REWEAVING THE TAPESTRY:
A SUPERTREE OF BIRDS

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Declaration

I attest that:

All material presented in this document was compiled and written by myself unless otherwise acknowledged. Part of the material included in this thesis is being prepared for submission in co-authorship with others:

- Chapter 2: Davis, K. E. and Dyke, G. J. In Prep for *Neues Jahrbuch für Geologie und Paläontologie*. “Two new specimens of *Primobucco* (Aves: Coraciiformes) from the Eocene of North America”. K. E. D. carried out the descriptive work, phylogenetic analyses and wrote the manuscript. G. J. D. provided the specimens and advised on description and writing of the manuscript.
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KATIE E. DAVIS, 2008

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Abstract

Supertrees are a useful method of constructing large-scale phylogenies by assembling numerous smaller phylogenies that have some, but not necessarily all, taxa in common. Birds are an obvious candidate for supertree construction as they are the most abundant land vertebrates on the planet and no comprehensive phylogeny of both extinct and extant species currently exists. In order to construct supertrees, primary analysis of characters is required. One such study, presented here, describes two new partial specimens belonging to the Primobucconidae from the Green River Formation of Wyoming (USA), which were assigned to the species *Primobucco mcgrewi*. Although incomplete, these specimens had preserved anatomical features not seen in other material. An attempt to further constrain their phylogenetic position was inconclusive, showing only that the Primobucconidae belong in a clade containing the extant Coraciiformes and related taxa. Over 700 such studies were used to construct a species-level supertree of Aves containing over 5000 taxa. The resulting tree shows the relationships between the main avian groups, with only a few novel clades, some of which can be explained by a lack of information regarding those taxa. The tree was constructed using a strict protocol which ensures robust, accurate and efficient data collection and processing; extending previous work by other authors. Before creating the species-level supertree the protocol was tested on the order Galliformes in order to determine the most efficient method of removing non-independent data. It was found that combining non-independent source trees via a "mini-supertree" analysis produced results more consistent with the input source data and, in addition, significantly reduced computational load. Another method for constructing large-scale trees is via a supermatrix, which is constructed from primary data collated into a single, large matrix. A molecular-only tree was constructed using both supertree and supermatrix methods, from the same data, again of the order Galliformes. Both methods performed equally as well in producing trees that fit the source data. The two methods could be considered complementary rather than conflicting as the supertree took a long time to construct but was very quick to calculate, but the supermatrix took longer to calculate, but was quicker to construct. Dependent upon the data at hand and the other factors involved, the choice of which method to use appears, from this small study, to be of little consequence. Finally an updated species-level supertree of the Dinosauria was also constructed and used to look at diversification rates in order to elucidate the "Cretaceous explosion of terrestrial life". Results from this study show that this apparent burst in diversity at the end of the Cretaceous is a sampling artefact and in fact, dinosaurs show most of their major diversification shifts in the first third of their history.

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Chapter 1

Introduction

1.1 Introduction

Birds (Aves) are a diverse class and are the most abundant land vertebrates on the planet. There are approximately 10,000 species of extant birds (Monroe and Sibley, 1993) occupying almost every geographical location, from ocean to desert, and from woodland to lake (Figure 1.1). Birds are widely considered to have evolved from therapod dinosaurs during the Jurassic period (Chiappe, 1995 and references therein), with the first known bird being the 150 million year old *Archaeopteryx lithographica*.

Figure 1.1: The diverse range of bird sizes and habitats. Top left: Ostrich (*Struthio camelus*) in an Israeli nature reserve (courtesy of Judith Anenberg). Top right: Yellow Warbler (*Dendroica petechia*) from Canada (courtesy of Wikimedia Commons). Bottom left: Laysan Albatross with chick (*Phoebastria immutabilis*) from Midway Atoll in the Pacific Ocean (courtesy of Ryan Haggerty). Bottom right: Lesser Bird of Paradise (*Paradisaea minor*) from New Guinea (courtesy of Roderick Eine).

Birds are an economically important group, providing food for humans, as well as fertilizer, and some species are kept as pets. However, human activity may be partly to blame for the 1,107 species currently on the endangered species list (IUCN Red List, 2007). Phylogenies are an important tool in conservation, as highlighted by Nee and May (1997), and allow testing of hypothetical extinction models to assess the loss of "phylogenetic diversity" (Bininda-Emonds *et al.,* 2002). Birds are also in particular need of phylogenetic assessment as no widely accepted phylogeny currently exists. In fact, no complete phylogeny of Aves has been attempted since Sibley and Ahlquist's "tapestry" (1990) was constructed using the much criticised technique of DNA-hybridisation. This phylogeny still only contained 1083 taxa, with most at genus-level. Smaller-scale attempts have also been made; the most recent of these being the large anatomical matrix of Livezey and Zusi (2007), which comprised just 150 taxa.

Phylogenies can be used for a range of practical applications in addition to aiding conservation, such as comparative biology and divergence times. A number of comparative studies using birds have been based on the tapestry of Sibley and Ahlquist (1990); these include the tempo and mode of bird evolution (Nee *et al.,* 1992), the effect of generation time on rates of avian molecular evolution (Mooers and Harvey, 1994) the evolution of avian mating systems and the association between mating systems and pair-bond length (Temrin and Sillen-Tullberg, 1994). The dependence of these comparative analyses on the tapestry is troubling as there are concerns about the validity of the method used (DNA – hybridisation) (Houde, 1987; Harshman, 1994; Sheldon and Bledsoe, 1993).

Given the lack of a comprehensive phylogeny of birds it is timely to create such a phylogeny. In order to include as many taxa as possible, a method must be used that allows the phylogeny to be as inclusive as possible. Supertree methods can be used to combine a large number of smaller individual phylogenies, each of which can be constructed using any phylogenetic techniques and any number of taxa, additionally these taxa may differ between these individual phylogenies. As such they give the widest possible view of phylogeny, both in terms of taxonomic coverage and in terms of the types of data incorporated.

Large-scale supertrees have now been produced for many groups of taxa including the Dinosauria (Pisani *et al.,* 2002; Lloyd *et al.* Chapter 6 of this thesis), marsupials (Cardillo *et al.,* 2004), bats (Jones *et al.,* 2002), early tetrapods (Ruta *et al.* 2003), grasses (Salamin *et al.* 2002), and a supertree of nearly all extant Mammalia (Bininda-Emonds *et al.,* 2007). Avian supertrees have been produced for the Procellariiformes (tube-nose seabirds) (Kennedy and Page, 2002) and the Charadriiformes (shorebirds) (Thomas *et al.,* 2004) but not for all of Aves. Supertrees have been used to look at cladogenesis of primates (Purvis, 1995) and diversification of the Dinosauria (Lloyd *et al.,* Chapter 6), amongst other things.

The purpose of this thesis is to construct a robust, and inclusive, phylogeny of Aves using supertree methods. As mentioned above, birds are a large important group of organisms, with nearly 10% of taxa currently on the endangered species list. Creating an inclusive phylogeny of birds will help elucidate their origins and help conservationists concentrate their efforts in preserving “biodiversity hotspots”.

1.2 Constructing large-scale phylogenies

There are two approaches used for creating large phylogenies. One is the supermatrix or “total evidence” method (Miyamoto, 1985; Kluge, 1989; Nixon and Carpenter, 1996). Here, all characters and taxa make up a single large matrix. A major drawback of this approach is that some types of data cannot be combined (e.g. immunological distance data and DNA-hybridisation data) and that combination of these data types introduces subjective decisions and is vastly time consuming (Sanderson *et al.,* 1998). There is also the potential for a large amount of missing data when combining information in this way (Sanderson *et al.,* 1998). Bird systematists have employed hard and soft body morphology, behaviour, allozymes, nucleotide sequences, and DNA-hybridisation to elucidate avian phylogeny. Consequently, a supermatrix approach would *a priori* eliminate many of these data sources.

However, supermatrices are based on primary character data and are thought to be capable of producing novel clades as a result of hidden character support with a well-characterised basis (Barrett *et al.,* 1991; Gatesy *et al.,* 1999; Lee and Huggal, 2003). When also taking into consideration the many issues with supertree construction, some workers believe that supermatrices are far superior to supertree methods of constructing large phylogenetic trees (Gatesy *et al.,* 2002; Gatesy *et al.,* 2004; Queiroz and Gatesy, 2006).

The second approach is the supertree method. A supertree is defined as an estimate of phylogeny assembled from smaller phylogenies. These partial phylogenies must have some taxa in common, but not necessarily all (Sanderson *et al.,* 1998). Supertrees are constructed, not from primary data, but from the combining of the topologies of partial phylogenies into a single comprehensive matrix (Bininda-Emonds *et al.,* 1999). Trees contributing to a supertree analysis are known as "source trees". The most commonly used supertree method is Matrix Representation with Parsimony (MRP) (Baum and Ragan, 2004). All taxa subtended by a given node in a source tree are scored as "1", taxa not subtended from that node are scored as "0", taxa not present in that source tree are scored as "?". Trees are rooted with a hypothetical, all-zero outgroup (Ragan, 1992) (Figure 1.2).

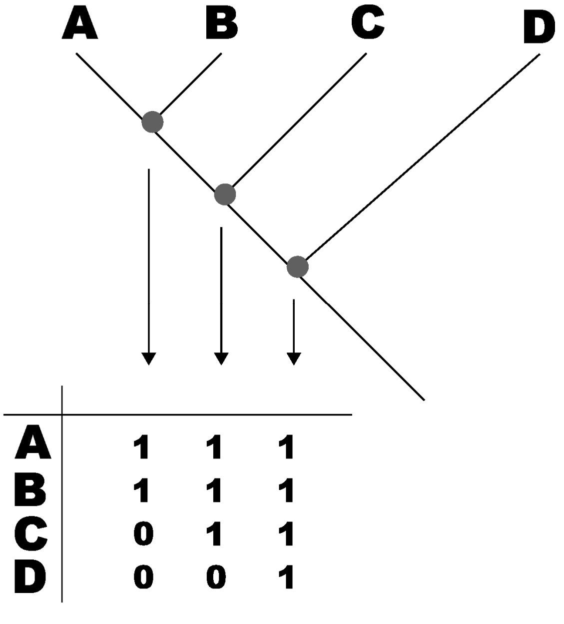

Figure 1.2: Example of Baum and Ragan coding. After Sanderson *et al.* (1998).

One of the justifications for the use of supertree methods is that they can combine trees derived from all data types to produce a single phylogeny (Sanderson *et al.,* 1998). However, the main advantages of supertrees are that they can handle very large numbers of taxa, combine numerous types of characters in a single tree, potentially summarise support, resolve groups that are poorly resolved in source trees, resolve taxon conflict (Ruta *et al.,* 2003) and highlight poor taxonomic sampling (Salamin *et al.,* 2002). However, it is not universally agreed that supertrees are a robust method for constructing phylogenies and criticisms include the use of poorly justified source data (Gatesy *et al.,* 2002) and biases in supertree methods (Wilkinson *et al.,* 2005b).

Some of these criticisms will be addressed in this thesis with the production of a rigorous supertree-building protocol, and in addition, supertree and supermatrix methods will be compared and contrasted using a case study. Supertree methods will also be used to construct species-level phylogenies for all Aves and Dinosauria. As discussed above, supertree methods are likely to be more efficient and will enable the incorporation of a wider variety of data, increasing taxonomic coverage. There are numerous different methods currently available for creating supertrees, not all of which have software implementation. These are discussed in more detail below.

1.3 Supertree methods

There are several implementations of the supertree approach. Of these the only widely used method is Matrix Representation with Parsimony (MRP). Methods can be split into two broad categories; “agreement” and “optimisation”. Agreement methods find common or uncontested groups within a set of source trees. In contrast, optimisation methods find the supertree (or set of supertrees) that has the maximum fit to the set of source trees according to an objective function (Bininda-Emonds, 2002). A summary table of all current supertree methods can be found in Table 1.1.

The main methods to date that have software implementation are Matrix Representation with Parsimony (MRP), Matrix Representation with Flipping (MRF), Matrix Representation with Compatibility (MRC), Mincut (MC) and Modified Mincut (MMC). These are all discussed in more detail in the section below.

Table 1.1: Summary of formal supertree methods according to category. After Bininda-Emonds (2004).

Agreement Supertrees	Optimisation Supertrees
MinCutSupertree	Average consensus (MRD)
Modified MinCut	Bayesian supertrees
RankedTree	Gene tree parsimony
Semi-labelled and AncestralBuild	Matrix representation using compatibility (MRC)
Semi-strict	Matrix representation using flipping (MRF or MinFlip)
Strict	Matrix representation with parsimony (MRP) and variants
Strict consensus merger	Most similar supertree method (dfit)
	Quartet supertree

1.3.1 Matrix Representation with Parsimony (MRP)

Matrix Representation with Parsimony (MRP) is by far the most widely used method and has been used to construct most large supertrees to date, for organisms ranging from dinosaurs (Pisani *et al.,* 2002) to flowering plants (Linder, 2000). This method can be used whether or not source trees are compatible, and converts the topology of a source tree into a data matrix of "characters" (Sanderson *et al.,* 1998). Once an MRP matrix has been constructed it can be analysed using a number of different computational algorithms. For example, the dinosaur supertrees (Pisani *et al.,* 2002; Lloyd *et al.,* Chapter 6 this thesis), mammals (Bininda-Emonds *et al.,* 1999; Cardillo *et al.,* 2004) and seabird supertrees (Kennedy and Page, 2002) have all been constructed using MRP. Matrix Representation with Parsimony methods seek to find a tree that requires the fewest number of steps based on the input matrices.

MRP is not however without criticisms. Gatesy *et al.* (2004) claim that although the majority of published supertree analyses have been constructed using MRP (e.g. Purvis, 1995; Bininda-Emonds *et al.,* 1999; Daubin *et al.,* 2001; Liu *et al.,* 2001; Jones *et al.,* 2002; Kennedy and Page, 2002; Salamin *et al.,* 2002) the logical basis, they claim, for this is unclear. They state that "using MRP to summarise the results of different analyses amounts to finding the arrangement of taxa that provides the best explanation of the conclusions of those analyses, not the best explanation of observations.".

Gatesy *et al.* (2002) also state that constructing supertrees is not the same as constructing cladograms from primary data and should not be interpreted as such as they are based on secondary representations of data. Bryant (2004), however, suggests that MRP could be operationally equivalent to the construction of cladograms using cladistic analysis of character data if consistent with cladistic principles and the following properties are upheld:

1) Must be based on source trees that were generated using well-designed cladistic analyses.

2) Matrix elements or sets of matrix elements should be weighted based on the relative character support for individual nodes on the source trees and to alleviate inappropriate biases associated with tree size.

3) Source trees should have high consistency indices.

4) The source trees must be based on different sets of characters to guarantee independence among the matrix elements.

Bryant (2004) concluded that all published MRP analyses failed to meet these criteria and therefore should be considered a synthesis of information rather than a rigorous phylogenetic analysis.

However, an advantage of Matrix Representation with Parsimony is that it has numerous software implementations including PAUP* 4.0b10 (Swofford, 2002) TNT (Goloboff *et al.,* 2008), POY (Varón *et al.,* 2007) and Clann (Creevey and McInerney, 2005).

1.3.2 Matrix Representation with Flipping (MRF)

Minimum flip (MRF) supertrees attempt to find the minimum number of changes (“flips”) to the matrix of source trees that will resolve incompatibilities (Eulenstein *et al.,* 2004). A cell in the matrix representation has either a 1 or a 0 and can be regarded as a potential error (Burleigh *et al.,* 2004). MRF determines the minimum number of flips required to turn this matrix into one that corresponds to a tree with no homoplasy (MRP seeks to find the tree with the least homoplasy). If the source trees are compatible and no flips are necessary the resulting supertree will display all the input trees.

MRF represents a philosophically different approach to that taken by MRP methods as it is based on error correction in the source trees, whereas MRP seeks to find the supertree with the minimum number of character changes with respect to the matrix representation (Eulenstein *et al.,* 2004).

Eulenstein *et al.* (2004) found that their MRF heuristic was at least as accurate as MRP methods and more accurate than MC or MMC supertrees. Accuracy was assessed by the use of MAST and triplet scores comparing the supertrees to the source data. Simulations showed that for calculating large phylogenies from a large collection of small input trees MRF should perform more accurately than any of MRP, MC or MMC supertrees. The major drawback of this method is the speed of the algorithm. In terms of speed, MRF was outperformed by MC (MinCut), MMC (Modified MinCut) and MRP (Matrix Representation with Parsimony) algorithms and it was only feasible to compute a 96 taxon supertree with the MRF algorithm. Obviously this becomes problematic when attempting to reconstruct phylogenies of groups containing, not just 100s, but 1000s of taxa.

1.3.3 Matrix Representation with Compatibility

Matrix Representation with Compatibility (MRC) identifies the largest set of mutually compatible characters in combined datasets represented by a binary matrix (Ross and Rodrigo, 2004). Compatible characters are those that either support, or are consistent with, a particular phylogenetic tree. These sets of characters are known as cliques and MRC seeks to find the largest set of these characters, known as the "maximum clique" (Ross and Rodrigo, 2004).

Overall, MRC does not perform as well as MRP. Both are successful but MRP is slightly more so for "large" datasets of 7-10 trees in which >50% taxa overlap is present (Ross and Rodrigo, 2004), although this clearly is not large in the context of most supertree analyses and certainly not in terms of this thesis. Ross and Rodrigo (2004) consider the main benefit of MRC to be that it "identifies the consistent and uncontradicted core of the dataset and excludes those nodes which logically cannot exist". Its main failing however is that it is not practical for the construction of large supertrees as it takes such a long time to find the maximum cliques in large datasets (Ross and Rodrigo, 2004).

1.3.4 MinCut

MinCut is derived from the OneTree algorithm (Ng and Wormald, 1996), which is a recursive algorithm that only returns a tree if all the input trees are compatible. MinCut (Semple and Steele, 2000) modifies OneTree such that it always returns a tree even if input trees are incompatible. MinCut contains slightly disconcerting properties when using simple test cases, for example, producing polytomies for uncontradicted data and maintaining relationships for contradicted data (Page, 2002). The algorithm uses a connective graph whose edges have a weight associated with them, this weight is the number of input trees that contain that relationship. Any edges that have the same weight as the number of input trees (i.e. unanimous/uncontradicted) are removed by merging the nodes. All edges that do not have the same weight as the number of source trees (i.e. contradicted) are placed in a polytomy. From this modified graph a new tree can be constructed.

1.3.5 Modified MinCut

Modified MinCut (Page, 2002) is based directly on MinCut but modifies the definition of "unanimous and uncontradicted". "Unanimous" means the same as in MinCut (Semple and Steele, 2000), however "uncontradicted" is defined as a nesting found in some of the source trees that is not contradicted by any of the source trees. This results in the collapsing of more nodes and removes the spurious groupings that can be returned by MinCut. Simulation studies (Eulenstein *et al.,* 2004) show that MinCut and Modified MinCut do not work as well as other methods, so it is reasonable to dismiss these *a priori* as potential supertree-building mechanisms for this study.

1.3.6 Other methods

A number of other methods exist in theory but have no software implementation as yet. A few of note are mentioned below.

Daniel and Semple (2004) described a supertree algorithm for higher taxa. This assumes that all operational taxonomic units (OTUs) are species and thus labels interior nodes as higher taxa, therefore trees with higher taxa can be included with no need for any processing. Also, the problem can be solved in polynomial time. A potential problem though is that it assumes that the taxonomy is correct.

Semi-strict supertrees (Goloboff and Pol, 2002) find a subset of the whole matrix where all possible subsets are compatible; this is known as the “ultra-clique”. Finding this ultra-clique is computationally complex but a heuristic method provides good results. If trees have no conflict or there are only two source trees then this method will get an exact result. When there are more than two and there is conflict, it eliminates spurious groups to find supertree. The drawback is that supertrees from matrices with very dissimilar sets of taxa (with not much overlap) should be interpreted with caution as they produce unresolved semi-strict supertrees.

1.4 Current estimates of Avian Phylogeny

1.4.1 The Sibley and Ahlquist tapestry

Current views on avian phylogeny are largely derived from Sibley and Ahlquist’s “tapestry” (1990). Many comparative studies have also been carried out using this work (Mooers and Harvey, 1994; Temrin and Sillen-Tullberg, 1994). The “tapestry” consisted of DNA work carried out by Sibley and Ahlquist over many years culminating in the publication of the book “Phylogeny and classification of birds – A study in molecular evolution” (1990). It covered 1083 taxa, most at genus level, and is the most comprehensive published study of avian phylogeny to date (Figure 1.3).

The DNA-hybridisation technique measures the genetic distance between taxa and Sibley and Ahlquist (1990) state that “a phylogeny based on DNA distances is a diagram of the degrees of genetic divergence among the included taxa”. The major criticisms of this technique are the fact that the authors did not publish the raw data (Houde, 1987), and that it was based on incomplete distance matrices and used an inappropriate tree-building algorithm (Harshman, 1994). Houde (1987) also points out that the avian molecular clock was assumed to be constant, but this is not the case in reality. The final point is that the method is phenetic, not cladistic, using distances instead of characters (Sheldon and Bledsoe, 1993). Some authors have, however, confirmed some of Sibley and Ahlquist's results (Harshman, 1994; Bleiweiss *et al.,* 1994).

In addition, Sibley and Ahlquist's tapestry was constructed largely at genus level and only covered 1083 taxa (including some higher taxa and vernacular names) out of an estimated 10,000 known species of birds (Monroe and Sibley, 1990). Therefore, it is clear that it is time for a new estimate of avian phylogeny, and supertree methods are an ideal way of exploring this in much greater detail than achieved previously.

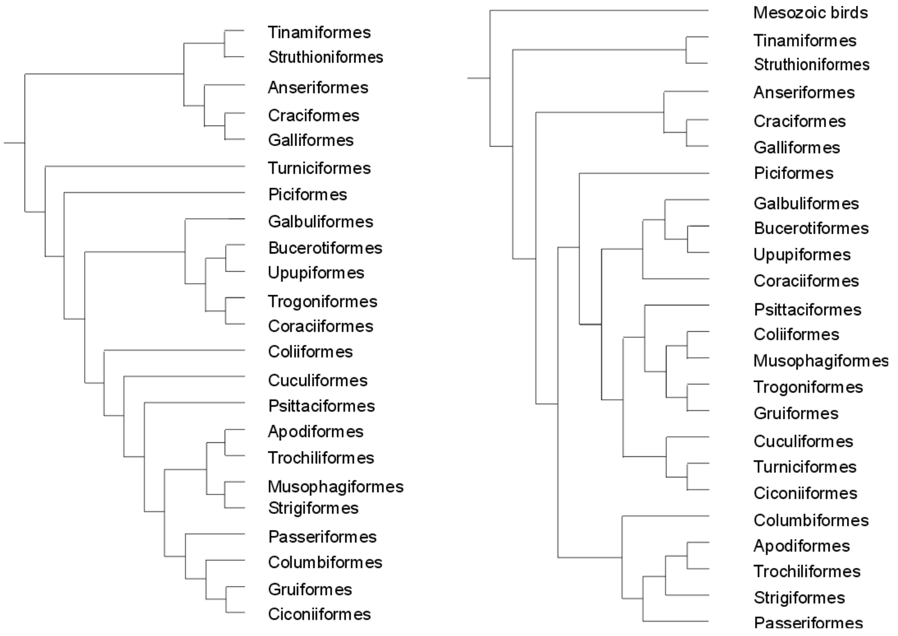

Figure 1.3: Comparison of Sibley and Ahlquist's "tapestry" (left) with the supertree of Davis (2003) (right).

1.4.2 Family-level supertree

To summarise knowledge of large-scale avian phylogeny prior to this thesis, the family-level supertree constructed as part of the author's M.Sc thesis will be used (Davis, 2003). In this study 124 source trees and 199 taxa were included. This supertree includes both extinct and extant taxa starting with the first known bird, the Jurassic *Archaeopteryx lithographica*. This supertree was a preliminary study of large-scale avian phylogeny and will be used in this thesis in lieu of a literature review in order to summarise current knowledge of avian phylogeny. The supertree provides a useful tool for this purpose and shows the current "state of the art".

Overview of avian phylogeny from the family-level supertree

The family-level supertree also included the use of QS values (Bininda-Emonds, 2003) to investigate clade support. This is described first below before discussing the supertree in depth.

The average QS value for the supertree was –0.043. Qualitative Support (QS index), is one of the first support measures that samples at the level of source trees rather than characters (Bininda-Emonds, 2003) and, as such, is possibly the first method that can be successfully applied to supertrees. The QS index works by comparing source trees with the supertree and assigning one of four "states" for the fit between the two. A hard match occurs where the source tree fits the supertree exactly, a soft match occurs where addition of missing taxa may support the clade but never contradict it and vice versa for a soft mismatch, finally, a hard mismatch occurs where the source tree contradicts the supertree. Hard matches are scored as +1, soft matches as +0.5, equivocal matches as 0, soft mismatches as –0.5 and hard mismatches as –1. These values are summed over the clade and divided by the number of source trees, therefore the QS value for a clade indicates the proportion of matches and mismatches in the clade. Generally speaking, more matches result in a positive QS value and more mismatches produce a negative value (Bininda-Emonds, 2003). Of 161 clades, none have hard support, which is to be expected as only highly overlapping datasets are likely to show hard support (Bininda-Emonds, 2003). Equally, no clades show hard conflict, indicating that there are no novel clades present in the supertree. Soft support was found in 37% of clades, while soft conflict was found in 58%. The remaining 5% were equivocal. The average clade size showing soft conflict was much larger than that for soft support (31.366 taxa as opposed to 9.250, respectively), this is due to the increasing possibility of disagreement between source trees as numbers of taxa increase (Bininda-Emonds, 2003). Equivocal clades have the highest average taxa number (179.375) and are all found near the base of the tree. This is in contrast to the results of Bininda-Emonds (2003), who found that equivocal clades largely follow the trends seen in clades with soft support. Overall, the tree is well resolved, with the exception of clades within the Passeriformes and a large part of the Ciconiiformes.

The resultant supertree (Figure 1.4) was the 50% majority rule consensus of 1,387 MPTs and had a length of 1109 steps. Low QS values reflect uncertainty in the positions of Mesozoic taxa relative to one another. The Mesozoic taxa were also the least well-represented among the source trees occurring, on average, in just 9% of the source trees. Despite the well-supported position of *Archaeopteryx* at the base of the tree (QS value of 0.5), only two clades have relatively high support; the Enantiornithes, which all have values higher than the tree average, and the Hesperornithiformes, which all have positive support values. This probably reflects the fact that the Enantiornithes and Hesperornithiformes are well studied groups, in contrast to other Mesozoic taxa many of which are represented by only a handful of fossils and have been included in few phylogenetic analyses.

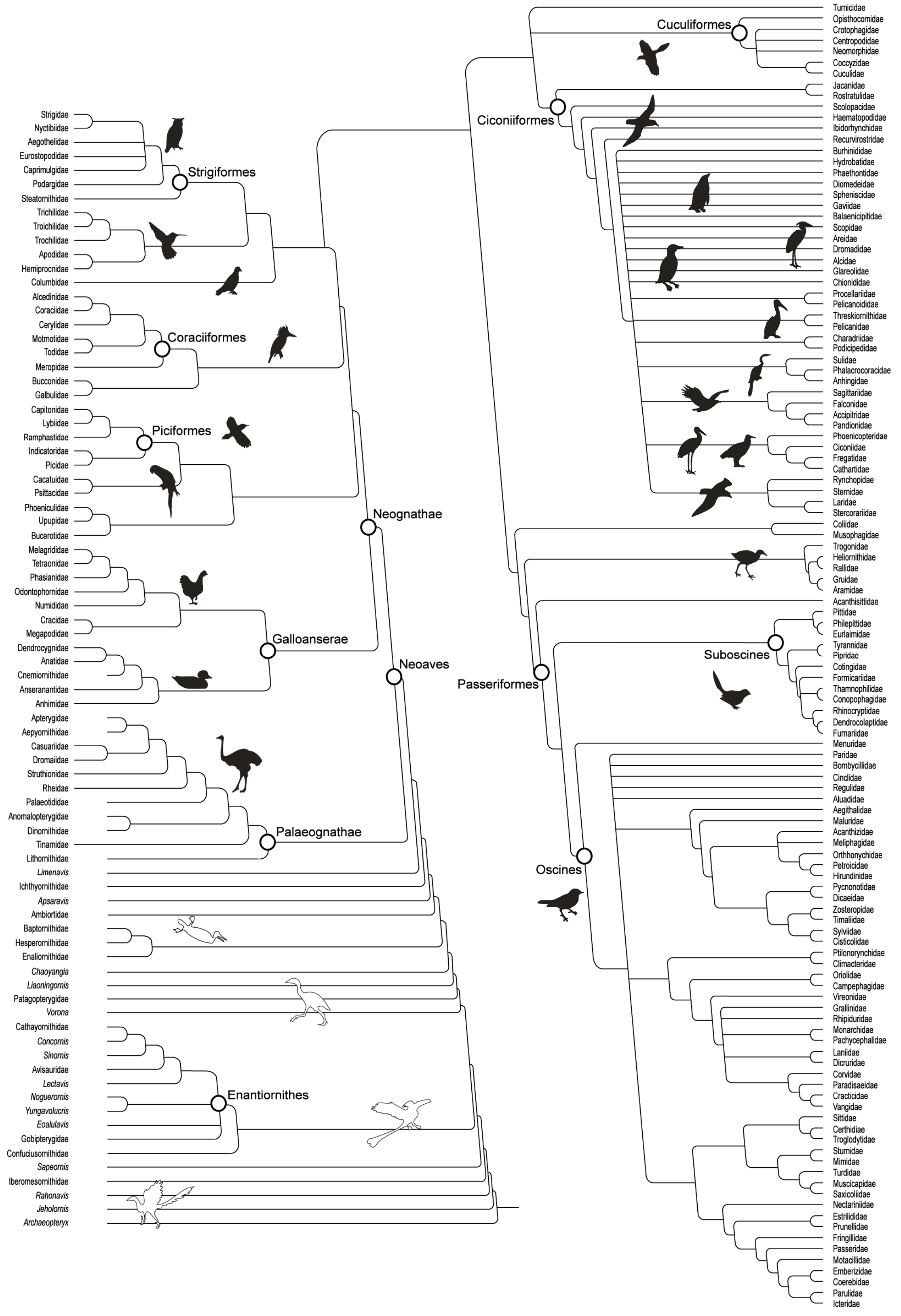

Figure 1.4: Family-level supertree from the analysis carried out by Davis (2003). This represents the most comprehensive known supertree of Aves to date.

Positions of extant orders are poorly understood, a fact that is reflected in the relatively low QS values for many clades. Palaeognath (ratites and tinamous) monophyly is retained; this clade is well supported compared to many others when QS values are taken into account. This result is in contrast to the proposal that the Palaeognathae are actually polyphyletic (Houde and Olson, 1981). The supertree also supports monophyly of the Galloanserae, a relatively recent proposal that the Anseriformes (waterfowl), Craciformes and Galliformes (landfowl) comprise a monophyletic group (Caspers *et al.,* 1997; Van Tuinen *et al.,* 2000; Sorenson *et al.,* 2003). The position of the Galloanserae with respect to other orders has been debated, specifically whether they form a monophyletic clade with the Palaeognathae (Sibley and Ahlquist, 1990) or occupy the position of sister group to the Neoaves (Neornithes minus Neognathae) (Cracraft, 1988; Van Tuinen *et al.,* 2000).

The traditional classification of the Piciformes (woodpeckers and allies) originally encompassed the clade now known as the Galbuliformes (puffbirds) (Simpson and Cracraft, 1981; Swierczewski and Raikow, 1981). Several authors have suggested that the traditional Piciformes were polyphyletic and that the Galbulae (the modern Galbuliformes) were more closely related to the Coraciiformes (kingfishers and allies) (Sibley and Ahlquist, 1972; Olson, 1983; Burton, 1984). The supertree places the Piciformes in a separate clade to the Coraciiformes and Galbuliformes, supporting the hypothesis that the latter two orders are more closely related to each other than either is to the Piciformes. These two clades are among the strongest in the tree, both with relatively high QS values compared to the tree average (0.012 and 0.016 respectively). Psittaciformes (parrots and allies) are traditionally considered to have no close living relatives (Sibley and Ahlquist, 1990) while the supertree suggests a sister group relationship with the Piciformes.

The closest relatives of the Columbiformes (doves and pigeons) are historically not well understood (Sibley and Ahlquist, 1990). This analysis suggests a sister group relationship with the Apodiformes (swifts) and Trochiliformes (hummingbirds), and with the Strigiformes (owls). This clade is also one of the stronger groupings within the tree with a QS value of -0.016. The association between Apodiformes and Trochiliformes is well recognised (Bleiweiss *et al.,* 1994; Van Tuinen *et al.,* 2000;

Johansson *et al.,* 2001; Mayr, 2002) and is not contradicted by any of the source trees. The positioning of Strigiformes as sister group to these taxa also agrees with that found by Bleiweiss *et al.* (1994).

Turniciformes (buttonquail), Cuculiformes (cuckoos and anis) and Ciconiiformes (storks and allies) comprise another clade, in agreement with Van Tuinen *et al.* (2000). The affiliation between Turniciformes and Ciconiiformes is also recovered by the analysis of Groth and Barrowclough (1999). Sibley and Ahlquist (1990) greatly expanded the definition of the Ciconiiformes to subsume the traditional orders Charadriiformes (shorebirds), Falconiformes (diurnal birds of prey), Pelicaniformes (totipalmate birds, e.g. tropicbirds and pelicans), Procellariiformes (tube-nose seabirds), Podicipediformes (grebes), Gaviiformes (loons) and Sphenisciformes (penguins). This is the most controversial part of Sibley and Ahlquist's classification and many of these taxa are placed within a large polytomy reflecting the high degree of incongruence between the source trees. These basal nodes within the Ciconiiformes have low QS values compared to the tree average, also indicating low support and high degrees of source tree conflict. Taxa that are resolved include the traditional "Falconiformes", a number of "pelicaniform" taxa and two clades of "procellariiform" taxa. All these groups retain monophyly according to the traditional classification of orders suggesting that their inclusion within this expanded Ciconiiformes may not be justified. In addition, they all possess positive QS values, indicating that their monophyletic status is largely uncontradicted. In addition to "falconiform" monophyly, the supertree confirms polyphyly of Old and New World vultures. Cathartidae (New World vultures) are closely related to Ciconiidae (storks), and Accipitridae (Old World vultures) are placed within the traditional Falconiformes. Three controversial taxa within the Ciconiiformes are the Spheniscidae (penguins), Gaviidae (loons) and Podicipedidae (grebes). These taxa have been placed in widely differing positions in previous analyses. They have been considered to be closely related (Cracraft, 1985) and some analyses (Sibley and Ahlquist, 1990) have claimed that loons and penguins are related to each other, and to Procellariiformes, while grebes have no close living relatives. A more recent analysis (Van Tuinen *et al.,* 2001) showed that grebes may be related to flamingos. This issue is not resolved with the current analysis as, although the Podicipedidae appear to be related to the Charadriidae, both the Gaviidae and Spheniscidae are part of the large polytomy.

The pairing of Musophagiformes (turacos) with Coliiformes (mousebirds), and Trogoniformes (trogons) with the Gruiformes, is supported by Van Tuinen *et al.* (2000). In the supertree these taxa are placed as sister groups to the Passeriformes (perching birds). The Passeriformes are traditionally considered to be a monophyletic group that evolved more recently than most other avian lineages (Johansson *et al.,* 2001). Some recent molecular analyses, however, have placed the passerines at the base of the avian phylogenetic tree (Härlid *et al.,* 1998; Mindell *et al.,* 1999) and also as a paraphyletic group (Mindell *et al.,* 1999), but this has since been rejected (Garcia-Moreno *et al.,* 2003). This view is also not supported by the supertree analysis, which agrees with the traditional view that the Passeriformes diverged relatively late compared to many other orders. However, QS values for Passeriformes are, on average, lower than the tree average, indicating the presence of conflict within the source trees. Acanthisittidae (New Zealand wrens) are placed at the base of the Passeriformes. This is as suggested by many workers who have been unable to assign them to either the suboscines or the oscines (e.g. Lovette and Bermingham, 2000). All other passeriform taxa are split into the suboscines and oscines. The suboscines are divided into well supported (QS higher than tree average) Old and New World clades, the latter being further subdivided into tracheophone and non-tracheophone clades.

Menuridae (lyrebirds) occupy the basal-most position within the oscines as proposed by many workers (e.g. Ericson *et al.,* 2002). The majority of the remaining oscines are grouped into three clades. Although QS values are low for these clades, the relationships fit very well the model proposed by Christidis and Schodde (1991) where the Australo-Papuan songbirds (Sibley and Ahlquist's "Corvida") are clustered into two main assemblages representing two endemic radiations. One includes the honeyeaters and allies (Meliphagidae, Acanthizidae and Orthhonychidae); the other contains the corvoid birds. These groups are analogous to Sibley and Ahlquist's Meliphagoidea and Corvoidea. The remaining families comprise the Eurasian radiation (Sibley and Ahlquist's "Passerida"). The supertree supports this model, although the "Corvida" are part of a polytomy and may or may not prove to be monophyletic. The "Passerida", however, form a distinct monophyletic clade, as also found by Christidis and Schodde (1991). This pattern of relationships has been used to suggest a Gondwanan origin for the Passeriformes (Ericson *et al.,* 2002), although the supertree has been unable to resolve the three clades with respect to each other, and therefore, while not in opposition to this hypothesis, does not directly support it.

Within the Eurasian oscines, it is generally accepted that the nine-primaried oscines comprises two sister clades; one being the family Fringillidae and the other made up of the Emberizidae, Coerebidae, Parulidae and Icteridae (Klicka *et al.,* 2000). The supertree shows that while the second clade forms a monophyletic group, the Fringillidae are more closely associated with the Passeridae and Motacillidae, as suggested by Groth (1998). Groth suggested that the term "New World nine-primaried oscines" might be best restricted to the emberizids (Emberizidae, Coerebidae, Parulidae and Icteridae) alone, as the traditional monophyletic grouping is not supported. The supertree suggests that this view may well be correct. In addition to this the fringillids are primarily an Old World group, which supports their separation from the New World nine-primaried oscines (Groth, 1998).

1.4.2.1 Limitations

The above section provides a good general overview of avian phylogeny, however, there are many areas for potential improvement. There was no attempt at standardising the taxonomy and, as a result, the tree will almost certainly contain synonyms that should be dealt with. The method used was cumbersome and error-prone as the data were processed largely by hand. There was a loss of important data, such as the method used in the original study, and finally, it would be much more useful to carry out meaningful comparisons on a supertree constructed at species-level. The support measures used (QS values) are also flawed as the categories defined by Bininda-Emonds (2003) were not mutually exclusive, for example the definitions of equivocal and soft support both contain no hard matches or mismatches and both contain soft mismatches (Wilkinson *et al.,* 2005a). For this reason, QS values will not be utilised for the supertrees in this thesis.

Issues surrounding data independence are also important in supertree construction. This study used 124 source trees and every effort was made to ensure the quality of the data used. However, ideas differ as to what constitutes an acceptable source tree and since this study was carried out, Bininda-Emonds *et al.* (2004) have proposed a protocol for selecting suitable source trees.

1.5 This thesis

There are clear issues that affect the family-level supertree (Davis, 2003) as outlined above. This thesis aims to construct species-level supertrees of all avian and dinosaurian taxa. The main challenges for this are data collection and processing; that is ensuring that data are faithfully recorded from the source and processed in a consistent and logical manner with minimal errors. The methodology used in the family-level supertree (Davis, 2003) is not suitable for such an endeavour as that study relied on manual data processing, which will not be possible for a significantly larger dataset. In addition, new ideas on how to minimise the problems associated with supertree construction have arisen since that study. It is therefore the aim of this study to implement and test these and see what effect they have on supertree construction. The questions posed in this thesis are:

1. Can a protocol for constructing supertrees be developed that is both methodologically robust and easy to implement?

2. Does this protocol result in supertrees that are good representations of the source data?

3. Can a supertree of all Aves be constructed at species-level using this protocol?

4. Can community-based tree-building help speed up the process in finding shorter tree?

5. Do supertree methods compare favourably with trees found from supermatrix analyses? Which, if either, produces superior results?

6. Can a new, updated supertree of the Dinosauria shed light on dinosaur diversification throughout the Cretaceous?

1.6 Thesis summary

The next chapter looks into the input for supertree construction; the source tree. Here, new specimens of the fossil taxon *Primobucco mcgrewi* are described and primary character diagnosis is encoded. The new information gleaned from these fossils is used to construct a phylogenetic tree, which can be used as input for a supertree. The results of this have not been included in the supertree in this thesis as it has not yet been published and this would violate the protocol designed and described in Chapter 3. This chapter has been written as a paper for submission to *Neues Jahrbuch für Geologie und Paläontologie* in collaboration with G. J. Dyke of University College Dublin.

Chapter 3 deals with the construction of supertrees. A protocol, based on that of Bininda-Emonds *et al.* (2004), is proposed and tested using a relatively small monophyletic group; the Galliformes (landfowl).

Once a suitable protocol is defined, and tested, the avian supertree is constructed and described in Chapter 4. This tree includes both extant and extinct species and is an order of magnitude greater in terms of taxa number than previous studies – a step-change in supertree size.

Given that the supertree method has been criticised, a small test, again involving the Galliformes, between supertree and supermatrix methods has been carried out in Chapter 5. The two methods were used on the same data, using identical numbers of taxa.

Dinosaurs are widely considered to be the ancestors of Aves (Chiappe, 1995 and references therein), and as such it is interesting to consider a supertree of Dinosauria. The first dinosaur supertree was published in 2002 (Pisani *et al.,* 2002) and this chapter details an updated tree with the inclusion of additional new data and the use of a strict protocol, adapted for extinct taxa. The tree is then used to look at diversification of the Dinosauria and to test the hypothesis of a major "burst" in diversification during the Campanian and Maastrichtian (Fastovksy *et al.,* 2004). This work was co-authored with G. T. Lloyd (University of Bristol), D. Pisani (National University of Ireland, Maynooth), J. Tarver (University of Bristol), M. Ruta (University of Bristol), M. Sakamoto (University of Bristol), D. W. E. Hone

(Bayerischen Staatssammlung für Paläontologie und Geologie), R. Jennings (University of Bristol), and M. J. Benton (University of Bristol).

Finally, the thesis is concluded in Chapter 7, which brings together the previous chapters, provides answers to the questions posed above and offers suggestions for future work.

Chapter 2

Two new specimens of *Primobucco* (Aves: Coraciiformes) from the Eocene of North America

2.1 Abstract

The Primobucconidae are fossil birds known from the Eocene of North America and Europe. This paper describes two new partial specimens from the Green River Formation of Wyoming (USA). Both specimens were assigned to the species *Primobucco mcgrewi*. Although incomplete, these specimens have preserved anatomical features not seen in other material and therefore add to our knowledge of these extinct birds. The two specimens were added to the large morphological matrix of Mayr and Clarke (2004) in an attempt to further constrain their phylogenetic position. The results of the analysis were inconclusive, showing only that the Primobucconidae appear to belong in a clade containing the extant Coraciiformes and related taxa. The new characters provided by these new specimens do, however, provide a wealth of new information and will surely prove invaluable in future analyses of these fossil birds.

2.2 Introduction

The Primobucconidae comprise a clade of fossil birds thought to be related to extant rollers (Mayr *et al.*, 2003), Coraciiformes. They are known from the Eocene of North America and Europe – fossil material has been described from the Lower Eocene Green River Formation of North America (Brodkorb, 1970; Houde and Olson, 1989; Mayr *et al.,* 2004), the Lower Eocene of France (Mayr *et al.,* 2004), and the Lower-Middle Eocene of Messel, Germany (Mayr *et al.,* 2004). However, in spite of recent discoveries, including some complete but crushed skeletons (Mayr *et al.,* 2004), their systematic position still remains somewhat uncertain (Mayr *et al.,* 2004).

The earliest described specimen of Primobucconidae, the holotype of *Primobucco mcgrewi*, was discovered in the Green River Formation (Brodkorb, 1970) and described based on an incomplete right wing. More recently, new specimens have been allocated to *Primobucco*, including two new species; *P. perneri* and *P. frugiligeus* (Mayr *et al.,* 2004). These specimens were incorporated into a cladistic analysis of morphological characters by Mayr *et al.* (2004) who considered Primobucconidae to occupy an unresolved basal position within Coraciiformes (*sensu* Mayr, 1998; see Mayr *et al.,* 2004: figure 6).

In this paper, we augment the known composition of Primobucconidae by describing two new specimens of *Primobucco mcgrewi* also from the Green River Formation of Wyoming (USA) (Figure 2.1). These specimens, although incomplete, add new anatomical features not seen in previously described material.

Abbreviation: FMNH, Field Museum, Chicago.

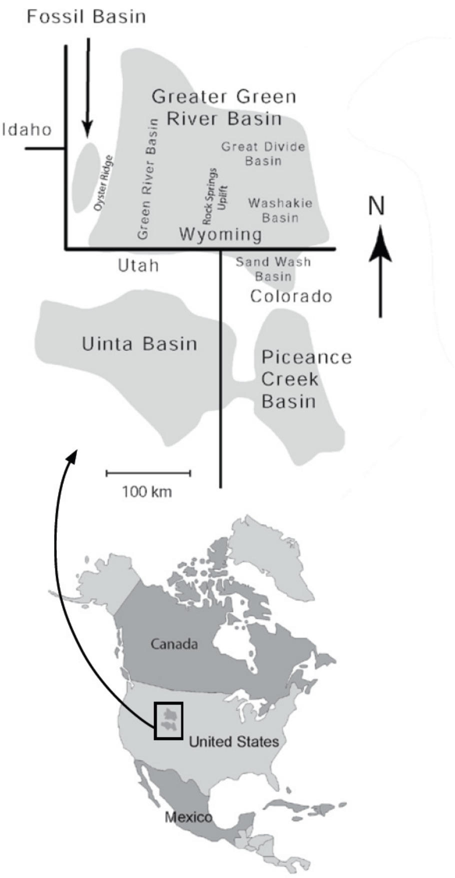

Figure 2.1: Map of the Green River Formation. From Buchheim and Eugster (1998).

2.3 Systematic palaeontology

Anatomical terminology used here follows Howard (1980) and Baumel (1979).

Order	Coraciiformes *sensu stricto* (see Mayr, 1998)
Family	Primobucconidae Feduccia and Martin, 1976
Genus	*Primobucco* Brodkorb, 1970

Species of *Primobucco* are all similar in their morphology and have been distinguished from one another based on differences in their limb proportions and overall size (Mayr *et al.,* 2004). Because of the compressed nature of many specimens, other osteological features have yet to be identified. These new specimens are therefore assigned to *P. mcgrewi* on the basis of limb measurements and ratios (see Table 2.1 for measurements and Figure 2.3) and inferences from modern rollers.

Primobucco mcgrewi Brodkorb, 1970

2.3.1 Original material

The holotype, UWGM 3299, consists of a right wing (Brodkorb, 1970).

2.3.2 Referred specimens

FMNH PA 611, slab containing right and left forelimbs, sternum and shoulder girdle (Figure 2.2 – top). The right wing is almost complete comprising the humerus, radius, ulna, carpometacarpus, phalanx digiti majoris and phalanx digiti minoris. The left wing is less complete; the humerus, radius, ulna, proximal end of the carpometacarpus and the phalanx digiti alulare are present. The sternum and incomplete disarticulated shoulder girdle are present consisting of both coracoids and a partial scapula. FMNH PA 345 a/b (part and counterpart), slab containing well-preserved forelimbs, sternum and shoulder girdle (Figure 2.2 – bottom). In this specimen, the right wing comprises the humerus, radius, ulna and the proximal carpometacarpus and the left comprises the proximal humerus and distal radius and ulna. The sternum is present with five costal processes preserved on its right side. The incomplete shoulder girdle includes the left and right coracoids.

2.3.3 Dimensions

Table 2.1: Comparison of limb dimensions of new specimens FMNH PA 611 and FMNH 345 a/b to other specimens of *Primobucco.* All measurements are in millimetres.

	Humerus (R/L)	Ulna (R/L)	Carpometacarpus (R/L)
Primobucco mcgrewi Brodkorb, 1970			
Holotype (after Brodkorb, 1970)	26.7/-	~34.2/-	~14.2/-
USNM 336284 (after Mayr *et al.*, 2004)	~27/~28	~32.5/~33	-/15.3
UWGM 14563 (after Mayr *et al.*, 2004)	-/26.8	-/33.8	-/15.7
FMNH PA 611	30.8/29.7	39.6/39.6	17.6/-
FMNH PA 345 a/b	27.5/-	35.2/-	-/-
Primobucco perneri Mayr *et al.* 2004			
Holotype (after Mayr *et al.*, 2004)	~29.3/~29.3	~36.3/36.0	15.4/15.1
SMF-ME 3793 (after Mayr *et al.*, 2004)	-/~25.8	-	-/~15.0
SMF-ME 516 (after Mayr *et al.*, 2004)	~25.2/~26.5	-/~32.0	15.0/15.0
SMF-ME 3546 (after Mayr *et al.*, 2004)	~28.6/~28.9	-/~34.0	-/~17.1
Primobucco frugilegus Mayr *et al.* 2004			
Holotype (after Mayr *et al.*, 2004)	~31.5/-	~37.8/-	18.7/-
SMF-ME 3794 (after Mayr *et al.*, 2004)	~32.7/~32.7	-/~38.4	~19.4/-

2.3.4 Collection history

Both FMNH PA 611 and FMNH PA 345 were collected from the Fossil Butte Member of the Green River Formation, Lincoln County, Wyoming (USA). FMNH PA 611 was collected by T. Lindgren and the Green River Geological Labs in 1990 while FMNH PA 345 was collected by J. E. Tynsky in 1983.

Figure 2.2. New specimens of *Primobucco mcgrewi*. Top – specimen A, bottom – specimen B.

2.3.5 Description

The Primobucconidae are small birds and both the specimens reported here have a wingspan of approximately 21 cm (see Table 2.1 for dimensions of individual elements).

The coracoid is long and thin with a broad distal end. The processus procoracoideus is short, but not abbreviate – it projects as far as the acrocoracoideus. The extremitas omalis is elongate and the processus lateralis of the extremitas sternalis is narrow. There is no notch on the medial margin of the sternal end. The processus lateralis is hooked cranially and the facies articularis sternalis located primarily on the dorsal surface.

The scapula is long and blade-like; the distal end is not preserved. The acromion is not bifurcate and has no distinct medial process. The extremitas caudalis is markedly hooked and deflected away from the plane of the bone.

The sternum is short and broad; being slightly longer than it is wide, there are four deep notches in the caudal end. Both pairs of incisions are very deep; the lateral ones are deeper than the medial ones, reaching to approximately half the length of the corpus sterni. The processus craniolaterales are long and prominent. The sternal keel is long and extends for most of the length of the corpus sterni. The spina externa is present and well-developed.

The humerus is elongate and slightly curved, its head is large, inflected medially and is short and broad. The distal border of the head merges into the shaft indistinctly; the entire caput humeri is medial to the inner border of the shaft. A small tuberculum dorsale is present and the crista deltopectoralis is short and protruding. The crista bicipitalis is shorter than the crista deltopectoralis and gently curved.

The ulna has an elongate, slightly curved shaft and distinctly exceeds the humerus in length (Table 2.1). The olecranon is long and well developed. The condylus dorsalis ulnae and the condylus ventralis ulnae are well developed with a marked sulcus intercondylaris. Papillae remigales are not visible.

The carpometacarpus is approximately half as long as the radius and is slender. The metacarpals are of equal length; the os metacarpale minus and the os metacarpale majus are straight. The spatium intermetacarpale is very narrow and the processus intermetacarpalis is very small. The proximal end of the os metacarpale minus bears a ventrally protruding projection, while the os metacarpale alulare is short and broad and its processus extensorius is large and protrudes cranially. The symphysis metacarpalis distalis is wide, the processus pisiformis is marked and the fovea carpalis cranialis is shallow. The phalanx proximalis digiti majoris is long and broad and lacks a large proximally directed process on the ventral side. The phalanx digiti alulae is also long and does not appear to possess a claw, in contrast to observations made by Mayr *et al.* (2004).

2.3.6 Ratios/measurements

The mean lengths of the humerus, ulna and carpometacarpus of each specimen in Table 2.1 were plotted to aid allocation of the new fossils to one of the *Primobucco* species. The graphs (Figure 2.3) show that there is a size distinction between the European species *P. frugilegus* and *P. perneri*, with the North American *P. mcgrewi* plotting at the lower end of the *P. perneri* range. For our new specimens FMNH PA 345 could only be plotted for humerus/ulna ratio and plotted in the same area as *P. mcgrewi*/*P. perneri*. FMNH PA 611 was a much larger specimen and plotted with *P. frugilegus* for all three sets of measurements.

Europe and North American have distinct avian faunas (Böhning-Gaese *et al.,* 1998). Based on our knowledge of modern avian faunal distribution and the absence of migratory behaviour in modern rollers it seems unlikely that *P. frugilegus* would have been present in both Europe and North America or to have been migratory between the two geographic regions. Specimen FMNH PA 345 plots well within the *P. mcgrewi* range and it is reasonable, given the above, to conclude that specimen FMNH PA 611 is simply a larger specimen of *P. mcgrewi* than those previously known. There is no other evidence to suggest that the latter specimen requires a new species designation and therefore we assign both specimens to *P. mcgrewi.*

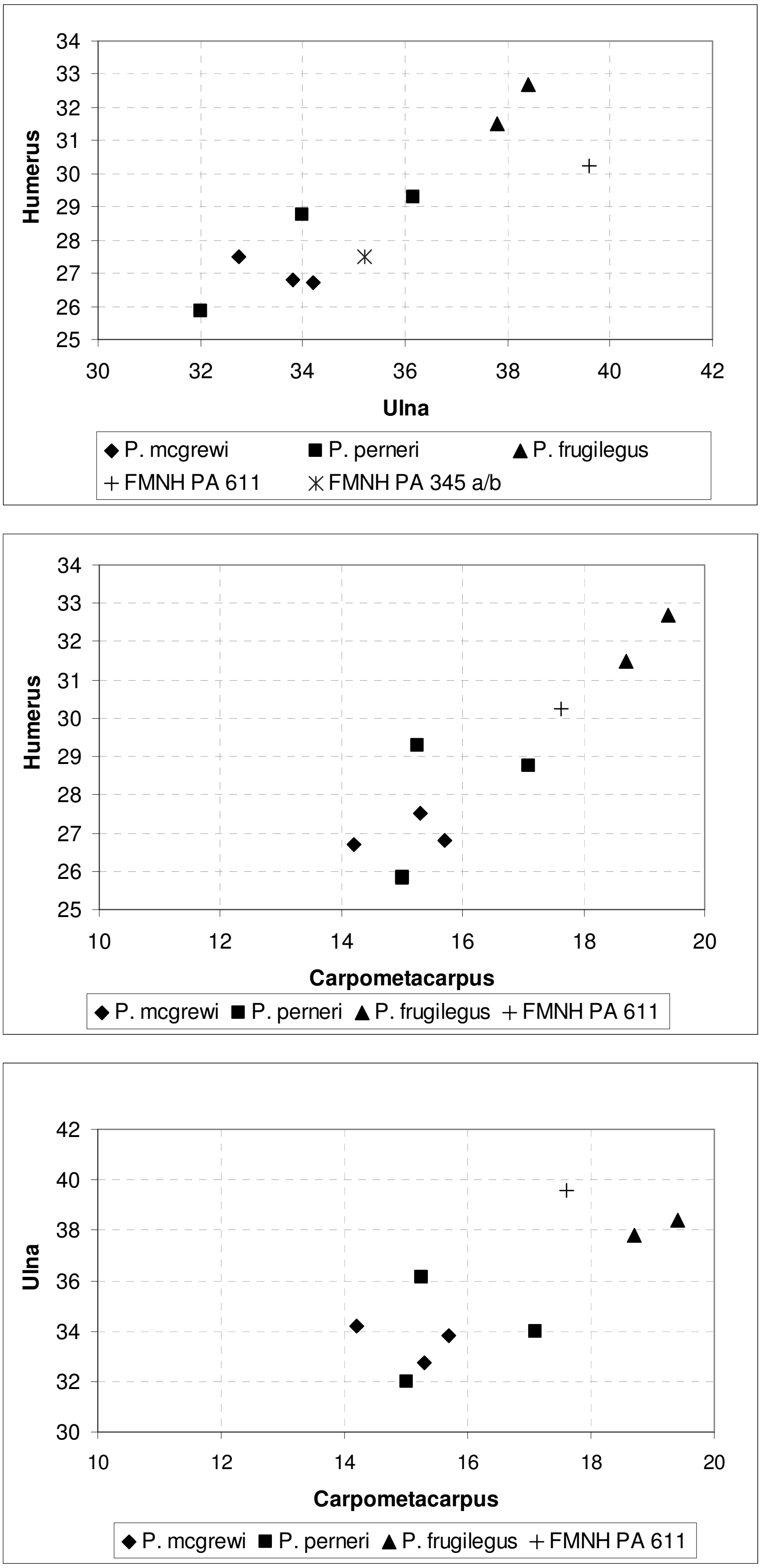

Figure 2.3: Biometric graphs showing mean limb ratios for species of *Primobucco*. All measurements are in mm and are taken from Table 2.1.

2.4 Phylogenetic Analysis

The Primobucconidae have been considered to be closely related to either the Galbulae (Brodkorb, 1970) or the rollers (Houde and Olson, 1989). More recently, Mayr *et al.* (2003) placed the Primobucconidae as sister taxon to the extant and fossil rollers (Coraciidae). However, this study was limited, with only 16 taxa and 36 characters examined. New character information from these new specimens of Primobucco, together with data from the matrix supplied by Mayr *et al*. (2004), were added to the anatomical matrix of Mayr and Clarke (2003) in an attempt to place the Primobucconidae in a wider context. This matrix contains 47 taxa and 148 characters.

The matrix (Appendix E) was analysed following Mayr and Clarke's (2003) methodology. As in their analysis three vertebral and sternal characters (55, 71 and 91) were ordered. The data matrix was analysed using PAUP* 4.0b10 (Swofford, 2002) using maximum parsimony. One thousand replicates of random stepwise addition (branch swapping: tree-bisection-reconnection) were carried out retaining only one tree at each step. A maximum of 10 trees one step longer than the shortest were retained in each replicate. Branches were collapsed to create soft polytomies if the minimum branch length was equal to zero.

2.5 Results

Analysis of the matrix resulted in 18 MPTs of length 721 (CI = 0.227, RI = 0.478, RC = 0.109). The strict consensus tree is shown in Figure 2.4. In the strict consensus the Primobucconidae are placed in a large polytomy at the base of the Neognathae minus Galloanserae. This unresolved position does not negate Mayr *et al.'s* (2004) conclusions drawn from their limited dataset, however it does not lend further support either. It is noticeable too that the tree produced by this study is significantly less well resolved than that of Mayr *et al.* (2004). The Adams consensus tree (Figure 2.5) shows that the Primobucconidae are "floating" in a clade that includes the Coraciidae but cannot resolve the relationships any further.

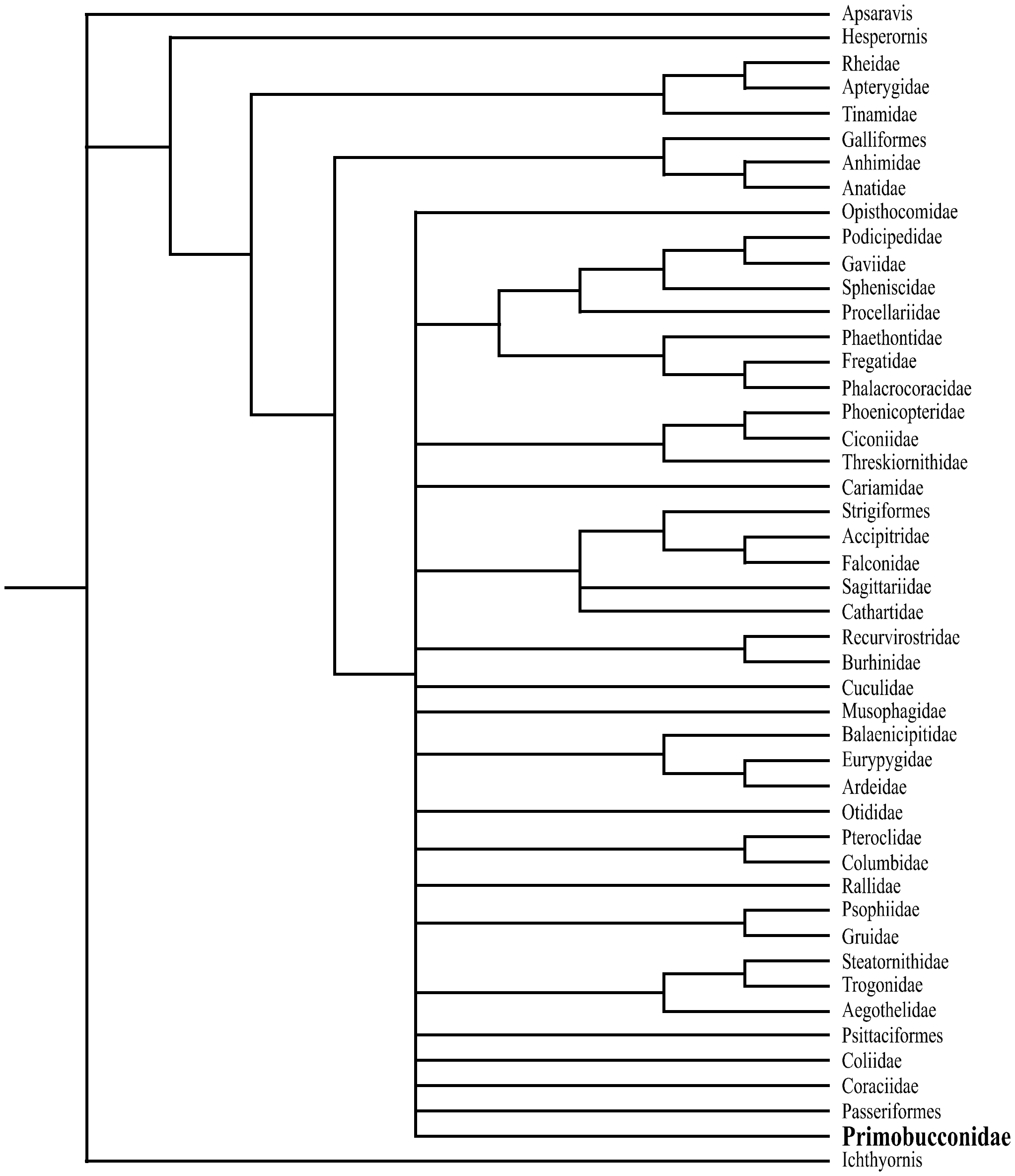

Figure 2.4: Strict consensus of the 18 most parsimonious trees resulting from analysis of the matrix in Appendix E (length = 721, CI = 0.227, RI = 0.478, RC = 0.109).

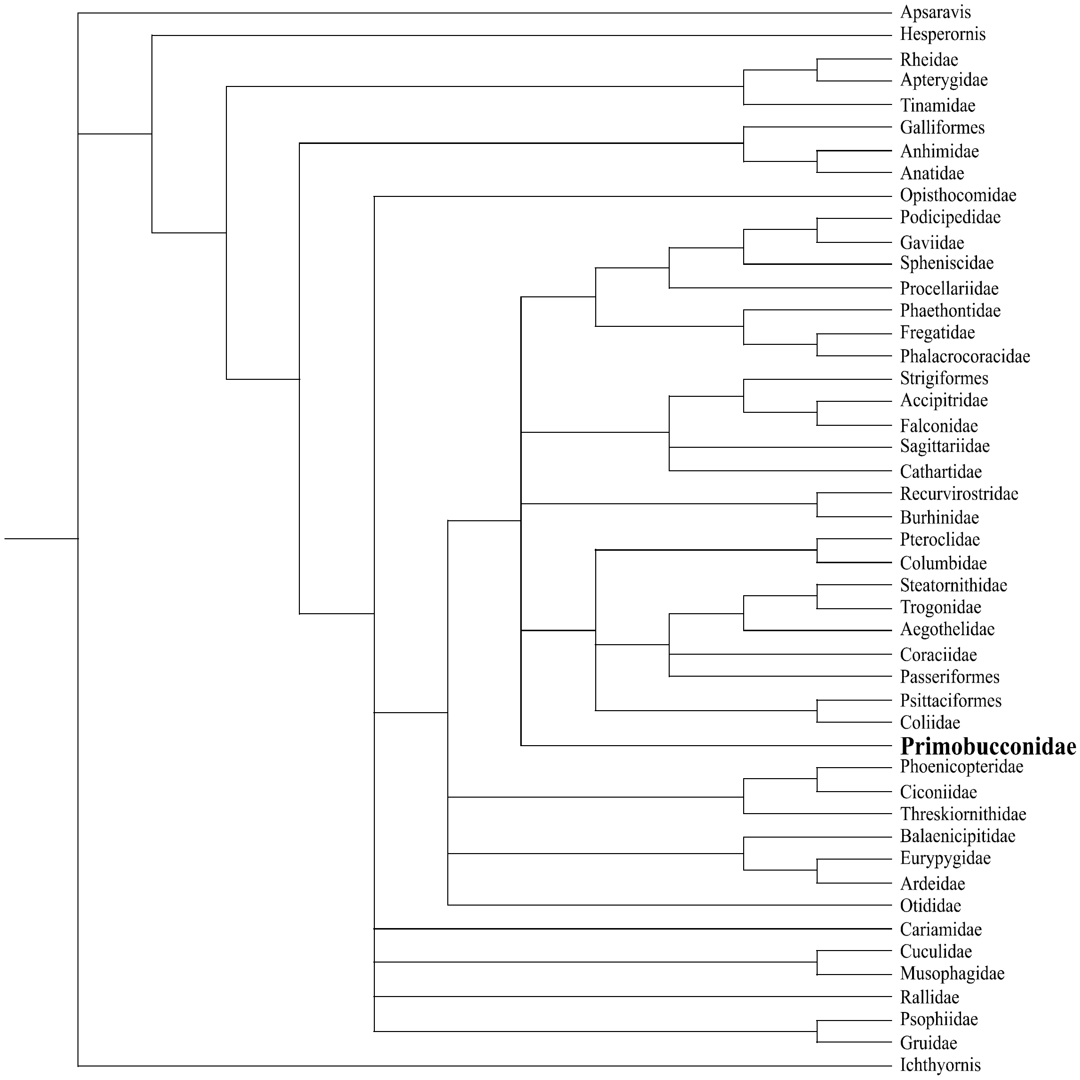

Figure 2.5: Adams consensus of the 18 most parsimonious trees resulting from analysis of the matrix in Appendix E (length = 721, CI = 0.227, RI = 0.478, RC = 0.109).

2.6 Discussion

Primobucco mcgrewi was first described by Brodkorb (1970) when it was placed in the family Bucconidae (puffbirds). The specimen consisted of only an incomplete right wing; therefore the description was necessarily limited. Feduccia and Martin (1976) created a new family, the Primobucconidae, and placed *P. mcgrewi* in this group, along with a number of other fossil birds. They considered the Primobucconidae to belong in the Piciformes and, within this, most closely related to the Bucconidae. More recently, Feduccia and Martin's "Primobucconidae" has been shown to be a polyphyletic assemblage including stem-group mousebirds (Houde and Olson, 1992; Mayr and Peters, 1998) and parrots (Mayr, 1998; Mayr, 2002). The only taxon originally placed in this family that remains there is *P. mcgrewi*, which, at the time, consisted of only the holotype (Brodkorb, 1970). Houde and Olson (1989) were the first to suggest that *P. mcgrewi* may belong with roller-like birds (Coraciiformes) and that other birds from the Green River Formation most closely resembled *P. mcgrewi* in morphology. Most recently, Mayr *et al.* (2004) have identified new specimens of *P. mcgrewi* and diagnosed two new species belonging to the Primobucconidae; *P. perneri* and *P. frugiligeus*. Their study described complete skeletons and conducted a cladistic analysis of the Primobucconidae. The analysis supports Houde and Olson's (1989) suggestion of the inclusion of Primobucconidae within the Coraciiformes. Mayr *et al.* (2004) identified two supporting characters, one of which is also present in the new specimens described here ("carpometacarpus, os metacarpale minus with ventrally protruding projection on ventral side of proximal end"). The other character concerns the tarsometatarsus and is not preserved in our specimens. Mayr *et al.'s* (2004) analysis was unable to provide any resolution on the position of Primobucconidae within the Coraciiformes. The dataset used contained a relatively limited number of only 36 characters. Of these, a large proportion were concerned with the morphology of the skull and legs. The new specimens have enabled detailed descriptions of the shoulder girdle and wing morphology, which were lacking in Mayr *et al.'s* (2004) analysis. The specimens described here provide detailed descriptions and hence many cladistic characters that help fill the gap in our knowledge of this part of the anatomy of *Primobucco*. Despite not adding to our knowledge of the relationships of the Primobucconidae at this present time these new characters may eventually help us to elucidate relationships of this extinct taxon with the help of further new discoveries.

As Primobucconidae have been described from the Eocene of both North America and Europe (Mayr *et al.,* 2004), while extant rollers have a distribution limited to the Old World, the confirmation of the affinities of the Primobucconidae is likely to have an impact on our understanding of the origins and evolutionary histories of extant taxa.

Chapter 3

Supertrees of Galliformes: A test case for a supertree-building protocol

3.1 Abstract

This chapter extends previous work by other authors on arriving at a robust protocol for determining good quality input data for supertree analyses. This mostly involves looking at issues surrounding source tree independence and data integrity. Two methods of combining non-independent source trees are assessed in an attempt to identify the most appropriate method of dealing with duplicated data. The order Galliformes was chosen as a test case due to the comparatively small number of taxa, making it suitable for detailed analysis on a relatively short timescale, and well-documented monophyly of the group. The results of this study produced a robust protocol for collecting, storing and processing data ready for inclusion in a supertree analysis. Both methods produced reasonable supertrees that represent current views on galliform phylogeny, however, it was found that combining non-independent source trees via a “mini-supertree” analysis produced results more consistent with the input source data and, in addition, significantly reduced computational load.

3.2 Introduction

Criticisms of supertrees have arisen for a variety of reasons, both practical and philosophical. Data quality is the main practical issue (Gatesy *et al.,* 2004) and is the main consideration of this chapter (see Chapter 1 for a full discussion of criticisms of supertrees in general) as the results can only be as good as the input data. In particular, a perceived, yet untested, problem with supertree analyses according to critics is the occurrence of weak, or poorly justified, data being included in supertree analyses (Gatesy *et al.,* 2004) for example the inclusion of duplicated datasets which are non-independent. An example of between study non-independence would be the re-using of the same character set by several different authors in different publications. Within study non-independence can arise due to the production of several estimates of phylogeny using the same data, for example due to the use of a number of different tree-building methods, a well-known case being the placental mammal supertree of Liu *et al.* (2001) which contained a single transferrin immunology data set for bats that was incorporated into five different source trees. The outcome of including this dataset five times is that the immunology dataset is then effectively up-weighted by a factor of five. Further criticisms arise from the inclusion of source trees that can be considered to be appeals to authority (Gatesy *et al.,* 2002). For example: source trees in which monophyly has been assumed and the topology accordingly constrained, source trees constructed from composite trees pieced together from previously published results, and source trees constructed from reviews of previous studies could all be classified as appeals to authority (Gatesy *et al.,* 2002). Other criticisms are based on the potential for bias in the results dependent upon source tree properties. Wilkinson *et al.* (2005b) proposed that unbalanced trees are more likely to be represented in a supertree than their balanced counterparts when using standard MRP (Matrix Representation with Parsimony). Size has also been suggested to have an influence (Bininda-Emonds *et al.,* 1999) and it is thought that larger source trees may "swamp" the dataset and therefore have a stronger influence on the resulting supertree than smaller source trees.

This chapter carries out a test study on a small group with well-documented monophyly, the Galliformes, in order to develop a protocol for selecting source trees. The approach is based on that designed by Bininda-Emonds *et al.* (2004), but resolves some of the issues with their protocol. The protocol developed here is subsequently used to construct the Aves supertree and a modified version is used to construct the Dinosauria supertree (Chapters 4 and 6 respectively).

3.3 Current Supertree Building Protocol

Many previous supertree studies have been rather *ad hoc* when it comes to data quality issues (e.g. Salamin *et al.,* 2002; Davies *et al.,* 2004; Thomas *et al.,* 2004). Some authors have made attempts to minimise data duplication and other data issues. Ruta *et al.* (2003) in their supertree of early tetrapods evidently recognised the problems caused by duplicated data as they ran two separate analyses in an attempt to remove some non-independent data. Their first analysis included all collected source trees, while the second removed any that were superseded by subsequent analyses of similar datasets. Jones *et al.* (2002) also made an attempt by applying differential weighting to source trees in their bat supertree. These are clear attempts to improve source data quality but were not implemented in a rigorous manner. Bininda-Emonds *et al.* (2004) have been the first to propose a stringent protocol in an attempt to minimise data quality issues and to standardise supertree construction.

Bininda-Emonds *et al.'s* (2004) protocol was designed to deal with the data independence and quality issue, but as yet remains untested. It was used as a basis for a supertree of the Cetartiodactylia (Price *et al.,* 2005) and the results were tested against a supermatrix, but the protocol itself was not tested in any way. Furthermore, Price *et al.* (2005) allowed the inclusion of informal phylogenies and two taxonomies. Therefore it was decided that before attempting a species-level supertree for all Aves, a strict protocol would be designed and tested. This protocol is based on that by Bininda-Emonds *et al.* (2004), but extends it and improves the practical aspects of it. In particular, although their protocol contains sensible ideas for source tree selection these are not backed up by any suggestions for implementation. As supertree analyses often contain large volumes of data some of the protocol stages are not easy to implement by hand or by eye and if attempted manually would likely be highly error-prone.

The following section gives a brief summary of the protocol of Bininda-Emonds *et al.* (2004) followed by the description of a revised and extended protocol intended for use in constructing a supertree of all Aves and tested here on the order Galliformes.

3.3.1 Summary of current protocol

Bininda-Emonds *et al.* (2004) identified the following factors to be considered:

1) Source tree independence

Possibly the single most important issue is concerned with the non-independence of data either between or within studies. An example of between study non-independence could be the re-using of the same character set by several different authors in different publications. Within study non-independence can arise due to the production of several estimates of phylogeny for the same data, e.g. due to the use of a number of different tree-building methods.

Also important here is the definition of "independent" source trees. Bininda-Emonds *et al.* (2004) define "independent" based on both the character data and taxa set.

Data considered independent:

- Non-overlapping datasets (e.g. different genes).
- Trees for non-overlapping taxa sets.
- Unique combinations of genes.

Data not considered independent:

- Trees derived from the same set of characters with the same taxa or where one taxa set is a subset of the other.
- Different portions of the same gene.

Figure 3.1 summarises Bininda-Emonds *et al.* (2004) suggestions on recognising independent source trees and how to deal with non-independence. Any sets of source trees that remain non-independent after processing can be combined by creating a "mini-supertree" to produce a summary of non-independent data, rendering it independent. These non-independent trees can therefore be represented in this way by a single independent source tree. This then removes any unnecessary up-weighting of source data. These "rules" have been challenged by other authors (Gatesy *et al.,* 2004), who point out that there is still a lot of scope for character duplication. However, Bininda-Emonds (2004) does not consider this to be problematic as "duplication can occur at this level and still result in independent phylogenetic hypotheses because a phylogenetic tree is composed of more than the data going into it".

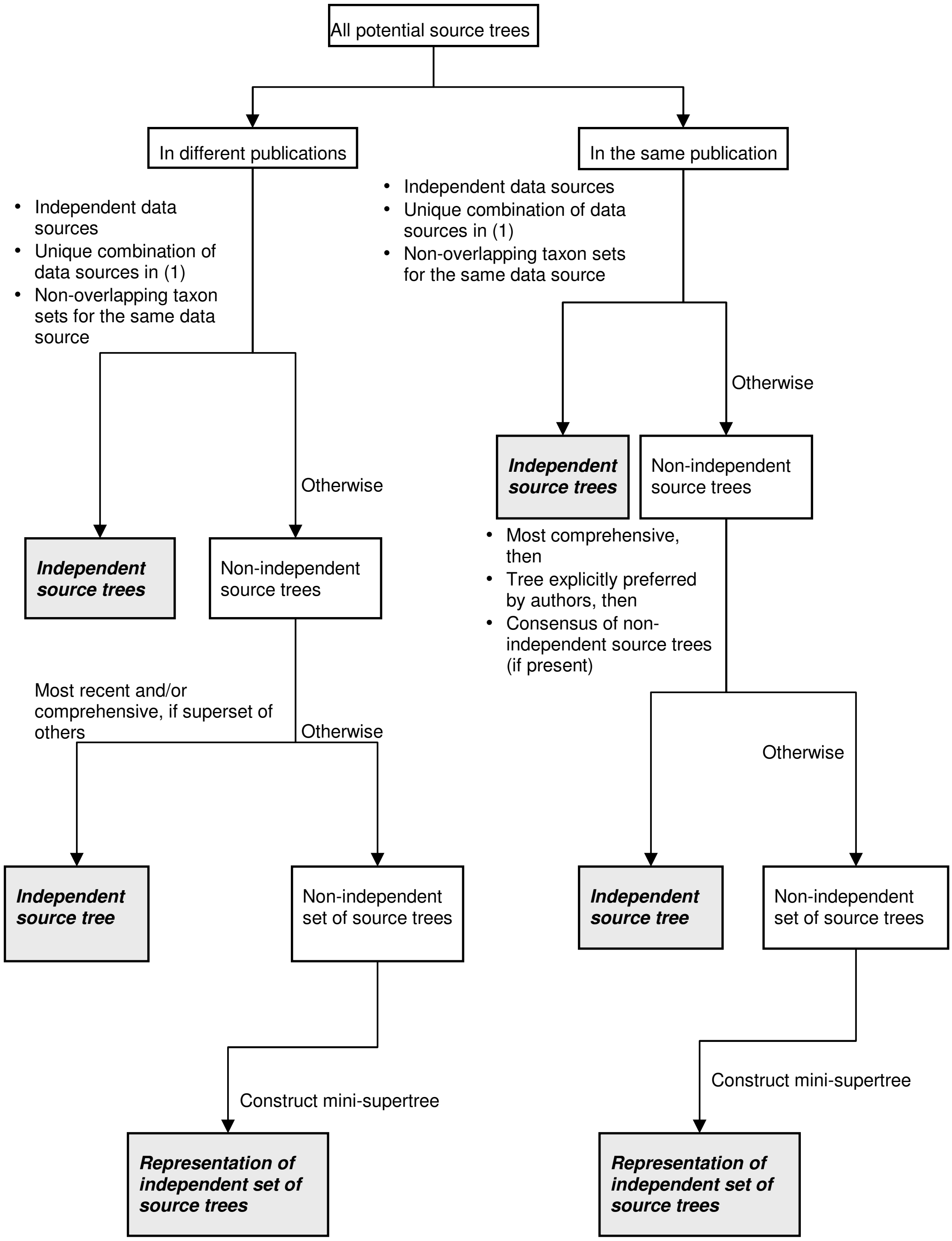

Figure 3.1: Summary of protocol for selecting source trees. After Bininda-Emonds *et al.* (2004).

2) Standardisation of terminal taxa

Terminal taxa must be comparable throughout the source data and therefore should be standardised before undertaking a supertree analysis. Problems arise when taxa are not standardised as synonyms artificially inflate taxon numbers and potentially mask phylogenetic signal.

Bininda-Emonds *et al.* (2004) do use a script for automatic standardisation of terminal taxa – synonoTree.pl – however, it appears to work via a user-input list of names and is therefore still manually labour intensive and potentially error-prone as it will not pick up any synonyms or misspellings not already known to the user.

2.1) Combination of trees at different taxonomic levels

Taxa at different taxonomic levels must be incorporated into the tree in order to retain as much phylogenetic information as possible. However, it is important to standardise these taxa to a comparable taxonomic level in order to retain as much of the phylogenetic signal as possible. It is meaningless, for example, to include the taxon "Passeriformes" alongside members of that order as the software used to construct the supertree does not intrinsically "know" which taxa belong within that order. In the case whereby a higher-level name is to be used in supertree construction, Bininda-Emonds *et al.* (2004) recommend that all constituent lower-level taxa take on that name, although this approach does make an assumption regarding the monophyly of the higher-level taxon. When wishing to use lower-level names for supertree construction, Bininda-Emonds *et al.'s* (2004) first suggestion for dealing with higher taxa is to identify the actual taxa examined in the source study. This is evidently the desired solution; however this approach is not always feasible. Where it is not possible two potential solutions are suggested. The first is to assume monophyly of the higher taxon and to create an extra node consisting of all its constituent taxa. They acknowledge that this approach will artificially elevate support for monophyly of the higher taxon and, as such, this support is derived from an appeal to authority rather than from genuine evidence of monophyly. Their preferred option is to identify the type species of the higher taxon and use this as a substitute, suggesting that this makes fewer assumptions of monophyly and therefore potentially influences the resultant supertree topology to a lesser extent.

2.2) Accommodation of paraphyletic taxa

There are two instances in which paraphyletic taxa may present a problem. The first is the case of genuine paraphyly, whereby a taxon does not represent a monophyletic grouping. The second is where taxonomy has been standardised (see above – section 2.1) and two taxa, which were not in the original tree, considered to be each other's closest relatives, become a single paraphyletic taxon in the standardised tree.

Both types of paraphyletic taxa need to be dealt with before inclusion in a supertree analysis as more than one node cannot have the same label within a tree, however both types of paraphyly can be dealt with in the same way.

Bininda-Emonds *et al.* (2004) recommended dealing with this scenario in one of two ways. Either a) where one of the paraphyletic taxa represents the type species this is taken as the reference species, or b) if this is not possible the position should be considered as uncertain and each source tree can be viewed as a number of different trees in which all the possible positions of the paraphyletic taxon are represented. These multiple source trees can then be dealt with in the same way as any other set of non-independent trees (Figure 3.2).

3) Source tree collection and selection

Bininda-Emonds *et al.* (2004) also point out the importance of careful source tree selection. They consider that only source trees based on original analyses should be considered valid and therefore collected. Any duplicated source trees as a result of secondary analyses should not be added to the dataset. They also suggest that it can be appropriate to include taxonomies in a supertree analysis but not other supertree analyses. In addition they recommend that only published source trees from reputable sources are collected.

Finally they state that all source trees to be included in an analysis should be collected as they appear in the source publication and thereafter modified to suit the particular supertree analysis to be performed.

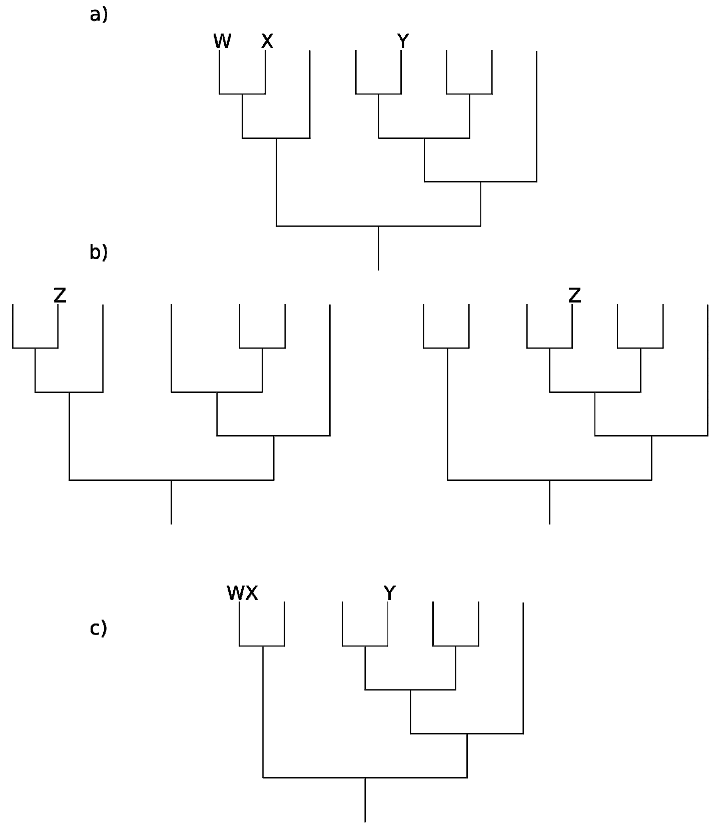

Figure 3.2: X and Y are the same species "Z", which renders Z paraphyletic in tree (a). One solution is to prune each of the source species to produce a set of source trees reflecting the uncertain position of Z (b). If two or more source species of Z form a monophyletic clade (W and X in tree (a)), this clade can be collapsed to a single terminal (c). After Bininda-Emonds *et al.* (2004).

3.4 Methods

The following proposed protocol is based on the above-described by Bininda-Emonds *et al.* (2004) but with a number of additional steps and methods of practical implementation. The data processing was split into individual stages, each of which dealt with a single issue. The stages were:

1. Data collection and entry (section 3.4.1).
2. Source tree independence (section 3.4.2).
3. Standardisation of terminal taxa (section 3.4.3).
4. Combination of trees at different taxonomic levels (section 3.4.4).
5. Accommodation of paraphyletic taxa (section 3.4.5).

6. Data integrity check (section 3.4.6).
7. Check adequate overlap of source trees (section 3.4.7).
8. Matrix creation (section 3.4.8).

With all these steps completed, the data will be in a state such that it is ready to be input into a supertree analysis. This protocol will also then be used to create a species-level supertree of Aves.

The main unanswered question is whether it is best to deal with non-independent source trees via combination into a "mini-supertree" ("method A" as suggested by Bininda-Emonds *et al.,* 2004) or by the appropriate weighting of source trees to avoid unintentional "up-weighting" of non-independent trees ("method B"). This question will be investigated and resolved as a part of this chapter (section 3.4.2).

3.4.1 Data collection and entry

Potential source trees were identified initially from online resources. The Web of Science[1], Science Citation Index was searched; covering the years 1981 to 2005. Papers potentially containing trees were examined. The reference lists within these papers were then searched for papers containing trees. All papers containing trees were retained and this process was continued until as many trees as possible were found. Papers were collected up to the end of December 2005 as at that point data processing commenced. A total of 589 papers were collected for the large Aves dataset that were deemed to contain potentially useful source trees, of these 39 were suitable for inclusion in this small test study. The majority of the relevant source trees were collected, but there is a great wealth of information regarding avian phylogeny and it is always possible that some have been missed. Reasons for source tree exclusion included the lack of cladistic methodology, i.e. trees drawn by hand or inferred from a taxonomy, use of a non-original tree, the use of a summary tree created from previous trees, and source tree non-independence. Bininda-Emonds *et al.* (2004) consider that it can be appropriate to include taxonomies and informal phylogenies in supertree analyses, and indeed have done so (e.g. in Price *et al.,*

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[1] http://wok.mimas.ac.uk

2005), however it was decided that as they are only summaries of phylogenetic knowledge, and therefore not derived from primary sources, that it would not be appropriate to include them in this analysis.

Diligent data entry and recording is of utmost importance as it ensures that all steps of data processing remain completely transparent. It also allows for easy identification of errors as all changes to the original data can be recorded during data processing. Crucially, when done in a consistent and sensible manner, it also leaves an audit trail for other researchers to enable further updates to the tree in future.

Data entry proceeded by converting each source tree into a Nexus format tree file (using the software TreeView 1.6.6, Page, 1996). In addition to this, each tree was accompanied by a XML file containing metadata about each source tree, such as source information, i.e. authors, journal, year etc., included taxa, and character information. This was to ensure that no information about the source data was lost during processing and ensures a consistent standard of data collection throughout. This format was chosen, rather than simply creating a document in Word or Excel, as it is very easy to extract trees required for any specific analysis, i.e. morphological or molecular data only or extant taxa only, by parsing the XML. A Java tool, which is available online[2] (Hill, pers. com.), was used to facilitate ease of data entry and ensure consistency of the XML files (see Figure 3.3). New data can also be easily added, an important factor as new phylogenies are constantly being published. It would even be possible to add other types of information if required at a later stage. The structure would also allow other workers to reconstruct exactly the steps taken here, or to investigate other possibilities, for example by only selecting data that are based on morphology. In addition, these files were later used to allow checking of data independence, substitution of higher taxa and gathering various statistics on the data by the use of various Perl scripts (see Appendix F).

The input data for the supertree essentially consist of tree files in Nexus format, which contain the taxa and phylogenetic relationship of the input tree. These are essentially all that is needed to construct a supertree. However, as discussed above,

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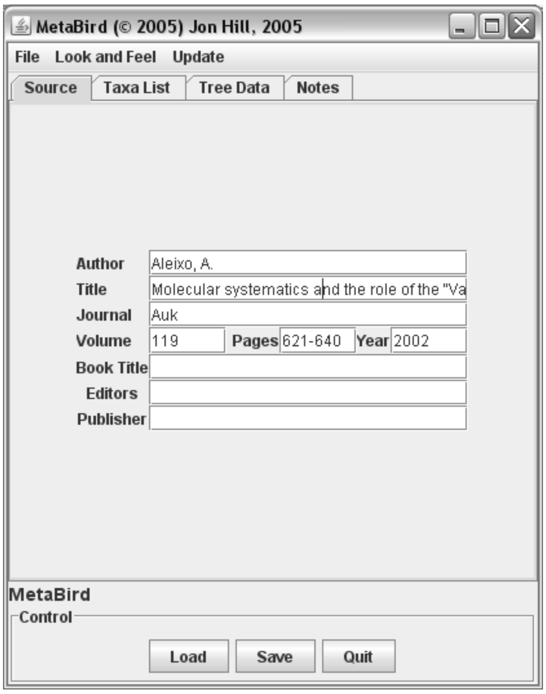
[2] http://www2.epcc.ed.ac.uk/~jon/

useful metadata can also be stored alongside these trees in the form of XML files. In order to organise the data, each paper that contained one or more source trees had a corresponding folder created which was labelled in the form of Author_Author2_Year. If more than two authors were listed, "etal" was used for Author2. Within each of these author folders, a further folder was created for each tree within the paper. The tree file and an accompanying XML file were then created within these folders. The result is a nested set of folders that have a predictable name and contain all data necessary to both construct a supertree and process the data further. This method proved much more efficient than that utilised in a previous project (Davis, 2003) which involved inputting trees by hand into Excel – a much more cumbersome and error-prone method.



Author: Aleixo, A.
Title: Molecular systematics and the role of the "Va
Journal: Auk
Volume: 119
Pages: 621-640
Year: 2002
Book Title:
Editors:
Publisher:

Figure 3.3: Screenshot of BirdXML; a Java client for easily creating the XML files.

All stages of source tree processing were retained in order to provide transparency should it be necessary to see what steps were carried out at an earlier stage.

3.4.2 Source tree independence

By and large, the suggestions made by Bininda-Emonds *et al.* (2004) were carried out as suggested (see Figure 3.1). However, the incorporation of non-independent sets of source trees via a mini-supertree analysis rather than by a method such as down-weighting the trees is not intuitive and has yet to be tested for validity. One concern is that combining source trees using Matrix Representation with Parsimony (MRP) could be taking the data a step even further away from the original. It could be argued, however, that supertrees are already removed from the original data and therefore any inaccuracies introduced by combination of source trees by MRP will be negligible. In this study these two methods will be compared and contrasted. Two separate supertrees of Galliformes will be built, the difference being in the way in which non-independent source trees are dealt with. One method (A) will take non-independent source trees and combine them into "mini-supertrees" using MRP, the other (method B) will down-weight them by an appropriate amount to remove any inappropriate up-weighting of character data. Comparisons to evaluate each method will be carried out using `ent` (Page, pers comm) and looking at two metrics – MASTd (Maximum Agreement SubTrees) and triplets – to investigate how well each supertree represents the source tree and whether one method outperforms the other. MAST compares each input tree to the supertree and calculates the ratio of leaves that appear in the same position in both trees to the total number of leaves in the input tree (Chen *et al.,* 2001). A perfect match is where the whole input tree is reproduced in the supertree and would score 1. If half of the leaves appeared in the same position, the score would be 0.5. Triplets are the rooted equivalents of quartets. For each input tree "T" that tree is compared with the subtree of the supertree that results when any taxa not in "T" are pruned. For any pair of triplets (one from each tree) there are five possible outcomes: a) the triplets are resolved in both trees and are identical, b) the triplets are resolved in both trees and are different, c) the triplet is resolved in one tree, or the other (d), but not both, and e) the triplet is unresolved in both trees. For the purpose of these comparisons only a), b) and d) are relevant. From these a score is calculated for each triplet pair using equation 1 (Page, 2002).

$$fit = 1 - {}^{(\mathrm{d} + \mathrm{r2})}\big/_{(\mathrm{d} + \mathrm{s} + \mathrm{r2})} \qquad (1)$$

Here, d is the number of triplets resolved differently in tree 1 and tree 2, s is the number of triplets resolved identically in tree 1 and tree 2, r1 is the number of triplets resolved in tree 1 but not in tree 2, and r2 is the number of triplets resolved in tree 2 but not in tree 1.

Before any of this could be implemented it was important to define what is meant by an "independent" source tree for the purpose of this study. For the purpose of this study source trees were considered to be independent or not according to the following criteria.

Data considered independent:

- Trees with non-overlapping datasets (e.g. different genes/different morphological characters).
- Trees for non-overlapping taxa sets.
- Unique combinations of genes.

Data not considered independent:

- Trees derived from the same set of characters with the same taxa or where one taxa set is a subset of the other. In this instance, trees were only considered non-independent if they shared *all* taxa or if one set was contained *entirely* within another. Trees from the same characters that shared some taxa, but not all were considered independent.
- Different portions of the same gene.

Non-independent trees were identified using a Perl script (Appendix F: check_independence.pl) that implemented the above rules. The script looks at the metadata and compares both the analysis type and character data. If the same characters and analysis are used within studies, the script checks the taxa list. If this is the same, the files are flagged as potentially non-independent. For each input tree file a list of tree files is given that are potentially non-independent. The script is designed to be pessimistic in judging independence. If there is doubt over the dependency of source trees, they are flagged as non-independent. The decision of dependency is then left to the user. The non-independent trees are then either a) removed if they are redundant (i.e. contained entirely within another dataset, not an original study or not a valid source tree for any other reason), or b) combined into a mini-supertree.

For method A combined trees were created using PAUP* 4.0b10 (Swofford, 2002) to make a "mini-supertree" of all the relevant overlapping source trees. In the vast majority of cases it was possible to use the "branch and bound" option for creating the trees, only a small number required "hsearch". In the case where PAUP* 4.0b10 (Swofford, 2002) found multiple MPTs (most parsimonious trees) a strict consensus was computed. These combined trees were then used in the analysis as independent source trees.

For method B trees were appropriately weighted (i.e. four synonymous trees were each given a weight of 0.25) in order to consider relations of non-independence among the input trees (Gatesy *et al.,* 2002; Bininda-Emonds *et al.,* 2004). In order to avoid the problem of weights being represented as floating point decimals (i.e. 0.33x3 ≠ 1 due to rounding errors) weights were initially worked out as a fraction of 1 but then the common factor was calculated and then all the weights were multiplied by this figure resulting in all weights being represented by integers. In this case the common factor was found to be 12 and therefore all independent trees carry a weight of 12 and down-weighted trees have various values dependent upon the number to be combined.

3.4.3 Standardisation of terminal taxa

It is necessary that terminal taxa be standardised in order to eliminate synonyms/misspellings, paraphyly in taxa and also to ensure that all taxa are represented at the same taxonomic level. Synonyms and misspellings are a major problem in avian taxonomy so this step is vital. The existence of non-standardised terminal taxa creates problems when constructing phylogenies as any given species may be known by very different names depending upon which classification is used. Many misspellings are also in existence, some have been perpetuated throughout the scientific literature accumulating yet more misspellings until they are almost unrecognisable from the original name. It is possible, even likely, that many ornithologists would disagree on the "correctness" of the names used in this thesis. However, the ultimate aim was to standardise the taxonomy and therefore it is more important that synonyms/misspellings/vernacular terms are identified and removed and less important that the names used as the standard are universally agreed upon. It is probably useful to think of this as a process of *standardising* taxonomy rather than one of taxonomic *correction*.

Bininda-Emonds *et al.* (2004) did not suggest any practical means of standardising terminal taxa so, bearing in mind that the Galliformes supertrees and the subsequent avian supertree were to be constructed at species-level, the following steps were taken:

- Taxa lists as found in published phylogenies were loaded into the Glasgow Taxonomic Name Server[3] (Page, 2005), which then returned the list corrected for any possible synonyms/misspellings. The Name Server was developed by Prof. R. D. M. Page and checks input names against those held in the database in an attempt to identify synonyms/misspellings of names.

- On occasions the name server identified an unrecognised name but was unable to suggest an alternative. In this situation the name was searched for in the Taxonomic Search Engine, which searches five databases (ITIS, Index Fungorum, IPNI, NCBI and uBIO) (Page, 2005). Any hits were then investigated and the correct name identified in this manner.

- As a last resort, names that did not appear in the Name Server or in any taxonomic database were input into Google[4] and search results investigated. It was usually the case that the name had been misspelt so badly that it was not recognised by the Name Server but could be identified by a process of elimination, some prior knowledge of the taxon in the question, and knowledge of common misspellings in avian taxonomy. For example the common endings of specific names "–a" and "–us" are often mixed up, i.e. *flava/flavus*, also the addition/subtraction of extra vowels as in *reevesi/reevesii.*

- The new taxa list was then used to create a new tree for the source phylogeny using TreeView 1.6.6 (Page, 2001). The standardising of names often

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[3] http://darwin.zoology.gla.ac.uk/~rpage/MyToL/www/index.php

[4] http://www.google.co.uk

resulted in paraphyly of previously monophyletic taxa, although sometimes the reverse was the case. In the former situation the paraphyletic taxa were dealt with as detailed in this section, point 4. The original tree direct from the source phylogeny was also retained, recorded exactly as in the source, both for completeness but also in order to enable further exploration into issues in avian taxonomy in the future.

It is accepted that there are still likely to be inconsistencies in the taxonomy used here, therefore a complete list of those synonyms/misspellings not found by the Glasgow Taxonomic Name Server, and the taxa they were deemed to be, is provided in Appendix A.

In some instances the name server allowed two variations of a single name, e.g. *Gallus sonnerati*/*G. sonneratti*. In this scenario the Howard and Moore (2003) checklist was consulted and the name given in there was used. In trees where vernacular names were used (e.g. Sibley and Ahlquist, 1990 – operational taxonomic units (OTUs), "New World quails" and "pheasants and turkeys"), Howard and Moore (2003) was also used. This checklist was chosen as the default position as it represents a conservative view of avian taxonomy. It was important to take a conservative view, as this is likely to invoke fewer assumptions that could be regarded as appeals to authority, such as regarding monophyly of higher taxa or the belonging of a particular taxon to a given group.

3.4.4 Combination of trees at different taxonomic levels

Where terminal taxa were referred to by a higher-level name (genus or higher) it was attempted to identify the particular species used in the analysis, in order to avoid unjustified assumptions of monophyly, and these were then coded into the tree. Where this was not possible, all members of that higher taxon were coded as a star polytomy, but only where those taxa were already present elsewhere in the supertree analysis. Bininda-Emonds *et al.* (2004) suggest inserting the type species, but it was felt that this made too strong an assumption as the original tree is not stating that just one species is present in that node but that *all* species in that higher taxon are present.

One exception to this substitution rule has been made in the case of species and sub-species. Sub-species are used much less frequently in analyses than species. Although it is desirable to make no changes to the original source tree, the adding of all known sub-species in the form of star polytomies in source trees in which only the species name is given would be cumbersome, unnecessarily increase computational time and then add little or no value to the resulting estimate of phylogeny (Pisani *et al.,* 2002). Although in some instances species can be shown to be paraphyletic (this issue is dealt with separately – see stage 5) the case for standardising all taxa at the species level far outweighs the evidence in favour of this approach. The second, and final, exception is in the case where species belonging to a higher taxon are not actually present in any of the source trees. No examples of this were present in the Galliformes dataset, but in the Aves species-level tree there exists a fossil family – Zygodactylidae (Mayr, 2004) that was left in the dataset at family-level rather than substituting the constituent taxa. All taxa falling into this category were left as higher taxa in order not to artificially inflate taxa numbers.

To facilitate an easy method for substituting higher taxa a Perl script (Appendix F: replace_higher_taxa.pl) was written to automate the process. Briefly, the script performs the following operations:

1. Scan all XML data to create a list of unique taxa.

2. Create a list of higher (than species) taxa by assuming any taxon which contains only a single word is a higher taxon.

3. If a species (i.e. a taxon consisting of two words – subspecies have already been removed) in the taxa list matches a higher taxa, add it to the substitution list. For example, if "*Gallus*" is found in the taxa list, then it becomes a "higher taxon". Then if "*Gallus gallus*" is found, this is added to the list to be substituted for "*Gallus*". Additionally, if "*Gallus varius*" is also found, "*Gallus*" will now be substituted with "*Gallus gallus*" and "*Gallus varius*". Note that the user can also input this list of substitutions if required (see below).

4. Go through all tree files and XML files performing the necessary substitutions depending on the following:

   a. If a species in the substitution list already exists in the tree, do not substitute this species in this particular tree.
   b. If the substitution is empty (i.e. because all the species belonging to that higher taxa are already in the tree) remove the higher taxon.

5. The substituted higher taxon is replaced by a polytomy.
6. Overwrite the existing files with the updated tree and XML data.

In step 3, the list generated makes the assumption that taxa with a single word as a label are generic names and taxa with two words as a label are specific names. This may not always be the case as, for example, there may be family or informal names within a tree (e.g. Sibley and Ahlquist, 1990 contains "pheasants and grouse" and "New World quails"). To resolve these cases, the user can specify substitutions that should be made via an optional input file. This can also be used to remove unwanted taxa (e.g. MRPOutgroup from combined mini-supertrees) very easily by specifying an empty substitution.

The replacement of higher taxa can take place in several stages, which assists verification of the substituted data, allows taxa that are higher than generic names to be replaced with generic names before being substituted with specific names, and removes unwanted taxa before any subsequent processing.

As in the case for synonyms, Howard and Moore (2003) was used to define inclusion of species within higher taxa, for the same reasons given above (section 3.4.3).

3.4.5 Accommodation of paraphyletic taxa

To accommodate paraphyletic taxa all possible permutations of the taxon's position were created in separate tree files, then all these trees were combined into a mini-supertree.

In order to create the trees containing all possible permutations of paraphyletic taxa the Nexus file was modified slightly. All paraphyletic taxa were input as the corrected taxon name with the characters %n, where n is an integer starting from one, appended onto the end. For example if the species *Aerodramus spodiopygius* appears in two locations within a tree, e.g. by removing a subspecies or after standardising a name, these are labelled as *'Aerodramus spodiopygius%1'* and *'Aerodramus spodiopygius%2'*. A Perl script (Appendix F: tree_permutation.pl) was then used to scan for names with the tagging characters, shuffle the taxa such that only one taxon from each paraphyletic group was contained in the tree, and save the resulting tree. A recursive function ensured that all possible permutations of paraphyletic positions were covered. This approach also worked in the terminal taxa standardisation stage in the case when paraphyletic subspecies needed to be removed.

Once all permutations were realised, a “mini supertree” was constructed, ensuring data independence.

3.4.6 Data integrity check

The data integrity between the tree files (Nexus text file) and the XML metadata is a key component of the dataset. The idea of using two separate files may seem unwieldy, but allows cross-checking of one against the other on common data to allow errors created during editing of one or both to be caught. To make testing easier, a short script (Appendix F: check_integrity.pl) which performs three checks was written. The first check is on the XML files, to ensure their validity. This is very simple to carry out and the XML parser will spot most errors. If an XML file contains an error, it is flagged to the user for checking. It could be made more robust by using Document Type Definition (DTD), but this was considered too high an overhead on this project as the XML may have been extended and/or altered. The next check was to ensure validity of the tree files. All the tree files encoded in this project were in "translated" format (see Box 3.1). An easy check for syntax errors is to translate the tree to normal nexus format (see Box 3.2). If the translation fails, the tree is flagged as possibly erroneous. Finally, the cross-check between XML and tree files checks that the same taxa are contained in both for each pair of files. The script checks that the same number of taxa are present in both files and then checks each taxon against the other file. If there are differences, these are flagged to the user to inspect.

```
#NEXUS
BEGIN TAXA;
      DIMENSIONS NTAX = 4;
      TAXLABELS
      Taxon_w
      Taxon_X
      Taxon_y
      Taxon_z
      ;
ENDBLOCK;
BEGIN TREES;
    TRANSLATE
        1   Taxon_w
        2   Taxon_x
        3   Taxon_y
        4   Taxon_z
        ;
     TREE * tree_1 = (1,2,(3,4));
ENDBLOCK;
```

Box 3.1: Example tree in translated Nexus format.

```
#NEXUS
BEGIN TREES;
     TREE * tree_1 = (Taxon_w,Taxon_x,(Taxon_y,Taxon_z));
ENDBLOCK;
```

Box 3.2: Example tree in standard Nexus format.

3.4.7 Check adequate overlap of source trees

This step is missing from the Bininda-Emonds *et al.* (2004) protocol, but is a fundamental requirement of constructing a supertree (Sanderson *et al.,* 1998). Each source tree must share at least two taxa with at least one other source tree in order to be included. Connections between sources trees were determined by a Perl script (Appendix F: tree_cluster.pl). Floating source trees that are not connected to any others and also “islands” of connected source trees (those that share two or more taxa between them, but do not join on to the main group of source tree) should also be eliminated. Figure 3.4 shows a graphical method of determining this using

GraphViz[5]. A node represents each source tree and edges are created between nodes when two or more taxa are shared between the corresponding source trees. The small island of trees 6, 7, 8 and 19 should be removed.

It was ensured that the source trees fulfilled the minimum requirement of overlap with other source trees (at least two taxa with at least one other source tree) before the trees were considered ready for the supertree analysis

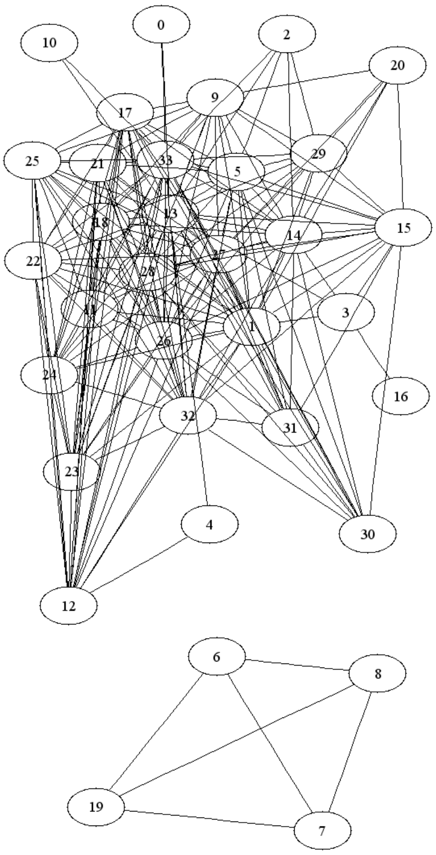

Figure 3.4: Graphical representation of minimal overlap of source trees (example from Chapter 5). Each node represents a source tree and edges represent an overlap of at least two taxa between those nodes. The island consisting of four source trees 6, 7, 8 and 19 should be removed from the study.

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[5] http://www.graphviz.org

3.4.8 Matrix creation

After all data processing there remained a total of 53 source trees from a total of 39 source references to be included in the analysis. There were a total of 202 taxa included in the analysis. See Appendix B for a list of source references.

First trees were combined into a single file (Appendix F: amalgamate_trees.pl), then MRP matrices for both datasets were created using a version of Bininda-Emonds' SuperMRP.pl Perl script (Bininda-Emonds *et al.,* 2005) which was modified to run in Windows. See Appendix E for the MRP matrix.

3.5 Analysis

Both datasets were run in PAUP* 4.0b10 (Swofford, 2002) using the Parsimony Ratchet (Nixon, 1999). A script of Bininda-Emonds (perlRat.pl[6]) was used to create the ratchet command file. The default parameters run 5 batches of 200 iterations. This was increased to 10 batches of 500 iterations in order to increase the chances of finding the shortest tree. The matrices were also run in TNT (Goloboff *et al.,* 2008) using the "xmult=level 10" command; an aggressive search designed to find the shortest trees. An attempt was also made to utilise POY (Varón *et al.,* 2007), as this is another recently developed piece of software for analysis of phylogenetic data, however POY requires 714Mb just to load the weighted Galliformes dataset and simple processing of the file uses 1.5Gb, which crashes the system.

Searches were carried out on an Apple MacBook 2.0GHz Intel Core 2 Duo with 2GB of RAM.

The resultant supertrees were compared to the source trees in order to assess fit and therefore which, if either, of method A (combining source trees) or method B (weighting source trees) provided better results. The program `ent` (Page, pers comm) was used for this. `Ent` compares the output (the supertree) to all the input trees (the source trees) and gives scores for each input tree (scores are between 0 and 1 with 0 being a complete mismatch and 1 being a perfect match).

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[6] http://www.personal.uni-jena.de/~b6biol2/ProgramsMain.html

3.6 Results

3.6.1 Galliformes supertrees

The shortest trees found by TNT (Goloboff *et al.,* 2008) were significantly shorter than the shortest trees found in PAUP* 4.0b10 (Swofford, 2002) using the Parsimony Ratchet (Nixon, 1999) for both datasets. For the combined data the Parsimony Ratchet found 178 MPTs of length 988, TNT found 8 MPTs of length 961. For the weighted data the Parsimony Ratchet (Nixon, 1999) found 220 MPTs of length 12458, whilst TNT found 17 MPTs of length 11912. The majority-rule consensuses of the trees found by TNT are shown in Figure 3.5 (combined supertree) and Figure 3.6 (weighted supertree).

The two trees are broadly similar and show essentially the same higher-level relationships. Both are concordant with generally accepted views of galliform phylogeny. The fossil taxon *Paraortygoides* (two species) is placed as the sister taxon to all extant Galliformes. The extant families are not all monophyletic but do broadly fall into the pattern of (Megapodiidae, (Cracidae, (Numididae, (Odontophoridae, (Phasianidae, (Meleagridinae, (Tetraonidae))))))).

Megapodiidae and Cracidae are resolved as monophyletic groups with the exception of *Penelope superciliaris* in the combined tree, which is placed as the sister taxon to Galliformes minus Megapodiidae and Paraortygoides. This is not supported by any of the source trees and, as such, can be considered to be a spurious result. Megapodiidae and Cracidae do not, however, form the monophyletic taxon Craciformes as proposed by Sibley and Ahlquist (1990). Instead, the supertree supports the more traditional view of the Megapodiidae forming the sister group to all other extant Galliformes (as in Dimcheff *et al.,* 2002; Dyke *et al.,* 2003; Gulas-Wroblewski and Wroblewski, 2003; Smith *et al.,* 2005).

A paraphyletic Numididae and monophyletic Odontophoridae are sister taxa to a monophyletic Phasianidae, which contains the majority of galliform species. In the combined tree the Numididae are rendered paraphyletic only by the grouping of *Agelastes niger* with the fossil taxon *Gallinuloides wyomingensis.* In the weighted tree it is the inclusion of the taxon *Francolinus lathami* within the Numididae that causes the paraphyly. Neither of these relationships is present in any source tree, however in Dyke and Gulas (2002) *F. lathami* (along with other francolin taxa) and the Numididae taxa are all present as part of the same large star polytomy, this could cause *F. lathami* to spuriously cluster with the Numididae. The fossil taxon *Gallinuloides wyomingensis* is placed as the sister taxon to Phasianidae + Odontophoridae + Numididae in the weighted tree, as suggested by Dyke (2003).

The Phasianidae is a large order and it is easier to consider the individual subfamilies that it comprises. Subfamilies have been defined according to Howard and Moore (2003) in keeping with earlier definitions for higher taxa within this chapter. Using this classification, the Phasianidae contains a paraphyletic Perdicinae (Old World partridges) and Phasianinae (pheasants). Pheasants and partridges were originally thought to represent monophyletic lineages (Johnsgard, 1986, 1988; Sibley and Ahlquist, 1990), however, more recent evidence (Kimball *et al.,* 1999; Geffen and Yom-Tov, 2001; Smith *et al.,* 2005) suggests that this is not actually the case. The supertrees are concordant with the non-monophyletic viewpoint. Within the Perdicinae the francolins are split into the quail francolins and partridge francolins as suggested by Crowe *et al.* (1992) and Bloomer and Crowe (1998) but are not monophyletic (as found in Bloomer and Crowe, 1998). The partridge francolins form a sister group to the *Coturnix* quails, Madagascar partridge (*Margaroperdix madagarensis*) and to the *Alectoris* partridges, again as in Bloomer and Crowe (1998). The Phasianinae are roughly split into two groups; a monophyletic group containing the peafowls and allies, and junglefowl; and a paraphyletic group containing the gallopheasants and allies, and the tragopans.

The monophyletic Meleagridinae (turkeys) and Tetraonidae (New World quail) are each other's closest relatives and cluster with the branch of the Phasianinae containing the gallopheasants and tragopans (as in Geffen and Yom-Tov, 2001; Dimcheff *et al.,* 2002). Kimball *et al.* (1999) support the clustering of the Meleagridinae and Tetraonidae but are not able to resolve the relationship of these to other Phasianidae.

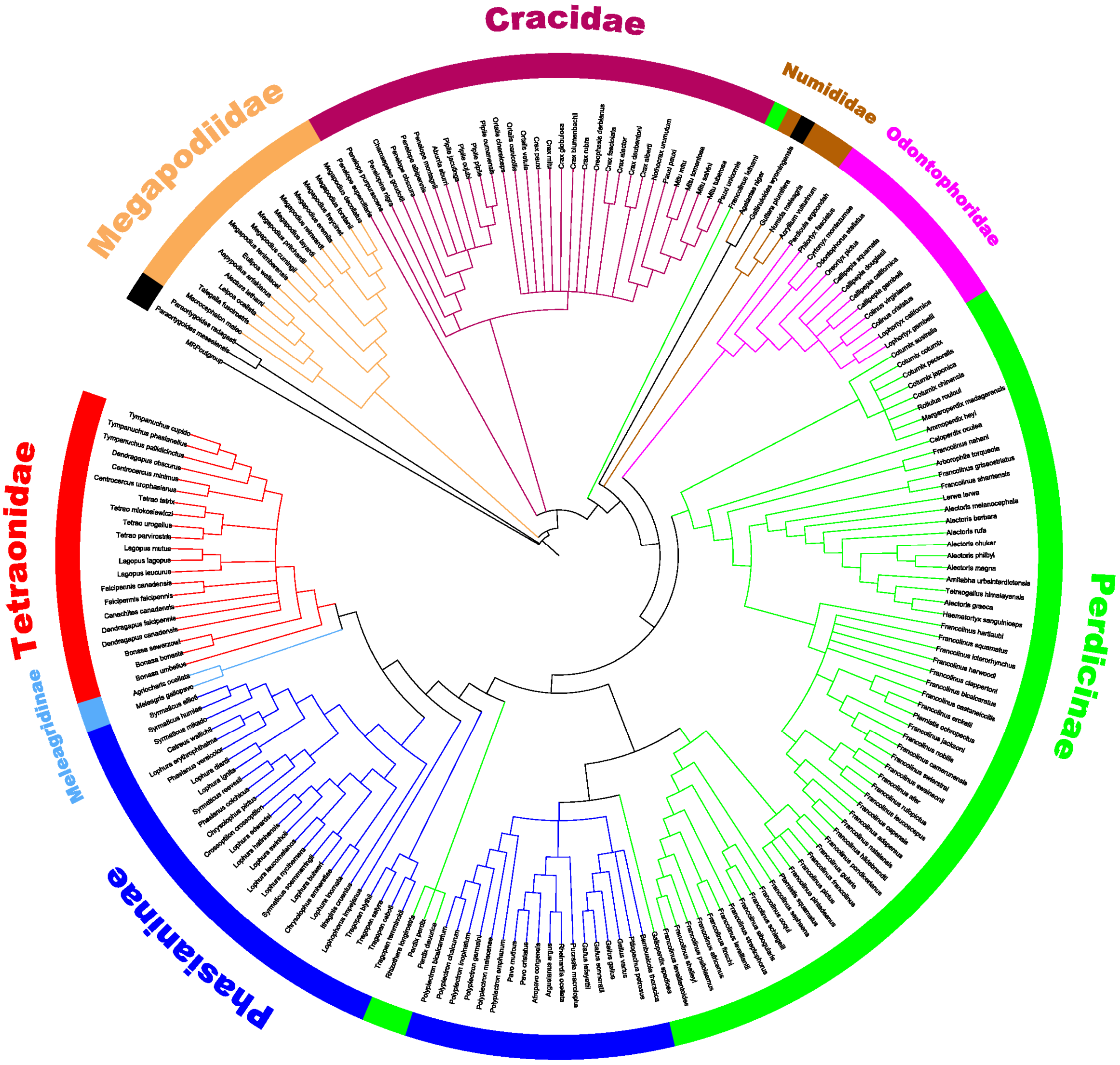

Figure 3.5: Combined supertree – shown is the 50% majority-rule consensus of 8 MPTs of length 961, found in TNT (Goloboff *et al.*, 2008).

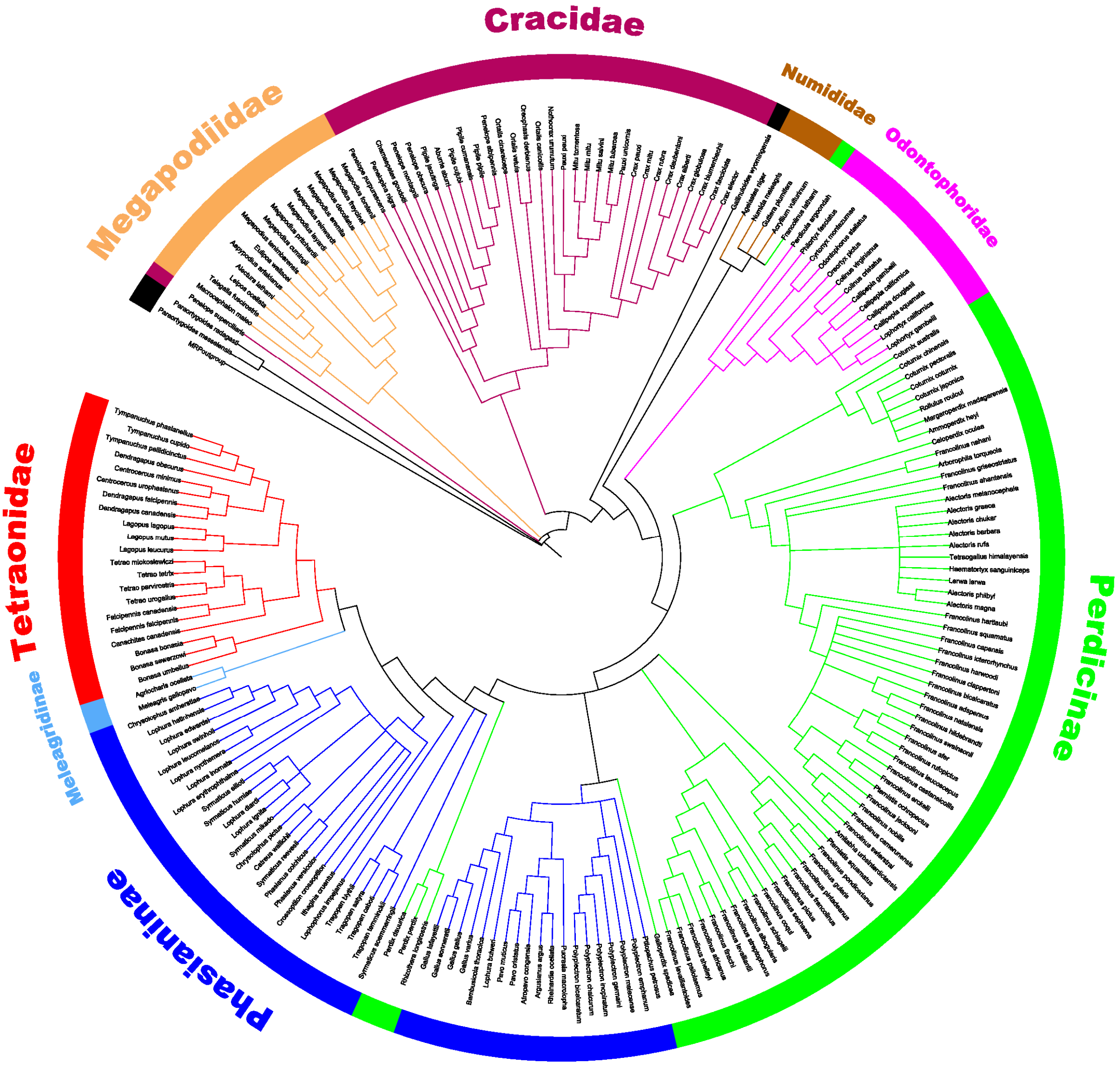

Figure 3.6: Weighted supertree - shown is the 50% majority-rule consensus of 17 MPTs of length 11912, found in TNT (Goloboff *et al.*, 2008).

Comparisons were made between the resulting supertrees and the set of source trees to assess the suitability of the two methods of dealing with overlapping data. As the data do not follow a Gaussian distribution (see Figure 3.7), a non-parametric test must be used to ascertain if the difference between the weighted and combined fit scores are statistically significant. Therefore the Mann-Whitney-U test was used to test if the difference between the means of the two samples was statistically significant.

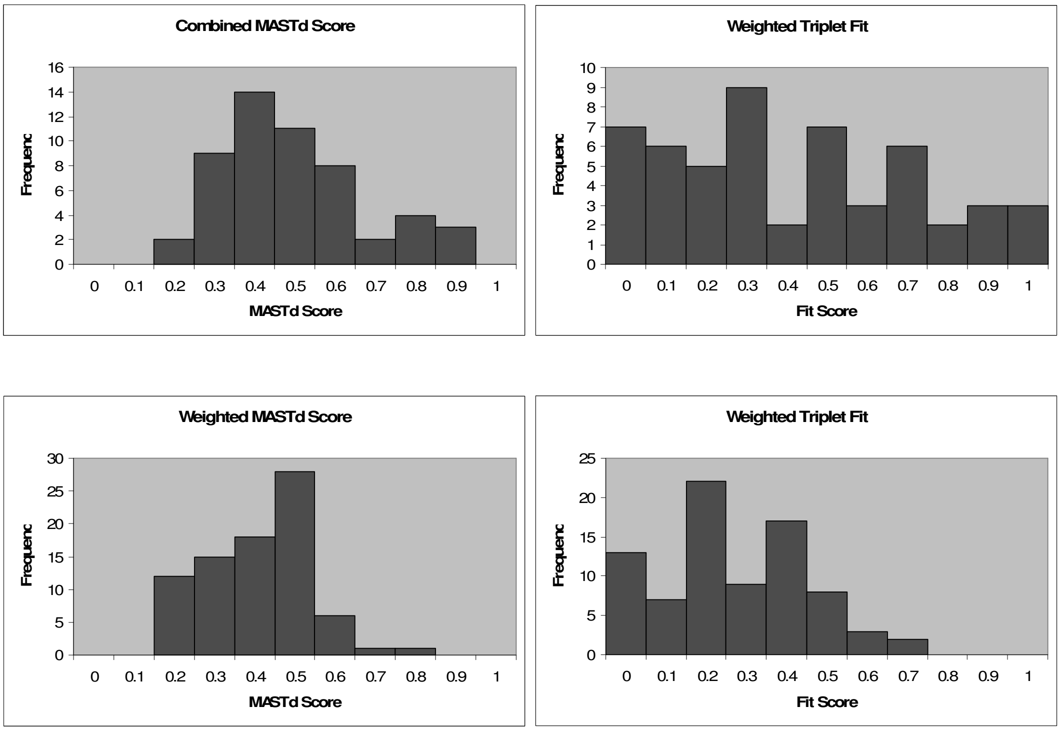

Figure 3.7: Histograms of fit scores for both combined and weighted methods. Note that neither method produces a Gaussian distribution (which is desirable as the optimum fit would be all trees with a score of 1 and hence give a non-Gaussian distribution).

The results show that for the combined dataset the mean fit scores are 0.37 for triplet fit and 0.45 for MASTd (higher score indicates better fit). For the weighted dataset the mean fit scores are 0.23 for triplet fit and 0.37 for MASTd (see Table 3.1) for full statistics). From these scores (Table 3.1) and the box plots (Figure 3.8) the combined supertree appears to be a better fit (higher mean score) to the source trees than the weighted supertree. To test if this is significant, the Mann-Whitney-U test was used, which showed that the higher mean fit for the combined dataset is statistically significant to a 0.99 confidence level for both MASTd and triplet fit. The calculated

P-value of 0.0104 is statistically significant; and shows that there is a significant difference between the means of the two samples.

Table 3.1: Statistical data for "fit" scores for both combined and weighted methods.

Method	Min	1st Qu	Median	Mean	3rd Qu	Max.
Weighted Triplets	0.00	0.11	0.19	0.23	0.35	0.64
Combined Triplets	0.00	0.11	0.30	0.37	0.63	1.0000
Weighted MASTd	0.12	0.28	0.35	0.37	0.44	0.71
Combined MASTd	0.15	0.32	0.43	0.45	0.55	0.90

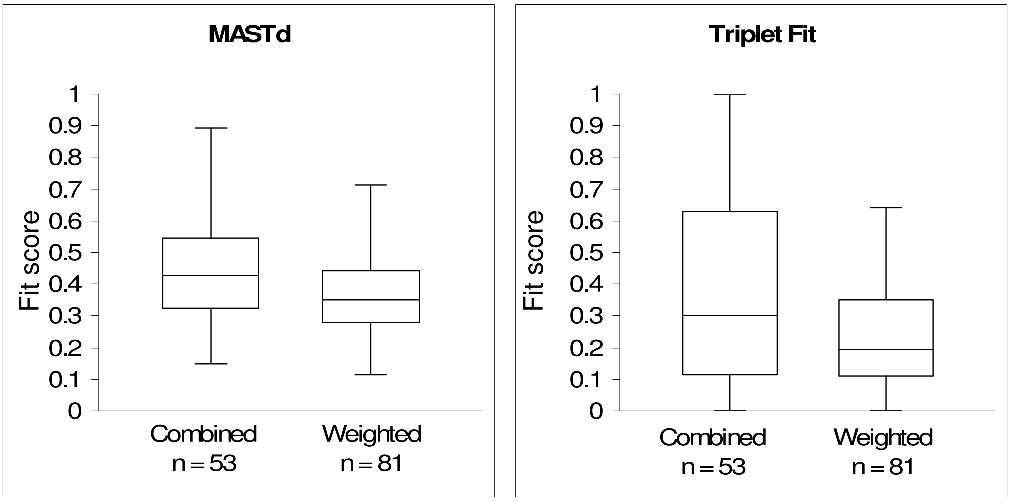

Figure 3.8: Box and whisker plots for combined and weighted data (see Table 3.1).

In addition to this, the time taken for each tree to compute was recorded (see Table 3.2). It was found that the combined dataset ran much more quickly in both programs. Therefore, combining non-independent source trees is much more efficient and saves significant computing time compared to weighting input trees, by running in just 60% of the time it takes to complete the weighted dataset when using the Parsimony Ratchet and 64% of the time when using TNT. In addition, TNT runs in just 12% of the time taken by the Parsimony Ratchet for both datasets. Yet another advantage of combining non-independent trees rather than applying differential weights was that it was much quicker and easier, when processing the data, to combine trees into mini-supertrees than it was to allocate weights and to create a weight set.

Table 3.2: Statistical data for "fit" scores for both combined and weighted methods

	PAUP (Parsimony Ratchet)	TNT
Combined	26 min 15.886 secs	3 min 14 secs
Weighted	43 min 29.463 secs	5 min 2 secs

3.7 Discussion

Both supertrees gave reasonable, sensible results with a minimum of spurious groups. There were no surprises in the results and both conformed well to currently accepted views on galliform phylogeny.

There was a statistically significant difference between combined and weighted methods to a 0.99 confidence level. Two scoring methods were used in order to provide a more robust test. These scoring methods are independent of each other and still gave the same result. This increases confidence in the result that combining non-independent data gives a supertree more consistent with the source data than by applying differential weights for this dataset.

Weighting of non-independent source trees seems more intuitive, however, as shown above; combining source trees gives results more consistent with the input data. Also, there are potential issues with any original weights of the source trees although this is only on a small scale and therefore relatively unimportant. Additionally, the weighted dataset takes longer to calculate and it can be tricky to load weighted data into some software (e.g. POY, TNT) without manual work. It is important for data to be as portable as possible to allow collaborative methods of tree-building (see Chapter 4) so that the matrix can be tested on as many different types of software as possible.

In addition to being statistically shown to produce a tree more compatible with the source trees than via weighting non-independent source trees, combining trees is much more convenient and allows utilisation of a wider variety of types of analysis, such as TNT (Goloboff *et al.,* 2008) and POY (Varón *et al.,* 2007) which have much more powerful algorithms than PAUP* 4.0b10 (Swofford, 2002). This method will be utilised for the main Aves dataset, which will be analysed in TNT, as this has been shown to consistently find the shortest trees in the shortest timescales. Run time and speed become increasingly important as datasets become larger so whilst a difference of a scale of minutes or 10s of minutes may seem unimportant on a dataset of this size, it has the potential to make a huge difference in the time taken to find the shortest trees on a much larger dataset.

3.8 Conclusions

The aim of this chapter was to develop and test a protocol for supertree construction using the Galliformes as a test case and with the ultimate aim of creating a robust protocol suitable for the construction of a supertree of Aves. This protocol was based on that outlined by Bininda-Emonds *et al.* (2004) but modified and extended, and tested on real data. The use of Perl scripts to automate data processing wherever possible greatly increases efficiency and reduces errors. This increased efficiency and reduction of errors will be even more vital for constructing a species-level supertree of Aves (see Chapter 4).

Several areas were identified that had not fully been explored by Bininda-Emonds *et al.* (2004); these were largely practical issues that had no clear implementation. These issues were resolved, often by the use of automated scripts, which had the dual effect of reducing error and also increasing efficiency. However, the greatest issue was whether to combine (via mini-supertree) or appropriately weight non-independent source trees. It was found that combining non-independent source trees produced a supertree that had a significantly higher mean fit to the original source trees than that produced by weighting of source trees. In addition, the combined datasets were much quicker to run in both programs, PAUP* 4.0b10 (Swofford, 2002) and TNT (Goloboff *et al.,* 2008), than the weighted dataset, and TNT was substantially quicker to run each dataset to completion than PAUP*4.0b10.

The supertrees were very similar in terms of large-scale relationships. Both gave sensible results and only a small number of spurious groups were identified. Neither tree should be regarded as a definitive representation of Galliformes phylogeny in any way but more as a summary of current knowledge.

Given the above discoveries and results, the species-level avian supertree, that is the main aim of this thesis, will be constructed as per the protocol developed in this chapter and via the combining of source trees to remove data non-independence.

The next chapter deals with the construction of the species-level avian supertree and explores the issues arising from the assembly of a supertree on such a large scale.

Chapter 4

A species-level supertree of Aves

4.1 Abstract

Supertrees are a useful method of constructing large-scale phylogenies by assembling numerous smaller phylogenies that have some, but not necessarily all, taxa in common. Supertrees have been produced for a diverse range of taxa including dinosaurs, mammals and crocodiles. Birds are an obvious candidate for supertree construction as they are the most abundant land vertebrate on the planet and no comprehensive phylogeny of both extinct and extant species currently exists. Here, a species-level supertree has been constructed containing over 5000 taxa from over 700 source trees. The tree shows the relationships between the main avian groups, with only a few novel clades, most of which can be explained by a lack of information regarding those taxa. The tree was constructed using the strict protocol described in Chapter 3, which ensures robust, accurate and efficient data collection and processing. In addition, the tree was constructed in a collaborative fashion by placing the source trees and MRP matrix on the World Wide Web for the scientific community to download. No shorter trees were found using this community-based method of tree-building but it still proved invaluable in the identifying of taxonomic errors that would otherwise have had a negative impact on the resultant supertree.

4.2 Introduction

Birds are an ideal candidate for supertree construction as they are of interest to vertebrate biologists and palaeontologists alike. They are diverse, with current estimates of nearly 10,000 extant species (Monroe and Sibley, 1990) occupying almost every geographical location, from ocean to desert. Birds evolved from therapod dinosaurs in the Jurassic (Chiappe, 1995 and references therein) and it is debated whether they experienced a huge burst in diversity during the Tertiary with many modern orders diversifying in a very short period of time (Feduccia, 1995) or whether the major orders of Neornithes were already present in the Cretaceous and survived the Cretacaeous-Tertiary event (Cracraft, 1973; Cracraft, 2001; Ericson *et al.,* 2002; Hope, 2002; Dyke, 2003; Ericson *et al.,* 2003; Van Tuinen *et al.,* 2003). Birds are in particular need of phylogenetic assessment as no widely accepted phylogeny currently exists that is at species level or contains both extinct and extant taxa.

Supertrees have now been produced for several groups of taxa including the Dinosauria (Pisani *et al.,* 2002), marsupials (Cardillo *et al.,* in 2004), bats (Jones *et al.,* 2002), Carnivora (Bininda-Emonds *et al.,* 1999), the Temnospondyli (Ruta *et al.,* 2007) and all extant mammals (Bininda-Emonds *et al.,* 2007). Supertrees can be used to address crucial questions in areas such as conservation and biodiversity studies to macroevolution (e.g. Purvis, 1995; Bininda-Emonds *et al.,* 1999; Jones *et al.,* 2002). Supertrees have also been constructed for some avian groups, such as the Procellariiformes (tube-nose seabirds) (Kennedy and Page, 2002) and Charadriformes (shorebirds) (Thomas *et al.,* 2004). In addition, Barker (2002) used supertree methods to construct an avian phylogeny to look at phylogenetic diversity. However, Barker (2002) used the Sibley and Ahlquist (1990) “tapestry” as a framework, then added in lower level taxa using supertree methods for individual clades in the tree, effectively pasting together smaller phylogenies into an informal supertree. No formal supertree has yet been constructed for all of Aves. This chapter will construct a formal supertree of Aves covering both extinct and extant species.

Supertrees lend themselves well to collaborative creation, in terms of data collection, but perhaps more readily to construction of the actual supertree as computational limits are often the reason for non-completion of analysis. Although some phylogenetic software can run on so-called supercomputers, utilising multiple processors on the same problem to reduce the amount of time taken to complete an analysis, they obviously require access to such hardware to run at their full potential. The supertree data in this chapter was therefore made freely available to the scientific community in an attempt to build the supertree in a collaborative fashion, with the hopes that this would increase efficiency, correct any errors missed by the author, and decrease the time taken to find shorter trees.

4.3 Methods

4.3.1 Data collection

As in Chapter 3, potential source trees were identified initially from online resources. The Web of Knowledge[1] Science Citation Index was searched; covering the years 1981 to 2005 and all papers potentially containing trees were examined. The reference lists within these papers were then searched for papers containing trees. All papers containing trees were retained and this process was continued until as many trees as possible were found. Papers were collected up to the end of December 2005 as at that point data processing commenced. A total of 589 papers were collected for the Aves species-level dataset that were deemed to contain potentially useful source trees, of these 30 were found to contain trees that were redundant because they a) reanalysed previous datasets and added no new data or taxa or b) did not contain an original tree. Category a) trees were dealt with according to the protocol (described fully in Chapter 3 and summarised below), while category b) source trees were discarded. While every effort was made to collect all references, there is a great wealth of information regarding avian phylogeny and it is always possible that some may have been missed.

The 589 papers yielded 1054 trees spanning 7384 taxa. After processing following the protocol described in Chapter 3, 307 trees were eliminated, leaving 747, from 556 source papers (see Appendix B), to be used to construct the supertree. These trees contained 5274 taxa. This drop in taxa numbers was due to the removal of higher taxa, vernacular names and synonyms during data processing.

Following the protocol, described in detail in Chapter 3, attempts were made to remove as much dubious data from the diverse range in input trees as possible. Briefly, the protocol aims to standardise taxonomy, remove non-independent trees, allow the combination of taxa at different levels, and accommodate paraphyletic taxa. The source trees, along with associated metadata, were first collected in their

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[1] http://wok.mimas.ac.uk

original form from the source papers collected. The next stage was to correct names using the Taxonomic Name Server (Page, 2005). Any names not validated using this tool were checked manually from a number of sources, including the original source (as was often the case for fossil taxa) and even Google[2] in an attempt to find the correct name (see Appendix A for a list). Any non-avian taxa (e.g. dinosaurian outgroups in fossil avian trees) were deleted before the matrix was created as "pruning a taxon from an MRP matrix will create a matrix that is not representative of the real topology of the pruned tree" (Pisani *et al.,* 2002).

Next, non-independent studies were identified using a Perl script which allows a semi-automated method of identifying such studies and bringing them to the attention of the user. Finally paraphyletic taxa and taxa at different taxonomic levels were dealt with using a range of Perl scripts (see Chapter 3 for full details of the protocol and Appendix F).

In the test case (Chapter 3) there were only a small number of supraspecific taxa and vernacular names in the source trees (e.g. "New World Quail" and "*Alectura*" as two examples in Sibley and Ahlquist, 1990). This meant that these OTUs (operational taxonomic units) could be replaced with the relevant species by hand. In the main supertree dataset this was not feasible. For example, a number of source trees contained the taxa "Neornithes", "Carinatae" or "modern birds", which requires the substitution of virtually every taxon contained within the supertree. It would be impossible, and hugely error-prone, to deal with this by hand and therefore a Perl script was employed to facilitate the substitution of these, and other, higher taxa and vernacular names (Appendix F: replace_higher_taxa.pl).

At this point the trees were checked for sufficient overlap (Sanderson *et al.,* 1998). All trees contained at least two taxa that overlapped with another source tree so all could be incorporated into the supertree analysis.

Once the data had been processed according to the protocol, the matrix was constructed using a version of Bininda-Emonds' SuperMRP.pl Perl script (Bininda-

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[2] http://www.google.co.uk

Emonds *et al.,* 2005) that was modified to run in Windows (see Appendix E for the matrix). A Nexus-formatted tree file containing all source trees was then constructed, again with a simple Perl script. The output from this is two tree files and a text file. One of the tree files contains all trees with correct labels according to the source from which they were taken. The second tree file contains the same trees, but they are labelled sequentially from 1 to n. The text file then contains a key indicated from which source each tree is from. It is this second tree file, along with the MRP matrix, that was uploaded to the Bird Supertree project website[3]. The website contained an online viewer for all trees uploaded (both source and any resulting supertrees), a 'blog' and information on the project. Researchers could then, independently, create a supertree using whatever methods they wished. The intention was that the person who uploaded the shortest tree would be asked to co-author a paper describing this work, while any persons finding shorter trees than that in the results section below would receive an acknowledgement.

Once all data processing was completed, the data contained 5274 taxa from 746 source trees, from 556 source references.

4.3.2 Analysis

The Galliformes supertree test study (Chapter 3) showed that TNT (Goloboff *et al.,* 2008) was far superior at finding shorter trees in a shorter timescale than PAUP* 4.0b10 (Swofford, 2002), either when using a standard heuristic search or when implementing the Parsimony Ratchet (Nixon, 1999). Therefore the MRP matrix was analysed in TNT (Goloboff *et al.,* 2008) using the "xmult level=10" option, an aggressive search strategy devised to find the shortest trees in as little time as possible. Although other supertree methods are available with software implementation (see Chapter 1), there are none that can handle such large numbers of taxa. Therefore it was necessary to use MRP (Matrix Representation with Parsimony) for this analysis, despite the various criticisms that the method has received (Gatesy *et al.,* 2002; Gatesy *et al.,* 2004; Wilkinson *et al.,* 2005b).

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[3] http://linnaeus.zoology.gla.ac.uk/~rpage/birdsupertree/

The analysis ran for 12 hours, the longest queue available on the machine used. Analyses were carried out on “Ness”, a 64 processor cluster, consisting of 2.6 GHz AMD Opteron (AMD64e) processors with 2 GB of memory per processor, hosted at EPCC, University of Edinburgh. Only a single processor was used for this study.

In addition to the above analysis, the data were made available publicly via the “Bird Supertree Project” website. To date (December 2007) a total of four trees have been uploaded. Trees uploaded used both TNT (Goloboff *et al.,* 2008) and PAUP* 4.0b10 (Swofford, 2002), however, no information was available on the machine used to run the analysis. In itself, this was a unique experiment in the social aspect of scientific collaboration.

4.4 Results

4.4.1 The supertree

The analysis ran for 12 hours and TNT (Goloboff *et al.,* 2008) found a single, remarkably well resolved, parsimonious tree of length 17899. This tree is displayed in full in Figure 4.1. Higher taxa have been labelled on the supertree as defined by Howard and Moore (2003). For a larger print version of the supertree see Appendix C.

It is worth mentioning that many of the groups discussed below, and this is particularly the case within the Passeriformes, are not perfectly monophyletic but where there is a clear distinction that allows the recognition of major groups and higher taxa they have been treated as such for the sake of brevity and clarity both in this description and in the accompanying diagram of the supertree (Figure 4.1).

General overview of the tree

The Mesozoic birds are at the base of the tree. The Neornithes (modern birds) are split into the Palaeognathae (tinamous and ratites) and the Neognathae (all other taxa). Both morphological and molecular data support this basal division (Cracraft, 1988; 2001; Groth and Barrowclough, 1999; Van Tuinen *et al.,* 2000; Livezey and Zusi, 2001). The Galloanserae (Galliformes – landfowl, and Anseriformes –

waterfowl) then form a monophyletic sister group to the Neoaves (Neognathae minus Galloanserae).

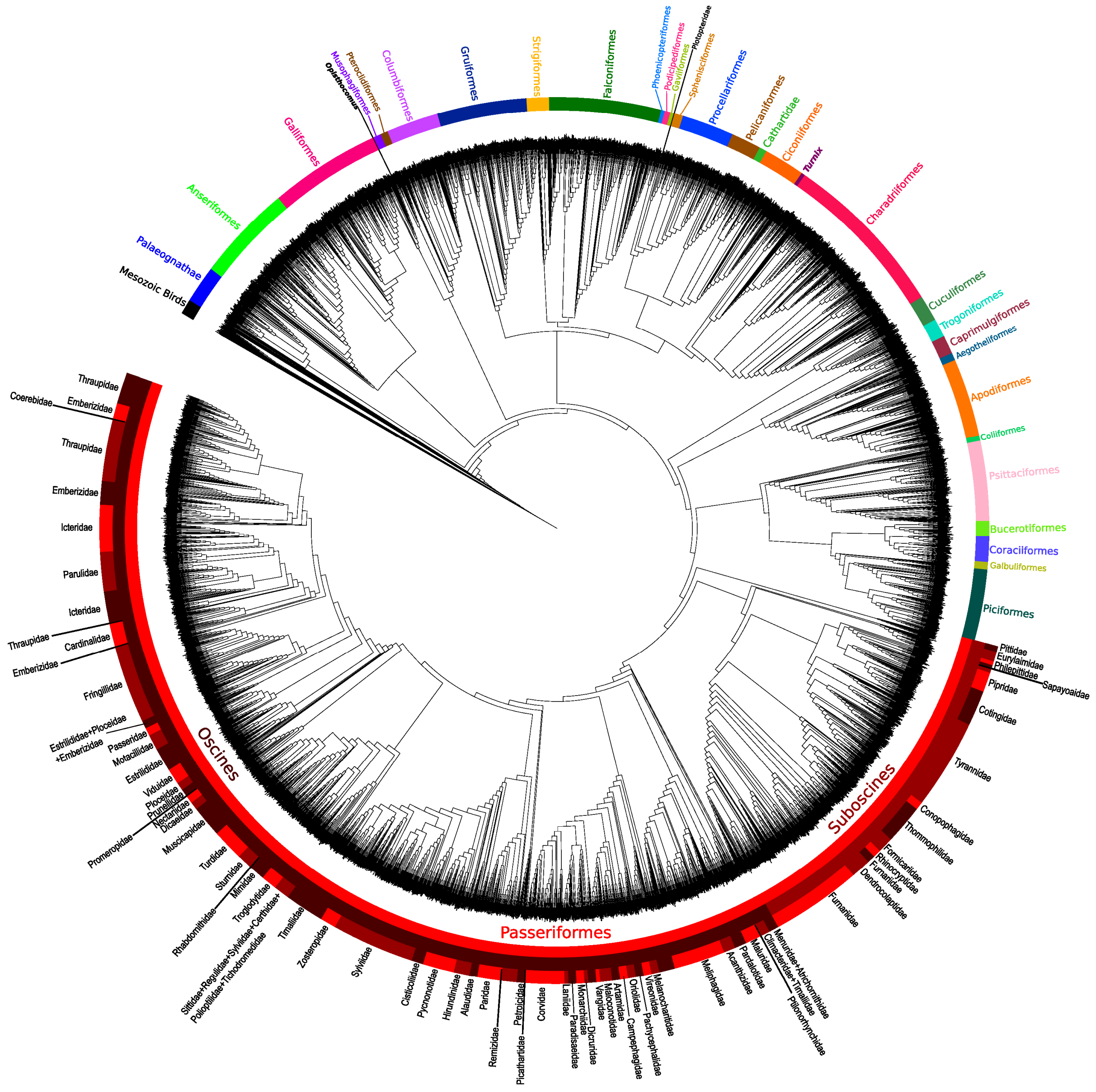

Figure 4.1: Single MPT of length 17899 found by TNT (Goloboff *et al.*, 2008). The inner ring shows orders, whilst the outer rings split the Passeriformes into more manageable sections (families and some genera) to better show areas of interest. Individual taxa are not visible, see Appendix C for a version of the tree in which all taxa can be read.

Within Neoaves, the hoatzin has been placed at the base of a clade containing the Musophagiformes (turacos and allies), Pteroclidiformes (sand grouse) and Columbiformes (doves and pigeons). The Phoenicopteridae (flamingos), Podicipedidae (grebes), Gaviiformes (loons), Sphenisciformes (penguins), Procellariiformes (tube-nose seabirds), Pelecaniformes (totipalamate birds), Ciconiiformes (storks and allies), Turnicidae (buttonquail) and Charadriiformes (shorebirds) all form a monophyletic group as in Sibley and Ahlquist's (1990) "Ciconiiformes". The one exception is the Falconiformes (diurnal birds of prey) which are placed with the Strigiformes (owls), then this clade is sister taxon to the other "ciconiiform" orders. The Cuculiformes (cuckoos and anis) are placed as sister to a clade containing the Trogoniformes (trogons), Caprimulgiformes (nightbirds), Aegotheliformes (owlet-nightjars) and Apodiformes (swifts and hummingbirds). The latter three have been placed together by both DNA-hybridisation data (Sibley and Ahlquist, 1990) and by cranial morphological characters (Livezey and Zusi, 2001). The Coliiformes (mousebirds) and Psittaciformes (parrots and allies) form the sister group to a clade containing the Bucerotiformes (hornbills), Coraciiformes (kingfishers and allies), Galbuliformes (puffbirds) and Piciformes (woodpeckers and allies). The affinities of the latter four to each other have been suggested by a number of workers (e.g. Espinosa de los Monteros, 2000; Johansson *et al.,* 2001). The Passeriformes (perching birds) form a large monophyletic group that is split into two fundamental divisions; the suboscines and the oscines (songbirds). The suboscines are further split into Old World and New World taxa. The oscines can be subdivided into a paraphyletic "Corvida" (*sensu* Sibley and Ahlquist, 1990), which contains two distinct clades (the honeyeaters and allies, and the corvoid birds), and the Passerida, which contains three superfamilies; the Sylvioidea, Muscicapoidea and Passeroidea. The taxa within these subfamilies are more concordant with the definition of Barker *et al.* (2002) than that of Sibley and Ahlquist (1990).

Lower-level relationships

The Mesozoic fossil birds are placed at the base of the tree with *Archaeopteryx lithographica* occupying the most basal position. Within these the Enantiornithes form a distinct monophyletic clade. The Enantiornithes are thought to represent a separate Mesozoic radiation to the Ornithurae (the direct ancestors of modern birds) that subsequently became extinct at the Cretaceous-Tertiary boundary (Sanz and Buscalioni, 1991; Feduccia, 1995; Hou *et al.,* 1996; Zhang *et al.,* 2001).

Within the Neornithes the Palaeognathae are sister to the remainder of Neornithes – the Neognathae, as in the traditional classification (Stapel *et al.,* 1984). The extinct palaeognath taxa *Lithornis* and the monophyletic moa – *Megalapteryx* (upland moa), *Dinornis* (giant moa), *Anomalopteryx* (lesser or bush moa), *Euryapteryx* (stout-legged moa), *Emeus* (eastern moa) and *Pachyornis* (heavy-footed moa) – are at the base of the extant palaeognaths. These are then split into two monophyletic clades comprising the Struthioniformes (ratites) and Tinamiformes (tinamous) with the extinct "elephant bird" (*Aepyornis*) at the base. The New Zealand ratites – Apterygidae (kiwis) and Dinornithidae (moa) do not form a monophyletic group, a grouping also found by Houde (1987) and Cooper *et al.* (1992) who suggest that this is evidence for a second colonisation of New Zealand by kiwis.

At the base of Neognathae the Galliformes (landfowl) and Anseriformes (waterfowl) form a monophyletic Galloanserae as proposed by Caspers *et al.* (1997), which is sister taxon to the remainder of extant birds (Neoaves) forming a monophyletic Neognathae as suggested by Cracraft (1988) and Van Tuinen *et al.* (2000) and in contrast to Sibley and Ahlquist's (1990) non-monophyletic Neognathae in which the Galloanserae are sister group to the Palaeognathae. Within the Anseriformes the extinct goose *Cnemiornis* is placed as a sister taxon to the Dendrocygnidae and Anatidae, as suggested by Livezey (1989; 1996). Within the Galliformes, the families and subfamilies follow the same large-scale pattern as that found in the galliform test cases of Chapter 3, i.e. (Megapodiidae, (Cracidae, (Numididae, (Odontophoridae, (Phasianidae, (Meleagridinae, (Tetraonidae))))))).

The hoatzin (*Opisthocomus hoazin*) is placed at the base of the next clade which contains the Musophagiformes (turacos and allies) and Pteroclidiformes (sand grouse) that then form the sister taxon to a monophyletic Columbiformes (doves and pigeons). Although *Opisthocomus* has often been placed with the Cuculiformes (cuckoos, coucals and anis) (Hughes, 2000; Johnson *et al.,* 2000; Hedges *et al.,* 1995) and even with the Gruiformes (crakes and rails) (Livezey and Zusi, 2001) some workers have suggested a relationship with the Musophagiformes (Hughes and Baker, 1999; Sorenson *et al.,* 2003) so this placing is not entirely unexpected.

Pteroclidiformes have been placed with the Columbiformes in a number of source trees (e.g. Rotthowe and Starck, 1998; Paton *et al.,* 2003). The relationships of the Columbiformes are quite uncertain (Sibley and Ahlquist, 1990). They have been placed close to the Passeriformes (Van Dijk *et al.,* 1999) but, as seen here, have also been placed with the Musophagiformes (Van Tuinen *et al.,* 2000). After this a monophyletic Gruiformes is sister to a clade containing Strigiformes (owls), Falconiformes (diurnal birds of prey), Phoenicopteridae (flamingos), Podicipedidae (grebes), Gaviiformes (loons), Sphenisciformes (penguins), Procellariiformes (tube-nose seabirds), Pelecaniformes (totipalmate birds), Ciconiiformes (storks and allies) and Charadriiformes (shorebirds) (with *Turnix* at the base). The Turniciformes (buttonquail – *Turnix*) have presented many problems in the history of avian phylogeny. Superficially they look like true quails but have traditionally been placed in the Gruiformes (Fürbringer, 1888; Sibley and Ahlquist, 1990). More recent analyses have placed them in the Ciconiiformes (Van Tuinen *et al.,* 2000) as is seen in the supertree. These relationships are similar to Sibley and Ahlquist's (1990) definition of "Ciconiiformes" containing the traditional orders Pelicaniformes, Procellariiformes, Charadriiformes, Falconiformes, Sphenisciformes, Podicipedidae and Gaviiformes, with the exception of the Falconiformes, which cluster with the Strigiformes as sister taxon to the main clade. Within Falconiformes are Accipitridae (Old World vultures) whilst the New World Vultures (Cathartidae) are placed close to the storks (Ciconiidae). All these clades are resolved largely as monophyletic groups (as in Storer, 1971; Griffiths, 1994; Paterson *et al.,* 1995; Nunn, 1998; Fain and Houde, 2007). The Sphenisciformes (penguins), Gaviiformes (loons) and Podicipedidae (grebes) have been considered to be closely related by Cracraft (1985), which is the outcome of the supertree analysis. Phoenicopteridae (flamingos) have been suggested to be related to grebes (Van Tuinen *et al.,* 2001) and in the supertree have been placed at the base of the clade containing the grebes, loons, penguins and tube-nose seabirds.

This clade is followed by a monophyletic Cuculiformes then a monophyletic Trogoniformes (trogons). The Cuculiformes is split into two clades containing the Neomorphinae (roadrunners) and Crotophaginae (anis) (Hedges *et al.,* 1995; Johnson *et al.,* 2000) and the Coccyzinae (New World cuckoos) and Cuculinae (Old World cuckoos) (Hedges *et al.,* 1995; Aragon *et al.,* 1999; Hughes, 1999; Johnson *et al.,* 2000). The next clade contains a monophyletic Caprimulgiformes (nightbirds), Aegotheliformes (owlet-nightjars) and Apodiformes (swifts and hummingbirds) (contains monophyletic Apodidae and Trochilidae – which supports Sibley and Ahlquist's (1990) suggested "Trochiliformes" for hummingbird taxa). The association between the Apodiformes (swifts) and Trochiliformes (hummingbirds) has long been recognised (Bleiweiss *et al.,* 1994; Van Tuinen *et al.,* 2000; Johansson *et al.,* 2001; Mayr, 2002) and is not contradicted by any of the source trees. Sibley and Ahlquist (1990) placed Caprimulgiformes within the Strigiformes (Caprimulgiformes was split and renamed Caprimulgi and Aegotheli), however, here the Caprimulgiformes are not placed in even the same clade as the Strigiformes (described earlier).

Next, the Coliiformes (mousebirds) form the sister taxon to a monophyletic Psittaciiformes (parrots and allies). Espinosa de los Monteros (2000) has suggested this relationship for the Psittaciformes, which are traditionally considered to have no close living relatives (Sibley and Ahlquist, 1990). These are sister to a clade containing the monophyletic Coraciiformes (kingfishers and allies), Galbuliformes (puffbirds) and Bucerotiformes (hornbills), which form a monphyletic sister group to the Piciformes (woodpeckers and allies). The Hoopoe, *Upupa epops*, is placed within the Coraciiformes in contrast to Sibley and Ahlquist's (1990) suggestion of a new order "Upupiformes". The Piciformes are split into two distinct clades, one containing the Ramphastidae (toucans) and the Capitonidae (New World barbets) (Simpson and Cracraft, 1981; Swiersczewski and Raikow, 1981; Lanyon and Zink, 1987; Lanyon and Hall, 1994) and the second containing the Picidae (woodpeckers) and the Indicatoridae (honeyguides) (Simpson and Cracraft, 1981; Swiersczewski and Raikow, 1981; Lanyon and Zink, 1987). This clade forms the sister group to a monophyletic Passeriformes (perching birds), which are placed in a derived position within the tree in agreement with traditional views on the timing of their divergence relative to other orders (Johansson *et al.,* 2001). The Passeriformes are the perching birds and contain more than half of all extant avian species.

Acanthisitta and *Xenicus* (New Zealand wrens) are at the base of the Passeriformes. The remainder of the Passeriformes are split into monophyletic suboscines and oscines (songbirds). This is the traditional view of passerine phylogeny and is supported by many previous analyses (e.g. Christidis *et al.,* 1996; Edwards *et al.,* 1997).

The suboscines are split into monophyletic Old World and New World groups. The Old World suboscines contain the Philepittidae (Asities), Eurylaimidae (broadbills) and Pittidae (pittas) and *Sapayoa,* which is at the base of the Eurylaimidae. *Sapayoa aenigma* is found in Panama and northwest South America and was traditionally placed in the New World suboscines, although it has more recently been placed in the Old World suboscines in varying positions (Prum, 1990; Fjeldsa *et al.,* 2003; Chesser, 2004a). Monophyly of the Old and New World suboscines is well-documented (e.g. Irestedt *et al.,* 2001; Irestedt *et al.,* 2002).

The New World suboscines are further split into two monophyletic groups; the tracheophone suboscines (Furnariidae – ovenbirds, Conopophagidae – gnat-eaters, Formicariidae – ground antbirds, Rhinocryptidae – tapaculos, Thamnophilidae – antbirds and Dendrocolaptidae - woodcreepers) and the non-tracheophone suboscines (Tyrannidae – tyrant-flycatchers, Pipridae – manakins and Cotingidae - cotingas).

The Pipridae and Cotingidae both form monophyletic groups. The vast majority of the Tyrannidae are found in a single monophyletic group, some however are placed at the base of the non-tracheophone suboscines and at the base of the suboscine/oscine clade. Within the remainder of the tracheophone suboscines, the Thamnophilidae and Rhinocryptidae are resolved as a monophyletic group, but the remainder of the families are paraphyletic.

The oscines, or songbirds, comprise the majority of the Passeriformes. Their relationships are poorly understood and are the subject of much confusion and controversy, a fact that probably explains the chaos and untidiness that characterises this portion of the supertree.

The Menuridae (lyrebirds) and Atrichornithidae (scrub-birds) have been placed at the base of Passeriformes in the supertree (as in Sibley and Ahlquist, 1990; Ericson *et al.,* 2002). These, with a monophyletic Climacteridae (treecreepers) and Ptilonorhynchidae (bowerbirds), form the sister group to the remainder of the oscines. This is a relationship supported by a number of workers (Sibley and

Ahlquist, 1990; Christidis *et al.,* 1996; Ericson *et al.,* 2002), although many analyses have widely separated these taxa with the bowerbirds placed close to the birds of paradise (Paradisaeidae) (Espinosa de los Monteros and Cracraft, 1997; Cibois and Pasquet, 1999) and also with the babblers (Timaliidae) (Edwards and Arctander, 1997).

The next portion of the tree comprises a number of large clades that correspond to Sibley and Ahlquist's (1990) "Corvida", although they form a paraphyletic group with the "Passerida" nested within. This part of the tree is split into two clades that correspond to the two main assemblages in Christidis and Schodde's (1991) Australo-Papuan songbirds. The first clade (honeyeaters and allies) contains the Irenidae (fairy bluebirds) which, with the Chloropsidae (leafbirds), form the sister taxon to a group containing the Maluridae ("wrens"), Meliphagidae (honeyeaters), Acanthizidae (Australian warblers) and Pardalotidae (pardalotes), in a larger clade with the Orthonychidae (logrunners) and Pomatostomidae (Australasian babblers). The Meliphagidae are monophyletic but the Acanthizidae and Pardalotidae are paraphyletic. The second clade contains the corvoid birds including the Melanocharitidae (berrypickers and longbills), Vireonidae (vireos), Pachycephalidae (whistlers and allies), Oriolidae (orioles), Campephagidae (cuckoo-shrike and allies), Artamidae (woodswallows), Malaconotidae (bushshrikes), Platysteiridae (wattle-eyes), Vangidae (vangas), Dicruridae (drongos), Monarchidae (monarchs), Paradisaeidae (birds of paradise), Laniidae (shrikes), Corvidae (crows and allies) and Petroicidae (Australian robins). Not all of these form perfectly monophyletic groups but they do all form well-defined clear clades. These two clades are thought to represent two endemic radiations (Christidis and Schodde, 1991).

The remainder of the passeriform birds represent the Eurasian radiation and correspond to Sibley and Ahlquist's (1990) "Passerida". Unlike the "Corvida" these form a monophyletic group.

The clade containing the Paridae (tits), Alaudidae (larks) and Hirundinidae (swallows) forming a sister to the Pycnonotidae (bulbuls), Cisticolidae (cisticolas and allies), Sylviidae (Old World warblers), Timaliidae (babblers) and Zosteropidae (white-eyes) corresponds to the superfamily Sylvioidea. First suggested by Sibley and Ahlquist (1990), the results shown here correspond more closely with the definition of Barker *et al.* (2002). It is important to note that although the large-scale relationships fit well with expectations, within these higher taxa the families, and even genera, are quite poorly defined and rarely form monophyletic groups.

Another clade containing the Regulidae (kinglets), Sittidae (nuthatches), Certhidae (treecreepers), Polioptilidae (gnatcatchers), Troglodytidae (wrens), Mimidae (mimids), Sturnidae (starlings), Turdidae (thrushes) and Muscicapidae (Old World flycatchers) represents the superfamily Muscicapoidea. Again, these families are not necessarily monophyletic.

The next clade contains the Promeropidae (sugarbirds), Dicaeidae (flower-peckers), Nectariniidae (sunbirds), Prunellidae (accentors), Estrilididae (Estrilid finches), Ploceidae (weavers), Passeridae (Old World sparrows), Motacillidae (wagtails) and the nine-primaried oscines. Many of these families are paraphyletic and this part of the tree is quite untidy and unclear. This clade does, however, correspond to the third superfamily, Passeroidea, again as defined by Barker *et al.* (2002).

Within the Passeroidea, the nine-primaried oscines, which contain approximately 10% of all extant species of bird (Klicka *et al.,* 2000), form a monophyletic clade. This contains a monophyletic Fringillidae (finches), Cardinalidae (cardinals) and Parulidae (New World warblers) then another monophyletic clade containing a paraphyletic Icteridae (blackbirds and allies), Emberizidae (American sparrows, buntings and allies) and Thraupidae (tanagers). The Coerebidae (bananaquits) are placed within the non-monophyletic Emberizidae and Thraupidae.

4.4.2 Novel clades

There were some novel clades present in the tree. An observation was that all those taxa examined were either a) only present in a small number (often only one) of source trees as part of a polytomy, or b) the taxa were in well-resolved positions in a single source tree and there was no obvious reason for MRP placing them in these spurious groups. Not all will be discussed here but a number have been considered below.

Those taxa whose positions can be explained by a lack of taxonomic constraint include: *Bombycilla japonica* which is placed within the Maluridae with the fossil taxon NHMM/RD 271. This is only found in one source tree (Pasquet *et al.,* 1999) in a polytomy. A large number of poorly-placed taxa are in a large polytomy at the base of the Passeriformes next to *Acanthisitta* and *Xenicus*. These are all passeriform birds (plus the fossil roller, *Geranopterus alatus*) and there is no logical basis for the positioning of these taxa. The following taxa are all part of this clade and each appear in only a single source tree and as part of polytomies: *Myiagra ferrocyanea* (steel-blue flycatcher) – in Filardi and Smith (2005); *Pteruthius xanthochlorus* (green shrike-babbler) and *Pteruthius rufiventer* – (black-headed shrike-babbler) – in Cibois (2003); *Andropadus curvirostris* (plain greenbul) and *Andropadus importunus* (sombre greenbul) – in Roy (1997).

Many of the novel clades were as a result of poorly constrained fossil taxa. *Eocoracias* (a middle Eocene roller) is placed with *Palaeotis* (a basal ratite) at the base of the Palaeognathae. This is a logical positioning for *Palaeotis* but there is no reason for *Eocoracias* to be placed here. It occurs in two source trees, one as sister to all other taxa (Mayr and Mourer-Chauvire, 2000) and in the other as part of a large polytomy (Mayr *et al.,* 2004). The Mesitornithidae (*Mesitornis* and *Monias*) are thought to be related to the cuckoos (Cuculiformes) (Mayr and Ericson, 2004) but have been placed within the Caprimulgiformes with *Steatornis* (oilbird) and the extinct oilbird taxon – *Prefica nivea*. The Quercypsittidae, which comprises two species of fossil parrot, is placed at the base of the clade containing the Coliiformes and Psittaciformes. *Pulchrapollia gracilis*, another fossil parrot, has been placed within the Coraciiformes. *Geranopterus alatus*, a fossil roller (Coraciiformes), is placed at the base of the Passeriformes with the New Zealand wrens. Another fossil roller of the same genus, *Geranopterus milneedwardsi,* has been placed within the Maluridae (Passeriformes). Finally, the unassigned fossil taxon NHMM/RD 271 was also placed within the Maluridae. Many of these fossil taxa are only represented in a single source tree and often only as part of a polytomy, for example, the fossil taxon NHMM/RD 271 is only found in Dyke *et al.* (2002) in a polytomy with *Anas* and *Ichthyornis*.

Less easy to explain are those that appear in well-resolved positions in source trees. Some examples are *Telophorus bocagei* (bushshrike) – in Smith *et al.* (1991); and

Catharus fuscater (slaty-backed nightingale-thrush) and *Catharus mexicanus* (black-headed nightingale-thrush) – both in Outlaw *et al.* (2003).

4.4.3 Results of the "community tree-building" approach

The community aspect of this project produced a total of four result trees at the time of writing (December 2007). Two of them were uploaded by the author. The trees uploaded by other interested parties were produced using TNT. Both were longer than the tree presented here and therefore have not been shown. Although not many trees were uploaded a number of errors, both taxonomic and syntactical, were identified in the source data by viewers of the uploaded source trees and, in this way, the community approach did greatly improve the quality of the supertree. As an example, the original uploaded source data was found to contain four duplicated albatross taxa, in the form of synonyms, which needed to be removed before any further analyses were carried out.

4.5 Discussion

The results show that the supertree is a reasonable assessment of the current understanding of avian phylogeny. As with the Galliformes supertree in Chapter 3 though, it would be advisable, at present, to view it only as an assessment rather than as a definitive statement of avian phylogeny and evolution. There are a number of novel clades, but these all occur at lower taxonomic levels and it is clear that the majority of these have arisen as a result of poor taxonomic sampling.

Many of the novel clades and poorly placed taxa are a result of low taxon sampling. This statement is made more robust as the protocol used to build the supertree ensured consistent naming of taxa, which may have exacerbated this problem. The protocol and data storage mechanisms (see Chapter 3) also made it very easy to pinpoint which sources trees contained taxa in novel clades and other spurious groupings. While novel clades are essentially an undesirable result, they are useful in that they pinpoint areas of phylogeny that need more research, which is, in fact, one of the justifications for supertrees in that they can highlight areas of poor taxonomic sampling (Bininda-Emonds *et al.,* 2002).

However, there were some taxa for which there was no obvious reason for their spurious placement in the tree. It is possible that this is an undesirable property of MRP (Matrix Representation with Parsimony). It is also possible that given more time to run the analysis (there was a queue length limit of 12 hours on the machine used) these anomalies would be resolved. Running the supertree on a similar machine for an increased length of time is an obvious next step to take in investigating these results as it is possible that further analysis of the data may find shorter trees. This could be surprisingly successful as the tree presented here was only four steps shorter than the second shortest tree found and yet was successful in resolving the positions of a number of the fossil taxa which had been placed in obviously spurious clades in the second shortest tree.

No measures of fit were added as there are currently none appropriate for supertrees in existence. Ruta *et al.* (2003) state that “statistical methods devised to assess branch support in character-based trees are problematic for supertrees”. Bininda-Emonds (2003) developed QS values, Qualitative Support, and applied them to a supertree of marsupials (Cardillo *et al.,* 2004). The QS index works by comparing source trees with the supertree and assigning one of four “states” for the fit between the two. A hard match occurs where the source tree fits the supertree exactly, a soft match occurs where addition of missing taxa may support the clade but never contradict it and vice versa for a soft mismatch, finally, a hard mismatch occurs where the source tree contradicts the supertree. However Wilkinson *et al.* (2005a) state that the QS values are flawed as the categories defined by Bininda-Emonds (2003) were not mutually exclusive, for example the definitions of equivocal and soft support both contain no hard matches or mismatches and both contain soft mismatches.

The community aspect of the project was not very successful. Although a few data problems were found by others (taxon duplication and a few erroneous trees) only one other person had uploaded a final tree at the time of writing. However, this approach did pick out problems such as duplicate taxa (albatrosses) and empty leaves, which were a result of a syntactical error in the taxa substitution script. These problems were subsequently dealt with before re-running the matrix. It is surprising that the project did not attract more attention as a large species-level supertree is very much in demand at the present time.

4.6 Conclusions

This study has produced the largest, to the author's knowledge, supertree of both extinct and extant avian species using robust data collection and processing methods. The tree contains over half of the known extant avian fauna. Over 5000 individual species or genera were included, covering 24 years worth of systematic research into Aves, and five times as inclusive as the next largest study, Sibley and Ahlquist's "tapestry" (1990). This level of taxonomic coverage would simply not have been possible with any other method of constructing large-scale phylogenies.

The results were sensible, giving a reasonable summary of the current knowledge of avian phylogeny. It is clear though that there is still much work to be done and there are a number of areas that require much more primary data collection and analysis. Many of these areas were identified by the presence of novel clades, which, on inspection, were evidently the result of poor taxonomic sampling. Other novel clades were as a result of the inclusion of fossil taxa, the only solution here is for more fossils to be described and included in phylogenetic analyses. Finally, there were some spurious groups that can not be easily explained. These could be due to undesirable properties of MRP or may be resolved simply be further analysis, as the current analysis was, by necessity, limited to a run time of just 12 hours.

The tree presented here is the largest species-level supertree constructed, to the author's knowledge, and will provide a useful resource for researchers studying avian macroevolution, biodiversity and character evolution. One such study would be to date the tree as in Bininda-Emonds *et al.* (2007) mammal supertree. This could be particularly interesting as the avian supertree presented here has incorporated fossils, something not covered by Bininda-Emonds (2007). In addition, the tree provides a "straw man" for further systematic research into Aves.

The next chapter takes a look at the supertree versus supermatrix "controversy" and builds two Galliformes phylogenies in order to compare and contrast the two methods.

Chapter 5

Supermatrix or Supertree? A comparison of supertree and supermatrix methods

5.1 Abstract

There are two distinct methods available to construct large-scale trees: supermatrix and supertree. Each has advantages and disadvantages, but supertrees in particular have come under heavy criticism from some authors. Supertrees are secondary constructions, built from individual phylogenetic trees, whereas a supermatrix is constructed from primary data collated into a single, large matrix. This chapter looks at the supertree vs. supermatrix "controversy" in order to assess which, if either, is a more suitable method of building large phylogenetic trees. A molecular-only tree was constructed using both methods, using the same data, thus ensuring that neither method had an advantage. Each output tree was then compared to the input source trees of the supertree as a method of assessing how each large-scale phylogeny represented the smaller, independent, source studies. Both methods performed equally as well in fitting the source data. The supermatrix was much quicker to construct, but took substantially longer to calculate. The supertree took a long time to construct, mainly due to the stringent data control protocols in place (see Chapter 3), but was very quick to calculate. Dependent upon the data at hand and the other factors involved, the choice of which method to use appears, from this small study, to be of little consequence.

5.2 Introduction

Supertree and supermatrix methods are two general approaches used to construct large trees from datasets with a diverse array of data. Supertrees have been discussed fully in previous chapters, however some workers believe that supertree methods cannot add anything to our knowledge of the tree of life and that supermatrices should instead be constructed (Gatesy *et al.*, 2002; Gatesy *et al.*, 2004; Queiroz and

Gatesy, 2006). A supermatrix represents the total evidence approach, where characters and taxa make up a single large matrix and the data are analysed simultaneously (Miyamoto, 1985; Kluge, 1989; Nixon and Carpenter, 1996).

Gatesy *et al.* (2002) argue that supertrees "are imprecise summaries of previous work" and that a supertree cannot be a better depiction of previous research (referring to Purvis, 1995; Bininda-Emonds *et al.*, 1999; Liu *et al.*, 2001; Jones *et al.*, 2002) than a supermatrix, due to the fact that supermatrices clearly review which characters have or have not been scored for particular taxa. These primary data are presented with no duplications or editing errors, and are easily accessible for examination by other researchers. In contrast, Queiroz and Gatesy (2006) state that in supertree analyses some of the character information is lost when sets of characters are combined as trees. The finding that trees produced by supermatrix analyses tend to be better resolved than those from supertree analyses is also thought "to reflect the greater information content of supermatrices and the associated emergence of hidden support" (Queiroz and Gatesy, 2006).

With regards to hidden support it is suggested that while supermatrices can produce novel clades as a result of hidden character support with a well-characterised basis (Barrett *et al.*, 1991; Gatesy *et al.*, 1999; Lee and Huggal, 2003), Matrix Representation with Parsimony (MRP), by far the most commonly utilised method of supertree construction, ignores or misinterprets hidden character support in different source data sets and produces novel clades with no logical basis (Gatesy *et al.*, 2004).

Simulations have shown that MRP can approximate total evidence (Bininda-Emonds and Sanderson, 2001). Gatesy *et al.* (2004) however, state that these simulations are run on ideal data and that none of these conditions are duplicated in published MRP supertree datasets. Therefore, they believe that these simulated results cannot be taken at face value.

A drawback of the supermatrix approach is that some types of data, such as from DNA-hybridisation and immunological distances, cannot be combined into a single data matrix (Sanderson *et al.*, 1998). However, Gatesy and Springer (2004) believe that the types of information that cannot be included in a supermatrix are limited to those which are partially redundant, obsolete, or have no clear empirical basis, and as such is “not a great loss of taxonomic information”.

The other issue with supermatrix analyses is that as more genes and characters are added and the datasets become ever larger, there are only a few taxa in common between datasets and as such, most of the data matrix will be scored as question marks, which requires a huge input of collective effort and time to fill in these gaps (Sanderson *et al.*, 1998). Therefore, the included taxa must be limited in order to avoid these problems, which results in supermatrices often offering much poorer taxonomic coverage than that possible from a supertree analysis. Figure 5.1 shows an example of a data availability matrix for green plants, showing that only a small number of genes (horizontal axis) have been sampled for a large number of taxa (vertical axis) and vice versa.

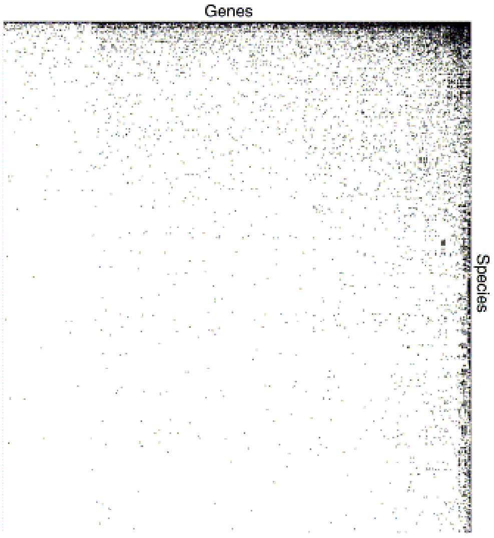

Figure 5.1: Data availability matrix for green plant proteins from GenBank (release 132). The figure shows that there are a large number of genes sampled for only a few taxa and many taxa sampled for just a few genes. Each dot represents a single gene sampled for a single taxon. Species were ordered according to the number of genes sampled, with better sampled species at the top. Similarly, the more commonly used genes are to the right, so the top right corner contains the densest concentration of data. The rest of the matrix is sparsely covered. From Sanderson and Driskell (2003).

As a response to these statements, Bininda-Emonds (2004) states the belief that supertrees and supermatrices analyse different data using different assumptions and methods, and therefore should be seen as complementary, not competing. Thus when these different approaches produce the same results there should be an increased level of confidence in those results. Where they disagree, this should indicate a need for further investigation.

Some previous studies have carried out some comparisons of supermatrix and supertree results. For example, Gatesy *et al.* (2002) looked at the percentage of shared key nodes and Price *et al.* (2005) considered clade congruence between the trees. The key difference with this work is that both these previous studies only considered how similar the trees were to each other rather than how well they represented the source data.

To investigate these issues, two trees for Galliformes will be compared. One will be created from a supermatrix and one from a supertree analysis constructed from source trees derived from the same data used to construct the supermatrix. The trees will also contain the same taxa. The aim is to determine which method, if either, produces results more consistent with the source data for the supertree. Galliformes were chosen as they are a well-known group with well-documented monophyly. Also, this group was used in Chapter 3 to test the supertree protocol so this provides a good opportunity to compare and contrast methods of creating large phylogenetic trees on a pre-existing dataset. It was decided that a molecular-only study would be carried out as this information is easy to collate from the pre-existing data collected for the supertree and from online sources, such as GenBank[1] for the supermatrix. The original Galliformes dataset from Chapter 3 was modified such that a molecular-only supertree (i.e. containing source trees derived from molecular only studies) analysis could be carried out. Only the data readily available for inclusion in a supermatrix analysis were retained for analysis in the molecular supertree so that an equivalent supermatrix analysis could be carried out. The trees were assessed against the input source data by using `ent` (Page, pers comm) (as in Chapter 3) to compare

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[1] http://www.ncbi.nlm.nih.gov/Genbank/index.html

each tree to the set of input data to assess which, if either, is more consistent with the source data.

5.3 Methods

5.3.1 Data collection

Sequences for Galliformes were obtained from GenBank using a Perl script. Given a list of all Galliformes nucleotide accession numbers available in GenBank on the 2nd September 2005, the script retrieved each sequence record in XML format using NCBI's Entrez Utilities service. The sequences were then stored in a MySQL database. Because the same gene may have multiple names, and different names may be used by different research groups when depositing their data, the database was manually edited to link gene name synonyms together. Sequences from the same genes were exported as FASTA format files for alignment.

Data for the supertree were taken from the Galliformes supertree dataset (Chapter 3). In order to make a fair comparison of methods this dataset was pruned to only contain source trees that were constructed using the same genes as those included in the supermatrix analysis. Due to the data collection methods employed, this was easy to carry out as the XML files already created for the supertree data contained all the necessary information.

After initial source tree pruning there remained a total of 30 source trees from 22 publications. The supertree dataset contained 153 taxa in the supertree dataset. The supermatrix data contained 151 taxa (152 with the outgroup *Aythya*), including a number of subspecies, which obviously were not present in the supertree dataset. The supertree dataset contained 9 taxa not present in the supermatrix data. After standardisation to remove taxa not present in both datasets, 144 taxa remained.

The taxa for the supertree were checked in the Glasgow Taxonomic Name Server[2] (Page, 2005) and any synonyms were corrected. This did not result in a change of

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[2] http://darwin.zoology.gla.ac.uk/~rpage/MyToL/www/index.php

taxa number therefore the data processing and analysis could proceed without any further modifications to the taxa.

5.3.2 Data processing

For the supermatrix, alignments were created in ClustalX 1.83 (Thompson *et al.,* 1997) using the default settings. The 16S rRNA alignment was trimmed and some taxa were removed from the CO1, COIII and tRNA-Trp sequences.

Supermatrix construction was automated using a Perl script. As when automating data processing elsewhere, this greatly reduced potential error and computational time. The taxon *Aythya americana* (redhead duck) was assigned as the outgroup. Within the matrix the data were organised into 41 character-based sets.

The supertree data had already been collated for the analysis described in Chapter 3 and were processed as described in the Chapter 3 protocol. The taxonomy had already been standardised for that analysis therefore it was only necessary to remove any source trees not based on molecular data included in the supermatrix. It was then possible to proceed as usual from the “check overlap” stage (see Chapter 3). This check showed that four trees were now no longer connected to the main cluster (Figure 5.2), therefore these were pruned from the dataset in order to fulfil the requirement of all trees overlapping by a minimum of two taxa with at least one other tree (Sanderson *et al.,* 1998). Once these trees were removed from the dataset the overlap was recalculated and it was found that all trees were now connected by the minimum required number of taxa (see Figure 5.3). Running a supertree analysis with these four pruned trees included produced obviously anomalous results. After carrying out this additional pruning of source trees the taxa number needed to be adjusted again and therefore the final trees contained 119 taxa. After all modifications to the included taxa, the final dataset contained 59% of the taxa included in the Galliformes supertrees of Chapter 3. See Appendix E for the final list of source trees.

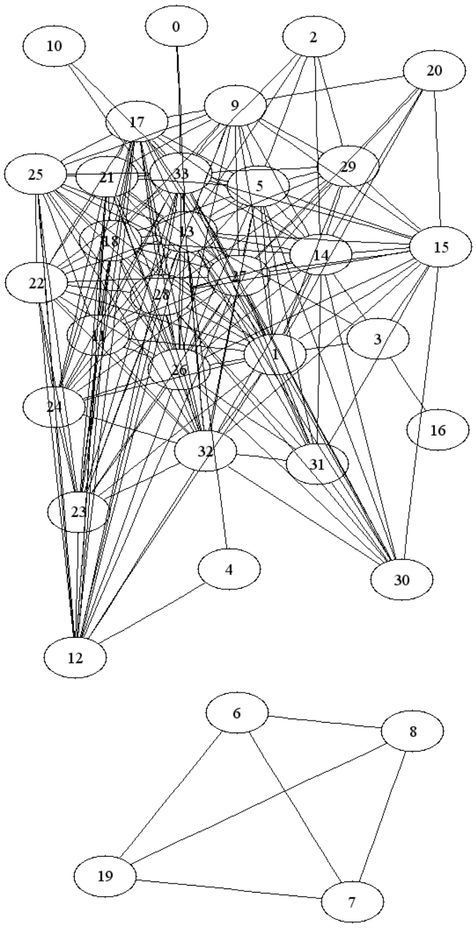

Figure 5.2: Graphical representation of minimal overlap of source trees after pruning of non-molecular source trees. The island consisting of four source trees needs to be removed from the study.

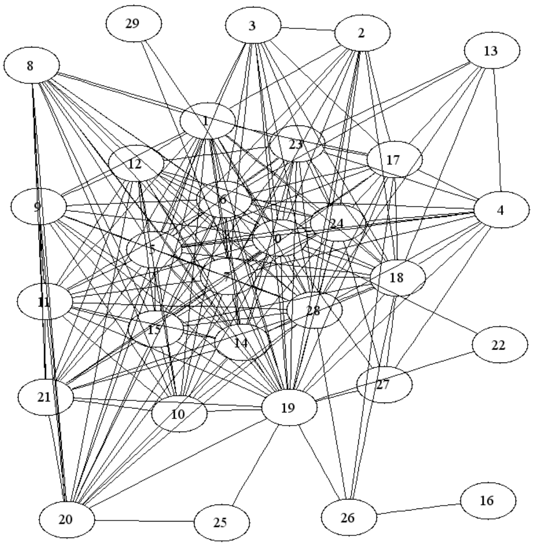

Figure 5.3: Graphical representation of minimum overlap after pruning of the four disconnected trees in Figure 5.2.

After a final check of the data integrity to ensure that no errors had been introduced, the MRP (Matrix Representation with Parsimony) matrix was created, first by combining the source trees into a single file (Appendix C), then the matrix was created using a version of Bininda-Emonds' SuperMRP.pl Perl script (Bininda-Emonds *et al.,* 2005) which had been modified to run in Windows.

5.3.3 Analysis

The supermatrix was analysed in PAUP* 4.0b10 (Swofford, 2002) using a heuristic search, with all characters unordered, equal weighting of transformations, indels treated as missing as data, 100 random taxon addition replicates, and tree bisection-reconnection branch swapping. An attempt was made to run the matrix in TNT (Goloboff *et al.,* 2008) as this has previously been found to find significantly shorter trees (see Chapter 3). Unfortunately it was not straightforward to reformat the matrix into a suitable format and therefore running the matrix in TNT was beyond the scope of this study due to time constraints. It seems unlikely though that this would have affected the results to a significant degree.

The supertree was analysed in both PAUP* 4.0b10 (Swofford, 2002) using the Parsimony Ratchet (Nixon, 1999) and in TNT (Goloboff *et al.,* 2008) using the "xmult=level 10" command; an aggressive search designed to find the shortest trees.

Searches were carried out on an Apple MacBook 2.0GHz Intel Core 2 Duo with 2GB of RAM.

The resulting trees from the supertree analysis and supermatrix analysis were compared to the source trees in order to assess fit and therefore which, if either provided results more consistent with the source studies. The program `ent` (Page, pers comm) was used for this. `Ent` compares the output (from the supertree or the result of the supermatrix analysis) to all the input trees (the source trees of the supertree analysis) and gives scores for each input tree (scores are between 0 and 1 with 0 being a complete mismatch and 1 being a perfect match). This was done for both the supermatrix tree and the supertree using the source trees for the supertree as input trees.

5.4 Results

In the supertree analysis PAUP* (Swofford, 2002) found 499 shortest trees of length 447 whilst TNT (Goloboff *et al.,* 2008) found 12 shortest trees of length 426. The strict consensus was poorly-resolved but the 50% majority rule consensus was reasonably well-resolved and is shown in Figure 5.4.

In the supermatrix analysis a total of 20400 most parsimonious trees (MPTs) of length 41225 were found. Both the strict consensus and 50% majority-rule consensus trees were well-resolved. The 50% majority-rule consensus is shown in Figure 5.5. See Figure 5.6 for a graph of the supermatrix tree showing gene coverage per taxon.

The two trees are broadly similar and show essentially the same higher-level relationships. Figure 5.7 depicts a tanglegram showing similarities and differences between the two trees. Both are concordant with generally accepted views of galliform phylogeny. The families are not all monophyletic but do broadly fall into the pattern of (Megapodiidae, (Cracidae, (Numididae, (Odontophoridae, (Phasianidae, (Meleagridinae, Tetraonidae)))))).

The Megapodiidae and Cracidae are resolved as monophyletic groups in the trees. These taxa do not, however, form the monophyletic taxon Craciformes as proposed by Sibley and Ahlquist (1990). Instead, the results support the more traditional view of the Megapodiidae forming the sister group to all other extant Galliformes (in agreement with Dimcheff *et al.,* 2002; Dyke *et al.,* 2003; Gulas-Wroblewski and Wroblewski, 2003; Smith *et al.,* 2005). A monophyletic Odontophoridae and the monospecific (in this study) Numididae are sister taxa to a monophyletic Phasianidae, which contains the majority of the galliform species.

The Phasianidae is a large order and is easier to consider as subfamilies. Subfamilies have been defined according to Howard and Moore (2003) in keeping with the definitions set for higher taxa within Chapter 3. Using this classification, the Phasianidae contains a paraphyletic Perdicinae (Old World partridges) and Phasianinae (pheasants). As already noted in Chapter 3, pheasants and partridges were originally thought to represent monophyletic lineages (Johnsgard, 1986, 1988; Sibley and Ahlquist, 1990), however, more recent evidence (Kimball *et al.,* 1999; Geffen and Yom-Tov 2001; Smith *et al.,* 2005) suggests that this is not actually the case. Both analyses produced results that are concordant with the non-monophyletic viewpoint. Within the Perdicinae the francolins are split into the quail francolins and partridge francolins as suggested by Crowe *et al.* (1992) and Bloomer and Crowe (1998) but are not monophyletic (in agreement with Bloomer and Crowe, 1998). The partridge francolins form a sister group to the *Coturnix* quails, Madagascar partridge (*Margaroperdix madagarensis*) and to the *Alectoris* partridges, again as in Bloomer and Crowe (1998). The Phasianinae are roughly split into two groups: a group containing the peafowls and allies, and junglefowl; and a group containing the gallopheasants and allies, and the tragopans. The former group is paraphyletic in the supertree and part of a polytomy with the quail francolins in the supermatrix tree.

Meleagris, the only member of the Meleagridinae (turkeys) in this analysis, and Tetraonidae (New World quail) are each other's closest relatives and cluster with the branch of the Phasianinae containing the gallopheasants and tragopans (as in Geffen and Yom-Tov, 2001; Dimcheff *et al.,* 2002). Kimball *et al.* (1999) support the clustering of the Meleagridinae and Tetraonidae but are not able to resolve the relationship of these to other Phasianidae. In the supermatrix analysis *Perdix* (Perdicinae) and *Pucrasia* (Phasianinae) are sister taxa to the Meleagridinae and together these form the sister group to the Tetraonidae.

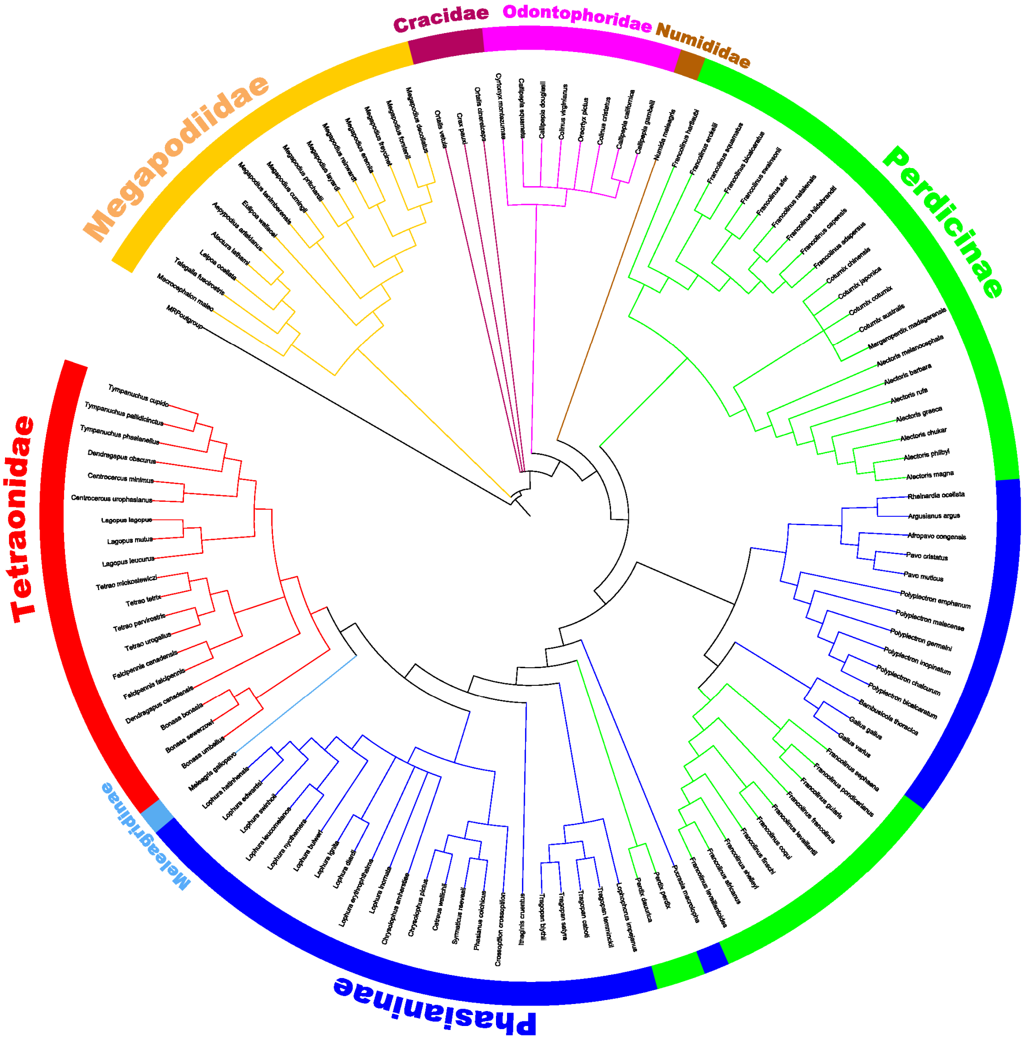

Figure 5.4: Galliformes molecular supertree – shown is the 50% majority-rule consensus of 12 MPTs of length 426 found in TNT (Goloboff *et al.*, 2008).

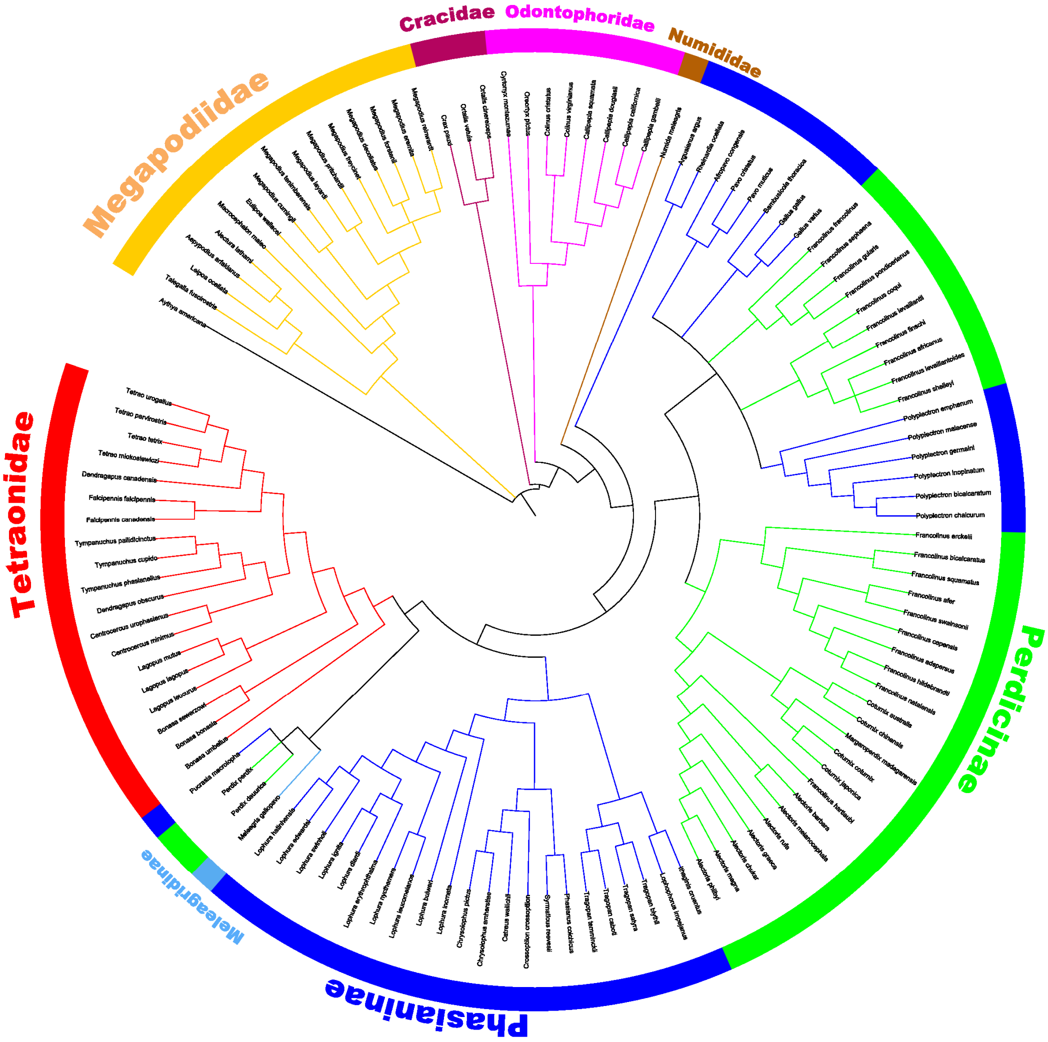

Figure 5.5: Galliformes tree from the supermatrix analysis - shown is the 50% majority-rule consensus of 20400 MPTs of length 41225 found in PAUP* 4.0b10 (Swofford, 2002).

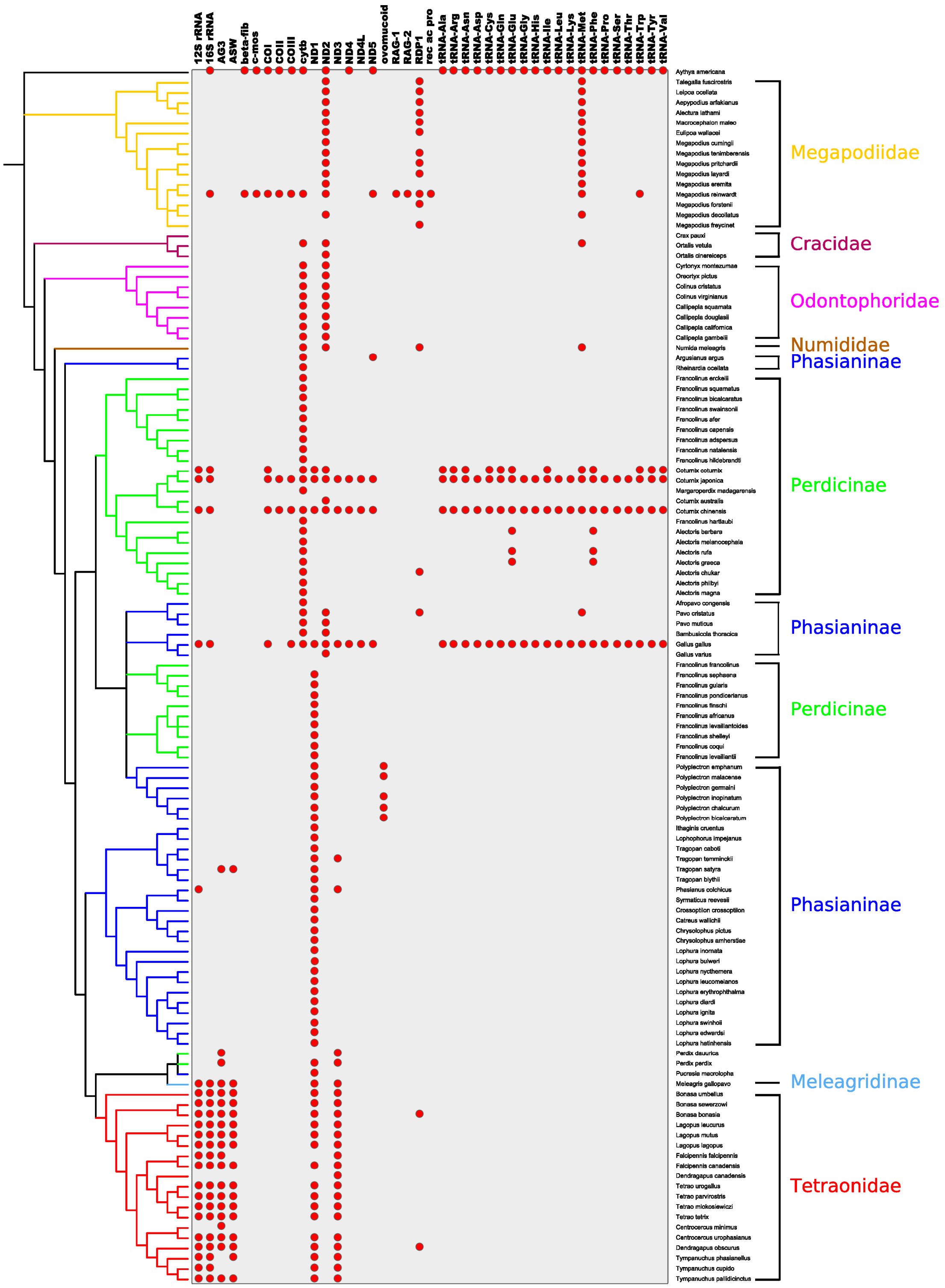

Figure 5.6: Graph of gene coverage for the Galliformes supermatrix. Red circles indicate characters sampled for each taxon, the shaded box shows missing data.

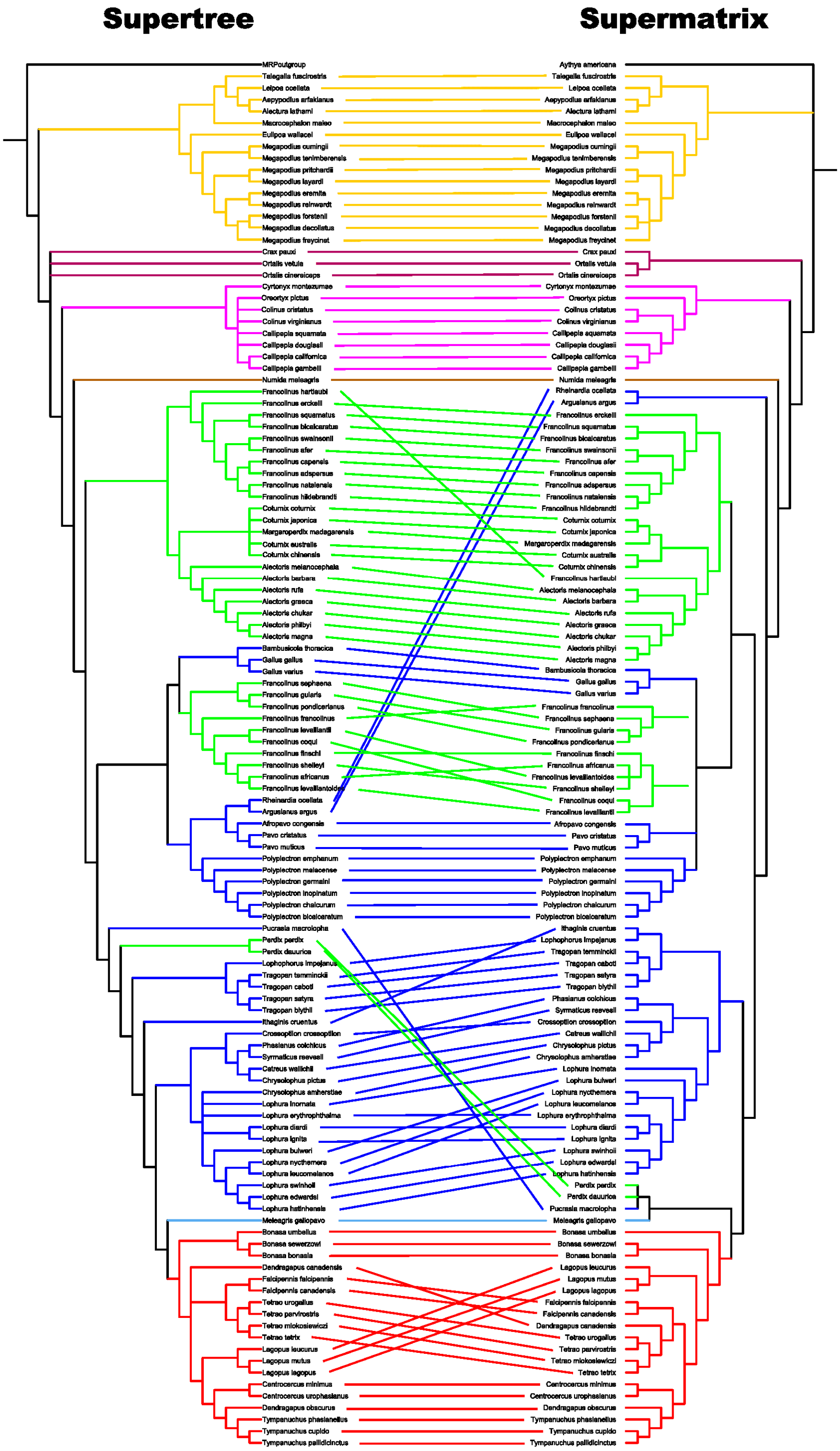

Figure 5.7: Tanglegram showing similarities and differences between the Galliformes supertree and supermatrix. Lines are drawn between corresponding taxa on each tree therefore the less lines that are crossed indicates higher similarity between the trees. Colours indicate families/subfamilies and are coded as in Figures 5.4, 5.5 and 5.6

Comparisons were made between the resulting trees and the set of source trees to assess the ability of each method to accurately represent the source trees. As the data do not follow a Gaussian distribution (this is desirable as the optimum fit would be all trees with a score of 1 and hence give a non-Gaussian distribution), a non-parametric test must be used to ascertain if the difference between the weighted and combined fit scores are statistically significant. Therefore, the Mann-Whitney-U test was used to test if the difference between the means of the two samples was statistically significant.

The results show that for the supertree the mean fit scores are 0.9071 for triplet fit and 0.7227 for MASTd (higher score indicates better fit). For the supermatrix the mean fit scores are 0.8976 for triplet fit and 0.7185 for MASTd (see Table 5.1) for full statistics). Interestingly, these are much higher than the equivalent results from Chapter 3. This could be as a result of “molecular vs. morphological” conflict being removed in the molecular only dataset. The two sets of trees do still show essentially the same higher level relationships, which suggests that the molecular/morphological conflict is within the shallower nodes, i.e. species-level.

From these scores (Table 1) and the box plots (Figure 5.8) the supertree and supermatrix appear to be equivalent representations of the source data. To test this, the Mann-Whitney-U test was used, which showed that the there is no statistically significant difference between the mean fit for the supertree and for the supermatrix to a 0.99 confidence level. The calculated P-value of 0.8824 is not at all statistically significant; and shows that there is no significant difference between the means of the two samples. The majority-rule consensus trees for each method were used to generate these results.

Table 5.1: Statistical data for "fit" scores for both the supertree and supermatrix.

Method	Min	1st Qu	Median	Mean	3rd Qu	Max.
Supertree Triplets	0.5760	0.8587	0.9205	0.9071	0.9990	1.0000
Supermatrix Triplets	0.6060	0.8407	0.9335	0.8976	0.9763	1.0000
Supertree MASTd	0.3680	0.6478	0.7140	0.7227	0.8330	1.0000
Supermatrix MASTtd	0.4000	0.6440	0.7530	0.7185	0.8397	1.0000

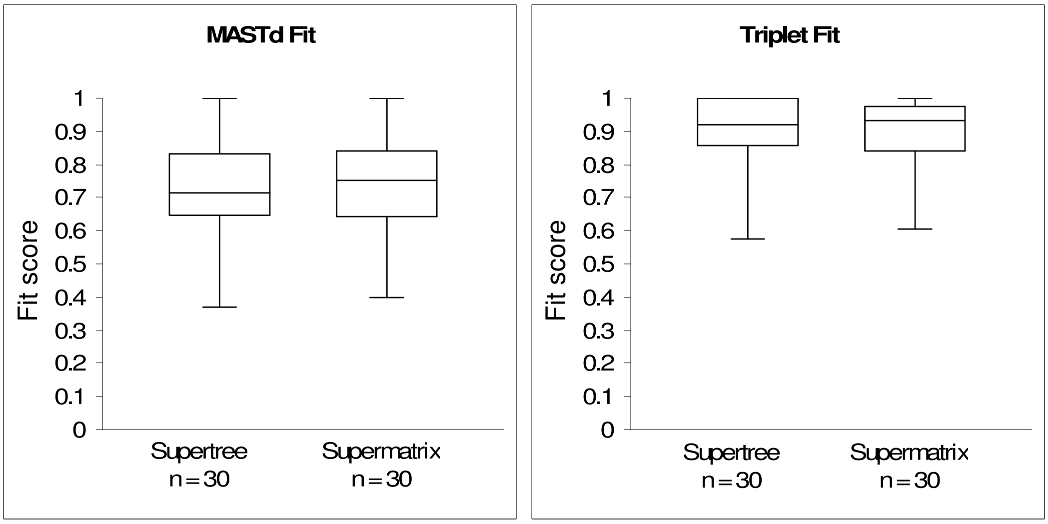

Figure 5.8: Box and whisker plots for the supertree and supermatrix (see Table 1 for individual figures).

In addition to this, the time taken for each tree to compute was recorded (see Table 5.2). The supertree took much less time to compute in both PAUP* (Swofford, 2002) and in TNT (Goloboff *et al.,* 2008) than the supermatrix analysis, with the TNT analysis completing in just 0.03% of the time taken by the PAUP* analysis.

Table 5.2: Run times for computation of both trees in two different programs.

	Paup	TNT
Supertree	24 min 15.18 secs	35 secs
Supermatrix	36 hrs 42 min 2secs	----

5.5 Discussion

Both trees gave reasonable, sensible results with no novel clades. There were no surprises in the results and both conformed well with currently accepted views on galliform phylogeny. The trees were based on equivalent data and it is therefore reasonable to compare both with the source trees used in the supertree analysis.

There was no statistically significant difference between supertree and supermatrix tree construction methods to a 0.99 confidence level. Two scoring methods were used in order to provide a more robust test. These scoring methods are independent of each other and still gave the same result. This increases confidence in the result that each method produces results as consistent with the source data as the other.

Although both methods were equally successful at representing the source data it was far easier to create the supermatrix analysis. From initial data collection to creating the matrix, both of which can be (and were) automated, the process was much quicker than creating a supertree analysis. A supertree analysis has the potential to be computationally much faster, however, in order to ensure data quality and integrity a strict protocol (as described in Chapter 3) must be followed and this is what lengthens the whole process by a considerable amount. Conversely though, the actual run time of the supertree analysis is far quicker than that taken by the supermatrix analysis. If the supermatrix was to be rerun using TNT (Goloboff *et al.,* 2008) it would quite probably find shorter tree in a shorter time, as found in the supertree analyses both here and in Chapter 3. However, it seems unlikely that it would complete in anywhere near as short a time as the 35 seconds taken by TNT to complete the molecular supertree analysis.

Given the above results it seems reasonable to suggest that, in this case at least, the supertree gives as valid results as does the supermatrix analysis. One difference to note is that the supertree was significantly less well-resolved in the strict consensus than the strict consensus of the trees found by the supermatrix analysis. It seems likely that this is due to conflict between the source trees that the supertree was unable to resolve and that, therefore, if resolution is a high priority it may be worthwhile constructing a tree using supermatrix methods, whilst bearing in mind the caveats of taxonomic limitations and increased computational time.

In this study the supertree and supermatrix are identical in terms of taxonomic coverage. This was intentional in order to provide a fairer comparison. In a "real-life" scenario it would be desirable to cover as many taxa as possible and in this case it is likely that the supermatrix would not be as taxonomically complete as a supertree.

5.6 Conclusions

The aim of this chapter was to compare and contrast supertree and supermatrix methods of tree-building in light of the controversies and discussion following these techniques for creating large phylogenetic trees (e.g. in Gatesy *et al.,* 2002; Bininda-Emonds *et al.,* 2003; Bininda-Emonds, 2004; Gatesy *et al.,* 2004; Queiroz and Gatesy, 2006).

The results were analysed in the same way as the Galliformes supertrees in Chapter 3 and show that there is no statistically significant difference between the tree constructed from a supermatrix and that constructed from a supertree analysis, i.e. each represents the input source data as well as the other. In this way, the two methods are complementary as suggested by Bininda-Emonds (2004), so it seems reasonable that these are good representations of galliform phylogeny.

Both trees were very similar in terms of large-scale relationships. Each gave sensible results and no spurious groups were identified. The higher-level relationships did not differ to those found in the taxonomically more inclusive Galliformes supertrees constructed in Chapter 3.

The next chapter moves on to describe a new supertree of the Dinosauria and describes the results found from the first quantitative study of diversification of the Dinosauria.

Chapter 6

Dinosaurs and the Cretaceous Terrestrial Revolution

This chapter has been submitted as a paper to Proceedings of the National Academy of Sciences.

6.1 Abstract

Dinosaurs were never more diverse than in the last 18 million years before their extinction, just as modern, angiosperm-dominated ecosystems were establishing themselves. This radiation of flowering plants was key to the Cretaceous Terrestrial Revolution (CTR), a time when lizards, birds, mammals and insects were adapting to the new ecological opportunities on offer. Others argue that dinosaurs were in decline long before their ultimate extinction. We show here that both views are incorrect, that the apparent explosion of dinosaurian diversity is a result of sampling, but that the group was not declining either. Results from the first quantitative study of diversification applied to a new supertree of dinosaurs suggest that this apparent burst in diversity at the end of the Cretaceous is a sampling artefact. In fact, dinosaurs showed most of their major diversification shifts in the first third of their history. Dinosaurs then were not progressively declining at the end of the Cretaceous; nor were they profiting from the new ecological opportunities offered by the CTR.

6.2 Introduction

Dinosaurs are icons of success and failure. According to a long-standing hypothesis (Sloan *et al.,* 1986; Sarjeant and Currie, 2001), the group was in decline long before its extinction at the end of the Cretaceous period, 65 Ma (million years) ago. However, new evidence (Wang and Dodson, 2006) suggests a major increase in diversification during the Campanian and Maastrichtian, spanning approximately the last 18 Ma of the Cretaceous, and so emphasizes the dramatic nature of their apparently sudden extinction at the end of the Cretaceous. This Late Cretaceous diversification has been seen as evidence that dinosaurs were part of the Cretaceous explosion of terrestrial life (Weishampel *et al.,* 2004) characterized by, among others, the rise of flowering plants, social insects, butterflies, as well as modern groups of lizards, mammals, and possibly birds (Hedges *et al.,* 1996; Grimaldi, 1999; Dilcher, 2000; Fountaine *et al.,* 2005; Bininda-Emonds *et al.,* 2007).

The Cretaceous period (145-65 Ma ago) has long been regarded as a time of major reorganization and modernisation of ecosystems. In the marine realm, these ecosystem changes have been named collectively the Mesozoic Marine Revolution (Vermeij, 1977), characterized by the appearance of new groups of planktonic organisms (e.g. coccoliths, foraminifera, dinoflagellates, diatoms) and new predators among crustaceans, teleost fishes, and marine reptiles. It has been postulated (Vermeij, 1987) that the emergence of such predators selectively favoured the appearance of thicker exoskeletons as a defensive measure in prey groups such as bivalves, gastropods, and echinoids. The evolution of land organisms was also characterized by a **Cretaceous Terrestrial Revolution** (CTR), as we term it here, marked by the replacement of ferns and gymnosperms by angiosperms (Dilcher, 2000). The huge radiation of angiosperms provided new evolutionary opportunities for pollinating insects, leaf-eating flies, as well as butterflies and moths, all of which diversified rapidly (Grimaldi, 1999). Among vertebrates, lizards, snakes, crocodilians, modern placental mammal superorders, and primitive groups of birds underwent major diversifications (Hedges *et al.,* 1996, Fountaine *et al.,* 2005, Bininda-Emonds *et al.,* 2007) although the timing of appearance of modern bird orders remains controversial (Hedges *et al.,* 1996; Dyke, 2001).

Dinosaur evolution was characterized by the appearance of truly spectacular new forms. Giant sauropods, the dominant herbivores of the Jurassic, were joined by new kinds of ornithischians at the beginning of the Cretaceous. Subsequent new waves of diversification at the beginning of the Late Cretaceous (some 100 Ma) produced a diverse fauna of hadrosaurs, ceratopsians, ankylosaurs, and pachycephalosaurs, among herbivores, as well as new theropod groups, including the giant tyrannosaurs and carcharodontosaurs, and the smaller troodontids, dromaeosaurs, and ornithomimosaurs. Qualitatively then dinosaurs appear to have been part of the CTR.

As is commonly the case, studies of dinosaur diversity through time have suffered from the lack of a conceptual framework in which ‘diversification’ is defined, detected, and quantified. Furthermore, a proper evaluation of sampling biases (Raup, 1972; Benton *et al.,* 2000; Alroy *et al.,* 2001) has not been taken into account. Two key sampling issues are that the fossil record of a group may be truncated (i.e. lacking its youngest and/or oldest members) and that the number of observed taxa depends to some extent on sampling intensity (a proxy for this is the number of localities investigated or the number of specimens collected). Here, we address both issues, and use analytical protocols to minimise or exclude them.

At the heart of our analysis is a new supertree of dinosaurs, which represents a development and expansion of an earlier study (Pisani *et al.,* 2002), and consists of 440 species (some 70% of the total number of valid species), and an additional 15 undescribed or indeterminate forms. Use of large trees in diversification analyses is commonly two-pronged. Previous workers have used them to fill implied gaps in the fossil record and correct raw species richness counts accordingly (Weishampel and Jianu, 2000; Upchurch and Barrett, 2005), though never for the whole group. A completely different approach is to use tree shape to search for and date perturbations consistent with divergence from a simple birth-death model (Forest *et al.,* 2007; Ruta *et al.,* 2007). Here we use both approaches to test whether dinosaurs responded to the CTR, by comparing the magnitude and rates of their diversification in the Cretaceous with their diversification characteristics in the Triassic and Jurassic.

6.3 Methods

6.3.1 Supertree Reconstruction

We expanded significantly upon the previous list of source trees (Pisani *et al.,* 2002) with publications up to the end of 2006. This list was then shortened by removing those trees without a corroborating cladistic analysis (i.e. a matrix and character list available either as part of the publication itself, as an electronic appendix, or explicitly available – and obtained – from the author). Retention of this information allowed determination of redundant source trees (Bininda-Emonds *et al.,* 2004), reinsertion of outgroup(s) discarded in published figures and the re-running of analyses where the source publication did not provide a standardized (strict) consensus tree. Not all trees could be considered novel, and hence independent (Bininda-Emonds *et al.,* 2004). When one analysis clearly superseded an earlier work we retained the later tree and discarded the original. When multiple later works had equal claim we included them all, but weighted them in tree searches so that their net contribution was equal to one independent tree. Overall these filters led to a strong skew in the data toward more recent analyses (Figure 6.1), greatly enhancing the chances of recovering a tree that represents current consensus.

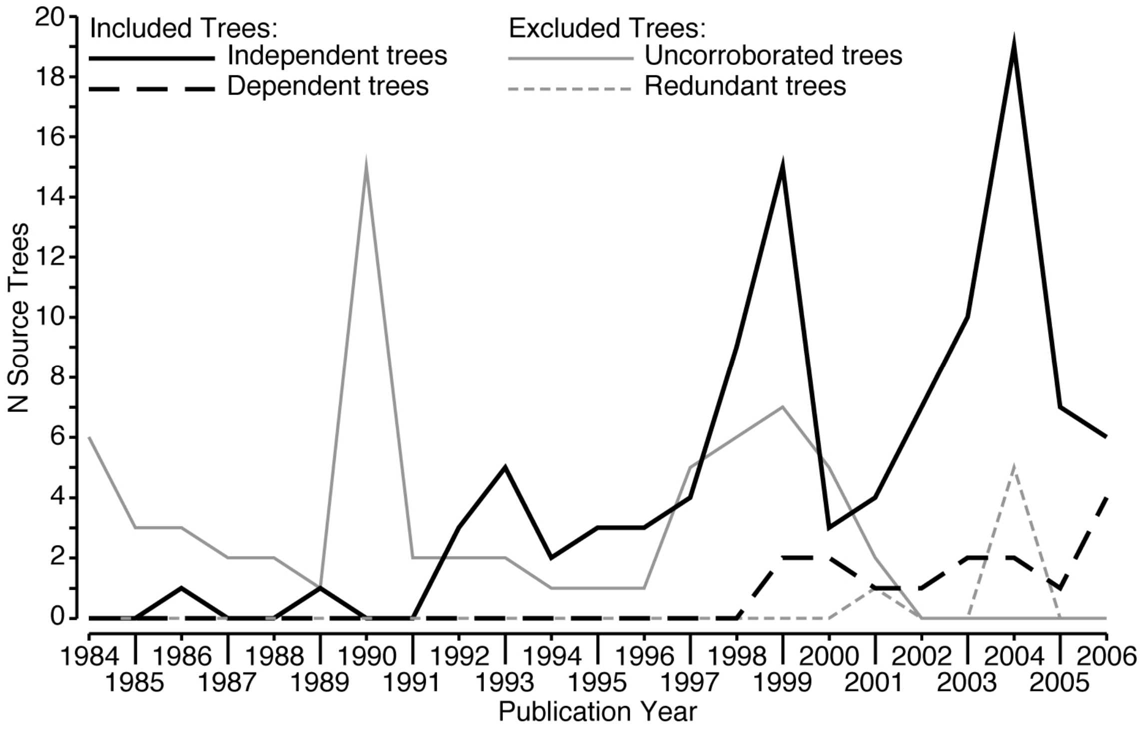

Figure 6.1: The year of publication of source trees shows a strong skew among included trees towards more recent analyses. The three major peaks (1990, 1999, 2004) correspond to the publication of The Dinosauria first edition (Weishampel *et al.,* 1990), a Science review paper (Sereno, 1999) and The Dinosauria second edition (Weishampel *et al.,* 2004) respectively.

Unlike the previous effort (Pisani *et al.,* 2002) we chose to produce a species-level supertree. This decision was bolstered by an authoritative recent compilation of valid names (Weishampel *et al.,* 2004) that served as our primary reference for nomina dubia, which were purged, and junior synonyms, which were replaced with their senior counterpart. Birds above *Archaeopteryx* and non-dinosaurian taxa were also purged from the source trees. Supraspecific taxa were replaced with all species that could be unequivocally assigned to that higher taxon based on the labelled nodes of source trees (Page, 2004), with the exception of genera, which were replaced by their type species, or, if more than one species exists, then the most completely known. Each source tree was processed in this way and both a tree (Page, 1996) and XML file produced. The latter contained metadata about the source publication, taxa and characters, ensuring a consistent standard of data collection and audit trail for future updates. Standard (Baum, 1992) and Purvis (Purvis, 1995) MRP matrices were then produced using a modified version of SuperMRP.pl (Bininda-Emonds *et al.,* 2006), Radcon (Thorley and Page, 2000) and CLANN (Creevey and McInerney, 2005).

Tree searches were performed following an established protocol (Pisani *et al.,* 2002; Pisani *et al.,* 2007). First, 5000 heuristic searches were performed in PAUP* 4.0b10 (Swofford, 2002) with the MulTree option turned off. Trees obtained from these searches were saved and swapped using the tree bisection reconnection algorithm, and the MulTree option on (to retain multiple equally optimal trees). The Parsimony Ratchet (Nixon, 1999) could not find a better tree. The split fit supertree (Wilkinson *et al.,* 2005) was built analysing the standard MRP matrix using Mix, which is part of the Phylip package (Felsenstein, 2000). To enforce Mix to run a compatibility analysis, the threshold parsimony option was set to 2. One hundred heuristic searches were performed, and characters were weighted (as described above) using a specifically generated weight file (Felsenstein, 2000).

In order to obtain a well-resolved tree we undertook some *post hoc* taxon pruning where poorly constrained species, producing unacceptably high numbers (> 5000) of equally likely supertrees, were removed. Choosing a tree for diversity analyses was based on overall supertree support. Here we used the V1 index (Wilkinson *et al.,* 2005), which indicated that support was highest for the standard MRP supertree (Figure 6.2).

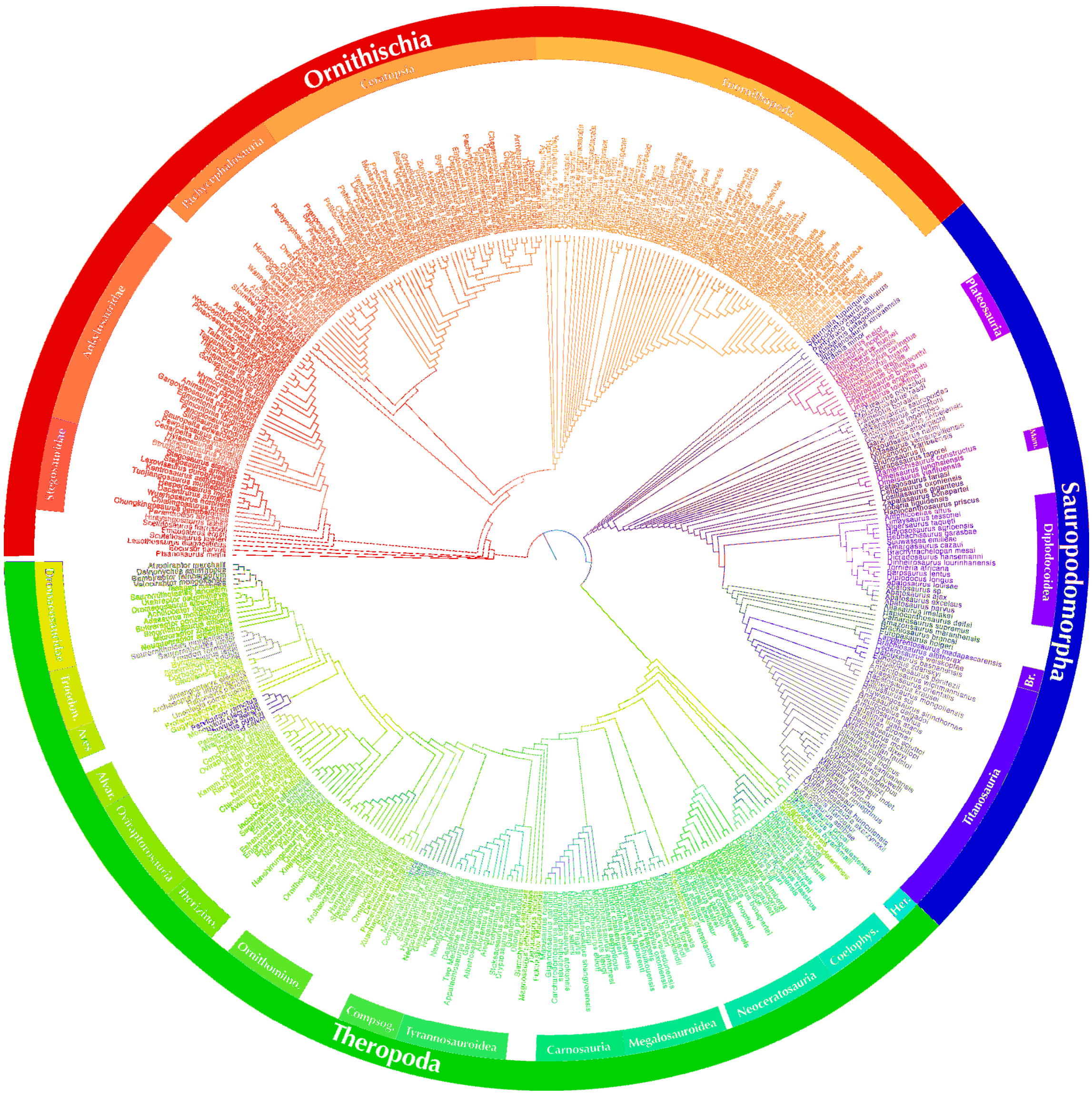

Figure 6.2: Standard MRP tree with clade labels. Majority-rule with minority components consensus tree of the reduced standard MRP matrix showing the major clades. Abbreviated clade names are: Mam. = Mamenchisauridae, Br. = Brachiosauridae, Her. = Herrerasauridae, Compsog. = "Compsognathoidea", Ornithomimo. = Ornithomimosauria, Therizino. = Therizinosauroidea, Alvar. = Alvarezsauridae and, Troodon. = Troodontidae.

6.3.2 Diversification Metrics

We calculated the percentage change, per million years, of global species richness among 12 successive time bins of subequal duration for three different datasets: 1) a recent database of the known dinosaur record (Weishampel *et al.,* 2004), 2) the same dataset but with some species' first appearances extended back in time as implied by a sister-group relationship with an older taxon (Norell, 1992) in the supertree and, 3) a subsampled dataset.

Subsampling methods have played an important role in ecology (Gotelli and Colwell, 2001) and palaeoecology (Raup, 1975; Tipper, 1979) as they offer the opportunity to examine the effects of taxonomic sampling on measures of species richness. Methodologically our approach is equivalent to setting the global quality of the record as equal to that of the worst part of it. Here we subsample the same dataset as above 1,000 times and record the number of species observed in a sample of 35 occurrences each time. Subsampling was performed using custom-built code (available on request from the lead author) in the freely available statistical programming language 'R'[1]. Note that in all cases diversification rates for each time bin were calculated using SymmeTREE version 1.0 (Chan and Moore, 2005). No diversification rate was calculated for the first bin as there are no unequivocal dinosaurian fossils, or for the second as there is no previous richness value – diversification is infinite. SymmeTREE implements a tree topology-dependent method for detecting diversification rate shifts (i.e. significant changes in lineage branching, based upon differences in the number of taxa and degree of imbalance on the left and right branches subtended by tree nodes) (Ruta *et al.,* 2007).

Phylogenetic shifts in diversification were also detected using SymmeTREE version 1.0 (Chan and Moore, 2005). In order to avoid non-monophyly biases associated with the exclusion of birds a 'dummy' branch representing a composite phylogeny of 72 Mesozoic species was inserted at the node subtending *Archaeopteryx* + *Jinfengopteryx*. Polytomies were treated as soft, with the size-sensitive ERM (Equal

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[1] http://cran.r-project.org

Rates Markov) algorithm set to perform 10,000 random resolutions per individual node and 1,000,000 random resolutions for the entire tree. Internal branches within the phylogeny on which diversification shifts are inferred to have occurred were identified using the Δ_2 shift statistic (a measure of the likelihood that a shift occurred). This process was repeated for time-slices of the whole tree as described in Ruta *et al*. (2007) to avoid violating the ERM-model.

6.4 Results

6.4.1 Ghost Ranges Account for Some Irregularities in the Diversity Curves

The supertree of dinosaur species is plotted on a geologic time scale (Gradstein *et al.,* 2004) (Figure 6.3a and Appendix G) split into twelve approximately equal-length time bins to assess the extent of ghost ranges (Norell, 1992). Ghost ranges, minimal basal stratigraphic range extensions implied by the geometry of the phylogenetic tree, indicate missing fossil data, and they allow us to correct diversity profiles for the group through the Mesozoic, and to compare diversification rates, the proportional change in observed species richness as a function of time, at different points (Figure 6.3b): note how the addition of ghost ranges smoothes the curve. In particular, peaks in observed diversification rate in the Norian and Campanian-Maastrichtian (bins 3 and 12) are greatly reduced when ghost ranges are introduced. This is a minimal correction that does not take account of unknown taxon ranges before the first appearance of the older of a pair of sister groups. In addition of course, this correction does not address possible upward range extensions. However, peaks in the earliest, Middle and Late Jurassic are still observed after introduction of ghost ranges (Figure 6.3).

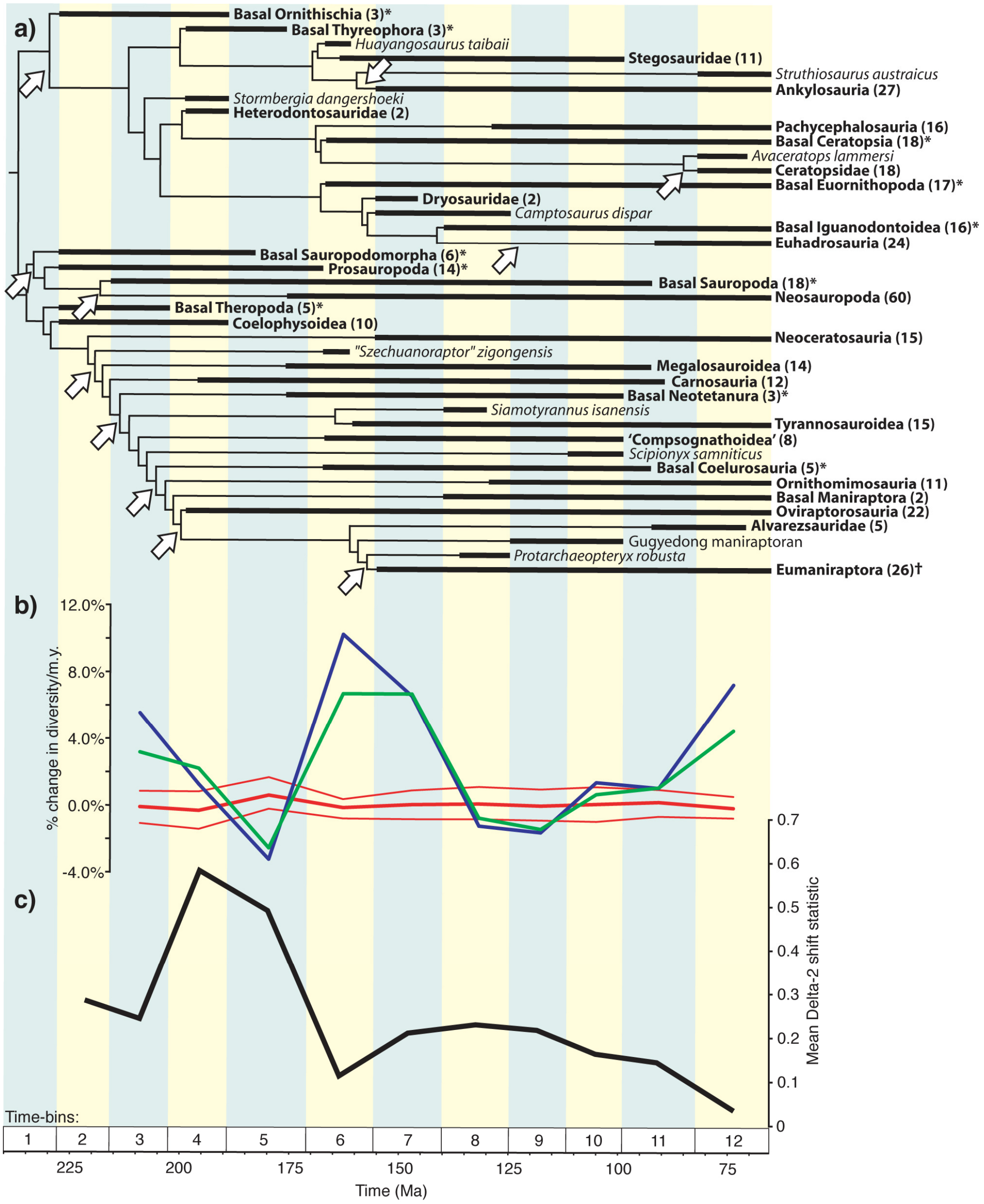

Figure 6.3: Results of different analyses of dinosaur diversification. a) A summary version of the supertree used here (Figure 6.2 for full tree); the eleven statistically significant diversification shifts present in both the entire tree and at least one time-slice are marked with white arrows denoting the branch leading to the more speciose clade. Taxa in bold represent the collapsing of a larger clade, the size of which is indicated in parentheses. An '*' indicates the collapsing of a paraphyletic clade and a '†' an extant clade (i.e. birds). b) Diversification rates based on the raw record (blue), the raw record plus additional 'ghost' ranges (green) and subsampled data (red; see text). c) Mean values of Δ_2 shift statistic through time (see text).

6.4.2 Correction for Sampling Removes Some Extreme Diversity Peaks

To test whether these peaks represent real diversification episodes or are simply the result of unusually intense sampling, we considered the number of dinosaur localities in each stratigraphic stage (Weishampel *et al.,* 2004). If localities sampled determine generic diversity, then the apparent diversification measures, once corrected for locality numbers, might be levelled. Our approach represents a subsampling method similar to rarefaction. Rarefaction methods have played an important role in ecology (Gotelli and Colwell, 2001) and palaeoecology (Raup, 1975*;* Tipper, 1979) as they offer the opportunity to examine the effects of taxonomic sampling on measures of species richness. Here we measure sample size as the total number of species occurrences by locality for each of our twelve time bins. When the same diversification calculations are applied to these subsamples (the mean and 95% bounds of which are plotted in Figure 6.3b), much lower values are recovered. These results suggest, but do not prove, that diversity estimates are heavily influenced by sampling, and further that the ghost range, i.e. tree-based, correction is indeed minimal. It follows that the fluctuations in diversification rate may not necessarily reflect evolutionary signal, and these must be tested rigorously.

6.4.3 Diversification Shifts are Concentrated in the Lower Half of the Dinosaur Tree

An alternative approach relies instead on phylogenetic tree shape. Phylogeny is determined by the available taxa and the inferred pattern of relationships, and phylogenetic tree shape reflects large-scale variations in speciation and extinction rates (Mooers and Heard, 1997). Topological methods (Bininda-Emonds *et al.,* 1999, Katzourakis *et al.,* 2001; Chan and Moore, 2005; Jones *et al.,* 2005) may be used to identify diversification rate shifts in phylogenetic trees, based on comparison between the observed tree and one expected under an ERM model. An ERM-model assumes that sister groups should contain a similar number of taxa as they originated at the same time; thus, if one group is significantly more speciose than the other a diversification rate shift may be inferred.

Analysis of diversification rates in the supertree using SymmeTREE shows that statistically significant ($p < 0.05$) and substantial ($0.05 < p < 0.1$) diversification shifts (i.e. multiplications of evolutionary lineages) were heavily concentrated in the first third of the evolution of the clade Dinosauria (Figure 6.3b and Appendix G). The majority are at the base of the Dinosauria, in the Late Triassic to Early Jurassic (230-175 Ma), and mark the origin of major clades (10 significant shifts; Genasauria, Eurypoda, Cerapoda, Sauropodomorpha, Neotheropoda, Tetanurae, Coelurosauria, Maniraptoriformes, Maniraptora, Oviraptorosauria). Later statistically significant diversification shifts occur in the Aalenian (1; Neosauropoda), Kimmeridigian (2; Ankylosauria, Eumaniraptora), Turonian (1; Euhadrosauria), and Campanian (1; Ceratopsidae). Of the 15 significant and 11 substantial diversification shifts, there are two significant and two substantial shifts in the Triassic, 11 significant and seven substantial in the Jurassic, and two significant, and two substantial shifts in the Cretaceous. This confirms that most diversification among Dinosauria occurred early, and very little is detected in the second two-thirds of their history, the 120 Ma from the Middle Jurassic onwards. When the mean Δ_2 shift statistic, which represents the likelihood that a shift occurred, is plotted against time (Figure 6.3c) there is a peak value of 0.58 during the Rhaetian-Sinemurian (Bin 4; 205-190 Ma) followed by an overall decrease towards the present. Two-thirds of significant pairwise comparisons between Δ_2-values (Kruskal-Wallis test; $p < 0.05$) show bins 4 and 5 (Rhaetian-Aalenian; 205-170 Ma) to have higher likelihoods of a diversification shift.

The robustness of these results was tested further by 'time-slicing' our tree to avoid issues surrounding violation of the ERM-model's assumptions (Ruta *et al.,* 2007). This involved creating eleven separate trees, one for each of our time bins, which included only the taxa that existed, or are posited to have existed, at that time. These results strongly support our whole-tree analysis, with 11 of the 15 significant shifts also occurring in the time-sliced trees. Only one novel significant shift was discovered in the time-sliced trees, coincident with the origin of Lithostrotia in the Valanginian (140 Ma). Again, the highest mean Δ_2 shift statistic (0.69) was found in bin 4, with a general decrease going forwards in time. Similarly, over half of the significant pairwise comparisons between Δ_2-values show time bins 4 and 5 to have had higher likelihoods of a diversification shift. All results are robust even if the controversial taxon *Eshanosaurus*, which is here placed as a therizinosaur and is responsible for dating four of the significant shifts (Tetanurae, Coelurosauria, Maniraptoriformes, Maniraptora), is removed.

6.5 Discussion

6.5.1 Diversification Shifts are not Always Concentrated in the Lower Half of a Tree

Geometric arguments might suggest that it is inevitable to find the majority of diversification shifts low in a tree. To an extent, of course, there must be statistically-significant diversification shifts at the base of the tree, as the founding taxa within the clade split and major branches become established. Bats, for example, show a similar early diversification pattern (Jones *et al.,* 2005), but ants do not (Forest *et al.,* 2007). The reason is that clades do not inevitably stop diversifying once they have become established. Studies of the distribution of clade shapes (Gould *et al.,* 1977; Valentine, 1990; Uhen, 1996; Nee, 2006) show all possible shapes (after paraphyly has been accounted for), ranging from bottom-heavy to top-heavy, tall and thin, short and fat, and even spindle-shaped, where the clade has been hit hard by an extinction event or other bottlenecking crisis, and has then recovered. In the case of Dinosauria here, the clade continues to expand up to the end of the Cretaceous, and yet, statistically speaking, the Cretaceous expansion cannot be distinguished from the normal expectation of an ERM.

6.5.2 Sampling Must be Taken into Account

The fossil record of continental vertebrates is clearly patchy, with large temporal gaps between sampling horizons. The seriousness of sampling bias is debated, with opinion ranging from assumptions that the fossil record offers more of a geological than a biological signal (Raup, 1972; Alroy *et al.,* 2001; Peters and Foote, 2002) to acceptance that sampling error does not much modify the apparent macroevolutionary patterns (Sepkoski *et al.,* 1981; Benton, 1999). Comparisons of cladograms with the fossil record show good congruence in most cases (Norell and Novacek, 1992; Benton *et al.,* 2000), so suggesting that the biological signal, assessed at the correct scale, is probably adequately represented. Current efforts (Smith, 2007) focus on methods to quantify sampling bias, and to determine parts of the fossil record signal that stand out after sampling has been considered.

In this paper, we have used the number of dinosaur localities in each time bin as a crude measure of sampling. Other measures could have been area of rock exposure, volume of rock deposited per unit time, total number of geological formations whether fossiliferous or not, or intensity of worker effort – number of palaeontologists, for example. All such measures are of course themselves subject to debate, and there is a risk that the crude use of a sampling measure to correct diversity figures automatically may be sufficiently heavy-handed that any biological signal is overwhelmed (Peters and Foote, 2002; Smith, 2007). For example, there is doubtless a species-area effect (Smith, 2001), in which rock area or volume, or number of formations, is linked with the diversity of life. For example, during times of high sea level, continental margins flood, and species on the continental shelf increase in abundance and diversity. To 'correct' those diversity figures by dividing by shelf area or rock volume, could perfectly remove the biological signal.

Our solution, to offer both the raw data and the sampling-modified data (Figure 6.3b), allows comparison of the data without making an assumption that one or the other version is correct, and points to the need for further examination of each of the undoubted biases in our understanding of this fossil record. Before applying a correction factor, we need evidence of how collecting intensity (i.e. number of palaeontologists; number of field days), rock availability, and other sampling factors affect the results. The relationship is almost certainly not linear, and that in itself speaks against crude application of sampling corrections. For example, discovery curves for dinosaurs and other fossil taxa, when calibrated against worker effort (Tarver *et al.,* 2007), show a classic logistic shape, where huge efforts at present do not necessarily yield huge numbers of new fossils.

6.5.3 Dinosaurs and the Cretaceous Terrestrial Revolution (CTR)

Previous studies have been equivocal about whether dinosaurs ate angiosperms. The Late Cretaceous expansion of dinosaurian diversity, founded especially on the diversification of herbivorous dinosaurs such as hadrosaurs, ceratopsians, and ankylosaurs, might have suggested that these groups, all of which either arose or diversified substantially only after the origin of angiosperms in the mid Cretaceous, were angiosperm specialists. Bakker (1978), for example, argued that the ornithopods of the Early Cretaceous fed close to the ground, and so favoured gymnosperms in their diet. Because of their intense low-level feeding, the only plants that could survive the onslaught were the earliest angiosperms that held their reproductive organs close to the ground. And so, in his words, dinosaurs invented flowers.

This view is disputed, and there is actually very limited evidence to demonstrate that Cretaceous dinosaurs fed on angiosperms (Barrett and Willis, 2001). The patterns of rises and falls in the diversity of Cretaceous dinosaurs and Cretaceous plants, as well as their palaeogeographic distributions, do not suggest any correlation. Coprolites, fossil faeces, are rare, and often cannot be attributed to their producer; Cretaceous examples include some with traces of the angiosperm biomarkers, oleananes, whereas others contain exclusively gymnosperm material. An Early Cretaceous ankylosaur, *Minmi*, has been reported (Molnar and Clifford, 2000) with remnants of angiosperm fruits in its gut, and some remarkable dinosaurian coprolites from India show that some dinosaurs ate early grasses (Prasad *et al.,* 2005). Fossil occurrences and studies of the teeth and postulated jaw functions of herbivorous dinosaurs suggest that angiosperms were a part of the diet of many dinosaurs, but that gymnosperms were still possibly the major constituent in many cases (Barrett and Willis, 2001). Plant-eating insects and mammals very likely benefited more from the new sources of plant food.

Detailed studies of dinosaurian herbivory and plant evolution (Barrett and Willis, 2001) had already suggested there was limited evidence that angiosperm diversification drove the Cretaceous diversification of dinosaurs. Our new evidence confirms that the Cretaceous Terrestrial Revolution was key in the origination of modern continental ecosystems, but that the dinosaurs were not a part of it. Hadrosaurs and ceratopsians showed late diversifications, but not enough to save the dinosaurs from their fate.

Chapter 7

Discussion and Conclusions

7.1 Introduction

This thesis has dealt with the construction of a large-scale supertree of extant and extinct avian taxa at species level. It is the largest such supertree ever constructed (to the author's knowledge) and contains over 5000 taxa. A robust protocol for collecting and processing source data for such as study has been detailed and tested. This protocol was also used to construct an updated, species-level supertree of dinosaurs containing 440 taxa. Put together, this constitutes an almost 6000 taxa species-level supertree of the archosaurs. This chapter gives a brief summary of the main findings of this thesis by assessing the questions asked in Chapter 1 and summarising the main conclusions of the study. It concludes with suggestions for future work.

7.2 Conclusions

The questions set out in Chapter 1 are reiterated and answered here.

1. **Can a protocol for constructing supertrees be developed that is both methodologically robust and easy to implement?**

Chapter 3 describes the protocol designed and implemented in this thesis. It was observed that the protocol described by Bininda-Emonds *et al.* (2004), although largely adequate and a novel idea, contained some gaps and a lack of suggestions for practical implementation. One such gap was how to deal with non-independent source trees either by combining into a "mini-supertree" (as in Bininda-Emonds *et al.,* 2004) or by down-weighting the trees by an appropriate factor. It was found that it is better to combine non-independent source trees than it is to down-weight those source trees as statistical results from MASTd and triplet fit of the supertree(s) to the source trees showed that the supertree constructed from combined data gave a result more concordant with the source trees than that from down-weighting the data. Additionally, it was much faster both to implement the combined method and analyse the resulting character matrix. For the main supertree analysis in Chapter 4, using this protocol reduced the taxa number from 7384 to 5274 by removing higher taxa, vernacular names and synonyms. Removing these taxa increases overlap between the source trees and hence is likely to produce a better result.

The protocol was straightforward to implement, but time-consuming. Scripts were used to largely automate the process. It took significantly longer to collect and process data ready for supertree construction than it took to collect and process data ready for supermatrix analysis (Chapter 5).

2. Does this protocol result in supertrees that are good representations of the source data?

Both supertrees constructed in Chapter 3 gave reasonable, sensible results with a minimum of spurious groups. There were no surprises in the results and both conformed well to currently accepted views on galliform phylogeny. Using the protocol for species-level trees of both Dinosauria and Aves produced sensible trees with few novel clades (given their size). In addition, a molecular-only supertree of the Galliformes was produced using the protocol. This resulted in a phylogeny very similar to that made via supermatrix methods (see below). Both these phylogenies (supertree and supermatrix) were very similar to the supertrees constructed in Chapter 3.

3. Can a supertree of all Aves be constructed at species-level using this protocol?

The species-level supertree of Aves contains 5274 taxa, both extinct and extant, more than half of all known extant taxa. The results were sensible, giving a reasonable summary of the current knowledge of avian phylogeny. Due to the stringent data processing methods, it is possible to pinpoint areas where primary data collection and analysis are required much more clearly. Many of these areas were identified by the presence of novel clades, which, on inspection, were evidently the result of poor taxonomic sampling. Other novel clades were as a result of the inclusion of fossil taxa, the only solution here is for more fossils to be described and included in phylogenetic analyses. Finally, there were some spurious groups that can not be easily explained. These could be due to undesirable properties of MRP or may be resolved simply by further analysis, as the current analysis was, by necessity, limited to a run time of just 12 hours. However, even with this limited run time, the tree is a good estimate of current understanding of bird phylogeny and will be very useful in future studies.

4. **Can community-based tree-building help speed up the process in finding shorter tree?**

The community aspect of the project was unfortunately not very successful. A few data problems were found by others (taxon duplication and a few erroneous trees), but only one other person uploaded a final tree. It is surprising that the project did not attract more attention as a large species-level supertree of birds is very much in demand at the present time.

5. **Do supertree methods compare favourably with trees found from supermatrix analyses? Which, if either, produces superior results?**

The results from both supermatrix and supertree analysis of molecular data were very similar (Chapter 5). Both trees were analysed in the same way as the Galliformes supertrees in Chapter 3 (i.e. compared to independent small-scale phylogenies using triplets and MASTd) and show that there is no statistically significant difference between the tree constructed from a supermatrix and that constructed from a supertree analysis, i.e. each represents the input source data as well as the other. Both trees were very similar in terms of large-scale relationships. Each gave sensible results and no spurious groups were identified. The higher-level relationships did not differ to those found in the taxonomically more inclusive trees constructed in Chapter 3. In this way, the two methods are complementary as suggested by Bininda-Emonds (2004).

6. **Can a new, updated supertree of the Dinosauria shed light on dinosaur diversification throughout the Cretaceous?**

The dinosaur supertree was created using a slightly modified version of the protocol designed and described in Chapter 3. The protocol was modified (in terms of the

XML file structure and down-weighted non-independent source trees rather than combining) in order to suit information related to fossil taxa. This was the first quantitative study of diversification applied to a supertree of dinosaurs and the results show that an apparent burst in diversity at the end of the Cretaceous is a sampling artefact and that dinosaurs show most of their major diversification shifts in the first third of their history. Dinosaurs then were not progressively declining at the end of the Cretaceous as previously thought; nor were they profiting from the new ecological opportunities offered by the Cretaceous modernisation of terrestrial ecosystems.

7.3 Further work

7.3.1 Further analysis of the tree

It would be interesting to investigate the tree further by running the analysis for a longer period of time as the current analysis was, by necessity, limited to a run time of just 12 hours. However, even with this limited run time, the tree is a good estimate of current understanding of bird phylogeny and will be very useful in future studies. It would also be of value to continue updating the tree, which is straightforward due to the data collection methods employed. The current tree includes all avian phylogenies up to January 2006 and more have been published since then. As phylogenies are continually being published, the supertree will always become out-of-date in a short period of time, but it is still valuable as a "snapshot” of currently accepted views of phylogeny.

7.3.2 Dating of the tree

An interesting study would be to date the tree as in Bininda-Emonds *et al.* (2007) mammal supertree, which was then used analyse to how extant lineages accumulated through time. This could be particularly interesting as the avian supertree presented here has incorporated fossils, something not covered by Bininda-Emonds *et al.* (2007). A supertree with dates could be used to explore the question of whether modern birds originated and diversified in the Tertiary or whether modern lineages originated in the Cretaceous and passed through the K-T boundary largely unaffected.

7.3.3 Taxonomy issues

This supertree of birds is a very comprehensive study of avian taxonomy; with over 5000 taxa in the final supertree. However, in order to create the best supertree possible the data were heavily sanitised; with replacement of synonyms and standardisation of names. Use of a consistent taxonomy is important because allowing synonyms and other invalid taxa to remain will artificially inflate the taxa number and, crucially, reduce the amount of overlap between source trees in a supertree analysis. From a wider viewpoint, use of a standardised taxonomy is essential in conservation issues.

For the main supertree analysis in Chapter 4, using this protocol reduced the taxa number from 7384 to 5274 by removing higher taxa, vernacular names and synonyms. This highlights the issues present in avian taxonomy, i.e. that there are a huge amount of invalid names present and this will obviously have an effect on the building of any phylogeny. For this thesis, both the standardised (regarding taxonomy) and original (as in the source trees) data were retained, which gives an opportunity to assess how “good” avian taxonomy is in terms of taxonomic stability and integrity. An investigation into the issues surrounding avian taxonomy was beyond the scope of this study but would be a worthwhile use of the large datasets collected, and retained, for this thesis.

7.3.4 Large-scale avian supermatrix

An interesting question is whether a species-level avian supermatrix could be constructed to the same, or near, level of taxonomic coverage as the supertree presented in this thesis. Supertree proponents often cite the inability to create such large supermatrices as a reason to build supertrees but it would be interesting to see just how large a matrix would be possible. As shown in Chapter 5, it would be relatively easy to assimilate the relevant data ready for analysis but computational time is likely to be the limiting factor.

It would also be interesting to download molecular data from GenBank and then use this to construct both individual source trees for each gene and then a supermatrix. The source trees could then be used to build a supertree, the results of which could then be compared to the supermatrix, as in Chapter 5, to look at how well each tree represents the source data. This was beyond the scope of this study with regards to time limitations, and also does not perhaps reflect “real-life” situations, in which source trees are not necessarily constructed under ideal conditions.

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Appendix A

List of names not found by Taxonomic Name Server

The table below shows queried names not found by the Taxonomic Name Server (1st column). The correct name is shown in the second column (which is not necessarily different fro the queried name). The 3rd column highlights those taxa which are extinct.

Queried name	Corrected name	
Acrocephalus scirpaceus avicenniae	Acrocephalus scirpaceus avicenniae	
Acrocephalus stentoreus australis	Acrocephalus australis	
Acrocephalus stentoreus harteri	Acrocephalus stentoreus harteri	
Acrocephalus stentoreus levantina	Acrocephalus stentoreus levantina	
Aegialornis gallicus	Aegialornis gallicus	Extinct
Aegialornis leenhardti	Aegialornis leenhardti	
Aegintha temporalis	Neochmia temporalis	
Aegotheles albertisi albertisi	Aegotheles albertisi albertisi	
Aegotheles albertisi salvadorii	Aegotheles albertisi salvadorii	
Aegotheles bennettii affinis	Aegotheles bennettii affinis	
Aegotheles bennettii bennettii	Aegotheles bennettii bennettii	
Aegotheles bennettii plumiferus	Aegotheles bennettii plumiferus	
Aegotheles bennettii terborghi	Aegotheles bennettii terborghi	
Aegotheles bennettii wiedenfeldi	Aegotheles bennettii wiedenfeldi	
Aegotheles novaezealandiae	Aegotheles novaezealandiae	
Aegotheles tatei	Euaegotheles tatei	
Aegotheles wallacii gigas	Aegotheles wallacii gigas	
Aegotheles wallacii wallacii	Aegotheles wallacii wallacii	
Aepyornis	Aepyornis	Extinct
Aerodramus brevirostris vulcanorum	Aerodramus brevirostris vulcanorum	
Aerodramus maximus lowi	Aerodramus maximus lowi	
Aerodramus salangana natunae	Aerodramus salangana natunae	
Aerodramus terraereginae terraereginae	Aerodramus terraereginae terraereginae	
Aerodramus vanikorensis lugubris	Aerodramus vanikorensis lugubris	
Aerodramus vanikorensis palawanensis	Aerodramus vanikorensis palawanensis	
Agelaioides badius	Molothrus badius	
Agelaius phoeniceus assimilis	Agelaius assimilis	
Agelasticus cyanopus	Agelaius cyanopus	
Agelasticus thilius	Agelaius thilius	
Agelasticus xanthophthalmus	Agelaius xanthophthalmus	
Aidemedia chascax	Aidemedia chascax	Extinct
Aidemedia lutetiae	Aidemedia lutetiae	Extinct
Aidemosyne modesta	Aidemosyne modesta	

Akialoa lanaiensis	Akialoa lanaiensis	Extinct
Akialoa obscurus	Akialoa obscurus	Extinct
Akialoa upupirostris	Akialoa upupirostris	Extinct
Alario alario	Serinus alario	
Alcedo cyanopecta cyanopecta	Alcedo cyanopectus cyanopectus	
Alcedo cyanopecta nigrirosta	Alcedo cyanopectus nigrirostris	
Alle alle polaris	Alle alle polaris	
Amazona aestiva aestva	Amazona aestiva aestiva	
Amazona aestiva xanthopteryx	Amazona aestiva xanthopteryx	
Amazona albifrons albifrons	Amazona albifrons albifrons	
Amazona albifrons nana	Amazona albifrons nana	
Amazona albifrons saltuensis	Amazona albifrons saltuensis	
Amazona auropalliata auropalliata	Amazona auropalliata auropalliata	
Amazona auropalliata parvipes	Amazona auropalliata parvipes	
Amazona autumnalis autumnalis	Amazona autumnalis autumnalis	
Amazona autumnalis lilacina	Amazona autumnalis lilacina	
Amazona farinosa farinosa	Amazona farinosa farinosa	
Amazona farinosa guatemalae	Amazona farinosa guatemalae	
Amazona farinosa inornata	Amazona farinosa inornata	
Amazona farinosa virenticeps	Amazona farinosa virenticeps	
Amazona festiva bodini	Amazona festiva bodini	
Amazona leucocephala leucocephala	Amazona leucocephala leucocephala	
Amazona ochrocephala nattereri	Amazona ochrocephala nattereri	
Amazona ochrocephala nattereri	Amazona ochrocephala nattereri	
Amazona ochrocephala ochrocephala	Amazona ochrocephala ochrocephala	
Amazona ochrocephala ochrocephala	Amazona ochrocephala ochrocephala	
Amazona ochrocephala xantholaema	Amazona ochrocephala xantholaema	
Amazona ochrocephala xantholaema	Amazona ochrocephala xantholaema	
Amazona oratrix belizensis	Amazona oratrix belizensis	
Amazona oratrix hondurensis	Amazona oratrix hondurensis	
Amazona oratrix oratrix	Amazona oratrix oratrix	
Ambiortus	Ambiortus	Extinct
Amitabha urbsinterdictensis	Amitabha urbsinterdictensis	Extinct
Ampelion sclateri	Doliornis sclateri	
Amytornis barbatus barbatus	Amytornis barbatus barbatus	
Amytornis barbatus diamantina	Amytornis barbatus diamantina	
Amytornis purnelli purnelli	Amytornis purnelli purnelli	
Amytornis striatus merrotsyi	Amytornis striatus merrotsyi	
Amytornis striatus striatus	Amytornis striatus striatus	
Amytornis textilis modestus	Amytornis textilis modestus	
Amytornis textilis myall	Amytornis textilis myall	
Anabazenops dorsalis	Automolus dorsalis	
Anatalavis	Anatalavis	Extinct
Anatalavis oxfordi	Anatalavis oxfordi	Extinct
Anneavis anneae	Anneavis anneae	Extinct
Anser rubrirostris	Anser anser	
Aplopelia simplex	Columba larvata simplex	
Apsaravis	Apsaravis	Extinct
Apsaravis ukhaana	Apsaravis ukhaana	Extinct
Apteryx mantelli	Apteryx australis	
Aquila pomarina hastata	Aquila pomarina hastata	

Archaeopteryx	Archaeopteryx	Extinct
Archaeopteryx lithographica	Archaeopteryx lithographica	Extinct
Argillornis emuinus	Argillornis emuinus	Extinct
Argornis caucasicus	Argornis caucasicus	
Asthenes arequipae	Asthenes dorbignyi arequipae	
Asthenes huancavelicae	Asthenes dorbignyi huancavelicae	
Asturina nitida costaricensis	Asturina nitida costaricensis	
Asturina nitida nitida	Asturina nitida nitida	
Asturina nitida plagiata	Asturina nitida plagiata	
Atlapetes latinuchus	Atlapetes latinuchus	
Avisaurus archibaldi	Avisaurus archibaldi	Extinct
Avisaurus gloriae	Avisaurus gloriae	Extinct
Baptornis advenus	Baptornis advenus	Extinct
Barnardius barnardi barnardi	Barnardius barnardi barnardi	
Barnardius barnardi macgillivaryi	Barnardius barnardi macgillivaryi	
Barnardius barnardi whitei	Barnardius barnardi whitei	
Berenicornis	Berenicornis	
Blythipicus pyrrhotis sinensis	Blythipicus pyrrhotis sinensis	
Bocagia minuta	Tchagra minuta	
Bowdleria punctata	Megalurus punctatus	
Bradornis mariquensis	Melaenornis mariquensis	
Branta hrota	Branta bernicla	
Breagyps clarki	Breagyps clarki	Extinct
Bubo zeylonensis	Ketupa zeylonensis	
Bucorvus cafer	Bucorvus leadbeateri	
Buteo albicaudatus colonus	Buteo albicaudatus colonus	
Buteo albonotatus albonotatus	Buteo albonotatus albonotatus	
Buteo brachyurus brachyurus	Buteo brachyurus brachyurus	
Buteo buteo arrigonii	Buteo buteo arrigonii	
Buteo buteo socotrae	Buteo buteo socotrae	
Buteo jamaicensis costaricensis	Buteo jamaicensis costaricensis	
Buteo japonicus	Buteo buteo japonicus	
Buteo japonicus toyoshimai	Buteo buteo toyoshimai	
Buteo magnirostris griseocauda	Buteo magnirostris griseocauda	
Buteo magnirostris magniplumis	Buteo magnirostris magniplumis	
Buteo magnirostris saturatus	Buteo magnirostris saturatus	
Buteo polyosoma exsul	Buteo polyosoma exsul	
Buteo polyosoma poecilochrous	Buteo poecilochrous	
Buteo polyosoma polyosoma	Buteo polyosoma polyosoma	
Buteo refectus	Buteo buteo refectus	
Buteogallus urubitinga urubitinga	Buteogallus urubitinga urubitinga	
Bycanistes	Ceratogymna	
Cabalus modestus	Cabalus modestus	Extinct
Cacatua roseicapilla	Eolophus roseicapillus	
Cacicus holosericeus	Amblycercus holosericus	
Calopelia puella brehmeri	Turtur brehmeri	
Canachites franklinii	Canachites canadensis	
Carduelis carduelis caniceps	Carduelis carduelis caniceps	
Carduelis carduelis parva	Carduelis carduelis parva	
Carduelis magellanicus	Carduelis magellanica	
Carduelis psaltria colombiana	Carduelis psaltria colombiana	

Carduelis psaltria hesperofila	Carduelis psaltria hesperofila	
Caryothaustes humeralis	Parkerthraustes humeralis	
Casuarius aruensis	Casuarius casuarius aruensis	
Catharacta skua hamiltoni	Catharacta skua hamiltoni	
Cathayornis	Cathayornis	Extinct
Cathayornis yandica	Cathayornis yandica	Extinct
Centrocercus minimus	Centrocercus minimus	Extinct
Ceranopterus	Ceranopterus	
Certhidea fusca	Certhidea olivacea fusca	
Ceryle maxima	Megaceryle maxima	
Ceyx melanurus melanurus	Ceyx melanurus melanurus	
Ceyx melanurus mindanensis	Ceyx melanurus mindanensis	
Ceyx melanurus samarensis	Ceyx melanurus samarensis	
Ceyx rufidorsum	Ceyx rufidorsa = Ceyx erithaca	
Changchengornis	Changchengornis	Extinct
Chaoyangia	Chaoyangia	Extinct
Charadrius venustus	Charadrius pallidus	
Chelychelynechen quassus	Chelychelynechen quassus	Extinct
Chenonetta finschi	Chenonetta finschi	Extinct
Chlamydotis houbara	Chlamydotis undulata	
Chlamydotis macqueenii	Chlamydotis macqueenii	
Chlamydotis undulata fuerteventurae	Chlamydotis undulata fuerteventurae	
Chloridops regiskongi	Chloridops regiskongi	Extinct
Chloridops wahi	Chloridops wahi	Extinct
Chloris chloris	Carduelis chloris	
Chloris sinica	Carduelis sinica	
Chloris spinoides	Carduelis spinoides	
Chlorophoneus dohertyi	Telophorus dohertyi	
Chlorophoneus nigrifrons	Telophorus nigrifrons	
Chlorophoneus sulfureopectus	Telophorus sulfureopectus	
Choreotis australis	Ardeotis australis	
Choriotis	Ardeotis	
Chroicocephalus cirrocephalus	Larus cirrocephalus	
Chroicocephalus genei	Larus genei	
Chroicocephalus philadelphia	Larus philadelphia	
Chroicocephalus ridibundus	Larus ridibundus	
Chroicocephalus scopulinus	Larus scopulinus	
Chroicocephalus serranus	Larus serranus	
Chrysomus icterocephalus	Agelaius icterocephalus	
Chrysomus ruficapillus	Agelaius ruficapillus	
Ciconia alba	Ciconia ciconia alba	
Cinclodes aricomae	Cinclodes aricomae	
Cinclosoma alisteri	Cinclosoma cinnamomeum alisteri	
Cinclosoma marginatum	Cinclosoma castaneothorax marginatum	
Cissopsis	Cissopis	Extinct
Clamator cafer	Clamator levaillantii	
Clamator levaillantii	Clamator levaillantii	
Cnemiornis	Cnemiornis	Extinct
Cnemiornis calcitrans	Cnemiornis calcitrans	Extinct
Cnemiornis gracilis	Cnemiornis gracilis	Extinct

Coccothraustes melanozanthos	Mycerobas melanozanthos	
Coccothraustes vespertinus brooksi	Coccothraustes vespertinus	
Coccothraustes vespertinus vespertinus	Coccothraustes vespertinus	
Coccycua	Piaya	
Collocalia esculenta becki	Collocalia esculenta becki	
Collocalia esculenta cyanoptila	Collocalia esculenta cyanoptila	
Collocalia esculenta nitens	Collocalia esculenta nitens	
Collocalia salangana	Aerodramus salanganus	
Collocalia vanikorensis	Aerodramus vanikorensis	
Columba albilinea	Columba fasciata	
Columba rufina	Columba cayennensis	
Columbigallina minuta	Columbina minuta	
Columbigallina passerina	Columbina passerina	
Columbigallina talpacoti	Columbina talpacoti	
Compsohalieus fuscescens	Phalacrocorax fuscescens	
Compsohalieus harrisi	Phalacrocorax harrisi	
Compsohalieus neglectus	Phalacrocorax neglectus	
Compsohalieus penicillatus	Phalacrocorax penicillatus	
Compsohalieus perspicillatus	Phalacrocorax perspicillatus	
Concornis	Concornis	Extinct
Concornis lacustris	Concornis lacustris	Extinct
Confuciusornis	Confuciusornis	Extinct
Confuciusornis sanctus	Confuciusornis sanctus	Extinct
Conirostrum cinereum fraseri	Conirostrum cinereum fraseri	
Copepteryx hexeris	Copepteryx hexeris	Extinct
Corythospis	Corythopis	Extinct
Cosmopelia elegans	Phaps elegans	
Cossyphicula roberti	Cossypha roberti	
Coturnix coturnix japonica	Coturnix japonica	
Crex albicollis	Porzana albicollis	
Crinifer concolor	Corythaixoides concolor	
Crinifer leucogaster	Corythaixoides leucogaster	
Crinifer personatus	Corythaixoides personatus	
Crithagra albogularis	Serinus albogularis	
Crithagra buchanani	Serinus buchanani	
Crithagra sulphurata	Serinus sulphuratus	
Cyanoramphus erythrotis	Cyanoramphus erythrotis	
Cyclarhis gujanensis contrerasi	Cyclarhis gujanensis contrerasi	
Cyclarhis gujanensis dorsalis	Cyclarhis gujanensis dorsalis	
Cygnus bewickii	Cygnus columbianus	
Dasylophus	Phaenicophaeus	
Dendragapus franklinii	Dendragapus canadensis	
Dendragapus fuliginosus	Dendragapus obscurus	
Dendrocolaptes concolor	Dendrocolaptes certhia concolor	
Dendrocopos leucotos leucotos	Dendrocopos leucotos leucotos	
Dendrocopos leucotos lilfordi	Dendrocopos leucotos lilfordi	
Dendrocopos leucotos subcirris	Dendrocopos leucotos subcirris	
Dendrocopos major brevirostris	Dendrocopos major brevirostris	
Dendrocopos major japonicus	Dendrocopos major japonicus	
Dendrocopos major pinetorum	Dendrocopos major pinetorum	

Dendroica auduboni	Dendroica coronata auduboni	
Dendroica nigrescens halseii	Dendroica nigrescens halseii	
Dendroica nigrescens nigrescens	Dendroica nigrescens nigrescens	
Dendrospiza capistrata	Serinus capistratus	
Dendrospiza hyposticta	Serinus hypostictus	
Dendrospiza koliensis	Serinus koliensis	
Dendrospiza scotops	Serinus scotops	
Diglossa carbonaria brunneiventris	Diglossa brunneiventris	
Diglossa carbonaria carbonaria	Diglossa carbonaria carbonaria	
Diglossa carbonaria gloriosa	Diglossa gloriosa	
Diglossa gloriosissima boylei	Diglossa gloriosissima boylei	
Diglossa gloriosissima gloriosissima	Diglossa gloriosissima gloriosissima	
Diglossa humeralis aterrima	Diglossa humeralis aterrima	
Diglossa humeralis humeralis	Diglossa humeralis humeralis	
Diglossa humeralis nocticolor	Diglossa humeralis nocticolor	
Diglossa mystacalis albilinea	Diglossa mystacalis albilinea	
Diglossa mystacalis mystacalis	Diglossa mystacalis mystacalis	
Diglossa mystacalis pectoralis	Diglossa mystacalis pectoralis	
Diglossa mystacalis unicincta	Diglossa mystacalis unicincta	
Dinornis maximus	Dinornis novaezealandiae	
Dinornis robustus	Dinornis giganteus	
Dinornis struthoides	Dinornis novaezealandiae	
Diomedea bassi	Thalassarche chlororhynchos bassi	
Diomedea exulans dabbenena	Diomedea exulans dabbenena	
Diopsittaca nobilis	Ara nobilis	
Dixiphia pipra	Pipra pipra	
Drepanornis albertisi	Epimachus albertisi	
Dromiceius novaehollandiae	Dromaius novaehollandiae	
Dyaphorophyia chalybea	Platysteira chalybea	
Emblema bella	Stagonopleura bella	
Emblema guttata	Stagonopleura guttata	
Emeus huttonii	Emeus crassus	
Enantiornis leali	Enantiornis leali	
Eoalulavis	Eoalulavis	Extinct
Eocoracias brachyptera	Eocoracias brachyptera	Extinct
Eocypselus vincenti	Eocypselus vincenti	Extinct
Eoglaucidium pallas	Eoglaucidium pallas	Extinct
Eogrus aeola	Eogrus aeola	Extinct
Eopsaltria capito	Tregellasia capito	
Eopsaltria leucops	Tregellasia leucops	
Ephippiorhynchus senegalis	Ephippiorhynchus senegalensis	
Eriocnemis sapphiropygia	Eriocnemis luciani sapphiropygia	
Erythrina mexicana	Carpodacus mexicanus	
Erythropygia	Cercotrichas	
Euaegotheles tatei	Euaegotheles tatei	
Euaegotheles tatei	Euaegotheles tatei	
Eudromia elegans albida	Eudromia elegans albida	
Eudromius morinellus	Charadrius morinellus	
Eudyptes chrysocome chrysocome	Eudyptes chrysocome chrysocome	
Eudyptes chrysocome moseleyi	Eudyptes chrysocome moseleyi	
Eudyptes chrysocome moseleyi	Eudyptes chrysocome moseleyi	

Eulabeornis cajanea	Aramides cajanea	
Euleucocarbo chalconotus	Phalacrocorax chalconotus	
Euleucocarbo colensoi	Phalacrocorax colensoi	
Euleucocarbo onslowi	Phalacrocorax onslowi	
Euleucocarbo ranfuriyi	Phalacrocorax ranfuriyi	
Euodice cantans	Lonchura cantans	
Euphagus carolinensis	Euphagus carolinus	
Euplectus hordeacea	Euplectes hordeaceus	
Euryanas finschi	Chenonetta finschi	
Euryapteryx exilis	Euryapteryx curtus	Extinct
Euryapteryx geranoides	Euryapteryx geranoides	Extinct
Excalfactoria sinensis/chinensis	Coturnix chinensis	
Falco peregrinus calidus	Falco peregrinus calidus	
Falco peregrinus peregrinus	Falco peregrinus peregrinus	
Finschia novaeseelandiae	Mohoua novaeseelandiae	
Fluvicola	Fluvicola	
Fluvicola pica albiventer	Fluvicola pica albiventer	
Francolinus ochropectus	Pternistis ochropectus	
Fringilla coelebs coelebs	Fringilla coelebs coelebs	
Fulica chathamensis chathamensis	Fulica chathamensis chathamensis	
Fulica chathamensis prisca	Fulica chathamensis prisca	
Gallinula martinica	Porphyrio martinica	
Gallinuloides wyomingensis	Gallinuloides wyomingensis	Extinct
Garritornis isidorei	Pomatostomus isidorei	
Geobates crassirostris	Geositta crassirostris	
Geobiastes	Brachypteracias	
Geobiastes squamigera	Brachypteracias squamigera	Extinct
Geochen rhuax	Geochen rhuax	
Geokichla princei	Zoothera princei	
Geranopterus alatus	Geranopterus alatus	Extinct
Geranopterus milneedwardsi	Geranopterus milneedwardsi	Extinct
Gobipteryx minuta	Gobipteryx minuta	Extinct
Guarouba guarouba	Aratinga guarouba	
Gyalophylax hellmayri	Synallaxis hellmayri	
Gymnogyps kofordi	Gymnogyps kofordi	Extinct
Gypopsitta aurantiocephala	Gypopsitta aurantiocephala	Extinct
Gypopsitta coccinicollaris	Gypopsitta coccinicollaris	
Haematopus frazari	Haematopus palliatus frazari	
Hagedashia hagedash	Bostrychia hagedash	
Halcyon leucopygia	Todirhamphus leucopygius	
Halcyon macleayii	Todirhamphus macleayii	
Halcyon sancta	Todirhamphus sanctus	
Halcyon winchelli	Todirhamphus winchelli	
Halietor pygmaeus	Phalacrocorax pygmeus	
Haplochelidon andecola	Hirundo andecola	
Hemignathus flava/flavus	Hemignathus chloris	
Hemignathus flavus	Hemignathus chloris	
Hemignathus lucidus affinis	Hemignathus lucidus affinis	
Hemignathus lucidus hanapepe	Hemignathus lucidus hanapepe	
Hemignathus lucidus lucidus	Hemignathus lucidus lucidus	
Hemignathus stejnegeri	Hemignathus stejnegeri	Extinct

Hemignathus virens chloris	Hemignathus virens chloris	
Hemignathus virens stejnegeri	Hemignathus virens stejnegeri	
Hemignathus virens virens	Hemignathus virens virens	
Hemignathus virens wilsoni	Hemignathus virens wilsoni	
Hemimacronyx chloris	Anthus chloris	
Hesperornis regalis	Hesperornis regalis	Extinct
Heterocnus	Tigrisoma	
Hieraaetus fasciatus fasciatus	Hieraaetus fasciatus fasciatus	
Hieraaetus fasciatus spilogaster	Hieraaetus spilogaster	
Hieraaetus morphnoides morphnoides	Hieraaetus morphnoides morphnoides	
Hieraaetus morphnoides weiskei	Hieraaetus morphnoides weiskei	
Hieraaetus wahlbergi	Aquila wahlbergi	
Himatione sanguinea sanguinea	Himatione sanguinea sanguinea	
Hippolais caligata caligata	Hippolais caligata caligata	
Hippolais caligata rama	Hippolais rama	
Hippolais pallida elaeica	Hippolais pallida elaeica	
Hydranassa caerula	Egretta caerula	
Hydranassa novaehollandiae	Egretta novaehollandiae	
Hydrocoleus minutus	Larus minutus	
Hylopsar	Lamprotornis	
Hypoleucos auritus	Phalacrocorax auritus	
Hypoleucos olivaceus	Phalacrocorax olivaceus	
Hypoleucos sulcirostris	Phalacrocorax sulcirostris	
Hypoleucos varius	Phalacrocorax varius	
Iberomesornis romerali	Iberomesornis romerali	Extinct
Ibycter americanus	Ibycter americanus	
Ichthyornis antecessor	Ichthyornis antecessor	Extinct
Ichthyornis dispar	Ichthyornis dispar	Extinct
Icterus cayanensis cayanensis	Icterus cayanensis cayanensis	
Icterus cayanensis periporphyrus	Icterus cayanensis periporphyrus	
Icterus galbula abeillei	Icterus galbula abeillei	
Icterus jamacaii croconotus	Icterus jamacaii croconotus	
Icterus leucopteryx leucopteryx	Icterus leucopteryx leucopteryx	
Icterus mesomelas taczanowskii	Icterus mesomelas taczanowskii	
Icterus nigrogularis nigrogularis	Icterus nigrogularis nigrogularis	
Icterus spurius spurius	Icterus spurius spurius	
Idioptilon	Hemitriccus	
Jeholornis prima	Jeholornis prima	Extinct
Jungornis tesselatus	Jungornis tesselatus	Extinct
Lagopus scoticus	Lagopus lagopus	
Laputa robusta	Laputa robusta	Extinct
Larus cirrocephalus poicephalus	Larus cirrocephalus poicephalus	
Larus kumlieni	Larus glaucoides kumlieni	
Larus novaehollandiae scopulinus	Larus novaehollandiae scopulinus	
Larus smithsonianus	Larus argentatus smithsonianus	
Lectavis bretincola	Lectavis bretincola	Extinct
Lepidogrammus	Phaenicophaeus	
Lepidothrix suavissima	Pipra suavissima	
Leptopterus madagascarinus	Cyanolanius madagascarinus	
Leptopterus viridis	Artamella viridis	
Leucocarbo bougainvilli	Phalacrocorax bougainvilli	

Leucocarbo capensis	Phalacrocorax capensis	
Leucocarbo nigrogularis	Phalacrocorax nigrogularis	
Leucophaeus scoresbii	Larus scoresbii	
Leucosticte arctoa littoralis	Leucosticte tephrocotis littoralis	
Leucosticte littoralis	Leucosticte tephrocotis littoralis	
Leucotreron cincta	Ptilinopus cinctus	
Leucotreron subgularis	Ptilinopus subgularis	
Liaoningornis	Liaoningornis	Extinct
Limenavis patagonica	Limenavis patagonica	Extinct
Limnoctites rectirostris	Hylocryptus rectirostris	
Linaria cannabina	Carduelis cannabina	
Lithoptila abdounensis	Lithoptila abdounensis	Extinct
Lithornis celetius	Lithornis celetius	Extinct
Lithornis plebius	Lithornis plebius	Extinct
Lithornis promiscuus	Lithornis promiscuus	Extinct
Lonchura cucullata cucullata	Lonchura cucullata cucullata	
Lonchura malacca atricapilla	Lonchura malacca atricapilla	
Lonchura pectoralis	Heteromunia pectoralis	
Lophophaps plumifera	Geophaps plumifera	
Lothyra nycthera	Lothura nycthemera	
Loxops coccineus caeruleirostris	Loxops caeruleirostris	
Loxops parvus	Hemignathus parvus	
Loxops sagittirostris	Hemignathus sagittirostris	
Loxops virens	Hemignathus virens	
Loxops/Akialoa stejnegeri	Hemignathus stejnegeri	
Lyrurus mlokosiewiczi	Tetrao mlokosiewiczi	
Lyrurus tetrix	Tetrao tetrix	
Malurus assimilis	Malurus lamberti assimilis	
Malurus dulcis	Malurus lamberti dulcis	
Malurus leuconotus	Malurus leucopterus leuconotus	
Malurus rogersi	Malurus lamberti rogersi	
Megabyas flammulatus	Bias flammulatus	
Megalapteryx benhami	Megalapteryx benhami	Extinct
Megaloprepria magnifica	Ptilinopus magnificus	
Megapodius duperryi	Megapodius freycinet duperryi	
Melaenornis pallidus	Melaenornis pallidus	
Melaenornis silens	Sigelus silens	
Melanitta americana	Melanitta americana	
Melanochlora sultanea gayeti	Melanochlora sultanea gayeti	
Melanochlora sultanea sultanea	Melanochlora sultanea sultanea	
Meliphaga penicillata	Lichenostomus penicillatus	
Messelastur gratulator	Messelastur gratulator	Extinct
Microcarbo africanus	Phalacrocorax africanus	
Microcarbo coronatus	Phalacrocorax coronatus	
Microcarbo melanoleucos	Phalacrocorax melanoleucos	
Microcarbo niger	Phalacrocorax niger	
Microcarbo pygmaeus	Phalacrocorax pygmaeus	
Microeca leucophaea	Microeca fascinans	
Micropalama himantopus	Calidris himantopus	
Miliaria calandra calandra	Miliaria calandra calandra	
Misocalius	Chalcites	

Misocalius osculans	Chrysococcyx osculans	
Monticola bensoni	Pseudocossyphus bensoni	
Monticola erythronota	Monticola erythronotus	
Motacilla baicalensis	Motacilla alba baicalensis	
Motacilla leucopsis	Motacilla alba leucopsis	
Motacilla lugens	Motacilla alba lugens	
Motacilla ocularis	Motacilla alba ocularis	
Myiarchus swainsoni swainsoni	Myiarchus swainsoni swainsoni	
Myiarchus tuberculifer atriceps	Myiarchus tuberculifer atriceps	
Myiarchus tuberculifer nigricapillus	Myiarchus tuberculifer nigricapillus	
Myiarchus tuberculifer platyrhynchus	Myiarchus tuberculifer platyrhynchus	
Myiarchus tyrannulus bahiae	Myiarchus tyrannulus bahiae	
Myiarchus tyrannulus insularum	Myiarchus tyrannulus insularum	
Myiobius sulphureipygius	Myiobius barbatus sulphureipygius	
Nannopterum harrisi	Phalacrocorax harrisi	
Nannus troglodytes	Troglodytes troglodytes	
Nectarinia humbloti humbloti	Nectarinia humbloti humbloti	
Nectarinia humbloti mohelica	Nectarinia humbloti mohelica	
Nectarinia notata moebii	Nectarinia notata moebii	
Nectarinia notata notata	Nectarinia notata notata	
Nectarinia notata voeltzkowi	Nectarinia notata voeltzkowi	
Nectarinia souimanga abbotti	Nectarinia sovimanga abbotti	
Nectarinia souimanga aldabrensis	Nectarinia sovimanga aldabrensis	
Nectarinia souimanga buchenorum	Nectarinia sovimanga buchenorum	
Nectarinia souimanga comorensis	Nectarinia sovimanga comorensis	
Nectarinia souimanga souimanga	Nectarinia sovimanga souimanga	
Nesocarbo campbelli	Phalacrocorax campbelli	
Neuquenornis volans	Neuquenornis volans	Extinct
Ninox sumbaensis	Ninox sumbaensis	Extinct
Noguerornis	Noguerornis	
Notocarbo atriceps	Phalacrocorax atriceps	
Notocarbo bransfieldensis	Phalacrocorax bransfieldensis	
Notocarbo georgianus	Phalacrocorax georgianus	
Notocarbo verrucosus	Phalacrocorax verrucosus	
Nyctiornis amicta	Nyctyornis amictus	
Oceanitidae	Hydrobatidae	
Ochetorhynchus certhioides	Upucerthia certhioides	
Ochraspiza reichenowi	Serinus reichenowi	
Ochrospiza atrogularis	Serinus atrogularis	
Ochrospiza dorsostriata	Serinus dorsostriatus	
Ochrospiza leucopygia	Serinus leucopygius	
Ochrospiza mozambica	Serinus mozambicus	
Ochrospiza xanthopygia	Serinus xanthopygius	
Ochthoeca pulchella	Silvicultrix pulchella	
Odontopteryx toliapica	Odontopteryx toliapica	Extinct
Odontospiza caniceps	Lonchura griseicapilla	
Oreopeleia	Geotrygon	
Oreopelia chrysia	Geotrygon chrysia	
Oreophylax moreirae	Schizoeaca moreirae	
Orthiospiza howarthi	Orthiospiza howarthi	Extinct
Orthonyx dorsalis	Orthonyx temminckii dorsalis	

Orthonyx novaeguineae	Orthonyx temminckii novaeguineae	
Orthonyx victoriana	Orthonyx temminckii victoriana	
Orthopsittaca manilata	Ara manilata	
Ortygospiza atricapilla	Ortygospiza atricollis	
Pachyornis australis	Pachyornis australis	Extinct
Pachyornis mappini	Pachyornis mappini	Extinct
Palaeotis	Palaeotis	Extinct
Paraortygoides messelensis	Paraortygoides messelensis	Extinct
Paraortygoides radagasti	Paraortygoides radagasti	Extinct
Paraprefica kelleri	Paraprefica kelleri	Extinct
Pareudiastes pacificus	Pareudiastes pacificus	Extinct
Pareudiastes sylvestris	Edithornis sylvestris	
Parisoma layardi	Sylvia layardi	
Parus bicolor atricristatus	Parus atricristatus	
Parus bicolor bicolor	Parus bicolor bicolor	
Parus dichrous	Lophophanes dichrous	
Parus niger niger	Parus niger niger	
Parus rubidiventris	Periparus rubidiventris	
Parus venustulus	Periparus venustulus	
Passer ammodendri ammodendri	Passer ammodendri ammodendri	
Passer griseus griseus	Passer griseus griseus	
Passer hispaniolensis hispaniolensis	Passer hispaniolensis hispaniolensis	
Passer melanurus melanurus	Passer melanurus melanurus	
Passer rutilans rutilans	Passer rutilans rutilans	
Passerella megarhyncha	Passerella iliaca megarhyncha	
Passerella schistacea	Passerella iliaca schistacea	
Passerella unalaschcensis	Passerella iliaca unalaschcensis	
Patagioenas fasciata	Columba fasciata	
Patagioenas plumbea	Columba plumbea	
Patagioenas speciosa	Columba speciosa	
Patagioenas subvinacea	Columba subvinacea	
Patagopteryx deferrariisi	Patagopteryx deferrariisi	Extinct
Pedionomus	Pedionomus	
Pelagornis	Pelagornis	Extinct
Pelecanus roseus	Pelecanus onocrotalus roseus	
Penthoceryx	Cacomantis	
Periparus ater ater	Periparus ater ater	
Periparus elegans elegans	Periparus elegans elegans	
Periparus elegans mindanensis	Periparus elegans mindanensis	
Petroica cucullata	Melanodryas cucullata	
Petronia petronia petronia	Petronia petronia petronia	
Petrophasa blaauwi	Geophaps smithii blaauwi	
Petrophasa ferruginea	Petrophassa plumifera ferruginea	
Petrophasa peninsulae	Petrophassa scripta	
Pezoporus wallicus wallicus	Pezoporus wallicus wallicus	
Phacellodomus maculipectus	Phacellodomus striaticollis maculipectus	
Pholia	Cinnyricinclus	
Phylloscopus abietinus	Phylloscopus collybita abietinus	
Phylloscopus bonelli orientalis	Phylloscopus bonelli orientalis	
Phylloscopus borealis kennecotti	Phylloscopus borealis kennecotti	

Phylloscopus borealis xanthodryas	Phylloscopus borealis xanthodryas	
Phylloscopus cantator cantator	Phylloscopus cantator cantator	
Phylloscopus collybita abietinus	Phylloscopus collybita abietinus	
Phylloscopus collybita abietinus	Phylloscopus collybita abietinus	
Phylloscopus collybita brevirostris	Phylloscopus collybita brevirostris	
Phylloscopus collybita caucasicus	Phylloscopus collybita caucasicus	
Phylloscopus collybita tristis	Phylloscopus collybita tristis	
Phylloscopus davisoni davisoni	Phylloscopus davisoni davisoni	
Phylloscopus davisoni disturbans	Phylloscopus davisoni disturbans	
Phylloscopus davisoni klossi	Phylloscopus davisoni klossi	
Phylloscopus davisoni ogilviegranti	Phylloscopus davisoni ogilviegranti	
Phylloscopus emeiensis	Phylloscopus emeiensis	
Phylloscopus hainanus	Phylloscopus hainanus	
Phylloscopus inornatus humei	Phylloscopus inornatus humei	
Phylloscopus kansuensis	Phylloscopus proregulus kansuensis	
Phylloscopus mackensianus	Phylloscopus umbrovirens mackensianus	
Phylloscopus maculipennis maculipennis	Phylloscopus maculipennis maculipennis	
Phylloscopus minullus	Phylloscopus ruficapillus minullus	
Phylloscopus orientalis	Phylloscopus orientalis	
Phylloscopus poliocephalus giulianettii	Phylloscopus poliocephalus giulianettii	
Phylloscopus presbytes floris	Phylloscopus presbytes floris	
Phylloscopus reguloides assamensis	Phylloscopus reguloides assamensis	
Phylloscopus reguloides claudiae	Phylloscopus reguloides claudiae	
Phylloscopus reguloides fokiensis	Phylloscopus reguloides fokiensis	
Phylloscopus reguloides goodsoni	Phylloscopus reguloides goodsoni	
Phylloscopus reguloides kashmiriensis	Phylloscopus reguloides kashmiriensis	
Phylloscopus reguloides reguloides	Phylloscopus reguloides reguloides	
Phylloscopus reguloides ticehursti	Phylloscopus reguloides ticehursti	
Phylloscopus ruficapilla minullus	Phylloscopus ruficapillus minullus	
Phylloscopus sarasinorum sarasinorum	Phylloscopus sarasinorum sarasinorum	
Phylloscopus sindianus lorenzii	Phylloscopus sindianus lorenzii	
Phylloscopus sindianus sindianus	Phylloscopus sindianus sindianus	
Phylloscopus trivirgatus benguetensis	Phylloscopus trivirgatus benguetensis	
Phylloscopus trivirgatus trivirgatus	Phylloscopus trivirgatus trivirgatus	
Phylloscopus trochiloides viridianus	Phylloscopus trochiloides viridianus	
Phylloscopus trochilus trochilus	Phylloscopus trochilus trochilus	
Phylloscopus umbrovirens fugglescouchmani	Phylloscopus umbrovirens fugglescouchmani	
Phylloscopus yunnanensis	Phylloscopus yunnanensis	
Pica pica camtschatica	Pica pica camtschatica	
Pica pica sericea	Pica pica sericea	
Picoides kizuki	Dendrocopos kizuki	
Picoides tridactylus alpinus	Picoides tridactylus alpinus	
Picus canus canus	Picus canus canus	
Picus canus jessoensis	Picus canus jessoensis	
Picus viridis viridis	Picus viridis viridis	
Pionopsitta coccinicollaris	Pionopsitta haematotis coccinicollaris	
Pionopsitta vulturina	Gypopsitta vulturina	
Piranga erythrocephala canida	Piranga erythrocephala canida	

Piranga flava lutea	Piranga flava lutea	
Piranga flava rosacea	Piranga flava rosacea	
Piranga flava testacea	Piranga flava testacea	
Piranga leucoptera ardens	Piranga leucoptera ardens	
Piranga leucoptera leucoptera	Piranga leucoptera leucoptera	
Pitylus grossus	Saltator grossus	
Platycercus adscitus adsiticus	Platycercus adscitus adsiticus	
Platycercus adscitus amathusiae	Platycercus adscitus amathusiae	
Platycercus adscitus mackaiensis	Platycercus adscitus mackaiensis	
Platycercus adscitus palliceps	Platycercus adscitus palliceps	
Platycercus elegans adelaidae	Platycercus elegans adelaidae	
Platycercus elegans elegans	Platycercus elegans elegans	
Platycercus elegans flaveolus	Platycercus elegans flaveolus	
Platycercus elegans nigrescens	Platycercus elegans nigrescens	
Platycercus eximius diemenensis	Platycercus eximius diemenensis	
Platycercus eximius eximius	Platycercus eximius eximius	
Platycercus icterotis xanthogenys	Platycercus icterotis xanthogenys	
Poecile carolinensis carolinensis	Poecile carolinensis carolinensis	
Poecile montanus borealis	Poecile montanus borealis	
Poecile montanus songarus	Poecile montanus songarus	
Poecile palustris brevirostris	Poecile palustris brevirostris	
Poecile palustris palustris	Poecile palustris palustris	
Poecile varius	Parus varius	
Poecilurus candei	Synallaxis candei	
Poecilurus scutatus	Synallaxis scutatus	
Poephila annulosa	Taeniopygia bichenovii annulosa	
Poephila atropygialis	Poephila cincta atropygialis	
Poephila bichenovii	Taeniopygia bichenovii	
Poephila castanotis	Taeniopygia guttata castanotis	
Poephila guttata	Taeniopygia guttata	
Poephila guttata	Taeniopygia guttata	
Poephila hecki	Poephila acuticauda hecki	
Poephila leucotis	Poephila personata leucotis	
Pogonotriccus orbitalis	Phylloscartes orbitalis	
Poliolimnas flaviventer	Porzana flaviventer	
Poliospiza burtoni	Serinus burtoni	
Poliospiza gularis	Serinus gularis	
Poliospiza leucoptera	Serinus leucopterus	
Poliospiza mennelli	Serinus mennelli	
Poliospiza striolata	Serinus striolatus	
Poliospiza tristriata	Serinus tristriatus	
Polyplancta aurescens	Heliodoxa aurescens	
Porphyrio hochstetteri	Porphyrio mantelli	
Porphyrio poliocephalus	Porphyrio porphyrio poliocephalus	
Porphyrio porphyrio madagascariensis	Porphyrio porphyrio madagascariensis	
Porphyrio porphyrio melanotus	Porphyrio porphyrio melanotus	
Porphyrio porphyrio pulverulentus	Porphyrio porphyrio pulverulentus	
Porphyrio porphyrio seistanicus	Porphyrio porphyrio seistanicus	
Porphyrio pulverulentus	Porphyrio porphyrio	
Porzana erythrops	Neocrex erythrops	
Porzana flavirostra	Amaurornis flavirostra	

Porzana olivieri	Amaurornis olivieri	
Prefica nivea	Prefica nivea	Extinct
Presbyornis pervetus	Presbyornis pervetus	Extinct
Primapus lacki	Primapus lacki	Extinct
Primobucco mcgrewi	Primobucco mcgrewi	Extinct
Primolius auricollis	Ara auricollis	
Primolius couloni	Ara couloni	
Primozygodactylus danielsi	Primozygodactylus danielsi	Extinct
Procarduelis vinacea	Carpodacus vinaceus	
Prophaethon shrubsolei	Prophaethon shrubsolei	Extinct
Protocypselomorphus manfredkelleri	Protocypselomorphus manfredkelleri	Extinct
Psarocolius latirostris	Ocyalus latirostris	
Psarocolius yuracares	Gymnostinops yuracares	
Pseudoalcippe abyssinica	Illadopsis abyssinica	
Pseudobulweria rostrata rostrata	Pseudobulweria rostrata rostrata	
Pseudobulweria rostrata trouessarti	Pseudobulweria rostrata trouessarti	
Pseudochloroptila totta	Serinus totta	
Pseudoseisuropsis cuelloi	Pseudoseisuropsis cuelloi	Extinct
Pseudoseisuropsis nehuen	Pseudoseisuropsis nehuen	Extinct
Psittacopes lepidus	Psittacopes lepidus	Extinct
Psittacula cyanocephala roseus	Psittacula cyanocephala	
Psittacula krameri borelis	Psittacula krameri borelis	
Psittacula krameri krameri	Psittacula krameri krameri	
Psittacula krameri manillensis	Psittacula krameri manillensis	
Psophodes lateralis	Psophodes olivaceus	
Psophodes leucogaster	Psophodes nigrogularis	
Pterodroma deserta	Pterodroma feae deserta	
Pteroglossus flavirostris	Pteroglossus azara flavirostris	
Pteroglossus humboldti	Pteroglossus inscriptus humboldti	
Pteroglossus reichenowi	Pteroglossus bitorquatus reichenowi	
Pteroglossus sturmii	Pteroglossus bitorquatus sturmii	
Ptilolaemus	Ptilolaemus	
Ptiloris alberti	Ptiloris magnificus alberti	
Puffinus bailloni	Puffinus lherminieri bailloni	
Puffinus baroli	Puffinus assimilis baroli	
Puffinus boydi	Puffinus assimilis boydi	
Puffinus colstoni	Puffinus lherminieri colstoni	
Puffinus dichrous	Puffinus lherminieri dichrous	
Puffinus elegans	Puffinus assimilis elegans	
Puffinus haurakiensis	Puffinus assimilis haurakiensis	
Puffinus kermadecensis	Puffinus assimilis kermadecensis	
Puffinus loyemilleri	Puffinus lherminieri loyemilleri	
Puffinus myrtae	Puffinus assimilis myrtae	
Puffinus nicolae	Puffinus lherminieri nicolae	
Puffinus polynesiae	Puffinus lherminieri polynesiae	
Puffinus puffinus mauretanicus	Puffinus mauretanicus	
Puffinus puffinus yelkouan	Puffinus yelkouan	
Puffinus subalaris	Puffinus lherminieri subalaris	
Puffinus temptator	Puffinus lherminieri temptator	
Puffinus tunneyi	Puffinus assimilis tunneyi	
Pulchrapollia gracilis	Pulchrapollia gracilis	Extinct

Purpureicephalus haematonotus	Purpureicephalus haematonotus	
Pyrrhula pyrrhula iberiae	Pyrrhula pyrrhula iberiae	
Quercypsitta ivani	Quercypsitta ivani	Extinct
Quercypsitta sudrei	Quercypsitta sudrei	Extinct
Quiscalus versicolor	Quiscalus quiscula versicolor	
Rahona	Rahonavis	Extinct
Rahonavis ostromi	Rahonavis ostromi	Extinct
Rallina amauroptera	Rallina eurizonoides amauroptera	
Rallina castaneiceps	Anurolimnas castaneiceps	
Rallus aquaticus aquaticus	Rallus aquaticus aquaticus	
Rallus modestus	Rallus modestus	
Rallus philippensis dieffenbachii	Rallus philippensis dieffenbachii	
Rallus sylvestris	Gallirallus sylvestris	
Ramphastos ariel	Ramphastos vitellinus	
Ramphastos sulfuratus brevicarinatus	Ramphastos sulfuratus brevicarinatus	
Ramphastos sulfuratus sulfuratus	Ramphastos sulfuratus sulfuratus	
Ramphastos tucanus cuvieri	Ramphastos tucanus cuvieri	
Ramphastos tucanus tucanus	Ramphastos tucanus tucanus	
Ramphastos vitellinus ariel	Ramphastos vitellinus ariel	
Ramphastos vitellinus vitellinus	Ramphastos vitellinus vitellinus	
Reinarda squamata	Tachornis squamata	
Rhamphococcyx	Phaenicophaeus	
Rhamphococcyx calyorhynchus	Zanclostomus calyorhynchus	
Rhinoplax	Ptilolaemus	
Rhinortha	Phaenicophaeus	
Rhopodytes	Phaenicophaeus	
Rhynchotus rufescens macullicollis	Rhynchotus rufescens maculicollis	
Rhynchotus rufescens pallescens	Rhynchotus rufescens pallescens	
Rhynoptynx	Pseudoscops	
Sandcoleus copiosus	Sandcoleus copiosus	Extinct
Sapeornis chaoyangensis	Sapeornis chaoyangensis	Extinct
Scaniacypselus szarskii	Scaniacypselus szarskii	Extinct
Scaniacypselus wardi	Scaniacypselus wardi	Extinct
Scenopoeetes dentirostris	Ailuroedus dentirostris	
Schistes geoffroyi	Schistes geoffroyi	
Schistocichla leucostigma	Percnostola leucostigma	
Scytalopus magellanicus simonsi	Scytalopus simonsi	
Scytalopus unicolor parvirostris	Scytalopus parvirostris	
Scythops	Scythrops	Extinct
Seicercus affinis intermedius	Seicercus affinis intermedius	
Seicercus affinis ocularis	Seicercus affinis ocularis	
Seicercus castaniceps castaniceps	Seicercus castaniceps castaniceps	
Seicercus cognitus	Seicercus affinis intermedius	
Seicercus omeiensis	Seicercus omeiensis	
Seicercus soror	Seicercus soror	
Seicercus tephrocephalus	Seicercus tephrocephalus	
Seicercus valentini	Seicercus valentini	
Seicercus whistleri whistleri	Seicercus whistleri whistleri	
Seicercus xanthoschistos tephrodiras	Seicercus xanthoschistos tephrodiras	
Seicercus xanthoschistos xanthoschistos	Seicercus xanthoschistos xanthoschistos	

Selenidera langsdorffii	Selenidera reinwardtii langsdorffii	
Semeiophorus	Macrodipteryx	
Sericornis citreogularis cairnsi	Sericornis citreogularis cairnsi	
Sericornis citreogularis citreogularis	Sericornis citreogularis citreogularis	
Sericornis magnirostris magnirostris	Sericornis magnirostris magnirostris	
Sericornis magnirostris viridior	Sericornis magnirostris viridior	
Serinops	Serinus	
Serinus canicollis canicollis	Serinus canicollis canicollis	
Serinus canicollis flavivertex	Serinus canicollis flavivertex	
Sicalis flaveola pelzelni	Sicalis flaveola pelzelni	
Sinornis santensis	Sinornis santensis	
Somateria borealis	Somateria mollissima borealis	
Somateria dresseri	Somateria mollissima dresseri	
Somateria v-nigrum	Somateria mollissima v-nigrum	
Soroavisaurus australis	Soroavisaurus australis	Extinct
Spermestes bicolor	Lonchura bicolor	
Spermestes cucullatus	Lonchura cucullatus=Lonchura cucullata	
Spermestes cucullatus	Lonchura cucullata	
Spermestes fringilloides	Lonchura fringilloides	
Sphecotheres flaviventris	Sphecotheres flaviventris	
Sphecotheres vieilloti	Sphecotheres vieilloti	
Sphenoeacus mentalis	Melocichla mentalis	
Sphenurus oxyura	Treron oxyura	
Spilaeornis	Spilornis	
Spindalis portoricensis	Spindalis zena portoricensis	
Spinus barbatus	Carduelis barbata	
Spinus cucullatus	Carduelis cucullata	
Spizaetus pinskeri	Spizaetus philippensis pinskeri	
Steganopus tricolor	Phalaropus tricolor	
Stercorarius maccormicki	Catharacta maccormicki	
Sterna nigra	Chlidonias niger	
Sterna sandvicensis acuflavida	Sterna sandvicensis acuflavida	
Sterna sandvicensis eurygnatha	Sterna sandvicensis eurygnatha	
Stictocarbo aristotelis	Phalacrocorax aristotelis	
Stictocarbo featherstoni	Phalacrocorax featherstoni	
Stictocarbo gaimardi	Phalacrocorax gaimardi	
Stictocarbo magellanicus	Phalacrocorax magellanicus	
Stictocarbo pelagicus	Phalacrocorax pelagicus	
Stictocarbo urile	Phalacrocorax urile	
Stigmatopelia senegalensis	Streptopelia senegalensis	
Stipiturus westernensis	Stipiturus malachurus	
Sylphornis bretouensis	Sylphornis bretouensis	Extinct
Sylvia abyssinica	Illadopsis abyssinica	
Sylvia balearica	Sylvia sarda balearica	
Sylvia crassirostris	Sylvia hortensis crassirostris	
Synallaxis chinchipensis	Synallaxis stictothorax chinchipensis	
Synallaxis gularis	Hellmayrea gularis	
Synoicus	Coturnix	
Synthliboramphus hypoleucus scrippsi	Synthliboramphus hypoleucus scrippsi	
Syrmaticus soemmerringii scintillans	Syrmaticus soemmerringii scintillans	

Taeniopygia bichenovii annulosa	Taeniopygia bichenovii annulosa	
Tangara pulcherrima	Iridophanes pulcherrima	
Tauraco corythaix livingstonii	Tauraco livingstonii	
Tauraco corythaix persa	Tauraco persa	
Tauraco corythaix schalowi	Tauraco schalowi	
Tauraco porphyreolophus	Gallirex porphyreolophus	
Telespiza cantans cantans	Telespiza cantans cantans	
Telespiza persecutrix	Telespiza persecutrix	Extinct
Telespiza ypsilon	Telespiza ypsilon	Extinct
Teratornis merriami	Teratornis merriami	Extinct
Thalassarche bassi	Thalassarche chlororhyncos bassi	
Thalasseus bergii	Sterna bergii	
Thambetochen xanion	Thambetochen xanion	Extinct
Tinamus tao kleei	Tinamus tao kleei	
Tonsala hildegardae	Tonsala hildegardae	Extinct
Totanus	?Tringa?	
Tregellasia albigularis	Tregellasia leucops albigularis	
Tregellasia nana	Tregellasia capito nana	
Trichastoma malaccense	Malacocincla malaccensis	
Tumbezia salvini	Ochthoeca salvini	
Turdus dauma	Zoothera dauma	
Tympanistria tympanistria	Turtur tympanistria	
Tympanuchus pinnatus	Tympanuchus cupido	
Tynskya eocaena	Tynskya eocaena	Extinct
Tyranniscus	Zimmerius	
Tyto pratincola	Tyto alba pratincola	
Vangulifer mirandus	Vangulifer mirandus	Extinct
Vangulifer neophasis	Vangulifer neophasis	Extinct
Vegavis iaai	Vegavis iaai	Extinct
Vireo olivaceus chivi	Vireo olivaceus chivi	
Vireo olivaceus diversus	Vireo olivaceus diversus	
Vireo olivaceus olivaceus	Vireo olivaceus olivaceus	
Vireo olivaceus solimoensis	Vireo olivaceus solimoensis	
Vireolanius leucotis simplex	Vireolanius leucotis simplex	
Viridonia virens	Hemignathus virens	
Vorona berivotrensis	Vorona berivotrensis	Extinct
Xenopipo holochlora	Xenopipo holochlora	
Xenopipo unicolor	Xenopipo unicolor	
Xenopipo uniformis	Xenopipo uniformis	
Xestospiza conica	Xestospiza conica	Extinct
Xestospiza fastigialis	Xestospiza fastigialis	Extinct
Yungavolucris brevipedalis	Yungavolucris brevipedalis	Extinct
Zanclostomus	Zanclostomus	Extinct
Zosterops conspicillatus rotensis	Zosterops rotensis	

Appendix B

Source trees used in Chapter 4

* Denotes a reference used for the Galliformes source data in Chapter 3.

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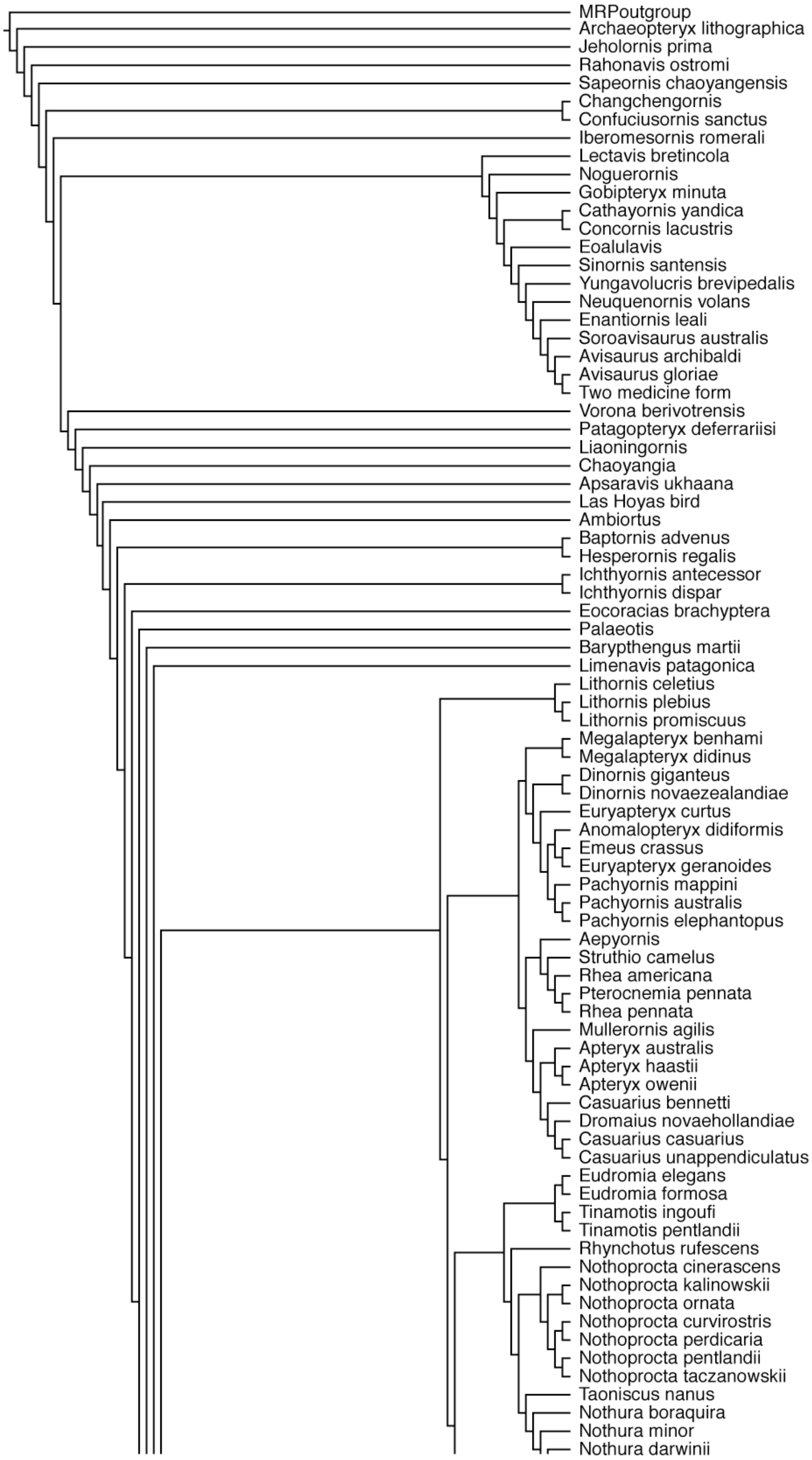
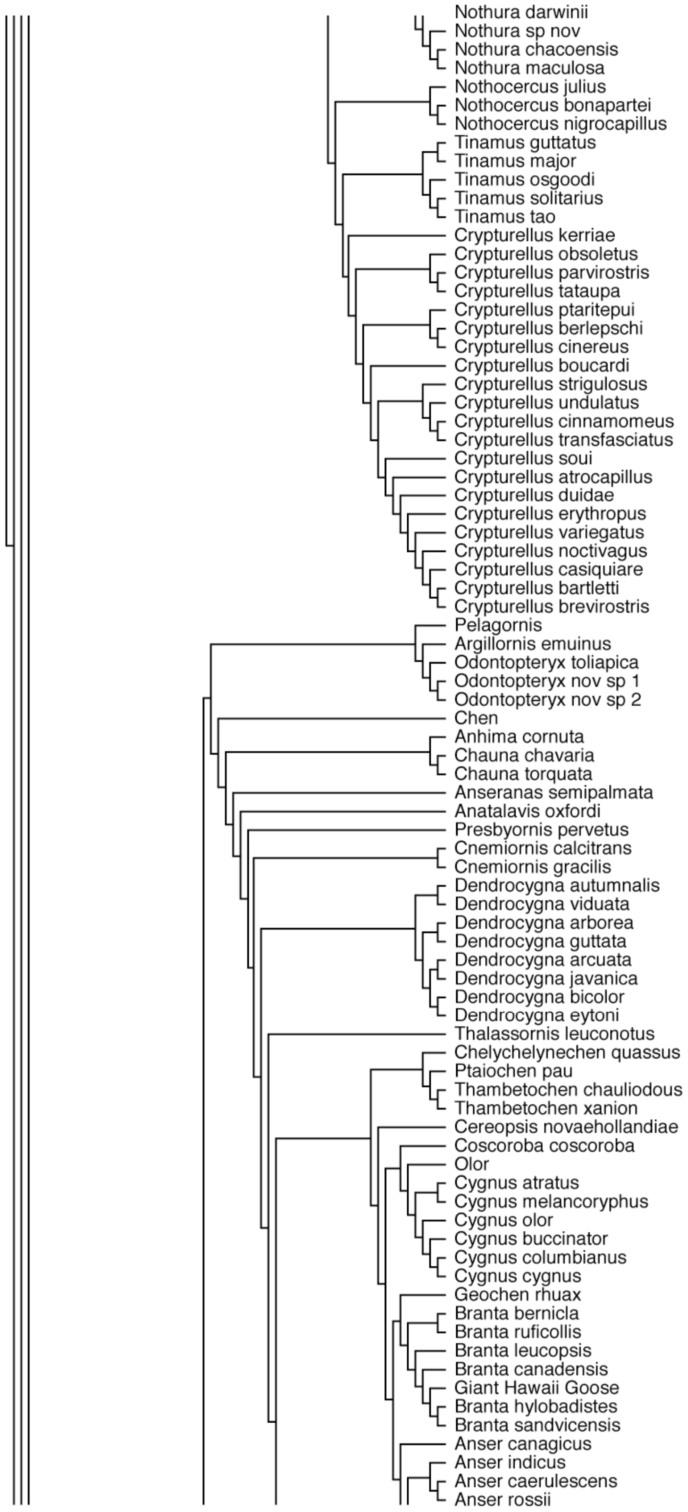
Appendix C

Avian Supertree

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Tinamus major
Tinamus osgoodi
Tinamus solitarius
Tinamus tao
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Crypturellus obsoletus
Crypturellus parvirostris
Crypturellus tataupa
Crypturellus ptaritepui
Crypturellus berlepschi
Crypturellus cinereus
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Crypturellus undulatus
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Crypturellus soui
Crypturellus atrocapillus
Crypturellus duidae
Crypturellus erythropus
Crypturellus variegatus
Crypturellus noctivagus
Crypturellus casiquiare
Crypturellus bartletti
Crypturellus brevirostris
Pelagornis
Argillornis emuinus
Odontopteryx toliapica
Odontopteryx nov sp 1
Odontopteryx nov sp 2
Chen
Anhima cornuta
Chauna chavaria
Chauna torquata
Anseranas semipalmata
Anatalavis oxfordi
Presbyornis pervetus
Cnemiornis calcitrans
Cnemiornis gracilis
Dendrocygna autumnalis
Dendrocygna viduata
Dendrocygna arborea
Dendrocygna guttata
Dendrocygna arcuata
Dendrocygna javanica
Dendrocygna bicolor
Dendrocygna eytoni
Thalassornis leuconotus
Chelychelynechen quassus
Ptaiochen pau
Thambetochen chauliodous
Thambetochen xanion
Cereopsis novaehollandiae
Coscoroba coscoroba
Olor
Cygnus atratus
Cygnus melancoryphus
Cygnus olor
Cygnus buccinator
Cygnus columbianus
Cygnus cygnus
Geochen rhuax
Branta bernicla
Branta ruficollis
Branta leucopsis
Branta canadensis
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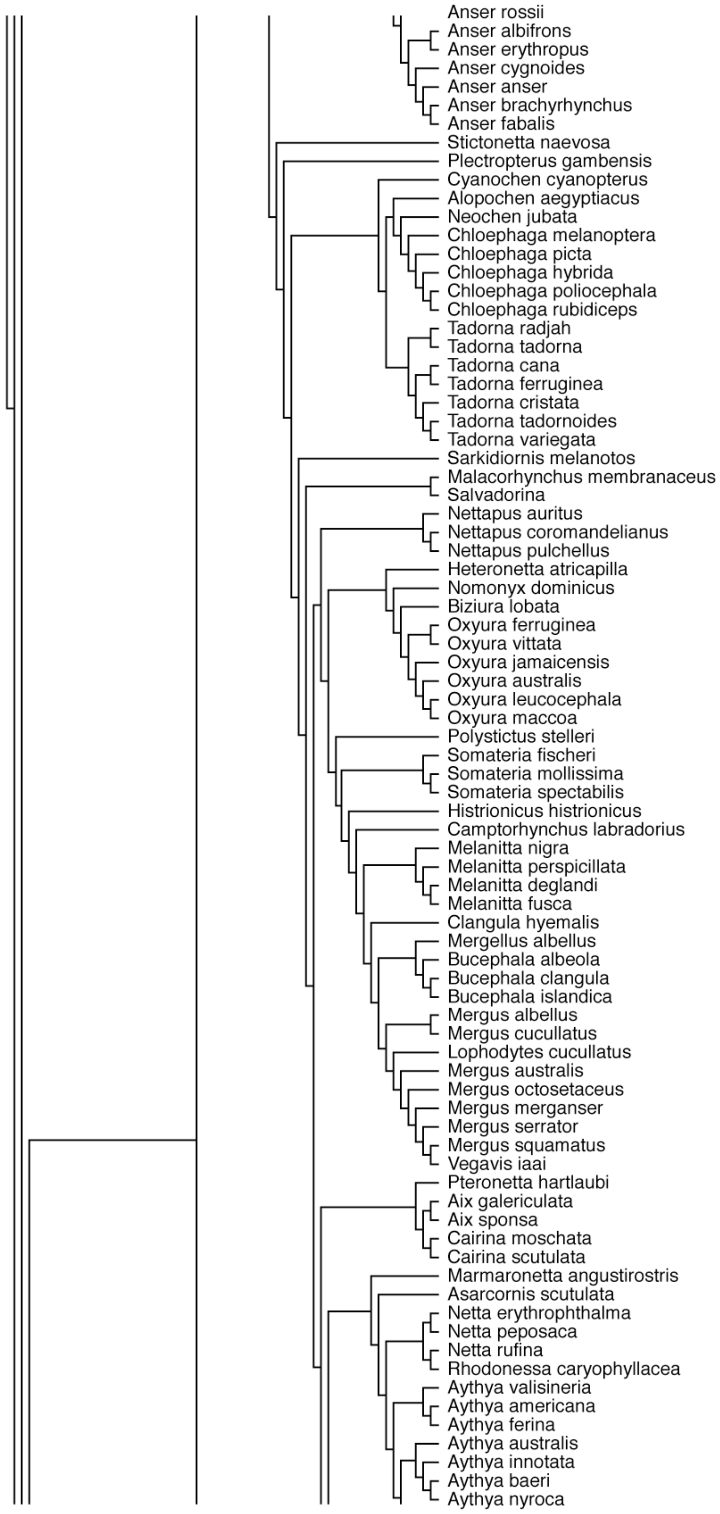
Branta hylobadistes
Branta sandvicensis
Anser canagicus
Anser indicus
Anser caerulescens
Anser rossii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Anser fabalis
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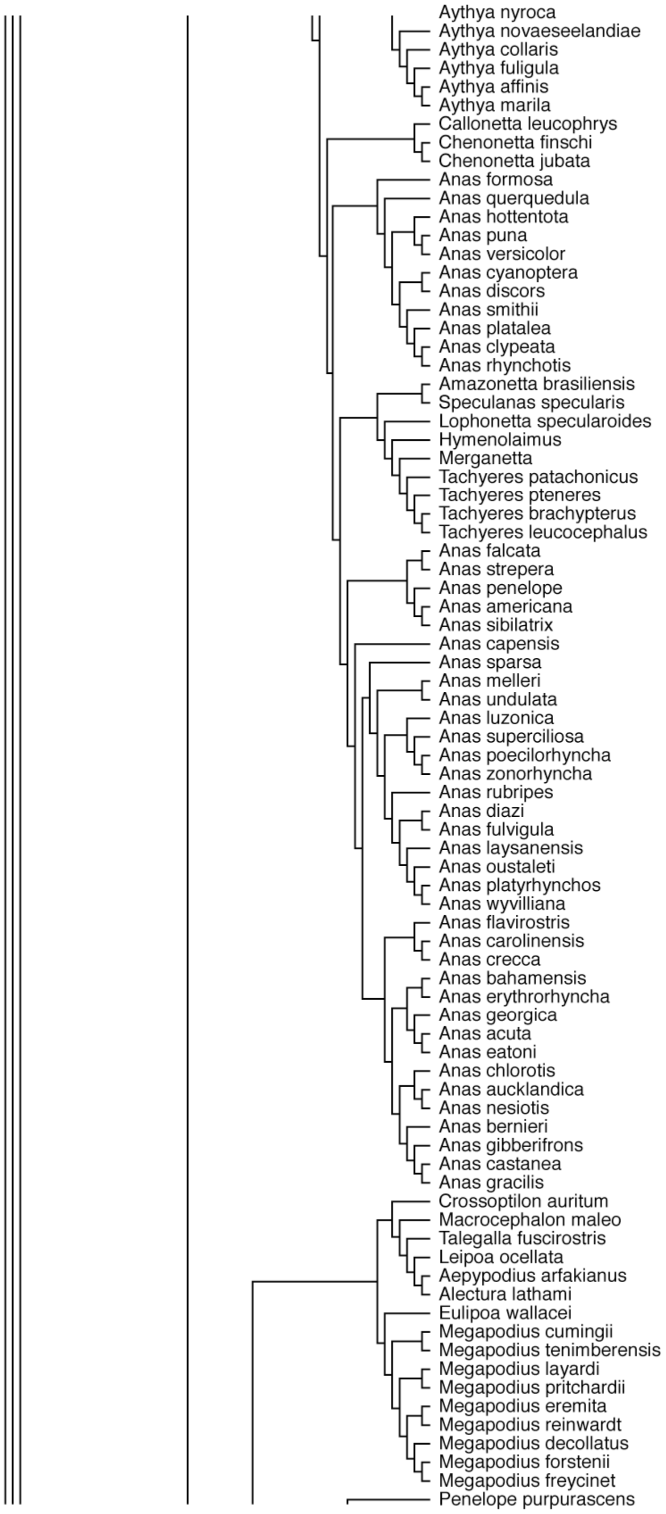
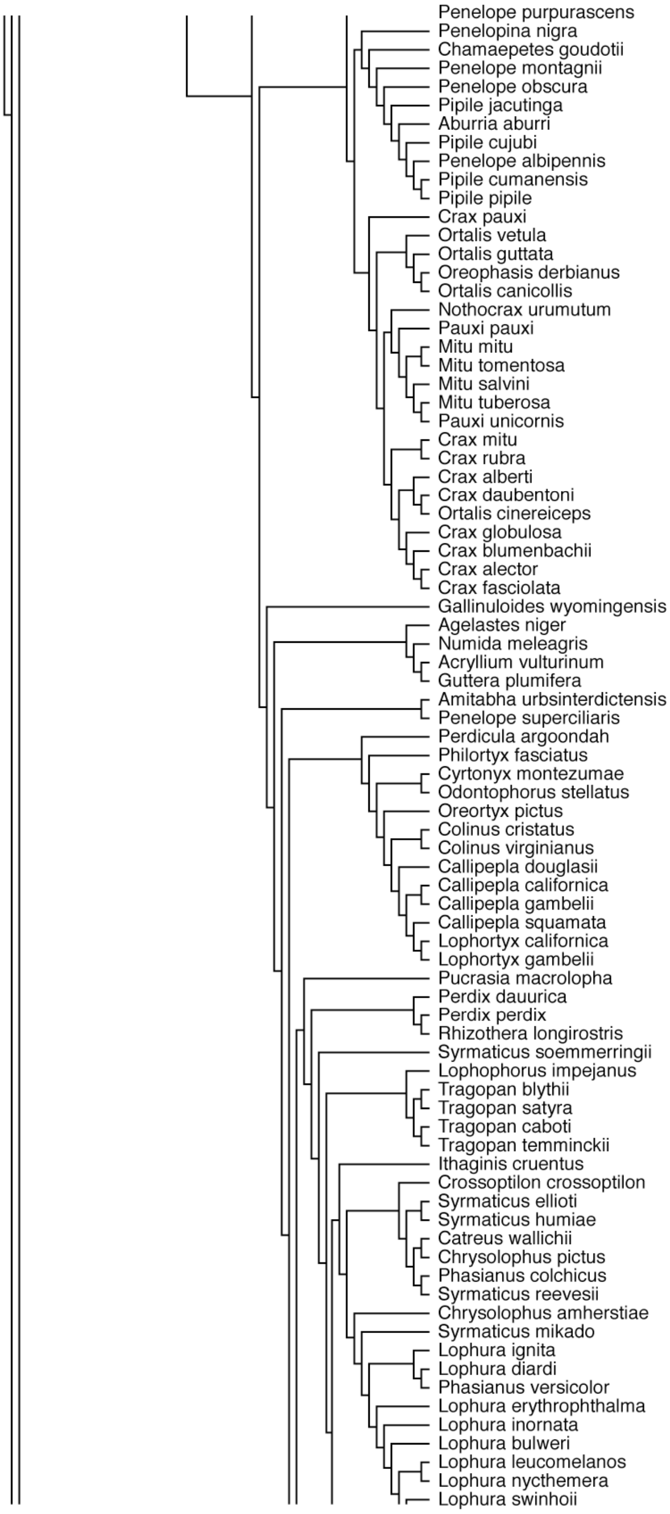
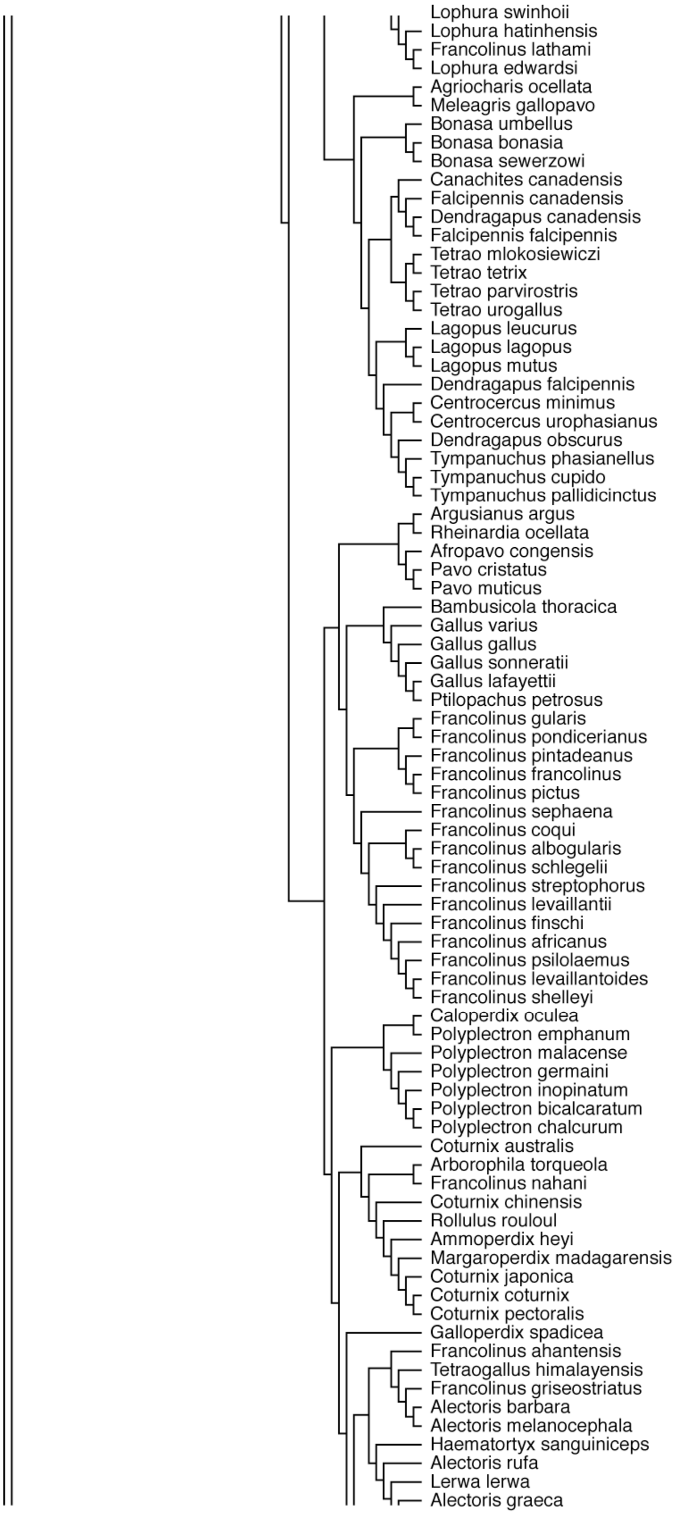
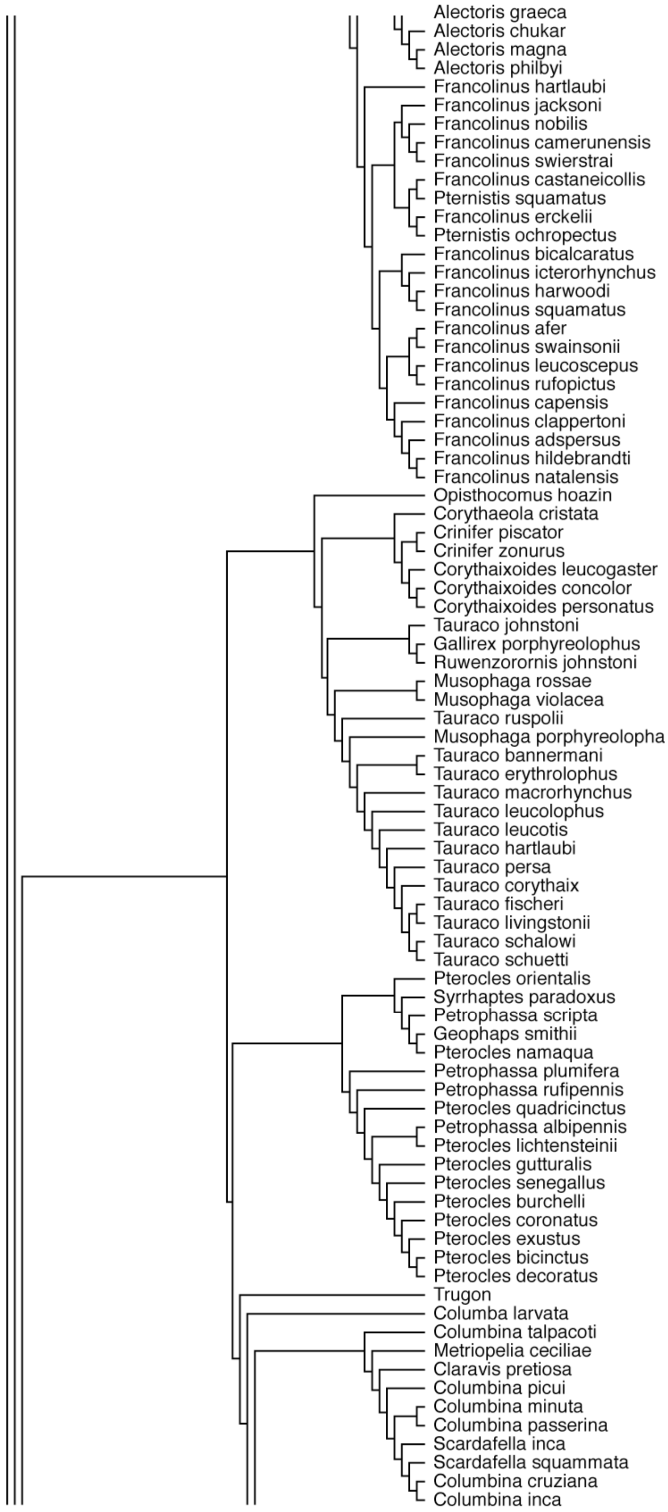
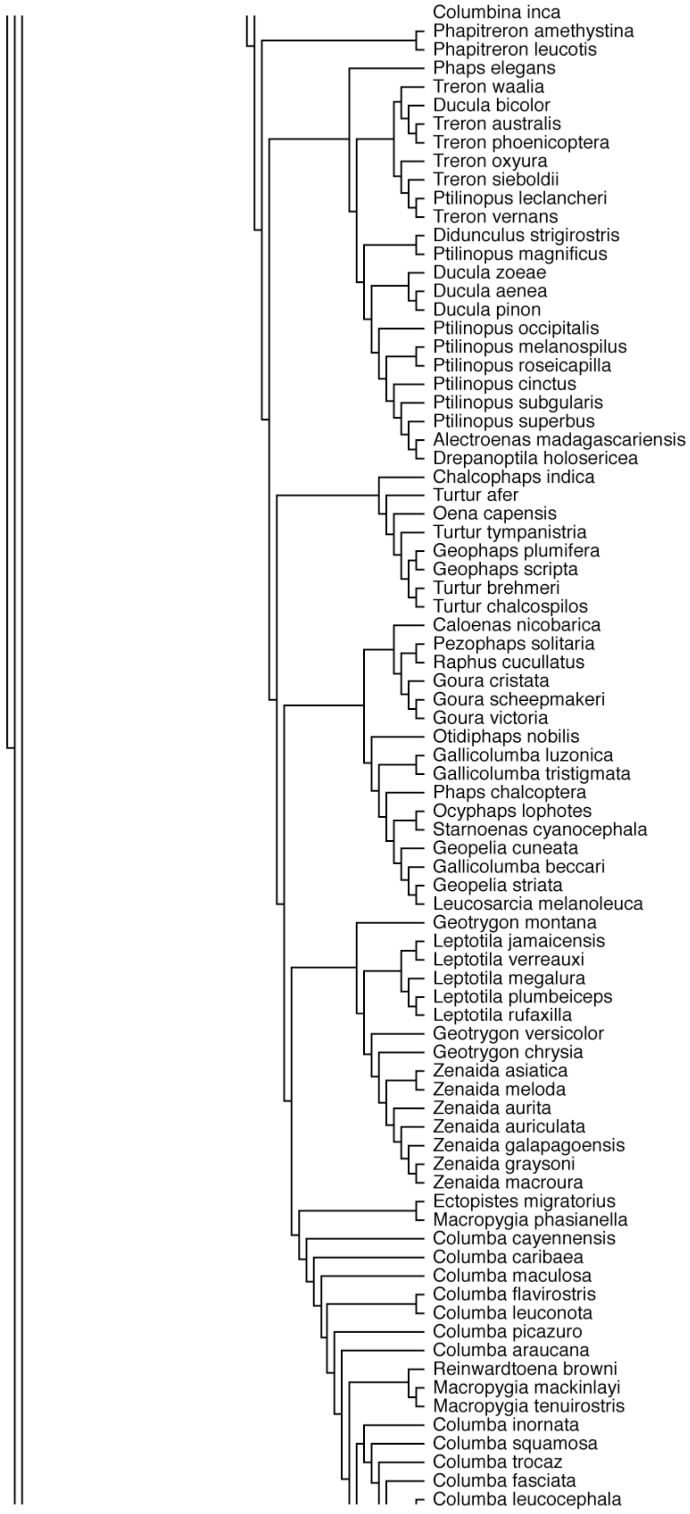
Plectropterus gambensis
Cyanochen cyanopterus
Alopochen aegyptiacus
Neochen jubata
Chloephaga melanoptera
Chloephaga picta
Chloephaga hybrida
Chloephaga poliocephala
Chloephaga rubidiceps
Tadorna radjah
Tadorna tadorna
Tadorna cana
Tadorna ferruginea
Tadorna cristata
Tadorna tadornoides
Tadorna variegata
Sarkidiornis melanotos
Malacorhynchus membranaceus
Salvadorina
Nettapus auritus
Nettapus coromandelianus
Nettapus pulchellus
Heteronetta atricapilla
Nomonyx dominicus
Biziura lobata
Oxyura ferruginea
Oxyura vittata
Oxyura jamaicensis
Oxyura australis
Oxyura leucocephala
Oxyura maccoa
Polystictus stelleri
Somateria fischeri
Somateria mollissima
Somateria spectabilis
Histrionicus histrionicus
Camptorhynchus labradorius
Melanitta nigra
Melanitta perspicillata
Melanitta deglandi
Melanitta fusca
Clangula hyemalis
Mergellus albellus
Bucephala albeola
Bucephala clangula
Bucephala islandica
Mergus albellus
Mergus cucullatus
Lophodytes cucullatus
Mergus australis
Mergus octosetaceus
Mergus merganser
Mergus serrator
Mergus squamatus
Vegavis iaai
Pteronetta hartlaubi
Aix galericulata
Aix sponsa
Cairina moschata
Cairina scutulata
Marmaronetta angustirostris
Asarcornis scutulata
Netta erythrophthalma
Netta peposaca
Netta rufina
Rhodonessa caryophyllacea
Aythya valisineria
Aythya americana
Aythya ferina
Aythya australis
Aythya innotata
Aythya baeri
Aythya nyroca

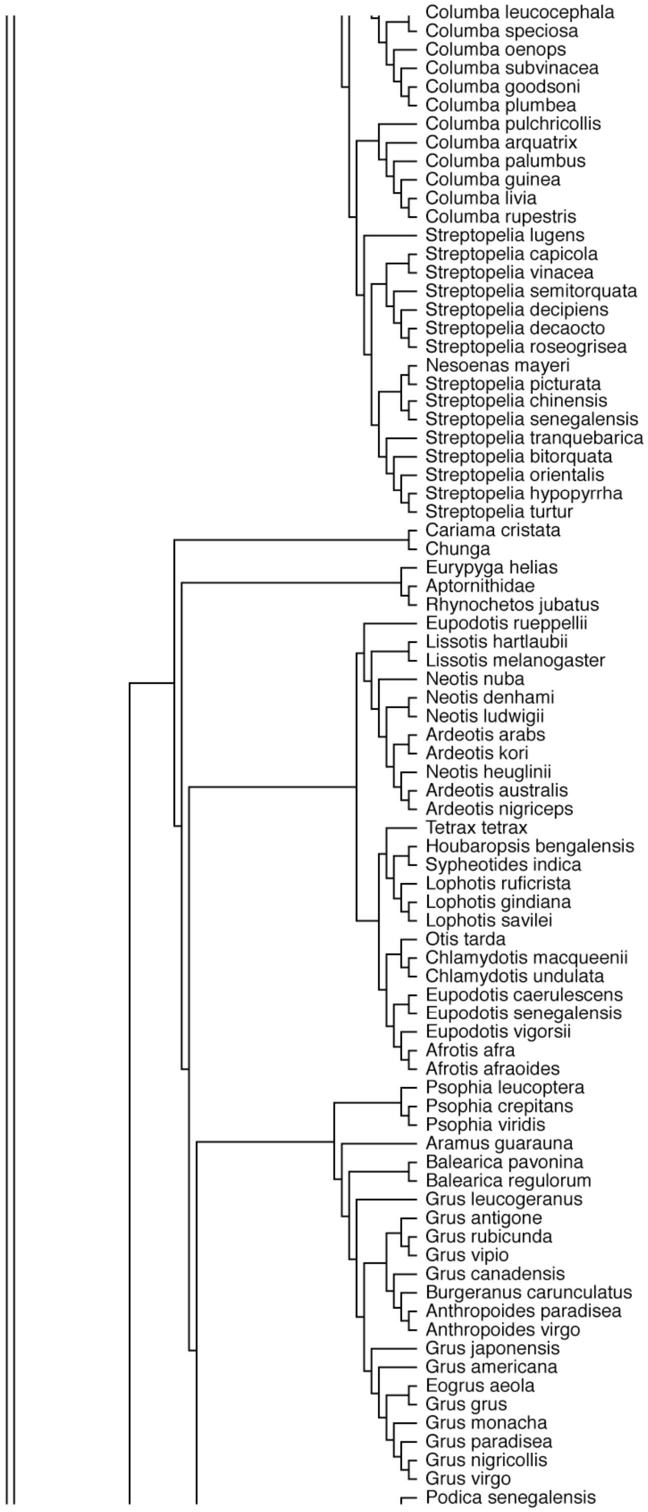

Aythya nyroca
Aythya novaeseelandiae
Aythya collaris
Aythya fuligula
Aythya affinis
Aythya marila
Callonetta leucophrys
Chenonetta finschi
Chenonetta jubata
Anas formosa
Anas querquedula
Anas hottentota
Anas puna
Anas versicolor
Anas cyanoptera
Anas discors
Anas smithii
Anas platalea
Anas clypeata
Anas rhynchotis
Amazonetta brasiliensis
Speculanas specularis
Lophonetta specularoides
Hymenolaimus
Merganetta
Tachyeres patachonicus
Tachyeres pteneres
Tachyeres brachypterus
Tachyeres leucocephalus
Anas falcata
Anas strepera
Anas penelope
Anas americana
Anas sibilatrix
Anas capensis
Anas sparsa
Anas melleri
Anas undulata
Anas luzonica
Anas superciliosa
Anas poecilorhyncha
Anas zonorhyncha
Anas rubripes
Anas diazi
Anas fulvigula
Anas laysanensis
Anas oustaleti
Anas platyrhynchos
Anas wyvilliana
Anas flavirostris
Anas carolinensis
Anas crecca
Anas bahamensis
Anas erythrorhyncha
Anas georgica
Anas acuta
Anas eatoni
Anas chlorotis
Anas aucklandica
Anas nesiotis
Anas bernieri
Anas gibberifrons
Anas castanea
Anas gracilis
Crossoptilon auritum
Macrocephalon maleo
Talegalla fuscirostris
Leipoa ocellata
Aepypodius arfakianus
Alectura lathami
Eulipoa wallacei
Megapodius cumingii
Megapodius tenimberensis
Megapodius layardi
Megapodius pritchardii
Megapodius eremita
Megapodius reinwardt
Megapodius decollatus
Megapodius forstenii
Megapodius freycinet
Penelope purpurascens

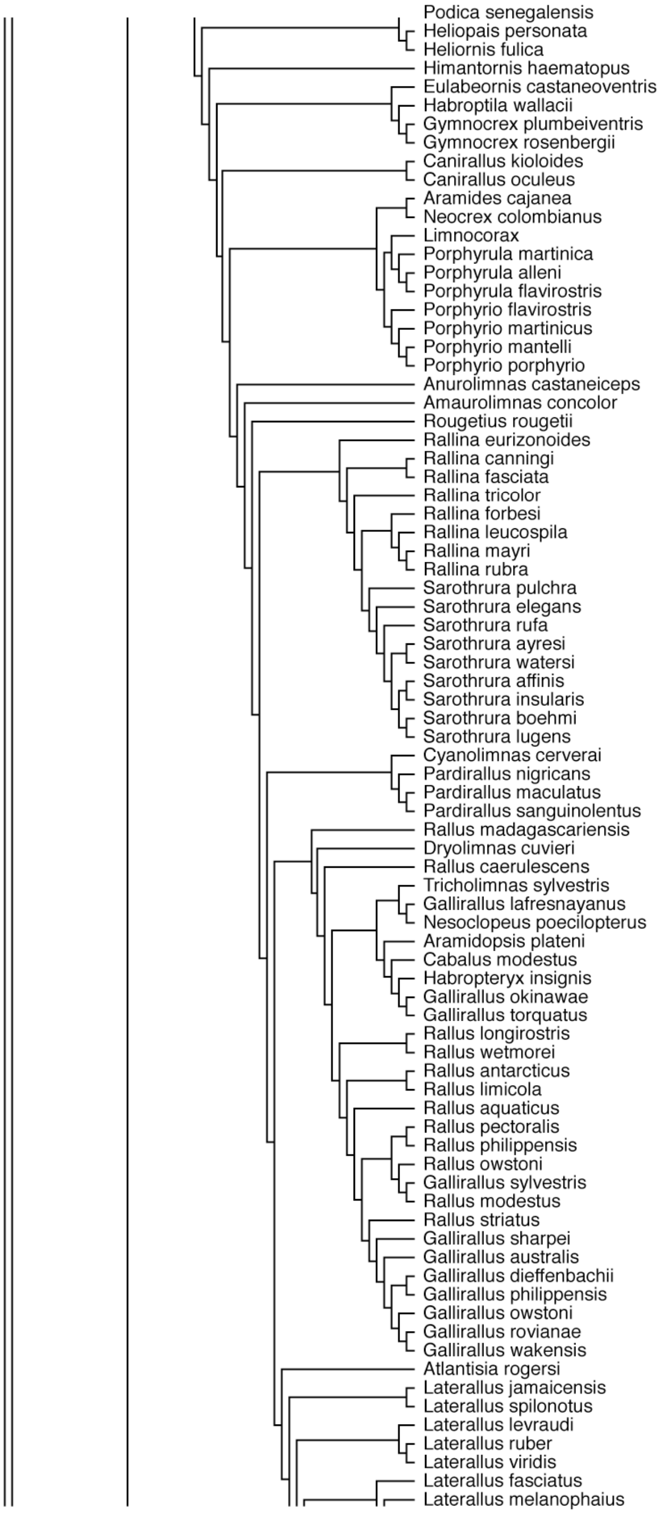

Penelope purpurascens
Penelopina nigra
Chamaepetes goudotii
Penelope montagnii
Penelope obscura
Pipile jacutinga
Aburria aburri
Pipile cujubi
Penelope albipennis
Pipile cumanensis
Pipile pipile
Crax pauxi
Ortalis vetula
Ortalis guttata
Oreophasis derbianus
Ortalis canicollis
Nothocrax urumutum
Pauxi pauxi
Mitu mitu
Mitu tomentosa
Mitu salvini
Mitu tuberosa
Pauxi unicornis
Crax mitu
Crax rubra
Crax alberti
Crax daubentoni
Ortalis cinereiceps
Crax globulosa
Crax blumenbachii
Crax alector
Crax fasciolata
Gallinuloides wyomingensis
Agelastes niger
Numida meleagris
Acryllium vulturinum
Guttera plumifera
Amitabha urbsinterdictensis
Penelope superciliaris
Perdicula argoondah
Philortyx fasciatus
Cyrtonyx montezumae
Odontophorus stellatus
Oreortyx pictus
Colinus cristatus
Colinus virginianus
Callipepla douglasii
Callipepla californica
Callipepla gambelii
Callipepla squamata
Lophortyx californica
Lophortyx gambelii
Pucrasia macrolopha
Perdix dauurica
Perdix perdix
Rhizothera longirostris
Syrmaticus soemmerringii
Lophophorus impejanus
Tragopan blythii
Tragopan satyra
Tragopan caboti
Tragopan temminckii
Ithaginis cruentus
Crossoptilon crossoptilon
Syrmaticus ellioti
Syrmaticus humiae
Catreus wallichii
Chrysolophus pictus
Phasianus colchicus
Syrmaticus reevesii
Chrysolophus amherstiae
Syrmaticus mikado
Lophura ignita
Lophura diardi
Phasianus versicolor
Lophura erythrophthalma
Lophura inornata
Lophura bulweri
Lophura leucomelanos
Lophura nycthemera
Lophura swinhoii

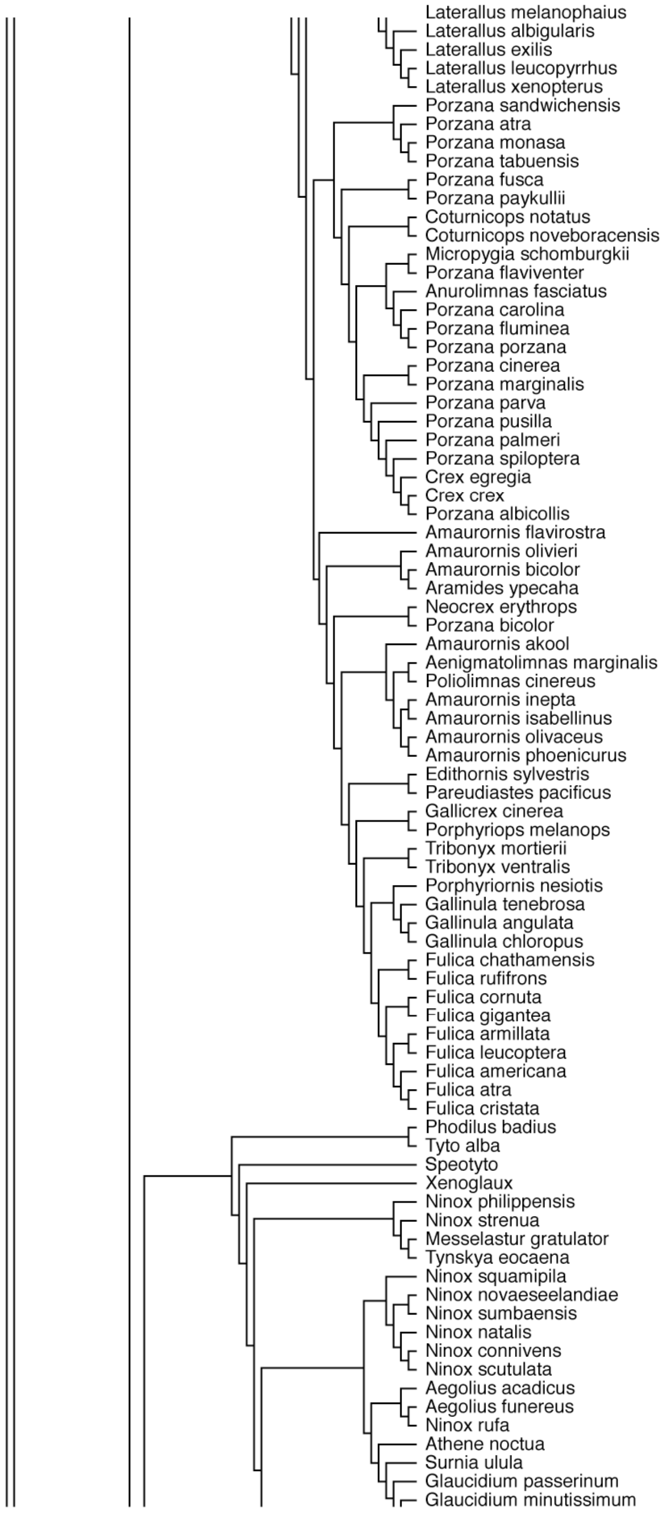

Lophura swinhoii
Lophura hatinhensis
Francolinus lathami
Lophura edwardsi
Agriocharis ocellata
Meleagris gallopavo
Bonasa umbellus
Bonasa bonasia
Bonasa sewerzowi
Canachites canadensis
Falcipennis canadensis
Dendragapus canadensis
Falcipennis falcipennis
Tetrao mlokosiewiczi
Tetrao tetrix
Tetrao parvirostris
Tetrao urogallus
Lagopus leucurus
Lagopus lagopus
Lagopus mutus
Dendragapus falcipennis
Centrocercus minimus
Centrocercus urophasianus
Dendragapus obscurus
Tympanuchus phasianellus
Tympanuchus cupido
Tympanuchus pallidicinctus
Argusianus argus
Rheinardia ocellata
Afropavo congensis
Pavo cristatus
Pavo muticus
Bambusicola thoracica
Gallus varius
Gallus gallus
Gallus sonneratii
Gallus lafayettii
Ptilopachus petrosus
Francolinus gularis
Francolinus pondicerianus
Francolinus pintadeanus
Francolinus francolinus
Francolinus pictus
Francolinus sephaena
Francolinus coqui
Francolinus albogularis
Francolinus schlegelii
Francolinus streptophorus
Francolinus levaillantii
Francolinus finschi
Francolinus africanus
Francolinus psilolaemus
Francolinus levaillantoides
Francolinus shelleyi
Caloperdix oculea
Polyplectron emphanum
Polyplectron malacense
Polyplectron germaini
Polyplectron inopinatum
Polyplectron bicalcaratum
Polyplectron chalcurum
Coturnix australis
Arborophila torqueola
Francolinus nahani
Coturnix chinensis
Rollulus rouloul
Ammoperdix heyi
Margaroperdix madagarensis
Coturnix japonica
Coturnix coturnix
Coturnix pectoralis
Galloperdix spadicea
Francolinus ahantensis
Tetraogallus himalayensis
Francolinus griseostriatus
Alectoris barbara
Alectoris melanocephala
Haematortyx sanguiniceps
Alectoris rufa
Lerwa lerwa
Alectoris graeca

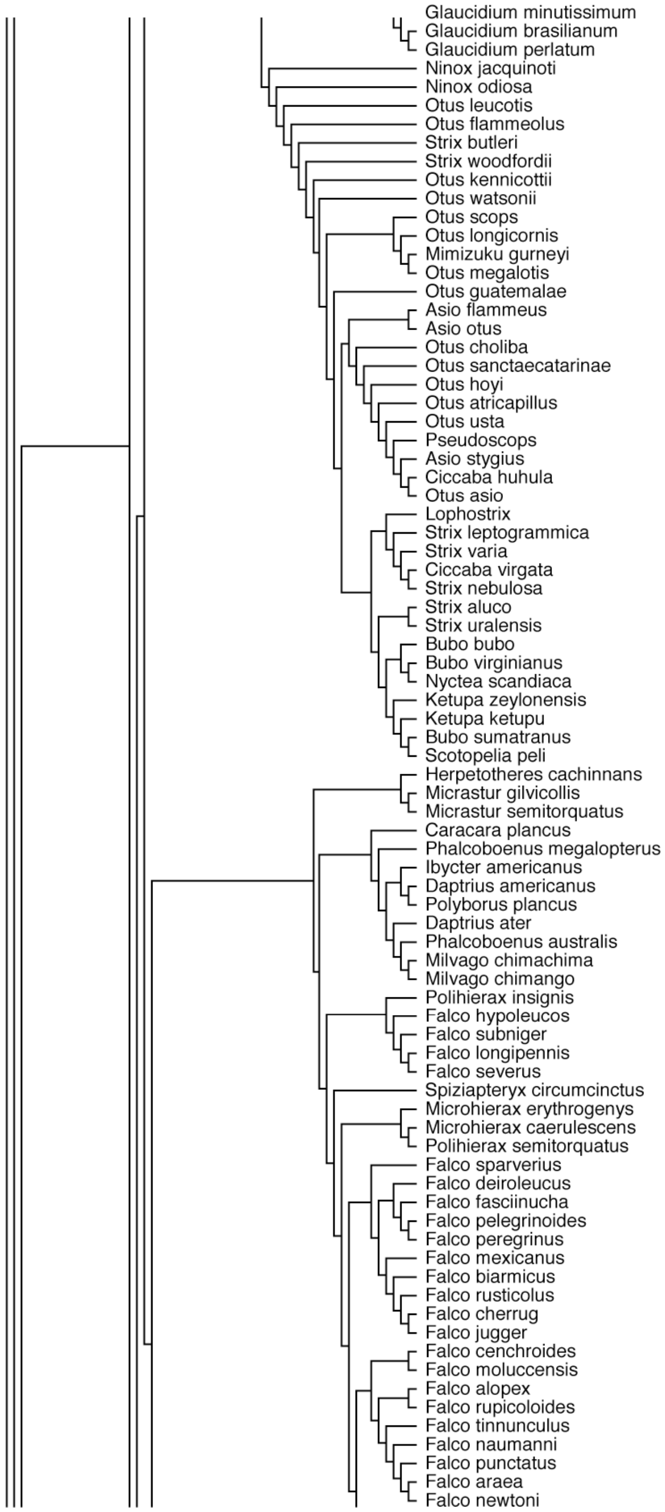

Alectoris graeca
Alectoris chukar
Alectoris magna
Alectoris philbyi
Francolinus hartlaubi
Francolinus jacksoni
Francolinus nobilis
Francolinus camerunensis
Francolinus swierstrai
Francolinus castaneicollis
Pternistis squamatus
Francolinus erckelii
Pternistis ochropectus
Francolinus bicalcaratus
Francolinus icterorhynchus
Francolinus harwoodi
Francolinus squamatus
Francolinus afer
Francolinus swainsonii
Francolinus leucoscepus
Francolinus rufopictus
Francolinus capensis
Francolinus clappertoni
Francolinus adspersus
Francolinus hildebrandti
Francolinus natalensis
Opisthocomus hoazin
Corythaeola cristata
Crinifer piscator
Crinifer zonurus
Corythaixoides leucogaster
Corythaixoides concolor
Corythaixoides personatus
Tauraco johnstoni
Gallirex porphyreolophus
Ruwenzorornis johnstoni
Musophaga rossae
Musophaga violacea
Tauraco ruspolii
Musophaga porphyreolopha
Tauraco bannermani
Tauraco erythrolophus
Tauraco macrorhynchus
Tauraco leucolophus
Tauraco leucotis
Tauraco hartlaubi
Tauraco persa
Tauraco corythaix
Tauraco fischeri
Tauraco livingstonii
Tauraco schalowi
Tauraco schuetti
Pterocles orientalis
Syrrhaptes paradoxus
Petrophassa scripta
Geophaps smithii
Pterocles namaqua
Petrophassa plumifera
Petrophassa rufipennis
Pterocles quadricinctus
Petrophassa albipennis
Pterocles lichtensteinii
Pterocles gutturalis
Pterocles senegallus
Pterocles burchelli
Pterocles coronatus
Pterocles exustus
Pterocles bicinctus
Pterocles decoratus
Trugon
Columba larvata
Columbina talpacoti
Metriopelia ceciliae
Claravis pretiosa
Columbina picui
Columbina minuta
Columbina passerina
Scardafella inca
Scardafella squammata
Columbina cruziana
Columbina inca

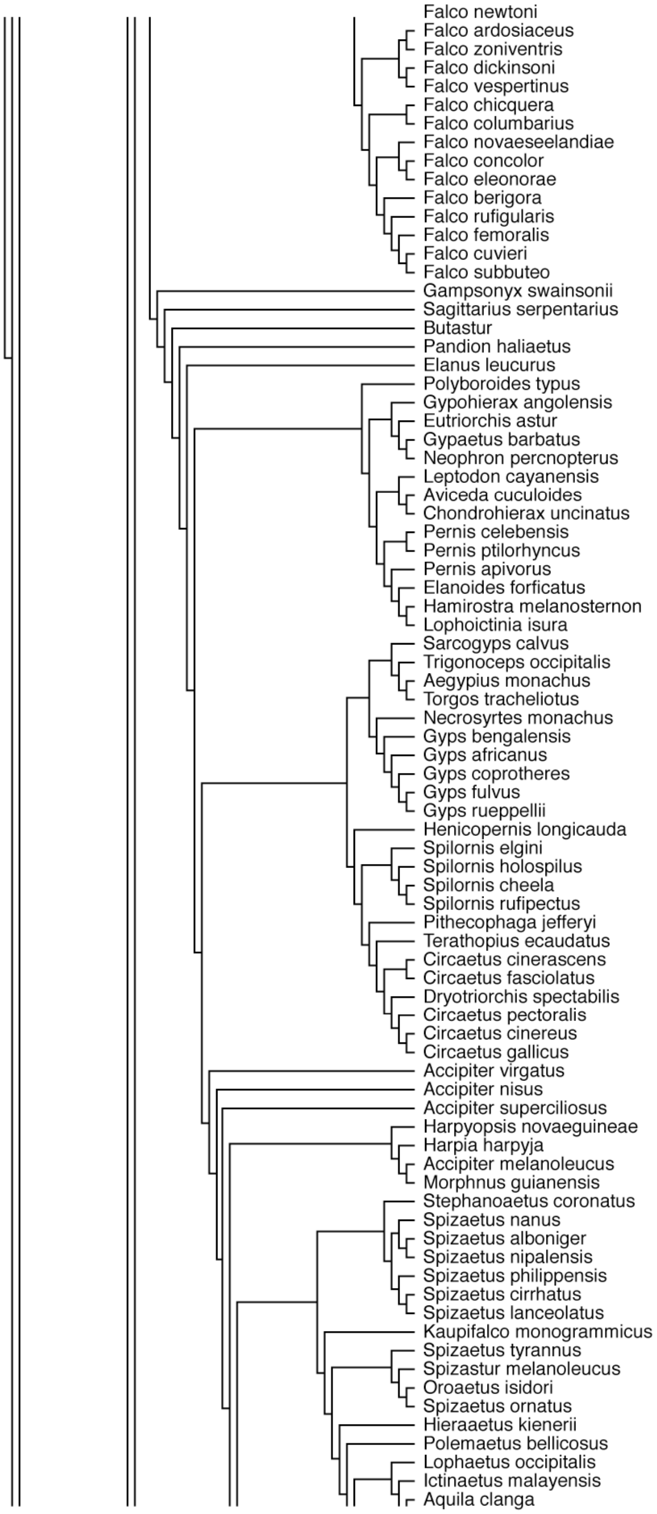

Columbina inca
Phapitreron amethystina
Phapitreron leucotis
Phaps elegans
Treron waalia
Ducula bicolor
Treron australis
Treron phoenicoptera
Treron oxyura
Treron sieboldii
Ptilinopus leclancheri
Treron vernans
Didunculus strigirostris
Ptilinopus magnificus
Ducula zoeae
Ducula aenea
Ducula pinon
Ptilinopus occipitalis
Ptilinopus melanospilus
Ptilinopus roseicapilla
Ptilinopus cinctus
Ptilinopus subgularis
Ptilinopus superbus
Alectroenas madagascariensis
Drepanoptila holosericea
Chalcophaps indica
Turtur afer
Oena capensis
Turtur tympanistria
Geophaps plumifera
Geophaps scripta
Turtur brehmeri
Turtur chalcospilos
Caloenas nicobarica
Pezophaps solitaria
Raphus cucullatus
Goura cristata
Goura scheepmakeri
Goura victoria
Otidiphaps nobilis
Gallicolumba luzonica
Gallicolumba tristigmata
Phaps chalcoptera
Ocyphaps lophotes
Starnoenas cyanocephala
Geopelia cuneata
Gallicolumba beccari
Geopelia striata
Leucosarcia melanoleuca
Geotrygon montana
Leptotila jamaicensis
Leptotila verreauxi
Leptotila megalura
Leptotila plumbeiceps
Leptotila rufaxilla
Geotrygon versicolor
Geotrygon chrysia
Zenaida asiatica
Zenaida meloda
Zenaida aurita
Zenaida auriculata
Zenaida galapagoensis
Zenaida graysoni
Zenaida macroura
Ectopistes migratorius
Macropygia phasianella
Columba cayennensis
Columba caribaea
Columba maculosa
Columba flavirostris
Columba leuconota
Columba picazuro
Columba araucana
Reinwardtoena browni
Macropygia mackinlayi
Macropygia tenuirostris
Columba inornata
Columba squamosa
Columba trocaz
Columba fasciata
Columba leucocephala

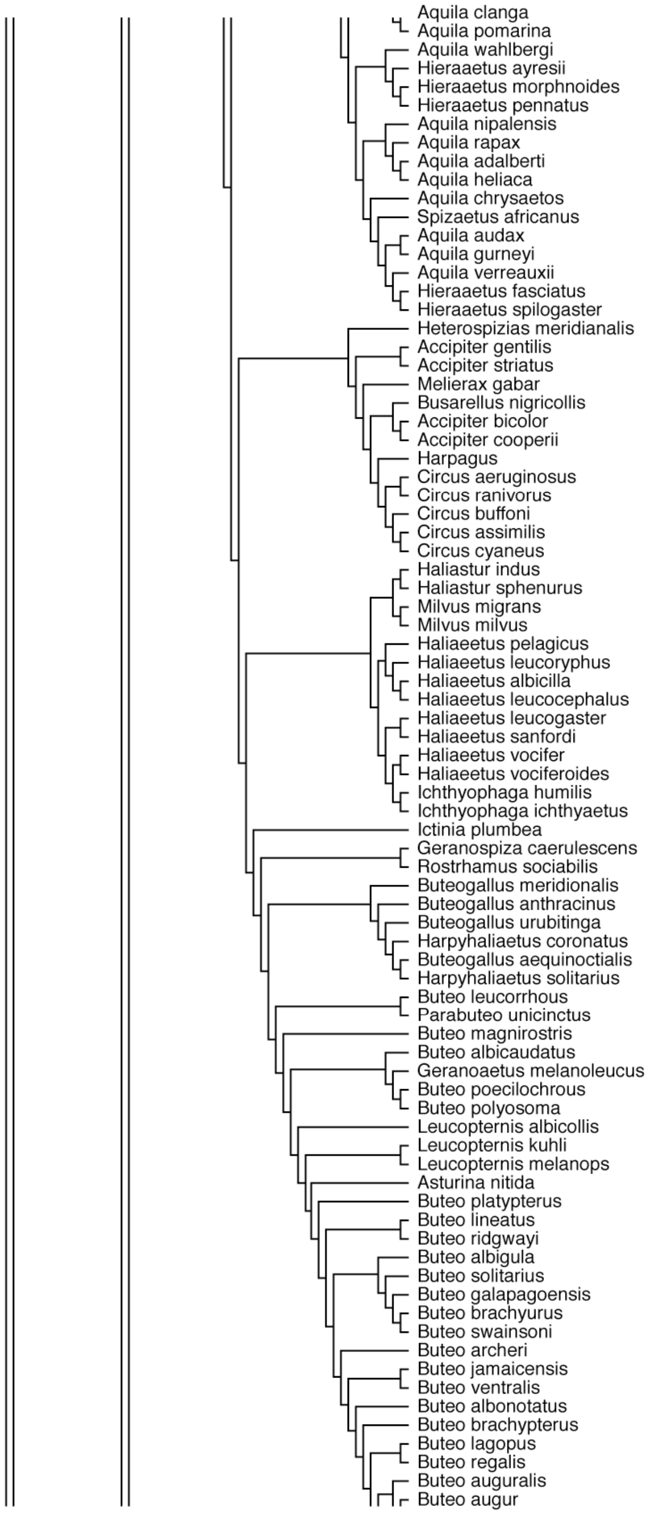

Columba leucocephala
Columba speciosa
Columba oenops
Columba subvinacea
Columba goodsoni
Columba plumbea
Columba pulchricollis
Columba arquatrix
Columba palumbus
Columba guinea
Columba livia
Columba rupestris
Streptopelia lugens
Streptopelia capicola
Streptopelia vinacea
Streptopelia semitorquata
Streptopelia decipiens
Streptopelia decaocto
Streptopelia roseogrisea
Nesoenas mayeri
Streptopelia picturata
Streptopelia chinensis
Streptopelia senegalensis
Streptopelia tranquebarica
Streptopelia bitorquata
Streptopelia orientalis
Streptopelia hypopyrrha
Streptopelia turtur
Cariama cristata
Chunga
Eurypyga helias
Aptornithidae
Rhynochetos jubatus
Eupodotis rueppellii
Lissotis hartlaubii
Lissotis melanogaster
Neotis nuba
Neotis denhami
Neotis ludwigii
Ardeotis arabs
Ardeotis kori
Neotis heuglinii
Ardeotis australis
Ardeotis nigriceps
Tetrax tetrax
Houbaropsis bengalensis
Sypheotides indica
Lophotis ruficrista
Lophotis gindiana
Lophotis savilei
Otis tarda
Chlamydotis macqueenii
Chlamydotis undulata
Eupodotis caerulescens
Eupodotis senegalensis
Eupodotis vigorsii
Afrotis afra
Afrotis afraoides
Psophia leucoptera
Psophia crepitans
Psophia viridis
Aramus guarauna
Balearica pavonina
Balearica regulorum
Grus leucogeranus
Grus antigone
Grus rubicunda
Grus vipio
Grus canadensis
Burgeranus carunculatus
Anthropoides paradisea
Anthropoides virgo
Grus japonensis
Grus americana
Eogrus aeola
Grus grus
Grus monacha
Grus paradisea
Grus nigricollis
Grus virgo
Podica senegalensis

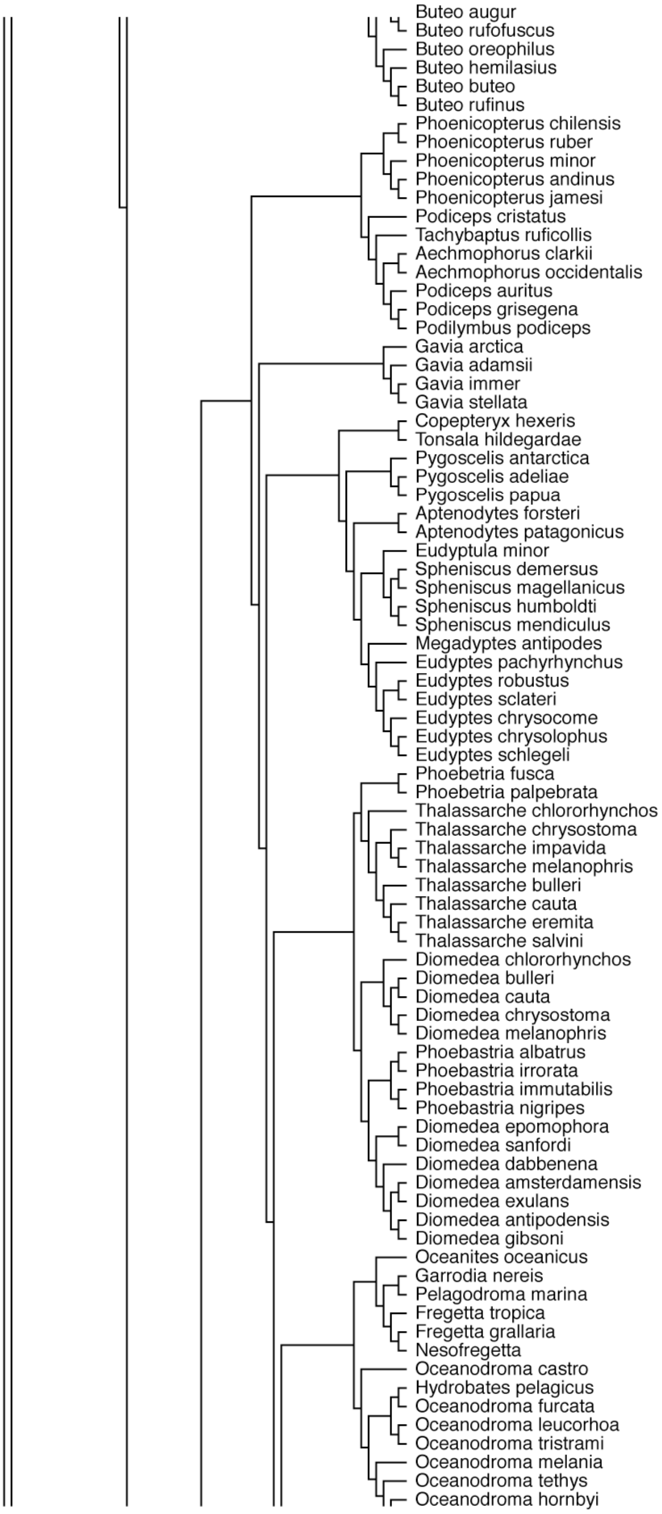

Podica senegalensis
Heliopais personata
Heliornis fulica
Himantornis haematopus
Eulabeornis castaneoventris
Habroptila wallacii
Gymnocrex plumbeiventris
Gymnocrex rosenbergii
Canirallus kioloides
Canirallus oculeus
Aramides cajanea
Neocrex colombianus
Limnocorax
Porphyrula martinica
Porphyrula alleni
Porphyrula flavirostris
Porphyrio flavirostris
Porphyrio martinicus
Porphyrio mantelli
Porphyrio porphyrio
Anurolimnas castaneiceps
Amaurolimnas concolor
Rougetius rougetii
Rallina eurizonoides
Rallina canningi
Rallina fasciata
Rallina tricolor
Rallina forbesi
Rallina leucospila
Rallina mayri
Rallina rubra
Sarothrura pulchra
Sarothrura elegans
Sarothrura rufa
Sarothrura ayresi
Sarothrura watersi
Sarothrura affinis
Sarothrura insularis
Sarothrura boehmi
Sarothrura lugens
Cyanolimnas cerverai
Pardirallus nigricans
Pardirallus maculatus
Pardirallus sanguinolentus
Rallus madagascariensis
Dryolimnas cuvieri
Rallus caerulescens
Tricholimnas sylvestris
Gallirallus lafresnayanus
Nesoclopeus poecilopterus
Aramidopsis plateni
Cabalus modestus
Habropteryx insignis
Gallirallus okinawae
Gallirallus torquatus
Rallus longirostris
Rallus wetmorei
Rallus antarcticus
Rallus limicola
Rallus aquaticus
Rallus pectoralis
Rallus philippensis
Rallus owstoni
Gallirallus sylvestris
Rallus modestus
Rallus striatus
Gallirallus sharpei
Gallirallus australis
Gallirallus dieffenbachii
Gallirallus philippensis
Gallirallus owstoni
Gallirallus rovianae
Gallirallus wakensis
Atlantisia rogersi
Laterallus jamaicensis
Laterallus spilonotus
Laterallus levraudi
Laterallus ruber
Laterallus viridis
Laterallus fasciatus
Laterallus melanophaius

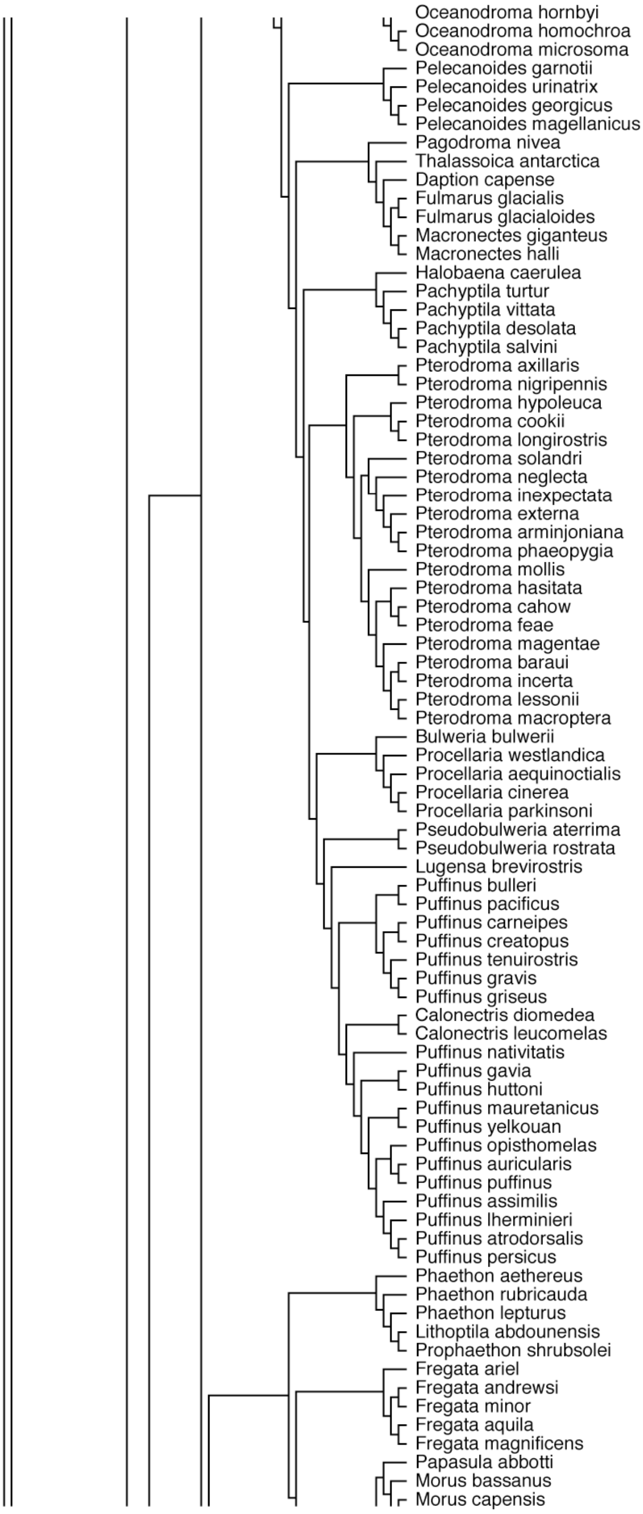

Laterallus melanophaius
Laterallus albigularis
Laterallus exilis
Laterallus leucopyrrhus
Laterallus xenopterus
Porzana sandwichensis
Porzana atra
Porzana monasa
Porzana tabuensis
Porzana fusca
Porzana paykullii
Coturnicops notatus
Coturnicops noveboracensis
Micropygia schomburgkii
Porzana flaviventer
Anurolimnas fasciatus
Porzana carolina
Porzana fluminea
Porzana porzana
Porzana cinerea
Porzana marginalis
Porzana parva
Porzana pusilla
Porzana palmeri
Porzana spiloptera
Crex egregia
Crex crex
Porzana albicollis
Amaurornis flavirostra
Amaurornis olivieri
Amaurornis bicolor
Aramides ypecaha
Neocrex erythrops
Porzana bicolor
Amaurornis akool
Aenigmatolimnas marginalis
Poliolimnas cinereus
Amaurornis inepta
Amaurornis isabellinus
Amaurornis olivaceus
Amaurornis phoenicurus
Edithornis sylvestris
Pareudiastes pacificus
Gallicrex cinerea
Porphyriops melanops
Tribonyx mortierii
Tribonyx ventralis
Porphyriornis nesiotis
Gallinula tenebrosa
Gallinula angulata
Gallinula chloropus
Fulica chathamensis
Fulica rufifrons
Fulica cornuta
Fulica gigantea
Fulica armillata
Fulica leucoptera
Fulica americana
Fulica atra
Fulica cristata
Phodilus badius
Tyto alba
Speotyto
Xenoglaux
Ninox philippensis
Ninox strenua
Messelastur gratulator
Tynskya eocaena
Ninox squamipila
Ninox novaeseelandiae
Ninox sumbaensis
Ninox natalis
Ninox connivens
Ninox scutulata
Aegolius acadicus
Aegolius funereus
Ninox rufa
Athene noctua
Surnia ulula
Glaucidium passerinum
Glaucidium minutissimum

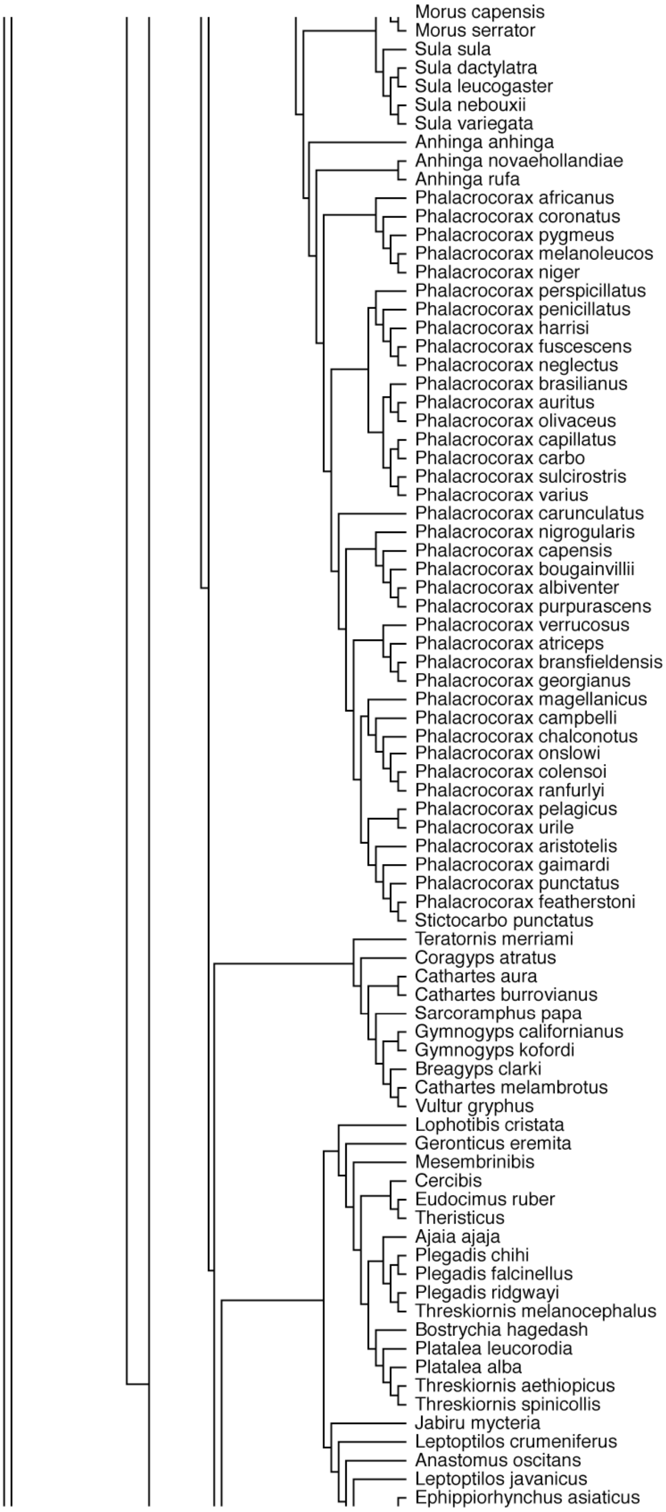

Glaucidium minutissimum
Glaucidium brasilianum
Glaucidium perlatum
Ninox jacquinoti
Ninox odiosa
Otus leucotis
Otus flammeolus
Strix butleri
Strix woodfordii
Otus kennicottii
Otus watsonii
Otus scops
Otus longicornis
Mimizuku gurneyi
Otus megalotis
Otus guatemalae
Asio flammeus
Asio otus
Otus choliba
Otus sanctaecatarinae
Otus hoyi
Otus atricapillus
Otus usta
Pseudoscops
Asio stygius
Ciccaba huhula
Otus asio
Lophostrix
Strix leptogrammica
Strix varia
Ciccaba virgata
Strix nebulosa
Strix aluco
Strix uralensis
Bubo bubo
Bubo virginianus
Nyctea scandiaca
Ketupa zeylonensis
Ketupa ketupu
Bubo sumatranus
Scotopelia peli
Herpetotheres cachinnans
Micrastur gilvicollis
Micrastur semitorquatus
Caracara plancus
Phalcoboenus megalopterus
Ibycter americanus
Daptrius americanus
Polyborus plancus
Daptrius ater
Phalcoboenus australis
Milvago chimachima
Milvago chimango
Polihierax insignis
Falco hypoleucos
Falco subniger
Falco longipennis
Falco severus
Spiziapteryx circumcinctus
Microhierax erythrogenys
Microhierax caerulescens
Polihierax semitorquatus
Falco sparverius
Falco deiroleucus
Falco fasciinucha
Falco pelegrinoides
Falco peregrinus
Falco mexicanus
Falco biarmicus
Falco rusticolus
Falco cherrug
Falco jugger
Falco cenchroides
Falco moluccensis
Falco alopex
Falco rupicoloides
Falco tinnunculus
Falco naumanni
Falco punctatus
Falco araea
Falco newtoni

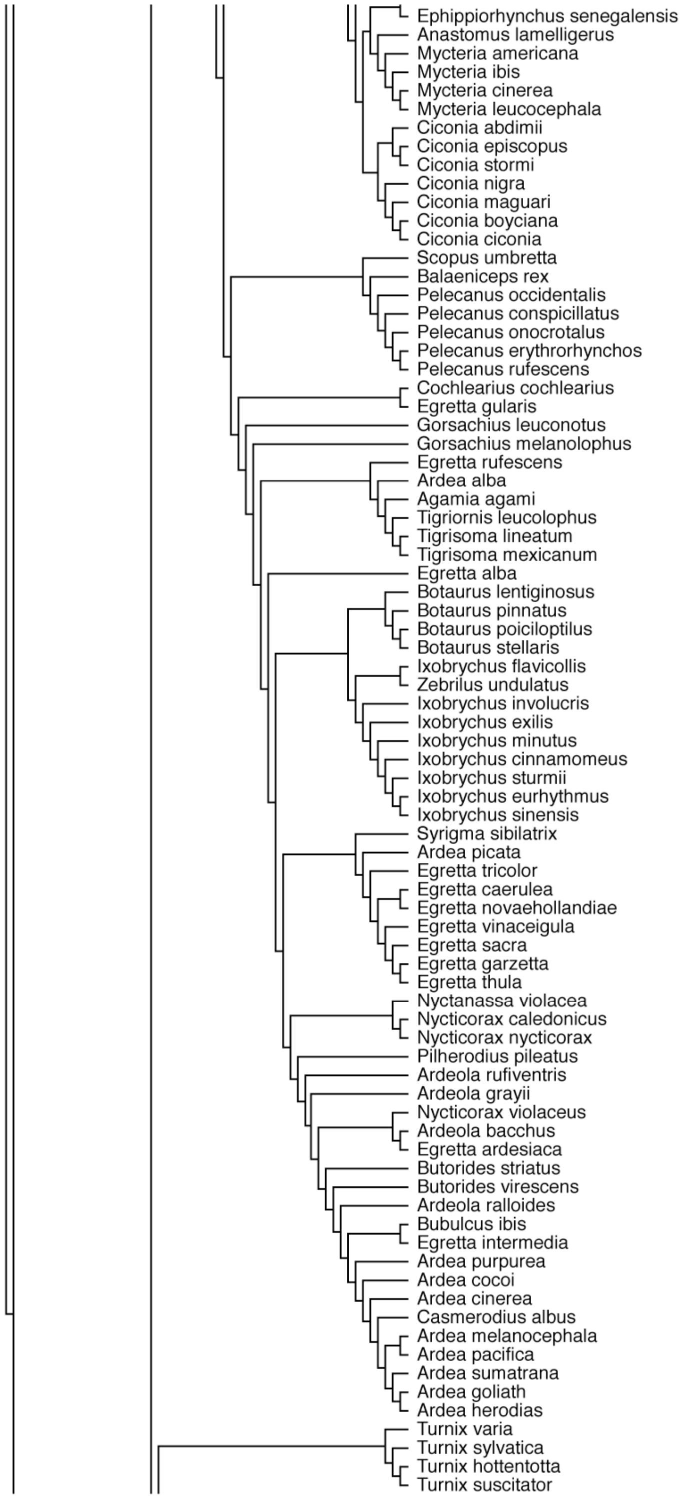

Falco newtoni
Falco ardosiaceus
Falco zoniventris
Falco dickinsoni
Falco vespertinus
Falco chicquera
Falco columbarius
Falco novaeseelandiae
Falco concolor
Falco eleonorae
Falco berigora
Falco rufigularis
Falco femoralis
Falco cuvieri
Falco subbuteo
Gampsonyx swainsonii
Sagittarius serpentarius
Butastur
Pandion haliaetus
Elanus leucurus
Polyboroides typus
Gypohierax angolensis
Eutriorchis astur
Gypaetus barbatus
Neophron percnopterus
Leptodon cayanensis
Aviceda cuculoides
Chondrohierax uncinatus
Pernis celebensis
Pernis ptilorhyncus
Pernis apivorus
Elanoides forficatus
Hamirostra melanosternon
Lophoictinia isura
Sarcogyps calvus
Trigonoceps occipitalis
Aegypius monachus
Torgos tracheliotus
Necrosyrtes monachus
Gyps bengalensis
Gyps africanus
Gyps coprotheres
Gyps fulvus
Gyps rueppellii
Henicopernis longicauda
Spilornis elgini
Spilornis holospilus
Spilornis cheela
Spilornis rufipectus
Pithecophaga jefferyi
Terathopius ecaudatus
Circaetus cinerascens
Circaetus fasciolatus
Dryotriorchis spectabilis
Circaetus pectoralis
Circaetus cinereus
Circaetus gallicus
Accipiter virgatus
Accipiter nisus
Accipiter superciliosus
Harpyopsis novaeguineae
Harpia harpyja
Accipiter melanoleucus
Morphnus guianensis
Stephanoaetus coronatus
Spizaetus nanus
Spizaetus alboniger
Spizaetus nipalensis
Spizaetus philippensis
Spizaetus cirrhatus
Spizaetus lanceolatus
Kaupifalco monogrammicus
Spizaetus tyrannus
Spizastur melanoleucus
Oroaetus isidori
Spizaetus ornatus
Hieraaetus kienerii
Polemaetus bellicosus
Lophaetus occipitalis
Ictinaetus malayensis
Aquila clanga

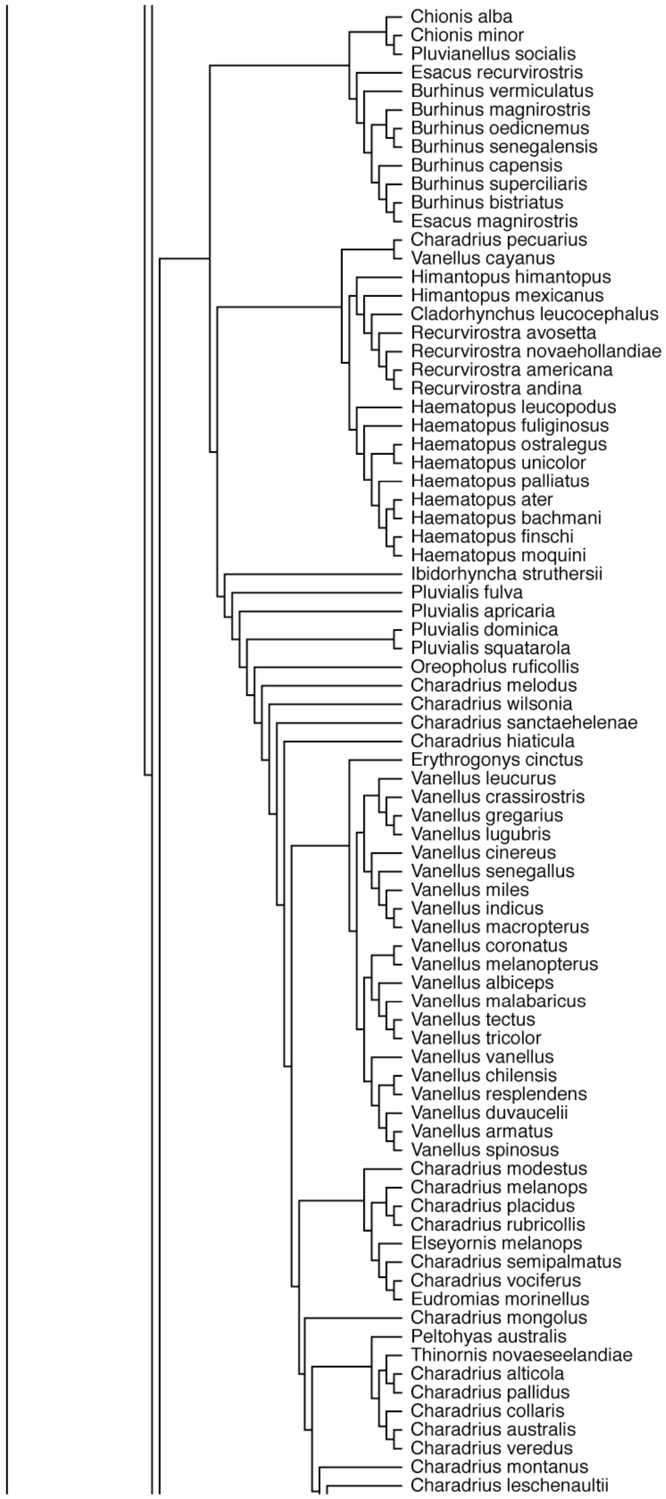

Aquila clanga
Aquila pomarina
Aquila wahlbergi
Hieraaetus ayresii
Hieraaetus morphnoides
Hieraaetus pennatus
Aquila nipalensis
Aquila rapax
Aquila adalberti
Aquila heliaca
Aquila chrysaetos
Spizaetus africanus
Aquila audax
Aquila gurneyi
Aquila verreauxii
Hieraaetus fasciatus
Hieraaetus spilogaster
Heterospizias meridianalis
Accipiter gentilis
Accipiter striatus
Melierax gabar
Busarellus nigricollis
Accipiter bicolor
Accipiter cooperii
Harpagus
Circus aeruginosus
Circus ranivorus
Circus buffoni
Circus assimilis
Circus cyaneus
Haliastur indus
Haliastur sphenurus
Milvus migrans
Milvus milvus
Haliaeetus pelagicus
Haliaeetus leucoryphus
Haliaeetus albicilla
Haliaeetus leucocephalus
Haliaeetus leucogaster
Haliaeetus sanfordi
Haliaeetus vocifer
Haliaeetus vociferoides
Ichthyophaga humilis
Ichthyophaga ichthyaetus
Ictinia plumbea
Geranospiza caerulescens
Rostrhamus sociabilis
Buteogallus meridionalis
Buteogallus anthracinus
Buteogallus urubitinga
Harpyhaliaetus coronatus
Buteogallus aequinoctialis
Harpyhaliaetus solitarius
Buteo leucorrhous
Parabuteo unicinctus
Buteo magnirostris
Buteo albicaudatus
Geranoaetus melanoleucus
Buteo poecilochrous
Buteo polyosoma
Leucopternis albicollis
Leucopternis kuhli
Leucopternis melanops
Asturina nitida
Buteo platypterus
Buteo lineatus
Buteo ridgwayi
Buteo albigula
Buteo solitarius
Buteo galapagoensis
Buteo brachyurus
Buteo swainsoni
Buteo archeri
Buteo jamaicensis
Buteo ventralis
Buteo albonotatus
Buteo brachypterus
Buteo lagopus
Buteo regalis
Buteo auguralis
Buteo augur

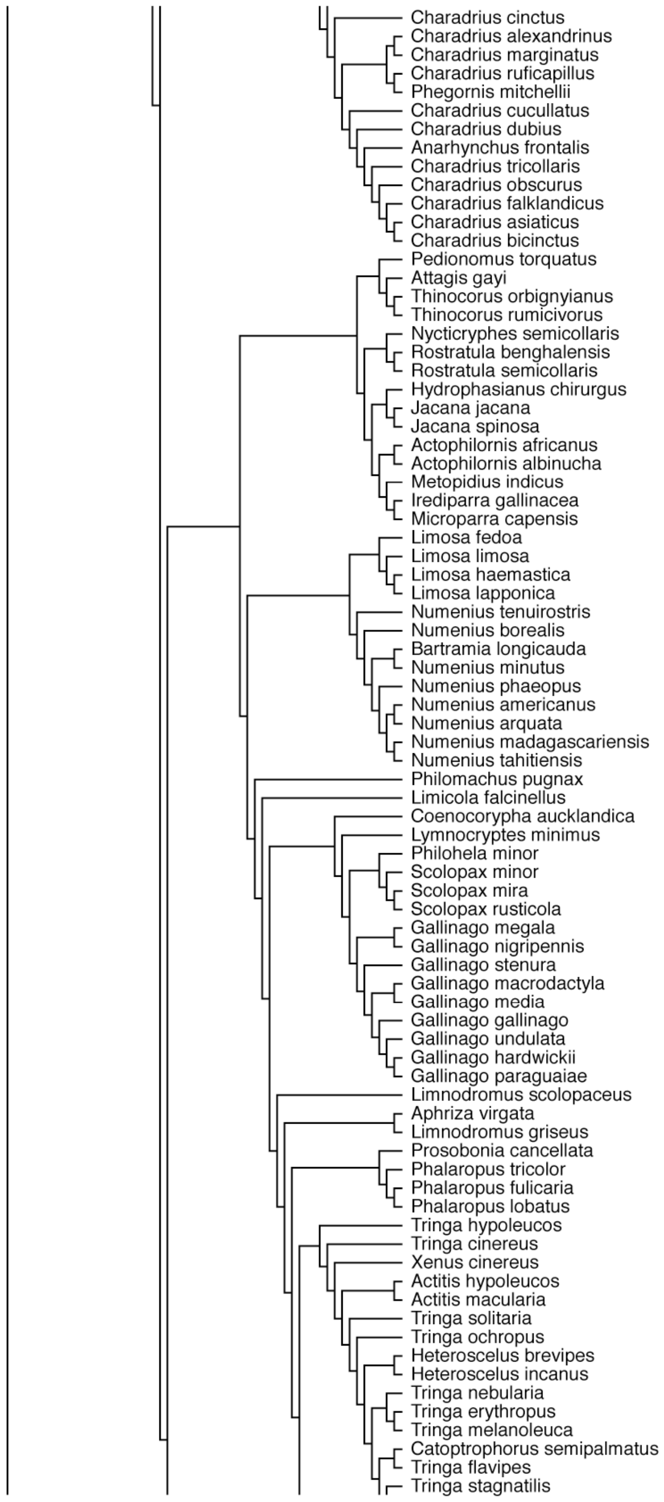

Buteo augur
Buteo rufofuscus
Buteo oreophilus
Buteo hemilasius
Buteo buteo
Buteo rufinus
Phoenicopterus chilensis
Phoenicopterus ruber
Phoenicopterus minor
Phoenicopterus andinus
Phoenicopterus jamesi
Podiceps cristatus
Tachybaptus ruficollis
Aechmophorus clarkii
Aechmophorus occidentalis
Podiceps auritus
Podiceps grisegena
Podilymbus podiceps
Gavia arctica
Gavia adamsii
Gavia immer
Gavia stellata
Copepteryx hexeris
Tonsala hildegardae
Pygoscelis antarctica
Pygoscelis adeliae
Pygoscelis papua
Aptenodytes forsteri
Aptenodytes patagonicus
Eudyptula minor
Spheniscus demersus
Spheniscus magellanicus
Spheniscus humboldti
Spheniscus mendiculus
Megadyptes antipodes
Eudyptes pachyrhynchus
Eudyptes robustus
Eudyptes sclateri
Eudyptes chrysocome
Eudyptes chrysolophus
Eudyptes schlegeli
Phoebetria fusca
Phoebetria palpebrata
Thalassarche chlororhynchos
Thalassarche chrysostoma
Thalassarche impavida
Thalassarche melanophris
Thalassarche bulleri
Thalassarche cauta
Thalassarche eremita
Thalassarche salvini
Diomedea chlororhynchos
Diomedea bulleri
Diomedea cauta
Diomedea chrysostoma
Diomedea melanophris
Phoebastria albatrus
Phoebastria irrorata
Phoebastria immutabilis
Phoebastria nigripes
Diomedea epomophora
Diomedea sanfordi
Diomedea dabbenena
Diomedea amsterdamensis
Diomedea exulans
Diomedea antipodensis
Diomedea gibsoni
Oceanites oceanicus
Garrodia nereis
Pelagodroma marina
Fregetta tropica
Fregetta grallaria
Nesofregetta
Oceanodroma castro
Hydrobates pelagicus
Oceanodroma furcata
Oceanodroma leucorhoa
Oceanodroma tristrami
Oceanodroma melania
Oceanodroma tethys
Oceanodroma hornbyi

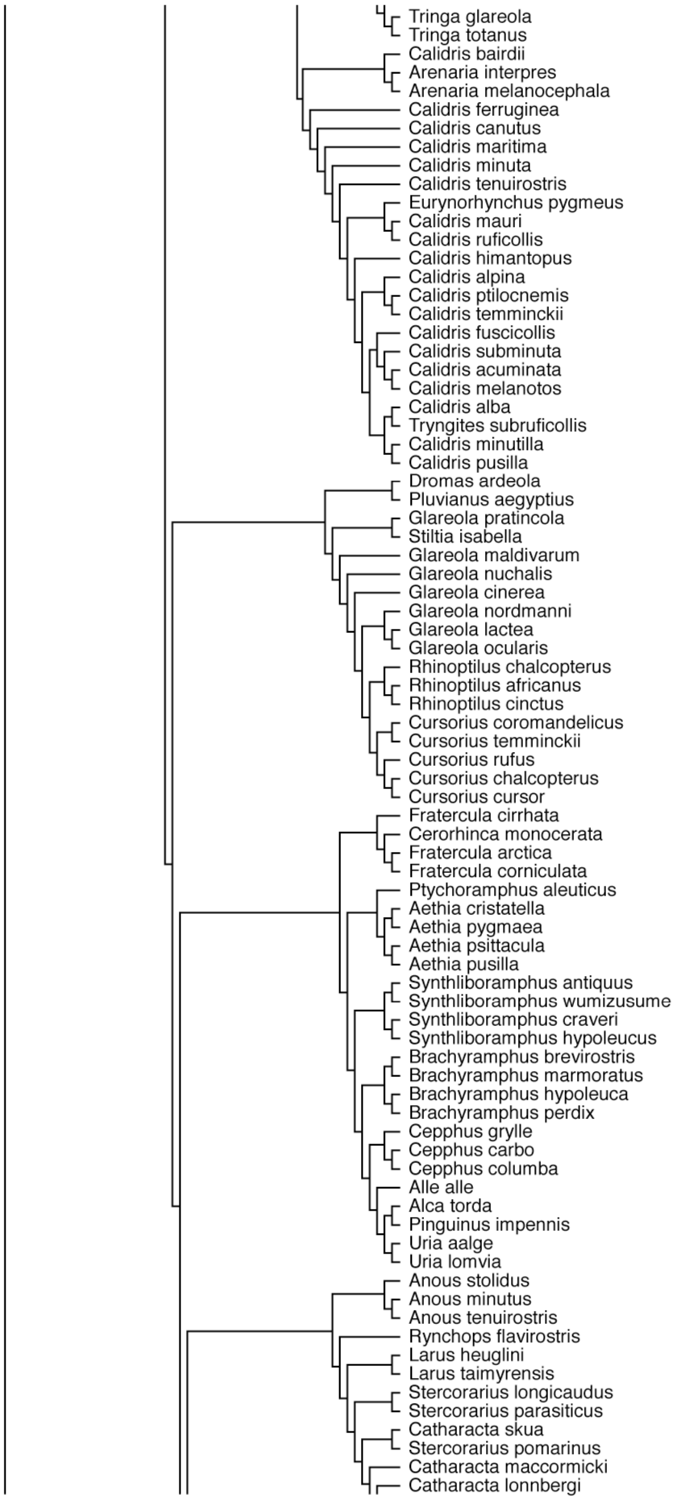

Oceanodroma hornbyi
Oceanodroma homochroa
Oceanodroma microsoma
Pelecanoides garnotii
Pelecanoides urinatrix
Pelecanoides georgicus
Pelecanoides magellanicus
Pagodroma nivea
Thalassoica antarctica
Daption capense
Fulmarus glacialis
Fulmarus glacialoides
Macronectes giganteus
Macronectes halli
Halobaena caerulea
Pachyptila turtur
Pachyptila vittata
Pachyptila desolata
Pachyptila salvini
Pterodroma axillaris
Pterodroma nigripennis
Pterodroma hypoleuca
Pterodroma cookii
Pterodroma longirostris
Pterodroma solandri
Pterodroma neglecta
Pterodroma inexpectata
Pterodroma externa
Pterodroma arminjoniana
Pterodroma phaeopygia
Pterodroma mollis
Pterodroma hasitata
Pterodroma cahow
Pterodroma feae
Pterodroma magentae
Pterodroma baraui
Pterodroma incerta
Pterodroma lessonii
Pterodroma macroptera
Bulweria bulwerii
Procellaria westlandica
Procellaria aequinoctialis
Procellaria cinerea
Procellaria parkinsoni
Pseudobulweria aterrima
Pseudobulweria rostrata
Lugensa brevirostris
Puffinus bulleri
Puffinus pacificus
Puffinus carneipes
Puffinus creatopus
Puffinus tenuirostris
Puffinus gravis
Puffinus griseus
Calonectris diomedea
Calonectris leucomelas
Puffinus nativitatis
Puffinus gavia
Puffinus huttoni
Puffinus mauretanicus
Puffinus yelkouan
Puffinus opisthomelas
Puffinus auricularis
Puffinus puffinus
Puffinus assimilis
Puffinus lherminieri
Puffinus atrodorsalis
Puffinus persicus
Phaethon aethereus
Phaethon rubricauda
Phaethon lepturus
Lithoptila abdounensis
Prophaethon shrubsolei
Fregata ariel
Fregata andrewsi
Fregata minor
Fregata aquila
Fregata magnificens
Papasula abbotti
Morus bassanus
Morus capensis

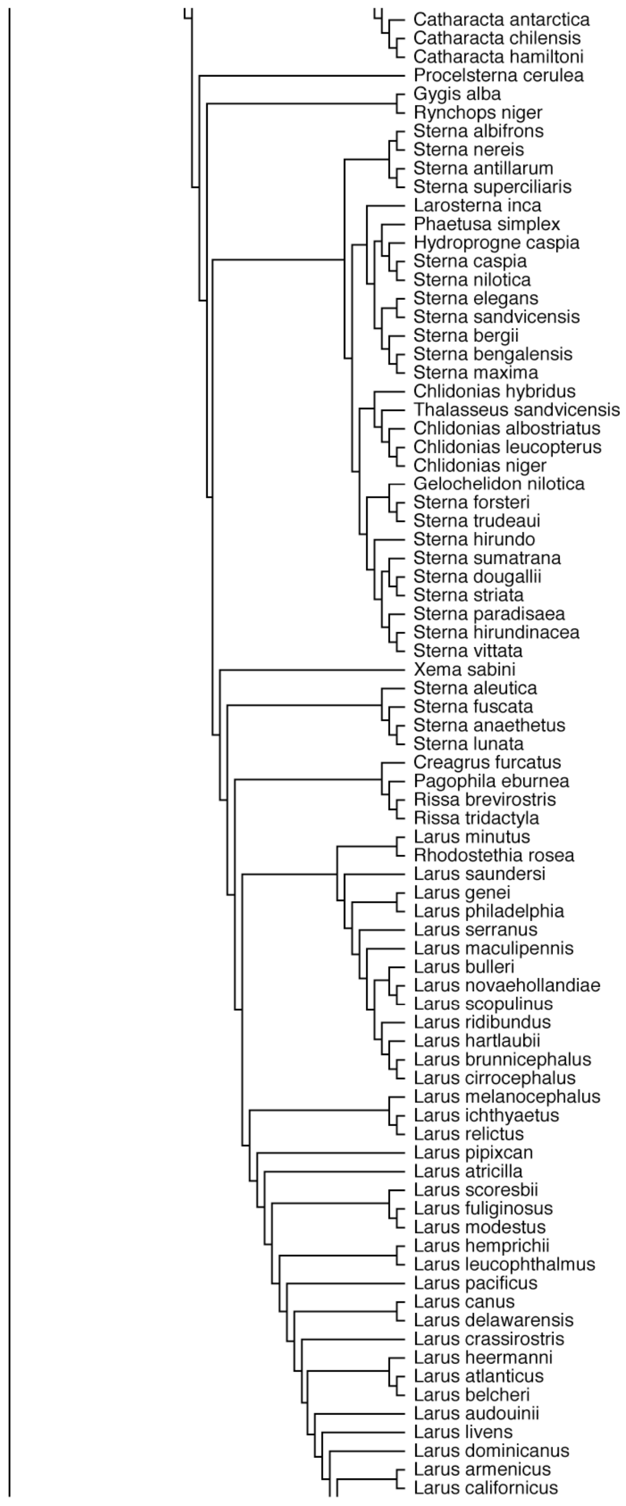

Morus capensis
Morus serrator
Sula sula
Sula dactylatra
Sula leucogaster
Sula nebouxii
Sula variegata
Anhinga anhinga
Anhinga novaehollandiae
Anhinga rufa
Phalacrocorax africanus
Phalacrocorax coronatus
Phalacrocorax pygmeus
Phalacrocorax melanoleucos
Phalacrocorax niger
Phalacrocorax perspicillatus
Phalacrocorax penicillatus
Phalacrocorax harrisi
Phalacrocorax fuscescens
Phalacrocorax neglectus
Phalacrocorax brasilianus
Phalacrocorax auritus
Phalacrocorax olivaceus
Phalacrocorax capillatus
Phalacrocorax carbo
Phalacrocorax sulcirostris
Phalacrocorax varius
Phalacrocorax carunculatus
Phalacrocorax nigrogularis
Phalacrocorax capensis
Phalacrocorax bougainvillii
Phalacrocorax albiventer
Phalacrocorax purpurascens
Phalacrocorax verrucosus
Phalacrocorax atriceps
Phalacrocorax bransfieldensis
Phalacrocorax georgianus
Phalacrocorax magellanicus
Phalacrocorax campbelli
Phalacrocorax chalconotus
Phalacrocorax onslowi
Phalacrocorax colensoi
Phalacrocorax ranfurlyi
Phalacrocorax pelagicus
Phalacrocorax urile
Phalacrocorax aristotelis
Phalacrocorax gaimardi
Phalacrocorax punctatus
Phalacrocorax featherstoni
Stictocarbo punctatus
Teratornis merriami
Coragyps atratus
Cathartes aura
Cathartes burrovianus
Sarcoramphus papa
Gymnogyps californianus
Gymnogyps kofordi
Breagyps clarki
Cathartes melambrotus
Vultur gryphus
Lophotibis cristata
Geronticus eremita
Mesembrinibis
Cercibis
Eudocimus ruber
Theristicus
Ajaia ajaja
Plegadis chihi
Plegadis falcinellus
Plegadis ridgwayi
Threskiornis melanocephalus
Bostrychia hagedash
Platalea leucorodia
Platalea alba
Threskiornis aethiopicus
Threskiornis spinicollis
Jabiru mycteria
Leptoptilos crumeniferus
Anastomus oscitans
Leptoptilos javanicus
Ephippiorhynchus asiaticus

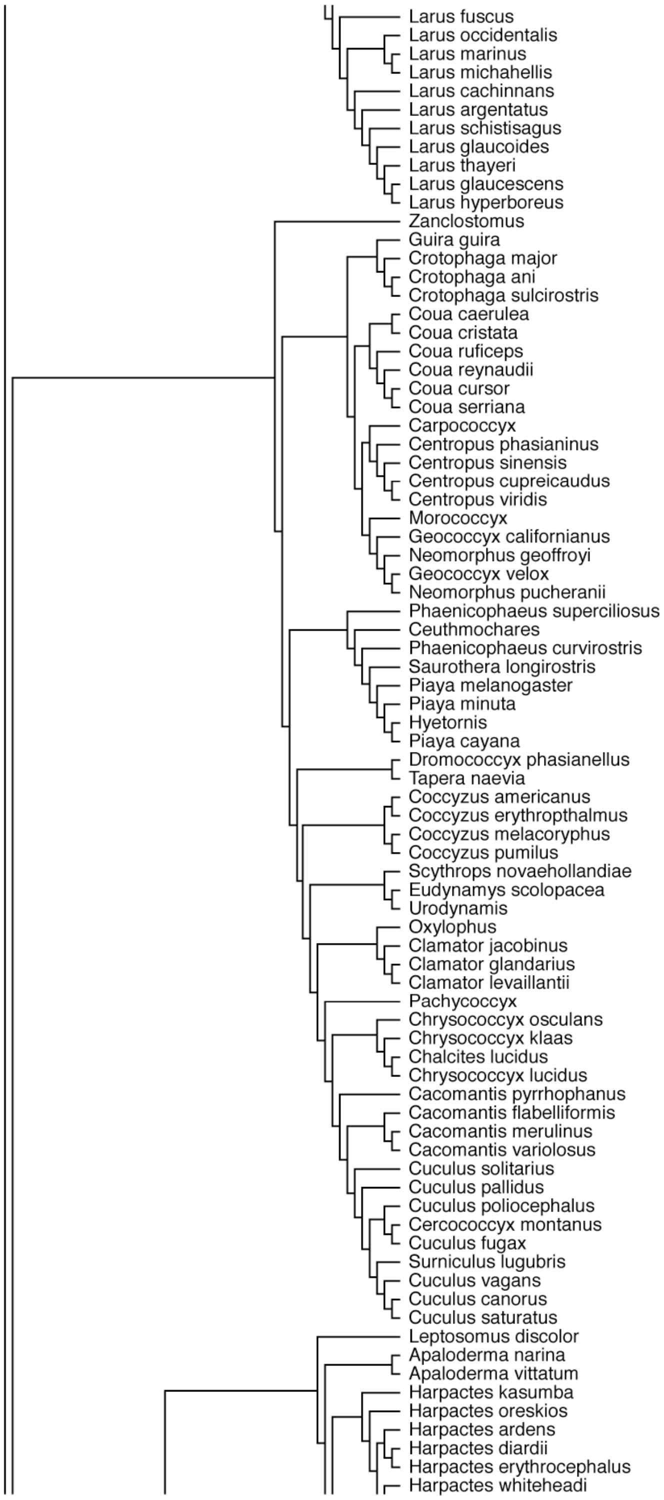

Ephippiorhynchus senegalensis
Anastomus lamelligerus
Mycteria americana
Mycteria ibis
Mycteria cinerea
Mycteria leucocephala
Ciconia abdimii
Ciconia episcopus
Ciconia stormi
Ciconia nigra
Ciconia maguari
Ciconia boyciana
Ciconia ciconia
Scopus umbretta
Balaeniceps rex
Pelecanus occidentalis
Pelecanus conspicillatus
Pelecanus onocrotalus
Pelecanus erythrorhynchos
Pelecanus rufescens
Cochlearius cochlearius
Egretta gularis
Gorsachius leuconotus
Gorsachius melanolophus
Egretta rufescens
Ardea alba
Agamia agami
Tigriornis leucolophus
Tigrisoma lineatum
Tigrisoma mexicanum
Egretta alba
Botaurus lentiginosus
Botaurus pinnatus
Botaurus poiciloptilus
Botaurus stellaris
Ixobrychus flavicollis
Zebrilus undulatus
Ixobrychus involucris
Ixobrychus exilis
Ixobrychus minutus
Ixobrychus cinnamomeus
Ixobrychus sturmii
Ixobrychus eurhythmus
Ixobrychus sinensis
Syrigma sibilatrix
Ardea picata
Egretta tricolor
Egretta caerulea
Egretta novaehollandiae
Egretta vinaceigula
Egretta sacra
Egretta garzetta
Egretta thula
Nyctanassa violacea
Nycticorax caledonicus
Nycticorax nycticorax
Pilherodius pileatus
Ardeola rufiventris
Ardeola grayii
Nycticorax violaceus
Ardeola bacchus
Egretta ardesiaca
Butorides striatus
Butorides virescens
Ardeola ralloides
Bubulcus ibis
Egretta intermedia
Ardea purpurea
Ardea cocoi
Ardea cinerea
Casmerodius albus
Ardea melanocephala
Ardea pacifica
Ardea sumatrana
Ardea goliath
Ardea herodias
Turnix varia
Turnix sylvatica
Turnix hottentotta
Turnix suscitator

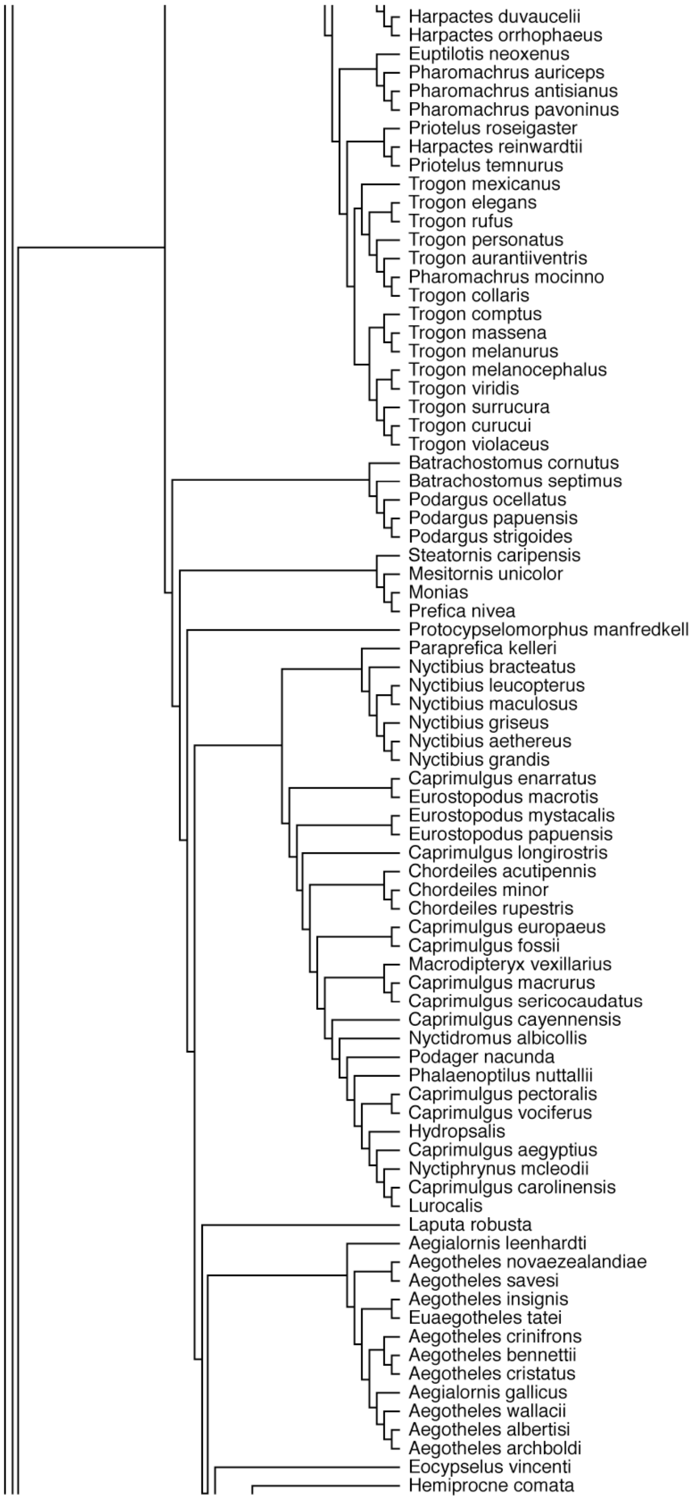

Chionis alba
Chionis minor
Pluvianellus socialis
Esacus recurvirostris
Burhinus vermiculatus
Burhinus magnirostris
Burhinus oedicnemus
Burhinus senegalensis
Burhinus capensis
Burhinus superciliaris
Burhinus bistriatus
Esacus magnirostris
Charadrius pecuarius
Vanellus cayanus
Himantopus himantopus
Himantopus mexicanus
Cladorhynchus leucocephalus
Recurvirostra avosetta
Recurvirostra novaehollandiae
Recurvirostra americana
Recurvirostra andina
Haematopus leucopodus
Haematopus fuliginosus
Haematopus ostralegus
Haematopus unicolor
Haematopus palliatus
Haematopus ater
Haematopus bachmani
Haematopus finschi
Haematopus moquini
Ibidorhyncha struthersii
Pluvialis fulva
Pluvialis apricaria
Pluvialis dominica
Pluvialis squatarola
Oreopholus ruficollis
Charadrius melodus
Charadrius wilsonia
Charadrius sanctaehelenae
Charadrius hiaticula
Erythrogonys cinctus
Vanellus leucurus
Vanellus crassirostris
Vanellus gregarius
Vanellus lugubris
Vanellus cinereus
Vanellus senegallus
Vanellus miles
Vanellus indicus
Vanellus macropterus
Vanellus coronatus
Vanellus melanopterus
Vanellus albiceps
Vanellus malabaricus
Vanellus tectus
Vanellus tricolor
Vanellus vanellus
Vanellus chilensis
Vanellus resplendens
Vanellus duvaucelii
Vanellus armatus
Vanellus spinosus
Charadrius modestus
Charadrius melanops
Charadrius placidus
Charadrius rubricollis
Elseyornis melanops
Charadrius semipalmatus
Charadrius vociferus
Eudromias morinellus
Charadrius mongolus
Peltohyas australis
Thinornis novaeseelandiae
Charadrius alticola
Charadrius pallidus
Charadrius collaris
Charadrius australis
Charadrius veredus
Charadrius montanus
Charadrius leschenaultii

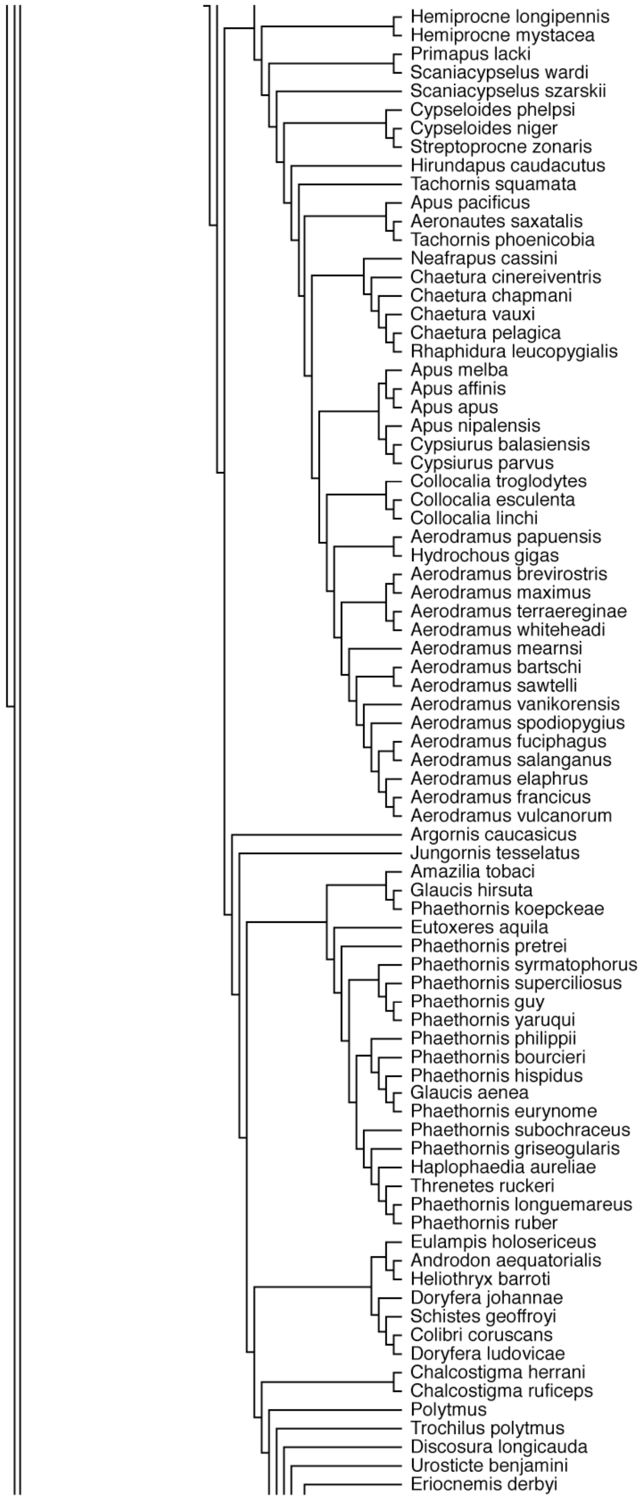

Charadrius cinctus
Charadrius alexandrinus
Charadrius marginatus
Charadrius ruficapillus
Phegornis mitchellii
Charadrius cucullatus
Charadrius dubius
Anarhynchus frontalis
Charadrius tricollaris
Charadrius obscurus
Charadrius falklandicus
Charadrius asiaticus
Charadrius bicinctus
Pedionomus torquatus
Attagis gayi
Thinocorus orbignyianus
Thinocorus rumicivorus
Nycticryphes semicollaris
Rostratula benghalensis
Rostratula semicollaris
Hydrophasianus chirurgus
Jacana jacana
Jacana spinosa
Actophilornis africanus
Actophilornis albinucha
Metopidius indicus
Irediparra gallinacea
Microparra capensis
Limosa fedoa
Limosa limosa
Limosa haemastica
Limosa lapponica
Numenius tenuirostris
Numenius borealis
Bartramia longicauda
Numenius minutus
Numenius phaeopus
Numenius americanus
Numenius arquata
Numenius madagascariensis
Numenius tahitiensis
Philomachus pugnax
Limicola falcinellus
Coenocorypha aucklandica
Lymnocryptes minimus
Philohela minor
Scolopax minor
Scolopax mira
Scolopax rusticola
Gallinago megala
Gallinago nigripennis
Gallinago stenura
Gallinago macrodactyla
Gallinago media
Gallinago gallinago
Gallinago undulata
Gallinago hardwickii
Gallinago paraguaiae
Limnodromus scolopaceus
Aphriza virgata
Limnodromus griseus
Prosobonia cancellata
Phalaropus tricolor
Phalaropus fulicaria
Phalaropus lobatus
Tringa hypoleucos
Tringa cinereus
Xenus cinereus
Actitis hypoleucos
Actitis macularia
Tringa solitaria
Tringa ochropus
Heteroscelus brevipes
Heteroscelus incanus
Tringa nebularia
Tringa erythropus
Tringa melanoleuca
Catoptrophorus semipalmatus
Tringa flavipes
Tringa stagnatilis

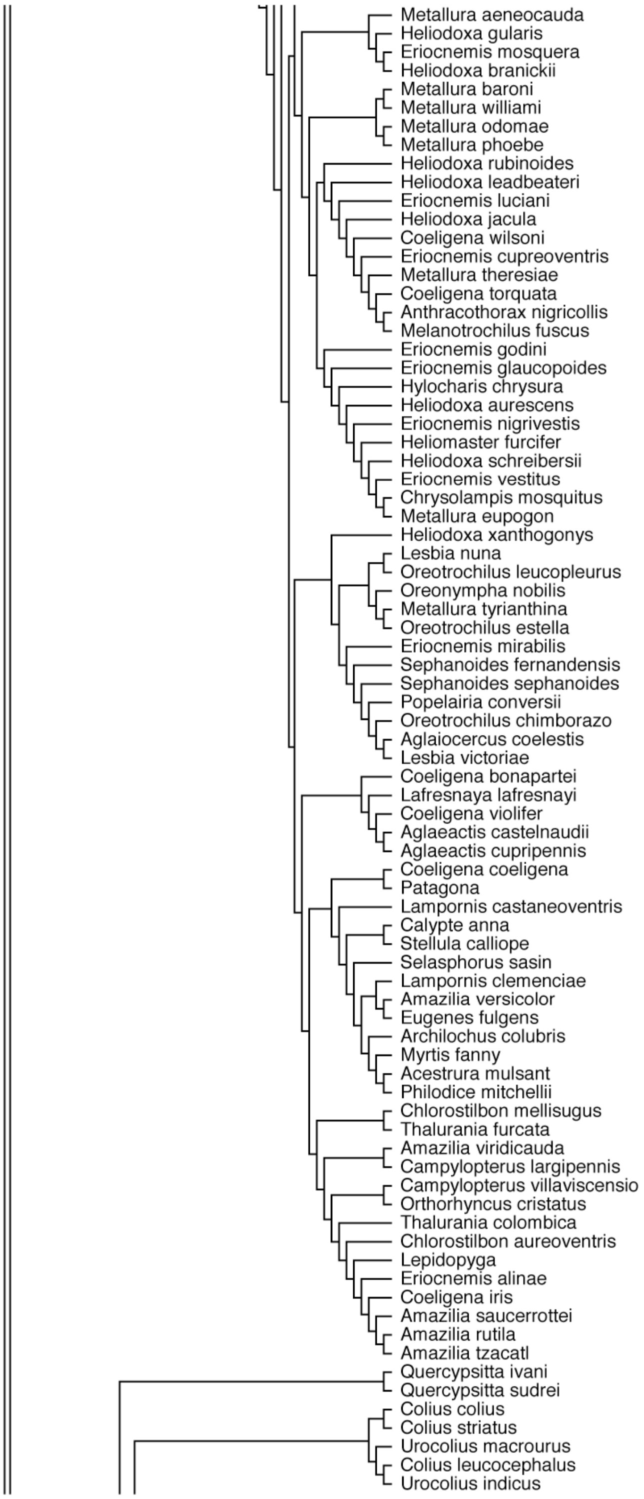

Tringa glareola
Tringa totanus
Calidris bairdii
Arenaria interpres
Arenaria melanocephala
Calidris ferruginea
Calidris canutus
Calidris maritima
Calidris minuta
Calidris tenuirostris
Eurynorhynchus pygmeus
Calidris mauri
Calidris ruficollis
Calidris himantopus
Calidris alpina
Calidris ptilocnemis
Calidris temminckii
Calidris fuscicollis
Calidris subminuta
Calidris acuminata
Calidris melanotos
Calidris alba
Tryngites subruficollis
Calidris minutilla
Calidris pusilla
Dromas ardeola
Pluvianus aegyptius
Glareola pratincola
Stiltia isabella
Glareola maldivarum
Glareola nuchalis
Glareola cinerea
Glareola nordmanni
Glareola lactea
Glareola ocularis
Rhinoptilus chalcopterus
Rhinoptilus africanus
Rhinoptilus cinctus
Cursorius coromandelicus
Cursorius temminckii
Cursorius rufus
Cursorius chalcopterus
Cursorius cursor
Fratercula cirrhata
Cerorhinca monocerata
Fratercula arctica
Fratercula corniculata
Ptychoramphus aleuticus
Aethia cristatella
Aethia pygmaea
Aethia psittacula
Aethia pusilla
Synthliboramphus antiquus
Synthliboramphus wumizusume
Synthliboramphus craveri
Synthliboramphus hypoleucus
Brachyramphus brevirostris
Brachyramphus marmoratus
Brachyramphus hypoleuca
Brachyramphus perdix
Cepphus grylle
Cepphus carbo
Cepphus columba
Alle alle
Alca torda
Pinguinus impennis
Uria aalge
Uria lomvia
Anous stolidus
Anous minutus
Anous tenuirostris
Rynchops flavirostris
Larus heuglini
Larus taimyrensis
Stercorarius longicaudus
Stercorarius parasiticus
Catharacta skua
Stercorarius pomarinus
Catharacta maccormicki
Catharacta lonnbergi

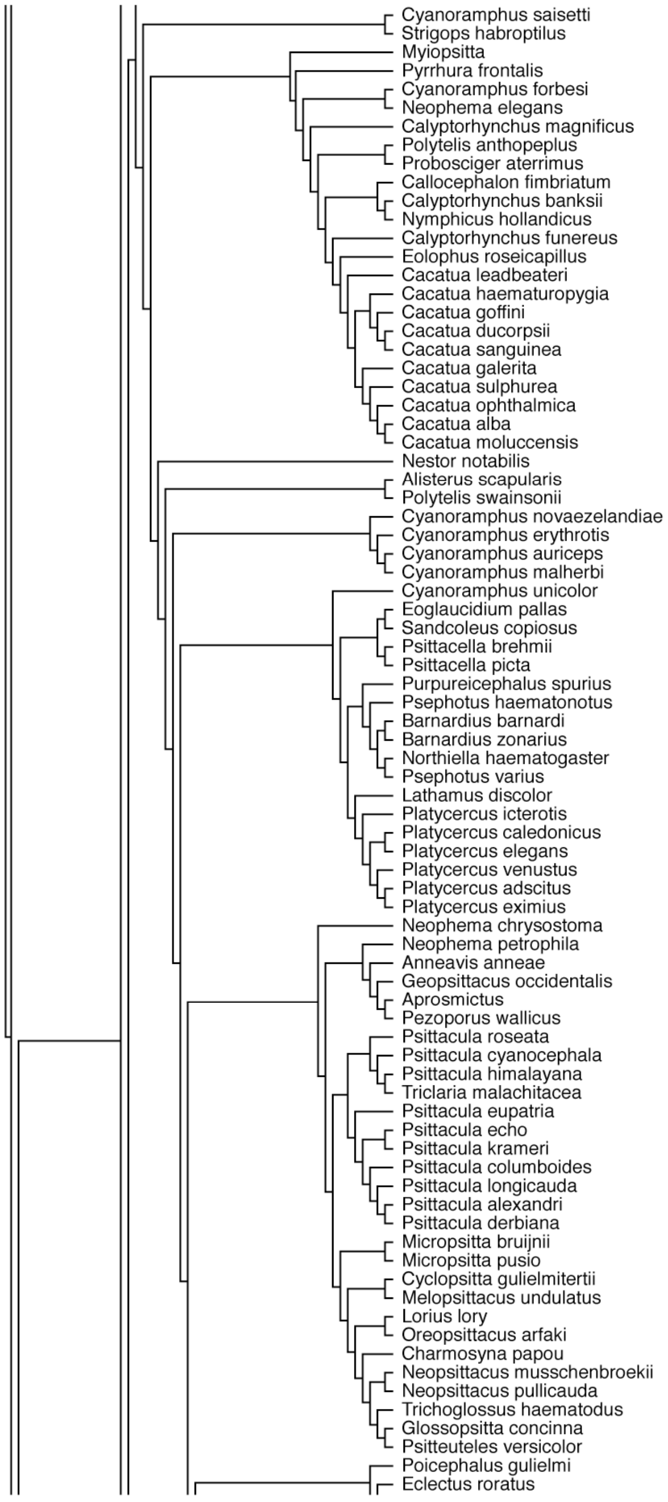

Catharacta antarctica
Catharacta chilensis
Catharacta hamiltoni
Procelsterna cerulea
Gygis alba
Rynchops niger
Sterna albifrons
Sterna nereis
Sterna antillarum
Sterna superciliaris
Larosterna inca
Phaetusa simplex
Hydroprogne caspia
Sterna caspia
Sterna nilotica
Sterna elegans
Sterna sandvicensis
Sterna bergii
Sterna bengalensis
Sterna maxima
Chlidonias hybridus
Thalasseus sandvicensis
Chlidonias albostriatus
Chlidonias leucopterus
Chlidonias niger
Gelochelidon nilotica
Sterna forsteri
Sterna trudeaui
Sterna hirundo
Sterna sumatrana
Sterna dougallii
Sterna striata
Sterna paradisaea
Sterna hirundinacea
Sterna vittata
Xema sabini
Sterna aleutica
Sterna fuscata
Sterna anaethetus
Sterna lunata
Creagrus furcatus
Pagophila eburnea
Rissa brevirostris
Rissa tridactyla
Larus minutus
Rhodostethia rosea
Larus saundersi
Larus genei
Larus philadelphia
Larus serranus
Larus maculipennis
Larus bulleri
Larus novaehollandiae
Larus scopulinus
Larus ridibundus
Larus hartlaubii
Larus brunnicephalus
Larus cirrocephalus
Larus melanocephalus
Larus ichthyaetus
Larus relictus
Larus pipixcan
Larus atricilla
Larus scoresbii
Larus fuliginosus
Larus modestus
Larus hemprichii
Larus leucophthalmus
Larus pacificus
Larus canus
Larus delawarensis
Larus crassirostris
Larus heermanni
Larus atlanticus
Larus belcheri
Larus audouinii
Larus livens
Larus dominicanus
Larus armenicus
Larus californicus

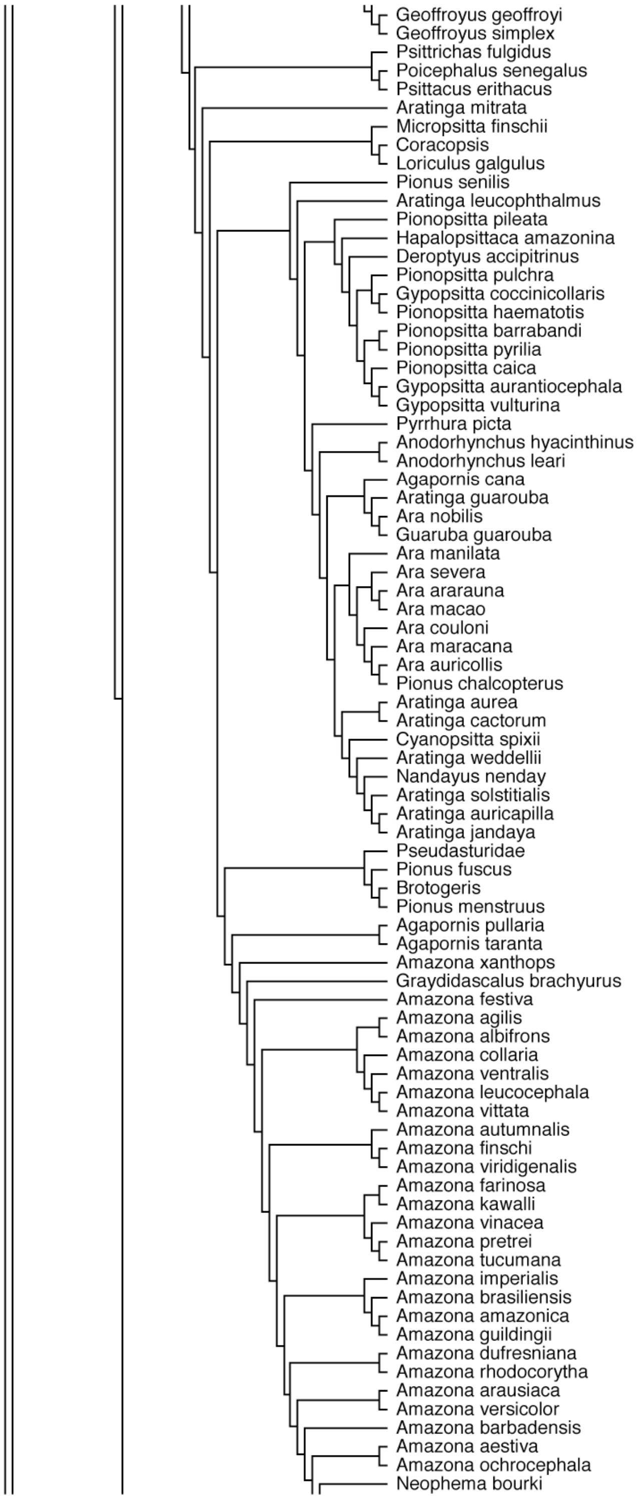

Larus fuscus
Larus occidentalis
Larus marinus
Larus michahellis
Larus cachinnans
Larus argentatus
Larus schistisagus
Larus glaucoides
Larus thayeri
Larus glaucescens
Larus hyperboreus
Zanclostomus
Guira guira
Crotophaga major
Crotophaga ani
Crotophaga sulcirostris
Coua caerulea
Coua cristata
Coua ruficeps
Coua reynaudii
Coua cursor
Coua serriana
Carpococcyx
Centropus phasianinus
Centropus sinensis
Centropus cupreicaudus
Centropus viridis
Morococcyx
Geococcyx californianus
Neomorphus geoffroyi
Geococcyx velox
Neomorphus pucheranii
Phaenicophaeus superciliosus
Ceuthmochares
Phaenicophaeus curvirostris
Saurothera longirostris
Piaya melanogaster
Piaya minuta
Hyetornis
Piaya cayana
Dromococcyx phasianellus
Tapera naevia
Coccyzus americanus
Coccyzus erythropthalmus
Coccyzus melacoryphus
Coccyzus pumilus
Scythrops novaehollandiae
Eudynamys scolopacea
Urodynamis
Oxylophus
Clamator jacobinus
Clamator glandarius
Clamator levaillantii
Pachycoccyx
Chrysococcyx osculans
Chrysococcyx klaas
Chalcites lucidus
Chrysococcyx lucidus
Cacomantis pyrrhophanus
Cacomantis flabelliformis
Cacomantis merulinus
Cacomantis variolosus
Cuculus solitarius
Cuculus pallidus
Cuculus poliocephalus
Cercococcyx montanus
Cuculus fugax
Surniculus lugubris
Cuculus vagans
Cuculus canorus
Cuculus saturatus
Leptosomus discolor
Apaloderma narina
Apaloderma vittatum
Harpactes kasumba
Harpactes oreskios
Harpactes ardens
Harpactes diardii
Harpactes erythrocephalus
Harpactes whiteheadi

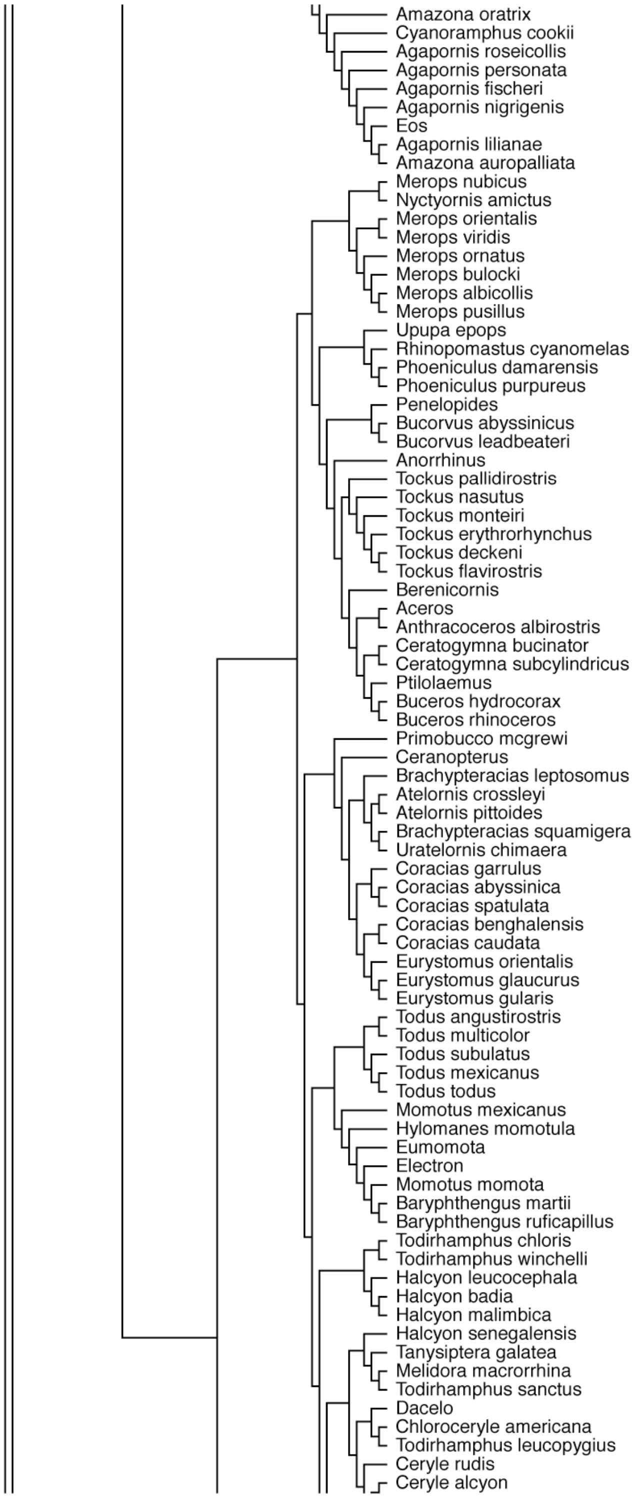

Harpactes duvaucelii
Harpactes orrhophaeus
Euptilotis neoxenus
Pharomachrus auriceps
Pharomachrus antisianus
Pharomachrus pavoninus
Priotelus roseigaster
Harpactes reinwardtii
Priotelus temnurus
Trogon mexicanus
Trogon elegans
Trogon rufus
Trogon personatus
Trogon aurantiiventris
Pharomachrus mocinno
Trogon collaris
Trogon comptus
Trogon massena
Trogon melanurus
Trogon melanocephalus
Trogon viridis
Trogon surrucura
Trogon curucui
Trogon violaceus
Batrachostomus cornutus
Batrachostomus septimus
Podargus ocellatus
Podargus papuensis
Podargus strigoides
Steatornis caripensis
Mesitornis unicolor
Monias
Prefica nivea
Protocypselomorphus manfredkell
Paraprefica kelleri
Nyctibius bracteatus
Nyctibius leucopterus
Nyctibius maculosus
Nyctibius griseus
Nyctibius aethereus
Nyctibius grandis
Caprimulgus enarratus
Eurostopodus macrotis
Eurostopodus mystacalis
Eurostopodus papuensis
Caprimulgus longirostris
Chordeiles acutipennis
Chordeiles minor
Chordeiles rupestris
Caprimulgus europaeus
Caprimulgus fossii
Macrodipteryx vexillarius
Caprimulgus macrurus
Caprimulgus sericocaudatus
Caprimulgus cayennensis
Nyctidromus albicollis
Podager nacunda
Phalaenoptilus nuttallii
Caprimulgus pectoralis
Caprimulgus vociferus
Hydropsalis
Caprimulgus aegyptius
Nyctiphrynus mcleodii
Caprimulgus carolinensis
Lurocalis
Laputa robusta
Aegialornis leenhardti
Aegotheles novaezealandiae
Aegotheles savesi
Aegotheles insignis
Euaegotheles tatei
Aegotheles crinifrons
Aegotheles bennettii
Aegotheles cristatus
Aegialornis gallicus
Aegotheles wallacii
Aegotheles albertisi
Aegotheles archboldi
Eocypselus vincenti
Hemiprocne comata

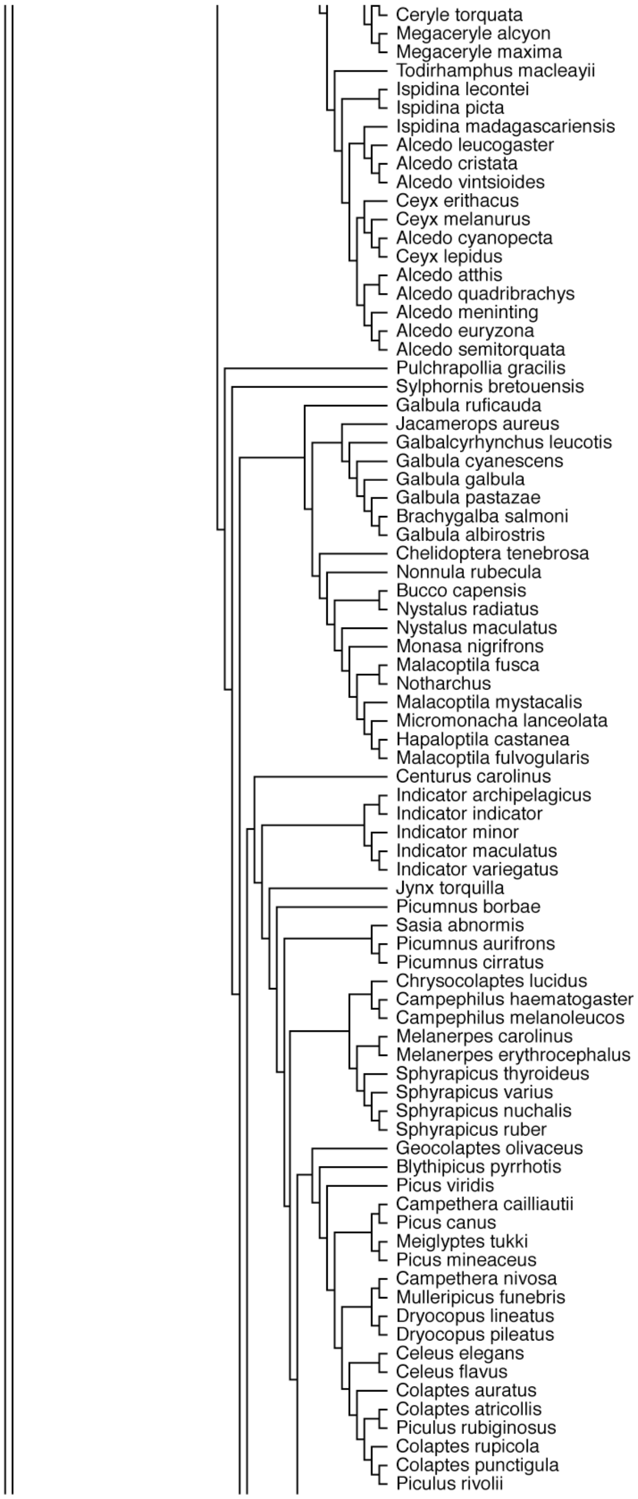

Hemiprocne longipennis
Hemiprocne mystacea
Primapus lacki
Scaniacypselus wardi
Scaniacypselus szarskii
Cypseloides phelpsi
Cypseloides niger
Streptoprocne zonaris
Hirundapus caudacutus
Tachornis squamata
Apus pacificus
Aeronautes saxatalis
Tachornis phoenicobia
Neafrapus cassini
Chaetura cinereiventris
Chaetura chapmani
Chaetura vauxi
Chaetura pelagica
Rhaphidura leucopygialis
Apus melba
Apus affinis
Apus apus
Apus nipalensis
Cypsiurus balasiensis
Cypsiurus parvus
Collocalia troglodytes
Collocalia esculenta
Collocalia linchi
Aerodramus papuensis
Hydrochous gigas
Aerodramus brevirostris
Aerodramus maximus
Aerodramus terraereginae
Aerodramus whiteheadi
Aerodramus mearnsi
Aerodramus bartschi
Aerodramus sawtelli
Aerodramus vanikorensis
Aerodramus spodiopygius
Aerodramus fuciphagus
Aerodramus salanganus
Aerodramus elaphrus
Aerodramus francicus
Aerodramus vulcanorum
Argornis caucasicus
Jungornis tesselatus
Amazilia tobaci
Glaucis hirsuta
Phaethornis koepckeae
Eutoxeres aquila
Phaethornis pretrei
Phaethornis syrmatophorus
Phaethornis superciliosus
Phaethornis guy
Phaethornis yaruqui
Phaethornis philippii
Phaethornis bourcieri
Phaethornis hispidus
Glaucis aenea
Phaethornis eurynome
Phaethornis subochraceus
Phaethornis griseogularis
Haplophaedia aureliae
Threnetes ruckeri
Phaethornis longuemareus
Phaethornis ruber
Eulampis holosericeus
Androdon aequatorialis
Heliothryx barroti
Doryfera johannae
Schistes geoffroyi
Colibri coruscans
Doryfera ludovicae
Chalcostigma herrani
Chalcostigma ruficeps
Polytmus
Trochilus polytmus
Discosura longicauda
Urosticte benjamini
Eriocnemis derbyi

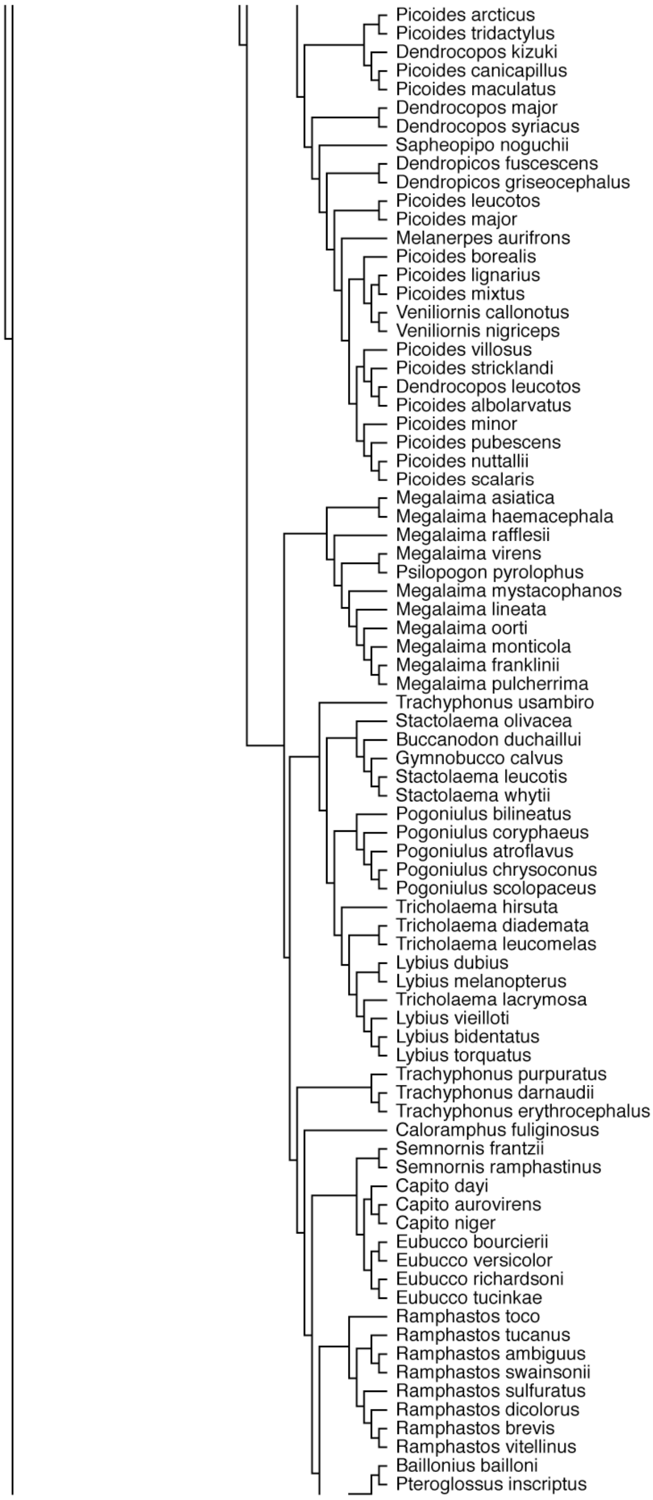

Metallura aeneocauda
Heliodoxa gularis
Eriocnemis mosquera
Heliodoxa branickii
Metallura baroni
Metallura williami
Metallura odomae
Metallura phoebe
Heliodoxa rubinoides
Heliodoxa leadbeateri
Eriocnemis luciani
Heliodoxa jacula
Coeligena wilsoni
Eriocnemis cupreoventris
Metallura theresiae
Coeligena torquata
Anthracothorax nigricollis
Melanotrochilus fuscus
Eriocnemis godini
Eriocnemis glaucopoides
Hylocharis chrysura
Heliodoxa aurescens
Eriocnemis nigrivestis
Heliomaster furcifer
Heliodoxa schreibersii
Eriocnemis vestitus
Chrysolampis mosquitus
Metallura eupogon
Heliodoxa xanthogonys
Lesbia nuna
Oreotrochilus leucopleurus
Oreonympha nobilis
Metallura tyrianthina
Oreotrochilus estella
Eriocnemis mirabilis
Sephanoides fernandensis
Sephanoides sephanoides
Popelairia conversii
Oreotrochilus chimborazo
Aglaiocercus coelestis
Lesbia victoriae
Coeligena bonapartei
Lafresnaya lafresnayi
Coeligena violifer
Aglaeactis castelnaudii
Aglaeactis cupripennis
Coeligena coeligena
Patagona
Lampornis castaneoventris
Calypte anna
Stellula calliope
Selasphorus sasin
Lampornis clemenciae
Amazilia versicolor
Eugenes fulgens
Archilochus colubris
Myrtis fanny
Acestrura mulsant
Philodice mitchellii
Chlorostilbon mellisugus
Thalurania furcata
Amazilia viridicauda
Campylopterus largipennis
Campylopterus villaviscensio
Orthorhyncus cristatus
Thalurania colombica
Chlorostilbon aureoventris
Lepidopyga
Eriocnemis alinae
Coeligena iris
Amazilia saucerrottei
Amazilia rutila
Amazilia tzacatl
Quercypsitta ivani
Quercypsitta sudrei
Colius colius
Colius striatus
Urocolius macrourus
Colius leucocephalus
Urocolius indicus

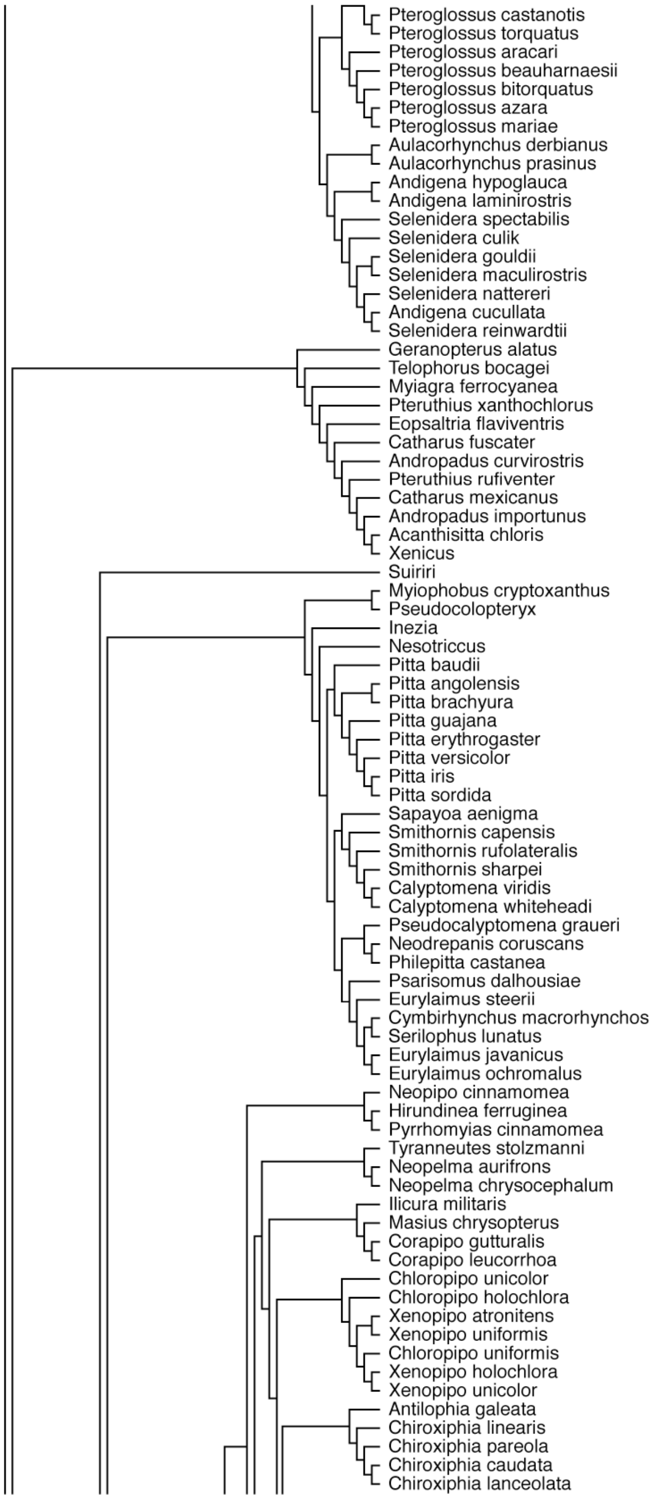

Cyanoramphus saisetti
Strigops habroptilus
Myiopsitta
Pyrrhura frontalis
Cyanoramphus forbesi
Neophema elegans
Calyptorhynchus magnificus
Polytelis anthopeplus
Probosciger aterrimus
Callocephalon fimbriatum
Calyptorhynchus banksii
Nymphicus hollandicus
Calyptorhynchus funereus
Eolophus roseicapillus
Cacatua leadbeateri
Cacatua haematuropygia
Cacatua goffini
Cacatua ducorpsii
Cacatua sanguinea
Cacatua galerita
Cacatua sulphurea
Cacatua ophthalmica
Cacatua alba
Cacatua moluccensis
Nestor notabilis
Alisterus scapularis
Polytelis swainsonii
Cyanoramphus novaezelandiae
Cyanoramphus erythrotis
Cyanoramphus auriceps
Cyanoramphus malherbi
Cyanoramphus unicolor
Eoglaucidium pallas
Sandcoleus copiosus
Psittacella brehmii
Psittacella picta
Purpureicephalus spurius
Psephotus haematonotus
Barnardius barnardi
Barnardius zonarius
Northiella haematogaster
Psephotus varius
Lathamus discolor
Platycercus icterotis
Platycercus caledonicus
Platycercus elegans
Platycercus venustus
Platycercus adscitus
Platycercus eximius
Neophema chrysostoma
Neophema petrophila
Anneavis anneae
Geopsittacus occidentalis
Aprosmictus
Pezoporus wallicus
Psittacula roseata
Psittacula cyanocephala
Psittacula himalayana
Triclaria malachitacea
Psittacula eupatria
Psittacula echo
Psittacula krameri
Psittacula columboides
Psittacula longicauda
Psittacula alexandri
Psittacula derbiana
Micropsitta bruijnii
Micropsitta pusio
Cyclopsitta gulielmitertii
Melopsittacus undulatus
Lorius lory
Oreopsittacus arfaki
Charmosyna papou
Neopsittacus musschenbroekii
Neopsittacus pullicauda
Trichoglossus haematodus
Glossopsitta concinna
Psitteuteles versicolor
Poicephalus gulielmi
Eclectus roratus

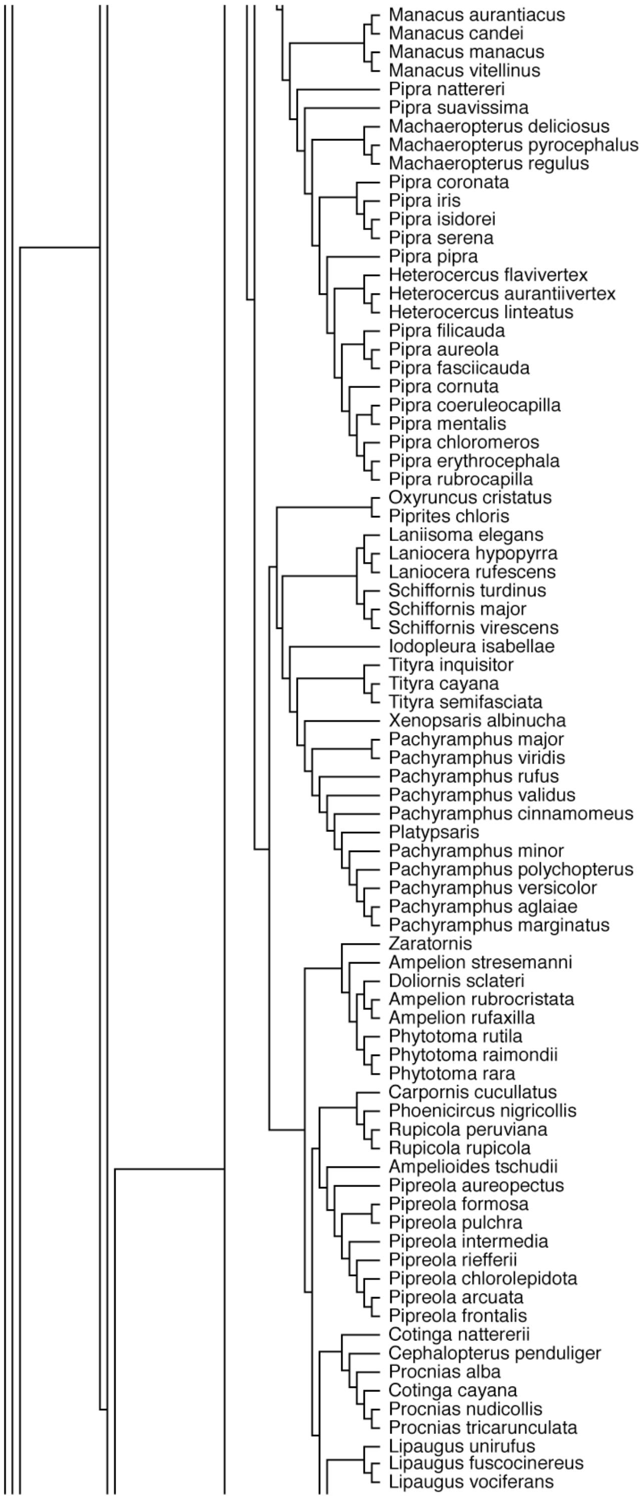

Geoffroyus geoffroyi
Geoffroyus simplex
Psittrichas fulgidus
Poicephalus senegalus
Psittacus erithacus
Aratinga mitrata
Micropsitta finschii
Coracopsis
Loriculus galgulus
Pionus senilis
Aratinga leucophthalmus
Pionopsitta pileata
Hapalopsittaca amazonina
Deroptyus accipitrinus
Pionopsitta pulchra
Gypopsitta coccinicollaris
Pionopsitta haematotis
Pionopsitta barrabandi
Pionopsitta pyrilia
Pionopsitta caica
Gypopsitta aurantiocephala
Gypopsitta vulturina
Pyrrhura picta
Anodorhynchus hyacinthinus
Anodorhynchus leari
Agapornis cana
Aratinga guarouba
Ara nobilis
Guaruba guarouba
Ara manilata
Ara severa
Ara ararauna
Ara macao
Ara couloni
Ara maracana
Ara auricollis
Pionus chalcopterus
Aratinga aurea
Aratinga cactorum
Cyanopsitta spixii
Aratinga weddellii
Nandayus nenday
Aratinga solstitialis
Aratinga auricapilla
Aratinga jandaya
Pseudasturidae
Pionus fuscus
Brotogeris
Pionus menstruus
Agapornis pullaria
Agapornis taranta
Amazona xanthops
Graydidascalus brachyurus
Amazona festiva
Amazona agilis
Amazona albifrons
Amazona collaria
Amazona ventralis
Amazona leucocephala
Amazona vittata
Amazona autumnalis
Amazona finschi
Amazona viridigenalis
Amazona farinosa
Amazona kawalli
Amazona vinacea
Amazona pretrei
Amazona tucumana
Amazona imperialis
Amazona brasiliensis
Amazona amazonica
Amazona guildingii
Amazona dufresniana
Amazona rhodocorytha
Amazona arausiaca
Amazona versicolor
Amazona barbadensis
Amazona aestiva
Amazona ochrocephala
Neophema bourki

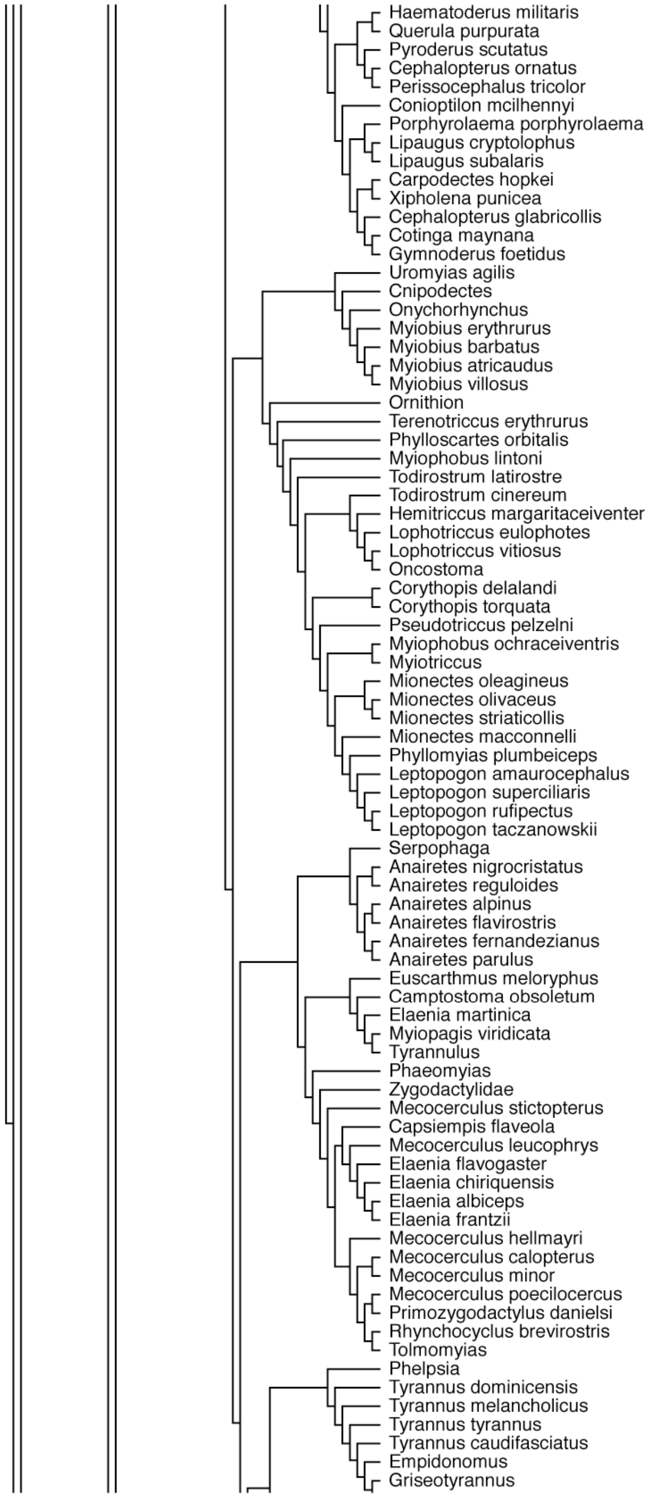

Amazona oratrix
Cyanoramphus cookii
Agapornis roseicollis
Agapornis personata
Agapornis fischeri
Agapornis nigrigenis
Eos
Agapornis lilianae
Amazona auropalliata
Merops nubicus
Nyctyornis amictus
Merops orientalis
Merops viridis
Merops ornatus
Merops bulocki
Merops albicollis
Merops pusillus
Upupa epops
Rhinopomastus cyanomelas
Phoeniculus damarensis
Phoeniculus purpureus
Penelopides
Bucorvus abyssinicus
Bucorvus leadbeateri
Anorrhinus
Tockus pallidirostris
Tockus nasutus
Tockus monteiri
Tockus erythrorhynchus
Tockus deckeni
Tockus flavirostris
Berenicornis
Aceros
Anthracoceros albirostris
Ceratogymna bucinator
Ceratogymna subcylindricus
Ptilolaemus
Buceros hydrocorax
Buceros rhinoceros
Primobucco mcgrewi
Ceranopterus
Brachypteracias leptosomus
Atelornis crossleyi
Atelornis pittoides
Brachypteracias squamigera
Uratelornis chimaera
Coracias garrulus
Coracias abyssinica
Coracias spatulata
Coracias benghalensis
Coracias caudata
Eurystomus orientalis
Eurystomus glaucurus
Eurystomus gularis
Todus angustirostris
Todus multicolor
Todus subulatus
Todus mexicanus
Todus todus
Momotus mexicanus
Hylomanes momotula
Eumomota
Electron
Momotus momota
Baryphthengus martii
Baryphthengus ruficapillus
Todirhamphus chloris
Todirhamphus winchelli
Halcyon leucocephala
Halcyon badia
Halcyon malimbica
Halcyon senegalensis
Tanysiptera galatea
Melidora macrorrhina
Todirhamphus sanctus
Dacelo
Chloroceryle americana
Todirhamphus leucopygius
Ceryle rudis
Ceryle alcyon

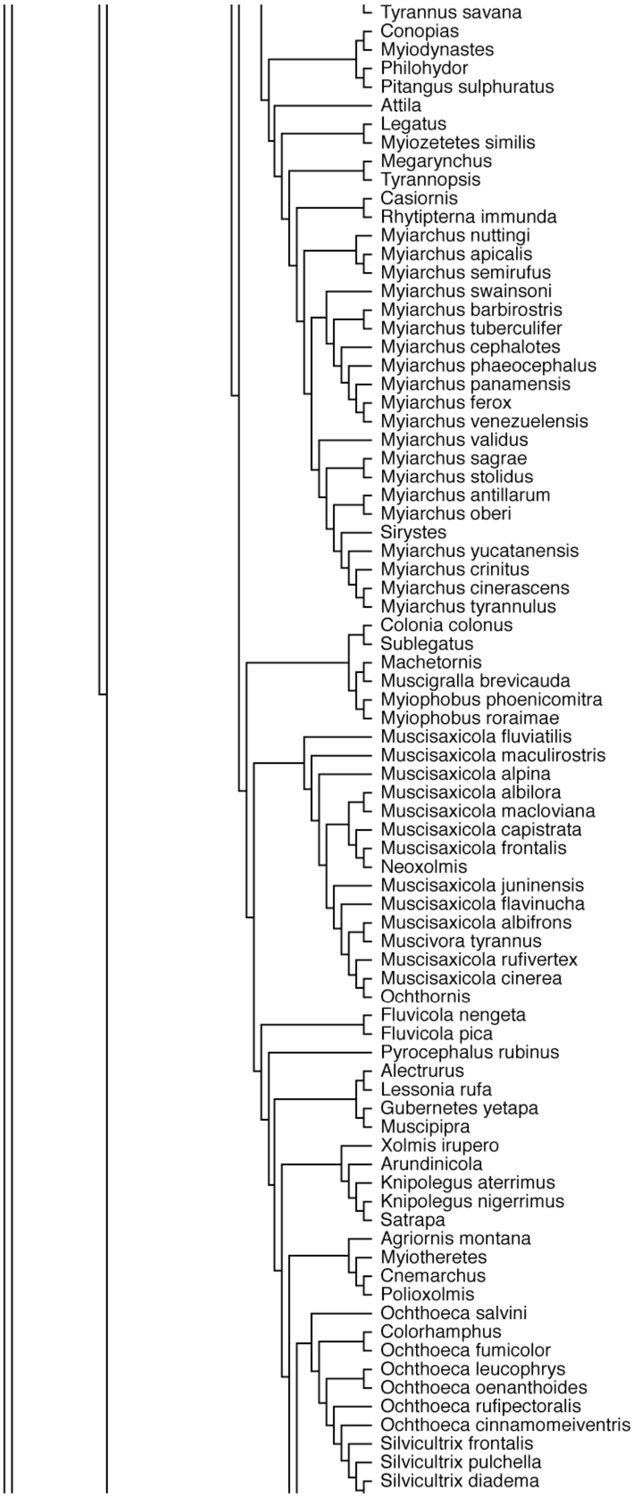

Ceryle torquata
Megaceryle alcyon
Megaceryle maxima
Todirhamphus macleayii
Ispidina lecontei
Ispidina picta
Ispidina madagascariensis
Alcedo leucogaster
Alcedo cristata
Alcedo vintsioides
Ceyx erithacus
Ceyx melanurus
Alcedo cyanopecta
Ceyx lepidus
Alcedo atthis
Alcedo quadribrachys
Alcedo meninting
Alcedo euryzona
Alcedo semitorquata
Pulchrapollia gracilis
Sylphornis bretouensis
Galbula ruficauda
Jacamerops aureus
Galbalcyrhynchus leucotis
Galbula cyanescens
Galbula galbula
Galbula pastazae
Brachygalba salmoni
Galbula albirostris
Chelidoptera tenebrosa
Nonnula rubecula
Bucco capensis
Nystalus radiatus
Nystalus maculatus
Monasa nigrifrons
Malacoptila fusca
Notharchus
Malacoptila mystacalis
Micromonacha lanceolata
Hapaloptila castanea
Malacoptila fulvogularis
Centurus carolinus
Indicator archipelagicus
Indicator indicator
Indicator minor
Indicator maculatus
Indicator variegatus
Jynx torquilla
Picumnus borbae
Sasia abnormis
Picumnus aurifrons
Picumnus cirratus
Chrysocolaptes lucidus
Campephilus haematogaster
Campephilus melanoleucos
Melanerpes carolinus
Melanerpes erythrocephalus
Sphyrapicus thyroideus
Sphyrapicus varius
Sphyrapicus nuchalis
Sphyrapicus ruber
Geocolaptes olivaceus
Blythipicus pyrrhotis
Picus viridis
Campethera cailliautii
Picus canus
Meiglyptes tukki
Picus mineaceus
Campethera nivosa
Mulleripicus funebris
Dryocopus lineatus
Dryocopus pileatus
Celeus elegans
Celeus flavus
Colaptes auratus
Colaptes atricollis
Piculus rubiginosus
Colaptes rupicola
Colaptes punctigula
Piculus rivolii

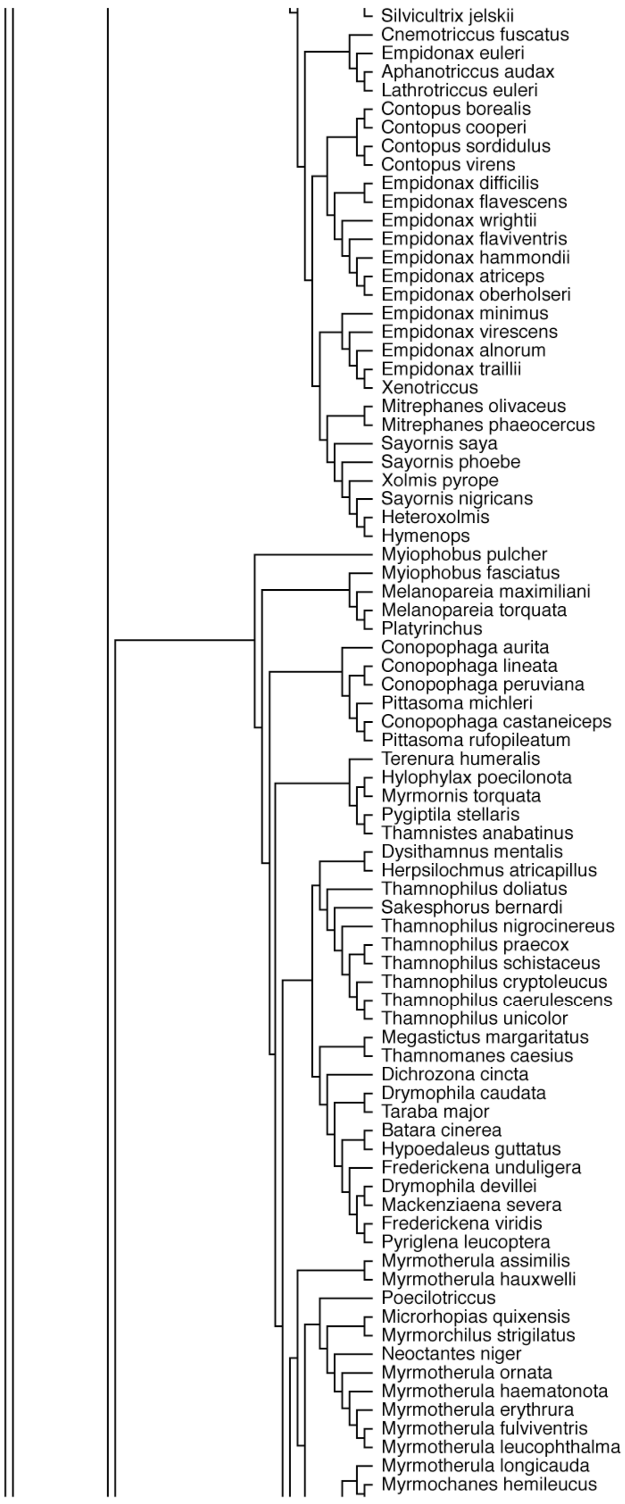

Picoides arcticus
Picoides tridactylus
Dendrocopos kizuki
Picoides canicapillus
Picoides maculatus
Dendrocopos major
Dendrocopos syriacus
Sapheopipo noguchii
Dendropicos fuscescens
Dendropicos griseocephalus
Picoides leucotos
Picoides major
Melanerpes aurifrons
Picoides borealis
Picoides lignarius
Picoides mixtus
Veniliornis callonotus
Veniliornis nigriceps
Picoides villosus
Picoides stricklandi
Dendrocopos leucotos
Picoides albolarvatus
Picoides minor
Picoides pubescens
Picoides nuttallii
Picoides scalaris
Megalaima asiatica
Megalaima haemacephala
Megalaima rafflesii
Megalaima virens
Psilopogon pyrolophus
Megalaima mystacophanos
Megalaima lineata
Megalaima oorti
Megalaima monticola
Megalaima franklinii
Megalaima pulcherrima
Trachyphonus usambiro
Stactolaema olivacea
Buccanodon duchaillui
Gymnobucco calvus
Stactolaema leucotis
Stactolaema whytii
Pogoniulus bilineatus
Pogoniulus coryphaeus
Pogoniulus atroflavus
Pogoniulus chrysoconus
Pogoniulus scolopaceus
Tricholaema hirsuta
Tricholaema diademata
Tricholaema leucomelas
Lybius dubius
Lybius melanopterus
Tricholaema lacrymosa
Lybius vieilloti
Lybius bidentatus
Lybius torquatus
Trachyphonus purpuratus
Trachyphonus darnaudii
Trachyphonus erythrocephalus
Caloramphus fuliginosus
Semnornis frantzii
Semnornis ramphastinus
Capito dayi
Capito aurovirens
Capito niger
Eubucco bourcierii
Eubucco versicolor
Eubucco richardsoni
Eubucco tucinkae
Ramphastos toco
Ramphastos tucanus
Ramphastos ambiguus
Ramphastos swainsonii
Ramphastos sulfuratus
Ramphastos dicolorus
Ramphastos brevis
Ramphastos vitellinus
Baillonius bailloni
Pteroglossus inscriptus

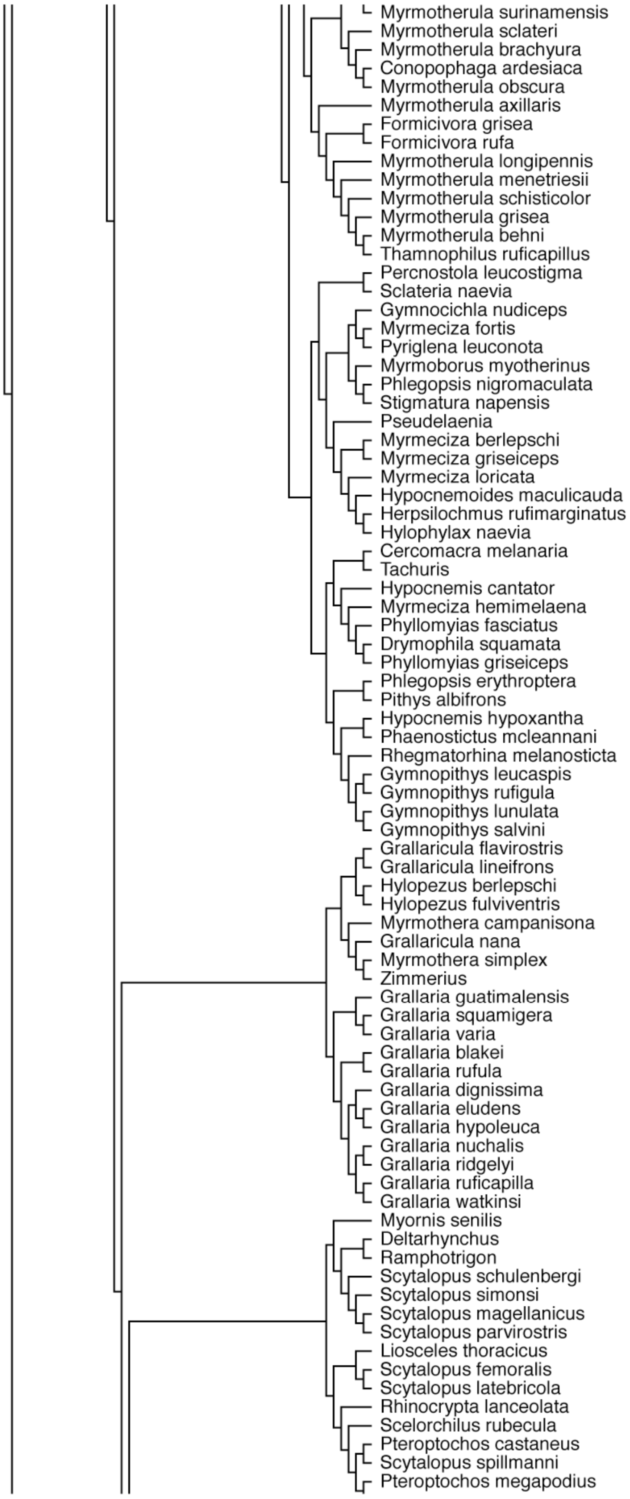

Pteroglossus castanotis
Pteroglossus torquatus
Pteroglossus aracari
Pteroglossus beauharnaesii
Pteroglossus bitorquatus
Pteroglossus azara
Pteroglossus mariae
Aulacorhynchus derbianus
Aulacorhynchus prasinus
Andigena hypoglauca
Andigena laminirostris
Selenidera spectabilis
Selenidera culik
Selenidera gouldii
Selenidera maculirostris
Selenidera nattereri
Andigena cucullata
Selenidera reinwardtii
Geranopterus alatus
Telophorus bocagei
Myiagra ferrocyanea
Pteruthius xanthochlorus
Eopsaltria flaviventris
Catharus fuscater
Andropadus curvirostris
Pteruthius rufiventer
Catharus mexicanus
Andropadus importunus
Acanthisitta chloris
Xenicus
Suiriri
Myiophobus cryptoxanthus
Pseudocolopteryx
Inezia
Nesotriccus
Pitta baudii
Pitta angolensis
Pitta brachyura
Pitta guajana
Pitta erythrogaster
Pitta versicolor
Pitta iris
Pitta sordida
Sapayoa aenigma
Smithornis capensis
Smithornis rufolateralis
Smithornis sharpei
Calyptomena viridis
Calyptomena whiteheadi
Pseudocalyptomena graueri
Neodrepanis coruscans
Philepitta castanea
Psarisomus dalhousiae
Eurylaimus steerii
Cymbirhynchus macrorhynchos
Serilophus lunatus
Eurylaimus javanicus
Eurylaimus ochromalus
Neopipo cinnamomea
Hirundinea ferruginea
Pyrrhomyias cinnamomea
Tyranneutes stolzmanni
Neopelma aurifrons
Neopelma chrysocephalum
Ilicura militaris
Masius chrysopterus
Corapipo gutturalis
Corapipo leucorrhoa
Chloropipo unicolor
Chloropipo holochlora
Xenopipo atronitens
Xenopipo uniformis
Chloropipo uniformis
Xenopipo holochlora
Xenopipo unicolor
Antilophia galeata
Chiroxiphia linearis
Chiroxiphia pareola
Chiroxiphia caudata
Chiroxiphia lanceolata

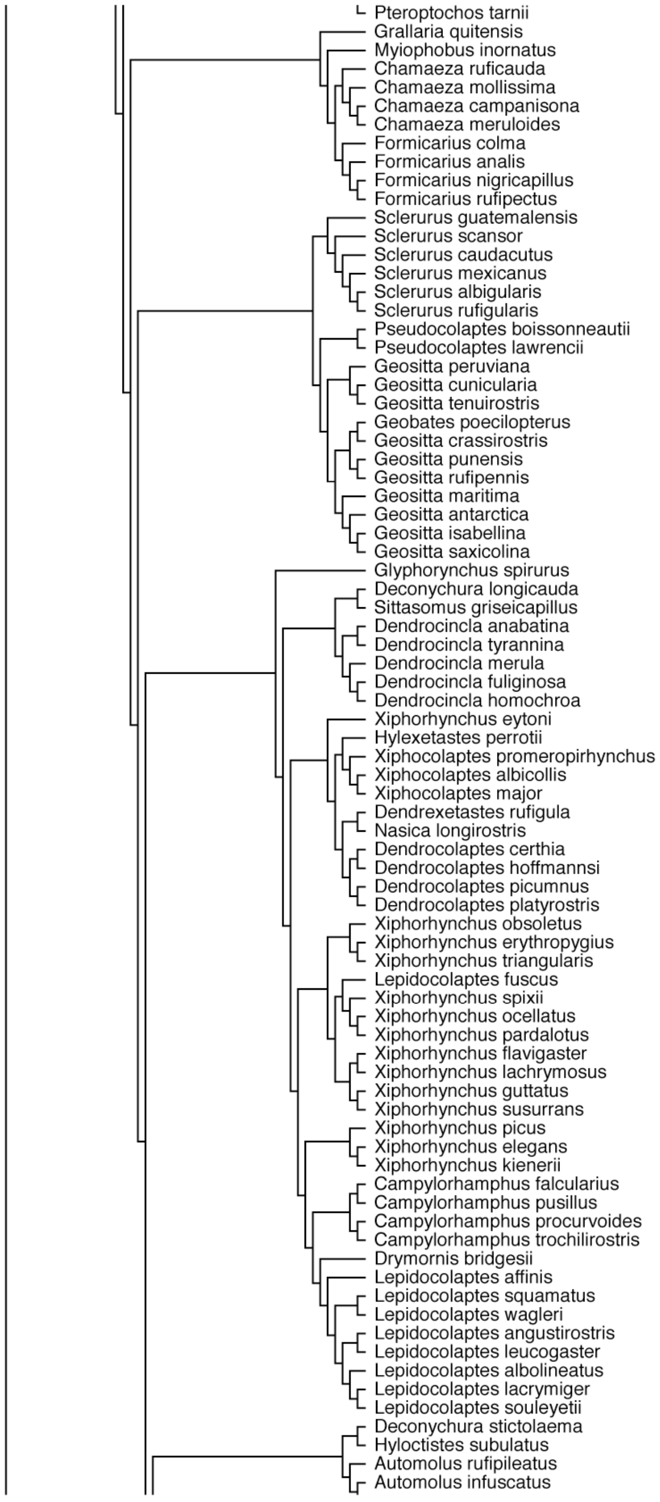

Manacus aurantiacus
Manacus candei
Manacus manacus
Manacus vitellinus
Pipra nattereri
Pipra suavissima
Machaeropterus deliciosus
Machaeropterus pyrocephalus
Machaeropterus regulus
Pipra coronata
Pipra iris
Pipra isidorei
Pipra serena
Pipra pipra
Heterocercus flavivertex
Heterocercus aurantiivertex
Heterocercus linteatus
Pipra filicauda
Pipra aureola
Pipra fasciicauda
Pipra cornuta
Pipra coeruleocapilla
Pipra mentalis
Pipra chloromeros
Pipra erythrocephala
Pipra rubrocapilla
Oxyruncus cristatus
Piprites chloris
Laniisoma elegans
Laniocera hypopyrra
Laniocera rufescens
Schiffornis turdinus
Schiffornis major
Schiffornis virescens
Iodopleura isabellae
Tityra inquisitor
Tityra cayana
Tityra semifasciata
Xenopsaris albinucha
Pachyramphus major
Pachyramphus viridis
Pachyramphus rufus
Pachyramphus validus
Pachyramphus cinnamomeus
Platypsaris
Pachyramphus minor
Pachyramphus polychopterus
Pachyramphus versicolor
Pachyramphus aglaiae
Pachyramphus marginatus
Zaratornis
Ampelion stresemanni
Doliornis sclateri
Ampelion rubrocristata
Ampelion rufaxilla
Phytotoma rutila
Phytotoma raimondii
Phytotoma rara
Carpornis cucullatus
Phoenicircus nigricollis
Rupicola peruviana
Rupicola rupicola
Ampelioides tschudii
Pipreola aureopectus
Pipreola formosa
Pipreola pulchra
Pipreola intermedia
Pipreola riefferii
Pipreola chlorolepidota
Pipreola arcuata
Pipreola frontalis
Cotinga nattererii
Cephalopterus penduliger
Procnias alba
Cotinga cayana
Procnias nudicollis
Procnias tricarunculata
Lipaugus unirufus
Lipaugus fuscocinereus
Lipaugus vociferans

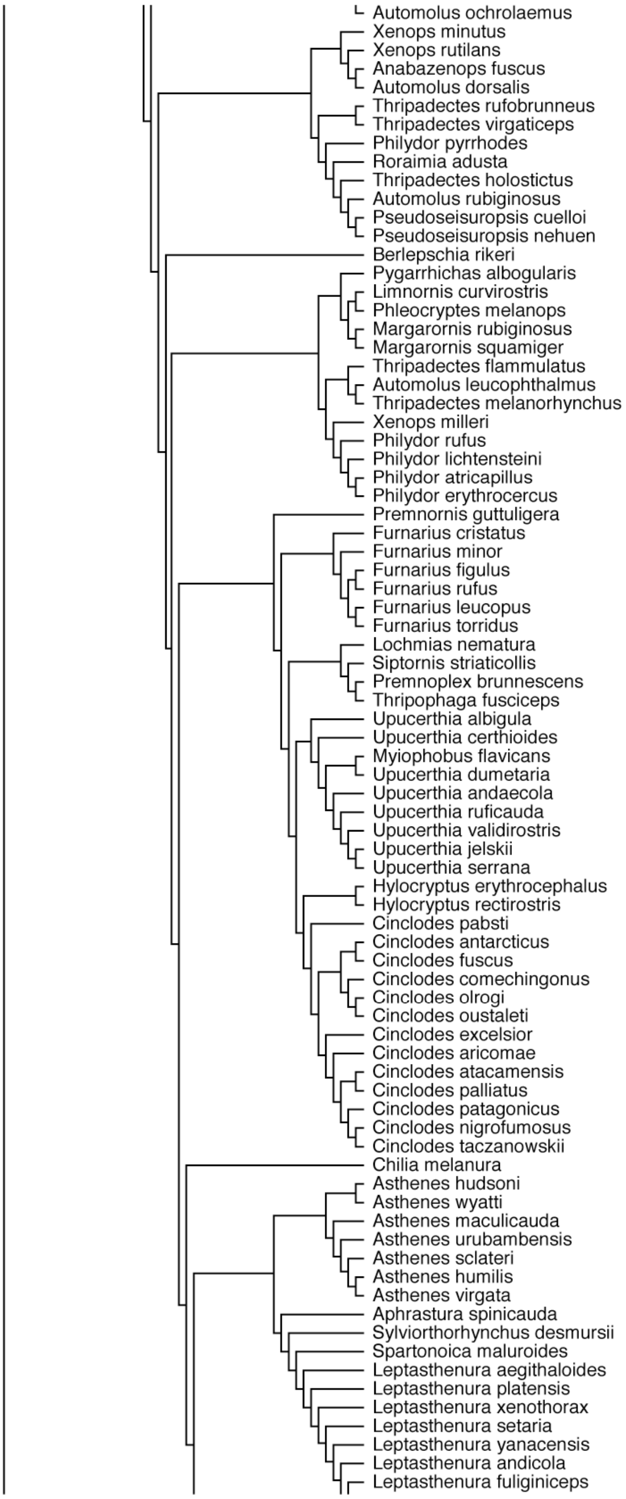

Haematoderus militaris
Querula purpurata
Pyroderus scutatus
Cephalopterus ornatus
Perissocephalus tricolor
Conioptilon mcilhennyi
Porphyrolaema porphyrolaema
Lipaugus cryptolophus
Lipaugus subalaris
Carpodectes hopkei
Xipholena punicea
Cephalopterus glabricollis
Cotinga maynana
Gymnoderus foetidus
Uromyias agilis
Cnipodectes
Onychorhynchus
Myiobius erythrurus
Myiobius barbatus
Myiobius atricaudus
Myiobius villosus
Ornithion
Terenotriccus erythrurus
Phylloscartes orbitalis
Myiophobus lintoni
Todirostrum latirostre
Todirostrum cinereum
Hemitriccus margaritaceiventer
Lophotriccus eulophotes
Lophotriccus vitiosus
Oncostoma
Corythopis delalandi
Corythopis torquata
Pseudotriccus pelzelni
Myiophobus ochraceiventris
Myiotriccus
Mionectes oleagineus
Mionectes olivaceus
Mionectes striaticollis
Mionectes macconnelli
Phyllomyias plumbeiceps
Leptopogon amaurocephalus
Leptopogon superciliaris
Leptopogon rufipectus
Leptopogon taczanowskii
Serpophaga
Anairetes nigrocristatus
Anairetes reguloides
Anairetes alpinus
Anairetes flavirostris
Anairetes fernandezianus
Anairetes parulus
Euscarthmus meloryphus
Camptostoma obsoletum
Elaenia martinica
Myiopagis viridicata
Tyrannulus
Phaeomyias
Zygodactylidae
Mecocerculus stictopterus
Capsiempis flaveola
Mecocerculus leucophrys
Elaenia flavogaster
Elaenia chiriquensis
Elaenia albiceps
Elaenia frantzii
Mecocerculus hellmayri
Mecocerculus calopterus
Mecocerculus minor
Mecocerculus poecilocercus
Primozygodactylus danielsi
Rhynchocyclus brevirostris
Tolmomyias
Phelpsia
Tyrannus dominicensis
Tyrannus melancholicus
Tyrannus tyrannus
Tyrannus caudifasciatus
Empidonomus
Griseotyrannus

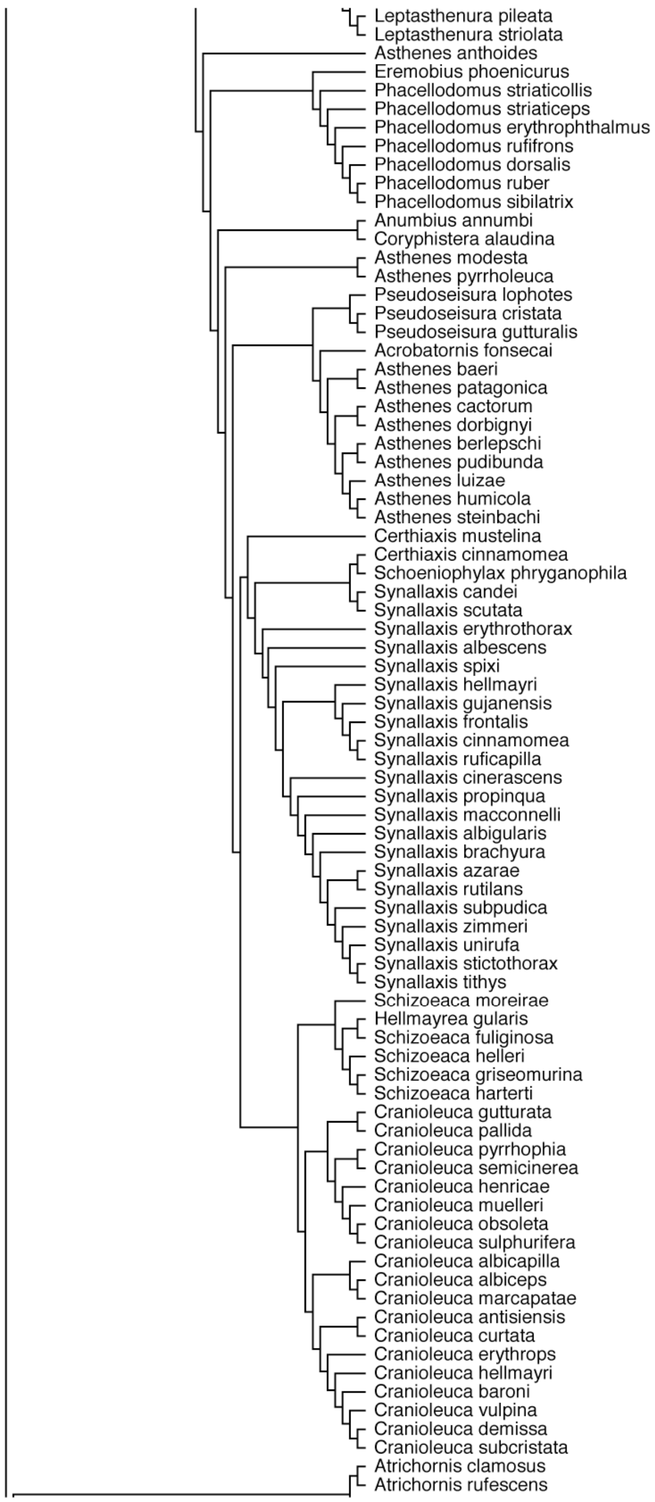

Tyrannus savana
Conopias
Myiodynastes
Philohydor
Pitangus sulphuratus
Attila
Legatus
Myiozetetes similis
Megarynchus
Tyrannopsis
Casiornis
Rhytipterna immunda
Myiarchus nuttingi
Myiarchus apicalis
Myiarchus semirufus
Myiarchus swainsoni
Myiarchus barbirostris
Myiarchus tuberculifer
Myiarchus cephalotes
Myiarchus phaeocephalus
Myiarchus panamensis
Myiarchus ferox
Myiarchus venezuelensis
Myiarchus validus
Myiarchus sagrae
Myiarchus stolidus
Myiarchus antillarum
Myiarchus oberi
Sirystes
Myiarchus yucatanensis
Myiarchus crinitus
Myiarchus cinerascens
Myiarchus tyrannulus
Colonia colonus
Sublegatus
Machetornis
Muscigralla brevicauda
Myiophobus phoenicomitra
Myiophobus roraimae
Muscisaxicola fluviatilis
Muscisaxicola maculirostris
Muscisaxicola alpina
Muscisaxicola albilora
Muscisaxicola macloviana
Muscisaxicola capistrata
Muscisaxicola frontalis
Neoxolmis
Muscisaxicola juninensis
Muscisaxicola flavinucha
Muscisaxicola albifrons
Muscivora tyrannus
Muscisaxicola rufivertex
Muscisaxicola cinerea
Ochthornis
Fluvicola nengeta
Fluvicola pica
Pyrocephalus rubinus
Alectrurus
Lessonia rufa
Gubernetes yetapa
Muscipipra
Xolmis irupero
Arundinicola
Knipolegus aterrimus
Knipolegus nigerrimus
Satrapa
Agriornis montana
Myiotheretes
Cnemarchus
Polioxolmis
Ochthoeca salvini
Colorhamphus
Ochthoeca fumicolor
Ochthoeca leucophrys
Ochthoeca oenanthoides
Ochthoeca rufipectoralis
Ochthoeca cinnamomeiventris
Silvicultrix frontalis
Silvicultrix pulchella
Silvicultrix diadema

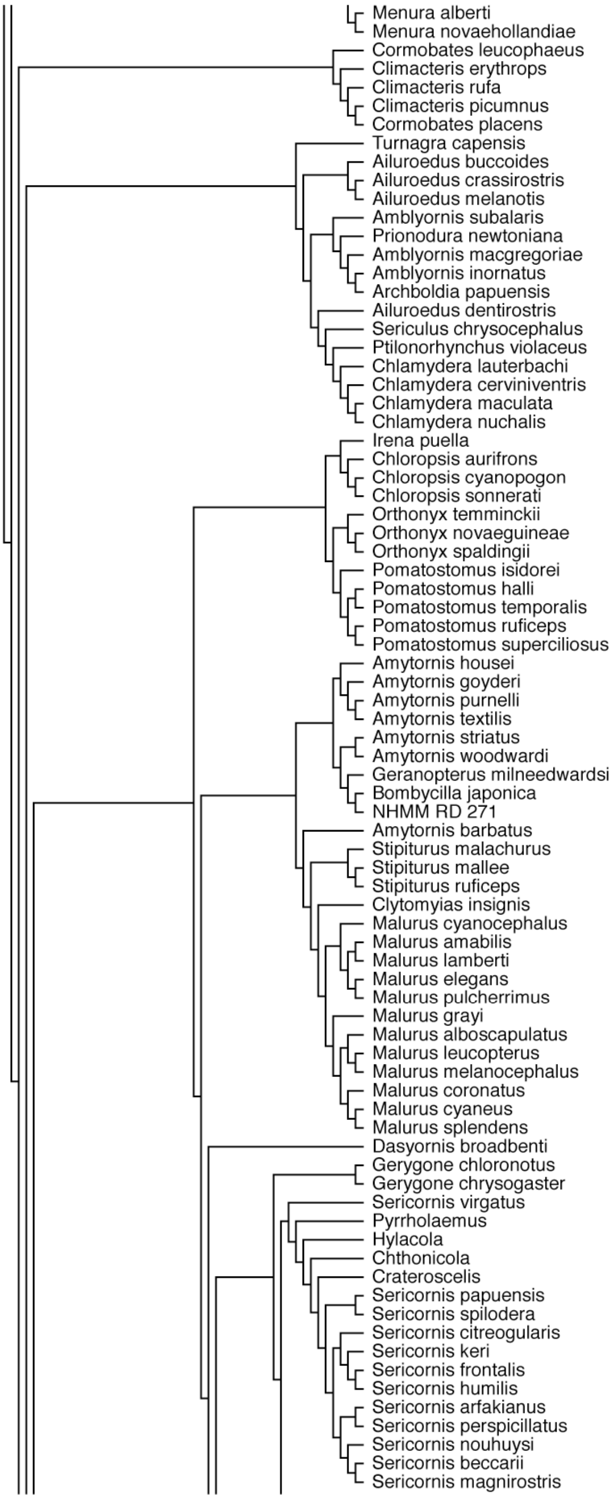

Silvicultrix jelskii
Cnemotriccus fuscatus
Empidonax euleri
Aphanotriccus audax
Lathrotriccus euleri
Contopus borealis
Contopus cooperi
Contopus sordidulus
Contopus virens
Empidonax difficilis
Empidonax flavescens
Empidonax wrightii
Empidonax flaviventris
Empidonax hammondii
Empidonax atriceps
Empidonax oberholseri
Empidonax minimus
Empidonax virescens
Empidonax alnorum
Empidonax traillii
Xenotriccus
Mitrephanes olivaceus
Mitrephanes phaeocercus
Sayornis saya
Sayornis phoebe
Xolmis pyrope
Sayornis nigricans
Heteroxolmis
Hymenops
Myiophobus pulcher
Myiophobus fasciatus
Melanopareia maximiliani
Melanopareia torquata
Platyrinchus
Conopophaga aurita
Conopophaga lineata
Conopophaga peruviana
Pittasoma michleri
Conopophaga castaneiceps
Pittasoma rufopileatum
Terenura humeralis
Hylophylax poecilonota
Myrmornis torquata
Pygiptila stellaris
Thamnistes anabatinus
Dysithamnus mentalis
Herpsilochmus atricapillus
Thamnophilus doliatus
Sakesphorus bernardi
Thamnophilus nigrocinereus
Thamnophilus praecox
Thamnophilus schistaceus
Thamnophilus cryptoleucus
Thamnophilus caerulescens
Thamnophilus unicolor
Megastictus margaritatus
Thamnomanes caesius
Dichrozona cincta
Drymophila caudata
Taraba major
Batara cinerea
Hypoedaleus guttatus
Frederickena unduligera
Drymophila devillei
Mackenziaena severa
Frederickena viridis
Pyriglena leucoptera
Myrmotherula assimilis
Myrmotherula hauxwelli
Poecilotriccus
Microrhopias quixensis
Myrmorchilus strigilatus
Neoctantes niger
Myrmotherula ornata
Myrmotherula haematonota
Myrmotherula erythrura
Myrmotherula fulviventris
Myrmotherula leucophthalma
Myrmotherula longicauda
Myrmochanes hemileucus

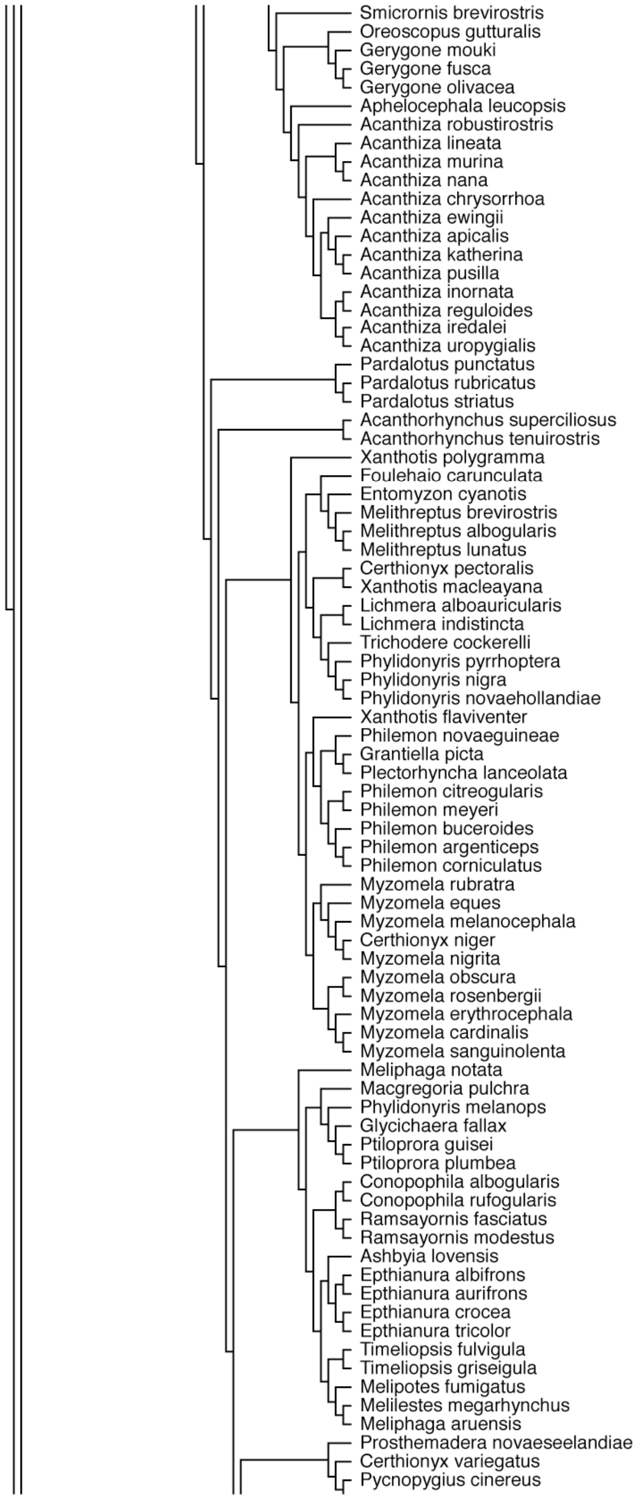

Myrmotherula surinamensis
Myrmotherula sclateri
Myrmotherula brachyura
Conopophaga ardesiaca
Myrmotherula obscura
Myrmotherula axillaris
Formicivora grisea
Formicivora rufa
Myrmotherula longipennis
Myrmotherula menetriesii
Myrmotherula schisticolor
Myrmotherula grisea
Myrmotherula behni
Thamnophilus ruficapillus
Percnostola leucostigma
Sclateria naevia
Gymnocichla nudiceps
Myrmeciza fortis
Pyriglena leuconota
Myrmoborus myotherinus
Phlegopsis nigromaculata
Stigmatura napensis
Pseudelaenia
Myrmeciza berlepschi
Myrmeciza griseiceps
Myrmeciza loricata
Hypocnemoides maculicauda
Herpsilochmus rufimarginatus
Hylophylax naevia
Cercomacra melanaria
Tachuris
Hypocnemis cantator
Myrmeciza hemimelaena
Phyllomyias fasciatus
Drymophila squamata
Phyllomyias griseiceps
Phlegopsis erythroptera
Pithys albifrons
Hypocnemis hypoxantha
Phaenostictus mcleannani
Rhegmatorhina melanosticta
Gymnopithys leucaspis
Gymnopithys rufigula
Gymnopithys lunulata
Gymnopithys salvini
Grallaricula flavirostris
Grallaricula lineifrons
Hylopezus berlepschi
Hylopezus fulviventris
Myrmothera campanisona
Grallaricula nana
Myrmothera simplex
Zimmerius
Grallaria guatimalensis
Grallaria squamigera
Grallaria varia
Grallaria blakei
Grallaria rufula
Grallaria dignissima
Grallaria eludens
Grallaria hypoleuca
Grallaria nuchalis
Grallaria ridgelyi
Grallaria ruficapilla
Grallaria watkinsi
Myornis senilis
Deltarhynchus
Ramphotrigon
Scytalopus schulenbergi
Scytalopus simonsi
Scytalopus magellanicus
Scytalopus parvirostris
Liosceles thoracicus
Scytalopus femoralis
Scytalopus latebricola
Rhinocrypta lanceolata
Scelorchilus rubecula
Pteroptochos castaneus
Scytalopus spillmanni
Pteroptochos megapodius

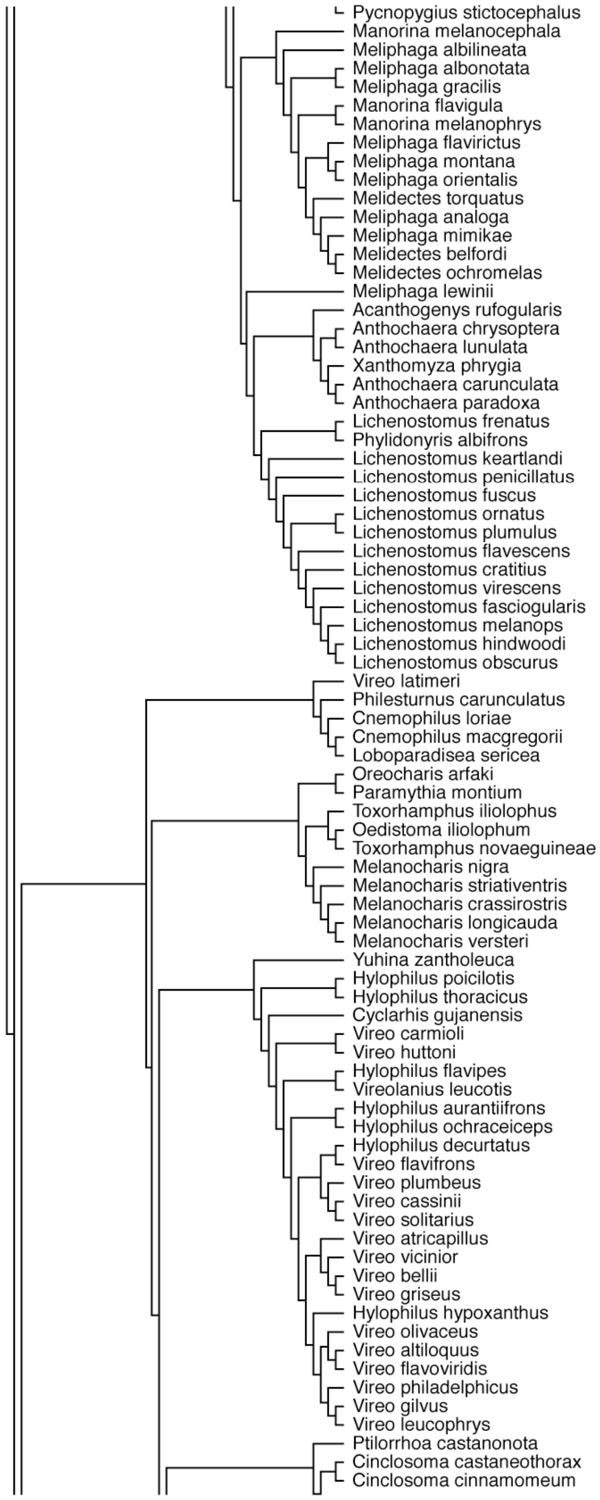

Pteroptochos tarnii
Grallaria quitensis
Myiophobus inornatus
Chamaeza ruficauda
Chamaeza mollissima
Chamaeza campanisona
Chamaeza meruloides
Formicarius colma
Formicarius analis
Formicarius nigricapillus
Formicarius rufipectus
Sclerurus guatemalensis
Sclerurus scansor
Sclerurus caudacutus
Sclerurus mexicanus
Sclerurus albigularis
Sclerurus rufigularis
Pseudocolaptes boissonneautii
Pseudocolaptes lawrencii
Geositta peruviana
Geositta cunicularia
Geositta tenuirostris
Geobates poecilopterus
Geositta crassirostris
Geositta punensis
Geositta rufipennis
Geositta maritima
Geositta antarctica
Geositta isabellina
Geositta saxicolina
Glyphorynchus spirurus
Deconychura longicauda
Sittasomus griseicapillus
Dendrocincla anabatina
Dendrocincla tyrannina
Dendrocincla merula
Dendrocincla fuliginosa
Dendrocincla homochroa
Xiphorhynchus eytoni
Hylexetastes perrotii
Xiphocolaptes promeropirhynchus
Xiphocolaptes albicollis
Xiphocolaptes major
Dendrexetastes rufigula
Nasica longirostris
Dendrocolaptes certhia
Dendrocolaptes hoffmannsi
Dendrocolaptes picumnus
Dendrocolaptes platyrostris
Xiphorhynchus obsoletus
Xiphorhynchus erythropygius
Xiphorhynchus triangularis
Lepidocolaptes fuscus
Xiphorhynchus spixii
Xiphorhynchus ocellatus
Xiphorhynchus pardalotus
Xiphorhynchus flavigaster
Xiphorhynchus lachrymosus
Xiphorhynchus guttatus
Xiphorhynchus susurrans
Xiphorhynchus picus
Xiphorhynchus elegans
Xiphorhynchus kienerii
Campylorhamphus falcularius
Campylorhamphus pusillus
Campylorhamphus procurvoides
Campylorhamphus trochilirostris
Drymornis bridgesii
Lepidocolaptes affinis
Lepidocolaptes squamatus
Lepidocolaptes wagleri
Lepidocolaptes angustirostris
Lepidocolaptes leucogaster
Lepidocolaptes albolineatus
Lepidocolaptes lacrymiger
Lepidocolaptes souleyetii
Deconychura stictolaema
Hyloctistes subulatus
Automolus rufipileatus
Automolus infuscatus

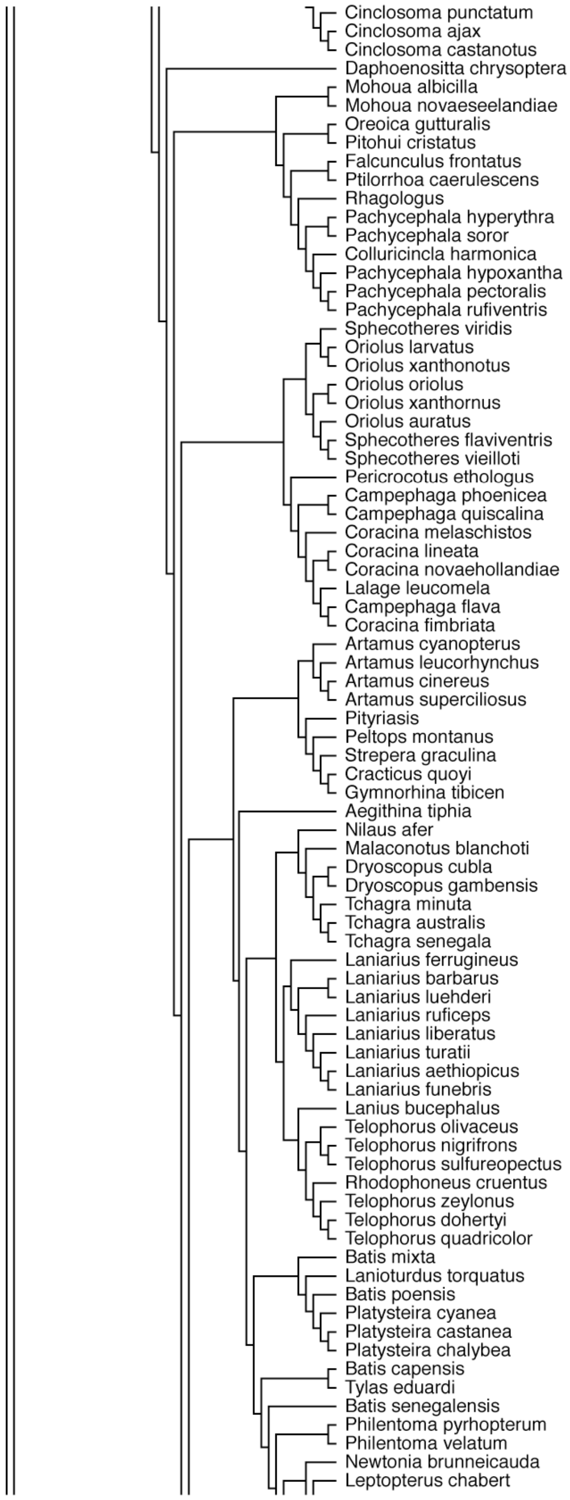

Automolus ochrolaemus
Xenops minutus
Xenops rutilans
Anabazenops fuscus
Automolus dorsalis
Thripadectes rufobrunneus
Thripadectes virgaticeps
Philydor pyrrhodes
Roraimia adusta
Thripadectes holostictus
Automolus rubiginosus
Pseudoseisuropsis cuelloi
Pseudoseisuropsis nehuen
Berlepschia rikeri
Pygarrhichas albogularis
Limnornis curvirostris
Phleocryptes melanops
Margarornis rubiginosus
Margarornis squamiger
Thripadectes flammulatus
Automolus leucophthalmus
Thripadectes melanorhynchus
Xenops milleri
Philydor rufus
Philydor lichtensteini
Philydor atricapillus
Philydor erythrocercus
Premnornis guttuligera
Furnarius cristatus
Furnarius minor
Furnarius figulus
Furnarius rufus
Furnarius leucopus
Furnarius torridus
Lochmias nematura
Siptornis striaticollis
Premnoplex brunnescens
Thripophaga fusciceps
Upucerthia albigula
Upucerthia certhioides
Myiophobus flavicans
Upucerthia dumetaria
Upucerthia andaecola
Upucerthia ruficauda
Upucerthia validirostris
Upucerthia jelskii
Upucerthia serrana
Hylocryptus erythrocephalus
Hylocryptus rectirostris
Cinclodes pabsti
Cinclodes antarcticus
Cinclodes fuscus
Cinclodes comechingonus
Cinclodes olrogi
Cinclodes oustaleti
Cinclodes excelsior
Cinclodes aricomae
Cinclodes atacamensis
Cinclodes palliatus
Cinclodes patagonicus
Cinclodes nigrofumosus
Cinclodes taczanowskii
Chilia melanura
Asthenes hudsoni
Asthenes wyatti
Asthenes maculicauda
Asthenes urubambensis
Asthenes sclateri
Asthenes humilis
Asthenes virgata
Aphrastura spinicauda
Sylviorthorhynchus desmursii
Spartonoica maluroides
Leptasthenura aegithaloides
Leptasthenura platensis
Leptasthenura xenothorax
Leptasthenura setaria
Leptasthenura yanacensis
Leptasthenura andicola
Leptasthenura fuliginiceps

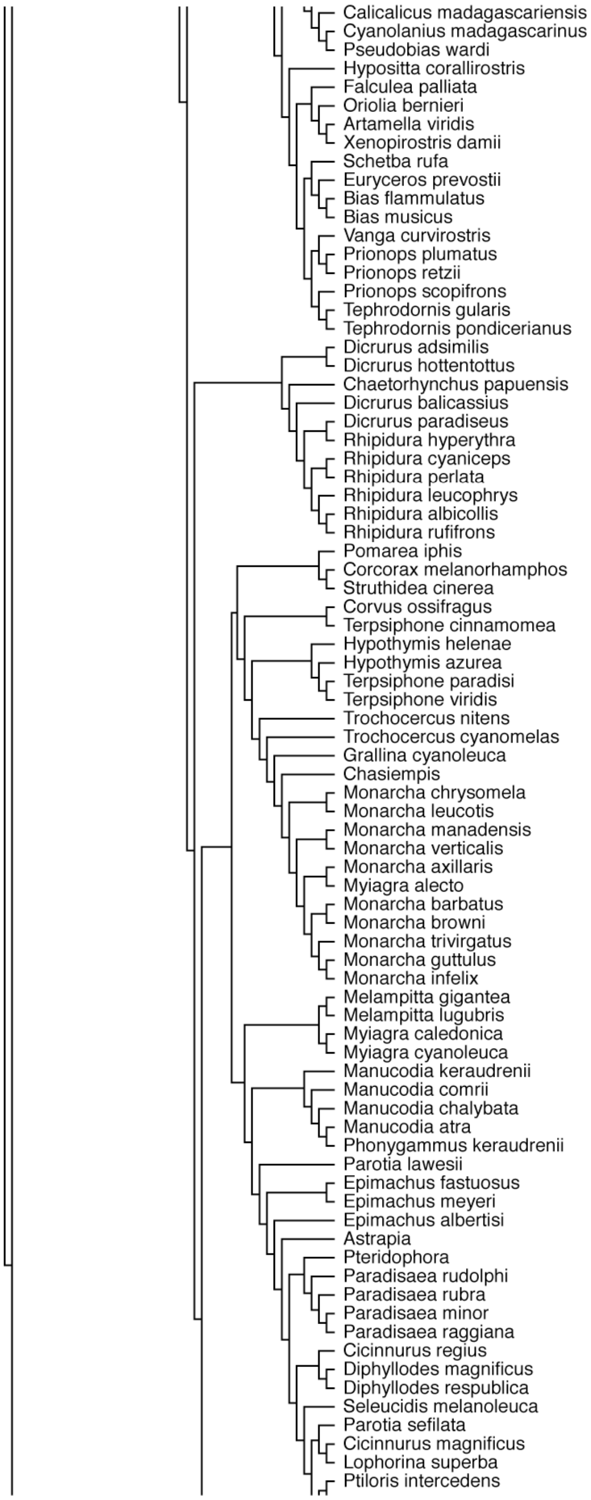

Leptasthenura pileata
Leptasthenura striolata
Asthenes anthoides
Eremobius phoenicurus
Phacellodomus striaticollis
Phacellodomus striaticeps
Phacellodomus erythrophthalmus
Phacellodomus rufifrons
Phacellodomus dorsalis
Phacellodomus ruber
Phacellodomus sibilatrix
Anumbius annumbi
Coryphistera alaudina
Asthenes modesta
Asthenes pyrrholeuca
Pseudoseisura lophotes
Pseudoseisura cristata
Pseudoseisura gutturalis
Acrobatornis fonsecai
Asthenes baeri
Asthenes patagonica
Asthenes cactorum
Asthenes dorbignyi
Asthenes berlepschi
Asthenes pudibunda
Asthenes luizae
Asthenes humicola
Asthenes steinbachi
Certhiaxis mustelina
Certhiaxis cinnamomea
Schoeniophylax phryganophila
Synallaxis candei
Synallaxis scutata
Synallaxis erythrothorax
Synallaxis albescens
Synallaxis spixi
Synallaxis hellmayri
Synallaxis gujanensis
Synallaxis frontalis
Synallaxis cinnamomea
Synallaxis ruficapilla
Synallaxis cinerascens
Synallaxis propinqua
Synallaxis macconnelli
Synallaxis albigularis
Synallaxis brachyura
Synallaxis azarae
Synallaxis rutilans
Synallaxis subpudica
Synallaxis zimmeri
Synallaxis unirufa
Synallaxis stictothorax
Synallaxis tithys
Schizoeaca moreirae
Hellmayrea gularis
Schizoeaca fuliginosa
Schizoeaca helleri
Schizoeaca griseomurina
Schizoeaca harterti
Cranioleuca gutturata
Cranioleuca pallida
Cranioleuca pyrrhophia
Cranioleuca semicinerea
Cranioleuca henricae
Cranioleuca muelleri
Cranioleuca obsoleta
Cranioleuca sulphurifera
Cranioleuca albicapilla
Cranioleuca albiceps
Cranioleuca marcapatae
Cranioleuca antisiensis
Cranioleuca curtata
Cranioleuca erythrops
Cranioleuca hellmayri
Cranioleuca baroni
Cranioleuca vulpina
Cranioleuca demissa
Cranioleuca subcristata
Atrichornis clamosus
Atrichornis rufescens

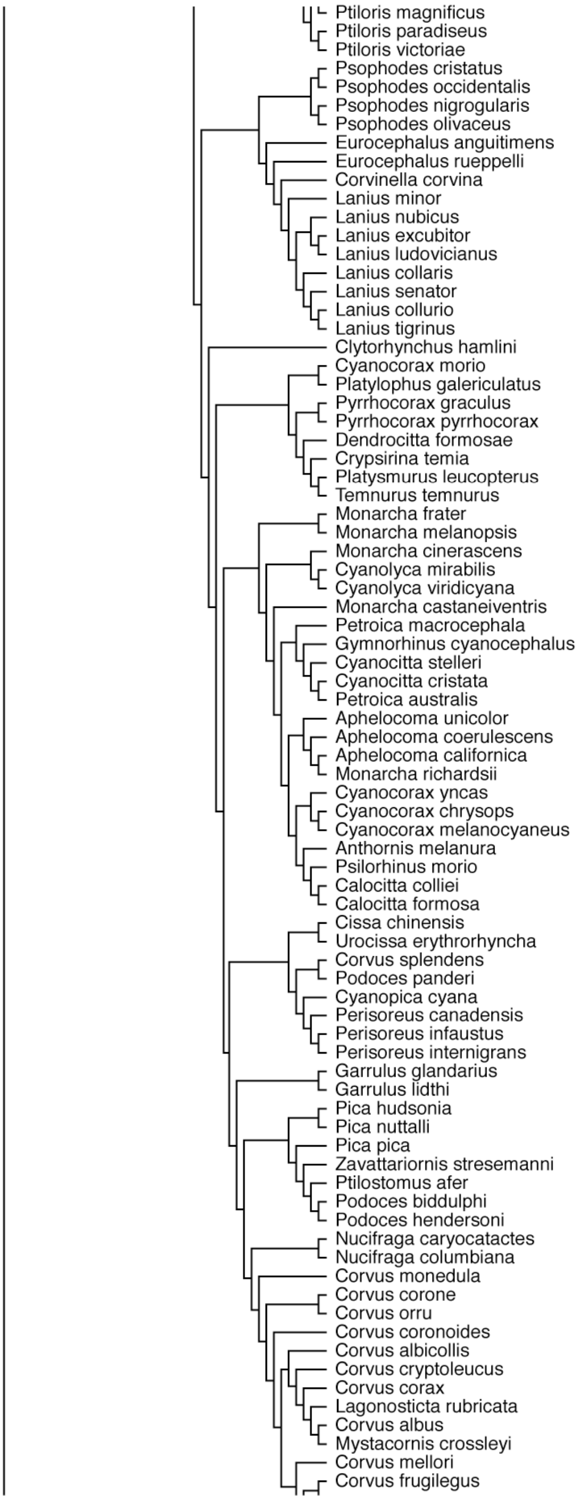

Menura alberti
Menura novaehollandiae
Cormobates leucophaeus
Climacteris erythrops
Climacteris rufa
Climacteris picumnus
Cormobates placens
Turnagra capensis
Ailuroedus buccoides
Ailuroedus crassirostris
Ailuroedus melanotis
Amblyornis subalaris
Prionodura newtoniana
Amblyornis macgregoriae
Amblyornis inornatus
Archboldia papuensis
Ailuroedus dentirostris
Sericulus chrysocephalus
Ptilonorhynchus violaceus
Chlamydera lauterbachi
Chlamydera cerviniventris
Chlamydera maculata
Chlamydera nuchalis
Irena puella
Chloropsis aurifrons
Chloropsis cyanopogon
Chloropsis sonnerati
Orthonyx temminckii
Orthonyx novaeguineae
Orthonyx spaldingii
Pomatostomus isidorei
Pomatostomus halli
Pomatostomus temporalis
Pomatostomus ruficeps
Pomatostomus superciliosus
Amytornis housei
Amytornis goyderi
Amytornis purnelli
Amytornis textilis
Amytornis striatus
Amytornis woodwardi
Geranopterus milneedwardsi
Bombycilla japonica
NHMM RD 271
Amytornis barbatus
Stipiturus malachurus
Stipiturus mallee
Stipiturus ruficeps
Clytomyias insignis
Malurus cyanocephalus
Malurus amabilis
Malurus lamberti
Malurus elegans
Malurus pulcherrimus
Malurus grayi
Malurus alboscapulatus
Malurus leucopterus
Malurus melanocephalus
Malurus coronatus
Malurus cyaneus
Malurus splendens
Dasyornis broadbenti
Gerygone chloronotus
Gerygone chrysogaster
Sericornis virgatus
Pyrrholaemus
Hylacola
Chthonicola
Crateroscelis
Sericornis papuensis
Sericornis spilodera
Sericornis citreogularis
Sericornis keri
Sericornis frontalis
Sericornis humilis
Sericornis arfakianus
Sericornis perspicillatus
Sericornis nouhuysi
Sericornis beccarii
Sericornis magnirostris

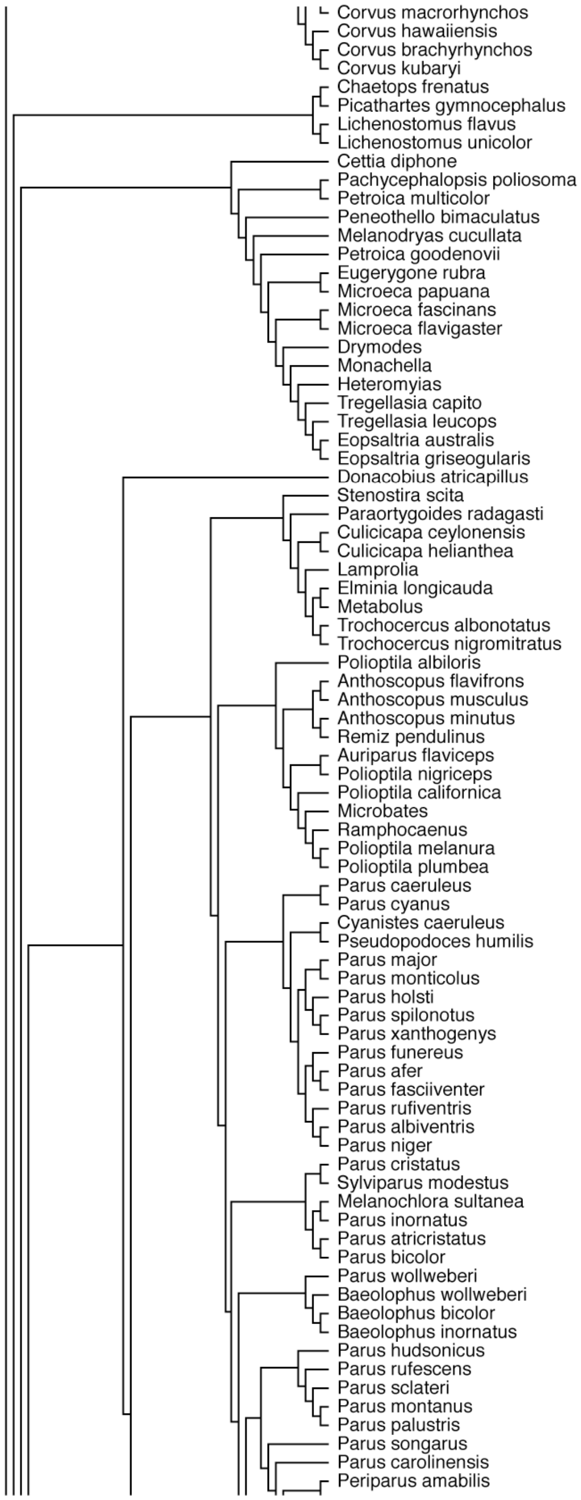

Smicrornis brevirostris
Oreoscopus gutturalis
Gerygone mouki
Gerygone fusca
Gerygone olivacea
Aphelocephala leucopsis
Acanthiza robustirostris
Acanthiza lineata
Acanthiza murina
Acanthiza nana
Acanthiza chrysorrhoa
Acanthiza ewingii
Acanthiza apicalis
Acanthiza katherina
Acanthiza pusilla
Acanthiza inornata
Acanthiza reguloides
Acanthiza iredalei
Acanthiza uropygialis
Pardalotus punctatus
Pardalotus rubricatus
Pardalotus striatus
Acanthorhynchus superciliosus
Acanthorhynchus tenuirostris
Xanthotis polygramma
Foulehaio carunculata
Entomyzon cyanotis
Melithreptus brevirostris
Melithreptus albogularis
Melithreptus lunatus
Certhionyx pectoralis
Xanthotis macleayana
Lichmera alboauricularis
Lichmera indistincta
Trichodere cockerelli
Phylidonyris pyrrhoptera
Phylidonyris nigra
Phylidonyris novaehollandiae
Xanthotis flaviventer
Philemon novaeguineae
Grantiella picta
Plectorhyncha lanceolata
Philemon citreogularis
Philemon meyeri
Philemon buceroides
Philemon argenticeps
Philemon corniculatus
Myzomela rubratra
Myzomela eques
Myzomela melanocephala
Certhionyx niger
Myzomela nigrita
Myzomela obscura
Myzomela rosenbergii
Myzomela erythrocephala
Myzomela cardinalis
Myzomela sanguinolenta
Meliphaga notata
Macgregoria pulchra
Phylidonyris melanops
Glycichaera fallax
Ptiloprora guisei
Ptiloprora plumbea
Conopophila albogularis
Conopophila rufogularis
Ramsayornis fasciatus
Ramsayornis modestus
Ashbyia lovensis
Epthianura albifrons
Epthianura aurifrons
Epthianura crocea
Epthianura tricolor
Timeliopsis fulvigula
Timeliopsis griseigula
Melipotes fumigatus
Melilestes megarhynchus
Meliphaga aruensis
Prosthemadera novaeseelandiae
Certhionyx variegatus
Pycnopygius cinereus

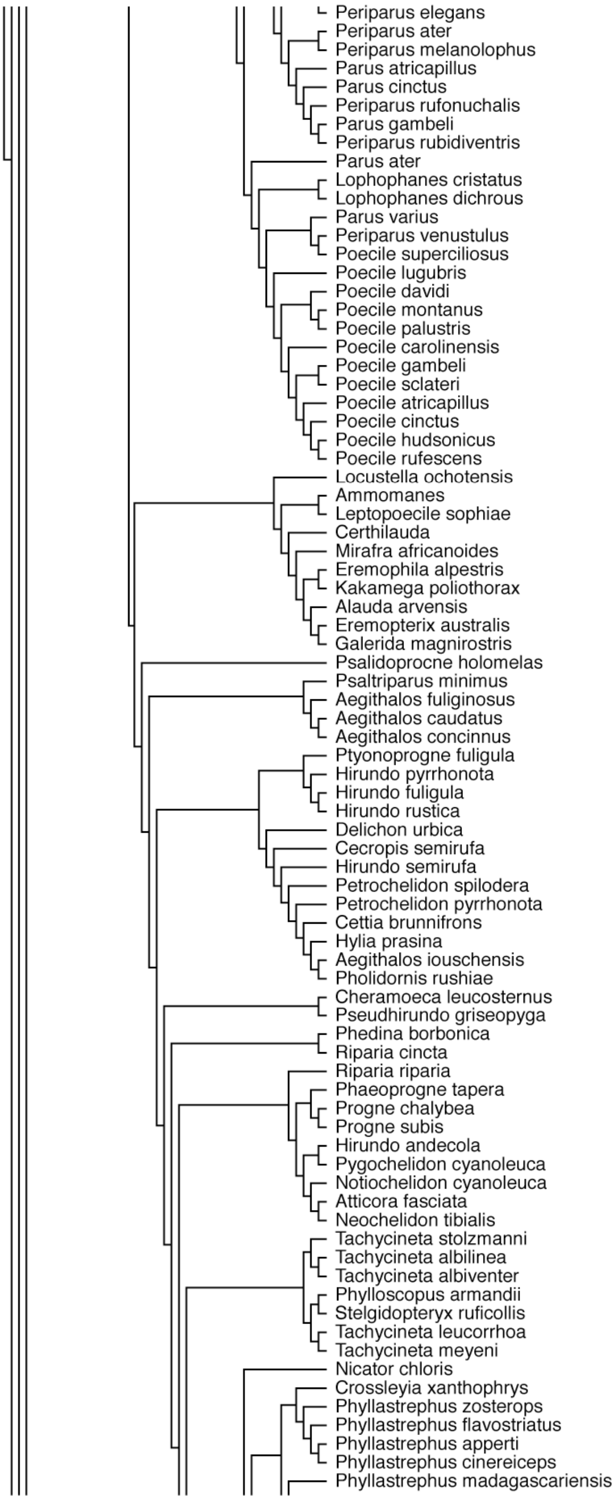

Pycnopygius stictocephalus
Manorina melanocephala
Meliphaga albilineata
Meliphaga albonotata
Meliphaga gracilis
Manorina flavigula
Manorina melanophrys
Meliphaga flavirictus
Meliphaga montana
Meliphaga orientalis
Melidectes torquatus
Meliphaga analoga
Meliphaga mimikae
Melidectes belfordi
Melidectes ochromelas
Meliphaga lewinii
Acanthogenys rufogularis
Anthochaera chrysoptera
Anthochaera lunulata
Xanthomyza phrygia
Anthochaera carunculata
Anthochaera paradoxa
Lichenostomus frenatus
Phylidonyris albifrons
Lichenostomus keartlandi
Lichenostomus penicillatus
Lichenostomus fuscus
Lichenostomus ornatus
Lichenostomus plumulus
Lichenostomus flavescens
Lichenostomus cratitius
Lichenostomus virescens
Lichenostomus fasciogularis
Lichenostomus melanops
Lichenostomus hindwoodi
Lichenostomus obscurus
Vireo latimeri
Philesturnus carunculatus
Cnemophilus loriae
Cnemophilus macgregorii
Loboparadisea sericea
Oreocharis arfaki
Paramythia montium
Toxorhamphus iliolophus
Oedistoma iliolophum
Toxorhamphus novaeguineae
Melanocharis nigra
Melanocharis striativentris
Melanocharis crassirostris
Melanocharis longicauda
Melanocharis versteri
Yuhina zantholeuca
Hylophilus poicilotis
Hylophilus thoracicus
Cyclarhis gujanensis
Vireo carmioli
Vireo huttoni
Hylophilus flavipes
Vireolanius leucotis
Hylophilus aurantiifrons
Hylophilus ochraceiceps
Hylophilus decurtatus
Vireo flavifrons
Vireo plumbeus
Vireo cassinii
Vireo solitarius
Vireo atricapillus
Vireo vicinior
Vireo bellii
Vireo griseus
Hylophilus hypoxanthus
Vireo olivaceus
Vireo altiloquus
Vireo flavoviridis
Vireo philadelphicus
Vireo gilvus
Vireo leucophrys
Ptilorrhoa castanonota
Cinclosoma castaneothorax
Cinclosoma cinnamomeum

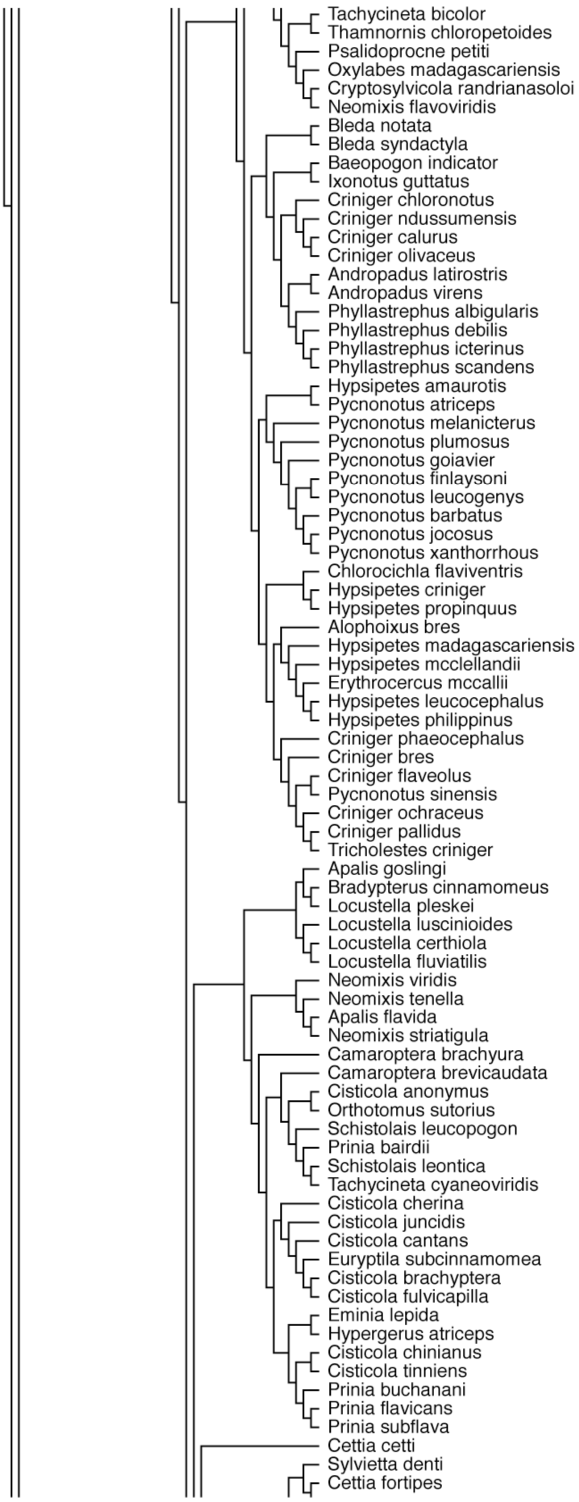

Cinclosoma punctatum
Cinclosoma ajax
Cinclosoma castanotus
Daphoenositta chrysoptera
Mohoua albicilla
Mohoua novaeseelandiae
Oreoica gutturalis
Pitohui cristatus
Falcunculus frontatus
Ptilorrhoa caerulescens
Rhagologus
Pachycephala hyperythra
Pachycephala soror
Colluricincla harmonica
Pachycephala hypoxantha
Pachycephala pectoralis
Pachycephala rufiventris
Sphecotheres viridis
Oriolus larvatus
Oriolus xanthonotus
Oriolus oriolus
Oriolus xanthornus
Oriolus auratus
Sphecotheres flaviventris
Sphecotheres vieilloti
Pericrocotus ethologus
Campephaga phoenicea
Campephaga quiscalina
Coracina melaschistos
Coracina lineata
Coracina novaehollandiae
Lalage leucomela
Campephaga flava
Coracina fimbriata
Artamus cyanopterus
Artamus leucorhynchus
Artamus cinereus
Artamus superciliosus
Pityriasis
Peltops montanus
Strepera graculina
Cracticus quoyi
Gymnorhina tibicen
Aegithina tiphia
Nilaus afer
Malaconotus blanchoti
Dryoscopus cubla
Dryoscopus gambensis
Tchagra minuta
Tchagra australis
Tchagra senegala
Laniarius ferrugineus
Laniarius barbarus
Laniarius luehderi
Laniarius ruficeps
Laniarius liberatus
Laniarius turatii
Laniarius aethiopicus
Laniarius funebris
Lanius bucephalus
Telophorus olivaceus
Telophorus nigrifrons
Telophorus sulfureopectus
Rhodophoneus cruentus
Telophorus zeylonus
Telophorus dohertyi
Telophorus quadricolor
Batis mixta
Lanioturdus torquatus
Batis poensis
Platysteira cyanea
Platysteira castanea
Platysteira chalybea
Batis capensis
Tylas eduardi
Batis senegalensis
Philentoma pyrhopterum
Philentoma velatum
Newtonia brunneicauda
Leptopterus chabert

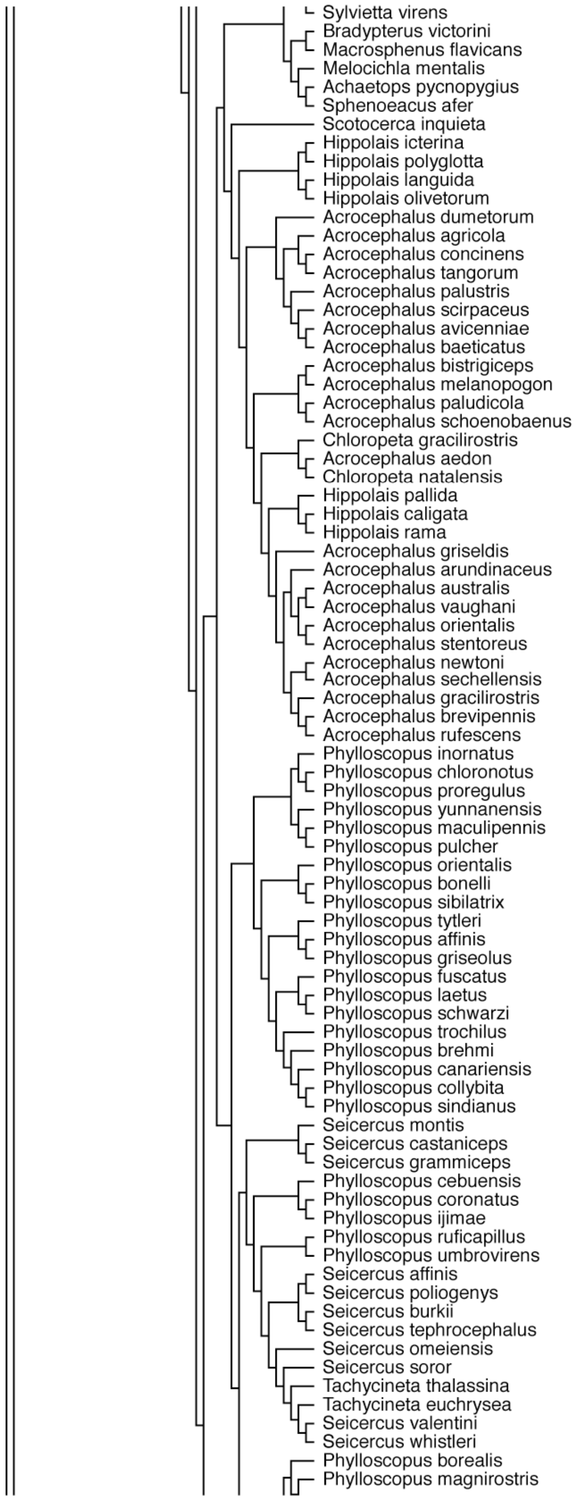

Calicalicus madagascariensis
Cyanolanius madagascarinus
Pseudobias wardi
Hypositta corallirostris
Falculea palliata
Oriolia bernieri
Artamella viridis
Xenopirostris damii
Schetba rufa
Euryceros prevostii
Bias flammulatus
Bias musicus
Vanga curvirostris
Prionops plumatus
Prionops retzii
Prionops scopifrons
Tephrodornis gularis
Tephrodornis pondicerianus
Dicrurus adsimilis
Dicrurus hottentottus
Chaetorhynchus papuensis
Dicrurus balicassius
Dicrurus paradiseus
Rhipidura hyperythra
Rhipidura cyaniceps
Rhipidura perlata
Rhipidura leucophrys
Rhipidura albicollis
Rhipidura rufifrons
Pomarea iphis
Corcorax melanorhamphos
Struthidea cinerea
Corvus ossifragus
Terpsiphone cinnamomea
Hypothymis helenae
Hypothymis azurea
Terpsiphone paradisi
Terpsiphone viridis
Trochocercus nitens
Trochocercus cyanomelas
Grallina cyanoleuca
Chasiempis
Monarcha chrysomela
Monarcha leucotis
Monarcha manadensis
Monarcha verticalis
Monarcha axillaris
Myiagra alecto
Monarcha barbatus
Monarcha browni
Monarcha trivirgatus
Monarcha guttulus
Monarcha infelix
Melampitta gigantea
Melampitta lugubris
Myiagra caledonica
Myiagra cyanoleuca
Manucodia keraudrenii
Manucodia comrii
Manucodia chalybata
Manucodia atra
Phonygammus keraudrenii
Parotia lawesii
Epimachus fastuosus
Epimachus meyeri
Epimachus albertisi
Astrapia
Pteridophora
Paradisaea rudolphi
Paradisaea rubra
Paradisaea minor
Paradisaea raggiana
Cicinnurus regius
Diphyllodes magnificus
Diphyllodes respublica
Seleucidis melanoleuca
Parotia sefilata
Cicinnurus magnificus
Lophorina superba
Ptiloris intercedens

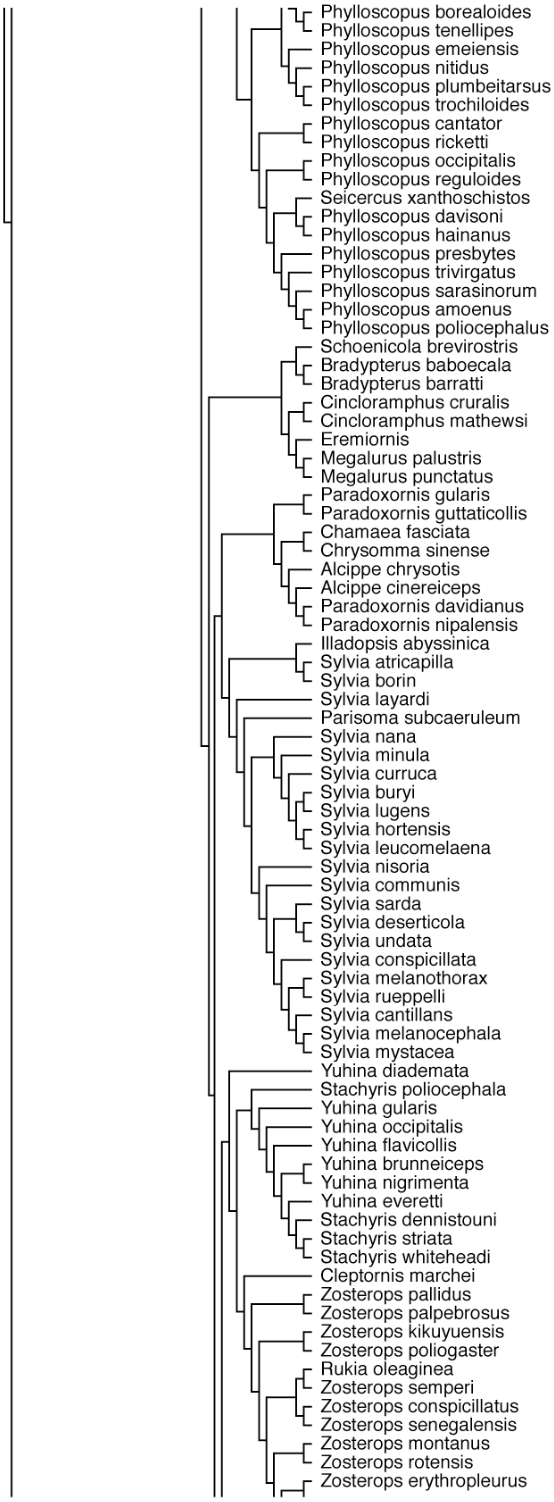

Ptiloris magnificus
Ptiloris paradiseus
Ptiloris victoriae
Psophodes cristatus
Psophodes occidentalis
Psophodes nigrogularis
Psophodes olivaceus
Eurocephalus anguitimens
Eurocephalus rueppelli
Corvinella corvina
Lanius minor
Lanius nubicus
Lanius excubitor
Lanius ludovicianus
Lanius collaris
Lanius senator
Lanius collurio
Lanius tigrinus
Clytorhynchus hamlini
Cyanocorax morio
Platylophus galericulatus
Pyrrhocorax graculus
Pyrrhocorax pyrrhocorax
Dendrocitta formosae
Crypsirina temia
Platysmurus leucopterus
Temnurus temnurus
Monarcha frater
Monarcha melanopsis
Monarcha cinerascens
Cyanolyca mirabilis
Cyanolyca viridicyana
Monarcha castaneiventris
Petroica macrocephala
Gymnorhinus cyanocephalus
Cyanocitta stelleri
Cyanocitta cristata
Petroica australis
Aphelocoma unicolor
Aphelocoma coerulescens
Aphelocoma californica
Monarcha richardsii
Cyanocorax yncas
Cyanocorax chrysops
Cyanocorax melanocyaneus
Anthornis melanura
Psilorhinus morio
Calocitta colliei
Calocitta formosa
Cissa chinensis
Urocissa erythrorhyncha
Corvus splendens
Podoces panderi
Cyanopica cyana
Perisoreus canadensis
Perisoreus infaustus
Perisoreus internigrans
Garrulus glandarius
Garrulus lidthi
Pica hudsonia
Pica nuttalli
Pica pica
Zavattariornis stresemanni
Ptilostomus afer
Podoces biddulphi
Podoces hendersoni
Nucifraga caryocatactes
Nucifraga columbiana
Corvus monedula
Corvus corone
Corvus orru
Corvus coronoides
Corvus albicollis
Corvus cryptoleucus
Corvus corax
Lagonosticta rubricata
Corvus albus
Mystacornis crossleyi
Corvus mellori
Corvus frugilegus

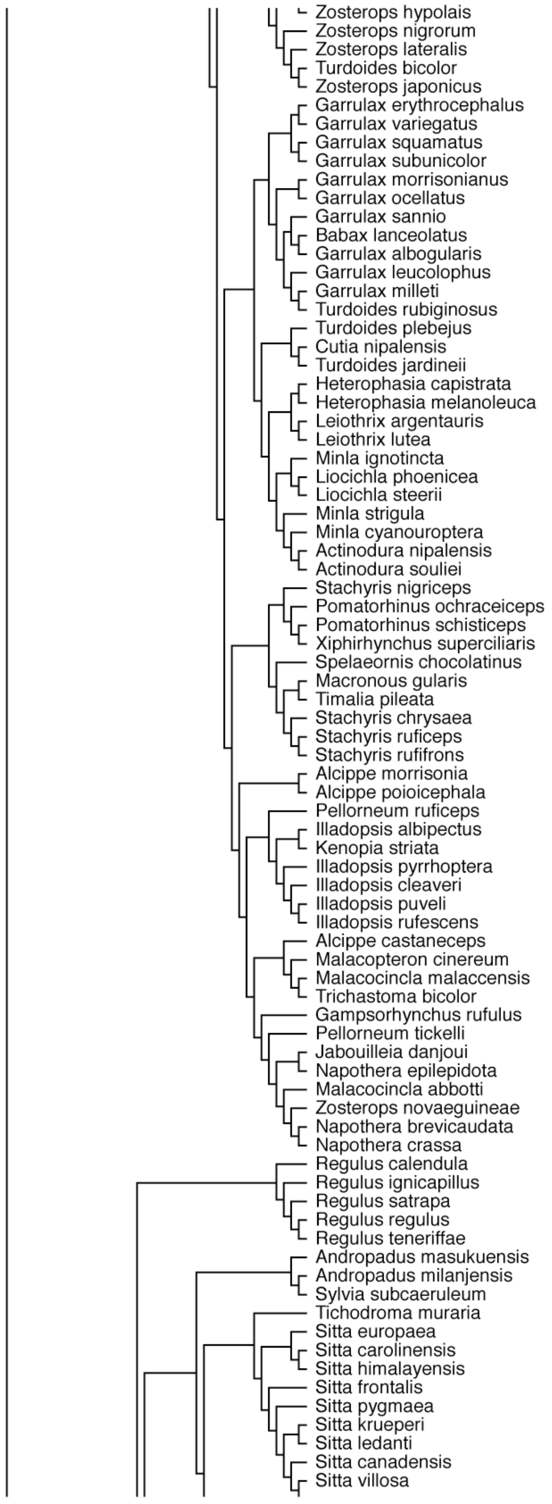

Corvus macrorhynchos
Corvus hawaiiensis
Corvus brachyrhynchos
Corvus kubaryi
Chaetops frenatus
Picathartes gymnocephalus
Lichenostomus flavus
Lichenostomus unicolor
Cettia diphone
Pachycephalopsis poliosoma
Petroica multicolor
Peneothello bimaculatus
Melanodryas cucullata
Petroica goodenovii
Eugerygone rubra
Microeca papuana
Microeca fascinans
Microeca flavigaster
Drymodes
Monachella
Heteromyias
Tregellasia capito
Tregellasia leucops
Eopsaltria australis
Eopsaltria griseogularis
Donacobius atricapillus
Stenostira scita
Paraortygoides radagasti
Culicicapa ceylonensis
Culicicapa helianthea
Lamprolia
Elminia longicauda
Metabolus
Trochocercus albonotatus
Trochocercus nigromitratus
Polioptila albiloris
Anthoscopus flavifrons
Anthoscopus musculus
Anthoscopus minutus
Remiz pendulinus
Auriparus flaviceps
Polioptila nigriceps
Polioptila californica
Microbates
Ramphocaenus
Polioptila melanura
Polioptila plumbea
Parus caeruleus
Parus cyanus
Cyanistes caeruleus
Pseudopodoces humilis
Parus major
Parus monticolus
Parus holsti
Parus spilonotus
Parus xanthogenys
Parus funereus
Parus afer
Parus fasciiventer
Parus rufiventris
Parus albiventris
Parus niger
Parus cristatus
Sylviparus modestus
Melanochlora sultanea
Parus inornatus
Parus atricristatus
Parus bicolor
Parus wollweberi
Baeolophus wollweberi
Baeolophus bicolor
Baeolophus inornatus
Parus hudsonicus
Parus rufescens
Parus sclateri
Parus montanus
Parus palustris
Parus songarus
Parus carolinensis
Periparus amabilis

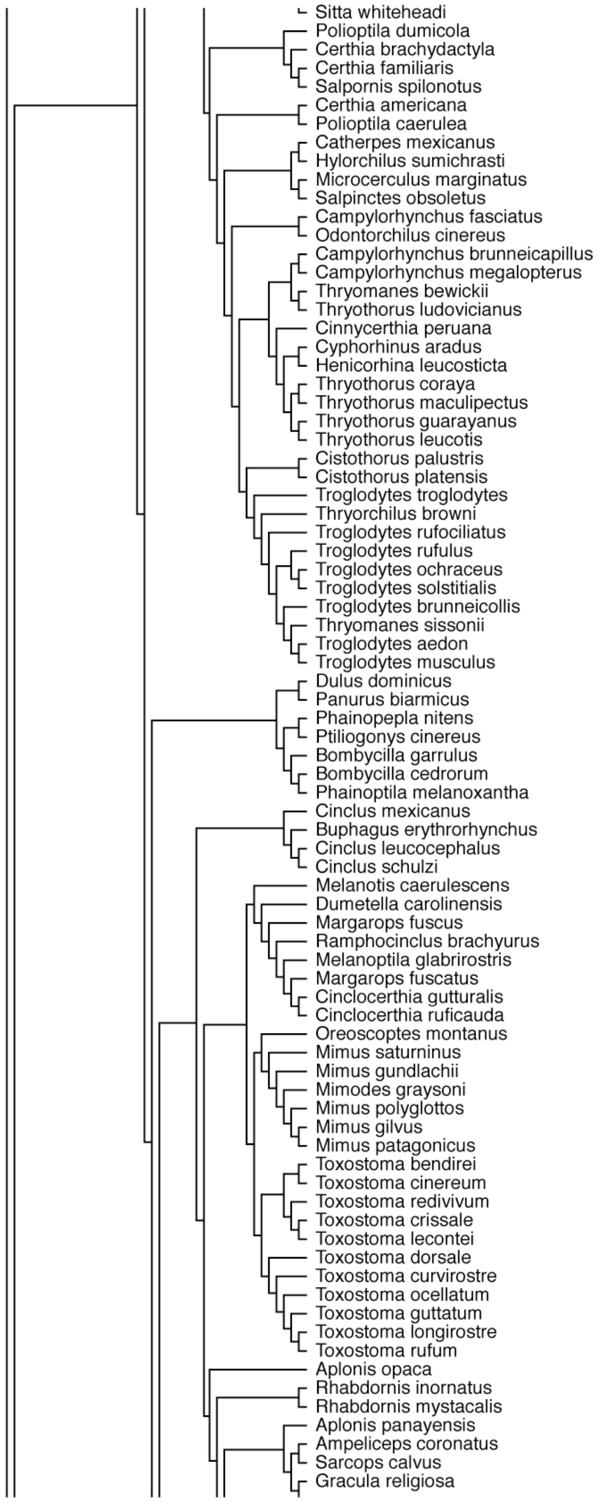

Periparus elegans
Periparus ater
Periparus melanolophus
Parus atricapillus
Parus cinctus
Periparus rufonuchalis
Parus gambeli
Periparus rubidiventris
Parus ater
Lophophanes cristatus
Lophophanes dichrous
Parus varius
Periparus venustulus
Poecile superciliosus
Poecile lugubris
Poecile davidi
Poecile montanus
Poecile palustris
Poecile carolinensis
Poecile gambeli
Poecile sclateri
Poecile atricapillus
Poecile cinctus
Poecile hudsonicus
Poecile rufescens
Locustella ochotensis
Ammomanes
Leptopoecile sophiae
Certhilauda
Mirafra africanoides
Eremophila alpestris
Kakamega poliothorax
Alauda arvensis
Eremopterix australis
Galerida magnirostris
Psalidoprocne holomelas
Psaltriparus minimus
Aegithalos fuliginosus
Aegithalos caudatus
Aegithalos concinnus
Ptyonoprogne fuligula
Hirundo pyrrhonota
Hirundo fuligula
Hirundo rustica
Delichon urbica
Cecropis semirufa
Hirundo semirufa
Petrochelidon spilodera
Petrochelidon pyrrhonota
Cettia brunnifrons
Hylia prasina
Aegithalos iouschensis
Pholidornis rushiae
Cheramoeca leucosternus
Pseudhirundo griseopyga
Phedina borbonica
Riparia cincta
Riparia riparia
Phaeoprogne tapera
Progne chalybea
Progne subis
Hirundo andecola
Pygochelidon cyanoleuca
Notiochelidon cyanoleuca
Atticora fasciata
Neochelidon tibialis
Tachycineta stolzmanni
Tachycineta albilinea
Tachycineta albiventer
Phylloscopus armandii
Stelgidopteryx ruficollis
Tachycineta leucorrhoa
Tachycineta meyeni
Nicator chloris
Crossleyia xanthophrys
Phyllastrephus zosterops
Phyllastrephus flavostriatus
Phyllastrephus apperti
Phyllastrephus cinereiceps
Phyllastrephus madagascariensis

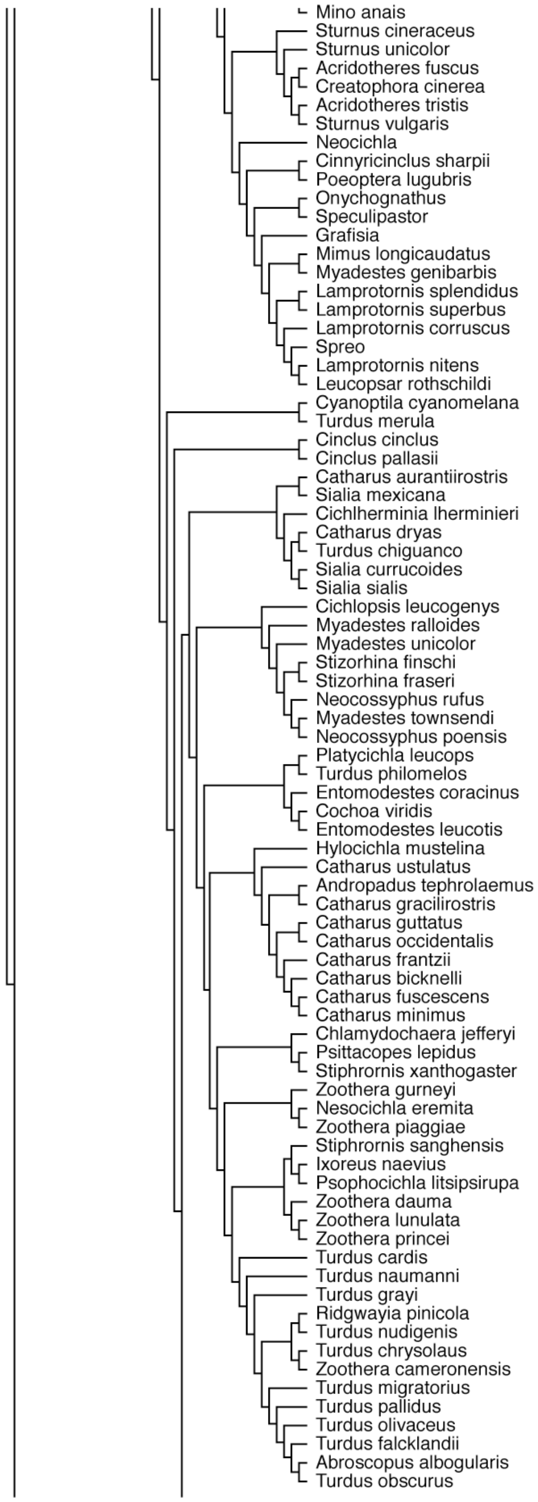

Tachycineta bicolor
Thamnornis chloropetoides
Psalidoprocne petiti
Oxylabes madagascariensis
Cryptosylvicola randrianasoloi
Neomixis flavoviridis
Bleda notata
Bleda syndactyla
Baeopogon indicator
Ixonotus guttatus
Criniger chloronotus
Criniger ndussumensis
Criniger calurus
Criniger olivaceus
Andropadus latirostris
Andropadus virens
Phyllastrephus albigularis
Phyllastrephus debilis
Phyllastrephus icterinus
Phyllastrephus scandens
Hypsipetes amaurotis
Pycnonotus atriceps
Pycnonotus melanicterus
Pycnonotus plumosus
Pycnonotus goiavier
Pycnonotus finlaysoni
Pycnonotus leucogenys
Pycnonotus barbatus
Pycnonotus jocosus
Pycnonotus xanthorrhous
Chlorocichla flaviventris
Hypsipetes criniger
Hypsipetes propinquus
Alophoixus bres
Hypsipetes madagascariensis
Hypsipetes mcclellandii
Erythrocercus mccallii
Hypsipetes leucocephalus
Hypsipetes philippinus
Criniger phaeocephalus
Criniger bres
Criniger flaveolus
Pycnonotus sinensis
Criniger ochraceus
Criniger pallidus
Tricholestes criniger
Apalis goslingi
Bradypterus cinnamomeus
Locustella pleskei
Locustella luscinioides
Locustella certhiola
Locustella fluviatilis
Neomixis viridis
Neomixis tenella
Apalis flavida
Neomixis striatigula
Camaroptera brachyura
Camaroptera brevicaudata
Cisticola anonymus
Orthotomus sutorius
Schistolais leucopogon
Prinia bairdii
Schistolais leontica
Tachycineta cyaneoviridis
Cisticola cherina
Cisticola juncidis
Cisticola cantans
Euryptila subcinnamomea
Cisticola brachyptera
Cisticola fulvicapilla
Eminia lepida
Hypergerus atriceps
Cisticola chinianus
Cisticola tinniens
Prinia buchanani
Prinia flavicans
Prinia subflava
Cettia cetti
Sylvietta denti
Cettia fortipes

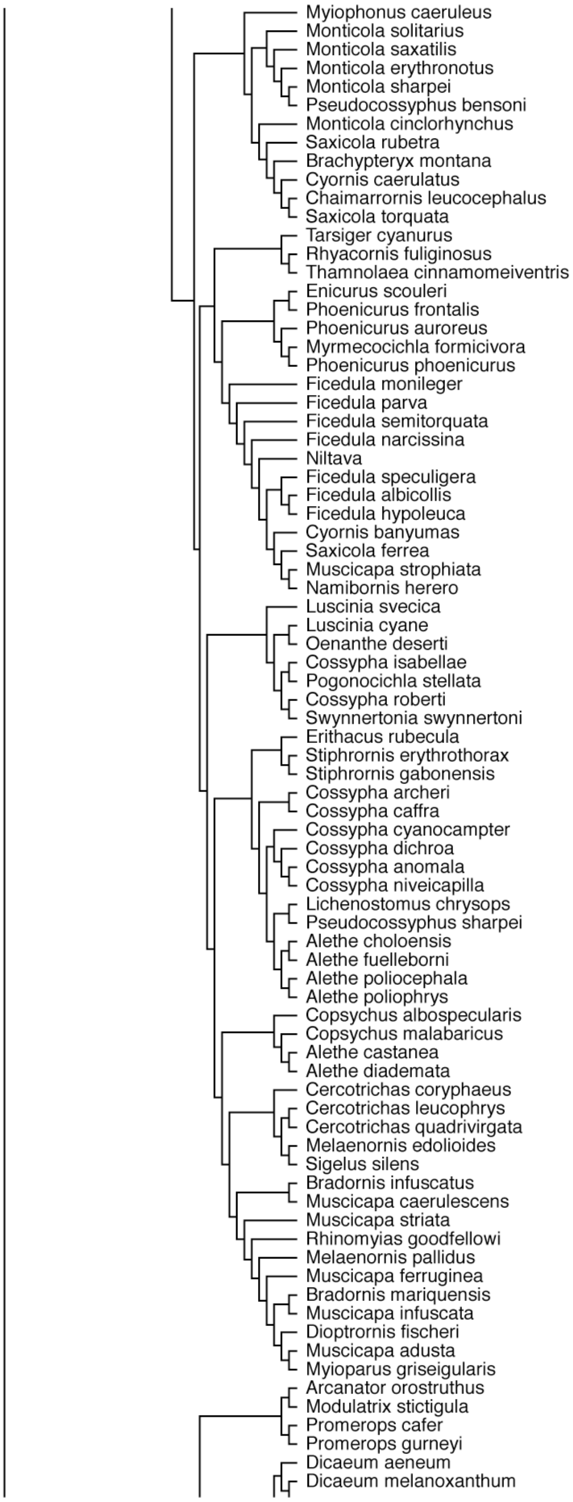

Sylvietta virens
Bradypterus victorini
Macrosphenus flavicans
Melocichla mentalis
Achaetops pycnopygius
Sphenoeacus afer
Scotocerca inquieta
Hippolais icterina
Hippolais polyglotta
Hippolais languida
Hippolais olivetorum
Acrocephalus dumetorum
Acrocephalus agricola
Acrocephalus concinens
Acrocephalus tangorum
Acrocephalus palustris
Acrocephalus scirpaceus
Acrocephalus avicenniae
Acrocephalus baeticatus
Acrocephalus bistrigiceps
Acrocephalus melanopogon
Acrocephalus paludicola
Acrocephalus schoenobaenus
Chloropeta gracilirostris
Acrocephalus aedon
Chloropeta natalensis
Hippolais pallida
Hippolais caligata
Hippolais rama
Acrocephalus griseldis
Acrocephalus arundinaceus
Acrocephalus australis
Acrocephalus vaughani
Acrocephalus orientalis
Acrocephalus stentoreus
Acrocephalus newtoni
Acrocephalus sechellensis
Acrocephalus gracilirostris
Acrocephalus brevipennis
Acrocephalus rufescens
Phylloscopus inornatus
Phylloscopus chloronotus
Phylloscopus proregulus
Phylloscopus yunnanensis
Phylloscopus maculipennis
Phylloscopus pulcher
Phylloscopus orientalis
Phylloscopus bonelli
Phylloscopus sibilatrix
Phylloscopus tytleri
Phylloscopus affinis
Phylloscopus griseolus
Phylloscopus fuscatus
Phylloscopus laetus
Phylloscopus schwarzi
Phylloscopus trochilus
Phylloscopus brehmi
Phylloscopus canariensis
Phylloscopus collybita
Phylloscopus sindianus
Seicercus montis
Seicercus castaniceps
Seicercus grammiceps
Phylloscopus cebuensis
Phylloscopus coronatus
Phylloscopus ijimae
Phylloscopus ruficapillus
Phylloscopus umbrovirens
Seicercus affinis
Seicercus poliogenys
Seicercus burkii
Seicercus tephrocephalus
Seicercus omeiensis
Seicercus soror
Tachycineta thalassina
Tachycineta euchrysea
Seicercus valentini
Seicercus whistleri
Phylloscopus borealis
Phylloscopus magnirostris

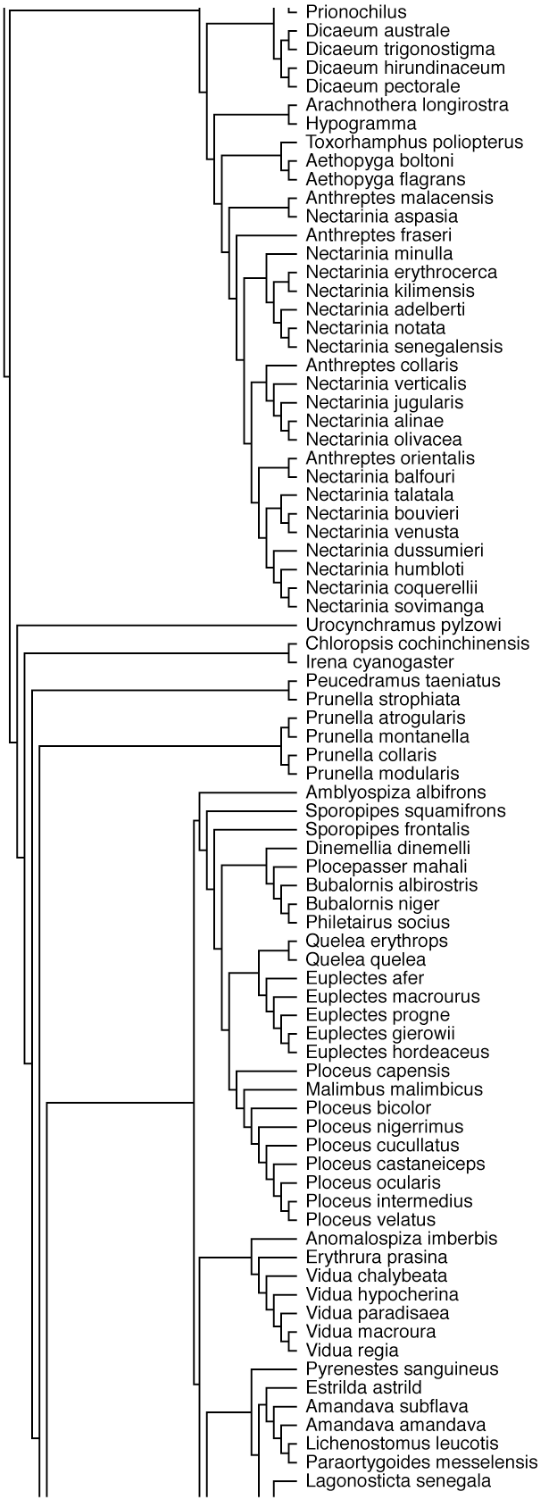

Phylloscopus borealoides
Phylloscopus tenellipes
Phylloscopus emeiensis
Phylloscopus nitidus
Phylloscopus plumbeitarsus
Phylloscopus trochiloides
Phylloscopus cantator
Phylloscopus ricketti
Phylloscopus occipitalis
Phylloscopus reguloides
Seicercus xanthoschistos
Phylloscopus davisoni
Phylloscopus hainanus
Phylloscopus presbytes
Phylloscopus trivirgatus
Phylloscopus sarasinorum
Phylloscopus amoenus
Phylloscopus poliocephalus
Schoenicola brevirostris
Bradypterus baboecala
Bradypterus barratti
Cincloramphus cruralis
Cincloramphus mathewsi
Eremiornis
Megalurus palustris
Megalurus punctatus
Paradoxornis gularis
Paradoxornis guttaticollis
Chamaea fasciata
Chrysomma sinense
Alcippe chrysotis
Alcippe cinereiceps
Paradoxornis davidianus
Paradoxornis nipalensis
Illadopsis abyssinica
Sylvia atricapilla
Sylvia borin
Sylvia layardi
Parisoma subcaeruleum
Sylvia nana
Sylvia minula
Sylvia curruca
Sylvia buryi
Sylvia lugens
Sylvia hortensis
Sylvia leucomelaena
Sylvia nisoria
Sylvia communis
Sylvia sarda
Sylvia deserticola
Sylvia undata
Sylvia conspicillata
Sylvia melanothorax
Sylvia rueppelli
Sylvia cantillans
Sylvia melanocephala
Sylvia mystacea
Yuhina diademata
Stachyris poliocephala
Yuhina gularis
Yuhina occipitalis
Yuhina flavicollis
Yuhina brunneiceps
Yuhina nigrimenta
Yuhina everetti
Stachyris dennistouni
Stachyris striata
Stachyris whiteheadi
Cleptornis marchei
Zosterops pallidus
Zosterops palpebrosus
Zosterops kikuyuensis
Zosterops poliogaster
Rukia oleaginea
Zosterops semperi
Zosterops conspicillatus
Zosterops senegalensis
Zosterops montanus
Zosterops rotensis
Zosterops erythropleurus

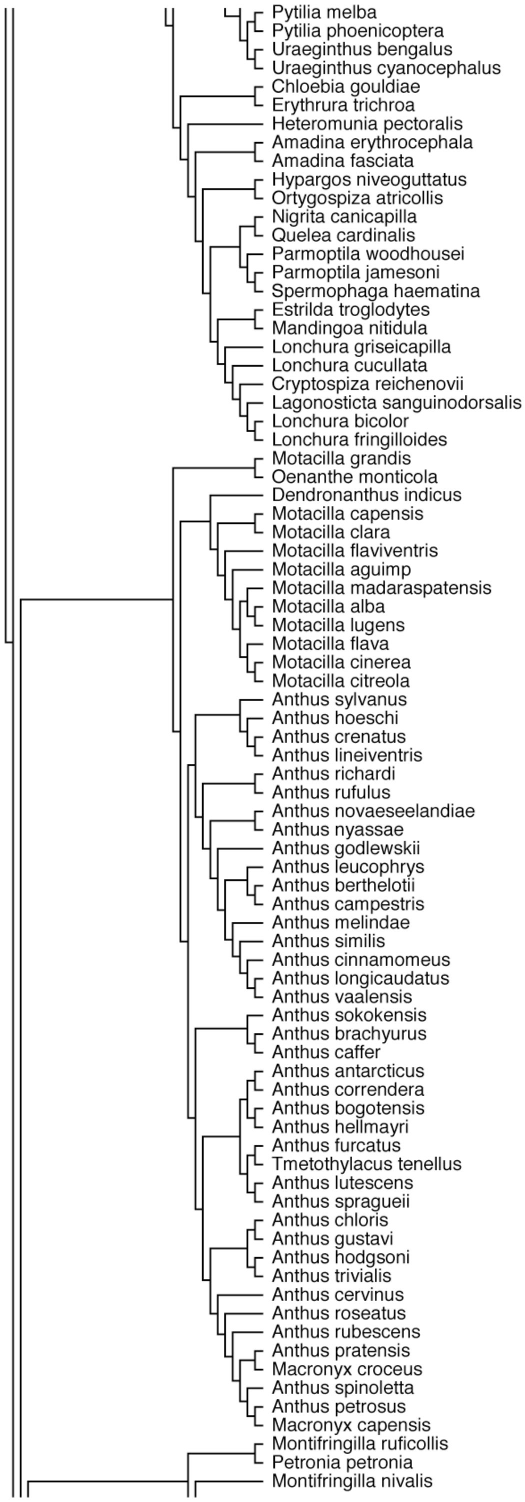

Zosterops hypolais
Zosterops nigrorum
Zosterops lateralis
Turdoides bicolor
Zosterops japonicus
Garrulax erythrocephalus
Garrulax variegatus
Garrulax squamatus
Garrulax subunicolor
Garrulax morrisonianus
Garrulax ocellatus
Garrulax sannio
Babax lanceolatus
Garrulax albogularis
Garrulax leucolophus
Garrulax milleti
Turdoides rubiginosus
Turdoides plebejus
Cutia nipalensis
Turdoides jardineii
Heterophasia capistrata
Heterophasia melanoleuca
Leiothrix argentauris
Leiothrix lutea
Minla ignotincta
Liocichla phoenicea
Liocichla steerii
Minla strigula
Minla cyanouroptera
Actinodura nipalensis
Actinodura souliei
Stachyris nigriceps
Pomatorhinus ochraceiceps
Pomatorhinus schisticeps
Xiphirhynchus superciliaris
Spelaeornis chocolatinus
Macronous gularis
Timalia pileata
Stachyris chrysaea
Stachyris ruficeps
Stachyris rufifrons
Alcippe morrisonia
Alcippe poioicephala
Pellorneum ruficeps
Illadopsis albipectus
Kenopia striata
Illadopsis pyrrhoptera
Illadopsis cleaveri
Illadopsis puveli
Illadopsis rufescens
Alcippe castaneceps
Malacopteron cinereum
Malacocincla malaccensis
Trichastoma bicolor
Gampsorhynchus rufulus
Pellorneum tickelli
Jabouilleia danjoui
Napothera epilepidota
Malacocincla abbotti
Zosterops novaeguineae
Napothera brevicaudata
Napothera crassa
Regulus calendula
Regulus ignicapillus
Regulus satrapa
Regulus regulus
Regulus teneriffae
Andropadus masukuensis
Andropadus milanjensis
Sylvia subcaeruleum
Tichodroma muraria
Sitta europaea
Sitta carolinensis
Sitta himalayensis
Sitta frontalis
Sitta pygmaea
Sitta krueperi
Sitta ledanti
Sitta canadensis
Sitta villosa

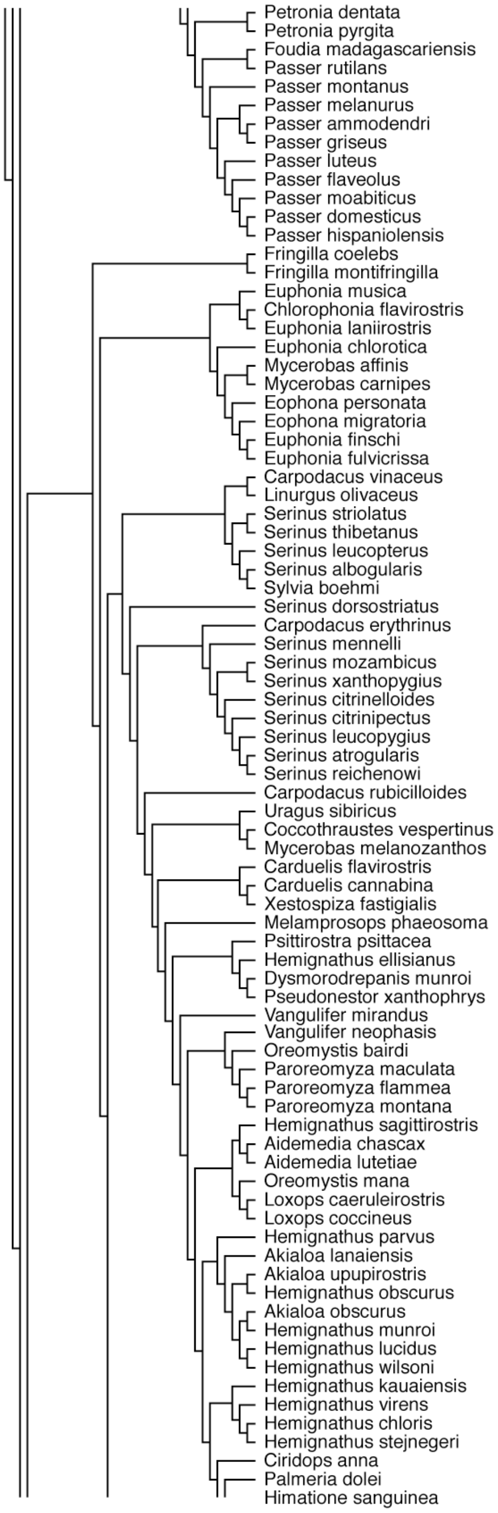

Sitta whiteheadi
Polioptila dumicola
Certhia brachydactyla
Certhia familiaris
Salpornis spilonotus
Certhia americana
Polioptila caerulea
Catherpes mexicanus
Hylorchilus sumichrasti
Microcerculus marginatus
Salpinctes obsoletus
Campylorhynchus fasciatus
Odontorchilus cinereus
Campylorhynchus brunneicapillus
Campylorhynchus megalopterus
Thryomanes bewickii
Thryothorus ludovicianus
Cinnycerthia peruana
Cyphorhinus aradus
Henicorhina leucosticta
Thryothorus coraya
Thryothorus maculipectus
Thryothorus guarayanus
Thryothorus leucotis
Cistothorus palustris
Cistothorus platensis
Troglodytes troglodytes
Thryorchilus browni
Troglodytes rufociliatus
Troglodytes rufulus
Troglodytes ochraceus
Troglodytes solstitialis
Troglodytes brunneicollis
Thryomanes sissonii
Troglodytes aedon
Troglodytes musculus
Dulus dominicus
Panurus biarmicus
Phainopepla nitens
Ptiliogonys cinereus
Bombycilla garrulus
Bombycilla cedrorum
Phainoptila melanoxantha
Cinclus mexicanus
Buphagus erythrorhynchus
Cinclus leucocephalus
Cinclus schulzi
Melanotis caerulescens
Dumetella carolinensis
Margarops fuscus
Ramphocinclus brachyurus
Melanoptila glabrirostris
Margarops fuscatus
Cinclocerthia gutturalis
Cinclocerthia ruficauda
Oreoscoptes montanus
Mimus saturninus
Mimus gundlachii
Mimodes graysoni
Mimus polyglottos
Mimus gilvus
Mimus patagonicus
Toxostoma bendirei
Toxostoma cinereum
Toxostoma redivivum
Toxostoma crissale
Toxostoma lecontei
Toxostoma dorsale
Toxostoma curvirostre
Toxostoma ocellatum
Toxostoma guttatum
Toxostoma longirostre
Toxostoma rufum
Aplonis opaca
Rhabdornis inornatus
Rhabdornis mystacalis
Aplonis panayensis
Ampeliceps coronatus
Sarcops calvus
Gracula religiosa

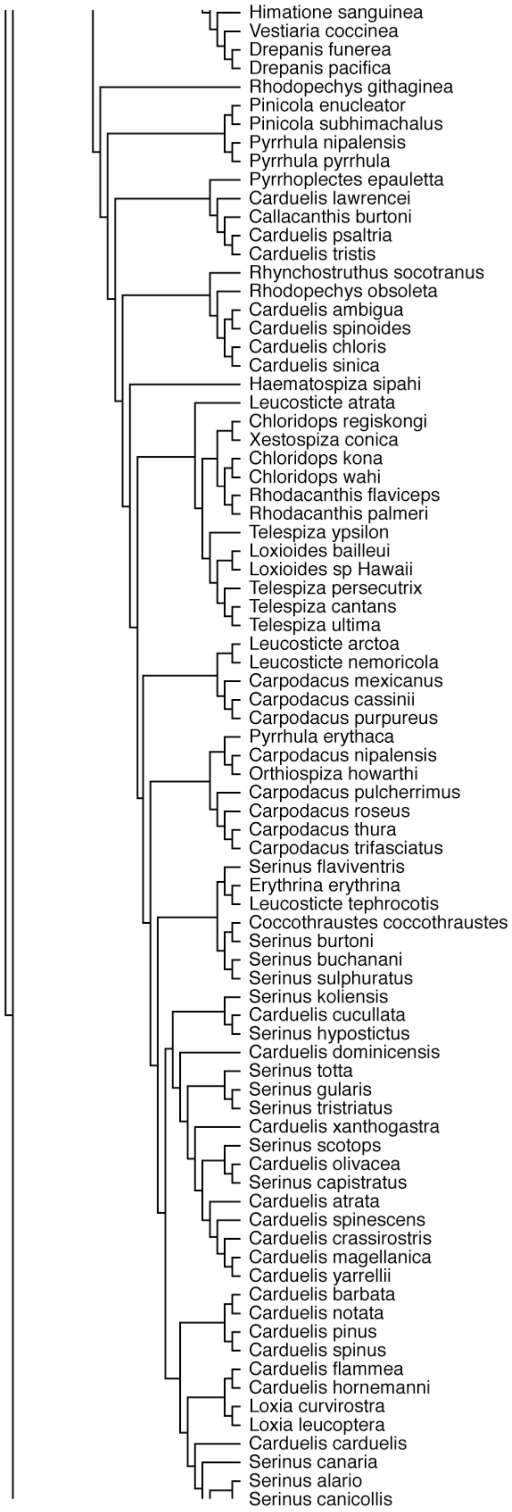

Mino anais
Sturnus cineraceus
Sturnus unicolor
Acridotheres fuscus
Creatophora cinerea
Acridotheres tristis
Sturnus vulgaris
Neocichla
Cinnyricinclus sharpii
Poeoptera lugubris
Onychognathus
Speculipastor
Grafisia
Mimus longicaudatus
Myadestes genibarbis
Lamprotornis splendidus
Lamprotornis superbus
Lamprotornis corruscus
Spreo
Lamprotornis nitens
Leucopsar rothschildi
Cyanoptila cyanomelana
Turdus merula
Cinclus cinclus
Cinclus pallasii
Catharus aurantiirostris
Sialia mexicana
Cichlherminia lherminieri
Catharus dryas
Turdus chiguanco
Sialia currucoides
Sialia sialis
Cichlopsis leucogenys
Myadestes ralloides
Myadestes unicolor
Stizorhina finschi
Stizorhina fraseri
Neocossyphus rufus
Myadestes townsendi
Neocossyphus poensis
Platycichla leucops
Turdus philomelos
Entomodestes coracinus
Cochoa viridis
Entomodestes leucotis
Hylocichla mustelina
Catharus ustulatus
Andropadus tephrolaemus
Catharus gracilirostris
Catharus guttatus
Catharus occidentalis
Catharus frantzii
Catharus bicknelli
Catharus fuscescens
Catharus minimus
Chlamydochaera jefferyi
Psittacopes lepidus
Stiphrornis xanthogaster
Zoothera gurneyi
Nesocichla eremita
Zoothera piaggiae
Stiphrornis sanghensis
Ixoreus naevius
Psophocichla litsipsirupa
Zoothera dauma
Zoothera lunulata
Zoothera princei
Turdus cardis
Turdus naumanni
Turdus grayi
Ridgwayia pinicola
Turdus nudigenis
Turdus chrysolaus
Zoothera cameronensis
Turdus migratorius
Turdus pallidus
Turdus olivaceus
Turdus falcklandii
Abroscopus albogularis
Turdus obscurus

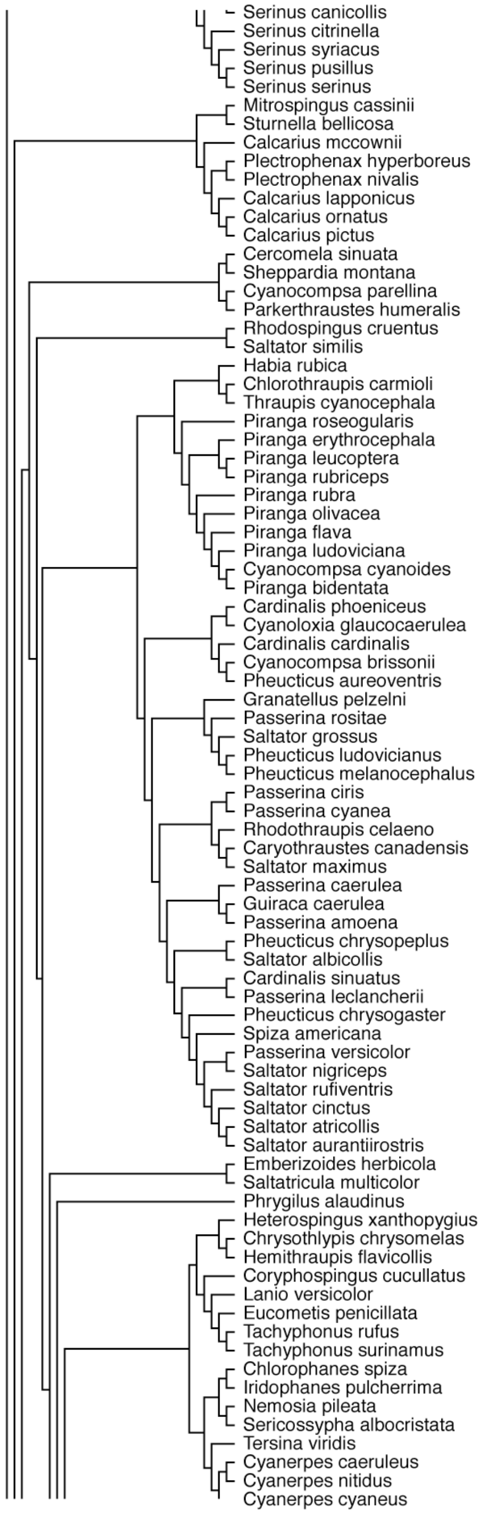

Myiophonus caeruleus
Monticola solitarius
Monticola saxatilis
Monticola erythronotus
Monticola sharpei
Pseudocossyphus bensoni
Monticola cinclorhynchus
Saxicola rubetra
Brachypteryx montana
Cyornis caerulatus
Chaimarrornis leucocephalus
Saxicola torquata
Tarsiger cyanurus
Rhyacornis fuliginosus
Thamnolaea cinnamomeiventris
Enicurus scouleri
Phoenicurus frontalis
Phoenicurus auroreus
Myrmecocichla formicivora
Phoenicurus phoenicurus
Ficedula monileger
Ficedula parva
Ficedula semitorquata
Ficedula narcissina
Niltava
Ficedula speculigera
Ficedula albicollis
Ficedula hypoleuca
Cyornis banyumas
Saxicola ferrea
Muscicapa strophiata
Namibornis herero
Luscinia svecica
Luscinia cyane
Oenanthe deserti
Cossypha isabellae
Pogonocichla stellata
Cossypha roberti
Swynnertonia swynnertoni
Erithacus rubecula
Stiphrornis erythrothorax
Stiphrornis gabonensis
Cossypha archeri
Cossypha caffra
Cossypha cyanocampter
Cossypha dichroa
Cossypha anomala
Cossypha niveicapilla
Lichenostomus chrysops
Pseudocossyphus sharpei
Alethe choloensis
Alethe fuelleborni
Alethe poliocephala
Alethe poliophrys
Copsychus albospecularis
Copsychus malabaricus
Alethe castanea
Alethe diademata
Cercotrichas coryphaeus
Cercotrichas leucophrys
Cercotrichas quadrivirgata
Melaenornis edolioides
Sigelus silens
Bradornis infuscatus
Muscicapa caerulescens
Muscicapa striata
Rhinomyias goodfellowi
Melaenornis pallidus
Muscicapa ferruginea
Bradornis mariquensis
Muscicapa infuscata
Dioptrornis fischeri
Muscicapa adusta
Myioparus griseigularis
Arcanator orostruthus
Modulatrix stictigula
Promerops cafer
Promerops gurneyi
Dicaeum aeneum
Dicaeum melanoxanthum

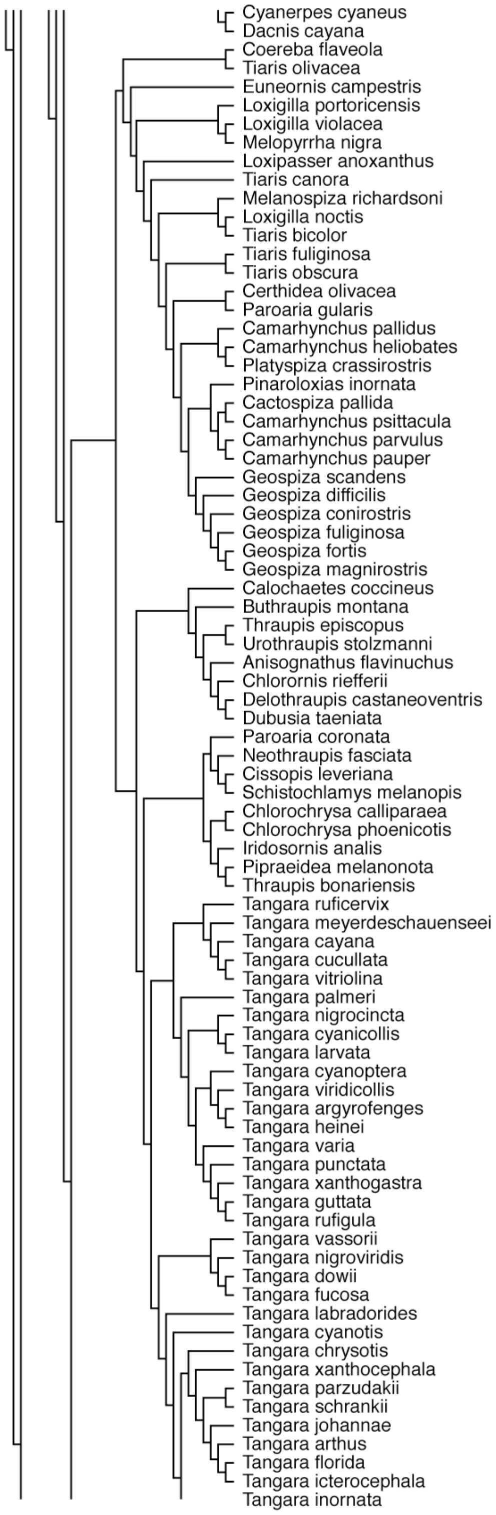

Prionochilus
Dicaeum australe
Dicaeum trigonostigma
Dicaeum hirundinaceum
Dicaeum pectorale
Arachnothera longirostra
Hypogramma
Toxorhamphus poliopterus
Aethopyga boltoni
Aethopyga flagrans
Anthreptes malacensis
Nectarinia aspasia
Anthreptes fraseri
Nectarinia minulla
Nectarinia erythrocerca
Nectarinia kilimensis
Nectarinia adelberti
Nectarinia notata
Nectarinia senegalensis
Anthreptes collaris
Nectarinia verticalis
Nectarinia jugularis
Nectarinia alinae
Nectarinia olivacea
Anthreptes orientalis
Nectarinia balfouri
Nectarinia talatala
Nectarinia bouvieri
Nectarinia venusta
Nectarinia dussumieri
Nectarinia humbloti
Nectarinia coquerellii
Nectarinia sovimanga
Urocynchramus pylzowi
Chloropsis cochinchinensis
Irena cyanogaster
Peucedramus taeniatus
Prunella strophiata
Prunella atrogularis
Prunella montanella
Prunella collaris
Prunella modularis
Amblyospiza albifrons
Sporopipes squamifrons
Sporopipes frontalis
Dinemellia dinemelli
Plocepasser mahali
Bubalornis albirostris
Bubalornis niger
Philetairus socius
Quelea erythrops
Quelea quelea
Euplectes afer
Euplectes macrourus
Euplectes progne
Euplectes gierowii
Euplectes hordeaceus
Ploceus capensis
Malimbus malimbicus
Ploceus bicolor
Ploceus nigerrimus
Ploceus cucullatus
Ploceus castaneiceps
Ploceus ocularis
Ploceus intermedius
Ploceus velatus
Anomalospiza imberbis
Erythrura prasina
Vidua chalybeata
Vidua hypocherina
Vidua paradisaea
Vidua macroura
Vidua regia
Pyrenestes sanguineus
Estrilda astrild
Amandava subflava
Amandava amandava
Lichenostomus leucotis
Paraortygoides messelensis
Lagonosticta senegala


Pytilia melba
Pytilia phoenicoptera
Uraeginthus bengalus
Uraeginthus cyanocephalus
Chloebia gouldiae
Erythrura trichroa
Heteromunia pectoralis
Amadina erythrocephala
Amadina fasciata
Hypargos niveoguttatus
Ortygospiza atricollis
Nigrita canicapilla
Quelea cardinalis
Parmoptila woodhousei
Parmoptila jamesoni
Spermophaga haematina
Estrilda troglodytes
Mandingoa nitidula
Lonchura griseicapilla
Lonchura cucullata
Cryptospiza reichenovii
Lagonosticta sanguinodorsalis
Lonchura bicolor
Lonchura fringilloides
Motacilla grandis
Oenanthe monticola
Dendronanthus indicus
Motacilla capensis
Motacilla clara
Motacilla flaviventris
Motacilla aguimp
Motacilla madaraspatensis
Motacilla alba
Motacilla lugens
Motacilla flava
Motacilla cinerea
Motacilla citreola
Anthus sylvanus
Anthus hoeschi
Anthus crenatus
Anthus lineiventris
Anthus richardi
Anthus rufulus
Anthus novaeseelandiae
Anthus nyassae
Anthus godlewskii
Anthus leucophrys
Anthus berthelotii
Anthus campestris
Anthus melindae
Anthus similis
Anthus cinnamomeus
Anthus longicaudatus
Anthus vaalensis
Anthus sokokensis
Anthus brachyurus
Anthus caffer
Anthus antarcticus
Anthus correndera
Anthus bogotensis
Anthus hellmayri
Anthus furcatus
Tmetothylacus tenellus
Anthus lutescens
Anthus spragueii
Anthus chloris
Anthus gustavi
Anthus hodgsoni
Anthus trivialis
Anthus cervinus
Anthus roseatus
Anthus rubescens
Anthus pratensis
Macronyx croceus
Anthus spinoletta
Anthus petrosus
Macronyx capensis
Montifringilla ruficollis
Petronia petronia
Montifringilla nivalis


Petronia dentata
Petronia pyrgita
Foudia madagascariensis
Passer rutilans
Passer montanus
Passer melanurus
Passer ammodendri
Passer griseus
Passer luteus
Passer flaveolus
Passer moabiticus
Passer domesticus
Passer hispaniolensis
Fringilla coelebs
Fringilla montifringilla
Euphonia musica
Chlorophonia flavirostris
Euphonia laniirostris
Euphonia chlorotica
Mycerobas affinis
Mycerobas carnipes
Eophona personata
Eophona migratoria
Euphonia finschi
Euphonia fulvicrissa
Carpodacus vinaceus
Linurgus olivaceus
Serinus striolatus
Serinus thibetanus
Serinus leucopterus
Serinus albogularis
Sylvia boehmi
Serinus dorsostriatus
Carpodacus erythrinus
Serinus mennelli
Serinus mozambicus
Serinus xanthopygius
Serinus citrinelloides
Serinus citrinipectus
Serinus leucopygius
Serinus atrogularis
Serinus reichenowi
Carpodacus rubicilloides
Uragus sibiricus
Coccothraustes vespertinus
Mycerobas melanozanthos
Carduelis flavirostris
Carduelis cannabina
Xestospiza fastigialis
Melamprosops phaeosoma
Psittirostra psittacea
Hemignathus ellisianus
Dysmorodrepanis munroi
Pseudonestor xanthophrys
Vangulifer mirandus
Vangulifer neophasis
Oreomystis bairdi
Paroreomyza maculata
Paroreomyza flammea
Paroreomyza montana
Hemignathus sagittirostris
Aidemedia chascax
Aidemedia lutetiae
Oreomystis mana
Loxops caeruleirostris
Loxops coccineus
Hemignathus parvus
Akialoa lanaiensis
Akialoa upupirostris
Hemignathus obscurus
Akialoa obscurus
Hemignathus munroi
Hemignathus lucidus
Hemignathus wilsoni
Hemignathus kauaiensis
Hemignathus virens
Hemignathus chloris
Hemignathus stejnegeri
Ciridops anna
Palmeria dolei
Himatione sanguinea


Himatione sanguinea
Vestiaria coccinea
Drepanis funerea
Drepanis pacifica
Rhodopechys githaginea
Pinicola enucleator
Pinicola subhimachalus
Pyrrhula nipalensis
Pyrrhula pyrrhula
Pyrrhoplectes epauletta
Carduelis lawrencei
Callacanthis burtoni
Carduelis psaltria
Carduelis tristis
Rhynchostruthus socotranus
Rhodopechys obsoleta
Carduelis ambigua
Carduelis spinoides
Carduelis chloris
Carduelis sinica
Haematospiza sipahi
Leucosticte atrata
Chloridops regiskongi
Xestospiza conica
Chloridops kona
Chloridops wahi
Rhodacanthis flaviceps
Rhodacanthis palmeri
Telespiza ypsilon
Loxioides bailleui
Loxioides sp Hawaii
Telespiza persecutrix
Telespiza cantans
Telespiza ultima
Leucosticte arctoa
Leucosticte nemoricola
Carpodacus mexicanus
Carpodacus cassinii
Carpodacus purpureus
Pyrrhula erythaca
Carpodacus nipalensis
Orthiospiza howarthi
Carpodacus pulcherrimus
Carpodacus roseus
Carpodacus thura
Carpodacus trifasciatus
Serinus flaviventris
Erythrina erythrina
Leucosticte tephrocotis
Coccothraustes coccothraustes
Serinus burtoni
Serinus buchanani
Serinus sulphuratus
Serinus koliensis
Carduelis cucullata
Serinus hypostictus
Carduelis dominicensis
Serinus totta
Serinus gularis
Serinus tristriatus
Carduelis xanthogastra
Serinus scotops
Carduelis olivacea
Serinus capistratus
Carduelis atrata
Carduelis spinescens
Carduelis crassirostris
Carduelis magellanica
Carduelis yarrellii
Carduelis barbata
Carduelis notata
Carduelis pinus
Carduelis spinus
Carduelis flammea
Carduelis hornemanni
Loxia curvirostra
Loxia leucoptera
Carduelis carduelis
Serinus canaria
Serinus alario
Serinus canicollis


Serinus canicollis
Serinus citrinella
Serinus syriacus
Serinus pusillus
Serinus serinus
Mitrospingus cassinii
Sturnella bellicosa
Calcarius mccownii
Plectrophenax hyperboreus
Plectrophenax nivalis
Calcarius lapponicus
Calcarius ornatus
Calcarius pictus
Cercomela sinuata
Sheppardia montana
Cyanocompsa parellina
Parkerthraustes humeralis
Rhodospingus cruentus
Saltator similis
Habia rubica
Chlorothraupis carmioli
Thraupis cyanocephala
Piranga roseogularis
Piranga erythrocephala
Piranga leucoptera
Piranga rubriceps
Piranga rubra
Piranga olivacea
Piranga flava
Piranga ludoviciana
Cyanocompsa cyanoides
Piranga bidentata
Cardinalis phoeniceus
Cyanoloxia glaucocaerulea
Cardinalis cardinalis
Cyanocompsa brissonii
Pheucticus aureoventris
Granatellus pelzelni
Passerina rositae
Saltator grossus
Pheucticus ludovicianus
Pheucticus melanocephalus
Passerina ciris
Passerina cyanea
Rhodothraupis celaeno
Caryothraustes canadensis
Saltator maximus
Passerina caerulea
Guiraca caerulea
Passerina amoena
Pheucticus chrysopeplus
Saltator albicollis
Cardinalis sinuatus
Passerina leclancherii
Pheucticus chrysogaster
Spiza americana
Passerina versicolor
Saltator nigriceps
Saltator rufiventris
Saltator cinctus
Saltator atricollis
Saltator aurantiirostris
Emberizoides herbicola
Saltatricula multicolor
Phrygilus alaudinus
Heterospingus xanthopygius
Chrysothlypis chrysomelas
Hemithraupis flavicollis
Coryphospingus cucullatus
Lanio versicolor
Eucometis penicillata
Tachyphonus rufus
Tachyphonus surinamus
Chlorophanes spiza
Iridophanes pulcherrima
Nemosia pileata
Sericossypha albocristata
Tersina viridis
Cyanerpes caeruleus
Cyanerpes nitidus
Cyanerpes cyaneus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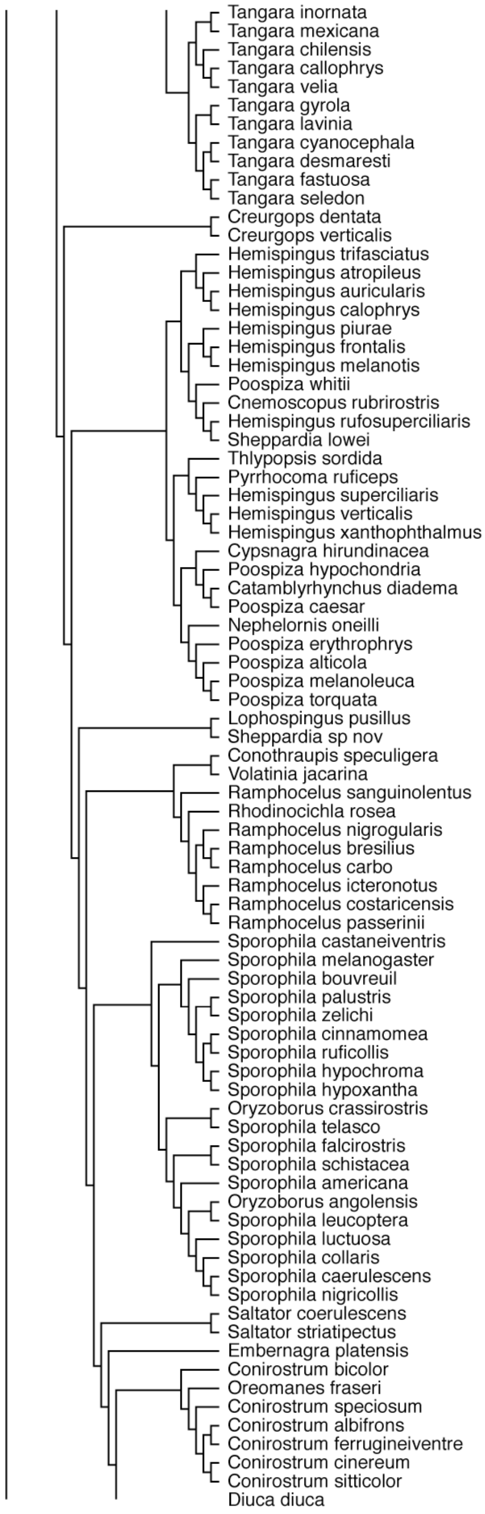
Dacnis cayana
Coereba flaveola
Tiaris olivacea
Euneornis campestris
Loxigilla portoricensis
Loxigilla violacea
Melopyrrha nigra
Loxipasser anoxanthus
Tiaris canora
Melanospiza richardsoni
Loxigilla noctis
Tiaris bicolor
Tiaris fuliginosa
Tiaris obscura
Certhidea olivacea
Paroaria gularis
Camarhynchus pallidus
Camarhynchus heliobates
Platyspiza crassirostris
Pinaroloxias inornata
Cactospiza pallida
Camarhynchus psittacula
Camarhynchus parvulus
Camarhynchus pauper
Geospiza scandens
Geospiza difficilis
Geospiza conirostris
Geospiza fuliginosa
Geospiza fortis
Geospiza magnirostris
Calochaetes coccineus
Buthraupis montana
Thraupis episcopus
Urothraupis stolzmanni
Anisognathus flavinuchus
Chlorornis riefferii
Delothraupis castaneoventris
Dubusia taeniata
Paroaria coronata
Neothraupis fasciata
Cissopis leveriana
Schistochlamys melanopis
Chlorochrysa calliparaea
Chlorochrysa phoenicotis
Iridosornis analis
Pipraeidea melanonota
Thraupis bonariensis
Tangara ruficervix
Tangara meyerdeschauenseei
Tangara cayana
Tangara cucullata
Tangara vitriolina
Tangara palmeri
Tangara nigrocincta
Tangara cyanicollis
Tangara larvata
Tangara cyanoptera
Tangara viridicollis
Tangara argyrofenges
Tangara heinei
Tangara varia
Tangara punctata
Tangara xanthogastra
Tangara guttata
Tangara rufigula
Tangara vassorii
Tangara nigroviridis
Tangara dowii
Tangara fucosa
Tangara labradorides
Tangara cyanotis
Tangara chrysotis
Tangara xanthocephala
Tangara parzudakii
Tangara schrankii
Tangara johannae
Tangara arthus
Tangara florida
Tangara icterocephala
Tangara inornata


Tangara inornata
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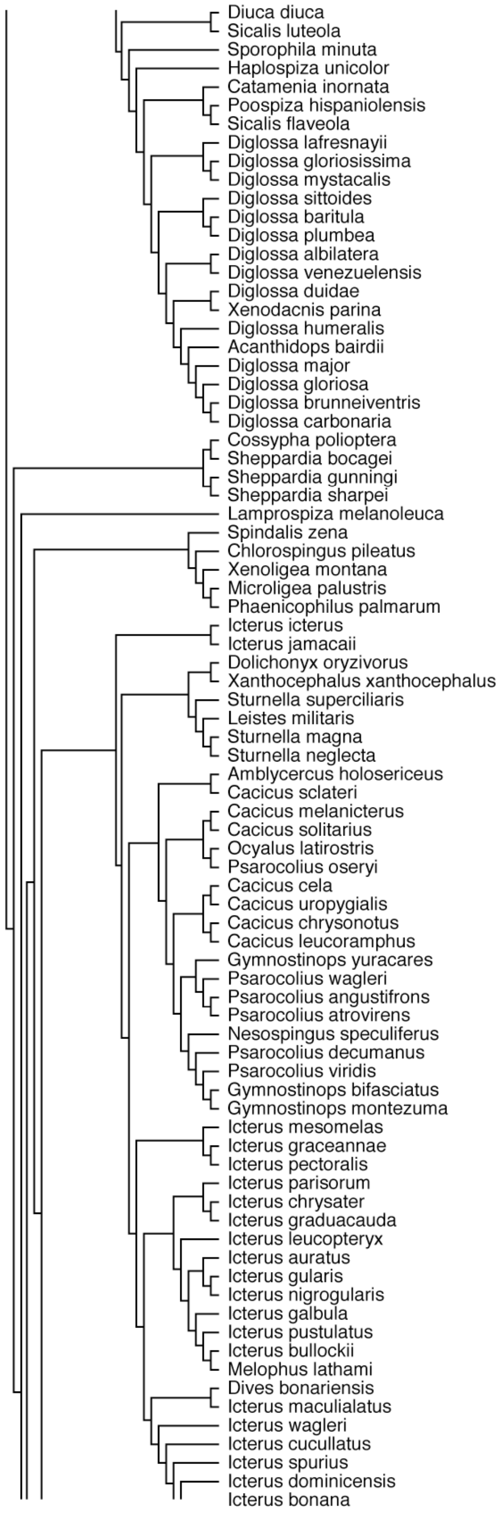
Tangara chilensis
Tangara callophrys
Tangara velia
Tangara gyrola
Tangara lavinia
Tangara cyanocephala
Tangara desmaresti
Tangara fastuosa
Tangara seledon
Creurgops dentata
Creurgops verticalis
Hemispingus trifasciatus
Hemispingus atropileus
Hemispingus auricularis
Hemispingus calophrys
Hemispingus piurae
Hemispingus frontalis
Hemispingus melanotis
Poospiza whitii
Cnemoscopus rubrirostris
Hemispingus rufosuperciliaris
Sheppardia lowei
Thlypopsis sordida
Pyrrhocoma ruficeps
Hemispingus superciliaris
Hemispingus verticalis
Hemispingus xanthophthalmus
Cypsnagra hirundinacea
Poospiza hypochondria
Catamblyrhynchus diadema
Poospiza caesar
Nephelornis oneilli
Poospiza erythrophrys
Poospiza alticola
Poospiza melanoleuca
Poospiza torquata
Lophospingus pusillus
Sheppardia sp nov
Conothraupis speculigera
Volatinia jacarina
Ramphocelus sanguinolentus
Rhodinocichla rosea
Ramphocelus nigrogularis
Ramphocelus bresilius
Ramphocelus carbo
Ramphocelus icteronotus
Ramphocelus costaricensis
Ramphocelus passerinii
Sporophila castaneiventris
Sporophila melanogaster
Sporophila bouvreuil
Sporophila palustris
Sporophila zelichi
Sporophila cinnamomea
Sporophila ruficollis
Sporophila hypochroma
Sporophila hypoxantha
Oryzoborus crassirostris
Sporophila telasco
Sporophila falcirostris
Sporophila schistacea
Sporophila americana
Oryzoborus angolensis
Sporophila leucoptera
Sporophila luctuosa
Sporophila collaris
Sporophila caerulescens
Sporophila nigricollis
Saltator coerulescens
Saltator striatipectus
Embernagra platensis
Conirostrum bicolor
Oreomanes fraseri
Conirostrum speciosum
Conirostrum albifrons
Conirostrum ferrugineiventre
Conirostrum cinereum
Conirostrum sitticolor
Diuca diuca


Diuca diuca
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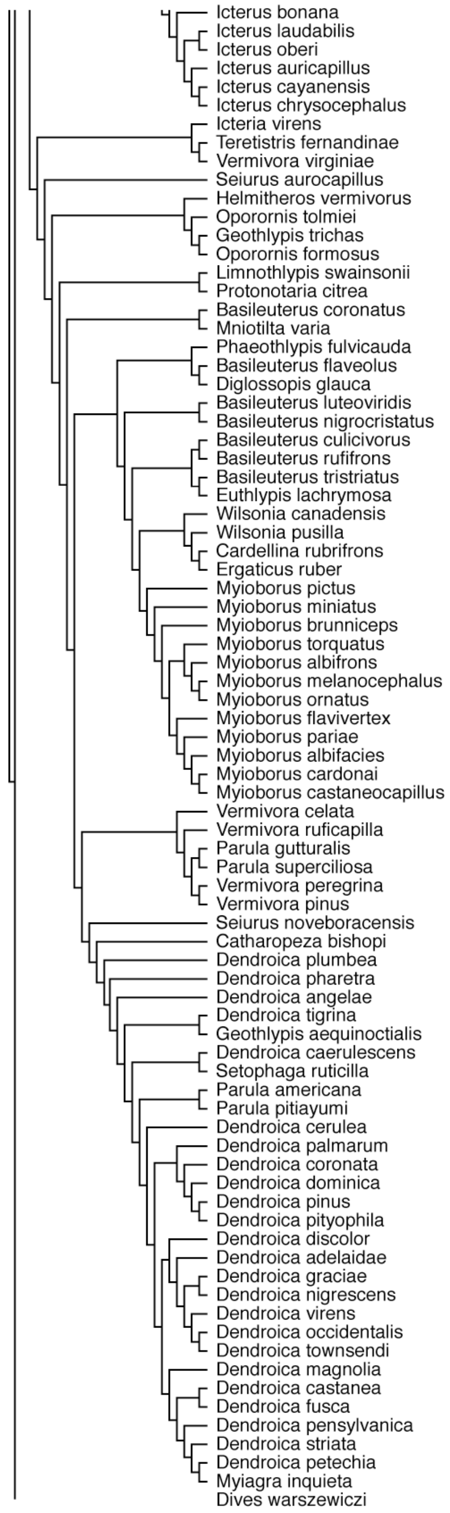
Sporophila minuta
Haplospiza unicolor
Catamenia inornata
Poospiza hispaniolensis
Sicalis flaveola
Diglossa lafresnayii
Diglossa gloriosissima
Diglossa mystacalis
Diglossa sittoides
Diglossa baritula
Diglossa plumbea
Diglossa albilatera
Diglossa venezuelensis
Diglossa duidae
Xenodacnis parina
Diglossa humeralis
Acanthidops bairdii
Diglossa major
Diglossa gloriosa
Diglossa brunneiventris
Diglossa carbonaria
Cossypha polioptera
Sheppardia bocagei
Sheppardia gunningi
Sheppardia sharpei
Lamprospiza melanoleuca
Spindalis zena
Chlorospingus pileatus
Xenoligea montana
Microligea palustris
Phaenicophilus palmarum
Icterus icterus
Icterus jamacaii
Dolichonyx oryzivorus
Xanthocephalus xanthocephalus
Sturnella superciliaris
Leistes militaris
Sturnella magna
Sturnella neglecta
Amblycercus holosericeus
Cacicus sclateri
Cacicus melanicterus
Cacicus solitarius
Ocyalus latirostris
Psarocolius oseryi
Cacicus cela
Cacicus uropygialis
Cacicus chrysonotus
Cacicus leucoramphus
Gymnostinops yuracares
Psarocolius wagleri
Psarocolius angustifrons
Psarocolius atrovirens
Nesospingus speculiferus
Psarocolius decumanus
Psarocolius viridis
Gymnostinops bifasciatus
Gymnostinops montezuma
Icterus mesomelas
Icterus graceannae
Icterus pectoralis
Icterus parisorum
Icterus chrysater
Icterus graduacauda
Icterus leucopteryx
Icterus auratus
Icterus gularis
Icterus nigrogularis
Icterus galbula
Icterus pustulatus
Icterus bullockii
Melophus lathami
Dives bonariensis
Icterus maculialatus
Icterus wagleri
Icterus cucullatus
Icterus spurius
Icterus dominicensis
Icterus bonana


Icterus bonana
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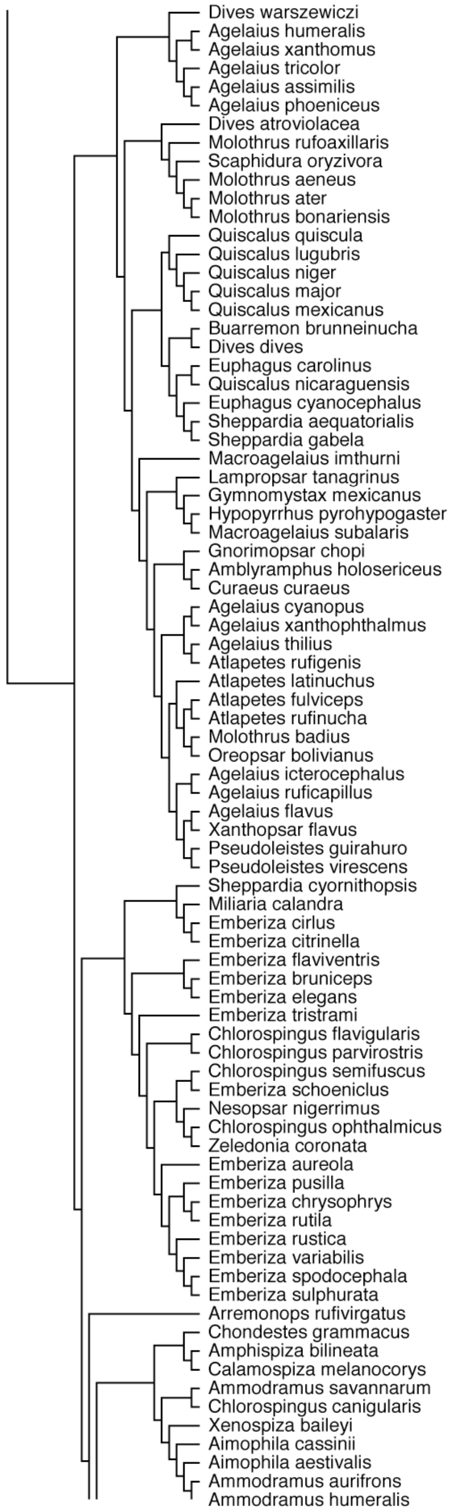
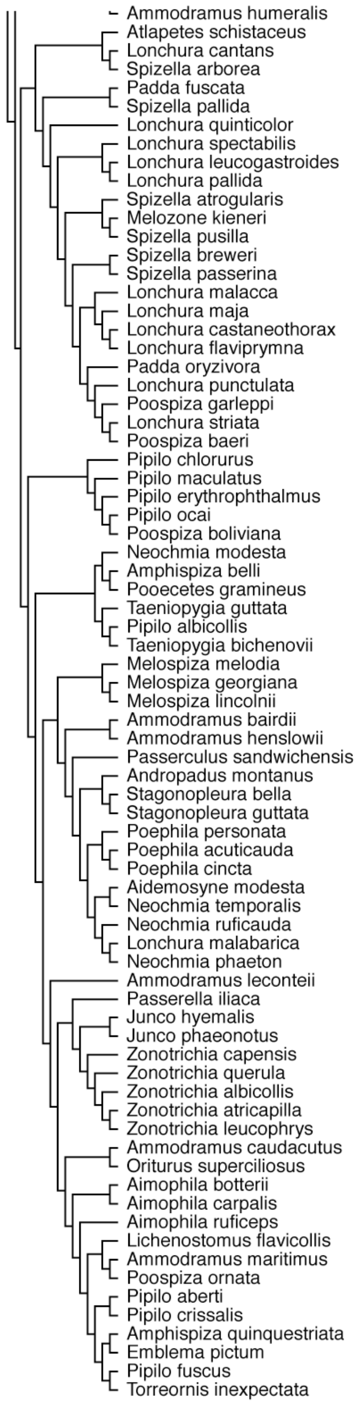
Icterus oberi
Icterus auricapillus
Icterus cayanensis
Icterus chrysocephalus
Icteria virens
Teretistris fernandinae
Vermivora virginiae
Seiurus aurocapillus
Helmitheros vermivorus
Oporornis tolmiei
Geothlypis trichas
Oporornis formosus
Limnothlypis swainsonii
Protonotaria citrea
Basileuterus coronatus
Mniotilta varia
Phaeothlypis fulvicauda
Basileuterus flaveolus
Diglossopis glauca
Basileuterus luteoviridis
Basileuterus nigrocristatus
Basileuterus culicivorus
Basileuterus rufifrons
Basileuterus tristriatus
Euthlypis lachrymosa
Wilsonia canadensis
Wilsonia pusilla
Cardellina rubrifrons
Ergaticus ruber
Myioborus pictus
Myioborus miniatus
Myioborus brunniceps
Myioborus torquatus
Myioborus albifrons
Myioborus melanocephalus
Myioborus ornatus
Myioborus flavivertex
Myioborus pariae
Myioborus albifacies
Myioborus cardonai
Myioborus castaneocapillus
Vermivora celata
Vermivora ruficapilla
Parula gutturalis
Parula superciliosa
Vermivora peregrina
Vermivora pinus
Seiurus noveboracensis
Catharopeza bishopi
Dendroica plumbea
Dendroica pharetra
Dendroica angelae
Dendroica tigrina
Geothlypis aequinoctialis
Dendroica caerulescens
Setophaga ruticilla
Parula americana
Parula pitiayumi
Dendroica cerulea
Dendroica palmarum
Dendroica coronata
Dendroica dominica
Dendroica pinus
Dendroica pityophila
Dendroica discolor
Dendroica adelaidae
Dendroica graciae
Dendroica nigrescens
Dendroica virens
Dendroica occidentalis
Dendroica townsendi
Dendroica magnolia
Dendroica castanea
Dendroica fusca
Dendroica pensylvanica
Dendroica striata
Dendroica petechia
Myiagra inquieta
Dives warszewiczi


Dives warszewiczi
Agelaius humeralis
Agelaius xanthomus
Agelaius tricolor
Agelaius assimilis
Agelaius phoeniceus
Dives atroviolacea
Molothrus rufoaxillaris
Scaphidura oryzivora
Molothrus aeneus
Molothrus ater
Molothrus bonariensis
Quiscalus quiscula
Quiscalus lugubris
Quiscalus niger
Quiscalus major
Quiscalus mexicanus
Buarremon brunneinucha
Dives dives
Euphagus carolinus
Quiscalus nicaraguensis
Euphagus cyanocephalus
Sheppardia aequatorialis
Sheppardia gabela
Macroagelaius imthurni
Lampropsar tanagrinus
Gymnomystax mexicanus
Hypopyrrhus pyrohypogaster
Macroagelaius subalaris
Gnorimopsar chopi
Amblyramphus holosericeus
Curaeus curaeus
Agelaius cyanopus
Agelaius xanthophthalmus
Agelaius thilius
Atlapetes rufigenis
Atlapetes latinuchus
Atlapetes fulviceps
Atlapetes rufinucha
Molothrus badius
Oreopsar bolivianus
Agelaius icterocephalus
Agelaius ruficapillus
Agelaius flavus
Xanthopsar flavus
Pseudoleistes guirahuro
Pseudoleistes virescens
Sheppardia cyornithopsis
Miliaria calandra
Emberiza cirlus
Emberiza citrinella
Emberiza flaviventris
Emberiza bruniceps
Emberiza elegans
Emberiza tristrami
Chlorospingus flavigularis
Chlorospingus parvirostris
Chlorospingus semifuscus
Emberiza schoeniclus
Nesopsar nigerrimus
Chlorospingus ophthalmicus
Zeledonia coronata
Emberiza aureola
Emberiza pusilla
Emberiza chrysophrys
Emberiza rutila
Emberiza rustica
Emberiza variabilis
Emberiza spodocephala
Emberiza sulphurata
Arremonops rufivirgatus
Chondestes grammacus
Amphispiza bilineata
Calamospiza melanocorys
Ammodramus savannarum
Chlorospingus canigularis
Xenospiza baileyi
Aimophila cassinii
Aimophila aestivalis
Ammodramus aurifrons
Ammodramus humeralis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Spizella arborea
Padda fuscata
Spizella pallida
Lonchura quinticolor
Lonchura spectabilis
Lonchura leucogastroides
Lonchura pallida
Spizella atrogularis
Melozone kieneri
Spizella pusilla
Spizella breweri
Spizella passerina
Lonchura malacca
Lonchura maja
Lonchura castaneothorax
Lonchura flaviprymna
Padda oryzivora
Lonchura punctulata
Poospiza garleppi
Lonchura striata
Poospiza baeri
Pipilo chlorurus
Pipilo maculatus
Pipilo erythrophthalmus
Pipilo ocai
Poospiza boliviana
Neochmia modesta
Amphispiza belli
Pooecetes gramineus
Taeniopygia guttata
Pipilo albicollis
Taeniopygia bichenovii
Melospiza melodia
Melospiza georgiana
Melospiza lincolnii
Ammodramus bairdii
Ammodramus henslowii
Passerculus sandwichensis
Andropadus montanus
Stagonopleura bella
Stagonopleura guttata
Poephila personata
Poephila acuticauda
Poephila cincta
Aidemosyne modesta
Neochmia temporalis
Neochmia ruficauda
Lonchura malabarica
Neochmia phaeton
Ammodramus leconteii
Passerella iliaca
Junco hyemalis
Junco phaeonotus
Zonotrichia capensis
Zonotrichia querula
Zonotrichia albicollis
Zonotrichia atricapilla
Zonotrichia leucophrys
Ammodramus caudacutus
Oriturus superciliosus
Aimophila botterii
Aimophila carpalis
Aimophila ruficeps
Lichenostomus flavicollis
Ammodramus maritimus
Poospiza ornata
Pipilo aberti
Pipilo crissalis
Amphispiza quinquestriata
Emblema pictum
Pipilo fuscus
Torreornis inexpectata

Appendix D

Source trees used in Chapter 5

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