
A phylogenetic supertree of the fowls (Galloanserae, Aves)

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The fowls (Anseriformes and Galliformes) comprise one of the major lineages of birds and occupy almost all biogeographical regions of the world. The group contains the most economically important of all bird species, each with a long history of domestication, and is an ideal model for studying ecological and evolutionary patterns. Yet, despite the relatively large amount of systematic attention fowls have attracted because of their socio-economic and biological importance, the species-level relationships within this clade remain controversial. Here we used the supertree method matrix representation with parsimony to generate a robust estimate of species-level relationships of fowls. The supertree represents one of the most comprehensive estimates for the group to date, including 376 species (83.2% of all species; all 162 Anseriformes and 214 Galliformes) and all but one genera. The supertree was well-resolved (81.1%) and supported the monophyly of both Anseriformes and Galliformes. The supertree supported the partitioning of Anseriformes into the three traditional families Anhimidae, Anseranatidae, and Anatidae, although it provided relatively poor resolution within Anatidae. For Galliformes, the majority-rule supertree was largely consistent with the hypothesis of sequential sister-group relationships between Megapodiidae, Cracidae, and the remaining Galliformes. However, our species-level supertree indicated that more than 30% of the polytypic genera examined were not monophyletic, suggesting that results from genus-level comparative studies using the average of the constituent species' traits should be interpreted with caution until analogous species-level comparative studies are available. Poorly resolved areas of the supertree reflect gaps or outstanding conflict within the existing phylogenetic database, highlighting areas in need of more study in addition to those species not present on the tree at all due to insufficient information. Even so, our supertree will provide a valuable foundation for understanding the diverse biology of fowls in a robust phylogenetic framework.

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Introduction

The fowls (Galloanserae; ducks, chicken, and allies) are generally regarded as a monophyletic group (Sorenson *et al.* 2003; Cracraft *et al.* 2004; but see Olson & Fecuccia 1980; Ericson 1996, 1997) that, according to Dickinson (2003), consist of eight families with 452 species. Fowls, which are typically separated into duck-like (Anseriformes) and chicken-like species (Galliformes), include the most economically important birds on earth. Many species in this group have a long history of domestication for socio-economic reasons (e.g. food, game, feather, or display, among others), including chicken (e.g. *Gallus gallus*), quails (e.g. *Coturnix japonica* and *Colinus virginianus*), ring-necked pheasants (*Phasianus colchicus*), turkeys (e.g. *Meleagris gallopavo*), guinea fowls (e.g. *Numida*

meleagris), peafowls (*Pavo cristatus*), ducks (e.g. *Anas platyrhynchos*), and geese (e.g. *Anser anser* and *A. cygnoides*). The global economic value of domesticated fowls is enormous. For example, more domestic chicken meat (over 68 million tons) than beef was produced worldwide in 2004 (FAO 2007). Income from eggs and poultry in the United States was approximately US\$29 billion in 2004 (USDA 2007). Hunting of migratory birds (e.g. ducks and geese) in the United States generates US\$1.3 billion annually for thousands of small businesses (USFWS 2007), and game shooting in the UK similarly supports some 70 000 full-time jobs (PACEC 2006).

Fowls are likewise of particular interest to many biologists. The group comprises the sister group of all remaining species of Neognathae [all living birds with the exception of

tinamous (Tinamidae) and ratites (Struthionidae, Rheidae, Casuariidae, Dromaiidae, and Apterygidae)], and occupies almost all major biogeographical regions of the world (Cra-craft *et al.* 2004). Despite this deep divergence and worldwide distribution, Anseriformes and Galliformes together possess extremely restricted extant species richness relative to their sister group (Neoaves), which covers over 9000 species (Dickinson 2003). Even so, fowls display a remarkable life-history and behavioural diversity as well as morphological plasticity (del Hoyo *et al.* 1992; Dunning 1993; del Hoyo *et al.* 1994; Kear 2005). For example, species within Galliformes show more than a 100-fold difference in body mass (e.g. from < 100 g for *C. japonica* to approximately 10 000 g for *M. gallopavo*), and more than a 20-fold difference in clutch size (e.g. from one for *Lophura bulweri* to approximately 20 for *Aepy-podius arfakianus*). Many galliform species tend to be sedentary, whereas most anseriform species migrate long distances. Within Galliformes, some grouse are characterized by adaptations to open habitats, whereas megapodes and cracids are adapted to forest habitats. Anseriformes are adapted generally to an aquatic lifestyle (e.g. webbed feet), but their reliance on the aquatic habitat differs widely among species. Swans and geese often feed on land at some distance from water, whereas most ducks forage in or close to water. Some fowl species (e.g. *Crax alberti* and *A. laysanensis*) are recognized as being critically endangered (IUCN 2007), whereas others (e.g. *P. colchicus* and *A. platyrhynchos*) are exploited as overabundant game species. Such remarkable diversity in Galloanserae makes it an exceptional group for studying a wide range of questions in ecology, evolution, conservation and management.

Biologists often employ a comparative approach to recognize, test, and interpret adaptive patterns and processes in ecology and evolution. To do so properly, a phylogenetic framework is essential to account for the nonindependence among taxa that arises through the process of descent with modification (Felsenstein 1985b; Harvey & Pagel 1991). Thus, a large, well-resolved (species-level) phylogeny, in addition to its systematic value, represents an indispensable tool for testing broad-scale hypotheses in nature, greatly increasing the statistical power of the associated comparative analyses. Currently, however, it is generally not possible to build large, comprehensive trees from a direct, conventional analysis of true biological characters, such as DNA sequences, due to uneven distribution of research effort across taxa resulting in insufficient homologous data (Sanderson *et al.* 2003; Bininda-Emonds 2005). This state of affairs also holds for Galloanserae, with a general lack of large species-level trees from any single molecular, morphological, or combined data set. To date, the most comprehensive trees for each of Anseriformes and Galliformes are genus-level trees, with Livezey (1997) summarizing the findings of several partial phylogenies for

Anseriformes based on morphology and Crowe *et al.* (2006) deriving a tree for Galliformes from an analysis of morphological and molecular data from 158 out of the 292 extant species.

Instead, supertree analysis provides an alternative method to generate comprehensive and rigorous estimates of phylogeny (Sanderson *et al.* 1998; Bininda-Emonds *et al.* 2004a). Using formal algorithmic procedures, this method combines multiple existing and overlapping source trees, each ideally based on independent data sets (see Gatesy *et al.* 2002), and therefore is able to use more of the information present in the global systematic database. Supertree construction remains a controversial technique and has attracted repeated criticism because it uses only the topological information of the source trees and thus loses contact with the raw data (e.g. Springer & de Jong 2001; Gatesy *et al.* 2002). Biases in some methods have also been noted (e.g. Wilkinson *et al.* 2005, 2007). However, simulation studies have repeatedly shown that supertrees built with sufficiently large and numerous source trees represent the phylogenetic information provided by the source trees accurately (Bininda-Emonds & Sanderson 2001; Chen *et al.* 2003; Levasseur & Lapointe 2003; Piaggio-Talice *et al.* 2004). With these advantages, comprehensive supertrees have been built for a wide range of animals and plants, including all extant mammal species (Bininda-Emonds *et al.* 2007), seabirds (Kennedy & Page 2002), shorebirds (Thomas *et al.* 2004), oscine passerine birds (Jönsson & Fjeldså 2006), dinosaurs (Pisani *et al.* 2002), grasses (Salamin *et al.* 2002) and angiosperms (Davies *et al.* 2004). It is beyond the scope of this article to outline the arguments for and against supertree construction and the reader is directed instead to the relevant literature (e.g. Gatesy *et al.* 2002; Bininda-Emonds *et al.* 2003).

Here, we use the supertree method of matrix representation with parsimony (MRP; Baum 1992; Ragan 1992) to generate a robust estimate of species-level phylogenetic relationships within Galloanserae. The major objectives of this study are: (i) to provide a comprehensive, global view of the group's phylogenetic relationships; (ii) to compare this topology to other comprehensive fowl phylogenies based on the conventional analysis of molecular or morphological characters (e.g. Livezey 1997; Crowe *et al.* 2006); and (iii) to provide a phylogenetic framework for future comparative studies of fowl ecology, evolution, conservation and management.

Materials and methods

Source tree collection

Phylogenetic information for Galloanserae was collated from the published literature by searching online databases, the Web of Science and Zoological Record for the years 1971–2006. We used the following search terms: phylogen*, phenogram*, cladogram*, cladistic*, taxonom*, or fossil* (where the asterisks represent wildcards) in combination with any scientific name of each fowl order, family, subfamily, or

genus (as given in Dickinson 2003) or any major fowl common name (e.g. fowl, gamebird, grouse, quail, pheasant, waterfowl, duck, goose, and swan). Additionally, we examined the references in the source articles we collected to obtain additional studies containing relevant phylogenetic information.

The protocol for inclusion or rejection of source trees was guided by the issues of data quality (e.g. data independence and duplication, see Gatesy *et al.* 2002) following the principles described in Bininda-Emonds *et al.* (2004b) and as implemented in Beck *et al.* (2006). Generally, only trees that were based on an actual analysis of a novel, independent data set were collected for our analysis. Reasons for the exclusion of potential source trees included the lack of any explicit underlying data set (e.g. as for taxonomies), the simple replication of the results of previous studies without any novel analysis, or an insufficient number of Galloanserae species for the tree to be phylogenetically informative in the context of this study. All nonindependent trees were retained at this stage, with corrections for any nonindependence being applied subsequently via downweighting (see below). Nonindependence could arise both between studies (e.g. through use of the same data set on an overlapping species sample) and/or within the same study (e.g. multiple analyses of the same data set using different optimization criteria). For example, gene trees derived from *MT-CYB* (cytochrome b) and *MT-RNR1* (12S rDNA) were held to be independent and independent from a tree based on morphological data, even if they all appeared in the same article. By contrast, all phylogenies based on *MT-CYB* would be classified as nonindependent, regardless of whether or not they occur in different articles or which optimization criteria was used for analysis.

A total of 400 phylogenetic trees derived from molecular and/or non-molecular (e.g. morphological or behavioural) data, and obtained using distance (e.g. neighbor-joining) or character-based methods (e.g. parsimony, maximum likelihood, and Bayesian analysis) were included initially as source trees. A topology equivalent to the classification of Dickinson (2003) was also included as a 'seed tree' to increase taxonomic overlap among source trees while providing only limited and usually uncontroversial phylogenetic information. The use of seed trees has been shown to improve the resolution of the supertree and to decrease computation time in simulation (Bininda-Emonds & Sanderson 2001) and when, suitably downweighted, does not distort the final topology compared to that dictated by the 'real' source trees (see Beck *et al.* 2006). All information in the source trees was coded and stored exactly as it appeared in the source publication (i.e. without any correction for apparent typos and/or synonyms in taxon names) into the tree window of MacClade (Maddison & Maddison 2000).

Standardization of taxon names

The set of 400 source trees, despite not including all extant species of Galloanserae, contained a total of 1368 taxon

names because of the inclusion of numerous typos and synonyms (including the use of common names) for a given species (e.g. 'Chicken' or '*Gallus gallus domesticus*' or '*Gallus gallus* 1' for *Gallus gallus*), of higher-level taxon names (e.g. *Gallus* or Galliformes), or of extinct species (e.g. the Turtle-jawed Moa-nalo, *Cheylchelynechen quassus*) or of non-fowl species (e.g. the Rock Pigeon, *Columba livia*).

Therefore, where possible, the names of all terminal taxa were standardized to those in Dickinson (2003). Appropriate synonyms for unrecognized names were obtained primarily from the Integrated Taxonomic Information Service (ITIS: www.itis.gov) and secondarily from additional searches. All non-fowl species were synonymized to 'outgroup' and higher-level terminal taxa were synonymized to the type species of the taxon (e.g. both *Gallus* and Galliformes were synonymized to *Gallus gallus*) following Bininda-Emonds *et al.* (2004b). Ambiguous names (e.g. 'Basal Anseriformes and Galliformes', 'Other Galliformes' or 'Partridge') and extinct taxa were pruned from the source trees. Synonymization was achieved using the Perl script synonoTree v2.1 (Bininda-Emonds *et al.* 2004b). SynonoTree also accounts for cases where the process of synonymization yields non-monophyletic species by outputting all possible permutations of a given source tree where each such species is represented only once in each of its possible placements. Finally, all trees containing the taxon 'outgroup' were rooted on this taxon, which was subsequently deleted. All other source trees were held to be unrooted. Trees that were synonymized so as to become phylogenetically uninformative (i.e. containing less than three or four species for rooted and unrooted trees, respectively) were deleted, as were any completely unresolved trees. Altogether the synonymization process reduced the number of source trees to 385 (from 108 published studies; including the seed tree) and 43 trees that represented additional permutations of 31 source trees. The identity of all trees, together with their final weights in the supertree analysis (see below) is provided in the online-only supplementary material I.

MRP supertree construction

Supertree construction used MRP, which represents by far the best investigated and most frequently used supertree method (Bininda-Emonds 2004). MRP operates by coding the topology of a tree as a series of binary pseudocharacters, each pseudocharacter representing one informative node in the tree. Taxa derived from the node are scored as 1, those that are not, but are still present on the tree are scored as 0, and taxa present only on other trees in the entire set are scored as ?. The matrix representations of each tree are then combined into a single matrix for parsimony analysis. Normally an all-zero outgroup is added to the matrix. However, we used semi-rooted MRP coding (Bininda-Emonds *et al.* 2005) as implemented in the Perl script SuperMRP v1.2.1 in which

the outgroup was scored with zeros only for rooted trees; for unrooted trees, it was scored as ?

The final MRP matrix consisted of 4713 pseudocharacters that were differentially weighted across trees to account for source-tree nonindependence, whether at the level of the underlying data or because of permutations of a given tree arising from non-monophyletic taxa, again following the guidelines of Bininda-Emonds *et al.* (2004b). The source trees were initially subdivided according to data type, with sets of nonindependent studies within each category being determined on a case-by-case basis: mixed-data analyses (six sets for seven trees), molecular data (83 sets for 236 trees), morphological data (1 set for 59 trees), other data types (13 sets for 22 trees), and unspecified data (13 sets for 13 trees). Weighting was applied in a hierarchical fashion, first according to data set nonindependence and then to permutation nonindependence. For example, pseudocharacters for each of the 59 trees in the single morphological data set received a weight of 0.017 (= 1/59). However, the pseudocharacters for the morphological study of Livezey (1991) were downweighted by an additional factor of two beyond this (to 0.008) to account for the two permutations of this tree generated by synonoTree. Similarly, weighting was applied separately for each set within a category. For example, of the 83 molecular data sets, those consisting of a single source tree received a relative weight of 1 (= 1/1), whereas those with five nonindependent trees (e.g. all *MT-CYB* trees) received a weight of 0.2 (= 1/5). Finally, the seed tree of Dickinson (2003) was given a weight of 0.001 (= at least six times smaller than any other source tree) to minimize its impact on the supertree topology beyond helping to stabilize the analysis. A nexus-formatted file listing the independent data sets and the weights applied to each is available from TreeBASE (Sanderson *et al.* 1994) under the study accession number xxx and matrix accession number xxx.

Parsimony analysis used PAUP* v4.0b10 (Swofford 2002) and employed a parsimony ratchet (Nixon 1999) consisting of 50 batches of 200 replicates initially, followed by a brute force search using all optimal trees found to that point as starting trees. During the reweighting steps, 25% of the MRP pseudocharacters were selected at random and given a weight of two before being returned to their initial differential weights. Starting trees for each batch were obtained using a single random-addition sequence. All searches used TBR branch-swapping. Ratchet searches allowed only a single tree to be retained at any given step, whereas the terminal brute-force search allowed multiple trees. All instructions for the ratchet were produced by the Perl script perlRat v1.0.9 and implemented in PAUP* as a PAUP block. The initial ratchet analysis saved a maximum of 10 050 equally most parsimonious trees. These trees then served as the starting trees for the extended brute-force search saving up to 100 000 trees. The

strict consensus trees from the initial and ratchet and subsequent brute force searches were identical, hinting that the ratchet had reached a form of 'convergence' in that the additional equally most parsimonious solutions showed conflict with existing areas of incongruence rather than generating new conflict (and thereby decreasing resolution). The final supertree was held to be the strict consensus of the set of 100 000 equally most parsimonious solutions (each of length 1418.607). Both it and a majority-rule consensus of the same set of trees have been deposited with TreeBASE (study accession number S2245).

Differential support within the supertree was determined using the rQS index as implemented in QualiTree v1.2.1 (Bininda-Emonds 2003; Price *et al.* 2005), which measures the amount of support and disagreement for a given node in the supertree among the set of source trees. As such, it avoids the inherent nonindependence between MRP pseudocharacters, which violates the assumptions underlying such conventional support measures as the bootstrap (Felsenstein 1985a) or Bremer support (Bremer 1988) and causing them to be invalid in this context. An rQS value varies between +1 and -1, indicating that all sources trees support or contradict the nodes in question, respectively. Empirically, rQS values usually tend to be slightly negative (e.g. Price *et al.* 2005; Beck *et al.* 2006), reflecting the fact that many phylogenies are uninformative for a given node (thereby scoring zero for it) and those that are informative tend to conflict with one another, even if slightly. Therefore, even slightly positive rQS values should be taken to indicate good support. All rQS values for each node on the supertree, together with how many source trees support, conflict, or are equivocal with a given node, are presented in the online-only supplementary material II. All Perl scripts used in this study are freely available from <http://www.uni-oldenburg.de/molekularesystematik/33997.html> or from the second author on request.

Results and discussion

Taxonomic coverage and resolution

Our fowl supertree includes 376 species, comprising over 83% of all 452 fowl species recognized by Dickinson (2003) (Table 1). All 162 Anseriformes species and 74% of all 290 Galliformes species are present in the supertree. The distribution of the 108 studies yielding source trees shows that the number of phylogenetic studies for fowls has increased rapidly since the late 1980s, with a sharp increase in particular for studies using molecular data, either alone or in combination with morphological or other data sources (Fig. 1). Overall, Galloanserae are relatively well-characterized phylogenetically. The number of source trees per fowl species present in the tree (1.0) was more than that in supertrees of well-studied mammalian groups of comparable size [e.g. 0.6 in primates or bats (Purvis 1995; Jones *et al.* 2002), and 0.7 in carnivores

Table 1 Information for major clades of Gallanserae, including number of taxa recognized and covered in this study and summary statistics for the supertrees. n/a, not available.

	Number of species recognized*	Number of species covered in this study	Percent coverage (%)	Percent resolution (%)		
				Strict consensus	Majority rule	rQS
Overall	452	376	83.2	81.1	96.3	0.265
Anseriformes	162	162	100	73.9	97.5	0.135
Anhimidae	3	3	100	100	100	0.091
Anseranatidae	1	1	100	0	0	0
Anatidae	158	158	100	72.6	97.5	0.044
Galliformes	290	214	73.8	86.9	95.8	0.252
Megapodiidae	22	17	77.3	93.8	93.8	0.099
Cracidae†	50	34	68	n/a	n/a	n/a
Numididae	6	6	100	100	100	0.026
Odontophoridae	32	13	40.6	91.7	100	0.021
Phasianidae†	180	144	80	n/a	n/a	n/a

*According to Dickinson (2003).

†Cracidae and Phasianidae were not monophyletic in the supertrees.

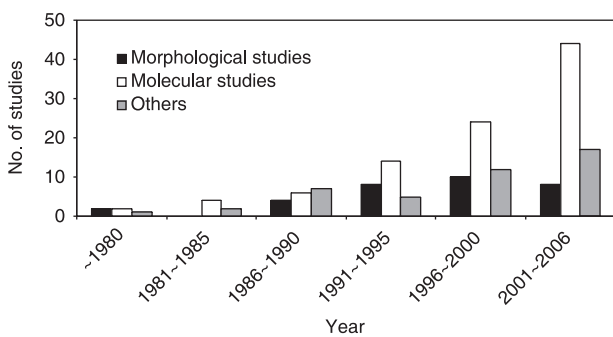


Fig. 1 Temporal distribution of source trees included in the Galloanserae supertree.

(Bininda-Emonds *et al.* 1999)], despite our more conservative source tree inclusion protocol. The value continues to exceed those of the mammalian supertrees even when we calculate it for all extant species, including those not present on the tree (0.83) to make it comparable to the mammal values.

The supertree highlights that poorly characterized species (i.e. those missing from the tree entirely or those found in only a few source trees) tend to belong to groups that themselves are not well-studied. For instance, the majority of species missing in the supertree are assigned to either Odontophoridae (59% missing), Cracidae (32% missing), or Phasianidae (20% missing). The uneven distribution of missing species often appears associated with issues of geography and/or accessibility of the species. For example, species of the genus *Odontophorus*, which represents almost half of all species in Odontophoridae (15 of 32), are found in Neotropical forests, but the genus is represented by only a single species (*Odontophorus gujanensis*)

in the supertree. Similarly, only a single species out of the 20 in *Arborophila* (*Arborophila torqueola*), which generally inhabit Southeast Asian tropical forests or high alpine meadows in the Himalayas and often in widely scattered populations, was present in the supertree. Obviously, deriving a complete phylogenetic estimate of Galloanserae will require an increase in future research effort towards these and other missing species.

Although the limit of 100 000 equally most parsimonious solutions was reached, the strict consensus of them was well-resolved, containing 304 of a maximum possible 375 nodes (= 81.1%; Table 1). This degree of resolution was higher than that for many other supertrees of comparable scale, including those for primates (79%; Purvis 1995), carnivores (78%; Bininda-Emonds *et al.* 1999), marsupials (74%; Cardillo *et al.* 2004), bats (46%; Jones *et al.* 2002), whale and even-toed hoofed mammals (60%; Price *et al.* 2005), shorebirds (50%; Thomas *et al.* 2004), and seabirds (63%; Kennedy & Page 2002). Again, the degree of resolution varied across the tree and among the (monophyletic) families in particular, ranging from 73% for Anatidae to 100% for Anhimidae and Numididae. Smaller families tended to show greater resolution, possibly because of their being fewer nodes that are likely to vary, but even some relatively large families showed high resolution (e.g. 73% for the 15 species of Anatidae) indicating general consensus over their internal relationships. Some cases of decreased resolution among and within families appear to derive more from a lack of agreement among the source trees than from a lack of available information. For example, nearly full resolution (94%) for Megapodiidae was achieved on the basis of 373 pseudocharacters. By contrast, relationships within *Coturnix* were completely unresolved despite having twice as much data

Table 2 Genera that were either ‘not monophyletic’ or of ‘questionable monophyly’ (due to being unresolved with respect to another taxon) in the strict consensus supertree.

Family	Genus	Status	
Anseriformes			
Anatidae	<i>Dendrocygna</i>	Not monophyletic	Fig. 3(B)
Anatidae	<i>Tachyeres</i>	Questionable monophyly	Fig. 3(B)
Anatidae	<i>Tadorna</i>	Not monophyletic	Fig. 3(B,F)
Anatidae	<i>Nettapus</i>	Not monophyletic	Fig. 3(C)
Anatidae	<i>Netta</i>	Questionable monophyly	Fig. 3(B)
Anatidae	<i>Aythya</i>	Questionable monophyly	Fig. 3(B)
Anatidae	<i>Melanitta</i>	Not monophyletic	Fig. 3(B,D)
Anatidae	<i>Bucephala</i>	Not monophyletic	Fig. 3(B,E)
Galliformes			
Megapodiidae	<i>Aepyodius</i>	Not monophyletic	Fig. 3(I)
Cracidae	<i>Pipile</i>	Not monophyletic	Fig. 3(A)
Cracidae	<i>Mitu</i>	Not monophyletic	Fig. 3(A)
Cracidae	<i>Pauxi</i>	Not monophyletic	Fig. 3(A)
Cracidae	<i>Ortalis</i>	Questionable monophyly	Fig. 3(A)
Cracidae	<i>Penelope</i>	Questionable monophyly	Fig. 3(A)
Phasianidae	<i>Francolinus</i>	Not monophyletic	Fig. 3(L,O)
Phasianidae	<i>Syrnaticus</i>	Not monophyletic	Fig. 3(N)
Phasianidae	<i>Coturnix</i>	Questionable monophyly	Fig. 3(O)

available (726 pseudocharacters). The occurrence of the poorly resolved groups in the supertree also highlights areas in need of more rigorous systematic analyses in the future.

To date, the most comprehensive phylogenies for Anseriformes and Galliformes (Livezey 1997 and Crowe *et al.* 2006, respectively) have been at the genus- and not species levels. These trees necessarily assume the monophyly of each genus, often forcing the wide range of ecological and evolutionary hypotheses that have been examined using these trees to be based on the average of the respective biological characters of the constituent species (e.g. Keane *et al.* 2005; Kolm *et al.* 2007). Crucially, however, our species-level supertree showed that more than 30% of the polytypic genera were not monophyletic or of questionable monophyly (Table 2). This suggests that the results from the genus-level comparative studies using the average of the species’ traits should be interpreted with caution until analogous species-level comparative studies are available.

Anseriformes–Galliformes relationships

The supertree supported the monophyly of each of the orders Anseriformes and Galliformes (Figs 2, 3), reflecting historical agreement on this point (but see Prager & Wilson 1976). In addition, both clades enjoyed high support as measured by the rQS index (0.252 for Anseriformes and 0.135 for Galliformes; node numbers 187 and 2, respectively), meaning that monophyly was directly specified by the majority of relevant source trees in each case.

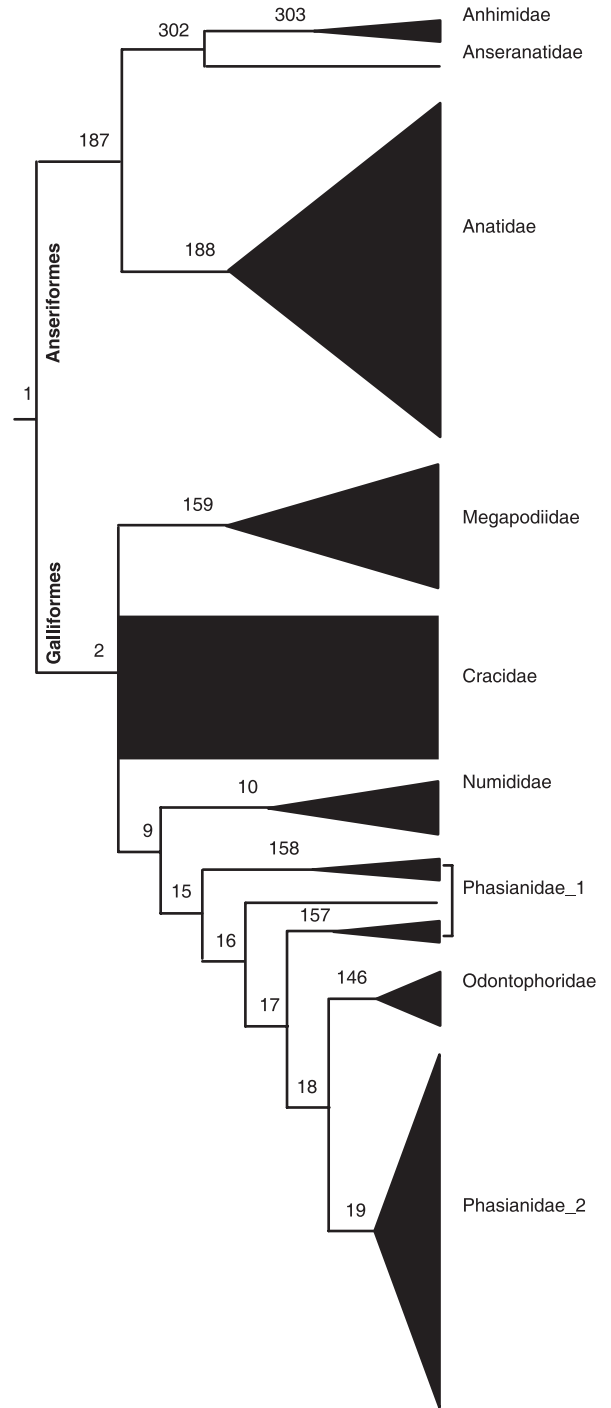


Fig. 2 Simplified representation of the Galloanserae supertree, showing interrelationships of and relative species richness of the major higher-level groups. Numbers on nodes represent node IDs.

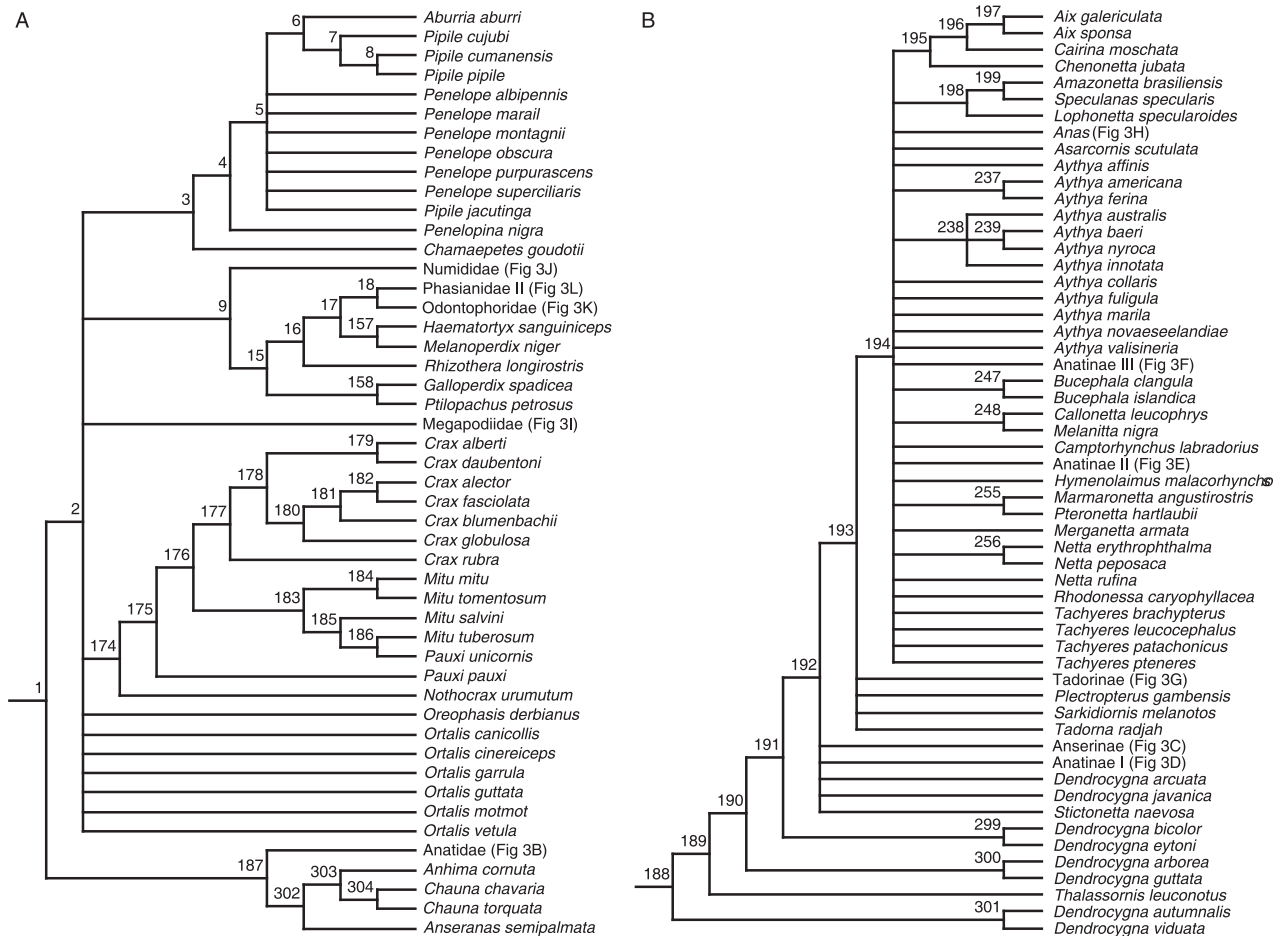


Fig. 3 A–P. Component supertrees of the fowl supertree showing species-level relationships.—A. Galloanserae. —B. Anatidae. —C. Anserinae. —D. Anatinae I. —E. Anatinae II. —F. Anatinae III. —G. Tadorinae. —H. *Anas*. —I. Megapodiidae. —J. Numididae. —K. Odontophoridae. —L. Phasianidae II. —M. Percidinae. —N. Tetraoninae. —O. Phasianinae I. —P. Phasianinae II. Numbers on nodes represent node IDs. rQS support values for each node on the supertree are presented in supplementary material II.

Anseriformes

The supertree supported the partitioning of Anseriformes into the three traditional families (Fig. 2) Anhimidae (screamers), the monotypic Anseranatidae (Magpie Goose), and Anatidae (ducks, geese, and swans). Anatidae was the sister group to the two other families, which was consistent with DNA-DNA hybridization (Sibley & Ahlquist 1990), and nuclear and mitochondrial DNA studies (e.g. Sorenson *et al.* 2003). This resolution, however, conflicted with some morphology-based topologies (e.g. Livezey 1997) and nuclear DNA studies (e.g. RAG-2 exon; see Cracraft *et al.* 2004), where Anhimidae formed the sister group. This uncertainty was also reflected in the slightly low rQS value (0.049; node number 302; Fig. 3A) for the clade containing both Anhimidae and Anseranatidae.

Based on behavioural patterns, Delacour & Mayr (1945) split Anatidae into the two subfamilies Anserinae and Anatinae, a pattern followed by del Hoyo *et al.* (1992). This classification was amended recently by Livezey (1997) and Dickinson (2003), who each recognized five subfamilies, splitting Dendrocygnae and the monotypic Stictonettinae (Freckled Duck) from a redefined Anserinae, and Tadorinae from Anatinae. However, the supertree did not provide strong support for either scheme, with only Anserinae *sensu* Livezey (1997) and Dickinson (2003) being found to be monophyletic within a paraphyletic Anatinae (Fig. 3B).

The supertree revealed a paraphyletic Dendrocygnae with respect to the remaining Anatidae, placing it as the first group to evolve in Anatidae (Fig. 3B). This basal position of

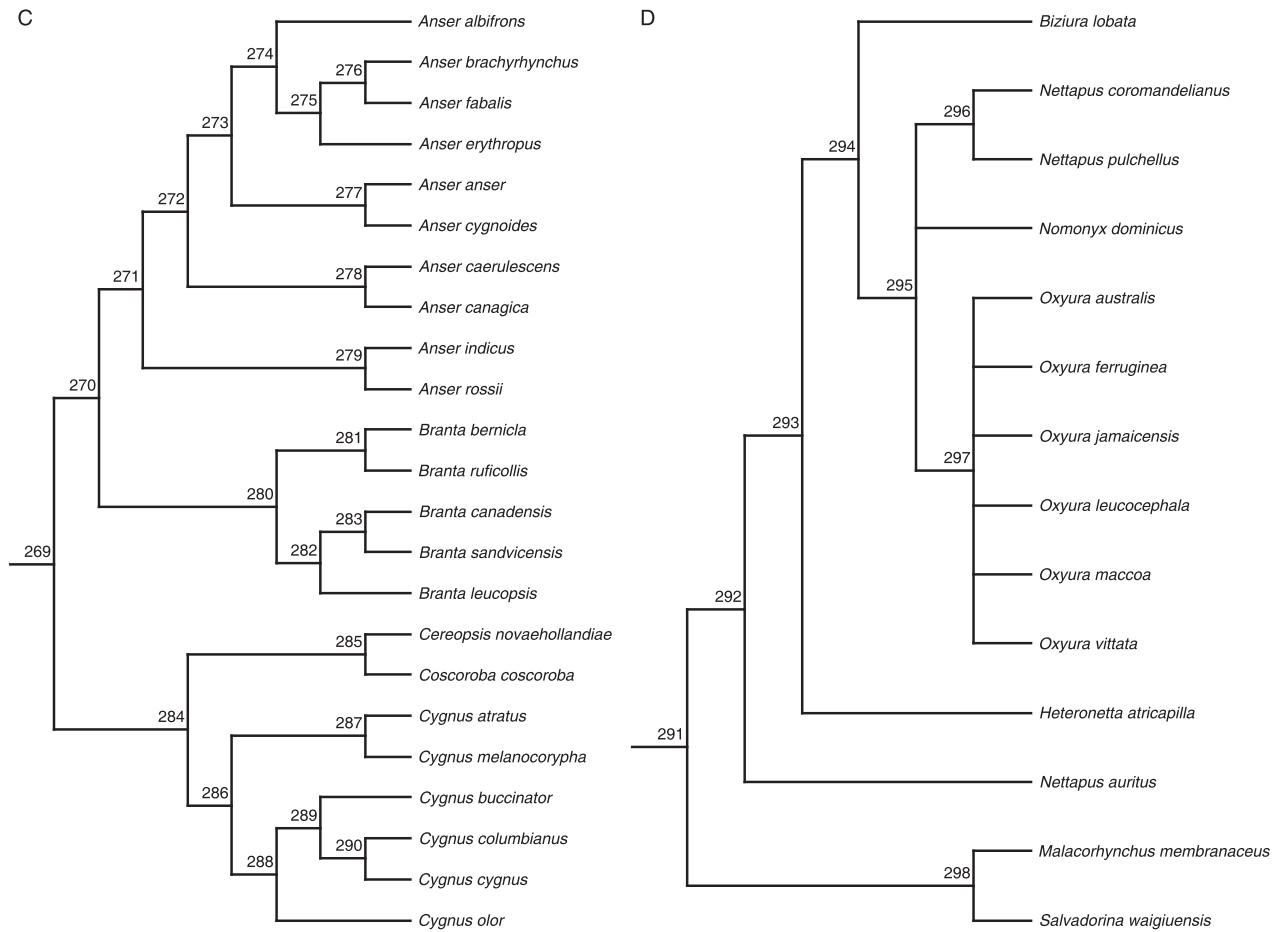


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the subfamily reflected the majority of the source topologies (e.g. Sibley & Ahlquist 1990; Livezey 1997). However, the internal relationships of Dendrocygnae in the supertree contradicted most traditional taxonomic groupings, including the monophyly of *Dendrocygna* (whistling ducks) and its sister group relationship with and *Thalassornis*.

The relative position of Stictonettinae also differed among the source references. Various authors have linked it with any of Dendrocygnae (Woolfenden 1961), Anserinae (Johnsgard 1965), or Tadorninae/Anatinae (Livezey 1997) based on morphological or behavioural characters. Our study also reflected this uncertainty, placing it in a polytomy with all other subfamilies (Fig. 3B).

Anserinae monophyly has been supported by both morphological (e.g. Livezey 1997) and molecular studies (e.g. Donne-Gousse *et al.* 2002), a fact reflected in our supertree (rQS = 0.042; node number 269; Fig. 3C), with 22 source trees supporting its monophyly and only six contradicting it. Resolution within Anserinae was complete and each of the

three polytypic genera recognized by Dickinson (2003) (*Anser*, *Branta*, and *Cygnus*) were recovered as monophyletic (Fig. 3C). *Anser* and *Branta* formed a clade (rQS = 0.042; node number 270; 20 source trees in agreement and only four in conflict), consistent with the majority of studies recognizing them as the tribe Anserini (true geese, e.g. Livezey 1997). However, disagreement among the source trees about the interrelationships of *Cygnus*, *Coscoroba* and *Cereopsis* lead the relative position of these genera being somewhat equivocal in the supertree (rQS = -0.003 for the clade as a whole and rQS = 0.003 for the grouping of *Coscoroba* and *Cereopsis*; Fig. 3C). For example, a morphological study (Livezey 1997) recognized the clade of *Cygnus* + *Coscoroba* as the tribe Cygnini (swans), and *Cereopsis* as the independent tribe Cereopsini, which was regarded as a distant relative to *Cygnus* + *Anser* + *Branta*. However, a recent molecular study placed *Cereopsis* and *Coscoroba* as sister genera, with *Cygnus* as sister to this clade (Donne-Gousse *et al.* 2002), as was found in this study (Fig. 3C). This latter branching pattern is also congruent with the disjunctive

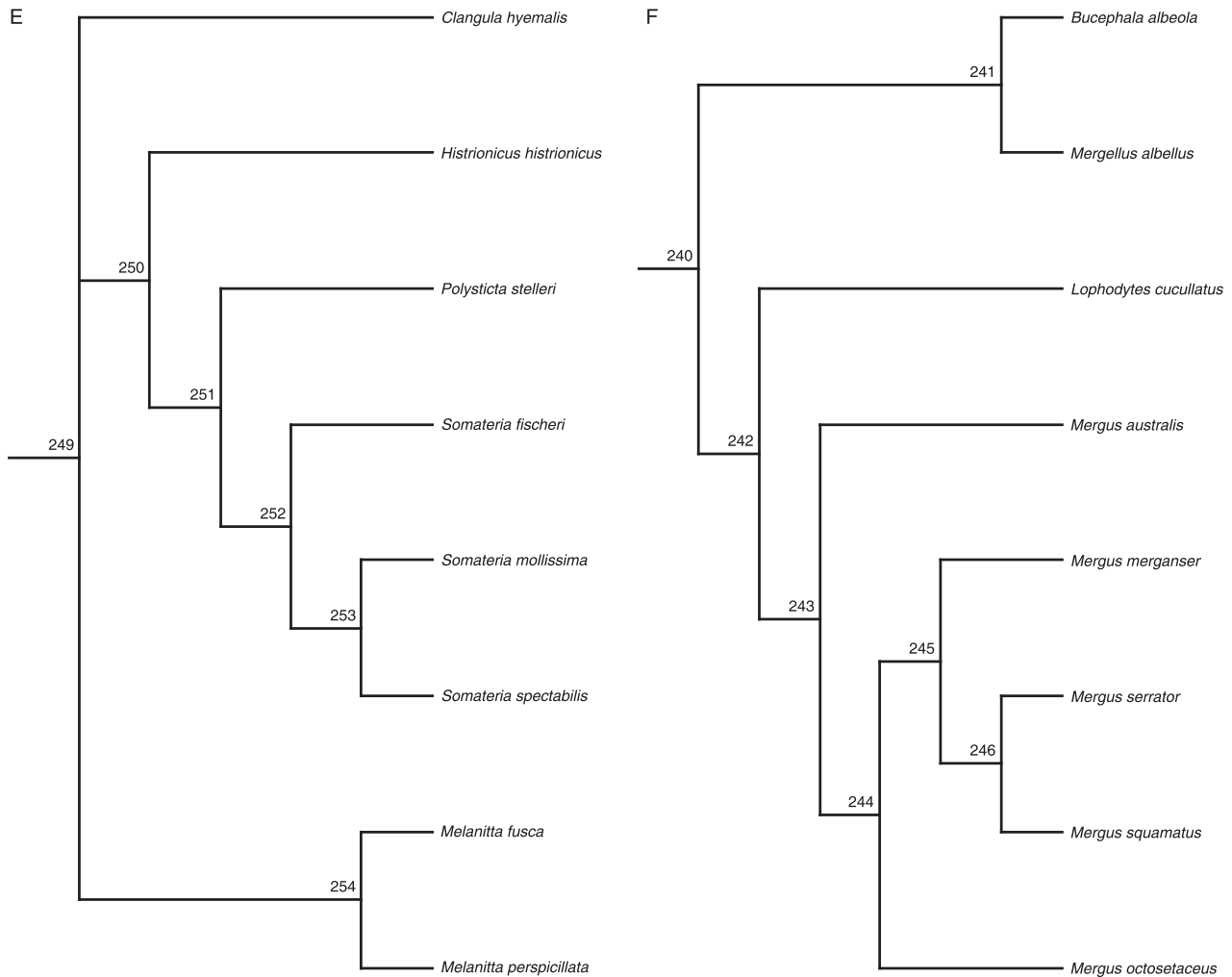


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geographical origins of the genera, with *Cygnus* originating in the Northern Hemisphere and the other two genera coming from the Southern Hemisphere (Donne-Gousse *et al.* 2002).

Strong disagreement exists with respect to the compositions of and interrelationships between Tadorninae and Anatinae, which is reflected in the supertree by neither subfamily being recovered as monophyletic (Fig. 3B). Nor do the two subfamilies form a clade (although the majority of their members do cluster together), with Anserinae embedded within them. For instance, whereas Dickinson (2003) did not delineate any tribes for the subfamilies in his classification, del Hoyo *et al.* (1992) divided Tadorninae + Anatinae into eight tribes. Independently of this, Livezey (1997) also divided Tadorninae into three tribes and Anatinae into five tribes. However, despite the similar numbers of tribes erected by these two authors, few are identical in terms of their composition (e.g. Tadornini, comprising *Tadorna*, *Chloephaga*, *Neochen*, *Alopochen*, and

Cyanochen). Instead, different compositions are the rule. For example, whereas Livezey (1997) included *Hymenolaimus* in Merganettini (Tadorninae), del Hoyo *et al.* 1992 considered it to be part of Anatini (Anatinae).

This supertree reflected these disagreements, with only the tribe Malacorhynchini (comprising *Malacorhynchus* and *Salvadorina*) being recovered unequivocally as monophyletic (Tadornini was monophyletic in the majority-rule supertree), and then strongly so, with 12 source trees supporting the clade and none opposing it ($rQS = 0.031$; node number 298; Fig. 3D). Moreover, whereas Malacorhynchini formed a clade with Oxyurini (*Heteronetta*, *Biziura*, *Nomonyx*, and *Oxyura*, but also unconventionally including *Nettapus*), this clade was positioned as part of a polytomy with Anserinae (or basal to it in the majority-rule supertree), hinting at the possible non-monophyly of Tadorninae + Anatinae (Fig. 3B). Again, however, this uncertainty simply reflects historical disagreement. For

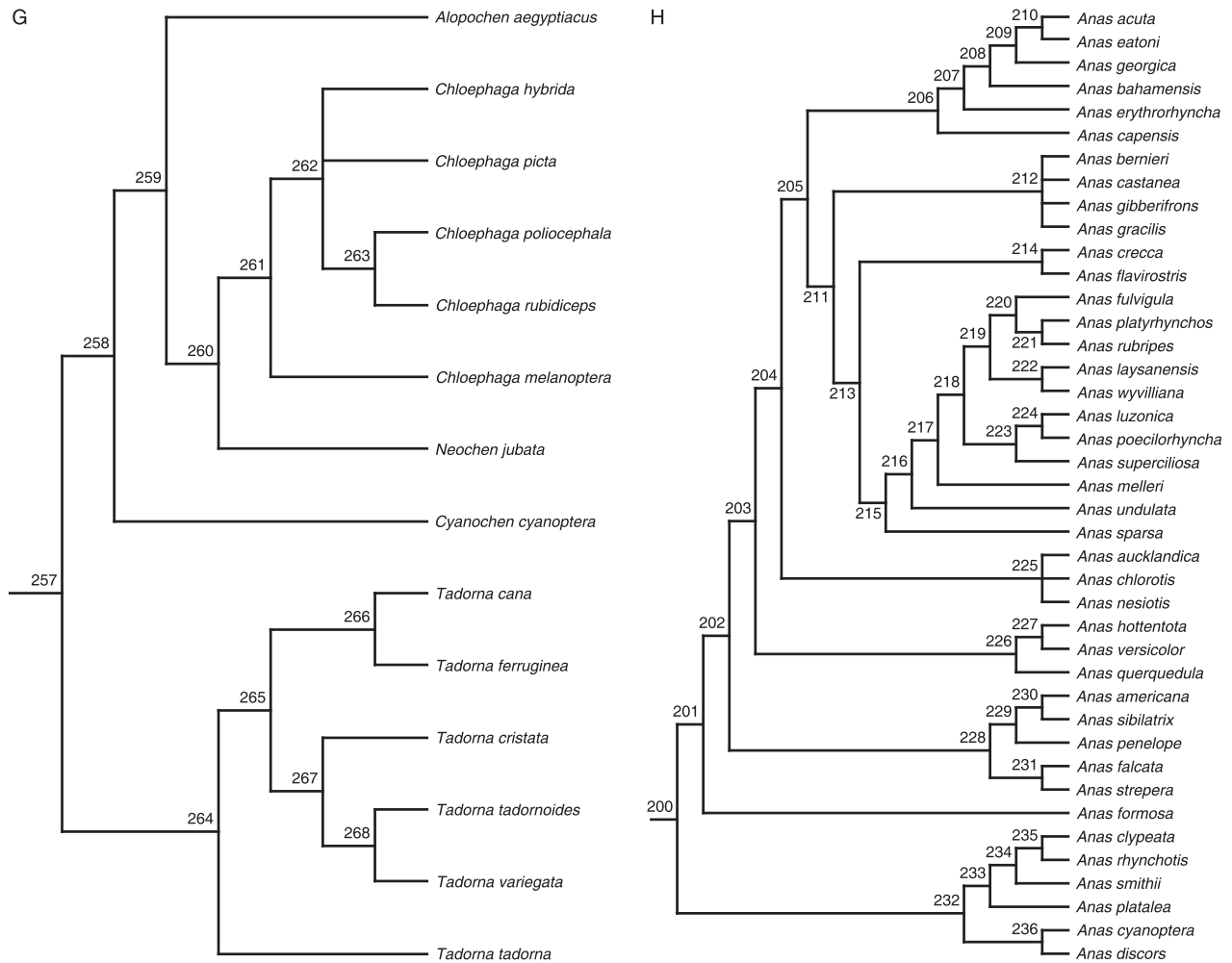


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example, the DNA-DNA hybridization study of Sibley & Ahlquist (1990) placed the *Oxyura* as sister to the remaining Anatidae, which is broadly consistent with our results, but Malacorhynchini in Anatinae, and therefore not directly related to *Oxyura*. By contrast, morphological evidence (e.g. Livezey 1997) tends to place Malacorhynchini at the base of the whole Anatinae. Thus, the relative positions of Malacorhynchini and Oxyurini appear to differ between molecular and morphological data. This conflict was also reflected in the rQS value of -0.018 for the relationship between Malacorhynchini and its sister clade, with six source trees in agreement and 17 source trees in disagreement with this arrangement (node number 291; Fig. 3D).

Resolution within the remaining members of Tadorninae and Anatinae (which formed a clade) was generally poor (Fig. 3B,D–H), with the clade displaying a large basal polytomy and the poor resolution also extending from the tribal-level

down through the genus- and species-levels. Only 46% (6 of 13) of the polytypic genera within Tadorninae + Anatinae were monophyletic in the supertree, and the entire clade was less than 70% resolved. The majority-rule supertree reveals better overall resolution for this clade (97%), and at the species- and the genus-levels in these subfamilies in particular. Resolution, however, remained poor at the higher taxonomic levels.

Galliformes

Traditionally, the relative positions between Megapodiidae (megapodes) and Cracidae (chachalacas, curassows, and guans), and among Numididae (guineafowls), Odontophoridae (New World quails), and Phasianidae (partridges, turkeys, grouse, and pheasants) have been contentious. Some authors suggested a sister-group relationship between Megapodiidae and Cracidae, designating them as the superfamily Cracoidea

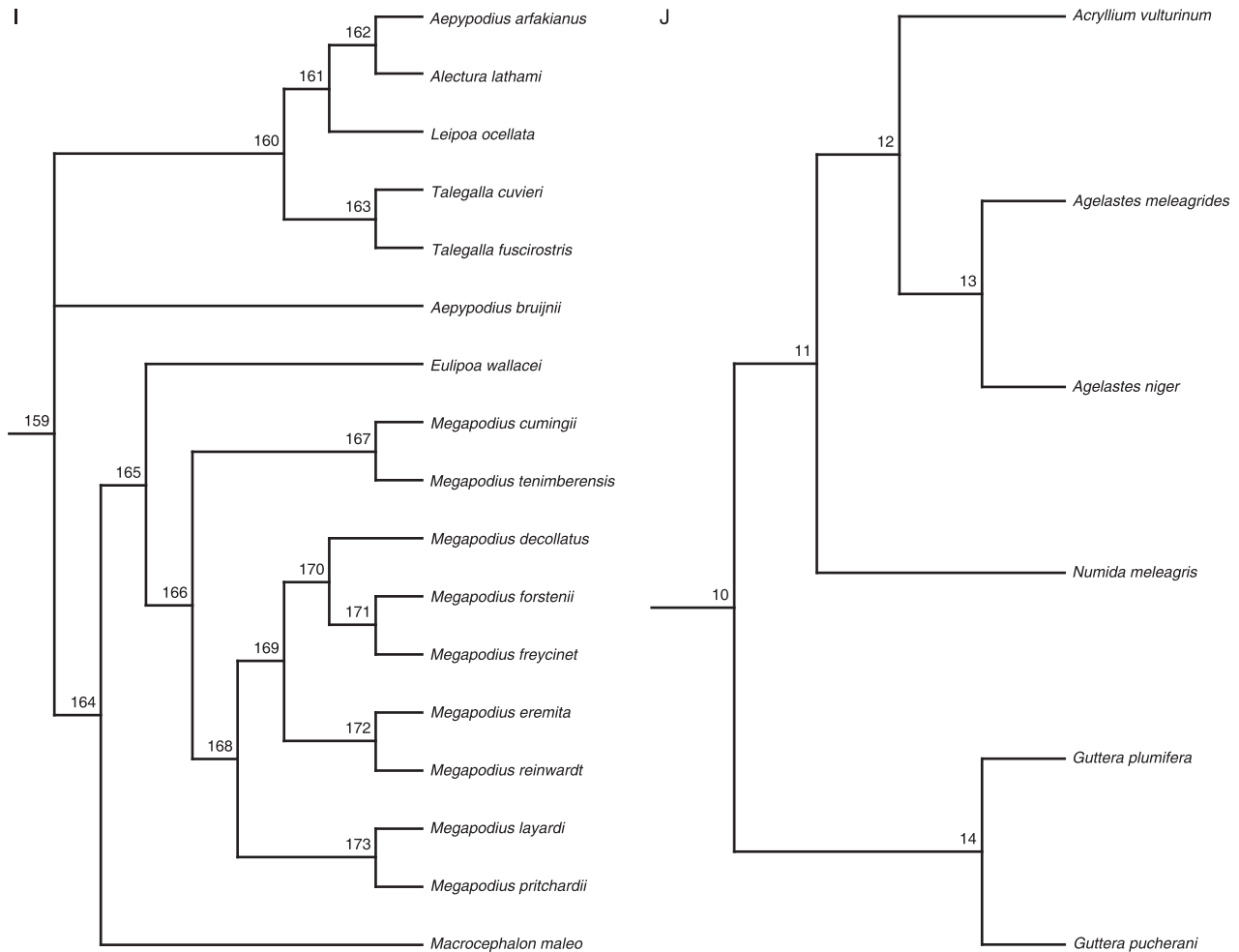


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(Wetmore 1960), the suborder Craci (del Hoyo *et al.* 1994), or even as the independent order Craciformes (Sibley & Ahlquist 1990). However, more recent phylogenies based on morphology (e.g. Dyke *et al.* 2003), molecular data (e.g. Dimcheff *et al.* 2002) or their combination (e.g. Crowe *et al.* 2006) all tend to support Megapodiidae as being sister to the remaining Galliformes (including Cracidae), with Cracidae then being sister to the remaining forms. Although relationships among these groups were unresolved in the strict consensus supertree (Fig. 3A), the majority-rule supertree broadly reflected this latter pattern, supporting the sequential sister-group relationships of Megapodiidae and Cracidae (with the exception of *Ortalis vetula*, thereby making Cracidae non-monophyletic), and the remaining Galliformes; these groups formed part of a large polytomy in the strict-consensus supertree (Figs 2, 3). Support for these sequential sister-group relationships also comes from recent studies based on

transposon data (Kriegs *et al.* 2007) that were published after completion of the supertree analyses.

Our supertree supported Numididae as being sister to the remaining families Odontophoridae and Phasianidae, with the clade comprising all three families having a high rQS value of 0.252 (node number 9; Fig. 3A). This arrangement agrees with those derived from nuclear (e.g. Armstrong *et al.* 2001), mitochondrial (e.g. Dimcheff *et al.* 2002), and combined morphological and molecular data (e.g. Crowe *et al.* 2006). That being said, the position of Odontophoridae remains largely unresolved. For example, recent phylogenetic trees derived from DNA–DNA hybridization (e.g. Sibley & Ahlquist 1990), morphological (e.g. Dyke *et al.* 2003), and combined morphological and molecular data (e.g. Crowe *et al.* 2006) place the family in a variety of positions within Phasianidae. Our supertree follows suit and recovers Odontophoridae as a relatively basal group within Phasianidae. However, it is

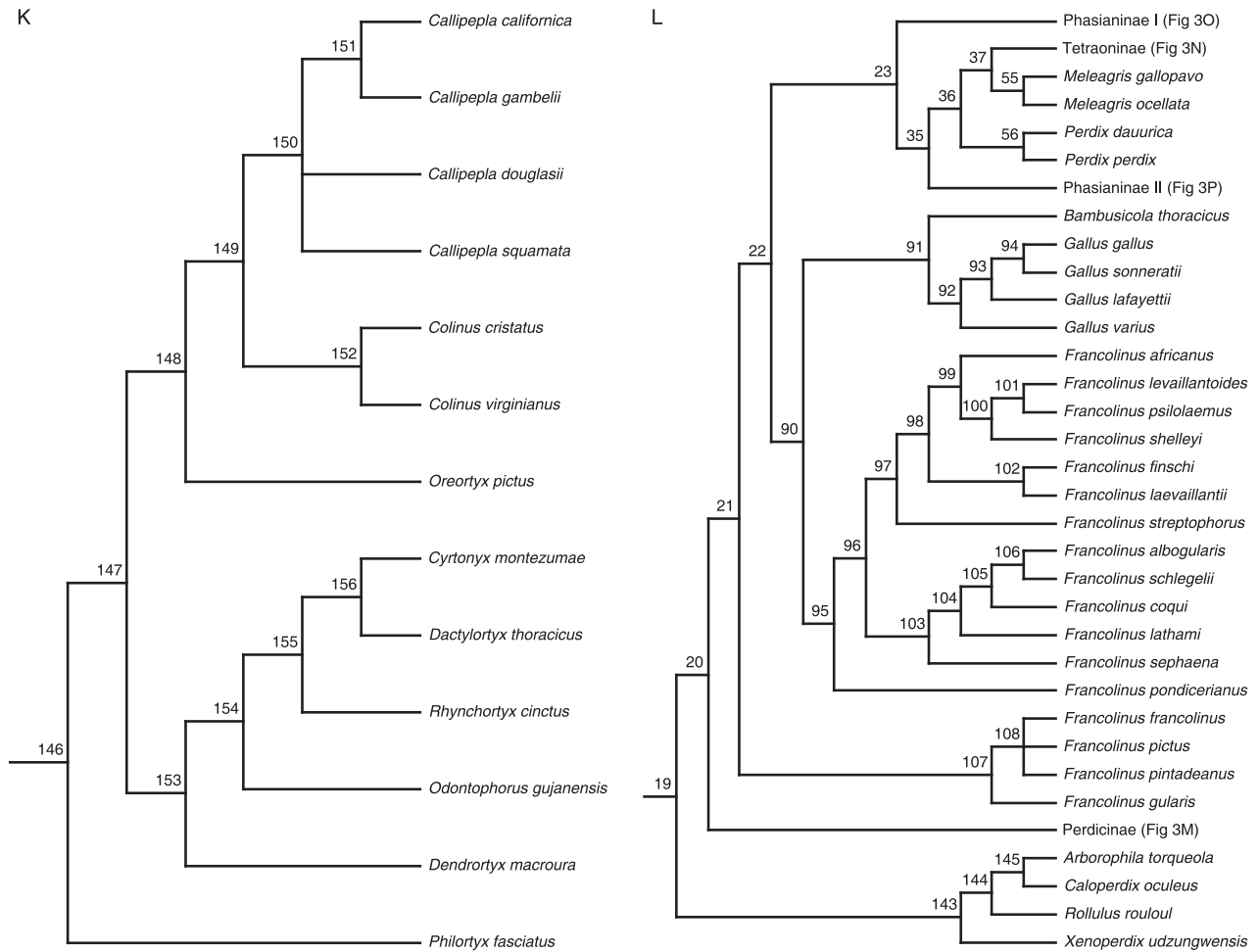


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noteworthy that most phylogenetic studies have included only a few species of Odontophoridae, such that we lack robust phylogenetic information for more than half of all species of this family. Thus, the relative position of Odontophoridae indicated here should likewise be regarded as tentative and should be revisited in the future with increased taxon sampling.

The monophyly of Megapodiidae was supported in the supertree (rQS = 0.099; node number 159; Fig. 3I) and relationships within the family were largely congruent with several traditional species-level phylogenies (e.g. Jones *et al.* 1995; Birks & Edwards 2002; Crowe *et al.* 2006). Support for the monophyly of the genus *Megapodius* in particular was strong, with 10 source trees supporting it and none directly opposing it (rQS = 0.026; node number 166). *Macrocephalon* was recovered as the sister to the clade of *Eulipoa* + *Megapodius* (rQS = 0.023; node number 164). Monophyly of *Aepyodius* was not supported.

The source trees did not support Cracidae monophyly absolutely (Fig. 3A), although the family is monophyletic in the majority-rule supertree (and found in 94% of all 100 000 equally most parsimonious solutions). Much of the conflict can be traced to the historical uncertainty regarding the two genera *Oreophasis* and *Ortalis*, which have been placed within either Cracinae (e.g. Crowe *et al.* 2006) or Penelopinae (e.g. del Hoyo *et al.* 1994; Dickinson 2003). The strict-consensus supertree makes no definitive statement to resolve this conflict (Fig. 3A); however, the majority-rule supertree suggests that the affinities of the two genera lie with Cracinae. However, *Ortalis* was not recovered as monophyletic in either supertree. Recent analyses combining molecular data with osteological, integumentary and behavioural characters placed *Oreophasis* and *Ortalis* within Penelopinae and not Cracinae, and with fairly robust bootstrap support (Frank-Hoeflich *et al.* 2007). As such, placement of these genera

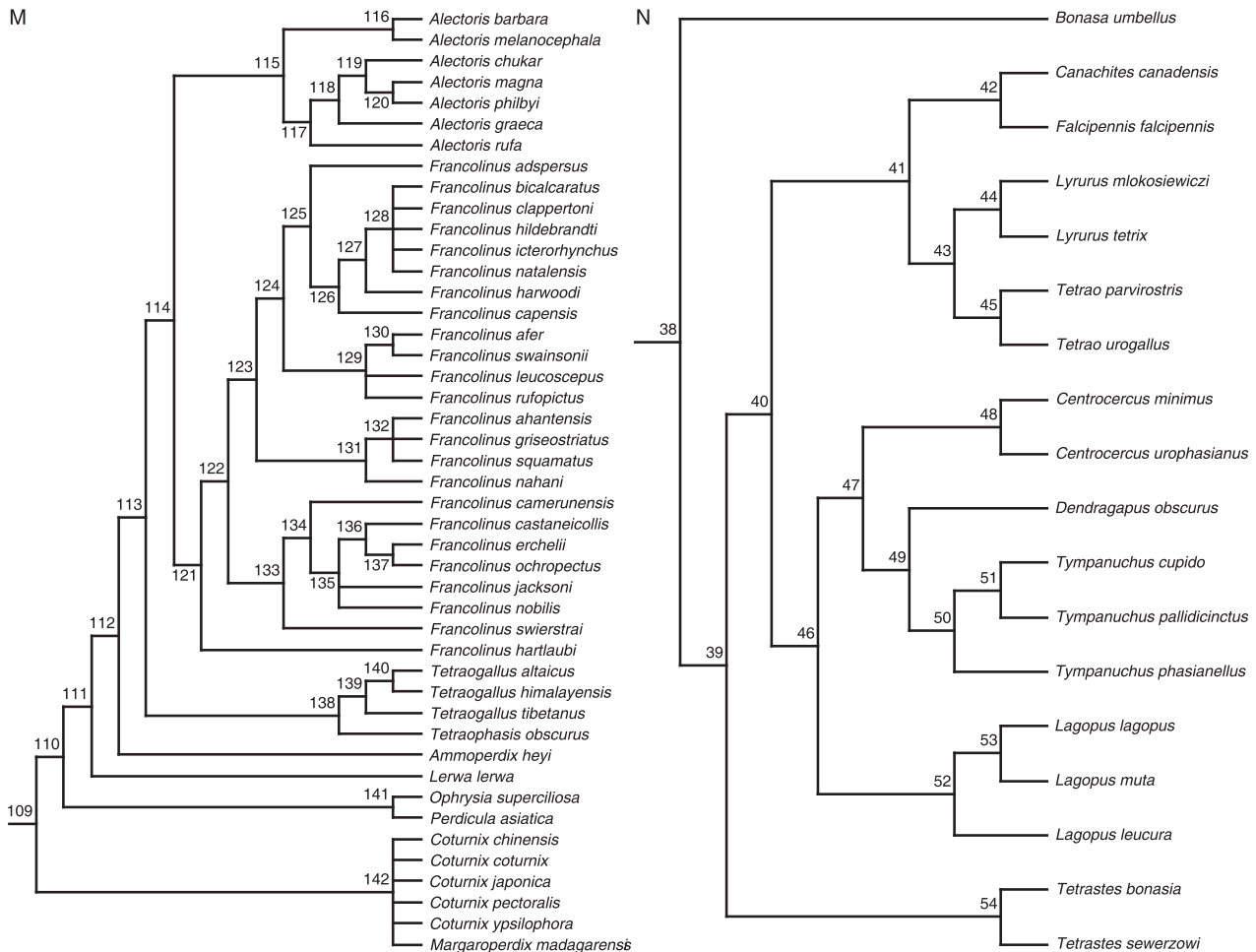


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should still be regarded as tentative and should be revisited with increased taxon sampling and possibly the use of other, novel data types. Beyond this, the subfamilies Cracinae (curassows) and Penelopinae (chachalacas and guans) were found to be monophyletic, although the degree of resolution within each varied considerably. Support for Cracinae was strong, with 26 source trees directly supporting and none directly contradicting it ($rQS = 0.068$; node number 174; Fig. 3A). By contrast, relationships within Penelopinae were unclear, largely because of the non-monophyly of *Penelope*.

Monophyly of Numididae was directly supported by 12 source trees and contradicted by only two ($rQS = 0.026$; node number 10; Fig. 3J). The species-level relationships in the family were completely resolved and each of the two polytypic genera (*Agelastes* and *Guttera*) was monophyletic. The branching pattern within the family disagreed with that presented by Crowe (1978), but was identical to that based later on combined morphological and molecular data (Crowe *et al.* 2006).

Similarly, monophyly of Odontophoridae was also supported, being present in eight source trees and none directly contradicting it ($rQS = 0.021$; node number 146; Fig. 3K). Relationships within the family were largely consistent with those based on a wide range of data types, including osteological (e.g. Holman 1961), ecological (e.g. Johnsgard 1983), allozyme (e.g. Gutierrez *et al.* 1983), and combined morphological and molecular data (e.g. Crowe *et al.* 2006). *Philortyx fasciatus* has been grouped traditionally with some genera adapted to the forest edge, such as *Colinus*, *Callipepla*, and *Oreortyx* (e.g. Holman 1961; Johnsgard 1983), but our supertree placed it as sister to the remaining Odontophoridae. Again, however, this relationship, and all other relationships within the family, should be interpreted with some degree of caution given the poor phylogenetic sampling effort in the family to date.

Within a polyphyletic Phasianidae, sequential sister-group relationships of the four subfamilies *Perdicinae* (partridges),

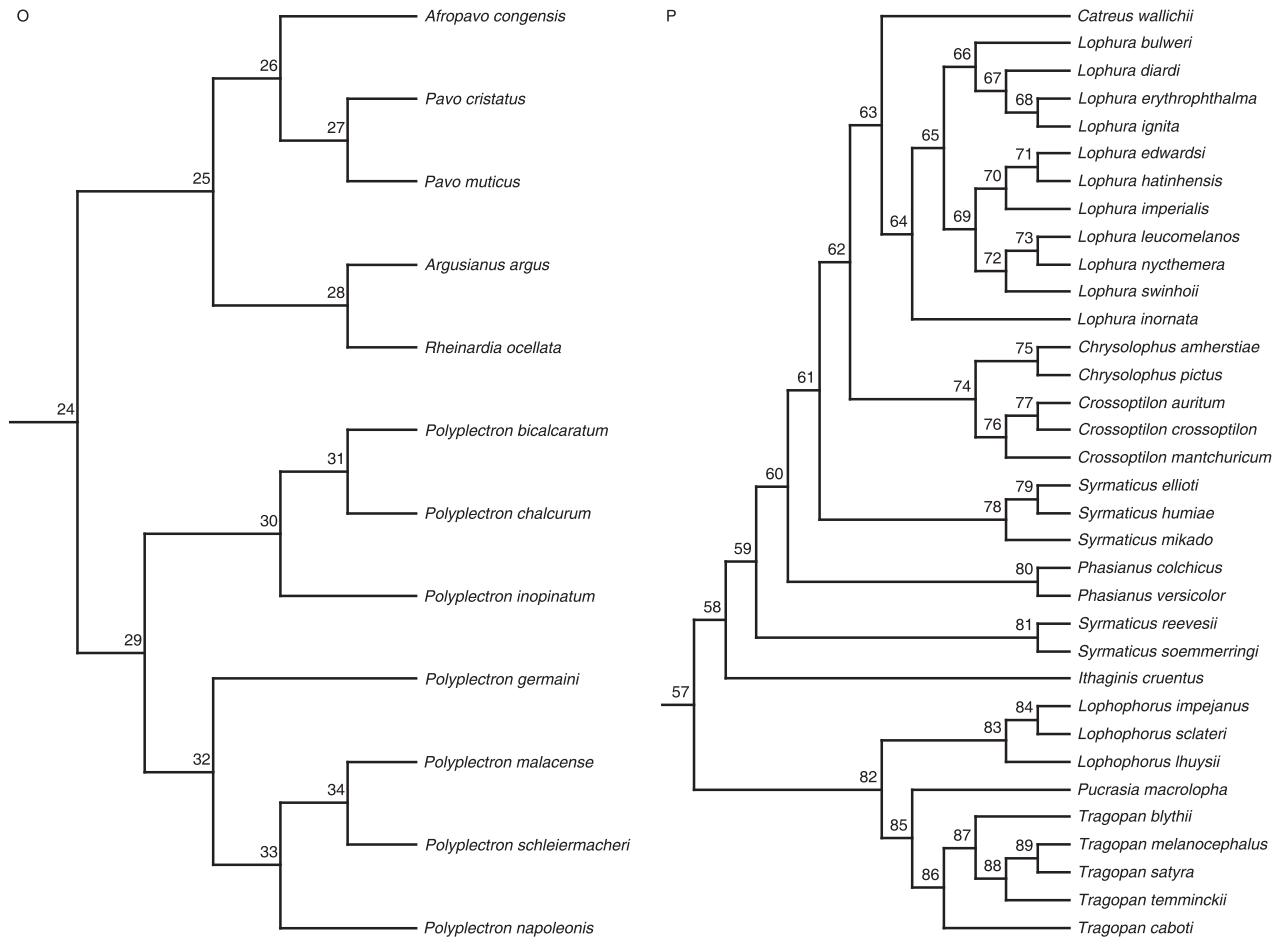


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Meleagridinae (turkeys), Tetraoninae (grouses), and Phasianinae (pheasants) were broadly recovered in the supertree, albeit with some exceptions (Fig. 3A,L–P). The supertree revealed seven subdivisions of *Perdicinae*, six of which were monophyletic. The first was a paraphyletic assemblage of *Rhizothera* and the monotypic genera *Galloperdix*, *Ptilopachus*, *Haematortyx*, and *Melanoperdix* situated basal to *Odontophoridae* and the remaining *Phasianidae* (Fig. 3A). Among these genera, a sister-group relationship between *Galloperdix* and *Ptilopachus* was recovered, concurring with the results of Crowe *et al.* (2006). The second group (rQS = 0.042; node number 143; Fig. 3L) included *Xenoperdix*, *Rollulus*, *Arborophila*, and *Caloperdix*. The species composition and branching pattern within the group was in agreement with Crowe *et al.* (2006), who designated this group as *Arborophilinae*. Similarly, the third group (rQS = 0.044; node number 109; Fig. 3M) corresponds to *Coturnicinae* of Crowe *et al.* (2006) and comprises Old World quails, the partridges *Coturnix* and *Alectoris*, and some *Francolinus* species. Relationships within *Coturnix* were

unresolved, however, and its monophyly could also not be assured. The fourth group (rQS = -0.013; node number 107; Fig. 3L) consisted of *Francolinus gularis*, *F. pictus*, *F. pintadeanus*, and *F. francolinus*. In the fifth group, the monotypic *Bambusicola* formed a clade with the four species of *Gallus* (Fig. 3L). Although *Gallus* is typically allocated to *Phasianinae*, the grouping found in our supertree does find support in Crowe *et al.* (2006), who named it *Gallinae*. In addition, the sister-group relationship between *Bambusicola* and *Gallus* was highly supported with an rQS value of 0.075 (node number 91; Fig. 3L). The sixth group (rQS = -0.018; node number 95; Fig. 3L) consisted of the remaining *Francolinus* species, meaning that the supertree did not support the monophyly of the 41 species of *Francolinus*. Some authors, however, have suggested on the basis of morphological and molecular data that this genus be subdivided into at least five different genera (*Pternistis*, *Francolinus*, *Dendroperdix*, *Peliperdix*, and *Scleroptila*, e.g. Crowe *et al.* 1992; Crowe *et al.* 2006). Although our results did not reflect these generic designations exactly, branching

patterns within *Francolinus* and its relationships with other genera were largely congruent with those in Crowe *et al.* (1992). The final group, the genus *Perdix* (rQS = 0.031; node number 56; Fig. 3L), was placed as the sister taxon to the clade of Meleagridinae + Tetraoninae, albeit with some uncertainty (rQS = -0.005; node number 36; Fig. 3L), with 30 source trees contradicting this placement and 28 supporting it.

The sister-group relationship of Meleagridinae (two species in the genus *Meleagris*) and Tetraoninae was also not strongly supported (rQS = 0.003; node number 37; Fig. 3L), although the monophyly of each showed better support (rQS = 0.018 and 0.106; node number 55 and 38; Fig. 3L,N). Relationships within Tetraoninae were congruent with molecular (e.g. Gutierrez *et al.* 2000; Dimcheff *et al.* 2002; Drovetski 2002) and combined morphological and molecular data (e.g. Crowe *et al.* 2006). The only exception was the position of *Lagopus*, with the low rQS value of the clade containing *Lagopus* and its sister group (-0.062; node number 46; Fig. 3N) suggesting disagreement among the source trees.

The remaining Phasianinae (with the exception of *Gallus*) was split into the peafowl (e.g. *Pavo* and *Polyplectron*; rQS = -0.003; node number 24; Fig. 3O) and pheasant groups (e.g. *Lophura* and *Tragopan*; rQS = 0.005; node number 57; Fig. 3P) separated by the clade comprising *Perdix*, Meleagridinae, and Tetraoninae. Apart from this, the species composition and branching pattern within each group was highly congruent with phylogenetic trees based on molecular and morphological data (e.g. Crowe *et al.* 2006).

Conclusion

Our supertree represents a first attempt to derive a comprehensive species-level phylogeny of Galloanserae, again highlighting the power of a traditional supertree approach (*sensu* Bininda-Emonds 2004) in this regard. Those areas where the supertree was either poorly resolved or incomplete tend to reflect gaps in the existing phylogenetic database (either ongoing disagreement and/or a lack of sufficient, robust phylogenetic information), and highlight areas in need of more study. Some of this missing information could perhaps be gleaned from taxonomies and other studies that are not based on the direct analysis of primary character data. However, given that strong disagreement often exists within the studies we have included here, we felt it prudent not to include these additional sources. Like any phylogenetic hypothesis, our supertree is naturally open to further revision and resolution. In the meantime, however, it will provide a valuable foundation to understand the diverse biology of Galloanserae in a robust phylogenetic framework.

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References

- Armstrong, M. H., Braun, E. L. & Kimball, R. T. (2001). Phylogenetic utility of avian ovomucoid intron G: a comparison of nuclear and mitochondrial phylogenies in Galliformes. *Auk*, *118*, 799–804.
- Baum, B. R. (1992). Combining trees as a way of combining datasets for phylogenetic inference, and the desirability of combining gene trees. *Taxon*, *41*, 3–10.
- Beck, R. M. D., Bininda-Emonds, O. R. P., Cardillo, M., Liu, F.-G. R. & Purvis, A. (2006). A higher-level MRP supertree of placental mammals. *BMC Evolutionary Biology*, *6*, 93.
- Bininda-Emonds, O. R. P. (2003). Novel versus unsupported clades: Assessing the qualitative support for clades in MRP supertrees. *Systematic Biology*, *52*, 839–848.
- Bininda-Emonds, O. R. P. (2004). The evolution of supertrees. *Trends in Ecology and Evolution*, *19*, 315–322.
- Bininda-Emonds, O. R. P. (2005). Supertree construction in the genomic age. In E. A. Zimmer & E. Roalson (Eds) *Molecular Evolution: Producing the Biochemical Data, Part B, Methods in Enzymology*, 395 (pp. 745–757). San Diego: Elsevier.
- Bininda-Emonds, O. R. P., Beck, R. M. D. & Purvis, A. (2005). Getting to the roots of matrix representation. *Systematic Biology*, *54*, 668–672.
- Bininda-Emonds, O. R. P., Cardillo, M., Jones, K. E., MacPhee, R. D. E., Beck, R. M. D., Grenyer, R. *et al.* (2007). The delayed rise of present-day mammals. *Nature*, *446*, 507–512.
- Bininda-Emonds, O. R. P., Gittleman, J. L. & Purvis, A. (1999). Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biological Reviews*, *74*, 143–175.
- Bininda-Emonds, O. R. P., Gittleman, J. L. & Steel, M. A. (2004a). The supertree of life: Procedures, problems, and prospects. *Annual Review of Ecology and Systematics*, *33*, 265–289.
- Bininda-Emonds, O. R. P., Jones, K. E., Price, S. A., Cardillo, M., Grenyer, R. & Purvis, A. (2004b). Garbage in, garbage out: Data issues in supertree construction. In O. R. P. Bininda-Emonds (Ed.) *Phylogenetic Supertrees: Combining Information to Reveal the Tree of Life* (pp. 267–280). Dordrecht: Kluwer.
- Bininda-Emonds, O. R. P. & Sanderson, M. J. (2001). An assessment of the accuracy of MRP supertree reconstruction. *Systematic Biology*, *50*, 565–579.
- Bininda-Emonds, O. R. P., Jones, K. E., Price, S. A., Grenyer, R., Cardillo, M., Habib, M., Purvis, A. & Gittleman, J. L. (2003). Supertrees are a necessary not-so-evil: a comment on Gatesy *et al.* *Systematic Biology*, *52*, 724–729.
- Birks, S. M. & Edwards, S. V. (2002). A phylogeny of the megapodes (aves: Megapodiidae) based on nuclear and mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, *23*, 408–421.
- Bremer, K. (1988). The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution*, *42*, 795–803.
- Cardillo, M., Bininda-Emonds, O. R. P., Boakes, E. & Purvis, A. (2004). A species-level phylogenetic supertree of marsupials. *Journal of Zoology*, *264*, 11–31.
- Chen, D., Diao, L., Eulenstein, O., Fernández-Baca, D. & Sanderson, M. (2003). Flipping: a supertree construction method. In M. F. Janowitz, F.-J. Lapointe, F. R. McMorris, B. Mirkin & F. S. Roberts

- (Eds) *Bioconsensus* (pp. 135–160). DIMACS Series in Discrete Mathematics and Theoretical Computer Sciences, Vol. 61. American Mathematical Society.
- Cracraft, J., Feinstein, J., Garcia-Moreno, J., Barker, F. K., Stanley, S., Sorenson, M. D. *et al.* (2004). Phylogenetic relationships among modern birds (Neornithes): Toward an avian tree of life. In J. Cracraft & M. J. Donoghue (Eds) *Assembling the Tree of Life* (pp. 468–489). Oxford: Oxford University Press.
- Crowe, T. M. (1978). The evolution of guinea-fowl (Galliformes, Phasianidae, Numidinae) taxonomy, phylogeny, speciation and biogeography. *Annals of the South African Museum*, 76, 43–136.
- Crowe, T. M., Harley, E. H., Jakutowicz, M. B., Komen, J. & Crowe, A. A. (1992). Phylogenetic, taxonomic and biogeographical implications of genetic, morphological, and behavioral variations in francolins (Phasianidae: *Francolinus*). *Auk*, 109, 24–42.
- Crowe, T. M., Bowie, R. C. K., Bloomer, P., Mandiwana, T. G., Hedderson, T. A. J., Randi, E. *et al.* (2006). Phylogenetics, biogeography and classification of, and character evolution in, gamebirds (Aves: Galliformes): Effects of character exclusion, data partitioning and missing data. *Cladistics*, 22, 495–532.
- Davies, T. J., Barraclough, T. G., Chase, M. W., Soltis, P. S., Soltis, D. E. & Savolainen, V. (2004). Darwin's abominable mystery: Insights from a supertree of the Angiosperms. *Proceedings of the National Academy of Sciences of USA*, 101, 1904–1909.
- Delacour, J. & Mayr, E. (1945). The family Anatidae. *Wilson Bulletin*, 57, 3–55.
- Dickinson, E. C. (2003). *The Howard and Moore Complete Checklist of the Birds of the World*. London: Christopher Helm.
- Dimcheff, D. E., Drovetski, S. V. & Mindell, D. P. (2002). Phylogeny of Tetraoninae and other galliform birds using mitochondrial 12S and ND2 genes. *Molecular Phylogenetics and Evolution*, 24, 203–215.
- Donne-Gousse, C., Laudet, V. & Hanni, C. (2002). A molecular phylogeny of Anseriformes based on mitochondrial DNA analysis. *Molecular Phylogenetics and Evolution*, 23, 339–356.
- Drovetski, S. V. (2002). Molecular phylogeny of grouse: Individual and combined performance of W-linked, autosomal, and mitochondrial loci. *Systematic Biology*, 51, 930–945.
- Dunning, J. B. (1993). *CRC Handbook of Avian Body Masses*. Ann Arbor: CRC Press.
- Dyke, G. J., Gulas, B. E. & Crowe, T. M. (2003). Suprageneric relationships of galliform birds (Aves, Galliformes): a cladistic analysis of morphological characters. *Zoological Journal of the Linnean Society*, 137, 227–244.
- Ericson, P. G. (1996). The skeletal evidence for a sister group relationship of anseriform and galliform birds—a critical evaluation. *Journal of Avian Biology*, 27, 195–202.
- Ericson, P. G. (1997). Systematic relationships of the paleogene family Presbyornithidae (Aves: Anseriformes). *Zoological Journal of the Linnean Society*, 121, 429–483.
- FAO. (2007). *FAO Statistical Yearbook*. (pp. 2005–2006). Rome: FAO.
- Felsenstein, J. (1985a). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, 39, 783–791.
- Felsenstein, J. (1985b). Phylogenies and the comparative method. *The American Naturalist*, 125, 1–15.
- Frank-Hoeflich, K., Silveira, L. F., Estudillo-López, J., García-Koch, A. M., Ongay-Larios, L. & Piñero, D. (2007). Increased taxon and character sampling reveals novel intergeneric relationships in the Cracidae (Aves: Galliformes). *Journal of Zoological Systematics and Evolutionary Research*, 45, 242–254.
- Gatesy, J., Matthee, C., DeSalle, R. & Hayashi, C. (2002). Resolution of a supertree/supermatrix paradox. *Systematic Biology*, 51, 652–664.
- Gutierrez, R. J., Zink, R. M. & Yang, S. Y. (1983). Genic variation, systematic, and biogeographic relationships of some galliform birds. *Auk*, 100, 33–47.
- Gutierrez, R. J., Barrowclough, G. F. & Groth, J. G. (2000). A classification of the grouse (Aves: Tetraoninae) based on mitochondrial DNA sequences. *Wildlife Biology*, 6, 205–211.
- Harvey, P. H. & Pagel, M. D. (1991). *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.
- Holman, J. A. (1961). Osteology of living and fossil new world quails (Aves, Galliformes). *Bulletin of Florida State of Museum Biological Sciences*, 6, 131–233.
- del Hoyo, J., Elliott, A. & Sargatal, J. (1992). *Handbook of the Birds of the World*, Vol. 1. Barcelona: Lynx Ediciones.
- del Hoyo, J., Elliott, A. & Sargatal, J. (1994). *Handbook of the Birds of the World*, Vol. 2. Barcelona: Lynx Ediciones.
- IUCN. (2007 December). IUCN red list of threatened species. Available via <http://www.iucnredlist.org/>.
- Johnsgard, P. A. (1965). *Handbook of Waterfowl Behavior*. Ithaca: Cornell University Press.
- Johnsgard, P. A. (1983). *The Grouse of the World*. Lincoln: University of Nebraska Press.
- Jones, D. N., Dekker, R. W. R. J. & Roselaar, C. S. (1995). *The Megapodes: Megapodiidae*. Oxford: Oxford University Press.
- Jones, K. E., Purvis, A., MacLarnon, A., Bininda-Emonds, O. R. P. & Simmons, N. B. (2002). A phylogenetic supertree of the bats (Mammalia: Chiroptera). *Biological Reviews*, 77, 223–259.
- Jönsson, K. A. & Fjeldså, J. (2006). A phylogenetic supertree of oscine passerine birds (Aves: Passeri). *Zoologica Scripta*, 35, 149–186.
- Keane, A., Brooke, M. D. L. & McGowan, P. J. K. (2005). Correlates of extinction risk and hunting pressure in gamebirds (Galliformes). *Biological Conservation*, 126, 216–233.
- Kear, J. (2005). *Ducks, Geese and Swans*. Oxford: Oxford University Press.
- Kennedy, M. & Page, R. D. M. (2002). Seabird supertrees: combining partial estimates of Procellariiform phylogeny. *Auk*, 119, 88–108.
- Kolm, N., Stein, R. W., Verspoor, J. J., Mooers, A. O. & Cunningham, E. J. (2007). Can sexual selection drive female life histories? A comparative study on galliform birds. *Journal of Evolutionary Biology*, 20, 627–638.
- Kriegs, J. O., Matzke, A., Churakov, G., Kuritzin, A., Mayr, G., Brosius, J. & Schmitz, J. (2007). Waves of genomic hitchhikers shed light on the evolution of gamebirds (Aves: Galliformes). *BMC Evolutionary Biology*, 7, 190.
- Leveseur, C. & Lapointe, F.-J. (2003). *Increasing Phylogenetic Accuracy with Global Congruence*. In M. F. Janowitz, F.-J. Lapointe, F. R. McMorris, B. Mirkin & F. S. Roberts (Eds) *Bioconsensus* (pp. 221–230). DIMACS Series in Discrete Mathematics and Theoretical Computer Sciences, Vol. 61. American Mathematical Society.
- Livezey, B. C. (1991). A phylogenetic analysis and classification of recent dabbling ducks (tribe Anatini) based on comparative morphology. *Auk*, 108, 471–507.
- Livezey, B. C. (1997). A phylogenetic classification of waterfowl (Aves: Anseriformes), including selected fossil species. *Annals of Carnegie Museum*, 66, 457–496.

- Maddison, D. R. & Maddison, W. P. (2000). *Macclade 4: Analysis of Phylogeny and Character Evolution*, Version 4.0. Sunderland: Sinauer Associates.
- Nixon, K. C. (1999). The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics*, 15, 407–414.
- Olson, S. L. & Fecuccia, A. (1980). *Presbyornis* and the origin of Anseriformes. *Smithsonian Contributions to Zoology*, 323, 1–24.
- PACEC. (2007 August). The economic and environmental impact of sports hunting. Available via <http://www.Shootingfacts.Co.Uk/>.
- Piaggio-Talice, R., Burleigh, J. G. & Eulenstein, O. (2004). Quartet supertrees. In O. R. P. Bininda-Emonds (ed.) *Phylogenetic Supertrees: Combining Information to Reveal the Tree of Life* (pp. 173–191) Dordrecht: Kluwer.
- Pisani, D., Yates, A. M., Langer, M. C. & Benton, M. J. (2002). A genus-level supertree of the Dinosauria. *Proceedings of the Royal Society B*, 269, 915–921.
- Prager, E. M. & Wilson, A. C. (1976). Congruency of phylogenies derived from different proteins: a molecular analysis of the phylogenetic position of cracid birds. *Journal of Molecular Evolution*, 9, 45–57.
- Price, S. A., Bininda-Emonds, O. R. P. & Gittleman, J. L. (2005). A complete phylogeny of the whales, dolphins and even-toed hoofed mammals (Cetartiodactyla). *Biological Reviews*, 80, 445–473.
- Purvis, A. (1995). A composite estimate of primate phylogeny. *Philosophical Transactions of the Royal Society B*, 348, 405–421.
- Ragan, M. A. (1992). Phylogenetic inference based on matrix representation of trees. *Molecular Phylogenetics and Evolution*, 1, 53–58.
- Salamin, N., Hodkinson, T. R. & Savolainen, V. (2002). Building supertrees: an empirical assessment using the grass family (Poaceae). *Systematic Biology*, 51, 136–150.
- Sanderson, M. J., Donoghue, M. J., Piel, W. & Eriksson, T. (1994). TreeBASE: a prototype database of phylogenetic analyses and an interactive tool for browsing the phylogeny of life. *American Journal of Botany*, 81, 183.
- Sanderson, M. J., Purvis, A. & Henze, C. (1998). Phylogenetic supertrees: Assembling the trees of life. *Trends in Ecology and Evolution*, 13, 105–109.
- Sanderson, M. J., Driskell, A. C., Ree, R. H., Eulenstein, O. & Langley, S. (2003). Obtaining maximal concatenated phylogenetic data sets from large sequence databases. *Molecular Biology and Evolution*, 20, 1036–1042.
- Sibley, C. G. & Ahlquist, J. E. (1990). *Phylogeny and Classification of Birds: a Study in Molecular Evolution*. New Heaven: Yale University Press.
- Sorenson, M. D., Oneal, E., Garcia-Moreno, J. & Mindell, D. P. (2003). More taxa, more characters: the hoatzin problem is still unresolved. *Molecular Biology and Evolution*, 20, 1484–1499.
- Springer, M. S. & de Jong, W. W. (2001). Phylogenetics: which mammalian supertree to bark up? *Science*, 291, 1709–1711.
- Swofford, D. L. (2002). *PAUP**. Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4. Sunderland, Massachusetts: Sinauer Associates.
- Thomas, G. H., Wills, M. A. & Szekely, T. (2004). A supertree approach to shorebird phylogeny. *BMC Evolutionary Biology*, 4, 28.
- USDA. (2007 August). Poultry yearbook. Available Via (<http://usda.Mannlib.Cornell.Edu/mannusda/viewdocumentinfo.Do?Documentid=1367>).
- USFWS. (2007 August). Economic Analysis of the Migratory Bird Hunting Regulations for the 2007–08 Season. Available Via (<http://www.Fws.Gov/migratorybirds/reports/specialtopics/economicanalysis-2007update.Pdf>).
- Wetmore, A. (1960). A classification for the birds of the world. *Smithsonian Miscellaneous Collection*, 139, 1–37.
- Wilkinson, M., Cotton, J. A., Creevey, C., Eulenstein, O., Harris, S. R., Lapointe, F.-J., Levasseur, C., McInerney, J. O., Pisani, D. & Thorley, J. L. (2005). The shape of supertrees to come: tree shape related properties of fourteen supertree methods. *Systematic Biology*, 54, 419–431.
- Wilkinson, M., Cotton, J. A., Lapointe, F.-J. & Pisani, D. (2007). Properties of supertree methods in the consensus setting. *Systematic Biology*, 56, 330–337.
- Woolfenden, G. (1961). Post-cranial osteology of the waterfowl. *Bulletin of the Florida State Museum Biological Sciences*, 6, 1–129.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Supplementary Material I Source trees used to construct the galloanserae supertree subdivided according to the independent data set they contributed to. The relative weights for the pseudocharacters associated with each source tree are also provided. Number of permutations refers to the number of trees that resulted from the synonymization process because of having to accommodate non-monophyletic taxa.

Supplementary Material II rQS values for the strict consensus supertree, indicating nodal support (\pm SE) among the set of source trees together with the number of source trees supporting, conflicting or equivocal with a given node. Node numbers refer to Figs 2 and 3.

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