Supplementary Information

Phylogenomic data yield new and robust insights into the phylogeny and evolution of weevils

Seunggwan Shin,[*,1,†] Dave J. Clarke,[*,1,†] Alan R. Lemmon,[2] Emily Moriarty Lemmon,[3] Alexander L. Aitken,[1] Stephanie Haddad,[1] Brian D. Farrell,[4] Adriana E. Marvaldi,[5] Rolf G. Oberprieler,[6] and Duane D. McKenna[1]

[1]Department of Biological Sciences, University of Memphis, 3700 Walker Avenue, Memphis, TN 38152

[2]Department of Scientific Computing, Florida State University, 400 Dirac Science Library, Tallahassee, FL 32306

[3]Department of Biological Science, Florida State University, 319 Stadium Drive, Tallahassee, FL 32306

[4]Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138

[5]CONICET, División Entomología, Universidad Nacional de La Plata, Paseo del Bosque s/n, 1900 La Plata, Buenos Aires, Argentina

[6]CSIRO, Australian National Insect Collection, GPO Box 1700, Canberra, ACT 2601

[†]**These authors contributed equally to this work**

Material and methods

Taxon sampling

We included all three subfamilies of the former Nemonychidae (Cimberidinae [*Cimberis*], Rhinorhynchinae [*Rhynchitomacerinus*, *Bunyaeus*] and Nemonychinae [*Nemonyx*]). However, *Nemonyx* failed at the enrichment stage and was excluded. We also sampled all three current subfamilies of Anthribidae (Anthribinae [*Dendropemon*], Urodontinae [*Urodontus*] and Choraginae [*Araecerus*]), and both subfamilies of Belidae (Oxycoryninae [*Hydnorobius*, *Rhopalotria*] and Belinae [*Rhinotia*]). However, *Rhinotia* was excluded from our sample at the post-sequencing informatics stage due to contamination with data from another species. We sampled both subfamilies of Attelabidae (Attelabinae [*Attelabus*, *Euops*] and Rhynchitinae [*Merhynchites*]), the family Caridae [*Car*] and all subfamilies of Brentidae (Apioninae [*Antliarhinus*, *Apion*, *Pterapion*, *Rhinorhynchidius*], Brentinae [*Cylas*, *Tracheloschizus*], Eurhynchinae [*Eurhynchus*], Ithycerinae [*Ithycerus*] and Microcerinae [*Episus*]) except for Nanophyinae (*Nanophyes*), which failed at enrichment and was therefore excluded. The large family Curculionidae was represented by 42 species in as many genera (supplementary table S3), representing all 11 former subfamilies (Brachycerinae, Conoderinae, Cossoninae, Curculioninae, Cyclominae, Dryophthorinae, Entiminae, Mesoptiliinae, Molytinae, Platypodinae and Scolytinae; Oberprieler 2014d) and 35 tribes. We sampled two families from the weevil sister group Chrysomeloidea (Wang et al. 2014; Haddad and McKenna 2016; Haddad et al. 2017) as outgroups: Chrysomelidae (*Diabrotica undecimpunctata*) and Orsodacnidae (*Orsodacne cerasi*). Two more distant outgroup families were also included, both from Cucujoidea (Robertson et al. 2015; McKenna 2016): Cucujidae (*Cucujus clavipes*) and Nitidulidae (*Aethina tumida*; GCKB00000000.1). A full list of the taxa included in this study can be found in supplementary table S3.

Phylogenetic analysis

Most analyses were run on the HPC (High Performance Computing) cluster at the University of Memphis. Model selection and partitioning for both the AA and NT datasets was performed using PartitionFinder 1.1.1 (Lanfear et al. 2012). For the AA matrix we used the Bayesian Information Criterion (BIC) in PartitionFinder 1.1.1 (rcluster with RaxML option) and RaxML 8.1.5 (AUTO option for model selection) for initial model testing. Our final dataset best fit the LG+G protein table according to results from both PartitionFinder 1.1.1 and RAxML 8.1.5. The GTRGAMMA and GTRGAMMA+I models were recommended for the NT data by PartitionFinder (BIC, rcluster with RaxML option) but 85.3 % (64 of a total of 75) of the partitions fit better with the GTRGAMMA+I model only, which we therefore used for all 75 partitions. The AA and NT matrices were analyzed separately in RAxML (10 replicate maximum likelihood [ML] searches; 1,000 rapid bootstrap

replicates). Results from the bootstrap analyses were mapped onto the resulting ML trees (AA and NT). Trees based on non-partitioned and partitioned NT and AA datasets are provided (supplementary figs. S1–S2 and S5–S6, respectively). The AA dataset was also recoded using the 'dayhoff6' scheme in PhyloBayes v4.1 (Lartillot et al. 2009) and analyzed with ML (supplementary fig. S11). We used the command line version MEGA7 (Kumar et al. 2016) to assist in codon usage bias analyses (assessing codon usage patterns, compiling data from four-fold degenerate sites for third codon positions, and skew; [supplementary figs. S16 and S17]—following Inagaki et al. 2004, Inagaki and Roger 2006, Rota-Stabelli et al. 2013 and Cox et al. 2014) based on the partitioned AA ML tree (supplementary fig. S6).

We also analyzed the NT and AA data using Bayesian inference (BI) implemented in MrBayes 3.2.5 (Ronquist et al. 2012). Bayesian analyses were only conducted on the non-partitioned (concatenated) dataset due to the prohibitively large size of our dataset, which precluded running partitioned analyses with available computational resources (an estimated $1x10^6$ generations with 24 CPU would take ~2–3 years on the super computer node of the University of Memphis HPC cluster). We analyzed the concatenated data using either the GTR+I+G model (NT dataset) or a mixed model (AA dataset). We implemented the Bayesian analyses using MPI (Message Passing Interface) and 24 chains, starting from a random tree and proceeding for $1x10^6$ Markov Chain Monte Carlo (MCMC) generations, sampling the chains every 1,000 generations. The runs converged quickly (at or before ~100,000 generations). Burn-in was set at 25 % of the sampled trees (~250,000 generations). Convergence was confirmed by graphically monitoring likelihood values in Tracer 1.6 (Rambaut et al. 2014). A 50 % majority-rule consensus tree was constructed from the remaining (post burn-in) trees and used to estimate posterior probabilities (PP) (supplementary figs. S3 and S4). The Bayesian analyses using the CAT-GTR model were performed for both non-partitioned AA and NT data using PhyloBayes-MPI v1.7a (Lartillot et al. 2013). We choose CAT-GTR, an among-site heterogeneous model (Lartillot and Philippe, 2004), to explore discrepancies between our AA and NT phylogenetic trees. We ran 2 independent chains until each chain converged on 24 CPU cores. We used the bpcomp program of the PhyloBayes package to compare the 2 chains using a burn-in of 500, and the results were returned with a meandiff <0.1. However, due to the size of the data and conflicts within the CEGH and CCCMS clades the maxdiff values for each were 1—an unsurprising result given the analytical challenges presented by applying CAT models in PhyloBayes analyses of datasets larger than 20000 positions (see PhyloBayes-MPI v1.5 manual[1]). We observed no discrepancies across at least the backbone of the phylogeny between the AA and NT results (supplementary figs. S12 and S13). The coalescent species tree analysis was performed on our AA and NT datasets. The gene trees were generated from each gene alignment in RaxML using 100 rapid bootstraps. We summarized a species tree using ASTRAL 4.11.1 (Mirarab et al. 2014a) using the weighted statistical binning scripts from Mirarab et al. (2014b) and Bayzid et al. (2015) using a 50 bootstrap score threshold for binning.

1 http://megasun.bch.umontreal.ca/People/lartillot/www/pb_mpiManual1.5.pdf, accessed 9/19/2017

Divergence time analyses

RelTime implements a timetree estimation method that allows for analysis of large phylogenomic datasets because analyses are up to 1000 times faster than the fastest Bayesian methods (Tamura et al. 2012). This dramatic time savings also enabled us to efficiently compare different hypotheses of divergence times based on alternative fossil calibrations and combinations of minimum and maximum age constraints (see below), which allowed for accommodation of differing interpretations of the age and classification (and therefore the value) of certain weevil fossils for divergence time analyses. Due to the computational time constraints under alternative timetree analysis frameworks, such an approach is not typically feasible—especially when analyzing genome-scale datasets. RelTime takes as input a data matrix, a reference tree, and a set of calibration constraints applied to one or more nodes. We used the 274,886 AA concatenated supermatrix, our preferred tree derived from analysis of this dataset as the reference tree (the partitioned AA ML best tree; Fig. 1, supplementary fig. S6), and a set of fossil constraints (see supplementary tables S4 and S5 for details).

In RelTime, a calibration constraint consists of a minimum and/or a maximum age for a node, with the overall constraint set in an analysis requiring at least one minimum age and one maximum age applied to one or more nodes, but not necessarily to the same node (Tamura et al. 2013, Mello et al. 2017). In our analyses we used dated fossils to apply constraints to up to ten nodes in the preferred phylogeny (Fig. 1), and tested different combinations of minimum/maximum ages to gauge the effect of including/excluding some key fossils and min-max combinations (see supplementary tables S4 and S5). The fossils we used were largely the same as those used in a recent study of weevil phylogeny (Gunter et al. 2016, supplementary materials: fossils were selected based on a critical review of the utility of weevil fossils for timetree analyses). Some differences between our study and Gunter et al. (2016) reflect new information about some key fossils and different taxon samples (e.g., we used a younger age for Brentidae, and applied a constraint to Rhinorhynchinae; see supplementary tables S4 and S5). In accordance with the node calibration scheme detailed in supplementary tables S4 and S5), for our maximum age constraints we used the age of the oldest beetle (Tshekardocoleidae: *Coleopsis archaica*: Kirejtshuk et al. 2014) or the oldest polyphagan beetle (Staphylinidae: *Leehermania prorova*: Chatzimanolis et al. 2012) for the non Curculionidae nodes, and the oldest definitive weevils (e.g., Arnoldi 1977; see also Oberprieler and Oberprieler 2012) for the Curculionidae nodes that we calibrate. For one of our comparisons, we tested the effect of using the supposed oldest reliable (see Gunter et al. 2016) scolytine fossil (*Microborus inertus*, described from ~100 Ma Burmese amber: Cognato and Grimaldi 2009) versus younger (Eocene) but more reliably aged and classified scolytine fossils (as used by Gunter et al. 2016) to calibrate one major node within higher weevils (the 'CCCMS' clade: Gunter et al. 2016). We also tested the effect of using alternative entimine fossils to calibrate the second major clade within higher weevils (the 'CEGH' clade: Gunter et al. 2016). These various combinations of fossils and minimum-maximum constraints yielded 8 separate time tree

analyses, and enabled us to gauge the effect of using alternative fossils that differ in ages by more than 50 million years on evolutionary inferences.

Result and discussion

Weevil Systematics

The superfamily Curculionoidea and all of its families except Nemonychidae are maximally supported as monophyletic groups in all of our main analyses (100 % ML bootstrap support [MLBS], 1.0 PP; fig. 1; supplementary figs. S1–S6; supplementary table S2), but the interrelationships of several higher taxa differed among analyses. In particular, although our analyses of the AA data recover a subset of relationships among weevil families (a phylogenetic backbone) with strong support (supplementary figs. S2, S4 and S6), not all of these strongly supported relationships are recovered in the analyses of NT data (fig. 1, supplementary figs. S1, S3 and S5). In contrast, the positions of subfamilies within each family are well supported in all analyses, except for the CCCMS subfamilies (fig. 1; supplementary figs. S1–S6).

Families of Curculionoidea

Cimberididae, *Nemonychidae and Anthribidae*

Cimberididae (Cimberidinae: *Cimberis*) are strongly supported as the sister group of all other weevils in all analyses of the NT and AA data (100 % MLBS, PP = 1.0; see supplementary table S2), except those for only 3rd codon positions and for the NT-based ASTRAL analyses (supplementary figs. S1-S8 and S10-S14). Our results are therefore similar to those of some other recent molecular phylogenetic analyses (e.g., Marvaldi et al. 2002, 2009; McKenna et al. 2009) in recovering a monophyletic Anthribidae adelphic to a clade comprising Nemonychidae (Rhinorhynchinae: *Rhynchitomacerinus* and *Bunyaeus* in our study) with strong support (fig. 1). In our ML results based on AA and in both BI results (supplementary figs. S2–S4 and S6), the placement of Cimberididae as sister group of the rest of Curculionoidea is strongly supported (more than 98%) and congruent with recent mitogenomic studies (Haran et al. 2013; Gillett et al. 2014). Haran et al. (2013) recovered Cimberidinae: *Doydirhynchus* and Anthribidae: *Platystomos* as successively branching taxa arising from the base of Curculionoidea, whereas Gillett et al. (2014) recovered Anthribidae (Anthribinae: *Platystomos* + an unidentified species) as monophyletic, split off at the most basal node of the phylogeny and adelphic to Cimberidinae: *Doydirhynchus* + the rest of Curculionoidea. Although the type genus *Nemonyx* (subfamily Nemonychinae) is not sampled in our study (because of enrichment failure; see Materials and Methods), a clade comprising *Nemonyx* (Nemonychinae; see fig. 1) + *Rhynchitomacerinus* (Rhinorhynchinae) was recovered by McKenna et al. (2009) with very strong support (1.0 PP, 99 MLBS). However, McKenna et al. (2015: fig. 15) found *Nemonyx* to be more closely related to Anthribidae (*Toxonotus* and *Urodontus*) than to *Rhynchitomacerinus*

(Rhinorhynchinae).

The monophyly of Anthribidae is maximally supported in all analyses (fig. 1, supplementary figs. S1–S15). An interesting difference between recent molecular results (Gunter et al. [2016] and our study) and one previous study (McKenna et al. 2009) is the position of the anthribid subfamily Urodontinae. The recovery of this small subfamily as sister group of the rest of Anthribidae (Anthribinae + Choraginae) is strongly supported in all analyses in Gunter et al. (2016) and in the present study (fig. 1). However, this contrasts with the results of McKenna et al. (2009), which recovered a polyphyletic Anthribidae, with Urodontinae (*Bruchela, Urodontus*) forming the sister group of the clade (Attelabidae (Caridae (Brentidae + Curculionidae))) but without strong nodal support (0.92 PP, <50 % MLBS) (McKenna et al. 2009). The Urodontinae have previously been proposed to constitute a family separate from Anthribidae (Hoffmann 1945; see also Crowson 1984; Thompson 1992) but were placed in Anthribidae by Kuschel (1995) based on four morphological synapomorphies. This placement was also strongly supported by Gunter et al. (2016), although no nemonychids were included in that study. In the present study, both the monophyly of Anthribidae *sensu* Kuschel (1995) and their placement as sister group of Nemonychidae (excluding Cimberidinae) are strongly supported in all analyses. Therefore, while the monophyly of Anthribidae is here corroborated, the constitution of former Nemonychidae remains unclear—there appears to be strong support only for a concept of Nemonychidae that excludes Cimberidinae (McKenna et al. 2009; Gillett et al. 2014; our study, fig. 1 and supplementary figs. S1–S15). Our results (along with those of McKenna et al. 2009; Gillett et al. 2014; McKenna et al. 2015) suggest that Cimberidinae are phylogenetically isolated and not closely related to anythe sister group of all other weevils, thus supporting the elevation of Cimberidinae to family rank.

These results of our large-scale sampling and analyses of molecular data show interesting points of corroboration with results from morphological phylogenetics: whereas Anthribidae have been suggested to form a strongly supported monophyletic group, with from 4 to 10 synapomorphies (Kuschel 1995; Marvaldi et al. 2002), and are likewise supported by analysis of our AHE dataset, the non-monophyly of Nemonychidae in our study and others is not necessarily a surprising result. Although nemonychids are morphologically well characterized (Kuschel 1994, 1995; Anderson et al. 2014), many of their diagnostic features are most likely plesiomophies and the support for monophyly of the group is weaker (three potential adult and larval synapomorphies: Kuschel [1994, 1995]; Marvaldi and Morrone [2000], Kuschel and Leschen [2010]; and see discussion in Anderson et al. [2014]). Furthermore, Nemonychidae are relatively primitive weevils and have the oldest fossil history of the extant families of Curculionoidea (Kuschel 1983, 2003; Kuschel and Leschen 2010; Davis and Engel 2014).

Attelabidae and Belidae

The positions of Attelabidae and Belidae are inconsistent among different analyses herein. In NT-

based partitioned ML analyses, the recovered relationship lacks strong nodal support (<65 % MLBS, supplementary fig. S5) due largely to the unstable placement of Belidae. In results of the NT-based analyses, Belidae are recovered either as the sister group of Attelabidae (supplementary fig. S5, 63 % MLBS) or as adelphic to the clade (Attelabidae (Caridae (Curculionidae + Brentidae))) (supplementary fig. S3, 0.5 PP), but in all AA-based analyses, Belidae are included in a strongly supported clade along with Nemonychidae: Rhinorhynchinae and Anthribidae (supplementary fig. S2, 97 %; supplementary fig. S6, 98 % MLBS; supplementary fig. S4, 1.0 PP), and Attelabidae are recovered as the sister group of the clade (Caridae (Brentidae + Curculionidae), with strong support (supplementary figs. S2, S6, both 99 % MLBS; supplementary fig. S4, 1.0 PP). The placement of Belidae in our AA-based analyses is unexpected and has never been recovered in any other phylogenetic study to date, unlike the positions of both of these families in the NT-based BI analyses, which are consistent with previously proposed phylogenetic and ecological hypotheses (Marvaldi et al. 2002; Marvaldi et al. 2009; McKenna et al. 2009). The relationships of these families therefore remain uncertain.

Relationships of Caridae, Brentidae and Curculionidae

Kuschel (1995) treated Carinae as a subfamily of Brentidae and in the first morphology-based phylogenetic classification of Curculionoidea recovered this taxon as the sister group of the rest of Brentidae (which in Kuschel´s sense excluded Microcerinae and Ithycerinae). In contrast, the most recent molecular phylogenetic analysis of weevils, which focused on the Australian fauna (Gunter et al. 2016), recovered the enigmatic Australian genus *Car* as adelphic to Attelabidae: Rhynchitinae, a somewhat intriguing result given the original placement in Rhynchitinae of the two carine genera known to Kuschel, *Car* and *Caenominurus* (Voss 1932, 1965). We recover a strongly supported relationship between Caridae and the clade (Brentidae + Curculionidae) in all of our analyses (fig. 1; supplementary figs. S1–S6). Our results therefore contrast with the aforementioned studies and agree instead with other systematic work that has treated carines as a distinct family and that benefited from knowledge of immature stages of *Car*, which were unknown to Kuschel (e.g., see Zimmerman 1994). Our results also corroborate those of previous key morphological phylogenetic hypotheses that included both adult and larval characters of Caridae (Marvaldi and Morrone 2000; Marvaldi et al. 2002), as well as the placement of the group (*Car* and *Caenominurus*) in the large-scale molecular phylogeny of McKenna et al. (2009). There is therefore strong support for the current concept of Caridae (Oberprieler 2014a) as a distinct family-level taxon, a concept based on all four of the now-known genera.

The recovery of a strongly supported sister group relationship between Brentidae and Curculionidae in all of our analyses (fig. 1; supplementary figs. S1–S15, supplementary table S2) is unsurprising, as all recent multi-gene molecular phylogenetic studies have also supported this relationship (McKenna et al. 2009; Haran et al. 2013; Gillett et al. 2014; Gunter et al. 2016).

Morphology-based and combined molecular and morphological phylogenetic analyses have also consistently recovered either this same relationship or else a close relationship between Brentidae and Curculionidae (Kuschel 1995; Marvaldi and Morrone 2000; Marvaldi et al. 2002), and the sister-group relationship between them now seems robustly supported, with several hypothesized synapomorphies (Marvaldi et al. 2002).

Brentidae

Brentidae in the present sense (Oberprieler 2000; 2014b; Oberprieler et al. 2007), which includes the subfamilies Brentinae, Apioninae, Nanophyinae, Eurhynchinae, Microcerinae and Ithycerinae, is maximally supported as a monophyletic group in all of our analyses (100 % MLBS and 1.0 PP in fig. 1 and supplementary figs. S1–S7 and S10–S15; Nanophyinae excluded from our analysis, see Materials and Methods). This is a significant finding as there is currently no strong morphological evidence for the monophyly of the family due to lack of, or inconclusive, morphological support (Oberprieler 2014b), and because the enigmatic subfamilies Ithycerinae and Microcerinae were both recovered within Curculionidae by McKenna et al. (2009) (though only two and one genes, respectively, were sampled for these subfamilies) and have had different systematic placements in the past (reviewed by Oberprieler 2014c). Although both these subfamilies are morphologically comparatively distinct, they share with other brentids several possible morphological synapomorphies, including the two hypothesized "key" synapomorphies (single median sensillum on the larval labrum and the reduction in number of Malpighian tubules to four: Oberprieler et al. 2007; Oberprieler 2014c).

In our analyses, the monotypic subfamily Ithycerinae is adelphic to the remaining Brentidae, which formed a clade comprised of a monophyletic subfamily Apioninae adelphic to a clade including Brentinae, Cyladinae, Eurhynchinae and Microcerinae (fig. 1, supplementary figs. S1–S6). The placement of Microcerinae in previous studies has varied: the subfamily has either been suggested to fall inside Brentidae (Oberprieler 2000; Oberprieler et al. 2007) or inside Curculionidae *sensu lato* (e.g., McKenna et al. 2009). It was most recently suggested to be an earlier, divergent brentid lineage because the larvae occur in the soil, where they feed externally on the roots of angiosperms – a more primitive ecological association within Brentidae (Oberprieler et al. 2007). Based on adult characters, previous studies proposed a placement of Microcerinae either close to Brachycerinae (Louw 1986) or in a family Brachyceridae (Thompson 1992). After larval characters became available, Louw (1986) suggested they belong within Curculionidae *sensu stricto* and related to Entiminae (Louw 1995), but results of the cladistic analysis by Marvaldi (1997) placed Microcerinae outside Brachycerinae and all other Curculionidae. Our results support the exclusion of Microcerinae from the family Curculionidae and their inclusion in Brentidae. Our results further suggest that Microcerinae (*Episus*) are a more derived brentid lineage (according to the brentids sampled; 100 % MLBS) and are related to the former subfamily Cyladinae (*Cylas formicarius,* now Brentinae: Cyladini) (except non partitioned NT

ML analyses, supplementary fig. S1). However, the clade Cyladini + Microcerinae has no support in our NT-based tree under ML analysis (supplementary figs. S1). Although the monophyly of Brentidae is recovered with maximal statistical support in all analyses, our study does not include a representative of Nanophyinae (failed at enrichment; see Materials and Methods). *Nanophyes* historically was placed in different groups of Curculionidae (summarized by Zimmerman 1993) on account of its apparent geniculate antennae (a putative synapomorphy of Curculionidae, probably independently evolved in Nanophyinae: Oberprieler et al. 2007), but all recent comparative morphological and phylogenetic studies have concurred in placing this taxon in Brentidae (McKenna et al. 2009; Gillett et al. 2014; Gunter et al. 2016) or at least outside of Curculionidae (Haran et al. 2013). For example, McKenna et al. (2009) recovered *N. marmoratus* in Brentidae and as sister group of *Cylas*. *Nanophyes* also shares with other brentids the two putative synapomorphies of Brentidae (see above; Oberprieler et al. 2007). Apioninae are recovered as a monophyletic group, and a clade comprising (Brentinae (Cyladini + Microcerinae)) is also strongly supported in AA-based analyses (supplementary figs. S2, S4 and S6, with maximum support) and most NT-based analyses (supplementary figs. S3 and S5; see supplementary fig. S1 for an alternative arrangement: [Microcerinae [Brentinae + Cyladinae]). The placement of Eurhynchinae differs among analyses (supplementary figs. S1–S6) and, considering the variation in placement of various taxa in our study, we conclude that the subfamily-level relationships within Brentidae remain uncertain and that alternative relationships may emerge with further sampling of characters and taxa.

Relationships within Curculionidae sensu lato

The family Curculionidae is recovered as a maximally supported monophyletic group in all of our analyses (fig. 1; supplementary figs. S1–S6; supplementary table S2; all 100 % MLBS and 1.0 PP) and is one of the main results of our study, because it firmly establishes the limits of the family (e.g., including Dryophthorinae and Platypodinae as nested within the family; and see below) with strong support and definitively excludes other groups from Curculionidae (e.g., the brentid subfamilies Microcerinae and Ithycerinae were placed in Curculionidae by Kuschel [1995] and also recovered in Curculionidae by McKenna et al. [2009]; see above). This result is also consistent with Marvaldi et al. (2009), McKenna et al. (2009), McKenna et al. (2015) and Gunter et al. (2016) in being among the molecular phylogenetic studies to recover a strongly supported monophyletic Curculionidae. Other molecular phylogenetic studies either did not recover Curculionidae as monophyletic (e.g., Hundsdörfer et al. 2009) or did so without strong nodal support (e.g., Haran et al. 2013; Gillett et al. 2014). Morphological synapomorphies supporting the monophyly of the family Curculionidae, in its current broad sense as sister group of Brentidae, are provided by Marvaldi et al. (2002: Appendix 2) (e.g., in the adult: geniculate antennae, compact antennal clubs, two radial sclerites in the hindwings, and tarsal segment 2 rounded at apical angles; and in the larva: fronto epicranial bracon separating frontal suture from mandible, the thoracic spiracles located on the prothorax, and three to four dorsal

folds in the abdominal segments). The Beetle Tree of Life morphological phylogenetic analysis (Lawrence et al. 2011) recovered the six taxa sampled from family Curculionidae as a monophyletic group.

Although most relationships between the subfamilies of Curculionidae are strongly supported in our study (fig. 1), no curculionid subfamily is consistently recovered as monophyletic among all of our analyses. Additionally, many lower-level relationships within some subfamilies lack robust support and others are not consistently supported among analyses. This is noteworthy given both the large size of our AHE dataset and the small number of taxa sampled from each of the subfamilies in our study. Nevertheless, we describe and discuss below several of the important findings from our analyses that do start to indicate the emergence of strongly supported natural lineages within the higher weevils.

The largely monocot-associated curculionids (e.g., Brachycerinae and Dryophthorinae) are early-diverging groups of Curculionidae in our results, which is consistent with various other phylogenetic studies (McKenna et al. 2009; Haran et al. 2013; Gillett et al. 2014; Gunter et al. 2016). In our study, taxon sampling for Brachycerinae constitutes the most extensive sampling in a molecular phylogenetic study for this group since McKenna et al. (2009). Under the current classification of Brachycerinae (Oberprieler 2014e; Pullen et al. 2014), in all of our analyses the group is polyphyletic and forms a grade at the base of Curculionidae, with the recovered relationships among brachycerine subgroups being strongly supported (fig. 1; supplementary figs. S1–S6). *Ocladius* and *Schizomicrus* form a clade with 100 % MLBS and 1.0 PP, which is adelphic to the remaining Curculionidae, whereas in McKenna et al. (2009) *Schizomicrus* was recovered as adelphic to *Brachycerus* with moderate support (0.89 PP) and *Ocladius* was recovered as sister group of a clade comprising a mixture of taxa from various curculionid subfamilies, including *Bagous*, but this relationship was poorly supported. In our study, however, a monophyletic tribe Brachycerini (*Brachycerus* and *Synthocus)* is recovered with strong support and as sister group of the remaining Curculionidae, suggesting that a change in the classification of Brachycerinae may be warranted, including a narrowing of the circumscription of that subfamily and modification of the ranks of currently included tribes.

The systematic position and rank of Platypodinae (pinhole borer beetles) has been the subject of considerable debate throughout the history of weevil classification. Sharing many morphological features with the similarly wood-boring/tunneling subfamily Scolytinae (bark beetles) (Kuschel et al. 2000; Marvaldi et al. 2002; Jordal et al. 2011; Hulcr et al. 2014), both groups have been considered either as distinct families (e.g., Morimoto and Kojima 2006) or as closely or distantly related subfamilies within Curculionidae *sensu lato*. It has even been suggested that Platypodinae are nested within Scolytinae (rejected family and subfamily status and combined with Scolytinae: Kuschel et al. 2000). In our analyses Platypodinae and Dryophthorinae form a monophyletic clade adelphic to a subset of Brachycerinae (the erirhinine genera *Tanysphyrus*, *Lissorhoptrus* and *Echinocnemus*) with

moderate to low support (fig. 1, supplementary figs. S1, S2, S4–S6), except in the NT BI analysis, in which *Australoplatypus* is adelphic to a monophyletic Dryophthorinae but *Notoplatypus* is instead nested in Scolytinae (supplementary fig. S3, 0.62 PP). This recovery of a sister group relationship between Dryophthorinae and Platypodinae is, on the one hand, unsurprising given the previously recovered close relationship between these taxa in McKenna et al. (2009), Haran et al. (2013) and Gillett et al. (2014) and also the support for this relationship from larval characters, particularly the subdivided abdominal pleura and the branched setae on the apical portion of the epipharynx (Marvaldi 1997), but on the other hand it is surprising given their very divergent anatomy and the greater morphological similarity between Platypodinae and Scolytinae that reflect their shared wood-boring habits (Jordal et al. 2011). Therefore, due to the only moderate support for a clade comprising Platypodinae and Dryophthorinae, it still remains unclear whether Platypodinae render Dryophthorinae paraphyletic or whether they are reciprocally monophyletic sister taxa.

We found the genus *Bagous* (in the formerly monotypic tribe Bagoini; here Bagoinae) to be adelphic to all remaining curculionid subfamilies (the "higher weevils"), with moderate (0.62 PP, >72 % MLBS in NT analyses) to high (all 100 % for AA analyses) support (supplementary figs. S1–S6). While *Bagous* has been considered to be more closely related to taxa with pedotectal male genitalia (Oberprieler et al. 2014; Gunter et al. 2016), our results (along with those of Gillett et al. 2014) suggest that Bagoini are indeed phylogenetically isolated and not closely related to other brachycerines, thus supporting the alternative recent classification that excluded the group from the clade comprising "higher" Curculionidae, and supports the treatment of *Bagous* and related genera (Caldara et al. 2017) as a distinct subfamily (Bagoinae) within Curculionidae (Gillett et al. 2014; Oberprieler 2014d) (fig. 1).

Our study indicates that taxa currently classified in Brachycerinae, together with Dryophthorinae and Platypodinae, form early-diverging lineages within Curculionidae as demonstrated by previous studies (Marvaldi 1997; McKenna et al. 2009; Haran et al. 2013; Gillett et al. 2014). The majority of species within these clades retain the plesiomorphic pedotectal type of male genitalia, although the structure of the male genitalia is unclear in Platypodinae (also in *Schizomicrus*) because of extreme reductions. The male genitalia of *Bagous* is also difficult to classify as a particular type (pedal vs. pedotectal), especially because the sclerotized dorsal part of the penis, although resembling a tectum, differs from that in other pedotectal taxa in that the apodemes of the penis are deflexed in a way similar to that seen in taxa with the derived pedal type of genitalia. The remaining curculionids (see next section) possess the derived pedal type of male genitalia and define a major lineage in Curculionidae here informally called "higher weevils" and which constitutes Thompson's (1992) more restricted concept of the family Curculionidae.

Curculionidae sensu stricto *and the CEGH and CCCMS clades*

A deep split dividing the higher weevils (Curculionidae*sensu stricto*) into two main clades is

beginning to emerge in results of molecular phylogenetic studies of Curculionidae (McKenna et al. 2009; Haran et al. 2013; Gillett et al. 2014; Gunter et al. 2016), and this split is also recovered in our analysis, albeit highly supported only by AA-based analyses (fig. 1, Higher Curculionidae). These clades comprise (1) the subfamilies Cyclominae and Entiminae along with the tribe Gonipterini and subfamily Hyperinae, formerly classified as *incertae sedis* (the "CEGH clade") and (2) the subfamilies Conoderinae, Cossoninae, Curculioninae, Molytinae and Scolytinae (the "CCCMS clade") (fig. 1; Marvaldi et al. 2002, in part; McKenna et al. 2009; Oberprieler et al. 2014; Gunter et al. 2016). Our results are largely compatible with those of Haran et al. (2013) and Gillett et al. (2014) in that *Hypera* is recovered as sister taxon of a clade including the broad-nosed weevil subfamilies Cyclominae (including Gonipterini) and Entiminae in the CEGH clade (fig. 1), supporting the classification of Hyperini (*Hypera*) as a subfamily (Hyperinae). But neither of these two large and diverse subfamilies is recovered as monophyletic in our analyses. Entiminae are paraphyletic with respect to Cyclominae and Gonipterini in analyses of NT data (fig. 1, supplementary figs. S1, S3 and S5) and polyphyletic in analyses of AA data (supplementary figs. S2, S4 and S6), and Cyclominae are paraphyletic with respect to Gonipterini in NT-based analyses (fig. 1, supplementary figs. S1, S3 and S5) but paraphyletic with respect to Entiminae: *Naupactus* + Gonipterini in AA-based analyses (supplementary figs. S2, S4 and S6). The nested position of Gonipterini within Cyclominae in our NT-based analysis as well as the strong support for this relationship suggest that the former placement of Gonipterini within Cyclominae may need to be restored. Previous morphological (Kuschel 1995; Marvaldi 1997; Marvaldi et al. 2002) and molecular phylogenetic analyses (Marvaldi et al. 2002; Hundsdörfer et al. 2009; McKenna et al. 2009) have disagreed on the placement of Gonipterini, and a recent morphology-based reclassification of Cyclominae excluded it from the subfamily (Oberprieler 2010), while also emphasizing both the lack of synapomorphies supporting the monophyly of Cyclominae and the putative monophyly of several of the morphologically well-defined tribes. Entiminae is among those few curculionid subfamilies that are relatively well characterized morphologically, and support for the monophyly of the group has been recovered from both previous molecular phylogenetic work (Haran et al. 2013; Gillett et al. 2014) and from morphology in which some larval and adult synapomorphies have been proposed, though none of these are unique or firmly established (see Marvaldi et al. 2014).

The monophyly of the CCCMS clade (fig. 1; Conoderinae, Cossoninae, Curculioninae, Molytinae [including Lixinae and Mesoptiliinae], Scolytinae), one of the most diverse plant-feeding groups of beetles, has not been strongly supported in previous molecular studies (McKenna et al. 2009; Haran et al. 2013; Gillett et al. 2014; Gunter et al. 2016). In our study the group is only moderately supported in NT-based analyses but strongly supported in AA-based analyses (fig. 1, supplementary table S2). In all of our analyses, relationships among the subfamilies within this clade are also not strongly supported due to many conflicting nodes, and so both the monophyly and subfamily-level relationships remain unclear. Despite this, some patterns within this clade have

425 emerged. Conoderinae are polyphyletic in all analyses (fig. 1; supplementary figs. S1–S6), and the
426 status of this subfamily is still uncertain due to incongruent AA and NT results. All remaining
427 subfamilies/tribes (Cionini, Cossoninae, Cryptorhynchini, Curculioninae, Mesoptiliinae, Molytinae
428 and Scolytinae) are recovered in variable positions and with low support (supplementary figs. S1–S6).
429 Scolytinae, while polyphyletic in all of our analyses, are clearly more closely related to Cionini,
430 Cossoninae, Conoderinae and Curculioninae than to Platypodinae (supplementary figs. S1–S6), the
431 latter being more closely related to Dryophthorinae (see above), as similarly suggested by larval
432 characters and recent molecular phylogenetic studies (Marvaldi 1997; McKenna et al. 2009; Haran et
433 al. 2013; Gillett et al. 2014; Gunter et al. 2016). Previous studies have also suggested that the
434 subfamily Molytinae is not monophyletic and that its members occupy relatively derived positions
435 within Curculionidae (Oberprieler et al. 2007; McKenna et al. 2009; Haran et al. 2013; Gillett et al.
436 2014), a result consistent with our analyses. Ultimately though, the classification of the higher
437 Curculionidae remains problematic; the poor support for the remaining nodes within the CCCMS
438 clade in our study continues an ongoing trend in weevil phylogenetics (e.g., Gunter et al. 2016), in
439 which robust conclusions about relationships are proving elusive, and consequently any significant
440 evolutionary inferences within this large assemblage continue to be difficult or nearly impossible to
441 pursue. Future studies will need to extensively sample both more taxa and more variable loci in order
442 to gain a reasonably comprehensive view of (especially higher) curculionid relationships.

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