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## Revision and Cladistic Analysis of the Nocturnal Social Wasp Genus, *Apoica* Lepeletier (Hymenoptera: Vespidae; Polistinae, Epiponini)

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### ABSTRACT

A revision of the nocturnal social wasp genus, *Apoica*, is presented. The revision is based on a cladistic analysis of morphological, behavioral, and molecular characters of the nine nominal species. The subgenera *Deuteraipoica* and *Apoica* are consistent with the phylogenetic results, and are thus retained. A new species, *Apoica ellenae*, whose phylogenetic position is uncertain, is described. A variant of *A. albimacula* from Peru is noted. This brings the total number of species in the genus to 10.

### INTRODUCTION

The paper wasp genus *Apoica* Lepeletier is one of the most bizarre genera of the swarm-founding Polistinae, or tribe Epiponini. Its nocturnal habit is unique within the Epiponini, and with the exception of the vespine *Provespa* (see review in Matsuura, 1991), no other social wasp genus is primarily nocturnal. Linked to its nocturnal habit, *Apoica* is characterized by unusually large ocelli. Caste determination within *Apoica* is

also unusual. In some cases, queens appear to be slightly smaller than workers (Richards, 1978), which runs counter to the typical situation. Other studies have demonstrated that queens and workers are approximately the same size (though queens are larger than workers posteriorly, and workers larger than queens anteriorly [Jeanne et al., 1995; Noll et al., 2004]), and this too seems to preclude the typical mode of caste determination, in which morphological caste differences are due to changes in size.

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Herein we revise the genus *Apoica*. Confusing issues of taxonomy are clarified, and new species described. We present the first morphological and molecular cladistic treatment of this phylogenetically important genus.

#### TAXONOMIC BACKGROUND

In 1792, Olivier (p. 675) described *Vespa pallida*, the first described species of what would later be the genus *Apoica*. Despite Olivier's specific epithet and his indication of the wasp as "GUEPE pâle", the description provided indicates an animal that is predominantly black to light brown, with traces of yellow coloration:

Elle a un peu plus de huit lignes de long. Les antennes font noirâtre, avec l'extrémité roussâtre. La tête est d'un fauve pâle. Les mandibules sont terminées par trois dents noires. Le corcelet est fauve, avec le dos obscur, un point de chaque côté, antérieurement, un sous l'origine des ailes, un autre à peine marqué, en arrière, trois sur l'écusson, dont deux à peine marqués, & deux autres en dessous, jaune, avec le dos obscur, marqué de quatre petites lignes postérieures, jaunes. Le pétiole est un peu allongé, d'un fauve pâle, avec un point jaune, de chaque côté de l'extrémité. L'abdomen est fauve pâle, sans taches. Les pattes sont de la couleur du corps. [It has little more than eight lines of length {i.e., ~18.0 mm}. The antennae are blackish, with reddish extremity. The head is of a pale fawn color {or perhaps *tawny*}. The mandibles are terminated by three black teeth. The corselet is fawn-colored, with the back dark, a point on each side, before, under the origin of the wings, another hardly marked, behind, three on the escutcheon {i.e., the scutellum}, including two hardly marked, and two others below, yellow, with the back dark, marked of four small posterior, yellow lines. The petiole is elongated a little, fawn-colored, with a yellow point, on each side of the end. The abdomen is pale fawn-colored, without spots. The legs are of the color of the body.]

Also, Olivier (1792) indicates that the pale to which he refers is "pallide rufa", not pale

yellow. A few years later, Fabricius (1804: 276) described *Polistes pallens* as having "Thorax pallide flavescens, dorso obscuriore, abdomen pallens." [Thorax pale yellow, dark dorsum, abdomen pale]. In the same work, Fabricius (1804: 277) described *Polistes albimacula*.

Not long after, *Apoica* was described by Lepeletier (1836) for two species: *Apoica lineolata* Lepeletier and *Apoica pallida*, although he immediately questioned the distinction, asking "Serait-ce une simple variété de la première espèce?" [Could it {*A. pallida*} be a simple variety of the first species?] (p. 539). Lepeletier described his *A. pallida* as having "... un tache double sur le métathorax, de couleur pâle. Abdomen pâle;" [a double spot on the metathorax, of pale color. Pale abdomen;] (p. 538). The abdomen of *A. pallida* (Olivier) is, at its palest, light brown ("corps fauve pâle" [body pale fawn (colored)]) in Olivier's original description (1792: 675). Thus, Lepeletier's description is not consistent with *A. pallida* (Olivier, 1792), but with *A. pallens* (Fabricius).

Like Lepeletier's *A. pallida*, Saussure's (1854: 107) *A. pallida* is pale yellow in color. It is clear from the plate alone that de Saussure's *A. pallida* is not the *A. pallida* of Olivier, but closer to *A. pallens* (see below). De Saussure's *A. pallida* may have also included the later described *A. flavissima* van der Vecht or *A. gelida* van der Vecht.

De Saussure (1854) determined that *Polistes virginea* F. (1804: 277, no. 37.) is a member of *Apoica*, and then synonymized *A. lineolata* (which he mistakenly called *Apoica bilineolata*) with *A. virginea* (p. 108). Saussure also noted that *A. virginea* is perhaps a variety of *A. pallida*. De Saussure's plate of *A. virginea* (1854: pl. XVII, fig. 2) suggests a light brown wasp with few pale markings on the abdominal terga, which is generally consistent with *A. pallida*. However, three of de Saussure's specimens, deposited in the MNHN, are clearly *A. strigata* Richards. Later, de Saussure (1854: 244) described a variant of *A. virginea* that is apparently *A. albimacula* (F.) (see below; noted by Bequaert 1943). It seems, therefore, that *A. pallida* (Olivier), *A. strigata*, and *A. albimacula* were included in de Saussure's concept of *A. virginea*.

De Saussure (1854: 108) also described *Apoica arborea*, separating it from other *Apoica* (and his *A. cubitalis*, a misidentification of *Polybia sericea* (Olivier)) as *Apoica* group II. Dalla Torre (1904) later referred to de Saussure's groups I and II as *Protapoica* and *Deuteroapoica*, respectively. Although *A. arborea* and *A. strigata* Richards (see below) are superficially similar, due to the alternating pale and dark vertical bands on the metanotum, it is clear from de Saussure's description and plate that he was not including *A. strigata* Richards in his concept of *A. arborea*. In his text, de Saussure (1854: 108) stated that *A. arborea* has a black mesonotum ("disque du mésothorax noir"), and the associated plate of *A. arborea* ("Planche XXVI") shows it to be uniformly black. No indication of pale-colored longitudinal stripes medial to the parapsidal furrows is mentioned, and this precludes *A. strigata*, which always has these.

Dalla Torre (1904: 79) considered *Vespa pallens* (lapses for *Polistes pallens* F. = *Apoica pallens*) a synonym of *A. pallida*; du Buysson (1906) also noted that Lepeletier's (1836) and de Saussure's (1854) *A. pallida* was *A. pallens* (Fabricius), and not the *A. pallida* of Olivier (described as *Vespa pallida*). After this, du Buysson (1906: 333), treated, *A. pallens* and *A. virginea* as varieties of *A. pallida*, stating:

Il n'y a qu'une seule espèce, se montrant avec diverses colorations qui ont été décrites comme autant d'espèces par les auteurs. Un simple examen suffit cependant pour se rendre compte que ce ne sont que des variations de couleurs. [There is only one species, showing itself with various colorations which have been described as many species by authors. A simple examination is enough however to realize that they are only variations of colors.]

It is worth noting du Buysson's description of *A. pallida* var. *virginea*. Of this variety, du Buysson (1906: 343) wrote:

Tête, thorax et abdomen testacés, presque sans taches. Presque toujours le 6<sup>e</sup> tergite abdominal est en grande partie flave. On trouve également des individus, pouvant se rattacher à cette variété, qui portent une

tache transversale flave, s'atténuant sur les côtés, au milieu du bord apical des tergites, 3, 4, et 5 de l'abdomen. D'autres fois c'est la majeure partie de ces mêmes segments, ainsi que le 6<sup>e</sup> qui deviennent flaves." [Head, thorax and abdomen testaceous, almost without spots. The sixth abdominal tergite is almost always mainly pale yellow. One also finds individuals, which can be attached to this variety, that wear a pale yellow transverse spot, attenuating on the sides, in the middle of the apical edge from the tergites, 3, 4, and 5 of the abdomen. At other times it is the major part of these same segments as well as the sixth that become pale yellow.]

It is clear from this statement that *A. pallida* var. *virginea* in du Buysson's sense applies to *A. pallida*, as well *A. strigata* and *A. pallens* (and perhaps *A. flavissima*). In the specimen list, du Buysson lists "Guyane française: Camopi (F. Geay 1900, Muséum de Paris)." As mentioned by Richards (1978: 268) and subsequently by Pickett (2003), these specimens are *A. albimacula* (F.).

Despite this action to combine all the named species into one concept, du Buysson (1906: 343) further subdivided the species by describing another variety of *A. pallida*, var. *thoracica*. In his original description, du Buysson mentions "Guyane française: Camopi (F. Geay 1900, Museum de Paris)" and "Brésil: Espiritu Santo (Musée de Hambourg)" in his list of specimens representing the distribution ("Patrie") of *A. thoracica*. As mentioned above, the former locality derives from specimens identified by Richards (1978: 268) and subsequently by Pickett (2003) as *A. albimacula*.

Du Buysson's (1906) treatment of all *Apoica* taxa as one species was completed by two actions. First, du Buysson (1906: 333) pointed out that *A. cubitalis* of de Saussure is *Polybia sericea* (Olivier). He also denied that *A. arborea* was a member of *Apoica*, claiming that it "ne possède aucun des caractères des *Apoica*" [has none of the characters of *Apoica*] (1906: 333). Zavattari (1906:10) and later Ducke (1910) correctly reestablished that *A. arborea* is indeed a member of *Apoica*.

Although de Saussure (1954) and du Buysson (1906) had seen specimens of *A.*

*albimacula* and had included the species in their concepts of various other *Apoica* species (see above), Schultz (1912) was the first to explicitly recognize that *P. albimacula* (F.) is both a valid species and a member of *Apoica*.

Like du Buysson 1906), Bequaert (1943) treated all *Apoica* species as varieties of *A. pallida*. Bequaert's varieties included a "typical" form of *A. pallida*, *A. pallida* var. *thoracica* du Buysson, *A. pallida* var. *pallens* (Fabricius), *A. pallida* var. *arborea* de Saussure and *A. pallida* var. *albimacula* (Fabricius). Bequaert (1943) followed de Saussure (1854) and du Buysson (1906), including *A. virginea* and *A. lineolata* as synonyms of his typical form of *A. pallida*. Bequaert stated (1943: 110), however, that *A. virginea* of de Saussure (1854) is not Fabricius' (1804) *Polistes virginea*, which is a species of *Synoeca*. Bequaert (1943: 113) later expanded the concept of *A. thoracica*, stating:

Although du Buysson's description was based on wasps in which the "testaceous" abdomen contrasted with the "black" head, thorax and tergite 1, I use his name to cover all females without or with scarcely any yellowish or whitish markings. All gradations occur between specimens colored as described by du Buysson and others which are uniformly mahogany or even blackish-brown. If pale markings are at all present, they are restricted to one or more of the following areas; hind margin of pronotum (usually very faint); a spot in the upper plate of mesepisternum (below the wing); a blotch on the tegula; a spot on the post scutellum; the narrow hind margin of the scutellum; and a very narrow apical streak on tergite 1. I have seen no specimen having all these markings at once. The head is unspotted and tergite 6 (female) is very rarely marked with yellow.

The reason Bequaert (1943) never saw any individual with all of the markings he described is that this description is one of *A. thoracica*, *A. pallida*, and possibly *A. ambracarina*. That he was including *A. pallida* is clear from his mention of a "spot on the post scutellum"; this feature is present in none of the *A. thoracica* we have seen, but is always

found in *A. pallida*. Specimens that are "uniformly mahogany" may correspond to *A. ambracarina*, as *A. thoracica* either (1) is uniformly dark brown to black, or (2) has dark brown to black head, thorax, and propodeum, and lighter brown metasoma (the latter as in *A. pallida*).

Later, Richards and Richards (1951) re-established the species status of the color varieties of du Buysson, and commented that there are two color varieties of *A. pallens*. Later, Van der Vecht (1972) concluded that there were three distinct species among specimens of *A. pallens* that he observed, and he described the new species *A. flavissima* and *A. gelida*. Van der Vecht (1972: 739) commented that although separation of species based on the females is difficult, the structure of the male genitalia provides good characters for identification.

In his revision of *Apoica*, Richards (1978) described *A. strigata*. Richards discussed the color similarities between *A. strigata* and *A. arborea*, and then designated the latter the type species of *Deuteroapoica* (Dalla Torre, 1904). Richards (1978) did not, however, include specimens from MNHN in his examined material, and was apparently unaware that specimens of his *A. strigata* had been included in the both de Saussure's and du Buysson's concepts of *A. virginea*.

#### NESTS

The only nests of *Apoica* that have been observed in any detail are members of subgenus *Apoica*. In fact, even among those, we know of no reports regarding the nests of *A. strigata*. The nests that have been studied suggest that *Apoica* nests are always composed of a single exposed comb of cells. The initial cells are attached directly to the surface, usually a broad tree branch, so the nests have no pedicel (see fig. 12: 743 of van der Vecht, 1972). As the nest grows, the dorsal surface of the nest is curved downward, such that cells built at the margin of the nest are not attached to the substrate. Young nests, viewed from below, can appear hexagonal in overall shape, but as the nest grows, it becomes increasingly rounded and oval. Thus, the resulting nest is superficially similar to the nests of *Polistes*.

However, the lack of the pedicel is not the only divergent feature of *Apoica* nests. The dorsal surface of the nests has a texture that is notably feltlike. The origin of this material is unknown, even though the material itself is known to be composed of hollow, branched plant hairs (Wenzel, 1991). KMP has observed workers masticating edges of the dorsal nest surface throughout the night. Often these workers, which were not building, would then expel water from their crops off the side of the nest. Thus, the ultimate pressure for this behavior may be water extraction, but this particular method (not seen in other social wasps) may inadvertently result in the cottony, feltlike nest dome. Richards (1978) likened the dorsal surface to a "rudimentary comb", but we see no justification for this assertion.

However, this outline of *Apoica* nests does not apply to *A. arborea*, the sole member of subgenus *Deuteroapoica* and sister to all other *Apoica* spp. (see Phylogenetic Analysis below). Van der Vecht (1972) described a single nest of what is reported as *A. arborea*. Though the associated photo (Photo I: 738) is poor, it does appear to indicate a nest attached broadly to a branch. No wasps are visible, but *A. arborea* is rather distinct. The nest is neither oval nor circular, but appears to conform to the shape of the tree branch. Apparently, all cells are attached to the branch, as is the case during initiation of *Apoica* sensu stricto nests (van der Vecht, 1972).

Richards (1978) placed *Apoica* in the stelocytarus-type nest group, but commented that *Apoica* lacked the defining character of that group, a pedicle-supported comb. Richards (1978: 19) said (caption of fig. 32): "*Apoica* with no real peduncle is a modified type." In fact, *Apoica* nests *never* resemble stelocytarus-type nests, and there is no peduncle of any kind at all. At the outset *Apoica* nest construction is like that of the astelocytarus-types, but diverges as the nest develops (Wenzel, 1991). The resulting nest is unlike any other in the family, and therefore cannot be placed easily into a previously named category. Accordingly, this excludes *Apoica* from the stelocytarus type, and therefore casts doubt on the assertion that *Apoica* nests are among the ancestral type of the Polistinae.

## BEHAVIOR

No doubt, owing to its primarily nocturnal habit, not much is known about the behavior of *Apoica*. Ducke (1906: 686) reported the unusual observation that males swarm with the females of the colony during colony emigration. This finding has been confirmed for absconding swarms by Howard et al. (2003), but not for primary reproductive swarms. However, examination by Richards (1978: 261) of young nests of *A. flavissima* suggests that this too is the case. *Apoica*, though nocturnal, has been reported to swarm in the daytime. With this exception, the wasps are mostly motionless during the daytime, and burst off the nest at dusk (Hunt et al., 1995), before foraging. This explosive activity is correlated with available moonlight (Hunt et al., 1995), and the colony will forgo this explosion into activity and foraging altogether if there is no moon or if the moon is occluded by clouds (KMP, personal obs.). As hypothesized in Hunt et al. (1995), *Apoica* engage in an otherwise unseen swarm emigration behavior in which they raise their metasoma and apparently release a volatile odor that "calls" the other wasps (Howard et al., 2003).

As in other polistines, *Apoica* workers police queens (KMP, personal obs.). While in Mato Grosso, Brazil, KMP observed five instances of worker *A. flavissima* biting at and harassing queens. S. Mateus, F. Nascimento and KMP identified and marked queens (using the color and morphological differences noted by Shima et al. (1994)) and observed them for three nights. On one instance, KMP observed a worker drive one of the queens from the nest onto a branch of the tree. By the end of the third night, all five marked queens were missing. Because of the size of the colony, it is likely that these five were not the only queens on the colony.

## PHYLOGENETICS

Phylogenetic placement of *Apoica* has been more or less consistent. De Saussure (1854) suggested that *Apoica* was intermediate between *Polistes* and *Polybia* plus the other Epiponines (=Polybiini; "Planche I"). This overly general view has never been doubted, but since, the details of *Apoica*'s position between *Polistes*

and the other epiponines have changed. Richards (1978) placed *Apoica* with *Mischocyttarus* plus the Epiponini in an unresolved trichotomy, uniting this group by his character 2, "Antenna with 12 segments female, 13 male". However, every taxon in his analysis shares this character except *Polybioides* and *Belonogaster*. As has been pointed out by Carpenter (1991), Richards' presented dendrogram cannot be obtained from his matrix.

The first cladistic treatment that addressed the position of *Apoica* relative to other paper wasps was Carpenter (1991). In that morphological study, *Apoica* was sister to all other epiponines, and required 16 fewer steps than did Richards' scheme. Wenzel (1993) conducted a cladistic analysis of the polistine genera based on nest architectural design, and the resulting phylogeny placed *Apoica* sister to Ropalidiini plus the remaining Epiponini, suggesting that swarm founding had evolved twice among the epiponines (or that it had been lost in the Ropalidiini). However, the simultaneous analysis (Nixon and Carpenter, 1996) of the data from Carpenter (1991) and Wenzel (1993) again placed *Apoica* sister to the other epiponines (Wenzel and Carpenter, 1994), as did Carpenter (1991).

Noll et al. (2004) found a sister relationship between *Apoica* and *Agelaia*, and that clade was not sister to the remaining epiponines. Noll's cladistic treatment used discretized caste morphometric data as characters in combination with the matrix of Wenzel and Carpenter (1994), but the (*Apoica* + *Agelaia*) result has not been unambiguously supported in subsequent investigations (F. B. Noll, personal commun.).

In all of these studies, *Apoica* has been coded as a single terminal. Carpenter (1991) used a summary coding for *Apoica* in his analysis. Wenzel (1993) also used a kind of ground-plan coding when deriving his nest architectural characters, and necessarily only coded the nests of *Apoica* subgenus *Apoica* in his matrix (as no nest of *Deuteroapoica* had been collected). As they augmented the matrix of Wenzel and Carpenter (1994), Noll et al. (2004) also represented *Apoica* in a single terminal.

Recently, Pickett et al. (2005) treated all nominal members of *Apoica* as terminals in an exclusively molecular analysis, which was

conducted for a purpose other than taxonomy. Accordingly, the present treatment is the only analysis of *Apoica* that uses morphological, molecular, and behavioral data coded for species.

## MATERIALS, METHODS, AND RESULTS

### CLADISTIC ANALYSIS

A more definitive elucidation of the placement of *Apoica* warrants a more robust treatment of the genus itself. If *Apoica* is sister to all other epiponines, then it may reflect some primitive or transitional aspects of social behavior that will inform us of the evolution of swarming behavior, worker policing, castes, and other characteristics of the Epiponini. However, it may be a highly apomorphic, aberrant genus of social wasps, and thus not be a good candidate to represent primitive or transitional social behavior, despite its phylogenetic position. These are issues that require a phylogeny. If *Apoica* is a primitive or transitional swarm-founder, the phylogenetic relationships both within *Apoica* and between *Apoica* and the other polistines may be of great general value, extending beyond taxonomy. In order to accomplish this, a cladistic analysis of *Apoica* and relevant outgroups is required. Below we report the data used, methods, and results of such an analysis that includes morphological, behavioral, and molecular data. Because male genitalia and DNA are not obtainable for *A. ellenae* (see below), we do not include that species in the phylogenetic analysis.

For the purpose of this treatment, we have employed the Phylogenetic Species Concept (Cracraft, 1983; Eldredge and Cracraft, 1980; Nixon and Wheeler, 1990) for species delimitations. To the extent possible, we have followed Nixon and Wheeler (1990), who defined the Phylogenetic Species Concept as "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)."

### MORPHOLOGICAL AND BEHAVIORAL DATA

A total of 34 parsimony-informative morphological characters—including 17 from ex-

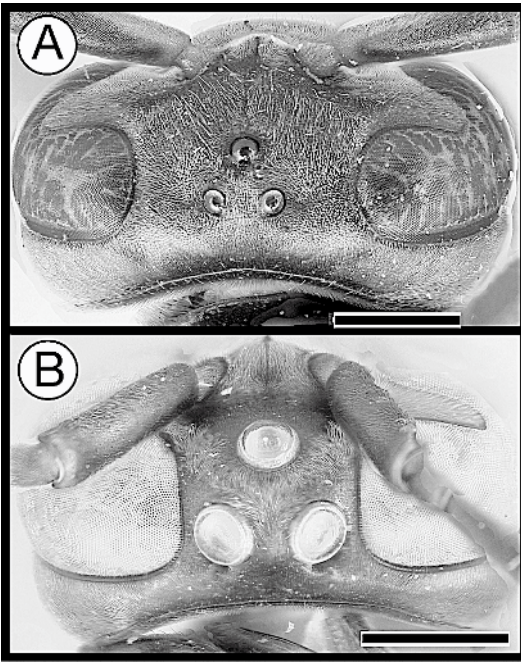


Fig. 1. Ocelli: **A**, *Polistes fuscatus*, typical (small); **B**, *Apoica ambracarina*, large. Scale bars = 1.0 mm.

ternal morphology, nine from male genitalia, and five from color—and three behavioral characters were used in the cladistic analysis. Some characters have been used in previous systematic studies, primarily cladistic analyses of polistine genera by Carpenter (1991). Character descriptions and figures accompany

new characters and characters never before treated in a cladistic framework. All characters are treated as nonadditive.

#### Characters from External Morphology:

**Character 1. Ocelli:** 0, typical; 1, large (fig. 1). This character is the best way to diagnose *Apoica*, as the ocelli are much larger than in other Polistinae.

**Character 2. Eye hairs:** 0, absent; 1, present (fig. 2). Carpenter (1991) originally treated state 0 as the ground plan for all *Apoica*. In fact, *A. thoracica* is the only species that lacks pronounced eye hairs. *A. thoracica* does, occasionally, have very short hairs, often near the genal border when present, and occasionally present sparsely across the surface (and this only when the metasoma is lighter in color; see below); usually, *A. thoracica* lacks hairs altogether. All other *Apoica* always have long, abundant eye hairs.

**Character 3. Median carina of metanotum I:** 0, absent; 1, present; 2, present and sharply carinate (fig. 3). Pickett (2003) used this character as the primary basis by which he separated *A. ambracarina* from within *A. thoracica*. The state is not the same as the sharp median carina of *A. albimacula*, which extends to the posterior border of the metanotum. In *A. ambracarina*, the carina is more rounded and occurs anteriorly only. *A. thoracica* does not have a metanotal carina. In his key to *Apoica*, Richards (1978: 262, 263) commented that *A. thoracica* “rarely has

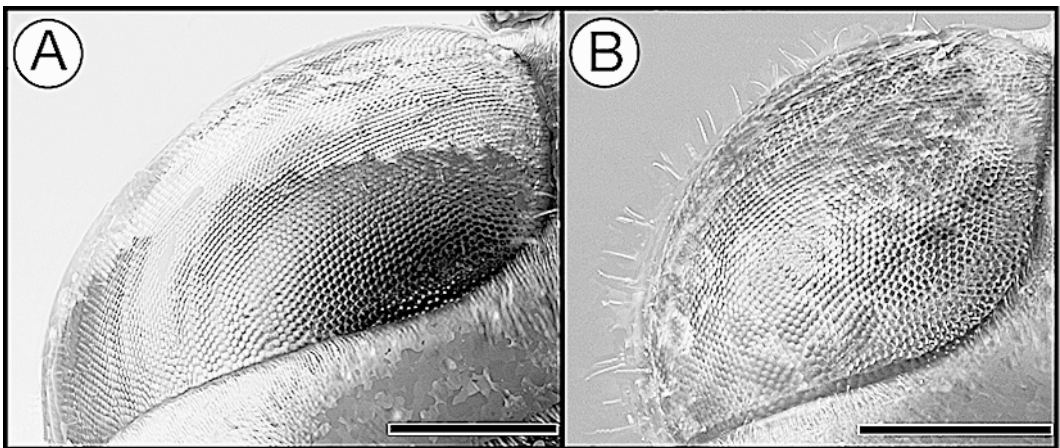


Fig. 2. Eye hairs: **A**, *Apoica thoracica*, absent; **B**, *Apoica pallida*, present. Scale bars = 0.5 mm.

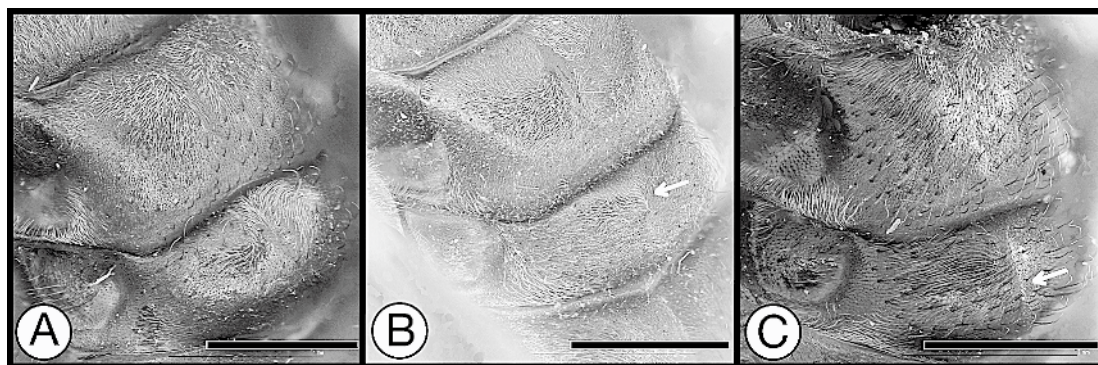


Fig. 3. Metanotum with central carina: **A**, *Apoica thoracica*, absent; **B**, *Apoica ambracarina*, anterior carina; **C**, *Apoica albimacula*, extending posteriorly and sharply carinate. Scale bars = 1.0 mm.

traces of a keel” and has a “weaker central tubercle”, but he may have included *A. ambracarina* in his concept of *A. thoracica* (Pickett, 2003).

Character 4. **Pronotal fovea**: 0, absent; 1, shallow; 2, deep (fig. 4). All *Apoica* have a pronotal fovea; however, the pronotal fovea may be either merely present, or recessed into a larger pit. Richards (1978: 262) used this character in his key to separate *A. albimacula* and *A. thoracica* from other *Apoica*. The new species, *A. ellenae*, though not included in the analysis, shares state 2.

Character 5. **Metanotum**: 0, rounded; 1, gradually angled; 2, sharply angled; 3, flat (fig. 5). Carpenter (1991) has used states 0 and 2 of this obvious structural character for

generic separation. The posterior metanotal angle that appears in some *Apoica* is sometimes difficult to diagnose because outstanding bristles can obscure the view or cause an otherwise rounded metanotum to appear angled. Richards (1978: 261) made use of this character in his key, describing the “rounded” state as “Metanotum less abruptly convex, not falling so perpendicularly onto the propodeum”, and the “angled” state as “Metanotum more abruptly convex”. However, Richards (1978) did not note the character’s variability across subgenera, considering it informative only in dividing the *Deuteroapoica* from *Apoica* sensu stricto.

Character 6. **Mesonotal bristles**: 0, absent; 1, not reaching anterior margin; 2, reaching

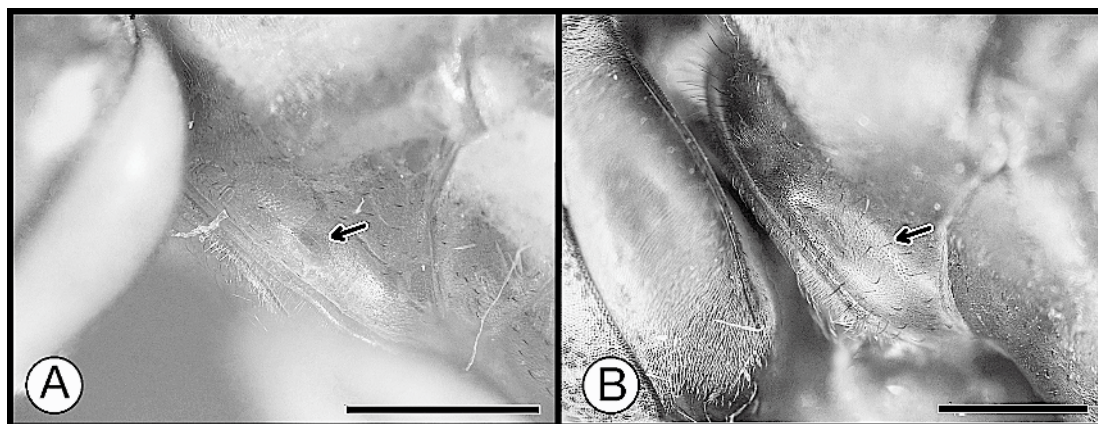


Fig. 4. Pronotal fovea: **A**, *Apoica flavissima*, shallow; **B**, *Apoica thoracica*, recessed into a pit. In **A**, the depression is the fovea. In **B**, the arrow indicates the border of the larger oval pit into which the fovea itself is recessed. Scale bars = 1.0 mm.

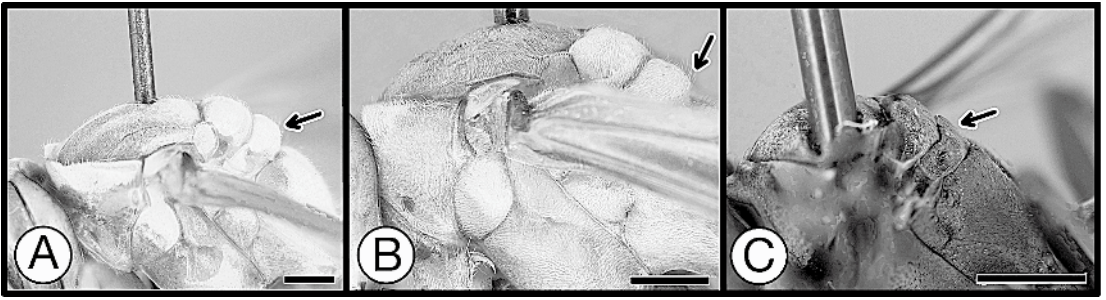


Fig. 5. Metanotal shape: **A**, *Apoica flavissima*, rounded; **B**, *Apoica gelida*, angled posteriorly; **C**, *Metapolybia cingulata*, flat. Scale bars = 1.0 mm.

anterior margin (fig. 6). Richards (1978) used this in his key to separate *A. flavissima* (state 2) from all other members of the subgenus *Apoica*. But state 2 also appears in *A. albimacula*, *A. strigata* and *A. thoracica*, in addition to *A. arborea*.

Character 7. **Meso- and metanotal bristles:** 0, absent; 1, erect; 2, apically bent towards midline (fig. 7). Van der Vecht (1972) discussed this character, saying that *A. arborea*'s

“outstanding, bristle-like hairs are short and only very slightly curved”. Although they are most certainly shorter than in all *Apoica* sensu stricto, we can detect no curvature in them, as is clear in other *Apoica*. This character was also used by Richards (1978) to divide *Deuteraipoica* from *Apoica* sensu stricto, but *A. ambracarina* also has erect, bristles, but here, the bristles are “slightly curved”. The curvature in the bristles of *A. ambracarina* is

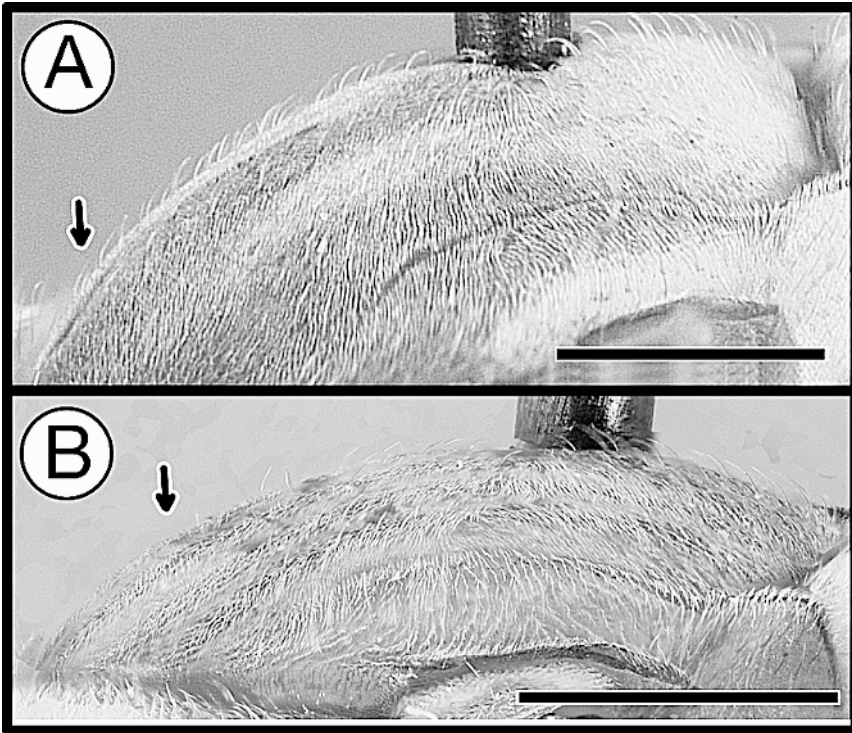


Fig. 6. Mesonotal bristles: **A**, *Apoica flavissima*, reaching anterior margin; **B**, *Apoica gelida*, not reaching anterior margin. Scale bars = 1.0 mm.

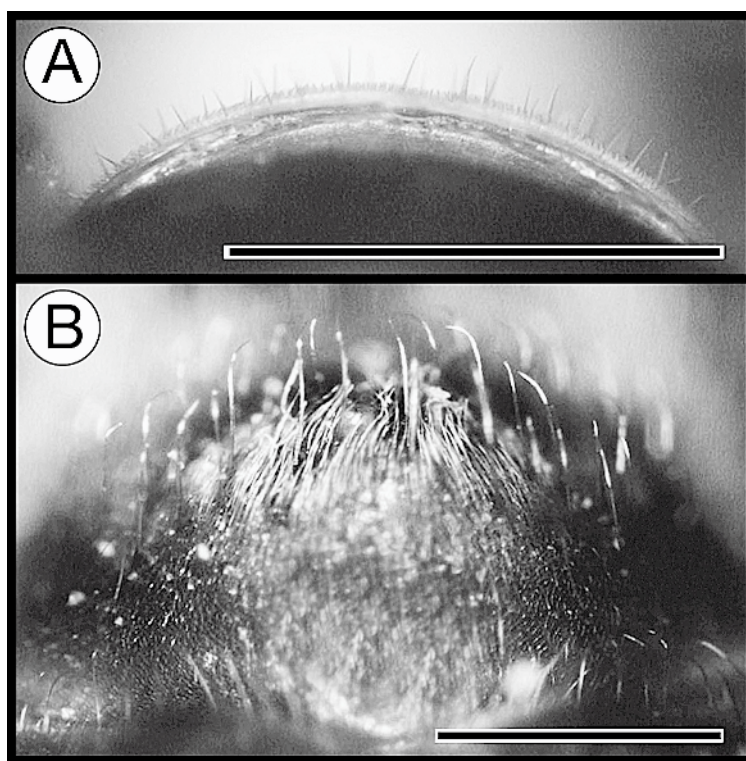


Fig. 7. Metanotal bristles in posterior view. **A.** *Apoica arborea*, erect. **B.** *Apoica thoracica*, apically bent towards midline. Scale bars = 1.0 mm.

far more subtle (and infrequent) than in other taxa.

The following characters derive from Carpenter (1991) and are not variable within *Apoica*, but serve to establish its monophyly. Other characters from Carpenter (1991) that are not used were excluded only because they were invariant or uninformative for the current taxa. See Carpenter (1991) for detailed descriptions of the characters and states.

Character 8. **Tyloides**: 0, present; 1, absent; 3, replaced by specialized flattened areas.

Character 9. **Clypeal apex**: 0, sharply pointed; 1, rounded to truncate.

Character 10. **Clypeal lateral lobes**: 0, well-developed; 1, reduced and rounded.

Character 11. **Dorsal groove**: 0, present; 1, absent.

Character 12. **Scrobal sulcus**: 0, present; 1, absent.

Character 13. **Epiclemum**: 0, carina present; 1, absent.

Character 14. **Scutal lamella**: 0, developed adjoining tegula; 1, reduced.

Character 15. **Metasomal petiole**: 0, absent; 1, segment I less than half the width of segment II; 2, linear.

Character 16. **Thyridium**: 0, linear transverse and basal; 1, not transverse or basal.

Character 17. **Van der Vecht's organ**: 0, externally modified area present; 1, absent.

Characters from Male Genitalia: Richards (1978) commented that the genitalia of *Apoica* probably provide good specific characters. The morphology of the genitalia is much more variable than external morphology, and in fact, male genitalia provide the best characters for species delimitation. This is somewhat unfortunate, as females are much more common in nature and in collections. Also, because the males are frequently paler in color than the females (as is often true among polistines), identifying males can be difficult without dissection.



Fig. 8. Digitus shape: **A**, *Apoica arborea*, posterior surface expanded, forming a triangular shape; **B**, *Apoica strigata*, fingerlike and curved. Scale bars = 1.0 mm.

Character 18. **Digitus shape**: 0, fingerlike and curved; 1, posterior surface expanded, forming a triangular shape (fig. 8). All members of subgenus *Apoica*, except *A. albimacula*, have fingerlike, curved digits, and this is modified from the typical state found throughout the Polistinae. *Apoica arborea* and *A. albimacula* have a more typical digitus that is expanded posteriorly (see arrow in fig. 8 below).

Character 19. **Digitus tip**: 0, rounded; 1, pointed (fig. 9). This character has not been discussed in the relevant literature.

Character 20. **Digitus setae**: 0, without setae; 1, with setae (fig. 10). Within *Apoica*, only *A. albimacula* has setae on its digitus, although this state occurs in other polistines.

Character 21. **Digitus contact with cuspis**: 0, apically to cuspis; 1, medially (fig. 11).

Character 22. **Paramere spine shape**: 0, blunt; 1, sharp (fig. 12).

Character 23. **Paramere spine shape**: 0, thick; 1, thin (fig. 12).

Character 24. **Paramere spine setae**: 0, without setae; 1, with setae (fig. 13).

Character 25. **Posterior lobe of paramere**: 0, angled; 1, rounded (fig. 13). Richards and Richards (1951: 151–152) made mention of this character in their abbreviated key to the males of *Apoica*, and it was used to identify *A. arborea*, essentially serving to separate *Deuteraipoica* from *Apoica* sensu stricto. However, *A. albimacula* also bears this character, but Richards and Richards (1951) did not have access to male *A. albimacula*.

Character 26. **Aedeagus**: 0, straight; 1, widening at posterior tip (fig. 14). Richards (1978) used this character in his key, but he

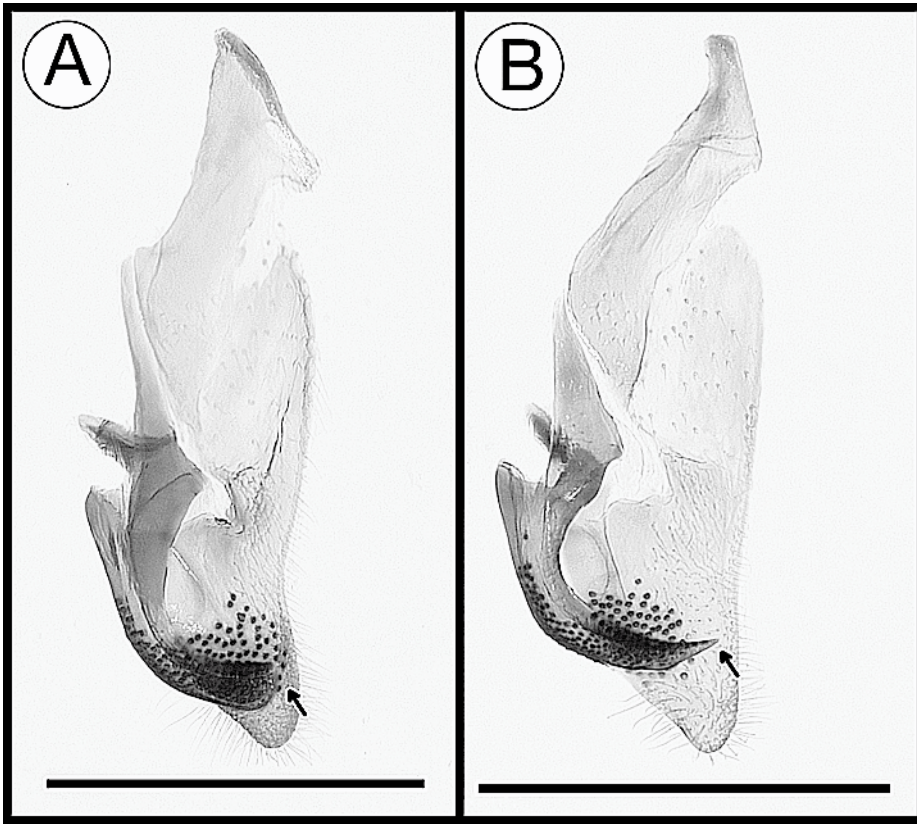


Fig. 9. Digitus tip: **A**, *Apoica ambracarina*, rounded; **B**, *Apoica gelida*, pointed. Scale bars = 1.0 mm.

wrote that *A. pallida* has a “uniformly wide stem” (p. 263). While it is true that the aedeagus of *A. pallida* is wider in general, and does not flare so gradually and severely as *A. gelida* (for example, see fig. 14), it does indeed widen at the posterior end. *A. arborea* is the only member of *Apoica* with a uniformly wide aedeagus.

**Color Characters:** Using color is often shunned because it is believed that it belongs to a class of characters that are particularly prone to plasticity, and are therefore unlikely to generate synapomorphy. However, the color characters discussed below appear to be fixed and stable across species boundaries and comprise valuable diagnostic and cladistic characters. With the exception of Character 28 (fig. 15), which involves shape and pattern in addition to color, none of the color characters are illustrated, because figures do not add any clarity.

**Character 27. Scutum color:** 0, dark brown to black; 1, yellow to light brown. This character has been used informally by many authors, including Bequaert (1943), Richards and Richards (1951), van der Vecht (1972), and Richards (1978) in general descriptions of the species differences.

**Character 28. Scutum with longitudinal stripes:** 0, absent; 1, pale; 2, dark (fig. 15). Certain states of this character have been mentioned by many authors, including Bequaert (1943), and Richards and Richards (1951) and Richards (1978). Richards (1978) used this character to separate *A. strigata* from within *A. arborea*, stating that *A. arborea* lacks the pale longitudinal stripes. But this is true only of female *A. arborea*; males have the stripes. Pickett (2003) used this character in his original description of *A. ambracarina*; unfortunately, he erroneously described the dark stripes as occurring over the parapsidal

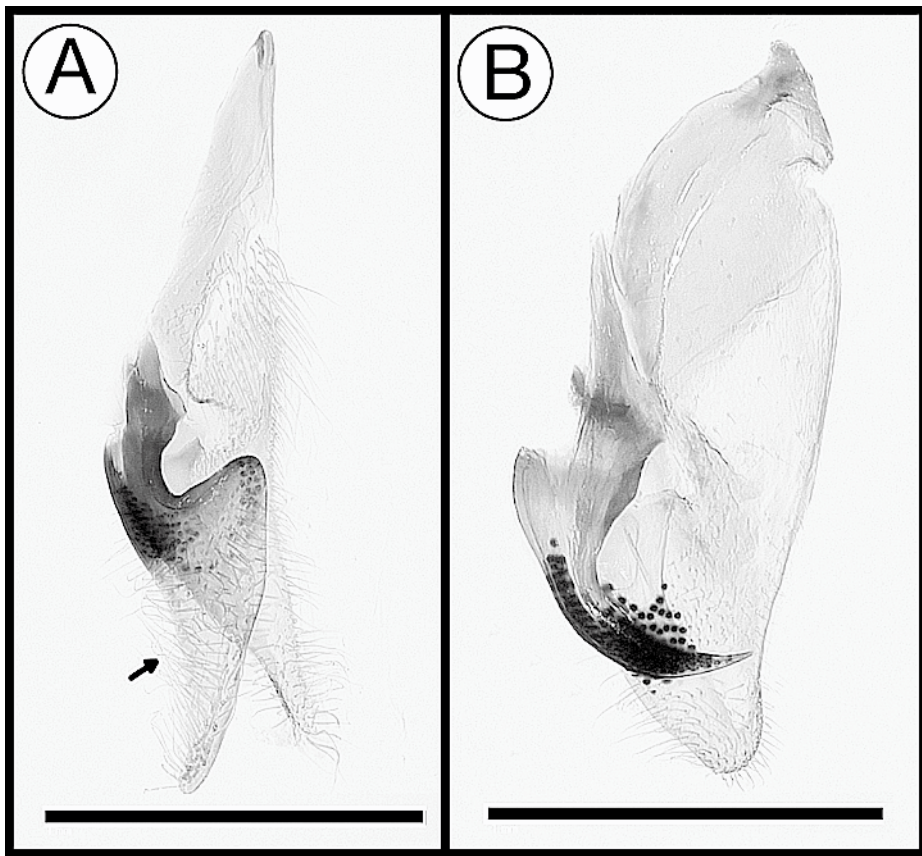


Fig. 10. Digitus setae: **A**, *Apoica albimacula*, with setae; **B**, *Apoica flavissima*, without setae. Scale bars = 1.0 mm.

furrows. In fact, the bands are medial to the furrows. At times, whether pale or dark, the stripes fuse posteriorly. Lateral to the parapsidal furrows, there are sometimes two additional stripes, one on each side.

Character 29. **Color of the scutellum**: 0, pale; 1, dark with pale spot; 2, entirely dark.

Character 30. **Metasomal terga** (excluding final tergum): 0, dark brown to black; 1, light brown; 2, pale yellow to white; 3, dark or light brown with pale posterior margin.

Character 31. **Metasomal sterna**: 0, dark brown to black; 1, light brown; 2, pale yellow to white; 3, dark or light brown with pale posterior margin.

**Behavioral Characters**: The following behavioral characters are valuable in both establishing the monophyly of *Apoica* and placing it within the Polistinae.

Character 32. **Nocturnal habit**: 0, absent; 1, present;

Character 33. **Nest structural variation**: 0, gymnodomous; 1, calyptodomous; 2, phragmocytarus; 3, astelocytarus.

Character 34. **Swarm founding**: 0, absent; 1, present;

The full matrix of these 34 morphological, color, and behavioral characters is shown in appendix 1.

#### MOLECULAR DATA

For all *Apoica* spp. and outgroups, except for *A. albimacula* and *A. arborea*, alcohol preserved specimens were used to obtain DNA from the mitochondrial CO1 subunit. A recently collected and rapidly dried *A. arborea* (from G. Melo) was used to obtain DNA, and the template from this specimen was less degraded than the alcohol-preserved specimens. The pinned *A. albimacula* specimen was collected in 1989, but this specimen's thoracic flight muscle provided



Fig. 11. Digitus contact with cuspis: Dark spots appearing on both digitus and cuspis correspond to places of potential contact. **A**, *Apoica albimacula*, unmodified relative to other Polistinae, expanded posteriorly (see above), the region of the digitus that is positionally most similar to the apical tip of the digitus in other *Apoica* (indicated by arrows) contacts the cuspis; **B**, *Apoica thoracica*, representing the modified, restricted digitus shape, contacting apically; **C**, *Apoica pallida*, contacting medially, with the tip extending freely beyond the body of the cuspis. Scale bars = 1.0 mm.

a good, unfragmented DNA template. Primers and amplification methodology are the same as set forth Pickett and Wenzel (2004), except that the use of internal, degenerate primers was unnecessary. Sequence fragments were aligned using the default setting of the multiple-alignment programs Clustal X and Malign (Wheeler and Gladstein, 1994), which both rendered the same alignment. The resulting matrix of aligned sequences contains 556 sites and 145 parsimony-informative characters (Genbank Accession numbers: AY663544–AY663559; data are available as individual sequences and alignment).

#### TREE SEARCH AND OPTIMALITY

The trees deriving from the phenotypic data, the molecular data, and both datasets combined were calculated under the parsimony criterion. The total-evidence tree(s) are preferred because simultaneous analysis of char-

acters provides the most robust test of homology assessments (Kluge, 1989; Nixon and Carpenter, 1996); the trees generated from phenotype or molecules alone are presented for comparison purposes only. All datasets were analyzed using the mult\* command in NONA (Goloboff, 1999). This command generates successive Wagner Trees (Kluge and Farris, 1969) from random taxon addition, and then rearranges the topologies according to the TBR method. All searches were implemented in WinClada version 1.00.18 (Nixon, 2002), spawning NONA 2.0 (Goloboff, 1999) as a daughter process. Two-hundred random addition sequences, holding two trees per replicate, were implemented for each analysis.

#### SUPPORT

Jackknife and Bremer support values were calculated for trees deriving from morphology and behavior alone, molecules alone, and the

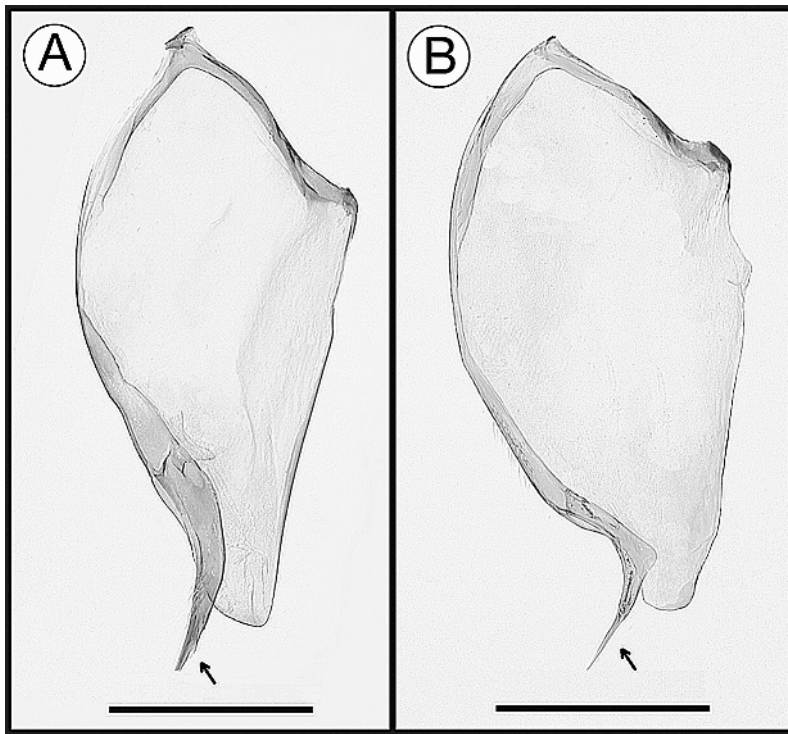


Fig. 12. Parameral spine: **A**, *Apoica albimaculata*, parameral spine thick and blunt; **B**, *Apoica gelida*, parameral spine thin and sharp. Both characters 22 and 23 are illustrated here only for efficiency; the different character states from the two characters do not always co-occur as in these species. Scale bars = 1.0 mm.

combined analysis. Jackknife-searching parameters were optimized for fastest asymptotic performance with the shortest amount of time (Freudenstein et al., 2004): 10,000 jackknife replicates; one random addition sequence replicate per jackknife replicate (“mult\*1” command in NONA); 1 starting tree held per rep (“hold/1” in NONA), TBR swapping on each rep (“max\*” command in NONA); tree buffer set to two trees. Jackknife support values are reported above clades on the strict consensus of the parsimony trees. Because all characters are equally weighted and are non-additive, the bias in typical resampling support that is corrected by symmetric resampling is not present (Goloboff et al., 2003). Bremer support values were calculated via the following series of commands, issued in NONA (search strategy due to D. Pol, personal commun.): “hold 150000; hold/1; sub 100; mult 1000; find\*”; this procedure generated

1,000 suboptimal trees of up to 100 steps longer than optimal from 1,000 random addition sequences. These trees were then subjected to TBR swapping, resulting in 150,000 suboptimal trees. The exact Bremer support was calculated from these 150,000 trees in TNT (Goloboff et al., 2000). Bremer support values are reported below clades on the strict consensus of the parsimony trees.

#### RESULTS OF CLADISTIC ANALYSES

Results from the analysis of morphology and behavior (fig. 16) alone, molecules (fig. 17), and the simultaneous analysis of both data sets (fig. 18) are shown below.

#### MORPHOLOGY AND BEHAVIOR ALONE

In many ways the phylogeny from morphology and behavior alone (presented in

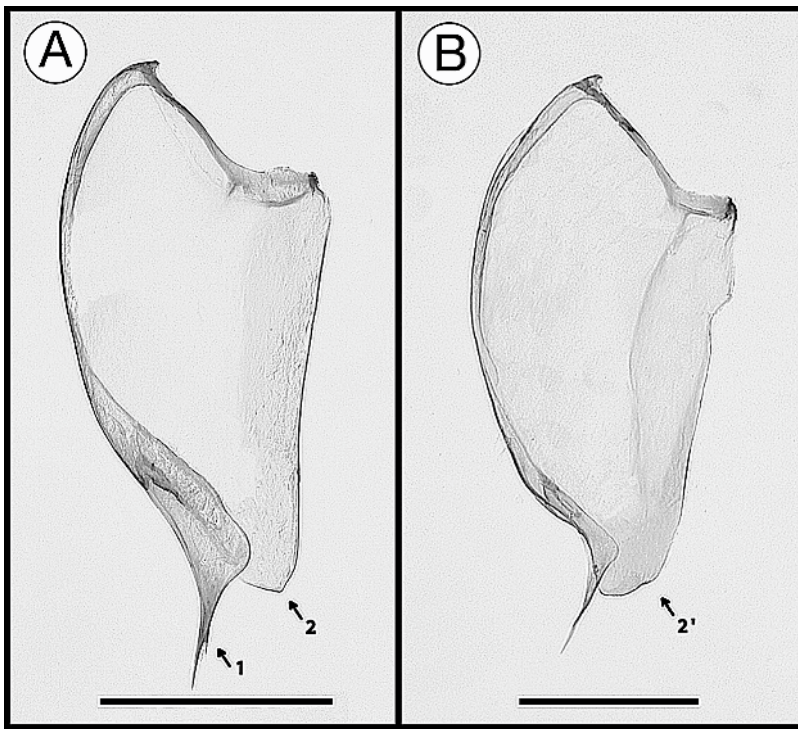


Fig. 13. Parameral spine: **A**, *Apoica arborea*, parameral spine with setae (1) and posterior lobe of paramere angled (2); **B**, *Apoica ambracarina*, parameral spine without setae and posterior lobe of paramere rounded (2'). Scale bars = 1.0 mm.

fig. 16) is not traditional. Most striking is the placement of *Ropalidia*, which renders Epiponini paraphyletic. The best hypothesis to date (i.e., that of Wenzel and Carpenter, 1994) of the position of the ropalidiines suggests that they should be basal to the epiponines. Certainly, such a placement of *Ropalidia* would require the loss of swarming behavior. However, this is not a study of the outgroups, and, assuming it is in error, one reason for this bizarre placement is that a single species cannot adequately represent the full breadth of the tribe.

More pertinent to the present study, *Apoica* is monophyletic with moderate support, but the relationships of the taxa inside *Apoica* have poor support. The placement of *Apoica* is unexpectedly inside Epiponini, as current views (Carpenter, 1991; Wenzel and Carpenter, 1994) suggest that *Apoica* is sister to the remaining swarm founders. However, the support for this position is marginal at best (51% jackknife support and Bremer support of 2).

#### MOLECULES ALONE

The tree obtained from molecular data (fig. 17) shows a monophyletic Epiponini, though the support for this clade is poor. *Mischocyttarus* and *Ropalidia* are shown as sisters, a relationship not previously suggested, although the relationship between the Mischocyttarini and Ropalidiini remains unclear (Wenzel and Carpenter, 1994).

Support for the monophyly of *Apoica* is rather poor (60% jackknife, 1 Bremer), but certain relationships within the genus are supported well. *A. arborea* (i.e., *Deuterapocica*) is separated from *Apoica* sensu stricto by strong support (87% jackknife, 4 Bremer), and other relationships are supported strongly.

#### TOTAL EVIDENCE

The optimal trees and their consensus (fig. 18) indicate a sister relationship between *Apoica* and all other Epiponines. This is

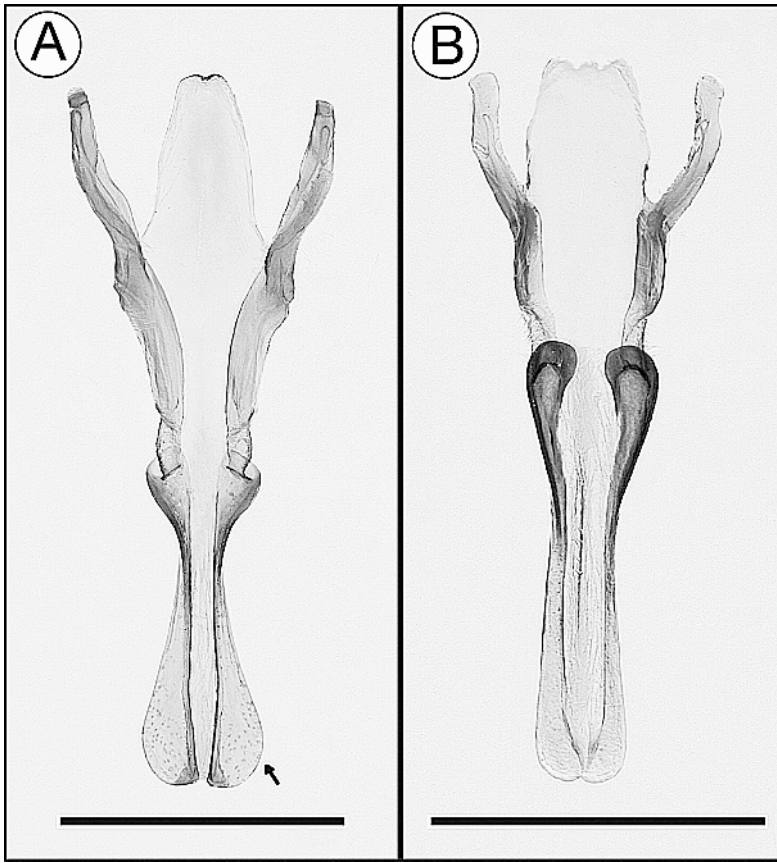


Fig. 14. Aedeagus: A, *Apoica gelida*, posterior end of aedeagus widening, B, *Apoica arborea*, posterior end of aedeagus straight. Scale bars = 1.0 mm.

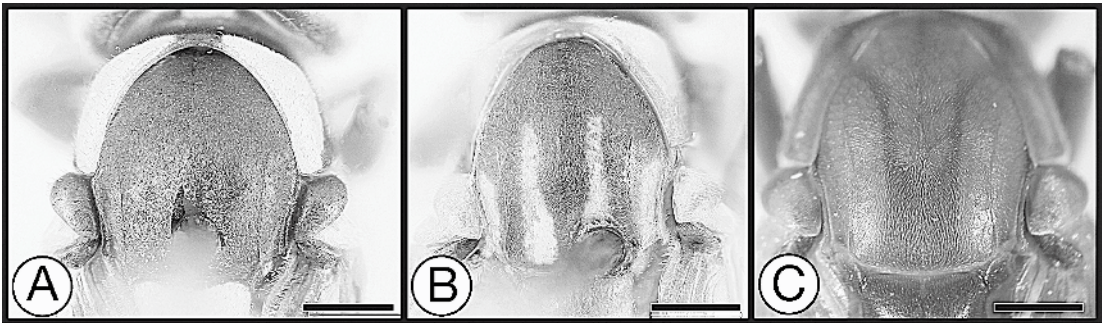


Fig. 15. Mesonotum with longitudinal stripes: A, *Apoica arborea* female, absent; B, *Apoica strigata*, 4 pale stripes, two on either side of the parapsidal furrows. The lateral two stripes are sometimes lacking. C, *Apoica ambracarina*, two dark stripes, medial to the parapsidal furrows, fusing posteriorly. Scale bars = 1.0 mm.

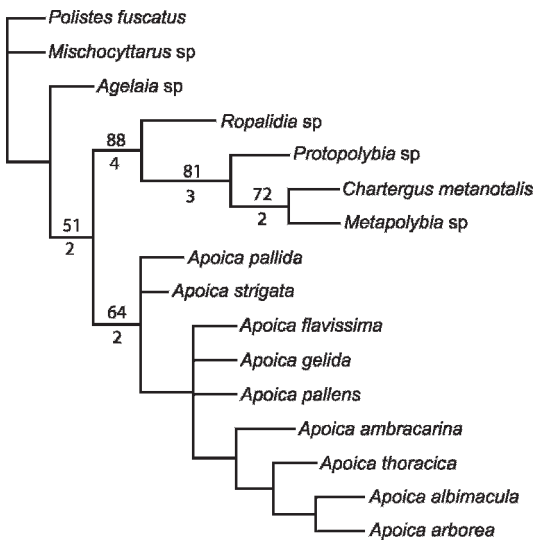


Fig. 16. Strict consensus ( $L = 94$ ;  $CI = 0.52$ ;  $RI = 0.64$ ) of three equally parsimonious topologies ( $L = 91$ ;  $CI = 0.53$ ;  $RI = 0.66$ ) of *Apoica* spp. and outgroups based on morphology and behavior. Numbers above and below each branch are jackknife and Bremer support values, respectively. Jackknife values below 50% and Bremer values of 1 are not reported.

consistent with the data of Carpenter (1991) and Wenzel and Carpenter (1994).

The monophyly of *Apoica* is strongly supported (98% jackknife, 9 Bremer). Relationships within *Apoica* are stronger than in either of the separate analyses (see figs. 16 and 17 above), which is common for simultaneous analyses. *A. arborea* is sister to the remaining *Apoica*, which is the only topology that is consistent with current subgeneric divisions. The placement of *A. albimacula* is not surprising, especially considering that its genitalia are markedly different than the other *Apoica* sensu stricto, and in many ways more similar to the genitalia of *A. arborea*. The well-supported, close relationship of *A. flavissima* and *A. pallens* is not surprising. However, the position of *A. gelida* is surprising, given that it has been thought a close relative of *A. pallens*. The clade to which it belongs is otherwise predictable. Richards (1978) predicted that *A. strigata* is close phylogenetically to *A. pallida*, and *A. ambracarina* is similar to these two in

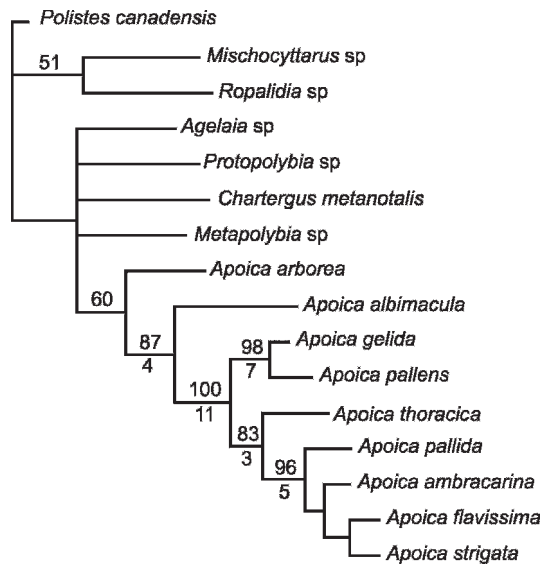


Fig. 17. Strict consensus ( $L = 500$ ;  $CI = 0.54$ ;  $RI = 0.47$ ) of three equally parsimonious topologies ( $L = 475$ ;  $CI = 0.57$ ;  $RI = 0.53$ ) of *Apoica* spp. and outgroups based on CO1. Numbers above and below each branch are jackknife and Bremer support values, respectively. Jackknife values below 50% and Bremer values of 1 are not reported.

the presence of a pale terminal metasomal tergum.

Contrary to general claims that molecular data override morphological signal, in this study, a number of traditional morphological characters performed more in line with prior expectation when analyzed in combination with molecules. For example, the CI for presence of tyloides (character 8) improves from 0.66 to perfect. Similarly, the presence of the epicnemial carina (character 13) improves from a CI of 0.50 to perfect. Remarkably, the complex suite of characters we call “swarming habit” (character 34), which is clearly a single origin with no known reversals within the Epiponinae, has only a CI of 0.50 when morphology and behavior alone are analyzed. This is because *Ropalidia* renders the Epiponini paraphyletic, another unexpected result. This unbelievable finding is rejected, and the traditional view supported only when molecules aid the morphology (swarm founding  $CI = 1.0$  under simultaneous analysis).

These improvements of morphological characters that have traditionally been viewed

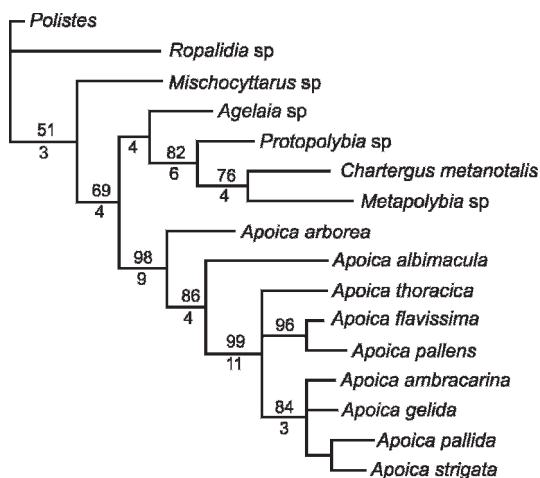


Fig. 18. Strict consensus ( $L = 592$ ;  $CI = 0.54$ ;  $RI = 0.52$ ) of two equally parsimonious topologies ( $L = 584$ ;  $CI = 0.54$ ;  $RI = 0.53$ ) of *Apoica* spp. and outgroups based on morphology, behavior, and CO1. Numbers above and below each branch are jackknife and Bremer support values, respectively. Jackknife values below 50% and Bremer values of 1 are not reported.

as homologous come at the cost of the performance of other morphological characters. However, the analysis of morphology and behavior already established the homoplastic nature of these characters—such as meso- and metapleural bristles (character 6), presence of the dorsal groove (character 11), various genitalic characters (digitus shape [18], digitus tip [19], paramere spine setae [24], posterior lobe of the paramere [25]), and color characters (scutum with longitudinal strips [28], color of the scutellum [29]). With the exception of the digitus shape character ( $CI = 1.0$  in tree from morphology and behavior;  $CI = 0.50$  in total evidence tree), all of these characters had  $CI$ 's of less than 0.50 in the tree based on morphology and behavior alone. So in this case, the equally weighted characters in the total-evidence analysis had an effect similar to successive approximations weighting (Farris, 1969; Carpenter, 1988) or implied weighting (Goloboff, 1993): Characters that performed well initially were perfected by minimizing the influence of characters that were already performing poorly.

## TAXONOMY

### Genus *Apoica* Lepeletier

*Apoica* Lepeletier, 1836: 536, genus (2 species).

Type species: *Apoica lineolata* Lepeletier, 1836 = *Vespa pallida* Olivier, 1792, by subsequent designation of Bequaert, 1943: 108.

### KEY TO SPECIES OF *APOICA* USING FEMALES

1. Flagellomeres clearly biconvex, almost beadlike (fig. 21A); hind wing with anal lobe present . . . . . Subgenus *DEUTERAPOICA* Dalla Torre, *arborea* de Saussure
  - 1a. Flagellomeres typically slightly convex dorsally, but ventrally almost flat (fig. 21B); hind wing with anal lobe absent or much reduced . . . . . 2, Subgenus *APOICA* Lepeletier
2. Dorsal surface of metasoma striped in appearance; metasoma light brown dorsally, light brown ventrally; pale apical margin of metasomal terga faint on T2 and T3, thin on T4 and T5; T6 entirely pale; scutum dark brown to black, always with at least two longitudinal pale stripes (fig. 15B) . . . . . *strigata* Richards
  - 2a. Dorsal surface of metasoma not striped in appearance. . . . . 3
3. Dorsal surface of metasoma entirely pale white to yellow, with no dark markings. . . . . 4
  - 3a. Dorsal surface of metasoma with obvious dark coloration . . . . . 6
4. Metanotal bristles reaching anterior margin of metanotum (fig. 6A); dorsal surface of propodeum and metasoma pale yellow in color; ventral surface also pale yellow, sometimes fading to light brown, but with no distinct separation from yellow of the dorsal surface; scutum light brown with 2 to 4 pale yellow longitudinal stripes . . . . . *flavissima* van der Vecht
  - 4a. Metanotal bristles not reaching anterior margin of metanotum (fig. 6B) . . . . . 5
5. Dorsal surface of metasoma pale white (worker) or cream (queen); ventral surface light brown with a distinct, sharp separation from the pale color of the dorsal surface; antennae mostly dark brown, pale at tips; scutum light brown with 2 to 4 darker brown longitudinal stripes . . . . . *gelida* van der Vecht
  - 5a. Dorsal surface of metasoma yellow, terga slightly darker apically; ventral surface light brown with a more or less distinct separation from the pale color of the ventral surface; antennae mostly dark brown, pale at tips;



Fig. 19. Habitus of the lone specimen and holotype of *Apoica ellenae*. Scale bar = 5.0 mm.

- scutum usually dark brown, occasionally light brown, with 2 to 4 pale yellow longitudinal stripes . . . . . *pallens* (Fabricius)

6. Posterior portion of first segment of metasoma and most of second metasomal tergum pale
- whitish-yellow; metanotum sharply angled posteriorly (fig. 5B) with prominent median carina (fig. 3C). . . . . *albimacula* (Fabricius)

6a. First and second terga of metasoma entirely dark brown to black, with no pale cuticular

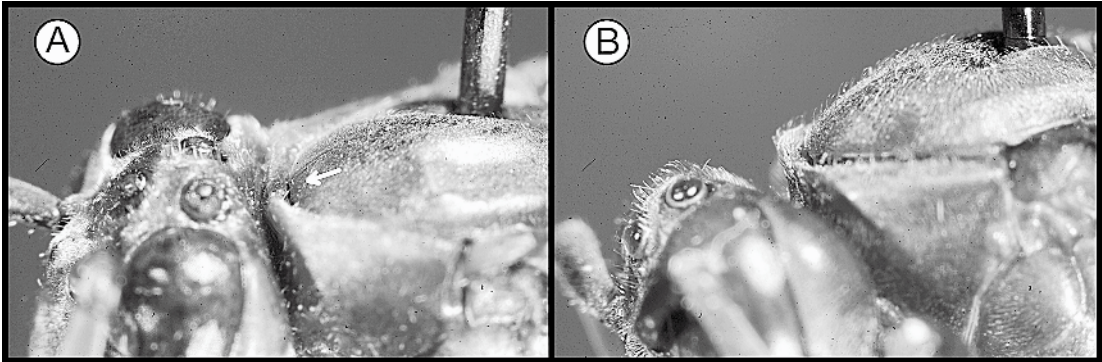


Fig. 20. A: *Apoica ellenae*. Mesonotum sits lower relative to pronotum, mesonotal bristles do not reach anterior margin; B: *Apoica thoracica*. Mesonotum sits higher (typical), mesonotal bristles reach anterior margin.

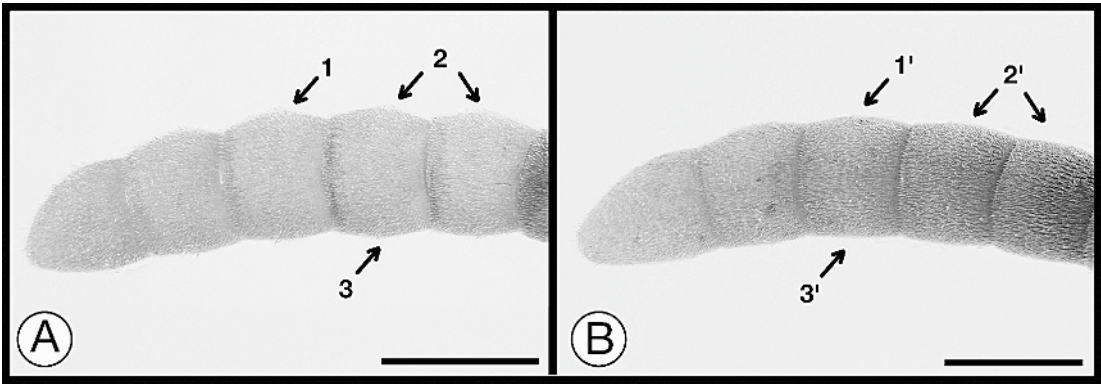


Fig. 21. Flagellomeres: **A**, *Apoica arborea*. Flagellomeres are “knotted”, or convex both dorsally (1 and 2) and ventrally (3); **B**, *Apoica pallida*. Dorsal flagellomeres are either slightly convex (1') or nearly flat (2'), as is typical of other vespids. Ventral flagellomeres are nearly flat (3').

- coloration as in 6; metanotum gently angled posteriorly (fig. 5A) . . . . . 7

7. Body almost entirely brown, with abdomen slightly lighter in color; final metasomal tergum either entirely pale or with pale color in V-shape apically; hairs prominent and present over surface of entire eye (fig. 2B) . . . . . 8

7a. Body entirely dark brown to black; final metasomal tergum never with strong pale color, occasionally with faint pale color on posterior tip of the tergum, but not in V-shape . . . . . 9

8. Mesonotum dark with central, strongly pale spot; meso- and metanotal bristles bent at nearly 90°, curving toward median (fig. 7B); metanotum without central carina (fig. 3A) . . . . . *pallida* (Olivier)

8a. Mesonotum entirely dark; meso- and metanotal bristles erect (fig. 7A), occasionally curving slightly, but not as extremely and uniformly as in other members of subgenus *Apoica*; metanotum with anterior, median carina (fig. 3B) . . . . . *ambracarina* Pickett

9. Fine pubescence generates a silvery-grey sheen over the meso- and metasoma, especially the metasoma . . . . . *ellenae* Pickett

9a. Lacking silvery-grey sheen; eye hairs absent or short and sparse at genal margin, rarely sparse across the entire surface (fig. 2A) . . . . . *thoracica* du Buysson

Subgenus *Apoica* Lepeletier

*Protapoica* Dalla Torre, 1904: 79, name for group I of genus *Apoica* Lepeletier in de Saussure, 1854, *Etudes sur la Famille des Vespides*. 2: 107 (two species).

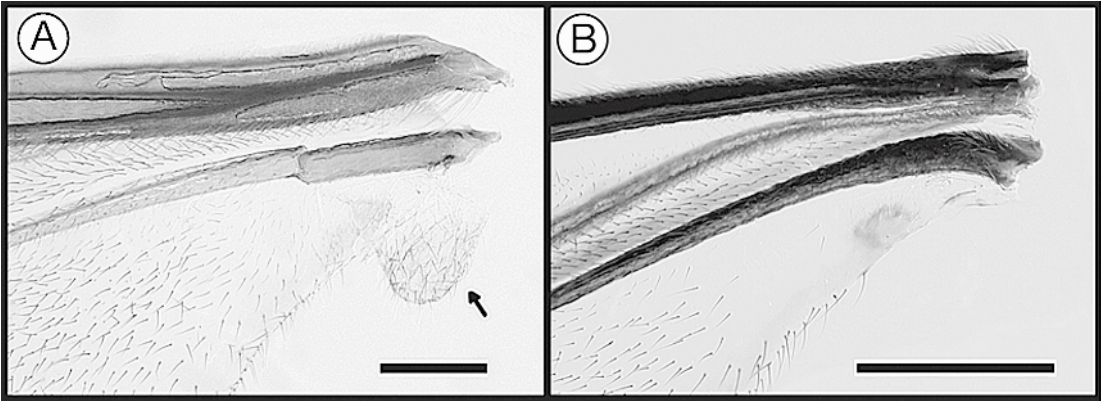


Fig. 22. Anal lobe: **A**, *Apoica arborea*, anal lobe present; **B**, *Apoica albimacula*, anal lobe absent (here severely reduced).

Type species: *Vespa pallida* Olivier, 1792, by subsequent designation of Richards, 1978: 264.

*Apoeca* Schulz, 1912, Berlin. Entomol. Zeitschr. 57: 84. Unjustified emendation.

*Apoica* (*Apoica*) *albimacula* (F.)

*Polistes albimacula* Fabricius, 1804: 277—"America meridionali" (Kobenhavn).

*Polybia albimaculata* [!]; de Saussure, 1854: 212, species dubiae. *Apoica virginea*, de Saussure, 1854: 212 [partim].

*Apoica pallida* var. *thoracica*, du Buysson, 1906: 343 [partim].

*Apoeca albimacula*, Schulz, 1912: 84. Unjustified emendation.

*Apoica pallida* var. *albimacula*; Bequaert, 1943: 117. *Apoica albimacula*; Richards, 1951, in Richards and Richards, 1951: 153; van der Vecht, 1972: 736. Richards, 1978: 262, 268.

DISTRIBUTION: Brazil: Amazonas, Pará; French Guiana; Guyana; Peru: Amazonas (new record), Suriname; Venezuela.

MATERIAL EXAMINED:<sup>4</sup> GUYANE: Massikiri-Oyapock, Nov 15 1969, "Balachowsky Gruner", det. J.v.d.Vecht, 1970 (3 females, MNHN); GUYANE, Itani, Ile de Touenké, Sep 19–21 1975, M. Boulard, P. Jauffret, det. B. Sigwalt, 1984 (1 female, MNHN); GUYANE, Itani, Molokoimené (Suriname), SEP 28 1975, M. Boulard P. Jauffret, (MNHN); FRENCH GUYANA, SAINT-ELIE, AUG 30–SEP 2 1975, M. Boulard P. Pompanon (MNHN); FRENCH GUYANA ("Guyane Franç"), Camopi, 1900, F. Geay, det. R. Du Buysson, 1906 as "*Apoica pallida* var. *thoracica*" (mentioned in Richards, 1978: 268; see Pickett, 2003: 597 for discussion) (2 females, MNHN); Brazil, Pará, "Bujaru", 04.viii.1978, P. Nolasco, (1 female, BMNH); Brazil, Pará, "Bujaru", 04.viii.1978, P. Nolasco, "Colônia no. 406", (1 female, BMNH); Brazil, Amazonas, Manaus "Reserva Ducke", 17/11/68, "caught at night" (1 female, 1 male, BMNH); Brit. Guiana, Moraballi Creek, 2-ix-29, "Oxf. Univ. Exp. Nest 1368", (2 females, BMNH); British Guiana, Esquito R. Moraballi Creek, 21.ix.29, "Oxf. Univ. Exp. N. 1368", (3 females, BMNH); N. Brazil: Pakaraima Mountains, 11–20.xi.32, C.V.-F.G. (2 females, BMNH [B.M. 1929-485]); SURINAME, Moengo, Boven "CotticaR", May 20, 1927, "Lot 760 Sub 68", det. J. C. Bequaert (as

"*Apoica pallida albimacula* Fab.") (1 male, CUIC). **New record**—Venezuela, Amazonas, Rio Mavaca Camp, 2°2'N, 65°06'W, 16–27/III/89, D. A. Grimaldi, "Phipps-FUDECI Exped. By Amer. Mus. Nat. Hist." (1 female, AMNH).

KMP has encountered some unusual specimens of *Apoica* (PERU: Dept. Amazonas, 5 km N. Pomacocha on road to Bioja. 2000 m; 7–8.X.1964; coll. P. C. Hutchinson & J. K. Write [CAS, 27 females, 1 male]; PERU: Vale, Cosñipata, F. Woytkowski, "ex - col Weyrauch", Collection Inst. Fund. M. Lillo (4000) - S. M. Tucuman, Tucuman, Argentina [1 female]) that are very similar to *A. albimacula*, except the pronotal fovea does not sit as recessed as typical *A. albimacula*, and nearly every metasomal tergum is anteriorly pale-yellowish, rather than the typical pale coloration of *A. albimacula*, which is restricted to metasomal segments one and two. However, KMP has dissected the lone male from the CAS series, and its genitalia are quite similar to typical *A. albimacula*. Therefore, unless further information comes to light, these specimens should be treated as *A. albimacula*.

*Apoica* (*Apoica*) *ambracarina* Pickett

*Apoica thoracica*; Richards, 1978: 268 [partim].

*Apoica ambracarina*; Pickett, 2003: 592. Holotype female, MZUSP.

DISTRIBUTION: Brazil: São Felix do Xingu; Colombia: Tuparro Cerro Tomas, Valle (new record).

MATERIAL EXAMINED: Brazil: Acre, Rio Branco, coll. S. Mateus and F. B. Noll, 10 X 1998. (Holotype) Paratypes: 40 workers, 5 males, and 5 queens (MZUSP); 20 workers, 3 males, 2 queens (OSUC); 20 workers, 3 males, 2 queens (AMNH). Colombia: Vichada PNN, Tuparro Cerro Tomas 140 m, 5°21'00"N 67°51'36"W, 8–28 aug 2000 W. Villalba, "Sample No 513" (1 female, coll. C. Sarmiento, IAVH); Colombia: Vichada PNN, Tuparro Cerro Tomas 140 m, 5°21'00"N 67°51'36"W, 18–28 aug 2000 W. Villalba, "Sample No 516" (1 female, coll. C. Sarmiento, IAVH); Colombia: Vichada PNN, Tuparro Cerro Tomas 140 m, 5°21'00"N 67°51'36"W, 29 jun–15 jul 2000 Malaise, "Sample No 269 W. Villalba" (1 female, coll. C. Sarmiento, IAVH); Brazil: "Moyen XINGU (Brésil)", Mission M. Boulard, P. Jauffret et P. Pompanon, Museum PARIS, SAO

<sup>4</sup>In all Materials Examined sections, with the exception of italicized species names, label content is reported with the intent to represent it exactly as it appears (i.e., variations in capitalization, etc. are respected). Quotation marks around label data indicate commentary information as it appears on the label.

FELIX DO XINGU, 1–4-X-1975 (5 females, MNHN); Moyon XINGU (Brésil), Mission M. Boulard, P. Jauffret et P. Pompanon, Museum PARIS, SAO FELIX DO XINGU, 29–30-IX-1975” (4 females, one determined *A. thoracica* B. Sigwalt 1984, MNHN). **New records:** COLOMBIA: Valle, Anchicaya nr. Buenaventura 300 m., 25.iv.1972, M. Cooper, (1 male, BMNH, B.M. 1972-275).

*Apoica (Apoica) ellenae* Pickett, new species

figures 19, 20A

**DIAGNOSIS:** Eye hairs sparsely present and prominent over the entire surface of the eyes. Mesonotum sits more deeply into the pronotum than in other *Apoica* (fig. 20A). Pronotal fovea recessed into a pit. Metanotal bristles curved; mesonotal bristles not reaching anterior margin; mesonotum, metanotum, and dorsal metasoma covered with fine, silvery-grey pubescence.

**DESCRIPTION:** Wing length 15.0 mm. *Color*—Brown cuticle with silvery-grey “frosting” (especially the dorsal metasoma) due to fine pubescence. Two short pale longitudinal mesonotal marks appear medial to parapsidal furrows, but not reaching anterior or posterior border of the mesonotum.

**DISTRIBUTION:** *Apoica ellenae* is known only from the type locality, Barro Colorado Island, Panama.

**TYPE MATERIAL:** Female holotype: Panama CZ, Barro Colorado I., 6–12 XI 1980, H. Wolda I. N. SM, deposited in the Bohart Museum of Natural History (UCD).

**ETYMOLOGY:** The name honors KMP’s late sister-in-law, Ellen English Pickett, who loved animals.

**REMARKS:** The phylogenetic placement of *A. ellenae* is uncertain, mainly because neither male genitalia characters nor DNA can be coded. *A. ellenae* is certainly a member of subgenus *Apoica*, due to its possession of a reduced anal lobe in the hind wing and the structure of the flagellomeres (see below). Its robust form would suggest a potentially close relationship with *A. albimacula* or *A. thoracica*; this is further supported by the presence of a pit into which the pronotal fovea is recessed. However, the silvery dorsal metasomal pubescence resembles that of *A. gelida*, which would tend to place *A. ellenae* among the more

derived *Apoica*. Resolution of this matter awaits the collection of males and other female specimens. Unfortunately, this may not be forthcoming. As Barro Colorado Island is so heavily trafficked by research scientists, it seems unlikely that the species could go uncollected, save a single specimen, if the species were extant. Perhaps fragmented populations persist elsewhere.

*Apoica (Apoica) flavissima* van der Vecht

*Apoica pallida*; Fox, 1898: 445 [partim].

*Apoica flavissima* van der Vecht, 1972: 736, 739, 741, figs. 1, 4, 12 (holotype male, RMNH).

**DISTRIBUTION:** Argentina: Salta; Bolivia: Beni; Brazil: Acre, Alagoas, Amazonas, Espírito Santo, Goiás, Maranhão, Mato Grosso, Minas Gerais, Pará, Paraíba, Rio de Janeiro, Rondônia, Roraima, São Paulo; Panama; French Guiana; Guyana; Paraguay; Peru: Cuzco, Huánuco, Loreto, Madre de Dios (new record); Suriname.

**MATERIAL EXAMINED:** British Guiana: Confluence of Oronoque & New Rivers, ix–xii.1937, *Apoica flavissima*, det. J.v.d. Vecht, 1970 (BMNH, B.M. 1938-319, 1 female); British Guiana: New River, 15–25.11.1938, C. A. Hudson, det. *Apoica flavissima*, J.v.d. Vecht, 1970 (BMNH, B.M. 1939-370, 1 female); Peru: Loreto, Pucallpa, 11.1.1961, J. M. Schunke, (BMNH, B.M. 1961-641 female); Bresil: Uberaba, 1900 (BMNH, B. M. 1942-95, 1 female); Brazil: Minas Gerais, Conceicao das Alagoas, iii.1973 (BMNH, 2 females); BRAZIL: Pará, Santerem, Taperinha, 2d54S, 54d20W, 2 xii 1978, (BMNH, 1 female); Brasil: Amazonas, Manaus “Res. Ducke” (BMNH, 1 male); PANAMA: Porto Armullis, July 1934, F. Peek, det. *Apoica flavissima*, “v.d.v.” (J.v.d. Vecht) (BMNH, 1 female); Brazil: Brasilia, Ninha Cab. De Veado, 12 Oct 1982, A. Raw (BMNH, 1 female); Brit. Guiana: Confluence of Oronoque & New Rivers, ix–xii.1937 (BMNH, B.M. 1938-319, 1 female); GUYANA: Demerara, CEIBA Biological Sta., 06d 18m N, 60d 35m W, 6 March 1997, J. H. Hunt (pers. coll. J. H. Hunt, 2 females); GUYANA: Berbice, Dubulay Ranch, 06d 21m N, 57d 60m W, 8–11 March 1997, J. H. Hunt and J. N. Seal (personal coll. J. H. Hunt, 1 female); Guyana: Essequibo Cnty, Potaro Dist., Kaieteur Falls National Park, 05d 10m N, 59d 30m W, 14 March 1997 and J. N. Seal (personal coll. J. H. Hunt, 1 female); BRAZIL: Goiás, Santa Isabel, Ilha do Bacanal, Rio Araguaia, VIII-12 to 22–57,

Borys Malkin (CAS, 2 females, 1 male); BRAZIL: Goiás, 5 mi. E. of E. branch Rio Araguaia, between Loroti & Rio Formosa, VII-15 to 25-57, Borys Malkin (CAS, 1 female); Peru: Madre de Dios, Rio Tambopata Reserve, 30 air km SW of Puerto Maldonado, November 1-26 1982, Edward S. Ross (CAS, 2 females); Peru: Monson Valley, Tingo Maria, IX-23-1954, E. I. Schlenger and E. S. Ross (CAS, 1 female); BRAZIL: Minas Gerais, Lassanoe, 9-19 Nov. 1919, R. G. Harris, det. Apoica flavissima, J. C. Bequaert, as Apoica pallida pallens Fab. (J. M. Carpenter det. one specimen in series as *A. flavissima* van der Vecht.) (CAS, Lot 569 Sub 110, 78 females, 1 male); Suriname: Dirkshoop, 21 May 1963, J.v.d. Vecht (RMNH, 8 females); Suriname, Sinaliwini, 9 March 1961, D.C. Geyskes (RMNH, 1 female); Suriname, Tafelbery, 19-X-1972, G.F. Mees (RMNH, 1 female).

*Apoica (Apoica) gelida* van der Vecht

*Apoica pallida*; Fox, 1898: 445 [partim].

*Apoica pallens* form C; Richards, 1951, in Richards and Richards, 1951: 156, fig. 24 [partim].

*Apoica gelida* van der Vecht, 1972: 736, 739, 741, figs. 2, 5 (holotype male, RMNH).

DISTRIBUTION: Brazil: Amazonas, D. F., Goiás, Mato Grosso, Minas Gerais, Pará, Rio de Janeiro; Colombia; French Guiana; Guyana; Peru: Huánuco; Suriname; Trinidad; Venezuela.

MATERIAL EXAMINED: Brazil: Mato Grosso, 12d 50m S, 51d 47m W, 14.IV.1968, O. W. Richards (BMNH, 12 females); Brazil: Goiás, Crystallina "Crystallandia", 9 Oct 68 (BMNH, 2 females); Trinidad: Siparia, 26.vII.1929, det. Apoica gelida, J.v.d. Vecht, 1971 (RMNH, 1 PARATYPE female); Trinidad, Mt. St. Benedict, VII-1929, Apoica gelida, J.v.d. Vecht, 1971 (RMNH, 4 PARATYPE females).

The dorsal metanota of *A. gelida* workers are nearly white, while those of the queens are cream colored (discovered by F. B. Noll). This is almost never apparent in pinned specimens, though it is clear in alcohol preserved specimens.

*Apoica (Apoica) pallens* (F.)

*Polistes pallens* Fabricius, 1804: 276—"America meridionali" (lectotype female Kobenhavn).

*Apoica pallida*; Lepeletier, 1836: 538 (misidentification).

*Apoica pallida* var. *pallens*; du Buysson, 1906: 342.

*Apoeca pallida*; Schulz, 1912: 84 (unjustified emendation).

*Apoica pallens*; Richards, 1951, in Richards and Richards, 1951: 153, fig. 23 [partim: form A].

DISTRIBUTION: Argentina: Misiones; Belize; Bolivia: Cochabamba, Santa Cruz; Brazil: Amapá, Amazonas, D. F., Goiás, Mato Grosso, Minas Gerais, Pará, Paraná, Rio Grande do Sul, Rio de Janeiro, Santa Catarina, São Paulo; Colombia: Amazonas, Bolívar, Cundinamarca, Putumayo; Costa Rica; El Salvador; Ecuador: Pichincha; French Guiana; Guatemala; Guyana; Mexico; Nicaragua; Panama; Paraguay; Peru: Cuzco, Huánuco, Junín, Loreto; Suriname; Trinidad; Venezuela: Amazonas, Aragua (new record), Barinas, Cojedes (new record), Guárico, Mérida, Yaracuy, Zulia.

MATERIAL EXAMINED: PANAMA: Barro Colorado Island, 9d 9m 30s N, 79d 51m W, 22-28-III-1977, H. Wolda (RMNH, 10 females); Brazil, Espirito Santo, Sta. Teresa, 19.ix.71, E.G. Mumiae (BMNH, 1 female); Panama: Canal Zone, 21.viii.1929, L. E. Cheesman (BMNH, 1 female); Colombia, Bolívar, 15.iv.70, F. Schremmer (BMNH, 1 female); PERU: Huanuco, Tingo Maria, 21-23.viii.1971, C. & M. Vardy (BMNH, B.M 1971-533, 1 female); Brazil: Mato Grosso, 12d 50m S, 51d 47m W, 14.IV.1968, O. W. Richards, (BMNH, 6 females); Brazil: Ribeirão Preto, 1.iii.74, D. Simões, "N. 221" (BMNH, 1 female); Trinidad: Coryal, 25-5-85, E. D. Bennett (BMNH, 1 female); Colombia: Rio Frio, 15-XII-1926, George Salt (BMNH, 1 female); PERU: Loreto, 03d 15m 30s S, 03d 54m 45s W, 16 June 1997, J. H. Hunt (personal coll. J. H. Hunt, 29 females); Costa Rica: Coto Brus, Las Cnjoes, 18 Feb 1996, M. Singer (personal coll. J. H. Hunt, 1 female); MEXICO: Chiapas, Ocozocoautia, 16-I-1972, D.E. Breedlove (CAS, 2 females); MEXICO, Chiapas, Palenque, 29-X-1976, Edward S. Ross (CAS, 4 females); MEXICO, Chiapas, Municipio de Ocosingo, 1.IX.1981, D.E.& P.M. Breedlove, 15 km SW. of Ocosingo on road to Sn Cristóbal de Las Casas (CAS, 1 female); **New records:** VENEZUELA, Cojedes, Hato Piñero, October 1993, R. Jeanne, M. Keeping, J. Hunt, det. Apoica pallens, J. M. Carpenter, 1994 (personal coll. J. H. Hunt, 14 females); VENEZUELA: Aragua, Rancho Grande Parque Nacional "Henry Pittier", III-4-1967, M.E. Irwin (CAS, 32 females).

*Apoica (Apoica) pallida* (Olivier)

*Vespa pallida* Olivier, 1792: 675, female—"l'isle de la Trinité" (type lost).

*Apoica lineolata* Lepeletier, 1836, Hist. Nat. Ins. Hym. 1: 537, female? —[Argentina] “Buenos-Ayres, Amérique méridionale” (type lost?).

*Polistes translucida* Spinola, 1851: 63—[Brazil] “Para” (Torino?).

*Apoica pallida*; de Saussure, 1854: 107, pl. XVIII fig. 1 (syn.: *P. pallens* Fabricius). *Apoica virginea*; de Saussure, 1854: 107 (syn.: *Apoica bilineolata* [!]), 244 [partim]. (misidentification).

*Vespa pallens*; Dalla Torre, 1904: 79 [lapsus].

*Apoica lineata* [!]; du Buysson, 1906: 359.

*Apoica pallida* var. *virginea*; Ducke, 1910: 517, fig. 11.

*Apoica pallida pallida*; Araújo, 1960: 251.

**DISTRIBUTION:** Belize; Bolivia: La Paz, Santa Cruz; Brazil: Acre, Amapá, Amazonas, Ceará, Goiás, Maranhão, Mato Grosso, Pará, Rondônia, Roraima, São Paulo; Colombia; Ecuador: Pichincha; French Guiana; Guyana; Peru: Huánuco, Junín, Loreto, Pasco; Trinidad; Suriname; Venezuela: Aragua, Monagas.

**MATERIAL EXAMINED:** BRAZIL: Pará, Santarem, Taperinha, 2d 54m S, 54d 20 W, 30 X 1978, R. L. Jeanne (BMNH, 1 female); BRAZIL, Pará, Belém, 10.7.64 (BMNH, 1 female); SURINAM: Marowijne River, vii.1965, E.A.M. Gale, “Cambridge Exped.” (BMNH, B.M. 1965-516, 1 female); ECUADOR: Pichincha, n. Nanegal, 19–20.ix.1977 (BMNH, 2 females); Bresil: Pará, Belém Mocambo, 23-viii.1978, R B Neto (BMNH, 1 female); PERU, Loreto, Pucallpa, lake Yarina Cocha, 26–27.viii.1971, C. & M. Vardy (BMNH, B.M. 1971-533, 1 female); TRINIDAD, St. George, St. Augustine, 16.iv.1976, J.S. Noyes (BMNH, 1 female); TRINIDAD, Toco, 11.xi.90, det. *Apoica pallida*, A. Polazsek 1992 (BMNH, 1 female); SURINAM, 1932, G. Bunzli (BMNH, 1 female); TRINIDAD, 14.IV.1937, Miss M.E. Fountaine, (BMNH, B.M. 1937-434, 1 female); Trinidad: Curepe, 17-5-1986, E. D. Bennet (BMNH, 1 female); Guyana: Berbice, CEIBA Biological Sta., 06d 18m N, 60d 35m W, 6 March 1997 (personal coll. J. H. Hunt, 1 female); Guyana: Berbice, CEIBA Biological Sta., 06d 18m N, 60d 35m W, 5 March 1997 (personal coll. J. H. Hunt, 1, female); Guyana: Berbice, Dubulay Ranch, 05d 21m N, 57d 60m W, 8–11 March 1997 (pers. coll. J. H. Hunt, 1 female); TRINIDAD, St. George, St. Augustine, iv.1977 (BMNH, 1 female); SURINAME: Maratakka River, Awarra-savanna, 26.II-3.III.1971, D.C. Geijskes, det. *Apoica pallida*, J.v.d. Vecht, 1971 (RMNH, 2 females); Suriname: “Marowijne creek”, 29 July 1964, D.C. Geijskes, det. *Apoica pallida*, J.v.d. Vecht, 1971 (RMNH, 1 female); Suriname: Zorgen Hoop, Paramaribo, 10 Okt 1963, J.W. Brockhuizen, det. *Apoica pallida*, J.v.d. Vecht, 1967, 55 (RMNH, 5 females);

Suriname, Paramaribo, 1 Nov 1963, J.W. Brockhuizen, det. *Apoica pallida*, J.v.d. Vecht, 1967 (RMNH, 1 female); Suriname, Luciekamp, 13 July 1963, H. P. Pijpers, det. *Apoica pallida*, J.v.d. Vecht, 1971 (RMNH, 1 female).

Although the type of *A. pallida* has been lost, and although the concept has had a convoluted history, we do not think the situation requires the designation of a neotype. The ICZN states (Article 75.2, page 84):

A neotype is not to be designated as an end in itself, or as a matter of curatorial routine, and any such neotype designation is invalid.

A valid neotype designation requires that, in addition to the loss of the name-bearing type, there be an “exceptional need” to solve “a complex zoological problem” (Article 75.3, page 84–85). At a minimum, the identity of the species must be in doubt, and this is not the case for *A. pallida*.

### *Apoica (Apoica) strigata* Richards

*Apoica virginea*; de Saussure, 1854: 107 [partim].

*Apoica pallida* “typical form”; Bequaert, 1943 (1942): 110 [partim].

*Apoica pallida* var. *arborea*; Bequaert, 1943 (1942): 116 [partim].

*Apoica strigata* Richards, 1978:262 (key), 267, fig. 107, female, male, “PERU: Junín, Chanchamayo” (holotype female, BMNH).

**DISTRIBUTION:** Brazil: Acre, Amazonas, Maranhão, Mato Grosso, Pará; Bolivia: Cochabamba; Costa Rica; Colombia: Amazonas, Caquetá, Meta; Ecuador: Napo, Pichincha; Guyana; Peru: Cuzco, Huánuco, Junín, Loreto; Trinidad.

**MATERIAL EXAMINED:** Brit. Guiana: Confluence of Oronoque & New Rivers, ix–xii.1937 (BMNH, Brit. Mus. 1938-319, 1 female); PERU, Loreto, Pucallpa (sic), 5.v.1962, J.M. Schunke, det. *Apoica strigata*, O. W. Richards (BMNH, B.M. 1962-491, 1 PARATYPE female); PERU: Chanchamayo, 4-iii-1949, J.M. Schunke, det. *Apoica strigata*, O. W. Richards (BMNH, B.M. 1962-645, 1 PARATYPE male); PERU: Huanuco, Tingo Maria, 21–23.viii.1971, C. & M. Vardy (BMNH, B.M. 1971-533, 2 males); GUYANA, 1974, S. Rawlins (BMNH, 1 male); Trinidad: May 1924, L.E. Cheesman, det. Cheesman as *Apoica virginea* (BMNH, 1 PARATYPE, male). ECUADOR: Pichincha n. Nanegal, 19–20.ix.1977 (BMNH, 1

male); PERU: Loreto, 03d 15m 30s S, 72d 54m 45s W, J. H. Hunt (personal coll. J. H. Hunt, 44 females); PERU: Huanuco, Rondos nr. Monzon, 24.ix.1960, J.M. Schunke (BMNH, B.M. 1961-64, 1 male).

Although Richards (1978) was correct to describe *A. strigata*, as it is clearly not *A. arborea*, he was incorrect when he said that *A. arborea* never has pale longitudinal stripes on its mesonotum. *A. arborea* males do have "striped" scuta, even though the females never have this character. In fact, male *A. arborea* look very much like male *A. strigata*, but *A. arborea* can always be distinguished from all other *Apoica* by its flagellomeres (fig. 21) and hind wing (fig. 22). In addition, the genitalia of *A. strigata* and *A. arborea* are quite distinct (for example, see fig. 8).

#### *Apoica (Apoica) thoracica* du Buysson

*Apoica pallida*; Fox, 1898: 445 [partim].

*Apoica pallida* var. *thoracica* du Buysson, 1906: 340, 343, female—"Brésil: Espírito Santo" (lectotype female, ZMH); also from French Guiana.

*Apoica thoracica*; Richards, 1951, in Richards and Richards, 1951: 152.

**DISTRIBUTION:** Bolivia: Cochabamba, La Paz, Santa Cruz; Brazil: Acre, Amapá, Amazonas, D. F., Espírito Santo, Goiás, Mato Grosso, Minas Gerais, Pará, Paraná, Rondônia, Roraima, São Paulo; Colombia: Amazonas, Caquetá, Meta, Putumayo, Valle; Costa Rica; Ecuador: Napo, Pichincha; French Guiana; Guatemala; Guyana; Honduras; Panama; Peru: Cuzco, Huánuco, Junín, Loreto, Pasco; Suriname; Venezuela: Amazonas, Barinas, Miranda.

**MATERIAL EXAMINED:** ECUADOR: Pichincha, n. Nangegal, 19-20.ix.1977 (BMNH, 1 female); BRAZIL: Mato Grosso, 12d 50m S, 51d 47m W, 19-X-1968, O. W. Richards, nest 1999 Oxf. Univ. Exp (BMNH, 1 female); Brit. Guiana: Moraballi Creek, 12.ix.1929 (BMNH, 1 female); PERU: Huanuco, Chinchao, 23.x.1973, J.M. Schunke, s-w of Tingo Maria (BMNH, B.M. 1974-37, 1 female); COLOMBIA: Putumayo, Mocoa, 24.ix.1974, M. Cooper (BMNH, B.M. 1975-33, 1 female); ECUADOR, Orinta, Zasayacu, 12.xi.68, L.E. Pena (BMNH, B.M. 1974-267, 1 female); British Guiana: Essequibo R., Moraballi Creek, 29/30.viii.1929, Oxf. Univ. Expedn. (BMNH, B.M. 1929-485, 1 female); PERU: Oxapampa, 1940,

Weyrauch, 1600 m (BMNH, 1 female); PERU: Chanchamayo, 7.iii.1949, J.M. Schunke (BMNH, B.M. 1952-645, 1 female); Brazil: Brasília, Lago Sul, 17.3.1977, A. Raw (BMNH, 1 female); Costa Rica, Coto Brus, Las Cnjoes, 18 Feb 1996, M. Singer, (pers. coll. J. H. Hunt, 1 female); Costa Rica, Turrialba, Cartago, 9-III-1967 (BMNH, 2 females); BRASIL, Amazonas, Rio Purus, between Beruri & Ariapua, 21.XI 1971, H. & P. Mass (RMNH, 2 females); BRASIL: Amazonas, Rio Purus, Tapaua, 21.XI 1971, H. & P. Mass (BMNH, 1 female).

Van der Vecht (1972) noted differences in the parameral spine of *A. thoracica*. The difference, whether "bent" or not, corresponds to true *A. thoracica* (which is not curved) and *A. ambracarina* (which is curved). Richards (1978) apparently included *A. ambracarina* in his concept of *A. thoracica* (see Pickett [2003]), but he also apparently included certain specimens of *A. pallida* in his concept of *A. thoracica*, as did Bequaert (1943; see above). This is evidenced by Richards' (1978: 262) key, which indicates that *A. thoracica* is "sometimes with a pale spot" on its metanotum. In reality, *A. thoracica* is a very dark animal that always lacks any pale coloration on its metanotum, as is always seen in *A. pallida*. *A. thoracica* also rarely has any pale coloration on its final metasomal tergum, and when this is present, it is also more faint than in *A. pallida* and restricted to the posterior tip of the tergum, but not in a V-shape as in *A. ambracarina*. When these faint pale colors appear in *A. thoracica*, the animal has a lighter dark brown metasoma and short, sparse eye hairs over the entire surface of the eye; the typical form, which is uniformly dark brown, lacks these pale spots and eye hairs (except perhaps at the genal border).

The confusion surrounding *A. thoracica* may because it is perhaps the most variable of all *Apoica* spp. With further study, additional species may be described from within *A. thoracica*. For example, *A. thoracica* has a typical form, which is uniformly dark brown to black and lacks eye hairs, and has no metanotal carina. But there are other specimens that have a lighter metasoma and have sparse eye hairs (similar to *A. ambracarina*), but lack a metanotal carina; the dorsal half of the terminal metasomal tergum of these specimens is also pale. This variant may be simply

a variant, or it may represent a distinct species or the worker caste. Until we have seen entire colonies of this variety, we are not content to describe it as a new species.

### Subgenus *Deuteraipoica* von Dalla Torre

*Deuteraipoica*. Dalla Torre, K. W. von. 1904 Hymenoptera, Vespidae. In Wytsmann's Genera Insectorum, 19. Brussels. Type-species: *Apoica arborea* de Saussure, Études sur la Famille des Vespides. 1954.

### *Apoica* (*Deuteraipoica*) *arborea* de Saussure

*Apoica arborea* de Saussure, 1854: 108; 1855: pl. XXVI, fig. 1. Holotype female, S. America (depository unknown).

*Apoica pallida* var. *arborea*: Bequaert, 1943: 116 [partim].

DISTRIBUTION: Bolivia: Santa Cruz; Guatemala (new record); Brazil: Acre, Amazonas, Goiás, Maranhão, Mato Grosso, Pará, Rondônia; Colombia: Caquetá; Ecuador: Napo; French Guiana; Guyana; Peru: Cuzco, Huánuco, Junín, Loreto; Suriname.

MATERIAL EXAMINED: GUYANE: SAUT-MARIPA, OYAPOCK, 24 Nov 1969, OCT-NOV-1969, (RMNH, 2 females). Suriname: Krakka, 19 Sept. 1962, G. v. Vreden (RMNH, 1, female); Suriname: Blakawatra, 12 June 1963 (RMNH, 2 females); Suriname: Sarakraak Dam, 17 Dec. 1963, D.C. Geyskes, (RMNH, 2 females); Suriname, Suriname River, 10 Dec 1962, D.C. Geyskes (RMNH, 1 female); British Guiana: New River, 20–23.iii.1938, C. A. Hudson (BMNH, B. M. 1979-106, 1 female); Colombia: Caqueta, Yuruyaco, M. Cooper (BMNH, 1 female); British Guiana, Kutari Sources, 10.i–10.ii.1936, G. A. Hudson (BMNH, B. M. 1936-360, 1 female); British Guiana: New River, 26–27.iii.1938, C. A. Hudson, (BMNH, B. M. 1936-370, 1 female); Guyana: Imbaimadai, 9.iv.1972, A. Harman (BMNH, B. M. 1936-308, 1 female); Brazil: Mato Grosso, 12d 50m S, 51d 47m W, 1–2.iii.1968, O. W. Richards (BMNH, B. M. 1968-260, 1 female); Brazil, Mato Grosso, 12d 50m S, 51d 47m W, 19.x.1968, O. W. Richards (BMNH, B. M. 1968-260, 1 female); Ecuador: Napo Pastaza, Dureno, 23–30.x.1977, L. E. Penna (BMNH, B. M. 1978-293, 1 female); British Guiana: Kaieteur: Savana, 8.ix.1937, Richards & Smart (BMNH; B. M. 1937-776, 1 female); Brasil: Amazonas, Manaus, Reserva Ducke (BMNH, 1 female); Brazil: Xambioa-bo, Sep 1972, F. G. Moreira, (BMNH, 1 female);

Brazil: Mato Grosso, 12d 50m S, 51d 47 W, 24.11.1968, O. W. Richards (BMNH, B. M. 1968-260, 1 female); British Guiana: Issororo, June 1915, G. E. Soika (BMNH, 1 female); PERU: Amazon Camp, Rio Momón, December 1–10, 1982, Edward S. Ross, det. *Apoica arborea*, H.K. Court, 1995 (CAS, 9 females); Guyana, Valle, Dubulay Ranch, 05d 21m N, 67d 60m W, 11 March 1997, J. H. Hunt, (personal coll. J. H. Hunt, 1 female); **New record:** GUATEMALA: Puerto Barrios, 1–10.I.1966, J. Geyskes, det. *Apoica, arborea*, J.v.d. Vecht, 1970 (RMNH, 2 females).

*A. strigata* was confused with *A. arborea* because, like *A. arborea*, its metasomal terga are dark with pale apical borders. However, the diagnostic character of *Deuteraipoica* is the biconvex, almost beadlike shape of the flagellomeres (fig. 21). This character is autapomorphic for *A. arborea*, and so was not included in the cladistic analysis (above). Richards (1978: 261) hinted at this character when he said that *Deuteraipoica* has “Antennae more knotted beneath.” However, as fig. 21 clearly shows, the dorsal surfaces of the flagellomeres are also much “more knotted” than in subgenus *Apoica*.

Members of subgenus *Apoica* also lack or nearly lack an anal lobe (fig. 22). Van der Vecht (1972) and Richards (1978) have noted that the anal lobe is reduced in subgenus *Apoica*. Other characteristics of *A. arborea* include mesonotal bristles reaching anterior margin, but bristles less than half as long as in other species; metasoma dark brown to black dorsally, brown ventrally; pale posterior margin of metasomal terga thick and prominent on all terga; scutum entirely dark brown to black, never with yellow stripes.

Even though the holotype is believed lost, we are not designating a neotype here, as this action is unnecessary in this case. As in the case of *A. pallida*, there is no “complex zoological problem”. In fact, *A. arborea* is easily the most monolithic of the species, and its identity is not in question.

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APPENDIX 1  
MORPHOLOGICAL MATRIX FOR CHARACTERS AND STATES USED IN ANALYSIS OF *Apoica*  
AND OUTGROUPS

|                               | 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
|-------------------------------|-----------------------------------------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|                               | 1                                                   | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 |   |   |   |
| <i>Polistes fuscatus</i>      | 0                                                   | 0 | 0 | 1 | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 3 | 3 | 0 | 0 | 0 |   |   |
| <i>Agelaia</i> sp.            | 0                                                   | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 |   |   |
| <i>Chartergus metanotalis</i> | 0                                                   | 0 | 0 | 0 | 3 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 3 | 3 | 0 | 2 | 1 |   |   |
| <i>Metapolybia</i> sp.        | 0                                                   | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 3 | 0 | 3 | 0 | 3 | 1 |   |   |
| <i>Mischocyttarus</i> sp.     | 0                                                   | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 2 | 3 | 3 | 0 | 0 | 0 |   |   |
| <i>Protopolybia</i> sp.       | 0                                                   | 0 | 0 | 2 | 3 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 2 | 3 | 3 | 0 | 2 | 1 |   |   |
| <i>Ropalidia</i> sp.          | 0                                                   | 0 | 0 | 0 | 3 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 3 | 3 | 0 | 0 | 0 |
| <i>Apoica albimacula</i>      | 1                                                   | 1 | 2 | 2 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 1 |   |
| <i>Apoica ambracarina</i>     | 1                                                   | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 2 | 1 | 1 | 1 | 0 | 1 |   |   |   |   |
| <i>Apoica arborea</i>         | 1                                                   | 1 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 1 | 0 | 1 |   |   |
| <i>Apoica flavissima</i>      | 1                                                   | 1 | 0 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 2 | 1 | 0 | 1 |   |   |   |
| <i>Apoica gelida</i>          | 1                                                   | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 1 | 1 | 0 | 1 |   |   |
| <i>Apoica pallens</i>         | 1                                                   | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 1 |   |   |
| <i>Apoica pallida</i>         | 1                                                   | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 |   |   |
| <i>Apoica strigata</i>        | 1                                                   | 1 | 0 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 3 | 1 | 0 | 1 |   |   |
| <i>Apoica thoracica</i>       | 1                                                   | 0 | 0 | 2 | 0 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 1 |   |   |   |



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