

The Fossil Calibration Database—A New Resource for Divergence Dating

DANIEL T. KSEPKA^{1,*}, JAMES F. PARHAM², JAMES F. ALLMAN³, MICHAEL J. BENTON⁴, MATTHEW T. CARRANO⁵,
KAREN A. CRANSTON⁶, PHILIP C. J. DONOGHUE⁴, JASON J. HEAD⁷, ELIZABETH J. HERMSEN⁸, RANDALL B. IRMIS⁹,
WALTER G. JOYCE¹⁰, MANPREET KOHLI¹¹, KRISTIN D. LAMM¹², DAN LEEHR^{6,13}, JOSÉS L. PATANÉ¹⁴, P. DAVID POLLY¹⁵,
MATTHEW J. PHILLIPS¹⁶, N. ADAM SMITH¹⁷, NATHAN D. SMITH¹⁸, MARCEL VAN TUINEN¹⁹, JESSICA L. WARE¹¹,
AND RACHEL C. M. WARNOCK⁵

¹Bruce Museum, 1 Museum Drive, Greenwich, CT 06830, USA; ²John D. Cooper Archaeological and Paleontological Center, Department of Geological Sciences, California State University, Fullerton, CA 92834, USA; ³Interrobang Digital Media, 1034 Pebblebrook Drive, Wake Forest, NC 27587, USA; ⁴School of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK; ⁵Department of Paleobiology, P.O. Box 37012, MRC 121, Smithsonian Institution, Washington DC 20013-7012, USA; ⁶National Evolutionary Synthesis Center, 2024 West Main Street Suite A200, Durham, NC 27705, USA; ⁷Department of Earth and Atmospheric Sciences, University of Nebraska-Lincoln, 228 Bessey Hall, Lincoln, NE 68588, USA; ⁸Department of Environmental and Plant Biology, Ohio University, Athens, OH 45701, USA; ⁹Natural History Museum of Utah and Department of Geology & Geophysics, University of Utah, 301 Wakara Way, Salt Lake City, UT 84108, USA; ¹⁰Department of Geosciences, University of Fribourg, Chemin du Musée 6, 1700 Fribourg, Switzerland; ¹¹Department of Biology, Rutgers University, 195 University Ave, Newark, NJ, 07102, USA; ¹²Bioinformatics Research Center, North Carolina State University, Raleigh, NC 27965, USA; ¹³Duke Center for Genomic and Computational Biology, Duke University, 101 Science Drive, Durham, NC 27708, USA; ¹⁴Departamento de Bioquímica, Instituto de Química, Universidade de São Paulo, 05508-000, Brazil; ¹⁵Department of Geological Sciences, Indiana University, 1001 E. 10th Street, Bloomington, IN 47401, USA; ¹⁶School of Earth, Environmental and Biological Sciences, Queensland University of Technology, Brisbane 4000, Australia; ¹⁷Field Museum of Natural History, 1400 S Lake Shore Drive, Chicago, IL 60605, USA; ¹⁸Department of Biology, Howard University, 415 College Street NW, Washington, DC, 20059, USA; ¹⁹Centre of Evolutionary and Ecological Studies, Marine Evolution and Conservation Group, University of Groningen, Nijenborgh 7, 9747 AG Groningen, The Netherlands;
*Correspondence to be sent to: Bruce Museum, 1 Museum Drive, Greenwich, CT 06830, USA;
E-mail: dksepka@brucemuseum.org.

Daniel T. Ksepka and James F. Parham contributed equally to this article.

Received 26 September 2014; reviews returned 2 December 2014; accepted 22 April 2015
Associate Editor: Laura Kubatko

Abstract.—Fossils provide the principal basis for temporal calibrations, which are critical to the accuracy of divergence dating analyses. Translating fossil data into minimum and maximum bounds for calibrations is the most important—often least appreciated—step of divergence dating. Properly justified calibrations require the synthesis of phylogenetic, paleontological, and geological evidence and can be difficult for nonspecialists to formulate. The dynamic nature of the fossil record (e.g., new discoveries, taxonomic revisions, updates of global or local stratigraphy) requires that calibration data be updated continually lest they become obsolete. Here, we announce the Fossil Calibration Database (<http://fossilcalibrations.org>), a new open-access resource providing vetted fossil calibrations to the scientific community. Calibrations accessioned into this database are based on individual fossil specimens and follow best practices for phylogenetic justification and geochronological constraint. The associated Fossil Calibration Series, a calibration-themed publication series at *Palaentologia Electronica*, will serve as a key pipeline for peer-reviewed calibrations to enter the database. [Calibration; divergence dating; fossil.]

Fossils provide a direct source of temporal data for evolutionary events. In concert with molecular sequence data, fossil-based calibrations provide the essential information for scaling phylogenetic trees to geological time. The proper translation of fossil data into calibrations is the single most important factor for establishing constraints for divergence dating (e.g., Brochu 2004; Parham and Irmis 2008; Joyce et al. 2013; Magallón et al. 2013; Warnock et al. 2015) which, in turn, is the most important factor influencing the accuracy of results (e.g., van Tuinen and Hadly 2004; Inoue et al. 2010; Sauquet et al. 2012; Warnock et al. 2012). Poor estimation of divergence dates as a result of inaccurate fossil calibrations has been demonstrated for both empirical (e.g., Joyce et al. 2013) and theoretical (e.g., dos Reis and Yang 2013) data sets. Similarly, the distribution of fossil calibrations across the phylogeny of interest (Brochu 2004), as well as the assignment of prior distributions to individual calibrations (e.g., Ho and Phillips 2009; Inoue et al. 2010; Clarke et al. 2011; Warnock et al.

2012), can have large effects on estimates of divergence dates.

Given the importance of fossil calibrations, there is a pressing need to increase their number and phylogenetic spread. Because calibrations can have a large impact on results throughout the tree (Ho and Phillips 2009; Clarke et al. 2011), quality control remains critical even when large numbers of calibrations are used. Furthermore, fossil calibrations are needed for poorly covered areas of the Tree of Life, where secondary calibrations continue to be used at a high rate despite widely acknowledged flaws in this approach (Hipsley and Müller 2014). Given these trends and concerns, it is necessary to increase the quality and quantity of fossil calibrations.

Unfortunately, methods for estimating the phylogenetic positions and geological ages of fossil specimens used for node-calibration are often treated less rigorously in divergence dating studies than steps such as sequence alignment, model selection, and searching for optimal trees. This weakness is due in

Palaeontologia Electronica
Fossil Calibration Database

Browse Calibrations Submit to PE FAQ About Contact Us

Search for calibrations in the database — you can also [browse the NCBI taxonomy](#)

marsupials Sort by relevance ▾

Advanced search filters

- By tip taxa
- By any clade
- By age (in Ma)
- By geological time

157.3–169.6 Ma Added Oct 13, 2014

Theria – from Benton et al. 2015
Benton, M.J., Donoghue, P.C.J., Asher, R.A., Friedman, M., Near, T.J., and Vinther, J. 2015. Constraints on the timescale of animal evolutionary history. *Palaeontologia Electronica*, 18.1.1FC. [more >](#)

47.6–131.3 Ma Added Oct 13, 2014

Marsupialia – from Benton et al. 2015
Benton, M.J., Donoghue, P.C.J., Asher, R.A., Friedman, M., Near, T.J., and Vinther, J. 2015. Constraints on the timescale of animal evolutionary history. *Palaeontologia Electronica*, 18.1.1FC. [more >](#)

15.97–54.65 Ma Added May 31, 2013

Macropodoidea – from Phillips, 2015
Phillips, M.J. 2015. Four mammal fossil calibrations: balancing competing palaeontological and molecular considerations. *Palaeontologia Electronica*, 18.1.5FC. [more >](#)

Sponsored by [Coquina Press](#) and [NESCent](#). • All data is released under a [CC0 waiver](#). To the extent possible under law, the authors have waived all copyright and related or neighboring rights to the data in the Fossil Calibrations database. • Full source code for this website (© 2013–2014, National Evolutionary Synthesis Center) is available under the [BSD \(2-clause\) license](#).

FIGURE 1. Example of the Fossil Calibration Database interface. The browse function allows users to enter any NCBI taxon name and to browse toward the root via the “Lineage” bread-crumbs trail or toward a tip by selecting any of the “Calibrations within clade” results. Searching via taxon, age, and/or author is also possible.

part to the breadth of interdisciplinary knowledge required to assess potential fossil calibrations, especially the difficulty in interpreting the relevant systematic, stratigraphic, and geochronological literature. Moreover, phylogenetic hypotheses and age estimates of fossils can, and often do, change over time. Widely used calibrations have been discarded due to new discoveries or revisions to ages and taxonomy (e.g., [Parham et al. 2012](#); [Benton et al. 2015](#)). These concerns are not obviated by the introduction of tip-based calibration methods (so-called ‘Total Evidence Dating’; e.g., [Pyron et al. 2011](#); [Ronquist et al. 2012](#)), which must also accommodate rigorous fossil dating. While tip-based approaches represent an exciting new class of methods for including fossil data, methodological concerns remain over the accuracy of “morphological clocks” (e.g., [Arcila et al. 2015](#)) and node-based calibrations are frequently used even within the context of tip-dating studies (e.g., [Beck and Lee 2014](#)). Furthermore, limitations of currently available software preclude tractable dating using data sets that combine genomic-scale molecular data and morphological data in a probabilistic framework ([Giribet 2015](#)). Thus, node-calibration approaches are likely to retain importance, especially as phylogenomic data sets become increasingly common.

A DATABASE APPROACH TO FOSSIL CALIBRATIONS

Background

We introduce the Fossil Calibration Database, (Figures 1–2) an open-access electronic resource for vetted, peer-reviewed fossil calibrations developed by a NESCent Working Group ([Ksepka et al. 2011](#)) and hosted in collaboration with the journal *Palaeontologia Electronica*. Calibrations must undergo peer review and meet the Best Practices (Table 1) articulated by [Parham et al. \(2012\)](#) to be accessioned into the database, offering a greater level of scientific rigor and clarity to users than might be obtained by harvesting putative dates from the general paleontological literature. In supplying calibrations to facilitate new analyses, the Fossil Calibration Database is distinct from *TimeTree* ([Hedges et al. 2006](#)), which serves as a database of published molecular divergence estimates.

A database approach is advantageous because the fossil record is not static. New fossil specimens are constantly being discovered, and the phylogenetic positions of known fossil taxa are frequently reinterpreted in light of new methods of study or phylogenetic revisions. Stratigraphic revisions regularly shift the best age estimates for individual fossils at both the local (e.g., new stratigraphic correlations or


Search by author, publication, species, etc. 

[Browse Calibrations](#) [Submit to PE](#) [FAQ](#) [About](#) [Contact Us](#)

Macropodoidea

[comment on this calibration](#)

Lineage (NCBI): root » Eukaryota » Opisthokonta » Metazoa » Eumetazoa » Bilateria » Coelomata » Deuterostomia » Chordata » Craniata <chordata> » Vertebrata <Metazoa> » Gnathostomata <vertebrate> » Euteleostomi » Sarcopterygii » Tetrapoda » Amniota » Mammalia » Theria <Mammalia> » Metatheria » Diprotodontia

calibration from:

Phillips, M.J. 2015. Four mammal fossil calibrations: balancing competing palaeontological and molecular considerations. *Palaeontologia Electronica*, 18.1.5FC.
[View electronic resource](#)

node name

Macropodoidea [Look for this name in NCBI](#) [Wikipedia](#) [Animal Diversity Web](#)

recommended citations

Phillips, 2015 <http://palaeo-electronica.org/content/fe-5>

node minimum age

15.97 Ma

Ganguroo bilamina occurs in Faunal Zones B and C of the Riversleigh local faunas (northwestern Queensland). The older of these is Faunal Zone B, from which *G. bilamina* is known from sites such as Wayne's Wok (including the holotype), Camel Sputum and Mike's Menagerie. Early Miocene dates have consistently been attributed to Faunal Zone B sites by biocorrelation (Black, 1997; Travouillon et al., 2006). More recently, Black et al. (2012) indicated that U/Pb radiometric dating of speleothems now confirms this timing. However, until the new dates are published I consider the top of the Early Miocene to provide a hard minimum for Riversleigh Faunal Zone B and hence, for the crown Macropodoidea divergence.

node maximum age

54.65 Ma

Several putative crown macropodoids occur in Late Oligocene (~25 Ma, Woodburne et al., 1993; Megirian et al., 2010) Etadunna and Riversleigh Faunal Zone A sites and as such, an older maximum bound is required for this clade. Unfortunately, the preceding hiatus in the Australasian terrestrial mammal fossil record stretches back to the earliest Eocene (54.6 ± 0.05 Ma) Tingamarra site near Murgon, Queensland (Godthelp et al., 1992). This gap provides for a very conservative maximum bound, because the Tingamarra Fauna represents an early stage in the evolution of Australian marsupials (Beck et al., 2008), well before the evolution of the highly derived kangaroos and potoroos.

primary fossil used to date this node

QM 19915

Ganguroo bilamina, Cooke, 1997

Location relative to the calibrated node: **Crown**

[\[show fossil details\]](#)

More information in [Fossilworks](#) [PaleoBioDB](#)

phylogenetic justification

The well-sampled, matrix-based cladistic analysis of Prideaux and Warburton (2010) provides 97% bootstrap support for grouping *Ganguroo* with or within Macropodidae to the exclusion of Potoroidae. Several mandibulo-dental and postcranial characters provided unambiguous synapomorphies for this relationship, including bilophodont molars and a straight acromion process on the scapula. All other cladistic analyses concur with this relationship for *Ganguroo*, although its precise position among basal macropodids is uncertain (see Kear and Pledge, 2007). The living macropodoid clades, Macropodidae and Potoroidae, are sister taxa in all recent molecular studies (e.g., Phillips and Pratt, 2008; Meredith et al., 2008a) and each of the morphological cladistic analyses that include *G. bilamina* (see above) is consistent with this relationship.

phylogenetic reference(s)

Prideaux, G.J. and Warburton, N.M. 2010. An osteology-based appraisal of the phylogeny and evolution of kangaroos and wallabies (Macropodidae: Marsupialia). *Zoological Journal of the Linnean Society*, 159:954-987.

tree image (click image for full size)

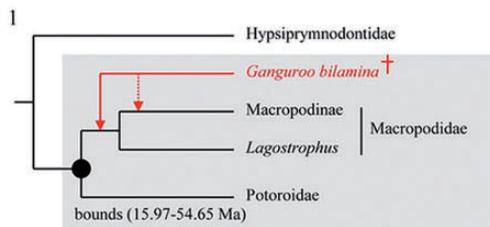


Figure 1 from Phillips (2015).

FIGURE 2. Example of the Fossil Calibration Database search result. Specimen data and the justifications for the recommended age and phylogenetic placements are provided, along with references, a tree image, and a link to the Fossil Calibration Series paper providing the full data.

TABLE 1. Best practices for justifying fossil calibrations (Parham et al. 2012), which must be met by calibrations accessioned into the Fossil Calibration Database

Best practices

1. Museum numbers of specimen(s) that demonstrate all the relevant characters and provenance data should be listed. Referrals of additional specimens to the focal taxon should be justified.
2. An apomorphy-based diagnosis of the specimen(s) or an explicit, up-to-date, phylogenetic analysis that includes the specimen(s) should be referenced.
3. Explicit statements on the reconciliation of morphological and molecular data sets should be given.
4. The locality and stratigraphic level (to the best of current knowledge) from which the calibrating fossil(s) was/were collected should be specified.
5. Reference to a published radioisotopic age and/or numeric timescale and details of numeric age selection should be given.

radiometric dates) and global scales (e.g., updates to major boundaries in the Geological Time Scale). The Fossil Calibration Database can accommodate such fluctuations by adding new calibrations as they are formulated, alerting users to alternate proposed calibrations for nodes, and flagging calibrations that have been superseded by newly discovered fossils.

A recent revision of fossil calibrations for major nodes in the animal phylogeny serves to illustrate the dynamic nature of fossil data. Benton (1990) compiled a suite of key fossil calibrations within Metazoa, which has been updated and revised several times (Benton and Donoghue 2007; Donoghue and Benton 2007; Benton et al. 2009). This compilation was most recently expanded and vetted against Best Practices as part of the Fossil Calibrations Database project (Benton et al. 2015). As may be expected, new discoveries are an important driver of updates: A different fossil now calibrates more than half of the 48 nodes that are examined in both the new and previous contributions (Table 2). It is illustrative to note that although new fossil discoveries are an important driver of revised dates, the majority of updates are due to phylogenetic and stratigraphic revisions.

Utilizing the Database

Fossil Calibration Database users can browse calibrations based on the extended NCBI taxonomy, or search by clade name, most recent common ancestor of the tip taxa of interest (MRCA of taxon A and taxon B), and/or age or geological time period. For each calibration result, the fossil specimen, hard minimum, soft maximum (if available), and recommended citation(s) are provided. Direct links to pdfs of papers in *Palaeontologia Electronica* are provided

for those calibrations whose justification has been published in the Fossil Calibration Series (FCS) (see below). A tree graphic is provided alongside every calibration to ensure phylogenetic placement is properly conveyed and avoid confusion due to variation in the application of NCBI taxon names (e.g., applying names to stem-based vs. crown-based clades). For all calibrations of named clades and/or based on fossils of named taxa, links are provided to relevant pages of the Paleobiology Database (paleodb.org), Animal Diversity Web (animaldiversity.org), and Wikipedia (en.wikipedia.org). Links to NCBI taxonomy pages for taxa within the clade of interest are also provided. The Fossil Calibration Database and Open Tree of Life both allow API access to their data, allowing for data integration. Fossil information will be useful for adding branch lengths to Open Tree of Life, or as an annotation layer on the Tree. The use of taxon names from the NCBI taxonomy in both resources will help facilitate future interaction.

The Fossil Calibration Database also includes an option to provide data and justification for maximum dates. Maximum dates are, of course, far more argumentative than minimum dates, which is why most methods use "soft" maxima. Nonetheless, most currently favored methods for divergence dating require at least one maximum date (whether in the form of a point calibration, hard maximum, or soft maximum) to operate. We do not require maximum bounds in calibration papers and the database, although where possible we encourage contributors to provide information relevant to users for choosing soft maximum bounds.

Although the primary function of the Fossil Calibration Database is to provide an easily accessible and updatable source for calibrations, the database is designed to encourage proper citation of the paleontological research that forms the basis for fossil calibrations. We recognize citing the database itself is useful in highlighting its utility, but we strongly encourage authors to also cite the primary literature for individual calibrations. To date, many divergence dating studies have cited a previous divergence dating study or a general review paper (which may lack primary data as a reference for calibrations), or provide no citations for calibrations at all. Directing database users to the appropriate literature for individual calibrations should ensure that an explicit and reproducible chain of evidence exists for use of these fossil calibrations. This approach will also increase the citation rates of papers laying out the justification for calibrations, thereby encouraging paleontologists to pursue the research required to translate fossil data into usable fossil calibrations.

Contributing to the Fossil Calibration Database

An important source of contribution to the Fossil Calibration Database will be the Fossil Calibration Series,

TABLE 2. Evolution of minimum clade age constraints

Crown clade	Benton 1990	Benton and Donoghue 2007	Donoghue and Benton 2007	Benton et al. 2009	Benton et al. 2015
Metazoa				634.9	550.25 ^a
Eumetazoa				531.5	550.25 ^a
Cnidaria				520.5	529 ^b
Bilateria		531.5	531.5	531.5	550.25 ^a
Protostomia				531.5	550.25 ^a
Deuterostomia			518.5	518.5	515.5 ^b
Chordata				518.5	514 ^b
Olfactores				518.5	514 ^b
Vertebrata				460.6	457.5 ^c
Gnathostomata				421.75	420.7 ^d
Osteichthyes		416.1	416 ^b	416	420.7 ^d
Clupeocephala		149.85	149.85	149.85	150.94 ^a
Ovalentaria– Tetraodontiformes		96.9	96.9	96.9	69.71 ^d
Gasterosteiformes– Tetraodontiformes		96.9	96.9	96.9	69.71 ^d
Tetraodontidae		32.25	32.25	32.25	32.02 ^b
Tetrapoda	363	330.4 ^a	330.4	330.4	337 ^a
Amniota	305	312.3 ^a	312.3	312.3	318 ^b
Diapsida	255	259.7 ^b	259.7	255.9 ^b	255.9
Archosauria	240	235 ^e	235	239 ^b	247.1 ^e
Neornithes	79	6 ^e	66	66	66
Neognathae	70	66 ^e	66	66	66
Mammalia	105	162.5 ^{e,d}	162.5	162.9 ^b	164.9 ^b
Marsupialia		61.5	61.5	61.5	47.6 ^d
Theria	94	124.6 ^e	124.3 ^b	124 ^b	156.3 ^e
Placentalia	59			62.5 ^e	61.6 ^{a,b}
Afrotheria		48.4	48.4	48.4	56 ^e
Atlantogenata				55.6	56 ^e
Bovidae		18.3	18 ^b	18	16 ^a
Whippomorpha-Ruminantia				52.4	52.4
Cetartiodactyla		48.3	48 ^b	52.4 ^e	52.4
Carnivora		42.8	43 ^b	39.68 ^a	37.3 ^b
Laurasiatheria			65.2	62.5 ^a	61.6 ^a
Lipotyphla			61.5	61.5	61.6 ^a
Boreoeutheria		95.3	71.2 ^d	61.5 ^a	61.6 ^b
Muridae		10	11 ^b	10.4 ^b	10.4
Rodentia			55.8	55.6	56 ^b
Lagomorpha				48.6	47.6 ^b
Glires	59	61.5 ^e	61.7 ^b	61.5 ^a	56 ^b
Archontoglires		61.5	61.7 ^b	61.5 ^a	61.6 ^{a,b}
Archonta	67		65.2 ^a	61.5 ^a	61.6 ^{a,b}
Primates			55.5	55.6 ^a	56 ^b
Strepsirhini				33.7	33.9 ^b
Anthropoidea				33.7	33.9 ^b
Catarrhini		23	23.5 ^b	23.5	24.44 ^a
Hominidae				11.2	11.6 ^b
Homininae		6.5	6.5	5.7 ^b	6.5 ^b
<i>Homo sapiens</i>				0.2	0.2

Note: Ages are in millions of years before present.

The clade age constraints required are principally by:

^aChange to a different but existing fossil.

^bRevision of timescale.

^cChange required to meet increased stringency of best practices.

^dRevision of phylogeny.

^eDiscovery of a new fossil.

a series of peer-reviewed articles in the open-access journal *Palaeontologia Electronica*. Articles published in the FCS will detail the phylogenetic and stratigraphic justifications for fossil calibrations, and these papers will be directly linked to individual calibrations in the Fossil Calibration Database. The FCS provides an important set of calibrations for the Fossil Calibration Database, with an initial set of 120 calibrations covered in the inaugural set of papers and many additional calibrations to follow in the second wave of FCS publications. These calibrations span a broad swath of the Tree of Life, and although vertebrates are best represented in the initial data set we are actively recruiting contributors working on sparsely represented clades. The FCS will be the main source of contributions to the data base, because it is peer reviewed. However, calibrations from other sources will also be considered by the Fossil Calibration Advisory Board, a rotating board of taxonomic and methodological experts, for entry into the database if they adhere to the Best Practices articulated by Parham et al. (2012).

This Fossil Calibration Advisory Board is also responsible for annotating the database to indicate updates and disagreements. Users can criticize existing calibrations using the "Comment on this Calibration" button. This allows the user to send a message to the FCD administrators, which can be used to alert them to incorrect or obsolete data. Beyond serving as a platform for new calibrations, the FCS welcomes papers discussing all aspects of calibration implementation, debates over contentious calibrations, and empirical calibration-based analyses.

Availability

The database is hosted by *Palaeontologia Electronica* and freely accessible at <http://fossilcalibrations.org>. Data are available through the graphical interface and search results can be downloaded as JavaScript Object Notation (JSON) or comma-separated values (csv). Data are also made available through an Application Programming Interface (API) that replicates the search capability of the graphical interface. The API adopts a RESTful architecture and documentation is available at <http://docs.fcdb.apiary.io>. All data are released with a CC0 waiver. The software is an open source and available at <http://github.com/nescent/fossilcalibrations> with a BSD 2-clause license. Ongoing hosting and support is provided by *Palaeontologia Electronica*.

FUNDING

This project was supported by the National Evolutionary Synthesis Center (NSF EF-0905606) as part of the Working Group grant "Synthesizing and Databasing Fossil Calibrations: Divergence Dating and Beyond" (to DTK and JFP), and funding from the John D. and Catherine T. MacArthur Foundation for the

Biodiversity Synthesis Group of the Encyclopedia of Life and a BioSynC Synthesis Meeting (to JFP). *Palaeontologia Electronica* is funded by the Palaeontological Association, the Paleontological Society, the Society of Vertebrate Paleontology, and the Western Interior Paleontological Society.

ACKNOWLEDGMENTS

We thank Barbara Dobrin, María A. Gandolfo-Nixon, and Christopher Torres for discussion; Mark Sutton and Vladimir Gapeyev for technical expertise; and Candace Brown Wiggins, Stephanie Ribson, Jeff Sturkey, and Danielle Wiggins for logistical support. We also wish to thank Editor Frank Anderson, Associate Editor David Posada, April Wright, and an anonymous reviewer for comments and suggestions that improved the quality of the article.

REFERENCES

- Arcila D., Pyron R.A., Tyler J.C., Ortí G., Betancur-R. R. 2015. An evaluation of fossil tip-dating versus node-age calibrations in tetraodontiform fishes (Teleostei: Percomorphaceae). *Mol. Phylogenet. Evol.* 82:131–145.
- Beck R.M.D., Lee M.S.Y. 2014. Ancient dates or accelerated rates? Morphological clocks and the antiquity of placental mammals. *Proc. R. Soc. B* 281:20141278.
- Benton M.J. 1990. Phylogeny of the major tetrapod groups: morphological data and divergence dates. *J. Mol. Evol.* 30: 409–424.
- Benton M.J., Donoghue P.C.J. 2007. Paleontological evidence to date the tree of life. *Mol. Biol. Evol.* 24:26–53.
- Benton M.J., Donoghue P.C.J., Asher R.J. 2009. Calibrating and constraining molecular clocks. In Hedges S.B., Kumar S., editors. *The timetree of life*. Oxford: Oxford University Press. p. 35–86.
- Benton M.J., Donoghue P.C.J., Asher R.J., Friedman M., Near T.J., Vinther J. 2015. Constraints on the timescale of animal evolutionary history. *Palaeontol. Electron.* 18.1:1FC.
- Brochu C.A. 2004. Patterns of calibration age sensitivity with quartet dating methods. *J. Paleontol.* 78:7–30.
- Clarke J.T., Warnock R.C.M., Donoghue P.C.J. 2011. Establishing a timescale for plant evolution. *New Phytol.* 192:266–301.
- Donoghue P.C.J., Benton M.J. 2007. Rocks and clocks: calibrating the Tree of Life using fossils and molecules. *Trends Ecol. Evol.* 22: 424–431.
- dos Reis M., Yang Z. 2013. The unbearable uncertainty of Bayesian divergence time estimation. *J. Syst. Evol.* 51:30–43.
- Giribet G. 2015. Morphology should not be forgotten in the era of genomics—a phylogenetic perspective. *Zool. Anz.* doi:10.1016/j.jcz.2015.01.003.
- Hedges S.B., Dudley J., Kumar S. 2006. TimeTree: A public knowledge-base of divergence times among organisms. *Bioinformatics* 22: 2971–2972.
- Hipsley C.A., Müller J. 2014. Beyond fossil calibrations: realities of molecular clock practices in evolutionary biology. *Front. Genet.* 5:1–11.
- Ho S.Y.W., Phillips M.J. 2009. Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence. *Syst. Biol.* 68:367–380.
- Inoue J., Donoghue P.C.J., Yang Z. 2010. The impact of the representation of fossil calibrations on Bayesian estimation of species divergence times. *Syst. Biol.* 59:74–89.
- Joyce W.G., Parham J.F., Lyson T.R., Warnock R.C.M., Donoghue P.C.J. 2013. A divergence dating analysis of turtles using fossil calibrations: an example of best practices. *J. Paleontol.* 87:612–634

- Ksepka D.T., Benton M. J., Carrano M.T., Gandolfo M.A., Head J.J., Hermesen E.J., Joyce W.G., Lamm K.S., Patané J.S.L., Phillips M.J., Polly P.D., van Tuinen M., Ware J.L., Warnock R.C.M., Parham J.F. 2011. Synthesizing and databasing fossil calibrations: divergence dating and beyond. *Biol. Lett.* 7:801–803.
- Magallón S., Hilu K.W., Kwanndt D. 2013. Land plant evolutionary timescale: gene effects are secondary to fossil constraints in relaxed clock estimation of age and substitution rates. *Am. J. Bot.* 100: 556–573.
- Parham J.F., Donoghue P.C.J., Bell C.J., Calway T.D., Head J.J., Holroyd P.A., Inoue J.G., Irmis R.B., Joyce W.G., Ksepka D.T., Patané J.S.L., Smith N.D., Tarver J.E., Van Tuinen M., Yang Z., Angielczyk K.D., Greenwood J., Hipsley C.A., Jacobs L., Makovicky P.J., Müller J., Smith K.T., Theodor J.M., Warnock R.C.M., Benton M.J. 2012. Best practices for justifying fossil calibrations. *Syst. Biol.* 61:346–359.
- Parham J.F., Irmis R.B. 2008. Caveats on the use of fossil calibrations for molecular dating: a comment on Near et al. *Am. Nat.* 171: 132–136.
- Pyron R.A. 2011. Divergence time estimation using fossils as terminal taxa and the origins of Lissamphibia. *Syst. Biol.* 60:466–481.
- Ronquist F., Klopfstein S., Vilhelmsen L., Schulmeister S., Murray D.L., Rasnitsyn A. P. 2012. A total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera. *Syst. Biol.* 61:973–999.
- Sauquet H., Ho S.Y., Gandolfo M.A., Jordan G.J., Wilf P., Cantrill D.J., Bayly M.J., Bromham L., Brown G.K., Carpenter R.J., Lee D.M., Murphy D.J., Kale Sniderman J.M., Udovicic F. 2012. Testing the impact of calibration on molecular divergence times using a fossil-rich group: the case of *Nothofagus* (Fagales). *Syst. Biol.* 61:289–313.
- van Tuinen M., Hadly E.A. 2004. Calibration and error in Placental molecular clocks: a conservative approach using the cetartiodactyl fossil record. *J. Hered.* 95:200–208.
- Warnock R.C.M., Parham J.F., Joyce W.G., Lyson T.R., Donoghue P.C.J. 2015. Calibration uncertainty in molecular dating analyses: there is no substitute for the prior evaluation of time priors. *Proc. R. Soc. B* 282: 20141013.
- Warnock R.C.M., Yang Z., Donoghue P. C. J. 2012. Exploring uncertainty in the calibration of the molecular clock. *Biol. Lett.* 8:156–159.