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THE NESTING HABITS OF *POLISTES RUBIGINOSIS*,  
WITH SPECIAL REFERENCE TO PLEOMETROSIS  
IN THIS AND OTHER SPECIES OF  
POLISTES WASPS

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The ingenuity of various species of *Polistes* in their task of nest-building, and the consistency with which each species adapts the nest to the chosen situation, have ever been the cause of pleasant surprise to the student of these wasps. In a paper recently published<sup>1</sup> on the habitat of *Polistes*, we find that each of the four species that are common hereabouts choose nesting-sites which are more or less distinct. *Polistes pallipes* build their symmetrical nests in sheds, barns, and under the eaves of roofs where space is not limited. *Polistes variatus* make their nests more compact, to fit small spaces under rocks on the ground or in pockets in banks of soil. *P. annularis* build nests in the tree-tops, with a side-wise tilt and a heavy roof to shed the rain. But *P. rubiginosis* long kept their secret of where they hid their nests. It was indeed puzzling that the literature contained so little on the habits of a wasp which is so common and conspicuous in the fields. The reason is evident when we learn that they habitually build in dark, inaccessible places, often high up out of reach, in hollow trees, or

<sup>1</sup> Ecology, 10:191-200. 1929.

behind the walls of old wooden buildings where they find ingress and egress through a tiny crack or knot-hole (Figs. 1 and 5) some distance from the actual site of the nest.

Under these conditions, I was indeed fortunate in finding a nest of *rubiginosis* unusually low so I could make observations on their behavior. Since these wasps prefer dark, inaccessible places, the queen which began this one



FIG. 1.

found an ideal spot here. The little shanty was one of a half-dozen huts which had been built for the storing of ammunition during the war. They stood in a large woods about seven miles from the city, but now were unused and abandoned. This was a sheet-metal structure among half a dozen wooden ones in a row, all windowless and dark, with only a small opening near the top of each for ventilation. With the door closed, the place was dark enough

to make happy the heart of any seclusion-loving creature. Here it was that, on opening the door on October 13, 1928, I was delighted to find a colony of these wasps. The nest was large, with all of the cells empty, and occupied by about fifty fine adults, which I supposed were queens. This was my opportunity to learn something of their habits of hibernation, and the founding of new colonies the next spring. I have already shown<sup>2</sup> that in *P. annularis* the queens hibernate some distance away from the nest, but on warm, sunny days of winter they often return to the old homestead, and when they make ready to found their own colonies, they do so in the vicinity of their former home, often with several queens co-operating in constructing one nest, and occasionally biting out the cell walls of their old nest for building materials for the new.

These, then, were the problems which I wished to solve for *rubiginosis*:

(a) Will these queens hibernate on the nest all winter, or will they disseminate?

(b) Will they revisit the old home during the warm days of winter?

(c) When they do build in the spring, will they choose nesting-sites near to the one where they were born?

Occasional visits to the shed yielded the following data in answer to the above questions:

On October 13, fifty queens were on the nest; on October 27, forty were there; on November 4, ten remained, and on December 3, three were on the wall near the site, the nest having fallen to the floor. A careful search through the five similar buildings nearby revealed none on these dates. This shows that they do not hibernate on the nest, but wander elsewhere; that they do not leave the nest in a body or swarm, and that some cling to the nest more tenaciously, literally and figuratively speaking, than do others. But the fact that they do not leave in a body does not mean that they do not hibernate gregariously, for

<sup>2</sup> *Annals Ent. Soc. Amer.* 23: 461-466, 1930.

during the previous year in January, I discovered about a hundred queens of this species huddled together in the galleries of the carpenter ant in a fallen tree. They were grouped in three masses, and when taken into the laboratory would often come out of the log when the room was warm, but would always huddle together in the galleries when the room became cold.

I cannot say with certainty whether they return on warm days to the old home, thereby refreshing their memories of the site. I was unable to visit the place during the winter as often as I intended: however, on three visits on very warm days in February no wasps were present.

Fortunately, we have a more positive reply to the question whether the queens build their new nests near the place where they were born, after having spent the winter elsewhere in hibernation. Likewise the question, does more than one queen work together on a nest, is answered in the affirmative, as the following data will show regarding these two points.

My next visit to the row of sheds was on June 8. There I found in the little house a new nest, just a few feet from the site of the old one. As mentioned before, the old one had fallen during the early winter, and I had left it on the floor, but it had been carried away during the winter. Hence the nest itself could hardly have been the object which they remembered or which attracted them, but the little building itself. This new nest was hexagonal, with 148 cells, only 8 of which were capped; the rest were shallow and filled with eggs and larvæ of various sizes. There were no full-sized empty cells from which adults could have emerged; in spite of this, however, seventeen adults were on the nest. These, then, were undoubtedly the queens which had emerged the previous autumn. Of course, when one finds more than one queen on the nest, one suspects that the surplus queens sink into the insignificant role of workers, while only one rules the nest in royal fashion. Whether or not this happens has yet to be ascertained, but here with so large a nest so early in the year, it is quite probable that all the queens had shared

in the labor of its construction. Not all of the queens were on the nest when I arrived at 9 a.m.; only eleven were there, but during the following three hours, six came in, some carrying materials and others left from time to time. Since all of these queens were given individual marks, I could make certain that the majority of them shared in the work.

The adjacent building, made of wood, similar in structure, equally dark and only two feet away, had contained no nest the previous year; now it harbored three nests of *rubiginosis*. One of these had four queens and 48 cells, another had two queens and 35 cells, and the third had one queen and 15 cells. The number of cells was only roughly in proportion to the number of queens per nest; the more queens, the more cells per nest. This, in turn, would mean, as one would expect, that all or most of the queens do work. However, it is evident that as the number of queens on the nest increases the work done by each individual is proportionally less. The nest with seventeen queens averaged nine cells per queen; the one with four queens averaged twelve cells each; the one with two queens averaged seventeen cells, while the lone queen had made fifteen cells. An individual *rubiginosis* mother, even though of larger size than *pallipes*, builds no faster than many queens of the latter; this is shown by a comparison of the size of the nest of this species with that of *pallipes*. Six nests of the latter in nearby buildings with one mother each, had 15, 20, 14, 12, 10 and 7 cells on this same date.

To summarize, then, we find that, like *P. annularis* of the tree-tops, this species remembered the old nesting-site and returned to it after hibernating elsewhere, and disseminated from the place of their birth, but did not go very far from it to build their own nests.<sup>3</sup> One or more queens founded the new nest and shared in the work. The founders

<sup>3</sup> Hoffer (Clements and Long, Experimental Pollination, p. 248. 1923) found that bumble bees remembered the place of their nest from the middle of October to April, when they returned. Also see article by Frison, *Canad. Entom.* 62: 51, 1930, who also finds that bumble bees remember the home site after spending the winter in hibernation.

of the nest were true sister queens, sharing in the activities alike, and so far as I could see no individual assumed the haughty role of queen.

At this point it will be well to digress from the nest-building habits of this species and discuss the facts of pleometrosis and its origin.

In a very interesting paper by Dr. J. Bequaert, entitled "Vestigial Pleometrosis in the North American *Polistes pallipes*,"<sup>4</sup> the term "pleometrosis" (which Wasmann introduced for ants) is used to signify the founding of a new colony by two or more fecundated females. Bequaert says that when pleometrosis occurs "among strictly monogynous wasps as with *Polistes*, it is well worthy of careful investigation, since it evidently is then one of those vestigial instincts whose study is of great value for a proper understanding of animal behavior."

Pleometrosis occurs here about St. Louis abundantly in *P. annularis*, occasionally in *P. rubiginosis* and but rarely in *P. pallipes*. This seems to be contrary to the findings for *P. pallipes* about New York.<sup>5</sup>

After viewing the occurrence of this habit in our *Polistes*, I am inclined to believe that pleometrosis in our northern species of *Polistes* had its origin in the "swarming" habit of tropical *Polistes*. In a paper now in course of publication on *Polistes canadensis* and *Polistes versicolor* of Barro Colorado Island in Panama, I show that when the colony grows too large or a catastrophe occurs to the nests,

<sup>4</sup> Bull. Brooklyn Entom. Soc. 18: 73-79, 1923.

<sup>5</sup> During a period of ten years, I have seen, among a thousand or more nests of *P. pallipes* examined, only six nests with two queens, and only one nest with three queens. I have always been on the lookout for the nests in the spring before the workers emerged, so that I could mark the queens with paint and find if one was truly a specialized egg-laying queen, and the other sank into the insignificant role of worker. In every case where this was tried, the queens deserted the nests soon after the ordeal of being marked, and the problem remains unsolved. Had I waited until larvæ were in the cells they might have been more faithful to their tasks; one must, however, mark the queens in *pallipes* before the young emerge, since it is not possible to distinguish workers from queens by either size or color. In course of two years I have been able to examine only about twenty-five nests of *P. variatus* in early spring, but I have never found more than one queen founding a nest.

swarming occurs much after the fashion of swarming of honey bees, with this difference; whereas the honey bee swarm seeks a new location in body, the swarm of *Polistes* wasps in the tropics breaks up into many smaller groups of few or many individuals, and these found the new homes. In the tropics where winter and hibernation do not occur, this is the method of dissemination. In the north, cold and hibernation interfere with this method, but we do see an adherence more or less complete (but in certain species no less complete) to the habit of pleometrosis, after assembling on the old home site which, after all, is very similar to swarming. This may or may not be vestigial in character, for it is difficult to tell whether pleometrosis is ascending to higher socialization, or is in a vestigial condition.

Thus we see that the occasional condition (more or less frequent according to the different species of *Polistes*) of more than one mother founding a colony has an analogous counterpart in the swarming of a sister species in the tropics. There seems to be but little difference between the psychological reactions of members of a colony when activities are cut short by the violent destruction of the nest in the tropics, or the violent curtailment of their activities in the north by the cold. In both cases, members of the colony disband and found new colonies with one, two or more queens present; however, in the tropics the founding of new colonies occurs immediately after adverse conditions occur, while in the north the founding of new colonies is interrupted by a period of hibernation in which the wasps are numb with cold. In any event, the long period of dormancy in the northern species apparently has not caused the wasps to forget how to behave like their tropical sisters when colonization occurs. Pleometrosis of *Polistes* in the tropics is due to the fact that with a twelve-month calendar, the colony splits up occasionally when it reaches great size, and one to many sister wasps go forth and found a new nest. But in the north where cold weather curtails the *Polistes* activities to only a fraction of a calendar year, pleometrosis undoubtedly has its origin in the queen's remembering the home

location, going there in the spring and meeting sister queens, and founding their nests near by. This marked difference between the two populations exists, however: in the northern *Polistes*, only the queens survive the winter and are ready to scatter in the spring, whereas in the tropical species, some of those which found new colonies may be workers. Bequaert (*loc. cit.* p. 76) says that in some species of tropical *Polistes*, "it is often hardly possible to distinguish externally workers from fertile females, and in some of the species it is even doubtful whether a differentiated worker caste is present."

Of course, if all of the wasps built close to the old home, there would be no world-wide distribution. Some of them fare forth alone to greater distances. Even so small a trait as this shows that they have individual psychological characteristics upon which selection may play. The inclination to stay near the old home or the inclination to venture farther may be very significant in the development of the habits of the species. It is the difference between conservatism and initiative, which, small in the beginning, may be vast in the end.

In this instance of fifty *P. rubiginosis* that were seen on the nest October 13, only twenty-four appeared the next spring, building the four nests already referred to. Some of the other 26 must have gone to greater distances to build, unless the mortality was that great. The powder-houses in which these nests were found had presented the same opportunities for this species to build for the past five years, but this is the first time that one of these pioneers found it good for a nest, and fixed a site for twenty-four of her less venturesome descendants. Of course, in studies of this kind we can follow only the lives of those conservative individuals which remain near home; of those venturesome pioneers which blaze new trails, we can have nothing to say. The first *rubiginosis* queen that came to this shed must have ventured some distance from her old home, perhaps in some hollow tree.

With these four new nests of *rubiginosis* at hand, all within easy reach of the eye (an unusual condition), I made plans for learning more of their habits, but unfortunately

the house containing the three nests was destroyed by the new owner of the grounds, and an accident befell the fourth which was in the metal house. The latter, however, gave me the following notes before the occurrence of the accident.

This nest with seventeen queens was revisited on June 19, after a nine-day absence. During this period, ten cells had been added to the nest, and instead of seventeen adults, only thirteen were on the nest. The others may have become easy prey to their enemies because of the conspicuous paint spots which I had placed on their bodies. The nest was attached to the ceiling about ten inches from two small ventilator-slits in one side-wall; through these slits the wasps came and went. On hot days, one, two or three wasps were stationed at these ventilators; they vibrated their wings rapidly for periods up to ten minutes. When the sun beat down upon the sheet-iron roof, it was indeed sweltering in there; hence I suppose this performance was for the purpose of cooling the nest, much after the manner of the trumpeter bees which ventilate the nests of bumblebees, or honey-bees that do the same at the entrance to the hive.

It is hard to see how this would be accomplished with the nest ten inches away; I sometimes wonder if the same behavior on the nest instead of at the opening would not do more good, but doubtless the wasps' judgment is better than mine in that. Their behavior agreed with that of other species of Hymenoptera which do their fanning at the hive entrance.

The incoming queens carried water, and placed much of it in large globules in the cells with the eggs or young larvæ. The lids of four sealed cells were thoroughly saturated with water, and another cell which had a concave instead of a convex cap had this cavity completely filled with water. This habit of spreading water on the outside of sealed cells was also noted for *pallipes* colonies elsewhere;<sup>6</sup> this precaution may protect the pupae from drying up. These *P. rubi-*

<sup>6</sup> See article to appear in *Ecology*, 1931, entitled "Polistes Wasps and their use of Water."

*ginosis* bring in large globules that glisten in their jaws as they fly. Sometimes if disturbed they lose their drops in flight or as they alight on the nest; by placing my notebook under the nest I have collected many such drops. At first I thought that the liquid might be a thin nectar, but when I substituted my tongue for my notebook, my taste told me it was clear water.

It is strange that so many of the wasps remained on the nest most of the time. In this colony of thirteen queens, from nine to thirteen were on the nest at all times; this means that sometimes none were out, and never more than four were out at one time. I could not understand why, with June still young, this group did not hustle to bring in pulp and increase the size of the nest. It appeared that they were merely waiting for the workers to emerge; with the first of their queenly instincts satisfied, they were remembering that they were queens, and now had only to await the vassals. Many of the larvæ were full-grown and ready to spin, and the younger larvæ could be sustained with only a few of the queens at work occasionally. While nine days ago only eight cells had been capped, today twenty-eight were capped. All this prospect of help from twenty-eight workers in the near future may account for the aristocratic languor of these queens.

With so many adults on the nest, it was hard to follow the activities of each, even though all bore distinguishing marks, but a few notes were so made. For instance, three certain wasps were seen more frequently than the others at the ventilating hole, vibrating their wings. "Red-thorax" gave special attention to inspecting the cells with larvae; "Blue-thorax" often left her ventilating post and flew afield, and when she returned to the nest the others would sip nectar or what not from her mouth. No paper pulp was being brought in now, and only a few shallow cells contained eggs. In one place instinct had miscarried; a cell with one-fourth grown larva contained also an egg, deposited a little below it. Since no cell is capable of bringing to maturity two larvæ, one must eventually perish.

The nest did not adhere well to the smooth iron ceiling, so when I attempted to pull off with the forceps a tightly

clinging queen, the whole nest crashed to the floor. I could not again fasten the nest to the metal ceiling, but since I had seen *P. pallipes* and *P. variatus* build again in the same spots after their nests had been taken, I hoped the same would occur here. Not knowing what to do with the nest, I placed it, open side down, on the shelf near the ventilating hole where the wasps would pass it on their way in and out. The wasps were furious for some time, and flew angrily about, and then one by one settled on the spot where the nest had been attached. After an hour, five queens left this congregation and assumed duties on the nest on the shelf. I left them with six wasps on the ceiling at the old site, and five on the nest on the shelf.

When their instincts are misled, one may expect almost anything. When I returned to the colony on June 23, I found the number of wasps complete, but they had left the ceiling and all were now at work on the nest on the shelf. Here, it seemed, would be something new in behavior; instead of all constructing a new nest, all now united in work on the old nest on the shelf, destroying it and carrying it out bit by bit. About fifteen cells had already been completely removed; the nest material and larvæ were being discarded, and even the capped cells were broken open and the pupæ carried out. Some of the queens would bite off pieces of the nest and drop them directly below, while others would fly out a distance and drop them while on the wing. One particular wasp would always drop her load below, six inches east, where already an accumulation of litter on the floor told of her diligence; another habitually dropped her loads toward the south. Eleven of the old, marked queens remained on the nest, but no new ones were there; this indicates that the maturing pupæ had been thoroughly destroyed.

The whole colony seemed to be demoralized, and several were seen eating and kneading the flesh of their own young. They were all restless, and appeared nervous and angry, working in helter-skelter fashion, destroying when they should be building, yet all seemed to be of one mind, intent upon demolishing the nest and its contents and getting it off the premises as soon as possible. At a short distance

from the nest, the chewing of paper pulp by the angry wasps sounded like the gnawing of a mouse in old papers. They were indeed as busy as they were angry, as they energetically poked their heads into the cells, as if in search for any that might remain. The larvæ seemed more the object of their wrath than the nest itself. The larvæ were always carried out and dropped at a great distance, while the bits of material were merely dropped below near by. Sometimes the larva was too heavy to permit a long flight; then the wasp would fly to the ground with it, but always drag it one to four feet away before abandoning it.

On June 30, a week later, they were still at the job; the nest was about two-thirds gone. Even two weeks later, July 14, a portion of the old nest still remained, with eight queens on board. They were unusually susceptible to intrusion, and one marked with green singled me out for attack during my entire stay of an hour. She stung me once, and came back to renew her attacks as often as I chased her out.

Perhaps their nervousness was increased by the fact that there was now a new nest also to be defended. On the ceiling, near the spot where the old nest had been, was the new nest with four of the queens on it. It was hexagonal in shape, and contained fifty-one cells, arranged in beautiful symmetry; the first row on one side had six cells, and the others in order contained 7, 8, 9, 8, 7 and 6 cells, respectively. Here they were at last doing what they probably would have done at first, had not the presence of the old, broken nest near by disconcerted them. They rebuilt the nest near the old site, just as *P. pallipes* and *P. variatus* had done elsewhere when their nests were removed.

By July 28 I found a thriving nest of eighty-two cells, all shallow, of course, each containing an egg, and every cell but the four newest ones at the edge had round, shiny pellets of honey. The globules in the cells varied in size and number. My sense of taste told me that these were really thin nectar, and not the drops of water which these wasps bring in when the larvæ are in an advanced stage or the cells are capped. Thus we find that this wasp pro-

vides honey for the first meal for the larvæ, just as do the other species of *Polistes*.<sup>7</sup>

Although eight or nine queens were on the new nest on the ceiling, they had not yet entirely abandoned the old one on the ledge. Three wasps, still wearing their identification marks, were on it, but all that was left of that beautiful nest of 175 cells was the mutilated stumps of about twenty-five cells. However, the wasps had tried to do something for the colony. Most of the cells contained eggs, but four cells had two eggs each, and two had three eggs. Perhaps it is no wonder their egg-laying instinct had gone astray amid such confusion.

The wasps guarded this new nest carefully. Only a few ventured out at any one time. Possibly they had something to fear from ants. A mouse made itself quite at home, running along the ledge nearby, not fearing even my presence; no doubt he would have made inroads on the eggs and larvæ if the guards had not been present.

We can readily see how *Polistes annularis*, coming back to the old home nest in the trees in the spring after a period of hibernation in a distant sheltered spot, can readily disseminate to similar branches near by. Obviously it is not so easy for *P. rubiginosus* to find nesting-places which fill her exacting requirements other than the immediate site of the parental nest. This difficulty, coupled with the innate tendency to return, probably accounts for the habit of nesting repeatedly near the same spot. In the photograph (fig. 1) the knot-hole<sup>8</sup> affords an entrance to a colony of *rubiginosus* situated in the dark space between the inside and outside wall. The paper nest was attached to the horizontal beam. Horizontal and vertical studding

<sup>7</sup> See article on "Honey Gathering Habits of *Polistes*." Biol. Bull. 54: 503-519, 1928.

<sup>8</sup> The knot-hole is the scene of the observations on behavior described under the title, "At the end of the season with *Polistes rubiginosus*." (Ent. News 40: 7-13. 1929.) There I have shown how the inhabitants of the nest congregate in clusters about the opening with nothing to do but wait for the impulse to seek hibernating quarters. I failed, however, to include one note on the return of these wasps to this knot-hole the following spring, which I wish to add here, because it shows how after a period of hibernation elsewhere, the wasps (like *annularis*) remember the home site and return to it.

made a small, square room surrounding this hole. For three years, returning queens in the spring congregated in abundance about this opening. The second year another colony appeared up under the roof, and later others appeared in various parts of this old building, wherever a knot-hole or a crack was available. When finally the building was wrecked, I found eight such nests between the lath and the outer wall.

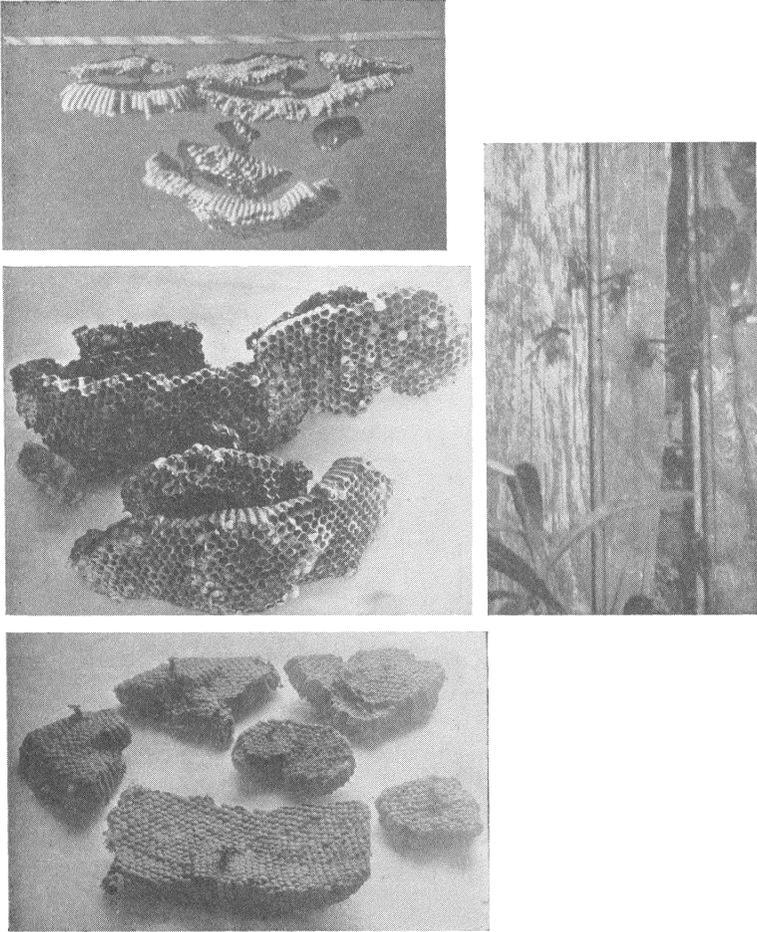
In two other distant localities in St. Louis County and Jefferson County the same condition prevailed and upon pulling off the boards which covered the nests I found in each several large combs which these wasps had built, one below another in true *Vespa* (not *Polistes*) fashion. In nest shown in fig. 2, each comb was attached to the one above by one or more pedicels, much after the manner of the comb attachment in nests of *Vespa*.<sup>9</sup> On the floor of this little square enclosure lay several old nests which had fallen of their own weight. Because of crowded conditions and the scarcity of proper dark nesting sites, these wasps had built tier below tier on the old nest; they had not used the old soiled cells, but each time had built anew, just below. Another new departure in habit also was apparent here: they were salvaging and rechewing the paper in the old combs for material for the new ones, as can be plainly seen in the top three sections in fig. 2. This certainly seemed like an ingenious step in the direction of economy. It was interesting to note that in reducing these old nests to pulp, they used only the clean, soft cells, but did not attack the roofs; these were extremely tough, and were contaminated by the many larvæ that had grown in the cells. Moreover, if the roofs had been broken, the support of their nests would have been weakened.

I say that the combs, attached one below the other, remind me of the nests of *Vespa*. It is easy to imagine this as the beginning of a new habit of nest building in *rubiginosis*, or to conjecture that it is a revival of some ancestral habit.

*Vespa* usually adds sheets of paper to enclose the

<sup>9</sup> A close-up of the same nest is shown in fig. 3.

combs. They make all of the combs in one season, instead of building a new comb each year. However, *Vespa*



Figs. 2-5. For explanation see text.

*crabro*<sup>10</sup> builds comb below comb in hollow trees, without paper covering-sheets, and builds the combs all in one

<sup>10</sup> Buetenmuller. Trans. New York Entom. Soc. 6, plate 9, 1911.

season. The indications are that in the course of<sup>11</sup> evolution, *P. rubiginosis* is becoming, in nest-building habits, more like *Vespa crabro* than it is like any other species of *Vespa* or *Polistes*, because they build in dark and inaccessible places, and build comb beneath comb.

A nest was taken at Wickes on September 7, 1919. Two days later, I noticed that one capped cell had an incision, and further observation showed a parasite in the act of emerging. The cap was removed, and under it I found the shrivelled pupa of *P. rubiginosis* pushed up toward the capped opening, and one-third of the distance down in the cell was a second cap or partition. This proved to be the covering of a series of elongated cocoons, each containing

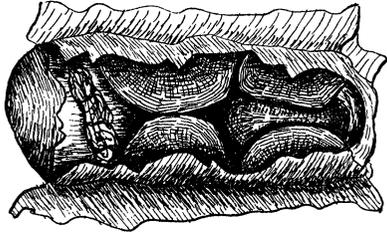


FIG. 6.

a parasite, *Christelia arvalis* Cress. [R. A. Cushman]. (fig. 6). In this particular case the host, despite parasitization, had succeeded in spinning its cap, but in four other cells in this nest infestation had occurred earlier, so the wasp larvæ had not the strength to spin their own coverings. Each parasite had spun its own cocoon; some had spun in nearly a horizontal position, others had spun in an upright position against the wall. The *Polistes* cells each contained about six cocoons of the parasite.

<sup>11</sup> When *rubiginosis* has sufficient room to build, the nests are very evenly made, and beautifully hexagonal in shape. When the conditions are crowded and space limited, the nests are made in various shapes, as shown in the collection of six in fig. 4. In fig. 3, which is another view of fig. 2, one can see more of the ill-shaped handiwork. However, if one looks closely in the center of the lowermost nest in the latter figure, one can see how the nest started out to be hexagonal, but the additions added to either side grew according to the available space.



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