

Caste in the swarming wasps: ‘queenless’ societies in highly social insects

FERNANDO B. NOLL^{1*} and JOHN W. WENZEL²

¹*Departamento de Zoologia e Botânica; Instituto de Biociências, Letras e Ciências Exatas, UNESP; Rua Cristóvão Colombo, 2265; 15054-000, São José do Rio Preto, SP, Brazil*

²*Department of Entomology, The Ohio State University, 1315 Kinnear Road, Columbus, Ohio, USA*

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Morphometric data for 30 species of swarming wasps (Vespidae: Polistinae: Epiponini) are presented, representing all currently recognized genera. Data are coded according to whether females that were shown by dissection to be egglayers are larger, similar, or smaller for each dimension than non-egglayers. These data are analysed in a phylogenetic framework with primitively social *Polistes* and *Mischocyttarus* as outgroups. Representative measurements are illustrated to show that most genera of Epiponini appear to have ancestry in a lineage that has no queen caste comparable with either the primitively social outgroups, or the more derived species of the tribe. This analysis indicates that a conspiracy of workers that operates without a queen characterizes the societies of many Epiponini, or their recent ancestors. © 2008 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2008, **93**, 509–522.

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INTRODUCTION

The origin of morphological variation that establishes social role (caste) is one of the definitive elements of the most sophisticated insect societies. The pinnacle of morphological caste is probably found in ants (Wilson, 1971), but the origin of morphological caste is usually studied in other groups. The basic distinction is between individuals that reproduce (customarily called ‘queens’) and those that do not (‘workers’). Social wasps present a challenge in this regard because characterization of queen and worker may be either indistinct or obvious. Among the primitively eusocial genera, such as *Polistes* and *Mischocyttarus*, animals representing a continuum of size compete directly to establish reproductive monopoly, based on dominance maintained by aggression (Fig. 1). At the other extreme, distinct queen/worker dimorphism is known to have evolved several times in social wasps: in Vespinae (Blackith, 1958), in Indoaustral *Ropa-*

lidia (Yamane, Kojima & Yamane, 1983), and in distantly related Malagasy *Ropalidia* (Wenzel, 1992). There is also a suggestion that reproductive monopoly has been lost in some lineages, such as palaeotropical *Ropalidia* where females express nearly solitary habit (Wenzel, 1987; Kojima *et al.*, 2002). Thus, the evolution of reproductive division of labour in social wasps is complex, and a general theory of caste in wasps is vague, to date. For example, Bourke’s (1999) excellent review of caste in social insects comments little on any general lesson learned from wasps.

The enigmatic swarming wasps of South America (the tribe Epiponini, formerly Polybiini) represent a particular difficulty with respect to interpreting the evolution of caste. Richards (1978) comments ‘In general the castes are not distinguished in the Polistinae, at any rate externally. . . In the Polybiini there are all stages from a morphologically very distinct queen (*Stelopolybia flavipennis*, *Stelopolybia areata*, *Protonectarina*) to forms such as *Parachartergus fraternus* or *Angiopolybia pallens* in which externally no even statistically distinct queen exists.’ One thing

*Corresponding author. E-mail: noll@ibilce.unesp.br

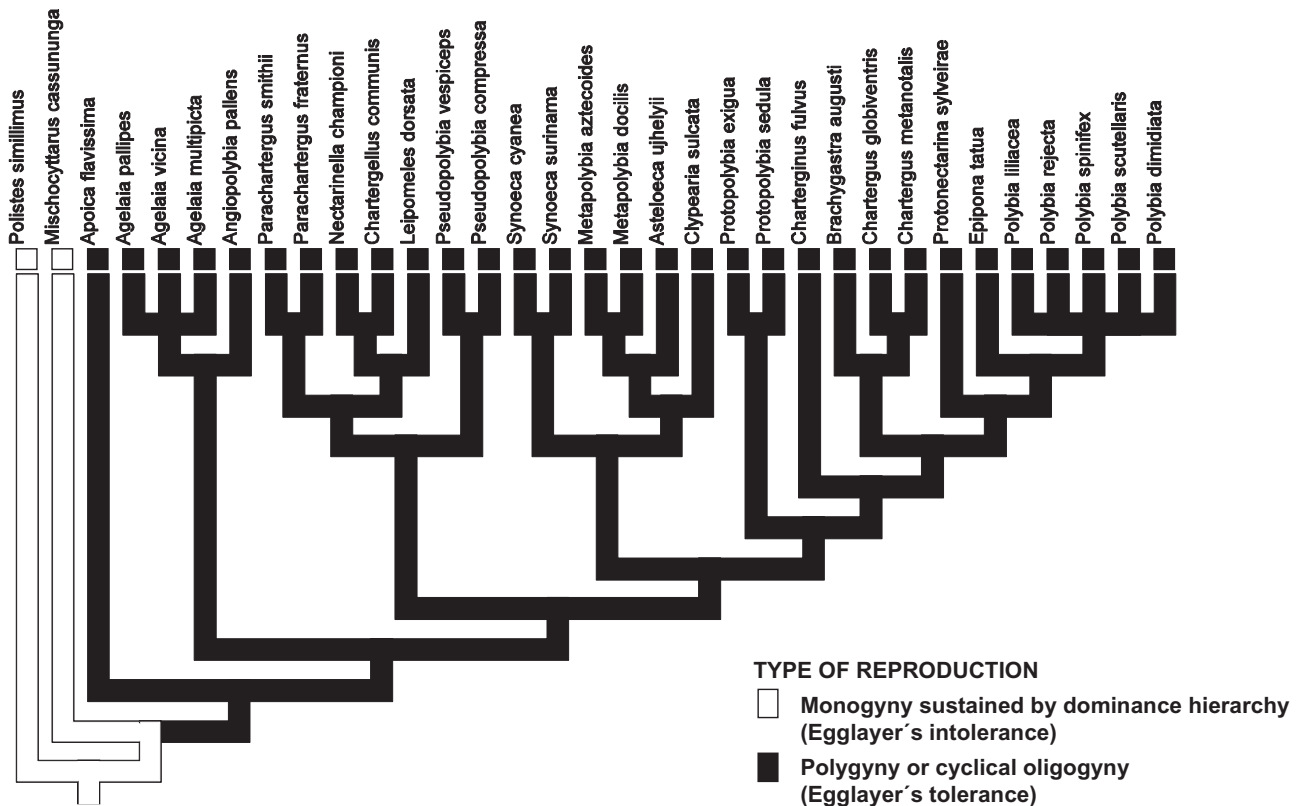


Figure 1. Phylogenetic hypothesis of the evolution of caste related to reproductive monopoly, maintained by the physical aggression of the egglayer, plotted on the tree presented by Wenzel & Carpenter (1994), with some genera expanded to denote the species analysed here.

these swarming wasps have in common is that all species (as far as is known) rely on a form of polygyny, in which many females lay eggs, tolerating each other, and these egglayers are tested and regulated in some manner by the sterile workers (Figs 1, 2). Species of swarming wasps communicate new sites with chemical trails, and an organized group starts a new nest (Jeanne, 1991). Many egglayers accompany the swarm (sometimes males also), and these gradually decrease in number (termed 'cyclical oligogyny'; West-Eberhard, 1978) until the next swarm, when the new colony begins again with many egglayers that are not aggressive towards each other. Careful studies show that many non-egglayers are reproductively potent, and can quickly become egglayers (Strassmann, Sullender & Queller, 2002). These females are considered to be the progenitors of females that emerge later, and are not comparable with the workers who lay trophic eggs or male eggs in other species. Consistent with having many mothers, degrees of relatedness are typically lower among colony mates in Epiponini than in *Polistes* (Queller, Strassmann & Hughes, 1988) until the number of queens is reduced (Strassmann *et al.*, 1991). Queen

reduction is achieved, at least partly, by workers challenging queens and eliminating those they find undesirable (West-Eberhard, 1978). Thus, queens are permissive of reproduction by others, and it is the workers that police the nest, suppressing certain reproductives (Fig. 2).

In some species of Epiponini, the distinction between reproductive and nonreproductive individuals may be impossible to make without dissection because there are no known external morphological correlates of reproductive status (Fig. 3). In other species, queens tend to be larger than workers, and intermediates (females with ambiguous ovarian status, containing usually one or two eggs, but with spermatheca empty, indicating that the female is not fertilized) may or may not appear periodically in association with swarming during the colony cycle (Fig. 4) In still other species, shape differences do exist, generally with reproductives having proportionally smaller heads and larger abdomens, a syndrome that is inferred to be adaptive according to the social role of the individuals (Jeanne & Fagen, 1974) (Fig. 5). To date, the research on this problem has been performed in small pieces, usually one species at

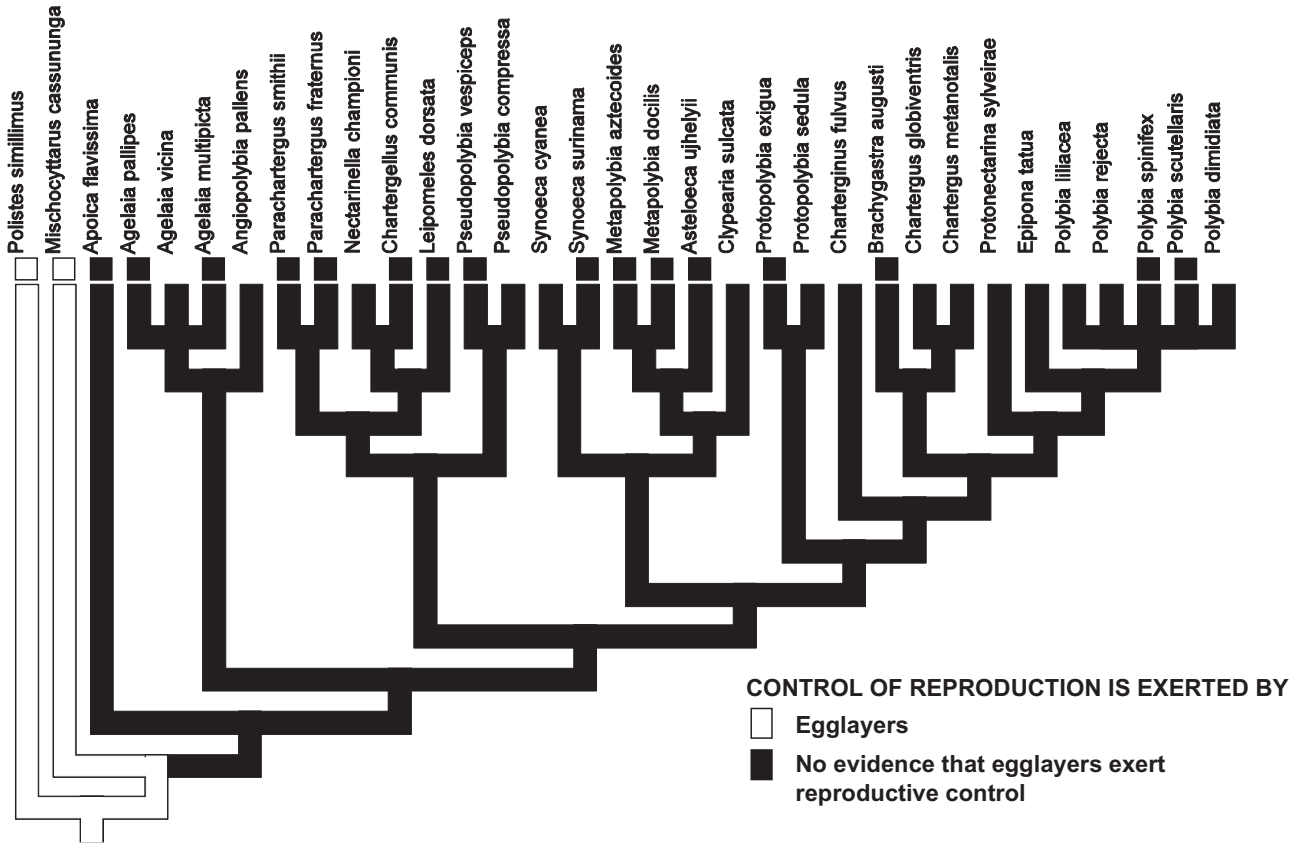


Figure 2. Phylogenetic hypothesis of the evolution of caste related to the control of reproduction, plotted on the tree presented by Wenzel & Carpenter (1994). Data sources: Pickett & Wenzel (2007) for *Apoica flavissima*; Simões (1977) for *Agelaiia pallipes*, *Agelaiia multipicta*, and *Protopolybia exigua*; Mateus (2005) for *Parachartergus fraternus*, *Parachartergus smithii*, *Chartergellus communis*, and *Pseudopolybia vespiceps*; West-Eberhard (1978, 1982) for *Metapolybia aztecoides* and *Synoeca surinama*, respectively; Baio *et al.* (2003) for *Metapolybia docilis* and *Brachygastra augusti*; Nascimento, Nascimento & Zucchi (2004) for *Asteloea ujhelyi*; Strassmann *et al.* (1992) for *Polybia spinifex* (data come from *Polybia emaciata*, from the same subgenus *Furnariana*); Queller *et al.* (1993) for *Polybia scutellaris* (data come from *Polybia occidentalis* from the same subgenus *Myrapetra*). Black squares denote the species in which only nonreproductives have been observed challenging egg-layers, and there is no evidence that egg-layers exert reproductive control on each other.

a time, which makes general patterns difficult to distinguish.

In a previous study (Noll, Wenzel & Zucchi, 2004), we offered enough data to analyse the entire Epiponini, using representatives of every genus currently recognized. Although some measurements of other species are available, Noll *et al.* (2004) represents by far the largest compilation of comparable data from mature colonies. Using these data, two phylogenetic comparisons were performed. In one, the individual differences (or lack of differences) between reproductives and nonreproductives were combined with the morphobehavioural matrix used in the most recent cladistic study of all Epiponini (Wenzel & Carpenter, 1994). The resulting analysis demonstrated that caste differences fall into several syndromes that are easily

interpreted phylogenetically. The sequence of transitions from one syndrome to another matches those proposed by Wheeler (1991) for ants, except for the presence of one syndrome not anticipated by Wheeler. Although Noll *et al.* (2004) demonstrated greater continuity in the morphological evolution of caste than was previously appreciated, there was still no discussion of the reorganization of behavioural patterns associated with the dramatic evolution of the swarming habit in wasps.

One impediment to understanding the evolution of reproduction in Epiponini is that efforts to explain ‘queen’ and ‘worker’ presuppose the definition of caste, and of the society itself. Because early studies recognized that honey bees and army ants define one extreme in the spectrum of colony size and order,

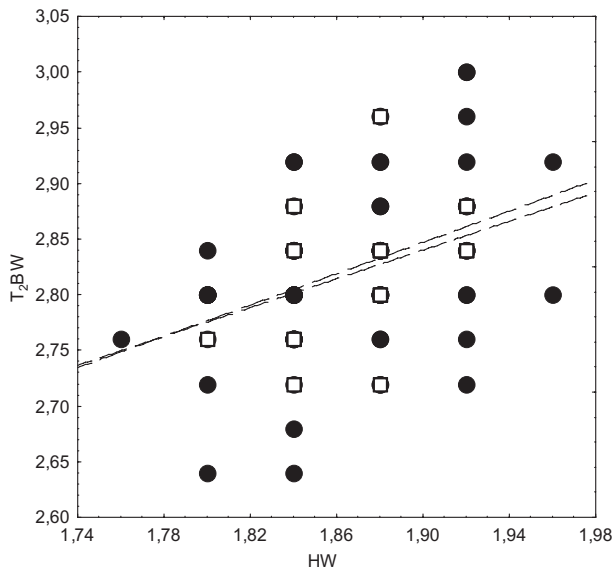


Figure 3. Morphometric data from several epiponines (*Metapolybia aztecoides*, *Angiopolybia pallens*, *Clypearia sulcata*, *Synoeca surinama*, *Leipomeles dorsata*, *Nectarinella championi*, and *Asteloecca ujhelyii*) without obvious morphological distinction (see Noll *et al.*, 2004 for more details). The width of head (HW) is plotted against the basal width of the second tergum of the apparent abdomen (T_2BW): □, egglayers; ●, non-egglayers.

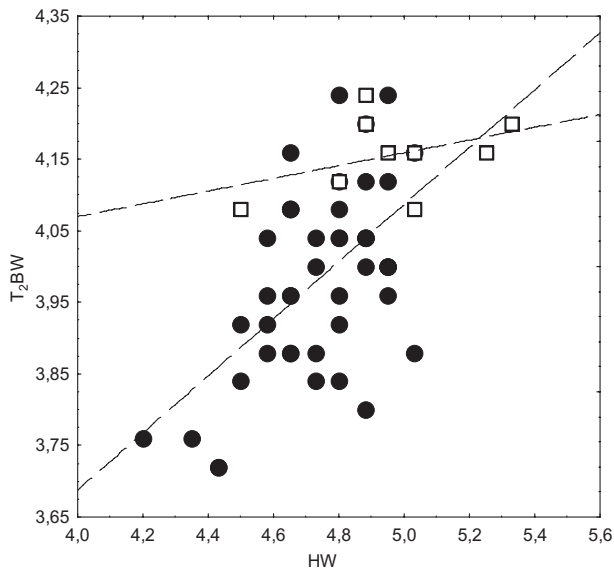


Figure 4. Morphometric data as in Figure 3, but for species in which egglayers are larger than non-egglayers (*Epiponina tatusa*, *Polybia liliacea*, *Polybia rejecta*, *Polybia spinifex*, *Chartergus metanotalis*, and *Charterginus fulvus*).

many authors use terminology that requires (by design or inadvertently) that reproduction be completely monopolized, as it is in honey bees and army ants, for an individual to be 'queen' and for a species

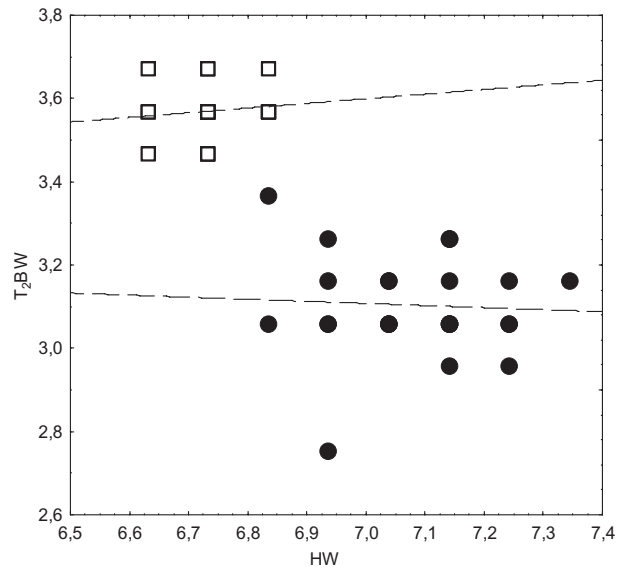


Figure 5. Morphometric data as in Figure 3, but for species in which egglayers are larger than non-egglayers in the abdomen, but are smaller in the head (*Apoica flavissima*, *Agelaia vicina*, *Agelaia pallipes*, and *Agelaia multipicta*).

to be 'highly social' (for a discussion of such terminology, see Costa & Fitzgerald, 1996). Yet, this classical perspective reduces all the diversity of sociobiology to the single question of 'who laid the eggs?' If laying eggs is the sole criterion for being queen, then there is no additional information provided by using the word 'queen.' Of course, sociobiologically, a queen is supposed to be something very much more than just a female who lays eggs, which is why our community has embraced terms such as 'laying worker': some individuals can lay eggs, but nonetheless are not queens. Similarly, if we say that polygynous Epiponini are not highly social because they are polygynous, then we deny the importance of all the other features of their life history that are just like those of honey bees: they are obliged to live in large colonies; they raise offspring exclusively by alloparental care; they reproduce these colonies by coordinated movement of swarms; they mobilize labour of hundreds or thousands of individuals to perform colony-level duties, such as nest construction; they use division of labour with task specialists to perform such feats; they socialize all resources; many of them are suicidal in defense of the colony. Thus, for either caste or society, it makes sense that measurement and description come first, and take priority over labels derived from studies of other systems (Costa & Fitzgerald, 1996). The challenge is to discover which elements of morphology and behaviour are associated with egg laying in different species, and to establish

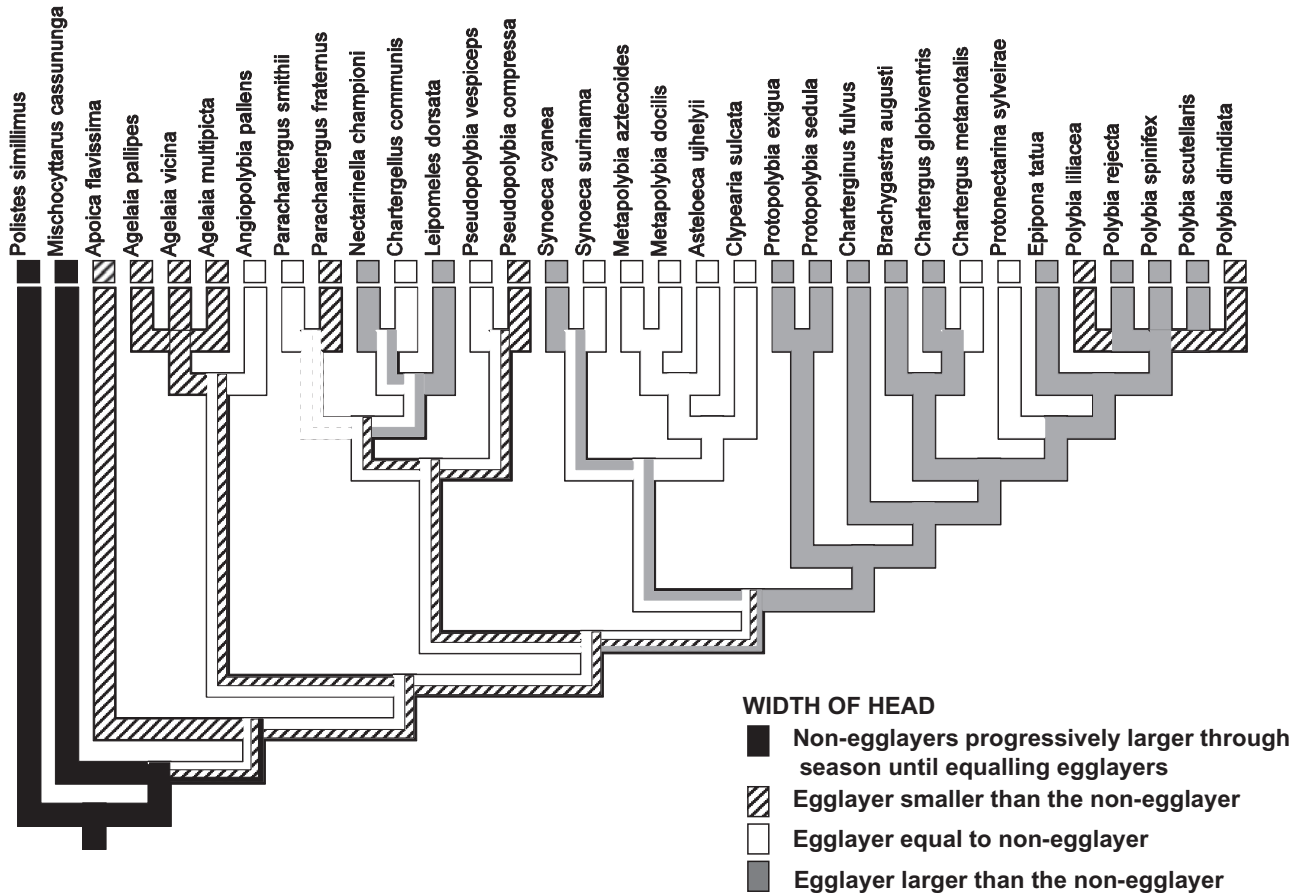


Figure 6. Phylogenetic hypothesis of the evolution of caste related to the width of the head, plotted on the tree presented by Wenzel & Carpenter (1994).

which features support meaningful definitions of queen and worker. To this end, we present morphometric data in a phylogenetic context, and integrate these with behavioural roles regarding the control of egg laying, and provide a simple solution to explain the curious phenomenon of polygynic swarms in Epiponini.

MATERIAL AND METHODS

Caste-differences data from seven body parts plus ovarian development were coded from 29 previously studied species of Epiponini, most of them present in Noll *et al.* (2004) except for the following species: *Parachartergus smithii* (Mateus, Noll & Zucchi, 1997), *Parachartergus fraternus* (Mateus, Noll & Zucchi, 2005), *Pseudopolybia vespiceps* (Shima *et al.*, 1998) and *Pseudopolybia compressa* (F. B. Noll, unpubl. data), *Chartergellus communis* (Mateus, Noll & Zucchi, 1999), *Brachygastra lecheguana* (Shima, Noll & Zucchi, 2000), *Synoeca cyanea* (Noda, Shima &

Noll, 2003), *Metapolybia docilis* (Baio, Noll & Zucchi, 2003), *Agelaia pallipes* and *Agelaia multipicta* (Noll, Simões & Zucchi, 1997); *Agelaia vicina* (Baio *et al.*, 1998), *Apoica flavissima* (Noll & Zucchi, 2002), *Chartergus globiventris* (Noll & Zucchi, 2002), *Prontonectarina sylveirae* (Shima, Noll & Zucchi, 2003), *Protopolybia exigua* (Noll & Zucchi, 2002); *Polybia scutellaris* (Noll & Zucchi, 2000). Given that at least one hundred females for each colony were sampled, our data corresponds to approximately 3200 females or 22 400 measurements. Terms queen and worker were not used, in order to avoid any unintended implication, rather females were classified upon dissection as egglayers (ovaries containing many mature or nearly mature eggs, spermatheca full), intermediates (one or few eggs, spermatheca empty), or non-eggayers (no ovarian development, spermatheca empty). Used as character data, comparisons between females of different ovarian status were plotted on the cladogram of Wenzel & Carpenter (1994), which is the current working hypothesis for the phylogeny of this group.

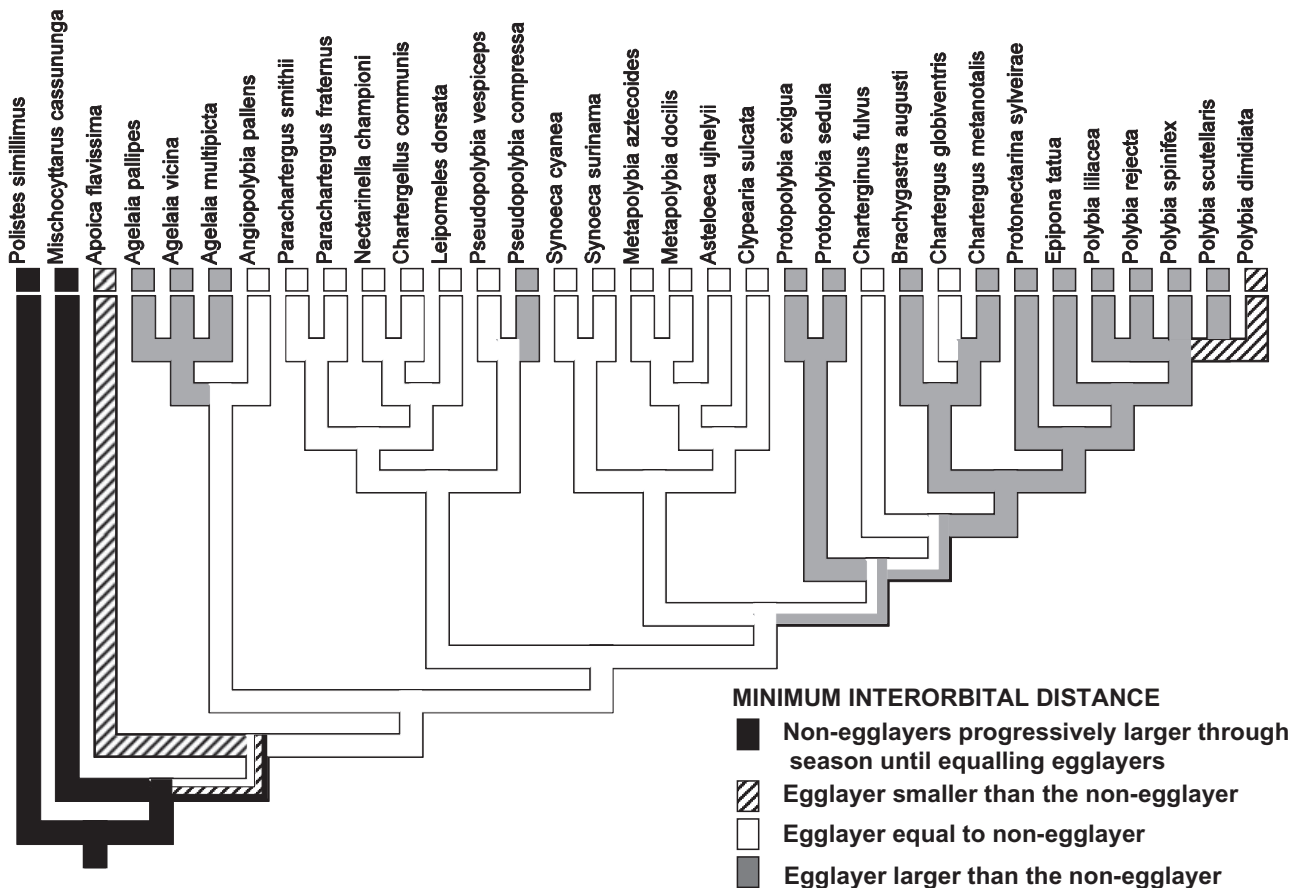


Figure 7. Phylogenetic hypothesis of the evolution of caste related to the minimum interorbital distance, plotted on the tree presented by Wenzel & Carpenter (1994).

RESULTS

CHARACTER PLOTTING

Polistes has dominant, egg-laying queens that are larger than subordinate workers, as does *Mischocyttarus*. Several studies show that when workers start feeding the queen's larvae they tend to be bigger, and that the size difference tends to be not significant (Dani, 1994). Hence, the progressive increase in body size, culminating in equality among females, is the condition at the root of the tree. No such progressive increase in body size is apparent in Epiponini, as far as is known today. Furthermore, a very different syndrome (egg-layers smaller in all measurements) is found in the most apical species shown, *Polybia dimidiata*.

Evolutionary change from the *Polistes* condition varies according to character and species. Representative measurements of head, thorax, abdomen, and wing are plotted here. In all measurements there are independent evolutionary steps from 'equal' to both 'egg-layer larger' and 'egg-layer smaller'. Head width presents an ambiguous optimization. One optimiza-

tion keeps 'equal' as the primitive condition in the component delimited by *Angiopolybia* and *Clypearia* ('component' meaning these terminals, including those that appear between them graphically in these illustrations, and not necessarily 'clades'), with many derivations of each of the other states more apically in the tree (Fig. 6). Minimum interorbital distance shows 'egg-layer smaller' in *Apoica*. 'Egg-layer equal to non-egg-layer' is the primitive condition in the component delimited by *Angiopolybia* and *Clypearia*. 'Egg-layer larger' is found in *Agelaima*, *P. compressa*, and in the component *Protopolybia*–*Polybia* (with reversion to 'same' in *Charterginus fulvus* and *C. globiventris*, and to 'egg-layer smaller' in *P. dimidiata*) (Fig. 7). Thorax size (width of mesoscutum) has ambiguous optimization. One optimization shows that 'egg-layer equal to non-egg-layer' is the primitive condition in the component delimited by *Angiopolybia* and *Charterginus*, with 'egg-layer larger' occurring several times, and for the entire component *Brachygastra*–*Polybia* (except *P. dimidiata*) (Fig. 8). Alitrunk length shows 'egg-layer equal to non-egg-layer' is the primitive condition in the component delimited by *Angiopolybia*

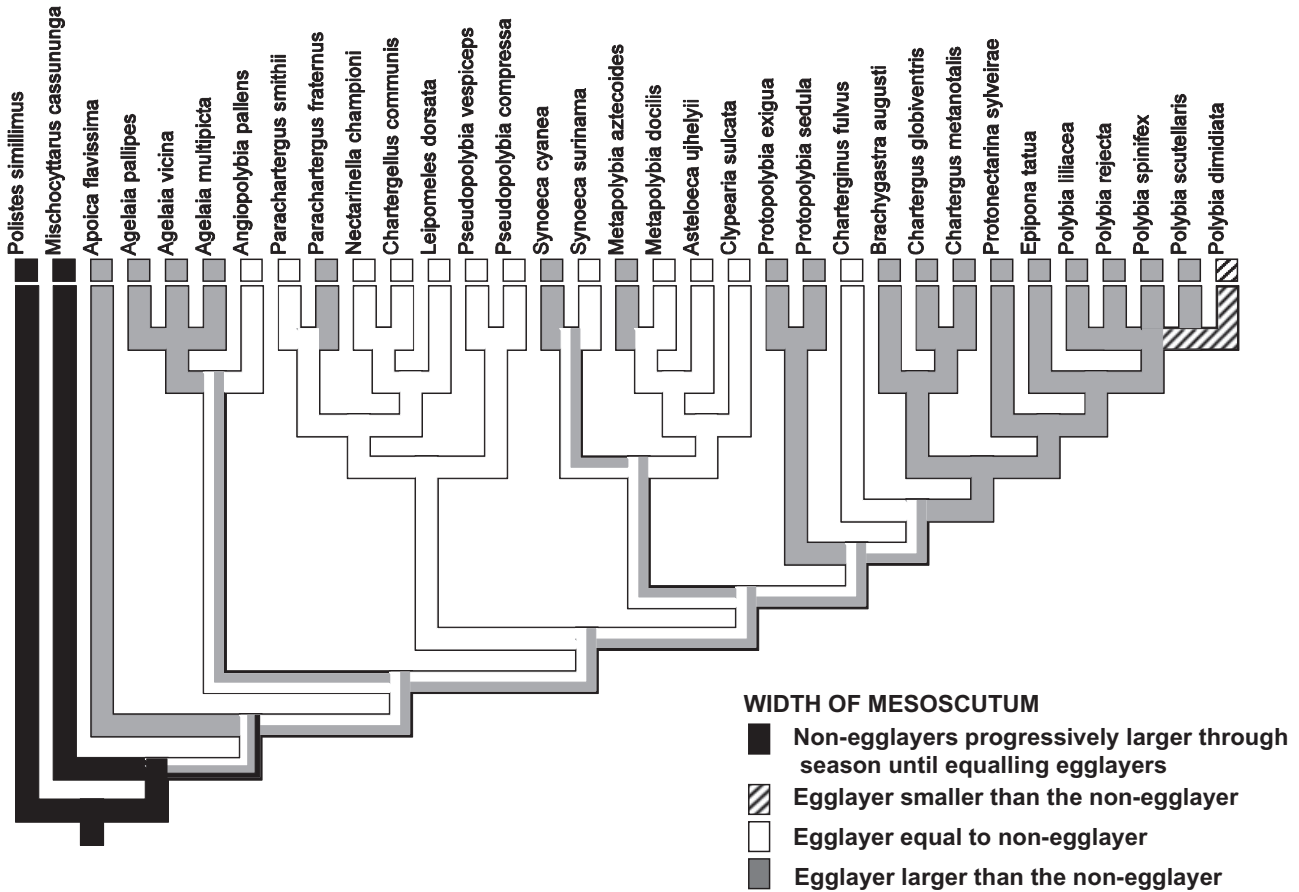


Figure 8. Phylogenetic hypothesis of the evolution of caste related to the width of the mesoscutum, plotted on the tree presented by Wenzel & Carpenter (1994).

and *Clypearia*, with ‘egglayer smaller’ in *Apoica*. ‘Egglayer larger’ is found several times more apically, and for the entire component *Brachygastra–Polybia* (except *P. dimidiata*) (Fig. 9). Evolution of the length of abdominal tergum I shows ambiguous optimizations, one of which has ‘egglayer equal to non-egglayer’ as the primitive condition in the component delimited by *Angiopolybia* and *Clypearia*, with ‘egglayer larger’ occurring several times, particularly in the clade of *Protopolybia–Polybia* (but with *P. dimidiata* smaller) (Fig. 10). Width of the abdominal tergite II shows ‘egglayer larger’ as ancestral, with independent changes to ‘equal’ in the components *Parachartergus–Leipomeles*, *Synoeca–Clypearia*, and in *Angiopolybia* (Fig. 11). Partial length of forewing shows ‘egglayer equal to non-egglayer’ is the primitive condition in the component delimited by *Angiopolybia* and *Clypearia*, ‘egglayers smaller’ in *Apoica* and *Pseudopolybia*, and ‘egglayers larger’ in *Agelaiia*, *Leipomeles*, and from *Protopolybia* to *Polybia* (except *P. dimidiata*) (Fig. 12). With respect to ovarian development, *Polistes* and *Mischocyttarus* are permissive

in the sense that even workers can develop ovaries to the point of laying eggs, and this permissiveness continues as the preferred optimization for most of the backbone of the tree, up to either *Charterginus* or *Brachygastra*, and again in *P. dimidiata* (Fig. 13). Ovarian development is restricted to egglayers only (that is, no intermediate females are found outside of the period of colony foundation) in *Apoica*, *Agelaiia*, the *Synoeca–Clypearia* component, and from about *Chartergus* to *Polybia* (except *P. dimidiata*) (Fig. 13).

DISCUSSION

PHYLOGENETIC PATTERN

Morphometric variables that compare body dimensions of egglayers to those of non-egglayers show patterns as described earlier (Noll *et al.*, 2004). It is important to note that the relative measurements of body parts do not covary exactly, indicating that to some degree head, thorax, abdomen, and wing can change with respect to each other. For example,

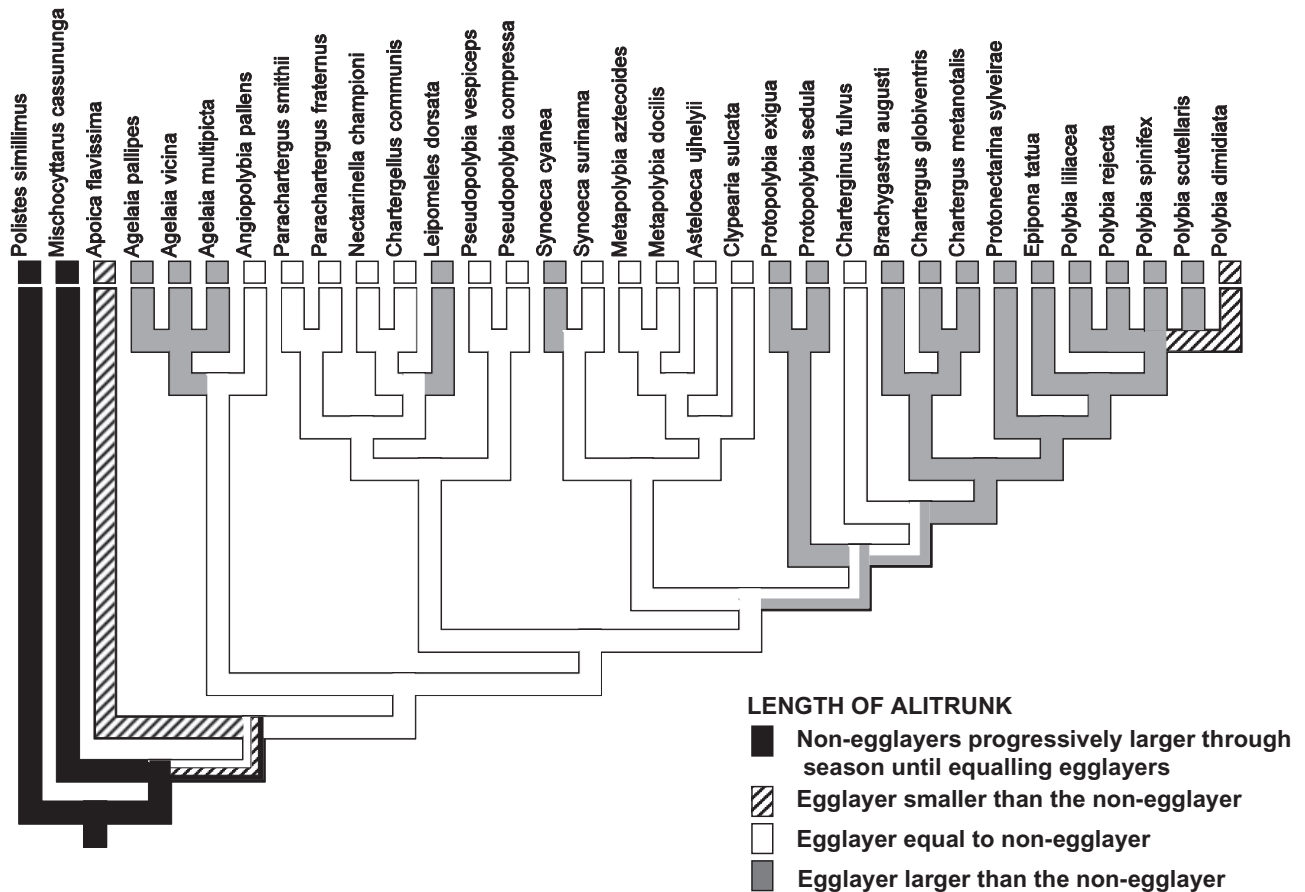


Figure 9. Phylogenetic hypothesis of the evolution of caste related to the length of the alitrunk, plotted on the tree presented by Wenzel & Carpenter (1994).

although the head of *Apoica* is smaller in egglayers than non-egglayers, the thorax is larger (for more detail on this interesting nocturnal genus, see the recent revision by Pickett & Wenzel, 2007). These events of disconnected proportionality indicate that our measurements can be independent, and that when they covary they may indicate something meaningful, rather than simply supply redundant measurements.

The data presented in Figures 6–13 demonstrate that the body plan of egglayers and that of non-egglayers have changed with respect to each other in several ways. *Polistes* and *Mischocyttarus* present the primitive system, by which egglayers are generally similar in all dimensions to non-egglayers, and we see that the Epiponini keep that same relationship as a ground plan, with independent origins of morphological differences, especially in *Apoica*, *Agelaiia*, and in the component *Protopolybia*–*Polybia*. The more ancient patterns in the Epiponini display a kind of disjunction, where either the egglayer is smaller in some measurements or there is no demonstrable difference between egglayer and non-egglayer. The body proportions are

dynamic, however, and no two measurements correspond exactly across the whole tree. There are repeated derivations of certain relationships, such as ‘egglayer head smaller than non-egglayer’, which has as many as six derivations in Figure 6, and species within the same genus may differ. It is important to note that we included measurements sufficient to detect caste in every species where caste was already known, and it is unlikely that we overlooked clear differences in the species in which we found none. Furthermore, if it were only that some unfortunate coincidence prevented us from finding caste in one or another species, then we would not expect such species to group together among close relatives along an evolutionary lineage. The coherence of the phylogenetic pattern is meaningful. One thing is made clear from the plots presented in Figures 6–13: several species of Epiponini are descended from a lineage that was characterized by no difference between egglayers and non-egglayers in most of these measurements.

Optimizations shown in Figures 6 and 10 have alternative resolutions on the Wenzel & Carpenter tree, such that the groundplan along the spine of the

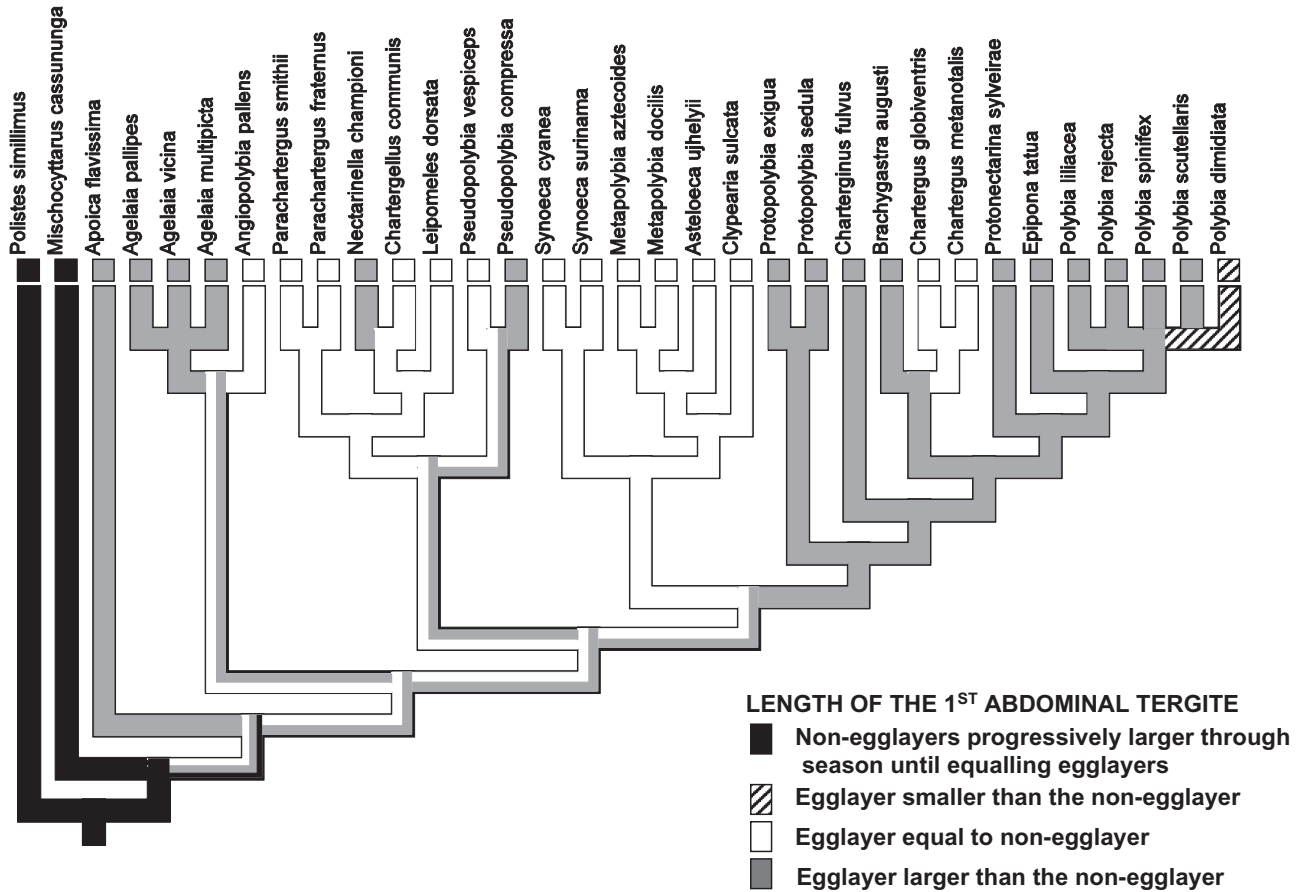


Figure 10. Phylogenetic hypothesis of the evolution of caste related to the length of tergite I, plotted on the tree presented by Wenzel & Carpenter (1994).

tree is ambiguous in certain details. However, the characters include an optimization that would have the spine in the condition of ‘egglayer equal to non-egglayer’ at the branch leading to all the Epiponini, with the exception of *Apoica* (Figs 6–10, 12). (It is accepted methodology to specify one or another optimization, as when a researcher specifies accelerated transformation, resolving homoplasy by invoking reversal, vs. specifying delayed transformation, resolving homoplasy by invoking convergence.) Thus, the separate characters illustrated in Figures 6–13 (except in Fig. 11) all mark the derivation of ‘egglayer equal to non-egglayer’ in the ancient ancestor of nearly all Epiponini. Control of reproduction by non-eggayers is also the character state at this branch. This optimization of data is logically satisfying because it could represent a single evolutionary event on that branch, rather than the scattered, disjunct evolutionary events that are obtained from optimizing all the characters to alternative nodes. The single evolutionary event that would capture all the character change shown in Figures 6–13 would be the lack

of caste distinction entirely. Derivation of qualitatively different queens generally does not appear until rather late in cladogenesis.

SOCIAL (R)EVOLUTION

The origin of most Epiponini via casteless societies represents a new perspective regarding swarming wasps. Traditional opinion considers industrial-scale reproduction in swarming wasps to be an extension of reproductive dominance in more primitive societies, like those of European and North America *Polistes*, which have served as general models in insect sociobiology right from the start (Wilson, 1971). In *Polistes*, one or a few females found a nest, and struggle for exclusive reproduction via physical domination of each other or of workers. Workers themselves are permissive of reproduction by others, whereas queens police the nest. Later, when there are offspring with developed ovaries, daughters may struggle to inherit the position of their mother (or aunt) as the dominant egglayer on that nest. The

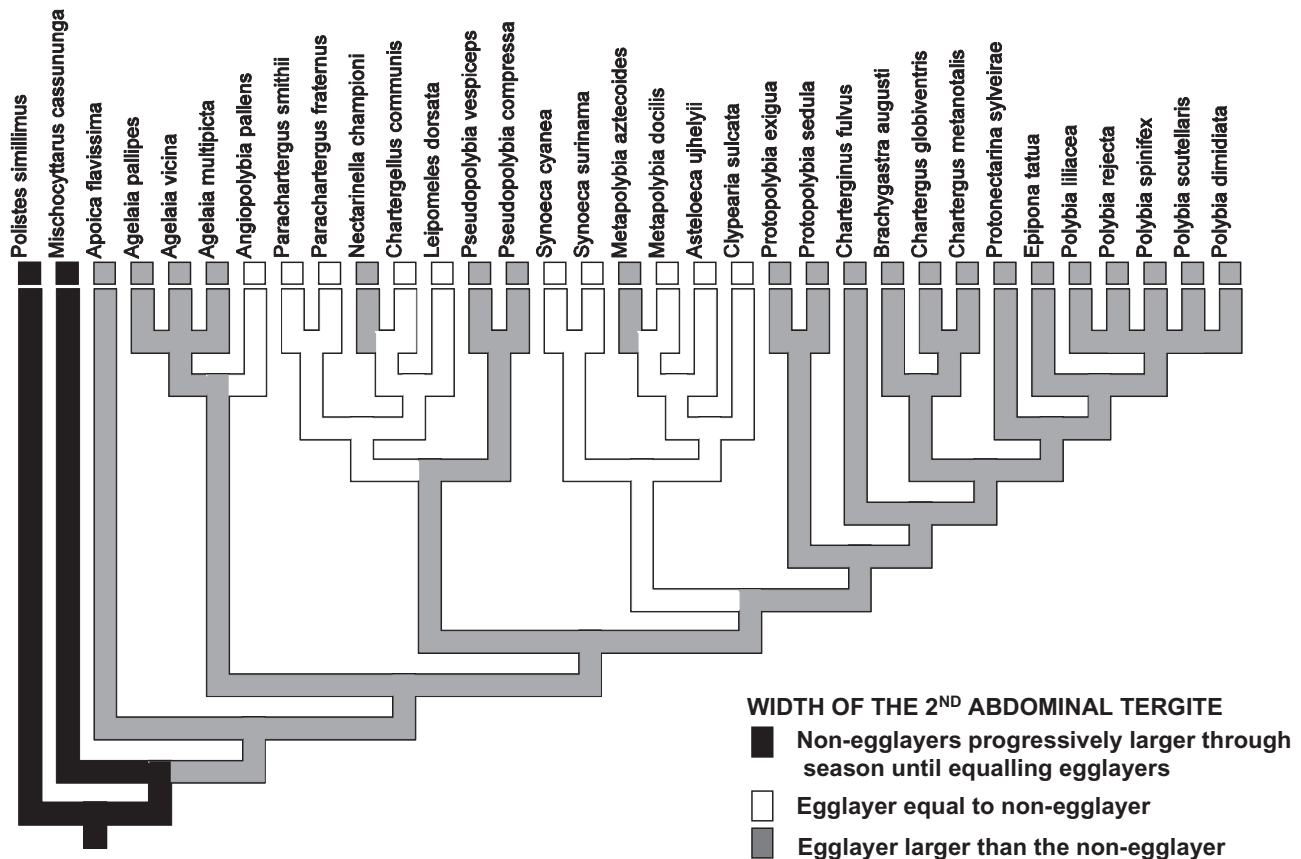


Figure 11. Phylogenetic hypothesis of the evolution of caste related to the width of the second abdominal tergite, plotted on the tree presented by Wenzel & Carpenter (1994).

great majority of dominance interactions are based on fighting, to achieve monopoly on the nest where the interaction takes place. However, there are few meaningful sociobiological similarities connecting *Polistes* with swarming wasps.

Each of the main characteristics of colony reproduction in Epiponini is a direct contrast to the models of colony foundation based on *Polistes*, but this simple fact seems to have been under-appreciated by the scientific community. Indeed, researchers of Epiponini apparently assume that the 'intermediate' females (those that have partly developed ovaries and might become future egg layers) should play a role comparable to the laying workers of *Polistes* on their natal nests (implicit in the genetic comparisons in Strassmann *et al.*, 1991). Intermediate females, however, are best seen as waiting not for the present egg layers to expire, but rather for a swarm to leave and start a new nest where they can be part of the initial group of egg layers founding the new colony. This is explicitly the point of cyclical oligogyny (West-Eberhard, 1978).

A second misconception seems to concern which comparisons are relevant to the study of caste across

these disparate taxa. Morphological studies of castes in *Polistes* generally compare a foundress with her nonreproductive daughters (which are rarely cofoundresses; West-Eberhard, 1969), whereas studies of Epiponini compare contemporaneous adults without attention to relationship (usually either cofoundresses or, mostly, cohorts of sisters derived from the cofoundresses, for example see Noll & Zucchi, 2000.) It is important that in this discussion we maintain a constant perspective, and compare egg layers to their own non-egg laying offspring throughout.

Sociobiologically, the change in dominance relating to caste is easy to interpret. As the workers of a large colony reinforce their interests in inclusive fitness, they reduce the possibility of succession among egg layers (Strassmann *et al.*, 1997) through policing the colony. Permissiveness with respect to egg laying is limited to the foundation period, and dominance among egg layers plays no role. Thus, the larger, dominant queen of *Polistes* does not exist in the basic groundplan of the major portion of Epiponini. This is demonstrated by the plots of Figures 6–13. In certain lineages, there is no detectable difference at all, such

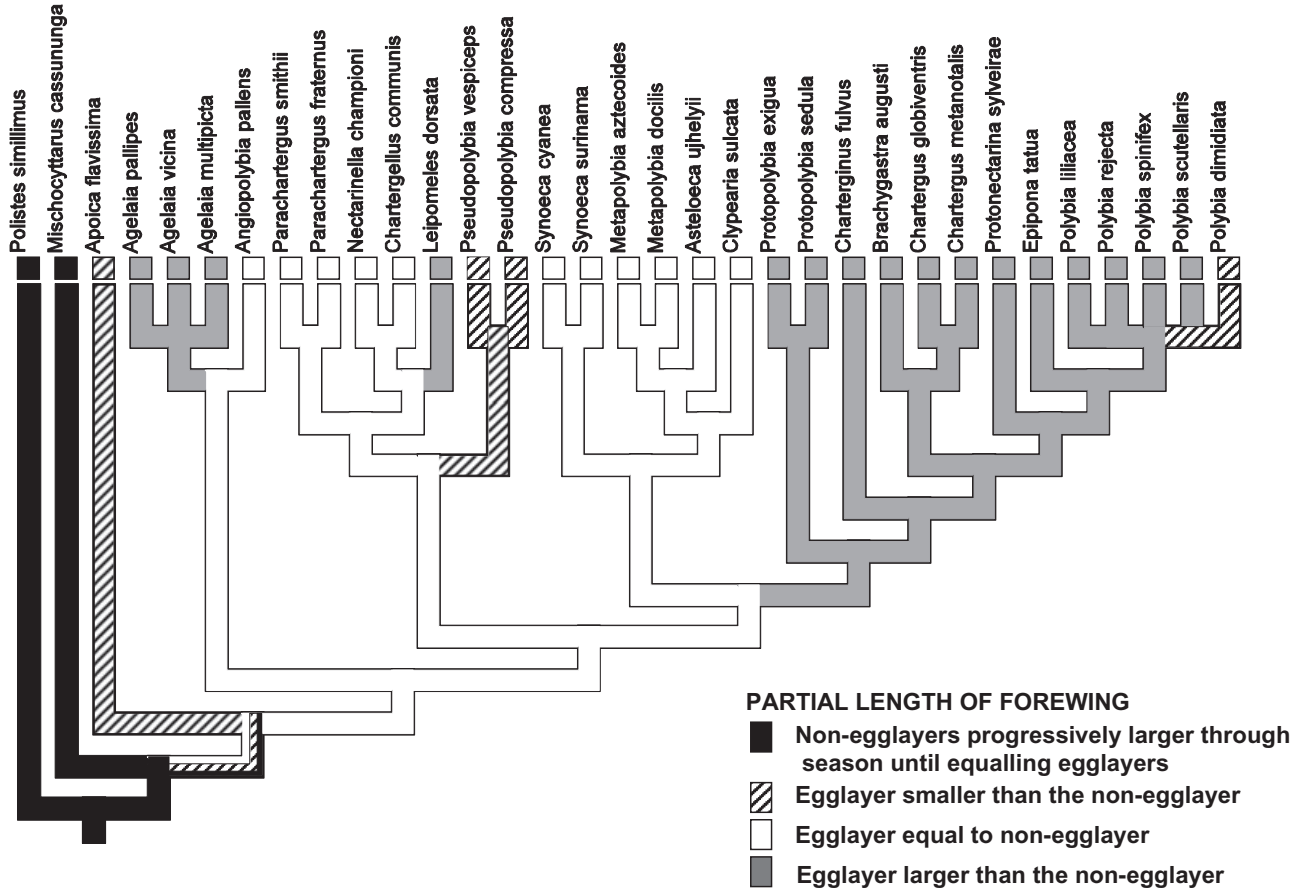


Figure 12. Phylogenetic hypothesis of the evolution of caste related to wing length, plotted on the tree presented by Wenzel & Carpenter (1994).

that these are essentially casteless societies. Specialization is strictly behavioural, with no meaningful morphological difference.

In social insects, a worker’s (here, we revert to traditional use of queen and worker) chance of becoming a replacement reproductive decreases as the colony size increases, because workers increase mutual reproductive inhibition (Ratnieks, 1988; Bourke, 1999). In epiponines, worker policing seems to be important to maintain the original cohort of queens, inhibit worker reproduction, and to maintain higher levels of relatedness (Queller *et al.*, 1993). Similarly, worker policing also acts towards increasing worker reproduction because, in contrast to *Polistes*, workers are usually more closely related to the sons of queens than the sons of other workers (Hastings *et al.*, 1998; Henshaw *et al.*, 2000). In epiponines, queens are tested by the workers (West-Eberhard, 1978, 1981; Herman, Queller & Strassmann, 2000), and they can be removed from the colony if they do not behave as queens (i.e. if they behave submissively), thereby keeping the levels of

genetic relatedness high enough to achieve ‘workers interests’ (Strassmann *et al.*, 1997, 1998). In this regard, the workers of swarming wasps resemble the swarming stingless bees and other large-colony social insects (Wilson, 1971) more than they do their own primitively social relatives living in small colonies. The workers control most colony functions, with the common interest being indirect fitness. Queens perform little or no service towards the social structure of the colony, and do not monopolize reproduction through aggressive dominance behaviours (but rather by ritualized display), remaining tolerant of other egglayers (Naumann, 1970; Simões, 1977; Herman *et al.*, 2000). Therefore, the most prominent difference between the more primitive caste systems of *Polistes* and those of most Epiponini is that (anciently) the Epiponini eliminated the intolerant monogynic egg-layer (the only thing that makes egglayers be ‘queens’ in *Polistes*) long before any other distinction was gained among egglayers. With no behaviourally determined ‘queen’ in ancient ancestors, and with morphological queens only developing recently, the

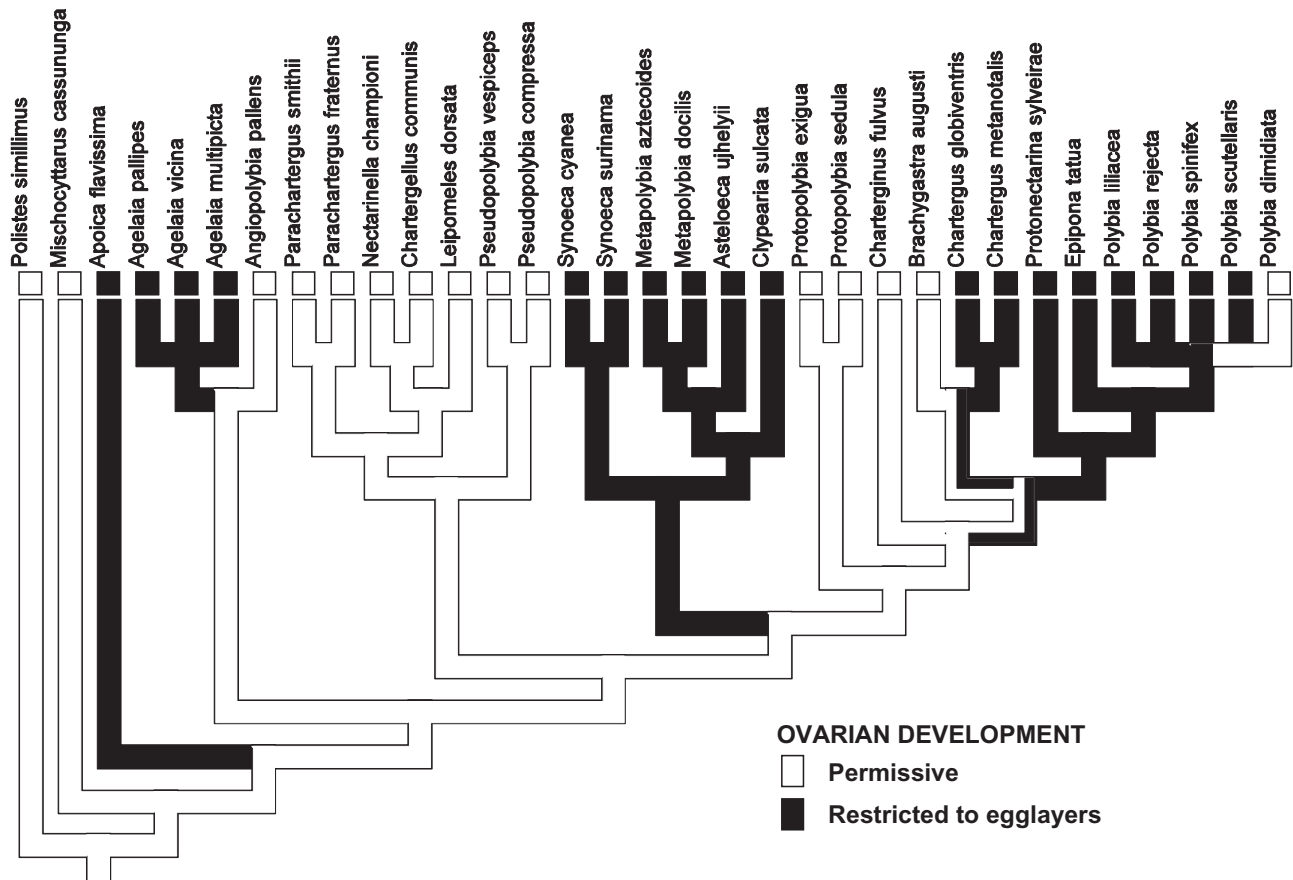


Figure 13. Phylogenetic hypothesis of the evolution of caste related to ovarian development, plotted on the tree presented by Wenzel & Carpenter (1994).

deep ancestry of Epiponini includes a long period with no 'queen' at all.

CONCLUSIONS

The swarming wasps, at their origin, are unlike primitively social *Polistes* and *Mischoctytarus* in that they do not produce progressively larger offspring, beginning with workers and ending with reproductives. Rather, reproductives are either smaller than nonreproductives by some measurement, or they are not different (see deep internal branches in Figs 6–10, 12). Those species of Epiponini that have reproductives larger than nonreproductives are more recently derived, and are not informative with respect to the derivation of the main lineages of the tribe. Indeed, only one measurement (width of abdominal tergum 2) may possibly represent an ancient distinction between reproductives and nonreproductives, and that distinction is nonetheless lost in several lineages (Fig. 11). In addition, in every species of Epiponini for which studies are available, it is found that nonreproductives regulate egg laying (Fig. 2). Thus, the

struggle for reproductive dominance as found in *Polistes* and *Mischoctytarus* does not apply to Epiponini, and there is no coherent morphological distinction between reproductives and nonreproductives in the deep lineages of Epiponini.

This comprehensive study demonstrates that the majority of Epiponini either have no meaningful reproductive caste, or are descended from ancestors who had none. The dominant, suppressive role of 'queen' as found in a primitively social colony of *Polistes* does not exist in Epiponini, and epiponine colonies are better characterized as a conspiracy of workers, some of whom lay eggs. In certain lineages, morphological queens have evolved anew, but these have no evolutionary connection to the classical queens of the simpler societies.

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