

Modern Phylogeny Debates

Compiled By Paul Nethercott

January 2013

1. Chance and Necessity in Eye Evolution, By Walter J. Gehring

“Neo-Darwinists introduced genetics into evolutionary biology, but eye evolution remained enigmatic because it was assumed that the evolution of the various eye types occurred 40–60 times independently in the different animal phyla. This was essentially incompatible with Darwin’s ideas, which assumed a rare stochastic event to give rise to prototypic eye. Recent molecular genetic work strongly supports the notion that the various eye types arose monophyletically.”

“What is still surprising is the rapidity of eye evolution, because compound eyes with over 3,000 ommatidia were discovered in the early Cambrian, some 515 Ma, in early arthropods. The analysis of the complex gene regulatory networks specifying eye development supports the unpredictability thesis of Monod.”

2. Evolutionary Patterns of the Mitochondrial Genome, By S. Castellana

“The processes by means of which mitochondrial DNA (mtDNA) replicates, expresses itself and evolves have been explored over the years, although various aspects are still debated.”

“Various models regarding the precise nature of the endosymbiotic process from the archaebacterium to the eukaryotes are still being debated (Gray et al. 1999; Embley and Martin 2006; Poole and Penny 2006). The main point of discussion is whether the endosymbiotic event directly promoted the development of eukaryotes in a single step or whether it is simply one of the evolutionary steps toward modern eukaryotes.”

“We focus attention here on the role of drift, purifying, and positive selection on the evolution of mtDNA in Metazoa, a topic regarding which available data are sometimes inconsistent and highly debated. Exactly how the mitochondrial genome evolved has been extensively debated: Some details about how it is inherited and how it changes are shown in box 2.”

“The results of Bazin et al. gave rise to extensive debate: Some authors criticized the manipulation and interpretation of the data (e.g., Meikeljohn et al. 2007); others are still convinced of the usefulness of the mtDNA for demography and conservation studies, even with draft (Mulligan et al. 2006; Berry 2006).”

3. Intron Gains and Losses , By Daniel Croll

“The presence of spliceosomal introns in genes is a major puzzle of eukaryotic genome evolution (Lynch and Richardson 2002).”

“Whether the emergence of introns predates the evolution of eukaryotes was a matter of considerable debate, however the currently favoured view is that prokaryotic genes were always devoid of introns.”

4. Dynamics of Gene Duplicates, By Anke Konrad

“Another current debate in the molecular evolution literature is on the relative importance of change at the gene expression and at the protein-coding levels.”

5. Patterns of Genomic Differentiation, By Kyanne R. Reidenbach

“At the heart of the debate is the role that genome structure plays in facilitating population divergence in the presence of gene flow.”

“However, as we discuss later, the extent of introgression is still an open question at the center of ongoing debate that has important ramifications for understanding M–S divergence.”

6. Evolutionary Rate and Duplicability, By David Alvarez-Ponce

“Identifying and understanding the factors responsible for this variability is one of the main open questions in Evolutionary Biology.”

“Although these trends are significant and consistent across all organisms studied to date, they are often weak, and whether they reflect a direct effect of network position on genes’ rates of evolution has been the subject of debate. In particular, some authors have suggested that these trends might be a by product of the distribution of confounding factors across the network.”

7. Short Arm of Chromosome 3, By Anne Roulin

“However, little is known about the variation in the dynamics of this process among plant lineages. Previous studies tried to estimate the mutation rate of LTR-retrotransposons in rice (Vitte and Panaud 2003; Ma and Bennetzen 2004) but the use of the molecular clock is still subject to debate.”

8. Homologous Recombination, By James R. Doroghazi

“Widespread evidence of horizontal gene transfer (HGT) among bacteria and archaea has provoked ongoing debate as to whether genetic clusters in these organisms represent species or simply represent points along a continuum of genetic exchange. A variety of evolutionary forces have been invoked in these debates, but chief among them are periodic selection, genetic drift, and the effects of both homologous recombination (HR) and non homologous recombination (NR). Several different models have been proposed to explain the evolution of microbial species (Fraser et al. 2009).”

9. Plethodontid Salamanders, By Cheng Sun

“Divergence dates in salamanders remain the topic of much debate. The basal split within plethodontids has been dated at ; 40 to 130 Myr, depending on data set and analytical technique; divergence time estimates for our six focal taxa are similarly varied, but all are >25 Myr”

10. Random Addition Concatenation, By Apurva Narechania

“In recent years, debates over the feasibility of the Tree of Life (TOL) have taken center stage in the phylogenetic research community (Ciccarelli et al. 2006; Baptiste et al. 2008). With respect to the prokaryotic portion of this tree, evidence for horizontal gene transfer (HGT) has polarized this debate (Baptiste et al. 2009; Degnan and Rosenberg 2009). One central issue is how best to combine information from individual genes that may have divergent histories or whether to combine them at all.”

11. Deep Genomic-Scale Analyses, By Therese A. Holton

“Uncertainty still persists pertaining to the early evolution of the Bilateria; an important group which includes all extant animals with the exclusion of the sponges, the Placozoa, the Cnidaria, and the Ctenophora (see, e.g., Nielsen 2001; Dunn et al. 2008; Hejnol et al. 2009; Philippe et al. 2009; Sperling et al. 2009). Central to this incertitude are the phylogenetic relationships of the “pseudocoelomates” (sensu Hyman 1940), particularly that of the Nematoda (i.e., the round worms), which remain an issue of debate (Telford et al. 2008).”

“Although there is ongoing debate over the phylogenetic relationships of these organisms, there is general agreement that both are nonbilaterian Metazoans.”

12. Genome Networks Root, By Tal Dagan

“Eukaryotes arose from prokaryotes, hence the root in the tree of life resides among the prokaryotic domains. The position of the root is still debated, although pinpointing it would aid our understanding of the early evolution of life. Because prokaryote evolution was long viewed as a tree-like process of lineage bifurcations, efforts to identify the most ancient microbial lineage split have traditionally focused on positioning a root on a phylogenetic tree constructed from one or several genes. Such studies have delivered widely conflicting results on the position of the root, this being mainly due to methodological problems inherent to deep gene phylogeny and the workings of lateral gene transfer among prokaryotes over evolutionary time.”

“The debate about the position of the root in the tree of life has focused mainly on its position and to some extent on the biology of the first organisms. The issues of microbial lifestyle (autotrophy vs. heterotrophy: Lane et al. 2010) and cellularity, that is, the transition from replicating molecules in inorganic compartments to genetically specified

replicating cells (Martin and Russell 2003; Koonin and Martin 2005; Branciamore et al. 2009) have received attention of late. However, by far the most heavily debated aspect of life at the root concerns temperature.”

13. Integration of the Genetic Map, By Wataru Kai

“The evolutionary significance of this phenomenon remains the subject of much debate (Lenormand 2003).”

14. Ecdysozoan Mitogenomics, By Omar Rota-Stabelli

“The same analyses also recover monophyly of traditionally recognized arthropod lineages such as Arachnida and of the highly debated clade Mandibulata.”

“In spite of an ongoing debate concerning their utility in phylogenetics (Curole and Kocher 1999, Delsuc et al. 2003, Cameron et al. 2004), mitogenomic studies have proven to be informative and insightful for phylogenetic studies (e.g., Boore et al. 1998, Lavrov and Lang 2005).”

“Although a monophyletic origin of the Ecdysozoa is now widely accepted (reviewed in Telford et al. 2008), the relationships among the eight extant ecdysozoan phyla, in particular the position of Tardigrada, are still vigorously debated.”

“However, the phylogenetic relationships among Pancrustacea, Myriapoda (millipedes, centipedes, symphylans), and Chelicerata (arachnids, ticks, and their allies) are hotly debated.”

15. Population Genomics of Intron Splicing, By Daniel A. Skelly

“The evolutionary forces governing intron dynamics have been subject to considerable debate”

16. Eukaryote Common Ancestor Polls, By Thorsten Thiergart

“Although the evolutionary details of the prokaryote-to-eukaryote transition are still incompletely resolved (Brown and Doolittle 1997; Koonin 2012), the crucial role that mitochondria played in that transition is becoming increasingly evident (Lane and Martin 2010; Lane 2011). Presently, two main categories of competing hypotheses address the prokaryote-to-eukaryote transition: autogenous and symbiogenic (Maynard-Smith and Szathmary 1995; Embley and Martin 2006; Pisani et al. 2007; Lane 2009). Autogenous models posit that eukaryotes arose from a single ancestral lineage via mutation in a gradualist type of evolutionary process. Symbiogenic models posit that eukaryotes arose via a symbiotic association of divergent prokaryotic cells, with symbiosis (and gene transfer from endosymbiont to host in some formulations) forging the prokaryote-to-eukaryote transition, with phases of evolutionary innovation marked by distinctly non-gradualist characteristics. Both the autogenous and the symbiogenic categories harbor a number of specific competing alternative hypotheses, respectively, each of which in turn generates testable predictions about the phylogenetic affinities of eukaryotic genes to prokaryotic homologues.”

“Much current thinking on eukaryote origins is still focused on debating the branching orders in alternative trees (Gribaldo et al. 2010): a tree x versus tree y debate. But a spectrum of alternatives that consider only trees is not broad enough.”

17. Widespread Recurrent Evolution, By Ignacio Maeso

“The recent explosion of genome sequences from all major phylogenetic groups has unveiled an unexpected wealth of cases of recurrent evolution of strikingly similar genomic features in different lineages.”

“In addition, many instances of a third more puzzling phylogenetic pattern have been observed: traits whose distribution is ‘scattered’ across the evolutionary tree (fig. 1), indicating repeated independent evolution of similar genomic features in different lineages.”

“Recurrent evolution has most commonly been studied at the level of organismal phenotype (fig. 2), comprising an extremely rich field with hundreds of articles spanning three centuries exploring a wide diversity of recurrent phenotypes and lineages (Scotland 2011). A central concern of phenotypic work has been understanding the physical or genetic causes for recurrence. This pursuit often focuses on distinguishing between convergent evolution and parallel evolution (a distinction which itself has been extensively debated; Arendt and Reznick 2008; Scotland 2011).”

18. The Human Genome Retains Relics, By David Alvarez-Ponce

“The relationships among the three domains of cellular life (Eubacteria, Archaeobacteria, and Eukaryotes; [Woese et al. 1990](#)) and in particular the exact phylogenetic placement of eukaryotes and the mechanisms underlying their origin (eukaryogenesis) have been the subject of ferocious debate for decades ([Martin et al. 2001](#); [Embley and Martin 2006](#); [Kurland et al. 2006](#); [Gribaldo et al. 2010](#)). A number of hypotheses have been proposed, many of which posit that eukaryotes arose from a fusion event involving a eubacterium (the ancestor of the present-day mitochondrion) and an archaeobacterium ([Sagan 1967](#); [Zillig et al. 1985](#); [Rivera and Lake 2004](#); [Pisani et al. 2007](#); [Lane and Martin 2010](#)).”

19. Mitochondrial Genome Sequences, By Andrew T. Beckenbach

“The origin of the Brachycera has long been subject to debate ([Woodley 1989](#)). All trees give strong support for monophyly of this suborder, and confirm that the Nematocera is paraphyletic to the Brachycera.”

20. Conserved Meiotic Machinery, By Sebastien Halar

“Although predominant throughout eukaryotes ([Malik et al. 2008](#)), the advantages versus costs of sexual reproduction and meiosis are still a matter of debate ([Ackerman et al. 2010](#); [Archetti 2010](#)). Indeed, although evolutionary theory predicts a rapid extinction of asexual lineages as a consequence of the accumulation of deleterious mutations ([Otto and Lenormand 2002](#); [Otto 2009](#)), a number of eukaryotes commonly referred to as “ancient asexuals” ([Maynard-Smith 1986](#)) have thrived across diverse ecosystems for millions of years without sex.”

21. Population Diversity of ORFan Genes, By Guoqin Yu

“The origin and evolution of “ORFans” (suspected genes without known relatives) remain unclear.”

“This would seem to be difficult without having some model of the evolution of ORFan sources outside of *E. coli*, currently a mystery.”

22. Evolutionary Effects of Translocations, By Jarrett D. Morrow

“Why some bacterial genomes have multiple chromosomes remains a mystery ([Mackenzie et al. 2004](#); [Egan et al. 2005](#)). Although additional chromosomes minimally offer an additional replication origin, which could speed replication or facilitate a larger genome, a broader question remains: to what extent does selection act on bacterial genome organization?”

23. Hyperexpression of the X Chromosome, By Eldon G. Prince

“A genome’s ability to produce two separate sexually dimorphic phenotypes is an intriguing biological mystery. Microarray based studies of a handful of model systems suggest that much of the mystery can be explained by sex-biased gene expression evolved in response to sexually antagonistic selection.”

24. Nuclearily Encoded Mitochondrial Genes, By Miguel Gallach

“How the pattern of expression of new genes evolves remains largely a mystery, especially for retrogenes because they do not inherit the promoter regions from their parental genes.”

25. Lacking the Carotenoid Pigment, By Deborah C. Holt

“The currently known global distribution of the CC75 lineage poses something of a mystery. Although the presence of this lineage in south east Asia can be broadly explained by geographical proximity to northern Australia, the discovery of ST1223 at a high frequency in carriage in a remote village in French Guiana is far more difficult to explain.”

26. Insect Phylogenomics, By Sabrina Simon

“In addition, we employ various approaches to evaluate data quality and highlight problematic nodes within the Insect Tree that still exist despite our phylogenomic approach.”

“One major problem in resolving insect relationships using phylogenomic data is the lack and/or overlap of genomic and/or transcriptomic data. There are more than one million described insect species ([Footit and Adler 2009](#)) but only 172 insect genomes have been sequenced or are in progress (<http://www.ncbi.nlm.nih.gov/genome>; last accessed April 2012).”

“The polyneopteran lineage still appears in an unresolved polytomy within the Insect Tree and even its monophyly is

disputed. Herein, especially the phylogenetic position of Plecoptera (Zwick 2009) and Zoraptera (Yoshizawa 2007) is far from settled (table 1). Both of them belong to the most phylogenetically ambiguous insect orders and even their placement within the polyneopteran lineage is still under discussion. To further clarify this most controversial problem among the higher systematics of insects”

“Especially, the exact position of Plecoptera and Dermaptera within Polyneoptera remains problematic even and despite using extensive molecular data sets.”

27. Seed Plant Phylogenomics, By Bojian Zhong

“Resolving the closest relatives of Gnetales has been an enigmatic problem in seed plant phylogeny. The problem is known to be difficult because of the extent of divergence between this diverse group of gymnosperms and their closest phylogenetic relatives.”

28. Genome Networks Root, By Tal Dagan

“Eukaryotes arose from prokaryotes, hence the root in the tree of life resides among the prokaryotic domains. The position of the root is still debated, although pinpointing it would aid our understanding of the early evolution of life. Because prokaryote evolution was long viewed as a tree-like process of lineage bifurcations, efforts to identify the most ancient microbial lineage split have traditionally focused on positioning a root on a phylogenetic tree constructed from one or several genes. Such studies have delivered widely conflicting results on the position of the root, this being mainly due to methodological problems inherent to deep gene phylogeny and the workings of lateral gene transfer among prokaryotes over evolutionary time.”

“Specific attempts to root the tree of life through data analyses deliver conflicting results, although most commonly a eubacterial root (Gogarten et al. 1989; Lake et al. 2009). Particularly problematic with any rooting of the tree of life within the eubacteria.”

29. An Evolutionary Network of Genes, By Thorsten Thiergart

“Common to autogenous theories is the assumption that mitochondria had no role in the prokaryote-to-eukaryote transition, a premise that has become increasingly problematic with data accrued over the last 10 years indicating 1) that mitochondria were present in the eukaryote common ancestor (Embley et al. 2003; van der Giezen 2009) and 2) that, for reasons of bioenergetics, mitochondria were strictly required for the origin of the molecular traits that make eukaryotic cells complex in comparison to their prokaryotic counterparts.”

“As discussed elsewhere, there are many serious fundamental problems with the view that the nucleus was ever a free-living prokaryote (Martin 1999a, 2005; Cavalier-Smith 2002).”

“Most studies aiming to identify the sister group to mitochondria have focused on genes encoded in mtDNA. But mtDNA-encoded proteins are often highly divergent or rapidly evolving and phylogenetic problems thus arise with their tendency to branch with proteins from other rapidly evolving lineages such as Rickettsias (Bridefalk et al. 2011; Georgiades and Raoult 2011; Thrash et al. 2011). In phylogenetics, the problem is well-known and called long-branch attraction (Lockhart et al. 1994).”

“If differential loss (instead of LGT) is invoked to explain the presence/absence patterns of all non universally distributed genes, the Genome of Eden problem (Doolittle et al. 2003) ensues: inferred ancestral genome sizes become orders of magnitude larger than any observed contemporary prokaryotic genome, an untenable proposition (Dagan and Martin 2007).”

“In the literature on endosymbiosis and gene transfer from organelles to the nucleus, it is commonplace to speak about ‘eukaryotic genes of a-proteobacterial origin.’ But the taxonomic or lineage designation ‘a-proteobacterial’ is in fact very problematic, and perhaps even more arbitrary than that. In the context of eukaryote gene origins, most readers will associate ‘a-proteobacterial’ with ‘mitochondrial,’ and attribution of a gene origin to a cellular partner is uncontroversial; the existence of a donor cell is inferred from an observation in a phylogenetic tree.”

“Thus, that avenue of interpretation (one cell per lineage) clearly problematic and leads to chaos because of the arbitrariness of choosing or defining the taxonomic level at which to seek or find a donor lineage.”

“That would solve the “one cell inferred per lineage identified” conundrum, but it is only half of the problem. The other half concerns the concept of a prokaryotic “lineage” in the context of the amount of geological time (about 1.8 billion years) that the fossil record implores us to keep in mind when considering eukaryote origins.”

30. Analysis of Rare Genomic Changes, By Igor B. Rogozin

“The deep phylogeny of eukaryotes is an important but extremely difficult problem of evolutionary biology. Five eukaryotic supergroups are relatively well established but the relationship between these supergroups remains elusive, and their divergence seems to best fit a “Big Bang” model.”

“The deep phylogeny of eukaryotes is an extremely difficult and controversial problem.”

“It should be noticed that molecular phylogeny methods that employ sophisticated models of sequence evolution, usually within the maximum likelihood framework, are not without their own serious problems that are related, mostly, to model over specification and misspecification.”

31. Eukaryotic RNA Polymerase, By Robert Carter

“Although functions have been attributed to the polymerase-specific subunits of eukaryotic RNAPI and RNAPIII, their origins in early eukaryotes remain a mystery and there exist little structural data describing these proteins.”

32. Genes in Homo Sapiens, By Etienne Loire

“The mystery of this apparent relaxed purifying selection needs more thought and data. In that respect, we think that there is a need for more theory along with a phylogenetic perspective on the evolution of coding SSR to gather further insight in this unclosed debate.”

33. UTR Intron Boundaries, By Scott William Roy

“Despite significant progress, the general functional and evolutionary significance of the untranslated regions (UTRs) of eukaryotic transcripts remain mysterious. Particularly mysterious is the common occurrence of spliceosomal introns in transcript UTRs because UTR splicing is not necessary for restoration of transcript coding sequence.”

“These results focus attention on the functional roles of eukaryotic UTRs and deepen the mystery of UTR intron splicing.”

“The apparent absence of a general function for introns, as well as their peculiar phylogenetic distribution across eukaryotic lineages, makes them a central mystery of genome evolution.”

“The evolutionary and functional significance of UTRs of eukaryotic transcripts remains a mystery.”

34. Oxidases Are an Ancient Innovation, By Anne-Lise Ducluzeau

“The evolutionary history of photosystem II is basically a mystery still today and controversial hypothetical scenarios abound in the literature (Blankenship and Hartman 1998; Baymann et al. 2001; Faller and Rutherford 2003; Mulkidjanian et al. 2006).”

35. Comparison of Diverse Protein Sequences, By Jayatri Das

“Although the evolutionary origin of the nuclear encoded subunits remains a mystery, they have subsequently evolved specialized functions.”

36. Birth and Death of Orphan Genes, By Haleh Amiri

“The origin and evolution of the thousands of species-specific genes with unknown functions, the so-called orphan genes, has been a mystery.”

“The source DNA from which the orphans have originated has been a mystery ever since the first genome sequences were made public.”

37. Remarkable Sequence Conservation, By Marianna Rodova

“Genes encoding eukaryotic mRNAs are usually interrupted by introns, whose origins and functions still remain mysteries. Theories for the origins of introns are that they coevolved with the earliest genes (intron-early) (Fedorov et al. 2001; Roy et al. 2001) and/or that they evolved after the earliest genes by insertion or duplication mechanisms (intron-late) (Logsdon, Stoltzfus, and Doolittle 1998; Fedorov et al. 2001).”

38. Widespread Intron Loss, By Scott William Roy

“Several facets of spliceosomal intron in apicomplexans remain mysterious. First, intron numbers vary across species by 2 orders of magnitude, indicating massive intron loss and/or gain. Second, previous studies have shown very different evolutionary patterns over different timescales, with 100-fold higher rates of intron loss/gain between genera than within genera. Third, the timing and dynamics of nearly complete intron loss in *Cryptosporidium* species, as well as reasons for retention of the few remaining introns, remain unknown.”

“We previously showed mysterious contrasting patterns of intron evolution in apicomplexans over different timescales. Rates of intron loss/gain are extremely low within genera (less than 1.5% intron loss/gain over 100 My for both *Plasmodium* and *Theileria*), but are 100 to 1,000-fold higher between genera (only one-sixth of intron positions are shared between *Plasmodium* and *Theileria*; Roy and Hartl 2006; Roy and Penny 2006).”

“A second evolutionary mystery involves near complete genome-wide intron loss, a surprisingly common occurrence in diverse eukaryotic lineages.”

“The dynamics of these dramatic reductions are not well understood: first whether loss in these lineages is episodic or ongoing, and second why these species retain their few remaining introns.”

39. Newly Evolved Genomic Variants, By A. I. Kalmykova

“The biological significance of this switch of expression strategy during intragenomic evolution of retrotransposon copies remains a mystery. We speculate that a selection of ‘single unprocessed ORF’ copies in the course of *Drosophila* genomes evolution might be forced by the requirement of a retrotransposon fused protein for host genome.”

40. Antisense Origin of Aminoacyl, By Tom A. Williams

“These enzymes fall into two unrelated structural classes whose evolution has not been explained.”

“The evolutionary origin of these enzymes, and therefore the system of translation as we know it, is a tantalizing mystery.”

41. Messenger RNA Surveillance, By Michael Lynch

“The mechanisms responsible for the proliferation and subsequent stabilization of introns within the eukaryotic lineage have remained elusive. In the early stages of eukaryotic evolution, most introns may have been mildly deleterious at the time of insertion, but enough of them eventually acquired integral roles in transcript processing that few eukaryotic species can any longer survive without them.”

“Some of the deepest unsolved mysteries of eukaryotic genome evolution concern introns.”

42. MIKC-type MADS-box Genes, By Katrin Henschel

“Although comparative morphological and phylogenetic analyses may have revealed the major patterns of land plant evolution, the mechanisms which generated the enormous diversity of land plant body plans have remained elusive. However, promising approaches are currently made to solve the mysteries of macroevolution, one of which is evolutionary developmental genetics (‘evo-devo’).”

43. Metazoan Transcription Factor, By Claire Larroux

“We know little about the genomic events that led to the advent of a multicellular grade of organization in animals, one of the most dramatic transitions in evolution. Metazoan multicellularity is correlated with the evolution of embryogenesis, which presumably was underpinned by a gene regulatory network reliant on the differential activation of signaling pathways and transcription factors. Many transcription factor genes that play critical roles in bilaterian development largely appear to have evolved before the divergence of cnidarian and bilaterian lineages.”

“Although the causal link between the evolution of a developmental regulatory network and the evolution of metazoan embryogenesis is currently a mystery, comparison of choanoflagellate and early branching metazoan genomes can provide a general indicator of the relative size and complexity of these networks in key ancestors.”

44. Evidence for the Inclusion of Cetaceans, By Dan Graur

“The transition in the cetaceans from terrestrial life to a fully aquatic existence is one of the most enduring evolutionary mysteries. Resolving the phylogenetic relationships between Cetacea and the other orders of eutherian mammals may provide us with important clues to the origin of whales and may help us date the evolutionary transition to aquatic life.”

“The origin of the order Cetacea (whales, dolphins, and porpoises) is an enduring evolutionary mystery (see, e.g., Flower and Garson 1884), more so since their adaptation to an exclusively aquatic lifestyle required an unprecedented number of unique, yet coordinated, changes in many biological systems. For example, the cetaceans are unique among extant mammals in completely lacking hind limbs, with the exception of an internal pair of rodlike pelvic vestiges that serve as attachments for the corpora cavernosa of the penis.”

45. Evolutionary Innovation of Angiosperms, By Judith Nardmann

“The evolutionary relationship between higher land plants, gymnosperms and angiosperms, jointly seed plants, is still a matter of debate.”

46. A Statistical Test of Phylogenies, By Wen-Hsiung Li

“Finally, the test, applied to the human-chimpanzee-gorilla problem, shows that the issue is not yet resolved.”

“How to test the significance of an inferred phylogeny is a difficult problem.”

47. Sand Dollar Phylogeny, By Charles R. Marshall

“Reconciling discordant morphological and molecular phylogenies remains a problem in modern systematics.”

48. Kingdoms Animalia, Plantae, and Fungi, By Naruo Nikoh

“The phylogenetic relationship among the kingdoms Animalia, Plantae, and Fungi remains uncertain, because of lack of solid fossil evidence. In spite of the extensive molecular phylogenetic analyses since the early report, this problem is a longstanding controversy; the proposed phylogenetic relationships differ for different authors, depending on the molecules and methods that they use.”

“The phylogenetic relationship among the kingdoms Animalia, Plantae, and Fungi, however, remains uncertain, because of lack of solid fossil evidence. Furthermore, for all the advantages of molecular phylogenetic analysis, this problem is a longstanding controversy among molecular evolutionists since the early reports”

49. Evolving Brain-Specific Genes, By Keichi Kuma

“The unified understanding of evolution at the two levels is a crucial problem that remains to be solved.”

50. Hypotheses on the Origin of Pinnipeds, By Gina M. Lento

“The evolutionary origin of the pinnipeds (seals, sea lions, and walrus) is still uncertain. Most authors support a hypothesis of a monophyletic origin of the pinnipeds from a caniform carnivore. A minority view suggests a diphyletic origin with true seals being related to the mustelids (otters and ferrets). The phylogenetic relationships of the walrus to other pinniped and carnivore families are also still particularly problematic.”

“The evolutionary origin of the pinnipeds (true seals, eared seals, and the walrus) has been the focus of considerable debate for over 100 yr”

51. Phylogenetic History of Murid Rodents, By Karen Usdin

“The single most difficult problem in phylogenetic analysis is deciding whether a shared taxonomic character is due to common ancestry or one that appeared independently due to convergence, parallelism, or reversion to an ancestral state.”

“The importance of accurate phylogenetic trees when studying evolution or using evolutionary information for other biological studies is obvious. However, despite significant advances and refinements in the techniques for generating phylogenetic trees, establishing correct phylogenies can still be extremely difficult”

“One frequently encountered problem is that ancestrally unrelated taxa may share the same or similar characters because of convergence, parallelisms, or reversion to an ancestral state. Such characters, called homoplasies, can prevent construction of a unique phylogenetic tree. In other cases, the number of taxa overwhelm the available data. Additionally, tree-building algorithms are sensitive to species sampling within the taxa of interest and depend on certain assumptions about evolutionary mechanisms or events that may not be warranted.”

52. Molecular Phylogeny of the Hominoids, By Maryellen Ruvolo

“Consensus on the evolutionary relationships of humans, chimpanzees, and gorillas has not been reached, despite the existence of a number of DNA sequence data sets relating to the phylogeny, partly because not all gene trees from these data sets agree.”

“Analysis of the hominoid problem has general implications for phylogenetic inference. It is likely that for any three closely related species, the pattern of support among genetic data sets would be similar to that observed for the hominoids-majority support for one hypothesis but not total agreement (Atchley and Fitch 1991).”

53. A Genetic Algorithm, By Paul O. Lewis

“Phylogeny reconstruction is a difficult computational problem, because the number of possible solutions increases with the number of included taxa. For example, for only 14 taxa, there are more than seven trillion possible unrooted phylogenetic trees.”

54. Factor 1-Alpha Sequences, By Cedric Berney

“The phylogenetic position of the Acoela is a key problem in the understanding of metazoan evolution.”

55. Cirripede Phylogeny, By Bernard Billoud

“The choice of this subclass of Crustacea was prompted by (1) the availability of several recently published sequences of the nuclear gene of the small-subunit (SSU) RNA (Spears, Abele, and Applegate 1994) and (2) the numerous phylogenetic problems posed by these organisms, still unsolved by previous molecular analyses.”

56. Evolution of the Wingless Gene, By Dana L. Campbell

“The last 40 years have seen considerable activity in the higher systematics and classification of the ‘true’ butterflies (Papilionoidea, including Hesperioidea). However, the multiple hypotheses that have arisen from these efforts do not provide a consistent interpretation of the evolution of the major butterfly lineages. In particular, assessing the monophyly and phylogenetic placement of the large family Riodinidae, which contains over 1,200 species, has been problematic, as can be seen by the conflicting phylogenetic hypotheses derived from morphological data.”

57. The Phylogeny of Cyclostomes, By Christiane Delarbre

“The relationships between hagfishes, lampreys, and jawed vertebrates (Gnathostoma) are one of the still-unresolved three-taxon problems in craniate phylogeny.”

58. The Phylogenetic Position of the Talpidae, By Suzette K. Mouchaty

“The relationship of the Lipotyphla to the other orders of eutherian mammals has remained a major problem in mammalian phylogeny (Butler 1972; Novacek 1992).”

59. Exploring a Phylogenetic Approach, By Pierre Tuffery

“The methods used to infer the ancestral amino acids at the interior nodes of an evolutionary tree still pose difficult problems. Each of the currently available methods, ML and P, has its own flaws”

60. Letter to the Editor, By Peter J. Waddell

“Furthermore, inconsistency has been shown to be a problem for all classes of phylogenetic analysis, including distance methods and maximum likelihood (Waddell 1995; Lockhart et al. 1996).”

61. The Crustacean *Penaeus monodon*, By Kate Wilson

“The former has been alluded to as ‘one of the most disconcerting problems of arthropod phylogeny’ by Tieggs and Manton (1958), who argued that Arthropoda were polyphyletic and hence that the malacostracan and insect eyes had evolved by convergence.”

62. Analysis Under Reticulate Evolution, By hizhongXu

“The usual assumption that species have evolved from a common ancestor by a simple branching process—where each branch is genetically isolated—has been challenged by the observation of frequent hybridization between species in natural populations. In fact, most plant species are thought to have hybrid origins. This reticulate pattern of species evolution has posed problems in the definition of speciation and in phylogenetic reconstruction, especially when molecular data are used. As a result, hybridization has been largely treated as an evolutionary accident or statistical error in phylogenetic analysis.”

63. Molecular Phylogeny and Divergence, By Ronald M. Adkins

“Although the order Rodentia is diagnosed by several derived morphological traits (Luckett and Hartenberger 1985), many phylogenetic and molecular evolutionary problems persist. For instance, relationships among major rodent families are confounded by mosaic patterns of derived and primitive morphological traits (Luckett and Hartenberger 1985). Characteristics of the zygomaseteric structure and jaw musculature have long been used for classifying rodent families and suborders, but many of these structures reveal parallelism and reversals throughout the rodent radiations (Nedbal, Honeycutt, and Schlitter 1996). Even more surprising is the failure of many recent molecular studies to find strong support for the monophyly of Rodentia.”

64. A New Theory of Phylogeny, By Yasuhiro Kitazoe

“The phylogeny of reptilians has been one of the most important problems in vertebrate evolution.”

65. Implications for Bat Evolution, By Yu-Hsin Lin

“The position of bats in the eutherian tree is uncertain.”

“Even the relationship between microbats and megabats is uncertain.”

66. Phylogenetic Signal and its Decay, By B. Misof

“The phylogeny of Anisoptera, dragonflies in the strict sense, has proven to be notoriously difficult to resolve. Based on morphological characters, several recent publications dealing with the phylogeny of dragonflies proposed contradicting inter- and intra-family relationships. We explored phylogenetic information content of mitochondrial large subunit (LSU) and small-subunit (SSU) ribosomal gene fragments for these systematic problems.”

67. Mitochondrial Versus Nuclear Gene, By Mark S. Springer

“Higher-level mammalian phylogenetics remains an outstanding problem in systematics.”

68. Early Mammalian Evolution, By H. Jow

“Determining the evolutionary relationship among placental mammals is one of the most controversial problems in evolutionary biology. Although molecular phylogeneticists appear to be making good progress on this group, striking inconsistencies between different studies remain.”

69. Evolution of Nuclear Genes, By Junko Kusumi

“The extent to which mutation and selection contribute to nucleotide substitutions has been one of the outstanding problems in molecular evolution since the proposal of the neutral theory by Kimura (1968).”

70. Experimental Genomic Evolution, By D. Rokytka

“An even more challenging problem is to understand how a genome evolves. Genome evolution depends not only on how the elements of a genome function and interact with each other but also on how mutations can change those functions and interactions. We have no easy assay of function that allows us to assess the overall role of different genes within the context of a complete genome, so the identification and significance of genetic changes during evolution has been laborious. Furthermore, although genomes evolve by a combination of point mutations and wholesale gene additions and losses or rearrangements, the contributions of these different scales of mutations to genome function are not easily delineated.”

71. Distribution of *Drosophila melanogaster*, By Lucia Alonso-Gonzalez

“Due to their significant influence on genomic diversity, the nature of forces affecting the transpositional spread of transposons and their distribution throughout the genome is a major problem of evolutionary genetics.”

72. Covariation of Larval Gene Expression, By Zoltan Bochdanovits

“Understanding adaptive phenotypic variation is one of the most fundamental problems in evolutionary biology.”

73. Selection on Coding Regions, By Mario Ali Fares

“The evolutionary forces determining the conservation or loss of Hox genes are poorly understood.”

74. Evolutionary Origin of a Brain, By Masumi Nakazawa

“The origin of the brain remains a challenging problem in evolutionary studies.”

“The evolutionary origin and processes of the brain, however, remain elusive.”

75. Evolution of the TCP Gene, By Patrick A. Reeves

“One of the most fundamental problems in modern evolutionary biology is the origin of morphological novelty.”

76. The Hoatzin Problem, By Michael D. Sorenson

“The apparently rapid and ancient diversification of many avian orders complicates the resolution of their relationships using molecular data.”

“The placement of hoatzin remains uncertain, however, and this kind of result may be a recurring problem for avian ordinal systematics—certain hypotheses will be relatively easily rejected, but their alternatives may remain poorly supported.”

“Given the magnitude of the avian orders problem, comprehensive analyses of relationships within avian families and orders may be more productive for individual researchers in the short term.”

77. Evolution of Clonality, By P. Stenberg

“Even though sex prevails in animals, asexual organisms may be both as successful as their sexual counterparts and as persistent through evolutionary time (Mark Welch and Meselson 2000, 2001). The reason for the persistence of clones over long periods is a challenging problem for biology.”

78. Identifying the Most Basal Angiosperm, By Vadim V. Goremykin

“Angiosperms (flowering plants) dominate contemporary terrestrial flora with roughly 250,000 species, but their origin and early evolution are still poorly understood.”

79. The Mitochondrial Genome, By Kevin G. Helfenbein

“The phylogenetic position of the lophophorates has long been controversial. Various studies have placed these taxa in widely disparate branches of the metazoan tree—in morphological analyses among the deuterostome animals”

“Resolution of the relationships within the Lophotrochozoa is an important and seemingly difficult problem in the study of animal evolution.”

80. Yeast Protein Interaction Network, By Victor Kunin

“Also, defining orthologous groups genes across vast phylogenetic distances, such as across domains of life, is a difficult problem because orthology is defined not only in terms of sequence similarity but also in terms of evolutionary relationships, which are not always known.”

81. Common Pattern of Evolution, By Sergev V. Nuzhdin

“The mechanism of adaptation remains a fundamental unsolved problem in evolutionary biology.”

82. Congruent Mammalian Trees, By Aurelio Reyes

“Mammalian phylogenetics at the ordinal level remains one of the outstanding problems in systematic because of the lack of congruence between different data sets.”

83. Oleosin-Like Gene Family, By Manja Schein

“Although several explanations for the rapid evolution of reproductive proteins have been proposed (e.g., sexual conflict, reproductive isolation, sexual selection, pathogen attacks; reviewed by Howard 1999; Swanson and Vacquier 2002b), differentiating between these hypotheses is difficult and still a largely unresolved problem.”

84. Evolution Revealed by Mutation Clocks, By Koichiro Tamura

“Despite this emphasis and the completion of its nuclear genome sequence, the timing of major speciation events leading to the origin of this fruit fly remain elusive because of the paucity of extensive fossil records and bio-geographic data. Use of molecular clocks as an alternative has been fraught with non clock-like accumulation of nucleotide and amino-acid substitutions.”

“This poses severe problems while inferring molecular time scales of fruit fly evolution.”

85. Origin of Photosynthetic Eukaryotes, By Hwan Su Yoon

“This is especially true for the estimation of ancient divergence times for which there is limited fossil evidence, and modelling DNA sequence evolution is the most error-prone because of the accumulation of superimposed mutations (Whelan, Lio, and Goldman 2001).”

“Assuming that our results (and the Paleoproterozoic model) are correct, we are left with an important problem, explaining the presence of algae significantly earlier than the eukaryotic diversification documented in Neoproterozoic fossils (Anbar and Knoll 2002). We believe that this discordance likely reflects a combination of factors.”

86. Genome Rearrangement Distances, By Eugeni Belda

“Symbiotic lineages present particular problems in phylogeny reconstruction due to their accelerated sequence evolution (Moran 1996; Itoh, Martin, and Nei 2002) and their biases in base and amino acid compositions (Moran 1996; Clark, Moran, and Baumann 1999; Shigenobu et al. 2001; Palacios and Wernegreen 2002; Rispe et al. 2004). In fact, the production of conflicting topologies is frequent.”

87. Analysis of *Acorus calamus*, By Vadim V. Goremykin

“Determining the phylogenetic relationships among the major lines of angiosperms is a long-standing problem, yet the uncertainty as to the phylogenetic affinity of these lines persists.”

“So far, application of molecular techniques has not been able to clarify the phylogenetic relationships among the major angiosperm lineages. Topologies suggested by cladistic studies are highly contradictory, especially regarding the placement of monocots, eumagnoliids, Piperales, Nymphaeales, Amborella, and Ceratophyllum.”

“Recent commentaries on the debate about angiosperm origins by Lockhart and Penny (2005) and Martin et al. (2005) both highlight why we expect this to be a challenging problem for current phylogenetic estimation methods.”

“Despite large numbers of characters for analysis, the issues of the basal most angiosperms and the monophyly of monocots are not, in our view, presently resolved. This confirms that the early phase of angiosperm lineage diversification is a difficult problem in molecular phylogenetics that will require a larger taxon sample and a large number of sites to resolve.”

88. Rooting Rapid Radiations, By Liat Shavit

“In such cases, where there is a combination of short internal and long external branches, correctly estimating and rooting phylogenetic trees is known to be a difficult problem.”

“The problem of tree reconstruction and rooting is known to be challenging, especially in cases of rapid radiations where there is a combination of short and long branches.”

89. Evolution of the *Caenorhabditis*, By Asher D. Cutter

“A fundamental problem in genome biology is to elucidate the evolutionary forces responsible for generating non random patterns of genome organization.”

“How does natural selection infringe upon neutral evolutionary processes to shape an organism’s genome? When do neutral forces, like mutation, genetic drift, and gene conversion, play a leading role in generating non random patterns in the genome? In what ways might demography and breeding system impact the character of sequences on a genomic scale? These are some of the broad questions that population genetics and molecular evolutionary theory seek to explain.”

90. Analyses Reveal Little Evidence, By Toni I. Gossmann

“The relative contribution of advantageous and neutral mutations to the evolutionary process is a central problem in evolutionary biology.”

“The contribution of adaptive evolution relative to genetic drift is a fundamental problem in molecular evolution.”

91. A Genome Phylogeny, By Christian Esser

“Chimaerism poses challenging and yet unsolved problems, regarding both the classification of unicellular organisms (Doolittle 1999) and the reconstruction of early eukaryotic evolution (Knoll 2003).”

92. Impacts of Molecular Oxygen, By Sara Vieira-Silva

“If one accepts the frequently held idea that eukaryotes derive from common ancestors with prokaryotes, this hypothesis leaves unsolved how oxygen-rich proteins in eukaryotes arose in the first place.”

93. Impacts of Gene Essentiality, By Ben-Yang Liao

“What determines the rate of protein sequence evolution is a fundamental question in molecular evolution.”

“Nonetheless, despite the availability of many mouse strains produced in targeted gene deletion experiments, whether gene essentiality influences mammalian protein evolution remains unsolved due to the lack of a comprehensive list of essential and nonessential genes.”

94. Neutralism in Molecular Evolution, By Masatoshi Nei

“Speciation or development of reproductive isolation is one of the most important unsolved problems in population genetics.”

95. A Phylogenomic Approach, By Sabrina Simon

“However, the origin of insect flight and the relationships of basal winged insect orders are still controversial. Three hypotheses have been proposed to explain the phylogeny of winged insects.”

“Considering the tremendous impact this change produced, the evolution of the flying insects is one of the most fascinating questions in evolutionary biology.”

“The monophyly of Palaeoptera has been controversial ever since. In contrast to the accepted monophyly of Neoptera, the so-called “Palaeoptera Problem” is one of the unsolved mysteries in insect systematics.”

96. Evolution of Modern Birds, By M. Andrena Pacheco

“Timing the radiation of modern birds (Neornithes) and assessing the evolutionary relationships among major orders are still controversial issues in avian biology.”

“In addition, the evolutionary relationships of several orders within the Neoaves phylogeny (e.g., parrots, columbiforms, coraciiforms, and cuculiforms) are still unsolved.”

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