

Phylogeny and evolution of the European Goldfinch (*Carduelis carduelis*) and its allies – a review of the “bird of the year”

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Abstract In 2017 the European Goldfinch (*Carduelis carduelis*) was voted to be the “bird of the year” in Hungary. This is a partially migrant species; most of the European populations are resident, however, its breeding range extends to East from the Sweden-Poland-Moldova axis towards the Yenisei with some of the populations wintering in Kazakhstan and South of Turkey. The European Goldfinch is classified within the Carduelinae subfamily including approximately a hundred species. Several taxonomic changes were introduced in this group during the last fifteen years, however, we still do not understand much of their origin and evolutionary history. My aim in this paper is to collect existing knowledge on the phylogeny and evolution of the Carduelinae finches and their allies, with a particular focus on the European Goldfinch and its closest relatives. Furthermore, here I point out uncertainties in different phylogenetic sources of finches, which careful consideration can be useful in similar evolutionary studies. Finally, I summarise some vision for future research.

Keywords: Carduelinae, finches, Fringillidae, evolution, phylogeny, taxonomy

Összefoglalás 2017-ben a tengelic (*Carduelis carduelis*) nyerte el az „év madara” címet Magyarországon. Egy részlegesen vonuló fajról van szó, melynek európai populációi jórészt egész évben megfigyelhetők, azonban költőterülete a Svédország-Lengyelország-Moldova vonaltól keletre, egészen Ázsia középső részéig kiterjed. Néhány populáció Kazahsztánban és Törökországtól délre telel. A tengelic a Carduelinae alcsaládba tartozik, mely közel száz fajt foglal magába. Számos taxonómiai változás történt a csoportban az elmúlt tizenöt évben, azonban fejlődéstörténetükről és eredetükről mégis keveset tudunk. Jelen tanulmányban megpróbálom összefoglalni a Carduelinae pintyek filogenetikájáról és evolúciójáról megszerzett tudásunkat, különös tekintettel a tengelicre és rokonaira. Továbbá szeretném felhívni a figyelmet a különböző forrásokban fellelhető filogenetikai bizonytalanságokra, melyek áttekintése más, hasonló tanulmányok kidolgozása esetében is hasznosak lehetnek. Végezetül összefoglalom a már említett taxonómiai változásokat és a lehetséges kutatási irányokat.

Kulcsszavak: Carduelinae, pintyek, Fringillidae, fejlődéstörténet, filogenetika, taxonómia

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Phylogenetic position of true finches (Fringillidae) among their bird allies

A wide variety of phylogenetic studies can be found in the literature ranging from those that explore connections among bird groups sampling one or a few species from each families (let me refer to this type of phylogeny as type-A), through robust analyses of genetic data of thousands of species (type-B), to those that describe deep phylogenetic relationships among species within a single family (type-C).

Based on the analysis of nuclear gene sequences of some randomly chosen species, Johansson *et al.* (2008) revised the phylogeny of Passerida and concluded that finches (Fringillidae) form a common clade with accentors, weavers, estrildine finches, sparrows, New World sparrows, and wagtails (type-A). This is fairly similar to previous (Ericson *et al.* 2003, Barker *et al.* 2004, Hackett *et al.* 2008) and more recent (Claramunt & Cracraft 2015, Prum *et al.* 2015, Moyle *et al.* 2016, Päckert *et al.* 2016) results indicating that true finches constitute one of the youngest evolutionary lineages in songbirds. Nevertheless, the deeper comparison of these studies is almost impossible due to the significantly different species sets they used to investigate relationships among genera or higher taxonomic units.

The only robust analysis to date (type-B) that contains more detailed information on relationships among finch lineages than the above mentioned studies (Burleigh *et al.* 2015, but see also Jetz *et al.* 2012, Kumar *et al.* 2017) showed that the Fringillidae is polyphyletic because all genera classified within the family are clustered together with a single genus from Emberizidae and/or Passeridae. This points to the need of revising the taxonomic and nomenclatural position of those genera, creating the possibility of narrowing evolutionary studies to monophyletic groups in which evolutionary hypotheses could be more acceptable.

Furthermore, these type of uncertainties imply the necessity of further gene sequencing studies in the so far uncovered groups which might be the reason why some researchers could only accept the usage of Jetz *et al.*'s (2012) phylogenetic trees in broad scale analyses instead of narrow, single-genus studies. Jetz *et al.* combined genetic data with taxonomic information for creating the phylogeny of all extant bird species. However, the most beneficial content of these trees the resolved bifurcations and available time scale at a species level.

Phylogenetic relationships of cardueline finches within the Fringillidae family

Before moving on to the detailed phylogenies of the Fringillidae family (type-C), more comprehensive studies (type-B) could help to summarise the relationships among the genera involved.

Based on the results of the TimeTree of Life project (Hedges *et al.* 2006, Hedges *et al.* 2015, Kumar *et al.* 2017), 11 cardueline genera can be distinguished among the 69 finch genera within the family (*Figure 1*). The Carduelinae subfamily appears to be polyphyletic on this tree, although the tree is poorly resolved due to multiple polytomies (non-bifurcated nodes).

Different studies use conflicting sources regarding to taxonomic classification of species. The number of species classified as finch largely varies up to an extreme 993 species (Payevsky 2015). While the above mentioned tree contains 235 species of finches, in the BirdLife Checklist (BirdLife International 2015) only 165 extant species are classified obviously as Fringillidae. Using this taxon list, phylogenies can be downloaded from the Birdtree site (Jetz *et al.* 2012), and comparing the trees, several further dissimilarity can be identified at the genus level. Many genera, including *Eremopsaltria*, *Hemignathus*, *Loxioides*, *Telespiza*, *Bucanetes*, *Pseudonestor*, *Oreomystis*, *Loxops*, *Palmeria*, *Vestiaria*, *Himatione* form a sister clade of Carduelinae on the TimeTree of Life (Kumar *et al.* 2017), whilst

they are merged into the cardueline finches on the Birdtree either choosing a random phylogeny or generating consensus tree from a larger set of trees (Jetz *et al.* 2012).

Specifically, these concise works motivate researchers to consider the optimal choice of phylogenetic sources for their studies. As mentioned above, Jetz *et al.*'s (2012) trees have resolved bifurcations, contrasting to the approach of Kumar *et al.* (2017), however, it is often challenging to choose an optimal number of trees. *Figure 2* allows the comparison of

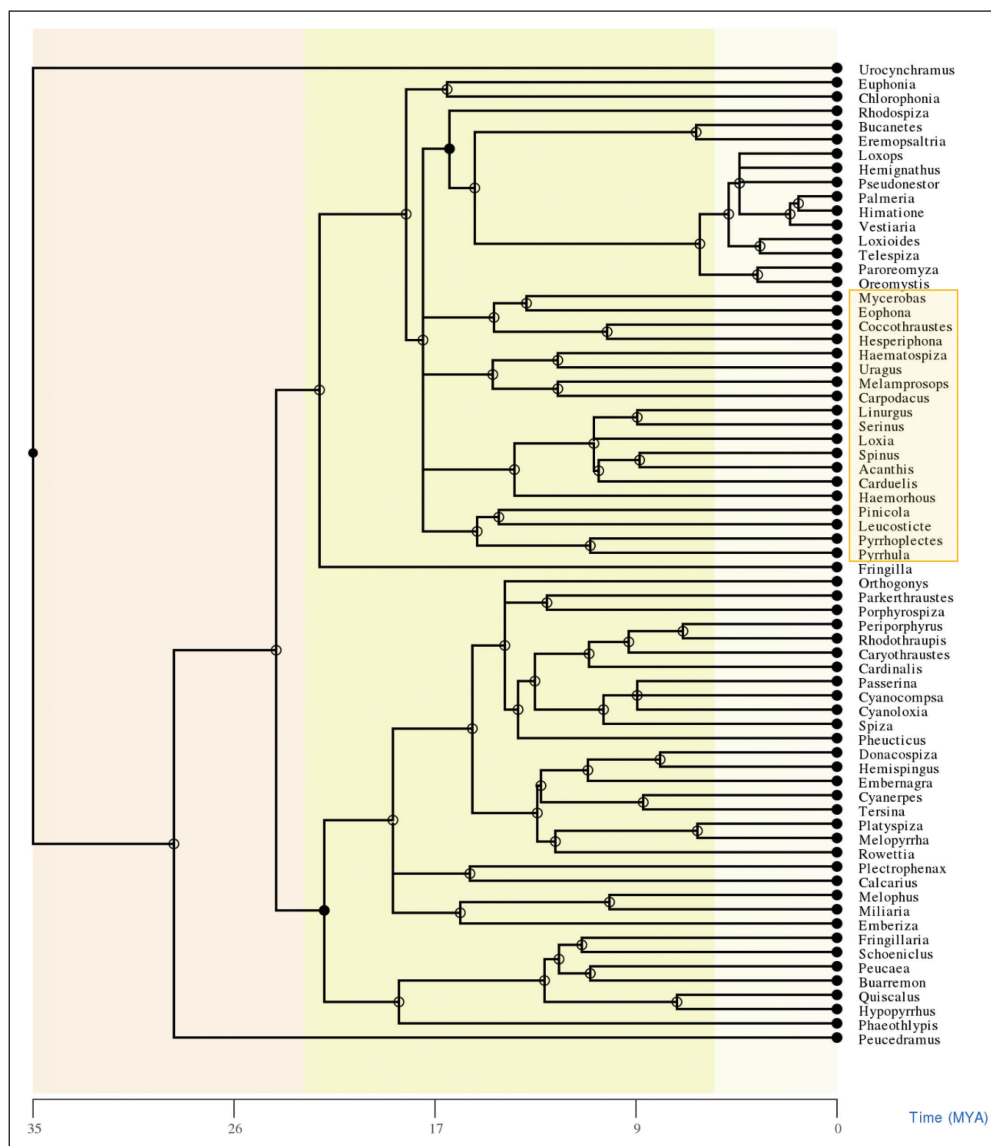


Figure 1. Phylogenetic position of cardueline taxa (boxed) among 69 true finch genera based on the tree of Kumar *et al.* (2017). (Enlargeable figures are available in the electronic version.)

1. ábra A cardueline pintyek (bekeretezett rész) filogenetikai helyzete 69 valódi pinyt nemzetség között (Kumar *et al.* 2017 nyomán). (Az elektronikus változatban nagyíthatóak a képek.)

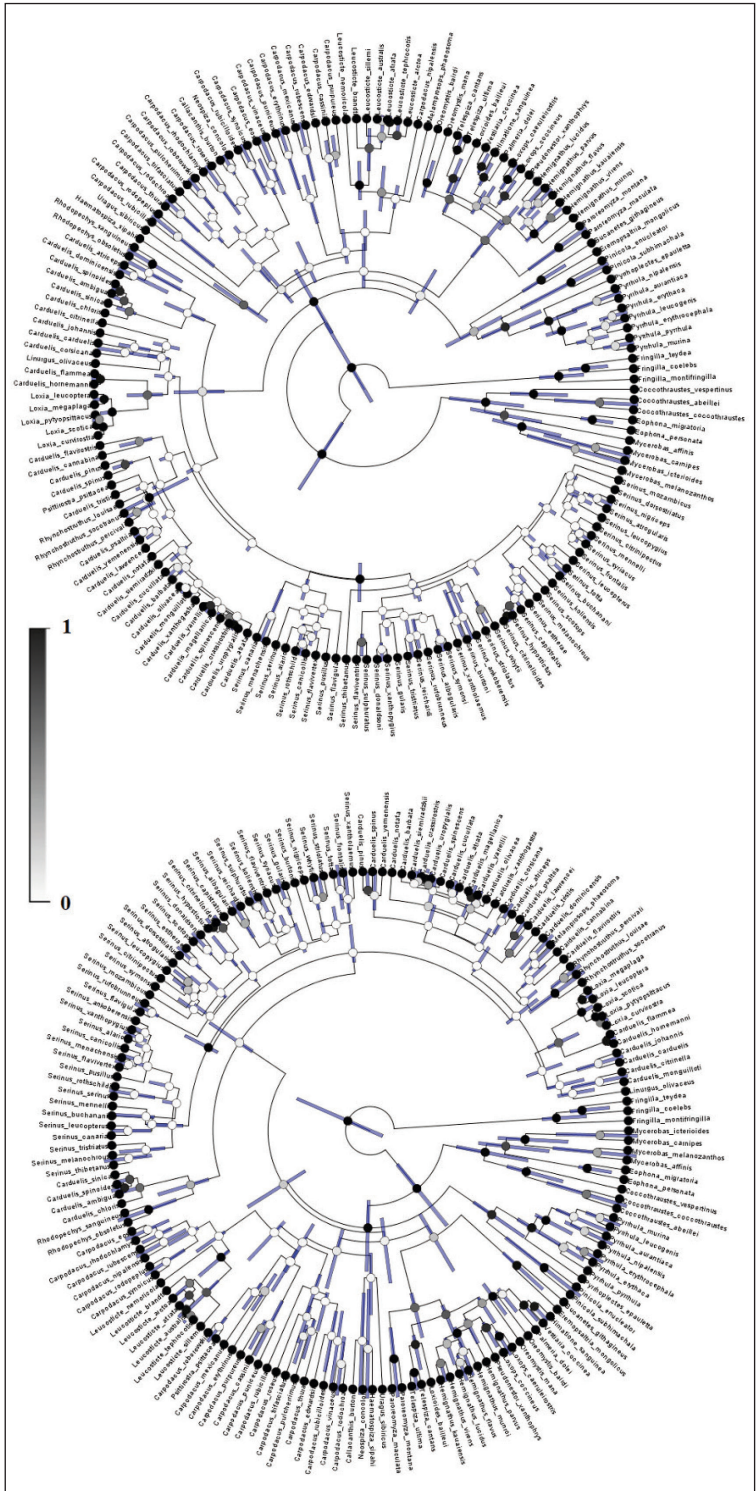


Figure 2. Consensus trees of 165 true finch species based on 1k and 10k trees using random phylogenies of Jetz *et al.* (2012). Circles show the posterior distribution of nodes (scale from white to black indicates 0 to 1 probability), and node bars represent the estimated range of node ages. (Enlargeable figures are available in the electronic version.)

2. ábra 165 pinty faj konszenzuszfa ezer, illetve tízezer véletlenszerű filogenetikus fa alapján (Jetz *et al.* 2012). A csomópontoknál lévő körök az egyes elágazások támogatottságát mutatják (a színskálán a fehér a 0, míg a fekete az 1 valószínűséget jelenti), a vonalak pedig a becsült időintervallumokat jelenítik meg. (Az elektronikus változatban nagyíthatók a képek.)

posterior distributions and node ages using one thousand and ten thousand randomly generated trees as input for creating a consensus tree for the 165 species. The root is aged 35 My (Kumar *et al.* 2017), whilst it ranges between 30.57 and 20.98 My on the 1k consensus tree, and 31.25 to 20.85 My on the 10k consensus tree (Jetz *et al.* 2012). Nevertheless, high amount of dissimilarities can be found in the relationships at the species level due to the significantly different number of trees used to make the consensus phylogenies.

Hence, more proper phylogenetic studies (type-C) are suggested to be examined and used in the case of well-defined groups if they are available in the literature and/or online databases, keeping type-B phylogenies for answering broad-scale, general questions in the evolution of birds. One of the earliest researches that studied Fringillidae using molecular phylogenetic approach (Yuri & Mindell 2002) supported the monophyly of the family, especially Fringillinae, which in fact, mainly formed by cardueline finches. At that time these species belonged to the subfamily under the tribe of Carduelini, however, a decade later they formed their own Carduelinae subfamily (Zuccon *et al.* 2012, Päckert *et al.* 2016), but the major clades still remained polyphyletic.

The taxonomy and phylogeny of the finch family is highly problematic and it has not been entirely clear to date (Payevsky 2015). The light circles in *Figure 2* represents these uncertainties that may occur as a result of the predominantly missing genetic data of species where previously published taxonomic positions were used to deduct the phylogenetic relationships.

The majority of the studies agreed in the basal position of *Fringilla* forming a sister subfamily to the rest of the species in interest (e.g. Yuri & Mindell 2002, Arnaiz-Villena *et al.* 2007, Zuccon *et al.* 2012, Arnaiz-Villena *et al.* 2014) and this relationship is also supported by the posterior probabilities on the phylogeny of Jetz *et al.* (*Figure 2, 3*). However, the position of euphonias to *Fringilla* and the Carduelinae varied in different studies (Yuri & Mindell 2002, Zuccon *et al.* 2012 and the references therein), but they suggested to be sister to Carduelinae as a single genus. Formerly, drepanids were recovered as sister taxa to the cardueline finches, but Zuccon *et al.* (2012) found support for their inclusion into the Carduelinae.

Payevsky (2015) reviewed the taxonomy of Fringillidae in more detail, ranging from ancient time histories to molecular systematics. Here, I focus on the field of the latter studies, further narrowing the focus on the Carduelinae subfamily which is considered to be monophyletic (Nguembock *et al.* 2009). Let us take a closer look.

Carduelinae

A pioneer study showed that North American cardueline finches originated 18–14 million years ago (Mya) and crossbills (*Loxia*) constitute the closest sister taxon to *Carduelis* (Marten & Johnson 1986). Papers based on *cytochrome b* sequences strengthened these results and described rapid radiation of Carduelinae between 14 and 2 Mya, including both Northern and Southern Hemisphere species (Arnaiz-Villena *et al.* 1998, 2001, 2007, 2008). The undoubted merit of these studies is the novel reflection to the taxonomy of goldfinches and allies. They provided suggestions for the classification of *Carduelis* species (Arnaiz-Villena *et al.* 1998) and recommend the renaming of North American goldfinches to siskins, due

to the distant relationships to European species, whereupon they belong to the *Spinus* genus today (BirdLife International 2015). The genera *Eophona* and *Mycerobas* form sister groups (but see also Zuccon *et al.* 2012) and represent one of the earliest splits in the subfamily, and crossbills are not sister taxa to *Carduelis* rather they are wedged into them (Arnaiz-Villena *et al.* 2001, 2007, 2008).

In molecular phylogenetic studies, the most important factors are the selected genes on that researchers would like to build their evolutionary hypotheses, and the species set on which the study is based on. Different genes often have different histories that could cause disharmonious results in the interpretation of phylogenies. Here, I recommend a thorough review on the effect of data types and species sets on avian trees by Reddy *et al.* (2017), but its deeper description exceeds the scope of the present study.

The studies already mentioned in this section were based on a single mitochondrial gene (cytochrome b). Quite a few researches examined cardueline phylogeny analysing sequences of more than one genes (e.g. Nguembock *et al.* 2009, Zuccon *et al.* 2012, Tietze *et al.* 2013). The most remarkable phenomenon is the amount of well-supported nodes in single-gene versus multiple-gene phylogenies. The large amount of analyses based on *cytochrome b* sequences alone does not mean that it would be more suitable for reconstructing phylogenies (e.g. Arnaiz-Villena *et al.* 1998, 2001) than other gene sequences (e.g. Sangster *et al.* 2016). The resolution of the generated trees are often poor (Arnaiz-Villena *et al.* 2008, 2012, 2014), which could partially be resulted by methodological differences. The figures in the work of Nguembock *et al.* (2009) perfectly illustrate these dissimilarities. The support of the nodes and the resolution of the tree is significantly lower when just one type of sequences was used, whilst a well-supported, bifurcated tree was resulted from the combination of all sources.

Nevertheless, including different sets of species into the analyses could also yield in distinct evolutionary hypotheses. For example, *Carduelis* species formed a monophyly in the first studies (Arnaiz-Villena *et al.* 1998, see also Arnaiz-Villena *et al.* 2012), however, this monophyly was supported in subsequent studies only when crossbills (Arnaiz-Villena *et al.* 2001), *Serinus* canaries and others were included (Arnaiz-Villena *et al.* 2007, 2008, 2014). The rosefinch (*Carpodacus*) genus have a similarly complicated history. It appears to be paraphyletic (Arnaiz-Villena *et al.* 2001, Nguembock *et al.* 2009, but see also Zuccon *et al.* 2012, Tietze *et al.* 2013) including also Sillem's Mountain Finch (*Leucosticte sillemi*) that was previously considered as a morph of Brandt's Mountain Finch *Leucosticte brandti* (Sangster *et al.* 2016). The grosbeaks (*Pinicola*) and bullfinches (*Pyrrhula*) constitute the only two genera that are clearly considered to be monophyletic, independently from what gene sources and methods applied, their species clustered together in all of the studies that contained both genera (Arnaiz-Villena *et al.* 2001, 2007, 2008, 2014, Zuccon *et al.* 2012, Huang *et al.* 2016, Sangster *et al.* 2016). Their monophyly is also supported by the phylogeny of Jetz *et al.* (2012) (Figure 2, 3).

The posterior probabilities show strong support for the common monophyly of the genera *Coccothraustes*, *Eophona* and *Mycerobas* (Jetz *et al.* 2012). The crossbills within the *Carduelis* finches, and the *Serinus* genus are also found to be monophyletic (Figure 3). However, the most comprehensive analysis of Fringillidae to date was done by Zuccon *et al.* (2012) and a detailed review was written by Payevsky (2015), which are highly recommended for interested readers.

Phylogeny of the European Goldfinch

The European Goldfinch (*Carduelis carduelis*) is the bird of the year in Hungary in 2017, hence I summarise here the knowledge about the evolution and phylogeny of this colourful species, especially focusing on its position among the Carduelinae.

The genus *Carduelis* is polyphyletic and, therefore, it is recommended to restrict the taxon to the European Goldfinch and Citril Finch (*C. citrinella*) due to their high posterior probability support (Zuccon *et al.* 2012). Formerly, the Citril Finch was named as *Serinus citrinella*, but its close relationship to the European Goldfinch has already been supported (Arnaiz-Villena *et al.* 1998, 2001, 2007, 2008, 2012, 2014, Nguembock *et al.* 2009). The broader relationship of this species pair (goldfinches) is not entirely clear. In the majority of the studies crossbills and redpolls form an earlier split and are in an outgroup position to goldfinches (Arnaiz-Villena *et al.* 1998, 2001, 2008, 2014, Zuccon *et al.* 2012). However, in some cases, *C. carduelis* and *C. citrinella* are basal to the clade including greenfinches, crossbills and redpolls (Arnaiz-Villena *et al.* 2007, 2012, Nguembock *et al.* 2009). Consensus trees based on the phylogenies of Jetz *et al.* (2012) show that crossbills and redpolls are sisters to goldfinches, but they are in a basal position to the clade containing greenfinches and *Serinus* canaries. Worth to note, however, that the support for these nodes are incredibly low.

Based on the various values of posterior probabilities, it is not yet possible to decide which hypothesis to accept for the evolution of goldfinches and allies, since none of the most important nodes are well-supported.

Summary

The European Goldfinch appeared as a new species within the clade of cardueline finches in a range of 8 to 0.2 Mya with a peak between 6.5 and 2 Mya (Marten & Johnson 1986, Arnaiz-Villena *et al.* 1998, 2001, 2008, 2012, 2014, Jetz *et al.* 2012).

However, the relationship among the cardueline lineages is still problematic in several points (Payevsky 2015). The Citril Finch is clearly a sister to the European Goldfinch, and the closest relatives of them are greenfinches, crossbills and redpolls (Arnaiz-Villena *et al.* 1998, 2001, 2007, 2008, 2012, 2014, Nguembock *et al.* 2009, Jetz *et al.* 2012, Zuccon *et al.* 2012).

Although different data sources often result in different phylogenetic histories, the monophyly of the Carduelinae subfamily as suggested by Nguembock *et al.* (2009) received a more powerful support from studies based on multiple gene sequences. Future studies should include as many cardueline species as possible for further taxonomic and phylogenetic comparative analyses.

Newly sampled gene sequences might help in resolving the “white patches” (Figure 2) of Jetz *et al.* (2012) in the phylogeny of goldfinches and allies.

The lack of biogeographical analyses (except the genus *Carpodacus*, Tietze *et al.* 2013) are conspicuous and only a few studies tried to form hypotheses on the spatial origin of cardueline finches (Arnaiz-Villena *et al.* 1998, 2001, 2012). Therefore, a well-designed

biogeographic analysis is also badly needed (e.g. Nagy & Tökölyi 2014, Moyle *et al.* 2016, Fuchs *et al.* 2017, Kennedy *et al.* 2017a, 2017b) that might be helpful in understanding the phylogenetic relationships within the group.

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