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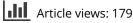
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Biology of the Trigonalyidae (Hymenoptera), with notes on the vespine parasitoid *Bareogonalos canadensis*

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Abstract The biology of the Trigonalyidae (Hymenoptera) is reviewed, with emphasis on adult behaviour. New observations on the vespine parasitoid *Bareogonalos canadensis* (Harrington) are presented, including oviposition behaviour in Douglas-fir foliage and overwintering in the egg stage. Potential use of *Bareogonalos* spp. in biological control of vespines is discussed.

Keywords *Bareogonalos*; Trigonalyidae; parasitoid; hosts; biological control; oviposition; overwintering; Vespidae

INTRODUCTION

Trigonalyidae are parasitoids with a most distinctive life history, which usually involves two successive, obligate hosts. Trigonalyid eggs are laid by the thousands in or on foliage and are ingested by folivorous caterpillars or sawfly larvae. After ingestion the eggs hatch inside the host gut, and the trigonalyid larvae make their way into the haemocoel. No other parasitic Hymenoptera larvae enter their hosts through the gut (Iwata 1976), but this behaviour is known in some Tachinidae (Diptera).

Trigonalyids use the folivorous larva as an intermediate host; the ultimate host being an ichneumonid wasp, tachinid fly, or vespid wasp (Clausen 1940). Because of the large numbers of eggs laid, many larvae may reach the ultimate host, but only one trigonalyid will emerge. Some Australian

species of the genus *Taeniogonalos* Schulz are unusual in that they can develop directly in sawfly larvae without a second host (Raff 1934; Carne 1969). Weinstein & Austin (1991) give additional information.

In 1835 Westwood described *Trigonalys* as "Genus anomalum familiae dubiae." Foerster (1877) separated the group as the "Diplomorpha," which he treated as equivalent to other groups of Hymenoptera recognised today as families. The genus *Trigonalys* was formally raised to family level by Cresson (1887).

The family Trigonalyidae is a distinctive monophyletic group based on their life history and morphology. This is a small family with 22 genera and almost 100 species. Most Trigonalyidae are relatively stocky, medium sized wasps, and most are black with yellow or white markings. Diagnostic morphological characters for the Trigonalyidae include front wings usually with 10 closed cells including a costal cell, 2-segmented trochanters, hyaline plantar lobes on the tarsi, cleft tarsal claws, ovipositor internal, antennae usually with 16–27 segments (the Nomadininae have as few as 13 antennal segments), and asymmetrical mandibular teeth (except *Bareogonalos* spp.).

There is considerable intraspecific variability in this family which has caused many species to be described repeatedly. It is quite probable that many of the currently recognised species are also synonyms (Marsakov 1981). Sexual dimorphism makes it difficult to associate males and females of some genera. Variation in colour patterns within a species can confuse identifications. Size and even the number of antennal segments is dependent on host size. Orthogonalys pulchella (Cresson) specimens longer than 1 cm are common, although some have been collected which were less than 0.5 cm. Bareogonalos canadensis (Harrington) from social wasp nest queen cells are much larger than those from worker cells (Carmean et al. 1981). Interestingly, adults of the family are large compared to other species of parasitoids from the same host species.

Attempts to establish phylogenetic relationships within the Hymenoptera have been unsatisfactory.

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Carlson (1979) stated that the phyletic position of the Trigonalyidae was "undeterminable." It has been placed with groups as far apart as the Chrysidoidea (Townes 1956) and the Ceraphronoidea (Rasnitsyn 1980). Boerner (1919) divided the "Terebrantia" into two subsections and, based on their primitive mouthparts, placed the Trigonalyidae alone in one subsection. The most recent classification places the Trigonalyidae in their own exclusive superfamily (Carlson 1979; Gauld & Bolton 1988).

Schulz described 12 of the 22 currently recognised genera and did the only major revision of the family (Schulz 1907). Bischoff (1938) catalogued the family and gave distribution, host, and bibliographical information. The classification by Bischoff, with additions from recent authors, is presented by Carmean (1988) and Weinstein & Austin (1991). Several regional studies are available: Townes (1956) reviewed the four North American species; Marsakov (1981) keys and discusses the nine species in the Soviet Union. There is only one species in Europe, Pseudogonalos hahnii (Spinola) (not Trigonalis, see Scaramozzino & Pagliano 1989). There is no review of neotropical species and other regional studies need to be updated. Riek (1954, 1962) gave keys to Australian species. Chen (1949) has keys to Chinese species, and Teranishi (1929) has a key to Japanese and Korean species. Benoit (1950, 1951) described species in Africa.

MATERIALS AND METHODS

Bareogonalos canadensis was studied in Benton County, Oregon, U.S.A. This species was found in 73 of 147 vespine nests collected in or near Douglasfir forests from 1986 to 1988. Vespid wasp colonies were found by the public in response to advertisment of a free wasp removal service. A vacuum aspirator was used to collect adults at the nest entrance and after most flight activity stopped (usually an hour) the nest was placed in a plastic bag. Nests were cooled in a refrigerator and the remaining adults removed. Combs from the nests were photocopied, making a permanent record of comb area, numbers of vespine larvae and pupal caps, as well as parasitoid pupal caps. Then, the combs were placed in screened emergence boxes to rear out Bareogonalos canadensis. Observations on adult behaviour and longevity were made in the laboratory under the conditions given in each section below.

Though generally considered rare, it is possible to collect long series of Trigonalyidae. The most

successful collection methods are the use of Malaise traps and rearing from hosts. Trigonalyids are most common in moist woods. D. R. Smith (pers. comm.) has collected over 700 Orthogonalys pulchella in 3 years using Malaise traps in the woods of Virginia, USA. This is probably more than all other collections of this species combined. Previous to my work rearing *Bareogonalos canadensis*, only 32 specimens were known from other collections, and all but two of these were also collected in association with vespine colonies.

Hosts

Hosts are known for less than 20 species of trigonalyids. Two species are known to be hyperparasites of tachinids and five of ichneumonids. Ten species (six genera) of trigonalyids are known to be parasitoids of vespid wasps. Little is known about how host specific trigonalyids are. Lycogaster pullata Shuckard is known from a caterpillar-provisioning eumenine wasp and from ichneumonid parasites of caterpillars (Cooper 1954; Carlson 1979). Pseudogonalos hahnii has been reared only from Lepidoptera pupae parasitised by ichneumonids, and never from vespines. Vespines are erroneously included in some host lists of *P. hahnii* (as in Clausen 1940; Thompson 1958), probably based on speculation by Dours (1874).

Bareogonalos spp. are the only Trigonalyidae known to parasitise Vespinae. Bareogonalos jezoensis (Uchida) parasitises several Vespa, Vespula, Paravespula, and Dolichovespula. Bareogonalos huisuni Yamane & Yamane and B. canadensis are only known from vespine wasps other than Vespa. The only other Bareogonalos species, B. scutellaris (Cameron), has not been associated with a host, but Vespula squamosa (Drury) is the only known Vespinae with an overlapping distribution.

The facultative nature of the intermediate host relationship was shown when *Poecilogonalos costalis* (Cresson), which was known only from tachinid parasitoids of caterpillars, was reared from a tachinid parasitoid of a tipulid detritivore (Gelhaus 1987). Presumably the tipulid had fed on fallen egg-laden leaves. This is the only record of a dipteran as an intermediate host. In Japan no trigonalyids emerged from any of the large numbers of Japanese scarab beetles parasitised by tachinids reared in localities where trigonalyids are known to occur (Clausen 1931).

Longevity

The short lifespan of trigonalyid adults has been noted in the literature for Australian species (Riek

1970), and *Pseudogonalos hahnii* (16 females, 5 days or less; 1 female, 8 days; Bischoff 1936). In my study, *Bareogonalos canadensis* females placed in 30 ml plastic cups and given water only lived $5.0 \pm$ 1.2 days at $22 \pm 2^{\circ}$ C (n = 8) and males lived 5.5 ± 1.5 days at $22 \pm 2^{\circ}$ C (n = 9). Individuals lived much longer when kept at cooler temperatures. At $15 \pm 2^{\circ}$ C males lived an average of 12.0 ± 3.6 days (n = 6) and females 10.2 ± 2.4 days (n = 5). At $12 \pm 2^{\circ}$ C females lived 11.5 ± 2.1 days (n = 6).

Mating

Mating has not been described in the Trigonalyidae. Clausen (1929) never observed mating in caged pairs of *Poecilogonalos thwaitesii* (Westwood), but found the males' appendages were mutilated after a few days. I placed adult *Bareogonalos canadensis* in flight cages with various foliage and flowers but did not observe mating. Mating was seen three times when pairs were placed in 30 ml plastic cups. The male was on top with his genitalia reaching down below the female genitalia. Mating was observed to last no more than 3 min.

Bareogonalos canadensis adults were collected in the nest entrance tunnels of Vespula vulgaris (L.) and Vespula pensylvanica (Saussure) during this study. Taylor (1898) also found them around the entrances of two V. pensylvanica colonies. Given the observed poor flight ability and relatively short adult life span they probably mate near the vespine colonies from which they emerge.

Some Trigonalyidae are parthenogenetic. Carne (1969) reared over a thousand *Taeniogonalos venatoria* Riek and only one was male. However, in most species males are common.

Oviposition

The complex and precarious life cycle of Trigonalyidae is compensated for by laying large numbers of eggs. Iwata (1955, 1960) found 14 000 mature eggs in the ovaries of one female *Poecilogonalos fasciata kibunensis* Uchida and 4400–13 200 in other trigonalyids. One female *Bareogonalos canadensis* taken from a worker cell of a *Vespula vulgaris* comb had about 11 000 eggs in her ovaries (Carmean 1988).

In many Trigonalyidae the eggs are laid on the margin of the underside surface of a leaf. Clausen (1929) observed a female *Poecilogonalos thwaitesii* lay 4376 eggs in 1 day. Bischoff (1936) observed a *Pseudogonalos hahnii* lay 3800 eggs in 7 days. Teranishi (1929) observed *Poecilogonalos maga* Teranishi laying eggs on bamboo foliage in the field and collected one female which laid 3599 eggs on bamboo foliage in a jar in 4 days. Two females laid "several eggs" on the legume *Lespedeza*.

From the limited observations so far published it appears trigonalyid females lay eggs without much discrimination. Poecilogonalos thwaitesii laid eggs on "a wide range of plants" and on paper (Clausen 1929). Bischoff (1936) found Pseudogonalos hahnii would oviposit on a variety of leaves, buds, petals, and also paper. Townes (1956) observed Orthogonalys pulchella ovipositing on a composite (?Aster) and Viburnum (Caprifoliaceae) in the woods, and on Liquidambar in the laboratory. Bareogonalos canadensis females laid eggs in a variety of foliage (and even paper) provided it was not too thick or pubescent (pers. obs.). In Japan, Tsuneki (1973) and Nozaka (1976) found B. jezoensis ovipositing (or at least thrusting) on mimosa (Albizzia julibrissin) and willows (Salix spp.). Tsuneki (1973) also observed Bareogonalos jezoensis ovipositing on several other deciduous trees, and bamboo and ferns. All other host plants recorded for Trigonalyidae are angiosperms (Carlson 1979).

In observations of *Bareogonalos canadensis*, tremendous numbers of eggs were rapidly oviposited in Douglas-fir, *Pseudotsuga menziesii* (Pinaceae). This is the first record of a coniferous plant host for a trigonalyid. I estimated oviposition rates of *Bareogonalos canadensis* on plants by counting ovipositional "thrusts." On Douglas-fir, thrusts occurred on the average of once every 2.2 s (36 observations totalling 908 s), and were observed to continue for as long as 30 min. If oviposition continued at this rate, 10 000 eggs could easily be laid in 1 day. Oviposition on hemlock, *Tsuga heterophylla* (Pinaceae), occurred at a similar rate. Oviposition on other foliage was less consistent and slower than on Douglas-fir, and was too erratic to measure.

In *Bareogonalos canadensis* the female grasped the edge of a leaf in a notch between the sternites of her abdomen and injected an egg into the leaf in a thrusting motion. A modification of the seventh sternite, not the ovipositor, pierced the leaf. Eggs were inserted into the spongy mesophyll, 0.2–0.5 mm from the edge of leaves, through a fine slit made in the underside of the leaf. Later a small heel shaped bruise would become visible on the upper surface. Females often started to oviposit within 5–15 s of being placed on Douglas-fir. They worked up and down the limb, laying a series of individual eggs in each leaf. When transferred from Douglas-fir to another plant species or paper, females generally stopped laying or laid very few eggs and remained motionless or dropped off the foliage. When replaced on the Douglas-fir, they normally resumed egg-laying.

Overwintering

Trigonalyids, as far as known, are univoltine. They have only been shown to overwinter as young larvae. In Australia *Taeniogonalos venatoria* eggs are ingested and hatch soon after they are laid, but do not continue development until the host prepares to pupate the next year (Carne 1969). *Poecilogonalos thwaitesii* appears to overwinter as a larva in its host caterpillar (Clausen 1929).

Unlike Sphecophaga vesparum burra (Cresson) (Ichneumonidae), which overwinters in dead wasp colonies, Bareogonalos spp. have no overwintering cocoon. Collection dates on museum specimens led Yamane (1973) to suggest that adult Bareogonalos jezoensis may overwinter, since males were collected in early June before vespine colonies would have pupae. Carmean et al. (1981) suggested that inseminated females of B. canadensis overwinter. However, Tsuneki (1973) observed B. jezoensis ovipositing in deciduous trees in the autumn after vespine colonies had died. Also, Bareogonalos canadensis eggs in leaves of potted and wild Douglasfir remained turgid after one winter (Carmean 1988) and the eggs of *Poecilogonalos* sp. remain viable on leaves for months (Clausen 1931). The apparent preference for oviposition in persistent coniferous foliage, and the short adult lifespan, indicate that the major, and perhaps only, overwintering stage of B. canadensis is the egg.

Biological control

Although most parasitoids lay their eggs in or on their hosts, or their larvae seek out the hosts, Trigonalyidae reach their hosts passively. This does not necessarily limit their effectiveness as biological control agents. Taeniogonalos venatoria may be a major factor in controlling pest sawfly populations, and may act in a density-related manner (Carne 1969). Bareogonalos spp. depend on the host to bring them back to the colony. A logical consequence of this is that a wasp colony with many foragers is more likely to be parasitised by Bareogonalos. In contrast, Sphecophaga vesparum burra depends on weakness in the colony defense to enter the nest as an adult and lay eggs onto the vespine pupae (Donovan & Read 1987, pers. obs.). As a result Bareogonalos may be more effective against stronger wasp colonies and may complement the biological control program

already being tried in New Zealand against wasps using Sphecophaga.

It is possible that a *Bareogonalos* species has already been successfully introduced to another area. *Bareogonalos jezoensis* is known from northern Japan, eastern Siberia, and Java (Indonesia). No collection localities have been recorded between Japan and Java. Yamane & Yamane (1975) expected to find *B. jezoensis* in Taiwan and instead found a species they described as *Bareogonalos huisuni* in a colony of *Vespula (Paravespula) ?karenkona* Sonan. The mountains in Java where *B. jezoensis* was found is a tourist area, and the Japanese may have introduced *B. jezoensis* to Java as eggs in the foliage of ornamental plants. *Bareogonalos jezoensis* may be functioning in Java as a classical biological control agent although there is no evidence of its effectiveness.

Biological control of wasps can be aimed at reducing the number of colonies, reducing worker populations, or reducing the number of reproductives produced by a colony. Under natural conditions B. canadensis appears unable to do any of these significantly. In addition, this parasitoid was only found in or adjacent to forested areas, not in urban or agricultural areas where most people come into contact with wasps. The ability of B. canadensis to disperse is limited by their weak flight, their short life, and because wasps rarely forage more than 1000 m from their nests. With more knowledge about the conditions required for *Bareogonalos* to parasitise wasps successfully, it may be possible to use the reproductive potential of Bareogonalos in areas where it is not found naturally. With its high fecundity, it may be suited for inundative releases.

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