JOURNAL OF NATURAL HISTORY, 2001, 35, 1507–1516

The biology and immature stages of *Thrybius togashii* Kusigemati (Hymenoptera: Ichneumonidae: Cryptinae), with a description of the male

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(*Accepted 20 March 2000*)

Thrybius togashii Kusigemati is found to be an ectoparasitoid of larvae of a phytophagous eurytomid, *Tetramesa* sp. (Hymenoptera), growing gregariously in internodal cavities of reeds (*Phragmites japonica* Steud.), in Japan. The female of *T. togashii* oviposits into reed canes and its predaceous larva consumes almost all eurytomid larvae in an internodal cavity. This species is bivoltine. The mode of parasitism of this species is unique in some respects. First, when the female oviposits, no food resources are available in the reed. Second, the parasitoid allows part of the host larvae to grow and exploits increasing food resources. The egg, pupa and first to final instar larvae and adult male are described and figured for the first time. Colour dimorphism in both sexes and adult morphology adapted to habitat and ovipositional substrate are also discussed.

KEYWORDS: Ichneumonidae, *Thrybius togashii*, biology, parasitism, immature stages.

Introduction

The genus *Thrybius* Townes is a small taxon of the subtribe Agrothereutina, belonging to the subfamily Cryptinae (Hymenoptera: Ichneumonidae). This genus comprises four species, *Thrybius praedator* (Rossi) from Europe, *T. ungulatus* (Gravenhorst) from Poland, *T. turkestanicus* (Szepligeti) from Kyrgyzstan and *T. togashii* Kusigemati from Japan.

The hosts of the subtribe Agrothereutina are various as follows (Townes, 1969): *Agrothereutes* Foerster, one of the largest genera of the subtribe, is known to attack cocoons of Lepidoptera and sawflies. The genera *Hidryta* Foerster, *Idiolispa* Foerster and *Trychosis* Foerster parasitize egg sacs of spiders. *Amauromorpha* Ashmead and *Aritranis* Foerster attack lepidopterous borers and some species of the latter attack

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Journal of Natural History
ISSN 0022-2933 print/ISSN 1464-5262 online © 2001 Taylor & Francis Ltd
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larvae of Hymenoptera: Aculeata in stems. The genus *Apsilops* is known to parasitize aquatic or semi-aquatic Lepidoptera. Although many host records have been reported for the subtribe as mentioned above, there are no host records for the genus *Thrybius*.

Many specimens of Japanese species, *T. togashii*, were collected by sweeping reeds (*Phragmites japonica* Steud.) along a stream in Fukuoka, Kyushu, in May 1998, and some females were observed ovipositing into reed canes. Upon this discovery observations were made on the host, mode of parasitism, life history, voltinism, immature stages and the hitherto unknown male of *T. togashii*, and described here as follows.

Materials and methods

Adult behaviour and immature stages were observed from April to December in 1998 at Kamiishigama (150 m alt.), along an upper stream of Muromi River in Fukuoka City, Kyushu, Japan (figure 1). Reed canes were cut and taken to the laboratory for examination.

Both mature eggs dissected from ovarioles and oviposited eggs were examined. The method of preparation of larval exuviae follows Wahl (1984), but after ultrasonification they were washed in distilled water directly and examined. After first and final instar larvae were killed in hot water, heads were removed and treated with 10% KOH solution for about 24 h at 25°C, transferred into 3% CH_3COOH and washed in distilled water. The treated head capsules were stained with Delafield's Hematoxylin and observed in pure glycerol under a stereoscopic microscope. Male genitalia were prepared by the method of Konishi (1985).

Terminology of larval cephalic structures follows Finlayson (1975) and Short (1978), and for adult morphology, Townes (1969).

All material used in this study is deposited in the collection of the Biosystematics Laboratory, Graduate School of Social and Cultural Studies, Kyushu University (BLKU).

Life history

Habitat

Adults of *T. togashii* were usually found resting on leaves of reeds, walking on reed canes, and rarely flew away from reed thickets. No specimens of this ichneumonid were captured by sweeping other plants around the observation site and by general collecting at other sites.

Host

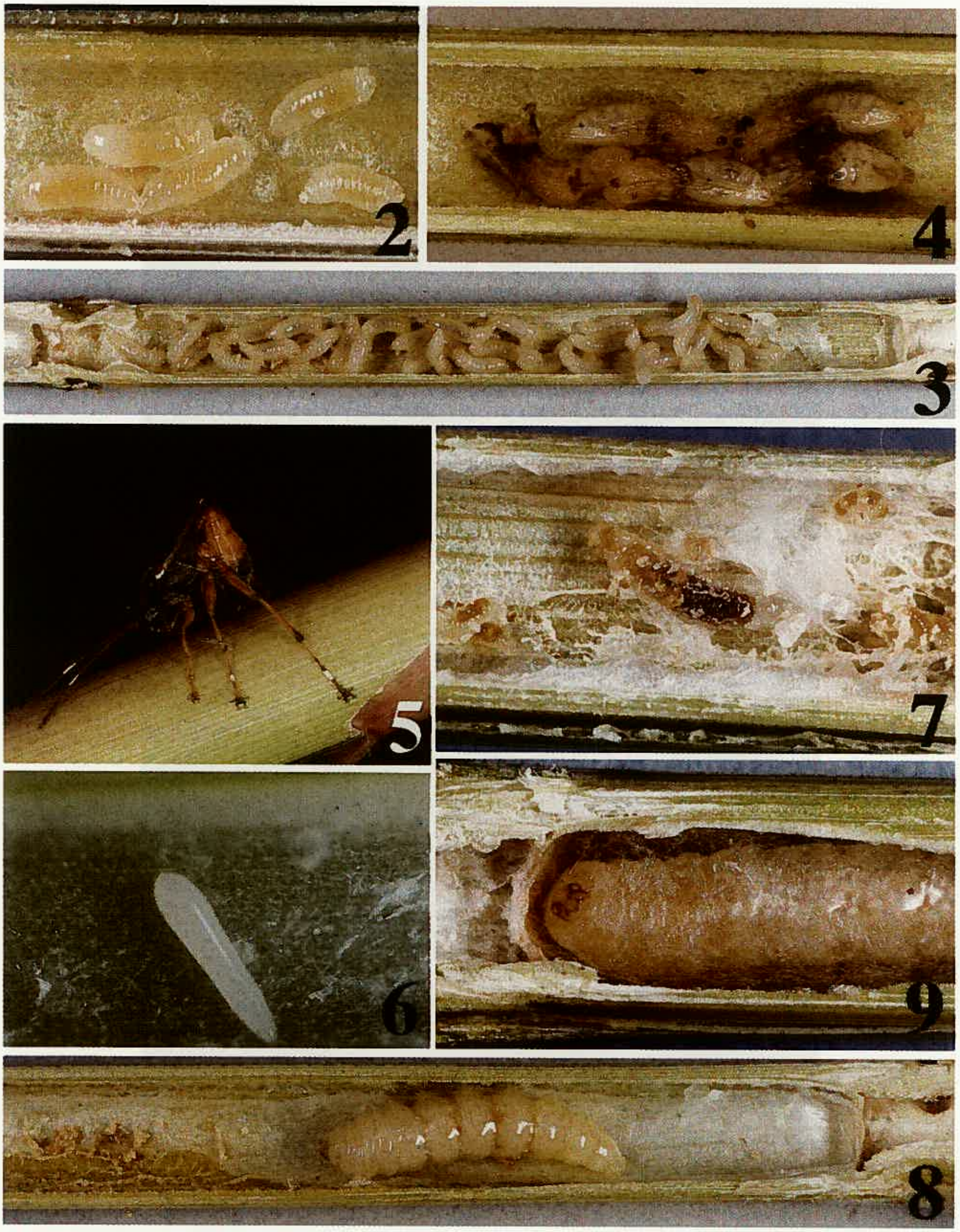
On the basis of the following, only larvae of an undescribed species of *Tetramesa* (Hymenoptera, Eurytomidae), which develop as gregarious phytophages (9–35 larvae per colony on an internode, 26 in average) feeding on the inner tissue of internodes of reeds (figures 2–4), are considered to be the hosts of *T. togashii*. The direct observations that larva of *T. togashii* fed on larvae of *Tetramesa* were made on 21 October 1998 for two host colonies. The inner wall of internodes containing a mature larva (figure 8) or a cocoon of *T. togashii* was always scraped and roughened, almost certainly through the feeding activity of larvae of *Tetramesa*, though no larvae of this species were found in these internodal cavities. In addition,

FIG. 1. Habitat of *T. togashii* in Kamiishigama, Fukuoka City, Kyushu.

these cavities exclusively contained only head capsules of larvae of *Tetramesa* or their fragments.

Ovipositing behaviour

Females of *T. togashii* were often observed drumming their antennae while walking along the reed canes. When a female located a suitable place for oviposition, she drummed it intensively. Then, she raised her metasoma high and acutely bent it between the first and second segments so that the ovipositor made a right angle with the cane (figure 5). At the same time, all legs were stretched out and held the cane tightly. In this posture the body was rocked back and forth, with the antennae stretched out forward, and the ovipositor was inserted into the cane. Movement stopped for about 5 s, at which point an egg was probably laid. All oviposition sequences took 1–2 min.



FIGS 2–9. (2–4)*Tetramesa* sp., the host of *T. togashii*, in the internodal cavity of the reed. (2) Immature larvae feeding on the inner tissue of internodal cavity. (3) Mature larvae. (4) Pupae. (5–9) *T. togashii*. (5) Female ovipositing. (6) Egg. (7) Third instar larva consuming *Tetramesa* sp. larvae. (8) Mature larva. (9) Mature larva spinning cocoon.

It is assumed one egg is oviposited because only a single egg or a first instar larva of the parasitoid was found in internodal cavities of randomly collected reeds. In addition, each internode which was attacked by *T. togashii* contained a single mature larva of this ichneumonid exclusively.

Life cycle

This species is bivoltine in Fukuoka. Adults of the first generation appear from early May to late July. No adults were observed in the field on 25 July 1998. But two pupae and three final instar larvae of *T. togashii* and three colonies of *Tetramesa* sp. (containing 12 and 23 larvae and nine pupae, respectively) were found when about 100 reeds were examined. The percentage parasitism of hosts was 62.5% (five ichneumonids to eight host colonies in about 100 reeds). From these pupae the adult wasps of *T. togashii* and *Tetramesa* sp. emerged within 7 days. Field emergence of the second generation also occurred at this time. Adults of the second generation disappeared by late September in the field. The population size of the second generation was somewhat smaller than that of the first generation.

On 21 October 1998 it was observed that most larvae of *T. togashii* had already matured and had begun to spin cocoons, except for two that were still feeding. The percentage parasitism of hosts was 73.4% (53 ichneumonids to 72 host colonies in 45 reeds). Under indoor conditions most of these ichneumonid larvae soon pupated, with some adults emerging towards the end of November. The emerged females had some mature eggs in their ovarioles. In the field, no adults were found in late November.

Sixteen ichneumonid larvae were found in 10 reeds that contained three unparasitized host colonies on 5 December 1998. These ichneumonid larvae had already finished feeding and were in the cocoon. Although most of them pupated in 15 days under indoor conditions, no pupae were found in the field on 19 December 1998 (nine ichneumonid larvae were found to 12 host colonies in 10 reeds).

Description

Immature stages

Four larval instars were recognized for *T. togashii* on the basis of cast skins in internodal cavities, although five instars have usually been recorded for Ichneumonidae (Gauld, 1984).

Egg (figures 6, 10). White, 1.2 mm long, elongate and sausage-shaped as usual in Cryptinae, curved and weakly tapered at one end. No differences were detected between the ovarian and the oviposited eggs.

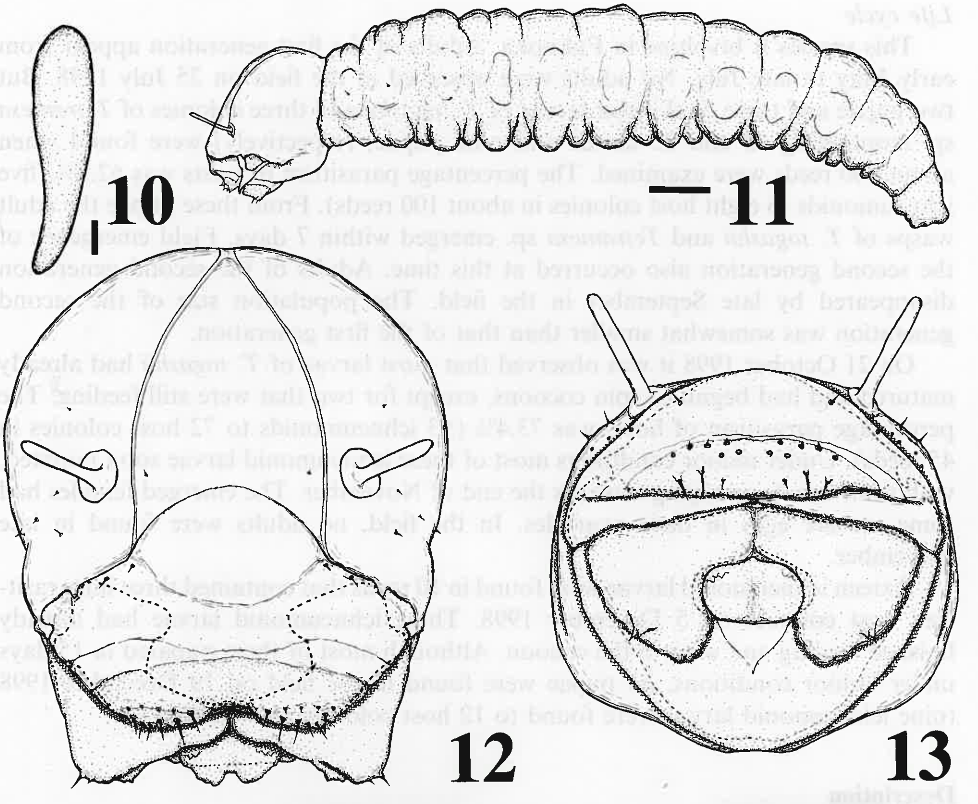
First instar larva (figures 11–13). Characteristic of Mandibulate and Polypodeiform type (Clausen, 1940). Body length about 2.4 mm. Head capsule well sclerotized, reddish brown, antenna elongate. Body white, somewhat translucent, with ventral transverse tubercles between each segment; each body segment with pair of tubercles ventrally.

Second instar larva (figure 14). Head capsule less sclerotized than in first instar; antenna short; stipital sclerite, pleurostoma and hypostoma well developed; labial and maxillary palpi present; mandible without teeth.

Third instar larva. Similar to second instar but slightly larger.

Final instar larva (figures 15–17). Body length 10.5–18.0 mm. Milky white in colour. Body 13-segmented, cylindrical, weakly tapered posteriorly beyond 2/3, with dorsal transverse tubercles on 4th to 10th segments. Vertex with pair of weakly sclerotized longitudinal patches near midline; hypostomal spar present; mandible without teeth; spiracle (figure 17) with closing apparatus adjoining atrium.

Pupa (figure 18). Body length 11.0–14.2 mm. Milky white just after pupation, with reddish brown compound eyes. Antenna reaching apex of 2nd metasomal



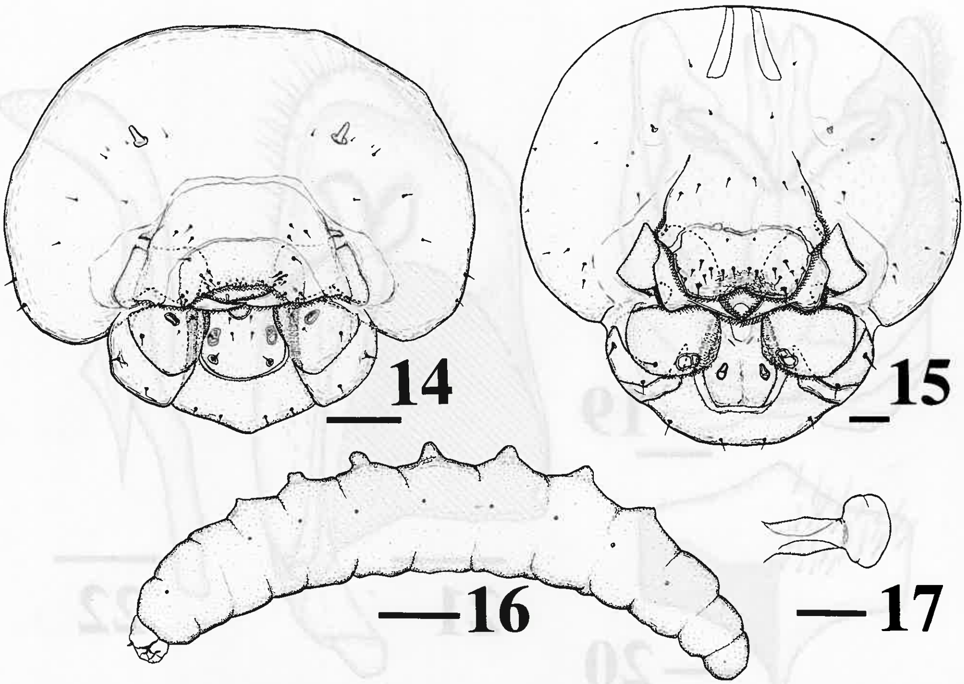
FIGS 10–13. 10–13. *T. togashii.* (10) Egg. (11–13) First instar larva. (11) Lateral aspect. (12) Head, frontal aspect. (13) Head, ventral aspect. Scales: 0.2 mm.

segment; 7th to 8th metasomal segments with a pair of hook-like projections curved posteriorly at tip. Ovipositor obliquely curved dorsally.

Adult morphology

See Kusigemati (1982) for description of the female. This species is dimorphic in colour pattern, with black and red forms, in both sexes. In contrast to the black form whose body is almost entirely black, the red form has 2nd to 4th abdominal segments (only basal half of the 4th in female) and legs almost entirely red. Specimens intermediate between the two forms were collected rarely.

Male, similar to female except as follows: flagellum 24–27-segmented, not clavated, with tyloids on subapical 7–8 segments, without subapical white band; apical segment of flagellum neither elongate nor truncate; fore femur and tibia not inflated unlike female; first metasomal segment more slender apically than in female, 1.9 times as long as wide at apex; subgenital plate (figure 20) with rather dense pubescence on apical half; both sides of apical margin of subgenital plate slightly concave; paramere (figures 19, 21) rather broad, with dense setae on outer side apically; apex of distivolsella with rather dense setae; gonolacinia slightly turned outward; aedeagus (figure 22) thickened subapically and tapered toward apex; 4th metasomal



FIGS 14–17. Larvae of *T. togashii*. (14) Head of second instar, frontal aspect. (15) Head of final instar, frontal aspect. (16) Final instar, lateral aspect. (17) Spiracle of first abdominal segment of final instar. Scales: 0.1 mm for (14, 15), 2.0 mm for (16), 0.05 mm for (17).

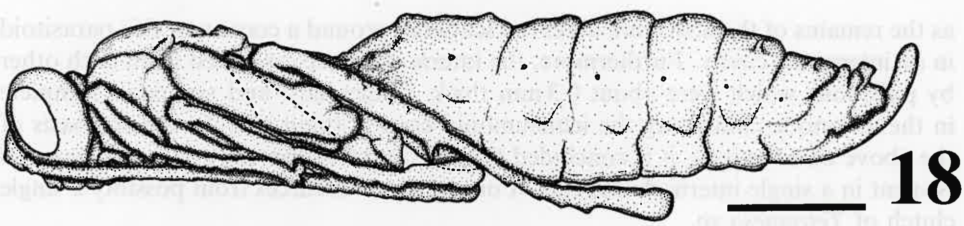


FIG. 18. Pupa of *T. togashii*, lateral aspect. Scale: 2.0 mm.

segment entirely red in red form; 5th to 7th metasomal terga with white markings medio-apically; paramere with longitudinal white marking on outer side.

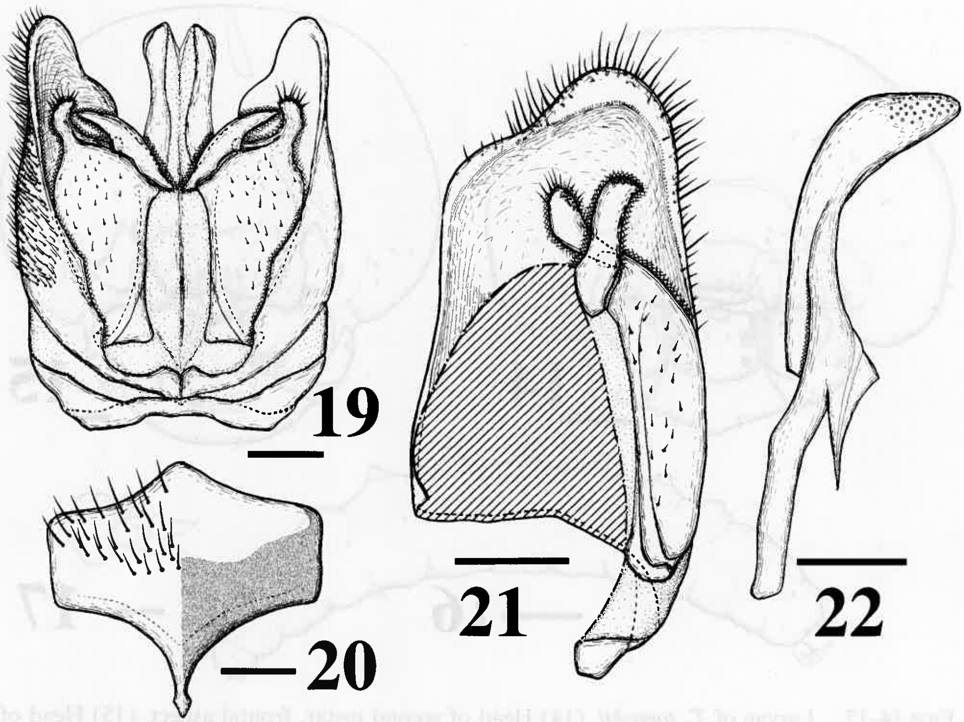
Length: Body 7.2–12.6 mm, fore wing 4.9–7.9 mm.

Discussion

Host utilization and parasitic strategy

Although most ichneumonids mainly parasitize larvae and/or pupae of Lepidoptera, Coleoptera and Symphyta, *T. togashii*, unusually attacks chalcidoid Hymenoptera.

Thrybius togashii is considered to be a solitary parasitoid, as a single egg was always found alone in an internode with no host larvae following an observed oviposition. In addition, exuviae of first to third instar larvae of *T. togashii* as well



FIGS 19–22. Male genitalia of *T. togashii*. (19) Ventral aspect. (20) Subgenital plate, ventral aspect. (21) Right paramere, inner aspect. (22) Aedeagus, lateral aspect. Scales: 0.2 mm.

as the remains of the host were observed scattered around a cocoon of this parasitoid in an internodal cavity. Furthermore, the internodes were separated from each other by partitions which were about 0.3 mm thick, rather hard and remained complete in the internode containing the ichneumonid cocoon (figures 8, 9). On the basis of the above observations, it is concluded that the entire immature cycle of *T. togashii* is spent in a single internode dependent on the food resources from possibly a single clutch of *Tetramesa* sp.

This parasitoid/host relationship appears quite unique because there is not enough food at the time of oviposition on which the larvae can grow and mature in the internodal cavity. It is hypothesized that the parasitoid larva probably consumes only some of the numerous individuals (see figure 3) of the host larvae per instar, allowing the remaining host larvae to grow, and therefore it can develop on the increasing food resources. Thus, *T. togashii* differs from idiobionts, although it may have arisen from this kind of parasitoid. In some ways its predatory biology parallels that of koinobionts in the way it exploits food resources.

There were 9–35 host larvae per internode which resulted in a significant size range for the parasitoid. For example, the length of the fore wing varied from 5.8 to 9.1 mm in females and from 4.9 to 7.9 mm in males.

Females of *T. togashii* possibly locate traces of oviposition by female eurytomids or detect hosts using a form of echo-location because they intensively drummed at certain positions along the cane before oviposition. But eggs of *Tetramesa* sp. could not be found in the internode into which the female of *T. togashii* was observed to oviposit. Consequently, it was assumed that the eggs of *Tetramesa* sp. were either microscopic in size and/or hidden in the inner tissue of the internodes.

This species was found to be strongly confined to reeds. A European species, *T. praedator*, was also reported to be restricted to reeds (*Phragmites australis*) (Schwarz and Shaw, 1988), which suggests that a similar mode of parasitism will be found in this species.

Hibernation

Thrybius togashii appears to hibernate as a mature larva in the cocoon which is spun in the autumn. Pupation of the overwintering generation is probably promoted by a rise in air temperature because larvae pupated soon after they were brought indoors. In the field, on the other hand, mature larvae did not pupate at least until late December.

Adaptation of body structure to habitat and ovipositional substrate

Thrybius is characterized by the following structures. Body entirely covered with dense pubescence; 5th tarsal segment long, curved, with large claws; ovipositor compressed, with lower valve strongly toothed.

The dense body pubescence may be an adaptation to moist habitats because adults appeared confined to an area within 100 cm of the water surface. The same character state is found in *Apsilops*, which attacks aquatic or semi-aquatic Lepidoptera.

The elongate 5th tarsal segment and large claws in the female appear to be an adaptation enabling her to firmly grasp the hard reed cane when she penetrates it with her ovipositor (figure 5). The compressed ovipositor and strongly toothed lower valve are used to rip the reed canes and are also considered as an adaptation to the hard, fibrous ovipositional substrate.

As noted in the larval description, the antenna of the first instar larva is very long (figure 11–13). This may be used to detect hosts in the internodal cavity of the reed.

Acknowledgements

The first author would like to express his sincere gratitude to Drs H. Shima and B. J. Sinclair (BLKU) for their critical reviews of early drafts of the manuscript, and to Dr O. Yata (BLKU) for his constant guidance and encouragement. The authors are also very grateful to Dr K. Kamijyo (Bibai, Hokkaido) and Mr Y. Higashiura (Department of Entomology, National Research Institute of Vegetables, Ornamental Plants & Tea, Kurume) for identification of the host, and to Dr K. Konishi (Laboratory of Insect Systematics, National Institute of Agro-Environmental Sciences, Tsukuba) and Dr K. Kanmiya (Biological Laboratory, Kurume University) for their valuable comments.

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