Caenocholax fenyesi (Strepsiptera: Myrmecolacidae) Parasitic in *Camponotus planatus* (Hymenoptera: Formicidae) in Mexico: Is This the Original Host?

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ABSTRACT The male of *Caenocholax fenyesi* Pierce (Strepsiptera) is widespread in South America, but no host records are known as the specimens examined were free-living males that came into traps. In southern USA *C. fenyesi* was found to parasitize the red imported fire ant, *Solenopsis wagneri* Santschi (Hymenoptera: Formicidae). We found a nest of the carpenter ant, *Camponotus planatus* Roger, in Veracruz, Mexico to be parasitized by *C. fenyesi.* This is the first record of a host of *C. fenyesi* from the Neotropics. At the same location Pierce (1909) found the type species of *C. fenyesi*, but there were no host records. As our findings were from the same location, we speculate whether *C. planatus* is the endemic host of *C. fenyesi.* If so, did *C. fenyesi* arrive in southern USA parasitic on *C. planatus*, and move to an exotic host, *S. wagneri* in an alien enviroment? We also synonomize *Myrmecolax ogloblini* Luna de Carvalho and *Caenocholax brasiliensis* Oliveira & Kogan from Brazil with *C. fenyesi*, based on the unique structure of the aedeagus of the latter.

KEY WORDS Strepsiptera, Myrmecolacidae, *Caenocholax fenyesi*, *Solonopsis wagneri*, *Camponotus planatus*

THERE HAS BEEN no comprehensive work on the Strepsiptera of Neotropica, except from Panama and MesoAmerica (Kathirithamby 1992). There have been reports of Strepsiptera from Argentina (Brethès 1923, Ogloblin 1939, Remes Lenicov 1970, Remes Lenicov and Teśon 1975, Téson and Remes Lenicov 1979), Bahamas (Kathirithamby and Peck 1994), Belize (Kifune and Brailovsky 1997), Brazil (Kogan 1958; Oliveira and Kogan 1959, 1960, 1962, 1963; Kogan and de Oliveira 1966; Luna de Carvalho 1978; Trois 1982, 1984a, 1984b, 1988), Chile (Hofmann1965, Téson and Remes Lenicov 1979), Galapagos (Peck and Peck 1989, Abedrabbo et al. 1990), Guatemala (Kifune 1979a, 1991; Kifune and Brailovsky 1988), Honduras (Kinzelbach 1969), Mexico (Pierce 1909; Brailovsky 1974, 1981; Brailovsky and Márquez 1974; Kifune 1979a; Kifune and Brailovsky 1987, 1988, 1991; Kathirithamby and Peck 1994; Kathirithamby and Moya-Raygoza 2000), Nicaragua (Maes and Kathirithamby 1993), Panama (Bohart 1941), Paraguay (Hoffman 1944), and Peru (Kifune 1979b). There are also records of Strepsiptera from Dominican amber (Kinzelbach 1983, Kathirithamby and Grimaldi 1993, Kinzelbach and Pohl 1994, and Pohl and Kinzelbach 1995). Pohl and Kinzelbach (2001) tentatively recorded a female myrmecolacid in a prionmyrmecine ant in Baltic amber, and speculated that the plesiomorphic habit of both sexes parasitizing a single species survived at least until the Eocene. Since there are no dignostic morphological characters of this female parasitic in the ant, we question this theory.

Here we report the host of the male strepsipteran, *Caenocholax fenyesi* Pierce, in Mexico. The type species was collected by Pierce (1909), but had no record of the host. However, 83 yr after its description, Kathirithamby and Johnston (1992) recorded the red imported fire ant, *Solenopsis wagneri* Santschi, in the southern United States as a host. It was assumed that the original host of *C. fenyesi* was the black fire ant, *Solenopsis richteri* Forel, in MesoAmerica, and it shifted to the red imported fire ant in the southern United States. We also provide records of *C. fenyesi* from Argentina, Costa Rica, Ecuador, Galapagos, Guatemala, Mexico, Panama, Trinidad, Venezuela,and the United States (Tennessee); and in one of the field collections from Mexico we found a nest of ants parasitized by *C. fenyesi.*

Materials and Methods

A nest of *C. planatus* was found occupying an abandoned wasp nest on the side of a building (2.5 m off the ground) at Los Tuxtlas Biological Station, Veracruz, Mexico (18° 35' N, 95° 5' W). The nest was collected at 1500 hours and the entire contents immediately sacrificed using chloroform. The nest contained 97 sexuals, 41 workers, and three pupae, which were either dissected or examined for the presence of

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Table 1. Total number of *Camponotus planatus* Roger found in nest and numbers parasitized by *Caencholax fenyesi* Pierce

Stage	Totals	Dissected	Parasitized
Sexuals	97	89	2
Workers	41	25	0
Pupae	3	2	2

Strepsiptera (Table 1). BMUCD-Bohart Museum, University of California, Davis. CMN-Canadian Museum of Nature, Aylmer, Quebec, Canada. OUMNH-Oxford University Museum of Natural History, Oxford, UK. SMNH-Smithsonian Museum of Natural History, Washington, DC USA. Ground (I), middle level (II) and canopy (III) levels in Panama.

Myrmecolacidae Saunders

Myrmecolacides Saunders, 1872: 20.
Myrmecolacidae Pierce, 1908: 76.
Stichotrematoidea Hofeneder, 1910: 49.
Stichotrematidae Hofeneder, 1910: 49.

Caenocholax Pierce

Caenocholax Pierce, 1909: 88.
Type Species: *Caenocholax fenyesi* Pierce 1909, Córdoba, Veracruz, Mexico.
Aedeagus with lateral spines and a ventral projection (Fig. 1).

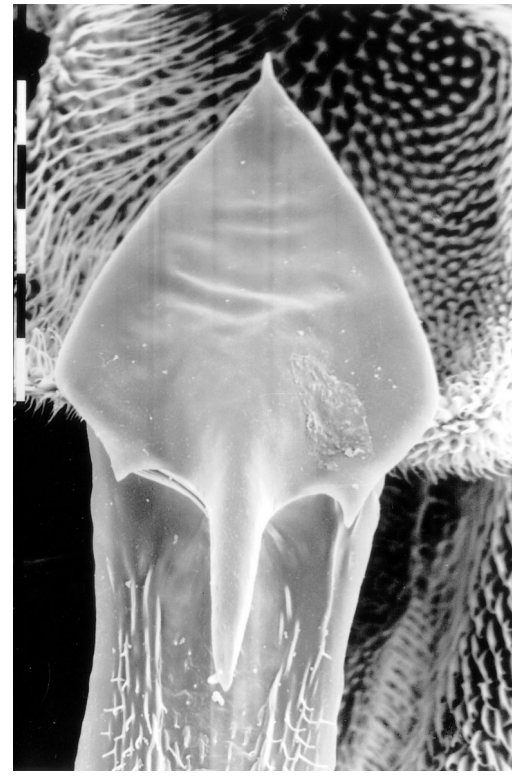

Fig. 1. Frontal view of shield on aedeagus of *Caenocholax fenyesi* Pierce. Bar = 10 mm.

Caenocholax fenyesi Pierce (Fig. 1)

Caenocholax fenyesi Pierce 1909: 88, Pierce, 1918: 433, Bohart, 1941: 120, Kifune and Brailovsky, 1987: 223, Kathirithamby and Johnston, 1992: 294, Maes and Kathirithamby, 1993: 52, Kathirithamby and Peck, 1994: 131, Kifune and Brailovsky, 1997: 436.

Caenocholax fenyesi was first described by Pierce (1909) from Mexico and since has been recorded from Argentina (Bohart 1941), Bahamas: Andros Island (Kathirithamby and Peck 1994), Belize (Kifune and Brailovsky 1997), Nicaragua (Maes and Kathirithamby 1993), Mexico (Kifune 1979a, Kifune and Brailovsky 1988), and the United States: Alabama (Jones et al. 1980), Arizona, and Georgia (Johnston and Morrison 1979), Florida (Meadows 1967, Kathirithamby and Peck 1994), Louisiana (Khalaf 1968), Mississippi (Khalaf 1969), and Texas (Kathirithamby and Johnston 1992, Kathirithamby and Peck 1994). Kifune (1979a) stated that, except for records from Panama in 1935 in the USNM (a dead male in banana thrash on a boat from Panama), and Argentina (Bohart 1941), no distributional data are available. All previously recorded specimens and the specimens examined in this study from the Neotropics are of male *C. fenyesi* that came into traps; hence the hosts are not known.

Synonymy

Mantidoxenos argentinus, Ogloblin 1939: 1277.
Myrmecolax ogloblini Luna de Carvalho 1973: 52 (syn. nov.).
Caenocholax brasiliensis Oliveira and Kogan, 1959: 221, Téson and Remes Lenicov, 1979: 120 (syn. nov.).

Based on the descriptions and figures by Oliveira and Kogan (1959, figures 2 and 3) and Téson and Remes Lenicov (1979, figures 20 and 20a), we synonymize *C. brasiliensis* with *C. fenyesi.* No type specimens of *C. brasiliensis* are available and hence were not examined. However, there is no doubt that *C. brasiliensis* is a synonym of *C. fenyesi* because of the unique shield-shaped aedeagus. In the latter paper, the authors examined first instars, pupae, and males of Ogloblin's (Ogloblin 1939) specimens which were *Mantidoxenos argentinus,* later described as *Myrmecolax ogloblini* Luna de Carvalho (1973), parasitic in the ant *Camponotus punctulatus cruentatus* Forel from Argentina. Although Téson and Remes Lenicov (1979) illustrated the adeagus they did not say if these specimens were parasitic on the hosts which they named as *Pheidole fallax emiliae* Forel and *P. radoschkowskyi reflexans* Santschi. They gave the range of this species as Brazil and Argentina (Table 2).

Material Examined. ARGENTINA: Salta Province: seven males, El Ray National Park, Pozo Verde Trail, 5 km, 950 m, Yungas forest, 5–15-XII-87, malaise FIT; two males, El Ray Nat. Park 200 m, 5–15.XII.87; five males, Rio La Sala, 5–15.XII.87, malaise-FIT, humid mossy chaco forest; two males, Pozo Verde Trail, 5 km,

Table 2. Hosts of male Myrmecolacidae

Species	Host of male (Hymenoptera: Formicidae)	Distribution
Myrmecolax nietneri Westwood 1861	*Camponotus maculatus-mitis* group	Sri Lanka, Malaysia
Myrmecolax borgmeieri Hofeneder 1949	*Eciton dulcius* Forel	Argentina
Caenocholax fenyesi Pierce 1909	*Solenopsis wagneri* Santschi [Kathirithamby and Johnston 1992][a]	S. America, S. USA
Myrmecolax ogloblini Luna de Carvalho 1973	*Camponotus punctulatus cruentatus* Forel	Argentina
Mantidoxeno argentinus Ogloblin 1939		
brasiliensis Oliveira & Kogan 1959	*Pheidole fallax emiliae* Far. *P. randoschkowskyi reflexans* Sants. [Teson and Lenicov 1979]	Neotropics
Stichotrema beckeri (Oliveira & Kogan 1959)		Neotropics
Caenocholax wygodzinskyl Oliveira & Kogan 1959	*Camponotus crassus* Mayr *C. puncutulatus cruentatus* Emery *Pseudomyrmexacanthobius virgo* Sants. *Solenopsis richteri* Forel [Teson and Lenicov 1979]	
Stichotrema robertsoni Kathirithamby 1991	*Pheidole* sp.	S. Africa

Authors of host records in square brackets.

5–15.XII.87, malaise, Yunus forest 950 m; four males, 7 km., 1,000 m, Yungas forest, 5–15-XII-87; 15 males, Rio La Sala, 900 m, humid mossy, Chaco Forest, 5–15-XII-87; 25 males, 1,000 m, Pozo Verde Trail, km 7, 5–15-XII-87; nine males, Rio Los Puestos, 880 m, Prosopis Forest, 6–16-XII-87; three males, Aguas Negras Trail, 900 m, Prosopis forest, 11–15- XII-87; three males, Arroyo Los Noques, 870 m, 13–14-XII-87, forest UV; Jujuy Province: N. Altagracia: one male, Miranda Guatopo, N.P., El Lucero, 700 m, 28 km, 31-V-7-VI-87, ravine FIT; 1–31.VIII.90, (I) (II). Calilegua Nat. Park, Estaca El Cero: six males, 900 m, 18–28-XII-87, forest Malaise – FIT. Calilegua Nat. Park, El Cortaderal: three males, km 6, 800 km, 18–28-XII-87, forest malaise-FIT, all collected by S. & J. Peck, (CMN).

COSTA RICA: Guanacaste Province: Santa Rosa National Park: six males, 17-IV-1-VII-85; five males, 3-VII-14-IX-85; two males, 5–26-X-85; three males, 16-XI-7-XII-85; one male, 14-IX-5-X-85; eight males, 7–28-XII-85; three males, 28-XII-85-8-II-86, P. Fretygae (OUMNH). 27 males, 18-I-2-III-86; 92 males, 23-III-3-IV-86; 24 males, 2–23-III-86; 30 males, 13-IV-4-V-86; 44 males, 4–24-V-86; six males, 24-V-14-VI-86; seven males, 5–26-VII-1986; five males, 26-VII-14-VIII-86; five males, 14-VIII-6-IX-86; four males, 29-XI-20-XII-86; 31 males, 20-XII-86–10-I-87; 66 males, 10–31-I-87; 94 males, 31-I-21-II-87; all by malaise trap; data as above, D. H. Janzen & I. Gould (OUMNH).

ECUADOR: Napo: Estación Biológica Jatum Sacha, one male, 2-VIII-89, blacklight, P. Freytag & T. Myers (OUMNH).

GUATEMALA: 1 male, Suchitepeque, Finca Moca Grande, hill behind lake MT, 24-II- 95, D. Quintero, (CMN).

PANAMA: Barro Colorado Island: Smithsonian Tropical Research Institute: Snyder Molino: 14 males, 1–30-XI-83; three males, 29-VIII-1-X-84, (I), (III), light; six males, 1–31-VIII-84; 34 males, 1–31-VIII-84; 23 males, 1–30-IX-84; 29 males, three males, 1–31-X-84; 30 males, 1–31-X-84 (I) (III); 29 males, 1–30-IX-84; 34 males, 1–31-VIII-84 (I) (III); five males, 7-XI-4-XII-84; eight males, 1–31-XII-84; one male, 1–3-I-85 (I) (III); two males, 1–30-II-85; one male, 1–28-II-85; two males 6-II-5 III-85; 17 males, 1–30-IV-85; three males, 1–31-V-85; one male, 1–30-VI-85 (I) (III); seven males, 1–31-VII-85; three males, 1–31-VIII-85; seven males, 1–30-IX-85; six males, 1–31-X-85; three males, 1–31-XI-85; 10 males, 1–31-III-86; three males, 1–31-IV-86 (I) (III); eight males, 1–31-VII-86; 20 males, 1–31-VIII-86 (I) (III); 13 males, 1–30-IX-86 (I) (III); 12 males, 1–31–X-86; 12 males, 1–31-XI-86; four males, 1–31-I-87; one male, 26.28.30-I-87; two males, 1–28-II-87; 17 males, 1–31-III-87; 15 males, 1–30-IV-87; 52 males, 1–31-V-87 (I) (III); five males, 11, 13, 15-V-87; 23 males, 1–30-VI-87; 13 males, 1–31-VII-87; 12 males, 1–30-VIII-87 (I) (III); 10 males, 1–30-IX-87; 17 males, 20-X-3-XI-87; one male, 28–31-XII-87; 11 males, 1–31-XII-87; 11 males, 1–31-XII-87; one male, 1–31-I-88 (I) (III); one male, 1–29-II-88 (I); −6 males, 1–31-III-88; 15 males, 1–31-IV-88; 53 males, 1–31-V-88; three males, 1–30-V-88; 12 males, 1–31-VI-88; 12 males, 1–31-VII-88; 12 males, 1–31-VIII-88; six males, 1–31-X-88; three males, 1–31-I-89; all same data as above, H. Wolda (BMUCD)

Snyder Molino: 3 males, 1–31-I-89 (I), light; one male, 1–30-IV-89 (I); one male, 1–31-V- 89 (I); 16 males, 1–30-VI-89 (I); six males, 1–31-VII-89 (I); nine males, 1–31-VIII-89, (I); seven males, 1–30-IX-89 (I); six males, 1–31-X-89 (I); 14 males, 1–30-XI-89 (I); five males, 1–31 × II-89 (I) (III); five males, 1–31-I-90 (I); one male, 9–15-II-90 (I); two males, 1–31-III-90 (I) (III); 12 males, 1–30-IV-90 (I); 35 males, 1–30-V-90 (I); 12 males, 1–30-VI-90 (1); eight males, 1–31-VII-90 (I); eight males, 1–31-VIII-90 (I); five males, 1–31-IX.90 (I); seven males, 9–31-X-90; two males, 1–30-XI-90 (I), same data as above, H. Wolda, (SMNH).

Las Cumbres: 5 males, 7-IX-4-XII-84, light; five males, 11.13.15-V-87, same data as above, H. Wolda (BMUCD).

TRINIDAD: Arima, Simla Research Station: two males, 7-VII-93; one male, 15 km, N, 260 m lower montane rainforest, 24-VI-8-VII-93, malaise; one male, 15 km N, Andrews Trace, 620 m up montane rainforest, 24-VI-7-VII-93, malaise, S. & J. Peck, collectors, (CMN).

UNITED STATES: Tennessee, Lexington: 1 male, 9–11-VI-72, S. & J. Peck, (CMN).

VENEZUELA: 1 male, Aragua, Parque, Nac. H. Pittier, Rancho Grande, env. 1,100 m, 10–14-IV-94, L. Masner; one male, Bolivar, Parupa, Gran Sabana, 27–30-VI-87, uv, grassland 1,500 m, S. & J. Peck; one male, Miranda, 700 m, 28 km N., Altagracia, Guatopo N.P., El Lucero 31-V-7-VI-87, Ravine FIT, S. & J. Peck (CMN).

New Records. MEXICO: Jalisco State: El Grulle, three males, 20–24-V-00, malaise, G. Moya Raygoza; one male, 31-X-00, same data as above (OUMNH). Veracruz: Los Tuxtlas Biological Station: one male extracted from pupa parasitic in *Camponotus planatus* Roger (Hymenoptera: Formicidae), 13-V-01, ex nest; one male pupa in *C. planatus*, same data as above; one male, 13-V- 01, light, D. Hughes (OUMNH).

Discussion

Kathirithamby and Hamilton (1995) suggested the use of the strepsipteran *C. fenyesi* (together with microbial and introduced phorids) to restore the balance of the red imported fire ant, *S. wagneri*, in the southern United States, and commented on the role of parasitism in structuring natural communities. In the southern United States the exotic *S. wagneri* has become an aggressive and abundant pest in an alien ecosystem without its natural parasites.

We have found a host of *C. fenyesi* in one of its endemic areas. The carpenter ant, *C. planatus*, was parasitized by *C. fenyesi*, in Veracruz, Mexico; the same locality where Pierce (1909) found the type species. Because the parasitized (stylopised) ant was found in the same locality as the type species described by Pierce (1909), we speculate that this might have been the original host of *C. fenyesi.*

As indicated in this article, the male of the strepsipteran *C. fenyesi* is widespread in South America and MesoAmerica. In the southern United States it has taken over a niche left by the natural parasite of *S. wagneri.* It is not known how this strepsipteran was introduced into the United States. We propose that *C. fenyesi* was introduced by the exotic carpenter ant, *C. planatus*, which was most probably its original host. The distribution of *C. planatus* ranges from Columbia in S. America through Mexico and into the southern states of the United States, being most widespread in southern Texas. *C. fenyesi* might have come to the southern states of the United States with *C. planatus* and then shifted hosts to *S. wagneri.*

Even with the discovery of a native host for the male, the female host remains conjectural. *C. fenyesi* belongs to the family Myrmecolacidae that exhibits an extreme form of heterotrophic heteronomy: a phenomenon that has never been found in any other insect parasite/parasitoid (Kathirithamby 1991). The usual form of heterotrophic heteronomy is when a mother selects a totally different host for male and female eggs. However, in the Myrmecolacidae (where first instars are the free-living host-seeking stage) the males develop in ants, and the females in grasshoppers, crickets and mantids (Kathirithamby and Hamilton 1992). Ogloblin (1939) was the first to report on the dual hosts of the Myrmecolacidae: the male *Mantidoxenos argentinus*, later described as *Myrmecolax ogloblini* (Luna de Carvalho 1973), parasitic in the ant *C. punctulatus cruentatus* Forel, and the female parasitic on *Acanthiotespis maculates* (Saussure) in Argentina.

Hosts of males caught in traps (sexes exhibit extreme sexual dimorphism) are largely unknown. As a consequence only six myrmecolacid males with their hosts have been described so far (Kathirithamby 1998, Kathirithamby et al. 2001).

Despite thorough searching, no females of *C. fenyesi* have been found although this species extends throughout the Neotropics. Two *Hapithus agitator* Uhler (Orthoptera: Gryllidae) from College Station, TX, were found parasitized by three strepsipteran females. The females were originally identified as *C. fenyesi* based on external morphological comparisons of shed first instar cuticles of male *C. fenyesi* and first instars, found in putative females (Cook et al. 1998). However, mitochondrial and nuclear phylogenetic analysis showed that this female strepersipteran is not *C. fenyesi* (Halbert et al. 2001).

Kathirithamby 2001 found that first-instar *Stichotrema dallatorreanum* Hofeneder enter their hosts via the foot-pads. Perhaps foot-pads of crickets, mantids and grasshoppers should be thoroughly examined for signs of stylopization.

Our data represent the only unambiguous case where the pharate male *C. fenyesi* was found in an ant host from Central South America. The abundant presence of *C. fenyesi* in the red imported fire ant in the southern USA is an excellent example of how an exotic parasite shifts and thrives in an exotic host within an alien ecosystem, but this time the introduction of the exotic parasite was not intentional and the shift to an alternate exotic host was to a pest species.

The recent entry of the red imported fire ant into Australia further fuels the debate on control mechanisms, and in a few years we shall see it's impact on the Australian ecosystem. Strepsiptera have great potential for integrated pest management (IPM) of the red imported fire ant, and our discovery of the original host of *C. fenyesi* has great significance in realizing this potential.

Based mainly on the diagrams by Oliveira and Kogan (1959), and Téson and Remes Lenicov (1979) (because the type material is unobtainable) *C. brasiliensis* Oliveira and Kogan (1959) and *M. ogloblini* Luna de Carvalho are symonized to *C. fenyesi.*

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