



RESEARCH ARTICLE - ANTS

Pheidole symbiotica Wasmann, 1909, an enigmatic supposed social parasite, is a nematode-infested form of *Pheidole pallidula* (Nylander, 1849) (Hymenoptera: Formicidae: Myrmicinae)

L BOROWIEC, S SALATA

University of Wrocław, Wrocław, Poland

Article History

Edited by

Rodrigo M. Feitosa, UFPR, Brazil

Received 27 November 2014

Initial acceptance 31 January 2015

Final acceptance 11 March 2015

Keywords

Hymenoptera, Formicinae, *Pheidole*, Myrmicinae, social parasite, Italy, redescription.

Corresponding author

Lech Borowiec

Department of Biodiversity and

Evolutionary Taxonomy

University of Wrocław

Przybyszewskiego 63/77, 51-148

Wrocław, Poland

E-Mail: cassidae@biol.uni.wroc.pl

Abstract

Pheidole symbiotica Wasmann, 1909 hitherto known only from type series collected in Portugal is recorded from Italy for the first time. Dissection of abdomen of this supposed social parasite of *Pheidole pallidula* (Nylander, 1849) showed that it is infested by a large mermithid nematode. That allows us to conclude that *Pheidole symbiotica* is only a teratological form of *Pheidole pallidula*. In consequence, we propose synonymy of *Pheidole symbiotica* Wasmann, 1909 under *Pheidole pallidula* (Nylander, 1849). High quality photographs of this form are presented for the first time and an illustration of its parasite is also given.

Introduction

Pheidole symbiotica Wasmann, 1909 is one of the most enigmatic European ants. It was described from material collected by P.W. Deckelmeyer in a *Pheidole pallidula* (Nylander, 1849) nest in Barrô [Portugal, Águeda county, 40° 32' 11" N 8° 28' 12" E]. In original description Wasmann (1909) noted only morphology of a specimen (no information about the number of examined specimens), presented sketch figures of dorsal view and head and discussed biological status of the species. He suggested that the described specimen may be a worker or ergatoid gyne. In subsequent supplementary paper (Wasmann, 1910) he provided information about four ergatoid gynes (two of them not fully sclerotized), one pupa with ergatoid gyne and six pupae with males collected by Deckelmeyer. The material contained also a specimens of host species including one major worker and 19 minor workers.

Unfortunately, present location of the type material is unknown. In supplementary description the putative male of

P. symbiotica is distinguished from male of *P. pallidula* only by the structure of antennae (basal segment slightly wider than subsequent segments and last segment twice longer than penultimate segment at *P. symbiotica* whereas male of *P. pallidula* has globular basal segment, twice wider than subsequent segments and last segment only 1.5 times as long as penultimate segment). According to these differences in male's body structure Wasmann (1910) definitely stated that *P. symbiotica* represents a distinct species, a social parasite of *P. pallidula*. In 1913 Forel published a note about a nest of *P. pallidula* (found by M. Sahlberg on the Corfu, Greece) in which apart from the typical major and minor workers occurred a specimen of intermediate size. He suggested that it represents *P. symbiotica* and concluded that this form is only a simple intermediate worker of *P. pallidula*. However, there is no certainty that the specimen studied by Forel (1913) represents the form described by Wasmann (1909) as a *P. symbiotica*. Emery (1915), in list of synonyms of *P. pallidula*, noted *P. symbiotica* as "var. ? *symbiotica* Wasm." with a short



comment “an sp. distinguenda?”. Collingwood (1978) in the checklist of Iberian ants noted *P. symbiotica* as a good species but missed this taxon in the key to Iberian species. In recent catalogues (Bolton, 1995; Bolton et al., 2006; Borowiec, 2014) *P. symbiotica* is treated as a good species.

Although *Pheidole pallidula*, a supposed host of *P. symbiotica*, is widely distributed and common species in the Mediterranean area (Borowiec, 2014) it is surprising that the form described by Wasmann (1909) under the name *P. symbiotica* has never been found again. *P. pallidula* is a pioneering species, one of the first to inhabit areas transformed by man, such as roadsides of new roads, mines, gravels and excavations of sand, but also it is common on sun-exposed rock walls, in grasslands and meadows. During our entomological travels to several Mediterranean countries we found several hundred nests of *P. pallidula* but we have never collected specimens distinguished from typical major and minor workers.

Such rarity of this enigmatic taxon suggested that perhaps *Pheidole symbiotica* is not a good species, but only a form of *P. pallidula*, teratological due to parasitic infections.

Some recent papers suggested that various ant parasites can affect the morphological changes of all castes. Trabalon et al. (2000) described modification of morphological characters of *Leptothorax nylanderi* (Förster) induced by cestodes. Csösz (2012), using noninvasive X-ray microtomography, proved that two *Myrmica* species: *M. myrmecophila* Wasmann, 1910 and *M. symbiotica* (Menozzi, 1925) are teratological forms of *Myrmica sulcinodis* Nylander, 1846 and *Myrmica scabrinodis* Nylander, 1846 developing as a result of infection by mermithid nematodes. Poinar (2012) gives an overview of examples of parasitic Nematoda infecting ants and affecting the morphology of workers and queens. The paper presents a photo of the nest of *Pheidole pallidula* with two atypical major workers infected by Nematoda. Unfortunately, lack of access to type material of *P. symbiotica* precluded verification of the hypothesis that this taxon is a teratological form of supposed host *P. pallidula*.

Unexpectedly, during senior author's trip to southern Italy (Campania and Calabria, August-September 2014) nine specimens with characters described for *P. symbiotica* were collected in two nests of *P. pallidula*. We dissected abdomen of two specimens and discovered that they are infested with large mermithid nematodes filling the entire abdomen (Fig 6).

Below we present a detailed redescription of “*symbiotica*” form with high-quality photographs and propose synonymization of *Pheidole symbiotica* Wasmann with *Pheidole pallidula* (Nylander).

Materials and Methods

Ants were collected in Italy, Campania, Salerno Prov., Cilento National Park, Monte Bulgheria n. Poderia. Description, measurements and photos were made under Nikon SMZ 1500 stereomicroscope, Nikon D5200 photo

camera and Helicon Focus software. Examined specimens are deposited in the collection of senior author.

Standard measurements and indices are as defined in Bolton (1975):

Measurements

HL – head length; measured in straight line from mid-point of anterior clypeal margin to mid-point of occipital margin; in full face view;

HW – head width; width of head at anterior margin of eyes in full-face view;

EL – eye length; measured along the maximum diameter of eye;

EW – eye width; measured along the maximum width of eye perpendicular to EL;

SH – scape width; measured in the widest point of the scape;

SL – scape length; maximum straight-line length of scape;

PNW – pronotum width; maximum width of pronotum in dorsal view;

ML – mesosoma length; measured as diagonal length from the anterior end of the neck shield to the posterior margin of the propodeal lobe;

PH – petiole height; maximum height of petiole in lateral view;

PL – petiole length; maximum length of petiole in lateral view;

PPH – postpetiole height; maximum height of postpetiole in lateral view;

PPL – postpetiole length; maximum length of postpetiole in lateral view;

HTL – hind tibia length; maximum length of hind tibia.

Example of measurements: 0.875 ± 0.032 ($0.838-0.927$) = the average measurement \pm standard deviation (range of variation).

Indices

CI – cephalic index; $HW/HL \times 100$;

SI1 – scape index 1; $SL/HL \times 100$;

SI2 – scape index 2; $SL/HW \times 100$;

MI – mesosoma index; $ML/PNW \times 100$;

PI – petiole index 1; $PL/PH \times 100$;

PPI – postpetiole index; $PPL/PPH \times 100$;

HTI – hind tibia index; $HTL/HW \times 100$.

All lengths are in mm.

Nomenclatorial notes

Pheidole pallidula (Nylander, 1849)

Myrmica pallidula Nylander, 1849: 42 (terra typica: Sicily).

Oecophthora subdentata Mayr, 1853: 145 (terra typica: Austria); Mayr, 1855: 456 (as synonym of *pallidula*).

Pheidole pallidula var. *arenarum* Ruzsky, 1905: 647 (terra typica: Kazakhstan); Atanassov & Dlussky, 1992: 123 (as synonym of *pallidula*).

Pheidole pallidula subsp. *koshewnikovi* Ruzsky, 1905: 648 (terra typica: Russia).

Pheidole pallidula var. *tristis* Forel, 1907: 204 (terra typica: Tunisia), not *Pheidole tristis* (Smith, 1858: 132).

Pheidole symbiotica Wasmann, 1909: 693 (terra typica: Portugal), **new synonymy**.

Pheidole pallidula var. *emeryi* Krausse, 1912: 169 (terra typica: Sardinia), not *Pheidole tristis* Mayr, 1887: 589; *Pheidole pallidula* var. *obscura* Santschi, 1936: 200 (= *Pheidole pallidula* var. *emeryi* Krausse 1912: 169 not Mayr, 1887: 589).

Pheidole pallidula var. *cicatricosa* Stitz, 1917: 340 (terra typica: Algeria); Collingwood, 1978: 68 (as synonym of *pallidula*).

Pheidole pallidula var. *inermis* Stitz, 1917: 340 (terra typica: Algeria), not *Pheidole inermis* Mayr, 1870: 984; *Pheidole pallidula selenia* Özdikmen, 2010: 805 (= *Pheidole pallidula* var. *inermis* Stitz, 1917: 340 not *Pheidole inermis* Mayr, 1870: 984).

Pheidole pallidula subsp. *orientalis* Müller, 1923: 69 (= *Pheidole pallidula* ssp. *arenarum* var. *orientalis* Emery, 1915: 230 unavailable name, terra typica: Russia); Baroni Urbani, 1964a: 3 (as synonym of *pallidula*).

Pheidole pallidula var. *recticeps* Menozzi, 1932: 452 (= *Pheidole pallidula* ssp. *tristis* var. *recticeps* Forel, 1909: 391 unavailable name, terra typica: Egypt).

Xenoaphaenogaster inquilina Baroni Urbani, 1964b: 50 (terra typica: Sicily), not *inquilina* Wheeler, 1903: 664; Bolton, 1987: 291 (as synonym of *pallidula*).

Redescription of “*symbiotica*” form (Figs 1-5)

Measurements: Infested workers (n = 9): HL: 0.875 ± 0.032 (0.838-0.927); HW: 0.869 ± 0.031 (0.816-0.916); SL: 0.721 ± 0.014 (0.704-0.739); SH: 0.085 ± 0.005 (0.078-0.089), EL: 0.151 ± 0.008 (0.134-0.156); EW: 0.108 ± 0.012 (0.089-0.123); ML: 1.04 ± 0.026 (0.993-1.079); HTL: 0.748 ± 0.028 (0.691-0.782); PL: 0.421 ± 0.039 (0.352-0.464); PPL: 0.313 ± 0.021 (0.279-0.345); PH: 0.261 ± 0.03 (0.212-0.302); PPH: 0.257 ± 0.025 (0.223-0.291); PNW: 0.542 ± 0.019 (0.514-0.564); CI: 99.3 ± 1.7 (97.4-101.3); SII: 82.5 ± 2.9 (78.3-87.0); SI2: 83.1 ± 2.5 (79.6-86.3); PI: 161.2 ± 18.7 (137.0-203.3); PPI: 122.7 ± 16.0 (107.6-154.7); HTI: 85.9 ± 1.8 (83.0-88.4); MI: 192.0 ± 6.2 (184.3-202.7)

Redescription: Forms were observed in two colors. In paler form the head is yellowish with brown frons and vertex, thorax, antennae and legs yellowish, abdomen brown, apical margins of abdominal segments yellowish (Figs 1, 2).

In darker form the head is mostly black with dark brown clypeus and yellowish brown underside, antennae and legs yellowish brown to partly brown, pronotum black, mesonotum brown, propodeum from brown to yellowish brown, petiole and postpetiole yellowish brown, abdomen brown, apical margins of abdominal segments yellowish (Figs 3, 4).

In full-face view head rectangular, almost as wide as long (Fig 5). Posterior margin shallowly concave, posterior corners rounded. Mandibles elongately triangular, their surface with setose, partly elongate punctures but without



Figs 1-2: Pale worker of teratological form “*symbiotica*” of *Pheidole pallidula*. 1. Dorsal; 2. Lateral. Scale bar = 1 mm.

striation, space between punctures shiny. Masticatory margin mostly straight, with large apical and slightly smaller preapical tooth, small tooth in the middle and two small teeth basally. Anterior margin of clypeus straight or shallowly emarginate, surface shiny, without striation or ridges, on sides with few fine, setose punctures, basal clypeal lobe triangular, deeply impressed, sharply bordered from triangular frontal lobes. Frons bicornute anterad, triangular anterior lobes with fine longitudinal striation, frontal lateral margins sharp, short, extending to 1/3 length of head, central part of frons shiny,



Figs 3-4: Dark worker of teratological form “*symbiotica*” of *Pheidole pallidula*. 3. Dorsal; 4. Lateral. Scale bar = 1 mm.

with sparse setose punctures. Antennal scrobes deep, with semicircular striation surrounding scrobe dorsally and laterally. Gena with longitudinal ridges, prolonged along inner margin of eyes up to 1/2-2/3 length of head, postocular area, top and venter of head without ridges or striation, with fine setose punctures. Eyes small, almost round, approximately 0.4 times as long as tempora and 0.5 times as long as gena. Whole surface of head shiny, covered with semi-erect and erect setae, the longest on clypeus, along frontal lateral ridges, on top of head and partly on ventral surface of head. The longest setae twice longer than eye length. Antennae moderately elongate, scapes slightly shorter than head width, funicles approximately 1.4 times as long as scapes, with large 3-segmented club 1.3 times as long as eight basal funicle segments joined. Scapus and funicles covered with long semierect to erect setae.

Mesosoma 1.9 times as long as wide, promesonotum subangulate in profile, pronotum separated from mesonotum by sharp margin. Dorsal surface of mesonotum almost flat with small tubercle laterally, distinctly separated from propodeum by moderately deep transverse sulcus. Dorsal surface of propodeum flat in profile, with small, triangular propodeal spines then with oblique, concave posterior surface (Figs 2, 4). Surface of pronotum shiny, with sparse, small setose punctures, top of mesonotum shiny, sides with distinct microreticulate sculpture, propodeum dorsally with transverse ridges and microreticulate sculpture, laterally with microreticulate sculpture and fine oblique to semicircular striation. Petiole elongate with long peduncle, its anterior face straight to shallowly concave, node triangular to slightly obtuse in profile. Posterior face of petiole straight, ventral margin straight, without spine or angulation. In dorsal view, petiole with concave sides and more or less angulate anterior and posterior corners. Postpetiole in profile rounded to subangulate. In dorsal view postpetiole 1.7 times as long as wide, regularly widened posteriorly, apical half with gently rounded sides.



Fig 5. Head of teratological form “symbiotica” of *Pheidole pallidula*. Scale bar = 0.5 mm.



Fig 6. Mermithid nematode prepared from abdomen of teratological form “symbiotica” of *Pheidole pallidula*. Scale bar = 0.5 mm.

Material: nine infested workers from two nests of *Pheidole pallidula*, Italy, Campania, Salerno Prov., Cilento National Park, Monte Bulgheria n. Poderia (40,08709N / 15,39717E), 380 m, leg. L. Borowiec.

Habitat and behavior notes: ants were collected in two nests of *P. pallidula* under limestone stones on the side of the road covered by a rock rubble which was scantily overgrown by xerothermophilic plants. After lifting the stone, the individuals of the “symbiotica” form immediately began to hide between the grains of gravel, while specimens of *P. pallidula*, in a manner typical for workers of this species, exhibited aggressive behavior. The area was placed on northern slope of Monte Bulgheria mountain which is exposed to sunlight in the middle of the day. The following ant species were recorded in the same area: *Camponotus aethiops* (Latreille), *Camponotus dalmaticus* (Nylander), *Camponotus lateralis* (Olivier), *Camponotus nylanderi* Emery, *Camponotus piceus* (Leach), *Camponotus vagus* (Scopoli), *Crematogaster scutellaris* (Olivier), *Crematogaster sordidula* (Nylander), *Formica gagates* Latreille, *Lasius emarginatus* (Olivier), *Lasius myops* Forel, *Lasius paraliensis* Seifert, *Messor structor* (Latreille), *Myrmica scabrinodis* Nylander, *Plagiolepis pygmaea* (Latreille), *Solenopsis fugax* Latreille, *Solenopsis* cf. *lusitanica*, *Temnothorax* cf. *exilis*, *Temnothorax flavicornis* (Emery), *Temnothorax krausseii* (Emery), *Temnothorax leviceps* (Emery), *Temnothorax lichtensteini* Bondroit, *Temnothorax luteus* (Forel), *Temnothorax recedens* (Nylander), and *Tetramorium bicarinatum* (Nylander). Finding of *Tetramorium bicarinatum* in natural habitat is very interesting because this exotic species is usually collected in anthropogenic areas such as city parks, greenhouses, ruderal areas and roadsides but it was previously recorded from open habitats in Italy near Cropani Marina, Catanzaro Province (Jucker et al., 2008).

Comments: At first glance the “symbiotica” form looks intermediate between minor and major workers of *P. pallidula*. The most striking feature is the very large abdomen in this form, which is longer than the summed total length of the head and thorax, while in typical workers of *Pheidole*

pallidula the abdomen is clearly shorter. The development of such a large abdomen is probably stimulated by the parasite, which is large and tightly fills the whole volume of the abdomen. Form “*symbiotica*” does not have any features of the gyne, even ergatoid form, there are no wing buds and body proportions and construction of trunk are similar to the body shape of a big major worker. The parasite is believed to stimulate the development of workers to such a large size, so that it could accommodate in abdominal cavity such a large nematode specimen (Csösz & Majoros, 2009; Csösz, 2012).

Discussion

True social parasitism was observed in the genus *Pheidole* Westwood (Buschinger, 2009). Although Wilson (1984) noted that this phenomenon is rare in tropical ants but pointed that Neotropical *Pheidole microgyna* Wheeler, 1928 is a temporary social parasite of *Pheidole minutula* Mayr, 1878 and described two species from the Oriental region: *Pheidole languinosa* and *Pheidole parasitica*, both parasitizing in common and widespread *Pheidole indica* Mayr, 1879. He listed another six *Pheidole* species as potential social parasites including *Pheidole symbiotica* (sic!) (Kusnezov, 1951) described from Argentina. This homonymic name was later replaced by *Pheidole kusnezovi* by Wilson (2003).

Our observations of the “*symbiotica*” form show that for the description of a new species of parasitic ant from a single specimen of caste is not enough. We confirm Csösz’s (2012) conclusion that especially taxa reported only once or only few times should be verified by allowing the possibility of infection by internal parasites. Thus far the most drastic changes in the morphology and development of ants was observed in the specimens infected by nematodes (Csösz & Majoros, 2009; Poinar, 2012), but there are also examples of altered host morphology resulting from infections by other internal parasites (Heinze et al., 1998; Tralabal et al., 2000; Miura et al., 2006).

Acknowledgements

Thanks to Jolanta Świętojańska (University of Wrocław, Poland) for her assistance during field trips of the senior author and Marek L. Borowiec (University of California, Davis, USA) for language verification and other comments. The junior author would like to thank the University of Wrocław for supporting grant no. 2127/M/KBTE/14.

References

- Atanassov, N. & Dlussky, G. M. (1992). Fauna of Bulgaria. Hymenoptera, Formicidae. [In Bulgarian.]. Fauna na Bŭlgariya, 22: 1-310.
- Baroni Urbani, C. (1964a). Su alcune formiche raccolte in Turchia. Annuario dell’Istituto e Museo di Zoologia dell’Università di Napoli, 16 :1-12.
- Baroni Urbani, C. (1964b). Studi sulla mirmecofauna d’Italia. II. Formiche di Sicilia. Atti dell’Accademia Gioenia di Scienze Naturali, (6)16: 25-66.
- Bolton, B. (1975). A revision of the ant genus *Leptogenys* Roger in the Ethiopian region, with a review of the Malagasy species. Bulletin of the British Museum (Natural History). Entomology, 31: 235-305.
- Bolton, B. (1987). A review of the *Solenopsis* genus-group and revision of Afrotropical *Monomorium* Mayr (Hymenoptera: Formicidae). Bulletin of the British Museum (Natural History). Entomology, 54: 263-452.
- Bolton, B. (1995). A New General Catalogue of the Ants of the World: Harvard University Press, Cambridge, Mass., 504 pp.
- Bolton, B., Alper, G., Ward, P. S. & Naskrecki, P. (2006). Bolton’s Catalogue of Ants of the World: 1758-2005. Harvard University Press, CD edition.
- Borowiec, L. (2014). Catalogue of ants of Europe, the Mediterranean Basin and adjacent regions (Hymenoptera: Formicidae). Genus (Wrocław), 25(1-2): 1-340.
- Buschinger, A. (2009). Social parasitism among ants: a review (Hymenoptera: Formicidae). Myrmecological News, 12: 219-235.
- Collingwood, C.A. (1978). A provisional list of Iberian Formicidae with a key to the worker caste (Hym. Aculeata). EOS. Revista Española de Entomología, 52 :65-95.
- Csösz, S. (2012). Nematode infection as significant source of unjustified taxonomic descriptions in ants (Hymenoptera: Formicidae). Myrmecological News, 17: 27-31.
- Csösz, S. & Majoros, G. (2009). Ontogenetic origin of mermithogenic *Myrmica* phenotypes (Hymenoptera, Formicidae). Insectes Sociaux, 56: 70-76. DOI 10.1007/s00040-008-1040-3
- Emery, C. (1915). Les *Pheidole* du groupe *megacephala* (Formicidae). Revue Zoologique Africaine (Brussels), 4: 223-250.
- Forel, A. (1907). Fourmis nouvelles de Kairouan et d’Orient. Annales de la Société Entomologique de Belgique, 51: 201-208.
- Forel, A. (1909). Études myrmécologiques en 1909. Fourmis de Barbarie et de Ceylan. Nidification des *Polyrhachis*. Bulletin de la Société Vaudoise des Sciences Naturelles, 45: 369-407.
- Forel, A. (1913). Fourmis de la faune méditerranéenne récoltées par MM. U. et J. Sahlberg. Revue Suisse de Zoologie, 21: 427-438.
- Heinze, J., Rŭppell, O., Foitzik, S. & Buschinger, A. (1998) First record of ants with Cestodes from western North-America. Florida Entomologist, 81:122-125.
- Jucker, C., Rigato, F. & Regalin, R. (2008) Exotic ant records from Italy (Hymenoptera, Formicidae). Bollettino di Zoologia Agraria e di Bachicoltura, Ser. 2, 40: 99-107.
- Krausse, A. H. (1912). Eine neue Ameisenform von Sardinien (*Pheidole pallidula* v. n. *Emeryi* m.). Internationale Entomologische Zeitschrift, 6: 169.

- Mayr, G. (1853). Einige neue Ameisen. Verhandlungen der Zoologisch-Botanischen Vereins in Wien, 2: 143-150.
- Mayr, G. (1855). Formicina austriaca. Beschreibung der bisher im österreichischen Kaiserstaate aufgefundenen Ameisen, nebst Hinzufügung jener in Deutschland, in der Schweiz und in Italien vorkommenden Arten. Verhandlungen der Zoologisch-Botanischen Vereins in Wien, 5: 273-478.
- Mayr, G. (1870). Neue Formiciden. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien, 20: 939-996.
- Mayr, G. (1887). Südamerikanische Formiciden. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien, 37: 511-632.
- Menozzi, C. (1932). Spedizione scientifica all'Oasi di Cufra (marzo-luglio 1931). Formiche. Annali del Museo Civico di Storia Naturale "Giacomo Doria", 55: 451-456.
- Miura, O., Kuris, A.M., Torchin, M.E., Hechinger, R.F. & Chiba, S. (2006). Parasites alter host phenotype and may create a new ecological niche for snail hosts. Proceedings of the Royal Society B: Biological Sciences, 273: 1323-1328.
- Müller, G. (1923). Le formiche della Venezia Giulia e della Dalmazia. Bollettino della Società Adriatica di Scienze Naturali in Trieste, 28: 11-180.
- Nylander, W. (1849). Additamentum alterum adnotationum in monographiam formicarum borealium. Acta Societatis Scientiarum Fennicae, 3 (1848): 25-48.
- Özdikmen, H. (2010). New names for the preoccupied specific and subspecific epithets in the genus *Pheidole* Westwood, 1839 (Hymenoptera: Formicidae). Munis Entomology and Zoology, 5: 804-806.
- Poinar, G. Jr. (2012). Nematode Parasites and Associates of Ants: Past and Present. Psyche, 2012, 13 pp. doi:10.1155/2012/192017.
- Ruzsky, M. (1905). The ants of Russia. (Formicariae Imperii Rossici). Systematics, geography and data on the biology of Russian ants. Part I. [In Russian.]. Trudy Obshchestva Estestvoispytatelei pri Imperatorskom Kazanskom Universitete, 38(4-6): 1-800.
- Santschi, F. (1936). Liste et descriptions de fourmis du Maroc. Bulletin de la Société des Sciences Naturelles du Maroc, 16: 198-210.
- Smith, F. (1858). Catalogue of hymenopterous insects in the collection of the British Museum. Part VI. Formicidae. London: British Museum, 216 pp.
- Stitz, H. (1917). Ameisen aus dem westlichen Mittelmeergebiet und von den Kanarischen Inseln. Mitteilungen aus dem Zoologischen Museum in Berlin, 8: 333-353.
- Trabalon, M., Plateaux, L., Peru, L., Bagnères, A.-G. & Hartmann, N. (2000). Modification of morphological characters and cuticular compounds in worker ants *Leptothorax nylanderi* induced by endoparasites *Anomotaenia brevis*. Journal of Insect Physiology, 46: 169-178.
- Wasmann, E. (1909). Über den Ursprung des sozialen Parasitismus, der Sklaverei und der Myrmekophilie bei den Ameisen. (Schluss.). Biologisches Centralblatt, 29: 683-703.
- Wasmann, E. (1910). Nachträge zum sozialen Parasitismus und der Sklaverei bei den Ameisen. [part]. Biologisches Centralblatt, 30: 515-524.
- Wheeler, W. M. (1903). Some new gynandromorphous ants, with a review of the previously recorded cases. Bulletin of the American Museum of Natural History, 19: 653-683.
- Wilson, E. O. (1984). Tropical social parasites in the ant genus *Pheidole*, with an analysis of the anatomical parasitic syndrome (Hymenoptera: Formicidae). Insectes Sociaux, 31: 316-334.
- Wilson, E. O. (2003). *Pheidole* in the New World. A dominant, hyperdiverse ant genus. Cambridge, Mass.: Harvard University Press, [ix] + 794 pp.

