“Basal” but not primitive: the nest of *Apoica arborea* de Saussure, 1854 (Insecta, Hymenoptera, Vespidae, Polistinae)

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ABSTRACT
The first nest of *Apoica arborea* ever collected is reported. Characteristics of the unusual nest design are discussed relative to other members of the genus *Apoica* and other epiponine genera. The characteristics of its nest architecture are a mosaic of primitive and derived features for the Polistinae, and thus the nest design is not properly interpreted as the primitive condition from which other swarm-founding wasp nest designs are derived. The frequent conflation of “basal” and primitive is discussed.

KEY WORDS
Insecta, Hymenoptera, Vespidae, Polistinae, *Apoica*, social wasps, nest architecture, mosaic evolution.

RÉSUMÉ
*« Basal » mais pas primitif : le nid d’*Apoica arborea *de Saussure, 1854 (Insecta, Hymenoptera, Vespidae, Polistinae).*
Le nid d’*Apoica arborea*, jamais collecté préalablement, est décrit pour la première fois. La structure peu commune de ce nid est étudiée en comparant ses caractéristiques à celles d’autres espèces d’*Apoica* et à d’autres genres d’Epiponini. En effet, l’architecture de ce nid correspond à une mosaïque de traits primitifs et dérivés pour les Polistinae, de sorte que ce type de nid ne peut pas être interprété comme étant un stade primitif à partir duquel les nids des Epiponini sont dérivés. La confusion fréquente entre « basal » et primitif est discutée.

MOTS CLÉS
Insecta, Hymenoptera, Vespidae, Polistinae, *Apoica*, guêpes sociales, architecture de nid, évolution mosaïque.

INTRODUCTION

The genus *Apoica* Lepeletier, 1836, comprises nocturnal swarming paper wasps, confined to the Neotropics and placed in the tribe Epiponini. It is divided into two subgenera, *Apoica* and *Deuterapoica* Dalla Torre, 1904. The monotypic *Deuterapoica* is sister to the subgenus *Apoica*, which contains the nine other nominal species of the genus (see Fig. 1, modified from Pickett & Wenzel 2007).

Richards (1978: 19) considered *Apoica* nests to be best categorized among the stelocyttarous nests, those with the comb attached to the substrate by a pedicel. Despite noting the fact that no *Apoica* nests have a pedicel, he suggested that these nests are "a modified type" of the "simple, exposed, stalked comb of *Polistes*". Of these latter he stated "Doubtless this is the ancestral type of nest" for Polistinae Lepeletier, 1836, as a whole. Any resemblance between nests of *Polistes* Latreille, 1802 and *Apoica* is superficial. As has been known since du Buysson (1906), species of *Apoica* begin nest construction with the cells attached directly to the substrate. After a few dozen cells are built, the wasps flare the nest construction away from the substrate, with felt added secondarily to the back of the comb, creating the characteristic subconical *Apoica* nest design (Wenzel 1998).

Van der Vecht (1972: pl. 1) published a photograph of a nest of *A. arborea* de Saussure, 1854, which could not be collected, and the photograph of which he characterized (p. 738) as "not perfect." This is the only descriptive information on the nest of this species hitherto published. Only the general shape of the comb can be ascertained from the photograph, and in particular, it does not show how the nest was attached. Van der Vecht (1972: 739) speculated "It seems possible that it was entirely 'sessile', and this would then be in marked contrast to the nests of other species in which only an initial cell group is in direct contact with the support." Here we report the collection of a nest of *A. arborea*. Just as van der Vecht suggested, the cells are sessile. The nest is different from all other species of *Apoica* as well in lacking added felt.

NEST DESCRIPTION

The nest of *A. arborea* is shown in Figure 2. It was collected near the HYDRECO Laboratory field station at Petit Saut, French Guiana (5°03'39"N, 53°02'36"W) on 6 December 2005 by A. Dejean. It was constructed on a *Cecropia obtusa* Trécul, which housed the ant *Azteca alfari* Emery, 1893 (Hymenoptera, Formicidae). The length of the nest is 41.4 cm; the width varies from 5 cm at the middle to under 2 cm at the ends of the comb; the height of the tallest cells on the edge in the middle is about 3 cm, while the cells at the ends are as low as 2 mm. The comb consists of at least 1114 cells, with 248 cells having pupal caps or with emerging adults (due to damage to some of the cells, counts are approximate, and not all of the very short cells were counted). The capped cells are concentrated towards either end (Fig. 2A), but some are scattered in between. Eggs were not seen. With the exception of a few very short semi-cells laterally (Fig. 2B), all cells appeared to be sessile, on the substrate, confirmed by probing. Flaring of the cells from the substrate was minimal (Fig. 2C). No patches of additional felt were observed anywhere on the comb. Collected with the nest were 423 females and 8 males.

The specimen is deposited in the American Museum of Natural History, nest # 051206-2.

Examination of the nest reveals that certain aspects of the nest of *A. arborea* are indeed primitive for the Polistinae. Among these are the construction of a single exposed comb and the absence of an envelope. The characteristics of the *A. arborea* nest also permit the optimization of derived characters within *Apoica* (see Fig. 1). Among these are loss of the pedicel and the sessile initiation with cell bases attached directly to the substrate. As all other *Apoica* initiate their nests in the same way, this is a synapomorphy for the genus. Species in the subgenus *Apoica* subsequently flare the nest off the substrate and add a felt-like covering, which obscures the bases of the cells and the foundation, creating the familiar subconical *Apoica* nest. Ontogenetic considerations and cladistic optimization suggest that the lack of such flaring and felt in *A. arborea* is the retention of the primitive condition; the flaring of the nest and addition of felt is derived within the genus, in the subgenus *Apoica*.

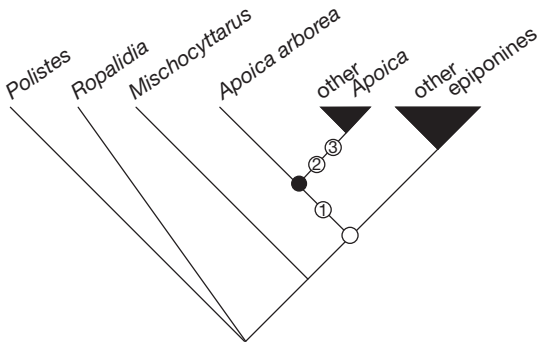

FIG. 1. — Phylogeny of *Apoica* Lepeletier, 1836 and relatives, after Pickett & Wenzel (2007). The open circle indicates the Epiponini; the closed circle indicates *Apoica*. Synapomorphies of interest include: **1**, the loss of the comb pedicel and the direct attachment of cells to the substrate; **2**, the nest's flaring away from the substrate, giving rise to a "dorsal surface" of the nest; **3**, the secondary thickening of the comb by the addition of felt material on the dorsal surface of the nest.

Van der Vecht (1972: 738) emphasized the elongate, narrow shape of the comb of *A. arborea*, stating "This is in marked contrast to the nests of other *Apoica* species, which, so far as known at present, are either circular, broadly oval, or hexagonal with more or less rounded angles, all as seen from below." The nest of *A. arborea* is basically confined to the substrate, a narrow one in both known specimens. If this elongate comb shape is confirmed as general in this species, it would represent a derived condition, relative the oval comb such as those seen in both *Polistes* and the subgenus *Apoica*.

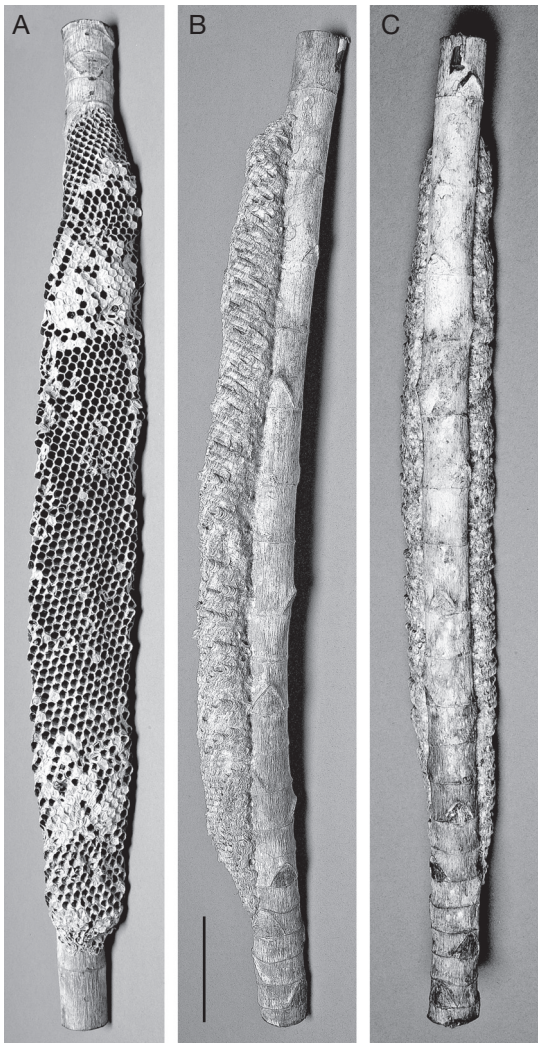

FIG. 2. — Nest of *Apoica arborea* de Saussure, 1854: **A**, comb seen from front; **B**, lateral view; **C**, comb seen from back. Scale bar: 5 cm.

DISCUSSION

A common view among biologists is that phylogenetic lineages that are "basal" to others – that is, a lineage that is sister to a larger group – will somehow represent the primitive condition of that larger group to which it is sister. The fallacy of this view was clearly pointed out in Hennig's (1965) discussion of the heterobathmy of characters as a necessity for phylogenetic inference. The combination of primitive and derived characters he described (Hennig 1965: 107) as "a fact which has long been known" and stated plainly: "In a phylogenetic system there can indeed be no solely primitive and no solely derivative groups." Certainly, primitive retention in the "basal" group is a possibility, but characters can evolve independently within lineages, and so it is more appropriate to discuss the primitiveness of particular characters. There is no reason to imagine that "basal" lineages retain all primitive characters – any more than their sister-group.

Apoica arborea has long been considered the most distinctive species in the genus (Richards & Richards

1951; Richards 1978), and van der Vecht (1972: 738), after discussing several characters of this species, stated that "*A. arborea* is less specialized than the other *Apoica* species". While *A. arborea* is plesiomorphic in lacking the flaring of the comb and addition of felt seen in other species of *Apoica*, it is perhaps apomorphic in the elongate, narrow comb shape – and it is just as derived as other species of *Apoica* in lacking a nest pedicel, while at the same time being just as primitive in lacking a nest envelope and having a single comb. Its characters are indeed a mosaic of primitive and derived, and terming such a species "primitive" is simply an error, the sort of error of evolutionary taxonomy that cladistics has corrected.

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