



REVIEW

“Marimbondos”: a review on the neotropical swarm-founding polistines

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Abstract

Neotropical swarm-founding polistines, the Epiponini, compose a highly social tribe of vespids which displays several complex social characteristics, such as: intricate nest building, polygyny, swarm reproduction, and the absence of morphology caste discontinuities, a trait that would not be expected for a highly eusocial group. The biology of Epiponini will be reviewed, evidencing the scarcity of information for this group and also that not all social insects might fit in traditional theories for the evolution of social behavior.

Introduction

Hymenoptera is the most well-known group of social insects (Wilson 1971). Ants and bees, probably because of their economical importance, are very well studied groups, while wasps are relegated to a marginal condition. Also, ants and bees are specific monophyletic groups (single evolutionary origin), while wasps are termed as everything other than ants and bees.

Vespidae is a family which comprises highly eusocial wasps, including Vespinae and Polistinae (Carpenter 1991). Yellow jackets and hornets (Vespinae) are commonly known for their solitary nest initiation, annual colony life cycle and strikingly divergent morphological variation between castes, attributed to a necessary condition of winter survival (West-Eberhard 1969).

Polistinae, on the other hand, is much more diverse in terms of social organization. *Polistes* is the group model for several sociobiological theories developed for wasps, but it does not reflect the real diversity and complexity of this subfamily which remains poorly known regarding some genera (Noll & Wenzel 2008).

Polistinae can be classified into two behavioral groups: the plesiomorphic (ancient) condition, shared with Vespinae,

which is the independent foundation, of which *Polistes*, *Mischocyttarus* and *Ropalidiini* (partially) are representatives. On the other hand, *Ropalidiini* in part (*Polybioides* and some *Ropalidia*) and Epiponini present colony foundation by organized swarms in which female filling different roles (castes) are highly dependent upon each other (Jeanne 1991).

In contrast to well-studied social insects, such as corbiculate bees, and temperate zone wasps and ants; neotropical swarm-founding wasps present a chimera of characteristics that make them singular and hard to accommodate in current theories on the evolution of social insects (Noll & Wenzel 2008). The main characteristics are: the complex and diverse nesting habits and construction, polygyny, swarm reproduction, castes lacking a strong morphology variation, and caste flexibility which creates a window for worker reproduction or a relaxation of ovarian control (West-Eberhard 1978). It is hard to sketch an evolutionary scenario for the origin of such complex traits consistent with classical theory based on *Polistes*. It is believed that the origin of such wasps is tropical (Evans & West-Eberhard 1970; Carpenter 1993). In contrast to temperate zone areas, seasonal variation is modest and may not constrain colony development, and as a consequence these wasps face a completely different situation in which colonies are perennial and asynchronous (Jeanne 1991). As a result,



colonies are multivoltine and not univoltine (when counting production of reproductive individuals) as observed in temperate zone wasps. Another important factor that may influence strongly the evolution of these wasps is the extensive predation of their colonies by ants (Jeanne 1979), which forces relocation of colonies unpredictably. Rapid nest abandonment and swarming, nest architecture, polygyny, and castes lacking clear-cut morphological discontinuities suggest evolutionary adaptations against ant predation as well as the optimization of work (Jeanne 1975; Wenzel 1998).

In this review, some important aspects of the biology of Neotropical swarm-founding wasps will be addressed, specifically systematics, swarming process, polygyny, castes and colony cycle of these insects that depart from standard theory.

Systematics and studied groups

Because theories of evolution are necessary exercises in reconstructing ancestral states, it is important to have an understanding of the state of the systematics and phylogenetic relationships among taxa in question. The Polistinae includes four tribes: Polistini (cosmopolitan, except in New Zealand), Mischocyttarini (Argentina through the southeastern United States and the western mountains to British Columbia), Ropalidiini (Australia, Sub-Sahara Africa, the Arabian Peninsula, Eastern Tropics, China, Korea, Japan, Iran, Equatorial Africa, and India) and Epiponini (Argentina through the southwestern United States (*Polybia* and *Brachygastra* occur in Texas and Arizona)). The Polistinae exhibits greater diversity in tropical regions, especially in the Neotropics. There are 26 genera worldwide, with approximately 900 species. Epiponini is diverse, especially in the Neotropical region, with 19 genera and approximately 234 species described. The first phylogenetic hypothesis for Polistinae was proposed by Carpenter (1991) (Fig. 1A) using primarily morphological data, which presented several polytomies. A much more well-resolved tree was proposed by Wenzel and Carpenter (1994) (Fig. 1C) with the combination of morphology of adults and larvae and nest architecture (Wenzel 1993) (Fig. 1B). Pickett and Carpenter (2010) proposed a phylogeny of Vespidae based on morphological and molecular data with a different topology for some clades of Polistinae determined previously by Wenzel and Carpenter (1994) (Fig. 1D). In general, the clade formed by *Synoeca*, *Clypearia*, *Metapolybia* and *Asteloeca* is placed quite differently, sometimes appearing as sister to the modular, enclosed, stacked brood comes nest building genera, such as *Polybia*, *Protonectarina*, *Epipona*, and sometimes as a component nested within this clade. In any case, irrespective of internal differences in the clades, it is clear that the Epiponini composes a monophyletic group.

The systematics for each genera of Epiponini is a very recent subject. Andena et al. (2007b) published the first phylogeny of the genus *Angiopolybia* using morphological data.

The other genera that have been subject to cladistic analyses were: *Pseudopolybia* (Andena et al. 2007a), *Angiopolybia* (Andena et al. 2007b), *Apoica* (Pickett & Wenzel 2007), *Synoeca* (Andena et al. 2009a), *Epipona* (Andena et al. 2009b), *Charterginus* (Andena et al. 2009c), and *Brachygastra* (Andena & Carpenter 2012). Larger genera still need review, such as *Agelaia* and *Polybia*, even though it is already in progress (Carpenter JM pers. com.).

Studies on polistines do not cover the diversity of genera and species well. A previous survey on the number of citations to all social wasps from the subfamily Polistinae showed the vast majority of the papers was written on *Polistes* and only on few species (Wenzel & Noll 2006). For the Epiponini, this scenario is not different, with a single genus (*Polybia*) representing the vast majority of studies (Wenzel & Noll 2006). Such restriction is problematic because using a few species as explanatory models may compromise the application of proposed theories for the whole group (see the section Caste for more details). In this regard, generalizations should be viewed with caution when they are based on a very small subset of the diversity of species.

Swarming

Highly eusocial insects that initiate their colonies by swarms migrate as a cohort of queen(s) and workers from the old nesting site to a new one. Brood predation by ants (Bouwma et al. 2007), parasites in the brood (West-Eberhard 1982), vertebrate attacks on the nest and storm damage (Richards 1978) are causes for absconding swarms and may happen at any time. In contrast, reproductive swarms (Forsyth 1978; West-Eberhard 1982) occur when the colonies are producing gynes (young queens and males) (Ezenwa et al 1998).

The coordination of a swarm to a new place requires some sort of communication, which is apparently mediated by pheromones (Jeanne 1980). In the Epiponini, it was observed that pheromones are released in the air to coordinate the swarm (Hunt et al. 1995; Howard et al. 2002; Mateus 2011), in other cases the workers rub their abdomen in leaves or substrates located between the old and new nest sites, as well as in the new nest site (Mateus 2011). Other colony members land on these marked points, apparently looking for new points along the route to the new nest site (Mateus 2011). Jeanne (1981) experimentally demonstrated that the secretion produced by Richards' gland, located at the fifth sternal metasomal segment, is used to mark the trail to the new nest in *Polybia sericea*. In *Parachartergus fraternus*, Mateus (2011) suggests that venom is used to mark the new nest site and the trail markings. In any case, it is still unknown how workers that mark the trail inform the rest of the colony about the new nest location (Sonnentag & Jeanne 2009). Scout wasps have to induce the rest of the colony to relocate to the new spot and guide them (Sonnentag & Jeanne 2009; Mateus 2011). It was proposed that mechanical signal, such as "bumping" be-

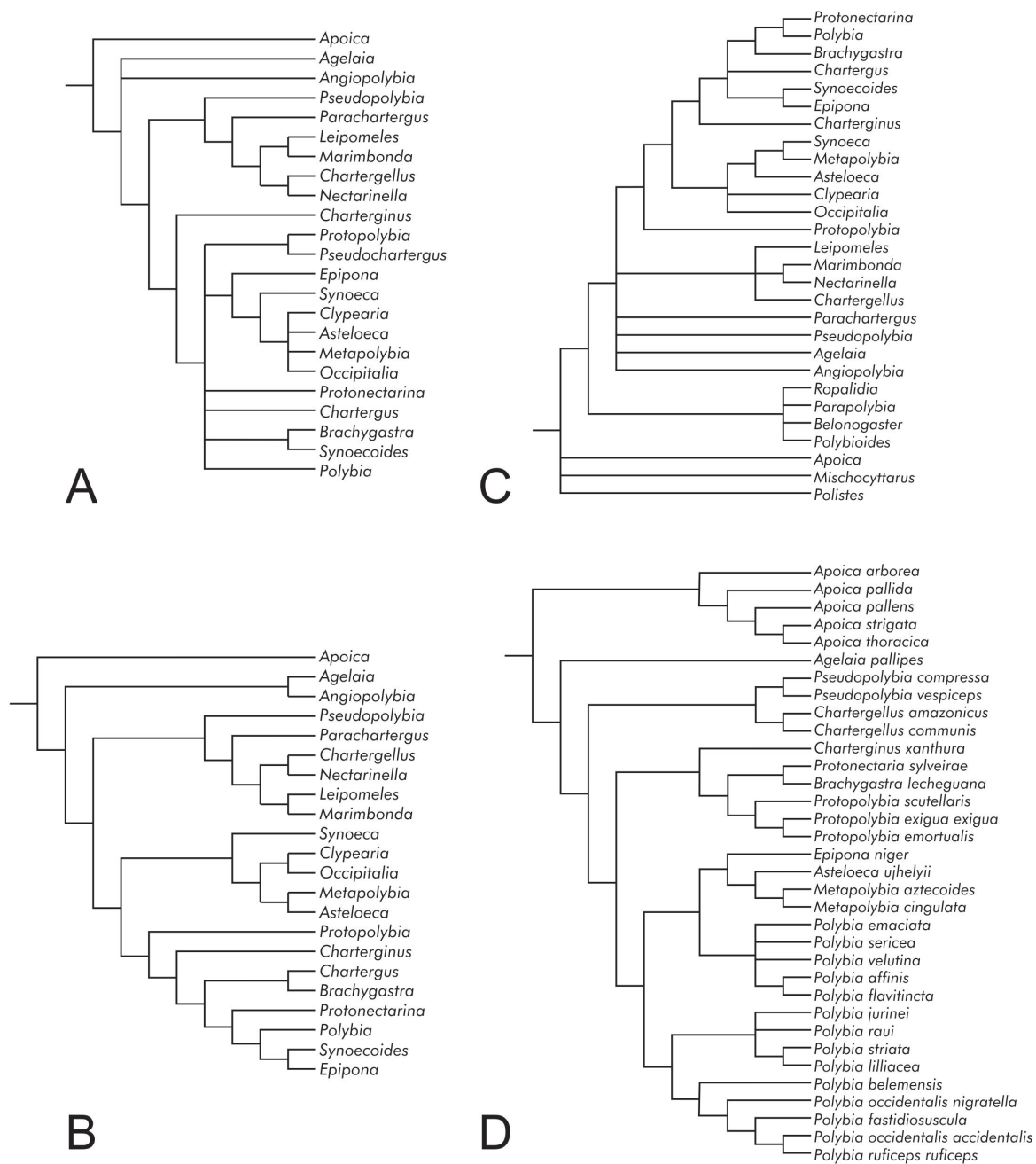


Figure 1 - Phylogenetic trees for the Epiponini based on: A - Carpenter (1991), B- Wenzel & Carpenter (1994), C- Wenzel (1993) and D- Pickett & Carpenter (2010).

haviors in which a female bumps her head against idle wasps are responsible for activation and migration to the new spot (Sonnentag & Jeanne 2009; Mateus 2011). A flight around the nest has been suggested by West-Eberhard (1982) as a stimulus to idle wasps to relocate as a swarm. A clear signal that a swarm is starting is the buzz running behavior in epiponines and it is triggered by older workers (Naumann 1970; Forsyth 1978; West-Eberhard 1982; Mateus 2011). Scout wasps are responsible for choosing the new nest site that will be suitable for the colony survival, depending on the type of substrate, height, solar incidence and, probably, food and water availability (Mateus 2011).

Polygyny

It is not hard to imagine that the origin of polygyny (presence of several egg-layers coexisting in a given nest) was molded by the same factors as swarming and nest design, for example, ant predation (Jeanne 1979). Considering that the loss of a single queen would be fatal, the origin of several queens would be advantageous for the colony in terms of survival. Among polistines, polygyny appeared three times: *Polybioides*, *Ropalidia* and Epiponini (Carpenter 1991). Epiponines are characterized as permanently polygynous or primarily polygynous with variation (decrease) in queen

number during the colony cycle, sometimes resulting in monogyny (West-Eberhard 1978; Richards 1978; Jeanne, 1991). The presence of polygyny in the basal clades of this tribe indicates that the common ancestor already presented long-term polygyny (Carpenter 1991).

The presence of several females laying eggs could represent a problem in the interpretation of the conflict of interests that usually occurs in social insect colonies. Even though relatedness is low in independent founding *Polistes* (Pickett et al., 2006), an additional problem arises in the Epiponini: because reproduction would be divided among several females, kinship rates would be even lower than what it is found in *Polistes*, and would not be high enough to justify the sterility of workers. However, relatedness studies in Epiponini colonies indicate that kinship is relatively high (Queller et al. 1988, 1993; Hughes et al. 1993). These findings are well understood by West-Eberhard (1978, 1981), which showed that after a swarm, colonies of *Metapolybia aztecoides* start with several queens and workers, and as the colony develops some queens disappear or adopt a worker role. As the colony develops further, the number of queens reduces until one or a few queens remain at last. Daughter queens and swarms occur predominantly after the establishment of monogyny or oligogyny, restricting the production of gynes to only a few individuals. Such a pattern is observed in several other species, such as in *Polybia occidentalis* (West-Eberhard 1978; Queller et al. 1993), *Parachartergus colobopterus* (Strassmann et al. 1991), *Polybia emaciata* (Strassmann et al. 1992), *Protopolybia exigua* (Gastreich et al. 1993), *Brachygastra mellifica* (Hastings et al. 1998), and *Agelaia multipicta* (West-Eberhard 1990). In this regard, the *cyclical oligogyny* was coined to define the decrease in the number of queens, with the production of gynes only during the period with fewer queens, increasing the kinship among daughter-queens, as predicted by the *kinselection* theory (Hamilton 1964 a, b; 1972). Another important point for the maintenance of high rates of relationship is that queens in epiponines are singly mated (Goodnight et al. 1996). Also, the possibility that epiponines may simply be inflexible in terms of losing sociality should not be discarded.

Castes

Size differences between castes appeared independently in various taxa and a phylogenetic interpretation shows several distinctly different syndromes, representing a picture more complex than formerly thought (reviewed in Noll et al. 2004; Noll & Wenzel 2008). Castes in this tribe challenge standard definitions. As expected for highly eusocial insects, pre-imaginal caste determination has been reported in at least five genera (Noll et al. 2004). However, in at least six genera (Noll et al. 2004), reproductive females resemble non-reproductives in terms of morphology, and castes also lack physiological discontinuities. In these cases, castes are flexible and determined by disputes among adults rather than by larval ma-

nipulation (West-Eberhard 1981; Mateus et al. 2004; Noll & Wenzel 2008). Also, in several colonies the absence of workers' sterility (termed "intermediates" by Richards & Richards 1951) has been identified. Their role is debatable, because they are considered as trophic egg or male producers (Richards 1971) or young queens (Forsyth 1978; West-Eberhard 1978; Gastreich et al. 1993). The level of ovarian development is inversely related to the number of queens, i.e. in the presence of a few females intermediates present more developed ovaries and vice versa (Richards 1971; West-Eberhard 1978). Also, they are absent in several other taxa (reviewed in Noll et al. 2004). Anyway, intermediates are part of a more complex scenario related to the evolution of castes and will be more detailed below.

The complex scenario of low morphological differentiation and non-sterility of workers is caused by the fact that pre-imaginal determination (Wheeler 1991) of castes, highly widespread in social insects, is not a plesiomorphic condition for all Epiponini. Instead, caste flexibility (West-Eberhard 1981) is probably plesiomorphic for these wasps. The classical theory for the origin of sociality in wasps is the polygynous family hypothesis (West-Eberhard 1978) in which *Polistes* would be the model. However, as pointed out by Noll and Wenzel (2008) this reasoning is not so straightforward because in primitive social vespids females compete for reproduction, restraining these societies to solitary or short-term monogynic conditions. That is the opposite of what is seen in the Epiponini, in which queens are more tolerant (Simões 1977; Naumann 1970; Herman et al. 2000). In this case, queens of epiponines seem similar to subordinates of *Polistes* that are tolerant of other's reproduction than the dominant, intolerant, monogynic queens of *Polistes* (Fig. 2).

If queens in epiponines are loose in terms of controlling reproduction, workers are not. Workers test and remove queens from the colony (West-Eberhard 1978, 1981; Herman et al. 2000, Platt et al. 2004) which seems to be important in keeping levels of genetic relatedness high enough to achieve "workers interests" (Strassmann 1997, 1998). Thus, the main difference between short-term monogyny and polygyny is that in the former, queen-policing is more prevalent and in the latter, worker-policing is (Platt et al. 2004). Figure 2 shows how eliminating the intolerant monogynic egg-layer and replacing her with her several tolerant subordinates could achieve the first step toward polygyny in the Epiponini.

The origin of highly tolerant egglayers can have some consequences. The first consequence is that many females would aspire for some chance of reproduction that would lead to caste totipotency (Strassmann et al. 2002). Thus, it would be expected to find ovary development widespread in members of polygynous societies, and, in fact, several epiponines have laying workers (Noll et al. 2004). Several basal genera of Epiponini fit in the scenario proposed for polygynous groups (West-Eberhard 1978, 1981) that is, caste flexibility due to the absence of morphological differences between castes and the

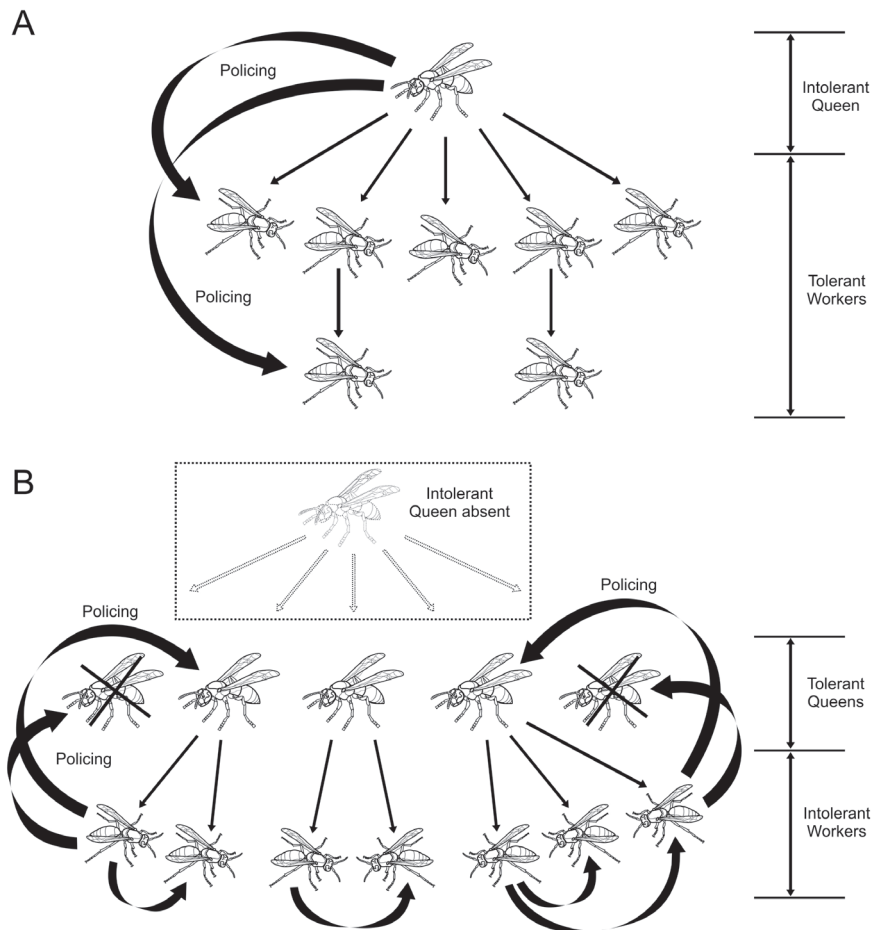


Figure 2. A model for the evolution of epiponine polygyny. A. Ancient (plesiomorphic) society, as seen in short-term, monogynic Polistinae, in which the dominant female is intolerant of reproduction by other females. The egg-layer performs policing tasks, whereas workers are tolerant of reproduction by others. Occasionally, workers do reproduce, perhaps as replacement reproductives. B. Epiponine polygyny, with no intolerant primary egg-layer. Rather, reproduction is performed by several tolerant females. The role of policing is adopted by workers, who suppress each other, and select among reproductives as well. This system is not what would result from merely adding several short-term queens together.

extensive ovarian activation in all females, which is primarily found in the genera *Angiopolybia*, *Pseudopolybia*, *Parachartergus*, *Chartergellus* and *Leipomelles* (Noll et al., 2004). Thus, the distribution of this characteristic is consistent with the presence of laying workers being, in fact, a primitive state rather than derived.

In contrast to the intuitive pattern of complex societies is that obligatorily two morphs, the queen and the worker, epiponines lack such a morphological skew, and so may have been thought to be less complex than species with morphological castes. However, epiponines show a unique set of advanced characteristics, such as that they do not maintain their reproductive position by aggression, present marked refined communication, show age polyethism, and display intricate nest construction (Jeanne 1991), all indicative of complexity. In fact, Jeanne (2003) suggested another definition that supports self-organization instead of morphological skew patterns. If self-organization is prevalent, there is no need to have an evolution of two morphs in some complex societies, as in the Epiponini. In fact, the egg-layer's role is a plesiomorphic condition, once all solitary Hymenoptera also lay eggs. It is possible that, at least in some societies, the evolution of complexity would drive selection favoring totipotent individuals that may develop complex tasks, related to worker castes, but keeping their reproductive potential. In fact, as suggested by

West-Eberhard (2003), the origin of morphologically distinct queens is much more a condition of colony stability and the level of defense rather than an indicative of social complexity. From this perspective, the complex societies of Epiponini may have passed through a phase of monomorphic, totipotent females (where egg laying has no relationship to dominance of *Polistes* queens) to various systems of morphologically distinct queens in different lineages. Noll et al. (2004) show that such a theory plots perfectly onto a cladogram of genera of Epiponini.

Colony cycle

The colony cycle in the swarm-founding polistine wasps is poorly known. As defined by Jeanne (1991) colony cycle "is the period of development lasting from the end of one reproductive episode to the end of the next" and, apparently, the tropical environment in which the Epiponini thrive has rendered colony cycles much more plastic (asynchronous) than those under the temperate climates (synchronic) (Jeanne 1991). The onset of nest foundation, for instance, which is limited to the start of the favorable season in the temperate zone species, shows a wide distributional pattern scattered along several months in the neotropics. In the rainy season, the population increases and a reproductive swarm

may occur (Jeanne 1991). An exception is in *Agelaisia vicina* (Oliveira et al. 2010) which shows an increase in population during the dry season. Interestingly, in new colonies or swarms, producing queens may not necessarily be linked to the production of swarms. In fact, in *Parachartergus colobopterus* (Strassmann et al. 1998), the queens present in swarms were rarely mothers of the workers of those swarms. It is suggested that the queens who join the swarms were losers in the race for dominance in original colonies. Because the production of queens and new colonies are not connected, the interests of workers in the production of males and queens prevail. As discussed above, castes develop in different ways for epiponines and the colony cycle certainly influences some of its aspects. In some species studied so far, morphological discontinuities might increase through the progression of the colony cycle (Noll & Zucchi 2000, 2002). Such a phenomenon has also been reported in some Ropalidiini (Fukuda et al. 2003 a, b). Combining morphological differences between castes, physiological potential of the females to develop ovaries and colony cycle, five different syndromes have been proposed (Noll & Zucchi 2000, 2002). In two syndromes, morphological differences between castes are absent and workers present a wide range of ovarian development in one case and in the other workers are physiologically distinct (sterile). In other two syndromes there are morphological and physiological discontinuities between castes, which are subjected to variation according to colony cycle, with queens larger than workers. Initially, queens have a variable size, but at the end of the cycle they are among the larger individuals (Noll & Zucchi 2000, 2002). These two syndromes differ from each other by the presence of non-inseminated laying females that appear always (in one case) or in some phases of the colony cycle (other syndrome). In the final syndrome, it is more similar to be basic pattern of social insects, in which castes are highly distinct based on both morphology and physiology.

Concluding remarks

This review demonstrates that the diversity and complexity that may be found in Epiponini cannot be easily explained by conventional theory extending a *Polistes*-like system, but seem instead to require a new perspective that separates egg-laying from dominance, and reproduction from regulation of work. From the other side, the scarcity of studies (and scholars) on this subject delays considerably the advance on the knowledge of this group. Hopefully, this review may serve as trigger to inspire young students to choose this group as their own.

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