DESCRIPTIONS OF FEMALE MYRMECOLACIDAE (STREPSIPTERA) PARASITIC IN ORTHOPTERA (TETTIGONIIDAE) IN PAPUA NEW GUINEA

Kathirithamby, J., T. Solulu & R. Caudwell, 2001. Descriptions of female Myrmecolacidae (Strepsiptera) parasitic in Orthoptera (Tettigoniidae) in Papua New Guinea. – Tijdschrift voor Entomologie 144: 187–196, figs. 1–16, tables 1–3. [ISSN 0040-7496]. Published 1 December 2001. *Stichotrema dallatorreanum* Hofeneder (Strepsiptera) is a parasite of *Sexava nubila* Stål, *Segestes decoratus* Redtenbacher and *Segestidea novaeguineae* (Brancsik) (Orthoptera: Tettigoniidae) in Oro Province, Papua New Guinea. These species of *Sexava* (a common name for this group of tettigoniids), which severely defoliate oil palm, are kept in check by the female strepsipteran *S. dallatorreanum*. In order to investigate whether there were other host reservoirs of *S. dallatorreanum* in Oro and West New Britain Provinces, various species of Orthoptera were sampled in these areas, in the bush, village oil palm blocks, and large oil palm plantations. Three species of Orthoptera (Tettigoniidae) (one from Oro Province and two in West New Britain) parasitised by female Strepsiptera were collected. Mitochondrial DNA analysis showed that female Myrmecolacidae found in these hosts were of three different species (Halbert et al.: pg. 179). Descriptions of the two new species of female Myrmecolacidae are provided: *Stichotrema jeyasothiae* Kathirithamby sp. n. and *S. waterhousei* Kathirithamby sp. n. There are no distinct external morphological characters to differentiate between the female Myrmecolacidae, and we here introduce the use of the shape and structure of the microvillate cells in the apron, as a possible taxonomic character.

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Strepsiptera are obligate entomophagous parasites, with free-living male adults and totally endoparasitic females (except in the family Mengenillidae). In all the eight extant families but one, the male and female parasitise (stylopise) the same host species. However, the family Myrmecolacidae is unusual, not only for Strepsiptera but for insect parasitoids in general, as the males and females parasitise different host orders (males parasitise Hymenoptera – ants, and female grasshoppers, crickets and mantids) (Kathirithamby & Hamilton 1992). Consequently, hosts of only a few myrmecolacid males and females are known: hosts of eight males and five females out of a total of 98 myrmecolacid species described so far (Kathirithamby 1998) (tables 1–3). A majority of the 98 species described are free-living males that have flown into traps. The hosts of only a few males are known as wandering stylopised ants are never encountered in the field, although ants are the most numerous of all known invertebrate species groups in any given ecosystem. Stylopised Hymeno-

ptera or Homoptera, however, are frequently encountered, the reason being that, when stylopised, ants remain in the nest and only come out to the open just before the emergence of the male myrmecolacid. To investigate stylopisation in Formicidae, therefore, whole nests have to be brought into the laboratory and individual specimens dissected for the presence of the parasitic strepsipteran. The female myrmecolacid is found in situ in the host, and, unlike other strepsipterans, the female cephalothorax in this family lies close to the host cuticle, and is not easily visible. The neotenic, totally endoparasitic, females do not have any outstanding morphological characters either, so that separation at the species level is impossible.

Female *Stichotrema dallatorreanum* Hofeneder (Strepsiptera) is a parasite of *Sexava nubila* Stål, *Segestes decoratus* Redtenbacher and *Segestidea novaeguineae* (Brancsik) (Orthoptera: Tettigoniidae) in Oro Province, Papua New Guinea. *S. decoratus*, *S. novae-*

Figs 1-4. *Stichotrema dallatorreanum* Hofeneder, morphology. – 1, Scanning Electron Micrograph of cephalothorax. Scale bar = 1 mm; 2, Cephalothorax. Scale bar = 0.5 mm; 3, Macrophotography of lateral view of neotenic female, after extrusion of cephalothorax (arrow) with apron (arrow head). Scale bar = 5 mm; 4, 5 µm section (stained with Haematoxylin) of apron in neotenic female with microvillate cells (arrow), (note irregular branches), $\times 15$.

Figs. 5-7. *Stichotrema jeyasothiae* sp. n., morphology. – 5, Scanning Electron Micrograph of cephalothorax. Scale bar = 1 mm; 6, cephalothorax. Scale bar = 0.5 mm; 7, 5 μ m section (stained with Haematoxylin) of apron in neotenic female with microvillate cells (arrow) (note tube-like structures with tapering tips and no branches), $\times 154$.

Table 1. Hosts of male and female Myrmecolacidae.

Species	Host of male Hymenoptera: Formicidae	Host of female Orthoptera	Distribution
1. <i>Myrmecolax ogloblini</i> Luna da Carvalho, 1973 <i>Mantidoxenos argentinus</i> Ogloblin, 1939	<i>Camponotus punctulatus</i> <i>cruentatus</i> Forel	<i>Acanthiotespis maculatus</i> (Saussure)	Argentina
2. <i>Stichotrema barrosmachadoi</i> Luna da Carvalho, 1956	<i>Crematogaster</i> sp.	<i>Sphodromantis lineola pinguis</i> La Greca	Angola

Table 2. Hosts of female Myrmecolacidae.

Species	Host of female Orthoptera	Distribution
1. <i>Stichotrema dallatorreanum</i> Hofeneder, 1910	<i>Segestes decoratus</i> Redtenbacher <i>Sexava nubila</i> (Stål) <i>Segestes novaeguineae</i> (Brancsik) <i>Segestes d. defoliaria</i> (Uravov) (new record) (all Tettigoniidae: Mecopodinae)	Papua New Guinea (Morobe Prov.) Pak Is. (Manus) (formerly Admiralty Isl.) Papua New Guinea (Oro Prov.) West New Britain
2. <i>Stichotrema yasumatsui</i> Kifune, 1983	<i>Euscirtus</i> sp. (Gryllidae: Eneopteridae)	Thailand
3. <i>Stichotrema asahinai</i> Hirashima & Kifune, 1974b	<i>Mecopoda elongata</i> L. (Tettigoniidae: Mecopodinae)	Japan
4. <i>Stichotrema jeyasothiae</i> Kathirithamby sp. n.	<i>Phyllophorella subinermis</i> Karny (Tettigoniidae: Phyllophorinae)	Papua New Guinea (West New Britain Prov.)
5. <i>Stichotrema waterhousi</i> Kathirithamby sp. n.	<i>Paracaedicia</i> sp. (Tettigoniidae: Phaneropterinae)	Papua New Guinea (West New Britain & Oro Prov.)

Table 3. Hosts of male Myrmecolacidae. Authors of host records in square brackets.

Species	Host of male (Hymenoptera: Formicidae)	Distribution
1. <i>Myrmecolax nietneri</i> Westwood 1861	<i>Camponotus maculatus-mitis</i> group	Sri Lanka, Malaysia
2. <i>Myrmecolax borgmeieri</i> Hofeneder 1949	<i>Eciton dulcius</i> Forel	Argentina
3. <i>Caenocholax fenyesi</i> Pierce, 1909	<i>Solenopsis invicta</i> Buren [Kathirithamby & Johnston 1992]	S. America, S. USA
<i>Caenocholax brasiliensis</i> Oliveira & Kogan, 1959	<i>Pheidole fallax emillae</i> Far. <i>P. randoschkowsky reflexana</i> Santa [Teson & Remes Lenicov 1979]	Neotropics
4. <i>Stichotrema beckeri</i> (Oliveira & Kogan, 1959) <i>Caenocholax wygodzinsky</i> Oliveira & Kogan, 1959	<i>Camponotus crassus</i> Mayr. <i>C. punctulatus cruentatus</i> Emery <i>Pseudomyrmex acanthobius virgo</i> Santschi <i>Solenopsis richteri</i> Forel [Teson & Remes Lenicov 1979]	Neotropics
6. <i>Stichotrema robertsoni</i> Kathirithamby, 1991	<i>Pheidole</i> sp.	S. Africa

guineae (in Oro province), *Segestidea defoliaria defoliaria* (Uvarov) (in West New Britain Province), and *Segestidea gracilis gracilis* (Willemse) (in New Ireland Province) are severe pests of oil palm. The female strepsipteran *S. dallatorreanum* keeps the first two species in check in Oro Province (Solulu 1996, Kathirithamby et al. 1998). *S. defoliaria defoliaria* (in West New Britain Province) and *S. gracilis gracilis* (New Ireland), which are not parasitised by *S. dallatorreanum*, cause severe defoliation of oil palm. Infectivity trials were conducted in Oro Province on *S. defoliaria defoliaria*, in which *S. dallatorreanum* successfully parasitised this species. During this period other orthopteran species were sampled in the bush, village oil palm blocks and in large plantations in Oro and West New Britain Provinces, to investigate if there were any reservoirs of *S. dallatorreanum* in alternate host species. One species (in Oro Province), and two species (in West New Britain Province) of Orthoptera (Tettigoniidae), were parasitised by female Myrmecolacidae. Mitochondrial DNA analysis showed that these were two distinct species (Halbert et al. 2001). We here provide descriptions of the two new species of female Myrmecolacidae and a re-description of *S. dallatorreanum* from Papua New Guinea. As there are no definite external morphological characters to differentiate between female Myrmecolacidae, we here show that the shape and structure of the microvillate cells in the apron of the neotenic female (Kathirithamby 2000) can be used as a reliable diagnostic character. We also provide figures and brief descriptions of the two Orthopteran hosts.

MATERIAL AND METHODS

Specimens were caught in the field and sent to Oxford for identification.

Measurements: width of cephalothorax – the broadest width; length – the length along the middle of the cephalothorax.

Abbreviations: OUMNH – Oxford University Museum of Natural History.

MYRMECOLACIDAE SAUNDERS

Myrmecolacides Saunders 1872: 20.

Myrmecolacidae Pierce 1908: 76.

Stichotrematoidea Hofeneder 1910: 49.

Stichotrematidae Hofeneder 1910: 49.

Diagnosis

Male. – Seven-segmented antennae with flabellum on the 3rd segment and shortened 4th segment. Mandibles knife-shaped, slender and crossing medially. Maxilla with short basal segment and long palpus. Tarsi: 4-segmented without claws. Aedeagus hook- or anchor-shaped. Hind wing with MA₁ short, MA₂

long, and R₅ longer than in any other family. The genus *Lychnocolax* with both CuA₁ and CuA₂ present. Veins between R₁ and R₄ variable.

Male host. – Hymenoptera: Formicidae (see tables 1 and 3).

Female. – Large with flat cephalothorax which lies close to the host cuticle. Opening of the apron (also known as the brood canal opening) crescent-shaped. Numerous genital tubes open into the apron on abdomen segments 1-3.

Female host. – Orthoptera (see table 2).

Remarks

There are four genera in the family Myrmecolacidae: *Caenocholax* Pierce 1909; *Lychnocolax* Bohart 1951; *Myrmecolax* Westwood 1861; *Stichotrema* Hofeneder 1910.

All female Myrmecolacidae described so far have been placed in *Stichotrema*. More molecular studies will be needed to verify the status of the four genera. The above classification will be followed here.

Stichotrema Hofeneder

Stichotrema Hofeneder 1910: 47.

Caenocholax; Pierce 1909: 88 pro parte

Mantidoxenos Ogloblin 1939: 1277.

Rhipidocolax Bohart 1951: 94.

Of the 47 descriptions of *Stichotrema*, four are of females, one of which (*Stichotrema dallatorreanum*) is from Papua New Guinea, and was the first female from the family Myrmecolacidae to be described. Three males belonging to the genus *Stichotrema* have been described from Australia (Kathirithamby 1993).

Stichotrema dallatorreanum Hofeneder (figs. 1-4)

Stichotrema dallatorreanum Hofeneder, 1910: 47.

Caenocholax (*Rhipidocolax*) *acutipennis* Kogan & Oliveira, 1964: 467.

Stichotrema dallatorreanum; Kinzelbach 1971: 159; Kifune 1986: 51.

Material examined. – 3 ♀: PAPUA NEW GUINEA, Oro Province, Popondetta, December 1995, T. Solulu (OUMNH).

Description

Female. – Size: total length varies according to number of females in a single host; largest strepsipteran female known (1.8-3.9 cm). Cephalothorax: dorsally circular and flat all round, length 1.30 mm; width 1.51 mm, dark brown in colour (n=10). Laterally with blunt-edged projections, and dorsally with spine-like hooks (figs. 1-2). Abdomen: segmentation obscure, 36 openings of the genital tubes into the apron on ab-

Figs. 8-12. *Stichtotrema jeyasothiae* sp. n. and its host *Phyllophorella subinermis* Karny. – 8, Macrophotography of host. Scale bar = 15; 9, Macrophotography of host with cephalothorax of parasite (arrow). Scale bar = 10 mm; 10, Scanning Electron Micrograph of metathoracic coxal plates of host (ventral view). Scale bar = 1 mm; 11, Scanning Electron Micrograph of metathoracic coxa with ridges (arrow head) and coxal plate with spines (arrows) host (lateral view). Scale bar = 1 mm; 12, Scanning Electron Micrograph of egg of *Phyllophorella subinermis*. Scale bar = 1 mm.

Figs. 13-16. *Stichtotrema waterhousi* sp. n. – 13, Macrophotography of host *Paracaedicia* sp. with *S. waterhousi* cephalothoraces (arrows). Scale bar = 14 mm; 14, Cephalothorax. Scale bar = 0.5 mm; 15, 5 μ m section (stained with Haematoxylin) of apron in neotenic female with microvillate cells (arrow) (note spine-like structures without branches), $\times 120$; 16, Scanning Electron Micrograph of stridulatory file (arrow) on the left forewing of *Paracaedicia* sp. Scale bar = 1 mm.

14

15

dominal segments 2-4. Microvillate cells in the apron are irregular, thick with no branches (figs. 3-4).

Multiparasitism. – This is rare in Strepsiptera but in Papua New Guinea the host is parasitized by *Exorista notabilis* Walker (Diptera: Tachinidae).

Superparasitism. – This is common in *S. novae-guineae*.

Hosts. – *Sexava nubila* (Stål) (Hofeneder 1910); *Segestidea novaeguineae* (Brancsik), *Segestes decoratus* Redtenbacher (O'Connor 1959) (Tettigoniidae: Mecopodinae) are the hosts of *S. dallatorreanum*.

New host record. – *Segestidea defoliaria defoliaria* (Uvarov), a pest of oil palm in West New Britain Province. Infectivity trials proved that *S. dallatorreanum* parasitised this species. Stylopised *S. defoliaria defoliaria* are being released in the plantations in West New Britain now.

Distribution. – Papua New Guinea: Pak Island (formerly Admiralty Is.) (Manus Province), Mapik, Schouten Is. (East Sepik Province) (recorded by Hofeneder 1910); Bubia (Morobe Province), Popondetta (Oro Province) (O'Connor 1959).

Remarks

On finding the aedeagus of *S. acutipenis* Kogan and Oliveira (1964) in the cephalothorax of *S. dallatorreanum*, Luna de Carvalho (1972) synonymised the two species. However, Kinzelbach (1971) and Kifune & Hirashima (1980, 1989) maintained them as separate species because the actual relationship between female *S. dallatorreanum* and male *S. acutipenis* had not been determined. In our studies we have found *S. dallatorreanum* to be parthenogenetic, since several generations were maintained in walk-in cages that were specially built to be male-proof. Whether they are obligate or occasional parthenogens is being studied now.

Hirashima & Kifune (1974a, b) reviewed the status of this species after their description of *S. asahinai*, which was the second female myrmecolacid to be described.

Stichotrema jeyasothiae Kathirithamby sp. n. (figs. 5-12)

Type material: Holotype, ♀ cephalothorax: PAPUA NEW GUINEA, West New Britain Province, Dami, August 1997, S. Solulu & S. Makai (Additional material with type: abdomen of ♀ with 1st instar larvae and host *Phyllophorella subinermis* Karny). – Paratypes: ♀: PAPUA NEW GUINEA, West New Britain Province, Hoskins, Kautu village oil palm block 312, 29 March 1994, T. Solulu; ♀ in ♂ host: Hoskins, Kasia village,

6 April 1994, (collected on cassava), T. Solulu & S. Makai; ♀ in host: Hoskins, 19 April 1994, (on cassava); 3 ♀: Hoskins, 19 April 1994, T. Solulu; ♀: Dami, 25 April 1995, T. Solulu & S. Makai; 3 ♀ in ♂ host: Hoskins, Kautu village oil palm block 312, 13 March 1996, T. Solulu & S. Makai; 2 ♀ in ♂ host: 16 March 1996, Hoskins, Kautu village oil palm block 312, S. Makai ♀: 17 March 1996, Hoskins, Kautu village oil palm block 312, S. Makai (OUMNH).

Description

Female. – Size: total length 1.8 mm (n=3). Cephalothorax: circular with blunt projections laterally and sharp hooks dorsally, with additional projection dorso-centrally placed; length 1.00 mm; width 1.40 mm (n=9); dark brown in colour (figs. 5-6). Abdomen: openings of the genital tubes into the apron on abdominal segments 2-4. The microvillate cells in the apron are straight, pyramid-shaped, tube-like structures, with fine branches at the tips (fig. 7).

Remarks

Diagnosis. – This species is represented by WNB-A/B in the data set by Halbert et al. (2001), forming a monophyletic group with a low level of sequence divergence (0.78%). The separation of this species from *S. dallatorreanum* is supported by approximately 20% sequence divergence and a 100% bootstrap value.

Biological notes. – Host: *Phyllophorella subinermis* Karny (Tettigoniidae: Phyllophorinae) (det. J. Kathirithamby). This is the first record of female Myrmecolacidae parasitising Phyllophorinae, a subfamily that is confined to the forests of the Indo-Malayan-Papuan-Australian region (Nickle & Naskrecki 1997) (figs. 8-9). The host has coxal stridulatory organs (figs. 10-11) where a pair of plates with serrated edges scrapes along a series of ridges on the coxae. The egg of the host has longitudinal ridges (fig. 12).

Distribution. – Papua New Guinea: West New Britain Province.

Etymology. – This new species is named in memory of my sister Jeyasothie.

Stichotrema waterhousi Kathirithamby sp. n. (figs. 13-15)

Type material. – Holotype, ♀: PAPUA NEW GUINEA, West New Britain Province, Dami Research Station, 18 March 1997, T. Solulu & S. Makai, (Additional material with type: host and abdomen with 1st instar larvae). – Paratypes: 3 ♀ in host: PAPUA NEW GUINEA, West New Britain Province, Dami Research Station, 1 September 1996, S. Maki; ♀: Oro Province, Po-

pondetta, 5 April 1997, T. Solulu (OUMNH).

Description

Female. – Smallest of the species found in Papua New Guinea but a whole specimen was not available. Cephalothorax: circular with blunt projections laterally and spine-like projections dorsally; length 0.68 mm; width 1.10 mm (n=5); dark brown in colour (figs. 13–14). Abdomen: 28 openings of genital tubes into apron. The microvillate cells in apron are spine-like without branches (fig. 15).

Remarks

Diagnosis. – This species is represented by WNB-C/POP in the data set by Halbert et al. (2001), forming a monophyletic group with a low level of sequence divergence (0.98%). The monophyly of this clade and the separation of *S. waterhousi* from the *S. dallatorreanum* / *S. jeyasothiae* clade is supported by a 97% bootstrap value.

Biological notes. – Male: unknown. Host: *Para-caedicia* sp. (Tettigoniidae: Phaneropterinae) (det. J. Kathirithamby); (fig. 13) with stridulatory organs: the file on the left forewing (fig. 16), and the mirror and frame on the right.

Distribution. – Papua New Guinea: West New Britain Province, Oro Province.

Etymology. – This species is named in memory of Dr. D. Waterhouse FRS (former Chief, Entomology Division, CSIRO, Canberra) who initially mentioned and discussed the female Myrmecolacidae parasitising *Sexava* in Papua New Guinea.

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