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Nest Structure: Social Wasps

John W. Wenzel
Powdermill Nature Reserve, Carnegie Museum of Natural History, Pittsburgh, PA, USA

Richness of Animal Architecture

Whether it is a palace or a hovel, every structure tells a story about its builder. We learn what functions are most important and sometimes what the builder anticipates. Does the builder invest in defensive structure? Does the builder store a bountiful harvest for the future? What do we learn about reproductive cycle from the habitation areas? Materials may indicate economic considerations, contrasting "cheap" against "durable." Engineering and design may reveal something about the builder's capacity to perceive or use information. Style indicates something about lineage. And, of course, the size of the structure provides important evidence of labor dedicated to the task.

Animal architecture is one of the more interesting areas of natural history, because it connects to many other topics [1, 2]. Construction behavior is well defined, and the animal's motivation is clear in most cases. As an extension of the animal's phenotype, a nest makes survival possible by providing protection from predators and the elements. In the case of social insects, the nest is center of colony life and bears information about colony size, growth rate or pattern, division of labor, brood demography and dynamics, food acquisition and storage, colony defense from anticipated enemies and against environmental challenges, economic considerations in construction itself, phylogenetic affinity, homeostasis and extended phenotype, and other parameters that have yet to be proposed.

In the animal kingdom, there are hundreds of origins of structures built by a single individual or mated pairs, but social insects are special because the nest is built as a collective effort by many individuals. This requires a set of interaction rules that permit an overall construction process to be broken into subtasks that may be completed by separate individuals, none of which has global knowledge of the overall effort. Thus, separate ants, bees, wasps, or termites can form teams that interact either directly or indirectly, even though none of them perceives the overall design. There is no job foreman, no clock coordinating shift workers, no understanding of how other teams are performing, nor even any necessary awareness of others on the same team.

Unlike other major groups of social insects, social wasps usually have nests above ground, subject to the weather, engineered to support their own weight by hanging from the substrate. The material is usually a kind of paper formed by

C. Starr (ed.), *Encyclopedia of Social Insects*,
https://doi.org/10.1007/978-3-319-90306-4_146-1

masticating pulp scraped from dead wood or plant hairs harvested from living plants or fragments of bark, dead leaves, or other plant tissues from the forest floor. Salivary secretions added to the plant matter provide a binding agent that may be akin to silk in composition, and that can be durable and strong. When wasps use long plant fibers, the product is usually grey, yellow, or even white and can be strong, flexible, and what humans would consider high quality paper, as in some *Parachartergus* or *Dolichovespula*. When new, such paper often can be rolled 180 ° around a pencil without tearing. Sometimes plant hairs are worked into a kind of felt, and the thick felt of *Chartergus* nests (probably composed of floss of the Bombacaceae, such as *Ceiba*) is stiff and largely indestructible. Other fine felts, such as the yellowish nests of *Protopolybia*, may be brittle (perhaps composed of trichomes from the underside of *Couepia* leaves, Chrysobalanaceae.) When the material is composed of leaf fragments or short chips of vegetable matter, the product is usually brown and brittle. Soil and mud are rarely used as building materials, although a few species use them exclusively. Whatever the wasps use, the choice is usually taxonomically specific, and all nests of a given species or sometimes a certain genus will have the same characteristic composition. Subtle differences allow a keen observer to identify most local species from the nest alone, based on structure and material composition. However, in speciose genera (*Polistes*, *Ropalidia*, *Mischocyttarus*, *Polybia*) it is not possible to distinguish all congeners everywhere by nest alone.

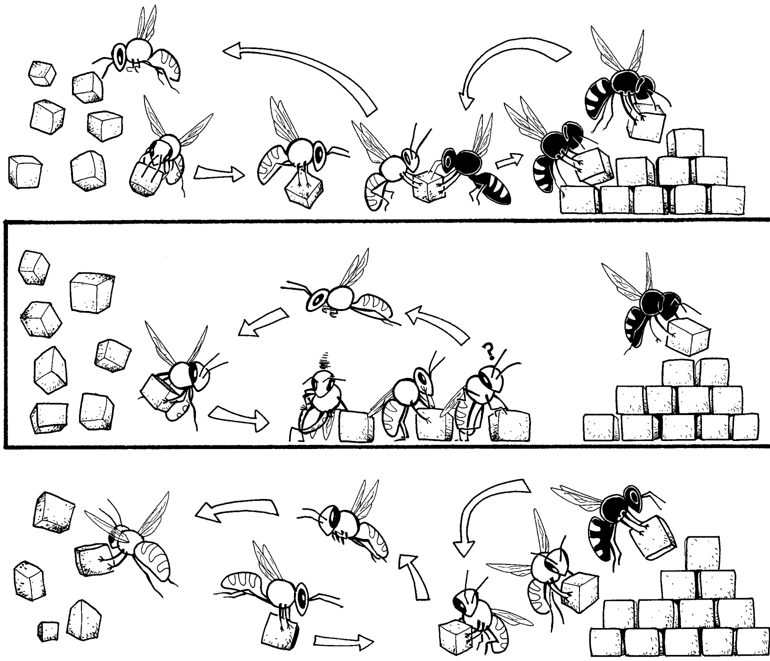
Organizing the Work

In a small colony of wasps, it is likely that a single individual may perform all types of building behavior, such as applying saliva to support structures, fetching water and pulp to make paper for the brood comb or envelope of the nest, or reinforcing paper sheets to add strength as the nest expands. When a colony has many workers, an individual may specialize to perform only one or a few of the necessary behaviors. This interruption of the total sequence leads to task partitioning that can increase efficiency through teams of specialists forming a kind of chain rather than many generalists working in parallel. Large colonies display a kind of swarm intelligence, or a property of ► self-organization that permits distributed decision making to take the place of a centralized command. Each worker bases her decisions of what to do upon her local experience and direct interactions, without ever knowing the status of the overall building project. Individual insects seem to use queuing time (how long they must wait to interact with a partner) as a general indication of whether the job they are doing is needed or not. First proposed in *Apis* by Martin Lindauer, a detailed demonstration of this principle was based on construction in *Polybia* wasps studied by Robert Jeanne. For example, if a pulp forager dispenses all her pulp quickly at the nest, then pulp is in demand by builders and she should repeat the task of foraging for pulp. If, on the other hand, she takes a long time to distribute her load of pulp, apparently pulp is not the limiting factor and she should do something else. When interaction rate is high (exchanges with a partner happen quickly), workers should repeat what they did before, becoming specialists in their given task. If the teams are not appropriately matched, a queue will develop where workers are waiting for partners of the other team. When a worker must wait a long time, those waiting should change tasks (Fig. 1).

Structural Variation

The elegance and variation in wasp nests is admired by scientists and the general public alike, and sometimes nests are sold in markets as attractive curios. A few archetypes from the range of designs across nearly 1000 species are illustrated here with emphasis on how researchers have come to understand the evolution of the broader variation.

In strong contrast with the ► nests of stingless bees, those of social wasps have relatively few design elements. The fundamental feature is a brood comb that is generally a one-sided bloc of hexagonal cells resembling a honeycomb, but



Nest Structure: Social Wasps, Fig. 1 Queuing time as a mechanism of team coordination. Apportioning labor to different teams can be optimized without global knowledge of the ratios of workers by measuring the time spent waiting for interaction with a partner of a different team. When teams are properly proportioned (a balanced number of foragers and builders in the top example here), interaction rate is high because one team is supplying a product at the same speed as the other team consumes it. Handoff times will be brief, and workers will maintain good efficiency if they repeat the job they just performed. If teams are not properly proportioned (middle frame), interaction rate decreases and handoff times increase as a queue forms. Workers waiting in the queue can judge that the rate-limiting step is someplace else in the chain, and some of them will change jobs. As labor is redistributed and the system approaches correct proportions in each task, interaction rate will increase and handoffs will be brief again (bottom panel). (Illustration by Jay Hosler)

built with greater precision than ► honey bees do. A mature nest can vary from fewer than 10 cells (some ► *Polistes*, ► *Mischocyttarus,* and ► *Ropalidia*) to millions (some *Agelaia*). While it is difficult to know how much of a very large nest is active simultaneously, counting the discarded silk caps from cocoons vacated by emerging adults demonstrated that as many as 12,000 new adults emerged per day in one *Agelaia* nest.

The brood comb may be suspended from the substrate or it may be built with cell bottoms flush against the surface, sessile in form. The comb may be surrounded by an envelope. Within these generalizations are modifications slight and great that represent one of the most interesting flourishes in all of behavioral evolution.

Several basic points of comparison of nest design were given names by Henri de Saussure in the 1850s, along with other authors. Saussure combined Greek roots to describe nest form, such as if cells were built on a pillar (stelocyttarous) or not (astelocyttarous). The many combinations of Greek roots provide an image of technical precision, but the forms themselves are multiply derived and do not indicate homologous structures in an evolutionary sense. As a result, the names do not communicate precisely and are not as useful as a careful plain-language description. More importantly, the names do not describe evolutionary lineages by capturing diagnostic features, of which there are many (21 characters with more than 50 contrasting conditions in the cladistic matrix of Wenzel [7]).

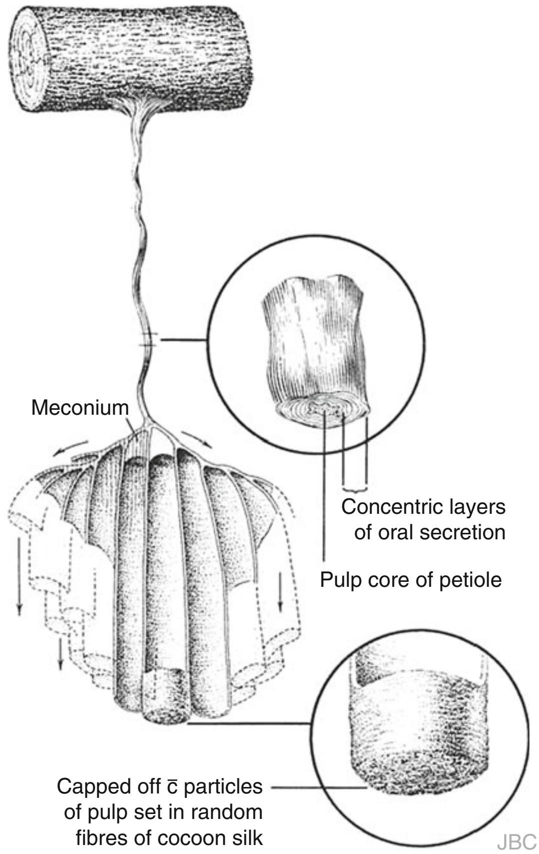
Social wasp nests usually are a composite of harvested plant fiber and salivary secretion. This contrasts with social bees, which rely primarily on their own secretions, or ants and termites, which generally excavate galleries. The actual construction behaviors are largely restricted to two main methods, termed "edge building" and "surface building" by Jeanne [3]. Edge building requires having one mandible on each side of the target space and masticating pulp into a sheet, either to enlarge an existing sheet or initiate one. The wasp usually walks backward slowly while doing this and leaves a narrow strip of paper that is much longer than it is deep. Separate building efforts may be visible if the builders use pulp of slightly different nature, and this gives some nests (particularly in the Vespinae) horizontal stripes. Successive efforts may be kept together to make a uniform sheet, or they may be organized as local structures that rest like roof tiles, one upon the other. By contrast, surface building is executed by the wasp being on one side of an existing paper sheet and spreading out a ball of pulp to make a more or less circular application directly on the surface. Sequential loads of pulp can be different colors.

Polistinae and Vespinae

Simple, petiolate nest. *Mischocyttarus*, Fig. 2. Similar forms are found in *Polistes, Belonogaster, Parapolybia*, and some *Ropalidia*. Nests are initiated by independent females or small groups. Using primarily salivary secretions, a resinous attachment and descending pillar (the petiole) is the main or sole support for the nest. This will be reinforced by oral secretions and occasionally pulp as the growing nest requires. The nest may point downward (Fig. 3) or sideways. A brood comb of carton expands outward from the petiole, adding cells to the margin of the comb, and may be highly variable in shape in either *Mischocyttarus* or *Ropalidia*, but generally a compact ovoid structure for *Polistes* and *Parapolybia*. *Belonogaster* may remove old cells completely to reuse material for new cells more distally, meaning that the nest is hollow at the top and supported only by a Y-shaped margin of the old comb. Usually no other structure is associated with the nest. In *Ropalidia*, *Parapolybia*, and *Belonogaster*, the back of the brood cell is removed to pull out larval meconium (the single fecal mass formed during development, passed just prior to pupation) as a sanitary behavior. The resulting hole in the carton and silk cocoon is repaired with oral secretion in *Ropalidia* and *Parapolybia*. Certain *Protopolybia*, *Agelaia*, or *Vespa* build nests in cavities and without envelopes even though some form of envelope is typical of other species in those genera when built in exposed sites. In these cases of cavity nesters omitting envelopes, the naked combs may superficially resemble this form, but these nests have wider, fibrous petioles rather than narrow, resinous petioles.

Petiolate combs, with envelope. *Angiopolybia*, Fig. 3. Similar forms are found in *Parachartergus, Chartergellus,* and *Leipomeles. Nectarinella* (sessile combs) and *Pseudopolybia* (multiple envelopes) probably represent modest modifications of this type. Nests are initiated by swarms. Fibrous petioles support pendant combs that may be supported from earlier combs above (*Angiopolybia* or *Pseudopolybia*) or separately from the substrate (other genera.) The envelope arises from substrate rather than the petiole or comb and is usually not in contact with these structures. The nest expands by addition of cells at the margin of the comb or by adding new combs below earlier ones. As the space in the envelope becomes limited, the envelope is partly removed and rebuilt to accommodate the growing combs. The entrance to the nest is usually at or near the lowest point in the envelope and is often the last gap left in construction. Envelope sheets are usually single, but *Pseudopolybia* has multiple sheets as parallel laminae that are not closely connected. *Nectarinella* builds a comb without a petiole, so that it is sessile on the substrate, a condition that may occur rarely in *Leipomeles*.

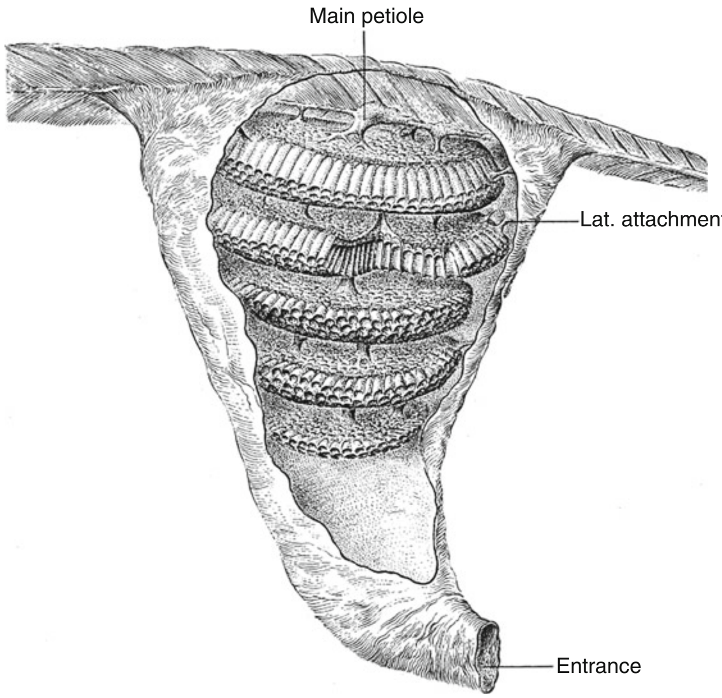
Sessile combs, with envelope, expanded along substrate. *Synoeca*, Fig. 4. Similar forms are found in *Metapolybia, Asteloeca*, and *Clypearia*. Nests are initiated by swarms. Cells are initiated directly on the substrate with no



Nest Structure: Social Wasps, Fig. 2 Nest of *Mischocyttarus*, simple, petiolate, comb. Similar forms may be found in *Polistes, Belonogaster, Parapolybia*, some *Ropalidia*, and some *Polybioides*. (From Jeanne [3])

petiole or other foundation. The comb is expanded outward. The envelope may arise directly from substrate and separate from the brood comb or may be supported by the comb as an extension of the walls of the most peripheral cells. The entrance to the nest is often built as a distinct structure separate from the last gap to close in the envelope. In *Synoeca* and *Metapolybia,* the entrance is directed upward. The nest is expanded along the substrate with a new envelope encompassing the old entrance. Earlier envelope that is made internal to new envelope may be retained as in the original design, but *Metapolybia* appears to strip away internalized envelope sheets. Envelope sheets in this type of nest are generally not reinforced except rarely by the surface-building method.

Sessile combs, with envelope, expanded by building on the previous envelope. *Chartergus*, Fig. 5. Similar forms are found in *Polybia, Brachygastra, Protonectarina*, and *Epipona*. Nests are initiated by swarms. Cells are initiated directly on the substrate with no petiole or other foundation (except the *Trichinothorax* subgenus of *Polybia,* females of which may build a pendant sheet as if it were a petiole). Cells may be limited entirely to the substrate, or comb may be expanded off the substrate as later cells arise from the walls of earlier ones. The envelope may arise directly from substrate and separate from the brood comb or may be supported by the comb as an extension of the walls of the most peripheral cells. The entrance to the nest is below the level of the comb, but usually not at the lowest point of the convex envelope (except for *Chartergus,* where the entrance is usually central and lowest). Expansion of the nest is in sudden, large bursts of building where a new comb is initiated on the lower surface of the old envelope, and a new envelope is built below that in a modular fashion such that the entire new capsule is built in a day or a few days. Sometimes many levels are built in the

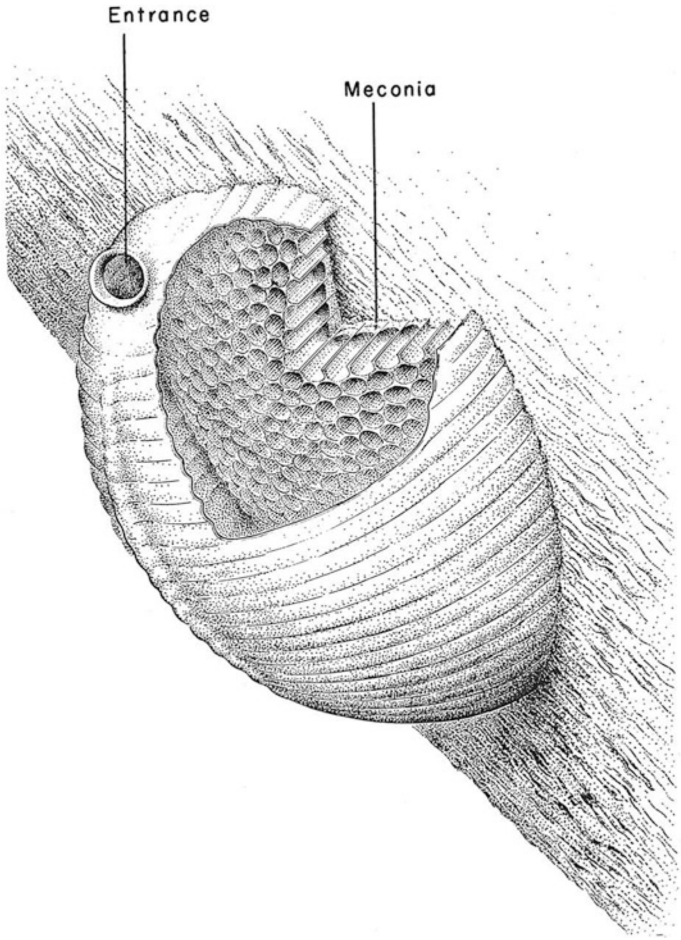


Nest Structure: Social Wasps, Fig. 3 Nest of *Angiopolybia*, petiolate combs, with envelope, entrance at bottom. Similar forms are found in *Parachartergus, Chartergellus, and Leipomeles. Nectarinella, Marimbonda* (sessile combs), and *Pseudopolybia* (multiple envelopes) probably represent modest modifications of this type. (From Jeanne [3])

course of a week or so, and then the nest is static for a year, with no visible expansion. Envelopes of this type are generally reinforced by either (or both) the surface-building method or by constructing via the edge-building method small shell-like structures that sit upon each other like imbricate roof tiles and may provide a great deal of strength and stiffness with little weight.

The archetypes above fail to encompass a few genera that are closely related to those that are listed. Among these are *Apoica*, which has a sessile comb growing off the substrate and no envelope. *Agelaia*, usually a cavity nester, generally makes no envelope, but some species will do so when exposed. *Protopolybia* may initiate with fibrous petioles or sessile upon the substrate (usually a leaf) and may have a complex pattern of expansion relying both on petioles and combs sessile on earlier envelopes. *Charterginus* builds only a few cells sessile on the substrate and the comb is immediately expanded off the surface by building new cells from the walls of the initial few. The nest may superficially resemble a *Polybia* nest with a single comb and envelope, but the entrance is on the dorsal side, through the brood comb, facing the substrate, and the comb is expanded laterally in the same plane as the original comb, not on the lower surface of the envelope. *Polybioides* in Africa build long combs hanging from an edge and surrounded by an envelope that resembles a bivalve to a greater (*P. tabidus*) or lesser (*P. melaina*) degree. *Polybioides raphigastra* in Southeast Asia builds a descending spiral comb whose margins connect with the comb above to close the nest. A fuller accounting of forms can be found in [6], and an illustrated identification key to genera is available in [8].

Sheet, followed by petiolate combs, and multiple envelopes, *Vespula*, Fig. 6. The entire subfamily Vespinae builds nests of similar and complex design despite the fact that they are generally independent founders (but *Provespa* founds by swarms). A small paper sheet or line of paper is applied to the substrate, and from that paper a petiole is suspended. This petiole is resinous oral secretion in *Dolichovespula* and fibrous in *Vespa, Vespula*, and *Provespa*. Promptly after initiating the first few cells, a globe-like paper envelope is constructed containing the nascent nest.

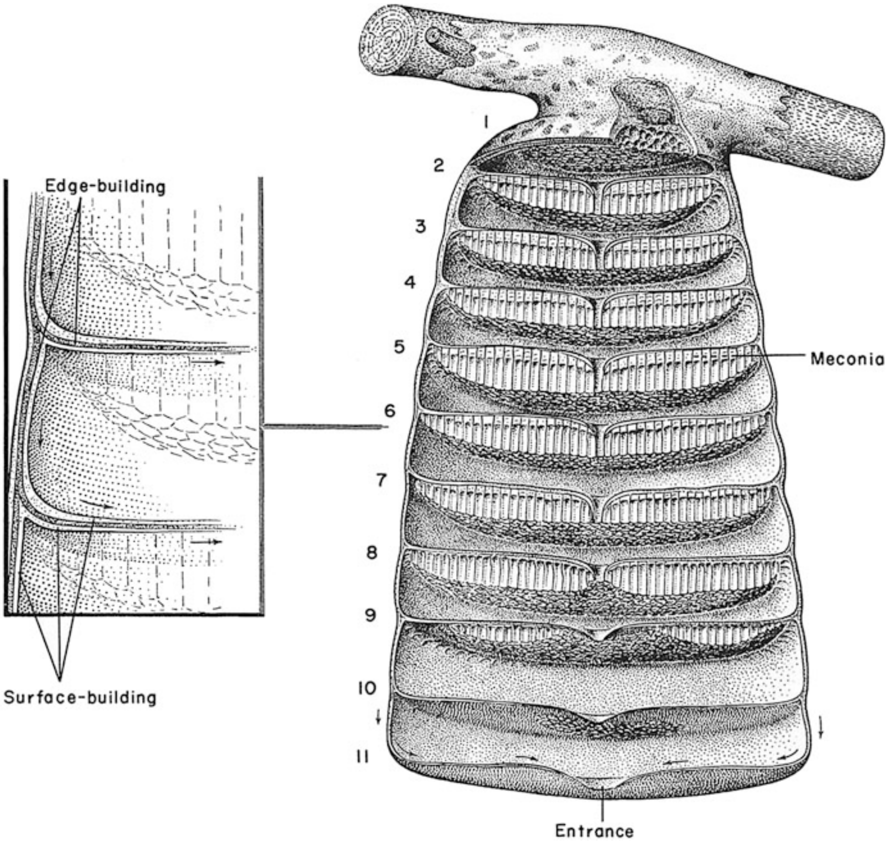


Nest Structure: Social Wasps, Fig. 4 Nest of *Synoeca,* sessile combs, with envelope, expanded along substrate. Similar forms are found in *Metapolybia, Asteloeca*, and *Clypearia*. (From Jeanne [3])

Only the Vespinae will have a lone queen inside a small nest covered by an envelope. Multiple sheets are built outside, and the inner sheets are stripped away as the comb grows. The envelope may have many smooth and laminar concentric sheets, as in some *Dolichovespula*, or may have interconnected, thickly imbricate tile-like structure as in most *Vespula* and some *Vespa*. Most species when nesting in exposed locations build a kind of imbricate cap over the nest that expands conically upward throughout the active period of the colony. The entrance is in the lower portion of the nest, but for large nests the entrance becomes peripheral as the envelope is expanded downward simply because it is more or less excluded from renovation as builders are interrupted and kept away from the entrance by arriving and departing traffic.

Stenogastrinae

The Stenogastrinae, commonly known as ► hover wasps, build nests unlike those other Polistinae and Vespinae. Their nests are extremely variable, given the modest number of species. Stenogastrinae as a group are not as salient ecologically nor as well known as Polistinae and Vespinae, and the total breadth of nest design in Stenogastrinae is still being discovered. Because colonies are small, nests are also small and often fragile. They are usually built in inconspicuous places, often dark and moist locations such as caves, eroding earthen banks, overhangs near falling water, or under low bridges crossing streams. In general, brood cells are attached either directly to the substrate or to another brood cell, without any defined petiole, although the

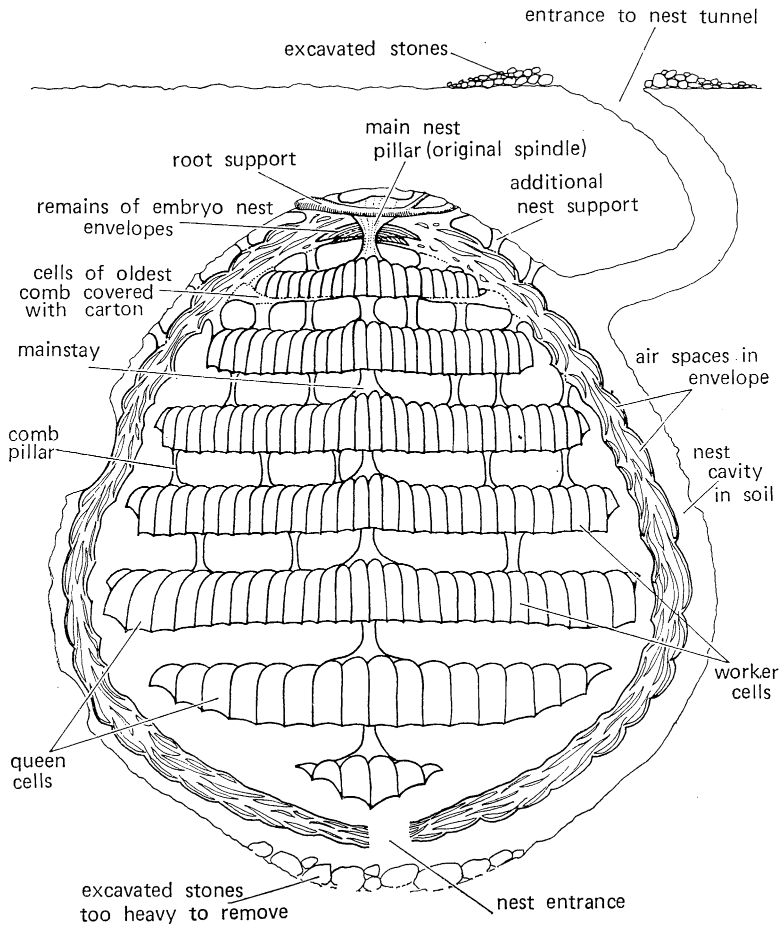


Nest Structure: Social Wasps, Fig. 5 Nest of *Chartergus,* sessile combs, with envelope, expanded by building on the previous envelope. Similar forms are found in *Polybia, Brachygastra, Protonectarina*, and *Epipona*. (From Jeanne [3])

substrate functions as a petiole when cells are attached to narrow, dangling rootlets or fungal hyphae (Fig. 7). Cells may be scattered such that they do not form a comb (*Parischnogaster jacobsoni* group), or organized in a hexagonal mat (*Liostenogaster flavolineata*, and *Eustenogaster*). In most genera, there is no protective envelope or other structure, although *Eustenogaster* builds an envelope descending from the margins of the brood comb. Stenogastrine nests are never large compared to Vespinae or Polistinae, and their fragile nature means one rarely finds abandoned nests from past seasons in large numbers.

Interpreting Variation

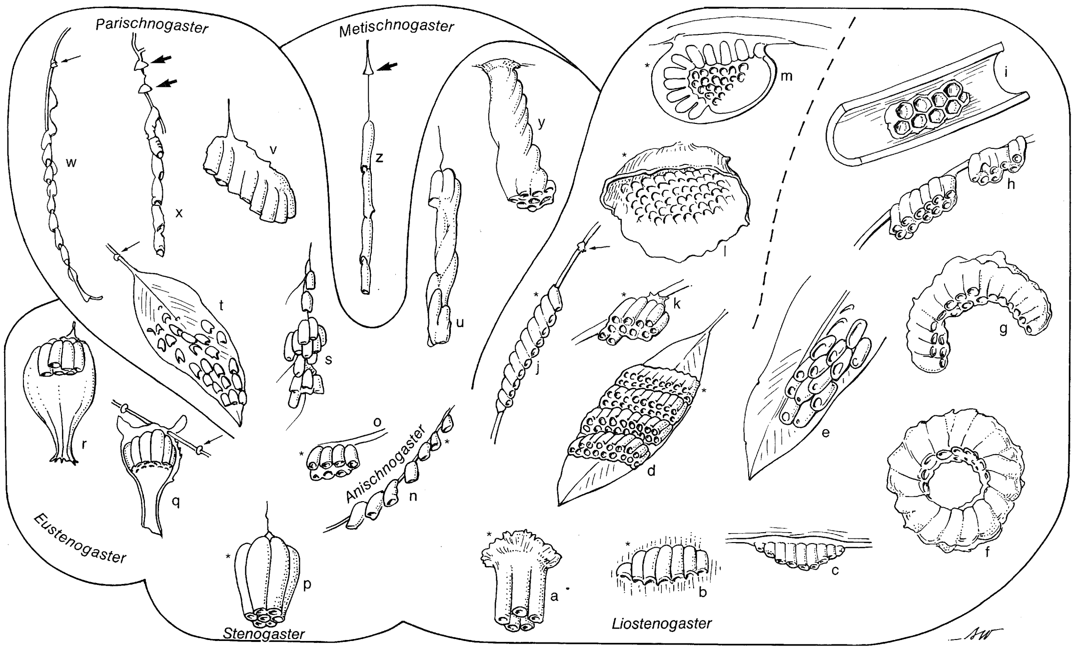
In his pioneering taxonomy of social wasps in the 1850s, Saussure used nest architecture as much as adult morphology to define genera. A fuller accounting of the systematics provided by Adolpho Ducke in 1914 retained the emphasis on nest forms, and Jacobus van der Vecht highlighted wasp nest architecture in 1967. Independent from taxonomic focus, Robert L. Jeanne [3] discussed the adaptiveness of this variation. He showed how different species solved the need to provide protection from ants by either suspending the brood comb on a petiole that can be defended physically or chemically against scouting ants, or by



Nest Structure: Social Wasps, Fig. 6 Nest of *Vespula,* sheet, followed by petiolate combs, and multiple envelopes. Nests may be subterranean (this figure), in a cavity, or arboreal. (From Spradbery [4])

enclosing the nest in an envelope that has a restricted entrance hole that can be defended similarly. Jeanne's celebration of adaptation also recognized that the wasps solved engineering problems of building pendant nests by reinforcing petioles and envelope walls as the nest grows and becomes more massive, and also that nest designs permit efficient and economic use of material. Jeanne also argued that general patterns are evident when one considers colony size. Species with small colony size usually have relatively simple nests (*Polistes, Mischocyttarus*, some *Ropalidia, Belonogaster, Parapolybia, Apoica*), whereas those that achieve large colony size have more complex nests (remaining genera, and some *Ropalidia*). Although this appears to be true in general, some genera that typically have large colony size seem to retain complex nest forms when individual species regress to few nest mates. Among species interesting in this regard would be *Polybia bistriata* and *P. chrysothorax,* species that may have mature colony sizes below 30 individuals, like *Polistes* or other small-colony wasps. Perhaps the key is how many females are present at initiation, and a small swarm is still "many" compared to an independent founding female.

Focusing on phylogenetic patterns, Wenzel [7] demonstrated that treating the construction of the nest as if it were a process of ontogeny obtains the same general patterns known as von Baer's law in embryology: Variation in elements that are evident early in development tend to plot to higher, more ancient taxonomic groups (subfamily, tribe, or ancestors of many genera) and variation in elements that appear late in development mark



Nest Structure: Social Wasps, Fig. 7 Nests of Stenogastrinae. An asterisk indicates construction using mud. Small arrows indicate chemical ant guards, while large arrows indicate rain deflectors. (**a**, **c**, **h**, **i**, **j**, **k**, **m**) undetermined *Liostenogaster* species; (**b**) *L. varipicta*; (**d**, **e**) *L. nitidipennis*; (**f**, **g**) *L. vechti*; (**i**) *L. flavolineata*; (**n**) undetermined *Anischnogaster* species; (**o**) *A. irridipennis*; (**p**) *Stenogaster concinna*; (**q**) *Eustenogaster fraterna*; (**r**) *E. calyptodoma*; (**s**) *Parischnogaster mellyi*; (**t**) *P. jacobsoni* group; (**u**) *P. striatula*; (**v**) *P. gracilipes*; (**w**) *P. nigricans serrei*; (**x**) *P. timida*; (**y**) *P. alternata*; (**z**) *Metischnogaster drewseni*. (From Turillazzi [5])

lower, more recent divergences (separating close genera, or clusters of species). Furthermore, coding more than 50 elements of architecture for 28 genera of Polistinae as if they were morphology and analyzing with the best computer algorithms of the day produced an evolutionary tree that compared favorably with a tree for the same genera based on morphology.

Some Functional Aspects

Crypsis

Venomous insects such as wasps often advertise themselves with bright, contrasting color patterns. However, they seem to prefer that their nests are inconspicuous, or even cryptic. A nest full of brood represents a substantial resource for a predator, and many birds and mammals are willing to risk being stung for the reward of a meal of wasp larvae. Nesting in cavities provides protection, and some species favor tree holes, rodent burrows, bamboo internodes, caves, the inside of termite nests, or wall voids and attics of human dwellings. Most species of *Agelaia* are cavity nesters, and their fidelity to a favorable site means they can obtain very large sizes (millions of cells) in a good cavity. Other species nest among leaves or include leaves in the envelope structures to be less evident than would be a nest pendant below a branch. *Protopolybia* and some *Ropalidia* are particularly good at this form of concealment. Still other species build a nest that is exposed, but the carton of the envelope is decorated with bark or colored pulp to create a camouflage that interrupts the image of the nest, as with black lines drawn on the white felt of *Chartergus*. Some *Brachygastra* that build with a brown carton will paint the bottom surface of the nest white such that the nest has contrasting colors like a fish or old warplane: When viewed from below, it is pale like the sky above, and when viewed from above, it matches the floor below. This is known as countershading. Other species may apply pulp to replicate the color and pattern of the substrate, such as *Metapolybia* and *Clypearia*, or some *Parachartergus*, *Chartergellus, Nectarinella,* and nearby genera. Of particular note, certain *Leipomeles* live in small colonies entirely supported by a single broad leaf, and they build envelopes that mimic the veination of a leaf. Crypsis can also be achieved simply by not displaying a clear brood comb of cells. The forest environment offers abundant irregular globs of earth suspended on rootlets, or old spider silk with leaf fragments attached, and a small open nest can be overlooked easily by being an irregular structure rather than a hexagonal comb. Many *Mischocyttarus* seem to have strange combs that may represent this class of crypsis. The pinnacle of this form of defense is found in the Stenogastrinae, where species vary greatly from one to another (Fig. 7), and some common species, such as *Parischnogaster mellyi*, vary from one to another nest. Traditionally, it is inferred that this great diversity of appearances is generated in part by the action of *Vespa* wasps that raid brood of other wasps. Of course, ants are also effective predators of wasp nests, and for this reason chemical defense has evolved including a class of chemical crypsis where the wasps mark their nest with the same compound that ants use to identify dead nestmates: Ants will not look for food if they think they have discovered an ant graveyard.

Naturalists have sometimes asked why there is relative uniformity of design in the simple nests of the cosmopolitan genus *Polistes,* whereas *Mischocyttarus* are far more variable in comb design despite having comparable numbers of species. Ignoring that some species of *Polistes* do have unique forms, it is apparent that *Mischocyttarus* appear to have experimented with ways to disguise the typical and obvious hexagonal comb, whereas *Polistes* relies on vigorous ► defense of the colony. There is still much to learn about the evolution of crypsis.

Food Storage

Unlike the ants and bees, social wasps have no special cavities for storing food in the nest. Exceptions are that some species (*Protonectarina* and some *Brachygastra*) will collect nectar and store it like honey, and some species (some *Polybia*) will capture flying ants or termites, remove wings and legs, and store them in empty brood cells. Most students of wasps have reported cannibalism and egg eating at relatively high rates, either as adults eat their own brood or as they feed some larvae to others. Cannibalism may manifest in a nonsensical way, where an older larva is destroyed and fed to a younger larva, thus moving backward in brood production. It is possible that some species treat the brood itself as a kind of storage device, rearing lots of larvae when prey are abundant and then feeding some to others in sparse times.

Homeostasis

Because nest structures physically isolate the colony from the environment, there is a belief that architectural designs provide a degree of homeothermy, humidity control, or other environmental stability. This view is based more on expectation than on data, and a few good examples may create a false impression of generality. Recent work indicating that desert termite nests are not evolved as air conditioners (*contra* traditional interpretation) demonstrates this point. *Apis* colonies are very homeostatic, but this is more due to the behavior of the bees than anything about the nest architecture itself. Wasp nests, although splendid in diversity, are relatively simple with respect to parts and mostly have not been examined in this regard. It does appear that montane *Polistes* may achieve some thermoregulation by having extra cell walls adjacent or distal to the developing brood. It is an obvious expectation that multiple envelopes of the northern groups *Vespa*, *Vespula*, and *Dolichovespula* provide a warmer internal environment for the brood. But note that tropical species of these taxa still have multiple envelopes, as do subterranean species where temperature variation would be quite modest. Physically isolating the brood from the atmosphere may produce a kind of homeostasis, but whether this property is the selective force that generated the architecture is largely unexplored. Thus, it cannot be said that the multiple envelopes are a Darwinian adaptation to cold climate. Homeostasis as a driving force *per se* is usually conjectural, whereas protection from predators, parasites, and inclement weather is easily demonstrated. Perhaps the clearest example of a structure that has evolved under this kind of selection is the long tubular entrance constructed by queens of some arboreal *Dolichovespula* and *Vespa* that help retain metabolic heat of the brood comb by reducing convection. It is interesting that in large nests of *Agelaia* the brood comb retains very much the same temperature, day or night, rather than tracking ambient air temperature. *Agelaia* typically nest in cavities, and the large mass of brood may be sufficient to achieve this metabolic stability without special architectural features.

Sanitation

Keeping a nest clean may answer either of two pressures: evading detection by enemies or control of disease. Because it is easy to eject material from an arboreal nest with little record remaining, it may be difficult to measure sanitary behavior. Nest structure may indicate the importance of these factors in some species. Pupal exuviae (cast skins) of parasitic flies are particularly common in wasp nests of the Old World stored in museum collections, indicating pressure from parasites that are likely olfactory in search behavior. Nests often develop an odor if they accumulate the organic debris of uneaten prey, failed brood, and feces of developed larvae. Among the Old World Polistinae, most species show hygienic behavior that is recorded in nest architecture. *Ropalidia*, *Belonogaster*, *Parapolybia*, and *Polybioides* all remove from the nest the larval meconium, a single fecal mass passed when the larva molts to the pupal stage. Adult wasps chew a hole through the back of the brood comb and extract the meconium. In *Belonogaster*, it appears that at least some species do not pass the meconium, but rather retain it until a worker wasp tears away the peri-anal region and pulls a sac-like meconium from the body of the prepupa. Unpublished data indicate that if the adult does not remove the meconium, the prepupa will retain it and die of necrosis during metamorphosis. In both *Ropalidia* and *Parapolybia*, the hole chewed by the adult wasp is repaired with oral secretion, a strong silk-like compound that consolidates the nest where it was made weak by the hole. *Belonogaster* and *Polybioides* do not repair the back of the brood comb. New World taxa generally do not remove meconia, allowing the number of meconia in a cell to indicate how many generations emerged from it. In contrast to the four Old World genera mentioned above, New World taxa rarely have fly pupae in museum nest specimens. Meconia can build up enough that, in a long-lived nest, such as those of *Chartergus*, the reduction in the length of the brood cell may explain why cells are abandoned from brood rearing (they are no longer deep enough), and more recent, lower levels of comb dominate production. New World wasps generally do not have sanitary behaviors to expel meconia, although some *Clypearia, Protonectarina, Polybia scutellaris,* and *Agelaia vicina* remove meconia through the open mouth of the cell.

Site Selection

Most species, and perhaps an entire genus, will have a preference for nesting sites such that there will be a syndrome that is common for them, at least locally. Typical nesting sites for a certain wasp might be below the broad surface of a large branch or roof line; under a rocky overhang; on the smooth trunk of a large tree; on a distal tip of a branch of a tree; at the top of a tall tree; among dense leaves in a tree; in a thicket of brush near the ground; in a burrow in the ground; in a tree cavity or wall void of a building; in a narrow cavity such as a bamboo internode or metal fence rail; or sun-warmed sites by high-latitude *Polistes*. At any single locality, a species commonly favors a typical site, although the nature of the site may vary across the geographical range. Among the synanthropes (those that choose to live beside humans), they may be so specific as to favor strongly the peak of the roof of houses, but not the straight line of the broad eaves of the roof, or beside the cross ties at the margin of railroad bridges, but not the long beams in the middle of the bridge. A student who recognizes the local pattern and searches for those sites will find more nests than someone who looks in all possible good locations. Uniformity across a species' range demonstrates that some preferences are probably evolved and deeply programmed. Other, local preferences may be learned, perhaps by classical imprinting. In an experiment that moved natural nests to inverted baskets nearby in an otherwise natural field, *Polistes annularis* that emerged from those nests chose to initiate their own nests in inverted baskets the following year rather than the ubiquitous natural sites in the same field, the natural sites their mothers chose before experimental transfer. This implies that local typical sites are learned. Perhaps the adaptive basis is "this worked for Mother, so I will do the same." The fact that widespread species vary in "typical" sites is consistent with this hypothesis. By contrast, an alternative, unspecified force of natural selection would have to be extremely strong and yet variable or arbitrary to generate differing, typical sites among widespread species. Recently, there has been a growing appreciation that site selection may suggest a greater sensitivity to environmental factors of climate than was recognized previously. Seasonal variation, or departures such as "a very wet year," may determine some aspects of site selection. In French Guiana, site selection of some species has been shown to relate to major weather patterns, such as El Niño years versus La Niña years. How wasps regulate these adaptive choices is unknown.

Curvature

People have admired for centuries the "honey comb" for its perfection as a flat field, but there has been little consideration given to the more challenging task of building curved surfaces. To examine curves, we must characterize what constitutes a planar array and what represents engineering through a third dimension by using curved surfaces. It is a good rule of thumb that the cells of the comb are essentially long prisms that are hexagonal in cross section, but that is not universal. Close examination of a honey bee comb will show irregularity, and wasps are actually far superior to *Apis* in their performance of building large planar fields of perfect hexagons. The species that build very large nests in genus *Agelaia* (*A. vicina,* for example) will build millions of perfect hexagonal prisms of uniform width without error. Builders start planar combs at different locations and may fuse combs when they run together with the rows properly matched. Viewing from the open, distal end of the cell, there may be no indication that the finished comb had multiple points of origin. A student looking at the back of the comb discovers the separate loads of pulp that were added to the margins of the separate combs, indicating the radial expansion of the initial combs centered on the focal points of origin, thus observing the excellence of stitching separate combs together in perfect planar array.

Some nests that rely on curved structures do not actually build curved combs. Examples include the spiral staircase nests of certain *Protopolybia* in the *P. sedula* group, or some perhaps some *Agelaia*, or *Ropalidia montana*, or *Polybioides raphigastra*. All these represent a descending spiral of all hexagons, a helix, without actually generating a 3-D curve in the comb itself. At their basis, they are a two-dimensional rotating mat of hexagons falling through a third dimension, but there is no necessity to generate a curve in the field of hexagons itself.

Species that build curves with precision through three dimensions must use nonhexagonal cells to achieve this, just as pentagons are used among hexagons to create the surface of a soccer ball or a geodesic dome. It is not yet well developed how we define the curve. Most commonly, combs develop a slight curvature because the brood cells are a little wider at the open, apical end than at the closed basal end. If the bases are all aligned, there will be a necessary curvature across the open face. Some curves appear to be improvised and disorderly, such as the deeply curved, hammock-like nests of *Belonogaster*. Such nests can be seen to have many widely expanding cells with some neighbors getting crowded out of contact. Cells may have six neighbors at their origin and only have five neighbors at their open ends (a "scutoid" shape). Note that a soccer ball is composed of hexagons and pentagons, indicating that pentagons are essential to permitting curvature in a field of hexagons. Building a five-sided cell drops a row from the pattern and allows curvature, like taking a pleat in a piece of cloth. A seven-sided cell (heptagon) inserts a row and counteracts the curvature, spreading out the surface of the nest slightly. It is helpful to examine *Polistes annularis,* which builds the largest nests of any *Polistes* in North America and often builds them deeply dished, like a soup bowl. Nests are initiated as inclined planes. As the comb is built downward, curvature allows the nest to face down. As the comb is built upward, the wasps must prevent the naked comb from pointing cells upward to expose the larvae to sun and rain. One study shows with statistical significance that nonhexagonal cells appear nonrandomly according to location, with the pentagons appearing below the nest's midline, permitting curvature and permitting cells to face downward (at a base rate of 6.5 per thousand hexagons) and heptagons appearing above the midline, preventing curvature and preventing cells from facing upward (base rate of 1.3 per thousand hexagons). It is unknown how a committee of builders regulates a global phenomenon such as comb curvature.

It is perhaps no coincidence that the genus that can make the most perfect planes of hexagons also makes the best curves. *Agelaia* includes species that build curves of various sorts: descending spirals (*A. xanthopus*), concentric hemispheres with regularly increasing radius of curvature (*A. angulata* or *A. testacea*), or outwardly expanding connected globes (*A. areata* or *A. flavipennis*). Their performance is extraordinary, and how the curvature is regulated by a very large committee of builder wasps is still unknown. It is clear that the regulation is sophisticated. If it was simply that the wasps drop rows of the matrix as they get crowded out, then *Agelaia* nests would appear chaotic (as with *Belonogaster* nests), but instead they are a stunning example of engineering. There is much to be learned about how the wasps individually and as a committee regulate curvarture. This will be one of the most sophisticated topics in self-organization addressed to date.

Cross-References

▶ Hover Wasps, Stenogastrinae
▶ *Mischocyttarus*
▶ Parapolybia
▶ *Polistes*
▶ *Ropalidia*
▶ Vespinae

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