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Systematics and Evolution of Eucharitidae (Hymenoptera: Chalcidoidea), With a Focus on the New World Kapala

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Systematics and Evolution of Eucharitidae (Hymenoptera: Chalcidoidea), With a Focus on the New World *Kapala*

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of the requirements for the degree of

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in

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by

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ABSTRACT OF THE DISSERTATION

Systematics and Evolution of Eucharitidae (Hymenoptera: Chalcidoidea), With a Focus on the New World *Kapala*

by

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Doctor of Philosophy, Graduate Program in Entomology
University of California, Riverside, December 2014
Dr. John Heraty, Chairperson

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. Eucharitidae (Chalcidoidea) contains 54 genera and over 500 described species. Worldwide, eucharitids attack five subfamilies across the ant phylogeny. To evaluate phylogenetic relationships, a molecular dataset was used (18S, 28S-D2, 28S-D3-5, COI, and COII). Eucharitid diversification is examined, including timing of key evolutionary events, biogeographic patterns, and potential cophylogeny with ant hosts. Eucharitidae arose approximately 50 mya after their hosts, during the time when the major ant lineages were already diversifying. 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.

A speciose group of eucharitids is the ‘Kapala clade’, which is a group of genera found mainly in the Neotropics. It includes some of the most morphologically bizarre members within the family. Their monophyly is supported in both morphological and molecular analyses. However, relationships among genera within the clade are not so easily resolved. Within this clade, *Kapala* Cameron is one of the most diverse and easily recognizable genera, with species distributed across the Neotropical region and one disjunct species found in the Afrotropical region. Divergence dating and estimated mutation rates suggest that the age of this species, *K. ivorensis*, is >1 my, thus predating a human introduction. A morphological matrix of 52 characters was analyzed both separately and combined with molecular data. There was support for the Kapala clade and the described genera sampled, with three major clades being recovered. The genus *Kapala* was rendered paraphyletic by two distinct clades of other kapaline genera. A redescription is provided for the type species, *Kapala furcata,* and for *Kapala cuprea* Cameron 1913. Three new species are described, *K. deltalis* **sp. nov.**, *K. parafurcata* **sp. nov.**, and *K. quasimodo* **sp. nov**.

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1. Introduction

Within Insecta, the Hymenoptera are tremendously diverse and one of the most speciose groups. There are over 115,000 described species, which puts it at the fourth-largest insect order, and this number is expected to greatly increase with further taxonomic scrutiny (Sharkey, 2007; Heraty *et al.*, 2011). Many of the members (sawflies, bees, wasps, and ants) are economically important for a variety of reasons, including pollination, biological control, and pest status (Sharkey, 2007). Within Hymenoptera, species of the superfamily Chalcidoidea present an amazing array of morphologies and behaviors. Many of the >22,500 described Chalcidoidea are minute or small insects that attack and parasitize a wide variety of insect hosts (Bouček, 1988; Gibson *et al.*, 1999; Gillespie *et al.*, 2005; Munro *et al.*, 2011; Heraty *et al.*, 2013). Convergent morphology is common across the families (Heraty *et al.*, 2013).

A unique group is the Eucharitidae, which is the only family of insects where all members attack Formicidae (Clausen, 1940a, b; Heraty, 2002; Lachaud & Pérez-Lachaud, 2012). The first eucharitid was described as *Cynips adscendens* (Fabricius 1787). Eucharitidae contains 54 genera and nearly 500 species. The number of subfamilies is cited as either three or four: Gollumiellinae, Oraseminae, and Eucharitinae are always included, and sometimes Akapalinae, though the host of this species is not known. Using morphology, Akapalinae was recovered as sister Eucharitidae with 85% bootstrap support (Heraty, 2002). Using 18s and 28S, *Jambyia* was recovered as the sister group to Eucharitidae with no branch support (Munro *et al.*, 2011). A combined analysis of 232 morphological characters and three gene regions indicated Akapalinae was sister to Eucharitidae *sensu stricto* (Heraty *et al.*, 2013). The analysis presented in chapter 1 also places Akapalinae as sister to the rest of the eucharitids.

The Eucharitidae are found across the world zoogeographic regions including the Nearctic, Neotropical, Ethiopian, Malagasy, Palearctic, Indo-Pacific, and Australian regions, and reach their greatest abundance pantropically (Heraty, 1994a; Heraty, 2002). Heraty (2002) proposed a late Cretaceous or early Eocene origin for the family, due to disjunct distributions in the southern hemisphere. Based on two species described from Baltic amber, *Perilampus pisticus* Heraty & Darling 2009 (Perilampinae) and *Palaeocharis rex* Heraty & Darling 2009 (Eucharitinae), a minimum age of 40 my was proposed for the subfamily Eucharitinae (Heraty & Darling, 2009).

There are a number of adult and larval synapomorphies to unite the family. In adults, the pronotum is ventral to the mesonotum, not overlapping it, and is reduced and hidden in dorsal view (Heraty & Darling, 1984; Heraty, 2002). There is no malar sulcus, and the mandibles are falcate and the labrum is digitate, though these latter two features have been secondarily lost in some genera (Heraty, 1994a). Stronger support for a monophyletic group is obtained from features of the immature wasps. Eggs are stalked, and the planidial larvae have secondarily lost dorsal setae on tergites VII and IX (of 12 tergites total).

The Eucharitidae biology depends plant and ant hosts. Females do not enter the ant nest but instead eggs are laid on host plants where they hatch into active, sclerotized first-instar larvae called planidia (Clausen, 1923; Clausen, 1940b, a; Das, 1963; Heraty & Darling, 1984; Lachaud & Pérez-Lachaud, 2012; Torréns, 2013). Host plant choice has not been assessed across the family, but some members of the Kapala clade appear to restrict oviposition to one or a few plant species (Clausen, 1940a; Heraty & Darling, 1984; Torréns, 2013). The active first instar must gain access to the host nest, either by phoresy on ants or on their prey items, but the processes are still being elucidated (Clausen, 1940a; Das, 1963; Wilson & Cooley, 1972; Heraty *et al.*, 2004; Carey *et al.*, 2012; Lachaud *et al.*, 2012). Within the nest, the planidium attaches to an ant larva eventually developing on the ant pupa as an ectoparasitoid (Clausen, 1941; Heraty, 1994b; Pérez-Lachaud *et al.*, 2006).

During adult eclosion there is apparent protection for the eucharitid due to chemical mimicry, which has also been demonstrated in other termitophiles and myrmecophiles (Vander Meer *et al.*, 1989; Howard *et al.*, 2001; Howard & Blomquist, 2005). Possible co-evolution is hypothesized to explain the overlap in ant and wasp cuticular hydrocarbon profiles. This semiochemical recognition may be one factor guiding the adult ants to carry the wasps out of the nest, usually without harm, though it is not sufficient to explain this process (Howard *et al.*, 2001) and brings up additional questions as to how one wasp species can then mimic various ant hosts. Semiochemical resemblance has been studied in host-parasitoid pairings of *Solenopsis invicta* Buren 1972 and *Orasema xanthopus* (Cameron 1909)*, Ectatomma ruidum* (Roger 1860) and *Kapala sulcifacies* (Cameron 1904), and *E. tuberculatum* (Olivier 1792) and *Dilocantha lachaudii* Heraty 1998 & *Isomerala coronata* (Westwood 1874) (Vander Meer *et al.*, 1989; Howard *et al.*, 2001; Pérez-Lachaud & Lachaud, pers. comm.). Immediately after eclosion, Orasema xanthopus males were shown to share 74.2% of hydrocarbons with the ant hosts, but the similarity dropped to 14.5% in males outside of the nest (Vander Meer *et al.*, 1989). *Dilocantha lachaudii* and *I. coronata* can simultaneously infest one host ant colony. These wasps share 91% and 72% of their cuticular hydrocarbons, respectively, with *E. tuberculatum* (Pérez-Lachaud & Lachaud, pers. comm.). Only 2/10 primary hydrocarbons are shared among the two wasps and the host, leading the researchers to believe the eucharitids synthesize their own hydrocarbons *de novo* instead of acquiring them through host contact. The hydrocarbon profile similarity is believed to temporarily inhibit ant agonistic behavior, as the wasps are carried by their spines out of the nest (Howard et al. 2001).

Ants support a huge variety of myrmecophiles and make a great impact on many ecosystems (Wilson, 2008). Interestingly, few parasitoids have been able to exploit this resource (Hölldobler & Wilson, 1990; Schmid-Hempel, 1998). Eucharitids are one of the few insect groups that have succeeded as ant parasitoids. Some of these species of eucharitids are under consideration as potential biological control agents due to their positive effects on pestiferous ants, but other eucharitids may negatively impact tropical agroecosystems due to parasitization of beneficial predatory ants. The capacity of eucharitids for ant biological control needs to be further explored (Heraty *et al.*, 1993; Heraty, 1994b; Pérez-Lachaud *et al.*, 2010; Varone *et al.*, 2010), especially since they attack both beneficial and injurious ants. Parasitism levels also may depend on habitat type and complexity (de la Mora & Philpott, 2010; Vásquez-Ordóñez *et al.*, 2012). Parasitism rates can reach over 50% of ant nests sampled (Lachaud & Pérez-Lachaud, 2009; Lachaud *et al.*, 2012) though effects on colony size are unknown.

As an example of a useful association, there are a number of *Orasema* species that parasitize pests. This genus attacks mainly Myrmicinae, including some economically-important ants. *Solenopsis invicta* and *Wasmannia auropunctata* (little fire ant) are each attacked by *Orasema* species, at average levels of 33.2% – 34.1% of nests parasitized (Heraty *et al.*, 1993; Varone & Briano, 2009). However, *Orasema* has also been implicated in damaging crop plants (bananas, tea leaves, and olives) (Kerrich, 1963) due to oviposition punctures, though this is rare. In a potentially negative wasp-ant interaction, studies suggest that Kapala clade parasitism on Ponerinae and Ectatomminae ants may be undesirable in agroecosystems. For example, *K. izapa* and *K. iridicolor* putatively play a role limiting these beneficial predatory ants in coffee plantations, and parasitize ~63.1% of *Ectatomma ruidum* nests, though effects on colony size are unknown (Lachaud & Pérez-Lachaud, 2009) and de la Mora and Philpott (2010) found parasitism in ~36% of the poneromorph ant colonies collected that had pupa.

My research involves phylogenetic breadth with studies ranging from family to species and will provide a solid background for future studies across Eucharitidae. Darwin repeatedly stressed the importance of a “natural system” of species arrangement, where organisms’ shared characters are used to determine the “propinquity of descent” (Darwin, 1859). Early molecular work on Eucharitidae showed that the evolutionary relationships of the group were not as expected under the past morphological hypotheses (Heraty, 2002; Heraty *et al.*, 2004). The systematic and taxonomic studies herein provide an updated interpretation of relationships in the group, with a focus on the New World Kapala clade.

In chapter 2, the dated molecular phylogeny and higher-level relationships of eucharitids are investigated. While ant colonies serve as host to a diverse array of myrmecophiles, few parasitoids are able to exploit this vast resource (Hölldobler & Wilson, 1990; Schmid-Hempel, 1998). A notable exception is the wasp family Eucharitidae, which is the only family of insects known to exclusively parasitize ants. Worldwide, ~700 (estimated, including undescribed) Eucharitidae species attack five subfamilies across the ant phylogeny. 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.

Chapter 3 provides a closer examination of a group of New World parasitoids attacking Ponerinae and Ectatomminae. The 'Kapala clade' is a group of 13 genera found mainly in the Neotropics (Heraty, 2002; Torréns & Heraty, 2013) and now but it has now been determined there is another diagnosable genus which will be described elsewhere. Their monophyly is strongly supported in both morphological and molecular analyses. However, relationships among genera within the clade are not so easily resolved. The Kapala clade includes some of the most morphologically bizarre members within the family. Within this clade, *Kapala* Cameron is one of the most common, diverse, and easily recognizable genera, with species distributed across the Neotropical region and one disjunct species found in the Afrotropical region. *Kapala* has been traditionally defined by pleisiomorphy, lacking the derived characters (synapomorphies) of the other Kapala clade genera. A new genus is recognized, bringing the total number of Kapala clade genera to 14.

Chapter 4 comprises the study of a disjunct distribution of one species of *Kapala* distributed in the Afrotropics. Oceanic dispersal has been gaining momentum as a credible explanation to account for some of the disjunct distributions of organisms present in South America and Africa. Examples of east-to-west dispersals are accumulating, but very few instances of dispersals in the opposite direction have been documented. *Kapala*, which is common and diverse in the New World, shows the intriguing pattern of having one derived species found in the Old World tropics, ranging across Africa and Madagascar. Divergence dating and estimated mutation rates suggest that the age of this species is >1 my, thus predating a human introduction. This is the first phylogenetic-based example of an insect that has successfully colonized the Old World via trans-Atlantic dispersal from South America.

Lastly, in chapter 5, a taxonomic revision of a species group is presented. Due to the importance of revising the generic boundaries of *Kapala*, it is crucial to revisit the type species, *Kapala furcata* (Fabricius 1804), and its related species. The taxonomy of *Kapala* has been in a state of disarray for over 100 years and this project will help to remedy this deficiency in our knowledge of a group of parasitoids of eusocial ants. Molecular phylogenetic relationships were used as a guide for sorting museum specimens and determining species boundaries in the complex. Six species are recognized in the furcata species complex. A redescription is provided for the type species, *Kapala furcata*, and for *Kapala cuprea* Cameron 1913. Three new species are described, K. deltalis **sp. nov.**, K. parafurcata **sp. nov.**, and K. quasimodo **sp. nov.** All new species names presented in this dissertation are not available for scientific use until properly published.

These objectives illustrate how systematic research incorporates morphology and molecules in areas such as lineage diversification, biogeography, and taxonomy. This work will allow a better understanding of the diversity and comparative studies on morphology, biology, and host relationships of *Kapala*.

2. Chapter 1

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

2.1 Introduction

Intimate ecological associations of parasites and their hosts have been considered important in shaping species evolution (Brooks, 1985; Klassen, 1992; Poulin, 1997), an idea tracing at least back to Darwin who stressed the co-dependency of these organisms (Darwin, 1859). Host diversity, host shifts, and niche diversification are significant influences in the radiation of parasitoids (Shaw, 1988; Smith *et al.*, 2008; Elizalde & Folgarait, 2010; McLeish *et al.*, 2010), which are a specialized group of parasites that develop in or on a single host, eventually killing it (Eggleton & Gaston, 1990). Studies of host-parasitoid relationships conclude that host range is often dependent on behavioral or ecological characteristics of the host (Shaw, 1988; Whitfield, 2003) 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 (Wilson, 2008). The roughly 15,000 ant taxa (antweb.org) support at least 17 orders of arthropod myrmecophiles including specialized predators, scavengers, commensals, parasites, and trophobionts (Wheeler, 1928; Hölldobler & Wilson, 1990). Ant parasitoids are known from three insect orders: Diptera, Strepsiptera, and Hymenoptera (Wojcik, 1989; Hölldobler & Wilson, 1990; Schmid-Hempel, 1998). Although roughly 77,000 species of parasitoids are described, and more than 600,000 are estimated (Heraty, 2009), only a fraction attack ants and even fewer can gain access inside the nest (Wilson, 1971; Schmid-Hempel, 1998).

Via a complex suite of behavioral, morphological and chemical adaptations, Eucharitidae are one of the few groups to successfully circumvent the formidable colony defense mechanisms and attack immature ants (Clausen, 1923; Ayre, 1962; Vander Meer *et al.*, 1989; Howard *et al.*, 2001; Buys *et al.*, 2010). Females deposit their eggs away from the ant nest on a host plant (Clausen, 1923; Das, 1963; Heraty & Darling, 1984). 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 (Clausen, 1940a; Das, 1963; Wilson & Cooley, 1972; Heraty *et al.*, 2004), and eventually develop as an ectoparasitoid of the ant pupae (Clausen, 1941; Heraty, 1994b). 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 (Ayre, 1962; Lachaud *et al.*, 1998; Buys *et al.*, 2010). This intimate interaction is based on semiochemical recognition involving similar hydrocarbon profiles between eucharitid parasitoids and their host ants (Vander Meer *et al.*, 1989; Howard *et al.*, 2001).

An examination of the nearest relatives of Eucharitidae is necessary to understand how this life cycle might have evolved. Their paraphyletic sister group, Perilampidae (Heraty & Darling, 1984, 2009; Munro *et al.*, 2011; Heraty *et al.*, 2013), parasitize a diverse array of species including several Hymenoptera (Darling, 1992), 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 (Smith, 1912; Clausen, 1940a).

Eucharitidae are known to attack five of the 21 subfamilies of ants: Ectatomminae, Formicinae, Myrmeciinae, Myrmicinae, and Ponerinae (as referenced in Lachaud & Pérez-Lachaud, 2012) (Table S1). Along with recent ant phylogenies (Brady *et al.*, 2006; Moreau *et al.*, 2006; Schmidt, 2009), 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 due to the close dependent association. There are few studies evaluating ants and their myrmecophiles within a phylogenetic framework (Navarrete-Heredia, 2001; Shingleton & Stern, 2003; Megens *et al.*, 2005; Komatsu *et al.*, 2008), 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 mya (Grimaldi & Engel, 2005; LaPolla *et al.*, 2013) which is in general agreement with molecular divergence dating analyses that estimate an age of 115-140 mya (Brady *et al.*, 2006; Moreau *et al.*, 2006; Schmidt, 2009) (Table 1.1). Ant fossils are rare in the Cretaceous, but show a gradual increase in representation from 5% of the total Baltic amber insects to 36% of the Dominican amber insect fossils (Ward, 2010). 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 (Wilson & Hölldobler, 2005; Brady *et al.*, 2006; Moreau *et al.*, 2006; LaPolla *et al.*, 2013).

Fossil evidence suggests that the superfamily Chalcidoidea arose in the early Cretaceous (Grimaldi & Engel, 2005; Schmidt *et al.*, 2010), yet most chalcidoid families do not appear until the Eocene (Heraty & Darling, 2009; Heraty *et al.*, 2013). The sole eucharitid fossil dates to the middle Eocene (Heraty & Darling, 2009), 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 my age of the fossils (Heraty & Darling, 2009).

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: 1) establish if there is evidence for cophylogeny between eucharitids and ants, 2) determine if diversification rates of eucharitids coincide with novel host colonization, and 3) 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.

2.2 Results and Discussion

2.2.1 Eucharitid Dated Phylogeny

The monophyly of Eucharitidae is strongly supported with a posterior probability (pp) of 1.0 (Figs 1.1A, 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 (Heraty, 2002) and analyses of molecular data (Heraty *et al.*, 2004; Munro *et al.*, 2011). Previous analyses have suggested both *Akapala* (Akapalinae) (Heraty *et al.*, 2013) and *Jambiya* (Perilampidae) (Munro *et al.*, 2011) 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) (Figs 1.1B, S1). Eucharitidae diverged from the perilampid non-ant parasitoids approximately 85.7 mya (95% highest posterior density interval (HPD) = 63.4-110.2 mya) and began diversifying by 72.0 mya (53.9-92.6 mya) (Fig. 1C, Table S3). Our study and others support a relationship in which Eucharitidae renders Perilampidae paraphyletic (Munro *et al.*, 2011; Heraty *et al.*, 2013). Perilampids and eucharitids are 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 mya (56.2-94.9 mya), as inferred from 200 taxa and six genes (Cruaud *et al.*, 2012). Both Eucharitidae and Agaonidae belong to a derived clade of larger hard-bodied chalcidoid wasps (Heraty *et al.*, 2013). Our dates provide evidence for a late Cretaceous origin for this group of related families, despite the lack of described fossils for this time period.

2.2.2 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 (Figs 2, 3; 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 (Conow *et al.*, 2010) offers support for phylogenetic host tracking. 0% of random sample solutions and of random parasitoid tree simulations (mean costs = 171 & 159) returned a lower cost than the original problem solution (min. 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 due to non-overlap in host and parasitoid node ages. By the time of eucharitid crown group diversification at 72.1 mya, most ant subfamilies were established (Brady *et al.*, 2006; Moreau *et al.*, 2006; Schmidt, 2009) (Fig. 1C, Table 1.1), and there is a lack of correspondence between dates for clades of Eucharitidae and their respective ant-subfamily hosts due to older ant ages.

The eucharitid-ant association developed during a period of high ant diversification 60-100 mya (Moreau *et al.*, 2006). To reconstruct historical host associations, ancestral states were calculated over a distribution of trees using BayesTraits (Pagel *et al.*, 2004). 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 (Fig. 3). Bayesian ancestral reconstruction indicates uncertainty but suggests that the ancestral host was likely Formicinae (58%), with other ant subfamily hosts possible at a much lower probability (<14%). There are several major host colonizations throughout the history of Eucharitidae. All but one ant subfamily (Myrmeciinae) were colonized prior to ~30 mya. 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 (Figs 3, S2). Additionally, 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 mya (6.6-19.8 mya) (Fig. 3). Ectatomminae and Ponerinae were historically treated as one subfamily (Ponerinae) (Bolton, 2003), but are now known to be distantly related (Brady *et al.*, 2006; Moreau *et al.*, 2006); they are mid- to large-bodied, "socially primitive" predators in a non-phylogenetic assemblage collectively referred to as the poneromorph ants

(Bolton, 2003; Wilson & Hölldobler, 2005). Myrmeciinae are also ground-nesting generalist predators/scavengers with a simple social structure (Hasegawa & Crozier, 2006; Ward, 2010). 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) (Fig. 1). Though the host associations in this terminal PEM parasitoid group are phylogenetically diverse, the ant hosts share similar morphology and behavior.

2.2.3 Eucharitidae Diversification and Biogeography

Under a homogenous birth-death model, there are potentially two rate shifts in Eucharitidae as compared to the background (r=0.0307). Though not necessarily causative, life history or geographic 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 (Figs 3, S2; 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 (Heraty, 2002) in characteristics of body size, antennal structure, and thoracic spines. The second diversification rate increase is at the base of the New World (NW) *Orasema* (r=0.1902). As in the Old World Oraseminae genera, NW *Orasema* are able to successfully exploit the hyperdiverse *Pheidole* (Moreau, 2008), but they also parasitize five additional ant genera in the Nearctic and Neotropics including the fire ants *Solenopsis* and *Wasmannia* (Heraty, 1994b; Varone *et al.*, 2010; Lachaud & Pérez-Lachaud, 2012).

Based on reconstruction of ancestral areas using the dispersal-extinction-cladogenesis model in Lagrange (Ree *et al.*, 2005; Ree & Smith, 2008), our results support an origin of Eucharitidae in the Old World. Stem eucharitids have a relative probability of 20.2% 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%. For each, there were multiple biogeographic areas included within the 2 log likelihood unit cutoff (Ree & Smith, 2008), 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 myrmicine, formicine, and PEM parasitoid groups invaded the New World in five separate events (Fig. 1A). Adult eucharitids typically live only a few days outside of the nest, and likely could not undergo long-distance dispersal (Clausen, 1923). The low probability of chance dispersal is supported by a high degree of geographic endemism for most genera and clades [53], 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 mya (0.5-2.6 mya) (Figs 1.1A, S1; bottom branches). This is the only instance of a dispersal event from the New World to the Old World.

Ants are incredibly diverse in the Neotropics (Moreau, 2011), and the New World ant groups evolved without parasitism pressure from eucharitids until approximately 43 mya. 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* + *Lophryocera*, *Pseudochalcura*, and the 13 genera comprising the Kapala Clade), while two (*Pseudometagea* and NW *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 my (~20-43 mya), as global landmasses and climate were changing (Zachos *et al.*, 2001; Scotese, 2003). Though 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 utilized a northern dispersal route. The age of the NW *Orasema* stem at ~20-23 mya suggests this dispersal likely overlapped with the late-Oligocene warming, when arctic climate was temperate (Zachos *et al.*, 2001; Brandley *et al.*, 2011). Remarkably, the major Old World Oraseminae ant host, *Pheidole*, may have moved in the opposing direction ~30 mya, dispersing from the New World to the Old World (Moreau, 2008).

It has also been shown that ants were dispersing worldwide during the time of eucharitid diversification (Moreau, 2008; Branstetter, 2012) and were likely utilizing northern Beringial routes to move from the Old to New World 10-30 mya (Jansen *et al.*, 2010), and southern land routes to move from the New to Old World ~30 mya (Ward *et al.*, 2010). 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.

2.2.4 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 (Wheeler, 1928), with parasitoids representing the ultimate nest symbionts (Kistner, 1979). 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 occasional ant subfamily colonization (host-switching) occurring 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 due to a taxonomic affinity (Fig. 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 (Shaw, 1988; Whitfield, 2003; Klimov *et al.*, 2007) as had been hypothesized in various historical studies (Brooks, 1985; Klassen, 1992; Whitfield, 2003).

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 (Klimov *et al.*, 2007), and host switches shaped by ecological fitting (Janzen, 1985; Harvey *et al.*, 2012), where organisms can succeed in a novel environment due to their suite of traits previously evolved. Eucharitids potentially have succeeded in diversifying on many ant taxa due to the mechanism by which the planidia unite with the hosts and subsequently by how immatures and adults mimic host hydrocarbon profiles (Vander Meer *et al.*, 1989). Evidence exists of other myrmecophiles that facilitate shifts among different ant hosts by exploiting communication codes (Kistner, 1979).

2.3 Conclusions

Eucharitids colonized ants by approximately 72 mya 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 utilize 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 (Wilson, 1971; Hölldobler & Wilson, 1990) .

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 >25% of pupae parasitized (Clausen, 1923; Pérez-Lachaud *et al.*, 2010). Their success suggests that they could form a promising model for the investigation of parasitoid impact on ant colonies (Lachaud & Pérez-Lachaud, 2012). 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 (see Whitfield, 2003). 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.

2.4 Materials and Methods

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 (Table S2). Five gene regions were sequenced: 18S, 28S-D2, and 28S-D3-D5 (nuclear), and COI and COII (mitochondrial) (Text S1). Genbank accession numbers are given in Table S2, and the aligned matrix is deposited in Dryad (datadryad.org; doi:10.5061/dryad.qn57t). Summary statistics and primers are compiled for each gene region in Tables S4 and S5. Specimen images can be found on Morphbank (morphbank.net) under collection number 816728.

2.4.1 Phylogenetic analyses, divergence dating, and rate diversification

Gene regions were partitioned into three unlinked groups: 18S, 28S D2-D5, and COI+COII (Table S4). To streamline computation and tree-drawing, monophyly was enforced for Perilampidae + Eucharitidae because this has been supported in previous studies (Heraty *et al.*, 2004; Munro *et* *al.*, 2011; Heraty *et al.*, 2013). 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. **1)** *Monodontomerus* sp. (Torymidae) (Brues, 1923) was used to constrain the crown outgroup Torymidae. **2)** *Perilampus pisticus* (Perilampidae: Perilampinae) (Heraty & Darling, 2009) was used to calibrate the crown node at the base of the present-day paraphyletic *Perilampus*. **3)** *Palaeocharis rex* (Eucharitidae: Eucharitinae) (Heraty & Darling, 2009), 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 ± 1.1 million years (Ritzkowski, 1997), 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 my for the included fossils, with the highest prior probability at 44.1 mya.

In BEAST v1.6.2 (Drummond & Rambaut, 2007), two MCMC chains were run to 200 million generations, logging parameters every 20,000. We also ran an empty alignment to verify that the data was driving the posterior probability distributions (Sanders & Lee, 2007). Subsequent to the phylogenetic analysis, Tracer v1.5.0 (Rambaut & Drummond, 2007) confirmed the effective sample size (ESS) of the posterior and all major clades reached >200. LogCombiner v1.6.2 and TreeAnnotator v1.6.2 were used to combine the trees from the two runs and then obtain a single tree of highest clade probabilities. 10,002 trees were removed as burnin, for a final distribution of 10,000 trees.

Eucharitidae clade diversification was analyzed using turboMEDUSA (Harmon *et al.*, 2011) in R (v2.13.1, R Development Core Team 2011). MEDUSA (modeling evolutionary diversification using stepwise AIC) uncovers diversification rate shifts in the phylogeny by fitting alternative models to the input chronogram (Alfaro *et al.*, 2009). 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 (2002) and the Universal Chalcidoidea Database (Noyes, 2012). The input combination of phylogeny and taxonomy is used to reveal clades that deviate statistically from the number of species expected due to age of the group.

2.4.2 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 utilized Jane 4 (Conow *et al.*, 2010) 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. (Moreau *et al.*, 2006). 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 due 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: 1) 'random tip mapping' of the two phylogenies, and 2) 'random parasite tree' calculation at beta=-1.0. A result of <5% of random solutions as better than the observed cost total is strong evidence for cophylogeny (Libeskind-Hadas, 2011).

Ant host associations are available for 29 of the 44 eucharitid genera in the dataset (Table S1). BayesTraits v1.0 (Pagel *et al.*, 2004) 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 mil generations. We employed 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%, which did result in mean acceptance rate of 24.5% of the 3000 post-burnin trees. Tracer v1.5.0 was used to confirm ESS >200 and to obtain the mean output value for all five subfamily probabilities at each node of interest. In addition, Mesquite v2.73 (Maddison & Maddison, 2010) 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) (Ree *et al.*, 2005; Ree & Smith, 2008), 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 (Ree *et al.*, 2005) with a script assembled via the online configurator. Seven areas were recognized: 1) North and Central America including Caribbean, 2) South America and Lesser Antilles, 3) Ethiopian, 4) Malagasy, 5) Indo-Pacific, and 6) Australian, following Heraty (2002). However, Central America/Caribbean is here included with North America instead of with South America as in (Heraty, 2002) due to its historic connection with the northern landmass. We developed dispersal constraints for four time periods (Text S2). All 229 terminals of Perilampidae and Eucharitidae were coded for geographic range according to specimen collection locality.

2.5 Figures and Tables

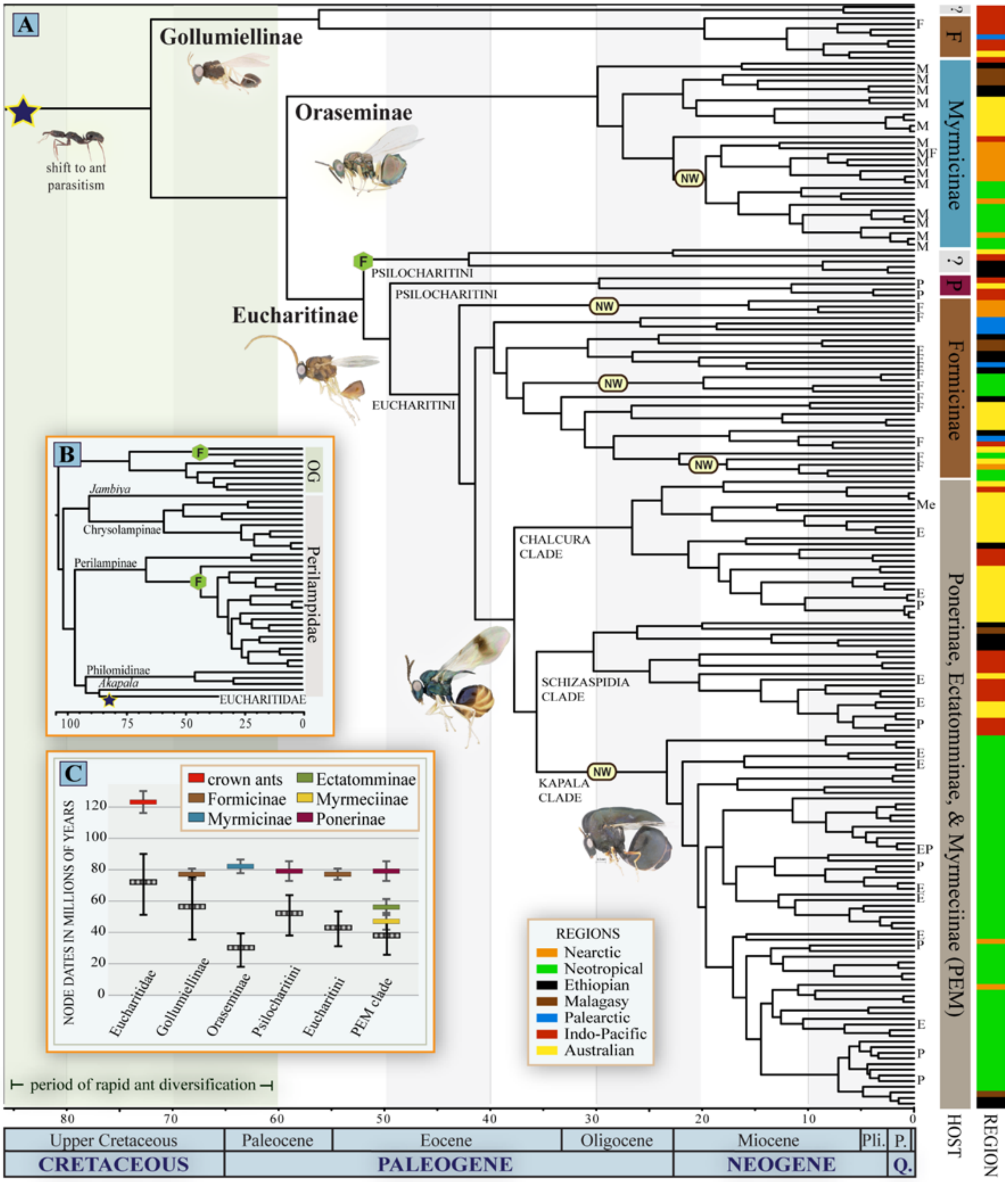


FIGURE 2.1.

A) Fossil-calibrated phylogeny of Eucharitidae. 237 taxa analyzed. Terminal labels, posterior probabilities, and error range of node ages found in Fig. S2.1 (Supplementary Information). 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=Myrmeciinae, M=Myrmicinae, P=Ponerinae. Ant image modified 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 (Schmidt, 2009), remaining from Brady et al. (Brady *et al.*, 2006)).

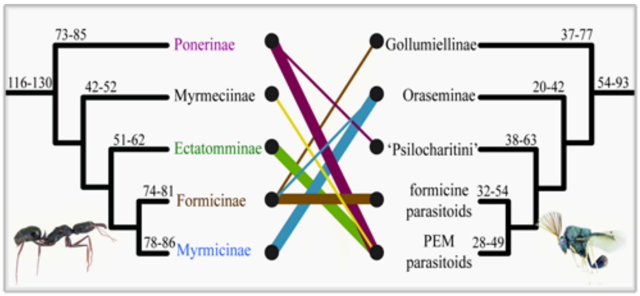


FIGURE 2.2.

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. (Moreau *et al.*, 2006). 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 Fig 2.1C.

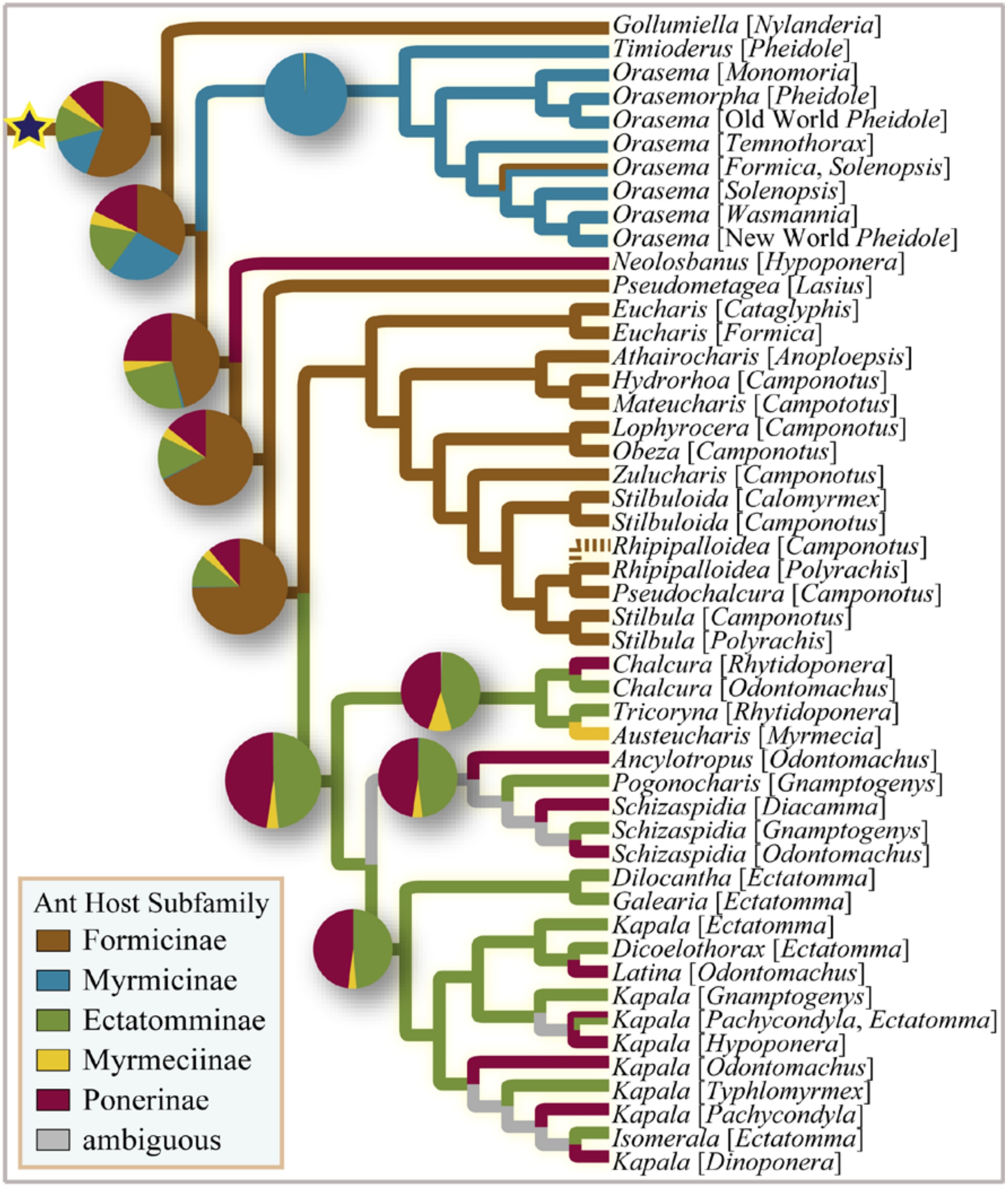


FIGURE 2.3.
Ancestral state reconstruction. 48 terminal taxa in analysis, with each genus of ant host represented by a parasitoid taxon (Table S2.1). Dashed line indicates the record was included for illustrative purposes (taxa not in data matrix). Pie charts at selected nodes display proportional probability under Bayesian inference. Colored branches show parsimony reconstruction. Terminals labeled by eucharitid genus, with ant genera in brackets.

	Moreau *et al.* (2006) **min. age fossils**	Brady *et al.* (2006) **145 MY root**	Schmidt (2009) **155 MY root**	oldest known fossils
Formicidae w/ Martialinae	n/a	n/a	123 (116-130)	100 (Dlussky, 1996)
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 (Grimaldi *et al.*, 1997)
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 (Archibald *et al.*, 2006)
Ectatomminae	79.5 (78.6-80.4)	56 (51.9-61.1)	n/a	79 (Engel & Grimaldi, 2005)
Formicinae	92.0 (91.8-92.2)	77 (73.5-80.5)	66 (56-76)	88.6-92 (Grimaldi & Agosti, 2000)
Myrmicinae	99.8 (95.6-104)	82 (77.7-86.3)	76 (66-85)	52 (Poinar Jr. *et al.*, 1999)

TABLE 2.1.
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.

3. Chapter 2

Tracing evolution in the Kapala clade ant parasitoids (Hymenoptera: Eucharitidae) using molecules and morphology

3.1 Introduction

Eucharitidae (Hymenoptera: Chalcidoidea) is a unique insect family in that all members are ant parasitoids (Heraty, 2002; Lachaud & Pérez-Lachaud, 2012). Eucharitids are one of the few groups to successfully evade colony defenses and parasitize immature ants in the nest (Clausen, 1923; Ayre, 1962; Pérez-Lachaud *et al.*, 2006b; Buys *et al.*, 2010) and are known to known to parasitize five of the sixteen ant subfamilies (Heraty, 2002; Lachaud & Pérez-Lachaud, 2012; Murray *et al.*, 2013; Torréns, 2013; Bolton, 2014).

Within Eucharitini (Eucharitinae), there is a monophyletic group that attacks ponerine, ectatommine and myrmeciine ants (PEM clade). The PEM clade is supported by molecular and some morphological analyses (Heraty, 2002; Murray *et al.*, 2013) and is composed of three groups: the Old World Chalcura and Schizaspidia clades and the New World Kapala clade (KC). Within the PEM clade, adults possess some of the most distinctive structures within Chalcidoidea. The Kapala clade and most of the Schizaspidia clade have scutellar projections originating posteriorly on the mesosoma, although these are believed to be independent characters; the Kapala clade has paired spines separated at the base, while the Schizaspidia clade has a forked projection (Heraty, 2002). No Chalcura clade genera possess scutellar spines.

The morphology and phylogenetic distribution of spine presence within the PEM clade suggest at least two independent origins of scutellar spines (Heraty, 2002; Murray *et al.*, 2013).

Murray *et al.* (2013) demonstrated that the Old World PEM parasitoids form a phylogenetic grade to the New World Kapala clade, with the Schizaspidia clade as the KC sister group. The Paleotropical Chalcura clade reaches its highest diversity in Australia and is found from Africa to the eastern Indo-Pacific islands, but is rare in mainland Asia and does not reach the Palearctic (Heraty, 2002). The primarily Paleotropical Schizaspidia clade is found in Africa and Australia and reaches north into Japan and the southeastern Palearctic region, but is most common in southeast Asia and the eastern Indo-Pacific islands (Heraty, 2002). Reconstruction of ancestral areas indicated the KC may have diverged from ancestors in the Ethiopian region, approximately 35 mya (26-46 mya) (Murray *et al.*, 2013). It reaches its highest diversity in the Neotropics (Heraty, 2002), but is found in the Nearctic region in Mexico and the southern US (Arizona, Florida, and Texas). It is found south to northern Argentina and is also in the Galapagos and across the Caribbean and West Indies, but is absent from Chile.

The KC members are the only New World eucharitids known to attack Ponerinae and Ectatomminae (Lachaud & Pérez-Lachaud, 2012; Murray *et al.*, 2013; Torréns, 2013). Ponerinae and Ectatomminae are included in the umbrella group of poneromorph ants, which are six subfamilies of mid- to large-bodied, typically specialist or generalist hypogaeic predators (Ward, 2000; Wilson & Hölldobler, 2005; Taylor, 2007). Poneromorph ants (Ponerinae *sensu lato*) are "globally successful yet socially primitive" (Wilson & Hölldobler, 2005). Ectatomminae was split from Ponerinae (Bolton, 2003), and subsequent large-scale phylogenies using molecular data showed that these two ant subfamilies are not closely related (Brady *et al.*, 2006; Moreau *et al.*, 2006). *Austeucharis* (Chalcura clade) is the only eucharitid known to parasitize Myrmeciinae (Cameron, 1891; Brues, 1919). Myrmeciinae, though not a poneromorph, is also considered to have “primitive” ecological, biological, and morphological characteristics and is composed of ground-nesting generalist predators or scavengers (Ward & Brady, 2003; Ward, 2010). This makes it apparent that the PEM parasitoids do not attack ants due to their phylogenetic relatedness, but likely utilize hosts based on shared convergent characteristics such as foraging behavior and body type (Murray *et al.*, 2013).

The availability of both host plants and ants restrict the distribution of Eucharitidae (Clausen, 1940b, 1941). Females do not enter the ant nest; eggs are laid on host plants where they hatch into active, sclerotized first-instar larvae called planidia (Clausen, 1923; Clausen, 1940b, a; Das, 1963; Heraty & Darling, 1984; Lachaud & Pérez-Lachaud, 2012; Torréns, 2013). Host plant choice has not been assessed across the family so there is no data on most genera, but it is observed that some members of the Kapala clade appear to restrict oviposition to one or a few plant species (Clausen, 1940b; Heraty & Darling, 1984; Torréns, 2013). The active first instar must gain access to the host nest, either by phoresy on ants or on their prey items (Clausen, 1940a; Das, 1963; Wilson & Cooley, 1972; Heraty *et al.*, 2004; Carey *et al.*, 2012; Lachaud *et al.*, 2012). Within the nest, the planidium attaches to an ant larva eventually developing on the ant pupa as an ectoparasitoid (Clausen, 1941; Heraty, 1994b; Pérez-Lachaud *et al.*, 2006b). While other eucharitid planidia may be endoparasitic or ectoparasitic, all records from the PEM clade indicate ectoparasitism (Wheeler & Wheeler, 1937; Ayre, 1962; Heraty, 1994a; Lachaud & Pérez-Lachaud, 2001; Heraty *et al.*, 2004; Pérez-Lachaud *et al.*, 2006b; Pérez-Lachaud *et al.*, 2006a;

Lachaud *et al.*, 2012; Torrens & Heraty, 2012; Vásquez-Ordóñez *et al.*, 2012; Heraty & Murray, 2013; Torréns & Heraty, 2013). Eucharitid biology is not conducive to dispersal independent of their hosts; females are proovigenic and oviposit near to the ant nest, flying no farther than necessary (Clausen, 1941). Those that lay eggs en masse do so typically on the day of emergence, even within the hour, while others may oviposit over the course of a week (Clausen, 1940b, 1941).

Eucharitidae are both plant-host and ant-host specific, though for some species, they do use multiple suitable plant hosts, with plant use often governed by the suitability of the site where the eggs are oviposited. There are a number of life history characteristics that unite the PEM clade and distinguish it from the other Eucharitidae. In the closet relatives to the PEM parasitoids, the formicine grade, females lay eggs in unripened fruits, in flower buds or under flower bracts, or within tree buds (Clausen, 1923; Clausen, 1940a; Heraty & Barber, 1990; Torréns, 2013). Members of the Chalcura and Schizaspidia clades are known to oviposit under bud scales, in leaf and flower buds, on the undersides of leaves (Clausen, 1928; Ishii, 1932; Clausen, 1940a; Heraty, 2002), and in at least one species (*Schizaspidia antennata* Gahan), into incisions in the undersides of fleshy leaves (Clausen, 1940b). The Old World Chalcura and Schizaspidia clades have been recorded from eight plant families: Boraginaceae, Euphorbiaceae, Fabaceae, Lamiaceae, Melastomataceae, Meliaceae, Moraceae, and Myrtaceae (Clausen, 1928; Ishii, 1932; Clausen, 1940b; Heraty, 2002). The New World KC is recorded from nine plant families: Amaranthaceae, Asclepiadaceae, Asteraceae, Boraginaceae, Euphorbiaceae, Malvaceae, Rubiaceae, Sapindaceae, and Verbenaceae (Clausen, 1940a; Berry, 1947; Torréns *et* *al.*, 2007; Torrens & Heraty, 2012; Torréns & Heraty, 2013), of which only Euphorbiaceae and Boragninaceae overlap with the Old World PEM parasitoid plant hosts for oviposition.

All of the PEM parasitoid clade larval stages possess a number of synapomorphies that support monophyly, despite a lack of adult morphological synapomorphies supporting the clade (Brues, 1919; Clausen, 1940a; Heraty, unpublished). These include the presence in the planidium of long spines on the terminal segments and stiff caudal cerci which allow it to stand erect while waiting for an ant worker (Clausen, 1923; Clausen, 1941). Mature PEM larvae possess a pronounced dorsal hump on the thorax (Clausen, 1940a) and the pupae possess a unique set of ocellar horns on the head and lateral abdominal projections of unknown function (Brues, 1919; Pérez-Lachaud *et al.*, 2006b).

Heraty (2002) used 88 morphological characters in an analysis of the genera of Eucharitidae and recovered a monophyletic New World Kapala clade (Fig. 2 inset). Diagnostic characters include: distinct anteclypeus, most with elongate, paired scutellar spines (habitus images, Fig. 1), small lateral axillar lobes, frenal line demarking a lateral shelf, emarginate propodeal spiracles, and marginal vein of hind wing incomplete (Heraty, 1998; Heraty, 2002). The KC is composed of 13 genera, and the genus *Kapala* Cameron is the most numerically abundant and diverse member, having the widest distribution and comprised of 18 described species. *Kapala* is easily recognizable, however there are no synapomorphies, and a monophyletic *Kapala* is has been proposed based only on similarity in morphology (Heraty, 2002) but is never recovered as monophyletic in molecular analyses at the family level (Heraty *et al.*, 2004; Murray *et al.*, 2013). One species, *Kapala ivorensis* Risbec, is the only Old World member of the clade, and it is widespread across the Afrotropical region (Heraty, 2002; Murray & Heraty, in prep.-b). The New World *Carletonia* Heraty was recovered as the sister genus outside the KC in a majority of analyses, based on what were recognized as homoplastic characters (Heraty, 2002). There is no molecular information to lend additional insight to phylogenetic placement on this rarely-collected genus. *Carletonia* resembles Old World genera *Eucharissa* Westwood and *Saccharissa* Kirby (in the Schizaspidia clade) and is morphologically distinct from the Kapala clade in that it has no scutellar spines and the male antennae are double-branched on the funicle (Heraty, 2002).

Across the Kapala clade (KC), multiple bizarre morphological modifications have led to the description of numerous genera. Head shape, antennal morphology, sculpture patterns, and spine morphology are particularly variable across the clade (Figs 1, 4). The extreme phenotypes are best exemplified by the paired spines; they vary from those in *Kapala* which are slightly curved and linearly carinate, to forms in other genera that differ from circularly striate to smooth (*Lasiokapala* Ashmead and some *Lirata* Cameron), dorsoventrally flattened and narrowly separated (*Dicoelothorax* Ashmead and *Dilocantha* Shipp), to broadly arched and forming a carapace over the gaster (*Galearia* Brullé and *Thoracantha* Latreille). Sexual dimorphism is mostly confined to differences in antennal morphology, morphology of the metasoma, and differences in scutellar spine morphology where the spines of the males are much more reduced and slender than those of females (*Dicoelothorax*, *Galearia,* and *Dilocantha)*. One of the other more bizarre modifications is in *Isomerala* Shipp, in which the eyes are conical-shaped and the frons has swollen protuberances (Fig. 3 inset), both features not seen elsewhere in Hymenoptera. While most KC genera are defined by features of the spines, the genus *Kapala* is recognized by its consistent phenotype across species and relatively invariable pleisiomorphic morphology in comparison to most other genera.

Using five gene regions and multiple analytic frameworks, we elucidate the relationships of the Kapala clade genera using the largest molecular data matrix of New World Eucharitidae to date. The historical disagreement in the relationships of the KC genera based on morphological hypotheses versus molecular hypotheses motivates us to explore relationships using a dataset focused specifically on broad sampling of the KC. We have all thirteen genera available for morphological coding, and have eleven genera available for molecular analyses. Understanding generic relationships in this clade is the foundation for interpreting biological data and morphological transformations across the group. A dated phylogeny will allow review the life history traits and behavior in a phylogenetic context. In addition, it allows us to explore the pattern of diversification rates across the clade. We aimed to test the diversification rate to find if specific clades which exhibited bizarre morphological phenotypes also had a higher rate of diversification. In morphological and molecular analyses, we find that the monophyly of each of the genera in the Kapala clade is supported, except for the polyphyletic *Kapala*. Molecular phylogenetic results are compared to morphology-based hypotheses of relationships, and the utility of genetic and phenotypic characters is discussed.

3.2 Materials and Methods

The molecular matrix has a total of 195 specimens, with 189 from the Kapala clade, representing an estimated 100 species (Table S1). Outgroup taxa are from the Old World sister group, three taxa each from the Chalcura and Schizaspidia clades. The monophyly of the KC in not in question, but we have sampled a variety of genera in order to polarize the morphological characters. Eleven of the 13 Kapala clade genera are included in the molecular matrix, from 25 countries, with only *Parakapala* Gemignani and *Liratella* Girault with no molecular data. We also lack molecular data for the putative Neotropical sister genus to the Kapala clade, *Carletonia*. These three genera were all included in the morphological character matrix.

Both fresh and dried specimens were used for DNA extraction. Specimens were non-destructively extracted using a chelex-proteinase-K protocol (see supplementary materials, Murray *et al.*, 2013) or DNeasy (Qiagen). Five gene regions were sequenced for three nuclear ribosomal (18S, 28S-D2, and 28S-D3-D5) and two mitochondrial (COI and COII) gene fragments with protocols following Murray *et al.* (2013). Amplified DNA was purified using GeneClean (MP Biomedicals) and sequenced at the IIGB Genomics Core Facility at UC Riverside. Sequencher 4.8 (Gene Codes Corp) was used to verify and edit chromatograms.

Individual genes were aligned using the MAFFT online server (Katoh *et al.*, 2005) under default settings. For nuclear ribosomal genes, the E-INS-i algorithmic strategy was applied, and for mitochondrial genes, the G-INS-I strategy was applied, with a post-alignment manual modification to correct a 3-bp COII insertion to be codon-aligned. SequenceMatrix 1.7.7 (Vaidya *et al.*, 2011) was used to concatenate genes for a final matrix.

Two data sets were used: ‘all taxa’ and ‘complete genes’ (Table S2). The ‘all taxa’ (AT) dataset (2942 bp) includes 195 taxa: 189 Kapala clade individuals and 6 outgroups. The ‘complete genes’ (CG) dataset includes 96 taxa: 92 Kapala Clade individuals and 4 outgroups, composed of the 94 specimens having data for all five gene regions, plus two additional taxa for sampling purposes (*Thoracantha*: no COI, *Lirata*: no COI or COII) – we needed to include *Thoracantha* and wanted a total of two *Lirata* taxa in order to get a dating estimate on the genus. In order to determine if the two taxa with incomplete data significantly affected tree topology, the symmetric distance (Robinson & Foulds, 1981) was calculated in phangorn (Schliep, 2011) to give an estimate of tree similarity of the 94 vs 96 taxa matrix by calculating branching difference. The normalized symmetric difference of the Bayesian results of the 94-taxa and the 96-taxa pruned of the two terminals was compared to the normalized symmetric difference of the 96-taxa Bayesian tree and the 96-taxa ML tree. The 94 vs 96 Robinson-Fould's metric was low, at 0.09, even smaller than the 96 ML vs 96 Bayesian difference of 0.28, and the two taxa were included in the final analyses.

The 18S and COI gene regions were often present in different lengths due to the use of differing primers by various researchers. Hence, the 96 taxa dataset is shorter (2350 bp total) than the 195 taxa matrix, due to removing the 5' and 3' ends of 18S that were not sequenced for all taxa (217 bp trimmed) and COI (372 bp trimmed). This was done because utilizing incompletely sequenced genes may be detrimental to an analysis (Roure *et al.*, 2013), so the aim was to use the portion that was present for all taxa.

Finally, morphological characters were coded for analysis alone and in a combined matrix with the taxa with complete genes. The characters had three origins: 1) directly from Heraty (2002) or Heraty and Woolley (1993), 2) modified from Heraty (2002), or 3) developed for the Kapala Clade. Of the 52 characters, 20 are of the head and antenna, 17 are from the mesosoma, 6 are on the gaster, and 9 are found on the leg and wing. See SI for the character list. All terminals were coded by species (not specimen) to allow for polymorphism and to incorporate male and female characters. Additionally, several terminals were coded at the genus-level: *Carletonia* (New World, unplaced PEM clade), *Liratella*, and *Parakapala* (New World KC), which matched with no molecular terminals, and *Austeucharis*, *Chalcura* (Old World Chalcura clade), *Ancylotropus*, and *Schizaspidia* (Old World Schizaspidia clade), which were outgroups. These were coded at the genus level to account for polymorphisms and encompass a larger amount of outgroup morphological variation. There were a total of 99 taxa in the morphological and combined analyses. Mesquite (Maddison & Maddison, 2010) was used for ancestral state reconstruction in a parsimony framework on the combined data topology.

3.3 Phylogenetic Analyses

Four phylogenetic methods were used to reconstruct the evolutionary history of the Kapala Clade: parsimony, maximum likelihood, Bayesian inference, and Bayesian molecular dating.

3.3.1 Parsimony

TNT vMay2014 (Goloboff *et al.*, 2008a) was used for parsimony reconstruction using the New Technology Search. Gaps were coded as missing data. For all analyses, sectorial search, ratchet, tree drifting, and tree fusing (10 rounds) were used. TNT was used for molecular data, morphological data, and for the combined molecular and morphological data. Implied weighting was used in the morphological and combined analyses to down-weight the most homoplasious characters using a concavity function (k=3, 15, or 45) (Goloboff *et al.*, 2008b). Branch support values are based on 1000 bootstrap replicates.

3.3.2 Maximum Likelihood

For maximum likelihood analyses, RAxML v8.0.24 (Stamatakis *et al.*, 2008) through the CIPRES interface (Miller *et al.*, 2010) was employed. Data were partitioned by gene, with the mtDNA each separated into positions (1+2) and (3). Branch support was assessed using 1000 rapid bootstrap replicates under GTRCAT. Other values were kept as default. After recovering the best tree under maximum likelihood, this topology was compared to a constraint tree, where all taxa morphologically recognized as *Kapala* were constrained as monophyletic, with the rest of the Kapala Clade taxa unconstrained in placement. This was based on current analyses, so that a clade identified as a New Genus was not included in the constrained *Kapala* set. RAxML was used with 1000 rbs and an identical starting seed for each. The Shimodaira-Hasegawa test (Shimodaira & Hasegawa, 1999) was employed in phangorn (Schliep, 2011) under a GTR model, with 10000 bootstrap replicates. This test assumes *a priori* that all hypotheses are equivalent.

3.3.3 Bayesian

Bayesian phylogenetic inference was performed in MrBayes v3.2.2 (Ronquist *et al.*, 2012) through the CIPRES interface (Miller *et al.*, 2010). Early analyses showed problems with stationarity and convergence, as diagnosed using the average standard deviation split frequencies and the posterior distribution of the log likelihood of each run in Tracer. In addition, the posterior probabilities of the rate multipliers for each gene did not coincide with expected relative mutation rates for ‘fast’ mtDNA and ‘slow’ rDNA partitions.

Previous studies have shown that the MrBayes’ initial starting tree length can contribute to errors in phylogeny estimation under partitioned datasets (Brown *et al.*, 2010; Marshall, 2010; Zhang *et al.*, 2012). This will drive a shift in other parameters, notably the rate multipliers for each data partition, leading the MCMC chain to commit to a “long-tree solution” (Marshall, 2010). Our hypothesis that the MCMC chain was not finding the best parameter space was supported by two pieces of evidence: 1) the uncorrected distance indicated more divergence in mtDNA than in rDNA; average base pair distance of the 92 Kapala clade taxa (from the CG matrix) was 10.05% in COII and 1.46% in D2. In addition, 2) the ML analyses produced a branch length an order of magnitude smaller than in the Bayesian maximum clade credibility trees when the analyses were run under five partitions (each gene substitution model unlinked). We addressed this problem by placing a more informative prior on branch length by increasing the rate of the exponential prior, utilizing an exponential distribution with a mean of 0.01 [exp(100)] instead of the default mean of 0.1 [exp (10)], to effectively shorten overall tree length. Molecular analyses were run under a five-partition scheme by gene region with mtDNA treated under a codon model and a seven-partition scheme by gene region, with COI and COII each split into positions (1+2) and (3). For a combined analysis with morphological data, the latter scheme was used with the addition of a morphological block under the Markov k-state 1-parameter (Lewis, 2001).

The Bayesian analyses were run to convergence as assessed using the split frequency of the two runs (<0.01 at completion) and the adequacy of the posterior parameter distributions (confirmed to be >200 ESS) in Tracer v1.5 (Rambaut & Drummond, 2007). Tracer was also instrumental in diagnosing early problems of convergence and appropriate posterior gene mutation rates. TreeAnnotator v1.8 (Drummond & Rambaut, 2007) was used to assemble the maximum clade credibility tree after burnin.

3.3.4 Dating

We wanted to compare the relative ages of the genera in the clade. There are no fossils within the Kapala Clade to calibrate internal nodes, so we used an estimate for the stem age of the entire KC clade from a previous analysis (Murray *et al.*, 2013). The previous fossil-calibrated dating analysis was run on the same five genes used here (though with differing parameters), incorporating 237 taxa across Eucharitidae and Perilampidae plus chalcidoid outgroups from Pteromalidae and Torymidae. For the current analyses presented, a normal distribution was set on the stem of the KC based on the node age posterior probability density of previous results, using a mean at 35.6 years, and a sigma of 6 to follow the 95% HPD range, in BEAUTi v2.2 (Bouckaert *et al.*, 2014). The genes were partitioned with the trees and clock rates linked and the nucleotide substitution rates unlinked; the ribosomal data were partitioned by gene, and in the AT dataset, COI and COII were each partitioned into positions 1+2 and position 3. In the CG dataset, the COI and COII were not split into (1+2),(3). The mutation rate of one gene, D2, was fixed to 1 (Drummond & Bouckaert, 2014) and analyses did not converge if this step was omitted. The add-on RBS v1.1 (Bouckaert *et al.*, 2013) was employed in BEAUTi v2.2 to allow for a reversible-jump MCMC in lieu of choosing each partition's nucleotide substitution model. Taxon D2782 was removed from the analysis, leaving 194 taxa, because it was jumping around the tree and was putatively producing topologies not consistent with the previous MrBayes analyses. The KC was constrained as monophyletic, the tree was built under a Yule process, and a diffuse gamma distribution was set on the birth rate and the UCLD clock mean (alpha=0.001, beta=1000). BEAST v2.2 (Bouckaert *et al.*, 2014) was run on a desktop computer, in conjunction with BEAGLE v2.1 (Ayres *et al.*, 2012). Two MCMC chains were run to 100 million generations, sampling every 10,000. Tracer v1.5.0 (Rambaut & Drummond, 2007) was used to confirm the effective sample size (ESS) of the posterior probability distributions. TreeAnnotator v1.8.0 was used to obtain a single tree of highest clade probabilities after removing burnin.

3.3.5 Branch Support

After reviewing phylogenetic tree results, we implemented a program designed to identify taxa that potentially contribute to low branch support and reduced resolution in the tree. We used the online interface of RogueNaRok (Aberer *et al.*, 2013), a tool for identifying 'rogue' taxa that are placed in contradictory positions in each topology over the course sampling of the ML bootstrap replicates or Bayesian generations. The support value increase that occurs if the rouge taxon or set of taxa are pruned is then calculated. The sampled tree set from the 96-taxa Bayesian analysis (10000 trees) was analyzed using RogueNaRok, using a threshold majority-rule consensus tree and a maximum dropped set of two taxa. AWTY (Nylander *et al.*, 2008) was used to summarize the distribution of trees containing alternative placements of the genus *Galearia*.

3.3.6 Diversification

Kapala clade diversification across a posterior distribution of trees was analyzed using MEDUSA (Alfaro *et al.*, 2009) v0.93-4-33 in R (v3.1.1, R Development Core Team). MEDUSA calculates diversification rate shifts in the phylogenies by fitting alternative models to the input chronogram. The input combination of phylogeny and taxonomy is used to reveal clades that deviate statistically from the number of species expected due to age of the group. From an initial model specifying one rate across the phylogeny, rate change breakpoints are inserted successively under a corrected AIC criterion. We included 26 terminals in the Kapala clade chronogram, representing the major species groups, and specified the estimated species richness of each genus using projected species numbers from Heraty (2002) and also estimated the species of *Kapala* subclades. The input of taxonomic diversity helps to amend the effects of incomplete phylogenetic sampling. Diversification shifts are calculated under mixed Yule and birth-death models, with shifts occurring at the nodes.

The normalized Colless index of imbalance (Colless, 1982) was used to test for tree balance, where a output value of 0 is completely balanced and 1 indicates pectinate or comb-like trees. The balance of a tree is the extent to which nodes define subgroups of equal size (Mooers & Heard, 1997) and imbalance potentially can indicate biased speciation (Blum & Francois, 2005).

3.4 Results

The Kapala clade is highly supported as a monophyletic group using both molecules and morphology for phylogenetic reconstruction. The overall Kapala clade topology is apportioned into three groups (Figs 2-4, S1-S5). Group 1 is sister to the rest of the Kapala Clade. The monophyly of Group 2 + Group 3 has support under most analyses. Overall relationships are reported below, with a short listing of diagnostic characters. A summary of major-clade support across analyses is found in Table 1, along with the figure numbers of phylogenies.

3.4.1 Molecular

The Bayesian maximum clade credibility tree of the ‘complete genes’ (CG) dataset of 96 taxa is shown in Fig. 1. Monophyly of the Kapala clade is supported with a posterior probability (pp) of 100. *Kapala* is rendered polyphyletic by eleven of the KC genera sampled, with only *Colocharis* and the New Genus not found within Kapala. The non-monophyly of *Kapala* is verified by the Shimodaira-Hasegawa test, which calculated a significantly smaller (worse) maximum likelihood for *Kapala* constrained as monophyletic (p =< 0.0001). All other genera having multiple taxa sampled are individually recovered as monophyletic under all molecular analyses and sampling regimes (see supplementary information for phylogenies and a list of figures in Table 3.1). Deeper divergences have short internodes, typically with low support. The timetree of ‘all taxa’ (AT) is shown in the Fig. 2 inset and in Fig S1. The crown age of the Kapala clade is estimated at 23.6 my (95% highest posterior density = 13.5-34.3) from the complete genes dataset and 25.4 my (15.5-37.1) from the large all taxa dataset. The primary difference from the Bayesian inference tree is monophyly of the Group 1 genera. Node ages for major clades below will be reported from the results of the large dataset. The ML trees tended to have variable topologies due to very little support for major clades, though it’s unclear why, so results and phylogenetic discussions will be centered on the Bayesian and parsimony topologies.

3.4.2 Morphological

A parsimony analysis of 52 morphological characters under implied weighting k=3 resulted in three shortest trees, which are summarized as a strict consensus tree (Fig. 3). The k=45 tree was similar in topology (not shown). The enigmatic New World genus, *Carletonia*, is recovered in the Old World outgroup and is not a sister group to the Kapala clade. Group 1 is a grade to the rest of the KC. The non-*Kapala* taxa from Groups 2 and 3 cluster together, with some *Kapala* within the group of genera (grade indicated by ‘3’ on backbone internode, Fig.2). All of the *Kapala* within this grade, besides *K. terminalis*, only have terminals coded for the male, due to lack of females to match with confidence. All of the remainder of *Kapala* form a monophyletic unit, composed of Group 2 and 3 *Kapala* species. The morphology-only tree is sufficient for distinguishing among genera, though within the genus *Kapala* the tree is unresolved or conflicts with DNA data in many areas.

3.4.3 Combined

The parsimony analysis of the morphology + DNA matrix resulted in one tree (Fig. 4). The phylogeny of the combined analysis appears to be dominated by the molecular data, since it follows the general topology of the TNT molecular tree. Bayesian inference was also used for the combined analysis, which gave a different topology from the parsimony analysis (Fig. S7) because the Lirata clade of (*Galearia*, (*Dilocantha*, (*Liratella*, *Lirata*))) is recovered as sister to the rest of Group 2+3. Most of the morphological characters (all but three of them) exhibit homoplasy across the Kapala clade. The retention index (RI) is used to measure the fit to the tree, and the RI of each character as optimized onto the combined tree is given in Table S3. The RI is 1.0 for the three characters: eye shape (char 2, *Isomerala*), male number of flagellomeres (char 17, 10 in all but *Carletonia* and *Colocharis*), and mesoscutal flange over tegula (char 28, *Lirata* + *Dilocantha)*.

3.4.4 Major Groups in the Kapala Clade

Synapomorphic characters for the KC include the cylindrical or flat scutellar processes (character 21) and male antennal flagellomeres uniformly branched, with F2 and F3 of similar length (char 20). All KC except *Colocharis* have the synapomorphy of a round propodeal spiracle having an incision of the ventral margin (char 37). The reconstruction of the KC ancestral number of flagellomeres on the combined analysis topology is ambiguous at 6, 8, or 9. Six flagellomeres is the ancestral state in *Colocharis*; 8 or 9 is ancestral for KC New Genus + Groups 2+3. Additionally, Groups 2+3 have the synapomorphic character of the maxillary palpomeres 3-segmented (char 7) [one anomalous specimen with 2, *K.* nr *furcata* sp2]. No synapomorphies were found for only *Kapala*.

3.4.4.1 Group 1

Group 1 is made of two clades that are together recovered both as monophyletic or paraphyletic under different analyses (i.e. Figs 2-4). When paraphyletic, *Colocharis* (Clade A) is sister to the New Genus (Clade B) and the rest of the KC. Molecular dating results give a crown age of 17.5 my for the monophyletic grouping (8.8-27.5) (Fig. 2 inset, Fig. S1, S2). Using MrBayes for the 96 dataset of CG as shown in Fig. 2, Group 1 is recovered as a grade. Morphology alone (Fig. 3) also indicates Group 1 is a grade to the remaining KC. Under dating reconstructions and the full 195 taxa Bayesian and ML analyses, Group 1 is monophyletic (Figs. S3, S5). Group 1 diagnostic characters include a smooth face, 6-7 labral digits, females with 6-8 flagellomeres, and marginal fringe on the forewing. It is distributed across South America (Fig. 4).

Clade A) *Colocharis* (pp=1, Fig.2)is sister to the remaining members when the Group 1 is recovered as a grade. It has an estimated crown age of 9.4 my (4.2-16.0), but when Group 1 is constrained to be paraphyletic, *Colocharis* is estimated to be older, at 14.1 my (7.1-23.5). *Colocharis* are easily-recognized by their very short paired scutellar spines, which is unique in the Kapala clade. Other diagnostic characters include a circular propodeal spiracle and males with only 8 flagellomeres (both unique within the KC). Females have 6 or 7 flagellomeres.

Clade B) KC New Genus is composed of a clade of Peruvian and Ecuadorian specimens previously identified as *Kapala*, with a crown age of 2.6 my (0.8-5.4) (pp=1, Fig.2). There are additional (non-molecular) specimens from Bolivia, Brazil, Paraguay, and Venezuela. This group was determined to be a new genus in the Kapala clade based on having a smooth face coupled with females having 8 flagellomeres and a 2/2 maxillary and labial palp formula, with the latter two features unique in the KC. Morphologically, these appear similar to species in the Kapala iridicolor complex (Group 2, Clade E) which also have a smooth face and low thoracic profile, but molecularly they are distinct in all analyses. This new genus will be described separately.

3.4.4.2 Group 2

Group 2 is supported with a pp of 1 based on the molecular data (Fig. 2) and as a clade but with no support in the combined analysis (Fig. 4), and is proposed to have originated 19.6 mya (10.8-28.8). Group 2 is not recovered using morphology-only analyses (Fig. 2). It is comprised of three clades, each strongly supported, however the relationship among the three is unclear, with very little pp or bootstrap support. The sister relationships of these three subclades are variable by analysis, so it is unclear if the two *Kapala* species-complexes, Clades D and E, in Group 2 are monophyletic. Of the *Kapala* specimens, all females have 9 or 10 flagellomeres (besides one anomalous specimen), which separate it from *Kapala* in Group 3.

Clade C) The Neolirata clade (pp=1, Fig. 2) is a monophyletic group of six genera, with an estimated crown age of 14.3 my (8.0-22.3). Five genera have molecular data (*Dicoelothorax*, *Lasiokapala, Latina* Gemignani, *Neolirata* Torrens & Heraty, and *Thoracantha*) and one with morphological only (*Parakapala).* In the combined analysis, *Parakapala* is placed in Clade C and was also a member of this clade in Heraty (2002); it shares more characters with *Dicoelothorax* than with any other genus. There are a wide variety of spine morphologies across the clade, including one of the few cases of extreme scutellar spine sexual dimorphism which is found in *Thoracantha*. The male of *Lasiokapala* is not known, but the female is the only one in the KC to have pectinate antennae. The six genera are easy to diagnose, based on Heraty (2002). *Neolirata* was since split from *Lirata* (Torréns & Heraty, 2013) and can be distinguished by a sharp carina separating the ocelli. Although more often placed with Clade 3, under a combined parsimony analysis with implied weighting k=15, *Liratella* also is placed in the Neolirata clade. The genera of the Neolirata clade are found across much of South America, and do not reach north to Central America.

Clade D) The Kapala furcata complex (pp= 1, Fig. 2) has a crown age of 13.3 my (6.6-20.7) and contains the type species of *Kapala*, *K. furcata* (Fabricius). Many of the specimens in this clade have thick longitudinally carinate spines and robust, heavy bodies, with the lateral midlobes of the mesoscutum enlarged. Females have 9 or 10 flagellomeres (with one known exception of a female with 8). The clade members generally have a rectangular upper prepectus and fine facial striae. The holotype of *K. furcata* is a female from Brazil, and although we have no molecular data from *K. furcata* from that country, the specimens from Argentina and Paraguay (*K.*nr *furcata* sp5) are very similar morphologically.

Clade E) The K. iridicolor complex is an estimated 11.4 my (6.3-18.8) and is always well-supported (pp=1, Fig. 2). All specimens have smooth faces and all females have 9-10 flagellomeres. Some individuals identified as *K. iridicolor* (*sensu stricto*) in have light striae on the frons, but not on the face. They are also typically found more northerly than the nr iridicolor group, in Honduras and Mexico (Figs S1, S3). Much of the diversity and species are found in northern South America. Many of the individuals in nr iridicolor clade (except nr iridicolor sp2 and 3) have scutellar spines that enlarge to a wide emarginate tip, unlike most Group 3 *Kapala*, which have spines that taper to a rounded or emarginate tip. The K. iridicolor complex is morphologically defined by a combination of characters including the females with 9-10 flagellomeres, smooth faces (or *K. iridicolor* sometimes with light striation on frons), a low profile of the mesoscutum, and a densely pilose mesosoma.

3.4.4.3 Group 3

Group 3 (pp=0.73, Fig.2) is the most speciose clade and exhibits low support for the bipartitions at the base of the clade across different analyses. It has an estimated crown age of 20.3 my (11.6-29.3). Group 3 is difficult to circumscribe but is made up of many *Kapala* typically identified as *K. sulcifacies* or 'near *K. sulcifacies*'. All Group 3 *Kapala* females have 8 flagellomeres. The described species of *Kapala* sampled are each monophyletic (e.g., *K. terminalis* (pp=1), *K. argentina* (pp=1), *K. ivorensis* (pp=0.98), Fig. S3), but there are many undescribed *Kapala* specimens of uncertain placement and low support. It will require more data for accurate determination of species boundaries. Group 3 has the largest range of the three main groups, with species found from Argentina to the southern US including Arizona, Texas and Florida.

Isomerala lacks clear sister group support but always comes out in embedded in Group 3. Morphologically, it looks extremely similar to *Kapala*, but has a modified head shape with nipple-shaped eyes. The age of *Isomerala* is estimated at 7.5 my (3.4-12.5). *Isomerala* is found in Central America and northern South America.

Clade F) The Lirata clade (usually recovered with Group 3) (Table 1) is estimated at 17.1 my (9.8-27.1). There are three genera: *Dilocantha* + *Lirata* (pp=1, Fig. 2) as sisters, with the problematic *Galearia* included under most reconstructions (Fig 2, pp=0.67). *Liratella* groups with Clade F under the combined parsimony analysis when the concavity constant for implied weights at k=3 (Fig. 4) or K=45, as sister to *Galearia* or *Lirata*, respectively. However, when k = 15, *Liratella* groups as sister to Clade C (Group 2). In the Bayesian combined analysis, *Liratella* is also found in Clade F, but Clade F is found as sister to Groups 2+3 and not within Group 3. It shares more characters with *Galearia* (also recovered as its sister in (Heraty, 2002)) than with *Lirata* and *Dilocantha*. In some dated BEAST analyses, the Lirata clade is recovered as sister to Group 2+3, but never in the MrBayes or RAxML molecular analyses. The Lirata clade has species found more northerly than the Neolirata Clade (Clade C). Both *Lirata* and Dilocantha are found in Trinidad. *Lirata* is found in Panama, and *Dilocantha* ranges as far north as Mexico.

Clade G) This clade is estimated at 7.9 my (3.7-13.3). The members would traditionally be described as *K. sulcifacies*. The clade is always recovered with high support (pp=1, Fig. 2), but the intra-clade relationships are not. Most of the individuals are from Trinidad, Colombia, and Costa Rica, with two sampled from Ecuador. The males have relatively long antennae (F2 branch 1.3-1.8 x the head height) and typically have serrated scutellar spines.

Clade H) This clade is always recovered and usually with high support (Table 1), with members typically described as near *K. sulcifacies*. The crown age is 11.4 my (7.7-21.7). *Kapala* nr *striata* is sister to the rest of the clade (Figs S1, S3, S5), a topological relationship that is recovered in all analyses. There is little internal support, and morphological variation may also obscure species boundaries. Clade H includes the only Old World species, *K. ivorensis,* which diverged from the New World sister taxa around 5.8 my (2.6-10.1) and has a crown age of 2.7 my (1.1-5.0). The *K. ivorensis* specimens are morphologically similar (Murray & Heraty, in prep.), especially in comparison to many other *Kapala* clades of comparable age. *Kapala izapa* (pp=0.31, Fig. S1) from Mexico are also in Clade H, and this species is difficult to circumscribe morphologically, with considerable intraspecific variation in the specimens examined.

3.4.5 Branch Support

Support for relationships of *Galearia* and Clade F: The placement of *Galearia* is not always stable across replicate analyses of the same parameters. *Galearia* is recovered as sister to *Lirata* + *Dilocantha* using the 96 taxa dataset in MrBayes and BEAST (Table 1). However, in some analyses is recovered with *Colocharis* (not shown) or as sister to Groups 2+3 (Fig. S4). In some reconstructions, it retains its relationship with *Lirata* and *Dilocantha*, but the entire clade is recovered as sister to Groups 2+3 instead of with Group 3. Therefore, we ran the 96 and 195 taxa sets in MrBayes and RAxML without *Galearia*, using the same parameters as the full datasets. We removed *Galearia* from analyses and analyzed the data under the same parameters in MrBayes. *Lirata* and *Dilocantha* are recovered as monophyletic in the best trees when phylogenetic analyses are run without *Galearia*, and in addition, they are monophyletic with Group 3 (Table 1, Fig. S8).

Additionally, AWTY was used to calculate the proportion of Bayesian post-burnin posterior distribution of trees supporting conflicting *Galearia* placement for the complete genes and all taxa MrBayes analysis. *Galearia* groups with *Lirata* and *Dilocantha* in 67% of the trees in the 96 taxa dataset (Fig. 2) and only 33% of trees in the 195 taxa dataset. However, the Lirata clade is not always found within Group 3 but is occasionally sister to Groups 2+3. The other common placement of *Galearia* is sister to *Colocharis* (6% trees and 29% of trees, respectively), which is rather unlikely because of the low support and because *Colocharis* has a small body and tiny spines. We believe *Galearia* has an effect on topology, potentially due to the molecular characters it shares with *Colocharis*.

RogueNaRok, a tool for identifying rogue taxa, was used to discern if the two *Galearia* in the 96 taxa dataset indeed jumped in various replicates, leading to a low pp value. Ten terminals were identified as rogue taxa but the two *Galearia* were not. Nonetheless, analyzing the dataset with the 10 suggested taxa removed resulted in an increase in branch support in the major clades not already at pp of 1 (Navajo rug, Fig. 2, Fig. S9, Table 1).

3.4.6 Diversification

The diversification rate of the Kapala clade was summarized across 10000 chronograms from the 96-taxon posterior probability distribution. Calculation of diversification rates with an incompletely sampled phylogeny and putative undescribed diversity should be considered as an educated estimate. There were two rate shifts in the clade, both in Group 3. In 52% of the trees there was a rate decrease for *K. terminalis* + *K*. sp4, D2802, and 19.1% of the trees exhibit a rate increase in Clade H.

3.5 Discussion

3.5.1 Phylogeny

We have developed a comprehensive, dated phylogeny for the Kapala Clade. We now recognize 14 genera within the KC, with a new genus being based on both molecules and several morphological synapomorphies (to be described separately). These results indicate that *Colocharis* and the New Genus (Group 1) are basal to the rest of the KC, but it is unclear if they form a grade or a clade. If a grade, then this would demonstrate a transition from the very short spines in *Colocharis* to the longer spines of the remaining members of the clade.

Based on our molecular results and our survey of museum collections, Group 3 has by far the most species and species complexes, mostly undescribed, within the Kapala Clade. Whereas Group 1 has two discrete genera and Group 2 is composed of three well-supported clades, Group 3 has less resolution. *Kapala* itself likely will need to be split, but due to the low branch support across the backbone of the tree, the circumscription of the genus should be subject to further analyses before implementing major taxonomic changes. The placement of *Galearia* and its relationships to *Lirata* and *Dilocantha* is also a concern for defining the limits of *Kapala*, since variability across analyses leaves ambiguity in placement of the Lirata clade. Additionally, *Kapala* lacks the shared, derived characters that define the other genera in the KC, and the split genera will still be defined by a suite of pleisiomorphic diagnostic characters.

Our parsimony combined analyses (Fig. 4) provided similar topological results to our molecular only analyses (Fig. 2). These combined analyses also included three genera without molecular data, *Carletonia* (outgroup), *Parakapala,* and *Liratella*. *Carletonia* was accurately placed in the outgroup, but not as the sister group to the Kapala clade (cf. Heraty, 2002), which could be a product of our reduced outgroup sampling or the lack of molecular data. What we term Groups 2 and 3 were recovered by Heraty, however *Lirata* and *Neolirata* (as *Lirata* in Heraty (2002)) separated in Groups 2 and 3 herein, and *Colocharis* was not previously found as the sister group to the rest of the clade. Compared to the morphology-only results from (Heraty, 2002), *Liratella* also was placed as the sister group of *Galearia*, and *Parakapala* included as part of the Neolirata clade, but here in a more apical position as the sister group of *Dicoelothorax*. Thus data combination and the inclusion of genera with only morphological data are providing results consistent with earlier studies.

The all taxa dataset had 34.75% of cells classified as gaps and undetermined characters while the complete genes dataset had 14.95%. Our preference is toward topologies resulting from the most complete gene region sampling (Figs 2, 4); the more taxon rich dataset (AT) with fewer genes sampled often gave variable topologies for the best tree, more often than the 96-taxa 'CG' dataset. The fear of missing data influences the design and execution of phylogenetic studies, though the researcher bias towards complete data may not be justified (Wiens, 2006). Here, two data sets were compared due to our concern of missing data affecting topology, since it has been shown that taxa missing data may have too few characters for accurate placement on the tree (Wiens, 2006). Additionally, in the probabilistic framework, each character affects the estimation of model parameters, even if the character is missing. In most major clades, removal of taxa with fewer than five genes paired with removal of sections of 18S and COI missing data did have a positive effect on the branch support (Table 1). In addition, sampling fewer taxa may allow for more easily-resolved bipartitions, potentially because internal branches have the opportunity to be longer due to fewer subdivisions (Roure *et al.*, 2013). The Kapala clade is always monophyletic when analyzing the 195 taxa dataset, but there were a select number of genera that jump between Group 1 and 3, believed to be due mainly to *Galearia*'s effect on relationships with *Colocharis* and the *Lirata* + *Dilocantha* clade.

The individual genera in the Kapala clade are straightforward to diagnose and those with molecular data are generally well-supported in phylogenetic reconstruction, but the relationships among them is more problematic. Phylogenetic relationships in Groups 1 and 3 are sensitive to the input parameters, models, and data completeness (Table 1). The lack of phylogenetic support in Group 3, originating at 20.3 mya (11.6-29.3), may be due to a radiation that is too rapid for our genetic markers to recover nodes accurately. Rapid radiations are often characterized by short internodes with low support (Whitfield & Kjer, 2008), which is exhibited in all of the backbone bipartitions in Group 3. The five individual gene phylogenies typically have little to no support along the backbone (Fig. S10). In the complete gene dataset, the mtDNA genes COI + COI have a mutation rate that is an average of 26.7 times faster than the D2 + D3-5 rDNA.

3.5.2 Clade Ages

We obtained an estimate of divergence times, using a secondary calibration point based off of a larger dataset of Eucharitidae. A previous analysis using three fossil-calibrated nodes gave an estimate of the crown age of the KC at 23.3 my (16.8-30.9) (Murray *et al.*, 2013) and here we recover 23.6 my (96 taxa) or 25.4 my (194 taxa). An Ethiopian ancestral area had been inferred for the KC, which may indicate a transatlantic dispersal event to South America. Some *Schizaspidia* are Palearctic, and another potential route to the New World is the Beringial land bridge between Asia and North America. This was effectively closing after the Eocene due to cooling temperatures, although the climate warmed slightly around 26-27 mya (Zachos *et al.*, 2001; Brandley *et al.*, 2011). Beringia in the late Oligocene was composed of temperate woodland and had moderate to temperate temperatures (Burbrink & Lawson, 2007), but most temperate fauna were prevented from dispersing by the cooler temperatures at the end of Eocene, ~35 mya (Sanmartin *et al.*, 2001). The Kapala Clade is currently found mainly in the tropics, which suggests it may not have been suited for survival or dispersal in the cooler climate.

The highly-supported K. furcata clade (Clade D) is estimated at 13.3 my (6.6-20.7), which is older than any KC genera sampled. Many of the genera have multiple species sampled, which gives a useful indication of the minimum genus age, though the with additional species sampling, the ages may increase. We see a range of 2.8-9.6 my for the age of genera having two or more species sampled. Much of the KC morphological differentiation and generic origins took place during the Miocene (5.3-23 mya), a time period which has been hypothesized to have facilitated diversification of many insect groups due to the cycles of warming and cooling across the earth opening new habitats (Condamine *et al.*, 2012), before a general trend in cooling starting ~14 mya (Potter & Szatmari, 2009). Insects exhibiting increased diversification include a genus of braconid wasps (Ceccarelli & Zaldivar-Riveron, 2013), a tribe of noctuid moths (Toussaint *et al.*, 2012), the clearwing butterfies (Elias *et al.*, 2009), swallowtail butterflies (Condamine *et al.*, 2012), a genus of leaf beetles (McKenna & Farrell, 2006), and a genus of leaf-mining flies (Winkler *et al.*, 2009). Andean uplift events (at 23, 12, and 4.5 my) had a great effect on all of South America, including rainfall, soil nutrient levels, and landscape evolution (Hoorn *et al.*, 2010) and influenced biotic diversification. In addition, the Isthmus of Panama started closing at 15 my with complete closure at 3.5 mya (Potter & Szatmari, 2009). Excluding *Kapala*, all Group 1 and 2 genera are only found in South America. In Group 3, three genera (of five) are found in Central America (including Trinidad): *Dilocantha*, *Isomerala*, and *Lirata* (Fig. 4). That Group 1 is restricted to South America could implicate that land mass as ancestral, corroborating the finding by Murray *et al.* (2013) that the Neotropic region -- and not the Nearctic -- was the ancestral area for the KC.

3.5.3 Diversity

We used the Colless index, normalized to account for incomplete sampling, to test for a balanced tree, meaning nodes define subgroups of equal sizes (Mooers & Heard, 1997). The KC all taxa dataset has a value of 0.05, which indicates the topology is balanced, though the recognition of genera across the tree is not. Most genus-level phenotypic change occurs in three different clades: Group 1, with 2 genera; the Neolirata clade (Group 2, Clade C), with 6-7 genera, dependent on inclusion of *Liratella*; and the Lirata clade (Group 3, Clade F), with 3-4 genera, dependent on *Liratella*. Bursts of morphological evolution is seen in clusters across the KC phylogeny. *Isomerala* is the only genus that is not paired with another non-*Kapala*, but instead is always placed within *Kapala* Group 3.

Apomorphic morphology may be nested within the clade exhibiting a pleisiomorphic phenotype, the pattern seen in a progenitor-derivative evolutionary event (Crawford, 2010). This is exemplified by the genus *Isomerala*, which is distinguished from *Kapala* by a modification of head morphology – displaying a bulging frons (Heraty, 2002) and conical-shaped eyes (char 2) (Fig. 3 inset). It is also genetically distinct, though with little divergence from *Kapala*. Using uncorrected distances of COI+COII, *Isomerala* has a 4.9% divergence from the nearest *Kapala*. Despite the issue that *Isomerala* is found within the middle of another group, we believe it is still useful at this juncture to recognize this genus based on its divergent diagnostic characters.

The varied phenotypes of the KC genera were not correlated to an increase in the rate of diversification, under these data. There is a large amount of morphological diversity across the KC, and we used MEDUSA to test for changes in the diversification rates. None of the three main groups of genera – Group 1, the Neolirata clade, or the Lirata clade – were recognized as having a shift in diversification rates. Morphological change that is recognized as taxonomically novel is likely not correlated to the five genes we are sampling. We recovered two shifts: one was a decrease in diversification at the node of *K. terminalis* + *Kapala* sp4. Of 10,000 trees in the 96 taxa dataset, the node was present and had a significant decrease (median value = -0.157) in 50.1% of trees. The second rate shift showed an increased rate of diversification at the crown of the *Kapala* Clade H, which had a significant increase of 0.219 in 14.7% of trees. This clade has a number of putative species and also contains the Old World *K. ivorensis*. Both of these clades are in Group 3, which is the most speciose KC clade and has a high amount of morphological variation in the genus *Kapala*.

3.5.4 Morphological data

Molecules and morphology are the most common data used to interpret phylogenetic relationships, and may be used independently or combined. Independent phylogeny reconstruction follows the concept of reciprocal illumination as applied to systematics (Hennig, 1966), in which a hypothesis is tested using another type of data to verify the two sources result in the same phylogenetic relationships. Unexpected molecular relationships of taxa should be checked against morphology. Yet there may be some instances where molecules are preferable for recovering evolutionary relationships. Two evolutionary processes can obscure phylogenetic signal as assessed from morphology: convergent evolution and retention of ancestral similarities by some taxa within a larger diversifying clade (Ward, 2011). In the Kapala Clade, both of these processes are apparent. The *Lirata* (Group 3) and *Neolirata* (Group 2) phenotypes are convergent according to molecules. They have similar body and spine shapes and are also the only two genera in the KC to possess an antennal scape reaching beyond the median ocellus (char 11, state 1). Four of the six genera in the Neolirata clade possess pronounced eye setae (bristles) (char 1, state 1), but outside of that group, only *Lirata* do. This indicates that in some of the KC genera, the presence of eye setae reveal evolutionary relatedness, but not in the case of *Lirata*. An example of retention of ancestral characters is the genus *Kapala*, which appears phenotypically similar and cohesive yet is polyphyletic under all molecular analyses and all genes. Dense taxon sampling shows non-monophyly of *Kapala*, but does not recover Groups 2 and 3 (Fig. 3).

We are recognizing a repeated pattern across related groups. Our tree supports a polyphyletic *Kapala* with morphologically divergent taxa embedded, resulting in a mixture of morphologically variable genera rendering the morphologically pleisiomorphic genus polyphyletic. This situation has been termed “budding”, which describes the origin of a new taxon that does not affect the existence or characters of the original stem group (Hörandl & Stuessy, 2010), meaning, it seems that Kapala retains its pleisiomorphic state while numerous other phenotypically divergent groups branch out of it. A similar pattern to that of *Kapala* has been observed in *Orasema* Cameron, with 57 described species, and *Perilampus* Latreille (Perilampidae), with 84 described species. These two genera also appear to be morphologically cohesive groups, but molecules show both to be intercalated by multiple other genera. This pattern of phenotypic bursts of evolution within a morphologically-conserved group has not yet been correlated with biology or life history in the KC. This is emphasized also in Brady *et al.* (2014), who note the heterogeneity of evolutionary rates in morphology in the doryline ants. For instance, the genus *Cerapachys* is now understood to have been recognized based on the collective retention of a generalized morphology, with other groups nested within (e.g., the army ants and other genera) undergoing divergent morphological evolution. We see similar results here, potentially due to the inability to both 1) identify *a priori* the phylogenetically-important characters amidst all phenotypic variation, and 2) effectively translate continuous morphological change into character states and discretize nuanced differences into phenetic gaps.

Ward (2011) has proposed a new protocol for taxonomy. In summary, Ward suggests: 1) estimate the molecular phylogeny, 2) reexamine the status of known groups and reconfigure if necessary to ensure monophyly, and 3) provide diagnostic morphological characters for the named clades. For example, the number of flagellomeres, the thickness and extent of facial striation, and the nature of the spine sculpturing were diagnostic for different *Kapala* species complexes. Additionally, some members of Clade B, the newly-recognized genus, had been previously identified as *K.* nr *iridicolor*, due to the smooth face and low mesoscutal profile. Molecules indicated it was a distinct group, leading to a new interpretation of morphology.

3.5.5 Life History

Clausen (1940b) identified six different plant parts eucharitids employed for oviposition: 1) overwintering buds, 2), expanding leaf and flower buds, 3) seed receptacles, 4) incisions in leaf tissue, 5) leaf surface, and 6) leaf surface but in association with thrips eggs. The PEM clade has been recorded to use divisions 2, 4, and 5, and the Kapala clade uses divisions 2 and 5.

The KC members most often oviposit onto leaves (Clausen, 1940b; Berry, 1947; Torréns *et al.*, 2007; Torrens & Heraty, 2012; Torréns & Heraty, 2013). Specifically, species of many genera oviposit on the ventral sides of the leaf with the eggs tucked under the plant spicules or pubescence, with the eggs parallel to the surface. Other records include oviposition in undeveloped flower spikes and flower buds, and on stems near the base of leaves (Clausen, 1940b; Heraty & Darling, 1984; Torréns, 2013). There are no data from Group 1 genera, but in Groups 2+3, there is oviposition information for six genera and four described *Kapala* species.

Character reconstruction in Mesquite on the combined data topology indicates the KC has an ancestral behavior of ovipositing in flower and leaf buds. The pruned tree and character matrix can be found in SI text. *Kapala* as a group have the most diverse oviposition habits. In *Kapala,* oviposition habits are known from four described species. *Kapala furcata* (Clausen, 1940b) and *K. iridicolor* (Heraty & Woolley, 1993) (Group 2) lay into flower buds, as do *K. sulcifacies* (Group 3) and other unidentified *Kapala* species (Heraty & Woolley, 1993; Torréns, 2013; Heraty, unpublished). *Kapala sulcifacies* and *K. iridicolor* (*sensu lato*) are often sympatric, and were reported ovipositing into the same species of plant just three meters from one another in Trinidad (Heraty & Woolley, 1993). *Kapala terminalis* (Clausen, 1940b) and another unidentified species lay on the undersides of leaves (Berry, 1947). Using the combined analysis phylogenetic reconstruction, a pattern emerges in host plant use in Group 2. All of the Neolirata clade (Clade C) oviposits on the undersides of leaves. This includes records for *Dicoelothorax*, *Latina*, *Neolirata*, and *Thoracantha* (Torréns, 2013; Torréns & Heraty, 2013). The two Kapala clades in Group 2 (furcata, D and iridicolor, E) oviposit into flower buds. In Group 3, there are fewer plant records. *Kapala* oviposit into both buds and under leaves. In Clade F, *Galearia* is known to oviposit at the base of leaves and also onto the stem by the base (Torréns, 2013) and *Dilocantha* oviposits near the base on the undersides of leaves (Heraty, unpublished). The ancestral reconstruction for Clade F is of oviposition under leaves. No information is known on Group 1.

The KC parasitoids are specific to two ant subfamilies, but records indicate that species may not be specific to either ant species or genera. *Kapala iridicolor* (likely, the K. iridicolor complex) have been recorded on *Ectatomma*, *Gnamptogenys* (Ectatomminae), and *Odontomachus* (Ponerinae) (Lachaud & Pérez-Lachaud, 2001; Pérez-Lachaud *et al.*, 2006b). There are even two separate genera, *Dilocantha lachaudii* and *Isomerala coronata*, that have been recorded concurrently feeding on an individual ant pupa of *Ectatomma tuberculatum* (Pérez-Lachaud *et al.*, 2006b). Ant host size and ant caste may influence the size and potentially also affect the morphology of the parasitoids, which presents interesting inquiries on host-induced phenotypic plasticity. In mapping the ant host onto the phylogeny, no pattern emerges in the utilization of ponerine or ectatommine hosts (Fig. 2). This suggests a lack of strict specialization within the Kapala clade and perhaps an opportunistic use of ants associated with the selected plant hosts.

3.6 Conclusions

The Kapala clade contains a remarkable amount of morphological diversity, and there are some groups where the evolutionary signal is obscured by bursts of phenotypic change, convergence, and retention of sympleisiomorphies by selected groups. Molecular data and a robust phylogeny are indispensable to help guide the interpretation of observed morphological characters. The genus *Kapala* will have to be revised to reflect the updated hypothesis of genus-level variation and phylogenetic relationships.

Taxonomists have recognized discrete genera in the Kapala clade based on gaps in phenotypic variation and novel morphologies. When making taxonomic decisions across the Kapala clade, it is worthwhile to consider the practicality of recognizing distinct taxa as they have been described and the utility of the present ordering systems (Hörandl & Stuessy, 2010; Stuessy & Hörandl, 2014) as more information is gathered about the evolutionary history. At this time, there is enough information content in the term *Kapala* that we are hesitant to split the group before having confidence in a stable topology. Prior to making the large-scale taxonomic revisions, due to the conflicting placement of some clades under different parameters, more data should be gathered. Future studies incorporating additional genomic information will potentially aid in establishing boundaries.

3.7 Figures and Tables

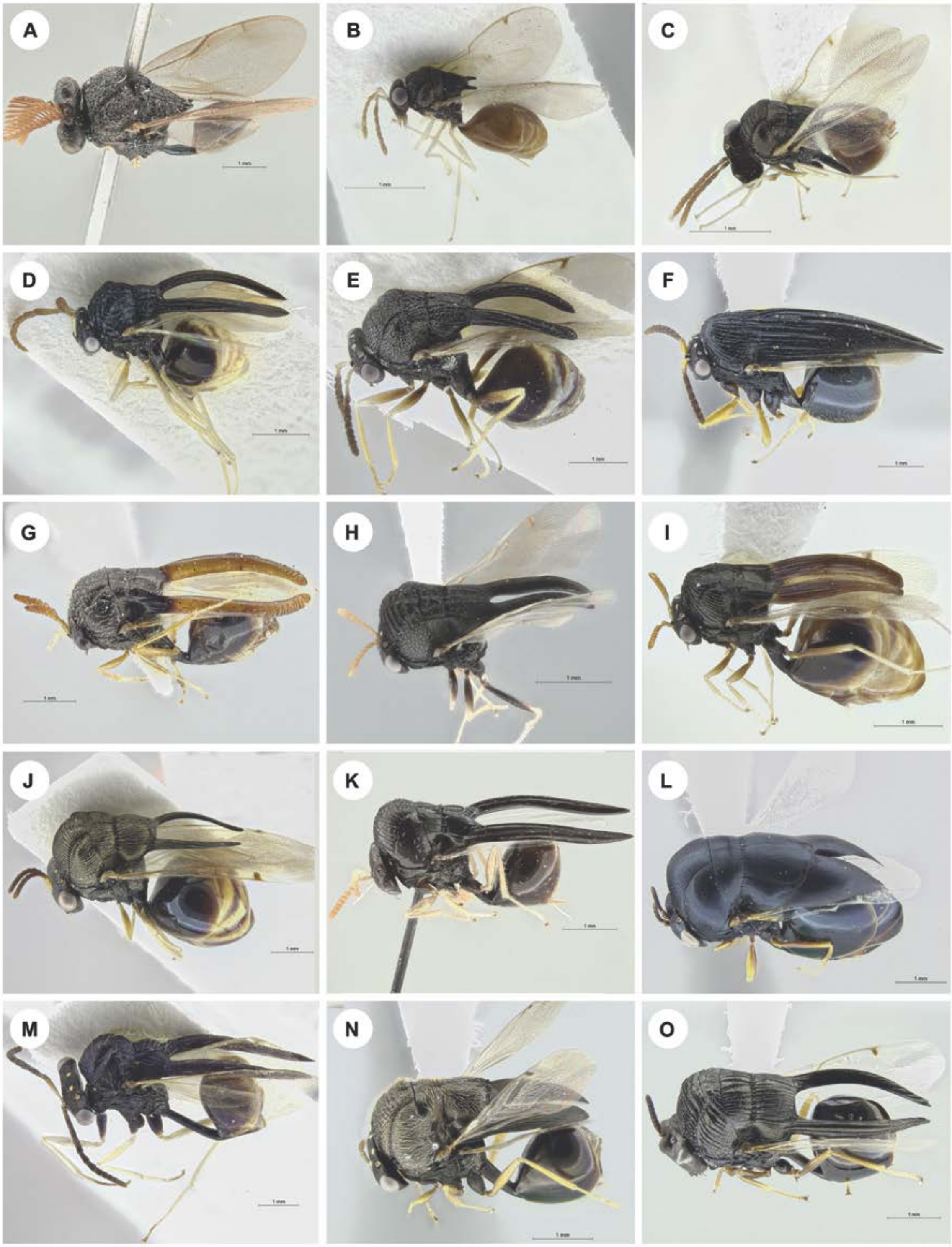


FIGURE 3.1.

Habitus images of the Kapala clade genera and related New World genus. All specimens are females except *Carletonia*, where only males are known. **A)** *Carletonia*; **B-C)** Group 1, B) *Colocharis*, C) New Genus; **D-I)** Clade C, Group 2, D) *Neolirata*, E) *Latina*, F) *Thoracantha*, G) *Lasiokapala*, H) *Parakapala*, I) *Dicoelothorax*; **J)** *Kapala,* with *K. furcata* representing genus; **K-N)** Clade F, Group 3, K) *Liratella*, L) *Galearia*, M) *Lirata*, N) *Dilocantha*; **O)** *Isomerala*, Group 3. All measurement bars are 1 mm.

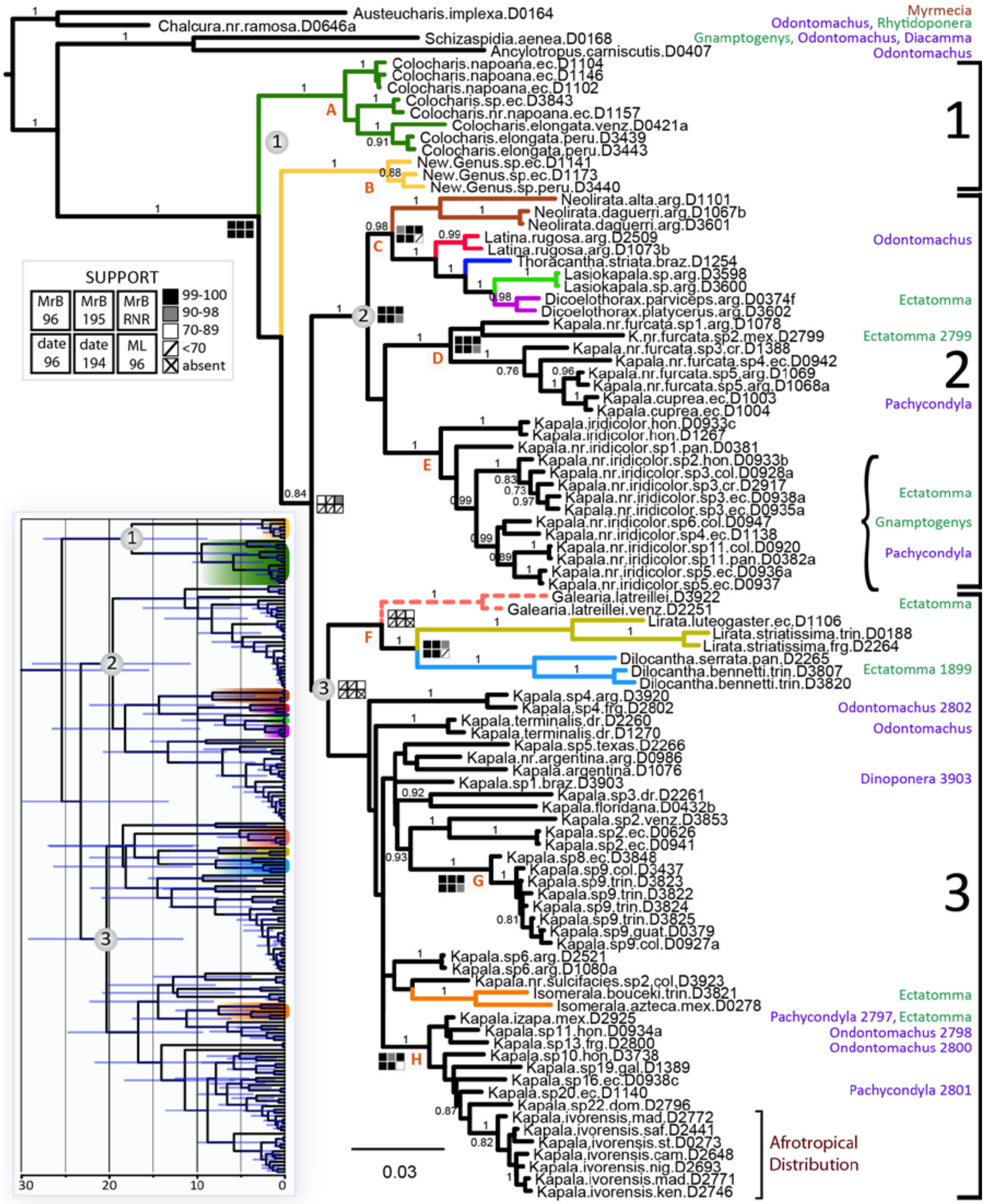

Austeucharis.implexa.D0164
Chalcura.nr.ramosa.D0646a
Schizaspidia.aenea.D0168
Ancylotropus.carniscutis.D0407
Myrmecia
Odontomachus, Rhytidoponera
Gnamptogenys, Odontomachus, Diacamma
Odontomachus
Colocharis.napoana.ec.D1104
Colocharis.napoana.ec.D1146
Colocharis.napoana.ec.D1102
Colocharis.sp.ec.D3843
Colocharis.nr.napoana.ec.D1157
Colocharis.elongata.venz.D0421a
Colocharis.elongata.peru.D3439
Colocharis.elongata.peru.D3443
New.Genus.sp.ec.D1141
New.Genus.sp.ec.D1173
New.Genus.sp.peru.D3440
A
B
C
D
E
F
G
H
1
2
3
0.91
0.88
0.98
0.99
0.76
0.96
0.84
0.83
0.73
0.97
0.89
0.92
0.93
0.81
0.87
0.82
Neolirata.alta.arg.D1101
Neolirata.daguerri.arg.D1067b
Neolirata.daguerri.arg.D3601
Latina.rugosa.arg.D2509
Latina.rugosa.arg.D1073b
Thoracantha.striata.braz.D1254
Lasiokapala.sp.arg.D3598
Lasiokapala.sp.arg.D3600
Dicoelothorax.parviceps.arg.D0374f
Dicoelothorax.platycerus.arg.D3602
Kapala.nr.furcata.sp1.arg.D1078
K.nr.furcata.sp2.mex.D2799
Kapala.nr.furcata.sp3.cr.D1388
Kapala.nr.furcata.sp4.ec.D0942
Kapala.nr.furcata.sp5.arg.D1069
Kapala.nr.furcata.sp5.arg.D1068a
Kapala.cuprea.ec.D1003
Kapala.cuprea.ec.D1004
Kapala.iridicolor.hon.D0933c
Kapala.iridicolor.hon.D1267
Kapala.nr.iridicolor.sp1.pan.D0381
Kapala.nr.iridicolor.sp2.hon.D0933b
Kapala.nr.iridicolor.sp3.col.D0928a
Kapala.nr.iridicolor.sp3.cr.D2917
Kapala.nr.iridicolor.sp3.ec.D0938a
Kapala.nr.iridicolor.sp3.ec.D0935a
Kapala.nr.iridicolor.sp6.col.D0947
Kapala.nr.iridicolor.sp4.ec.D1138
Kapala.nr.iridicolor.sp11.col.D0920
Kapala.nr.iridicolor.sp11.pan.D0382a
Kapala.nr.iridicolor.sp5.ec.D0936a
Kapala.nr.iridicolor.sp5.ec.D0937
Odontomachus
Ectatomma
Ectatomma 2799
Pachycondyla
Ectatomma
Gnamptogenys
Pachycondyla
SUPPORT
MrB 96
MrB 195
MrB RNR
date 96
date 194
ML 96
99-100
90-98
70-89
<70
absent
Galearia.latreillei.D3922
Galearia.latreillei.venz.D2251
Lirata.luteogaster.ec.D1106
Lirata.striatissima.trin.D0188
Lirata.striatissima.frg.D2264
Dilocantha.serrata.pan.D2265
Dilocantha.bennetti.trin.D3807
Dilocantha.bennetti.trin.D3820
Ectatomma
Ectatomma 1899
Kapala.sp4.arg.D3920
Kapala.sp4.frg.D2802
Kapala.terminalis.dr.D2260
Kapala.terminalis.dr.D1270
Kapala.sp5.texas.D2266
Kapala.nr.argentina.arg.D0986
Kapala.argentina.D1076
Kapala.sp1.braz.D3903
Kapala.sp3.dr.D2261
Kapala.floridana.D0432b
Kapala.sp2.venz.D3853
Kapala.sp2.ec.D0626
Kapala.sp2.ec.D0941
Kapala.sp8.ec.D3848
Kapala.sp9.col.D3437
Kapala.sp9.trin.D3823
Kapala.sp9.trin.D3822
Kapala.sp9.trin.D3824
Kapala.sp9.trin.D3825
Kapala.sp9.guat.D0379
Kapala.sp9.col.D0927a
Kapala.sp6.arg.D2521
Kapala.sp6.arg.D1080a
Kapala.nr.sulcifacies.sp2.col.D3923
Isomerala.bouceki.trin.D3821
Isomerala.azteca.mex.D0278
Kapala.izapa.mex.D2925
Kapala.sp11.hon.D0934a
Kapala.sp13.frg.D2800
Kapala.sp10.hon.D3738
Kapala.sp19.gal.D1389
Kapala.sp16.ec.D0938c
Kapala.sp20.ec.D1140
Kapala.sp22.dom.D2796
Kapala.ivorensis.mad.D2772
Kapala.ivorensis.saf.D2441
Kapala.ivorensis.st.D0273
Kapala.ivorensis.cam.D2648
Kapala.ivorensis.nig.D2693
Kapala.ivorensis.mad.D2771
Kapala.ivorensis.ken.D2746
Odontomachus 2802
Odontomachus
Dinoponera 3903
Ectatomma
Pachycondyla 2797, Ectatomma
Ondontomachus 2798
Ondontomachus 2800
Pachycondyla 2801
Afrotropical Distribution
0.03
30
20
10
0

FIGURE 3.2.

Bayesian maximum clade credibility phylogeny from 96 taxa and five gene regions. Posterior probabilities are given above branches. Support for major clades is shown at nodes by use of Navajo rugs; phylogenies can be found in supplementary materials (see Table 3.1). The three major groups are labeled as 1, 2, and 3. To the left of the phylogeny, large clades are indicated by orange letters below the appropriate branches . All genera have variously colored branches, and *Kapala* have black branches. Ant hosts are designated to the right of the tree. A D# following a host genus indicates the specimen with the host record is found directly in the analyses. Host data from several specimens from the larger analyses were included on this figure in the applicable phylogenetic position, though they are not found as terminals in the small dataset. Hosts colored green are Ectatomminae, hosts colored blue are Ponerinae. Inset: Dated BEAST phylogeny using all taxa. Full phylogeny is Figure S1. *Galearia* is shown with a dotted line due to uncertain placement.

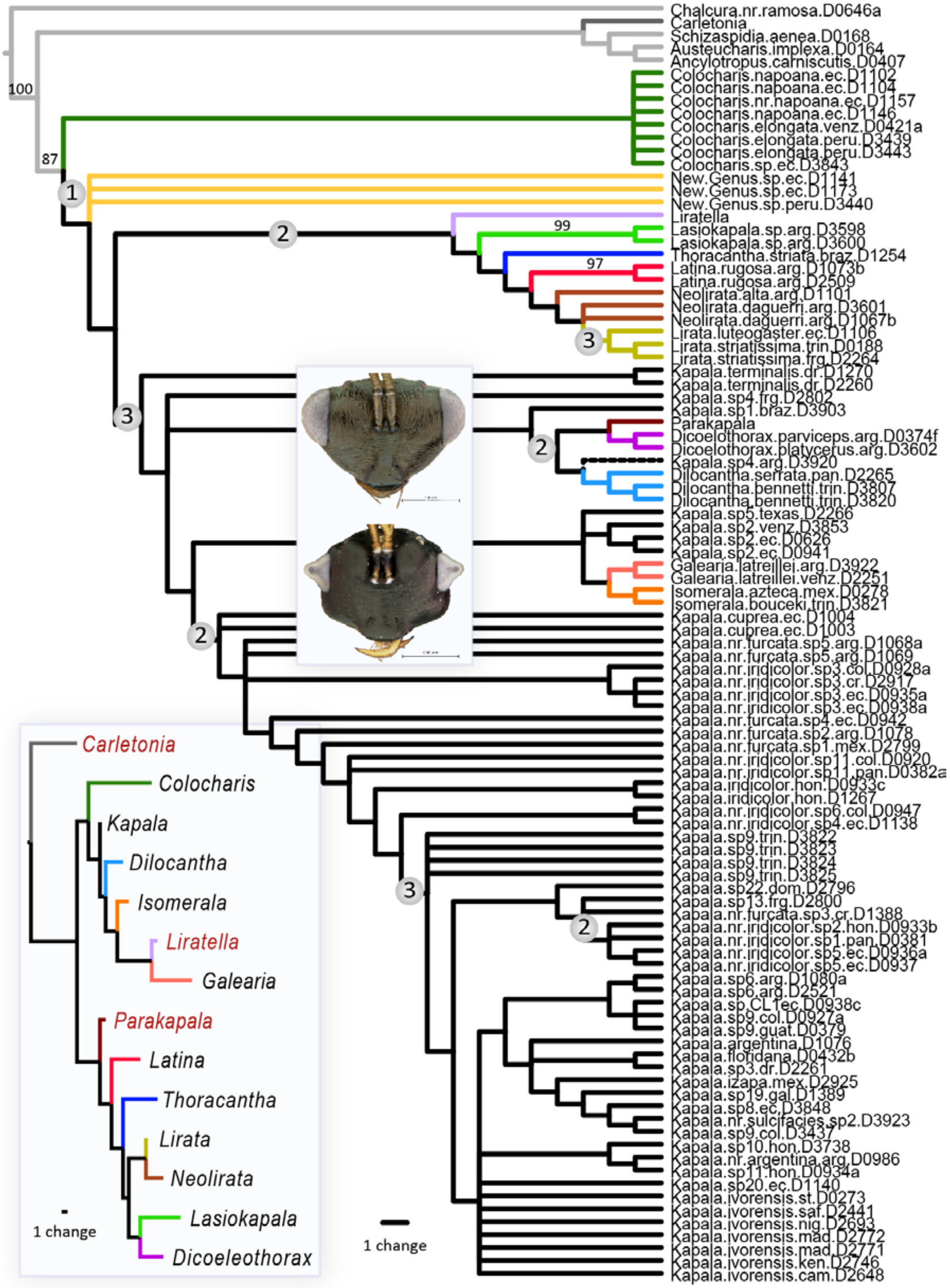
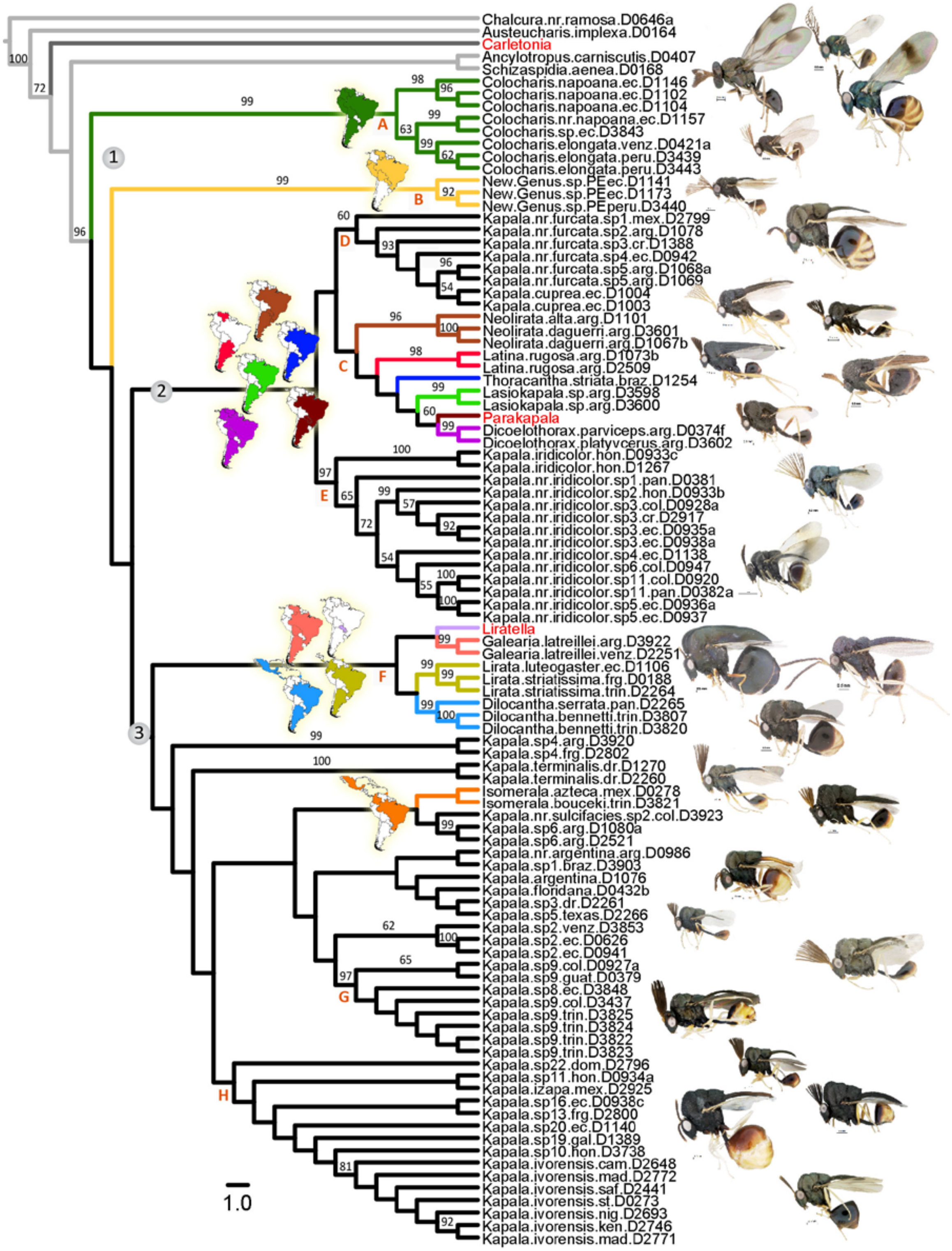

Chalcura.nr.ramosa.D0646a
Carletonia
Schizaspidia.aenea.D0168
Austeucharis.implexa.D0164
Ancylotropus.carniscutis.D0407
Colocharis.napoana.ec.D1102
Colocharis.napoana.ec.D1104
Colocharis.nr.napoana.ec.D1157
Colocharis.napoana.ec.D1146
Colocharis.elongata.venz.D0421a
Colocharis.elongata.peru.D3439
Colocharis.elongata.peru.D3443
Colocharis.sp.ec.D3843
New.Genus.sp.ec.D1141
New.Genus.sp.ec.D1173
New.Genus.sp.peru.D3440
Liratella
Lasiokapala.sp.arg.D3598
Lasiokapala.sp.arg.D3600
Thoracantha.striata.braz.D1254
Latina.rugosa.arg.D1073b
Latina.rugosa.arg.D2509
Neolirata.alta.arg.D1101
Neolirata.daguerri.arg.D3601
Neolirata.daguerri.arg.D1067b
Lirata.luteogaster.ec.D1106
Lirata.striatissima.trin.D0188
Lirata.striatissima.frg.D2264
Kapala.terminalis.dr.D1270
Kapala.terminalis.dr.D2260
Kapala.sp4.frg.D2802
Kapala.sp1.braz.D3903
Parakapala
Dicoelothorax.parviceps.arg.D0374f
Dicoelothorax.platycerus.arg.D3602
Kapala.sp4.arg.D3920
Dilocantha.serrata.pan.D2265
Dilocantha.bennetti.trin.D3807
Dilocantha.bennetti.trin.D3820
Kapala.sp5.texas.D2266
Kapala.sp2.venz.D3853
Kapala.sp2.ec.D0626
Kapala.sp2.ec.D0941
Galearia.latreillei.arg.D3922
Galearia.latreillei.venz.D2251
Isomerala.azteca.mex.D0278
Isomerala.bouceki.trin.D3821
Kapala.cuprea.ec.D1004
Kapala.cuprea.ec.D1003
Kapala.nr.furcata.sp5.arg.D1068a
Kapala.nr.furcata.sp5.arg.D1069
Kapala.nr.iridicolor.sp3.col.D0928a
Kapala.nr.iridicolor.sp3.cr.D2917
Kapala.nr.iridicolor.sp3.ec.D0935a
Kapala.nr.iridicolor.sp3.ec.D0938a
Kapala.nr.furcata.sp4.ec.D0942
Kapala.nr.furcata.sp2.arg.D1078
Kapala.nr.furcata.sp1.mex.D2799
Kapala.nr.iridicolor.sp11.col.D0920
Kapala.nr.iridicolor.sp11.pan.D0382a
Kapala.iridicolor.hon.D0933c
Kapala.iridicolor.hon.D1267
Kapala.nr.iridicolor.sp6.col.D0947
Kapala.nr.iridicolor.sp4.ec.D1138
Kapala.sp9.trin.D3822
Kapala.sp9.trin.D3823
Kapala.sp9.trin.D3824
Kapala.sp9.trin.D3825
Kapala.sp22.dom.D2796
Kapala.sp13.frg.D2800
Kapala.nr.furcata.sp3.cr.D1388
Kapala.nr.iridicolor.sp2.hon.D0933b
Kapala.nr.iridicolor.sp1.pan.D0381
Kapala.nr.iridicolor.sp5.ec.D0936a
Kapala.nr.iridicolor.sp5.ec.D0937
Kapala.sp6.arg.D1080a
Kapala.sp6.arg.D2521
Kapala.sp.CL1ec.D0938c
Kapala.sp9.col.D0927a
Kapala.sp9.guat.D0379
Kapala.argentina.D1076
Kapala.floridana.D0432b
Kapala.sp3.dr.D2261
Kapala.izapa.mex.D2925
Kapala.sp19.gal.D1389
Kapala.sp8.ec.D3848
Kapala.nr.sulcifacies.sp2.D3923
Kapala.sp9.col.D3437
Kapala.sp10.hon.D3738
Kapala.nr.argentina.arg.D0986
Kapala.sp11.hon.D0934a
Kapala.sp20.ec.D1140
Kapala.ivorensis.st.D0273
Kapala.ivorensis.saf.D2441
Kapala.ivorensis.nig.D2693
Kapala.ivorensis.mad.D2772
Kapala.ivorensis.mad.D2771
Kapala.ivorensis.ken.D2746
Kapala.ivorensis.cam.D2648
100
87
1
2
99
97
3
3
2
2
3
2
1 change
Carletonia
Colocharis
Kapala
Dilocantha
Isomerala
Liratella
Galearia
Parakapala
Latina
Thoracantha
Lirata
Neolirata
Lasiokapala
Dicoeleothorax
1 change

FIGURE 3.3.

Morphological parsimony phylogeny of 99 taxa from 52 characters. Strict consensus topology of 3 trees under implied weights (k=3). Retention index = 0.745, consistency index = 0.311. Bootstrap values from 1000 replicates are shown above branches, and the three major groups (as recovered by molecules) are labeled across the tree. Inset tree: Kapala Clade relationships from Heraty, 2002. Inset images: *Kapala* and *Isomerala* faces. *Isomerala* is easily-recognized by its facial characteristics is the only genus that comes out alone in the middle of a group of *Kapala. Kapala* sp4 D3920 had mostly missing data, and is indicated by a dotted terminal branch.


Chalcura.nr.ramosa.D0646a
Austeucharis.implexa.D0164
Carletonia
Ancylotropus.carniscutis.D0407
Schizaspidia.aenea.D0168
Colocharis.napoana.ec.D1146
Colocharis.napoana.ec.D1102
Colocharis.napoana.ec.D1104
Colocharis.nr.napoana.ec.D1157
Colocharis.sp.ec.D3843
Colocharis.elongata.venz.D0421a
Colocharis.elongata.peru.D3439
Colocharis.elongata.peru.D3443
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New.Genus.sp.PEec.D1173
New.Genus.sp.PEperu.D3440
Kapala.nr.furcata.sp1.mex.D2799
Kapala.nr.furcata.sp2.arg.D1078
Kapala.nr.furcata.sp3.cr.D1388
Kapala.nr.furcata.sp4.ec.D0942
Kapala.nr.furcata.sp5.arg.D1068a
Kapala.nr.furcata.sp5.arg.D1069
Kapala.cuprea.ec.D1004
Kapala.cuprea.ec.D1003
Neolirata.alta.arg.D1101
Neolirata.daguerri.arg.D3601
Neolirata.daguerri.arg.D1067b
Latina.rugosa.arg.D1073b
Latina.rugosa.arg.D2509
Thoracantha.striata.braz.D1254
Lasiokapala.sp.arg.D3598
Lasiokapala.sp.arg.D3600
Parakapala
Dicoelothorax.parviceps.arg.D0374f
Dicoelothorax.platyvcerus.arg.D3602
Kapala.iridicolor.hon.D0933c
Kapala.iridicolor.hon.D1267
Kapala.nr.iridicolor.sp1.pan.D0381
Kapala.nr.iridicolor.sp2.hon.D0933b
Kapala.nr.iridicolor.sp3.col.D0928a
Kapala.nr.iridicolor.sp3.cr.D2917
Kapala.nr.iridicolor.sp3.ec.D0935a
Kapala.nr.iridicolor.sp3.ec.D0938a
Kapala.nr.iridicolor.sp4.ec.D1138
Kapala.nr.iridicolor.sp6.col.D0947
Kapala.nr.iridicolor.sp11.col.D0920
Kapala.nr.iridicolor.sp11.pan.D0382a
Kapala.nr.iridicolor.sp5.ec.D0936a
Kapala.nr.iridicolor.sp5.ec.D0937
Liratella
Galearia.latreillei.arg.D3922
Galearia.latreillei.venz.D2251
Lirata.luteogaster.ec.D1106
Lirata.striatissima.frg.D0188
Lirata.striatissima.trin.D2264
Dilocantha.serrata.pan.D2265
Dilocantha.bennetti.trin.D3807
Dilocantha.bennetti.trin.D3820
Kapala.sp4.arg.D3920
Kapala.sp4.frg.D2802
Kapala.terminalis.dr.D1270
Kapala.terminalis.dr.D2260
Isomerala.azteca.mex.D0278
Isomerala.bouceki.trin.D3821
Kapala.nr.sulcifacies.sp2.col.D3923
Kapala.sp6.arg.D1080a
Kapala.sp6.arg.D2521
Kapala.nr.argentina.arg.D0986
Kapala.sp1.braz.D3903
Kapala.argentina.D1076
Kapala.floridana.D0432b
Kapala.sp3.dr.D2261
Kapala.sp5.texas.D2266
Kapala.sp2.venz.D3853
Kapala.sp2.ec.D0626
Kapala.sp2.ec.D0941
Kapala.sp9.col.D0927a
Kapala.sp9.guat.D0379
Kapala.sp8.ec.D3848
Kapala.sp9.col.D3437
Kapala.sp9.trin.D3825
Kapala.sp9.trin.D3824
Kapala.sp9.trin.D3822
Kapala.sp9.trin.D3823
Kapala.sp22.dom.D2796
Kapala.sp11.hon.D0934a
Kapala.izapa.mex.D2925
Kapala.sp16.ec.D0938c
Kapala.sp13.frg.D2800
Kapala.sp20.ec.D1140
Kapala.sp19.gal.D1389
Kapala.sp10.hon.D3738
Kapala.ivorensis.cam.D2648
Kapala.ivorensis.mad.D2772
Kapala.ivorensis.saf.D2441
Kapala.ivorensis.st.D0273
Kapala.ivorensis.nig.D2693
Kapala.ivorensis.ken.D2746
Kapala.ivorensis.mad.D2771
100
72
96
99
98
96
99
63
99
62
A
1
99
92
B
60
D
93
96
54
96
100
98
C
99
60
99
2
100
97
E
65
99
57
72
92
54
100
55
100
99
99
99
F
99
100
3
99
100
99
62
100
65
97
G
H
81
92
1.0

FIGURE 3.4.

Combined morphological and molecular hypothesis. Single best tree under parsimony using implied weighting (k=3). Retention index = 0.657, consistency index = 0.342. Groups 1, 2, and 3 are indicated at the nodes and bootstrap support shown above branches. Distributions of genera are shown by maps colored by country. On the right are images of taxa.

	BEAST		MrBayes					RAxML		TNT		
	96 taxa	195 taxa	96 taxa	86 RNR	195 taxa	'195' no Gal.	96 taxa combined	96 taxa	195 taxa	99 taxa morph	99 taxa combined	96 taxa DNA
	Fig. S2	Fig. S1	Fig. 2	Fig. S9	Fig. S3	Fig. S8	Fig. S7	Fig. S4	Fig. S5	Fig. 3	Fig. 4	Fig. S6
Kapala Clade	100	100	100	100	100	100	100	100	100	87	96	99
Group 1	65	88	grade	grade	32	22	grade	grade	9	grade	grade	grade
Groups 2+3	80	53	84	92	34	83	75	23	4	<50	<50	<50
Group 2	100	100	100	100	100	100	100	89	80	n/a	<50	<50
K. furcata+iridicolor clades, Clades D+E	n/a	n/a	54	n/a	n/a	n/a	53	n/a	n/a	n/a	<50	<50
Group 3	52	57	47	72	24	84	99 no GLD	17 no G.	3	n/a	<50	<50 no GLD
Galearia +*Lirata* +*Dilocantha* (GLD), Clade F	92	52	67	75	33	100*	97 w/ *Liratella*	n/a	8	n/a	<50 w/ *Liratella*	<50
K. sulcifacies group, Clade H	100	89	100	100	94	93	100	84	72	n/a	<50	<50

TABLE 3.1.

Support values for major clades across all four types of analyses. A 'n/a' indicates the clade was not recovered in the topology.

4. Chapter 3

Transatlantic dispersal: an Old World invasion by a New World ant parasitoid (Eucharitidae: Hymenoptera)

4.1 Introduction

The explanation of disjunct distributions is one of the "intriguing problems" in biogeography (Morrone & Crisci, 1995). Dispersal was a dominant explanation for centuries, until vicariance eclipsed it as the reigning hypothesis in the 1960s due in part to the recognition of plate tectonics and a non-static earth (Crisci, 2001; Posadas *et al.*, 2006), additionally facilitated by its explicit analytical methodologies as a discipline (Rosen, 1978). Dispersal was consequently regarded by many as an *ad hoc* explanation that could be invoked to describe any distribution pattern and therefore as a random process could not be expected to produce concordant patterns over multiple groups (Nelson & Platnick, 1981; Sanmartin & Ronquist, 2004). More recently, novel methods that include molecular divergence dating have allowed for a reexamination of these hypotheses of vicariance, and hence, for those divergences found to be too young to be explained by vicariance, oceanic dispersal as a viable explanation has made a resurgence (Cook & Crisp, 2005; de Queiroz, 2005; Renner, 2005; Christenhusz & Chase, 2013; de Queiroz, 2014). Many animal and plant groups exhibiting a present-day pantropical range were previously postulated to be Gondwanan in origin, while newer analyses have shown these taxa to be too young to support hypotheses of ancient divergence (Sanmartin & Ronquist, 2004; Clayton *et al.*, 2009; Vidal *et al.*, 2010; Rowson *et al.*, 2011).

Our focus is on the disjunction of a genus of ant parasitoids across present-day South America and Africa, two landmasses which separated ~100-106 mya (McLoughlin, 2001; Eagles, 2007; Moulin *et al.*, 2010; Seton *et al.*, 2012), while the genus of interest, *Kapala*, putatively emerged during the late Eocene or early Miocene (Murray & Heraty, in prep.-a). The majority of tropical trans-Atlantic plant and animal crossings invoked by dispersal are proposed to have occurred in an east to west direction (Renner, 2004; Cook & Crisp, 2005; Monaghan *et al.*, 2005; Trenel *et al.*, 2007; Gamble *et al.*, 2011; Price *et al.*, 2011; Blaimer, 2012; Banasiak *et al.*, 2013; Uit de Weerd & Gittenberger, 2013). In plants, there are several examples of postulated west to east dispersals of species in over a dozen different plant families (Renner *et al.*, 2001; Pennington, 2003; Givnish *et al.*, 2004; Renner, 2004; Prince & Kress, 2006; Dick *et al.*, 2007; Bouetard *et al.*, 2010; Duchen & Renner, 2010; Michalak *et al.*, 2010; Nie *et al.*, 2012; Christenhusz & Chase, 2013). Animal examples are far rarer.

In the several plant groups with dated phylogenies, it is estimated that transatlantic dispersals from South America occurred throughout a time period of 2-30 mya. For example, African *Ampelopsis* (Vitaceae) and African *Vanilla* (Orchidaceae) diverged, respectively, from their New World ancestors 30.5 mya (Nie *et al.*, 2012) and ~25 mya (Bouetard *et al.*, 2010). Vitaceae are often bird-dispersed, and *Vanilla* hypothetically may be dispersed by migratory birds or floating vegetation. The ancestor of the Paleotropical tribe Melastomeae (Melastomataceae) is believed to have dispersed to Africa 12-14 mya, and later nearly 50 species reached Madagascar (Renner *et al.*, 2001). *Pitcairnia feliciana* (Bromeliceae) and *Maschalocephalus* (Rapateaceae) diverged from their New World sister groups around 12 and 7.3 mya, respectively, and subsequently colonized Africa no later than an estimated 6-8 mya (Givnish *et al.*, 2004). *Cayaponia* reached

Africa 2-5 mya and is also found on Madagascar, though it is unresolved as to whether that second event was an anthropogenic introduction (Duchen & Renner, 2010). In another recent event, *Hernandia beninensis* (Hernandiaceae) is tentatively postulated to have dispersed ~3 mya and is endemic to the islands of São Tomé and Bioko but not on the mainland (Michalak *et al.*, 2010). Hernandiaceae can tolerate a broad range of conditions and the fruits can be dispersed by many methods, including wind, water, birds, and bats.

In contrast to the multiple instances of east to west plant dispersal, we are aware of only two examples in the literature of an animal colonizing Africa after a trans-Atlantic dispersal. One is the thrush genus (*Turdus*) which exhibits two separate dispersal events to Africa after divergence from New World ancestors. Both groups diverged from ancestors in the West Indies or northern South America region an estimated 5.7 mya (five extant species) and 4.7 mya (one species) (Voelker *et al.*, 2009). Postulated as another group displaying east to west dispersal are the circumtropical crocodiles (*Crocodylus*) (Oaks, 2011), though there is evidence to refute this hypothesis. Oaks (2011) tested several dispersal models, and the South America to Africa dispersal reconstruction is not recovered under all models. Additionally it conflicts with the conclusions of Meredith *et al.* (2011) which suggest origin dispersal out of Africa to the New World.

We investigate an unusual event of an insect species which potentially dispersed from South America to Africa and Madagascar. *Kapala ivorensis* Risbec (Hymenoptera: Eucharitidae) is the only member of the Kapala clade that is found in the Old World with the majority of the clade being primarily Neotropical with some Nearctic in the southern US. The Kapala clade is a diverse group of 13 genera whose monophyly is supported in both morphological and molecular analyses (Heraty, 2002; Heraty *et al.*, 2004; Murray *et al.*, 2013; Murray & Heraty, in prep.-a). *Kapala ivorensis* is the only species of this clade known to occur outside of the New World, and has a widespread distribution across sub-Saharan Africa, Madagascar, and São Tomé.

Kapala is a commonly collected genus in the ant parasitoid family Eucharitidae (Chalcidoidea: Hymenoptera) (Heraty & Woolley, 1993; Heraty, 2002; Pérez-Lachaud *et al.*, 2006b; Lachaud & Pérez-Lachaud, 2012). Eucharitidae are found in nearly every zoographic region, with an estimated 700 species attacking the immature stages of ants of five different subfamilies (Heraty, 2002; Lachaud & Pérez-Lachaud, 2012; Torréns, 2013). Results of molecular dating indicate that eucharitids diversified at a minimum age of 72.0 mya (95% probability = 53.9-92.6 mya) (Murray *et al.*, 2013). It was proposed that Eucharitidae originated in the Old World (OW) and multiple groups subsequently colonized the New World (NW) via a series of dispersal events occurring ~20-40 mya, some potentially following northern land bridge connections to the NW (Murray *et al.*, 2013).

Previous phylogenetic analyses support two Old World sister groups, the Chalcura and Schizaspidia clades, which form a paraphyletic grade to the New World taxa (Murray *et al.*, 2013). These three clades together make up the PEM parasitoids, which are united in attacking Ponerinae, Ectatomminae and Myrmeciinae ants (Heraty, 2002; Lachaud & Pérez-Lachaud, 2012; Murray *et al.*, 2013). The five genera of the Chalcura clade are found in the Ethiopian, Indo-Pacific, and Australian regions (terminology of biogeographic regions following Schuh & Stonedahl, 1986). The six genera of the Schizaspidia clade are found in the Afrotropical

(Ethiopian+Malagasy), Indo-Pacific, Palearctic, and Australian regions (distributional data from Heraty, 2002; Heraty, 2014). The Chalcura clade is widespread in Australia and rare on the Asian mainland, while the Schizaspidia clade is uncommon in Australia and most diverse in the Indo-Pacific, reaching as far north as Japan (Palearctic). To the east, species of both groups are often island endemics, potentially resulting from steppingstone dispersal and speciation. Species in both the genera *Chalcura* and *Schizaspidia* are distributed eastward into the Pacific in the Oriental and Paupan subregions, with endemic *Chalcura* species found in Samoa and the Marshall Islands and endemic *Schizaspidia* species are found in Fiji, Tonga, and American Samoa (Heraty, 2002; Heraty, 2014). However, there are no genera of either the Chalcura or Schizaspidia clades known from the New World.

In seven of the eleven genera of the Chalcura and Schizaspidia clades, short oceanic dispersals are inferred to have produced disjunct distributions, but long-distance dispersal is rare. One enigmatic genus in the PEM clade is the unplaced New World *Carletonia*, which is rarely collected and for which there is no molecular data available. It is morphologically similar to some members of the Schizaspidia clade and was recovered as sister to the Kapala clade based on potentially homoplastic characters (Heraty, 2002). However, phylogenetic placement has not yet been determined, because subsequent morphological analyses give conflicting results, placing *Carletonia* within the Old World grade (Murray & Heraty, in prep.-a). Within the Kapala clade, only the genus *Kapala* shows evidence of short oceanic dispersals as it is found across islands in the Caribbean, along with at least one *Kapala* species known from the Galapagos.

Based on molecular evidence, it is estimated that the Kapala clade diverged from the Old World taxa approximately 35.6 mya (25.7-46.4) (Murray *et al.*, 2013) and diversified within the New World at 25.4 my (15.5-37.1) (Murray & Heraty, in prep.-a). The only other eucharitid genus that has a pattern of a shared OW to NW distribution is *Orasema* (Oraseminae), which is proposed to have colonized the NW ~20 mya, potentially via a northern land bridge (Murray *et al.*, 2013).

Kapala is paraphyletic, but other genera within the clade are monophyletic (Murray & Heraty, in prep.-a). All members of the clade possess paired scutellar spines separated basally, a small lateral axillar lobe, an incomplete hind wing marginal vein, and males are distinguished from females by their long-branched antennae (Heraty, 2002). These wasps are ectoparasitoids on the larvae of large-bodied predatory ants in the subfamilies Ectatomminae and Ponerinae (Heraty, 2002; Lachaud & Pérez-Lachaud, 2012; Murray *et al.*, 2013). As with other Eucharitidae, female wasps lay eggs away from the host in or on plant tissue. The active planidial stage (first-instar larva) is responsible for obtaining entry to the host nest, where it attaches to the host ant larvae. Larval and pupal development is completed on a single host pupa, and after emergence, adult eucharitids must exit the nest to mate (reviewed in Lachaud & Pérez-Lachaud, 2012).

Kapala is especially common and speciose in the Neotropical region, though its entire range extends from the southern US (Arizona, Texas, and Florida) to Argentina and it is not found in Chile. *Kapala* is known to attack three genera of Ponerinae and three genera of Ectatomminae (Lachaud & Pérez-Lachaud, 2012; Murray *et al.*, 2013). There are currently 18 species described, though this number has been predicted to increase to 25-60 species (Heraty, 2002). Based on results from Murray and Heraty (in prep.-a), along with over 4000 specimens from museum collections, the number of species of *Kapala* is at the high end of that estimate and the genus may potentially comprise up to 75 species.

Kapala ivorensis is an anomaly. While the majority of species and morphological diversity is confined to the New World, a single widespread species occupies a range extending across the Afrotropics. Risbec (1954) first described *K. ivorensis* from a single female specimen from the Ivory Coast, though he had misidentified it as a male. Heraty (2002) further documented a range that spanned seven African countries and Madagascar. No males had been collected by that time, and it was proposed that *K. ivorensis* might be a thelytokous species. While males have since been collected, the female to male ratio of museum specimens is approximately 15:1. Currently, *K. ivorensis* has been recorded from Madagascar and 12 African countries across sub Saharan Africa (Fig. 1), including the island of São Tomé which is located in the Gulf of Guinea >200 km west of the continent. Currents from both the Congo and Niger Rivers flow towards São Tomé (Measey *et al.*, 2006) providing a potential dispersal mechanism for oceanic rafting from the mainland, but no other eucharitids have been recorded for São Tomé.

There is no question that *K. ivorensis* is a derived member of the Kapala clade. Genetically and phenotypically it has no commonalities with any of the members of the Chalcura and Schizaspidia clades in Africa and Madagascar. The question then becomes whether this is a human-mediated introduction. Prior to dated analyses, the disjunct distribution of *K. ivorensis* from the remainder of the genus was interpreted by Heraty (2002) as a recent anthropogenic movement because of the presumed rarity of oceanic dispersal events. It was posited that the wasps and their ant hosts could survive in the ship ballast carried across transcontinental trading routes.

Kapala ivorensis has been included in two previous dated molecular analyses: Murray *et al.* (2013) used three *K. ivorensis* specimens in a fossil-calibrated family-level phylogeny (237 taxa) that included five gene regions, 18S, 28S-D2, 28S-D3, COI, and COII. The estimated crown age of *K. ivorensis* was 2.22 my (0.78-3.88), with divergence from the New World estimated at 4.80 my (2.35-7.44). Murray and Heraty (in prep.-a) focused on the Kapala clade and analyzed 195 taxa with the same five gene regions, with a secondary calibration on the divergence of the New World Kapala clade from the Old World taxa. Eleven *K. ivorensis* specimens were included, with a resulting crown age of 2.69 mya (1.1-4.98), and the New World split at 5.78 my (2.65-10.1).

Herein we will verify the age of the relaxed molecular clock estimates with a strict molecular clock calculation. We address the species status by examining population level divergence and morphological variation. DeSalle *et al.* (2005) recommend using multiple lines of evidence to delineate species, and here is presented evidence of DNA, morphology, and geography to show that *K. ivorensis* is one widespread species. Additionally, we postulate the expected origin of the OW *Kapala* and the potential for natural dispersal versus anthropogenic means in its movement to the Old World.

4.2 Materials and Methods

4.2.1 Dataset

Kapala ivorensis has been collected from: Democratic Republic of São Tomé and Príncipe, Democratic Republic of the Congo, Federal Republic of Nigeria, Republic of Cameroon, Republic of Côte d'Ivoire, Republic of Guinea, Republic of Kenya, Republic of Madagascar, Republic of Sierra Leone, Republic of South Africa, Republic of the Congo, Republic of Uganda, and The Gambia. We have molecular data from nine of these countries (Fig. 1 map, dots indicate DNA specimens). All DNA specimens are mounted and vouchered (see Table 1) and sequences will be submitted to Genbank (Table 2). Morphological characters were diagnosed based upon ~75 *K. ivorensis* specimens accessed through museum collections (distribution in Fig. 1, map inset). *Kapala ivorensis* georeference data were submitted to the Hymenoptera Online database, and individual specimen records can be accessed at hol.osu.edu.

The molecular matrix was derived from the Kapala clade dataset of Murray and Heraty (in prep.-a) with only the monophyletic clade of the nearest relatives of *K. ivorensis* retained for reanalysis of their relationships herein (Table 1). A summary of the Kapala clade is presented in simplified format in the Fig. 1 inset phylogeny, with the specimens used in this study circled. These specimens are within Group 3, a clade which is made of five genera, including a portion of *Kapala*. The monophyletic group of 39 individuals used here includes *K. ivorensis* and also several New World specimens historically loosely defined as “near” *K. sulcifacies* Cameron due to their vaulted mesosoma and striate facial sculpturing (Heraty & Woolley, 1993). We have also identified some of the New World specimens included here as *Kapala izapa* Carmichael. The molecular matrix analyzed includes 14 *K. ivorensis* collected from nine Afrotropical countries (Table 1).

4.2.2 DNA extraction, sequencing, and alignment

We used the alignment from Murray and Heraty (in prep.-a), which included three nuclear ribosomal gene regions: 18S, 28S D2, and 28S D3-5, and two mitochondrial gene regions: COI and COII. In addition, a fast-evolving ITS2 gene region (second internal transcribed spacer) was added to the matrix, using primers ITS2F, 5'-TGT GAA CTG CAG GAC ACA TG-3' and ITS2Ra, 5'-TCT CGC CTG CTC TGA GGT-3'. ITS2 immediately precedes the 28S large ribosomal subunit and is useful for intraspecies to genus level phylogenetic inference (Rokas *et al.*, 2002). ITS2 was aligned using the MAFFT v7 online server (Katoh *et al.*, 2005), using the Q-INS-i model for RNA data. DNA was extracted from three additional *K. ivorensis* taxa representing two previously-unsampled African countries (Table 1) using a DNeasy kit (Qiagen), and the gene regions were amplified via PCR following protocols of Murray *et al.* (2013). The COI portion amplified is a modified NJ-MD region (Simon *et al.*, 1994), with forward NJ, 5'-TAT ATT TTA ATT YTW CCW GGA TTT GG-3', and reverse C1-N-2594, 5'-ATT GCA AAT ACT GGA CCT AT-3' which is shorter than some of the other COI included in the phylogenetic analysis of Murray and Heraty (in prep.-a). DNA templates were prepared using GeneClean (MP Biomedicals) and submitted to the IIGB Genomics Core at University of California Riverside for sequencing. Sequencher 4.8 (Gene Codes Corp) was used to edit chromatograms.

The number of parsimony-informative and constant sites in each gene were calculated using PAUP* (Swofford, 2002) (Table 2). Uncorrected distances of mtDNA were used to summarize inter- and intra-specific divergence.

4.2.3 Phylogenetic Analyses, Molecular Distances, and Haplotype Network

We endeavored to implement the best fit of data and partitioning model for Bayesian inference of phylogeny, and therefore compared different partitioning schemes in order to choose the phylogeny with the best likelihood. Bayesian phylogenetic inference and stepping-stone importance sampling were performed using MrBayes v3.2.2 (Ronquist *et al.*, 2012) through CIPRES (Miller *et al.*, 2010). Ultimately, two different partitioning schemes were compared in a likelihood framework using MrBayes for stepping-stone sampling (Fan *et al.*, 2011; Xie *et al.*, 2011). This method uses both the posterior and the prior distributions, computing the marginal likelihood, and is considered superior to using the harmonic mean. Two schemes were analyzed for best fit: Scheme 1, ‘8 partitions’: [18S], [28S D2], [28S D3], [ITS2], [COI positions 1+2], [COII pos 1+2], [COI pos 3], and [COII pos 3]; and scheme 2, ‘4 partitions’: [18S + 28S D2 + 28S D3], [ITS2], [COI + COII pos 1+2], and [COI + COII pos 3]. The stepping-stone analyses were run for a total of 200 mil generations sampling every 500, with the default 50 steps, resulting in 7843 samples per step after burnin.

For phylogenetic inference, partitioned data was run under reversible jump MCMC using the mixed nucleotide substitution model, with a gamma distribution to account for rate heterogeneity. Each partition was unlinked and the branch length prior was set to an exponential distribution with a mean of 0.01. The dataset and program commands will be deposited in Dryad. The concatenated analysis was run for 50 mil generations, sampling every 5000, and 50% of each run was removed as burnin. A likelihood posterior parameter distributions of ESS >200 of the was confirmed in Tracer v1.5 (Rambaut & Drummond, 2007). The two independent runs for the analysis were combined, and TreeAnnotator v1.8 (Drummond & Rambaut, 2007) was used to determine the maximum clade credibility tree.

In addition to phylogenetic inference of relationships in *K. ivorensis* plus the NW sister taxon (D2796), a haplotype network was constructed, allowing for non-bifurcating relationships, meaning that reticulated relationships are allowed. The ribosomal genes were not analyzed since there were so few differences between *K. ivorensis* and D2796: none in 18S or D3-5 and one in D2. For the three fastest-evolving genes – COI, COII, and ITS2 – intraspecific connections were graphed using TCS (Templeton *et al.*, 1995; Clement *et al.*, 2000). This employs statistical parsimony, which first seeks most-parsimonious connections, but then allows nonparsimonious alternatives to build the network (Templeton *et al.*, 1992). Indels in ITS2 were treated as a 5th base (five sites).

To independently assess previous fossil-calibrated dating results of the age of *K. ivorensis* (Murray *et al.*, 2013; Murray & Heraty, in prep.-a), we calculated a strict molecular clock estimate of age from a constant global nucleotide substitution rate based on two previously-published mtDNA rates. However, we note that this method is used as a means of approximate comparison to the previously-published dating analysis due to the fact that our likelihood ratio test rejected clock-like evolution (chi-square dist., p=0.0019). We acknowledge drawbacks of the clock method (Ho & Lo, 2013) but believe the short time period lends itself to a rough estimate to corroborate the fossil calibration since there is a shorter time to accumulate error or account for substitution rate heterotachy. Two published estimates were used: 1) the commonly-cited arthropod estimate of 0.015 substitutions/site/million years (Brower, 1994), and 2) an estimate of 0.019 subs/site/my from the agaonid fig wasps, another family in Chalcidoidea (Machado *et al.*, 2001). Crown Agaonidae are estimated to be approximately as old as Eucharitidae, at 75.1 my (56.2-94.9 my) (Cruaud *et al.*, 2012) or older (Lopez-Vaamonde *et al.*, 2009). We used nine *K. ivorensis* specimens along with the NW sister taxon *K.* sp. 13 Dominica (D2796) recovered in phylogenetic analyses, for a total of ten taxa that had both COI NJ-MD and COII data. We calculated corrected pairwise distances from the nucleotide substitution model as determined in jModelTest v2.1 (Darriba *et al.*, 2012), using the Akaike Information Criterion corrected for small sample size as the model selection metric.

Lastly, the correlation between genetic distance and geographic distance of the OW populations was tested using Isolation by Distance Web Service v3.23 (IBDWS) (Jensen *et al.*, 2005). This program follows the hypothesis that there will be a decrease in genetic similarity as populations become progressively geographically distant (Wright, 1940, 1943). We analyzed mtDNA (COI NJ-MD and COII) using 10 of the *K. ivorensis* specimens, because only one population is allowed to have less than two individuals. Included taxa were: Congo (3), Madagascar (2), São Tomé (2), South Africa (1), and Uganda (2). Two of the Congo specimens were from the same locality and the third was 5 km apart, and we grouped them as one population. Geographic distances were calculated from pairwise coordinates using the ellipsoid model of the shape of the Earth in the R package sp (Bivand *et al.*, 2013). In IBDWS, the genetic distances were log-transformed before analysis, and 10,000 randomizations were run. Genetic distances were computed based on the sequence data under a K2P substitution model, which was the most parameter-rich available; sites with missing data (only Congo specimens missing COI) allowed to match to everything (instead of being ignored). Final results are based on phi$_{ST}$ values, which measure differentiation of populations using DNA sequences instead of numerical distances (as in the F_{ST}). Correlation is reported as a reduced major access regression value and statistical significance is based on a nonparametric Mantel test built into the online program.

4.3 Results

4.3.1 Molecular data collection and model choice

There were few base pair differences, so alignment of the molecular data was trivial. Generally, the mitochondrial genes aligned without gaps or stop codons. However, there were suspected COI numts (nuclear mitochondrial DNAs) from the three individuals from the Republic of the Congo (D2922-24). All three individuals were identical for what amplified as the 'COI region', which was 16 bases shorter than other *K. ivorensis*, had stop codons within the sequence, and also had gaps present in non-triplicate; these results were verified by a second amplification. DNA contamination by another organism was excluded because a BLAST search revealed 89% maximum identity with other species of *Kapala*. Numts were not recovered in the COII region.

We implemented a test for the best-fit partition model as a statistical approach to choose a phylogeny, prompted by the low branch support on preliminary trees. Marginal likelihood from the stepping-stone analysis was -6244.90 for ‘8 partitions’ and -6202.75 for ‘4 partitions’. The resulting Bayes factor is 42.15 which can be interpreted as strong support for ‘4 partitions’ (Kass & Raftery, 1995). The phylogenetic results presented are based on a 4-partition regimen.

4.3.2 Phylogenetic relationships

Using six gene regions, we analyzed the previously-recovered monophyletic group of 39 specimens in Group 3 of the Kapala clade (Murray & Heraty, in prep.-a) along with three additional specimens of *K. ivorensis*. The Bayesian maximum clade credibility tree is shown in Fig. 1. Monophyly of the OW *Kapala ivorensis* group is supported with a posterior probability (pp) of 98, and it renders the NW *Kapala* paraphyletic . What we regard as an undescribed species from Dominica in the “K. sulcifacies complex”, *Kapala* sp. 13 (D2976), is recovered as the sister to a monophyletic *K. ivorensis* (97 pp) and it has also been recovered under different sampling regimes (Murray *et al.*, 2013; Murray & Heraty, in prep.-a). Another specimen from Dominica, *Kapala* sp. 7 (D2785), does not have any support as being closely related.

Only one internal branch within *K. ivorensis* has support above 70 pp, the stem of two specimens from the same location in the Republic of Congo (88 pp). To assess relationships below the species level, individual haplotype networks were analyzed for COI (10 ind.), COII (15 ind.), and ITS2 (9 ind.) (COII, Fig. 2; COI and ITS2, Fig. S1). Results show reticulated networks in *K. ivorensis* for both COI and COII and the Dominican sister taxon being treated as part of a different COI network cluster. For the 9 taxa analyzed for ITS2, *K. ivorensis* is split into three haplotypes, and the Dominican specimen (*K.* sp. 13, D2796) is removed by seven changes from the Old World species, four of which are indels. There are no geographic clusters in any of the three genes.

4.3.3 Morphology

Kapala ivorensis specimens are extremely similar in morphology, and exhibit little variation across their Old World range. A diagnosis of *Kapala ivorensi*s: *Kapala ivorensis* can be distinguished from related *Kapala* species by a combination of characters (Fig. 3D-L). In lateral view, the midlobe of the mesosoma is rounded but not vaulted, the apex of the scutellum is approximately 1 X the height of the spines, with a 35-45° angle from tip to base. The upper prepectus is triangular and narrowed to the posterior tip, and the pleuron has light striations, with a weakly-impressed, curving femoral groove. In dorsal view, the spines are 1.8 - 2.0 X the length of the scutellum from the transscutal articulation to the posterior scutellar apex between the spines, and the spines have an evenly convex curve in dorsal view and laterally emarginate apices. The propodeal disc is flat and shallowly punctate, with a carinal border. As in other *Kapala*, the males are more striate across the face (both frons and gena) and mesosoma than females (Fig. 3K). There is very little morphological variation over the entire range of *K. ivorensis*, supporting the relationships observed in the molecular results. Spine shape can differ slightly, but spines tend to show variation across other species. *Kapala ivorensis* is very similar to the sister Dominican species that is predicted to be its sister group (top row, Fig. 2), but has a more evenly rounded and less carinate mesosoma, narrower prepectus, lighter striae on the pleuron, and few to no setae on the mesepimeron (Fig S2).

4.3.4 Molecular distances, dating, and geography

Intraspecifically, for ribosomal DNA 18S, 28S D2, and 28S D3-5, all *K. ivorensis* individuals are identical, excepting D0273 (one of two from São Tomé), which has two polymorphisms in 28S-D3-D5. In the three fast-evolving genes, the number of polymorphic characters for the 14 *K. ivorensis* is as follows: COI NJ-MD: 16, COII: 16, ITS2:3. Interspecifically, *K. ivorensis* exhibits four unambiguous synapomorphies from the New World specimens sampled. In COI NJ-MD, there is a transition (pos 15, G→A) and a transversion (pos 297, A/G →T) (both 3rd positions), in COII, there is a transition (pos 171, A→T) (3rd position), and in ITS2 there is a transition (pos 246, T→A).

All mtDNA nucleotide changes in *K. ivorensis* but one are synonymous substitutions. In the nine *K. ivorensis* with both COI+COII, the individuals exhibit an average uncorrected p distance of 1.2% (range = 0.5%-2.0%). This value does not overlap with their mean interspecific distance to the closest known relative from Dominica, at 3.7% (range = 3.0%-4.1%). Other NW species have similar uncorrected distances, though covering less geographic space and with fewer sampled specimens (Table 3).

The HKY + I (I=0.86) was chosen as the best-fit nucleotide substitution model for COI+COII of all *K. ivorensis* + the NW sister from Dominica, D2796. Absolute age was calculated by dividing the corrected pairwise distance of mtDNA by the substitution rate from independent estimates of 0.015 subs/site/my (arthropod) and 0.019 subs/site/my (chalcid). No error is associated with the clock estimation. The resulting age of crown *K. ivorensis* is 2.03 my using the slower arthropod rate, and 1.23 my using the faster agaonid rate. The minimum age for the *K. ivorensis* split from the NW Dominica D2796 is 3.50 my under the slow rate or 2.12 my under the fast rate.

The populations of *K. ivorensis* sampled are geographically extremely distant from one another and it may be expected that closer populations tend to be more genetically similar. Specimens are difficult to obtain, but we do have four localities with more than one individual sampled. We find there is no statistical correlation between the genetic distance and geographic distance of the populations (r=-0.19, Mantel test, one-sided p=0.7036) (Fig. S3). Additionally, on the phi_{ST} scale of 0-1 (indicating complete panmixis vs. population fixation), the five *K. ivorensis* populations range from 0 to 0.467 meaning that there is no or little population fixation of alleles.

4.4 Discussion

4.4.1 Phylogeny

Kapala ivorensis potentially colonized tropical Africa and Madagascar over 1.23 mya according to clock and fossil-calibrated dating (Murray *et al.*, 2013; Murray & Heraty, in prep.-a). The monophyly of *K. ivorensis* is always supported suggesting a single ancestral establishment event. Intraspecifically, there are many short branches and little internal resolution. Within the large geographic range of specimens, there is no morphological differentiation or genetic signal that correlates to geography. The sister group of New World specimens are not highly genetically or phenotypically differentiated from each other. However, there are subtle morphological variations that distinguish the NW species from the OW species, with the Dominican sister being the most similar to *K. ivorensis*. The low amount of variation among putative species sampled in the New World serves as a contrast to the long internal branch leading to the Old World *K. ivorensis*.

4.4.2 Species status of *K. ivorensis*

There is little phylogenetic signal within *K. ivorensis* but it is clearly genetically distinct from the New World relatives. Though we have limited population-level information, there is no overall pattern of phylogeographic structure within *K. ivorensis*. Haplotype networks show connections that transverse the African mainland along with spanning two bodies of water to reach São Tomé and Madagascar (Fig. 2). It is surprising the populations are so similar genetically and morphologically despite the geographic distance. Four pairs of specimens were each collected from the same locality, and only one of these (Republic of the Congo) are identical; conversely the pairs from São Tomé, Uganda, and Madagascar are not each other's closest relatives in a haplotype or phylogenetic analysis (though with no pp support). Statistically there is no correspondence between the geographic position and the genetic distance of the populations (Fig. S3). If there were structure, we would expect higher phi_{ST} values and close populations to be more genetically similar than distant ones.

Additionally, morphology indicates one species due to the similarity of the individuals in characters such as facial striation patterns, antennal length, spine shape and length, scutellar apex, and pleuron sculpturing (Fig. 3D-L, S2, bottom row). The lack of morphological diversity of

Kapala in the OW is in contrast to that of the NW, which includes many more species than sampled here (e.g. Murray & Heraty, in prep.-a). The Dominican sister taxon, *Kapala* sp. 13 D2796, is closest in phenotype of all other New World specimens sampled. Another specimen from Dominica, *Kapala* sp. 7, D2785, is not closely related genetically.

The lack of geographic structure and pattern of population differentiation (Scheffer & Grissell, 2003) points to recognition of only one species in the Old World. DeSalle *et al.* (2005) recommend using multiple lines of evidence to delineate species, drawing at least two arguments from evidence of DNA, morphology, ecology, geography, or reproduction. We have information on three data types that indicate *K. ivorensis* is a distinct species from the New World taxa: the disjunct range, low intraspecific molecular divergence coupled with interspecific synapomorphies, and cohesive intra-species morphology.

4.4.3 Biogeography and dispersal

In contrast to the numerical abundance and morphological diversity in the NW is the infrequently-collected *K. ivorensis*. The large geographic range is atypical for a *Kapala* species, especially considering the low amount of molecular (max 2.0% in mtDNA) and phenotypic variation stretching roughly 8000 km across the expanse from Gambia to Kenya, including the islands of São Tomé and Madagascar.

Most genera of Eucharitidae exhibit geographic endemism (Heraty, 2002), suggesting a low probability of long-distance dispersal events. No other genera of Eucharitini (Eucharitinae; over

40 genera) are shared between the Old and New Worlds. Eucharitid species are restricted in range due to their dependence on host plants and host ants, low vagility exhibited by larvae and adults, and the propensity to remain near the emergence site (Clausen, 1940a, 1941). *Kapala ivorensis* is proposed to be the only eucharitid to have successfully dispersed from the NW to OW (Murray *et al.*, 2013), likely in a transatlantic sweepstakes dispersal. We reject the hypothesis of multiple New World sources that might lead to a greater mitochondrial diversity, since the OW *Kapala* sampled have one phylogenetic origin.

There is a general expectation that introduced species undergo a genetic bottleneck and will exhibit less genetic diversity than its source, and this general pattern is supported in many studies, though the founder effects may be rather small (Nei *et al.*, 1975; Hufbauer *et al.*, 2004; Kolbe *et al.*, 2012; Shirk *et al.*, 2014). For instance, Scheffer and Grissell (2003) studied the disjunct distribution of an African seed-eating chalcidoid, *Megastigmus transvaalensis* (Hussey) (Torymidae) which was dispersed along with its host (*Schinus* seeds) via human-mediated means. All introduced populations in Brazil, California, Florida, and Hawaii share the same haplotype as the putative source population. This pattern is in contrast to the genetic diversity seen in *K. ivorensis*, which leads us to believe the species was not recently introduced. *Kapala ivorensis* has genetic heterozygosity comparable to species in the New World. Two other species with a similar age to *K. ivorensis* have comparable mtDNA distances (Murray & Heraty, in prep.-a): *K. terminalis*, dated at ~2 my, has a distance of 1.4%, but is only found across the Caribbean from Cuba to the Virgin Islands. The *K. furcata* species group dated at ~2.5 my shows a distance of 2.3%, across a geographic range of 1000 km across Argentina and Paraguay.

We believe that a fossil-calibrated relaxed molecular clock estimate is preferable (Murray *et al.*, 2013; Murray & Heraty, in prep.-a), yet we wanted to explore the ages returned using a strict clock. The strict molecular clock estimate provided here corresponds surprisingly well with the previous estimate based on fossil calibrations. The strict clock estimates based on mtDNA distances are younger; however even at the most recent end of the divergence range date, this age is too old for anthropogenic dispersal to be a viable explanation (Campbell & Tishkoff, 2010), since the clock estimate of crown *K. ivorensis* is 1.23 and 2.03, under the fast and slow rates.

We hypothesize for *K. ivorensis* a west-to-east transatlantic dispersal. The potential means for a transatlantic dispersal event would be the North Equatorial Countercurrent originating off northeastern South America, with winds playing a very important role, though neither the current nor winds originate directly on the coast (Grodsky, 2003; Renner, 2004). Dispersing across water on floating islands – rafting on tangled plants and soil – has been postulated for other transoceanic dispersal by animals (Houle, 1998; Poux *et al.*, 2006; Vidal *et al.*, 2008; de Oliveira *et al.*, 2009; Rowe *et al.*, 2010; Mayr *et al.*, 2011; Gillespie *et al.*, 2012; Pyron, 2014), and the total oceanic trip riding an equatorial current can take under two weeks in either direction under ideal conditions (Renner, 2004). Heraty (2002) had hypothesized dispersal by means of ship ballast, as part of an intercontinental trade route. We cannot rule out recent anthropogenic transport of the species if *K. ivorensis* was sufficiently diverse in the New World and then was established in the Old World while maintaining the variation in mitochondrial haplotypes. However, we have not found populations of this species in the NW and we would also not expect both speciation and generation of such mitochondrial diversity in only a few hundred years. Therefore, we believe this is a more ancient dispersal.

Adult eucharitids typically live only a few days outside of the nest (Clausen, 1923) so this group likely could not undergo long-distance dispersal without their ant hosts. Was there concurrent ant host dispersal through Africa or a host-range expansion by *K. ivorensis* to novel ants? Since this information could shed light on *Kapala* dispersal speed and historical biogeography, it is unfortunate that the host/s of *K. ivorensis* is unknown. A search of Antweb.org (accessed 21 Feb 2013) was undertaken to determine which of the six known *Kapala* host ant genera were shared across South America and Africa or Madagascar. Of these, *Hypoponera*, *Odontomachus*, and *Pachycondyla* are found in Africa / Madagascar. Only a small tramp ant (*Hypoponera punctissima*) is shared between the NW and OW, and it is much smaller than the parasitoid. Therefore, there are no clear candidates for a specific ant introduced host species. *Odontomachus troglodytes*, *Pachycondyla ambigua*, and *P. darwinii madecassa* are shared across Africa and Madagascar, so these are potential candidates due to their distribution. *Odontomachus troglodytes* is exceptionally widespread and found in open areas and secondary forest (Fisher & Smith, 2008). Its range overlaps with *K. ivorensis*: it is documented across much of sub-Saharan Africa, is found in eastern South Africa and also Madagascar. Additionally, there is the possibility that *K. ivorensis* attacks a different genus ponerine or ectatommine ant. For example, *Anochetus* (Ponerinae), which is closely related to *Odontomachus* (Fisher & Smith, 2008), is found in the New World, including Dominica (Wheeler, 1913), and across sub-Saharan Africa and Madagascar (Antweb.org). We encourage further exploration of the parasitoids of potential ant hosts and further work on the ecology and population genetics of *Kapala ivorensis.*

4.5 Conclusions

Kapala ivorensis is different from many other species in *Kapala* in that it exhibits a wide distribution but shows little morphological variation. It shows no general phylogeographic pattern, such that specimens united geographically do not group together phylogenetically. It is proposed to have been in the Old World for 2.2 my, presumably from a source population dispersing in association with its ant host and then undergoing allopatric speciation.

Historical biogeography is an interdisciplinary pursuit (Crisci, 2001) and we have attempted to incorporate many forms of evidence including fossil-calibrated divergences, multi-gene phylogenetic analyses, inter- and intraspecific genetic distances, morphology, and geography. *K. ivorensis* is the first recorded example of an insect species that has successfully dispersed from South America to Africa across the Atlantic to colonize the Old World. Likely there will be additional reports of long-distance oceanic dispersal as more disjunct distributions are studied using dated phylogenies.

4.6 Figures and Tables

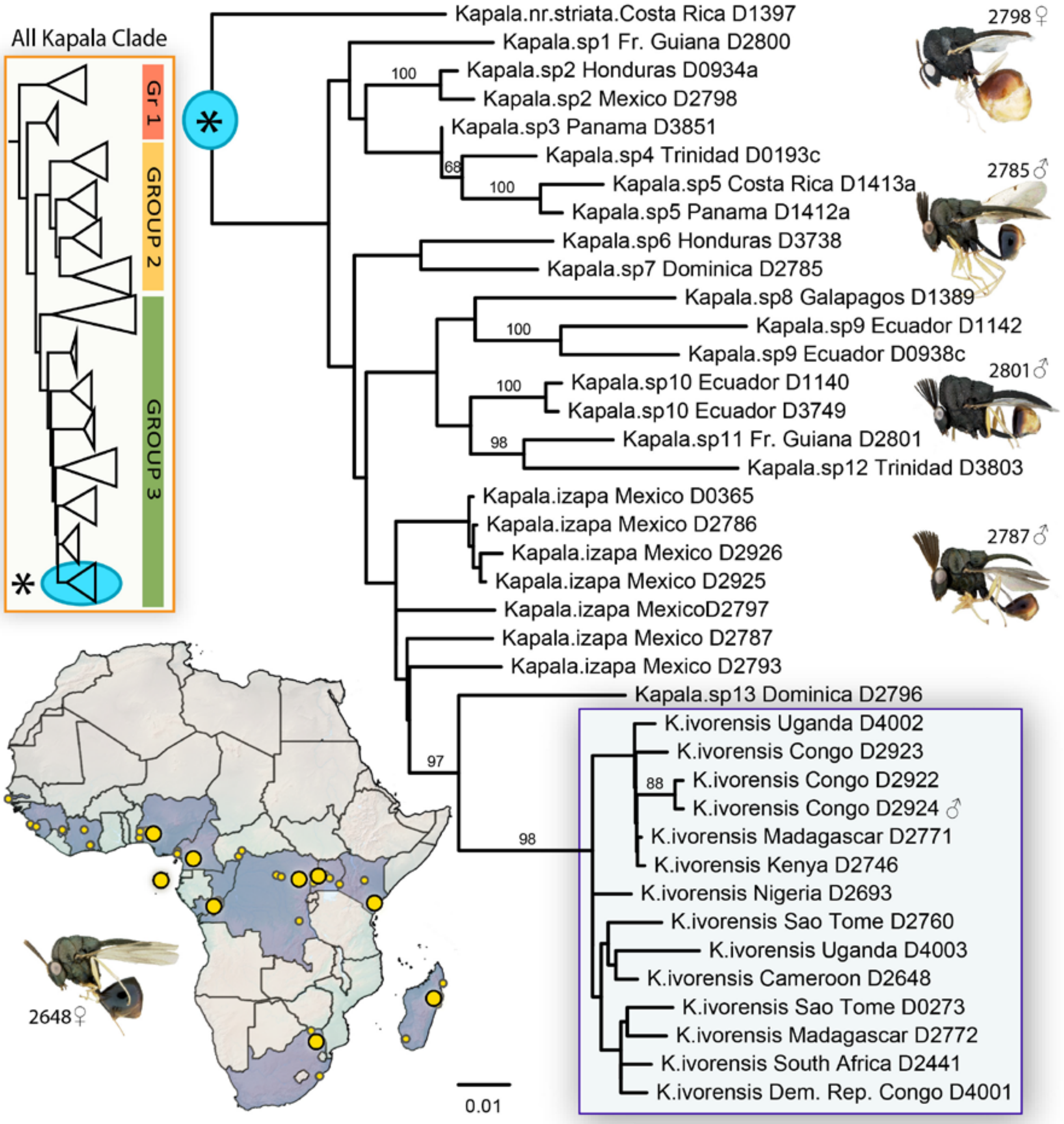

FIGURE 4.1.
Bayesian inference maximum clade credibility tree of *Kapala ivorensis* and the nearest New World relatives, from six gene regions. Inset tree shows the entire Kapala Clade (13 described genera) redrawn from an analysis of 195 taxa Murray and Heraty (in prep.), with a blue circle around the monophyletic group analyzed in current study. Map inset of Africa with the thirteen countries colored in light blue where *K. ivorensis* have been recorded, of which nine countries are represented in the molecular matrix. Localities of DNA collections are shown as large yellow dots and other museum collections are shown in small yellow dots, with some points representing multiple taxa (map from SimpleMappr.net). Specimen images from top to bottom: D2798♀, D2785♂, D2801♂, D2787♂, and *K. ivorensis* D2648♀.

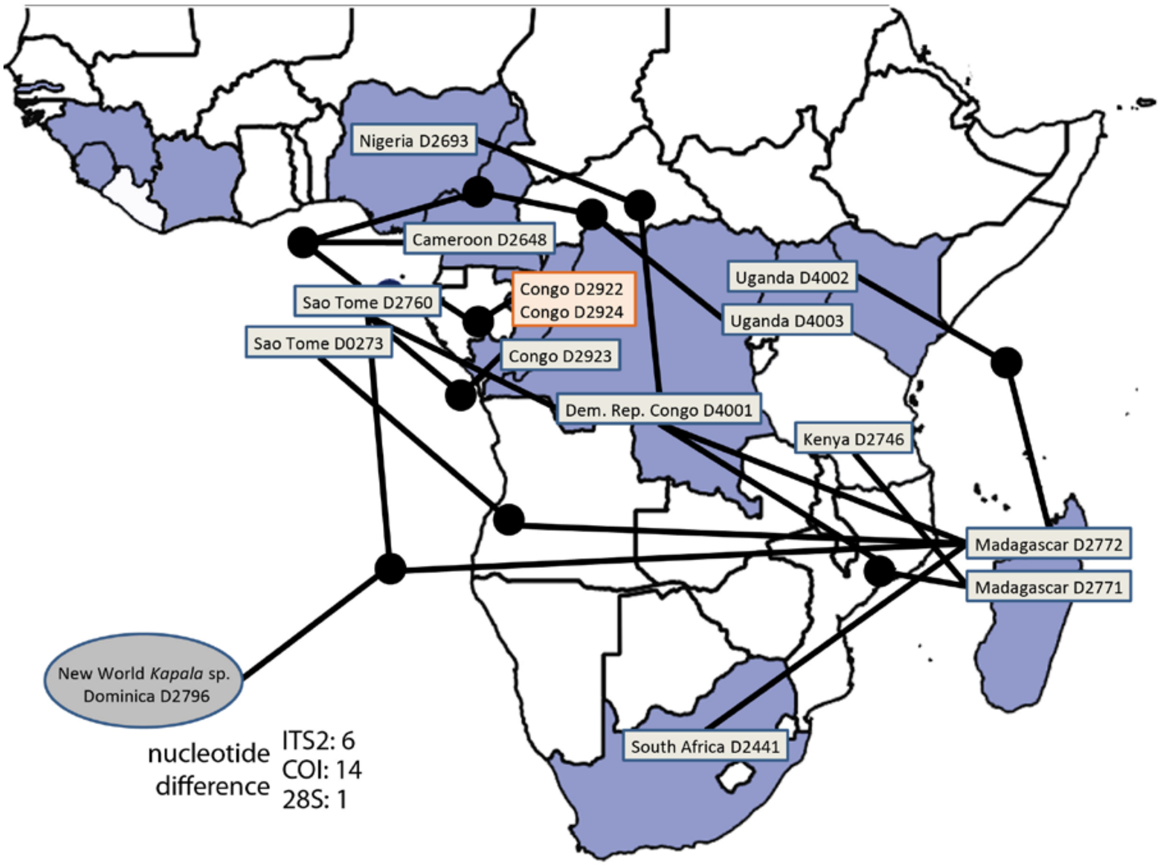

FIGURE 4.2.
COII haplotype network. All 14 *K. ivorensis* and the New World sister taxon. Each circle indicates one nucleotide change when there is more than one along a connection. Line length has no relation to genetic distance. Congo D2922-23 are the only two specimens with identical data.

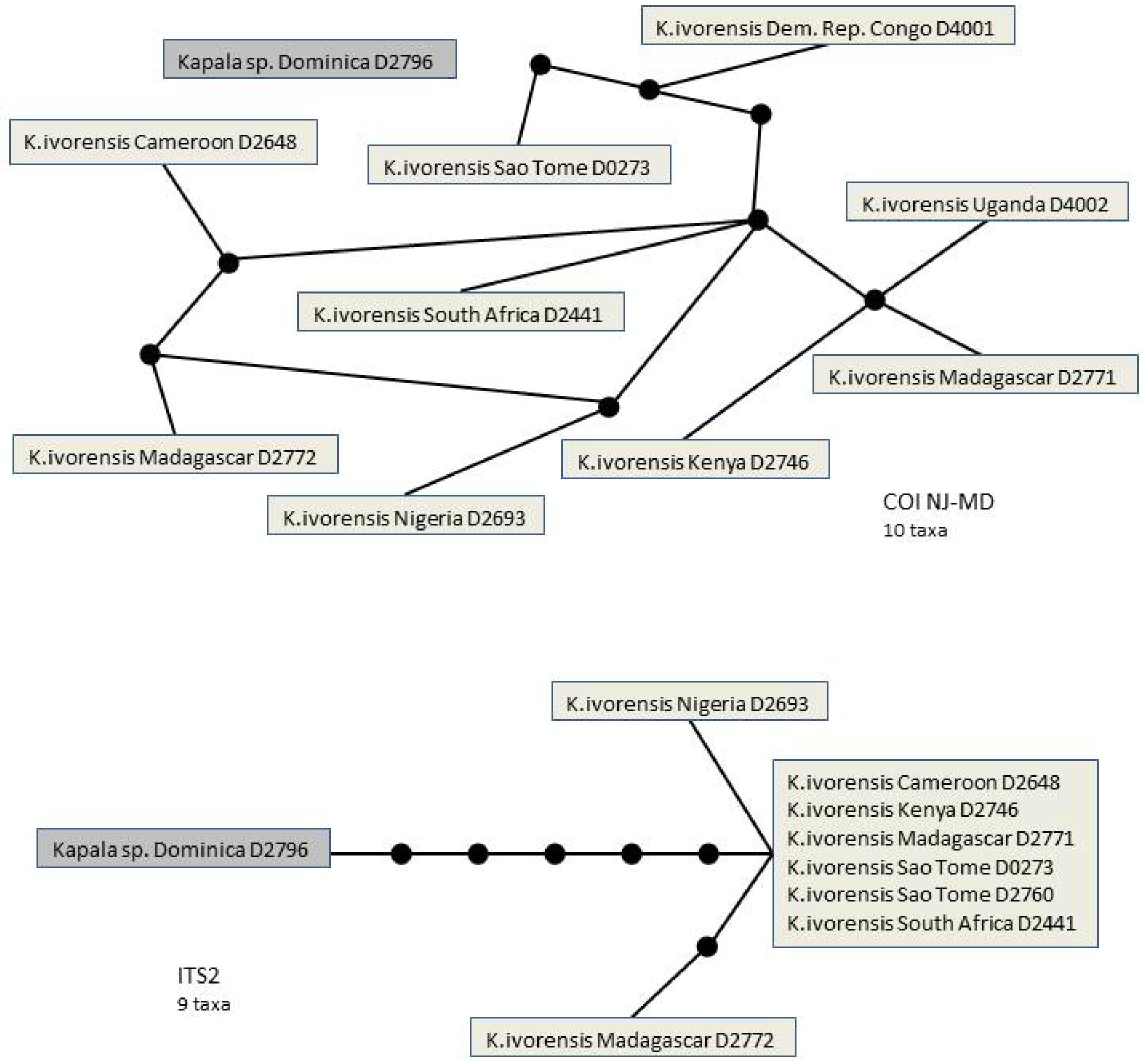

FIGURE 4.3.
COI and ITS2 haplotype networks. Each circle indicates one nucleotide change when there is more than one along a connection. Line length has no relation to genetic distance.

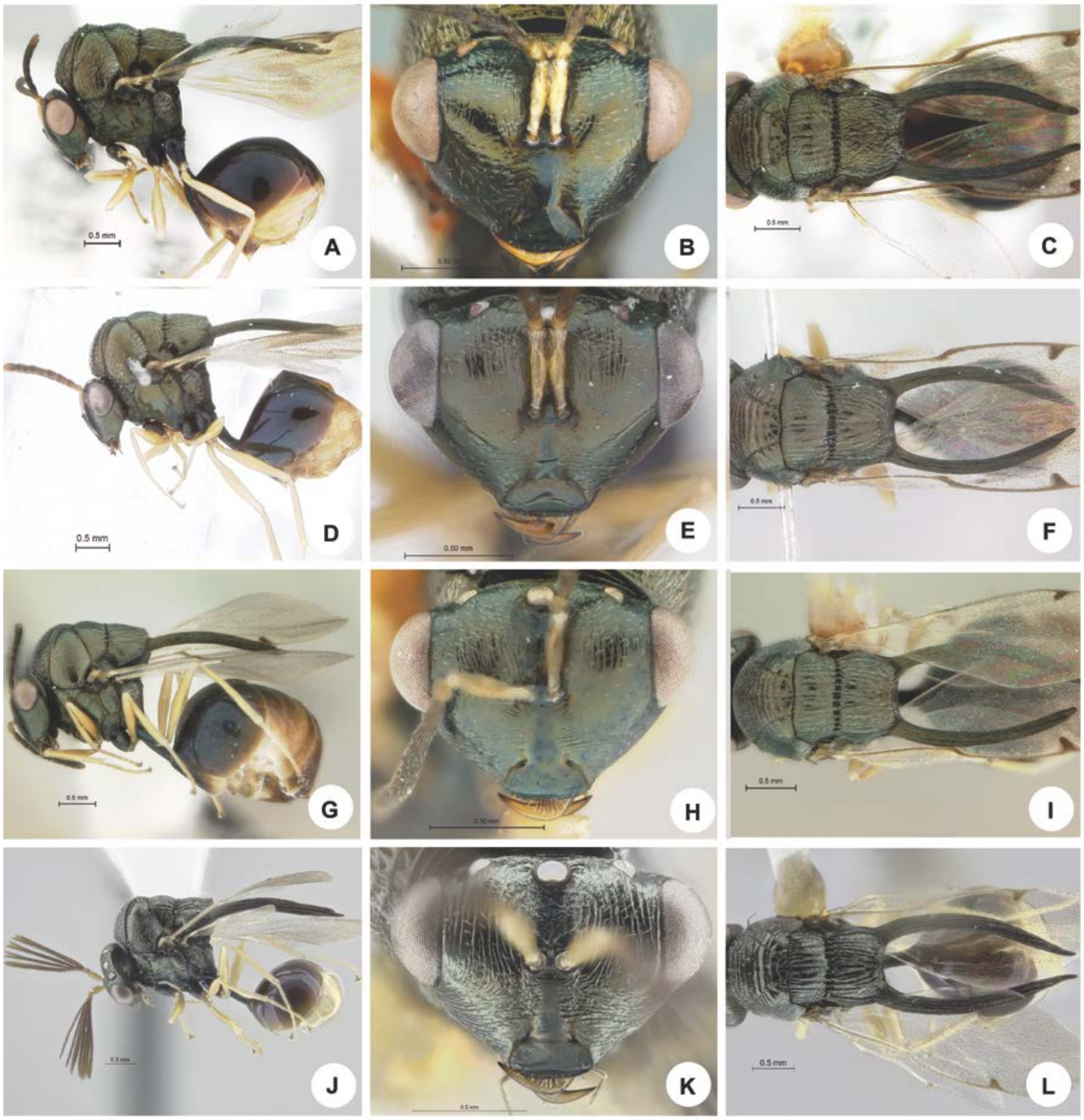

FIGURE 4.4.
Kapala. A-C) *Kapala* n. sp. 13, D2796♀, New World sister to *K. ivorensis*, from Dominica, D-F) *K. ivorensis* D2746♀ from Kenya, G-I) *K. ivorensis* D2772♀ from Madagascar, and J-L) *K. ivorensis* D2924♂ from the Congo.

	species	DNA ID	sex	specimen identifier	museum	locality
1	*Kapala ivorensis*	0273	♀	UCRC_ENT 00092140	UCRC	Sao Tome: Poto CIAT compound, 0°14'33"N 6°36'34"E 7-12.Jun.1999 A. Polaszek MT
2	*Kapala ivorensis*	2441	♀	UCRC_ENT 00278291	UCRC	South Africa: Mpumalanga: Stridjum tunnel area, 730m 24°27'47"S 30°36'31"E 31.Jan.2006 J.Heraty H06-008
3	*Kapala ivorensis*	2648	♀	UCRC_ENT 00235916	MNHN	Cameroon: Centre Pr: Messamendongo, 3°48'35"N 11°31'17"E 1-13.Apr.2003 T. Marc MT
4	*Kapala ivorensis*	2693	♀	UCRC_ENT 00000313	UCRC	Nigeria: Ondo: 1.6 km E Owena, 268m 7°11'54"N 5°01'50"E 19.Jul.2008 J. Mottern swp cacao plantation M08-017
5	*Kapala ivorensis*	2746	♀	UCRC_ENT 00302068	UCRC	Kenya: Coast Pr: Arabuko-Sokoke Forest, 3°25'13"S 39°53'49"E 8-9.Jan.2000 R. Copeland swp
6	*Kapala ivorensis*	2760	♀	UCRC_ENT 00092139	UCRC	Sao Tome: Poto CIAT compound, 0°14'33"N 6°36'34"E 7-12.Jun.1999 A. Polaszek MT
7	*Kapala ivorensis*	2771	♀	UCR_ENT 00018899	CASC	Madagascar: Toamasina Pr: Mobot site, Analalava 7 km SW Foulpointe, 18m 17°41'36"S 49°27'37"E 3-11.Jan.2008 M. Irwin, R. Harin'Hala MT sand in low alt. dense humid forest MG-37B-17
8	*Kapala ivorensis*	2772	♀	UCR_ENT 00018900	CASC	Madagascar: Toamasina Pr: Mobot site, Analalava 7 km SW Foulpointe, 18m 17°41'36"S 49°27'37"E 28.Sep-5.Oct.2007 M. Irwin, R. Harin'Hala MT sand in low alt. dense humid forest MG-37B-03
9	*Kapala ivorensis*	2922	♀	UCRC_ENT 00241581	HIC	Republic of Congo: Pool Dept: Abio: Lesio-Louna Pk., 330m 3°06'1"S 15°31'26"E 11-18.Sep.2008 Sharkey & Braet
10	*Kapala ivorensis*	2923	♀	UCRC_ENT 00241571	HIC	Republic of Congo: Pool Dept: Iboubikro: Lesio-Louna Pk., 330m 3°06'1"S 15°28'16"E Sep.2008 Sharkey & Braet MT
11	*Kapala ivorensis*	2924	♂	UCRC_ENT 00241604	HIC	Republic of Congo: Pool Dept: Abio: Lesio-Louna Pk., 330m 3°06'1"S 15°31'26"E 30.Sep-7.Oct.2008 Sharkey & Braet MT
12	*Kapala ivorensis**	4001	♀	UCRC_ENT 00320312	UCRC	Democratic Republic of the Congo: Univeristy of Kisangani, maise field, 0°30'51"N 25°10'34"E 18.Jan.2013
13	*Kapala ivorensis**	4002	♀	UCRC_ENT 00320309	UCRC	Uganda: Bwamba Co.: Semuliki Nat. Pk., north +/- savannah part inside Nat'l Park, 0°50'0"N 30°03'0"E 16.Mar.2013 A. Gumovsky
14	*Kapala ivorensis**	4003	unk	UCRC_ENT 00320310	UCRC	Uganda: Bwamba Co.: Semuliki Nat. Pk., north +/- savannah part inside Nat'l Park, 0°50'0"N 30°03'0"E 16.Mar.2013 A. Gumovsky
15	*Kapala izapa*	2925		UCRC_ENT 00356033	UCRC	Mexico: Chiapas: Playón de la Gloria, 180m 16°09'36"N 90°54'7"W 24.Jun.2008 MT LLAMA# Ma-A-09-1-02
16	*Kapala izapa*	2926	♂	UCRC_ENT 00397279	UCRC	Mexico: Chiapas: Playón de la Gloria, 180m 16°09'36"N 90°54'7"W 24.Jun.2008 MT LLAMA# Ma-A-09-1-02
17	*Kapala izapa*	2797	♀	UCRC_ENT 00252081	UCRC	Mexico: Chiapas: Rosario Izapa, 14°58'0"N 92°09'0"W 19.Jan.2004 J.P. Lachaud ex. *Pachycondyla stigma*
18	*Kapala izapa*	0365	unk	none	UCRC	Mexico: Quintana Roo: El Eden, M. Gates swp secondary vegetation along forest road
19	*Kapala izapa*	2787	♂	UCRC_ENT 00235920	UCRC	Mexico: Quintana Roo: Lazaro Cardena: 25 km NNE Leona Vicario Reserva Ecologia El Eden, 21°13'0"N 87°11'0"W 10.Aug.1998 R. Rodriguez swp secondary growth near greenhouse
20	*Kapala izapa*	2786	♂	UCRC_ENT 00235919	UCRC	Mexico: Quintana Roo: Lazaro Cardena: 25 km NNE Leona Vicario Reserva Ecologia El Eden, 21°13'0"N 87°11'0"W 19.Aug.1998 R. Rodriguez swp savannah de cabana
21	*Kapala izapa*	2793	♂	UCRC_ENT 00235954	UCRC	Mexico: Quintana Roo: Lazaro Cardena: 25 km NNE Leona Vicario Reserva Ecologia El Eden, 21°13'0"N 87°11'0"W 23.Aug.1998 M. Gates swp secondary growth near greenhouse
22	*Kapala* nr. *striata*	1397	♂	UCRC_ENT 00092034	UCRC	Costa Rica: Puntarenas Pr: Monteverde, 1500m 10°18'25"N 84°48'35"W Feb.1980 W.R. Mason & M. Wood cloud forest
23	*Kapala* sp. 1	2800	♀	UCRC_ENT 00252084	UCRC	French Guiana: PK 24; 24 km to Barrage Petit Saut, 21.Mar.2008 G. Perez-Lachaud & J.-P. Lachaud ex. *Odontomachus hastatus*
24	*Kapala* sp. 2	0934a	♀	UCRC_ENT 00092082	UCRC	Honduras: Olancho: Montana del Malacate, 15°08'4"N 85°35'36"W 3.Jul.2002 D. Yanega
25	*Kapala* sp. 2	2798	♀	UCRC_ENT 00252082	UCRC	Mexico: Chiapas: Ejido 2 de Mayo, 13.Apr.2005 G. Perez-Lachaud ex. *Odontomachus opaciventris*
26	*Kapala* sp. 3	3851	♀	UCRC_ENT 00320841	CNC	Panama: Darién Pr: Cana, 530m 7°45'0"N 77°41'0"W 3-7.Jun.1996 J. Ashe & R. Brooks PIT #65
27	*Kapala* sp. 4	0193c	♂	UCRC_ENT 00092214	UCRC	Trinidad & Tobago: Peck 93-58
28	*Kapala* sp. 5	1413a	♂	UCRC_ENT 00092126	UCRC	Costa Rica: Puntarenas: PN Corcovado, Est. Agujas, S. Coroma, 245m 8°32'25"N 83°34'15"W 23.Apr.2002 J. Azofeifa swp L-5275500 S21000
29	*Kapala* sp. 5	1412a	♂	UCRC_ENT 00092229	UCRC	Panama: Corcovado
30	*Kapala* sp. 6	3738	♀	UCRC_ENT 00397254	UCRC	Honduras: Olancho Dept.: La Muralla, visitor's center, 1467m 15°05'49"N 86°44'19"W 26-30.Apr.2013 O. Schlein MT (6m)
31	*Kapala* sp. 7	2785	♂	UCRC_ENT 00235918	UCRC	Dominica: Parish of St. Joseph Springfield Estate, 430m 15°20'48"N 61°22'6"W 15-20.Mar.2003 M.E. Irwin, E. Benson, G. Carner, M.B. Shepard MT
32	*Kapala* sp. 8	1389	♂	UCRC_ENT 00092031	UCRC	Ecuador: Galapagos: Isabela Island 13 km NW Villamil, 125m 0°49'45"S 91°08'7"W 24-30.Apr.1996 Peck MT Trans forest
33	*Kapala* sp. 9	0938c	♂	UCRC_ENT 00092127	UCRC	Ecuador: Esmeraldas: Bilsa Biol. Sta., 500m 0°20'24"N 79°42'36"W 10.May-4.Jun.1996 P. Hibbs MT
34	*Kapala* sp. 9	1142	♀	UCRC_ENT 00091926	UCRC	Ecuador: Orellana: 1 km S. Onkone Gare Camp, Reserva Etnica Waorani, 216m 0°39'25"S 76°27'10"W 2.Oct.1996 T.L. Erwin et al. fogging terre firme forest Lot 1705
35	*Kapala* sp. 10	3749	♂	UCRC_ENT 00364771	USNM	Ecuador: Orellana: Northern Production Facility, Reserva Etnica Waorani, 216.3m 0°39'25"S 76°27'10"W 23.Feb.1995 T.L. Erwin et al fogging terre firme forest Lot # 1057
36	*Kapala* sp. 10	1140	♂	UCRC_ENT 00092030	UCRC	Ecuador: Orellana: Tiputini Biodiversity Station nr Yasuni National Pk, Erwin Transect - T/5, 220-250m 0°37'55"S 76°08'39"W 26.Oct.1998 T.L. Erwin et al. fogging terre firme forest Lot 1942
37	*Kapala* sp. 11	2801	♂	UCRC_ENT 00252085	UCRC	French Guiana: Camp Patawa, 4°32'10"N 52°09'8"W 14.Mar-30.Apr.2007 R. de Souza Ferreira ex. *Pachycondyla verenae*
38	*Kapala* sp. 12	3803	♀	UCRC_ENT 00412121	UCRC	Trinidad: Brasso Seco, Rd to Paria Bay, 148m 10°44'57"N 61°15'53"W 25.Jul.2013 Heraty & Baker swp forest H13-079
39	*Kapala* sp. 13	2796	♀	UCRC_ENT 00235957	UCRC	Dominica: St. David: 11 km NE Pont Casse, 15°27'36"N 61°18'53"W 20.Jun.2004 R.Turnbow

TABLE 4.1

List of specimens and locality information. Asterisks indicate taxa that are newly sequenced for this study.

					Genbank accession numbers					
	species	**DNA ID**	**genes**	**specimen identifier**	**18S**	**28S-D2**	**28S-D3-5**	**ITS2**	**COI**	**COII**
1	*Kapala ivorensis*	0273	6	UCRC_ENT 00092140	KC008564	AY672990	KC008161	unpub.	KC008294	KC008483
2	*Kapala ivorensis*	2441	6	UCRC_ENT 00278291	unpub.	unpub.	unpub.	unpub.	unpub.	unpub.
3	*Kapala ivorensis*	2648	6	UCRC_ENT 00235916	unpub.	unpub.	unpub.	unpub.	unpub.	unpub.
4	*Kapala ivorensis*	2693	6	UCRC_ENT 00000313	KC008565	KC008135	KC008162	unpub.	KC008295	KC008484
5	*Kapala ivorensis*	2746	6	UCRC_ENT 00302068	unpub.	unpub.	unpub.	unpub.	unpub.	unpub.
6	*Kapala ivorensis*	2760	4	UCRC_ENT 00092139	x	unpub.	unpub.	unpub.	x	unpub.
7	*Kapala ivorensis*	2771	6	UCR_ENT 00018899	unpub.	unpub.	unpub.	unpub.	unpub.	unpub.
8	*Kapala ivorensis*	2772	6	UCR_ENT 00018900	KC008566	KC008136	KC008163	unpub.	KC008296	KC008485
9	*Kapala ivorensis*	2922	4	UCRC_ENT 00241581	unpub.	unpub.	unpub.	x	x	unpub.
10	*Kapala ivorensis*	2923	4	UCRC_ENT 00241571	unpub.	unpub.	unpub.	x	x	unpub.
11	*Kapala ivorensis*	2924	4	UCRC_ENT 00241604	unpub.	unpub.	unpub.	x	x	unpub.
12	*Kapala ivorensis*	4001	5	UCRC_ENT 00320312	unpub.	unpub.	unpub.	x	unpub.	unpub.
13	*Kapala ivorensis*	4002	5	UCRC_ENT 00320309	unpub.	unpub.	unpub.	unpub.	x	unpub.
14	*Kapala ivorensis*	4003	2	UCRC_ENT 00320310	x	unpub.	x	x	x	unpub.
15	*Kapala izapa*	2925	5	UCRC_ENT 00356033	KC008533	KC008119	KC008151	x	KC008252	KC008440
16	*Kapala izapa*	2926	3	UCRC_ENT 00397279	unpub.	x	unpub.	x	x	unpub.
17	*Kapala izapa*	2797	4	UCRC_ENT 00252081	x	unpub.	unpub.	x	unpub.	unpub.
18	*Kapala izapa*	0365	5	none	unpub.	unpub.	unpub.	x	unpub.	unpub.
19	*Kapala izapa*	2787	4	UCRC_ENT 00235920	x	unpub.	unpub.	unpub.	x	unpub.
20	*Kapala izapa*	2786	4	UCRC_ENT 00235919	x	unpub.	unpub.	unpub.	x	unpub.
21	*Kapala izapa*	2793	4	UCRC_ENT 00235954	unpub.	x	unpub.	x	unpub.	unpub.
22	*Kapala* nr. *striata*	1397	5	UCRC_ENT 00092034	unpub.	unpub.	unpub.	unpub.	x	unpub.
23	*Kapala* sp. 1	2800	5	UCRC_ENT 00252084	KC008540	KC008125	KC008155	x	KC008263	KC008450
24	*Kapala* sp. 2	0934a	6	UCRC_ENT 00092082	KC008545	AY671860	AY671860	unpub.	KC008270	KC008458
25	*Kapala* sp. 2	2798	3	UCRC_ENT 00252082	x	unpub.	unpub.	x	x	unpub.
26	*Kapala* sp. 3	3851	4	UCRC_ENT 00320841	unpub.	unpub.	unpub.	x	unpub.	x
27	*Kapala* sp. 4	0193c	3	UCRC_ENT 00092214	x	unpub.	unpub.	x	x	unpub.
28	*Kapala* sp. 5	1413a	5	UCRC_ENT 00092126	unpub.	unpub.	unpub.	unpub.	x	unpub.
29	*Kapala* sp. 5	1412a	4	UCRC_ENT 00092229	x	KC008130	unpub.	x	KC008269	KC008456
30	*Kapala* sp. 6	3738	5	UCRC_ENT 00397254	unpub.	unpub.	unpub.	x	unpub.	unpub.
31	*Kapala* sp. 7	2785	4	UCRC_ENT 00235918	x	unpub.	unpub.	unpub.	x	unpub.
32	*Kapala* sp. 8	1389	6	UCRC_ENT 00092031	KC008535	KC008120	unpub.	unpub.	KC008255	KC008443
33	*Kapala* sp. 9	0938c	6	UCRC_ENT 00092127	KC008546	AY671865	AY671865	unpub.	KC008271	KC008459
34	*Kapala* sp. 9	1142	5	UCRC_ENT 00091926	unpub.	unpub.	unpub.	unpub.	x	unpub.
35	*Kapala* sp. 10	3749	3	UCRC_ENT 00364771	x	unpub.	x	x	unpub.	unpub.
36	*Kapala* sp. 10	1140	5	UCRC_ENT 00092030	KC008534	AY671888	AY671888	x	KC008254	KC008442
37	*Kapala* sp. 11	2801	4	UCRC_ENT 00252085	x	KC008127	KC008157	x	KC008265	KC008452
38	*Kapala* sp. 12	3803	4	UCRC_ENT 00412121	x	unpub.	unpub.	x	unpub.	unpub.
39	*Kapala* sp. 13	2796	6	UCRC_ENT 00235957	KC008539	KC008124	KC008154	unpub.	KC008262	KC008449

TABLE 4.2.

Genbank accession numbers and information on gene completeness for each taxa. Cells with an ‘x’ indicate no data. All ITS2 are newly sequenced for this study.

gene	length	# taxa	PI sites	constant
18S	757	26	1	756 (99.9%)
28S D2	585	37	9	565 (99.6%)
28S D3-5	539	37	4	527 (97.8%)
ITS2	271	19	7	246 (90.8%)
COI	762	26	37	662 (86.9%)
COI NJ-MD	390	26	25	328 (84.1%)
COII	246	37	25	198 (80.5%)

TABLE 4.3.
Gene coverage across the 39 taxa. COI NJ-MD was amplified for this study, but eight other taxa from previous work have additional COI data, including the 3' portion of the barcode region. The full COI region was used in phylogenetic analysis, while the NJ-MD region was used for haplotype network and distance calculations.

species	intraspecific distance	distance to *K. ivorensis*	# taxa	geographic sampling
K. ivorensis	1.2%	-	9	13 OW countries
K. izapa	1.1%	2.2 - 3.8%	7	Mexico
***K.* sp. 2**	0.8%	2.9 - 5.1%	2	Honduras, Mexico
***K.* sp. 5**	1.2%	3.2 - 5.5%	2	Costa Rica, Panama
***K.* sp. 9**	2.6%	3.3 - 5.1%	2	Ecuador
***K.* sp. 10**	0.3%	2.1 - 3.5%	2	Ecuador

TABLE 4.4.
Genetic distances calculated from mtDNA.

5. Chapter 4

Taxonomic revision and phylogenetic relationships of Kapala furcata clade (Hymenoptera: Eucharitidae)

5.1 Introduction

Kapala Cameron 1886 (Chalcidoidea: Eucharitidae) is one of the most commonly encountered eucharitid wasps in the Neotropics (Heraty & Woolley, 1993; Heraty, 2002). This genus has a wide distribution and exhibits a large amount of external morphological variation, yet the boundaries of most species of this charismatic ant parasitoid have not been established. It has long been recognized that there is high diversity and few diagnostic characters across the genus (Heraty & Woolley, 1993). Although *Kapala* is phenotypically distinctive from related genera, there are no morphological or molecular synapomorphies to unite the genus (Heraty, 2002; Murray & Heraty, in prep.-a) and in both molecular and combined molecular and morphological analyses *Kapala* is not monophyletic, despite its phenotypic similarity (Heraty *et al.*, 2004; Murray & Heraty, in prep.-a).

Kapala is part of a clade of 14 New World genera that diverged from their Old World sister approximately 35 mya (Murray *et al.*, 2013). All members of the Kapala clade possess paired scutellar spines separated basally, a small lateral axillar lobe, an incomplete hind wing marginal vein, and long-branched antennae in the males (Heraty, 2002). Each of the 14 described genera is morphologically distinctive and straightforward to recognize using macromorphological characters, notably the scutellar spines and antennae. The Kapala clade is also united in attacking only ants in the subfamilies Ectatomminae and Ponerinae (Lachaud *et al.*, 2012; Lachaud & Pérez-Lachaud, 2012; Murray *et al.*, 2013). Within the Kapala clade, *Kapala* is the most numerically abundant and diverse member, with the widest distribution and 18 described species. The genus is defined by a suite of sympleisiomorphies including carinate lyre-shaped spines, eyes bare, body lacking stiff bristles, male antennal branches longer than height of head, female basal flagellomeres rarely more than twice as long as broad, and typically the posterior apex of the scutellar disc is elevated (Heraty, 2002). *Kapala* are found within two of the three defined groups of the Kapala clade, with the furcata and iridicolor complexes in Group 2, and the sulcifacies complex and multiple other described and undescribed species in Group 3 (Murray & Heraty, in prep.-a). These three clades of Kapala are separated phylogenetically by two clusters of morphologically distinct genera and by the genus *Isomerala*.

Due to the importance of establishing the new boundaries of the paraphyletic *Kapala* (Murray & Heraty, in prep.-a), we deem it a primary task to revisit the type species and establish diagnostic characters for its identification. The type species, *Kapala furcata* (Fabricius) 1804 was described from a single female collected in South America (Fabricius, 1804). The name has been consistently misapplied to many museum specimens and has led to problems association both biological data and geographic limits (Heraty, 2002). Within the Kapala clade, the furcata clade is monophyletic with high support in all molecular analyses, and was estimated to have a crown age of 13.3 my (6.6-20.7)(Murray & Heraty, in prep.-a). Herein we define and describe the six species in the furcata species group.

5.2 Materials and Methods

5.2.1 Specimens and Morphology

Measurements were taken using a micrometer with a Zeiss Stemi SV 6 light microscope with a 5x objective and 10x eyepiece. Terminology follows Heraty *et al.* (2013) and measurements generally follow those of Heraty and Woolley (1993), with some of these summarized in Figure 5.1 (descriptions in Table 5.1). The stigmal vein on the fore wing is often irregular in shape and so was measured at the widest point and the longest point from the wing margin. All measurements were taken from the left side of the specimen when possible. The facial striation patterns are an important character for designation of *Kapala* groups. The frons and lower face are considered separately, as areas defined as above and below the torulus. Oblique striae above the frons may extend from the torulus to the lateral ocelli, following the antennal scrobal depression, or, conversely, the striae may extend from the median ocelli to the gena, following the margin of the compound eye. Below the torulus, the striae may continue obliquely or may be transverse, and run horizontally on the lower face adjacent to the clypeus. The length of the scutellum is considered to be the sum of the axilla (from the transscutal articulation to the scutoscutellar sulcus) and scutellar disc (from the scutoscutellar sulcus to the posterior apex of the mesosoma), but not including the spine length (Fig. 5.1). Striation of the spines is considered longitudinal when extending the length of the spine, and oblique when it follows an outward spiral direction at the apical half.

All specimen records including label and locality information are deposited in the internal lab FileMakerPro database maintained at UCR. Images will be deposited in Morphbank.

Abbreviations for museum depositories in the materials examined are as follows: American Museum of Natural History (AMNH), Natural History Museum of London (BMNH), California Academy of Sciences (CASC), Cleveland Museum of Natural History (CMNH), Canadian National Collection (CNC), Florida State Collection of Arthropods (FSCA), Universidad Nacional de Tucuman (IMLA), Instituto Nacional de Biodiversidad in Costa Rica (INBIO), Lost Angeles County Museum (LACM), Museo Argentino de Ciencias Naturales (MACN), The Museum of Comparative Zoology at Harvard (MCZ), Lund University in Sweden (MZLU), Polish Academy of Science Institute of Systematic Zoology (MZPW), Naturhistorisches Museum, Wein, Austria (NMW), Royal Ontario Museum in Canada (ROME), Staatliches Museum für Natrukunde in Stuttgart (SMNS), University of Connecticut Museum at Storrs (UCMS), University of California Riverside Entomology Research Museum (UCRC), Universidade Federal do Espirito Santo in Brazil (UFES),United States Nation Museum of Natural History (USNM), and Bavarian Natural History Museum in Munich (ZSMC). In the materials examined, all museum numbers with no museum deposition but just a UCRC# are deposited in UCRC

5.2.2 Molecular Methods

Boundaries of the furcata complex were identified based upon previous molecular analyses (Murray & Heraty, in prep.-a), allowing us to build a targeted molecular matrix of *Kapala* individuals of interest. Included in our subset phylogenetic analysis are 24 individuals recovered as part of the furcata clade and two outgroup taxa from the putative sister, the K. iridicolor complex (Table S1). We wanted to reanalyze a small dataset to remove missing data introduced from a more taxon-rich dataset and to add more data to these analyses. The matrix includes three nuclear ribosomal (partial 18S, 28S-D2, and 28S-D3-D5) and two mitochondrial (partial COI and COII) gene fragments from (Murray & Heraty, in prep.-a). Five specimens are additionally sequenced for COII. PCR amplification and sequencing protocols are described in Murray *et al.* (2013). In addition to the museum identification code, all molecular specimens are given a unique DNA voucher number (D#).

5.2.3 Phylogenetic Analyses

Maximum likelihood using RAxML v8.0.24 (Stamatakis *et al.*, 2008) was implemented through the CIPRES Science Gateway (Miller *et al.*, 2010). One thousand rapid bootstrap replicates were performed, with other parameters kept at default. The dataset was partitioned by gene, and COI and COII were split into 1+2 and 3. COI and COII were also analyzed separately. Bayesian phylogenetic inference was performed in MrBayes v3.2.2 (Ronquist *et al.*, 2012) through the CIPRES interface (Miller *et al.*, 2010). The matrix was partitioned by gene, with COI and COII each analyzed under codon models. The posterior parameter distributions were confirmed to be >200 ESS in Tracer v1.5 (Rambaut & Drummond, 2007) and burnin was removed. A majority rule consensus tree was assembled in the R package ape (Paradis *et al.*, 2004). The program phangorn (Schliep, 2011) was used to map cladogram terminals to geographic locality.

5.2.4 Analytical species delimitation

The taxonomy-independent method PTP (Poisson tree process) was used via the online interface (Zhang *et al.*, 2013). It is a species discovery approach to delimiting species and the user gives no *a priori* classes (Carstens *et al.*, 2013). This program models speciations using the number of substitutions on a gene tree and searches for transition points where the branching pattern changes from among-species to within-species, based on the phylogenetic species concept as in Baum and Shaw (1995). It is intended to be used with single-locus data; we tested both COI and COII ML phylogenies independently. The ML phylogenies were built using RAxML through CIPRES. Of the 24 taxa, 20 had COI and 21 had COII. We analyzed each topology in a ML framework.

5.3 Results and Discussion

5.3.1 Phylogeny

We were able to recognize six discrete clades within the *K. furcata* complex in both the ML results (Fig. 5.2) and the Bayesian codon model phylogeny (Fig. S5.1). As in our previous analyses with a much larger taxon sampling, the single specimen from Mexico (D2799) was sister to the rest of the furcata complex with relatively strong support (Murray & Heraty, in prep.-a). The sister to the rest of the furcata clade, D2799, is not described. It is a single specimen, and given the variation in the group it is not justified to describe it at this time. The furcata clade is distributed from southern Mexico to central Argentina (Fig. 5.3)

Kapala furcata is distinguished from the rest by the facial striation patterns (Fig. 5.4). It overlaps with K. parafurcata, but *K. parafurcata* is easily-recognized due to the weaker, oblique striations. *Kapala deltalis* and *K. quasimodo* form a phylogenetic grade, but share similar facial striation with weak striae weakly punctate. They also show a gradient in the morphology of the lateral lobes, with *K. deltalis* having extremely large and conical lobes and *K. quasimodo* having less pronounced lobes (Figs 5.5, 5.6).

Kapala parafurcata and *K. cuprea* Cameron 1913 are distinctive and form separate clades, but they have little divergence between them as compared to the branch lengths leading to the remaining species. Potentially the two constitute one species instead of separate species. Both have identical facial striation, but exhibit differences in spines. *K. cuprea* has relatively shorter spines than *K. parafurcata* that generally have oblique, sometimes spiral, striations. In COI+COII using uncorrected distances, *K. cuprea* has a maximum of 1.70% intraspecific divergence and *K. parafurcata* has a maximum of 1.84%. The interspecific distance is 1.15% – 3.74%. There is little genetic difference between the two, but they form distinct groups in phylogenetic analyses (Figs 5.2, S5.1) . The geographic distribution of *K. cuprea* is northern South America (7 localities with molecular sampling), and *K. parafurcata* is distributed centrally to southerly (6 localities with molecular sampling); the two overlap in part of the range (Fig. 5.3).

5.3.2 Analytical Species Determination

The species discovery method under ML resulted in six species using both COI and COII individual gene phylogenetic analyses. This result was of interest because the species status of *K. cuprea* and *K. parafurcata* was questioned due to the low amount of molecular divergence and the paucity of morphological characters. The statistical methodology did not combine these two species into one. Absent from molecular sampling are representatives from Brazil. It was determined to designate the two as separate species. Species limits of the furcata complex are based upon phylogenetic patterns in combination with morphological diagnostic characters of the groups.

5.3.3 Diagnosis of Kapala furcata complex

Features of the *K. furcata* complex generally correspond with the generic description of Heraty (2002), and general features of the furcata complex correspond with the genus description. This species complex is diagnosed by combination of a striate face and females with 9-10 flagellomeres, or rarely appearing as 8 on small specimens. When there are 10 flagellomeres present, F8-F10 are generally broader than long (Fig. 5.7). Some *K. parafurcata* have flagellomeres 8 and 9 distinct in lateral and dorsal view, but not well-divided in ventral and medial view. One small *K. parafurcata* (D1086, missing one antenna) appears to only have a very long F8, though there is faint division in lateral view. Facial setae sparse, more prominent on upper frons, with a row of short transverse setae on anteclypeus. There is variation in facial striae (Fig. 5.5); most species have the frons adjacent to the scrobes with oblique striate, traversing between middle ocellar triangle medially to lower eye margin; lower face below toruli with striae broadly curved from torulus to posterior genal margin. One species, *K. furcata*, however, has striae oblique from the scrobes to the lateral ocelli and the lower face with transverse striae adjacent to the clypeus. The species sister to the remaining clade, D2799, has barely discernable striae. Facial striae are generally absent in the iridicolor complex (also Kapala clade Group 2), and present and distinct in all of the Group 3. The dorsolateral projection of the furcata complex prepectus is typically an elongate triangle, broadly rounded or sometimes squared at the apical point (Fig. 5.8). Species near *K. sulcifacies* typically have a more strongly acute posterior tip of the dorsolateral projection of the prepectus. Propodeal disc flat and broad, with shallow areolate crenulations on dorsal margin; callus swollen, irregularly crenulate, and setose.

Many of the specimens in this clade have thick spines and robust bodies (Fig. 5.5), with striate faces as compared the sister complex, the iridicolor clade, which have smooth faces (Murray & Heraty, in prep.-a). Typically, the two clades are easily distinguished, but here D2799 has only a lightly striate face, and some of the K. iridicolor *sensu stricto* also have weak striae on the upper frons. The distantly-related *Kapala* that are near *K. sulcifacies* ('Group 3' in Murray & Heraty, in prep.-a) always have 8 flagellomeres in females and the striae below the torulus is always transverse. Small-bodied male K. furcata clade specimens may be misidentified as *K. sulcifacies* due to the striate face.

Known ant host associations: specimen D2799 from Mexico on *Ectatomma ruidum* (Ectatomminae) and *K. cynipsea* (as *K. cuprea*) from Trinidad on *Pachycondyla crassinoda* (Ponerinae) (Myers, 1931). Plant associations were reported for *K. furcata* from the Panama Canal Zone (Clausen, 1940a), but under current definition, this species is not what would be *K. furcata*.

5.4 Key to the species groups of Kapala and the furcata complex

Species groups and the new genus follow Chapter 3 (Murray and Heraty (in prep.-a)).

1. Smooth face. Rare exceptions with faint striae on the frons, only found in specimens from Central America. If striations present, mid lobe of mesoscutum typically rounded in lateral view and not abruptly angular………………………………………………………………………………………… 2

-- Striate face. Striations both above and below the torulus, may be faint. Mid lobe of mesoscutum typically elevated and angular in lateral view (as in Fig. 5.6B-F) 3

2. Females with 8 flagellomeres and males typically with spiraling carinae on spines. Maxillary and labial palpomere formula 2/2 …………………………... KC New Genus (description pending)

-- Females with 9 to 10 flagellomeres. Maxillary and labial palpomere formula 3/2 or 3/3 ……... iridicolor species complex

3. Females with 8 flagellomeres, palpi 3/3 or rarely 3/2. Facial striation transverse on face below torulus …….. sulcifacies species complex

-- Females with 9 to 10 flagellomeres, palpi 3/3, 3/2, or 2/2. Facial striation nearly always oblique on face below torulus, if transverse than females with 9 flagellomeres .... furcata species complex

4. Lateral lobes of mesoscutum subconical and projecting dorsolaterally to the approximate height of the mid lobe. Mexico and Costa Rica (Fig. 5.6A) .... *K. deltalis*

-- Lateral lobes lower than height of midlobe and not conical (Fig. 5.6B-D) 5

5. Face with extremely faint striae over face, nearly indiscernible. Females with 9 flagellomeres, palpi 3/2. Male unknown. Mexico .... *K.* undet. sp D2799

-- Face with distinct striae on both frons and lower face. Females with 9 to 10 flagellomeres. Palpi 3/3, 3/2, or 2/2. From Central America, Caribbean, or South America; not known from Mexico 6

6. Striation of frons oblique from scrobes to lateral ocelli, striation of lower face transverse to sub-transverse adjacent to clypeus (Fig. 5.4B). Facial striations may be widely spaced. Maxillary-labial palpomere formula 2/2 or 3/2 .... *K. furcata*

-- Facial striation oblique from medial ocelli to gena and continuing as oblique on face below torulus. Facial striations closely spaced. Maxillary and labial palpomere formula 3/3 7

7. Face with fine shallow striae, in combination with weak punctuations below torulus. Lateral lobes enlarged, and mid lobe raised with two medial swellings (Fig. 5.6B). Scutellar spines often parallel or widening in dorsal view (Fig. 5.5D). Males known .... *K. quasimodo*

-- Facial striation more deeply impressed. Lateral and midlobes may project, but lateral lobes not rectangular (5.6C,D). Females nearly always with 9 flagellomeres, but rarely appearing as 10 in ventral view...8

8. Scutellar spines longitudinal, extending from base to tips, spines 1.3-1.8× the length of scutellum (Fig. 5.5E). Females with 9 or very rarely 10 flagellomeres .... *K. parafurcata*

-- Scutellar spines longitudinal in basal half, and in apical half oblique or spiraling outwards around spines, spines generally 1.0-1.3× the length of scutellum (Fig. 5.5F) .... *K. cuprea*

5.5 Species descriptions

5.5.1 *Kapala cuprea* Cameron 1913

Figs 5.4F, 5.5F, 5.8F. ♀

Kapala cuprea Syntype: French Guiana: [1♂, BMNH: UCRCENT00310005]. "*Kapala cuprea* Cameron type Fr. Guiana / P. Cameron coll. 1914-110 / B.M. Type Hym 5.390"

Following information is from Heraty, 2002; pg 170:

Kapala cuprea Cameron, 1913: 116–117. Type data: Guyana and Trinidad. Syntypes, M. Type depository: BMNH; type no. 5.390. Description of male. Male from Trinidad (31.xii.1928) mounted with host cocoon, in which the cap is almost completely bitten off in a neat circle. Additional citation: De Santis, 1979: 103 (catalog).

Kapala cynipsea MALE Syntype: Villa Nova, Brazil: [1♂, BMNH: UCRCENT00310055]. "*Kapala cynipsea* Walker / B.M. Type Hym 5.636.b"

Following information is from Heraty, 2002; pg 170:

Thoracantha cynipsea Walker 1862: 379. Type data: Brazil: Santarem and Villa Nova. Syntypes (examined). Type depository: BMNH; type no. 5.636a and 5.636b. Description of both sexes. Additional citation: Dalla Torre, 1898: 365 (catalog).

Schizaspidia cynipsea; Walker, 1871: 66. Change of combination.

Kapala cynipsea; Ashmead, 1904: 473. Change of combination. Additional citation: De Santis, 1980: 208 (catalog).

Diagnosis:

Recognized by a combination of face with regularly-spaced, oblique striations in combination with scutellar spines 1.0-1.3× as long as length of scutellum, and is found in northern South America and the Caribbean. Distinguished from *K. parafurcata* which has tapering spines 1.3-1.8× as long as length of scutellum and occurs south of central Brazil.

Redescription of male, first description of female:

FEMALE: Body length 4.5-5.4 mm; length of mesosoma excluding spines 2.8-3.1 mm. Head, mesosoma, and scutellar spines black with greenish reflections, coxa and petiole black; flagellum brown, scape yellow to brown; femora pale yellowish to light brown first gastral tergite (Gt_1) brown, subsequent tergites yellow to light brown. Wing membranes hyaline to an even light infuscation, venation brown.

Head. 1.4× as broad as high. Face with a pattern of fine uniform striations, excluding the smooth supraclypeal and clypeal area (Fig. 5.4). Frons adjacent to scrobes with oblique striate, traversing between middle ocellar triangle medially to lower eye margin; lower face below toruli with striae broadly curved from torulus to posterior genal margin; occiput circularly carinate. Eyes separated by 1.8-2.0× their height. Malar space 0.8-1.0× eye height. Labrum with 8-10 digits. Maxillary/labial palpi 3/3-segmented. Flagellum 9 segmented, basal flagellomeres cylindrical or slightly serrate, clava rounded, length of flagellum 0.9-1.0× head height; basal flagellomere of female 0.4-0.5× length of scape, 1.3-1.4× as long as apical width, and 1.1-1.3× as long as following flagellomere; scape 3.1-3.4× as long as broad and 0.3× head height.

Mesosoma. Midlobe and lateral lobes of mesoscutum with regular transverse striae, axilla and scutellar disc with regular longitudinal striae; midlobe with flattened anterior face; lateral lobes elevated to approximately height of medial midlobe. Scutellar disc 1.3-1.9× as long as axilla, with medial apex raised 1.0-1.4× height of spines in lateral view (Fig. 5.8). Mesepisternum and upper mesepimeron with light transverse carinae, femoral groove impressed as a crenulate furrow. Scutellar spines 5.9-7.9× as long as basally broad, cylindrical, 1.0-1.3× as long as length of axillae and scutellar disc; arched in lateral view and in dorsal view often parallel at basal half and tapering only at the apical half, spines weakly to strongly obliquely carinate in apical half (Fig. 5.5). Metacoxa with medial row of setae, semiglobose, 1.5-2.0× as long as broad. Metafemur with appressed setae, 6.1-7.2× as long as broad. Fore wing 2.3-2.7× as long as broad, stigmal vein 1.8-2.1× as long as broad.

Metasoma. Petiole cylindrical and with fine parallel longitudinal carinae, slightly flattened dorsally. Gastral terga bare except for sparse minute setae; tergal scar on Gt_1 long. Petiole 2.6-3.0× as long as broad and 1.5× as long as metacoxa.

MALE: Body length: 2.6-4.9 mm (type=4.4mm), length of mesosoma excluding spines: 1.4-2.8 mm (type=2.7 mm). Similar to female except for the following; length of first antennal branch 1.0-1.2× head height; scape 2.1-2.6× as long as broad and 0.3× head height; petiole 3.8-4.2× as long as broad and 1.7-1.9× as long as metacoxa.

Distribution (Fig. 5.3):

Northern South America; Bolivia, Brazil, Ecuador, French Guiana, Guyana, Peru, West Indies

Discussion:

The syntypes examined of *K. cuprea* is a male from French Guiana (BM 5.390, BM: British Museum type) and the *K. cynipsea* (Walker 1862) female (BM 5.636a) and male (BM 5.636b) syntypes are from Brazil; the female is from Santarem and the male from Villa Nova. Examination of the syntype of *K. cuprea* and the male syntype of *K. cynipsea* indicate that these specimens represent the same species. The male *K. cynipsea* appears nearly identical to the *K. cuprea* type. The *K. cynipsea* male and female vary more in spine shape than the *K. cuprea* and *K. cynipsea* males, due to the female spines tapering more at the apex, while the male spines remain uniformly thick. All three specimens do possess thick spines relative to other *Kapala*. The female syntype of *K. cynipsea* was described preceding the male in the original manuscript. We propose that the male and female syntypes of *K. cynipsea* are split and the male syntype of *K. cynipsea* (Walker 1862) be synonymized with *K. cuprea* and the female syntype remain as *K. cynipsea*, which needs to be reexamined to determine if the female is part of the furcata group.

Eleven specimens were sequenced and attributed to *K. cuprea* (Ecuador: ♀= D1003 and D3838; ♂=D1004, D3833, D3836, D3837, D3852; Trinidad: ♀=D3804, ♂=3805, D3806, and D3815). Facial striation is similar in all 11 molecular specimens determined to be *K. cuprea*, and the patterns correspond to the type specimen. Measurements from the *K. cuprea* and from the *K. cynipsea* male syntypes overlap with the range of measurements from the molecular specimens.

Host associations:

Pachycondyla crassinoda (Ponerinae) in Trinidad (Myers, 1931).

Material Examined:

Bolivia: Santa Cruz Dept.: 5km SSE Buena Vista, Hotel Fauna y Flora, 440m, 17°29'56"S, 63°39'08"W, 6-15 Dec 2003, S. & J. Peck, forest, flight intercept trap [2♂, CNC: UCRCENT00300676 - 77]. Santa Cruz: Buena Vista, 17°27'32"S, 63°39'33"W, 8 Jul 1973, C. Potter, L. Styange & E. Demares [2♂, IMLA: UCRCENT00242080 - 81]. Estac. Experimental General Saavedra, 430m, 17°47'38"S, 63°11'00"W, 9 Jul 1972, C. Porter & L. Stange [1♂, IMLA: UCRCENT00313142]. **Brazil:** Para: Aldeia Coraci 12 km W Caninde, Rio Gurupi, 1°48'38"S, 46°24'03"W, 16-26 Apr 1963, B. Malkin [1♂, AMNH: UCRCENT00237855]. Santarem, 0°57'27"S, 46°59'38"W [1♀, CMNH: UCRCENT00172445]. Turcurui, 3°42'00"S, 49°42'00"W, Jan 1978, M. Alvarenga [1♂, UCRC: UCRCENT00305549]. **Ecuador:** Napo: Sacha, 1°04'59.3"S, 77°37'05"W, 9 Mar 1983, L. Huggert [1♂, MZLU: UCRCENT00242568]. Orellana: 1 km S. Onkone Gare Camp, Reserva Etnica Waorani, 216m, 0°39'25.7"S, 76°27'10.8"W, 2 Jul 1995, T.L. Erwin et al., terre firme forest, fogging [1♀, UCRC: UCRCENT00091807]. 1 km. S. Onkone Gare Camp, Reserva Etnica Waorani, 216m, 0°39'25"S, 76°27'11"W, 9 Jul 1995, T.L. Erwin et al., terre firme forest, fogging [1♂, UCRC: UCRCENT00092227]. Rio Piraña Bridge, Reserva Etnica Waorani, Onkone Gare Camp, 216.3m, 0°39'25.7"S, 76°27'10.8"W, 17 Oct 2005, T.L. Erwin, M.C. Pimienta et al, terre firme forest, Fogging [1♀, USNM: UCRCENT00247775]. Transect Ent. at Rio Piraña Bridge Reserva Etnica Waorani Onkone Gare Camp, 216.3m, 0°39'25.7"S, 76°27'10.8"W, 17 Oct 2005, T.L. Erwin, M.C. Pimienta et al, terre firme forest, Fogging [1♂, USNM: UCRCENT00247778].

Sucumbíos: Napo River, Sacha Lodge, 230m, 0°30'00"S, 76°30'00"W, 13-23 Apr 1994, P. Hibbs, malaise trap [1♂, CNC: UCRCENT00320767]. Napo River, Sacha Lodge, 290m, 0°30'00"S, 76°30'00"W, 3-13 Jun 1994, P. Hibbs [1♂, CNC: UCRCENT00320768]. Napo River, Sacha Lodge, 290m, 0°30'00"S, 76°30'00"W, 4-14 May 1994, P. Hibbs [1♂, CNC: UCRCENT00320853]. **Guyana:** Bartica, Kartabo, 0-30m, 5°45'15"N, 57°42'16"W, 24 Mar 1924 [1♀, AMNH: UCRCENT00238159]. **Peru:** Madre de Dios: Los Amigos Bio. St., 300m, 12°33'44.4"S, 70°05'47.1"W, 25 Dec 2010, J. Heraty, trail 10, swp [1♂, UCRC: UCRCENT00301932]. Rio Tambopata Res., 30 km air SW P to. Maldanado, 290m, 12°50'00"S, 69°20'00"W, 6 Dec 1982, J.J. Anderson [1♂, FSCA: UCRCENT00411912]. **Trinidad:** 10°41'26"N, 61°13'16"W, May 2004 [1♂, UCRC: UCRCENT00172511]. Brasso Seco, Rd to Paria Bay, 148m, 10°44'57"N, 61°15'53"W, 25 Jul 2013, Heraty & Baker, forest, swp [2♂ 1♀, UCRC: UCRCENT00412122 - 24]. Curepe, 10°38'48"N, 61°24'56"W, 21 Jul 1978, malaise trap [1♂, UCRC: UCRCENT00305559]. nr. Chaguaramas, 400m, 10°43'01"N, 61°11'52"W, 24 Nov 1977, W. & E. Mason [1♂, CNC: UCRCENT00425741]. Simla Field Station, Arima Valley, 10°41'49"N, 61°17'06"W, 8-9 Mar 1977, P. Feinsinger, tropical rain forest, malaise trap [1♀, FSCA: UCRCENT00306377]. Simla Res. St., 250m, 10°41'34"N, 61°17'23"W, 22 Jul 2013, Heraty&Baker, station, Malaise [1♂, UCRC: UCRCENT00412133]. Tunapuna, Mt. St. Benedict , 500m, 10°40'20"N, 61°23'51"W, 21 Jun-8 Jul 1993, S&J Peck, Mt. Tabor rainforest, Malaise [15♂, UCRC: UCRCENT00320102 - 03, UCRC: UCRCENT00320105 - 17]. **U.S. Virgin Islands:** St. Thomas , 1500m, 18°20'17"N, 64°53'39"W, 1859, Thoreg [1♂, NMW: UCRCENT00317112].

5.5.2 *Kapala deltalis* **sp. nov.**

Figs 5.4C, 5.5C, 5.6A, 5.8C.

Diagnosis:

Recognized by the distinctive subconical dorsolateral swelling of the mesoscutal sidelobes and by apex of the scutellar disc with a medially acute, sharp apical crest (Fig. 5.8C). Another species in the furcata complex, *K. quasimodo*, also has enlarged lateral lobes, but they do not reach the height of the midlobe (Fig. 5.6A,B).

Description:

FEMALE: Body length 5.0-5.8 mm; length of mesosoma excluding spines 2.7-3.1 mm. Head, coxae, scutellar spines, and petiole black, mesosoma black with reddish copper metallic reflection; flagellum and scape brown; femora pale yellowish to light brown; first gastral tergite (Gt_1) black, subsequent tergites dark orange. Wing membranes hyaline to an even light infuscation, venation brown.

Head. 1.4-1.5× as broad as high. Face with a pattern of fine uniform striations and punctations, excluding the smooth supraclypeal and clypeal area (Fig. 5.4F), frons adjacent to scrobes with oblique striate, traversing between middle ocellar triangle medially to lower eye margin; lower face below toruli with striae broadly curved from torulus to posterior genal margin; occiput circularly carinate; facial setae sparse, more prominent on upper frons, with a row of short transverse setae on anteclypeus. Supraclypeal area defined by weakly impressed sulci. Eyes separated by 2.1-2.4× their height. Malar space 0.9-1.1× eye height. Labrum with 8-11 digits.

Maxillary/labial palpi 3/3-segmented. Flagellum 9-10 segmented, basal flagellomeres cylindrical or slightly serrate, clava rounded and sometimes subdivided resulting in 10 flagellomeres, length of flagellum 1.1-1.3× head height; basal flagellomere of female 0.5-0.6× length of scape, 1.8-2.2× as long as apical width, and 1.3-1.7× as long as following flagellomere; scape 3.6-4.0× as long as broad and 0.3× head height.

Mesosoma. 1.3× broader than head; midlobe and lateral lobes of mesoscutum with fine, regular transverse striae, axilla and scutellar disc with shallow, regular longitudinal striae; midlobe with flattened anterior face; lateral lobes elevated to approximately the height of medial midlobe. Axilla raised convexly in lateral view; scutellar disc 1.3-1.8× as long as axilla, with apex raised ~2× height of spines in lateral view (Fig. 5.8) and bordered by a strong carina posteriorly. Posteriodorsal prepectus with sparse setae, elongated triangle with rounded tip. Mesepisternum smooth and shining except for weak rugose crenulae ventrally; upper mesepimeron smooth or with weak punctations, femoral groove impressed as a crenulate furrow. Propodeal disc flat and broad, with shallow areolate crenulations on dorsal margin; callus swollen, irregularly crenulate, and setose. Scutellar spines 7.1-10.6× as long as basally broad, and tapering apically, cylindrical, arched in lateral view and convexly rounded in dorsal view, 1.3-1.9× as long as length of axillae and scutellar disc (Fig. 5.5), with spines longitudinally carinate and apically emarginate. Metacoxa with medial row of setae, semiglobose, 1.6-2.0× as long as broad. Metafemur with appressed setae, 6.2-7.2× as long as broad. Fore wing 2.1-2.8× as long as broad, stigmal vein 1.5-2.3× as long as broad.

Metasoma. Petiole cylindrical and with fine parallel longitudinal carinae, slightly flattened dorsally. Gastral terga bare except for sparse minute setae; tergal scar on Gt_1 short. Petiole 3.3-3.6× as long as broad and 1.3-1.5× as long as metacoxa.

MALE: Body length: 3.3-5.2 mm, length of mesosoma excluding spines: 1.6-2.8 mm. Similar to female except for the following; length of first antennal branch 1.0-1.3× head height; scape 2.4-3.0× as long as broad and 0.3× head height; petiole 4.6-5.0× as long as broad and 1.6-1.9× as long as metacoxa.

Distribution (Fig. 5.3):

Costa Rica and Mexico.

Discussion:

There is little morphological variation. Male to female ratio in museum collections is approximately 20:1. One specimen sequenced (D1388; ♂ Costa Rica).

Host associations:

Unknown.

Etymology:

From the Greek letter delta, Δ. The shape of the mesosoma resembles an inverted triangle from the anterior aspect.

Holotype: ♀, “**Costa Rica:** Prov. Guanacaste, Macizo Miravalles, Estación Cabro Muco, 1100m 23-28 SEP 2003. J. Azofeifa, TP de Luz, L N 299769 411243 #75484” / “INB0003778914 INBIOCRI COSTA RICA” . Calculated coordinates: 10°43'0"N 85°08'34"W. Deposited in INBIO, Costa Rica.

Paratypes (6♀, 47♂**): Costa Rica:** Alajuela: P.N. Rincon de la Vieja, 2 km N Colonia Blanca, 800m, 18-28 Jun 1992, III curso Parataoxon [1♂ 1♀, INBIOCRI00703908, INBIOCRI00704253]. Guanacaste Prov.: Est. Cacao, 2 km SW del Cerro Cacao, 800-1400m, 10°55'59"N, 85°28'03"W, 7-18 Feb 1995, M. Iobo [2♂, INBIOCRI00235220 - 21]. Est. Cacao, Send. a la Cima. 2 km SW del Cerro Cacao, 1500m, 10°55'59"N, 85°28'03"W, Mar 1996, C. Moraga, Sombrereta [1♂, INBIOCRI00473635]. Est. Cacao, SW side Volcan Cacao, 1000-1400m, 10°55'42"N, 85°28'06"W, Nov-Dec 1989, URCG R. Blanco & C. Chaves [6♂, INBIOCRI00143717, INBIOCRI00143797, INBIOCRI00144236, INBIOCRI00144249, INBIOCRI00144251, INBIOCRI00146357]. Estac. Mengo, SW Volcan Cacao, 1100m, 10°56'03"N, 85°27'22"W, 1988-1989 [2♂, INBIO: UCRCENT00305583, INBIO: UCRCENT00305593]. Guanacaste N.P., Biol. Sta. Cacao, 900m, 10°35'03"N, 85°22'46"W, 13 Feb 1995, L. Masner, screen sweep [11♂ 1♀, CNC: UCRCENT00316290 - 95, UCRC: UCRCENT00305703 - 08]. Macizo Miravalles, Estación Cabro Muco, 1100m, 10°43'00"N, 85°08'34"W, 22 Sep-5 Oct 2003, J.D. Gutierrez, MT #2 [2♂, INBIOCRI03983169 - 70]. Macizo Miravalles, Estación Cabro Muco, 1100m, 10°43'00"N, 85°08'34"W, 24 Sep-5 Oct 2003, B. Hernandez, MT #1 [13♂ 3♀, INBIOCRI00097313, INBIOCRI00097315, INBIOCRI00097317, INBIOCRI00097320, INBIOCRI00097322 - 23, INBIOCRI00097325, INBIOCRI00097331, INBIOCRI00097333 - 34, INBIOCRI00097341, INBIOCRI03730848, INBIOCRI03983084, INBIOCRI03983089, INBIOCRI03983129, INBIOCRI03983131]. Rio San Lorenzo, Tierras Morenas, 1050m, Oct 1995, G. Rodriguez [1♂, INBIOCRI00453881]. Guanacaste: Estac. Mongo, SW Volcan

Cacao, 1100m, 10°56'03"N, 85°27'22"W, Jul 1988, P. Hanson [1♂, INBIO: UCRCENT00305586]. Puntarenas Prov.: San Luis, Monteverde, 1000-1350m, 10°16'31"N, 84°47'40"W, Feb 1995, Z. Fuentes [1♂, INBIOCRI00165650]. San Luis, Monteverde, 1040m, 10°16'25"N, 84°49'27"W, Apr 1994, Z. Fuentes [1♂, INBIOCRI00796351]. San Luis, R.B. Monteverde, 1040m, 10°16'25"N, 84°49'27"W, 24 Aug-15 Sep 1992, F.A. Quesada [1♀, INBIOCRI00856129]. San Luis, R.B. Monteverde, 1040m, 10°16'25"N, 84°49'27"W, Aug 1992, Z. Fuentes [1♂, INBIOCRI00754455]. San Luis, R.B. Monteverde, 1040m, 10°16'25"N, 84°49'27"W, Dec 1992, Z. Fuentes [1♂, INBIOCRI00958023]. San Luis, R.B. Monteverde, 1040m, 10°16'25"N, 84°49'27"W, Jul 1992, Z. Fuentes [1♂, INBIOCRI00722852]. **Mexico:** Chiapas: 32 km N. of Ocozocoautla, on road to Malpaso, 762m, 16°59'01"N, 93°30'17"W, 6 Oct 1974, D.E. & J.A. Breedlove [1♂ 1♀, CASC: CASENT02174570, CASC: UCRCENT00292310]. All INBIOCRI specimens are deposited in INBIO.

5.5.3 *Kapala furcata* (Fabricius, 1804)

Figs 5.4B, 5.5B 5.7B, 5.8B.

Holotype: South America. “*E. furcata* ex. Am. mer: Schmidt” ♀, ZMUC00241187

Eucharis furcata Fabricius, 1804: 158. Type data: South America. Type depository: ZMUC. Description of female.

Eucharis furcata Fabricius, 1804: 158.

Lectotype was designated by (Heraty, 2002), illustrated, fig. 173. Type depository: ZMUC. Type data: Brasilia. Description of female. However, this conflicts with the type specimen with label information from South America (“Am.: mer.”).

Following information is from Heraty, 2002; pg 172:

Additional citations:Latreille (1809): 21 (subsequent description of female);Lamarck (1817): 160 (catalog);Walker (1839): 65 (subsequent description of female). *Thoracantha furcata*; Walker (1839): 22. Change of combination. List of species and new distribution; distribution from Sierra Leone refers to *K. ivorensis.* Incorrectly places *E. flabellatus* Fabricius as junior synonym of *furcata*. Additional citation: Walker (1841): pl. P. (illustrated).

Chirocerus furcatus; Brullé (1846): 571, illustrated. Change of combination. Kirby (1886) questions the identity of Brullé's drawing and suggests that it looks closer to *Thoracantha atrata* Walker than to either of the Fabrician species. In opinion of JMH, the drawing appears closer to

Kapala sulcifacies (Cameron). The figure legend in Brullé (1846: pl.38) refers to *Chirocerus furcatus* Westwood not Fabricius, and probably refers to a species identified by Westwood.

Chirocera furcata; Chenu [(Desmarest, 1860)], 1860: 161, illustrated.

Schizaspidia furcata; Walker (1871): 66. Change of combination.

Schisaspidia furcata; Walker (1872): 65, illustrated and misspelling of generic epithet.

Kapala furcata Cameron (1884): 103, pl.5, fig. 17. Change of combination and designation by monotypy as type of *Kapala*. It is likely that none of the specimens listed in the specimens examined section actually belong to *K. furcata*, but rather to *K. sulcifacies* (Cameron). Additional citations: Kirby (1886): 30 (catalog);Dalla Torre (1898): 364 (catalog);Kieffer (1904): 243–244 (subsequent description of female, but probably not this species); Ashmead (1904): 472 (refers to specimens in Berlin bearing MS names:

"*Thoracantha elevata* Westw., *T. spinosa* Illiger, etc."); Brues (1907): 105–106 (probably not this species; from Brownsville, Texas); Peck (1963): 509 (catalog); Burks (1979): 877 (catalog); De Santis (1979): 103 (catalog); De Santis (1980): 209 (catalog).

Diagnosis:

Determined a combination of a pattern of facial striations on the frons oblique from the torulus to the lateral ocelli, and with transverse striae adjacent to clypeus, often deeply impressed across ventral half of face. Female with 9-10 flagellomeres. The scutellar apex apical crest is lower than other species of the furcata clade, and in lateral view is <1× height of the base of the scutellar spines (Fig. 5.8).

Redescription:

FEMALE: Body length 5.0-5.8 mm; length of mesosoma excluding spines 2.7-3.1 mm. Head, mesosoma, and scutellar spines black to green-black, coxa and petiole black; flagellum brown to dark brown, scape brown; femora pale yellowish to light brown; Wing membranes hyaline to an even light infuscation, venation brown.

Head. 1.3-1.5× as broad as high. Face with a pattern of fine uniform striations and punctations, excluding the smooth supraclypeal and clypeal area (Fig. 5.5). Frons adjacent to scrobes with oblique striate, traversing between middle ocellar triangle medially to lower eye margin; lower face below toruli with striae broadly curved from torulus to posterior genal margin; occiput circularly carinate; facial setae sparse, more prominent on upper frons, with a row of short transverse setae on anteclypeus. Supraclypeal area defined by weakly impressed sulci. Eyes separated by 2.1-2.3× their height. Malar space 0.9-1.0× eye height. Labrum with 8-12 digits. Maxillary/labial palpi variously segmented as 2/2 or 3/2. Flagellum 9-10 segmented (Fig. 5.7), basal flagellomeres cylindrical or slightly serrate, clava rounded, length of flagellum 1.0-1.1× head height; basal flagellomere of female 0.6-0.7× length of scape, 1.8-2.3× as long as apical width, and 1.2-1.6× as long as following flagellomere; scape 2.7-3.0× as long as broad and 0.3× head height.

Mesosoma. Mid lobe and lateral lobes with regular transverse striae, axilla and scutellar disc with regular longitudinal striae. Scutellar disc 1.3-2.1× as long as axilla, with posterior apex raised 0.7-0.9× height of spines in lateral view (Fig. 5.8). Mesepisternum and upper mesepimeron with weak transverse striae, femoral groove impressed as a crenulate furrow.

Propodeal disc flat and broad, typically with at most weak longitudinal carinae on the disc. Scutellar spines 6.7-8.0× as long as basally broad, and tapering apically, with the widest distance between the two 1.0-2.6× the narrowest distance, arched in lateral view and convexly rounded in dorsal view (Fig. 5.4), 1.0-1.3× as long as length of axillae and scutellar disc, with spines longitudinally carinate and apically rounded or emarginate. Metacoxa with medial row of setae, semiglobose, 1.6-2.0× as long as broad. Metafemur with appressed setae, 6.1-6.4× as long as broad. Fore wing 2.5-2.9× as long as broad, stigmal vein 1.5-2.0× as long as broad.

Metasoma. Petiole cylindrical and with fine parallel longitudinal carinae, slightly flattened dorsally. Gastral terga bare except for sparse minute setae; tergal scar on Gt_1 absent or present and short or faint. Petiole 2.7-3.4× as long as broad and 1.3-1.4× as long as metacoxa.

MALE: Body length: 4.1-4.6 mm, length of mesosoma excluding spines: 2.3-2.7 mm. Similar to female except for the following; length of first antennal branch 1.2× head height; scape 2.2-2.3× as long as broad and 0.3× head height; petiole 5.0-6.3× as long as broad and 2.3-2.6× as long as metacoxa.

Distribution (Fig. 5.3):

Central South America: Argentina, Brazil, and Uruguay.

Discussion:

The lectotype of *K. furcata* is a female from South America, and the specimen from northern Argentina (D1078) is very similar morphologically. The molecular specimen D1078 is united to *K.*

furcata type in having horizontal facial striae below torulus, which is not seen in other K. furcata complex specimens. The collection of female morphospecies matched to D1078 closely fit *K. furcata* body and spine phenotype. The male specimens exhibit the facial striae but often have thicker spines at the base, which are more deeply carinate. Interestingly, there is variation in the museum collection specimens in the number of flagellomeres being 9-10 and the number of maxillary palpomeres being 2 or 3. Two palpomeres is not seen in other *Kapala* species. The *K. furcata* type has 3 maxillary palpomeres, but many of the paratypes have 2. At this time all of these individuals are grouped as *K. furcata*, because there are no apparent patterns in the polymorphism or a geographic correlation. Facial striation is typically more deeply impressed in northern specimens from Brazil and less impressed in specimens from southern Argentina.

Two male specimens from Uruguay UCRCENT_00237807 and 237115 are an example of spine morphotypes that do not match as closely the type *K. furcata*. They exhibit the *K. furcata* facial striation but have spines that are much thicker and deeply carinate.

Kapala furcata is extremely similar morphologically to *K. parafurcata*. However, *K. furcata* has 2-3 maxillary palpomeres and has vertical striations below the torulus, which is not found in other members of the furcata complex sampled.

Host associations:

Unknown.

Material Examined:

Argentina: Misiones Prov.: Santa Ana, near Loreto, 84m, 27°20'11"S, 55°31'51"W, 27 Mar 2003, J. Heraty, humid forest [1♀, UCRC: UCRCENT00092093]. Salta: Finca El Rey, 1000m, 24°42'00"S, 64°38'00"W, Feb 1953, N. Kusnezov [1♀, IMLA: UCRCENT00313148]. Tucuman Prov.: Siambon, 26°42'00"S, 65°27'00"W, Jan 1945, D. Olea [1♂, IMLA: UCRCENT00242082]. Tucuman: Tucuman, 26°48'30"S, 65°13'03"W, Jan 1947, Cordoba [1♀, IMLA: UCRCENT00313138]. **Brazil:** Rio Grande do Sul: , 29°32'04"S, 53°23'26"W, Stieglmayr [4♂ 6♀, NMW: UCRCENT00242559 - 62, NMW: UCRCENT00242564, NMW: UCRCENT00242566, NMW: UCRCENT00317114, NMW: UCRCENT00317115, NMW: UCRCENT00317118 - 19]. CPCN Pro-Mata, 325m, 29°30'00"S, 50°10'00"W, 4 Apr 1997, J. Ketterl [1♂, SMNS: UCRCENT00318556]. Pro-Mata, 325m, 29°30'00"S, 50°10'00"W, 30 Apr 1997, J. Ketterl [1♂, SMNS: UCRCENT00318557]. Santa Catarina: Corupa (Hansa Humbolt), 26°25'34"S, 49°14'36"W, Dec 1940, A. Maller [1♀, AMNH: UCRCENT00238157]. Pinhal, 27°14'00"S, 51°55'00"W, Apr 1947, A. Maller [1♂, AMNH: UCRCENT00238160]. Rio Natal, 26°21'00"S, 49°18'00"W, Jan 1945, A. Maller [2♀, AMNH: UCRCENT00238153 - 54]. Rio Natal, 26°21'00"S, 49°18'00"W, Mar 1945, A. Maller [1♀, AMNH: UCRCENT00238151]. Rio Vermelho, 27°29'28"S, 48°24'32"W, Feb 1945, A. Maller [2♀, AMNH: UCRCENT00238150, AMNH: UCRCENT00238152]. **Uruguay:** Tacuarembo: 40 km NW Tacuarembo, 200-300m, 31°29'45"S, 56°18'08"W, 2-9 Feb 1963, J.K. Bouseman [2♂, AMNH: UCRCENT00237807, AMNH: UCRCENT00238155].

5.5.4 *Kapala parafurcata* **sp. nov.**

Figs 5.4E, 5.5E, 5.7C, 5.8E.

Diagnosis:

Determined by a combination of face with regularly-spaced, oblique striations in upper and lower face in combination with scutellar spines tapering to apex and 1.3-1.8× as long as length of scutellum (Fig. 5.8E), and is found in central South America. Distinguished from *K. cuprea* which has spines 1.0-1.3× as long as length of scutellum (Fig. 5.8F) and occurs more northerly.

Description:

FEMALE: Body length 2.6-5.0 m;, length of mesosoma excluding spines 1.4-2.8 mm. Head, mesosoma, and scutellar spines black to green-black, coxa and petiole black; flagellum and scape yellow to brown; femora pale yellowish to light brown; first gastral tergite (Gt_1) brown, subsequent tergites light brown.

Head. 1.4-1.5× as broad as high. Face with a pattern of fine uniform striations, excluding the smooth supraclypeal and clypeal area (Fig. 5.4). Frons adjacent to scrobes with oblique striate, traversing between middle ocellar triangle medially to lower eye margin; lower face below toruli with striae broadly curved from torulus to posterior genal margin; occiput circularly carinate. Eyes separated by 2.1-2.4× their height. Malar space 0.8-0.9× eye height. Labrum with 6-11 digits. Maxillary/labial palpi 3/3-segmented. Flagellum 9-10 segmented, basal flagellomeres cylindrical or slightly serrate, clava rounded and sometimes subdivided resulting in 10 flagellomeres, length of flagellum 0.9-1.0× head height; basal flagellomere of female 0.5-0.7×

length of scape, 1.7-2.0× as long as apical width, and 1.1-1.3× as long as following flagellomere; scape 3.0-3.4× as long as broad and 0.3× head height.

Mesosoma. Mid lobe and lateral lobes with regular transverse striae, axilla and scutellar disc with regular longitudinal striae; lateral lobes elevated to approximately the height of medial midlobe. Scutellar disc 1.5-1.8× as long as axilla, with apex raised 1.1-1.5× height of spines in lateral view (Fig. 5.8). Mesepisternum and upper mesepimeron with weak to strong transverse striae, femoral groove impressed as a crenulate furrow. Scutellar spines 7.0-11.0× as long as basally broad, and tapering apically, cylindrical, arched in lateral view and parallel convexly rounded in dorsal view, 1.3-1.8× as long as length of scutellum (Fig. 5.5), with spines longitudinally carinate and apically emarginate. Metacoxa with medial row of setae, semiglobose, 1.4-2.1× as long as broad. Metafemur with appressed setae, 5.1-5.9× as long as broad. Fore wing 2.3-2.8× as long as broad, stigmal vein 1.5-2.4× as long as broad.

Metasoma. Petiole cylindrical and with fine parallel longitudinal carinae, slightly flattened dorsally. Gastral terga bare except for sparse minute setae; tergal scar on Gt_1 long. Petiole 3.0-3.6× as long as broad and 1.4-1.6× as long as metacoxa.

MALE: Body length: 2.2-4.8 mm, length of mesosoma excluding spines: 1.0-2.5 mm. Similar to female except for the following; length of first antennal branch 1.2-1.5× head height (Fig. 5.7); scape 2.8-3.0× as long as broad and 0.3× head height; petiole 4.5-5.3× as long as broad and 1.8-2.3× as long as metacoxa.

Distribution (Fig. 5.3):

Central South America: Argentina, Brazil, Paraguay, Peru.

Discussion:

K. parafurcata is very closely in molecules and morphology to *K. cuprea*. The two share extremely similar facial striation. They can be distinguished by the spines. K parafurcata has longer spines in comparison to the scutellum. In addition, K. parafurcata generally has more parallel or slightly convex spines. The maximum to minimum dorsal distance between the spines is 1.7-2.5×, whereas in *K. cuprea*, the spine interdistance is variable, at 1.7-9.8×, but spines are often directed inward and very close at the tips.

Eight specimens have been sequenced (Argentina: ♀= D0711, D1086, D2518; ♂=D1068a, D1069, D2519, D2520; Paraguay: ♂=3436).

Host associations:

Unknown.

Etymology:

The name derives from the close similarity to *K. furcata* in body shape, and due to many museum specimens of this species previously having been identified as “near *K. furcata*”.

Holotype: Argentina: Misiones Prov.: Loreto, Ruinas Jesuiticas, 27°29'59"S, 55°31'59"W, 4 Nov 2001, S.O. Martinez, P. Fidalgo, malaise trap [1♀, UCRC: UCRCENT00091817].

Paratypes: Argentina: Buenos Aires, 34°36'30"S, 58°22'23"W, Antigua [1♂, MACN: UCRCENT00242244]. Corrientes: Las Marias, Ca. Virasoro, 28°05'33"S, 56°02'42"W, 7 Nov 1971, C. Porter [2♂, IMLA: UCRCENT00242086, IMLA: UCRCENT00313140]. Misiones : Dos de Mayo , 27°02'00"S, 54°39'00"W, Dec 1973, Fritz [2♂, AMNH: UCRCENT00237787 - 88]. Misiones Prov.: Cataratas del Iguazu, 25°40'00"S, 54°27'00"W, 5-9 Nov 1970, C. Potter & L. Stange [7♂, IMLA: UCRCENT00242084 - 85, IMLA: UCRCENT00274414 - 15, IMLA: UCRCENT00274417, IMLA: UCRCENT00313134 - 35]. Iguazu, 25°55'25"S, 54°21'51"W, 30 Jan-13 Mar 1945, Hayward, Willink & Golbach [1♂ 2♀, IMLA: UCRCENT00313137, IMLA: UCRCENT00313139, IMLA: UCRCENT00313141]. Parque Nacional Iguazu, 200m, 25°40'48"S, 54°27'00"W, 2-7 Dec 2003, B.V. Brown & G. Kung, malaise trap [1♂, UCRC: UCRCENT00316349]. Reserva de Vide Silvestre Urugua-I, 400m, 25°58'28"S, 54°06'59"W, 7-9 Dec 2003, B. Brown & G. Kung , malaise trap [3♂, UCRC: UCRCENT00172510, UCRC: UCRCENT00172515 - 16]. RN 12, N of Puerto Bosseti, 221m, 25°48'20"S, 54°32'19"W, 25 Mar 2007, J.&J. Heraty & J. Torrens, Aurac.for. [1♀, UCRC: UCRCENT00000325]. Rt17, E of 9 de Julio, 212m, 26°24'02"S, 54°27'54"W, 26 Mar 2007, J.&J. Heraty & J. Torrens, roadside [2♂, UCRC: UCRCENT00000324, UCRC: UCRCENT00161498]. Santa Ana, near Loreto, 84m, 27°20'11"S, 55°31'51"W, 27 Mar 2003, J. Heraty, humid forest [2♂ 1♀, UCRC: UCRCENT00091803, UCRC: UCRCENT00091921, UCRC: UCRCENT00172312]. Misiones: Aristobulo del Valle, 27°05'51"S, 54°53'47"W, 28 Nov 1951, Montes &Willink [1♂, IMLA: UCRCENT00313136]. Loreto, Ruinas Jesuiticas, 285m, 27°30'00"S, 55°32'00"W, 26 Jan-20 Feb 2001, S.O. Martinez, P. Fidalgo, MT [1♂, UCRC: UCRCENT00302400]. Los Helechos, 350m, 27°32'05"S, 55°05'07"W, May 1949, Duret [1♂, AMNH: UCRCENT00237791]. Puerto Bemberg, 25°55'10"S, 54°35'08"W [1♂, MACN: UCRCENT00242245]. Salta Prov.: Oran, Rd to San Andres along Rio Blanca, 399m, 23°05'30"S, 64°21'57"W, 22 Mar 2003, J. Heraty, sclerophyll scrub [1♂, UCRC: UCRCENT00092070]. **Brazil:** Nova Teutonia , 27°11'00"S, 52°23'00"W, 7 Apr 1937, Fritz Plaumann [2♀, BMNH: UCRCENT00309840, BMNH: UCRCENT00309843]. Nova Teutonia, 300-500m, 27°11'00"S, 52°23'00"W, 30 Mar 1966, Fritz Plaumann [1♂, CNC: UCRCENT00300619]. Nova Teutonia, 300-500m, 27°11'00"S, 52°23'00"W, 9 Feb 1967, Fritz Plaumann [1♀, CNC: UCRCENT00300603]. Nova Teutonia, 300-500m, 27°11'00"S, 52°23'00"W, Apr 1968, Fritz Plaumann [5♂ 1♀, CNC: UCRCENT00172444, CNC: UCRCENT00300604, CNC: UCRCENT00300607, CNC: UCRCENT00300609, CNC: UCRCENT00300616, CNC: UCRCENT00300628]. Nova Teutonia, 300-500m, 27°11'00"S, 52°23'00"W, Dec 1968, Fritz Plaumann [7♂, CNC: UCRCENT00300608, CNC: UCRCENT00300610, CNC: UCRCENT00300620 - 22, CNC: UCRCENT00300625 - 26]. Nova Teutonia, 300-500m, 27°11'00"S, 52°23'00"W, Feb 1968, Fritz Plaumann [3♂, CNC: UCRCENT00300605, CNC: UCRCENT00300612-13]. Nova Teutonia, 300-500m, 27°11'00"S, 52°23'00"W, Jan 1969, Fritz Plaumann [2♂, CNC: UCRCENT00300627, CNC: UCRCENT00300629]. Nova Teutonia, 300-500m, 27°11'00"S, 52°23'00"W, Mar 1968, Fritz Plaumann [3♂, CNC: UCRCENT00300606, CNC: UCRCENT00300618, CNC: UCRCENT00300623]. Nova Teutonia, 300-500m, 27°11'00"S, 52°23'00"W, Mar 1969, Fritz Plaumann [1♂ 2♀, CNC: UCRCENT00300601 - 02, CNC: UCRCENT00300611]. Nova Teutonia, 300-500m, 27°11'00"S, 52°23'00"W, Mar 1971, Fritz Plaumann [2♂, CNC: UCRCENT00300614, CNC: UCRCENT00300624]. Mato Grosso: Maracaju, 21°37'08"S, 55°10'02"W, Apr-May 1937, G. Fairchild [1♂ 1♀, MCZ: UCRCENT00242335, MCZ: UCRCENT00242337]. Nova Teutonia: , 861m, 27°02'58"S, 52°23'55"W, 23 Jan 1939, Fritz Plaumann [1♂ 1♀, BMNH: UCRCENT00309842, BMNH: UCRCENT00309844]. Parana: Prudentopolis, 25°12'56"S, 50°58'08"W, 23-25 Feb 1969, C. Porter & A. Garcia [1♂, MCZ: UCRCENT00242336]. Pernambuco: Caruaru, 900m, 8°16'51"S, 35°58'32"W, Jun 1972, J. Lima [1♂, ROME: UCRCENT00242713]. Rio de Janeiro: Rio de Janeiro, 22°54'13"S, 43°12'35"W, Westwood [1♂, ZMUC: UCRCENT00245090]. Rondonia Pr. : Faz. Rancho Grande 62 km S Ariquemes , 10°17'57"S, 62°52'12"W, 12-22 Nov 1991, E. Fischer [1♂, UCRC: UCRCENT00172322]. Santa Catarina: 26°25'34"S, 49°14'36"W, Luderwaldt [1♂ 1♀, MZPW: UCRCENT00242646, MZPW: UCRCENT00242680]. São Paulo: Am. Brasiliense Cerradão Clube Nautico , 21°42'12.1"S, 48°01'24.7"W, 5 May 2000, M.T. Tavares et al., Varredura Vegetação (5 min.) horas 12:15 [1♂, UFES: UFES00002697]. Am. Brasiliense Cerradão Clube Nautico , 21°42'21.1"S, 48°01'24.7"W, 5 May 2000, M.T. Tavares et al., Varredura Vegetação (5 min.) horas 10:44 [2♂, UFES: UFES00002695 - 96]. Am. Brasiliense Cerradão Clube Nautico , 21°42'21.1"S, 48°01'24.7"W, 5 May 2000, M.T. Tavares et al., Varredura Vegetação (5 min.) horas 11:55 [1♂, UFES: UFES00002694]. Am. 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Colonia Independencia, 25°41'43"S, 56°15'34"W, Dec 1950, Foerster [1♂, AMNH: UCRCENT00237797]. Villarrica, 25°47'04"S, 56°27'03"W, Jun, F. Schade [1♂, MCZ: UCRCENT00242334]. Itapua: 17 km N. Hohenau, 200m, 26°57'14"S, 55°32'32"W, 2-4 Feb 1983, E.G. Riley [1♀, AMNH: UCRCENT00237790]. **Peru:** Madre de Dios: Rio Tambopata Res. 30km (air) SW Pto. Maldonado. , 290m, 15°50'02"S, 70°01'31"W, 14 Sep 1984, T.L.Erwin et al., Fogging [1♂, UCRC: UCRCENT00172319].

5.5.5 *Kapala quasimodo* **sp. nov.**

Figs 5.4D, 5.5D, 5.6B, 5.8D.

Diagnosis:

Recognizable by the finely striate and punctate face in combination with the enlarged lateral lobes and two dorsal swellings of the midlobe of the mesoscutum (Fig. 5.6B). Another species in the furcata complex, *K. deltalis* has much larger lateral lobes, reaching the height of the midlobe. Distance between spines typically as wide at apex as at base, forming a U shape (Fig. 5.8D). Spines weakly carinate.

Description:

MALE: Body length 3.4-4.7 mm; length of mesosoma excluding spines 1.8-2.4 mm. Head, mesosoma, coxae, scutellar spines, and petiole black; flagellum brown, scape light brown; femora pale yellow to light brown; first gastral tergite (Gt_1) black, subsequent tergites dark orange. Wing membranes hyaline to an even light infuscation, venation light brown to brown.

Head. 1.5× as broad as high. Face with a pattern of fine uniform striations and punctations, excluding the smooth supraclypeal and clypeal area (Fig. 5.4D). Frons adjacent to scrobes with oblique striate, traversing between middle ocellar triangle medially to lower eye margin; lower face below toruli with striae broadly curved from torulus to posterior genal margin; occiput circularly carinate; facial setae sparse, more prominent on upper frons, with a row of short transverse setae on anteclypeus. Supraclypeal area defined by ventral weakly impressed sulci.

Eyes separated by 2.0× their height. Malar space 0.9-1.0× eye height. Labrum with 8-11 digits. Maxillary/labial palpi 3/3-segmented. Length of first antennal branch 1.2× head height; scape 2.9-3.2× as long as broad and 0.3× head height.

Mesosoma. Mid lobe and lateral lobes with regular transverse striae, axilla and scutellar disc with regular longitudinal striae; midlobe with two dorsal swellings; lateral lobes enlarged but do not reach height of medial midlobe (Fig. 5.6). Scutellar disc 1.4-1.7× as long as axilla. Mesepisternum and upper mesepimeron striate, femoral groove impressed as a crenulate furrow (Fig. 5.8D). Scutellar spines 9.0-10.8× as long as basally broad, and tapering apically, cylindrical, with the widest distance between the two 0.9-1.7× the narrowest distance, 1.6-1.7× as long as length of axillae and scutellar disc, with spines longitudinally carinate and apically rounded (Fig. 5.5D). Metacoxa with medial row of setae, semiglobose, 1.6-1.9× as long as broad. Metafemur with appressed setae, 6.1-6.9× as long as broad. Fore wing 2.4-2.6× as long as broad, stigmal vein 1.3-2.4× as long as broad.

Metasoma. Petiole cylindrical and with fine parallel longitudinal carinae, slightly flattened dorsally. Gastral terga bare except for sparse minute setae; tergal scar on Gt_1 long. Petiole 4.9-6.3× as long as broad and 2.2-2.6× as long as metacoxa.

FEMALE: Unknown.

Distribution (Fig. 5.3):

Brazil, Ecuador and Venezuela.

Discussion:

Two specimens from the same locality in Ecuador were sequenced (D0938b and D0942a; ♂ Ecuador).

Host associations:

Unknown.

Etymology:

Named for Quasimodo, Victor Hugo's protagonist of the Hunchback of Notre Dame. This species has a projections of the mesosoma mid and lateral lobes, giving it a hunched appearance.

Holotype: Venezuela: Aragua: Rancho Grande N.P., 1100m, 10°24'13"N, 67°34'26"W, 18 Aug-3 Sep 1992, L. Masner, cloud forest, maxinet [1♂, UCRC: UCRCENT00172446].

Paratypes: Brazil: : Nova Teutonia , 300-500m, 27°11'00"S, 52°23'00"W, 1 Apr 1937, Fritz Plaumann [1♂, LACM: UCRCENT00242214]. **Ecuador:** Esmeraldas: Bilsa Biol. Sta., 500m, 0°20'24"N, 79°42'36"W, 10 May-4 Jun 1996, P. Hibbs, malaise trap [1♂, UCRC: UCRCENT00092084]. Bilsa Biol. Station, 500m, 0°20'24"N, 79°42'36"W, 7-19 Jul 1996, P. Hibbs, malaise trap/flight intercept trap [1♂, UCRC: UCRCENT00092002]. **Venezuela:** Aragua: Rancho Grande N.P., 1100m, 10°24'13"N, 67°34'26"W, 18 Aug-3 Sep 1992, L. Masner, cloud forest, maxinet [17♂, UCMS: UCRCENT00397267, UCRC: UCRCENT00172447 - 60, UCRC: UCRCENT00397263 - 64]. Rancho Grande, 1150m, 10°04'00"N, 67°32'36"W, 4 Jul-9 Aug 1986, B. Gill [3♂, CNC: UCRCENT00425738 - 40].

5.6 Figures and Tables

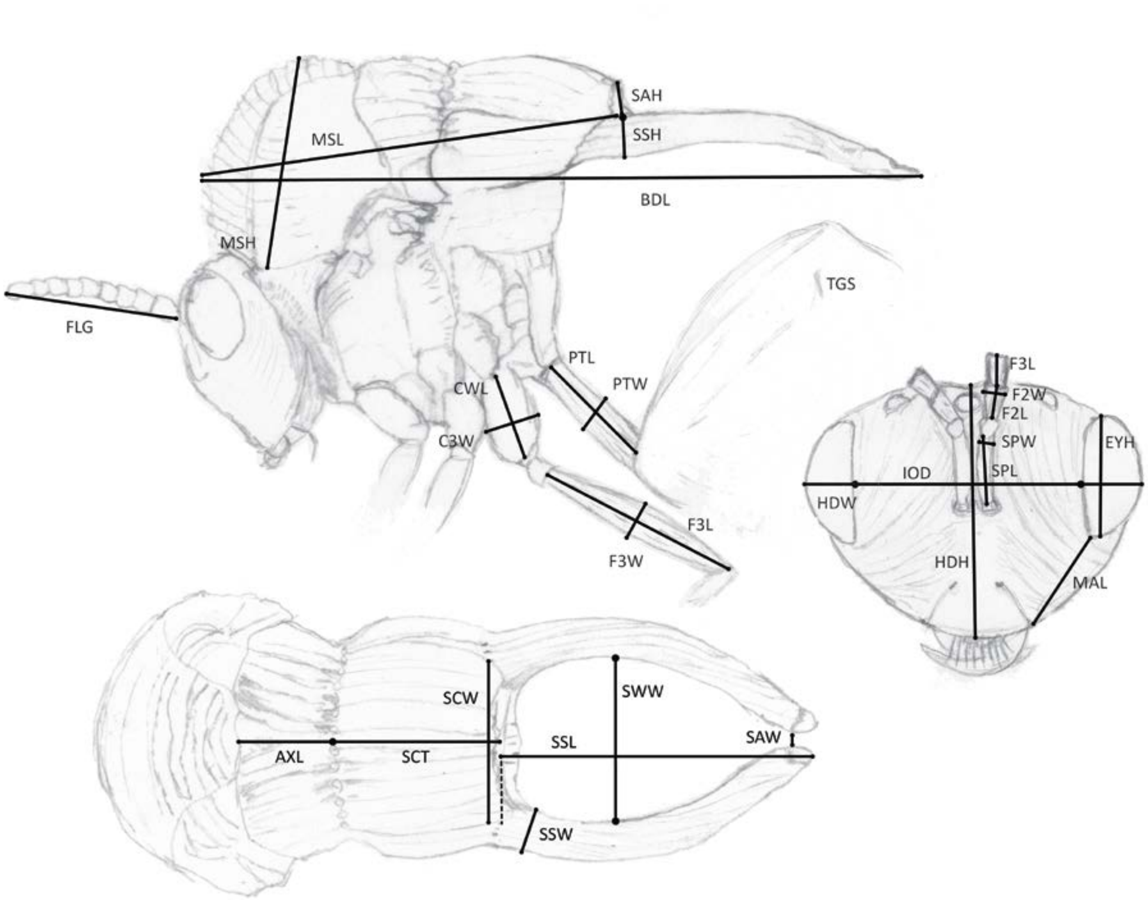


FIGURE 5.1.
Specimen measurements. Explanation of abbreviations and landmarks found in Table 1.

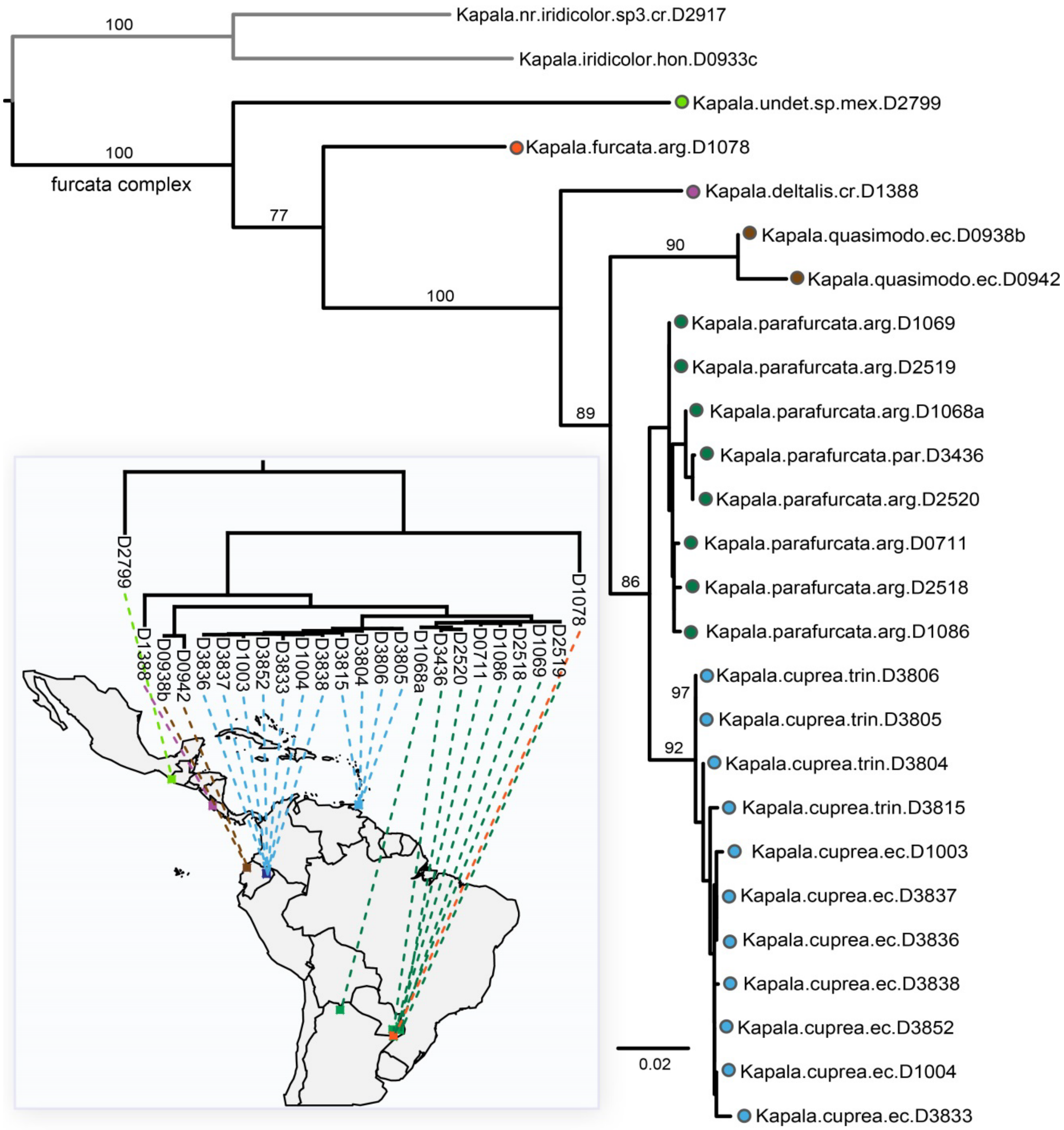


FIGURE 5.2.

ML phylogeny of the 24 furcata complex specimens and two outgroups from the iridicolor complex. Bootstrap values over 70 shown. The inset shows the tree mapped to the geographic localities.

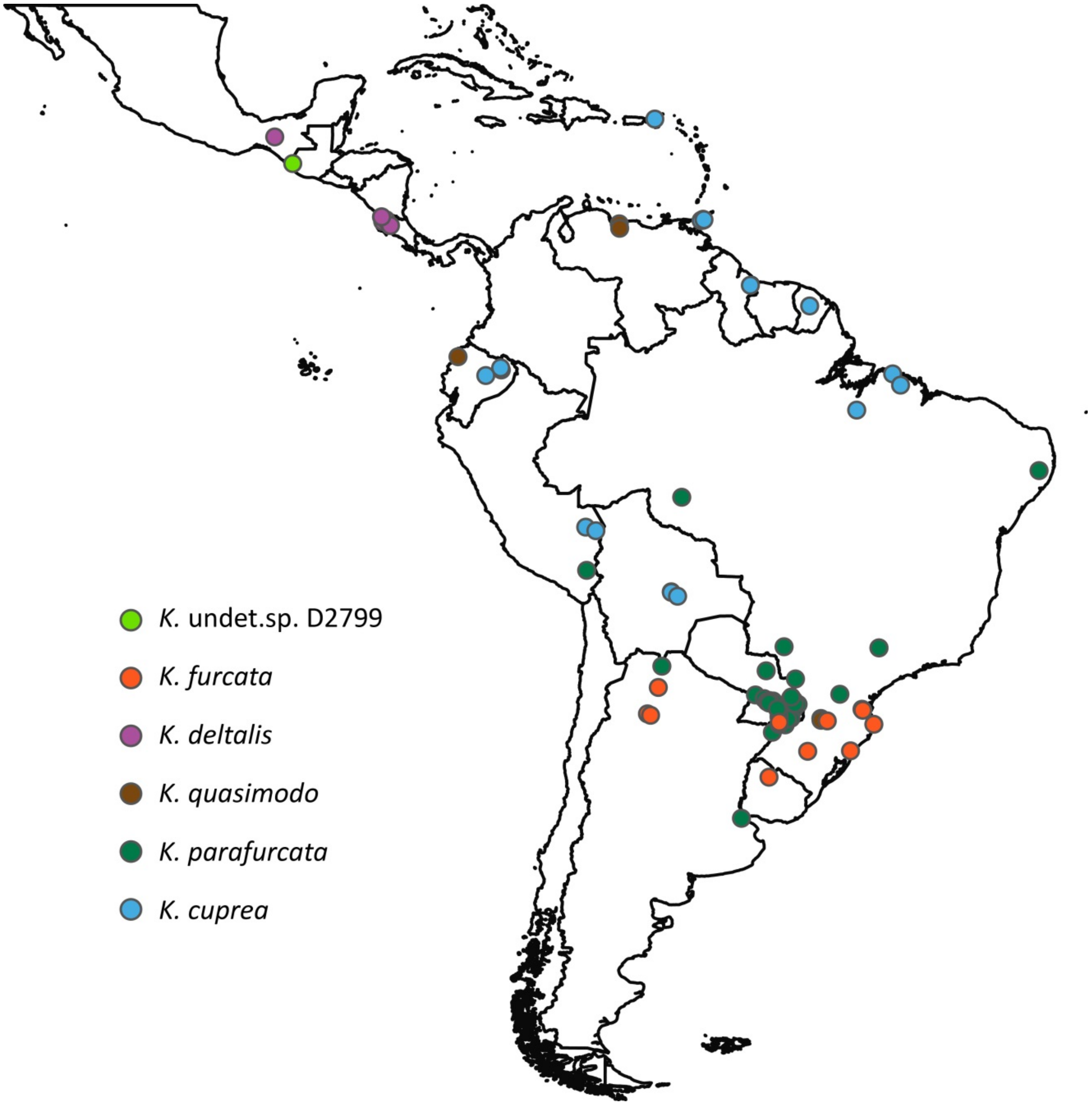


FIGURE 5.3.
Species distribution maps, from holotype and paratype material. Points mapped in SimpleMappr.net.

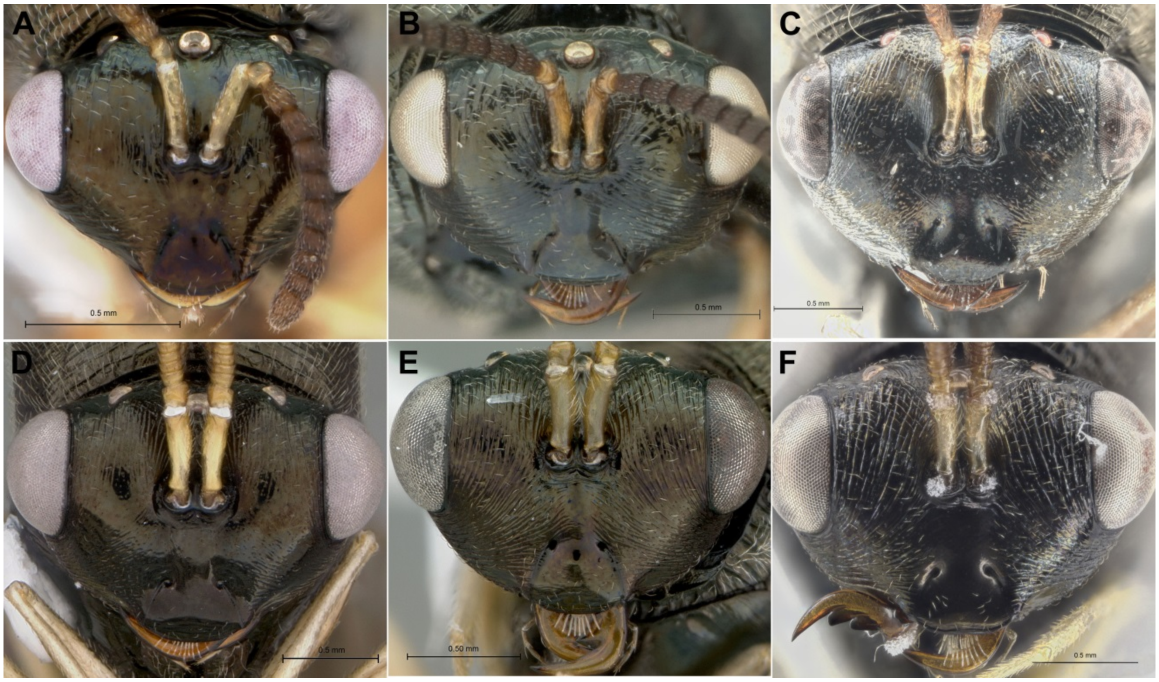


FIGURE 5.4.
Kapala furcata clade faces. A. *K.* undet D2799. B. *K. furcata*. C. *K. deltalis*. D. *K. quasimodo*. E. *K. parafurcata*. F. *K. cuprea*. All measurement bars 1.0 mm.

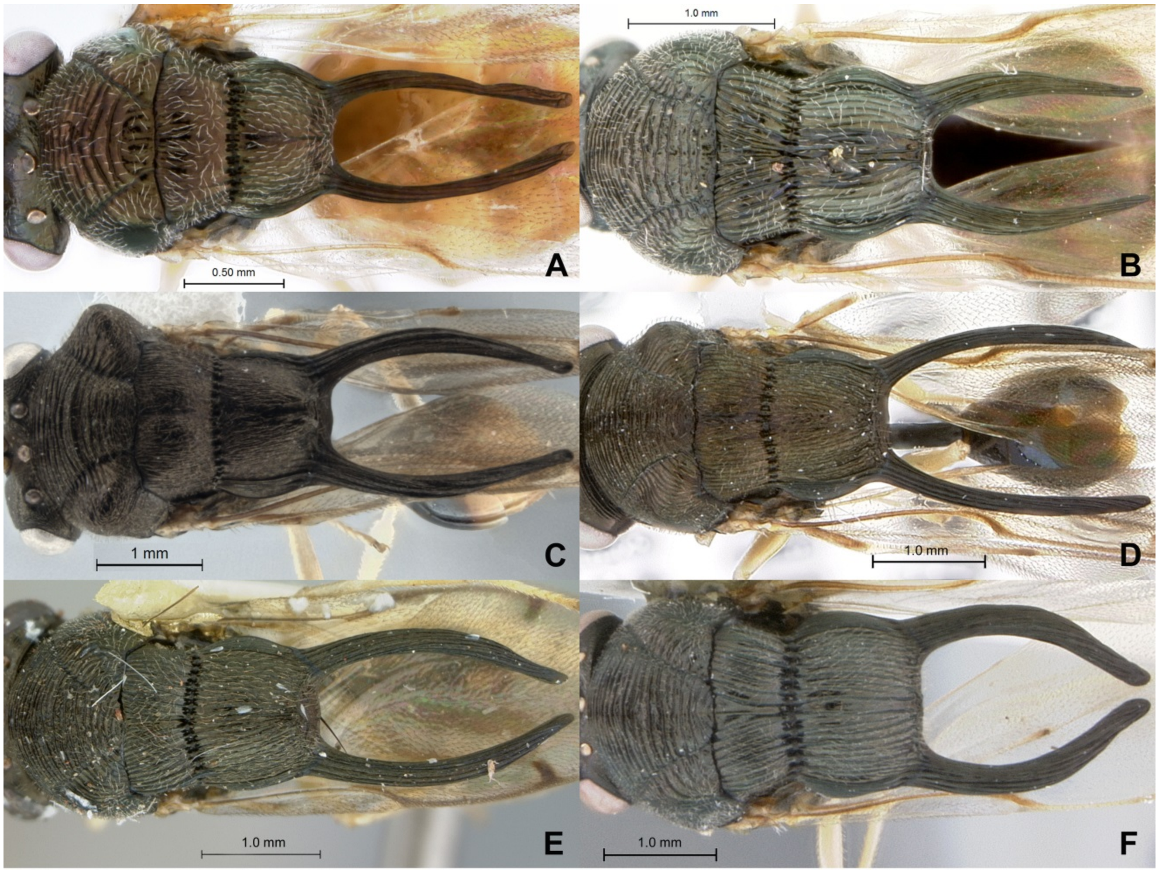


FIGURE 5.5.
Kapala furcata clade dorsal view of mesosoma. A. *K.* undet D2799. B. *K. furcata*. C. *K. deltalis*. D. *K. quasimodo*. E. *K. parafurcata*. F. *K. cuprea*. All measurement bars 1.0 mm.

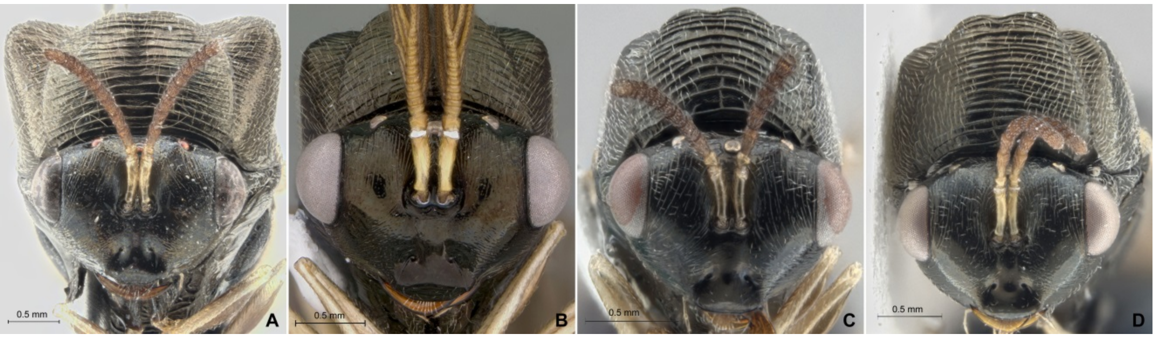


FIGURE 5.6.
Head and mesosoma, anterior view. A. *K. deltalis* holotype. B. *K. quasimodo*. C. *K. cuprea.* D. *K. parafurcata*. All measurement bars 0.5 mm.

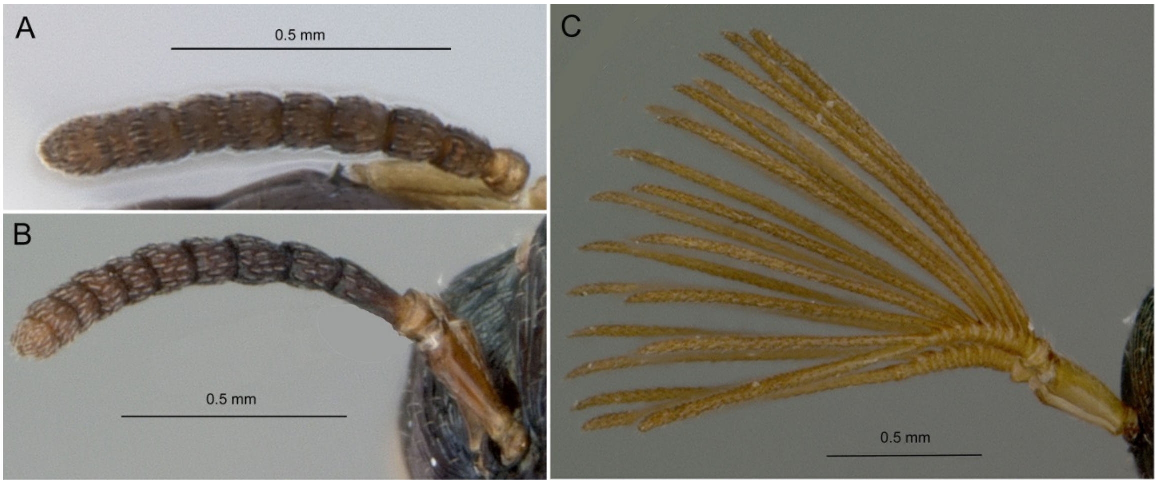


FIGURE 5.7.
Antennae. A. *K.* undet D2799 ♀, 9 flagellomeres. B. *K. furcata* ♀, 10 flagellomeres. C. *K. parafurcata* ♂, 10 flagellomeres, as in all *Kapala*. All measurement bars 0.5 mm.

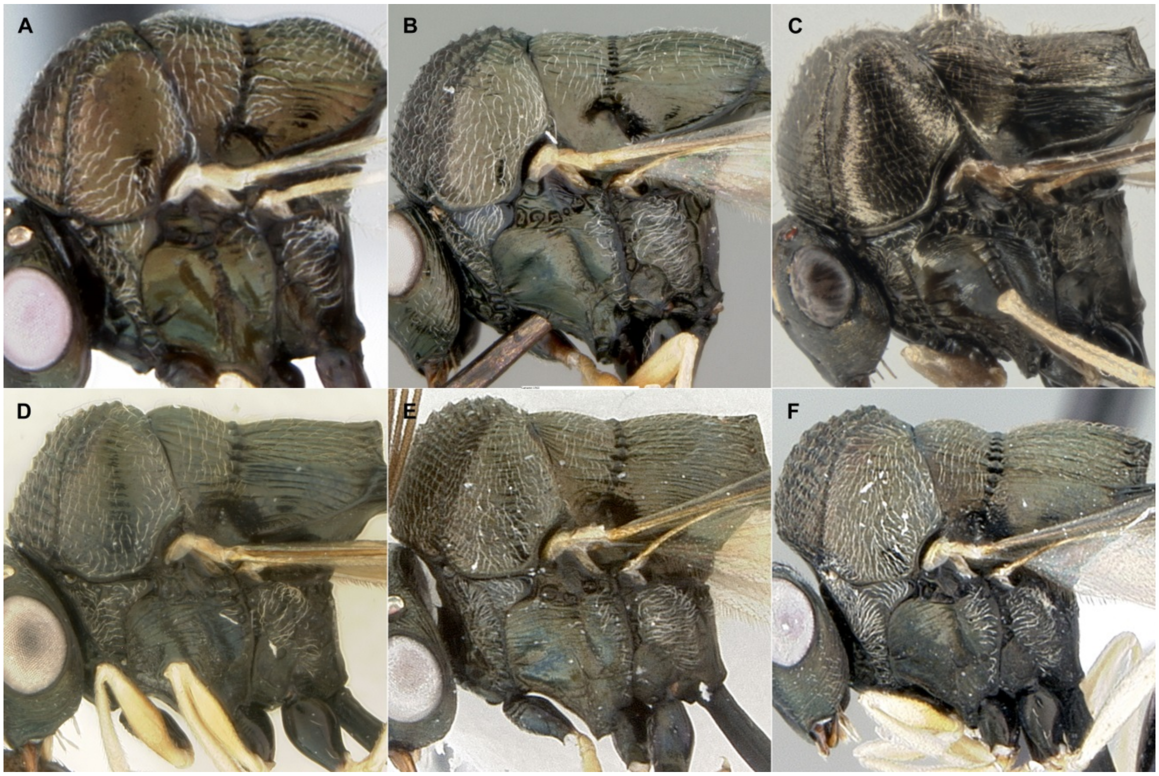


FIGURE 5.8.
Kapala furcata clade lateral habitus of mesosoma. A. *K.* undet D2799. B. *K. furcata*. C. *K. deltalis*. D. *K. quasimodo*. E. *K. parafurcata*. F. *K. cuprea*. All measurement bars 1.0 mm.

	Code	Character	Description
1	BDL	Body length	Lateral length of mesonotum at longest, from anterior point of midlobe to apex of scutellar spines
2	MSL	Mesonotum length	Lateral length of mesonotum not including the spines, from midlobe to apex of scutellum
3	HDH	Head height	Height measured from dorsal margin of median ocellus to median apex of clypeus
4	HDW	Head width	Distance across face at widest point from outer margins of eyes
5	IOD	Interocular distance	Distance between eyes measured across dorsal margin of eyes
6	EYH	Eye height	Vertical height of eye
7	MAL	Malar space	Length measured from ventral margin of eye to base of mandibles
8	FLG	Flagellum length	Female length of all flagellomeres from margin at pecicel to apex of club
9	FL2	Flagellomere 2 length	Length of F2 (female) or F2 ramus (male, not shown) of "first" flagellomere from lateral margin at pedicel to apex
10	FLW	Flagellomere 2 width	Width of flagellomere at apex, female only
11	FL3	Flagellomere 3 length	Length of F3 from dorsal margin at pedicel to apex, female only
12	SPL	Scape length	Measured from base to the apical margin
13	SPW	Scape width	Width measured at apex
14	MSH	Mesoscutum	Lateral height from anteriolateral ventral margin to dorsal margin at highest point
15	AXL	Axillar length	Dorsal length of axilla from TSA to scutoscutellar sulcus (SSS)
16	SCL	Scutellar length	Dorsal length of scutellum from SSS to apex between apical spines
17	SCW	Scutellar width	Width of scutellum at base of spines and between axillular carinae
18	SAH	Scutellum apex height	Lateral height of crest from dorsal base of spine to dorsal margin
19	SSH	Scutellar spine height	Lateral height of spine at base
20	SSL	Scutellar spine length	Dorsal length of apical scutellar spines, from medial point of spine base on frenal line
21	SSW	Scutellar spine width	Dorsal width across spine, taken after frenum fully merges into a cylindrical spine
22	SWW	Scutellar spine widest	Maximum inner distance between spines from dorsal view
23	SAW	Scutellar spine narrowest	Min imum inner distance between spines from dorsal view, at narrowest point at the apex
24	PTL	Petiole length	Dorsal length of petiole from flange at base to apex
25	PTW	Petiole width	Width of petiole across medial
26	C3L	Metacoxa length	Length of coxa from basal to apical margin
27	C3W	Metacoxa width	Width at widest point
28	F3L	Metafemur length	Length of femur from interiolateral view
29	F3W	Metafemur width	Width in center from interiolateral view
30	TGS	tergal scar	Recorded for presence or absence

TABLE 5.1.

Description of the measurements shown in Figure 5.1. Wing and male antennal illustrations are as in Heraty and Woolley (1993).

6. Conclusions

Eucharitid ant parasitoids are one of the few groups to successfully circumvent colony defense mechanisms and attack immature ants (Clausen, 1923; Ayre, 1962; Vander Meer *et al.*, 1989; Howard *et al.*, 2001; Buys *et al.*, 2010). Eucharitid species encompass many morphological forms and have successfully colonized five different ant subfamilies. In chapter 2, it is reported that despite the evidence for ancient ant host shifts, there is high host affinity and apparent ecological constraints maintaining host-specificity in the Eucharitidae.

The Kapala clade contains a remarkable amount of morphological diversity, and there are some groups where the evolutionary signal is obscured by bursts of phenotypic change, convergence, and retention of sympleisiomorphies by selected groups. Molecular data and a robust phylogeny are indispensable to help guide the interpretation of observed morphological characters. Often, conflicting molecular and morphological results lead to a redefinition of morphological characters and states or the recognition of new patterns of morphological diversity, as exhibited in chapter 3. The genus *Kapala* will have to be revised to reflect the updated hypothesis of genus-level variation and phylogenetic relationships. Additional molecular sampling from Brazil would also contribute to the analyses, if data were obtained. At this time, there is enough information content in the term *Kapala* that we are hesitant to split the group before having confidence in a stable topology.

Two targeted species groups within the Kapala clade were addressed for further analyses, in chapters 4 and 5. The Afrotropical species, *K. ivorensis*, is shown to be putatively the first insect example of a dispersal from South America to Africa. It is a widely distributed species with extremely little morphological variation, which supports its status as a single species, along with the phylogenetic reconstruction. Additionally, in chapter 4, phylogenetic relationships and geographic distributions of species in the furcata clade were established. Three new species were described and *K. furcata*, the type species, is redescribed. Both studies involved a combination of molecular and morphological data to support the conclusions.

More data should be gathered for the Kapala clade prior to making large-scale taxonomic revisions, due to the conflicting placement of some clades under different parameters. Several higher-level branches have low support and require further investigation. Variable topological results may be due to multiple factors, including those such as: the initial taxon sampling, the type of data collected, and how available data ties in the taxa having incomplete data (Wiens, 2006; Cho *et al.*, 2011; Wiens & Tiu, 2012), methodological choice, model specification and rate heterogeneity across sites, and the inclusion of ambiguous characters (Lemmon *et al.*, 2009; Wiens & Morrill, 2011), the number of unique site patterns in the sampled data (Drummond & Bouckaert, 2014),and the evolutionary process underlying site patterns, and the influential sites driving the results, including the distribution of the missing data or taxa (Roure *et al.*, 2013; Shavit Grievink *et al.*, 2013). The effects of missing data in phylogenetic reconstruction has been under scrutiny for a number of years, prompting studies employing empirical and simulated data, though there is not a clear consensus on the impacts of inclusion incomplete data (Lemmon *et al.*, 2009; Wiens & Morrill, 2011; Roure *et al.*, 2013), some of which may be expected owning to the variability across datasets and conditions. In the case of the Kapala clade, potentially what is needed is to sample more gene regions. Future studies incorporating additional genomic information will potentially aid in establishing boundaries.

Delineating species boundaries is crucial to the discovery of biodiversity (Dayrat, 2006), while implicit in this expression of biodiversity is the necessity of consideration of variation within and among species. The amount of molecular and morphological intra- and interspecific variation in the Kapala clade is an interesting question to be addressed in the future. The framework of the comprehensive phylogenies of Eucharitidae and the Kapala clade will aid in encouraging future research on the group.

7. Supplementary Information

7.1 Chapter 2

DNA extraction, sequencing, and alignment:

Fresh or dried museum specimens were utilized for DNA extraction. Chelex + proteinase-K extractions were performed (Walsh *et al.*, 1991) 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 10µL reaction contained: 2.0 µL buffer, 0.4µL dNTPs, 0.5µL forward and reverse primer, 0.5µL Taq polymerase, 4.0µL Q solution [replaced with water in COI & COII reactions], and 11.2µL water. PCR profiles followed the format: 3 min at 93ºC, 35 cycles of 93ºC for 15 sec, 46ºC for 45 sec, and 68ºC for 45 sec, ending with 68ºC 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 (Katoh *et al.*, 2005) 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 (Vaidya *et al.*, 2011) 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 (Posada, 2008). 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) under collection reference number 816728. 482 new sequence fragments were deposited in Genbank; accession numbers are found in Table S2.

Ancestral Area Reconstruction

LAGRANGE (Ree *et al.*, 2005; Ree & Smith, 2008) dispersal constraints. Dispersal constraints over four time periods were constructed based on historic landmass distribution (Scotese, 2003). No probabilities are below 0.5, as these constraints were not intended to be entirely prohibitive.

<u>**Geographic Areas**</u>
1 = North and Central America and Caribbean Islands

2 = South America, including Lesser Antilles

3 = Ethiopian

4 = Malagasy

5 = Palearctic

6 = Indo-Pacific

7 = Australian

0-10 mya

	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]
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]
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]]

10-30 mya

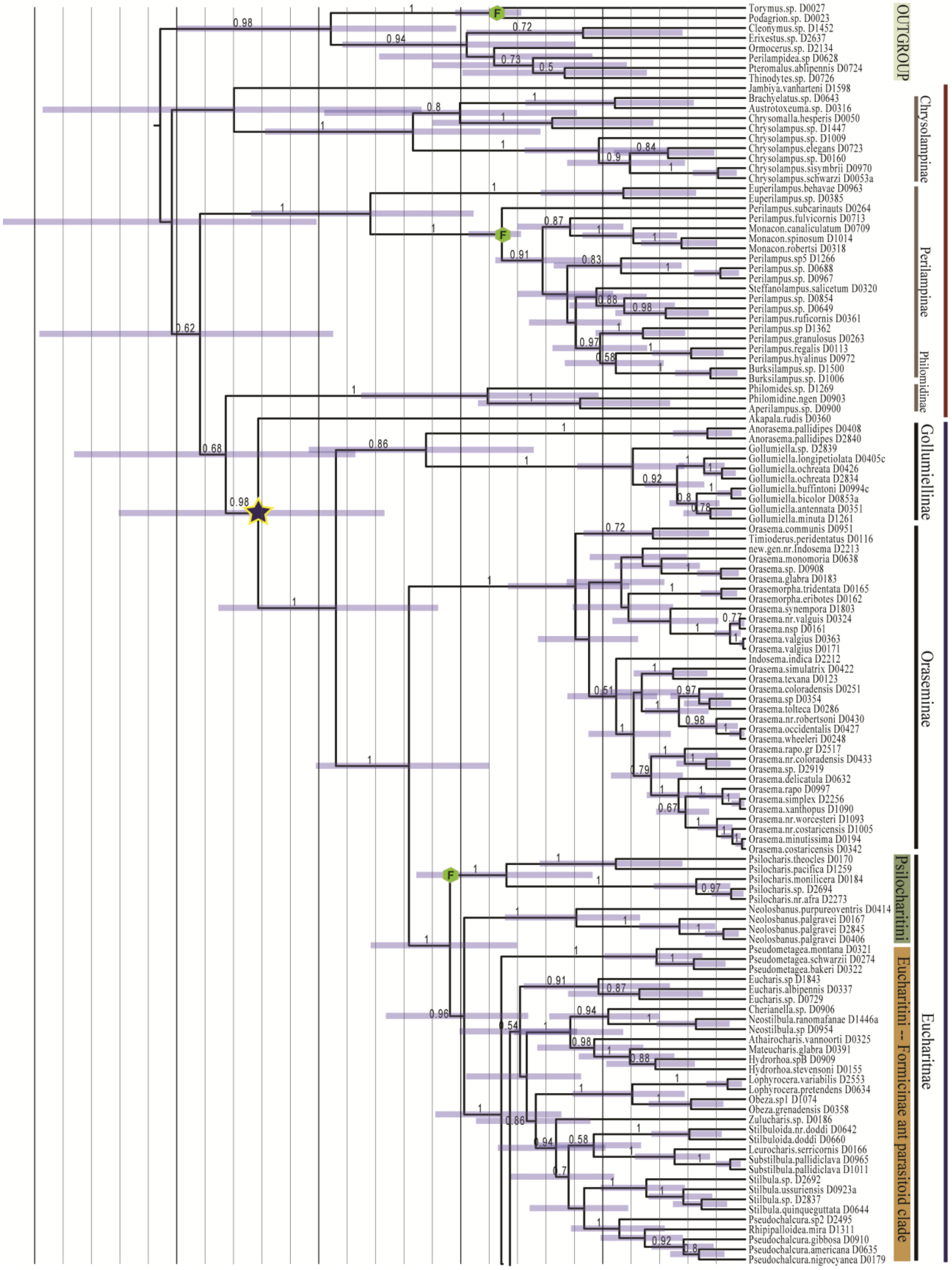
	1	2	3	4	5	6	7
1	[[1.0,	0.75,	0.5,	0.5,	0.75,	0.5,	0.5]
2	[0.75,	1.0,	0.5,	0.5,	0.5,	0.5,	0.5]
3	[0.5,	0.5,	1.0,	1.0,	1.0,	0.75,	0.75]
4	[0.5,	0.5,	1.0,	1.0,	0.75,	0.75,	0.75]
5	[0.75,	0.5,	1.0,	0.75,	1.0,	1.0,	0.75]
6	[0.5,	0.5,	0.75,	0.75,	1.0,	1.0,	0.75]
7	[0.5,	0.5,	0.75,	0.75,	0.75,	0.75,	1.0]]

30-65 mya

	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]]

65-101 (root) mya

	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]]



Continued next page

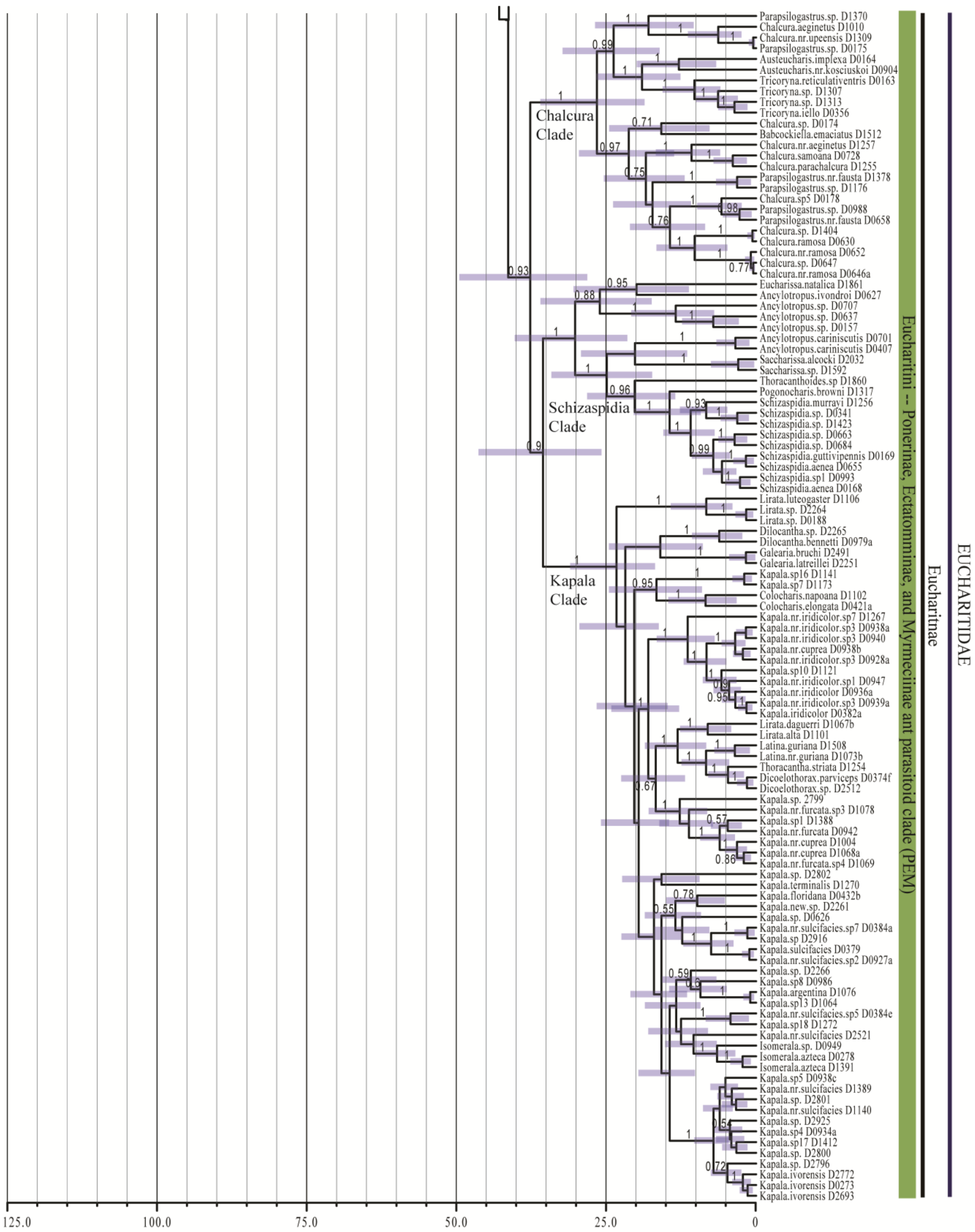


Figure S2.1. Fossil-calibrated phylogeny of Eucharitidae, as shown in Fig. 2.1. 237 taxa analyzed, 95% highest posterior density error bars shown in blue. Posterior probability support shown above branches. Starred node indicates Eucharitidae origin, 'F' symbol indicates fossil placement. Taxonomic groups shown on right. Taxa localities found in Table S2.

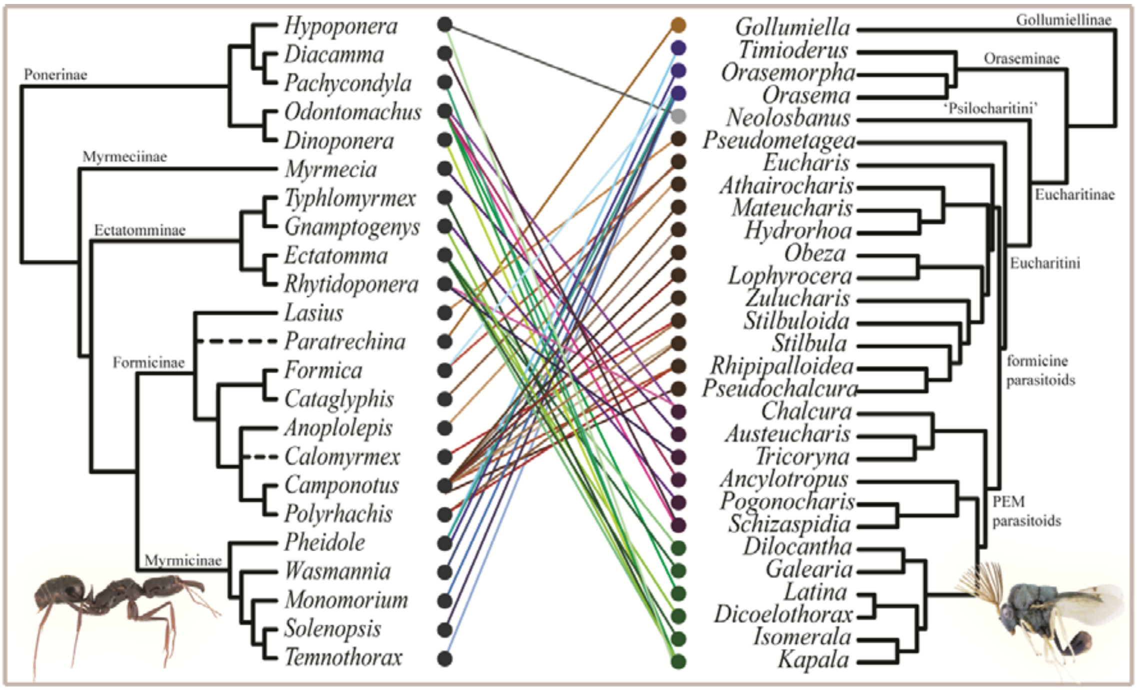


Figure S2.2. Host-parasitoid taxonomic associations. Tanglegram of 29 eucharitid genera and 23 formicid genera (Table S1). Formicidae cladogram on left adapted from Moreau et al. (Moreau *et al.*, 2006), ant image from antweb.org. *Paratrechina* and *Calomyrmex* placement was estimated (dashed line) 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.

wasp subfamily	wasp genus	ant genus	ant subfamily	references
Gollumiellinae	*Gollumiella*	*Nylanderia*	Formicinae	(Heraty *et al.*, 2004)
Oraseminae	*Orasema*	*Formica*	Formicinae	(Johnson *et al.*, 1986)
		Monomorium	Myrmicinae	(Heraty, 2000)
		Pheidole	Myrmicinae	(Wheeler, 1907; Girault, 1913; Gemignani, 1933; Wheeler & Wheeler, 1937; Gahan, 1940; Clausen, 1941; van Pelt, 1950; Das, 1963; Kerrich, 1963; Heraty, 1994a; Heraty, 1994b; Heraty, 2000; Carey *et al.*, 2012)
		Solenopsis	Myrmicinae	(Wheeler, 1907; Wheeler & Wheeler, 1937; Wojcik, 1989; Heraty *et al.*, 1993; Heraty, 1994a; Varone & Briano, 2009; Varone *et al.*, 2010)
		Temnothorax	Myrmicinae	(Heraty, 1994b, 2002; Lachaud & Pérez-Lachaud, 2012)
		Wasmannia	Myrmicinae	(Mann, 1918; Heraty, 1994b)
	Orasemorpha	*Pheidole*	Myrmicinae	(Brues, 1934; Bouček, 1988; Heraty, 1994a)
	Timioderus	*Pheidole*	Myrmicinae	(Heraty, 2000)
Eucharitinae	*Ancylotropus*	*Odontomachus*	Ponerinae	(Heraty, 2002)
	Athairocharis	*Anoploepsis*	Formicinae	(Heraty, 2002)
	Austeucharis	*Myrmecia*	Myrmeciinae	(Cameron, 1891; Brues, 1919; De Santis, 1968)
	Chalcura	*Rhytidoponera*	Ectatomminae	(Dodd, 1906; Heraty, 1994a; Heraty, 2002)
		Odontomachus	Ponerinae	(Dodd, 1906; Clausen, 1941; Heraty, 2002)
	Dicoelothorax	*Ectatomma*	Ectatomminae	(Torrens & Heraty, 2012)
	Dilocantha	*Ectatomma*	Ectatomminae	(Lachaud *et al.*, 1998; Lachaud & Pérez-Lachaud, 2001; Pérez-Lachaud *et al.*, 2006a)
	Eucharis	*Cataglyphis*	Formicinae	(Cameron, 1891; Bouček, 1956)
		Formica	Formicinae	(Clausen, 1941)
	Galearia	*Ectatomma*	Ectatomminae	(Torréns, 2011)
	Hydrorhoa	*Camponotus*	Formicinae	(Heraty, 2002)
	Isomerala	*Ectatomma*	Ectatomminae	(Bouček, 1956; Lachaud & Pérez-Lachaud, 2001; Pérez-Lachaud *et al.*, 2006a)
	Kapala	*Ectatomma*	Ectatomminae	(Lachaud & Pérez-Lachaud, 2001; Pérez-Lachaud *et al.*, 2006b; Pérez-Lachaud *et al.*, 2006a; Lachaud *et al.*, 2012; Vásquez-Ordóñez *et al.*, 2012)
		Gnamptogenys	Ectatomminae	(Dodd, 1906; Lachaud & Pérez-Lachaud, 2001; de la Mora & Philpott, 2010; Lachaud *et al.*, 2012)
		Typhlomyrmex	Ectatomminae	(de la Mora & Philpott, 2010)
		Dinoponera	Ponerinae	(Buys *et al.*, 2010)
		Hypoponera	Ponerinae	(de la Mora & Philpott, 2010)
		Odontomachus	Ponerinae	(Clausen, 1941; Heraty, 2002; de la Mora & Philpott, 2010; Lachaud *et al.*, 2012)
		Pachycondyla	Ponerinae	(Bouček, 1956; Lachaud & Pérez-Lachaud, 2001; Heraty, 2002; de la Mora & Philpott, 2010; Lachaud *et al.*, 2012)
	Latina	*Odontomachus*	Ponerinae	(Torréns, 2011)

	Lophyrocera	*Camponotus*	Formicinae	(Gemignani, 1933)
	Mateucharis	*Camponotus*	Formicinae	(Heraty, 2002)
	Neolosbanus	*Hypoponera*	Ponerinae	(Heraty, 1994a)
	Obeza	*Camponotus*	Formicinae	(Davis Jr. & Jouvenaz, 1990)
	Pogonocharis	*Gnamptogenys*	Ectatomminae	(Heraty, 2002)
	Pseudochalcura	*Camponotus*	Formicinae	(Wheeler, 1907; Heraty, 1986; Heraty & Barber, 1990; Heraty *et al.*, 2009)
	Pseudometagea	*Lasius*	Formicinae	(Ayre, 1962)
	Rhipipalloidea	*Camponotus*	Formicinae	(Maeyama *et al.*, 1999)
		Polyrachis	Formicinae	(Heraty, 2002)
	Schizaspidia	*Gnamptogenys*	Ectatomminae	(Heraty, 1994a)
		Diacamma	Ponerinae	museum specimen
		Odontomachus	Ponerinae	(Clausen, 1941; Heraty, 1994a; Heraty, 2002)
	Stilbula	*Camponotus*	Formicinae	(Clausen, 1923; Parker, 1932; Clausen, 1941)
		Polyrhachis	Formicinae	(Wheeler, 1924; Bouček, 1988)
	Stiluboida	*Calomyrmex*	Formicinae	(Brues, 1934)
		Camponotus	Formicinae	(Dodd, 1906)
	Tricoryna	*Rhytidoponera*	Ectatomminae	(Brues, 1934; Heraty, 1994a)
	Zulucharis	*Camponotus*	Formicinae	(Heraty, 2002)

Table S2.1. Eucharitidae ant hosts.

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

Table S2.2. List of taxa, ID codes, and Genbank accession numbers. Accessions with prefix 'KC' were added from this study. Family abbreviations: 'Ptero'=Pteromalidae, 'Peri'=Perilampidae, and 'Euch'=Eucharitidae.

Table S2.2 continued

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

Table S2.**2** **c**ontinued

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

Table S2.2 continued

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

Table S2.2 continued

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

	mean	95% HPD
Eucharitidae origin (stem)	85.7	63.4-110.2
Eucharitidae (crown)	72.0	53.9-92.6
Gollumiellinae	56.2	37.1-76.7
Oraseminae	29.9	20.3-41.6
New World clade	19.6	13.0-27.5
Eucharitinae	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 S2.3. Mean minimum age of major eucharitid clades and the 95% highest posterior density range, in millions of years.

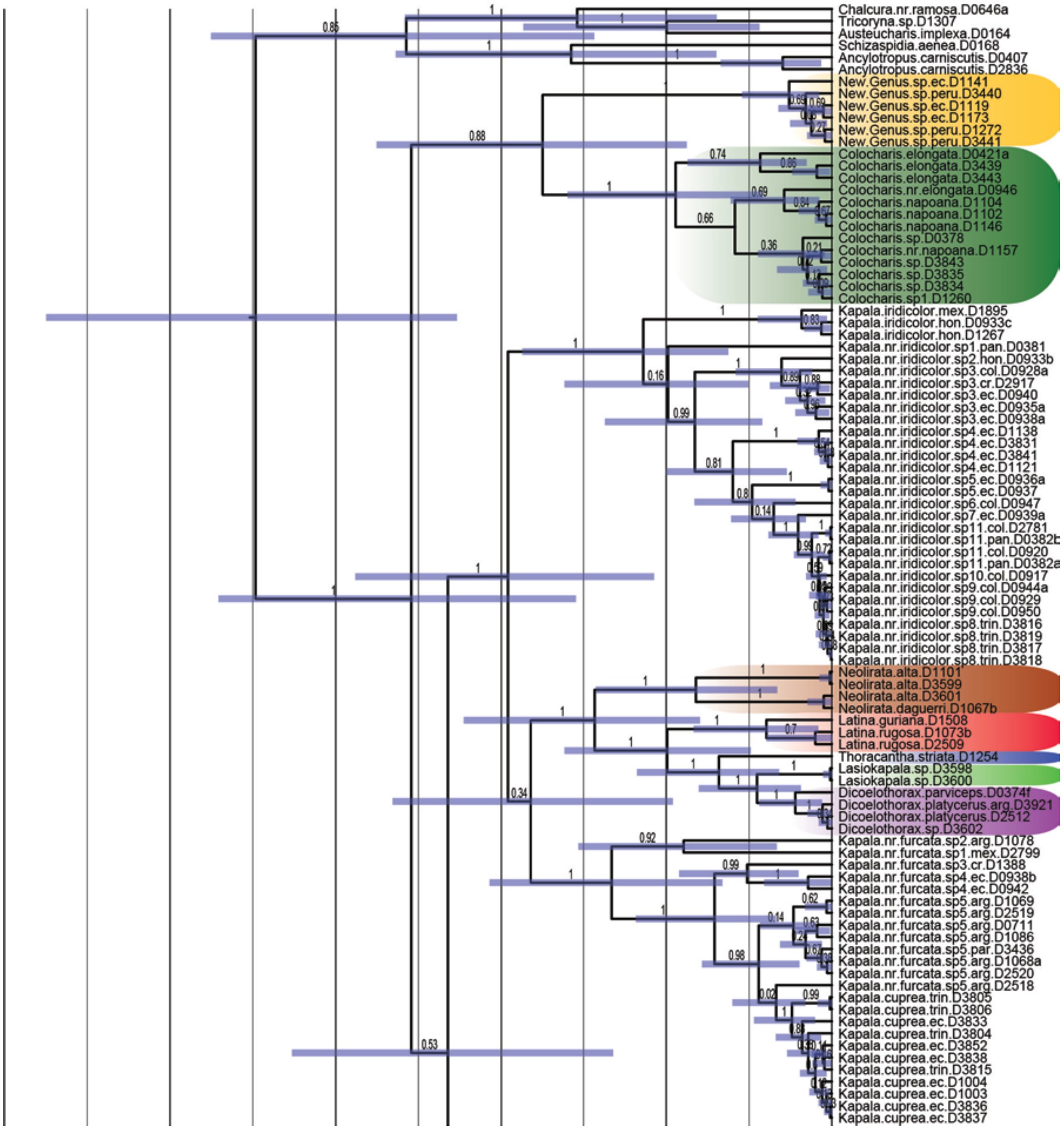
	aligned length	% taxa complete	parsimony-inf. sites **%**	constant sites **%**	AIC model	Analysis partition
18S	780	71.3	7.4	89.0	GTR+G	1
28S-D2	680	99.6	43.6	47.4	HKY+G	2
28S-D3-D5	613	98.7	17.7	73.7	HKY+G	2
COI	780	67.9	41.5	49.5	GTR+G	3
pos 1 & 2	520		20.6	70.2	n/a	
pos 3	258		84.1	8.1	n/a	
COII	258	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 S2.4. Gene regions utilized and summary statistics. Partition 3 employed a codon model ((1+2),3), recommended by Brandley *et al.* (2011).

gene	**primer**	**sequence**	**references**
18S			
	18S F (mid)	5'-AAA TTA CCC ACT CCC GGC A-3'	(Munro *et al.*, 2011)
	18S R (mid)	5'-TGG TGA GGT TTC CCG TGT T-3'	(Munro *et al.*, 2011)
	18Si F (inside mid)	5'-ATC GCT CGC GAT GTT TAA CT-3'	(Heraty *et al.*, 2004)
	18Si R (inside mid)	5'-AGA ACC GAG GTC CTA TTC CA-3'	(Heraty *et al.*, 2004)
	18S1 F (5' end)	5'-TAC CTG GTT GAT CCT GCC AGT-3'	(Ouvrard *et al.*, 2000)*
	18S4 R (5' end)	5'-GAA TTA CCG CGG CTG CTG G-3'	(Schulmeister, 2003)
	18Sa F (3' end)	5'-ATG GTT GCA AAG CTG AAA C-3'	(Schulmeister, 2003)
	18S9 R (3' end)	5'-GAT CCT TCC GCA GGT TCA CCT-3'	(Ouvrard *et al.*, 2000)*
28S D2			
	D2-3551 F	5’-CGG GTT GCT TGA GAG TGC AGC-3’	(Campbell *et al.*, 2000)*
	D2Ra R	5’-CTC CTT GGT CCG TGT TTC-3’	(Campbell *et al.*, 2000)*
28S D3-5			
	D3-4046 F	5’-TTG AAA CAC GGA CCA AGG AG-3’	(Nunn *et al.*, 1996)*
	D3-4413 R	5'-TCG GAA GGA ACC AGC TAC TA-3'	(Nunn *et al.*, 1996)*
	D5-4625 R	5’-CGC CAG TTC TGC TTA CCA-3’	(Schulmeister, 2003)*
COI			
	COI-NJ F	5’-TAT ATT TTA ATT YTW CCW GGA TTT GG-3’	(Simon *et al.*, 1994)*
	COI-MD R	5’-ATT GCA AAT ACT GGA CCT AT-3’	(Dowton & Austin, 1997)*
COII			
	COII-MTD16 F	5’-ATT GGA CAT CAA TGA TAT TGA-3’	(Simon *et al.*, 1994)
	COII-MTD18 R	5’-CCA CAA ATT TCT GAA CAT TGA CCA-3’	(Dowton & Austin, 1997)

Table S2.5. Primer oligonucleotides used in this study. Sequences marked with an ‘*’ have been modified from the original reference publication.

7.2 Chapter 3



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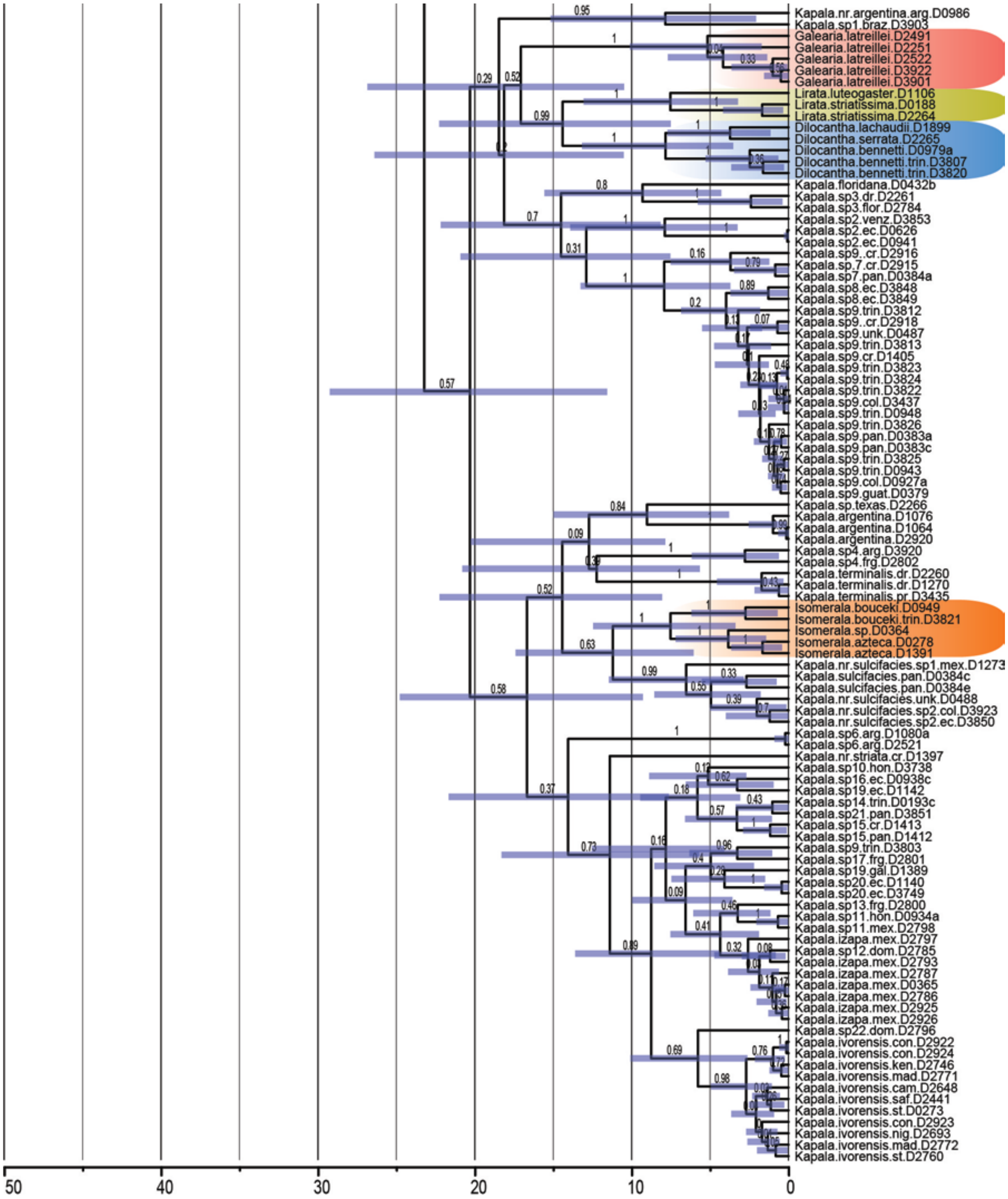

Figure S3.1. Dated phylogeny of all taxa. Genera are highlighted. Blue bars indicate the 95% highest posterior density values for the nodes. Node heights are the calculated median ages after burnin.

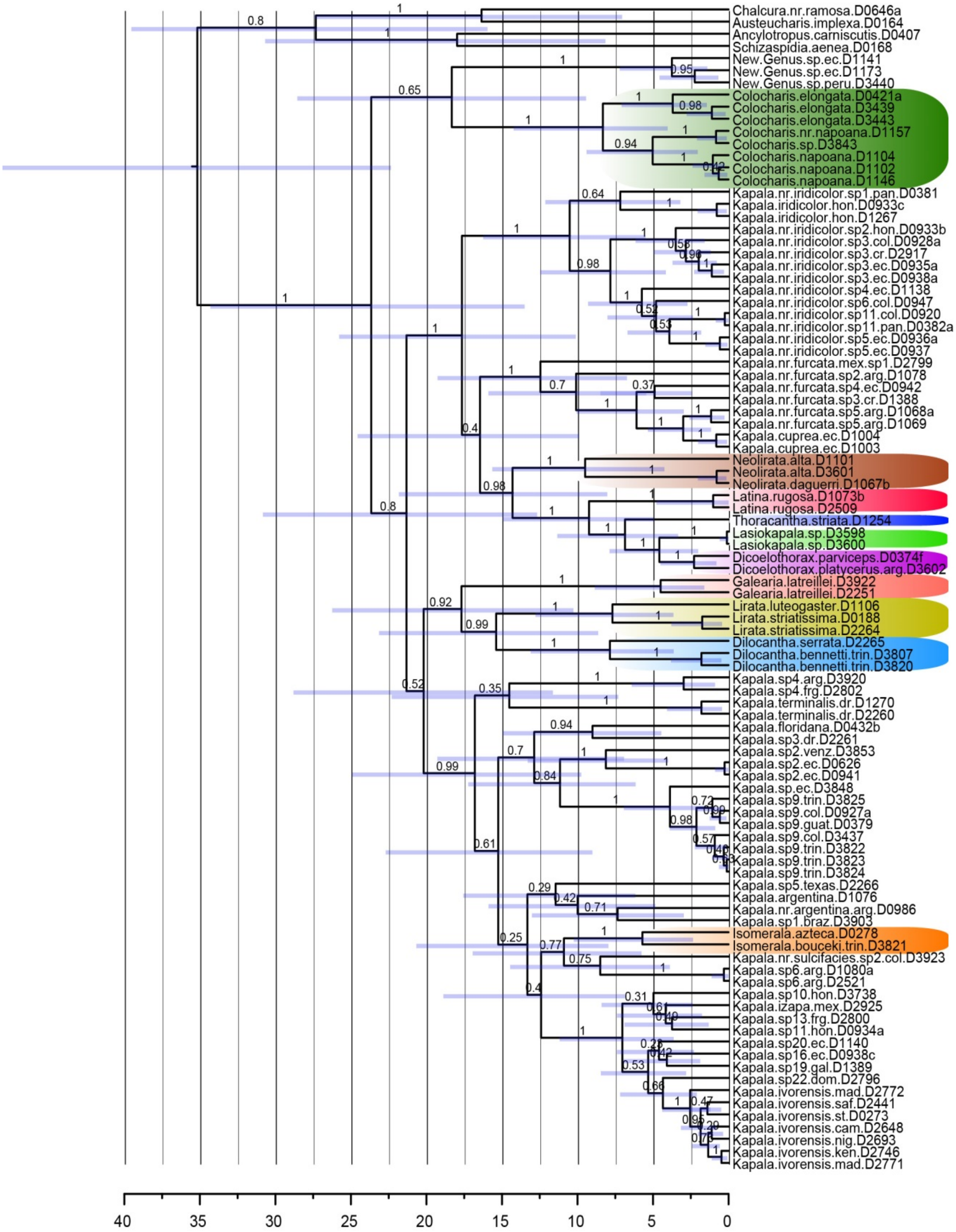

Figure S3.2. Dated phylogeny of taxa with complete genes. Genera are highlighted. Blue bars indicate the 95% highest posterior density values for the nodes. Node heights are the calculated median ages after burnin.

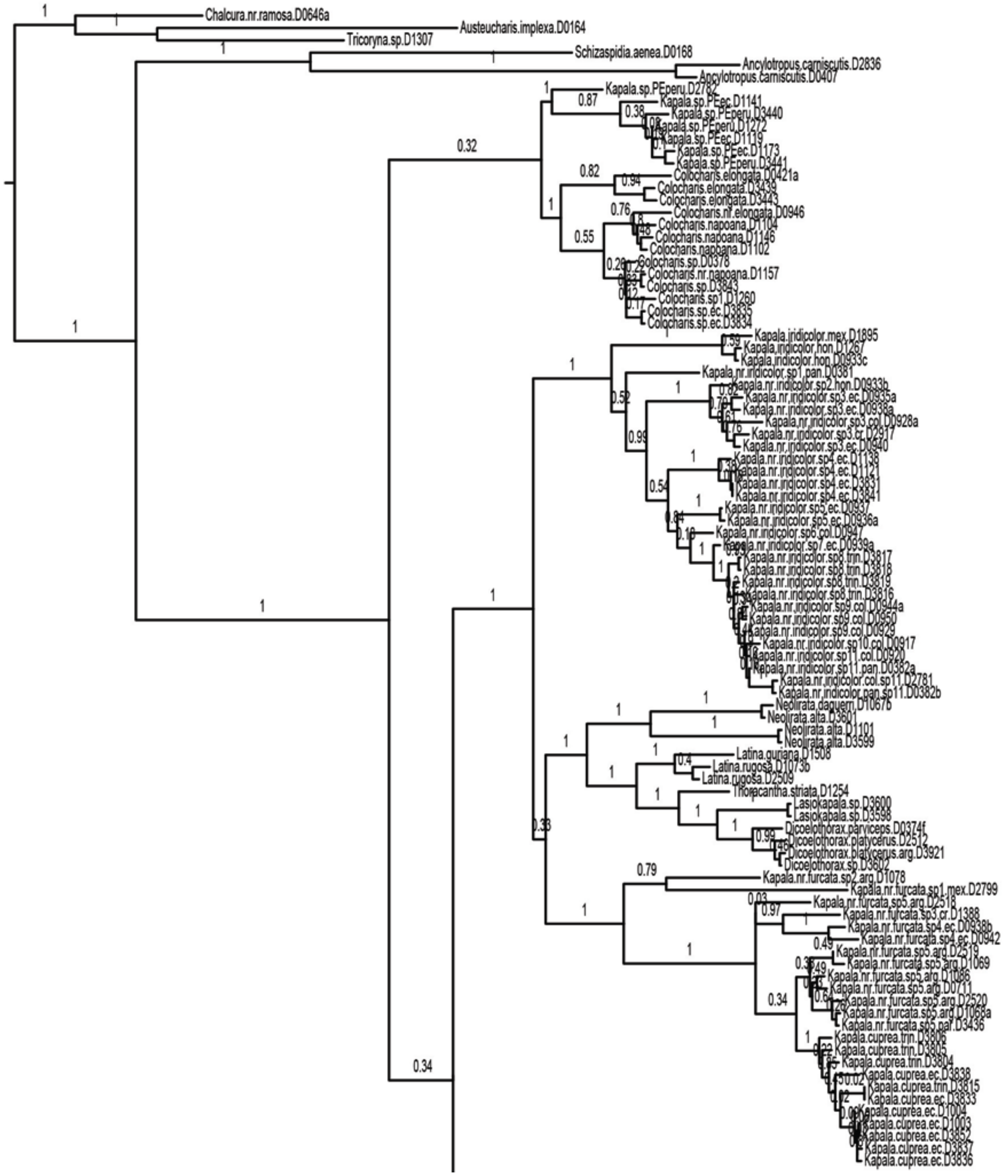

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Figure S3.3. Bayesian phylogeny of all 195 taxa. Maximum clade credibility tree shown.

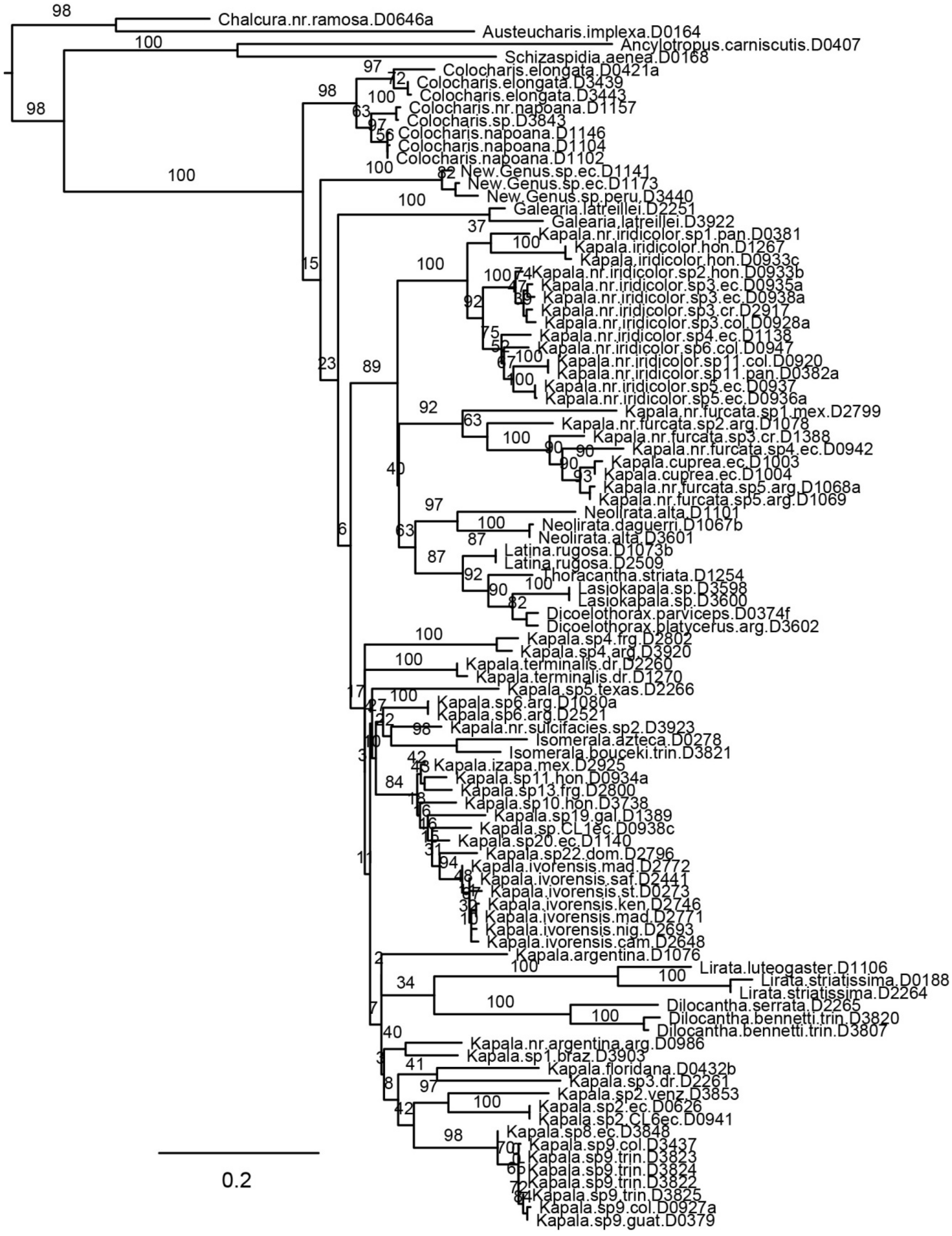

Figure S3.4. RAxML phylogeny of 96 taxa.

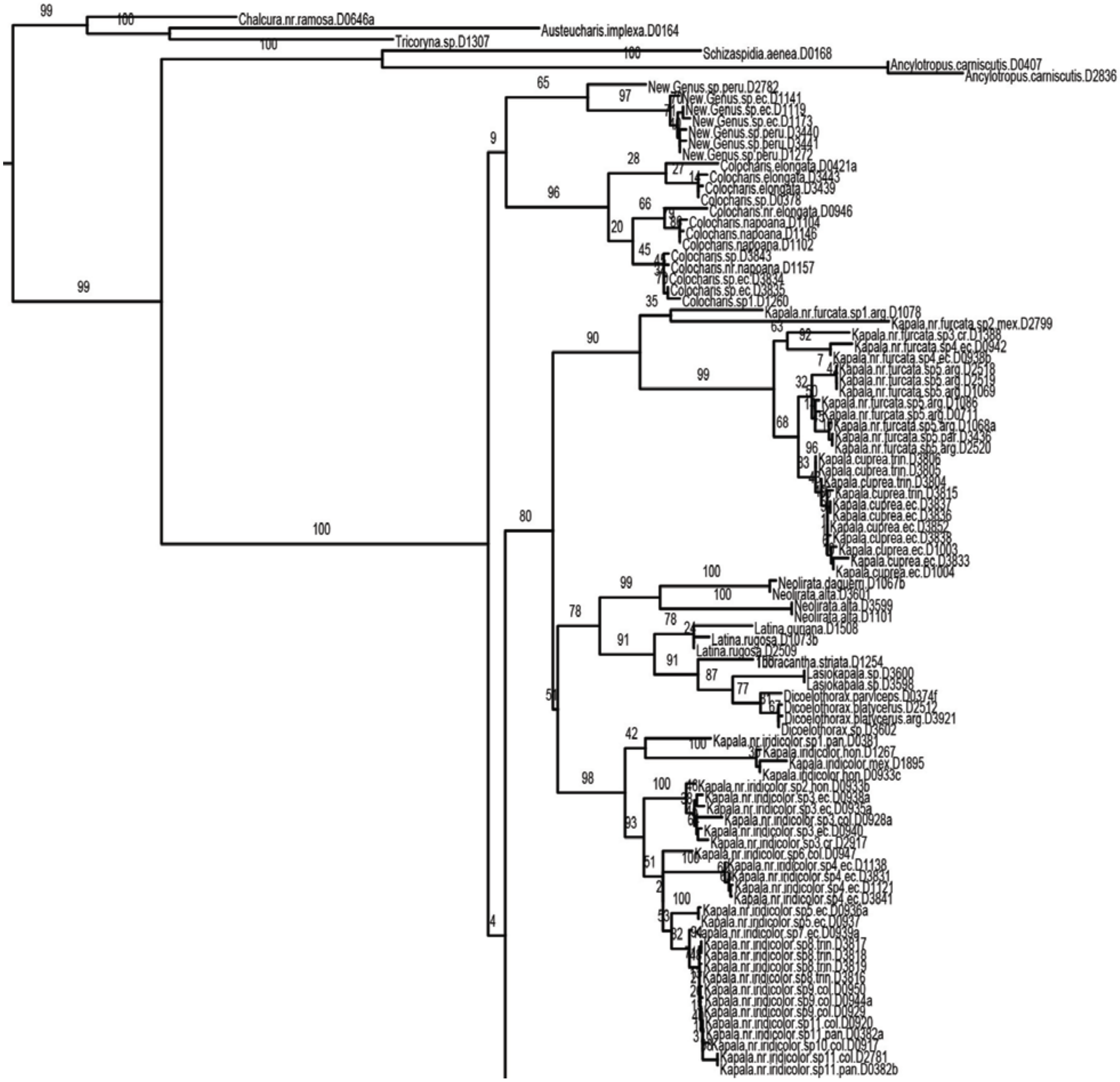

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Figure S3.5. RAxML phylogeny of 195 taxa.

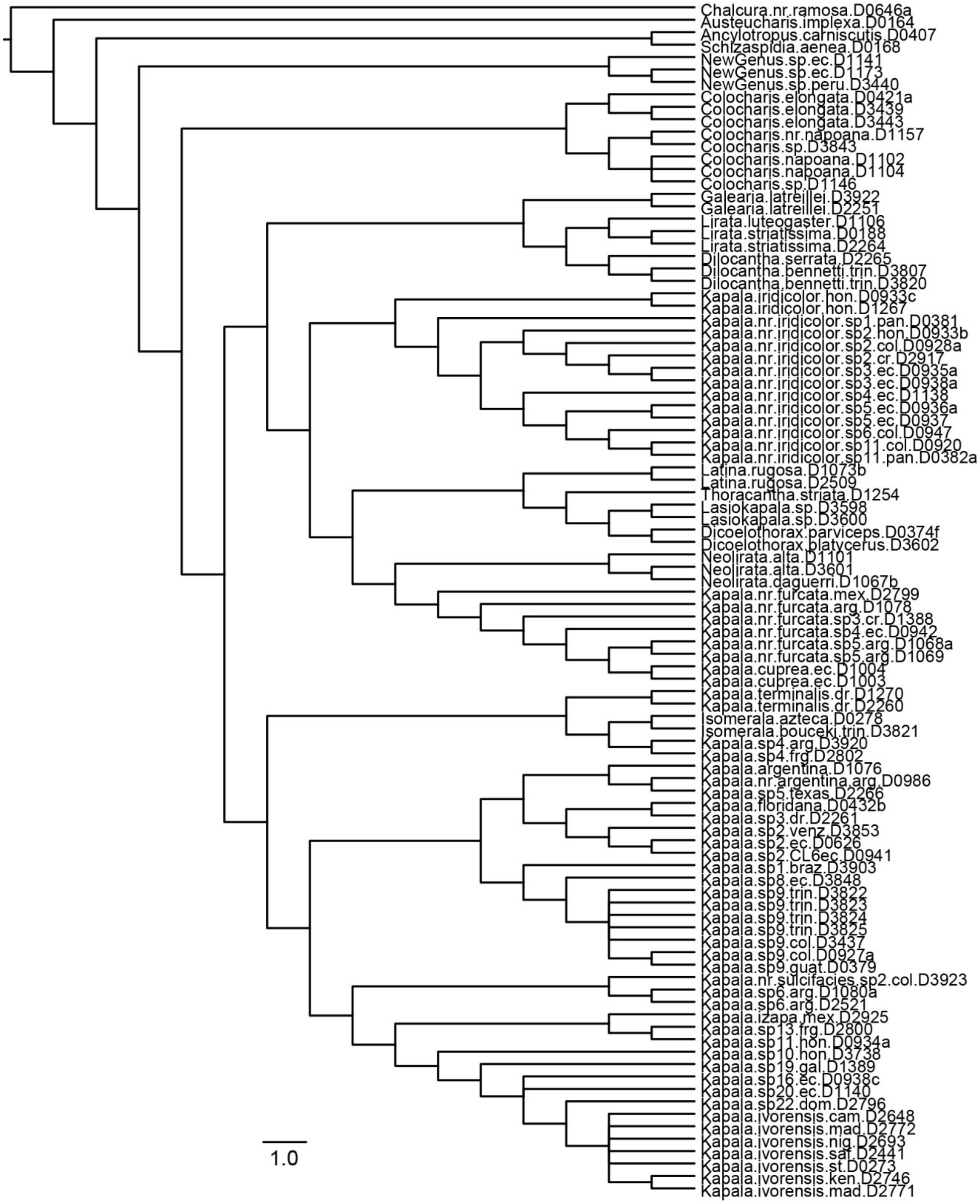

Figure S3.6. Parsimony analysis of 96 taxa molecular dataset under equal weights. Results are shown as a 50% majority rule tree. Retention index = 0.683, consistency index = 0.357.

Figure S3.7. Combined molecular and morphological tree using Bayesian inference.

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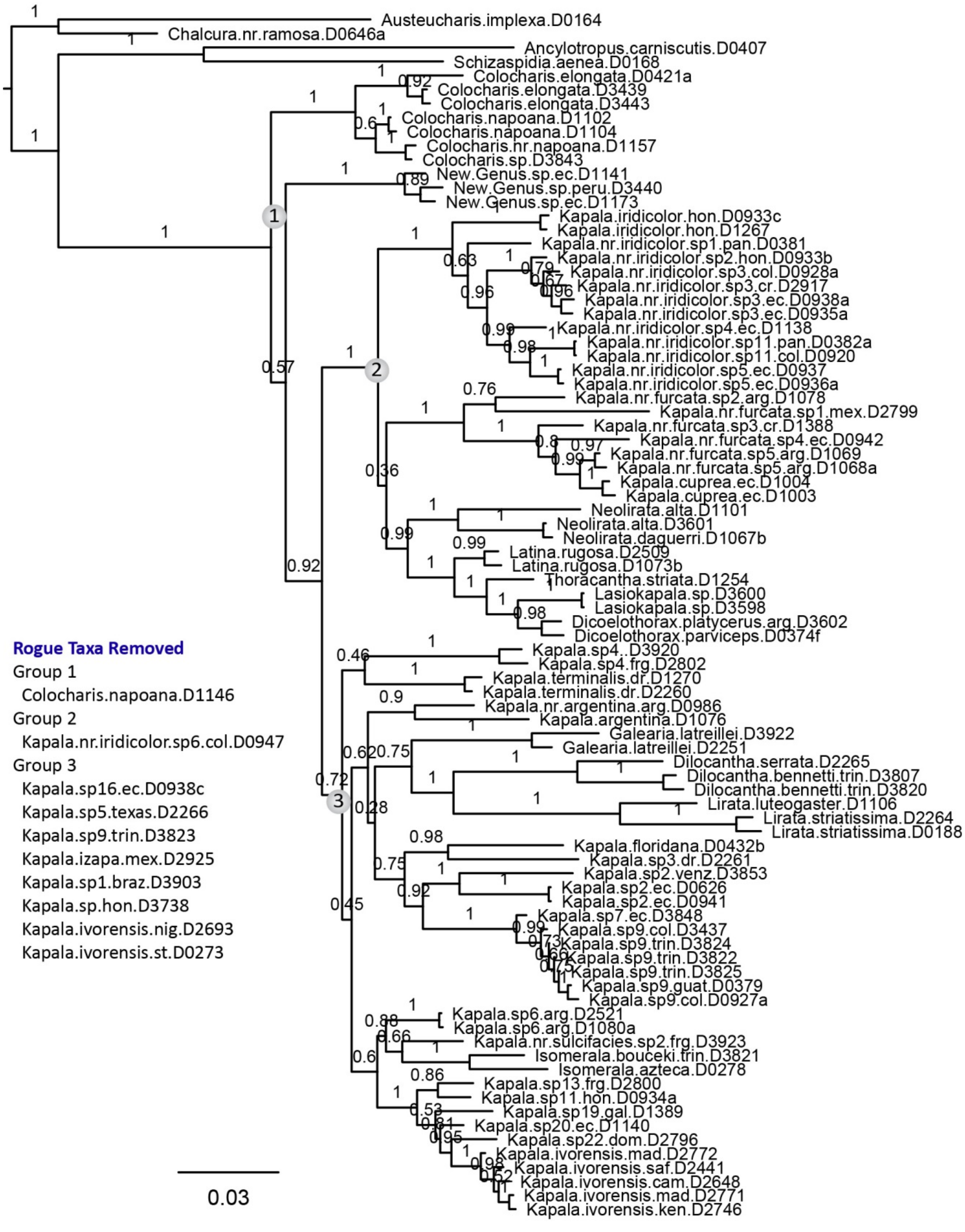
Figure S3.8. *Galearia* removed from the 'all taxa' dataset, leaving 190 taxa. Bayesian maximum clade credibility tree shown.

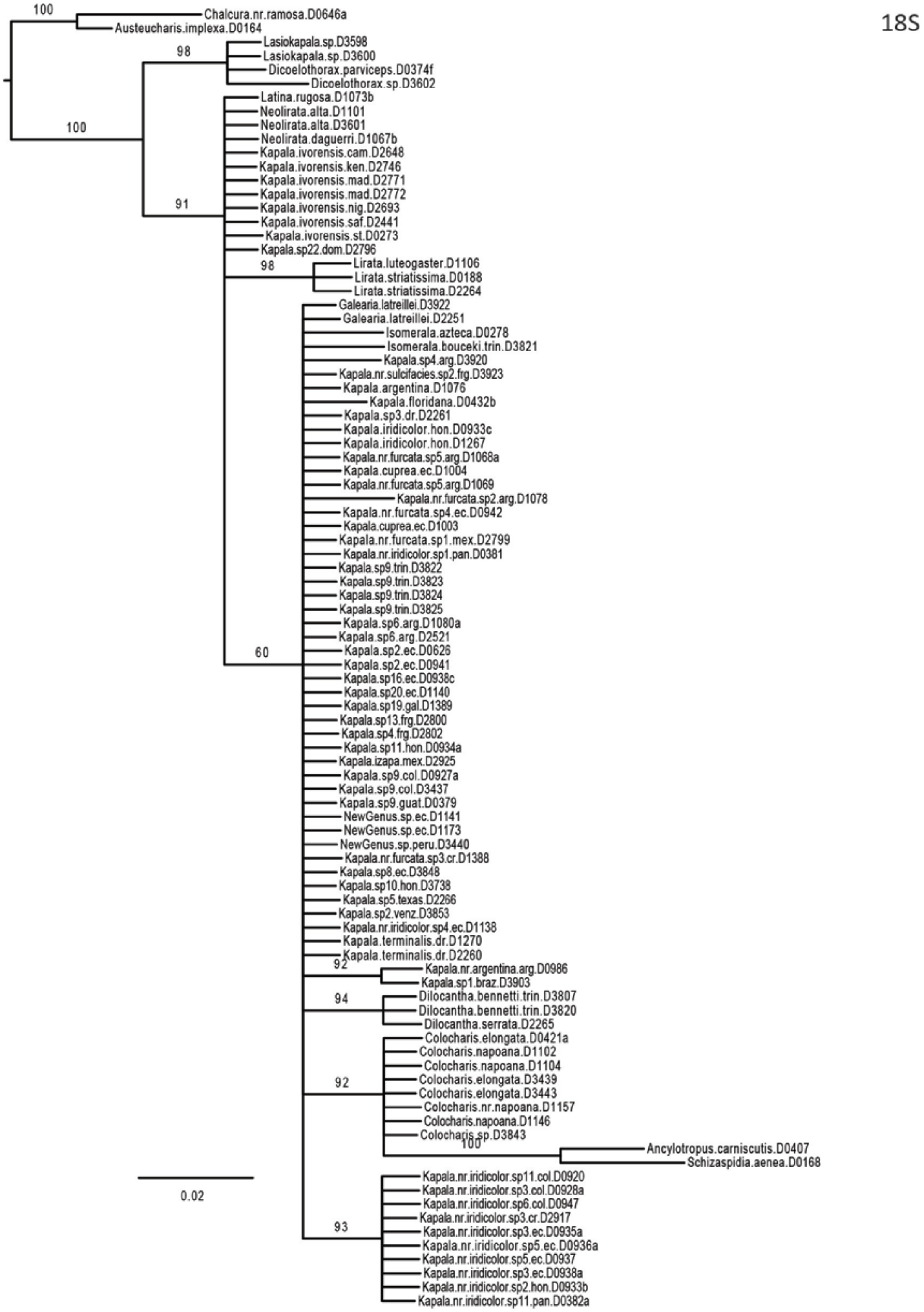


Rogue Taxa Removed

Group 1
  Colocharis.napoana.D1146
Group 2
  Kapala.nr.iridicolor.sp6.col.D0947
Group 3
  Kapala.sp16.ec.D0938c
  Kapala.sp5.texas.D2266
  Kapala.sp9.trin.D3823
  Kapala.izapa.mex.D2925
  Kapala.sp1.braz.D3903
  Kapala.sp.hon.D3738
  Kapala.ivorensis.nig.D2693
  Kapala.ivorensis.st.D0273

Figure S3.9. Complete genes dataset trimmed of the 10 taxa suggested by RogueNaRok, leaving 86 taxa. Bayesian maximum clade credibility phylogeny.

Note: Figure 3.10 is distributed onto the following five pages.



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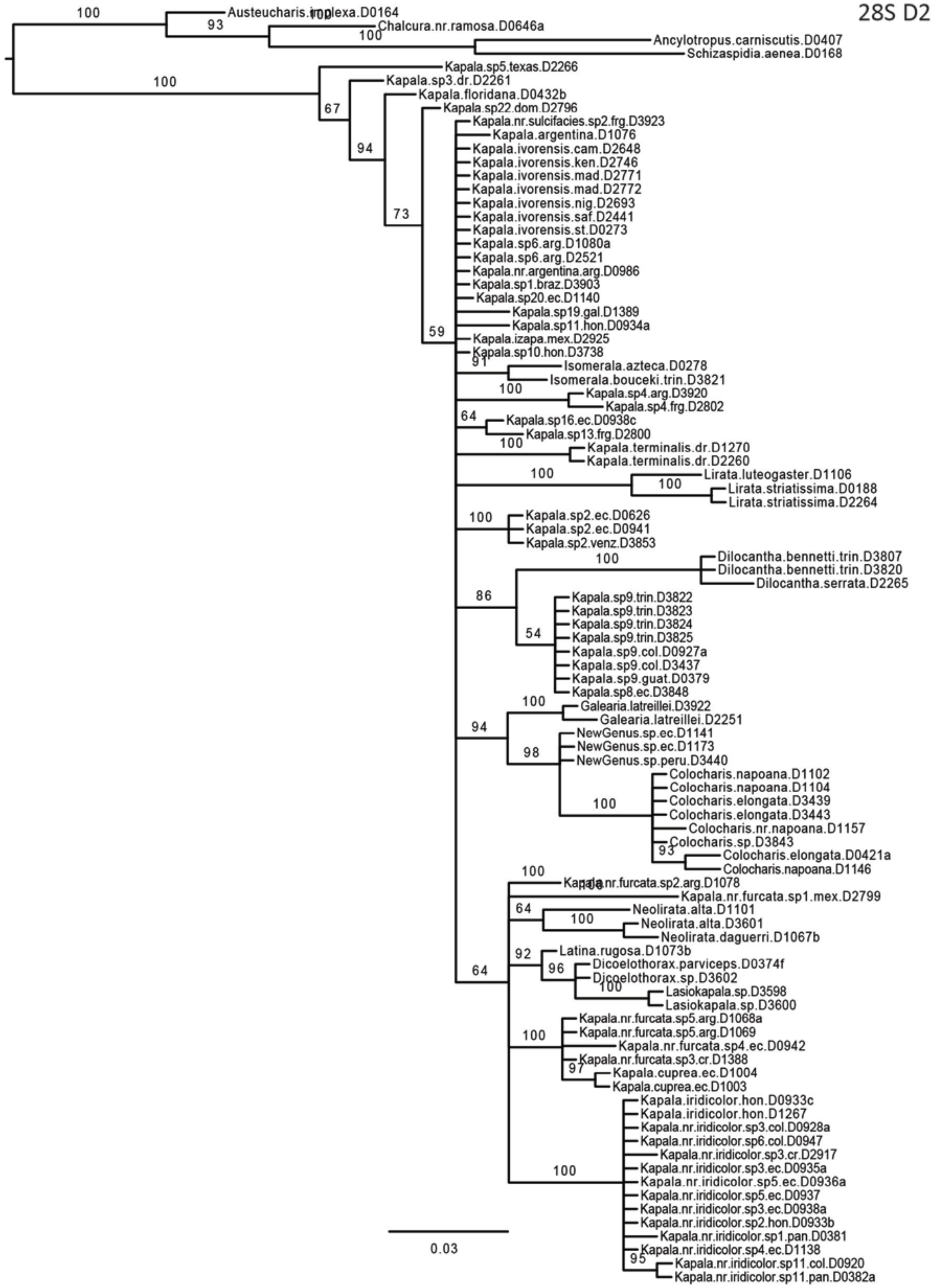

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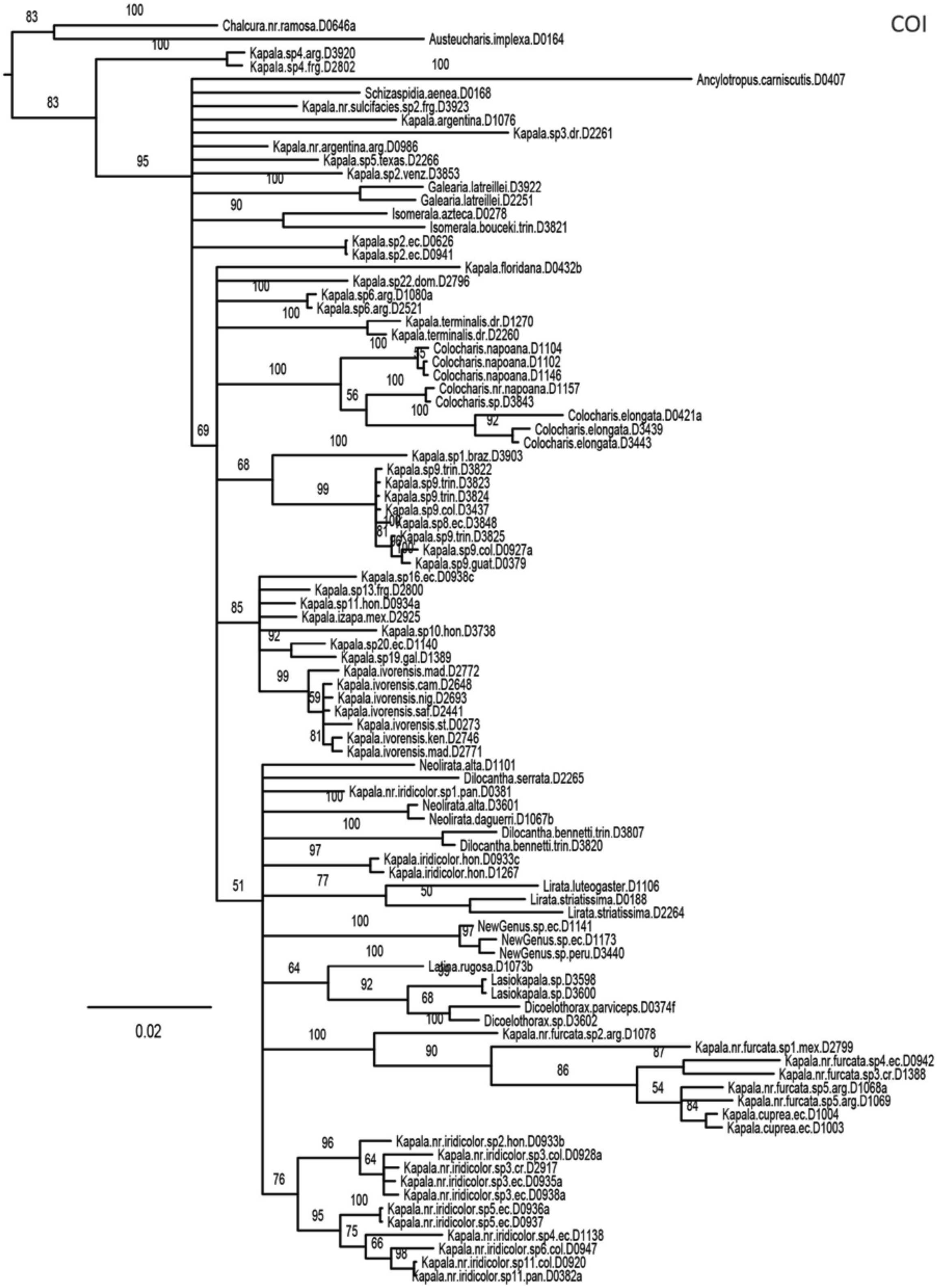

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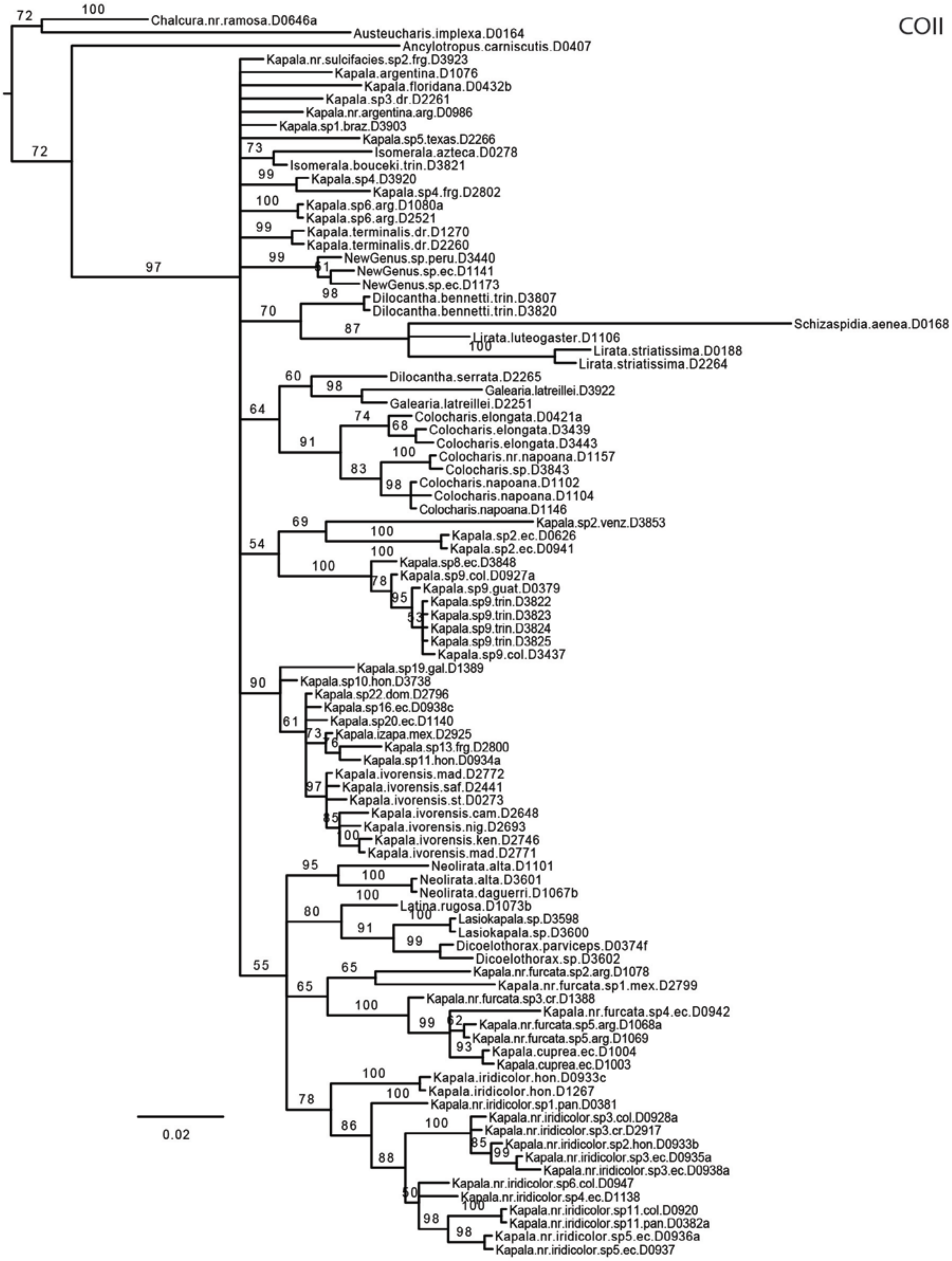

Fig. S3.10. Individual gene analyses (from the 96 taxa dataset) under Bayesian inference. The 50% majority rule trees are shown.

		clade	genus	species	DNA ID	Specimen identifier	museum	sex	locality
1	OG	Chal	Austeucharis	implexa	0164	UCRC_ENT 00091767	UCRC	♂	Australia: SA: Mt. Barker , 511m 35°03'51"S 138°51'29"E 22-23.Jan.1999 J. Heraty Eucalyptus scrub H99/024a
2	OG	Chal	Chalcura	ramosa	0646a	UCRC_ENT 00091769	UCRC	♀	Australia: NT: W. of Alice Spr. 3 km E Ellery's Hole, 650m 23°48'35"S 133°11'26"E 15.Mar.2002 J. Heraty eucalypt/creekbed H02-042
3	OG	Chal	Tricoryna	sp.	1307	UCRC_ENT 00092241	UCRC	unk	Australia: QLD: Samsonvale Cemetery, 8.5 SSE Dayboro, 50m 27°16'0"S 152°51'0"E 22.Nov.2002 C. Burwell, C. Desjardins swp 51087
4	OG	Schiz	Ancylotropus	cariniscutis	0407	UCRC_ENT 00091771	UCRC	♂	Malaysia: Selangor: forest road behind quarry 13km E Gombak, 284m 3°18'11"N 101°44'43"E 5.Sep.2001 J. Heraty H01-014
5	OG	Schiz	Ancylotropus	cariniscutis	2836	UCRC_ENT 00237302	UCRC	♂	Singapore: National Botanical Gardens, 68m 1°18'42"N 103°48'55"E 7.Jul.2010 J. Heraty swp rainforest trail H10-096
6	OG	Schiz	Schizaspidia	aenea	0168	UCRC_ENT 00091398	UCRC	unk	Australia: QLD: 11 km N Ellis Beach , 50m 16°43'17"S 145°38'31"E 30.Jan.1999 J.M. Heraty H99/041
7	Gr1	A	Colocharis	napoana	0378	none	UCRC	unk	Ecuador
8	Gr1	A	Colocharis	elongata	0421	UCRC_ENT 00091867	CNC	♂	Venezuela: Aragua: Parque Nac. H. Pittier Portachullo Pass, 1000m 13.Apr.1994 L. Masner V94-3
9	Gr1	A	Colocharis	sp.	1260	UCRC_ENT 00092065	CNC	♂	Bolivia: Cochabamba Dept.: Villa Tunari, 16°54'55"S 65°22'6"W 15.Mar.2001 H. Heider MT
10	Gr1	A	Colocharis	nr elongata	0946	UCRC_ENT 00092132	UCRC	♂	Colombia: Caquetá: San Jose de Fragua, R Yuru Yaco, 1300m 1°20'55"N 76°06'11"W 9-13.Sep.2000 E. Gonzales MT Malaise 5
11	Gr1	A	Colocharis	napoana	1102	UCRC_ENT 00091450	USNM	♀	Ecuador: Orellana: Tiputini Biodiversity Sta. nr. Yasuni National Park, Erwin Transect - T/6, 220-250m 0°37'55"S 76°08'39"W 26.Oct.1998 T.L. Erwin et al. Fogging terre firme forest Lot 1958
12	Gr1	A	Colocharis	napoana	1104	UCRC_ENT 00092220	USNM	♂	Ecuador: Orellana: Tiputini Biodiversity Sta. nr. Yasuni National Park, Erwin Transect - T/6, 220-250m 0°37'55"S 76°08'39"W 26.Oct.1998 T.L. Erwin et al. Fogging terre firme forest Lot 1956
13	Gr1	A	Colocharis	napoana	1146	none	UCRC	unk	Ecuador: Orellana: Tiputini Biodiversity Sta. nr. Yasuni National Park, erwin Transect - T/10, 220-250m 0°37'55"S 76°08'39"W 5.Feb.1999 T.L. Erwin et al. Fogging terre firme forest Lot 2099
14	Gr1	A	Colocharis	elongata	3439	UCRC_ENT 00320311	UCRC	♂	Peru: Manu Pr.: Villa Carmen, Pillcopata, 526m 12°53'7"S 71°23'48"W 27.Nov.2011 J.M. Heraty swp secondary forest H11-157
15	Gr1	A	Colocharis	elongata	3443	UCRC_ENT 00320315	UCRC	♂	Peru: Manu Pr.: Villa Carmen, Pillcopata, 518m 12°53'3"S 71°24'16"W 28.Nov.2011 J.M. Heraty swp mature forest H11-158
16	Gr1	A	Colocharis	sp.	3834	UCRC_ENT 00247776	USNM	♂	Ecuador: Orellana: Transect Ent. Rio Piraña Bridge Reserva Etnica Waorani Onkone Gare Camp, 216.3m 0°39'25"S 76°27'10"W 9.Jul.2006 T.L. Erwin, M.C. Pimienta et al Fogging terre firme forest Lot 3262
17	Gr1	A	Colocharis	sp.	3843	UCRC_ENT 00247777	USNM	♀	Ecuador: Orellana: Transect Ent. Rio Piraña Bridge Reserva Etnica Waorani Onkone Gare Camp, 216.3m 0°39'25"S 76°27'10"W 9.Jul.2006 T.L. Erwin, M.C. Pimienta et al Fogging terre firme forest Lot 3262
18	Gr1	A	Colocharis	sp.	3835	UCRC_ENT 00247780	USNM	♀	Ecuador: Orellana: Transect Ent. Rio Piraña Bridge Reserva Etnica Waorani Onkone Gare Camp, 216.3m 0°39'25"S 76°27'10"W 7.Jul.2006 T.L. Erwin, M.C. Pimienta et al Fogging terre firme forest Lot 3208
19	Gr1	A	Colocharis	nr napoana	1157	UCRC_ENT 00092033	USNM	♀	Ecuador: Napo: Transect Ent. 1 km S. Onkone Gare Camp Reserva Etinica Waorani, 220mm 0°39'25"S 76°27'0"W 10.Feb.1995 T.L. Erwin et al. fogging terre firme forest lot #993
20	Gr1	B	New Genus	sp.	1119	UCRC_ENT 00092192	UCRC	♂	Ecuador: Orellana: Tiputini Biodiversity Sta. nr. Yasuni National Park, 220-250m 0°37'55"S 76°08'39"W 7.Feb.1999 T.L. Erwin et al. fogging terre firme forest Lot 2050 Trans.6 Sta.1
21	Gr1	B	New Genus	sp.	1141	UCRdb 00010304	UCRC	♂	Ecuador: Orellana: Tiputini Biodiversity Station nr Yasuni National Park, Erwin Transect - T/7, 220-250m 0°37'55"S 76°08'39"W 2.Jun.1999 T.L. Erwin et al. fogging terre firme forest Lot 2069
22	Gr1	B	New Genus	sp.	1173	UCRC_ENT 00092029	UCRC	♂	Ecuador: Orellana: Tiputini Biodiversity Station nr Yasuni National Park, Erwin Transect - T/6, 220-250m 0°37'55"S 76°08'39"W 2.Jun.1999 T.L. Erwin et al. fogging terre firme forest Lot 2069
23	Gr1	B	New Genus	sp.	1272	UCRC_ENT 00091868	UCRC	♀	Peru: Madre de Dios: Rio Tambopata Res.30 km air SW Pto., 290m 12°50'0"S 69°17'0"W Maldonado
24	Gr1	B	New Genus	sp.	3440	UCRC_ENT 00397251	UCRC	♂	Peru: Madre de Dios: Los Amigos Bio. St., 231m 12°34'17"S 70°05'43"W 22.Dec.2010 J. Heraty trail 13, 15, 14, 19 H10-152
25	Gr1	B	New Genus	sp.	3441	UCRC_ENT 00397284	UCRC	♂	Peru: Madre de Dios: Los Amigos Bio. St., 255m 12°33'31"S 70°05'35"W 26.Dec.2010 J. Heraty swp trail 10&28 H10-165
26	Gr2	B	New Genus	n. sp. 1	2782	UCRC_ENT 00235922	UCRC	♂	Peru: Madre de Dios: Tambopata Research Center, 13°08'24"S 69°36'36"W 16-22.Jul.2001 B. Brown, G. Kung MT
27	Gr2	C	Dicoelothorax	parviceps	0374-f	UCRC_ENT 00184099	UCRC	♀	Colombia: Vichada: PNN Tuparro, 5°15'9"N 68°25'48"W 16.Jun.2000 M. Sharkey SS
28	Gr2	C	Dicoelothorax	platycerus	2512	UCRC_ENT 00161497	UCRI	♂	Argentina: Salta Pr.: Cabeza de Buey, RN34, 781m 24°47'38"S 64°01'56"W 15.Mar.2007 J.&J. Heraty & J. Torrens chaco H07-016
29	Gr2	C	Dicoelothorax	platycerus	3602	UCRC_ENT 00333658	TUC	♀	Argentina: Santiago del Estero Pr.: Rt5, cerca de La Unión, 26°18'14"S 62°50'9"W 21.Mar.2012 J.Torréns & P. Fidalgo T12-011
30	Gr2	C	Dicoelothorax	platycerus	3921	none	TUC	♀	Argentina: Santiago del Estero Pr: La Unión (Colonia Negrito), 26°16'51"S 62°50'7"W 29.Mar.2013 J.Torréns T13-009
31	Gr2	C	Thoracantha	striata	1254	none	UCRC	unk	Brazil: Rondônia Prov., Rancho Grande
32	Gr2	C	Lasiokapala	sp.	3598	UCRC_ENT 00333654	TUC	♀	Argentina: Santiago del Estero Pr.: La Unión (Colonia Negrito), 26°16'51"S 62°50'7"W 20.Mar.2012 J.Torréns & P. Fidalgo T12-009
33	Gr2	C	Lasiokapala	sp.	3600	UCRC_ENT 00333656	TUC	♂	Argentina: Santiago del Estero Pr.: La Unión (Colonia Negrito), 26°16'51"S 62°50'7"W 20.Mar.2012 J.Torréns & P. Fidalgo T12-009
34	Gr2	C	Latina	rugosa	1073b	UCRC_ENT 00091466	UCRC	♂	Argentina: Salta Pr.: Rosario de la Frontera, Hotel Termal , 25°50'14"S 64°55'55"W 21.Mar.2003 P. Fidalgo sclerophyll forest H03-010b
35	Gr2	C	Latina	guriana	1508	UCRC_ENT 00242338	MCZ	♂	Venezuela: Guri, Isla Rocas, isolated islands in Guri reservoir, near Puerto Ordaz , Doug Yu seasonal tropical forest
36	Gr2	C	Latina	rugosa	2509	UCRC_ENT 00000323	IMLA	♀	Argentina: Chaco Pr.: E of Pampa del Infierno, 116m 26°38'43"S 60°51'2"W 28.Mar.2007 J.&J. Heraty & J. Torrens chaco H07-037
37	Gr2	C	Neolirata	alta	1101	UCRC_ENT 00092091	UCRC	♀	Argentina: Salta Prov.
38	Gr2	C	Neolirata	daguerrei	1067b	UCRC_ENT 00091838	UCRC	♂	Argentina: Formosa Pr.: RN 11; south of Formosa, 60m 26°15'54"S 58°15'57"W 26.Mar.2003 J. Heraty H03-031
39	Gr2	C	Neolirata	alta	3599	UCRC_ENT 00333655	TUC	♀	Argentina: Tucumán Pr.: Tapia, 26°34'27"S 65°17'6"W 20.Mar.2012 J. Torréns chaco T12-013
40	Gr2	C	Neolirata	daguerri	3601	UCRC_ENT 00333657	TUC	♂	Argentina: Tucumán Pr.: Tapia, 26°34'27"S 65°17'6"W 20.Mar.2012 J. Torréns chaco T12-013
41	Gr3	F	Lirata	striatissima	0188	UCRC_ENT 00092235	CNC	unk	Trinidad: Maracas Valley, above Loango Village, 600m 10°44'0"N 61°25'40"W 22.Jun-6.Jul.1993 S&J Peck MT montane rainforest 93-42
42	Gr3	F	Lirata	luteogaster	1106	UCRC_ENT 00092211	UCRC	♀	Ecuador: Orellana: Tiputini Biodiversity Sta. nr. Yasuni National Park, Erwin Transect - T/6, 220-250m 0°37'55"S 76°08'39"W 7.Feb.1999 T.L. Erwin et al. Fogging terre firme forest Lot 2054
43	Gr3	F	Lirata	striatissima	2264	UCRC_ENT 00161521	UCRC	♂	French Guiana: Regina Road Roura-Kaw, 276m 4°32'1"N 32°07'45"W Jul.2004 O. Morvan
44	Gr3	F	Dilocantha	bennetii	0979a	none	UCRC	unk	Trinidad: Curepe, 10°38'48"N 61°24'56" 23-27.Nov.1977 W.R.M. Mason
45	Gr3	F	Dilocantha	lachaudii	1899	UCRdb 00010487	UCRC	♀	Mexico: Chiapas: Cacahoatan: Rosario Izapa, 14°58'0"N 92°09'0"W 29.Jan.1998 P. Lachaud ex. *E. tuberculatum*
46	Gr3	F	Dilocantha	serrata	2265	UCRC_ENT 00161522	TAMU	♀	Panama: Com de San Blas, 2 km N of Nusagadi , 320-400m 9°21'29"N 78°58'42"W 14.Jan.2001 M. Yoder & J. B. Woolley screen swp 2001/044
47	Gr3	F	Dilocantha	bennetti	3820	UCRC_ENT 00412138	UCRC	♀	Trinidad: Mt. St. Benedict Trail, 330m 10°40'1"N 61°24'2"W 18.Jul.2013 Heraty&Baker swp H13-048
48	Gr3	F	Dilocantha	bennetti	3807	UCRC_ENT 00412125	UCRC	♂	Trinidad: Mt. St. Benedict Trail, 330m 10°40'1"N 61°24'2"W 19.Jul.2013 Heraty&Baker swp H13-066
49	Gr3	F	Galearia	latreillei	2251	UCRC_ENT 00161520	UCRI	♀	Venezuela: Bolivar: Guyana mer. or., Kavanayen vill. env. (ca 80 km SW of Kilometer 88), 1268m 5°35'9"N 61°44'54"W 26-28.Feb.2005 P. Jansta & Z. Musilova light
50	Gr3	F	Galearia	latreillei	2491	none	IMLA	unk	Argentina: Salta Pr.: Cabeza de Buey, RN34, 771m 24°47'36"S 65°01'57"W 16.Mar.2007 J.&J. Heraty & J. Torrens chaco H07-018
51	Gr3	F	Galearia	latreillei	2522	UCRC_ENT 00161480	UCRC	♀	Argentina: Santiago del Estero Pr.: Rt 5, S of Campo Gallo, 196m 26°41'53"S 62°45'54"W 29-30.Mar.2007 J.&J. Heraty & J. Torrens chaco H07-039
52	Gr3	F	Galearia	latreillei	3901	UCRC_ENT 00161535	UCRC	♀	Argentina: Santiago del Estero Pr.: Rt 5, S of Campo Gallo, 196m 26°41'53"S 62°45'54"W 29-30.Mar.2007 J.&J. Heraty & J. Torrens chaco H07-039
53	Gr3	F	Galearia	latreillei	3922	none	TUC	♀	Argentina: Santiago del Estero Pr: La Unión (Colonia Negrito), 26°16'51"S 62°50'7"W 29.Mar.2013 J.Torréns T13-009
54	Gr3		Isomerala	azteca	0278	UCRC_ENT 00091773	UCRC	♀	Mexico: Chiapas: Rosario Izapa, 14°57'50"N 92°08'56"W 13.Feb.1998 G Perez
55	Gr3		Isomerala	coronata	0364	unknown	UCRC	unk	Mexico: Quintana Roo: El Eden, M. Gates swp secondary vegetation along forest road

Table S3.1. Locality and museum information for 195 taxa. Major groups and clades are labeled.

Table S3.1 continued

		clade	genus	species	DNA ID	Specimen identifier	museum	sex	locality
56	Gr3		Isomerala	bouceki	0949	UCRC_ENT 00092014	UCRC	♂	Colombia: Vichada: PNN Tuparro Cerro Tomás, 140m 5°21'0"N 67°51'36"W 18-28.Aug.2000 W. Villalba
57	Gr3		Isomerala	azteca	1391	UCRC_ENT 00092016	UCRC	♂	Mexico: Chiapas: Munic. Ocozocoautla, El Aguacero, 1800-2200m 8.Aug.1990 J.B. Woolley 90/055b
58	Gr3		Isomerala	bouceki	3821	UCRC_ENT 00412139	UCRC	♀	Trinidad: Tucuche Tr., Caura Valley, 293m 10°41'13"N 61°22'33"W 24.Jul.2013 Heraty & Baker swp forest H13-075
59	Gr2	D	Kapala	nr furcata sp 1	2799	UCRC_ENT 00252083	UCRC	♀	Mexico: Chiapas: Rosario Izapa, 14°58'0"N 92°09'0"W Apr.2008 J.P. Lachaud ex. *Ectatomma ruidum* , nest 46
60	Gr2	D	Kapala	nr furcata sp 2	1078	UCRC_ENT 00092093	UCRC	♀	Argentina: Misiones Pr.: Santa Ana, near Loreto, 84m 27°20'11"S 55°31'51"W 27.Mar.2003 J. Heraty humid forest H03-038
61	Gr2	D	Kapala	nr furcata sp 3	1388	UCRC_ENT 00092109	UCRC	♂	Costa Rica: Guanacaste Pr.: Guanacaste N.P., Biol. Sta. Cacao, 900m 10°35'3"N 85°22'46"W 13.Feb.1995 L. Masner screen swp
62	Gr2	D	Kapala	nr furcata sp 4	0938b	UCRC_ENT 00092084	UCRC	♂	Ecuador: Esmeraldas: Bilsa Biol. Sta., 500m 0°20'24"N 79°42'36"W 10.May-4.Jun.1996 P. Hibbs MT
63	Gr2	D	Kapala	nr furcata sp 4	0942a	UCRC_ENT 00092002	UCRC	♂	Ecuador: Esmeraldas: Bilsa Biol. Station, 500m 0°20'24"N 79°42'36"W 7-19.Jul.1996 P. Hibbs MT/FIT
64	Gr2	D	Kapala	cuprea	3815	UCRC_ENT 00412133	UCRC	♂	Trinidad: Simla Res.St., 250m 10°41'34"N 61°17'23"W 22.Jul.2013 Heraty&Baker MT station H13-071
65	Gr2	D	Kapala	furcata	0711	UCRC_ENT 00091817	UCRC	♀	Argentina: Misiones Pr.: Loreto: Ruinas Jesuiticas, 27°29'59"S 55°31'59"W 4.Nov.2001 S.O. Martinez, P. Fidalgo MT
66	Gr2	D	Kapala	furcata	1068a	UCRC_ENT 00092070	UCRC	♂	Argentina: Salta Pr.: Oran: Rd to San Andres along Rio Blanca, 399m 23°05'30"S 64°21'57"W 22.Mar.2003 J. Heraty sclerophyll scrub H03-015
67	Gr2	D	Kapala	furcata	1069	UCRC_ENT 00091921	UCRC	♂	Argentina: Misiones Pr.: Santa Ana, near Loreto, 84m 27°20'11"S 55°31'51"W 27.Mar.2003 J. Heraty humid forest H03-038
68	Gr2	D	Kapala	furcata	3436	UCRC_ENT 00397274	UCRC	♂	Paraguay: Caazapá: Estancia Condesa/Toro Blanco, San Rafael Reserve, 110m 26°19'11"S 55°39'57"W 8-10.Dec.2000 Z.H. Falin FIT
69	Gr2	D	Kapala	furcata	2518	UCRC_ENT 00000325	UCRI	♀	Argentina: Misiones Pr.: RN 12, N of Puerto Bosseti, 221m 25°48'20"S 54°32'19"W 25.Mar.2007 J.&J. Heraty & J. Torrens Aurac.for. H07-025
70	Gr2	D	Kapala	furcata	2519	UCRC_ENT 00161498	UCRI	♂	Argentina: Misiones Pr.: Rt17, E of 9 de Julio, 212m 26°24'2"S 54°27'54"W 26.Mar.2007 J.&J. Heraty & J. Torrens roadside H07-031
71	Gr2	D	Kapala	furcata	2520	UCRC_ENT 00000324	UCRI	♂	Argentina: Misiones Pr.: Rt17, E of 9 de Julio, 212m 26°24'2"S 54°27'54"W 26.Mar.2007 J.&J. Heraty & J. Torrens roadside H07-031
72	Gr2	D	Kapala	furcata	1086	UCRC_ENT 00091803	UCRC	♀	Argentina: Misiones Pr.: Santa Ana, near Loreto, 84m 27°20'11"S 55°31'51"W 27.Mar.2003 J. Heraty humid forest H03-038
73	Gr2	D	Kapala	cuprea	1003	UCRC_ENT 00091807	UCRC	♀	Ecuador: Orellana: 1 km S. Onkone Gare Camp, Reserva Etnica Waorani, 216m 0°39'25"S 76°27'10"W 2.Jul.1995 T.L. Erwin et al. fogging terre firme forest Lot 1068
74	Gr2	D	Kapala	cuprea	3836	UCRC_ENT 00320767	CNC	♂	Ecuador: Sucumbíos: Napo River, Sacha Lodge, 230m 0°30'0"S 76°30'0"W 13-23.Apr.1994 P. Hibbs MT
75	Gr2	D	Kapala	cuprea	3852	UCRC_ENT 00320853	CNC	♂	Ecuador: Sucumbíos: Napo River, Sacha Lodge, 290m 0°30'0"S 76°30'0"W 4-14.May.1994 P. Hibbs
76	Gr2	D	Kapala	cuprea	3837	UCRC_ENT 00320768	CNC	♂	Ecuador: Sucumbíos: Napo River, Sacha Lodge, 290m 0°30'0"S 76°30'0"W 3-13.Jun.1994 P. Hibbs
77	Gr2	D	Kapala	cuprea	1004	UCRC_ENT 00092227	UCRC	♂	Ecuador: Orellana: Transect Ent. 1km S Onkone Gare Camp, Res. Etnica Waorani, 216.3m 0°39'25"S 76°27'10"W 9.Jul.1995 TL Erwin et al. Fogging terre firme forest Lot 1135
78	Gr2	D	Kapala	cuprea	3838	UCRC_ENT 00247775	USNM	♀	Ecuador: Orellana: Rio Piraña Bridge, Reserva Etnica Waorani, Onkone Gare Camp, 216.3m 0°39'25"S 76°27'10"W 17.Oct.2005 T.L. Erwin, M.C. Pimienta et al Fogging terre firme forest Lot 3088
79	Gr3	D	Kapala	cuprea	3804	UCRC_ENT 00412122	UCRC	♀	Trinidad: Brasso Seco, Rd to Paria Bay, 148m 10°44'57"N 61°15'53"W 25.Jul.2013 Heraty & Baker swp forest H13-079
80	Gr3	D	Kapala	cuprea	3805	UCRC_ENT 00412123	UCRC	♂	Trinidad: Brasso Seco, Rd to Paria Bay, 148m 10°44'57"N 61°15'53"W 25.Jul.2013 Heraty & Baker swp forest H13-079
81	Gr3	D	Kapala	cuprea	3806	UCRC_ENT 00412124	UCRC	♂	Trinidad: Brasso Seco, Rd to Paria Bay, 148m 10°44'57"N 61°15'53"W 25.Jul.2013 Heraty & Baker swp forest H13-079
82	Gr2	D	Kapala	cuprea	3833	UCRC_ENT 00247778	USNM	♂	Ecuador: Orellana: Transect Ent. Rio Piraña Bridge Reserva Etnica Waorani Onkone Gare Camp, 216.3m 0°39'25"S 76°27'10"W 17.Oct.2005 T.L. Erwin, M.C. Pimienta et al Fogging terre firme forest Lot 3084
83	Gr3	E	Kapala	iridicolor	1267	UCRC_ENT 00092059	UCRC	♂	Honduras: Feo. Morazan: Zamorano Campus, 840m 14°00'43"N 87°00'50"W 1.Jul.2002 D. Yanega
84	Gr2	E	Kapala	iridicolor	1895	UCRC_ENT 00002411	UCRC	♀	Mexico: Chiapas: Rosario Izapa, 14°58'0"N 92°09'0"W 11.Aug.1997 P. Lachaud
85	Gr3	E	Kapala	iridicolor	0933c	UCRC_ENT 00092075	UCRC	♂	Honduras: Olancho: El Boquerón Nat. Mon., 14°47'6"N 86°00'42"W 2.Jul.2002 D. Yanega
86	Gr2	E	Kapala	nr iridicolor sp 1	0381	UCRC_ENT 00091879	UCRC	♀	Panama: Nusagandi Lodge , 390m 9°20'31"N 78°59'38"W 21.Jan.2001 L. Masner swp open road
87	Gr2	E	Kapala	nr iridicolor sp 2	0933b	UCRC_ENT 00092077	UCRC	♂	Honduras: Olancho: El Boquerón Nat. Mon., 14°47'6"N 86°00'42"W 2.Jul.2002 D. Yanega
88	Gr2	E	Kapala	nr iridicolor sp 3	0928a	UCRC_ENT 00091816	UCRC	♂	Colombia: Magdalena: PNN Tayrona Zaino, 50m 11°20'11"N 74°02'1"W 28.Apr-13.May.2000 R. Henriquez M.133
89	Gr2	E	Kapala	nr iridicolor sp 3	0935a	UCRC_ENT 00092125	UCRC	♂	Ecuador: Pichincha: Rio Palenque, 200m 0°08'48"S 78°50'18"W 6.Mar-1.Apr.1996 P. Hibbs MT/PT
90	Gr2	E	Kapala	nr iridicolor sp 3	0938a	UCRC_ENT 00092085	UCRC	♂	Ecuador: Esmeraldas: Bilsa Biol. Sta., 500m 0°20'24"N 79°42'36"W 10.May-4.Jun.1996 P. Hibbs MT
91	Gr2	E	Kapala	nr iridicolor sp 3	0940	UCRC_ENT 00091809	UCRC	♂	Ecuador: Pichincha: Rio Palenque Science Ctr, 200m 0°36'0"S 79°21'0"W 25.Apr-6.Jul.1996 P. Hibbs FIT/MT
92	Gr2	E	Kapala	nr iridicolor sp 3	2917	UCRC_ENT 00282474	UCRC	♀	Costa Rica: Heredia Pr.: La Selva Biol. Sta., 64m 10°25'49"N 84°00'26"W 14.Aug.2010 J. Heraty swp *Hamelia patens* and nearby bushes H10-125
93	Gr2	E	Kapala	nr iridicolor sp 4	3831	UCRC_ENT 00247782	USNM	♀	Ecuador: Orellana: Rio Piraña Bridge, Reserva Etnica Waorani, Onkone Gare Camp, 216.3m 0°39'25"S 76°27'10"W 20.Oct.2005 T.L. Erwin, M.C. Pimienta et al Fogging terre firme forest Lot 3056
94	Gr2	E	Kapala	nr iridicolor sp 4	3841	UCRC_ENT 00247783	USNM	♀	Ecuador: Orellana: Rio Piraña Bridge, Reserva Etnica Waorani, Onkone Gare Camp, 216.3m 0°39'25"S 76°27'10"W 20.Oct.2005 T.L. Erwin, M.C. Pimienta et al Fogging terre firme forest Lot 3056
95	Gr2	E	Kapala	nr iridicolor sp 4	1121	UCRC_ENT 00092008	UCRC	♂	Ecuador: Orellana: Tiputini Biodiversity Sta. nr. Yasuni National Park, Erwin Transect - T/4, 220-250m 0°37'55"S 76°08'55"W 8.Feb.1999 T.L. Erwin et al. Fogging terre firme forest Lot 2032
96	Gr2	E	Kapala	nr iridicolor sp 4	1138	UCRC_ENT 00092246	UCRC	♀	Ecuador: Orellana: 1 km S. Onkone Gare Camp, Reserva Etnica Waorani, 216.3m 0°39'25"S 76°27'10"W 1.Oct.1996 T.L. Erwin et al. fogging terre firme forest Lot 1684
97	Gr2	E	Kapala	nr iridicolor sp 5	0936a	UCRC_ENT 00092073	UCRC	♂	Ecuador: Pichincha: Rio Palenque, 200m 0°08'48"S 78°50'18"W 6.Mar-1.Apr.1996 P. Hibbs MT/PT
98	Gr2	E	Kapala	nr iridicolor sp 5	0937	UCRC_ENT 00175171	UCRC	♂	Ecuador: Pichincha: Rio Palenque, 200m 0°08'48"S 78°50'18"W 6.Mar-1.Apr.1996 P. Hibbs MT/PT
99	Gr2	E	Kapala	nr iridicolor sp 6	0947	UCRC_ENT 00092092	UCRC	♀	Colombia: Cauca: PNN Gorgona Alto el Mirador, 180m 2°58'0"N 78°11'0"W 4-24.Mar.2000 R. Duque MT M.47
100	Gr2	E	Kapala	nr iridicolor sp 7	0939a	UCRC_ENT 00092081	UCRC	♂	Ecuador: Pichincha: Rio Palenque Science Ctr, 200m 0°36'0"S 79°21'0"W 25.Apr-6.Jul.1996 P. Hibbs MT/ FIT
101	Gr2	E	Kapala	nr iridicolor sp 8	3818	UCRC_ENT 00412136	UCRC	♂	Trinidad: Simla Res.St., 250m 10°41'34"N 61°17'23"W 22.Jul.2013 Heraty&Baker MT station H13-071
102	Gr2	E	Kapala	nr iridicolor sp 8	3819	UCRC_ENT 00412137	UCRC	♀	Trinidad: Simla Res.St., 250m 10°41'34"N 61°17'23"W 22.Jul.2013 Heraty&Baker MT station H13-071
103	Gr2	E	Kapala	nr iridicolor sp 8	3816	UCRC_ENT 00412134	UCRC	♂	Trinidad: Simla Res.St., 250m 10°41'34"N 61°17'23"W 22.Jul.2013 Heraty&Baker MT station H13-071
104	Gr2	E	Kapala	nr iridicolor sp 8	3817	UCRC_ENT 00412135	UCRC	♂	Trinidad: Simla Res.St., 250m 10°41'34"N 61°17'23"W 22.Jul.2013 Heraty&Baker MT station H13-071
105	Gr2	E	Kapala	nr iridicolor sp 9	0929	UCRC_ENT 00092120	UCRC	♂	Colombia: Magdalena: PNN Tayrona Zaino, 50m 11°20'11"N 74°02'1"W 28.Apr-13.May.2000 R. Henriquez M.133
106	Gr2	E	Kapala	nr iridicolor sp 9	0944a	UCRC_ENT 00092072	UCRC	♂	Colombia: Magdalena: PNN Tayrona Pueblito, 225m 11°20'0"N 74°02'0"W 29.Jun-14.Jul.2000 R. Henriquez MT M.277
107	Gr2	E	Kapala	nr iridicolor sp 9	0950	UCRC_ENT 00091804	UCRC	♂	Colombia: Magdalena: PNN Tayrona Pueblito, 225m 11°20'0"N 74°02'0"W 12-29.May.2000 R. Henriquez MT M.135
108	Gr2	E	Kapala	nr iridicolor sp 10	0917	UCRC_ENT 00092074	UCRC	♂	Colombia: Magdalena: PNN Tayrona Zaino, 50m 11°20'0"N 74°02'0"W 28.Jun-17.Jul.2000 R. Henriquez MT M.301
109	Gr2	E	Kapala	nr iridicolor sp 11	2781	UCRC_ENT 00235921	UCRC	♂	Colombia: Chocó: PNN UTRIA C. Visitantes, 2m 6°01'9"N 77°20'55"W 5-19.Jul.2000 J. Perez
110	Gr2	E	Kapala	nr iridicolor sp 11	0920	UCRC_ENT 00091969	UCRC	♂	Colombia: Magdalena: PNN Tayrona Zaino, 50m 11°20'0"N 74°02'0"W 28.Jun-17.Jul.2000 R. Henriquez MT M.301

Table S3.1 continued

		clade	genus	species	DNA ID	Specimen identifier	museum	sex	locality
111	Gr2	E	Kapala	nr iridicolor sp 11	0382a	UCRC_ENT 00091869	UCRC	♂	Panama: Panama: P.N. Soberania Plantation, 9°04'43"N 79°40'1"W 21.Jan.2001 L. Masner swp rainforest
112	Gr2	E	Kapala	nr iridicolor sp 11	0382b	UCRC_ENT 00092055	UCRC	♂	Panama: Panama: P.N. Soberania Plantation, 9°04'43"N 79°40'1"W 21.Jan.2001 L. Masner swp rainforest
113	Gr3	G	Kapala	sp 7	2915	UCRC_ENT 00282472	UCRC	♀	Costa Rica: Heredia Pr.: La Selva Biol. Sta., 64m 10°25'49"N 84°00'26"W 10.Aug.2010 J. Heraty swp *Hamelia patens* (Rubiaceae) H10-103
114	Gr3	G	Kapala	sp 7	0384a	UCRC_ENT 00092114	CNC	♂	Panama: 2 km S Torti, Serrania de Maje, 8°53'0"N 8°24'0"W 18.Jan.2001 L. Masner swp
115	Gr3	G	Kapala	sp 8	3848	UCRC_ENT 00320794	CNC	♂	Ecuador: Napo: Rio Palenque, 1°26'59"S 79°44'25"W Feb.1983 M. Sharkey MT
116	Gr3	G	Kapala	sp 8	3849	UCRC_ENT 00320797	CNC	♂	Ecuador: Napo: Rio Palenque, 1°26'59"S 79°44'25"W Feb.1983 M. Sharkey MT
117	Gr3	G	Kapala	sp 9	0487	unknown	UCRC	unk	unkown
118	Gr3	G	Kapala	sp 9	0948	UCRC_ENT 00091967	UCRC	♂	Trinidad: La Gloria, Tableland, 10°16'41"N 61°16'15"W 9.Mar.1995 R.L. Manuel in citrus
119	Gr3	G	Kapala	sp 9	2916	UCRC_ENT 00282473	UCRC	♂	Costa Rica: Heredia Pr.: La Selva Biol. Sta., 64m 10°25'49"N 84°00'26"W 10.Aug.2010 J. Heraty swp *Hamelia patens* (Rubiaceae) H10-103
120	Gr3	G	Kapala	sp 9	2918	UCRC_ENT 00282475	UCRC	♂	Costa Rica: Heredia Pr.: La Selva Biol. Sta., 64m 10°25'49"N 84°00'26"W 14.Aug.2010 J. Heraty swp *Hamelia patens* and nearby bushes H10-125
121	Gr3	G	Kapala	sp 9	0383a	UCRC_ENT 00091865	CNC	♂	Panama: Bocas del Toro: Rio La Gloria, 8 km W Rambaia, 35mm 8°59'4"N 82°13'57"W 8.Jan.2001 L. Masner swp forest
122	Gr3	G	Kapala	sp 9	0383c	UCRC_ENT 00092129	CNC	♂	Panama: Bocas del Toro: Rio La Gloria, 8 km W Rambaia, 35mm 8°59'4"N 82°13'57"W 8.Jan.2001 L. Masner swp forest
123	Gr3	G	Kapala	sp 9	3437	UCRC_ENT 00397262	UCRC	♂	Colombia: Meta: San Martin, Reserva Natural El Caduceo, 380m 3°40'12"N 73°39'36"W 21.Oct.2010 G. Zhang & J. Avendaño CO10-L7
124	Gr3	G	Kapala	sp 9	3812	UCRC_ENT 00412129	UCRC	♀	Trinidad: Mt. St. Benedict Trail, 330m 10°40'1"N 61°24'2"W 24.Jul.2013 Heraty&Baker swp H13-074
125	Gr3	G	Kapala	sp 9	3813	UCRC_ENT 00412130	UCRC	♂	Trinidad: Mt. St. Benedict Trail, 330m 10°40'1"N 61°24'2"W 24.Jul.2013 Heraty&Baker swp H13-074
126	Gr3	G	Kapala	sp 9	3822	UCRC_ENT 00412140	UCRC	♀	Trinidad: Tucuche Tr., Caura Valley, 293m 10°41'13"N 61°22'33"W 24.Jul.2013 Heraty & Baker swp forest H13-075
127	Gr3	G	Kapala	sp 9	3824	UCRC_ENT 00412142	UCRC	♀	Trinidad: Tucuche Tr., Caura Valley, 293m 10°41'13"N 61°22'33"W 24.Jul.2013 Heraty & Baker swp forest H13-075
128	Gr3	G	Kapala	sp 9	0379	UCRC_ENT 00092110	UCRC	♂	Guatemala: 250m 14°33'58"N 91°43'42"W D. Hawks
129	Gr3	G	Kapala	sp 9	3823	UCRC_ENT 00412141	UCRC	♀	Trinidad: Tucuche Tr., Caura Valley, 293m 10°41'13"N 61°22'33"W 24.Jul.2013 Heraty & Baker swp forest H13-075
130	Gr3	G	Kapala	sp 9	3825	UCRC_ENT 00412143	UCRC	♀	Trinidad: Tucuche Tr., Caura Valley, 293m 10°41'13"N 61°22'33"W 24.Jul.2013 Heraty & Baker swp forest H13-075
131	Gr3	G	Kapala	sp 9	3826	UCRC_ENT 00412144	UCRC	♀	Trinidad: Tucuche Tr., Caura Valley, 293m 10°41'13"N 61°22'33"W 24.Jul.2013 Heraty & Baker swp forest H13-075
132	Gr3	G	Kapala	sp 9	0927a	UCRC_ENT 00092121	UCRC	♂	Colombia: Magdalena: PNN Tayrona Zaino, 50m 11°20'11"N 74°02'1"W 28.Apr-13.May.2000 R. Henriquez M.133
133	Gr3	G	Kapala	sp 9	0943a	UCRC_ENT 00091808	UCRC	♂	Trinidad: Las Cuevas, 10°47'2"N 61°23'20"W 16.Mar.1995 R.L. Manuel along roadside
134	Gr3	G	Kapala	sp 9	1405	UCRC_ENT 00091835	UCRC	♂	Costa Rica: Heredia Pr.: La Selva Biol. Sta., 15m 10°24'0"N 84°00'0"W 15-17.Feb.1988 B. Hubley & D.C. Darling screen swp rainforest ROM880027
135	Gr3	H	Kapala	ivorensis	0273	UCRC_ENT 00092140	UCRC	♀	Sao Tome: Poto CIAT compound, 0°14'33"N 6°36'34"E 7-12.Jun.1999 A. Polaszek MT
136	Gr3	H	Kapala	ivorensis	2441	UCRC_ENT 00278291	UCRC	♀	South Africa: Mpumalanga: Stridjum tunnel area, 730m 24°27'47"S 30°36'31"E 31.Jan.2006 J.Heraty H06-008
137	Gr3	H	Kapala	ivorensis	2648	UCRC_ENT 00235916	MNHN	♀	Cameroon: Centre Pr.: Messamendongo, 3°48'35"N 11°31'17"E 1-13.Apr.2003 T. Marc MT
138	Gr3	H	Kapala	ivorensis	2693	UCRC_ENT 00000313	UCRC	♀	Nigeria: Ondo: 1.6 km E Owena, 268m 7°11'54"N 5°01'50"E 19.Jul.2008 J. Mottern swp cacao plantation M08-017
139	Gr3	H	Kapala	ivorensis	2760	UCRC_ENT 00092139	UCRC	♀	Sao Tome: Poto CIAT compound, 0°14'33"N 6°36'34"E 7-12.Jun.1999 A. Polaszek MT
140	Gr3	H	Kapala	ivorensis	2746	UCRC_ENT 00302068	UCRC	♀	Kenya: Coast Pr.: Arabuko-Sokoke Forest, 3°25'13"S 39°53'49"E 8-9.Jan.2000 R. Copeland swp
141	Gr3	H	Kapala	ivorensis	2771	UCRC_ENT 00018899	CASC	♀	Madagascar: Toamasina Pr: Mobot site, Analalava 7 km SW Foulpointe, 18m 17°41'36"S 49°27'37"E 3-11.Jan.2008 M. Irwin, R. Harin'Hala MT sand low alt dense humid forest MG-37B-17
142	Gr3	H	Kapala	ivorensis	2772	UCR_ENT 00018900	CASC	♀	Madagascar: Toamasina Pr: Mobot site, Analalava 7 km SW Foulpointe, 18m 17°41'36"S 49°27'37"E 28.Sep-5.Oct.2007 M. Irwin, R. Harin'Hala MT sand low alt dense humid forest MG-37B-03
143	Gr3	H	Kapala	ivorensis	2924	UCRC_ENT 00241604	HIC	♂	Republic of Congo: Pool Dept.: Abio: Lesio-Louna Pk., 330m 3°06'1"S 15°31'26"E 30.Sep-7.Oct.2008 Sharkey & Braet MT
144	Gr3	H	Kapala	ivorensis	2923	UCRC_ENT 00241571	HIC	♀	Republic of Congo: Dept. Pool: Iboubikro: Lesio-Louna Pk., 330m 3°06'1"S 15°28'16"E Sep.2008 Sharkey & Braet MT
145	Gr3	H	Kapala	ivorensis	2922	UCRC_ENT 00241581	HIC	♀	Republic of Congo: Pool Dept.: Abio: Lesio-Louna Pk., 330m 3°06'1"S 15°31'26"E 11-18.Sep.2008 Sharkey & Braet
146	Gr3	H	Kapala	izapa	2787	UCRC_ENT 00235920	UCRC	♂	Mexico: Quintana Roo: Lazaro Cardena: 25 km NNE Leona Vicario Reserva Ecologia El Eden, 21°13'0"N 87°11'0"W 10.Aug.1998 R. Rodriguez swp secondary growth near greenhouse
147	Gr3	H	Kapala	izapa	2793	UCRC_ENT 00235954	UCRC	♂	Mexico: Quintana Roo: Lazaro Cardena: 25 km NNE Leona Vicario Reserva Ecologia El Eden, 21°13'0"N 87°11'0"W 23.Aug.1998 M. Gates swp secondary growth near greenhouse
148	Gr3	H	Kapala	izapa	2797	UCRC_ENT 00252081	UCRC	♀	Mexico: Chiapas: Rosario Izapa, 14°58'0"N 92°09'0"W 19.Jan.2004 J.P. Lachaud ex. *Pachycondyla stigma*
149	Gr3	H	Kapala	izapa	2925	UCRC_ENT 00356033	UCRC	♂	Mexico: Chiapas: Playón de la Gloria, 180m 16°09'36"N 90°54'7"W 24.Jun.2008 MT LLAMA# Ma-A-09-1-02
150	Gr3	H	Kapala	izapa	2926	UCRC_ENT 00397279	UCRC	♂	Mexico: Chiapas: Playón de la Gloria, 180m 16°09'36"N 90°54'7"W 24.Jun.2008 MT LLAMA# Ma-A-09-1-02
151	Gr3	H	Kapala	izapa	0365	unknown	UCRC	unk	Mexico: Quintana Roo: El Eden, M. Gates swp secondary vegetation along forest road
152	Gr3	H	Kapala	izapa	2786	UCRC_ENT 00235919	UCRC	♂	Mexico: Quintana Roo: Lazaro Cardena: 25 km NNE Leona Vicario Reserva Ecologia El Eden, 21°13'0"N 87°11'0"W 19.Aug.1998 R. Rodriguez swp savannah de cabana
153	Gr3	H	Kapala	nr *striata*	1397	UCRC_ENT 00092034	UCRC	♂	Costa Rica: Puntarenas Pr.: Monteverde, 1500m 10°18'25"N 84°48'35"W Feb.1980 W.R. Mason & M. Wood cloud forest
154	Gr3	H	Kapala	sp 10	3738	UCRC_ENT 00397254	UCRC	♀	Honduras: Olancho Dept.: La Muralla, visitor's center, 1467m 15°05'49"N 86°44'19"W 26-30.Apr.2013 O. Schlein MT (6m)
155	Gr3	H	Kapala	sp 10	3851	UCRC_ENT 00320841	CNC	♀	Panama: Darién Pr.: Cana, 530m 7°45'0"N 77°41'0"W 3-7.Jun.1996 J. Ashe & R. Brooks PIT #65
156	Gr3	H	Kapala	sp 12	2798	UCRC_ENT 00252082	UCRC	♀	Mexico: Chiapas: Ejido 2 de Mayo, 13.Apr.2005 G. Perez-Lachaud ex. *Odontomachus opaciventris*
157	Gr3	H	Kapala	sp 12	0934a	UCRC_ENT 00092082	UCRC	♀	Honduras: Olancho: Montana del Malacate, 15°08'4"N 85°35'36"W 3.Jul.2002 D. Yanega
158	Gr3	H	Kapala	sp 12	2785	UCRC_ENT 00235918	UCRC	♂	Dominica: Parish of St. Joseph Springfield Estate, 430m 15°20'48"N 61°22'6"W 15-20.Mar.2003 M.E. Irwin, E. Benson, G. Carner, M.B. Shepard MT
159	Gr3	H	Kapala	sp 13	2800	UCRC_ENT 00252084	UCRC	♀	French Guiana: PK 24; 24 km to Barrage Petit Saut, 21.Mar.2008 G. Perez-Lachaud & J.-P. Lachaud ex. *Odontomachus hastatus*
160	Gr3	H	Kapala	sp 14	0193c	UCRC_ENT 00092214	UCRC	♂	Trinidad: Peck 93-58
161	Gr3	H	Kapala	sp 15	1413a	UCRC_ENT 00092126	UCRC	♂	Costa Rica: Puntarenas: PN Corcovado, Est. Agujas, S. Coroma, 245m 8°32'25"N 83°34'15"W 23.Apr.2002 J. Azofeifa swp L-5275500 S21000
162	Gr3	H	Kapala	sp 15	1412a	UCRC_ENT 00092229	UCRC	♂	Panama: Corcovado
163	Gr3	H	Kapala	sp 16	0938c	UCRC_ENT 00092127	UCRC	♂	Ecuador: Esmeraldas: Bilsa Biol. Sta., 500m 0°20'24"N 79°42'36"W 10.May-4.Jun.1996 P. Hibbs MT
164	Gr3	H	Kapala	sp 17	2801	UCRC_ENT 00252085	UCRC	♂	French Guiana: Camp Patawa, 4°32'10"N 52°09'8"W 14.Mar-30.Apr.2007 R. de Souza Ferreira ex. *Pachycondyla verenae*
165	Gr3	H	Kapala	sp 18	3803	UCRC_ENT 00412121	UCRC	♀	Trinidad: Brasso Seco, Rd to Paria Bay, 148m 10°44'57"N 61°15'53"W 25.Jul.2013 Heraty & Baker swp forest H13-079

Table S3.1 continued

		clade	genus	species	DNA ID	Specimen identifier	museum	sex	locality
166	Gr3	H	Kapala	sp 19	1389	UCRC_ENT 00092031	UCRC	♂	Ecuador: Galapagos: Isabela Island 13 km NW Villamil, 125m 0°49'45"S 91°08'7"W 24-30.Apr.1996 Peck MT Trans forest
167	Gr3	H	Kapala	sp 20	1140	UCRC_ENT 00092030	UCRC	♂	Ecuador: Orellana: Tiputini Biodiversity Station nr Yasuni National Park, Erwin Transect - T/5, 220-250m 0°37'55"S 76°08'39"W 26.Oct.1998 T.L. Erwin et al. fogging terre firme forest Lot 1942
168	Gr3	H	Kapala	sp 20	1142	UCRC_ENT 00091926	UCRC	♀	Ecuador: Orellana: 1 km S. Onkone Gare Camp, Reserva Etnica Waorani, 216m 0°39'25"S 76°27'10"W 2.Oct.1996 T.L. Erwin et al. fogging terre firme forest Lot 1705
169	Gr3	H	Kapala	sp 21	3749	UCRC_ENT 00364771	USNM	♂	Ecuador: Orellana: Northern Production Facility, Reserva Etnica Waorani, 216.3m 0°39'25"S 76°27'10"W 23.Feb.1995 T.L. Erwin et al fogging terre firme forest Lot # 1057
170	Gr3	H	Kapala	sp 22	2796	UCRC_ENT 00235957	UCRC	♀	Dominica: St. David: 11 km NE Pont Casse, 15°27'36"N 61°18'53"W 20.Jun.2004 R.Turnbow
171	Gr3	n/a	Kapala	argentina	1064	UCRdb 00010184	UCRC	♀	Argentina: Salta Pr.: Rosario de la Frontera, Hotel Termal, Cambriceto path, 741m 25°50'14"S 64°55'55"W 21.Mar.2003 J.Heraty swp sclerophyll forest H03-010a
172	Gr3	n/a	Kapala	argentina	1076	UCRC_ENT 00091827	UCRC	♀	Argentina: Salta Pr.: Rosario de la Frontera, Hwy 34, 745m 25°50'3"S 64°52'31"W 21.Mar.2003 J. Munro swp forest/chaco H03-009a
173	Gr3	n/a	Kapala	argentina	2920	UCRC_ENT 00282476	UCRC	♂	Argentina: Salta Pr.: RN9 Rosario de la Frontera, 730m 25°50'2"S 64°52'35"W 13-14.Mar.2007 J.&J. Heraty & J. Torrens chaco/past. H07-013
174	Gr3	n/a	Kapala	nr argentina	0986	UCRC_ENT 00091929	UCRC	♂	Argentina: Tucuman Pr.: Horco Molle, 26°46'38"S 65°19'50"W 15.Jan.1996 M.J. Sharkey swp
175	Gr3	n/a	Kapala	floridana	0432b	UCRdb 00092111	UCRC	♂	USA: FL: Marion Co.: Juniper Spr Rd. , 41m 29°13'33"N 81°43'35"W 19.Sep.2001 J. Heraty sand/oak scrub H01-046
176	Gr3	n/a	Kapala	nr sulcifacies	0488	unknown	UCRC	unk	unknown
177	Gr3	n/a	Kapala	nr sulcifacies sp 1	1273	UCRC_ENT 00091851	UCRC	♂	Mexico: Tamaulipas: Gomez Farias, Farias Road to Rancho Cielo , 700mm 23°01'49"N 99°08'53"W 4.Oct.1999 R. Jones tropical decidous forest
178	Gr3	n/a	Kapala	nr sulcifacies sp 2	3923	UCRC_ENT 00397281	UCRC	♂	French Guiana
179	Gr3	n/a	Kapala	nr sulcifacies sp 2	3850	UCRC_ENT 00320844	CNC	♂	Ecuador: Loja Pr.: Macara, La Tacocha, 650m 4°22'59"S 79°56'47"W 14.Aug.1977
180	Gr3	n/a	Kapala	sp 1	3903	UCRC_ENT 00397256	UCRC	♂	Brazil: Bahia: Belmonte, Barrolândia CEPLAC reserve, 19.Mar.2012 J.R.M. dos Santos ex. *Dinoponera lucida*
181	Gr3	n/a	Kapala	sp 2	0626	UCRC_ENT 00092243	UCRC	♂	Ecuador: Esmereldas: Bilsa Biol. Sta., 500m 0°20'24"N 79°42'36"W 5.Jun-7.Jul.1996 P. Hibbs MT
182	Gr3	n/a	Kapala	sp 2	0941	UCRC_ENT 00091920	UCRC	♂	Ecuador: Esmeraldas: Bilsa Biol. Station, 500m 0°20'24"N 79°42'36"W 7-19.Jul.1996 P. Hibbs MT/FIT
183	Gr3	n/a	Kapala	sp 2	3853	UCRC_ENT 00320852	CNC	♂	Venezuela: Aragua: Rancho Grande Biol. Sta., 1550m 10°21'38"N 67°41'38"W 12-14.May.1998 J. Ashe, R. Brooks, & R. Hanley
184	Gr3	n/a	Kapala	sp 3	2261	UCRC_ENT 00161512	UCRC	♀	Dominican Republic: Punta Cana, Reserva, 18°30'40"N 68°22'38"W 11-14.Nov.2005 L. Masner screen swp forest
185	Gr3	n/a	Kapala	sp 3	2784	UCRC_ENT 00172257	UCRC	♀	USA: FL: Monroe Co.: Big Pine Key, SW 1/4 S4, 0m 24°40'12"N 81°21'14"W 1-31.Aug.1986 S. & J. Peck MT mangrove/hardwood trnsition
186	Gr3	n/a	Kapala	sp 4	3920	none	TUC	unk	Argentina: Santiago del Estero Pr: La Unión (Colonia Negrito), 26°16'51"S 62°50'7"W 21.Mar.2012 J.Torréns & P. Fidalgo T12-012
187	Gr3	n/a	Kapala	sp 4	2802	UCRC_ENT 00252086	UCRC	♀	French Guiana: "Paracou", Km 100.3 RN1 from Kourou to Sinnamary, 5°16'12"N 52°55'3"W 9.Mar.2008 G. Perez-Lachaud ex. *Odontomachus* sp.2
188	Gr3	n/a	Kapala	sp 5	2266	UCRC_ENT 00161514	UCRC	♂	USA: TX: Brewster Co.: Big Bend Nat.Pk Buttrill Spg., 29°19'42"N 103°12'21"W 10-21.Jul.1991 R. Vogtsberger
189	Gr3	n/a	Kapala	sp 6	2521	UCRC_ENT 00161501	UCRI	♀	Argentina: Santiago del Estero Pr.: Rt5, S of Tintina, 168m 27°05'27"S 62°48'1"W 30.Mar.2007 J.&J. Heraty & J. Torrens chaco H07-042
190	Gr4	n/a	Kapala	sp 6	1080a	UCRC_ENT 00091805	UCRC	♂	Argentina: Salta Pr.: Cabaze de Buey, 781m 24°47'38"S 64°01'46"W 21.Mar.2003 J. Heraty
191	Gr3	n/a	Kapala	sulcifacies	0384c	UCRC_ENT 00092221	CNC	♂	Panama: 2 km S Torti, Serrania de Maje, 8°53'0"N 8°24'0"W 18.Jan.2001 L. Masner swp
192	Gr3	n/a	Kapala	sulcifacies	0384e	UCRC_ENT 00092058	CNC	♂	Panama: 2 km S Torti, Serrania de Maje, 8°53'0"N 8°24'0"W 18.Jan.2001 L. Masner swp
193	Gr3	n/a	Kapala	terminalis	1270	UCRC_ENT 00091880	UCRC	♂	Dominican Republic: Puerto Plata, 19°47'0"N 70°41'0"W 23.Jan.1989 L. Masner suburban
194	Gr3	n/a	Kapala	terminalis	2260	UCRC_ENT 00161511	UCRC	♂	Dominican Republic: Punta Cana, Reserva, 18°30'40"N 68°22'38"W 11-14.Nov.2005 L. Masner screen swp forest
195	Gr3	n/a	Kapala	terminalis	3435	UCRC_ENT 00397249	UCRC	♂	USA: Puerto Rico: Cerezos, circle 38, 28.Feb.2004 L Yunes MT 72d

	96	Grp	clade	genus	species	DNA ID	genes	18S	D2	D3-5	COI	COII
1	X	OG	Ch	Austeucharis	implexa	0164	5	AY552310	AY552233	AY552233	KC008219	KC008397
2	X	OG	Ch	Chalcura	ramosa	0646a	5	AY552314	AY552237	AY552237	KC008204	KC008380
3		OG	Ch	Tricoryna	sp.	1307	4	x	KC008104	unpub	KC008223	KC008401
4	X	OG	Sc	Ancylotropus	cariniscutis	0407	5	JN623228	AY552239	JN624005	KC008234	KC008413
5		OG	Sc	Ancylotropus	cariniscutis	2836	4	unpub	unpub	unpub	x	unpub
6	X	OG	Sc	Schizaspidia	aenea	0168	5	AY552317	AY552240	AY552240	KC008225	KC008403
7		Gr1	A	Colocharis	napoana	0378	3	unpub	unpub	unpub	x	x
8	X	Gr1	A	Colocharis	elongata	0421	5	KC008522	AY671837	AY671837	KC008238	KC008422
9		Gr1	A	Colocharis	sp.	1260	4	unpub	unpub	unpub	x	unpub
10		Gr1	A	Colocharis	nr elongata	0946	4	unpub	unpub	unpub	x	unpub
11	X	Gr1	A	Colocharis	napoana	1102	5	AY552323	AY552246	AY552246	KC008239	KC008423
12	X	Gr1	A	Colocharis	napoana	1104	5	unpub	unpub	unpub	unpub	unpub
13	X	Gr1	A	Colocharis	napoana	1146	5	unpub	unpub	unpub	unpub	unpub
14	X	Gr1	A	Colocharis	elongata	3439	5	unpub	unpub	unpub	unpub	unpub
15	X	Gr1	A	Colocharis	elongata	3443	5	unpub	unpub	unpub	unpub	unpub
16		Gr1	A	Colocharis	sp.	3834	4	unpub	unpub	unpub	unpub	x
17	X	Gr1	A	Colocharis	sp.	3843	5	unpub	unpub	unpub	unpub	unpub
18		Gr1	A	Colocharis	sp.	3835	3	x	unpub	unpub	unpub	x
19	X	Gr1	A	Colocharis	nr napoana	1157	5	unpub	unpub	unpub	unpub	unpub
20		Gr1	B	New Genus	sp.	1119	3	x	AY671886	AY671886	x	unpub
21	X	Gr1	B	New Genus	sp.	1141	5	KC008543	KC008129	unpub	KC008268	KC008455
22	X	Gr1	B	New Genus	sp.	1173	5	KC008547	AY671890	AY671890	KC008272	KC008460
23		Gr1	B	New Genus	sp.	1272	4	KC008544	KC008131	unpub	x	KC008457
24	X	Gr1	B	New Genus	sp.	3440	5	unpub	unpub	unpub	unpub	unpub
25		Gr1	B	New Genus	sp.	3441	3	x	unpub	unpub	unpub	x
26		Gr2	B	New Genus	n. sp. 1	2782	4	x	unpub	unpub	unpub	unpub
27	X	Gr2	C	Dicoelothorax	parviceps	0374f	5	KC008528	AY671835	AY671835	KC008245	KC008430
28		Gr2	C	Dicoelothorax	platycerus	2512	3	x	KC008115	KC008149	x	KC008431
29	X	Gr2	C	Dicoelothorax	platycerus	3602	5	unpub	unpub	unpub	unpub	unpub
30		Gr2	C	Dicoelothorax	platycerus	3921	4	x	unpub	unpub	unpub	unpub
31	X	Gr2	C	Thoracantha	striata	1254	4	KC008530	AY671896	AY671896	x	KC008435
32	X	Gr2	C	Lasiokapala	sp.	3598	5	unpub	unpub	unpub	unpub	unpub
33	X	Gr2	C	Lasiokapala	sp.	3600	5	unpub	unpub	unpub	unpub	unpub
34	X	Gr2	C	Latina	rugosa	1073b	5	AY552319	AY552242	AY552242	KC008246	KC008433
35		Gr2	C	Latina	guriana	1508	3	x	AY671894	unpub	x	KC008432
36	X	Gr2	C	Latina	rugosa	2509	3	unpub	unpub	unpub	x	x
37	X	Gr2	C	Neolirata	alta	1101	5	KC008523	AY671894	AY671894	KC008240	KC008424
38	X	Gr2	C	Neolirata	daguerrei	1067b	5	AY552322	AY552245	AY552245	KC008241	KC008425
39		Gr2	C	Neolirata	alta	3599	4	unpub	unpub	unpub	unpub	x
40	X	Gr2	C	Neolirata	daguerri	3601	5	unpub	unpub	unpub	unpub	unpub
41	X	Gr3	F	Lirata	striatissima	0188	5	KC008529	KC008116	unpub	KC008247	KC008434
42	X	Gr3	F	Lirata	luteogaster	1106	5	KC008524	AY671895	AY671895	KC008242	KC008426
43	X	Gr3	F	Lirata	striatissima	2264	5	KC008525	KC008112	KC008147	KC008243	KC008427
44		Gr3	F	Dilocantha	bennetii	0979a	4	KC008526	KC008113	unpub	x	KC008428
45		Gr3	F	Dilocantha	lachaudii	1899	3	x	unpub	unpub	x	unpub
46	X	Gr3	F	Dilocantha	serrata	2265	5	KC008527	KC008114	KC008148	KC008244	KC008429
47	X	Gr3	F	Dilocantha	bennetti	3820	5	unpub	unpub	unpub	unpub	unpub
48	X	Gr3	F	Dilocantha	bennetti	3807	5	unpub	unpub	unpub	unpub	unpub
49	X	Gr3	F	Galearia	latreillei	2251	5	KC008532	KC008118	KC008150	KC008248	KC008436
50		Gr3	F	Galearia	latreillei	2491	3	KC008531	KC008117	unpub	x	x
51		Gr3	F	Galearia	latreillei	2522	3	unpub	unpub	unpub	x	x

Table S3.2. Genbank information. The taxa used for the complete genes dataset are indicated in the ‘96’ column. The total number of genes is listed. An ‘x’ in one of the gene region cells indicates no data.

Table S3.2 continued

	96	Grp	clade	genus	species	DNA ID	genes	18S	D2	D3-5	COI	COII
52		Gr3	F	Galearia	latreillei	3901	**1**	x	x	x	x	unpub
53	**X**	Gr3	F	Galearia	latreillei	3922	**5**	unpub	unpub	unpub	unpub	unpub
54	**X**	Gr3		Isomerala	azteca	0278	**5**	AY552318	AY552241	AY552241	KC008249	KC008437
55		Gr3		Isomerala	coronata	0364	**4**	x	unpub	unpub	unpub	unpub
56		Gr3		Isomerala	bouceki	0949	**4**	x	AY671833	AY671833	KC008251	KC008439
57		Gr3		Isomerala	azteca	1391	**4**	x	AY671834	AY671834	KC008250	KC008438
58	**X**	Gr3		Isomerala	bouceki	3821	**5**	unpub	unpub	unpub	unpub	unpub
59	**X**	Gr2	D	Kapala	nr furcata sp 1	2799	**5**	KC008542	KC008128	KC008158	KC008266	KC008453
60	**X**	Gr2	D	Kapala	nr furcata sp 2	1078	**5**	unpub	AY671883	AY671883	KC008253	KC008441
61	**X**	Gr2	D	Kapala	nr furcata sp 3	1388	**5**	KC008555	AY671892	AY671892	KC008280	KC008469
62		Gr2	D	Kapala	nr furcata sp 4	0938b	**3**	KC008550	AY671864	AY671864	x	x (error GB)
63	**X**	Gr2	D	Kapala	nr furcata sp 4	0942a	**5**	KC008553	AY671869	AY671869	KC008278	KC008467
64		Gr2	D	Kapala	nr furcata sp 5	3815	**4**	x	unpub	unpub	unpub	unpub
65		Gr2	D	Kapala	nr furcata sp 5	0711	**4**	x	AY671852	AY671852	unpub	unpub
66	**X**	Gr2	D	Kapala	nr furcata sp 5	1068a	**5**	KC008552	AY671880	AY671880	KC008277	KC008466
67	**X**	Gr2	D	Kapala	nr furcata sp 5	1069	**5**	KC008554	AY671881	AY671881	KC008279	KC008468
68		Gr2	D	Kapala	nr furcata sp 5	3436	**4**	unpub	unpub	unpub	unpub	x
69		Gr2	D	Kapala	nr furcata sp 5	2518	**2**	x	unpub	unpub	x	x
70		Gr2	D	Kapala	nr furcata sp 5	2519	**3**	x	unpub	unpub	x	unpub
71		Gr2	D	Kapala	nr furcata sp 5	2520	**2**	x	unpub	unpub	x	unpub
72		Gr2	D	Kapala	furcata	1086	**4**	x	unpub	unpub	unpub	unpub
73	**X**	Gr2	D	Kapala	cuprea	1003	**5**	unpub	AY671878	AY671878	unpub	unpub
74		Gr2	D	Kapala	cuprea	3836	**3**	x	unpub	unpub	unpub	x
75		Gr2	D	Kapala	cuprea	3852	**4**	unpub	unpub	unpub	unpub	x
76		Gr2	D	Kapala	cuprea	3837	**3**	x	unpub	unpub	unpub	x
77	**X**	Gr2	D	Kapala	cuprea	1004	**5**	KC008551	AY671879	AY671879	KC008276	KC008465
78		Gr2	D	Kapala	cuprea	3838	**3**	x	unpub	unpub	unpub	x
79		Gr3	D	Kapala	cuprea	3804	**4**	x	unpub	unpub	unpub	unpub
80		Gr3	D	Kapala	cuprea	3805	**4**	x	unpub	unpub	unpub	unpub
81		Gr3	D	Kapala	cuprea	3806	**4**	x	unpub	unpub	unpub	unpub
82		Gr2	D	Kapala	cuprea	3833	**3**	x	unpub	unpub	unpub	x
83	**X**	Gr3	E	Kapala	iridicolor	1267	**5**	KC008560	KC008133	unpub	KC008288	KC008477
84		Gr2	E	Kapala	iridicolor	1895	**3**	x	unpub	unpub	x	unpub
85	**X**	Gr3	E	Kapala	iridicolor	0933c	**5**	unpub	AY671859	AY671859	unpub	unpub
86	**X**	Gr2	E	Kapala	nr iridicolor sp 1	0381	**5**	unpub	AY671841	AY671841	unpub	unpub
87	**X**	Gr2	E	Kapala	nr iridicolor sp 2	0933b	**5**	unpub	unpub	unpub	unpub	unpub
88	**X**	Gr2	E	Kapala	nr iridicolor sp 3	0928a	**5**	KC008558	AY671856	AY671856	KC008284	KC008473
89	**X**	Gr2	E	Kapala	nr iridicolor sp 3	0935a	**5**	unpub	unpub	unpub	unpub	unpub
90	**X**	Gr2	E	Kapala	nr iridicolor sp 3	0938a	**5**	KC008559	AY671863	AY671863	KC008285	KC008474
91		Gr2	E	Kapala	nr iridicolor sp 3	0940	**4**	x	AY671867	AY671867	KC008287	KC008476
92	**X**	Gr2	E	Kapala	nr iridicolor sp 3	2917	**5**	unpub	unpub	unpub	unpub	unpub
93		Gr2	E	Kapala	nr iridicolor sp 4	3831	**3**	x	unpub	unpub	unpub	x
94		Gr2	E	Kapala	nr iridicolor sp 4	3841	**3**	x	unpub	unpub	unpub	x
95		Gr2	E	Kapala	nr iridicolor sp 4	1121	**4**	x	AY671887	AY671887	KC008289	KC008478
96	**X**	Gr2	E	Kapala	nr iridicolor sp 4	1138	**5**	unpub	unpub	unpub	unpub	unpub
97	**X**	Gr2	E	Kapala	nr iridicolor sp 5	0936a	**5**	KC008556	AY671862	AY671862	KC008282	KC008471
98	**X**	Gr2	E	Kapala	nr iridicolor sp 5	0937	**5**	unpub	unpub	unpub	unpub	unpub
99	**X**	Gr2	E	Kapala	nr iridicolor sp 6	0947	**5**	KC008557	AY671874	AY671874	KC008283	KC008472
100		Gr2	E	Kapala	nr iridicolor sp 7	0939a	**4**	x	AY671866	AY671866	KC008286	KC008475
101		Gr2	E	Kapala	nr iridicolor sp 8	3818	**4**	x	unpub	unpub	unpub	unpub
102		Gr2	E	Kapala	nr iridicolor sp 8	3819	**4**	x	unpub	unpub	unpub	unpub

Table S3.2 continued

	96	Grp	clade	genus	species	DNA ID	genes	18S	D2	D3-5	COI	COII
103		Gr2	E	Kapala	nr iridicolor sp 8	3816	4	x	unpub	unpub	unpub	unpub
104		Gr2	E	Kapala	nr iridicolor sp 8	3817	4	x	unpub	unpub	unpub	unpub
105		Gr2	E	Kapala	nr iridicolor sp 9	0929	4	x	AY671857	AY671857	unpub	unpub
106		Gr2	E	Kapala	nr iridicolor sp 9	0944a	4	x	AY671871	AY671871	unpub	unpub
107		Gr2	E	Kapala	nr iridicolor sp 9	0950	4	x	AY671874	AY671874	unpub	unpub
108		Gr2	E	Kapala	nr iridicolor sp 10	0917	4	x	AY671853	AY671853	unpub	unpub
109		Gr2	E	Kapala	nr iridicolor sp 11	2781	2	x	unpub	x	x	unpub
110	X	Gr2	E	Kapala	nr iridicolor sp 11	0920	5	unpub	AY671854	AY671854	unpub	unpub
111	X	Gr2	E	Kapala	nr iridicolor sp 11	0382a	5	AY552321	AY552244	AY552244	KC008281	KC008470
112		Gr2	E	Kapala	nr iridicolor sp 11	0382b	4	x	unpub	unpub	unpub	unpub
113		Gr3	G	Kapala	sp 7	2915	3	x	unpub	unpub	unpub	x
114		Gr3	G	Kapala	sp 7	0384a	4	x	AY671846	AY671846	KC008259	KC008447
115	X	Gr3	G	Kapala	sp 8	3848	5	unpub	unpub	unpub	unpub	unpub
116		Gr3	G	Kapala	sp 8	3849	4	unpub	unpub	unpub	x	unpub
117		Gr3	G	Kapala	sp 9	0487	2	x	unpub	unpub	x	x
118		Gr3	G	Kapala	sp 9	0948	3	x	AY671873	AY671873	x	unpub
119		Gr3	G	Kapala	sp 9	2916	4	unpub (15 bp)	KC008122	KC008153	KC008260	x
120		Gr3	G	Kapala	sp 9	2918	4	x	unpub	unpub	unpub	unpub
121		Gr3	G	Kapala	sp 9	0383a	4	x	unpub	unpub	unpub	unpub
122		Gr3	G	Kapala	sp 9	0383c	4	x	unpub	unpub	unpub	unpub
123	X	Gr3	G	Kapala	sp 9	3437	5	unpub	unpub	unpub	unpub	unpub
124		Gr3	G	Kapala	sp 9	3812	4	x	unpub	unpub	unpub	unpub
125		Gr3	G	Kapala	sp 9	3813	4	x	unpub	unpub	unpub	unpub
126	X	Gr3	G	Kapala	sp 9	3822	5	unpub	unpub	unpub	unpub	unpub
127	X	Gr3	G	Kapala	sp 9	3824	5	unpub	unpub	unpub	unpub	unpub
128	X	Gr3	G	Kapala	sp 9	0379	5	AY552320	AY552243	AY552243	KC008274	KC008462
129	X	Gr3	G	Kapala	sp 9	3823	5	unpub	unpub	unpub	unpub	unpub
130	X	Gr3	G	Kapala	sp 9	3825	5	unpub	unpub	unpub	unpub	unpub
131		Gr3	G	Kapala	sp 9	3826	4	unpub	unpub	unpub	unpub	x
132	X	Gr3	G	Kapala	sp 9	0927a	5	KC008537	AY671855	AY671855	KC008257	KC008445
133		Gr3	G	Kapala	sp 9	0943a	4	x	AY671870	AY671870	unpub	unpub
134		Gr3	G	Kapala	sp 9	1405	3	x	AY671893	AY671893	x	unpub
135	X	Gr3	H	Kapala	ivorensis	0273	5	KC008564	AY672990	KC008161	KC008294	KC008483
136	X	Gr3	H	Kapala	ivorensis	2441	5	unpub	unpub	unpub	unpub	unpub
137	X	Gr3	H	Kapala	ivorensis	2648	5	unpub	unpub	unpub	unpub	unpub
138	X	Gr3	H	Kapala	ivorensis	2693	5	KC008565	KC008135	KC008162	KC008295	KC008484
139		Gr3	H	Kapala	ivorensis	2760	3	x	unpub	unpub	x	unpub
140	X	Gr3	H	Kapala	ivorensis	2746	5	unpub	unpub	unpub	unpub	unpub
141	X	Gr3	H	Kapala	ivorensis	2771	5	unpub	unpub	unpub	unpub	unpub
142	X	Gr3	H	Kapala	ivorensis	2772	5	KC008566	KC008136	KC008163	KC008296	KC008485
143		Gr3	H	Kapala	ivorensis	2924	4	unpub	unpub	unpub	x	unpub
144		Gr3	H	Kapala	ivorensis	2923	4	unpub	unpub	unpub	x	unpub
145		Gr3	H	Kapala	ivorensis	2922	4	unpub	unpub	unpub	x	unpub
146		Gr3	H	Kapala	izapa	2787	3	x	unpub	unpub	x	unpub
147		Gr3	H	Kapala	izapa	2793	4	unpub	x	unpub	unpub	unpub
148		Gr3	H	Kapala	izapa	2797	4	x	unpub	unpub	unpub	unpub
149		Gr3	H	Kapala	izapa	2925	5	KC008533	KC008119	KC008151	KC008252	KC008440
150	X	Gr3	H	Kapala	izapa	2926	3	unpub	x	unpub	unpub	x
151		Gr3	H	Kapala	izapa	0365	4	x	unpub	unpub	unpub	unpub
152	X	Gr3	H	Kapala	izapa	2786	3	x	unpub	unpub	x	unpub
153	X	Gr3	H	Kapala	nr striata	2796	5	KC008539	KC008124	KC008154	KC008262	KC008449

Table S3.2 continued

	96	Grp	clade	genus	species	DNA ID	genes	18S	D2	D3-5	COI	COII
154	**X**	Gr3	H	Kapala	sp 10	3738	**5**	unpub	unpub	unpub	unpub	unpub
155		Gr3	H	Kapala	sp 10	3851	**4**	unpub	unpub	unpub	x	unpub
156		Gr3	H	Kapala	sp 12	2798	**3**	x	unpub	unpub	x	unpub
157		Gr3	H	Kapala	sp 12	0934a	**5**	KC008545	AY671860	AY671860	KC008270	KC008458
158		Gr3	H	Kapala	sp 12	2785	**3**	x	unpub	unpub	x	unpub
159	**X**	Gr3	H	Kapala	sp 13	2800	**5**	KC008540	KC008125	KC008155	KC008263	KC008450
160		Gr3	H	Kapala	sp 14	0193c	**3**	x	unpub	unpub	x	unpub
161		Gr3	H	Kapala	sp 15	1413a	**4**	unpub	unpub	unpub	x	unpub
162	**X**	Gr3	H	Kapala	sp 15	1412a	**4**	x	KC008130	unpub	KC008269	KC008456
163		Gr3	H	Kapala	sp 16	0938c	**5**	KC008546	AY671865	AY671865	KC008271	KC008459
164		Gr3	H	Kapala	sp 17	2801	**4**	x	KC008127	KC008157	KC008265	KC008452
165	**X**	Gr3	H	Kapala	sp 18	3803	**4**	x	unpub	unpub	unpub	unpub
166		Gr3	H	Kapala	sp 19	1389	**5**	KC008535	KC008120	unpub	KC008255	KC008443
167		Gr3	H	Kapala	sp 20	1140	**5**	KC008534	AY671888	AY671888	KC008254	KC008442
168	**X**	Gr3	H	Kapala	sp 20	1142	**4**	unpub	AY671889	AY671889	x	unpub
169		Gr3	H	Kapala	sp 21	3749	**3**	x	unpub	x	unpub	unpub
170		Gr3	H	Kapala	sp 22	1397	**4**	unpub	unpub	unpub	x	unpub
171		Gr3		Kapala	argentina	1064	**4**	x	unpub	unpub	KC008267	KC008454
172	**X**	Gr3		Kapala	argentina	1076	**5**	KC008562	AY671882	AY671882	KC008291	KC008480
173		Gr3		Kapala	argentina	2920	**4**	unpub	unpub	unpub	unpub	x
174	**X**	Gr3		Kapala	nr argentina	0986	**5**	KC008548	AY671875	AY671875	KC008273	KC008461
175	**X**	Gr3		Kapala	floridana	0432b	**5**	JN623234	AY671850	AY671850	KC008293	KC008482
176		Gr3		Kapala	nr sulcifacies	0488	**2**	x	unpub	unpub	x	x
177		Gr3		Kapala	nr sulcifacies sp 1	1273	**3**	x	unpub	unpub	x	unpub
178	**X**	Gr3		Kapala	nr sulcifacies sp 2	3923	**5**	unpub	unpub	unpub	unpub	unpub
179		Gr3		Kapala	nr sulcifacies sp 2	3850	**1**	x	x	x	x	unpub
180	**X**	Gr3		Kapala	sp 1	3903	**5**	unpub	unpub	unpub	unpub	unpub
181	**X**	Gr3		Kapala	sp 2	0626	**5**	KC008538	AY671851	AY671851	KC008261	KC008448
182	**X**	Gr3		Kapala	sp 2	0941	**5**	unpub	AY671868	AY671868	unpub	unpub
183	**X**	Gr3		Kapala	sp 2	3853	**5**	unpub	unpub	unpub	unpub	unpub
184	**X**	Gr3		Kapala	sp 3	2261	**5**	KC008563	KC008134	KC008160	KC008292	KC008481
185		Gr3		Kapala	sp 3	2784	**1**	x	x	x	x	unpub
186	**X**	Gr3		Kapala	sp 4	3920	**5**	unpub	unpub	unpub	unpub	unpub
187	**X**	Gr3		Kapala	sp 4	2802	**5**	KC008541	KC008126	KC008156	KC008264	KC008451
188	**X**	Gr3		Kapala	sp 5	2266	**5**	KC008549	KC008132	KC008159	KC008275	KC008463
189	**X**	Gr3		Kapala	sp 6	2521	**5**	KC008536	KC008121	KC008152	KC008256	KC008444
190	**X**	Gr4		Kapala	sp 6	1080a	**5**	unpub	AY671884	AY671884	unpub	unpub
191		Gr3		Kapala	sulcifacies	0384c	**4**	x	unpub	unpub	unpub	unpub
192		Gr3		Kapala	sulcifacies	0384e	**4**	x	AY671848	AY671848	KC008258	KC008446
193	**X**	Gr3		Kapala	terminalis	1270	**5**	KC008561	AY671891	AY671891	KC008290	KC008479
194	**X**	Gr3		Kapala	terminalis	2260	**5**	unpub	unpub	unpub	unpub	unpub
195		Gr3		Kapala	terminalis	3435	**3**	unpub	unpub	unpub	x	x

		eye setae	nipple eye	anteclypeus	supraclypeal lateral margins	supraclypeal area sculpture	facial sculpture above torulus	facial sculpture below torulus	labral digits	maxillary palp	labial palp	scape length	F # flagell.	F flg L: head ht	F F2 length vs width	F shape of F2	F shape of F3	M # flagell.	M flg L: head ht, only branch	M F2 length vs width, no branch	M shape of funicular segments	scutellar projection	spine length	spine shape	spine setae	spine sculpture	spine apex	axillular groove	mesocutal flange over tegula	shape of prepectus	posterior scutellar margin
	coded terminals	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
	RI, combined data tree	0.7	1	0	0.5	0.417	0.76	0.824	0.75	0.731	0.667	0.8	0.656	0.618	0.4	0.519	0.455	1	0.455	0.375	0	0.5	0.607	0.615	0.556	0.375	0.805	0	1	0.286	0.607
1	Chalcura	[0 1]	0	2	1	0	[0 1]	[0 3]	[1 2]	[2 3]	[2 3]	0	[7 8 9]	1	1	4	0	0	1	1	1	0	4	-	-	-	-	0	0	1	0
2	Austeucharis	0	0	[1 2]	[0 1]	0	2	3	[1 2]	[1 2 3]	[0 1 2]	0	[8 9 0]	[1 2]	2	0	0	0	3	2	0	[1 0]	4	-	-	-	-	0	0	1	0
3	Ancylotropus	0	0	[0 1]	0	0	[0 1 3]	[0 1 3]	[1 2]	[0 1 2 3	[0 1 2]	0	[9 0]	1	1	0	0	0	3	2	0	[0 2]	0	1	1	3	0	[0 1]	0	1	[0 1]
4	Schizaspidia	0	0	[1 2]	0	0	[0 1]	0	1	[2 3]	[2 3]	0	[9 0]	1	1	0	1	0	0	1	1	2	3	1	1	3	0	[0 1]	0	0	0
5	Carletonia	0	0	0	1	0	2	1	[0 1]	0	0	0	?	?	?	?	?	[1 3]	0	1	1	1	4	-	-	-	-	0	0	1	0
6	Colocharis.elongata.D0421a	0	0	0	1	0	0	0	0	2	0	0	6	[2 3]	1	4	0	8	[1 2]	0	2	3	0	0	0	1	0	1	0	0	1
7	Colocharis.elongata.D3439	0	0	0	1	0	0	0	0	2	0	0	6	[2 3]	1	4	0	8	[1 2]	0	2	3	0	0	0	1	0	1	0	0	1
8	Colocharis.elongata.D3443	0	0	0	1	0	0	0	0	2	0	0	6	[2 3]	1	4	0	8	[1 2]	0	2	3	0	0	0	1	0	1	0	0	1
9	Colocharis.napoana.D1102	0	0	0	1	0	0	0	0	[2 3]	0	0	7	2	1	4	0	8	1	0	2	3	0	0	0	1	0	1	0	0	1
10	Colocharis.napoana.D1104	0	0	0	1	0	0	0	0	[2 3]	0	0	7	2	1	4	0	8	1	0	2	3	0	0	0	1	0	1	0	0	1
11	Colocharis.napoana.D1146	0	0	0	1	0	0	0	0	[2 3]	0	0	6	2	1	4	0	8	1	0	2	3	0	0	0	1	0	1	0	0	1
12	Colocharis.nr.napoana.D1157	0	0	0	1	0	0	0	0	[2 3]	0	0	6	2	1	4	0	8	1	0	2	3	0	0	0	1	0	1	0	0	1
13	Colocharis.sp.D3843	0	0	0	0	0	0	0	0	2	1	0	6	2	2	1	0	?	?	?	2	3	0	0	0	1	0	1	0	0	1
14	New.Genus.sp.ec.D1141	0	0	0	1	0	0	0	0	2	2	0	8	2	1	1	1	0	[1 2]	0	2	3	1	0	0	1	0	1	0	0	1
15	New.Genus.sp.ec.D1173	0	0	0	1	0	0	0	0	2	2	0	8	2	1	1	1	0	[1 2]	0	2	3	1	0	0	1	0	1	0	0	1
16	New.Genus.sp.peru.D3440	0	0	0	1	0	0	0	0	2	2	0	8	2	1	1	1	0	[1 2]	0	2	3	1	0	0	1	0	1	0	0	1
17	Lasiokapala.sp.D3598	1	0	0	0	0	0	0	0	2	0	0	6	2	1	3	3	?	?	?	?	3	2	0	1	0	0	1	0	0	3
18	Lasiokapala.sp.D3600	1	0	0	0	0	0	0	0	2	0	0	6	2	1	3	3	?	?	?	?	3	2	0	1	0	0	1	0	0	3
19	Latina.rugosa.D1073b	1	0	0	1	[2 3]	2	2	0	1	0	0	9	3	2	0	1	0	1	0	2	3	2	0	1	3	0	1	0	0	0
20	Latina.rugosa.D2509	1	0	0	1	[2 3]	2	2	0	1	0	0	9	3	2	0	1	0	1	0	2	3	2	0	1	3	0	1	0	0	0
21	Thoracantha.striata.D1254	1	0	0	0	1	1	1	0	0	0	0	8	2	1	1	1	0	0	0	2	3	2	2	1	1	0	0	0	0	3
22	Lirata.luteogaster.D1106	1	0	0	1	2	2	2	0	2	1	1	8	3	2	0	1	0	0	2	2	3	2	0	1	2	0	[0 1]	1	0	3
23	Lirata.striatissima.D0188	1	0	0	0	0	0	0	0	2	1	1	?	?	?	?	?	0	0	[1 2]	2	3	2	0	1	1	0	1	1	1	3
24	Lirata.striatissima.D2264	1	0	0	0	0	0	0	0	2	1	1	?	?	?	?	?	0	0	[1 2]	2	3	2	0	1	1	0	1	1	1	3
25	Neolirata.alta.D1101	1	0	0	1	1	1	0	0	1	1	1	0	3	1	1	1	0	1	0	2	3	2	0	1	1	0	1	0	0	0
26	Neolirata.daguerri.D3601	1	0	0	0	0	0	0	0	[1 2]	1	1	9	3	2	1	1	0	1	2	2	3	2	0	1	1	0	1	0	0	[0 3]
27	Neolirata.daguerri.D1067b	1	0	0	0	0	0	0	0	[1 2]	1	1	9	3	2	1	1	0	1	2	2	3	2	0	1	1	0	1	0	0	[0 3]
28	Parakapala	0	0	0	1	3	3	3	[0 1]	0	0	0	6	0	1	1	1	0	0	0	2	3	1	1	0	1	0	1	0	0	3
29	Liratella	0	0	0	0	0	0	0	0	2	2	0	8	0	1	0	0	0	0	0	2	3	2	0	1	1	0	1	0	0	3
30	Dicoelothorax.parviceps.D0374f	0	0	0	1	[2 3]	[2 3]	[2 3]	0	0	0	0	5	0	1	2	2	0	1	0	2	3	[1 2]	1	0	1	0	1	0	0	2
31	Dicoelothorax.parviceps.D3602	0	0	0	1	[2 3]	[2 3]	[2 3]	0	0	0	0	5	0	1	2	2	0	1	0	2	3	[1 2]	1	0	1	0	1	0	0	2
32	Dilocantha.bennetti.trin.D3807	0	0	0	0	3	3	3	0	2	2	0	0	0	0	0	0	0	1	0	2	3	1	1	0	0	0	1	1	0	2
33	Dilocantha.bennetti.trin.D3820	0	0	0	0	3	3	3	0	2	1	0	0	0	0	0	0	0	1	0	2	3	1	1	0	0	0	1	1	0	2
34	Dilocantha.serrata.D2265	0	0	0	1	3	3	3	0	2	1	0	8	1	1	1	1	0	1	0	2	3	1	1	0	1	0	1	1	0	2
35	Galearia.latreillei.D3922	0	0	0	1	1	4	4	0	1	1	0	8	0	1	0	0	0	0	0	2	3	3	2	0	[0 2]	0	1	0	1	[0 1]
36	Galearia.latreillei.D2251	0	0	0	1	1	4	4	0	1	1	0	8	0	1	0	0	0	0	0	2	3	3	2	0	[0 2]	0	1	0	1	[0 1]
37	Isomerala.azteca.D0278	0	1	0	1	1	1	1	1	3	3	0	8	0	0	0	0	0	0	0	2	3	1	0	0	1	0	1	0	0	2
38	Isomerala.bouceki.trin.D3821	0	1	0	0	3	3	3	1	3	3	0	8	0	1	0	0	0	?	0	2	3	2	0	0	1	1	1	0	0	1
39	Kapala.nr.furcata.sp1.mex.D2799	0	0	0	1	0	4	4	1	3	2	0	9	1	1	0	0	?	?	?	2	3	1	0	0	1	1	1	0	0	0
40	Kapala.nr.furcata.sp2.arg.D1078	0	0	0	1	0	4	4	1	2	2	0	0	1	1	0	0	?	?	?	2	3	1	0	0	1	0	1	0	0	1
41	Kapala.nr.furcata.sp3.cr.D1388	0	0	0	1	0	1	1	2	3	3	0	8	0	1	1	1	0	1	0	2	3	1	0	0	1	1	1	0	0	2
42	Kapala.nr.furcata.sp4.ec.D0942	0	0	0	1	0	4	4	1	3	3	0	?	?	?	?	?	0	1	0	2	3	?	0	0	1	0	1	0	0	1
43	Kapala.nr.furcata.sp5.arg.D1068a	0	0	0	0	0	4	4	[1 2]	3	3	0	[8 9]	1	1	0	0	0	[1 2]	0	2	3	1	0	0	1	[0 1]	1	0	0	[1 2]
44	Kapala.nr.furcata.sp5.arg.D1069	0	0	0	0	0	4	4	[1 2]	3	3	0	[8 9]	1	1	0	0	0	[1 2]	0	2	3	1	0	0	1	[0 1]	1	0	0	[1 2]
45	Kapala.cuprea.ec.D1003	0	0	0	0	0	4	4	[1 2]	3	3	0	9	0	1	0	0	0	1	0	2	3	1	0	0	1	[0 1]	1	0	0	[1 2]
46	Kapala.cuprea.ec.D1004	0	0	0	0	0	4	4	[1 2]	3	3	0	9	0	1	0	0	0	1	0	2	3	1	0	0	1	[0 1]	1	0	0	[1 2]
47	Kapala.iridicolor.hon.D0933c	0	0	0	1	0	[0 1]	0	1	3	3	0	9	1	1	0	0	0	1	0	2	3	1	0	0	1	1	1	0	0	1
48	Kapala.iridicolor.hon.D1267	0	0	0	1	0	[0 1]	0	1	3	3	0	9	1	1	0	0	0	1	0	2	3	1	0	0	1	1	1	0	0	1
49	Kapala.nr.iridicolor.sp1.pan.D0381	0	0	0	0	0	0	0	1	3	3	0	0	1	1	1	1	?	?	?	2	3	1	0	0	1	1	1	0	0	1
50	Kapala.nr.iridicolor.sp2.hon.D0933b	0	0	0	0	0	0	0	1	3	3	0	?	?	?	?	?	0	1	0	2	3	1	0	0	1	1	1	0	0	1
51	Kapala.nr.iridicolor.sp3.col.D0928a	0	0	0	[0 1]	0	0	0	[0 1]	3	[2 3]	0	9	1	1	0	0	0	1	0	2	3	[1 3]	0	0	1	0	1	0	0	1
52	Kapala.nr.iridicolor.sp3.cr.D2917	0	0	0	0	0	0	0	[0 1]	3	[2 3]	0	9	1	1	0	0	0	1	0	2	3	[1 3]	0	0	1	0	1	0	0	1
53	Kapala.nr.iridicolor.sp3.ec.D0935a	0	0	0	[0 1]	0	0	0	[0 1]	3	[2 3]	0	9	1	1	0	0	0	1	0	2	3	[1 3]	0	0	1	0	1	0	0	1
54	Kapala.nr.iridicolor.sp3.ec.D0938a	0	0	0	[0 1]	0	0	0	[0 1]	3	[2 3]	0	9	1	1	0	0	0	1	0	2	3	[1 3]	0	0	1	0	1	0	0	1
55	Kapala.nr.iridicolor.sp4.ec.D1138	0	0	0	0	0	0	0	2	3	3	0	0	1	1	0	0	?	?	?	2	3	1	0	0	1	1	1	0	0	1
56	Kapala.nr.iridicolor.sp5.ec.D0936a	0	0	0	[0 1]	0	0	0	2	3	3	0	0	1	1	1	1	0	1	0	2	3	1	0	0	1	1	1	0	0	1
57	Kapala.nr.iridicolor.sp5.ec.D0937	0	0	0	[0 1]	0	0	0	2	3	3	0	0	1	1	1	1	0	1	0	2	3	1	0	0	1	1	1	0	0	1
58	Kapala.nr.iridicolor.sp6.col.D0947	0	0	0	0	0	0	0	2	3	3	0	9	1	1	0	0	?	?	?	2	3	1	0	0	1	1	1	0	0	1
59	Kapala.nr.iridicolor.sp11.col.D0920	0	0	0	1	0	0	0	1	3	2	0	?	?	?	?	?	0	1	0	2	3	1	0	0	1	1	1	0	0	1
60	Kapala.nr.iridicolor.sp11.pan.D0382a	0	0	0	1	0	0	0	1	3	2	0	?	?	?	?	?	0	1	0	2	3	1	0	0	1	1	1	0	0	1
61	Kapala.argentina.D1076	0	0	0	0	1	1	1	2	3	3	0	8	0	1	0	0	0	1	0	2	3	1	0	0	1	1	1	0	0	1
62	Kapala.floridana.D0432b	0	0	0	1	1	2	1	[0 1]	3	2	0	8	1	1	0	0	0	1	0	2	3	1	0	0	1	1	1	0	0	0
63	Kapala.nr.argentina.arg.D0986	0	0	0	0	0	1	1	?	3	3	0	?	?	?	?	?	0	2	0	2	3	1	0	0	1	1	1	0	0	1
64	Kapala.nr.sulcifacies.sp2.col.D3923	0	0	0	1	1	1	1	0	?	?	0	?	?	?	?	?	0	2	0	2	3	1	0	0	1	1	1	0	0	1

Table S3.3. Character coding and retention indices. Outgroups were coded at the genus level. The retention indices are calculated from the fit to the parsimony combined analysis. An RI value of 1 shows perfect fit to the tree, and 0 indicates the character was parsimony uninformative.

Table S3.3 continued

		eye setae	nipple eye	anteclypeus	supraclypeal lateral margins	supraclypeal area sculpture	facial sculpture above torulus	facial sculpture below torulus	labral digits	maxillary palp	labial palp	scape length	F # flagell.	F flg L: head ht	F F2 length vs width	F shape of F2	F shape of F3	M # flagell.	M flg L: head ht, only branch	M F2 length vs width, no branch	M shape of funicular segments	scutellar projection	spine length	spine shape	spine setae	spine sculpture	spine apex	axillular groove	mesocutal flange over tegula	shape of prepectus	posterior scutellar margin
	coded terminals	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
	RI, combined data tree	0.7	1	0	0.5	0.417	0.76	0.824	0.75	0.731	0.667	0.8	0.656	0.618	0.4	0.519	0.455	1	0.455	0.375	0	0.5	0.607	0.615	0.556	0.375	0.805	0	1	0.286	0.607
65	Kapala.sp1.braz.D3903	0	0	0	0	0	1	1	?	3	3	0	?	?	?	?	?	0	1	0	2	3	3	0	0	4	0	1	0	0	2
66	Kapala.sp2.ec.D0626	0	0	0	0	1	1	1	2	3	3	0	?	?	?	?	?	0	2	0	2	3	1	0	0	1	0	1	0	0	2
67	Kapala.sp2.ec.D0941	0	0	0	0	1	1	1	2	3	3	0	?	?	?	?	?	0	2	0	2	3	1	0	0	1	0	1	0	0	2
68	Kapala.sp2.venz.D3853	0	0	0	1	1	1	1	1	3	3	0	?	?	?	?	?	0	2	0	2	3	1	0	0	0	0	1	0	0	2
69	Kapala.sp3.dr.D2261	0	0	0	1	1	1	1	1	3	3	0	8	1	1	0	0	0	1	0	2	3	1	0	0	1	1	1	0	0	2
70	Kapala.sp4.arg.D3920	0	0	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	2	3	?	?	?	?	?	?	?	?	?
71	Kapala.sp4.frg.D2802	0	0	0	0	0	1	1	?	3	2	0	8	0	1	1	1	?	?	?	2	3	1	0	0	1	0	1	0	0	1
72	Kapala.sp5.texas.D2266	0	0	0	0	1	1	1	1	3	2	0	?	?	?	?	?	0	0	0	2	3	1	0	0	4	0	1	0	0	1
73	Kapala.sp6.arg.D1080a	0	0	0	0	0	1	1	0	3	3	0	8	1	1	0	0	0	0	0	2	3	1	0	0	1	1	1	0	0	1
74	Kapala.sp6.arg.D2521	0	0	0	0	0	1	1	0	3	3	0	8	1	1	0	0	0	0	0	2	3	1	0	0	1	1	1	0	0	1
75	Kapala.sp8.ec.D3848	0	0	0	1	1	1	1	1	3	3	0	?	?	?	?	?	0	2	0	2	3	1	0	0	4	1	1	0	0	1
76	Kapala.sp9.col.D0927a	0	0	0	0	0	1	1	[0 1]	3	3	0	?	?	?	?	?	0	[1 2]	0	2	3	1	0	0	4	[1 2]	1	0	0	1
77	Kapala.sp9.col.D3437	0	0	0	1	1	1	1	?	3	3	0	?	?	?	?	?	0	2	0	2	3	1	0	0	4	2	1	0	0	1
78	Kapala.sp9.guat.D0379	0	0	0	0	0	1	1	[0 1]	3	3	0	?	?	?	?	?	0	[1 2]	0	2	3	1	0	0	4	[1 2]	1	0	0	1
79	Kapala.sp9.trin.D3822	0	0	0	[0 1]	0	1	1	1	3	3	0	8	1	1	0	0	?	?	?	2	3	1	0	0	1	1	1	0	0	1
80	Kapala.sp9.trin.D3823	0	0	0	[0 1]	0	1	1	1	3	3	0	8	1	1	0	0	?	?	?	2	3	1	0	0	1	1	1	0	0	1
81	Kapala.sp9.trin.D3824	0	0	0	[0 1]	0	1	1	1	3	3	0	8	1	1	0	0	?	?	?	2	3	1	0	0	1	1	1	0	0	1
82	Kapala.sp9.trin.D3825	0	0	0	[0 1]	0	1	1	1	3	3	0	8	1	1	0	0	?	?	?	2	3	1	0	0	1	1	1	0	0	1
83	Kapala.sp10.hon.D3738	0	0	0	0	0	1	1	1	3	3	0	8	1	1	0	0	?	?	?	2	3	2	0	0	1	1	1	0	0	1
84	Kapala.sp11.hon.D0934a	0	0	0	0	0	1	1	1	3	3	0	8	1	1	0	0	?	?	?	2	3	1	0	0	1	1	1	0	0	1
85	Kapala.sp13.frg.D2800	0	0	0	0	0	1	1	1	3	3	0	8	1	1	1	1	?	?	?	2	3	2	0	0	1	1	1	0	0	1
86	Kapala.sp16.ec.D0938c	0	0	0	1	0	1	1	0	3	2	0	?	?	?	?	?	0	1	0	2	3	2	0	0	4	1	1	0	0	1
87	Kapala.sp19.gal.D1389	0	0	0	1	1	1	1	1	3	3	0	8	1	1	0	0	0	1	0	2	3	1	0	0	4	1	1	0	0	1
88	Kapala.sp20.ec.D1140	0	0	0	0	0	1	1	1	3	3	0	?	?	?	?	?	0	1	0	2	3	1	0	0	1	1	1	0	0	1
89	Kapala.sp22.dom.D2796	0	0	0	0	0	1	1	1	3	3	0	8	1	1	1	0	?	?	?	2	3	1	0	0	1	1	1	0	0	1
90	Kapala.ivorensis.cam.D2648	0	0	0	0	0	1	1	1	3	3	0	8	1	1	0	0	0	1	0	2	3	1	0	0	1	1	1	0	0	1
91	Kapala.ivorensis.ken.D2746	0	0	0	0	0	1	1	1	3	3	0	8	1	1	0	0	0	1	0	2	3	1	0	0	1	1	1	0	0	1
92	Kapala.ivorensis.mad.D2771	0	0	0	0	0	1	1	1	3	3	0	8	1	1	0	0	0	1	0	2	3	1	0	0	1	1	1	0	0	1
93	Kapala.ivorensis.mad.D2772	0	0	0	0	0	1	1	1	3	3	0	8	1	1	0	0	0	1	0	2	3	1	0	0	1	1	1	0	0	1
94	Kapala.ivorensis.nig.D2693	0	0	0	0	0	1	1	1	3	3	0	8	1	1	0	0	0	1	0	2	3	1	0	0	1	1	1	0	0	1
95	Kapala.ivorensis.saf.D2441	0	0	0	0	0	1	1	1	3	3	0	8	1	1	0	0	0	1	0	2	3	1	0	0	1	1	1	0	0	1
96	Kapala.ivorensis.st.D0273	0	0	0	0	0	1	1	1	3	3	0	8	1	1	0	0	0	1	0	2	3	1	0	0	1	1	1	0	0	1
97	Kapala.izapa.mex.D2925	0	0	0	0	1	1	1	1	3	3	0	8	1	1	0	0	0	[1 2]	0	2	3	1	0	0	1	1	1	0	0	1
98	Kapala.terminalis.dr.D1270	0	0	0	0	[0 1]	2	1	[0 1]	3	3	0	8	2	2	1	1	0	2	0	2	3	1	0	0	1	0	1	0	0	1
99	Kapala.terminalis.dr.D2260	0	0	0	0	[0 1]	2	1	[0 1]	3	3	0	8	2	2	1	1	0	2	0	2	3	1	0	0	1	0	1	0	0	1

Table S3.3 continued

		mesepisternum	mesepimeron	callous sculpture	callus pilosity	propodeal disc	propodeal carina	propodial spiracle	1st gastral tergite	erect setae over >1/2 of area	tergal scar	hypopygium	ovipositor shape	ovipositor shape tip	calcar	# hind tibial spurs	wing, infuscate	venation of forewing	stigmal vein	L postmarginal vein of forewing	pilosity of forewing wingdisc	marginal fringe on forewing	marginal fringe on hindwing
	coded terminals	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**
	RI, combined data tree	0.682	0.514	0.583	0.6	0.333	0.667	0.75	0.5	0.636	0.474	0.789	n/a	0	0.556	0.8	0	0.65	0.4	0.667	0.5	0.75	0.833
1	Chalcura	0	[0 2]	0	0	0	0	0	0	0	1	0	0	0	0	2	[0 1]	0	0	0	[0 1]	[0 1]	1
2	Austeucharis	2	2	1	1	0	0	0	0	0	[0 1]	2	0	1	0	2	0	0	0	[0 1]	0	0	1
3	Ancylotropus	[0 2]	[0 2]	1	[0 1]	0	0	0	0	0	[0 1]	2	[0 1]	0	0	2	0	0	0	0	0	0	1
4	Schizaspidia	2	2	1	1	[0 1]	0	0	0	0	[0 1]	[0 2]	[0 2]	0	0	[1 2]	[0 1]	0	0	0	0	1	1
5	Carletonia	0	2	1	1	0	0	0	0	0	1	?	?	?	0	1	1	0	1	0	0	1	1
6	Colocharis.elongata.D0421a	0	0	1	0	1	1	0	0	0	[0 1]	0	0	0	0	0	0	0	0	1	0	1	1
7	Colocharis.elongata.D3439	0	0	1	0	1	1	0	0	0	[0 1]	0	0	0	0	0	0	0	0	1	0	1	1
8	Colocharis.elongata.D3443	0	0	1	0	1	1	0	0	0	[0 1]	0	0	0	0	0	0	0	0	1	0	1	1
9	Colocharis.napoana.D1102	0	1	1	0	1	1	0	0	0	[0 1]	0	0	0	0	0	0	0	0	1	0	1	1
10	Colocharis.napoana.D1104	0	1	1	0	1	1	0	0	0	[0 1]	0	0	0	0	0	0	0	0	1	0	1	1
11	Colocharis.napoana.D1146	0	1	1	0	1	1	0	0	0	[0 1]	0	0	0	0	0	0	0	0	1	0	1	1
12	Colocharis.nr.napoana.D1157	0	1	1	0	1	1	0	0	0	[0 1]	0	0	0	0	0	0	0	0	1	0	1	1
13	Colocharis.sp.D3843	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
14	New.Genus.sp.ec.D1141	0	[0 1]	1	1	1	[0 1]	1	0	0	[0 1]	1	0	0	0	2	0	1	0	1	0	1	1
15	New.Genus.sp.ec.D1173	0	[0 1]	1	1	1	[0 1]	1	0	0	[0 1]	1	0	0	0	2	0	1	0	1	0	1	1
16	New.Genus.sp.peru.D3440	0	[0 1]	1	1	1	[0 1]	1	0	0	0	1	0	0	0	2	0	1	0	1	0	1	1
17	Lasiokapala.sp.D3598	0	0	0	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1
18	Lasiokapala.sp.D3600	0	0	0	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1
19	Latina.rugosa.D1073b	1	1	1	1	1	1	1	0	1	1	1	0	0	[0 1]	[1 2]	0	0	0	1	0	0	1
20	Latina.rugosa.D2509	1	1	1	1	1	1	1	0	1	1	1	0	0	[0 1]	[1 2]	0	0	0	1	0	0	1
21	Thoracantha.striata.D1254	1	1	[1 2]	0	1	2	1	1	1	1	1	0	0	1	1	0	0	1	1	0	0	1
22	Lirata.luteogaster.D1106	0	1	2	0	[0 1]	1	1	0	1	1	1	0	0	1	0	0	1	0	2	[0 1]	0	0
23	Lirata.striatissima.D0188	0	0	[1 2]	0	[0 1]	1	1	0	1	1	1	0	0	1	0	0	1	0	2	[0 1]	0	0
24	Lirata.striatissima.D2264	0	0	[1 2]	0	[0 1]	1	1	0	1	1	1	0	0	1	0	0	1	0	2	[0 1]	0	0
25	Neolirata.alta.D1101	0	2	1	1	[0 1]	1	1	0	1	1	1	0	0	1	1	0	1	0	1	0	0	1
26	Neolirata.daguerri.D3601	0	2	[1 2]	0	[0 1]	1	1	0	1	1	1	0	0	1	1	0	1	0	1	0	0	1
27	Neolirata.daguerri.D1067b	2	2	[1 2]	0	[0 1]	1	1	0	1	1	1	0	0	1	1	0	1	0	1	0	0	1
28	Parakapala	0	0	0	0	1	0	1	0	0	1	2	0	?	1	2	0	1	1	1	0	0	1
29	Liratella	0	0	1	0	1	1	1	0	1	1	2	0	0	0	2	0	1	1	2	1	0	1
30	Dicoelothorax.parviceps.D0374f	1	1	[0 2]	0	1	0	1	0	0	1	1	0	0	1	1	0	1	0	0	[0 1]	0	1
31	Dicoelothorax.parviceps.D3602	1	1	[0 2]	0	1	0	1	0	0	1	1	0	0	1	1	0	1	0	0	[0 1]	0	1
32	Dilocantha.bennetti.trin.D3807	1	1	[0 2]	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
33	Dilocantha.bennetti.trin.D3820	1	1	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
34	Dilocantha.serrata.D2265	1	1	2	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
35	Galearia.latreillei.D3922	1	1	2	1	1	2	1	1	0	1	0	0	0	0	0	0	1	0	0	1	0	1
36	Galearia.latreillei.D2251	1	1	2	1	1	2	1	1	0	1	0	0	0	0	0	0	1	0	0	1	0	1
37	Isomerala.azteca.D0278	1	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1
38	Isomerala.bouceki.trin.D3821	3	3	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1
39	Kapala.nr.furcata.sp1.mex.D2799	0	1	0	1	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
40	Kapala.nr.furcata.sp2.arg.D1078	0	0	1	1	1	1	1	0	0	[0 1]	1	0	0	0	2	0	1	0	1	0	0	1
41	Kapala.nr.furcata.sp3.cr.D1388	0	3	1	1	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
42	Kapala.nr.furcata.sp4.ec.D0942	1	1	1	1	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
43	Kapala.nr.furcata.sp5.arg.D1068a	1	1	1	1	1	1	1	0	0	[0 1]	1	0	0	0	2	0	1	0	1	0	0	1
44	Kapala.nr.furcata.sp5.arg.D1069	1	1	1	1	1	1	1	0	0	[0 1]	1	0	0	0	2	0	1	0	1	0	0	1
45	Kapala.cuprea.ec.D1003	1	1	1	1	1	1	1	0	0	[0 1]	1	0	0	0	2	0	1	0	1	0	0	1
46	Kapala.cuprea.ec.D1004	1	1	1	1	1	1	1	0	0	[0 1]	1	0	0	0	2	0	1	0	1	0	0	1
47	Kapala.iridicolor.hon.D0933c	0	0	1	1	1	1	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	1
48	Kapala.iridicolor.hon.D1267	0	0	1	1	1	1	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	1
49	Kapala.nr.iridicolor.sp1.pan.D0381	0	0	1	1	1	0	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	1
50	Kapala.nr.iridicolor.sp2.hon.D0933b	0	0	1	1	1	1	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	1
51	Kapala.nr.iridicolor.sp3.col.D0928a	1	[0 1]	1	1	1	1	1	0	0	?	1	0	0	0	2	0	1	0	1	0	0	1
52	Kapala.nr.iridicolor.sp3.cr.D2917	0	[0 1]	1	1	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
53	Kapala.nr.iridicolor.sp3.ec.D0935a	0	[0 1]	1	1	1	1	1	0	0	?	1	0	0	0	2	0	1	0	1	0	0	1
54	Kapala.nr.iridicolor.sp3.ec.D0938a	0	[0 1]	1	1	1	1	1	0	0	?	1	0	0	0	2	0	1	0	1	0	0	1
55	Kapala.nr.iridicolor.sp4.ec.D1138	0	0	1	1	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
56	Kapala.nr.iridicolor.sp5.ec.D0936a	0	[0 1]	1	1	1	1	1	0	0	?	1	0	0	0	2	0	1	0	1	0	0	1
57	Kapala.nr.iridicolor.sp5.ec.D0937	0	[0 1]	1	1	1	1	1	0	0	?	1	0	0	0	2	0	1	0	1	0	0	1
58	Kapala.nr.iridicolor.sp6.col.D0947	0	0	1	1	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
59	Kapala.nr.iridicolor.sp11.col.D0920	[0 1]	[0 1]	1	1	1	1	1	0	0	?	1	0	0	0	2	0	1	0	1	0	0	1
60	Kapala.nr.iridicolor.sp11.pan.D0382a	[0 1]	[0 1]	1	1	1	1	1	0	0	?	1	0	0	0	2	0	1	0	1	0	0	1
61	Kapala.argentina.D1076	1	1	1	1	1	1	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	1
62	Kapala.floridana.D0432b	1	1	3	1	1	1	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	1
63	Kapala.nr.argentina.arg.D0986	1	1	1	0	1	1	1	0	0	?	1	0	0	0	2	0	1	0	1	0	0	1
64	Kapala.nr.sulcifacies.sp2.col.D3923	0	0	1	0	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1

Table S3.3 continued

		mesepisternum	mesepimeron	callous sculpture	callus pilosity	propodeal disc	propodeal carina	propodial spiracle	1st gastral tergite	erect setae over >1/2 of area	tergal scar	hypopygium	ovipositor shape	ovipositor shape tip	calcar	# hind tibial spurs	wing, infuscate	venation of forewing	stigmal vein	L postmarginal vein of forewing	pilosity of forewing wingdisc	marginal fringe on forewing	marginal fringe on hindwing
	coded terminals	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**
	RI, combined data tree	0.682	0.514	0.583	0.6	0.333	0.667	0.75	0.5	0.636	0.474	0.789	n/a	0	0.556	0.8	0	0.65	0.4	0.667	0.5	0.75	0.833
65	Kapala.sp1.braz.D3903	0	1	1	1	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
66	Kapala.sp2.ec.D0626	1	1	1	0	1	1	?	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
67	Kapala.sp2.ec.D0941	1	1	1	0	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
68	Kapala.sp2.venz.D3853	1	1	1	0	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
69	Kapala.sp3.dr.D2261	1	1	1	1	1	1	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	1
70	Kapala.sp4.arg.D3920	?	?	?	?	1	?	?	0	0	?	1	0	0	0	2	0	1	0	1	0	?	0
71	Kapala.sp4.frg.D2802	1	1	1	1	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
72	Kapala.sp5.texas.D2266	2	2	1	0	1	1	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	1
73	Kapala.sp6.arg.D1080a	1	1	1	0	1	1	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	1
74	Kapala.sp6.arg.D2521	1	0	1	0	1	1	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	1
75	Kapala.sp8.ec.D3848	1	0	1	1	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
76	Kapala.sp9.col.D0927a	[0 1]	1	1	1	1	1	1	0	0	?	1	0	0	0	2	0	1	0	1	0	0	1
77	Kapala.sp9.col.D3437	0	0	1	1	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
78	Kapala.sp9.guat.D0379	[0 1]	1	1	1	1	1	1	0	0	?	1	0	0	0	2	0	1	0	1	0	0	1
79	Kapala.sp9.trin.D3822	0	0	1	1	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
80	Kapala.sp9.trin.D3823	0	0	1	1	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
81	Kapala.sp9.trin.D3824	0	0	1	1	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
82	Kapala.sp9.trin.D3825	0	0	1	1	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
83	Kapala.sp10.hon.D3738	1	0	1	0	1	1	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	1
84	Kapala.sp11.hon.D0934a	0	1	0	0	1	1	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	1
85	Kapala.sp13.frg.D2800	0	1	1	1	1	1	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	1
86	Kapala.sp16.ec.D0938c	1	1	1	1	1	1	1	0	0	?	1	0	0	0	2	0	1	0	1	0	0	1
87	Kapala.sp19.gal.D1389	1	1	1	1	1	1	1	0	0	?	1	0	0	0	2	0	1	0	1	0	0	1
88	Kapala.sp20.ec.D1140	1	0	1	1	1	1	1	0	0	?	1	0	0	0	2	0	1	0	1	0	0	1
89	Kapala.sp22.dom.D2796	0	0	1	1	1	1	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	1
90	Kapala.ivorensis.cam.D2648	1	[0 1]	1	1	1	1	1	0	0	[0 1]	1	0	0	0	2	0	1	0	1	0	0	1
91	Kapala.ivorensis.ken.D2746	1	[0 1]	1	1	1	1	1	0	0	[0 1]	1	0	0	0	2	0	1	0	1	0	0	1
92	Kapala.ivorensis.mad.D2771	1	[0 1]	1	1	1	1	1	0	0	[0 1]	1	0	0	0	2	0	1	0	1	0	0	1
93	Kapala.ivorensis.mad.D2772	1	[0 1]	1	1	1	1	1	0	0	[0 1]	1	0	0	0	2	0	1	0	1	0	0	1
94	Kapala.ivorensis.nig.D2693	1	[0 1]	1	1	1	1	1	0	0	[0 1]	1	0	0	0	2	0	1	0	1	0	0	1
95	Kapala.ivorensis.saf.D2441	1	[0 1]	1	1	1	1	1	0	0	[0 1]	1	0	0	0	2	0	1	0	1	0	0	1
96	Kapala.ivorensis.st.D0273	1	[0 1]	1	1	1	1	1	0	0	[0 1]	1	0	0	0	2	0	1	0	1	0	0	1
97	Kapala.izapa.mex.D2925	1	1	1	1	1	1	1	0	0	1	1	0	0	0	2	0	1	0	1	0	0	1
98	Kapala.terminalis.dr.D1270	1	1	[0 1]	1	1	1	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	1
99	Kapala.terminalis.dr.D2260	1	1	[0 1]	1	1	1	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	1

Character State Reconstruction, with focus on the mode of oviposition

```
#NEXUS
BEGIN CHARACTERS;
        DIMENSIONS  NCHAR=12;
        FORMAT DATATYPE = STANDARD GAP = - MISSING = ? SYMBOLS = "  0 1 2 3 4 5 6 7 8 9";
        CHARSTATELABELS
                1 eye_setae, 2 oviposition_habits, 3 labral_digits, 4 max._palp, 5
labial_palp, 6 female_#_flag, 7 male_#_flag, 8 scutellar_projection, 9
male_shape_funicular_seg, 10 spine_length, 11 spine_setae, 12 forewing_marg_fringe ;

[oviposition habits -> 0 =into flower buds, 1 =undersides of leaves, 2 =stem by base of
leaf, 3 =into incisions on undersides of leaves)]

        MATRIX
        Chalcura.nr.ramosa.D0646a      (0 1)0(1 2)(2 3)(2 3)(7 8 9)0014?(0 1)
        Austeucharis.implexa.D0164     0?(1 2)(1 2 3)(0 1 2)(0 8 9)0(0 1)04?0
        Ancylotropus.carniscutis.D0407 0(0 1)(1 2)(0 1 2 3)(0 1 2)(0 9)0(0 2)0010
        Schizaspidia.aenea.D0168       0(0 1 3)1(2 3)(2 3)(0 9)021311
        Carletonia                     0?(0 1)00?(1 2)114?1
        Parakapala                     0?(0 1)006032100
        Liratella                      0?0228032210
        Colocharis.napoana.D1102       0?0(2 3)0(6 7)832001
        Lasiokapala.serrata.D3598      1?0216?3?210
        Latina.rugosa.D2509            110109032210
        Thoracantha.striata.D1254      110008032210
        Lirata.luteogaster.D1106       1?0218032210
        Neolirata.alta.D1101           110(1 2)1(0 9)032210
        Dicoelothorax.parviceps.D3602  010005032(1 2)00
        Dilocantha.bennetti.trin.D3807 0?02(1 2)(0 8)032100
        Galearia.latreillei.D2251      0(1 2)0118032300
        Isomerala.azteca.D0278         0?1338032(1 2)00
        Kapala.nr.furcata.ec.D0942     00(1 2)3(2 3)8032100
        Kapala.iridicolor.hon.D0933c   00(0 1 2)3(2 3)8032(1 3)00
        Kapala.sp.guat.D0379           0(0 1)(0 1 2)3(2 3)8032(1 2)00
        New.Genus.D1173                0?0228032101;
END;

BEGIN TREES;
        TRANSLATE
                1 Chalcura.nr.ramosa.D0646a,
                2 Austeucharis.implexa.D0164,
                3 Ancylotropus.carniscutis.D0407,
                4 Schizaspidia.aenea.D0168,
                5 Carletonia,
                6 Parakapala,
                7 Liratella,
                8 Colocharis.napoana.D1102,
                9 Lasiokapala.serrata.D3598,
                10 Latina.rugosa.D2509,
                11 Thoracantha.striata.D1254,
                12 Lirata.luteogaster.D1106,
                13 Neolirata.alta.D1101,
                14 Dicoelothorax.parviceps.D3602,
                15 Dilocantha.bennetti.trin.D3807,
                16 Galearia.latreillei.D2251,
                17 Isomerala.azteca.D0278,
                18 Kapala.nr.furcata.ec.D0942,
                19 Kapala.iridicolor.hon.D0933c,
                20 Kapala.sp.CL5guat.D0379,
                21 Kapala.sp.PEec.D1173;
        TREE UNTITLED =
(1,(2,(5,((3,4),(8,((((((11,(9,(6,14))),10),13),18),19),(((12,15),(7,16)),(17,20))),21))
))));

END;
```

Characters and character states used in the morphological matrix. Characters identified as (Heraty, 2002) were coded previously for a phylogenetic investigation of the entire Eucharitidae, including Perilampidae outgroups. These characters were either taken as coded due to applicability at the genus level, or the character coding was modified to be more discriminatory for the Kapala clade. Figures labeled as "Fig. S3.C" are found immediately following all character descriptions.

Morphological Coding:

HEAD

1. Eye setae (Heraty, 2002) [character 1].
   0. absent or with setae barely discernable
   1. present, erect and bristle-like (in Heraty, 2002, figs 32, 87, 180, 201)

2. Shape of compound eye. This character is diagnostic for *Isomerala*, which has the eye protruding medially, as in Fig. 3.3.
   0. globular and convex
   1. conical-shaped

3. Anteclypeus (Heraty, 2002) [char. 7, modified].
   0. distinct and linear (in Heraty, 2002, figs 6, 375, 376, 398,400)
   1. indistinct with lower clypeal margin not produced and evenly convex to margin(in Heraty, 2002, fig. 410)
   2. clypeal margin extended as rounded flange over mouthparts and evenly convex to margin (in Heraty, 2002, figs 374, 432)

4. Supraclypeal area (Heraty, 2002) [char. 8, modified].
   0. indistinct lateral sulci (area absent) or impressed <1/2 distance to torulus (in Heraty, 2002, figs 400, 410)
   1. lateral margins impressed for > 1/2 distance to torulus (in Heraty, 2002, figs 6, 18, 375, 398, 403, 421, 425, 432)

5. Supraclypeal area, sculpture.
   0. Smooth (Fig. S3.C1)
   1. striate or sculptured (margins at anterior tentorial pits to outer base of torulus) (Fig. S3.C2)
   2. rugose (Fig. S3.C3)
   3. punctate (Fig. S3.C4)

6. Facial sculpture above torulus (lateral to scrobes).
   0. smooth or with only weak, scattered punctations (Fig. S3.C5)
   1. wide striae (Fig. S3.C2)
   2. rugose (Fig. S3.C3)
   3. punctate (Fig. S3.C6)
   4. fine, close striae (Fig.S3.C1)

7. Facial sculpture below torulus (lateral to clypeal region).
   0. smooth or with only weak, scattered punctations
   1. wide striae
   2. rugose
   3. punctate
   4. fine, close striae

8. Number of labral digits (used as a range; typically variable within species) (Heraty, 2002) [char. 17, modified] (in Heraty, 2002, figs 4, 6, 238, 432).
   0. 4-6 digits
   1. 7-9 digits
   2. 10-13 digits

9. Maxillary palp (Heraty, 2002) [char. 18, but unordered].
   0. absent
   1. 1-segmented
   2. 2-segmented
   3. 3-segmented

10. Labial palp (Heraty, 2002) [char. 19, but unordered].
   0. absent
   1. 1-segmented
   2. 2-segmented

ANTENNA

11. Scape length (Heraty, 2002) [char. 21, modified].
   0. not reaching to median ocellus (in Heraty, 2002, figs 388, 389, 392)
   1. exceeding bottom margin of median ocellus

12. Female: number of flagellomeres. In some cases, the terminal flagellomere is divided and more easily distinguished from the penultimate on the inner, medial surface but not the outer lateral surface. In these instances, the flagellomeres were recorded as two and not one.
recorded as counted (6-10), ‘0’ indicates 10, which is the maximum number

13. Female: flagellum length to head height ratio (Heraty & Woolley, 1993) [see in Heraty, 2002, fig. 2] (Fig. 5.1). If the flagellum was in a curved position, the measurement was taken with one pivot point along the length.
   0. < 1.0
   1. 1.0-1.4
   2. 1.41-1.99
   3. >2

14. Female: flagellomere 2 (F2) (basal flagellomere) length vs width (Heraty, 2002) [char. 26, modified] (Fig. 5.1).
   0. as wide as high; approximately transverse but <1.5x
   1. length vs width = 1.5 to 3x
   2. length vs width > 3x

15. Female: shape of F2 (Heraty, 2002) [char. 28, modified]. Character states 0 and 1 may show too much continuity between simple and serrate to be useful. Intraspecific variation is high.
   0. simple, cylindrical
   1. serrate
   2. oblique serrate, obvious sharp point
   3. pectinate, elongate branches (only *Lasiokapala*)

16. Female: shape of F3. Character states 0 and 1 may show too much continuity between simple and serrate to be useful. Intraspecific variation is high.
   0. simple, cylindrical
   1. serrate
   2. oblique serrate, obvious sharp point
   3. pectinate, elongate branches (only *Lasiokapala*)

17. Male: number of flagellomeres.
recorded as counted (8-13), “0 – 3” coding indicates 10 – 13 flagellomeres

18. Male: F2 branch length to head height ratio (Heraty & Woolley, 1993) [see in Heraty, 2002, fig. 2].
   0. < 1.0
   1. 1.0-1.4
   2. 1.41-1.99
   3. >2

19. Male: flagellomere 2 (F2) (basal flagellomere) length vs width, not including flagellar branch (Heraty, 2002) [char. 32, modified].
   0. as wide as high; approximately transverse but <1.5x
   1. length vs width = 1.5 to 3x
   2. length vs width > 3x

20. Male: shape of funicular segment [char. 35].

0. all segments simple, serrate, or moniliform (in Heraty, 2002, figs 31, 39, 101, 126, 433)
1. unevenly branched, F2 very different from F3 (in Heraty, 2002, figs 75, 80, 81, 231, 345, 411)
2. uniformly branched, F2 and F3 similar (in Heraty, 2002, figs 105, 120, 131, 141, 408)
3. uniformly pectinate with thick branches (figs 188, 359)

MESOSOMA

21. Posterior scutellar margin projection (Heraty, 2002) [char. 50, partial, modified].

0. rounded apically / no projection
1. apical margin emarginate or only slightly produced
2. cylindrical or flat process, 1 origin; may fork apically; “spine”
3. cylindrical or flat process, 2 origins; “spine”

22. Scutellar spine length (landmarks as in Fig. 5.1).

0. shorter than length of scutellum
1. 1-2x the length of transscutal articulation to the apex of scutellar disc between spines
2. >2x length of scutellar disc from transscutal articulation to apex of scutellar disc
3. longer than scutellum, but shorter than 1x length of scutellar disc from transscutal articulation to apex of scutellum

23. Female: scutellar spine shape (Heraty, 2002) [char. 50, partial, modified].

0. relatively thin paired cylindrical processes
1. broad dorsoventrally flattened processes of female
2. forming an arching carapace over gaster of female

24. Spine bristles.

0. absent (Fig. 3.1, J, L, O)
1. present over length of spine (Fig. 3.1, F, K)

25. Scutellar spine sculpture (dorsal aspect). This character is homoplastic and difficult to discretize. *Lasiokapala* exhibits transverse striae apically, but >half of the spine is smooth and rounded, and was coded as state 0.

0. smooth or appearing nearly smooth for majority (Fig. 3.1, G, L)
1. longitudinal or oblique striae along entire length (Fig. 3.1, J, K, O)
2. transverse striae (Heraty, 2002, fig. 194)
3. rugose for over one quarter of length (some outgroups; Heraty, 2002, fig. 33)
4. serrated for over one quarter of length (Fig. S3.C9)

26. Scutellar spine apex. Concave emarginate is used to describe a tip where the dorsal margin curves inward before making contact to the ventral tip.
   0. rounded or acute, without any emargination (Fig. S3.C7, S3.C12)
   1. emarginate (Fig. S3.C8, S3.C10)
   2. concave-emarginate (Fig. S3.C9)

27. Axillular groove (Heraty, 2002) [char. 47, with state numbers reversed].
   0. absent (in Heraty, 2002, fig. 412)
   1. present (in Heraty, 2002, fig. 7)

28. Mesoscutal flange over tegula (Heraty, 2002) [char. 41].
   0. at most a very thin even flange along the margin of the tegula (in Heraty, 2002, figs 377, 393, 427, 429)
   1. triangular flange projecting posteriorly from the posterolateral corner of the mesoscutum over the tegula (in Heraty, 2002, fig. 200, arrow).

29. Shape of prepectus dorsolaterally (Heraty, 2002) [char. 64, modified].
   0. triangular to sub-rectangular (in Heraty, 2002, figs 1, 108, 399, 402, 427)
   1. narrow and fingerlike (in Heraty, 2002, figs 52, 62, 393)

30. Posterior medial margin of scutellar disc in lateral view.
   0. rounded or flattening to apex (Fig. S3.C10)
   1. ending in crested apex; apex ≤ 1.5x scutellar spine height (Fig. S3.C11)
   2. ending in crested apex; apex >1.5x spine height (Fig. S3.C12)
   3. medially depressed, raised and rounded scutellum laterally (Fig. S3.C13)

31. Mesepisternum.
   0. smooth (Fig. S3.C14)
   1. striations on more than one quarter of the surface (Fig. S3.C10)
   2. crenulate or rugose on more than one quarter of the surface
   3. punctate

32. Mesepimeron.
   0. smooth (Fig. S3.C14)
   1. striations on more than one quarter of the surface (Fig. S3.C10)
   2. crenulate or rugose on more than one quarter of the surface
   3. punctate

33. Callus sculpture.
   0. smooth or slight punctations
   1. rugose or crenulate
   2. striate

34. Callus pilosity (Heraty, 2002) [char. 57, modified].
  0. bare or with a few small setae (in Heraty, 2002, fig. 428)
  1. densely pilose (in Heraty, 2002, figs 384, 418)

35. Propodeal disc (Heraty, 2002) [char. 53, modified].
  0. convex (in Heraty, 2002, figs 7, 412, 434, 435)
  1. flat (in Heraty, 2002, fig. 124)

36. Carina bordering propodeal disc (Heraty, 2002) [char. 54, but unordered]. This character was coded at genus level directly from the character matrix of Heraty, 2002, but with the KC New Genus examined separately from the remainder of *Kapala*.
  0. absent
  1. present
  2. produced as a prominent flange that fits closely with the anterior face of the gaster

37. Propodeal spiracle (Heraty, 2002) [char. 55, modified].
  0. circular (in Heraty, 2002, figs 380, 418)
  1. circular with an incision / rounded notch ventrally (keyhole-like) (in Heraty, 2002, figs 177, 391)

GASTER

38. First gastral tergite (Heraty, 2002) [char. 87]. This character was coded at genus level directly from the character matrix of Heraty, 2002, but with the KC New Genus examined separately from the remainder of *Kapala*.
  0. relatively soft and pliable
  1. hardened and plate-like

39. Erect setae present on more than half of first gastral tergite.
  0. absent
  1. present, though may be very sparse

40. Tergal scar (Heraty, 2002) [char. 90].
  0. absent
  1. present (in Heraty, 2002, fig. 181)

41. Hypopygium (Heraty, 2002) [char. 94]. This character was coded at genus level directly from the character matrix of Heraty, 2002, but with the KC New Genus examined separately from the remainder of *Kapala*.
  0. with few or no setae apically surrounding mucro (in Heraty, 2002, figs 1, 45, 62, 106, 154)
  1. with a single linear ring of long curved hairs apically (in Heraty, 2002, figs 38, 156
  2. with a tuft of setae apically around mucro (in Heraty, 2002, figs 26, 229)

42. Ovipositor shape (Heraty, 2002) [char. 95].

0. acicular or needle-like (in Heraty, 2002, figs 307, 381)
1. expanded along entire length (in Heraty, 2002, fig. 26)

43. Ovipositor shape at extreme apex (Heraty, 2002) [char. 96].

0. straight or very slightly curved (in Heraty, 2002, figs 2, 65)
1. bent and slightly clubbed at tip (in Heraty, 2002, fig. 59)

LEGS AND WINGS

44. Calcar (Heraty, 2002) [char. 72, modified]. This character was coded at genus level directly from the character matrix of Heraty, 2002, but with the KC New Genus examined separately from the remainder of *Kapala*.

0. long, curved and bifid
1. thin, straight and acuminate

45. Number of hind tibial spurs (Heraty, 2002) [char. 73]. This character was coded at genus level directly from the character matrix of Heraty, 2002, but with the KC New Genus examined separately from the remainder of *Kapala*.

0. spurs absent
1. one
2. two

46. Infuscation of fore wing disc. This character was coded at genus level directly from the character matrix of Heraty, 2002, but with the KC New Genus examined separately from the remainder of *Kapala*.

0. uniformly transparent or slightly tinted
1. with darkened infuscate patch or patches

47. Venation of forewing (Heraty, 2002) [char. 77, modified]. This character was coded at genus level directly from the character matrix of Heraty, 2002, but with the KC New Genus examined separately from the remainder of *Kapala*.

0. distinct (in Heraty, 2002, figs 57, 115)
1. faint, venation beyond submarginal essentially absent (in Heraty, 2002, figs 51, 86, 108, 128, 189)

48. Stigmal vein.

0. darkened
1. nearly transparent, opaque

49. Length of postmarginal vein of forewing (Heraty, 2002) [char. 78]. This character was coded at genus level directly from the character matrix of Heraty, 2002, but with the KC New Genus examined separately from the remainder of *Kapala*.

0. absent (in Heraty, 2002, figs 86, 108, 128)
1. 3-4x as long as broad (in Heraty, 2002, figs 62, 115)
2. >5x as long as broad (in Heraty, 2002, figs 43, 57)

50. Pilosity of forewing wing disc (Heraty, 2002) [char. 79]. This character was coded at genus level directly from the character matrix of Heraty, 2002, but with the KC New Genus examined separately from the remainder of *Kapala*.

0. densely pilose with long setae (in Heraty, 2002, figs 1, 25, 57)
1. moderately pilose, usually with shorter setae (in Heraty, 2002, fig. 115)
2. bare or with only microtrichiae (in Heraty, 2002, figs 128, 189)

51. Marginal fringe on forewing (Heraty, 2002) [char. 80]. This character was coded at genus level directly from the character matrix of Heraty, 2002, but with the KC New Genus examined separately from the remainder of *Kapala*.

0. absent (in Heraty, 2002, fig. 86)
1. present (in Heraty, 2002, figs 1, 128)

52. Marginal fringe on hindwing (Heraty, 2002) [char. 82]. This character was coded at genus level directly from the character matrix of Heraty, 2002, but with the KC New Genus examined separately from the remainder of *Kapala*.

0. absent
1. present

FIGURES

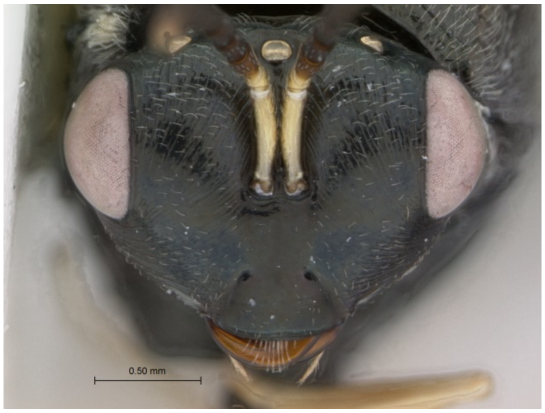

Fig. S3.C1. *Kapala cuprea* ♀.

Fig. S3.C2. *Kapala* sp2 venz ♂.

Fig. S3.C3. *Lirata luteogaster* ♀.

Fig. S3.C4. *Dicoelothorax platycerus* ♀.

Fig. S3.C5. *Kapala* iridicolor complex, *K.* nr *iridicolor* sp 2 ♂.

Fig. S3.C6. *Dilocantha serrata* ♂.

Fig. S3.C7. *K. terminalis* ♂.

Fig. S3.C8. *K. ivorensis* ♀.

Fig. S3.C9. *K.* sp 9 ♂, Clade G.

Fig. S3.C10. *K. floridana* ♀.

Fig. S3.C11. *K. argentina*♀.

Fig. S3.C12. *K*. sp2 venz ♂.

Fig. S3.C13. *Dicoelothorax parviceps* ♀.

Fig. S3.C14. *Kapala iridicolor* ♀.

7.3 Chapter 4

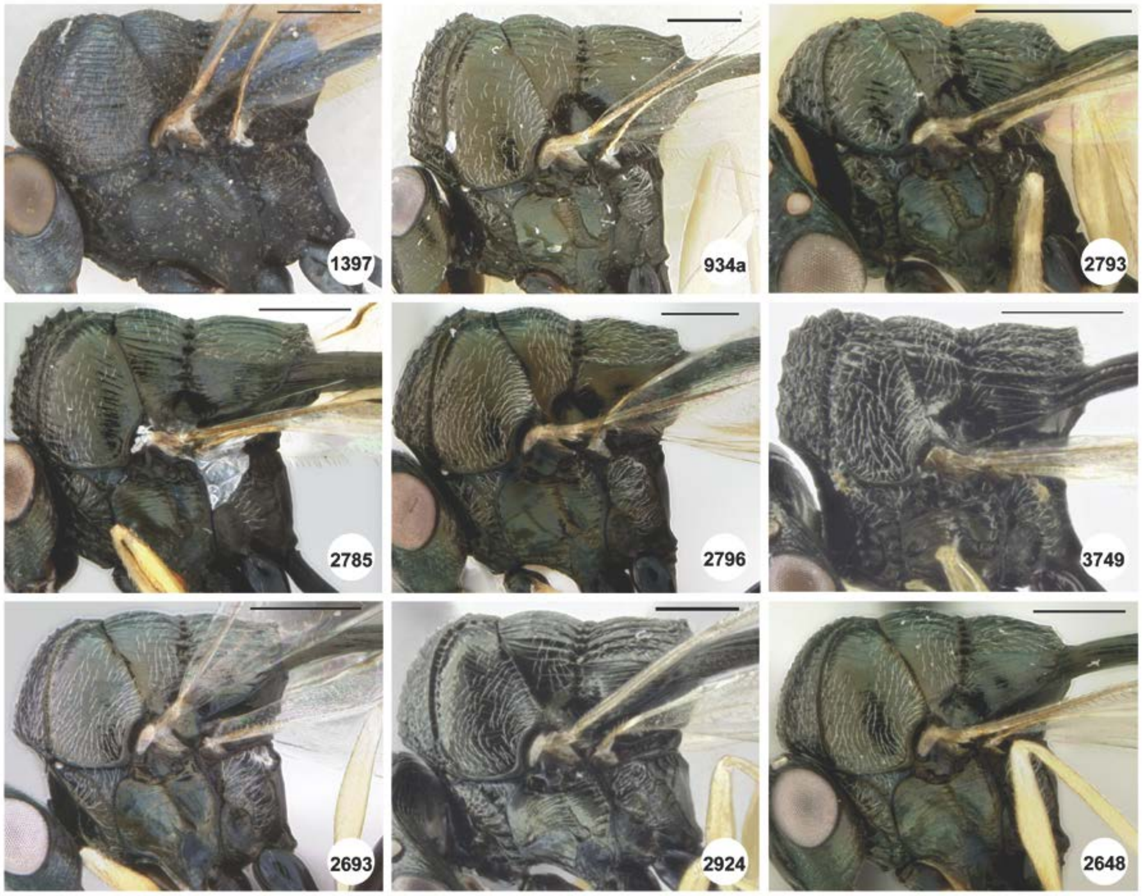

Figure S4.1. *Kapala*. Top and middle rows are New World *Kapala*, identified by DNA ID number. Bottom row is *K. ivorensis.*

		1	2	3	4	5
Congo	1	-				
Madagascar	2	0.000	-			
South Africa	3	0.467	0.000	-		
São Tomé	4	0.209	0.002	0.274	-	
Uganda	5	0.171	0.000	0.000	0.041	-

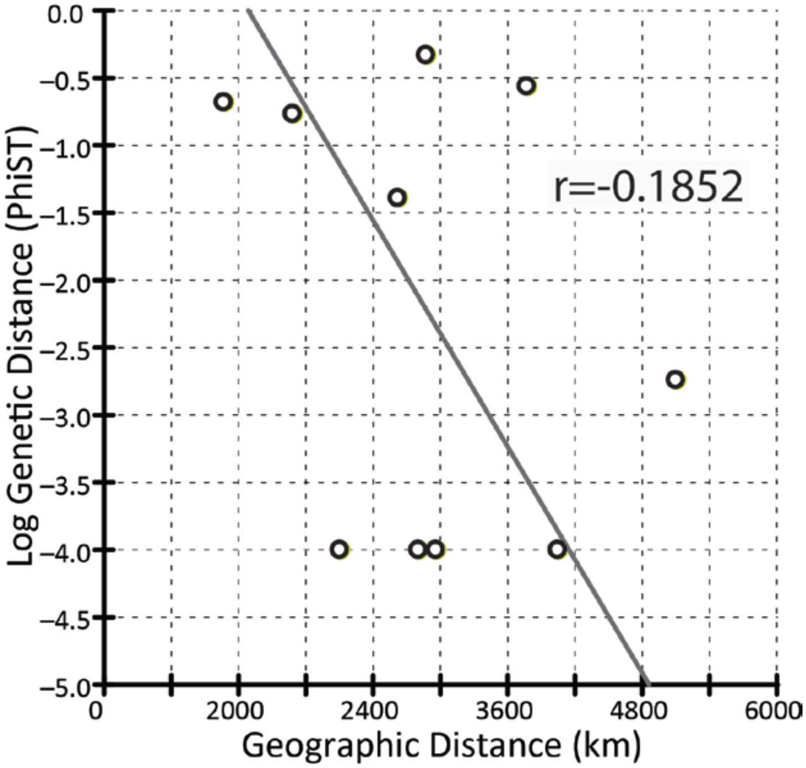

Figure S4.2. *Kapala ivorensis* populations. Top table is the phi$_{ST}$ values of the populations. Negative values were converted to zero distance. Bottom chart shows the lack of significant correlation between the genetic and geographic distances of the five populations.

7.4 Chapter 5

	species	DNA ID	UCRCENT ID	genes	18S	D2	D3-5	COI	COII
1	Kapala cuprea	1003	91807	**5**	unpub	AY671878	AY671878	unpub	unpub
2	Kapala cuprea	1004	92227	**5**	KC008551	AY671879	AY671879	KC008276	KC008465
3	Kapala cuprea	3804	412122	**4**	x	unpub	unpub	unpub	unpub
4	Kapala cuprea	3805	412123	**4**	x	unpub	unpub	unpub	unpub
5	Kapala cuprea	3806	412124	**4**	x	unpub	unpub	unpub	unpub
6	Kapala cuprea	3815	412133	**4**	x	unpub	unpub	unpub	unpub
7	Kapala cuprea	3833	247778	**4**	x	unpub	unpub	unpub	unpub
8	Kapala cuprea	3836	320767	**4**	x	unpub	unpub	unpub	unpub
9	Kapala cuprea	3837	320768	**3**	x	unpub	unpub	unpub	x
10	Kapala cuprea	3838	247775	**3**	x	unpub	unpub	unpub	unpub
11	Kapala cuprea	3852	320853	**5**	unpub	unpub	unpub	unpub	unpub
12	Kapala deltalis	1388	92109	**5**	KC008555	AY671892	AY671892	KC008280	KC008469
13	Kapala furcata	1078	92093	**5**	unpub	AY671883	AY671883	KC008253	KC008441
14	Kapala parafurcata	0711	91817	**4**	x	AY671852	AY671852	unpub	unpub
15	Kapala parafurcata	1069	91921	**5**	KC008554	AY671881	AY671881	KC008279	KC008468
16	Kapala parafurcata	1086	91803	**4**	x	unpub	unpub	unpub	unpub
17	Kapala parafurcata	2518	325	**4**	x	unpub	unpub	x	unpub
18	Kapala parafurcata	2519	161498	**3**	x	unpub	unpub	x	unpub
19	Kapala parafurcata	2520	324	**2**	x	unpub	x	x	unpub
20	Kapala parafurcata	3436	397274	**4**	unpub	unpub	unpub	unpub	x
21	Kapala parafurcata	1068a	92070	**5**	KC008552	AY671880	AY671880	KC008277	KC008466
22	Kapala quasimodo	0938b	92084	**3**	KC008550	AY671864	AY671864	x	x

Table S5.1. Gene information for the 26 molecular terminals. Five new COII gene fragments were added for this study: D2518, D3833, D3836, D3838, and D3852. An ‘x’ indicates no data.

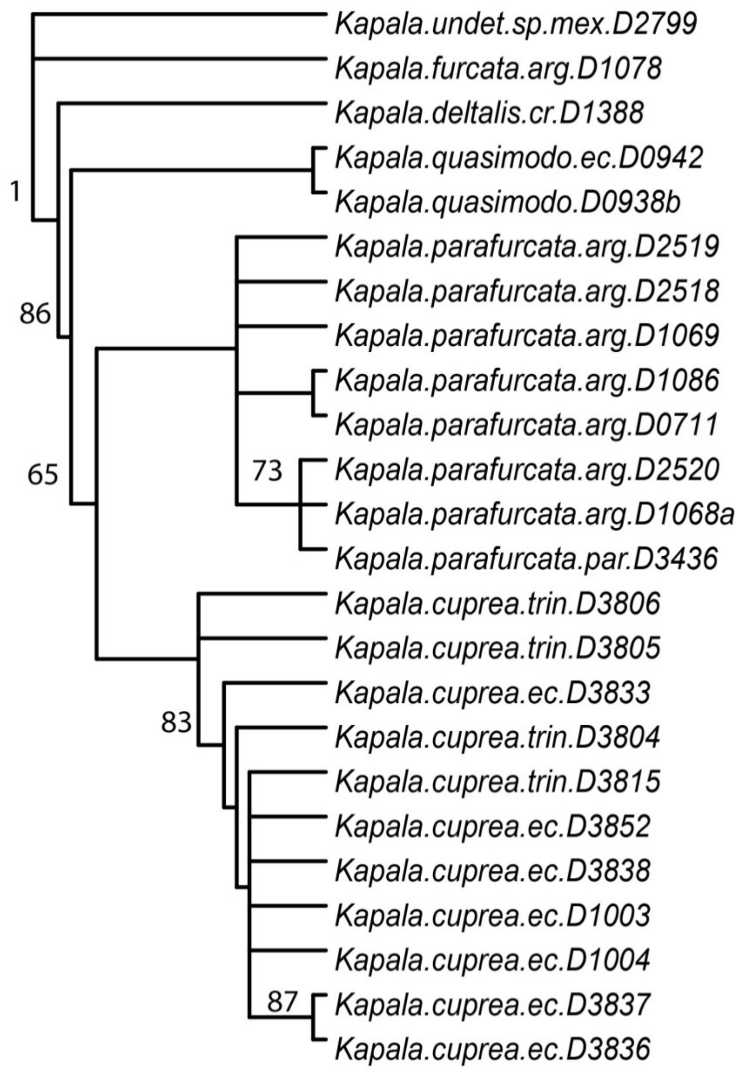

Figure S5.1. Bayesian phylogeny of furcata clade, 50% majority rule consensus tree. Five gene partitions: 18S, 28S-D2, 28S-D3, COI, and COII. COI and COII were analyzed under a codon model. Posterior probabilities over 70 shown.

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