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justification exists for recognizing *T. gloveri* as a species distinct from *T. tumidus*, especially in view of the consistent differences between the males of the two species, and the biological distinctions and reproductive isolation exhibited.

Male and female specimens of *T. gloveri* have been deposited in the United States National Museum.

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STUDIES ON THE NESTING BEHAVIOR OF DIGGER WASPS OF THE TRIBE SPHECINI. PART I: GENUS PRIONONYX DAHLBOM[1]

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ABSTRACT

Few attempts have been made to correlate the many observations recorded on nesting behavior in this group so that its evolution can be understood. Some original observations are presented here on several species of *Priononyx*, and the recorded observations on species of this genus are reviewed briefly. Four Nearctic species (*P. atratus*, *thomae*, *pubidorsus*, and *striatus*) and one Palaearctic species (*P. subfuscatus*) all appear to be very similar in their nesting behavior. The prey always consists of Acrididae; it is paralyzed lightly, carried forward over the ground in a characteristic manner, and left in a protected place during digging. The nest is dug after the prey has been captured, and is simple, shallow, and unicellular; it is dug and filled very rapidly and in a characteristic manner. The prey is placed in the cell head-in, dorsum-up, and the egg is laid with one end in contact with the membrane of a hind coxa. Certain Neotropical species are reported to differ from this type of behavior. *P. spinolae* prepares the nest before hunting, makes several cells per nest, places 5 to 10 grasshoppers in a cell, and lays the egg on the thoracic venter. *P. spinolae* resembles *Sphex* species in these respects, and it seems possible that this species represents something of a link between these two genera.

The large and conspicuous wasps of the tribe Sphecini have attracted the attention of many persons, and a complete bibliography of published notes on these wasps would fill many pages. Yet, aside from the very valuable survey by Iwata (1942), few attempts have been made to bring any of this information together from the point of view of understanding the evolution of behavior in the group. Since the Sphecinae are, at least in my opinion, the most primitive subfamily of the large family Sphecidae (exclusive of the Ampulicidae), it is important to understand the ethology of the group if we are ever to understand the over-all evolution of behavioral characters in the Sphecidae.

There is by no means full agreement on the correct classification of the Sphecini. The most common practice has been to recognize but a single genus, *Sphex* (or *Chlorion* of most recent American authors), with several subgenera. Personally I feel that this tends to obscure the diversity of structure and of ethology within the group. It is true that some of these groups are "weaker" than others, and some species of rather doubtful position. Surely a careful survey of the ethological characters of the Sphecini is in order if we are ever to settle upon a satisfactory classification of the tribe.

In the present paper I shall present some original observations on several species of *Priononyx* and review the published observations on the species of this genus. In a second paper I hope to discuss more briefly the other genera of the tribe and to attempt to draw some conclusions on the evolution and classification of the Sphecini.

The field work for this study was undertaken as part of a project on the comparative behavior of solitary wasps, supported by the National Science Foundation. Note numbers in the text refer to field notes and associated specimens now

[1]Accepted for publication September 3, 1957.

on permanent file at Cornell University. In the studies of *P. atratus*, I was assisted by C. S. Lin and C. M. Yoshimoto. All the grasshoppers were identified by A. B. Gurney of the Entomology Research Division, U. S. Department of Agriculture, whom I particularly wish to thank. I also wish to thank Ernest C. Bay for providing the nesting data and photographs for *P. striatus*.

Some information is available on all of the North American species of this genus except *ferrugineus* (Fox). In South America, *striatus* Smith, *striatulus* (Brèthes), and *spinolae* (Kohl) have received some attention, and in Eurasia *subfuscatus* (Dahlbom) has been studied in detail. Members of this genus are rather striking in appearance: they are stout-bodied, with heavy, spinose legs which terminate in tarsal claws bearing from two to six teeth along their inner margin. The gaster is somewhat globose, the first tergite rising almost perpendicularly from the rather short petiole. In the front wing the second submarginal cell is higher than wide, and in the female the clypeus has a median notch.

Prionony x atratus (Lepeletier)

This is a widely distributed species, occurring from coast to coast from the Lower Austral well into the Transition Zone. It is a particularly common species in midsummer in the Great

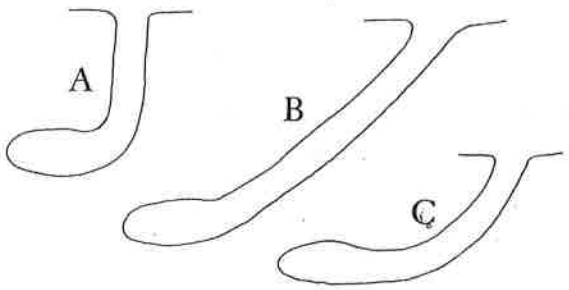

FIG. 1.—Three typical nests of *Prionony x atratus*. A, an L-shaped nest, no. HE46, Blackjack Creek, Pottawatomie Co., Kansas. B, a diagonal nest, no. HE57, Little Gobi Desert, Pottawatomie Co., Kansas. C, a curved nest, no. 573, Sun City, Barber Co., Kansas.

Plains, where there is an ever-constant supply of the short-horned grasshoppers which serve as its prey. There are several published notes on this species, and Williams (1913) and the Raus (1918) have published fairly full accounts of its biology; a shorter account by Strandtmann (1945) is somewhat out of accord with earlier observations. The present studies are based on 22 field notes made in Kansas during the summers of 1952 and 1953. Most of them were made in two localities in Pottawatomie Co., in northeast-central Kansas, and a few were made in several places in southern and western Kansas.

P. atratus does not appear to be strongly restricted ecologically; I have found it nesting in localities varying from a moist sandy stream bottom to the much drier sand of an upland blow-out and to a grassy prairie. The species does not occur in open sand dunes or in areas of woodland or dense herbaceous growth. It is not a gregarious species, although in suitable areas several individuals may nest in relatively close proximity. Both sexes commonly visit flowers for nectar; I have taken them in abundance on *Asclepias*, *Petalostemon*, *Melilotus*, and several other plants. The Raus report that mating occurs on flowers. The night is spent clinging to low vegetation (e.g., *Asclepias*) and individuals sometimes rest on vegetation during the heat of the day. In Kansas, the species is on the wing from June well into September; during this time it has several generations, the life cycle, from egg to adult, requiring not more than a month.

Hunting behavior.—Females search for grasshoppers in grass and other low vegetation, particularly bunch-grass. Often they land on a clump of grass and walk down inside; if a grasshopper flies out they pursue if swiftly on the wing. Very commonly they fail to pursue it successfully, perhaps being deceived by the cryptic coloration of the hopper when it lands on the soil. If a female succeeds in leaping on the back of a hopper, she embraces it firmly with her legs and mandibles, and in the ensuing struggle bends her abdomen beneath the body of the hopper and stings it quickly one or more times at random on the ventral side. The grasshopper immediately ceases to struggle and the wasp then stings it once more, rather slowly, on the ventral side of the thorax, probably through the cervical membrane. She may then lap up fluids exuding from the wound or from the mouth-parts of the grasshopper for a minute or two (note No. CY73).

Apparently any short-horned grasshopper of moderate or rather large size is found suitable as prey. Adults are most commonly used, but there are a few records for last-instar nymphs (see Table I).

Carriage of prey.—The prey is dragged over the ground in a characteristic manner which has been noted by many observers. The wasp spreads her legs wide and straddles the grasshopper, holding the base of the antennae in her mandibles and supporting the prothorax with her front legs. Walking on the middle and hind legs, and often buzzing the wings at the same time, she proceeds rapidly forward over the ground. The grasshopper often weighs much more than the wasp and frequently extends out behind the wasp a considerable distance. The grasshopper is invariable held dorsum-up, and its hind legs drag along behind. The sight of such a pair proceeding over the ground is enough to cause even the most blasé of persons to stop and stare.

Since *P. atratus* nests in much the same area in which it hunts for grasshoppers, the prey is

usually carried only a short distance (a few centimeters to several meters) before it is deposited while the wasp searches for a place to dig the nest. Rarely is the hopper merely dropped on the ground; rather it is placed in or beneath a clump of grass or a few centimeters up in an herb. The prey is often moved from place to place as the wasp searches for a suitable nesting site or digs a bit here and there. Once the nest is begun, the wasp may visit the grasshopper occasionally and commonly moves it to a new place closer to the burrow.

According to Strandtmann, the one individual which he observed dug the nest first and then captured a grasshopper and carried it to the nest. However, he notes that apparently the wasp paralyzed the prey immediately and without a struggle, "for it never moved, except for twitchings of the antennae and tarsi." In all probability this grasshopper had been stung previously and hidden in the vegetation while the wasp dug the nest. In all of the numerous observations of Williams, the Raus, and myself, this species has never been seen to prepare its nest until after the prey has been captured and paralyzed.

TABLE I

PREY RECORDS FOR PRIONONYX ATRATUS

SPECIES	NOTE NO. OR SOURCE
Acrididae	
Acridinae	
Ageneotettix deorum deorum Scudd., adult ♀	CL63
Aulocara elliotti Thom., adult	Williams, 1913
Mermiria neomexicana Thom., adult ♀	Williams, 1913
Oedipodinae	
Arphia xanthoptera Burm., nymph	Rau, 1918
Dissosteira carolina L.	Rau, 1918; Peckham, 1898
Pardalophora phoenicoptera Burm., adult ♂	HE57
Spharagemon collare Scudd., nymph	374
Trimerotropis citrina Scudd., adult ♀ ♀	HE46, 767
Cyrtacanthacridinae	
Melanoplus angustipennis Dodge, adult ♂ ♂	HE47, CY58, CY79, CL58, CL61
M. arizonae Scudd., adult ♀	573
M. bispinosus Scudd., adult ♂, ♀	HE83, HE119
M. bivittatus Say, adult ♀	CL74; Rau, 1922
M. devastator Scudd.	Coquillett, 1886
M. differentialis Thom., adult	Williams, 1913; Rau, 1918
M. femur-rubrum Deg., adult	Rau, 1918
M. foedus Scudd, adult ♂	HE66
M. lakinus Scudd., adult	Williams, 1913
M. spretus Walsh	Rau, 1918 (after Riley)
M. spp., adult ♀ ♀	CL59, CL62
Schistocerca lineata Scudd., adult ♂	CY76

Digging the nest.—The wasp uses her mandibles to loosen the soil or break it into lumps; she removes the soil from the burrow with the front legs assisted by the mandibles and scrapes it back a short distance (1–3 cm.) from the entrance. She moves in and out of the burrow very rapidly, "mechanically, like a toy wound up", to use an apt expression of the Raus. Rather commonly a hole is abandoned after the wasp has dug down a short distance; when this happens, the wasp turns around and fills it as rapidly as she dug it, packing the soil with her head and sometimes even scraping soil over the surface for concealment. Wasp No. HE47 began a burrow at 1811 on July 28, 1952, then at 1820 refilled the burrow and began a new one 25 cm. away in a footprint. At 1828 she also abandoned this hole and for two minutes walked about in an irregular pattern, then started a new nest two meters away. This was completed at 1842 (total time, 12 minutes) and she retrieved her grasshopper, which had been left on top of a flat tuft of grass near the first hole. She carried the hopper to within 15 cm. of the nest, left it and went into the nest, came out and carried the hopper to the edge of the hole, then backed in and pulled the hopper behind her by the antennae. Another individual (No. CY64) required 15 minutes to complete her nest, another (CL58) 17 minutes, and still another (CY58) 20 minutes. Williams timed one individual and found that she required 34 minutes to dig her nest, but part of this time was taken up by three visits to the prey. The Raus also noted that these wasps usually fill up burrows which they abandon, but they watched one individual which abandoned six successive holes without filling up any of them.

Williams found the nests he dug to have a

nearly vertical burrow leading to a horizontal cell, and therefore to be L-shaped; one nest he measured was 2 inches deep. The Raus found the burrow to be about 3/8 inch in diameter, starting vertically and curving gradually to the cell; they give 3 to 4 inches as the usual length of the burrow and 1½ inches as the usual depth of the cell. Strandtmann's nest had a gently inclined burrow which suddenly dipped down vertically and entered the horizontal cell; the burrow was 6 inches long, the cell 3¼ inches below the surface.

In the present studies (as also noted by the Raus) it appeared that nests were relatively constant in size and form regardless of the type of soil in which they were constructed. For this reason I have combined the data from all 17 nests which were dug. Burrow length (including cell) averaged 10.5 cm. (6.5–15 cm.); depth of the bottom of the cell from the surface averaged 6 cm. (4–9 cm.). Cell length varied from 2.5 to 5 cm. and cell diameter from 1.2 to 1.8 cm.; burrow diameter always approximated one centimeter. The figures reported by earlier workers fall within these extremes. Nest types included the L-shaped nest reported by Williams (fig. 1, A), the curved burrow of the Raus (C) and the diagonal burrow of Strandtmann (B), though without the vertical dip which he found. The three types of nest grade imperceptibly into one another, but in general it may be said that 3 of the 17 nests were L-shaped, 8 curved, and 6 diagonal. Thus individual or ecological variation appears to account readily for the apparent lack of agreement in the observations of earlier workers.

Placement of prey and oviposition.—The grasshopper is placed in the nest in the manner described above, i.e., it is dragged to the edge of the burrow, then pulled in by the antennae. Oviposition is completed in a matter of seconds and the wasp begins filling her burrow. The grasshopper is invariably found to be head-in; indeed, no other orientation is possible, since the burrow and cell are not large enough to turn the grasshopper around. The hopper is nearly always dorsum-up, although occasionally it tilts slightly to one side or another. Strandtmann's sketch shows the grasshopper lying venter-up in a cell of unusually large size relative to the prey. This may be an instance of abnormal behavior, or the grasshopper may have been turned over accidentally in the course of digging.

The egg is slender, strongly curved, and about 6 mm. long. The position in which the egg is laid is constant. It is glued to the membrane just above one of the hind coxae, and curves backward over the base of the femur. This has been noted by all who have worked on the species, and Williams' figure 6 shows the position of the egg nicely.

Closing the nest.—*P. atratus* closes the nest with the same speed and efficiency she exhibits in digging it. Very soon after placing the grasshopper in the nest, she reappears at the entrance, scrapes soil rapidly from the pile at the entrance into the burrow, then turns around, rushes into the nest head-first, and presses the soil in place in the burrow with her head. She uses the ventral portion of the head, especially the clypeus and spread mandibles, for packing the burrow, and during this process emits a loud buzz. Very soon she again appears at the entrance, scrapes some more soil into the burrow, then re-enters and presses the soil into place again. These actions are repeated quickly many times, until the burrow is filled level with the surface of the soil, an operation which may require no more than three to five minutes. The body is always held nearly vertically during the packing of the burrow. The Raus note that when the burrow is nearly full the wasp may pick up chunks of earth and break them up with her head in the burrow, "rubbing and pressing down the soil with them until they [become] part of the firm part of the pulverized earth." Having filled the burrow, the wasp then rakes sand in various directions over the place and frequently picks up lumps of soil, twigs, and other objects and places them over the nest. These actions may take considerably longer than the actual filling of the burrow.

After completing the filling and concealment of the nest, the wasp flies off and not uncommonly begins to hunt another grasshopper immediately. One individual observed by Williams captured another grasshopper only ten minutes after completing her previous nest. Individuals apparently make consecutive nests in the same small area. The time taken for the entire nesting process, from the stinging of the grasshopper to the concealment of the finished nest, may be no more than one hour. Presumably a female may complete several nests in a single day if conditions are favorable.

Development.—There is general agreement that the grasshoppers captured by *P. atratus* are paralyzed very lightly. Within a few hours after the nest is closed, the hopper begins to show spontaneous movements of the legs and antennae, and within a day is able to kick vigorously and move its wings, mouthparts, and antennae considerably. Probably such movements are restricted within the confines of the narrow cell, but in a rearing tin they are pronounced and make rearing difficult, since the egg is often dislodged.

The following extract from my notes (No. HE47) will illustrate the progessive development of the wasp larva on the grasshopper and the eventual death of the hopper:

July 28 (1952): Nest completed 1855; dug out at that time and contents placed in tin. Hopper is *Melanoplus angustipennis*, adult ♂; egg in usual position.

July 29: Hopper is very active, showing much

movement of the legs, but is unable to move about in a co-ordinated manner.

July 30: Condition of hopper same. Egg had not hatched 0900 but at 2100 small larva had begun to feed through the membrane above the hind coxa.

July 31: Condition of hopper same. Larva about 4 mm. long, body external but head extending inside the body through the coxal membrane.

August 1: Hopper still responds to stimulation, but shows no spontaneous movements. Larva is 8 mm. long, feeding in same manner.

August 2: Hopper dead. Larva about 18 mm. long, feeding in same position, extending its head and thorax into the body through the coxal cavity. Entire thorax of hopper hollowed out as well as much of abdomen.

August 3: Larva is about 20 mm. long and is lying free from the now completely dismembered grasshopper.

August 4: Cocoon is complete.

August 27: Adult ♂ *P. atratus* emerged.

Three others were reared successfully (HE57, CL58, CL61) with very similar results. Without exception the egg stage required two days, the larval stage four. Two of the larvae were preserved as they began to spin and have been described elsewhere (Evans and Lin, 1955). One other spun its cocoon on August 5 and gave rise to an adult on August 29.

Natural enemies.—Williams noted a small fly lurking about the nest of a *P. atratus* as it was being dug; when the wasp disappeared into the tunnel the fly larviposited at the base of the front wing of the grasshopper. The Raus noted a small fly hovering around a nest and apparently trying to enter while the wasp was filling. When they dug this nest only fifteen minutes later, the egg and the prey were "teeming with tiny Dipterous larvae." They found other instances of this, and in every case the egg of the wasp was destroyed before the maggots consumed the grasshopper. Adams (1915) found *Metopia leucocephala* Rossi (Sarcophagidae, Miltogramminae) hovering about an *atratus* nest. In the present studies, miltogrammines were noticed only once hovering behind an *atratus* as she carried her grasshopper (CL65); the flies were not captured, but they appeared to belong to the genus *Senotainia*. *S. trilineata* (v.d.W.) commonly attacks *Sphex ichneumoneus* L. (Ristich, 1953) and is not at all host-specific, so it is quite possible that it attacks *Priononyx atratus*. Flies of the genus *Senotainia* larviposit on the prey before it is placed in the nest, while flies of the genus *Metopia* are reported to enter nests for larviposition. It is probable that both genera attack *Priononyx*.

There is also much evidence that this species is attacked by the cleptoparasitic stizine wasp *Stizoides unicinctus* (Say). Williams found this species smoothing over a filled burrow of *P. atratus*; when he dug this nest he found that the *Priononyx* egg had been destroyed and another, shorter egg laid on the grasshopper. I have several times seen *S. unicinctus* in close association with filled nests of *atratus*, but have never made observations on the exact relationships between the two species.

Adult *P. atratus* occasionally fall prey to asilids, and I once found an adult on the blossoms of *Petalostemon* in the clutches of a reduviid bug, *Apiomerus spissipes* (Say) (note No. 309).

Priononyx thomae (Fabricius)

This is essentially a Neotropical species, ranging from Argentina north to the southern part of the United States. There are several published notes on its biology, including those of Hartman (1905) made in Texas, those of Williams (1913) made in Kansas, and those of the Raus (1918) made in Missouri. My observations on this species are rather brief, consisting of two notes made at McKinney Lake, Kearny Co., Kansas, on August 20, 1952 (note Nos. HE108, 109), and one note made near Port Isabel, Cameron Co., Texas, on June 24, 1956 (note No. 1175).

As in the case of *atratus*, the adults visit a wide variety of flowers. Williams (1913) reports that they pass the night and periods of unfavorable weather clustering on weeds. Like *atratus*, the species does not seem to be strongly restricted ecologically, and occurs in many types of open country. Hartman and the Raus found the species nesting in relatively hard-packed soil, but I have found it nesting in relatively soft sand. Individuals apparently return to the same place again and again to nest; Hartman reports finding nine nests in an area only a few centimeters square, all apparently made by the same wasp over a period of several days.

Hunting behavior.—I have observed *thomae* hunting in bunchgrass in much the manner of *atratus*. The Raus found a female with her "sting buried deep" in a grasshopper's thorax for over a minute while the hopper struggled violently. Apparently *thomae*, like *atratus*, preys upon almost any short-horned grasshopper of suitable size which she is able to capture. The species which have been taken as prey of this species are listed in Table II.

Carriage of prey.—The wasp grasps the grasshopper by the base of the antennae with her mandibles, straddles it, the hopper dorsum-up, and proceeds rapidly forward, often moving her wings rapidly at the same time. The prey is commonly placed in a tuft of grass or a similar place of concealment while the wasp first seeks a place to dig and then digs her nest. During the digging, the wasp commonly visits the prey one or more times and each time carries it to a place closer to nest. Eventually the hopper is placed on the edge of the burrow and pulled into the nest by the antennae. Hartman, Williams, and

the Raus all agree that the prey is captured before the nest is dug.

Digging the nest.—The wasp makes use of her mandibles to break up the soil, which is then scraped with the fore legs into a pile a short distance from the entrance. Large pieces of earth are carried out with the mandibles. Hartman remarks that the wasp moves with "almost machine-like regularity . . . darting in and out so quickly and smoothly that I can best compare her movements to those of a rubber ball attached to the end of an elastic band". Hartman's wasp abandoned her first hole and filled it up before starting another. One wasp which I watched (No. HE108) started and abandoned six successive nests between 1730 and 1757, filling each hole at least partially with sand before leaving it, but in no case using the head to press the soil into place. This wasp was able to dig the length of her body in about two minutes. She began her seventh hole at 1758 and was still working on it at 1830

Placement of prey and oviposition.—All observers are in agreement that the hopper is placed in the cell head-in, dorsum-up, and the egg laid just above the hind coxa on either side. One end of the egg is glued to the coxal membrane and the other curved over the base of the femur, exactly as in *atratus*.

Closing the nest.—The burrow is filled from the mound of earth outside the entrance. The wasp first scrapes some of the soil into the burrow with her fore legs, then turns around and rushes into the nest and presses it into place with her head while buzzing loudly. She then reappears at the entrance and repeats the procedure. When the burrow is filled to the surface, she picks up lumps of earth and small pebbles which are lying about the entrance and places them in a pile over the entrance. These pellets are not selected carefully, but picked up quickly and without apparent discrimination. This has been noted by Hartman, the Raus, and myself, and seems to be very

TABLE II

PREY RECORDS FOR PRIONONYX THOMAE

SPECIES	NOTE NO. OR SOURCE
Acrididae	
Acridinae	
Amphitornus sp.	Williams, 1913
Aulocara sp.	Williams, 1913
Orphulella p. pelidna Burm., adult ♂	HE108
Oedipodinae	
Arphia xanthoptera Burm., adult	Rau, 1918
Dissosteira carolina L., adult	Rau, 1918
Encoptolophus subgracilis texensis Br., adult ♀	1175B
Cyrtacanthacridinae	
Paraidemona sp., probably fratercula Heb., adult ♀	1175A

when overtaken by rain and cool winds. The next morning at 0900 the hole was still open, but at 1915 the wasp appeared with a grasshopper which was stored in the nest in the usual manner. If this was a freshly caught hopper, as seems likely, then the wasp was capable of reversing the usual prey→nest sequence and utilizing a previously prepared nest.

The nest of this species is in every respect similar to that of *atratus*, except that it averages slightly smaller in all dimensions due to the slightly smaller average size of this species. The burrow may be vertical, curved, or oblique; the cell is elongate and horizontal. Hartman found the cell to be about two inches below the surface, the Raus about one inch. In the two nests which I dug in Kearny Co., Kansas, the burrow length (including the cell) was 8.5 and 9 cm., the depth of the cell from the surface 5 and 7 cm. (between 2 and 3 inches). In both cases the cell was about 1 cm. in diameter and 2.5 cm. in length.

characteristic of this species. The Raus watched one pile cinders over the entrance for sixteen minutes; the wasp then flew about the nest for two minutes, and finally added a few more cinders to the pile. This wasp took fifty-four minutes to dig her burrow, provision it, and close and conceal the nest. As noted earlier, wasps often prepare successive nests in very close proximity.

Development.—One larva was reared to maturity in the present studies (No. HE109). The egg was laid on August 20 and hatched on the 22nd. The larva fed in the manner described for *atratus* and reached full size and began to spin on August 26. The larva was preserved and has been described elsewhere (Evans and Lin, 1955). As in *atratus*, the grasshopper remains lively for several days, until the larva consumes the vital organs. The Raus dug out a nest which had been prepared on July 14 and obtained a completed cocoon on July 19; a female wasp emerged

from this cocoon on August 15. Apparently this species, like *atratus*, has a series of generations throughout the summer.

Natural enemies.—There appear to be no records of miltogrammine flies attacking this species, although such attacks may well be common. The Raus discuss at considerable length the apparent cleptoparasitic relationship of *Stizoides unicinctus* with *P. thomae.*

Priononyx pubidorsus (Costa)

This wasp, like the preceding two, is widely distributed and not uncommon throughout the southern half of the United States. The only published notes on its biology known to me are those of Rau (1922), under the name *bifoveolatum.* I have observed the nesting of this species three times, once at Lake Charles, La., August 2, 1953 (No. 579) and twice at Arcadia, Florida, April 27, 1955, and March 27, 1957 (Nos. 964 and 1029).

Rau watched a single individual carrying her grasshopper (*Melanoplus scudderi* Uhler, Cyrtacanthacridinae) along a mud bank with sparse vegetation near St. Louis, Missouri. The manner of carriage was the same as in *atratus* and *thomae*, and as in those species the hopper was left at the mouth of the burrow and pulled in from the inside. The nest was "a small, sloping pocket in the earth, similar to that of *P. atratum* but somewhat smaller". The egg was laid at the base of a hind leg in the same manner as in *atratus* and *thomae.*

The individual I observed at Lake Charles, Louisiana, was carrying a grasshopper along a sandy roadside in the usual manner. The hopper was deposited in a clump of grass while the wasp walked about and eventually began a nest a short distance away. Since I was pressed for time, I captured the wasp and prey before the nest was finished; the grasshopper was determined as *Trimerotropis citrina* Scudder, adult ♀ (Oedipodinae).

Wasp No. 1029, at Arcadia, Florida, had at 1615 just begun a nest in a heel print in sand along the banks of the Peace River. The grasshopper (*Melanoplus femur-rubrum propinquus* Scudd., adult ♂) was lying on top of a weed 3 cm. above the ground about half a meter away. At about five minute intervals the wasp left her digging to visit the prey, but she did not move it. In all she visited the prey four times. Finally, at 1650, she grasped the hopper and carried it over rough terrain directly to the edge of the burrow, then went in, turned around inside, and drew the hopper into the burrow by the antennae. She reappeared in about a minute, then began filling. She was captured before the nest was completely filled and the nest dug out. The burrow was at a sharp angle with the horizontal, about 80°, and about 7 cm. long, leading to a cell 2 cm. long and 8 cm. beneath the surface (the burrow had been started from the edge of a heel print about 2 cm. deep). The hopper was in the cell dorsum-up, head-in, the egg laid above the hind coxa in the usual manner of this genus.

Wasp No. 964 began digging her burrow at 1035 in a small bare place surrounded by grass. She brought out the sand in large lumps carried in her mandibles and front legs, each time backing out about one centimeter from the entrance, dropping her sand, and scraping it back with her front legs. She flicked her wings constantly while outside the nest and made a slight buzzing noise while digging. In two minutes she had dug the length of her body. After 10 minutes she left the nest, making a few circles about it on the ground and then flying off in a straight line to her prey, which was lying on a small mound of sand two meters away. She carried it in the usual manner directly to the hole and then beyond it about 20 cm., where she placed it on top of a clump of grass 3 cm. above the ground. She then resumed her digging until 1055 (total time 20 minutes minus three for retrieving the prey). The sand accumulated in a small mound 1–2 cm. from the entrance. On finishing the nest, she went directly to her prey and carried it to the edge of the burrow, then went in and drew it in from the inside by the antennae. In 45 seconds she began filling. She would first scrape in a little sand, then go in head first to pack it, each time emitting 7–10 distinct buzzing sounds. As filling progressed, it could be seen that she packed with her head with the mandibles spread, the head going up and down vertically. At 1100 she had finished filling and began scuffing sand over the entrance. One small stick and one piece of cow dung were picked up and placed over the entrance. She then cleaned her antennae and mouthparts with her front legs and at 1107 flew off. She had cleaned herself in a similar manner before each of her trips for her prey. The nest was very shallow and the egg was dislodged during the digging. The grasshopper was a nymphal *Scireletica marmorata picta* (Scudder) (Oedipodinae).

A second individual (No. 964b) was seen that same day with a nymphal grasshopper of the same species. This individual dug a short burrow and then abandoned it, filling it partially with sand as she did so. The grasshopper was collected and remained alive for five days, when it died and began to deteriorate.

Natural enemies.—As No. 1029 was visiting her prey during the digging, a small fly hovered behind her. Later, a fly was noted perched on a lump of earth over looking the nest. Just after the hopper was placed in the nest, and while the wasp was still inside, this fly darted into the nest and immediately came out. I do not know exactly when larviposition occurred—it may have occurred earlier than this—but at any rate it obviously did occur at some point. The next morning the egg had disappeared and was replaced by a mass of small maggots. At the end of four days these maggots had consumed the

entire grasshopper except for the exoskeleton and had entered the soil for pupation. Ten specimens of *Senotainia rubriventris* Macq. (det. C. W. Sabrosky) later emerged from these puparia.

Priononyx striatus Smith

This is a larger species than the preceding three. Its known range extends from Argentina north to Arizona and Nevada. Apparently it has not been recorded from Texas, but on June 23, 1957, I took a female at Port Isabel, Cameron Co., Texas, on flowers of black mangrove (*Avicennia nitida* Jacq.). I have made no observations on the nesting of this species myself. I am greatly indebted to Ernest C. Bay for the following notes and the accompanying photographs, made on January 3, 1956, at La Ventosa, Oaxaca, Mexico.

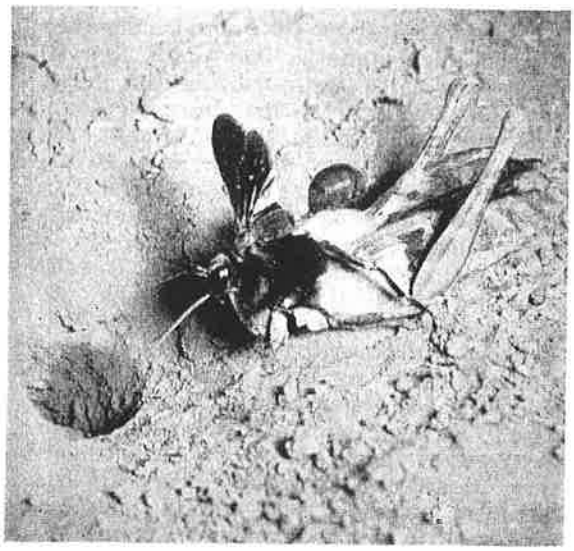

FIG. 2.—Female *Priononyx striatus* approaching nest with her prey, a female *Xyleus* sp. Note that the wasp's mandibles grasp the antennae of the grasshopper and the front legs the lower sides of the thorax. The middle and hind legs of the wasp are thrust out to the side for walking and the wings are extended. From a Kodachrome by Ernest C. Bay.

Mr. Bay observed a female digging her nest in a slopping sandy road cut in scrubby, semi-desert country. Her grasshopper, a female *Xyleus* sp., probably *centralis* Rehn (Oedipodinae), was lying paralyzed on the ground about 30 cm. away. After digging for about an hour, the wasp came after the grasshopper and carried it to the edge of the burrow. The grasshopper was very much larger than the wasp, measuring 58 mm. (exclusive of the wings) to the wasp's 27 mm. The wasp held the base of the hopper's antennae in her mandibles and grasped the bottom of the prothoracic lobes with her front tarsal claws; she walked on her middle and hind legs and vibrated her wings rapidly (fig. 2). After leaving the grasshopper at the edge of the burrow, she entered the nest, turned around inside, and drew the hopper in by the base of the antennae. Oviposition and closure occurred rapidly, and the wasp was not seen to place pellets of earth over the nest entrance. This nest was dug out and found to be about 9 cm. deep. The grasshopper was head-in, lying on its side, with the wasp's egg laid on the base of the hind coxa in the usual manner of this genus (fig. 3).

This species has also been studied by Conil in Argentina, under the name *Enodia fervens* (Willink, 1951). According to Conil, the wasps prepare their nest first and then hunt their prey, *Schistocerca cancellata* (Serville) (Cyrtacanthacridinae). A single locust is used per nest. In most respects Conil's observations appear to agree well with those of other workers on *Priononyx*, and it seems strange that his wasps apparently dug their nests before taking their prey.

FIG. 3.—Cell of *Priononyx striatus* cut away from the side. The burrow approaches from the left. Note the position of the egg on the base of the hind leg of the grasshopper. From a Kodachrome by Ernest C. Bay.

Priononyx subfuscatus (Dahlbom)

This widely distributed Old World species has been studied in Europe by Ferton (1902, 1905, 1921) and in China by Piel (1935). In every respect it closely resembles the North American species of the group.

The prey consists of adults and nymphs of at least eight genera belonging to all three major subfamilies of Acrididae. The wasp usually stings the grasshopper twice, then may lap up the fluids exuding from its mouth. The prey is then placed on a tuft of vegetation while the wasp seeks a place to dig. The nest is simple and of the same form as in *atratus* and other North American species. The grasshopper is carried to the nest and placed in it in the usual manner; the curved egg is attached to the membrane of one of the posterior coxae. Paralysis of the prey is very light. The burrow is filled rapidly, the

pile at the entrance being used as fill; the soil is pressed in the burrow with the head and the surface carefully leveled when the burrow is full.

Prionoyx striatulus (Brèthes)

This South America species has been studied in some detail by Liebermann (1931) under the name *Sphex caridei* Lieb. In Argentina it is an important enemy of the destructive locust *Trigonophymus arrogans* Stål (Cyrtacanthacridinae). According to Liebermann, the burrow is dug before hunting begins and may eventually contain up to three cells; it is vertical and rather shallow, and apparently is closed while the wasp is away hunting. The stinging of the prey is said to take a considerable time, after which the wasp cleans herself and then straddles the grasshopper and drags it to her burrow. The manner of carriage does not appear to differ from that of the North American *Prionyx*. On approaching her nest, the wasp drops the prey, then opens and enters her nest. She then returns to her prey and drags it backwards to and into the nest. After oviposition the burrow is filled rapidly and the surface eventually leveled carefully, the wasp often picking up small pebbles and putting them in place over the nest.

Prononyx spinolae (Kohl)

This neotropical species apparently belongs to *Prionyx*, although the notch in the anterior margin of the clypeus is weakly developed. However, if Claude-Joseph's observations (1928, under the name *Sphex chilensis* Spinola) are correct in all details, the species departs radically from the usual nesting behavior of the genus.

Claude-Joseph reports that the species nests in colonies of up to about a hundred individuals. The burrows are dug horizontally or obliquely in clay banks and reach a depth of 10 to 12 cm. The cells are ovoid, with smooth walls, and are prepared more or less in series starting at the bottom of the burrow and working back toward the entrance. They are separated by only a small barrier of sand; the final cell is close to the surface and covered by only a little earth.

The prey consists of two or three species of *Acridium* (*?=Schistocerca*), both adults and immatures. The grasshoppers are carried to the nest on the wing; the wasp lands from 10 to 20 cm. from the nest, then deposits the prey, opens the nest, returns to the prey and carries it into the nest. When she leaves she again closes the nest with a small amount of soil. Five to ten grasshoppers are provided for each cell. The egg is laid on the first hopper in the cell, on the venter of the thorax between the hind legs, and requires about a week to hatch. The larva feeds for about ten days before reaching maturity.

DISCUSSION

In reviewing the ethological data on various species of *Prionyx*, one is at once impressed by the close similarity in the nesting behavior of all the Nearctic and Palaearctic species which have been studied. Indeed, if there are real differences in the behavior of these species they have yet to be found. Since the species of *Prionyx*, at least in North America, are not strongly restricted ecologically and are often more or less sympatric, one wonders why they do not compete seriously with one another for prey and for nesting sites. The answer is perhaps that short-horned grasshoppers are always abundant and virtually any species is acceptable; furthermore, since any more or less bare place is adequate for nesting, the number of potential nesting sites is almost infinite. Actually, one rarely finds two or more species of *Prionyx* nesting in close proximity, and there may be ecological preferences which are not apparent from the existing data.

It may be of interest to list some of the ethological characters shared in common by all *Prionyx* (at least so far as known):

(1) The prey always consists of Acrididae.
(2) The prey is paralyzed lightly and remains fairly active for several days.
(3) The wasp often laps the fluid exuding from the grasshopper's mouthparts following stinging.
(4) The nest is built in a bare, flat place and is dug and filled with great rapidity.
(5) Abandoned incomplete burrows are generally partially filled up.
(6) The grasshopper is drawn into the cell by the antennae.
(7) The grasshopper is placed in the cell head-in, usually dorsum-up.
(8) The wasp uses her head for pressing the soil in place during the final closure of the nest.
(9) Various objects are placed over the filled burrow.

Some of the following characters are perhaps of greater importance than some of the above, but exceptions are known:

(10) The species are essentially solitary. Exception: *spinolae*, which nests in colonies.
(11) Prey carriage is forward over the ground, the prey being straddled and held by the antennae; the wings may be used for added propulsion on the ground. Exception: *spinolae*, which flies with the prey.
(12) The nest is prepared after the prey is captured. Exception: *striatulus*, *spinolae*, *?striatus*.
(13) The nest is shallow and unicellular. Exceptions: *striatulus*, *spinolae*.
(14) One grasshopper is provided per cell. Exception: *spinolae*.

(15) The egg is laid with one end attached to the hind coxal membrane. Exception: *spinolae*, which lays the egg on the venter between the hind coxae.

(16) The prey is usually placed on a tuft of grass or slight elevation while the wasp digs her nest. Exceptions: *striatulus*, *spinolae*.

These exceptions are of considerable interest. n every case they represent a convergence toward ıe genus *Sphex*, which usually nests in colonies, ies with the prey, makes moderately deep, multi-ellular nests with several prey per cell, lays the gg on the venter of the pro- or mesothorax, and repares the nest before hunting prey. As I have lready noted, the usual clypeal notch of *'riononyx* is nearly wanting in *spinolae*. This otch is probably an adaptation for holding on to ıe rather thick antennae of Acrididae, but it is osent in *Sphex*, which grasps the very much ıinner antennae of Tettigoniidae. Also, the aws of *spinolae* have only two teeth, while most :her *Priononyx* have four to six teeth. In *phex* and in *Palmodes* there are two teeth on the aws.

Structurally, *Priononyx* is more specialized than *phex* with regard to the claws, the wing venation, ıe clypeal notch, and the shape of the abdomen. it is a derivative of *Sphex*, then such a species *spinolae* would seem to provide an excellent pro-type. But in its behavior *Priononyx* is in many ays more primitive than *Sphex* (and than *P. inolae*). In the wasps, the sequence prey→ st is clearly more primitive than the sequence st→prey, and shallow, unicellular nests con-ining a single host specimen are clearly more imitive than deeper, multicellular nests con-ining several prey per cell. For the present I erely wish to pose this enigma; its solution must vait a careful consideration of the structure and hology of the remaining genera of Sphecini.

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OBSERVATIONS ON TWO SPECIES OF PINE CONE FEEDING DEATHWATCH BEETLES IN CALIFORNIA (COLEOPTERA: ANOBIIDAE)

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Allen (1956) observed that *Ernobius granulatus* Conte attacks first year cones of longleaf pine, *nus palustris*, in the southeastern United States ıere it causes serious damage to cone crops. sig (1936) mentions that *E. cupressi* Van Dyke (*E. conicola* Fisher) breeds in green and dry cones and dead wood of Monterey cypress, *Cupressus macrocarpa*. My recent studies of insects infesting the cones and seeds of pines in California, have shown that each year a small percentage of the cones of Jeffrey pine, *Pinus jeffreyi*, never reach maturity and cone growth has ceased early in the second year of cone development. Dissection of these "aborted" cones revealed the

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