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# Mini review of the Family Crabronidae (Insecta: Hymenoptera) sand wasps: Natural history, behavior and taxonomy

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## Abstract

The family of the Crabronidae wasps are important ecological interactions such as predation or parasitism, in addition to pollination. They stock their nests with food of animal origin, whereas adult wasps normally feed on nectar. Two factors are important for the maintenance of populations of predatory wasps in the environment where they live: suitable places for building nests and a sufficient amount of prey for their provisioning. Therefore, changes in nesting site availability and prey abundance should produce corresponding variations in nest structure and population density, as well as species diversity. The objective of the current manuscript was to determine the natural history, behavior and taxonomy of the Familia Crabronidae (Insecta: Hymenoptera) sand wasps. Concerned about drawing a public profile of quality research in the area, we sought to answer these questions based on a literature review in the main journals in the area (national and international) classified by the Coordination for the Improvement of Higher Education Personnel (CAPES)). In order to complement this analysis with other types of documents such as books, theses, dissertations, scientific journals, documents and digital platforms.

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**Keywords:** Ecological Interactions, Predation, Parasitism, Nests, Behavior.

## 1. Introduction

Vespoidea is a superfamily of the order Hymenoptera, although older taxonomic schemes vary in this categorization,



particularly in recognizing that the superfamily Scoliidea is now obsolete. Members of this group are wasps and ants. Predatory wasps included in the superfamily Apoidea are distinguished because of their diversity of habits and behavioral complexity, ranging from solitary to eusocial species. Apoidea is advanced culeates considered the most economically important insect group in biological control (Figures 1-3) [1][2].



**Figure 1.** *Philanthus triangulum* (Fabricius, 1775). *Trypoxylon lactitarse* Saussure, 1867.

Sources: Photo 16305457, (c) Henk Wallays, all rights reserved, <https://www.biodiversity4all.org/photos/16305457> and <https://bugguide.net/node/view/2092643>.



**Figure 2.** *Crabro latipes* Smith, 1856.

Sources: Photo 4009185, (c) Denis Doucet, some rights reserved (CC BY-NC) and <https://www.biodiversity4all.org/photos/4009185>





**Figure 3.** *Sphecius speciosus* (Drury 1773).

Sources: Photo 22644093, (c) Danny Goodding, All Rights Reserved, uploaded by and <https://www.biodiversity4all.org/photos/22644093>.

## 1.2. Description

Small size, black integument with off-white markings on mesosoma and legs; pubescence short, silvery; clypeal lobe with large deep punctuations, mainly in females; metapostnotum with subparallel longitudinal lines running from anterior to posterior margin, some of them branching apically; last antennal segment of male slightly longer than the two preceding conjoined. A combination of characters separates it from the Cuban species and from known Nearctic species. Among these characters is the shape of the apical margin of the clypeus, the sculpture of the integument of the metapostnotum, and the length of the last antennal segment of the male (Figures 4-7) <sup>[1][2][3]</sup>.

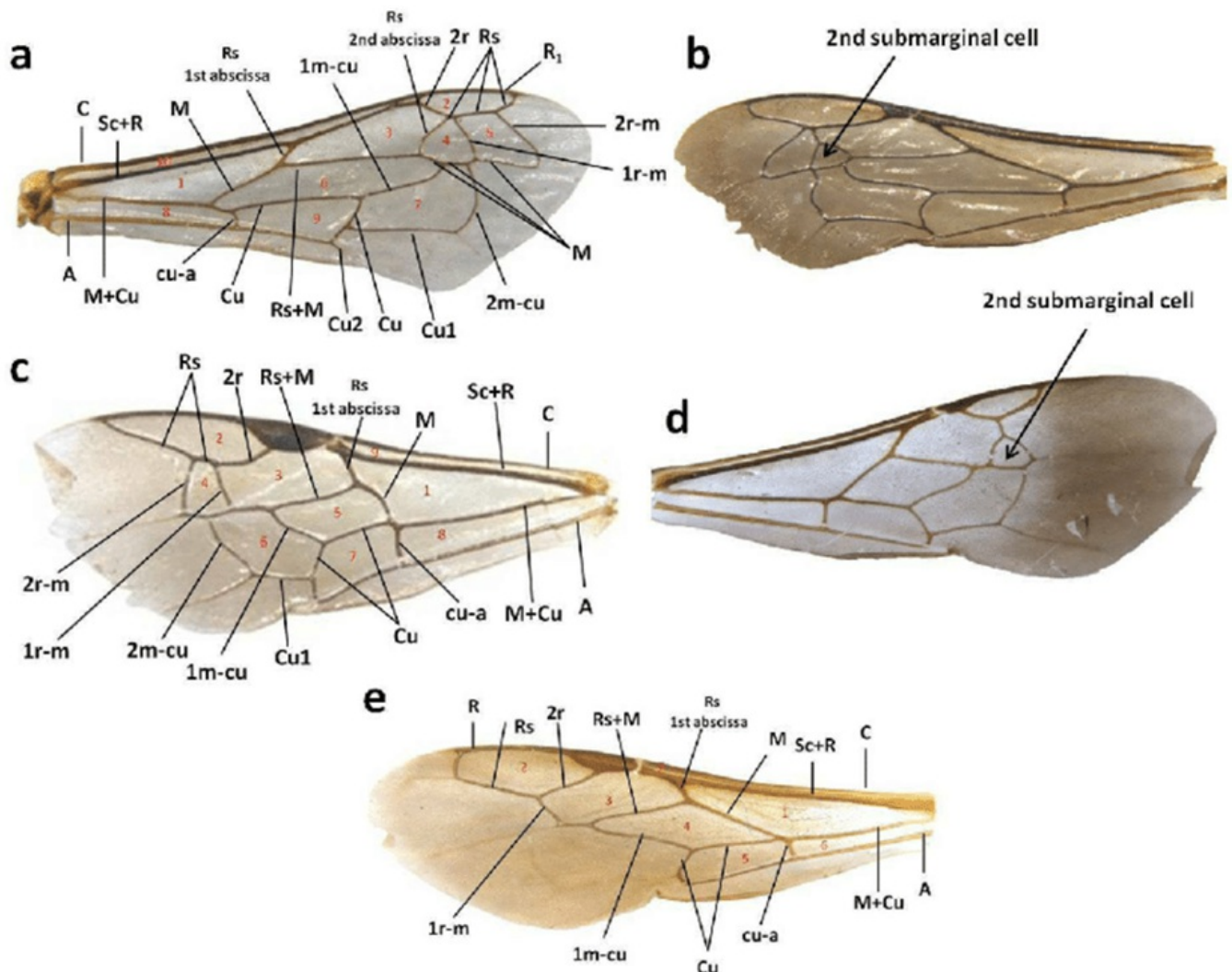


**Figure 4.** Crabronidae sting is a transformed ovipositor that mostly lost its primary function of egg-laying and is used for prey capture, attack and as a defense weapon in some digger wasps, Crabronidae the sting is also used for prey transportation Adult Crabronidae



feed on nectar and pollen, whereas. There are three types of prey carriage in different wasps: with mandibles (mandibular transport), with legs (pedal transport), and impaled on the sting (abdominal transport).

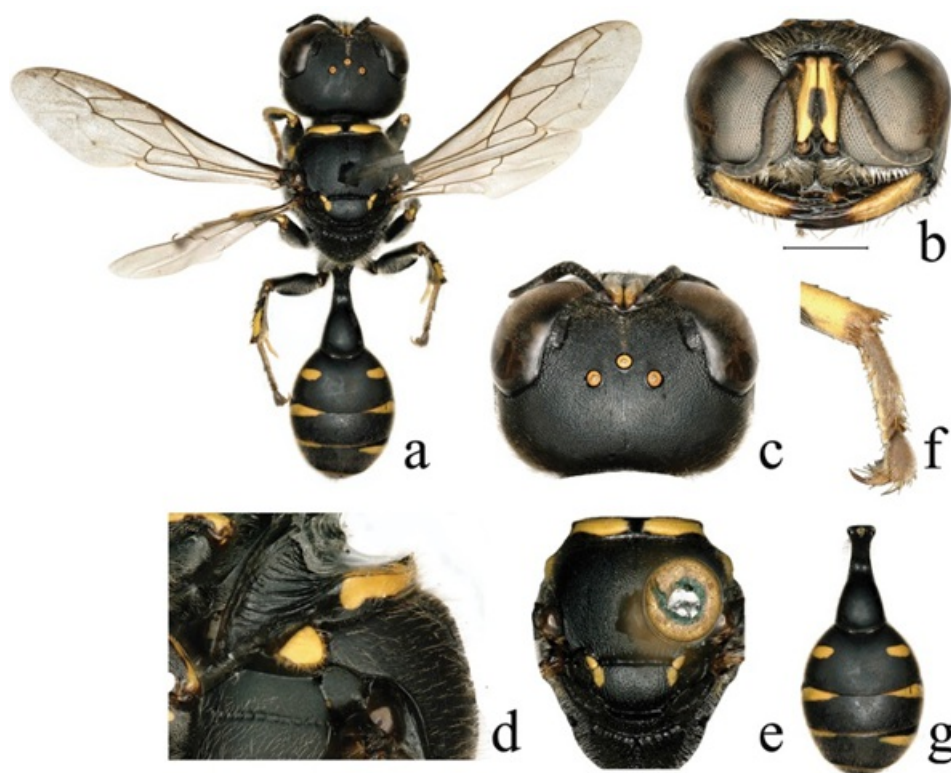
Source: <https://www.sciencedirect.com/science/article/abs/pii/S1467803919300325>.



**Figure 5.** Different types of forewings in the Crabronidae family in terms of cell number and veins. a) Right forewing of *Bembecinus tridens* (Fabricius, 1781) with three submarginal cells representing cell and vein names. Cell names (1-10): (1). Medial, (2). Marginal, 3. Submarginal I, (4). Submarginal II, (5). Submarginal III, (6). Discoidal I, (7). Discoidal II, 8. Submedial, (9). Subdiscoidal, (10). Costal. Vein names: (A). Anal, (C). Costal, Cu. Cubital, M. Medial, R. Radial, Rs. Radial sector, Sc. Subcostal; b) Left forewing of *Brachystegus scalaris* (Illiger, 1807), with a petiolated second submarginal cell; c) Left forewing of *Diodontus minutus* (Fabricius, 1793), with two submarginal cells representing names of cells and veins. Cell names (1-9): (1). Medial, (2). Marginal, (3). Submarginal I, (4). Submarginal II, (5). Discoidal I, (6). Discoidal II, (7). Subdiscoidal, (8). Submedial, (9). Costal. d) Right forewing of *Miscophus pretiosus* Kohl, 1884, with a petiolated second submarginal cell; e) Left forewing of *Ectemnius crassicornis* (Spinola, 1808), with one submarginal cell representing names of cells and veins. Cell names (1-7): (1). Medial, (2). Marginal, (3). Submarginal, (4). Discoidal, (5). Subdiscoidal, (6). Submedial, (7). Costal.

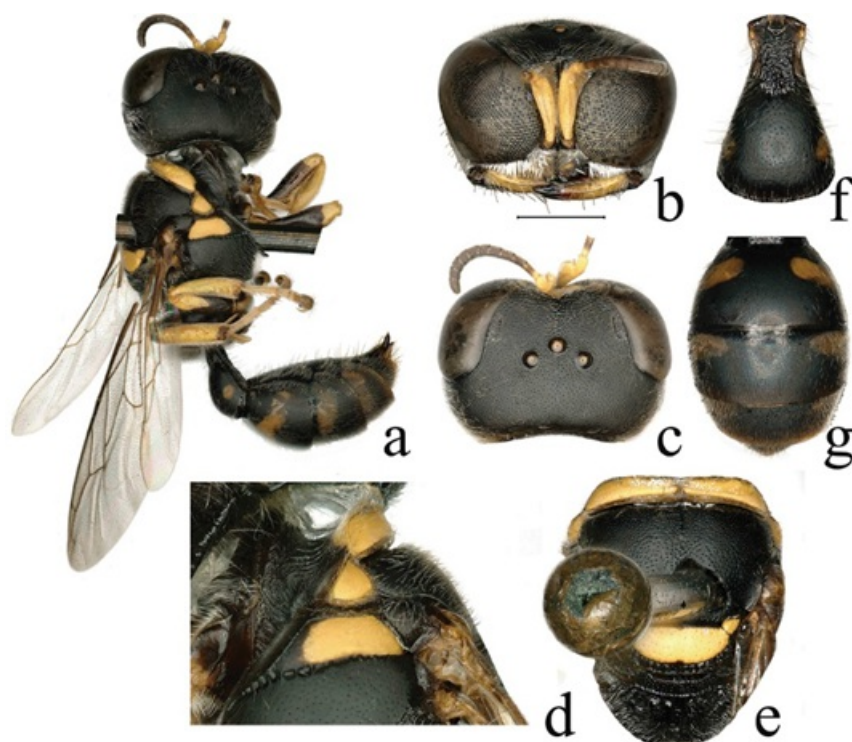
Source: [https://www.researchgate.net/figure/Different-types-of-forewings-in-the-Crabronidae-family-in-terms-of-cell-number-and-veins\\_fig1\\_362279087](https://www.researchgate.net/figure/Different-types-of-forewings-in-the-Crabronidae-family-in-terms-of-cell-number-and-veins_fig1_362279087).





**Figure 6.** *Dasyproctus amplicarinalis* Yue & Ma, sp. nov., ♀. (a) habitus, dorsal view (b) head, frontal view (c) head, dorsal view (d) collar, lateral view (e) mesosoma, dorsal view (f) fore tarsomere I, dorsal view (g) metasoma, dorsal view.

Source: <https://zookeys.pensoft.net/article/59920/>.



**Figure 7.** *Dasyproctus hainanensis* Yue & Li, sp. nov., ♀ (a) habitus, lateral view (b) head, frontal view (c) head, dorsal view (d) collar, lateral view and mesosome, dorsal view (f) petiole, gastral tergum I, dorsal view (g) gastral terga II–V, dorsal view.

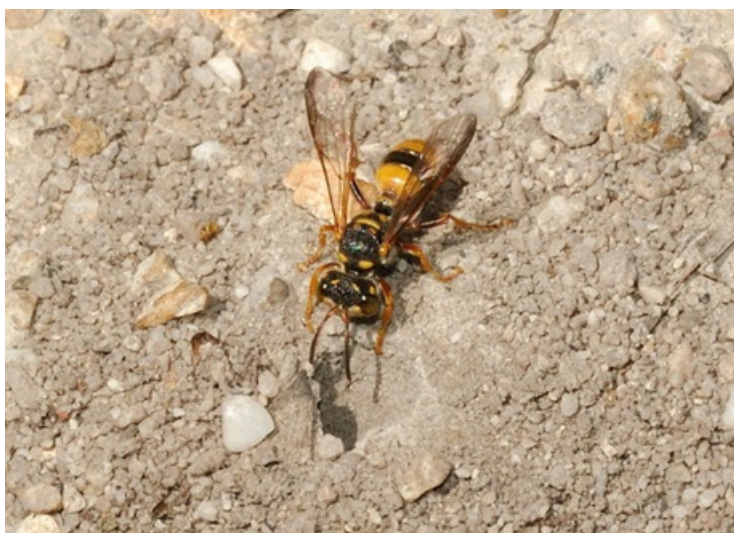


Source: <https://zookeys.pensoft.net/article/59920/>.

### 1.3. Biology and Ecology

Wasps are important ecological interactions such as predation or parasitism, in addition to pollination. They stock their nests with food of animal origin, whereas adult wasps normally feed on nectar. Two factors are important for the maintenance of populations of predatory wasps in the environment where they live: suitable places for building nests and a sufficient amount of prey for their provisioning. Therefore, changes in nesting site availability and prey abundance should produce corresponding variations in nest structure and population density, as well as species diversity (Figures 8-13) [4][5][6].

3.2.1. *Cerceris* Digger wasp 1 - *Cerceris* sp. Family Crabronidae, subfamily Philanthinae. This page contains pictures and information about *Cerceris* digger wasps that we found in the Brisbane area, Queensland, Australia.



**Figure 8.** Digger wasp in the subfamily Philanthinae is medium in size. There is the petiole segment between the thorax and abdomen. The abdomen is constricted between segments. The head is large and wide. The hind legs or femur, are expanded and flattened.

Source:

[https://www.brisbaneinsects.com/brisbane\\_apoidwasps/CercerisDiggerWasp.htm](https://www.brisbaneinsects.com/brisbane_apoidwasps/CercerisDiggerWasp.htm).





**Figure 9.** Digger wasps nest in bare, firm ground. They nest communally and there is some division of labor. All Australian wasps in this subfamily are in the *Cerceris* genus.

Source: [https://www.brisbaneinsects.com/brisbane\\_apoidwasps/CercerisDiggerWasp.htm](https://www.brisbaneinsects.com/brisbane_apoidwasps/CercerisDiggerWasp.htm).

## First Encounter



**Figure 10.** The wasps do not close the entry. A wasp was always guarding the entry. In our 10 minutes of watching, we saw one wasp fly out from the nest. There were no wasps flying, except the one with prey trying to get in, as mentioned below.

Source: [https://www.brisbaneinsects.com/brisbane\\_apoidwasps/CercerisDiggerWasp.htm](https://www.brisbaneinsects.com/brisbane_apoidwasps/CercerisDiggerWasp.htm).



**Figure 10.** We found two nests near the sand patch where we were looking for the *Bembix*. They were about ten meters apart. The entry was a small hole 6mm in diameter. The entry was a dome of loose soil with a diameter of 80mm and 40mm height.

Source: [https://www.brisbaneinsects.com/brisbane\\_apoidwasps/CercerisDiggerWasp.htm](https://www.brisbaneinsects.com/brisbane_apoidwasps/CercerisDiggerWasp.htm).





**Figure 11.** A wasp carrying prey was coming back to the nest. Because we were inspecting the nest, it just rested on a small plant and waited. When we came close to it, it dropped the prey and flew away. The wasp was about 10mm in body length, with lemon-yellow and black body patterns. The prey was a small beetle (family Cleridae), 5mm in body length. It was metallic brown in color. It was paralyzed, but its legs still moved. Source: [https://www.brisbaneinsects.com/brisbane\\_apoidwasps/CercerisDiggerWasp.htm](https://www.brisbaneinsects.com/brisbane_apoidwasps/CercerisDiggerWasp.htm).



**Figure 12.** The whole afternoon waited and we rarely saw them coming in and out. When they did, they did it very quickly. We couldn't get good enough pictures to identify them. The second photo above was out of focus, but it's the only full-body photo we took. We took this photo signaling the guardian wasp that left the nest (a bit like fishing), then quickly blocked the entrance with a dry leaf. Anyway, the wasp was back in the nest within 10 seconds. Source: [https://www.brisbaneinsects.com/brisbane\\_apoidwasps/CercerisDiggerWasp.htm](https://www.brisbaneinsects.com/brisbane_apoidwasps/CercerisDiggerWasp.htm).





**Figure 13.** Beetle wasp, male, *Cerceris sextoides* Banks, 1947, subfamily Philanthinae, family Crabronidae (the crabronid wasps, including the mud daubers and sand wasps). The photographer noted that this male beetle wasp has a tiny yellow dot behind its eye, a feature he did not see in the female.

Source: [www.flickr.com/photos/myobservatory/45095536722/](https://www.flickr.com/photos/myobservatory/45095536722/).

Many species make their nests on the ground, others in hollow stems or tunnels in wood. The larvae are fed on captured prey and brought to the nest. The type of prey varies with the species; includes aphids, beetles, lepidopterans, hemipterans, cicadas, crickets, flies, etc. Some species are kleptoparasites, feeding their larvae prey that they steal from other wasp nests [7][8][9].

Many of the excavator wasps of the Crabronidae family are found in aggregates, which can range from a few individuals to hundreds of nests in the same area this behavior is considered a possible precursor of eusociality in Hymenoptera. It is common to observe in this group adult female wasps excavating new nests to imprison their prey and lay eggs, but in some cases, some species reuse previously excavated nests, sometimes for which the individuals themselves. These insects keep captured prey inside their burrows and provision eggs in the body of still-living hosts (Figures 14-17B) [10][11][12].





**Figure 14.** Adult of *Oxybelus variegatus* Wesmael, 1852. (A) Male; (B) female in front of the nest entrance; (C–E) female with prey.

Source: <https://www.mdpi.com/2075-4450/12/2/100>.





**Figure 15** Developmental stages of *Oxybelus variegatus* Wesmael, 1852. (A) Egg; (B–H) larva and pupa.

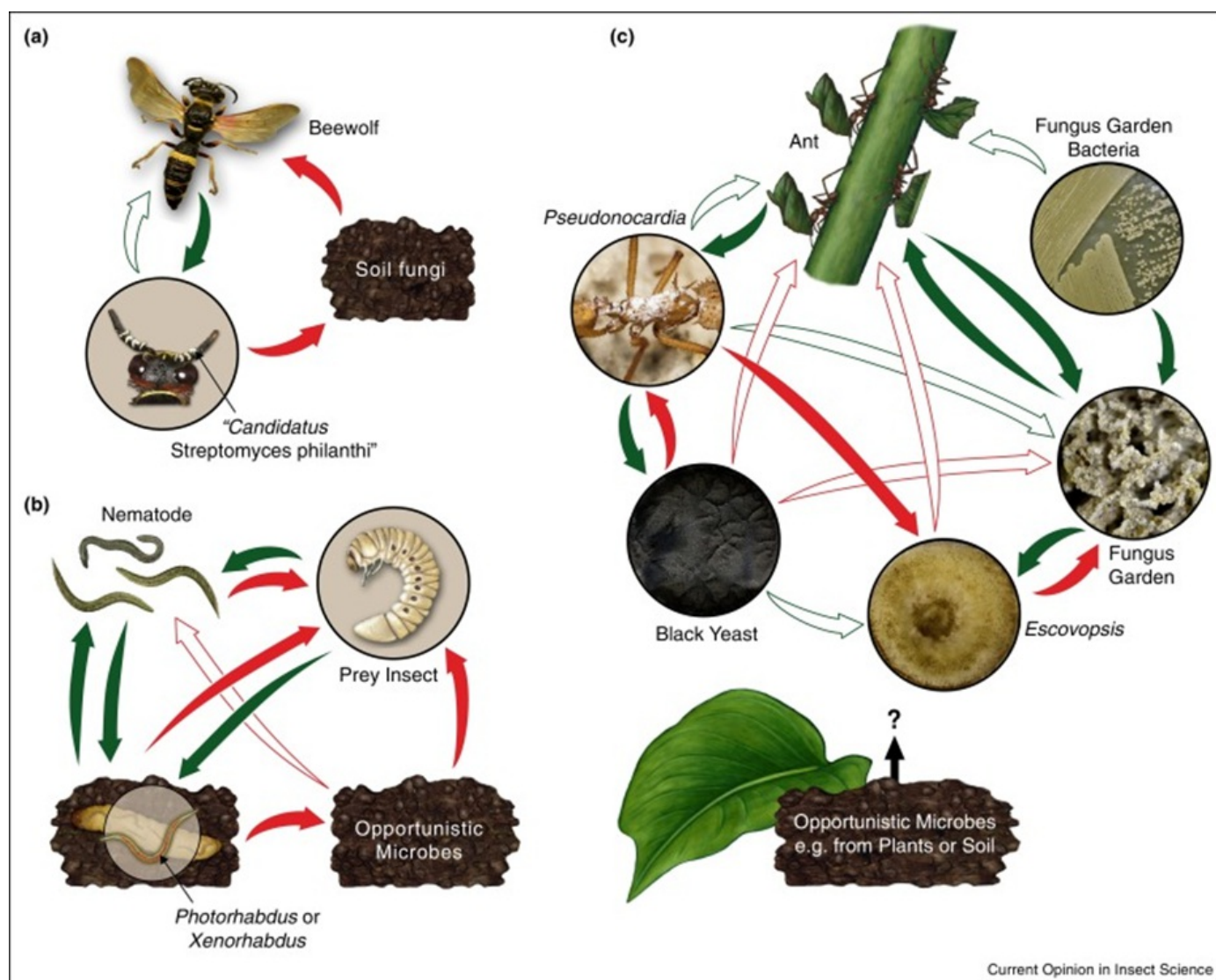
Source: <https://www.mdpi.com/2075-4450/12/2/100>.



**Figure 16.** *Sphecius speciosus* carrying its prey (Cicadellidae).

Source: Photo 2355203, (c) Rob Curtis, some rights reserved (CC BY-NC-SA), uploaded by Rob Curtis and <https://www.biodiversity4all.org/photos/2355203>.





Current Opinion in Insect Science

**Figure 17A.** Schematic of interactions between symbionts of (a) beewolves; (b) entomopathogenic nematodes; and (c) fungus-growing ants. Positive interactions are indicated in green, negative ones in red, and ones with unclear fitness effects in black. Solid arrows indicate direct interactions and outlined arrows indirect ones.

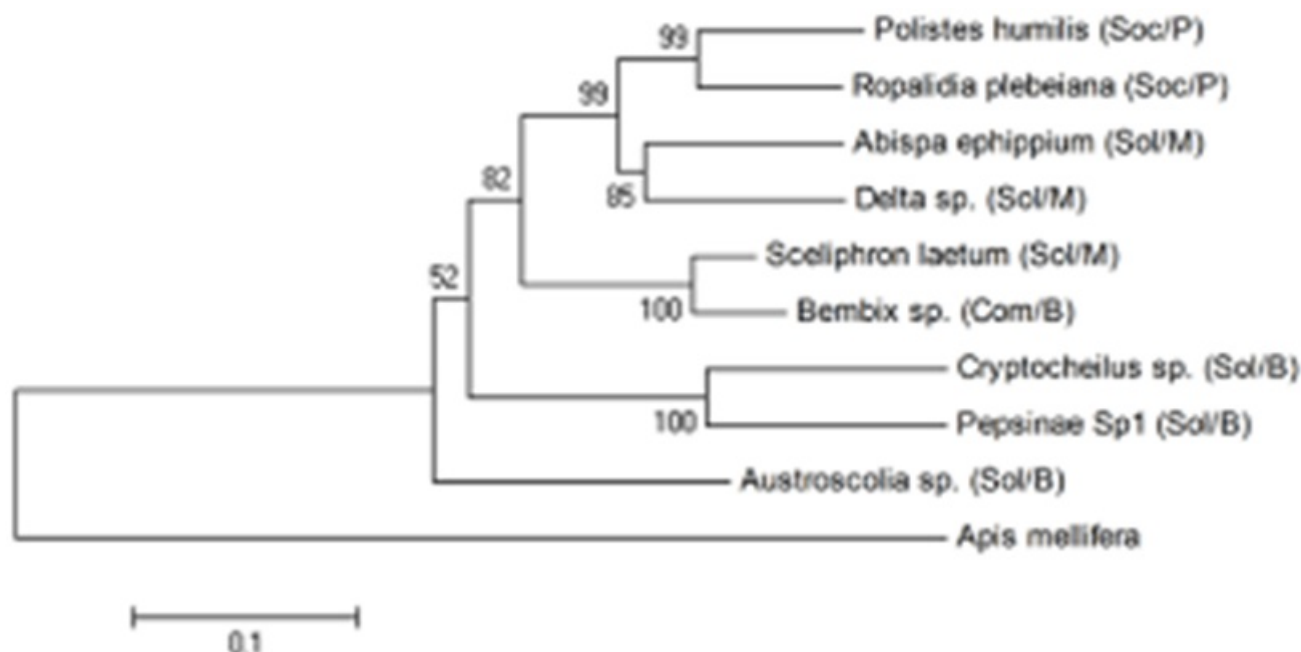
Source: <https://www.sciencedirect.com/topics/agricultural-and-biological-sciences/crabronidae>.

## 1.4. Taxonomy

The family Crabronidae represents 89% of the species present in the Americas from the opioid wasps, followed by Sphecidae (8%) and Ampulicidae with 2%. Crabronidae is a large family of hymenopteran insects in the superfamily Apoidea that includes most of the species that were formerly included in the superfamily Sphecoidea, which no longer exists [13][14][15].

It contains 20 genera and more than 9 thousand species. It is possible that some of your subfamilies will acquire the family level in the future. The Crabronidae family (Hymenoptera), formerly considered a subfamily of Sphecidae, comprises 8,774 species distributed in 243 genera around the world (Figure 17B) [16][17].





**Figure 17B.** Distance-based neighbor-joining tree. Neighbor-joining phylogenetic reconstruction of nine wasp species using a 941 bp sequence generated by concatenating the two gene fragments: 28S nrDNA (484 bp) and COI mtDNA (457 bp). Social complexity and nest type are indicated after the species names; social (Sol), communal aggregator (Com), solitary (Soc), paper nest (P), mud nest (M), and burrower (B). Bootstrap values were obtained using 10000 replicate.

## 1.5. Objective

The objective of the current manuscript was to determine the natural history, behavior, and taxonomy of the Familia Crabronidae (Insecta: Hymenoptera) sand wasps.

## 2. Methods

Concerned about drawing a public profile of quality research in the area, we sought to answer these questions based on a literature review in the main journals in the area (national and international) classified by the Coordination for the Improvement of Higher Education Personnel (CAPES)). In order to complement this analysis with other types of documents such as books, theses, dissertations, scientific journals, documents and digital platforms.

## 3. Selected Studies following the documents listed in the methods.

### 3.1. Study 1

**Subfamilies:** Astatinae, Bembicinae, Crabroninae, Dinetus, Eremiasphecinae, Mellininae, Pemphredoninae and Philanthinae [18][19][20].

**Distribution** Worldwide.



**Biology:** Solitary predatory wasps, provisioning nest with paralyzed prey for consumption by the larvae.



1



2





3



4



5





6



7



8

**Figure 18.** Subfamilies: Astatinae (1), Bembicinae (2), Crabroninae (3), Dinetus (4), Eremiasphecinae (5), Mellininae (6,



Pemphredoninae (7) and Philanthinae (8).

Source: Photographs © Simon van Noort (Iziko Museums of South Africa).

1-Subfamily Astatinae

**Genus:** *Astata*, *Diploplectron*, and *Dryudella*,

**Distribution:** Worldwide [18][19][20].

**Biology:** Prey on adults and nymphs of Pentatomidae.

**Some Species:** *Astata albopilosella* Arnold, 1946 (South Africa), *Astata nana* Arnold, 1946 (South Africa), *Astata gracilicornis* Arnold, 1924 (Zimbabwe), *Astata melanaria*, Cameron, 1905 (South Africa), *Astata minax*

**Distribution:** Kenya, Madagascar, Malawi, Namibia, South Africa, Zambia and Zimbabwe (Figures 19-20) [18][19][20].



**Figure 19.** Genus *Diploplectron*

Source: <https://www.dreamstime.com/photos-images/genus-astata.html>.





**Figure 20.** *Astata boops* (Schrank, 1781).

Source: [https://pt.wikipedia.org/wiki/Astata\\_boops](https://pt.wikipedia.org/wiki/Astata_boops).

### 3. Subfamily: Bembicinae

**Genus:** *Alysson* and *Didineis*.

**Distribution:** Ethiopia, Lesotho, Madagascar, South Africa. Also Palaearctic region.

**Biology:** Solitary predatory wasps, provisioning nest with paralyzed prey for consumption by the larvae.

**Specie:** *Didineis* species (South Africa).

**Distribution:** Ethiopia: South Africa. Also Palaearctic region.<sup>[18][19][20]</sup>

**Some Species:** *Alysson guichardi* Arnold, 1951 (Ethiopia) and *Alysson guillarmodi* Arnold, 1944 (Lesotho).

**Distribution:** Ethiopia, Lesotho, Madagascar, South Africa. Also Palaearctic region.

**Some Genus:** *Bembecinus*, *Bembix*, and *Handlirscha*<sup>[18][19][20]</sup>.

**Distribution:** Worldwide.

**Biology:** Solitary predatory wasps, provisioning nest with paralyzed prey for consumption by the larvae. For further details on this situation, nest structure, method of nest construction, prey provisioning and oviposition, life history, sleeping and associated organisms <sup>[18][19][20]</sup>.

**Some Species:** *Bembecinus caffer* (de Saussure, 1854) (South Africa, Zambia) and *Bembecinus chilwae* Bohart, 1997 (Malawi) (Figure 21).





**Figure 21.** *Bembecinus nanus* (Handlirsch, 1892)

Sources: Photo 30466295, (c) Angella Moorehouse, All rights reserved and <https://www.biodiversity4all.org/photos/30466295>.

**Distribution:** Worldwide.

**Biology:** Females excavate burrows in hard or sandy soil, often in large colonies. Females feed their developing larvae progressively with leafhoppers and other Homoptera (Hemiptera). Some species use sand-filled or empty snail shells as nesting sites.

**Some Species:** *Bembecinus somalicus* Arnold, 1940 (Ethiopia, Kenya, Tanzania) and *Bembecinus spinicornis* (de Saussure, 1887) (Madagascar) <sup>[18][19][20]</sup>.

3-Subfamily: Crabroninae

**Some Genus:** *Entomognathus*, *Rhopalum* and *Crossocerus*.

**Distribution:** Worldwide.

**Biology:** Solitary predatory wasps, provisioning nests constructed in-ground or plant stems with paralyzed prey for consumption by the larvae <sup>[18][19][20]</sup>.

**Some Species:** *Crossocerus gaboni* Leclercq, 2008 (Gabon), *Crossocerus glabricornis* (Arnold, 1926) (South Africa) and *Crossocerus hirtitibia* (Arnold, 1944) (Madagascar) (Figure 22) <sup>[18][19][20]</sup>.





**Figure 22.** *Crossocerus glabricornis* (Arnold, 1926) (South Africa)

Source:

<http://www.waspweb.org/Apoidea/Crabronidae/Crabroninae/Crabronini/Crossocerus/index.htm>.

**Distribution:** Afrotropical, Oriental and Australasian regions.

**Biology:** Females make their nests in plant stems and provision with flies (Chloropidae, Lonchaeidae, Muscidae, Otitidae, Syrphidae and Tephritidae are commonly used) <sup>[18][19][20]</sup>.

#### 4. Subfamily Dinetinae

**Genus:** *Dianthus*

**Distribution:** Oriental and Palaearctic regions.

**Biology:** Solitary predatory wasps, provisioning nest with paralyzed prey (Lygaeidae, Nabidae) for consumption by the larvae.

**Some Species:** *Dinetus pulawskii* Beaumont, 1960 (Egypt), *Dinetus simplicities* Saunders, 1910 (Algeria) *Dinetus turanicus* Kazenas, 1993 (Kazakhstan, Turkmenistan and Uzbekistan) (Figure 23) <sup>[18][19][20]</sup>.





**Figure 23.** *Dinetus politus* Turner, 1917.

Source: Photographs © Norman Larsen (Iziko Museums of South Africa).

**Distribution and Biology:** Same as above: [\[18\]](#)[\[19\]](#)[\[20\]](#).

#### 5. Subfamily Eremiasphecinae

**Genus:** *Eremiasphecium* and *Laphyragogus*

**Distribution:** Afrotropical, Oriental and Palaearctic regions.

**Biology:** Solitary predatory wasps, provisioning nest with paralyzed prey (Thysanoptera, or adult Lepidoptera) for consumption by the larvae.

**Some Species:** *Eremiasphecium pulawskii* Schmid-Egger, 2011 (United Arab Emirates), *Eremiasphecium sahelense* Simon Thomas, 1994 (Mauritania, Niger, Senegal, United Arab Emirates, Yemen) and *Eremiasphecium schmiedeknechtii* Kohl, 1897 (Canary Islands, Egypt, Kazakhstan, Oman, Russia, Turkmenistan, United Arab Emirates, Uzbekistan) (Figure 24) [\[18\]](#)[\[19\]](#)[\[20\]](#).





**Figure 24.** *Eremiasphecium sahelense* Simon Thomas, 1994.

Source: Photographs © Norman Larsen (Iziko Museums of South Africa).

**Genus:** *Laphyragogus*

**Distribution:** Oriental and Palaearctic regions.

**Biology:** Solitary predatory wasps, provisioning nest with paralyzed prey (adult Lepidoptera) for consumption by the larvae.

**Some Species:** *Laphyragogus pictus* Kohl, 1889 (Egypt, Israel, Kuwait, United Arab Emirates, Western Sahara), *Laphyragogus strakai* Schmid-Egger, 2011 (United Arab Emirates) and *Laphyragogus visnagae* de Beaumont, 1959 (Algeria) (Figure 25) <sup>[18][19][20]</sup>.



**Figure 25.** *Laphyragogus kohlii* (Bingham, 1897).

Source: <https://ru.wikipedia.org/wiki/Laphyragogus>.



## 6. Subfamily: Mellininae

**Genus:** *Mellinus* and *Xenosphex*:

**Distribution:** Nearctic, Neotropical, Oriental and Palaearctic regions.

**Biology:** Solitary predatory wasps, provisioning nest with paralyzed prey (Diptera) for consumption by the larvae [18][19][20].

**Species:** *Mellinus hansonii* Menke, 1996, *Mellinus iani* Menke, 1996, *Mellinus imperialis* Bohart, 1968 and *Mellinus obscurus* Handlirsch, 1888 (Figure 26).



**Figure 26.** *Mellinus arvensis* (Linnaeus, 1758).

Source: <https://en.wikipedia.org/wiki/Mellinus>.

**Distribution:** Nearctic: USA.

Species: *Xenosphex boharti* F. Parker, 1966 (USA), *Xenosphex timberlakei* Williams, 1956 (USA) and *Xenosphex xerophilus* Williams, 1954 (USA) (Figure 27) [18][19][20][21].





**Figure 27.** *XenospheX timberlakei* Williams, 1955.

Source: [https://ru.wikipedia.org/wiki/XenospheX\\_timberlakei](https://ru.wikipedia.org/wiki/XenospheX_timberlakei).

7. Subfamily: Pemphredoninae

**Genus:** *Ammoplanus*, *Carinostigmus*, *Diodontus* and *Mimesa*

**Distribution:** Worldwide.

**Biology:** Females provision their nests with Homoptera, Thysanoptera, or Collembola (Bohart & Menke, 1976).

**Some Species:** *Polemistus apterinus* (Leclercq, 1959), *Polemistus macilentus* de Saussure, 1892 and *Polemistus schoutedeni* (Leclercq, 1959) (Figure 28) <sup>[20][21][22]</sup>.





**Figure 28.** *Polemistus macilentus* de Saussure, 1892.

Source: <https://eol.org/pages/2760686>.

**Distribution:** Democratic Republic of Congo, Madagascar, South Africa.

**Biology:** Nest in existing holes in dead wood and provision with aphids. The nests are sealed with a transparent resin-like substance [22][23][24][25].

8. Subfamily: Philanthinae

**Genus:** *Cerceris*, *Philanthus* and *Pseudoscolia*.

**Distribution:** Afrotropical, Nearctic, Neotropical, Oriental and Palearctic regions. Absent from Australia.

**Biology:** Provision their nests with Hymenoptera, especially bees.

**Some Species:** *Cerceris xosa* Brauns, 1926 (South Africa), *Cerceris yalensis* R.Turner, 1913 (Kenya), *Cerceris yngvei* Cameron, 1908 (Kenya, Zimbabwe) and *Cerceris zavattarii* Guiglia, 1939 (Ethiopia) (Figure 29) [23][24][25].





**Figure 29.** *Cercheris rybyensis* (Linnaeus, 1771).

Source: [https://pt.wikipedia.org/wiki/Cercheris\\_rybyensis](https://pt.wikipedia.org/wiki/Cercheris_rybyensis).

**Distribution:** Worldwide.

**Biology:** Nest in bare, sand clay or gravel soil aggregations. Nests are usually provisioned with beetles (Bruchidae, Buprestidae, Cerambycidae, Chrysomelidae, Curculionidae, Scareabaieidae, Tenebrionidae) or sometimes with bees or wasps (Hymenoptera).

**Some Species:** *Philanthus triangulum* (Fabricius, 1775) (Widespread in Afrotropical & Palaearctic regions), *Philanthus turneri* Arnod, 1925 (South Africa) and *Philanthus variolosus* Arnold, 1932 (Ethiopia) (Figure 30) [22][23][24][25].



**Figure 30.** *Philanthus triangulum* (Fabricius, 1775).

Source: [https://pt.wikipedia.org/wiki/Philanthus\\_triangulum](https://pt.wikipedia.org/wiki/Philanthus_triangulum).



**Distribution:** Afrotropical, Nearctic, Neotropical (Cuba & Central America), Oriental and Palaearctic regions. Absent from South America and Australia.

**Biology:** Nest in small to large aggregations in bare, sandy soil. Nests are provisioned with bees or wasps<sup>[23][24][25]</sup>.

### 3.2. Study 2

The group's species of bees, wasps and ants present different levels of social organization. About 90% of wasp species exhibit solitary behavior, characterized by the independence of females in building and provisioning brood cells. Some species build their nests in preexisting cavities, such as representatives of the Vespidae, Pompilidae, Sphecidae and Crabronidae families (Figures 31-35)<sup>[26][27]</sup>.



**Figure 31.** *Trypoxylon* female flying to nest with a load of wet mud.

Source: <https://spidersinohio.net/trypoxylon-vs-parasteatoda/>.



**Figure 32.** *Trypoxylon* female landing at nest with mud.



Source: <https://spidersinohio.net/trypoxylon-vs-parasteatoda/>.



**Figure 33.** *Trypoxylon* female at nest adding mud to lip. Here is another series of photos of a female arriving with a mud ball and spreading the mud along the edge of the tube forming a new extension.

Source: <https://spidersinohio.net/trypoxylon-vs-parasteatoda/>.



**Figure 34.** *Trypoxylon* female arrives with a mud ball, male attending below.

Source: <https://spidersinohio.net/trypoxylon-vs-parasteatoda/>.





**Figure 35.** *Trypoxylon politum* Drury, 1773 female adding mud to her tube, male attending below.

Source: <https://spidersinohio.net/trypoxylon-vs-parasteatoda/>.

“She will fly out and capture a spider when a tube is ready. After she captures a spider, she paralyzes it with a sting, then stuffs it into the tube. The spiders aren’t dead, just immobilized. They are alive and will remain so until they are eaten by the baby wasp (larva). As she provisions her nest tubes, a second wasp often hangs around near the entrance. This is a male *Trypoxylon*, guarding the female and her nest. I assume he is likely protecting his mate from other males who might try to mate with her” (Figures 36-37) <sup>[26][27]</sup>.





**Figure 36.** Male *Trypoxylon* wasp guarding the entrance to a tube with a female inside.

Source: <https://spidersinohio.net/trypoxylon-vs-parasteatoda/>.



**Figure 37.** Fresh tube of *Trypoxylon* wasp with pair present, male visible at the entrance.

Source: <https://spidersinohio.net/trypoxylon-vs-parasteatoda/>.

When the mother wasp has provided enough zombie spiders as food she will lay an egg on one of the spiders and then seal up that section of the tube. The pair of wasps actually mate inside the tube and the male holds the female as she lays the egg. The female now seals the zombie spider prey and her egg by making a mud partition. Eventually, each tube will have several compartments, each with a supply of paralyzed spiders and wasp eggs (Figures 38-40) [28][29].





**Figure 38.** Back view of *Trypoxylon* nest tubes revealing wasp pupal cases and some spider bodies (at left).

Source: <https://spidersinohio.net/trypoxylon-vs-parasteatoda/>.



**Figure 39.** Dissected the *Trypoxylon* tube revealing the successful emergence.

Source: <https://spidersinohio.net/trypoxylon-vs-parasteatoda/>.





**Figure 40.** Dissected *Trypoxylon* tube revealing successful emergence.

Source: <https://spidersinohio.net/trypoxylon-vs-parasteatoda/>.

*Trypoxylon* Latreille, 1796 is the most diverse genus within the Crabronidae family. It has a wide geographic distribution, but its greatest diversity is in the Neotropics. They are solitary wasps and the female exhibits maternal care in the form of building and provisioning the nests, where the immature ones develop to the adult stage (Figure 41) [28][29].



**Figure 41.** *Trypoxylon* Latreille, 1796.

Source: Chapelin-Viscardi JD.

The subgenus *Trypargilum* Richards, 1934, restricted to the New World, consists of solitary wasps whose females stock their nests with paralyzed spiders. In this group, the males present the male-guard behavior, remaining close to the nest during its construction (Figures 42-43) [28][29].





**Figure 42.** *Neoscona arabesca* (Walckenaer 1841) (Araneae: Araneidae) female.

Source: <https://spidersinohio.net/typoxylon-vs-parasteatoda/>.





**Figure 43.** Common house spider with male *Trypoxylon* wasp prey (also note that some of her spiderlings are emerging from another egg case above).

Source: <https://spidersinohio.net/trypoxylon-vs-parasteatoda/>.

These wasps usually successfully nest in artificial cavities and trap-nests facilitate their sampling, producing data on abundance, richness and seasonality intranidal architecture, use of prey and natural enemies male guard behavior and parental investment (Figures 44-45) <sup>[28][29]</sup>.

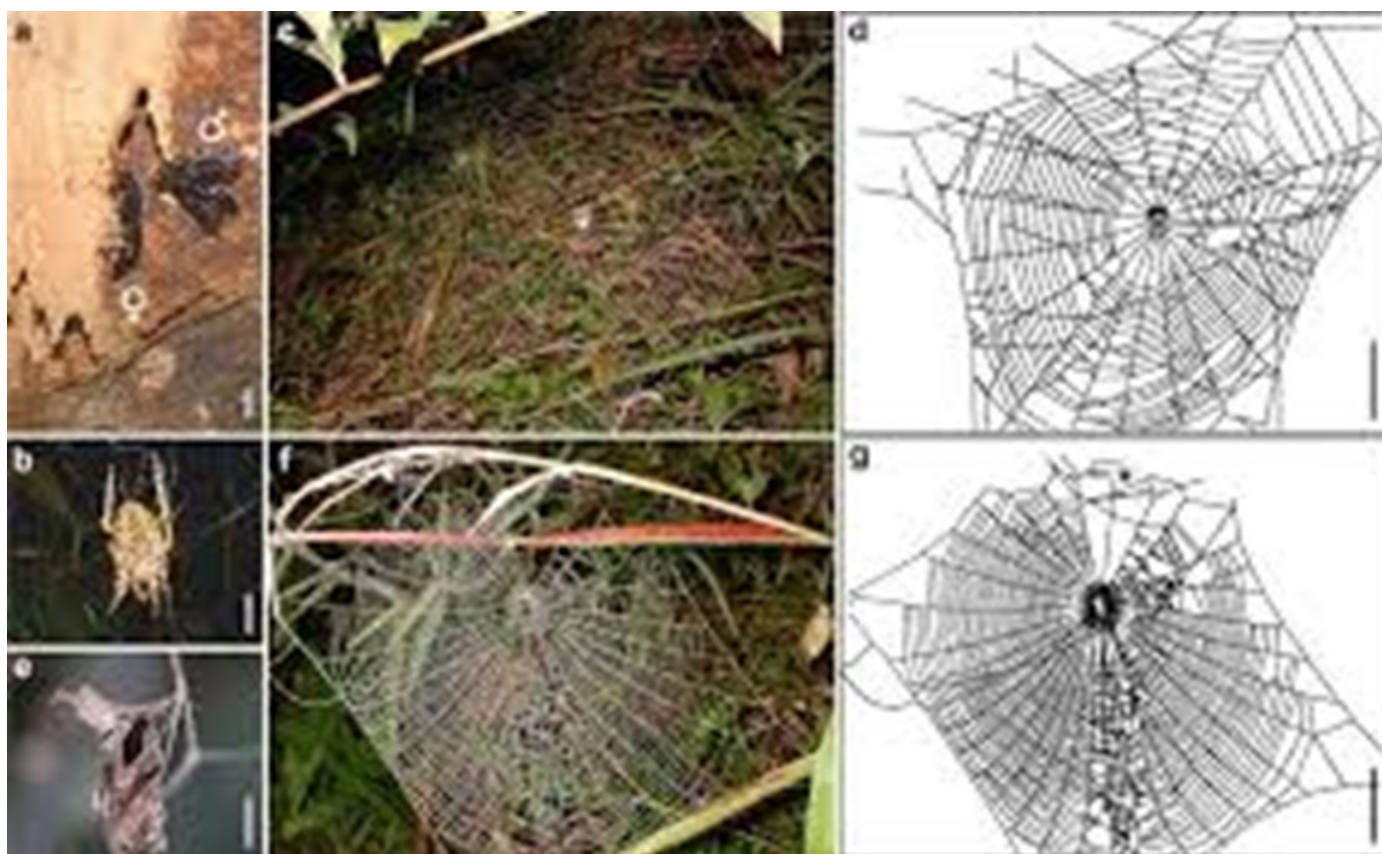




**Figure 44.** Common house spider feeding on a male Trypoxylon wasp prey.

Source: <https://spidersinohio.net/trypoxylon-vs-parasteatoda/>.





**Figure 45.** (a) Female of *Trypoxylon* (*Trypargilum*) *albonigrum* Richards, 1934 building a mud nest. The other wasp in the picture is the male. (b) The female of *Parawixia audax* (Blackwall, 1863). (c, d) Web of *P. audax* showing the position occupied by the spider during the day, in the center of the orb. (e) The female of *Eustala* sp. (f, g) Web of *Eustala* sp. shows the peripheral position occupied and the free sector in the web. The spider remains in the vegetation, holding a thread connected to the hub of the orb.

Source: [https://ib.rc.unesp.br/Home/Departamentos47/ecologia/laboratoriodeecologiaevolutiva/araujo-e-gonzaga\\_2007.pdf](https://ib.rc.unesp.br/Home/Departamentos47/ecologia/laboratoriodeecologiaevolutiva/araujo-e-gonzaga_2007.pdf).

### 3.3. Study 3

This species is native to eastern Asia and has not previously been reported from Europe. The description of the species, as well as information on its nest architecture, cocoon shape, the identity of the spiders captured to provision the nests, and mortality rates, including parasitism by a native cleptoparasitic. The term kleptoparasitism ('kleptein', from Greek: 'to steal') was introduced to describe the theft of food previously collected or processed by someone else [30].

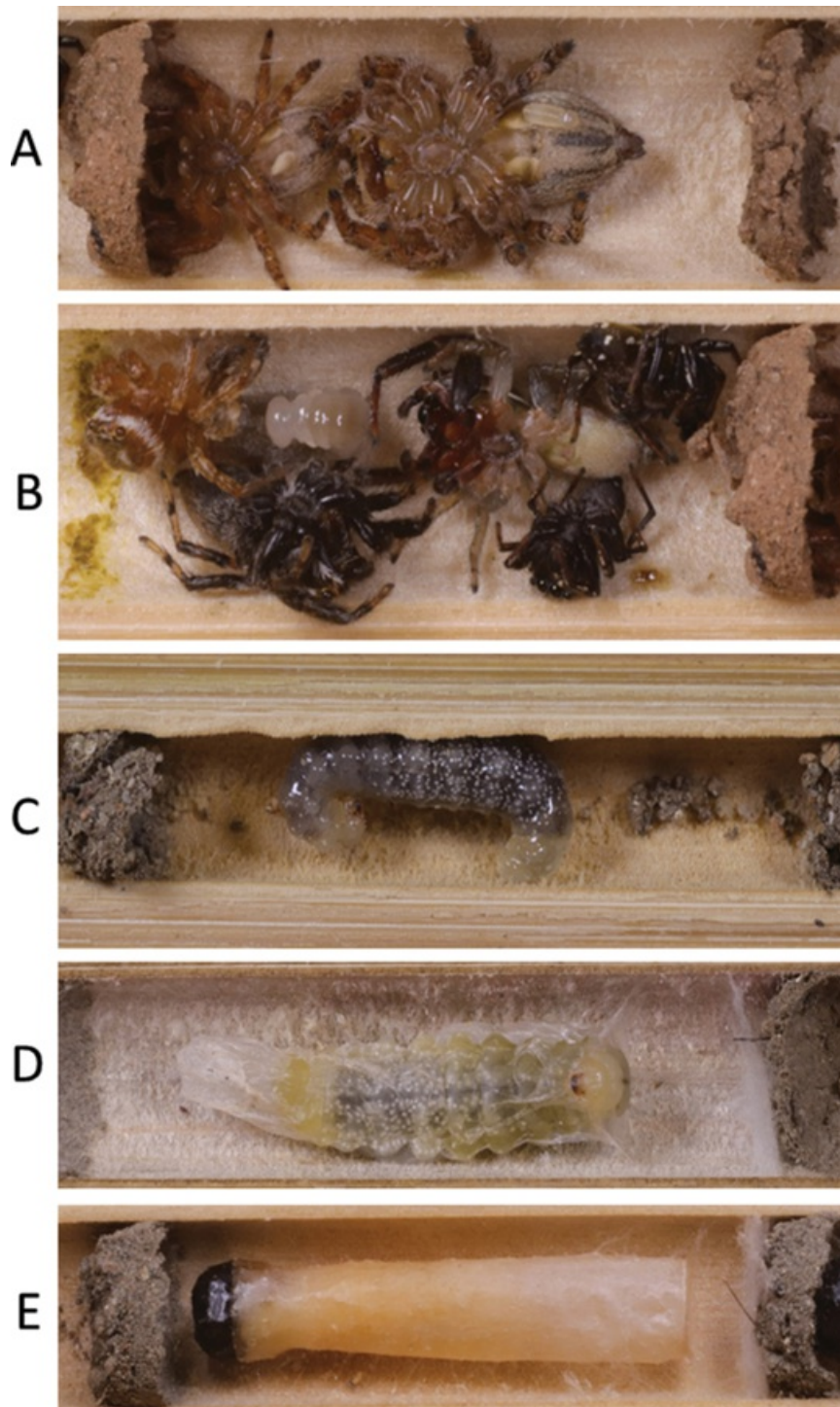
This type of behavior is also called feeding parasitism, piracy or stealing behavior, being recognized as an important feeding strategy recorded in large groups such as marine invertebrates, insects and spiders. *Amobia signata* (Diptera: Sarcophagidae) and a native parasitoid wasp *Melittobia acasta* (Hymenoptera: Eulophidae) (Figures 46-48) [30].





**Figure 46.** Cell provisioned with *Heliophanus apiatus* Simon, 1868 (6 females, 1 male) and *Heliophanus tribulosus* Simon, 1868 (Aranaea) (2 females).





**Figure 47.** Larval development of *Trypoxylon petiolatum* Smith, 1858 (A) first instar larva on the abdomen of a spider prey (B) instar 2-3 larva consuming a spider prey (C) post-feeding instar 5 larva (D) larva spinning its cocoon (E) completed cocoon.





**Figure 48.** Puparia (A), habitus (B), and head (C) of male adult *Amobia signata* (Meigen, 1824) (Diptera: Sarcophagidae).

Source: <https://jhr.pensoft.net/article/78581/list/1/>.

### 3.4. Study 4

The objective of this work is to understand the morphometric variations of the wings of two species of wasps *Bembix* sp. (Crabronidae: Bembecini) and *Scieliphron* sp. (Sphecidae) in order to evaluate the effect of the environmental gradient in relation to the flood pulse on the morphometric variation in different areas of the Pantanal since the wasps use different strategies for nesting, one digs nests on the ground and the other makes high nests (Figure 49) [31].





**Figure 49.** *Bembix* sp. (Family Crabronidae)

<https://www.flickr.com/photos/luisgaifem/14574244403/>.

Samplings were carried out in 19 areas of the Pantanal with Malaise and Moericke traps and active search to capture specimens. Seven individuals of *Bembix* sp. were collected and measured. and 22 individuals of *Sceliphron* sp., being who in *Bembix* sp. the greatest variation between points was found, and more anatomical points with variations, when compared with *Sceliphron* sp., indicating that there is a difference between the study areas and the relation of wing shape between species. It also showed more and greater variations in the PCA scores analyzing the landmarks (Figure 50) <sup>[31]</sup>.



**Figure 50.** *Sceliphron* sp. (Family Sphecidae).

Source: <https://bugguide.net/node/view/124289>.

For *Sceliphron* sp., the variations were 1 2 Universidade Federal de Rondonópolis, less significant, and only a few points



stood out more in comparison with *Bembix spp* the variations in the PCA scores were less frequent and in smaller amplitudes. Thus, as expected, the group that belongs to *Bembix* sp, as it is more associated with soil characteristics, responded with greater amplitudes to the influence of the flood pulse [31].

### 3.6. Study 6

**Crabronidae and Sphecidae (Hymenoptera: Apoidea) type specimens were deposited in the Museu de Zoologia da Universidade de São Paulo, Brazil [32].**

#### Crabronidae

#### Bembicinae

##### 1-Bembicini

#### *Liogorytes*

*Liogorytes brasilius* Bohart, 2000.

*Stictia Illiger* Schrottky, 1913/ *Stictia maculitarsis* Schrottky, 1913 (Figure 51).



**Figure 51.** *Liogorytes brasilius* Bohart, 2000.

Source:



<https://treatment.plazi.org/id/6D263559FFAEFFDFF9E01DFFD3B7134>.

## 2-Crabroninae

### **Bothynostethini**

#### *Bohartella* Menke

*Bohartella hypopsia* Menke & Vardy, 1980.

## 3-Crabronini

#### *Podagritus* Spinola

*Podagritus jordaonis* Leclercq, 2000.

*Podagritus ypirangae* Leclercq, 2000.

## 4-larrini

*Tachysphex* Koh (Figure 52).

*Tachysphex advenus* Pulawski, 1974.



*Tachytes* Panzer (Figure 53).





**Figure 53.** Genus *Tachytes*.

Source: <https://scan-bugs.org/portal/taxa/index.php?taxauthid=1&taxon=263386&cl=175>.

- *Tachytes catarinae* Bohart, 1978.
- *Tachytes coloratus* Bohart, 1978.
- *Tachytes fraternoides* Bohart, 1978.
- *Tachytes menkei* Bohart, 1978.
- *Tachytes pubescens* Bohart, 1978.
- *Tachytes richardsi* Bohart, 1978.
- *Tachytes roraimae* Bohart, 1978.
- *Tachytes rubioi* Bohart, 1978.
- *Tachytes sexdens* Bohart, 1978.
- *Tachytes stangei* Bohart, 1978.

#### 5-Oxybelini

*Oxybelus* Latreille





**Figure 54.** Genus *Oxybelus*.

Sources: Photo 15020021, (c) Henk Wallays, All rights reserved and <https://inaturalist.ca/photos/15020021>.

- *Oxybelus cinemucro* Bohart, 1993.
- *Oxybelus genisei* Bohart, 1993.
- *Oxybelus Irwin* Bohart, 1993.
- *Oxybelus plaumanni* Bohart, 1993b.
- *Oxybelus roraimae* Bohart, 1993b:
- *Trypoxylon* Latreille 1796 (Figure 55).



**Figure 55.** *Trypoxylon lactitarse* Saussure, 1867 on the nest.

Sources: Browsing by Author Hallett, Peter and <https://tspace.library.utoronto.ca/browse?type=author&value=Hallett%2C+Peter+>.



- *Trypoxylon lenkoi*, Amarante, 1991.
- *Trypoxylon mojuba* Amarante, 1995.
- *Trypoxylon personatum* Amarante, 1991.

### 3.7. Study 7

#### **Taxonomy of Crabronidae (Insecta, Hymenoptera) from the Entomological Collection of Santa Cruz do Sul (Cesc), Rs, Brazil [33].**

The objective of this work was the taxonomic analysis of specimens of the Crabronidae family at the genus and morphospecies level [33].

The material analyzed is listed in the Entomological Collection of Santa Cruz do Sul (CESC) of the University of Santa Cruz do Sul. Individuals belonging to the Crabronidae were separated by subfamilies and later identified at the genus level using the specific taxonomic keys of "Introducción a los Hymenoptera de la Región Neotropical" and "Chaves ilustradas para las subfamilies, tribus y genera de esfécidos neotropicales". The material separated by genus level was stored in entomological boxes at CESC [33].

A total of 455 individuals were identified, belonging to three subfamilies and nine tribes (Aphilanthopini, Bembicini, Cercerini, Gorytini, Larrini, Pemphredonini, Philanthini, Psenini, Stizini, and Trypoxylini), with the subfamily Philanthinae being the most abundant. Twenty-one genera were identified, with *Cerceris* being the richest in terms of morphospecies (10) and *Trypoxylon* being the most abundant in the number of individuals (70) [33].

Individuals of the genus *Cerceris* were mostly collected in the months of December, January and February, in 16 different municipalities in RS, with a higher incidence in Santa Cruz do Sul, Candelária and Sobradinho, but there are also individuals collected in the states of Mato Grosso do Sul and Paraná [33].

*Trypoxylon* was collected more frequently in the same months and also in 16 municipalities, with greater frequency in the municipality of Santa Cruz do Sul. The taxonomic study of these genera, the places where they were collected and the ecosystems in which they are inserted are important for the analysis of the faunal richness of this family in the different regions [33].

### 3.3. Study 8

#### **Crabronidade in Mexico and provide data on species with potential use as biological control agents.**

This study aimed to update the number of species of the family Crabronidade in Mexico and provide data on species with potential use as biological control agents [34].

According to the reviewed literature, a total of 769 species representing 99 genera of the family Crabronidae are reported in Mexico. The subfamilies Crabroninae and Philanthinae exhibited the highest numbers of species, with 338 and 187



species, respectively. The genera *Cerceris* and *Trypoxylon* were the most diverse with 130 and 58 species, respectively. Baja California Norte, Sonora, and Tamaulipas represented the most diverse Mexican states with 144, 125, and 106 species, respectively [34].

Regarding the agroecological importance, the genera *Astata*, *Bicyrtes*, *Cerceris*, *Larra*, *Liris*, *Oxybelus*, *Rubrica*, *Solierella*, *Tachysphex* and *Tachytes*, which include species that are used as biological control agents, are reported in Mexico. Also, at the species level, seven species *Astata unicolor* Say, 1824, *Cerceris californica* Cresson, 1865, *Cerceris dilatata* Spinola, 1841, *Cerceris fumipennis* Say, 1837, *Cerceris grandis* Banks, 1913, *Solierella blaisdelli* (Bridwell, 1920) and *Solierella peckhami* (Ashmead, 1897) have been recorded in the country (Figure 55) [34].



**Figure 55.** *Astata unicolor* Say, 1824.

Source: <https://bugguide.net/node/view/467930/bgpage>.



**Figure 56.** *Cerceris dilatata* Spinola, 1841.

Source: Photo 5362202, (c) conabio\_bancodeimágenes, some rights reserved (CC BY-NC-ND), uploaded by conabio\_bancodeimágenes and <https://inaturalist.lu/photos/5362202>.



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