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Anchored hybrid enrichment provides new insights into the phylogeny and evolution of longhorned beetles (Cerambycidae)

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Abstract. Cerambycidae is a species-rich family of mostly wood-feeding (xylophagous) beetles containing nearly 35 000 known species. The higher-level phylogeny of Cerambycidae has never been robustly reconstructed using molecular phylogenetic data or a comprehensive sample of higher taxa, and its internal relationships and evolutionary history remain the subjects of ongoing debate. We reconstructed the higher-level phylogeny of Cerambycidae using phylogenomic data from 522 single copy nuclear genes, generated via anchored hybrid enrichment. Our taxon sample (31 Chrysomeloidea, four outgroup taxa: two Curculionoidea and two Cucujoidea) included exemplars of all families and 23 of 30 subfamilies of Chrysomeloidea (18 of 19 non-chrysomelid Chrysomeloidea), with a focus on the large family Cerambycidae. Our results reveal a monophyletic Cerambycidae *s.s.* in all but one analysis, and a polyphyletic Cerambycidae *s.l.* When monophyletic, Cerambycidae *s.s.* was sister to the family Disteniidae. Relationships among the subfamilies of Cerambycidae *s.s.* were also recovered with strong statistical support except for Cerambycinae being made paraphyletic by *Dorcasomus* Audinet-Serville (Dorcasominae) in the nucleotide (but not amino acid) trees. Most other chrysomeloid families represented by more than one terminal taxon – Chrysomelidae, Disteniidae, Vesperidae and Orsodacnidae – were monophyletic, but Megalopodidae was rendered paraphyletic by *Cheloderus* Gray (Oxypeltidae). Our study corroborates some relationships within Chrysomeloidea that were previously inferred from morphological data, while also reporting several novel relationships. The present work thus provides a robust framework for future, more deeply taxon-sampled, phylogenetic and evolutionary studies of the families and subfamilies of Cerambycidae *s.l.* and other Chrysomeloidea.

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Introduction

Longhorned beetles (family Cerambycidae Latreille) comprise one of the most species-rich families of animals, with an estimated 4000 genera and 35 000 described extant species (Monné *et al.*, 2009; Svacha & Lawrence, 2014). Cerambycidae *s.s.* (see Fig. 1 for representatives) is usually divided into eight subfamilies: Lamiinae (>20 000 species), Cerambycinae

(∼11 000 species), Lepturinae (∼1500 species), Prioninae (>1000 species), Dorcasominae (>300 species), Parandrinae (119 species), Spondylidinae (∼100 species) and Necydalinae (∼70 species) (Svacha & Lawrence, 2014). Cerambycidae *s.s.* plus the families Disteniidae (>300 species), Oxypeltidae (three species) and Vesperidae (∼80 species) comprise the informal grouping Cerambycidae *s.l.*, equivalent to the Cerambycidae or Longicornia of most earlier authors, the Cerambycoidea of, for example, Böving & Craighead (1931) or Svacha & Danilevsky (1987), the cerambycid lineage/Cerambycidae *s.l.* of Reid (1995) or the cerambyciform assemblage of Svacha *et al.* (1997).

Cerambycidae *s.l.* occur worldwide but attain maximum species richness in the tropics, where Lamiinae, Cerambycinae, and Prioninae typically dominate, although Dorcasominae is the second largest subfamily in Madagascar (Berkov & Tavakilian, 1999; Svacha & Lawrence, 2014). Cerambycidae *s.l.* belongs to the informal grouping Phytophaga, a clade of mostly phytophagous beetles consisting of the sister superfamilies Curculionoidea Latreille (weevils *s.l.* including bark beetles) and Chrysomeloidea Latreille (leaf beetles, longhorned beetles and relatives). According to Ślipiński *et al.* (2011), the clade Phytophaga contains 125 237 described species (61 854 described species in Curculionoidea and 63 383 described species in Chrysomeloidea).

The earliest fossil Cerambycidae *s.l.* (Wang *et al.*, 2013; possibly Yu *et al.*, 2015) are from the Early Cretaceous. The earliest known unambiguous fossil angiosperms (e.g. Friis *et al.*, 2006) are also from that epoch. The diversity of Chrysomeloidea and other phytophagous insects has been attributed by some to their co-diversification with angiosperms (e.g. Farrell, 1998; Mitter & Farrell, 1991; McKenna & Farrell, 2006; McKenna *et al.*, 2009; McKenna, 2011). This seems only partially true for cerambycids. Although they quite possibly pre-date angiosperms, whose increasing diversity later contributed to cerambycid diversity, cerambycids (even at low taxonomic levels) are often highly polyphagous in the larval stage and some species may even feed on both gymnospermous and angiospermous plants. There were undoubtedly multiple host switches between gymnosperms and angiosperms in cerambycid evolution.

Larvae of Cerambycidae *s.l.* are mostly internal borers in woody plants (xylophagous in the broadest sense) and feed on living or dead (including rotten and fungus-infested) plant tissue, although larvae of some Cerambycidae *s.s.* feed in herbs, and those of some Lamiinae, Prioninae, Lepturinae and all Vesperidae are terricolous and feed externally on plant roots. Unlike in Chrysomelidae (leaf beetles), no free-living cerambycid larvae (such as defoliators or external bark grazers) are known. Most wood-boring species feed on nutrient-rich subcortical tissues (inner bark, cambium and immature xylem), with some species feeding on nutrient-poor outer bark, sapwood, heartwood and pith (Linsley, 1959; Hanks, 1999). Adult feeding (Butovitsch, 1939; Linsley, 1959) is often poorly known; some Cerambycidae *s.s.* and possibly all Vesperidae apparently do not feed, whereas adults of the subfamily Lamiinae undergo obligate maturation feeding, which is thought to be an apomorphy for the subfamily (Svacha & Lawrence, 2014). Adult food includes various plant parts (leaves, conifer needles and cones, bark, stems of herbs or flowers in Lamiinae), pollen and nectar (some Lepturinae, Necydalinae, Dorcasominae and Cerambycinae), sap (some Prioninae, Cerambycinae and Lepturinae), fruit (e.g. various Cerambycinae and Lamiinae), and fungal spores or fruiting bodies (known in some Lepturinae and Lamiinae).

Adult feeding usually has little impact on the environment by itself, but some Lamiinae may transfer pathogens or parasites such as the nematode *Bursaphelenchus xylophilus* (Steiner and Buhrer) Nickle causing Pine Wilt Disease (e.g. Togashi & Shigesada, 2006). The extensive larval feeding makes cerambycids an important component of both natural and managed forest ecosystems. They are major recyclers of dead wood, and through their feeding activities they create access routes into wood for other decomposing agents, such as fungi, and other invertebrates (Ślipiński & Escalona, 2013). However, larval feeding can also seriously damage or even kill the host plant, either directly, or when the larval tunnels and adult emergence holes provide access points for pathogenic fungi (e.g. Schowalter, 2009). For instance, some Cerambycinae and Lamiinae are especially notorious pests of trees in urban, suburban and forest ecosystems (Linsley, 1959). Some Cerambycinae are capable of infesting dry seasoned wood and may seriously damage structural timber. Compared to the subfamilies Lepturinae, Prioninae and Parandrinae, whose larvae mostly develop in decaying wood, species of Cerambycinae and Lamiinae also have higher capacities for introduction in living or freshly dead plants or construction wood and wood products (Cocquempot & Lindelöw, 2010; Raje *et al.*, 2016). For instance, the Asian longhorned beetle, *Anoplophora glabripennis* Motschulsky, has recently shown the potential to spread after introduction and cause significant ecological and economic damage (Nowak *et al.*, 2001; Meng *et al.*, 2015; McKenna *et al.*, 2016). Also, some terricolous root feeders (such as *Philus* Saunders or *Migdolus* Westwood of Vesperidae) may cause considerable damage to forest or agricultural plantations (Svacha *et al.*, 1997; Machado & Habib, 2006).

As in other similarly extensive and diverse groups, it is often extremely difficult to even *distinguish* cerambycid higher taxa on a worldwide scale based on classical adult characters. Larval morphology appears more promising in this group (perhaps because of the universally concealed larval habits resulting in lower morphological diversity), but particularly in some exotic regions, the larvae are known only for a fraction of described species. Under such conditions, it is problematic to use the 'exemplar' approach in morphological phylogenetic studies (as done by Napp, 1994, who sampled 12 of the current 14 subfamilies; Vesperinae and Dorcasominae were not included), particularly if the exemplars are few. As a result of the obvious multiple parallelisms, Napp was forced to somewhat arbitrarily polarize characters by rooting with a 'hypothetical ancestor', and she also rather subjectively coded some characters. Despite this, Napp (1994) remains the only modern phylogenetic study specifically focused on resolving higher-level relationships within Cerambycidae *s.l.* Subsequent phylogenetic studies (whether based on morphological data, molecular data or employing a combined approach) did not specifically address the relationships among the families and subfamilies of Cerambycidae *s.l.* They all lack

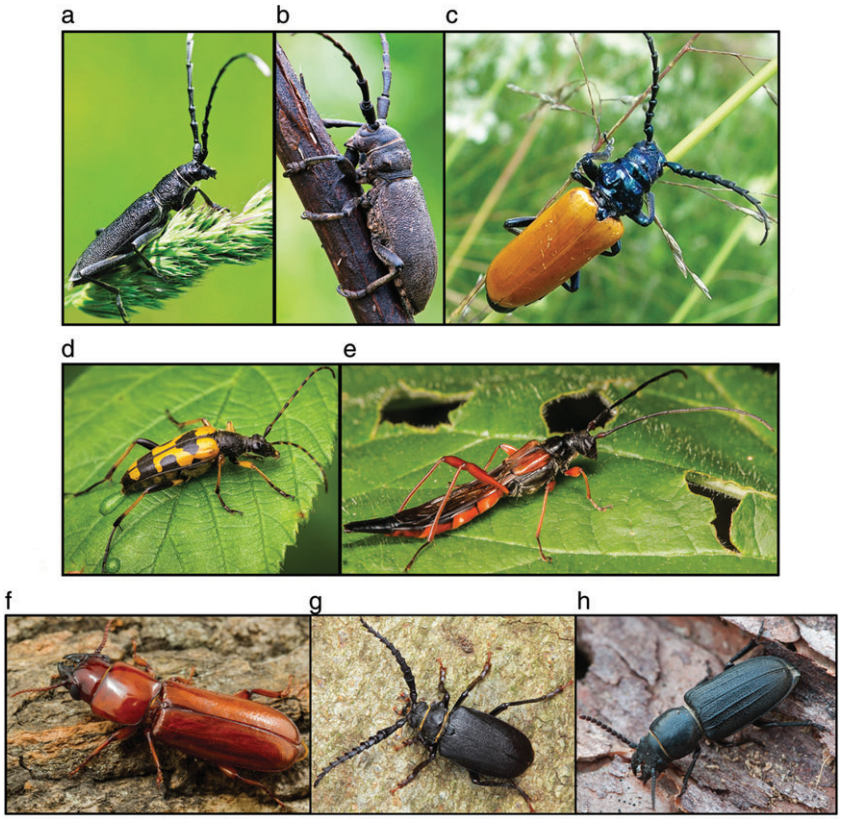

Fig. 1. Representatives of the subfamilies of Cerambycidae *s.s.* (a) *Cerambyx cerdo* Linnaeus (Cerambycinae; image courtesy of Stefano Trucco), (b) *Lamia textor* Linnaeus (Lamiinae; image courtesy of Serhey Ruban), (c) *Dorcasomus* sp. (Dorcasominae; image courtesy of Petr Malec), (d) *Rutpela maculata* Poda (Lepturinae; image courtesy of Paul Mitchy), (e) *Necydalis mellita* Say (Necydalinae; image courtesy of Jeff Gruber), (f) *Parandra polita* Say (Parandrinae; image courtesy of John and Kendra Abbott/Abbott Nature Photography), (g) *Prionus coriarius* Linnaeus (Prioninae; image courtesy of Nikola Rahmé), (h) *Spondylis buprestoides* Linnaeus (Spondylidinae; image courtesy of Serhey Ruban). [Colour figure can be viewed at wileyonlinelibrary.com].

some important higher taxa and/or the relationships within Cerambycidae *s.l.* lack consistent resolution and strong statistical support (see Haddad & McKenna, 2016 for review) whether the studies focused on Phytophaga (Farrell, 1998; Marvaldi *et al.*, 2009), Chrysomeloidea (Reid, 1995; Farrell, 1998; Farrell & Sequeira, 2004; Gómez-Zurita *et al.*, 2007, 2008; Wang *et al.*, 2013), Coleoptera (Hunt *et al.*, 2007; Lawrence *et al.*, 2011; Bocak *et al.*, 2014; McKenna *et al.*, 2015) or even Cerambycidae *s.s.* (Raje *et al.*, 2016). Consequently, many aspects of chrysomeloid classification and evolution, particularly those concerning Cerambycidae *s.l.*, remain the subject of considerable debate: the monophyly of Cerambycidae *s.s.* and *s.l.*; the phylogenetic positions of Megalopodidae and Orsodacnidae relative to Cerambycidae *s.l.*; possible Southern (?Gondwanan) versus Northern (?Laurasian) origins of the subfamilies of Cerambycidae *s.s.* (see Svacha & Lawrence, 2014); early host plant associations (gymnosperms versus angiosperms); etc. Without a reliable phylogeny, morphological ground plans of individual subtaxa cannot be reconstructed. This also makes it difficult to interpret fossils that are not clearly related to extant taxa, on account of the limited set of characters available for fossils.

Due to recent methodological advances (both analytical and wet-lab), a decrease in the cost of DNA sequencing, and a concomitant increase in available genomic resources, it is now possible to efficiently obtain and analyse DNA sequence data from hundreds of genes/loci from all kinds of organisms (e.g. Niehuis *et al.*, 2012; Lemmon & Lemmon, 2013; Hulcr *et al.*, 2014; Misof *et al.*, 2014; Young *et al.*, 2016). Recent studies have effectively employed whole genome sequencing (WGS; e.g. Niehuis *et al.*, 2012; Prum *et al.*, 2015), transcriptome sequencing (e.g. Bi *et al.*, 2012; Kawahara & Breinholt, 2014; Misof *et al.*, 2014; Kjer *et al.*, 2015; Lei & Dong, 2016) or target enrichment (e.g. Faircloth *et al.*, 2012; Lemmon *et al.*, 2012; Smith *et al.*, 2014; Brandley *et al.*, 2015; Eytan *et al.*, 2015; Prum *et al.*, 2015; Hamilton *et al.*, 2016; Young *et al.*, 2016; Breinholt *et al.*, 2017), to generate large-scale phylogenomic datasets for use in phylogeny reconstruction, particularly in groups for which relationships have been difficult to resolve using smaller samples of molecular data (see Lemmon & Lemmon, 2013 for a review of alternative approaches). WGS produces the most data, but is the most expensive of these approaches and also carries a high bioinformatic and computational burden. Transcriptome sequencing requires tissues that are preserved for RNA and such tissues are often not available for all taxa of interest. Therefore, in cases where high-quality RNA is unobtainable, hybrid enrichment is typically the

preferred approach (Lemmon & Lemmon, 2013). Hybrid enrichment has also demonstrated utility across a broad spectrum of taxonomic scales, and is an extremely cost-effective and efficient strategy (e.g. Faircloth *et al.*, 2012; Lemmon *et al.*, 2012; Lemmon & Lemmon, 2013). However, this approach requires that at least some 'model' DNA sequences are available for designing probes to target the loci of interest. Hybrid enrichment is a comparatively versatile approach, and has been successfully used with museum specimens (Bi *et al.*, 2013) and ancient DNA (Burbano *et al.*, 2010; Carpenter *et al.*, 2013). Anchored Hybrid Enrichment (AHE) (Lemmon *et al.*, 2012) is a relatively recent approach for hybrid enrichment that is now being used rather widely in phylogenomic studies of vertebrates (e.g. Brandley *et al.*, 2015; Eytan *et al.*, 2015; Prum *et al.*, 2015) and most recently invertebrates (Diptera: Young *et al.*, 2016; Arachnida: Hamilton *et al.*, 2016; Lepidoptera: Breinholt *et al.*, 2017). It is a fast and cost-efficient method for enriching hundreds of *a priori* targeted loci for use in phylogeny reconstruction. Ideally, organisms with sequenced genomes or other genomic resources are used to design enrichment probes that capture sequence data from organisms lacking genomic resources. These probes are designed based on select conserved 'anchor regions' in the model organisms' genomes that are adjacent to less conserved regions. As such, these probes can be used to obtain conserved anchor regions in addition to the more rapidly evolving flanking regions. The resulting captured fragments are then sequenced using high-throughput Next Generation Sequencing (NGS) methods, assembled into contigs, evaluated for orthology and used in phylogenetic analyses (Lemmon *et al.*, 2012).

This is the first study to use hybrid enrichment on nuclear protein coding genes in beetles, the first molecular phylogenetic study focused on resolving relationships among the families and subfamilies of Cerambycidae *s.l.* and *s.s.*, and the first study to determine the phylogenetic placement of Megalopodidae and Orsodacnidae in the context of a higher-level phylogeny of Chrysomeloidea. Although the sampling within the subfamilies had to be limited because of the demanding methodology, we believe that the present work will serve as a robust framework for future, more deeply taxon-sampled phylogenetic studies of the families and subfamilies of the superfamily Chrysomeloidea. It will also facilitate future evolutionary studies of Cerambycidae (e.g. pertaining to morphology, host associations, biogeographic origins, pheromones, mimicry), and promote studies on the biological control, monitoring and conservation of this ecologically and economically significant group of beetles.

Materials and methods

Taxon sampling

Exemplars were selected based on the availability of specimens suitable for DNA, and type genera and species of families and subfamilies were sampled when possible (see Table 1; refer to Table S1 for the number of recovered loci for each taxon used in this study). We included 14 taxa representing all eight subfamilies of Cerambycidae *s.s.*, seven exemplars from other families of Cerambycidae *s.l.* (two Disteniidae, one Oxypeltidae, four Vesperidae), four exemplars of presumed close relatives in the families Megalopodidae and Orsodacnidae, and six exemplars representing six subfamilies of Chrysomelidae. Four outgroups were sampled, including two Curculionoidea (sister group to Chrysomeloidea; McKenna, 2014) and two Cucujoidea *s.s.* (sister group to Phytophaga; Robertson *et al.*, 2015). All trees were rooted with the Cucujoidea [*Aethina* Erichson (Nitidulidae) and *Cucujus* Fabricius (Cucujidae)] based on recent studies (e.g. McKenna *et al.*, 2015).

DNA extraction, library preparation and sequencing

DNA extraction, library preparation, enrichment and sequencing were performed for all but two taxa in Table 1 (the sequenced genome of *Anoplophora glabripennis* and the transcriptome shotgun assembly from NCBI of *Aethina tumida* Murray were used in our phylogenetic analyses). Depending on the size of the specimen, genomic DNA was extracted from one to six legs, thoracic muscle, a piece of larval tissue or the whole body of the specimen. Specimens were live-frozen, alcohol-preserved (80–100% ethanol), or pinned/dry. Total genomic DNA was extracted from air-dried specimens using the Omniprep™ kit (G-biosciences, St. Louis, MO, U.S.A.) and treated with RNase A. The recommended minimum amount of DNA required for library prep is 200 ng, which can be readily obtained from cerambycids of any size. Genomic DNA QC statistics were generated for each extracted specimen/sample using a Qubit fluorometer, and DNA quality (fragmentation/degradation and/or contamination with RNA) was further assessed via gel electrophoresis. Remaining specimen parts (intact and/or ground pieces) are preserved in 99% ethanol and retained in the McKenna Lab (University of Memphis) as vouchers. Extracted DNA was sent to the Center for Anchored Phylogenomics at Florida State University, Talahassee, FL (www.anchoredphylogeny.com) for library preparation, hybrid enrichment and DNA sequencing. Protocols for library preparation, enrichment, sequencing and probe design followed Lemmon *et al.* (2012). Genomic DNA samples were sonicated to a fragment size of ~150–350 bp using a Covaris E220 Focused-ultrasonicator with Covaris microTUBES. Library preparation and indexing were performed on a Beckman-Coulter Biomek FXp liquid-handling robot following a protocol modified from Meyer & Kircher (2010), that included size-selection after blunt-end repair using SPRIselect beads (Beckman-Coulter Inc.; 0.9× ratio of bead to sample volume). Indexed samples were then pooled at equal quantities (~12–16 samples/pool), and enrichments were performed on each multi-sample pool using an Agilent Custom SureSelect kit (Agilent Technologies), which contained probes designed for anchored loci from the selected model beetle genomes/transcriptomes. After enrichment, the three enrichment pools were pooled in equal quantities for sequencing in three PE150 Illumina HiSeq 2000 lanes, shared with samples from other projects (a total of 27 714 941 100 bp were collected

Table 1. Nomenclature and terminal taxa used in this study. Note that Cerambycidae *s.l.* were polyphyletic and Megalopodidae paraphyletic in all analyses because the genus *Cheloderus* (Oxypeltidae) was invariably recovered as sister to *Palophagoides* (Megalopodidae: Palophaginae).

Superfamily		Family		Subfamily (Type genus)	Genus	Species
'Phytophaga'	Chrysomeloidea	Cerambycidae *s.l.*	Cerambycidae *s.s.*	Cerambycinae (*Cerambyx*)	*Callisphyris* Newman	*macropus* Newman
					Megacyllene Casey	*robiniae* (Forster)
				Dorcasominae (*Dorcasomus*)	*Dorcasomus* Audinet-Serville	*mirabilis* Quentin & Villiers
				Prioninae (*Prionus*)	*Prionus* Geoffroy	*coriarius* (Linnaeus)
					Tragosoma Audinet-Serville	*depsarium* (Linnaeus)
				Parandrinae (*Parandra*)	*Acutandra* Santos-Silva	*araucana* (Bosq)
				Lepturinae (*Leptura*)	*Desmocerus* Dejean	*palliatus* (Forster)
					Rutpela Nakane & Ohbayashi	*maculata* (Poda)
				Necydalinae (*Necydalis*)	*Necydalis* Linnaeus	*formosana* Kano
				Lamiinae (*Lamia*)	*Lamia* Fabricius	*textor* (Linnaeus)
					Anoplophora Hope	*glabripennis* (Motschulsky)
					Tetraopes Dalman	*tetrophthalmus* (Forster)
				Spondylidinae (*Spondylis*)	*Asemum* Eschscholtz	*striatum* (Linnaeus)
					Spondylis Fabricius	*buprestoides* (Linnaeus)
			Disteniidae	Disteniinae (*Distenia*)	*Cyrtonops* White	*punctipennis* White
					Distenia Le Peletier & Audinet-Serville	*japonica* Bates
			Vesperidae	Vesperinae (*Vesperus*)	*Vesperus* Dejean	*sanzi* Reitter
				Philinae (*Philus*)	*Philus* Saunders	*pallescens* Bates
				Anoplodermatinae (*Anoploderma*)	*Migdolus* Westwood	*fryanus* Westwood
					Mysteria Thomson	*darwini* (Lameere)
			Oxypeltidae	Oxypeltinae (*Oxypeltus*)	*Cheloderus* Gray	*childreni* Gray
		Orsodacnidae		Orsodacninae (*Orsodacne*)	*Orsodacne* Latreille	*cerasi* (Linnaeus)
				Aulacoscelidinae (*Aulacoscelis*)	*Aulacoscelis* Duponchel & Chevrolat	*costaricensis* Bechyne
		Megalopodidae		Zeugophorinae (*Zeugophora*)	*Zeugophora* Kunze	*varians* Crotch
				Palophaginae (*Palophagus*)	*Palophagoides* Kuschel	*vargasorum* Kuschel
		Chrysomelidae		Bruchinae (*Bruchus*)	*Caryobruchus* Bridwell	*gleditsiae* (Linnaeus)
				Sagrinae (*Sagra*)	*Sagra* Fabricius	*femorata* (Drury)
				Criocerinae (*Crioceris*)	*Lilioceris* Reitter	*lilii* (Scopoli)
				Galerucinae (*Galeruca*)	*Diabrotica* Chevrolat	*undecimpunctata* Mannerheim
				Cryptocephalinae (*Cryptocephalus*)	*Neochlamisus* Karren	*bebbianae* (Brown)

Table 1. continued

Superfamily	Family	Subfamily (Type genus)	Genus	Species
		Cassidinae (*Cassida*)	*Chelobasis* Gray	*perplexa* (Baly)
Curculionoidea	Nemonychidae	Rhinorhynchinae (*Rhinorhynchus*)	*Rhynchitomacerinus* Kuschel	*kuscheli* (Voss)
	Attelabidae	Rhynchitinae (*Rhynchites*)	*Merhynchites* Sharp	*bicolor* (Fabricius)
Cucujoidea	Nitidulidae	Nitidulinae (*Nitidula*)	*Aethina* Erichson	*tumida* Murray
	Cucujidae	Cucujinae (*Cucujus*)	*Cucujus* O. F. Müller	*clavipes* Fabricius

for the samples used in this study). Sequencing was performed by the Translational Science Laboratory in the College of Medicine at Florida State University.

Probe design and identification of conserved orthologous loci

Probes for Coleoptera were designed using methods similar to those used for a recently published probe set for Diptera (Young *et al.*, 2016) and Lepidoptera (Breinholt *et al.*, 2017). Specifically, we obtained nucleotide alignments of 4485 protein-coding genes for 13 insect species from Niehuis *et al.* (2012). These alignments included 11 species of Holometabola from five orders (Diptera, Hymenoptera, Lepidoptera, Strepsiptera and Coleoptera) and two nonholometabolous outgroups from the insect orders Anoplura and Hemiptera (See Young *et al.*, 2016, Table 1 for details). A preliminary set of loci was then selected containing greater than or equal to six taxa, and at least one consecutive 120 bp region with >50% pairwise sequence identity. Exon boundaries were then identified using custom scripts that identified matches between the beetle model genomes/transcriptomes and the genomes obtained from Niehuis *et al.* (2012) using 40-mers (see Young *et al.*, 2016 for details and scripts).

In order to develop the beetle probe kit, 26 taxa (see Table 2) with sequenced genomes and/or transcriptomes representing the major lineages of interest and near outgroups in Cucujiformia (McKenna *et al.*, 2015) were chosen for consideration: four cerambycids, six chrysomelids, five curculionids, one brentid, one carabid, one coccinellid, one hydroscaphid, one cupedid, one byturid, one clerid, one cryptophagid, one tenebrionid, one mengenillid and one corydalid. We refer to these taxa as the model species.

Enrichment probes were developed targeting 941 orthologous nuclear loci (average length 440 bp) pre-determined to be useful for phylogeny reconstruction in beetles based on their location in conserved anchor regions (flanked by less conserved regions) of the genomes/transcriptomes of the model species, and their status as 1:1 orthologs in the model species. The 941 target loci were selected from a pool of ∼1200 candidate loci that constituted the intersection of a genome-based dataset (4485 1:1 orthologs from Holometabola; Niehuis *et al.*, 2012) with a transcriptome-based dataset (1478 1:1 orthologs from 139 representative Arthropoda, mostly insects; Misof *et al.*, 2014). They comprise a core set of 236 loci with utility across Arthropoda, but primarily focused on Insecta, plus 705 loci selected from a 1:1 ortholog set for Neuropteroidea (Coleoptera + Strepsiptera and Neuropterida) (McKenna & Farrell, 2010; Beutel & McKenna, 2016; McKenna, 2016). The 941 target loci were sought in each of the genomes and transcriptomes of the model species to confirm their presence and further assess their phylogenetic utility (e.g. copy number, length, % identity, GC content). Alignments for the 941 target loci containing the 26 model species were used to identify enrichment probes. Probes were tiled approximately every 50 bp for each of 26 model species (2.4× coverage per species), starting at the beginning of the alignment. Final alignments and probe sequences will be made available on Dryad (the beetle probes are continuously being refined; Contact D. D. McKenna for the latest versions).

Read processing, assembly and orthology assessment

Quality-filtered sequencing reads were processed following the methods described in Lemmon *et al.* (2012) and Prum *et al.* (2015). In short, reads were quality filtered and demultiplexed (with no mismatches tolerated), and overlapping reads were identified and merged following Rokyta *et al.* (2012). Reads were then assembled following Prum *et al.* (2015), except that the following models were used as references: *Callosobruchus maculatus* Fabricius (genome), *Leptinotarsa decemlineata* Say (transcriptome), *Diabrotica undecimpunctata* Linnaeus (genome), *Rhamnusium bicolor* Schrank (transcriptome), *Anoplophora glabripennis* (genome) and *Tribolium castaneum* Herbst (genome; Richards *et al.*, 2008). *T. castaneum* covered 100% of the target loci which is why it was selected as the main reference gene set. The remaining reference taxa covered approximately 82–92% of the target loci, with the lowest being *C. maculatus* at 72.3%. After assembly, we checked for possible cross contamination using an all-vs.-all blast search for each taxon (Camacho *et al.*, 2009).

Table 2. Data used to design anchored hybrid enrichment probes for Coleoptera.

Family	Subfamily	Genus	Species	Data Type	Source
Cerambycidae	Cerambycinae	*Phymatodes*	*amoenus*	Genome	Robert Mitchell (University of WI Oshkosh)
Cerambycidae	Cerambycinae	*Xylotrechus*	*colonus*	Genome	Robert Mitchell (University of WI Oshkosh)
Cerambycidae	Lamiinae	*Anoplophora*	*glabripennis*	Genome	Asian Longhorned Beetle Genome Project (https://www.hgsc.bcm.edu/arthropods/asian-long-horned-beetle-genome-project)
Cerambycidae	Lepturinae	*Rhamnusium*	*bicolor*	Transcriptome	1000 Insect Transcriptome Evolution project (http://www.1kite.org/)[a]
Chrysomelidae	Bruchinae	*Callosobruchus*	*maculatus*	Genome	http://www.beanbeetles.org/genome/
Chrysomelidae	Chrysomelinae	*Chrysomela*	*tremulae*	Transcriptome	Yannick Pauchet (Max Planck Institute of Chemical Ecology)
Chrysomelidae	Chrysomelinae	*Gastrophysa*	*viridula*	Transcriptome	Yannick Pauchet (Max Planck Institute of Chemical Ecology)
Chrysomelidae	Chrysomelinae	*Leptinotarsa*	*decemlineata*	Transcriptome	Yannick Pauchet (Max Planck Institute of Chemical Ecology)
Chrysomelidae	Donaciinae	*Donacia*	*marginata*	Transcriptome	1000 Insect Transcriptome Evolution project (http://www.1kite.org/)
Chrysomelidae	Galerucinae	*Diabrotica*	*undecimpunctata*	Genome	Hugh Robertson (University of Illinois at Urbana-Champaign)
Brentidae	Brentinae	*Arrhenodes*	sp.	Transcriptome	1000 Insect Transcriptome Evolution project (http://www.1kite.org/)
Curculionidae	Dryophthorinae	*Sitophilus*	*oryzae*	Transcriptome	Yannick Pauchet (Max Planck Institute of Chemical Ecology)
Curculionidae	Dryophthorinae	*Rhynchophorus*	*ferrugineus*	Transcriptome	GenBank: PRJNA79205
Curculionidae	Molytinae	*Pissodes*	*strobi*	Transcriptome	GenBank: PRJNA186387
Curculionidae	Scolytinae	*Dendroctonus*	*ponderosae*	Transcriptome	GenBank: PRJNA178770
Curculionidae	Scolytinae	*Ips*	*typographus*	Transcriptome	1000 Insect Transcriptome Evolution project (http://www.1kite.org/)
Cryptophagidae	Atomariinae	*Atomaria*	*fuscata*	Transcriptome	1000 Insect Transcriptome Evolution project (http://www.1kite.org/)
Tenebrionidae	Tenebrioninae	*Tribolium*	*castaneum*	Genome	http://beetlebase.org/ Richards *et al.* (2008)
Carabidae	Carabinae	*Calosoma*	*scrutator*	Genome	D. D. McKenna (Unpublished data)
Coccinellidae	Coccinellinae	*Harmonia*	*axyridis*	Genome	D. D. McKenna (Unpublished data)
Hydroscaphidae	Hydroscaphinae	*Hydroscapha*	*redfordi*	Genome	D. D. McKenna (Unpublished data)
Cupedidae	Cupedinae	*Priacma*	*serrata*	Genome	D. D. McKenna (Unpublished data)
Byturidae	Byturinae	*Byturus*	*ochraceus*	Transcriptome	1000 Insect Transcriptome Evolution project (http://www.1kite.org/)
Cleridae	Clerinae	*Thanasimus*	*formicarius*	Transcriptome	1000 Insect Transcriptome Evolution project (http://www.1kite.org/)
Mengenillidae	Mengenillinae	*Mengenilla*	*moldryzki*	Genome	GenBank: PRJNA181027
Corydalidae	Chauliodinae	*Chauliodes*	*pectinicornis*	Genome	D. D. McKenna (Unpublished data)

[a]An earlier version of the 1KITE assembly was used (as in Misof *et al.*, 2014) for all 1KITE references. The latest assembly version (E3) is not yet available. Umbrella Comparative Genomics project https://www.ncbi.nlm.nih.gov/bioproject/1832

Orthologous genes were identified using Orthograph (Petersen *et al.*, 2017), a protein-based orthology search pipeline. It removes possible paralogous genes using Hidden Markov Model (HMM)-based orthology searches of protein-translated sequences. Three official gene sets (OGS) of three insect taxa from OrthoDB7 (online database of orthologous protein-coding genes across major radiations in the tree of life) were used as references for orthology prediction: *Danaus plexippus* Linnaeus (Lepidoptera: Danaidae) (Zhan *et al.*, 2011), *Nasonia vitripennis* Walker (Hymenoptera: Pteromalidae) (Werren *et al.*, 2010) and *T. castaneum* (Coleoptera: Tenebrionidae) (Richards *et al.*, 2008). The OGS for *T. castaneum* is the only beetle OGS available in OrthoDB7, and the other two insect taxa were chosen based on their high-quality genomes and OGSs. OrthoDB7 (Waterhouse *et al.*, 2013; Kriventseva *et al.*, 2015) was used to generate a table of clusters of orthologous groups (COGs) for each of the three chosen OGSs. In particular, the 941 AHE reference locus set for *T. castaneum* was remapped by BLASTX (E-value threshold $<1e{-}6$) against the reference OGS for *T. castaneum* (OGS 3.0; Richards *et al.*, 2008). This recovered 663 genes, each an assembly of sequences from one or more of the targeted AHE loci. AHE reference assemblies can generate duplicates of single-copy orthologs if the flanking regions of different targeted loci (different exons from the same gene) overlap. Based on the BLASTX results, these duplicate loci were removed. Thus, we settled on 522 COGs that matched

with all single-copy COGs of the aforementioned three OGSs in the Orthograph pipeline (141 of the 663 genes represented by our 941 target loci were excluded because they had multiple copies in at least one of the three OGSs).

The resulting COG tables and OGS sequences were loaded into Orthograph as the reference database for subsequent strict protein-based orthology searches. First, all DNA sequences were translated in all 6 possible reading frames, then the resulting library of amino acid (AA) sequences was searched using profile HMMs (pHMMs) that were trained by the three OGSs previously selected from OrthoDB7. Each of the 522 genes was then assessed for orthology in Orthograph using a reciprocal blast search, and this was done for each taxon-based result from the Orthograph pipeline. Results were stored in both AA and nucleotide (NT) format for each taxon-based result (following Petersen *et al.*, 2017). The resulting fasta formatted NT files for each species were screened for vector contamination using UniVec (Cochrane & Galperin, 2010). Finally, an all-vs.-all blast search was used to further assess our dataset for cross-contamination.

Phylogenomic pipeline

Orthograph generates fasta files that include OrthoDB7 IDs for every taxon and gene and include descriptive information concerning the results in their headers. They also include three OGS sequences for each gene. As a result, we employed a custom bioinformatics pipeline to process these files. First, headers of all files were modified using orthograph2hamstrad.pl (Perl script provided from the Orthograph package; Petersen *et al.*, 2017). Second, reference genes (OGSs) are removed for each file, such that each of them contained only one target sequence for each gene and a clear taxon name (or taxon code) that includes an OrthoDB7 ID. Next, fasta files for each taxon were combined using Perl script *summarize_orthograph_results.pl* (from Orthograph package; Petersen *et al.*, 2017). Genes were then aligned in MAFFT v7 (Katoh & Standley, 2013) with L-ins-i and default options. The resulting file names were then changed from the HaMStRad header to simple taxon names using the custom script *change_taxon_names.sh* (requires an input file of custom taxon names/codes to be created by the user). Finally, aligned files were concatenated with a modified *AMAS.sh* (alignment manipulation and summary statistics) script executed in AMAS 0.97 (Borowiec, 2015). Custom scripts used in this pipeline will be made available in Shin *et al.* (submitted).

Phylogenetic analysis

Phylogenetic analyses were conducted using maximum-likelihood (ML) and Bayesian inference (BI) for both nucleotide (781 446 bp) and amino acid (257 303 aa) data. ML analyses were performed in RAXML 8.1.5 (Stamatakis, 2014) and Bayesian analyses were performed in MRBAYES 3.2.5 (Ronquist *et al.*, 2012). Most analyses were carried out on the HPC (high performance computing) cluster at the University of Memphis. We chose to carry out both partitioned (Figs 2, 3) and unpartitioned (Figures S1 and S2) ML analyses for both the amino acid and nucleotide datasets. Trees resulting from the partitioned ML analyses are our preferred trees. Partitioning optimizes the selection of appropriate models of molecular evolution and has been determined to account for among-site heterogeneity in the rates and patterns of evolution of sequence alignments (e.g. Lanfear *et al.*, 2012) which has been shown to improve various aspects of phylogenetic inference (e.g. see Poux *et al.*, 2008; Rota & Wahlberg, 2012; Leavitt *et al.*, 2013).

Partitioned analyses were carried out using PARTITIONFINDER 2.0.0 (PF; Lanfear *et al.*, 2012) with the RAXML option to determine optimal partitioning schemes and best-fit models of substitution for both AA and NT data. For the AA PF analysis (Fig. 3), we specified use of the strict hierarchal clustering algorithm (hcluster) to search for the best partitioning scheme using the Bayesian Information Criterion (BIC). PF recommended both LG + G (60 subsets) and WAG + G (nine subsets) models for the AA data, but only 13% of the data was fitted to the WAG + G model, so we used the LG + G model for the AA ML analysis.

For the NT PF analysis (Fig. 2), we also specified the use of the h-cluster algorithm to search for the best partitioning scheme using the BIC criterion. The GTR+I+G model was recommended by PF for all of the NT data (16 subsets), so we used that model for the NT ML analysis.

The AA and NT datasets were analysed separately in RAXML (10 replicate ML searches and 1000 rapid bootstrap replicates). Results from the bootstrap analyses were mapped onto the resulting ML trees. A node with a ML bootstrap support (MLBS) value greater or equal to 95% was considered strongly supported.

The Bayesian analyses for both unpartitioned AA (Figure S4) and NT (Figure S3) datasets were also performed on the HPC cluster of the University of Memphis. Concatenated datasets were analysed using the GTR + I + G model for the NT dataset and mixed models for the AA dataset; 24 chains were executed using the MPI (Message Passing Interface) version of MRBAYES for both datasets respectively, starting with a random tree and running for 1 million MCMC (Markov Chain Monte Carlo) generations, with trees sampled every 1000 generations. Burn-in was set at 25% of the sampled number of trees (~250 000 generations). We used TRACER 1.6 (Rambaut *et al.*, 2014) to monitor convergence of the MCMC runs, which was also confirmed by monitoring the value of split frequencies between runs (value fell below 0.01). The runs converged at or before approximately 100 000 generations. A 50% majority rule consensus tree was constructed from the remaining (post burn-in) trees to estimate posterior probability (PP) values, with nodes having PP $\geq$0.95 considered strongly supported.

Results

The nomenclature and terminal taxa used in this study are shown in Table 1. For clarity, in the following text, we usually refer to taxa by their family-level names. We also do this for the families or subfamilies represented only by a single terminal taxon (such

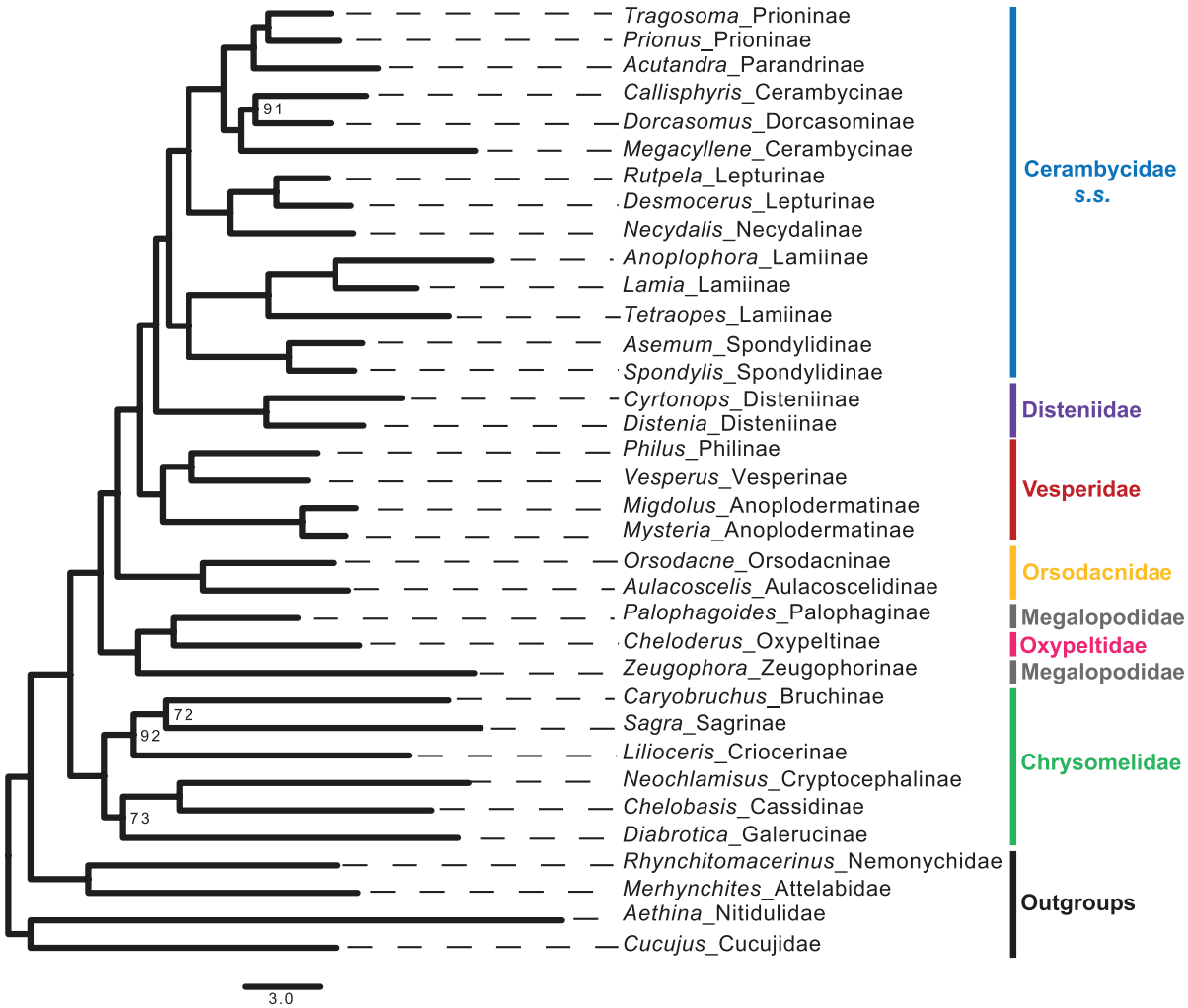

Fig. 2. Maximum-likelihood phylogeny for nucleotide data partitioned in PARTITIONFINDER v2.0 with the RAXML option, and using the hcluster algorithm to search for the best partitioning scheme using the BIC criterion. Maximum-likelihood bootstrap support (MLBS) is shown only for nodes with MLBS <100%. Information regarding the systematics of the sampled exemplars is indicated on the right of the tree. [Colour figure can be viewed at wileyonlinelibrary.com].

as Oxypeltidae by *Cheloderus childreni* Gray), although the monophyly of such family-level taxa remains entirely untested.

Relationships recovered from all analyses

Within the Phytophaga, at the superfamily and family level, all trees (Figs 2, 3, Figures S1–S4) recovered the following clades (which had maximum support in all trees, except where noted): (1) Curculionoidea sister to Chrysomeloidea; (2) Chrysomelidae sister to all remaining Chrysomeloidea (the latter had 99% MLBS in the unpartitioned ML tree of NT data); (3) Orsodacnidae; (4) a clade containing Oxypeltidae and paraphyletic Megalopodidae [(Zeugophorinae + (Palophaginae + Oxypeltidae))] (99% MLBS in the unpartitioned ML tree of NT data); Cerambycidae *s.l.* were thus polyphyletic in all analyses; (5) Vesperidae [as ((Vesperinae + Philinae) + Anoplodermatinae)] (MLBS for Vesperidae was 95% and 94% in the partitioned and unpartitioned ML trees of AA data, respectively, and the clade Vesperinae + Philinae had 99% MLBS in the partitioned ML tree of AA data); and (6) Disteniidae.

Cerambycidae *s.s.* were monophyletic (although with low support in the ML trees of AA data) and sister to Disteniidae in all trees except for the Bayesian AA tree (Figure S4) where they were rendered paraphyletic by the disteniids. Whether monophyletic or paraphyletic, Cerambycidae *s.s.* consistently contained the following clades (with maximum support in all trees, except where noted): (1) Spondylidinae sister to Lamiinae; (2) Lepturinae sister to Necydalinae; (3) a clade containing Dorcasominae and a paraphyletic (NT trees) or monophyletic (AA trees) Cerambycinae; and (4) Prioninae sister to Parandrinae. Clade 3 had maximum support in all trees, but the

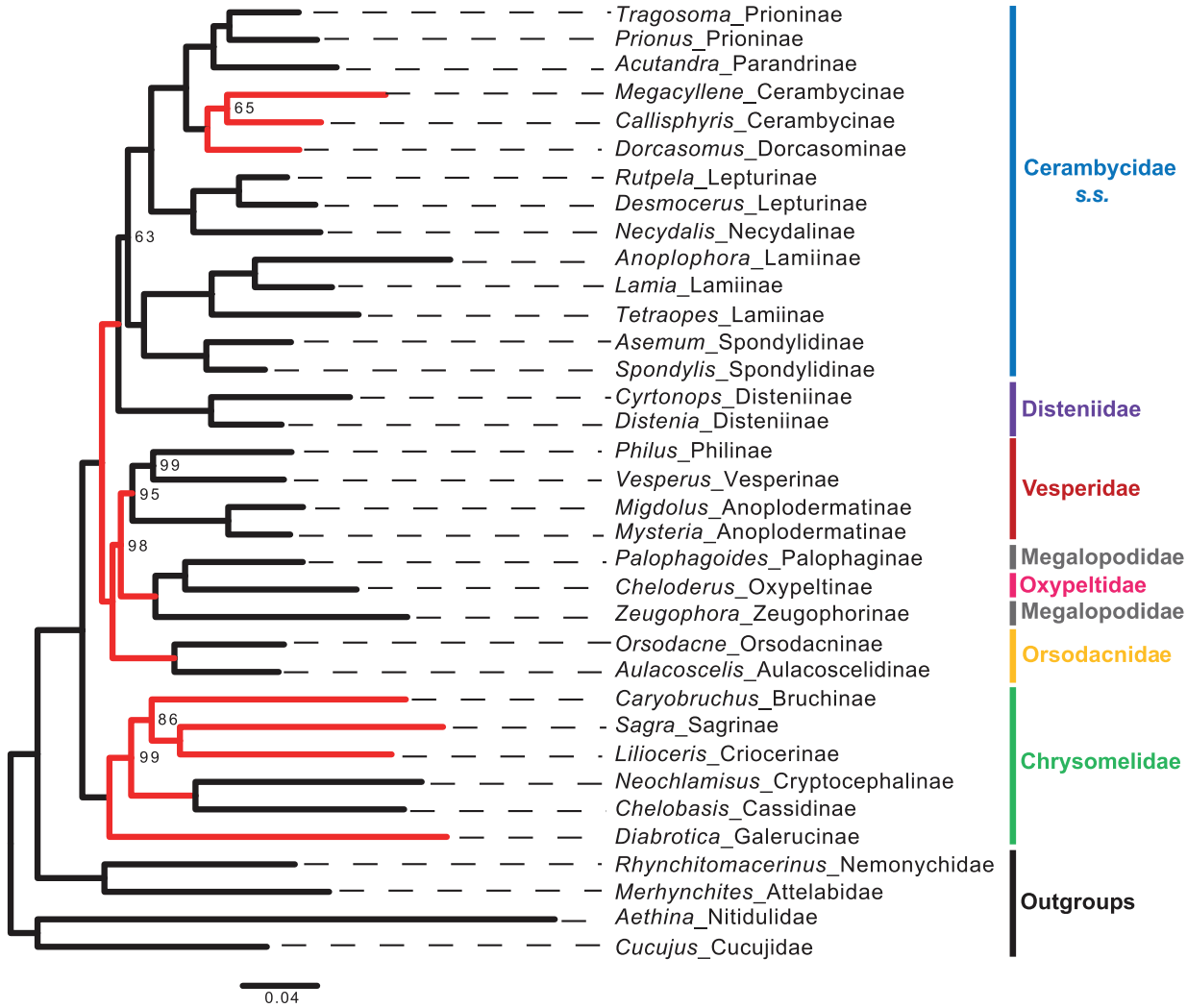

Fig. 3. Maximum-likelihood phylogeny for amino acid data partitioned in PARTITIONFINDER v2.0 with the RAXML option, and using the hcluster algorithm to search for the best partitioning scheme using the BIC criterion. Maximum-likelihood bootstrap support (MLBS) is shown only for nodes with MLBS <100%. Information regarding the systematics of the sampled exemplars is indicated on the right of the tree. Branches in red indicate differences in relationships between this phylogeny and that in Fig. 2. [Colour figure can be viewed at wileyonlinelibrary.com].

internal relationship of *Callisphyris* Newman (whether with *Dorcasomus* in the NT trees or with *Megacyllene* Casey in the AA trees) did not, except in the Bayesian trees where *both* alternatives had maximum support (Figures S3 and S4). In addition, the relationship among the clades 2–4 was always (2 + (3 + 4)) with maximum support, and within the monophyletic Cerambycidae *s.s.*, clade 1 (Spondylidinae + Lamiinae) was the most basal.

Comparing the NT and AA trees

The trees obtained from the three different analyses of NT data (Fig. 2, Figures S1 and S3) were identical in topology but varied slightly in nodal support. The tree resulting from the Bayesian analysis of NT data (Figure S3) had maximal support for all nodes, and the greatest variation in nodal support among the three NT trees was within the very selectively sampled chrysomelid clade. Notably, all NT analyses showed maximal support (100% MLBS and PP = 1) for Cerambycidae *s.s.*, Vesperidae and all of its internal clades, and for the relationships (Orsodacnidae + (Vesperidae + (Disteniidae + Cerambycidae *s.s.*))). This latter group was sister to a clade containing Oxypeltidae and a paraphyletic Megalopodidae with high support (MLBS of 99–100% and PP = 1). Within the Cerambycidae *s.s.*, Cerambycinae (represented by two very different genera *Callisphyris* and *Megacyllene*) was rendered paraphyletic by *Dorcasomus* (Dorcasominae). Relationships within the Chrysomelidae were recovered as (((Bruchinae + Sagrinae) + Criocerinae) + ((Cryptocephalinae + Cassidinae) + Galerucinae)), but none of the internal clades except for Cryptocephalinae + Cassidinae had maximum support in the ML trees.

The analyses of AA data recovered slightly different results. The partitioned (Fig. 3) and unpartitioned (Figure S2) ML analyses resulted in identical tree topologies with a monophyletic but poorly supported Cerambycidae *s.s.* (63% and 50% MLBS for the partitioned and unpartitioned analyses, respectively). The sister-group relationship between Cerambycidae *s.s.* and Disteniidae was maximally supported in both. The Cerambycidae *s.s.* + Disteniidae clade was sister (with maximal nodal support) to a likewise maximally supported clade comprised of the Orsodacnidae (sister to the following two), Vesperidae, and the clade containing Oxypeltidae and a paraphyletic Megalopodidae. Within Cerambycidae *s.s.*, the two Cerambycinae (*Callisphyris* + *Megacyllene*) grouped together but with low support (MLBS of 65% and 61% in the partitioned and unpartitioned trees, respectively). Relationships within the Chrysomelidae were recovered as (((Bruchinae + (Sagrinae + Criocerinae)) + (Cryptocephalinae + Cassidinae)) + Galerucinae); the Sagrinae + Criocerinae and Cryptocephalinae + Cassidinae clades had maximum support in the ML trees. The Bayesian AA tree (Figure S4) had an identical topology to the ML trees of AA data, except for recovering a paraphyletic Cerambycidae *s.s.* due to Disteniidae becoming sister to all cerambycid subfamilies except Spondylidinae and Lamiinae; this clade had PP = 0.9807 (the only node with support lower than 1 in both Bayesian trees). All remaining nodes in the Bayesian AA tree had maximum support.

Discussion

This study was not aimed at elucidating relations between the Curculionoidea and Chrysomeloidea or within the Chrysomelidae *s.s.* Both the Curculionoidea and Chrysomelidae were sampled very selectively. Yet all the trees (rooted by two cucujoids) reliably recovered Curculionoidea as a sister group to Chrysomeloidea, and Chrysomelidae *s.s.* as a monophyletic group (even if the internal relationships were variable) sister to all remaining Chrysomeloidea. The following discussion will be mostly restricted to the non-chrysomelid Chrysomeloidea, particularly to the Cerambycidae *s.l.*

Brief summary of chrysomeloid classification

It is beyond the scope of this paper to review the rich taxonomic history of the Chrysomeloidea in the present broad sense and of the Cerambycidae *s.l.* (Cerambycoidea, Longicornia, etc.) of various authors. For the Chrysomeloidea, see Crowson (1955), Kuschel & May (1990) and Reid (1995, 2000, 2014), unlike Crowson, the latter authors focused mainly on the chrysomelid cluster in the traditional sense including the former Bruchidae). For the Cerambycidae *s.l.*, see Crowson (1955), Linsley (1961), Napp (1994) or Svacha & Lawrence (2014).

Briefly, within the chrysomelid cluster, the long-reigning system of the families Chrysomelidae (including the present Orsodacnidae and Megalopodidae, e.g. Seeno & Wilcox, 1982) and Bruchidae has been, in recent literature, almost universally replaced by another (supported also by our results), placing Bruchinae as a chrysomelid subfamily (exceptions are uncommon, e.g. Kingsolver, 2002, accepted Bruchidae as a family), whereas Megalopodidae (including Palophaginae as a subfamily following Kuschel & May, 1990) and Orsodacnidae (including Aulacoscelidinae as a subfamily following Kuschel & May, 1990 and Reid, 1995) are separate families (e.g. Clark & Riley, 2002; Riley *et al.*, 2003; Clark *et al.*, 2004; Lawrence & Ślipiński, 2013, 2014a,b; Löbl & Smetana, 2010; Bouchard *et al.*, 2011).

The situation is much more unsettled within Cerambycidae *s.l.* We had to disregard the enigmatic Mexican *Vesperoctenus flohri* Bates in our study due to the lack of necessary data (larvae unknown, no material available for molecular study). Earlier authors had placed it in Lepturinae, and it was later preliminarily classified as a taxon (genus or monogeneric tribe Vesperoctenini Vives) *incertae sedis* close to *Vesperus* Dejean or within the present Vesperidae (Svacha *et al.*, 1997; Vives, 2001, 2005; Svacha & Lawrence, 2014). Additionally, it was moved for unexplained reasons to Prioninae by Bousquet *et al.* (2009) and Bouchard *et al.* (2011). All remaining current families and subfamilies of the Cerambycidae *s.l.* (Table 1), except for Dorcasominae, had already been mentioned either as cerambycid subfamilies or at least as taxa of problematic taxonomic status (Oxypeltini, *Vesperus*) by Crowson (1955). Subsequent authors raised the subfamilies Oxypeltinae (Duffy, 1960), Dorcasominae (Danilevsky, 1979b, as Apatophysinae, misspelling of Apatophyseinae, and containing the single genus *Apatophysis* Chevrolat) and Vesperinae (Crowson, 1981, within his broad Disteniidae and including Oxypeltinae and Philinae, but excluding Anoplodermatinae; the family should have been named Vesperidae for priority reasons). Svacha & Danilevsky (1987, pp. 14, 66) added *Dorcasomus* [whose larva, unlike the pupa, was considered 'unquestionably lepturine' by Duffy (1957), although it lacks several typical lepturine characters] to Apatophyseinae but failed to appropriately rename the subfamily to Dorcasominae (this was formally done by Özdikmen, 2008). Svacha & Danilevsky (1987) also suggested that nearly all Afrotropical and Madagascan taxa that were then classified in Lepturinae might belong to Apatophyseinae. This was later confirmed by larval morphology (Svacha *et al.*, 1997, p. 364). Following those changes, the number and extent of subfamilies recognized within the Cerambycidae *s.l.* were relatively stable in major cerambycid publications. The exceptions were the gradual but now prevailing acceptance of the subfamily Dorcasominae (the bulk of which were previously classified in Lepturinae), and the occasional recognition of separate subfamilies Spondylidinae and Aseminae (e.g. Napp, 1994); such division is neither supported by larval morphology (Duffy, 1953; Svacha & Danilevsky, 1987) nor molecular studies where any genera of Spondylidini (*Spondylis* Fabricius, *Neospondylis* Sama or *Scaphinus* LeConte) were included together with several Asemini or even other tribes of Spondylidinae (Sýkorová, 2008, where Spondylidinae is well sampled; Raje *et al.*, 2016, where Spondylidinae is monophyletic but *both* Asemini *and* Spondylidini are not). Based on the remark by Danilevsky (in Löbl & Smetana, 2010, p. 48) who rejected the inclusion of

Apatophysis in Dorcasominae, and retained the name Apatophyseinae, Bouchard *et al.* (2011) accepted separate subfamilies Apatophyseinae and Dorcasominae. This was considered unsupported by Svacha & Lawrence (2014, p. 143) even with the lack of a phylogeny and reliable synapomorphies for Dorcasominae. Svacha & Lawrence (2014) also summarized some confirmed or suspected misclassifications at the subfamily level.

However, even if the number and definition of subfamilies within the Cerambycidae *s.l.* gradually stabilize, their relationships and rank are unclear or not agreed upon and various alternatives can be found in recent literature. The system of families and subfamilies as proposed predominantly on larval characters by Svacha *et al.* (1997) and used in Bouchard *et al.* (2011) and Svacha & Lawrence (2014) was used in the present study. Various intermediate solutions exist and particularly some primarily nomenclatural or cataloguing publications (such as Bousquet *et al.*, 2009, or Löbl & Smetana, 2010) place all subfamilies within a single broad family Cerambycidae. In addition, relationships of Cerambycidae with Orsodacnidae and Megalopodidae, even if occasionally indicated (e.g. Crowson, 1955, p. 150, 1960; Schmitt, 1994a; Svacha *et al.*, 1997, p. 360; Svacha & Lawrence, 2014, p. 59), have not been studied using a sufficiently representative taxon sample and the monophyly of Cerambycidae *s.l.* has not been convincingly demonstrated.

Discrepancies among our trees

Although our analyses mostly recover the same monophyletic families and subfamilies (the only exceptions being the paraphyletic Cerambycidae *s.s.* in the Bayesian AA tree and the paraphyletic vs monophyletic Cerambycinae in the NT and AA trees, respectively), there is clearly some incongruity in support and topology between the AA and NT analyses, which is not uncommon (e.g. Regier *et al.*, 2010). On the one hand, generally, in protein-coding sequences, NT data are more informative than AA data for phylogenetic reconstruction of recent divergences due to the increased likelihood of substitutions at synonymous sites (Rota-Stabelli *et al.*, 2013). On the other, in phylogenetic reconstructions of deep-level relationships, the NT data may suffer from saturation and convergence affecting those variable synonymous sites, which may result in poorly supported or false phylogenies (Rota-Stabelli *et al.*, 2013). In such cases, either AA data are preferentially used, or the NT data are modified to alleviate those issues (e.g. by removing third codon positions or via R-Y recoding). Nevertheless, studies continue to disagree over which data type should be prioritized for phylogenetic reconstruction, with analyses of AA data oftentimes preferred for reconstructing phylogenies of deeper-level relationships, despite some studies arguing for the preference of NT data in all cases for phylogenetic analysis (e.g. Townsend *et al.*, 2008, for vertebrates, but see discussion therein; Holder *et al.*, 2008). Some recent studies argue that incongruence between AA and NT analyses is the result of poor modelling methods for AA analyses, and that NT data can still be utilized but require better methods of nucleotide degeneracy coding (Zwick *et al.*, 2012), whereas others suggest that given the current state of things, AA data should be preferred (Rota-Stabelli *et al.*, 2013). Taking all this into consideration, we included separate analyses for both AA and NT data with the intention of comparing the resulting phylogenetic hypotheses. We consider cases of congruence in topology across the different analyses to reflect the robustness of those recovered relationships, whereas cases of incongruence require further investigation.

Families of Chrysomeloidea and their relationships

Chrysomeloid families listed in Table 1 were represented by more than one terminal taxon except for Oxypeltidae, but both known oxypeltid genera (*Cheloderus* and *Oxypeltus* Blanchard) have similar adult and larval morphology with some unique synapomorphies (Svacha & Lawrence, 2014). As such, there is little doubt of the monophyly of Oxypeltidae. *Oxypeltus* and *Cheloderus* were recovered as sister taxa in Bocak *et al.* (2014; *Cheloderus* was misplaced and miscoloured in their figure S1 as a curculionoid).

All of our analyses (Figs 2, 3, Figures S1–S4) divide Chrysomeloidea into two sister clades, Chrysomelidae and all remaining Chrysomeloidea. The same two clades were obtained in McKenna *et al.* (2015) based on different molecular data, but not in any previous molecular or morphological analyses. Within the non-chrysomelid Chrysomeloidea, four clades are universally recovered: (1) paraphyletic Megalopodidae including Oxypeltidae as sister to Palophaginae, (2) Orsodacnidae, (3) Vesperidae, and (4) Disteniidae and Cerambycidae *s.s.* as sister groups except for the Bayesian AA tree where Cerambycidae *s.s.* is paraphyletic (Figure S4). However, the relationships of those four clades differ between the NT trees $(1+(2+(3+4)))$ and AA trees $((2+(1+3))+4)$. Specifically, each of the four clades has a different sister group in the NT versus AA trees. Cerambycidae *s.l.* is not recovered as monophyletic either in the NT trees (Oxypeltidae and a clade containing Vesperidae, Disteniidae and Cerambycidae *s.s.*) or in the AA trees (Oxypeltidae, Vesperidae, and a clade containing Disteniidae and Cerambycidae *s.s.*). Thus, the higher-level relationships within the non-chrysomelid group particularly require a more focused and better sampled analysis.

As mentioned in the above section on chrysomeloid classification, Megalopodidae and Orsodacnidae were historically treated within Chrysomelidae, but are currently widely accepted as separate families and thought to occupy transitional (but uncertain) positions between Chrysomelidae and Cerambycidae or even being closer to the latter (e.g. Crowson, 1955, p. 150; Schmitt, 1994a; Reid, 1995, 2000). Orsodacnidae and Megalopodidae occur in variable positions in recent molecular phylogenetic studies, either recovered closer in affinity to Chrysomelidae or to Cerambycidae (e.g. Farrell, 1998; Farrell & Sequeira, 2004; Gómez-Zurita *et al.*, 2007, 2008; Hunt *et al.*, 2007; Marvaldi *et al.*, 2009; Bocak *et al.*, 2014; McKenna *et al.*, 2015). Our analyses place both Orsodacnidae and (paraphyletic) Megalopodidae reliably in the non-chrysomelid clade

of Chrysomeloidea together with Cerambycidae *s.l.* All of our analyses reliably recovered a monophyletic Orsodacnidae including Aulacoscelidinae as proposed by Kuschel & May (1990) and Reid (1995). However, Megalopodidae in the classical sense was equally reliably rendered paraphyletic by Oxypeltidae (placed as sister to Palophaginae). Both families, but particularly Megalopodidae (24 genera and an estimated 450 species; Lawrence & Ślipiński, 2014a) should be better sampled in future phylogenetic studies.

The sister-group relationship of Palophaginae and Oxypeltidae has been recovered in several molecular studies to date: Prado *et al.* (2012), McKenna *et al.* (2015), and in part in Bocak *et al.* (2014), who recovered a clade ((*Oxypeltus* + *Cheloderus*) + *Palophagus* Kuschel) with *Palophagoides* Kuschel recovered outside it, but within the same small clade of nine taxa. However, the results of these studies are difficult to interpret either due to the poor sampling of Cerambycidae *s.l.*, or (in Bocak *et al.*, 2014 where Cerambycidae *s.l.* is well sampled) because the two oxypeltids and two palophagines were recovered in an improbable clade sister to all other Chrysomeloidea and containing also three species of *Zeugophora* Kunze (other species were elsewhere in the tree), a species of *Aulacoscelis* Duponchel & Chevrolat (again not the only one in the tree) and an obviously misidentified taxon labelled as the genus *Collops* Erichson of Melyridae. However, there is not a single molecular study containing both oxypeltids and palophagines that has not recovered them as sister taxa, or at least in very close phylogenetic positions (*Palophagoides* in Bocak *et al.*, 2014). To verify whether purely mitochondrial DNA provides the same signal, we performed a ML analysis of *COI* sequence data obtained from GenBank (not shown here) in which we included an exemplar for every chrysomeloid subfamily for which *COI* sequence data were available, and we also recovered Oxypeltidae and Palophaginae as sister groups. The Oxypeltidae, although placed as a possible sister group to Vesperidae on very doubtful characters, were considered 'perhaps the greatest jeopardy for the monophyly of the cerambyciform lineage' (= Cerambycidae *s.l.*) by Svacha *et al.* (1997). Oxypeltidae and Palophaginae share a fused immovable larval clypeolabrum (possible synapomorphy; Svacha & Lawrence, 2014), an apomorphy absent in all other Phytophaga except the cryptocephaline cluster ('Camptosomata') within Chrysomelidae where the larval head morphology is very different and the character undoubtedly arose because of convergent evolution. Kuschel & May (1990, p. 702) mentioned the shared clypeolabral fusion in Palophaginae and Oxypeltidae, but considered it a parallelism. They were apparently not aware that their key to families of Chrysomeloidea based on male and female genitalia did not fit the peculiar genitalia of Oxypeltidae (see Fragoso, 1985; Svacha & Lawrence, 2014). Oxypeltidae and Palophaginae share a 'Gondwanan' distribution (southern South America, Palophaginae also occur in Australia) and their known hosts – *Araucaria* and probably *Agathis* (Araucariaceae) for Palophaginae (Lawrence & Ślipiński, 2014a) and *Nothofagus* (Nothofagaceae) for Oxypeltidae – are currently also restricted to the Southern Hemisphere. Thus, despite the dissimilar adults and biology (tree boring vs pollen feeding larvae), the relationship of Oxypeltidae and Palophaginae is supported, or at least not contradicted, by a variety of data in addition to the consistent support from molecular data.

The family Vesperidae in the present sense (Table 1; see taxonomic overview above for comments on the Mexican *Vesperoctenus* Bates not sampled here) was first proposed by Svacha *et al.* (1997) on larval characters and biology. The family continues to be almost impossible to define based on adult characters when it includes the Neotropical Anoplodermatinae (the extraordinary genus *Hypocephalus* Desmarest makes almost any group it would be included in difficult to define), although a close relationship between *Vesperus* (Mediterranean) and Philinae (basically Oriental with one species in tropical Africa) has been proposed previously (e.g. Gahan, 1906; Saito, 1990, on female genitalia). Anoplodermatinae have previously been associated with the Prioninae and Parandrinae based on adult characters (e.g. Napp, 1994), but many of those characters are inconsistent (Svacha & Lawrence, 2014, p. 133) and anoplodermatines differ from all Prioninae and Parandrinae, for example by the internally and externally closed procoxal cavities (the only known prionine with internally closed procoxal cavities, the genus *Anoeme* Gahan, has them broadly open externally). *Vesperus* (and *Vesperoctenus*) were most often placed with the cerambycid subfamily Lepturinae because of the posteriorly constricted head, and the position of Philinae was very unstable in different systems. The monophyly of Vesperidae sensu Svacha *et al.* (1997) has been repeatedly questioned, particularly with respect to adult characters (e.g. Svacha & Lawrence, 2014; Vives, 2001). Vesperidae were not recovered monophyletic based on morphological characters by Napp (1994; *Philus* and *Anoploderma* Guérin-Méneville sampled), Reid (1995) or Lawrence *et al.* (2011); *Vesperus* and *Sypilus* Guérin-Méneville sampled), and were not monophyletic in the only two molecular phylogenies which included Anoplodermatinae and at least one other vesperid subfamily (Bocak *et al.*, 2014; McKenna *et al.*, 2015; see Table 1 in Haddad & McKenna, 2016). Our data recovered a monophyletic Vesperidae with high to maximum support in all analyses. Svacha *et al.* (1997) proposed a (Vesperinae + (Philinae + Anoplodermatinae)) relationship of vesperid subfamilies, whereas our results clearly place Philinae and Vesperinae as sister groups which agrees with the morphology of female genitalia (unlike the females of Vesperinae and Philinae studied by Saito, 1990, the anoplodermatine females dissected by Svacha & Lawrence, 2014 had distinct sclerotized presumably plesiomorphic spermatheca). This suggests that either the larva of *Vesperus* is strongly derived and the proposal of Svacha *et al.* (1997) was based on larval plesiomorphies, or that the larval characters joining Philinae and Anoplodermatinae were parallelisms (Svacha & Lawrence, 2014, p. 35).

There were attempts in earlier literature to divide the broad Cerambycidae into more than one family (usually either Prionidae or Lamiidae were raised to family level; see Crowson, 1955) and some authors effectively treated cerambycids as a superfamily rather than a family. Disteniidae was the first group in the modern cerambycid taxonomic history to be given the family rank (Linsley, 1961, 1962), in part on larval characters (mainly

the absence of the ventral external sclerotized cranial closure, the gula and more retracted ventral mouthparts; first described by Craighead, 1923, and Böving & Craighead, 1931). The absence of a larval gula is very probably plesiomorphic as it is shared with virtually all other Phytophaga, except Cerambycidae *s.s.* (where the gula is invariably present), and thus cannot be used to establish disteniid relationships. Disteniid larvae are unfortunately known only in a few genera of the nominotypical tribe Disteniini, but all known larvae are very similar and unlike any other Chrysomeloidea. None of the adult characters listed by Linsley (1962, p. 1) can define disteniids on a worldwide basis because they occur in some Cerambycidae *s.s.* (clypeus oblique to frons, 'non-hylecoetoid' metendosternite, wing crossvein r4 without spur, truncate 'scalpriform' mandibular apex; the latter character is also not universally present within Disteniidae). Gahan (1906), who defined the group (as a cerambycid subfamily) in the present extent, listed some additional characters but none are universal and exclusive. A possible morphological character exclusive to Disteniidae (and undoubtedly apomorphic because it is unknown in any other chrysomeloids) is the presence of a row of very long setae (lying in a groove at repose) along at least some antennal flagellomeres (mentioned by Gahan but not by Linsley). However, those setae are absent in *Cyrtonops* White and reduced in *Dynamostes* Pascoe (Gahan, 1906; Svacha & Lawrence, 2014).

All of our analyses recovered Disteniidae (*Distenia* Le Peletier & Audinet-Serville + *Cyrtonops*) in a monophyletic clade with Cerambycidae *s.s.* The latter family was paraphyletic in the Bayesian AA tree (Figure S4; note that the clade containing disteniids and cerambycids other than Spondylidinae and Lamiinae was the only one in both Bayesian trees which did not have maximum support). A sister-group relationship between Disteniidae and Cerambycidae *s.s.* (recovered in all remaining trees) was proposed by Svacha *et al.* (1997) based on larval characters, notably the identical and apomorphic fusion of the larval postclypeus with frons (forming the so-called epistomal margin bearing epistomal – originally postclypeal – setae) and possibly the annular-multiforous spiracles in later-instar larvae (annular in Vesperidae and apparently in the only known later-instar orsodacnid larva described by Prado *et al.*, 2012; annular-biforous in Megalopodidae and Oxypeltidae). The first character is difficult to evaluate in some other chrysomeloid larvae (e.g. in the Palophaginae and Oxypeltidae with fused clypeolabrum), and although annular-multiforous spiracles may be a groundplan character in Cerambycidae *s.s.*, its spiracle morphology is very variable (annular, annular-biforous, annular-multiforous). Svacha *et al.* (1997) also remarked that Disteniidae was the only chrysomeloid group sharing the dead wood feeding habit widespread (and possibly plesiomorphic) in Cerambycidae *s.s.* There are no known adult synapomorphies indicating a relationship between Disteniidae and any other group within Chrysomeloidea (Svacha & Lawrence, 2014); Napp (1994) retained Disteniidae as a separate family requiring further study, and those subsequent phylogenetic studies that included disteniids (see Haddad & McKenna, 2016) recovered the group in rather variable positions.

Monophyly of Cerambycidae s.s. *and relationships within the family*

For a summary of cerambycid classification, adult and larval morphology, and distribution and biology see Svacha & Lawrence (2014) and references therein. Our results do not all firmly support the monophyly of Cerambycidae *s.s.* with respect to Disteniidae, and the maximal versus poor nodal support (or even paraphyly in the Bayesian AA tree) is a major difference between the NT versus AA trees. Mann & Crowson (1981); key to chrysomeloid higher taxa), Svacha & Danilevsky (1987), and Svacha *et al.* (1997) proposed the larval gula as a possible synapomorphy for Cerambycidae *s.s.* As a summary of classical and (partly unpublished) molecular data, Svacha & Lawrence (2014) proposed a preliminary phylogeny of Cerambycidae *s.s.* as an unresolved basal trichotomy with three branches: Prioninae and Parandrinae (with no synapomorphies available for the former which could thus be paraphyletic), Dorcasominae and Cerambycinae (no clear synapomorphies known for the former), and a third branch (which they and others suspect may not be monophyletic) including the remaining four subfamilies as (Spondylidinae + (Lepturinae + Necydalinae) + Lamiinae).

In our present analyses, the eight subfamilies of Cerambycidae *s.s.* (Table 1, Figs 2, 3, Figures S1–S4) form four maximally supported clades composed of two subfamilies each (see Results): (1) Spondylidinae + Lamiinae, (2) Lepturinae + Necydalinae, (3) Dorcasominae and Cerambycinae, the latter paraphyletic in NT trees, and (4) Prioninae + Parandrinae. The relationship of those four clades is (1 + (2 + (3 + 4))) in all trees where Cerambycidae *s.s.* is monophyletic, and would be the same also in the Bayesian AA tree (where Cerambycidae *s.s.* is rendered paraphyletic by Disteniidae; Figure S4) if the disteniids were disregarded.

Clade 4. The relationship of Parandrinae to Prioninae is currently widely accepted. The two subfamilies have previously been recovered as sister groups in some trees resulting from molecular or combined phylogenetic analyses with limited sampling (Farrell, 1998; Farrell & Sequeira, 2004; Gómez-Zurita *et al.*, 2007, 2008; Marvaldi *et al.*, 2009; Wang *et al.*, 2013; McKenna *et al.*, 2015). In fact, it is possible that the first may be an ingroup of the second (Nearns, 2013). A close relationship between the two subfamilies has been consistently suggested based on larval morphology; either the two groups formed a single subfamily (Craighead, 1915, 1923) or, at the very least, were considered closely related. The previous proposal of some authors of Parandrinae being the most basal group of Cerambycidae *s.l.*, or even related to other Cucujiformia has been discussed and criticised (e.g. by Crowson, 1955) and is today virtually abandoned. Prioninae and Parandrinae have often been associated with Anoplodermatinae based on adult morphology (Crowson, 1955; Napp, 1994), but such an association greatly contradicts larval characters (Svacha & Danilevsky, 1987; Svacha *et al.*, 1997) and our results support the larval conclusions in placing Anoplodermatinae within Vesperidae and not near Cerambycidae *s.s.* Adults of Parandrinae and Prioninae share the internally open procoxal cavities (a character virtually unique in Chrysomeloidea; the prionine genus *Anoeme* Gahan is

the single known exception with the procoxal cavities internally closed), the absence of a mesonotal stridulatory plate (present in at least some taxa of all other subfamilies of Cerambycidae *s.s.* and in Disteniidae), and the presence of lateral pronotal carina in most species (also present in some other Chrysomeloidea but very seldom in other Cerambycidae *s.s.* and never in Disteniidae). Larvae possess the combination of a short gula *and* a relatively broad firm tentorial bridge (unique in Chrysomeloidea), and in later instars, the flat (not conical) antennal sensorium which is nearly unknown in remaining Cerambycidae *s.s.* and in Disteniidae.

Clade 3. Most Dorcasominae were previously classified within or near Lepturinae (or its equivalent) mainly based on the similarity in the superficial adult morphology of some floricolous species. Danilevsky (1979b) proposed a close relationship with Cerambycinae based on larval characters when he raised the subfamily Dorcasominae (as Apatophysinae) based on the genus *Apatophysis*, and this was confirmed for all dorcasomine larvae discovered since then (Svacha *et al.*, 1997; Svacha & Lawrence, 2014; P. Svacha, unpublished). Our analyses confirm a close relationship to Cerambycinae for *Dorcasomus*; we did not sample any exemplars for the largest dorcasomine tribe Apatophyseini (we attempted the Madagascan genus *Logisticus* Waterhouse but DNA obtained from the specimen was not suitable) and we thus cannot evaluate the monophyly of Dorcasominae. Sýkorová (2008) also recovered dorcasomine genera belonging to Apatophyseini (*Apatophysis* and *Tsivoka* Villiers) in a cluster containing Cerambycinae, Prioninae and Parandrinae (and away from Lepturinae). Additional sampling of cerambycine species is needed to clarify the contradiction between the subfamily's paraphyly and monophyly in the NT versus AA trees. Nodal support for *Callisphyris* + *Dorcasomus* in the NT trees was reasonably high (91% and 96% for partitioned and unpartitioned ML analyses, respectively) whereas support for a monophyletic Cerambycinae (*Callisphyris* + *Megacyllene*) in the AA trees was low (65% and 61% for partitioned and unpartitioned ML analyses, respectively). A nonmonophyletic Cerambycinae would be unexpected because the subfamily appears to have distinct larval apomorphies (such as a constricted clypeus or round 'gouge-like' mandibles; see Svacha & Lawrence, 2014). Dorcasomines were mostly absent from the taxon sample of recent phylogenetic studies (see Table 1 in Haddad & McKenna, 2016); they have no obvious larval or adult apomorphies supporting their monophyly, and there are no reliable adult characters distinguishing them from cerambycines (Svacha & Lawrence, 2014). Clade 3 (Dorcasominae and Cerambycinae) is difficult to define by apomorphies. Both subfamilies invariably lack the wedge cell in the wing (it may be present in all three remaining clades, namely in almost all Prioninae, some Lepturinae and some Spondylidinae), but it was lost several times in parallel in cerambycids. Both subfamilies lack the characters listed for Clade 4 above, and although adult dorcasomines are frequently habitually similar to lepturines, Clade 3 universally lacks the mandibular molar sclerite present in most species of Clade 2 (Lepturinae and Necydalinae) (see Svacha & Lawrence, 2014, figs 2.4.12K, L). Larvae almost universally differ from Clades 2 and 1 (Lamiinae and Spondylidinae) by the presence of a postnotal fold (if it is absent in a few Cerambycinae, the cerambycine larval apomorphies mentioned above are present). Lamiinae has a number of unique larval and adult apomorphies, but it is difficult to distinguish some cerambycine adults with rich wing venation from those spondylidine taxa lacking the wing wedge cell, and misclassifications between Cerambycinae and Spondylidinae on external adult morphology were common (such confusion is impossible in the case of larval morphology).

Clade 2. The close relationship between Necydalinae and Lepturinae is also widely accepted. It is possible that necydalines may be a lepturine ingroup and some authors placed Necydalini as a tribe of Lepturinae (e.g. Linsley, 1940; Linsley & Chemsak, 1972; Monné, 2006). Napp (1994) consistently recovered *Necydalis* Linnaeus within Lepturinae, but on debatable characters and with poor sampling. A separate subfamily Necydalinae prevails in recent literature. Necydalinae is a morphologically distinct subfamily whose adults have very short elytra and exposed hindwings and both morphologically and behaviorally mimic certain Hymenoptera. Similar mimics occur in some other subfamilies (particularly in Cerambycinae) and were occasionally incorrectly associated with necydalines. Most of those misclassifications have already been corrected, but some persist. Svacha & Lawrence (2014, p. 152) suggested that the subfamily Necydalinae includes only two genera (*Necydalis* and *Ulochaetes* LeConte), which are nearly completely restricted to the Northern Hemisphere. They also noted that the ten additional American (predominantly Neotropical) genera placed in Necydalinae (most recently in Bezark, 2016) are Cerambycinae that are misclassified based on adult parallelisms (larvae are known for two of them, *Callisphyris* and presumed *Hephaestion* Newman, and bear the characteristic cerambycine apomorphies; Duffy, 1960, Appendix; Svacha & Lawrence, 2014 and fig.2.4.24D therein). *Callisphyris*, the most '*Necydalis*-like' of those Neotropical genera, was included in our study and was reliably recovered within the clade also containing *Dorcasomus* (Dorcasominae) and *Megacyllene* (Cerambycinae), thus confirming that the placement of *Callisphyris* in Necydalinae is a misclassification. We sampled only one species of *Necydalis*, but the only molecular study that contained both *Necydalis* (three species) and *Ulochaetes* (Sýkorová, 2008) recovered a monophyletic Necydalinae, even if often with poor support. In Lepturinae, we sampled a typical member of the nominotypical tribe Lepturini (*Rutpela* Nakane & Ohbayashi) and the Nearctic genus *Desmocerus* Dejean which has usually been classified by American authors in a separate tribe Desmocerini (e.g. Linsley & Chemsak, 1972; Bezark, 2016). However, *Desmocerus* also clusters in Lepturini *s.s.* in Sýkorová (2008). Thus, additional sampling of taxa is needed to investigate the monophyly of the Lepturinae. Svacha & Lawrence (2014) suggested a possible larval apomorphy for each of Lepturinae (reduction or absence of larval pronotal lateral furrows) and Necydalinae (duplicate lateral impressions of the ventral larval ambulatory ampullae) that would distinguish their otherwise relatively similar larvae.

Adults of Necydalinae are highly apomorphic (see above), but it would be difficult to name any apomorphies for the relatively large Lepturinae with an estimated 200 described extant genera (Svacha & Lawrence, 2014). Both subfamilies share some characters that could be considered plesiomorphic compared with all other Cerambycidae *s.s.*: in adults, the mandibular molar sclerite (very seldom rudimentary); in larvae, the relatively long legs bearing (with the exception of the Oriental *Pyrocalymma* Thomson) a distinct mesal pretarsal seta or the almost always broadly separate dorsal epicranial halves. However, as none of these characters occur in the basalmost Spondylidinae + Lamiinae clade and the long legs with pretarsal seta also do not occur in Disteniidae (plus the mandibular mola in adult disteniids, when present, is constructed somewhat differently), at least some of those characters might be in fact synapomorphies of the present clade. In addition, this clade lacks all characters listed for Clade 4, the larval postnotal fold almost universally present in Clade 3, several characteristic larval and adult apomorphies of the Lamiinae (see below), and the long distinct larval lateral pronotal furrows of the Spondylidinae (although they are somewhat intermediate in necydalines).

Clade 1. The only pair of subfamilies which is currently not commonly accepted is Spondylidinae + Lamiinae. This relationship has previously been proposed (e.g. by Crowson, 1955, based on some adult characters, even if those mentioned by him also occur in some other cerambycid subfamilies or may be plesiomorphic) and larval characters do not contradict such a relationship (Danilevsky, 1979a; Svacha & Danilevsky, 1987, p. 15). One larval synapomorphy might be the split retractors of dorsal ambulatory ampullae in the spondylidine and lamiine groundplan causing two pairs of lateral impressions (Svacha & Danilevsky, 1987), although lamiines show a vast array of various modifications and there is only one pair of impressions in the spondylidine genus *Pectoctenus* Fairmaire. Two pairs of impressions also occur in Necydalinae, but on both dorsal and ventral ampullae and the muscle split may have occurred independently. Although the spondylidine larval and adult groundplan is one of a relatively generalized cerambycid, the huge subfamily Lamiinae is highly derived in both adult and larval characters: in larvae, the (at most) rudimentary legs, elongate cranium jointly rounded posteriorly and bearing a deep dorsomedian intracranial crest, and the reduced immovable maxillary cardo; in the adult groundplan, the perpendicular or receding frons (more or less prognathous forms appear to be secondary reversals), the asymmetrical mesonotal carina, a peculiar bilobed or bidentate prominent sclerite at base of tibial flexor apodeme, and a few others. This makes Lamiinae easy to define, but at the same time, difficult to associate with its closest relatives based on morphological characters. It would be difficult to list any adult or larval synapomorphies for Spondylidinae, and although spondylidine larvae can be easily distinguished from all other subfamilies, we lack reliable adult distinguishing characters. Some Spondylidinae were frequently misclassified in Cerambycinae, and vice versa, and even the generally richer spondylidine wing venation has not been entirely reliable in defining the group (see Clade 3 and Svacha & Lawrence, 2014). Both larval morphology and molecular data make it impossible to accept separate subfamilies Spondylidinae and Aseminae (see section on classification). Sýkorová (2008) recovered the subfamily (whose relationships to other subfamilies were unfortunately inconclusive) as composed of two distinct branches, one comprising *Spondylis* (tribe Spondylidini) and the usually paraphyletic Asemini, and the other including the Anisarthrini, Saphanini and Atimiini. However, the subfamily gradually came together only after including a sufficient sample of taxa (see her fig. 8a and b with 11 and 4 spondylidine species, respectively). Our study includes only two genera of the Spondylidini-Asemini branch (type genera of both tribes) and inclusion of taxa from the other branch would be desirable. However, Spondylidinae was also recovered sister to Lamiinae in at least some trees by Gómez-Zurita *et al.* (2007, 2008), Marvaldi *et al.* (2009) and Wang *et al.* (2013), and in the first and last of these, spondylidines were represented by *Drymochares* Mulsant (a genus of Saphanini). Lamiinae was often associated with Cerambycinae (figs 2.4.19A–D in Svacha & Lawrence, 2014), but generally based on problematic and nonexclusive or misinterpreted adult characters. In addition to the characters of Napp (1994) critically discussed in Svacha & Lawrence (*l. c.*, p. 133), the 'undivided' mesonotal stridulatory plate was occasionally listed as a shared character (e.g. Linsley, 1961), but whereas the typical 'undivided' plate in Cerambycinae resulted from disappearance of the median mesonotal endocarina, in most Lamiinae that endocarina is present but shifted sidewise and asymmetrical (Crowson, 1955; fig. 2.4.14G in Svacha & Lawrence, 2014) and the endocarina is present in some Cerambycinae (Svacha & Lawrence, 2014; some photographs in Ślipiński & Escalona, 2016).

Although none of the latter four recovered clades are very surprising, their relationships as recovered in this study (disregarding for the moment the invasion of disteniids in the Bayesian AA tree, Figure S4, which requires further investigation) are far from commonly accepted. We cannot comprehensively discuss even the more recent classification systems as they are too many (for an incomplete sample, see figs 2.4.19A–F in Svacha & Lawrence, 2014, and references therein). Briefly, Parandrinae and Prioninae were traditionally considered basal (and occasionally associated with Anoplodermatinae based on adult characters) in the Cerambycidae *s.l.*, or at least basal in Cerambycidae *s.s.* after removal of some taxa as separate families (e.g. Crowson, 1955; Linsley, 1961; Svacha & Danilevsky, 1987; Napp, 1994; Svacha *et al.*, 1997) based on the following: the laterally margined pronotum, broad fore coxae or absence of mesonotal stridulatory plate in adults if considered plesiomorphic, and the occipital foramen apparently divided in two parts by a broad and ventrally visible tentorial bridge in larvae. Both subfamilies also held basal (although in details different) positions in some molecular or combined phylogenies (e.g. Farrell, 1998; Hunt *et al.*, 2007). Conversely, our results place Prioninae and Parandrinae in a more derived phylogenetic position within Cerambycidae *s.s.* (and far from Anoplodermatinae). This is similar to the phylogenetic placement of Prioninae as recovered in other recent molecular phylogenetic studies (some cladograms in Gillett, 2006; Raje, 2012; Nearns, 2013; Raje *et al.*,

2016). This would necessitate re-evaluation of some prionine and parandrine adult characters which have been so far treated as plesiomorphic or of uncertain polarity. The questionable homology of lateral pronotal margins in various chrysomeloid taxa was pointed out by Reid (1995), for example. The absence of a mesonotal stridulatory file should be apomorphic as the file occurs (even if not universally) in all other cerambycid subfamilies, in Disteniidae, some Vesperidae (always absent in Anoplodermatinae), in Megalopodidae, perhaps in some Chrysomelidae (Schmitt, 1994b), and in some Nemonychidae of Curculionoidea (Kuschel & May, 1990). Broad largely exposed fore coxae also occur in some other subfamilies and their almost universal presence in Prioninae and Parandrinae may be associated with the internally open procoxal cavities which is an apparently unique character within the entire Chrysomeloidea (even if the closing bridge is very narrow in some other groups) and thus also probably an apomorphy. The larval tentorial bridge is discussed in the following paragraph.

The relationship between the prionine-parandrine clade and the dorcasomine-cerambycine clade is also a nontraditional feature. In addition to our results, some recent molecular studies also indicate a similar relationship (although most of them did not sample dorcasomines): some cladograms in Gillett (2006), Nearns (2013), and Raje *et al.* (2016). Almost no such earlier opinions exist except for Danilevsky (1979a; see fig. 24.19F in Svacha & Lawrence, 2014) who proposed a close relationship between Cerambycinae and the Prioninae-Parandrinae clade based on the 'divided' larval occipital foramen (later found also in many Dorcasominae): the tentorial bridge lies on the ventral cranial plane (i.e. is not sunken into the cranial cavity) well behind the gula and thus divides the occipital foramen into a smaller anterior part and a larger posterior part. However, as long as the broad larval tentorial bridge in all known Disteniidae, Vesperidae, Oxypeltidae, and Prioninae and Parandrinae (of Cerambycidae *s.s.*) was regarded as a possible symplesiomorphy lost in the six remaining subfamilies of the Cerambycidae *s.s.* (most recently Svacha & Lawrence, 2014; see the figures of larval heads therein), it was impossible to accept the proposition of Danilevsky because the bridge in Cerambycinae (and Dorcasominae) is narrow and thus a potential synapomorphy with the subfamilies Spondylidinae, Lamiinae, Lepturinae and Necydalinae. However, the conformation of our present trees suggests that the groundplan of Cerambycidae *s.s.* might include a narrow and possibly partially internalized tentorial bridge with distinct metatentorial pits (a narrow bridge occurs in Clades 1–3, distinct metatentorial pits in clades 1 and 2 and in some Dorcasominae). Thus, the broad bridge in Prioninae and Parandrinae may be an independent apomorphic parallelism, and consequently the proposal by Danilevsky (1979a) may be correct. If the broad larval tentorial bridge of the prionine-parandrine clade is independent and apomorphic, then so is the very short larval gula (shortest of all cerambycids) in those two subfamilies.

The 'second most basal' Clade 2 (Lepturinae + Necydalinae) is difficult to comment on with respect to classical characters. Its position is neither expected nor surprising, but it would be difficult to propose any synapomorphies with Clades 3 + 4. Given the unorthodox relationships recovered in this study, the morphology of Cerambycidae *s.s.* will have to be carefully revisited.

The basalmost Clade 1 (Spondylidinae + Lamiinae) comprises two morphologically and biologically different subfamilies. Spondylidinae (some taxa are pronouncedly relict) is the second smallest subfamily. Its adults are typically somber-coloured and nonfeeding, and usually crepuscular or nocturnal. Its larvae are uniformly wood-boring or subcortical. Taking our results into consideration, the subfamily has no obvious larval or adult apomorphies. Lamiinae (containing more than half of described cerambycid species) has diversified larvae and adults, obligate adult maturation feeding on plant tissues or fungi, many different types of larval feeding (including terricolous taxa), and numerous adult and larval apomorphies (see above). As such, the biology and morphology of Lamiinae would not aid in reconstructing the cerambycid groundplan. Thus, considering the present results and the difficulty of defining Spondylidinae based on adult characters, the morphology of the surviving spondylidine taxa needs to be carefully revised.

After taking into consideration the distribution, preliminary molecular phylogenetic results, the geographical distribution of plesiomorphic characters (e.g. in wing venation) in the worldwide subfamilies, and the presence of related low-rank taxa on different continents, Svacha & Lawrence (2014, p. 135) proposed that the subfamilies Prioninae, Parandrinae, Dorcasominae and Cerambycinae might be of 'southern' (Gondwanan) origin (Dorcasominae has since been found in Australia, unpublished record), whereas the remaining four subfamilies (Spondylidinae, Lamiinae, Lepturinae and Necydalinae; placed as a questionable monophylum in the preliminary phylogenetic tree of Svacha and Lawrence) could be of 'northern' (Laurasian) provenience. Interestingly, the proposed 'southern' subfamilies form a monophyletic and phylogenetically advanced group in our cladograms whereas the presumably 'northern' subfamilies remain as a paraphyletic base.

Relationships within Chrysomelidae

Resolving relationships within the Chrysomelidae was not within the scope of this study. Nonetheless, our analyses corroborate some previous findings on the phylogenies of Chrysomelidae and Chrysomeloidea. Chrysomelidae was recovered monophyletic with maximum nodal support in all our analyses (Figs 2, 3, Figures S1–S4) and including Bruchinae, which is consistent with many previous phylogenetic studies (e.g. Reid, 1995, 2000; Farrell, 1998; Duckett *et al.*, 2004; Farrell & Sequeira, 2004; Gómez-Zurita *et al.*, 2007, 2008; Hunt *et al.*, 2007; Marvaldi *et al.*, 2009; Lawrence *et al.*, 2011; Bocak *et al.*, 2014; McKenna *et al.*, 2015). We sampled only six of the approximately 12 currently recognized chrysomelid subfamilies (classifications differ), each represented by a single species (Table 1). Their interrelationships differed between NT and AA trees (with some clades not maximally supported) with the following points in common: Criocerinae, Sagrinae and Bruchinae formed one clade in both NT and AA trees, although Sagrinae was sister to Bruchinae in the former but to Criocerinae in the latter.

Cassidinae was sister to Cryptocephalinae and thus the subfamilies Cassidinae, Criocerinae, Sagrinae and Bruchinae whose members share the bifid tarsal setae (see Stork, 1980; Mann & Crowson, 1981) did not form a monophyletic group, similar to Gómez-Zurita *et al.* (2008) and Marvaldi *et al.* (2009). The position of Galerucinae differed between NT trees (sister to Cassidinae + Cryptocephalinae) and AA trees (sister to all other Chrysomelidae).

Practical classification

The families and subfamilies of Cerambycidae *s.l.* are relatively clear-cut based on larval morphology (what is known so far), but often difficult or impossible to define based on adult morphology. For details of the characters mentioned in this section see Svacha & Lawrence (2014).

The practical classification system is subjective, particularly concerning the extent and rank of higher taxa. However, if the relationships reliably recovered in *all* our analyses are sound, the following should be accepted: (1) Cerambycidae *s.l.* in the present extent (Table 1) is polyphyletic and should be abandoned. The non-chrysomelid Chrysomeloidea (Cerambycidae *s.l.*, Orsodacnidae and Megalopodidae) form a monophyletic group in all our analyses and could be classified as a single broad family Cerambycidae *sensu latissimo* (as was in fact suggested by Schmitt, 1994a on some morphological characters, but his proposal was not accepted by subsequent authors). Such a nomenclatural change would represent a major departure from all systems currently in use and would profoundly influence cataloguing and retrieval of information among other things. The group would also be more difficult to characterize based on morphological characters as many of its members bear some plesiomorphies compared with most or all Chrysomelidae. Therefore, we suspect that such a proposal would not be favourably accepted by chrysomeloid workers. Additionally, Cerambycidae and Megalopodidae originate from the same paper (Latreille, 1802) and we would have to establish priority. (2) Oxypeltidae cannot be accepted as a family so long as Palophaginae is included in Megalopodidae; either Oxypeltinae should be included as a subfamily of Megalopodidae, or Palophaginae should be placed as a subfamily of Oxypeltidae. Our study does not include any member of the nominotypical subfamily Megalopodinae, but both molecular and morphological analyses indicate that it is closer to Zeugophorinae than to Palophaginae (e.g. Reid, 1995, 2000; Duckett *et al.*, 2004; Farrell & Sequeira, 2004; Marvaldi *et al.*, 2009) and some include Zeugophorinae in Megalopodinae (Kuschel & May, 1990) or at least suspect that Megalopodinae without Zeugophorinae may be paraphyletic (Reid, 1995, p. 605). Thus, both the above alternatives would be phylogenetically acceptable. Considering the generally accepted placement of Palophaginae in Megalopodidae, we would prefer the former solution (Oxypeltinae as a subfamily of Megalopodidae sister to Palophaginae). (3) Vesperidae (and any of its subgroups sampled here) should not be placed in Cerambycidae *s.s.* when Disteniidae is accepted as a separate family. (4) Because the results recovered from the AA analyses would make inclusion of Vesperidae in Cerambycidae possible only if Cerambycidae included all non-chrysomelid Chrysomeloidea (a solution questioned above), we recommend retaining Vesperidae as a separate family (containing the subfamilies Vesperinae, Philinae and Anoplodermatinae) until its relationships are clarified by additional analyses. (5) Disteniidae (we sampled two of its four tribes, Disteniini and Cyrtonopini) could be included in the Cerambycidae as a subfamily because our cladograms place Disteniidae as sister group or even ingroup (Bayesian analysis of AA data) of Cerambycidae *s.s.* However, it may be acceptable to classify Disteniidae and Cerambycidae as separate families because Disteniidae as a separate family has already become relatively widespread and the apomorphic presence of the larval gula conveniently (and without any known exceptions) defines the Cerambycidae *s.s.* (whereas disteniid larvae, like those of all other Phytophaga, lack the gula).

Our results basically support the current division of Cerambycidae *s.s.* into eight subfamilies (except for the paraphyletic Cerambycinae in the NT trees), although their relationships are in part unexpected and enforce revision of some widespread assumptions (see above). Further research may reveal Parandrinae and Necydalinae as ingroups of Prioninae and Lepturinae respectively (our sampling is insufficient to test that), but presently, we recommend accepting the former two as separate subfamilies to emphasize their uncertain status. Currently, there are no clear synapomorphies available for the subfamily Dorcasominae, only larval synapomorphies for the subfamily Cerambycinae, and no reliable distinguishing characters between adults of the two subfamilies (Svacha & Lawrence, 2014). We recommend retaining both Dorcasomini and Apatophyseini (the latter not sampled here), plus some related tribes of uncertain status (Protaxini if not considered synonymous with Apatophyseini; Trigonarthrini; see Svacha & Lawrence, 2014), in one broad subfamily Dorcasominae, at least until its limits and relationships to the Cerambycinae can be further investigated.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12257

Figure S1. Unpartitioned maximum-likelihood phylogenetic tree for nucleotide data inferred in RAXML 8.1.5. Maximum-likelihood bootstrap support (MLBS) is shown only for nodes with MLBS <100%. Information regarding the systematics of the sampled exemplars is indicated on the right of the tree.

Figure S2. Unpartitioned maximum-likelihood phylogenetic tree for amino acid data inferred in RAXML 8.1.5. Maximum likelihood bootstrap support (MLBS) is shown only for nodes with MLBS <100%. Information regarding the systematics of the sampled exemplars is indicated on the right of the tree. Branches in red indicate differences in relationships between this phylogeny and that in Figure S1.

Figure S3. Phylogeny based on Bayesian inference for nucleotide data inferred in MRBAYES 3.2.5. All nodes had a Bayesian posterior probability (PP) value of 1. Information regarding the systematics of the sampled exemplars is indicated on the right of the tree.

Figure S4. Phylogeny based on Bayesian inference for amino acid data inferred in MRBAYES 3.2.5. Bayesian posterior probability (PP) values are shown only for nodes with PP < 1. Information regarding the systematics of the sampled exemplars is indicated on the right of the tree. Branches in red indicate differences in relationships between this phylogeny and that in Figure S3.

Table S1. Number of loci analysed for each taxon used in this study.

Supplementary material. Dryad accession numbers (AHE probes and final sequence alignments will be uploaded to Dryad).

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