

¹ DateLife: leveraging databases and analytical tools to reveal the dated Tree of Life

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17

Abstract

18 Achieving a high-quality reconstruction of a phylogenetic tree with branch lengths
19 proportional to absolute time (chronogram) is a difficult and time-consuming task. But the
20 increased availability of fossil and molecular data, and time-efficient analytical techniques
21 has resulted in many recent publications of large chronograms for a large number and wide
22 diversity of organisms. Knowledge of the evolutionary time frame of organisms is key for
23 research in the natural sciences. It also represent valuable information for education, science
24 communication, and policy decisions. When chronograms are shared in public, open
25 databases this wealth of expertly-curated and peer-reviewed data on evolutionary timeframe
26 is exposed in a programmatic and reusable way, as intensive and localized efforts have
27 improved data sharing practices, as well as incentivized open science in biology. Here we
28 present DateLife, a service implemented as an R package and an R Shiny website application
29 available at www.datelife.org, that provides functionalities for efficient and easy finding,
30 summary, reuse, and reanalysis of expert, peer-reviewed, public data on time frame of
31 evolution. The main DateLife workflow constructs a chronogram for any given combination
32 of taxon names by searching a local chronogram database constructed and curated from the
33 Open Tree of Life Phylesystem phylogenetic database, which incorporates phylogenetic data
34 from the TreeBASE database as well. We implement and test methods for summarizing time
35 data from multiple source chronograms using supertree and congruification algorithms, and
36 using age data extracted from source chronograms as secondary calibration points to add
37 branch lengths proportional to absolute time to a tree topology. DateLife will be useful to
38 increase awareness of the existing variation in alternative hypothesis of evolutionary time for
39 the same organisms, and can foster exploration of the effect of alternative evolutionary
40 timing hypotheses on the results of downstream analyses, providing a framework for a more
41 informed interpretation of evolutionary results.

42

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⁴³ Congruification; Supertree; Calibrations; Secondary calibrations

⁴⁴ Word count: 4834

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46 **Introduction**

47 Chronograms –phylogenies with branch lengths proportional to time– provide key data
48 on evolutionary time frame for the study of natural processes in many areas of biological
49 research, such as developmental biology (Delsuc et al., 2018; Laubichler & Maienschein,
50 2009), conservation biology (Felsenstein, 1985; C. Webb, 2000), historical biogeography
51 (Posadas, Crisci, & Katinas, 2006), and species diversification (Magallon & Sanderson, 2001;
52 Morlon, 2014).

53 Building a chronogram is not an easy task. It requires obtaining and curating data to
54 construct a phylogeny, selecting and placing appropriate calibrations on the phylogeny using
55 independent age data points from the fossil record or other dated events, and inferring the
56 full dated tree; it also generally requires specialized biological training, taxonomic domain
57 knowledge, and a non-negligible amount of research time, computational resources and
58 funding.

59 Here we present the DateLife project which has the main goal of capturing age data
60 from published chronograms, and making these data readily accessible to the community for
61 reuse and reanalysis. DateLife’s core software application is available as an R package
62 (Sanchez-Reyes et al., 2022), and as an online Rshiny interactive website at www.datelife.org.
63 It features key elements for scientific reproducibility, such as a versioned, open and fully
64 public source database (McTavish et al., 2015), data stored and available in a computer
65 readable format (Vos et al., 2012), automated and programmatic ways of accessing the data
66 (Stoltzfus et al., 2013) and methods to summarize and compare the data.

67 **Description**

68 DateLife’s core software application consists of the R package `datelife`. Its latest
69 stable version – v0.6.2, is available from the CRAN repository (Sanchez-Reyes et al., 2022),

70 and relies on functionalities from various biological R packages: ape (Paradis, Claude, &
71 Strimmer, 2004), bold (Chamberlain et al., 2019), geiger (Pennell et al., 2014), paleotree
72 (Bapst, 2012), phyloch (Heibl, 2008), phylocomr (Ooms & Chamberlain, 2018), phytools
73 (Revell, 2012), rotl (Michonneau, Brown, & Winter, 2016), and taxize (Chamberlain & Szöcs,
74 2013; Chamberlain et al., 2019). Figure 1 provides a graphical summary of the three main
75 steps of the DateLife algorithm: creating a search query, searching a database, and
76 summarizing results from the search.

77 Creating a search query

78 DateLife starts by processing an input consisting of at least two taxon names, which
79 can be provided as a comma separated character string or as tip labels on a tree. If the input
80 is a tree, it can be provided as a classic newick character string (Archie et al., 1986), or as a
81 “phylo” R object (Paradis et al., 2004). The input tree is not required to have branch lengths,
82 and its topology is used in the summary steps described in the next section.

83 DateLife accepts scientific names that can belong to any inclusive taxonomic group
84 (e.g., genus, family, tribe, etc.) or a binomial species name. Subspecies and variants are
85 ignored. If an input taxon name belongs to an inclusive taxonomic group, the algorithm has
86 two alternative behaviors defined by the “get species from taxon” flag. If the flag is active,
87 DateLife retrieves all species names within the inclusive taxonomic group (following a
88 taxonomy of choice; current options are Open Tree of Life, NCBI, GBIF, or IRMNG
89 taxonomies) and adds them to the input string. If the flag is inactive, DateLife excludes any
90 taxon names above the species level from the search query.

91 DateLife processes input scientific names using a Taxonomic Name Resolution Service
92 (TNRS), which increases the probability of correctly finding the queried taxon names in the
93 chronogram database. TNRS detects, corrects and standardizes name misspellings and typos,
94 variant spellings and authorities, and nomenclatural synonyms to a single taxonomic

95 standard (Boyle et al., 2013). DateLife implements TNRS using OpenTree's unified
96 taxonomy as standard (Open Tree Of Life et al., 2016; Rees & Cranston, 2017), storing
97 OpenTree's Taxonomy identification numbers for further processing.

98 The processed input taxon names are saved as an R object of a newly defined class,
99 `datelifeQuery`, that is used in the following steps. This object contains the standardized
100 names, the corresponding OpenTree taxonomic id numbers, and the topology of the input
101 tree if any was provided.

102 Searching a chronogram database

103 At the time of writing of this manuscript , DateLife's chronogram database latest
104 version consist of 253 chronograms published in 187 different studies. It is curated from
105 OpenTree's phylogenetic database, the Phylesystem, which constitutes an open source of
106 expert and peer-reviewed phylogenetic knowledge with rich metadata (McTavish et al., 2015),
107 which allows automatic and reproducible assembly of our chronogram database. Datelife's
108 chronogram database is navigable as an R data object within the `datelife` R package.

109 A unique feature of OpenTree's Phylesystem is that the community can add new
110 published, state-of-the-art chronograms any time through their curator application
111 (<https://tree.opentreeoflife.org/curator>). As chronograms are added to Phylesystem, they are
112 incorporated into an updated `datelife`'s database that is assigned a new version number,
113 followed by a package release on CRAN. `datelife`'s chronogram database is updated as new
114 chronogram data is added to Phylesystem, at a minimum of once a month and a maximum
115 of every 6 months. Users can also upload and curate new chronograms to OpenTree
116 themselves. Then, trigger an update of their local `datelife` database to incorporate the new
117 chronograms and have them available for their current analysis.

118 A DateLife search is implemented by matching processed taxon names provided by the
119 user to tip labels in the chronogram database. Chronograms with at least two matching

120 taxon names on their tip labels are identified and pruned down to preserve only the matched
121 taxa. These matching pruned chronograms are referred to as source chronograms. Total
122 distance (in units of millions of years) between taxon pairs within each source chronogram
123 are stored as a patristic distance matrix (Figure 1). The matrix format speeds up extraction
124 of pairwise taxon ages of any queried taxa, as opposed to searching the ancestor node of a
125 pair of taxa in a “phylo” object or newick string. Finally, the patristic matrices are
126 associated to the study citation where the original chronogram was published, and stored as
127 an R object of the newly defined class `datelifeResult`.

128 **Summarizing search results**

129 Summary information is extracted from the `datelifeResult` object to inform
130 decisions for subsequent steps in the analysis workflow. Basic summary information available
131 to the user is:

- 132 1. The matching pruned chronograms as newick strings or “phylo” objects.
- 133 2. The ages of the root of all source chronograms. These ages can correspond to the age
134 of the most recent common ancestor (mrca) of the user’s group of interest if the source
135 chronograms have all taxa belonging to the group. If not, the root corresponds to the
136 mrca of a subgroup within the group of interest.
- 137 3. Study citations where original chronograms were published.
- 138 4. A report of input taxon names matches across source chronograms.
- 139 5. The source chronogram(s) with the most input taxon names.
- 140 6. Various single summary chronograms resulting from summarizing age data, generated
141 using the methodology described next.

142 ***Choosing a topology.***— DateLife requires a tree topology to summarize age data
143 upon. We recommend that users provide a tree topology as input from the literature, or one
144 of their own making. If no topology is provided, DateLife automatically obtains one from the

¹⁴⁵ OpenTree synthetic tree (Open Tree Of Life et al., 2019). These are known as “induced”
¹⁴⁶ OpenTree subtrees, which do not necessarily correspond to a monophyletic group.
¹⁴⁷ Alternatively, DateLife can combine topologies from source chronograms using a supertree
¹⁴⁸ approach. To combine topologies from source chronograms into a single summary (or
¹⁴⁹ supertree) topology, the DateLife algorithm starts by identifying the source chronograms
¹⁵⁰ that form a grove, roughly, a sufficiently overlapping set of taxa between trees, by
¹⁵¹ implementing definition 2.8 for n-overlap from Ané et al. (2009). In rare cases, a group of
¹⁵² trees can have multiple groves. By default, DateLife chooses the grove with the most taxa,
¹⁵³ however, the “criterion = trees” flag allows the user to choose the grove with the most trees
¹⁵⁴ instead. If source chronograms do not form a grove, the supertree reconstruction will fail.

¹⁵⁵ ***Dating the topology.***— Input topologies from OpenTree or the supertree approach
¹⁵⁶ described above do not include branch length estimates of any kind. Optionally, to estimate
¹⁵⁷ branch lengths proportional to substitution rates on these topologies, DateLife can mine the
¹⁵⁸ Barcode of Life Data System, BOLD (Ratnasingham & Hebert, 2007) to obtain genetic
¹⁵⁹ markers for the input taxa. These markers are aligned with MUSCLE (Edgar, 2004) (by
¹⁶⁰ default) or MAFFT (Katoh, Asimenos, & Toh, 2009). This alignment can be used to
¹⁶¹ estimate branch lengths on input topologies that lack branch lengths. Currently, branch
¹⁶² length reconstruction in DateLife is performed using parsimony and the likelihood of the
¹⁶³ phylogenetic tree given a sequence alignment is computed (Schliep, 2011). While relative
¹⁶⁴ branch length information provides additional data for nodes without secondary date
¹⁶⁵ calibrations, topologies without branch lengths can also be dated.

¹⁶⁶ Once a topology is chosen, DateLife applies the congruification method (Eastman,
¹⁶⁷ Harmon, & Tank, 2013) to find nodes belonging to the same clade across source
¹⁶⁸ chronograms, and extract the corresponding node ages from the patristic distance matrices
¹⁶⁹ stored as `datelifeResult`. By definition, the matrices store total distance (time from tip to
¹⁷⁰ tip), hence, node ages correspond to half the values stored in the patristic distance matrices.

171 This assumes that the terminal taxa are coeval and occur at the present. A table of
172 congruified node ages that can be used as calibrations for a dating analysis is stored as a
173 `congruifiedCalibrations` object.

174 For each congruent node, the pairwise distances that traverse that node are
175 summarized into a single summary matrix using classic summary statistics (i.e., mean,
176 median, minimum and maximum ages), and the Supermatrix Distance Method [SDM;
177 Criscuolo, Berry, Douzery, and Gascuel (2006)], which deforms patristic distance matrices by
178 minimizing variance and then averaging them. These single summary taxon pair age
179 matrices (Summarized calibrations) can be applied as calibrations to date a tree topology,
180 using different dating methods currently supported within DateLife: MrBayes (Huelsenbeck
181 & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), PATHd8 (Britton, Anderson, Jacquet,
182 Lundqvist, & Bremer, 2007), BLADJ (Campbell O. Webb, Ackerly, & Kembel, 2008;
183 Campbell O. Webb & Donoghue, 2005), and treePL (Stephen A. Smith & O'Meara, 2012).

184 By default, DateLife implements the Branch Length Adjuster (BLADJ) algorithm to
185 obtain a fully dated topology. BLADJ fixes node ages that have calibration data, and
186 distributes time between nodes with no data evenly between nodes with calibration data.
187 This minimizes age variance in the resulting chronogram (Campbell O. Webb et al., 2008).
188 BLADJ does not use branch lengths even when they are present in the input tree or
189 summarizing topology. When there is conflict in ages between nodes with calibration data,
190 the algorithm ignores node ages that are older than the age of a parent node. BLADJ
191 requires a root age estimate. If there is no information on the age of the root in the
192 chronogram database, users can provide an estimate from the literature. If none is provided,
193 DateLife assigns an arbitrary age to the root as 10% older than the oldest age available
194 within the group.

195 Alternative options supported in DateLife (MrBayes, PATHd8, TreePL) incorporate
196 branch length information from the input topology in combination with the calibrations.

197 PATHd8 is a non-clock, rate-smoothing method (Britton et al., 2007) to date trees. treePL
198 (Stephen A. Smith & O'Meara, 2012), is a semi-parametric, rate-smoothing, penalized
199 likelihood dating method (Michael J. Sanderson, 2002). The MrBayes (Huelsenbeck &
200 Ronquist, 2001; Ronquist & Huelsenbeck, 2003) approach in datelife uses the calibrations as
201 priors on node ages.

202 **Visualizing results.**— Finally, users can save all source and summary chronograms in
203 formats that permit reuse and reanalyses (newick and R “phylo” format), as well as visualize
204 and compare results graphically, or construct their own graphs using `datelife`’s chronogram
205 plot generation functions available from the R package `datelifeplot` (Sanchez-Reyes &
206 O’Meara, 2022).

207 Benchmark

208 `datelife`’s code speed was tested on an Apple iMac with one 3.4 GHz Intel Core i5
209 processor. We registered variation in computing time of query processing and search through
210 the database relative to number of queried taxon names. Query processing time increases
211 roughly linearly with number of input taxon names, and increases considerably if Taxonomic
212 Name Resolution Service (TNRS) is activated. Up to ten thousand names can be processed
213 and searched in less than 30 minutes with the most time consuming settings. Once names
214 have been processed as described in methods, a name search through the chronogram
215 database can be performed in less than a minute, even with a very large number of taxon
216 names (Fig. 2). `datelife`’s code performance was evaluated with a set of unit tests designed
217 and implemented with the R package `testthat` (R Core Team, 2018) that were run both
218 locally with the `devtools` package (R Core Team, 2018), and on a public server –via GitHub,
219 using the continuous integration tool Travis CI (<https://travis-ci.org>). At present, unit tests
220 cover more than 40% of `datelife`’s code (<https://codecov.io/gh/phylotastic/datelife>). Unit
221 testing helps identify potential issues as code is updated or, more critically, as services code
222 relies upon may change.

223

Case studies

224 We illustrate the DateLife algorithm using a family within the Passeriform birds
225 encompassing the true finches, Fringillidae, as case study. The first example analyses 6 bird
226 species and shows all steps of the algorithm. The second example is an application analysing
227 289 species in the family Fringillidae that are included in the NCBI taxonomy.

228 **A small example**

229 ***Creating a search query.***- We chose 6 bird species within the Passeriformes. The
230 sample includes two species of cardinals: the black-thighed grosbeak – *Pheucticus tibialis*
231 and the crimson-collared grosbeak – *Rhodothraupis celaeno*; three species of buntings: the
232 yellowhammer – *Emberiza citrinella*, the pine bunting – *Emberiza leucocephalos* and the
233 yellow-throated bunting – *Emberiza elegans*; and one species of tanager, the vegetarian finch –
234 *Platyspiza crassirostris*.

235 Processing input names found that *Emberiza elegans* is synonym for *Schoeniclus*
236 *elegans* in the default reference taxonomy [Open Tree of Life Taxonomy v3.3, June 1, 2021].
237 For a detailed discussion on the state of the synonym refer to Avibase (Avibase, 2022;
238 Lepage, 2004; Lepage, Vaidya, & Guralnick, 2014). Discovering this synonym allowed
239 assigning five age data points for the parent node of *Emberiza elegans*, shown as *Schoeniclus*
240 *elegans* in figure 3A, which would not have had any data otherwise.

241 ***Searching the database.***- DateLife used the processed input names to search the
242 local chronogram database and found 9 matching chronograms in 6 different studies (Fig.
243 3B). Three studies matched five input names (Barker, Burns, Klicka, Lanyon, & Lovette,
244 2015; Hedges, Marin, Suleski, Paymer, & Kumar, 2015; Jetz, Thomas, Joy, Hartmann, &
245 Mooers, 2012), one study matched four input names (Hooper & Price, 2017) and two studies
246 matched two input names (Barker, Burns, Klicka, Lanyon, & Lovette, 2013; Burns et al.,
247 2014). No studies matched all input names. Together, source chronograms provide 28 unique

248 age data points, covering all nodes on our chosen tree topology to date (Table 1).

249 ***Summarizing search results.-*** DateLife obtained OpenTree's synthetic tree
250 topology for these taxa (Fig. 3C), and mapped age data to nodes in this chosen topology. As
251 expected, more inclusive nodes (e.g., node "n1") have more variance in age data than less
252 inclusive nodes (e.g., node "n5"). The name processing step allowed including five data
253 points for node "n4" (parent of *Schoeniclus elegans*; Fig. 3A) that would not have had any
254 data otherwise due to name mismatch. Age summary statistics per node were calculated and
255 used as calibrations to date the tree topology using the BLADJ algorithm. Age data for
256 node "n2" was excluded as final calibration because it is older than age data of the more
257 inclusive node "n1" (Fig. 3C4).

258 **The family Fringillidae**

259 ***Creating a query.-*** To obtain ages for all species within the family of true finches,
260 Fringillidae, we ran a DateLife query using the "get species from taxon" flag, which gets all
261 recognized species names within a named group from a taxonomy of choice. Following the
262 NCBI taxonomy, our DateLife query has 289 Fringillidae species. This taxon-constrained
263 approach implies that the final results of a full DateLife analysis will be done using a tree
264 topology and ages for the species in a named group, which do not necessarily correspond to a
265 monophyletic group. Users can change this behaviour by providing a monophyletic tree as
266 input for a DateLife search, or as a tree topology for a DateLife summary.

267 ***Searching the database.-*** Next, we used the processed species names in our DateLife
268 query to identify chronograms with at least two Fringillidae species. The DateLife search
269 identified 13 chronograms containing at least two Fringillidae species, published in 9 different
270 studies (Barker et al., 2013, 2015; Burns et al., 2014; Claramunt & Cracraft, 2015; Gibb et
271 al., 2015; Hedges et al., 2015; Hooper & Price, 2017; Jetz et al., 2012; Price et al., 2014).
272 Once identified, DateLife pruned matching chronograms to keep Fringillidae species names

273 on tips only, and transformed these pruned chronograms to pairwise distance matrices.

274 ***Summarizing search results.-*** The final step is to summarize the age data available
275 for the Fringillidae species into single summary chronograms, using different types of
276 summary ages, median and SDM. As explained in the “Description” section, a tree topology
277 to summarize age data upon is required. By default, DateLife uses the portion of OpenTree
278 synthetic phylogeny that contains the species provided as search query as summarizing
279 topology. According to this phylogeny, species belonging to the family Fringillidae do not
280 form a monophyletic group (Fig. 4). Age data from source chronograms is summarised into
281 a single patristic distance matrix and then the available node ages are used as fixed node
282 calibrations over a consensus tree topology, to obtain a fully dated phylogeny with the
283 program BLADJ (Fig. 5). Median summary chronograms are older and have wider variation
284 in maximum ages than chronograms obtained with SDM.

285 **Cross-validation test**

286 We performed a cross validation analysis of the DateLife workflow using the
287 Fringillidae chronograms. We used the individual tree topologies from each of the 19 source
288 chronograms from 13 studies as inputs, treating their node ages as unknown. We then
289 estimated dates for these topologies using the node ages from the chronograms from the
290 other studies as calibrations and smoothing using BLADJ.

291 We found that node ages from original study, and ages estimated using all other age
292 data available are correlated (Supplementary Fig. 6).

293 For five studies, Datelife tended to underestimate ages for topologically deeper nodes
294 (those with many descendant taxa, aka ‘closer to the root’) relative to the orginal estimate,
295 and overestimate ages for nodes closer to the tips. Accordingly, root ages are generally older
296 in the original study than estimated using cross-validated ages (Supplementary Fig. 7).

Discussion

297 **datelife** makes state-of-the-art data on evolutionary time frame easily accessible for
298 comparison, reuse, and reanalysis, to researchers in all areas of science and with all levels of
299 expertise in the matter. It is an open service that does not require any expert biological
300 knowledge from users –besides the names of the species or group they want to work with, for
301 any of its functionality.

303 A total of 99474 unique terminal taxa are represented in **datelife**'s database.

304 Incorporation of more chronograms into **datelife**'s database will continue to improve its
305 services. One option to increase the number of chronograms in the DateLife database is the
306 Dryad data repository. Methods to automatically mine chronograms from Dryad could be
307 designed and implemented. However, Dryad's metadata system has no information to
308 automatically detect branch length units, and those would still need to be determined
309 manually by a human curator. We would like to emphasize on the importance of sharing
310 chronogram data, including systematically curated metadata, into open repositories, such as
311 OpenTree's Phylesystem (McTavish et al., 2015) for the benefit of the scientific community
312 as a whole.

313 Primary vs Secondary calibrations in dating analyses

314 While most chronograms in DateLife's database are constructed using primary
315 calibrations (molecular substitution rates or ages obtained from the fossil record or geological
316 events), DateLife summarizes chronograms using secondary calibrations only (ages coming
317 from other chronograms).

318 Graur and Martin (2004) cautioned on the increased error and uncertainty in estimated
319 ages when using secondary calibrations in dating analyses. Schenk (2016) showed that, in
320 simulations, divergence times inferred using secondary calibrations are significantly younger
321 than those inferred with primary calibrations, when obtained with Bayesian inference

322 methods, and when priors are implemented in similar ways in both analyses. Accordingly, the
323 scientific community seems to have more confidence in chronograms obtained from a single
324 analysis, using fossil data as primary sources of calibrations (Schenk, 2016), and using fossils
325 that have been widely discussed and curated as calibrations to date other trees, making sure
326 that all data used in the analysis reflect a coherent evolutionary history (Sauquet, 2013), as
327 for example done by (Antonelli et al., 2017). There have been attempts to create fossil
328 calibration databases (Ksepka et al., 2015), though these still have room to grow.

329 **LLSR: What does our cross validation analysis show in relation to diffs between**
330 **primary and secondary calibrations?**

331 It seems that using several (as opposed to just a few) secondary calibrations can
332 provide sufficient information to alleviate or even neutralize potential biases (Sauquet, 2013).
333 Certainly, further studies are required to fully understand the effect of secondary calibrations
334 on outputs from different tree dating methods, and on downstream analyses. It is possible
335 that secondary calibrations can be safely used with dating methods that do not require
336 setting priors, such as penalized likelihood (Michael J. Sanderson, 2003), methods that do
337 not make any assumptions on the ages and fix them to a node on a tree topology, such as
338 BLADJ (Campbell O. Webb et al., 2008; Campbell O. Webb & Donoghue, 2005), or
339 methods that summarize age data unto a tree topology.

340 **Variation in source chronograms**

341 Conflict among alternative dating studies is common in the literature (see, for example,
342 the robust ongoing debate about crown group age of angiosperms (Barba-Montoya, Reis,
343 Schneider, Donoghue, & Yang, 2018; Magallón, Gómez-Acevedo, Sánchez-Reyes, &
344 Hernández-Hernández, 2015; Ramshaw et al., 1972; Michael J. Sanderson & Doyle, 2001;
345 Sauquet, Ramírez-Barahona, & Magallón, 2021)).

346 Source chronograms may have been estimated using different types of primary

347 calibrations (fossil record, geologic or biogeographic events, molecular substitution rates).
348 These differences in approach can deepen the already substantial variation in time estimates
349 between lineages, as observed from the comparison of source chronograms in the Fringillidae
350 example. For example, the chronograms from Burns et al. (2014) tend to have much older
351 date estimates for the same nodes than other inferences (Figure 5). This study inferred dates
352 using molecular substitution rate estimates across birds (Weir & Schluter, 2008) **EJM:**
353 **MORE ON the FINCH examples and the cross validation here**

354 Different chronograms might also imply fundamentally distinct evolutionary
355 hypotheses. For example, two different researchers working on the same clade could both
356 carefully select and argue for their choices of fossil calibrations. Still, if one researcher
357 decides a fossil will calibrate the ingroup of a clade, while another researcher uses the same
358 one to calibrate outside the clade, the resulting age estimates will often differ substantially,
359 as the placement of calibrations as stem or crown group is proved to deeply affect estimated
360 times of lineage divergence (Sauquet, 2013).

361 Sumarizing chronograms

362 By default, DateLife currently summarizes all source chronograms that overlap with at
363 least two species names. Users can exclude source chronograms if they have reasons to do so.
364 Strictly speaking, a good chronogram should reflect the real time of lineage divergence
365 accurately and precisely. To our knowledge, there are no tested measures to determine
366 independently when a chronogram is better than another. Yet, several characteristics of the
367 data used for dating analyses, as well as from the output chronogram itself, could be used to
368 score the quality of source chronograms.

369 Some measures that have been proposed are the proportion of lineage sampling and the
370 number of calibrations used Magallón et al. (2015). Some characteristics that are often cited
371 in published studies as a measure of improved age estimates as compared to previously

372 published estimates are: quality of alignment (missing data, GC content), lineage sampling
373 (strategy and proportion), phylogenetic and dating inference method, number of fossils used
374 as calibrations, support for nodes and ages, and magnitude of confidence intervals.

375 DateLife provides an opportunity to capture concordance and conflict among date
376 estimates, which can also be used as a metric for chronogram reliability. Its open database of
377 chronograms allows other researchers to do such analyses themselves reproducibly, and
378 without needing permission. Though, of course, they should follow proper citation practices,
379 especially for the source chronogram studies.

380 The exercise of summarizing age data from across multiple studies provides the
381 opportunity to work with a more inclusive chronogram, that reflects a unified evolutionary
382 history for a lineage, by putting together evidence from different hypotheses. The largest,
383 and taxonomically broadest chronogram currently available from OpenTree was constructed
384 summarizing age data from 2,274 published chronograms using NCBI's taxonomic tree as
385 backbone (Hedges et al., 2015). A summarizing exercise may also amplify the effect of
386 uncertainty and errors in source data, and blur parts of the evolutionary history of a lineage
387 that might only be reflected in source chronograms and lost on the summary chronogram
388 (Sauquet et al., 2021). **EJM: ??? it's not clear to me what this last part means! What might**
389 **you be losing? LLSR: I changed loosing to blurring. But I will elaborate more on it**
390 Choosing source chronograms that we are going to keep and the ones that we are going to
391 discard might be key. **LLSR: Example**

392 **Effects on downstream analyses**

393 For downstream analyses, using alternative chronogram may deeply affect our
394 inferences (Title & Rabosky, 2016), particularly when studying phenomena dependent on the
395 timing of species diversification events, such as macroevolutionary processes.

396 In ecology and conservation biology, incorporating at least some data on lineage

397 divergence times represents a relevant improvement for testing alternative hypothesis using
398 phylogenetic distance (Campbell O. Webb et al., 2008). Hence, DateLife's workflow features
399 different ways of estimating node ages in the absence of calibrations and branch length
400 information for certain taxa. "Making up" branch lengths is a common practice in scientific
401 publications: Jetz et al. (2012), created a time-calibrated tree of all 9,993 bird species, where
402 67% had molecular data and the rest was simulated; Rabosky et al. (2018) created a
403 time-calibrated tree of 31,536 ray-finned fishes, of which only 37% had molecular data;
404 Stephen A. Smith and Brown (2018) constructed a tree of 353,185 seed plants where only
405 23% had molecular data.

406 Notably, risks come with this practice. Taken to the extreme, one could make a fully
407 resolved, calibrated tree of all modern and extinct taxa using a single taxonomy and a single
408 calibration, using polytomy resolution and branch estimation methods. There has yet to be
409 a thorough analysis of what can go wrong when one extends inferences beyond the data in
410 this way, so we urge caution; we also urge readers to follow the example of the large tree
411 papers cited above, by carefully considering the statistical assumptions being made, and
412 assessing the consistency of the results with prior work.

413 Conclusions

414 Knowledge of the evolutionary time frame of organisms is key to many research areas:
415 trait evolution, species diversification, biogeography, macroecology and more. It is also
416 crucial for education, science communication and policy, but generating chronograms is
417 difficult, especially for those who want to use phylogenies but who are not systematists, or
418 do not have the time to acquire and develop the necessary knowledge and skills to construct
419 them on their own. Importantly, years of primarily public funded research have resulted in
420 vast amounts of chronograms that are already available on scientific publications, but hidden
421 to the public and scientific community for reuse.

The DateLife project allows for easy and fast summary of public and state-of-the-art data on time of lineage divergence. It provides a straightforward way to get an informed idea on the state of knowledge of the time frame of evolution of different regions of the tree of life, and allows identification of regions that require more research, or that have conflicting information. It is available as an R package, and as a web-based R shiny application at www.datelife.org. Both summary and newly generated trees are useful to evaluate evolutionary hypotheses in different areas of research. The DateLife project helps with awareness of the existing variation in expert time of divergence data, and will foster exploration of the effect of alternative divergence time hypothesis on the results of analyses, nurturing a culture of more cautious interpretation of evolutionary results.

Availability

The `datelife` software is free and open source and it can be used through its R shiny web application at <http://www.datelife.org>, through the `datelife` R package, and through Phylotastic's project web portal <https://phylo.cs.nmsu.edu/>. DateLife's web application is maintained using RStudio's shiny server and the shiny package open infrastructure, as well as Docker and Open Tree of Life's infrastructure (dates.opentreeoflife.org/datelife).
The `datelife`'s R package stable version is available for installation from the CRAN repository (<https://cran.r-project.org/package=datelife>) using the command `install.packages(pkgs = "datelife")` from within R. Development versions are available from the GitHub repository (<https://github.com/phylotastic/datelife>) and can be installed using the command `devtools::install_github("phylotastic/datelife")`.

Supplementary Material

Code used to generate all versions of this manuscript, the biological examples, as well as the benchmark of functionalities are available at `datelifeMS1`, `datelife_examples`, and `datelife_benchmark` repositories in LLSR's GitHub account.

447

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452

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732 Ecology*, 17(10), 2321–2328.

Table 1

Ages of congruified nodes belonging to step C3 from Figure 3

Node Name	Taxon A	Taxon B	Node Age	Study chronogram
1 n1	<i>Emberiza citrinella</i>	<i>Platyspiza crassirostris</i>	9.6509881	Jetz et al. 2012 – chronogram 1
2 n1	<i>Pheucticus tibialis</i>	<i>Schoeniclus elegans</i>	14.3336520	Barker et al. 2015 – chronogram 1
3 n1	<i>Rhodothraupis celaeno</i>	<i>Schoeniclus elegans</i>	16.2984859	Barker et al. 2015 – chronogram 2
4 n1	<i>Emberiza citrinella</i>	<i>Platyspiza crassirostris</i>	16.9499615	Hooper et al. 2017
5 n1	<i>Rhodothraupis celaeno</i>	<i>Schoeniclus elegans</i>	21.5140867	Jetz et al. 2012 – chronogram 2
6 n1	<i>Emberiza leucocephalos</i>	<i>Platyspiza crassirostris</i>	22.0000000	Hedges et al. 2015 – chronogram 2
7 n1	<i>Emberiza citrinella</i>	<i>Platyspiza crassirostris</i>	22.3757277	Hedges et al. 2015 – chronogram 1
8 n2	<i>Platyspiza crassirostris</i>	<i>Rhodothraupis celaeno</i>	7.9691925	Jetz et al. 2012 – chronogram 1
9 n2	<i>Platyspiza crassirostris</i>	<i>Rhodothraupis celaeno</i>	19.7085830	Jetz et al. 2012 – chronogram 2
10 n2	<i>Platyspiza crassirostris</i>	<i>Rhodothraupis celaeno</i>	19.7085900	Hedges et al. 2015 – chronogram 2
11 n2	<i>Platyspiza crassirostris</i>	<i>Rhodothraupis celaeno</i>	19.7128363	Hedges et al. 2015 – chronogram 1
12 n2	<i>Pheucticus tibialis</i>	<i>Platyspiza crassirostris</i>	44.2958603	Burns et al. 2014
13 n3	<i>Pheucticus tibialis</i>	<i>Rhodothraupis celaeno</i>	10.5304440	Barker et al. 2015 – chronogram 1
14 n3	<i>Pheucticus tibialis</i>	<i>Rhodothraupis celaeno</i>	10.5379092	Barker et al. 2013
15 n3	<i>Pheucticus tibialis</i>	<i>Rhodothraupis celaeno</i>	11.2095375	Barker et al. 2015 – chronogram 2
16 n3	<i>Pheucticus tibialis</i>	<i>Rhodothraupis celaeno</i>	18.1570685	Hedges et al. 2015 – chronogram 1
17 n4	<i>Emberiza citrinella</i>	<i>Schoeniclus elegans</i>	5.3238969	Jetz et al. 2012 – chronogram 1
18 n4	<i>Emberiza leucocephalos</i>	<i>Schoeniclus elegans</i>	9.8622460	Barker et al. 2015 – chronogram 1
19 n4	<i>Emberiza leucocephalos</i>	<i>Schoeniclus elegans</i>	10.3391445	Jetz et al. 2012 – chronogram 2
20 n4	<i>Emberiza leucocephalos</i>	<i>Schoeniclus elegans</i>	11.7317630	Barker et al. 2015 – chronogram 2
21 n4	<i>Emberiza citrinella</i>	<i>Schoeniclus elegans</i>	12.5133870	Hooper et al. 2017
22 n5	<i>Emberiza citrinella</i>	<i>Emberiza leucocephalos</i>	0.1407015	Jetz et al. 2012 – chronogram 1
23 n5	<i>Emberiza citrinella</i>	<i>Emberiza leucocephalos</i>	0.1516230	Hedges et al. 2015 – chronogram 2
24 n5	<i>Emberiza citrinella</i>	<i>Emberiza leucocephalos</i>	0.2011990	Barker et al. 2015 – chronogram 1
25 n5	<i>Emberiza citrinella</i>	<i>Emberiza leucocephalos</i>	0.2409300	Barker et al. 2015 – chronogram 2
26 n5	<i>Emberiza citrinella</i>	<i>Emberiza leucocephalos</i>	0.2732460	Jetz et al. 2012 – chronogram 2
27 n5	<i>Emberiza citrinella</i>	<i>Emberiza leucocephalos</i>	0.5760260	Hedges et al. 2015 – chronogram 1
28 n5	<i>Emberiza citrinella</i>	<i>Emberiza leucocephalos</i>	2.2898230	Hooper et al. 2017

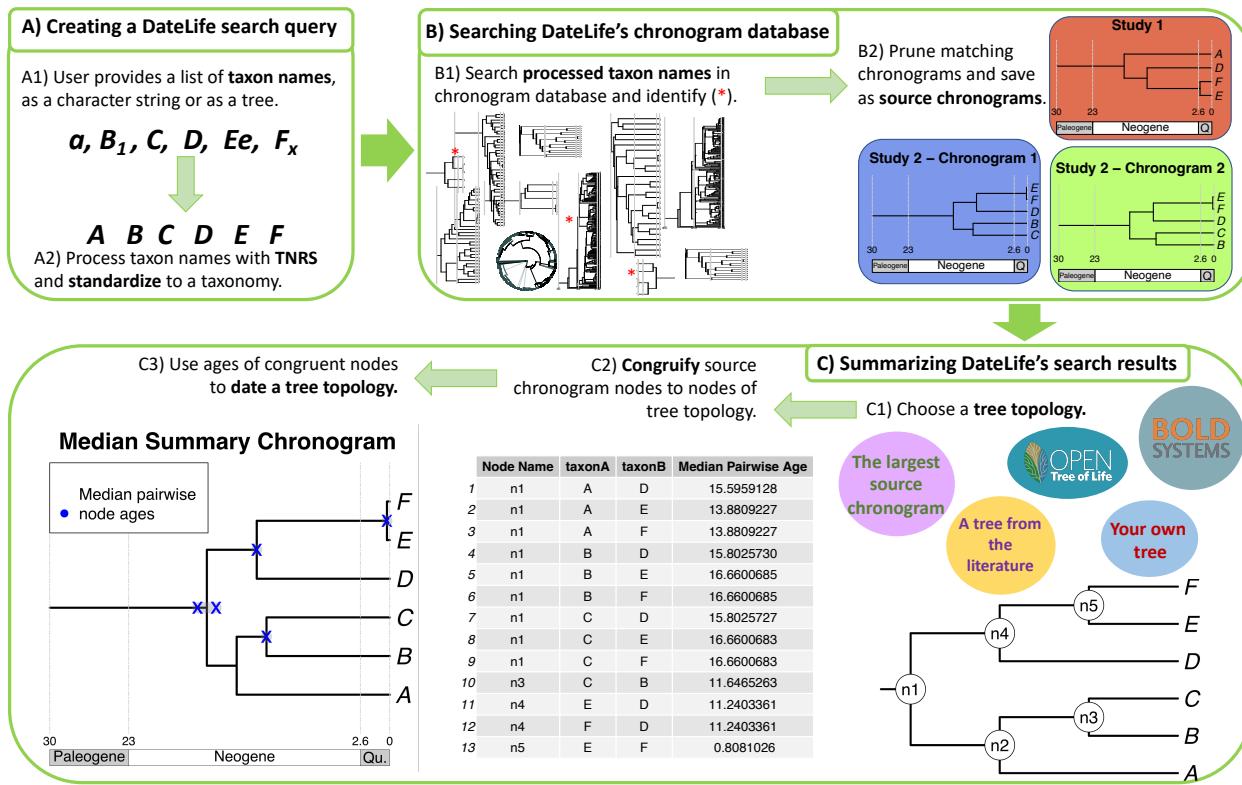


FIGURE 1. Stylized DateLife workflow. This shows the general workflows and analyses that can be performed with `datelife`, via the R package or through the website at <http://www.datelife.org/>. Details on the functions involved on each workflow are shown in `datelife`'s R package vignette.

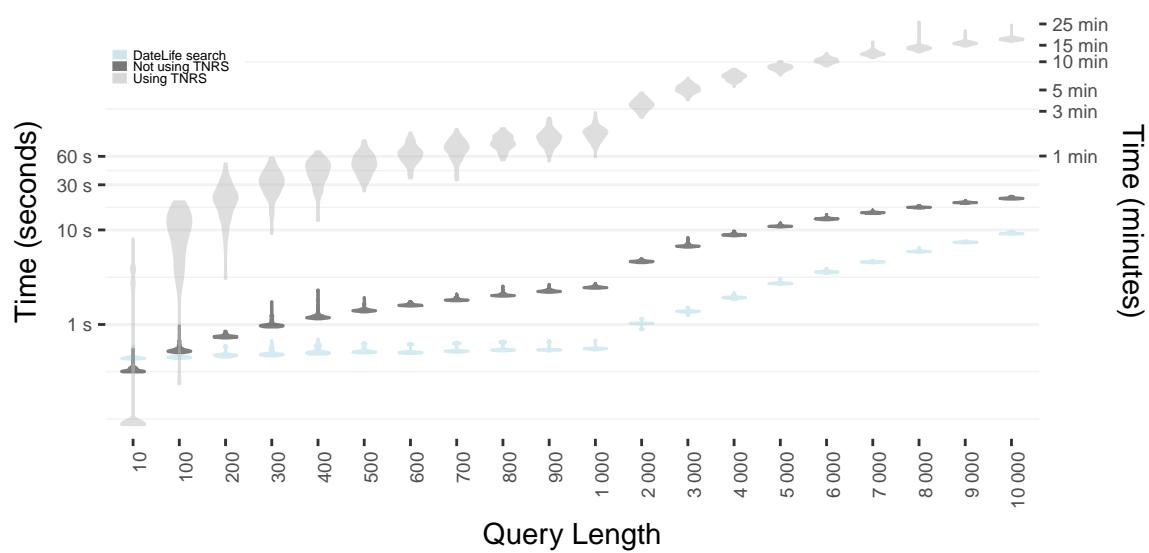


FIGURE 2. Computation time of query processing and search across **datelife**'s chronogram database relative to number of input taxon names. We sampled N names from the class Aves for each cohort 100 times and then performed a search with query processing not using the Taxon Names Resolution Service (TNRS; dark gray), and using TNRS (light gray). We also performed a search using the already processed query for comparison (light blue).

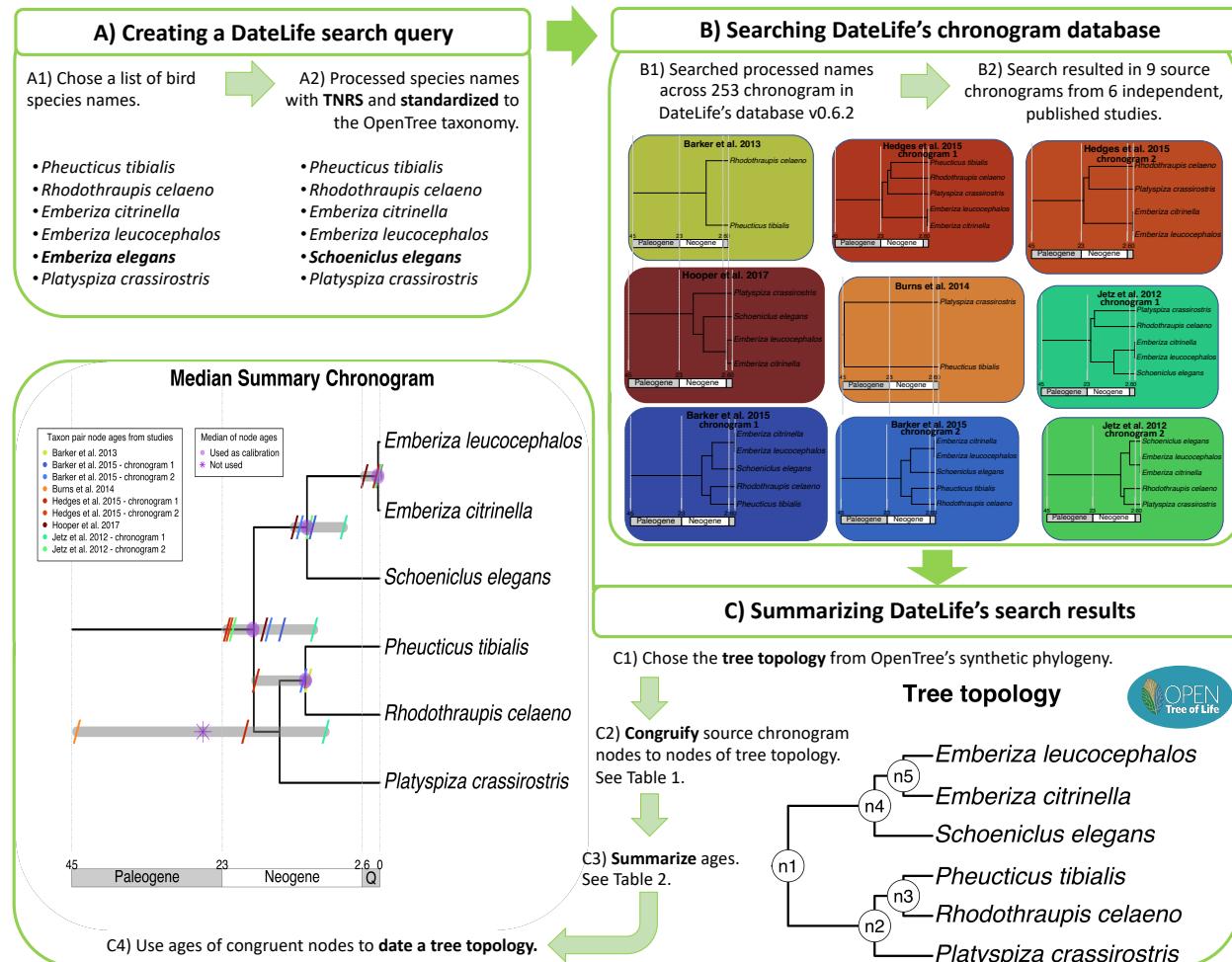


FIGURE 3. DateLife analysis results for a small sample of A) 6 bird species within the Passeriformes. B) Processed species names were found across 9 chronograms within 6 independent studies (Barker et al. (2012), Barker et al. (2015), Burns et al. (2014), Hedges et al. (2015), Hooper and Price (2017), Jetz et al. (2012).) C) This revealed 28 source age data points for the queried species names. Summarized age data is used as secondary calibrations to date a tree topology obtained from OpenTree's synthetic tree, resulting in a summary chronogram of source ages.

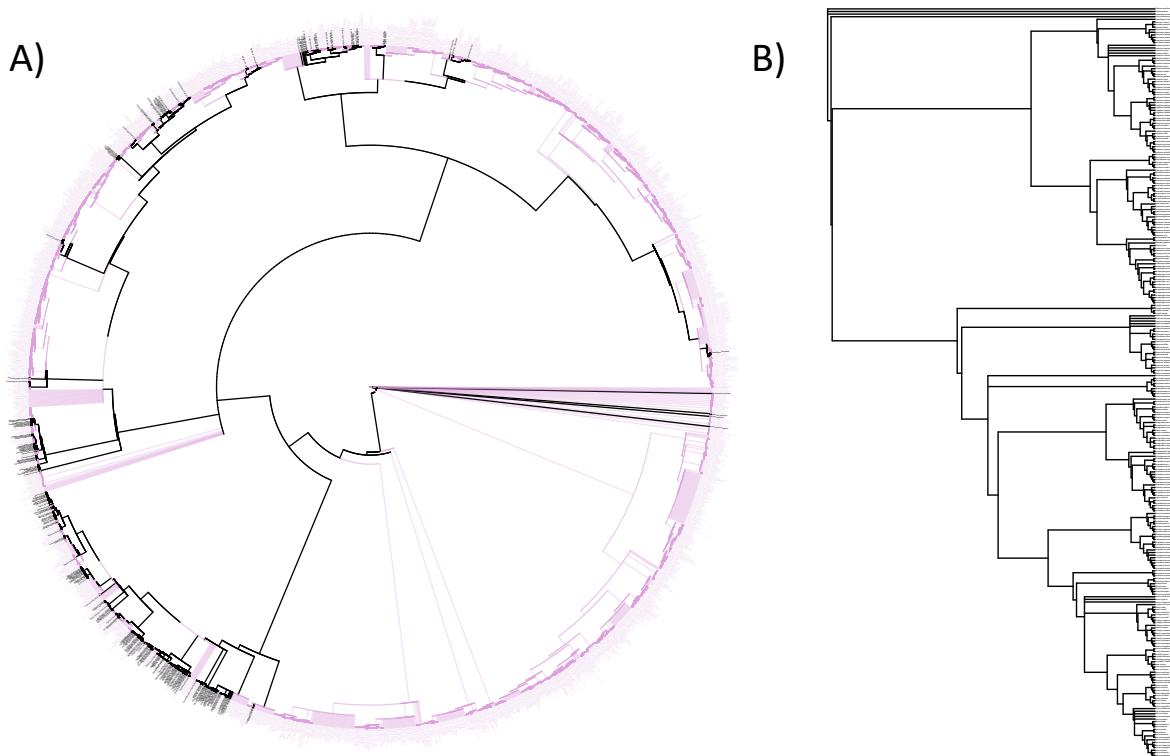


FIGURE 4. Tree topologies obtained from Open Tree of Life's (OpenTree) synthetic phylogenetic tree. A) Topology of 2,333 tips and 1,305 internal nodes, encompassing bird species within the family Fringillidae following the NCBI taxonomy (black), as well as all other bird species that share the same mrca node in OpenTree's synthetic tree (purple). B) Topology of 289 tips and 253 internal nodes, encompassing bird species within the Fringillidae only. This tree results from pruning species that are not assigned to the family Fringillidae (purple branches in topology A) but that form a monophyletic group with them. Bird species within the Fringillidae are paraphyletic (Alström et al. 2014, Barker, Cibois, Schikler, Feinstein, & Cracraft 2004, Barker et al. 2013, Barker 2014, Barker et al. 2015, Beresford, Barker, Ryan, & Crowe 2005, Bryson Jr et al. 2014, Burleigh, Kimball, & Braun 2015, Burns et al. 2014, Chaves, Hidalgo, & Klicka 2013, Claramunt & Cracraft 2015, Gibb et al. 2015, Hackett et al. 2008, Jetz et al. 2012, Johansson, Fjeldså, & Bowi 200, Kimball et al. 2019, Klicka et al. 2014, Lamichhaney et al. 2015, Lerner, Meyer, James, Hofreiter, & Fleischer 2011, Lovette et al. 2010, Moyle et al. 2016, Ödeen, Håstad, & Alström 2011, Oliveros et al. 2019, Päckert et al. 2012, Parchman, Benkman, & Mezquida 2007, Powell et al. 2014, Price et al. 2014, Pulgarín-R, Smith, Bryson Jr, Spellman, & Klicka 2013, Selvatti, Gonzaga, & Moraes Russo 2015, Tietze, Päckert, Martens, Lehmann, & Sun 2013, Treplin et al. 2008, Zuccon, Prŷs-Jones, Rasmussen, & Ericson 2012).

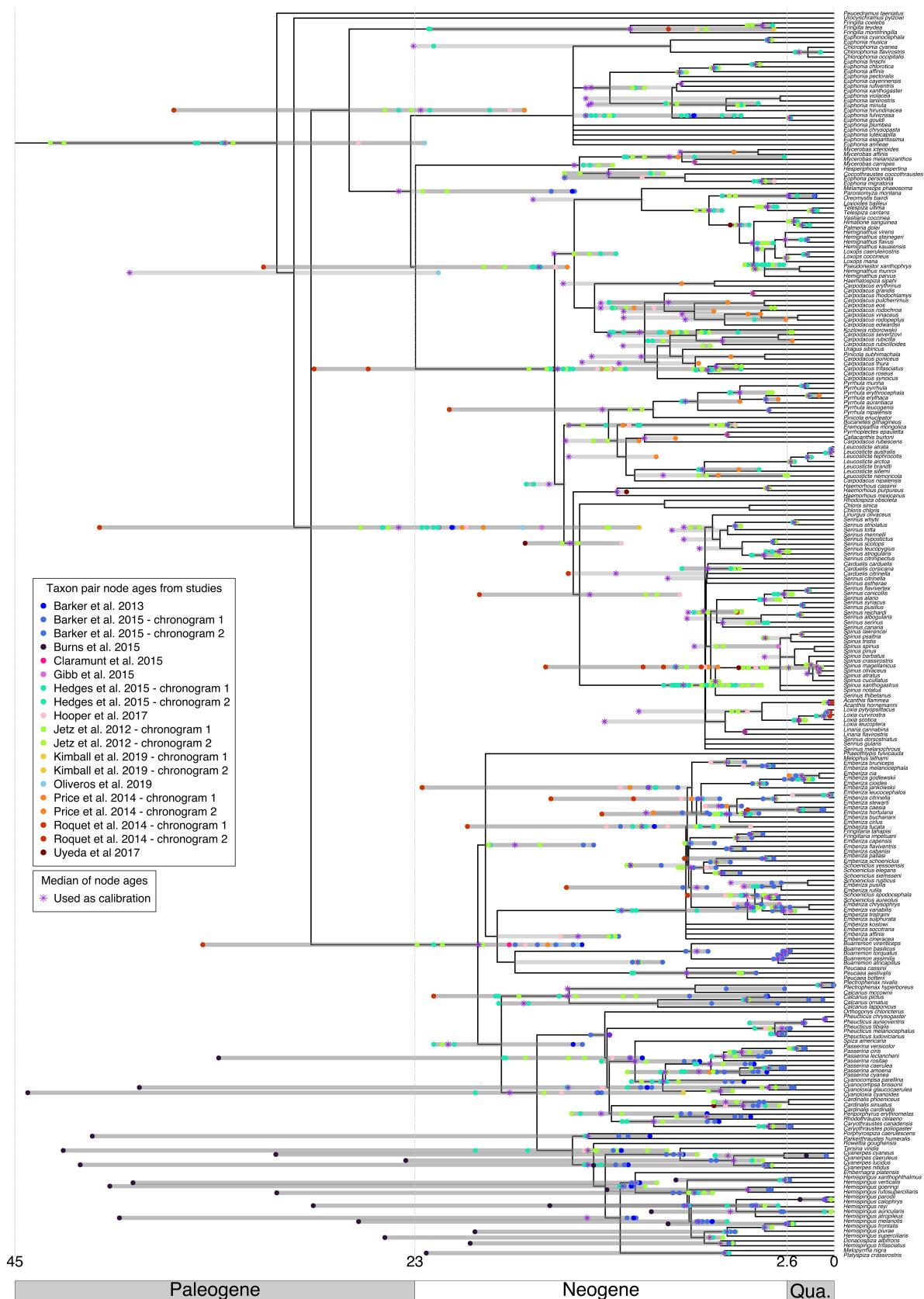


FIGURE 5. Fringillidae median summary chronogram generated with DateLife. It has 256 tips and 233 nodes.

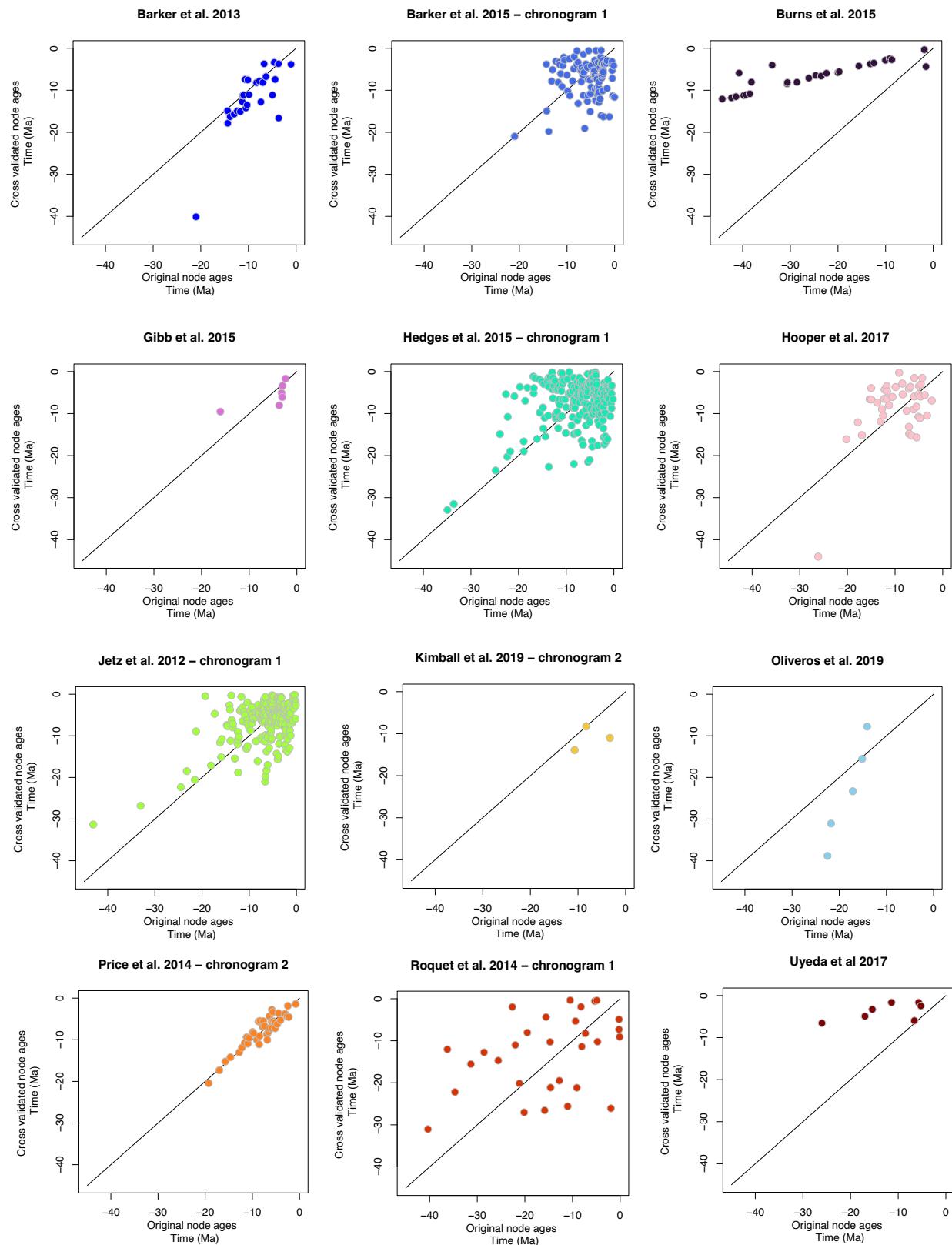


FIGURE 6. Results from cross validation analysis.

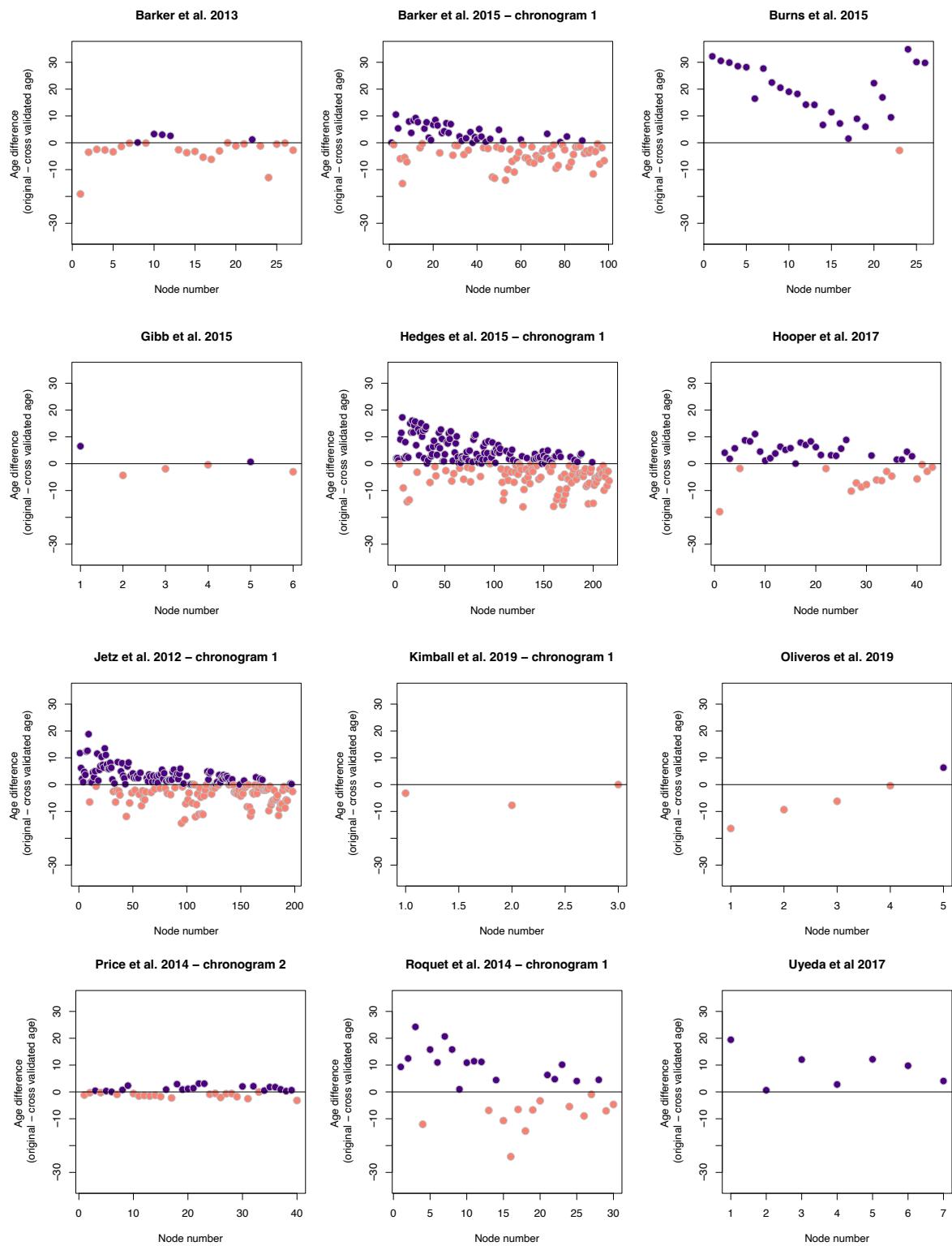


FIGURE 7. Results from cross validation analysis.

Barker et al. 2015 - chronogram 1

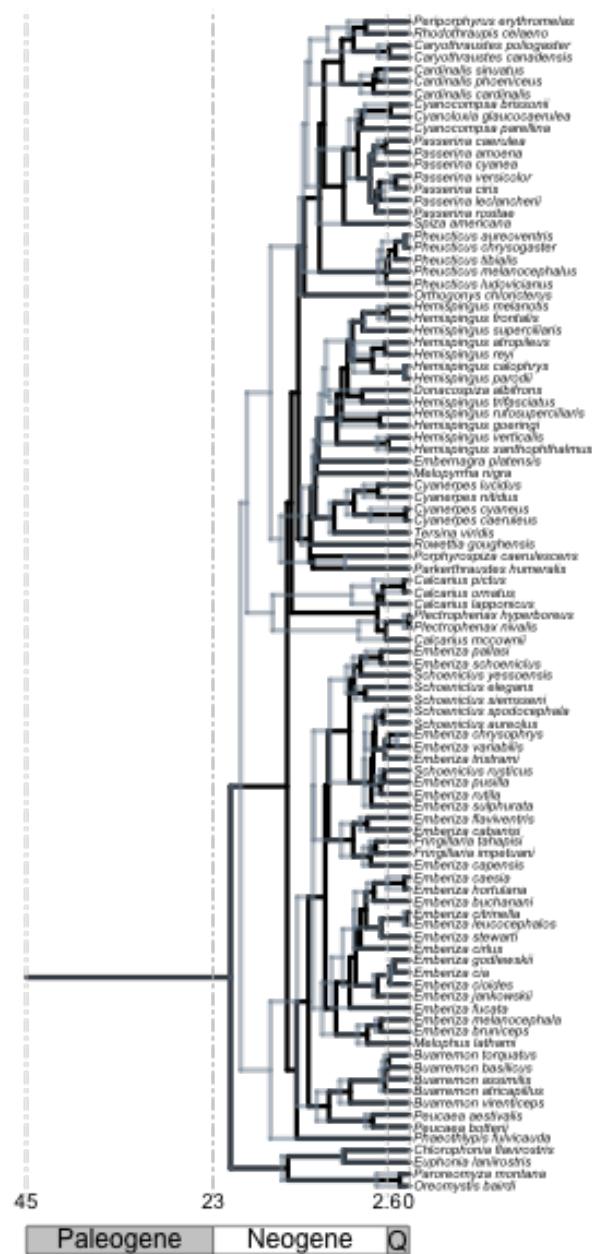


FIGURE 8. Cross validation of second source chronogram. The chronogram shown in black corresponds to the dates published in the original study. The gray chronogram corresponds to

Barker et al. 2015 - chronogram 2

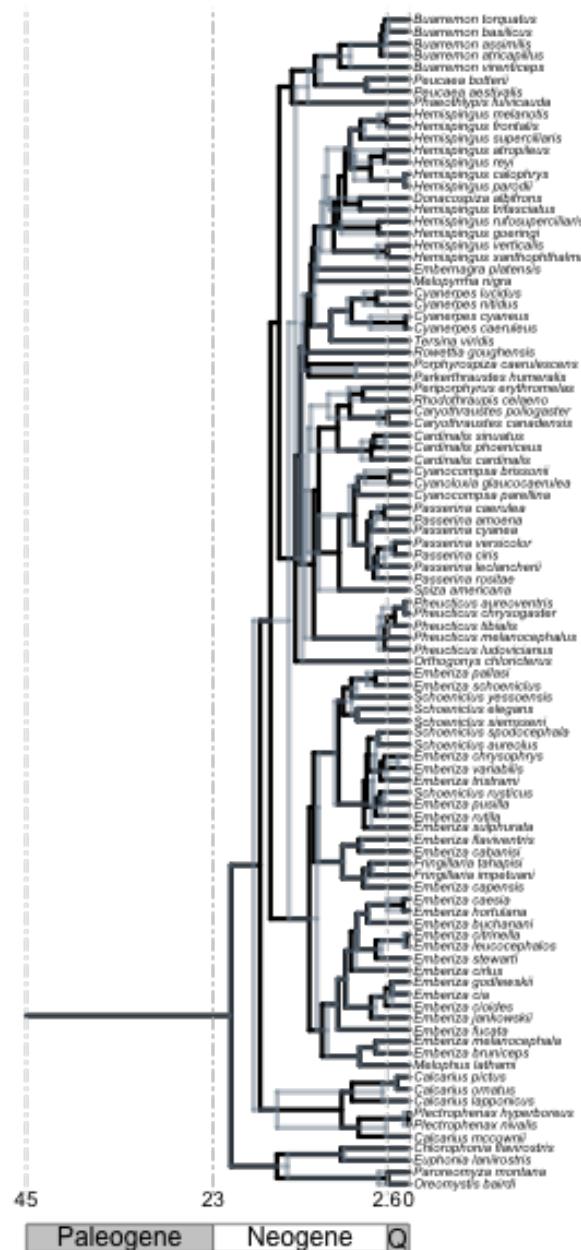


FIGURE 9. Cross validation of third source chronogram. The chronogram shown in black corresponds to the dates published in the original study. The gray chronogram corresponds to

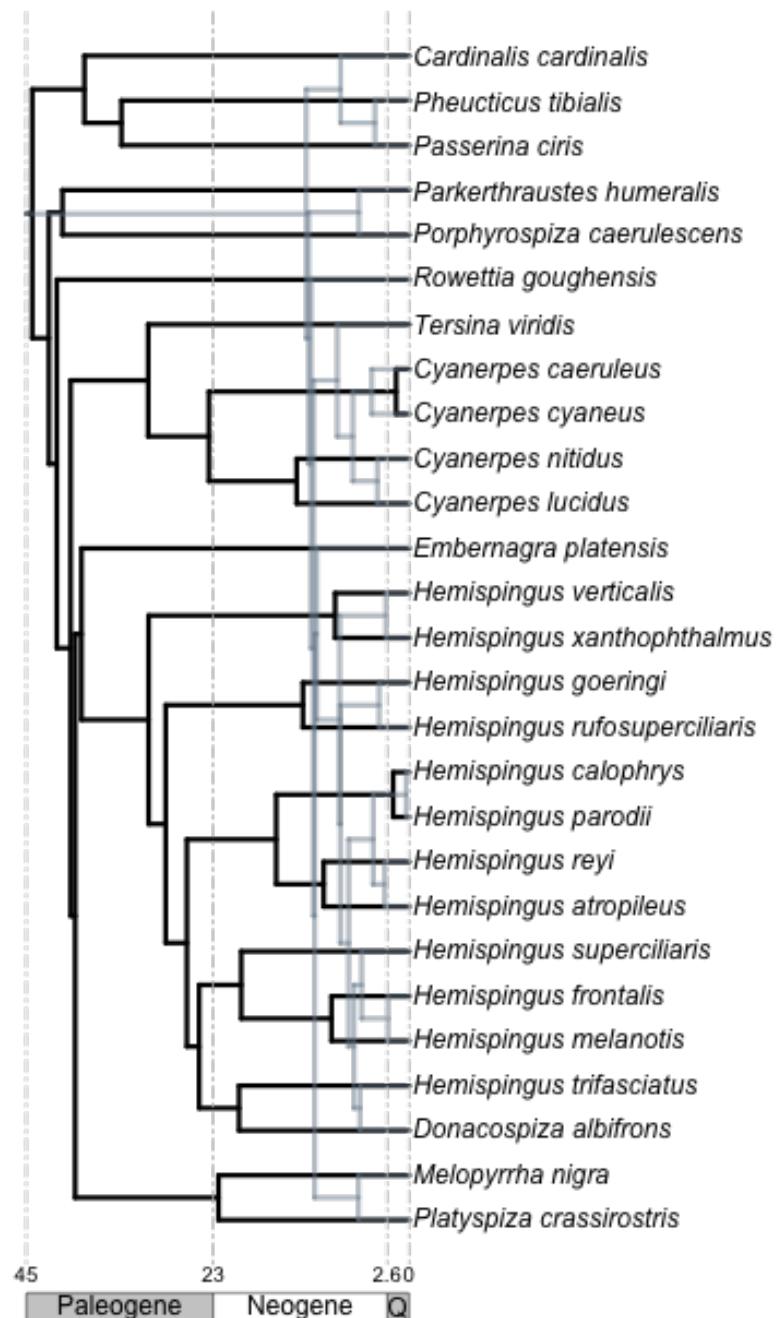
Burns et al. 2015

FIGURE 10. Cross validation of fourth source chronogram. The chronogram shown in black corresponds to the dates published in the original study. The gray chronogram corresponds to the dates calculated with BLADJ, i.e., under a fossil calibration.

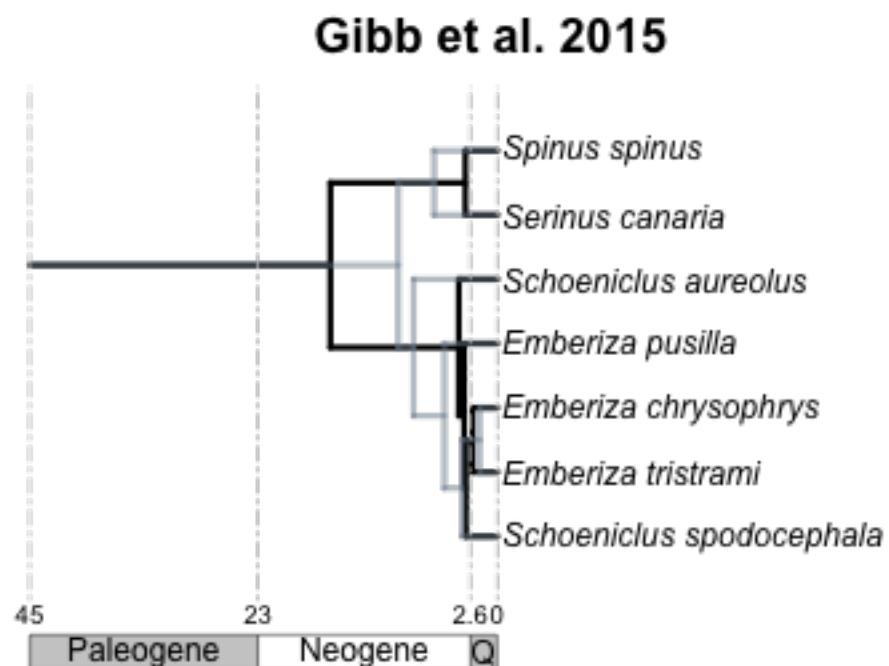


FIGURE 11. Cross validation of sixth source chronogram. The chronogram shown in black corresponds to the dates published in the original study. The gray chronogram corresponds to the same tree topology dated with BLADJ using node ages from all other source chronograms as secondary calibrations.

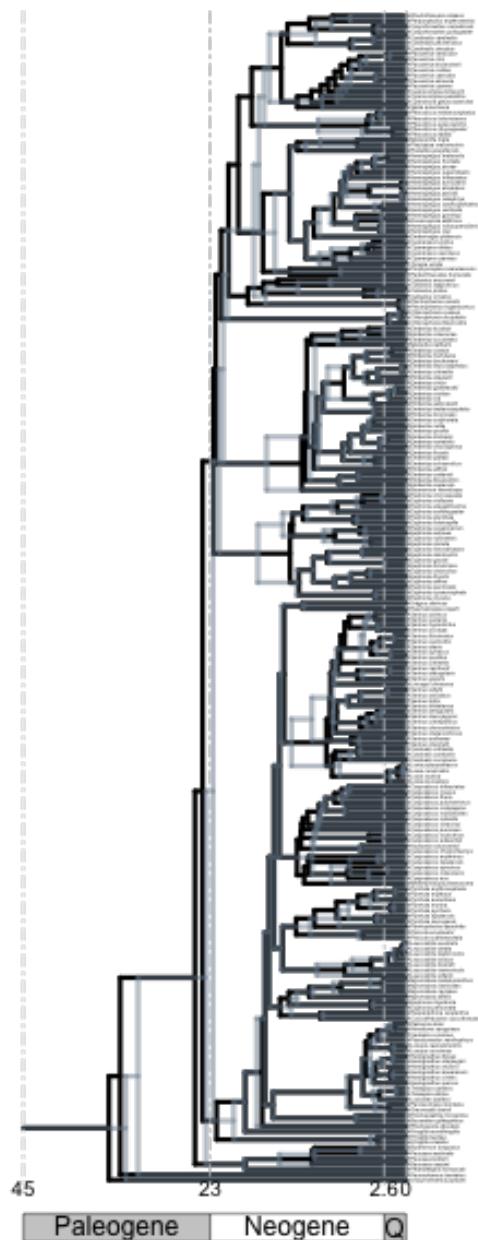
Hedges et al. 2015 - chronogram 1

FIGURE 12. Cross validation of seventh source chronogram. The chronogram shown in black corresponds to the dates published in the original study. The gray chronogram corresponds to the dates calculated with BLADe. In order to facilitate the comparison, the two chronograms are plotted side-by-side.

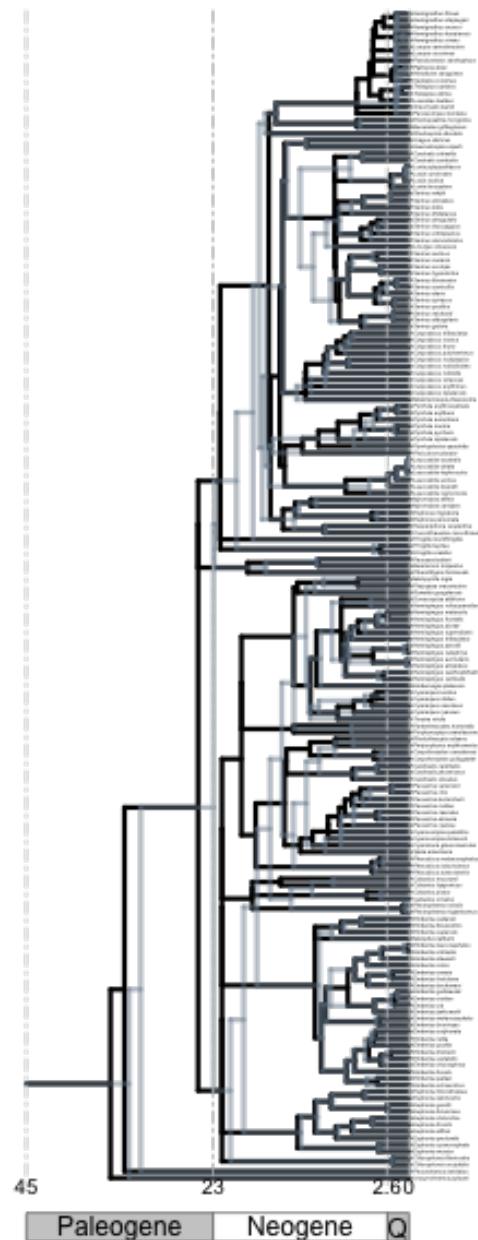
Hedges et al. 2015 - chronogram 2

FIGURE 13. Cross validation of eight source chronogram. The chronogram shown in black corresponds to the dates published in the original study. The gray chronogram corresponds to the dates calculated with BLADJ, i.e., the cross-validation procedure.

Hooper et al. 2017

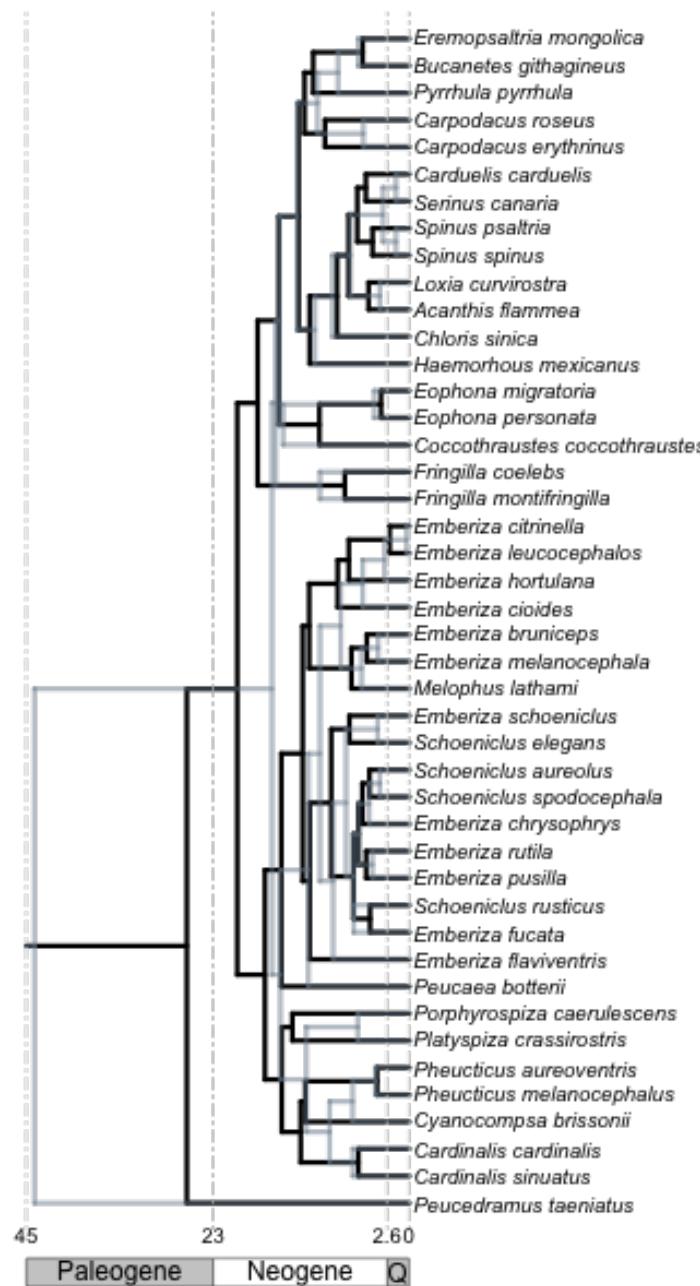


FIGURE 14. Cross validation of ninth source chronogram. The chronogram shown in black corresponds to the dates published in the original study. The gray chronogram corresponds to the dates calculated with BLADJ, i.e., the ones from the ninth source.

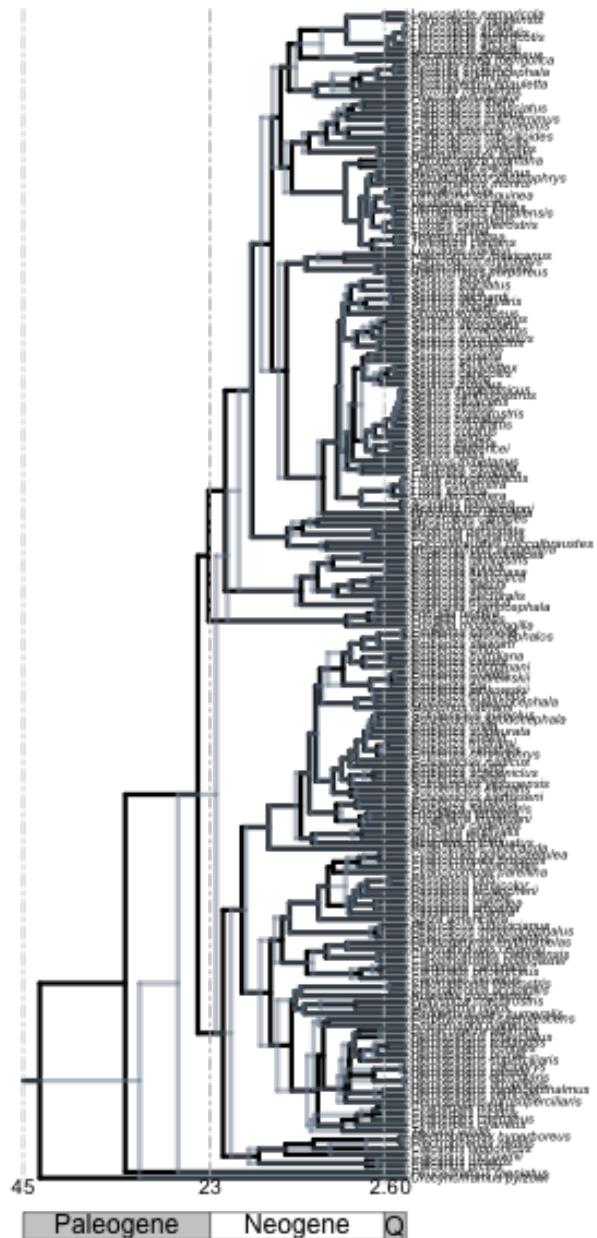
Jetz et al. 2012 - chronogram 1

FIGURE 15. Cross validation of tenth source chronogram. The chronogram shown in black corresponds to the dates published in the original study. The gray chronogram corresponds to the dates calculated with BLADe. In each case, the tree is the same.