

Summary of Laurasiatheria (Mammalia) Phylogeny

Jingyang HU^{1,2}, Yaping ZHANG^{1,3}, Li YU^{1,2,*}

1. Laboratory for Conservation and Utilization of Bio-resource, Yunnan University, Kunming 650091, China

2. Key Laboratory for Animal Genetic Diversity and Evolution of High Education in Yunnan Province, Yunnan University, Kunming 650091, China

3. State Key Laboratory of Genetic Resources and Evolution, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming 650223, China

Abstract: Laurasiatheria is one of the richest and most diverse superorders of placental mammals. Because this group had a rapid evolutionary radiation, the phylogenetic relationships among the six orders of Laurasiatheria remain a subject of heated debate and several issues related to its phylogeny remain open. Reconstructing the true phylogenetic relationships of Laurasiatheria is a significant case study in evolutionary biology due to the diversity of this suborder and such research will have significant implications for biodiversity conservation. We review the higher-level (inter-ordinal) phylogenies of Laurasiatheria based on previous cytogenetic, morphological and molecular data, and discuss the controversies of its phylogenetic relationship. This review aims to outline future researches on Laurasiatheria phylogeny and adaptive evolution.

Keywords: Laurasiatheria; Phylogeny; Mitochondrial DNA; Nuclear genes; Phylogenomics

Placental mammals, which diverged from marsupials about 160 million years ago (Mya) (Luo et al, 2011, Dos Reis et al, 2012), consist of four super-orders, i.e., Afrotheria, Xenarthra, Euarchontoglires, and Laurasiatheria. (Asher & Helgen, 2010; Carter, 2001; Eizirik et al, 2001; Hallström et al, 2011; Kriegs et al, 2006; Kulemzina et al, 2010; Lin et al, 2002; Murphy et al, 2001a,b; Murphy et al, 2007; Nikolaev et al, 2007; Nishihara et al, 2006; Prasad et al, 2008; Springer et al, 2004; Wildman et al, 2006; Zhou & Yang, 2010; Zhou et al, 2011a). Among them, Laurasiatheria is one of the richest and most-diverse, with an origin and a primary distribution on the supercontinent of Laurasia (including North America, Europe and Asia) during their early history (Springer et al, 2011; Waddell et al, 1999b). Although the root of placental mammals is unclear, Laurasiatheria has been consistently recognized as a sub-clade of Boreoeutheria (=Laurasiatheria+Euarchontoglires) (Dos Reis et al, 2012; Gibson et al, 2005; Hallström & Janke, 2008; Song et al, 2012; Madsen et al, 2001; McCormack et al, 2012; Murphy et al, 2001a, b; Nishihara et al, 2006; Springer & Murphy, 2007; Springer et al, 2011; Wildman et al, 2006). Many Laurasiatheria species have attracted great interest in relation to the conservation of wild animals and are also crucial animal models for studies on adaptive evolution.

As a mammalian group bearing important evolutionary significance and conservation value, Laurasiatheria has long been a focus of researches.

Current classifications of Laurasiatheria recognize six orders, namely Eulipotyphla (hedgehogs, shrews, and moles), Perissodactyla (rhinoceroses, horses, and tapirs), Carnivora (carnivores), Cetartiodactyla (artiodactyls and cetaceans), Chiroptera (bats), and Pholidota (pangolins) (Hallström et al, 2011; Lin et al, 2002; Waddell et al, 1999a; Wildman et al, 2006; Wilson & Reeder, 2005; Zhou et al, 2011a). However, the phylogeny and evolution of Laurasiatheria remain subjects of heated debate and are not yet well-established. The origins of Laurasiatheria have been dated to the Cretaceous, ranging from 100 to 78.5–93 mya according to several molecular estimates (Cao et al, 2000; Hallström & Janke 2008, 2010; Hallström et al, 2011; Hasegawa et al, 2003; Ji et al, 2002; Kitazoe et al, 2007; Meredith et al, 2011; Murphy et al, 2004; Springer & Murphy, 2007; Zhou et al, 2011b). However, most morphological studies place the origins of this super-order in the Paleocene (Asher et

Received: 06 September 2012; Accepted: 15 November 2012

Foundation Item: This work was supported by Program for New Century Excellent Talents in University (NCET)

* Corresponding author, E-mail: yuli1220@yahoo.com.cn

al, 2003; Wible et al, 2007, 2009; Luo et al, 2011). The diversification of mammalian species within Laurasiatherian orders appear to have radiated within 1–4 mya in the Eocene (Hallström & Janke 2008, 2010; Zhou et al, 2011b). So, attempts to clarify relationships among the six Laurasiatheria orders from a variety of studies have encountered serious challenges due to the rapid evolutionary radiations and recent speciation events. Although there has been a general consensus regarding the earliest divergence of the order Eulipotyphla (Dos Reis et al, 2012; Hallström et al, 2011;

Lin et al, 2002; Murphy et al, 2001a, b; Nery et al, 2012; Nishihara et al, 2006; Romiguier et al, 2010; Song et al, 2012; Wildman et al, 2006; Zhou et al, 2011a, b), conflicting phylogenetic hypotheses exist for the other orders that evolved subsequently (Figure 1). In this article, we review the higher-level (inter-ordinal) phylogenies of Laurasiatheria based on previous cytogenetic, morphological and molecular data, and discuss the controversies of its phylogenetic relationship. This review aims to outline future research of Laurasiatheria phylogeny and adaptive evolution.

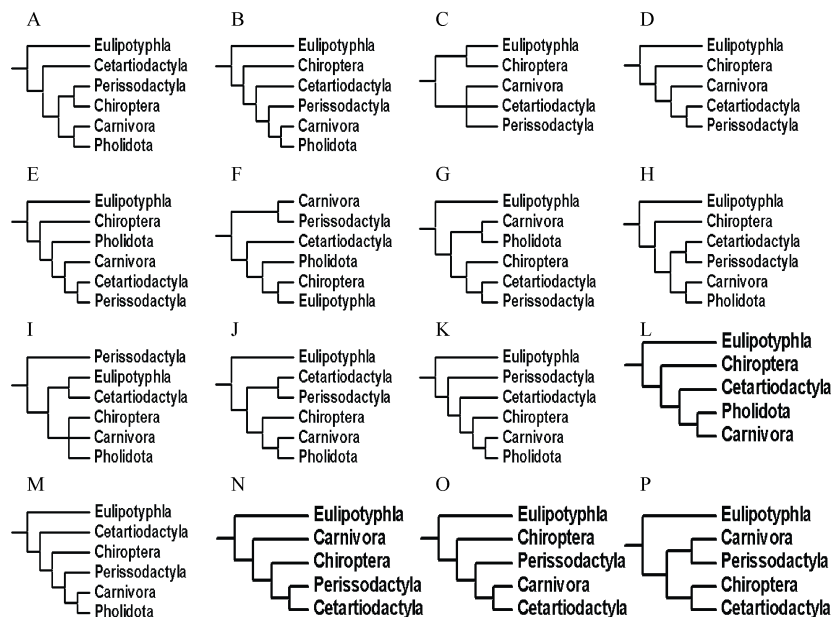


Figure 1 Sixteen different tree topologies proposed in previous studies

A: Waddell & Shelley, 2003; Murphy et al, 2007; Kulemzina et al, 2010. B: Waddell et al, 1999a; Murphy et al, 2001b; Arnason et al, 2002; Arnason & Janke, 2002; Amrine-Madsen et al, 2003; Springer et al, 2004; Wildman et al, 2006; Hallström et al, 2011; Song et al, 2012. C: Mouchaty et al, 2000; Nikaido et al, 2001. D: Jow et al, 2002; Gibson et al, 2005. E: Hudelot et al, 2003. F: Madsen et al, 2001, Figure 1A. G: Madsen et al, 2001, Figure 1B; Meredith et al, 2011. H: Murphy et al, 2001a; Waddell et al, 2001; Beck et al, 2006; Springer et al, 2007; Bininda-Emonds et al, 2007; Zhou et al, 2011b. I: Madsen et al, 2002. J: Asher et al, 2003; Kullberg et al, 2006. K: Matthee et al, 2007. L: Kriegs et al, 2006; Nikolaev et al, 2007. M: Nishihara et al, 2006; Romiguier et al, 2010; McCormack et al, 2011; Zhou et al, 2011a; Dos Reis et al, 2012. N: Prasad et al, 2008, O: Prasad et al, 2008, P: Hou et al, 2009; Nery et al, 2012.

Laurasiatheria phylogeny inferred from cytogenetic and morphological evidence

Early karyotype studies of Laurasiatheria have suggested there are significant differences in chromosome number, morphology and banding pattern among the six orders (Ao et al, 2007; Frönicke et al, 1997; Kulemzina et al, 2009; Nie et al, 2011; Sotero-Caio et al, 2011; Trifonov et al, 2008; Yang & Graphodatsky, 2004; Yang et al, 2006; Ye et al, 2006). Kulemzina et al (2010) investigated the phylogenetic relationships among Laurasiatheria orders by comparing their karyotypes with human karyotype, and proposed the Laurasiatheria phylogeny as (Eulipotyphla, (Cetartiodactyla, ((Perissodactyla, Chiroptera), (Carnivora,

Pholidota)))) (Figure 1A, Table 1). Their study therefore supports the basal placement of Eulipotyphla, and the close relationship between Carnivora and Pholidota, as well as that between Perissodactyla and Chiroptera. However, the trichotomy among Cetartiodactyla, Carnivora + Pholidota, and Perissodactyla + Chiroptera is unresolved.

Compared with limited karyotype studies, numerous morphological studies have been conducted on Laurasiatheria phylogeny reaching a variety of conclusions. In early morphological studies, Laurasiatheria monophyly was not even supported (Asher et al, 2003; Novacek, 1992, 2001; Simpson, 1945; Wible et al, 2007, 2009). For examples, Perissodactyla was originally classified into clade Ungulata (Shoshani & McKenna, 1998), whereas Chiroptera was often associated with

Table 1 Major studies on phylogenetics of laurasiatherian groups

Study evidence	Main studies	Data	Data size	Number of orders	Number of species	
Cytogenetic	Kulemzina et al, 2010			6	37	
	Shoshani and McKenna, 1998	260 morphological characteristics				
Morpho-logical	Asher et al, 2003	433 morphological characteristics				
	Wildman et al, 2006	13 placenta features		6	20	
	Wilb et al, 2007	408 morphological characters				
	Wilb et al, 2009	408 morphological characters				
	Pumo et al, 1998	mt genome	~16 kb	5 (lack Pholidota)	12	
	Cao et al, 1998	<i>ATP6, ATP8, Co I, Co II, Co III, Cytb, ND1, ND2, ND3, ND4, ND4L, ND5</i>	~16 kb	4 (lack Chiroptera and Eulipotyphl)	9	
	Waddell et al, 1999b	mt genome, t RNA, <i>ND6</i>	~1 Mb	4 (lack Pholidota and Chiroptera)	9	
	Cao et al, 2000	mt genome	~16 kb	5 (lack Pholidota)	17	
	Mitochondrial genes	Arnason et al, 2002	mt genome, <i>Cytb</i> , 12S r RNA	~16 kb	6	25
		Lin et al, 2002	mt genome, r RNA, t RNA	~16 kb	5 (lack Pholidota)	29
Jow et al, 2002		mt genome, r RNA, t RNA	~16 kb	5 (lack Pholidota)	24	
Hudelot et al, 2003		r RNA, t RNA	~3.5 kb	6	31	
Kern & Kondrashov, 2004		t RNA		6	30	
Gibson et al, 2005		mt genome	~16 kb	6	31	
Kjer et al, 2007		mt genome, r RNA, t RNA, <i>ND6</i>	~1.4 Mb	6	42	
Madson et al, 2001		4 nu DNA (<i>A2AB, IRBP, Vwf, BRCA1</i>); mt r RNA	~5 kb	6	21	
Murphy et al, 2001a		15 nu DNA (<i>ADORA3, ADRB2, APP-3'UTR, ATP7A, BDNF, BMI1-3'UTR, CNRI, CREM-3'UTR, EDG1, PLCB4-3'UTR, PNOC, RAG1, RAG2, TYR, ZFX</i>); mt DNA	~1 kb	6	24	
Murphy et al, 2001b		19 nuDNA (Murphy et al, 2001a; Madsen et al, 2001); mt DNA	~16 kb	6	20	
Waddell et al, 2001		19 nu DNA (Madson et al, 2001; Murphy et al, 2001b); mt DNA	~10 kb	6	20	
Eizirik et al, 2001		15 nuDNA (Murphy et al, 2001a); mtDNA	~1 Mb	6	24	
Madsen et al, 2002		1 nuDNA (<i>A2AB</i>)	~1 kb	6	19	
Asher et al, 2003		18 nuDNA (Murphy et al, 2001a; 2001b; Madsen et al, 2001); mt DNA; 196 morphological characters	~17 kb	6	20	
Nuclear genes		Amrine-Madsen et al, 2003	20 nuDNA (Murphy et al, 2001b, <i>apolipoprotein B</i>)	~17 kb	6	20
		Wandell & Shelley, 2003	27 nuDNA (Amrine-Madsen et al, 2003, <i>RAG1, c-fibrinogen, ND6, RNA, c-MYC, e-globin, and GHR</i>)	~20 kb	6	38
		Kullberg et al, 2006	8 housekeeping genes (<i>NAD [mt], SDSA, SDHB, RPL18, G3PD, isocitrate dehydrogenase I, ATP synthase, citrate synthase</i>)	~5.8 kb	4 (lack Eulipotyphl and Pholidota)	10
		Matthee et al, 2007	introns (<i>THY, PRKC, MGF</i>)	~6 kb	6	114
	Asher et al, 2007	19 nuDNA and mt DNA (Murphy et al, 2001b); 196 morphological characters (Asher et al, 2003)	~17 kb	6	19	
	Springer et al, 2007	20 nuDNA (Amrine-Madsen et al, 2003); 175 morphological characters	~1.4 kb	6	22	
	Meredith et al, 2011	26 nuDNA (<i>A2AB, ApoB, BRCA, DMP1, ENAM, GHR, IRBP, Rag1, vWF, TTN, CNRI, BCHE, EDG1, RAG1, RAG2, ATP7A, TYR1, BDNF, ADRB2, APP, BMI1, CREM, FBNI, PLCB4, ADORA3, PNOC</i>)	~2 Mb	6	69	
	Bashir et al, 2005	1000 orthologous genes	~1.5 Mb	4 (lack Pholidota and Chiroptera)	4	
	Kriegs et al, 2006	retroposed elements		5 (lack Perissodactyla)	15	
	Nishihara et al, 2006	retroposon insertion (long interspersed elements; L1) loci		5 (lack Pholidota)	8	
	Nikolaev et al, 2007	218 orthologous genes	~200 kb	4 (lack Perissodactyla and Pholidota)	4	
	Prasad et al, 2008	protein-coding sequence and non-coding sequence	~1.9 Mb	5 (lack Pholidota)	13	
	Hallström & Janke, 2008	3012 orthologous genes	~280 kb	4 (lack Perissodactyla and Pholidota)	6	
	Phylogenomics	Hou et al, 2009	2705 orthologous genes	~40 MB	4 (lack Pholidota and Eulipotyphla)	4
		Romiguier et al, 2010	1138 orthologous genes	~300 kb	5 (lack Pholidota)	10
Hallström et al, 2011		4775 orthologous genes	~6 Mb	5 (lack Pholidota)	12	
McCormack et al, 2011		683 loci of ultraconserved elements		5 (lack Pholidota)	6	
Zhou et al, 2011a		8 orthologous genes	~5 kb	6	11	
Zhou et al, 2011b		97 orthologous genes	~46 kb	6	13	
Nery et al, 2012		3733 orthologous genes	~50 Mb	5 (lack Pholidota)	6	
Dos Reis et al, 2012		857 orthologous genes and 153 mt genome	~2 Gb	5 (lack Pholidota)	153	
Song et al, 2012		447 orthologous genes	~7 Mb	5 (lack Pholidota)	11	

Dermoptera (flying lemur) (Asher et al, 2003; Novacek, 1992; Shoshani & McKenna, 1998; Simmons & Geisler, 1998). Gunnell & Simmons (2005) proposed that the grouping of Chiroptera with Dermoptera was spurious due to the homoplasious morphological characters. Based on analyses of 13 placenta features, Wildman et al (2006) first supported that Laurasiatheria formed a monophyletic clade, which was confirmed by later molecular studies, and favored the Laurasiatheria phylogeny as (Eulipotyphla, (Chiroptera, (Cetartiodactyla, (Perissodactyla, (Carnivora, Pholidota)))) (Figure 1B, Table 1).

Similar to the karyotype studies, the earliest divergence of Eulipotyphla and the close association between Carnivora and Pholidota were supported. Regarding the phylogenetic placements of the other three orders, however, morphological studies demonstrated more resolutions and debates than the karyotype studies.

Laurasiatheria phylogeny inferred from molecular evidence

Phylogenetic estimate from mitochondrial genes

Due to relatively small effective population size and lack of recombination as well as easy obtainment, mitochondrial DNA (mtDNA) has often been chosen as a preferred molecular marker in early molecular phylogenetics (Bargelloni et al, 2000; Brito & Edwards, 2009; Phillips & Penny, 2003; Sánchez-Gracia & Castresana, 2012; Springer et al, 2001; Sturmbauer & Meyer, 1993; Yu et al, 2007),

Pumo et al (1998) analyzed 12 complete mt genome sequences of five Laurasiatheria orders, placing Chiroptera as the sister group of Cetartiodactyla, Perissodactyla and Carnivora, while positioning Eulipotyphla as the most basal order of placental mammals, thus rejecting Laurasiatheria monophyly. Cao et al (1998) investigated the mt genome sequences of three orders, placing Cetartiodactyla as the sister group of Perissodactyla and Carnivora. By summarizing the results proposed in the "International Symposium on the Origin of Mammalian Orders", Waddell et al (1999b) suggested the Laurasiatheria phylogeny as (Eulipotyphla, (Chiroptera, (Cetartiodactyla, (Perissodactyla, (Carnivora, Pholidota)))) (Figure 1B, Table 1). These relationships are consistent with those from the morphological study of Wildman et al (2006). Moreover, these relationships are also supported by later analysis of 13 important rare genomic changes (RGCs) (Springer et al, 2004). By adding the mtDNA genome sequences of other orders and by using different tree-building schemes, later studies obtained the same phylogenetic relationships as those from Waddell et al (1999b) and Wildman et al (2006) (Arnason et al, 2002; Arnason & Janke, 2002; Cao et al, 2000; Gibson et al, 2005; Kern & Kondrashov,

2004; Kjer & Honeycutt, 2007; Lin et al, 2002; Reyes et al, 2004) (Figure 1B, Table 1) with the exception of Eulipotyphla positioned as the most basal order of placental mammals, and Cetartiodactyla as the sister group of Perissodactyla and Carnivora (Waddell et al, 1999a).

Conversely, Nikaido et al (2001) and Mouchaty et al (2000) proposed that Eulipotyphla and Chiroptera were clustered together, which were closely related to Perissodactyla, Carnivora and Cetartiodactyla (Figure 1C, Table 1). Jow et al (2002) utilized all mt tRNAs and rRNAs to reconstruct the Laurasiatheria phylogeny among orders except for Pholidota. The resulting tree topology was (Eulipotyphla, (Chiroptera, (Carnivora, (Cetartiodactyla, Perissodactyla)))) (Figure 1D, Table 1). Subsequently, by adding the mt tRNAs and rRNAs of Pholidota, Hudelot et al (2003) claimed the Laurasiatheria phylogeny was (Eulipotyphla, (Chiroptera, (Pholidota, (Carnivora, (Cetartiodactyla, Perissodactyla)))) (Figure 1E, Table 1). Notably, their study rejected the general view of the clustering of Carnivora and Pholidota (Arnason et al, 2002; Arnason & Janke, 2002). Therefore, except for the early divergences of Eulipotyphla and Chiroptera, the phylogenetic relationships among the other four orders are inconsistent with all the previous studies.

Phylogenetic estimate from nuclear genes

Although analyses of mtDNA sequences have provided insights into the phylogeny and evolution of Laurasiatheria, the fact that all genes comprising mt genome are inherited as a single, haploid linkage unit is a well-known limitation on phylogenetic reconstruction because the resulting mt gene trees are unlikely to reflect one independent estimate of the species tree (Giannasi et al, 2001; Johnson & Clayton, 2000; Moore, 1995; Page, 2000; Yu et al, 2004; Yu & Zhang, 2006a). Therefore, when much longer nuclear DNA sequences become widely available, nuclear genes received more and more attention in molecular phylogenetic studies, and demonstrated superiority in resolving deep phylogenies (Springer et al, 1999, 2001). Since 2001, a series of Laurasiatheria studies based on analyses of nuclear genes made important contributions to the resolution of relationships among Laurasiatheria orders, entering into an unprecedented progress.

Madsen et al (2001) first use three nuclear genes, combined with mt tRNA and rRNAs (~5 kb in total), to investigate Laurasiatheria relationships and proposed a tree topology of ((Carnivora, Perissodactyla), (Cetartiodactyla, (Pholidota, (Chiroptera, Eulipotyphla)))) (Figure 1F, Table 1). When another nuclear gene (*BRCAL*) was added and the taxon of representatives was increased to test the stability of the resulting tree, the tree topology changed to (Eulipotyphla, ((Carnivora, Pholidota),

(Chiroptera, (Cetartiodactyla, Perissodactyla)))) (Figure 1G, Table 1), indicating that Laurasiatheria phylogeny varied with the genes and species used in the analyses.

In the same year, by screening 15 nuclear genes (~10 kb) and three mt genes, Murphy et al (2001a) supported a Laurasiatheria phylogeny of (Eulipotyphla, (Chiroptera, ((Cetartiodactyla, Perissodactyla), (Carnivora, Pholidota)))) (Figure 1H, Table 1). Interestingly, their study clustered Cetartiodactyla with Perissodactyla, though this relationship received low statistical support. The subsequent study of Waddell et al (2001) using 12 nuclear genes (~10 kb) and mt genome sequences retrieved the same Laurasiatheria phylogeny and similar nodal supports (Figure 1H, Table 1). These results were also supported by the analysis of 20 nuclear genes and 175 morphological characters by Springer et al (2007) (Figure 1H, Table 1).

Remarkably, when the dataset is increased to 19 nuclear genes and three mt genes (~16 kb), Murphy et al (2001b) showed that the Laurasiatheria phylogeny was (Eulipotyphla, (Chiroptera, (Cetartiodactyla, (Perissodactyla, (Carnivora, Pholidota)))) (Figure 1b and Table 1). Differences from other nuclear trees thus mainly lie in the phylogenetic positions of Cetartiodactyla and Perissodactyla. By adding a new nuclear marker (*apolipoprotein B* gene) to Murphy et al (2001b)'s dataset, Amrine-Madsen et al (2003) achieved the same phylogenetic results (Figure 1B, Table 1). These results were congruent with those from the morphological and mt genome analyses (Arnason et al, 2002; Arnason & Janke, 2002; Springer et al, 2004; Wildman et al, 2006).

Madsen et al (2002) attempted to evaluate the utility of *Alpha 2B* adrenergic receptor gene in the Laurasiatheria phylogeny, which showed the tree as (Perissodactyla, ((Eulipotyphla, Cetartiodactyla), (Chiroptera, Carnivora, Pholidota))) (Figure 1I, Table 1). Surprisingly, Perissodactyla was placed as the basal and Eulipotyphla was the sister-group of Cetartiodactyla. Waddell & Shelley (2003) developed seven nuclear gene fragments and determined the Laurasiatheria phylogeny to be (Eulipotyphla, (Cetartiodactyla, ((Perissodactyla, Chiroptera), (Carnivora, Pholidota)))) (Figure 1A, Table 1).

Asher et al (2003) examined 18 nuclear genes, in combination with three mt genes and 196 morphological characters, and presented the Laurasiatheria phylogeny as (Eulipotyphla, ((Cetartiodactyla, Perissodactyla), (Chiroptera, (Carnivora, Pholidota)))) (Figure 1J, Table 1). Notably, Chiroptera was not placed at the second diverging lineage in Laurasiatheria, as suggested in most previous studies (Madsen et al, 2001; Murphy et al, 2001b), but displayed a close relationship with Carnivora + Pholidota. Using 8 housekeeping genes from four Laurasiatheria orders, Kullberg et al (2006) retrieved a

phylogeny of (Chiroptera, (Cetartiodactyla, (Perissodactyla, Carnivora))) (Figure 1J, Table 1). Despite weak support, this result was consistent with most mt phylogenies (Cao et al, 2000; Lin et al, 2002).

Different from those protein-coding nuclear genes commonly used in previous studies, Matthee et al (2007) first utilize three nuclear introns (~6 kb) from 114 Laurasiatheria species to rebuild the relationships among the six orders. Their study supported the phylogeny of (Eulipotyphla, (Perissodactyla, (Cetartiodactyla, (Chiroptera, (Carnivora, Pholidota)))) (Figure 1K, Table 1). However, these relationships were poorly supported. Asher (2007) reanalyzed 19 nuclear and three mt sequences data from Murphy et al (2001b) as well as 196 morphological characters from Asher et al (2003) (Table 1). By incorporating indels of sequence data, the study suggested that the phylogenetic relationships among the Laurasiatheria orders changed with the combinations of characters and the analytic methods.

Based on the above studies, Laurasiatheria phylogeny at the ordinal level remains an outstanding problem in mammalian systematics due to the contradicting conclusions reached under different datasets, especially in the case of the phylogenetic positions of Perissodactyla, Cetartiodactyla and Chiroptera.

Phylogenomics of Laurasiatheria

With the increasing availability of genomic data of more species, phylogenetic analysis, which use genomic data to infer evolutionary relationships, is entering a new era (Delsuc et al, 2005; Rokas & Chatzimanolis, 2008; Yu & Zhang, 2006a, b). By performing phylogenomic studies, a reliable phylogenetic tree can be reconstructed using many more characters than those in previous studies, including gene families, large insertion and deletion gene fragments, and gene rearrangement, etc. (Meslin et al, 2011; Wu et al, 2012; Yu et al, 2011). These characters might be useful for distinguishing nodes resulting from rapid radiation episodes such as the Laurasiatheria speciation events.

Bashir et al (2005) attempted to reconstruct the Laurasiatheria phylogeny of four orders (Eulipotyphla, Cetartiodactyla, Perissodactyla, and Carnivora) based on more than 1000 orthologous repetitive elements obtained from publically available genome sequence data. In their study, Perissodactyla and Carnivora were grouped together, whereas the placements of the other two orders remained unclear.

Using retroposed elements as new markers to reconstruct the Laurasiatheria phylogeny with the exception of Perissodactyla, Kriegs et al (2006) determined the tree as (Eulipotyphla, (Chiroptera, (Cetartiodactyla, (Pholidota, Carnivora)))) (Figure 1L, Table 1). On the other hand, Nishihara et al (2006) performed a comprehensive comparison of orthologous

retropon insertion (long interspersed elements; L1) loci among five orders of Laurasiatheria (lacking Pholidota). These loci supported the phylogeny as (Eulipotyphla, (Cetartiodactyla, (Chiroptera, (Perissodactyla, Carnivora)))) (Figure 1M, Table 1). Their most interesting finding was that Carnivora, Perissodactyla, and Chiroptera were grouped together, excluding Cetartiodactyla and Eulipotyphla, which has not been recovered by previous studies.

Based on 218 protein-coding genes (~200 kb) obtained from the analysis of 18 placental mammalian genomes, Nikolaev et al (2007) suggested that Eulipotyphla diverged first, followed by Chiroptera, and Cetartiodactyla and Carnivora were sister-group (Figure 1L, Table 1). Subsequently, by searching for informative coding indels within whole-genome sequence data and amplifying them in Laurasiatheria species, Murphy et al (2007) yielded a new tree topology as (Eulipotyphla, (Cetartiodactyla, ((Chiroptera, Perissodactyla), (Carnivora, Pholidota)))) (Figure 1A, Table 1). The close relatedness of Chiroptera and Perissodactyla has been only recovered in karyotype research (Kulemzina et al, 2010).

Prasad et al (2008) reconstructed the phylogeny of Laurasiatheria except for Pholidota based on 1.9 Mb gene regions. The protein-coding sequence analyses supported the tree as (Eulipotyphla, (Carnivora, (Chiroptera, (Perissodactyla, Cetartiodactyla)))) (Figure 1N, Table 1), whereas the combination of coding and non-coding sequence analyses favored the tree as (Eulipotyphla, (Chiroptera, (Perissodactyla, (Carnivora, Cetartiodactyla)))) (Figure 1O, Table 1), showing a lack of consistency in Laurasiatheria phylogeny under different kinds of characters used. The lack of consistency with such large amounts of data can be also evidenced from Hou et al (2009), in which 2705 orthologous genes (~40 Mb) from Cetartiodactyla, Perissodactyla, and Carnivora were used, and different tree topologies were produced under different tree-building methods. When Chiroptera was added into the analysis, they found close relatedness of Perissodactyla with Carnivora, and that of Cetartiodactyla with Chiroptera (Figure 1P, Table 1).

Hallström & Janke (2008) screened 3 012 genes (~280 kb) from four orders with available genome sequences (Eulipotyphla, Chiroptera, Carnivora, and Cetartiodactyla). Their results only recovered the basal placement of Eulipotyphla, and failed to resolve the relationships of the other three orders. The rapid radiation of Laurasiatheria within a narrow time scale was proposed to explain the irresolution using such large amounts of data. By utilizing the third codon position GC content (GC3) of 1 138 protein-coding orthologous genes (~300 kb), Romiguier et al (2010) revealed the Laurasiatheria phylogeny to be (Eulipotyphla,

(Cetartiodactyla, (Chiroptera, (Perissodactyla, Carnivora)))) (Figure 1M, Table 1).

Hallström et al (2011) analysed 4 775 protein-coding genes (~6 Mb) screened from the available genome sequences of five Laurasiatheria orders and determined the tree as (Eulipotyphla, (Chiroptera, (Cetartiodactyla, (Perissodactyla, Carnivora)))) (Figure 1B, Table 1). Their results were more consistent with morphological and mt genome analyses as well as nuclear analyses of Murphy et al (2001b). However, Pholidota was not included in the analyses. When the retropon insertions from these genome sequences were analysed, their study supported the earliest divergence of Eulipotyphla, but failed to resolve the relationships among the other four orders. Additionally, McCormack et al (2011) analysed 683 loci of ultraconserved elements, supporting the tree topology (Eulipotyphla, (Cetartiodactyla, (Chiroptera, (Perissodactyla, Carnivora))))), which was consistent with Nishihara et al (2006) (Figure 1M, Table 1).

By screening protein-coding genes within genome sequence data and amplifying them in Laurasiatheria species, Zhou et al (2011a) analyzed 8 markers (~5 kb) and reconstructed the Laurasiatheria phylogeny as (Eulipotyphla, (Cetartiodactyla, (Chiroptera, (Perissodactyla, Carnivora)))) (Figure 1M, Table 1), consistent with the results from Nishihara et al (2006) and McCormack et al (2011). Subsequently, Zhou et al (2011b) investigated Laurasiatheria phylogeny based on 97 orthologous genes (~46 kb) from six orders. Regardless of datasets and analytic methods used, they obtained an identical tree topology of (Eulipotyphla, (Chiroptera, ((Carnivora, Pholidota), (Cetartiodactyla, Perissodactyla)))) (Figure 1H, Table 1). This result was consistent with those from Murphy et al (2001a) and Waddell et al (2001).

Recently, Nery et al (2012) choose 3 733 orthologous genes (~50 Mb) obtained from available genome sequences of five orders, namely Eulipotyphla, Chiroptera, Carnivora, Cetartiodactyla, and Perissodactyla. They obtained a Laurasiatheria phylogeny of (Eulipotyphla, ((Chiroptera, Cetartiodactyla), (Perissodactyla, Carnivora))) with high supports (Figure 1P, Table 1).

As the most comprehensive study so far, Dos Reis et al (2012) studied 11 available whole genomes of five Laurasiatheria orders (except Pholidota). Based on 857 nuclear genes and 153 mt genomes (~2 Gb), they reconstructed the tree topology as (Eulipotyphla, (Cetartiodactyla, (Chiroptera, (Perissodactyla, (Carnivora, Pholidota)))) (Figure 1M, Table 1), which was consistent with Nishihara et al (2006) and McCormack et al (2011).

Most recently, Song et al (2012) analyzed 447 orthologous genes (~7 Mb) and used multispecies coalescent model analysis to investigate the phylogenetic relationships among the five orders of Laurasiatheria

(except Pholidota). Their results strongly favored (Eulipotyphla, (Chiroptera, (Cetartiodactyla, (Perissodactyla, Carnivora)))) (Figure 1B), supporting Waddell et al (1999a), Murphy et al (2001b), Arnason et al (2002), Arnason & Janke (2002), Amrine-Madsen et al (2003), Springer et al (2004), Wildman et al (2006), and Hallström et al (2011).

Perspectives

The phylogeny of Laurasiatheria, which is characterized by rapid species radiations and short internal tree branches, has long been one of the most controversial and challenging problems in mammalian systematics. So far, only the earliest divergence of Eulipotyphla and the close relationship between Carnivora and Pholidota has been generally accepted. The main controversies are concentrated on the phylogenetic positions of the other three orders, i.e., Chiroptera, Cetartiodactyla and Perissodactyla.

References

- Amrine-Madsen H, Koepfli KP, Wayne RK, Spring MS. 2003. A new phylogenetic marker, apolipoprotein B, provides compelling evidence for eutherian relationships. *Mol Phylogenet Evol*, **28**(2): 225-240.
- Ao L, Mao X, Nie W, Gu X, Feng Q, Wang JH, Su Weiting, Wang YX, Volleth M, Yang FT. 2007. Karyotypic evolution and phylogenetic relationships in the order Chiroptera as revealed by G-banding comparison and chromosome painting. *Chromosome Res*, **15**(3): 257-267.
- Arnason U, Janke A. 2002. Mitogenomic analyses of eutherian relationships. *Cytogenet Genome Res*, **96**(1-4): 20-32.
- Arnason U, Adegoké JA, Bodin K, Born EW, Esa YB, Gullberg A, Nilsson M, Short RV, Xu XF, Janke A. 2002. Mammalian mitogenomic relationships and the root of the eutherian tree. *Proc Natl Acad Sci USA*, **99**(12): 8151-8156.
- Asher RJ. 2007. A web-database of mammalian morphology and a reanalysis of placental phylogeny. *BMC Evol Biol*, **7**(1): 108-118.
- Asher RJ, Helgen KM. 2010. Nomenclature and placental mammal phylogeny. *BMC Evol Biol*, **10**: 102-111.
- Asher RJ, Novacek MJ, Geisler JH. 2003. Relationships of endemic African mammals and their fossil relatives based on morphological and molecular evidence. *J Mamm Evol*, **10**(1-2): 131-194.
- Bargelloni L, Marcato S, Zane L, Patarnello T. 2000. Mitochondrial phylogeny of notothenioids: a molecular approach to Antarctic fish evolution and biogeography. *Syst Biol*, **49**(1): 114-129.
- Bashir A, Ye C, Price AL, Bafna V. 2005. Orthologous repeats and mammalian phylogenetic inference. *Genome Res*, **15**(7): 998-1006.
- Brito PH, Edwards SV. 2009. Multilocus phylogeography and phylogenetics using sequence-based markers. *Genetica*, **135**(3): 439-455.
- Cao Y, Fujiwara M, Nikaido M, Okada N, Hasegawa M. 2000. Interordinal relationships and timescale of eutherian evolution as inferred from mitochondrial genome data. *Gene*, **259**(1-2): 149-158.
- Cao Y, Janke A, Waddell PJ, Westerman M, Takenaka O, Murata S, Oksa N, Pääbo S, Hasegawa M. 1998. Conflict among individual mitochondrial proteins in resolving the phylogeny of eutherian orders. *J Mol Evol*, **47**(3): 307-322.
- Carter AM. 2001. Evolution of the placenta and fetal membranes seen in the light of molecular phylogenetics. *Placenta*, **22**(10): 800-807.
- Delsuc F, Brinkmann H, Philippe H. 2005. Phylogenomics and the reconstruction of the tree of life. *Nat Rev Genet*, **6**(5): 361-375.
- Dos Reis M, Inoue J, Hasegawa M, Asher RJ, Donoghue PCJ, Yang ZH. 2012. Phylogenomic datasets provide both precision and accuracy in estimating the timescale of placental mammal phylogeny. *Proc R Soc B*, **279**(1742): 3491-3500.
- Eizirik E, Murphy WJ, O'Brien SJ. 2001. Molecular dating and biogeography of the early placental mammal radiation. *J Hered*, **92**(2): 212-219.
- Frönicke L, Müller-Navia J, Romanakis K, Scherthan H. 1997. Chromosomal homeologies between human, harbor seal (*Phoca vitulina*) and the putative ancestral carnivore karyotype revealed by Zoo-FISH. *Chromosoma*, **106**(2): 108-113.
- Giannasi N, Thorpe RS, Malhotra A. 2001. The use of amplified fragment length polymorphism in determining species trees at fine taxonomic levels: analysis of a medically important snake, *Trimeresurus albolabris*. *Mol Ecol*, **10**(2): 419-426.
- Gibson A, Gowri-Shankar V, Higgs PG, Rattray M. 2005. A comprehensive analysis of mammalian mitochondrial genome base composition and improved phylogenetic methods. *Mol Bio Evol*, **22**(2): 251-264.

- Gunnell GF, Simmons NB. 2005. Fossil evidence and the origin of bats. *J MammEvol*, **12**(1-2): 209-246.
- Hallström BM, Janke A. 2008. Resolution among major placental mammal interordinal relationships with genome data imply that speciation influenced their earliest radiations. *BMC Evol Biol*, **8**:162-175.
- Hallström BM, Janke A. 2010. Mammalian evolution may not be strictly bifurcating. *Mol Biol Evol*, **27**(12): 2804-2816.
- Hallström BM, Schneider A, Zoller S, Janke A. 2011. A genomic approach to examine the complex evolution of laurasiatherian mammals. *PLoS One*, **6**(12): e28199.
- Hasegawa M, Thorne JL, Kishino H. 2003. Time scale of eutherian evolution estimated without assuming a constant rate of molecular evolution. *Genes Genet Syst*, **78**(4): 267-283.
- Hou ZC, Romero R, Wildman DE. 2009. Phylogeny of the Ferungulata (Mammalia: Laurasiatheria) as determined from phylogenomic data. *Mol Phylogenet Evol*, **52**(3): 660-664.
- Hudlot C, Gowri-Shankar V, Jow H, Rattray M, Higgs PG. 2003. RNA-based phylogenetic methods: application to mammalian mitochondrial RNA sequences. *Mol Phylogenetics Evol*, **28**(2): 241-252.
- Ji Q, Luo ZX, Yuan CX, Wible JR, Zhang JP, Georgi JA. 2002. The earliest known eutherian mammal. *Nature*, **416**(6883): 816-822.
- Johnson KP, Clayton DH. 2000. A molecular phylogeny of the dove genus *Zenaida*: mitochondrial and nuclear DNA sequences. *Condor*, **102**(4): 864-870.
- Jow H, Hudlot C, Rattray M, Higgs PG. 2002. Bayesian phylogenetics using an RNA substitution model applied to early mammalian evolution. *Mol Biol Evol*, **19**(9): 1591-1601.
- Kern AD, Kondrashov FA. 2004. Mechanisms and convergence of compensatory evolution in mammalian mitochondrial tRNAs. *Nat Genet*, **36**(11): 1207-1212.
- Kitazoe Y, Kishino H, Waddell PJ, Nakajima N, Okabayashi T, Watabe T, Okuhara Y. 2007. Robust time estimation reconciles views of the antiquity of placental mammals. *PLoS One*, **2**(4): e384.
- Kjer KM, Honeycutt RL. 2007. Site specific rates of mitochondrial genomes and the phylogeny of eutheria. *BMC Evol Biol*, **7**: 8-17.
- Krieger JO, 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**(4): e91.
- Kulemzina AI, Trifonov VA, Perelman PL, Rubtsova NV, Volobuev V, Ferguson-Smith MA, Stanyon R, Yang FT, Graphodatsky AS. 2009. Cross-species chromosome painting in Cetartiodactyla: reconstructing the karyotype evolution in key phylogenetic lineages. *Chromosome Res*, **17**(3): 419-436.
- Kulemzina I, Biltueva L, Trifonov VA, Perelman PL, Staroselec YY, Beklemisheva VR, Vorobieva NV, Serdukova NA, Graphodatsky AS. 2010. Comparative cytogenetics of main Laurasiatheria taxa. *Russ J Genet*, **46**(9): 1132-1137.
- Kullberg M, Nilsson MA, Arnason U, Harley EH, Janke A. 2006. Housekeeping genes for phylogenetic analysis of eutherian relationships. *Mol Biol Evol*, **23**(8): 1493-1503.
- Lin YH, McLenachan PA, Gore AR, Phillips MJ, Ota R, Hendy MD, Penny D. 2002. Four new mitochondrial genomes and the increased stability of evolutionary trees of mammals from improved taxon sampling. *Mol Biol Evol*, **19**(12): 2060-2070.
- Luo ZX, Yuan CX, Meng QJ, Ji Q. 2011. A Jurassic eutherian mammal and divergence of marsupials and placentals. *Nature*, **476**(7361): 442-445.
- Madsen O, Willemsen D, Ursing BM, Arnason U, de Jong WW. 2002. Molecular evolution of the mammalian *alpha 2B* adrenergic receptor. *Mol Biol Evol*, **19**(12): 2150-2160.
- Madsen O, Scally M, Douady CJ, Kao DJ, DeBry RW, Adkins R, Amrine HM, Stanhope MJ, de Jong WW, Springer MS. 2001. Parallel adaptive radiations in two major clades of placental mammals. *Nature*, **409**(6820): 610-614.
- Matthee CA, Eick G, Willows-Munro S, Montgelard C, Pardini AT, Robinson TJ. 2007. Indel evolution of mammalian introns and the utility of non-coding nuclear markers in eutherian phylogenetics. *Mol Phylogenet Evol*, **42**(3): 827-837.
- McCormack JE, Faircloth BC, Crawford NG, Gowaty PA, Brumfield RT, Glenn TC. 2012. Ultraconserved elements are novel phylogenomic markers that resolve placental mammal phylogeny when combined with species-tree analysis. *Genome Res*, **22**(10): 746-754.
- Meredith RW, Janecka JE, Gatesy J, Ryder OA, Fisher CA, Teeling EC, Goodbla A, Eizirik E, Simão TLL, Stadler T, Rabosky DL, Honeycutt RL, Flynn JJ, Ingram CM, Steiner C, Williams TL, Robinson TJ, Burkherrick A, Westerman M, Ayoub NA, Springer MS, Murphy WJ. 2011. Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science*, **334**(6055): 521-524.
- Meslin C, Brimau F, Meillour PNL, Callebaut I, Pascal G, Monget P. 2011. The evolutionary history of the SAL1 gene family in eutherian mammals. *BMC Evol Biol*, **11**: 148-162.
- Moore WS. 1995. Inferring phylogenies from mtDNA variation: mitochondrial-gene trees versus nuclear-gene trees. *Evolution*, **49**(4): 718-726.
- Mouchaty SK, Gullberg A, Janke A, Arnason U. 2000. The phylogenetic position of the talpidae within eutheria based on analysis of complete mitochondrial sequences. *Mol Biol Evol*, **17**(1): 60-67.
- Murphy WJ, Pevzner PA, O'Brien SJ. 2004. Mammalian phylogenomics comes of age. *Trends Genet*, **20**(12): 631-639.
- Murphy WJ, Pringle TH, Crider TA, Springer MS. 2007. Using genomic data to unravel the root of the placental mammal phylogeny. *Genome Res*, **17**(4): 413-421.
- Murphy WJ, Eizirik E, Johnson WE, Zhang YP, Ryder OA, O'Brien. 2001a. Molecular phylogenetics and the origins of placental mammals. *Nature*, **409**(6820): 614-618.
- Murphy WJ, Eizirik E, O'Brien SJ, Madsen O, Scally M, Douady CJ, Teeling E, Ryder OA, Stanhope MJ, de Jong WW, Springer MS. 2001b. Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science*, **294**(5550): 2348-2351.
- Nery MF, González DJ, Hoffmann FG, Opazo JC. 2012. Resolution of the laurasiatherian phylogeny: evidence from genomic data. *Mol*

- Phylogenetics Evol*, **64**(3): 685-689.
- Nie W, Wang J, Su W, Wang D, Tanomtong A, Perelman PL, Grahodatsky AS, Yang F. 2011. Chromosomal rearrangements and karyotype evolution in carnivores revealed by chromosome painting. *Heredity*, **108**(1): 17-27.
- Nikaido M, Kawai K, Harada M, Tomita S, Okada N, Hasegawa M. 2001. Maximum likelihood analysis of the complete mitochondrial genomes of eutherians and a reevaluation of the phylogeny of bats and insectivores. *J Mol Evol*, **53**(4-5):508-516.
- Nikolaev S, Montoya-Burgos JI, Margulies EH, NISC Comparative Sequencing Program, Rougemont J, Nyffeler B, Antonarakis SE. 2007. Early history of mammals is elucidated with the ENCODE multiple species sequencing data. *PLoS Genet*, **3**(1): e2.
- Nishihara H, Hasegawa M, Okada N. 2006. Pegasoferae, an unexpected mammalian clade revealed by tracking ancient retroposon insertions. *Proc Natl Acad Sci USA*, **103**(26): 9929-9934.
- Novacek MJ. 1992. Mammalian phylogeny: shaking the tree. *Nature*, **356**(6365): 121-125.
- Novacek MJ. 2001. Mammalian phylogeny: genes and supertrees. *Curr Biol*, **11**(14): 573-575.
- Page RDM. 2000. Extracting species trees from complex gene trees: reconciled trees and vertebrate phylogeny. *Mol Phylogenetics Evol*, **14**(1): 89-106.
- Phillips MJ, Penny D. 2003. The root of the mammalian tree inferred from whole mitochondrial genomes. *Mol Biol Evo*, **28**(2): 171-185.
- Prasad AB, Allard MW, Green ED. 2008. Confirming the phylogeny of mammals by use of large comparative sequence data sets. *Mol Biol Evol*, **25**(9): 1795-1808.
- Pumo DE, Finamore PS, Franek WR, Phillips CJ, Tarzami S, Balzarano D. 1998. Complete mitochondrial genome of a neotropical fruit bat, *Artibeus jamaicensis*, and a new hypothesis of the relationships of bats to other eutherian mammals. *J Mol Evol*, **47**(6): 709-717.
- Reyes A, Gissi C, Catzeflis F, Nevo E, Pesole G, Saccone C. 2004. Congruent mammalian trees from mitochondrial and nuclear genes using Bayesian methods. *Mol Biol Evol*, **21**(2): 397-403.
- Rokas A, Chatzimanolis S. 2008. From gene-scale to genome-scale phylogenetics: the data flood in, but the challenges remain. *Methods Mol Biol*, **422**: 1-12.
- Romiguier J, Ranwez V, Douzery EJP, Galtier N. 2010. Contrasting GC-content dynamics across 33 mammalian genomes: relationship with life-history traits and chromosome sizes. *Genome Resh*, **20**(8): 1001-1009.
- Sánchez-Gracia A, Castresana J. 2012. Impact of deep coalescence on the reliability of species tree inference from different types of DNA markers in mammals. *PLoS One*, **7**(1): e30239.
- Shoshani J, McKenna MC. 1998. Higher taxonomic relationships among extant mammals based on morphology, with selected comparisons of results from molecular data. *Mol Phylogenetics Evol*, **3**(9): 572-584.
- Simmons NB, Geisler JH. 1998. Phylogenetic relationships of Icaronycteris, Archaeonycteris, Hassianycteris, and Palaeochiropteryx to extant bat lineages, with comments on the evolution of echolocation and foraging strategies in Microchiroptera. *Bulletin AMNH*, **235**: 1-182.
- Simpson GG. 1945. The principles of classification and a classification of mammals. *Bull Amer Mus Nat Hist*, **85**: 1-350.
- Song S, Liu L, Edwards SV, Wu SY. 2012. Resolving conflict in eutherian mammal phylogeny using phylogenomics and the multispecies coalescent model. *Proc Natl Acad Sci USA*, **109**(37): 14942-14947.
- Sotero-Caio CG, Pieczarka JC, Nagamachi CY, Gomes AJB, Lira TC, O'Brien PCM, Ferguson-Smith MA, Souza MJ, Santos N. 2011. Chromosomal homologies among vampire bats revealed by chromosome painting (Phyllostomidae, Chiroptera). *Cytogenet Genome Res*, **132**(3): 156-164.
- Springer MS, Murphy WJ. 2007. Mammalian evolution and biomedicine: new views from phylogeny. *Biol Rev Camb Philos Soc*, **82**(3): 375-392.
- Springer MS, Amrine HM, Burk A, Stanhope MJ. 1999. Additional support for Afrotheria and Paenungulata, the performance of mitochondrial versus nuclear genes, and the impact of data partitions with heterogeneous base composition. *Syst Biol*, **48**(1): 65-75.
- Springer MS, Stanhope MJ, Madsen O, de Jong WW. 2004. Molecules consolidate the placental mammal tree. *Trends Ecol Evol*, **19**(8): 430-438.
- Springer MS, Meredith RW, Janecka JE, Murphy WJ. 2011. The historical biogeography of Mammalia. *Philos Trans R Soc Lond B Biol Sci*, **366**(1577): 2478-2502.
- Springer MS, Burk-Herrick A, Meredith R, Eizirik E, Teeling E, O'Brien SJ, Murphy WJ. 2007. The adequacy of morphology for reconstructing the early history of placental mammals. *Syst Biol*, **56**(4): 673-684.
- Springer MS, DeBry RW, Douady C, Amrine HM, Madsen O, de Jong WW, Stanhope MJ. 2001. Mitochondrial versus nuclear gene sequences in deep-level mammalian phylogeny reconstruction. *Mol Bio Evol*, **18**(2): 132-143.
- Sturmbauer C, Meyer A. 1993. Mitochondrial phylogeny of the endemic mouthbrooding lineages of cichlid fishes from Lake Tanganyika in eastern Africa. *Mol Biol Evol*, **10**(4): 751-768.
- Trifonov VA, Stanyon R, Nesterenko AI, Fu BY, Perelman PL, O'Brien PCM, Stone G, Rubtsova NV, Houck ML, Robinson TJ, Ferguson-Smith MA, Dobigny G, Grahodatsky AS, Yang FT. 2008. Multidirectional cross-species painting illuminates the history of karyotypic evolution in Perissodactyla. *Chromosome Res*, **16**(1): 89-107.
- Waddell PJ, Shelley S. 2003. Evaluating placental inter-ordinal phylogenies with novel sequences including *RAG1*, γ -fibrinogen, *ND6*, and mt-tRNA, plus MCMC-driven nucleotide, amino acid, and codon models. *Mol Phylogenet Evol*, **28**(2): 197-224.
- Waddell PJ, Okada N, Hasegawa M. 1999a. Towards resolving the interordinal relationships of placental mammals. *Syst Biol*, **48**(1): 1-5.
- Waddell PJ, Kishino H, Ota R. 2001. A phylogenetic foundation for comparative mammalian genomics. *Genome Inform*, **12**: 141-154.
- Waddell PJ, Cao Y, Hauf J, Hasegawa M. 1999b. Using novel

- phylogenetic methods to evaluate mammalian mtDNA, including amino acid-invariant sites-LogDet plus site stripping, to detect internal conflicts in the data, with special reference to the positions of hedgehog, armadillo, and elephant. *Syst Biol*, **48**(1): 31-53.
- Wible JR, Rougier GW, Novacek MJ, Asher RJ. 2007. Cretaceous eutherians and Laurasian origin for placental mammals near the K/T boundary. *Nature*, **447**(7147): 1003-1006.
- Wible JR, Rougier GW, Novacek MJ, Asher RJ. 2009. The eutherian mammal *Maelestes gobiensis* from the Late Cretaceous of Mongolia and the phylogeny of Cretaceous Eutheria. *Bio One*, **327**: 1-123.
- Wildman DE, Chen CY, Erez O, Grossman LI, Goodman M, Romero R. 2006. Evolution of the mammalian placenta revealed by phylogenetic analysis. *Proc Natl Acad Sci USA*, **103**(9): 3203-3208.
- Wilson DE, Reeder DM. 2005. *Mammal Species of the World: A Taxonomic and Geographic Reference*. 3rd ed. Baltimore: Johns Hopkins University Press.
- Wu YC, Rasmussen MD, Kellis M. 2012. Evolution at the subgene level: domain rearrangements in the drosophila phylogeny. *Mol Bio Evol*, **29**(2): 689-705.
- Yang FT, Graphodatsky AS. 2004. Integrated comparative genome maps and their implications for karyotype evolution of carnivores. *Chromosomes Today*, **14**: 215-244.
- Yang FT, Graphodatsky AS, Li TL, Fu BY, Dobigny G, Wang JH, Perelman PL, Serdukova NA, Su WT, O'Brien PCM, Wang YX, Ferguson-Smith MA, Volobouev V, Nie WH. 2006. Comparative genome maps of the pangolin, hedgehog, sloth, anteater and human revealed by cross-species chromosome painting: further insight into the ancestral karyotype and genome evolution of eutherian mammals. *Chromosome Res*, **14**(3): 283-296.
- Ye JP, Biltueva L, Huang L, Nie WH, Wang JH, Jing MD, Su WT, Volobouev V, Jiang XL, Graphodatsky AS, Yang FT. 2006. Cross-species chromosome painting unveils cytogenetic signatures for the Eulipotyphla and evidence for the polyphyly of Insectivora. *Chromosome Res*, **14**(2): 151-159.
- Yu L, Zhang YP. 2006a. Phylogenomics—An attractive avenue to reconstruct "Tree of Life". *Genetics*, **28**(11): 1445-1450. (in Chinese)
- Yu L, Zhang YP. 2006b. Summary of phylogeny in mammalian order carnivora. *Zool Res*, **27**(6): 657-665. (in Chinese)
- Yu L, Li YW, Ryder OA, Zhang YP. 2004. Phylogeny of the *bears* (Ursidae) based on nuclear and mitochondrial genes. *Mol Phylogenet Evol*, **32**(2): 480-494.
- Yu L, Li YW, Ryder OA, Zhang YP. 2007. Analysis of complete mitochondrial genome sequences increases phylogenetic resolution of *bears* (Ursidae), a mammalian family that experienced rapid speciation. *BMC Evol Biol*, **7**: 198-209.
- Yu L, Luan PT, Jin W, Ryder OA, Chemnick LG, Davis HA, Zhang YP. 2011. Phylogenetic utility of nuclear introns in interfamilial relationships of Caniformia (order Carnivora). *Syst Biol*, **60**(2): 175-187.
- Zhou XM, Yang G. 2010. A review on the progress in mammalian phylogenomics. *Acta Theriol Sin*, **30**(3): 339-345. (in Chinese)
- Zhou XM, Xu SX, Zhang P, Yang G. 2011a. Developing a series of conservative anchor markers and their application to phylogenomics of Laurasiatherian mammals. *Mol Ecol Resour*, **11**(1): 134-140.
- Zhou XM, Xu SX, Xu JX, Chen BY, Zhou KY, Yang G. 2011b. Phylogenomic analysis resolves the interordinal relationships and rapid diversification of the laurasiatherian mammals. *Syst Biol*, **61**(1): 150-164.