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## A Generic Key to the Nests of Hornets, Yellowjackets, and Paper Wasps Worldwide (Vespidae: Vespinae, Polistinae)

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### ABSTRACT

The 31 genera of Vespinae and Polistinae worldwide are identified in a key to nest structure. Fifty-nine couplets and more than 80 photographs and illustrations permit both specialists and amateurs to recognize these nests in the field or museum collections. A brief overview explains the distinction between nests of these social wasps and those of other social or soli-

tary Hymenoptera with which they may be confused. Many characteristics are illustrated or described here for the first time, with notes on both anomalous species and anomalous forms of nests of common species. Pertinent published figures and museum collections are cited to assist the professional in finding reference material.

### INTRODUCTION

All over the world, both entomologists and the lay public recognize and fear colonies of social wasps. More than 900 species range from the Arctic to Tasmania, from prairie to rain forest to desert, from pristine habitats to industrial cities. Their sophisticated, all-female societies provided the inspiration for several of the major discoveries in insect behavior and sociobiology (Wilson, 1971: 7). Mature colonies may consist of a single

female (Wenzel, 1987) or millions (Zucchi et al., 1995). The aggressive, boldly striped adults advertise their unforgettable stings, and many moths, flies, and other defenseless insects have developed elaborate morphological and behavioral mimicry to benefit from a general desire among most animals to avoid wasps. In addition to supporting these mimicry complexes, their large numbers make wasps important predators of other in-

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sects in many ecosystems, composing up to about 6% of total insect biomass (Fittkau and Klinge, 1973). They are well known for symbioses with each other (Windsor, 1972) and with other organisms such as ants (Espelie and Hermann, 1988), honeydew insects (Le-tourneau and Choe, 1987), and birds (Hindwood, 1955, Joyce, 1993, Dejean and Fotso, 1995). This commensalism attracted artists of ancient civilizations (Coe, 1982) and forms the foundation of the mythology and rituals of certain indigenous peoples (Schoepf, 1990). The architecture of wasp nests has been cited for its perfection as evidence against modern evolutionary theory (Anon., 1986). Yet, despite this rich resource wasps provide for behaviorists, ecologists, anthropologists, and others, identifying wasps to genus has always required the care of a few overburdened specialists with extensive libraries and reference collections. The present key to nests is offered to provide an alternative that will be useful to specialists and amateurs alike.

The wasps' industriousness as builders and cleverness as architects are appreciated even by those of us who dread unexpectedly discovering them making their home in the shelter of our own. Their elegant paper nests sometimes attract attention as decorative curios in markets. These nests can be the size of a thimble or more than a meter long, as durable as hard felt or more fragile than egg shells, more regular and uniform than the much-celebrated honeybee comb or wildly chaotic with an intricate mazelike interior. Indeed, variation in nest architecture between distantly related species is far more striking than is the morphological variation, and some species were initially sorted into certain genera primarily based on their nests. Recent treatments demonstrate that architecture-related behaviors are particularly useful at tracing phylogenetic lineages in many animals (Wenzel, 1992a) and that architectural details of wasp nests reflect well the relationships derived from morphological study (Wenzel, 1993).

The nests of Vespinae (hornets and yellowjackets) and Polistinae (paper wasps) are easy to recognize. Except for four Neotropical species that build nests of mud, the nest are all made of vegetable fiber without wax

or plant resins. Soil or glandular secretion may be used to reinforce or repair nests, but they rarely constitute the primary building material for mature colonies. Brood combs are usually one sided, with an hexagonal arrangement of cells sharing thin (less than 0.5 mm) walls. There are no specialized storage chambers, but one may find honey or prey ants and termites stored in ordinary brood cells or in spaces between envelope sheets.

In Southeast Asia, nests of Stenogastrinae (hover wasps) may be confused with those of Vespinae and Polistinae, but stenogastrine nests can be separated by the following characters: cells more than 1.3 times as large as the head diameter of the wasp; cells usually narrowed at their openings by a short collar and may be closed with carton by the adults when the larva pupates; pupae naked and leaving no cocoon inside the cell; carton fragile and brittle; nest lacking a narrow, tough pedicel (although sometimes producing illusion of one by hanging from rootlets, fungal hyphae, or other such substrate); cells sometimes connected to the substrate along their side walls; and cells easily separated from the substrate (except when built of clay). In contrast, Vespinae and Polistinae build cells barely larger than the head diameter of the wasp; cell openings not narrowed by a collar nor closed over pupae by adults (occasionally closed in some *Vespa*) but rather capped by a portion of the silk cocoons found in the cells; carton either fragile and brittle or tough and supple; nest with or without pedicel (mostly with pedicels in Southeast Asia); cells rarely connected to the substrate along their side walls; and, in living colonies without pedicels, cells usually not easily separated from the substrate.

Nests of a few more distant relatives of Vespinae and Polistinae may be confused with them occasionally. The eumenine genera *Zethus* and *Calligaster* build clusters of cells of resin and plant material, often with pieces cut from leaves, but each of these barrel shaped cells has its own thick walls rather than sharing thin, common walls with neighboring cells, and rarely are all cells parallel. Clay nests of the Neotropical sphecids *Trypoxylon fabricator*, *T. maraballi*, and some other species may be confused occasionally with those of paper wasps, but the former are

naked combs of closely adjacent, circular cells each with its own walls, built without a pedicel, and often plastered with mud on the sides of the comb. Social vespid nests built in cavities have an entrance that is a simple hole or crack, never an entrance tube of resin as found in stingless bees, for example, *Trigona* or *Melipona* (Apidae). Carton nests of ants are usually composed of a coarse uneven envelope only, and never include a hexagonal comb. A few Neotropical polistines live inside the carton nests of ants or termites, and observers should take care not to confuse the structures built by these latter with the parallel, naked, carton combs of the wasps that will be found within a cavity.

Museum nest specimens are often decayed, discolored, distorted, lacking parts, or confused with parts and adults of other nests. Therefore, one must be cautious in certain decisions, such as whether a given specimen naturally lacks an envelope or has merely lost it in handling. I have made use of biogeographic and other information that will help identification in the field or with properly labeled material, but some information, such as "in a cavity," may not be evident in museum specimens. Although some nests have survived two centuries in collections (Wenzel, 1992b), I do not recommend borrowing nest specimens from museums because they are bulky and travel poorly, and there is generally little the novice will gain from examining a specimen that could not have been learned from published accounts.

This is the first effort to include all 31 genera of Vespinae and Polistinae worldwide. It is not possible to identify all specimens to genus without error before investing a great deal of study, and several genera may not be separable on the basis of very young nests. Effort is rewarded, though, because an experienced observer can identify nearly all nests to genus from a distance of a meter or more, and many to species. In my experience, indigenous people who are alert to insects can identify the majority of local species by nest structure alone.

Despite much variation, I do not believe that every species has a distinctive nest architecture. As a premise, species specificity requires an assumption about evolution that I am not willing to make: that speciation, by

whatever means, be accompanied by a change in architecture in one or both descendant lineages. Eberhard's (1990: 342) appraisal that apparent species specificity of spider webs is an illusion due to lack of data probably applies to wasp nests as well. Intraspecific variation between habitats or populations can be great, and limited sampling may lead to generalizations that are false or hold for only one part of the species' range.

The illustrations offered are only to assist the user in deciding if he or she has found roughly the right description of the nest. Nests are far more variable than are the morphologies of the animals who build them, and some identifiable nests will not match closely the figure chosen to characterize the genus. Problematic nests, such as those included among the diverse architectural forms of Paleotropical *Ropalidia*, are sometimes best determined by excluding the other possibilities (i.e., the nest does not resemble *Polistes*, *Belonogaster*, *Polybioides*, or *Parapolybia*). In the neotropics the number of alternatives is much larger, and several genera present problems due to their diversity of nest forms or a superficial resemblance to other taxa. *Parachartergus* includes forms similar to *Leipomeles* and *Chartergellus*. *Protopolybia* and *Agelaia* both have forms that may resemble other genera, depending on the exact details of the site and colony size. *Pseudopolybia* sometimes superficially resembles Vespinae (but fortunately the most similar forms are allopatric). Some nests of *Polybia* can be separated from *Brachygastra* only with difficulty and both of these from *Protonectarina* only by destructive examination. Neotropical, naked, pedicelate combs in exposed sites are usually *Polistes* or *Mischocyttarus*, but the key helps separate these from particular forms of other genera (usually *Agelaia* or *Protopolybia*). *Polybioides*, *Synoecoides*, *Marimbonda*, *Clypearia* (including *Occipitalia*), and *Asteloea* are poorly known and may not be properly characterized here. Among nests of the approximately 350 species I have studied (appendix 1) are several anomalous ones that will run through this key to an incorrect genus (e.g., the long-fiber nests of *Mischocyttarus carbonarius* in Brazil and *M. flavitarsis* in the Rocky Mountains may key to *Polistes*; *Ro-*

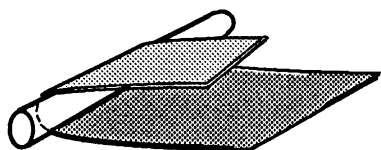


Fig. 1. Supple paper, rolled around a pencil without breaking into separate pieces.

*palidia loriana* will key to *Parapolybia*; the short-chip nests of *Polistes stenopus* in the South Pacific or Neotropical *Polistes bicolor* resemble *Mischocyttarus*). I believe most of these exceptions are encountered rarely, but as this key is used and improved, perhaps these exceptions will be treated better.

The generic nomenclature used here is that of Carpenter (1996) or essentially that of Richards (1978) with the addition of *Asteioeca* (Raw, 1985), synonymies of *Protopolybia* and *Pseudochartergus* (Carpenter and Wenzel, 1989) and *Clypearia* and *Occipitalia* (Carpenter et al., 1996), and the replacement of *Stelopolybia* with *Agelaia* (Carpenter and Day, 1988). *Dolichovespula* is separated from *Vespula*, but *Paravespula* is not recognized as separate from *Vespula*. Although phylogenetic relationships of the genera of paper wasps are not yet definitively established, an interim cladogram is available from Wenzel and Carpenter (1994) and is modified and reproduced here as figure 14. This cladogram may be useful for interpreting information presented here and elsewhere, but it is to be considered preliminary and is presented here only for reference and without discussion. A thorough treatment of the phylogeny of social Vespidae is yet forthcoming.

#### INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York
BMNH	The Natural History Museum, London
CMNH	The Carnegie Museum, Pittsburgh, Pennsylvania
CUIC	Cornell University Insect Collection, Ithaca, New York
FMNH	Field Museum of Natural History, Chicago
HMCZ	Harvard Museum of Comparative Zoology, Cambridge, Massachusetts
HUMB	Humboldt Universität, Berlin

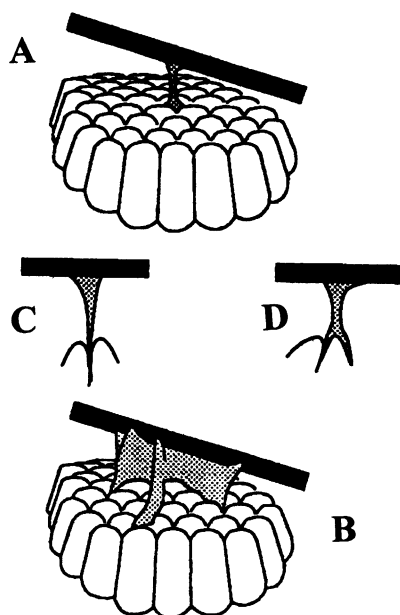


Fig. 2. Suspension. A. Narrow pedicel. B. Buttressed sheet. C. Cell-marginal pedicel, becoming flat apically and serving as the wall between the first two cells, typical of *Polistes*, *Mischocyttarus*, and others. D. Cell-central pedicel, becoming cone shaped apically and serving as the base of the first cell, unique to *Ropalidia*, *Parapolybia*, and *Belonogaster*.

IMLT	Instituto Miguel Lillo, Tucumán, Argentina
KUSM	University of Kansas Snow Museum, Lawrence, Kansas
MALS	Museum am Löwentor, Stuttgart
MNHN	Muséum National d'Histoire Naturelle, Paris
MRAT	Musée Royal de l'Afrique, Tervuren, Belgium
NMBS	Naturhistorische Museums, Bern
NNML	Nationaal Natuurhistorische Museum, Leiden
WDH	William D. Hamilton personal collection, Oxford

#### DEFINITIONS

**Brittle:** Carton that breaks into separate fragments when rolled around to the opposite side of a pencil. Contrasts with "supple" (fig. 1). Dry museum specimens may become brittle despite being supple in nature.

**Carton:** Material composed of masticated vegetable matter or soil, bound in a matrix of dried



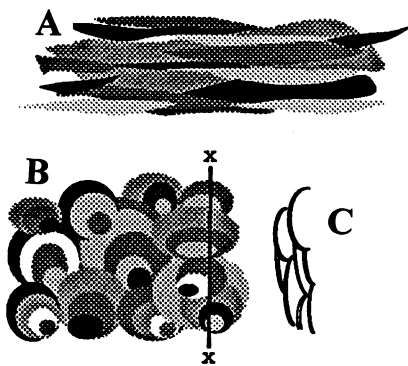


Fig. 3. Lines of construction. **A.** Parallel lines of pulp, as in laminate envelope. **B.** Concentric arcs of pulp and imbricate pattern. **C.** Cross section showing superimposed structure of imbricate envelope.

salivary secretions. May have the consistency of paper, felt, or dried mud.

**Cell-central:** Condition in which the apex of the pedicel is gently flared into a cone that becomes the base of the first cell of the comb (fig. 2). Found in *Ropalidia*, *Belonogaster*, and *Parapolybia*. Contrasts with “cell-marginal.”

**Cell-marginal:** Condition in which the apex of the pedicel is flattened to become the side wall of the first cell (fig. 2), usually the common wall between the first two cells. Found in *Polistes*, *Mischocyttarus*, and other New World taxa. Contrasts with “cell-central.”

**Envelope:** A sheet of carton, mud, or secretion protecting the combs and hiding them from the environment.

**Imbricate:** Built or reinforced with shell-like structures usually less than 10 cm in breadth; lines of construction often tightly arced structures superimposed upon each other like roof tiles or fish scales (fig. 3).

**Laminate:** Built or reinforced with sheetlike structures usually more than 10 cm in breadth, lines of construction usually nearly linear and parallel, sheets mostly parallel and interconnected only intermittently (fig. 3).

**Lines of construction:** A pattern visible in the carton due to the successive addition of separate loads of building material to the margin of the envelope (fig. 3).

**Long fiber:** Vegetable fiber that is slender and more than four times as long as wide, usually supple. Contrasts with “short chips” (fig. 4).

**Pedicel:** A tough, sometimes resinous, structure that supports the nest from above or from the side, capable of function when diameter is 1 mm. It may become broad, branched, or buttresslike in

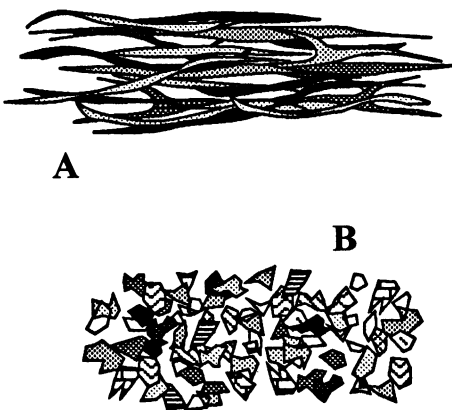


Fig. 4. Composition of paper, low magnification. **A.** Long fiber, typical of supple paper. **B.** Short chips, typical of brittle paper.

mature nests (fig. 2). Synonymous with “petiole” or “peduncle” of other authors. Short connections that do not function until they are several millimeters across are excluded from this definition, although other authors sometimes include them.

**Secretion:** Resinous, glossy material of glandular origin, added to pulp for strength and water resistance. May be clear or any color; often resembles the basic color of the wasps’ cuticle.

**Short chips:** Vegetable fragments less than four times as long as wide, usually brittle. Contrasts with “long fiber” (fig. 4).

**Supple:** Carton that can be rolled around to the opposite side of a pencil without breaking apart into separate fragments (fig. 1). Contrasts with “brittle.” Dry museum specimens may become brittle despite being supple in nature.

KEY TO NESTS OF VESPINAE  
AND POLISTINAE

In case of error, the reader may trace decisions backwards by following the numerals in parentheses to find the couplet at which the alternative branch was more appropriate than the path chosen originally. An asterisk means that the nest of this taxon is rarely seen or infrequently takes a form that will key to the place given.

- 1. Nest exposed . . . . . 2
- Nest concealed in folded leaf, hole in tree or ground, hollow wall, attic, or other cavity . . . . . 48
- 2(1). Without envelope . . . . . 3
- With envelope . . . . . 9
- 3(2). Vacated pupal cells with bottoms lacking

- carton, either replaced by translucent secretion or completely open revealing interior. No meconia in older cells (Old World only) . . . . . 4
- Vacated pupal cell bottoms of carton. With or without meconia (New World only or cosmopolitan *Polistes*) . . . . 6
- 4(3). Cell bottoms open, revealing cocoons. Single comb, usually hammock or ball shaped and hung from one edge, sometimes a linear string of cells (Madagascar only). Sparse carton, silk cocoons providing most of the structure. Sometimes all material removed from region of old cells and only reinforced comb margin remains; Africa to India . . . . .
- . . . . . *Belonogaster*
- Cell bottoms replaced by translucent secretion, not open to cocoons . . . . . 5
- 5(4). Combs single or multiple, elongate, and hung from one edge. Mature combs may have single pedicel several centimeters across. Carton sometimes translucent, sometimes lacelike when new, composed of profuse secretion and yellow or amber long fibers, rarely white or brown; Iran to New Guinea, north to Korea and Japan (fig. 5) . . . . .
- . . . . . *Parapolybia*
- Combs single or multiple, shape variable, hung from one edge or supported centrally. Carton generally opaque (except for cell bottoms), usually composed of short vegetable chips and profuse secretion, inorganic matter, or, rarely, long fiber. Pedicles narrow but possibly numerous. Envelope sometimes present; Africa, Asia, and Australia (fig. 5) . . . . .
- . . . . . *Ropalidia*
- 6(3). Pedicel absent. Comb single, horizontal, broadly attached to branch or limb; upper surface composed of soft felt 3 mm or more thick, forming a hemispherical or slightly peaked cap that conceals cell bases and usually encompasses supporting branch; Central and South America . . . . .
- . . . . . *Apoica*
- Pedicel single or multiple. Combs single or multiple, orientation variable, attached to leaves, human domicile, or other substrate. Without thick felt cap . . . . . 7
- 7(6). Comb beneath *Heliconia* leaf, deeply lobed. Pedicels multiple and numerous. Cell walls uniform in height; Central and South America . . . . .
- . . . . . *Protopolybia scutellaris*

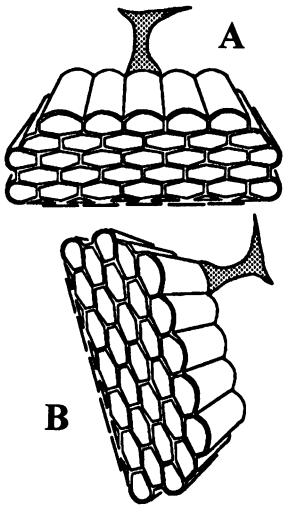


Fig. 5. Pedicellate combs. A. Horizontal, suspended from center. B. Inclined, suspended from one edge.

- Comb not deeply lobed, or, if so, then with only one or few pedicels. Cell walls usually higher in older region of nest and gradually shorter toward newer marginal regions . . . . . 8
- 8(7). Carton composed mostly of short vegetable chips, gray or brown in color. Cells not larger than 3 mm wide, or, if so, then with single pedicel more than 20 mm long (except in USA); South America, Carribean, southern USA, and Colorado, and occasionally farther North along Great Basin (fig. 5) . . . . .
- . . . . . *Mischocyttarus*
- Carton composed mostly of long, woody fibers, usually gray in color, cells larger than 3 mm wide in Americas; cosmopolitan (fig. 5) . . . . . *Polistes*
- 9(2). Nest broadly appressed to trunk or limb, longest axis along line of attachment, not on a leaf (figs. 6, 7); Mexico south to central South America and Trinidad . . . . . 10
- Nest clearly pendant from leaves, branches or limbs. Shape variable (figs. 8, 9, 10, 11, 13) . . . . . 18
- 10(9). Nest shaped like inverted flask, remodelled mostly downward. Envelope carton gray, usually streaked with other colors. Entrance in lowermost region of envelope (fig. 6) . . . . . 11
- Nest dome shaped, remodelled mostly laterally or upward. Envelope not papery, often very brittle, brown, gray, or

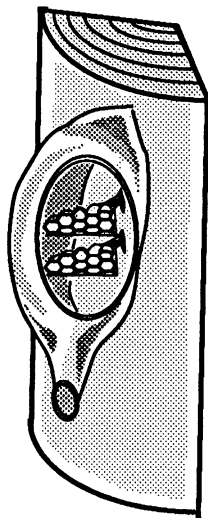


Fig. 6. Inverted flask appressed to broad surface or leaf (rarely among twigs); entrance as downward spout; cut away to show pedicelate combs; *Parachartergus*, *Chartergellus*, and *Leipomeles*. *Nectarinella* and *Marimbonda* with sessile comb.

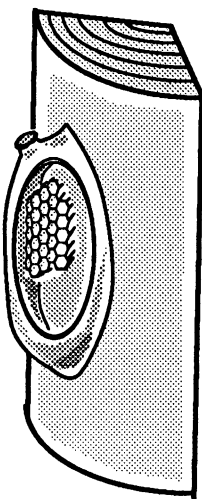


Fig. 7. Dome appressed to broad surface; entrance as short upward spout; cut away to show sessile comb; *Synoecca* and *Metapolybia*; *Clypearia* and *Asteloeca* with entrance variable.

- tan, often spotted or mottled. Entrance variable (fig. 7) ..... 14
- 11(10). Entrance distinct, gently narrowed, downward spout ..... 12
- Entrance simple, not a spout ..... 13
- 12(11). Envelope bearing numerous fine carton pillars 1–2 mm high and tipped with a sticky secretion. Carton color closely resembling substrate. Comb sessile upon substrate; Central America and South America ..... *Nectarinella*\* (possibly *Marimbonda*\*, but without pillars)
- Envelope without sticky pillars, sometimes corrugated with orderly ridges and furrows. Carton color not closely resembling substrate. Combs pedicellate, oval to kidney shaped; Central and tropical South America ..... *Parachartergus*
- 13(11). Envelope without carton pillars or floss, funnel shaped, very supple and soft. Lines of construction only weakly visible. Entrance simple hole. Combs pedicellate, oval to kidney shaped; Central and tropical South America ..... *Parachartergus*
- Envelope with fine carton pillars or floss at envelope margin, especially on inner side of upper margin; envelope flat,

- rough, and variable, sometimes brittle. Lines of construction strong. Entrance short collar; Central and tropical South America ..... *Chartergellus*\*
- 14(10). Envelope more than 4 cm deep, often corrugated with orderly ridges and furrows converging on a central longitudinal line. Carton coarse, with little evident secretion. Entrance usually in upper part of nest, separate from final gap in construction, ringed by short collar ..... *Synoecca*
- Envelope less than 4 cm deep, no corrugation. Carton with profuse secretion and short vegetable chips, including small windows or layers of pure, glossy, transparent secretion ..... 15
- 15(14). Nest projecting beyond margin of narrow support ..... 16
- Nest wrapping around narrow support, or on broad support ..... 17
- 16(15). Comb back showing cell bases, comb sides showing cell contours. Carton smooth, glossy. Lines of construction long, parallel, clear ..... *Asteloeca*\*
- Comb back thick, obscuring cell bases, comb sides generally not showing cell contours. Carton rough, many fine particles. Lines of construction short, irregular, or obscured ..... *Clypearia*\*
- 17(15). Envelope shallow, may be flat, sometimes sharply angled and resembling eaves where side walls meet dome. En-

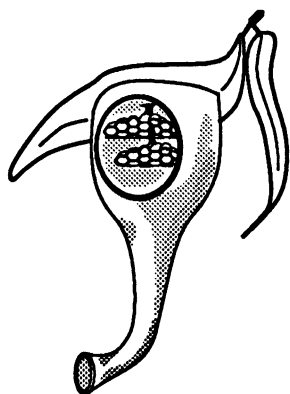


Fig. 8. Inverted flask pendant below leaves; entrance as downward, curved spout; cut away to show pedicellate combs suspended from those above; *Angiopolybia*.

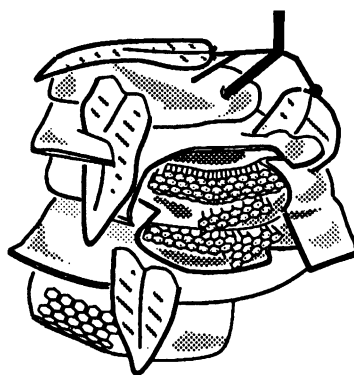


Fig. 10. Chaotic nest; cut away to show multiple combs sessile on multiple envelopes; possibly multiple entrances; usually incorporating nearby vegetation; *Protopolybia*, *Brachygastra*, and *Ropalidia*.

- trance separate from final gap in construction, upward spout or short collar. Cells 2.5 mm in diameter or less . . . . . *Metapolybia*
- Envelope dome arching gradually. Entrance at final gap in construction, simple hole or short collar . . . . . *Clypearia*\*
- 18(9). New World south from California, Arizona, Texas . . . . . 19
- Old World or North America to southern USA . . . . . 43
- 19(18). Envelope simple sheet or shaped like inverted flask, smoothly curved and gently narrowed below, widest above midline, or, if ball shaped, then with smooth and uniform exterior. Entrance lowest structure, often spoutlike. Combs' position not reflected on envelope exterior (figs. 6, 8) . . . . . 20

- Envelope variably shaped, widest below midline, sometimes angled abruptly where rounded bottom meets sides, or, if ball shaped, then with rough and irregular exterior. Entrance variable, but, if spoutlike, then not at lowest region of the nest. Combs' position often strongly marked on envelope exterior (figs. 9, 10, 11) . . . . . 27
- 20(19). Nest supported primarily by single broad leaf, sometimes a few leaves, or a few twigs that terminate in leaves touching or very close to nest . . . . . 21
- Nest suspended from limb or twigs several centimeters from leaves, or attached to a broad vertical surface such

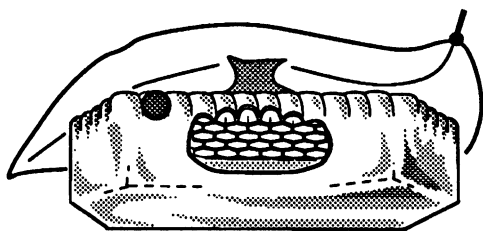


Fig. 9. Inverted mushroom pendant below leaves; central pedicel or distinct short stalk; cut away to show primary envelope from margin of comb; *Protopolybia* and *Charterginus* (some *Polybia* similar).

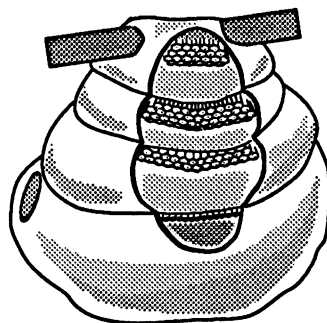


Fig. 11. Pendant nest; widest below midline; cut away to show combs sessile on previous envelopes (envelope sometimes imbricate in upper region, not shown); tiers of combs strongly marked on exterior of side wall; *Brachygastra*, *Polybia*, *Protonectarina*, and *Synoecoides*.

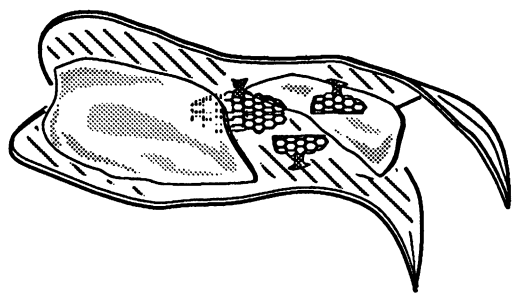


Fig. 12. Nest between leaves or in other cavity; envelope as simple sheets across gaps (rarely from margin of comb); combs variable; *Agelaia*, *Protopolybia*, and some *Ropalidia*.

- as a trunk; usually white or gray, rarely yellow or brown, sometimes streaked with other colors ..... 26
- 21(20). Envelope not domed more than 2 cm from leaf surface, color variable .. 22
  - Envelope domed more than 2 cm from leaf surface, usually amber or brown ..... 24
- 22(21). Envelope color variable, usually yellow or amber, rarely brown, green, or gray, sometimes nearly transparent with profuse secretion, often with ridges or streaks of color suggesting leaf veins. Entrance usually 5 mm wide or less. Sometimes with inconspicuous, fine sticky carton pillars 1–2 mm high around leaf petiole. Combs often highly recurved, often overlapping but rarely fusing with others. Cocoons extending above cell mouths by more than cell diameter ..... *Leipomeles* (possibly *Marimbonda*\*, but with sessile combs)
  - Envelope gray or white, uniform in texture and color, or if streaked then not so as to suggest veins of a leaf. Entrance usually more than 5 mm wide, with or without spout. Combs planar to slightly recurved, sometimes fusing. Cocoons barely if at all domed above cell walls ..... 23
- 23(22). Fine carton pillars or floss at envelope margin, especially on inner side of upper margin ..... *Chartergellus*\*
  - No such pillars or floss ..... *Parachartergus smithii*, *colobopterus*, *amazonensis*
- 24(21). Envelope shaped like funnel or inverted bottle. Entrance at bottom of narrow spout ..... 25
  - Envelope as simple sheet. Entrance merely a gap between envelope and substrate (fig. 12) .. *Agelaia cajennensis*

- 25(24). Envelope a broad funnel. Entrance a simple hole at bottom. Combs never hung one from another, often highly recurved, overlapping but rarely fusing with others. Cocoons domed above cell walls by more than cell diameter ...
  - ..... *Leipomeles*
- Envelope more bottle shaped. Entrance a long downward spout with flared opening directed sideways. Combs may be suspended from those above by central pedicel, neighboring combs may fuse. Cocoons domed barely, if at all, above cell walls ..... *Angiopolybia*
- 26(20). Envelope laminate, layers either supple, pale gray, and joining smoothly (*compressa*, *difficilis*), or with horizontal stripes of more brittle brown carton and long vertical lines where two layers meet (*vespiceps*). Combs round or oval, secondary combs suspended from those above by central pedicel. Cocoon caps simple. Entrance simple at lowest point ..... *Pseudopolybia*
  - Envelope mostly single layer or a few layers skewed and not closely parallel, usually gray or beige, with orderly ridges and furrows or sometimes lumpy and irregular. Combs kidney shaped and attached to substrate, rarely (Central America) secondary combs oval and suspended from those above. Cocoon caps often crossed with walls of pulp. Entrance usually at least a short spout ..... *Parachartergus*
- 27(19). Primary comb suspended from leaf by a central pedicel or short distinct stalk and bearing from its margin a domed primary envelope not more than about 2 cm deep, sometimes resembling an inverted mushroom (fig. 9) ..... 28
  - Primary comb not suspended from a pedicel or short distinct stalk, or, if so, then envelope much more than 2 cm high and not resembling a mushroom (fig. 11) ..... 30
- 28(27). Envelope same color as pulp of carton. Nest shape variable. Entrance lateral or ventrolateral. Secondary comb distinguishable from primary. Contours of cells visible around much of external comb margin ..... 29
  - Envelope painted partly or completely white externally, remaining yellow, amber, or brown internally. Nest mushroom shaped, sometimes star shaped with six points, with single, stout, central pedicel. Entrance dorsolateral or

- dorsal through comb. Secondary comb continuous with primary, indistinguishable from it when mature. Contours of cells rarely visible around external margin of comb . . . . . *Charterginus*
- 29(28). Carton composed of long fiber, often very fine, usually pale. Pedicels often multiple, sometimes very fine. Secondary combs either continuous with primary comb, pedicellate, and with single lateral entrance, or secondary combs sessile upon primary envelope and nest with separate lateral entrances for each comb. Cells less than 2 mm in diameter . . . . . *Protopolybia*
- Carton composed of short dark chips. Single stout stalk never resembling a fine pedicel. Secondary combs sessile upon primary envelope and nest with single ventrolateral entrance and internal passage connecting separate levels of combs. Envelope sometimes bears long extensions of carton at margins. Cells over 2 mm in diameter . . . . . *Polybia bistriata, platycephala, bicyttarella, catillifex, incerta, scrobalis* sometimes *occidentalis* (Central America)
- 30(27). Carton composed of fine, soft, durable, white plant hairs resembling cotton, often with blots of dark material painted on surface. Entrance ventrally in center of bottom envelope; South America only  
*Charterginus*
- Not as above . . . . . 31
- 31(30). Envelope abruptly angled where bottom meets side wall. Carton brittle, dark brown, composed of plant chips; portions of side walls and most of bottom envelope painted white. Entrance lateral, may be long slit . . . . . *Brachygastra bilineolata, scutellaris, smithii*
- Not as above . . . . . 32
- 32(31). Carton supple, resilient . . . . . 33
- Carton brittle, stiff . . . . . 38
- 33(32). Carton yellow or amber . . . . . 34
- Carton gray . . . . . 35
- 34(33). Comb continuous spiral or concentric spheres, forming a ball growing in all directions. Cell diameter more than 2 mm . . . . . *Agelaia areata, flavipennis*
- Comb many separate blocks, or, if continuous spiral, then expanding downward. Cell diameter 2 mm or less. Nest may be chaotic in structure (fig. 10) . . . . .  
. . . . . *Protopolybia sedula, acutiscutis, eximia, weyrauchi*
- 35(33). Mexico; if elsewhere, then with new envelope and comb added chaotically at several places at the bottom and side walls of nest (fig. 10). May have multiple entrances. Sometimes contains honey . . . . . *Brachygastra azteca, mellifica, lecheguana*
- Not Mexico; if in Mexico, then with combs added in orderly fashion one below the other (fig. 11) . . . . . 36
- 36(35). Cell walls easily peel away from backing sheet to yield an intact mat of hollow hexagons. Entrance in center of lowest envelope. Upper combs spherical, so that small nests are ball shaped; lower combs more planar (but curvature and spacing irregular), so large nests cylindrical or sausage shaped. Seams marking successive envelopes sinuous and irregular. Carton sometimes glossy. Nest sometimes contains honey; southern Brazil, Paraguay, northern Argentina . . . . . *Protonectarina*
- Cell walls firmly joined to backing, cannot be peeled off without destroying the hexagons. Combs curved similarly. Seams marking successive envelopes straight or gently curving. Carton dull . . . . . 37
- 37(36). Entrance lateral or ventrolateral, sometimes with a short lateral or upward spout, no honey . . . . . *Polybia ruficeps*, sometimes *occidentalis*, some other *Polybia*
- Entrance dorsal. Nest sometimes with honey . . . . . *Brachygastra moebiana*
- 38(32). Carton thin and fragile. Lines of construction obvious in upper region. Often imbricate in upper region . . . . . 39
- Carton dense and firm, sometimes resonating when struck with a finger or stick. Lines of construction not obvious. Imbrication weak or absent in upper region . . . . . 40
- 39(38). Entrance lateral, long vertical slit at least three times as high as wide . . . . .  
. . . . . *Brachygastra augusti*
- Entrance circular or oval . . . . . *Polybia*
- 40(38). Mud or clay . . . . . *Polybia emaciata, spinifex, singularis, furnaria*
- Vegetable fiber . . . . . 41
- 41(40). Bottom of nest convex, roughly radially symmetrical. Entrance lateral . . . . . 42
- Bottom flat or slightly concave, distinctly asymmetrical, sometimes with one side drooping lower than other. Entrance clearly ventral and opposite drooping lower side . . . . . *Epipona*

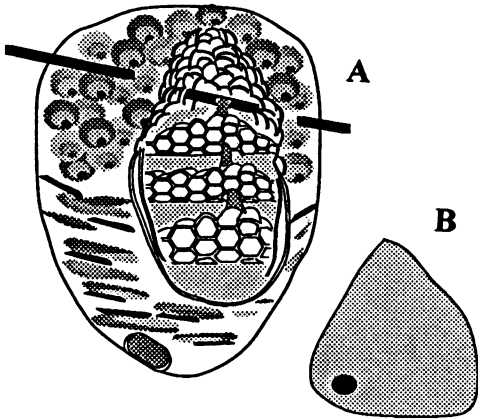


Fig. 13. A. Nest pendant (sometimes subterranean); upper region imbricate, lower region more laminate; pedicellate combs suspended from those above; entrance simple; abrupt switch to queen cells. B. Sometimes with conical roof; *Dolichovespula*, *Vespula*, *Vespa*, and *Provespa*. *Pseudopolybia* arboreal only, without queen cells, no conical roof.

- 42(41). Envelope extensively painted white . . . . . *Synoecoides*\*
- Envelope brown or gray, not painted white . . . . . *Polybia*
- 43(18). Carton flexible, supple (fig. 1) . . . . . 44
- Carton stiff, brittle . . . . . 47
- 44(43). Not ball or flask shaped, or, if so, then new carton is yellow or tan and not striped. Envelope either of simple separate sheets or many irregular, fused sheets . . . . . 45
- Nest ball or flask shaped, sometimes with a tall peaked cap above point of support. Envelope striped blue gray, lower region consisting of many complete or partly circumferential arcs. Combs horizontal, hanging from those above (fig. 13) . . . . . 46
- 45(44). Envelope resembling bivalve shell, bilaterally symmetrical with sheets hanging on each side of combs. Entrance ventral, horizontal slit where envelope sheets fail to fuse. Combs vertical, hanging from one edge without a narrow pedicel and rarely in contact with each other. Often hanging over water; central and western Africa . . . . . *Polybioides*
- Envelope not like a bivalve, variable. Entrance usually a simple slit or hole, sometimes multiple. Comb orientation variable, sometimes growing spirally,

- sometimes sessile marginally on substrate or basally on envelope; southern India to northern Australia, New Guinea, and Philippines . . . . . *Ropalidia*
- 46(44). Envelope often of independent arcs 10 cm wide to completely circumferential. Internal surface of envelope smoothed and almost continuous. Combs slightly recurved and connected by broad flattened buttresses. Cell walls slightly curved; Holarctic . . . . . *Dolichovespula*
- Envelope arcs usually less than 10 cm wide and overlapping. Internal surface of envelope usually rough and revealing many pockets between separate imbricate arcs. Combs flat and connected by stout posts especially in lower levels of nest, or by several buttresses not continuous across back of comb. Nests sometimes more than 1 m in diameter; northern Europe, introduced into USA, Australia, New Zealand, Chile, South Africa, and Argentina . . . . . *Vespula germanica*\* (rarely nests in the open, usually in cavities)
- 47(43). Carton entirely of coarse, short chips. Lines of construction strong. Primary comb supported by one or more flattened pedicels spread across comb back. Face of combs sometimes covered over with carton to block cells. Nest sometimes with conical cap above point of support . . . . . *Vespa*
- Carton at least partly of long amber plant hairs. Lines of construction sometimes not visible on upper envelope. Primary comb supported by parallel, rodlike pedicels from the substrate, or by a broad buttress formed by fusion of these pedicels. Nest without conical cap. Back of primary comb sometimes glossy, sometimes with furrows between cell bases partly filled with carton; Southeast Asia . . . . . *Provespa*
- 48(1). Nest of multiple combs (except in early stage) surrounded by an envelope . . . . . 49
- Single naked comb without an envelope . . . . . 55
- 49(48). Envelope mostly of many interconnected layers. Cell diameter varying within or between combs, never less than 3 mm. If envelope encloses combs, then entrance ventral or ventrolateral . . . . . 50
- Envelope mostly a simple sheet, sometimes a few layers, sometimes transparent and

- celophanelike. Cell diameter uniform throughout nest, 3 mm or less. Entrance variable (fig. 12) . . . . . 52
- 50(49). Envelope blue gray, supple; Holarctic, historically south through montane Mexico and Guatemala . . . . . *Vespula rufa* group (Palearctic), *V. germanica*, *pensylvanica*, *squamosa* (New World), *V. pensylvanica* (introduced) Hawaii, *V. germanica* (introduced) Australia, New Zealand, Chile, South Africa, and Argentina
- Envelope tan or brown, brittle . . . . . 51
- 51(50). Envelope usually completely enclosing nest; most imbricate patches closed completely to the outside; often many pillars connecting envelope to cavity ceiling. Older cells mostly less than 5 mm in diameter; Holarctic . . . . . *Vespula vulgaris* group except *germanica* and *pensylvanica*
- Envelope often broadly open below combs, or reduced to sheets closing access to cavity. Older cells mostly more than 6 mm in diameter. Palearctic and Southeast Asia, eastern USA . . . . . *Vespa*
- 52(49). Older cell bottoms removed and without carton . . . . . 53
- Older cell bottoms retaining carton, or sessile . . . . . 54
- 53(52). Comb carton composed of short chips. Older cell bottoms replaced with windows of clear secretion. Comb, if spiral shaped, separate from envelope; southern India to northern Australia, New Guinea, and Philippines . . . . . *Ropalidia*
- Comb carton composed of long plant fiber. Older cell bottoms open, not replaced with secretion. Comb, if spiral shaped, continuous with envelope; Southeast Asia and Indonesia . . . . . *Polybioides*
- 54(52). Envelope supported by walls of cavity and composed of yellow or amber long fiber. Comb usually over 50 cm<sup>2</sup> in area when mature. Nest with or without pedicel . . . . . *Agelaia cajennensis*
- Envelope supported by comb margin and variable in color, or supported by walls of cavity and transparent with little or no vegetable fiber. Comb usually less than 50 cm<sup>2</sup> in area when mature, pedicellate . . . . . *Protopolybia*
- 55(48). Carton composed of short chips; sometimes glossy with profuse secretion, sometimes with patches of pure, transparent secretion . . . . . 56
- Carton of long fiber; duller, glossy only near pedicel . . . . . 58
- 56(55). Comb sessile inside sheathing leaf of a bromeliad; South America . . . . . *Metapolybia bromelicola*
- Comb pedicellate . . . . . 57
- 57(56). Older cell bottoms replaced with windows of clear secretion; Africa, India to Australia, New Guinea, and Japan . . . . . *Ropalidia*
- Older cell bottoms retaining carton; Central and South America . . . . . *Mischocyttarus*
- 58(55). Carton and pedicels fibrous, brown, amber, or yellow, with very little secretion. Combs often orderly parallel or concentrically arched, interconnected by pedicels; Central and South America . . . . . *Agelaia*
- Carton brown or gray. Usually a single continuous comb; if multiple, then separate and not as above . . . . . 59
- 59(58). Pedicels fibrous, easily broken or detached; cells less than 3 mm in diameter; Central and tropical South America . . . . . *Protopolybia*
- Pedicels resinous, tough, and well anchored; cells more than 3 mm in diameter in Central and South America, variable elsewhere; cosmopolitan . . . . . *Polistes*

## ILLUSTRATIONS

In addition to the photographs presented here, previously published photographs and detailed illustrations are cited for the reader to consult. Some of these are obscure, but they are included so that thorough students will not overlook certain noteworthy works. Boxed arrow in figures indicates upward. All photographs are by the author unless otherwise stated. Scale bar equals 25 mm unless otherwise noted. Nomenclature is cited parenthetically where modern nomenclature differs from that used by earlier authors. Readers who wish to consult a few texts that cover the diversity well should examine Berland and Grassé (1951), Jeanne (1975), Wenzel (1991), or scattered photographs in the Ross and Matthews (1991) volume. Many fine illustrations are available in the classical works by Saussure (1853–1858) and Möbius (1856), though these are not commonly available and their nomenclature is archaic. Institutions housing certain specimens are abbreviated on page 4, and localities are offered for photographs from the field for which no specimen was retained. A cladistic



matrix of architectural characters for the genera of Polistinae is offered in Wenzel (1993). An interim cladogram of genera of social Vespidae is offered in figure 14. Ranges of the genera are approximate.

## DESCRIPTIONS OF NESTS

*Agelaia*: Variable. Swarm-founded. In cavities or subterranean, sometimes exposed arboreal. Nests can grow to millions of cells (*A. vicina*). Pedicels multiple, fibrous, cell-marginal, vertical or horizontal, from cavity walls; sometimes sessile initiation. Carton supple, long fiber, amber or yellow. Combs growing gradually at margins, may be suspended from each other, fusing, double sided (*A. lobipleura*), planar, conical, or spiralling outward. Cell walls straight, parallel to divergent. Cavity species without envelope or sometimes with a reduced envelope restricting access to cavity (*A. cajennensis*); exposed arboreal nests (*A. areata* and *flavipennis*) with single or multiple ball shaped envelope supported by combs within or by pedicels arising from combs, not removed but rather built over as nest expands in all directions. Mexico to Argentina. See figures 5, 12, 17C, D, 23C; Vesey-Fitzgerald (1938: fig. 12, as *Gymnopolybia*); Evans and West Eberhard (1970: fig. 91, as *Stelopolybia*); Jeanne (1970: as *Stelopolybia*, 1973); Richards (1978: figs. 28–30, as *Stelopolybia*); Wenzel (1991, 1992b); and Zucchi et al. (1995).

*Angiopolybia*: Swarm-founded. Arboreal, often on leaves. Pedicel initially single, sometimes later multiple, fibrous, cell-marginal, vertical. Carton supple, long fiber, amber or yellow, rarely brown. Combs growing gradually at margins, adjacent and fusing or suspended from each other, slightly recurved, not in contact with envelope. Cell walls straight, subparallel. Envelope from substrate, single sheet, flask shaped, partly removed to allow downward expansion. Entrance long downward spout with hole facing horizontally. Panama to Brazil. See figures 8, 17B, 23F; Ducke (1910: fig. 12, as *Stelopolybia*); Vesey-Fitzgerald (1938: fig. 3, as *Stelopolybia*); and Jeanne (1975).

*Apoica*: Swarm-founded. Arboreal, usually on narrow branch. Sessile initiation, sometimes resembling fibrous, short, broad, ver-

tical pedicel. Carton supple, long fiber, felt-like, amber or yellow, rarely brown. Comb single, growing gradually off substrate at margins, facing downward, sometimes resembling an inverted bowl or plate. Foundation and back of comb thickened secondarily by addition of felt, obscuring cell bases, often including supporting branch into comb apex. Cell walls straight and parallel. No envelope. Mexico to Argentina. See figures 17A, 21B; Buysson (1906); Ducke (1910); Evans and West Eberhard (1970); Vecht (1972); Richards (1978); and Schremmer (1986).

*Asteloeca*: Poorly known. I have seen one complete specimen and a fragment of a second. Swarm-founded. Arboreal. Sessile initiation on a narrow branch. Carton brittle, of short chips, very glossy. Comb single, growing off narrow substrate, expansion probably suddenly in blocks. Cell bases visible on back of comb, cell walls straight and parallel. Envelope a single sheet, from comb margin, abruptly angled where walls meet flattened dome, about one cell length distant from comb face, initial sheet apparently covered with clear secretion, may be partly removed to allow contiguous expansion. Entrance hole a short collar, apparently at center of dome, at final remaining gap in envelope construction. Amazonian Peru and Bolivia, Brazil, and French Guyana. See figures 7, 19D, 24B and Garcia (1978, as *Polybia trailii*).

*Belonogaster*: Independent-founded. Arboreal. Pedicel resinous, cell-central, vertical. Carton supple, long fiber but sometimes very spare with cocoons or re-used silk providing structure. Comb single, growing gradually at margins, usually hammock shaped due to divergent cell walls (sometimes vertical string of adjacent cells—Madagascar only). Cell bottoms removed but not replaced, cocoons slit open, no meconium in old cells, sometimes old cells near top completely removed and only reinforced comb margin supplies support in mature nests. No envelope. Africa, Arabian Peninsula, and perhaps India. See figure 16F; Iwata (1966); Marino Piccioli and Pardi (1970, 1978); Pardi and Marino Piccioli (1970); Keeping and Crewe (1983); and Gadagkar (1991).

*Brachygastra*: Variable. Swarm-founded. Arboreal. Sessile initiation. Carton either

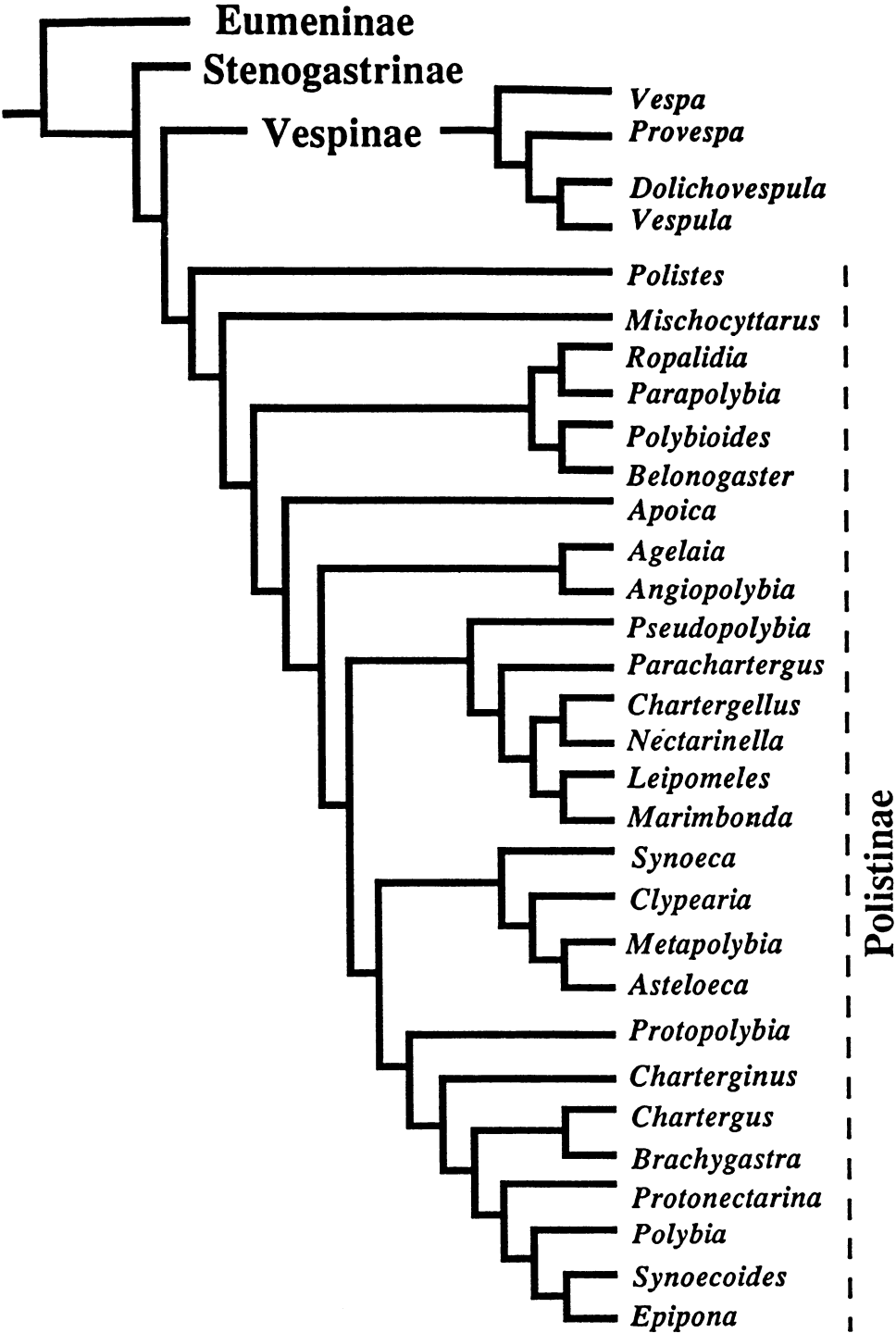


Fig. 14. A preliminary cladogram for social wasps. Provided for basic reference only, this tree is modified from Wenzel and Carpenter (1994) and is not definitive.

brown, brittle, and of short chips or gray, supple, and of long fiber; without obvious secretion reinforcement. Primary comb built rapidly to full size, entirely sessile beneath broad surface or growing off narrow or upright surface; may be planar or spherical. Secondary combs strictly sessile on preceding envelope, sometimes chaotic and starting at several places in gray nests; orderly in brown nests. Cell walls straight and subparallel. Primary envelope from comb margin or substrate, usually a deep dome. Secondary envelope built from previous envelope (brown nests), sometimes partly from substrate (gray nests). Brown nest side wall often reinforced by imbrication or surface blots peripherally, but not on area destined to support secondary combs. Brown nests may be painted white on sides and below. Entrance simple, sometimes aligned to form an internal passage between stories, sometimes peripheral, long, vertical slit (brown nests), or multiple and chaotic (gray nests only). May contain honey. Arizona and Texas to northern Argentina. See figures 10, 11, 21D, 25F; Buysson (1905); Ducke (1910: fig. 4, as *Nectarina*); Richards (1978); and Starr (1991).

*Chartergellus*: Swarm-founded. Arboreal, Pedicel fibrous, cell-marginal, horizontal to margin of downward-facing comb. Carton of long, gray fiber, either supple, smooth, and uniform or brittle and irregular with prominent lines of construction. Combs multiple, growing gradually at margins, suspended from substrate one below the other, not in contact with envelope. Cell walls straight, subparallel. Envelope from substrate, a single sheet, flask shaped, sometimes much flattened when substrate is broad, partly removed to allow downward expansion. Fine paper pillars or floss between substrate and envelope margin, particularly on inside of upper region. Entrance short downward spout. Costa Rica to Brazil. See figures 6, 18C, 23A, B and Richards (1978).

*Charterginus*: Swarm-founded. Arboreal, often on broad leaf. Sessile initiation, resembling a stout pedicel. Carton of fine, long fiber, feltlike but brittle. Comb single, resembling an inverted mushroom, only a few initial cells reaching substrate, nest growing by sudden blocks contiguous with existing comb. Cell walls straight and subparallel.

Envelope from comb margin, a single sheet, dome, sometimes deep with acute ridges and broad furrows or flattened with hollow points protruding hexagonally. Lines of construction obscured externally by pulp. Surface of nest sometimes spotted or entirely covered with white substance externally. Envelope margin partly removed to allow contiguous expansion. Entrance hole simple, peripheral or dorsal. Panama to Brazil. See figures 9, 17F, 26F; Ducke (1905: pl. 1); Bequaert (1938); Evans and West Eberhard (1970); and Schremmer (1978).

*Chartergus*: Swarm-founded. Arboreal, often high in tree. Sessile initiation, point of contact later encompassing branch. Carton of fine, long white fiber resembling cotton, felt-like, supple when thin, later stiff and easily withstanding strong pressure of fingers. Combs multiple, sessile on envelope, growing by rapid construction of several layers. Cell walls straight and subparallel. Primary envelope from substrate or comb margin, secondary envelopes from preceding envelope, initially a single sheet but rapidly reinforced to become thick, heavy, and durable dome, usually angled abruptly where side walls meet bottom cell-bearing region of dome. Lines of construction obscured by pulp, surface of nest sometimes spotted with dark pulp externally. Entrance hole simple, in ventral center of dome which may become funnel shaped, little more than one head-width in diameter, aligned to form internal passage between stories. Colombia to Brazil. See figure 26C; Ducke (1910); Berland and Grassé (1951); Evans and West Eberhard (1970); Wilson (1971); Spradbery (1973); and Richards (1978).

*Clypearia* (= *Occipitalia*): Poorly known. Swarm-founded. Arboreal. Sessile initiation on trunk or branch. Carton brittle, of short chips. Comb single, entirely sessile on broad surface or growing off narrow substrate; in latter case back of comb reinforced with pulp obscuring cell bases. Cell walls straight and parallel or subparallel. Envelope single sheet, from substrate or comb margin, dome shaped, sometimes less than 1 cm distant from comb face. Initial sheet apparently covered with clear secretion (except in *C. sulcata*) and distinctive, nonpapery particles applied to the secretion separately. Envelope

margin may be partly removed to allow contiguous expansion. Entrance hole simple or a short collar, corresponding to final remaining gap in envelope construction at top, periphery, or center of dome. *C. sulcata* often situated near arboreal ant nests, such as those of *Azteca*. Panama to southern Brazil, and Bolivia. See figures 7, 24C, D, F; Dücke (1910); Araujo (1955: fig. 8); Evans and West Eberhard (1970: fig. 92); and Jeanne (1979). See Carpenter et al. (1996) for synonymy.

*Dolichovespula*: Independent-founded. Arboreal, occasionally subterranean (western plains of USA and Canada). Hanging sheet of fibrous paper from substrate precedes pedicel. Pedicel single, twisted, and reinforced with secretion in new nests, fibrous in mature nests, cell-marginal, vertical. Carton supple, gray. Combs recurved, suspended from each other by buttresses, cell walls curved, divergent, with abrupt switch to large queen cells, not in contact with envelope. Envelope from hanging sheet or substrate, mostly laminar, sometimes with imbricate conical roof, removed and smoothed internally as nest grows. Lines of construction obvious. Entrance hole long downward spout in young nests, simple in mature nests. Holarctic, Asia excluding India and Indochina. See figures 13, 26A; Hungerford (1930); Duncan (1939); Berland and Grassé (1951); Spradbery (1973); Akre et al. (1980); Edwards (1980); Mastuura and Yamane (1984); and Greene (1991).

*Epipona*: Swarm-founded. Arboreal, usually high in tree. Sessile initiation, point of contact encompassing branch. Carton of short chips and coarse matter, gray or brown, brittle, very dense, without obvious secretion, easily withstanding pressure and resonating if struck with a finger. Combs multiple, sessile on envelope, growing by rapid construction of several layers. Cell walls straight and subparallel. Primary envelope from substrate or comb margin. Secondary envelopes from preceding envelope, single sheet but rapidly reinforced to become thick, usually abruptly angled where side walls meet bottom cell-bearing region of dome, peripheral walls drooping lower on side opposite entrance than elsewhere and sometimes unsuitable for comb in lower stories. Lines

of construction obscured by pulp added externally. Cross section of nest sometimes increasing for several layers then gradually decreasing. Entrance hole simple, very near shorter side wall of dome, aligned to form an internal passage between stories. Mexico to Brazil. See figures 20D, 26E; Vesey-Fitzgerald (1938: fig. 7, as *Tatua*); Berland and Grassé (1951: fig. 1026); Wilson (1971); Jeanne (1975); Richards (1978); and Wenzel (1991, 1992b).

*Leipomeles*: Swarm-founded. Arboreal, beneath single or among few leaves, sometimes with leaf petiole bearing pillars 1–2 mm long tipped with sticky secretion. Pedicel fibrous, cell-marginal, vertical or oblique from leaf veins, single or multiple. Carton supple, long fiber, thin and often translucent. Combs adjacent, growing gradually at margins, rarely fusing, planar to highly recurved, not in contact with envelope. Cell walls straight, subparallel to divergent. Cocoons domed 1–2 mm above cell walls. Envelope from leaf, single sheet, flattened dome to funnel shape, may be any color including green, sometimes with ridges or streaks mimicking leaf venation, sometimes with a central, impressed, longitudinal furrow composed of tight arches of pulp. Envelope margin partly removed to allow downward or peripheral expansion. Entrance toward tip of leaf, sometimes with downward spout. Brazil to Costa Rica. See figures 6, 18E, 23E, 24A; Dücke (1910); Richards (1978); Schremmer (1983, 1986); and Wenzel and Carpenter (1994).

*Marimbonda*: Poorly known. I have seen only two specimens that I believe are of this genus. Swarm-founded. Arboreal on vertical branch or leaf. Sessile initiation. Carton supple, long fiber. Comb probably expanding gradually at margins and mostly downward, restricted to substrate. Envelope flattened, rather similar to some *Leipomeles* but without leaf venation, sometimes with central, longitudinal crease composed of tight arches of pulp. Brazil, probably Amazonian Peru, Ecuador, and Colombia. See figures 6 (but sessile), 23D.

*Metapolybia*: Swarm-founded. Arboreal. Sessile initiation on broad surface. Carton of short chips, supple when new, brittle later. Single comb expanded suddenly in blocks on substrate adjacent to earlier comb and on any

side of it when nest is on horizontal surface, growing mostly upward when on vertical surface, growing around a curved substrate rather than off it. Cell walls straight and usually parallel (except where nest grows around curve). Envelope (lacking in *M. bromelicola*) from substrate or from fully elongated cell walls (*M. docilis*), single sheet, not papery, generous secretion often forming clear windows. Short envelope walls perpendicular to substrate, straight or curving outward, eaves often forming an acute angle with the flattened, rough, and uneven central region of dome. Envelope margin partly removed and expanded to cover contiguous combs together. Entrance spout peripheral, curved upward, built separately from final remaining gap in envelope construction. Mexico to Paraguay. See figures 7, 19A, 24E; Vesey-Fitzgerald (1938); Richards (1978); and Schremmer (1984).

*Mischocyttarus*: Independent-founded. Arboreal, sometimes in cavities. Pedicel resinous, cell-marginal, vertical or oblique. Carton supple or brittle, short chips (except *M. carbonarius* in eastern Brazil), sometimes with conspicuous glossy secretion. Comb may be any shape, may be multiple. No envelope. Southwestern Canada to northern Argentina. See figures 5, 15D, E, F, 16A, B, C, 22A; Ducke (1914); Richards (1945); Zikán (1949); Jeanne (1975); Herre et al. (1986); Carpenter and Wenzel (1988); Gadagkar (1991); and Starr (1991).

*Nectarinella*: Swarm-founded. Arboreal on broad vertical or slanting surface. Sessile initiation. Carton supple, long, gray fiber. Single oval comb expanding gradually at margins but primarily downward. Envelope from substrate, flattened dome with irregular small ridges and furrows, externally bearing paper pillars 1–2 mm long and tipped with sticky secretion, often blotted with lichens and fragments of bark as camouflage, sometimes many fine paper pillars or floss between substrate and envelope margin or downward entrance spout. Costa Rica to Colombia, also Mato Grosso, Brazil. See figures 6 (but sessile), 18D and Schremmer (1977, 1986).

*Parachartergus*: Variable. Swarm-founded. Arboreal. Pedicel fibrous, cell-marginal, vertical to horizontal, sometimes multiple.

Carton supple, long fiber. Combs adjacent (sometimes fusing), or one below the other, or suspended from each other (Central America only), growing gradually at margins. Cell walls straight, subparallel, sometimes pulp aligned with neighboring walls extending across pupal caps. Envelope from substrate, single sheet, flat dome or flask shaped, sometimes contacting combs. Envelope margin partly removed to allow expansion in any direction but primarily downward, sometimes with regular corrugations converging on a weak keel. Entrance usually a downward spout. Mexico to Argentina. See figures 6, 17E, 18A, B; Ducke (1910: fig. 16); Vesey-Fitzgerald (1938); Berland and Grassé (1951: fig. 1025); Spradbery (1973); Richards (1978); Schremmer (1978, 1986); Strassmann et al. (1990); and Wenzel (1992b).

*Parapolybia*: Independent-founded. Arboreal. Pedicel resinous, cell-central, vertical to oblique, sometimes absent in secondary combs, may be several centimeters wide in mature combs. Carton supple, long fiber with conspicuous glossy secretion, usually yellow or light brown, sometimes very pale, sometimes translucent or lacelike when new. Combs long and slender, hung from one edge, may be multiple and closely packed. Cell bottoms and base of cocoons removed and replaced with transparent secretion, no meconium in old cells. No envelope. Iran to New Guinea, north to Korea and Japan. See figures 5, 22C; Vecht (1966); Sekijima et al. (1980); Yamane (1984); and Gadagkar (1991).

*Polistes*: Independent-founded. Arboreal, sometimes in cavities. Pedicel resinous, cell-marginal, vertical or oblique. Carton supple, of long fiber (except *P. stenopus* in South Pacific or Neotropical *P. bicolor*), usually glossy only near pedicel but sometimes extensively over comb back. Comb planar or recurved, rarely as a long string of cells (*P. goeldi*, South America and *P. stenopus*, South Pacific); single, rarely multiple. Indopacific species sometimes with two brood per cell in tandem. No envelope. Cosmopolitan. See figures 5, 15C; Rau (1928); Yoshikawa (1964); Evans and West Eberhard (1970); Yamane and Okazawa (1977); Schremmer (1986); and Starr (1991).

*Polybia*: Variable. Swarm-founded. Arbo-

real. Sessile initiation or suspended by buttressed sheet from substrate (subgenus *Trichinothorax*). Carton brittle, of short chips or mud (*P. emaciata*, *furnaria*, *singularis*, and *spinifex*), and without obvious secretion reinforcement. Primary comb entirely sessile and built rapidly to full size beneath broad and horizontal surface, or growing gradually at margins off narrow or upright surface. Secondary combs strictly sessile on preceding envelope, often growing by rapid construction of several layers. Cell walls straight and subparallel. Primary envelope from comb margin or substrate, usually a deep dome, rarely resembling an inverted mushroom (few one-level nests of *P. bicyttarella*, *bistriata*, *catillifex*, *incerta*, *platycephala*, and *scrobalis*), sometimes with projections extending radially outward (particularly *P. catillifex*). Secondary envelopes built from previous envelope, each envelope as a single sheet, built to full size rapidly, side wall often quickly reinforced by imbrication or surface blots peripherally but not on area destined to support secondary combs. Upper region of nest sometimes slightly glossy on exterior (subgenus *Trichinothorax*). Entrance simple, peripheral or in lower region of dome, aligned to form internal passage between stories, modified in mud nesters into a small ventral hole (*P. furnaria*), projecting snout (*P. emaciata*), or vertical slit continued across all combs (*P. singularis*, and *spinifex*). *Polybia richardsi* (Cooper, 1993) builds an initial nest of thick walls (AMNH) that is expanded to peculiar chaotic shape with multiple entrances and extraneous flanges or blisters of carton. The interior may be secondarily smoothed with carton, unique among *Polybia*. Arizona and Texas to Argentina. See figures 9, 11, 20A, B, C, E, F, 21F, 25E; Dücke (1910); Vesey-Fitzgerald (1938); Berland and Grassé (1951); Windsor (1972); Spradbery (1973); Jeanne (1975, 1986); Garcia (1978); Richards (1978); Höfling and Machado (1985); Schremmer (1986); and Cooper (1993).

*Polybioides*: Asian species poorly known. Swarm-founded. Arboreal or in cavities (Asia). Sessile initiation, but supporting margin of comb may become reinforced with dark secretion to resemble a fat pedicel (Africa). Carton supple, long fiber, usually yel-

low or amber, sometimes brown. Combs multiple, long, hung from one edge, and parallel, facing outward from original back-to-back pair and growing gradually at the margins (Africa), or single, horizontal, and as a downward spiral (Asia). Cell walls straight and subparallel, cell bottoms and base of cocoons removed and not replaced, no meconium in old cells. Envelope of separate, incompletely fused sheets perpendicular to combs, open below, resembling bivalve shell (Africa), or formed by marginal fusion of spiral comb with subtle imbricate reinforcement above (Asia). West and Central Africa and Southeast Asia. See figures 21A, B, 22F; Bequaert (1918: pl. 19); Pagden (1958); Walrecht (1963); Vecht (1966); Richards (1969); and Turillazzi and Francescato (1994).

*Protonectarina*: Swarm-founded. Arboreal. Sessile initiation. Carton gray, supple, of long fiber, slightly glossy. Primary comb built rapidly to full size, spherical. Secondary combs strictly sessile on preceding envelope and successively less curved, but curvature and spacing of combs irregular. Nest developing from ball to sausage shaped, often growing by rapid orderly construction of several layers. Cell walls straight and subparallel. Comb backing (internalized envelope) is easily peeled away from hexagonal pattern of cell walls leaving hollow cell walls behind. Primary envelope from substrate, usually a deep dome. Secondary envelope built from previous envelope or partly from substrate, seams marking successive envelopes sinuous and irregular. Entrance simple, in ventral surface of nest, aligned to form internal passage between stories. Nest sometimes contains honey. Southern Brazil, Paraguay, and northeastern Argentina. See figures 11, 21E, 25D; Shima et al. (1996).

*Protopolybia* (= *Pseudochartergus*): Highly variable, including within species. Swarm-founded. Arboreal, frequently on leaves or in cavities. Pedicel fibrous, cell-marginal, vertical, multiple, or sessile initiation on surface (*P. acutiscutis*, and *sedula*). Carton supple to brittle, long fiber. Comb and cell walls may be constructed rapidly to large or final size. Cell walls straight and subparallel. Secondary combs may be built rapidly to large or final size from margin of primary comb and coplanar with it, or sessile on the

primary envelope, sometimes spiraling downward (*P. acutiscutis*, and *sedula*). Envelope, when arising from margin of comb or cell walls, then partly removed and expanded to cover contiguous, pedicelate combs together; when from primary envelope or substrate, then covering successive, sessile combs separately. Envelope as a single sheet, dome, or absent; or as a dry, clear sheet of secretion without wood pulp, arising from substrate and restricting access to the cavity (usually folded leaves). Envelope not reinforced by imbrication or lamination, rarely thickened by blots of pulp. Entrance hole simple, usually peripheral, often multiple providing separate access to each layer, not aligned to form internal passage between stories. Honduras to Brazil. See figures 9, 10, 12, 19E, F, 25A, B, C; Duce (1910: figs. 2, 3; 1914, as *Pseudochartergus*); Jeanne (1970, as *Pseudochartergus*); and Schremmer (1984, as *Pseudochartergus*). For synonymy, see Carpenter and Wenzel (1989).

*Provespa*: Swarm-founded. Arboreal or in tree cavities. Pedicel fibrous, cell-marginal, vertical, multiple but later fused to form single broad pedicel. Carton supple to brittle, of short chips to long fiber. Combs suspended from each other, usually with one central pedicel between combs, growing gradually at margins, queen cells mixed with worker cells, not in contact with envelope. Back of comb sometimes with pulp placed in furrows between cell bases. Cell walls straight, subparallel. Envelope from substrate or base of pedicel, laminate to imbricate. Entrance hole simple. Southeast Asia. See figures 13, 15B; Matsuura and Yamane (1984: figs 7.3, 7.4); Maschwitz and Hänel (1988); and Matsuura (1991).

*Pseudopolybia*: Swarm-founded. Arboreal. Pedicel fibrous, cell-marginal, vertical, single, sometimes becoming broad. Carton supple. Combs stacked downward, occasionally multipedicellate, growing gradually at margins, slightly recurved, not fused with envelope. Cell walls straight. Envelope from substrate, laminar or loosely imbricate, spherical or tapering below, removed internally and smoothed as nest grows. Entrance hole simple at lowest point. Nicaragua to Brazil. See figure 18F; Duce (1910: figs.

13–15, as *Parachartergus*; 1914); and Richards (1978).

*Ropalida*: Highly variable. Independent- or swarm-founded. Arboreal or in cavities. Pedicel resinous, cell-central, vertical to horizontal, or initiation sessile. Carton supple or brittle, usually short chips with conspicuous glossy secretion. Comb may be any shape, may be multiple; large single comb may be cut to produce separate daughter combs. Cells bottoms and base of cocoons removed and replaced with transparent secretion, no meconium in old cells. If envelope present, then as simple sheets, often joined chaotically or closing gap between leaves or nearby objects, may be pure secretion without pulp. Entrances simple, may be multiple, but do not align to form internal passage. Africa, India to Australia and New Guinea, and north to Japan. See figures 5, 10, 12, 16D, E, 21C, 22D, E; Carl (1934); Vecht (1962); Yoshikawa (1964); Hook and Evans (1982); Kojima (1982, 1984, 1988); Itô (1986); Kojima and Jeanne (1986); Itô et al. (1988); Spradbery and Kojima (1989); Maschwitz et al. (1990); Gadagkar (1991); Starr (1991); Yamane et al. (1991); and Makino et al. (1994).

*Synoeca*: Swarm-founded. Arboreal, usually on broad slanting surface, often near arboreal ant nest. Sessile initiation. Carton brittle, short chips, often coarse. Each comb expanding gradually at margins but mostly downward. Secondary combs built contiguous with primary but mostly higher on substrate, may be built partly on envelope when substrate is narrow. Cell walls straight, parallel to divergent. Envelope from substrate or margin of comb, each a single sheet, deep dome sometimes with regular transverse corrugations, sometimes chaotically supported from previous envelope. Entrance as a short upward collar near top of envelope. Lower, older levels of nest may be abandoned while upper levels are active. Mexico to Argentina. See figures 7, 19B; Buysson (1906); Duce (1910); Vesey-Fitzgerald (1938); Schremmer (1973, 1986); Jeanne (1975); Richards (1978); and Castellón (1980).

*Synoecoides*: Poorly known. I have seen one specimen. Swarm-founded. Arboreal. Sessile initiation, point of contact encompassing branch. Carton brittle, of short chips, without obvious secretion. Primary comb

sessile on substrate, growing off it gradually at margins. Secondary comb sessile on previous envelope. Cell walls straight and subparallel. Primary envelope from substrate. Secondary envelopes from preceding envelope, single sheet, lines of construction obscured by long fiber pulp added externally, sometimes pale or white. Colombia, Ecuador, Peru, Bolivia, and Brazil. See figures 11, 26D and Araujo (1944).

*Vespa*: Independent-founded. Arboreal, in cavities, or subterranean. Pedicel fibrous, cell-marginal, vertical, sometimes multiple. Carton brittle, of short chips. Cell walls straight or slightly curved, subparallel. Secondary combs with single or multiple pedicels, stacked downward. Cell size increasing gradually to queen size, some cells may have open ends closed with paper. Envelope from substrate or base of pedicel, laminate to imbricate, removed internally as nest grows and internal surface left rough, revealing many pockets between separate imbricate arcs. Envelope sometimes reduced to restrict natural access to a cavity, or absent in cavity nesters. Nest may develop imbricate conical roof in exposed sites. Entrance often as long downward spout when nest is young, simple hole in mature nests. Southeast Asia, Palearctic, and introduced to eastern USA. See figures 13, 15A; Vecht (1957); Matsuura (1971, 1984, 1991); Edwards (1980); Seeley and Seeley (1980); Starr and Jacobson (1990); and Starr (1991).

*Vespula* (= *Paravespula*): ***Vespula vulgaris* group**. Independent-founded. In cavities or subterranean. Hanging sheet of fibrous paper from substrate precedes pedicel. Pedicel fibrous, cell-marginal, vertical, twisted, single. Multiple pedicels occurring between secondary combs, peripheral pedicels from combs to envelope, sometimes between envelope and cavity wall, buttresses sometimes built secondarily above primary comb. Carton supple to brittle. Combs stacked downward, abruptly switching to large queen cells pe-

ripherally or in lower combs. Cell walls straight to slightly curved, subparallel. Envelope from hanging sheet or from previous sheet of envelope, imbricate in upper region, but more laminar below, highly imbricate when nest is mature. Envelope removed internally as nest grows and internal surface left rough, revealing many pockets between separate imbricate arcs, often very brittle and tan in color. Entrance hole simple. ***Vespula rufa* group**. As *V. vulgaris* but carton always supple and gray. Usually with buttressed sheets between combs. Comb planar. Cell walls curved, divergent. Envelope laminar or loosely interconnected, imbrication vague or absent. Entrance hole simple. Holarctic, with some extension into southern Asia and Central America, introduced into Australia, New Zealand, Chile, South Africa, and Hawaii. See figures 13, 26B; Duncan (1939); Spradbery (1973); Edwards (1980); Akre et al. (1981); Yamane et al. (1981); Matsuura and Yamane (1984); Schremmer (1986); and Vasic (1986, as *Vespa*).

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## Appendix 1

### SPECIES FOR WHICH NESTS HAVE BEEN EXAMINED

Genera are presented in phylogenetic order (see fig. 14). Nomenclature for *Polistes* follows Carpenter (1996), but Richards (1978) subgenera are listed in parentheses under *Aphanilopterus*, with which Carpenter synonymized them. Following Kojima and Carpenter (1996) for *Ropalidia*, no subgenera are listed. A list of institutions where these specimens may be found is available at <http://iris.biosci.ohio-state.edu/people/jww/specieslist.html>.

#### VESPINAE

##### Genus *Vespa*

*affinis*  
*analis*  
*cincta*  
*crabro*  
*mongolica*  
*parallela*  
*tropica*  
*velutina*

##### Genus *Provespa*

*anomala*

##### Genus *Dolichovespula*

*arenaria*  
*maculata*  
*media*  
*norvegica*  
*sylvestris*

##### Genus *Vespula*

*germanica*  
*maculifrons*  
*pennsylvanica*  
*rufa*  
*squamosa*  
*vulgaris*

*cavapyta*  
*cinctus*  
*comanchus*  
*crinitus*  
*cubensis*  
*dominica*  
*erythrocephalus*  
*exclamans*  
*goeldii*  
*infuscatus*  
*instabilis*  
*versicolor*  
(*Epicnemius*)  
*bicolor*  
*billardieri*  
*cinerascens*  
*pacificus*  
*testaceicolor*  
(*Fuscopolistes*)

*apachus*  
*carolina*  
*dorsalis*  
*fuscatus*  
*metricus*  
*poei*  
(*Onerarius*)  
*carnifex*  
(*Palisotius*)  
*major*

Subgenus *Gyrostoma*  
(including *Nygmopolistes*)  
*diabolicus*  
*jadwigae*  
*olivaceus*  
*minor*

*stenopus*  
*tenebricosus*  
*tepidus*

##### Subgenus *Polistella* (including *Stenopolistes*)

*albocalcaratus*  
*aquilinus*  
*bernardii*  
*defectivus*  
*fastidiosus*  
*flavobilineatus*  
*haugi*  
*humilis*  
*madecassus*  
*mandarinus*  
*mandiburens*  
*manillensis*  
*nigrifrons stotheri*  
*sagittarius*  
*saussurei*  
*sikorae*  
*smithii*  
*smithii neavei*  
*stigma*  
*takasagonus*

##### Subgenus *Polistes* (including *Sulcopolistes*)

*africanus*  
*associus*  
*badius*  
*dominulus*  
*gallicus*  
*marginalis*  
*nimpha*  
*tenellus*

#### POLISTINAE

##### Genus *Polistes*

##### Subgenus *Aphanilopterus*

*annularis*  
*apicalis*  
*aterrimus*  
*buyssoni*  
*canadensis*

- Genus *Mischocyttarus*
- Subgenus *Clypeopolybia*  
*carbonarius*  
*piger*
- Subgenus *Haplometrobius*  
*alboniger*  
*artifex*  
*cerberus*  
*cooperi*  
*decimus*  
*dimorphus*  
*iheringi*  
*illusorius*  
*mirificus*  
*nigropygialis*  
*oecothrix*  
*ornatus*  
*prominulus*  
*silvicola*  
*stenoecus*  
*surinamensis*  
*sylvestris*  
*tenius*  
*undulatus*  
*vredeni*  
*weyrauchi*  
*xanthocerus*  
*ypiranguensis*
- Subgenus *Kappa*  
*atramentaris*  
*bertoni*  
*comunalis*  
*injuncundus*  
*latior*  
*latissimus*  
*metathoracicus*  
*pseudomimeticus*  
*shunkei*  
*socialis*  
*tolensis*
- Subgenus *Megacanthopus*  
*collarellus*  
*collaris*  
*melanopygus*  
*parallelogrammus*  
*saturatus*  
*superus*
- Subgenus *Mischocyttarus*  
*cinerascens*  
*drewseni*  
*gynandormorphus*  
*labiatus*  
*matograssoensis*  
*melananus*  
*rotundicollis*  
*tomentosus*
- Subgenus *Monacanthocnemis*  
*buyssoni*  
*punctatus*  
*vaqueroi*
- Subgenus *Monogynoecus*  
*alienus*  
*fraudulentus*  
*insolitus*  
*metoecus*  
*moralesi*  
*pelor*
- Subgenus *Phi*  
*alfkeni*  
*araujoi*  
*barbatulus*  
*barbatus*  
*basimacula*  
*cassununga*  
*cubensis*  
*flavicornis*  
*flavoniger*  
*hirsutus*  
*imeldai*  
*lilae*  
*lules*  
*mexicanus*  
*oreophilus*  
*pallidipectus*  
*paraguaensis*  
*phthisicus*  
*tarmensis*  
*wagneri*
- Genus *Ropalidia*  
*ambigua*  
*anarchica*  
*antennata*  
*aristocratica*  
*artifex*  
*bambusae*  
*bicincta*  
*bilineata*  
*brazzai*  
*cabeti*  
*capensis*  
*carinata*  
*cincta*  
*constitutionalis*  
*cyathiformis*  
*distigma*  
*fasciata*  
*ferruginea*  
*flavopicta*  
*flavoviridis*  
*formosa*  
*galimatia*  
*guttatipennis*  
*grandidieri*
- granulata*  
*gregaria*  
*honkongensis*  
*horni*  
*ignobilis*  
*jacobsoni*  
*lacustris*  
*latebalteata*  
*maculiventris*  
*madecassa*  
*malayana*  
*marginata*  
*mathematica*  
*melania*  
*minor*  
*morosa*  
*nitidula*  
*nobilis*  
*opifex*  
*phalansterica*  
*picta*  
*plebeiana*  
*prasina*  
*ranavali*  
*revolutionalis*  
*romandi*  
*rufoplagiata*  
*schultessi*  
*shestakovi*  
*stigma*  
*sumatrae*  
*timida*  
*tomentosa*  
*turneri*  
*variabilis*  
*variegata*  
*vitripennis*  
*xanthura*
- Genus *Parapolybia*  
*nodosa*  
*orientalis*  
*varia*
- Genus *Polybioides*  
*melainus*  
*raphigastra*  
*tabidus*
- Genus *Belonogaster*  
*abyssinica*  
*brachycera*  
*brevipetiolata*  
*brunnea*  
*clypeata*  
*discifera*  
*dubia*  
*eumenoides*  
*filiventris*  
*fulvipennis*

- grisea*  
*guerini*  
*junceae*  
*rufipennis*  
*vassae*  
 Genus *Apoica*  
*flavissima*  
*gelida*  
*pallens*  
*pallida*  
*thoracica*  
 Genus *Agelaia*  
*angulata*  
*areata*  
*cajennensis*  
*flavipennis*  
*fulvofasciata*  
*lobipleura*  
*myrmecophila*  
*pallipes*  
*vicina*  
*xanthopus*  
 Genus *Angiopolybia*  
*pallens*  
*paraensis*  
 Genus *Pseudopolybia*  
*compressa*  
*difficilis*  
*vespiceps*  
 Genus *Parachartergus*  
*apicalis*  
*aztecus*  
*colobopterus*  
*fraternus*  
*fulgidipennis*  
*richardsi*  
*smithii*  
*weyrauchi*  
 Genus *Chartergellus*  
*amazonicus*  
*communis*  
*punctator*  
 Genus *Nectarinella*  
*championi*  
 Genus *Leipomeles*  
*dorsata*  
*nana*  
 Genus *Marimbonda*  
*albogrisea*  
 Genus *Synoeca*  
*chalibea*  
*cyanea*  
*septentrionalis*  
*surinama*  
*virginea*  
 Genus *Clypearia*  
*duckei*  
*sulcata*  
*weyrauchi*  
 Genus *Metapolybia*  
*acincta*  
*azteca*  
*aztecoides*  
*cingulata*  
*docilis*  
*suffusa*  
 Genus *Asteloea*  
*traili*  
 Genus *Protopolybia*  
 (including *Pseudochartergus*)  
*acutiscutis*  
*biguttata*  
*chanchamayensis*  
*chartergoides*  
*exigua*  
*fuscatus*  
*holoxantha*  
*minutissima*  
*pallidibaleatus*  
*panamensis*  
*picteti*  
*sedula*  
*scutellaris*  
*weyrauchi*  
*wheeleri*  
 Genus *Charterginus*  
*aberrans*  
*fulvus*  
*nevermanni*  
 Genus *Chartergus*  
*chartarius*  
*globiventris*  
*metanotalis*  
 Genus *Brachygastra*  
*augusti*  
*azteca*  
*bilineolata*  
*lechequana*  
*mellifica*  
*scutellaris*  
*smithii*  
 Genus *Protonectarina*  
*sylveirae*  
 Genus *Polybia*  
 Subgenus *Alpha*  
*bifasciata*  
 Subgenus *Apopolybia*  
*jurinei*  
 Subgenus *Cylindroeca*  
*dimidiata*  
 Subgenus *Formicicola*  
*rejecta*  
 Subgenus *Furnariana*  
*furnaria*  
*richardsi*  
 Subgenus *Myrapetra*  
*belemensis*  
*bicyttarella*  
*bistriata*  
*catillifex*  
*digueta*  
*dimorpha*  
*erythrothorax*  
*flavifrons*  
*juruana*  
*occidentalis*  
*parvulina*  
*paulista*  
*platycephala*  
*ruficeps*  
*scrobalis*  
*scutellaris*  
 Subgenus *Pedotheca*  
*emaciata*  
*singularis*  
*spinifex*  
 Subgenus *Polybia*  
*liliacea*  
*striata*  
 Subgenus *Platypolybia*  
*incerta*  
*procellosa*  
 Subgenus *Trichinothorax*  
*affinis*  
*chrysothorax*  
*flavitincta*  
*rufitarsis*  
*sericea*  
*tinctipennis*  
*velutina*  
 Genus *Synoecoides*  
*depressus*  
 Genus *Epipona*  
*guerini*  
*tatua*

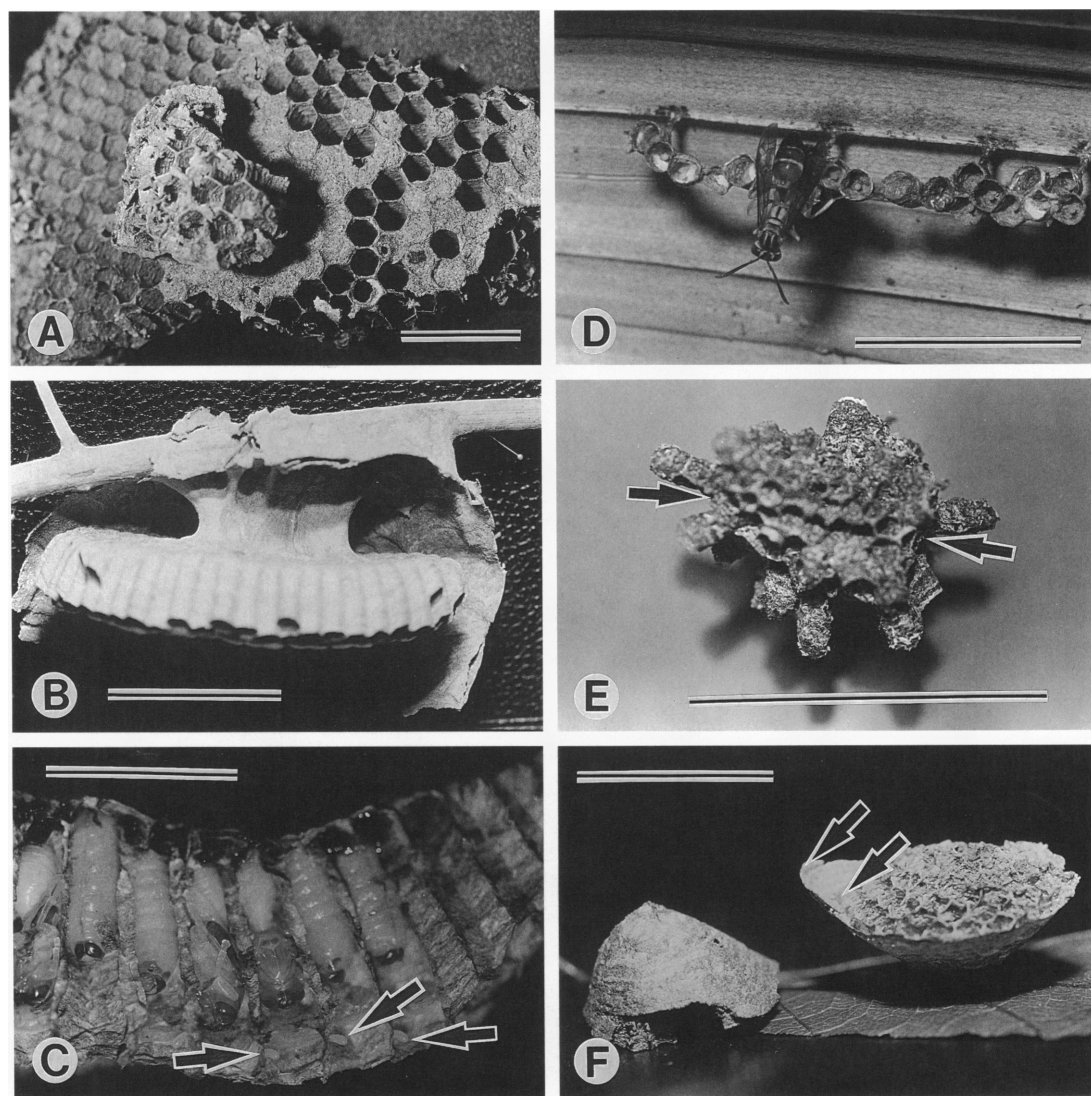


Fig. 15. **A.** *Vespa tropica*. Cells papered over (FMNH). **B.** *Provespa anomala*. Broad pedicel formed of secondarily fused, rod-like pedicels (BMNH). **C.** *Polistes olivaceus*. Tandem brood, eggs (arrows) distal to pupae (Toamasina, Madagascar). **D.** *Mischocyttarus fraudulentus*, from below. Multiple pedicels; comb fusion (Costa Rica; photo by C. K. Starr). **E.** *Mischocyttarus pelor*, from below. Comb two-sided, expanding outward from central row (between arrows) (Turrialba, Costa Rica; USNM). **F.** *Mischocyttarus decimus*, two nests from side, natural orientation (left) and inverted (right). Nest on midrib of leaf; paper cone smooth, extending beyond cell walls (arrows), not composed of separate cell bases (left) (Mazaruni Settlement, Guyana; BMNH).



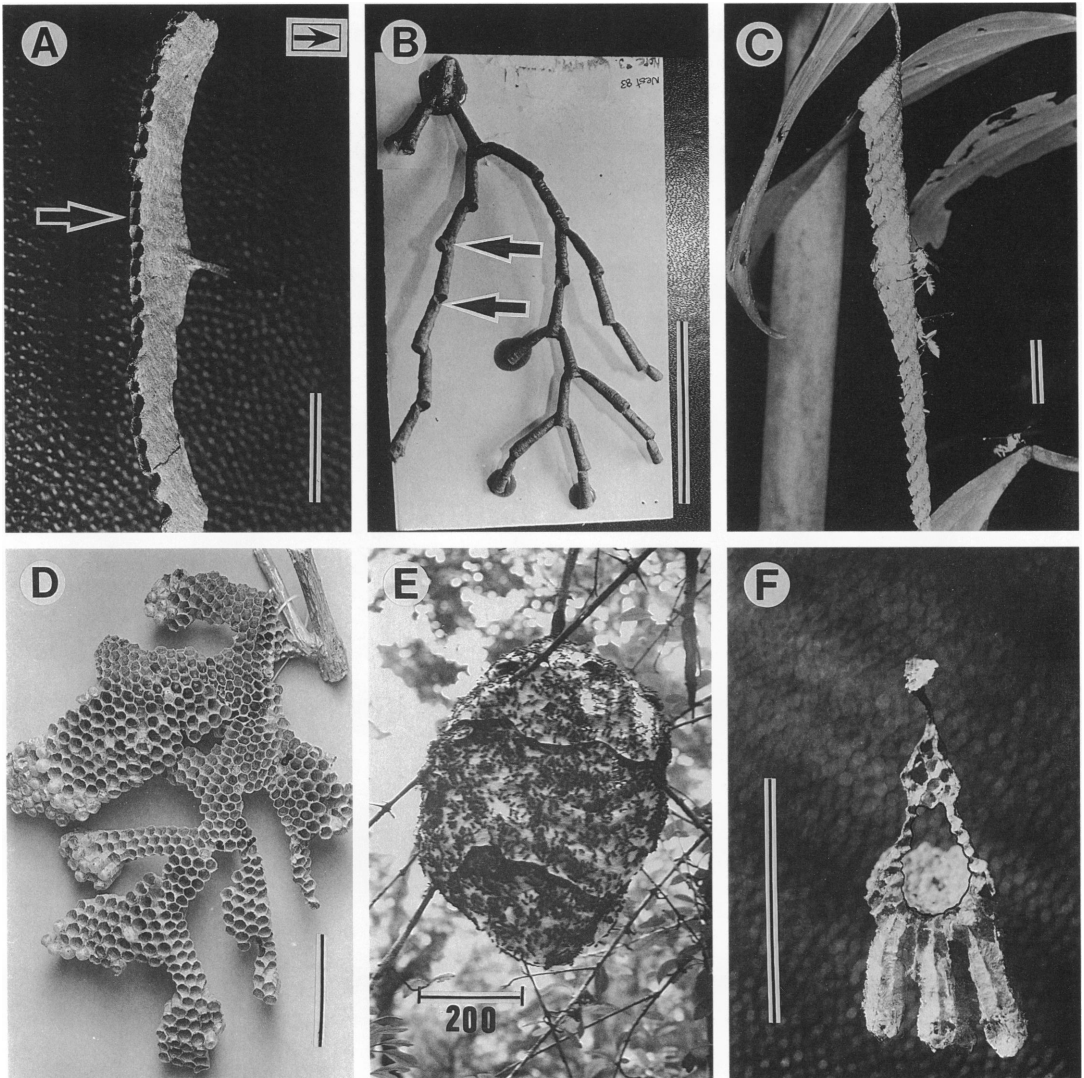


Fig. 16. **A.** *Mischocyttarus weyrauchi* (or possibly variant of *nigropygialis*), from above. Pedicel short; comb single row supported centrally; cells face horizontally; furrows between cells reduced; some cells rectangular in cross section (arrow) (Chapada, Mato Grosso, Brazil, CMNH). **B.** *Mischocyttarus* new species near *punctatus*. Cells round in cross section, from lip of preceeding cell (arrows). Terminal dark spots are glue fastening nest to card (BMNH). **C.** *Mischocyttarus* near *alienus*. Pedicel long; comb single verticle row of cells (Puerto Viejo, Costa Rica). **D.** *Ropalidia bicincta*. Comb pinnate; central rib built by foundresses, lateral branches added by workers (Antseranana, Madagascar; KUSM). **E.** *Ropalidia montana*. Envelope sheets multiple; entrances variable and multiple (Mudumulai Preserve, Tamil Nadu, India). **F.** *Belonogaster* sp. Comb removed as pupae emerge, leaving hole. Back of comb visible through hole; comb supported by marginal strips of reinforced carton bordering hole (margin retouched for clarity) (HUMB).

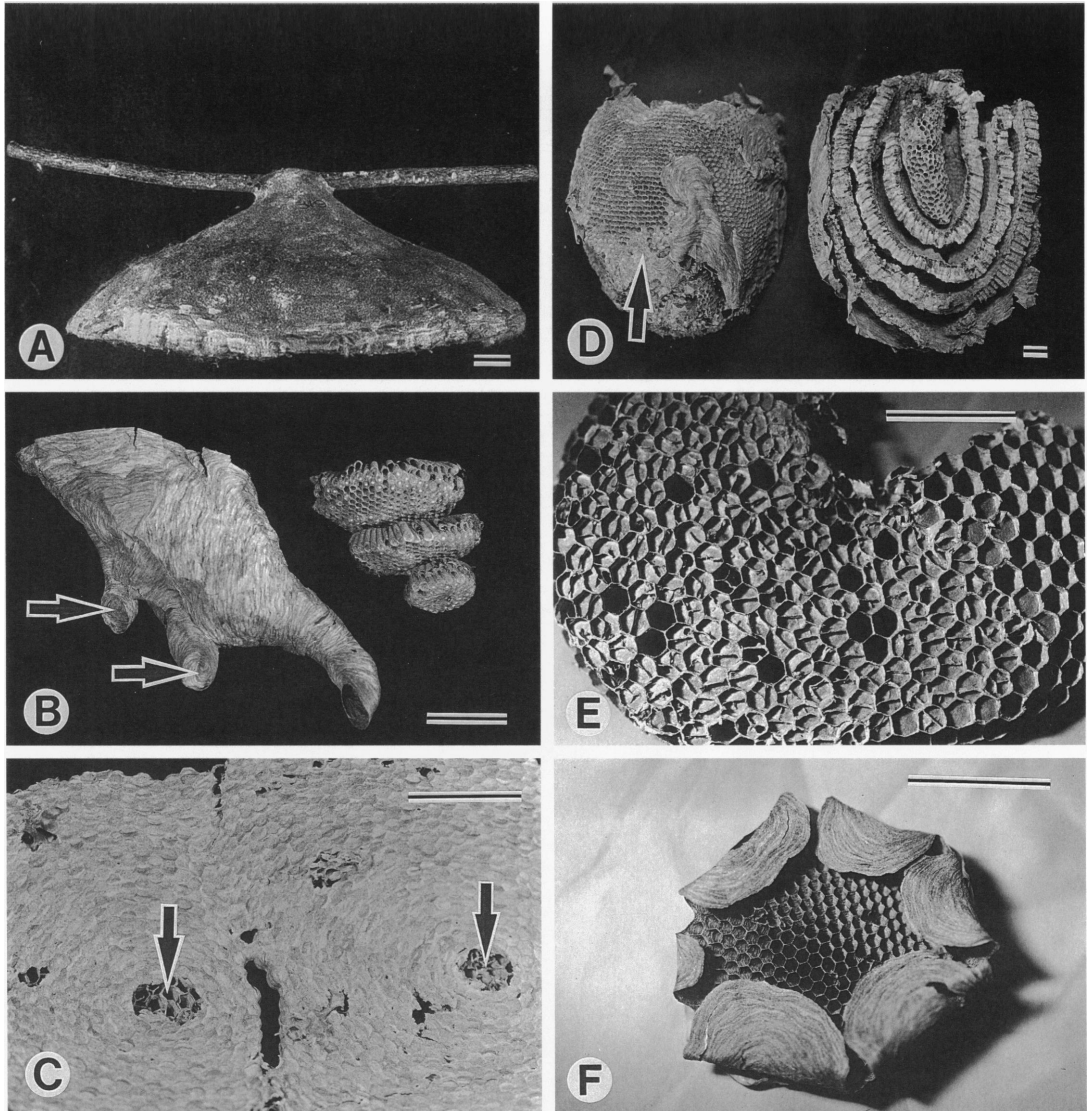


Fig. 17. Comb expansions. **A.** *Apoica* sp. Broad attachment to branch; back of comb felt-like, showing no cell bases (HMCZ). **B.** *Angiopolybia pallens*, combs removed. Repeated expansion of envelope corresponding to lateral growth of combs and addition of new combs suspended from those above; old entrances plugged (arrows) but not removed in this anomalous nest, current entrance open (KUSM). See typical form, figure 23F. **C.** *Agelaia testacea*, comb back. Radial comb growth from point of initiation (arrows, pedicels removed); comb fusion, hexagonal pattern becoming continuous across both combs (upper region) (Santarém, Pará, Brazil; HMCZ). **D.** *Agelaia areata*, nest bisected. Spiral envelope expanding over itself; entrances multiple; some cells destined to hold brood, others (arrow) papered over to provide support (KUSM). **E.** *Parachartergus* (*apicalis* group), comb, from below. Secondary crosswalls on top of pupal caps (Suriname; CUIC). **F.** *Charterginus fulvus*, incipient nest, from below. Lateral margins drawn across face of completed comb, eventually fusing to create six-pointed nest; entrance simple hole dorsally or at apex of one point (Suriname; CUIC).

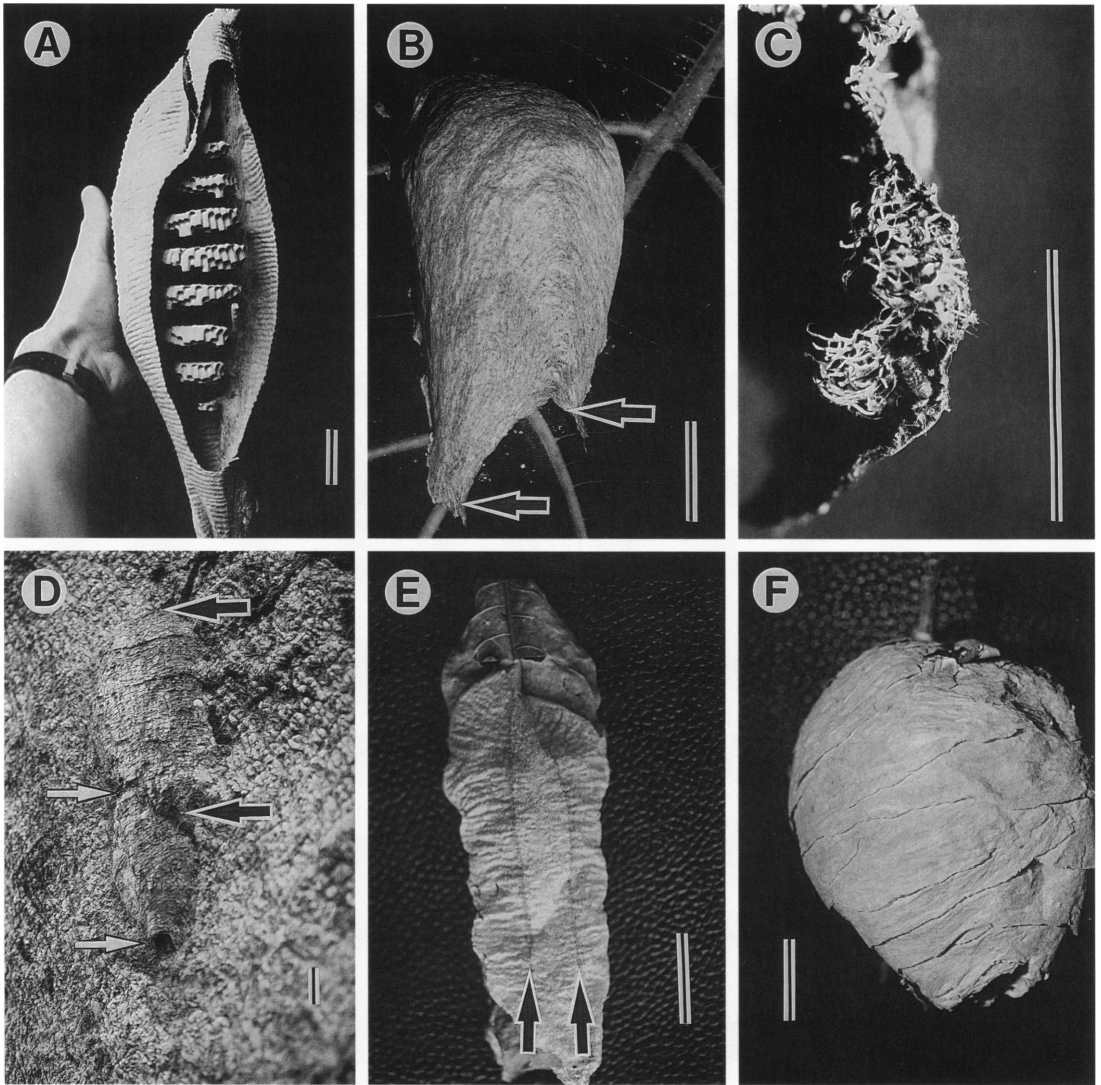


Fig. 18. **A.** *Parachartergus apicalis*, sectioned. Envelope generally single sheet with large regular corrugation, remodelled to allow comb expansion; pedicelate combs supported independently from vertical or inclined branch; new combs added either above or below older combs (Suriname, NNML). **B.** *Parachartergus amazonensis*. Envelope simple or flattened dome; entrance simple gap in lower region (between arrows) (near Iquitos, Peru, AMNH). **C.** *Chartergellus punctator*. Margin of envelope bearing flossy, paper pillars internally, particularly in top region. Beetle carcass from museum pest (Barbacoas; Colombia, BMNH). **D.** *Nectarinella championi*. Envelope with fine irregular corrugations, highly cryptic on broad trunk; primary envelope (between black arrows) expanded by adding secondary envelope below and contiguous with it (between white arrows); entrance simple or spout at lowest region (white arrow) (Atena, Costa Rica; AMNH). **E.** *Leipomeles dorsata*, corrugated form. Envelope with fine, irregular corrugations laterally, smooth central region bordered by dark bands of pulp (arrows); entrance simple gap at leaf apex (Barcellos, Brazil; NMBS). **F.** *Pseudopolybia difficilis*. Envelope round or ovoid, multiple, laminae closely spaced; entrance simple hole in lower region (Suriname; CUIC).

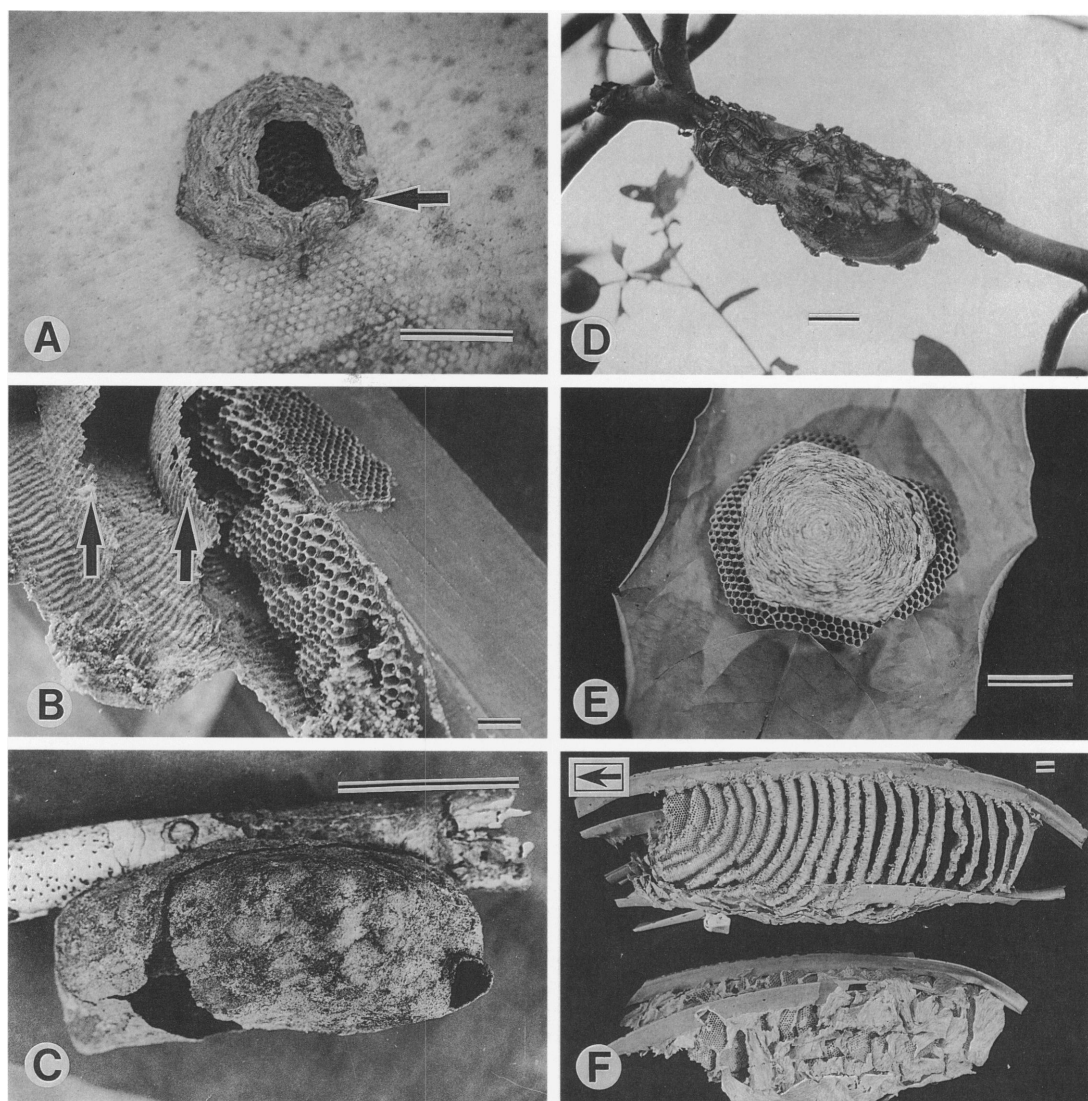


Fig. 19. **A.** *Metpolybia cingulata*, incipient nest, from below. Small swarm rebuilding sessile comb on site of destroyed nest (cement ceiling); entrance (arrow) distinct, away from last gap in envelope, which will be closed completely (Tena, Ecuador; AMNH). **B.** *Synoeca septentrionalis*, section through lower uninhabited levels of large, active nest. Comb sessile; old envelopes (arrows) not removed as nest expands upward; entrance (not shown) at top (San Vito; Costa Rica). **C.** *Clypearia duckei*, damaged nest. Sessile beneath branch distal to ant nest; envelope rough, reinforced with blots, rounded, not showing cell walls; entrance short collar, lateral or upward (near Manaus, Brazil; WDH, photo by W. D. Hamilton). **D.** *Asteloeca traili*, from below. Sessile beneath branch; envelope smooth, not concealing marginal cell walls or bases; entrance central, short collar. This nest was expanded once (near Iquitos, Peru; AMNH). **E.** *Protopolybia* near *holoxantha*, incipient expansion of mature nest. Pedicellate comb expanded contiguously with older comb; envelope ultimately arising from marginal cell walls and closed with old envelope; entrance simple, dorsal or dorsolateral, sometimes distinct from last gap in incipient envelope (KUSM). **F.** *Protopolybia acutiscutis*, dry season nest, bisected. Envelope multiple, sometimes chaotic; entrances multiple, lateral or ventrolateral; later combs sessile upon preceding envelope (Canal Zone, Panama; KUSM).



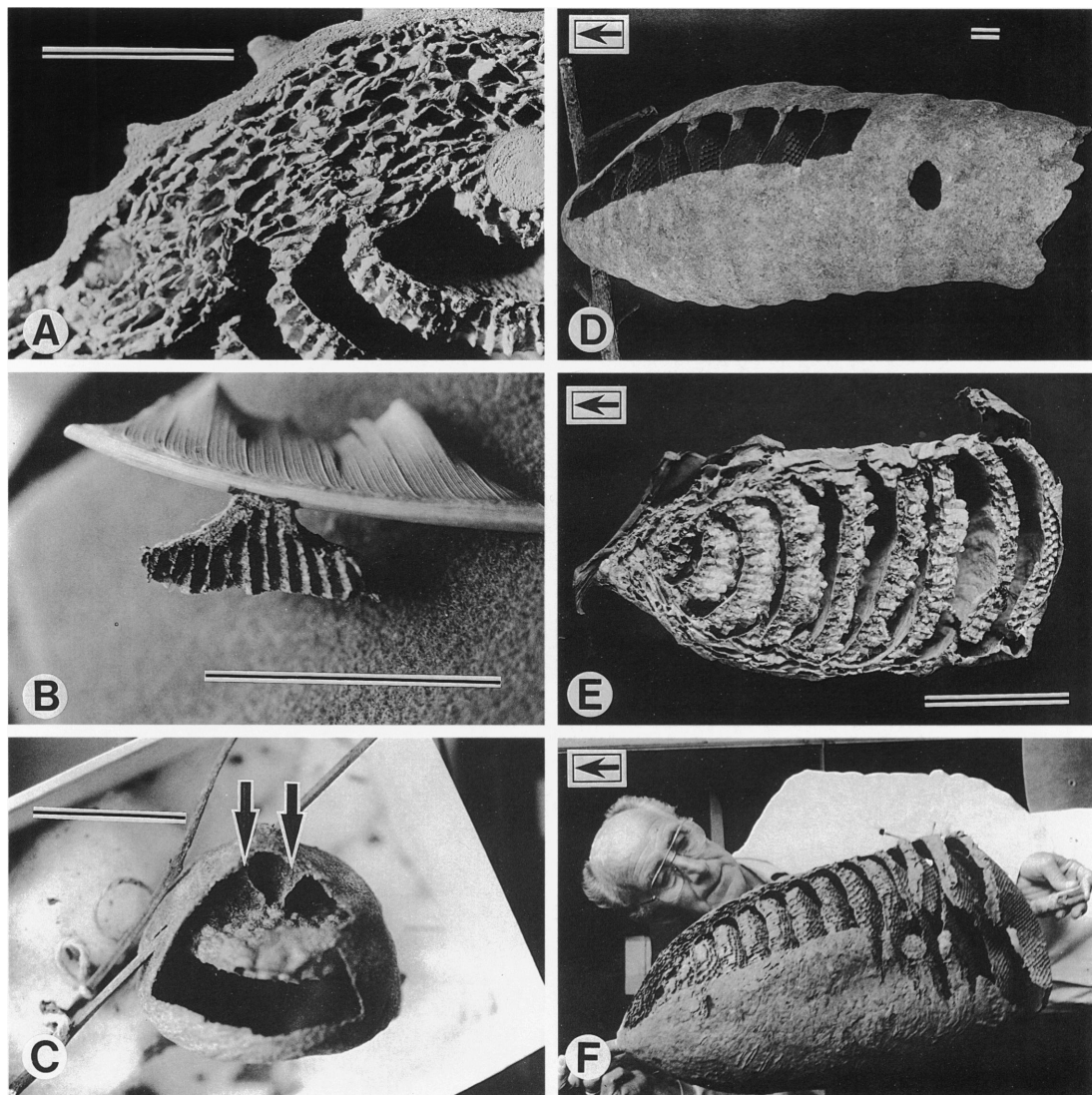


Fig. 20. **A.** *Polybia scutellaris*, sectioned. Envelope reinforced initially by fine, imbricate carton, exterior ultimately thickened by blots; stout spines are typical of this species but rare in the genus. Genera *Chartergus* and *Epipona* are similarly heavily reinforced, but without spines (half of nest at MNHN, other half in Geneva; see Wenzel 1992b). **B.** *Polybia bistriata*, bisected. Initial cells are sessile on substrate, but comb grows off it, creating illusion of having a pedicel. Some *Apoica*, *Brachygastra*, *Chartergus*, and *Charterginus* are similar (Suriname, NNML). **C.** *Polybia affinis*, sectioned. Primary comb suspended by buttressed sheet (arrows), typical of subgenus *Trichinothorax* (NNML). **D.** *Epipona* sp., sectioned and damaged. Nest of 13 levels completed before the hatching larvae in the top (oldest) level required cell walls to be elongated, hence construction in as rapidly as 10-15 days. Some nests of this genus are not expanded beyond the effort of the original swarm for several years (but see fig. 26E). The hole in the lower center and the broken lowest level are the result of damage during collecting (Costa Rica?; KUSM). **E.** *Polybia diguetana* (?), bisected. Envelope with imbricate reinforcement; lower combs with successively greater radius of curvature (KUSM). **F.** *Polybia dimidiata*, sectioned, and M. Hennigan. Nest surrounds vertical support; envelope with thick imbrication in upper portion (NNML).

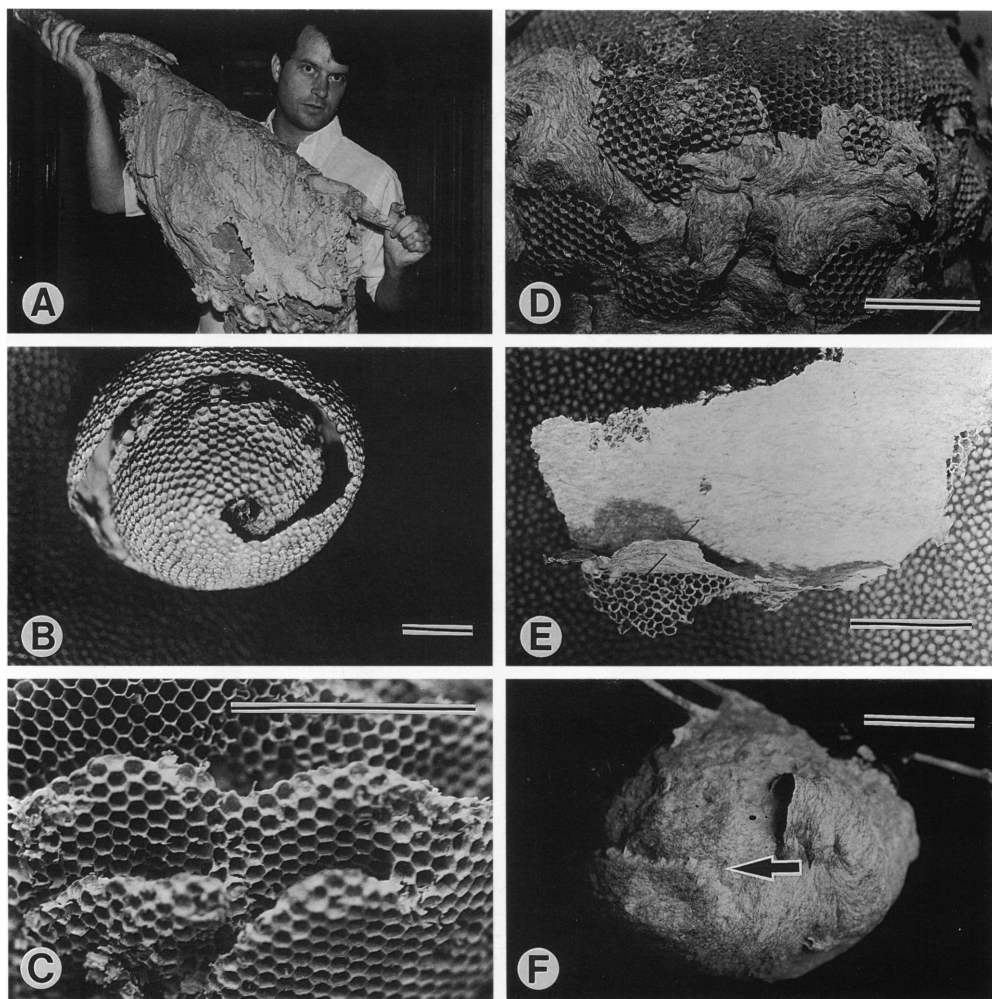


Fig. 21. Comb expansions. **A.** *Polybioides melaina* and the author. This species achieves the largest colony size of any African social wasp (MRAT, photo by J. M. Carpenter). **B.** *Polybioides raphigastra*, from below. Built in cavities, this comb spirals outward and downward. Imbricate reinforcement of the margins of the comb provide added support and form a protective envelope around more centrally located cells (BMNH). **C.** *Ropalidia montana*, comb. Protected inside a separate envelope, continuous combs growing in a downward spiral (= klimakatocytarus sensu Carl, 1934) allow this and some other *Ropalidia* to create huge nests without requiring many distinct structures for support or modifications thereof to allow expansion (see also fig. 16E) (AMNH). **D.** *Brachygastra mellifica*, from below. Chaotic expansion of comb and envelope in mature nests produces many entrances and loosely interconnected regions of cells. Young nests are more orderly and form discrete levels with a single entrance (not shown) (USNM). **E.** *Protoneectarina sylveirae*, comb, from above. The supple paper of the comb back (a former envelope) can be easily peeled away to leave the hexagonal walls of brood comb behind (see also fig. 25D) (Brazil; HMCZ). **F.** *Polybia ruficeps*. Many *Polybia* have the entrance as a lateral or dorsolateral hole or short spout above the level of the lowest brood comb. This species exaggerates the form to resemble a tea pot with the spout pressed back against the pot. The entrance (center) is well above the level of the lowest comb (arrow), with which it communicates by a curved passage. Subsequent envelopes must incorporate the old entrance, becoming increasingly asymmetrical and protruding on one side (Chapada, Mato Grosso, Brazil; CMNH).

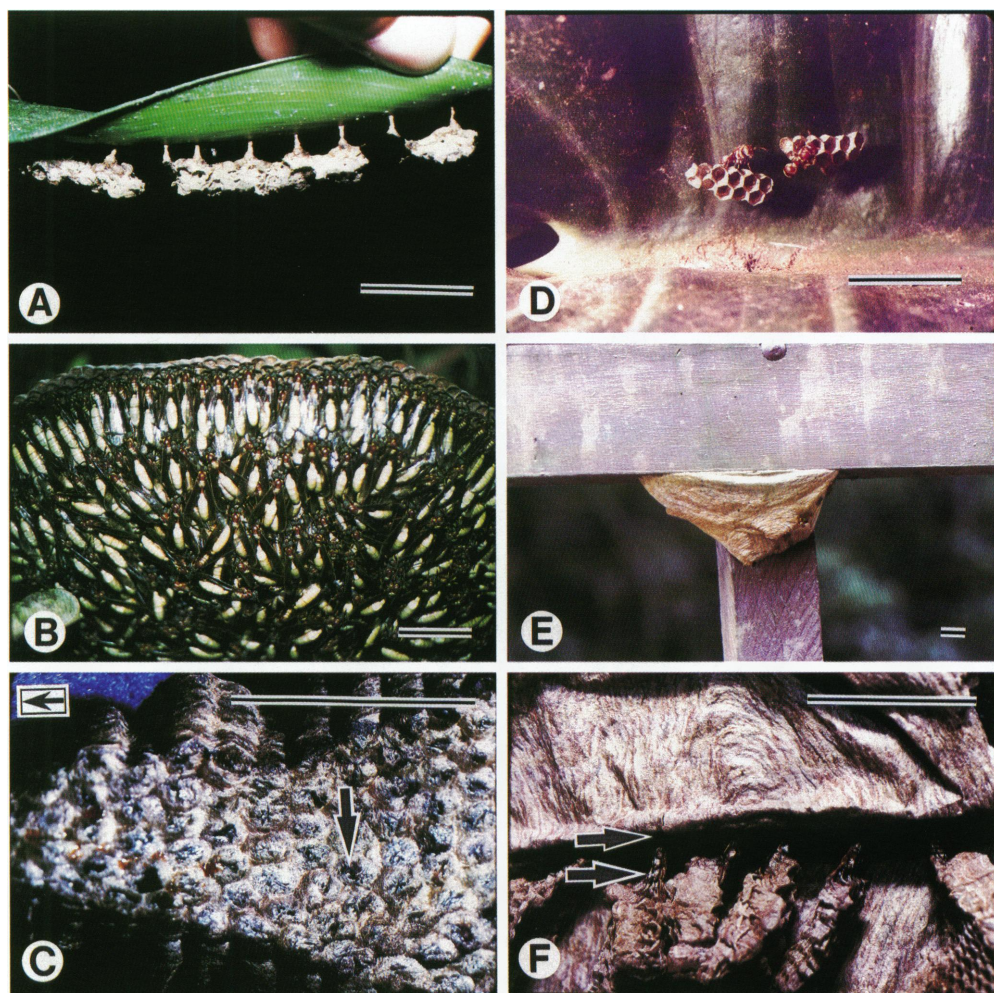


Fig. 22. A. *Mischocyttarus* sp., dead nest. Multiple pedicels and comb fusion can produce linear nests of dozens of cells. Such *Mischocyttarus* nests are usually built on leaves guarded basally by dolichoderine ants (San Vito, Costa Rica). B. *Apoica flavissima*. Nocturnal habits of *Apoica* allow the entire workforce to remain on the nest in the day, where they may be so numerous as to completely cover the face of the nest and hang from the bodies of their nestmates. Pale-bodied species make an impressive display (Iguazú, Argentina; AMNH). C. *Parapolybia varia*, comb back. Removal of meconium through the back of the cell leaves a hole that is closed by transparent oral secretion, appearing dark here. Such "windows" in the back of the comb are unique to *Ropalidia* and *Parapolybia* (AMNH). D. *Ropalidia marginata*, from below. Many *Ropalidia* begin nests with multiple combs, which generally proliferate separately but may fuse (Bangalore, India). E. *Ropalidia romandi*. *Ropalidia* that build envelopes tend to make amorphous structures of multiple layers, but the exterior is generally smooth in appearance (Queensland, Australia; AMNH; photo by J.M. Carpenter). F. *Polybioides tabidus*, one envelope sheet folded up. The origin of the nest is revealed by the first pair of back-to-back combs, which also correspond to the oldest region of the bivalve-like envelope. The first cells of each comb are sessile by their walls on the branch, but are chewed down and reinforced with secretion to produce a narrow support resembling a pedicel (between arrows) for the comb that hangs from it. This species has two simple envelope sheets, one on either side, but *P. melaina* is complex (see fig. 20A) (MNHN).



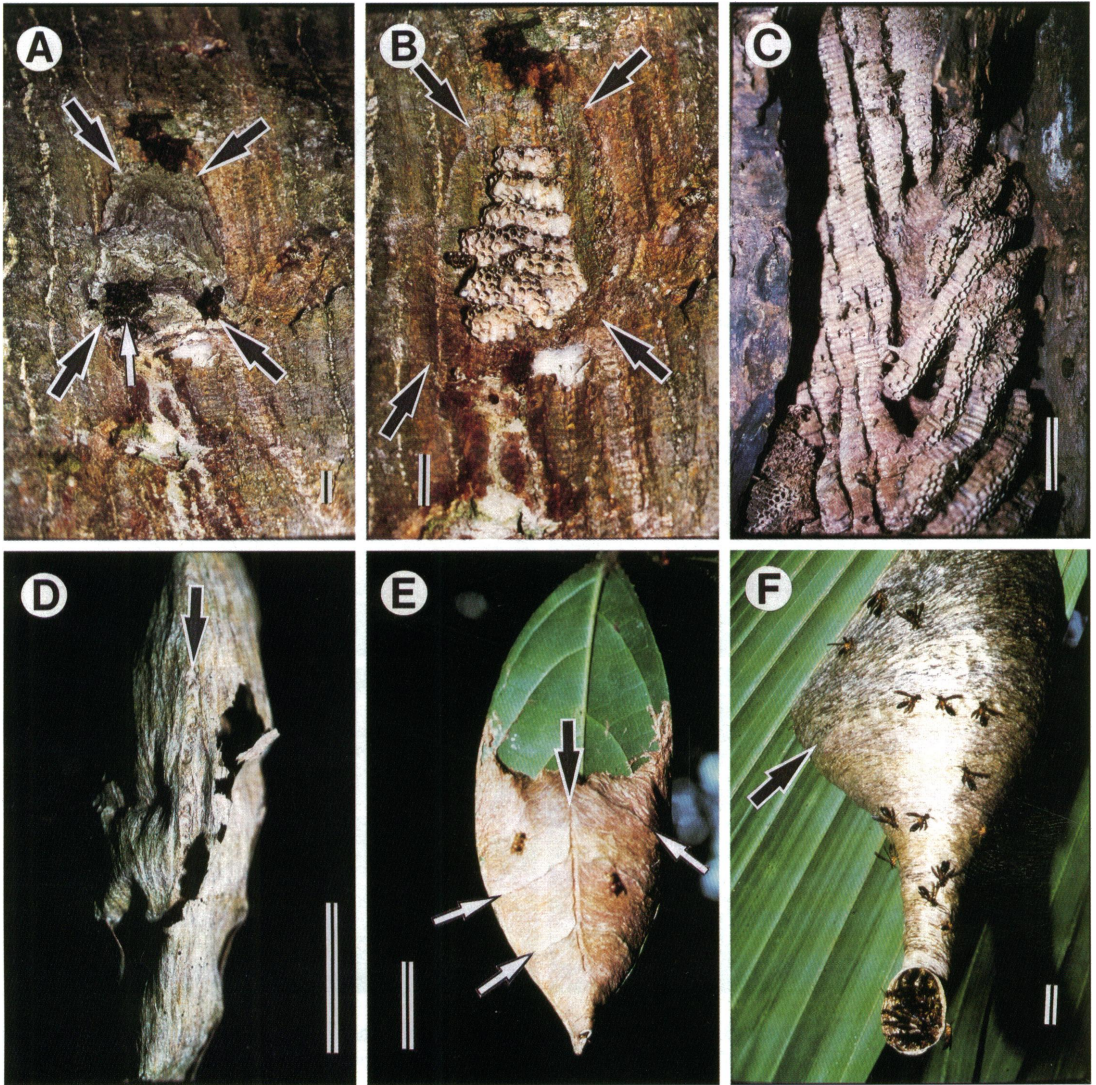


Fig. 23. **A.** *Chartergellus punctatior*. Envelope is a flattened dome (black arrows), rough, uneven, and cryptic against a broad trunk; entrance (white arrow) is a short spout easily concealed by loitering wasps (Tena, Ecuador; AMNH). **B.** Same as **A**, with envelope removed, revealing combs. Former margin of envelope denoted by arrows; dark area above is a wound in the tree, white area just below combs is a spider egg sac. **C.** *Agelaia xanthopus*, in a tree cavity. Combs stacked, conical, and partly spiral and fused. See also cross-section photo in Wenzel (1992b) (Mexico, MNHN). **D.** *Marimbonda* (?). Envelope simple on the underside of a narrow leaf; central furrow (arrow) like *Leipomeles* (see **E**) (BMNH). **E.** *Leipomeles dorsata*, furrow form. Central furrow (black arrow) mimics leaf midrib, ridges (white arrows) mimic veins; entrance at apex of leaf (Santarém, Pará, Brazil; photo by R. L. Jeanne). **F.** *Angiopolybia pallens*. Typical form; smooth envelope with elegant flared spout. Boundary between carton of different colors (arrow) marks beginning of new lower construction to accommodate growing combs (see also fig. 17B) (Misahualli, Ecuador; photo by J. M. Carpenter).



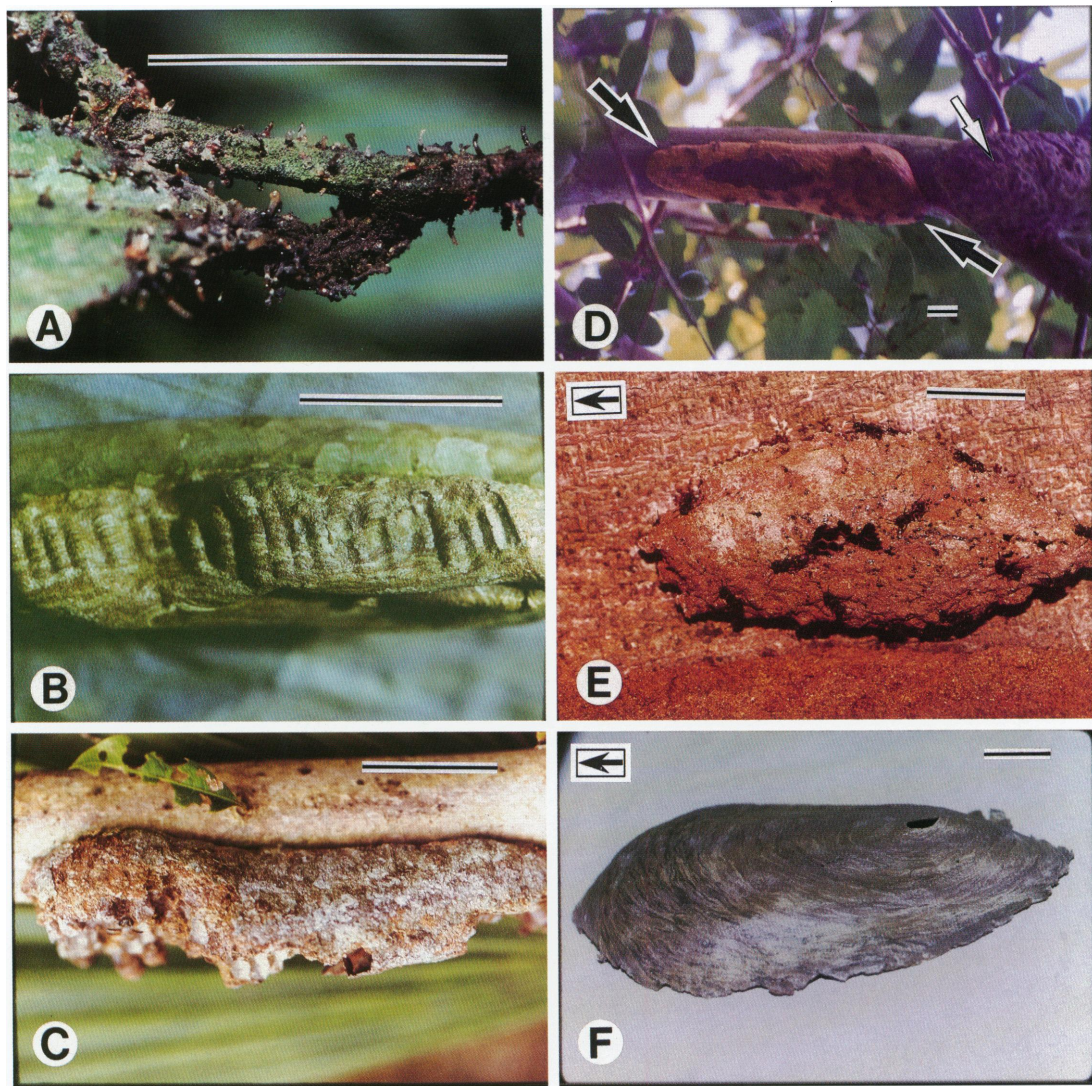


Fig. 24. **A.** *Leipomeles dorsata*, ant guard on leaf petiole. (Belem, Brazil; photo by R. L. Jeanne). **B.** *Asteloeca traili*. Smooth carton, margin of nest showing lines of construction, cell bases, and walls (near Iquitos, Peru; AMNH). **C.** *Clypearia* (= *Occipitalia*) *sulcata*, broken. Rough, thick carton, reinforced to obscure lines of construction, cell bases, and walls (near Iquitos, Peru; AMNH). **D.** *Clypearia sulcata*, incipient, from below. Nest (between black arrows) in close proximity and apical to *Azteca* ant nest (white arrow) (Iquitos, Peru). **E.** *Metapolybia cingulata*. Brittle envelope damaged slightly, revealing comb within. Envelope rough, sometimes glossy, rarely showing lines of construction. Entrance at top concealed by sharp eaves around envelope margin (Tena, Ecuador; AMNH). **F.** *Clypearia weyrauchi*, oblique side view. Envelope glossy, smooth, lines of construction obvious (IMLT).

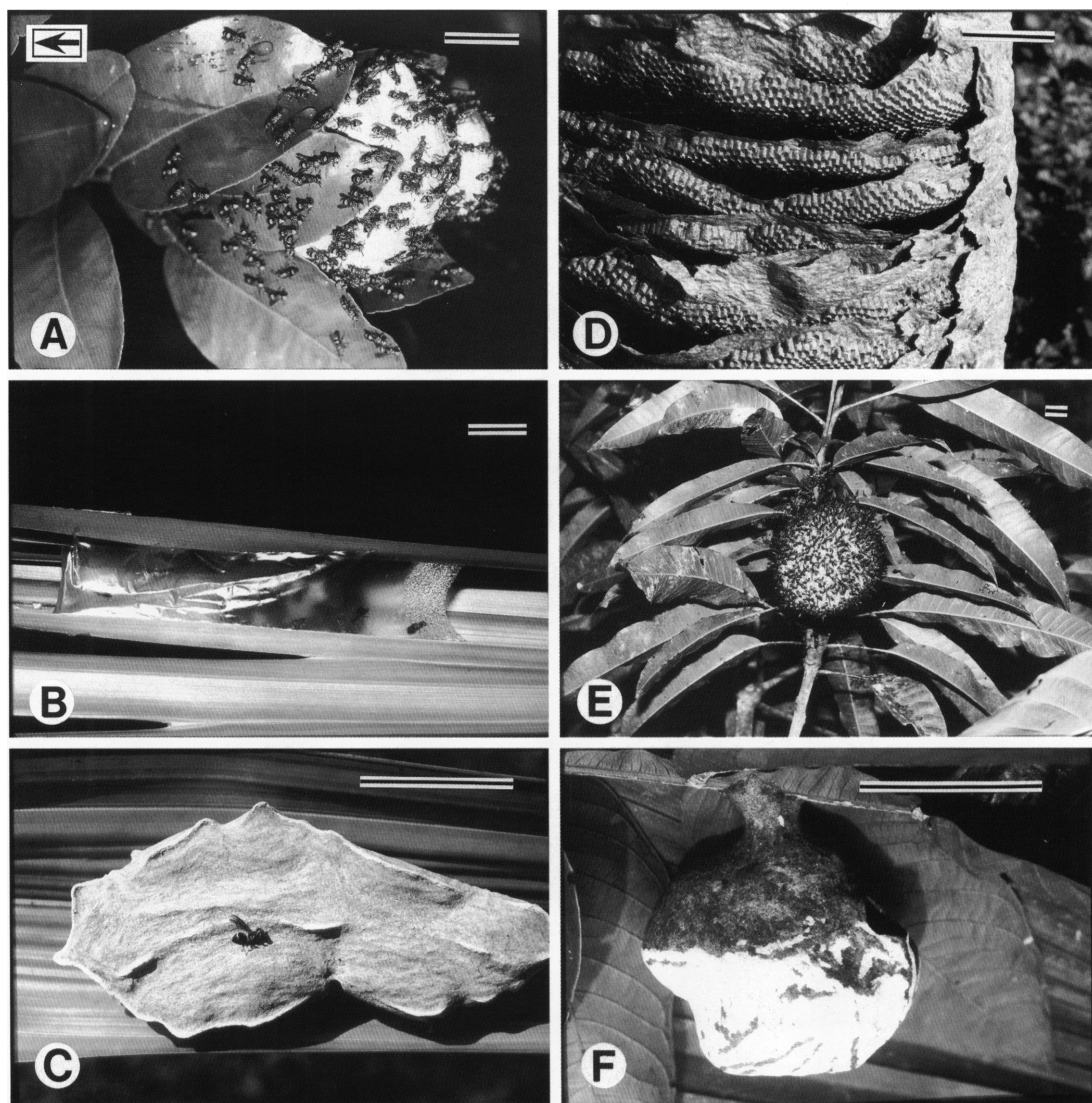


Fig. 25. **A.** *Protopolybia exigua*. Multilevel form among leaves (near Santa Cruz, Bolivia; AMNH). **B.** *Protopolybia chartergoides*, in curled leaf, from below. Transparent form, envelope consists of salivary matrix only, no pulp, restricting access to cavity; entrance is simple gap on right side where new membrane appears rough; comb visible as ordinary brown carton beyond transparent envelope (near confluence of Rio Napo and Rio Amazon, Loreto, Peru; AMNH). **C.** *Protopolybia exigua binominata*, from below. Planar form (in situ), envelope exterior green (fading in collections), acute margins of envelope remain natural pale color of carton (near Tena, Ecuador; AMNH). **D.** *Protonectarina sylveirae*, lower region, sectioned. Supple, gray wavy carton; seams marking successive combs wiggly and irregular (see also fig. 21E) (MALS, photo by T. Osten). **E.** *Polybia* sp., from below. Defense display: wasps cover nest and nearby branches with wings upraised, next response is to attack moving or alien objects (Iquitos, Peru). **F.** *Brachygastra scutellaris*. Nest is sessile despite image of narrow pedicel (cf. *P. bistriata*, fig. 20B). Carton is naturally brown, but lower region of envelope is later colored white below (see also fig. 26D, F). This form found in *B. scutellaris* and *B. smithii* (near Iquitos, Peru; AMNH).





Fig. 26. **A.** *Dolichovespula maculata*, sectioned. Laminae of concentric envelope sheets (Islip, New York). **B.** *Vespula maculifrons*, mature envelope surface. Tight imbricate reinforcement, lines of construction evident (Lawrence, Kansas; KUSM). **C.** *Chartergus chartarius*, broken, and P. J. DeVries. Cylindrical white nest, entrance in center of combs (left arrow), top of nest encompassing branch (right arrow) (Sucumbios, Ecuador; photo by J. Clark). **D.** *Synoecoides depressus*. Carton is naturally brown, but lower region of envelope is later colored white (see also figs. 23F, 26F) (BMNH). **E.** *Epipona niger*, expanded nest. Original nest was tapered below, second construction effort represented by broader lower region; comb becomes increasingly sloping, entrance near comb margin on higher side of incline (arrow). Cotton stuffed in entrance and area damaged during collection (Gamboa, Panama). **F.** *Charterginus nevermanni*, broken. Comb reveals natural amber color of carton, exterior of envelope later colored white (see also figs. 25F, 26D) (La Selva, Costa Rica; photo by R. M. Timm).

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