A NEW SPECIES AND NEST TYPE OF *MISCHOCYTTARUS* FROM COSTA RICA (HYMENOPTERA: VESPIDAE; POLISTINAE), WITH DESCRIPTIONS OF NESTS OF THREE RELATED SPECIES

By JAMES M. CARPENTER¹ AND JOHN W. WENZEL²

While engaged in a study of the nest architecture of paper wasps, one of us (JWW) discovered a remarkable nest of *Mischocyttarus* in the collection of the U.S. National Museum. The four associated adults proved to be an undescribed species. The genus *Mischocyttarus* is the most speciose among social wasps, with 189 species recognized in the recent revision by Richards (1978). Snelling (1983) synonymized one of these species, but described one new one and raised one subspecies, and Raw (1985) described two more for a total of 192 presently recognized species. Nest architecture in the genus differs mainly in detail (Richards, 1978), but the new species builds a nest very different from its congeners. It is described below to bring it to the attention of behaviorists working in Costa Rica.

Mischocyttarus pelor Carpenter, NEW SPECIES

Diagnosis: A member of the subgenus *Monogynoecus* Richards, with a short pronotal carina, weak pronotal fovea, and weakly asymmetrical third segment of the midtarsus. In Richards (1978) it keys to *fraudulentus* Richards, with which it shares a blunt enlarged hindclaw. It differs in the shape of the first metasomal segment (*cf.* Figs. 1 and 2), in having the propodeum with the longitudinal carina more effaced dorsally (*cf.* Figs. 2 and 3), and all metasomal terga are brown and banded with yellow.

Type material: Holotype Q and three paratype QQ, Turrialba, Costa Rica, 31 May 1951 (O. L. Cartwright). The holotype, two paratypes and nest are deposited in the U.S. National Museum; one paratype is in the Museum of Comparative Zoology.

¹Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

²Snow Entomological Museum, Snow Hall, University of Kansas, Lawrence, Kansas 66045.

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Description of holotype: Forewing length 8.6 mm. Structure-Clypeus weakly bidentate below, emargination narrower than an antennal socket; pronotal carina ending at about level of secondary spiracular entrance; pronotal fovea shallow, obtuse prominence present below this; propodeum with longitudinal carina and posterior cavity essentially obliterated dorsally (Fig. 3); third segment of midtarsus almost symmetrical; inner lobe of third segment of hindtarsus short (Fig. 6); enlarged claw of hindtarsus thick and blunt (Fig. 6); metasomal tergum I more than twice as long as wide, flask-shaped (Fig. 1). Integument finely granulate throughout, dull. Vestiture consisting of scattered yellow hairs shorter than an ocellar diameter. Color-(Discolored by alcohol). Brown. Red are mandibular teeth, ventral margin of clypeus and tips of claws. Yellow are antennae beneath, clypeus, marks above and below interantennal area, inner margins of eyes extending above and behind ocelli, most of genae narrowing to stripes above, mandibles, pronotal carina, anterior and posterior margins of pronotum, longitudinal stripes below humeri, two longitudinal stripes on scutum, tegulae, anterior margin and posterior transverse stripes on scutellum, metanotum except posterior margin, two broad longitudinal stripes on propodeum, a large spot above dorsal groove, broad anterior and posterior stripes on mesepisternum, connected below, metapleura broadly above, metasomal sternum I posteriorly, posterior bands on terga I-VI and sterna II-V, forecoxae, anterior half of midcoxae, three stripes on hindcoxae, foretrochanters and distal margins of mid and hindtrochanters, forefemora and tibiae mostly, mid and hindfemora anteriorly, mid and hindtibiae except for stripes, tarsi and claws except for mid and hind first tarsal segments proximally. Wings hyaline with veins yellowish, verging into brown basally.

Male: Unknown.

Etymology: The name, a noun in apposition, is taken from the Greek word pelor, meaning monster or prodigy, and refers to the nest.

Remarks: There is little variation among the paratypes. Taking forewing length as an indicator of size, the paratypes are all 8.4 mm. The yellow is more extensive on the pronotum in two of the paratypes, and on the mesepisterna, metapleura and propodeum of one of these specimens.

During a recent visit to the British Museum, JMC compared the type series with the types of *M. fraudulentus* and *alienus*, the two



Figs. 1-2. Metasomal petiole. 1, M. pelor, $11 \times .2$, M. fraudlulentus, $12 \times .$ Fig. 3. M. pelor, propodeum, $17 \times .$ Figs. 4-6. Hindtarsus. 4, M. alienus, $15 \times .5$, M. fraudlulentus, $17 \times .6$, M. pelor, $11 \times .$

species at the couplet to which *pelor* keys. Both species were originally described from Colombian specimens. Now, in addition to the type material mentioned in Richards (1978), there are two specimens and one nest of *alienus* and four specimens and two nests of *fraudulentus* in the British Museum, all determined by Richards. The *alienus* are from Bolivia ("La Paz, Caranavi 1000 m., 15-V-1979, M. Cooper") and Costa Rica ("Cartago, Prov. Tapanti, 2 July 1963 4000 ft., C. D. Michener" determined as "sp. nr. *alienus*"; the hindtarsi are missing). The *fraudulentus* are all from the type locality, Barbacoas in Div. Nariño in Colombia, collected on 5-IV-1974, 20-VII-1974 and 6-I-1975 by M. Cooper. Besides this material, three

additional *alienus* specimens from Costa Rica in the collection of the Snow Entomological Museum were seen; these have identical collection data to the one in the British Museum and are labelled as "from nest #CR 04" and "Det. Starr, 1981." Finally, another specimen of *fraudulentus* from the collection of the Museum of Natural History of the University of Georgia was examined. This was collected in Costa Rica ("Sirena, Corcovado Nat. Pk., Puntarenas 22-III-1981, C. K. Starr, nest series no. 204"), determined as "? *fraudulentus*" by Richards, and was accompanied by a nest.

M. alienus is distinguished from pelor by its larger size (forewing length 9.5-10.6 mm), less asymmetrical third segment of the mid and hindtarsi (Fig. 4), and nest (see below), but is similar in having the propodeal longitudinal carina dorsally effaced. The enlarged hindclaw is usually narrower in alienus (Fig. 4), but this feature varies somewhat. M. fraudulentus is more similar to pelor: the third segment of the mid and hindtarsi is similarly asymmetrical and the enlarged hindclaw is blunt (Figs. 5 and 6), the size overlaps (forewing length 8.0-9.1 mm), and the nest (see below) is similar. But the shape of metasomal segment I and propodeal sculpture are different. Segment I is relatively narrower basally and more abruptly expanded posteriorly in pelor (cf. Figs. 1 and 2), and the propodeal carina is more reduced dorsally (cf. Figs. 2 and 3). The color is also distinctive. M. fraudulentus is lighter on the mesosoma, with more yellow on the sides of the thorax and propodeum, and the legs brown. The metasoma is black, at most tinged with yellow apically, on the three posterior segments in *fraudulentus*. It is brown and banded with yellow in pelor.

These three species together with *M. moralesi* Zikán may form a monophyletic group, sharing the apomorphy of an emarginate clypeus. Other species in *Monogynoecus* have the clypeus pointed or rounded (Richards, 1978). The emargination is broader in *moralesi*, which may be derived, and the other morphological features shared by *pelor*, *fraudulentus* and *alienus* appear primitive in the subgenus, e.g. pronotal fovea present. But the nests of *pelor* and *fraudulentus* probably show derived similarity (see below), so these species may be sister-groups. They are generally quite similar, and further collecting may yet show that the differences represent geographical variation in one species. At present, they are best regarded as distinct species.

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Nest diagnosis: Since the nest of *pelor* is a museum specimen not accompanied by notes, its original substrate and orientation are unknown. It may have been on the underside of a leaf, as suggested by an impressed central furrow along the line of pedicels. In the following description we assume that the substrate was horizontal and that the nest hung beneath it. This nest differs from those of all other known Mischocyttarus by its presumed mode of expansion (Fig. 7). A line of short pedicels supports cells which grow laterally parallel to the substrate. Successive rows of cells apparently point to alternate sides of the central line of pedicels. A central plate, probably homologous to the back side of an ordinary Mischocyttarus nest, serves as the common base of back-to-back rows. Near either end of the rows, cells may grow at angles intermediate between the alternate rows and some cells are initiated on the walls of others, giving the nest the false appearance of a hemisphere of radially expanding cells (Fig. 8).

Nest description: Egg-shaped with long axis parallel to substrate, slightly flattened vertically, 34 mm long, 24 mm wide, 11 mm deep from substrate to lowest margin of downward pointing cells. Carton mottled brown with some pale stripes, brittle, composed of coarse, inflexible wood fiber and chips, reinforced with glossy secretion in region of pedicels and adjoining sheet. Three pedicels less than 2 mm long, aligned on central axis, initially supporting separated cells; fourth colinear pedicel secondarily added between wall of growing cell and substrate (Fig. 8c). Sheet (27 mm by 24 mm, but fragmented in specimen) fibrous and irregular, covering substrate, impressed along central line of pedicels with shallow furrow suggestive of the rib of a leaf; probably built outward from pedicels, peripherally fusing to side walls of those cells that contact substrate. Eight closed pupal cocoons (one broken), strongly domed about 2 mm beyond end of cells 10 mm long and covered over with wood fiber applied to silk, nine open cocoons. Eighty-four irregular cells, initial three laterally pointing to same side of the line of pedicels (primary side), younger cells radiating outward in all directions, more irregular on primary than secondary side, most parallel to substrate, may have walls straight or curved through 45 degrees, up to 6 mm deeper than their adjacent neighbors, may support younger cells of different orientation on their walls when divergent from or deeper than neighbors, one row of five short (less than 2 mm) cells pointing



Fig. 7. Hypothetical cross-section through an expanding nest, edge view, perpendicular to row of pedicels. 7a: LB = leaf blade, P = pedicel, S1 = primary side of comb. 7b: S2 = secondary side of comb, CP = central plate axis, with central row of downward cells. 7c: SS = substrate sheet.

directly away from the substrate. Shining bright light through nest reveals between younger rows (but perhaps not between older cells) a central plate perpendicular to substrate, roughly coplanar with line of pedicels, dividing the nest into halves and supporting on its lower edge the row of five downward pointing cells.

Remarks: Unusual architecture involving unconvential comb design and multiple pedicels upon a leaf rib is known for other Mischocyttarus, such as insolitus Zikán or latissimus Richards (Herre et al., 1986, JWW unpubl. data). The nest of pelor is most similar to that of the closely related fraudulentus, which builds on a leaf midrib. One fraudulentus specimen (BMNH #279) on an arum leaf has four short (2 mm) pedicels supporting 13 cells (one missing) which are parallel to the leaf blade and fused to form a continuous horizontal row (Fig. 9). A fifth pedicel (broken) supports six cells in a regular hexagonal array, separated from the row. All cells point to the same side of the rib, many bearing acute longitudinal ridges. The nest has three intact long cells; one of 10 mm is capped by the 1 mm dome of a cocoon. Unlike M. pelor, the carton is thoroughly reinforced with clear secretion forming irregular transparent windows as large as 1 mm², and there is no sign of a substrate sheet of paper. The specimen in the Museum of Natural History of the University of Georgia is similar. Separated by 13, 12 and 9 mm are four pedicels 2 mm long on the rib of a leaf and supporting 22 shallow (2-3 mm) cells (one broken), arranged very like the British Museum specimen in one or two rows and all pointing to the same side of the rib. The remnant of a fifth pedicel 9 mm from the last marks either an incipient pedicel or a broken and missing section of the nest. Like



Fig. 8. Nest of *M. pelor.* 8a: Oblique top view. SS = substrate sheet (outlined), CF = central furrow, S1 = primary side, S2 = secondary side. 8b: Oblique bottom view. CR = central row of five downward cells; scale bar equals 10 mm. 8c: Edge view. Cp = central plate axis viewed on edge, P4 = fourth pedicel. 8d: Retouched to highlight cell walls. SS = substrate sheet.



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Fig. 9. Nest of *M. fraudulentus* (BMNH #279). 9a: Front view. 9b: Rear view.

Fig. 10. Nest of M. alienus (BMNH #216), lateral view. Arrows mark ends of pedicel, previously perpendicular but now unnaturally subparallel to leaf due to preservation.

the British Museum specimen, the carton is glossy with clear secretion, but there are neither windows nor longitudinal ridges on the cell walls. A photograph (by C. K. Starr) of this nest *in situ* shows that the nest contained only or mostly eggs. If larger *fraudulentus* nests also have cells pointing opposite to the first row, they would be very similar to *pelor* nests.

The closely related *M. alienus* (BMNH #216) and *moralesi* Weyrauch (in the Museum of Comparative Zoology) hang a single vertical row of cells from a long pedicel, which is pale in color, contains little pulp and apparently incorporates air bubbles. The *alienus* specimen is a nest of eight cells, including a pupa 13 mm long, suspended from a 12 mm pedicel (Fig. 9). The *moralesi* specimen is similar but smaller; an 8 mm pedicel supports 6 cells of which 3 are pupae, one 12 mm long. Although this design is very different from those described above, these two species share with *fraudulentus* the longitudinal ridges on the cell walls and the glossy carton with windows. All four species described here apparently initiate pedicels

on leaf veins, point cells roughly laterally (as opposed to vertically), build some cells much deeper than neighboring cells, and paste carton onto the silk caps of cocoons strongly domed beyond the end of the cells.

DISCUSSION

Recognition of this new species, defined morphologically, should not be interpreted as support for the widespread and probably erroneous opinion that every species of paper wasp has a distinctive nest form of its own. However, the obvious differences between the nests described here demonstrate that closely related species may vary greatly in architecture. *M. alienus* and *moralesi* build a long, pale pedicel and continue mostly along the vertical axis. *M. fraudulentus* builds simultaneously several short pedicels and separate groups of cells that fuse mostly horizontally. *M. pelor* probably begins like *fraudulentus* but shows the peculiar back-to-back arrangement of cells in subsequent construction.

It is rare to find pupae in polistine nests as small as those described for *M. alienus, moralesi* and *fraudulentus.* With several nests now examined, it seems that founding females of these species ordinarily provision few larvae simultaneously, and provision unevenly, producing few pupae per comb. This would result in unusually small colony size after worker emergence. To accommodate for this low productivity, perhaps females simultaneously maintain several nests separately, as is known for *Polistes* (Jeanne, 1979) and *Ropalidia* (Itô, 1986), or build and abandon several nests sequentially, as suggested for one *Ropalidia* species (Wenzel, 1987). Present information is inadequate to determine if either of these possibilities occurs. Unlike these three species, the size of the *M. pelor* nest (and presumably the colony) is not unusual for *Mischocyttarus*.

The architecture of the *M. pelor* nest is perhaps caused by continuous building in a confined place or by inversion of a small comb and subsequent disorientation of ordinary cues used by the builders. However, several facts support the opinion that this nest is not such a monstrosity. Most nests built in too small a cavity are soon abandoned or modified to fit the space available. If the nest was built on the rib of a leaf, it probably would not have been confined in such a way as to explain the architecture. In many genera, including *Mischocyttarus*, most nests which have been rotated or inverted during construction are not remodeled completely, but rather older

regions remain as they were built and new sections are soon built normally within the new orientation (JWW, unpubl. data). This nest has pupae pointing in all directions in the uppermost cells, suggesting that they were built back-to-back early in the nest's history, just as are the younger cells below them.

Back-to-back cells originating at the margin of a central plate have long been falsely reported for the Old World genus *Polybioides* (van der Vecht, 1966). This design is currently known in the South American *Stelopolybia lobipleura* Richards (Richards, 1978), which builds such combs in cavities. Whether the nest described here is typical for its species and how it expands await confirmation by observers in the field.

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