THE TAXONOMIC POSITION OF THE PACHYNEURINI (CHALCIDOIDEA, PTEROMALIDAE) AS JUDGED BY CHARACTERISTICS OF COURTSHIP BEHAVIOUR

by

J. VAN DEN ASSEM & M. J. GIJSWIJT

ABSTRACT

Assem, J. van den & M. J. Gijswijt, 1989. The taxonomic position of the Pachyneurini (Chalcidoidea, Pteromalidae) as judged by characteristics of courtship behaviour. — Tijdschrift voor Entomologie 132: 149-154, tabs 1-2. [ISSN 0040-7496]. Published 3 July 1989.

Characteristics of courtship behaviour seem to be of considerable interest from a comparative point of view. A syndrome of behavioural features was used for separating a group of pteromalids (*viz.* the Pachyneurini) from the Pteromalinae, a subfamily to which they were formerly assigned.

Key words. – Pteromalidae; Pachyneurini; taxonomy; behaviour.

Dr. J. van den Assem, Zoological Laboratory, Division of Ethology, University of Leiden, P.O. Box 9516, 2300 RA Leiden, The Netherlands.

INTRODUCTION

Current classification of the Chalcidoidea is still far from what must be the ultimate aim: an arrangement of taxa reflecting the group's phylogeny. Comparative studies of chalcidoid mating behaviour can make a contribution to this end (Gauld 1986) because they provide, in principle, independent tests of classifications that were based on morphological criteria only (the usual practice). Features of behaviour may serve as characters on different levels. Such features are often species-characteristic; sibling species in particular may be identified more easily on characteristics of mating behaviour than of morphology (e.g. Van den Assem & Povel 1973). Just as well, behaviour elements can serve to separate genera or families (e.g. Van den Assem et al. 1982b). Actually, the use of behavioural features as criteria of classification is of a long standing (e.g. the classification of Anatidae – ducks and relatives –: Heinroth 1910, Lorenz 1941). In the entomological practice severe limitations abound since living specimens are not usually the kind of material at the disposal of taxonomists and, moreover, far from all species will "behave" under laboratory conditions. However, this is no excuse; phylogenetic classifications require supportive evidence from various biological sources.

Those components of courtship repertoires which function as intra-specific signals qualify as useful characters in the first place. They are supposed to have acquired their more or less fixed quality during evolution in a process called ritualisation. Fixation means minimal variation in performance – a necessary quality of unambiguous signals and, likewise, of reliable diagnostic characters. Courtship signals produced by chalcidoid males are, at least partly, of a chemical and/or of an acoustic nature, and cannot be recorded or analysed without sophisticated equipment (Van den Assem 1986). On the other hand, signal emission usually coincides with overt movements of one or more limbs, and these movements can be described and quantified in a simple way (in terms of number of occurrences or of durations; e.g. Barrass 1960; Martin & Bateson 1986).

Previous studies of chalcidoid mating behaviour have corroborated current classifications (e.g. Kogan & Legner 1970, Van den Assem & Povel 1973), or suggested changes (e.g. Van den Assem et al. 1982a, Dahms 1984, In den Bosch & Van den Assem 1986). In the present paper we want to point out an apparent discrepancy, and suggest a change.

MATERIAL AND METHOD

Parasitized hosts were collected in the field and individual parasitoids were isolated prior to emergence, as far as possible, to obtain virgin specimens. (Females of several species are known to

mate only once in a lifetime; in some species they appear no longer attractive to males following mating. Obviously, virgin specimens are necessary for studying courtship and mating behaviour in such cases). A list of the material that was used for the observations mentioned in this paper is given in the appendix.

All observations were made with a low-power binocular microscope. Prior to the observations, a male and a female specimen were introduced into a small, perspex cell that was closed with a glass cover slip. The cell's diameter (ca 2.5 cm) corresponded to the visual field of the microscope. Magnifications of 10 or 15 × proved to be sufficient. Many sequences of courtship and mating behaviour were recorded on video tape.

COURTSHIP BEHAVIOUR OF PTEROMALINAE

Among taxonomists there is consensus that several large families of Chalcidoidea (e.g. Encyrtidae, Eulophidae, Eurytomidae) represent monophyletic entities while others do not (e.g. Pteromalidae, Torymidae). Many lower ranking taxa appear to be non-holophyletic assemblages: the Pteromalinae, a sub-family of Pteromalidae, may serve as an example. Clearly, the Pteromalinae are a "rest" group. Positive morphological criteria for separating Pteromalinae from alternative groups do not exist. Unifying behavioural characteristics do not exist either. Yet, within this group, several clusters of distinctly related genera can be defined, some of which were already recognized by Thomson (1878). Similar clusters are apparent in the checklist of Chalcidoidea by Bouček & Graham (1978): genera are arranged in a non-random order, suggestive of varying degrees of relatedness (never explicitly stated by the authors). Examples are: *Psilonotus-Anogmus-Mesopolobus; Nasonia-Trichomalopsis (= Eupteromalus); Caenasis-Cecidostiba-Hobbya-Ablaxia-Aggelma.* Details of courtship and mating procedures give support to these assumed relationships (unpubl. data).

For the Pteromalinae as a whole, unifying features of courtship and mating behaviour cannot be defined. Yet, for what seems to be a large majority, an assemblage that we refer to as the Pteromalinae s.s., such features do exist. Earlier (Van den Assem 1974), this group has been characterized as "those pteromalids in which the male takes up a frontal position on the female for courtship (by placing his front feet on her head) and produces a sequence of motor coordinations in which the antennae are moved synchronously as each other's mirror image, the general direction of these movements being up and down; the female indicates her readiness to copulate by a special antennal signal (she draws her flagellae tightly to her head capsule) and maintains a frozen posture for some time". This definition – which was based on observations of 14 species – may still serve, although the importance of mouthpart extrusions (see below) as taxonomic criteria was not appreciated at the time.

The elements of courtship and mating which characterize the Pteromalinae s.s. are mentioned below. Actually, it is the syndrome of elements that is characteristic; taken separately, alle features can be found in many other groups as well. Our observations now refer to 37 species (mentioned in the appendix) belonging to the 20 genera enumerated in table 1. We assume that many more can be added to the Pteromalinae s.s. once courtship and mating procedures are known. Our prediction is that the rules which refer to general characteristics of movements, temporal structure, and frontal position of the male (see below) will apply to all near-relatives of the genera mentioned in table 1.

Characteristic behaviour patterns

Courtship position. – The male courts from a frontal position on top of the female, with its fore tarsi placed on the female's head. The precise placement differs between species (e.g. laterally on the female's eyes, on its nape, near the base of its scapes, etc.). By necessity, a male has to back up from its courtship position before it can copulate.

Antennal movements. – The male's antennae, whatever the precise motor coordinations, move as each other's mirror image. The details of these movements, and the corresponding temporal patterns, are usually characteristic for a species or for a group of species. Several kinds of movements are involved; one of them is most conspicuous: the antennal sweep, a swift up-and-down large amplitude movement, and performed just before or synchronously with a mouthpart extrusion (below).

Extrusion of the mouthparts. – The male extrudes (lowers) its mouthparts periodically in a conspicuous way (as if "vomitting"). Extrusions may be combined with head-nodding movements. If so, an extrusion coincides with the upstroke of a nod.

Female receptivity signal. – At the onset of sexual receptivity (i.e. coinciding with the exposure of the genital orifice) the female lowers its antennae (previously held horizontally). It draws the flagellae tightly in to the front of its head (flagellae pointing downwards).

Table 1. Genera of Pteromalinae s.s.; courtship and mating procedures were observed in one or more species

Anisopteromalus Ruschka, 1912
Anogmus Förster, 1856
Caenasis Förster, 1856
Cecidostiba Thomson, 1878
Dibrachys Förster, 1856
Dinarmus Thomson, 1878
Hobbya Delucchi, 1957
Hypopteromalus Ashmead, 1900
Lariophagus Crawford, 1909
Meraporus Walker, 1834
Mesopolobus Westwood, 1833
Muscidifurax Girault & Sanders, 1910
Nasonia Ashmead, 1903
Peridesmia Förster, 1856
Psilonotus Walker, 1834
Pteromalus Swederus, 1795 (including the subgenus *Habrocytus* Thomson, 1878)
Stenomalina Ghesquière, 1946
Trichomalopsis Crawford, 1913
Trichomalus Thomson, 1878
Trychnosoma Graham, 1957

Duration of genital contact. – In Pteromalinae s.s. the duration of genital contact (at 20 °C) is relatively long, ranging between 10 secs (in e.g. *Nasonia*) and ca 1 minute (in e.g. *Lariophagus*).

An experimental analysis of the displays of a few species of Pteromalinae s.s. has revealed (Van den Assem 1986) that mouthpart extrusions are associated with the release of chemical stimuli (pheromones). Head-noddings probably enhance the effects of pheromone release. There are (slight) differences in the precise motor coordinations between clusters of related genera (e.g. the nodding movements of *Anogmus – Mesopolobus* species differ from those of *Nasonia vitripennis* and relatives). Several clusters include genera with nodding and non-nodding species. Also, within certain genera (e.g. *Habrocytus*) species may differ in the extent of nodding. Apparently, nodding has been "invented" a number of times, which means that not all nods are truly homologous.

Courtship behaviour of Pachyneurini

Courtship displays in one section of Pteromalinae (i.e. the Pachyneurini sensu Ashmead, 1904) do not correspond to those of the Pteromalinae s.s. We believe that the differences are of a fundamental kind (see Discussion), and we suggest to separate the Pachyneurini from the Pteromalinae and preferably raise it to sub-family rank, the Pachyneurinae. Ours is not the only argument: Copland & King (1972) found consistent differences in the

structure of the female reproductive system of *Pachyneuron* versus other species of Pteromalinae. Moreover, Bouček and Graham (1978) placed the Pachyneurini at the end of the Pteromalinae in their checklist; not because they believed it to be the most apomorphic section, but because it was unclear where to place it at all (Bouček, pers. comm.). Earlier, Bouček (1961) has suggested that the (then newly described) genus *Vrestovia* was close to *Synedrus* Graham, 1956, *Ablaxia* Delucchi, 1957 or *Caenasis* Förster, 1856, but this suggestion was dropped later. Features of courtship would not support such a relationship either: *Caenasis* males court in the way of Pteromalinae s.s.; males of the two *Vrestovia* species we have seen do not.

Judged by general characteristics of their mating behaviour, the Pachyneurini represent a natural unit. The diagnostic syndrome comprises the following features:

Characteristic behaviour patterns

Courtship position. – The male's fore tarsi are placed at the frontal edge of the female's pronotum (on its "shoulders") or on top of its thorax. In *Pachycrepoideus vindemmiae* the placement is variable: sometimes on the female's thorax, sometimes on its head (but never stereotypical on the head).

Phase shifts. – There are periodic shifts in the orientation of the courting male with respect to the female below. Foreward-backward movements with the entire body occur which coincide with bending-stretching movements of the fore legs while the fore tarsi remain in the same place throughout. (These postural changes are the equivalents of the periodic low phase-high phase shifts described by Van den Assem et al. 1982b.)

Antennal movements. – All displays include movements with the antennae; however, not in all phases are the antennae moved as each other's mirror image. There is no antennal sweep of the kind seen in Pteromalinae s.s., but there is a more distinct forward-backward component in the antennal motions.

Mouthpart movements by the male. – Forward-backward movements are always present, but of an inconspicuous kind which is easily overlooked. There are no real extrusions which suggest "licking" actions, as in the Pteromalinae s.s., and the motor patterns involved differ greatly. (In the Pteromalinae s.s. mouthpart extrusion is a prominent element of a male's display.)

Position of the female antennae. – During courtship, females point their antennae more or less vertically upward, forming an acute figure V. This posture never occurs in female Pteromalinae s.s.

Mouthparts female. – Typically, females hold their mandibles agape as soon as they are mounted.

Female antennal signal and duration of genital contact. – Antennal movements made by the female at the onset of receptivity occur in some species, but judged from direct observations it seems doubtful that they serve a signal function as found in Pteromalinae s.s. Backing up by courting males may involve considerable delays. Antennal movements by the female were absent in *Vrestovia* and *Pachyneuron* species (antennae remain in the upright position throughout) and of a variable quality in *Pachycrepoideus*, from upright to horizontal or below. In *Toxeumorpha* the antennae go into a low position. But even when low, the ensuing posture is less "complete" than in the Pteromalinae s.s. (the flagellae are not tightly drawn in to the front of the head) (table 2).

The duration of genital contact varies between species. In most it is very short (a matter of a few seconds only); in *Toxeumorpha* contacts may last for over a minute.

DISCUSSION

The courtship procedures of species of Pteromalinae s.s. have many features in common. Species of Pachyneurini were found to be different in this respect, not just in a matter of degree but in a fundamental way because they lack a number of what we consider to be synapomorphic features.

By examining the display behaviour of many species, it is possible to uncover phylogenetic trends (i.e. successively more advanced combinations of behavioural traits). Similar trends can be traced in several large families of Chalcidoidea, suggestive of parallel developments. Two of these are relevant in the context of this paper: the switch of the male's courtship position from the rear to the front, in connection with the development of a (secondary) receptivity signal, and the omission of periodic shifts in the position of the courting male relative to the female (Van den Assem 1986). In this respect the Pteromalinae s.s. qualify as synapomorphic: the position of the courting male has moved to the extreme front, the male's head is just above the female's antennae and the male releases a necessary, receptivity inducing stimulus periodically – probably a product of its mandibular glands – by means of extruding its mouthparts. Head-noddings enhance the effectiveness of stimu-

Table 2. Genera and species (in alphabetical order) which were observed to deviate from the courtship and mating procedures of the Pteromalinae s.s.

Pachycrepoideus Ashmead, 1904; *Pachyneuron* Walker, 1833; *Toxeumorpha* Girault, 1915; *Vrestovia* Bouček, 1961.

Pachycrepoideus vindemmiae (Rondani): Curepe, Trinidad, from pupae of an antomid fly September 1971; Hanoi, Vietnam, from pupae of *Drosophila* spec. Laboratory culture on *D. melanogaster*.

Pachyneuron muscarum (L.): Vleuten, The Netherlands, parasite of *Leptomastix dactylopii* Girault, on *Planococcus citri* in a glasshouse; May 1988.

Pachyneuron planiscuta Thomson: Leiden, The Netherlands, emerged from reed stalks, host unknown, March 1974.

Toxeumorpha nigricola (Ferriere): Natal, Rep S Africa, from pupae of *Zaprionius* spec. in tomato fields, 1980. Laboratory stock on *D. melanogaster*.

Vrestovia fidenas (Walker). Zuidwijk, Wassenaar The Netherlands, on pupae of *Drosophila* spec.; April 1987.

Vrestovia spec.: Amherst. Mass USA, on pupae of *Drosophila* spec.; October 1979. (Bouček in litt).

lus release. Females have developed a secondary receptivity signal which is a sufficient stimulus for the male to stop courting and back up (Van den Assem & Jachmann 1982). Phase-shifts in the male's position are absent, males court in a low-phase position throughout. Pachyneurini give evidence of a less advanced condition. The position of the courting male is less extreme; males change their posture periodically during a display (without shifting the position of the forefeet); there is no evidence for pheromonal stimulation by way of specialized movements with the mouthparts. A secondary antennal signal is absent, or, where antennal movements occur, evidence that males take them as a cue for switching to copulatory behaviour is missing. Actually, we often observed a delay between the moment of overt receptivety (the moment the female exposes its genital orifice) and the male backing up, and it seems to be longer, on average, than in the Pteromalinae s.s., although in this group as well males are variable in this respect. To delay backing up to copulate may have serious consequences for a courting male because sneaking competitors may take precedence and mate first (which always means: inseminate more successfully). In this respect the procedures of *Pachyneuron muscarum* are of interest. Males produce a single courtship cycle, back up immediately and attempt to copulate. If the female is not yet receptive then the frontal courtship position is taken up again, a new cycle follows, etc. A similar organization of the courtship display has been observed in *Pteromalus*

puparum; it was hypothesized that it might be understood as an adaptation to a high level of competition (Van den Assem 1974). *Pteromalus* is a parasitoid of the chrysalids of butterflies from which hundreds of wasps may emerge more or less synchronously. The same explanation may hold for the *Pachyneuron muscarum* display. Moreover, males hold their wings low while backing up, in a cape-like fashion (as do some tetrastichids in an attempt to ward off competitors) thus providing an additional argument. This rapid-pendulum type of temporal organization will prolong the time required to induce receptivity in a female but this loss will probably be more than evened out by losing a copulation to a competitor less often.

For *Pteromalus*, it was argued that the pendulum procedures were probably not an original feature (*Pteromalus* females have a fully developed antennal signal), but for *Pachyneuron* it may be different. Courting males provide conspecific females with stimuli that may induce sexual receptivity. In probably genuinely primitive groups (such as Cerocephalinae) males stay in a caudal position throughout, and a successful courter can thus perceive the onset of receptivity immediately (it receives a tactile stimulus, the effect of the female's abdomen-raising). Pachyneurini males are small enough, and the position on the female is enough to the front to make a direct perception of receptivity unlikely. The most effective strategy would then be to make an inspection on the spot repeatedly, which is what *Pachyneuron muscarum* males do. However, males of other species, which likewise lack a secondary signal, do produce a sequence of cycles before backing up. We have no idea on what cues they might act.

We have argued that the Pachyneurini should be separated from the Pteromalinae and be made a sub-family in its own right. Judged by characteristics of display behaviour, the Pteromalidae comprise an array of subfamilies which combine original character states (e.g. Cerocephalinae, Spalanginae), highly derived character states (Pteromalinae s.s.), or intermediate conditions (e.g. Miscogastrinae, Asaphinae). The Pachyneurini belong to the latter category but they do not fit into one of the existing subfamilies. The conspicuous position of the females' antennae offers no cues (similar positions are observed in many groups throughout the Chalcidoidae). The movements of the males' mouthparts do not provide cues either, nor do characteristics of the respective repertoires. For the time being the Pachyneurini should be kept apart from other groups, awaiting a more profound analysis of mutual relationships.

REFERENCES

Assem, J. van den, 1974. Male courtship patterns and female receptivity signal of Pteromalidae, with a consideration of some evolutionary trends and a comment on the taxonomic position of *Pachycrepoideus vinde-miae*. – Netherlands Journal of Zoology 24: 253-278.

Assem, J. van den, 1986. Mating behaviour in parasitic wasps. – In: Insect Parasitoids (J. K. Waage & D. Greathead eds). 13th Symposium Royal Entomological Society London: 137-167.

Assem, J. van den, H. A. J. in den Bosch & E. Prooy, 1982a. *Melittobia* courtship behaviour: a comparative study of the evolution of a display. – Netherlands Journal of Zoology 32: 427-471.

Assem, J. van den, M. J. Gijswijt & B. K. Nübel, 1982b. Characteristics of courtship and mating behaviour used as classificatory criteria in Eulophidae – Tetrastichinae, with special reference to the genus *Tetrastichus*. – Tijdschrift voor Entomologie 125: 205-220.

Assem, J. van den & F. Jachmann, 1982. The coevolution of receptivity signalling and body-size dimorphism in the Chalcidoidea. – Behaviour 80: 96-105.

Assem, J. van den & G. D. E. Povel, 1973. Courtship behaviour of some *Muscidifurax* species (Hym. Pteromalidae): a possible example of a recently evolved ethological isolating mechanism. – Netherlands Journal of Zoology 23: 465-487.

Barrass, R., 1960. The courtship behaviour of *Mormoniella vitripennis*. – Behaviour 15: 185-209.

Barrass, R. 1976. Courtship behaviour in *Meraporus graminicola* and other Pteromalinae. – Physiological Entomology 1: 77-81.

Bosch, H. A. J. in den & J. van den Assem, 1986. The taxonomic position of *Aceratoneuromyia granularis* (Hym. Eulophidae), as judged by characteristics of its courtship behaviour. – Systematic Entomology 11: 19-23.

Bouček, Z., 1961. Beiträge zur Kenntnis der Pteromaliden-Fauna von Mitteleuropa, mit Beschreibungen neuer Arten und Gattungen (Hym). – Acta Entomologica Musei Nationalis Pragae 34: 55-95.

Bouček, Z. & M. W. R. de V. Graham, 1978. Hymenoptera. – Checklist of British insects (G. S. Kloet & W. D. Hincks eds) 4: 67-110.

Copland, M. J. W., & P. E. King, 1972. The structure of the female reproductive system in the Pteromalidae. – Entomologist 105: 7-96.

Dahms, E. C., 1984. Revision of the genus *Melittobia* (Chalcidoidea Eulophidae) with the description of seven new species. – Memoirs of the Queensland Museum 21: 271-336.

Gauld, I. D., 1986. Taxonomy, its limitations and its role

in understanding parasitoid biology. – In: Insect Parasitoids (J. K. Waage & D. Greathead, eds). 13th Symposium Royal Entomologial Society London: 137-167.

Heinroth, O., 1910. Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. – Internationational Congress of Ornithology 5: 589-702.

Kogan, M. & E. F. Legner, 1970. A biosystematic revision of the genus *Muscidifurax* (Hym. Pteromalidae) with descriptions of four new species. – Canadian Entomologist 102: 1268-1290.

Lorenz, K., 1941. Vergleichende Bewegungsstudien an Anatiden. – Journal für Ornithologie 89: 194-294.

Martin, P. & P. Bateson, 1986. Measuring behaviour. An introductory guide: 1-200. – Cambridge University Press.

Miller, M. C., R. White & C. Smith, 1973. Courtship behaviour of *Peridesmia discus*. – Entomophaga 17: 20-25.

Thomson, C. G., 1878. Hymenoptera Scandinaviae V. – Lund.

APPENDIX

Anisopteromalus calandrae (Howard): Savannah Georgia USA, on weevils in wheat stored in warehouse; January 1971. Laboratory culture on *Sitophilus*.

Anogmus hohenheimensis (Ratzeburg): Oberstdorf BRD, on cecidomyids in cones of *Picea abies*; January 1979.

Anogmus piceae (Ruschka): Kiental Switzerland, on idem; August 1978.

Anogmus strobilorum Thomson: Oberstdorf BRD, on idem; February 1977.

Anogmus vala (Walker): Oberstdorf BRD, on idem; February 1977.

Caenasis lauta (Walker): Leiden The Netherlands, from galls of *Cynips divisa*; February 1986.

Cecidostiba semifascia (Walker): Mt Ventoux France, from galls on *Quercus* spec.; August 1978.

Dibrachys boarmiae (Walker): Meyendel Wassenaar The Netherlands, parasitic on a dipterous parasite of an earwig inside stems of *Asparagus* spec.; April 1978; laboratory culture on *Calliphora*.

Dibrachys cavus (Walker): Wageningen The Netherlands, from *Apantheles* pupae on *Pieris* spec.; March 1972.

Dinarmus basalis (Rondani): Slough England, from a laboratory culture on *Callosobruchus chinensis* in beans; May 1981.

Habrocytus bedeguaris Thomson: Bentheim BRD, from galls on *Rosa* spec.; April 1974.

Habrocytus elevatus (Walker): Oberstdorf BRD, on trypetids in flowerheads of *Centaurea* spec.; February 1978; Oegstgeest The Netherlands, on idem in flowerheads of *Arctia* spec.; June 1978.

Habrocytus sequester (Walker): Wijster The Netherlands, from seedpods of *Linaria vulgaris*; September 1977.

Hobbya stenonota (Ratzeburg): Mt Ventoux France, from galls on *Quercus* spec.; August 1978.

Hypopteromalus tabacum Ashmead: McNeil in litt 1974.

Lariophagus distinguendus (Förster): Leiden The Netherlands, obtained as an infection of our laboratory culture of *Sitophilus granarius* on wheat.

Meraporus graminicola Walker: quoted by Barrass (1976).

Mesopolobus rhabdophagae (Graham): Wassenaar The Netherlands, from galls on *Salix repens*; July 1983.

Mesopolobus dubius (Walker): Antequera Spain, from galls of *Plagiotrochus* on *Quercus* spec.; March 1978.

Mesopolobus mediterraneus (Mayr): Antequera Spain, idem.

Mesopolobus fasciiventris Westwood: Bunde The Netherlands, from galls of *Pediaspis aceris* on *Acer*; June 1974.

Muscidifurax raptor Girault & Sanders Riverside California USA, obtained from laboratory cultures on *Musca domestica*, details quoted in Kogan & Legner (1970).

Muscidifurax raptorellus Kogan & Legner: idem.

Muscidifurax uniraptor Kogan & Legner: idem; September 1975.

Muscidifurax zaraptor Kogan & Legner: idem, as *M. raptor*.

Nasonia vitripennis (Walker): Leiden The Netherlands, on pupae of *Calliphora* spec.; August 1971.

Nasonia spec. nov.: Rochester NY USA, from bird nests in nestboxes; August 1987 (this species has long-winged males).

Peridesmia discus (Walker): in Miller, White & Smith (1973), and Miller in litt, 1974.

Psilonotus achaeus Walker: Meyendel Wassenaar The Netherlands, from *Semudobia* galls on *Betula* spec.; October 1976; Oberstdorf BRD, idem; March 1978; 's Graveland The Netherlands, idem; April 1985.

Psilonotus adamas Walker: Meyendel Wassenaar The Netherlands, idem; August 1976.

Pteromalus puparum (L): Ales France, from chrysalids of *Pieris* spec.; August 1971.

Pteromalus venustus Walker: Lethbridge Alberta Canada, from pupae of *Megachile rotundata*; November 1974.

Stenomalina liparae (Walker): Leiden The Netherlands, from galls of *Lipara lucens* in *Phragmites* spec. January 1971.

Trichomalopsis (Eupteromalus) micropterus (Lindemann): Oegstgeest The Netherlands, on drosophilids in apple orchard, August 1986.

Trichomalopsis (Eupteromalus) spec.: Riverside California USA, from a laboratory culture on *Drosophila* spec. from locally collected material.

Trichomalopsis (Eupteromalus) tigasis (Walker): De Lemmer The Netherlands, collected as adults on a window; October 1973.

Trychnosoma punctipleura (Thomson): Oberstdorf BRD, from cecidomyids in cones of *Picea abies*; February 1977.