

Review Article

Diversity of Species and Behavior of Hymenopteran Parasitoids of Ants: A Review

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Reports of hymenopterans associated with ants involve more than 500 species, but only a fraction unambiguously pertain to actual parasitoids. In this paper, we attempt to provide an overview of both the diversity of these parasitoid wasps and the diversity of the types of interactions they have formed with their ant hosts. The reliable list of parasitoid wasps using ants as primary hosts includes at least 138 species, reported between 1852 and 2011, distributed among 9 families from 3 superfamilies. These parasitoids exhibit a wide array of biologies and developmental strategies: ecto- or endoparasitism, solitary or gregarious, and idio- or koinobiosis. All castes of ants and all developmental stages, excepting eggs, are possible targets. Some species parasitize adult worker ants while foraging or performing other activities outside the nest; however, in most cases, parasitoids attack ant larvae either inside or outside their nests. Based on their abundance and success in attacking ants, some parasitoid wasps like diapriids and eucharitids seem excellent potential models to explore how parasitoids impact ant colony demography, population biology, and ant community structure. Despite a significant increase in our knowledge of hymenopteran parasitoids of ants, most of them remain to be discovered.

1. Introduction

Ants are distributed all over the world, and their colonies provide both a stable food resource and numerous niches for thousands of other organisms, termed myrmecophiles, that exhibit a diverse array of relationships with their hosts [1–7]. Among myrmecophiles, numerous species of hymenopterans are associated with ants through predation, parasitism on the brood and/or adults, cleptoparasitism, parabiosis, mimetism, true symphily, or indirect parasitism through trophobionts and/or social parasites. However, in most cases, the precise nature of their relationship with their ant hosts remains obscure.

A review of the diversity of parasitoid wasps attacking ants has not been attempted since the work of Schmid-Hempel [7]. In his extensive review of the parasites of social insects, he pointed out the wide variety of hymenopteran parasitoids that attack these insects but, with the exception

of the family Eucharitidae (with 33 valid species really involved), his list provided very few other examples (only 10) of true parasitoidism, that is, cases where the attack of the wasp species on ants (adults or brood) has been reliably demonstrated.

Knowledge has increased greatly in the intervening years, and numerous cases of parasitic associations involving wasps and ants have been reported. Moreover, changes in nomenclature and phylogeny have been numerous in the last two decades (see, e.g., [8–15]), and many species names of both the parasitoids and their ant hosts required emendations.

In the present paper, we address only hymenopteran parasitoids and focus strictly on ant-parasitoid wasp associations in which parasitism has been established beyond any doubt, and where ants are proved to be the primary hosts. Therefore, no bethylid species are considered here even though various members of the genera *Pseudisobrachium* and

Dissomphalus are strongly suspected of being parasitoids of ant brood [16–18]. Neither are any species of ceraphronid, dryinid, figitid, platygastriid, proctotrupid, or pteromalid wasps considered although several species belonging to the genera *Ceraphron*, *Conostigmus*, *Gonatopus*, *Kleidotoma*, *Platygaster*, *Exallonyx*, and *Spalangia* are known to be associated with ants, most of them probably as parasitoids [2, 19–24]. All of these species were omitted from the present paper because wasps have not been reliably reared from ants or their brood. Moreover, according to the definition of “parasitoid” which implies the killing of a single host, associations such as those involving numerous sphecid species, particularly those of the genera *Aphilanthops*, *Clypeadon*, and *Tracheliodes*, which are known to specialize with preying on and storing numerous adult ants (of the genus *Formica*, *Pogonomyrmex*, or *Liometopum*, resp.) [25–27] are not dealt with. Likewise, the highly interesting associations of ants with some braconid species such as *Compsobraconoides* sp. [28] and *Trigastrotheca laikipiensis* Quicke [29], which are known to consume various stages of their ant hosts (*Azteca* spp. and *Crematogaster* spp., resp.) during their development, are not covered in the present paper.

In spite of such restrictions, the list of hymenopteran species reliably involved in parasitic associations with ants remains impressive and represents more than a quarter of all of the hymenopteran species known to be associated with ants [30]. Here, we attempt to provide an overview of both the diversity of the species of parasitoid wasps known to attack ants and the diversity of the interactions they have developed with their hosts. By so doing, we also call attention to this little known biodiversity.

2. Checklist of Hymenopteran Parasitoids of Ants

Records of associations of hymenopteran wasps with ants involve more than 500 wasp species [30], but only a fraction have unambiguously been reported as parasitoids. The term parasitoid applies to organisms whose juvenile stages are parasites of a single host individual, eventually sterilizing, killing, or even consuming their host, while the adult parasitoid is free living [31]. With few exceptions, female parasitoid wasps oviposit on or inside the body of their host, typically another arthropod, and all stages of development of the host are susceptible to attack. After hatching, the parasitoid larva feeds on the host’s tissues, gradually killing it. A survey of the literature since 1852 and some of our own unpublished results have allowed us to identify at least 138 species (see Table 1 and Supplementary Material available online at doi:10.1155/2012/134746) reported as primary endo- or ectoparasitoids of larvae, pupae, or adult ants. All of these species are included in 3 superfamilies: Chalcidoidea (with 6 families concerned), Ichneumonoidea (2 families), and Diaprioidea (only 1 family) (Table 1). In 2007, Sharkey [12] estimated that there were approximately 115,000 described species of Hymenoptera (perhaps up to 1,000,000 if undescribed species—especially species of parasitoid wasps—were included), and that Chalcidoidea and

Ichneumonoidea were the most species-rich superfamilies among the parasitoid hymenopterans. So, it is not surprising that most of the parasitoid wasps attacking ants belong to these two superfamilies, especially the Chalcidoidea which alone includes more than 70% of all of wasp species parasitizing ants registered until now.

In the following text, we follow Sharkey [12] for the higher-level phylogeny of the order Hymenoptera (see also [15]). The taxonomic validity of the scientific names is in accordance with Bolton [8, 9] for ants, and with different databases available on the web for other hymenopterans: Hymenoptera Name Server (version 1.5) (http://osuc.biosci.ohio-state.edu/hymDB/nomenclator.home_page), Global Name Index (version 0.9.34) (http://gni.globalnames.org/name_strings), Universal Chalcidoidea Database [32] (<http://www.nhm.ac.uk/chalcidoidea>), and Home of Ichneumonoidea (version 2011) (<http://www.ichneumonoidea.name/index.php>). Authors of all scientific names are given throughout the text only when they are not already reported in Table 1.

2.1. Diaprioidea. The superfamily Diaprioidea is a monophyletic group, with 4 recognized families [15], and accounts for more than 4000 species around the world in over 210 genera [8, 155–157], almost all in the family Diapriidae. Most diaprioids are primary endoparasitoids of dipterans (eggs, larvae, or pupae), but several species are known to attack Hymenoptera, Homoptera, or Coleoptera, and some are facultative or obligate hyperparasitoids. Some of the species attacking Diptera have been considered as potential biological control agents, but their efficiency has not been demonstrated [157, 158].

2.1.1. Diapriidae. Despite their number, the members of this large family are relatively unknown and less than half of the 4000 species estimated to occur worldwide have been described [8, 156, 159]. Three subfamilies are currently recognized: Ambositrinae, Belytinae, and Diapriinae [15]. Their biologies are diverse, but most species are primary parasitoids of puparia of Diptera [156–160].

Although some diapriids have only occasionally been found in ant nests, a number of species are closely associated with ants (all belonging to the Belytinae and Diapriinae subfamilies). However, there are few behavioral data on host-diapriid myrmecophile interactions (but see [36]). These symphytes are often highly adapted to their hosts, exhibiting morphological and behavioral adaptations to living with ants (extensive morphological mimicry of the host ants—coloration, ocellus regression, convergence in sculpture—, presence of appeasement substances in specialized structures and trichomes, trophallaxis, etc., [161–166]), which presumably aid them in avoiding detection and/or aggression by host ants [34]. The adaptations can include secondary apterism in which the wings of the wasps are assumed to have been bitten off by either the parasite itself or its host (e.g., *Mimopria*, *Bruchopria*, *Lepidopria*, and *Solenopsia*, [156, 161, 164, 167, 168]). Most often, the presence of a diapriid in an ant nest is suspected to be just circumstantial [160] and related to its

TABLE 1: List of parasitic wasps recorded as true primary parasitoids of ants (brood or adult). As all of the eucharitids are true parasitoids of ants, all known associations with ants have been included, but see **. For further details, see text.

| Hymenopterous parasitoids | | Associated ant host | | References |
|---|---------------------------------|---|------------------------|------------|
| Species | Referred to as | Species | Referred to as | |
| Diaprioidea: Diapriidae (26) | | | | |
| <i>Acanthopria</i> sp. | — | <i>Cyphomyrmex salvini</i> Forel | — | [33] |
| <i>Acanthopria</i> sp. | — | <i>Trachymyrmex</i> cf. <i>zeteki</i> Weber | — | [34] |
| <i>Acanthopria</i> sp. no. 1 | — | <i>Cyphomyrmex transversus</i> Emery | — | [35] |
| <i>Acanthopria</i> sp. no. 2 | — | <i>Cyphomyrmex transversus</i> Emery | — | [35] |
| <i>Acanthopria</i> sp. no. 3 | — | <i>Cyphomyrmex transversus</i> Emery | — | [35] |
| <i>Acanthopria</i> sp. no. 4 | — | <i>Cyphomyrmex transversus</i> Emery | — | [35] |
| <i>Acanthopria</i> sp. no. 5 | — | <i>Cyphomyrmex transversus</i> Emery | — | [35] |
| <i>Acanthopria</i> sp. no. 6 | — | <i>Cyphomyrmex transversus</i> Emery | — | [35] |
| <i>Acanthopria</i> sp. no. 7 | — | <i>Cyphomyrmex transversus</i> Emery | — | [35] |
| <i>Acanthopria</i> sp. no. 8 | — | <i>Cyphomyrmex transversus</i> Emery | — | [35] |
| <i>Acanthopria</i> sp. 1 | — | <i>Cyphomyrmex minutus</i> Mayr | — | [36] |
| <i>Acanthopria</i> sp. no. 1' | — | <i>Cyphomyrmex rimosus</i> (Spinola) | — | [36] |
| <i>Acanthopria</i> sp. no. 2' | — | <i>Cyphomyrmex rimosus</i> (Spinola) | — | [36] |
| <i>Acanthopria</i> sp. no. 3' | — | <i>Cyphomyrmex rimosus</i> (Spinola) | — | [36] |
| <i>Acanthopria</i> sp. no. 4' | — | <i>Cyphomyrmex rimosus</i> (Spinola) | — | [36] |
| <i>Mimopriella</i> sp. | — | <i>Cyphomyrmex rimosus</i> (Spinola) | — | [36] |
| <i>Mimopriella</i> sp. 1 | — | <i>Trachymyrmex</i> cf. <i>zeteki</i> Weber | — | [34] |
| <i>Mimopriella</i> sp. 2 | — | <i>Trachymyrmex</i> cf. <i>zeteki</i> Weber | — | [34] |
| <i>Oxypria</i> sp. | — | <i>Trachymyrmex</i> cf. <i>zeteki</i> Weber | — | [34] |
| <i>Plagiopria passerai</i> Huggert and Masner | — | <i>Plagiolepis pygmaea</i> (Latr.) | — | [37] |
| <i>Szelenyopria lucens</i> (Loiácono) | <i>Gymnopria lucens</i> | <i>Acromyrmex ambiguus</i> (Emery) | — | [38] |
| <i>Szelenyopria pampeana</i> (Loiácono) | <i>Gymnopria pampeana</i> | <i>Acromyrmex lobicornis</i> (Emery) | — | [39] |
| <i>Szelenyopria</i> sp. 1 | — | <i>Trachymyrmex</i> cf. <i>zeteki</i> Weber | — | [34] |
| <i>Szelenyopria</i> sp. 2 | — | <i>Trachymyrmex</i> cf. <i>zeteki</i> Weber | — | [34] |
| <i>Trichopria formicans</i> Loiácono | — | <i>Acromyrmex lobicornis</i> (Emery) | — | [40] |
| <i>Trichopria</i> sp. | — | <i>Acromyrmex lobicornis</i> (Emery) | — | [40] |
| Chalcidoidea: Chalcididae (2 + 2*) | | | | |
| <i>Smicromorpha doddi</i> Girault | — | <i>Oecophylla smaragdina</i> (Fabr.) | — | [41, 42] |
| <i>Smicromorpha keralensis</i> Narendran* | — | <i>Oecophylla smaragdina</i> (Fabr.) | — | [43] |
| <i>Smicromorpha masneri</i> Darling | — | <i>Oecophylla smaragdina</i> (Fabr.) | — | [44] |
| <i>Smicromorpha minera</i> Girault * | — | <i>Oecophylla smaragdina</i> (Fabr.) | — | [42] |
| Chalcidoidea: Encyrtidae (1) | | | | |
| <i>Blanchardiscus</i> sp. ? <i>pollux</i> Noyes | — | <i>Pachycondyla goeldii</i> (Forel) | — | [45] |
| Chalcidoidea: Eucharitidae (86 + 7** + 1***) | | | | |
| <i>Ancyлотropus manipurensis</i> | — | <i>Camponotus</i> sp.*** | — | [11, 46] |
| <i>Ancyлотropus</i> sp. | — | <i>Odontomachus troglodytes</i> Santschi | — | [11] |
| <i>Athairocharis vannaorti</i> Heraty | — | <i>Anoplolepis</i> sp. | <i>Anaplolepis</i> sp. | [11] |
| <i>Austeucharis fasciventris</i> (Brues) | <i>Psilogaster fasciventris</i> | <i>Myrmecia gulosa</i> (Fabr.) | — | [47] |
| <i>Austeucharis implexa</i> (Walker) | — | <i>Myrmecia pilosula</i> F. Smith | — | [11] |

TABLE 1: Continued.

| Hymenopterous parasitoids | | Associated ant host | | References |
|--|---|---|--|------------|
| Species | Referred to as | Species | Referred to as | |
| <i>Austeucharis myrmeciae</i> (Forel) | <i>Eucharis myrmeciae</i> Cameron | <i>Myrmecia forficata</i> (Fabr.) | — | [48] |
| <i>Austeucharis</i> sp. | — | <i>Myrmecia pavidata</i> Clark | <i>M. atrata</i> Clark | [49, 50] |
| | — | <i>Myrmecia nigriceps</i> Mayr | <i>M. nigriceps</i> Smith | [49, 50] |
| | — | <i>Myrmecia pilosula</i> F. Smith | — | [50] |
| | <i>Epimetagea</i> sp. | <i>Myrmecia pyriformis</i> F. Smith | — | [51] |
| | — | <i>Myrmecia tarsata</i> F. Smith | — | [50] |
| | — | <i>Myrmecia vindex</i> F. Smith | <i>M. vindex</i> Forel | [50] |
| <i>Chalcura affinis</i> (Bingham) | <i>Rhipipallus affinis</i> | <i>Odontomachus ruficeps</i> F. Smith | <i>O. ruficeps</i> subsp. <i>coriarius</i> Mayr | [52] |
| | <i>Chalcuroides versicolor</i> Girault | <i>Odontomachus</i> sp. | <i>Myrmecia</i> sp. | [53, 54] |
| <i>Chalcura deprivata</i> (Walker) | — | <i>Odontomachus haematodus</i> (L.) | <i>O. haematodes</i> | [55] |
| <i>Chalcura nigricyanea</i> (Girault) | — | <i>Rhytidoponera metallica</i> (F. Smith) | <i>R. metallicum</i> | [11] |
| <i>Chalcura polita</i> (Girault) | — | <i>Rhytidoponera metallica</i> (F. Smith) | <i>R. metallicum</i> | [11] |
| <i>Chalcura</i> sp. | — | <i>Formica rufa</i> L. | — | [56] |
| <i>Chalcura</i> sp. nr. <i>polita</i> (Girault) | — | <i>Rhytidoponera chalybaea</i> Emery | — | [11] |
| <i>Dicoelothorax platycerus</i> Ashmead | — | <i>Ectatomma brunneum</i> F. Smith | — | [57] |
| <i>Dilocantha lachaudii</i> Heraty | — | <i>Ectatomma tuberculatum</i> (Olivier) | — | [58, 59] |
| <i>Eucharis adscendens</i> (Fabr.) | — | <i>Formica ?cunicularia</i> Latr.** | <i>F. glauca</i> Ruzsky | [60] |
| | — | <i>Formica rufa</i> L. | — | [61] |
| | — | <i>Messor barbarus</i> (L.)** | <i>Aphaenogaster</i> <i>barbara</i> L. | [62] |
| <i>Eucharis bedeli</i> (Cameron) | — | <i>Cataglyphis bicolor</i> (Fabr.)*** | <i>C. viaticus</i> | [63] |
| | <i>Chalcura bedeli</i> | <i>Cataglyphis viaticus</i> (Fabr.) | <i>Myrmecocystus</i> <i>viaticus</i> | [64, 65] |
| | <i>Chalcura bedeli</i> | <i>Formica rufa</i> L.*** | — | [61, 65] |
| <i>Eucharis esakii</i> Ishii | <i>E. scutellaris</i> Gahan | <i>Formica japonica</i> Motschoulski | <i>F. fusca fusca japonica</i> Mots. | [66] |
| | <i>E. scutellaris</i> Gahan | <i>Formica</i> sp. | — | [55] |
| <i>Eucharis microcephala</i> Bouček | — | <i>Cataglyphis nodus</i> (Brullé) | <i>C. bicolor</i> ssp. <i>nodus</i> <i>M. barbarus</i> r. | [67] |
| <i>Eucharis punctata</i> Förster | — | <i>Messor concolor</i> Santschi** | <i>semirufus</i> v. <i>concolor</i> Sm. | [68] |
| <i>Eucharis rugulosa</i> Gussakovskiy | — | <i>Cataglyphis</i> sp.** | — | [60] |
| <i>Eucharis shestakovi</i> Gussakovskiy | — | <i>Messor structor</i> (Latr.)** | — | [69] |
| <i>Eucharis</i> sp. | — | <i>Formica neorufibarbis</i> Emery** | <i>F. fusca neorufibarbis</i> | [70] |
| | — | <i>Myrmica incompleta</i> Provancher** | <i>M. brevinodis</i> Emery | [70] |
| <i>Galearia latreillei</i> (Guérin-Méneville) | <i>Thoracantha bruchi</i> | <i>Pogonomyrmex cunicularius</i> Mayr** | <i>P. carnivora</i> Santschi | [11, 71] |
| <i>Gollumiella longipetiolata</i> Hedqvist | — | <i>Paratrechina</i> sp. | — | [72] |
| <i>Hydrorhoa</i> sp. <i>striaticeps</i> Kieffer complex | — | <i>Camponotus maculatus</i> (Fabr.) | <i>C. maculatus</i> Mayr | [11] |
| <i>Isomerula coronata</i> (Westwood) | <i>Isomaralia coronata</i> | <i>Ectatomma tuberculatum</i> (Olivier) | — | [73] |
| | — | <i>Ectatomma ruidum</i> Roger*** | — | [11] |
| <i>Kapala atrata</i> (Walker) | <i>K. surgens</i> | <i>Pachycondyla harpax</i> (Fabr.) | — | [11] |
| <i>Kapala cuprea</i> Cameron | — | <i>Pachycondyla crassinoda</i> (Latr.) | — | [74] |
| <i>Kapala floridana</i> (Ashmead) | — | <i>Pogonomyrmex badius</i> (Latr.)** | — | [70] |
| <i>Kapala iridicolor</i> (Cameron) | <i>K. sulcifacies</i> (Cameron) | <i>Ectatomma ruidum</i> Roger | — | [75, 76] |

TABLE 1: Continued.

| Hymenopterous parasitoids | | Associated ant host | | References |
|---|-----------------------------------|---|---|------------|
| Species | Referred to as | Species | Referred to as | |
| | — | <i>Gnamptogenys regularis</i> Mayr | — | [76] |
| | — | <i>Gnamptogenys striatula</i> Mayr | — | [76] |
| | — | <i>Gnamptogenys sulcata</i> (F. Smith) | — | [76] |
| | — | <i>Pachycondyla stigma</i> (Fabr.) | — | [76] |
| <i>Kapala izapa</i> Carmichael | — | <i>Ectatomma ruidum</i> Roger | — | [76] |
| <i>Kapala</i> sp. | — | <i>Dinoponera lucida</i> Emery | — | [77] |
| | — | <i>Ectatomma brunneum</i> F. Smith | — | [78] |
| | — | <i>Ectatomma tuberculatum</i> (Olivier) | — | [79] |
| | — | <i>Gnamptogenys sulcata</i> (F. Smith) | — | [80] |
| | — | <i>Gnamptogenys tortuolosa</i> (F. Smith) | — | [78] |
| | — | <i>Hypoponera nitidula</i> (Emery) | — | [81] |
| | — | <i>Odontomachus bauri</i> Emery | — | [11] |
| | — | <i>Odontomachus brunneus</i> (Patton) | — | [80] |
| | — | <i>Odontomachus haematodus</i> (L.) | — | [77] |
| | — | <i>Odontomachus hastatus</i> (Fabr.) | — | [11] |
| | — | <i>Odontomachus insularis</i> Guérin-Méneville | <i>O. haematodes</i> <i>insularis pallens</i> Wheeler | [66] |
| | — | <i>Odontomachus laticeps</i> Roger | — | [80] |
| | — | <i>Odontomachus mayi</i> Mann | — | [78] |
| | — | <i>Odontomachus meinerti</i> Forel | — | [81] |
| | — | <i>Odontomachus opaciventris</i> Forel | — | [80] |
| | — | <i>Pachycondyla apicalis</i> (Latr.) | — | [80] |
| | — | <i>Pachycondyla harpax</i> (Fabr.) | — | [81] |
| | — | <i>Pachycondyla stigma</i> (Fabr.) | — | [81] |
| | — | <i>Pachycondyla verena</i> (Forel) | — | [78] |
| | — | <i>Typhlomyrmex rogenhoferi</i> Mayr | — | [81] |
| <i>Kapala terminalis</i> Ashmead | — | <i>Odontomachus insularis</i> Guérin-Méneville | <i>O. haematodes</i> <i>insularis pallens</i> Wheeler | [66] |
| <i>Lophyrocera variabilis</i> Torrén, Heraty and Fidalgo | — | <i>Camponotus</i> sp. | — | [82] |
| <i>Mateucharis rugulosa</i> Heraty | — | <i>Camponotus</i> sp. | — | [11] |
| <i>Neolosbanus gemma</i> (Girault) | — | <i>Hypoponera</i> sp. | — | [83] |
| <i>Neolosbanus palgravei</i> (Girault) | — | <i>Hypoponera</i> sp. | — | [83] |
| <i>Obeza floridana</i> (Ashmead) | — | <i>Camponotus floridanus</i> (Buckley) | <i>C. abdominalis</i> <i>floridanus</i> | [84] |
| <i>Orasema aenea</i> Gahan | — | <i>Solenopsis quinquecupis</i> Forel | — | [85] |
| <i>Orasema argentina</i> Gemignani | — | <i>Pheidole nitidula</i> Santschi | <i>P. strobili misera</i> Snts. | [71] |
| <i>Orasema assectator</i> Kerrich | — | <i>Pheidole</i> sp. | — | [86, 87] |
| <i>Orasema coloradensis</i> Wheeler | <i>O. coloradensis</i> Ashmead | <i>Diplorhoptum validiusculum</i> (Emery) | <i>Solenopsis molesta</i> <i>validiuscula</i> | [70] |
| | <i>O. coloradensis</i> Gahan | <i>Formica oreas comptula</i> Wheeler | — | [88] |
| | <i>O. coloradensis</i> Gahan | <i>Formica subnitens</i> Creighton | — | [88] |
| | <i>O. coloradensis</i> Ashmead | <i>Pheidole bicarinata</i> Mayr | <i>P. vinelandica</i> Forel | [70] |
| <i>Orasema costaricensis</i> Wheeler and Wheeler | — | <i>Pheidole flavens</i> Roger | — | [63] |

TABLE 1: Continued.

| Hymenopterous parasitoids | | Associated ant host | | References |
|--|------------------------------------|---|--|------------|
| Species | Referred to as | Species | Referred to as | |
| | — | <i>Pheidole vallifica</i> Forel | — | [89] |
| <i>Orasema fraudulenta</i> (Reichensperger) | <i>Psilogaster fraudulentus</i> | <i>Pheidole megacephala</i> (Fabr.) | — | [90] |
| <i>Orasema minuta</i> Ashmead | — | <i>Pheidole</i> nr. <i>tetra</i> Creighton | — | [11, 83] |
| | — | <i>Temnothorax allardycei</i> (Mann) | — | [11, 83] |
| <i>Orasema minutissima</i> Howard | — | <i>Wasmannia auropunctata</i> (Roger) | — | [91] |
| | — | <i>Wasmannia sigmoidea</i> (Mayr) | — | [92] |
| <i>Orasema monomoria</i> Heraty | — | <i>Monomorium</i> sp. | — | [93] |
| <i>Orasema occidentalis</i> Ashmead | — | <i>Pheidole pilifera</i> (Roger) | — | [94] |
| <i>Orasema pireta</i> Heraty | — | <i>Solenopsis</i> sp. | — | [85] |
| <i>Orasema rapo</i> (Walker) | — | <i>Eciton quadriglume</i> (Haliday)** | — | [83] |
| <i>Orasema robertsoni</i> Gahan | — | <i>Pheidole dentata</i> Mayr | — | [95] |
| <i>Orasema salebrosa</i> Heraty | — | <i>Solenopsis invicta</i> Buren | — | [85] |
| | — | <i>Solenopsis richteri</i> Forel | — | [96] |
| <i>Orasema simplex</i> Heraty | — | <i>Solenopsis invicta</i> Buren | — | [97] |
| | — | <i>Solenopsis macdonaghi</i> Santschi | — | [85] |
| | — | <i>Solenopsis quinquecuspis</i> Forel | — | [85] |
| | — | <i>Solenopsis richteri</i> Forel | — | [96] |
| <i>Orasema simulatrix</i> Gahan | — | <i>Pheidole desertorum</i> Wheeler | — | [98] |
| <i>Orasema sixaolae</i> Wheeler and Wheeler | — | <i>Solenopsis tenuis</i> Mayr | — | [63] |
| <i>Orasema</i> sp. | B1 nr. <i>bakeri</i> | <i>Solenopsis geminata</i> (Fabr.) | — | [83] |
| | B1 nr. <i>bakeri</i> | <i>Solenopsis xyloni</i> MacCook | — | [83] |
| <i>Orasema</i> sp. | B2 nr. <i>bakeri</i> | <i>Pheidole</i> nr. <i>californica</i> Mayr | — | [83] |
| | B2 nr. <i>bakeri</i> | <i>Pheidole</i> nr. <i>clementensis</i> Gregg | — | [83] |
| | B2 nr. <i>bakeri</i> | <i>Pheidole</i> sp. | — | [83] |
| | B2 nr. <i>bakeri</i> | <i>Tetramorium</i> sp. | — | [83] |
| <i>Orasema</i> sp. | C1 nr. <i>costaricensis</i> | <i>Pheidole dentata</i> Mayr | — | [83] |
| <i>Orasema</i> sp. | — | <i>Pheidole bilimeki</i> Mayr | <i>P. anastasii</i> Emery | [99] |
| <i>Orasema</i> sp. | — | <i>Pheidole paiute</i> Gregg | — | [94] |
| <i>Orasema</i> sp. nr. <i>bouceki</i> Heraty | — | <i>Pheidole</i> sp. | — | [83] |
| <i>Orasema</i> sp. <i>uichancoi</i> -group | — | <i>Pheidole</i> sp. | — | [93] |
| <i>Orasema susanae</i> Gemignani | — | <i>Pheidole</i> nr. <i>tetra</i> Creighton | — | [83] |
| <i>Orasema tolteca</i> Mann | — | <i>Pheidole hirtula</i> Forel | <i>P. vasleti</i> var. <i>acohlma</i> | [100] |
| <i>Orasema valgius</i> (Walker) | <i>O. pheidolophaga</i> Girault | <i>Pheidole</i> sp. | — | [53] |
| <i>Orasema wheeleri</i> Wheeler | <i>O. wheeleri</i> Ashmead | <i>Pheidole ceres</i> Wheeler | — | [70] |
| | <i>O. viridis</i> Ashmead | <i>Pheidole dentata</i> Mayr | — | [55, 70] |
| | <i>O. viridis</i> Ashmead | <i>Pheidole sciophila</i> Wheeler | — | [55, 70] |
| | <i>O. viridis</i> Ashmead | <i>Pheidole tepicana</i> Pergande | <i>P. kingi</i> subsp. <i>instabilis</i> Emery | [55, 70] |
| | <i>O. viridis</i> Ashmead | <i>Pheidole tepicana</i> Pergande | <i>P. carbonaria</i> Pergande | [55, 70] |
| <i>Orasema worcesteri</i> (Girault) | <i>O. doello-juradoi</i> Gemignani | <i>Pheidole radoszkowskii</i> Mayr | <i>P. nitidula</i> Emery | [71, 96] |
| <i>Orasema xanthopus</i> (Cameron) | — | <i>Solenopsis invicta</i> Buren | — | [83, 96] |
| | — | <i>Solenopsis quinquecuspis</i> Forel | — | [85] |
| | — | <i>Solenopsis richteri</i> Forel | — | [101] |
| | — | <i>Solenopsis saevissima</i> (F. Smith) | — | [102] |

TABLE 1: Continued.

| Hymenopterous parasitoids | | Associated ant host | | References |
|---|------------------------------------|---|--|------------|
| Species | Referred to as | Species | Referred to as | |
| <i>Orasemomorpha eribotes</i> (Walker) | — | <i>Pheidole</i> sp. | — | [54] |
| <i>Orasemomorpha myrmicae</i> (Girault) | — | <i>Pheidole</i> sp. | — | [83] |
| <i>Orasemomorpha tridentata</i> (Girault) | <i>Eucaromorpha wheeleri</i> Brues | <i>Pheidole proxima</i> Mayr | — | [103] |
| <i>Orasemomorpha xeniades</i> (Walker) | — | <i>Pheidole tasmaniensis</i> Mayr | — | [83] |
| <i>Pogonocharis browni</i> Heraty | — | <i>Gnamptogenys menadensis</i> (Mayr) | — | [11] |
| <i>Pseudochalcura gibbosa</i> (Provancher) | — | <i>Camponotus herculeanus</i> (L.) | — | [46] |
| | — | <i>Camponotus laevigatus</i> (F. Smith) | — | [104] |
| | — | <i>Camponotus novaeboracensis</i> (Fitch) | <i>C. ligniperdus</i> var. <i>novaeboracensis</i> | [70] |
| | — | <i>Camponotus</i> sp. ? <i>vicinus</i> Mayr | — | [104] |
| <i>Pseudochalcura nigrocyanea</i> Ashmead | — | <i>Camponotus</i> sp. | — | [105] |
| <i>Pseudochalcura sculpturata</i> Heraty | — | <i>Camponotus planatus</i> Roger | — | [11] |
| <i>Pseudometagea schwarzii</i> (Ashmead) | — | <i>Lasius neoniger</i> Emery | — | [106] |
| <i>Rhipipalloidea madangensis</i> Maeyama, Machida, and Terayama | — | <i>Camponotus</i> (<i>Tanaemyrmex</i>) sp. | — | [107] |
| <i>Rhipipalloidea mira</i> Girault | — | <i>Polyrhachis femorata</i> F. Smith | — | [11] |
| <i>Schizaspidia convergens</i> (Walker) | — | <i>Odontomachus haematodus</i> (L.) | <i>O. haematodes</i> | [55] |
| <i>Schizaspidia nasua</i> (Walker) | — | <i>Odontomachus rixosus</i> F. Smith | — | [11] |
| <i>Stilbula arenae</i> Girault | — | <i>Polyrhachis</i> sp. | <i>Cyrtomyrma</i> sp. | [54] |
| <i>Stilbula cyniformis</i> (Rossi) | <i>S. cynipiformis</i> | <i>Camponotus aethiops</i> (Latr.) | <i>C. marginatus</i> Latr. | [68] |
| | <i>Schizaspidia tenuicornis</i> | <i>Camponotus japonicus</i> Mayr | <i>C. herculeanus</i> ssp. <i>japonicus</i> | [108] |
| | <i>Schizaspidia tenuicornis</i> | <i>Camponotus obscuripes</i> Mayr | <i>C. herculeanus</i> ssp. <i>ligniperdus</i> v. <i>obscuripes</i> | [66, 108] |
| | <i>S. cynipiformis</i> | <i>Camponotus sanctus</i> Forel | <i>C. maculatus</i> r. <i>sanctus</i> | [62] |
| <i>Stilbula polyrhachicida</i> (Wheeler and Wheeler) | <i>Schizaspidia polyrhachicida</i> | <i>Polyrhachis dives</i> F. Smith | <i>Polyrhachis</i> (<i>Myrmhopla</i>) <i>dives</i> | [109] |
| <i>Stilbuloida calomyrmecis</i> (Brues) | <i>Schizaspidia calomyrmecis</i> | <i>Calomyrmex purpureus</i> (Mayr) | — | [103] |
| <i>Stilbuloida doddi</i> (Bingham) | <i>Schizaspidia doddi</i> | <i>Camponotus</i> sp. | — | [52] |
| <i>Timioderus acuminatus</i> Heraty | — | <i>Pheidole capensis</i> Mayr | — | [93] |
| <i>Tricoryna chalcoponerae</i> Brues | — | <i>Rhytidoponera metallica</i> (F. Smith) | <i>Chalcoponera metallica</i> var. <i>critulata</i> | [103] |
| <i>Tricoryna ectatommae</i> Girault | — | <i>Rhytidoponera</i> sp. | <i>Ectatomma</i> sp. | [110] |
| <i>Tricoryna iello</i> (Walker) | — | <i>Rhytidoponera</i> sp. | — | [11] |
| <i>Tricoryna minor</i> (Girault) | — | <i>Rhytidoponera metallica</i> (F. Smith) | — | [11] |
| | — | <i>Rhytidoponera victoriae</i> (André) | — | [11] |
| <i>Tricoryna</i> sp. nr. <i>alcicornis</i> (Bouček) | — | <i>Rhytidoponera violacea</i> (Forel) | — | [11] |
| <i>Zulucharis campbelli</i> Heraty | — | <i>Camponotus</i> sp. | — | [11] |
| Chalcidoidea: Eulophidae (5) | | | | |
| <i>Horismenus floridensis</i> (Schauff and Bouček) | <i>Alachua floridensis</i> | <i>Camponotus atriceps</i> (F. Smith) | <i>C. abdominalis</i> (Fabr.) | [111] |
| | <i>Alachua floridensis</i> | <i>Camponotus floridanus</i> (Buckley) | — | [111] |
| <i>Horismenus myrmecophagus</i> Hansson, Lachaud, and Pérez-Lachaud | — | <i>Camponotus</i> sp. ca. <i>textor</i> Forel | — | [112] |

TABLE 1: Continued.

| Hymenopterous parasitoids | | Associated ant host | | References |
|---|---|--|---|-----------------|
| Species | Referred to as | Species | Referred to as | |
| <i>Myrmokata diparoides</i> Bouček | — | <i>Crematogaster</i> sp. | — | [113] |
| <i>Pediobius marjoriae</i> Kerrich | — | <i>Lepisotia</i> sp. | <i>Acantholepis</i> sp. | [114] |
| Unidentified sp. (? <i>Horismenus</i>) | nr. <i>Paracrias</i> | <i>Crematogaster acuta</i> (Fabr.) | — | [109, 112] |
| Chalcidoidea: Eurytomidae (4) | | | | |
| <i>Aximopsis affinis</i> (Brues) | <i>Conoaxima affinis</i> | <i>Azteca</i> sp. | — | [115] |
| | <i>Conoaxima affinis</i> | <i>Azteca alfari</i> Emery | <i>Azteca alfari</i> subsp. <i>lucidula</i> var. <i>canalis</i> | [116] |
| | <i>Conoaxima affinis</i> | <i>Azteca pittieri</i> Forel | — | [117] |
| <i>Aximopsis aztecicida</i> (Brues) | <i>Conoaxima aztecicida</i> | <i>Azteca alfari</i> Emery | <i>Azteca alfaroi</i> | [115] |
| | <i>Conoaxima aztecicida</i> | <i>Azteca constructor</i> Emery | — | [115] |
| <i>Aximopsis</i> sp. | <i>Conoaxima</i> sp. | <i>Azteca salti</i> Wheeler | <i>Azteca xanthochroa</i> (Roger) subsp. <i>salti</i> | [116] |
| <i>Aximopsis</i> sp. (? <i>aztecicida</i>) | <i>Conoaxima</i> sp. (? <i>aztecicida</i>) | <i>Azteca alfari</i> Emery | — | [118] |
| | <i>Conoaxima</i> sp. (? <i>aztecicida</i>) | <i>Azteca australis</i> Wheeler | — | [118] |
| | <i>Conoaxima</i> sp. (? <i>aztecicida</i>) | <i>Azteca ovaticeps</i> Forel | — | [119] |
| | <i>Conoaxima</i> sp. (? <i>aztecicida</i>) | <i>Camponotus balzani</i> Emery | — | [118] |
| Chalcidoidea: Perilampidae (1) | | | | |
| Unidentified sp. | — | <i>Pachycondyla luteola</i> (Roger) | — | [119] |
| Ichneumonoidea: Braconidae (11 + 4*) | | | | |
| <i>Elasmosoma berlinense</i> Ruthe | — | <i>Camponotus</i> spp. | — | [120] |
| | — | <i>Camponotus vagus</i> (Scopoli) | — | [121] |
| | — | <i>Formica fusca</i> L. | — | [48] |
| | — | <i>Formica japonica</i> Motschoulsky | — | [122] |
| | — | <i>Formica pratensis</i> Retzius | — | [123] |
| | — | <i>Formica rufa</i> L. | — | [124–126] |
| | — | <i>Formica sanguinea</i> Latr. | — | [48] |
| | — | <i>Formica</i> spp. | — | [120] |
| | — | <i>Lasius niger</i> (L.) | — | [48, 56] |
| | — | <i>Polyergus</i> sp. | — | [127] |
| <i>Elasmosoma luxemburgense</i> Wasmann | — | <i>Formica rufibarbis</i> Fabr. | — | [128, 129] |
| <i>Elasmosoma michaeli</i> Shaw | — | <i>Formica obscuripes</i> Forel | — | [130] |
| | <i>E. sp. nr. pergandei</i> Ashmead | <i>Formica obscuriventris clivia</i> Creighton | — | [131] |
| <i>Elasmosoma pergandei</i> Ashmead* | — | <i>Camponotus castaneus</i> (Latr.) | <i>C. melleus</i> (Say) | [132] |
| | — | <i>Formica integra</i> Nylander | — | [126] |
| | — | <i>Formica subsericea</i> Say | — | [126] |
| <i>Elasmosoma petulans</i> Muesebeck* | — | <i>Formica integra</i> Nylander | — | [133] |
| | — | <i>Formica opaciventris</i> Emery | — | [127, 133, 134] |
| | — | <i>Formica pergandei</i> Emery | <i>F. rubicunda</i> Emery | [133, 134] |
| | — | <i>Formica rubicunda</i> Emery*** | — | [127, 133, 134] |
| | — | <i>Formica subintegra</i> Wheeler | <i>F. subintegra</i> Emery | [133] |
| | — | <i>Formica subsericea</i> Say | — | [133] |

TABLE 1: Continued.

| Hymenopterous parasitoids | | Associated ant host | | References |
|---|--------------------------------------|--|---|------------|
| Species | Referred to as | Species | Referred to as | |
| <i>Elasmosoma schwarzi</i> Ashmead* | — | <i>Formica schaufussi</i> Mayr | — | [127] |
| | — | <i>Polyergus lucidus</i> Mayr | — | [127] |
| <i>Elasmosoma vigilans</i> Cockerell | — | <i>Formica perpilosa</i> Wheeler | — | [94] |
| | — | <i>Formica subpolita</i> Mayr | — | [135] |
| <i>Elasmosomites primordialis</i> Brues | — | <i>Lasius</i> sp. (? <i>schiefferdeckeri</i> Mayr) | — | [136] |
| <i>Kollasmosoma marikovskii</i> (Tobias) | — | <i>Formica pratensis</i> Retzius | — | [137] |
| <i>Kollasmosoma platamonense</i> (Huddleston) | <i>Elasmosoma platamonense</i> | <i>Cataglyphis bicolor</i> (Fabr.) | — | [127] |
| | — | <i>Messor semirufus</i> (André) | — | [138] |
| <i>Kollasmosoma sentum</i> van Achterberg and Gómez | — | <i>Cataglyphis ibericus</i> (Emery) | — | [129] |
| <i>Neoneurus auctus</i> (Thomson) | <i>Euphorus bistigmaticus</i> Morley | <i>Formica pratensis</i> Retzius | — | [139, 140] |
| | <i>Euphorus bistigmaticus</i> Morley | <i>Formica rufa</i> L. | — | [139, 140] |
| <i>Neoneurus clypeatus</i> (Förster)* | <i>Elasmosoma viennense</i> Giraud | <i>Formica rufa</i> L. | — | [141] |
| <i>Neoneurus mantis</i> Shaw | — | <i>Formica podzolica</i> Francoeur | — | [142, 143] |
| <i>Neoneurus vesculus</i> van Achterberg and Gómez | — | <i>Formica cunicularia</i> Latr. | — | [129] |
| Ichneumonoidea: Ichneumonidae (3 + 2*) | | | | |
| <i>Eurypterna cremieri</i> (de Romand) | <i>Pachylomma cremieri</i> | <i>Formica rufa</i> L. | — | [144] |
| | <i>Pachylomma cremieri</i> | <i>Lasius fuliginosus</i> (Latr.) | <i>Formica fuliginosa</i> | [145–148] |
| | — | <i>Lasius niger</i> (L.) | — | [123] |
| | <i>Pachylomma cremieri</i> | <i>Lasius nipponensis</i> Forel | — | [149] |
| <i>Ghilaromma fuliginosi</i> (Donisthorpe and Wilkinson)* | <i>Paxylomma fuliginosi</i> | <i>Lasius fuliginosus</i> (Latr.) | — | [150, 151] |
| <i>Hybrizon buccatus</i> (Brébisson) | <i>Pachylomma buccata</i> | <i>Formica rufa</i> L. | <i>F. rufa</i> var. <i>rufo-pratensis</i> | [152] |
| | <i>Pachylomma buccata</i> | <i>Formica rufibarbis</i> Fabr. | — | [152] |
| | <i>Pachylomma buccata</i> | <i>Formica sanguinea</i> Latr. | — | [152] |
| | <i>Pachylomma buccata</i> Nees | <i>Lasius alienus</i> (Förster) | <i>Donisthorpea aliena</i> | [24] |
| | <i>Pachylomma buccatum</i> | <i>Lasius brunneus</i> (Latr.) | — | [144] |
| | <i>Pachylomma buccata</i> | <i>Lasius flavus</i> (Fabr.) | — | [152] |
| | — | <i>Lasius grandis</i> Forel | — | [129] |
| | <i>Pachylomma buccata</i> | <i>Lasius niger</i> (L.) | — | [140] |
| | <i>Pachylomma buccata</i> Nees | <i>Myrmica lobicornis</i> Nylander | — | [24] |
| | <i>Pachylomma buccata</i> Nees | <i>Myrmica ruginodis</i> Nylander | — | [24] |
| | <i>Pachylomma buccata</i> | <i>Myrmica scabrinodis</i> Nylander | — | [153] |
| | <i>Pachylomma buccata</i> | <i>Tapinoma erraticum</i> (Latr.) | — | [152] |
| <i>Hybrizon rileyi</i> (Ashmead)* | — | <i>Lasius alienus</i> (Förster) | — | [154] |
| Unidentified Hybrizontinae (gen. nov. sp. nov.) | — | <i>Myrmica kotokui</i> Forel | — | [149] |

*: attack was not observed, but there is strong evidence that all of the species of this genus reported as associated with an ant species are true primary parasitoids of this host.

** : uncertain report of association with the host (e.g., ants of the genera *Pogonomyrmex* and *Messor* do not have cocoons—contrary to what is reported in the original reference—and were probably misidentified), uncertain identification of the ant host (ambiguity between 2 or more species), or wasps not found directly within the nest of the presumed host (e.g., found near a nest—perhaps only by chance—or found on refuse deposit—perhaps as a prey—).

***: erroneous report (misidentification of either the parasitoid or the ant host), or erroneous emendation of the host species.

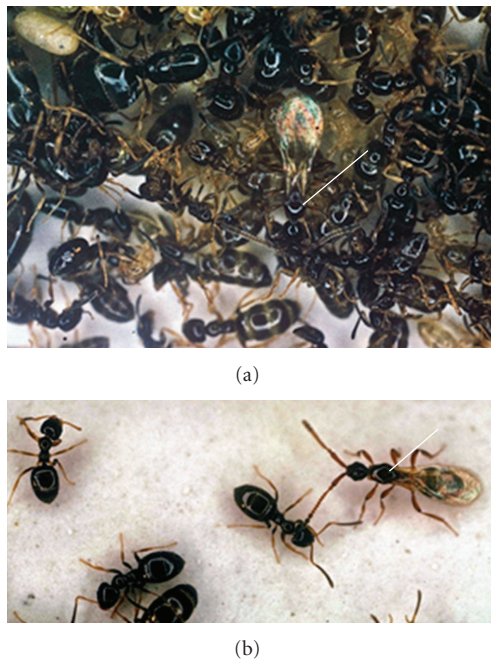


FIGURE 1: Winged females of the diapiiid wasp, *Plagiopria passerai* (white pointer) in a nest of the formicine ant *Plagiolepis pygmaea*, just after emergence from queen pupae. Photos courtesy of L. Passera.

search for dipterous hosts, such as *Tetramopria aurocincta* Wasmann found in nests of *Tetramorium caespitum* (L.) [128]. This wasp is in fact a parasitoid of the puparia of *Compsilura concinnata* Meigen (Diptera: Tachinidae), a primary parasite of the lepidopteran *Hyphantria cunea* (Drury) [160]. Occasionally, diapiiids enter ant nests for temporary shelter since some species hibernate in the host nest as do *Solenopsis imitatrix* Wasmann and *Lepidopria pedestris* Kieffer in the nests of *Solenopsis fugax* (Latr.) [37, 164].

Only a few diapiiids are true parasitoids of ant brood. Ever since the pioneering work of Wasmann in 1899 [128], most diapiiids found in ant nests were assumed either to parasitize insect myrmecophiles (dipteran or coleopteran) inside the host nest or, less frequently, to be primary parasitoids of ant larvae. However, the first record of a diapiiid positively reared from ant brood was reported just in 1982 by Lachaud and Passera [37], who reared *Plagiopria passerai* from cocoons of queens of the formicine *Plagiolepis pygmaea* (Figures 1(a) and 1(b)). As far as known, diapiiid parasitoids attacking ants develop as solitary or gregarious, koinobiont endoparasitoids of the host larvae [34, 36, 38, 169], and worker and/or reproductive immature stages can be parasitized [37, 169, 170]. Ramos-Lacau et al. [35] observed oviposition of *Acanthopria* sp. in young ant larvae under laboratory conditions. Late parasitized larvae are easily recognized by their dark coloration, compared to nonparasitized larvae, due to the developing wasp visible through the cuticle [35, 36, 38]. Worker ants do not discriminate between parasitized and nonparasitized larvae

[35, 38, 169], but adult parasitoids are aggressively attacked by their hosts under laboratory conditions [35, 36].

From the 121 diapiiine species in 34 genera that have been collected in association with ants [30], development of immature stages as parasitoids of ant larvae has been demonstrated for only 26 species in 7 genera, most of which are only known at the level of morphospecies (Table 1): 15 species of *Acanthopria*, 3 of *Mimopriella*, 1 of *Oxypria*, 1 of *Plagiopria* (*P. passerai*), 4 of *Szelenyopria*, and 2 of *Trichopria* (*T. formicans* and *Trichopria* sp.) [34–38, 169, 170]. The ant hosts of these diapiiines belong to 8 species in only 4 genera: the myrmecine fungus-growing ants *Cyphomyrmex*, *Trachymyrmex*, and *Acromyrmex* and the formicine *Plagiolepis*. Fifteen species of Belytinae belonging to 11 genera have also been reported from ant nests [30, 171–173], but none has been reliably reared from the ants, and their actual relationship with their hosts remains unknown.

In some cases, the rate of parasitism can reach high levels. Two recent studies have provided important details of the biology of diapiiids and have also investigated their impact on ant-host populations. Fernández-Marín et al. [36] found that between 27 and 70% of the colonies of 2 species of *Cyphomyrmex* were parasitized by one species in Puerto Rico and by up to 4 concurrent morphospecies of diapiiids in Panama. Similarly, the work of Pérez-Ortega et al. [34] showed that another fungus-growing ant, *Trachymyrmex* cf. *zeteki*, was attacked by a diverse community of diapiiids in Panama, with a mean intensity of larval parasitism per ant colony of 33.9%, and a prevalence across all ant populations of 27.2% (global data for all 6 diapiiid morphospecies present at the study site).

2.2. Chalcidoidea. The superfamily Chalcidoidea is considered as one of the most abundant, species-rich, and biologically diverse groups of insects with 23,000 species described and a conservative estimation of about 400,000 to 500,000 species in over 2040 genera distributed in 19 families [32, 174–178]. Though some species are phytophagous, most Chalcidoidea are parasitoids of other insects, and numerous species are currently used as biological control agents against insect pests.

2.2.1. Chalcididae. Chalcididae is a moderate-sized family with more than 1450 species and over 85 genera. Chalcids are primary parasitoids of Lepidoptera or, to a much lesser extent, of Coleoptera, Diptera, Hymenoptera, and Neuroptera, and various species are hyperparasitoids of other hymenopterous parasitoids [179]. Most often they parasitize host larvae or pupae, but a few species can parasitize eggs.

Very few species, like *Epitranus chilkaensis* (Mani) (referred to as *Anacryptus chilkaensis*) found with the formicine *Camponotus compressus* (Fabr.) in the Barkuda Island (India) [180], are known to be associated with ants [179, 181], but true parasitoidism has rarely been documented. Only species of the genus *Smicromorpha* seem to be specialized as parasitoids of the larvae of the green ant, *Oecophylla smaragdina*. The only unquestionable (see [44]) record of parasitoidism is that of Dodd in the early 20th century, describing *Smicromorpha doddi* in North

Queensland (Australia) parasitizing larvae of this weaver ant, “depositing eggs upon them when the workers are using their silk-spinning larvae for the purpose of binding the leaves together when building a new nest” [41]. No other example of true parasitoidism has ever been quoted for the genus *Smicromorpha* but, more recently, adults of another species of this genus, *S. masneri*, were reported emerging from *O. smaragdina* nests collected in Vietnam and maintained in controlled green-house conditions in the USA, which strongly suggests that these wasps are also primary parasitoids of weaver ants [44]. Moreover, two other species, *S. keralensis* [43] and *S. minera* [42], have been observed hovering over nests of *O. smaragdina* in India and Australia, respectively, a behavior likely to be related to parasitism of ants (see below under Braconidae and Ichneumonidae). For such reasons, all these members of the genus *Smicromorpha* can reasonably be suspected of being true parasitoids of the larvae of this ant host and were included in our list (Table 1).

2.2.2. Encyrtidae. Encyrtidae is a large family of parasitic wasps, currently including more than 460 genera and 3700 species, and is one of the key chalcidoid families for the biological control of insect pests [178, 182, 183]. Most encyrtids are primary endoparasitoids of immatures or, less commonly, adults of Coccidae and Pseudococcidae; others are hyperparasitic through other hymenopterous parasitoids, and some can attack insects in other orders, mites, ticks, or spiders [184, 185]. Some species are polyembryonic, a single egg multiplying clonally in the host, producing large numbers of identical adult wasps.

At least 25 species of encyrtid wasps representing 16 genera are known to be indirectly associated with ants through primary parasitism of the trophobionts they exploit and protect [32]; for example, the species *Anagyrus ananatis* Gahan is indirectly associated with the ant *Pheidole megacephala* through the trophobiotic Pseudococcidae present in their nest [186]. However, very few encyrtids have been reported as directly associated with ants. Apart from *Taftia prodeniae* Ashmead, which was found to exhibit a phoretic association (wasps were found clinging to the ant’s antennae) with the dolichoderine ant *Dolichoderus thoracicus* (F. Smith) (referred to as *D. bituberculatus* (Mayr)) [187], and an unidentified species recently reported from a refuse deposit of the ecitonine ant *Eciton burchellii* [188], only *Holcencyrtus wheeleri* (Ashmead) (referred to as *Pheidoloxenus wheeleri*), found in nests of the myrmicine ants *Pheidole tepicana* Pergande (referred to as *P. instabilis*) [70] and *P. ceres* Wheeler (referred to as *P. ceres* var. *tepaneca* Wheeler) [100], has been suspected of being “probably also entoparasitic on these ants or their progeny during its larval stages” [1]. However, the parasitic relationship was never proved. Only very recently a Neotropical, gregarious endoparasitoid species, *Blanchardiscus* sp. (?*pollux*) (determination by J. S. Noyes), was recorded from French Guiana attacking pupae of the ponerine ant *Pachycondyla goeldii* [45] and thus constitutes the first true case of parasitism on ants for this family. However, no information has yet been published, and the exact identification of the species still needs to be confirmed.

2.2.3. Eucharitidae. This is a small family but the largest and most diverse group of hymenopteran parasitoids attacking ants since all of its members, where the host is known, parasitize ant brood [11, 66, 72, 78, 83, 189–191]. Fifty-three genera and more than 470 species are currently described and distributed in three subfamilies: Oraseminae, Eucharitinae, and Gollumiellinae.

All of the species have a highly modified life cycle [63, 66, 76, 83, 108]. Like the Perilampidae [191] and the ichneumonid species *Euceros frigidus* [192], but unlike most parasitic wasp species, eucharitid females deposit their eggs away from the host nest, in or on plant tissue (leaves and buds) [72, 189] (Figures 2(a) and 2(b)), and the very active, minute (less than 0.13 mm), strongly sclerotized first-instar larva is termed a “planidium” (Supplementary material 2 available online at doi:10.1155/2012/134746). It is responsible for gaining access to the host ant brood by using various phoretic behaviors including either attachment to an intermediate host (as in some orasemine species [11, 72, 83, 86, 88, 93] and, possibly, in *Gollumiella antennata* (Gahan) ([190] but see [72]) or, more generally, to foraging ant workers. On occasions (as is apparently the case for *Pseudochalcura gibbosa* and *Gollumiella longipetiolata*), attractive substances are suspected to be present in or on the eggs [46, 72]. Within the nest, the planidium attaches itself to an ant larva (Figures 2(c) and 2(d)): Eucharitine planidia attach externally to the host larva, whereas orasemine and gollumielline planidia partially burrow into the host larva, in the thoracic region just posterior to the head capsule [11, 70, 72]. All of the Eucharitidae develop as koinobiont, larval-pupal ectoparasitoids. At molting of the host larva, the planidium migrates to the ventral region, just under the legs (Figure 2(e)), of the newly formed ant pupa for further development which is only completed when the host pupates [76, 83, 93, 189] (Supplementary material 3 available online at doi:10.1155/2012/134746). In general, only one parasitoid develops per host but, occasionally, more than one adult eucharitid can develop in a single host (superparasitism) (Figure 2(f)) [72, 83], especially when larger brood (sexual brood) is parasitized [193, 194], and one exceptional case of multiparasitism involving two different species from two different eucharitid genera (*Dilocantha lachaudii* and *Isomeralla coronata*) has even been reported from a single pupa of the ectatommine ant *Ectatomma tuberculatum* [79]. In almost all of the cases, adults emerge among ant brood (but see [77]), and, even if in some cases they are well treated within the nest by their hosts (as is the case for *Orasema coloradensis* which is transported, cared for, and even fed by the workers of *Pheidole bicarinata* [70]), they have to leave the host nest to reproduce. Ants show only moderate aggression to newly emerged eucharitids [58, 70, 75, 106, 189, 195, 196], suggesting passive or active chemical mimicry of the host ants [58, 75, 195]. If the parasitoid wasps do not exit their host nest by themselves, ant workers transport them outside (Figure 2(g)) as if they were refuse [58, 77, 196], ultimately enhancing wasp dispersal. Parasitism is very variable and localized in time and space [106, 193, 194]. A very high local prevalence may lead to only a low impact at the regional scale, suggesting that these parasitoids do not

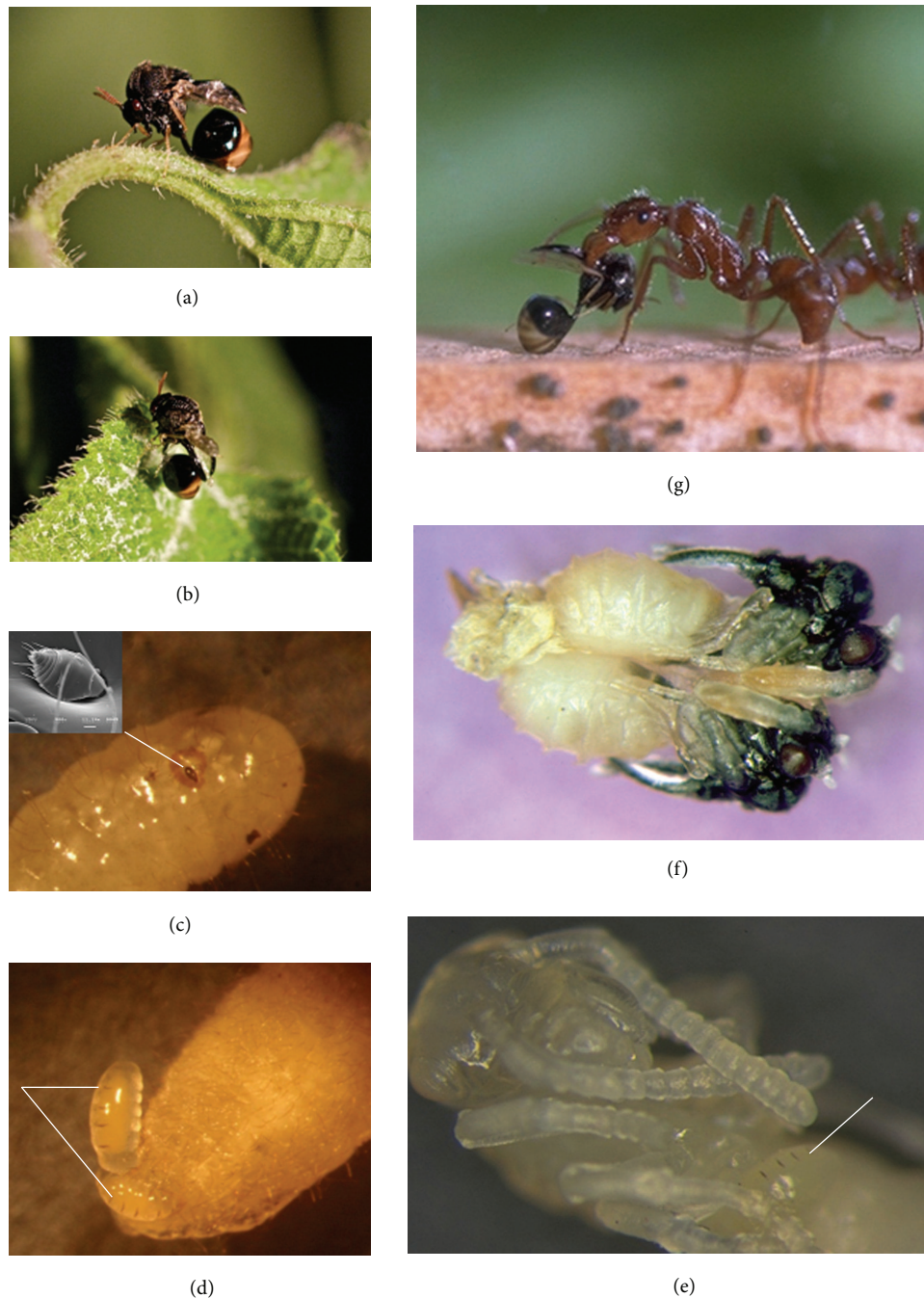


FIGURE 2: Life cycle of a typical eucharitid wasp. (a) Female *Dilocantha lachaudii* ovipositing on *Lantana camara* L. (Verbenaceae). (b) *D. lachaudii* female with eggs scattered on leaf surface. (c) Planidium (white pointer) attached upon an *Ectatomma tuberculatum* larva. Insert: SEM picture of a planidium. (d) Two *D. lachaudii* swollen planidia (white pointers) feeding upon an *E. tuberculatum* larva. (e) 2nd instar larva (white pointer) relocated after host pupation. (f) Two *D. lachaudii* pupae from a single host pupa. The host cocoon has been removed. (g) *E. tuberculatum* worker transporting a recently emerged *D. lachaudii* female. Photos: J.-P. Lachaud and G. Pérez-Lachaud.

have a major influence on the dynamics of their ant host population [194].

According to Heraty [11], the hypothesized phylogeny of Eucharitidae is highly correlated with the subfamilies of their ant hosts and responsible for differences in behavior related with egg placement, activity of the planidium, and

access to the ant host. Oraseminae (*Orasema*, *Orasemorpha*, and *Timioderus*) primarily attack myrmicine ants (numerous species of *Pheidole* and *Solenopsis*, and some species of *Diplorhoptrum*, *Monomorium*, *Temnothorax*, *Tetramorium*, and *Wasmannia*, see Table 1), and exceptionally formicines (*Formica subnitens* and *F. oreas comptula* in the case of

O. coloradensis, [88]) or ecitonines (*Eciton quadriglume* in the questionable case of *O. rapo*, [11, 83]). For Eucharitinae, the only two host records for the tribe Psilocharitini (*Neolosbanus*) concern the ponerine genus *Hypoponera* [83], while the numerous members of the tribe Eucharitini are essentially parasitic on medium to large ponerines (*Pachycondyla*, *Odontomachus*, and *Dinoponera*) and ectatommines (*Ectatomma*, *Gnamptogenys*, *Typhlomyrmex*, and *Rhytidoponera*), but also on myrmeciines (*Myrmecia*) and numerous formicines (*Anoplolepis*, *Calomyrmex*, *Camponotus*, *Cataglyphis*, *Formica*, *Lasius*, and *Polyrhachis*); without exception, all of the scarce records of associations of eucharitines with myrmicine ants (*Messor*, *Myrmica*, and *Pogonomyrmex*) are highly doubtful (Table 1). Finally, the only host record for the Gollumiellinae concerns a formicine (*Paratrechina*).

The hosts of most eucharitid genera seem to be restricted to only one or a few closely related ant genera and, for a long time, all species were considered as host-specific parasitoids, at least at the host genus level [83]. However, recent results [76, 78, 79] raised questions concerning the degree of host specificity in eucharitids and about the factors that determine the association of these parasitoids and their hosts. Results in the guild of eucharitid parasitoids associated with ponerine ant species in southeastern Mexico and French Guiana suggest that some eucharitid wasps tend to be oligophagous in their host choice: some eucharitid species can attack different hosts from different genera and different subfamilies such as *Kapala iridicolor*, which parasitizes one species of *Ectatomma*, two of *Gnamptogenys*, and one of *Pachycondyla* [76, 78]. Furthermore, concurrent parasitism has been reported for *Ectatomma tuberculatum*, which is simultaneously parasitized by *Dilocantha lachaudii*, *Isomerula coronata*, and *Kapala* sp. [79], or for *E. ruidum* parasitized by two *Kapala* species, *K. iridicolor*, and *K. izapa* [76, 193].

2.2.4. Eulophidae. The family Eulophidae is the largest of the Chalcidoidea with up to 4470 species in 297 genera. The majority of the species are primary parasitoids attacking a large variety of insects (mainly Lepidoptera and Coleoptera, but also Diptera, Thysanoptera, and Hymenoptera), and occasionally mites or spiders. Many species are facultative or obligate hyperparasitoids of other Hymenoptera, and some are even phytophagous. Entomophagous larvae can develop as koino- or idiobionts, gregarious or solitary, and ecto- or endoparasitoids, and according to the species, eulophids can attack eggs, larvae, pupae, or even the adults of their hosts [197].

Despite the large number of species in this family, parasitization of ants is uncommon among Eulophidae, and only few associations involving eulophid wasps and ant hosts have been reported to date. Almost all are from genera belonging to the subfamily Entedoninae. Three concern species indirectly associated with ants as they parasitize insects living in ant nests: *Pediobius acraconae* Kerrich which has been reported [114] from a last instar larva of the pyralid lepidopteran *Acracona remipedalis* Karsch found in a nest of *Crematogaster depressa* (Latr.) or *C. africana* Mayr in Nigeria, and both *Microdonophagus woodleyi* Schauff in Panama



FIGURE 3: Larva of the neotropical weaver ant *Camponotus* sp. ca. *textor* parasitized by the gregarious endoparasitoid *Horismenus myrmecophagus* (Eulophidae). Several wasp larvae can be observed through the host cuticle. Photo: G. Pérez-Lachaud.

and *Horismenus microdonophagus* Hansson et al. in Mexico, which parasitize larvae of *Microdon* sp. syrphid flies living in nests of the dolichoderine *Technomyrmex fulvus* (Wheeler) (referred to as *Tapinoma fulvum*) [198] and of the formicine *Camponotus* sp. ca. *textor* [112], respectively. Three other species (two Entedoninae and a Tetrastichinae) have been reported associated with ant nests, but direct parasitism on the ant brood was not clearly established in any of these cases: *Myrmobomyia malayana* Gumovsky and Bouček with nests of an ant species of the genus *Dolichoderus* in Malaysia [199], an unidentified species of *Horismenus* from the bivouac and refuse deposits of the army ant *Eciton burchellii* [188], and an unidentified species of *Tetrastichus* from a nest of the formicine *Myrmecocystus mexicanus* Wesmael in Nevada [94].

In fact, only five species are known as true primary parasitoids of ants (Table 1). An unidentified gregarious parasitoid, apparently closely related to the genus *Paracrius* (according to Gahan in [109]), possibly *Horismenus* sp. [112], was recorded parasitizing larvae of the myrmicine *Crematogaster acuta* in Guyana, the prepupae of another unidentified species of *Crematogaster* were parasitized by *Myrmokata diparoides* [113] in Cameroon, *Pediobius marjorariae* was reared from cocoons of the formicine ant *Lepisiota* sp. in Uganda [114], and two species of *Horismenus*, *H. floridensis* and *H. myrmecophagus*, were found parasitizing the pupae of *Camponotus atriceps* and *C. floridanus* in Florida [111], and of the weaver ant *Camponotus* sp. ca. *textor* in Mexico [112], respectively. In the latter two cases, *Horismenus* larvae develop as gregarious endoparasitoids of the ant larvae (Figure 3), and large numbers of parasitoid individuals can develop from the same host: up to 21 for *H. floridensis* and between 4 and 12 for *H. myrmecophagus*. Finally, two other cases deserve to be added to this list since two other ant species have recently been found parasitized by eulophids: the ponerine ant *Pachycondyla crenata* (Roger) in Mexico and an unidentified species of *Camponotus* (*Dendromyrmex*) in French Guiana [112]; however, the identity of the parasitoids has not been confirmed yet.

2.2.5. Eurytomidae. Eurytomidae is a moderate-sized family with 90 genera and at least 1400 nominal species [13, 32, 200, 201]. Eurytomid wasps exhibit a wide range of biologies, but most of the larvae are endophytic either as seed or plant stem eaters or as parasitoids of gall formers or other phytophagous insects. Most species are primary or secondary parasitoids, attacking eggs, larvae, or pupae of various arthropods (Diptera, Coleoptera, Hymenoptera, Lepidoptera, Orthoptera, and Araneae).

A few species have been reported as indirectly associated with ants, like *Eurytoma rosae* Nees von Esenbeck found with *Lasius flavus* and *Eurytoma* sp. found with *Formica* (?) *rufibarbis* (misidentified as *Polyergus rufibarbis*) [20], but most probably these eurytomids only fed on the gall-forming cynipid larvae and/or on the gall tissue on *Rosa* spp. which are visited by these ant species, without any direct relationship with the ants. Recently, various adults of a new genus and species, *Camponotophilus delvarei* Gates, were found within nests of the weaver ant *Camponotus* sp. ca. *textor* [202], but the exact nature of their relationship with the ants remains unclear. As a matter of fact, only 3 or 4 species from the single genus *Aximopsis* (see Table 1) have been reported from Guatemala, Costa Rica, Guyana, Colombia, and Peru as parasitoids of queens of various species of dolichoderine ants (*Azteca alfari*, *A. australis*, *A. constructor*, *A. pitieri*, *A. ovaticeps*, and *A. salti*) and one formicine (*Camponotus balzani*), all of which colonize *Cecropia* spp. internode chambers by chewing a hole through a prostoma and entering the internode. The parasitoids attack only founding queens and feed on their host, while the internode chamber is sealed with parenchyma scraped from the internal stem walls [115, 116, 118]; there is never more than one wasp larva or pupa per foundress ant [117]. Queen parasitization was thought to occur before they entered their dwellings (Bailey, in [115]); however, as suggested by Davidson and Fisher [119], the location of the ant host may occur through searching for host plants since female *Aximopsis* were observed to visit various seedlings, where they inspected newly sealed prostoma. This fact has been confirmed recently. A picture of an *A. affinis* female ovipositing through a prostoma into an *Azteca* queen at La Selva Biological Station, Costa Rica, was provided by Weng et al. [203] (their Figure 16). In this site, among the internodes that harbored *Azteca* ants, 43% contained dead queens, of which 13% contained *A. affinis* [203].

2.2.6. Perilampidae. Perilampidae is a small family closely related to the Eucharitidae, composed of up to 270 species from 15 genera. A feature shared with Eucharitidae is that the first-instar larva, the “planidium”, is responsible for gaining access to the host, rather than the egg-laying female [191]. Most species are hyperparasitoids on ichneumonid wasps or tachinid flies which are primary parasitoids of Hymenoptera or Lepidoptera, or parasitoids of wood-boring platypodid and anobiid beetles, and some species can attack Orthoptera, Neuroptera, or Hymenoptera [190, 204].

Association of perilampids with ants seems extremely casual. The only report deals with an unidentified species from Peru found parasitizing cocoons of the ponerine ant

Pachycondyla luteola, inhabiting internode chambers of a *Cecropia*, with as many as nine perilampid wasps emerging from a single pupa of this ant [119]. However, no other details were ever published, and the species apparently remained undescribed.

2.3. Ichneumonoidea. The superfamily Ichneumonoidea, with only two extant families, accounts for more than 40,000 species around the world, and there are estimated to be approximately 100,000 species [205–207]. Most are primary ecto- or endoparasitoids, idio- or koinobionts, especially attacking immature stages of a wide variety of insects and arachnids, and more occasionally adults. Some members use many different insects as hosts, and others are very specific in host choice. Various ichneumonoids are successfully employed as biological control agents in controlling insect pests such as flies or beetles.

2.3.1. Braconidae. This is a very large family with 48 subfamilies, more than 1050 genera and about 17,600 described species worldwide and exhibiting a variety of biologies [207–209]. The total number of species is estimated to be 40–50,000. Many braconids parasitize nymphal stages of Hemiptera, Isoptera, and Psocoptera; a few genera also parasitize adult Coleoptera and Hymenoptera [209]. Two major lineages occur within the Braconidae: (a) the cyclostome braconids, most of which are idiobiont ectoparasitoids of concealed Lepidoptera and Coleoptera larvae although many are koinobiont endoparasitoids of Diptera and Hemiptera, and (b) the noncyclostome braconids which are all endoparasitoids, and most generally koinobionts, typically attacking an early instar of their hosts (see [210] for a comprehensive overview of their biology).

Numerous braconid species have been reported in association with ants. Some, such as *Compsobraconoides* sp. [28] and *Trigastrotheca laikipiensis* [29], are predatory on several developmental stages of ants. Others, such as *Aclitus sappaphis* Takada and Shiga found in nests of *Pheidole fervida* Smith [211, 212], *Paralipsis enervis* (Nees von Esenbeck) found with *Lasius niger* [213], or *P. eikoeae* (Yasumatsu) found with *L. japonicus* Santschi (referred to as *L. niger* (L.)) and *L. sakagami* Yamauchi and Hayashida [212, 214], are in fact primary parasitoids of root aphids and can only be considered as indirectly associated with the aphid-attending ants; however, they have developed highly sophisticated relationships with their hosts involving chemical mimicry and chemical and tactile communication to obtain regurgitated food (trophallaxis).

For several other species, the exact nature of the association with the ant host has not been clearly established, but at least 15 euphorine species can be considered as true parasitoids of adult ants even if direct evidence of oviposition has been obtained for only 11 of them (see Table 1). All of these parasitoids are grouped in three extant genera, *Elasmosoma*, *Kollasmosoma*, and *Neoneurus*, and one fossil genus, *Elasmosomites*, all belonging to the tribe Neoneurini. Evidence from Eocene Baltic amber, as demonstrated from an individual of *Elasmosomites primordialis* emerging from the abdomen of a *Lasius* worker (Figure 4(a)), indicates that

the parasitoid association between neoneurine braconids and ants has been in existence for at least 40 million years [136]. Although oviposition into the abdomen of adult worker ants has been reported on several occasions [56, 120, 121, 126, 127, 140], detailed descriptions were rare and, until recently, restricted to only two species. In the case of *N. mantis* attacking *Formica podzolica*, Shaw [142, 143] gave interesting information both on the “perching” behavior displayed by the parasitoid females in their ambush strategy to locate their hosts and on the attack sequence which is completed in less than 1 s and is characterized by a reduction of the usual braconid oviposition sequence, the first two steps (antennation of the host and ovipositor probing) being entirely lost in favor of speed. For *E. michaeli*, Poinar [131] not only described the attack behavior, exclusively focused on major workers of *Formica obscuriventris clivia* (Figure 4(b)), but also provided invaluable information on the altered behavior of parasitized ants, on the development of the immature stages, and on cocoon formation and adult emergence. Immature stages of Neoneurini parasitoids attacking adult ants develop as koinobiont endoparasitoids in the abdomen of workers, and fully developed larvae leave the host to pupate in the soil [131].

Very recently, slow motion video recordings were used to describe the oviposition behavior in adult ants for 3 other species [129], and we refer the reader to their excellent films, which show the variability in oviposition behavior within the tribe. Neoneurini wasps parasitize worker ants in the vicinity of the nest entrance(s), or while foraging. Females of *Elasmosoma luxemburgense* hover over the nest entrance of *Formica rufibarbis* and attack workers from behind, grasping the ant abdomen with the three pairs of legs involved, and probably ovipositing through the anus. The whole behavioral sequence (alighting, grasping, ovipositor insertion, and takeoff) lasted a mean of 0.73 s. The ants were aware of these attacks, turning around and chasing the wasps with open mandibles ([129] doi: 10.3897/zookeys.125.1754.app1). Females of *Kollasmosoma sentum* attack workers of *Cataglyphis iberica* in the vicinity of nest entrances, or when carrying prey and walking more slowly than usual. Attacks usually occurred during the brief stops characterizing *Cataglyphis* workers walks. The wasps were extremely fast and attacked the ants from behind. Oviposition took place in both the dorsal and ventral surfaces of the ant’s gaster, likely through intersegmental membranes. Wasps adjusted their alighting strategies according to the direction of their own approach to the targeted ant, and to the position of the ant’s gaster (horizontal or vertical position, distinctive for the genus *Cataglyphis*), and accomplished extraordinary pirouettes. The whole oviposition behavior lasted only 0.05 s on average. The ants were often aware of the presence of the parasitoids, aggressively turning around with open mandibles, or extending their hind or middle legs to hit them ([129] doi: 10.3897/zookeys.125.1754.app2). Finally, *N. vesculus* females alight and probably oviposit in the mesosoma of *Formica cunicularia* workers. As for *N. mantis* [142, 143], they were observed ambushing or hovering over the nest entrance. Females preferentially attacked ants while at a vertical



(a)



(b)

FIGURE 4: (a) *Elasmosomites primordialis* larva (white pointer) emerging from the abdomen of a *Lasius* worker in Baltic amber. Photo courtesy of G. Poinar Jr. (see [136]). (b) *Elasmosoma michaeli* larva leaving its *Formica obscuriventris clivia* host to pupate in the soil. Photo courtesy of G. Poinar Jr.

position (going up a tree trunk, e.g.). The wasps approached the ants from behind, alighted, held the ant’s thorax with their raptorial fore legs, bent their abdomen towards the postero-lower part of the ant’s thorax, and oviposited. The ovipositor is thought to be inserted near the posterior coxal cavities. The whole oviposition behavior lasted a mean of 2.02 s ([128] doi: 10.3897/zookeys.125.1754.app3).

With few exceptions, neoneurine wasps have been found in association with formicine ants [129, 207, 215, 216]. It is thought that formic acid used by these ants could serve also as a kairomonal stimulant to host-seeking hymenopterous parasitoids [120, 127, 129]. Far less is known about the fate of parasitized ants. According to Poinar [131], *Formica* ants parasitized by *E. michaeli* form an assembly along the edge of their superficial nest when the parasitoid larvae are about to leave the host to pupate. This behavioral modification is thought to increase the survival of adult wasps.

Several morphological and behavioral adaptations, apart from rapidity of attack, contribute to the success of these wasps in parasitizing aggressive adult ants: for example, the vestigial tarsal claws and enlarged pulvilli (suction like disks, [130, 131, 217]) of *Elasmosoma* spp., or the raptorial fore

legs of *Neoneurus* spp., enable wasps to grasp and hold the ant firmly while ovipositing. Likewise, the peculiar ventral spine of *K. sentum* females, located on the fifth sternite, could help to fix the wasp's position during oviposition, when the body of the wasp goes back tending to the vertical position, and fore legs detach from the ant's cuticle. Finally, the longitudinal disposition of *K. sentum* females's tarsi on the ant metasoma, one over the other, enables the necessary rotation of the body to adjust itself to the position of the ant's gaster, before oviposition. The wasp rotates counterclockwise if the right tarsus is placed over the left one; and if the left tarsus is placed over the right one, the rotation is clockwise.

2.3.2. Ichneumonidae. Ichneumonidae is the largest family in the Hymenoptera with about 23,330 described species worldwide in 46 subfamilies and 1207 genera; the total number of species is estimated to be more than 60,000 [207, 218, 219]. Most of the members of this large family are parasites of holometabolous insects, but a few species parasitize spiders (egg sacs, spiderlings, or adults) or egg sacs of pseudoscorpions. Many ichneumonids are hyperparasitoids of other ichneumonoids or of tachinid flies, and some species are egg-larval parasitoids, laying an egg in the host egg but consuming the host in its larval stage [218, 219].

Various species of the genus *Gelis* (all of them initially referred to as *Pezomachus*) and a few others of the genera *Agrothereutes*, *Aptesis*, *Pleolophus*, and *Thaumtogelis* have been reported by various authors to be associated with ants of the genera *Lasius*, *Formica*, *Myrmica*, *Temnothorax*, and *Solenopsis* [24, 56, 220–222]. However, no information is available on the exact relationship with their ant host, except that in some cases (such as *Pleolopus micropterus* (Gravenhost) (referred to as *Pezomachus micropterus*) and *T. vulpinus* (Gravenhorst) (referred to as *Pezomachus vulpinus*)), they were clearly reported as “found in the nest of *Formica rufa*, not reared from cocoons” [220]. Until now, true ichneumonid parasitism on ants has been demonstrated only for 3 species, all belonging to the subfamily Hybrizontinae and very likely to the same tribe Hybrizontini. The most ancient report dates back to 1852 [145] and concerns *Eurypterna cremieri* described as hovering over a nest of *Lasius fuliginosus* in Germany. This behavior, suspected to be related to the search of an appropriate host, was later confirmed by different authors not only for the same host species in France and Italy [146–148] but also for three other species of ants in the genera *Lasius* and *Formica* in France, England, and Japan [123, 144, 149]. In the early 20th century, Cobeli [148] described how four females of *E. cremieri* were hovering over trails of *L. fuliginosus*, while ants were moving their nest to another nest site, inspecting each ant worker that was transporting a larva. The female parasitoids quickly drew closer to the larva, and folding up the abdomen touched it, presumably depositing an egg. Such behavior was only observed with ants transporting a larva and did not trigger any reaction from the workers. In spite of the interesting information supplied, this report passed more or less unnoticed until 2010 when the parasitic nature of this behavior could be confirmed (and even photographed) concerning *Lasius nipponensis* transporting brood between

two nests [149]. Only workers carrying something in their mandibles were tracked by *E. cremieri* females hovering about 2 cm above them. And only those carrying a larva were attacked after a sudden dive of the wasp which gripped the targeted larva with the tarsi of its fore and middle legs, bent its abdomen down, exerted its ovipositor, and oviposited in the larva before flying away in search of a new host. The complete sequence lasted less than 1 s and elicited some brief excitement from the worker ant. Dissection of a stung ant larva showed that a wasp egg was present in the somatic cavity. Another undescribed Hybrizontinae species (gen. nov. sp. nov.) was similarly reported by the same authors as hovering over workers of the slow moving ant *Myrmica kotokui* which were holding something in their mandibles. As for *E. cremieri*, only those carrying a larva were more closely inspected and were attacked in a similar manner as previously described, but in that case, the complete attack sequence lasted longer (3–4 s), and oviposition itself took at least 1 s. A third case of ant larval parasitism has very recently been confirmed and involves *Hybrizon buccatus* females. This species had been frequently reported in association with (or hovering over) different ant species from various genera (*Myrmica*, *Lasius*, *Formica*, and *Tapinoma*, see Table 1) [24, 140, 144, 146, 152, 153] and was reared from nests of *Lasius alienus* where the ichneumonid naked pupae had been found among ant-host cocoons [150]. But it was not until 2011 that the oviposition into larvae transported by *Lasius grandis* workers could be observed and filmed during brood transfer between two nest entrances [129]. Only final instar larvae were attacked, in a very similar way to that previously described for *E. cremieri*, and the complete sequence lasted between 0.40 and 0.58 s. Chemical and/or visual cues are likely to be involved in the location of the ants' trail since *H. buccatus* females have been observed continuously hovering over the trail for a period of time, even in the absence of ants. Finally, considering both the hovering behavior as a reliable evidence of parasitism and the fact that all three ichneumonid parasitoids known until now to attack ants are restricted to the Hybrizontinae, two other cases are likely to be added to our list: *Ghilaromma fuliginosi* and *H. rileyi* which have been reported swarming and hovering over the nests of *Lasius fuliginosus* [150, 151] or attracted to a disturbed nest of *L. alienus* [154], respectively. However, in both cases, direct oviposition into ant larvae or adults needs to be confirmed.

3. Conclusions

Since the last paper on parasites of social insects by Schmid-Hempel [7], the number of reliable records of parasitoid wasps attacking ants and their brood has grown dramatically from about 43 species to at least 138 belonging to 9 hymenopteran families. Furthermore, the knowledge of the biology and behavior of those wasps and the nature of their interactions with ants has significantly progressed, though many gaps still remain. Most likely, hymenopterous parasitoids of ants are more abundant than suggested by our list of reliable records, and future studies focusing on the

immature stages of ants under close scrutiny would certainly increase this list substantially.

All castes of ants and all developmental stages, excepting eggs, are the target of parasitoid wasps. For example, neoneurine braconids parasitize adult worker ants while foraging or performing other activities outside the nest [129, 131, 143], while eurytomids of the genus *Aximopsis* attack adult queens at the very moment of nest foundation [115, 116, 118, 119]. However, in most cases, ant larvae are the target of parasitoid attacks, either inside or outside their nests. Larvae can be parasitized outside the protective walls of the nest during transportation when ants move from one nest to another as for some euphorine braconids and hybridontine ichneumonids [129, 149], or while being employed to fix or build a new nest as occurred for the green weaver ant larvae attacked by the chalcidid *Smicromorpha* [41]. Most often, ant larvae are attacked inside the nest, notwithstanding the pugnacious character of ants. For eucharitid and perilampid wasps, planidia are transported by phoresis into the targeted nest where they actively search for a larval host. The extremely small size of the planidia is assumed to facilitate both entrance into the host colony and initial parasitization [195], but in most other parasitoid wasps (diapriids, encyrtids, entedonine eulophids, and some eurytomids), it has been assumed that it is the female that searches for a host nest, enters it, and oviposits on or in the larval host. So far, however, how the females gain access into the ant nest and complete the oviposition process has never been described, and the initial stages of development of these parasitoids are in most cases unknown (but see [35, 131]).

Hymenopterous parasitoids attacking ants exhibit a wide array of biological and developmental strategies: ecto- or endoparasitism, solitary or gregarious, and idio- or koinobiosis. Besides, the behavioral strategies evolved to cope with ant aggression or to exploit the communication system of ants are also impressive. Most of these parasitoids belong to families with species using a wide range of insects or arthropods as primary hosts, and in many cases of recorded associations between parasitic wasps and ants [20, 23, 112, 114, 128, 160, 186, 198], the primary host of the parasitoids is not the ant but another insect species present in the ant nests. Such indirect association through parasitism of trophobionts or other myrmecophiles suggests that a possible path to the parasitization of ants by hymenopterous parasitoids could have evolved as a shift from the initial primary host (Diptera, Coleoptera, or other insect myrmecophiles) to the ant host larvae through a gradual process of association and integration with the ant hosts. Such a hypothesis proposed for diapriids by Huggert and Masner [160] and widened by Hanson et al. [223] to hymenopterous parasitoids in general might apply for numerous families, and a supporting example has recently been suggested among eulophids [112]. However, other evolutionary paths are likely to be involved in the case of eucharitids and perilampids and those species that attack adult ants and deserve further study.

Despite a significant increase in our knowledge of hymenopterous parasitoids of ants in the last 15 years, the remark of Schmid-Hempel [7] concerning parasitism in social insects in general: “the existing knowledge is bound to

be a massive underestimation, since the true abundance and distribution of parasites remain to be discovered” is still, more than ever, a topical subject. Most hymenopterous parasitoids attacking ants remain to be discovered. Moreover, despite the presumed importance of some of them as natural enemies of ants, few quantitative data are available on the impact of these natural enemies on their hosts (see [224]). Based on their abundance and success in attacking ant hosts [36, 83, 193, 194], some parasitoid wasps like, for example, diapriids and eucharitids, seem excellent potential models to explore how parasitoids impact ant colony demography, population biology, and ant community structure, and further studies focusing on these issues will certainly contribute to deepening our knowledge on this important group of parasites.

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