O P I N I O N

Can higher-level phylogenies of weevils explain their evolutionary success? A critical review

N I C O M . F R A N Z[1] and M I C H A E L S . E N G E L[2]

[1]Department of Biology, University of Puerto Rico, Mayagüez, PR, U.S.A. and [2]Division of Entomology, Natural History Museum, University of Kansas, Lawrence, KS, U.S.A.

Abstract. We review a series of related publications that combine higher-level phylogenies of weevils (Coleoptera: Curculionoidea) with host plant information to explain the success of this megadiverse lineage in the context of a co-evolutionary escape-and-radiation hypothesis. We argue that the authors' approach is marred by the cumulative effect of: (1) inadequate taxon sampling, particularly within the most diverse family Curculionidae; (2) insufficient reconciliation of systematic evidence, including the reassessment of morphological characters and necessary classificatory emendations; (3) exceedingly wide concepts of ecological similarity, leading to uninformative tests of adaptation; (4) insufficient resolution of the temporal sequence of associated weevil and angiosperm radiations; and (5) inadequate consideration of alternatives to the escape-and-radiation hypothesis. As a result, there are very few new and reliable inferences about the evolutionary success of weevils that depend precisely on the phylogenetic data presented in these studies. Improved taxon sampling alone is not the solution, because the existing mid-level classification of weevils is too deficient to permit inferences about natural lineages and their ancestral traits. We therefore recommend abandoning such an approach in favour of more narrowly focused reconstructions of the evolutionary history of generic and tribal groupings.

'Most damagingly, I find it has become profitable to ignore or hide results that do not fit with the story being sold – a mix of evidence tends to make a paper look messy and lower its appeal' (Lawrence, 2007: R584).

'Some biologists will reply to our arguments by saying that it is better to proceed with admittedly weak techniques than to do nothing. We argue that it is better to do nothing than to misinform' (Wenzel & Carpenter, 1994: 97).

Introduction

The evolutionary success of the Coleoptera has engaged the minds of preeminent natural historians for centuries. Nonetheless, a coherent and compelling explanatory account of the diversification of beetles remains elusive, not least because

of the magnitude of outstanding taxonomic and phylogenetic research challenges. Looking beyond the systematic hurdles, reliable inferences from present-day phenomena (i.e. beetle diversity) to their historical causes are challenging epistemologically; they require a fine-tuned body of clearly stated, predictive theories about the historical unfolding of particular lineages, as well as suitable data to permit discrimination among each of these. Such inferential scrutiny may well lead to the insight that different beetle lineages have diversified due to varying factors at different times and in different places.

To avoid the charge of presenting 'just so stories', studies of beetle diversification should adhere to the highest scientific standards, both in terms of data quality and methods. It is in this sense that we review critically a series of related publications on the higher-level phylogeny and evolutionary success of weevils in the superfamily Curculionoidea, authored by Farrell (1998), Marvaldi *et al.* (2002) and McKenna *et al.* (2009). We explore shortcomings in these studies – hereafter collectively called FMM – arguing that science is served through a discourse about the merits of the underlying observations and inference methods. Our comments are pertinent more generally

Correspondence: Nico M. Franz, Department of Biology, University of Puerto Rico, Call Box 9000, Mayagüez, PR 00681-9000, U.S.A. E-mail: nico.franz@upr.edu

to large-scale phylogenetic studies of insects that address the theme of evolutionary success, in particular Hunt *et al*. (2007), and hopefully will contribute to more rigorous analyses [see also Mayhew (2007)].

Conceptual origins of the weevil phylogeny/evolutionary success studies

The central contention of FMM is that the high diversity of weevils, and specifically of members of the family Curculionidae, has been facilitated by multiple independent shifts of ancestral weevil lineages from gymnosperm to angiosperm host plants and subsequent specialization on angiosperm organs and tissues, mediated through a series of morphological, physiological and ecological adaptations. Conceptually, this account is rooted in Simpson's (1953) notion of accelerated radiation after entering an 'adaptive zone' via 'key innovations' (Mitter *et al*., 1988). Ehrlich & Raven's (1964) influential paper adopted these concepts, and argued specifically that the diversification of plants and papilionoid lepidopterans has been driven by a stepwise series of chemical adaptations that conferred temporary reductions in the levels of herbivory and herbivore competition, respectively, thus allowing the newly adapted lineages to undergo rapid radiation. Properly interpreted, their cause-and-effect hypothesis predicts certain patterns of plant toxicity and herbivore specialization that can be assessed in present time (Cornell & Hawkins, 2003). Moreover, when translated into a phylogenetic framework, the escape-and-radiation hypothesis predicts a topological correspondence among associated plant and herbivore lineages (Farrell *et al*., 1992). However, as formulated it cannot differentiate between, or selectively prohibit, a range of 'co-evolutionary' phenomena (cf. Thompson, 1989), including: (i) specific co-adaptation among pairs or communities of interacting species, (ii) co-speciation ('parallel cladogenesis', with or without simultaneous reciprocal or unilateral adaptation), (iii) sequential evolution (herbivore lineages adapting to plant metabolites that had evolved in response to previous unrelated pressures), and (iv) resource tracking of chemically convergent plants with little or no phylogenetic constraints.

The inherent ambiguity of Ehrlich & Raven's (1964) hypothesis was not lost on those who attempted to apply it in the context of historical co-evolutionary analyses of weevils. Lacking extensive species-level phylogenies for curculionoid lineages and their hosts that would suggest either reciprocal adaptation and/or parallel cladogenesis (Anderson, 1993), some authors have opted to test for the repeated existence of a correlation of particular ecological traits (e.g. an association with angiosperms) and higher species numbers in independent sister clade comparisons (Harvey & Pagel, 1991). Subsequent analyses have incorporated fossil data to determine the divergence time intervals (Arbogast *et al*., 2002) of weevil 'stem' lineages, and thus distinguish between simultaneous and sequential diversification on the respective host plant lineages. It is in this context that FMM's studies were carried out.

Acknowledging the scientific merits of higher-level analyses of weevils

Prior to launching our critique, we wish to fully acknowledge that FMM's studies represent the best information on higher-level weevil phylogenetics published to date. Indeed, each of the three analyses was a landmark in curculionoid phylogenetics at the respective time of publication. In particular, Marvaldi *et al*. (2002) remains the most comprehensive analysis combining morphological and molecular information to resolve weevil phylogeny. McKenna *et al*.'s (2009) study, although employing fewer focal taxa (135 species) than Hundsdoerfer *et al*. (2009; 157 species) and Hunt *et al*. (2007; 222 species), is arguably superior to either study in taxon coverage at a global and phylogenetic scale. McKenna *et al*. (2009) also sampled nearly twice as many gene sequences (more than 500 sequences; six loci) as any other analysis. FMM are therefore highly valuable contributions towards reconstructing weevil phylogeny.

We furthermore recognize that singling out FMM for discussion may seem unfair given that their inferential approach is widespread. We nevertheless submit that their studies do form a coherent set of incremental analyses aimed at explaining the evolutionary success of weevils. These studies jointly share authors, primary morphological and molecular information, inference methods and evolutionary conclusions. In this they differ from (e.g.) Hundsdoerfer *et al*. (2009), who focused more narrowly on assessing the aptitude of molecular loci for resolving weevil phylogeny and refrain from any inferences about probable causes for evolutionary success. On the other hand, Hunt *et al*.'s (2007) study is similar methodologically to FMM and thus susceptible to many of the criticisms discussed below.

Overview of criticism: inadequate phylogenetic information and unconnected evolutionary inferences

Our critique of FMM's analyses is not aimed primarily at their central contention concerning the factors promoting diversification of weevils (see above). That contention has inherited a certain attractiveness from Ehrlich & Raven (1964), and remains partially relevant, albeit too vague. Instead, we take issue with the quality of the phylogenetic and natural history information provided in these analyses, and above all with the lack of an epistemological correspondence between the data presented and the evolutionary inferences derived therefrom. Producing the most or best phylogenetic data does not necessarily translate into making reliable inferences about weevil evolution, particularly if the available data – DNA sequences, fossil species, etc. – are inadequate, or unsuited, to test for specific evolutionary hypotheses [see also Reid (2000)]. We argue that such poor data-to-hypothesis fit largely renders FMM's analyses devoid of new, sufficiently precise and reliable insights about the causal evolutionary mechanisms that have promoted the great radiation of weevils. The following point-by-point discussion suggests that the profundity of these

problems should deter from further pursuit of similar higher-level phylogeny/evolutionary success analyses of weevils or other megadiverse and understudied lineages, such as beetles as a whole (Hunt *et al.*, 2007).

Specific points of criticism

Inadequate taxon sampling of curculionid lineages

FMM's studies suffer from extremely low taxon sampling, particularly within the Curculionidae, which include 51 000 species described to date, or ∼82% of the documented weevil diversity at the species level (Oberprieler *et al.*, 2007). Farrell (1998) sampled 35 species of Curculionidae, Marvaldi *et al.* (2002) sequenced 82 species and McKenna *et al.* (2009) analysed 97 species of this diverse family. The sampling strategy of the three studies was mostly incremental, although no more than 50 curculionid species sequenced in Marvaldi *et al.* (2002) were also included in the subsequent publication.

McKenna *et al.* (2009: 7083) stated that theirs was a large-scale analysis that represented 'all families and subfamilies' of weevils, which is true in the context of their preferred reference classification (Oberprieler *et al.*, 2007). However, that classification is rather inclusive in its subfamily concepts, recognizing only ten curculionid subfamilies. Of these, the Baridinae (8000 species; 35 tribes), Curculioninae (8400 species; ∼35 tribes), Entiminae (12 000 species; 55 tribes) and Molytinae (10 000 species; ∼48 tribes) are the four most diverse subfamilies. The corresponding numbers of tribes were taken from the more traditional mid-level classification of Alonso-Zarazaga & Lyal (1999). Viewed at this intermediate taxonomic level, McKenna *et al.* (2009) sampled only four tribes (11.4%) of Baridinae, 14 tribes (40.0%) of Curculioninae, nine tribes (16.3%) of Entiminae and ten tribes (20.8%) of Molytinae. As many as 31 of these 37 tribes were represented by a single species.

We contend that such a sampling protocol, i.e. one to two species for approximately 22% of ∼170 tribes that jointly contain more than 38 000 species, is not suited to support reliable conclusions about the sequence of evolutionary life strategies within the Curculionidae. Although measuring taxon coverage at the tribal is somewhat arbitrary, it is at least repeatable, and is further validated because significantly different life history traits of weevils tend to occur at this and at lower taxonomic levels (e.g. Anderson, 2002). Precise inferences of evolutionary change across such a vast and ecologically variable lineage as the weevils cannot be inferred if four-fifths of the current tribal concepts are unrepresented even by a single species.

Insufficient reconciliation of molecular, morphological and classificatory information

One might expect that the sequencing of weevil species will increase rapidly in the coming years, thereby gradually resolving the sampling issue. Nonetheless, the emerging molecular insights must be integrated rigorously with morphological information and translated into natural classifications. It is no secret that the existing subfamiliar, tribal and generic concepts for weevils remain largely those of the 19th century (Kuschel, 1995; Oberprieler *et al.*, 2007). Many of them are highly polyphyletic. Any molecular study using these concepts starts out with an intractable mix of mid-level names that represent non-monophyletic groups and therefore negatively affect both the sampling design and the ability to associate existing taxonomic names with the resulting clades and optimized life history traits. Thus, the Curculioninae and Molytinae are polyphyletic in all of FMM's analyses, precluding any reliable inferences about the evolutionary history of these 'taxa'.

Whenever molecular information suggests the nonmonophyly or nontraditional placement of previously circumscribed groups, the proper course of reaction is to reinvestigate the morphological evidence, resolve apparent conflicts and propose concrete classificatory changes where necessary (Franz, 2005). However, such procedures are rarely applied in FMM's analyses, as detailed below.

Neither the combined matrix nor the 18S ribosomal DNA sequence alignment of Farrell (1998) was published, although the sequence lengths submitted to GenBank vary from 1688 to 1914 nucleotides. An attempt to align 50 weevil sequences (including outgroups) yielded 213 parsimony-informative characters (N. Franz, personal observation); compared with 106 morphological characters in Kuschel's (1995) matrix, which was adopted for the combined analysis. The 18S rDNA partition of that analysis showed little resolution between weevil families under parsimony (1740 most-parsimonious trees; 30 nodes collapsed in the strict consensus; N. Franz, personal observation). The reference topology in Farrell (1998: figure 1A) is therefore largely driven by Kuschel's (1995) morphological data. Similar conclusions were reached by Reid (2000), who presented additional criticism regarding the chrysomeloid component of Farrell's (1998) analysis.

The strength of the morphological signal is also apparent in Marvaldi *et al.* (2002), where under parsimony the 18S rDNA partition (Marvaldi *et al.*, 2002: figure 2) produces a phylogenetic sequence of Belidae → Nemonychidae (in part) → Anthribidae → Nemonychidae (in part) → Attelabidae → Brentidae (in part) → Caridae → Curculionidae → Brentidae (in part). On the other hand, the morphological analysis (Marvaldi *et al.*, 2002: figure 3) recovered all families as monophyletic, arranged in the same overall sequence as in Kuschel (1995) and also in Marvaldi *et al.*'s (2002) reference tree (figure 5), namely: Nemonychidae → Anthribidae → Belidae → Attelabidae → Caridae → Brentidae → Curculionidae. Evidently, morphology outweighed the molecular data to determine the family-level arrangement. Nevertheless, the morphological matrix (100 taxa, 115 characters) was not published in the actual paper and is no longer accessible via the journal website, although it was subsequently submitted to TreeBASE (http://www.treebase.org/) in IUPAC mode and without character state specifications. The morphological character states and optimizations for Marvaldi *et al.*'s (2002) reference tree were published in appendices 1 and 2, representing the most comprehensive effort yet to code the morphological evolution of

weevils, and containing many potentially relevant phylogenetic insights. Remarkably, this is accompanied by no discussion of any of these traits, or promotion of newly discovered synapomorphies, or necessary classificatory amendments.

McKenna *et al.*'s (2009) study was based on molecular data only, with two to six loci sequenced per species. We are unaware of an available sequence alignment. The Bayesian tree (figure 2) is fully resolved, yet displays numerous nontraditional placements. For instance, McKenna *et al.* (2009) showed the Dryophthorinae (in part) and Platypodinae (ambrosia beetles) as sister lineages, a nontraditional placement that accords with at least four larval and pupal synapomorphies proposed in Marvaldi (1997; see also Thompson, 1992), but conflicts (i) with many adult characters (Kuschel *et al.*, 2000; although this latter study had its own sampling biases favouring a platypodine–scolytine relationship), as well as (ii) with published molecular evidence (e.g. Jordal *et al.*, 2008). Our point is not that one placement is correct or incorrect; rather, that such apparent conflicts are not reconciled with existing phylogenetic information. Instead, McKenna *et al.* (2009: 7084) remain largely uncommitted to their own results. Referring to the Platypodinae as 'enigmatic', they discuss the probability of alternative phylogenetic placements under Bayesian and maximum likelihood inference, but do not re-examine the implications for platypodine morphology, character evolution and classification.

The pattern of presenting unconventional and unreconciled placements is common in FMM's analyses [see e.g. Cossoninae, Ithycerinae, Microcerinae, *Gonipterus* Schoenherr, *Gymnetron* Schoenherr, *Haplonyx* Schoenherr, *Hypera* Germar and *Oxyops* Schoenherr (all Curculioninae) in McKenna *et al.* (2009); *Myrmex* Sturm (Curculioninae) in Farrell (1998); or Derelominae in Marvaldi *et al.* (2002)]. In particular, the 'higher Curculionidae' of McKenna *et al.* (2009) are a morphologically intractable mix of tribes and subfamilies [e.g. *Baris* Germar (Baridinae) as sister to *Smicronyx* Schoenherr (Curculioninae); *Cionus* Clairville (Curculioninae) as sister to *Cossonus* Clairville (Cossoninae); *Heilipodus* Kuschel (Molytinae) as sister to *Meriphus* Erichson (Curculioninae), etc.]. If nothing else, the authors have shown that the preferred subfamily-level classification (Oberprieler *et al.*, 2007) is of very limited use for communicating the results of their multi-gene analysis of the 'higher Curculionidae'. More importantly, their treatment of these issues implies that there is a lower standard for making reliable evolutionary inferences than for resolving phylogenetic uncertainties; apparently one can achieve the former without the latter.

Inadequate assessments and tests of ecological similarity

To derive evolutionary conclusions from their analyses, FMM first mapped ecological similarities on to a reference phylogeny and subsequently performed statistical tests for the presence of multiple 'independent contrasts' among sister lineages with different life histories and species numbers (Mitter *et al.*, 1988; Harvey & Pagel, 1991). In doing so, they defined

the contrasting life histories so broadly as to sacrifice the ability to represent evolutionary comparable conditions across lineages. According to Proctor (1996: 144), the probable reasons for this practice are: 'first, because the phenomenon of interest may occur in a wide range of taxa and thus is unlikely to be similar in the narrow, phylogenetically homologous sense; second, because statistical power increases with the sample size (number of independent evolutions). The [researchers] define their characters of interest very broadly in order to maximize the probability of homoplasy'. In other words, such tests of presumably recurrent adaptation and diversification are susceptible to yielding false positives.

FMM's analyses include many oversimplifications and some misrepresentations of the natural history of particular weevil lineages. For instance, one of the two weevil-related comparisons in Farrell (1998) concerns the 'primitively gymnosperm-associated' Oxycoryninae-Allocoryninae (30 species) versus the 'primitively angiosperm-associated' Belinae (150 species). This five-fold increase in species diversity seems noteworthy at first. However, the ecological characterization of the former lineage is superficial if checked against Marvaldi *et al.*'s (2006) detailed homology-based reconstruction of host plant shifts and feeding habits in the Oxycoryninae. Accordingly, the Metrioxenina are palm-associated, whereas weevils in the sister lineage Afrocorynina possibly reproduce in stems or flower buds of conifers or angiosperms. Members of the Aglycyderina are associated with at least 20 phylogenetically diverse families of angiosperms, and contain species that feed on dead branches and mine leaves. The Oxycraspedina include associates of conifer sporophylls, whereas species in the Allocorynina are highly host-specific pollinators of cycads. Furthermore, Oxycorynina occur on the inflorescences of root-parasitic angiosperms in the Balanophoraceae and Hydnoraceae. In Marvaldi *et al.*'s (2006: 465) own assessment: '[t]he most evident pattern is that of several shifts to distantly related host-plant taxa having occurred from the indicated ancestral association of the Belidae with conifers'. This homology-based reconstruction of oxycorynine natural history differs dramatically from that of Farrell (1998), to the point that a simple 'gymnosperm/angiosperm' contrast and its statistical implementation are inadequate. The aforementioned contrast is also invalid for the Belinae, whose oldest lineages (Pachyurini) all are associated with conifers (Zimmerman, 1994).

In another example, Marvaldi *et al.* (2002: 768) characterize the life history of the curculionine genus *Perelleschus* Wibmer & O'Brien as follows (character state numbers as used in source): major taxon used – monocots (4); larval habit – endophagous (0); tissue consumed by larvae – seed (4); state of host plant tissue – living (0). This superficially valid characterization oversimplifies the nature and homology of plant-related adaptations in this lineage. As reviewed in Franz & Valente (2005), *Perelleschus* weevils are associated exclusively with inflorescences of *Carludovica* Ruíz & Pavón (Cyclanthaceae). The adults function as secondary pollinators of their hosts, and the larvae develop mainly in the pulp of maturing fruits, but occasionally may perforate the seeds. In contrast, the larvae of the putative sister group, *Systenotelus*

Anderson & Gómez, are obligatory seed predators. The larvae of *Ganglionus* Franz & O'Brien, the next closest relative to the *Perelleschus–Systenotelus* clade, breed in the male flowers and mature in decaying plant matter. Other members of the subtribe Phyllotrogina occur on a variety of dicot families. Had one of these alternative yet closely related taxa been selected, Marvaldi *et al.*'s (2002) 4040 coding for *Perelleschus* would have changed, presumably either to 4351 for *Ganglionus* or 3331 for some species of *Phyllotrox* Schoenherr. In the end, no available states in Marvaldi *et al.* (2002) properly reflect any of the 30 narrowly homologous life history traits that Franz & Valente (2005: 16) identified at the genus level within the tribe. Moreover, the cyclanth-pollinating *Perelleschus* received the same coding as the stored grain pest *Sitophilus granarius* (Linnaeus) (Dryophthorinae). In short, the standards for ecological similarity lack adequate vocabulary to test rigorously for the presence of life history adaptations or convergent evolution. An additional comparison of Marvaldi *et al.*'s (2002) analysis and Anderson's (1993) review confirms that this pattern extends to other curculionid groups.

McKenna *et al.* (2009) make wide ranging inferences about the traits causing success in curculionids. A key passage (p. 7087) reads: 'increased specialization is apparent in terms of larval host organ/tissue associations in increasingly more derived weevil groups, loosely following the general sequence (in order of increasing specialization): roots and stems (most Brachycerinae, Cyclominae, Dryophthorinae, Entiminae, Ithycerinae, Microcerinae) → wood (most Cossoninae, Molytinae, Scolytinae) → fruits and seeds (most Baridinae, Curculioninae)'. As conceded later in the same paragraph, one cannot accurately map these similarities on to their phylogeny to perform statistical tests. Therefore, the authors' conclusions are largely unconnected to the very particular topology they represent, and their ecological characterizations of curculionid subfamilies are unsuited for tracing the historical diversification of these taxa.

Here we briefly revisit the general shortcomings of the method of independent contrasts. As reviewed by Wenzel & Carpenter (1994) and Proctor (1996), advocates of this approach tend to de-emphasize the inferential disconnect between a correlation and a causal relationship, and frequently dilute homology statements to increase the test sample size. However, relaxing the focus on homology also means relaxing the focus on precisely defined evolutionary similarity and change. The method is thus susceptible to yielding multiple alternative, somewhat arbitrary (or even 'cherry-picked') ecological characterizations of higher-level clades, with little semantic or phylogenetic precision.

This kind of arbitrariness is evident when comparing Farrell (1998) with Hunt *et al.* (2007) who re-examined the herbivory/success explanation. They expanded the sample significantly to represent better all Coleoptera and added a limited set of choice ecological categories to the modified test data. Although their results seem to refute Farrell's (1998) main hypothesis, their analysis similarly fails to advance from selectively mapped similarities to a reconstruction of homologous life history traits.

Although we cannot expect to reconstruct every historical condition in exactly the right way, it is critical to get as close as possible to this goal in order to make a strong argument for the causes of evolutionary success. Neither FMM nor Hunt *et al.* (2007) met this standard. No ancestral or extant coleopteran species ever was, or currently is, 'herbivorous' or 'mostly fungivorous', in the sense that it fed or feeds on all plants or mostly on all fungi. No individual or species, and certainly no clade, has ever perceived its environment in a way that is causally congruent with such imprecise terms. In a truly phylogenetic sense, no weevil reproduces on 'angiosperms', 'cycads' or 'seeds'. A more narrow and precise semantic characterization of ancestral and extant life habits of particular lineages is not only possible, but necessary to address the causal realm of evolutionary transformation. Until we reach that level of inferential precision, accounts of evolutionary success will remain stuck in a semi-arbitrary, semi-referential stage.

Insufficient temporal resolution based on fossil data

FMM's analyses depend on a plausible reconstruction of the temporal occurrence of ancestral weevil taxa and their feeding habits. Although this strategy is adequate in principle, it involves many pitfalls in practice. Our present knowledge of the weevil fossil record is fragmentary and several published placements of important fossil taxa are doubtful or incorrect (Kuschel, 1992; Oberprieler *et al.*, 2007; R. Oberprieler & G. Kuschel, personal communication). For instance, the Triassic Obrieniidae, initially placed in the Curculionoidea (Zherikhin & Gratshev, 1993), is now considered to be a member of the Archostemata (Reid, 2000; Kuschel, 2003). This transfer has led to an adjustment of the minimum age of weevils from ∼230 million years in Farrell (1998) to ∼180 million years in McKenna *et al.* (2009). Clearly, more properly diagnosed fossils are needed to reconstruct the diversification of ancestral weevil lineages and life history traits. The situation is perhaps most wanting for the megadiverse curculionids, whose oldest documented fossils appear in the Lower Cretaceous (Aptian). An unpublished reanalysis of 148 'weevil' species from the Mesozoic represents a major step ahead (R. Oberprieler & G. Kuschel, personal communication), but included only eight fossil species placed to the family Curculionidae, none of which was assignable unambiguously to subfamilies or tribes. According to Gratshev & Zherikhin (2003), much of the available material from the Tertiary also needs reassessment. To date, no higher-level morphology-based phylogenetic analysis combining fossil and living weevils has been undertaken.

McKenna *et al.*'s (2009) analysis was particularly affected by the aforementioned lacunae in the weevil fossil record, given that their primary goal (p. 7083) was ' [t]o gain insight into the degree and nature of contemporaneity in weevil and angiosperm diversification'. Even acknowledging these limitations as unavoidable, the sampling strategy remained too incomplete to attain the stated goal. In all, the authors utilized only eight taxa to determine the probable divergence

times of major lineages within the Curculionoidea. Only four of these fall within the Curculionidae; including one platypodine, one scolytine, one dryophthorine, and one ambiguously identified species whose overall form and sculpture 'suggests a true weevil (family Curculionidae) of possibly a molytine or cryptorhynchine type' (Kuschel *et al.*, 1994: 143). Presumably based on this vague diagnosis, McKenna *et al.* (2009) placed the unnamed taxon at the root of the Curculionidae (figure 2, 'E'). This means that there is not a single precisely defined fossil to anchor the lineage divergence times in the 'higher Curculionidae' in the authors' sense, even though the latter represent at least 38 000 extant species. Considering the scope of the problem being investigated and the time scale involved, the sampling of fossils is disappointing. Although the weevil fossil record is scattered and imprecise, significantly more definitive and assignable records exist than were employed by FMM's studies (Kuschel, 1992; Gratshev & Zherikhin, 2003; Poinar, 2009; reviewed in R. Oberprieler & G. Kuschel, personal communication).

The authors provided no homology-based evidence for the assignment of the few fossils to particular ancestral nodes of their reference phylogeny (see Reid, 1995; Grimaldi & Engel, 2005; Beutel *et al.*, 2008; Ware *et al.*, 2010). Whether the chosen taxa are members of a 'stem' or 'crown' group within their constituent lineage remains unclear, which may result in considerable over- or underestimation of clade ages (Rutschmann *et al.*, 2007; Engel *et al.*, 2009; Ksepka, 2009). As it stands, the 95% confidence intervals for the estimated minimum ages for 12 selected ancestral nodes range from 7.8 million years (Caridae) to 65.5 million years (Anthribidae, excluding Urodontinae), with an average of 45.4 ± 17.4 million years. This is the level of temporal (im)precision at which the issue of contemporaneity among angiosperm and weevil radiations is assessed.

For proper calibration of divergence times one must rely on a series of fossil taxa for any particular lineage, rather than isolated records. For instance, using a single putative scolytine fossil from the London Clay (55 million years) to date this lineage, which includes crown group taxa that extend into the Mid Cretaceous and stem groups from the Early Cretaceous (Jarzembowski, 1990; Cognato & Grimaldi, 2009; Kirejtshuk *et al.*, 2009), would be analogous to using a single fossil horse to calibrate a phylogeny of vertebrates or to estimate the timing of the tetrapod origin. Inferences of evolutionary scenarios based on fossil taxa lose power quickly when such extinct species are not representative of crown groups, unless representatives of successively earlier lineages share precise life histories with the crown lineage under investigation. Extinct species may have their own unique and apomorphic attributes, and these naturally may include elements of their ecology and life history. Thus, the earliest representatives of an angiosperm-associated lineage may have specialized on extinct gymnosperms, or exhibited some unknown ecological traits specific to their palaeoenvironment and not represented among living relatives. Timing the origin of a transition to angiosperms on such extinct taxa would only serve to artificially 'age' this evolutionary event, and may obscure more significant evolutionary novelties.

Apart from the issue of reliable clade divergence estimation, the 'super-imposed stem group' representation of McKenna *et al.* (2009: figure 3), therein interpreted as evidence for 'codiversification' among weevils and angiosperms as well as sequential evolution/resource tracking, requires numerous additional inference leaps. For one, the appearance of a temporal lag in the radiation of various curculionid lineages hinges upon the authors' decision to depict the minimum estimated ages for each lineage. Had they instead opted to extend the grey rectangles that represent the clades' existence to the estimated median or maximum ages, then the resulting figure would show that most curculionid radiations predated those of the angiosperms. Moreover, accepting the authors' interpretation requires equation of: (i) an increase in relative species richness of angiosperms in Cretaceous northern hemisphere macrofossil and palynomorph assemblages (Lidgard & Crane, 1990) with (ii) an increased diversification of 'major' angiosperm lineages that facilitated weevil diversification. Such a correlation is probably neither linear nor clade independent (Magallón & Castillo, 2009); and in any case, the black line in figure 3 is not suited to demonstrate a truly phylogenetic diversification of angiosperms.

Moreover, if the goal is to establish a sustained causal relationship among increased rates in angiosperm/herbivore cladogenesis (sensu Ehrlich & Raven, 1964), then it is not sufficient to focus solely on the timing of the first appearance of select associated lineages. The radiation of curculionids was probably a 100+ million year process (R. Oberprieler & G. Kuschel, personal communication), and thus it is essential to reconstruct a sequence of key events from the time of origin of an association to its present complexity and species richness. McKenna *et al.*'s (2009) 'super-imposed stem groups' graphic lacks such evidence about specific historical associations or reciprocal/unilateral specializations in angiosperms and weevils. In the authors' own assessment of the graphic's message (p. 7086): '[p]atterns of weevil diversification during the time interval between the origin of each major weevil clade and the present remain unclear'.

Inferential overreach and failure to properly discriminate alternative hypotheses

FMM's approach to interpreting their results is at times highly conjectural, to the point where presumptions about the validity of the escape-and-radiation hypothesis (Ehrlich & Raven, 1964) overshadows the lack of strong supporting evidence and consideration for additional or alternative explanations. This is perhaps best illustrated by revisiting a few passages from the respective discussions.

Farrell wrote (1998: 558): '[i]n contrast with the strobilus feeding of conifer- and cycad-associated ancestors, diversification of the subfamilies that attack flowering plants has been accompanied by larval folivory, leaf mining, and seed and root feeding, which exemplify the concept of adaptive radiation'. Although plausible, it does not derive from the phylogeny and mapping of gymnosperm/angiosperm associations of Farrell

(1998); any more than it would from a traditional group-by-group review of Curculionoidea systematics and natural history (e.g. Kuschel, 1995; Oberprieler *et al.*, 2007). If adaptation is to be an onerous concept (Williams, 1966), then the above statement would have to be subtended (*inter alia*) by a more precise reconstruction of evolutionary transformations of larval feeding habitats in particular weevil lineages.

Similar speculative extrapolations were made by McKenna *et al.* (2009: 7087): '[f]ine-tuning and elaboration of the weevil trophic repertoire, for example conveying the ability to metabolize additional- or new-plant secondary metabolites, or to oviposit deep into plant material, not only facilitated colonization and exploitation of diverse living tissues of nearly all other kinds of landplants, but also equipped Curculionidae to adapt to and track [. . .] the increasing complexity and diversity in chemistry, structure, growth form and habits, habitat associations, and life histories of angiosperms over the course of their evolution'. Furthermore (p. 7087): 'Monocots have less strongly differentiated tissues with fewer numbers and kinds of secondary metabolites and other defences than most eudicots [. . .], and are predominantly herbaceous, lacking the true woody tissues of eudicots. As a result, they offered rapid growth life histories, Grime's 'ruderal growth strategy' [. . .], and had accommodationist rather than well-defended life-history patterns for deflecting insect herbivores. Thus, monocots may have also offered competition-free and plant-defense-free space relative to other early divergent groups of angiosperms'. Here, and elsewhere, it is unclear how the authors establish a precise inferential link between their phylogenetic data on one side and 'radiation-promoting' adaptations to chemical, physiological and structural transformations in host plant lineages on the other side (cf. Barkman, 2001; Butler *et al.*, 2009).

FMM point out on various occasions that their results were consistent with certain elements of Ehrlich & Raven's (1964) hypothesis, but did not rank its plausibility systematically against additional or alternative hypotheses, as would be required for a reliable inference to the best explanation (Lipton, 2004). The situation is alleviated neither by the inherent vagueness of the escape-and-radiation hypothesis (Thompson, 1989); nor by adopting terms such as 'codiversification' (e.g. McKenna *et al.*, 2009) and thereby blurring the definitional line between (i) co-adaptation and (ii) co-speciation. Each phenomenon can occur, and may be tested for, independently (Franz, 2004).

Aside from these ambiguities, FMM did not discuss thoroughly the relative explanatory contribution of habitat structure (Anderson, 1993), biogeography (Machado, 2007), sexual selection (Franz, 2003), parasitism (Lill *et al.*, 2002) and other more or less tractable phenomena, such as high lineage survival (Hunt *et al.*, 2007). For instance, the Entiminae, with more than 12 000 species described to date, seem to present a particularly poor match with the notion that reciprocal chemical and physiological adaptations have been the primary drivers of weevil diversification. Most entimines tend to feed on a broad range of phylogenetically distant hosts (Oberprieler *et al.*, 2007).

Proper evaluation of competing lineage-specific explanations for the evolutionary success of weevils is critical to understanding the inferential reach of the escape-and-radiation hypothesis. There are many plausible competitors; Mayhew's (2007) insightful review ranked as many as 18 commonly invoked mechanisms for increased insect species richness. The timing of weevil diversification is *prima facie* not that different from other nonherbivorous beetle lineages (Zherikhin, 2002; Grimaldi & Engel, 2005; Hunt *et al.*, 2007). One would expect that many of the mechanisms that led to the success of (for example) the Staphylinidae were also selectively operative in weevils (Anderson & Ashe, 2000).

Conclusions and outlook

With probably more than 200 000 extant species (Oberprieler *et al.*, 2007), weevils undoubtedly constitute a megadiverse lineage whose evolutionary success merits explanation. The vast majority of weevil species are associated with particular lineages of angiosperms. There is consensus that weevils and plants somehow have influenced their respective evolutionary trajectories, resulting in increased speciation rates in diversifying weevil lineages and possibly also in the hosts. The challenge for phylogenetic analyses, then, is to reconstruct these trajectories so as to corroborate the sequential occurrence of specific associations and character state transformations, and examine plausible alternative hypotheses for a radiation's success critically. Evidential support for Ehrlich & Raven's (1964) hypothesis in particular would require evidence for transformations in secondary plant metabolites and causally related physiological adaptations in the associated herbivores (e.g. Berenbaum, 1983; Becerra, 1997; Schneider *et al.*, 2002).

FMM's analyses lack the inferential quality standard necessary to explain the remarkable diversification of weevils. Their approach is marred by the cumulative effect of inadequate taxon sampling, insufficient reconciliation of systematic evidence, exceedingly wide concepts of ecological similarity, insufficient resolution of the temporal sequence of associated weevil and angiosperm radiations and inadequate consideration of alternatives to the escape-and-radiation hypothesis. As a result, there are very few new and reliable inferences concerning the evolutionary success of weevils that depend precisely on the phylogenetic data presented in these studies. Reassessment of relevant prior work, e.g. Anderson (1993) and Kuschel (1995), would yield almost the same inferential precision. Moreover, the purported consistency with Ehrlich & Raven's (1964) complex and ambiguous hypothesis has only limited explanatory power. Ultimately, FMM's phylogenetic studies have uncovered no concrete examples of causally sustained co-adaptation, co-speciation or sequential, chemically mediated radiation in weevils and their host plants.

In discussing their results, FMM mentioned that an improved taxon sampling will provide added phylogenetic resolution and thus also lead to improved tests and explanations. To the contrary, we submit that the aforementioned shortcomings will persist even if the sampling is increased to include 500 or 1000 extant weevil species and a better representation of fossil taxa. This is so because the existing mid-level classification

of weevils, and particularly of the Curculionidae, is simply too deficient to permit reliable inferences about natural groups and their ancestral traits (Kuschel, 1995; Oberprieler *et al.*, 2007; R. Oberprieler & G. Kuschel, personal communication). In other words, many of the 'labels' with which we address traditional curculionid genera, tribes, subfamilies and other intermediate taxonomic levels will require comprehensive phylogenetic testing and reclassification before they can support the evolutionary inferences that FMM intend to make. Thus, a phylogenetic revision of the curculionine tribe Acalyptini, which includes some 40 genera, resulted in a total of 17 generic transfers to and from seven affected tribes, some of which are classified outside the subfamily Curculioninae (Franz, 2006). Carrying out these taxonomic adjustments was essential to characterizing the tribe in terms of its morphological and life history synapomorphies. In the absence of such groundwork, it would make little sense to employ the traditional tribal concept to explain acalyptine weevil evolution.

Our recommendation concerning FMM's analyses is to abandon the higher-level approach and to focus more narrowly on reconstructions of the evolutionary history of assuredly monophyletic generic and tribal groupings. That approach can potentially mitigate all criticisms levelled against their studies, especially if it is accompanied by more precise characterizations of homologous and convergent morphological and ecological adaptations. Studies that concentrate on a taxonomically manageable lineage tend to yield rather conclusive results (e.g. Anderson, 1988; Franz & Valente, 2005; Marvaldi *et al.*, 2006; Velázquez de Castro *et al.*, 2007; Sequeira *et al.*, 2008), and jointly contribute more to our understanding of weevil evolution than a singular higher-level approach.

The messages that emerge from lower- and mid-level analyses are more precise and at the same time more heterogeneous than the main theme promoted in FMM's studies. There is a growing pool of evidence suggesting that secondary plant metabolites form but one of many factors in response to which particular weevil lineages have radiated. It remains unclear whether higher-level analyses of weevil families and subfamilies are suited to differentiate adequately between these factors. Studies that attempt to explain the evolution of the taxonomically intractable 'Curculioninae' or 'Molytinae' in the context of a central theme are unlikely to explain very much. Higher-level analyses of weevils are well advised to remain constrained within a strictly phylogenetic context (Marvaldi *et al.*, 2008; Hundsdoerfer *et al.*, 2009).

In conclusion, the diversity of weevils is not only fascinating, but may be epistemologically overwhelming. We hope that our discussion will help foster more studies that balance with rigor our preference for unifying explanations with the true complexity of the mechanisms that have shaped the evolution of particular weevil lineages.

Acknowledgements

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