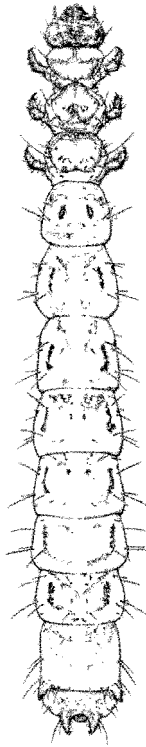


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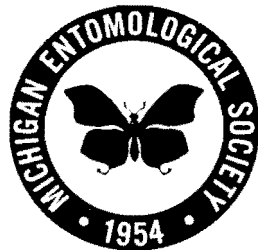
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Larva of *Lecontia discicollis* (LeConte) (Coleoptera: Boridae). Drawing by Lana Tackett.

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THE TRUE LARVA OF *LECONTIA DISCICOLLIS* AND CHANGE IN  
THE SYSTEMATIC POSITION OF THE GENUS  
(COLEOPTERA: BORIDAE)

Daniel K. Young<sup>1</sup>

ABSTRACT

The mature larva of *Lecontia discicollis* is described and illustrated. The presence of well-developed hypostomal rods, fine setae associated with the thoracic legs, two urogomphal pits, and lack of a series of asperities along the anterior margin of the ninth abdominal sternite obviate the placement of *Lecontia* within the Pythidae. Additional features of the larva (urogomphal plate) and adult (head and thorax) indicate a close relationship between *Lecontia* and *Boros*, and *Lecontia* is transferred to the Boridae.

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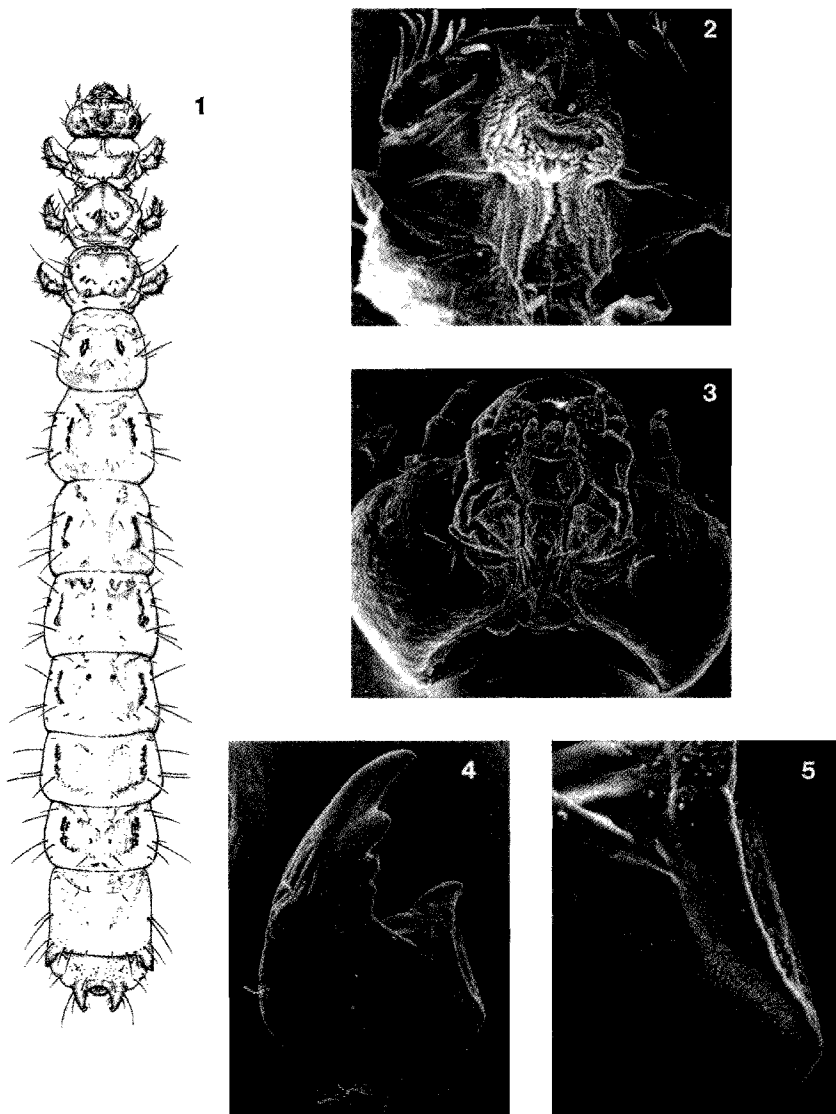
While hosting the December 1983 workshop on beetle larvae held at Ohio State University, in conjunction with the tribute to John LeConte, I discovered several vials of odd-looking "Pyrochroidae-Pythidae" in the Peterson collection of immature insects. All of the 24 specimens came from the eastern Upper Peninsula of Michigan; most were collected in Chippewa County during the summer and fall of 1935. The largest, and presumably mature, larvae ranged from 38 to 45 mm long. Based on numerous rearings of pyrochroid larvae, the ensuing adults could be expected to range from about 14 to 21 mm in length. Given the geographical data, body size, and salient anatomical features discussed below, the specimens can only be *Lecontia discicollis* (LeConte).

DESCRIPTION OF LARVA

Mature larvae (Fig. 1) attain lengths of 38–45 mm and widths of 3.7–5.5 mm. Body somewhat flattened, sides subparallel through length; sclerotization heaviest in head region and 9th abdominal tergite. Vestiture consisting of scattered short to moderately elongate setae; posteromesal margin of pronotum bearing two posteriorly directed, dentiform processes, surface of body otherwise generally smooth. Body yellowish-brown, reddish-brown to nearly black in areas of heavy sclerotization. **Head** Prognathous, exerted from prothorax. Epicranial suture with stem short, anterior arms lyriform and complete to posterior margins of antennal insertions; endocarinae absent. Symmetrical labrum present anterad of fused frons and clypeus; epipharynx (Fig. 2) bearing two spine-like setae along each anterolateral margin, two peg-like setae mesally along the anterior margin, and dense brushes of mesally and posteromesally directed setae along either side of the meson. Stemmata lacking. Antennal insertions fully exposed, **antennae** elongate, three-segmented, small dome-like sensory appendix associated with penultimate segment. **Mouthparts** (Fig. 3) retracted, supported ventrally by well developed, posteriorly divergent hypostomal rods. **Mandibles** (Figs. 4–7) heavily sclerotized, movable, asymmetrical: left mandible (Fig. 4) bearing prominent molar tooth, right mandible with deeply notched, cusp-like mola (Fig. 7); apices of mandibles tridentate. **Maxilla** with

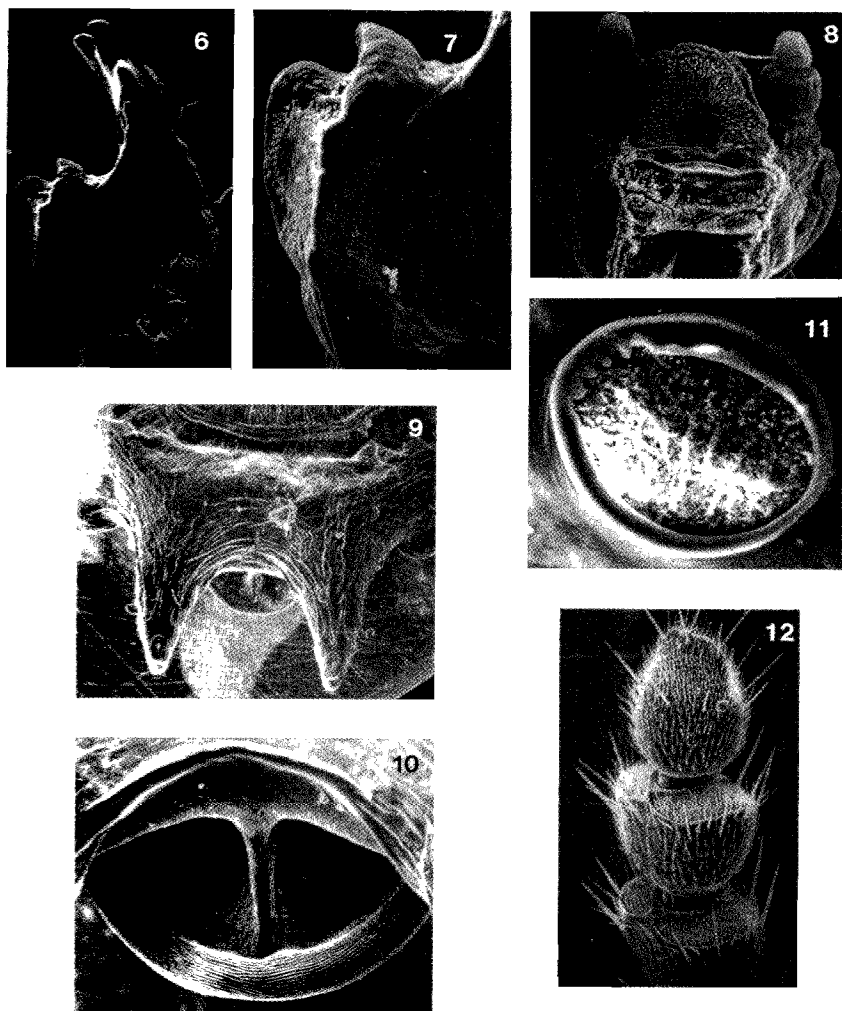
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Figs. 1-5. *Lecontia discicollis* larva. (1) habitus, dorsal view; (2) epipharynx; (3) head, ventral view; (4) left mandible, dorsal view; (5) left mandible, mola and dorsal microtrichia.

cardo folded upon itself and thus appearing 2-segmented, well developed, triangular maxillary articulating area, undivided maxillary mala, and 3-segmented palpus. **Labium** free to base of mentum and possessing elongate, distally rounded ligula and stout, two-segmented palpi. Hypopharyngeal sclerome (Fig. 8) well developed, transversely



Figs. 6-12. (6-11) *Leconia discicollis* larva. (6) right mandible, dorsal view; (7) right mandible, molar surface and dorsal microtrichia; (8) hypopharynx; (9) abdominal tergite 9 (wrinkled surface is artifactual); (10) microsculpturing of urogomphal pits, caudodorsal view; (11) second abdominal spiracle, left side. (12) *Borus unicolor* adult. Antennal segments 9-11 and paired reniform sensory regions on distal ends of 9-10.

subrectangular. Mentum slightly wider than long, anterior margin slightly emarginate; submentum quadrate; gular region transversely rectangular.

**Thorax and abdomen.** Thorax elongate with sides subparallel. cervicosternum divided into three plates, posterior margin of pronotum bearing two posteriorly directed, flat,

Table 1. Comparative anatomical features of adult Boridae (*Boros unicolor*), Pythidae (*Pytho* spp., *Priognathus monilicornis*, *Sphalma quadricollis* Horn), and *Lecontia discicollis*.

	Boridae	<i>Lecontia</i>	Pythidae
Eyes slightly emarginate.....	+	+	+/-
Antennal insertions concealed from above by extension of frons.....	+	+	-
Antennal segments 9 & 10 with reniform sensory regions (Fig. 12).....	+	+	-
Sides of pronotum with longitudinal suture.....	+	+	-
Prosternal process well developed (extending to posterior margin of coxal cavities).....	+	+	-

dentiform processes along meson. Legs well developed, five-segmented including tarsungulus, legs similar in size and shape, bearing numerous scattered fine setae. Abdomen somewhat flattened; tergite 9 (Fig. 9) heavily sclerotized, hinged, extending ventrally to form the entire terminal region or urogomphal plate, ventral aspect divided along meson by deep, wide, longitudinal sulcus, caudoventral margin bearing two well developed urogomphal pits between the paired, fixed urogomphi. Urogomphi upcurved distally, each urogomphus terminating as a single blunt, dorsally oriented ovate knob; urogomphal pits with striate microsculpturing (Fig. 10). Sternite 9 transversely rectangular, partially recessed into emargination of 8th sternite, bearing a single asperity on each side. Segment 10 reduced, visible ventrally surrounding anal orifice.

**Spiracles.** Thoracic spiracle ovate with peritreme partially crenulated; abdominal spiracles (Fig. 11) annular-ovate with dorsal aspect of peritreme crenulate.

#### SYSTEMATIC POSITION

If the larva described above is that of the monotypic *Lecontia*, as I believe it must be, two critical problems must be dealt with. First, the larva figured by Peterson (1960:189; Figs. F,G) and referred to as *Lecontia* does not fit the above description. The solution to this apparent dilemma is quite simple: the larva that Peterson saw was not that of *Lecontia*. This possibility was first suggested to me some time ago by John Lawrence, who felt that Peterson's figures represented another monotypic genus, *Priognathus*. I have collected larvae like the one figured by Peterson in the same log with adults of *P. monilicornis* (Randall), which supports this notion.

*Lecontia* has previously been associated with *Pytho* and related genera, and is presently assigned to the Pythidae (Crowson 1955, Lawrence 1982). However, larvae of *Lecontia* have well developed hypostomal rods, thoracic legs which bear fine setae, two well developed urogomphal pits, and lack a series of asperities along the anterior margin of the ninth abdominal sternite. Pythid larvae (*Priognathus*, *Pytho*, *Sphalma*) lack hypostomal rods, possess stout, spine-like setae on the thoracic legs, have but a single urogomphal pit, and possess a conspicuous series of 12 or more asperities in the form of a double arch along the anterior margin of the ninth abdominal sternite. An additional character which differentiates *Lecontia* larvae from those of Pythidae is the ninth abdominal tergite. It forms a terminal, hinged plate similar to the urogomphal plate of Boridae, Inopeplidae,

Mycteridae, Prostomidae, and Pyrochroidae. Of these taxa, borids, pyrochroids, and some mycterids (*Lacconotus*) possess two urogomphal pits. Those of *Lecontia*, borids, and pyrochroids are typically well-developed and heavily sclerotized, while those of *Lacconotus* are quite small. Mycterids also differ from *Lecontia* in lacking an enlarged maxillary articulating area and by having nearly symmetrical mandibles with reduced molae (except Hemipeplinae which possess a median endocarina in association with the epicranial suture).

Larvae of *Boros unicolor* Say, our only North American borid, and *B. schneideri* (Panzer), have the ventral aspect of the urogomphal plate conspicuously divided along the meson by a longitudinal suture (St. George 1931, 1940). The broad, longitudinal sulcus associated with the ventral urogomphal plate in *Lecontia* appears to be the structural homologue. Larvae of Pyrochroidae (Pyrochroinae) differ significantly from those of *Lecontia* by possessing an arch of asperities along the anterior margin of the ninth abdominal sternite.

The data presented above lead me to conclude that *Lecontia* cannot be a pythid, and I recommend that it be transferred to the Boridae. An examination of adult Boridae, Pythidae, and *Lecontia* provides further support (Table 1). The dorsal concealment of the antennal insertions by the projection of the frons, and unique sensory regions (Arnett 1968:715) associated with the distal ends of the 9th and 10th antennal segments (Fig. 12) are particularly convincing characters. They may well be synapomorphies and point to the hypothesis that *Boros* and *Lecontia* are sister groups.

#### ACKNOWLEDGMENTS

It seems quite fitting that the larval stages of *Lecontia* should be discovered during the course of a symposium and series of workshops held in honor of Dr. John Lawrence LeConte. I am grateful to Michael Ivie and James Stribling for inviting me to host the workshop on beetle larvae and for their warm welcome during my stay in Columbus. Thanks are extended to Charles Triplehorn and Ohio State University for the loan of *Lecontia* larvae, and to Lana Tackett for the habitus illustration. I should also like to thank Stanley Carlson for the use of SEM facilities at the University of Wisconsin and Martin Garment for taking the scanning electron photographs.

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## THE SLAVE-MAKING ANT *FORMICA GYNOCRATES* (HYMENOPTERA: FORMICIDAE)

Mary Talbot<sup>1</sup>

### ABSTRACT

*Formica gynocrates*, a recently described species of slave-making ant, was found at the E. S. George Reserve in southern Michigan. It contrasted with the other five *sanguinea* group species found there by living in dry fields and enslaving a field-dwelling ant, *Formica vinculans*. Slave raids were carried on from 16 June to 11 September and flights occurred between 5 July and 14 August. Three other *sanguinea* group species, *F. subintegra*, *F. pergandei*, and *F. rubicunda*, were most common along field-wood ecotones. They enslaved *F. subsericea*, and *F. pergandei* occasionally took *F. pallidefulva nitidiventris*. *F. subnuda* lived in and under logs and usually had no slaves or a limited number of *F. subsericea*. *F. creightoni* was rare, lived in woods, and enslaved *F. neogagates* and *F. lasioides*. Raids of *subintegra*, *pergandei*, and *rubicunda* took place from late June to September, and flights occurred from the first or second week of July until early August.

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The two square miles of the Edwin S. George Reserve in Livingston County in southern Michigan harbor all of the six known eastern species of the slavemaking *Formica* of the *sanguinea* group. Of these, *Formica subintegra* Emery, *F. pergandei* Emery, and *F. subnuda* Emery are common at the borders of fields or in open spots in woods; *F. subnuda* is less common and is associated with logs or stumps in open to dense woods; *F. creightoni* Buren is rare and seems to be confined to woods; and *F. gynocrates* Snelling and Buren is the only one found in the middle of dry fields.

Between 1951 and 1973, 23 colonies of *F. gynocrates* were discovered on the George Reserve. Some colonies have been found and later lost in a number of different fields. They were easily lost since colonies move frequently. However four colonies have been known for 10, 5, 4, and 3 years respectively.

*Formica gynocrates* is restricted to living where there are numerous nests of its host ant *F. vinculans* Wheeler. This latter species will not tolerate fields with grass cover thick enough to obscure the ground, nor is it found in woods or even woods edge if the soil is heavily matted with dead leaves.

Thus, *F. gynocrates* lives in rather sterile, sandy, upland fields where rapid drainage prevents a lush growth of vegetation. Associations of Canada bluegrass (*Poa compressa* L.) and three-awned grass (*Aristida purpurascens* Poir.) are typical. These, together with a few other grasses, form a sparse ground cover. There are usually small patches of bare soil and larger patches of red-tipped lichen (*Cladonia cristatella* var. *vestita* Tuck) or moss (*Polytrichum juniperinum* Hedw. and *P. piliferum* Hedw.). Beds of pussy's toes (*Antennaria neglecta* Greene and *A. fallax* Greene) are frequent and other scattered forbs form a slightly higher layer. The most conspicuous of these are bush-clover (*Lespedeza capitata* Michx. and *L. virginica* (L.) Britt.), St. John's-wort (*Hypericum perforatum* L.), blazing-star (*Liatriis aspera* Michx.) and several species of goldenrod (*Solidago* spp.).

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The ants (*Aphaenogaster treatae* Forel and *Lasius neoniger* (Emery) are typical of these fields and in some places *Formica pallidefulva nitidiventris* Emery is present. *Myrmica americana* Weber, *Solenopsis molesta* (Say), *Monomorium minimum* (Buckley), and *Paratrechina parvula* (Mayr) are usually found on the lower parts of field slopes, while *Formica lasioides* Emery sometimes nests in little swales or near trees where the soil is slightly more moist.

### NEST STRUCTURE

Colonies of the host ant *F. vinculans* are usually inconspicuous because workers do not pile up soil around nest entrances nor do they make large, semi-bare nest areas. The mixed colonies are sometimes easier to see because *F. gynocrates* workers, which help with the excavation, are more apt to leave a covering of soil near the openings. This may occur after rains and especially during flight periods when a vague circle may reach 30–60 cm d. This does not mark the limits of the nest and alates may emerge from other openings in the grass beyond. It is characteristic of *F. vinculans* that nests extend for some distance just under the surface of the soil.

*Formica vinculans* has another characteristic which is carried over into the mixed colonies. It builds small piles of debris around bases of plants on or near the nest. The thatch for these small cones varies and may consist of any mixture of sand grains, tiny pebbles, leaf scales, and bits of dried leaves, lichen, and moss. The shelters may be built among the small leaves of *Antennaria* or around the bases of many kinds of plants such as clumps of grass, rosette leaves of hawkweed, or stems of goldenrod, mullein, star thistle, or blazing-star. These small structures are 2.5–7.5 cm across and usually enclose aphids. They also serve as aboveground chambers for incubating pupae and as a loitering place for alates.

### DAILY ACTIVITIES

Excavation of chambers and galleries, performed by both species, was especially conspicuous after rains, when a colony had moved, and during the flight period. Foraging was carried out primarily by *F. vinculans* workers. They attended aphids and brought in numerous small bits of food, usually working singly. *F. gynocrates* carried home larger bits of food and often cooperated in dragging in bulky pieces such as caterpillars or tree hoppers.

Both species were high-temperature ants, becoming more active as the day became warmer. Usually both stayed underground at night and began coming out in the morning as the surface warmed. They walked slowly on the nest at 18°C, ground temperature; at 21° they were moving normally and foraging off the nest. *F. gynocrates* raided normally at 35° and on a raid could run across soil which registered 39.5°C. *F. vinculans* has been seen foraging at 40.5°, ground temperature. At high temperatures they ran rapidly and climbed up off the soil as much as possible. Activity did not depend directly upon temperature because sometimes one colony would be raiding or foraging vigorously while another would be inactive. Three times during the summer one colony was disturbed by a bird (probably a flicker) which made 7.5-cm deep holes over the nest. Each time all excavation and most foraging ceased for half a day or more before the usual activity was resumed.

### MOVING

*Formica gynocrates* colonies did a great deal of moving, typical of species in the *sanguinea* group. During these activities some workers of both species excavated a new site while other *F. gynocrates* carried adults, pupae, and larvae. A few *F. vinculans*

Table 1. Earliest and latest records of brood, alates, flights, and raids of the ants of the *sanguinea* group at the Edwin S. George Reserve.<sup>a</sup>

Species	Larvae		Worker Pupae		Alate Pupae	
<i>F. gynocrates</i>	4-6-70	29-8-57	4-6-70	21-9-70	4-6-70	17-7-73
<i>F. subintegra</i>	2-6-69	22-8-73	4-6-70	8-9-69	10-6-70	31-7-56
<i>F. rubicunda</i>	3-6-75	29-8-71	14-6-69	25-9-70	14-6-70	4-8-69
<i>F. pergandei</i>	3-6-71	25-8-56	3-6-71	21-9-71	6-6-73	29-7-69
<i>F. subnuda</i>	4-6-70	24-8-56	5-6-69	28-8-56	6-6-63	20-7-56
	Alates		Flights		Raids	
<i>F. gynocrates</i>	21-6-71	16-8-72	5-7-73	14-8-73	16-6-73	11-9-72
<i>F. subintegra</i>	1-7-70	14-8-56	7-7-70	8-8-56	1-7-70	24-8-73
<i>F. rubicunda</i>	3-7-73	6-8-69	12-7-70	4-8-73	17-6-70	1-9-69
<i>F. pergandei</i>	1-7-70	8-8-69	6-7-73	27-7-56	18-6-70	6-8-69
<i>F. subnuda</i>	16-6-58	28-7-60	15-7-60	18-7-62	— <sup>b</sup>	—

<sup>a</sup>No observations were made before the first week in June.

<sup>b</sup>No raids of *F. subnuda* were seen.

workers carried some of the smaller (*vinculans*) pupae. As is usual when ants change nest location, a few ants carried brood and adults back to the old nest while others were taking them to the new. Ordinarily moving was completed within 7-12 days.

Colonies commonly stayed in place during the maturing of the alate brood and until after flights were over. This could be by the end of July for some colonies to the middle of August for others. Some became restless as soon as flying ceased but more waited until raids had slowed or stopped. Most changing of nest sites took place in late August and throughout September.

Distances shifted were often very short, 1-3 m, with most colonies changing nest sites only once in a season. One colony, living on a ditch bank, moved to the flat surface 3 m above in August 1972. In late July 1973 it shifted 2.4 m down the bank, and in late August moved up to a spot just below the 1972 nest. This much moving was unusual. Some colonies remained in one place for a number of years.

In contrast to these short moves, some ants traveled long distances. Three such colonies were lost and not found again. One other, observed while moving, settled on a spot 28 m away from the original nest and another moved 29.3 m. This latter colony, in early September 1973, invaded and took over a colony of *F. vinculans* which it had been seen to raid on 13 July, 1973. It was a large vigorous colony which had put up a full-scale defense at the time. Evidently there was also resistance when *F. gynocrates* moved in because inside the nest were many dead *F. vinculans* workers. Probably this capturing of a *F. vinculans* colony is common procedure when *F. gynocrates* move for a long distance.

## BROOD DEVELOPMENT

Larvae and a few worker and alate pupae were already present when observations began in early June (Table 1). Larvae are not overwintered and all had developed into pupae by 19 August. A few worker pupae have been found as late as 21 September. Most records of alate pupae were obtained between 4 June and 8 July, a period of just over a month,

Table 2. Data from 15 flights of *Formica gynocrates* in Southern Michigan.

Nest	Date	Alates climbing			Beginning of flight			Height of flight		
		Time	°C <sup>a</sup>	klx	Time	°C <sup>a</sup>	klx	Time	°C <sup>a</sup>	klx
20	8-7-73	0639	22.2	12.9	0656	23.3	12.9	0703	23.9	15.1
20	9-7-73	0638	22.2	15.1	0657	23.3	15.1	0713	24.4	19.4
18	9-7-73	0650	22.8	15.1	0743	24.4	19.4	0747	26.1	28.0
20	14-7-73	—	—	—	0730	23.3	21.5	0812	25.0	36.6
18	14-7-73	0804	21.7	28.0	0812	23.9	36.6	0817	22.2	23.7
3	20-7-73	0710	22.8	11.8	0840	23.9	17.2	0742	25.0	23.7
3	22-7-73	0646	24.4	10.8	0705	25.0	11.8	0712	26.1	11.8
3	24-7-72	0745	24.4	28.0	0800	26.1	36.6	0812	26.7	40.9
21	29-7-73	0810	22.8	43.0	0833	23.3	56.0	0851	23.9	64.6
6	1-8-73	—	—	—	0905	23.9	60.3	0910	25.0	49.5
21	4-8-73	0759	22.2	28.0	0815	23.9	47.3	0835	26.7	51.6
5	5-8-72	0848	22.2	54.9	0910	23.3	60.3	0930	24.4	65.6
6	7-8-73	0745	21.7	19.4	0809	24.4	28.0	0812	24.4	30.1
21	12-8-73	0748	23.3	36.6	0806	23.9	28.7	0812	24.4	38.7
21	13-8-73	0811	22.8	34.4	0832	23.9	51.6	0838	25.0	45.2
Mean		0735	22.8	26.0	0804	23.9	34.2	0811	25.0	36.3

but in 1973 a few were still present on 17 July. These records were kept over a number of years and during some seasons there is a longer development period than in others.

Adult alates were first seen on 21 June and last seen on 16 August, a period of eight weeks. For a week or two after the first emerged there were still more alate pupae than adults in the colony and adults continued to emerge from the pupal stage for another week or two. Flights began within one or two weeks after the emergence of the first winged adults and considerably before all of the alate pupae had become adult.

### FLIGHTS

The flight season in 1973 was from 5 July through 14 August (Table 2). One colony had flights during the entire season but others ran out of alates by 25 July–11 August. Thirty-four flights have been seen in other years but none earlier or later than these except in 1972 when one last male flew on 16 August. There were 16 days of flights in 1973 and 22 days when unfavorable weather conditions prevented flights.

Entire flight records could be secured from only one nest at a time (except for a few cases when a helper was available), so different nests were watched on different days. Sometimes, instead of watching one colony, a survey was made of all the six colonies used. It was found that the colonies were principally either male- or female-producing. Two had only males and one had only females throughout the flights, while two produced only males until near the end of the season when a few females were found, and one produced females with only a few males.

During each of 21 watched flights in 1972 and 1973, an attempt was made to check all of the alates which flew. This could be done fairly accurately because all flights were sparse, but still probably undercounted them. The most alates seen to fly in one day from a male colony was 46, while the greatest number from a female colony was 21. Mean

Table 2 (continued).

Nest	Date	Time	End of flight		Length of flight min	Number flying	
			°C <sup>a</sup>	klx		♂	♀
20	8-7-73	0712	24.4	17.2	17	5	—
20	9-7-73	0758	25.0	30.1	62	6	—
18	9-7-73	0800	27.2	28.0	18	—	8
20	14-7-73	0902	25.0	60.3	93	14	—
18	14-7-73	0845	23.3	28.0	34	—	19
3	20-7-73	0755	24.4	17.2	16	—	13
3	22-7-73	0720	26.7	13.7	15	—	20
3	24-7-72	0825	27.8	40.9	25	—	8
21	29-7-73	0917	30.6	79.6	45	46	—
6	1-8-73	0916	26.1	47.3	12	22	—
21	4-8-73	0847	27.2	51.6	33	45	—
5	5-8-72	0953	25.6	73.2	43	—	21
6	7-8-73	0815	24.4	36.6	7	4	—
21	12-8-73	0842	24.4	62.4	37	22	—
21	13-8-73	0845	25.6	53.8	14	7	—
Mean		0830	26.1	42.0	31	19	15

<sup>a</sup>Air temperature measured 25 cm above the ground; many ants flew from vegetation at approximately this height.

number of alates flying per day on the 21 days was 16.1 The 14 male flights averaged 17.6 males released and the seven female flights averaged 15.9 females. Flights were especially sparse toward the end of flight season when colonies were running out of alates and also at the beginning of the season when few alates were mature.

All flights took place in early to mid-morning and flying might begin as early as 0656 hr (EST) or as late as 0910. Flights ended from 0712 to 0953. This variation in time took place because the ants were reacting primarily to warming soil and air. On sunny mornings the first alates could be seen when air temperature was about 17–18°C (25 cm above the ground); on hazy mornings they might stay underground until the temperature reached 21–22°. As soon as the air and the alates warmed sufficiently, some began to climb vegetation. Actual flying usually began when the air temperature reached 23–24°. Females sometimes delayed until it was a bit warmer. Ends of flights did not seem so dependent upon a certain temperature and the last alates might leave at temperatures anywhere from 23° to 30.5°. Light also played an important role; dimming or fluctuating light could delay or stop a flight. The best flight days were those after a cool night when the morning sun was bright, the temperature was rising steadily, and there were no clouds and little or no wind.

During the 1973 season there were 22 days without flights. On some days no alates were out; on the other days a few appeared but there was no true flight. On two days conditions seemed satisfactory but for some unknown reason workers kept the alates from flying.

Before flights began workers of both species engaged in vigorous digging-out of chambers just under the surface and in adding openings. These extra chambers and exits were usually in places where patches of grasses or forbs grew on the nest area or at its rim. Workers were not very active in trying to keep alates from flying. On most days no interference was seen but a few *F. vinculans* workers would intervene when conditions were unfavorable, especially at the beginning or end of a flight. A *vinculans* worker might pull back a male by an antenna, leg, or mandible, or induce it to turn around by nipping

or lunging at it. They were less successful with the larger females and rarely disturbed them. Occasionally a *F. gynocrates* worker would nip a female.

Males and females both tended to climb vegetation to fly. Males usually flew from near the place where they had come from the nest, while females generally walked about on the ground for short distances before climbing. Males could fly from grasses but females usually chose more sturdy stems of *Rumex*, *Lespedeza*, *Solidago*, etc. When ready to fly the alates stretched forward, moved antennae, opened wings, and flew. Sometimes they fluttered wings vigorously before flying, especially if conditions were not ideal.

There was no mass climbing of plants and during most flights only a few alates could be seen on the vegetation at any one time. However, more might accumulate if conditions became unsatisfactory. Once, when females began to climb at 23°C, the temperature dropped 1° and light dimmed from 11.8 to 11.4 klx. At this time 24 females were counted on plants, the most ever seen. As soon as the temperature rose to 24° and light to 17.2 klx, they began to fly and most left in the next 3 min. Males reacted in the same way and never were more than 17 counted on vegetation at one time. These had gathered when the temperature was not rising and light remained dim.

Both males and females climbed down stems when conditions became unsatisfactory, as when a slight wind swayed the plants or the temperature lowered slightly. At times they tended to drop, either while standing still or while trying to take off for flight. Dropping was more frequent toward the end of a flight when temperature rose too high, but might also occur at any time when conditions were not right.

Flights of *F. gynocrates* took place under essentially the same conditions as those of *F. vinculans*. Flights of *F. vinculans*, misidentified as *F. neogagates* Emery, have been reported by Talbot (1966).

## RAIDS

The main raiding season extended from about 24 June to 25 August and there were numerous raids on *F. vinculans* colonies during that time. Two, observed on 16 and 19 June 1973, were weak exploratory forays; no nests were found. The latest raid seen was on 11 September 1973, when a colony was entered and a few workers were captured, but no brood was brought out of the nest. Two other late raids, 29 August 1957 and 10 September 1972, were unusual in that they were directed against *Lasius neoniger* colonies. Evidently the raiding season begins when alates are emerging from the pupal state, about two weeks before flights begin, and continues until the time when larvae are scarce in the nest.

Many raids were seen over a number of years but the most concentrated study was made between 12 and 25 August, 1972. These observations covered the latter part of the raiding season when raids were less frequent, but nevertheless the colony made successful raids on seven colonies of *F. vinculans* in spite of a number of days of bad weather. One was raided for two days with *F. gynocrates* workers remaining in the nest overnight and once two colonies were raided on one day. Distances to the raided nests were 3, 4.9, 7.3, 12.5, 15.2, 28 and 31.7 m. In addition to the successful raids, some groups failed to find a colony.

During this period the ants maintained five basic, invisible trails, which were followed by the ants leaving the nest. All led toward the open field and not back to scattered trees at woods edge (where *F. subsericea* Say were abundant but unmolested). Ants leaving by such a trail might deviate from it almost immediately or might follow it for a long distance. Once, workers followed a trail to within 1.5 m of a previously raided colony and then branched off to find a new nest. Sometimes the ants moved quickly to a colony as if they had a good odor trail. More often they took a long time along the way as if they were hunting a colony by searching the ground thoroughly. (Regnier and Wilson [1971] found that they could induce raids of *F. subintegra* and *F. rubicunda* by laying down odor trails made with ether extracts of crushed whole workers or of hindgut.)

Raids might start at any time of day from 0645 to 1645. They were most frequent in early to mid-morning and when the day began to cool in the afternoon, but sometimes started at mid-day if temperatures were not too high. The ants seemed not as sensitive to heat as the other *sanguinea* group species on the Reserve, and were not so apt to have a mid-day lull.

The beginning of a raid was not an especially clear-cut activity. Workers would become more numerous on the nest and then a little group would start off on one of the trails. At first they traveled close together but soon would spread out as individuals wandered back and forth and from side to side, exploring the terrain. As workers moved farther apart the line would become indistinct. Usually other groups left the nest at intervals, followed the first, and extended the line. If any workers found what seemed to be a *F. vinculus* nest others would gather, searching very carefully for openings. If they failed to find a colony quickly some continued to hunt at that place while others would either increase the area of search, move forward, or start back home. Colonies were sometimes easy to find because entrances were obvious; others were so thoroughly concealed and blocked that considerable searching and digging was necessary.

*F. vinculus* had a characteristic habit when attacked. Some workers rushed out carrying brood up nearby plant stems so that sometimes they were a conspicuous sight, a whole area of grass covered with dozens of workers, each holding a pupa or, more rarely, a larva. Usually the attacking ants did not pursue them but waited until they came down and then took their brood.

Some *F. vinculus* colonies staged a good defense of the nest, either above-ground or down in the nest. Sometimes no defense was attempted; perhaps these colonies had been raided before, possibly several times.

On the morning of 13 July 1973, one *F. gynocrates* colony raided three nests. The first two did not resist but the third did. The first raid began at 0744. By this time many workers were on the home nest and were starting to wander off along a trail. Out in denser grasses the line became sparse and wide, then dwindled to individual workers and was lost. Other groups went out and by 0815 some had found a nest 22 m away. Then the line became well populated. There was no fighting at the *F. vinculus* colony and only a few workers ran up onto grasses holding brood. Almost immediately the raiding ants began to take pupae from the nest, going back over the same trail and meeting others coming out. Very few pupae were found and within 5 min a group began to push uphill, exploring carefully and moving slowly. They found a second colony 3.7 m away in a large clump of dead grass. Here again there was no resistance and brood was carried off for the next 15 min.

A cluster of *F. gynocrates* then found a third nest only 1.2 m above the second. This colony was large and belligerent, staging a good defense. Workers rushed out in great numbers and, while some carried brood up slope from the nest, a great many formed a half circle 25 cm below the three main openings. They fought vigorously all along the line and held the *F. gynocrates* at bay for 40 min. Fighting involved two or three ants of one species holding an ant of the other species by legs and antennae and stretching it until it died. Sometimes this was unsuccessful and, after tumbling about a bit, the group fell apart without any being hurt. Defenders greatly outnumbered aggressors and it looked as if they might win, but a large group of *F. gynocrates* reinforcements arrived, fighting was accelerated, and the tide of battle turned.

At this time it was noted that certain *F. gynocrates* were running forward for short distances among the *F. vinculus* and then retreating swiftly. It could not be seen if they were spraying but it seemed possible that they were releasing an intimidating allomone. (Regnier and Wilson [1971] reported that acetates from Dufour's glands of *F. subintegra* and *F. pergandei* were discharged at defending workers of the slave species *F. subsericea*, causing panic and rapid retreat. They called the chemicals "propaganda substances" because they attract the slave-makers but disperse the defenders.)

Ten minutes later the *F. gynocrates* workers had broken through the *F. vinculus* line and were moving all over the nest site. They did not find many pupae and half an hour later most had returned home. By this time (1030) ground temperature was 49° and workers were running fast and keeping up off the ground as much as possible.

Some colonies carried on their defense within the nest instead of on the surface. One such colony had nested in a bed of moss and its entrances were thoroughly concealed. At 1345, 13 July 1973, *F. gynocrates* workers were digging into the moss at one place and others were exploring for 0.3–1.2 m in all directions. Evidently the hole they opened led to a nest, for soon a *F. vinculans* worker was dragged out and stretched by two *F. gynocrates*. Then several more were extracted. A half hour later the raiding workers were still trying to penetrate farther into this entrance and had made another hole 10 cm away from which they pulled an occasional worker. After another 40 min they began pouring out with brood. Evidently the defense had broken down. At this time there were about 50 *F. gynocrates* at the nest, more were traveling to it, and brood was being carried off at a rate of 6.6/min. By 1555 230 pupae and 89 larvae had been captured. As the stream of pupae dwindled some ants spread out seeking dead *vinculans* workers, which they carried home, and four discarded *F. gynocrates* workers were found.

Not all of the raids were successful. Sometimes exploratory groups started out on a trail, branched from it, and spread out searching, but failed to find a colony. In these cases workers gradually returned home along the trail.

#### COMPARISON WITH OTHER *SANGUINEA* GROUP SPECIES

Five species of the *sanguinea* groups were well known at the Reserve. The sixth, *F. creightoni*, was collected only four times; no flights and only two raids were seen. Similarities among the species were great. They developed brood at approximately the same rate, had flights at about the same time, and raided over roughly the same period (Table 1). Differences seemed primarily associated with degree of tolerance to heat and to variations in the slave species captured.

Locations of nests were perhaps mainly determined by exposure to heat. *F. gynocrates* was distinct in that it could occupy open fields with no shade. Some colonies of *F. pergandei* were far enough away from trees that they were shaded for only a short time each day. A little over half of the *F. pergandei*, *F. subintegra*, and *F. rubicunda* colonies occupied overlapping habitat. A colony at the edge of a field near a woods, fence row, or clump of trees might be any one of the three species. All three were also found in open woods or openings in woods. A few *F. subintegra* penetrated into dense woods, and a few *F. pergandei* lived in low fields bordering swamp or marsh. *F. subnuda* seemed limited to the shade of woods and perhaps *F. creightoni* was also.

Flight activities were similar for all species but here again *F. gynocrates* showed a preference for high temperatures. Its males and females were never seen to fly at less than 23°C (25 cm above ground) and they flew best at 24–26°. *F. pergandei* could begin flights at temperatures as low as 19° and flew well at 21–23°. *F. subintegra* and *F. rubicunda* followed this same pattern. *F. subnuda* could fly in the shade at temperatures as low as 17° and had no difficulty in flying at 18° if it was warmer in nearby sunny areas.

It was common in all of the species for a colony to produce only males or females, or a predominance of one; consequently many flights were all male or all female. *F. gynocrates* seemed to produce fewer alates than did the other species. The greatest number seen to fly on one day was 46, in contrast with the several hundred alates which might be released in a good flight of the other species.

Tolerance of high temperatures allowed *F. gynocrates* to raid and forage in heat intense enough to cause the characteristic mid-day lull for *F. subintegra*, *rubicunda*, and *F. pergandei*.

Slaves captured by *F. gynocrates* were the field-dwelling *F. vinculans*. A few *F. lasioides* workers also have been found with *F. gynocrates*. These could have been living in a small swale in a field. The *F. creightoni* found were enslaving *F. neogagates* and *F. lasioides*, which differ from *F. vinculans* in forming smaller colonies in more sheltered



places. Usually *F. subnuda* colonies contained a few *F. subsericea* but several nests had no slaves. *F. rubicunda*, *F. pergandei*, and *F. subintegra* typically had an abundance of captured *F. subsericea*. A few *F. pergandei* colonies, living in drier places, had both *F. subsericea* and *F. pallidefulva nitidiventris* Emery or only the latter.

In rare instances brood of other species was brought in, presumably used for food. *F. gynocrates* has raided *Lasius neoniger* Emery and *F. rubicunda* has captured brood of *Myrmica*. *F. pergandei* has plundered colonies of *Aphaenogaster treatae* Forel, *A. rudis* Emery, and *Lasius pallitarsis* Provancher.

Type of nest structure was at least partly determined by the slave species although members of the *sanguinea* group always helped in construction. *F. gynocrates* nested in soil and did not make mounds. The *F. creightoni* colonies found were in piles of leaves or in and under logs. *F. subintegra*, *F. rubicunda*, and *F. pergandei* usually nested in soil and most often formed a "nest area" at the surface (a circle or oblong of openings where excavated soil has slightly or mostly restricted the growth of plants) but they sometimes constructed low mounds. *F. subintegra* and *F. rubicunda* occasionally occupied a log and leaves to its side but *F. pergandei* was never found in this type of nest. *F. subnuda* used logs or stumps almost exclusively and these might be near swamp or in rather open woods. They used thatch to fill in gaps between logs and the matted leaves beside them, and might cover the side of a log with it, forming added chambers outside the logs. *F. subsericea* is quite versatile in its type of nest building which allows latitude in the nesting habits of species enslaving it.

*F. gynocrates* seemed more willing to fight and did so more fiercely than the others, but this may be due to the pugnacity of the *F. vinculans*. *F. subsericea* rarely offered resistance. However, a vigorous colony might carry on a rather spectacular battle. One such occurred on 15 and 16 July 1970. On the first morning a large colony of *F. pergandei* had a raid line extending 40 m to a fire lane which they were unable to cross because *F. subsericea* workers were defending it. Fighting consisted of individual combats in which one, two, or three ants of one species pulled and mauled an ant of the other species until it died or escaped. Five to seven such groups were fighting at any one time and many ants were moving about until 1200 hr when most of the *F. pergandei* returned to their nest. In late afternoon they returned in great number and formed a mass of ants along 2 m of the fire lane and extending 2.4 m back from it. Fighting increased but none could get across the fire lane. Next morning there were fighting groups all across the lane and some *F. pergandei* had reached the other side, but it was not until 1800 hr that they were crossing in large numbers and were exploring on the other side. They found the *F. subsericea* nest, entered it without resistance, and by 1845 were taking home larvae and pupae. Next day they were in full control of the captured nest and in the afternoon used it as a base for bringing in plundered *F. pallidefulva nitidiventris* brood. The afternoon was very warm and they were storing the larvae and pupae until the evening cool when they carried them to their nest. At the same time they were also bringing in brood from an *Aphaenogaster treatae* colony which they had found nearby.

Like *F. gynocrates*, some colonies of the other species remained in one spot for a number of years, but many moved frequently. Usually moves were late or very early in the season but colonies could move at other times. One *F. pergandei* colony moved during the flight period. The workers had captured, with some fighting, a *F. subsericea* colony on 17, 18, and 19 July 1956, and began moving into the captured nest on 20 July. The moving was accomplished in 11 days during which some females walked to the new nest over the workers' trail. Workers tried to carry some females but had difficulty because when one grasped a female by her mandibles, pulled her back, and then moved forward, the female did not curl up as carried workers do. A worker, then, might try to drag a female or just abandon her. During this time there were four flights with females flying from the old and new nests and the path between.

No complete colonies were counted but from observations of raids, it seems probable that *F. gynocrates* forms smaller colonies than are characteristic of other *sanguinea* group species on the Edwin S. George Reserve.

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## A NEW HOST FAMILY FOR *LYRODA SUBITA* (HYMENOPTERA: SPHECIDAE)

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### ABSTRACT

*Lyroda subita*, a sphecid that ordinarily stocks its cells with Gryllidae, is reported provisioning a two-celled nest in upstate New York with Tridactylidae. The structure of the nest, depth of cells, stages of wasps, and degree of paralysis of the prey are described.

In 1984 Evans and Hook reported on an undescribed species of *Lyroda* from Australia that preys upon Tridactylidae. This record is remarkable because species of *Lyroda* ordinarily capture Gryllidae (Evans 1964, Kurczewski and Peckham 1982) or Tetrigidae (Iwata 1938, 1963, 1964; Tsuneki and Iida 1969). Furthermore the hunting components of sphecids that capture Tridactylidae are unique (Krombein and Kurczewski 1963, Kurczewski 1966a, Kurczewski and Kurczewski 1984), and such a tridactylid-hunting species of *Lyroda* would have to alter its manner of searching for prey in contrast to the more basic prey searching components exhibited by the gryllid- and tetrigid-hunting species. Previously only two genera of Sphecidae, *Tachytes* and *Gastrosericus*, both in the subfamily Larrinae, were known to contain species that prey upon Tridactylidae (summary in Bohart and Menke [1976]), and now another larrine genus, *Lyroda*, represents a third.

On 20 July 1984, in a man-made sand pit near Owasco Lake on the outskirts of Auburn, Cayuga County, New York we were astonished to observe a female of *Lyroda subita* (Say) provisioning with Tridactylidae. The wasp with prey flew into an abandoned *Cerceris fumipennis* Say entrance. The burrow was traced obliquely downward to a depth of 7 cm. A few centimeters to the side at a depth of 10 cm we found two fully-provisioned cells of *L. subita* separated by 2–3 cm of sand. The oldest cell contained a large larva and the remains of several Tridactylidae. The most recent cell held a small larva and four adult *Neotridactylus apicalis* (Say) (det. I. J. Cantrall, Museum of Zoology, The University of Michigan). The pygmy mole-crickets were rather thoroughly paralyzed in contrast to stored prey of *Tachytes intermedius* (Viereck) and *T. mergus* (Fox) which often leap from the cell when unearthed (Krombein and Kurczewski 1963, Kurczewski and Kurczewski 1984). Because *L. subita* is a larger species it may inject relatively more venom into its small prey.

The use of Tridactylidae as prey by *L. subita* is surprising when one considers that this sphecid has been studied in some detail by Patton (1892), Peckham and Peckham (1898), Evans (1964) and Kurczewski and Peckham (1982), and, in all cases, the prey comprised Gryllidae. Kurczewski and Peckham (1982), for example, recorded 67 individual gryllid prey in their study on *L. subita*. In our current study of sphecid wasps and their cleptoparasitic miltogrammine flies we have observed an additional 65 gryllid prey items from *L. subita* cells and provisioning females.

The use of atypical prey by species of solitary wasps is indeed a rarity. Evans's (1948) record of *Anoplius marginatus* (Say) (Pompilidae) capturing a harvestman and Kurczewski's (1966b) observation of *Tachysphex terminatus* (Smith) (Sphecidae) storing false katydids exemplify the capture of atypical prey by common, well-studied species of

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wasps. Kurczewski (1966b) attributed the use of false katydids, instead of the usual acridid prey, to a scarcity of grasshopper nymphs of suitable size at a particular time of year. One record of *Ammophila azteca* Cameron, a species which usually uses lepidopterous and sawfly larvae, storing larval weevils is also exceptional (Evans 1965). Evans believed that caterpillars are the "preferred" prey of *A. azteca* but that sawfly or, rarely, weevil larvae may be taken when caterpillars are in "short supply." According to Evans (1963), wasps do not normally "make mistakes" in capturing prey. The prey taken by a wasp may vary over time from cell to cell, indicating that one source of prey has been exhausted and another has been found, but a sudden drastic switch to an atypical family of prey is highly unusual.

The reason for the female of *L. subita* storing Tridactylidae is unknown but this observation is certainly unique in view of the fact that 14 conspecifics nesting at this locality preyed entirely upon gryllids and that both adult and nymphal gryllids were plentiful under fallen bark, in cavities in the soil, and in grasses at the edge of a field. The *L. subita* female probably unearthed the pygmy mole-crickets; exactly how remains a mystery. Did she excavate them with her mandibles in the manner of *Tachytes intermedius* and *T. mergus*, or did she obtain them in some other way? Perhaps the answer will never be known in view of this rare occurrence.

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**TEMPERATURE AND CROWDING EFFECTS ON VIRUS  
MANIFESTATION IN *NEODIPRION SERTIFER*  
(HYMENOPTERA: DIPRIONIDAE) LARVAE**

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**ABSTRACT**

Temperature and (or) crowding (larval density) functioned as stressors in the induction of symptoms associated with the nucleopolyhedrosis virus of the European pine sawfly, *Neodiprion sertifer*. Subsamples of larvae maintained at 30 and 35°C, with three levels of larval density each (20, 60, and 100/shoot) which had died under these conditions, revealed the presence of polyhedral inclusion bodies under microscopic examination. In contrast, larvae maintained at 25°C with the same three larval density levels experienced no symptoms of virus infection or mortality. The latter was consistent with field observations when temperatures during larval development ranged from 14°C to 27°C and larval densities were in the same general range.

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The vertical transmission of sawfly nucleopolyhedrosis virus (NPV) between generations generally falls into two categories: environmental persistence and persistence in the host development sequence (Cunningham and Entwistle 1981). Environmental persistence has been well documented from foliage and soil samples; however, different explanations exist as to how the virus is maintained and spread by the adult sawflies. According to Cunningham and Entwistle (1981) there is no evidence that sawfly virus is transmitted from adults to progeny either within the egg or on it, even though Bird (1961) suggested ovarian transmission for both the European spruce sawfly, *Gilpinia hercyniae* (Hartig), and the European pine sawfly, *Neodiprion sertifer* (Geoffroy). It is established that infected adults are capable of contaminating the foliage with virus which may later be consumed by developing larvae. Bird (1961) did not favor the latent virus infection theory as a transmission possibility. Latent virus infection has been demonstrated in several lepidopteran species, manifesting itself in spontaneous outbreaks under various stressors including temperature and crowding (Steinhaus 1958). With coniferous sawflies, the only documented case of a spontaneous epizootic in North America was with the European spruce sawfly (Bird and Elgee 1957). The causative factors of this outbreak are unknown, though it is generally accepted that the virus was introduced from Europe through the release of contaminated exotic parasitoids. This paper provides some evidence for the possibility of latent viral infection in *N. sertifer* and the roles of temperature and crowding in disease expression.

**MATERIALS AND METHODS**

Second-instar larvae of *N. sertifer* were selected from a "virus-free" population in the Kettle Moraine State Forest in southeastern Wisconsin. Red pine shoots, with foliage from the previous year, were cut at the base and inserted in waxed, 1-pt containers filled with

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Table 1. Percent mortality ( $\bar{x} \pm SE$ ) of *N. sertifer* larvae from nucleopolyhedrosis virus at three levels and three temperature regimes.<sup>a</sup>

Temperature (°C)	Density (larvae/shoot)		
	20	60	100
25	0%	0%	0%
30	77 ± 1%	84 ± 7%	95 ± 5%
35	100%	100%	100%

<sup>a</sup>At each temperature/density combination there were two replicates for a total of 18 units.

Table 2. Analysis of variance of virus-induced mortality in *N. sertifer* larvae.

Effect	F ratio	P
Density	$F(2,9) = 4.036$	$0.01 < P < 0.05$
Temperature	$F(2,9) = 1271$	$P < 0.005$
Temperature and density	$F(4,9) = 4.036$	$0.01 < P < 0.05$

water (400 ml). Larvae were transferred to the shoots at rates of 20, 60, and 100/shoot. These densities were comparable to those observed in the field on similar units of foliage. Six replicates were provided at each density. Each unit was sealed with a glass lantern globe and covered with cheesecloth for ventilation. The units were placed in controlled chambers at  $25 \pm 1^\circ\text{C}$ ,  $30 \pm 1^\circ\text{C}$ , and  $35 \pm 1^\circ\text{C}$ , RH at 50–60%, and a 16:8 photoperiod. The latter provided two replicates for each density and temperature combination or a total of six units in each chamber.

Each unit was monitored for 21 days with fresh foliage added when necessary. Dead larvae were removed at three-day intervals and stored singly in disposable test tubes at  $0^\circ\text{C}$ . From these larvae, three were picked at random from each replicate at each temperature-density combination. Each larva was macerated in a sterile glass tissue homogenizer and examined for polyhedral inclusion bodies (PIB) with brightfield microscopy at 600X. The number of PIB/larva was counted using a Levy chamber. Larvae in the field were monitored concurrently for symptoms of NPV infections.

Data were analysed using a multifactor analysis of variance. This allowed testing of the response (percent mortality), and PIB accumulation, as a function of temperature, density (crowding), or a combination of the two.

## RESULTS AND DISCUSSION

Mortality due to NPV at the three levels of temperature and density (Table 1) shows that there was no mortality due to NPV at  $25^\circ\text{C}$ . This was consistent with the absence of any symptoms of NPV infection of larvae in the field under daily average temperatures which ranged from  $13.9$  to  $27.0^\circ\text{C}$ . during the same time period. At  $30^\circ\text{C}$ , the virus manifested itself in a progressive differential mortality directly related to the increase in larval densities. And lastly, there was a small temperature-density interaction that appeared to affect the response. To quantify the latter, a multifactor analysis of variance (Table 2) showed that the density and temperature interaction on the response was significant at  $p < 0.05$ . However, if the significance level was set at  $p = 0.01$ , it would appear that temperature alone was the significant factor in the induction of mortality by a latent virus. *Neodiprion sertifer* larvae are colonial feeders and one would expect that crowding (larval density) would have less effect than some of the other stressors.

Table 3. Average number of polyhedral inclusion bodies (PIB) ( $\log_{10}$  units) observed in *N. sertifer* larvae at various densities or temperature conditions.

Larval density	PIB/larva <sup>a</sup> $\bar{x} \pm SD$	Temp. °C	PIB/larva <sup>b</sup> $\bar{x} \pm SD$
20	4.74 $\pm$ 0.61 (n = 12)A	30	4.87 $\pm$ 0.54 (n = 18)
60	4.80 $\pm$ 0.46 (n = 12)A	35	4.31 $\pm$ 0.33 (n = 18)
100	4.23 $\pm$ 0.28 (n = 12)B		

<sup>a</sup>Means followed by same letter not significantly different, and, those by different letters significantly different at  $P = 0.05$  (df = 33) by Least Significant Difference Test.

<sup>b</sup>Means significantly different  $P < 0.001$ , df = 28 (*t*-test with unequal variances).

To analyse the accumulation of PIB in NPV-killed larvae, three larvae/replicate were subsampled at random from each temperature (30°C and 35°C) and density combination. Each of the 36 larvae was checked microscopically for the number of PIB present. Using  $\log_{10}$  values to normalize the data, analysis of variance showed that temperature-density interaction on the accumulation of virus in the larvae was not statistically significant ( $F(2,30) = 2.87$ ,  $p > 0.05$ ). However, either density or temperature was significant in larval virus accumulation ( $F(2,30) = 9.21$ ,  $p < 0.01$ ;  $F(1,30) = 15.43$ ,  $p < 0.01$ , respectively). Examination of the individual means (Table 3) showed that more virus was accumulated in the larvae at the lower densities (20 and 60 larvae/colony) and temperature (30°C) than at the higher density (100 larvae/colony) and temperature (35°C). These results suggest that temperature or density may limit the net accumulation of virus in the larvae.

Given the conditions of this experiment where the most stringent care was exercised in maintaining sterility in all objects and instruments used, and the choice of larvae from an area with no known history of NPV, it is possible to conclude that *N. sertifer* does harbor a latent virus. The conditions under which it manifests itself in the laboratory are harsh, particularly with regard to high temperatures. Thus, it is unlikely that epizootics caused by latent virus will be observed in the current range of this species where temperatures above 30°C are infrequent. It is possible, however, that latent virus could limit the southern range of *N. sertifer* where temperatures may average above 30°C.

#### ACKNOWLEDGMENTS

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## NEARCTIC *RHYACIONIA* PINE TIP MOTHS: A REVISED IDENTITY AND A NEW SPECIES (LEPIDOPTERA: TORTRICIDAE)

William E. Miller<sup>1</sup>

### ABSTRACT

Moths now identified as *Rhyacionia busckana* are a mix of two long-confused sibling species. The name *R. busckana* applies to the species with male antennal pecten length subequal to antennal segment length, and with female sterigma width three-fold or more ostium bursae width. The name *R. granti* applies to the previously undescribed species (type locality Iron Bridge, Algoma District, Ontario) with male antennal pecten length at least two-fold antennal segment length, and with female sterigma width less than three-fold ostium bursae width. Structural differences were discovered after sex attractant studies revealed differences in behavioral physiology and phenology. In the Great Lakes region, *R. busckana* larvae feed on *Pinus resinosa* and *P. sylvestris*, and *Rhyacionia granti* larvae feed on *Pinus banksiana*.

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*Rhyacionia* is one of the better-known North American tortricid genera, both taxonomically and biologically (Powell and Miller 1978). Without notable exception, the known larvae feed on needle, bud, and shoot tissues of *Pinus* spp. Several of the more than 20 Nearctic *Rhyacionia* species are considered forest, ornamental, or nursery pests.

The two species treated here have long been confused under one name, *Rhyacionia busckana* Heinrich. That two species were involved was suggested by sex attractant studies at the Forest Pest Management Institute, Canadian Forestry Service, Sault Ste. Marie, Ontario (G. G. Grant, pers. comm.). These studies revealed differences in behavioral physiology and phenology. I examined specimens thus segregated and found consistent morphological correlates. When applied more widely, these results showed that the original type series and a large existing collection of *R. busckana* were species mixtures. Although distinct and separable morphospecies, the pair can be viewed as sibling species because of sympatry and great similarity.

In this paper I identify the species to which the name *R. busckana* applies, and describe the other sibling, which lacks a valid name.

*Rhyacionia busckana* Heinrich  
(Figs. 1-4)

*Rhyacionia busckana* Heinrich (1923: 17) (holotype: male, Bellmore, Long Island, New York, 7-IV-13, genit. prep. CH 15-I-20, No. 24785 in National Museum of Natural History, Washington, D. C., forewing length 7.5 mm, genitalia illustrated in Heinrich 1923: Fig. 51, basal part of antenna illustrated here in Fig. 4), Powell and Miller (1978: 19) (part).

**Discussion.** Male antennal pecten length is subequal to antennal segment length (Fig. 4) (16n). The male uncus is subequal in length and width, and the aedeagus has a

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pronounced asymmetry (Fig. 3) (16n). The female sterigma widens caudally, and its greatest width is three-fold or more ostium bursae width (Fig. 2) (5n). Adults of both sexes usually, but not always, have red crown scaling, which in old specimens may be faded (21n). Red crown scaling and host species were used to associate the sexes. In Ontario, adults developed from larvae found on *Pinus resinosa* Ait. and *P. sylvestris* L. (8n). At least three *Rhyacionia busckana* paratypes are not that species, but represent the sibling species described below. Voucher specimens of *R. busckana* originated in Ontario and New York. They are in the Great Lakes Forest Research Centre, Sault Ste. Marie, Ontario, Canadian National Collection, Ottawa, University of Minnesota, St. Paul, University of California, Berkeley, and National Museum of Natural History, Washington, D. C.

*Rhyacionia granti* new species  
(Figs. 5–8)

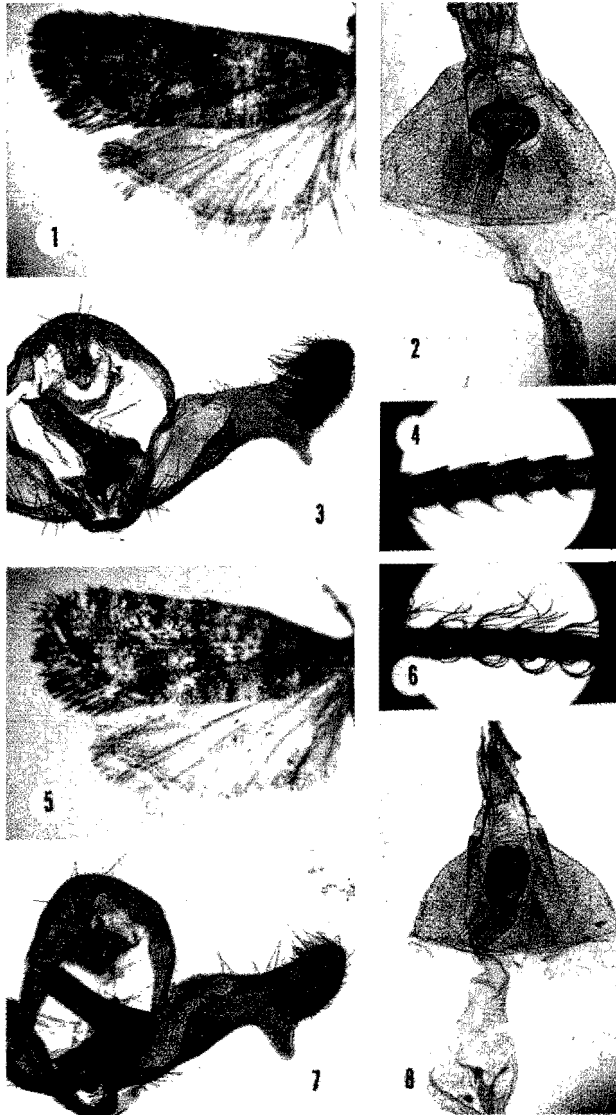
*Rhyacionia busckana* Heinrich; Powell and Miller (1978: 19) (part), Lindquist (1961: 2), Heppner (1975: 121). Misidentification.

**Male.** Forewing length 6.5–8.0 mm (holotype 7.0 mm) (8n). **Head:** Labial palpus clothed with brownish black white-tipped scales, sometimes also red scales, length of second segment subequal to eye diameter, length of third segment one-fourth that of second; front brownish black; crown scales brownish black and white tipped, sometimes red, partly obscuring antennal bases; antennal pecten length at least two-fold antennal segment length (Fig. 6). **Thorax:** Dorsally clothed with white-tipped brownish black scales, sometimes also red, ventrally paler; leg scaling similar to thoracic; forewing upper sides clothed on basal two-thirds with brownish black white-tipped scales forming faint dark and pale crossbands, on apical one-third with red and yellow scales (Fig. 5); hindwing upper sides uniformly light gray. **Abdomen:** Shiny gray. **Genitalia** (Fig. 7) (7n): Uncus ventrally recurved, length at least two-fold mid-width; socii rudimentary; neck of valva ventrally constricted, sculpted out on inner aspect, clasper broad, pollex one-third dorsal-ventral length of cucullus; apical one-fourth of aedeagus slightly asymmetrical, ending in a spur, with 7 to 13 spinules on dorsal and one lateral surface; vesica with two to eight cornuti.

**Female.** Forewing length 6.0–7.5 mm (9n). Similar exteriorly to male. **Genitalia** (Fig. 8) (9n): Margin of ostium bursae ring-like, sterigma often wrinkled, greatest width less than three-fold ostium bursae width; ductus bursae sclerotized near ostium bursae on one side; corpus bursae with two thorn-like signa subequal in size.

**Type Data.** Holotype: male, Iron Bridge, Algoma Dist., Ontario, 25-IV-84, Grant, ant. and genit. prep. WEM 267843 (Figs. 6, 7), in Canadian National Collection, Ottawa. Seven male and nine female paratypes in voucher depositories listed in previous section: ONTARIO: three males, Iron Bridge, 25-IV-84 and 14-V-82, Grant, ant. and genit. preps. WEM 287844 and 317842; one male, Kirkwood Forest, near Thessalon, 2-V-84, Grant, genit. prep. WEM 307841; one male, Sault Ste. Marie, em. Forest Insect Survey (FIS) 9-V-57, genit. prep. WEM 52475a; one female, Nestor Falls, em. FIS 18-I-61, genit. prep. WEM 410841 (Fig. 8); two females, English River, em. FIS 18-I-61, genit. preps. WEM 7575a and b; one female, Calstock, em. FIS 20-I-61, genit. prep. 7575c; one female, Sioux Lookout, em. FIS 16-I-61 (Fig. 5), genit. prep. 52375a; NEW YORK: two females, Central Park, Long Is., 10-IV-13, genit. preps. ME 3-VIII-27-4 and WEM 251851 (from *R. busckana* paratypes); PENNSYLVANIA: one male, Harrisburg, 26-III-11 (from *R. busckana* paratypes); FLORIDA: one male and female, Cedar Key, Levy Co., 21-XI-73, Heppner, genit. preps. WEM 123743 and 123741; MARYLAND: one female, Beltsville, 5-IV-55, Miller, genit. prep. WEM 22-XI-58.

**Discussion.** Superficially, *R. granti* resembles *R. zozana* (Kearfott), *R. fumosana* Powell, *R. jenningsi* Powell, *R. adana* Heinrich, *R. blanchardi* Miller, and its sibling, *R. busckana*. Structurally, it most resembles the last. The two species differ as follows. In *R. granti* males, antennal pecten is coarser and at least twice as long as that in *R. busckana*;



Figs. 1-8. *Rhyacionia busckana*: (1) wings of female from Barrie, Ont.; (2) genitalia of female from Barrie, Ont.; (3) genitalia of male from Iron Bridge, Ont.; (4) basal part of holotype male antenna. *R. granti*: (5) wings of female from Sioux Lookout, Ont.; (6) basal part of holotype male antenna; the pecten curled in process of preparation; (7) genitalia of holotype male; (8) genitalia of female from Nestor Falls, Ont.

the uncus is usually narrower; and aedeagal asymmetry less pronounced (Figs. 3, 7) (7n and 16n, respectively). In *R. granti* females, caudal widening of the sterigma is usually slight, while in *R. busckana* it is pronounced; sterigma width in the former is less than three-fold ostium bursae width, while in the latter it is three-fold or more (Figs. 2, 8) (9n and 5n, respectively).

*Rhyacionia granti* adults of both sexes usually, but not always, have brownish black crown scaling. Brownish black crown scaling and host species were used to associate the sexes.

In Ontario, the larval host of *R. granti* is *Pinus banksiana* Lamb. (8n). Larvae complete feeding in early July and drop to the ground to pupate (Lindquist 1961).

The species is named for its discoverer, Gary G. Grant.

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**AN ILLUSTRATED KEY TO THE PUPAE OF SIX SPECIES OF  
*HYDROPSYCHE* (TRICHOPTERA: HYDROPSYCHIDAE) COMMON  
IN SOUTHERN ONTARIO STREAMS**

Jane E. Rutherford<sup>1</sup>

**ABSTRACT**

I present a key for the identification of pupae and pupal exuviae of six species of *Hydropsyche* that are widely distributed throughout northeastern North America and that are particularly abundant in the streams of southern Ontario. Use of the pupal key requires less manipulation of a specimen than either removing larval sclerites from the pupal case or attempting to discern the adult genitalia through the pupal integument.

Net-spinning caddisflies of the family Hydropsychidae are among the most abundant of the aquatic insects in the streams and rivers of southern Ontario. Two genera, *Cheumatopsyche* Wallengren and *Hydropsyche* Pictet, occur throughout many drainage systems, from headwater streams to river mouths, and often assemblages of several species of both genera are found together on the same rock. In the Credit and Humber rivers, the longitudinal distributions of the common species of *Hydropsyche* overlap, so that at upstream stations (orders 3-4), *Hydropsyche slossonae* Banks and *Hydropsyche sparna* Ross co-occur, whereas at downstream stations (orders 5-6), *H. sparna* is found with *Hydropsyche morosa* Hagen and *Hydropsyche bronta* Ross. At some downstream stations, *Hydropsyche betteni* Ross, *Hydropsyche dicantha* Ross, and *Hydropsyche scalaris* Hagen are present as well (Mackay 1979). *Hydropsyche betteni* has also been collected from fourth-order Humber River stations (Mackay 1979, Rutherford 1984), and is particularly abundant below dams (Mackay 1979). Collection of hydropsychid pupae, with particular emphasis on the timing of pupation, the relative densities of pupae, and the incidence of pupal mortality, has contributed to a better understanding of the life history patterns of *H. slossonae*, *H. sparna*, *H. bronta*, and *H. morosa*.

Hydropsychid pupae are more abundant on the undersides of large rocks, and on the underlying stones and gravel, than on the uppermost surfaces of the streambed substrates where larvae are most abundant. Because considerable effort is required to collect representative samples of pupae it is important to be able to identify every specimen. Often pupae may be identified by characteristics of the larval sclerites remaining within the pupal case, or, when mature, by the adult genitalia visible through the pupal integument. However, in many instances, it is desirable to identify the insect by pupal characteristics. Unless metamorphosis is nearly complete, the genitalia are not well enough developed for identification. The larval sclerites may not be present within the pupal case, as sometimes happens naturally (Scott 1983, and personal observation). Pupal cases that have been infested by either inquiline or predatory chironomid larvae (Parker and Voshell 1979, Vinikour and Anderson 1981, Rutherford 1984) may no longer retain the larval sclerites. Similarly, the activities of the invading chironomid larvae can damage the tissues (including the genitalia) of the developing hydropsychid pupae beyond recognition, although the pupal integument usually remains almost intact.

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Accordingly, I have developed a key for the identification of the pupae of six species of *Hydropsyche* common in southern Ontario. To my knowledge, this is the first published key for the identification of hydropsychid pupae at the species level. My object was to produce a guide for the rapid identification of hydropsychid pupae which did not require excessive manipulation of specimens, or the clearing and mounting of any portion of the insect. I have used features of the dorsum of the pupal abdomen that are easily discerned under a dissecting microscope. Intact specimens are not required for positive identification; consequently, damaged insects or even empty pupal exuviae may be identified using this key. The ability to identify almost every pupa collected, no matter what its condition, allowed me to undertake two studies of pupal mortality in hydropsychids (Rutherford 1984). It is my hope that the features of the pupal integument used here will be examined in other species found in southern Ontario, so that a more comprehensive key can be developed. The species common in southern Ontario are widely distributed throughout northeastern North America (Wiggins 1977), so that a key based on Ontario species would be more than locally useful.

The systematics of the Hydropsychidae have received considerable attention recently. Several workers have proposed the splitting the genus *Hydropsyche* into as many as three genera: *Hydropsyche*, *Symphitopsyche* Ulmer, and *Ceratopsyche* Ross and Unzicker (Schuster and Etnier 1978, Schuster 1984, Morse and Holzenthal 1984). By this scheme, two of the species represented in this pupal key, *betteni* and *dicantha*, would remain in the genus *Hydropsyche*, while the remaining four species, all members of the *bifida* group, would belong to the genus *Ceratopsyche*. Other workers who recognize the taxonomic complexities of the *bifida-morosa* complex do not favour the splitting of *Hydropsyche* into separate genera (Scheffer 1982, Scheffer and Unzicker 1984). Until this matter is resolved, I prefer to retain the use of the name *Hydropsyche* for all the species considered in this paper.

## MATERIALS AND METHODS

Four sampling stations were established on each of the Credit and Humber rivers (Fig. 1); these have been described in detail elsewhere (Mackay 1979, Rutherford 1984). Weekly collections of hydropsychid pupal cases were made from 15 May to 9 September, 1980, to obtain pupae for rearing in the laboratory. Pupae were maintained in small rearing pots at 18°C under a 12:12 h light-dark photoregime (details are described in Rutherford 1984). The pots were checked daily for newly emerged adults and cast exuviae. Adults were removed to holding jars for a few days to allow hardening of their sclerotized tissues, then preserved in Kahle's solution in individual vials in which the associated pupal exuviae were already preserved. Exuviae were easy to associate with individual adults despite the fact that pupae were reared in small groups (up to 30 per pot). Adults emerged sporadically; my records show that for those days on which adults were collected, the rate of emergence was  $1.71 \pm 0.049$  ( $\bar{x} \pm 1$  SE,  $n = 555$ ) adults per pot. Not all collected pupae gave rise to adults (emergence success was about 33%) (Rutherford 1984); however, all specimens were identified using adult characters where possible (Ross 1944), or setal lengths and colour patterns of larval sclerites retained within the pupal case (Mackay 1978, 1984a). These identifications were used to confirm identifications based on characteristics of the hook plates and hairs of the pupal abdomen. Some pupal exuviae were mounted in Permount<sup>TM</sup> on microscope slides to facilitate measurement of the dimensions of the abdomen and hook plates. In total, 2332 specimens were examined (Table 1) to develop the key to six species of *Hydropsyche*. Mounted specimens of *H. morosa* and *H. bronta* were measured at 12 X magnification using a dissecting microscope equipped with an ocular micrometer. Abdominal length was measured along a dorsal midline extending from the thoracic-abdominal suture to the distal end of segment VIII. Width was measured at a perpendicular to the midline, across the 4p hook plates. Hook plate widths were measured at 50X. Drawings of mounted specimens were rendered using both a dissecting microscope and a compound microscope fitted with drawing tubes.

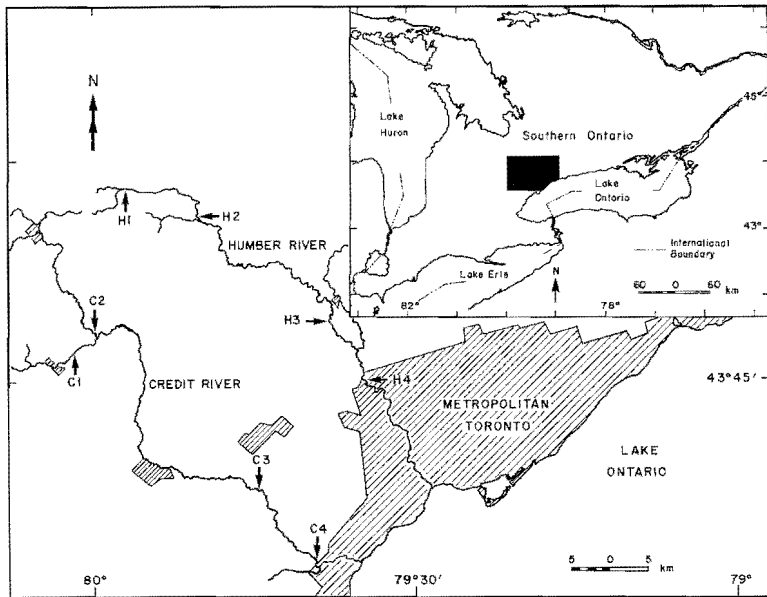


Fig. 1. Location of sampling-stations on the Credit and Humber rivers, southern Ontario.

Table 1. Specimens examined for development of the key to six species of *Hydropsyche*.

Taxon	Identified	Exuviae mounted
<i>Cheumatopsyche</i>	247	13
<i>H. slossonae</i>	677	51
<i>H. sparna</i>	453	49
<i>H. betteni</i>	5	4
<i>H. dicantha</i>	1	1
<i>H. bronta</i>	374	33
<i>H. morosa</i>	575	63
Total	2332	214

## RESULTS AND DISCUSSION

Trichopteran pupae may be identified to family using the keys of Ross (1944). The hydropsychid pupal abdomen lacks a lateral fringe of setae, but has lateral gills; the mandibles have several conspicuous sub-apical teeth in addition to a prominent apical point; the dorsum of segment III bears two pairs of hook plates. In many streams of southern Ontario, the two genera *Hydropsyche* and *Cheumatopsyche* co-exist in abundance. *Cheumatopsyche* pupae may be distinguished from *Hydropsyche* by the shape of the 3p hook plates, which in *Cheumatopsyche* are ovoid to round and in *Hydropsyche* are elongated ovals (Ross 1944). Certain features of the dorsum of the pupal abdomen of *Hydropsyche* are important to note (Fig. 2): segment I is moderately hairy but does not have a spined ridge (as in Limnephilidae); segments II to VIII (in some species, III to VIII) bear paired hook plates with an anterior and posterior pair on each of segments III and IV.

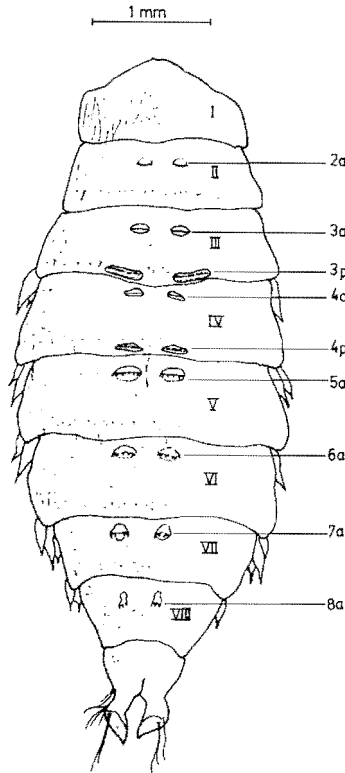


Fig. 2. Generalized drawing of a hydropsychid pupal abdomen showing segments I to VIII, lateral gills, terminal anal processes, and location of paired hook plates (a = anterior, p = posterior); rows of hairs (shown here on the left side of the drawing only) extending across dorsum of each segment are usually well-developed on segments IV to VI, less well-defined on other segments.

On the other segments the hook plates are in the anterior position. Hairs are scattered over the dorsal surface; on some segments (particularly IV to VI) there is a well developed row of hairs on the posterior third of the segment. The presence or absence of the 2a hook plates, the relative size, shape and spacing of the other hook plates, and the stoutness of hairs on the dorsal surface are the main characters used to separate six species of *Hydropsyche* in the following key.

#### KEY TO PUPAE

1. 3p hook plates ovoid to round ..... *Cheumatopsyche*
- 1'. 3p hook plates elongated ovals (*Hydropsyche*) ..... 2
- 2(1'). 2a hook plates absent ..... 3
- 2'. 2a hook plates present (Fig. 2), but may be reduced to as little as a single hook (Fig. 5b) ..... 5
- 3(2). Hairs at lateral margins of dorsum of segments VI to VIII short and coarse, twice as thick at base but only 1/3 to 1/2 as long as hairs of postero-lateral margin of



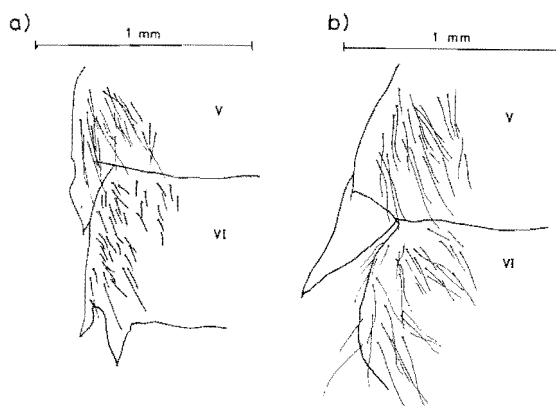


Fig. 3. (a) detail of lateral margin of dorsal surface of *H. bronta* with fine hairs on segment V, coarse hairs on segment VI; (b) lateral margin on *H. sparna* with fine hairs on segments V and VI.

- segment V (Fig. 3a) (short coarse hairs 0.007–0.01 mm long, slender hairs of segment V 0.02–0.03 mm long)..... *H. bronta* (in part)
- 3'. Hairs at lateral margins of dorsum of segments VI to VIII slender, similar in length and thickness to hairs found on lateral margins of segments III to V (Fig. 2 and Fig. 3b) ..... 4
- 4(3'). 4a hook plates small, 0.10–0.12 mm wide, with 4 short hooks, each about as long as they are broad at the base (Fig. 4a); 3a hook plates 0.08–0.10 mm wide, with number of hooks variable (4–8) (Fig. 4c); hook plates on segments V to VII (i.e. pairs 5a, 6a and 7a) 0.10–0.14 mm wide with 4–6 hooks (Fig. 4e, g and i) ... *H. dicantha*
- 4'. 4a hook plates wider, range 0.16–0.18 mm, with more than 4 hooks (number variable, usually 7–9), each about twice as long as they are broad at the base (Fig. 4b); 3a hook plates 0.16–0.18 mm wide, with 7–11 hooks (Fig. 4d); hook plates on segments V to VII (i.e. pairs 5a, 6a and 7a) 0.15–0.19 mm wide with 4–7 hooks (Fig. 4f, h and i) ..... *H. betteni*
- 5(2'). Hairs at lateral margins of dorsum of segments VI to VIII short and coarse, twice as thick at base but 1/3 to 1/2 as long as hairs at lateral margins of segment V (Fig. 3a); 3p hook plates wider than other hook plates, with 4a hook plates 1/2 to 2/3 as wide as 3p hook plates (Fig. 2) ..... 6
- 5'. Hairs at lateral margins of dorsum of segments VI to VII slender not coarse, similar to hairs at lateral margins of segments I to V (Fig. 3b); 3p, 4a, 4p and 5a hook plates approximately equal in width, with 4a plates at least 2/3 as wide as the 3p plates, and the 4p and 5a hook plates both slightly wider than the 3p plates (Fig. 6a) ..... 7
- 6(5). 2a hook plates present, clearly visible at 50X, each with well-developed hooks, number variable (2–13) but usually 6 or 7 (Fig. 5a); complete row of short hairs present on the anterior portion of dorsum of segments III and IV with some arising at the anterior margins of hook plates 3a and 4a (Fig. 5c); 6a hook plates with sturdy hooks, intermediate hooks generally as long and as heavily-sclerotized as lateral hooks (Fig. 5e) ..... *H. morosa*
- 6'. 2a hook plates usually present but can be difficult to see clearly at 50X, often reduced in size with few hooks (range 0–8, but usually 3) (Fig. 5b); some short hairs may be present on anterior portions of segments III and IV, but do not form a well-defined row and none arise at the anterior margins of hook plates 3a and

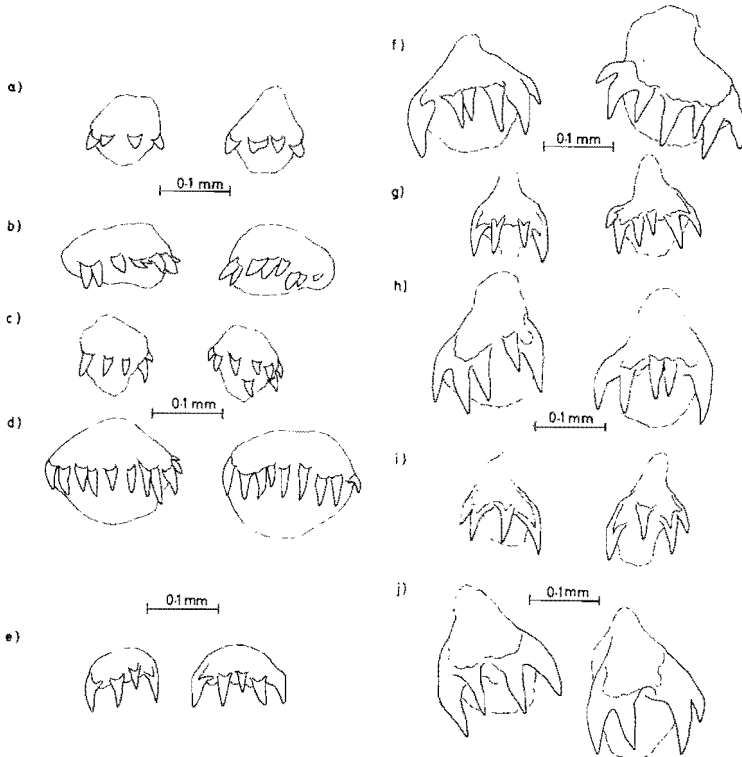


Fig. 4. Comparison of hook plates of *H. dicantha* and *H. betteni* (two examples of each): 4a hook plates, (a) *H. dicantha*, (b) *H. betteni*; 3a hook plates, (c) *H. dicantha*, (d) *H. betteni*; 5a hook plates, (e) *H. dicantha*, (f) *H. betteni*; 6a hook plates, (g) *H. dicantha*, (h) *H. betteni*; 7a hook plates, (i) *H. dicantha*, (j) *H. betteni*.

- 4a (Fig. 5d); lateral hooks on 6a hook plates heavily sclerotized, about twice as long and sturdy as intermediate hooks (Fig. 5f) ..... *H. bronta* (in part)
- 7(5'). Pupa small, abdominal length 5.8–7.3 mm ( $\bar{x} = 6.5 \pm 0.58$  mm,  $n = 37$ ), does not have a dense patch of fine hairs on dorsum of segment IV, but has well-developed posterior row of hairs across dorsum of segments IV, V and VI (Fig. 6a); left and right plates of each pair on segment III close together, sometimes almost touching, with maximum distance between paired plates less than a single plate-width (Fig. 6a) ..... *H. sparna*
- 7'. Pupa large, abdominal length 6.9–9.0 mm ( $\bar{x} = 7.8 \pm 1.00$  mm,  $n = 43$ ) with a dense patch of fine hairs present on dorsum of segment IV but the rest of the dorsal surface relatively hairless (Fig. 6b); left and right plates of each pair on segment III well-separated by at least 1 hook-plate width (Fig. 6b) ..... *H. slossonae*

At upstream stations *H. slossonae* and *H. sparna* are often equally abundant. *H. slossonae* pupae may be recognized immediately by the dense patch of fine hairs on the

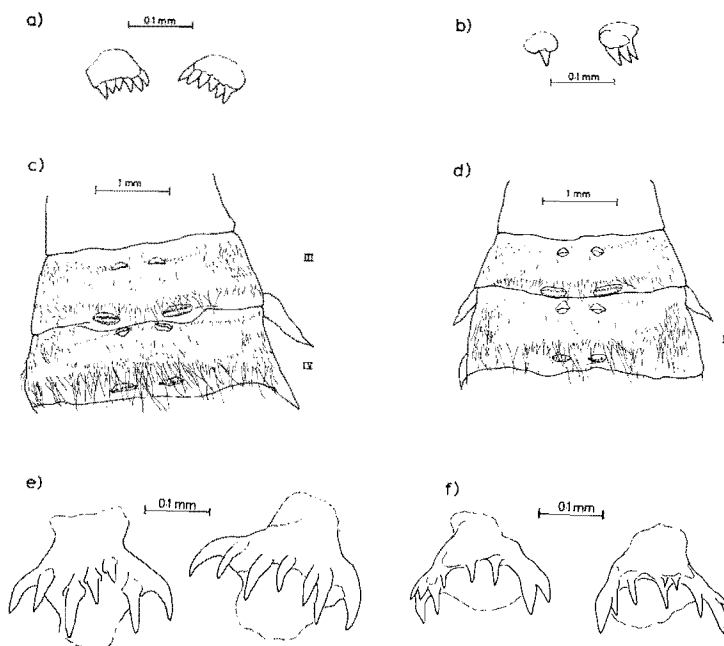


Fig. 5. (a) 2a hook plates of *H. morosa*; (b) 2a hook plates of *H. bronta*; (c) *H. morosa*: detail of dorsum of segments III and IV. Note row of short hairs at anterior of segments, extending to the 3a and 4a hook plates; bases of some hairs arise from anterior margin of hook plates. (d) *H. bronta*: detail of dorsum of segments III and IV. Anterior row of short hairs on each segment not as well-defined as on *H. morosa* (compare to Fig. 5c); no hairs arise from anterior margin of 3a or 4a hook plates. (e) 6a hook plates of *H. morosa*; (f) 6a hook plates of *H. bronta*.

dorsum of segment IV, which contrasts with the rather hairless appearance of the rest of the dorsal surface (Fig. 6b). On *H. sparna*, the hook plates of segment IV are wide, about as wide as the 3p hook plates, but are set very close together (Fig. 6a); the dorsum of segment IV is not markedly hairier than the rest of the abdomen. Both these species are easily distinguished from *H. bronta* and *H. morosa* which are chiefly confined to downstream stations. These latter species have distinctly coarser hairs on the edges of segments VI to VIII than on segments I to V (Fig. 3a); the lateral hairs of *H. slossonae*, *H. sparna*, as well as *H. dicantha* and *H. betteni*, do not become coarser on the three terminal segments (Fig. 3b and Fig. 6a and 6b). *H. dicantha* and *H. betteni* co-occur with *H. bronta*, *H. morosa* and *H. sparna* at some downstream stations. *H. dicantha* and *H. betteni* lack the 2a hook plates, whereas they are well-developed in *H. sparna* and *H. morosa* and usually present (although often reduced in size) in *H. bronta*. Details of the hook plates of segments III to VII may be used to separate *H. dicantha* from *H. betteni* (Fig. 4). *H. morosa* and *H. bronta* are the most difficult to distinguish in the pupal stage, as they are in the larval stage (Mackay 1978, 1984a). In general *H. morosa* pupae are larger and relatively hairier than *H. bronta* pupae (Fig. 5c and d) but because of sexual dimorphism as well as seasonal differences in size attained (Mackay 1984b), length and width alone are not adequate for separation of the two species (Table 2). Close attention must be paid to the size of the 2a hook plates, and the presence of short hairs on the anterior dorsum of segments III and IV for reliable separation of the species (Fig. 5).

Table 2. Comparison of length and width of pupal abdomens (mounted pupal exuviae) in females and males of *H. morosa* and *H. bronta*.<sup>a</sup>

Dimension		<i>H. morosa</i>			<i>H. bronta</i>		
		F	M	Both	F	M	Both
Length (mm)	Mean	6.91 <sup>A</sup>	6.27 <sup>A,B</sup>	6.67	6.10 <sup>A,B</sup>	5.30 <sup>B</sup>	5.64
	S.E.	0.078	0.093	0.085	0.195	0.098	0.130
	n	17	10	27	11	15	26
Width (mm)	Mean	3.09 <sup>C</sup>	2.74 <sup>C</sup>	2.96	2.76 <sup>C</sup>	2.33 <sup>C</sup>	2.50
	S.E.	0.037	0.070	0.047	0.131	0.055	0.075
	n	17	10	27	11	15	26

<sup>a</sup>Lengths and widths of females and males of the species were compared by two separate *a posteriori* tests (using the Student-Newman-Keuls test): (1) lengths, letters denote means that are significantly different, *P* < 0.05; (2) widths, no significant differences were found.

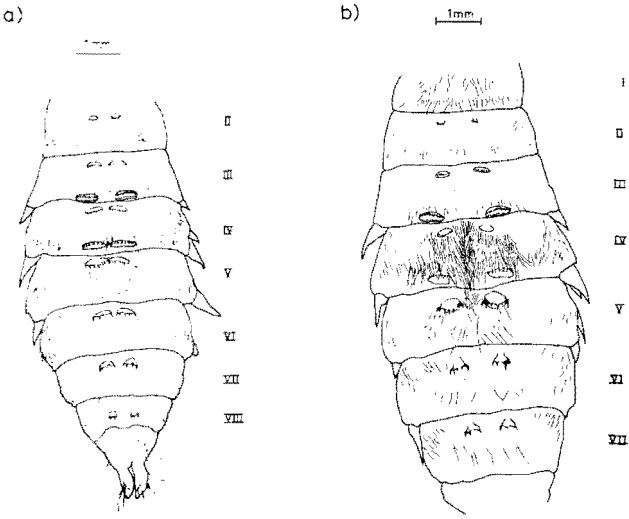


Fig. 6. (a) Dorsal view of *H. sparna* pupal abdomen: hook plates 4a, 4p and 5a approximately the same width as 3p hook plates; plates of each pair separated by less than 1 plate-width; (b) dorsal view of *H. slossonae* pupal abdomen: note dense patch of fine hairs on segment IV; other segments bear relatively few hairs.

Other species of *Hydropsyche* are known to occur at stations on the Credit and Humber rivers. *H. walkeri* is rare at C3 and C4, and *H. scalaris* is moderately abundant at H3 and C3 (Mackay 1979). However, in this study no specimens of these species were successfully reared to adulthood, so that adults and pupal exuviae could not be associated.

Perhaps the most difficult feature to use confidently is the detection of the 2a hook plates on some specimens. This leads us once again to the nomenclatural and systematic problem of the recognition of one, two, or three generic names, as opposed to my use of the single name *Hydropsyche*. The 16 Afrotropical species of the proposed *Symphitopsyche*, and the members of the larger proposed genus *Ceratopsyche*, all possess dorsal hook plates on segment II whereas the members of *Hydropsyche* (*sensu stricto*) do not (Scott 1983, Shuster 1984). By this scheme, *sparna*, *slossonae*, *morosa*, and *bronta* all belong to *Ceratopsyche*. However, the 2a hook plates on pupae of *bronta* are often very difficult to distinguish and, in my experience, are sometimes completely missing. For this reason, two distinct pathways lead to the identification of *bronta* in my key. For these problematic specimens, the choice of either alternative in couplet 2 will lead to the correct identification.

The pupal key presented here was tested in 1981 in a study of pupal mortality in which 4721 pupal cases were collected and preserved immediately in Kahle's solution (Rutherford 1984). Frequently these insects had just pupated so that the genitalia were not developed. In 1–2% of the cases, the larval sclerites were not present. For these specimens, the pupal key provided the only means of identification. Even when larval sclerites were retained in the pupal case, they were tedious to extract, and often the characteristic pronotal setae were broken. Identification of these specimens using pupal characters was easier and more efficient than relying on the colour pattern of the larval head capsule sclerites, and required less handling of the insects.

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