The biological context and evolution of Pendergrast's organs of Acanthosomatidae (Heteroptera, Pentatomoidea)[1]

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Abstract: The Pendergrast's organs of Acanthosomatidae have been the subjects of many investigations. The present study summarizes and reviews previous data and hypotheses. In addition a survey on the presence of Pendergrast's organs of more than 100 acanthosomatid species is presented for the first time. Transformations of the Pendergrast's organs within the Acanthosomatidae are discussed. The reproductive behaviour of *Cyphostethus tristriatus* is described for the first time. It reveals that the Pendergrast's organs are involved in the biological context of oviposition. Female acanthosomatids rub their hind tarsi over the setose area of the Pendergrast's organs, spin the eggs, then place and attach them with their hind tarsi to the oviposition site. The smearing behaviour of Acanthosomatidae performed during oviposition is homologised with the grooming behaviour of Heteroptera. A scenario on the evolution of Pendergrast's organs and the involved oviposition behaviour is presented.

Key words: Acanthosomatidae, behaviour, grooming, Heteroptera, Lestoniidae, oviposition, Pendergrast's organs.

Introduction

Many authors have contributed to the study of Pendergrast's organs (PENDERGRAST 1953; CARAYON 1981; STADDON 1990; FISCHER 1994a, 1994b, 2000) and proposed several – sometimes quite conflicting – hypotheses on the biological role of these organs. BREDDIN (1903) was the first to recognise the setose areas on the female abdomen of Acanthosomatidae and used the term „Copulationsgruben" (copulation grooves), which suggests that the Pendergrast's organs are involved in mating behaviour. Other authors favoured a hypothesis that Pendergrast's organs are involved in oviposition. In order to be able to verify each of the hypotheses, the mating and oviposition behaviour of *Cyphostethus tristriatus* (FABRICIUS 1787) was studied. Both nymphs and adults of *Cyphostethus tristriatus* feed on the fruits of *Juniperus communis*, a shrub. *Juniperus communis* is also used as the mating and oviposition site of *Cyphostethus tristriatus*.

Pendergrast's organs are grooves on each side of the sternum and can be present on female abdominal segments V, VI and VII. The majority of acanthosomatid species have Pendergrast's organs on the abdominal segments VI and VII (Tab. 1). The grooves bear numerous bristles and have a more or less oval shape with the greater diameter usually orientated in the dorsoventral axis. In *Elasmostethus* spp. the dorsoventral diameter measures about 0.5 mm (FISCHER 1994b). Size and number of bristles differ between the grooves of the abdominal segments VI and VII. In most species of the Acanthosomatidae the grooves of the abdominal segment VII are bigger and bear more bristles than those of segment VI. The length of the bristles varies from 0.4 mm up to 0.6 mm. From SEM-photographs, ductules opening into pores with a diameter of 10 μm can be detected between the bristles (Fig. 11). The epidermis underlying the setose areas is much thicker than the surrounding epidermal tissue (Fig. 12). TEM-

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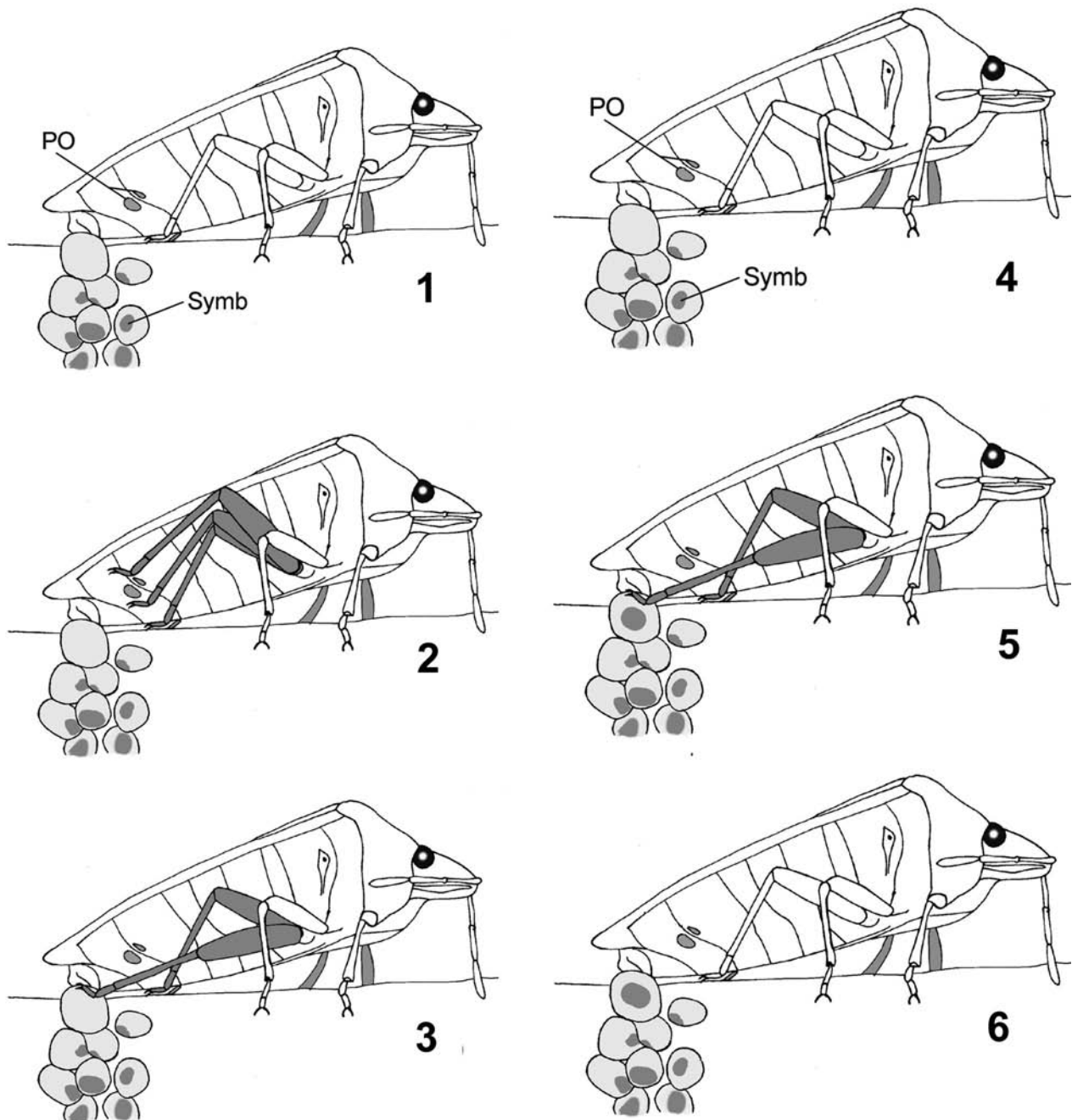
Figs 1-6: Oviposition of *Cyphostethus tristriatus* (Acanthosomatidae) (**1**) egg just deposited (**2**) after egg is deposited the female rubs her hindtarsi across the Pendergrast's organs (po) (**3**) secretion is applied by rotating the egg with both hindtarsi before glue hardens (**4-6**) a microsymbiont sac (symb) is applied onto the egg surface. Microsymbionts, which are transferred onto the egg, originate from a unique cuticular pouch of the female genitalia in Acanthosomatidae.

sections clearly display that the cells contain numerous vacuoles. The contents of these cells are still unknown. Nevertheless, a secretory function of the Pendergrast's organs is most likely. Cross-sections display ductules, which open into pores between the bristles. SEM-photographs of the inner side of the cuticle exhibit typical gland cells (FISCHER 1994b, 2000).
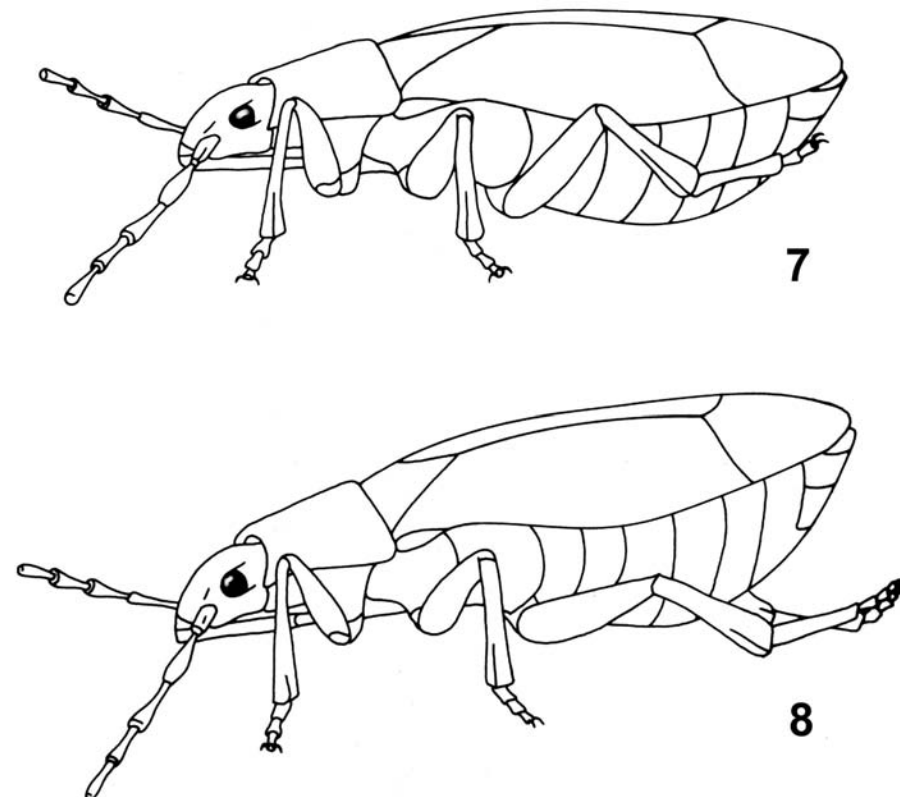
Phylogenetic analysis of Acanthosomatidae has demonstrated that paired Pendergrast's organs on the female abdominal sternum of segment VI and VII belong to the stem-species pattern of Acanthosomatidae (FISCHER 1993, 1994a). This character was thought to be an apomorphy of the Acanthosomatidae until the „disc-like organs" of Lestoniidae (Pentatomoidea) were studied using lightmicroscopical and SEM-techniques (FISCHER 2000). It became evident that the disc-like organs present only in female Lestoniidae are homologous to the Pendergrast's organs of female Acanthosomatidae (FISCHER 2000). The disc-like organs of Lestoniidae are present only on the abdominal segment VII. Being homologous as paired abdominal sternal glands in fe-

males, Pendergrast's organs of Acanthosomatidae and disc-like organs of Lestoniidae are hypothesized as a synapomorphy supporting a sistergroup relationship of these two taxa (FISCHER 2000). Additionally, several other morphological characters (FISCHER 2000) and combined analyses of morphological and molecular data (GRAZIA et al., in press) support a sistergroup relationship of Acanthosomatidae and Lestoniidae. For the stem-species of Acanthosomatidae, paired Pendergrast's organs on the female abdominal segment VII are a plesiomorphy and paired Pendergrast's organs on the abdominal segment VI are an apomorphy.

The self-stimulation hypothesis

As mentioned above, several conflicting hypotheses on the function and biological role of Pendergrast's organs were proposed during the last 100 years. PENDERGRAST (1953) investigated the morphology of the female setose areas in detail with light-microscopical techniques. Although he was not very confident in his interpretation of the „cell-like bodies" as being nerve cells, he proposed a stimulating function for the setose areas. He proposed that rubbing the hindtarsi across the setose areas should self stimulate the female to oviposit her eggs. It should be clearly stated that Pendergrast himself was not very convinced by this hypothesis. Indeed, self-stimulation by the female does not make much sense. Several arguments can be put forward against this hypothesis. First, why should a female stimulate herself to oviposit her eggs? There are countless other insects that deposit their eggs without any evidence of mechanical self-stimulation. Second, transformations within the Acanthosomatidae, e.g. neither the enlarged Pendergrast's organs areas over three abdominal segments of *Sniploa obsoletus* nor the complete loss of Pendergrast's organs in *Elasmucha*-species can be explained by this self-stimulation-hypothesis. Third, if there really is a self-stimulation, a rather complex system must be present. A signal must be sent to the hindtarsi rubbing across the setose. These setose areas must be sensitive and send signals to stimulate the oviposition behaviour. This is neither very likely nor parsimonious.

Figs 7-8: *Pyrrhocoris apterus* grooming abdomen (**7**) Note the position of the hindtarsi while taking up dirt and particles, which is similar to the position of the hindtarsi of *Cyphostethus tristriatus* while taking up secretion from the Pendergrast's organs (see Fig. 2) (**8**) brushing off uptaken dirt by rubbing both hindtarsi against each other (compare with Fig. 3) (drawings by courtesy of Antje Fischer).

The egg-clutch protection hypothesis

PENDERGRAST (1953) also considered a possible secretory function for this organ. In his view the secretion should be transferred onto the eggs by the hind tarsi. Because of the lack of evidence of secretion, Pendergrast discarded this hypothesis. The hypothesis of a secretion transfer onto the eggs gained new evidence from a phylogenetic analysis of Acanthosomatidae (FISCHER 1993, 1994a). Indeed, the egg-smearing behaviour can be observed, as it is described for *Cyphostethus tristriatus* in this study.

The secretion of the Pendergrast's organs most likely functions as a repellent against predators and parasitoids. An indirect indication comes from *Elasmucha* species. It has been known for a long time that females of *Elasmucha*-species perform maternal care. *Elasmucha*-species do not have Pendergrast´s organs (Tab. 1). As paired Pendergrast's organs on the female abdominal segments VI and VII belong to the stem-species pattern of Acanthosomatidae, the absence of Pendergrast's organs in *Elasmucha* species has to be considered as a secondary loss in the stem-species pattern of

Tab. 1: Presence of Pendergrast's organs on the pregenitalia segments of Acanthosomatidae-species.

	V	VI	VII	Reference
Abulites fuscosparsus (Stål 1854)	-	-	+	Kumar 1974
Abulites sparsus Germar 1837	-	-	+	CF
Acanthosoma axillaris Jakowleff 1889	-	+	+	CF
Acanthosoma dentata De Geer 1773	-	+	+	CF
Acanthosoma forciparum Reuter 1881	-	+	+	CF
Acanthosoma haemorrhoidale (Linnaeus 1758)	-	+	+	Pendergrast 1953, CF
Acrophyma frigidula Bergroth 1916	-	+	+	Kumar 1974
Aesepus signoretii Stål 1876	-	-	+	Kumar 1974
Agamedes pilicornis Stål 1876	-	-	-	Kumar 1974
Amphaces elongata Distant 1910	-	+	-	CF
Amphaces ferruginea Dallas 1851	-	+	-	CF
Amphaces proxima Dallas 1851	-	+	-	CF
Amphaces subrufescens (Van Duzee 1905)	-	+	-	CF
Andriscus amartus (Dallas 1851)	-	+	+	CF
Andriscus recurvus Walker 1867	-	+	+	Kumar 1974
Andriscus telifer (Walker 1867)	-	+	+	CF
Anischys luteovarius (Westwood 1837)	-	+	+	Kumar 1974
Bebaeus punctipes Dallas 1851	-	-	-	Kumar 1974, CF
Blaudus ruficornis Stål 1872	-	+	+	Kumar 1974
Catadipson aper Breddin 1903	-	-	-	Kumar 1974, CF
Catadipson imernensis (Cachan 1952)	-	-	-	Kment 2005
Catadipson sus Breddin 1906	-	-	-	CF
Cylindrocnemia plana Mayr 1864	-	+	+	Kumar 1974, CF
Cyphostethus tristriatus (Fabricius 1787)	-	+	+	CF
Elasmostethus elasmosthethoides (Breddin 1903)	-	+	+	Breddin 1903, CF
Elasmostethus tenuispinum (Breddin 1903)	-	+	+	Breddin 1903
Elasmostethus sastragaloides (Breddin 1903)	-	+	+	Breddin 1903, CF
Ditomotarsus punctiventris Spinola 1852	-	+	+	Kumar 1974, CF
Duadicus pallidus Dallas 1851	-	+	+	Kumar 1974, CF
Ea australis Distant 1911	-	+	+	Kumar 1974, CF
Elasmostethus atricornis (Van Duzee 1904)	-	+	+	Thomas 1991, Carter & Hoebeke 2003
Elasmostethus cruciatus (Say 1831)	-	+	+	Thomas 1991
Elasmostethus interstinctus (Linnaeus 1758)	-	+	+	Pendergrast 1953, Thomas 1991, CF
Elasmostethus minor Horváth 1899				CF
Elasmucha amurensis Kerzhner 1972	-	-	-	CF
Elasmucha aspersa (Walker 1867)	-	-	-	Kumar 1974
Elasmucha cordillera Thomas 1991	-	-	-	Thomas 1991
Elasmucha dorsalis (Jakovlev 1876)	-	-	-	CF
Elasmucha ferrugata (Fabricius 1787)	-	-	-	Kumar 1974, CF
Elasmucha fieberi (Jakovlev 1865)	-	-	-	CF
Elasmucha flammatum (Distant 1974)	-	-	-	Thomas 1991
Elasmucha grisea (Linnaeus 1758)	-	-	-	Pendergrast 1953, Kumar 1974, CF
Elasmucha lateralis (Say 1831)	-	-	-	Thomas 1991, CF
Elasmucha nipponica (Esaki & Ishihara 1950)	-	-	-	CF
Elasmucha punctata (Dallas 1851)	-	-	-	Kumar 1974
Elasmucha putoni Scott 1874	-	-	-	Kumar 1974, CF
Elasmucha salebrosa (Breddin 1903)	-	-	-	Breddin 1903, CF
Elasmucha signoreti Scott 1874	-	-	-	Kumar 1974, CF
Elasmucha truncatula (Walker 1867)	-	-	-	Kumar 1974
Esbenia major Jensen-Haarup 1931	-	+	+	Kumar 1974
Esbenia minor Jensen-Haarup 1931	-	+	+	CF
Eupolemus picturatus Distant 1910	?	?	?	Kumar 1974
Galgacus labidus (Erichson 1842)	-	-	+	Kumar 1974, CF

Elasmucha (Fischer 1993, 1994a). Females that protect eggs and nymphs against predators and parasitoids should have a higher fitness. Indeed, the maternal care of the *Elasmucha* females is very effective (Frost & Haber 1944; Strawinski 1951; Jordan 1958; Melber et al. 1980; Melber & Schmidt 1984; Honbo & Nakamura 1985; Kudo et al. 1989; Mappes & Kaitala 1994) with nearly 100 % of the deposited eggs surviving. If maternal care is an effective way of protecting eggs and nymphs against predators and parasitoids, and if the secretion of Pendergrast's organs has a protective function, Pendergrast's organs became absent, but not before maternal care evolved in the stem-lineage of *Elasmucha*.

Why do phytophagous insects have to protect their eggs?

Additional support for the function of Pendergrast's organs can be gained from a comparison to the biology of other phytophagous insects. With the exception of Asopinae, all Pentatomoidea are phytophagous (Schaefer & Ahmad 1987). Phytophagous insects face several problems and require evolving solutions to these problems. Mitter et al. (1988) gave a general outlook on the evolutionary steps that insects have to confront when crossing the barrier between zoophagy and phytophagy. Phytophagy not only means exploiting the nutrient resources of plants, but also involves ethological and morphological characters that can be attributed to phytophagy. Females of a phytophagous species often lay their eggs on the host-plants, which the nymphs can use as a food resource. After hatching, the nymphs are already on the host-plant. Choosing the food plant as an oviposition site is certainly an advantage for the offspring, but causes some disadvantages, too. Eggs that are deposited on plants are exposed and therefore easily visible and accessible for predators and parasites. To minimise the loss of eggs, females insert eggs into the plant tissues or protect them by chemical or behavioural strategies (Hilker 1994).

Materials and Methods

Specimens of 60 species of Acanthosomatidae and Lestoniidae were studied by the author; bring the total number of species observed to more than 100 (Tab. 1). Specimens in the collection of the following museums were studied: British Museum of Natural History London, American Museum of Natural History New York, Museum für Naturkunde der Humboldt-Universität Berlin, Naturhistorisches Museum Vienna, National Museum of Natural History Washington, Zoological Collection of the Zoological Institute of Freie Universität Berlin, Staatliches Museum für Naturkunde Karlsruhe, Zoological Museum of St. Petersburg, Zoological Museum University of Copenhagen.

The mating and oviposition behaviour of *Cyphostethus tristriatus* was observed in the field (Eschwege, Germany). Four males and three females of *Cyphostethus tristriatus* were collected in the field and kept in insect boxes (20 cm x 20 cm x 10 cm) in the laboratory. Branches of *Juniperus communis* were placed in the boxes to provide resources as food and oviposition sites for *Cyphostethus tristriatus*.

Macrophotographs were used to prepare ink drawings of the oviposition behaviour.

The biological role of Pendergrast's organs

Different functions of the Pendergrast's organs in several biological contexts had been assumed previously 1) mating and 2) egg laying self-stimulation and/or egg smearing (see introduction).

Mating behaviour of *Cyphostethus tristriatus*

Males approach the female from behind. With his antennae the male drums the female's abdomen at first, then the thorax and the head. While the male mounts on the dorsum, he continues drumming with his antennae. Finally, the male exposes his genital capsule and makes contact with the female's genital segments. Still maintaining the contact with the female genitalia, the male turns to the right side and dismounts from the female dorsum. This procedure re-

	V	VI	VII	Reference
Hellica nitida Haglund 1868	-	-	+	CF
Hiarchas crassicornis (Walker 1867)	?	?	?	Kumar 1974
Hyperbius geniculatus (Signoret 1863)	-	+	+	Kumar 1974, CF
Ibocoris ficivora Roche 1947	-	-	-	Kumar 1974, Kment 2005, CF
Laccophorella bornemiszae Horváth 1904	-	+	+	Kumar 1974, CF
Lanopis rugosus Signoret 1863	-	+	+	Kumar 1974
Lindbergicoris armifer (Lindberg 1934)	-	+	+	Zheng & Wang 1995
Lindbergicoris difficilis (Liu 1988)	-	+	+	Zheng & Wang 1995
Lindbergicoris distinctus (Liu 1988)	-	+	+	Zheng & Wang 1995
Lindbergicoris elegans Zheng & Wang 1995	-	-	+	Zheng & Wang 1995
Lindbergicoris elegantulus Zheng & Wang 1995	-	-	+	Zheng & Wang 1995
Lindbergicoris forfex (Dallas 1851)	-	+	+	Zheng & Wang 1995
Lindbergicoris hochii (Yang 1933)	-	+	+	Zheng & Wang 1995
Lindbergicoris pulchellus Zheng & Wang 1995	-	-	+	Zheng & Wang 1995
Mahea andriai (Cachan 1952)	-	-	-	Kment 2005
Mahea distanti Kment 2005	-	-	-	Kment 2005
Mahea durrelli Kment 2005	-	-	-	Kment 2005
Mahea parvula Kment 2005	-	-	-	Kment 2005
Mahea sexualis Distant 1909	-	-	-	Kment 2005
Mazanoma variada Rolston & Kumar 1974	-	+	+	Rolston & Kumar 1974
Microdeuterus aequalis Walker 1867	-	-	+	CF
Microdeuterus megacephalus (Herrich-Schaeffer 1845)	-	-	+	Kumar 1974, CF
Mochus fortis Distant 1910	?	?	?	Kumar 1974, CF no females
Monteithiessa distincta Kumar 1974	-	+	-	Kumar 1974
Nopalis sulcatus Signoret 1863	-	-	+	Kumar 1974, CF
Noualhierida rufa Cachan 1952	?	?	?	Kment 2005
Noualhieridia marginata Cachan 1952	?	?	?	Kment 2005
Noualhieridia ornatula Breddin 1898	-	+	+	Kumar 1974, Kment 2005
Oncacontias brunneipennis Breddin 1903	-	+	+	Breddin 1903
Oncacontias vittatus (Fabricius 1787)	-	+	+	Pendergrast 1953, Kumar 1974, CF
Panaetius lobulatus Stål 1866	-	+	+	Kumar 1974, CF
Phorbanta variabilis (Signoret 1863)	-	-	-	CF
Planois bimaculatus (Spinola 1852)	-	+	+	Kumar 1974, CF
Praesus incarnatus Stål 1872	-	-	2	Kumar 1974
Proctophantasta colax Breddin 1903	-	-	-	Kumar 1974, CF
Proctophantasta diabolus Breddin 1903	-	-	-	CF
Proctophantasta pseustes Breddin 1903	-	-	-	CF
Rhopalimorpha alpina (Woodward 1953)	-	+	+	Kumar 1974
Rhopalimorpha lineolaris Pendergrast 1950	-	+	+	Pendergrast 1953, Kumar 1974, CF
Rhopalimorpha obscura Dallas 1842	-	+	+	Pendergrast 1953, Kumar 1974
Sangarius paradoxus Stål 1866	-	-	+	Kumar 1974
Sastragala guttasanguiis Breddin 1903	-	-	-	CF
Sastragala scutellata (Scott 1874)	-	-	-	CF
Sinopla perpunctatus Signoret 1863	-	+	+	Kumar 1974, CF (some ♀♀ without, some with p.o. on VII or VI+VII)
Sniploa obsoletus Signoret 1863	+	+	+	Kumar 1974, CF
Stauralia chlorocantha Dallas 1851	-	-	+	CF
Stauralia compuncta Bergroth 1895	-	-	+	CF
Tolono decoratus Rolston & Kumar 1974	-	-	+	Rolston & Kumar 1974
Uhlunga typica Distant 1892	-	-	-	Kumar 1974, CF
Xosa lugubris (Thunberg 1822)	-	+	+	Kumar 1974, CF

grooming behaviour of Heteroptera

take up dirt from abdomen

brush off uptaken dirt from hindtarsi

egg-smearing behaviour of Acanthosomatidae

take up secretion from setae of pendergrast organ

apply secretion onto egg

spin and rotate egg

place sac with symbiont onto egg

egg-smearing behaviour of *Apiomeris* (Reduviidae)

take up secretion from abdominal setose area

apply secretion onto eggs

set of structure and process

wiping hindtarsi over abdomen in a dorso-ventrally direction

rubbing hindtarsi against each other

Fig. 9: Diagram showing the homologization of grooming behaviour with egg-smearing behaviour in Acanthosomatidae (Pentatomoidea) and *Apiomeris flaviventris* (Reduviidae). As the egg-smearing behaviour in both taxa are derived from the grooming behaviour, but the smearing behaviour itself is not homologous, this case qualifies as an example of homoiology (refer to text for further information and discussion).

sults in a rotation of the male genitalia segments of 180°. While the tail-to-tail copulation position is kept for several hours, the couple is able to walk around. Typically, the female goes in front with the male walking backwards. When not walking around, the male and female hold their abdomens in an elevated position, forming an angle of about 30°. During these periods, the couple performs jerky vertical and faint lateral body movements. Finally, the female drums the male pregenital abdominal segments with her hindtarsi. During 16 hours of observation on four mating pairs, neither the male nor the female was ever observed touching the Pendergrast's organs. Pendergrast's organs were not involved in mating behaviour or copulation.

Oviposition in *Cyphostethus tristriatus* and the involvement of the Pendergrast's organs

Immediately after copulation, which can last a couple of days, the females can be observed searching for an oviposition site.

Oviposition starts with heavy contractions of the genital segments of the female. The egg's movement can be observed through the slightly opened genitalia plates. The egg is then rotated within the vagina for several seconds before it eventually leaves the vagina, passing the now fully opened genitalia plates. The glue for attaching the egg to the plant surface is clearly visible on the pole of the egg as it emerges. The egg is attached to the plant surface in an upright orientation. However, the glue does not harden until the female puts the secretions of the Pendergrast's organs onto the egg.

Repeatedly the female touches the setose areas of the Pendergrast's organs with the distal part of the hindtibia and hindtarsi about five times. The secretion is transferred onto the surface of the egg while the female spins the egg around 360°. During this treatment, the egg remains glued to the plant surface. The egg is moved around by the hindleg, which has been touching the Pendergrast's organs, while the other hindleg gives support to the distal end of the egg, where it is glued to the plant surface.

A typical egg-clutch of *Cyphostethus tristriatus* comprises 14 eggs, which are arranged in two parallel rows on a needle of *Juniperus communis* (see Tab. 2). The number of eggs per clutch corresponds well with the number of ovarioles. Each of the two ovaries of *Cyphostethus tristriatus* is composed of seven telotrophic ovarioles, each producing at least four eggs. At a given time, fourteen eggs are within a corresponding developmental stage.

However, there are deviations from the number of fourteen eggs within the egg-clutch and from the arrangement of the clutch. Two egg-clutches were laid onto the plain surface of the insect boxes. These two clutches lacked the typical arrangement of the eggs in two rows. This may indicate that the needle of *Juniperus* is essential to provide
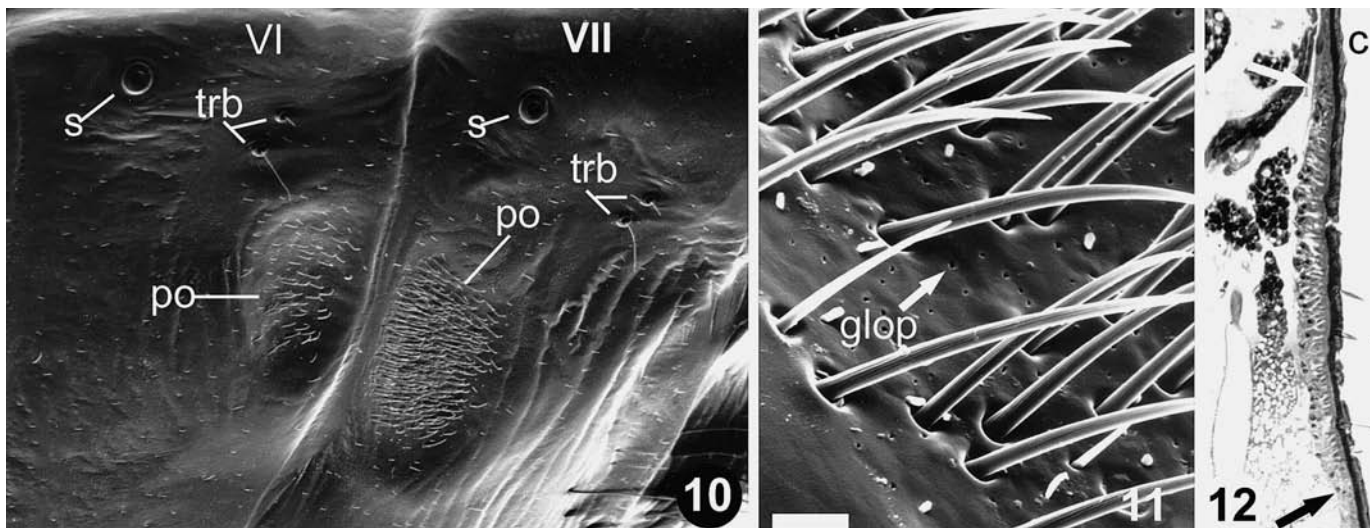
Figs 10-12: Morphology of Pendergrast's organs of female *Elasmostethus interstinctus* (Acanthosomatidae) (**10**) SEM-photograph of pregenitalia segments VI and VII. There are less bristles on the abdominal segment VI than on the abdominal segment VII (**11**) The ductules of the subepidermal gland cells open into pores (glop) between the bristles. (**12**) semi-thin-section of Pendergrast's organs. Epidermis underlaying the setose area of the Pendergrast's organs is much thicker (arrows) (modified from Fischer 1993). Glop = pore opening of gland cells, Po = Pendergrast's organs, S = stigma, Trb = trichobothria.

some structural guidance for female *Cyphostethus tristriatus* to produce a two-row egg-clutch. In those cases where the female laid fewer than 14 eggs she might have been disturbed and was consequently not able to lay a 14 egg clutch.

Placement of symbiont droplet

The placement of the symbiont droplet has never been taken into consideration to be involved with the Pendergrast's organs. As the present study aimed to describe the whole process of oviposition of *Cyphostethus tristriatus*, the placement of the symbiont droplet was carefully observed. There is no evidence of any involvement of the Pendergrast's organs in the symbiont droplet transfer.

Shortly after the egg is deposited, a brown secretion sac becomes visible, which issues from the female genital opening. The brown sac is moved under the egg using the hindlegs. The brown sac contains microsymbionts, which are essential for the hatched nymph (MÜLLER 1956). Immediately after hatching, the nymphs suck on the contents of the brown sac. Before the next egg is issued, the female moves fore- and backward repeatedly touching the just deposited egg with the bristles of the genitalia plates.

The placement of the microsymbiontical sac in Acanthosomatidae differs from that of Pentatomidae. In Pentatomidae the microsymbiontical droplet is placed in the gap between the eggs. In contrast to other pentatomoid Heteroptera, females of Acan-thosomatidae bear unique symbiont transfer organs (ROSENKRANZ 1939; FISCHER 1993). A fold of the second valviferes enveloped by the first valviferes forms this paired structure.
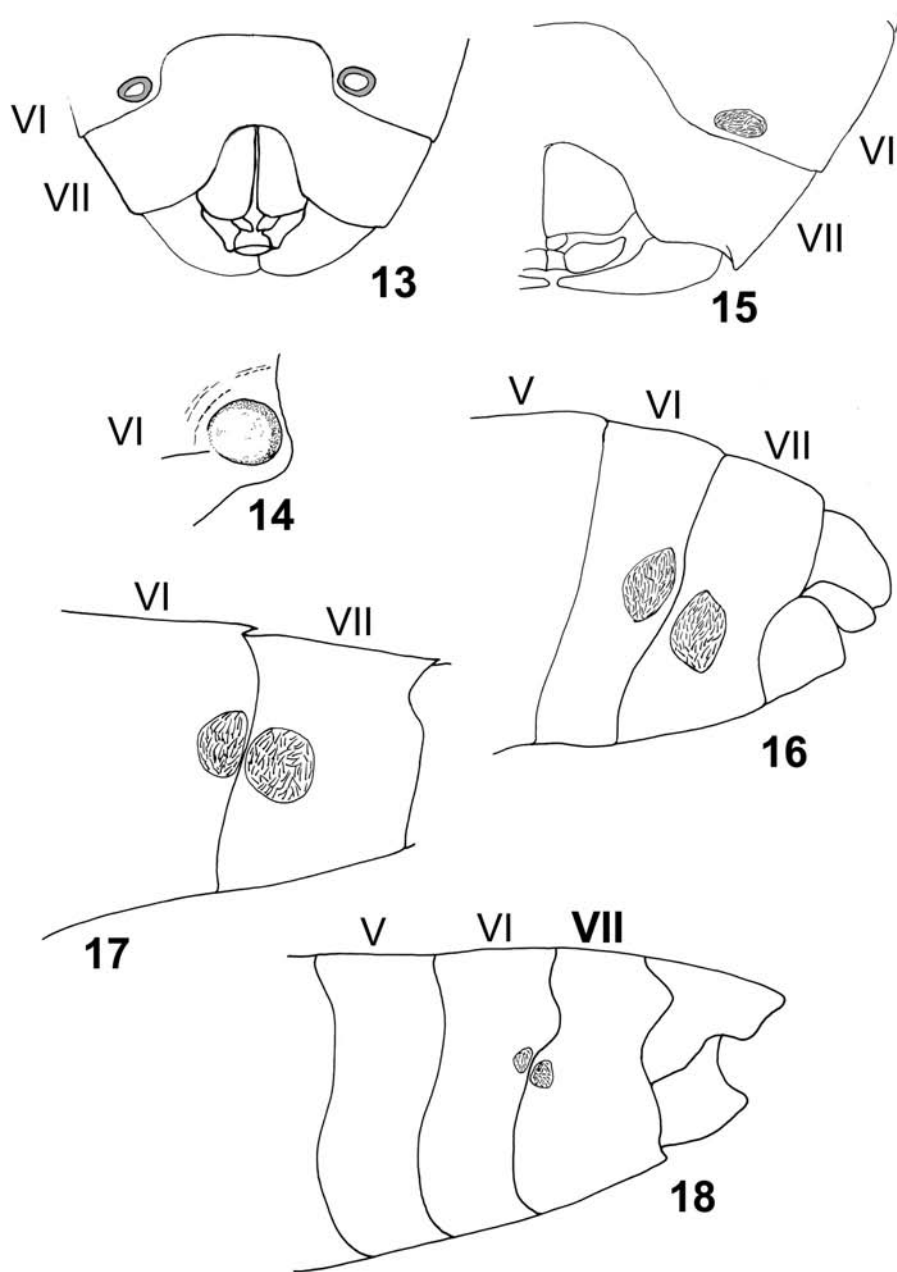
Presence of Pendergrast's organs in Acanthosomatidae-species

The presence of Pendergrast's organs in Acanthosomatidae has been recorded and studied by numerous authors (BREDDIN 1903; PENDERGRAST 1953; KUMAR 1974; ROLSTON & KUMAR 1974; THOMAS 1991; FISCHER 1993,1994a, 1994b, 2000; ZHENG & WANG 1995; CARTER & HOEBEKE 2003). Since then, several new Acanthosomatidae species have been described.

For the first time, a list of acanthosomatid species is presented referring to the presence of Pendergrast's organs. So far, this is the most comprehensive data available of Pendergrast's organs in Acanthosomatidae. Table 1 includes data from literature as well as results of my own studies. The data of species, which had been studied by others, were checked as far as specimens were available. Tab. 1 also includes acanthosomatid species, where data with respect to the Pendergrast's organs is not available. In most of

Tab. 2: Egg-clutch size of *Cyphostethus tristriatus*.

Egg-clutch no.	Number of eggs	Shape of clutch	Egg-clutch attached to
1	14	two parallel rows	needle of *J. communis*
2	14	two parallel rows	needle of *J. communis*
3	12	two parallel rows	needle of *J. communis*
4	9	two parallel rows	needle of *J. communis*
5	14	two parallel rows	needle of *J. communis*
6	3	not arranged	insect box
7	16 + 4	not arranged	insect box

Figs 13-18: Pendergrast's organs on female pregenitalia segments of Acanthosomatidae **(13)** ventral view of abdomen of *Amphaces ferruginea* **(14)** Pendergrast´s organs of *Amphaces ferruginea* on abdominal segment VI with raised cuticular ring **(15)** ventral view of abdomen of *Amphaces elongata* **(16-18)** lateral view of abdomen **(16)** *Ea australis* **(17)** *Xosa lugubris* **(18)** *Esbenia minor*.

ever, there are several deviations from this stem-species pattern. In all these species, except two, we find a reduced number of Pendergrast´s organs. Pendergrast's organs are present only on the abdominal segment VI in four *Amphaces*-species (Figs 13-15). However, KUMAR (1974) noted *Elasmostethus nebulosum* and *Monteithiessa distincta* also possess this condition, but I have been unable to verify these data.

In all of the investigated species of *Abulites*, *Aesepus*, *Duadicus*, *Microdeuterus* (Fig. 19), *Nopalis*, *Sangarius*, *Stauralia* and *Tolono*, Pendergrast's organs are present only on the abdominal segment VII. While most of the species of the genus *Lindbergicoris* resemble the stem-species pattern of Acanthosomatidae with respect to the Pendergrast's organs, *L. pulchellus*, *L. elegantulus* and *L. elegans* have Pendergrast's organs only on abdominal segment VII. In contradiction to KUMAR (1974), Pendergrast's organs in *Galgacus labidus* are only present on abdominal segment VII based on my own observations. In species of the genera *Agamedes*, *Bebaeus*, *Catadipson*, *Mahea*, *Phorbanta*, *Elasmucha*, *Ibocoris*, *Proctophantasta* (Figs 20-21), and *Uhlunga*, Pendergrast's organs are totally absent.

Sniploa obsoletus and *Praesus incarnatus* are unique with regard to the number and shape of setose areas. In *Sniploa obsoletus* the setose area of the Pendergrast's organs not only covers the abdominal segments V, VI and VII, but also forms a uniform, single area (Fig. 22). *Praesus incarnatus* differs from all other Acanthosomatidae in having two setose patches on each side of abdominal segment VII, but lacks setose areas on any other abdominal segments. I have not been able to check any specimens of *Praesus incarnatus* and the description of KUMAR (1974) does not reveal any further details. Therefore, it is pure speculation whether the pair of setose areas develops from a single patch, which became divided during ontogenesis or is the result of duplication.

Setose areas on the abdominal segments of male Acanthosomatidae

While this study deals with the setose areas of Pendergrast's organs of female Acanthosomatidae, it is noteworthy to

these cases, females were not present in the studied collections or specimens were of questionable condition.

The results of this study corroborate most of the data of previous investigations, but reveal some conflicts and contradictions. In Acanthosomatidae, Pendergrast's organs can be present on the female abdominal sterna of segment V, VI and VII. Nearly half of the investigated Acanthosomatidae-species have Pendergrast's organs on abdominal segments VI and VII. This character state represents the stem-species pattern of Acanthosomatidae based on cladistic analyses (FISCHER 1993, 1994, 2000). How-

mention some unique features of the male abdomen found in two acanthosomatid species. In *Panaetius lobulatus* both sexes possess setose areas on the posterior pregenitalian segments. While Pendergrast's organs are present on the female abdominal segments VI and VII (Figs 23, 24), setose areas are also present on the male abdominal segments V, VI and VII (Figs 25, 26). The setose areas of the male *Panaetius lobulatus* specimens resemble the morphology of the female Pendergrast's organs. The male setose areas are shallow grooves with numerous bristles and pores. These similarities with the Pendergrast's organs of the female might allow us to assume that the male setose areas have a glandular character. In contrast to the female setose areas, the males have an additional paired setose area on abdominal segment V. There are no detailed morphological, chemical, or behavioural studies. STADDON (1990) described male sternal pheromone glands in Acanthosomatidae from Great Britain. However, these glands are typically present on the pregenital segments V and VI. In male *Acanthosoma haemorrhoidale* and *Elasmucha grisea* gland areas are present on the sterna of the abdominal segments III, IV, V, and VI. In contrast to the setose areas of male *Panaetius lobulatus*, the sternal gland areas of male *Acanthosoma haemorrhoidale*, *Cyphostethus tristriatus*, *Elasmostethus interstinctus*, and *Elasmucha grisea* bear neither bristles nor shallow grooves.

As nothing is known about the biology of *Panaetius lobulatus*, an ad hoc hypothesis that the male setose areas do have a similar function as proposed for the females is no more than speculation, but can provide some interesting predictions on the male behaviour. The males of *Panaetius lobulatus* should perform paternal investment by transferring their own secretion to the female or directly onto the eggs.

Another unique feature of the male abdomen is found in *Mochus fortis*. A long, inclined groove is present on the abdominal segment V (Fig. 27). The groove starts with a slight impression until it reaches its deepest point in the segment midline. The shape and proportions resemble those of the hindtarsus. Nothing is known about the biology
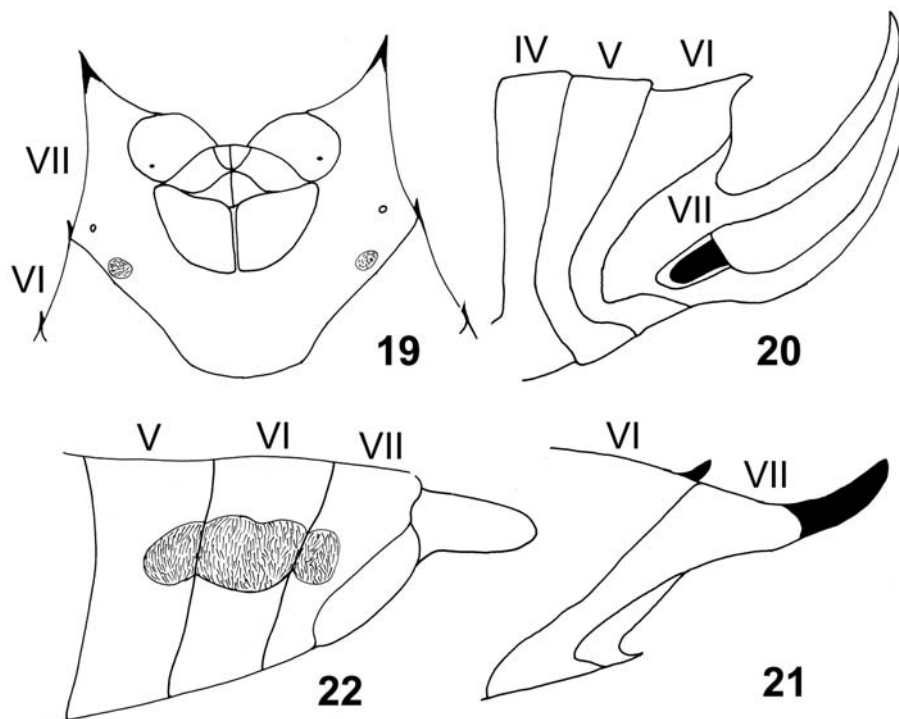

of *Mochus fortis* and there is no data available on the presence of Pendergrast's organs in female *Mochus fortis* (see Tab. 1).

Although I discuss a similar function of the male setose areas to the female Pendergrast's organs at least for *Panaetius lobulatus*, another likely hypothesis may be that these areas produce pheromones, which may play an important role during the mating behaviour. Sternal abdominal gland areas are described as occurring in both sexes of diverse Pentatomoidea (CARAYON 1981; STADDON 1990). It will be a subject for future investigations to address these interesting questions.

Discussion

It is evident from this study on the mating and oviposition behaviour of *Cyphostethus tristriatus* that Pendergrast's organs function only within the context of oviposition. The same behaviour is known from two other European and one North American acanthosomatid species: *Acanthosoma haemorrhoidale* (FISCHER 1993), *Elasmostethus interstinctus* (Fischer unpubl.), and *Elasmostethus atricornis* (CARTER & HOEBEKE 2003). Although some questions on the biological role of the Pendergrast's organs still remain unanswered, two major aspects of

Figs 19-22: Transformations of Pendergrast's organs within the Acanthosomatidae (**19**) ventral view of the abdomen of *Microdeuterus megacephalus*. Only a small, paired setose area is present on the abdominal segment VII (**20**) lateral view of the abdomen of *Proctophantasta pahangiensis*. Pendergrast's organs are absent. *Proctophansta* is closely related to *Elasmucha*, which perfom maternal care (**21**) lateral view of abdomen of *Proctophantasta colax* (**22**) lateral view of the abdomen of *Sniploa obsoletus*. Note the extended setose area, which covers the abdominal segment V, VI and VII. This is an unique feature within the Acanthosomatidae.
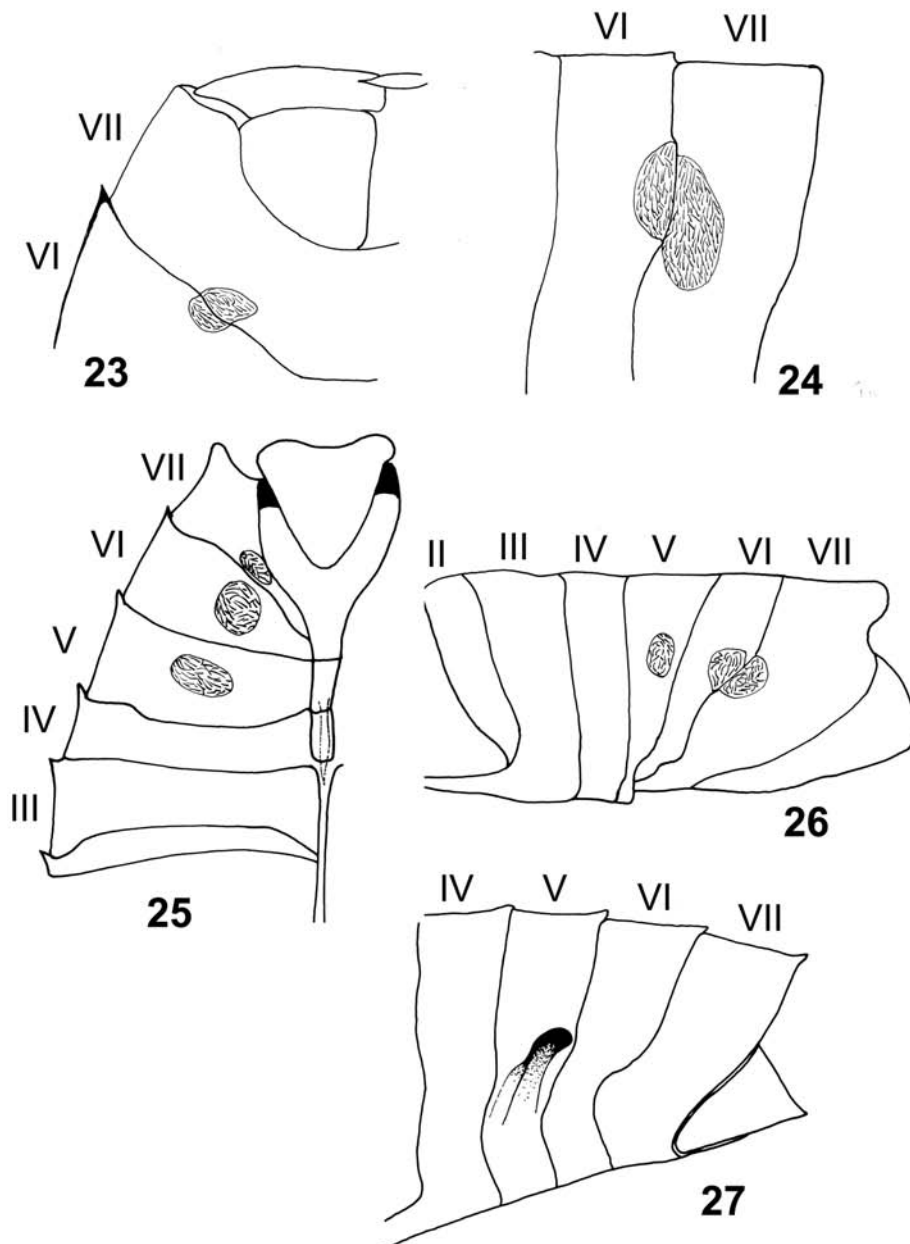
Figs 23-27: Setose areas of female and male Acanthosomatidae (**23**) ventral view of the female abdomen of *Panaetius lobulatus* (**24**) lateral view of the female abdomen of *Panaetius lobulatus* (**25**) ventral view of the male abdomen of *Panaetius lobulatus* (**26**) lateral view of the male abdomen of *Panaetius lobulatus* (**27**) lateral view of the male abdomen of *Mochus fortis*. Abdominal segment V has an inclining groove.

the Pendergrast's organs are clear: the biological context and morphological-behavioural function. These two results provide a sound basis for addressing one of the always-new „old" questions of evolutionary biologists: How did this complex of structures and behaviour evolve?

Evolution of smearing behaviour is derived from grooming

Every morphological structure and behavioural character is used in a specific biological context. Behavioural characters are properties of an organism just like morphological characters are properties of an organism. Both are subject to natural selection.

Some characters can have a main function and one or more additional functions. In evolutionary terms, we assume that both functions were present in the past, with the main function preceding the additional function. In some cases the main function can be reduced or totally lost and it is only the additional function that persists.

The concept of homology and evolutionary transformation can be applied to all properties of organisms. As behavioural characters are properties of an organism, we can make hypotheses on the homology of behavioural characters.

The oviposition of Acanthosomatidae is composed of several behavioural aspects and morphological structures. Females touch the setose areas of their Pendergrast's organs, rubbing the tarsi onto the eggs, spinning the egg and finally placing the symbiont sac under the egg. This reveals that the hind legs are used in a rather elaborate way. On the morphological side, we have to note the evolution of sternal abdominal glands and the setose areas to hold and store the secretion.

How did this complex of behaviour and structure evolve? To take this question a step further: What was first: behaviour or structure?

An answer to this question can be given easily as it is true for nearly all organisms. Most evolutionary changes start with a change of behaviour. But what did each component of this behavioural-morphological complex of oviposition of Acanthosomatidae derive from? In order to address this question, the oviposition complex has to be taken in pieces (Fig. 9).

Homology of behavioural elements in oviposition

Oviposition of acanthosomatid species is composed of several behavioural elements. In fact, there are two main sub-complexes: deposition of the egg and applying the secretion of the Pendergrast's organs onto the eggs. In evolutionary terms, the placement of an egg within the clutch is achieved by the position of the genitalia opening and the hindlegs to arrange the form of the clutch is a common shared char-

acter of pentatomoidean taxa. Females produce an egg clutch in which the eggs are carefully arranged in parallel rows. The hindlegs are used to place an egg next to the previously deposited egg. Sensilla on the genital plates seem to play an important role in achieving the complex egg clutch arrangement. As soon as the egg is placed in the right position the female touches the egg clutch with her genital plates while moving her body for- and backwards and swinging from left to right. Eventually the female moves her body slightly forwards and either to the left or to the right, depending where the next egg is going to be placed within the clutch.

The second sub-complex of oviposition in Acanthosomatidae refers to the application of the secretion of the Pendergrast's organs onto the eggs. In this section, I will particularly focus on the behavioural elements. After the egg is deposited on the leaf, the female rubs the Pendergrast's organs on her abdomen with her hind legs. With the hindtarsi she takes up and transfers the secretion onto the eggs. This behaviour resembles the grooming behaviour of other Heteroptera (FISCHER & ZAKRZEWSKI 2005). Bugs are grooming their abdomen with their hindlegs (Figs 7, 8). The hindlegs start rubbing across the abdomen. Numerous bristles on the hindtarsi function as a brush to wipe off dirt and other particles from the abdominal sternites and pleurites. The hindlegs even reach the abdominal tergites and wings. Dirt accumulated in bristles of the hindtarsi is brushed off by rubbing both hindtarsi against each other. While the bugs keep attached to the substrate with the fore and middle legs, the hindlegs are totally stretched posteriorly (Fig. 8). Both structure and process of grooming behaviour and applying the Pendergrast's organs secretion onto the eggs are very similar. Based on these similarities I conclude that the grooming behaviour and the transfer behaviour of Pendergrast´s organs secretion is homologous.

The homology of grooming behaviour and the transfer of Pendergrast's organs secretion provokes the question which is plesiomorphic and which apomorphic. Grooming the abdomen with the hindlegs belongs to the stem-species pattern of Heteroptera.

As the Pendergrast's organs on the abdominal segment VII are an apomorphy of the stem-species of Acanthosomatidae + Lestoniidae the behavioural elements in transferring the secretion have to be considered as an apomorphy of the stem-species of Acanthosomatidae + Lestoniidae too. Rubbing the hindlegs across the abdomen has to be homologised with grooming (main function) and the transfer of Pendergrast's organs secretion is an additional function which evolved in the common ancestral lineage of Acanthosomatidae + Lestoniidae.

Evolution of Pendergrast's organs

As described in detail in the morphology section, Pendergrast's organs are a complex of abdominal epidermal glands with pores opening into abdominal grooves. Numerous bristles hold the secretion, which is taken up by the hindtarsi. Epidermal glands are present in all insects. Many pentatomoid Heteroptera have sternal gland complexes on the abdominal segments (CARAYON 1981; STADDON 1990). Sternal abdominal glands may be already present in the stem-species of Acanthosomatidae + Lestoniidae. Using the hindtarsi for grooming and oviposition it may have occurred that particles from the abdomen have been transferred to eggs, but also secretion from the sternal abdominal glands. In the beginning, the secretion of these glands should have small effect on the eggs. However, they should not decrease the viability of eggs. Within the population, a variability of the secretion components has to be assumed. Females that produce secretion with protective chemical components should have an increased fitness. Over time, there should be an increase of females within the population producing protective secretion.

Why are Pendergrast's organs present solely on the posterior pregenitalic segments? The midline of the abdominal segments VI and VII are within an area that can be reached most easily by the hindtarsi during the grooming behaviour. In fact, setose areas of the Pendergrast's organs evolved first on the abdominal segment VII. This viewpoint is supported by the reconstructed stem-species pattern of Acanthosomatidae + Lestoniidae. The anterior abdom-

inal segments are much more difficult to reach. In fact, no Pendergrast's organs are present on the abdominal segments II, III, IV or V. There are more species that lack Pendergrast's organs on the abdominal segment VI than species that lack Pendergrast´s organs on the abdominal segment VII.

In a next hypothetical step, grooves and bristles evolved. Grooves and bristles are able to hold back the secretion. Additionally, a bigger amount of secretion can be easily stored and picked up for use in a single transfer. While the majority of acanthosomatid species have shallow grooves, some species evolved deeper grooves. Another evolutionary solution to achieve a bigger storage evolved in *Sniploa obsoletus*, where females possess a unique large area of Pendergrast's organs (Fig. 22). The Pendergrast's organs on the abdominal segments V, VI and VII is enlarged and fused to form a uniform Pendergrast's organs. A different way of increasing the volume of setose areas can be found in the genus *Amphaces*. The cuticle grooves are deeper than in other species and are surrounded by an additional cuticular ring (Fig. 13). *Amphaces*-species have Pendergrast's organs only on the abdominal segment VI, while Pendergrast's organs are absent on the abdominal segment VII. The presence of a double pair of setose areas on the abdominal segment VII in *Praesus incarnatus* is unique in Acanthosomatidae (KUMAR 1974). However, *Praesus incarnatus* lacks Pendergrast's organs on abdominal segment VI.

Pendergrast's organs are totally absent in species of the genera *Agamedes*, *Bebaeus*, *Catadipson*, *Elasmucha*, *Ibocoris*, *Mahea*, *Phorbanta*, *Proctophantasta*, and *Uhlunga*. The absence of Pendergrast's organs in *Elasmucha*-species correlates with the presence of maternal care, which the females of these species perform (FROST & HABER 1944; STRAWINSKI 1951; JORDAN 1958b; MELBER et al. 1980; MELBER & SCHMIDT 1984; HONBO & NAKAMURA 1985; KUDO et al. 1989). The females guard their eggs and nymphs. *Catadipson*, *Ibocoris*, *Proctophantasta*, and *Uhlunga are* closely related to *Elasmucha* (FISCHER 1993). Corresponding studies to these of *Elasmucha*-species are welcome for these African and Oriental species.

Egg-clutch protection in *Apiomeris flaviventris*: A case of homoiology

Most interestingly, females of the reduviid *Apiomeris flaviventris* have similar structures, and perform a behaviour, which shows some remarkable similarities to the oviposition behaviour of Acanthosomatidae-species that possess Pendergrast's organs. *Apiomeris flaviventris* bears setose areas on its abdominal segments and uses camphor, which it takes from plants not only to hunt prey but also to protect its eggs against predators and parasites (EISNER 1988). Camphor is known to be a very effective insecticide. In contrast to the Acanthosomatidae, *Apiomeris flaviventris* does not produce a repellent by itself, but rather is able to use a plant repellent, which evolved to protect the plant against insects.

The analogous behaviour and structures of *Apiomeris flaviventris* and Acanthosomatidae can be used to support the egg-protection hypothesis proposed for Acanthosomatidae. Moreover, the above-discussed hypothesis on the evolution of egg-smearing behaviour in Acanthosomatidae gains further support. It clearly shows that comparable evolutionary pressure leads to similar solutions under the given constraints and possibilities of the same body plan.

Females of *A. flaviventris* take up camphor fluids from plants with their tarsi and store them in unique setose patches on the venter of the abdominal segments. This reduviid species catches prey by using its forelegs. The stored camphor fluids are applied onto the foretibia, which exhibits an enormous area of bristles (fossula spongiosa). Females also transfer camphor fluids to their egg-clutches. The fluids are taken up by the hindtarsi rubbing across the setose areas on the abdomen.

The egg-smearing behaviour of *A. flaviventris* shows remarkable similarities with both the grooming behaviour and the smearing behaviour described for Acanthosomatidae. The similarities of the egg-smearing behaviour of *A. flaviventris* with the grooming behaviour can be easily interpreted as homologous (Fig. 9). Arguments that are used to homologize the smearing behaviour of Acan-

thosomatidae with the grooming behaviour can be applied in the same manner. However, the egg smearing of Acanthosomatidae and A. *flaviventris* is not homologous. There is no support for a close relationship, i.e. sistergroup relationship, of A. *flaviventris* and Acanthosomatidae. *Apiomeris flaviventris* belongs to the Reduviidae which are a subordinated taxon of the Cimicomorpha. Acanthosomatidae are a subordinated taxon of Pentatomoidea, which belong to the Pentatomomorpha, the sistergroup of the Cimicomorpha. As no further cases of such an egg-smearing behaviour in other cimicomorphan and pentatomomorphan species have been described, it is most parsimonious to assume a convergent evolution of egg-smearing in A. *flaviventris* and the Acanthosomatidae. If the hypothesis of homology of egg smearing of these both taxa would be proposed one would be forced to assume that their last common stem-species would have that property, whilst it got lost in all other taxa. This is not very parsimonious.

In summary the egg smearing in A. *flaviventris* and Acanthosomatidae evolved independently, but derived from the homologous grooming behaviour. This type of convergent evolution based on a homologous pattern is named homoiology.

Acknowledgements

Zusammenfassung

Die vorliegende Studie fasst alle bisherigen morphologischen Untersuchungen und Hypothesen zur Funktion der Pendergrast'schen Organe der Acanthosomatidae zusammen. Zum ersten Mal wird das Vorhandensein von Pendergrast'schen Organen bei über 100 Acanthosomatidae-Arten aufgelistet. Evolutive Transformationen der Pendergrast'schen Organe innerhalb der Acantho-

somatidae werden dargestellt und diskutiert. Das Fortpflanzungs- und Eiablageverhalten von *Cyphostethus tristriatus* wird erstmals beschrieben. Dabei zeigt sich, dass die Pendergrast'schen Organe eine wichtige Rolle bei der Eiablage spielen. Weibchen reiben mit ihren Hintertarsen über das Borstenfeld der Pendergrast'schen Organe, drehen das Ei mehrmals und platzieren es mit ihren Hintertarsen auf der Pflanze. Das Beschmieren der Eier mit den Sekreten der Pendergrast'schen Organe bei den Acanthosomatidae wird als Verhalten mit dem Putzverhalten der Heteropteren homologisiert. Die Evolution der Pendergrast'schen Organe und des damit verbundenen Verhaltens wird Schritt für Schritt erklärt.

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