

# Incorporating fossils into hypotheses of insect phylogeny

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Fossils represent stem and crown lineages, and their inclusion in phylogenetic reconstruction influences branch lengths, topology, and divergence time estimation. In addition, paleontological data may inform trends in morphological evolution as well as biogeographic history. Here we review the incorporation of fossils in studies of insect evolution, from morphological analyses to combined ‘total evidence’ node dating analyses. We discuss challenges associated with fossil based phylogenetics, and suggest best practices for use in tree reconstruction.

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## Introduction

The fate of every species is to go extinct. This results in a mixture of crown lineages [which have living representatives currently] and stem lineages [for which there are no extant representatives] in the fossil record. How to best incorporate such fossils into insect phylogenetic hypotheses has been a matter of debate. Those in favor of incorporating fossils in phylogenetic studies argue that although fossilization is rare, the vast majority of insect species have gone extinct [1] and therefore fossil taxa offer otherwise unknowable insight into the morphological, biogeographic, and temporal history of extant lineages. Initially, phylogenetic analyses that included fossils were based on morphology-only datasets [2], making their incorporation relatively straightforward. The advent of molecular-based phylogenetic and comparative analysis has made the incorporation of fossil data into combined datasets less clear. So-called ‘total-evidence’ methods of integrating molecular and morphological data arose with the aim of addressing incongruence between datasets while allowing fossils to impact phylogenetic reconstruction [3]. However, these combined analysis

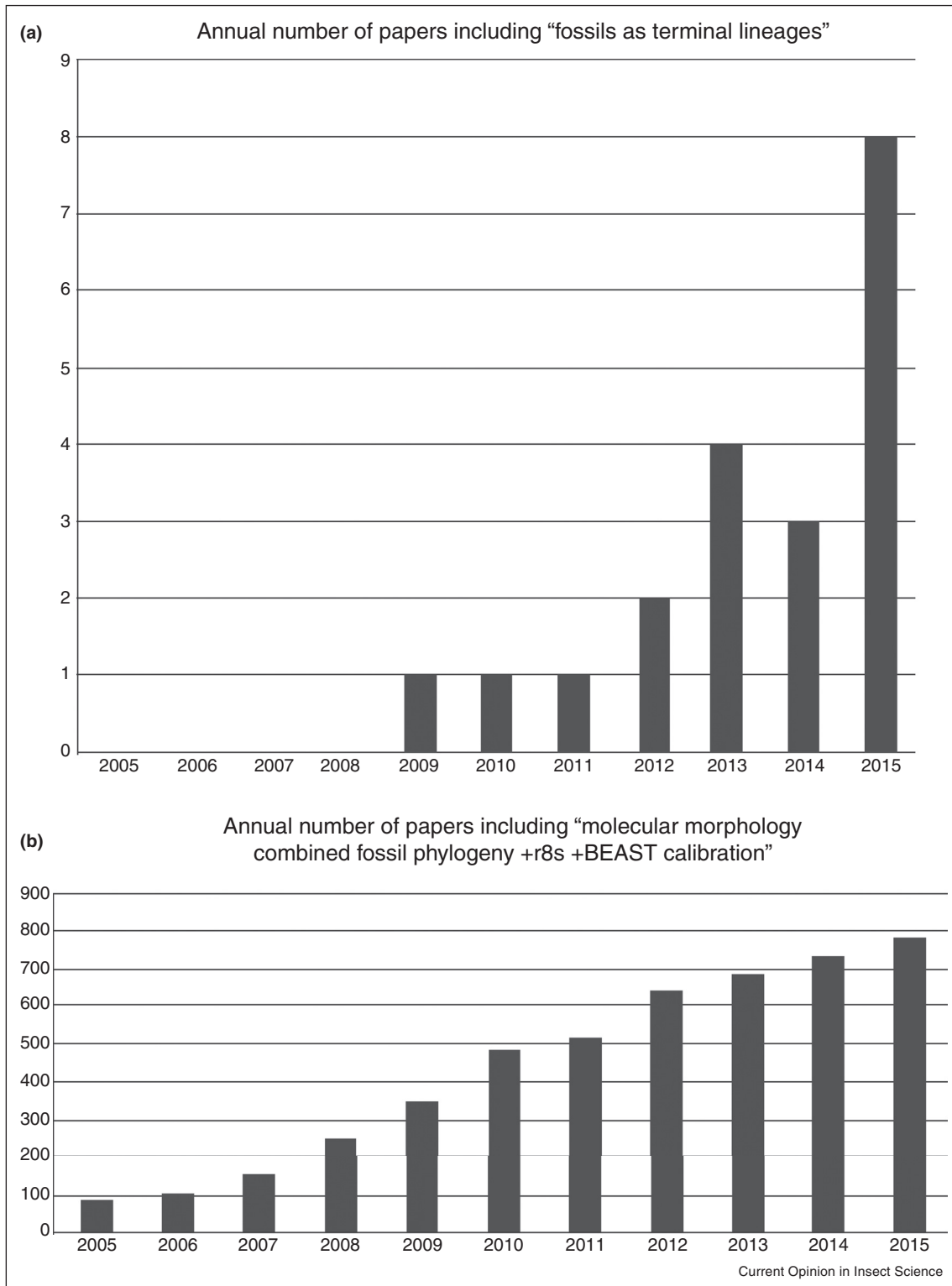
techniques were challenging, as initial model-based procedures prohibited simultaneous optimization of molecular and morphological characters. In the last decade, after implementation of the mk model by several software applications [4], fossils have become increasingly common in combined molecular and morphological phylogenetic datasets (e.g. [5]). In addition, divergence time [‘dating’] estimates are now widely considered integral information when interpreting the evolution of organisms from a phylogenetic perspective; these estimates rely on fossil calibrations to estimate node ages. In these dating studies, fossils may be stem or crown, treated as terminal lineages [Figure 1, Top] (e.g. [6–19,20<sup>••</sup>,21–23,24<sup>••</sup>]) or, more frequently [Figure 1, Bottom] used as node calibrations modeled with uniform or non-uniform distributions (e.g. [25<sup>••</sup>,26–29]). For groups with poor fossil records, secondary calibrations [i.e., dates from prior studies, biogeographic constraints] have become more commonly used when estimating divergence times, which is problematic (see [30<sup>••</sup>] for review; briefly, node ages calibrated by secondary calibrations were found to be younger and give spurious estimates of precision].

Whether for chronogram or phylogenetic reconstruction, the use of fossils has often been contentious due to a lack of agreement about how to use stem and crown fossils, in particular when considering mixed types of data (e.g. [31–36,73<sup>••</sup>74]). Here we review the use of fossils in past phylogenetic datasets, discuss current methodology, and the challenges facing future dataset analyses.

## Traditional fossil treatments in phylogenetics: ‘total evidence’ analyses

Hennig [37,38] incorporated fossils in a phylogenetic treatment of insects, based on morphological synapomorphies [Figure 2a]; this was the first phylogenetic evaluation of extant and living insect lineages. When reconstructing evolutionary relationships among insects, authors have argued that fossils provide vital information about character polarity (e.g. [39]). Several have argued further that fossil inclusion may reduce long-branch attraction [2,40]. Donoghue *et al.* [41] tested the effect of fossils on amniote and seed-plant morphological phylogeny, and suggested that fossil inclusion may result in topological differences. Similarly, Lee [42] found that potentially incorrect relationships resulted when fossils were omitted from phylogenetic reconstructions of lizards. Further, the results from Wiens [43] support the inclusion of even incomplete fossils in phylogenetic reconstruction despite some level of missing data,

Figure 1



Comparison of publication rates for alternative divergence time estimation protocols. **Top** total papers per year found on Google Scholar, which include 'fossils as terminal lineages' in text. **Bottom** total annual papers on Google Scholar including the terms 'molecular morphology combined fossil phylogeny calibration' which utilized the phylogenetic programs r8s or BEAST.

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