

A survey of the Western European Rhipiphoridae including the first record of a *Macrosiagon* species in The Netherlands (Coleoptera)

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WIJNAND R.B. HEITMANS, THEO M.J. PEETERS, JEROEN DE ROND & JAN SMIT

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Abstract: The Palaearctic Rhipiphoridae of Western Europe are listed for The Netherlands and the surrounding countries. Triungulin larvae close to the species of *Macrosiagon ferrugineum* are reported as new to the Dutch fauna. The phoretic association with *Nitela borealis* (Sphecidae), *Chrysis angustula* and *Trichrysis cyanea* (Chrysididae) in nature has not been recorded earlier. Westervoort (province of Gelderland) represents the most northern locality in Western Europe of a representative of the genus *Macrosiagon*, which has a mainly Mediterranean distribution.

W.R.B. Heitmans, Institute of Evolutionary and Ecological Sciences, University of Leiden, P.O. Box 9516, 2300 RA Leiden, The Netherlands.

T.M.J. Peeters, National Museum of Natural History, P.O. Box 9517, 2300 RA Leiden, The Netherlands.

J. de Rond, Rietmeent 1, 1357 CC Almere Haven, The Netherlands.

J. Smit, Plattenbergerweg 7, 6824 ER Arnhem, The Netherlands.

Introduction

Rhipiphoridae are beetles parasitic on insects of diverse orders including beetle larvae (Cerambycidae and possibly Anobiidae), the larvae of aculeate Hymenoptera and nymphal cockroaches (Clausen, 1940; Selander, 1957). Some species are highly specialized and attack just one host species, while others attack hosts belonging to a number of genera or even families. The Palaearctic species belong to four different subfamilies: Pelecotominae, Ptilophorinae, Rhipiphorinae and Rhipidiinae.

Records of rhipiphorid beetles are scarce and, because of their complex life history, descriptions of developmental stages are often incomplete and the life cycle of many of the better studied European and American species is still based on fragmentary results of observation and inferences from the habits of the hosts.

In this paper we summarize the general life history of the Western European Rhipiphoridae and list the species and their hosts known from The Netherlands and the neighbouring countries using records from literature and from different Dutch museum collections

(National Museum of Natural History Leiden (NNM); Zoological Museum Amsterdam (ZMA)) and the private collections of C.M.J. Berger (CB), P. Poot (PP) and A.P.J.A. Teunissen (AT). Because some Mediterranean species are known from northerly localities we admit the species from southern France to our list. The presence of a *Macrosiagon* species on previously unknown phoretic associates is established as new to the Dutch fauna. The original descriptions and the reports on the associations of the beetles and their hosts need to be consulted to identify the larval stages, since neither identification tables nor recently published surveys exist. The adult beetles were identified by the descriptions in literature (Gerstaecker, 1855; Chobaut, 1891, 1906a, b; Bétis, 1912; Besuchet, 1956) and via the identification table given by Yablokhov-Khnzoryan (1976). The biological nomenclature as disposed by Selander (1957) is adopted. We discuss a number of factors concerning the potential dispersal capacity of *Macrosiagon* species, such as the climatic condition of the habitat, the vegetation, host finding, the range of suitable (carrier) hosts and the life cycle.

Life history

Female rhipiphorids are short-lived and have a high fecundity: they may produce several hundreds to thousands of small eggs (0.4-0.5 mm) either produced separately or in a number of clutches. The number of eggs in the ovaries is determined by the body size of the adult beetles, which is, in turn, dependent on host size. Hence, body size and fecundity are expected to be most variable in the solitary species that use different host species of different size. Large differences in body size of the species in the collections indicate that they use different host species in nature.

The beetle larvae go through three to four different developmental stages, all adapted to display different biological functions. The number of moults and the characteristic forms of the larvae may differ in the distinguished subfamilies. The first stage larva is of a campodeid or triungulin (= three claw) form. Triungulins possess a prognathous head with strong mandibles, antennae, eyes (or ocelli) and a body with well-developed legs often with the tarsi terminated in transparent leaf-like pulvillae. The mandibles and legs are adapted to cling to an insect that happens to pass near the triungulin or is actively hunted. Triungulins may show fast movements to cling to a host. The larva of *Rhipiphorus* species also have a terminal abdominal segment adapted as a sucker to attach to a wing of a carrier host (Chobaut, 1906a, Tomlin & Miller, 1989). The second stage larva is grub-like, legless and eyeless and lives in or attached to its host. In the species of the temperate climatic zone this stage may go into diapause. In the Rhipidiinae the diapausing form is followed by a third instar larva, but in the Rhipiphorinae no such diapausing larva seems to exist. The second instar probably develops directly in the third and final stage that consumes the host (see below). The mature instar larva spins a cocoon before pupation.

Rhipiphorinae are idiobiont parasitoids of the mature larvae of aculeate Hymenoptera. The Macrosiagonini use solitary (Tiphidae, Scoliidae, Eumenidae, Sphecidae) and social

(Vespidae) wasps, whereas the Rhipiphorini parasitize solitary (Andrenidae, Anthophoridae, Megachilidae) and subsocial (Halictidae) bees. The subfamily is considered as an advanced taxon (Selander, 1957). It is the best studied of the four subfamilies. The triungulin uses a wasp or bee as carrier (phoresy) to get into a nest where a full-grown larva is attacked. If no carrier is found, or when no suitable host is available in the nest, the triungulin starves. Inside the nest the triungulin larva first enters its host and feeds on haemolymph, but later emerges again with the body expanded 6 to 8 times the original length. It then moults into a grub-like second instar larva that lives as an ectoparasitoid on its still living host, subsequently, followed by the third stage larva that consumes the host completely. The third and presumably last stage larva is elongate and greatly curved, with large fleshy processes on all segments, and the legs short, fleshy, and non-functional. The mature beetle larva first seals the cell of its former host and spins a cocoon before pupation. (Chapman, 1870; Grandi, 1936; Clausen, 1940). The adult beetles leave the host's nest and mate outside.

Rhipidiinae are highly specialized and known as koinobiont endoparasitoids of cockroaches. That they also use caterpillars as hosts (De Peyerimhoff, 1942) is unlikely, since Barbier (1947), Riek (1955) and Besuchet (1956) showed that cockroaches are the exclusive hosts for quite a large number of species. All Rhipidiinae are probably highly host specific parasitoids. The female beetles are larviform with small eyes, atrophied mouth parts and no traces of wings. The elytra of the males are also strongly reduced, but they can fly with the hind wings. The triungulins do not use a phoretic carrier, but actively hunt for a young cockroach nymph. The pulvillae of the tarsi are absent. The triungulin will partly enter the body of the captured host. Then it moults by leaving the triungulin exuvium outside and develops into a legless endoparasitic second instar larva. In *Rhipidius* species from the temperate climate the second instar larva may go into diapause and hibernate in the living cockroach. Next year the

third instar then slowly grows in its growing host and finally kills it by consuming the internal parts of the by then mature nymph or adult cockroach. The mature, fourth stage larva has six small, but functional legs. It leaves the body of the dead cockroach. Subsequently, it searches a place to spin a cocoon to pupate (Sundevall, 1831; Stamm, 1936; Barbier, 1947; Riek, 1955; Besuchet, 1956).

The Pelecotominae and Ptilophorinae contain the least specialized members of the group. Their systematic position is very different from both the Rhipiphorinae and Rhipidiinae (Selander, 1957). For example, the elytra and hind wings of the adult beetles are not reduced and the mouth particles are less atrophied. Their life history is obscure; immature stages are unknown. The hosts are virtually unknown, although the larvae of *Rhipistena cryptartha* Broun likely feed on larval Cerambycidae of the genus *Prionoplus* Westwood in New Zealand, whereas the adult beetles of the European *Pelecotoma fennica* (Paykull) have been associated with wood burrows of *Ptilinus* beetles (Anobiidae) in old willows (*Salix* spp.) near rivers in June and July (C. Besuchet, personal communication). It has been suggested that the triungulins might be active hunters like the Rhipidiinae preying upon the larvae of different species of wood boring beetles. Schumann (1899) suggests that *P. fennica* might also parasitize larvae of the sphecid *Trypoxylon clavicerum* (Lepelletier & Serville) nesting in the abandoned burrows of Anobiidae, but substantive evidence is lacking.

Survey of rhipiphorid species of The Netherlands and neighbouring countries

Pelecotominae

Pelecotoma fennica (Paykull)

The beetle is probably a parasitoid of wood boring Anobiidae in decaying wood (see above). It is a small and slender species (3.8-5.0 mm, n=12, NNM, ZMA).

Pelecotoma fennica is a northern species,

rarely found in woodlands in Germany, Poland, Austria and further into northeastern Europe (Horion, 1956; Lucht, 1987). The species has never been collected in The Netherlands and Belgium.

Ptilophorinae

Evaniocera dufouri (Latreille)

Immature stages and the host(s) of this species are unknown. The adult beetles remarkably vary in body length from 3.8 to 11.2 mm (n=46) in both the males and females (NNM, ZMA, AT, CB).

Evaniocera dufouri is known from southern France and is widely distributed in Mediterranean countries up to the Caucasus (Csiki, 1913). It also occurs in Algeria and Morocco. The most northerly locality in Europe is Hungary (NNM).

Rhipiphorinae

(Macrosiagonini)

Metoecus paradoxus (Linnaeus)

Metoecus paradoxus is chiefly a parasitoid of the larvae of the common yellow jacket wasp *Vespula vulgaris* (Linnaeus), but it may occasionally occur in the nests of *V. germanica* (Fabricius) and *V. rufa* (Linnaeus). Body length varies from 7.8 to 13.3 mm (n=73).

The species is commonly found in almost all European countries and further into eastern Europe and Russia (Chapman, 1870, 1891; Hoffer, 1883; Horion, 1956; Yablokhov-Khnzoryan, 1976; Lucht, 1987; Drees, 1994). It was previously the only autochthonous rhipiphorid known from The Netherlands. Brakman (1966) still refers to the localities Soest (central part of The Netherlands) and Roermond (southern part) as given by Everts (1903) (NNM, ZMA). More recent records show that *M. paradoxus* occurs in almost all Dutch provinces (Peeters & Heitmans, unpublished).

Macrosiagon ferrugineum (Fabricius)

Macrosiagon ferrugineum is a parasitoid of a number of different hollow stem and twig nesting eumenid wasp species including *Euodynerus variegatus* (Fabricius) (syn. *Odynerus crenatus* (Lepeletier)), *E. disconotatus* (Lichtenstein) (syn. *O. crenatus* sensu Blütgen), *Symmorphus murarius* (Linnaeus) (syn. *O. nidulator* Saussure) and *Rhynchium oculatum* (Fabricius), but it is also reared from a nest of a *Eumenes* species (Chobaut, 1891; Bétis, 1912; Grandi, 1936; Hubenthal, 1929; Van der Vecht & Fischer, 1972). Body length varies in females: 4.9-8.1 mm (n=14) (NNM, ZMA, CB), the only male present: 7.1 mm (ZMA).

Distribution: southern France and almost all other Mediterranean countries; the species is also known from (sub)tropical countries in Asia (India), North Africa (Egypt) and even West Africa (Senegal) (Gerstaecker, 1855; Csiki, 1913).

Macrosiagon tricuspidatum Lepechin

Macrosiagon tricuspidatum uses a number of different eumenid wasp species and perhaps *Megachile* bees as hosts (Chobaut, 1906b; Bétis, 1912). *Euodynerus* species may have their nest in abandoned nests of other aculeates. Therefore, the record of *Megachile* as host may be incorrect.

The beetles vary greatly in body size. Most specimens are females. Female body length: 4.0-12.8 mm (n=80), male: 6.0-8.0 mm (n=2) (NNM, ZMA, CB, PP, AT).

Distribution: southern France and almost all other Mediterranean countries; also known from Russia and Egypt. The records of *M. tricuspidatum* in southwestern Germany including Hessen, Nordbaden (Mannheim) and the Alsace (France) are all from the nineteenth century. Horion (1956) and Lucht (1987) do not confirm the presence of any *Macrosiagon* species in Germany and doubt whether *M. tricuspidatum* really occurs in Kärnten and Steiermark (southern Austria). However, 13 specimens of *M. tricuspidatum* from neighbouring Hungary and one from Bulgaria are present in the collections of NNM and ZMA.

Macrosiagon praeustum (Gebler)

Immature stages of this species and host(s) are unknown. Female body length: 3.3-7.1 mm (n=7) (NNM, ZMA), males are not present in the collections examined.

Distribution: southern France and almost all other Mediterranean countries, also known from Algeria, Russia and Siberia (Csiki, 1913; Yablokhov-Khinzoryan, 1976).

(Rhipiphorini)

Rhipiphorus subdipterus Bosc

This species is a parasitoid of solitary and sub-social bees, e.g. *Halictus sexcinctus* (Fabricius) (Chobaut, 1906a; Bétis, 1912). Most specimens in the collections are females (NNM, ITZ, AT). Female body length: 4.5-9.2 mm (n=29), males: 6.5-8.4 mm (n=4).

Distribution: southern France and almost all other Mediterranean countries.

Rhipidiinae

Rhipidius pectinicornis Thunberg

Rhipidius pectinicornis is a parasitoid of the German cockroach (*Blattella germanica* (Linnaeus)), a household pest of tropical origin. At the beginning of this century De Meijere reared two larviform females of this species emerged from cockroaches from Amsterdam. It is unknown whether these specimens emerged from one single host or from two hosts. The specimens are of equal body length: 5.0 mm (NNM). *Rhipidius pectinicornis* was listed as part of the Dutch fauna by Everts (1922). The beetle is known particularly from ships infested with German cockroaches in Calcutta (Sundevall, 1831), in Denmark (Stamm, 1936) and in Egypt (Barbier, 1947). In cooler areas *R. pectinicornis* can possibly maintain itself in heated buildings with its host, but no new records were reported in the world since 1947. The origin

Fig. 1. Ventral view of triungulin larva of *Macrosiagon* sp. on *Nitela borealis* from Westervoort, attached to the arolium between claws of left hind tarsus.



and natural habitat of *R. pectinicornis* are unknown.

Rhipidius quadriceps Abeille de Perrin

This species is parasitic on *Ectobius* cockroaches, particularly *E. sylvestris* (Poda).

Rhipidius quadriceps is known from Germany, Austria, Switzerland, France, Italy, Spain, Russia, Finland and North Africa (Kraatz, 1891; Chobaut, 1919a, b, 1922; Español Coll, 1942; Lindberg, 1955; Horion, 1956; Besuchet, 1956; Yablokhov-Khnzo-

ryan, 1976; Lucht, 1987). The species is present in the collection of AT from Switzerland, but we do not know any record from The Netherlands and Belgium.

Rhipidius abeillei Chobaut

Rhipidius abeillei is closely related to *R. quadriceps*. It is likely to be a parasitoid of ectobiid cockroaches. Body length of males from France: 5.0-6.5 mm (n= 21) (AT, ZMA). The female and immature stages are unknown.

Rhipidius abeillei has a more southern distri-



Fig. 2. Dorsal view of triungulin larva of *Macrosiagon* sp. on *Nitela borealis* from Westervoort, anchored to metatarsus under the apical spores.



Fig. 3. Lateral view of triungulin of *Macrosiagon* sp. on *Chrysis angustula* from Westervoort, attached to seta of right mid tibia.

bution than *R. quadriceps*; France, Spain, Algeria (Español Coll, 1942; Besuchet, 1956).

Rhizostylops inquirendus Silvestri

This species is only known from one single, larviform female, her eggs and the emerged triungulin larvae from Italy once taken from a soil sample (not seen) (Silvestri, 1905). The male and other immature stages as well as the host(s) are unknown.

New Dutch records

In 1990 and 1991 five identical triungulin larvae attached to three different species of aculeate wasps were collected at a railway siding on a sandy embankment in Westervoort near the city of Arnhem. The collecting site faces south and rises ± 5 m above the surroundings that consist of a clay soil deposited by the IJssel river. Oak and elm trees surround the territory; shrubs such as *Symphoricarpos rivularis* Suksd., *Syringa vulgaris* L., *Crataegus*



Fig. 4. Close-up of head with mandibles, maxillary palps, antennae and the light sensitive organs (ocelli) of triungulin of *Macrosiagon* sp.

Table 1. Carrier host species and family, sex of the carrier, collecting date, number and position of the triungulins.

carrier host	host family	sex of carrier	coll. date	no. of triungulins	position of triungulins
<i>Chrysis angustula</i> Schenck	Chrysididae (Chrysidinae)	♀	June 1, 1990	2	one on left and one on right mid tibia
<i>Trichrysis cyanea</i> (Linnaeus)	Chrysididae (Chrysidinae)	♂	July 2, 1991	1	right hind tibia
<i>Nitela borealis</i> Valkeila	Sphecidae (Larrinae)	♂	July 2, 1991	2	both on left hind tarsus

monogyna Jacq., *Rubus saxatilis* L. and *R. idaeus* L. are present in abundance. The insect and plant species at the site were listed in a KNNV-report (Smit, 1991).

The wasps with triungulins were part of a sample of insects collected by hand near and on a dead oak tree (table 1). The triungulins did not release their grip during preservation of the wasps. The triungulins attached to the tibia of *Chrysis angustula* Schenck and *Trichrysis cyanea* (Linnaeus) all firmly held a seta in the mandibles (fig. 3). One triungulin on *Nitela borealis* Valkeila clung to the arolium between the claws of the tarsus (fig. 1) and another specimen was found under the spores of the tibia on the tarsal base holding a piece of soft cuticula of the articulation (fig. 2). Fig. 4 shows the head of a released triungulin.

Description

Hexapod larva. Average length of the body of dried triungulins (without the caudal setae): 0.33 ± 0.06 mm (n=4), strongly dorso-ventrally flattened.

Body colour: overall dark brown; head, tergites, sternites and legs strongly sclerotised, only the tarsal pulvillae and a similar structure posterior of the abdomen are transparent.

Head large, 0.12 ± 0.03 mm, somewhat triangular of shape, tapering off in front, considerably longer than the combined lengths of the first and second thoracic tergites. Frons indistinctly fused with the clypeus. Simple eyes placed laterally on the back of the head behind the antennae. Eyes consist of four light sensitive structures (Grandi (1936) calls them ocelli): three above the im-

plantation of the antenna, one below of it (fig. 4). Antennae implanted in the margin of the head, length 0.096 mm. They consist of 3 segments: I, the shortest and widest segment in the form of ring, II, the longest segment, flattened, III, of a thin pin-like structure. Flattened sensory appendix on antennal joint II forming a fork-like structure with the apical part of the joint (figs 3 and 4). Labrum very prognathous, distinct, split into two halves ending in a dorsal furrow, that extends further backwards and has half the length of the head (not visible in figs 1-4). Mandibles strong, curved to hold a structure in a firm grip. Maxillary palps consist of 3 cylindrical segments, I and II short and about equal in length, III about 2 times as long as II; labial palps rudimentary or absent (fig. 4). Two small pairs of dorsal setae in front of the head, a single pair of small setae on the margin of the head and another single pair of posterior setae implanted just above the eyes (figs 2 and 4).

One single pair of setae on each of the thoracic tergites and sternites. Trochanters with a single seta as long as the coxa (fig. 1).

Three pairs of setae on the abdominal tergites: one dorsal pair, one pair on the marginal edges and another single pair on the lateral tergites. The eighth and ninth segment have only 2 pairs of setae of which the outer pair on the ninth is extremely long, 0.10 mm. Also, 3 pairs of setae on the abdominal sternites, except for the eighth segment with 2 pairs of which the outer pair is longer and both the ninth and tenth segment with only a single pair (figs 1 and 2). (Grandi (1936) illustrated a fourth outer pair of very small setae on the second and third abdominal sternite, but that could not be observed

in our dry material). Terminal abdominal segment with a small pulvillus-like structure (fig. 3), unlike the sucker of *Rhipiphorus* species (Tomlin & Miller, 1989).

Identification

The identification of triungulin larvae to the subfamily level offers no particular problems, although the information is far from complete. Differences are sufficiently described and illustrated for the Rhipiphorinae and Rhipidiinae (Sundevall, 1831; Chapman, 1870; Chobaut, 1891, 1906a, b, 1919; Silvestri, 1905; Grandi, 1936; Barbier, 1947; Besuchet, 1956; Tomlin & Miller, 1989). Species are best recognized by the chaetotaxy and the presence of tarsal pulvillae. In combination with the type of carrier host it was easily to identify the species as Macrosiagonini, Rhipiphorinae. Primary larvae of Macrosiagonini have a dorsal furrow from the front to the middle of the head. Triungulins of the genus *Macrosiagon* are characterized by one dorsal pair of remarkably long setae on the ninth abdominal segment as described above. Another pair of ventral setae on the eighth abdominal segment is about 1/3 of this length (fig. 1). Both these abdominal setae are much smaller in *Metoecus* and are lacking in *Rhipiphorus* (Rhipiphorini).

The triungulins of *M. ferrugineum* and *M. tricuspidatum* are very similar. The main differences given by Chobaut (1891, 1906b) are that the head of *M. tricuspidatum* is considerably smaller and that the anterior edge is much more rounded than in *M. ferrugineum*. The eighth and ninth abdominal segments are also shorter and the edges of the three thoracic tergites are much more rounded in *M. tricuspidatum* than in *M. ferrugineum*. These differences are clear, although the triungulins are poorly illustrated and the chaetotaxy of both species is not described. Grandi (1936) illustrated the triungulin of *M. ferrugineum* and gives a more precise description than the previous papers. Except for the total body length of the living triungulin (0.5 mm.) no other anatomical measurements are given. The triungulins presented in figs 1-4 are very similar in almost all

details to those illustrated and described by Grandi (1936), yet we can only conclude that the triungulins from Westervoort are closer to *M. ferrugineum* than to *M. tricuspidatum*. Without knowing the adult beetle it is not possible to identify a *Macrosiagon* triungulin correctly to species level. Unfortunately, the adult beetle has not been captured.

Discussion

The finding of *Macrosiagon* triungulin larvae in two successive years on the same spot suggests that a population has become established in the most northerly locality of Western Europe known for this genus. All European *Macrosiagon* species are generally considered to be faunistic elements of the Mediterranean region (Schilder, 1926). It is most likely that one of the three species mentioned in this paper from southern France up to the Haute Loire is the best candidate to migrate to the cooler northwestern part of Europe. In Eastern Europe all three *Macrosiagon* species seem to be distributed as far as the Caucasus, whereas early records of *M. praeustum* are even reported from Siberia (Csiki, 1913; Yablokhov-Khnzoryan, 1976).

European *Macrosiagon* species are known from arid zones, such as sand dunes and warm mountain slopes. Northern populations may survive when suitable climatic conditions are met. It is possible that *Macrosiagon* species disperse from their dry and warm Mediterranean habitat to other arid zones where potential hosts are present. *Macrosiagon tricuspidatum* specimens were collected in the Hungarian puszta (NNM, ITZ). Other arid zones are present along railway tracks throughout Europe suggesting a possibility how *Macrosiagon* species may have come even that far north. However, we do not think that rhipiphorids disperse easily over large distances in one generation. The adult beetles do not eat, are short-lived and were only kept alive for a maximum of 8 days in captivity (Chobaut, 1891). Adult beetles are also poor flyers. The dispersal of triungulins depends on the activities of carrier hosts, which will not move far from their nest(s).

Macrosiagon beetles as well as their triungulins are usually found on flowers, e.g. *Eryngium campestre* L., *E. maritimum* L. and *Solidago* spec. (Chobaut, 1891, 1906b, Balduf, 1935; A.P.J.A. Teunissen, personal communication). Both *E. campestre* and *S. canadensis* L. are present at the railway siding in Westervoort (Smit, 1991). Triungulins sit and wait in flowers for an opportunity to cling to a visiting insect. This behaviour allows them to encounter a variety of flying insects.

Triungulins do not seem to distinguish the sex of a carrier host (table 1; Linsley et al., 1952; Tomlin & Miller, 1989). If they board a male they might never come to a nest with larvae. It is suggested that *Rhipiphorus (smithi)* triungulins on halictid bees may get a second chance changing from male to a hibernating female host during a copulation (Tomlin & Miller, 1989). Copulatory sessions of these bees often occur in their underground burrows and last some minutes. However, copulation in wasps often takes less than one minute. Females usually mate only once in their life time. So, it is unlikely that a triungulin ever gets the opportunity to give up its firm grip and exchange carrier host.

Macrosiagon species use a broad spectrum of different eumenid host species, including the large Mediterranean wasp *Rhynchium oculatum* (14.5-18 mm) and the more slender and smaller *Eumenes* (14-16 mm), *Euodynerus* and *Symmorphus* (9-13 mm) species (Chobaut, 1891; Bétis, 1912; Balduf, 1935; Grandi, 1936). Indeed, the highly variable body size of the examined beetles indicates that different wasp species are used as hosts between and within different populations. It is possible that the range of suitable hosts extends far over the species that are previously mentioned for the Mediterranean region. A broad range of host species will increase the probability to establish in an invaded area, but also facilitates dispersal activities. *Rhynchium oculatum* is absent in The Netherlands, but two *Euodynerus* and four *Eumenes* species are known from the Dutch fauna. Other solitary eumenids, such as *Symmorphus* and *Ancistrocerus* with 8 and 12 Dutch species respectively, are much more common (Hensen,

1985). In Westervoort at least five different *Ancistrocerus* species were listed and recently, the larger *Eumenes papillarius* (Christ) was found (Smit, 1991; Smit, unpublished). The occurrence of a triungulin on the sphecid *Nitela borealis* (table 1) may indicate that the beetle may use an even broader range of hosts including the subfamilies Larrinae and Pemphredoninae (Sphecidae), most of which have their nests in hollow stems or twigs (Lomholdt, 1975). However, we wonder whether the small *Nitela borealis* (3.5-4 mm) is large enough to be a suitable host for *Macrosiagon*.

This is the first time that Chrysididae have been observed as carrier hosts in nature. Balduf (1935) previously referred to an experiment done by Cros who collected triungulin larvae of *M. tricuspidatum* from flowers and observed that they clinged to a variety of hymenopteran hosts including *Chrysis*, *Osmia* bees, *Polistes* and *Eumenes* wasps offered in captivity. In this experiment it was found that 12 triungulins adhered to one *Eumenes* wasp.

The use of Chrysididae as carriers will undoubtedly contribute to both the dispersal and the survival of triungulins (table 1). Both *Chrysis angustula* and *Trichrysis cyanea* visit a number of different twig nesting Eumenidae, Sphecidae (Pemphredoninae, Larrinae) and sometimes solitary bees (Morgan, 1984). By using Chrysididae, the triungulin will have the opportunity to be transported to several different host species. Moreover, clinging to a female chrysidid may avoid the risk that a carrier will not get offspring, while the chrysidid wasp prefers to enter the nests of successful wasps only. It is also possible that a triungulin uses a chrysidid larva itself as host after the latter has destroyed the legitimate cell owner. Using chrysidid wasps as carriers may, however, incur disadvantages, because the triungulin and the developing chrysidid larva may have to compete for food when both feeding simultaneously on the same host larva. Nothing is known about the outcome of a contest between triungulins and a chrysidid larva nor that between two or more solitary living triungulins. The record of two or more triungulins on one carrier is not uncommon (table

1; Balduf, 1935; Tomlin & Miller, 1989). So, more than one triungulin may be introduced in a nest at once. Grandi (1936) found that 1 to 4 larvae of *M. ferrugineum* developed from the four examined nests of *Rhynchium oculatum*, whereas every nest also produced at least one new wasp. More spectacular is a record of more than 50 *Metoecus paradoxus* beetles in a nest of *Vespula vulgaris* by S. C. Langeveld (unpublished). In the Rhipiphorinae one single beetle develops per nest cell. Triungulins of *Rhipidius pectinicornis* are the only facultatively gregarious rhipiphorids known: 1 or 2 and sometimes even 5 beetle larvae may develop in one cockroach under natural circumstances (Stamm, 1936; Barbier, 1947).

The life cycle and the number of generations of many Rhipiphorinae are insufficiently known. Our record of *Macrosiagon* triungulins as early as June 1, 1990 is the earliest observation known so far. Our records of July 2, 1991 can also be rated among the early observations. In Pisa (Italy) the triungulin and mature larvae of *M. ferrugineum* were found in *Rhynchium* nests in the second half of July and early August (Grandi, 1936). In southern France Chobaut (1891) observed *M. ferrugineum* laying the eggs in July and the emerged triungulins in August. Triungulins of *Rhipiphorus subdipterus* were collected in early August and those of *M. tricuspidatum* as late as August 26 (Chobaut, 1906a, b). Unfortunately, the possible presence of *Macrosiagon* triungulins or adult beetles in Westervoort could not be established in late summer as the frequency of sampling then was less intensive. Balduf (1935) postulates that the appearance of triungulins coincides with the period that the carrier wasps have mature larvae. Both *Macrosiagon pectinatum* (Fabricius) in Indiana and *Rhipiphorus solidaginis* (Pierce) in Nebraska (USA) hibernate as mature larva, pupate the following spring and emerge as adults in July. A similar seasonal distribution of stages has been demonstrated in Mediterranean *Macrosiagon ferrugineum*: the larvae hibernate and pupation has been observed in June. The postulated life cycle is, however, inconsistent with our earliest record of *Macrosiagon* triungulins on June 1. It is possible that *Macrosiagon*

in northern regions is able to hibernate as diapausing triungulin outside a nest, becoming active next spring to find a carrier similar to *Metoecus paradoxus*. *Metoecus* is thought to have always one generation per year like its host *Vespula vulgaris*, since adult beetles were never taken early in the season. *Metoecus paradoxus* emerges and deposits the eggs from late July until early October (Hoffer, 1883). The diapausing triungulin is thought to survive for more than 8 months in their egg shell (Chapman, 1891). The life cycle of *M. paradoxus* is similar to another northern species of *Rhipiphorus* from Canada of which the triungulins hibernate attached to the wing of diapausing female bees (Tomlin & Miller, 1989). Southern *Macrosiagon* populations may have more than one generation per year and adapt the number of generations to that of their hosts. The presence of the beetles during the entire summer period supports the idea that they do not belong to a single cohort. The adult beetles of *M. praeustum*, for example, have been collected near Zaragoza (northern Spain) as early as May 26 and 28, 1958 (NNM). On the other hand, an adult beetle of *M. ferrugineum* has been captured in Policoro (South Italy) as late as October 7, 1977 (NNM). More knowledge about the rhipiphorid life cycle may lead to more observations of these rarely collected beetles and to a better understanding of their geographical distribution and life history.

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References

- BALDUF, W.V., 1935. *The bionomics of entomophagous Coleoptera*: 1-220. John S. Swift, St. Louis.

- BARBIER, J., 1947. Observations sur les mœurs de *Rhipidius pectinicornis* Thunbg. et descriptions de la larve primaire. – *Entomologiste* 3: 163-180.
- BESUCHET, C., 1956. Biologie, morphologie et systématique des *Rhipidius* (Col.: Rhipiphoridae). – *Mitt. schweiz. ent. Ges.* 2: 73-144.
- BÉTIS, L., 1912. Les rhipiphorides Gallo-Rhénans. – *Annls Soc. Hist. nat. Toulon* 3: 125-155.
- BRAKMAN, P.J., 1966. Lijst van Coleoptera uit Nederland en het omliggend gebied. – *Monogr. ned. ent. Ver.* 2: i-x, 1-219.
- CHAPMAN, T.A., 1870. Some facts towards a life history of *Rhipiphorus paradoxus*. – *Ann. Mag. nat. Hist.* [4] 6: 314-328.
- CHAPMAN, T.A., 1891. On the oviposition of *Metoecus* (*Rhipiphorus*) *paradoxus*. – *Entomologist's mon. Mag.* [2] 2: 18-20.
- CHOBOUT, A., 1891. Mœurs et métamorphoses de *Eumenia flabellata* F., insecte Coléoptère de la famille des Rhipiphorides. – *Annls Soc. ent. Fr.* 8: 447-456.
- CHOBOUT, A., 1906a. Le triongulinide du *Myiodes subdip-terus* Bosc (Col.). – *Annls Soc. ent. Fr.* 19: 238-244.
- CHOBOUT, A., 1906b. Le triongulinide du *Macrosiagon tricuspidata* Lepech (Col.). – *Annls Soc. ent. Fr.* 19: 270-272.
- CHOBOUT, A., 1919. Description des deux sexes, de l'oeuf et de larve primaire d'un nouveau *Rhipidius* de Provence. – *Bull. Soc. ent. Fr.* [1919]: 200-206.
- CLAUSEN, C.P., 1940. *Entomophagous insects*: 1-688. McGraw-Hill, New York.
- CSIKI, E., 1913. Rhipiphoridae: 1-29 (G. Schenkling), *Coleopterorum Catalogus* 17, pars. 54. W. Junk, Berlin.
- DREES, M., 1994. Eine Gebäudebrut von *Metoecus paradoxus* (L.) (Insecta, Coleoptera, Rhipiphoridae). – *Ent. Bl. Biol. Syst. Käfer* 90: 117-121.
- EVERTS, E., 1903. *Coleoptera Neerlandica* 2: i-iv, 1-796. Nijhoff, 's-Gravenhage.
- EVERTS, E., 1922. *Coleoptera Neerlandica* 3: v-xviii, 1-668. Nijhoff, 's-Gravenhage.
- ESPAÑOL COLL, F., 1942. Los representantes catalanes de la familia Rhipiphoridae. – *An. Esc. Peritos Agri. Barcelona* 2: 335-346.
- GERSTAECKER, C.E.A., 1855. *Rhipiphoridum Coleopterorum familiae dispositio systematica*: 1-36. Libreria Frederici Nicolai, Berolini.
- GRANDI, G., 1936. Morfologia ed etologia comparate di insetti a regime specializzato, 12: *Macrosiagon ferrugineum flabellatum* F. – *Boll. Ist. ent. Univ. Bologna* 9: 33-64.
- HENSEN, R., 1985. *De plooiwleugelwespen (Hymenoptera: Vespidae)*: 1-60. Jeugdbondsuitgeverij, Utrecht.
- HOFFER, E., 1883. Über die Lebensweise des *Metoecus paradoxus* L.. – *Ent. Nachr. Dresden* 9: 45-49.
- HORION, A., 1956. *Faunistik der mitteleuropäischen Käfer*, 5: *Heteromera*: 1-336. G. Frey, Tutzing.
- HUBENTHAL, W., 1929. *Macrosiagon ferrugineum* vs. *flabellatum* F. – *Ent. Bl. Biol. Syst. Käfer* 25: 53.
- KRAATZ, G., 1891. *Rhipidius apicipennis* nov. spec. aus Thüringen. – *Dt. ent. Z.* 2: 358-360.
- LINDBERG, H., 1955. *Rhipidius apicipennis* Kraatz i Finland. – *Notul. ent.* 35: 53-55.
- LINSLEY, E.G., J.W. MACSWAIN & R.F. SMITH, 1952. The life history and development of *Rhipiphorus smithi* with notes on their phylogenetic significance. – *Univ. Calif. Publ. Ent.* 9: 291-314.
- LOMHOLDT, O., 1975. The Sphecidae (Hymenoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica*, [4], 1 and 2. Scandinavian Science Press, Klampenborg.
- LUCHT, W.H., 1987. *Die Käfer Mitteleuropas, Katalog*: 1-342. Goecke & Evers, Krefeld.
- MORGAN, D., 1984. Cuckoo-wasps (Hymenoptera: Chrysididae). – *Handbk Ident. Br. Insects* [6] 5: 1-37.
- PEYERIMHOFF, P. DE, 1942. Les Rhipidiens peuvent-ils parasiter les chenilles? – *Bull. Soc. ent. Fr.* 1: 172-177.
- RIEK, E.F., 1955. The Australian rhipidiine parasites of cockroaches (Coleoptera: Rhipiphoridae). – *Aust. J. Zool.* 3: 71-91.
- SCHILDER, F.A., 1926. Rhipiphoriden-Studien. – *Ent. Bl. Biol. Syst. Käfer* 22: 114-117.
- SCHUMANN, E., 1899. *Pelecoma fennica* Payk. – *Z. wiss. Insektbiol.* 4: 153.
- SELANDER, R.B., 1957. The systematic position of the genus *Nephrites* and the phylogenetic relationships of the higher groups of Rhipiphoridae (Coleoptera). – *Ann. ent. Soc. Am.* 50: 88-103.
- SILVESTRI, F., 1905. Descrizione di un nuovo genere di Rhipiphoridae. – *Redia* 3: 315-324.
- SMIT, J., 1991. *Insekteninventarisatie Spoorwegemplacement Westervoort*: 1-26. Insekten Werkgroep KNNV Arnhem, Arnhem.
- STAMM, R.H., 1936. A new find of *Rhipidius pectinicornis* Thbg. (*Symbius blattarum* Sund.). – *Ent. Meddr* 19: 286-297.
- SUNDEVALL, J.C., 1831. Beschreibung einer neuen Coleopteren-Gattung, *Symbius Blattarum*. – *Isis, Jena* 11: 1222-1228.
- TOMLIN, A.D. & J.J. MILLER, 1989. Physical and behavioural factors governing the pattern and distribution of Rhipiphoridae (Coleoptera) attached to wings of Halictidae (Hymenoptera). – *Ann. ent. Soc. Am.* 82: 785-790.
- VECHT, J. VAN DER & F. C. J. FISCHER, 1972. Palaeartic Eumenidae (Hymenoptera, Vespoidea). – *Hym. Cat. (Nova Editio)* 8: 1-199.
- YABLOKHOV-KHNZORYAN, S.M., 1976. Beetles of the family Rhipiphoridae (Coleoptera) in the USSR., part 2. – *Ent. Obozr.* 55(2): 410-424. [in Russian, translated in: *-Ent. Rev., Wash.* 55(2):104-113].

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