A REVIEW OF NESTING BEHAVIOR OF DIGGER WASPS OF THE GENUS *APHILANTHOPS*, WITH SPECIAL ATTENTION TO THE MECHANICS OF PREY CARRIAGE

by

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(With 5 Figs)
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The digger wasp genus *Aphilanthops* (Hymenoptera, Sphecidae, Philanthinae) includes about 15 species which collectively range throughout temperate North America. There are three subgenera: *Aphilanthops*, with one eastern and several western species; *Clypeadon*, with the several species occurring chiefly in semiarid or arid regions of the Southwest and Mexico; and the recently described *Listropygia*, with a single species from southern California. It has been known for some time that at least one member of the subgenus *Aphilanthops* preys upon queen ants of the genus *Formica* and that at least two members of the subgenus *Clypeadon* prey upon worker ants of the genus *Pogonomyrmex*. The papers of WHEELER (1913) and HICKS (1927, 1933) contain considerable information on nesting behavior but leave a number of questions unanswered or incorrectly answered. For example, WHEELER believed that *A. (A.) frigidus* provisions its cells progressively and HICKS believed that *A. (Clypeadon) laticinctus* carries its prey on its sting. Present evidence indicates that neither of these statements is strictly correct and that the manner of prey carriage is, in fact, even more unusual than HICKS believed.

In the pages which follow I have reviewed what is known about the nesting behavior of two species of the subgenus *Aphilanthops*, six species of subgenus *Clypeadon*, and the one known species of *Listropygia*. The discussions of individual species are based partly on my own observations, partly on data associated with museum specimens, and partly on published information. In two concluding sections I have presented a brief review of the ethology of the genus and a discussion of the unique method of prey carriage employed by the species of *Clypeadon*.

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Some of the observations reported for *A. frigidus* were made by CHENG SHAN LIN and by MARY ALICE EVANS. The observations on *A. (Clypeaddon) haigi* were made while I spent a very profitable six weeks at the Southwestern Research Station of the American Museum of Natural History, MONT A. CAZIER, director. The ants of the genus *Formica* were determined by M. R. SMITH, those of the genus *Pogonomyrmex* by A. C. COLE. R. M. BOHART, the current authority on the systematics of *Aphilanthops,* identified the wasps. The parasitic flies were determined by C. W. SABROSKY and W. L. DOWNES. I wish to express my thanks to all of these persons.

APHILANTHOPS (APHILANTHOPS) FRIGIDUS (SMITH)

The range of this species includes most of temperate North America east of the Rockies. It is characteristic of restricted areas of bare sand or gravel, and the wasps apparently do not range far from their nesting sites. The species has been studied by the PECKHAMS (1905) in Wisconsin, by WHEELER (1913) in Massachusetts, and briefly by RISTICH (1956) in Maine. The present report is based on 31 field notes made at three sites in Tompkins Co., N. Y., and one site in Oswego Co., N. Y., during the summers of 1954 and 1955. Although these observations largely confirm those of earlier workers, they do provide more detail on nest structure and indicate that WHEELER's impressions of provisioning were partially incorrect.

In the northeastern states, *frigidus* has but one generation a year. In central New York, adults appear suddenly during the last few days of June and the females are active for about six weeks thereafter, disappearing in mid-August almost as suddenly as they appeared. As noted by both the PECKHAMS and by WHEELER, the females nest gregariously, though I have only occasionally observed colonies as large and concentrated as those described by those authors. More commonly, the nest entrances are separated by at least several centimeters, and the nests may be interspersed with those of other digger wasps such as species of *Philanthus, Crabro,* and *Oxybelus.* Nests are usually constructed in slightly sloping soil, as noted by WHEELER.

In starting a nest, the female bites into the soil with her mandibles, twisting the body in corkscrew fashion so as to make a circular bore. After making a small hole, the female often faces out while biting at the walls of the burrow, then turns about and kicks the soil from the entranceway. The sand particles and small pebbles are kicked a considerable distance, falling up to 20 cm. away, sometimes twice that far. At no time does any real mound of earth form at the entrance. Digging females can often be

heard before they are seen, especially if there are dried leaves about, because of the pattering of earth on the soil. At any time during digging, the female may come out of the burrow head first, then turn about and enter head first kicking soil. Apparently at least a full day is required to complete a nest. The PECKHAMS believed that a single nest serves the female for the entire season. This is a possibility, although we have sometimes seen females digging late in the nesting season.

There are many records of this wasp preying exclusively upon winged queen ants of the genus *Formica*. In central New York, *F. fusca* L. is used as prey very commonly, *F. pallide-fulva nitidiventris* Emery somewhat less commonly. WHEELER records these two species and also *F. neogagates* Emery. He also presents records for *fusca* from Ontario and Michigan, and RISTICH found *fusca* to be used in Maine. WHEELER notes that these ants are all of "cowardly disposition" and that *Aphilanthops* has apparently "learned to discriminate between different species of *Formica* and to avoid the more vigorous and aggressive queens of the *sanguinea, rufa,* and *exsecta* groups". WHEELER determined that the queens are taken "during the few hours that intervene between the nuptial flight and the loss of their wings". My observations confirm those of WHEELER that the wasps do not respond to dealate queens. There is no evidence that these wasps enter the nests of the ants or take the queens from the immediate vicinity of the nest; rather, they are captured at various places on the ground, after they land from their nuptial flight. WHEELER saw an *Aphilanthops* swoop down upon a queen that had just landed and very quickly sting her and begin to carry her away.

The wasp carries the prey by grasping its antennae with her mandibles and taking flight, during flight embracing the ant with the legs. The ant may be venter-up or sideways, rarely even dorsum-up. The hind legs of the wasp support the sides of the abdomen of the ant, the middle legs clamp around the thorax, and the front legs loosely embrace the head or prothorax. The wasp comes in to the nest entrance with a loud buzz and drops heavily in front of it, at this time generally retaining the grip with the middle legs while standing on the hind legs and scraping open the entrance with the front legs. Sometimes, particularly if the wasp has some occasion to walk about with the prey, the ant is grasped only by the antennae with the mandibles. Although the ant is sometimes carried directly into the burrow, more commonly it is left at or just inside the entrance while the wasp turns around inside the burrow and then pulls in the ant by an antenna. The entrance is often, though not always, closed from the outside when the female leaves to hunt for an ant. When the female is not actively

provisioning the nest entrance may be closed from the inside or it may be open, in which case the female may often be seen peering out the entranceway.

Both the PECKHAMS and WHEELER remark that the nests of this species are unusually difficult to dig out, a fact which I can most emphatically confirm. The PECKHAMS found "clumps of ants at different levels, some with larvae feeding on them. The deepest were eighteen inches down [45 cm.]". WHEELER remarks that "the burrow descends obliquely and abruptly to a depth of only 6 to 8 inches [15-20 cm.], where it terminates in a small cell. There are also two or three other cells, but it was found impossible to determine their precise relations to the other portions of the nest . . .". WHEELER also observed that ants are stored in the burrow and that the wings of the ants are cut off and left in the burrow before the ants are "carried to the lower portion of the nest".

In fact, all of these observations are essentially correct, and the difference in depth noted by the PECKHAMS and by WHEELER is easily accounted for. The burrow is very irregular and difficult to follow; usually it forms about a 45° angle with the soil surface, but parts of it may be at a much steeper angle. Usually there are sharp, almost angular lateral curves in the burrow; in some instances curves to the left more or less alternate with curves to the right, such that the general direction of the burrow remains the same. On other occasions all or most of the curves are in the same direction, such that the burrow descends much like a circular staircase. The bottom of this burrow is somewhat enlarged and can often be said to terminate in a definite "cell", though this is no more than a storage cell. Measurements of 13 nests in central New York showed a depth ranging from 12.5 to 25 cm. (mean 17.5 cm.). The figures given by WHEELER are in close agreement with these. I found no more than four winged ants in this storage cell, and the cell does not seem large enough to hold more than this. In one nest (no. 1098) there were three *Formica fusca* in the cell and two *F. pallide-fulva nitidiventris* a few centimeters up the burrow. The wings of ants which have been used for provisioning the brood cells can be found either in the storage cell or in the burrow.

The brood cells are situated well below the storage cell and as soon as provisioning and oviposition occur are closed off by a sizable plug of soil; thus it is almost never posible to trace the burrow all the way from the surface to a brood cell. I found 37 brood cells in various nests and found them to vary in depth from 23 to 45 cm. (mean 30 cm.). The deepest cells thus were at precisely the same depth as were the deepest cells of the PECKHAMS. Only two or (less commonly) three dealated ants are supplied per cell.

On several occasions I found cells with a full complement of ants in which oviposition had not occurred. For example, nest no. 1328 had one cell with three ants and another with two, but neither contained an egg. No. 1332, by contrast, had one cell with a larva of small size, another with a newly hatched larva, and a third (the deepest) with an egg on the top of the top ant (figure 1a). The evidence suggests that the female lays about one egg

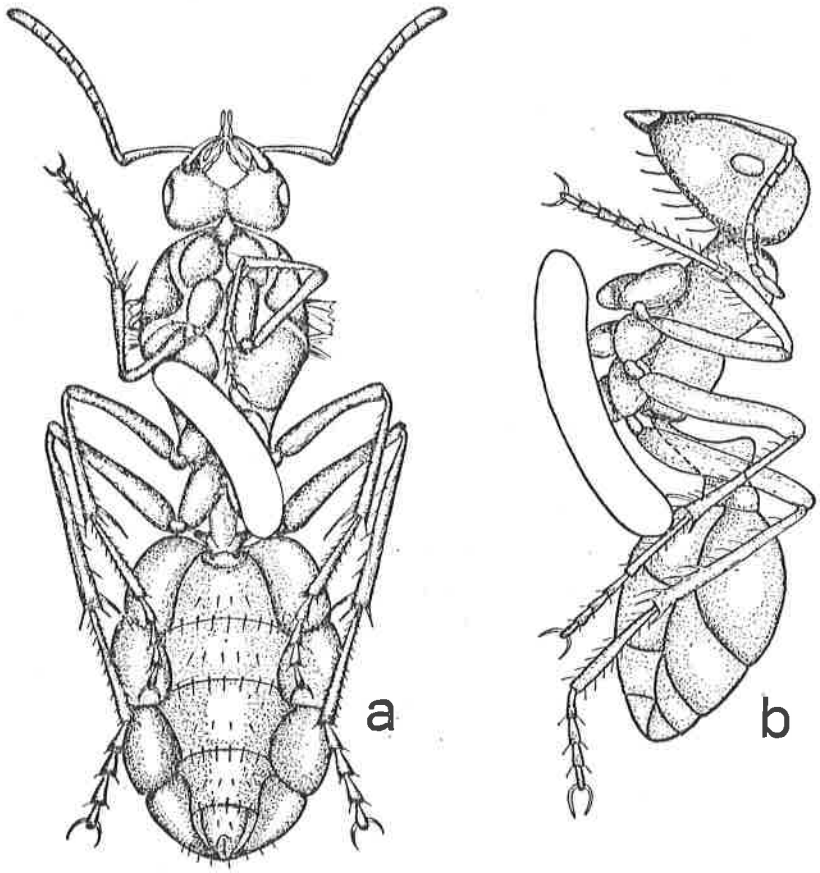

Fig. 1a. Egg of *Aphilanthops (Aphilanthops) frigidus* in place on the venter of a dealate queen *Formica fusca*. — Fig. 1b. Egg of *A. (Clypeadon) haigi* in place on venter of a worker *Pogonomyrmex barbatus rugosus*. In normal position in the cell of the wasp, the ant lies on its back.

per day, but during periods of successful hunting may provision more than one cell and also accumulate several ants in the storage cell and even in the upper part of the burrow. The adaptive value of this behavior is obvious: the nuptial flights of *Formica* ants are distinctly periodic, and the wasps must on some days take many queens, on other days few or none. In order to compensate for the fact that the wasp produces her eggs at a slow and regular pace, some storage of ants is a necessity.

The brood cells of a given nest generally form a rather close cluster; they are commonly separated by about 2 or 3 cm. of earth and vary in depth only slightly (in one nest not more than by about 5 cm.). The maximum number of cells which I could definitely associate with a specific nest was four (nest nos. 1334, 1341). Since the nest entrances were often close together and the burrows of irregular course, many situations arise where it is impossible to be certain to which nest a given cell belongs. In nest no. 1118, dug out late in the season, I was able to find 14 cells, all between 25 and 32 cm. deep and all almost directly beneath a storage cell containing a dead female *Aphilanthops*. Most of these cells contained cocoons. These cells may or may not have all belonged to this one nest. Since the female may perhaps remain with a single nest all season, and certainly must not make more than two or three nests, it seems certain that the maximum number of cells is more than four.

All my evidence indicates that as soon as the female lays her egg on the top ant she closes the cell. She then lays another egg in another cell, generally the next day, and closes this off. WHEELER came to entirely different conclusions. He believed that the wasp lays her egg on a single ant which is cut in two so that the larva can have access to the soft body contents. He believed that the larva is fed progressively from the supply of ants in storage. I found larvae in all stages of development, and in every case the cell contained the full complement of ants; also, the egg was found to be laid in cells containing the full number of ants. I believe that WHEELER simply drew erroneous conclusions from rather fragmentary observations, and that *Aphilanthops frigidus* mass-provisions its cells in the manner of *Philanthus* and other related genera.

The ants stung by *A. frigidus* remain in permanent deep paralysis. Several were kept in a rearing tin for two weeks, by the end of which time they were still well relaxed and in apparently fresh condition. In nature, the ants are normally consumed in about nine days, as the egg takes two days to hatch, the larva about seven days to complete its feeding. The cocoon is semitransparent, elongate-elliptical and tapering to a point at one end; it is suspended horizontally in the cell by a network of fine threads.

The PECKHAMS watched a female laden with prey approach her nest again and again, but always circle away without entering; they discovered that she was pursued by two small flies. WHEELER also reported a "small gray Tachinid fly" watching provisioning females. RISTICH (1956) found the miltogrammine fly *Senotainia trilineata* (Wulp) attacking *Aphilanthops frigidus* with much success in Maine. He found that "most of the winged ants carried by *Aphilanthops* had one or more maggots on some parts of

its anatomy. Some had as many as nine maggots distributed over their appendages either singly or in groups". He believed that the fact that these wasps carry the prey rather loosely beneath the body (as compared, for example, to *Philanthus*) made them especially vulnerable to these flies, which larviposit on the prey while it is being taken to the nest. *S. trilineata* was common in the areas studied both in Tompkins and in Oswego Cos., N. Y., and on many occasions the flies were observed trailing provisioning wasps. A high percentage of the cells dug out appeared to have had the contents destroyed by maggots, but I made no special effort to determine the percentage of parasitism or to determine whether or not *S. trilineata* was the only parasite involved. *Metopia leucocephala* (Rossi) was common in one nesting area near Ithaca, although not actually incriminated as attacking *Aphilanthops*. On one occasion, also at Ithaca (no. 1328) a fly was seen entering a nest just as the wasp entered with prey. The fly remained in the nest two minutes and was captured when it left. This fly was determined as *Euaraba tergata* (Coq.). All three species of flies belong to the Sarcophagidae, subfamily Miltogramminae.

APHILANTHOPS (APHILANTHOPS) SUBFRIGIDUS DUNNING

A specimen of this species in the U. S. National Museum is labeled simply "Wash.", undoubtedly the state of Washington rather than the city, since this species is characteristic of the northwestern states. It is pinned with a queen ant of the *Formica fusca* group which has the abdomen missing.

APHILANTHOPS (CLYPEADON) HAIGI BOHART

During the late summer of 1959 I discovered a small nesting aggregation of this species about a mile north of the town of Rodeo, in extreme southwestern New Mexico. In this area there were several small patches of open sand, some of them slightly elevated above the general level of the desert. The vegetation consisted of scattered mesquite and yuccas, considerable tall grass, and great numbers of annuals, particularly prickly saltbush (*Salsola kali tenuifolia*) and various composites. Most observations were made in a single small dune surrounded by tall vegetation and with a few nearby patches of bare, heavier soil (Plate XVII, fig. 2). About ten nests of this species were found and marked with stakes, but only four of these were dug out. Males were not uncommon in the nesting area and were often observed perched motionless on vertical stems around the nesting area; invariably they were oriented head-down and had their antennae extended rigidly forward. Mating was not observed.

The first observations were made in the late afternoon of August 31. At 1700 a female *haigi* flew into the nesting area carrying a worker *Pogonomyrmex barbatus rugosus* Emery. The ant was carried well back beneath the venter of the wasp and the wasp appeared to walk on all three pairs of legs when she landed in front of the nest. The nest entrance was not closed, and the wasp entered directly carrying the ant behind her. There was only a small, well-spread mound of sand at the nest entrance, and it was later discovered that this species digs in much the manner of *frigidus,* scattering the sand widely as she digs. This wasp left the nest again in a few moments, leaving the entrance open. At 17.30 it was noted that the entrance was closed from within, presumably for the night.

When it was discovered that *Pogonomyrmex* workers were being used as prey, attention was directed to the nests of these ants. There were several nests of *P. barbatus rugosus* in areas of flat, bare soil near the small dune where the *Aphilanthops* were nesting. Each nest had the usual large entrance hole surrounded by a certain amount of litter from the nest. Over a period of days several *Aphilanthops* females were observed capturing these ants at the nest entrances. The wasp lands near a column of ants leaving or entering a nest and pauses motionless or pivots about, apparently awaiting an opportunity to seize one. Now and then the wasp dashes up to a worker ant from the side, often retreating quickly if unable to overcome the ant with a quick thrust of the sting. When the wasp is successful, the ant collapses immediately. The wasp quickly picks it up in a characteristic manner and flies off to her nest. On one occasion an *Aphilanthops* was seen to land at an ant nest which had no workers about the entrance. The wasp actually entered the nest briefly and succeeded in flushing an ant from it; she pursued this ant a short distance and stung it. This species of ant is a relatively aggressive one, and the workers are able to sting and bite effectively. However, they seemed very ineffective in avoiding or fighting off the wasps.

Over a two-week period I made many observations both at ant nests and at wasp nests and also dug out four wasp nests. Over 50 ants were taken from wasps or their nests, and in every case they were workers of this same species of ant, *Pogonomyrmex barbatus rugosus.* This was true in spite of the fact that there were in the area many nests of another, paler species of *Pogonomyrmex, maricopa* Wheeler. In fact, the nests of *maricopa* tended to be in sandier soil, and there were several of them actually within the nesting area of the *Aphilanthops.* Not infrequently these pale harvester ants were seen about the nest entrances of the wasps, and on several occasions the wasps were seen to drive them away from their nests. In spite of this, these ants

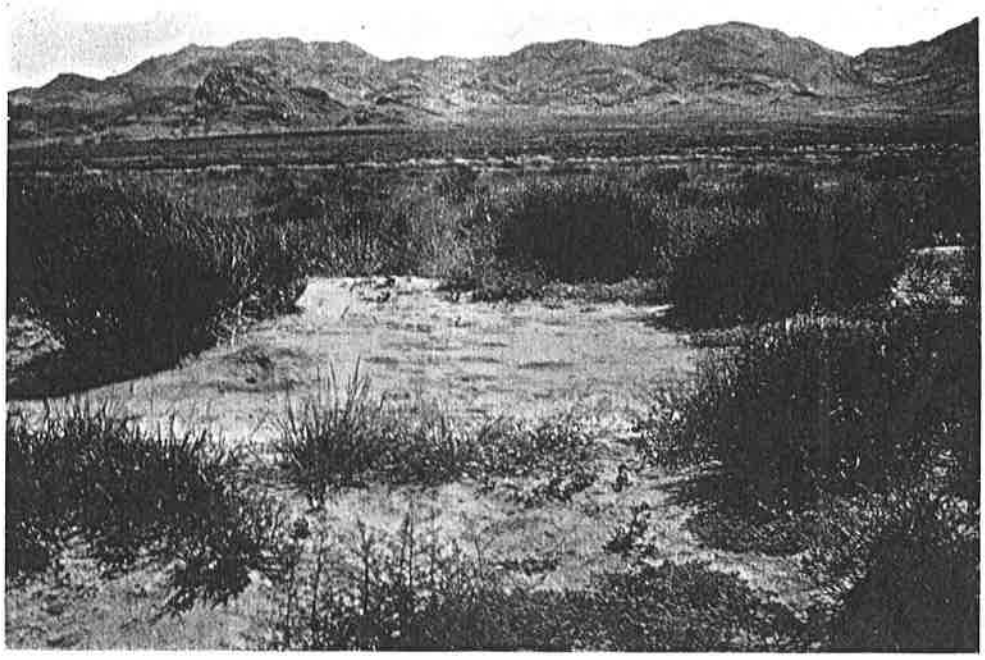

Fig. 2. View of desert one mile north of Rodeo, New Mexico, during August 1959. A nesting aggregation of *Aphilanthops (Clypeadon) haigi* occupied the sandy elevation in the foreground.

Fig. 3. A female *Aphilanthops (Clypeadon) haigi* arriving in front of the nest entrance carrying a worker *Pogonomyrmex*. Note that the end of the wasp's abdomen is turned sharply downward and inserted between the coxae of the ant. The middle and hind legs of the wasp are out to the side and in no way associated with the ant.

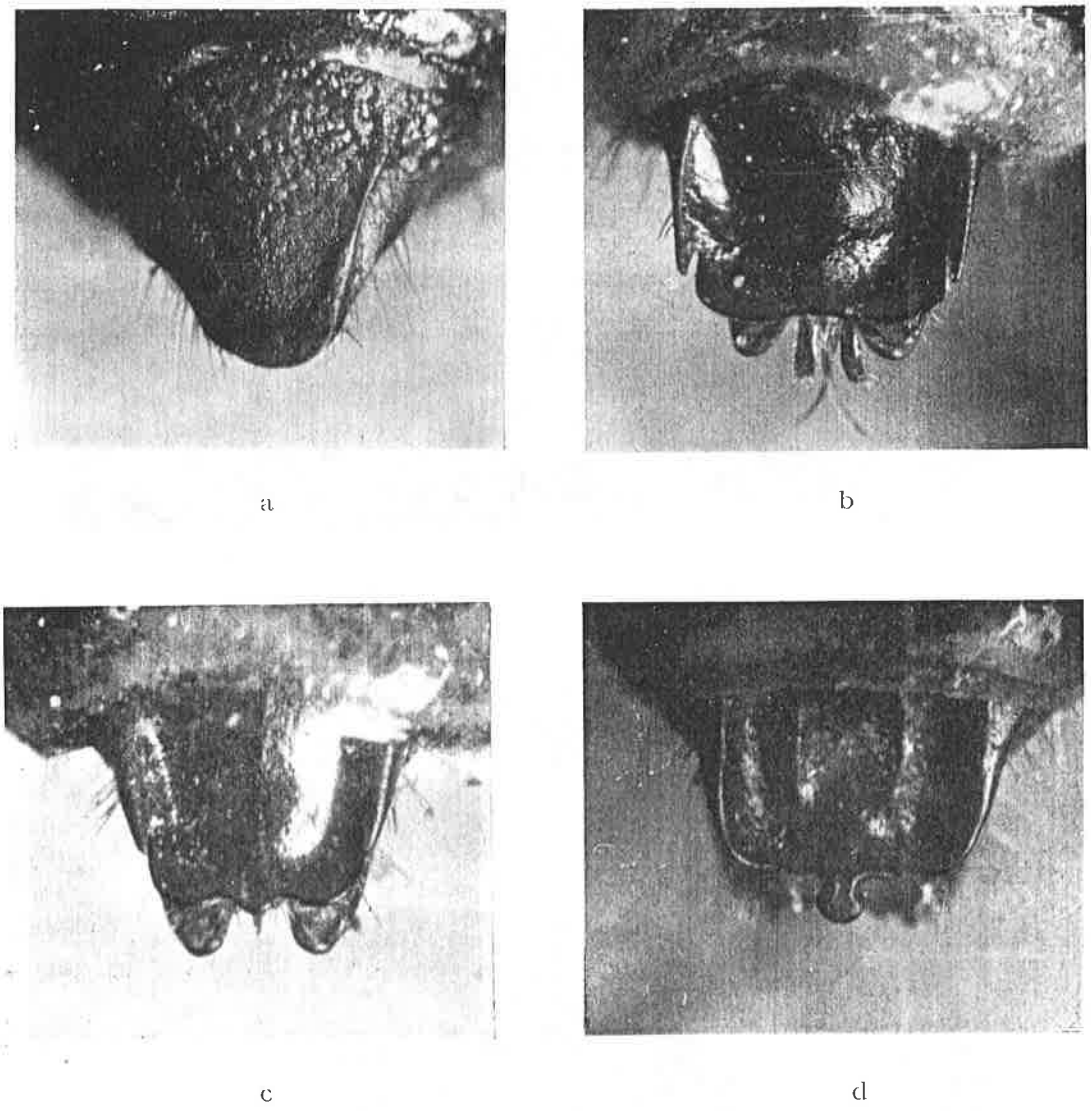

Fig. 4. Pygidia of four species of *Aphilanthops*. a: *A. (Aphilanthops) frigidus;* b: *A. (Clypeadon) haigi;* c: *A. (Clypeadon) concinnula;* d: *A. (Listropygia) bechteli.*
In b, c, and d the apical lobes of the hypopygium may be seen beneath the pygidium and extending slightly beyond it; in b the sting and sting-sheaths are visible.

were never used as prey. On September 7, I did see one *Aphilanthops* (no. 1634B) land near the nest entrance of an active colony of *Pogonomyrmex maricopa*. This wasp approached several ants rather closely, as if about to attack them, but in each case she backed away. The wasp then returned to her nest, which she was still digging. This may have been a freshly emerged female which had not yet begun active hunting; she may have been attracted to the ants but on closer contact had perceived some factor which told her that they were not "the proper species".

Several days of observation left me still confused as to precisely how these wasps carried their ants, so I began to pay special attention to this aspect of the behavior. The wasps leave the ant nest quickly and arrive at and enter their own nests with equal rapidity, the nest entrances normally being left open between trips for prey. It was apparent that the wasps held the ants well back beneath their abdomen and did not employ their legs or mandibles for holding the ant. By artificially closing nest entrances with sand, I was able to delay entry of the wasps long enough to observe that they carry the ant solely by means of the apical abdominal segment, which is curved downward and inserted between the middle and hind coxae of the ant. The ant is, of course, venter-up, and its gaster extends vertically upward or horizontally outward beyond the end of the wasp's abdomen (fig. 3). This mechanism, which is discussed more fully in a later section, appeared to be highly efficient, as no wasps were seen to drop their ants even when prevented from immediate entry into their nests.

Four nests of *haigi* were dug out between September 5 and 12. The burrow of the first one (no. 1629) entered the ground at a 30° angle with the surface, then after 10 cm. went down at a 45° angle for another 16 cm., finally terminating blindly at a vertical depth of 14 cm. There were three ants in the burrow, one about 10 cm. from the entrance, one at 18 cm., and one at 22 cm., only 4 cm. from the end of the burrow. Although I dug out the area to a depth of 35 cm., I was unable to find any cells.

A second nest (no. 1649) appeared to show a somewhat more advanced stage in the nesting process. This burrow started at about a 20° angle with the surface, but curved gradually downward until it was nearly vertical at the bottom; there was a single sharp lateral bend 27 cm. along the burrow. Nineteen cm. along the burrow, at a depth of 5 cm., was a single ant, and 24-26 cm. along the burrow, at a depth of 9 cm., were nine additional ants in some loose filling. The burrow went on for another 10 cm., terminating blindly at 36 cm., at a vertical depth of 15 cm. At a depth of 18 cm., several centimeters off to one side of the bottom of the burrow, a

completed cell was located. The burrow connecting this cell to the main burrow could not be located and had apparently been closed off. The cell was subspherical, slightly flattened on the bottom, about 12 mm. in diameter. It contained 14 ants, all venter-up. The top ant bore an egg in the manner shown in figure 1b; the egg was glued firmly to the venter of the abdomen and adhered more loosely to the coxae. The cell contents were removed to a rearing tin but the egg failed to hatch.

The third nest (no. 1634) was very similar in structure but contained three cells, all at a depth of about 25 cm. and separated by about 8 cm. of sand. This burrow also started out at a small angle from the horizontal and then dipped down much more sharply; it had a single weak lateral bend. The burrow was 26 cm. long and reached a vertical depth of 14 cm. The first cell (which had the freshest contents and was therefore the last cell chronologically) was directly below the end of the burrow; it contained 16 ants, but apparently no egg or larva. It appeared to have been closed off, and it is possible that I overlooked the egg. The other two cells each contained one fly maggot which had partially consumed the cell contents. The flies were removed to rearing tins, where they grew rapidly and formed puparia within a few days. Unfortunately no adult flies were reared from these pupuria.

The fourth nest (no. 1642) also contained three cells, at depths of 16, 18, and 23 cm. All three cells contained the remains of ants, but no wasp larvae, and it seems probable that the contents of all three had been destroyed by fly maggots which had left the cell and formed puparia in the soil. The wasp which made this nest had been observed several days earlier being trailed by a small fly which entered the nest after the wasp had entered. The fly was presumably a sarcophagid, subfamily Miltogramminae, but I was unable to capture it for identification.

The last active female was seen on September 11, only twelve days after the first one was seen. Presumably the species had been active for some time before it was discovered. There was no obvious reason for the sudden termination of activity on the 11th. During the active period, most provisioning appeared to occur in the late afternoon, between 1600 and 1800, although some females were also observed hunting and carrying ants in the late morning and early afternoon.

APHILANTHOPS (CLYPEADON) SPECIES A

This undescribed species was encountered in the same place as the preceding, but it appeared to be less common. A few males were captured as they perched on vegetation around the nesting area in exactly the same manner

as in *haigi*. Only one female was observed nesting, September 7-9 (no. 1637). This female was bringing in ants over a two day period to a nest only a few centimeters from a nest of *haigi*. The nest entrance was left open between trips for prey and the ants carried in the same manner as *haigi*. Over 50 ants were eventually recovered from this nest, and all proved to be worker *Pogonomyrmex barbatus rugosus* Emery.

This nest was dug out on September 9th while the wasp was actively provisioning. The burrow entered the ground at about a 35° angle; only a few centimeters deep there were five fresh ants in the burrow. Beyond this point I lost track of the burrow, but by digging out the area I located 5 cells. These had much the same dimensions as in *haigi* and varied in depth from 12 to 16 cm.; they were separated by from 5 to 12 cm. of sand. The shallowest cell appeared to be the most recently prepared, as it contained 12 ants with an egg on the top ant. The ants were venter up, and the egg appeared to be glued to the top ant in exactly the same manner described for *haigi*. Two other cells contained half-grown larvae, each lying in a semicircle on top of the pile of ants (in each case about 12). Another cell contained 11 ants but no egg or larva. The final cell contained two large maggots which had nearly finished consuming the cell contents. One wasp larva reached full size in a rearing tin and was preserved for future morphological study. The maggots formed puparia and one adult miltogrammine fly (*Senotainia trilineata* Wulp) emerged the following spring. It is probable that this is the same species of fly that was attacking *haigi*.

APHILANTHOPS (CLYPEADON) DREISBACHI BOHART

I have examined a specimen of this species in the collection of the University of California at Berkeley which is pinned with a worker *Pogonomyrmex barbatus rugosus* Emery. This specimen was taken 17 miles north of Fresnillo, Zacatecas, Mexico, 16 July 1954, by J. W. MacSwain. Dr MacSwain made some notes on these specimens, and has written me as follows:

"The wasp was observed near the entrance of a small nest of the ant. At intervals the wasp approached close to the large slit-like opening of the ant nest and two or more ants would come out of the nest and approach the wasp. As the ants ran toward the wasp the wasp would move away from the nest a foot or more. This pattern was repeated about a dozen times until only a single ant left the nest and approached the wasp. After several unrecorded movements on the part of the wasp, the ant was grasped and I presume stung by the wasp. At this point the two insects were captured."

APHILANTHOPS (CLYPEADON) CONCINNULA COCKERELL

A specimen of this species in the collection of the University of California at Davis is pinned with a worker *Pogonomyrmex barbatus* (F. Smith). This specimen was taken at Walker Pass, Kern Co., Calif., 26 Sept. 1957, by E. I. SCHLINGER.

APHILANTHOPS (CLYPEADON) TAURULUS COCKERELL

AINSLIE (1909) observed females of this species preying upon worker *Pogonomyrmex barbatus rugosus* Emery in Albuquerque, New Mexico. He described the hunting behavior as follows:

"I noticed a small quadrate-headed wasp drop from the upper air to the hard-trodden soil, alighting without previous reconnoitering. She stood perfectly motionless, not even dressing herself after the manner of her kind when idle. Presently an ant hurried by . . . when instantly the wasp gave chase. The ant dodged and doubled as it fled, but the wasp overtook and seized it after a very brief and intensely active resistance . . . and . . . rose heavily into the air and ascended at a sharp angle of flight. During the next few minutes I saw the same performance repeated again and again . . . Occasionally an ant, when pursued, would dodge around a blade of grass or rush beneath some welcome shelter and elude its hunter, but this happened in only a few cases ... The wasps never, so far as I observed, assisted themselves with their wings to gain speed, but . . . ran them down."

AINSLIE did not note the manner of prey carriage or discover the nests of the wasps. His observations on the hunting behavior are in close agreement with mine on *haigi*.

APHILANTHOPS (CLYPEADON) SCULLENI BOHART

On August 12, 1961, JAMES E. GILLASPY, Research Associate at the Museum of Comparative Zoology, collected a female of this species in dunes at the Waterfowl Refuge, La Joya, Socorro Co., New Mexico. This female was carrying a worker *Pogonomyrmex maricopa barnesi* M. R. Smith. This record is of special interest inasmuch as I found *P. maricopa* being rejected by *Aphilanthops* (*Clypeadon*) *haigi* in southwestern New Mexico.

APHILANTHOPS (CLYPEADON) LATICINCTUS (CRESSON)

HICKS published two short papers on this species (1927, 1933) under the name *quadrinotatus* Ashmead, which is a synonym. He found two nesting aggregations of this species, both in sandy soil, one near Boulder and another at Roggen, Colorado. He noted that the females, when digging the nest, kick the sand some distance from the hole. The burrow was found

to be 15 cm. long, the cells from 3.3 to 17.4 cm. deep, each cell containing from 8 to 12 worker *Pogonomyrmex occidentalis* Cresson. HICKS described the cocoon at some length but apparently did not discover the egg. He does not mention storage of ants in the burrow, but some of the cells close to the surface may have been storage places; at least 3.3 cm. seems to be remarkably shallow for an *Aphilanthops* cell.

HICKS made several observations on the hunting behavior, and his account bears much similarity to those already presented for other species. "A wasp would often alight", he says, "at the edge of the bare area about the [ant] hill... Her antennae were held forward, slightly at right angles to her body, and her eyes appeared intently fastened upon her prey as she seemed to watch or follow their every movement. She would suddenly rush in after an ant... following it closely until she was in a favorable position to jump upon it, or until, as more often was the case, it could successfully evade her... But eventually and in a comparatively brief time... the wasp would throw herself upon or grab an ant, overcome and sting it, impale it upon her sting and be quickly away with it to the nest." He watched some females actually digging into ant nests in much the same manner in which they dig their own nest; one such female, having cleared a burrow into an ant nest, "emerged head-first with her ant carried on her sting."

HICKS conceded the possibility that the ant might not actually be carried on the sting but by the apical abdominal segments, but "on examination at the laboratory they did not appear modified for the purpose". He was aware that the legs play no part in prey transport. He remarks that the wasp may rearrange the position of the ant either right after capture, on the way to her nest, or even after arriving at the nest. He states that at such time the wasp "twists her head back to the impaled ant and appears to use her jaws in quieting, re-arranging, or better holding it."

The interesting fact that the species of *Aphilanthops* are relatively uncommon as compared to the great abundance of their host was considered by HICKS. He believed that parasitism might be important, and listed several insects found in or around the nests of *laticinctus* which might have been acting as parasites. One of them was the miltogrammine fly *Senotainia* (? *trilineata* Wulp).

Since writing the above, I have had an unexpected opportunity to study *laticinctus* myself. About fifteen nests were located at Great Sand Dunes National Monument, Alamosa Co., Colorado, August 25-27, 1961. The nests were in small patches of bare sand in a sparsely vegetated area on the edge of the dunes proper. Some of the nest entrances were only 2-5 cm. apart, while others were much more widely spaced. Males were common in the

area, and could often be seen sitting on the ground or on twigs near the nests of the females, motionless and with their antennae extended rigidly. Some males were actually seen to enter nests, but they remained inside only very briefly.

Digging behavior of the females was similar to that of other species of the genus. The females come out to the threshold of the burrow, pause, rock the body up and down slightly, then turn around quickly and plunge into the burrow kicking sand. The sand falls at some distance from the entrance, but does tend to form a flat mound measuring 6-10 cm. long, 4-5 cm. wide. The burrow is oblique for a few centimeters, then becomes almost vertical. As usual in the genus, the ants are stored in the burrow (at a depth of 7 to 15 cm.), then later moved to a cell deeper in the soil. A total of 13 cells were uncovered in 5 nests, no one nest having over 3 cells. Since females were seen starting new nests rather frequently, it is probable that 3 cells is close to the maximum for one nest. The cells found varied in depth from 10 to 21 cm., and in any one nest the cells were separated by several centimeters of sand. Apparently when one cell is fully provisioned and the egg laid, a fairly long section of burrow is filled and another long section excavated. This is confirmed by the fact that periods of provisioning are separated by fairly long periods of digging.

The cells are fairly large, 8-10 mm. in diameter, and are nearly spherical. The ants are piled in the cells venter-up, head-in, and the egg is laid on one of the topmost ants in the manner figured for *haigi*. The number of ants in fully provisioned cells varied from 15 to 26. All ants taken from the 5 nests dug out proved to be worker *Pogonomyrmex occidentalis* Cresson. These were evidently being captured at several large nests of this ant in and around the nesting area of the wasps. Female *Aphilanthops* were commonly seen hunting around the ant nests, and several were seen entering the nests as described by HICKS. The manner of prey carriage was similar to that of *haigi*, the ant being quickly adjusted on the apex of the abdomen after stinging, and carried quickly to and into the nest of the wasp, the nest entrances always being left open during provisioning. If the ant was taken close to the nest of the wasp, the wasp would often walk with it to its nest. More commonly, the wasp would fly with the ant, land some distance from its nest, then walk or fly to the entrance. I did not observe any wasps readjust their ants during transport as described by HICKS. There were, in the area, many formicine ants (*Formica bradleyi* Wheeler) of about the same size and color as the *Pogonomyrmex*. The wasps would sometimes approach these ants closely as if about to attack them, but they would always back away at the last moment.

Miltogrammine flies were common in this area and were often seen perching about nest entrances or actually pursuing wasps carrying ants. One of these was captured and determined as *Senotainia* sp. nr. *trilineata* (Wulp). Of the 13 cells examined, 7 had apparently had the cell contents destroyed by miltogrammine maggots.

APHILANTHOPS (LISTROPYGIA) BECHTELI BOHART

This species and subgenus were described only recently by BOHART (1959). One of the paratypes was taken by Dr BOHART in dunes in Borrego Valley, San Diego Co., Calif., on April 18, 1957, with a worker *Pogonomyrmex californicus* Buck.

SUMMARY AND DISCUSSION

Aphilanthops is very much the sort of genus that an ethologically-oriented systematist likes to discuss. In many details of nesting behavior it typifies the subfamily to which it belongs. The practice of storing the prey in various places in the burrow, but especially at the bottom, and then preparing cells at a lower level and provisioning them from the stored prey is characteristic of *Philanthus* and *Cerceris* as well as *Aphilanthops*. The egg is laid on the top prey in the cell and the larva feeds on top of the pile in a somewhat coiled position, using its anal pseudopod to push itself about in the cell. The cocoon is a thin-walled, narrowly elliptical structure suspended in the middle of the cell by a network of fine threads. These statements are true of most if not all Philanthinae. In common with the other genera of the tribe Philanthini, *Philanthus* and *Trachypus* (also with a few *Cerceris*), the species of *Aphilanthops* prey upon adult Hymenoptera. In the use of ants rather than bees (or rarely wasps), and the differences in hunting behavior that this implies, the genus *Aphilanthops* differs sharply from *Philanthus* and *Trachypus*. And obviously the type of ants employed provides a good subgeneric character in *Aphilanthops*. Thus the usual classification of these wasps, based on morphological evidence, is well supported by ethology. (Other characters than these can, of course, be called to mind, such as the rather different nest entrances and manner of entering and leaving the nest in the Cercerini, differences in manner of prey carriage, *etc.*)

When it comes to interpreting these similarities and differences in terms of evolution, the matter is not simple. In my study of the larvae (EVANS, 1959) I concluded that both the Philanthini and the Cercerini show some primitive and some derived characters. I believe that the study of adult structure leads to much the same conclusion. For example, the presence of a

prepectal suture is a derived character found in the Philanthini but not the Cercerini, while the nodose first gastric segment and modifications of the clypeus are derived characters found in the Cercerini but not the Philanthini. Larval and adult structure suggest that *Cerceris* is more primitive than *Eucerceris, Aphilanthops* more primitive than *Philanthus* and *Trachypus*. The Philanthinae as a whole may have shared a common ancestry with the Nyssoninae.

There is little question in my mind that in the manner of digging the nest, in the manner of carrying the prey with the middle legs, usually not assisted by the mandibles, and in other details of the nesting behavior, *Philanthus* is more like other digger wasps, particularly the Nyssoninae, than is *Aphilanthops* (or *Cerceris*). (For a recent review of the ethology of the North American species of *Philanthus*, see EVANS and LIN, 1959.) In *Aphilanthops* no particular mound of earth accumulates at the nest entrance (as it does in most digger wasps) because the female digs in such a way that the soil particles are well scattered. In the subgenus *Aphilanthops* the middle legs are employed somewhat as in *Philanthus*, but the prey is held rather more loosely and not always venter-up as in *Philanthus*; also, the mandibles are employed for grasping the antenna of the ant (the mandibles form the major device for carrying prey in *Cerceris*). In *Clypeadon* (and doubtless in *Listropygia*) the manner of prey carriage is very different and clearly specialized. Surely the hunting behavior of these subgenera can also be considered specialized.

The use of ants as prey is not entirely restricted to the genus *Aphilanthops*. Several genera of Crabroninae are known to employ ants either occasionally or exclusively. For example, HICKS (1936) found that *Trachelioides hicksi* Sandhouse provisions its nests with worker dolichoderine ants. However, the consistent use of queen ants is, so far as I know, restricted to the typical subgenus of *Aphilanthops*, while the other two subgenera are the only wasps employing as prey aggressive worker myrmicine ants such as *Pogonomyrmex*. HICKS has asked the obvious question: why are not wasps of the genus *Aphilanthops* not far more abundant, since the supply of ants is almost infinite. It appears from the records that these wasps are notably unsuccessful in avoiding the attacks of miltogrammine flies, a fact which may be related to the rather "disjointed" bodies of their prey, rendering it difficult to grasp them close to the body where they might be less accessible for larviposition by miltogrammines. The high degree of host specificity of these wasps is unusual and may also help explain why they are not more abundant. For example, *A. frigidus* takes only queens of certain species of the genus *Formica* (why not *Lasius* or *Camponotus*?), while all evidence

indicates that each species of *Clypeadon* attacks only one species of harvester ant, even when more than one species is readily available.

Whatever may be the answer to this question, *Aphilanthops* clearly occupies its own adaptive zone, and the subgenera *Aphilanthops* and *Clypeadon* each its own adaptive subzone. The various species of each subgenus appear to be very similar in their behavior so far as present evidence goes. The admittedly fragmentary records reveal no important differences between the hunting behavior of *A.* (*Clypeadon*) *haigi*, species A, *dreisbachi*, and *taurulus*; all four species are, so far as known, restricted to *Pogonomyrmex barbatus rugosus*, a very common ant in the Southwest. *A.* (*C.*) *laticinctus* is apparently very similar, though preying upon *P. occidentalis*, the prairie mound-building ant. *A.* (*C.*) *sculleni* preys upon *P. maricopa*, a species rejected by *haigi*. *A.* (*Listropygia*) *bechteli* apparently preys upon *P. californicus*. A closer study of the relationship between the species of this genus and their ant prey might be rewarding. Why, for example, does *haigi* reject *P. maricopa* as prey even when it is abundant in the nesting area of the wasps? Why do no less than five species prey upon *P. barbatus*? Are these species able to occupy similar ecological niches because their prey is in unlimited supply but their populations kept low by parasite pressure?

THE MECHANICS OF PREY CARRIAGE

As indicated above, *frigidus* (and presumably other members of the subgenus *Aphilanthops*) carries its prey by employing both its legs and its mandibles. The middle legs appear to clamp about the thorax of the queen ant in much the manner of *Philanthus*, and during flight the other legs appear to embrace the ant more loosely. When the wasp lands at the nest entrance, she stands on the hind legs, opens the nest entrance with the fore legs, and continues to hold the ant with the middle legs. During all this time the wasp also holds on to the ant's antennae with her mandibles. If the wasp lands elsewhere than at the nest entrance, or has occasion to walk about before entering the nest, she may walk on all three pairs of legs, merely dragging the ant beneath by the antennae.

There is nothing particularly remarkable about the manner of prey transport in *frigidus*. The prey is relatively large and decidedly "loose-jointed", and the use of the mandibles as well as the legs may be related to this fact. Females laden with prey fly rather slowly, land heavily, and are capable of very little manoeuvering. It is a curious fact that only winged queens are accepted as prey, even though dealate queens are often available

and would presumably be somewhat less awkward to carry. Yet the wasps remove the wings of the ants before using them for provisioning cells.

In *frigidus* the abdomen is in no way involved in prey carriage. The apical tergite has a distinct, margined pygidial plate (Plate XVIII, fig. 4a). This plate resembles that of many digger wasps and is undoubtedly used (as in most Sphecidae except Sphecinae) for packing soil into the burrows. In these wasps the burrows leading to the cells are invariably tightly packed with sand and it is probably these burrows, rather than the entrance burrow, which require the major use of this pygidial plate. The apical sternite (hypopygium) of *frigidus* is relatively unmodified, but does have an elongate median groove of unknown function.

In recently describing a new subgenus of *Aphilanthops*, Bohart (1959) selected the name *Listropygia* (shovel-tail) on the perfectly natural assumption that the pygidium of these wasps also served in moving soil (Plate XVIII, fig. 4d). In the light of my studies of *A.* (*Clypeadon*) *haigi*, it now seems much more probable that the unusual pygidia and hypopygia of all species of *Clypeadon* and *Listropygia* serve as devices for clamping onto the ants, thus releasing all the legs as well as the mandibles of the wasp for other functions.

It will be recalled that Hicks believed that these wasps carry the prey on their sting, as is known to occur in the crabronine genus *Oxybelus*. I cannot prove that the sting does not play some role in holding the ant, but the sting and sting-sheaths of *Clypeadon* appear remarkably small and fragile (Plate XVIII, fig. 4b). In *Oxybelus* the sting is robust and the entire situation very different from that prevailing here (see, for example, Olberg, 1959, figs on pp. 376-388). So far as I know, carriage of the prey on the sting is restricted to certain Crabroninae, and the method of prey carriage employed by *Clypeadon* occurs in no other wasps.

If one watches a female *Clypeadon* either immediately after she has subdued an ant or later as she arrives at the entrance to her nest, he notes that the end of the wasp's abdomen turns sharply downward and is inserted firmly between the middle and hind coxae of the ant (Plate XVII, fig. 3). Hicks, in his study of *laticinctus*, noted that the wasps often rearrange the prey en route to the nest. However, I failed to note this in my studies of *haigi*; rather, the wasps seemed to proceed very rapidly from ant nest to their own nest, encountering no difficulties at all with their prey. In fact, I was much impressed with the efficiency of this remarkable method of prey transport, which left the wasp with full use of its legs and mandibles when entering the nest.

It was not until I was able to study the pygidium and hypopygium of these wasps in the laboratory that I was able to arrive at any sort of understanding

of how the "ant-clamp" worked. The pygidium of *haigi* is broad and biconcave, with strong lateral margins, bearing a subapical notch (Plate XVIII, fig. 4b). The hypopygium is deeply concave and polished, with its apex in the form of paired lobes (the tips of which are visible in Plate XVIII, fig. 4b). When this apparatus is thrust between the middle and hind coxae of the ant, the biconcave pygidium neatly embraces the hind coxae, the deeply concave and bilobed hypopygium the middle coxae. It is possible that the lateral notches and paired lobes play some role in locking into the coxal cavities and sclerotized supports at the base of the coxae. Two linear series of setae on the hypopygium may conceivably be tactile receptors which convey information to the wasp that "the clamp is set". By using dead, relaxed specimens I have been able to simulate the method of prey carriage closely, but the ant does not remain fixed between the coxae. Presumably in life the wasp is able to effect a separation of the pygidium and hypopygium, thus exerting pressure against the two pairs of coxae. It is possible that this is done by increasing the blood pressure in the abdomen or by employing muscles normally used in copulation or oviposition.

The different species of *Clypeadon* exhibit various modifications of the pygidium and hypopygium. The pygidium of *concinnula,* which also preys upon *Pogonomyrmex barbatus,* has a small median projection (Plate XVIII, fig. 4c). I suspect that this may enter the base of the U-shaped concavity at the base of the petiolar articulating groove between the hind coxae (fig. 5). It is possible that a pygidium such as that of *concinnula* may represent an intermediate step between the simpler pygidium of species such as *haigi* and the more elaborate pygidium of *Listropygia.*

Although I have never encountered *Aphilanthops* (*Listropygia*) *bechteli* in the field, I have worked with relaxed specimens of wasps and prey and have come to some tentative conclusions regarding the functions of the specializations of that species. The median prolongation of the pygidium is knob-like (Plate XVIII, fig. 4b) and fits well into the basal concavity of the petiolar articulating groove (fig. 5). At the same time the paired carinae in the pygidial concavities may provide added pressure against the hind coxae. The hypopygium of this species is also of unusual interest. It is deeply divided apically and each of the lobes deeply concave in itself. One can conceive of this providing a more effective device for embracing the middle coxae than in the species of *Clypeadon.* At the apex of each lobe is a small notch (fig. 5; barely visible in Plate XVIII, fig. 4) ; laterad of each notch the hypopygium is distinctly thicker than it is mesad. It is probable that these notches hook onto the transverse intercoxal carinae (fig. 5), with the thicker, lateral sections of the hypopygial margin remaining behind the carinae, the

thinner, mesal sections being in front of the higher, mesal ends of the carinae. This would mean that the apical margins of the pygidium and hypopygium would actually be in close approximation rather than being pushed apart as I have visualised in *Clypeadon*. Working with relaxed specimens, I have been able to catch the apices of both the pygidium and hypopygium into the body parts indicated above, proving that they do in fact fit. However, I have been

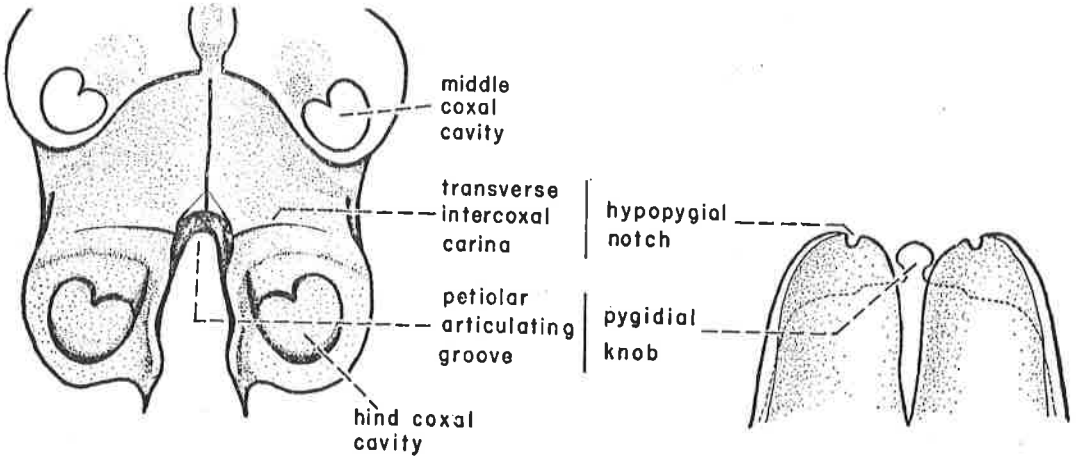

Fig. 5. On left, ventral surface of meso- and metathorax of a worker *Pogonomyrmex* with the coxae removed (the coxae are very much larger than the cavities in which they articulate). On right, hypopygium and pygidium of *Aphilanthops (Listropygia) bechteli*. It is assumed that the hypopygial notches fit over the transverse intercoxal carina, as explained in the text, while the pygidial notch fits into the concavity at the base of the petiolar articulating groove. Although the structures are here shown in one plane, in fact the pygidium and hypopygium of the wasp contact the ant perpendicularly or nearly so.

unable to catch both pygidium and hypopygium simultaneously in intact specimens.

Whether or not my explanation of the function of the various structures found in *Listropygia* is correct can only be established by careful studies of living specimens. I am confident, from my field studies of species of *Clypeadon*, that these explanations are correct at least in their broader aspects. There can be no question that the unusual pygidia and hypopygia of *Clypeadon* and *Listropygia* function as "ant-clamps". So far as I know, such modifications of the abdomen for holding prey are unique in the Hymenoptera.

SUMMARY

The digger wasp genus *Aphilanthops* is divisible into three subgenera. Two species of the subgenus *Aphilanthops* are known to prey upon winged queen ants of the genus *Formica.* One of these species, *frigidus,* has been studied in some detail by WHEELER and by the present writer. In carrying the ant, the female grasps the antennae with her mandibles and holds the ant's body beneath her with her legs. The ants are stored at the bottom of the burrow, where the wings are removed; later they are moved to cells deeper in the soil. Two or three ants are used per cell; when the cell is fully provisioned the egg is laid on the top ant and the cell closed. WHEELER reported that the cells are provisioned progressively, as the larva grows, but the present studies indicate that this is not the case.

Members of the subgenera *Clypeadon* and *Listropygia* prey upon worker ants of the genus *Pogonomyrmex.* Some information is available on six species of *Clypeadon* and the one known species of *Listropygia,* but the only detailed studies are those made by the writer on *A. (Clypeadon) haigi.* The general details of the nesting behavior of this species are much as in *frigidus.* Storage of ants in the burrow occurs, and 14 to 16 ants are supplied per cell. The ants are captured and stung at or inside the entrances to their nests. They are carried fastened to the apical segment of the wasp's abdomen by the base of the ant's middle and hind legs, thus leaving the mandibles and legs of the wasp free.

The peculiar "ant-clamp" formed by the apical body segment of members of the subgenera *Clypeadon* and *Listropygia* is unique among digger wasps. Apparently it arose as a modification of the simple pygidial plate of members of the subgenus *Aphilanthops,* which is probably used for packing soil in the burrow as it is in other digger wasps. The pydigium and hypopygium of the species of *Clypeadon* are biconcave and have various processes which seem to be well fitted for clamping on to the middle and hind coxae of the ant (probably with the aid of blood pressure or muscular action). In *Listropygia* these modifications have become quite elaborate. While no one has observed closely the manner of prey carriage in *Listropygia,* it is possible to postulate how some of the various processes and notches fit into specific structures on the ant to provide a more effective device for holding the ant.

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ZUSAMMENFASSUNG

Die Grabwespengattung *Aphilanthops* zerfällt in 3 Untergattungen. Zwei Arten der Untergattung *Aphilanthops* erbeuten geflügelte Ameisenköniginnen der Gattung *Formica*. Die schon von WHEELER genauer untersuchte Art *frigidus* wurde jetzt nochmals untersucht. Zum Heimtransport packt das ♀ die Antennen der Königin mit den Mandibeln und hält ihren Körper mit den Beinen unter sich; es entflügelt und speichert die Opfer am Ende des Ganges, später bringt es zwei bis drei in je eine tiefer gelegene Zelle, legt ihr Ei auf die oberste und schliesst die Zelle. WHEELER's Angabe, die Zelle würde entsprechend dem Wachstum der Larve wiederholt versorgt, hat sich nicht bestätigt.

Sechs Arten der Untergattung *Clypeadon* und eine von *Listropygia* tragen *Pogonomyrmex*-Arbeiterinnen ein. Die allein eingehender beobachtete *A. (Clypeadon) haigi* verhält sich im grossen ganzen wie *frigidus*. Sie sticht die Ameisen erst am oder im Nesteingang und lagert 14-16 in einer Zelle. Beim Eintragen behält sie ihre Mandibeln und Beine frei: sie klemmt die Arbeiterin unter sich, indem ihr Hinterleibsende die Mittel- und Hinterhüften der Ameise umgreift.

Von allen Grabwespen haben nur die Untergattungen *Clypeadon* und *Listropygia* so als „Ameisenklammer" gestaltete Hinterleibsenden. Wahrscheinlich ist diese Struktur aus dem einfach plattenförmigen Pygidium der Untergattung *Aphilanthops* entstanden, die, wie bei anderen Grabwespen, als Bodengreifer dient. Bei den *Clypeadon*-arten sind das Pygidium und Hypopygium bikonkav und haben verschiedene Fortsätze, die, sei es durch Blutdruck oder Muskeln, die Mittel- und Hinterhüften der Ameisen umklammern. Am kompliziertesten sind sie wohl bei *Listropygia*. Zwar hat man diese beim Ameisentragen noch nicht genau beobachtet, kann sich aber gut vorstellen, wie die verschiedenen Vorsprünge und Vertiefungen in entsprechende Ameisenstrukturen passen, um die Beute ganz fest zu halten.