



The global phylogeny of the subfamily Sycoryctinae (Pteromalidae): Parasites of an obligate mutualism

Simon T. Segar^a, Carlos Lopez-Vaamonde^b, Jean-Yves Rasplus^c, James M. Cook^{a,d,*}

^a School of Biological Sciences, University of Reading, Reading RG6 6AS, UK

^b INRA, UR 633 Zoologie Forestière, F-45075 Orléans, France

^c INRA, Centre de Biologie et de Gestion des Populations, Campus International de Baillarguet, CS 30 016, 34988 Montferrier-sur Lez, France

^d Hawkesbury Institute for the Environment, University of Western Sydney, Locked Bag 1797, Penrith South DC, New South Wales 1797, Australia

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ABSTRACT

The inflorescences of fig trees (*Ficus*, Moraceae) host well-defined, host plant specific wasp communities that lend themselves to tests of hypotheses on insect diversification. We provide the first estimate of the global molecular phylogeny for the Sycoryctinae – a large subfamily of fig wasps consisting mainly of parasitoids of fig-pollinating wasps. We find strong support for a large Old World clade that contains eight of the eleven genera, in the tribes Sycoryctini and Philotrypesini. The sister taxon is tribe Apocryptini, comprising the genera *Apocrypta* and *Bouceka*. Finally, a new tribe, Critogastrini, is raised for the genus *Critogaster*, sister to all other sycoryctines. At the genus level, we found a general pattern of strong host conservatism, in which closely related wasps associate with closely related figs. Despite this, there is also evidence for multiple host shifts between more distantly related figs in some wasp genera (especially *Philotrypesis*). We estimate Sycoryctinae to have originated 49–64 Ma, after the initial co-radiation of the host figs and pollinators. Further, conservative assumptions in our analyses probably overestimate the age of the sycoryctines. Together, patterns of host association, evidence for a mix of host constraints and host shifting, and molecular dating suggest that sycoryctine parasites radiated through delayed phylogenetic tracking of their hosts. This contributes to the growing body of literature suggesting that coevolving parasites often radiate after their hosts.

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1. Introduction

A large proportion of all known species are insects and many of these are either insect herbivores or the parasitoids that attack them. Consequently, the processes by which parasitoids and their insect hosts radiate across plants are responsible for the evolution of much of our extant terrestrial biodiversity (Bailey et al., 2009; Cruaud et al., 2010a). Coevolution has an important role in generating extant biodiversity (Chapela et al., 1994; Thompson, 1994; Peek et al., 1998; Rowan, 1998) and interactions between insects and plants, ranging from antagonistic herbivory (Ronquist and Liljeblad, 2001; Stireman et al., 2010) to obligate mutualism (Pellmyr and Leebens-Mack, 1999; Cook and Rasplus, 2003; Kawakita et al., 2004), often form the basis of complex multi-trophic communities (Nyman et al., 2007).

In general, insect herbivores are relatively host-specific, attacking only a few closely related host plant taxa (Strong et al., 1984;

Janz and Nylin, 1998; Schoonhoven et al., 2005). Similarly, many parasitoids attack only a small number of related insect hosts (Smith et al., 2007). These observations lead to the linked hypotheses that herbivores often cospeciate with their host plants, and parasitoids often cospeciate with their insect hosts. The first hypothesis has been tested in several studies (Ehrlich and Raven, 1964; Percy et al., 2004) with the general conclusion that, although insects often coevolve with plants they rarely cospeciate (Becerra, 1997; Smith and Bush, 1997; Cook et al., 2002; Winkler and Mitter, 2008; but see Roderick, 1997; Farrell and Mitter, 1998). Instead, many herbivore lineages appear to have radiated millions of years after their hosts (Lopez-Vaamonde et al., 2006; Gómez-Zurita et al., 2007; McKenna et al., 2009; but see Becerra, 2003). Indeed, figs and fig-pollinating wasps seem to provide the only strong case for the long-term co-radiation of an insect and a plant lineage (Rønsted et al., 2005).

Far less is understood about the radiation of parasitoids with respect to their host insects and host plants (Godfray, 1994; Quicke, 1997; Nicholls et al., 2010). Moreover, the ‘cascading’ impact of one trophic level (e.g. herbivores) on the one above it (e.g. parasitoids), in terms of radiation, has been emphasised only recently

* Corresponding author at: School of Biological Sciences, University of Reading, Reading RG6 6AS, UK.

E-mail address: james.cook@reading.ac.uk (J.M. Cook).

(Lopez-Vaamonde et al., 2005; Stireman et al., 2006; Nyman et al., 2007). Host shifting, either to a novel insect host or to a novel host plant, has been hypothesised as the main driver of parasitoid diversification (Godfray, 1994), but this idea awaits large-scale tests. What are the dominant modes of parasitoid radiation and how do they compare to those of their phytophagous hosts? To what degree is parasitoid speciation constrained by host insect or host plant phylogeny? To answer these questions we need robust estimates of molecular phylogenies of parasitoid taxa matched with high quality information on host associations.

The enclosed communities associated with insect galls offer excellent opportunities to study insect community evolution and compare radiation patterns between co-associated lineages of herbivores and parasitoids (e.g. Hayward and Stone, 2005). Figs (*Ficus*) and fig wasps provide one such system that is being used increasingly for studies of coevolution and community evolution (Kerdelhué et al., 2000; Cook and Segar, 2010). The genus *Ficus* is pantropical and species rich (Berg and Corner, 2005) and is dependent on symbiosis with tiny host-specific wasps (family Agaonidae) for pollination. The larvae of these wasps gall the fig flowers, as do the larvae of several other lineages of wasps that do not pollinate the trees. The galling wasps, in turn, are hosts for various lineages of parasitoid wasps whose larvae either feed directly on their insect hosts (Tzeng et al., 2008) or kill them while usurping their galls (Joseph, 1959).

There have been recent molecular estimates of global phylogenies of figs (Rønsted et al., 2005, 2008), fig-pollinating wasps (Lopez-Vaamonde et al., 2009; Cruaud et al., 2010b) and one lineage (subfamily Sycophaginae) of non-pollinating gallers (Cruaud et al., 2010a). Such studies allow comparisons of the age and biogeographic history of different lineages and there is strong support for long-term co-radiation of figs and pollinators (Rønsted et al., 2005). Recent studies provide independent support for the origin of both figs and their pollinators at least 60 Ma (although the mutualism may be up to 150 million years old) (Rønsted et al., 2005; Lopez-Vaamonde et al., 2009), but the area of origin remains controversial. Nevertheless, it seems clear that the sycophagine gallers originated later (ca. 40 Ma) and probably in a different continent (Australia) to their hosts. However, we cannot yet extend these comparisons to a third trophic level, because there have been no global phylogenies of lineages of parasitoid fig wasps.

The largest and most geographically widespread parasitoid lineage is the subfamily Sycoryctinae. These wasps are associated with all six *Ficus* subgenera and at least 15/19 sections (Jiang et al., 2006; this study). Assuming that sycoryctines occur on even just half of all Old World *Ficus* species we estimate a total species richness of 826 in this region (2.7 species per *Ficus* (McLeish et al., 2010) for 306 *Ficus* species (Berg and Corner, 2005)). The next richest group is the Sycophaginae with an estimated richness of 702 species (Cruaud et al., 2010a). Female sycoryctines lay eggs into the galls of fig-pollinating wasps, or more rarely other gall-inducing fig wasps, and kill their hosts either directly as parasitoids (Tzeng et al., 2008), or indirectly as cleptoparasites (Joseph, 1959). Most sycoryctines use pollinating wasps as hosts, but at least one genus (*Watshamiella*) appears to include some hyperparasitoids of other sycoryctines (Compton et al., 2009), while another (*Apocrypta*) includes parasitoids of non-pollinating gall-formers (Silvieus et al., 2008).

Despite the diversity and ecological importance of Sycoryctinae as parasites of fig-pollinating wasps (Dunn et al., 2008), the systematics of the subfamily remains controversial (Bouček, 1988; Munro et al., 2011) and hampers comparative studies. Sycoryctinae is currently placed in family Pteromalidae within the superfamily Chalcidoidea (Rasplus et al., 1998) and has three tribes (Wiebes, 1966): Apocryptini consisting only of *Apocrypta*; Philotrypesini containing *Philotrypesis* and *Philoverdane*; and Sycoryctini comprising 10 genera (Table 1) (Bouček, 1988; Pridyadarsanan,

2000). However, five genera are monotypic (Table 1) and taxonomists debate their validity, with several being synonymised by Bouček (1988) under *Sycoscapter*. At a higher level, the monophyly of the subfamily itself has been questioned repeatedly on both molecular and morphological grounds (Rasplus et al., 1998; Gibson et al., 1999; Munro et al., 2011). However, the only previous dedicated study of sycoryctine molecular systematics was restricted to species from one continent (Africa–McLeish et al., 2010). We therefore designed our sampling to cover all genera and continents.

We estimated the global sycoryctine phylogeny using three molecular markers on 130 species, representing 12 of the 13 genera, and covering all relevant continents. We used this to test the validity of currently recognised tribes and genera and propose appropriate changes to the classification. We then used multiple estimates of the sycoryctine phylogeny to test how often different sycoryctine genera have switched hosts between different *Ficus* sections. Finally, we also estimated the age and region of origin of the subfamily to test when and where these parasitoids entered the communities of wasps centred on fig fruits.

2. Methods

2.1. Taxon sampling

We sampled throughout the geographic range of the subfamily, with sampling effort (the Neotropics: 6 spp., Africa: 33 spp., Asia only: 10 spp., Australasia only: 27 spp., and Asia and Australasia: 54 spp.) fitted to regional diversity. Sampling density was therefore lowest in the Neotropics, but only *Critogaster* is found in this region. Described species or those included in previous publications are listed as previously described, while other taxa were identified to genus level for this study. Sycoryctinae belongs to the family Pteromalidae and we used 16 species from two other pteromalid fig wasp subfamilies (Otitesellinae and Sycoecinae) as outgroups.

2.2. DNA sequencing

We extracted genomic DNA using the chelex method of Lopez-Vaamonde et al. (2001) and then amplified fragments of three genes. The mitochondrial protein-coding gene cytochrome-*b* (*cyt-b*) was amplified using the primers CB1 and CB2 (Jermiin and Crozier, 1994). The D1–D3 region of the nuclear ribosomal gene 28S (28S) was amplified with the primers D1F and D3R (Campbell et al., 2000). Both of these genes were amplified following Lopez-Vaamonde et al. (2001). Finally, we amplified a fragment of the nuclear protein-coding gene elongation factor-one alpha (EF1a) using the primers EF1a-070333 and EF1a-073534, following the protocol of McLeish et al. (2010). We sequenced 120 new taxa for this study for three gene regions (28S: 108, EF-1a: 110 and *cyt-b*: 106) and their sequences were uploaded to EMBL under accession numbers HE793199–HE793306 and HE800211–HE800426 (Table A.1).

2.3. Sequence alignment and estimation of phylogenetic relationships

Edited *cyt-b* and EF-1a sequences were 417 and 335 bp long respectively, apart from two *cyt-b* sequences, which had 18 bp indels. All protein-coding sequences had full open reading frames and were aligned by eye. The alignments were shortened to 383 (*cyt-b*) and 322 (EF-1a) bp respectively in analyses to match the data available for species from McLeish et al. (2010). Sequence length varied more for 28S (920–974 bp) and sequences were aligned using the structural methods of Kjer (1995) and Gillespie et al. (2005).

We estimated the phylogenetic relationships between sycoryctines using Bayesian methods. These are thought to be

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