Chapter 5
Nesting Habits of Neotropical Social Wasps

Bruno Corrêa Barbosa, Tatiane Tagliatti Maciel, and Fábio Prezoto

Abstract With the main functions of providing a microenvironment for the offspring and providing protection for the colony against vertebrate and invertebrate predators, the complex architecture of social wasp nests varies from group to group. The nests can have from one to multiple combs covered or not by a protective envelope, presenting an important taxonomic value for the classification of the groups to which they belong. Here, we propose a brief overview of the nesting habits, foundation strategies, and the distinction and identification of the genera of social wasps (Polistinae) occurring in Brazil.

Keywords Nesting habits · Nesting substrate · Paper wasps

When talking about social insects, we can say that social wasps are superorganisms because they function as if they were a single organism when they are together, with a diversity of behaviors which is directly reflected in varying nesting strategies exhibited by their different genera, such as nest architecture and material used in nest construction (Wenzel 1998).

In addition, the main function of social wasp nests is colony protection against natural enemies (Jeanne 1975; Wenzel 1998), as well as accumulating auxiliary functions such as weather protection structure, offspring care, and, in some species cases, food storage (cf. Jeanne 1991; Prezoto and Gobbi 2003; Guimaraes et al. 2008; Rocha 2012).

Like bees, social wasp nests are very diverse and are made up of combs, cells, and protective envelopes and may contain a single discovered comb with a few dozen brood cells fixed by a pedicel (Fig. 5.1a) or several layers of combs with brood cells overlapped and encased in the protective envelopes (Fig. 5.1b).

Some characteristics regarding studies of nesting habits of social wasps may hinder a researcher's observation process, such as species aggressiveness and

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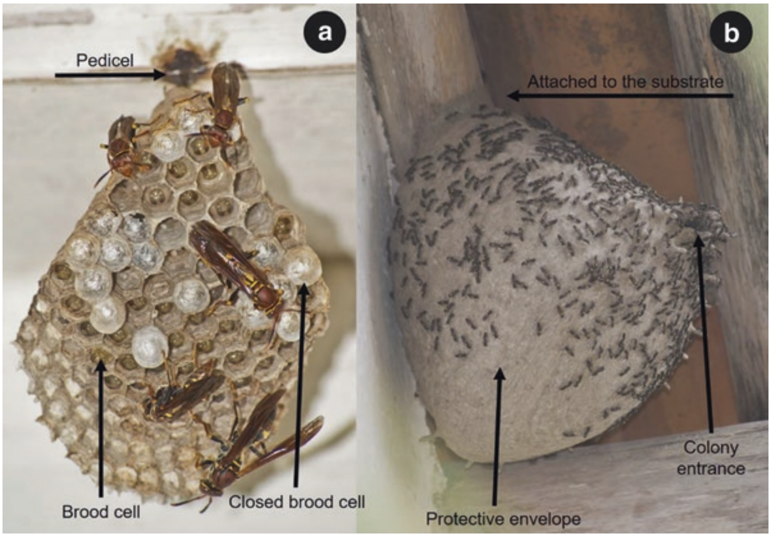

Fig. 5.1 Examples of social wasp nest types: (**a**) open nest fixed by a pedicel (*Polistes versicolor*); (**b**) closed nest attached to a substrate (*Polybia scutellaris*)

especially because nests are usually covered by envelopes and are difficult to access. For these reasons, except very specific cases involving direct observations of Epiponini behavior, they can still be considered a poorly studied group (e.g., Mateus 2005; Gelin et al. 2008; Kudô et al. 2016).

These difficulties are not found for Mischocyttarini and Polistini due to the fact that their nests are open, facilitating behavioral observations in loco; therefore, they are the best-studied groups (e.g., Oliveira et al. 2006; De Souza et al. 2012; Castro et al. 2014; Barbosa et al. 2016).

In this chapter, we will present several subjects and curiosities that are part of the nesting habits of neotropical social wasps, starting with nesting strategies and ending with an illustrated key for the genres of Brazilian social wasps.

5.1 Foundation Strategies

Social wasps are traditionally divided into two large groups considering their foundation strategy: an independent foundation and a swarming foundation species (Jeanne 1972; Jeanne 1980) (Fig. 5.2a, d).

The independent foundation is only practiced by species of the Polistini and Mischocyttarini tribes in the neotropical region, usually with relatively small colonies when compared to swarming species (Carpenter and Marques 2001). The independent foundation can occur in two ways: with nest building initiated by a single inseminated female (haplometrose) and a group of them (pleometrose) (Wenzel 1991; West-Eberhard 1969) (Fig. 5.2a, b).

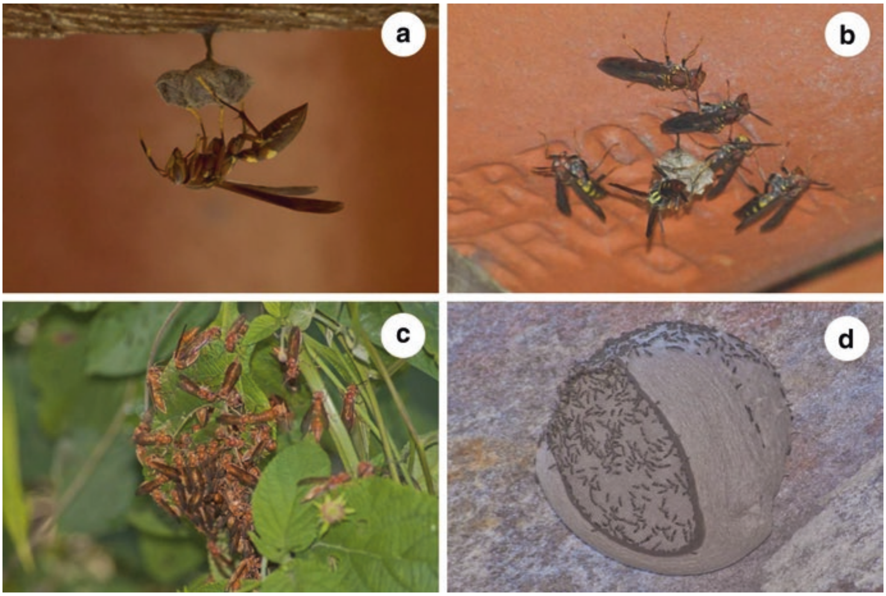

Fig. 5.2 (**a**) *Polistes simillimus* colony with haplometrose foundation; (**b**) *Polistes versicolor* colony with pleometrose foundation; (**c**) swarming behavior (*Synoeca virginea*); (**d**) a swarming social wasp colony (*Polybia paulista*) under construction

Other females join the process after the foundation begins in some species where haplometrosis occurs; however, the original founder maintains oviposition exclusivity through aggressive behavior such as persecution and subjugation (Carpenter and Marques 2001). The founder participates in building the nest and foraging until the first workers emerge and is then restricted to reproduction.

One behavior associated with the independent foundation strategy is usurpation. This behavior can come from a founder abandoning her own nest, which may be by choice or after being expelled by co-founders; the usurpation itself consists of a foreign founder invading an existing nest and becoming dominant (breeding) through aggressive interactions with resident females (Iwahashi 1989; Turillazzi 1992). Field (1992) elaborated hypotheses about the conditions which stimulate usurpation behavior to the detriment of founding a new nest, such as ecological constraints, temporal limitations, behavioral stimuli, and phenotypic tendencies.

Swarming foundation only occurs in Epiponini in the neotropical region (Fig. 5.2c, d). Swarming behavior can occur for two reasons; one is for the reproductive division of the colony which is in the production phase of new sexed individuals, also called the "reproductive swarm" (cf. Richards and Richards 1951). In this case, the workers (sterile females) of an established colony go out to select a new nesting site and indicate it to the colony by pheromone trails, called trail making (cf. Naumann 1975), which causes the swarm to move and form a new colony (West-Eberhard 1982; Carpenter and Marques 2001). The queens in this foundation strategy are already defined from the beginning, being responsible for oviposition; the swarms are polygenic, i.e., they have multiple functional queens (Hölldobler and Wilson 1977; Mateus 2005).

The second reason for swarming is forced migration or an evacuating swarm (cf. Richards and Richards 1951), in which the swarm is induced by adverse mechanisms such as predation where predators damage structural parts of the nest or parts of the substrate or by biotic factors such as rain and wind which can damage the nest, making it impossible to rebuild the site, in addition to other accidental facts.

Different foundation strategies in swarming have advantages over independent foundation, especially in relation to the size that swarming colonies reach, enabling greater defense against predators and adverse conditions (Jeanne 1991). However, the independent foundation also has positive points, as its small size increases the chance of being overlooked by predators, as well as requiring a much smaller nesting area, making it possible to colonize a larger group of substrates.

There are records of various sizes that a colony can reach in terms of both nest size and number of colony individuals. The largest numbers among all social wasps belong to the *Agelaia* genus, which has the largest nest size and the largest concentration of individuals which can reach more than 1 million adults in a colony and can contain 956 thousand cells weighing over 13 kg (cf. Zucchi et al. 1995; Oliveira 2008).

5.2 Materials Used in Nest Construction

The materials used in building social wasp nests are indicators of the wasps' interaction with the environment and have a strong influence on the architecture and physical appearance of nests (Wenzel 1991). A significant part of the adult resource-gathering effort is directed toward collecting nest building materials (Giannotti et al. 1995).

Neotropical social wasps build nests from plant fibers collected by scraping their mandible on the plant substrate (Fig. 5.3a). The foragers collect the material, crush, and mix it with water and salivary secretion resulting in a mass which is then applied in the construction and repair of new nest and envelope cells (Fig. 5.3b), as well as reinforcing the pedicel. As a result, this obtained mass is a paperlike fiber, being responsible for the popular name paper wasps. The thickness can vary considerably, being thick in most Epiponini and thinner in Polistini and Mischocyttarini (Gallo et al. 1988; Wenzel 1991; Wenzel 1998).

There are exceptions such as the *Polybia emaciata* Lucas, 1879 species which uses nesting clay, and *Mischocyttarus iheringi* Zikán, 1935 specie which uses unprocessed plant materials such as algae, bryophytes and trichomes (Fig. 5.3c) (cf. Wenzel 1991; Barbosa et al. 2016).

Fig. 5.3 (**a**) Collection of nest building or repair material (*Parachartergus fraternus*); (**b**) nest building behavior (*Parachartergus fraternus*); (**c**) *Mischocyttarus iheringi* nest; this species uses an unprocessed plant material for camouflage

5.3 Choice of Nesting Substrate

The choice of nesting site is the focus of studies on social wasps, given the importance of the theme and its ecology (e.g., Corbara et al. 2009; Alvarenga et al. 2010; Castro et al. 2014; Barbosa 2015; Virgínio et al. 2016). Factors taken into consideration when choosing a location include concealability, weather protection, and the risk of predation (Richards and Richards 1951; Downing and Jeanne 1986; Dejean et al. 2010).

Species commonly build nests under or on leaves, branches, and logs and within natural cavities in a natural environment (Jeanne 1991). Social wasp nesting in vegetation seems to be generally influenced by broadleaf and evergreen plants (Fig. 5.4a) concentrated in understory species (e.g., Dejean et al. 1998; Souza et al. 2014; Barbosa 2015), which keeps the nests more concealed and protected against abiotic factors due to the density, such that the vegetation morphology and height are more relevant for choosing the social nesting site than any specific plant species.

In parallel, social wasp nests are commonly found in urban areas, especially in man-made structures. This relationship indicates the synanthropism of the group which is most observed in *Mischocyttarus* and *Polistes* species, sometimes preferring human to natural substrates (e.g., Yeison-López et al. 2012; Barbosa 2015). Although there are several materials in man-made substrates such as concrete, metals, plastics, and glass, wood stands out due to its plant origin, suggesting that social wasps are still undergoing a process of synanthropic adaptation, as they tend to nest in substrates of plant origin.

Fig. 5.4 (**a**) *Polybia fastidiosuscula* colony nested on *Dracaena fragrans*, a broadleaf and evergreen plant species; (**b**) difference in concealability of nests on human substrates for species of independent and swarming foundations, highlighting a *Polistes versicolor* nest next to a *Polybia fastidiosuscula* nest

It can also be noted that the use of man-made substrates is limited for some species due to the need for the nest to be fixed onto the substrate and its concealability, and which the size of the nest influences, i.e., independently found wasp nests are generally small and remain concealed, while on the other hand swarming species present larger, much more visible colonies and lose their concealability, as observed in Fig. 5.4b.

5.4 Colonial Cycle and Seasonality

Less-defined annual seasons in tropical regions also lead to less-defined phases of the colonial cycle. West-Eberhard (1969) showed the existence of asynchrony in the social wasp cycle in tropical regions, since nests can be started at any time of the year; for this very reason, the cycle is strictly related to the environment in which they are inserted, and may go through distinct phases, as characterized by Reeve (1991):

- *Foundation*: it begins with the construction of the nest and goes until the emergence of the first female offspring wasp (Fig. 5.5a).
- *Development*: it begins with the appearance of the first female offspring and extends until the appearance of reproductive forms (new queens). This phase is also known as the colony growth period which can last several months, and the colony increases in size several times (both in physical and population structures) (Fig. 5.5b).
- *Decline*: this period is characterized by ceasing nest expansion activities; irreversible reduction of the population, mainly immature forms (eggs, larvae, and pupae); and the appearance of reproductive forms (males) (Fig. 5.5c).
- *Abandonment*: the colony will only be made up of adult individuals at some point during the decline phase, who eventually abandon it and may disperse throughout the region to found new colonies or form an aggregate.

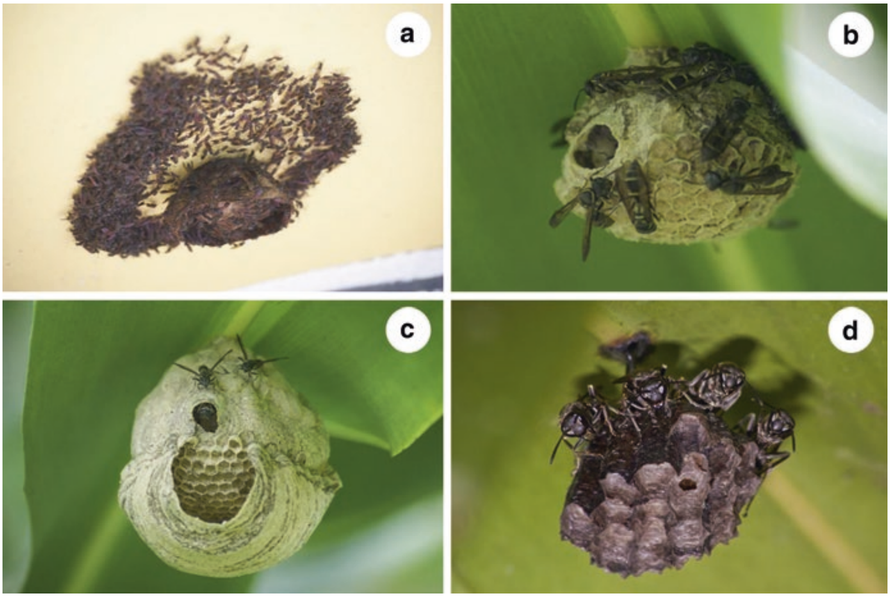

Fig. 5.5 (**a**) Foundation phase, nest building and first egg laying; (**b**) development phase, emergence of the first lineage and colony expansion; (**c**) decline phase, decrease in new comb construction, population, and male production; (**d**) aggregation, optional behavior performed in cold seasons

- *Aggregated*: it has a very variable duration (from a few days to several months), being an optional event which is mainly dependent on climatic conditions. This phenomenon can be frequently observed during the dry season. Aggregation is similar to mammalian hibernation and is performed by a group of adults, usually relatives, gathering over the nest to spend times of drought protected (Fig. 5.5d).

Cycles in tropical regions often do not follow the sequence suggested by Reeve (1991) and can repeat, skip, or recycle phases as needed by colonies, increasing or decreasing colony life, such as in records of a *Polybia scutellaris* colony which is over 4 years old. However, it is still possible to see some seasonality in the cycles even in asynchronous nests, even though the weather seasons are not so defined; Jeanne (1972) argues that this is due to intrinsic control.

According to the author, aggressive queen-worker interactions are essential to maintain the queen's reproductive exclusivity; as the colony expands, the dominant female cannot control all workers, leading to a large proportion of non-working females and males in the nest, which causes marked declines in productivity, leading to hunger and ultimately nest abandonment. In addition to the influence of environmental seasonality and intrinsic factors, extrinsic factors such as direct predation interference can occur, in which nests can be destroyed and adults disperse and start a new foundation (Maciel et al. 2016).

5.5 Nest Architecture

Several classifications of neotropical social wasp nests have been proposed over the years due to the diversity of their shapes; the classical and most widely accepted system by Polistinae researchers was created by Saussure (1853–1858) and was later revised by Richards and Richards (1951). This classification is separated into three major divisions which will be presented next.

Stelocyttarus nests They attach to the nesting substrate via pedicels or pillars; they can be formed by one or more combs, and subsequent combs can be linked to the previous ones by means of peduncles. Although the peduncles are of equal origin to the envelope, they are made of a stronger resinous material. Stelocyte nests are further divided into two subtypes: Gymnodornous, which usually have only one comb and do not have a protective envelope, and Calyptodomous, which have a protective envelope involving their combs and great structural diversity. The Gymnodornous nest type is represented in *Mischocyttarus*, *Polistes*, and some *Agelaia* species, while Calyptodomous nests can be seen in *Angiopolybia*, *Charteginus*, *Leipomeles*, *Parachartergus*, *Pseudopolybia*, and some *Agelaia* and *Protopolybia* species.

Astelocyttarus nests Only one comb is attached directly to the substrate, protected by a dome-shaped envelope; nest enlargement occurs through expansion of the initial comb under the substrate as well as the protective envelope. The genera which build astelocyte nests are *Asteloeca*, *Clypearia*, *Marimbonda*, *Metapolybia*, *Nectarinella*, and *Synoeca*.

Phragmocyttarus nests They are initially composed of a comb connected directly to the substrate from which a protective envelope is constructed; the subsequent comb is added to the envelope surface which is enlarged to cover the new comb and so on. The genera which present this type of nest are *Brachygastra*, *Epipona*, *Chartergus*, *Polybia*, and *Protonectarina*.

5.6 Generic Key for Nests of Genera Found in Brazil

As there is a known difficulty in identifying the morphological characteristics of social wasp nests which occur in Brazil, this chapter will conclude by presenting an illustrated key to the neotropical social wasp genera based on the structural characteristics of the nests:

1. Nests are usually built in natural cavities such as tree trunks and termites (Fig. 5.6a) or in abandoned houses; they are exposed nests, unenveloped and with brood cells of size up to 4 mm. .... *Agelaia*

   - Nests fully exposed and fixed to the substrate; generally exposed nests with or without envelope and brood cell size of 5 mm (Fig. 5.6b) **2**

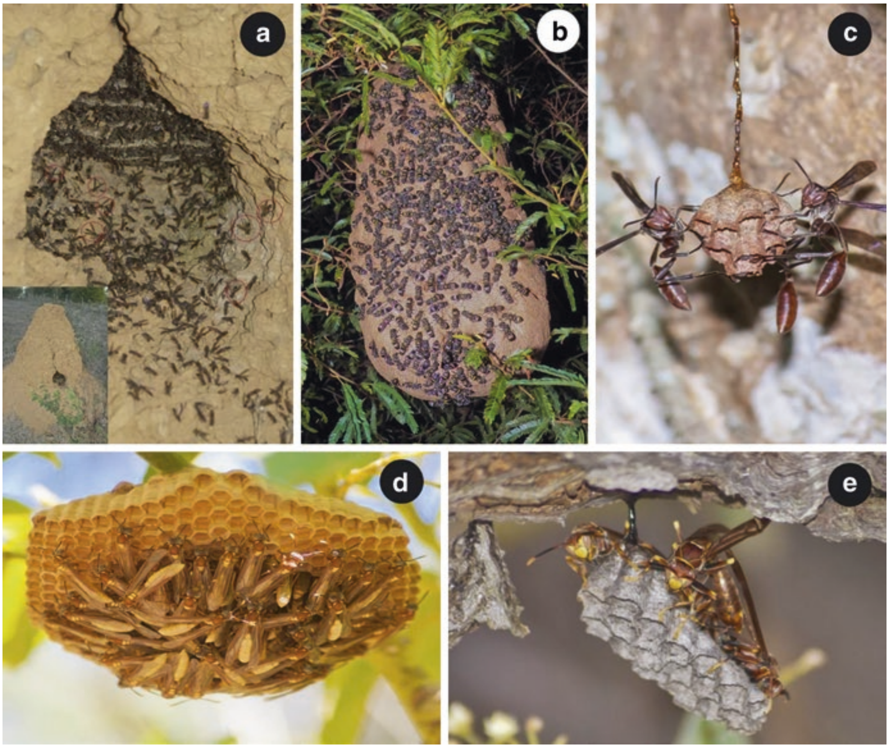

Fig. 5.6 (**a**) Cavity (termite) housing *Agelaia vicina* colony; (**b**) *Polybia bifasciata* nest; (**c**) *Mischocyttarus rotundicollis* nest; (**d**) *Apoica pallens* nest; (**e**) *Polistes similimus* nest

2. Uncoated nests with fully exposed brood cells (Fig. 5.6c). **3**
   - Enveloped nests with hidden/concealed brood cells (Fig. 5.6b) **5**
3. Pedicel absent (Fig. 5.6d); single layer of brood cells facing downward in a horizontal position, with the largest portion in contact with the substrate and completely enveloped therein; usually the nests are light in color and have a hat or shower shape. .... *Apoica*
   - Pedicel present (Fig. 5.6c), which may be single or multiple; composed of only one layer of brood cells; variable cell orientation (vertical or horizontal) found fixed on leaves or human buildings; colored nests which can vary..... **4**
4. Brood cells smaller than 4 mm in diameter (Fig. 5.6c); nests are composed of short vegetable fibers. ….. *Mischocyttarus*
   - Brood cells larger than 4 mm in diameter (Fig. 5.6e); nests are composed of long and woody fibers…... *Polistes*
5. Nest with a single sessile comb, built directly on the surface of the trunk....... **6**
   - All combs hung by pedicels or at least with sessile initiation.................. **10**

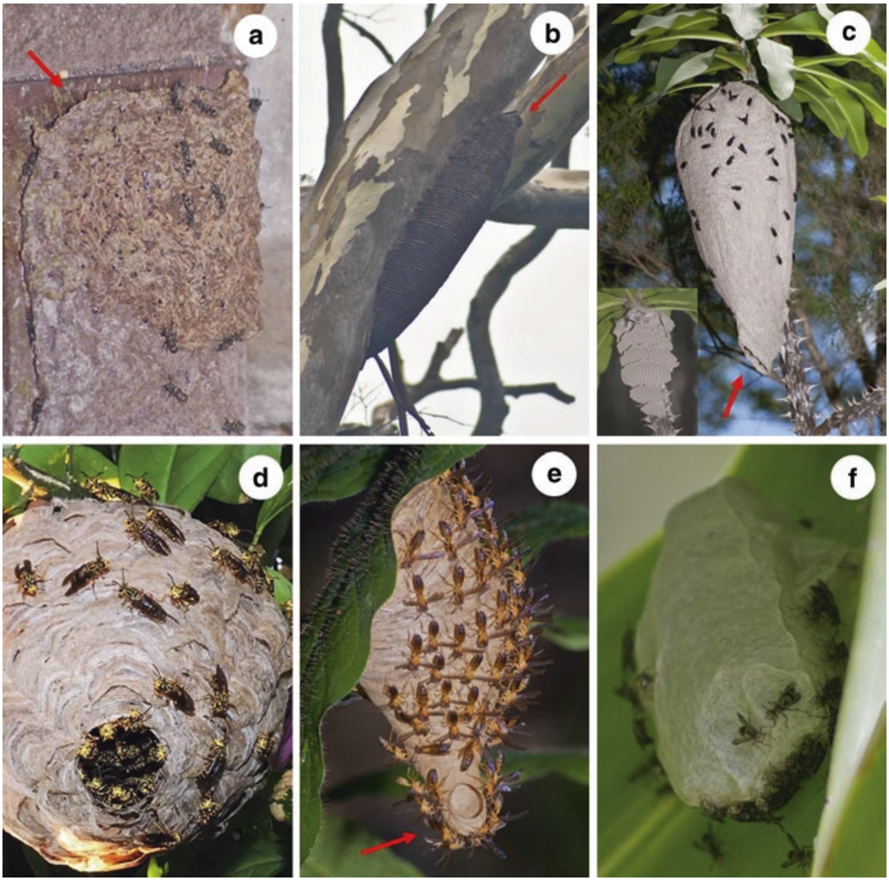

Fig. 5.7 (**a**) *Metapolybia* sp nest, the darkest and brightest areas are transparent windows elaborated with a secretion; (**b**) *Synoeca cyanea* nest; (**c**) *Parachartergus fraternus* nest; (**d**) *Pseudopolybia* nest; (**e**) *Angiopolybia pallens* nest; (**f**) *Protopolybia exigua* nest. Red arrow points to the nest entrance

6. Nest entrance in the lower half of envelope (Fig. 5.7c, e)................................ **7**
   - Nest entrance in the upper half or central part of the envelope (Fig. 5.7b)..**8**
7. Substrate around the nest entrance with small droplets of sticky substance; cells are 3.5–3.7 mm wide. ……..*Nectarinella*
   - Substrate around nest entrance and no droplets of sticky substance; 1.8-mm-wide cells…... *Leipomeles*

8. Envelope forms eaves (Fig. 5.7a) extending laterally; envelope with transparent windows of some secretion. …... *Metapolybia*

   • Envelope does not form eaves.. **9**

9. Some areas of the envelope show added bark particles and other plant materials; envelope with transparent windows is made up of some secretion; the entrance is positioned below the middle of the nest............................... *Clypearia* or *Asteloeca*

   • Nests with brood cells parallel to the substrate and larger than 4 mm in diameter; envelope with transverse undulations except for *Synoeca virginea* (Fig. 5.7b) .... *Synoeca*

10. Envelope against or covering substrate. **11**

    • Envelope does not touch the substrate.. **14**

11. Combs are supported by one or more pedicels.. **12**

    • First sessile comb or suspended by a broad leaf-shaped pedicel; when smaller combs are present, they are built over the upper comb envelope (Fig. 5.8a) **15**

12. Nests with brood cells horizontal to substrate ….. .... *Parachartergus* (Fig. 5.7a) or *Chartergellus*

    • Combs supported by an approximately central pedicel............................ **13**

13. First and following combs supported by a single central pedicel; envelope has more than one layer (Fig. 5.7d)..*Pseudopolybia*

    • First comb is supported by more than one pedicel; the nest entrance is located in the lower portion of the tubular envelope projection in some species (Fig. 5.7e) .... *Angiopolybia*

14. Nests with one or more layers of brood cells are 1 mm in diameter; usually they are attached to leaves by multiple pedicels, which are very small; they are light-colored, very fragile, and thin or have no leaflike wrapper playing a protective role (Fig. 5.7f). .... *Protopolybia*

    • Nest entrance located on the comb floor through an opening between the enclosure and the substrate; often star-shaped nests….............. *Charterginus*

15. Nests involving and/or attached to tree trunks, branches, or leaves, with a single opening in the lower region; the envelope is mostly fragile (Fig. 5.8a).............. .... *Polybia*

    • Nest built differently from the above **16**

16. Rigid nest with a hard and fibrous envelope. …... **17**

    • Nest with a soft and friable envelope... **18**

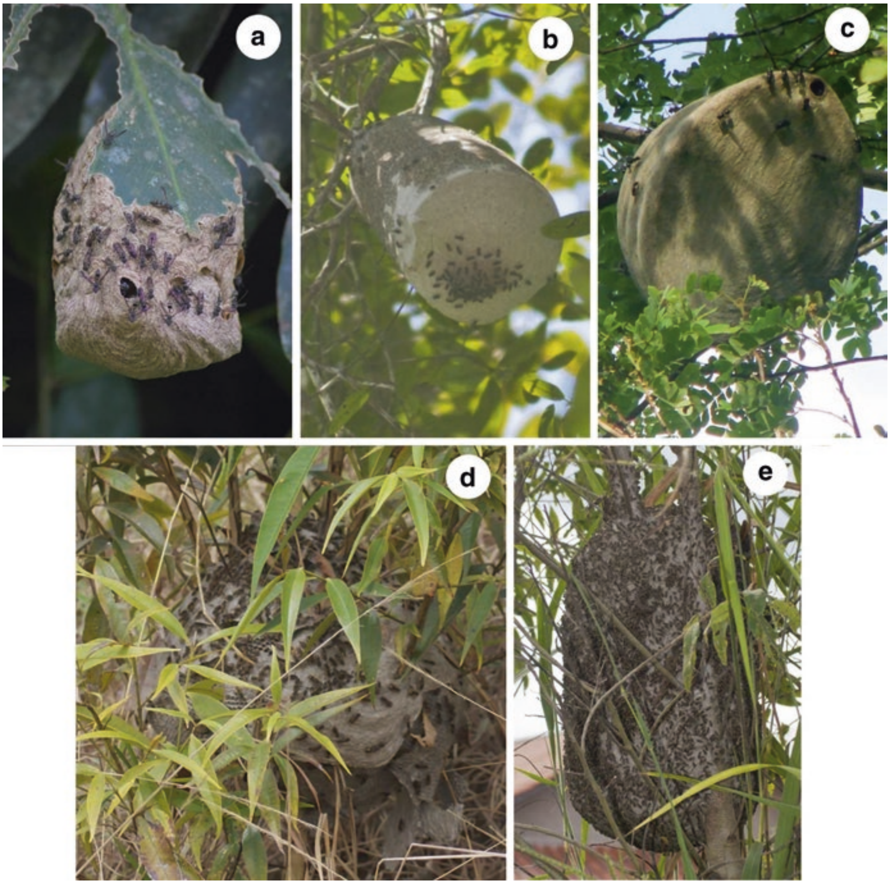

Fig. 5.8 (**a**) *Polybia platycephala* nest; (**b**) *Chartergus* nest; (**c**) *Epipona tatua* nest; (**d**) *Brachygastra lecheguana* nest; (**e**) *Protonectarina sylveirae* nest

17. Nest with a flat or conical bottom; entrance is located in the center of the nest and between the combs (Fig. 5.8b).. *Chartergus*

    - Nest with bottom projecting ever further sideways; entrance is located in the bottom projected portion of the nest (Fig. 5.8c).............................. *Epipona*

18. Nests involving tree trunks or branches with more than one layer of brood cells, small or medium in size; some species have thin and fragile envelope; other species may use clay in the envelope, making it very sturdy and well expressed, and may have irregular, ever-present auburns of varying color, usually lighter, resembling a gas canister (Fig. 5.8d). .... *Brachygastra*

    - Nests involving tree trunks or branches with more than one layer of brood cells; these are small, ever-present envelopes of varying coloration, usually darker and more resistant (Fig. 5.8e).............................. *Protonectarina*

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