Biology of *Diastrophus Nebulosus* (Hymenoptera: Cynipidae) and Its Parasitoid/Inquiline Complex in Galls on *Rubus Flagellaris* (Rosaceae)

H. C. Gordinier

BIOLOGY OF *DIASTROPHUS NEBULOSUS* (HYMENOPTERA: CYNIPIDAE) AND ITS PARASITOID/INQUILINE COMPLEX IN GALLS ON *RUBUS FLAGELLARIS* (ROSACEAE)

H. C. Gordinier[1]

ABSTRACT

Rubus flagellaris patches occasionally harbor colonies of compound stem-galls initiated by the cynipid, *Diastrophus nebulosus*. These isolated colonies host a parasitoid/inquiline complex made up of five principal and three incidental chalcidoid species and one cynipid inquiline. Over 1-2 seasons, parasitoid/inquiline infestation reduced primary host populations to lows of 2-0% in some colonies. Despite heavy parasitism in most colonies, dispersal of *D. nebulosus* out of infested colonies resulted in a survival rate of 22%. Among parasitoids, a new species, *Eurytoma rubrigalla*, was revealed along with new records for *Eupelmella vesicularis* and an unidentified *Habrocytus* species. Immature stages and life histories of *D. nebulosus* and members of its parasitoid/inquiline complex are illustrated and described with notes on gall genesis and development. Courtship and mating is summarized for *Eurytoma diastrophi* and arrhenotoky is here first reported for a Nearctic species in *Diastrophus*.

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Hartig (1840) erected the genus *Diastrophus* around the Palearctic monotype, *D. rubi* (= *Cynips rubi* Bouche). Seventy years later, Beutenmuller (1909) redescribed the 10 then recognized Nearctic species, summarized their ranges and host plants and figured their galls. The species is included in regional listings of various galls and host plants (Cook 1910, Winterringer 1961). Another 65 years passed before any biological investigations were made into two of the presently recognized 14 species (Burks 1979d); these include Matthews' (1975) account of courtship and mating for *Diastrophus nebulosus* (Osten Sacken), and the first comprehensive biology for a member of the genus published by Wangberg (1975, 1976) on *D. kincaidii* Gillette. Further work on *D. kincaidii* was done by Jones (1983) and Kraft and Erbisch (1990), the latter authors extending its former range from the far northwest to Michigan's Upper Peninsula. Their report, in conjunction with my comparative data, suggests *D. kincaidii* to be the most abundant of *Diastrophus* spp. on *Rubus*. This is the first comprehensive study of the biology of *D. nebulosus* and its gall complex.

Diastrophus spp. produce galls on *Rubus, Fragaria, Potentilla*, and possibly on *Smilax* (Weld 1959). *Diastrophus nebulosus* initiates stem galls on *Rubus flagellaris* (= *villosus*) (Beutenmuller 1909) and is therefore the primary host; its numbers are reduced by both the entomophagous ectoparasitoid complex and the phytophagous inquiline, *Synophromorpha sylvestris* Osten Sacken (Cynipidae) (Fig. 1). Principal chalcidoid parasitoids are *Eurytoma diastrophi* Walsh, *E. rubrigalla* Bugbee (Eurytomidae), *Ormyrus labotus* Walker (Ormyridae), *Torymus flavicoxa* (Osten Sacken) (Torymidae) and *Habrocytus* sp. A (Pteromalidae). The three incidental chalcidoids include *Tenuipetiolus ruber* Bugbee (Eurytomidae), *Torymus advenus* (Osten Sacken) and previously unreported *Eupelmella vesicularis* (Retzius) (Eupelmidae). The role of the single unidentified ichneumonid (near *Orthopelma*) remains unknown. Another *D. nebulosus* parasitoid reported in Krombein et al. (1979) but not found in the present study is *Torymus fagopirum* (Provancher). With the exception of the inquiline, these parasitoids are also found in congeneric and noncongeneric
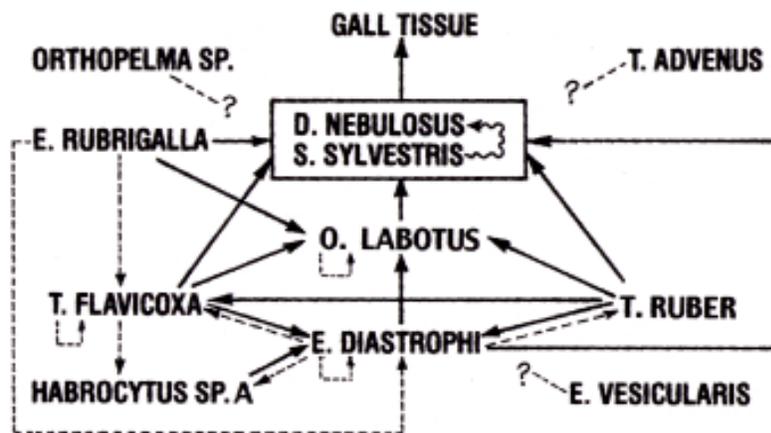
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Figure 1. The resource web in the Diastrophus nebulosus gall complex. Solid lines = frequent observations. Dashed lines = 4 or fewer observations. Turned-in dashed lines = autoparasitism. The sinuous line = indirect destruction of the host by the inquiline.

galls; literature review, synonymies and other hosts for the chalcidoid species discussed are surveyed in Krombein et al. (1979).

Nearctic *R. flagellaris* ranges from southern Ontario and Quebec, south to Florida and west to Colorado and New Mexico (Beutenmuller 1909, Fernald 1950, Bugbee 1967). Voss (1985) reports that *R. flagellaris* occurs essentially throughout Michigan, but I have found galliferous plants only in the southern Lower Peninsula. In this study, *R. flagellaris* appeared most often in the more acidic soils associated with *Quercus* spp.

MATERIALS AND METHODS

Most study material and data were gathered in Macomb and Oakland Counties in southeastern Michigan, beginning in winter of 1965-66 through winter of 1969 (Table 1). A few galls were later taken in Pennsylvania and Virginia for comparative host/predator data. Random collections of roughly 109 galls yielded many hundreds of gall inhabitants through rearing and dissection. Study material was represented by 13 series from seven noncontiguous *R. flagellaris* patches. Study areas were separated by 3-20 km. Loss of autumn foliage facilitated gall collection. Some galliferous plants were transplanted to my yard yielding natural emergences, oviposition sequences (Fig. 2) and gall development data. Six others were potted and caged in the laboratory (Gordinier 1977) to allow study of adult host/predator dynamics and the selective introduction of adult predators. Summer gall collections were kept fresh by immersing their stems in water. Dissection was accomplished with a No.16 Exacto blade and larvae removed with a No.1 sable brush. Late instar larvae were placed in 10×40 mm stoppered vials to prevent desiccation and then into 10 cm movie-film cans to eliminate light. These were then kept outdoors or refrigerated to facilitate diapause and later reared to adults at room temperature. One calendar year was required to identify species and to relate immatures to adults. Gall dissections in all stages of development elucidated morphologies, life histories and larval host/predator dynamics. Parasitoids were often found feeding on their hosts. Mandibles embedded in dried exuvial pellets were separated by soaking in alcohol yielding one, or in the case of hyperparasites, two or more

Table 1. Field sites and collection records.

| Site Name	Location (Long./Lat.)	Collection Dates		No. Galls Collected
MACOMB CO.				
Dodge Bros. St. Pk. #8	T2N:R12E:S14	30 Dec	1965	5
		Dec	1966	25
		Jan	1968	14
		10 Feb	1969	9
Fraser Village	T1N:R12E:S1	26 Feb	1966	4
Utica Rd.	T2N:R12E:S14	22 May	1966	2
		11 May	1968	8
Plumbrook Golf Cs. (fence row)	T2N:R12E:S23	Jan to Feb	1968	13
Warren Twp.	T1N:R12E:S12	Dec	1967	13
(Gloede Rd.)		15 Dec	1968	5
OAKLAND CO.				
Troy (old field)	T2N:R11E:S3	Oct	1967	5
Stony Crk. Mtrpk.	T3N:R12E:S5	9 Apr	1966	6
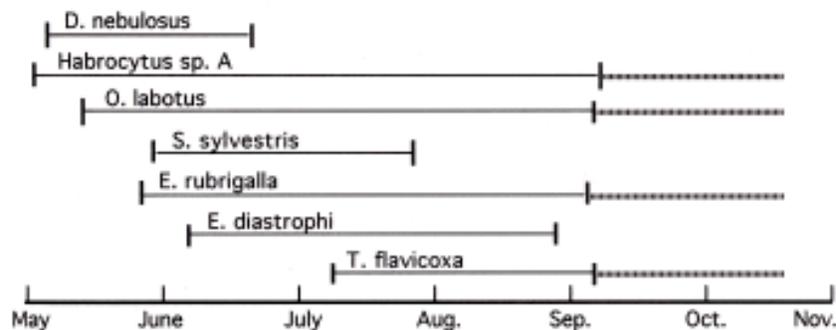
Figure 2. Emergence and flight periods of Diastrophus nebulosus gall inhabitants. Second brood emergences and ovipositions begin at hatched lines. Predators emerge sequentially, perhaps for optimal host competition. Regional and climatic variables will offset specific dates.

sets. Mandibles were often found adhering to the viscous integuments of parasitoid larvae or to chamber walls. Species' measurements were taken through normal body arcuations and all specimens were examined at 40× from which figures were subsequently made by the author (Gordinier 1967). Pertinent material was cataloged and labeled; a number of slide preparations were made. Representative series of insects discussed are in the author's collection.

Plant nomenclature generally follows that of Bailey (1941-1945), Billington (1949) and Fernald (1950).

Predator is a term herein used collectively for parasitoids and inquilines.

Due to extensive parasitism and oophagy within the gall, original species diversity was obscured. Therefore, the term "gall inhabitants" refers to the recording of any stage of a gall species through dissection, rearing or natural emergence.

RESULTS AND DISCUSSION

Gall genesis and development. Blackberry knot-galls are morphologically variable, roughly obovate to oblongate, averaging 35-50 mm in length by 20-30 mm in diameter and may bear typical stem prickles. Matured ovate chambers measure 1.5-3.8 mm across and radiate transversely from the axis. Chambers can number up to 150 but average 50, with each compound gall being considered a fusiform group of individual galls with no communal function among *D. nebulosus* inhabitants. However, the formation of large galls with their more deeply embedded chambers offers some communal protection against predators (Jones 1983). Incipient galls are dark green tinged with red, turning deep reddish-brown in the fall, matching the host plant. Eggs are implanted in the vascular and medullar regions of the stem (Houard 1903, Mani 1964) and gall initiation begins when large numbers of hatchling *D. nebulosus* larvae begin to feed on lateral meristem cells. Larval saliva causes cellular enlargement (hypertrophy) and proliferation (hyperplasy) of adjacent tissues (Mani 1964). The stimulated *Rubus* stem area turns pale luminous-green within two days of the hatch, owing to enlarged phloem and xylem cells with a perceptible swelling at the basal limits of the gall. This swelling radiates in all directions from the axis forcing inflating softer tissues through more resistant, verticular endodermal bundles resulting in typical longitudinal furrows, dividing the gall into 4-5 irregularly convoluted portions (Figs. 3,4). Rudimentary gall chambers are surrounded by continuously forming, enlarged, white, spongiose nutritive cells upon which cynipid larvae feed. Arcuate galls (Fig. 4) result from females laying eggs on one side of the host plant stem as discussed further. Nodular or deformed specimens (Fig. 5) result from few eggs implanted or tissue-severing excavations and elimination of cynipid hosts by parasitoids causing localized cessation of gall genesis. Unfurrowed smoother galls (Figs. 6,7) are associated with poor sandy soils. Gall genesis and growth are phytologically independent, the former continuing normally while the latter may be retarded or accelerated by ecologic variables (Mani 1964). Accordingly, less developed *D. nebulosus* galls on host plants growing in poor soils were seen to contain the same numbers of chambers as in larger succulent specimens, but have thinner tissues, compacted chambers and smaller inhabitants. In mid-October, cessation of both plant
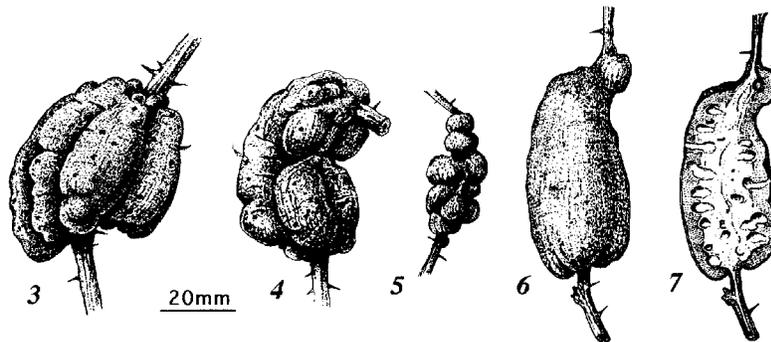
Figures 3-7. Diastrophus nebulosus galls: (3) furrowed, (4) furrowed and arcuate, (5) nodular, (6) smooth, (7) longitudinal section showing larval chambers, parasitoid excavations, and emergence passages.

metabolic activity and cynipid feeding results in pithy cork-like vascular tissues while outer cortical layers become hard and woody. The meristem layer surrounding inquiline and gallmaker chambers dries to form a thin, white shell-like integument. Outer epidermal tissues remain viable throughout the winter, producing floricane branchlets in the spring. Although primocanes and floricanes grow concurrently, *D. nebulosus* normally selects vigorous primocanes, perhaps owing to the hard texture and ultimate fall dying-off of floricanes. In the laboratory, formation of small, distorted rudimentary galls yielding smaller adults on tender floricane branchlets, and even leaf petioles, was accomplished. Some *D. nebulosus* galls are formed basally on the stem and are easily mistaken for those of its crown galling congener, *D. bassetti* Beutenmuller.

Instars of all species exhibit no morphological changes other than size, so a mid-to-last instar description is provided. In general, minute first instars measured from size of the egg to $\geq$ 0.7 mm, vermiform; 13 segments; head capsules nearly as wide or wider than the supernumerary segment. Identification is determined through examination of described setation patterns where present. Dates given for starting emergences and flight periods will vary by 1-2 weeks depending on weather. Described orientation of eggs is based on the first-produced end being the posterior end.

### Species Descriptions and Life Histories.

Family Cynipidae

Diastrophus nebulosus (Osten Sacken) (Figs. 8-13).

Egg (Fig. 8). Bipolar; size of egg body $\geq$ 0.4 mm, with peduncle and club, $\geq$ 0.8 mm (N = 2); egg body nearly transparent turning opaque ivory with age, narrowly elliptic, anterior end producing a long peduncle or stalk terminating in a small elliptic club; peduncle elastic and as long or longer than the egg, becoming wiry upon drying; chorion smooth, viscous when fresh and unpigmented.

Mid-to-last-instar (Fig. 9). Size, 2-2.9 mm (N = 2), rotund; a distinct ventral angulation beginning at the third thoracic segment, but arcuate dorsally; no setae, opaque, smooth, abdominal segments creamy-yellow, thoracic segments creamy white, all segments deeply invaginate and nearly equal in circumference, tapering abruptly from the eighth abdominal to the anal segment. Six visible pairs of spiracles; a pair of ovate mesad-oblique pigmentations on the supernumerary segment are well-defined; head capsule prominent, smaller than the supernumerary segment, smooth, with a distinct epicranial suture and indistinct, transverse eye-like sulci; nasale jutting ventrally. Mandibles (Fig. 10) sclerotized, sub-falciform and weakly recurving, strongly tridentate, dark brown, and larger than those of the inquiline. In April, the once blind larval gut develops and several pellets of greenish, dark brown frass are evacuated. The head capsule is shed and the ovate pigmentations advance anteriorly on the supernumerary segment, apparently forming the compound eyes.

Diastrophus nebulosus larvae are distinguished from those of parasitoids in all instars by its tridentate mandibles and lack of setae, and from *S. sylvestris* by the greater rotundity and stronger arcuation in the latter. The mature larva nearly fills its chamber and frequently shifts its position through a rhythmic snapping movement. Feeding ceases in mid-October with the onset of colder temperatures. *Diastrophus nebulosus* larvae are attacked by all members of the predator complex with up to three nonconspecific predator eggs often found in single chambers.

Pseudo-oophagy was displayed by mid-instars that successfully broke the chorion of inquiline eggs but did not ingest the hemolymph. Also, *D. nebulosus* ineffectively bit at the chorion of parasitoid eggs for long intervals with intermittent feedings on meristem. This behavior continued for 1-3 days and up to hatching of the intruding egg. Parasitoid chorions are perhaps harder than that of the inquiline; age, shape and texture may also determine their resistance. In
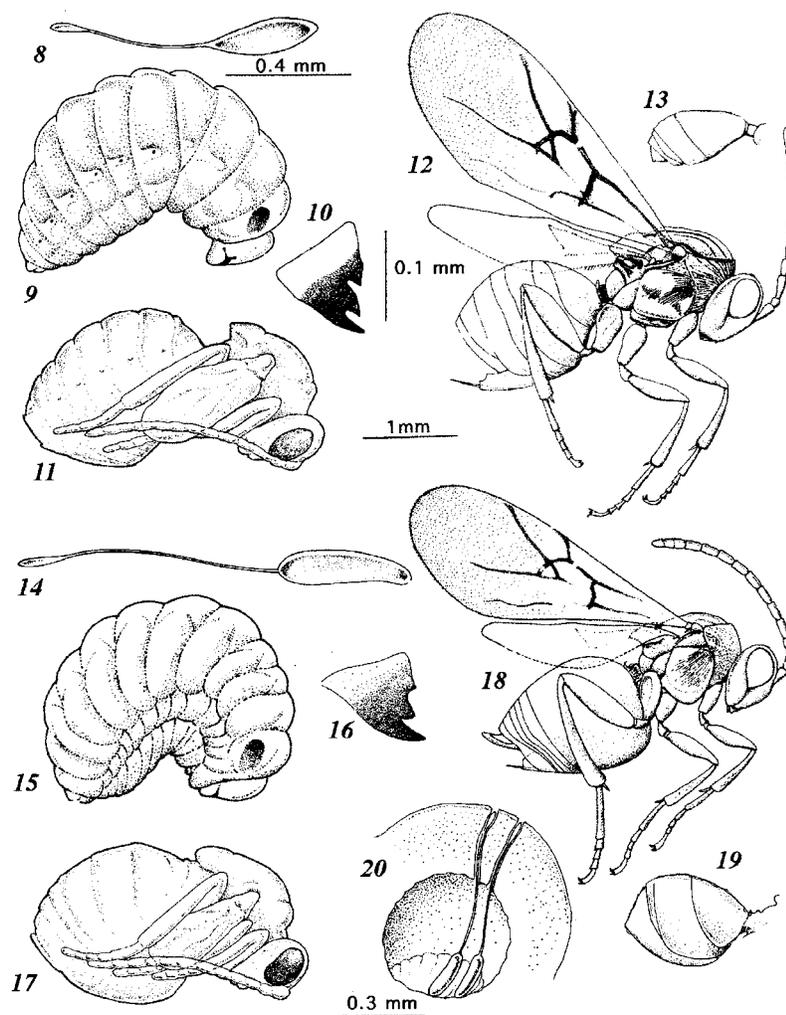
Figures 8-20. Egg measurements are without peduncle. *Diastrophus nebulosus*: (8) egg, (9) larva, (10) larval mandible, (11) female pupa, (12) adult female, (13) male metasoma; *Synophromorpha sylvestris*: (14) egg, (15) larva, (16) larval mandible, (17) female pupa, (18) adult female, (19) male metasoma, (20) *S. sylvestris* multioviposition in a *D. nebulosus* gall chamber.

any event, once the parasitoid egg hatches, the minute larva probably remains unnoticed up to attachment to its host.

Pupa (Fig. 11)**.** Size, 2-3.2 mm (N = 2); creamy-white when newly formed, gradually darkening to deep brown. Pupation lasts 12-17 days after which a large clear drop of fluid is exuded anally. *Diastrophus nebulosus* pupae are distinguished from those of *S. sylvestris* by the smaller size and less rotund metasoma of the former.

Adult. (Figs. 12,13). Female length 2-3 mm; males, 1.5-2 mm (N = 3). Univoltine. Males emerge about 5 May, females over 10-25 May. Rare sightings of adults occurred in the field as late as 22 June. Sex ratios in parasitized galls yielded females 1.5:1, while rare unparasitized galls, such as one found near Richmond, Virginia, produced 163 adults with females 5.79:1. A large unparasitized *D. nebulosus* gall collected near Reamstown, Pennsylvania, produced a series of 38 males only. This arrhenotoky, first reported here for a Nearctic *Diastrophus* species was previously reported in the European *D. rubi* (Bouche) (Folliot 1960).

Emergent gravid females had egg loads of approximately 150 and mated immediately with waiting males. Jones (1983) reports egg loads of 200 in *D. kincaidii* females perhaps explaining their larger comparative numbers (Kraft and Erbisch 1990).

Matthews (1975) reported on the mating and courtship habits of *D. nebulosus* and showed that subtle variations in courtship behavior between closely related groups are significant clues that even permit identification of species (Khasimuddin and DeBach 1975, Matthews 1975).

After mating, females oviposit in rapidly growing primocanes, their stems and lateral shoots measuring from 3-10 mm in diameter and 40-60 cm in height with several developing leafbuds. Eggs are implanted in the axis or shoot junctures but never within a leaf bud. Later on, more tender lateral shoots are used as the stem axis hardens with age. Both *D. nebulosus* and *Diastrophus cuscutaeformis* Osten Sacken females face basally while ovipositing, as was also noted in the rose galling *Diplolepis polita* Ashmead (Shorthouse 1973). Two to 10 minutes are required for each implantation. Moving ≥1 mm for each egg, some short vertical rows are sporadically produced around the axis, seemingly ideal for symmetrical galls, but this factor was countered with many more eggs laid among the rows. The basal and apical boundaries are also indistinct owing to overlapped egg-laying.

On shaded stems, eggs were laid on the shaded side, producing arcuate galls as explained further. Eggs are oviposited along 12-25 mm of the stem with the array of eggs gradually becoming more dense at the apical gall boundary, perhaps indicating female sensitivity to gall symmetry. The occasionally formed secondary galls, 10 cm or so distal to the first are generally smaller. Ovipositor wounds are visible as black specks that disappear in several days. This is perhaps due to oxidation of exposed plant tissue but Wangberg (1975) reports that *D. kincaidii* females produce a brownish fluid with each egg which may account for the darkened egg sites. With the egg body implanted in deeper stem tissues, the small anterior club remains near the surface, an archaic ovipositional mode employed as well by the cynipid inquiline, *S. sylvestris*. Adler and Straton (1894) and Clausen (1940) suggest that terminal clubs are remnants, having lost in vigorously metabolizing plant tissue, their original use as respiratory organs. They exemplify with the European oak galling species, *Biorhiza aptera* Fabricius (sexual gen.= *B. pallida* Olivier). Egg bodies of this species, deeply implanted between bud scales of *Quercus pedunculata*, effect gas exchange through the exposed club since no gas exchange occurs through the dormant bud tissue. In contrast, vigorously metabolizing tissues of plants bearing *Diastrophus* spp. and other cynipid galls, allow gas exchange and would permit total egg implantation by inquiline and parasitoids alike. Indeed, the entire

pedunculate eggs of *Eurytoma diastrophi* and *E. rubrigalla* are so implanted in *D. nebulosus* gall chambers.

In the laboratory, two to three *D. nebulosus* females frequently oviposited simultaneously at the same gall site, a behavior Adler and Straton (1894) suggest is a rudiment of inquilinous behavior. Many average-sized galls in established colonies are perhaps the shared work of several females who apportion their individual egg-loads over neighboring gall sites. Single, large, isolated galls, however, forming a remote, frontier colony, showed near depletion of one female's egg-load.

Diastrophus nebulosus females oviposit over 1-2 days with infrequent rest periods and eggs hatch in 4-6 days. No nocturnal ovipositions in the laboratory were seen. Females retired to the underside of a leaf after dark. Eggs were implanted on the shaded sides of *Rubus* stems, suggesting a phototropic response to the harmful effects of solar rays and heat on delicate eggs in semi-transparent *Rubu*s stems and premature hardening of galls that are exposed to sunshine. Similar behavior is exhibited by the rose galling *Diplolepis rosae* (L.) (personal observation) and *D. polita* (Shorthouse 1973). Constant shade on one side of the stem, however, leads to lop-sided ovipositions resulting in arcuate galls, a more frequent form in galls of *D. kincaidii* (Kraft and Erbisch 1990). Galls semi-sheltered by *Rubus* foliage, however, are more symmetrical and succulent throughout winter. After oviposition, notably weakened females probably die soon thereafter. No adults were observed nectaring but water was readily taken in the laboratory.

Adult *D. nebulosus* are quite docile and when disturbed, "play possum," i.e., fold their legs and antennae, drop from the plant and remain motionless for 2-3 seconds, a characteristic common to many cynipids. These wasps fly poorly, if at all, and habitually walk over plants or make short erratic jumps.

Principal Parasitoid/Inquiline Complex

Family Cynipidae

***Synophromorpha sylvestris* Osten Sacken** (Figs. 14-20). The small, Holarctic genus *Synophromorpha* is largely restricted to *Diastrophus* spp. galls on *Rubus* and perhaps *Diplolepis ignota* (Osten Sacken) galls on Rosa (Weld 1952a, Burks 1979d). I have found *S. sylvestris* only in *D. nebulosus* galls.

Egg (Fig. 14). Bipolar. Size of egg body $\geq$ 0.4 mm, with peduncle and club, $\geq$ 1.2 mm (N = 2); egg body oblo-arcuate, wider anteriorly, gradually tapering posteriorly, anterior end producing a long thread-like elastic peduncle, twice as long as the egg body, terminating in a small elliptic club; eggs are transparent when fresh, becoming opaque with age; chorion and peduncle smooth, viscous and unpigmented.

Mid-to-last instar. (Fig. 15); size, 1.8-2.6 mm (N = 2); very rotund, strongly arcuate, segments convoluted and invaginate; spiracles obscured by mesad secondary segmental convolutions; segments 2-9 nearly equal in circumference, tapering abruptly caudad; integument smooth, viscous, opaque, creamy-yellow; head capsule smooth, smaller than the supernumerary segment, somewhat retracted with a shallow epicranial fossa above the adfrontal area; a pair of ovate, oblique pigmentations appear on the supernumerary segment as in *D. nebulosus*. Mandibles (Fig. 16) falcate, tridentate, dark brown, moderately opposed and smaller than in *D. nebulosus*.

Synophromorpha sylvestris larvae nearly fill their host chambers in late instar and must access fresh meristem with the same snapping tactic employed by *D. nebulosus* larvae. With the onset of autumn, instars are quite immobile, reacting slightly or not at all to the touch of a probe. Dark, greenish frass is excreted two days prior to pupation. The smaller head capsule, epicranial fossa, greater arcuation and rotundity distinguish this larva from that of *D. nebulosus*. *Synophromorpha sylvestris* larvae are attacked by all members of the parasitoid complex.

Pupa (Fig. 17). Size, 2.3-2.8 mm (N = 2); robust, opaque, creamy yellow, becoming dark brown and anally exuding a large drop of clear fluid two days prior to emergence. The larger, more ovate, ventrally projected metasoma with its dorsally fused scutellum distinguish this pupa from that of *D. nebulosus*. The pupal state, beginning in mid-May, lasts 12 days for the male and 17 for the female.

Adult. (Figs. 18, 19). Female length, 2.6-3 mm, males 1.3-2 mm (N = 3). Univoltine. Males emerge around 28 May, gravid females 2-3 days later, roughly two weeks after *D. nebulosus* has initiated new galls. Females outnumbered males 2.75:1. Mating proceeds immediately and appears similar in behavior to *D. nebulosus* (Matthews 1975) except for more rapid movements by *S. sylvestris*. Egg loads are roughly 80 and eggs are larger than those of *D. nebulosus*. Adults, unlike those of *D. nebulosus* are robust, very active and capable of fairly sustained flight. Like *D. nebulosus*, *S. sylvestris* "plays possum" when disturbed. After mating, females seek out galls roughly two weeks old and beginning to swell. At this stage, inquilinous behavior is similar to that of *D. nebulosus* as both oviposit into the same gall sites and their larvae feed on gall tissues. The hatchling larvae of *S. sylvestris*, however, as with other cynipid inquilines have lost their ability to initiate gall tissues and thus females must introduce their eggs into existing *D. nebulosus* gall chambers. After suffocation or immobilization of early instar *D. nebulosus* larvae, *S. sylvestris* larvae commence stimulating and feeding on preinitiated tissues. Gall genesis proceeds normally in these inquiline inhabited chambers.

Oviposition may continue over a six week period (Fig. 2). Ovipositing females move rapidly over the gall substrate with nervously probing antennae. Intruding conspecific females are rushed upon with fanning wings and ejected with split-second mandibular and head contact. Females display a remarkable tenacity for a given gall, guarding it against conspecifics and parasitoids over 1-2 days. A laboratory female was removed from a gall 6-7 times but, in each instance, returned 2-3 minutes later and continued oviposition. Nocturnal oviposition was often noted in the laboratory and almost certainly occurs in the field. One to four minutes are required to deposit each egg, the female remaining motionless except for a slow rising and falling of her body as she guides and releases the egg; she then resumes her spider-like movements while probing out another host site. The medium-sized ovipositor allows implantation of eggs into the deeper chambers of incipient galls and shallower chambers in later gall stages, allowing a flight period from late May to mid-July with peak activity noted about 24 June.

The egg body is guided near or upon the host larva with the club anchored in outer gall tissues. Viscous *S. sylvestris* eggs laid in newly initiated chambers smother or otherwise immobilize first instar larvae of *D. nebulosus* until they die. The method employed in destroying mid-to-late instar *D. nebulosus* larvae revealed that the long peduncle had evolved toward a remarkably different role than that of its archaic respiratory function. With one or more egg bodies deposited in the chamber and their clubs anchored in outer tissues (Fig. 20), the peduncles cross chamber space and serve as an elastic, viscous snare. *Diastrophus nebulosus* mid-instars were frequently observed writhing against adhesive eggs and peduncles, completely immobilized and dying soon thereafter. *Synophromorpha sylvestris* multiovipositions are common, with occasionally two or rarely four eggs implanted. Eggs hatch in 6-10 days.

Among parasitoid species, first-hatched larvae were seen to destroy remaining eggs and/or hatchling larvae resulting in a single occupant per chamber. Shorthouse (1973) and Wangberg (1976) noted like behavior in *Diplolepis polita* and *Diastrophus kincaidii* galls respectively. However, in otherwise barren chambers containing several *S. sylvestris* eggs, the last-hatched larva survives, the earlier hatchlings having been destroyed by conspecific eggs and peduncles. Although Malyshev (1966) suggests that inquiline multioviposition is probably a remnant of its archaic gallforming behavior; such activity is exhibited as well by parasitoid members of the *D. nebulosus* complex.

The replacement of primary host *D. nebulosus* by *S. sylvestris* presents the disadvantage of its becoming the secondary host to parasitoids; ultimately comprising only 9% of total gall inhabitants.

Superfamily Chalcidoidea

Eurytoma diastrophi **Walsh** (Figs. 21-25). Bugbee (1967) and Burks (1979b) review the literature and report this species as indigenous to galls of *D. nebulosus, D. cuscutaeformis* and *D. niger* Bassett. I have reared *E. diastrophi* from *Rubus* crown galls of *D. bassetti* and root galls of *Diastrophus radicum* Bassett, the latter of which are occasionally found adjacent to *D. nebulosus* colonies utilizing the same host plants. I have not reared *E. diastrophi* from *D. cuscutaeformis* galls. The nutritive need of *E. diastrophi* for two or more larvae through excavating into adjacent chambers would not be met by a single host larva in the small, unilocular galls of *D. cuscutaeformis*.

Egg (Fig. 21). Bipolar; size of egg body, ≥ 0.4 mm, with peduncle ≥ 0.7 mm (N = 3); egg body ovoid-elliptic; white when fresh, turning dark brown to black with age; posterior end with a fine stylet that withers with age; anterior end bearing a transluscent peduncle or stalk as long as the egg body, terminating in a small club; peduncle is soft and elastic when fresh, becoming dry, wiry and curling in a day or two; chorion smooth, viscous when fresh, becoming drier with age.

Mid-to-last instar (Fig. 22). Size, 1.5-2.9 mm (N = 2); off-white; sparse rows of setae on all segments, lacking dorsally caudad of third thoracic segment; several pairs of setae on adfrontal head capsule; head capsule nearly as large as the supernumerary segment; mandibles (Fig. 23) large, sclerotized, dark brown, bidentate, strongly falcate and opposed; nine dorsal protuberances or lobes, beginning at the third thoracic segment and prominently displayed when relaxed; strong latero-ventral segmental lobes; integument dry with a wrinkled appearance due to oblique intersegmental invaginations separating the dorsal lobes; eight visible spiracles; body rotund in cross-section with gut contents visible and peristalsis noted. In April, the formerly blind gut develops two days prior to pupation when several pellets of black, semi-solid frass are evacuated. The larger head capsule, setation pattern and larger mandibles readily distinguish this larva from others in the gall.

Pupa (Fig. 24). Size, 2.5-3.2 mm (N = 2); white when formed, turning glossy black with age. Female pupae are larger, more robust and less arcuate than pupae of other eurytomids in the gall. Pupal state lasts from 12-17 days at the end of which a large drop of clear fluid is exuded anally.

Adult. (Fig. 25). Female length 2.7-3.6 mm; males 1.3-2.8 mm (N = 3). Univoltine. Males emerge about 6 June, females about 10 June. *Eurytoma diastrophi* was fourth in sequence to emerge, parasitizing *D. nebulosus* and *S. sylvestris* and hyperparasitizing *O. labotus, E. rubrigalla* and *Habrocytus* sp. A. Among the Eurytomidae, females either equal or outnumber males (Bugbee 1951a) and in this species the ratio was 4:1. Males waited on leaves of a *Populus* sp., some 20 meters from the nearest gall, later approaching the galls where they mated with emergent females. Females have egg loads of roughly 12. *Eurytoma diastrophi* is the most frequent and devastating species in the gall, comprising 33% of inhabitants. Although females of *E. diastrophi* lay relatively fewer eggs, these larvae consume 2-4 host larvae and survive in larger numbers in extremely hardened or dry-rotted galls.

Mating and courtship. An observation of complex courtship and mating activity began with the much smaller male swiftly approaching a female, stopping abruptly several mm away. The male engages in head-bobbing and rapid side-to-side teetering with legs in fixed position lasting for intervals of several seconds. A variation of this behavior was intermittent lateral teetering while quickly approaching in a zig-zag pattern. The male then antennates the female's antennae with a rapid "swimming" motion, the female seemingly non-receptive with antennae elbowed down or receptive with antennae vertical (Assem 1970).
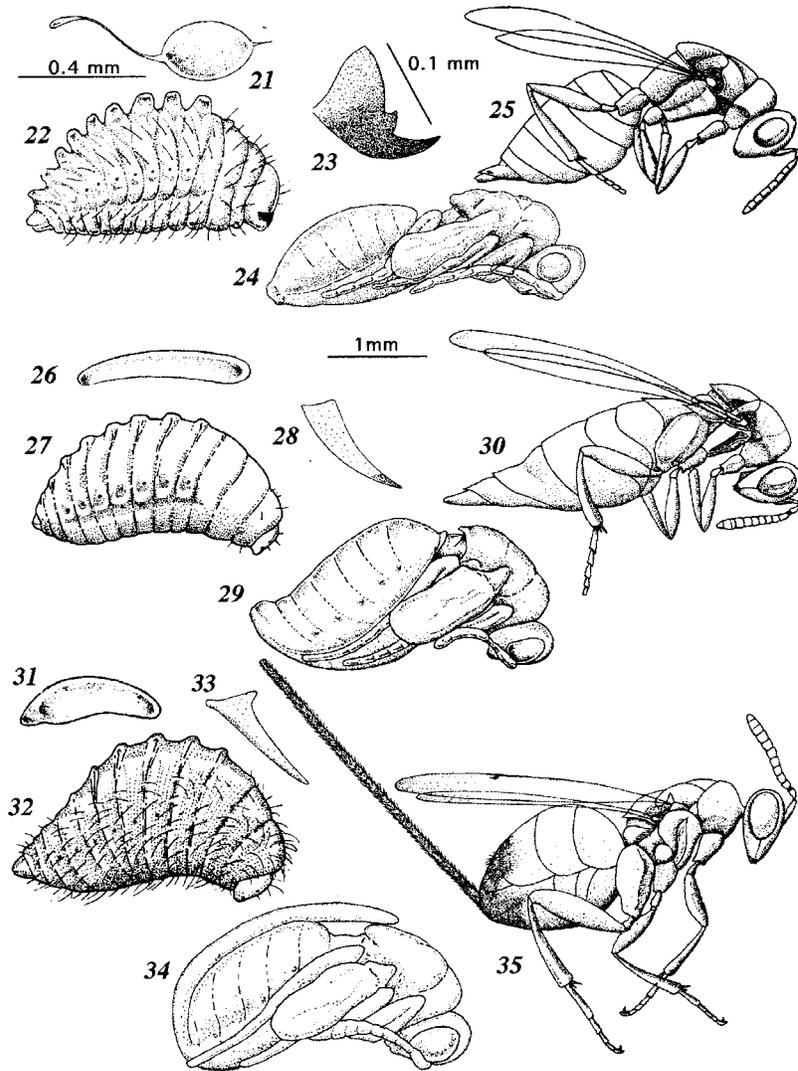
Figures 21-35. *Eurytoma diastrophi*: (21) egg, (22) larva in relaxed state, (23) larval mandible, (24) female pupa, (25) adult female; *Ormyrus labotus*: (26) egg, (27) larva, (28) larval mandible, (29) female pupa, (30) adult female; *Torymus flavicoxa*: (31) egg, (32) larva, (33) larval mandible, (34) female pupa, (35) adult female.

If a non-receptive state remains, the male mounts the female's prothorax with his fore-tarsi atop the female's head. With antennae elbowed down and outward in front of the female's antennae, the male begins a rhythmic bobbing of his head and thorax in abrupt stabbing motions at approximately two beats per second, touching the substrate with his antennae directly in front, or under the tips, of the female's antennae. If still non-receptive, the mounted male strongly fans his wings in roughly two-second repetitions, the force of which pulls his body forward and downward in front of the female; this behavior lasts 20-30 seconds. Should receptivity occur after several such stimuli displays, the male quickly moves latero-ventrally, effecting copulation. In related behavior, a male will mount and remain atop a female's prothorax and is so carried about the gall and stem substrates for $10-25$ minutes. This appears to be a male territorial display to discourage the approach of nearby males. Considerable aggression was shown by males who were in larger numbers as females began emerging. Males rushed at mounted courting pairs, occasionally making body contact causing the mounted male to depart. Females oviposit beginning in early June, implanting one or more eggs into host chambers.

 Upon consuming its initial host larva, *E. diastrophi* excavates into adjacent chambers, ingesting two to four host larvae over its development. The large sclerotized *E. diastrophi* mandibles chew erosively through gall tissues generating sizable amounts of masticated tissues that readily identifies the chamber occupant. Well-developed dorsal and lateral lobes act as tractile and motile organs allowing the larva to exert greater mandibular pressure against gall tissues, and also as "conveyors," moving excavated material posteriorly. Phytophagy was not discerned in *E. diastrophi* but some ingestion of gall tissues may occur during excavation. Eurytomid phytophages are known (Bugbee 1966).

The strong entomophagy of *E. diastrophi* was displayed in the laboratory when a mid-instar larva, having devoured its initial host, was placed in a 10 x 40 mm vial and presented with individual host larvae. Over 19-26 July, this *E. diastrophi* larva consecutively consumed two conspecific and eight *D. nebulosus* larvae beyond its initial host. In two instances, the *E. diastrophi* larva crawled a distance of 10-12 mm to attack and devour the hosts. Consumption time was from 1-4 hours. Nocturnal feeding was not observed suggesting an obligate rest period. On 28 July, two days after feeding ceased, premature metamorphosis occurred as the once blind gut developed and frass was evacuated, but the *E. diastrophi* larva died. The overt aggressiveness of these larvae was exhibited when a fine probe touched to mid-venter was attacked and after removal of the probe, the larvae continued biting at the site. Host larvae fed to late instar *E. diastrophi* in the fall were ignored or weakly grasped and released indicating waning entomophagous response.

Besides its autoparasitism, *E. diastrophi* is attacked by four hyperparasites (Fig. 1) whose method of subjugating aggressive mid-instar *E. diastrophi* larvae would appear to require a sting as commonly administered by certain *Habrocytus* spp. (Clausen 1940).

***Ormyrus labotus* Walker** (Figs. 26-30). Hanson (1992) recently revised and provided a key to *Ormyrus* spp. and summarized their hosts and ranges. *Ormyrus labotus* attacks five hosts on *Quercus*, one on *Rubus* and one on *Lactuca* spp. (Peck 1963). I have reared *O. labotus* from *D. nebulosus* and from the previously unreported hosts *D. bassetti* and *D. cuscutaeformis*.

Egg (Fig. 26). Size, ≥ 0.4 mm (N = 2), banana-like, wider posteriorly,

terminating abruptly at its ends; chorion smooth, unpigmented, viscous and transparent when fresh, becoming opaque and drier with age.

Mid-to-last instar (Fig. 27). Size, 2-2.5 mm (N = 3); light gray, rotund, with weak intersegmental lateral and dorsal lobes, prominent when active; segments 3-8 equally wide, tapering abruptly caudad and gradually cephalad; head capsule smaller than the supernumerary segment; seven visible spiracles; integument

finely punctate; short, sparse rows of setae only on the supernumerary segment and frontal head capsule; mandibles (Fig. 28) small, sickle-like, moderately opposed and unpigmented except for light brown tips; mid-gut transparent and black with gut contents; peristalsis noted while feeding. The sickulate mandibles and relative lack of setae distinguish this larva from others in the gall.

Pupa (Fig. 29). Size, 2.5-3.2 mm (N = 2); distinquished from others by the dorsally projected anal tergites of the female and greater rotundity. Pupal state lasts 15-17 days.

Adult. (Fig. 30). Female length 2.4-3.2 mm; males 1.5-1.9 mm (N = 3). Bivoltine. In spite of two generations, *O. labotus* adults were equal in numbers to those of the univoltine inquiline, *S. sylvestris*, comprising 9% of inhabitants. Although *Ormyrus labotus* is found in *D. nebulosus* and *D. bassetti* galls, it appears more often in *D. cuscutaeformis* galls, comprising 20% of its inhabitants. Both sexes emerge about 10 May; second generation males emerge around 5 September, females about 9 September. Spring-emergent females outnumbered males 1.8:1 with fall ratio unknown. Females emerged in the laboratory but no mating activity was observed.

Ovipositing females nervously flex their metasomas while antennating the gall surface and require 6-7 seconds to implant each egg, with multiovipositions into several host chambers per gall a common occurrence. Females do not linger on the gall but depart after implanting several eggs. The shorter ovipositor is ideally suited to the externally produced, seed-like galls of *D. cuscutaeformis* and reveals why eggs are laid in the outermost compound chambers of *D. nebulosus* galls. Moreover, its relatively early emergence allows its use of smaller, less developed *D. nebulosus* galls.

Ormyrus labotus exhibits considerable autoparasitism, especially in the fall brood, probably due to depleted or inaccessible primary host resource. Females attack conspecific larvae, pupae and even fall preemergent adults whose intact integuments then resemble the result of endoparasitism. A remarkable aspect of its autoparasitism was frequent ovipositions on conspecific male pupae, subsequently producing male *O. labotus* adults. While perhaps coincidental displays, the stratagem for deliberate replacement of fall-brood with spring-brood males is unclear. *Ormyrus labotus* larvae require a single host larva for development. Second generation, overwintering *O. labotus* larvae are found in all instars on their hosts, their feeding commencing with rising temperatures.

***Torymus flavicoxa* (Osten Sacken)** (Figs. 31-35). *Torymus flavicoxa* is reported parasitic on the cynipids *Liposthenes glechomae* (L.) in galls on *Glechoma hederacea, Belonocnema treatae* Mayr in root galls on *Quercus virginiana* and *Diplolepis radicum* (Osten Sacken) in root galls on a *Rosa* sp. (Grissell 1979).

Egg (Fig. 31). Size, ≥ 0.4 mm (N = 2), widely oblo-arcuate, wider posteriorly, constricting into a smaller bulbous protuberance; chorion smooth, translucent and unpigmented when freshly laid, becoming opaque with age.

Mid-to-last instar (Fig. 32). Size, 2.5-3 mm (N = 3), rotund when relaxed; weakly projected dorsal intersegmental lobes beginning at the third abdominal segment; integument opaque, darker gray than *O. labotus* and finely punctate or matte in texture; rows of numerous long setae overall except dorsally from the third thoracic, caudad to the eighth abdominal segment; black in mid-gut with peristalsis noted; head capsule small, having several long setae on adfrontal area with a pair of minute tubercles projecting from the adfrontal margins. Mandibles (Fig. 33) lacking in pigmentation, scarcely sickulate and opposed. The pair of tubercles on the adfrontal margins and heavier setation separate this larva from others in the gall.

Pupa (Fig. 34). Size, 3.4-4 mm (N = 2). Female pupae are easily separated from others by the large ovipositor sheath produced postero-ventrally and fused dorsally. Pupation periods were about 12 days for males, 18 days for females.

Adult. (Fig. 35). Female length, 3.5-4.1 mm (excluding ovipositor); males 1.6-2.5 mm (N = 3). Bivoltine. *Torymus flavicoxa* was fifth in frequency, comprising 4% of total inhabitants. The smaller males emerge sporadically in early summer, about 10-24 July, females around 13-28 July. Summer brood females outnumber males 1.50:1. Fall brood males emerge about 7-27 August, and females, 13 August to 28 September, with fall brood sex ratio unknown.

Torymus flavicoxa females gain sufficient clearance for their 4-5 mm ovipositor by typically arising full height on extended middle and hind legs. Some rising and falling of the body is noted as the ovipositor is slowly inserted into the gall. One or more eggs are implanted in each host chamber and require 7-10 days to hatch. Both generations are closely interwoven with emergences overlapping ovipositions from midsummer to late fall. With the arrival of spring, *T. flavicoxa* larvae enter a prolonged diapause, emerging around 10 July. Higher mid-to-late summer temperatures appear to activate development in both generations. Similar protracted diapause is reported for *T. bedeguaris* (L.) (Shorthouse 1973) in the rose galls of *D. polita*. Host relations include attacks by hyperparasites and autoparasitism (Fig. 1). *Torymus flavicoxa* feeds on a single larva and displays no excavating behavior. The typically long ovipositor allows implantation into both shallow and more deeply positioned host chambers in fully matured galls. Immatures are observed in all instars throughout winter, remaining fastened to their hosts until rising temperatures trigger feeding response.

Eurytoma rubrigalla **Bugbee** (Figs. 36-39). Similarities of adult characters in this genus belied the presence of a congener within the series in my earlier collections of *E. diastrophi*. Evidence of such, however, was revealed through immature morphology, host relations and bivoltinism of this second species. Series of immatures and adults were submitted to R.E. Bugbee who described the new species (Bugbee 1968). Examination of my older *E. diastrophi* series turned up proportionate numbers of *E. rubrigalla*. I have reared several small series of unconfirmed *E. rubrigalla* from the *Rubus* crown galls of *D. bassetti*, the rose galls *of Diplolepis dichlocerus* Harris and *Lactuca* galls of *Aulacidea tumida* (Bassett). In each case, *E. rubrigalla* occurred with *E. diastrophi, E. spongiosa* Bugbee and *E. bicolor* Walsh, respectively.

Egg. Undetermined, but would resemble that of *E. diastrophi*.

Mid-to-last instar (Fig. 36). Size, 1-2.3 mm (N = 3). A late instar was recorded based on scant material. Creamy white, opaque, 13 apparent segments; six pairs of visible spiracles beginning at the fourth abdominal segment; elliptical in cross section; midsegments wider, narrowing gradually caudad and cephalad to the supernumerary segment, the latter nearly as wide as the head capsule; flange-like latero-ventral protuberances beginning at the fourth segment, more pronounced when relaxed; pairs of setae on the lateral and ventral aspects of all but the anal segment, lacking dorsally except on the first two thoracic segments. Head capsule small with weakly bifurcate nasale and sparse adfrontal setae; mandibles (Fig. 37) small, unpigmented except for dark tips, falcate, opposed and bidentate.

Pupa (Fig. 38). Size, 1.2-2.4 mm (N = 2); distinguished from *E. diastrophi* by its smaller size, more ovate metasoma and ventral arcuation in the female. Pupation period for females was approximately 18 days.

Adult (Fig. 39). Female length 2.2-2.7 mm, males 1.5-2.1 mm (N = 2). Bivoltine. *Eurytoma rubrigalla* comprised 3% of total inhabitants. Though eurytomid females are generally equal or greater in number than males (Bugbee 1951a, Shorthouse 1973), *E. rubrigalla* males outnumbered females 1.4:1 but larger samplings are needed to show truer ratios. Males emerge earlier than *E. diastrophi*, around 26 May, and females about 2 June. Fall males emerge around 27 August, females about 5 September, and were found ovipositing on 9 September. *Eurytoma rubrigalla* attacks the primary and secondary hosts and is
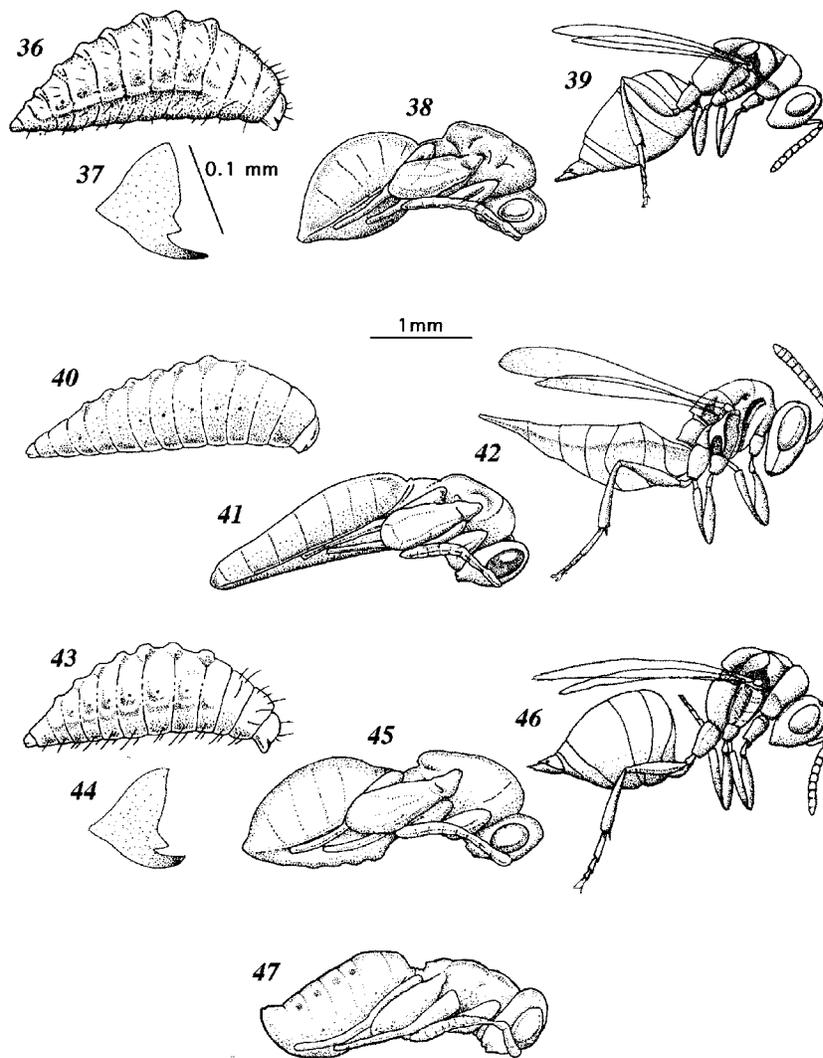
Figures 36-47. *Eurytoma rubrigalla*: (36) larva, (37) larval mandible, (38) female pupa, (39) adult female; *Habrocytus* sp. A: (40) larva, (41) female pupa, (42) adult female; *Tenuipetiolus ruber*: (43) larva, (44) larval mandible, (45) female pupa, (46) adult female; *Eupelmella vesicularis*: (47) female pupa.

hyperparasitic *on E. diastrophi, O. labotus* and fall brood pupae of *T. flavicoxa*. In both generations, *E. rubrigalla* implants one or more eggs into each host chamber and exhibits no excavating behavior, requiring only one host larva for development. Adults are smaller than *E. diastrophi* and are distinguished from the latter by black infuscation on the profemora and protibia of the female, the squarish flagellar segments of the male and the white tarsi present in both sexes (Bugbee 1968).

Habrocytus **sp. A.** (Figs. 40-42). Systematics problems in the Pteromalidae disallowed identification of this species (B. D. Burks, personal communication).

Egg. Undetermined.

Mid-to-last instar (Fig. 40). Scant material allowed only a description of late instar larvae. Size, 2-2.1 mm (N = 2), vermiform, elongate, ivory white, smooth and lacking setae, semi-transparent and somewhat round in cross section, 13 weakly produced segments, with eight pairs of visible spiracles, indistinct dorsal lobes, fourth segment wider, others tapering caudad and cephalad; head capsule ovate, dome-like laterally and as wide as the supernumerary segment; mandibles unpigmented, small, sub-falciform and strongly opposed.

Pupa (Fig. 41). Size, 3-3.7 mm (N = 2), metasoma elongate; gradually tapering posteriorly, separating this species from the others. Early pupation in mid-April lasts 12-15 days.

Adult. (Fig. 42). Female length, 3-3.5 mm; male, 2-2.5 mm (N = 2). Bivoltine. *Habrocytus* sp. A. was the least frequent gall member, comprising 2% of inhabitants and was not previously reported from *D. nebulosus* galls. First generation *Habrocytus* sp. A. emerged around 25 April, roughly two weeks prior to *D. nebulosus*. Second generation males appeared about 8 September, females about 11 September. Spring-emergent females outnumbered males 3.17:1. Though *Habrocytus* sp. A. is first to emerge from *D. nebulosus* galls, it did not appear in their galls until mid-June to early July. Clausen (1940) surmises that certain *Habrocytus* spp. remain at large and infertile for many weeks until a suitable host becomes available. Such late entry into the gall may suggest its nutritive need for larger hosts. Unidentified *Habrocytus* spp. are also reported from galls of *D. polita* (Shorthouse 1973) and galls of *D. kincaidii* (Wangberg 1976) and reflect the multiparasitism found in the genus (Burks 1979c). The few *Habrocytus* sp. A. found in *D. nebulosus* galls were hyperparasitic on second instar *E. diastrophi* larvae in mid-July. Up to two larvae are required for development; a straight narrow tunnel is excavated into a second host chamber. The precarious habit of *Habrocytus* sp. A. mining into *E. diastrophi* chambers occasionally resulted in the former being consumed by *E. diastrophi*. Stinging by *Habrocytus* spp. (Clausen 1940, Wangberg 1976) of other gall hosts may also be the subjugation method used by *Habrocytus* sp. A. on its obligate mid-to-late instar hosts in *D. nebulosus* galls. Overwintering *Habrocytus* sp. A. instars were noted latero-dorsally attached to unconsumed *E. diastrophi* hosts with feeding commencing with rising temperatures. Four to six days are required to ingest a single larva after which the once blind gut develops in the prepupa. Only two instances of hyperparasitism were observed on *Habrocytus* sp. A.: *E. diastrophi* fed on its pupa and *T. flavicoxa* fed on its larva.

Incidental Parasitoid/Inquiline Complex
Superfamily Chalcidoidea

Tenuipetiolus ruber **Bugbee** (Figs. 43-46). Bugbee (1951b) offers systematics and range of this species. Recorded hosts for *T. ruber* include *D. nebulosus, D. cuscutaeformis* and the rose galls of *D. rosae* (Burks 1979b). I have reared larger numbers of *T. ruber* from *D. cuscutaeformis* galls than from *D. nebulosus* galls and from the unreported galls of *D. fusiformans* Ashmead on *Potentilla* species.

Egg. Unidentified.

Mid-to-last instar (Fig. 43). Size, 1.5-2.2 mm (N = 2); vermiform, integument white; weak dorsal and lateral intersegmental lobes; segments indistinct, somewhat oval in cross section; long ventral setae on all segments, including sparse dorsal rows on the second thoracic segment and all around the supernumerary segment; several pairs of setae on the adfrontal head capsule; mandibles (Fig. 44) small, bidentate, unpigmented except for light-brown tips, closely resembling those of *E. rubrigalla* but more falcate. Other larval characters are close to *E. rubrigalla*, the latter showing stronger segmentation and overall latero-dorsal setae.

Pupa (Fig. 45). Size, 2-3.5 mm (N = 2); female pupae are easily distinguished from those of other species in the gall by the ventral ridges on the metasoma. Pupal stage for females was roughly 11 days.

Adult (Fig. 46). Female length, 2-3.7 mm (N = 2). Apparently univoltine. Only 15 specimens were reared. According to Bugbee (1951b), *T. ruber* emerges throughout May and early June, the females outnumbering males 3:1. This ratio in the present study was 2.5:1. *Tenuipetiolus ruber* is a parasitoid of *D. nebulosus* and *S. sylvestris* in immature galls, and later became hyperparasitic on *E. diastrophi, O. labotus* and *T. flavicoxa. Tenuipetiolus ruber* occasionally feeds on a second larva by excavating a straight, narrow passage into the host's chamber, its clean excavations differing from the erosive mining of *E. diastrophi*. Excavating by *T. ruber* in *D. nebulosus* galls would be curtailed in the unilocular galls of *D. cuscutaeformis*, indicating facultative feeding habits. Adults are readily distinguished from adults of other species in the gall by the metasoma's long petiole and long whorls of setae on the scape of the female (Bugbee 1951b).

Eupelmella vesicularis **(Retzius)** (Fig. 47). Adult female length, 2.5-2.8 mm (N = 2); distinquished from other adults by the larger head capsule, enlongate thorax, and an oblate gaster bearing a pair of spinules on the anal tergite. Synonymies, literature review and long host list for this parasitoid are given in Peck (1963) and Burks (1979a). Personal rearings from incidentally collected *D. nebulosus* gall material have turned up further *E. vesicularis* specimens, but the species is incidental in most hosts and biological data have thus far been incremental. Wangberg (1976) described its egg as white and stalked, and its larva was hyperparasitic on *Eurytoma brevitergis* Bugbee in *D. kincaidii* galls. *Eupelmella vesicularis* larvae were observed to excavate in *D. nebulosus* galls but no host data was revealed. Only 5-6 females were reared and no males were observed in the field or otherwise recorded.

Torymus advenus **(Osten Sacken).** This parasitoid has been tentatively reported from *D. nebulosus* galls (Grissell 1979), and appeared in this study in a series of four females from one gall. Nothing was revealed of its immature stages or life history.

Family Ichneumonidae

Unidentified ichneumonid (near *Orthopelma* Taschenberg) sp. A. One specimen was found as a preemergent adult in a large chamber. *Orthopelma* is reported as endoparasitic and indigenous to *Rubus, Ribes* and *Rosa* galls (Wangberg 1976, Barron 1977, Carlson 1979).

Numbers of inhabitants. The total disposition of 109 galls from 13 series collected in four years is shown in Table 2. Parasitoid infestation resulted in occasional extinction of *D. nebulosus* in some habitats as seen in Series X (Table 2). Nearly 100% of *D. nebulosus* galls were parasitized, but absence of one or more species occurred in some series. Each randomly collected series displayed distinct populational stages and are accordingly classified (Table 2) as having frontier, succession or climax status, the latter two combined outnumbering frontier colonies by 11:2. Second brood emergence-hole counts from overwintered galls totaled 410 from all series, their numbers nearly equal to spring broods.

Table 2. Total numbers of gall inhabitants from all series, 1965-1969.

Date Coll.	Series	No. Galls	1	2	3	4	5	6	7	8	Totals	% D. nebulosus in Galls	Colony[b] Status	Site Locale
12-65	I	5	83	11	1	44	0	2	3	19	163	51	S	Dodge Park
2-66	II	4	65	0	4	1	7	0	0	0	77	84	F	Fraser
4-66	III	6	13	21	6	63	21	5	1	71	201	6	C	Stony Creek
5-66	IV	2	101	0	0	2	0	0	0	0	103	98	F	Utica Rd.
12-66	V	25	36	39	13	205	52	17	7	118	487	7	C	Dodge Park
10-67	VI	5	83	4	18	10	0	3	9	13	140	59	S	Troy
12-67	VII	13	27	73	33	125	4	22	2	62	348	8	C	Warren
1-68	VIII	5	4	18	69	51	0	1	0	0	143	3	C	Plumbrook
1-68	IX	14	4	8	21	120	2	9	17	18	199	2	C	Dodge Park
2-68	X	8	0	3	25	44	0	0	0	27	99	0	C	Plumbrook
5-68	XI	8	65	4	0	36	12	0	0	11	128	51	S	Utica Rd.
12-68	XII	5	30	39	4	23	2	1	0	40	139	22	C	Warren
2-69	XIII	9	12	4	11	61	6	9	2	31	136	9	C	Dodge Park
Totals:	13	109	523	224	205	785	106	69	41	410	2,363			
Mean Nos. per gall			4.7	2	1.9	7.2	1	0.6	0.4	3.8	21.7			

[a]Key:
1 = D. nebulosus   5 = T. flavicoxa*
2 = S. sylvestris   6 = E. rubrigalla*
3 = O. labotus*   7 = Habrocytus sp. A*
4 = E. diastrophi   8 = Fall brood
    *bivoltine
[b]Populational stage of colony: F = frontier, S = sucession, C = climax

Figure 48A-B illustrates population trends at two sites where several annual samplings were made. Two series totaling 10 galls were collected in an intermittent three year sampling at Site A (Utica Rd., fencerow colony), showing a frontier gallmaker-dominated colony trending toward predator dominance by 1969-1970. The succession curves are typically reciprocal and reveal the rapidity of populational shifts. The small samplings at Site A are indicative of the few galls found in remote frontier colonies; therefore, 1967 was estimated due to overcollection concerns. The successful dispersal of parasitoids in a single season out of old infested colonies becomes evident in the 1968 sampling.

Site B (Dodge Park No.8), with four annual samplings totaling 53 galls, revealed a sharp *D. nebulosus* decline from frontier status in the winter of 1965-66 to predator succession beginning in 1967. This trend culminated in 1968 with predators reaching a 98% climactic level. A 0-2% gallmaker population within a colony would lead to parasitoid/inquiline dispersal owing to lack of resource, forcing them to move to newly established colonies or perish which may account for the slight *D. nebulosus* rebound in 1969. These slight rallies, occurring in 2-3 years, would not result in more than continuing low numbers or annihilation of *D. nebulosus* populations. The infested Dodge Park site annually produced small numbers of galls, persisting as Janzen's (1970) parasite "sinks" or "generators," depending on one's point of view.

The disposition of host-predator percentages from all colonies over four years (Fig. 49) shows *D. nebulosus* having a survival rate of 22%. Recurring reports of other gall species sustaining low gallmaker populations (Askew 1961, Evans 1967, Shorthouse 1973) affirms their successful adaptation to seemingly marginal populations.

Host/predator dynamics. *Rubus flagellaris* forms habitat patches for relatively small, isolated colonies of *D. nebulosus* galls that both define and delimit competitive resources. Patch-confinement of hosts results in predator
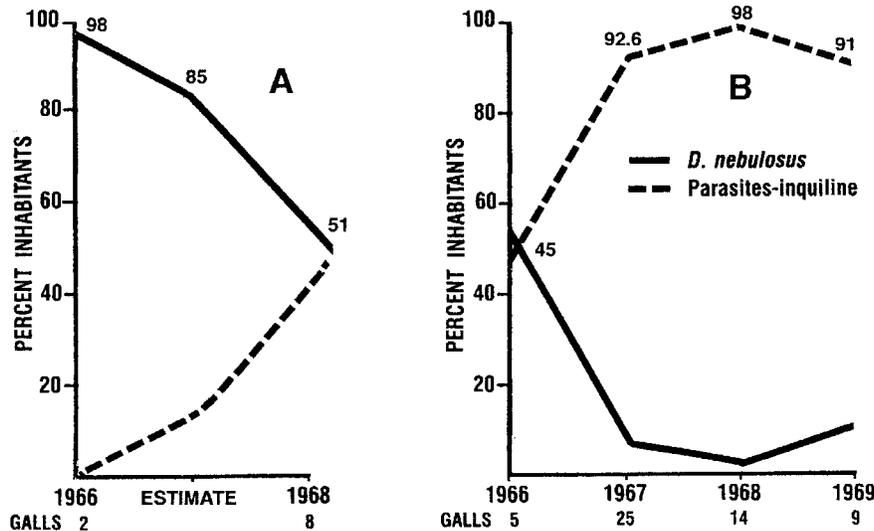

Figure 48(A-B). Reciprocal climax and succession of *Diastrophus nebulosus* and its parasitoid/inquiline complex respectively in three and four year samplings at two sites. Site A. Utica Road fencerow, Series IV, XI, 10 galls; Site B. Dodge Bros. Park, No. 8, Series I, V, IX, XIII, 53 galls.
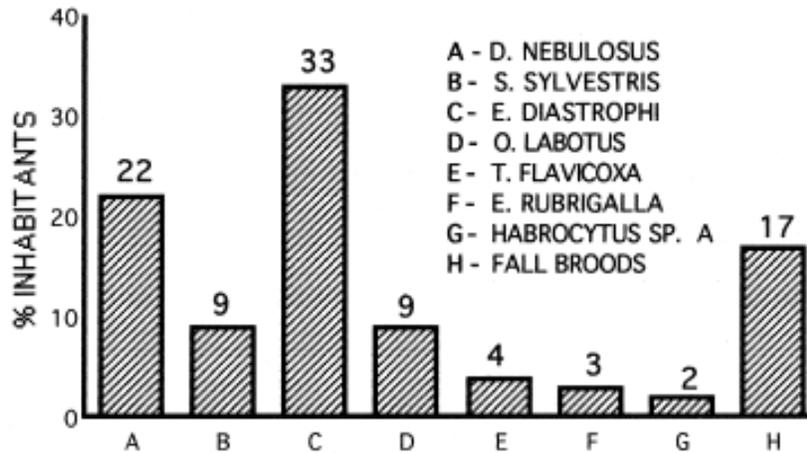
Figure 49. Species percentages in all samplings over four years.

group response to strong olfactory attractants (Salt 1937) from adjacent, newly initiated galls. This irresistible predator recycling and resultant annual populational degradation of *D. nebulosus* resource to single-digit numbers in some cases, may perhaps be seen as a predator diversion stratagem (analogously in Janzen 1970), allowing hosts in remote frontier colonies to proliferate. *Diastrophus nebulosus* disperal success, however, is transitory, with predators locating and infesting frontier colonies over one or two seasons.

Little or no host discrimination was displayed by adult parasitoids that introduced eggs into previously visited conspecific and nonconspecific chambers. The *S. sylvestris* inquiline, however, always discriminates for *D. nebulosus* larvae but may not detect a cohabiting parasitoid egg. Certain defensive cues were evident when attacking predator females were noted reluctant to alight upon occupied galls. Although such attempts were made, intruding females were chased away by the first-ovipositing female.

In evaluating competitor success, the ovipositor length of *D. nebulosus* predators indicated that all but that of the much larger *T. flavicoxa* ovipositor allowed access to only the shallower outer chambers, depending on gall maturation. The eventual replacement of cynipid resource by parasitoids leads to facultative hyperparasitism and autoparasitism when competition approaches parasitoid climax by mid-July. Though *D. nebulosus* parasitoids also use other hosts, their olfactory link to an established *D. nebulosus* colony annually assures a strong parasitoid presence.

Attacking *D. nebulosus* larvae in early stages of gall development is thus essential to most of its parasitoids. Jones' (1983) morphological studies of compound galls of *D. kincaidii*, showed that the more deeply located gall chambers offered escape from parasitoids. However, the small numbers of surviving cynipid hosts in the deeper but fewer *D. nebulosus* chambers suggest the need for their augmented dispersal to ungalled patches in order to maintain their 22% populational level. Kinsey (1929) and Malyshev (1966) regarded compound galls as primitive forms, the latter suggesting that such galls are a less efficient adaptation since predator infestation occurs at early stages of gall development and the hardening of outer protective tissues in the fall occurs too late. In addition, the large olfactory "targets" presented by compound galls increases their vulnerability.

My observations of host plant biotas and those of Kuster (1911), Winterringer (1961), and Shorthouse (personal communication) confirm that vast areas of apparently suitable host plants remain devoid of galls. Patch underpopulations may be simply due to normally low dispersal success out of infested colonies. The common, dipterous midge galls of *Lasioptera nodulosa* Beutenmuller, for example, a species with the apparent advantages of greater flight ability and fewer parasitoids, are found on the same *Rubus* host stems and in far greater numbers and range.

To summarize, *D. nebulosus* hosts an indigenous predator complex of one cynipid inquiline, and five principal and three incidental chalcidoid parasitoids. The disclosure of three definitive colony types — frontier, succession and climax colonies — suggest a successful *D. nebulosus* strategy where succession and climax colonies are seen as predator diversions from frontier colonies. Pseudo-oophagy of inquiline eggs by *D. nebulosus* indicate some ability to reduce inquiline numbers. The percentages of a *D. nebulosus* emergent patch population are fair predictors of the following season's population in both succession and climax colonies. The single appearance of arrhenotoky in an isolated *D. nebulosus* gall (outside of the study area) occurred after the rearing of 109 galls produced only bisexual generations. This disclosure suggests that prenuptial dispersal and lack of mating opportunities in new *Rubus* habitats may result in selective pressures leading to sexual polarizations commonly found in *Diplolepis* species (Kinsey and Ayres 1922, Shorthouse 1973). Owing to the limited size of ovipositors, all parasitoids but *T. flavicoxa* and *Habrocytus* sp. A. require early entry into galls to reach their hosts. Despite larger egg loads and two generations in certain *D. nebulosus* predators, competitor success is greatest in *E. diastrophi*, whose univoltinism and minimal egg-loads are evidently more than offset by superior physiological and behavioral attributes of its larvae. On the other hand, *Ormyrus labotus* with its two generations, displayed a strong autoparasitism, particularly by its second brood depleting much of its own population.

ACKNOWLEDGMENTS

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