

Metoecus paradoxus in The Netherlands (Coleoptera: Rhipiphoridae)

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Abstract: *Metoecus paradoxus* is predominantly a parasitoid of *Vespula vulgaris*, but has a wide range of host species. Before 1966 there were only three records of this northern Palaearctic species from The Netherlands, but during the last three decades the beetle was present in ten of the twelve Dutch provinces. The beetle occurs in various rural and urban environments. In this paper we summarize the beetle's complex life history and discuss the recent increase of records. Possible mechanisms for differential parasitism and coexistence of different *Metoecus* species are also discussed.

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Introduction

Metoecus paradoxus (Linnaeus) belongs to the subfamily Rhipiphorinae of which all species are solitary, idiobiont parasitoids of the fullgrown larvae of various taxa of solitary and social aculeate Hymenoptera. Species of the genus *Metoecus* are exclusively found on the eusocial Vespidae.

The Rhipiphorinae are widely distributed in tropical and subtropical areas. Only a few species occur in regions with temperate climates. *Metoecus paradoxus* is found throughout the Palaearctic region, including almost all northern European countries, the northern parts of the Mediterranean area and northern Asia as far as Hokkaidô, northern Japan (Csiki, 1913; Hattori & Yamane, 1975; Yablokhov-Khnzoryan, 1976; Lucht, 1987; Heitmans et al., 1994). The species was possibly introduced in the USA (Missouri) and in Brazil (Schilder, 1924), but recent records could not be found. In the most recent overviews only a few records of the beetle are given from The Netherlands (Everts, 1922; Brakman, 1966), but in the last decades the species is increasingly observed (Peeters, 1990; Langeveld, 1992; Knotters, 1994). The scarce findings of *M. paradoxus* may be closely connected with its parasitic and largely cryptic way of life.

Ramdohr (1813) first found the species emerging from a *Vespula* nest in Germany, but the biology and much of the beetle's complex life-history was unravelled by Chapman (1870, 1891, 1897). The more recent studies by Spradbery (1973), Carl & Wagner (1982) and Švácha (1994) greatly contribute to the understanding of the general ecology and the host relationships of *M. paradoxus*. These studies may have stimulated entomologists to pay more attention to the presence and habits of the species. In this paper we shall give a brief description of the adult beetle and summarize its life-history. The new localities and the former and present distribution are given for The Netherlands. We also discuss the beetle's abundance in wasp colonies, the possible mechanisms of host selection and the occurrence of differential parasitism in different *Metoecus* species.

Description and life-history

The adult *Metoecus paradoxus* beetle can easily be recognized by its relatively small head (fig. 1) with the eyes moderate in size, antennae pectinate with the third to tenth joint subequal in length bearing very long and slender thread-like prolongations in the male, antennae subpectinate in the female, prothorax



Fig. 1. *Metoecus paradoxus*, male, head.



Fig. 2. *Metoecus paradoxus*, female, dorsal side.

as wide as long with a median furrow, elytra 2.5-3.0 times as long as the prothorax, gradually tapered and acuminate posteriorly, surface closely and finely punctured (fig. 2). The colour patterns are remarkably variable: Rouget (1873) and Schilder (1924) distinguish 21 different colour varieties of which many combinations are fairly well related to sex and the host species.

Metoecus paradoxus is often found in the nests of the common yellow jacket wasps of the genus *Vespula* (Hoffer, 1883; Newstead, 1891; Tuck, 1897; Spradbery, 1973; Carl & Wagner, 1982). The beetle probably mates and always lays the eggs outside the nest. The female deposits her small eggs (0.5 mm) in crevices of decaying wood. The egg hibernates. The first larval instar is of the triungulinid form, which hatches the following spring or summer. *Vespula* wasp workers that collect wood to build the nest may coincidentally visit natal sites of triungulinids. The phoretic first-larval instar clings to the body of the wasp and is carried to the wasp's nest. After arriving in the nest, the larva leaves the wasp and searches for a suitable host in the comb. The beetle larva uses one fullgrown wasp larva for its development and pupates in the cell that is closed by the wasp larva before it is almost completely consumed by the parasitoid. Summaries of the successive feeding processes of the larva and its development to adult beetle are given in Clausen (1940), Edwards (1980) and Švácha (1994). The development from triungulinid to adult beetle is completed within 3.5 weeks. The beetles emerge from late July until early

October. The adult insects do probably not feed and are short-lived. Rouget (1873) reported 12 days for an extremely large female. Carl & Wagner (1982) noted an average longevity of seven days for females and eight days for males. H. Vogel (personal communication) kept five adult beetles (four non-reproducing females, one male) alive for six days. The species is univoltine.

Several authors observed that *M. paradoxus* can lay hundreds of eggs in small (10-50) to large clusters (500) (Rouget, 1873; Chapman, 1897; Carl & Wagner, 1982). Usually the ovarioles contain 600 to 700 mature eggs (Carl & Wagner, 1982). The number of eggs may increase with increasing body size, which is, in turn, probably dependent on host size. Gradl (1879b) and Hattori & Yamane (1975) found that beetles from host larvae in queen cells are significantly larger than those from worker cells. In Dutch museums and private collections the total body length of adult females varies from 8.1 to 13.3 mm (n= 49).

In contrast with the short life expectancy of the adult beetles the triungulinids were observed to survive at least two months without food waiting for a carrier (Carl & Wagner, 1982). Observations of emerging beetles during a period of about 12 weeks reflect the idea that triungulinids have gradually entered the nest during most of the summer period (Rouget, 1873; Hoffer, 1883; Tuck, 1897; Langeveld, 1992; Drees, 1994; Švácha, personal communication).

Localities and distribution patterns

The first beetle was recorded in The Netherlands in Soest in the province of Utrecht in 1875 and several specimens were collected in 1895 in Roermond (province of Limburg) (Everts, 1876; van der Hoop, 1896). These records from the nineteenth century are represented by specimens in the collections of the National Natural History Museum (NNM, Leiden) and in the Zoological Museum of Amsterdam (ZMA). A third finding from Hulsberg (province of Limburg) was reported by Schmitz (1936); this specimen is kept in the Natural History Museum of Maastricht (NHMM). Rüschkamp (1919) considered a previous record of one (male) beetle from Valkenburg (also from the southern part of Limburg) as erroneous and no such specimen is present in the NHMM (F.N. Dingemans-Bakels, personal communication). We do not know why Everts (1922) still mentioned a new record from Valkenburg, but it is possible that he pointed out another specimen that could not be traced by us. Brakman (1966) only referred to records of provinces and did not specify any localities. In this paper we therefore map the records over three periods starting with the nineteenth century, followed by the period from 1900 until the publication of Brakman's list (1966) and the more recent period starting from 1966. Faunistic data were checked from the material deposited in different museum and private collections, from the records registered by The Inspectorate of the Environment (= Afdeling Bestrijding van Dierplagen (ABD), Ministerie VROM) and from a number of field observations.

Fig. 3 gives the former and present distribution of *M. paradoxus* in The Netherlands in 10 x 10 km UTM-squares. Before 1966 *M. paradoxus* was considered to be rare, as it was only known from 3 UTM-squares. Since then the number of records has increased to the present 22 UTM-squares. *M. paradoxus* is present in many regions of The Netherlands, including the dunes and the Holocene coastal districts, the different Pleistocene interior areas and in the paleogeographical older part of the south-

ern district of the province of Limburg. Records from the West Frisian Islands and also from the provinces of Flevoland and Drenthe are still lacking.

Unlike former articles by Gradl (1879a, 1879b) and Reineck (1909) and reference books by Spradbery (1973) and Edwards (1980) that report *Metoecus paradoxus* especially to occur in underground nests, we also recorded specimens from nests in buildings. Many authors did not take into account that subterranean nests were more frequently examined than 'aerial' nests (Hoffer, 1883; Tuck, 1897; Carl & Wagner, 1982). Ten of our 22 recent records came from pest control operators (PCOs) who destroyed wasp colonies under roofs, in chimneys and in cavity walls. The beetle was also captured twice by light traps in Zuid-Limburg and also once in Rhoon and The Staelduinse Bosch (province of Zuid-Holland). Both male and female beetles are attracted to light. Single beetles were collected in quite different localities: two specimens were found on a reed stem (*Phragmites australis* (Cav.) Steudel) in Zeist (province of

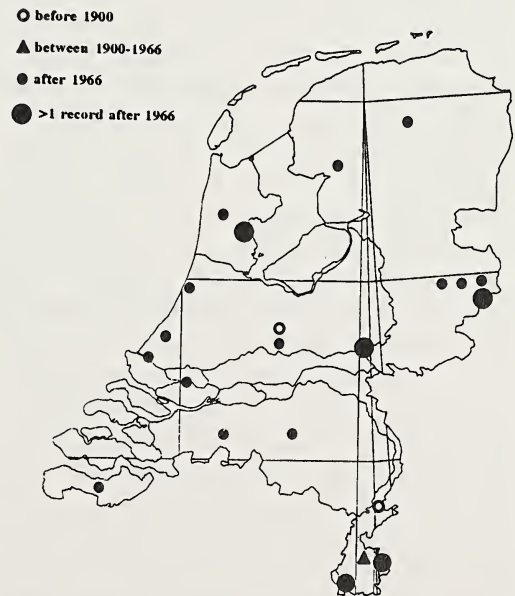


Fig. 3. Records of *Metoecus paradoxus* in The Netherlands. A record consists of an observation of a single beetle in the field or an infested colony of wasps with one or more parasitoids.

Utrecht) and on a leaf of *Scrophularia nodosa* L. in Leek (province of Groningen) respectively. The last one was collected as early as July, 25 (1992). A flying male beetle was captured with an insect net on the banks of the river Beerze near Boxtel (province of Noord-Brabant) (Peeters, 1990). Another female beetle had landed on a windowpane in Oldenzaal (province of Overijssel) and one specimen was encountered on a table in a office building in Leidschendam (province of Zuid-Holland). Although the data in this paper give a picture that is far from complete, the presence of hosts seems to be the only criterion for the occurrence of *M. paradoxus* in The Netherlands. Potential hosts such as the common *Vespula* species and the less abundant *Dolichovespula* species are found in all provinces.

Host species, parasitism and abundance

A summary of the host species as listed from the literature available from The Netherlands, the neighbouring countries and also from Japan, including some unpublished reports and observations, is given in table 1. Most records show that *M. paradoxus* is predominantly found in the nests of *Vespula vulgaris* (Linnaeus). Extensive studies show that the number of *V. vulgaris* nests infested by the parasitoid varies from 20 to 67% (Tuck, 1897; Spradbery, 1973; Carl & Wagner, 1982). Examination of many nests of *V. germanica* (Fabricius) often did not yield a single specimen: the number of infested nests of *V. germanica* does not exceed 13% (Carl & Wagner, 1982). In the Netherlands the use of *V. germanica* as host was confirmed by the presence of a female in Breda (province of Noord-Brabant) (leg. H. v.d. Krift, 1970; coll. A.P.J.A. Teunissen; table 1). Unfortunately, we were unable to record the host species of the records obtained via PCOs, because the wasps are not preserved and their nests destroyed. Records of specimens from the nests of *Vespula rufa* (Linnaeus), *Dolichovespula sylvestris* (Scopoli) and *D. media* (Retzius) could not be established. The latter species are considered to be potential hosts, but the nests were often found

to be under-represented in different samples. Carl & Wagner (1982) for the first time reported a record from a nest of *Dolichovespula saxonica* (Fabricius) in a survey of 54 nests. *Vespula lewisi* (Cameron) (= *V. flaviceps* (Smith)) is the host species in Hokkaidō, northern Japan (Hattori & Yamane, 1975).

Metoecus paradoxus was found in the nests from late July until the first week of October. In June and early July the beetles are absent (Hoffer, 1883; Carl & Wagner, 1982). Most observations of emerging specimens are reported from August. Old nests with a dead beetle were reported twice by PCOs in February.

The number of beetles per nest usually varied between 1 and 25. Only in a few cases the numbers exceeded 50 beetles per nest (table 1). The highest number of emerging beetles ever observed in The Netherlands was made by Langeveld (1992) in a visitor centre of a nature park in the dunes (table 1). The nest of *V. vulgaris* was hidden under a roof and the emergence of far over 80 beetles was observed. The beetles were caught close to the nest from late July until late August. Unfortunately, at this time, the nest was destroyed with insecticides (S.C. Langeveld, personal communication).

Discussion

Increase of records

There is no straightforward explanation for the increase of records of *Metoecus paradoxus* since 1966. One reason is simple, that entomologists have paid more attention to collect the species. However, Schmitz (1936) already noted that there have been made many unsuccessful attempts to collect the species in the southern part of the province of Limburg. Another possible explanation is the drastically increased urbanization of The Netherlands in this century providing more nesting space for wasps in buildings. At present, new findings of the beetle are in many cases related to a better co-ordinated, national control of urban pest insects. Most beetles recorded presently were found by PCOs in 'aerial' nests in office buildings and in roof and chimney constructions.

Table 1. Host species, period of observation, number of examined nests and presence or absence of *Metacoelus paradoxus*. In case the exact number of wasp nests examined and the presence of beetles were not given we labelled the records as "many", "some" or "several". Codes and abbreviations; in column 2, 6=June, 7=July, 8=August, 9=September, 10=October; in column 3-5; a: aerial nests, s: subterranean nests; in column 6; A= Austria, DK= Denmark, D= Germany, F= France; J= Japan, NL= The Netherlands, CH= Switzerland; GB= United Kingdom.

Host species	period of observations (months)	number of nests examined (subterranean or aerial)	nests with parasitoids	number of parasitoids counted per nest	locality	reference
<i>Vespula vulgaris</i> (L.)	7-10	±75 (s)	many	up to 78	Dijon, F	Rouget, 1873
	9-10	±25	several	up to 46	Egerthai, D	Gradi, 1879a,b, 1883
	6	5 (s)	0	-	Styria, A	Hoffer, 1883
	7	10 (s)	0	-	Styria, A	Hoffer, 1883
	7-9	many (s)	many	9->50	Styria, A	Hoffer, 1883
	10	some (s)	1	1	Styria, A	Hoffer, 1883
	-	several	1	not given	Cheshire, Denbighshire, GB	Newstead, 1891
	-	1 (s)	1	7	Roermond, NL	van der Hoop, 1896
	7-10	106	22	not given	Bury St. Edmunds, GB	Tuck, 1897
	-	5	4	resp.1;1;9;24	Leighton Buzzard, GB	Crawshaw, 1905
	8	1	1	118	Leipzig, D	Reichert, 1914
	8	1 (s)	1	55	Nordsjælland, DK	Suenson, 1921
	10	1	1	1	Valkenburg, NL	Everts, 1922; Schmitz, 1936
	10	1 (s)	1	1	Hulsberg, NL	Schmitz, 1936
	throughout the season	many	several	?	GB	Potter, 1965 (cited in Spradbery, 1973)
<i>V. germanica</i>	7-10	115 (a and s)	77	not given	Hertfordshire, GB	Spradbery, 1973
	7-9	220 (a and s)	106	1-54 (average: 2.2)	Styria, A; Rhine valley, D; Jura, CH	Carl & Wagner, 1982
	7-8	1 (a)	1	>>80	Amsterdam Waterleiding Dunes, NL	Langeveld, 1992; Knoters, 1994
	-	1	1	25	Enschede, NL	F. van Stuivenberg, 1981, unpubl.
	8	13 (a and s)	1 (a); 1 (s)	3 (a); 5 (s)	Purmerend, NL	H. Vogel, 1995, unpubl.
	8	1 (a)	1	12	Hagen, D	Drees, 1994
	7-9	±75 (s)	several	up to 34	Dijon, F	Rouget, 1873
	9-10	±18 (s)	several	up to 14	Egerthai, D	Gradi, 1879a, b, 1883
	7-10	60 (s)	0	-	Styria, A	Hoffer, 1883
	-	many	0	-	Cheshire, Denbighshire, GB	Newstead, 1891
	-	30	0	-	Bury St. Edmunds, GB	Tuck, 1897
	7	1	1	1 (not hatched)	Breda, NL	H.J. van der Krift, 1970, unpubl.
	-	40 (most s)	0	-	Hertfordshire, GB	Spradbery, 1973
	7-9	54 (s)	7	1-20 (average: 2.2)	Styria, A; Rhine valley, D; Jura, CH	Carl & Wagner, 1982
	8-10	5 (s)	0	-	Amsterdam, NL	W.R.B. Heitmans (1982-'94), unpubl.
<i>V. rufa</i>	-	7 (s)	0	-	Styria, A	Hoffer, 1883
	-	1	0	-	Bury St. Edmunds, GB	Tuck, 1897
	7-9	5	0	-	Rhine valley, D; Jura, CH	Carl & Wagner, 1982
	-	several	4	resp.5;16;21;86	Hokkaido, J	Hattori & Yamane, 1975
	6-8	54 (most a)	1	not given	Styria, A; Rhine valley, D; Jura, CH	Carl & Wagner, 1982
	6-8	many (a and s)	0	-	Styria, A	Hoffer, 1883
	-	3	0	-	Bury St. Edmunds, GB	Tuck, 1897
	6-9	15 (a)	0	-	Styria, A	Hoffer, 1883
	6-9	4 (a)	0	-	Rhine valley (D) and Jura (CH)	Carl & Wagner, 1982

V. flaviceps
Dolichovespula saxonica
D. sylvestris

D. media

However, recent findings include five field observations and three captures with light traps, of which six were clearly away from the urban areas.

Whether the population of *M. paradoxus* is growing is unknown. Older reports seldom present the percentage of nests infested with the parasitoid, so that the results of previous investigations cannot be compared with the newer studies on the abundance of the beetle. The most recent, extensive study by Carl & Wagner (1982) of the occurrence of the species in Switzerland, Germany and Austria shows that often about half of the examined nests of *Vespula vulgaris* is parasitized. However, the number of beetles per nest is usually very low compared to the numbers of available hosts. Colonies that were only investigated as late as September and October may have contained more parasitoids at earlier dates. Carl & Wagner (1982) show that colony size of the wasps, i.e. the number of nest cells, is not correlated to the number of beetles. This is not much of surprise, because it is not the number of wasps, but rather their foraging pattern which determines the number of triungulinids carried in. The behaviour of wasps forms the most crucial step in the beetle's life cycle. High numbers of parasitoids will be expected when many wasp foragers for wood-pulp repeatedly return to the same place(s) with triungulinids.

When many triungulinids enter the nest in a short period superparasitism may occur. Sometimes a dozen of fourth and fifth stage wasp larvae may contain more than one parasite of various stage of development, but only one larva per host survives (Hattori & Yamane, 1975). The beetle larvae do also not successfully develop on smaller (fourth instar) hosts (Švácha, personal communication). Superparasitism drastically suppresses the ultimate number of emerging beetles per nest and hence, it may be of great influence on the population dynamics of the parasitoid.

Host selection and differential parasitism

An intriguing question is whether *Metoecus*

paradoxus is able to choose between different host species. It is obvious that the parasitoid uses *Vespula vulgaris* more often than *V. germanica* as a host in areas where both wasp species coexist (table 1). *Vespula vulgaris* is about as common as *V. germanica* in all kinds of biotopes, but both species are much more common in both rural and urban areas than other *Vespula* and *Dolichovespula* species in western Europe (Spradbery, 1973; Edwards, 1980). Moreover, foragers in *Vespula* nests are usually much more numerous than those in *Dolichovespula* nests, so that the probability of encountering a *Vespula* species is much higher. Scarce findings of the beetle in *Dolichovespula* nests need not to rely upon selective behaviour only, but may also be explained by the relatively low availability of these host species.

Host selection can occur at two stages of the life cycle of a *Metoecus* beetle. First, there is the way of entering a host colony by the phoretic first larval instars and secondly, the selection of particular oviposition sites by the adult beetle. Choosing whether to attach to particular carriers offers a potential mechanism, if larvae are able to manipulate the process by selecting the preferred carriers (Heitmans et al., 1994). However, Švácha (personal communication) observed that *M. paradoxus* triungulinids respond to living insects as well as non-living objects, such as a dead bee or a camel hair brush. The larva reacts on approaching objects by raising its body and stretching the legs to all sides in the air so, that it only receives support of the tip of the abdomen, waiting. This behaviour does not indicate host selection, many offspring might starve on the wrong carrier, or not encounter a carrier at all. This is also indicated by the relatively low numbers of *M. paradoxus* in the wasp nests compared to the high fecundity of adult beetles (table 1).

Spradbery (1973) argues that differential parasitism in *M. paradoxus* may be due to the combination of beetle oviposition in the cracks of rotten, moist wood which is favoured by foraging *V. vulgaris*, whereas *V. germanica* utilizes sound and drier wood. How-

Table 2. *Metoecus* species of the world with information on host species and geographical distribution.

<i>Metoecus</i> species	Host species	Geographical distribution
<i>M. paradoxus</i> (Linnaeus)	<i>Vespula vulgaris</i> (L.) <i>V. germanica</i> (F.) <i>V. flaviceps</i> (Smith) <i>Dolichovespula saxonica</i> (F.)	NW and NE Palaearctic Regions: from the UK to central and northern Japan
<i>Metoecus</i> spec. 1	<i>D. media media</i> (Retzius)	NE Palaearctic Region: Hokkaidô, northern Japan
<i>M. vespae</i> Kôno	<i>V. rufa schrencki</i> (Rad.)	NE Palaearctic Region: Hokkaidô, northern Japan
<i>M. satanas</i> Schilder	<i>V. flaviceps</i> (Smith)	SE Palaearctic Region: Tibet, Nepal, southern China, central and southern Japan
<i>M. morawitzi</i> (Semenov)	unknown	SE Palaearctic Region: Chinese Turkistan
<i>M. javanus</i> Pic	unknown	SE Asia: West Java
<i>M. sumatrensis</i> Nakane & Yamane	<i>Vespa multimaculata</i> Pérez	SE Asia: West Sumatra
<i>Metoecus</i> spec. 2	<i>V. velutina</i> Lepeletier	SE Asia: West Java

ever, empirical evidence to test this proposition is hardly available. Chapman (1897) and Švácha (1994) observed that oviposition can be stimulated by offering half-rotten oakwood. Carl & Wagner (1982) found that oviposition also occurs on moist corrugated cardboard. So, oviposition may take place on different kinds of woody substrates, but it is not clear whether females show particular preferences. If *M. paradoxus* can select its host species it is not understood how they do it.

Differential parasitism is a form of niche differentiation that facilitates the coexistence of different sympatric species of *Metoecus*. For example, in Europe *Metoecus paradoxus* is mainly associated with *Vespula vulgaris* and less often with *V. germanica*, but in Japan this parasitoid is reported from *V. flaviceps* (tables 1-2). Here *M. paradoxus* is separated by the host species from another Asiatic and partly sympatric species *Metoecus vespae* Kôno that uses *Vespula rufa schrencki* (Radoszkowski) as host (Hattori & Yamane, 1975). The Asiatic *Vespula flaviceps* is related to the European *V. vulgaris* and *V. germanica*. Archer (1989) placed the latter species in the genus *Paravespula* Blüthgen. Likewise, both the Asiatic *Vespula rufa schrencki* and the European *V. rufa* are classified in the *V. rufa* group; Archer (1989) considered this taxon as

Vespula sensu stricto. So, it seems likely that both sympatric populations of *Metoecus paradoxus* and *M. vespae* attack different groups of hosts. Whether this also occurs in other *Metoecus* species remains to be studied. *Metoecus paradoxus* may have recently (in the geological time scale) dispersed westwards into Europe, mainly using *Paravespula* species even in regions where other competitive *Metoecus* species are absent. All other *Metoecus* species are known from the East Palaearctic Region and South-East Asia.

Knowledge of the hosts of other *Metoecus* species is slowly increasing. Makino (1982) first recorded an unidentified *Metoecus* species from *Dolichovespula media media* (Retzius) in Hokkaidô, northern Japan as did Carl & Wagner (1982) for *M. paradoxus* from a *D. saxonica* nest in western Europe (table 1). The more southern Asiatic species, *Metoecus satanas* Schilder, originally described from an arid climate in Kuku-Nor, East Tibet, is probably widely distributed both in arid and humid climates. In southern Japan the host of *M. satanus* is *Vespula flaviceps*, the same as for *M. paradoxus* in northern Japan (Hattori & Yamane, 1975; Matsuura & Yamane, 1990; table 2). Schawaller (1987) suggested that in Nepal *M. satanas* deposits her eggs on the bark of a *Rhododendron* species. It is possible

that in Japan *M. satanas* shares similar habitats with the northern species *M. paradoxus* or *M. vespae*, but it is insufficiently studied whether they also share the same hosts in those cases.

The host(s) of a second, southern Asiatic species, *Metoecus morawitzi* (Semenov) also described from an arid climate in Shache (=Yarkant), Chinese Turkestan, is unknown to us. The taxonomic status of *M. morawitzi* is doubtful; the species may be conspecific to *M. paradoxus* or to *M. satanas* (Schawaller, 1987). The holotype of *M. morawitzi* could not be traced by Yablokov-Khnzoryan (1976). *Metoecus morawitzi* and *M. satanas* may also be (partly) sympatric.

We further identified Van der Vecht's (1957) rhipiphorid from Telaga Warna, Puncak Pass, near Bogor, West-Java deposited in NNM as a true *Metoecus*. This species is the first known *Metoecus* found in a colony of the hornet *Vespa velutina* Lepelletier (table 2). *Metoecus sumatrensis* Nakane & Yamane from Lubuk Gadang, West Sumatra, is also found in a hornet's nest: *Vespa multimaculata pendleburyi* van der Vecht (Nakane & Yamane, 1990; table 2). Both *Vespa velutina* and *V. multimaculata* are phylogenetically closely related and are usually placed in the *V. affinis* group, but they belong to different sister groups (Archer, 1993). The *Metoecus* species of Van der Vecht (1957) is probably identical or closely related to *M. sumatrensis*. Nakane & Yamane (1990) described *M. sumatrensis* without comparing it with the type material of *M. javanus* Pic from Sukabumi, West Java (Pic, 1913). It is possible that both the *Metoecus* species of Van der Vecht (1957) and *M. sumatrensis* are synonyms of *M. javanus*. Further study should elucidate the taxonomic status of the three Indonesian species of *Metoecus*, which may all be specialized in attacking (a particular group of) hornets.

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References

- ARCHER, M.E., 1989. A key to the world species of the Vespinae (Hymenoptera). – *Res. Monogr. Coll. Ripon & York St. John* 2: 1-75.
- ARCHER, M.E., 1993. A phylogenetic study of the species of the genus *Vespa* (Hymenoptera: Vespinae). – *Ent. scand.* 24: 469-478.
- BRAKMAN, P.J., 1966. Lijst van Coleoptera uit Nederland en het omliggend gebied. – *Monogr. ned. ent. Ver.* 2: i-x, 1-219.
- CARL, K.P. & A. WAGNER, 1982. Investigations on *Spheco-phaga vesparum* Curtis (Ichneumonidae) and *Metoecus paradoxus* L. (Rhipiphoridae) for the biological control of *Vespula germanica* F. (Vespidae) in New Zealand. Silwood Park, UK: Commonwealth Institute of Biological Control, Working Report: 1-15.
- 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: 18-20.
- CHAPMAN, T.A., 1897. Sketch on the life-history of *Metoecus* (*Rhipiphorus*) *paradoxus*. – *Entomologist's Rec. J. Var.* 9: 321-322.
- CLAUSEN, C.P., 1940. *Entomophagous insects*: 1-688. McGraw-Hill, New York.
- CRAWSHAY, G.A., 1905. A large community of *Vespa vulgaris*. – *Entomologist's mon. Mag.* 41: 8-10.
- 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.
- EDWARDS, R., 1980. *Social wasps. Their biology and control*: 1-342. East Grinstead.
- EVERTS, E.J.G., 1876. Verslag 36e Zomervergadering NEV. – *Tijdschr. Ent.* 19: 27.
- EVERTS, E.J.G., 1922. *Coleoptera Neerlandica* 3: v-xviii, 1-668. Nijhoff, 's-Gravenhage.

- GRADL, H., 1879a. Biologische Notizen. – *Ent. Nachr.* 5: 224-225.
- GRADL, H., 1879b. *Metoecus paradoxus* L., weitere Beobachtungen. – *Ent. Nachr.* 5: 326-327.
- GRADL, H., 1883. Ad *Metoecum* et *Phytodectas*. – *Ent. Nachr.* 9: 68-69.
- HATTORI, T. & SK. YAMANE, 1975. Notes on *Metoecus paradoxus* and *M. vespae* parasitic on the *Vespula* species in northern Japan (Coleoptera, Rhipiphoridae; Hymenoptera, Vespidae) (I) – *New Entomologist* (Ueda) 24: 1-7.
- HEITMANS, W.R.B., T.M.J. PEETERS, J. DE ROND & J. SMIT, 1994. A survey of the Western European Rhipiphoridae including the first record of a Macroasiagon species in The Netherlands (Coleoptera). – *Ent. Ber., Amst.* 54: 201-211.
- HOFFER, E., 1883. Über die Lebensweise des *Metoecus paradoxus* L.. – *Ent. Nachr. Dresden* 9: 45-49.
- HOOP, D. VAN DER, 1896. Verslag 29e Wintervergadering NEV – *Tijdschr. Ent.* 39: 89.
- KNOTTERS, C., 1994. Waaikever, Wespe-moorder, een zeldzame keversoort. – *Natura* 91: 195.
- LANGEVELD, S.C., 1992. *Metoecus paradoxus*: vreemde gasten in het bezoekerscentrum. – *Nieuwsbrief Natuuronderzoek Amsterdamse Waterleidingduinen* 2: 8.
- LUCHT, W.H., 1987. *Die Käfer Mitteleuropas, Katalog*: 1-342. Goecke & Evers, Krefeld.
- MAKINO, S., 1982. Nest structure, colony composition, and productivity of *Dolichovespula media media* and *D. saxonica nipponica* in Japan (Hymenoptera, Vespidae). – *Kontyû* 50: 212-224.
- MATSUURA, M. & SK. YAMANE, 1990. *Biology of vespine wasps*: 1-303. Springer, Berlin.
- NAKANE, T. & SK. YAMANE, 1990. A new species of the genus *Metoecus* Gerstaecker (Coleoptera, Rhipiphoridae) from West Sumatra, Indonesia. – *South Pacific Study* 10: 305-308.
- NEWSTEAD, R., 1891. Insects, &c., taken in the nests of British Vespidae. – *Entomologist's mon. Mag.* 27: 39-41.
- PEETERS, T.M.J., 1990. De zonderlinge waaierkever. – *Veelpoot* 1 (1): 24-25.
- PIC, M., 1913. Descriptions de 29 espèces et de plusieurs variétés. – *Mélang. exot.-ent.* 5: 5-20.
- POTTER, N.B., 1965. *Some aspects of the biology of Vespula vulgaris* L. Ph. D. Thesis, University of Bristol. [cited in Spradbery, 1973]
- RAMDOHR, K., 1813. Rhipiphorus paradoxus (in Wespennestern). – *Mag. Ent., Halle* 1: 137.
- REICHERT, A., 1914. Die Parasiten unseren heimischen Wespen. – *Illustr. Z. Leipzig*, no. 3682.
- REINECK, G., 1909. Über die Lebensweise und den Fang von Rhipiphorus paradoxus L. und Velleius dilatatus F. – *Ent. Rdsch.* 26: 89-90.
- ROUGET, A., 1873. Sur les Coléoptères parasites des Vésrides. – *Mém. Acad. Dijon* (3) 1: 161-288.
- RÜSCHKAMP, F., 1919. Coleoptera Neerlandica und die Lokalfauna Süd-Limburgs. – *Natuurhistorisch Genootschap in Limburg, jaarboek* 1919: 35-80.
- SCHAWALLER, W., 1987. Rhipiphoridae aus dem Nepal-Himalaya (Insecta: Coleoptera). – *Cour. Forschungsinst. Senckenberg* 93: 477-479.
- SCHILDER, F.A., 1924. Rhipiphoriden-Studien. VI. Revision des Genus *Metoecus* – *Dt. ent. Z.* 1924: 237-244.
- SCHMITZ, P., 1936. Verslag van de maandelijke vergadering op woensdag 7 Oct. 1936. – *Natuurh. Maandbl.* 25: 122.
- SPRADBERY, J.P., 1973. *Wasps. An account of the biology and natural history of solitary and social wasps*: 1-408. Sidgwick & Jackson, London.
- ŠVÁCHA, P., 1994. Bionomics, behaviour and immature stages of *Pelecotoma fennica* (Paykull) (Coleoptera: Rhipiphoridae). – *J. nat. Hist.* 28: 585-618.
- SUENSON, E., 1921. Om Klæklingen af *Metoecus paradoxus* L. – *Ent. Medd.* 13: 17-22.
- TUCK, W.H., 1896. Inquiline and other inhabitants in nests of aculeate Hymenoptera. – *Entomologist's mon. Mag.* 32: 153-155.
- TUCK, W.H., 1897. Coleoptera, &c., in the nests of aculeate Hymenoptera. – *Entomologist's mon. Mag.* 33: 58-60.
- VECHT, J. VAN DER, 1957. The Vespinae of the Indo-Malyan and Papuan areas (Hymenoptera, Vespidae). – *Zool. Verh. Leiden* 34: 1-83.
- 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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