*Eur. J. Entomol.* **98**: 195–199, 2001
ISSN 1210-5759

# Dorsal sex pheromone glands in female Geometridae (Lepidoptera: Geometroidea): a new apomorphy of the family

AMEL BENDIB

Muséum national d'Histoire naturelle, Laboratoire d'Entomologie, ESA-8043 CNRS, 45, rue Buffon, F-75005 Paris, France; e-mail: bendib@mnhn.fr

**Key words.** Lepidoptera, Geometroidea, dorsal sex pheromone glands, female, apomorphy

**Abstract**. The female Geometridae are characterized by the presence of saccular pheromone glands. They are paired structures, invaginated anteriorly and located dorso-laterally to the rectum. The opening of dorsal saccular glands varies from wide to narrow and opens up on the 9th abdominal segment. These saccular glands are widely distributed in the family. Morphological variability of these glands can be observed. In certain species of Geometridae, the paired glands vary from short to long. Pheromone production is an established function of these glands, in the case of *Rheumaptera hastata.*

## INTRODUCTION

The sex pheromone-producing glands in Lepidoptera are usually found in the intersegmental fold between the eighth and ninth abdominal segments. These glands are derived from hypodermal cells and are described by several authors: e.g. Urbahn (1913), Götz (1951), Steinbrecht (1964), Weatherston & Percy (1968), Roelofs & Feng (1968), Jefferson & Rubbin (1970), Yin et al. (1991), and many other authors see – Percy-Cunningham & Mac Donald (1987). Certain females of the Geometridae (e.g. *Eupithecia* Curtis, 1825, and *Scotopteryx* Hübner, 1825) possess glandulae odoriferae (Petersen, 1900). Later, Werner (1977) described this type of gland in *Rheumaptera hastata* (L., 1758). They are paired structures, invaginated anteriorly and located dorso-lateral to the rectum. Similar glands are found in other lepidopterous groups, e. g. Nymphalidae and Zygaenidae (Naumann, 1988), but morphologically, these glands are completely different in the Nymphalidae, the Zygaenidae and the Geometridae and it can be assumed that these glands have evolved independently in three unrelated families and cannot be expected to be homologous. Another type of gland was described by Ostaff et al. (1974) in *Lambdina fiscellaria* (Guenée, 1857) (Geometridae: Ennominae), a species which possesses paired pheromone glands situated ventro-laterally in the eighth segment.

The Geometridae include about 21 000 described species (Scoble et al., 1995), making it one of the three largest families of Lepidoptera. The taxonomy of the family has developed over a long period, but the infrafamilial classification has not received critical attention. The history of the classification of Geometridae to early in this century was chronicled by Prout (1910). Nine subfamilies are recognized now (Parsons et al., 1999), but the system is unsatisfactory with the monophyly of all being, at least, in some doubt (e.g. Oenochrominae *sensu lato* is a polyphyletic grouping) (Minet & Scoble, 1998). A tentative classification of the Geometridae of Borneo was proposed by Holloway (1997, Fig. 2: 11).

The Geometridae are monophyletic and characterized by two apomorphies:

- first, the presence of distinctive, paired tympanal organs situated at the base of the abdomen (e.g. Cook & Scoble, 1992). These structures have been reduced independently or lost (because of a few being wingless) in several Geometridae (Sattler, 1991).
- second, the larvae can be distinguished from those of other families by their "looping" progression, although "semi-loopers" occur among the Noctuidae. This distinctive movement is caused by the reduction of the number of pairs of prolegs typically to two pairs on abdominal segments 6 and 10. A full lepidopteran complement of prolegs exists in some species (i.e., on abdominal segments 3–6 and 10), but the size of these structures tends to be reduced (e.g. in Archiearinae). In some species of Oenochrominae and Ennominae, more than the minimum number of two pairs of prolegs occur, but fewer than the full lepidopteran complement.

The present paper aims at improving the knowledge of the distribution and the morphological variability of these dorsal saccular glands within the Geometridae and to assess their possible value for phylogenetic studies.

## MATERIAL AND METHODS

Dried museum specimens representing nine subfamilies of Geometridae were used to examine the internal female genitalia. The abdomens were dissected after 15 minutes maceration in hot 10% KOH and the genitalia slides were prepared by following the standard method (Robinson, 1976). The preparations were stained with chlorazol black (Carayon, 1969) and Euparal was used as the mounting medium. For the investigation of pheromone glands, the internal genitalia and segment A8 were removed; the ovipositor integument was incised midventrally and spread flat between glass slide and coverslip. I dissected 48 geometrid species from various parts of the world (mostly from Palearctic region) (Appendix 1).

## RESULTS

The glands consist of a pair of internal saccular organs (term proposed by Bendib, 1998) that are located dorso-laterally to the rectum. Morphological variability of these dorsal saccular glands can be observed (*cf.* Appendix 1): in *Philereme vetulata* (Larentiinae), the pheromone glands are characterized by the shortness of their lobes (0,18–0,3mm) and a narrow opening (Fig. 8). Other Larentiinae (e.g. *Horisme tersata*, *Melanthia procellata*) and Alsophilinae (*Alsophila aescularia*, Fig. 4) exemplify this type of gland (with minor variation). The glands are also short, (though separate) in Orthostixinae (*Gypsochroa renitidata*) (Fig. 5), certain Sterrhinae (*Rhodostrophia vibicaria, Rhodometra sacraria*), *Lycia zonaria* (Ennominae) and several Larentiinae (*Xanthorhoe montanata*, *Catarhoe rubidata*, *Pelurga comitata*, *Pareulype berberata, Triphosa sabaudiata*, *Anticollix sparsata* and *Venusia cambrica*).

In *Archiearis parthenias* (Fig. 2) (Archiearinae), the dorsal saccular glands are mid-length (0,6–0,9mm) (*cf.* Appendix 1) with a moderately wide opening. This type of gland occurs in species of Desmobathrinae (e.g. *Brachytrita cervinaria* (Fig. 1), *Conolophia conscitaria*) and Larentiinae (e.g. *Chloroclysta cinereata*, *Cidaria fulvata*, *Pennithera firmata*, *Pterapherapteryx sexalata*, *Trichopteryx polycommata* and *Eupithecia linariata*). In *Alcis repandata* (Ennominae) (Fig. 3) and *Euphyia frustata* (Larentiinae) (Fig. 9), the glands lobes are also mid-length but with a narrow opening.

In some Larentiinae (e.g. *Mesoleuca albicillata*, *Rheumaptera subhastata* (Fig. 7) and *Minoa murinata*), the saccular glands are long (1–3,5 mm) (*cf.* Appendix 1) and provided with a wide opening. In other Larentiinae (e.g. *Plemyria rubiginata*, *Photoscotosia miniosata* and *Gymnoscelis pumilata*) the gland shape is intermediate between those in Fig. 5 and Fig. 7. In the Geometrinae, the glands are very elongate and tapered (Fig. 6) with a narrow opening (e.g. *Geometra valida*, *Idiochlora ussuriaria* and *Eucrostes indigenata*) or a moderately wide opening (e.g. *Jodis lactearia*, *Xenochlorodes beryllaria* and *Bustilloxia saturata*).

Glands in different taxa are of various length (*cf.* Appendix 1). The location of the gland opening shows significant variation. In most species, it is situated laterally on the rectum but in some cases more on the distal part (Fig. 3: *Alcis repandata*, Ennominae; Fig. 8: *Philereme vetulata*, Fig. 9: *Euphyia frustata*, Larentiinae), sometimes on the subterminal part (Fig. 1: *Brachytrita cervinaria*, Desmobathrinae; Fig. 2: *Archiearis parthenias*, Archiearinae), or also in an intermediate position on the rectum (Fig. 4: *Alsophila aescularia*, Alsophilinae). In some cases, the opening is inserted much more laterally in the mid-width of the papillae anales (Fig. 6: *Geometra valida,* Geometrinae; Fig. 7: *Rheumaptera subhastata*, Larentiinae). This character is observed in all geometrine species examined and in *Mesoleuca albicillata*, *Rheumaptera subhastata*, and *Eupithecia linariata* (Larentiinae) and finally, the opening can reach the antero-medial margin of the papillae anales (Fig. 5: *Gypsochroa renitidata*, Orthostixinae).

## DISCUSSION

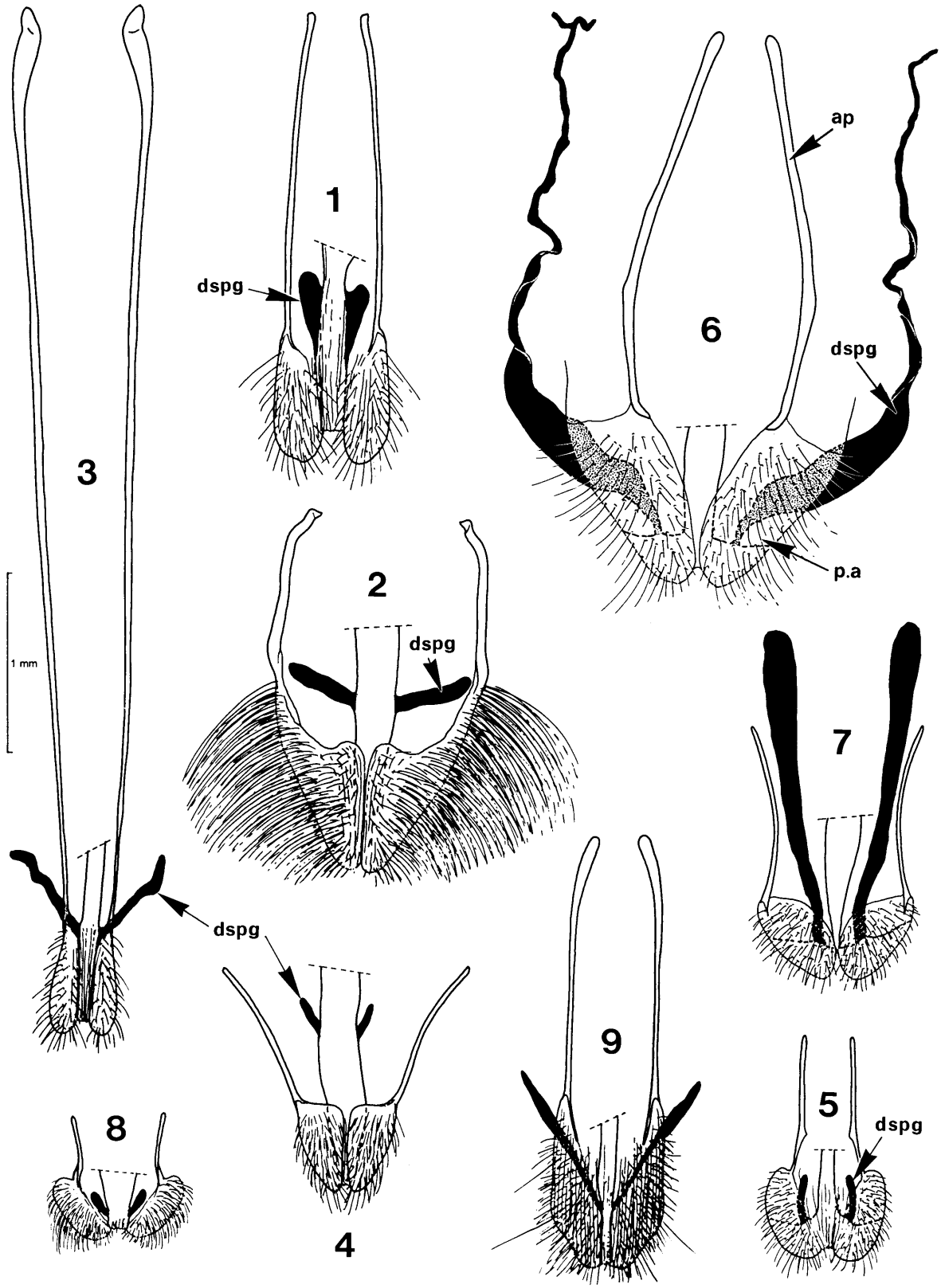
In addition to both apomorphies quoted in the introduction, dorsal saccular glands inserted on the rectum represent a third autapomorphy which has been unknown until now, and characterize Geometridae as a monophyletic group. The opening of saccular glands varies from wide to narrow and opens up on the 9 th abdominal segment. It should allow the pheromone to disperse when the abdominal tip is extended. Werner (1977) provided bioassay evidence that the glands of *Rheumaptera hastata* produce a sex pheromone and described the morphology and histology of the sex pheromone gland of this species. The location of gland opening shows variation (see Results) and could be a character shared in some groups or subfamilies, but now it is not easy to characterise the ground plan of this trait. The opening of glands situated in mid-width of the papillae anales (Figs. 6, 7) is observed in all species examined of Geometrinae (see Appendix 1) and in certain Larentiinae (e.g. *Mesoleuca albicillata*, *Rheumaptera subhastata* (Fig. 7) and *Eupithecia linariata*). This situation may be clarified, when more species have been studied.

The dorsal saccular glands are widely distributed in the family; indeed they are widespread in all subfamilies. This apomorphy can be ascribed to the ground plan of the Geometridae, with the possible exception of certain species which are devoid of dorsal saccular glands. These glands have disappeared secondarily, on several occasions, notably in some Ennominae (e.g. *Abraxas grossulariata*, *Colotois pennaria*, *Gnophos furvatus*, *Ourapteryx sambucaria, Bupalus piniaria*, *Theria rupicapraria*, *Hylaea fasciaria* and *Gnophos furvatus*), certain Sterrhinae (e.g. *Cyclophora punctaria* and *Scopula decorata*) and Oenochrominae (*Gastrophora henricaria*). However, I tentatively interpret the absence of dorsal saccular glands in a few members of the family as a secondary loss since the dorsal glands are present in other taxa of the Ennominae (e.g. *Lycia zonaria*, *Alcis repandata*) and Sterrhinae (e.g. *Rhodostrophia vibicaria*, *Rhodometra sacraria*). Nevertheless, the absence of glands could help to clarify relationships within Sterrhinae and Ennominae.

Both the geometrid *Rheumaptera hastata* and some species of Arctiidae (a family that belongs to the Noctuoidea, and which is characterized by the presence of one or two dorsal saccular glands situated on the A8–A9 intersegmental membrane – see Bendib & Minet; 1998 are reported to pulse the abdomen rhythmically during calling (Krasnoff & Roelofs, 1988).

It would be interesting to use histological methods which could help to establish the micromorphology of the gland.

ACKNOWLEDGEMENTS. I thank J. Minet and P. Grandcolas for their diverse suggestions and I am grateful for the perceptive comments of an anonymous reviewer.




Figs 1–9. Geometrid dorsal sex pheromone glands of female (ventral view). dspg – dorsal saccular pheromone glands, ap – apophysis posterior, pa – papilla analis. 1 – *Brachytrita cervinaria* Swinhoe, 1904; 2 – *Archiearis parthenias* (L., 1761); 3 – *Alcis repandata* (L., 1758); 4 – *Alsophila aescularia* (Denis & Schiffermüller,1775); 5 – *Gypsochroa renitidata* (Hübner, 1825); 6 – *Geometra valida* Felder & Rogenhofer, 1875; 7 – *Rheumaptera subhastata* (Nolcken, 1870); 8 – *Philereme vetulata* (Denis & Schiffermüller, 1775); 9 – *Euphyia frustata* Treitschke, 1828. Scale bar: 1mm.

TABLE 1. *Appendix 1. List of species examined of Geometridae. The distribution and morphological variability of dorsal saccular glands in the family. Location of the gland opening: distal part of the rectum (dpr); subterminal part of the rectum (spr); intermediate position on the rectum (ipr); antero-medial of the papillae anales (ampa); more laterally in mid-width of the papillae anales (mwpa).

| | Dorsal saccular glands | | Length of glands (mm) | | | Location of gland opening |
|---|---|---|---|---|---|---|
| | Presence of dorsal saccular glands | Absence of dorsal saccular glands | short 0,18-0,3 | mid-length 0,6-0,9 | long 1-3,5 | |
| **Desmobathrinae** (formerly included in Oenochrominae) | | | | | | |
| *Brachytrita cervinaria* Swinhoe, 1904 | + | | | + | | spr |
| *Conolophia conscitaria* (Walker, 1861) | + | | | + | | spr |
| **Archiearinae (= Brephinae)** | | | | | | |
| *Archiearis parthenias* (L., 1761) | + | | | + | | spr |
| **Ennominae** | | | | | | |
| *Abraxas grossulariata* (L., 1758) | | - | | | | |
| *Ourapteryx sambucaria* (L., 1758) | | - | | | | |
| *Colotois pennaria* (L., 1761) | | - | | | | |
| *Lycia zonaria* (Denis & Schiffermüller, 1775) | + | | + | | | dpr |
| *Alcis repandata* (L., 1758) | + | - | | + | | dpr |
| *Bupalus piniaria* (L., 1758) | | - | | | | |
| *Theria rupicapraria* (Denis & Schiffermüller, 1775) | | - | | | | |
| *Hylaea fasciaria* (L., 1758) | | - | | | | |
| *Gnophos furvatus* (Denis & Schiffermüller, 1775) | | | | | | |
| **Oenochrominae** | | | | | | |
| *Gastrophora henricaria* Guenée, 1857 | | - | | | | |
| **Alsophilinae** | | | | | | |
| *Alsophila aescularia* (Denis & Schiffermüller, 1775) | + | | + | | | ipr |
| **Orthostixinae** | | | | | | |
| *Gypsochroa renitidata* (Hübner, 1817) | + | | + | | | ampa |
| **Geometrinae (=Hemitheinae)** | | | | | | |
| *Geometra valida* Felder & Rogenhofer, 1875 | + | | | | + | mwpa |
| *Idiochlora ussuriaria* (Bremer, 1864) | + | | | | + | mwpa |
| *Bustilloxia saturata* (Bang-Haas, 1906) | + | | | | + | mwpa |
| *Jodis lactearia* (L., 1758) | + | | | | + | mwpa |
| *Eucrostes indigenata* (Villers, 1789) | + | | | | + | mwpa |
| *Xenochlorodes beryllaria* (Mann, 1853) | + | | | | + | mwpa |
| **Sterrhinae (= Acidaliinae)** | | | | | | |
| *Cyclophora punctaria* (L., 1758) | | - | | | | |
| *Scopula decorata* (Denis & Schiffermüller, 1775) | | - | | | | |
| *Rhodostrophia tabidaria* Zeller, 1847 | + | | + | | | ampa |
| *Rhodometra sacraria* (L., 1767) | + | | + | | | ampa |
| **Larentiinae** ( = **Hydriomeninae**) | | | | | | |
| *Xanthorhoe montanata* (Denis & Schiffermüller, 1775) | + | | + | | | dpr |
| *Catarhoe rubidata* (Denis & Schiffermüller, 1775) | + | | + | | | dpr |
| *Mesoleuca albicillata* (L., 1758) | + | | | | + | mwpa |
| *Pelurga comitata* (L., 1758) | + | | + | | | dpr |
| *Chloroclysta cinereata* Moore, 1868 | + | | | + | | dpr |
| *Cidaria fulvata* (Forster, 1771) | + | | | + | | ipr |

| | | | | | |
|---|---|---|---|---|---|
| *Plemyria rubiginata* (Denis & Schiffermüller, 1775) | + | | | + | dpr |
| *Pennithera firmata* (Hübner, 1822) | + | | | + | dpr |
| *Pareulype berberata* (Denis & Schiffermüller, 1775) | + | | + | | dpr |
| *Rheumaptera subhastata* (Nolcken, 1870) | + | | | | + mwpa |
| *Eupithecia linariata* (Denis & Schiffermüller, 1775) | + | | | + | mwpa |
| *Triphosa sabaudiata* (Duponchel, 1830) | + | | + | | dpr |
| *Philereme vetulata* (Denis & Schiffermüller, 1775) | + | | + | | dpr |
| *Photoscotosia miniosata* (Walker, 1862) | + | | | + | dpr |
| *Euphyia frustata* (Treitschke, 1828) | + | | | + | dpr |
| *Gymnoscelis pumilata* (Hübner, [1813]) | + | | | + | dpr |
| *Anticollix sparsata* (Treitschke, 1828) | + | | + | | ipr |
| *Horisme tersata* (Denis & Schiffermüller, 1775) | + | | + | | dpr |
| *Melanthia procellata* (Denis & Schiffermüller, 1775) | + | | + | | dpr |
| *Venusia cambrica* Curtis, 1839 | + | | + | | dpr |
| *Minoa murinata* (Scopoli, 1763) | + | | | | + dpr |
| *Pterapherapteryx sexalata* (Retzius, 1783) | + | | | + | dpr |
| *Trichopteryx polycommata* (Denis & Schiffermüller, 1975) | + | | | + | dpr |

## REFERENCES


Bendib A. 1998: Evolution of saccular sex pheromone glands in female Arctiidae. *Abstr. XI Eur. Congr. Lepid. Malle, Belgium*: 27–28.

Bendib A. & Minet J. 1998: Female pheromone glands in Arctiidae (Lepidoptera: Noctuoidea): evolution and phylogenetic significance. *C. R. Acad. Sci.* **321**: 1007–1014.

Carayon J. 1969: Emploi du noir chlorazol en anatomie microscopique des insectes. *Ann. Soc. Entomol. Fr. (N.S.)* **5** *(1)*: 179–193.

Cook M.A. & Scoble M.J. 1992: Tympanal organs of geometrid moths: a review of their morphology, function and systematic importance. *Syst. Entomol.* **17** (3): 219–232.

Götz B. 1951: Die Sexualduftstoffe an Lepidopteren. *Experientia* **7** (11): 406–418.

Holloway J.D. 1997: The moths of Borneo. Family Geometridae, subfamilies Sterrhinae and Larentiinae *Malay. Nat. J.* **51**: 242 pp.

Jefferson R.N. & Rubin R.E. 1970: Sex pheromones of noctuid moths. XVII: A clarification of the description of the female sex pheromone glands of Prodenia litura. *Ann. Entomol. Soc. Am.* **63**: 431–433.

Krasnoff S.B. & Roelofs W.L. 1988: Sex pheromone released as an aerosol by the moth Pyrrharctia isabella. *Nature Lond.* **333**: 263–265.

Minet J. & Scoble M. J. 1998: The Drepanoid/Geometroid Assemblage. *In*: Kristensen N.P. (ed.), *Lepidoptera, Moths and Butterflies, vol. 1: Evolution, Systematic, and Biogeography* (Handbuch der Zoologie [founded by Willy Kükenthal; ed.: Fischer M.], Band 4, Teilband 35), Walter de Gruyter, Berlin, pp. 305–320.

Naumann C.M. 1988: The internal female genitalia of some Zygaenidae (Insecta, Lepidoptera): their morphology and remarks on their phylogenetic significance. *Syst. Entomol.* **13**: 85–99.

Ostaff D.P., Shepherd R.F. & Borden J.H. 1974: Sex attraction and courtship behavior in Lambdina fiscellaria lugubrosa (Lepidoptera: Geometridae). *Can. Entomol.* **106**: 493–501.

Parsons M.S., Scoble M.J., Honey M.R. Pitkin L.M. & Pitkin B.R. 1999: *Geometrid Moths of the World: A catalogue (Lepidoptera: Geometridae)*. Vol. 1: 5–482, Vol. 2: 485–1016, Index vol. 1 & 2 I-1– I-129; ed.: Scoble M.J. Nat. Hist. Mus. London, Apollo books, Stenstrup, Denmark.

Percy-Cunningham J.E. & MacDonald J.A. 1987: Biology and ultrastructure of sex pheromone-producing glands: In: Prestwich G.D. & Blonquist G.J. (eds), *Pheromone biochemistry*. Academic Press, Orlando, pp. 27–75.

Petersen W. 1900: Beiträge zur Morphologie der Lepidopteren. *Zapiski Imperatorskoj Akademij Nauk po Fisiko-Matematitscheskomu Otdjeljeniyu* **9** (6): 1–142.

Prout L.B. 1910: Lepidoptera Heterocera. Fam. Geometridae: subfam. Oenochrominae. In Wytsman P. (ed.). *Genera Insect.* **104**: 1–120 + 2pls.

Robinson G.S. 1976: The preparation of slides of Lepidoptera genitalia with special reference to the Microlepidoptera. *Entomologist's Gaz* **27**: 127–132.

Roelofs W.L. & Feng K.C. 1968: Sex pheromone specificity tests in the Tortricidae introductory report. *Ann. Entomol. Soc. Am.* **61**: 312–316.

Sattler K. 1991: Der "Achselkamm" der Lepidoptera und seine Funktion. *Dtsch. Ent. Z.* **38**: 7–11.

Scoble M.I., Gaston K.J. & Crook A. 1995: Using taxonomic data to estimate species richness in Geometridae. *J. Lepid. Soc.* **49** *(2)*: 136–147.

Steinbrecht R.A. 1964: Feinstructure und Histochemie der Sexualduftdrüse des Seidenspinners Bombyx mori. L. *Z. Zellforsch.* **64**: 227–261.

Urbahn E. 1913: Abdominale Duftorgane bei weiblichen Schmetterlingen. *Jena. Z. Naturw.* **50**: 277–358 + 2 pls.

Weatherston J. & Percy J.E. 1968: Studies of physiologically active arthropod secretions. I: Evidence for a sex pheromone in female Vitula edmandsae (Lepidoptera: Phycitidae). *Can. Entomol.* **100**: 1065–1070.

Werner R.A. 1977: Morphology and histology of the sex pheromone gland of a geometrid, Rheumaptera hastata. *Ann. Entomol. Soc. Am.* **70** *(2)*: 264–266.

Yin L.R.S., Schal C. & Cardé R.T. 1991: Sex pheromone gland of the female tiger moth Holomelina lamae (Lepidoptera: Arctiidae). *Can. J. Zool.* **69**: 1916–1921.


Received July 14, 2000; revised January 17, 2001; accepted March 19, 2001