Eur. J. Entomol. **94**: 503–510, 1997
ISSN 1210–5759

The unusual male brush apparatus of *Hypopteridia* (Lepidoptera: Noctuidae)

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Lepidoptera, Noctuidae, *Mythimna-Leucania* complex, androconial organs, male scent organs, trifine brush organs

Abstract. The male scent organs of *Hypopteridia reversa* (Moore) are described and compared with other androconial organs occurring in the Mythimnini. Abdominal segments A1–A4 possess an organ composed of a pair of little brushes that are linked to the ends of levers which branch off the posterior margin of sternum A2 and a pair of large pleural hair tufts. In the resting position, the tufts are contained in a complex ventral pouch that consists of a base covered by lateral flaps, the latter of which were created by extensive modifications of segments A3–A4. This configuration has no correspondence in other Noctuidae so far examined and is considered autapomorphic to *Hypopteridia*. Another large posterior abdominal brush is also present on sternum A8. Phylogenetic value of the profound deviations from the groundplan of the abdominal brush organ morphology of trifine Noctuidae is emphasized.

INTRODUCTION

Despite the vast number of species recognized within the Mythimnini (or *Mythimna-Leucania* complex auct.), a group of the trifine subfamily Hadeninae, the assemblage shows remarkable morphological homogeneity and following several taxonomic rearrangements (e.g. Franclemont, 1951; Rungs, 1953; Calora, 1966; Sukhareva, 1973; Beck, 1996) inclusion of most of the species into a single genus is occasionally proposed (e.g. Holloway, 1989; Yoshimatsu, 1994). However, a recent survey of most of the European species (Zilli & Di Giulio, 1996) revealed an unrivalled variety of male scent organs, which provides useful insights into the phylogenetic architecture of the whole complex.

Several male structures involved with chemical communication between individuals are known in the Lepidoptera (Stobbe, 1912; Varley, 1962a; Birch, 1979; Birch & Hefetz, 1987; Birch et al., 1990; Scoble, 1992). It is generally assumed that male pheromones play a major role during courtship and promote species isolation (Phelan & Baker, 1987; Birch et al., 1990; Andersson, 1994). It should be noted, however, that multiple functions by the male scents have also been evidenced, including use in defense and intrasexual signalling (Boppré, 1984), and the isolating role still requires exhaustive substantiation (Zilli, 1992).

Androconial organs (brush organs, inflatable coremata, eversible hair tufts, etc.) can be found on almost any part of the body in the Noctuidae, but occur most commonly on the abdomen. In particular, a complex set of paired structures known collectively as "trifine brush organ" (TBO) occur throughout most of the "trifine" lineages (viz. Noctuidae with hindwing vein M_2 obliterated), and some quadrifine species as well (Speidel & Naumann, 1995; Zilli, 1995; Speidel et al., 1996). TBOs typically consist of five parts: a sclerotized lever directed anteriorly from the posterior corner of sternum A2; a long brush supported by the distal end of the lever; a lateral pocket that conceals the brush when the subject is in resting position; a scent gland (Stobbe's gland) inside segment A1+2 with secretory hairs that discharge onto the brush; and a lateral apodeme that protrudes from anterior margin of sternum A3 (cf. Stobbe, 1912; Varley, 1962a; Birch, 1972, 1979; Kobayashi, 1977).

Reasons for the high diversity of brush organs in the Mythimnini are still obscure and might be explained by rapid evolution of sex-limited scent organs due to the uneven nature of sexual selection, either epigamic or intrasexual. Nevertheless, many of the detected organs do not consist of simple assemblages of androconial scales as in many other Lepidoptera; rather they involve massive exoskeletal modifications, that are of interest in taxonomic studies (Zilli & Di Giulio, 1996). The evolutionary stability of other structures may provide an alternative explanation for the high diversity of brush organs; the Mythimnini are distinctively specialized for exploitation of gramineous host plants, and this involves some ecological constraints.

Members of the Mythimnini found in continents other than Europe are being studied in order to trace major trends in the evolution of male scent organs. The opportunity to check the type species of *Hypopteridia* Warren, 1912, namely *Aletia reversa* Moore, 1885, provided unexpected evidence of morphological complexity attained by androconial structures within the group. This species possesses a very unusual, hitherto undescribed, organ on the abdomen (Figs 1–2). It was reported by Calora (1966) and Yoshimatsu (1994) in their keystone revisions of subsets of the Oriental and east Palaearctic faunas, although they failed to take note of the actual morphology of the structure. Actually, Warren (1912a) himself substantiated his description of *Hypopteridia* because of "large lateral tufts, expansible as winglets, beneath the hindwings" occurring in male *Aletia reversa* (the name *Hypopteridia* means "inferior winglets"). Nonetheless, Warren (1912a,b) incorrectly presumed that such winglets arose from beneath the thorax.

MATERIAL AND METHODS

Pinned male specimens of *Hypopteridia reversa* (Moore, 1885) from Borneo and Sumatra were carefully examined to locate areas with thick scale vestiture. The abdomina were then detached from the specimens and macerated in a 10% KOH solution. At regular intervals they were rinsed in distilled water, partially descaled and observed through a dissecting microscope in order to elucidate the morphofunctional relationships between component parts. After cutting the terga with sharp scissors and removing loose tissues with a fine paint-brush, the abdomina were eventually soaked in ethanol (95%) and mounted in Euparal.

DESCRIPTION

Sternum A2 (apparently first). Greatly modified; anterior margin sinuous, V-shaped, posterior margin deeply excised, possessing a pair of slightly divergent lobate paramesial notches, which result in short, flat median process; pair of elongated hollows below anterior margin, at approx. 45° to the median plane, each spanning from base of anterolateral processes to middle of sternum; pair of long, sclerotized levers that branch from posterior corners of sternum and extend to base of abdomen (Fig. 2). Levers are slightly divergent and closely resemble those of common TBOs (cf. Birch, 1972), but lack central flat piece in which they usually displace themselves laterally. Apices of levers are joined with a cupular structure from which flimsy brush is hanging; hairs sparse and barely shorter than levers.

Hair tufts. Pair of large hair tufts inserted in basal pleura located adjacent to apices of levers, although superimposed on both levers and little brushes when in natural position. In resting position hair tufts directed ventrally, basal portion held within hollows of sternum A2 and distal half contained in complex median pouch (Figs 1–2). Attempts to evert pleural bases of tufts from inside body cavity indicate that they do not function as tubular coremata, rather they just evaginate partially and allow spreading of tufts.

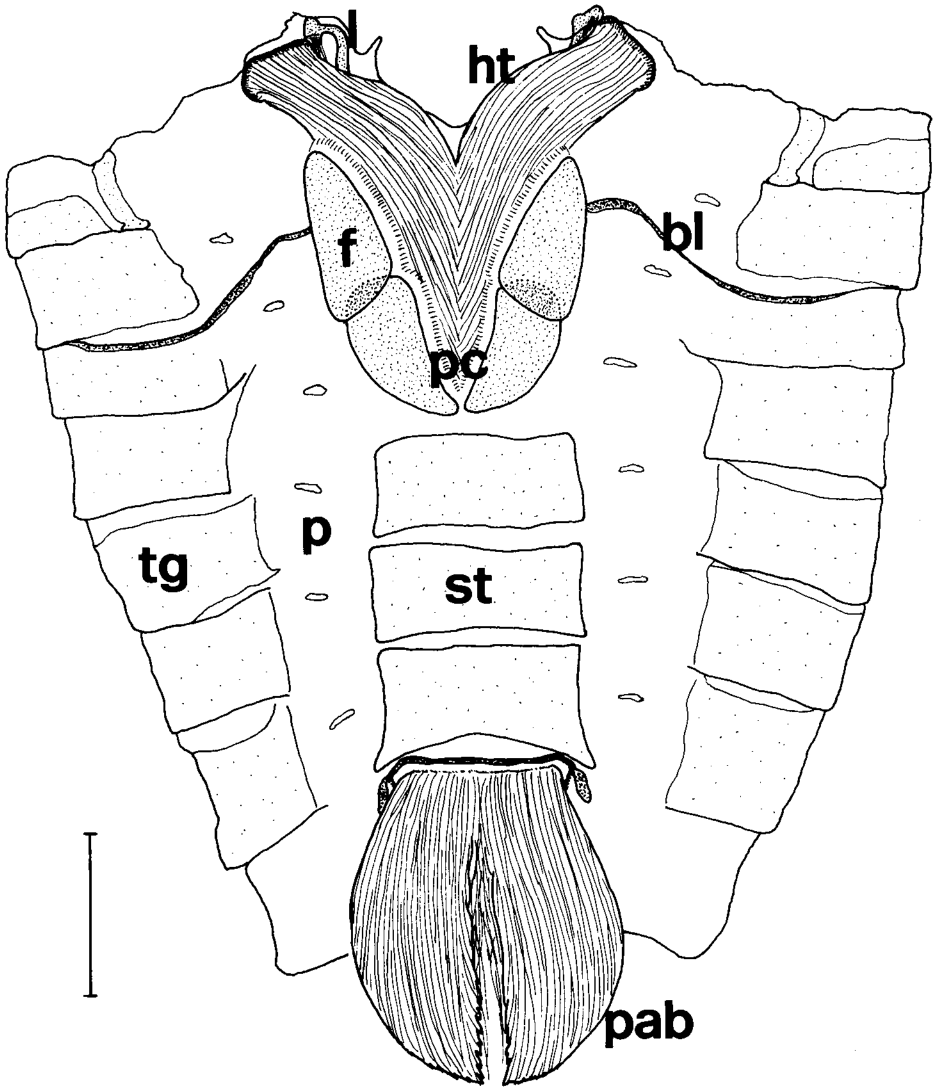

Fig. 1. Dissected abdomen of male *Hypopteridia reversa* (ventral side in the middle) showing the brush apparatus consisting of a basal organ and a posterior abdominal brush (bl – belt, f – flap, ht – hair tuft, l – lever, p – pleuron, pab – posterior abdominal brush, pc – pouch, st – sternum, tg – tergum). Scale = 2 mm.

Median pouch. Base represented by sterna A3–A4; covering consists of pleural flaps on corresponding segments that work as shutters (Figs 1–3). Sternum A3 remarkably modified; consists of small median plate; posterior portion is approximately square-shaped and weakly sclerotized and anterior portion consists of a pair of long, heavily sclerotized rods. In resting position both rods gradually diverge from each other; basal half of sternum well invaginated beneath sternum A2. Sternum A4 poorly sclerotized and serves as bottom of pouch; mesially flat, nearly square-shaped, sides are convex but possess very marginal concave areas (Figs 3–4). Brushes adpressed onto base of pouch; lateral flaps protrude from pleura A3–A4 and greatly overlap on corresponding sterna. Posterior flaps on pleura A4 gradually converge and almost join each other at median plane and thus confer shape of shield to closed pouch. Outer side of flaps are well sclerotized, covered by massive coat of flat, tightly adpressed scales which, projecting well out from distal margin, greatly enhance closing of pouch; inner side membranous, that of A3 extensively filled with hairs. Sclerotized anterior ridge of tergum A3 continues along pleura to base of flaps, thus constituting characteristic dorsolateral belt (cf. Speidel & Naumann, 1995) which evidently plays mechanical role in opening flaps. During eversion, posterior part of sternum A2 rises upward from sternum A3, assisted by wide intersegmental membrane and levering pitchfork-like anterior rods of sternum A3.

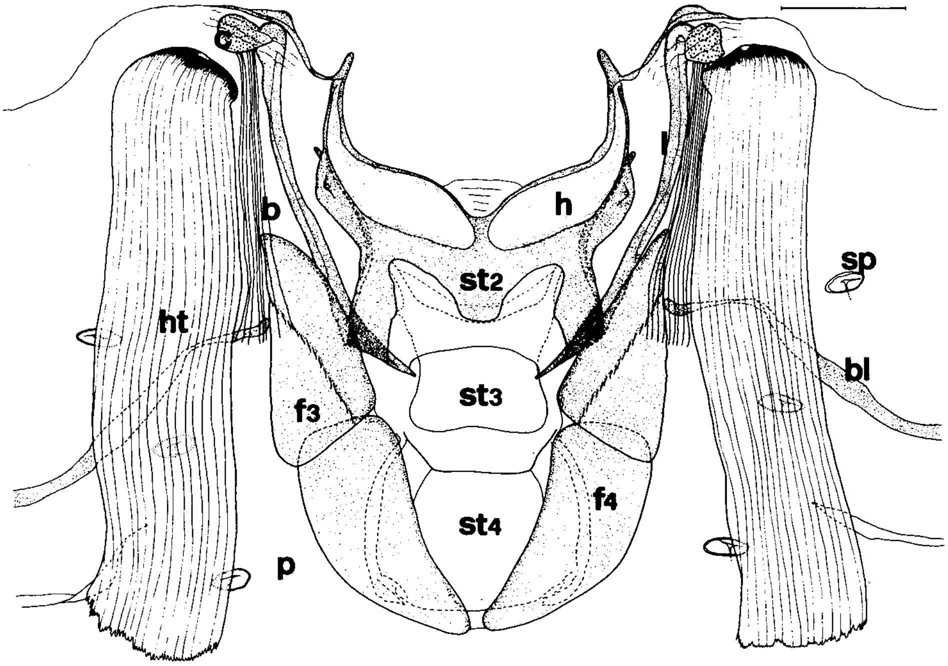

Fig. 2. Basal abdominal androconial organ of *Hypopteridia reversa* (ventral view; brushes and hair tufts set aside from the median pouch to show its details) (b – brush, bl – belt, c – cupular base of brush, f – flap, h – hollow, ht – hair tuft, l – lever, p – pleuron, sp – spiracle, st – sternum, numbering indicates abdominal segments). Scale = 1 mm.

Posterior abdominal brush. As usual for most Mythimnini and several other noctuids, a posterior abdominal brush is present on sternum A8; in this case the brush is very large and is partially bisected (Fig. 1).

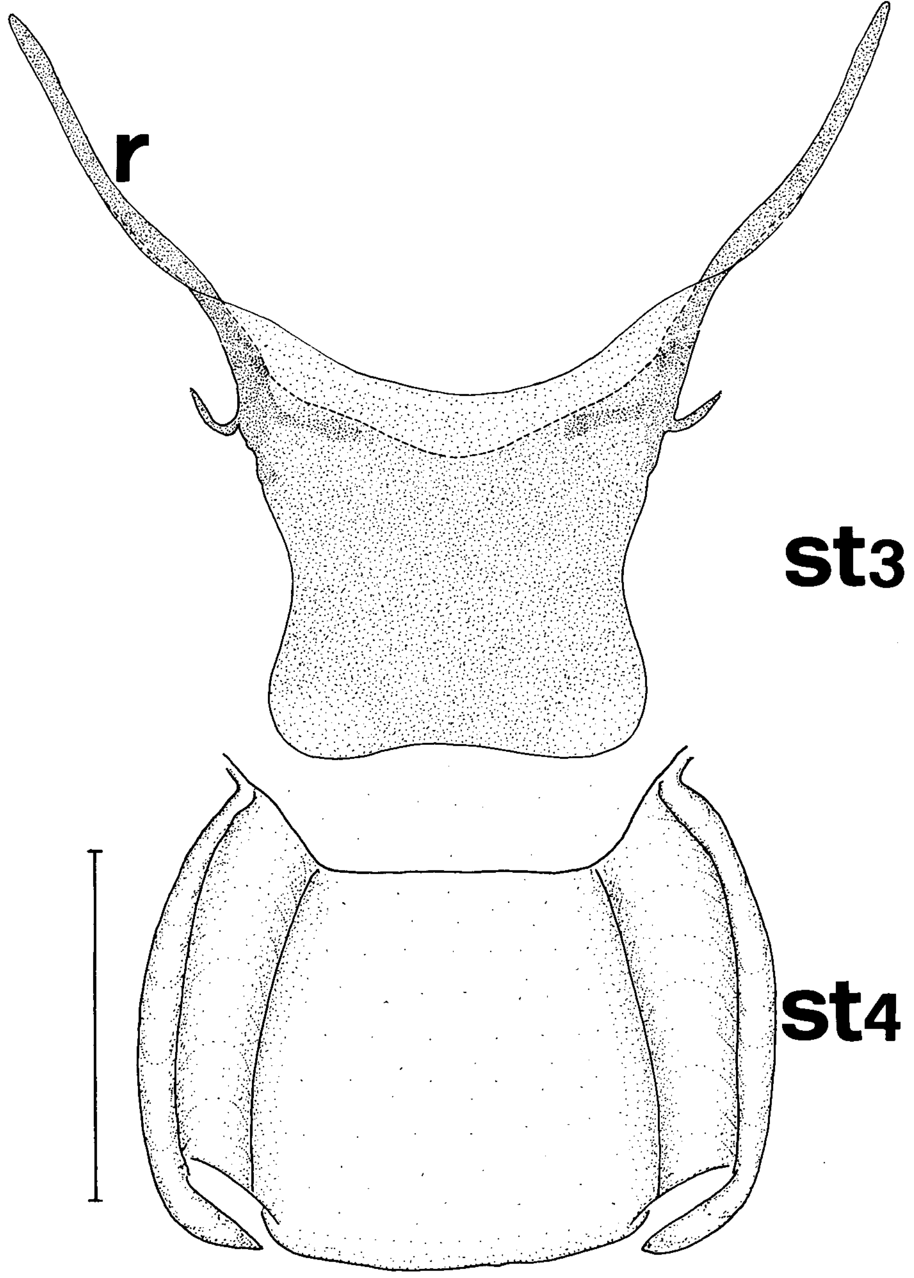

Fig. 3. Configuration of sterna A3–A4 of male *Hypopteridia reversa* (r – rod, st – sternum, numbering indicates abdominal segments). Scale = 1 mm.

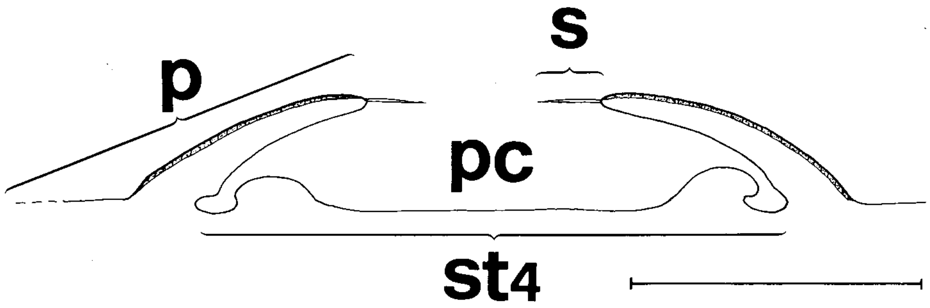

Fig. 4. Diagrammatic transverse section of the median pouch of male *Hypopteridia reversa* on segment A4 showing the relationships between pleural flaps and sternum (p – pleuron, pc – pouch, s – scales protruding from the flap, st4 – sternum A4). Scale = 1 mm.

DISCUSSION

The basal abdominal brush organ that occurs in *Hypopteridia reversa* and, according to Warren (1912b), Calora (1966) and Yoshimatsu (1994), in *H. albipuncta* Warren, 1912 and *H. amplia* Calora, 1966, shows very little affinity to the androconial structures so far studied in the Mythimnini (cf. Varley, 1962b; Birch, 1972; Kobayashi, 1977; Yoshimatsu, 1994; Zilli & Di Giulio, 1996). In fact, despite some minor differences, only the sclerotized levers protruding from the posterolateral corners of sternum A2 and the little brushes at their ends can be considered homologous with those characteristic of the plesiomorphic trifine brush organ (TBO) (cf. Introduction) that occurs in several noctuid subfamilies and in many Mythimnini as well (Birch, 1972; Kobayashi, 1977; Yoshimatsu, 1994; Speidel & Naumann, 1995; Zilli, 1995; Zilli & Di Giulio, 1996; Speidel et al., 1996). In other Mythimnini single parts of the ancestral TBOs underwent modifications (becoming even rudimentary) and were rearranged with newly arisen structures into more derived organs peculiar to smaller groups.

For example, in *Sablia* Sukhareva, 1973, the levers rotated and are perpendicular to the median plane; thus the brushes, instead of being held in paired longitudinal pockets as in TBOs, are placed transversely in the markedly concave sternum A2. Other median pouches, derived from an invagination in the middle of sternum A2, are known in some *Leucania* Ochsenheimer, 1816; in this case, however, they do not contain true brushes but rather collapsed, hairy coremata. It is worth noting that the remarkably complex median pouch of *H. reversa*, involving segments A3–A4, does not show any similarity with the analogous structures found in *Sablia* and *Leucania* (cf. Zilli & Di Giulio, 1996).

Sparse hairs of *H. reversa* hang below the cupular structures linked to the apex of the levers; the basal section of these hairs shows faint undulated ridges (cf. Kobayashi, 1977) at magnification of 1,000 x with the optical microscope. Both these facts suggest homology with the brushes of the TBOs. However, in the TBOs, the brushes uptake pheromone precursors from Stobbe's glands located at the base of the abdomen; while in *Sablia* glandular vesicles filling sternum A2 are responsible for secretion. Accordingly, the hairs might simply represent brushes undergoing regression or alternatively may play a direct role in pheromone secretion, due to their intimate contact with the hair tufts, which may act as dispersants. Other candidates for roles in pheromone elaboration or secretion are the hairs that fill the inner side of the flaps on segment A3.

Some limited similarities between *H. reversa* and other Mythimnini offer analogous solutions to comparable problems and may suggest such similarities are better regarded as homoplasies, which nonetheless reveal the existence of similar trends. In particular, the basal hollows of sternum A2 are reminescent of some *Leucania* in which the hairs of collapsed coremata are partly lodged. Moreover, pleural sclerotizations are also known in species of *Sablia* and *Leucania* with brushes or coremata directed mesially in the resting position, although these show a totally different configuration and do not involve segment A4 (cf. Zilli & Di Giulio, 1996). More intriguing for phylogenetic analyses are correspondences of *H. reversa* with *Leucania consanguis* Guenée, 1852 in the shape of sternum A2 and presence of pleural hair tufts (cf. Kobayashi, 1977). This species, however, differs sharply by possessing normal sterna A3–A4 and lateral pockets characteristic of TBOs. It is interesting to note that should the pleural pockets of *L. consanguis* attain eversion a major step toward the evolution of pleural flaps would be accomplished.

The unique features shown by *H. reversa* and its close allies, i.e. the radically changed segments A3–A4 forming a complex ventral pouch and a dorsolateral belt on A3, support the view that *Hypopteridia* is a highly apomorphic branch within the Mythimnini. The synapomorphy is shared by a least three species to which the name *Hypopteridia* should then be restricted (Warren, 1912b; Calora, 1966; Yoshimatsu, 1994), i.e. *H. reversa* (Moore, 1885), *H. amplia* Calora, 1966, and *H. albipuncta* Warren, 1912. Other species that from time to time were delegated to *Hypopteridia* (cf. Holloway, 1976; Poole, 1989) were later proven to belong to *Apospasta* Fletcher, 1959 (Holloway, 1989); whereas a proper placement of "*Leucania acontosema*" Turner, 1903, which was transferred to *Hypopteridia* by Edwards (1996) without attention to the male brush organs, will largely depend on re-examination of this species.

ACKNOWLEDGEMENTS. The author's most sincere gratitude goes to P. Provera (Lugano), who kindly loaned study materials described herein, to H. Hacker (Staffelstein) and E. Tremblay (Napoli) for their kind bibliographic assistance, and to the referees for their useful comments. This work is part of research programmes MURST (40%) and CNR.

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Received June 11, 1996; accepted November 21, 1996