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FURTHER STUDIES ON THE WASPS OF JACKSON HOLE, WYOMING (HYMENOPTERA, ACULEATA)

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ABSTRACT.— In a report published in 1970, 190 species of wasps were reported from Jackson Hole, Wyoming, and notes were presented on the biology of several ground-nesting species. In this paper, records of 18 additional species are presented. A short account of the biology of a ground-nesting species, *Tachysphex aethiops* Cresson, is included. Also included are accounts of four species that accepted wooden trap nests during the summer of 1971: *Symmorphus cristatus* (Saussure), *Ancistrocerus adiabatus* (Saussure), both Eumenidae; *Trypoxylon aldrichi* Sandhouse, *Passaloecus cuspidatus* Smith, both Sphecidae. Notes are presented on nest structure, prey, and parasites in each instance.

This is a brief supplement to my study of the ecology and behavior of the wasps of Jackson Hole, Wyoming (Evans, 1970). That paper summarized three summers of study over a six-year period (1961-1967). I returned to Jackson Hole in the summer of 1971, primarily to round out my work on the digger wasp genus *Philanthus*. My data on *Philanthus* will be saved for a proposed survey of the comparative behavior of members of that genus. The present paper includes additions to the faunal list and notes on the nesting behavior of five species not or only briefly studied earlier.

In my 1970 paper I reported 190 species of wasps from Jackson Hole. Eighteen species are here added to the list, bringing the total to 208. Since my earlier studies were concerned with ground-nesting wasps, I put out 300 wooden trap nests in 1971, hoping to learn something of the distribution and behavior of twig-nesting species. Although the percentage of acceptance was high, only four species of wasps occupied these nests. The results of the trap-nesting work are summarized in the last section of this paper.

A general description of the study areas will be found in my 1970 paper. Study area no. 3, listed as 4 miles SW of the Elk post office and indicated by the word *Elk* in the text of that paper, should perhaps be qualified, since there is evidently no longer a post office at Elk. This area is on the Snake River some 9.5 km southwest of Moran Junction, about 11 km south of the research station. For the sake of consistency, I have continued to call it Elk in the present paper.

I am, as usual, much indebted to the authorities of Grand Teton National Park for permission to collect specimens for identification, and particularly to the staff of the Jackson Hole Biological Research Station for use of their facilities. I am indebted to several specialists for identifying certain Sphecidae: Frank Parker (Astatinae), David Vincent (*Passaloecus*), Richard Bohart (*Gorytes*), and Joanne E. Slanky (*Nitelopterus*). Insect prey were identified by specialists of the Entomology Research Laboratory, U.S. Department of Agri-

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culture, as indicated in the text. Spider prey were identified by H. W. Levi of the Museum of Comparative Zoology.

I. Additions to the Faunal List

Family Chrysididae

Omalus cressoni (Aaron). Pilgrim Creek, 1 ♀, note no. 2299B: trap-nest collected 22 Aug. 1971, 1 ♀ emerged 7 May 1972 (nest was that of *Passaloecus cuspidatus;* female of host had emerged 24 April 1972).

Family Tiphiidae

Publication of Allen's (1971) study of the genus *Tiphia* in western North America permits me to clarify the species listed as "near *essigi*" and to add two additional species to the list.

Tiphia anguis Allen. This species was described by Allen (1971), the ♂ holotype and several paratypes (2 ♀♀, 3 ♂♂) being from Elk, 4-10 July 1964, with additional paratypes from Moran (1 ♀, 1 ♂, 11 Aug. 1964) and from Jenny Lake (1 ♀, 20 July 1936).

Tiphia barberi Allen. Allen reports 3 ♀♀ and 1 ♂ from the Grand Tetons, collected by E. C. VanDyke in June 1938.

Tiphia nevadana Cameron. This is a senior synonym of *T. essigi* Allen, and the records for "sp. near *essigi*" from Moran and Elk should be transferred to this species; they are so recorded by Allen (1971).

Family Masaridae

Pseudomasaris marginalis (Cresson). Death Canyon, 17 July 1971, 3 ♀♀, 2 ♂♂, ♀♀ on *Phacelia sericea.*

Pseudomasaris zonalis (Cresson). Pilgrim Creek, 2 Aug. 1971, 2 ♀♀, 2 ♂♂; Death Canyon, 17 July 1971, 2 ♀♀, 1 ♂.

Family Pompilidae

Anoplius (*Pompilinus*) *insolens* (Banks). Signal Mt., 7300-7700 feet, 28 July 1971, 1 ♀.

Family Sphecidae

Subfamily Pemphredoninae

Passaloecus relativus Fox. This species should be deleted from my original list. David Vincent, of Utah State University, is currently studying this genus and has examined the specimens reported as *P. relativus* and found them to consist of the following three species.

Passaloecus cuspidatus Smith. Moran, 6 July - 23 Aug. 1964, 1967, 4 ♀♀, 2 ♂♂, 1 ♀, note no. 1992: taken as prey of *Philanthus pulcher;* Huckleberry Hot Springs, 11-31 Aug. 1967, 2 ♀♀; Snake River, Elk, 9 Aug. 1967, 1 ♀, note no. 2144: taken as prey of *Philanthus pacificus.* This species accepted trap nests in considerable numbers during 1971; the results of trap nesting are discussed on a later page.

Passaloecus armeniacae Cockerell and Fox. Moran, Aug. 1967, 2 ♀♀.

Passaloecus melanocrus Rohwer. Moran, July-Aug. 1967, 1 ♀, 1 ♂.

Subfamily Astatinae

Astata mexicana Cresson. Signal Mt., 7300-7700 feet, 28 July 1971, 5 ♂♂.
Astata nevadica Cresson. Signal Mt., 7300-7700 feet, 28 July 1971, 1 ♀.

Diploplectron brunneipes (Cresson). Pilgrim Creek, 2 Aug. 1964, 1 ♀; String Lake, 3 Aug. 1961, 1 ♀; Snake River, Elk, 14-26 July 1971, 1 ♀; Moran, 19 July - 17 Aug. 1967, 1 ♀, 2 ♂♂, 1 ♀, note no. 2163: taken from nest of *Philanthus pacificus*, as prey.

Diploplectron fossor Rohwer. Moran, 4-30 July 1961, 2 ♀♀, 2 ♂♂; Snake River, Elk, 9 Aug. 1967, 1 ♀, note no. 2144: taken from nest of *Philanthus pacificus*, as prey.

Diploplectron peglowi Krombein. Moran, 18 July 1967, 1 ♂.

Subfamily Larrinae

Nitelopterus laticeps Ashmead. Pacific Creek, 12 Aug. 1971, 1 ♀. This species has been studied by Powell (1967) under the name *N. californicus* (Ashmead).

Nitelopterus maurus Rohwer. Moran, July 16, 1961, 2 ♂♂. This record was originally entered under the name *N. cyanurus* (Rohwer), but I am informed by Joanne E. Slansky that they should be called *N. maurus*.

Subfamily Nyssoninae

Gorytes flagellatus Bohart. Snake River, Elk, 4-10 Aug. 1964, 1 ♂; Moran, 6 Aug. 1964, 1 ♀ on *Perideridia gairdneri*.

Gorytes provancheri Handlirsch. Signal Mt., 7300-7700 feet, 28 July 1971, 2 ♀♀.

Subfamily Philanthinae

Cerceris calcohorti Rohwer. Snake River, Elk, 29 July 1971, 2 ♂♂, note no. 2260: taken from nest of *Philanthus zebratus nitens* Banks, as prey.

II. Notes on a Ground-nesting Sphecid

Tachysphex aethiops Cresson

This is a common wasp in sandy soil along the Snake River, but I was able to report only one incomplete, parasitized nest in 1970. At 4:00 p.m. on 16 August 1971, I observed a female at a nest in firm, flat sand about 5 meters from the river (area MOR-A2 of the 1970 paper). The hole was open and there was a low, spreading mound of sand, 8 cm wide by 5 cm long, in front of the entrance. The female emerged from the burrow periodically and rose in the air to a height of 0.8 m, with her feet dangling, facing the burrow. The significance of this behavior was not apparent, as she soon began filling the burrow persistently, emerging again and again to scrape in sand from the entrance. I captured the wasp when the burrow was nearly filled and excavated the nest. It proved to be surprisingly shallow, an oblique burrow only 10 cm long terminating in a cell only 4 cm deep. This cell contained a paralyzed immature acridid grasshopper, *Trimerotropis* sp., probably *T. suffusa* Scudder [det. A. B. Gurney], bearing the egg of the wasp. Immediately beyond it, separated by only a thin barrier of soil, there was a second cell, containing an immature acridid of the same species, also bearing an egg. In both cases the egg was laid on the "throat" of the prey, with one end glued to the left front coxal membrane, the egg extending transversely over the right coxa, its posterior end free. Both cells obviously contained the full complement of prey, as the female was

making a final closure, and both grasshoppers exceeded the wasp in size (12 and 17 mm in length, as compared to 11 mm for the wasp). This compares favorably with data reported in 1970, for that nest also contained a single immature grasshopper somewhat larger than the wasp.

III. Results of Trap Nesting

During the first week in July 1971, I put out 300 trap nests, about half near the research station at Moran and half along Pilgrim Creek in Teton National Forest. Techniques were those described by Krombein (1967) in his well-known book on this subject; for terminology see his book, p. 18. Of the 300 nests, 200 were pieces of pine of the type used by Krombein, while 100 were sections of *Sambucus* stems cut to about the same length (15 cm), part of them bored and part with the pith intact. The *Sambucus* stems proved unsuccessful, only one being accepted by a wasp and 5 by bees. Of the 200 standard type, 65 were accepted by wasps in the course of the summer, 57 by bees. Those accepted by bees were turned over for study to Stephen L. Clement of the University of California at Davis; they are not considered here except in cases of supercedure involving a bee and a wasp. Trap nests were overwintered in Massachusetts, and all emergence occurred in April and May, 1972, there being but one generation per year of these species in Jackson Hole.

Although the percentage of acceptance was reasonably high, I was surprised to find that only four species of wasps (2 Eumenidae, 2 Sphecidae) were involved. Many other twig-nesting wasps are recorded from Jackson Hole, but evidently they did not lend themselves to these techniques. Although these four species occurred in much the same habitats, the kinds and numbers of parasites emerging from the nests were very different. *Symmorphus cristatus*, for example, was very heavily parasitized by the miltogrammine fly *Amobia distorta* Allen, and the other two mud-users had a low incidence of parasitism by *Amobia*. On the other hand, the resin-user *Passaloecus cuspidatus* appeared to be immune from attacks by *Amobia*, although it was the only one of the four to be parasitized by *Omalus* cuckoo wasps. Table I summarizes the results of the rearing of parasites.

Table 1. Parasites reared from nests of trap-nesting wasps.

Species of Wasp	No. Nests	Approx. No. Cells	No. Parasites Reared		
			Amobia	Anthrax	Chrysididae
Symmorphus cristatus	25	75	36[1]	1	0
Ancistrocerus adiabatus	6	40	1[2]	1	2[3]
Trypoxylon aldrichi	14	50	2[1]	0	0
Passaloecus cuspidatus	20	120	0	1	6[4]

[1]*Amobia distorta* (Allen)
[2]*A. floridensis* (Townsend)
[3]*Chrysis caerulans* Fabr.
[4]*Omalus*, 3 species

Symmorphus cristatus (Saussure)

This was the most abundant wasp in trap nests and also the most heavily parasitized. Twenty-five trap nests were accepted, all at Moran. Most were associated with dead wood, either on the walls of log cabins or on stumps or standing or fallen dead pines and aspens. Only four of the nests were on live pines, one on a live willow. Traps accepted were from 0.3 to 2.5 meters high. Of the 25, 18 were in 4 mm borings, 7 in 6 mm borings. The number of cells per 13 cm boring was small compared to *Ancistrocerus adiabatus*: from 2 to 6, the majority having 3 or 4. Cell length varied from 8 to 24 mm (mean 15.5). Nest architecture was remarkably varied and is difficult to summarize. Closing plugs varied in thickness from 2 to 15 mm, most being 3 to 5 mm. As in Krombein's (1967) nests from New York and Virginia, all had an empty vestibular cell just inside the closing plug, and several of these cells were subdivided by partitions. Altogether the vestibular cells varied in length from 17 to 55 mm in length, with one exceptional one measuring only 5 mm. In addition to several having one or two partitions within the vestibular cell, two had barriers 3-4 mm thick (as compared to 1-2 mm thick partitions) essentially dividing the vestibular cell into two. For example, one nest had two cells at the end of the boring followed by two long, empty cells, 35 and 45 mm long, separated by a barrier 4 mm thick and closed on the outside by a plug 5 mm thick.

Intercalary cells, between filled cells, were also variable in occurrence and in length. In many cases they consisted of no more than two partitions separated by a space of only 1-3 mm; two nests had all or most of the cells separated by such double partitions, and one of these had one triple partition. One other nest had two distinct intercalary cells measuring 4 and 9 mm. The first cell was normally placed at the terminus of the boring, with no preliminary plug, but several had empty spaces preceding the first partition and cell, these spaces varying in length from 12 to 73 mm. A number of the more heavily parasitized nests had partitions that were partly destroyed by maggots when they were harvested; hence it is not possible to present accurate quantitative data on nest architecture.

Eggs were found in several cells, without exception suspended from the roof of the cell by a short filament, near the partition at the deep end of the cell. The prey are brought in after the egg is laid, from 3 to 10 (usually 4 to 6) being supplied per cell. Without exception the prey consisted of a single species of external, leaf-feeding beetle larvae (Chrysomelidae, Chrysomelinae [det. R. E. White]).

There were four instances of supercedure. In two cases *Symmorphus cristatus* had built 3-5 cells following 3-4 cells of the bee *Hoplitis* (*Formicapis*) *robusta* (Nylander).[2] In one case the bee superceded was an unidentified species of *Hylaeus*. In still another case a *Symmorphus* had filled a single cell deep in a boring and was

[2]Determination by Dr. G. C. Eickwort of Cornell University. Dr. Eickwort informs me that this species has usually been called *H. clypeata* (Sladen) and that *H. robusta* represents a new combination. Nothing has been published regarding the biology of this bee, but Stephen Clement and Richard Rust, of the University of California at Davis, are preparing a paper on this and several other species of *Hoplitis*.

superceded by the wasp *Passaloecus cuspidatus*, which prepared seven cells. In this instance the *Symmorphus* male that developed was eventually found dead in the cell, apparently unable to penetrate the resin partitions made by the *Passaloecus*.

No less than 14 of the 25 nests proved to have been parasitized by the miltogrammine fly *Amobia distorta* Allen [det. R. J. Gagne]. In all, 36 flies were reared from these 14 nests, a maximum of 6 flies emerging from each of 2 nests. Within the nests, the maggots moved freely from cell to cell, in some cases reducing the entire interior to loose bits of mud, pieces of prey, and maggots or puparia. A single bombyliid fly, *Anthrax irroratus* Say [det. L. V. Knutson], was reared from one nest.

In all, only 12 adult *Symmorphus cristatus* were reared from these nests, partly a result of the high incidence of parasitism. The remaining nests were presumed to belong to this species on the basis of the prey and, in two cases, on the basis of larvae preserved when the nest was opened.

Krombein (1967) has studied this species in some detail and has reviewed previous observations by Fye (1965). My own observations, so far as they go, are reasonably consistent with the results of those authors.

Ancistrocerus adiabatus (Saussure)

I obtained six nests of this species, five at Moran and one at Pilgrim Creek. These were in diverse situations: one on a tree root only 0.3 m high, two on dead trees about 1 m high, one on a cabin 1.3 m high, one on live willow, and one on live sagebrush 0.3-0.5 m high. Four of the nests were in 6 mm borings and had from 9 to 11 cells measuring from 8 to 22 mm in length; each had one or two empty vestibular cells measuring 10-15 mm in length. A fifth nest in a 6 mm boring had a single cell 15 mm long following several cells of a bee and followed by a long vestibular cell, 52 mm long. A single nest in a 4 mm boring had several cells (not counted) measuring 11-14 mm in length and followed by a vestibular cell 14 mm long. Closing plugs were of mud and measured 2-3 mm in thickness; partitions between cells were also of mud, but no more than 1 mm thick; none of the nests had preliminary plugs at the extremity of the boring. There were no intercalary cells or double partitions in these nests (in contrast to those of *Symmorphus*).

Provisioned cells were packed tightly with small caterpillars, 15-20 per cell. A sampling of these, 56 specimens from two separate nests, all proved to be *Coleotechnites* sp. (Gelechiidae) [det. D. M. Weisman]. Cocoons were whitish, very thin and delicate. The only case of supercedure was the one mentioned above, in which a single cell of *Ancistrocerus* followed several cells of a leafcutter bee (not reared, but probably *Hoplitis robusta*).

One nest was found to contain maggots in two cells; this nest later yielded one adult fly, *Amobia floridensis* (Townsend) [det. R. J. Gagne]. Another nest contained two brown, parchment-like cocoons; these later yielded cuckoo wasps, *Chrysis caerulans*

Fabricius. A third nest yielded a bombyliid fly, *Anthrax irroratus* Say [det. L. V. Knutson]. This fly emerged from a pupa that had worked its way out of the nest and into the rearing container; a second, dead pupa was inside the nest.

There are several published accounts of the nesting behavior of this widely distributed species, mostly under the name *A. tigris* (Saussure). My observations are consistent with Krombein's (1967) much more detailed studies. *Chrysis caerulans* has been reared from nests of this species on several occasions, and flies of the genera *Amobia* and *Anthrax* have often been reared from this and other species of the genus *Ancistrocerus*. Krombein found the prey to consist of microlepidopterous larvae of five families.

Trypoxylon aldrichi Sandhouse

Fourteen trap nests were accepted by wasps of this species, 10 at Pilgrim Creek and 4 at Moran. Five accepted 4 mm borings, 8 accepted 6 mm borings, and one nested in a 5 mm boring in a *Sambucus* stem. Traps accepted were from 0.3 to 1.2 meters high and were in a variety of situations: live alders, standing dead aspens, standing live or dead pines, and prostrate logs. The number of cells per 13 cm boring varied from 4 to 7, with two exceptions: one with 1 and one with 2 cells. The nest in the *Sambucus* stem had two cells in a boring only 4 cm long; both cells were 8 mm long. In 4 mm borings, cells varied in length from 8 to 20 mm (mean 13.5), while in 6 mm borings, cells varied in length from 7 to 20 mm (mean 12.0). An empty vestibular cell, 8-13 mm in length, was present in four nests. Empty intercalary cells, 2-5 mm in length, were found in two nests. Closing plugs varied in thickness from 2 to 7 mm, and in several cases were recessed slightly from the opening of the boring. Partitions between the cells were very thin; all partitions and plugs were of mud.

From 5 to 16 spiders were provided per cell, the larger number occurring in larger cells or when the spiders themselves were small in size. Spiders of four families were utilized, all of them web spinners, either orb webs, sheet webs, or the irregular webs of theridiids. The species are chiefly those occurring on tree trunks, in bushes, close to the ground, or under bark or stones. The following is a list of those spiders saved for identification and the numbers of each [determinations by H. W. Levi].

THERIDIIDAE

Achaearanea sp. 2 ♀♀
Chrysso nordica (C. and I.) 1 ♀
Steatoda sp. 2 juveniles
Theridion aurantium Emerton 24 ♀♀
T. differens Emerton 1 ♂

LINYPHIIDAE

Lepthyphantes spp. 7 ♀♀
Meioneta sp. 3 ♀♀
Pityohyphantes sp. 12 juveniles

ARANEIDAE
Genera and spp. ? 24 juveniles

TETRAGNATHIDAE
Genus and sp. ? 1 juvenile

The egg of the wasp was found to be laid obliquely on the dorsum of the abdomen of one of the spiders deep in the cell. Twenty-nine *T. aldrichi* were eventually reared from eight of these nests, and although none were reared from the remaining six, I feel confident that all were nests of this species.

Only one instance of supercedure was found. In this case a bee (*Hoplitis robusta* Nylander) [det. G. C. Eickwort] had constructed four cells at the extremity of the boring, and the *Trypoxylon* had then constructed four more, a vestibular cell, and a closing plug.

I noted no maggots or puparia of parasitic flies when these nests were first examined, but one nest yielded two flies, *Amobia distorta* (Allen) [det. R. J. Gagne]. Two nests were, however, found to contain a small larva of a clerid beetle. In both nests there was evidence that the clerid had destroyed the egg or small larvae of the wasp; probably some feeding on the spiders also occurred. The clerids were not successfully reared to the adult stage.

Passaloecus cuspidatus Smith

Twenty trap nests were accepted by wasps of this species, 7 at Moran and 13 at Pilgrim Creek. These trap nests were from 0.3 to 1.5 m high and were in diverse situations: on our cabin at Moran, on pine and aspen stumps and logs, and attached to low branches of live pines. Twelve were in 4 mm borings, 8 in 6 mm borings. Brood cells in 4 mm borings averaged considerably longer than in 6 mm borings (mean 11 mm, range 7-17 mm, as compared to mean 8.5 mm, range 5-12 mm in 6 mm borings). The number of cells per 13 cm boring ranged from 2 to 16, all of those having more than 10 cells being in 6 mm borings. Partitions were of resin and were very thin, no more than 0.3 mm; in no case was there a partition at the extreme end of the boring. Closing plugs were from 2 to 5 mm thick and were also of clear resin except that several had dirt particles or wood chips mixed with the resin. As reported by Krombein (1967) from New York and Virginia, none of these nests had an empty intercalary cell, but all had empty vestibular cells; the latter varied in length from 12 to 58 mm, and one of them was divided in half by a thin partition.

Provisioned cells were packed tightly with aphids, usually wingless forms and often immatures. I counted the aphids in 14 cells and found the number to vary from 10 to 40 (mean 21), much of this variation the result of differences in the size of the aphids. The egg was found to be 1.3 mm long and to be laid on the venter of an aphid, one end attached just behind the hind coxae and the other end extending free, obliquely forward and upward.

In most of the nests, all the aphids were dark in color; I preserved 80 aphids from several cells of two nests, and all proved to be *Ptero-*

comma bicolor (Oestlund) [det. L. M. Russell]. However, two nests from Moran, collected on 9 and 13 August, were provisioned with aphids of paler coloration; I preserved 9 of these and all proved to be *Macrosiphum euphorbiae* (Thos.) [det. L. M. Russell]. Since there were over 2000 aphids in the 120 cells of this wasp and I preserved fewer than 100, I cannot be sure that other species of aphids were not involved. However, I noted none that were superficially different from these two species.

There were three instances of supercedure, in each case the *Passaloecus* usurping the nest of another wasp or bee. In one case *P. cuspidatus* built 6 cells following one cell of *Symmorphus cristatus;* in the other two cases *P. cuspidatus* built 4-10 cells following 3 cells of a bee. The bees were not reared successfully but were probably *Hoplitis robusta.*

Passaloecus appeared to be free from attacks of miltogrammine flies, possibly because of the nature of the partitions. One bombyliid fly, *Anthrax irroratus* Say [det. L. V. Knutson], was reared from a nest, but this was one of the nests containing three cells of a bee, and it was not determined in what cell that parasite had developed. An eight-celled nest yielded an ichneumon wasp, *Poemenia americana nebulosa* Habeck and Townes [det. H. K. Townes], as well as a chrysidid, *Omalus aeneus* Fabr. Both *O. aeneus* and *P. a. americana* (Cresson) have been reared from this host by Krombein (1967). I reared *Omalus aeneus* from one additional nest and also reared *O. cressoni* (Aaron) from one nest and *O. purpuratus* (Provancher) from two.

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