ISSN 0013-8738, Entomological Review, 2010, Vol. 90, No. 5, pp. 548–555. © Pleiades Publishing, Inc., 2010.
Original Russian Text © A.V. Antropov, N.A. Khrustalyova, 2010, published in Zoologicheskii Zhurnal, 2010, Vol. 89, No. 3, pp. 294–301.

Worker Ants of *Myrmica rubra* (Hymenoptera, Formicidae) as an Unusual Prey of the Digger Wasp *Crossocerus vagabundus* (Hymenoptera, Crabronidae)

A. V. Antropov[a] and N. A. Khrustalyova[b]

[a]*Zoological Museum, Moscow State University, Moscow, 125009 Russia*
e-mail: antropov@zmmu.msu.ru
[b]*Research Institute of Disinfectology, Federal Service for Supervision in Consumer Rights Protection and Human Welfare, Moscow, 117246 Russia*
e-mail: khrustalyova-n@rambler.ru

Received June 1, 2009

Abstract—The digger wasp *Crossocerus vagabundus* (Panzer, 1798) (Hymenoptera, Crabronidae, Crabronini) hunting for workers of *Myrmica rubra* (Linnaeus, 1758) was recorded for the first time. Various dipterans, mostly crane flies (Tipulidae), were the only known prey for this species. The modes of wasp hunting for worker ants are described. The reasons for unusual choice of prey are discussed.

DOI: 10.1134/S0013873810050027

At present, the digger wasp family Crabronidae comprises 144 genera (Pulawski, 2009). Virtually all of them are active hunters, except for *Krombeinictus nordenae* Leclercq, 1996; females of this species feed their larvae on pollen of *Humboldtia laurifolia* M. Vahl, 1794 (Fabaceae, Caesalpinioideae) (Krombein et al., 1999). Digger wasps of the family Crabronidae hunt for different insects (mainly adults), including minute thrips (Thysanoptera) and aphids (Homoptera), and also wasps and bees (Hymenoptera, Vespoidea, Apoidea) and spiders (Arachnida), however, relatively small number of crabronid wasps hunt for ants (Hymenoptera, Vespoidea, Formicidae).

Actually, representatives of only three genera of the family Crabronidae are exclusive ant hunters. They comprise 13 species of mainly Nearctic genera *Aphilanthops* Patton, 1881 and *Clypeadon* Patton, 1897 (= *Listropygia* R. Bohart, 1959) (Philanthinae, Aphilanthopini), and also 15 modern species of the genus *Tracheliodes* A. Morawitz, 1866 (Crabroninae, Crabronini), dwelling in the Holarctic and Neotropical zones.

On the whole, representatives of the subfamily Philanthinae hunt for stinging hymenopterans, mainly for bees.

Females of the genus *Aphilanthops* hunt for stingless winged females of the genus *Formica* Linnaeus, 1758 (Formicinae). For example, the prey of *A. frigidus* (F. Smith, 1856) and *A. subfrigidus* Dunning, 1898 is represented by the ants *F. fusca* Linnaeus, 1758, *F. pallidefulva* Latreille, 1802 (= *F. pallidefulva nitidiventris* Emeri, 1893), *F. neogagates* Viereck, 1903 (= *F. neogagates* Emery, 1893) and *F. subpolita* Mayr, 1886 (Peckham and Peckham, 1905; Wheeler, 1913; Evans, 1962; Krombein, 1967a, 1979; Evans, 1970; O'Neill, 1994).

At the same time, the prey of females of the genus *Clypeadon* is represented by stingy worker ants of the genus *Pogonomyrmex* Mayr, 1868 (Myrmicinae). In particular, females of *Clypeadon bechteli* (R. Bohart, 1959) hunt for worker ants *Pogonomyrmex californicus* (Buckley, 1867) (Evans, 1962); *C. dreisbachi* (R. Bohart, 1959), for *P. barbatus* (F. Smith, 1858) and *P. rugosus* Emery, 1895 (Evans, 1962, 1977; Krombein, 1979); *C. evansi* R. Bohart, 1966 and *C. haigi* (R. Bohart, 1959), for *P. rugosus* (= *P. barbatus rugosus* Emery, 1895) (Evans, 1962; Alcock and Gamboa, 1975; Krombein, 1979); *C. laticinctus* (Cresson, 1865), for *P. occidentalis* (Cresson, 1865) (Hicks, 1927, 1933; Alexander, 1985; Evans, 1962, 1977); *C. sculleni* (R. Bohart, 1959), for *P. maricopa* Wheeler, 1914 (= *P. maricopa barnesi* M.R. Smith, 1929) (Evans, 1962; Krombein, 1979); and *C. utahensis* (Baker, 1895), for *P. barbatus* and *P. californicus* (Evans, 1962, 1977; Krombein, 1967a).

Species of the genus *Tracheliodes* fill their nests with stingless workers of the genera *Liometopum* Wheeler, 1905 and *Tapinoma* Forster, 1850 (Dolychoderinae). For example, females of the Nearctic species *Tracheliodes amu* Pate, 1942, *T. foveolineatus* (Viereck, 1909), and *T. hicksi* Sandhouse, 1936 hunt for *Liometopum luctuosum* Wheeler, 1905 (= *L. occidentale luctuosum* Wheeler, 1905) (Hicks, 1936; Parker and Bohart, 1966; Krombein, 1967, 1979), whereas females of the western Palaearctic species *Tracheliodes curvitarsis* (Herrich-Schaeffer, 1841) and *T. varus* (Panzer, 1799) hunt for *L. microcephalum* (Panzer, 1798) (Adlerz, 1904; Zettel et al., 2004); *Tracheliodes quinquenotatus* (Jurine, 1807), for *Tapinoma erraticum* (Latreille, 1798) and *T. nigerrimum* (Nylander, 1856) (Ferton, 1892; Adlerz, 1904; Bernard, 1934; Bohart and Menke, 1976). Finally, species dwelling in the Russian Far East, namely, *Tracheliodes alinae* Nemkov, 1988 and *T. ghilarovi* Nemkov, 1988 hunt for worker ants *L. orientale* Karawajew, 1927, differing in size (Nemkov, 1988). Together with these specialized digger wasp genera of the family Crabronidae, females of some genera also hunt for ants.

In particular, the most complicated data on the known prey of the genus *Palarus* Latreille, 1802 is given in the latest revision of the tribe Palarini (Pulawski and Prentice, 2008). Species of this genus are specialized hunters for other hymenopterans, frequently for stinging species, including representatives of the families Ichneumonidae, Tiphiidae, Scoliidae, Mutillidae, Pompilidae, Sphecidae, Crabronidae, and also the solitary and social Vespidae and Apidae. Ants, however, were recorded as prey only in two cases. They were found in the nest of a Middle Asiatic species *P. funerarius* F. Morawitz, 1889 (winged ants, without indicating the species and sex) (Myartseva, 1976), and in the nest of the widespread and the most plastic in relation to prey Palaearctic species *P. variegatus* (Fabricius, 1781) [*Camponotus* Mayr, 1861 (Formicinae) (Tsuneki, 1969)].

Similar data are also known for some representatives of the subtribe Crabronina (Crabronidae, Crabronini).

Winged ant males were found among prey together with small dipterans of the families Culicidae, Chironomidae, Bombyliidae, Sapromyzidae, small butterflies, and even mayflies *Ephemera vitripennis* Blanchard, 1851 (Ephemeridae), in nests of the South American species *Podagritus rufotaeniatus* (Kohl, 1905) (Janvier, 1928), and also in the nest of the Australian species *Rhopalum carnegiacum* Leclercq, 1979 (Leclercq, 1997) (in both cases, no taxonomic data on ants was mentioned).

In nests of the western Palaearctic species *Lindenius pygmaeus armatus* (Van der Linden, 1829), winged males of the genus *Leptothorax nylanderi* (Forster, 1850) (Myrmicinae) (Marchal, 1893; Ferton, 1901; Grandi, 1928; Minkiewicz, 1933; Maneval, 1937) were found among prey together with small dipterans (Ceratopogonidae and Sciaridae) and hymenopterans (Pteromalidae and Braconidae).

In another case, male ants of the genus *Lasius* Fabricius, 1804, (Formicinae) were found in nests of the Nearctic species *Lindenius columbianus* (Kohl, 1892), together with other prey, represented by dipterans (Ceratopogonidae, Chironomidae, Sciaridae, Scatopsidae, Cecidomiidae, Hybotidae, Empididae, Chamaemyiidae, Milichiidae, Ephydridae, Chloropidae, and Agromyzidae), bugs (Anthocoridae, Miridae, and Lygaeidae), aphids (Aphididae), and hymenopterans (Aphidiidae, Ichneumonidae, Mymaridae, Eulophidae, Encyrtidae, Eupelmidae, Eucharitidae, Torymidae, Pteromalidae, Eurytomidae, Chalcididae, Ceraphronidae, and Crabronidae) (Miller and Kurczewski, 1975; Krombein, 1979).

Only solitary specimens of small mirmecine workers were revealed among the prey of some species of *Lindenius* Lepeletier de Saint Fargeau et Brulle, 1835, frequently hunting for hymenopterans. For example, a single ant *Monomorium minimum* (Buckley, 1867) (Myrmicinae) worker was found in a nest of *Lindenius buccadentis* Mickel, 1916, together with small parasitic hymenopterans (including mainly Braconidae, Eulophidae, and Pteromalidae, and also Ichneumonidae, Perilampidae, Ormyridae, Eurytomidae, Chalcididae, Cynipidae, and Bethylidae) and a single fly of the genus *Drapetis* Meigen, 1822 (Empididae). Two workers of *M. minimum* and a single male of *Tapinoma sessile* (Say, 1836) (Dolichoderinae) were found in another nest of the same species (Miller and Kurczewski, 1975; Krombein, 1979).

It should be noted that in all the above cases female wasps hunted either for winged ant males looking like their ordinary prey or, less frequently, for small stingless workers. In addition, the presence of solitary ant specimens in the nests of the abovementioned wasp species testifies to the occasional character of this prey.

On the whole, purposeful hunting of female crabronine wasps for stinging workers was recorded only once. Not only was the Southern African species *Encopognathus chirindensis* (Arnold, 1932) (Crabronini, Anacrabronina) (= *Thyreopus chirindensis* Arnold, 1932) recorded attacking *Tetramorium setuliferum* Emery, 1895 (Myrmicinae) workers, but a nest was found full of worker ants of several similar species (Arnold, 1932). Unfortunately, the glass tube with the collected material was accidentally broken and the ant species were not determined. No additional data concerning this species was ever obtained.

MATERIALS AND METHODS

A brilliantly colored digging wasp female, attacking a plastic street flowerbox (in an orchard situated approximately 63 km SSE from Moscow), was noted by us at 16.30 (July 14, 2008) during observation of ant nesting behavior. This box with flat "legs" was placed on a concrete plate at a height of approximately 70 cm above ground.

We planned watching the activity of this wasp for as long time as possible and did not try to catch it. Instead, we repeatedly photographed it from different views and distances, which later helped us to determine the species of this wasp. All the shots were made using a Canon EOS-40D camera with a Canon EF 100 f/2.8 Macro lens and a Canon Twin Macro Lite MT-24 EX).

Forewing venation reduced to a single discoidal and a single submarginal cell, together with an apically truncate marginal cell, is characteristic of digging wasps of the tribe Crabronini. Among the latter, several species of the genera *Crabro* Fabricius, 1775, *Crossocerus* Lepeletier de Saint Fargeau et Brulle, 1835, and *Ectemnius* Dahlbom, 1845 are most similar to the wasp observed, in yellow spots on abdominal tergites.

At the same time, the end of the recurrent vein near the middle of the submarginal cell rules out the species of the genus *Ectemnius*, whereas the thickened head with ocelli on the vertex forming nearly equal-sided triangle, together with the laterally compressed pygidial area, rules out all the species of the genus *Crabro*.

Only five species of the genus *Crossocerus* with yellow spots on abdominal tergites are known from East Europe: *C. binotatus* Lepeletier de Saint Fargeau et Brulle, 1835, *C. dimidiatus* (Fabricius, 1781), *C. quadrimaculatus* (Fabricius, 1793), *C. subulatus* (Dahlbom, 1845), and *C. vagabundus* (Panzer, 1798).

Crossocerus binotatus, *C. dimidiatus*, and *C. subulatus* possess elongate abdominal segment I, entirely black tergites II and IV, yellow tergite VI, and mainly yellow mandibles, whereas *C. quadrimaculatus* is distinguished by pointed mandible apices, the presence of triangular teeth in lower corners of the occipital carina, entirely yellow (virtually always) postscutellum, brown distal half of hind tibiae, and a flat pygidial area.

As a result, the wasp observed was determined as *Crossocerus* (*Acanthocrabro*) *vagabundus* (Panzer, 1798), a species repeatedly collected by us in this orchard.

The object of female wasp attacks appeared to be well-recognized ants *Myrmica rubra* (Linnaeus, 1758) (Formicidae, Myrmicinae), which had built their nest under the flowerbox bottom. In this part of the orchard, we annually found about half a dozen of small active nests of this ant species. They were usually situated between plastic plates bordering flowerbeds, under flat stones of the rockery and ground vases, or under the partly detached bark layer of fallen tree branches. *Myrmica rubra* is easily distinguished from formicine ants *Lasius niger* Linnaeus, 1758 and *Formica fusca* Linnaeus, 1758, commonly found in this orchard and dwelling in ground nests, by brown-rufous body color, 2-segmented propodeum, and a pair of pointed spines on posteriorly rounded epinotum.

RESULTS

The observed female of *C. vagabundus* performed regular attacks on worker ants *M. rubra*. The behavioral tactics of the wasp was unchanged and similar to that recorded to other crabronid wasps hunting for slowly moving prey. It included approaching, hovering, selecting of a solitary prey, estimating darts, and the final attack.

We distinguished the following main stages in the wasp's hunting behavior:

(1) the wasp landed on the concrete plate approximately at a distance of 3–5 cm from the base of the container (because usually ants hide in the nest before the appearance of the wasp) and then crawled to the nest entrance, touched it with the antennae, and started digging the substrate near the entrance, instigating the ants to leave their nest (Fig. 1);

Fig. 1. *Crossocerus vagabundus* female instigating ants *Myrmica rubra* to leave the nest.

Fig. 2. *Crossocerus vagabundus* female hovering and waiting for ants *Myrmica rubra*.

Fig. 3. *Crossocerus vagabundus* female immediately before the final attack on a worker of *Myrmica rubra*.

(2) as soon as the first workers came from the nest the wasp took off vertically, hovering at a distance of about 7–10 cm from ants (Fig. 2);

(3) the wasp did not attack groups of workers but waited for a single ant to walk away from the group;

(4) when one of the ants moved for a distance of about 3-4 cm from the group, the wasp performed 2–4 short darts toward this ant, followed by the final attack (Fig. 3);

(5) capturing the ant, the wasp flew away to a distance of about 10 cm, fell down on the concrete plate and, bending its abdomen, performed a single sting bite; after that, the wasp immediately flew away with its prey;

(6) each time the wasp flew away toward the free side of the plate to the right of the ant nest entrance; judging by the absence of any ant fragments, the wasp used its sting rather than mandibles, piercing the only unprotected place in the worker ant body, namely, the membrane near the base of the head.

—All the wasp's actions from the final attack to leaving for the nest lasted for about 3–4 s on average, testifying to a well-elaborated behavioral tactics. During nearly one and a half hours we watched one and the same female, judging by the characteristic spot of some foreign particles sticking to its pronotum. During this time, we recorded six successful wasp's attacks, followed by capture and removal of a single worker. Hence, about 15 min were spent by the female wasp on each ant capture. According to the wasp's flight rate and the intervals between the attacks, the nest of this wasp was situated at a distance of about 10 m (or less) from the attack site. The last appearance of the wasp was recorded at 9 min past 6 p. m. With the coming of twilight the ants' activity outside the nest stopped completely; so did the visits of the wasp.

Unfortunately, a strong night shower washed the ant nest from under the flower box, and neither the wasp no ants could be seen near it since that day.

DISCUSSION

According to the present data, females of *C. vagabundus* make nests in hollow stems of herbaceous plants and shrubs or in dead wood, occupying empty tunnels of xylophagous insects, only cleaning out frass. The majority of entomologists (Sickmann, 1893; Borries, 1897; Jansson, 1919; Fahringer, 1922; Bris-

towe, 1925; Gronblom, 1925; Hamm and Richards, 1926; Masuda, 1940) mentioned midges (Diptera, Tipulidae) as the only prey of these wasps. Only Tsuneki (1947) mentioned snipe flies (Diptera, Rhagionidae) and, in rare cases, even leaf-rollers (Lepidoptera, Tortricidae) among the wasp prey. Nowadays, no hymenopterans were ever revealed in the prey of the species of the genus *Crossocerus* and of *C. vagabundus* in particular.

Our observations resulted in distinguishing several aspects in the unusual hunting behavior of *C. vagabundus*.

The first question concerns transition from midge (Tipulidae) and snipe-fly (Rhagonidae) hunting to ant hunting, the latter prey being very unusual for the wasps mentioned. *Crossocerus vagabundus* usually hunts in the same layer where it nests, among high herbaceous plants, shrubs, and tree branches. According to our observations, midges of the family Tipulidae and similar representatives of the family Limoniidae could be frequently observed sitting on the lower sides of leaves, whereas snipe flies could also be seen on flowers and tree trunks in their usual numbers.

Normally, the soil ants *M. rubra* do not attract the attention of hunting *C. vagabundus* females, but in our case, they turned out in its hunting layer since they built their nest at a distance of about 70 cm above ground level and, thus, attracted the wasp's attention. At the same time, in contrast to *Liometopum microcephalum*, the ants that met the attacking wasp (*Tracheliodes varus*) in bark crevices with dangerously exposed mandibles (Zettel et al., 2004), *M. rubra* workers were indifferent to the hovering wasp, testifying to the fact that they were not the regular prey of *C. vagabundus*. *C. vagabundus* does not seem to be so narrowly specialized in relation to its prey as it is believed and can hunt for any available prey. This fact is supported by the wasp's tactics and the rate of its actions when immobilizing its prey, and also by the data on a wide prey spectrum of the abovementioned Nearctic species *L. columbianus*, testifying to the fact that the hunting preferences of wasps of the family Crabronidae can be associated with their nesting sites. In particular, in near-water nesting sites of this species, midges of the family Chironomidae were the main prey, whereas in other biotopes, the greatest prey fraction was represented by small parasitic hymenopterans (mainly, Pteromalidae, Eulophidae, and Eucharitidae), dipterans (Scatopsidae, Chloropidae, Ceratopogonidae, Milichiidae, and Cecidomyiidae), and bugs (Anthocoridae) (Miller and Kurczewski, 1975). In this case, prey selection was determined by its abundance in certain biotopes.

The second aspect deals with the reason, why it was *M. rubra* ants that were selected as the prey, whereas more numerous and less protected *L. niger* dwell in the same biotope; at the same time, *M. rubra* possess significantly harder integument and can protect themselves using their sting.

Our observations on both ant families revealed significant differences in their nest defense tactics. Disturbed *M. rubra* do not attack an alien, but try to remove exposed eggs, larvae, and pupae into the inner galleries of their nest, hiding themselves there too. By contrast, in the same situation, the large number of *L. niger* workers come to the outside, attacking an alien in groups. Although they do not possess such a dangerous weapon as the sting, they can bite alien integument with their mandibles, injecting acid into the wound. As a result, their grouped defense appears to be more effective in comparison with the solitary actions of *M. rubra* workers.

Finally, we agree that the available data on the biology of *C. vagabundus* is very insufficient, taking into account the fact that the latest observations were performed about half a century ago. Probably, special studies will reveal many peculiarities of the hunting behavior and biology of this wasp species.

ACKNOWLEDGMENTS

We are grateful to al the colleagues who helped us in preparation of the manuscript, in particular, to Prof. P.A. Rasnitsyn (PIN RAS, Moscow), Prof. G.M. Dlussky (Biological Faculty, Moscow State University), Dr. A.G. Radchenko (Institute of Zoology, National Academy of Sciences of the Ukraine, Kiev), and to Dr. E.B. Fedoseeva (Zoological Museum, Moscow State University) for fruitful discussions. We are especially grateful to Dr W.J. Pulawski (California Academy of Sciences, San Francisco, CA, USA), and Mrs. H.K. Court, California Academy of Sciences, San Francisco, USA) for very valuable information support and comments, and also to Dr. Robert L. Zuparko, California Academy of Sciences, San Francisco, USA), for his reading of our manuscript and making corrections in its English variant.

REFERENCES

1. Adlerz, G., "Lefnadsförhåallanden och instinkter inom familjerna Pompilidae och Sphegidae," Kungliga Svenska Vetenskapsakademiens Handlingar **37** (5), 1–181 [1904 (1903)].

2. Alcock, J. and Gamboa, G.J., "The Nesting Behavior of Some Sphecid Wasps of Arizona, including *Bembix*, *Microbembix*, and *Philanthus*," J. Ariz. Acad. Sci. **10**, 160–165 (1975).
3. Alexander, B.A., "Predator-prey Interactions between the Digger Wasp *Clypeadon laticinctus* and the Harvester Ant *Pogonomyrmex occidentalis*," J. Nat. Hist. **19**, 1139–1154 (1985).
4. Arnold, G., "New Species of Ethiopian Sphegidae," Occasion Papers of the Rhodesian Museum **1** (1), 1–31 (1932).
5. Bernard, F., "Observations sur les proies de quelques Hyménoptères," Bull. Soc. Entomol. France **39**, 247–250 (1934).
6. Bohart, R.M. and Menke, A.S., *Sphecid Wasps of the World. A Generic Revision* (Univ. California Press, Berkeley, 1976).
7. Borries, H., "Bidrag til danske Gravehvepses Biologi," Videnskabelige Meddelelser fra den Dansk Naturhistorisk Forening i Kjobenhavn **1897**, 1–163 (1897).
8. Bristowe, W.S., "Solitary Wasps and Their Prey, with Special Reference to the Mantid-Hunters," Ann. Mag. Nat. Hist. (Ser. 9) **16**, 278–285 (1925).
9. Evans, H.E., "A Review of Nesting Behavior of Digger Wasps of the Genus *Aphilanthops*, with Special Attention to the Mechanics of Prey Carriage," Behaviour **19**, 239–260 (1962).
10. Evans, H.E., "Ecological-Behavioral Studies on the Wasps of Jackson Hole, Wyoming," Bull. Mus. Comp. Zool. **140**, 451–511 (1970).
11. Evans, H.E., "Prey Specificity in *Clypeadon* (Hymenoptera: Sphecidae)," Pan-Pacific Entomol. **53**, 144 (1977).
12. Fahringer, J., "Hymenopterologische Ergebnisse einer wissenschaftlichen Studienreise nach der Türkei und Kleinasien (mit Ausschluss des Amanusgebirge)," Archiv für Naturgeschichte, Abteilung A **88** (9), 149–222 (1922).
13. Ferton, Ch., "Un Hymenoptere ravisseur de fourmis," Actes la Société Linnéenne de Bordeaux **44**, 341–346 [1892 (1890)].
14. Ferton, Ch., "Notes détachées sur l'instinct des Hyménoptères melliferes et ravisseurs avec la description de quelques espèces," Ann. Soc. Entomol. France **70**, 83–148 (1901).
15. Grandi, G., "Contributi alla conoscenza biologica e morfologica degli Imenotteri melliferi e predatori. VII," Bol. Laborat. Entomol. R. Inst. Super. Agrar. Bologna **1**, 259–326 [1928 (1929)].
16. Gronblom, T., "Bidrag till kännedom om levnadssättet hos våra rovsteklar (Hymenopt., Sphegidae) I," Notul. Entomol. **5**, 1–9 (1925).
17. Hamm, A.H. and Richards, O.W., "The Biology of the British Crabronidae," Trans. Entomol. Soc. London **74**, 297–331 (1926).
18. Hicks, Ch.H., "*Aphilanthops quadrinotatus* Ashmead, a Wasp which Carries Her Prey on Her Sting," Can. Entomol. **59**, 51–53, 55 (1927).
19. Hicks, Ch.H., "Further Notes on *Aphilanghops quadrinotatus* Ashmead (Hymenopt.)," Can. Entomol. **65**, 141–144 (1933).
20. Hicks, Ch.H., "Tracheloides hicksi Sandhouse Hunting Ants (Hymen.: Sphecidae)," Entomol. News **47**, 4–7 (1936).
21. Jansson, A., "Zur Lebensweise einiger Hymenopteren," Arkiv Zool. **12** (12), 1–5 (1919).
22. Janvier, H., "Recherches biologiques sur les predateurs du Chili," Ann. Sci. Natur. Zool. (Ser. 10) **11**, 67–207 (1928).
23. Krombein, K.V., *Trap-nesting Wasps and Bees: Life Histories, Nests, and Associates*. (Smithsonian Inst. Press, Washington, D.C., 1967).
24. Krombein, K.V., "Superfamily Sphecoidea," in *Hymenoptera of America North of Mexico, Synoptic Catalog* (U.S. Department of Agriculture, Washington, D.C., 1967a) Supplement 2, pp. 386–421.
25. Krombein, K.V., "Superfamily Sphecoidea," in *Catalog of Hymenoptera in America North of Mexico; Vol. 1, Symphyta and Apocrita (Parasitica); Vol. 2, Apocrita (Aculeata); Vol. 3, Indexes*. (Smithsonian Inst. Press, Washington, D.C., 1979), pp. 1573–1740.
26. Krombein, K.V., Norden, B.B., Rickson, M.M., and Rickson, F.R., "Biodiversity of Domatia Occupants (Ants, Wasps, Bees, and Others) of the Sri Lankan Myrmecophyte *Humboldtia laurifolia* Vahl (Fabacaeae)," Smithsonian Contrib. Zool. **603**, 1–34 (1999).
27. Leclercq, J., "Hymenopteres Sphecides Crabroniens d'Australie, du genre *Rhopalum* Stephens, 1829," Notes Fauniques de Gembloux **32**, 1–101 (1997).
28. Maneval, H., "Notes sur les Hyménoptères (5^{e} série)," Rev. Franç. Entomol. **4**, 162–181 (1937).
29. Marchal, P., "Observations biologiques sur les Crabronides," Ann. Soc. Entomol. France **62**, 331–338 (1893).
30. Masuda, H., "Biological Notes on *Crabro* (*Acanthocrabro*) *vagabundus* (Panzer, 1798) (Hymenoptera, Crabronidae)," Mushi **13**, 33–39 (1940).
31. Miller, R.C. and Kurczewski, F.E., "Comparative Behavior of Wasps in the Genus *Lindenius* (Hymenoptera: Sphecidae, Crabroninae)," J. NY Entomol. Soc. **83**, 82–120 (1975).
32. Minkiewicz, R., "Gniazda i zwierzyna lowna Grzebaczowatych—Nids et proies des Sphégiens de Pologne. Deuxième série de fragments éthologiques," Polsk. Pismo Entomol. **11**, 98–112 [1933 (1932)].
33. Myartseva, S.N., "Notes on the Biology of Poorly Known Sphecid Wasps of Turkmenia (Hymenoptera, Sphecidae)," in *Ecology and Economical Significance of Insects in Turkmenia* (Ilym, Ashkhabad, 1976), pp. 72–82 [in Russian].
34. Nemkov, P.G., "A Review of Holarctic Digging Wasps of the Genus *Tracheliodes* A. Morawitz (Hymenoptera, Sphecidae, Crabronini), with the Description of Two New Species for the Russian Far East," Trudy Vses. En-

tomol. O-va **70**, 116–124 (1988).
35. O'Neill, K.M., "The Mating Strategy of the Ant *Formica subpolita* Mayr (Hymenoptera: Formicidae): Swarming, Mating, and Predation Risk," Psyche **101**, 93–108 (1994).
36. Parker, F.D. and Bohart, R.M., "Host-Parasite Associations in Some Twig-Nesting Hymenoptera from Western North America," The Pan-Pacific Entomol. **42** (2), 91–98 (1966).
37. Peckham, G.W. and Peckham, E.G., *Wasps, Social and Solitary* (Univ. Press, Cambridge, 1905).
38. Pulawski, W.J., "Catalog of Specidae sensu lato (= Apoidea excluding Apidae). Catalog of Genera and Species. Last updated: 27 June 2009 // http://research.calacademy.org/research/entomology/Entomology_Resources/Hymenoptera/sphecidae/Genera_and_species_PDF/PDF_links.html (2009).
39. Pulawski, W.J. and Prentice, M.A., "A Revision of the Wasp Tribe Palarini Schrottky, 1909 (Hymenoptera: Apoidea: Crabronidae)," Proc. California Acad. Sci. (Ser. 4) **59**, 307–479 (2008).
40. Sickmann, F., "Die Hymenopterenfauna von Iburg und seiner nächsten Umgebung, mit biologischen und kritischen Bemerkungen. I. Abteilung: Die Grabwespen," Jahresbericht des Naturwissenschaftlichen Vereins zu Osnabrück **9**, 39–112 (1893).
41. Tsuneki, K., "Crabronidae-Fauna of Korea (Hymenoptera)," J. Facul. Sci., Hokkaido Imp. Univ. (Ser. VI, Zool.) **9**, 281–295 (1947).
42. Tsuneki, K., "Gleanings on the Bionomics of the East-Asiatic Non-Social Wasps (Hymenoptera): II. Some Species of Tachytini, Larrini and Palarini (Sphecidae)," Etizenia **39**, 1–22 (1969).
43. Wheeler, W.M., "A Solitary Wasp (*Aphilanthops frigidus* F. Smith) that Provisions Its Nest with Queen Ants," J. Animal Behavior **3**, 374–387 (1913).
44. Zettel, H., Ljubomirov, T, Steiner, F.M., Schlick-Steiner, B.C., et al., "The European Ant Hunters *Tracheliodes curvitarsis* and *T. varus* (Hymenoptera: Crabronidae): Taxonomy, Species Discrimination, Distribution, and Biology," Myrmecologische Nachrichten **6**, 39–47 (2004).