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## Research

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# Ancient host shifts followed by host conservatism in a group of ant parasitoids

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While ant colonies serve as host to a diverse array of myrmecophiles, few parasitoids are able to exploit this vast resource. A notable exception is the wasp family Eucharitidae, which is the only family of insects known to exclusively parasitize ants. Worldwide, approximately 700 Eucharitidae species attack five subfamilies across the ant phylogeny. Our goal is to uncover the pattern of eucharitid diversification, including timing of key evolutionary events, biogeographic patterns and potential cophylogeny with ant hosts. We present the most comprehensive molecular phylogeny of Eucharitidae to date, including 44 of the 53 genera and fossil-calibrated estimates of divergence dates. Eucharitidae arose approximately 50 Ma after their hosts, during the time when the major ant lineages were already established and diversifying. We incorporate host association data to test for congruence between eucharitid and ant phylogenies and find that their evolutionary histories are more similar than expected at random. After a series of initial host shifts, clades within Eucharitidae maintained their host affinity. Even after multiple dispersal events to the New World and extensive speciation within biogeographic regions, eucharitids remain parasitic on the same ant subfamilies as their Old World relatives, suggesting host conservatism despite access to a diverse novel ant fauna.

## 1. Introduction

Intimate ecological associations of parasites and their hosts have been considered important in shaping species evolution [1–3], an idea tracing at least back to Darwin who stressed the co-dependency of these organisms [4]. Host diversity, host shifts and niche diversification are significant influences in the radiation of parasitoids [5–8], which are a specialized group of parasites that develop in or on a single host, eventually killing it [9]. Studies of host–parasitoid relationships conclude that host range is often dependent on behavioural or ecological characteristics of the host [5,10] rather than being limited to taxonomic relatedness of host. To contribute to the understanding of host–parasitoid interactions, we elucidate the evolutionary history of an association between ants and a specialized group of parasitoid wasps, the Eucharitidae (Hymenoptera: Chalcidoidea).

Ants represent one of the most successful radiations within the insects, and in terms of available biomass, distribution and diversity, they offer a tremendous resource for a variety of nest associates [11]. The roughly 15 000 ant taxa ([antweb.org](http://antweb.org), AntWeb (accessed September 2012). Hosted by the California Academy of Sciences) support at least 17 orders of arthropod myrmecophiles, including specialized predators, scavengers, commensals, parasites and trophobionts [12,13]. Ant parasitoids are known from three insect orders: Diptera, Strepsiptera and Hymenoptera [13–15]. Although roughly 77 000 species of parasitoids are described, and more than 600 000 are estimated [16], only a fraction attack ants and even fewer can gain access inside the nest [15,17].

Via a complex suite of behavioural, morphological and chemical adaptations, Eucharitidae are one of the few groups to successfully circumvent the formidable colony defence mechanisms and attack immature ants [18–22]. Females deposit their eggs away from the ant nest on a host plant [18,23,24]. The eucharitid planidia (active, first instar larvae) enter the ant nest via phoresy, either directly on worker ants or on prey items carried by ants [23,25–27], and

**Table 1.** Comparison of relevant ant clade estimated ages from three previous studies, along with taxon appearance in the fossil record. Age and range given in millions of years.

	Moreau <i>et al.</i> [37] min. age fossils	Brady <i>et al.</i> [38] 145 Myr root	Schmidt [39] 155 Myr root	oldest known fossils
Formicidae w/Martialinae	n.a.	n.a.	123 (116–130)	100 [46]
Formicidae w/o Martialinae	140.6 (132.6–148.6)	116 (112.2–119.8)	118 (112–124)	
poneroid clade	128.2 (122.3–134.1)	100 (103.9–116.1)	107 (99–115)	
Ponerinae	110.7 (104.4–117)	79 (72.7–85.3)	94 (85–104)	88.6–92 [47]
formicoid clade	124.7 (118.2–131.2)	105 (101.5–108.5)	104 (98–111)	
Myrmeciinae	108.3 (105.3–111.3)	47 (41.6–52.4)	n.a.	54.5 [48]
Ectatomminae	79.5 (78.6–80.4)	56 (51.9–61.1)	n.a.	79 [49]
Formicinae	92.0 (91.8–92.2)	77 (73.5–80.5)	66 (56–76)	88.6–92 [50]
Myrmicinae	99.8 (95.6–104)	82 (77.7–86.3)	76 (66–85)	52 [51]

eventually develop as an ectoparasitoid of the ant pupae [28,29]. Within the nest, both adults and immature stages are generally accepted by the ants, being groomed, carried or protected if the colony is under attack [19,22,30]. This intimate interaction is based on semiochemical recognition involving similar hydrocarbon profiles between eucharitid parasitoids and their host ants [20,21].

An examination of the nearest relatives of Eucharitidae is necessary to understand how this life cycle might have evolved. Their paraphyletic sister group, Perilampidae [24, 31–33], parasitize a diverse array of species, including several Hymenoptera [34], but never attack ants. Both families possess planidial larvae and oviposit away from the host, which are shared life-history traits exhibited by no other Chalcidoidea [25,35].

Eucharitidae are known to attack five of the 21 subfamilies of ants: Ectatomminae, Formicinae, Myrmeciinae, Myrmicinae and Ponerinae (as referenced in [36]; electronic supplementary material, table S1). Along with recent ant phylogenies [37–39], a comprehensive, dated phylogenetic analysis of Eucharitidae makes possible an investigation of the historical evolutionary relationships of the two families, one where congruence of parasitoids to their host could be expected owing to the close dependent association. There are few studies evaluating ants and their myrmecophiles within a phylogenetic framework [40–43], thus this large-scale examination is a significant contribution to our understanding of ant-associates.

Fossil data place the origin of ants at 110–120 Ma [44,45] which is in general agreement with molecular divergence dating analyses that estimate an age of 115–140 Ma ([37–39]; table 1). Ant fossils are rare in the Cretaceous, but show a gradual increase in representation from 5 per cent of the total Baltic amber insects to 36 per cent of the Dominican amber insect fossils [52]. While the major ant lineages were established and had diversified by the end of the Cretaceous, it was not until the Eocene that ants attained ecological dominance [37,38,45,53].

Fossil evidence suggests that the superfamily Chalcidoidea arose in the Early Cretaceous [44,54], yet most chalcidoid families do not appear until the Eocene [31,33]. The sole eucharitid fossil dates to the Middle Eocene [31], which coincides with the rise in dominance of ants. Previous taxonomic analysis of Baltic amber fossils of both Eucharitidae

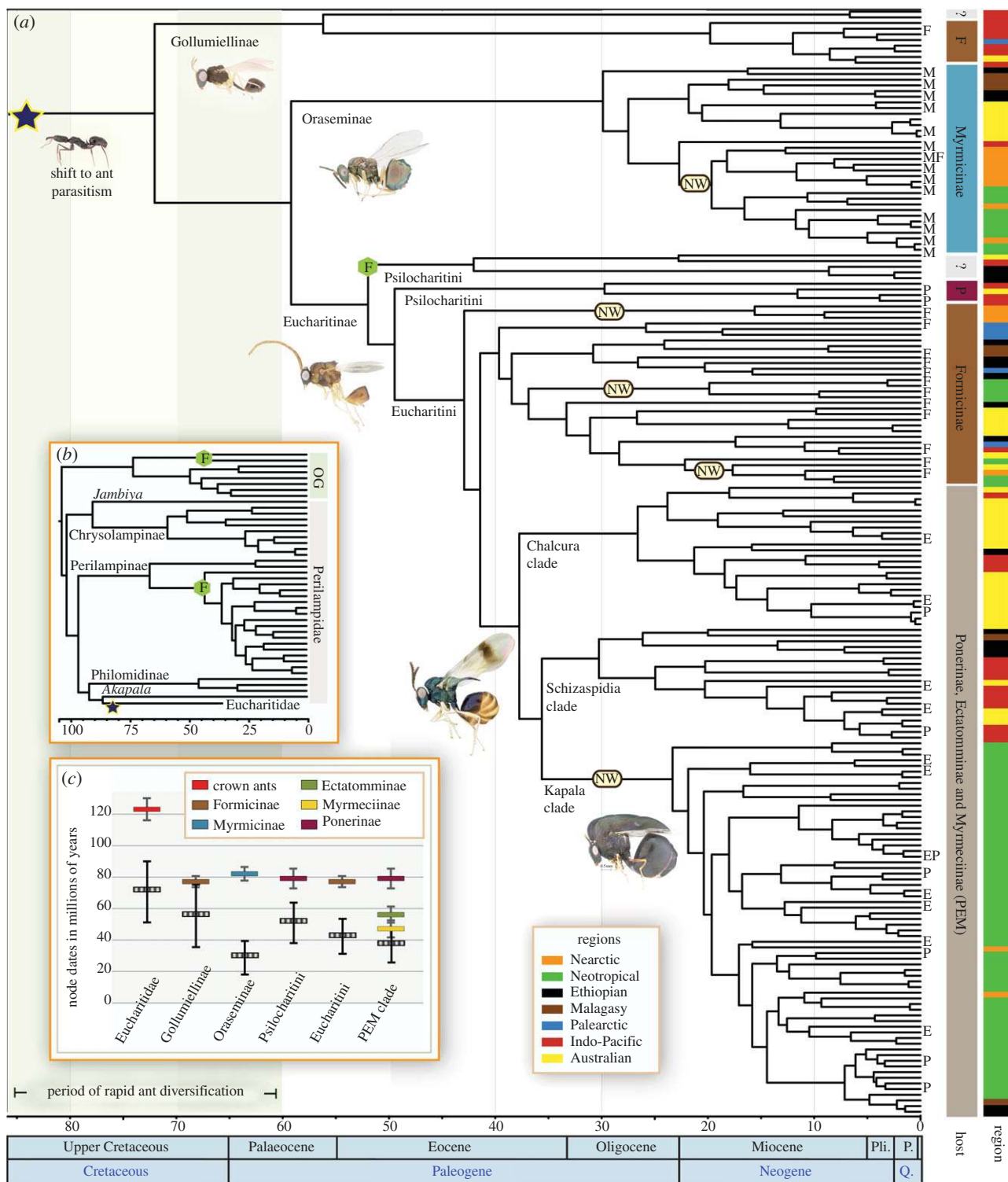
(*Palaeocharis rex*) and their nearest relative Perilampidae (*Perilampus pisticus*) indicates a relatively derived phylogenetic placement of these extinct species, leading to the conclusion that the two families diverged considerably earlier than the approximate 45 Myr age of the fossils [31].

To examine the evolutionary history of this ant–eucharitid association, we first present a molecular phylogeny of the Eucharitidae (237 taxa) that includes calibrated divergence time estimates. We then use this phylogeny combined with cophylogenetic analysis, ancestral host reconstruction and biogeographic analysis to address three objectives: (i) establish if there is evidence for cophylogeny between eucharitids and ants, (ii) determine if diversification rates of eucharitids coincide with novel host colonization, and (iii) resolve the parasitoid biogeographic history and consider its overlap with ant distribution. We find that despite the evidence for ancient ant host shifts, there is high host affinity and apparent ecological constraints maintaining host-specificity in the Eucharitidae.

## 2. Results and discussion

### (a) Eucharitid dated phylogeny

The monophyly of Eucharitidae is strongly supported with a posterior probability (pp) of 1.0 (see figure 1a and electronic supplementary material, S1). The subfamilies Gollumiellinae, Oraseminae and Eucharitinae are each recovered as monophyletic, and relationships among them are strongly supported, with Gollumiellinae sister to Oraseminae + Eucharitinae. These results are in general agreement with phylogenetic relationships based on morphology [55] and analyses of molecular data [27,32]. Previous analyses have suggested both *Akapala* (Akapalinae; [33]) and *Jambiya* (Perilampidae; [32]) as sister to Eucharitidae, but with low support; we found high support for *Akapala* as the sister group of the remaining Eucharitidae (0.98 pp; figure 1b; electronic supplementary material, S1). Eucharitidae diverged from the perilampid non-ant parasitoids approximately 85.7 Ma (95% highest posterior density interval = 63.4–110.2 Ma) and began diversifying by 72.0 Ma (53.9–92.6 Ma; figure 1c; electronic supplementary material, table S3). Our study and others support a relationship in which Eucharitidae renders Perilampidae paraphyletic [32,33]. Perilampids and eucharitids are

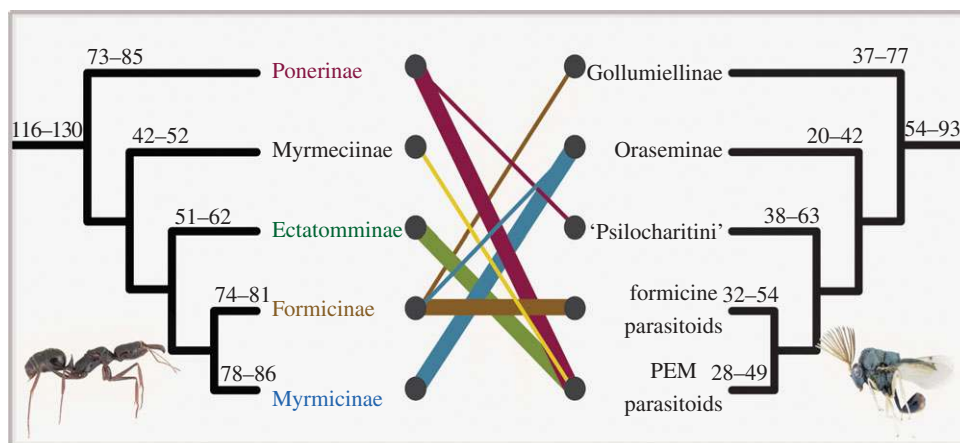


**Figure 1.** (a) Fossil-calibrated phylogeny of Eucharitidae. Two hundred and thirty-seven taxa were analysed. Terminal labels, posterior probabilities and error range of node ages found in the electronic supplementary material, figure S1. Blue star signifies eucharitid origin (stem node). Green shading on left indicates the major period of ant diversification, which coincides with the origin of their eucharitid parasitoids. 'F' symbols indicate the three fossil constraints, and 'NW' indicates that the subtending clade members are found in the New World, whereas ancestral eucharitids are Old World. Bars to the right indicate ant hosts and biogeography, with the specific ant-subfamily host indicated by abbreviation at tree terminals: E, Ectatomminae; F, Formicinae; Me, Myrmecinae; M, Myrmicinae; P, Ponerinae. Ant image (adapted from [11]). (b) Portion of tree showing age and relationships of the paraphyletic Perilampidae relative to Eucharitidae. (c) Ages of major eucharitid groups and their respective ant host subfamilies (crown ant age from Schmidt [39], remaining from Brady *et al.* [38]).

united by their common strategy of host accession via planidia, but the host association preceding Formicidae in the eucharitid ancestor remains elusive because perilampids attack a wide range of insect orders, including Coleoptera, Diptera and Hymenoptera; the hosts for *Akapala* and *Jambiya* are unknown.

Molecular dating techniques have been applied to only two chalcidoid families: Eucharitidae and the pollinating fig

wasps, Agaonidae. Our results indicate that Eucharitidae originated in the Late Cretaceous. Likewise, the most recent study from Agaonidae suggests an origin shortly prior to the Cretaceous boundary at 75.1 Ma (56.2–94.9 Ma), as inferred from 200 taxa and six genes [56]. Both Eucharitidae and Agaonidae belong to a derived clade of larger hard-bodied chalcidoid wasps [33]. Our dates provide evidence



**Figure 2.** Host–parasitoid taxonomic associations. Tanglegram simplified from analysis of 29 eucharitid genera and 23 formicid genera. Ant cladogram on left (adapted from Moreau *et al.* [37]). Thin interaction lines indicate utilization of just one host genus, thick lines indicate multiple hosts. Psilocharitini and the formicine parasitoid groups are non-monophyletic. Estimated node age ranges above branches, as in figure 1c.

for a Late Cretaceous origin for this group of related families, despite the lack of described fossils for this time period.

### (b) Cophylogeny test and ancestral host mapping

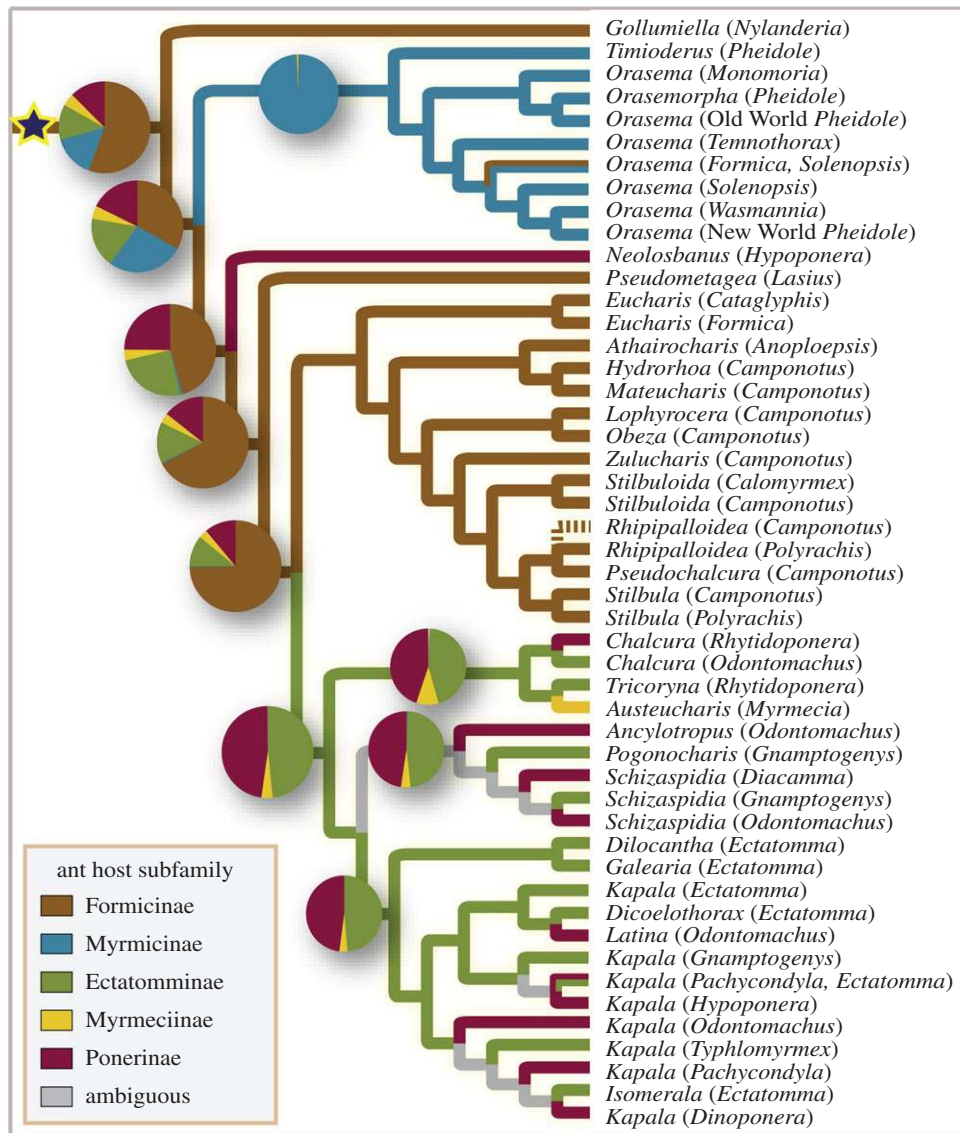
Host–parasitoid relationships at the subfamily and generic level show a conserved pattern of host use within major clades of Eucharitidae (see figures 2 and 3 and electronic supplementary material, table S1). We found that the eucharitid and ant host phylogeny were statistically more similar than expected by chance, under event-based reconstruction methods. Cophylogeny reconciliation in Jane [57] offers support for phylogenetic host tracking. Zero per cent of random sample solutions and of random parasitoid tree simulations (mean costs = 171 and 159) returned a lower cost than the original problem solution (minimum cost = 97). This provides high support ( $p < 0.01$ ) for non-random patterns of the two phylogenies. There is topological congruence, but we were unable to incorporate temporal data owing to non-overlap in host and parasitoid node ages. By the time of eucharitid crown group diversification at 72.1 Ma, most ant subfamilies were established ([37–39]; figure 1c and table 1), and there is a lack of correspondence between dates for clades of Eucharitidae and their respective ant-subfamily hosts owing to older ant ages.

The eucharitid–ant association developed during a period of high ant diversification 60–100 Ma [37]. To reconstruct historical host associations, ancestral states were calculated over a distribution of trees using BAYESTRAITS [58]. General patterns across major clades in Eucharitidae indicate a series of host jumps to a new ant subfamily and then range expansion within each group, typically extending to several host ant genera. Diverse clades of Eucharitidae also exhibit a high degree of endemism, suggesting that much of the host diversification took place after major continental dispersal routes were closed. Under parsimony, Formicinae are mapped as the ancestral host (figure 3). Bayesian ancestral reconstruction indicates uncertainty but suggests that the ancestral host was likely to be Formicinae (58%), with other ant-subfamily hosts possible at a much lower probability (less than 14%). There are several major host colonizations throughout the history of Eucharitidae. All but one ant subfamily (Myrmeciinae) were colonized prior to approximately 30 Ma. Reconstruction shows a series of shifts away from the ancestral formicine host in three wasp groups: Oraseminae, Psilocharitini and the ‘Ponerinae–

Ectatomminae–Myrmeciinae’ (PEM) parasitoids (see figure 3 and electronic supplementary material, S2). In addition, there is a host-use shift within Formicinae, from Plagiolepidini (Gollumiellinae wasp host) to Lasiini, Formicini and Camponotini (Eucharitini wasp hosts). Also within Eucharitini, a major host shift occurs in the PEM parasitoids. The ancestral host in this clade is equally likely to be Ponerinae or Ectatomminae, with one recent jump to Myrmeciinae in the Australian genus *Austeucharis* 12.9 Ma (6.6–19.8 Ma; figure 3). Ectatomminae and Ponerinae were historically treated as one subfamily (Ponerinae; [59]), but are now known to be distantly related [37,38]; they are mid- to large-bodied, ‘socially primitive’ predators in a non-phylogenetic assemblage collectively referred to as the poneromorph ants [53,59]. Myrmeciinae are also ground-nesting generalist predators/scavengers with a simple social structure [52,60]. While Myrmeciinae (*Myrmecia*) is a unique host association for one eucharitid taxon, both Ectatomminae and Ponerinae are hosts for each of the three clades attacking the PEM ants (Chalcura, Schizaspidia and Kapala clades; figure 1). Although the host associations in this terminal PEM parasitoid group are phylogenetically diverse, the ant hosts share similar morphology and behaviour.

### (c) Eucharitidae diversification and biogeography

Under a homogeneous birth–death model, there are potentially two rate shifts in Eucharitidae as compared with the background ( $r = 0.0307$ ). Although not necessarily causative, life-history or geographical transitions can be correlated to diversification rate shifts. One rate increase occurs in Eucharitini, excluding *Pseudometagea* ( $r = 0.0988$ ). The group encompassed in the rate transition includes both formicine and PEM parasitoids. These increases coincide with eucharitid expansion on speciose groups of ants, including the worldwide ponerine, ectatommine and camponotine ants (see figure 3 and electronic supplementary material, S2 and table S1). Members of the Eucharitini switched to attacking ants with their pupae in cocoons, and these wasps also exhibit an extraordinary amount of morphological variation [55] in characteristics of body size, antennal structure and thoracic spines. The second diversification rate increase is at the base of the New World *Orasema* ( $r = 0.1902$ ). As in the Old World *Oraseminae* genera, New World *Orasema* are able to successfully exploit



**Figure 3.** Ancestral state reconstruction. Forty-eight terminal taxa in analysis, with each genus of ant host represented by a parasitoid taxon (see the electronic supplementary material, table S1). Dashed line indicates the record was included for illustrative purposes (taxon not in data matrix). Pie charts at selected nodes display proportional probability under Bayesian inference. Coloured branches show parsimony reconstruction. Terminals labelled by eucharitid genus, with ant genera in parenthesis.

the hyperdiverse *Pheidole* [61], but they also parasitize five additional ant genera in the Nearctic and Neotropics, including the fire ants *Solenopsis* and *Wasmannia* [29,36,62].

Based on reconstruction of ancestral areas using the dispersal-extinction-cladogenesis model in Lagrange [63,64], our results support an origin of Eucharitidae in the Old World. Stem eucharitids have a relative probability of 20.2 per cent of originating in ancient Australia (locality of sister group *Akapala*), and the crown Eucharitidae have the highest probability of their ancestral area being the Indo-Pacific region, at 24.6 per cent. For each, there were multiple biogeographic areas included within the 2 log likelihood unit cut-off [64], indicating uncertainty in reconstruction. The major eucharitid clades, excluding the Old World Gollumiellinae, are distributed in both the Old and New World, and ancestral area reconstruction suggests members of the myrmecine, formicine and PEM parasitoid groups invaded the New World in five separate events (figure 1a). Adult eucharitids typically live only a few days outside the nest, and likely could not undergo long-distance dispersal [18]. The low probability of chance dispersal is supported by a high degree of

geographical endemism for most genera and clades [52], although we know of one case in the PEM parasitoids in which a single-derived species (*Kapala ivorensis*) of the diverse Neotropical *Kapala* clade colonized sub-Saharan Africa and Madagascar, presumably 1.4 Ma (0.5–2.6 Ma; figure 1a; electronic supplementary material, S1; bottom branches). This is the only instance of a dispersal event from the New to the Old World.

Ants are incredibly diverse in the Neotropics [65], and the New World ant groups evolved without parasitism pressure from eucharitids until approximately 43 Ma. At this point, we hypothesize multiple dispersals of eucharitid wasps from the Old World into the New World. Lagrange reconstruction points to South American ancestral areas for three New World clades (*Obeza* + *Lophyrocera*, *Pseudochalcura*, and the 13 genera comprising the *Kapala* Clade), whereas two (*Pseudometagea* and New World *Orasema*) exhibit a North American ancestral area.

Our evidence points to the possibility of multiple dispersal mechanisms and routes for different groups to colonize New World ants. The five dispersals potentially occurred throughout a time period greater than 20 Myr (approx. 20–43 Ma), as

global landmasses and climate were changing [66,67]. Although land routes were intermittently open for eucharitid passage, long-distance oceanic rafting cannot be ruled out. Both North and South American ancestral areas are hypothesized, indicating a possibility for both northern and southern dispersal. *Orasema* may have used a northern dispersal route. The age of the New World *Orasema* stem at approximately 20–23 Ma suggests this dispersal likely overlapped with the Late Oligocene warming, when arctic climate was temperate [66,68]. Remarkably, the major Old World Oraseminae ant host, *Pheidole*, may have moved in the opposing direction approximately 30 Ma, dispersing from the New to the Old World [61].

It has also been shown that ants were dispersing worldwide during the time of eucharitid diversification [61,69] and were likely using Northern Beringian routes to move from the Old World to New 10–30 Ma [70], and southern land routes to move from the New to Old World approximately 30 Ma [71]. Through each movement to the New World, despite the abundance of available ant taxa, eucharitids remained constrained to the same ant subfamilies as their Old World relatives. Thus, established host constraints remained in place despite the availability of new host niches.

#### (d) Ant–eucharitid associations

It has been postulated that the coevolution of ants and their associates follows a gradual progression from predaceous hostile invader to the eventual integration of the species into the ant colony [12], with parasitoids representing the ultimate nest symbionts [72]. In the case of Eucharitidae, however, they successfully colonized Formicidae directly as brood parasitoids via planidial larvae shared with perilampid relatives.

Eucharitidae exhibit a general trend of ant subfamily colonization (host-switching) occurring infrequently at an early time period, followed by high host conservatism (phylogenetic affinity) at the ant-subfamily level in extant lineages. In the PEM parasitoids attacking three different subfamilies, these eucharitids seem to be successful on ants with a similar ecological niche as opposed to success owing to a taxonomic affinity (figure 3). These findings are in agreement with previous research on arthropod host–parasitoid or parasite associations concluding that host use is not determined by host phylogeny [5,10,73] as had been hypothesized in various historical studies [1,2,10].

If ecological similarity rather than host phylogeny accounts for the high amount of host-switching within the PEM parasitoids, this leads to the hypothesis that parasitoid host range may be limited by ecological constraints [73], and host switches shaped by ecological fitting [74,75], where organisms can succeed in a novel environment owing to their suite of traits previously evolved. Eucharitids potentially have succeeded in diversifying on many ant taxa owing to the mechanism by which the planidia unite with the hosts and subsequently by how immatures and adults mimic host hydrocarbon profiles [20]. Evidence exists of other myrmecophiles that facilitate shifts among different ant hosts by exploiting communication codes [72].

### 3. Conclusions

Eucharitids colonized ants by approximately 72 Ma and have since proliferated worldwide and are known to parasitize 23 genera in 12 tribes. These wasps are able to break the

communication codes used in kin recognition among colony members to successfully escape harm as both immatures and adults while in the ant nest. Eucharitidae use ants across the phylogeny, yet there are still empty niches in speciose or resource-rich ant groups, namely the dolichoderine ants, fungus ants (attines) and the driver and army ants (dorylomorphs) which typically support diverse symbionts and myrmecophiles that need the ‘protection’ of large, long-lived colonies [13,17].

Eucharitidae are abundant and diverse but the ecological effects they have on their hosts are still not quantified, though adults and larvae have been recorded in nests year-round and can reach nest parasitism rates of greater than 25 per cent of pupae parasitized [18,76]. Their success suggests that they could form a promising model for the investigation of parasitoid impact on ant colonies [36]. The major eucharitid clades display phylogenetic conservatism through a pattern of ancient novel host colonization and subsequent host tracking; this lack of strict cophylogeny coincides with other documented host–parasitoid relationships [10]. Together, the evolutionary and biogeographic histories of ant and eucharitid have produced the unique association where hundreds of diverse parasitoid species have profited by proliferating on a eusocial host family.

## 4. Material and methods

### (a) Taxon sampling

The molecular dataset includes 237 specimens, with dense taxonomic sampling across Eucharitidae comprising 44 of the 53 eucharitid genera from 41 countries. Eight taxa are outgroup Chalcidoidea, 34 are Perilampidae and 195 are Eucharitidae (see the electronic supplementary material, table S2). Five gene regions were sequenced: 18S, 28S-D2 and 28S-D3-D5 (nuclear), and COI and COII (mitochondrial; electronic supplementary material, text S1). Genbank accession nos. are given in the electronic supplementary material, table S2, and the aligned matrix is deposited in the Dryad Depository ([datadryad.org](http://datadryad.org); doi:10.5061/dryad.qn57t). Summary statistics and primers are compiled for each gene region in the electronic supplementary material, tables S4 and S5. Specimen images can be found on Morphbank ([morphbank.net](http://morphbank.net)) under collection no. 816728.

### (b) Phylogenetic analyses, divergence dating and rate diversification

Gene regions were partitioned into three unlinked groups: 18S, 28S-D2–D5 and COI + COII (electronic supplementary material, table S4). To streamline computation and tree-drawing, monophyly was enforced for Perilampidae + Eucharitidae because this has been supported in previous studies [27,32,33]. A birth–death process was used for the tree priors, using a starting tree generated from the same dataset under a Yule model. The trees were calculated under an uncorrelated lognormal relaxed clock.

Three Baltic amber fossils were used to calibrate nodes. (i) *Monodontomerus* sp. (Torymidae; [77]) was used to constrain the crown outgroup Torymidae. (ii) *Perilampus pisticus* (Perilampidae: Perilampinae; [31]) was used to calibrate the crown node at the base of the present-day paraphyletic *Perilampus*. (iii) *Palaeocharis rex* (Eucharitidae: Eucharitinae; [31]), sister to present-day *Psilocharis*, was used to constrain the node of the stem of *Psilocharis*. The mean date of the Baltic amber was estimated at  $44.1 \pm 1.1$  Myr [78], corresponding to the age of the fossil-rich blue earth stratigraphic layer. To accommodate uncertainty in the date, the prior

for all three nodes was specified as a lognormal distribution at 44.1, mean 8.08, offset 39.2 (in real space), which translates to a 95% probability range of 40.2–64.6 Myr for the included fossils, with the highest prior probability at 44.1 Ma.

In BEAST v. 1.6.2 [79], two Markov chain Monte Carlo (MCMC) chains were run to 200 million generations, logging parameters every 20 000. We also ran an empty alignment to verify that the data were driving the pp distributions [80]. Subsequent to the phylogenetic analysis, TRACER v. 1.5.0 [81] confirmed the effective sample size (ESS) of the posterior and all major clades reached greater than 200. LOGCOMBINER v. 1.6.2 and TREEANNOTATOR v. 1.6.2 were used to combine the trees from the two runs and then obtain a single tree of highest clade probabilities. A total of 10 002 trees were removed as burnin, for a final distribution of 10 000 trees.

Eucharitidae clade diversification was analysed using turboMEDUSA [82] in R (v. 2.13.1, R Development Core Team 2011). MEDUSA (modelling evolutionary diversification using stepwise Akaike information criterion (AIC)) uncovers diversification rate shifts in the phylogeny by fitting alternative models to the input chronogram [83]. From an initial model specifying one rate across the phylogeny, rate change breakpoints are inserted successively at internal nodes until the optimal corrected AIC is reached. We included 68 genera in the eucharitid + perilampid chronogram and specified the estimated species richness of each genus; required if the tree is not completely sampled. The projected diversity values were from Heraty [55] and the Universal Chalcidoidea Database [84]. The input combination of phylogeny and taxonomy is used to reveal clades that deviate statistically from the number of species expected owing to age of the group.

### (c) Cophylogenetic reconstruction, character mapping and biogeography

Cophylogeny reconstruction methods were used to explore the possibility of parallel patterns of phylogeny between host and parasitoid. We used Jane 4 [57] for reconstruction and statistical analysis. Jane 4 implements event-cost methods and a genetic algorithm to map the parasite tree to the host tree as based on the ant phylogeny of Moreau *et al.* [37]. We reduced the datasets of ants and eucharitids down to the genera that had a host record pairing it to the opposing family, resulting in 23 host genera and 29 parasitoid genera. The cost matrix used the following settings (cospeciation = 0, duplication, loss, failure to diverge = 1 and duplication + host switch = 2), and the analysis was run to 200 generations with a population size of 400. We could not implement timing capabilities for incorporating temporal congruence owing to the large gap in origin of host and parasitoid species; host switches for nodes in different time zones are not permitted in Jane. Statistical significance was assessed by randomly permutating the tree tip pairings and re-assessing the cost distribution to determine if the input pairings remain as

the lowest-cost scenario. Two statistical analyses were run to a sample size of 200: (i) 'random tip mapping' of the two phylogenies and (ii) 'random parasite tree' calculation at beta = -1.0. A result of less than 5 per cent of random solutions as better than the observed cost total is strong evidence for cophylogeny [85].

Ant host associations are available for 29 of the 44 eucharitid genera in the dataset (electronic supplementary material, table S1). BAYES TRAITS v.1.0 [58] MultiState analysis was used for reconstruction of an ancestral character state at specified nodes. A fully Bayesian implementation was used, with a distribution of 10 000 trees (from the dating analysis). The trees were pruned to 48 taxa, which represented the unique ant genera records for each wasp genus available in the molecular phylogeny. Each eucharitid terminal was coded by ant subfamily, for a total of five discrete states. Analyses were run to 200 million generations, sampling every 20 000, discarding the first 50 million generations. We used the reversible-jump MCMC option, using an exponentially distributed prior and a uniform hyperprior drawn from the interval [0,10], with an additional parameter of a rate deviation of 0.015 to ensure that acceptance rates were above 20 per cent, which did result in mean acceptance rate of 24.5 per cent of the 3000 post-burnin trees. TRACER v. 1.5.0 was used to confirm ESS greater than 200 and to obtain the mean output value for all five subfamily probabilities at each node of interest. In addition, MESQUITE v. 2.73 [86] was used to trace host associations on the topology using parsimony reconstruction.

For the reconstruction of ancestral areas, we used LAGRANGE v. 20120508 (likelihood analysis of geographical range evolution; [63,64]), which implements a stochastic model of range evolution, incorporating dispersal, extinction and cladogenesis. This program uses a given set of areas with their connections (dispersal routes) in conjunction with an input chronogram to estimate the ancestral area likelihoods at each node of the tree [63] with a script assembled via the online configurator. Seven areas were recognized: (i) North and Central America including Caribbean, (ii) South America and Lesser Antilles, (iii) Ethiopian, (iv) Malagasy, (v) Indo-Pacific and (vi) Australian, following Heraty [55]. However, Central America/Caribbean is here included with North America instead of with South America as in [55] owing to its historic connection with the northern landmass. We developed dispersal constraints for four time periods (electronic supplementary material, text S2). All 229 terminals of Perilampidae and Eucharitidae were coded for geographical range according to specimen collection locality.

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## References

- Brooks DR. 1985 Historical ecology: a new approach to studying the evolution of ecological associations. *Ann. Mo. Botanical Garden* **72**, 660–680. (doi:10.2307/2399219)
- Klassen GJ. 1992 Coevolution: a history of the macroevolutionary approach to studying host-parasite associations. *J. Parasitol.* **78**, 573–587. (doi:10.2307/3283532)
- Poulin R. 1997 Species richness of parasite assemblages: evolution and patterns. *Annu. Rev. Ecol. Syst.* **28**, 341–358. (doi:10.1146/annurev.ecolsys.28.1.341)
- Darwin C. 1859 *On the origin of species. A facsimile of the first edition*, 513 p. Cambridge, MA: Harvard University Press.
- Shaw SR. 1988 Euphorine phylogeny: the evolution of diversity in host-utilization by parasitoid wasps (Hymenoptera: Braconidae). *Ecol. Entomol.* **13**, 323–335. (doi:10.1111/j.1365-2311.1988.tb00363.x)
- Smith MA, Rodriguez JJ, Whitfield JB, Deans AR, Janzen DH, Hallwachs W, Hebert PD. 2008 Extreme diversity of tropical parasitoid wasps exposed by iterative integration of natural history, DNA barcoding, morphology, and collections. *Proc. Natl Acad. Sci. USA* **105**, 12 359–12 364. (doi:10.1073/pnas.0805319105)
- McLeish MJ, van Noort S, Tolley KA. 2010 Parasitoid fig-wasp evolutionary diversification and variation in ecological opportunity. *Mol. Ecol.* **19**, 1483–1496. (doi:10.1111/j.1365-294X.2010.04583.x)



8. Elizalde L, Folgarait PJ. 2010 Host diversity and environmental variables as determinants of the species richness of the parasitoids of leaf-cutting ants. *J. Biogeogr.* **37**, 2305–2316. (doi:10.1111/j.1365-2699.2010.02361.x)
9. Eggleton P, Gaston KJ. 1990 'Parasitoid' species and assemblages: convenient definitions or misleading compromises? *Oikos* **59**, 417–421. (doi:10.2307/3545155)
10. Whitfield JB. 2003 Phylogenetic insights into the evolution of parasitism in Hymenoptera. In *The evolution of parasitism—a phylogenetic perspective* (ed. D Littlewood), pp. 69–101. Amsterdam, The Netherlands: Elsevier.
11. Wilson EO. 2008 One giant leap: how insects achieved altruism and colonial life. *BioScience* **58**, 17. (doi:10.1641/b580106)
12. Wheeler WM. 1928 *The social insects*, 378 p. New York, NY: Harcourt Brace and Company.
13. Hölldobler B, Wilson EO. 1990 *The ants*. Cambridge, MA: Harvard University Press.
14. Wojcik DP. 1989 Behavioral interactions between ants and their parasites. *Fla. Entomol.* **72**, 43–51. (doi:10.2307/3494966)
15. Schmid-Hempel P. 1998 *Parasites in social insects*, p. 409. Princeton, NJ: Princeton University Press.
16. Heraty J. 2009 Parasitoid biodiversity and insect pest management. In *Insect biodiversity: science and society* (eds RG Foottit, PH Alder), pp. 445–462. Hague, The Netherlands: Springer.
17. Wilson EO. 1971 *The insect societies*, 548 p. Cambridge, MA: Belknap Press.
18. Clausen CP. 1923 The biology of *Schizaspidia tenuicornis* Ashm., a eucharid parasite of *Camponotus*. *Ann. Entomol. Soc. Am.* **16**, 195–219.
19. Ayre GL. 1962 *Pseudometagea schwarzii* (Ashm.) (Eucharitidae: Hymenoptera), a parasite of *Lasius neoniger* Emery (Formicidae: Hymenoptera). *Can. J. Zool.* **40**, 157–164. (doi:10.1139/z62-020)
20. Vander Meer RK, Jouvenaz DP, Wojcik DP. 1989 Chemical mimicry in a parasitoid (Hymenoptera: Eucharitidae) of fire ants (Hymenoptera: Formicidae). *J. Chem. Ecol.* **15**, 2247–2261. (doi:10.1007/bf01014113)
21. Howard RW, Pérez-Lachaud G, Lachaud JP. 2001 Cuticular hydrocarbons of *Kapala sulcifacies* (Hymenoptera: Eucharitidae) and its host, the ponerine ant *Ectatomma ruidum* (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am.* **94**, 707–716. (doi:10.1603/0013-8746(2001)094[0707:choksh]2.0.co;2)
22. Buys SC, Cassaro R, Salomon D. 2010 Biological observations on *Kapala* Cameron 1884 (Hymenoptera Eucharitidae) in parasitic association with *Dinoponera lucida* Emery 1901 (Hymenoptera Formicidae) in Brazil. *Trop. Zool.* **23**, 29–34.
23. Das GM. 1963 Preliminary studies on the biology of *Oraesema assectator* Kerrich (Hym., Eucharitidae), parasitic on *Pheidole* and causing damage to leaves of tea in Assam. *Bull. Entomol. Res.* **54**, 373–378. (doi:10.1017/S0007485300048884)
24. Heraty JM, Darling DC. 1984 Comparative morphology of the planidial larvae of Eucharitidae and Perilampidae (Hymenoptera: Chalcidoidea). *Syst. Entomol.* **9**, 309–328. (doi:10.1111/j.1365-3113.1984.tb00056.x)
25. Clausen CP. 1940 The oviposition habits of the Eucharitidae. *J. Wash. Acad. Sci.* **30**, 504–516.
26. Wilson TH, Cooley TA. 1972 A chalcidoid planidium and an entomophilic nematode associated with the Western Flower Thrips. *Ann. Entomol. Soc. Am.* **65**, 414–418.
27. Heraty J, Hawks D, Kostecki JS, Carmichael A. 2004 Phylogeny and behaviour of the Gollumiellinae, a new subfamily of the ant-parasitic Eucharitidae (Hymenoptera: Chalcidoidea). *Syst. Entomol.* **29**, 544–559. (doi:10.1111/j.0307-6970.2004.00267.x)
28. Clausen CP. 1941 The habits of the Eucharitidae. *Psyche* **48**, 57–69. (doi:10.1155/1941/21539)
29. Heraty JM. 1994 Biology and importance of two eucharitid parasites of *Wasmannia* and *Solenopsis*. In *Exotic ants: biology, impact and control of introduced species* (ed. D Williams), p. 332. Boulder, CO: Westview Press.
30. Lachaud J-P, Perez-Lachaud G, Heraty JM. 1998 Parasites associated with the ponerine ant *Ectatomma tuberculatum* (Hymenoptera: Formicidae): first host record for the genus *Dilocantha* (Hymenoptera: Eucharitidae). *Fla. Entomol.* **81**, 570–574. (doi:10.2307/3495962)
31. Heraty JM, Darling DC. 2009 Fossil Eucharitidae and Perilampidae (Hymenoptera: Chalcidoidea) from Baltic amber. *Zootaxa* **2306**, 1–16.
32. Munro JB, Heraty JM, Burks R, Hawks D, Mottern J, Cruaud A, Rasplus J-Y, Jansta P. 2011 A molecular phylogeny of the Chalcidoidea (Hymenoptera). *PLoS ONE* **6**, 1–27. (doi:10.1371/journal.pone.0027023)
33. Heraty JM *et al.* 2013 A phylogenetic analysis of the megadiverse Chalcidoidea (Hymenoptera). *Cladistics*. (doi:10.1111/cla.12006)
34. Darling DC. 1992 The life history and larval morphology of *Aperilampus* (Hymenoptera: Chalcidoidea: Philomidinae), with a discussion of the phylogenetic affinities of the Philomidinae. *Syst. Entomol.* **17**, 331–339. (doi:10.1111/j.1365-3113.1992.tb00554.x)
35. Smith HS. 1912 The chalcidoid genus *Perilampus* and its relations to the problem of parasite introduction. *USDA Tech. Ser.* **19**, 33–69.
36. Lachaud J-P, Pérez-Lachaud G. 2012 Diversity of species and behavior of Hymenopteran parasitoids of ants: a review. *Psyche* **2012**, 1–24. (doi:10.1155/2012/134746)
37. Moreau CS, Bell CD, Vila R, Archibald SB, Pierce NE. 2006 Phylogeny of the ants: diversification in the age of angiosperms. *Science* **312**, 101–104. (doi:10.1126/science.1124891)
38. Brady SG, Schultz TR, Fisher BL, Ward PS. 2006 Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proc. Natl Acad. Sci. USA* **103**, 18 172–18 177. (doi:10.1073/pnas.0605858103)
39. Schmidt CA. 2009 Molecular phylogenetics and taxonomic revision of ponerine ants (Hymenoptera: Formicidae: Ponerinae). PhD thesis, University of Arizona, Tucson, AZ, USA.
40. Navarrete-Heredia JL. 2001 Beetles associated with *Atta* and *Acromyrmex* ants (Hymenoptera: Formicidae: Attini). *Trans. Am. Entomol. Soc.* **127**, 381–429.
41. Shingleton AW, Stern DL. 2003 Molecular phylogenetic evidence for multiple gains or losses of ant mutualism within the aphid genus *Chaitophorus*. *Mol. Phylogenet. Evol.* **26**, 26–35. (doi:10.1016/S1055-7903(02)00328-7)
42. Megens H-J, De Jong R, Konrad F. 2005 Phylogenetic patterns in larval host plant and ant association of Indo-Australian Arhopalini butterflies (Lycaenidae: Theclinae). *Biol. J. Linn. Soc.* **84**, 225–241. (doi:10.1111/j.1095-8312.2005.00426.x)
43. Komatsu T, Maruyama M, Ueda S, Itino T. 2008 mtDNA phylogeny of Japanese ant crickets (Orthoptera: Myrmecophilidae): diversification in host specificity and habitat use. *Sociobiology* **52**, 1–12.
44. Grimaldi D, Engel MS. 2005 *Evolution of the insects*, 755 p. Hong Kong: Cambridge University Press.
45. LaPolla JS, Dlussky GM, Perrichot V. 2013 Ants and the fossil record. *Annu. Rev. Entomol.* **58**, 609–630. (doi:10.1146/annurev-ento-120710-100600)
46. Dlussky GM. 1996 Ants (Hymenoptera: Formicidae) from Burmese amber. *Paleontol. J.* **30**, 449–454.
47. Grimaldi D, Agosti D, Carpenter JM. 1997 New and rediscovered primitive ants (Hymenoptera: Formicidae) in Cretaceous amber from New Jersey, and their phylogenetic relationships. *Am. Mus. Novit.* **3208**, 1–43.
48. Archibald SB, Cover SP, Moreau CS. 2006 Bulldog ants of the Eocene Okanagan Highlands and history of the subfamily (Hymenoptera: Formicidae: Myrmeciinae). *Ann. Entomol. Soc. Am.* **99**, 487–523. (doi:10.1603/0013-8746(2006)99[487:BAOTEJ]2.0.CO;2)
49. Engel MS, Grimaldi DA. 2005 Primitive new ants in Cretaceous amber from Myanmar, New Jersey, and Canada (Hymenoptera: Formicidae). *Am. Mus. Novit.* **3485**, 1–24. (doi:10.1206/0003-0082(2005)485[0001:PNAICA]2.0.CO;2)
50. Grimaldi D, Agosti D. 2000 A formicine in New Jersey Cretaceous amber (Hymenoptera: Formicidae) and early evolution of the ants. *Proc. Natl Acad. Sci. USA* **97**, 13 678–13 683. (doi:10.1073/pnas.240452097)
51. Poinar Jr G, Archibald B, Brown A. 1999 New amber deposit provides evidence of early Paleogene extinctions, paleoclimates, and past distributions. *Can. Entomol.* **131**, 171–177. (doi:10.4039/Ent131171-2)
52. Ward PS. 2010 Taxonomy, phylogenetics, and evolution. In *Ant ecology* (eds L Lach, CL Parr, KL Abbot), pp. 3–17. Oxford, UK: Oxford University Press.
53. Wilson EO, Hölldobler B. 2005 The rise of the ants: a phylogenetic and ecological explanation. *Proc. Natl Acad. Sci. USA* **102**, 7411–7414. (doi:10.1073/pnas.0502264102)
54. Schmidt AR *et al.* 2010 Cretaceous African life captured in amber. *Proc. Natl Acad. Sci. USA* **107**, 7329–7334. (doi:10.1073/pnas.1000948107)

55. Heraty JM. 2002 *A revision of the genera of Eucharitidae (Hymenoptera: Chalcidoidea) of the world*, 359 p. Gainesville, FL: American Entomological Institute.
56. Cruaud A *et al.* 2012 An extreme case of plant–insect co-diversification: figs and fig-pollinating wasps. *Syst. Biol.* **61**, 1029–1047. (doi:10.1093/sysbio/sys068)
57. Conow C, Fielder D, Ovadia Y, Libeskind-Hadas R. 2010 Jane: a new tool for the cophylogeny reconstruction problem. *Algorithms Mol. Biol.* **5**, 16. (doi:10.1186/1748-7188-5-16)
58. Pagel M, Meade A, Barker D. 2004 Bayesian estimation of ancestral character states on phylogenies. *Syst. Biol.* **53**, 673–684. (doi:10.1080/10635150490522232)
59. Bolton B. 2003 *Synopsis and classification of Formicidae*. Gainesville, FL: American Entomological Institute.
60. Hasegawa E, Crozier RH. 2006 Phylogenetic relationships among species groups of the ant genus *Myrmecia*. *Mol. Phylogenet. Evol.* **38**, 575–582. (doi:10.1016/j.ympev.2005.09.021)
61. Moreau CS. 2008 Unraveling the evolutionary history of the hyperdiverse ant genus *Pheidole* (Hymenoptera: Formicidae). *Mol. Phylogenet. Evol.* **48**, 224–239. (doi:10.1016/j.ympev.2008.02.020)
62. Varone L, Heraty JM, Calcaterra LA. 2010 Distribution, abundance and persistence of species of *Orasema* (Hym: Eucharitidae) parasitic on fire ants in South America. *Biol. Control* **55**, 72–78. (doi:10.1016/j.biocontrol.2010.06.017)
63. Ree RH, Moore BR, Webb CO, Donoghue MJ. 2005 A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution* **59**, 2299–2311. (doi:10.1554/05-172.1)
64. Ree RH, Smith SA. 2008 Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Syst. Biol.* **57**, 4–14. (doi:10.1080/10635150701883881)
65. Moreau CS. 2011 What do molecular clocks tell us about the evolution of ants? *Am. Entomol.* **57**, 52–53.
66. Zachos J, Pagani M, Sloan L, Thomas E, Billups K. 2001 Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**, 686–693. (doi:10.1126/science.1059412)
67. Scotese CR. 2003 *PALEOMAP Project*. See [www.scotese.com](http://www.scotese.com) (accessed September 2012)
68. Brandley MC, Wang Y, Guo X, de Oca AN, Fera-Ortiz M, Hikida T, Ota H. 2011 Accommodating heterogeneous rates of evolution in molecular divergence dating methods: an example using intercontinental dispersal of *Plestiodon* (*Eumeces*) lizards. *Syst. Biol.* **60**, 3–15. (doi:10.1093/sysbio/syq045)
69. Branstetter MG. 2012 Origin and diversification of the cryptic ant genus *Stenamamma* Westwood (Hymenoptera: Formicidae), inferred from multilocus molecular data, biogeography and natural history. *Syst. Entomol.* **37**, 478–496. (doi:10.1111/j.1365-3113.2012.00624.x)
70. Jansen G, Savolainen R, Vepsäläinen K. 2010 Phylogeny, divergence-time estimation, biogeography and social parasite–host relationships of the Holarctic ant genus *Myrmica* (Hymenoptera: Formicidae). *Mol. Phylogenet. Evol.* **56**, 294–304. (doi:10.1016/j.ympev.2010.01.029)
71. Ward PS, Brady SG, Fisher BL, Schultz TR. 2010 Phylogeny and biogeography of dolichoderine ants: effects of data partitioning and relict taxa on historical inference. *Syst. Biol.* **59**, 342–362. (doi:10.1093/sysbio/syq012)
72. Kistner DH. 1979 *Social and evolutionary significance of social insect symbionts*, p. 437 New York, NY: Academic Press.
73. Klimov PB, O'Connor BM, Knowles LL. 2007 Museum specimens and phylogenies elucidate ecology's role in coevolutionary associations between mites and their bee hosts. *Evolution* **61**, 1368–1379. (doi:10.1111/j.1558-5646.2007.00119.x)
74. Janzen DH. 1985 On ecological fitting. *Oikos* **45**, 308–310. (doi:10.2307/3565565)
75. Harvey JA, Ximenez de Embun MG, Bukovinsky T, Gols R. 2012 The roles of ecological fitting, phylogeny and physiological equivalence in understanding realized and fundamental host ranges in endoparasitoid wasps. *J. Evol. Biol.* **25**, 2139–2148. (doi:10.1111/j.1420-9101.2012.02596.x)
76. Pérez-Lachaud G, López-Méndez JA, Beugnon G, Winterton P, Lachaud J-P. 2010 High prevalence but relatively low impact of two eucharitid parasitoids attacking the Neotropical ant *Ectatomma tuberculatum* (Olivier). *Biol. Control* **52**, 131–139. (doi:10.1016/j.biocontrol.2009.10.016)
77. Brues CT. 1923 Some new fossil parasitic Hymenoptera from Baltic amber. *Proc. Am. Acad. Arts Sci.* **58**, 327–346. (doi:10.2307/20025999)
78. Ritzkowski S. 1997 K-Ar-Altersbestimmungen der bernsteinführenden sedimente des Samlandes (Paläogen, Bezirk Kaliningrad). *Metalla, Sonderheft* **66**, 19–23.
79. Drummond AJ, Rambaut A. 2007 BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol. Biol.* **7**, 214. (doi:10.1186/1471-2148-7-214)
80. Sanders KL, Lee MS. 2007 Evaluating molecular clock calibrations using Bayesian analyses with soft and hard bounds. *Biol. Lett.* **3**, 275–279. (doi:10.1098/rsbl.2007.0063)
81. Rambaut A, Drummond AJ. 2007 Tracer v1.5. See [beast.bio.ed.ac.uk/Tracer](http://beast.bio.ed.ac.uk/Tracer) (accessed August 2010)
82. Harmon LJ, Rabosky DL, FitzJohn RG, Brown JW. 2011 turboMEDUSA. See [webpages.uidaho.edu/~lukeh/software/software](http://webpages.uidaho.edu/~lukeh/software/software) (accessed July 2011)
83. Alfaro ME, Santini F, Brock C, Alamillo H, Dornburg A, Rabosky DL, Carnevale G, Harmon LJ. 2009 Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proc. Natl Acad. Sci. USA* **106**, 13 410–13 414. (doi:10.1073/pnas.0811087106)
84. Noyes J. 2012 Universal Chalcidoidea database. The Natural History Museum. See [nhm.ac.uk/research-curation/research/projects/chalcidoids](http://nhm.ac.uk/research-curation/research/projects/chalcidoids) (accessed August 2011)
85. Libeskind-Hadas R. 2011 Figs, wasps, gophers, and lice: a computational exploration of coevolution. In *Bioinformatics for biologists* (eds P Pevzner, R Shamir), pp. 227–247. Cambridge, UK: Cambridge University Press.
86. Maddison WP, Maddison DR. 2010 Mesquite: a modular system for evolutionary analysis, v2.73. See [mesquiteproject.org](http://mesquiteproject.org).

## Electronic Supplementary Information

### Text S1.

#### **DNA extraction, sequencing, and alignment:**

Fresh or dried museum specimens were utilized for DNA extraction. Chelex + proteinase-K extractions were performed [1] using non-destructive sampling to preserve the integrity of the wasp for retainment as a voucher specimen. Portions of five gene regions were amplified: 18S, 28S-D2, 28S-D3-D5, COI, and COII; primers are reported in Table S5. Qiagen (Valencia, CA) reagents were used for PCR; each 10 $\mu$ L reaction contained: 2.0  $\mu$ L buffer, 0.4 $\mu$ L dNTPs, 0.5 $\mu$ L forward and reverse primer, 0.5 $\mu$ L Taq polymerase, 4.0 $\mu$ L Q solution [replaced with water in COI & COII reactions], and 11.2 $\mu$ L water. PCR profiles followed the format: 3 min at 93°C, 35 cycles of 93°C for 15 sec, 46°C for 45 sec, and 68°C for 45 sec, ending with 68°C for 7 min. For COII amplification, all temperatures and durations were increased slightly. DNA templates were prepared using GeneClean (MP Biomedicals, Salon, Ohio) and subsequently outsourced to either University of California Riverside or University of San Diego facilities for sequencing. Sequencher 4.8 (Gene Codes Corp, Ann Arbor, MI) was used to edit chromatograms to final sequences; primers were not included in the final sequence contigs. DNA sequences have been deposited in Genbank.

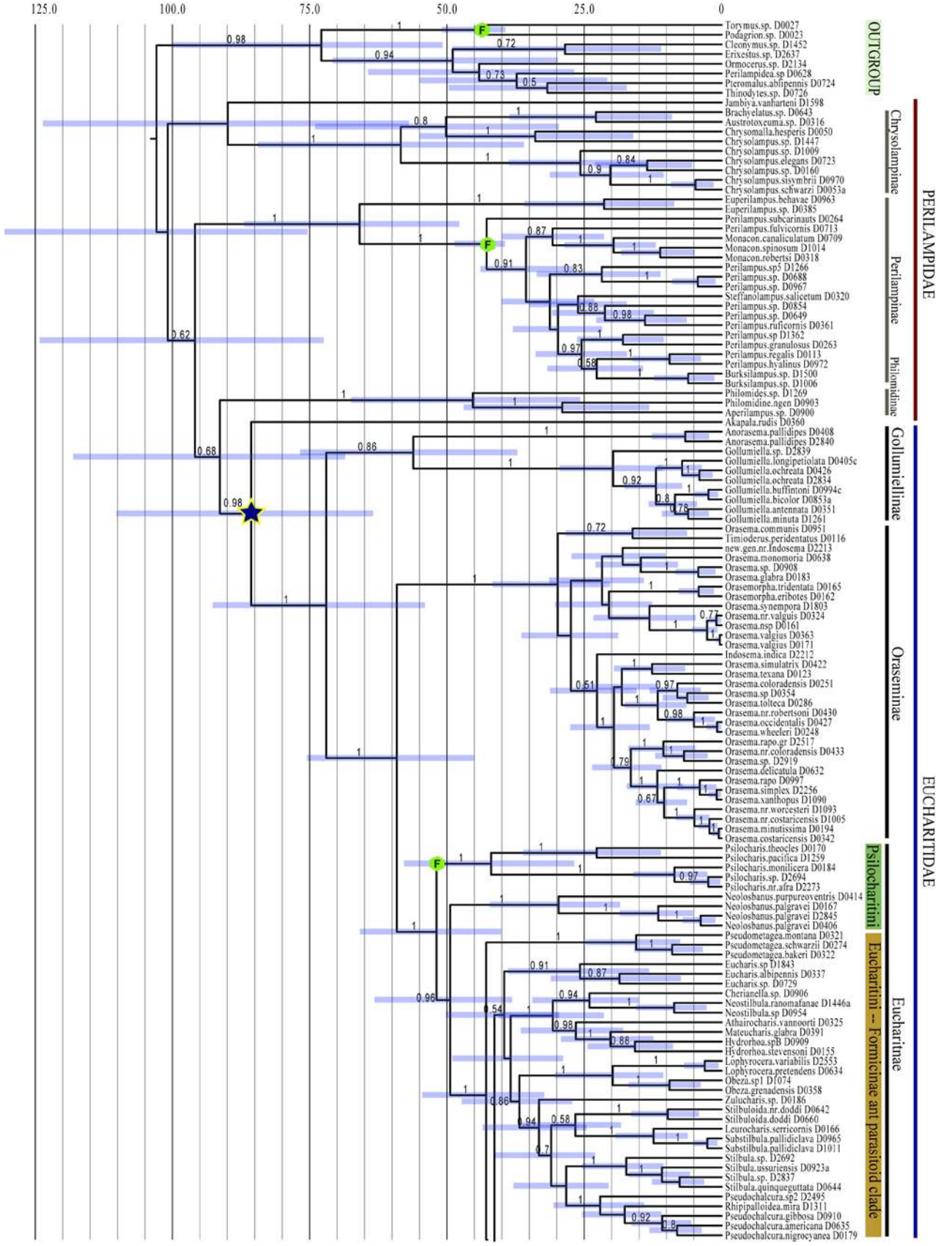
Individual genes were aligned first using the online version of MUSCLE as a first pass to remove taxa in the matrix having no data, then genes were aligned using the MAFFT [2] online server. For nuclear ribosomal genes, we applied the E-INS-i algorithmic strategy under default settings, and mitochondrial genes were aligned using the G-INS-I strategy under default settings. We used a limited number of manual adjustments for egregious alignment errors. SequenceMatrix 1.7.7 [3] was used to concatenate genes with terminal gaps coded as missing (data lost due to amplification and sequencing). Nearly all taxa included in the molecular matrix have data for at least 2 of the 5 genes (Table S3). Gene region substitution models were based on results from jModelTest [4]. The aligned concatenated matrix was submitted to Dryad (datadryad.org; doi:10.5061/dryad.qn57t).

The majority of specimens are deposited at the University of California, Riverside. Most specimens or their secondary (representative) vouchers have been imaged and are available through Morphbank ([www.morphbank.net](http://www.morphbank.net)) under collection reference number 816728. 482 new sequence fragments were deposited in Genbank; accession numbers are found in Table S2.

**Text S2.**

**LAGRANGE [5, 6] dispersal constraints.** Dispersal constraints over four time periods were constructed based on historic landmass distribution [7]. No probabilities are below 0.5, as these constraints were not intended to be entirely prohibitive.

<b>Geographic Areas</b>		<b>0-10 mya</b>						
<b>1</b>	North and Central America and Caribbean Islands	1	2	3	4	5	6	7
		1	[[1.0, 1.0,	0.5,	0.5,	0.5,	0.5,	0.5]
		2	[1.0, 1.0,	0.5,	0.5,	0.5,	0.5,	0.5]
<b>2</b>	South America, including Lesser Antilles	3	[0.5, 0.5,	1.0,	1.0,	1.0,	0.75,	0.75]
		4	[0.5, 0.5,	1.0,	1.0,	0.75,	0.75,	0.75]
		5	[0.5, 0.5,	1.0,	0.75,	1.0,	1.0,	0.75]
<b>3</b>	Ethiopian	6	[0.5, 0.5,	0.75,	0.75,	1.0,	1.0,	1.0]
		7	[0.5, 0.5,	0.75,	0.75,	0.75,	1.0,	1.0]]
<b>4</b>	Malagasy	<b>10-30 mya</b>						
		1	2	3	4	5	6	7
<b>5</b>	Palaearctic	1	[[1.0, 0.75,	0.5,	0.5,	0.75,	0.5,	0.5]
		2	[0.75, 1.0,	0.5,	0.5,	0.5,	0.5,	0.5]
<b>6</b>	Indo-Pacific	3	[0.5, 0.5,	1.0,	1.0,	1.0,	0.75,	0.75]
		4	[0.5, 0.5,	1.0,	1.0,	0.75,	0.75,	0.75]
		5	[0.75, 0.5,	1.0,	0.75,	1.0,	1.0,	0.75]
<b>7</b>	Australian	6	[0.5, 0.5,	0.75,	0.75,	1.0,	1.0,	0.75]
		7	[0.5, 0.5,	0.75,	0.75,	0.75,	0.75,	1.0]]
		<b>30-65 mya</b>						
		1	2	3	4	5	6	7
		1	[[1.0, 0.75,	0.75,	0.5,	1.0,	0.5,	0.5]
		2	[0.75, 1.0,	0.75,	0.5,	0.5,	0.75,	0.75]
		3	[0.75, 0.75,	1.0,	1.0,	0.75,	0.75,	0.75]
		4	[0.5, 0.5,	1.0,	1.0,	0.75,	0.75,	0.75]
		5	[1.0, 0.5,	0.75,	0.75,	1.0,	0.75,	0.75]
		6	[0.5, 0.75,	0.75,	0.75,	0.75,	1.0,	0.75]
		7	[0.5, 0.75,	0.75,	0.75,	0.75,	0.75,	1.0]]
		<b>65-101 (root) mya</b>						
		1	2	3	4	5	6	7
		1	[[1.0, 0.75,	0.75,	0.5,	1.0,	0.5,	0.5]
		2	[0.75, 1.0,	0.75,	0.5,	0.5,	0.75,	0.75]
		3	[0.75, 0.75,	1.0,	1.0,	0.75,	0.75,	0.75]
		4	[0.5, 0.5,	1.0,	1.0,	0.75,	0.75,	0.75]
		5	[1.0, 0.5,	0.75,	0.75,	1.0,	0.75,	0.75]
		6	[0.5, 0.75,	0.75,	0.75,	0.75,	1.0,	0.75]
		7	[0.5, 0.75,	0.75,	0.75,	0.75,	0.75,	1.0]]



OUTGROUP

Chrysolampinae

Perlampinae

Philomidae

Gollumiellinae

Oraseminae

Psilocharini

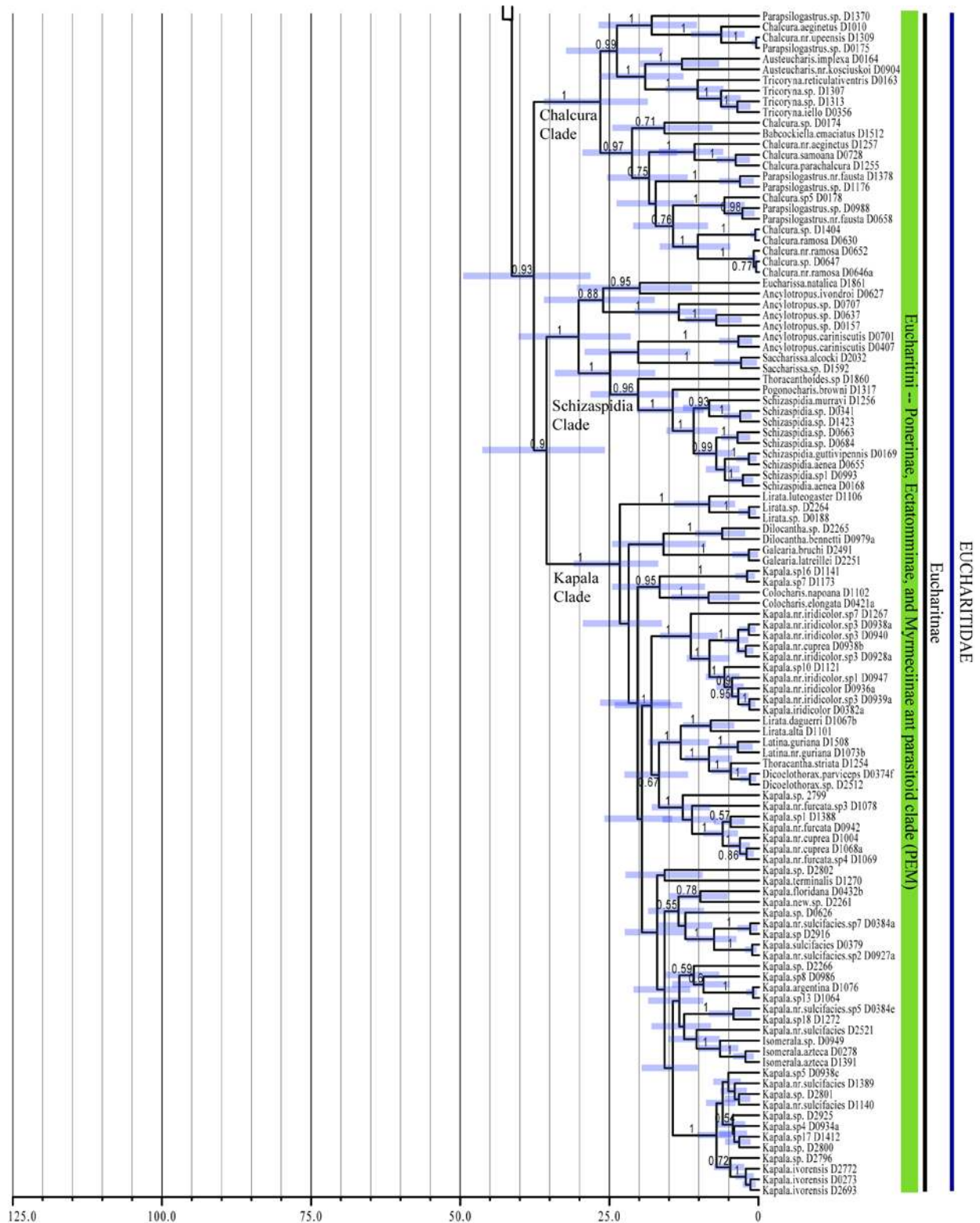
Eucharitini - Formicinae ant. parasitoid clade

Eucharitinae

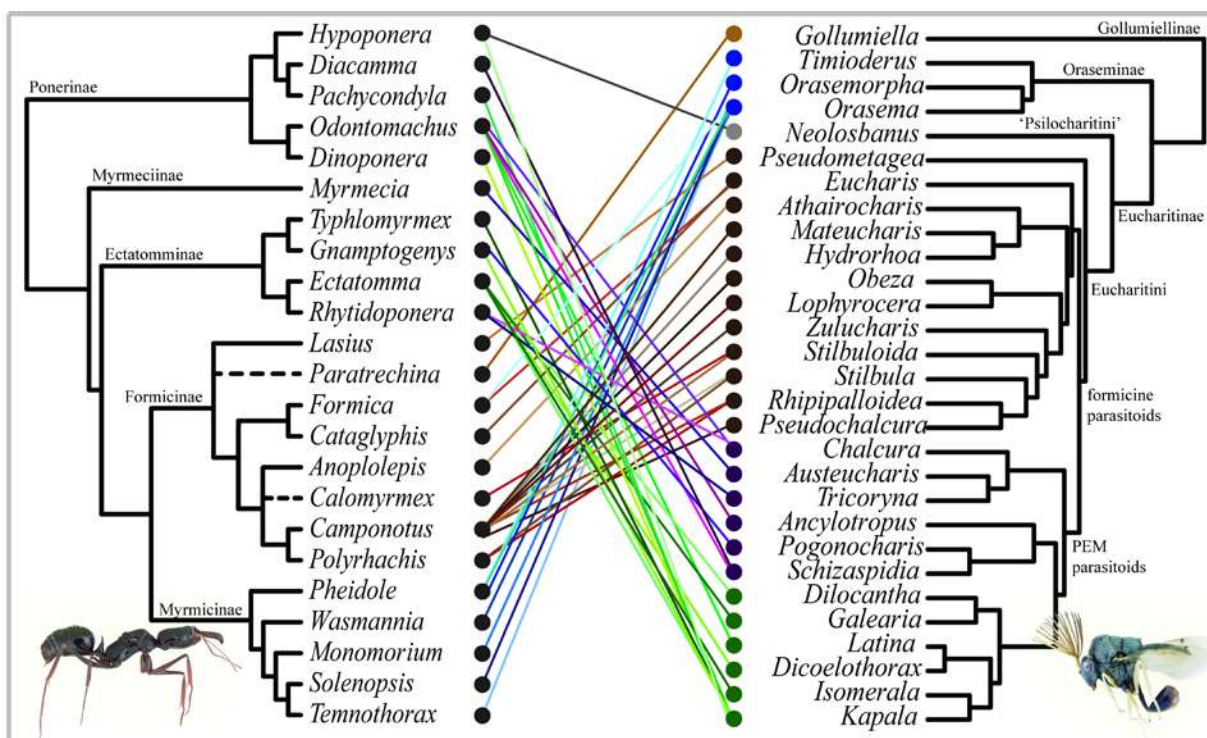
PERILAMPIDAE

EUCHARITIDAE

- Torymus.sp. D0027
- Podagron.sp. D0023
- Cleonymus.sp. D1452
- Erivestus.sp. D2637
- Ormocerus.sp. D2134
- Perilampidea.sp. D0628
- Peromalus.abipemnis D0724
- Thinodytes.sp. D0726
- Jambiva.vanharteni D1598
- Brachyelatus.sp. D0643
- Austrotocuma.sp. D0316
- Chrysomalla.hesperis D0050
- Chrysolampus.sp. D1447
- Chrysolampus.sp. D1009
- Chrysolampus.elegans D0723
- Chrysolampus.sp. D0160
- Chrysolampus.sisymbrii D0970
- Chrysolampus.schwarzii D0053a
- Euperilampus.behavae D0963
- Euperilampus.sp. D0385
- Perilampus.subcarinatus D0264
- Perilampus.fulvicornis D0713
- Monacon.canaliculatum D0709
- Monacon.sphaosum D1014
- Monacon.robertsi D0318
- Perilampus.sp. D1266
- Perilampus.sp. D0688
- Perilampus.sp. D0967
- Stelamlampus.salicetum D0320
- Perilampus.sp. D0854
- Perilampus.sp. D0649
- Perilampus.ruficornis D0361
- Perilampus.sp. D1362
- Perilampus.granulosus D0263
- Perilampus.regalis D0113
- Perilampus.bivalinus D0972
- Burksilampus.sp. D1500
- Burksilampus.sp. D1006
- Philomides.sp. D1269
- Philomidine.ngen D0903
- Aperilampus.sp. D0900
- Akapalla.rudis D0350
- Anorasema.pallidipes D0408
- Anorasema.pallidipes D2840
- Gollumiella.sp. D2839
- Gollumiella.longipetiolata D0405c
- Gollumiella.ochreata D0426
- Gollumiella.ochreata D2834
- Gollumiella.buffinoni D0994c
- Gollumiella.bicolor D0853a
- Gollumiella.antennata D0351
- Gollumiella.minuta D1261
- Orasema.communis D0951
- Timioderus.peridentatus D0116
- new.gen.nr.Indosema D2213
- Orasema.monomorpha D0638
- Orasema.sp. D0908
- Orasema.glabra D0183
- Orasemomorpha.tridentata D0165
- Orasemomorpha.eribotes D0162
- Orasema.synempora D1803
- Orasema.nr.valgus D0324
- Orasema.nsp D0161
- Orasema.valgus D0363
- Orasema.valgus D0171
- Indosema.indica D2212
- Orasema.simulatrix D0422
- Orasema.texana D0123
- Orasema.coloradensis D0251
- Orasema.sp. D0354
- Orasema.tolteca D0286
- Orasema.nr.robertsoni D0430
- Orasema occidentalis D0427
- Orasema.wheeleri D0248
- Orasema.rapo.gr D2517
- Orasema.nr.coloradensis D0433
- Orasema.sp. D2919
- Orasema.delicatula D0632
- Orasema.rapo D0997
- Orasema.simplex D2256
- Orasema.xanthopus D1090
- Orasema.nr.worcesteri D1093
- Orasema.nr.costaricensis D1005
- Orasema.minutissima D0194
- Orasema.costaricensis D0342
- Psilocharis.theocles D0170
- Psilocharis.pacifici D1259
- Psilocharis.monticera D0184
- Psilocharis.sp. D2694
- Psilocharis.nr.afra D2273
- Neolosbanus.purpureiventris D0414
- Neolosbanus.paigravesi D0167
- Neolosbanus.paigravesi D2845
- Neolosbanus.paigravesi D0406
- Pseudometagea.montana D0321
- Pseudometagea.schwarzii D0274
- Pseudometagea.bakeri D0322
- Eucharis.sp. D1843
- Eucharis.albipennis D0337
- Eucharis.sp. D0729
- Cherianella.sp. D0906
- Neostilbula.ranomafanae D1446a
- Neostilbula.sp. D0954
- Atharocharis.vannootti D0325
- Mateuecharis.alabra D0391
- Hydrothoa.sp.B D0909
- Hydrothoa.stevensoni D0155
- Lophyroceria.variabilis D2553
- Lophyroceria.pretendens D0634
- Obeza.sp. D1074
- Obeza.grenadensis D0358
- Zulucharis.sp. D0186
- Stilbuloida.nr.doddi D0642
- Stilbuloida.doddi D0660
- Leurocharis.serricornis D0166
- Substilbula.pallidiclava D0965
- Substilbula.pallidiclava D1011
- Stilbula.sp. D2692
- Stilbula.usuariensis D0923a
- Stilbula.sp. D2837
- Stilbula.quinqueguttata D0644
- Pseudochalcura.sp. D2495
- Rhippalloidea.mira D1311
- Pseudochalcura.gibbosa D0910
- Pseudochalcura.americana D0635
- Pseudochalcura.nigrocyanea D0179



**Figure S1.** Fossil-calibrated phylogeny of Eucharitidae, as shown in Fig. 1. 237 taxa analyzed, 95% highest posterior density error bars shown in blue. Posterior probability support shown above branches. Starred node indicates Eucharitidae origin, 'F' symbol indicates fossil placement. Taxonomic groups shown on right. Taxa localities found in Table S2.



**Figure S2.** Host-parasitoid taxonomic associations. Tanglegram of 29 eucharitid genera and 23 formicid genera (Table S1). Formicidae cladogram on left adapted from Moreau et al. [8], ant image from antweb.org. *Paratrechina* and *Calomyrmex* placement was estimated (dashed line) because the terminals were not included in original phylogeny. Eucharitidae cladogram on right modified from Fig. 1. Only genera with parasitoid-host associations are included. Eucharitid groups coded by colored lines and terminal dots: Gollumiellinae = **orange** and Oraseminae = **blue**. Eucharitinae is broken into four subgroups: the paraphyletic Psilocharitini = **gray**, and the Eucharitini is further divided: formicine parasitoid clade = **brown**, Old World PEM parasitoid clade = **purple**, and New World PEM parasitoid clade = **green**. Patterns of host use emerge at subfamily level and below.

**Table S1.** Eucharitidae ant hosts.

wasp subfamily	wasp genus	ant genus	ant subfamily	references	
Gollumiellinae	<i>Gollumiella</i>	<i>Nylanderia</i>	Formicinae	[9]	
	Oraseminae	<i>Orasema</i>	<i>Formica</i>	Formicinae	[10]
		<i>Monomorium</i>	Myrmicinae	[11]	
		<i>Pheidole</i>	Myrmicinae	[11-23]	
		<i>Solenopsis</i>	Myrmicinae	[12, 15, 21, 24-27]	
		<i>Temnothorax</i>	Myrmicinae	[22, 28, 29]	
		<i>Wasmannia</i>	Myrmicinae	[22, 30]	
		<i>Orasemorpha</i>	<i>Pheidole</i>	Myrmicinae	[21, 31, 32]
		<i>Timioderus</i>	<i>Pheidole</i>	Myrmicinae	[11]
Eucharitinae		<i>Ancylotropus</i>	<i>Odontomachus</i>	Ponerinae	[28]
		<i>Athairocharis</i>	<i>Anoploepsis</i>	Formicinae	[28]
		<i>Austeucharis</i>	<i>Myrmecia</i>	Myrmeciinae	[33-35]
		<i>Chalcura</i>	<i>Rhytidoponera</i>	Ectatomminae	[21, 28, 36]
			<i>Odontomachus</i>	Ponerinae	[17, 28, 36]
		<i>Dicoelothorax</i>	<i>Ectatomma</i>	Ectatomminae	[37]
		<i>Dilocantha</i>	<i>Ectatomma</i>	Ectatomminae	[38-40]
	<i>Cataglyphis</i>		Formicinae	[33, 41]	
	<i>Eucharis</i>	<i>Formica</i>	Formicinae	[17]	
		<i>Ectatomma</i>	Ectatomminae	[42]	
	<i>Galearia</i>	<i>Camponotus</i>	Formicinae	[28]	
	<i>Hydrorhoa</i>	<i>Ectatomma</i>	Ectatomminae	[39-41]	
	<i>Isomerala</i>	<i>Ectatomma</i>	Ectatomminae	[39, 40, 43-45]	
		<i>Gnamptogenys</i>	Ectatomminae	[36, 39, 44, 46]	
	<i>Kapala</i>	<i>Typhlomyrmex</i>	Ectatomminae	[46]	
		<i>Dinoponera</i>	Ponerinae	[47]	
		<i>Hypoponera</i>	Ponerinae	[46]	
		<i>Odontomachus</i>	Ponerinae	[17, 28, 44, 46]	
		<i>Pachycondyla</i>	Ponerinae	[28, 39, 41, 44, 46]	
		<i>Odontomachus</i>	Ponerinae	[42]	
	<i>Latina</i>	<i>Camponotus</i>	Formicinae	[14]	
	<i>Lophyrocera</i>	<i>Camponotus</i>	Formicinae	[28]	
	<i>Mateucharis</i>	<i>Hypoconera</i>	Ponerinae	[21]	
	<i>Neolosbanus</i>	<i>Camponotus</i>	Formicinae	[48]	
	<i>Obeza</i>	<i>Gnamptogenys</i>	Ectatomminae	[28]	
	<i>Pogonocharis</i>	<i>Camponotus</i>	Formicinae	[12, 49-51]	
	<i>Pseudochalcura</i>	<i>Lasius</i>	Formicinae	[52]	
	<i>Pseudometagea</i>	<i>Camponotus</i>	Formicinae	[53]	
	<i>Rhipipalloidea</i>	<i>Polyrachis</i>	Formicinae	[28]	
		<i>Gnamptogenys</i>	Ectatomminae	[21]	
	<i>Schizaspidia</i>	<i>Diacamma</i>	Ponerinae	museum specimen	
		<i>Odontomachus</i>	Ponerinae	[17, 21, 28]	
	<i>Stilbula</i>	<i>Camponotus</i>	Formicinae	[17, 54, 55]	
<i>Polyrhachis</i>		Formicinae	[32, 56]		
<i>Stiluboida</i>	<i>Calomyrmex</i>	Formicinae	[31]		
	<i>Camponotus</i>	Formicinae	[36]		
<i>Tricoryna</i>	<i>Rhytidoponera</i>	Ectatomminae	[21, 31]		
<i>Zulucharis</i>	<i>Camponotus</i>	Formicinae	[28]		



**Table S2.** List of taxa, ID codes, and Genbank accession numbers. Accessions with prefix ‘KC’ were added from this study. Family name abbreviations: ‘Ptero.’ = Pteromalidae, ‘Peri.’ = Perilampidae, and ‘Euch.’ = Eucharitidae.

	taxon name	voucher	family: subfamily	UCRC ID	GenBank Accession Number				locality information
					18S	28S D2-D5	COI	COII	
1	<i>Cleonymus</i> sp	D1452	Ptero.: Cleonyminae	x	GQ410678	AY599278, JN624099	KC008297		USA: CA: Los Angeles Co., Rancho Palos Verdes
2	<i>Erixestus</i> sp	D2637	Ptero.: <i>incertae sedis</i>	117000	JN623478	JN623832, JN624205			Ecuador: Orellana: Tiputini Biodiversity Sta.
3	<i>Nodisoplata</i> sp	D2134	Ptero.: Miscogasterinae	161348	JN623438	JN623798, JN624169			USA: CA: Riverside Co., Harford Spg. Pk.
4	<i>Perilampidea</i> sp	D0628	Ptero.: Pteromalinae	161402	JN623461	JN623819, JN624190			Mexico: San Luis Potosi, Las Pozas
5	<i>Pteromalus albipennis</i>	D0724	Ptero.: Pteromalinae	91131	KC008494	AY552170	KC008299	KC008486	USA: CA: San Bernardino, San Bernardino Mtns
6	<i>Thinodytes</i> sp	D0726	Ptero.: Miscogasterinae	91133	JN623431	AY552172, JN624161	KC008300		USA: CA: San Bernardino, San Bernardino Mtns
7	<i>Podagrion</i> sp	D0023	Torymidae: Toryminae	175285	JN623524	AY599269	KC008298		USA: CA
8	<i>Torymus</i> sp	D0027	Torymidae: Toryminae	175224	JN623528	AY599270, JN624247	KC008301		USA: CA
9	<i>Aperilampus</i> sp	D0900	Peri.: Philomidinae	184055	JN623332	AY672941, JN624072	KC008302		Yemen: NW of Manakhah
10	<i>Philomides</i> sp	D1269	Peri.: Philomidinae	161226	JN623333	JN623712, JN624073	KC008303		Madagascar: Toliara Prov.: Frut de Mete
11	<i>Philomidinae</i> ngen	D0903	Peri.: Philomidinae	92160	JN623334	AY672942, JN624074	KC008304		Yemen: NW of Manakhah
12	<i>Brachyelatus</i> sp	D0316	Peri.: Chrysolampinae	91144	JN623321	AY552187, JN624067	KC008305		Australia: SA: Kangaroo Island, Finders Chase NP
13	<i>Austrotoxeuma</i> sp	D0643	Peri.: Chrysolampinae	91141	JN623322	AY552184, JN624068	KC008306		Australia: NT: W of Alice Springs
14	<i>Chrysolampus elegans</i>	D0723	Peri.: Chrysolampinae	x	JN623324	AY552186	KC008307		USA: CA: San Bernardino, San Bernardino Mtns
15	<i>Chrysolampus schwarzi</i>	D0053a	Peri.: Chrysolampinae	x	JN623325	AY672937	KC008308		USA: CA: Anza Borrego State Park
16	<i>Chrysolampus sisymbrii</i>	D0970	Peri.: Chrysolampinae	91147	JN623326	AY552188	KC008309		USA: CA: Howler Junction
17	<i>Chrysolampus</i> sp	D0160	Peri.: Chrysolampinae	91142	JN623327	AY552185, JN624069			Australia: Kangaroo Island
18	<i>Chrysolampus</i> sp	D1009	Peri.: Chrysolampinae	91171	JN623329	AY672939	KC008310		Australia: WA: Stirling Range Nat'l Park
19	<i>Chrysolampus</i> sp	D1447	Peri.: Chrysolampinae	175145	JN623328	JN623710, JN624070			Madagascar: Fianarantsoa: Parc Nat'l Ranomafana
20	<i>Chrysomalla hesperis</i>	D0050	Peri.: Chrysolampinae	91180	JN623330	AY672940			USA: CA: Anza Borrego State Park
21	<i>Burksilampus</i> sp	D1006	Peri.: Perilampinae	91154	JN623335	AY552183, JN624075	KC008311		Colombia: Boyaca: Carrizal
22	<i>Burksilampus</i> sp	D1500	Peri.: Perilampinae	x	JN623336	JN623713		KC008487	Colombia: Boyaca: Arabuco, SSF Iguaque
23	<i>Euperilampus behavae</i>	D0963	Peri.: Perilampinae	x	JN623337	AY672932	KC008312		Madagascar
24	<i>Euperilampus triangularis</i>	D0385	Peri.: Perilampinae	91387	JN623338	AY552174	KC008313	KC008488	USA: VA: Clark Co., U Va. Blandy Experiment Sta.
25	<i>Monacon</i> sp	D0709	Peri.: Perilampinae	91152	JN623339	AY552182, JN624077	KC008314		Kenya: Kakamega: Yala R. Nat'l Res.
26	<i>Monacon robertsi</i>	D0318	Peri.: Perilampinae	91150	JN623340	AY552181, JN624078	KC008315		Indonesia: Seram: Maluku
27	<i>Monacon spinosum</i>	D1014	Peri.: Perilampinae	91170	JN623341	KC008080, JN624079			Australia: QLD: Great Sandy NP
28	<i>Perilampus</i> sp5	D1266	Peri.: Perilampinae	302333	JN623351	JN623725, JN624086	KC008216		Australia: ACT: Canberra, Jerrabomberra Wetlands NR
29	<i>Perilampus fulvicornis</i>	D0713	Peri.: Perilampinae	x	JN623342	JN623717, JN624080	KC008217	KC008489	USA: CA: Riverside Co.
30	<i>Perilampus granulosus</i>	D0263	Peri.: Perilampinae	91178	JN623343	AY672934			USA: TX: Jim Wells Co., 7 mi W of Ben Bolt
31	<i>Perilampus hyalinus</i>	D0972	Peri.: Perilampinae	x	AY552257	AY552180	KC008318		Canada: ON: Algonquin lab ex <i>Neodiprion</i>
32	<i>Perilampus regalis</i>	D0113	Peri.: Perilampinae	91177	JN623345	AY552178	KC008319		USA: AZ: Cochise Co., Sam Simeon Rd.
33	<i>Perilampus ruficornis</i>	D0361	Peri.: Perilampinae	91158	JN623346	JN623720, JN624082	KC008320	KC008490	Russia
34	<i>Perilampus</i> sp1	D0649	Peri.: Perilampinae	302331	JN623347	JN623721, JN624083			Australia: NT: W of Alice Springs
35	<i>Perilampus</i> sp2	D0688	Peri.: Perilampinae	91156	JN623348	JN623722, JN624084			Australia: QLD: Mt. Isa, Moondaara Lake Rd
36	<i>Perilampus</i> sp3	D0854	Peri.: Perilampinae	x	JN623349	JN623723			China: Beijing, Fragrant Hills Park
37	<i>Perilampus</i> sp4	D0967	Peri.: Perilampinae	302332	JN623350	JN623724, JN624085			Australia: QLD: Brisbane Forest Park, Northbrook Prkwy
38	<i>Perilampus</i> sp6	D1362	Peri.: Perilampinae	184042	JN623352	JN623726	KC008321		Argentina: Salta Prov.: RN 81, 25 km east Jst RP24
39	<i>Perilampus subcarinatus</i>	D0264	Peri.: Perilampinae	91157	JN623353	AY552175, JN624087	KC008322		USA: TX: Jim Wells Co., La Copita
40	<i>Steffanolampus salicetum</i>	D0320	Peri.: Perilampinae	824	JN623354	AY552177, JN624088	KC008323		Canada: Ontario: Joker's Hill NW of Newmarket
41	<i>Akapala rudis</i>	D0360a	Peri.: Akapalinae	91182	JN623320	AY672943, JN624066	KC008324	KC008491	Australia: QLD: Mica Ck., Mt Isa
42	<i>Jambiya vanharteni</i>	D1598	Peri.: <i>incertae sedis</i>	184056	JN623331	JN623711, JN624071		KC008492	Yemen: NW Manakhah
43	<i>Anorasema pallidipes</i>	D0408	Euch.: Gollumiellinae	x	JN623250	AY552189, JN624019		KC008325	Malaysia: Selangor, 13 km E Gombak
44	<i>Anorasema pallidipes</i>	D2840	Euch.: Gollumiellinae	274984		KC008081	KC008164	KC008326	Brunei: Temburong Dist.: Temburong NP

45	<i>Gollumiella antennata</i>	D0351a	Euch.: Gollumiellinae	91199	JN623251	AY552190			Sri Lanka: Mount Lavinia
46	<i>Gollumiella bicolor</i>	D0853a	Euch.: Gollumiellinae	91201	AY552270	AY552193	KC008165	KC008327	China: Beijing, Fragrant Hills Park
47	<i>Gollumiella longipetiolata</i>	D0405c	Euch.: Gollumiellinae	91183	JN623252	AY552191, JN624020	KC008166	KC008328	Malaysia: Selangor, Univ. Malaya, Rimba Ilmu
48	<i>Gollumiella minuta</i>	D1261	Euch.: Gollumiellinae	x	AY552271	AY552194	KC008167	KC008329	Australia: QLD: SF50 nr Expedition, Range NP
49	<i>Gollumiella ochreatea</i>	D0426	Euch.: Gollumiellinae	91314	AY552269	AY552192	KC008168		Malaysia: Selangor, K.L. Univ. Malaya, Rimba Ilmu
50	<i>Gollumiella ochreatea</i>	D2834	Euch.: Gollumiellinae	237300		KC008082, KC008137	KC008169		Singapore: National Botanical Gardens
51	<i>Gollumiella buffingtoni</i>	D0994c	Euch.: Gollumiellinae	91216	KC008499	AY552193	KC008170		Japan: Niigata: Kurokawa, Tainai Riv.
52	<i>Gollumiella sp</i>	D2839	Euch.: Gollumiellinae	274981		KC008083, KC008138	KC008171	KC008330	Brunei: Belait Dist.: Labi Road
53	<i>Orasemorpha eribotes</i>	D0162	Euch.: Oraseminae	91283	JN623263	AY552199, JN624032	KC008172	KC008331	Australia: SA: Kangaroo Is., Flinders Chase NP
54	<i>Orasemorpha tridentata</i>	D0165	Euch.: Oraseminae	91448	JN623265	AY552200	KC008173	KC008332	Australia: SEQ: Mt. Glorius, Bryce's Road
55	<i>Indosema indica</i>	D2212	Euch.: Oraseminae	161364	JN623253	JN623661, JN624021			India: Uttar Pradesh, New Delhi, IARI
56	new gen nr <i>Indosema</i>	D2213	Euch.: Oraseminae	175146		KC008084, KC008139		KC008333	Madagascar: Toliara
57	<i>Timioderus peridentatus</i>	D0116	Euch.: Oraseminae	91288	JN623266	AY552195, JN624034		KC008334	South Africa: W Cape: Bainskloof Pass
58	<i>Orasema coloradensis</i>	D0251	Euch.: Oraseminae	92176		AY672958		KC008335	USA: TX: Jim Wells Co., 7 mi W Ben Bolt
59	<i>Orasema communis</i>	D0951	Euch.: Oraseminae	91472	JN623254	AY552196, JN624022	KC008174	KC008336	Madagascar: Province d'Antananarivo, nr Andasibe NP
60	<i>Orasema costaricensis</i>	D0342	Euch.: Oraseminae	1375		AY672931			St. Lucia, West Indies
61	<i>Orasema delicatula</i>	D0632	Euch.: Oraseminae	91402	JN623255	AY552202, JN624023	KC008175	KC008337	Colombia: Amazonas, PNN Amacayacu San Martin
62	<i>Orasema glabra</i>	D0183	Euch.: Oraseminae	x	JN623256	AY672948, JN624024			South Africa: Natal: btwn Mineral Springs & Nylstrom
63	<i>Orasema minutissima</i>	D0194	Euch.: Oraseminae	x	AY552281	AY552204	KC008176	KC008338	Cuba: Santiago Prov., 16 km NE of Caney
64	<i>Orasema monomoria</i>	D0638	Euch.: Oraseminae	278241		KC008085			Madagascar: Antananarivo Prov., 3km 41'NE Andranomay
65	<i>Orasema nr coloradensis</i>	D0433	Euch.: Oraseminae	91429	JN623257	AY552207, JN624025		KC008339	USA: IN: Lake Co., Indiana Dunes N.L.
66	<i>Orasema nr costaricensis</i>	D1005	Euch.: Oraseminae	91468	AY552208	AY552203	KC008177		USA: NC: Carteret Co., Moorehead City
67	<i>Orasema nr robertsoni</i>	D0430	Euch.: Oraseminae	x	AY552285	AY552208	KC008178	KC008340	USA: FL: Gainesville, NE of airport, Indust. Pk.
68	<i>Orasema nr valguis</i>	D0324	Euch.: Oraseminae	91415	AY552274	AY552197	KC008179		Australia: QLD: Mt. Glorious
69	<i>Orasema nr worcesteri</i>	D1093	Euch.: Oraseminae	x	KC008502	KC008086, KC008140			Argentina: Salta Pr., Rosario de la Frontera, RN 9
70	<i>Orasema nsp</i>	D0161	Euch.: Oraseminae	92152		KC008087			Australia: SEQ: Blackbutt Range
71	<i>Orasema occidentalis</i>	D0427	Euch.: Oraseminae	92155	KC008503	AY672963			USA: CA: Riverside Co., Lake Skinner
72	<i>Orasema rapo</i>	D0997	Euch.: Oraseminae	91462	AY552287	AY552201	KC008180	KC008341	Ecuador: Orellana: Res. Etnica Waorani
73	<i>Orasema rapo group</i>	D2517	Euch.: Oraseminae	161481		KC008088, KC008141	KC008181		Argentina: La Rioja Prov., Santa Cruz
74	<i>Orasema simplex</i>	D2256	Euch.: Oraseminae	768	JN623258	JN623663, JN624026			Argentina: Corrientes Pr., EBCo
75	<i>Orasema simulatrix</i>	D0422	Euch.: Oraseminae	91444	JN623259	AY552206, JN624027	KC008181		USA: AZ: Pima Co., Box Cyn. Coronado Nat'l For.
76	<i>Orasema sp</i>	D0354	Euch.: Oraseminae	103431	KC008504	KC008089			Argentina
77	<i>Orasema sp</i>	D0908	Euch.: Oraseminae	92148	KC008505	KC008090, JN624029			Yemen: Ar Rujum
78	<i>Orasema sp</i>	D2919	Euch.: Oraseminae	278358	KC008506	KC008091, KC008142	KC008182		Costa Rica: Heredia Prov.: La Selva Biol. Sta.
79	<i>Orasema synempora</i>	D1803	Euch.: Oraseminae	175151	JN623261	JN623665, JN624030			Australia: QLD: Station Creek, 17 km N Mt Malloy
80	<i>Orasema texana</i>	D0123	Euch.: Oraseminae	x	JN623262	AY552205, JN624031	KC008183		USA: AZ
81	<i>Orasema tolteca</i>	D0286	Euch.: Oraseminae	175176	KC008508	AY672961		KC008342	USA: AZ: Cochise Co, Harshaw Ck
82	<i>Orasema valgius</i>	D0171	Euch.: Oraseminae	91307	AY552275	AY552198	KC008184	KC008343	Australia: SA: Mt. Barker
83	<i>Orasema valgius</i>	D0363	Euch.: Oraseminae	x	KC008509	KC008092			Australia: SA: Mt. Barker
84	<i>Orasema wheeleri</i>	D0248	Euch.: Oraseminae	91353		AY672955, KC008493			TX: Corpus Cristi Lake State Rec. Area
85	<i>Orasema xanthopus</i>	D1090	Euch.: Oraseminae	278287	KC008510	KC008093, KC008143			Argentina: SA: Orán, rd to San Andres, along Rio Blanca
86	<i>Psilocharis monilicera</i>	D0184	Euch.: Eucharitinae	x	KC008511	KC008094, KC008144			South Africa: Natal: btwn Mineral Springs & Nylstrom
87	<i>Psilocharis afra</i>	D2273	Euch.: Eucharitinae	184095	JN623244	JN623657, JN624015			South Africa: Mpumalanga, 2 km E R532 God's Window
88	<i>Psilocharis pacifica</i>	D1259	Euch.: Eucharitinae	91474	JN623245	GQ453403, JN624016		KC008344	Fiji: Viti Levu, Ba Prov., Koroyanitu, Abaca Village
89	<i>Psilocharis sp</i>	D2694	Euch.: Eucharitinae	314		KC008095, KC008145	KC008185		Nigeria: Ondo State, 4.4 km E Owena
90	<i>Psilocharis theocles</i>	D0170b	Euch.: Eucharitinae	91237	JN623246	AY552209		KC008345	Australia: NSW: Monga State For.
91	<i>Neolosbanus palgravei</i>	D0167	Euch.: Eucharitinae	x	AY552289	AY552212		KC008346	Australia: NEQ: 2 km N Black, mt. road
92	<i>Neolosbanus palgravei</i>	D0406	Euch.: Eucharitinae	91412	JN623236	AY552213, JN624010		KC008347	Malaysia: Selangor, road by Quarry, 13 km E Gombak
93	<i>Neolosbanus palgravei</i>	D2845	Euch.: Eucharitinae	274985		KC008096, KC008146	KC008186	KC008348	Brunei: Temburong Dist: Temburong NP, Ulu-Ulu Pipe Rd
94	<i>Neolosbanus purpureoventris</i>	D0414	Euch.: Eucharitinae	91470	JN623237	AY552214, JN624011		KC008349	Malaysia: Selangor, by Quarry, 13 km E Gombak
95	<i>Pseudometagea bakeri</i>	D0322	Euch.: Eucharitinae	91252	JN623240	AY672971, JN624013		KC008350	Canada: Saskatchewan, Beaver Creek Cons. Area
96	<i>Pseudometagea montana</i>	D0321	Euch.: Eucharitinae	91473	JN623241	AY552216	KC008187	KC008351	Canada, Ont: 12 km W SS Marie, Pte de Chenes Pk

97	<i>Pseudometagea schwarzii</i>	D0274	Euch.: Eucharitinae	91457	AY552292	AY552215	KC008188	KC008352	USA: MO: St. Clair Co., Taberville Prairie Cons. Area
98	<i>Eucharis albipennis</i>	D0337	Euch.: Eucharitinae	92166		AY672978			Kyrgyzstan: Osh Karakuldzha, Lajsu Ravine
99	<i>Eucharis</i> sp	D0729	Euch.: Eucharitinae	91257	JN623231	AY552229, JN624007	KC008189	KC008353	Israel: Sde Boqer
100	<i>Eucharis</i> sp	D1843	Euch.: Eucharitinae	175167	JN623232	JN623654, KC008494		KC008354	Tunisia
101	<i>Hydrorhoa</i> spB	D0909	Euch.: Eucharitinae	91389	AY552309	AY552232	KC008190	KC008355	Yemen: 12 km NW of Manakhah
102	<i>Hydrorhoa stvensoni</i>	D0155	Euch.: Eucharitinae	91399	AY552307	AY552230		KC008356	South Africa: Sutton Game Farm
103	<i>Mateucharis glabra</i>	D0391	Euch.: Eucharitinae	92173	KC008513	AY672981		KC008357	Tanzania: Amani Hills
104	<i>Zulucharis</i> sp	D0186	Euch.: Eucharitinae	x	AY552305	AY552228	KC008191	KC008358	South Africa: Natal: Percy Fyfe N.R.
105	<i>Cherianella</i> sp	D0906	Euch.: Eucharitinae	92161	KC008514	AY672982		KC008359	Yemen: Suq Bani Mansour
106	<i>Athairocharis vannoorti</i>	D0325	Euch.: Eucharitinae	92163	KC008515	AY672980		KC008360	South Africa: Eastern Cape Prov. 6 km N Steytierville
107	<i>Neostilbula ranomafanae</i>	D1446a	Euch.: Eucharitinae	184096	JN623238	JN623656, JN624012			Madagascar: Prov. Fianarantsoa, Parc Nat'l Ranomafana
108	<i>Neostilbula</i> sp	D0954	Euch.: Eucharitinae	x	KC008516	AY672983		KC008361	Madagascar: Prov Diego-Suarez, Montagne d'Ambre NP
109	<i>Leurocharis serricornis</i>	D0166	Euch.: Eucharitinae	91409	AY552296	AY552219	KC008192	KC008362	Australia: SA: Bookmark Reserve, Amalia Dam
110	<i>Substilbula pallidiclava</i>	D0965	Euch.: Eucharitinae	91416	AY552297	AY552220, AY552220	KC008193	KC008363	Australia: QLD: Brisbane Forest Park, S of Mt. Nebo
111	<i>Substilbula pallidiclava</i>	D1011	Euch.: Eucharitinae	103430		GQ331926	KC008194	KC008364	Australia: QLD: Brisbane Forest Pk. off Mount Nebo Rd
112	<i>Rhipipalloidea mira</i>	D1311	Euch.: Eucharitinae	91861		GQ331921		KC008365	Australia: SEQ: Mt Scoria
113	<i>Stilbula quinqueguttata</i>	D0644	Euch.: Eucharitinae	91439	AY552299	AY552222	KC008195	KC008366	Australia: QLD: Mt. Isa, Moondaara Lake
114	<i>Stilbula</i> sp	D2692	Euch.: Eucharitinae	315	AY552301	GQ331923, KC008495		KC008367	Nigeria: Ondo State: Idanre Hills
115	<i>Stilbula</i> sp	D2837	Euch.: Eucharitinae	237301	KC008517	KC008097	KC008196	KC008368	Singapore: Kent Ridge Rd at Nat'l University Singapore
116	<i>Stilbula ussuriensis</i>	D0923a	Euch.: Eucharitinae	103422		GQ331922	KC008197	KC008369	Russia: Primorskiy Krai, Ussuriysk Dist, Gornotayozhnoye
117	<i>Stilbuloida doddi</i>	D0660	Euch.: Eucharitinae	91438	AY552301	AY552224	KC008198	KC008370	Australia: NT: W of Alice Springs, rd to Ellery's Hole
118	<i>Stilbuloida nr doddi</i>	D0642	Euch.: Eucharitinae	x	AY552300	AY552223		KC008371	Australia: QLD: Mt. Isa, 4 km N on Lake Julius Rd.
119	<i>Pseudochalcura americana</i>	D0635	Euch.: Eucharitinae	91425	AY552294	AY552217		KC008372	Colombia: Chocó, PNN Utría Centro de Visitantes
120	<i>Pseudochalcura gibbosa</i>	D0910	Euch.: Eucharitinae	91401	AY552295	AY552218	KC008199	KC008373	USA: WY: Grand Teton Nat'l Pk, UW-NPS Research St.
121	<i>Pseudochalcura nigrocyanea</i>	D0179	Euch.: Eucharitinae	92174	GQ331910	AY672972		KC008374	Brazil: Rondonia, ~60 km SE Ariquemes, Rancho Grande
122	<i>Pseudochalcura</i> sp2	D2495	Euch.: Eucharitinae	x		GQ331920, KC008496		KC008375	Argentina: Sant. del Est. Pr. Rt 5, S of Campo Gallo
123	<i>Obeza grenadensis</i>	D0358	Euch.: Eucharitinae	x	AY552302	AY552225	KC008200	KC008376	St. Lucia
124	<i>Obeza</i> sp1	D1074	Euch.: Eucharitinae	91454	AY552303	AY552226		KC008377	Argentina: Salta Province, Cabeza de Buey
125	<i>Lophrocera pretendens</i>	D0634	Euch.: Eucharitinae	91397	AY552304	AY552227, JN624009			Colombia: Caquetá PNN Chiribiquete Puerto Abeja
126	<i>Lophrocera variabilis</i>	D2553	Euch.: Eucharitinae	161496		GQ331914, KC008497	KC008201		Argentina: Tucuman, Los Chorillos
127	<i>Chalcura aeginetus</i>	D1010	Euch.: Eucharitinae	91264		AY671810	KC008202	KC008378	Australia: QLD: Bunya Mtns NP, Paradise
128	<i>Chalcura aeginetus</i>	D1257	Euch.: Eucharitinae	92097		AY671812	KC008203	KC008379	Fiji: Viti Levu Ba Prov., Koroyanitu, Abaca Vall.
129	<i>Chalcura nr ramosa</i>	D0646a	Euch.: Eucharitinae	91769	AY552314	AY552237	KC008204	KC008380	Australia: NT: W of Alice Springs, 3 km E Ellery's Hole
130	<i>Chalcura nr ramosa</i>	D0652	Euch.: Eucharitinae	91966		KC008098	KC008205	KC008381	Australia: NT: W of Alice Springs, Standley Chasm
131	<i>Chalcura nr upeensis</i>	D1309	Euch.: Eucharitinae	92056		AY671816	KC008206	KC008382	Australia: QLD: North Tamborine
132	<i>Chalcura parachalcura</i>	D1255	Euch.: Eucharitinae	175166		AY671811	KC008207	KC008383	Fiji: E. Sigatoka
133	<i>Chalcura ramosa</i>	D0630	Euch.: Eucharitinae	91761		AY671808	KC008208	KC008384	Australia: QLD: Brisbane Forest Park
134	<i>Chalcura samoana</i>	D0728	Euch.: Eucharitinae	91930		AY671809	KC008209	KC008385	American Samoa: Mapusaga, Tutuila Island
135	<i>Chalcura</i> sp	D1404	Euch.: Eucharitinae	91839		AY671817	KC008210	KC008386	Australia: QLD: Wongabel, 8 km S of Atherton
136	<i>Chalcura</i> sp	D0647	Euch.: Eucharitinae	91770		KC008099	KC008211	KC008387	Australia: NT: W of Alice Springs, 3 km E Ellery's Hole
137	<i>Chalcura</i> sp	D0174	Euch.: Eucharitinae	91426	AY552313	AY552236	KC008212	KC008388	Australia: NSW: Shoalhaven River & Hwy 52
138	<i>Chalcura</i> sp5	D0178	Euch.: Eucharitinae	91911		KC008100	KC008213	KC008389	Australia: NSW: Monga State For.
139	<i>Parapsilogastrus nr fausta</i>	D0658	Euch.: Eucharitinae	91888	KC008519	AY671819		KC008390	Australia: NSW: Monga State Forest, 3.7 km S River Rd
140	<i>Parapsilogastrus</i> sp	D0175	Euch.: Eucharitinae	91912		AY671815	KC008214	KC008391	Australia: SEQ: Lansborough
141	<i>Parapsilogastrus</i> sp	D1176	Euch.: Eucharitinae	x		KC008101	KC008215	KC008392	Australia: ACT: Canberra Nature Prk. Black Mtn.
142	<i>Parapsilogastrus</i> sp	D1370	Euch.: Eucharitinae	x		AY671822	KC008216	KC008393	Australia: QLD, Mt. Glorious
143	<i>Parapsilogastrus nr fausta</i>	D1378	Euch.: Eucharitinae	x		KC008102	KC008217	KC008394	Australia: QLD, Mt. Glorious
144	<i>Parapsilogastrus</i> sp	D0988	Euch.: Eucharitinae	x		AY671821	KC008218	KC008395	Australia: ACT: Canberra. Black Mtn.
145	<i>Babcockiella emaciatus</i>	D1512	Euch.: Eucharitinae	x		KC008103		KC008396	South Africa
146	<i>Austeucharis implexa</i>	D0164	Euch.: Eucharitinae	91767	AY552310	AY552233	KC008219	KC008397	Australia: SA: Mt. Barker
147	<i>Austeucharis nr kosciuskoi</i>	D0904	Euch.: Eucharitinae	92124		AY671806	KC008220	KC008398	Australia: NSW: Styx River State Forest, Falls Road
148	<i>Tricornyna iello</i>	D0356	Euch.: Eucharitinae	91449	AY552312	AY552235	KC008221	KC008399	Australia: ACT: Namadgi Nat'l Park

149	<i>Tricoryna reticulativentris</i>	D0163	Euch.: Eucharitinae	x	AY552311	AY552234	KC008222	KC008400	Australia: SEQ: 10 km N Crows Nest
150	<i>Tricoryna</i> sp	D1307	Euch.: Eucharitinae	x		KC008104	KC008223	KC008401	Australia: QLD: Samsonvale Cemetery, SSE Dayboro
151	<i>Tricoryna</i> sp	D1313	Euch.: Eucharitinae	x	KC008520	KC008105	KC008224	KC008402	Australia: SEQ: Pine Mt. Summit
152	<i>Schizaspidia aenea</i>	D0168	Euch.: Eucharitinae	91398	AY552317	AY552240	KC008225	KC008403	Australia: NEQ: 11 km N Ellis Beach
153	<i>Schizaspidia aenea</i>	D0655	Euch.: Eucharitinae	91764	JN623249	AY552240, JN624018		KC008404	Australia: QLD: Kingfisher Park, ~5 km E Mt. Malloy
154	<i>Schizaspidia guttivipennis</i>	D0169	Euch.: Eucharitinae	x		AY671827	KC008226	KC008405	Australia: NEQ: Tam O'Shanter Forest, Mission Beach
155	<i>Schizaspidia murrayi</i>	D1256	Euch.: Eucharitinae	175165		AY671831	KC008227	KC008406	Fiji: E. Sigatoka
156	<i>Schizaspidia</i> sp	D0341	Euch.: Eucharitinae	x		AY671828	KC008228	KC008407	Thailand
157	<i>Schizaspidia</i> sp	D0663	Euch.: Eucharitinae	x		AY671830	KC008229	KC008408	Australia: QLD: Kingfisher Park, ~5 km E Mt. Malloy
158	<i>Schizaspidia</i> sp	D0684	Euch.: Eucharitinae	x		KC008106	KC008230	KC008409	Australia: QLD: Kingfisher Park, ~5 km E Mt. Malloy
159	<i>Schizaspidia</i> sp	D1423	Euch.: Eucharitinae	92224		KC008107	KC008231	KC008410	India
160	<i>Schizaspidia</i> sp1	D0993	Euch.: Eucharitinae	x		KC008108	KC008232	KC008411	Papua New Guinea: East New Britain, Bainings Mtns
161	<i>Ancylotropus cariniscutis</i>	D0701	Euch.: Eucharitinae	x		KC008109	KC008233	KC008412	Malaysia: Selangor Gombak
162	<i>Ancylotropus cariniscutis</i>	D0407	Euch.: Eucharitinae	91771	JN623228	AY552239, JN624005	KC008234	KC008413	Thailand: Trang Pr., Forest Reseach Sta., Khao Chong
163	<i>Ancylotropus ivondroi</i>	D0627	Euch.: Eucharitinae	92238	KC008521	AY671824		KC008414	Madagascar: Antananarivo Prov, Ambohitantely Res.
164	<i>Ancylotropus</i> sp	D0157	Euch.: Eucharitinae	92222		AY671823	KC008235	KC008415	South Africa: Umhalazi
165	<i>Ancylotropus</i> sp	D0637	Euch.: Eucharitinae	92023		AY671825	KC008236	KC008416	South Africa: Kwazulu Natal; Umhalazi N.R.
166	<i>Ancylotropus</i> sp	D0707	Euch.: Eucharitinae	91813		AY671826	KC008237	KC008417	Kenya: Kakamega D., Yala R. Nat'l Res.
167	<i>Eucharissa natalica</i>	D1861	Euch.: Eucharitinae	x		AY672989		KC008418	South Africa: Cape Prov.
168	<i>Saccharissa alcocki</i>	D2032	Euch.: Eucharitinae	161230	JN623247	JN623659, JN624017			Thailand: Trang Prov. Khao Chong
169	<i>Saccharissa vicina</i>	D1592	Euch.: Eucharitinae	92023	JN623248	JN623660		KC008419	Uganda: 20 km SE Fort Portal
170	<i>Thoracanthoides</i> sp	D1860	Euch.: Eucharitinae	x		KC008110		KC008420	Australia: QLD
171	<i>Pogonocharis browni</i>	D1317	Euch.: Eucharitinae	x		KC008111		KC008421	Indonesia: Borneo: Balampesoang For.
172	<i>Colocharis elongata</i>	D0421a	Euch.: Eucharitinae	91867	KC008522	AY671837	KC008238	KC008422	Venezuela: Aragua: Henri Pittier NP, Portachuelo Pass
173	<i>Colocharis napoana</i>	D1102	Euch.: Eucharitinae	91450	AY552323	AY552246	KC008239	KC008423	Ecuador: Orellana: Tiputini Biodiversity Sta nr Yasuni NP
174	<i>Lirata alta</i>	D1101	Euch.: Eucharitinae	92091	KC008523	AY671894	KC008240	KC008424	Argentina: Salta Prov.
175	<i>Lirata daguerri</i>	D1067b	Euch.: Eucharitinae	91838	AY552322	AY552245	KC008241	KC008425	Argentina: Formosa Prov., RN 11; S of Formosa
176	<i>Lirata luteogaster</i>	D1106	Euch.: Eucharitinae	92211	KC008524	AY671895	KC008242	KC008426	Ecuador: Orellana: Tiputini Biodiversity Sta nr Yasuni NP
177	<i>Lirata</i> sp	D2264	Euch.: Eucharitinae	161521	KC008525	KC008112, KC008147	KC008243	KC008427	French Guiana: Regina Road Reserva Kaw
178	<i>Dilocantha bennetti</i>	D979a	Euch.: Eucharitinae	x	KC008526	KC008113		KC008428	Trinidad: Curepe
179	<i>Dilocantha</i> sp	D2265	Euch.: Eucharitinae	161522	KC008527	KC008114, KC008148	KC008244	KC008429	Panama: Com de San Blas, 2 km N. Nusagadi
180	<i>Dicoelothorax parviceps</i>	D0374f	Euch.: Eucharitinae	184099	KC008528	AY671835	KC008245	KC008430	Colombia: Vichada PNN
181	<i>Dicoelothorax</i> sp	D2512	Euch.: Eucharitinae	161497		KC008115, KC008149		KC008431	Argentina: Salta Province, Cabeza de Buey
182	<i>Latina guriana</i>	D1508	Euch.: Eucharitinae	242338		AY671894		KC008432	Venezuela: Guri, Isla Rocas
183	<i>Latina nr guriana</i>	D1073b	Euch.: Eucharitinae	91466	AY552319	AY552242	KC008246	KC008433	Argentina: Salta
184	<i>Lirata</i> sp	D0188	Euch.: Eucharitinae	92235	KC008529	KC008116	KC008247	KC008434	Trinidad
185	<i>Thoracantha striata</i>	D1254	Euch.: Eucharitinae	x	KC008530	AY671896		KC008435	Brazil: Rondônia Prov., Rancho Grande
186	<i>Galearia bruchi</i>	D2491	Euch.: Eucharitinae	x	KC008531	KC008117			Argentina: Salta Province, Cabeza de Buey
187	<i>Galearia latreillei</i>	D2251	Euch.: Eucharitinae	161520	KC008532	KC008118, KC008150	KC008248	KC008436	Venezuela: Guayana mer. or.
188	<i>Isomerala azteca</i>	D0278	Euch.: Eucharitinae	91773	AY552318	AY552241	KC008249	KC008437	Mexico: Chiapas, Rosario Izapa
189	<i>Isomerala azteca</i>	D1391	Euch.: Eucharitinae	92016		AY671834	KC008250	KC008438	Mexico: Chiapas, Munic. Ocozocautla El Aguacero
190	<i>Isomerala</i> sp	D0949	Euch.: Eucharitinae	92014		AY671833	KC008251	KC008439	Colombia: Vichada, PNN Tuparou
191	<i>Kapala</i> sp.	D2925	Euch.: Eucharitinae	356033	KC008533	KC008119, KC008151	KC008252	KC008440	Mexico: Chiapas: 8 km SE Salto de Agua
192	<i>Kapala nr furcata</i> sp3	D1078	Euch.: Eucharitinae	92093		AY671883	KC008253	KC008441	Argentina: Misiones Prov., Santa Ana, near Loreto
193	<i>Kapala nr sulcifacies</i>	D1140	Euch.: Eucharitinae	92030	KC008534	AY671888	KC008254	KC008442	Ecuador: Orellana: Tiputini Biodiversity Sta nr Yasuni NP
194	<i>Kapala nr sulcifacies</i>	D1389	Euch.: Eucharitinae	92031	KC008535	KC008120	KC008255	KC008443	Ecuador: Galapagos: Isabela Island 13 km NW Villamil
195	<i>Kapala nr sulcifacies</i>	D2521	Euch.: Eucharitinae	161501	KC008536	KC008121, KC008152	KC008256	KC008444	Argentina: Santiago del Estero Prov., S of Tintina
196	<i>Kapala nr sulcifacies</i> sp2	D0927a	Euch.: Eucharitinae	92121	KC008537	AY671855	KC008257	KC008445	Colombia: Magdalena, PNN Tayrona Zaino
197	<i>Kapala nr sulcifacies</i> sp5	D0384e	Euch.: Eucharitinae	92058		AY671848	KC008258	KC008446	Panama: Panama, 2 km S Torti, Serrania de Maje
198	<i>Kapala nr sulcifacies</i> sp7	D0384a	Euch.: Eucharitinae	92114		AY671846	KC008259	KC008447	Panama: Panama, 2 km S Torti, Serrania de Maje
199	<i>Kapala</i> sp	D0626	Euch.: Eucharitinae	92243	KC008538	AY671851	KC008261	KC008448	Ecuador: Esmeraldas Prov, Bilsa Biol. Sta.
200	<i>Kapala</i> sp	D2796	Euch.: Eucharitinae	235957	KC008539	KC008124, KC008154	KC008262	KC008449	Dominica: Parish of St. David, 11 km NE Pont Casse

201	<i>Kapala</i> sp	D2916	Euch.: Eucharitinae	282473		KC008122, KC008153	KC008260		Costa Rica: Heredia Prov, La Selva Biol. Sta.
202	<i>Kapala</i> sp	D2800	Euch.: Eucharitinae	252084	KC008540	KC008125, KC008155	KC008263	KC008450	French Guiana: PK 24; 24 km to Barrage Petit Saut
203	<i>Kapala</i> sp	D2802	Euch.: Eucharitinae	252086	KC008541	KC008126, KC008156	KC008264	KC008451	French Guiana: Km 100.3 RN1 fm Kourou to Sinnamary
204	<i>Kapala</i> sp	D2801	Euch.: Eucharitinae	252085		KC008127, KC008157	KC008265	KC008452	French Guiana: Camp Patawa
205	<i>Kapala</i> sp	D2799	Euch.: Eucharitinae	252083	KC008542	KC008128, KC008158	KC008266	KC008453	Mexico: Chiapas, Rosario Izapa
206	<i>Kapala</i> sp13	D1064	Euch.: Eucharitinae	10184			KC008267	KC008454	Argentina: Salta Prov., Rosario de la Frontera
207	<i>Kapala</i> sp16	D1141	Euch.: Eucharitinae	10304	KC008543	KC008129	KC008268	KC008455	Ecuador: Orellana: Tiputini Biodiversity Sta nr Yasuni NP
208	<i>Kapala</i> sp17	D1412	Euch.: Eucharitinae	175159		KC008130	KC008269	KC008456	Panama: Corcovado
209	<i>Kapala</i> sp18	D1272	Euch.: Eucharitinae	91868	KC008544	KC008131		KC008457	Peru: Madre de Dios, Tambopata Research Center
210	<i>Kapala</i> sp4	D0934a	Euch.: Eucharitinae	92082	KC008545	AY671860	KC008270	KC008458	Honduras: Olancho, Montana del Malcate
211	<i>Kapala</i> sp5	D0938c	Euch.: Eucharitinae	92127	KC008546	AY671865	KC008271	KC008459	Ecuador: Esmeraldas Prov, Bilsa Biol. Sta.
212	<i>Kapala</i> sp7	D1173	Euch.: Eucharitinae	92029	KC008547	AY671890	KC008272	KC008460	Ecuador: Orellana: Tiputini Biodiversity Sta nr Yasuni NP
213	<i>Kapala</i> sp8	D0986	Euch.: Eucharitinae	91929	KC008548	AY671875	KC008273	KC008461	Argentina: Tucuman, Horco Molle
214	<i>Kapala sulcifacies</i>	D0379	Euch.: Eucharitinae	10296	AY552320	AY552243	KC008274	KC008462	Guatemala: Retalhuleu
215	<i>Kapala</i>	D2266	Euch.: Eucharitinae	161514	KC008549	KC008132, KC008159	KC008275	KC008463	USA: TX: Brewster Co., Big Bend Nat'l Pk, Buttrill Spg.
216	<i>Kapala nr cuprea</i>	D0938b	Euch.: Eucharitinae	92084	KC008550	AY671864		KC008464	Ecuador: Esmeraldas Prov, Bilsa Biol. Sta.
217	<i>Kapala nr cuprea</i>	D1004	Euch.: Eucharitinae	92227	KC008551	AY671879	KC008276	KC008465	Ecuador: Orellana: Res. Etnica Waorani
218	<i>Kapala nr cuprea</i>	D1068a	Euch.: Eucharitinae	92070	KC008552	AY671880	KC008277	KC008466	Argentina: Salta Prov., Oran
219	<i>Kapala nr furcata</i>	D0942	Euch.: Eucharitinae	92002	KC008553	AY671869	KC008278	KC008467	Ecuador: Esmeraldas Prov, Bilsa Biol. Sta.
220	<i>Kapala nr furcata</i> sp4	D1069	Euch.: Eucharitinae	91921	KC008554	AY671881	KC008279	KC008468	Argentina: Misiones Prov., Santa Ana, near Loreto
221	<i>Kapala</i> sp1	D1388	Euch.: Eucharitinae	92109	KC008555	AY671892	KC008280	KC008469	Costa Rica: Guanacaste Prov, Cacao Biol. Sta.
222	<i>Kapala iridicolor</i>	D0382a	Euch.: Eucharitinae	91869	AY552321	AY552244	KC008281	KC008470	Panama: Panama Prov, Soberania NP
223	<i>Kapala nr iridicolor</i>	D0936a	Euch.: Eucharitinae	92073	KC008556	AY671862	KC008282	KC008471	Ecuador: Pichincha: Rio Palenque
224	<i>Kapala nr iridicolor</i> sp1	D0947	Euch.: Eucharitinae	92092	KC008557	AY671874	KC008283	KC008472	Colombia: Cauca, NN Gorgona Alto el Mirador
225	<i>Kapala nr iridicolor</i> sp3	D0928a	Euch.: Eucharitinae	91816	KC008558	AY671856	KC008284	KC008473	Colombia: Magdalena, PNN Tayrona Zaino
226	<i>Kapala nr iridicolor</i> sp3	D0938a	Euch.: Eucharitinae	92085	KC008559	AY671863	KC008285	KC008474	Ecuador: Esmeraldas Prov, Bilsa Biol. Sta.
227	<i>Kapala nr iridicolor</i> sp3	D0939a	Euch.: Eucharitinae	92081		AY671866	KC008286	KC008475	Ecuador: Pichincha: Rio Palenque
228	<i>Kapala nr iridicolor</i> sp3	D0940	Euch.: Eucharitinae	91809		AY671867	KC008287	KC008476	Ecuador: Pichincha: Rio Palenque
229	<i>Kapala nr iridicolor</i> sp7	D1267	Euch.: Eucharitinae	92059	KC008560	KC008133	KC008288	KC008477	Honduras: Francisco Morazan, Zamorano Campus
230	<i>Kapala</i> sp10	D1121	Euch.: Eucharitinae	92008		AY671887	KC008289	KC008478	Ecuador: Orellana: Tiputini Biodiversity Sta nr Yasuni NP
231	<i>Kapala terminalis</i>	D1270	Euch.: Eucharitinae	10303	KC008561	AY671891	KC008290	KC008479	Dominican Republic: Puerto Plata
232	<i>Kapala argentina</i>	D1076	Euch.: Eucharitinae	10186	KC008562	AY671882	KC008291	KC008480	Argentina: Salta Pr., Rosario de la Frontera
233	<i>Kapala</i> nsp 17	D2261	Euch.: Eucharitinae	161512	KC008563	KC008134, KC008160	KC008292	KC008481	Dominican Republic: Punta Cana
234	<i>Kapala floridana</i>	D0432b	Euch.: Eucharitinae	92111	JN623234	AY671850	KC008293	KC008482	USA: FL: Marion Co, Juniper Spr Rd
235	<i>Kapala ivorensis</i>	D0273	Euch.: Eucharitinae	92140	KC008564	AY672990, KC008161	KC008294	KC008483	Sao Tome: Poto CIAT Compoud
236	<i>Kapala ivorensis</i>	D2693	Euch.: Eucharitinae	313	KC008565	KC008135, KC008162	KC008295	KC008484	Nigeria: Ondo State, E of Owena
237	<i>Kapala ivorensis</i>	D2772	Euch.: Eucharitinae	18900	KC008566	KC008136, KC008163	KC008296	KC008485	Madagascar: Toamasina Prov., SW of Foulpointe

**Table S3.** Mean minimum age of major eucharitid clades and the 95% highest posterior density range, in millions of years.

	mean	95% HPD
Eucharitidae origin (stem)	85.7	63.4-110.2
<b>Eucharitidae</b> (crown)	72.0	53.9-92.6
<b>Gollumiellinae</b>	56.2	37.1-76.7
<b>Oraseminae</b>	29.9	20.3-41.6
New World clade	19.6	13.0-27.5
<b>Eucharitinae</b>	52.0	40.1-65.8
formicine grade	42.9	32.2-54.4
PEM clade	37.7	28.1-49.5
Chalcura clade	26.6	18.5-35.9
Schizaspidia clade	30.3	21.4-40.2
Kapala clade	23.3	16.8-30.9

**Table S4.** Gene regions utilized and summary statistics. Partition 3 employed a codon model ((1+2),3), recommended by Brandley et al. [57].

	aligned length	% taxa complete	parsimony-inf. sites %	constant sites %	AIC model	Analysis partition
<b>18S</b>	780	71.3	7.4	89.0	GTR+G	1
<b>28S-D2</b>	680	99.6	43.6	47.4	HKY+G	2
<b>28S-D3-D5</b>	613	98.7	17.7	73.7	HKY+G	2
<b>COI</b>	780	67.9	41.5	49.5	GTR+G	3
pos 1 & 2	520		20.6	70.2	n/a	
pos 3	258		84.1	8.1	n/a	
<b>COII</b>	258	70.9	62.8	29.5	GTR+G	3
pos 1 & 2	172		47.7	41.9	n/a	
pos 3	86		93.0	4.7	n/a	

**Table S5.** Primer oligonucleotides used in this study. Sequences marked with an ‘\*’ have been modified from the original reference publication.

gene	primer	sequence	Ref.
<b>18S</b>			
	18S F (mid)	5'-AAA TTA CCC ACT CCC GGC A-3'	[58]
	18S R (mid)	5'-TGG TGA GGT TTC CCG TGT T-3'	[58]
	18Si F (inside mid)	5'-ATC GCT CGC GAT GTT TAA CT-3'	[9]
	18Si R (inside mid)	5'-AGA ACC GAG GTC CTA TTC CA-3'	[9]
	18S1 F (5' end)	5'-TAC CTG GTT GAT CCT GCC AGT-3'	[59]*
	18S4 R (5' end)	5'-GAA TTA CCG CGG CTG CTG G-3'	[60]
	18Sa F (3' end)	5'-ATG GTT GCA AAG CTG AAA C-3'	[60]
	18S9 R (3' end)	5'-GAT CCT TCC GCA GGT TCA CCT-3'	[59]*
<b>28S D2</b>			
	D2-3551 F	5'-CGG GTT GCT TGA GAG TGC AGC-3'	[61]*
	D2Ra R	5'-CTC CTT GGT CCG TGT TTC-3'	[61]*
<b>28S D3-5</b>			
	D3-4046 F	5'-TTG AAA CAC GGA CCA AGG AG-3'	[62]*
	D3-4413 R	5'-TCG GAA GGA ACC AGC TAC TA-3'	[62]*
	D5-4625 R	5'-CGC CAG TTC TGC TTA CCA-3'	[60]*
<b>COI</b>			
	COI-NJ F	5'-TAT ATT TTA ATT YTW CCW GGA TTT GG-3'	[63]*
	COI-MD R	5'-ATT GCA AAT ACT GGA CCT AT-3'	[64]*
<b>COII</b>			
	COII-MTD16 F	5'-ATT GGA CAT CAA TGA TAT TGA-3'	[63]
	COII-MTD18 R	5'-CCA CAA ATT TCT GAA CAT TGA CCA-3'	[64]

## ESM References

- Walsh P.A., Metzger D.A., Higuchi R. 1991 Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. *Biotechniques* **10**, 506-513.
- Katoh K., Kuma K., Toh H., Miyata T. 2005 MAFFT version 5: improvement in accuracy of multiple sequence alignment. *Nucleic Acids Res.* **33**(2), 511-518. (doi:10.1093/nar/gki198).
- Vaidya G., Lohman D.J., Meier R. 2011 SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. *Cladistics* **27**(2), 171-180. (doi:10.1111/j.1096-0031.2010.00329.x).
- Posada D. 2008 jModelTest: phylogenetic model averaging. *Mol. Biol. Evol.* **25**(7), 1253-1256. (doi:10.1093/molbev/msn083).
- Ree R.H., Moore B.R., Webb C.O., Donoghue M.J. 2005 A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution* **59**(11), 2299-2311.
- Ree R.H., Smith S.A. 2008 Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Syst. Biol.* **57**(1), 4-14. (doi:10.1080/10635150701883881).
- Scotese C.R. 2003 PALEOMAP Project. Accessed Sept 2012.

8. Moreau C.S., Bell C.D., Vila R., Archibald S.B., Pierce N.E. 2006 Phylogeny of the ants: Diversification in the age of angiosperms. *Science* **312**(5770), 101-104. (doi:10.1126/science.1124891).
9. Heraty J., Hawks D., Kostecki J.S., Carmichael A. 2004 Phylogeny and behaviour of the Gollumiellinae, a new subfamily of the ant-parasitic Eucharitidae (Hymenoptera: Chalcidoidea). *Syst. Entomol.* **29**(4), 544-559. (doi:10.1111/j.0307-6970.2004.00267.x).
10. Johnson J.B., Miller T.D., Heraty J.M., Merickel F.W. 1986 Observations on the biology of two species of *Orasema* (Hymenoptera: Eucharitidae). *Entomol. Soc. Wash.* **88**(3), 542-549.
11. Heraty J.M. 2000 Phylogenetic Relationships of Oraseminae (Hymenoptera: Eucharitidae). *Ann. Entomol. Soc. Am.* **93**(3), 374-390. (doi:10.1603/0013-8746(2000)093[0374:proohe]2.0.co;2).
12. Wheeler W.M. 1907 The polymorphism of ants, with an account of some singular abnormalities due to parasitism. *Bull. Am. Mus. Nat. Hist.* **23**, 1-18.
13. Girault A.A. 1913 New genera and species of chalcidoid Hymenoptera in the South Australian Museum. *Trans. R. Soc. S. Aust.* **37**, 67-115.
14. Gemignani E.V. 1933 La familia "Eucharidae" (Hymenoptera: Chalcidoidea) en la Republica Argentina. *An. Mus. Nac. Hist. Nat.* **37**, 477-493.
15. Wheeler G.C., Wheeler E.W. 1937 New hymenopterous parasites of ants (Chalcidoidea: Eucharidae). *Ann. Entomol. Soc. Am.* **30**, 163-175.
16. Gahan A.B. 1940 A contribution to the knowledge of the Eucharidae (Hymenoptera: Chalcidoidea). *Proc. US Nat. Mus.* **88**, 425-458.
17. Clausen C.P. 1941 The habits of the Eucharidae. *Psyche* **48**(2-3), 57-69.
18. van Pelt A.F. 1950 *Orasema* in nests of *Pheidole dentata* Mayr (Hymenoptera: Formicidae). *Entomol. News* **61**(6), 161-163.
19. Kerrich G.J. 1963 Descriptions of two species of Eucharitidae damaging tea, with comparative notes on other species (Hym., Chalcidoidea). *Bull. Entomol. Res.* **54**, 365-372.
20. Das G.M. 1963 Preliminary studies on the biology of *Orasema assectator* Kerrich (Hym., Eucharitidae), parasitic on *Pheidole* and causing damage to leaves of tea in Assam. *Bull. Entomol. Res.* **54**(03), 373-378. (doi:10.1017/S0007485300048884).
21. Heraty J.M. 1994 *Classification and evolution of the Oraseminae in the Old World, including revisions of two closely related genera of Eucharitinae* (Hymenoptera: Eucharitidae). Toronto, Royal Ontario Museum; 176 p.
22. Heraty J.M. 1994 Biology and importance of two eucharitid parasites of *Wasmannia* and *Solenopsis*. In *Exotic ants: Biology, impact and control of introduced species* (ed. Williams D.), p. 332. Boulder, CO, Westview Press.
23. Carey B., Visscher K., Heraty J. 2012 Nectary use for gaining access to an ant host by the parasitoid *Orasema simulatrix* (Hymenoptera, Eucharitidae). *J. Hymenopt. Res.* **27**, 47-65. (doi:10.3897/JHR.27.3067).
24. Wojcik D.P. 1989 Behavioral interactions between ants and their parasites. *Fla. Entomol.* **72**(1), 43-51.
25. Heraty J.M., Wojcik D.P., Jouvenaz D.P. 1993 Species of *Orasema* parasitic on the *Solenopsis saevissima*-complex in South America (Hymenoptera: Eucharitidae, Formicidae). *J. Hymenopt. Res.* **2**(1), 169-182.
26. Varone L., Briano J. 2009 Bionomics of *Orasema simplex* (Hymenoptera: Eucharitidae), a parasitoid of *Solenopsis* fire ants (Hymenoptera: Formicidae) in Argentina. *Biol. Control* **48**(2), 204-209. (doi:10.1016/j.biocontrol.2008.10.003).
27. Varone L., Heraty J.M., Calcaterra L.A. 2010 Distribution, abundance and persistence of species of *Orasema* (Hym: Eucharitidae) parasitic on fire ants in South America. *Biol. Control* **55**(1), 72-78. (doi:10.1016/j.biocontrol.2010.06.017).
28. Heraty J.M. 2002 *A revision of the genera of Eucharitidae (Hymenoptera: Chalcidoidea) of the world*. Gainesville, FL, American Entomological Institute; 359 p.



29. Lachaud J.-P., Pérez-Lachaud G. 2012 Diversity of species and behavior of Hymenopteran parasitoids of ants: A review. *Psyche* **2012**, 1-24. (doi:10.1155/2012/134746).
30. Mann W.M. 1918 Some myrmecophilous insects from Cuba. *Psyche* **25**, 104-106.
31. Brues C.T. 1934 Some new eucharidid parasites of Australian ants. *Bull. Brooklyn Entom. Soc.* **29**(5), 201-207.
32. Bouček Z. 1988 *Australasian Chalcidoidea (Hymenoptera). A biosystematic revision of genera of fourteen families, with a reclassification of species*. Wallingford, UK, C. A. B. International; 832 p.
33. Cameron P. 1891 Hymenopterological Notices. II. Two new species of Eucharinae. *Mem. Proc. Manch. Lit. Philos. Soc.* **4**, 182-194, pl 181.
34. Brues C.T. 1919 A new chalcid-fly parasitic on the Australian bull-dog ant. *Ann. Entomol. Soc. Am.* **12**, 13-23.
35. De Santis L. 1968 Una nueva especie de *Orasema* del Uruguay (Hymenoptera: Eucharitidae). *Rev. Soc. Uruguaya Ent.* **7**, 1-3.
36. Dodd F. 1906 Notes upon some remarkable parasitic insects from North Queensland. *Trans. Entom. Soc. London* **1**, 119-132.
37. Torrens J., Heraty J.M. 2012 Description of the species of *Dicoelothorax* Ashmead (Chalcidoidea, Eucharitidae) and biology of *D. platycerus* Ashmead. *ZooKeys* (165), 33-46. (doi:10.3897/zookeys.165.2089).
38. Lachaud J.-P., Perez-Lachaud G., Heraty J.M. 1998 Parasites associated with the ponerine ant *Ectatomma tuberculatum* (Hymenoptera: Formicidae): first host record for the genus *Dilocantha* (Hymenoptera: Eucharitidae). *Fla. Entomol.* **81**(4), 570-574.
39. Lachaud J.-P., Pérez-Lachaud G. 2001 Fourmis ponérines associées aux parasitoïdes du genre *Kapala* Cameron (Hymenoptera, Eucharitidae). *Actes Coll. Insectes Soc.* **14**, 101-105.
40. Pérez-Lachaud G., López-Mendez J.A., Lachaud J.-P. 2006 Eucharitid parasitism of the neotropical ant *Ectatomma tuberculatum*: parasitoid co-occurrence, seasonal variation, and multiparasitism. *Biotropica* **38**(4), 574-576. (doi:10.1111/j.1744-7429.2006.00169.x).
41. Bouček Z. 1956 A contribution to the knowledge of the Chalcididae, Leucospididae and Eucharitidae (Hymenoptera, Chalcidoidea) of the Near East. *B. Res. Counc. Israel* **5**(3-4), 227-259.
42. Torrén J. 2011 Estudios de biología y taxonomía de Eucharitidae (Hymenoptera: Parasitica) de Argentina, parasitoides de Formicidae (Hymenoptera: Aculeata), Universidad Nacional de Tucuman.
43. Pérez-Lachaud G., Heraty J.M., Carmichael A., Lachaud J.-P. 2006 Biology and behavior of *Kapala* (Hymenoptera: Eucharitidae) attacking *Ectatomma*, *Gnamptogenys*, and *Pachycondyla* (Formicidae: Ectatomminae and Ponerinae) in Chiapas, Mexico. *Ann. Entomol. Soc. Am.* **99**(3), 567-576. (doi:10.1603/0013-8746(2006)99[567:babokh]2.0.co;2).
44. Lachaud J.-P., Cerdan P., Pérez-Lachaud G. 2012 Poneromorph ants associated with parasitoid wasps of the genus *Kapala* Cameron (Hymenoptera: Eucharitidae) in French Guiana. *Psyche* **2012**, 1-6. (doi:10.1155/2012/393486).
45. Vásquez-Ordóñez A.A., Armbrecht I., Pérez-Lachaud G. 2012 Effect of habitat type on parasitism of *Ectatomma ruidum* by eucharitid wasps. *Psyche* **2012**, 1-7. (doi:10.1155/2012/170483).
46. de la Mora A., Philpott S.M. 2010 Wood-nesting ants and their parasites in forests and coffee agroecosystems. *Environ. Entomol.* **39**(5), 1473-1481. (doi:10.1603/en09295).
47. Buys S.C., Cassaro R., Salomon D. 2010 Biological observations on *Kapala* Cameron 1884 (Hymenoptera Eucharitidae) in parasitic association with *Dinoponera lucida* Emery 1901 (Hymenoptera Formicidae) in Brazil. *Trop. Zool.* **23**, 29-34.
48. Davis Jr. L.R., Jouvenaz D.P. 1990 *Obeza floridana*, a parasitoid of *Camponotus abdominalis floridanus* from Florida (Hymenoptera: Eucharitidae, Formicidae). *Fla. Entomol.* **73**(2), 335-337.
49. Heraty J.M. 1986 *Pseudochalcura* (Hymenoptera: Eucharitidae): a New World genus parasitic upon ants. *Syst. Entomol.* **11**, 183-212.
50. Heraty J.M., Barber K.N. 1990 Biology of *Obeza floridana* (Ashmead) and *Pseudochalcura gibbosa* (Provancher) (Hymenoptera: Eucharitidae). *Proc. Entomol. Soc. Wash.* **92**(2), 248-258.

51. Heraty J., Heraty J., Torr ns J. 2009 A new species of *Pseudochalcura* (Hymenoptera, Eucharitidae), with a review of antennal morphology from a phylogenetic perspective. *ZooKeys* **20**. (doi:10.3897/zookeys.20.126).
52. Ayre G.L. 1962 *Pseudometagea schwarzii* (Ashm.) (Eucharitidae: Hymenoptera), a parasite of *Lasius neoniger* Emery (Formicidae: Hymenoptera). *Can. J. Zool.* **40**, 157-164.
53. Maeyama T., Machida M., Terayama M. 1999 The ant-parasitic genus *Rhipipalloidea* Girault (Hymenoptera: Eucharitidae), with a description of a new species. *Aust. J. Entomol.* **38**(4), 305-309.
54. Clausen C.P. 1923 The biology of *Schizaspidia tenuicornis* Ashm., a eucharid parasite of *Camponotus*. *Ann. Entomol. Soc. Am.* **16**(3), 195-219.
55. Parker H.L. 1932 Notes on a collecting spot in France and a chalcid larva (*Stilbula cynipiformis* Rossi). (Hymenop.: Eucharidae). *Entomol. News* **43**(1), 1-6.
56. Wheeler G.C.W.a.E.H. 1924 A new species of *Schizaspidia* (Eucharidae) with notes on a eulophid ant parasite. *Psyche* **31**, 49-56.
57. Brandley M.C., Wang Y., Guo X., de Oca A.N., Fera-Ortiz M., Hikida T., Ota H. 2011 Accommodating heterogenous rates of evolution in molecular divergence dating methods: an example using intercontinental dispersal of Plestiodon (Eumeces) lizards. *Syst. Biol.* **60**(1), 3-15. (doi:10.1093/sysbio/syq045).
58. Munro J.B., Heraty J.M., Burks R., Hawks D., Mottern J., Cruaud A., Rasplus J.-Y., Jansta P. 2011 A molecular phylogeny of the Chalcidoidea (Hymenoptera). *PLoS One* **6**(11), 1-27.
59. Ouvrard D., Campbell B.C., Bourgoin T., Chan K.L. 2000 18S rRNA secondary structure and phylogenetic position of Peloridiidae (Insecta, Hemiptera). *Mol. Phylogenet. Evol.* **16**(3), 403-417. (doi:10.1006/mpev.2000.0797).
60. Schulmeister S. 2003 Simultaneous analysis of basal Hymenoptera (Insecta): Introducing robust-choice sensitivity analysis. *Biol. J. Linnean Soc.* **79**, 245-275.
61. Campbell B., Heraty J., Rasplus J., Chan K., Steffan-Campbell J., Babcock C. 2000 Molecular systematics of the Chalcidoidea using 28S-D2 rDNA. In *The Hymenoptera: Evolution, biodiversity and biological control* (eds. Austin A., Dowton M.), pp. 59-73. Canberra, CSIRO.
62. Nunn G.B., Theisen F., Christensen B., Arctande P. 1996 Simplicity-correlated size growth of the nuclear 28S ribosomal RNA D3 expansion segment in the crustacean order Isopoda. *J. Mol. Evol.* **42**, 211-223.
63. Simon C., Frati F., Beckenbach A., Crespi B., Liu H., P F. 1994 Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Ann. Entomol. Soc. Am.* **87**(6), 651-701.
64. Dowton M., Austin A.D. 1997 Evidence for AT-transversion bias in wasp (Hymenoptera: Symphyta) mitochondrial genes and its implications for the origin of parasitism. *J. Mol. Evol.* **44**, 398-405.