ETHOLOGICAL STUDIES ON DIGGER WASPS OF THE GENUS ASTATA (HYMENOPTERA, SPHECIDAE)

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Astata is a genus of worldwide distribution containing approximately 100 species. It is sufficiently unique structurally to justify being placed in its own subfamily, the Astatinae. The one other genus of this subfamily, *Diploplectron,* is smaller and has a discontinuous distribution; it is closely related to *Astata* and perhaps more primitive, although the wing venation seems more specialized. Adult Astatinae share some structural characters in common with the Sphecinae and particularly with the Larrinae. The larvae, however, are not at all similar to those of either of those groups (Evans, 1958).

Most commonly, the Astatinae are placed first among the subfamilies of Sphecidae, implying that they are primitive. If this is so, the ethology of the group should be particularly interesting and should shed light on the ancestral type of behavior in the family. In order to characterize the ethology of the subfamily, it is necessary to know the behavior of several species in some detail and to establish their similarities. Also, it is possible that any species differences may give clues as to the evolution of behavior within the group.

Unfortunately almost nothing is known about the behavior of the North America species of *Astata,* and still less about *Diploplectron.* The Peckhams (1898) presented a short account of some aspects of the nesting behavior of three species of *Astata,* and Barth (1910) published an even briefer note on two of these same species. More recently Williams (1946) has discussed the biology of *Astata immigrans,* a species apparently introduced into Hawaii from the Western United States. Even the Eurasian species are not particularly well studied, although considerable information has accumulated regarding the widely distributed *Astata boops,* a recent paper by Tsuneki (1947) on this species being particularly valuable. Minkiewicz (1933, 1934) has also discussed the behavior of *Astata minor* at considerable length.

Almost by accident, I have recently had an opportunity to study two species of *Astata* in moderate detail. One of them, *Astata unicolor,* has nested for the past two summers in the vegetable garden at my home in Ithaca, New York. The other, *occidentalis,* happened to be nesting in some numbers in the midst of a colony of *Bembix nubilipennis* which I was studying in Versailles, Indiana. I also found *Astata leuthstromi* nesting once. After describing the behavior of these three species, I have summarized briefly what is known of other species of the genus and have attempted to come to some conclusions regarding the position of the Astatinae as suggested by ethological characters.

This study was supported by a grant from the National Science Foundation. Note numbers in the text refer to field notes and associated specimens now on permanent file at Cornell University. I would like to express my appreciation to Herbert Ruckes for identifying the hemipterous prey of *Astata,* to Curtis W. Sabrosky for identifying the dipterous parasites, and to Karl V. Krombein for checking the identity of the species of *Astata.*

OBSERVATIONS ON ASTATA UNICOLOR SAY

Astata unicolor is a relatively common species throughout much of temperate North America. In the Northeast, there is clearly only one generation a year. I have seen no specimens collected earlier than July 12 or later than September 10, and August is clearly the month of greatest abundance and most nesting activity. The species is not strongly restricted ecologically, but occurs in many types of open country: fields, meadows, gardens, waste places, and bare sandy areas. The wasps are particularly apt to be encountered on the flowers of *Daucus carota,* and have been so recorded by Krombein (1936). Mickel (1918) and Robertson (1938) record the species from many different flowers.

BEHAVIOR OF THE MALE. Males are on the wing for at least two weeks before the females appear in numbers. Aside from visiting flowers for nectar, the males often perch on flowers for considerable periods of time, flying off occasionally and returning again in a few seconds. More commonly, they perch on a slight elevation in an area of bare soil, for example, on a stone or clod of earth. Here the male may remain for several hours

during the warmest part of the day, at short intervals (from a few seconds to up to three minutes) flying swiftly, obliquely upward, then in an arc and back again to the perch. Back on the perch, he rotates his body in various directions and walks about a bit before finally coming to rest with the antennae extended rigidly. The flights vary in length from one to several meters, and are so swift that they often cannot be followed with the eye. These flights appear to be "spontaneous," that is, they are in response to no obvious stimulus. They cannot be elicited regularly by tossing pebbles over the perches, as can the precopulatory flights of certain other digger wasps. When two or more males perch in the same area, as often happens, they take up stations from .5 to 1 meter apart and show no obvious response to one another. At least I have never seen them attack one another as if defending a territory. However, Minkiewicz (1934), who observed very much this same type of behavior in *Astata minor* in Poland, found that if one male approached the perch of another too closely, the two rolled together "dans un corps-à-corps formidable."

The most curious aspect of this behavior of the male is that it occurs at some distance from the nesting area of the females (also noted by Minkiewicz in *minor*). During the summer of 1957, several males occupied their perches at the south edge of my garden from July 29 to August 17. No females were found nesting until the second week in August, and then they nested in another part of the garden, at least 8 meters away. Although I watched the males for brief periods on several different days, I never saw a female in this part of the garden. Presumably the females must enter the area patrolled by the males and be fecundated during one of their characteristic flights. Probably the females do this shortly after they first emerge. I have never observed copulation in *unicolor* and am not aware that it has been observed in *boops* or *minor*.

NESTING BEHAVIOR OF THE FEMALE. *Astata unicolor* appears to nest in almost any type of bare soil. Ferton (1901) remarks that "toutes les *Astata* de France et de Corse . . . creusent volontiers leurs terriers dans les sols sableux et durs, mais elles habitent aussi les terrains argileux. . . ." This seems to be equally true of *unicolor*. I have frequently seen both sexes in sand pits and small dunes, but have only one record of their nesting in

sandy soil. On August 14, 1954, C. S. Lin observed a female carrying a stinkbug into a nest in a sandy-gravel slope near Ithaca, New York (note no. 1346). He dug out the nest and found the burrow to be 17 cm. long, but gently curved so that the bottom was only 10 cm. beneath the surface; the upper 5 cm. were open, but the lower 12 cm. were loosely filled with earth. The stinkbug was found in the bottom of the burrow. From what is now known of the behavior of *unicolor,* it seems probable that this was a new nest and the wasp had not yet actually made a cell.

All the remainder of the observations reported here were made by myself in a very different habitat: the garden at my home two miles south of Ithaca. The soil here is a heavy clay containing much organic matter and many stones. It is difficult to dig in with a trowel, and must present infinitely greater problems to *Astata* than sand, not only because of its firmness but because it holds moisture to a much greater extent. Nevertheless, there were several individuals nesting here both in 1956 and in 1957. In all I found and eventually dug out five nests, but there were undoubtedly others which I did not discover. In 1956, all the nests were situated in a strip about .5 to 1.5 meters in size along two rows of carrots; in every case the nest entrances were beneath and well hidden by the drooping leaves of the carrots. In 1957, the nests were located in approximately the same place, but beneath the foliage of tomato plants, which happened to have been planted there that year. The Peckhams (1898) found *unicolor* nesting in their garden, and Barth (1910) remarks that the species "prefers ground to sand."

I did not observe the digging of the nest. The Peckhams report that the soil is pushed out of the burrow with the end of the abdomen and cleared away from the entrance with the hind legs. The initial burrow enters the ground at an angle of from 45 to 75 degrees with the surface and reaches a depth of from 7 to 15 cm. The diameter of the burrow is about 7 mm., slightly wider (about 9 mm.) at the entrance. The earth dug from the burrow is cleared from the entranceway only slightly, and comes to form a pile about 5 cm. wide and 7 cm. long, with the hole near one end of it. This pile of earth is never leveled by the female nor is any of it ever used for closing the burrow; only rarely is it added to. After a period of days it tends to weather away, and eventually it may disappear altogether. The Peckhams (1898)

also noted similar mounds of earth at the nest entrance. They found the burrow to be about 9 cm. long. Barth (1910) states that the burrow extends to a depth of from 8 to 14 inches (about 20 to 35 cm.), which is somewhat out of accord with the figures obtained by the Peckhams and myself.

The lower part of the burrow is kept filled loosely with soil. When the stinkbugs are brought in they are stored near the bottom of the burrow beneath this loose filling. Only after several

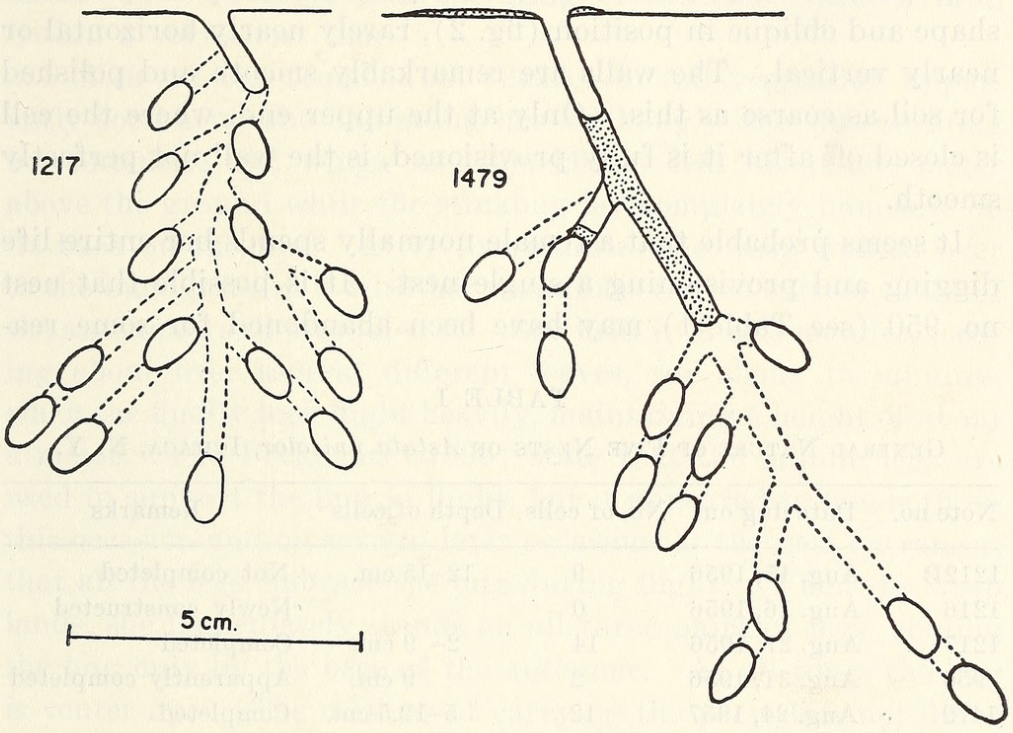


FIG. 1. Two nests of *Astata unicolor*, Ithaca, N. Y. Burrows indicated by dashed lines were filled solidly with soil and could not be traced, hence are somewhat hypothetical. Stippling in the burrows indicates a loose filling of earth.

stinkbugs have been stored in this manner is a cell constructed and provisioned. The first cell is constructed near the bottom of the burrow, provisioned from the bugs stored in the burrow, then closed off with soil. Successive cells are constructed progressively upward as the burrow is gradually shortened. Thus, in a nest containing several cells, the lower cells invariably contain cocoons or fully grown larvae, while the topmost cells contain eggs or small larvae (see Table II). The exact arrangement of the cells varies considerably from nest to nest, but in general it appears that many of them are constructed in short side-burrows (fig. 1). A single side-burrow may eventually contain two cells

in the same series, separated by a substantial barrier of earth (at least 3 mm.). In no case did I find more than two cells in a single series. The deepest cell found in any nest was 15 cm., the shallowest only 2 cm. One would expect a larva in a cell only 2 cm. deep to be subject to much higher temperatures and lower humidity than a larva in a cell 15 cm. deep, but such factors are apparently of little importance in this species.

The cells of this species measure approximately 12 mm. in length and 8 mm. in diameter. They are broadly elliptical in shape and oblique in position (fig. 2), rarely nearly horizontal or nearly vertical. The walls are remarkably smooth and polished for soil as coarse as this. Only at the upper end, where the cell is closed off after it is fully provisioned, is the wall not perfectly smooth.

It seems probable that a female normally spends her entire life digging and provisioning a single nest. It is possible that nest no. 950 (see Table I) may have been abandoned for some reason, or the female may have met an untimely death. The full complement of cells seems to be from 12 to 14 per nest. It is possible that under ideal conditions the total number is considerably higher than this.

TABLE I

GENERAL NATURE OF FIVE NESTS OF *Astata unicolor*, ITHACA, N. Y.

Note no.	Date dug out	No. of cells	Depth of cells	Remarks
1212B	Aug. 15, 1956	9	12–15 cm.	Not completed
1216	Aug. 16, 1956	0		Newly constructed
1217	Aug. 27, 1956	14	2– 9 cm.	Completed
950	Aug. 31, 1956	2	9 cm.	Apparently completed
1479	Aug. 24, 1957	12	5–12.5 cm.	Completed

HUNTING AND PROVISIONING ACTIVITIES. The prey of *Astata unicolor* consists of immature stinkbugs (Pentatomidae). Generally speaking, last instar nymphs are taken, but occasionally earlier instars are used. The Peckhams (1898) recorded *Podisus modestus* Fabr. as prey. In 1956, I found the prey to consist entirely of two species of *Euschistus, tristigmus* Say and another species which was probably *euschistoides* Voll. The two species were well mixed in all the nests studied. The one nest

dug in 1957 contained all *E. tristigmus* except for one specimen of *Podisus maculiventris* (Say). The collections of the U. S. National Museum include one specimen from Clifton, Va., pinned with a nymph of *Euschistus tristigmus*.

The females appear to hunt their prey in the tall vegetation of fields and meadows. I have not observed the actually stinging of the prey. All bugs taken from nests or from wasps entering nests were very thoroughly paralyzed if not dead. The Peckhams (1898) observe that the sting of *unicolor* "proves fatal within a very short time."

I observed one female (no. 1212A) in tall vegetation apparently soon after she had stung her stinkbug. She was cleaning her antennae and wings on a blackberry leaf about one meter above the ground while the stinkbug lay completely immobile on its back on the leaf. After five minutes the wasp walked over to the bug, grasped it with her mandibles by the extreme base of the antennae, and straddled it. She held it in this manner, moving about over several different leaves, for about 15 minutes, when she finally took flight heavily, maintaining a height of about a meter. The Peckhams (1898) state that the middle legs are used to support the bug in flight, but it appeared to me, both on this occasion and on several later occasions at the nest entrances, that all the legs embrace the bug during flight. When the wasp lands, she immediately stands on all three pairs of legs, holding the bug only by the base of the antennae. At all times the bug is venter-up. (The manner of carrying the prey does not differ from that of *occidentalis*, shown in fig. 6).

After arriving in the nesting area, the wasp lands on vegetation near the nest, then proceeds circuitously by walking and short flights to the nest entrance, which is left open at all times during provisioning. She enters the nest still straddling the bug and holding it by the antennae with her mandibles. Frequently the bug is left just inside the entrance for a moment and then drawn in from the inside. On leaving the nest the female again takes a somewhat circuitous course from the entrance before flying off. This behavior has been described and figured by the Peckhams (1898), who state that their wasps "almost invariably made a long locality study, first running about on the ground . . . and then rising and circling all around the place."

I interpreted this as analogous to the usual rather devious manner of entering the nest, perhaps serving to deceive potential parasites. Certainly this manner of entering and leaving the nest, added to the fact that the nest entrances are invariably located beneath overhanging vegetation, makes the nests exceedingly difficult for a human observer to find.

The bugs brought in are not taken directly to a cell, but are left in the bottom of the burrow, usually venter-up. Only after a certain number of bugs accumulate (often, probably, after the completion of a day's hunting) is a new cell prepared and the bugs placed in it in a very specific manner. Tsuneki (1947) found this to be true in *boops*, and he believes the wasps may

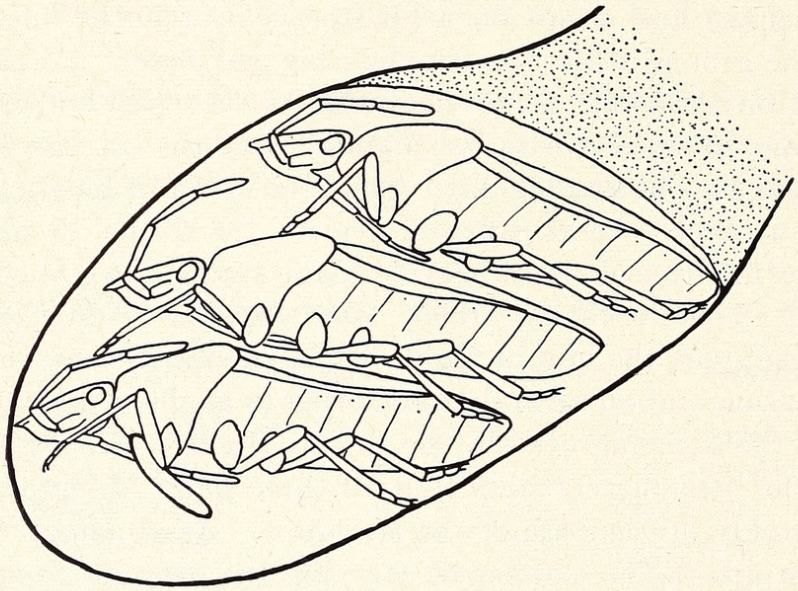


FIG. 2. A cell of *Astata unicolor* provisioned with stinkbugs and closed off. The egg is attached to the prosternum of the bottom bug.

prepare and provision several cells at a time in this manner. This unusual manner of provisioning has confused many earlier workers and led to a number of erroneous statements. Both the Peckhams (1898) and Barth (1910) are incorrect on details of cell structure and egg position, and Ferton (1901) is led to the paradoxical statement that the egg of *Astata* is laid on the bottom bug in the cell but not until after the cell is fully provisioned!

Actually, the egg is laid on the first bug placed in the cell from the supply in the burrow. This bug is placed in the bottom of the cell, venter-down, more or less horizontally, in such a way that there is a small open space beneath it formed by the smooth, oval contours of the cell (fig. 2). The egg is attached

to the prosternum and extends backward along the midline of the body with its posterior end free from the body. It is about 2 mm. long. The remaining stinkbugs are placed on top of the first one, also venter-down, and the cell is closed off from above, the closure being made directly on the dorsum of the top bug. The number of bugs per cell varies from 2 to 4, with an average of 2.8. The bugs fit the cell very tightly, the only appreciable free space being beneath the bottom bug surrounding the egg and later the small larva.

As already mentioned, the entrance to the burrow is never closed during provisioning. During periods of inactivity, that is, from late afternoon until morning and during inclement weather, a closure of the burrow is ordinarily visible not at the entrance, but at a distance from one to two centimeters inside the entrance.

DEVELOPMENT. The egg hatches in about three days. The larva remains attached for about two days at the point of attach-

TABLE II

CONTENT OF NEST 1212B, ITHACA, N. Y., AUG. 15, 1956

Cell no.	Depth	No. of bugs	State of wasp progeny	Development
1	15 cm.	Pasty mass (3?)	Larva 12 mm. long	Accidentally killed
2	14 cm.	Pasty mass (3?)	Larva 10 mm. long	Full grown August 16
3	14 cm.	3	Larva 5 mm. long	Full grown August 20
4	13.5 cm.	2	Larva 3 mm. long	Full grown August 22
5	13 cm.	2	Larva 2.5 mm. long	Full grown August 24
6	12.5 cm.	2	Larva 2.5 mm. long	Full grown August 24
7	12.5 cm.	3	Egg	Hatched Aug. 16; Full grown Aug. 25
8	12 cm.	2	Egg	Hatched Aug. 18; Full grown Aug. 26
9	12 cm.	4 (small)	Egg	Hatched Aug. 18; Full grown Aug. 26

ment of the egg, feeding through the front coxal membrane or in the neck region. Then it loses its attachment, but remains in

an inverted position, hollowing out the first bug from the ventral side and then the other bugs in turn. The larva possesses a strong mid-dorsal lobe on the fourth abdominal segment, and this lobe apparently serves as a pseudopod and assists the larva in moving about in the cell. As the larva approaches maturity, the bugs become reduced to a pasty mass. About eight days are required for the larva to reach maturity (see Table II).

In spinning its cocoon, the larva apparently merely lines the smooth walls of the cell with silk. The resulting cocoon is unusually frail, and seems particularly so at the upper end, where the cell walls are somewhat more irregular. A certain amount of earth tends to adhere to the outside of the cocoon, but none is incorporated into the cocoon itself. Having spun the cocoon, the larva enters diapause and remains in diapause throughout the winter months.

NATURAL ENEMIES. The Peckhams (1898) observed a cuckoo wasp of the genus *Chrysis* lurking about a nest of *unicolor* and even entering it, but they did not determine whether or not it was actually parasitizing the wasp. They also found "a parasitic larva" in the cells of one nest. None of the nests which I studied appeared to be parasitized, and I saw no cuckoo wasps or miltogrammine flies around the nest entrances.

OBSERVATIONS ON ASTATA OCCIDENTALIS CRESSON

This species also occurs from coast to coast in North America, but its center of distribution appears to be somewhat more southerly than that of *unicolor*. Nothing has previously been recorded on its biology except for a prey record by Townes (1951) and a brief note by Ashmead (1894). Townes records the stink-bug *Peribalus limbolarius* Stål as prey. His record is based on a series of 33 adult bugs of that species in the U. S. National Museum, taken as prey of *occidentalis* at the "So. End of Long Bridge, Va.," July 18, 1920, by J. C. Bridwell. In the National Museum there is also an adult *Thyanta custator* Fabr. taken as prey of this species in Los Angeles Co., Calif., Oct. 15, 1893, by D. W. Coquillett. This is apparently the specimen referred to by Ashmead (1894); Ashmead calls the wasp *Astata nubecula*, but the specimen in the National Museum is clearly *occidentalis*. According to Ashmead, Coquillett found this wasp storing bugs "in a burrow formed in a limestone formation."

I found a considerable aggregation of nests of this species at Versailles, Indiana, July 17–23, 1957, and was able to work out many of the details of the nesting behavior. No males were observed during this period, and it is possible that they had completed their period of activity and disappeared. The nesting of the females seemed well advanced. The nesting site was a baseball diamond one mile east of the town of Versailles. The soil here was a hard-packed clay, throughout the nesting area completely devoid of vegetation of any kind. *Bembix nubilipennis*

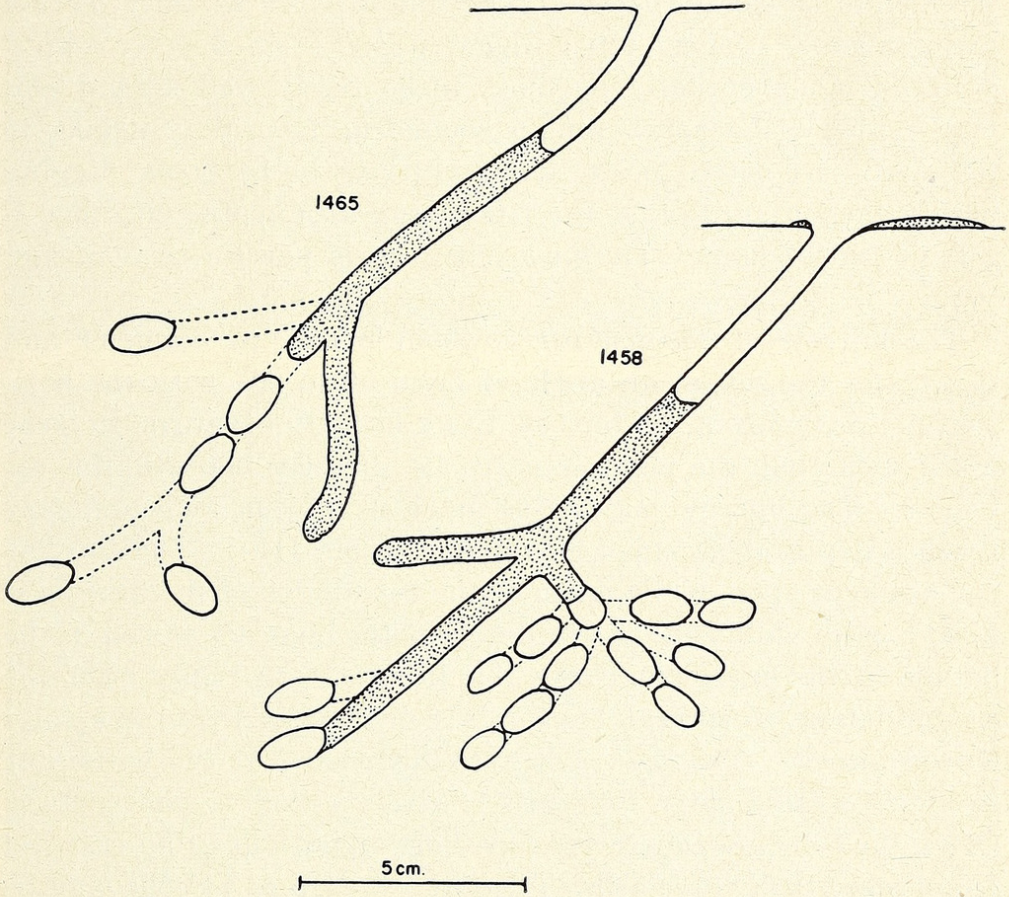


FIG. 3. Two nests of *Astata occidentalis*, Versailles, Ind. Burrows indicated by dashed lines were filled solidly with soil and could not be traced, hence are somewhat hypothetical. Stippling indicates a loose filling of earth.

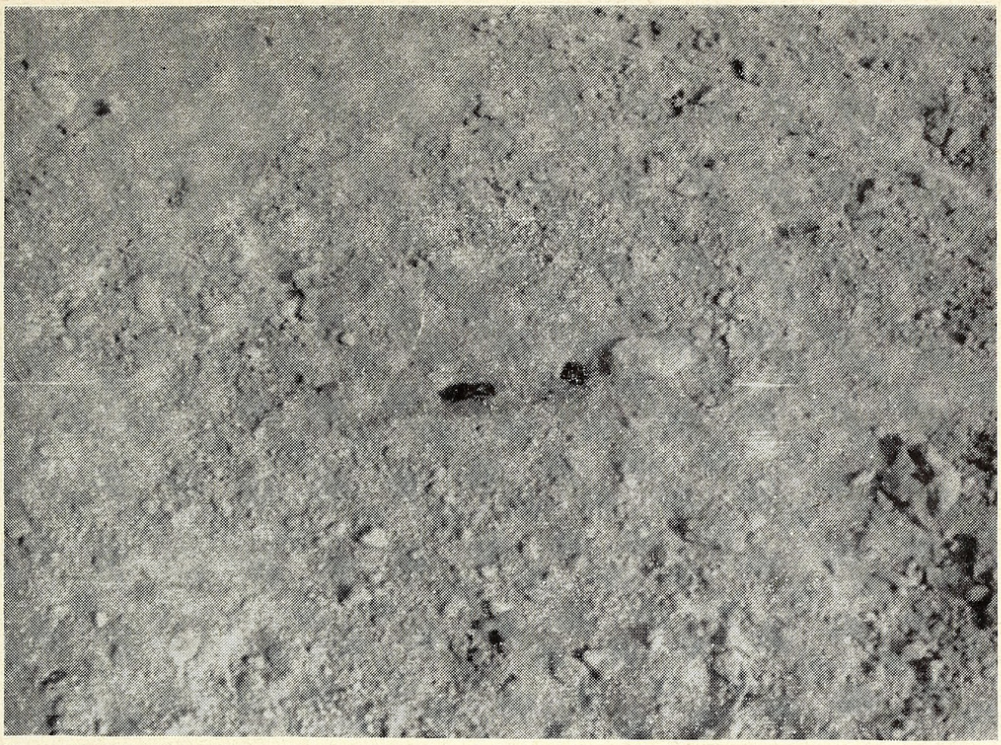
and *Cerceris fumipennis* also nested in considerable numbers in this very hard soil. In all, I marked and eventually dug out eight nests of *Astata occidentalis*, but the actual number of nesting females was probably at least twice this. All the nests were located in an area about five meters square, with no two nests closer together than about half a meter. Each nest entrance was

surrounded by a rim of soil and was very conspicuous on the bare, smooth surface of the baseball diamond.

NESTING BEHAVIOR. The wasps break the soil with their mandibles and produce a weak buzzing sound as they do so. The soil is scraped back with the fore legs, rather slowly, while the body is held rather low, the middle hind legs spread widely. The soil is permitted to plug the entrance to the burrow, and the wasp then comes out and clears it away. As she backs away from the entrance scraping soil, she produces a small trough in the mound of earth (fig. 4). The soil is never actually leveled in the manner of some other digger wasps (e.g., *Bembix nubilipennis*), but eventually it comes to be fairly well spread out, with evidence of several troughs emanating from the entrance to the nest. In active nests, there appears to be fresh digging nearly every day, so that the rim of soil around the entrance is always conspicuous. The nest entrance is never closed at any time.

The burrow of *occidentalis* is about 8 mm. in diameter and penetrates the soil at an angle of from 50 to 80° with the horizontal. Very often the burrow has a lateral curvature, in some cases such that the cells actually lie directly beneath the entrance. The burrow may be as much as 18 cm. long and may reach a depth of as much as 12 cm. (Table III). The top 2–5 cm. are kept open, while much of the remainder of the burrow is filled loosely with soil. As in *unicolor*, the bugs are stored in the bottom of the burrow, beneath this loose soil, and only after the accumulation of several bugs is a cell prepared and the bugs moved into it. The first cells are constructed at the bottom of the burrow, and later cells progressively closer to the surface. Often the cells are constructed in short series, but in no case did I find more than three cells in one series. Up to 14 cells may be constructed per nest (probably more under some conditions) (Table III; figs. 3, 5).

The cells of this species are broadly elliptical and usually oblique, occasionally nearly horizontal or nearly vertical. They are smooth-walled and measure, on the average, about 8×15 mm. The closure of the cell is made directly on the back of the top stinkbug. When cells are in series, the closure between them may consist of no more than a very thin barrier of soil (1–3 mm.).



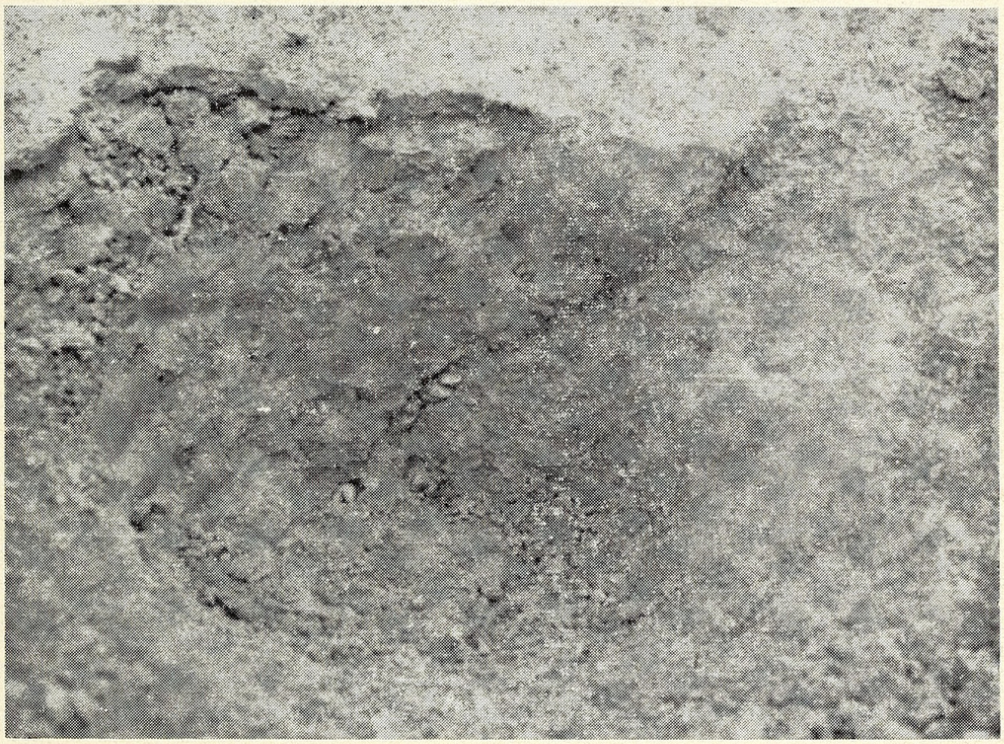


Fig. 4. (Above) *Astata occidentalis* digging at the nest entrance. Note the trough extending from the open entrance.

Fig. 5. (Below) A nest of *A. occidentalis* showing four cells. This is nest no. 1465, shown also, after further excavation, in figure 3. The cell on the lower left contains a full-grown larva; the two upper cells contain stink bugs and small larvae; the cell on the lower right contains the remains of several bugs which have been consumed by maggots of *Senotainia*.

All of the 58 cells dug out were within the narrow range of 6–12 cm. in depth; in individual nests the cells were often grouped very close together (in nest 1466, 14 cells between 8 and 11.5 cm. deep). The exact arrangement of the cells showed much

TABLE III

NATURE OF EIGHT NESTS OF *Astata occidentalis*, VERSAILLES, IND.

Note no.	Date dug out	No. of cells	Depth of cells	Remarks
992	July 18, 1957	2	6–7 cm.	Relatively new nest
1452	July 20, 1957	11	8–11 cm.	Wasp still active
1458	July 21, 1957	12	8–10 cm.	Wasp still active
1459	July 22, 1957	5	8–10.5 cm.	Wasp still active
1462	July 22, 1957	6	7–9 cm.	Wasp still active
1463	July 22, 1957	3	7–10 cm.	Apparently an inactive nest
1465	July 23, 1957	5	8–12 cm.	Wasp still active
1466	July 23, 1957	14	8–11.5 cm.	Wasp still active

variation from nest to nest; apparently cells are constructed both in the main burrow, in short side-burrows, and in major branches of the burrow (fig. 3).

HUNTING AND PROVISIONING ACTIVITIES. The wasps in this nesting aggregation preyed exclusively on adult Pentatomidae. The 122 bugs taken from cells or from wasps represented 6 species in the following numbers:

Hymenarcys nervosa (Say)	57
Thyanta calceata (Say)	27
Thyanta pallidovirens accerra (McAtee)	19
Euschistus variolarius (Beauv.)	14
Peribalus limbolarius Stål	4
Banasa calva (Say)	1

Individual wasps seemed to prey on one or a very few species of bugs. For example, of the 52 bugs taken from the 12 cells of nest no. 1458, 51 were *Hymenarcys nervosa* and 1 was *Thyanta calceata*. The 13 identifiable bugs taken from nest no. 1466 were all *Euschistus variolarius*. But 13 bugs taken from nest no. 1462 represented four species! Apparently individual wasps tend to

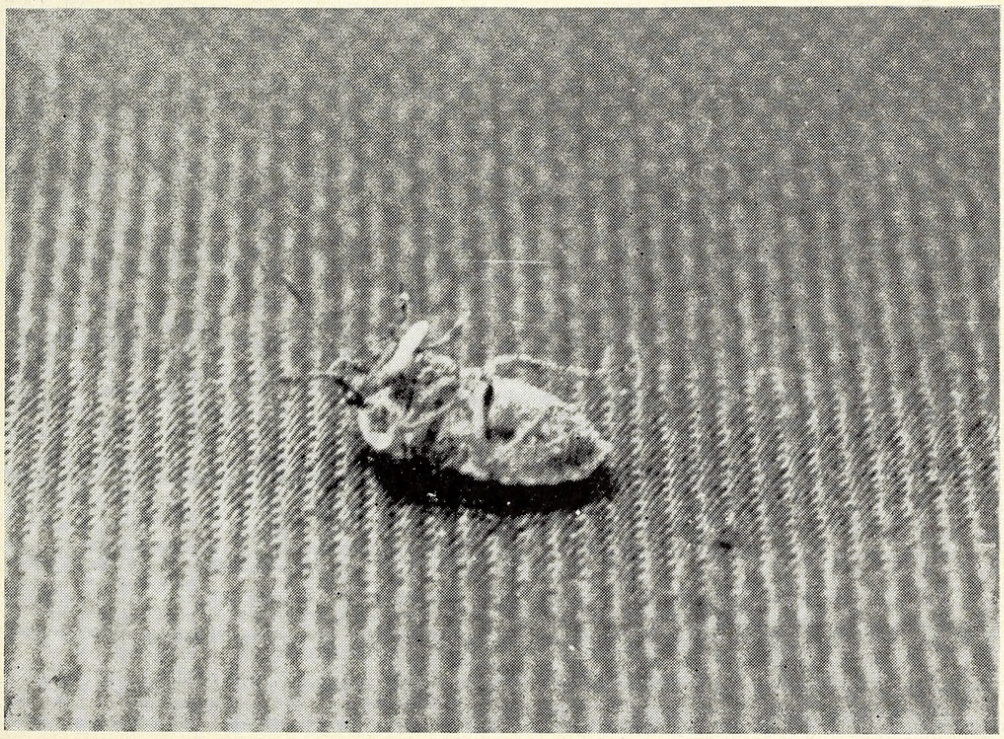


Fig. 6. (Above) *A. occidentalis* female carrying a stinkbug toward the nest entrance. Note that the bug is held venter-up by the base of the antennae.

Fig. 7. (Below) The egg of *A. occidentalis* on a stinkbug which has been removed from a cell. In normal position, the bug is venter-down and the egg extends downward as shown in figure 2.

return to the same place each time for their bugs, but the species may be characterized as able to utilize virtually any species of adult stinkbug of medium size.

The number of bugs per cell varies from 3 to 6, with an average of 3.8. The bugs are placed in the cell head-in, venter-down, exactly as in *unicolor*. The egg is about 2 mm. long and is attached to the first bug placed in the cell in the same manner as in *unicolor* (fig. 7). The larva is very similar to that of *unicolor* and feeds in the same manner.

Females enter the nesting area from various directions and usually at a considerable height (roughly 2 meters). Characteristically, they land on the ground a short distance from the entrance of their burrow. They carry the stinkbug beneath their body venter-up, holding the base of the antennae (or apparently sometimes the base of the beak) with their mandibles. In flight, the bug is also embraced with all three pairs of legs, but upon landing the wasp stands upon all the legs and holds the bug only with her mandibles (fig. 6). When a wasp lands with her bug, she produces a fairly loud "plop," apparently a result of the back of the stinkbug hitting the hard ground. The wasp proceeds to the open nest entrance by a somewhat devious path and may not actually enter the nest for several minutes after arriving in the area. Eventually she enters the nest straddling the bug in the usual manner, leaves the bug just inside the entrance, then a moment later pulls it in from the inside. When the wasp reappears (after a period of several minutes, often as long as 30 minutes) she usually again walks in a circuitous path before taking flight. Provisioning proceeds at a very slow pace. Wasp no. 1457B brought in her first bug on July 21 at 1000, her second bug at 1108; by noon she had not yet brought in a third. The condition of the bugs stung by *occidentalis* seems to vary considerably. Most bugs seemed thoroughly paralyzed if not dead, and some taken from relatively new cells were actually stiff. On the other hand, it was not uncommon to find a bug, even in a cell which had been provisioning 2–3 days earlier, which still exhibited movements of the legs and antennae. Development of the egg and larva and spinning of the cocoon are so similar to *unicolor* that they need not be described separately.

In the morning, many wasps could always be seen digging at

the entrances of their nests, presumably clearing away some of the soil which accumulates in the course of digging new cells. After a period of digging, each wasp would move away from the nest entrance by a devious path before finally flying off to hunt a stinkbug. For example, no. 1457A dug at her nest from 0835 until 0910 on July 21. Then she walked and flew around the nest in approximately the pattern shown in figure 8, finally flying

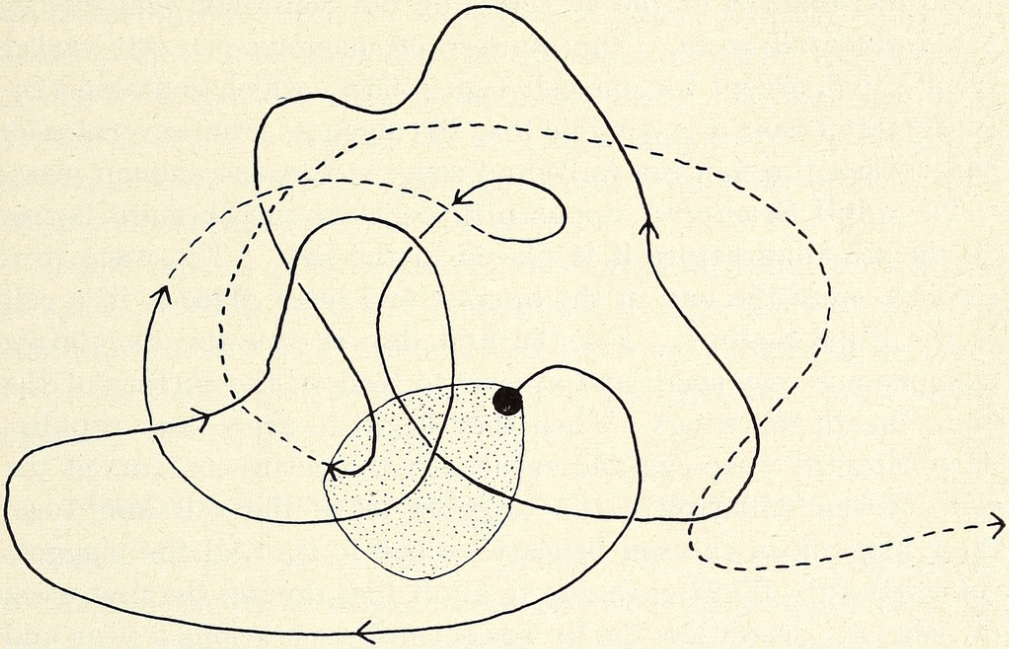


FIG. 8. Movements of wasp no. 1457A away from the nest entrance. Walking is indicated by a solid line, flying by a dashed line. The mound of earth at the nest entrance is stippled.

off at 0913. Later in the day, wasps leaving their nests behave similarly, but take fewer loops and turns and less time in the process. Doubtless this behavior is primarily concerned with orientation, but since the wasp also behaves similarly when entering the nest with its prey, it seems possible that it also functions to deter parasitism.

NATURAL ENEMIES. This colony of *Astata occidentalis* was very heavily parasitized by the fly *Senotainia trilineata* Wulp (Sarcophagidae, Miltogramminae). On many occasions wasps approaching their nests with prey were seen to be trailed by these flies, which would hover a few centimeters behind the wasp and await an opportunity to larviposit on the bug. Some wasps trailed by flies would leave the area and re-enter, or fly about

from one part of the nesting area to another, in an apparent effort to shake off the pursuers. On one occasion I watched an *Astata* fly about for over ten minutes in an unsuccessful effort to escape a *Senotainia;* finally the wasp left the bug on the earth and flew off. Several times I found stinkbugs lying on the ground, apparently abandoned by wasps which had not been able to reach their nests safely.

No less than 26 of the 58 cells dug out contained maggots of *Senotainia trilineata.* The number of maggots per cell varied from 1 to 6, except for one cell (no. 1466A) which contained 24. In the latter case it is possible that the maggots from several cells had broken through the walls and come to form a common mass.

The adult *Senotainia* apparently deposits one or more larvae on the stinkbug before it is placed in the nest. The wasp proceeds to store the bug in the burrow and later place it in a cell in the usual manner. For the first day or two the *Senotainia* maggots are very small and appear to feed on the surface of the bug beneath the wings. Then they begin to grow very rapidly, devouring the wasp egg and eventually the entire contents of the cell. When full-grown, the maggots leave the cell and form their puparia in the soil beneath or beside it. All the maggots collected July 17–23 gave rise to adult flies during the first week of August. Doubtless the fly has several generations a year and attacks several different digger wasps.

OBSERVATIONS ON ASTATA LEUTHSTROMI ASHMEAD

This is a small and relatively uncommon species. I have found it nesting in the garden at my home near Ithaca, but in smaller numbers than *unicolor.* On August 7, 1956, a female was seen raking earth over the entrance to a nest located beneath a dead weed which was lying on the ground (no. 1213). She scraped earth from several directions over the entrance, but left before the nest was fully concealed. Believing this to be a temporary closure, I marked the nest and observed it intermittently over the next week. However, the wasp was not seen again, and when the nest was dug out on August 14 the burrow could not be traced. Two cells in close proximity were discovered only 4 cm. beneath the surface. Each cell contained several pentatomid nymphs, but the cell contents were completely molded.

While digging this nest, I accidentally uncovered another nest only 10 cm. away. This one contained two (or perhaps three) cells, also in a close group about 4 cm. deep. Unfortunately the cells were destroyed before I could observe their structure. In all they contained 13 nymphs of the small pentatomid *Cosmopepla bimaculata* Thom. One small wasp larva was found, but it failed to grow in a rearing tin. While I was digging, the adult *Astata* returned with another stinkbug nymph, again the same species. She landed on the ground and began walking and flying from place to place around her nest. The bug was held venter-up by the base of the antennae, exactly as in *unicolor,* and apparently supported in flight by all three pairs of legs. The wasp was captured for identification.

The Peckhams (1898) observed a single individual of this species, also in their garden. They noted that there was a heap of earth around the entrance and that the wasp closed the entrance from the inside for the night. They were not successful in excavating the nest.

ETHOLOGY OF OTHER NORTH AMERICAN SPECIES OF ASTATA

Astata bicolor Say. The Peckhams (1898) found this species nesting in the hard soil of their garden. They noted that the nests are usually located beneath overhanging vegetation and have a small mound of earth at the entrance as in *unicolor.* The wasps enter and leave the nest in the usual circuitous manner and leave the entrance open during provisioning. The one nest they dug out was very shallow, a burrow about 6 cm. long leading to a group of cells only about 4 cm. beneath the surface. The Peckhams observed malaxation and stinging of the prey in a jar and found that most of the bugs were killed by the sting. Although they speak of *bicolor* as preferring a certain species of bug, they do not state the species, or even the family, of the bug; at one point they mention a wasp carrying a "small homopterous insect." Mickel (1918) took a specimen at Lincoln, Nebr., which "had attacked a nymph of *Pentatomidae* sp. and was dragging it away." Mickel also presents several flower records.

Astata nubecula Cresson. Ashmead's (1894) note on this species should properly be referred to *occidentalis,* as indicated under that species. In the U. S. National Museum there is a

specimen of *nubecula* from Salt Lake, Utah, pinned with an immature stinkbug identified by H. G. Barber simply as "Gen. & sp.?".

Astata immigrans Williams. Williams (1946) found that this species, described from Hawaii but apparently native to western United States, preys upon immature lygaeid bugs of the genus *Nysius*. Williams was able to observe mating, stinging and malaxation of the prey, and nesting activities all in large glass jars. Digging, he reports, is done with the mandibles, and the earth thrown out with the front legs. The bugs are carried in the same manner as I have described for *unicolor* and *occidentalis*. The nest is always left open and is "a short affair of more than one cell." The egg is "glued obliquely to the bug's breast." Williams also describes the behavior of the male, who "stations himself upon some stem or other convenient object" and "pivots about alertly or pursues some passing insect, to return to or near his station again. He appears to mate frequently and is often carried about by the female."

ETHOLOGY OF EURASIAN SPECIES OF ASTATA

Astata boops (Schrank). There are many published notes on this widely distributed species, and I shall not attempt to review all of them. Apparently Shuckard (1837) was the first to publish on its behavior, and later Fabre (1856), Ferton (1901), Adlerz (1903), and several others contributed additional observations from western Europe. Piel (1936) made some fairly detailed studies on the species in China, and Tsuneki (1947) in Korea. Tsuneki's paper is in Japanese, but his tables and his English summary provide the best single source of information on the behavior of this species.

The behavior of the male is in general similar to that of *unicolor*; Shuckard noted long ago that the male flies very rapidly and "settles upon small clods, whence it momentarily makes wide circumvolations." The females dig their burrows in various situations but chiefly in hard soil; in eastern Asia burrows are often constructed in the clay plaster of the walls of stone buildings. As many as 12 cells may be built in a single nest. These are constructed in various branches, many of them in series of up to three cells, the cells separated by thin partitions of earth.

The cells are broadly elliptical, oblique or almost vertical, and the walls are very smooth. From 2 to 15 (usually 3 to 6) bugs are placed in a cell, and the egg is laid in the same manner as in *unicolor* and *occidentalis*. To the best of my knowledge, all of the numerous bugs recorded as prey of this species are immature Pentatomidae and Cydnidae.

The bug is usually killed by the sting of the wasp. It is carried to the nest in flight, the wasp grasping it by the antennae with its mandibles and supporting it with the middle legs (Tsuneki) or with all three pairs of legs (Piel). At the nest entrance the wasp deposits the bug while she clears the entrance, enters, comes out, grasps the bug by the antennae, and drags it in backwards. The bugs are stored temporarily in various places in the burrow surrounded by loose sand; Tsuneki found as many as nine bugs in one burrow, and believes the wasp normally makes and provisions several cells at a time from the bugs stored in the burrow.

Astata minor Kohl. This species has been studied briefly by Ferton (1901) in Corsica and at considerable length by Minkiewicz (1933, 1934) in Poland. I have already mentioned, under *unicolor*, Minkiewicz' studies on the males. The females nest chiefly in bare, hard soil, often digging their nests in small depressions. The soil is cleared away from the entrance so that no mound of earth accumulates there. The nest is shallow and contains at least two cells; the cells vary considerably in depth. The prey consists of immature bugs of several genera, chiefly Pentatomidae but including a few Cydnidae and Lygaeidae. The bugs are stored in the cells in much the manner of the species already described; the usual number is about five per cell. According to Minkiewicz, the entrance is invariably closed from the outside when the wasp leaves the nest. When the wasp arrives with a bug, she drops it at the entrance, opens the nest, enters, and draws the bug into the nest. The manner of prey carriage and oviposition are said to be the same as in *boops*.

Astata picea Costa. This species is recorded as preying upon immature bugs of the family Pentatomidae and, less commonly, Coreidae. Ferton (1901) observed stinging and malaxation of the prey. Apparently the behavior resembles that of *boops* in most details.

Astata costai Piccioli. According to Ferton (1901), this species

also attacks pentatomid nymphs, but lays its egg with its long axis perpendicular to that of the body of the prey.

Astata rufipes Mocsary. Ferton (1901, 1908) and Berland (1925) record as prey several genera of immature bugs, all Cydnidae.

Astata tricolor Van der Linden. Ferton (1901, 1908) records two genera of immature Lygaeidae as prey of this species.

Astata stigma Panzer. Verhoeff (1951) cites two prey records for this species, one a pentatomid and the other a scutellerid. Earlier prey records for this species cannot be trusted, since several species have been confused under the same name.

Astata pinguis (Dahlbom). Verhoeff (1951) lists three prey records for this species, all Lygaeidae.

Astata freygessneri Carl. Verhoeff (1951) cites two prey records, both Pentatomidae.

ETHOLOGY OF THE SPECIES OF DIPLOPLECTRON

These very small wasps are poorly known both taxonomically and ethologically. The genus is known to occur only in North America and in South Africa. Judging from the few published observations, these insects seem to occur mostly in sandy areas, the female digging her nest in open sand. Rohwer (1909) described several species from Colorado which were taken "flying over dry sand." Krombein (1939) found *D. peglowi* "on sandy knolls sparsely covered with grass." He states that "the species evidently constructs its burrows in the sand since three females were taken while burrowing." Williams (1946) found an unidentified species nesting in the sand at San Francisco, California. This species was found to prey on immature Lygaeidae and store several bugs per cell, laying the egg "on the breast of one of these bugs." The prey is grasped by the antennae and carried to the nest in flight. Williams found another unidentified species preying upon adult and immature Lygaeidae.

From these very limited observations, it seems probable that the species of *Diploplectron* resemble *Astata* in many details of behavior. They do, however, exploit a different type of soil for nesting purposes, for the species of *Astata* only rarely nest in open sand.

DISCUSSION

The preceding survey of ethological data on the Astatinae is not exhaustive (except, I believe, for the North American species) but it will suffice for a few general remarks on the behavioral characteristics of the group. In general, the species which have been studied appear to be remarkably similar in their behavior. Only three species, *Astata unicolor, occidentalis,* and *boops,* have been studied in sufficient detail to permit any real comparison (Table IV), and I find it difficult to attach any particular significance to the rather minor differences between these species. The practice of building the nest beneath overhanging vegetation, observed in *unicolor,* may well be an adaptation for escaping the attacks of certain natural enemies such as miltogrammine flies. The building of cells in series is an efficient way of exploiting very hard soil, since it involves less digging than if each cell occupied a separate branch of the nest. Both *occidentalis* and *boops* nest in extremely hard soil, while *unicolor* nests in the clay-loam of gardens; the latter species appears to have less tendency to build cells in series.

A. occidentalis differs not only from *boops* and *unicolor* but from virtually all species of *Astata* in preying exclusively on adult Hemiptera rather than immatures. It is interesting to note that while Pentatomidae form the major prey of *Astata,* a number of species employ Cydnidae, Scutelleridae, Coreidae, or Lygaeidae, either instead of or along with Pentatomidae. Several of the species which use Lygaeidae show structural convergence toward the genus *Diploplectron,* which also preys on Lygaeidae. This includes *immigrans, tricolor,* and *pinguis,* all of which belong to the subgenus *Dryudella.* This subgenus approaches *Diploplectron* in such characters as the small size, delicate habitus, and very short marginal cell.

The close similarity of the species which have been studied makes it feasible to generalize regarding the behavior of the group as a whole and to enquire as to the relationships of the group as suggested by ethology. This is best done by considering some of the more outstanding characters of the group one by one. Useful in interpreting the significance of these characters are the papers of Nielsen (1936), Iwata (1942), and Leclercq (1954).

TABLE IV

COMPARISON OF SOME ASPECTS OF NESTING BEHAVIOR OF THREE SPECIES OF *Astata*

Species	Location of nest	No. cells per nest	Arrangement of cells	Manner of entering nest	Type of prey
unicolor	Beneath overhanging vegetation	Up to 14	Individually or two in series, separated by thick barriers of earth.	No closure during provisioning; female enters with prey, leaves prey well inside entrance and draws further in from inside.	Immature Pentatomidae
occidentalis	Bare places devoid of vegetation	Up to 14	Often in series of up to 3 cells, separated by very thin barriers of earth.	As above	Adult Pentatomidae
boops	Bare places devoid of vegetation	Up to 12	As above	Nest closed during provisioning; female drops prey outside entrance, clears entrance, then pulls in prey.	Immature Pentatomidae and Cydnidae

(1). The nest is many-celled and relatively complex, the cells smooth-walled and often in short series separated by barriers of earth. This is a highly specialized type of nest and not strongly reminiscent of that of any other digger wasp.

(2). The prey is allowed to accumulate in the burrow, more or less covered with soil, and only later is a cell prepared and the prey moved into it. This practice is common in the Philanthinae, but uncommon in other groups of Sphecidae.

(3). The prey is placed in deep paralysis by the sting of the wasp. This characteristic is shared with many of the more specialized Sphecidae.

(4). The prey consists of Hemiptera, suborder Heteroptera, with Pentatomidae the family most commonly used. Few other wasps use Pentatomidae, but they form the major prey of *Bicyrtes* (Nyssoninae) and *Paranysson* (Larrinae). Many Nyssoninae employ Homoptera and several genera of Larrinae employ Heteroptera.

(5). The bugs are placed tightly in the cell, venter-down, with the egg beneath the bottom bug; the larva feeds in an inverted position. I am not familiar with any other digger wasps exhibiting this behavior.

(6). The egg is attached to the prosternum of the prey and extends backward along the midline of the body. This type of oviposition is termed by Iwata a modified "Sphex-type"; it is similar but not identical to the common type in the Sphecinae and Larrinae.

(7). The prey is grasped in the mandibles and carried to the nest in flight. This is a relatively unspecialized method of prey transport, and occurs in several groups, including the Larrinae and Sphecinae, where, however, the prey is usually held dorsum-up rather than venter-up.

On the whole there seems little justification for regarding the Astatinae a particularly primitive group. Certainly there are genera in the Sphecinae and the Larrinae in which the behavior is much less advanced in every respect. Yet it can hardly be denied that the Astatinae bear some relationship to these two groups. This is borne out by adult structure and by behavioral characters 6 and 7 above. Yet I do not feel the relationship is a close one. Probably the Astatinae split off long ago from a

primitive sphecine stock and evolved independently of other groups of Sphecidae. Their predilection for Hemiptera, their manner of carrying the prey venter-up in flight and storing it in the burrow before placing it in a cell, and their complex, many-celled nests all suggest that the Astatinae may actually have split off (rather early) from that stock which gave rise to the two related subfamilies Nyssoninae and Philanthinae. This is supported by larval morphology. Obviously, a linear arrangement of the subfamilies which is also phylogenetic is impossible. Because the Astatinae appear first in catalogs, one should not necessarily look to them for indications of primitive behavior. If one does, he will be most disappointed, for the Astatinae are in many ways highly advanced. In some aspects of their nesting behavior, and also in the male behavior, they are in fact unique.

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