and 51.40% for all species, and the nucleotide composition at each of the three codon positions is very similar among the 11 taxa (Supplementary Table 1).

Table 1
Data composition.

Alignment strategy	Alignment length ^a	Matrix size ^a	Best tree likelihood score
<i>Concatenated dataset</i>			
MAFFT	5162,886	56,791,746	−14,978,822
MUSCLE	5154,748	56,702,228	−15,009,354
T-COFFE	5155,772	56,713,492	−15,013,920

^a After removing third codon positions.

3.2. Phylogenetic analyses

In the case of the maximum likelihood and Bayesian trees derived from the different concatenated alignments of 3733 1:1 orthologs produced the same tree topology with slight differences in the likelihood score (Table 1). Irrespective of the alignment strategy used, all of the nodes within Laurasiatheria received maximal bootstrap support and posterior probabilities (Fig. 1). In all our phylogenies Perissodactyla, as represented by horse, was placed sister to Carnivora, as represented by dog, and Chiroptera, as represented by flying fox, was placed sister to Cetartiodactyla, as represented by cow and dolphin. These four orders formed a monophyletic clade sister to the order Eulipotyphla, as represented by hedgehog. In the case of the consensus of the independent trees from each of the 3733 1:1 orthologs, phylogenetic relationships within Laurasiatheria were not resolved.

As in other previous studies, phylogenetic accuracy was most efficient when using the concatenated dataset, showing that the concatenation of genes may result in better-resolved tree topologies (e.g. Rokas et al., 2003; Gadagkar et al., 2005; Zhou et al., 2011a,b). Gatesy et al. (1999) named this increased support for a clade in a combined analysis relative to the sum of support in the separate analyses as “hidden support”. The hidden support emerges because separate analyses of individual data sets could retrieve incongruent trees since “individual orthologs may experience events that cause parts of their history to diverge from the species phylogeny” (Gatesy and Baker, 2005). Instead, the concatenated data is expected to amplify the phylogenetic signal,

whereas noise (e.g. convergence, base composition bias, stochastic effects) will be masked, leading to better resolution in phylogenetic estimation (Gatesy and Baker, 2005). The hidden support can also explain why several previous studies, most of which relied on sequence from a relatively small number of genes, could not adequately resolve phylogenetic relationships among the taxa studied.

The placement of Perissodactyla has been a source of controversy among recent phylogenomic studies. Hou et al. (2009) reported a sister relationship between Cetartiodactyla and Perissodactyla, to the exclusion of Carnivora, with 79–97.5% of bootstrap support (Fig. 3, Hou et al., 2009), depending on the background model used. However, our analyses placed Perissodactyla as sister group to Carnivora, with a 100% of bootstrap support and 1.0 posterior probability (Fig. 1). This relationship was recovered in the majority of previous studies (e.g. Murphy et al., 2001; Arnason et al., 2008; Campbell and Lapointe, 2011), but with lower levels of bootstrap support and/or posterior probability.

The phylogenetic position of Chiroptera was insufficiently supported or even unresolved by the majority of previous studies. However, our results resolved the node joining Chiroptera and Cetartiodactyla with maximal support (100% bootstrap support, and 1.0 posterior probability), probably due to the significant increase in sequence data used, and also a phylogenetic design that minimized the amount of missing data. Interestingly, the unusual phylogenetic position of Chiroptera as sister to Cetartiodactyla had also been recovered by Hallström and Janke (2008, 2010), who did not find support to resolve the corresponding node. Similarly, Hou et al. (2009) analyzed a dataset that included 1255 genes, and found a laurasiatherian tree topology in which a cow-bat clade was sister to a horse-dog clade, but decided to treat this result with caution and placed little confidence on the relevant node because it had not been reported before.

The maximal branch support values obtained in this study could be explained by three different factors. First, the amount of sequence data included in this study is substantially larger than what has been included by previous studies: the total length of the alignment, after removing third codon positions, ranged from 5,162,886 to 5,154,748 depending on the alignment strategy (Table 1). Secondly, our alignment did not have “gene gaps”, that is we obtained sequence data from all genes for all species analyzed.

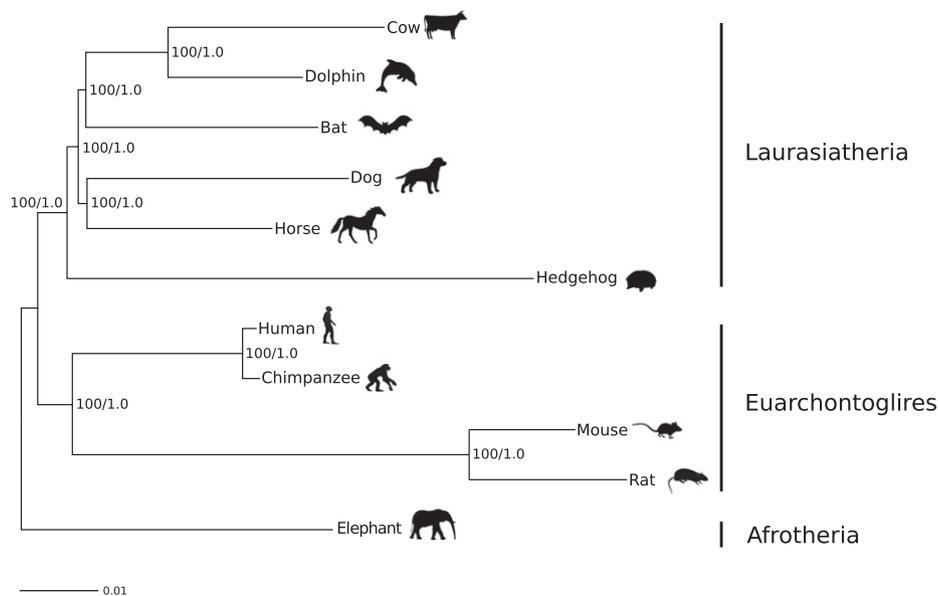


Fig. 1. Maximum likelihood tree ($\ln L = -14,978,822$) derived from the analysis of the concatenated sequence of 3733 protein-coding genes for 11 eutherian species, excluding third codon position. Values on the nodes correspond to maximum likelihood bootstrap support and Bayesian posterior probabilities, respectively. The African elephant was the outgroup used to root the tree.

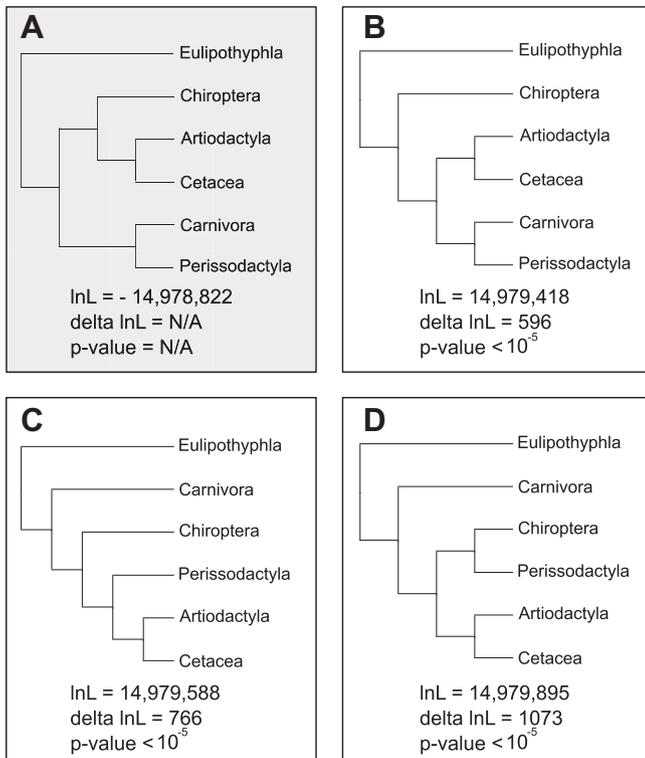


Fig. 2. Competing hypotheses regarding the relationships among laurasiatherian orders. (A) Chiroptera as sister group to Cetartiodactyla and Perissodactyla as sister taxon to Carnivora (our study, Hallström and Janke, 2008, 2010). (B) Chiroptera as sister group to Fereuungulata (e.g. Kitazoe et al., 2007; Arnason et al., 2008; Murphy et al., 2001, 2007; Reyes et al., 2004; Kjer and Honeycutt, 2007; Nikolaev et al., 2007). (C) Perissodactyla as sister-group to Cetartiodactyla (e.g. Prasad et al., 2008; Hou et al., 2009; Kitazoe et al., 2007). (D) Chiroptera and Perissodactyla group together (e.g. Murphy et al., 2007).

Thirdly, as this study was designed to resolve phylogenetic relationships among laurasiatherian orders, we restricted our choice of outgroup sequences to five additional eutherian species reducing genetic divergence in our data set, and thus improving the alignment quality.

3.3. Topology test

The likelihood score of the phylogenetic tree obtained in our study (Fig. 2A) was compared to the score of three other competing hypotheses depicted in Fig. 2 (panels B–D) using the Shimodaira–Hasegawa test. In all comparisons the likelihood value of the topology obtained in our study (Figs. 1 and 2A) was significantly better than the likelihood score of the competing phylogenetic hypotheses (Fig. 1, panels B–D; $P < 10^{-5}$). This result also represents an important improvement in comparison with previous studies (Hallström and Janke, 2008, 2010), in which alternative topologies could not be rejected by topology tests.

3.4. Conclusions

Through analyses of an unprecedented amount of data, and a phylogenetic design focused on minimizing the amount of missing data we were able to obtain a robust estimate of interordinal relationships within Laurasiatheria. Our phylogenomic analyses of 3733 genes, corresponding to over 5 million nucleotides for each taxon, resolved all nodes within Laurasiatheria with maximal bootstrap support values and maximal posterior probabilities as well. Our trees place Chiroptera as sister to Cetartiodactyla, as Perissodactyla as sister to Carnivora, as well as the placement of

Eulipotyphla as sister to all other laurasiatherian orders. Aside from resolving long-standing question in mammalian systematics, our study also underscores the potential of using massive amounts of well-curated sequence data to address challenging problems and to resolve controversial and weakly supported branches.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ympcv.2012.04.012>.

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