

A review of the nesting habits and socioecology of the ant genus *Polyrhachis* Fr. Smith

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Abstract. We provide a summary of the nesting and socioecological habits of 197 species of *Polyrhachis* ants. Nesting habits range from subterranean to terrestrial, lignicolous, lithocolous and arboreal with varying levels of consistency at the subgeneric level. Species are predominantly either subterranean or terrestrial nesting within the subgenera *Campomyrma*, *Chariomyrma* and *Hagiomyrma*; mainly arboreal nesting within *Aulacomyrma*, *Cyrtomyrma*, *Hedomyrma*, *Hemioptica*, *Myrmatopa* and *Myrmothrinax*; lignicolous within *Hedomyrma*, and variable within *Myrma*, *Myrmhopta* and *Polyrhachis*. The majority of species within a particular subgenus demonstrate a consistent nesting type but a few species can be highly variable, demonstrating both subterranean and arboreal habits. The inclusion of larval silk in the nests is correlated almost entirely with arboreal nesting, but the presence of spider silk in the nests of at least four species suggests caution when inferring silk origin. Pupal cocoons are present in all but *Cyrtomyrma* and *Myrmatopa*. Polydomy and polygyny are known from a number of species and may be more common in arboreal nesting species, but limited data sets prevent definitive interpretations at this time.

Keywords: *Polyrhachis*, Formicidae, nesting ecology, socioecology, mating systems

INTRODUCTION

The Old-World ant genus *Polyrhachis* Fr. Smith includes approximately 500 described species organised into 12 subgenera, and is the subject of extensive and ongoing taxonomic revisions (Bolton 1973; Dorow 1995; Kohout 2006b). The taxonomic diversity of the genus is matched with an equally diverse socioecology. Nesting habits, for example, range from subterranean and terrestrial, to lignicolous, lithocolous and arboreal (Robson & Kohout 2005). Nest walls can include both larval and spider silk (Robson 2004), and nests can even be found in such unusual habitats as intertidal mangrove mud (Nielsen 1997) or within the colonies of other ant species (Maschwitz *et al.* 2003).

Studies of the socioecology of ants have provided an important framework for the testing and development of numerous evolutionary theories (Hölldobler & Wilson 1990) and with improved phylogenetic knowledge ants are becoming even more significant model systems to explore the evolution of a variety of ecological, social and behavioural characters (Brady *et al.* 2006; Moreau *et al.* 2006). The ant genus *Polyrhachis* is ideally suited to such approaches due its highly diverse socioecological habits, but unfortunately much of the information on these attributes of the genus is located in equally scattered sources. There exists a variety of ecological or behavioural studies summarising particular biogeographical subgroups or ecological communities (e.g. Lieke *et al.* 1998; Kohout 1999)

and the socioecology of a number of species has been studied in detail (e.g. Ofer 1970; Yamauchi 1987; van Zweden *et al.* 2007), but much valuable information remains embedded within the primary taxonomic literature. In combination with ongoing taxonomic revisions, this makes it difficult to determine the socioecological state of individual species and subgenera, and the potential significance of new descriptions to our understanding of the evolution of these traits as a whole.

The goal of this paper is to review the entire literature on *Polyrhachis* in order to consolidate our knowledge of the nesting habits and socioecology of the genus. We hope this information and the conclusions we draw from it will provide a solid basis for ongoing socioecological and phylogenetic studies, and prompt fellow researchers to further the collection of such information.

MATERIALS AND METHODS

Information on the nesting and socioecological characteristics of *Polyrhachis* was derived from both the primary literature and our own unpublished field observations and museum inspections. In order to optimise the information presented in the face of ongoing taxonomic revisions, records are provided only for described species. Further information will be provided on additional species once they are described.

The taxonomic classification, spelling of species epithets and authors' names follows that established by Bolton (1995a) with additions from Kohout (2006b, 2006a). Informal species groups within *Myrma* follow those proposed by Bolton (1973) and Kohout (2006a), while species groups within *Myrmhopla* and *Polyrhachis* follow those of Dorow (1995).

Individual nests were described as being located in either subterranean (in the soil with or without any cover such as rocks or fallen logs), terrestrial (on the ground beneath logs and stones, in or between grass stems), lignicolous (within the cavities of living or dead plants, including hollow

stems, bamboo internodes, the base of ferns in trees, cavities under bark, or within myrmecophyte plants), lithocolous (on or within rock crevices) or arboreal (among leaves or twigs, either against a single surface such as a trunk or between adjacent surfaces such as leaves) sites. In a single case, 'laboratory' was used to describe the nesting location of a captive but originally subterranean colony.

The determination of the number of colonies and queens per nest was made with reference to published literature and our own field studies. Polydomy was inferred if either workers were observed moving between nests or the transfer of workers between nests did not invoke aggressive interactions. Polygyny was inferred if more than one dealate queen was observed in a single nest. In a single case this interpretation was confirmed by molecular studies (van Zweden *et al.* 2007).

Additional nest material was classified as either silk (typically flat sheets thought to arise from larval silk glands), carton (fine plant material), spider silk (silk known to be removed from spider webs or egg sacks) or none (where the absence of either silk, carton or spider silk was confirmed). All types were described if more than one type of nesting material was found in a single nest.

The presence or absence of pupal cocoons is noted, based on existing literature or direct observations of field and laboratory colonies.

The source of the information typically indicates the earliest published reference to the character state of a particular species. We have deliberately restricted the sources to those that specifically refer to an actual identified species, and give precedence to published records over our own unpublished observations. The following abbreviations are used in addition to literature citations where required, and refer to reliable sources such as field notes, laboratory observations or information accompanying museum specimen label data: BBL (Bede B. Lowery, unpublished), JRF (John R. Fellowes, unpublished), MCZC (Museum of Comparative Zoology, Harvard University, Cambridge, Mass.,

USA), NMNH (National Museum of Natural History, DC, USA), SKR (Simon K.A. Robson, unpublished), RJK (Rudolf J. Kohout, unpublished). In all cases, the absence of information means that a particular character state has been neither explicitly described in the literature, nor determined through our own unpublished studies.

RESULTS

Nesting and socioecological data were determined from 197 of the approximately 500 described species of *Polyrhachis*. Representative species were included from all 12 subgenera, but the extent to which each subgenus is sampled is variable (Table 1). Records are particularly sparse from the smaller subgenera (*Aulacomyrma*, *Hemioptica*), perhaps due to their limited distribution and relative rarity.

Within the subgenus *Aulacomyrma*, all three species for which nesting habits have been described are lignicolous. The nests of *P. dohrni* Forel were lined with silk and cocoons have been confirmed in two species.

Within the subgenus *Campomyrma*, the majority of species are subterranean-nesting, though lignicolous and arboreal nesting are known in two and one species respectively. Silk has been described in the field nest of only a single species, *Polyrhachis phryne* Forel, though a captive colony of *Polyrhachis hexacantha* Erichson lined their test-tube nest with silk. Pupal cocoons have been described in 12 species. Nothing is known of the queen number or colony structure of any species in this genus.

Within the subgenus *Chariomyrma*, the majority of species are subterranean-nesting but a few species have been described with lignicolous nests and with one exception silk has never been found as part of their nests. The single exceptional species, *Polyrhachis schoopae* Forel, has been found in a silk nests on the sides of rock faces, but based on the type of nests and the identity of other *Polyrhachis* species at the same locality we believe this unusual example is a case

of *P. schoopae* moving into an abandoned *Polyrhachis turneri* Forel nest. Pupal cocoons are present in the eight *Chariomyrma* species for which this trait has been described.

Within the subgenus *Cyrtomyrma*, all species form arboreal nests, all nests include larval silk (though some such as *Polyrhachis australis* Mayr and *Polyrhachis pilosa* Donisthorpe are known to also include spider silk), and all larvae appear to pupate without cocoons. Both monodomous and polydomous nests, and single vs. multiple queen colonies, have been described.

Within the subgenus *Hagiomyrma*, the majority of species are subterranean or terrestrial, with a few lignicolous species. There is no evidence for the incorporation of silk into their nest structures, and all larvae pupate in cocoons. Nothing is known of the queen number or colony structure.

Within the subgenus *Hedomyrma*, the majority of species are lignicolous, with a few species also nesting in the ground or inhabiting nests constructed of spider silk on the side of rock walls. Colonies are monodomous in the single species for which information is available, *P. turneri*. The presence of silk is variable and all larvae pupate in cocoons.

Within the subgenus *Hemioptica*, all species are arboreal nesting, incorporate silk into their nests, and appear to produce pupal cocoons. There is support for monodomous nesting habits in a single species, *Polyrhachis bugnioni* Forel.

Nesting and socioecological habits within the subgenus *Myrma* are extremely variable, and there appears to be a loose correlation between the various species groups and their habits. All species within the *alexisi* and *monista* species groups, for example, are arboreal nesting, while nesting habits range from terrestrial to lignicolous and arboreal within the *relucens* species group. Nests can include either carton, silk or neither, though the presence of pupal cocoons appears consistent within the subgenus. Both monodomous and

polydomous nests, and single vs. multiple queen colonies, have been described.

Within the subgenus *Myrmatopa*, all species have arboreal nests, and with the exception of one variable species, *Polyrhachis schang* Forel, all species can include silk in their nests. The larvae of this subgenus appear to pupate without cocoons.

Nesting and socioecological habits within the subgenus *Myrmhopla* are also extremely variable. Nest habits range from subterranean to lignicolous and arboreal, and at least one species (*Polyrhachis lacteipennis* Fr. Smith) appears capable of nesting in all three localities. The incorporation of silk (and occasionally carton) appears to occur in all arboreal species. Both monodomous and polydomous nests, and single vs. multiple queen colonies, have been described, and all larvae appear to pupate in cocoons. The *viehmeyeri* species group stands out as an almost entirely parasitic group, with no evidence for the incorporation of silk into their (or their hosts) nest.

Within the subgenus *Myrmothrinax*, the majority of species are arboreal nesting, with two species, *Polyrhachis eudora* Fr. Smith and *Polyrhachis ternatae* Karawajew, forming lignicolous nests. At least two species are known to form polydomous colonies, and silk and pupal cocoons are present in all nests described.

Nesting and socioecological habits within the subgenus *Polyrhachis* are variable, including examples of subterranean, terrestrial, lignicolous and arboreal nesting. Nesting habits of *Polyrhachis lamellidens* Fr. Smith appear highly variable, including all but lithocolous habits. Examples of polydomous and both monogynous and polygynous colonies are known; silk is incorporated into the nest of arboreal nesting species in which nest-wall structure was described, but appears to be absent in the case of the ground-nesting *P. olybria* Forel. All larvae appear to pupate in cocoons.

DISCUSSION

The diversity of nesting habits described within *Polyrhachis* ants is in accordance with previous descriptions of the nesting habits of the genus as a whole (Dorow 1995), but a number of previously undetected patterns are now evident. Arboreal nesting appears to be universal in species of the subgenera *Aulacomyrma*, *Cyrtomyrma* and *Myrmatopa* and almost so in *Hedomyrma* and *Myrmothrinax*, where a number of species have adopted lignicolous nesting habits. Species of *Campomyrma*, *Chariomyrma* and *Hagiomyrma* are predominantly subterranean-nesting, with a few species in each subgenus utilising alternative nest sites. Within the subgenus *Campomyrma* at least one species, *P. halidayi*, can be found in arboreal nests and a number of undescribed species are known to be lignicolous in the Australian tropics (C. Burwell, personal communication, 2006). Similarly in *Chariomyrma*, a few species occupy lignicolous or lithocolous nest sites. *Myrma* and *Myrmhopla* stand out among the *Polyrhachis* subgenera for the diversity of nesting habits, ranging from subterranean to arboreal and in the case of *Myrmhopla*, even as parasites within the nests of other ant species. This diversity is perhaps not surprising given that *Myrmhopla* is most likely polyphyletic (Dorow 1995). The subgenus *Polyrhachis* is predominantly an arboreal-nesting group, but at least one member of the bihamata species group (*P. bihamata* Drury), and the single member of the *lamellidens*-group (*P. lamellidens* Fr. Smith) can nest in the soil (Table 1).

Information on the presence of silk in the nests of *Polyrhachis* is less detailed than knowledge of their nest locations, but a number of general patterns can be discerned. The incorporation of silk into the nests is restricted almost entirely to arboreal-nesting species, though it has been recorded occasionally in lignicolous species. Silk has never been reported in species of the two predominantly ground-nesting subgenera, *Chariomyrma* or *Hagiomyrma*, and within those subgenera containing a diversity of nesting types it is restricted almost entirely to lignicolous or arboreal-nesting species. The presence of silk in a

laboratory colony of the normally soil-nesting *P. (Campomyrma) hexacantha* and “woven material” in the soil-nesting *P. (Myrma) esarata* Bolton suggest that silk production may be facultative or even maintained in a number of subterranean species.

Despite the consistent pattern of nest habits in some subgenera, caution still needs to be exercised when reviewing published descriptions of nest habits. Donisthorpe (1941c, 1941a, 1943), for example, appears to have used “carton” and “silk” almost synonymously when describing *Polyrhachis* nests and so it is not always clear if “carton” implies the absence of silk, as it is typically interpreted to mean at present. The location of described nest material should also be noted, as carton can also be present at the entrance of a number of lignicolous and subterranean-nesting species (Table 1). The partial inclusion of spider silk in *P. (Cyrtomyrma) australis*, *P. (Cyrtomyrma) pilosa* and *P. (Myrma) laboriosa* Fr. Smith and the construction of silk nests made entirely of spider silk in *P. (Hedomyrma) turneri* also raise the possibility that “silk” nests need not always imply the use of larval silk only. We suspect that most published descriptions of silk nests imply a larval origin, as the fluffy spider-silk nests of *P. turneri* are quite different from the larval-derived flat sheets of silk found in the nests of most weaving *Polyrhachis* (Robson 2004), but field observers should be aware that multiple sources of silk exist.

Many important socioecological aspects of the genus are currently poorly known. The absence of pupal cocoons appears limited to species in the subgenus *Cyrtomyrma* and *Myrmatopa* (Table 1; Kohout 1999), but cocoon status in the majority of species remains to be described. This is unfortunate as the loss of cocoons has been correlated with the evolution of nest-weaving within ants as a whole (Hölldobler & Wilson 1983). Species that produce the most extensive silk nests, such as *Oecophylla smaragdina* (Fabricius), pupate without cocoons, while species such as *Dendromyrmex chartifex* (Fr. Smith), considered to represent the lowest grade of nest weaving, continue to produce cocoons (Hölldobler &

Wilson 1977). Similarly, knowledge of the presence of polydomous or polygynous nests is extremely limited and it is not yet possible to draw ecological conclusions. Arboreality seems to be the most common nesting habit of those species described as being either polydomous or polygynous (Table 1) but this may reflect the ease with which arboreal nests can be sampled, rather than an ecological correlate of arboreality *per se*.

In conclusion, the ant genus *Polyrhachis* demonstrates a significant diversity in nesting habits but much information remains to be gathered. The recent descriptions of inter-tidal nesting habits (Nielsen 1997) and the occupation of nests on rock faces constructed entirely of spider silk (Robson 2004) suggest that unique habits remain to be discovered. *Polyrhachis* ants comprise a significant component of the Southeast Asian ant fauna (Bolton 1995b) and play an important role in a variety of environmental studies in this region (Yamane *et al.* 1996; Brühl *et al.* 1998; Maryati Mohamed 1998; Hashimoto *et al.* 2000), yet we have knowledge of the nesting habits of less than half of the described species. Future studies that report on the presence and type of silk, the presence or absence of larval cocoons, and the number of queens in sampled colonies, would be extremely informative.

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Table 1: Nesting and social habits of the ant genus *Polyrhachis*

Subgenus Species	Nest location	Multiple nests/colony?	Multiple queens/colony?	Additional nest material	Pupal cocoon	Source
<i>Aulacomyrma</i> Emery, 1921						
<i>dohrni</i> Forel, 1901	lignicolous				present	Kohout (in press)
<i>orokana</i> Kohout, 2007	lignicolous				present	Kohout (in press)
<i>wardi</i> Kohout, 2007	lignicolous				present	Kohout (in press)
<i>Campomyrma</i> Wheeler, 1911						
<i>creusa</i> Emery, 1897	subterranean				present	Kohout (2000)
<i>femorata</i> Fr. Smith, 1858	subterranean lignicolous subterranean			none	present	RJK Kohout (2000) Wheeler (1915a)
<i>flavibasis</i> Clark, 1930	lignicolous				present	RJK Kohout (2000)
<i>fuscipes</i> Mayr, 1862	lignicolous				present	RJK SKR
<i>gravis</i> Clark, 1930	subterranean			carton entrance	present	RJK Bingham (1903)
<i>halidayi</i> Emery, 1889	arboreal				present	JRF
<i>hexacantha</i> Erichson, 1842	subterranean / lignicolous				present	BBL
<i>hirsuta</i> Mayr, 1876	laboratory				present	RJK
<i>insularis</i> Emery, 1887	subterranean				present	RJK
<i>macropa</i> Wheeler, 1916	subterranean				present	Kohout (2000)
<i>maculata</i> Forel, 1915	subterranean				present	Wheeler (1910)
<i>micans</i> Mayr, 1876	subterranean			none	present	SKR
<i>ops</i> Forel, 1907	lignicolous				present	RJK
<i>patiens</i> Santschi, 1920	subterranean				present	RJK
<i>phryne</i> Forel, 1907	subterranean				present	Wheeler (1915a)
<i>prometheus</i> Santschi, 1920	subterranean				present	RJK BBL
<i>schwiedlandi</i> Forel, 1902	subterranean				present	Brown, pers. comm. cited in Hung (1967)
<i>semipolita</i> André, 1896	subterranean				present	Kohout (1990)
<i>sidnica</i> Mayr, 1866	subterranean				present	RJK Kohout (2000)
	subterranean				present	RJK BBL
	subterranean				present	Wheeler (1915a)

Subgenus Species	Nest Location	Multiple Nests/Colony?	Multiple Queens/Colony?	Additional Nest Material	Pupal Cocoons	Source
<i>templi</i> Forel, 1902	subterranean lignicolous				present present	RJK RJK
<i>Charitomyrma</i> Forel, 1915						
<i>aurea</i> Mayr, 1876	subterranean					RJK
<i>constricta</i> Emery, 1897	subterranean			none	present	Clay & Anderson (1996) RJK
<i>cyrus</i> Forel, 1901	lignicolous			none	present	SKR
<i>gab</i> Forel, 1879	subterranean				present	Kohout (2000)
<i>heinlethii</i> Forel, 1895	subterranean / lignicolous				present	RJK Kohout (1988a)
<i>hookeri</i> Lowne, 1865	subterranean				present	RJK Kohout (1990)
<i>lata</i> Emery, 1895	subterranean				present	Kohout (1990) Kohout (2000)
<i>limbata</i> Emery, 1897	subterranean / terrestrial				present	RJK Kohout (1988a)
<i>lownei</i> Forel, 1895	subterranean / lignicolous				present	RJK Kohout (1988a)
<i>nitens</i> Donisthorpe, 1943	lignicolous				present	BBL Donisthorpe (1943)
<i>obscura</i> Forel, 1895	subterranean				present	BBL Donisthorpe (1943)
<i>punctiventris</i> Mayr, 1876	subterranean				present	Kohout (2000)
<i>schoopae</i> Forel, 1902	lithocolous				present	Kohout (1999)
<i>senilis</i> Forel, 1902	subterranean / lignicolous				present	Kohout (1988a)
<i>sokolova</i> Forel, 1902	subterranean				present	RJK Kohout (1988b)
<i>vermiculosa</i> Mayr, 1876	subterranean				present	SKR Kohout & Taylor (1990)
<i>vermiculosa</i> Mayr, 1876	subterranean				present	RJK
<i>Cyrtomyrma</i> Forel, 1915						
<i>abbreviata</i> Kohout, 2006	arboreal				absent	Kohout (2006b)
<i>aporema</i> Kohout, 2006	arboreal			silk	absent	RJK
<i>australis</i> Mayr, 1870	arboreal			silk	absent	Turner (1897)
<i>brevinoda</i> Kohout, 2006	arboreal	yes	yes	silk	absent	Wheeler (1915b)
<i>debilis</i> Emery, 1887	arboreal			silk	absent	Hinman (1994)
<i>decumbens</i> Kohout, 2006	arboreal		no	spider silk	absent	Dwyer & Ebert (1994)
	arboreal			silk	absent	Kohout (2006b)
	arboreal			silk	absent	SKR
	arboreal			silk	absent	Donisthorpe (1938b)
	arboreal			silk	absent	Kohout (2006b)

Subgenus Species	Nest Location	Multiple Nests/Colony?	Multiple Queens/Colony?	Additional Nest Material	Pupal Cocoons	Source
<i>delecta</i> Kohout, 2006	arboreal			silk	absent	Kohout (2006b)
<i>dorsena</i> Kohout, 2006	arboreal			silk	absent	RJK
<i>kyawthani</i> Kohout, 2006	arboreal			silk	absent	RJK
<i>laevissima</i> Fr. Smith, 1858	arboreal			carton		Karawajew (1928)
<i>mackayi</i> Donisthorpe, 1938	arboreal			silk		Karawajew (1929)
<i>montithi</i> Kohout 2006	arboreal			silk	absent	Robson & Kohout (2005)
<i>pilosa</i> Donisthorpe, 1938	arboreal			silk	absent	SKR
<i>rastellata</i> (Latreille, 1802)	arboreal			silk		Kohout (2006b)
<i>robsoni</i> Kohout, 2006	arboreal			spider silk		Kohout & Taylor (1990)
<i>yorkana</i> Forel, 1915	arboreal			silk	absent	Dwyer & Ebert (1994)
	arboreal			silk		SKR
	arboreal			silk		Turner (1897)
	arboreal			carton / silk		Mann (1919)
	arboreal	yes		silk	absent	Kohout (2006b)
	arboreal	yes	yes	silk		van Zweden et al. (2007)
	arboreal		yes	silk		Heinze & Holldobler (1993)
	arboreal			silk		Wheeler (1915a)
	arboreal	yes		silk		Kohout (2006b)
	arboreal		no	silk	absent	SKR
Hagiomyrma Wheeler, 1911						
<i>ammon</i> (Fabricius, 1775)	subterranean				present	RJK
<i>ammonooides</i> Roger, 1863	subterranean					BBL
<i>angusta</i> Forel, 1902	subterranean				cocoons	RJK
<i>crawleyi</i> Forel, 1916	subterranean				present	Kohout (1988c)
<i>denticalata</i> Karawajew, 1927	subterranean/often in old rotting tree stumps					Kohout (1988c)
<i>lachesis</i> Forel, 1897	lignicolous				present	Kohout (1999)
<i>lydiae</i> Forel, 1902	subterranean					RJK
<i>metella</i> Fr. Smith, 1860	subterranean				present	Kohout (2000)
<i>paxilla</i> Fr. Smith, 1863	subterranean				present	Kohout (1988c)
<i>schenkii</i> Forel, 1886	lignicolous				present	Donisthorpe (1943)
<i>semiaurata</i> Mayr, 1876	subterranean					Kohout (1988c)
	terrestrial / lignicolous				present	RJK
	terrestrial					Froggatt (1905)
						Wheeler (1922a)
<i>semiobscura</i> Donisthorpe, 1944	lignicolous				present	RJK
<i>thusnelda</i> Forel, 1902	lithocolous			carton	present	Kohout & Taylor (1990)
	lignicolous	no		carton	present	Robson (2004)
						SKR

Subgenus Species	Nest Location	Multiple Nests/Colony?	Multiple Queens/Colony?	Additional Nest Material	Pupal Cocoon	Source
<i>trapezoidea</i> Mayr, 1876	subterranean				present	RJK
<i>tubifera</i> Forel, 1902	subterranean				present	RJK
<i>Hedomyrma</i> Forel, 1915						
<i>annae</i> Mann, 1919	subterranean / lignicolous					Mann (1919)
<i>argentina</i> Forel, 1902	lignicolous				present	Kohout (1988c) RJK
<i>atropos</i> Fr. Smith, 1860	lignicolous				present	Kohout & Taylor (1990)
<i>clio</i> Forel, 1902	lignicolous				present	RJK
<i>cupreata</i> Emery, 1895	arboreal			silk		Kohout (1988c)
	lignicolous			none	present	SKR
<i>daemeli</i> Mayr, 1876	lignicolous					RJK
	lignicolous					Turner (1897)
	lignicolous			no	present	Robson & Kohout (2005)
<i>erato</i> Forel, 1902	lignicolous				present	SKR
<i>fervens</i> Fr. Smith, 1860	arboreal			no	present	Kohout (1988c)
	lignicolous			carton		Smith (1871)
	lignicolous				present	Robson & Kohout (2005)
<i>malaensis</i> Mann, 1919	lignicolous					SKR
	subterranean					Mann (1919)
<i>melpomene</i> Emery, 1897	lignicolous					RJK
<i>mjoberti</i> Forel, 1915	lignicolous					RJK
	lignicolous				present	Kohout (1988c)
<i>ornata</i> Mayr, 1876	lignicolous					RJK
	lignicolous				present	Turner (1897)
<i>ruffemur</i> Forel, 1907	lignicolous				present	RJK
	lignicolous				present	Kohout (1988c)
<i>terpsichore</i> Forel, 1893	lignicolous				present	RJK
<i>turneri</i> Forel, 1895	lithocolous			spider silk	present	SKR
	lithocolous		no	spider silk	present	Robson (2004) SKR
<i>Hemiptica</i> Roger, 1862						
<i>boltoni</i> Dorrow & Kohout, 1995	arboreal			silk	present	Dorow & Kohout (1995)
<i>bugnioni</i> Forel, 1908	arboreal		no	silk	present	Krombein & Norden cited in Dorow & Kohout (1995)
<i>scissa</i> Roger, 1862	arboreal			silk		Wroughton (1892)
<i>Myrma</i> Billberg, 1820						
<i>alexisi</i> -group						

Subgenus Species	Nest Location	Multiple Nests/Colony?	Multiple Queens/Colony?	Additional Nest Material	Pupal Cocoons	Source
<i>curta</i> André, 1890 <i>latharis</i> Bolton, 1973	arboreal arboreal					Bolton (1973) Bolton (1973)
<i>continua</i>-group <i>conops</i> Forel, 1901 <i>spinifera</i> Stitz, 1911	lignicolous / tree stumps lignicolous / terrestrial					Forel (1901) RJK
<i>inermis</i>-group <i>hosei</i> Donisthorpe, 1942 <i>vindex</i> Fr. Smith, 1857	lignicolous lignicolous					Donisthorpe (1942) Wheeler (1919)
<i>militaris</i>-group <i>alluaudi</i> Emery, 1892 in Bolton	arboreal					Emery (1892), cited (1973)
<i>concana</i> André, 1889 <i>decedentata</i> André, 1889 <i>esarata</i> Bolton, 1973 in Bolton	arboreal lignicolous subterranean subterranean			'woven material'		Bolton (1973) Bolton (1973) Bolton (1973) Arnold (1924), cited (1973)
<i>fissa</i> Mayr, 1902 <i>gagates</i> Fr. Smith, 1858 <i>laboriosa</i> Fr. Smith, 1858	arboreal subterranean arboreal arboreal arboreal arboreal			silk 'paper like material' silk silk	present	Wheeler (1922a) Wheeler (1922b) Karawajew (1928) Bolton (1973) Wheeler (1922a) Collart (1932) Lenir & Dejean Eidmann (1944), (1973)
(1994) <i>latispina</i> Emery, 1925 cited in Bolton	lignicolous			spider silk no silk carton		
<i>militaris</i> (Fabricius, 1782)	lignicolous subterranean / terrestrial			none		Bolton (1973) Wheeler (1922a)
<i>rufipalpis</i> Santschi, 1910 <i>schistacea</i> Gerstäcker, 1859	arboreal subterranean terrestrial			silk silk		Lévieux (1976) Bolton (1973) Wheeler (1922b) MCZC
<i>monista</i>-group <i>monista</i> Santschi, 1910 Bolton	arboreal arboreal			silk carton		Bolton (1973) Forel (1916), cited in (1973)
<i>parabiotica</i>-group <i>chapmani</i> Kohout, 2006 <i>parabiotica</i> Chapman, 1963	lignicolous				present present	RJK Chapman (1963) RJK

Subgenus Species	Nest Location	Multiple Nests/Colony?	Multiple Queens/Colony?	Additional Nest Material	Pupal Cocoons	Source
relucens-group						
<i>andromache</i> Roger, 1863b	arboreal / lignicolous lignicolous			silk none / carton	present	Kohout (1988c) Robson & Kohout (2005) RJK
<i>foreli</i> Kohout, 1989	lignicolous/subterranean terrestrial					Kohout (1989) Kohout (2000)
<i>illaudata</i> Walker, 1859	terrestrial / lignicolous		no	none	present	Robson & Kohout (2005) SKR
<i>litigiosa</i> Emery, 1897	terrestrial	yes		none		Liefke et al. (1998) Hung (1962)
<i>nigropilosa</i> Mayr, 1872	lignicolous lignicolous / terrestrial lignicolous		no	none	present	RJK RJK Liefke et al. (1998)
<i>obliqua</i> Stütz, 1911	lignicolous	yes	yes	none		RJK Liefke et al. (1998)
<i>proxima</i> Roger, 1863	subterranean					MCZ
<i>pubescens</i> Mayr, 1879	lignicolous					Mann (1919)
<i>relucens</i> (Latreille, 1802)	lignicolous terrestrial					Hung (1962) Kohout (1989)
<i>rufofemorata</i> Fr. Smith, 1859	lignicolous		no	no	present	SKR
<i>salomo</i> Forel, 1910	lignicolous / subterranean	yes		silk	present	Mann (1919) RJK
<i>semitestacea</i> Emery, 1900	lignicolous	yes				Donisthorpe (1943)
<i>sericata</i> (Guérin-Méneville, 1831)	terrestrial					
revolit-group						
<i>olleti</i> Forel, 1916	lignicolous			silk		Forel (1916) cited in Hung (1967)
<i>transiens</i> Bolton, 1973	arboreal			carton		Bolton (1973)
<i>weissi</i> Santischi, 1910	arboreal			silk		Bolton (1973)
viscosa-group						
<i>arnoldi</i> Forel, 1914	arboreal			silk		Arnold (1924), cited in Bolton (1973)
<i>cubaensis</i> Mayr, 1862	lignicolous			silk		Arnold (1924), cited in Bolton (1973)
<i>viscosa</i> Fr. Smith, 1858	subterranean					Bolton (1973)
zopyra-group						
<i>zopyra</i> Fr. Smith, 1861					present	Donisthorpe (1941b)

Subgenus Species	Nest Location	Multiple Nests/Colony?	Multiple Queens/Colony?	Additional Nest Material	Pupal Cocoons	Source
<i>Myrmatopa</i> Forel, 1915						
<i>alpheia</i> Fr. Smith, 1863	arboreal			carton	absent	RJK Donisthorpe (1943) listed as <i>taurus</i> Donisthorpe, 1937
<i>derecyna</i> Fr. Smith, 1871	arboreal	yes				Smith (1871) Kohout & Taylor (1990)
<i>dolomedes</i> Fr. Smith, 1863	arboreal		no	silk	absent	SKR
<i>lombokensis</i> Emery, 1898	arboreal		yes	silk/carton carton/silk		Mann (1919)
<i>osae</i> Mann, 1919	arboreal			carton/silk/none carton / silk		Karawajew (1928) Karawajew (1906) listed as <i>alexandri</i> Karawajew, 1906
<i>schang</i> Forel, 1879	arboreal			carton/silk		Karawajew (1928)
<i>solmsi</i> Emery, 1887	arboreal			silk	absent	Robson & Kohout (2005) SKR
<i>subritidens</i> Emery, 1900	arboreal					
<i>ulysses</i> Forel, 1910	arboreal					
<i>Myrmhopta</i> Forel, 1915						
<i>arachne</i>-group						
<i>arachne</i> Emery, 1896	arboreal			none		Karawajew (1928)
	arboreal			silk		Dorow & Maschwitz (1990)
	arboreal			silk		Robson & Kohout (2005) Bingham (1903)
	lignicolous					Liefke et al. (1998)
	lignicolous	yes	no	none		RJK Dorow & Maschwitz (1990) Bingham (1903)
<i>hodgsoni</i> Forel, 1902	arboreal			silk	present	
	lignicolous					
<i>armata</i>-group						
<i>armata</i> (Le Guillou, 1842)	arboreal			silk		Karawajew (1928)
	arboreal / lignicolous			silk		RJK
	arboreal			silk	present	SKR
	arboreal			silk		Mann (1919) listed as <i>argentea</i> Mayr, 1862
<i>saeuissima</i> Fr. Smith, 1860	arboreal			carton		Karawajew (1928)
	arboreal			silk		Robson & Kohout (2005)
	arboreal			silk		Mann (1919)
<i>tibialis</i> Fr. Smith, 1858	arboreal					
	arboreal					
<i>wheeleri</i> Mann, 1919	arboreal					
<i>bicolor</i>-group						
<i>bicolor</i> Fr. Smith 1858	arboreal	yes	no	silk		Liefke et al. (1998)
	arboreal			silk	present	SKR

Subgenus Species	Nest Location	Multiple Nests/Colony?	Multiple Queens/Colony?	Additional Nest Material	Pupal Cocoons	Source
<i>bicolor atrocastanea</i> Karaw., 1927	arboreal			silk	present	Karawajew (1928)
<i>bicolour concolor</i> Forel, 1910					present	RJK
<i>bicolour nigripes</i> Emery, 1897					present	RJK
cryptoceroides-group						
<i>cryptoceroides</i> Emery, 1887	lignicolous arboreal			silk silk		Dorow (1995) Karawajew (1928) listed as <i>mysitica</i> Karawajew, 1927
<i>jerdonii</i> Forel, 1892	arboreal / lignicolous arboreal			silk silk		Karawajew (1928) Forel (1894), cited in Wheeler (1910)
daphne-group						
<i>daphne</i> Wheeler, 1919	arboreal	yes		silk		Dorow (1995)
dives-group						
<i>dives</i> Fr. Smith, 1857	arboreal arboreal arboreal terrestrial arboreal	yes	yes	silk carton silk silk silk	present	Forel (1894), cited in Wheeler (1910) Kohout (1988c) Yamauchi et al. (1987) Karawajew (1928) SKR
<i>lacteipennis</i> Fr. Smith, 1858	arboreal subterranean / lignicolous / arboreal subterranean / arboreal subterranean	yes		silk silk silk silk	present	Dorow (1995) Ofer (1970) Wheeler & Mann (1916) Hung (1962)
flavoflagellata-group						
<i>flavoflagellata</i> Karawajew, 1927	arboreal			silk		Karawajew (1928)
furcata-group						
<i>etheli</i> Chapman, 1963	lignicolous					Chapman (1963)
<i>furcata</i> Fr. Smith, 1858	arboreal	yes	no	silk	present	Liefke et al. (1998) RJK
<i>rufipes</i> Fr. Smith, 1858	lignicolous				present	RJK
hector-group						
<i>abdominalis</i> Fr. Smith, 1858	arboreal lignicolous			carton / silk	present	Karawajew (1928) RJK
<i>hector</i> Fr. Smith, 1857	arboreal				present	RJK
<i>muelleri</i> Forel, 1893	arboreal arboreal arboreal			silk silk silk	present	Karawajew (1929). Dorow & Maschwitz (1992)
<i>schellerichae</i> Dorow, 1996	arboreal	yes	no	silk	present	Liefke et al. (1998)
<i>tubifex</i> Karawajew, 1926	lignicolous arboreal	yes	no	none silk	present	Schellerich-Kaaden et al. (1997) Karawajew (1928)

Subgenus Species	Nest Location	Multiple Nests/Colony?	Multiple Queens/Colony?	Additional Nest Material	Pupal Cocoons	Source
<i>mucronata</i>-group						
<i>bismarckensis</i> Forel, 1901	arboreal		yes	silk		SKR
<i>follicula</i> Menozzi, 1926	arboreal			silk		Robson & Kohout (2005)
<i>Keratifera</i> Karawajew, 1927	arboreal			carton/silk		NMNH
<i>mitrata</i> Menozzi, 1932	arboreal					Karawajew (1928)
<i>mucronata</i> Fr. Smith, 1859	arboreal					Menozzi (1932)
<i>paromala</i> Fr. Smith, 1863	arboreal	no	no	silk	present	Kohout & Taylor (1990)
<i>ochracea</i>-group						
<i>ochracea</i> Karawajew, 1927	arboreal			silk		SKR Smith (1871)
<i>sexpinosa</i>-group						
<i>aureovestita</i> Donisthorpe, 1937	arboreal/ lignicolous					Dorow (1995)
<i>bubastes</i> F. Smith 1863	arboreal			carton	present	Donisthorpe (1937)
<i>calypso</i> Forel, 1911	arboreal			silk		RJK Donisthorpe (1943)
<i>esuriens</i> Emery, 1897	arboreal			carton	present	Robson & Kohout (2005)
<i>glabrinota</i> Clark, 1930	arboreal					RJK Donisthorpe (1941c) listed as <i>arcuspinoxa</i> Donisthorpe 1941
<i>reclinata</i> Emery, 1887	arboreal / lignicolous	no	no	silk	present	RJK Kohout & Taylor (1990)
<i>rugifrons</i> Fr. Smith, 1860	lignicolous			silk		SKR
<i>sexpinosa</i> (Latreille, 1802)	arboreal	no / yes		carton	present	Robson & Kohout (2005)
	arboreal			silk		Karawajew (1928)
	arboreal			carton		Kohout & Taylor (1990)
	arboreal					SKR
	lignicolous			carton	present	Robson & Kohout (2005)
				carton/silk		Smith (1871)
				silk		Karawajew (1928)
				silk		Robson & Kohout (2005)
						SKR
					present	Kohout (1999)
<i>viehmeyeri</i>-group						
<i>loweryi</i> Kohout, 1990	subterranean					Kohout (1990)
<i>rustica</i> Kohout, 1990	subterranean		no	none		Maschwitz et al. (2003)
<i>lama</i> Kohout, 1994	subterranean					Kohout (1990)
	subterranean					Maschwitz et al. (2000)

Subgenus Species	Nest Location	Multiple Nests/Colony?	Multiple Queens/Colony?	Additional Nest Material	Pupal Cocoons	Source
<i>Myrmotherinx</i> Forel, 1915						
<i>abnormis</i> Donisthorpe, 1948	arboreal			silk	present	Robson & Kohout (2005) RJK
<i>cheesmanae</i> Donisthorpe, 1937	arboreal					Donisthorpe (1937)
<i>dirvillei</i> Donisthorpe, 1938	arboreal			silk		Donisthorpe (1938a)
<i>delicata</i> Crawley, 1915	arboreal	yes		silk		Kohout (1999)
<i>eudora</i> F. Smith, 1860	arboreal lignicolous			silk	present	SKR Smith (1871) (species inquirenda see Kohout (1998))
<i>frauenfeldi</i> Mayr, 1862	arboreal			carton / silk		Karawajew (1928)
<i>queenstandica</i> Emery, 1895	arboreal			carton / silk		Kohout (1999)
<i>saigonensis</i> Forel, 1886	arboreal			silk	present	RJK
<i>ternatae</i> Karawajew, 1933	arboreal lignicolous			silk		Robson & Kohout (2005)
<i>textor</i> Fr. Smith, 1857	arboreal	yes				Karawajew (1933)
<i>thrinax</i> Roger, 1863	arboreal			carton / silk		Smith (1871) Karawajew (1928)
<i>Polyrhachis</i> Fr. Smith, 1957						
<i>bihamata</i>-group						
<i>bellicosa</i> Fr. Smith, 1859	arboreal		no	carton / silk		Wilson (1959)
	arboreal				present	Kohout (1988b)
	arboreal					SKR
<i>bihamata</i> (Drury, 1773)	arboreal			silk		Bingham (1903)
	subterranean					SKR
<i>erosispina</i> Emery, 1900	arboreal		no	silk		Kohout (1988b)
	arboreal			silk		Kohout (2005)
<i>olybria</i> Forel, 1912	terrestrial		no	none		Liefke et al. (1998)
<i>taylori</i> Kohout, 1988	lignicolous	yes	yes	silk	present	Kohout (1988b)
<i>ypsilon</i> Emery, 1887	arboreal			silk		SKR
<i>lamellidens</i>-group						
<i>lamellidens</i> Fr. Smith, 1874	subterranean / terrestrial / lignicolous					Yano (1911) cited in Hung (1967)

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