The evolution of the female postabdomen and genitalia in mecopterid insects (Insecta: Mecopterida)

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1. Introduction

Mecopterida are an immensely diverse group of endopterygote insects with more than 300 000 described species. The lineage comprises the traditional "orders" Trichoptera (caddisflies; 10 500 spp.), Lepidoptera (moths and butterflies; 160 000 spp.), Mecoptera (scorpion flies, hanging-flies and snow fleas; 600 spp.), Siphonaptera (fleas; 2 200 spp.) and Diptera (true flies, crane flies and mosquitoes; 134 000 spp.). As the numbers of species show, Lepidoptera and Diptera belong to the megadiverse groups of organisms; their species richness is only surpassed by Coleoptera (beetles; > 300 000 spp.) and probably Hymenoptera (bees, wasps and saw-flies), with 132 000 species described yet, but possibly the most diverse of insect orders (Grimaldi & Engel 2005).
Mecopterid insects occur in all parts of the world with the exception of the circumpolar regions, and in a large variety of terrestrial habitats. Aquatic habits of larvae have secondarily evolved in several lineages such as Trichoptera, Nannochoristidae, and several groups of Diptera (e.g., Kristensen 1997, Mey 2003, Willmann 2003b, Ziegler 2003). The oldest fossils are known from the upper permian and were assigned to Nannochoristidae (see Willmann 2003b).

The monophyly of Mecopterida was already suggested by Hennig (1969) (see also Kristensen 1975, 1999), and was also supported in recent analyses of combined data sets (Hünefeld & Kjer, unpublished: Fig. 1), the phylogenetic relationships within the group are still highly ambiguous, with the notable exception of the sister-group- relationship between Trichoptera and Lepidoptera, which is arguably the best supported in insect systematics, both from morphological and from molecular evidence (e.g., Hennig 1969, Kristensen 1999, Wheeler et al. 2001; Hünefeld & Kjer, unpublished). The concept of a monophyletic group Antliophora, which has largely been undisputed for several decades (e.g., Hennig 1969, Kristensen 1999, Wheeler et al. 2001), was greatly affected by the rejection of the strongest presumptive synapomorphy of its subgroups, the presence of a sperm pump in the adult males (see Hünefeld & Beutel 2005; but see also Mickoleit 2009). The monophyly of Mecoptera in the traditional sense was seriously challenged (Whiting 2002b) and seems more and more unlikely considering recent molecular and morphological studies. The question of the basal branching events within Antliophora, especially the phylogenetic position of Nannochoristidae, Boreidae, and Siphonaptera, is one of the pertinent problems in recent insect systematics (e.g., Whiting 2002a; Beutel & Baum 2008). Within Diptera, likewise the basal splitting events are discussed controversially (Tipulomorpha or Culicomorpha-Ptychopteromorpha; see, e.g., Hennig 1973, Oosterbroek & Courtney 1995, Sinclair 1992, Wood & Borkent 1989, Wood et al. 1991, Yeates et al. 2003, Yeates & Wiegmann 1999). An inclusion of Strepsiptera into Mecopterida was proposed, namely as the sister-taxon of Diptera (e.g., Chalwatzis et al. 1996, Whiting et al. 1997, Whiting 1998, Wheeler et al. 2001). However, this challenging hypothesis (Halteria concept) is only supported by 18S-rDNA- data so far. Recent phylogenetic hypotheses based on comprehensive morphological and molecular data sets tentatively support a placement of Strepsiptera near the base of Endopterygota, or close to Coleoptera (e.g., Beutel & Gorb 2001, 2006, Bonneton et al. 2006, Kristensen 1999, Kukalová-Peck & Lawrence 2004).

As pointed out in Beutel & Pohl (2006), the lack of well documented morphological data established for a well chosen taxon sampling, is still a major drawback in endopterygote systematics, and also for insects systematics in general. This is true for different body parts and developmental stages and includes the morphology of the female postabdomen, which was hitherto scarcely used in formal phylogenetic investigations of endopterygote insects. The character system as such was addressed in a considerable number of studies on mecopterid taxa (e.g., Davis 1978, Dugdale 1974, Evans 1942, Ferris & Rees 1939, Frommer 1963, Gerry 1932, Herting 1957, Kristensen 1984, 1998, 2003b, Matsuda 1976, Mickoleit 1975, 1976, Mutuura 1972, Rees & Ferris 1939, Schmid 1989, Snodgrass 1935, Willmann 1982, Wood 1891). However, in-detail- information on the internal parts of the female genitalia is restricted to a few representatives, which belong to more or less specialised subordinate taxa, and are therefore not suitable for the reconstruction of the ordinal ground plans (see Grell 1942: *Panorpa*; Nielsen 1980: Trichoptera; Stekolnikov 1967: *Micropterix*, *Eriocrania*). An evolutionary scenario addressing the principal lineages within Amphiesmenoptera was presented by Kristensen (1997). However, this was not based on a formal character evaluation, and detailed accounts addressing the musculature of the female postabdomen were almost completely lacking for presumably basal taxa within the traditional orders. Consequently, the first aim of the present contribution is to improve the morphological knowledge of the female postabdomen of mecopterid representatives and enodpterygote and non-endopterygote outgroup taxa. The understudied character system apparently displays a high number of features that are potentially relevant for the phylogenetic reconstruction of higher-level relationships (see e.g., Mickoleit 1975).

The taxon sampling was focused on presumably basal representatives of the orders, taking into account intra-ordinal phylogenies that are recently discussed. Most of the mecopterid "key taxa" could be included such as representatives of Nannochoristidae, Boreidae, Limoniidae, Tipulidae, Culicidae, Rhyacophilidae, Micropterigidae, Agathiphagidae, and Eriocraniidae. As pointed out above, the species poor Nannochoristidae and Boreidae, both traditionally placed in Mecoptera, are presently under debate with respect to their phylogenetic position. Affinities with Siphonaptera or Diptera or both, were suggested in different combinations (see e.g., Beutel & Pohl 2006; Beutel & Baum, 2008). Culicomorpha and Tipulomorpha are both candidates for a basal position within Diptera, and the same applies to Micropterigidae and Agathiphagidae within Lepidoptera. Agathiphagidae ("Kauri moths") strongly resemble caddis-flies. They comprise only 2 species occurring in Queensland (Australia) and on some South Pacific islands, respectively. Heterobathmiidae, the third non-glossatan family, are most likely the sister-group of Lepidoptera-Glossata; Eriocraniidae represent the basal branch within Glossata. Rhyacophilidae are probably closest to the groundplan of Trichoptera, with free living larvae and largely plesiomorphic wing venation and male genitalia (see Mey 2003). Additionally, a recently described Vietnamese caddisfly, *Fansipangana vernalis* Mey, 1996, addressed as exceptionally "primitive" (Mey, 1996), was examined and its female postabdomen and genitalia described and depicted in detail. The information available from the brief original description of this species was critically evaluated. Strepsiptera, which are potentially the sister group of Diptera (Wheeler et al. 2001, Whiting et al. 1997) were not included, as the female genital apparatus is generally extremely reduced in these insects.

A consistent nomenclature for the musculature of the female postabdomen of insects was not available so far. In almost all studies addressing this character system different individual nomenclatures were used by the authors, which caused considerably terminological confusion. Therefore, in the framework of the present study a new muscle nomenclature is presented using neutral terms and based on estimated homologies throughout the investigated taxa. This approach also allows later additions or corrections by other authors in a convenient way.

A total of 102 characters related to the female postabdomen and genitalia and 8 characters related to the habits of oviposition were defined and coded in a character matrix. This data set was combined with a matrix with larval and adults characters developed in the framework of a comprehensive project (DFG – no.: BE1789/4-1: The phylogeny and evolution of Endopterygota; see **Appendix B**). For outgroup comparison, selected representatives of Orthoptera, Hymenoptera and Neuroptera were included in the cladistic analysis. A preliminary phylogenetic hypothesis is proposed, based on the above mentioned data sets. An evolutionary scenario for the female postabdomen is presented based on the phylogenetic results. The detailed morphological information presented here will be part of a comprehensive morphological data set for a future "total evidence" analysis aiming at reliable clarification of the higher-level- relationships within Endopterygota.

Summarizing, the major aims of the present study are:

(1) improvement of the knowledge on the female postabdomen and genitalia of mecopterid insects

(2) complete inventarisation and homologization of all postabdominal muscles found in the taxa under consideration

(3) an approach to clarify the homology of the ventral sclerotized elements on segments VIII and IX in mecopterid females

(4) a preliminary phylogenetic hypothesis including the information from the female postabdomen

(5) an evolutionary scenario for the character system.

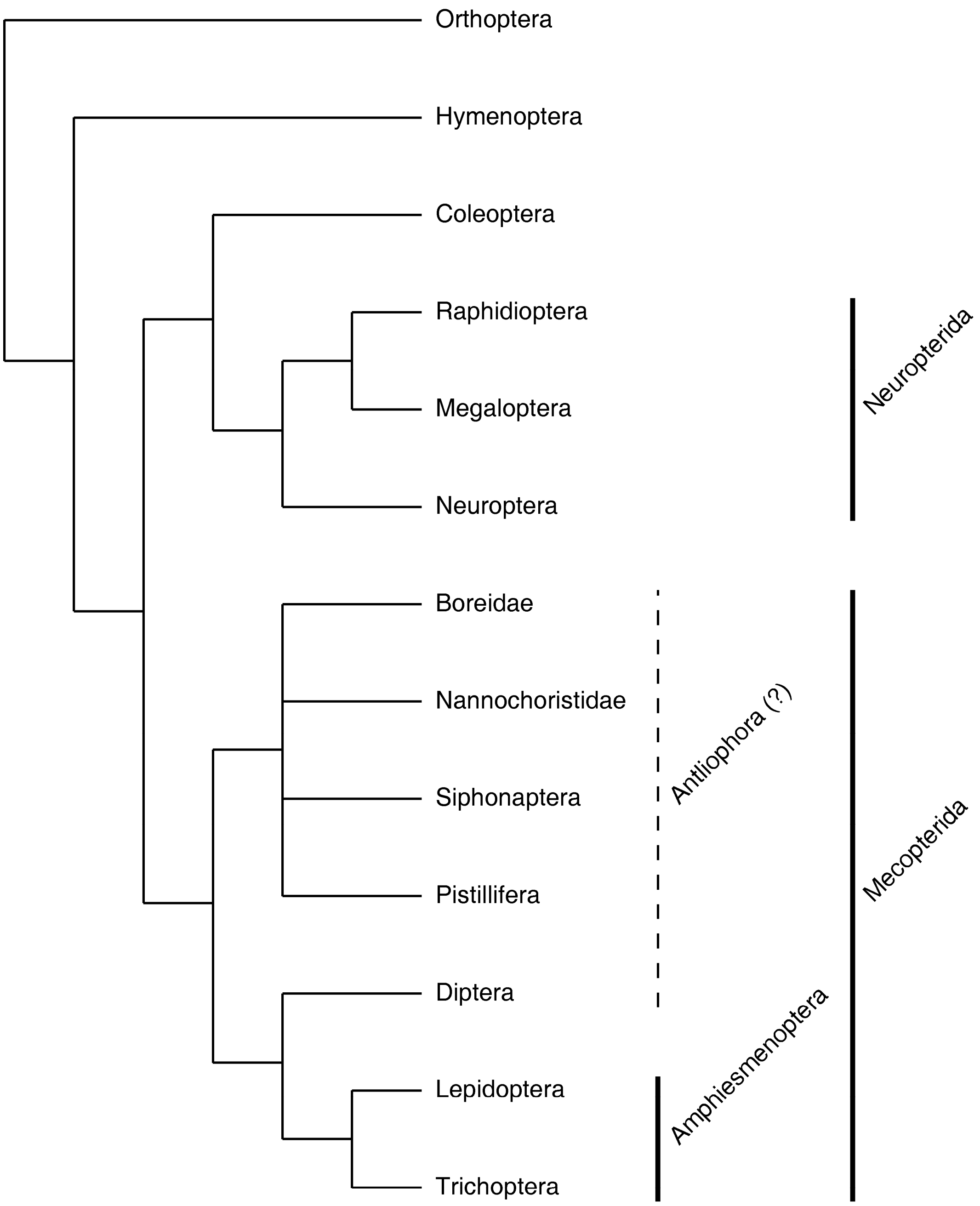

Fig. 1. Maximum parsimony analysis of 18S- and 28S-rDNA – sequence data and 205 morphological characters; strict consensus. Note the basal position of Hymenoptera within Endopterygota, the monophyly of Mecopterida and Amphiesmenoptera, but also the non-monophyly of Antliophora and the polytomy between Boreidae, Nannochoristidae, Siphonaptera and Pistillifera. Hünefeld & Kjer (unpublished), modified.

2. Material and methods

2.1. List of taxa examined

Fifteen representatives of Mecopterida (ingroup) were examined. The taxon sampling was focussed on presumably basal lineages according to recent intraordinal phylogenetic hypotheses (see e.g., Klass [ed.] 2003). The ingroup taxa and the morphological techniques applied are listed in Tab. 1. For a brachyceran fly (Bombylidae: *Toxophora*) and an apoditrysian member of Lepidoptera (Tortricidae: *Cydia*) data were obtained from the literature (Mühlenberg 1971, Kuznetzov & Stekolnikov 2001).

Tab. 1 List of taxa examined / ingroup: mecopterid representatives. **CLSM** – confocal laser scanning microscopy, **Dis.** – dissection, **His.** – histological section series, **µCT** – Micro-Xray-Computertomography, **3-D** – 3-dimensional reconstruction.

Taxon	Origin of material	CLSM	Dis.	His.	µCT	3-D
Siphonaptera Pulicidae *Archaeopsylla erinacei* Bouché, 1835	Germany / Thuringia / Jena leg. F. Hünefeld / 2004 (on hedgehog)				x	x
Nannomecoptera Nannochoristidae *Nannochorista neotropica* Navas, 1928	N. P. Kristensen / Denmark University of Copenhagen	x		x 1,0µm		x
Neomecoptera Boreidae *Boreus hiemalis* Linnaeus, 1767	Germany / Hessen / Darmstadt leg. H. Pohl / 1997	x				
Pistillifera Bittacidae *Anabittacus iridipennis* Kimmins, 1929	N. P. Kristensen / Denmark University of Copenhagen	x		x 1,0µm		x
Pistillifera Panorpidae *Panorpa communis* Linnaeus, 1758	Germany / Thuringia / Jena leg. F. Hünefeld / 2008	x				
Diptera Limoniidae *Limonia* sp.	Germany / Thuringia / Jena leg. F. Hünefeld / 2003	x		x 1,0µm		x
Diptera Tipulidae *Tipula* sp.	Germany / Thuringia / Jena leg. F. Hünefeld / 2007	x				
Diptera Culicidae *Aedes* sp.	R. Beutel / Germany University of Jena / Thuringia				x	x
Trichoptera Rhyacophilidae *Fansipangana vernalis* Mey, 1996	W. Mey / Germany University of Berlin **Paratypus**			x 1,0µm		x
Trichoptera Rhyacophilidae *Rhyacophila* sp.	Germany / Thuringia / Jena leg. F. Hünefeld / 2006			x 1,5µm		x
Trichoptera Hydrobiosidae *Ulmerochorema* sp.	N. P. Kristensen / Denmark University of Copenhagen			x 1,0µm		x

Taxon	Origin of material	CLSM	Dis.	His.	µCT	3-D
Lepidoptera Micropterigidae *Micropterix calthella* Linnaeus, 1761	N. P. Kristensen / Denmark University of Copenhagen	x		x 1,0µm		x
Lepidoptera Agathiphagidae *Agathiphaga vitiensis* Dumbleton, 1952	N. P. Kristensen / Denmark University of Copenhagen			x 1,0µm		x
Lepidoptera Heterobathmiidae *Heterobathmia pseuderiocrania* Kristensen & Nielsen, 1979	N. P. Kristensen / Denmark University of Copenhagen	x		x 1,5µm		x
Lepidoptera Eriocraniidae *Eriocrania cicatricella* Zetterstedt, 1839	N. P. Kristensen / Denmark University of Copenhagen			x 1,0µm		x

Representatives of 2 endopterygote groups and 1 non-endopterygote group were used as outgroups (Tab. 2). The female postabdomen of another basal hymenopteran representative (Xyelidae: *Xyela julii* Brebisson, 1818) was recently described in detail by Vilhelmsen (2001).

Tab. 2 List of taxa examined / outgroup: non-mecopterid insects. **CLSM** – confocal laser scanning microscopy, **Dis.** – dissection, **His.** – histological section series, **µCT** – Micro-Xray-Computertomography, **3-D** – 3-dimensional reconstruction.

Taxon	Origin of material	CLSM	Dis.	His.	µCT	3-D
Orthoptera Gryllidae *Gryllus assimilis* Fabricius, 1775	Zoological Institute / FSU Jena rearing stock		x			
Orthoptera Tettigoniidae *Tettigonia viridissima* Linnaeus, 1758	Germany / Thuringia / Jena leg. F. Hünefeld / 2008		x			
Hymenoptera Tenthredinidae *Tenthredo vespa* Retzius, 1783	Germany / Thuringia / Jena leg. F. Hünefeld / 2007				x	
Neuroptera Osmylidae *Osmylus fulvicephalus* Scopoli, 1763	Germany/ Thuringia / Camburg leg. R. Bellstedt / 2007				x	

2.2. Morphological techniques

External features were examined and drawn using a stereo microscope MZ 12.5 with a camera lucida (LEICA). A confocal laser scanning microscope LSM 510 (Zeiss, Göttingen, Germany) was used for cuticular structures and the general arrangement of muscles. As insect cuticle and musculature are auto-fluorescent, treatment with antibodies is not necessary for CLSM investigations (see Klaus et al. 2003). Macroscopic preparations were carried out under stereo microscopes MS 5 and MZ 12.5 (LEICA).

For semithin section series specimens were embedded in Araldite CY 212® (Agar Scientific, Stansted/Essex, England) and cut at 1,0 µm or 1,5 µm with a diamond knife (Elementsix, Cuijk, Netherlands) using a microtome HM 360 (Microm, Walldorf, Germany). The sections were stained with Toluidin blue and Pyronin G (Waldeck GmbH & Co. KG / Division Chroma, Münster, Germany).

Pictures of selected sections were made using a Zeiss Axioplan (Göttingen, Germany) and the AnalySIS® (Soft Imaging Systems, Münster, Germany) documentation system. Figures were processed in Adobe Photoshop® and Adobe Illustrator® (San Jose, California, USA).

For µ-Xray-computertomography (µCT) the synchrotrone facilities of DESY / HASYLAB (Hamburg, Germany) were used. For sample preparation the specimens were dried to the critical point (CPD / K850, EmiTech) and mounted on specimen holders compatible to the experimental setup at DESY / HASYLAB. Measurements were done at beamline BW2 using stable, relatively low energy beams (8kEV) (see Friedrich et al. 2008).

Three-dimensional reconstructions were carried out with Imaris (Bitplane AG, Zürich, Suisse) and MAYA7® software (Alias Wavefront, Toronto/Ontario, Canada) based on cross section series or µCT-data.

2.3. Cladistic analysis

For entering the character state matrix, tree calculation and character analysis winclada / NONA software, version 2.0 (Goloboff 1999) was used. For the parsimony analysis heuristic methods were applied with the following parameters: “rs0” (random choice after time), “hold2001” (keep 2001 trees), “hold/20” (keep 20 trees after each replicate), “mult*100” (randomized taxa, build Wagner tree, TBR branch swapping and 100 replicates). Bremer indices, Jackknife- and Bootstrap- values were calculated.

3. Terminology

3.1. External sclerotized parts

In the present study it is attempted to use neutral terms consistently in the descriptions of the results-section, following the principle: the same term for homologous structures. Reciprocally, non-homologues are strictly distinguished by consequent use of different terms. This is mainly important for the ventral sclerotized parts of the abdominal segments VIII – XI. The use of the terms “(gono)coxite” and “(gono)stylus” (Mickoleit 1973, 1975) is avoided here, as there is no conclusive evidence for homology with true coxites or styli. Terms used in the present study are listed in Tab. 3, as well as the terms used for the same structures by Snodgrass (1935), Matsuda (1976) and Mickoleit (1973, 1975).

It has to be noted that the term “subgenital plate” is omitted here. Structures designated with this term in literature can be plate-like ventral sclerotized elements of segments VII, VIII or even IX that are clearly not homologues, but use of the term might suggest homology to the reader and is therefore predestinated to be misleading.

Tab. 3 List of terms applied on external sclerotized elements of abdominal segments VII – XI.

present study	**Snodgrass (1935)**	**Matsuda (1976)**	**Mickoleit (1973, 1975)**
tergum VII – X ***tgVII-X***	tergum VII – X	tergum VII - X	Tergum VII – X
tergum XI ***tgXI***	epiproct	supraanal lobe	Tergum XI
sternum VII ***stVII***	sternum VII	sternum VII	Sternum VII
ventral sclerotization of segment VIII ***vsVIII***			Gonocoxosternit VIII
ventral sclerotization VIII, proximal part ***vsVIII-p***	valvifer 1	valvifer 1	Gonocoxit VIII
ventral sclerotization VIII, distal part ***vsVIII-d***	valvula 1	valvula 1	Gonapophyse VIII
ventral sclerotization of segment IX ***vsIX***			Gonocoxosternit IX
ventral sclerotization IX, proximal part (1) ***vsIX-p(1)***	valvifer 2	valvifer 2	Gonocoxit IX
ventral sclerotization IX, proximal part (2) ***vsIX-p(2)***	anterior intervalvula	anterior intervalvula	
ventral sclerotization IX, proximal part (3) ***vsIX-p(3)***	posterior intervalvula	posterior intervalvula	
ventral sclerotization IX, distal part (1) ***vsIX-d(1)***	valvula 2	valvula 2	Gonapophyse IX
ventral sclerotization IX, distal part (2) ***vsIX-d(2)***	valvula 3	valvula 3	Gonostylus IX
ventral sclerotization of segment X ***vsX***	sternum X	sternum X	
ventral sclerotization of segment XI ***vsXI***	paraproct(s)	subanal lobe(s)	Subanalplatte
laterotergite of segments VIII and IX ***ltgVIII / IX***	laterotergite		Laterotergit

3.2. Musculature of the female postabdomen

A new nomenclature for the musculature of the female postabdomen was worked out in the framework of the present study, grouping the muscles with regard to their sites of origination and insertion. Compared to the numerous different nomenclatures which are in use, even for "low level taxa" as genera within the same family, this approach allows a later addition of muscles that will be found in other holometabolous taxa (and, in principal, even in insect taxa in general) in a comparatively simple and convenient way.

The advantages of the new nomenclature presented here are: **(1)** neutral muscle names for consistent use in endopterygote morphology, based on homology estimates; **(2)** the possibility to make additions and / or corrections to the system in an easy and quick way; and **(3)** the possibility to extend it onto insects in general.

The postabdominal muscles are sorted into the following groups:

is – intersegmental muscles in general
seX-ce01 – cercal muscle, usually originating from tergum X
intra – muscles with origin and insertion sites at the same sclerotized part of a segment
dv – dorso-ventral muscles
t – transverse muscles
se-gc – muscles originating from the external segmental sclerotizations or adjacent membranous parts and with insertion at the genital chamber
intra-gc – muscles running between parts of the genital chamber
rec/clo01 – muscle inserting at the rectal / cloacal aperture
add – muscles that can not be ascribed to one of the above mentioned groups

A complete, numbered list of all muscles identified in the female postabdomen of the taxa under consideration, including the sites of origin and insertion as well as notes on observed or assumed function, is provided in **Appendix A** of this study.

3.3. Internal parts of the genital system

The terminology applied on the internal parts of the female genital system widely follows Snodgrass, 1935 (also adopted in general by most authors, as Kéler 1961, Matsuda 1976). The few exceptions are briefly explained in the subsequent list of terms used in the present study. Without further comments, the definitions of the terms are conform to those given by Snodgrass (1935).

genital chamber, *gc* The term is used here in the comparatively wide sense as defined by Snodgrass (1935). The terms "vagina" and "uterus" are not used here, as they refer just to a special state in which a genital chamber in the sense of Snodgrass´ definition can occur, or to a certain part of it. So, restriction onto the term genital chamber appears to be most appropriate to avoid terminological confusion.

gland duct, *agd* duct connecting the accessory glands with the lumen of the genital chamber

accessory glands, *ag*

spermathecal process, *prc* more or less cone-like region of strengthened cuticle derived from the roof of the genital chamber with the opening of the spermathecal duct on its tip, often sclerotized; Mickoleit 1973 / 75: Receptaculumpapille

spermathecal duct, *spd* Matsuda 1976, Mickoleit 1973 / 75: ductus receptaculi

spermatheca, *sp* Matsuda 1976: also termed receptaculum seminis

spermathecal gland, *spg* Kéler: receptacular gland

ductus bursae, *bcd* duct connecting the lumina of the genital chamber and the bursa copulatrix

bursa copulatrix, *bc* Following Snodgrass´and Matsuda´s definition, the bursa copulatrix has to be addressed just as an (anterior) compartment of the genital chamber. In fact it is in almost all cases separated from the latter by way of a distinct ductus bursae. Both the walls of the bursa itself as well as that of the ductus bursae mostly display striking differentiations in cell morphology and cuticular structure, compared to the genital chamber. Consequently, the bursa copulatrix is treated here as a certain part of the female internal genital system on its own.

common oviduct, *ovc*

lateral oviducts, *ovc*

It has to be mentioned that the treatment of the above listed parts of the genital system as "internal parts of the genitalia" just refers to the spatial relations in the animals body (i.e., parts of the genital system that are not exposed) and does not mirror the developmental origin of the structures in any way. The following of the above listed parts are of ectodermal origin and have to be addressed as invaginations of the external cuticle: genital chamber, gland duct, spermathecal duct and spermatheca, ductus bursae and bursa copulatrix, common oviduct. The ectodermal origin of these structures is indicated by the cuticular outline (**intima, *i***) of their lumina. Of mesodermal origin are: the lateral oviducts and the ovaries ("inner genitalia" *sensu strictu*), and the glands (accessory glands, spermathecal gland). However, for fluent and easily capable descriptions in the results section, it seemed more useful to treat together structures that form functional units (as "gland duct and accessory glands").

The ovaries and ovarioles were not subject of the present study, as comprehensive accounts addressing these parts of the reproductive system are already available.

4. Results

4.1. Outgroup

4.1.1. Orthoptera

4.1.1.1. Gryllidae: *Gryllus assimilis*

The external morphology as well as the internal parts of the genital system of *G. assimilis* are sufficiently described (see Snodgrass 1935). New results mainly concern the muscular equipment.

Musculature (Fig. 2). The female postabdomen is equipped with 21 muscles. In Snodgrass (1935) only 8 muscles directly associated with the ovipositor are depicted: **05** *isVII-VIII05*, **34** *intraIX03*, **38** *dvVIII02*, **40** *dvIX01*, **41** *dvIX02*, **42** *dvIX03*, **43** *dvIX04*, **68** *add01*. The presence of these muscles can be confirmed here.

In addition, the following muscles were identified: **01** *isVII-VIII01* (short, 2 bundles), **02** *isVII-VIII02* (short, 2 bundles), **03** *isVII-VIII03* (short, 2 bundles), **04** *isVII-VIII04* (short, 2 bundles), **07** *isVII-VIII07* (short, 2 bundles), **14** *isVIII-IX01* (short, 2 bundles), **15** *isVIII-IX02* (short, 2 bundles), **16** *isVIII-IX03* (short, 2 bundles), **25** *isIX-X01* (short, 2 bundles), **26** *isIX-X02* (short, 2 bundles), **28** *isX-XI01* (short, 2 small bundles), **30** *seX-ce01*, **36** *dvVII01* (2 compact bundles). Transverse postabdominal muscles are absent as well as muscles of the genital-chamber. A genital chamber corresponding to the definition given by Snodgrass (1935) is not developed in orthopterans; the common oviduct directly opens by way of the primary gonopore.

The skeleto-muscular situation was cross-checked with that of *Tettigonia viridissima* (Orthoptera: Tettigoniidae). Compared to *G. campestris*, no essential differences in the skeletal and muscular equipment were found.

4.1.2. Hymenoptera

4.1.2.1. Tenthredinidae: *Tenthredo vespa*

The external morphology of the female postabdomen of tenthredinid wasps is well known, and also the internal parts of the genital system are sufficiently described (Togashi, 1970). The results presented here address the muscle system.

Musculature (Fig. 3). The muscle set of the female postabdomen comprises 20 muscles: **01** *isVII-VIII01*, **02** *isVII-VIII02*, **03** *isVII-VIII03* (site of origin shifted to an area dorsad of the origin of isVII-VIII02, muscle crosses laterad to *isVII-VIII02*), **04** *isVII-VIII04*, **05** *isVII-VIII05* (2 bundles: one bundle inserts on sclerite vsVIII-p, the other on the ramus of sclerite vsVIII-d), **07** *isVII-VIII07*, **14** *isVIII-IX01* (2 distinct bundles), **15** *isVIII-IX02* (2 bundles), **16** *isVIII-IX03*, **28** *isX-XI01,* **30** *seX-ce01*, **34** *intraIX03*, **35** *intraIX04*, **36** *dvVII01* (2 compact

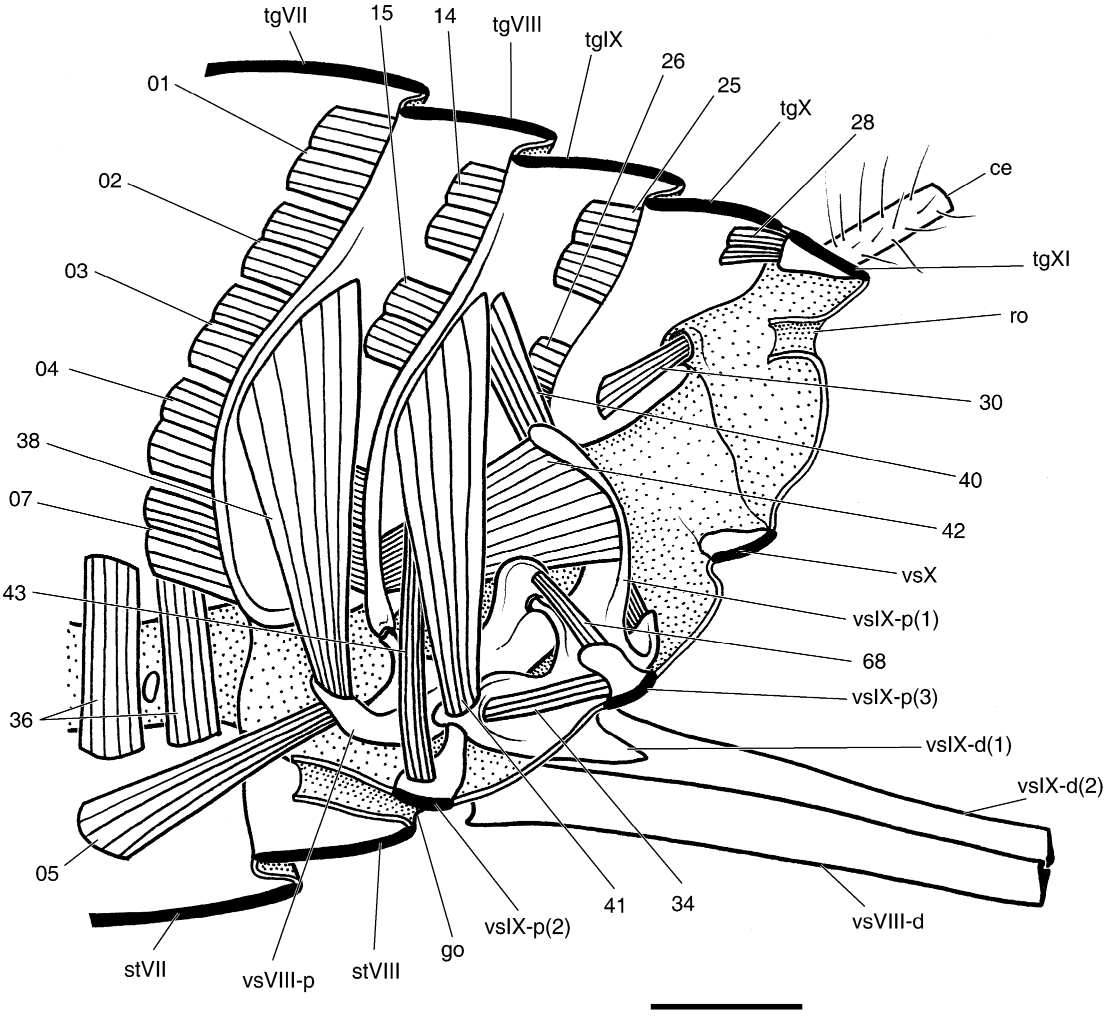

Fig. 2. *Gryllus assimilis*, skeleto-muscular arrangement of the female postabdomen. Cut along the median line, left body half, internal parts of the genitalia, soft tissue and fat body removed. Scale bar: 1 mm.

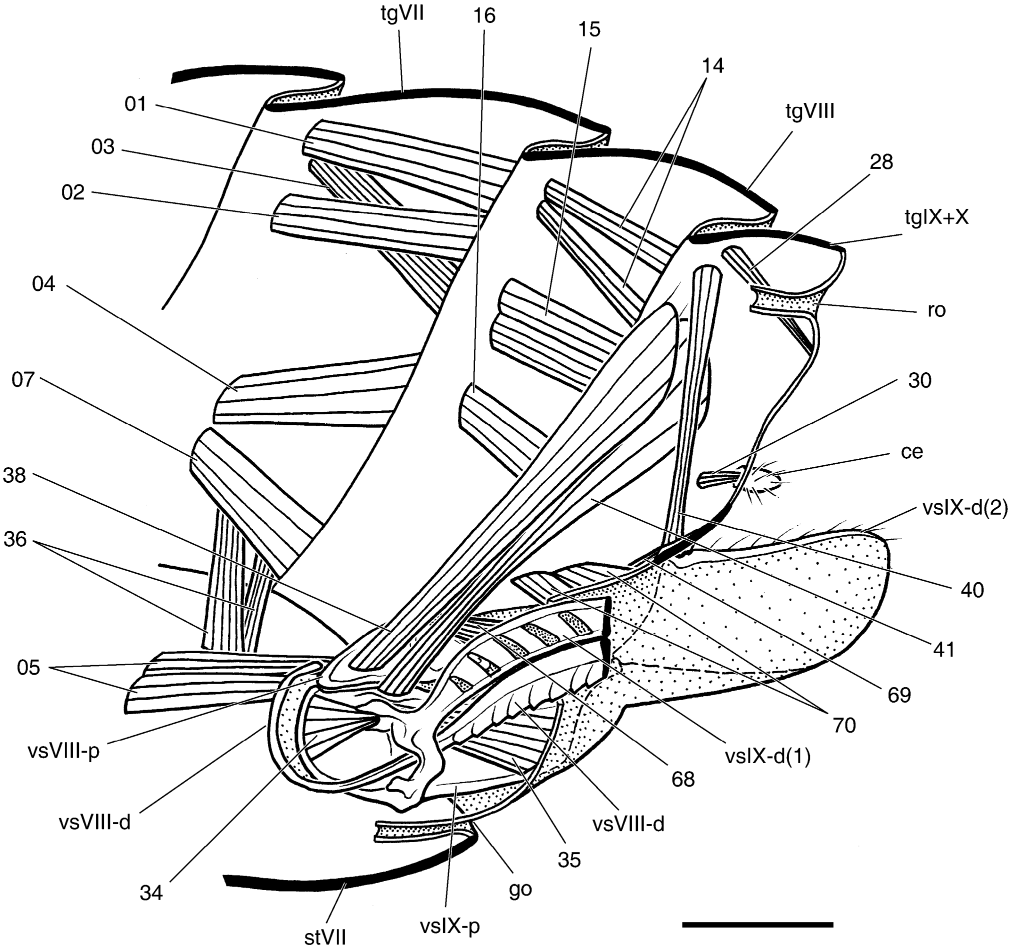

Fig. 3. *Tenthredo vespa*, skeleto-muscular arrangement of the female postabdomen. Left body half, internal parts of the genitalia, soft tissue and fat body are not depicted. Scale bar: 500 µm.

bundles), **38** *dvVIII02* (origin shifted posterad to tergum IX), **40** *dvIX01*, **41** *dvIX02*, **68** *add01*, **69** *add02*, **70** *add03*. Transverse muscles and muscles of the genital-chamber are absent (a "true" genital chamber is lacking in Tenthredinidae).

For a xyelid wasp, *Xyela julii* (Hymenoptera: Xyelidae), the skeletal parts of the female postabdomen and the musculature associated with the ovipositor were worked out in great detail by Vilhelmsen (2001). All skeletal elements and ovipositors muscle of *X. julii* have an exact equivalent in *T. vespa*, with one exception: muscle **38** *dvVIII02* originates on tergumVIII in *X. julii*, but on an anterior region of tergumIX in *T. vespa*. The sites of insertion of the muscle are identical in both species (sclerite ***vsVIII-p***).

4.1.3. Neuroptera

4.1.3.1. Osmylidae: *Osmylus fulvicephalus*

The external postabdominal morphology of *Osmylus* was addressed by Aspöck & Aspöck (2008) and Mickoleit (1973) and does not require further scrutiny. A very detailed account on the female postabdominal musculature of *O. fulvicephalus* was recently presented by Feuerstein (2008). The results can be fully confirmed and need no additions. Some contributions can be made here concerning the internal parts of the genital system.

Internal parts of the genital system (Fig. 4)**.** The ***genital chamber*** opens ventrally, behind the small ventral sclerotization of segment VIII. It has the shape of a bilobed sac, with the common oviduct evaginating from the chamber lumen ventrally, just a very short distance anterad of the genital opening. The epithelium of the chamber does not display any specific features. A cuticular intima is present, as well as a muscularis that is mainly composed of longitudinal fibres.

The paired ***spermathecal ducts*** evaginate ventrally from the anterior quarter of the genital chamber. The slender ducts are simple, without any specialized regions; they form 5 – 6 loops before they enter the spermatheca. The epithelium is composed of unspecialized cubic cells. An intima is present but a muscularis is lacking. The paired ***spermathecae*** are large and balloon-shaped. The epithelium is formed of prismatic cells with glandular appearance (numerous vesicles visible in the cytoplasm). A cuticular intima and a muscular envelope are absent. Spermathecal glands are not developed.

The ***gland duct*** evaginates from the roof of the most posterior part of the genital chamber, in the region of the genital opening. The duct is short and slender, and not surrounded by a muscularis. The unpaired ***accessory gland*** is located asymmetrically in the left body half. Its shape is simple and it is not divided into distinct lobes. The epithelium is composed of prismatic cells with vesicles visible in the cell bodies.

Both, the ***common oviduct*** and the ***lateral oviducts*** display a flattened, squamose epithelium. The oviducts are surrounded by a loose, single-layered meshwork of single muscle fibres.

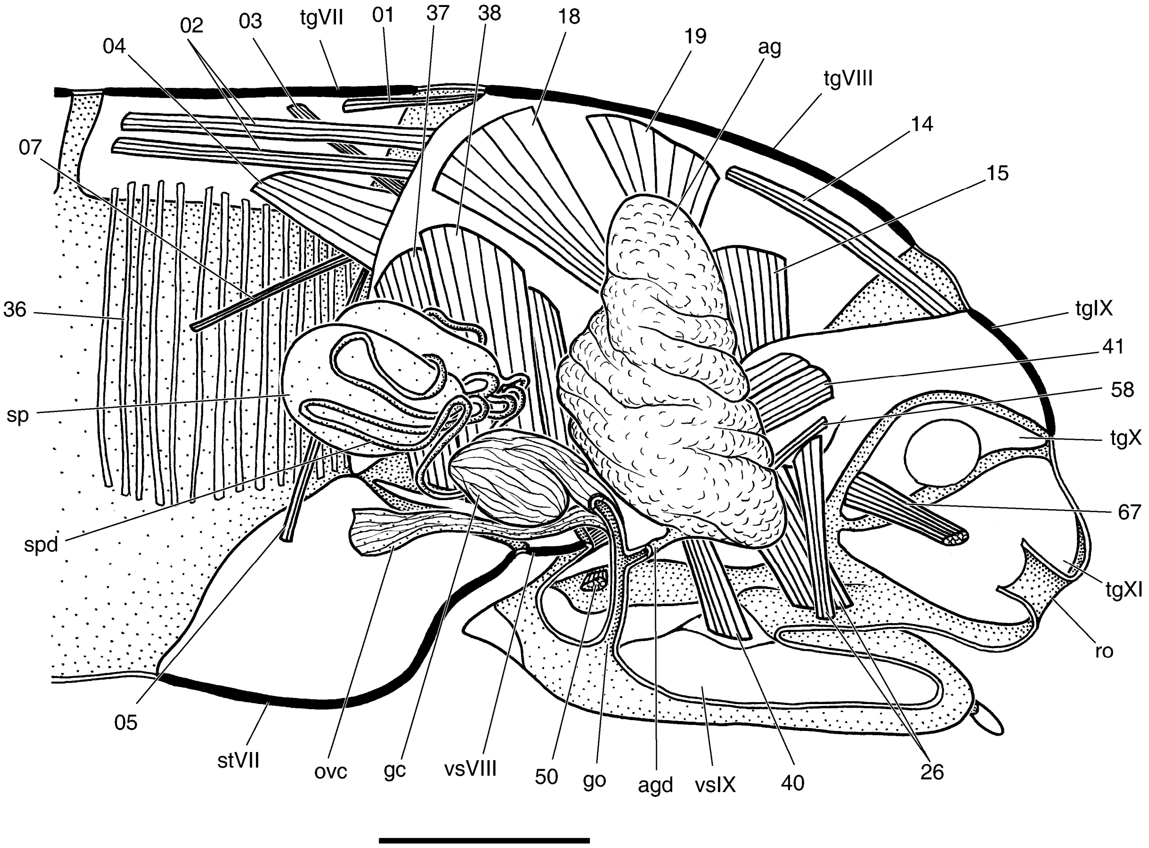

Fig. 4. *Osmylus fulvicephalus*, female postabdomen. Cut along the median line. Scale bar: 500 μm. Skeleto-muscular arrangement after Feuerstein (2008), modified.

4.2. Ingroup

4.2.1. Siphonaptera

4.2.1.1. Pulicidae: *Archaeopsylla erinacei*

Exoskeleton (Figs. 5A, B). Accounts of the external morphology of the female postabdomen were given by several authors (see Kinzelbach 2003). However, only very few figures explaining the spatial relations of the external sclerotized elements in more detail seem are available. The habitus of the female postabdomen of *A. erinacei* is shown in Fig. 5 (A, B).

Musculature (Fig. 5C). Composed of 18 muscles: **01** *isVII-VIII01*, **02** *isVII-VIII02*, **05** *isVII-VIII05*, **14** *isVIII-IX01* (2 bundles), **25** *isIX-X01*, **26** *isIX-X02*, **28** *isX-XI01* (site of insertion shifted ventrad), **29** *isX-XI02*, **33** *intraIX02*, **36** *dvVII01*, **37** *dvVIII01*, **47** *tVII01*, **49** *tVIII02*, **50** *tIX01*, **55** *seVIII-gc01*, **58** *seIX-gc01*, **59** *seIX-gc02*, and **62** *intra-gc01*.

Internal parts of the genital system. The ***genital chamber*** is short and compact and the lumen strongly flattened dorso-ventrally. The epithelium is squamose. A ***spermatheca*** is present, but minute. It is connected with the genital chamber by way of a slender ***spermathecal duct*** that evaginates from the genital chamber in a dorso-median position, just a short distance in front of the genital opening. The epithelium of both the spermatheca and the spermathecal duct does not display any peculiarities. A ***spermathecal gland*** is lacking. The short ***common oviduct*** evaginates from the anterior end of the genital chamber. After a short distance it branches off into the ***lateral oviducts***. The epithelium of the oviducts is composed of cubic cells.

4.2.2. Nannomecoptera

4.2.2.1. Nannochoristidae: *Nannochorista neotropica*

A detailed account of the external morphology of the female postabdomen was given by Mickoleit (1975) and can be fully confirmed by the results of the present study, with one exception: distinct laterotergites were not found in *N. neotropica*. The muscular equipment and the internal parts of the genital system are described in the following.

Musculature (Fig. 6B). The postabdominal muscle set of *N. neotropica* comprises 23 muscles: **01** *isVII-VIII01*, **02** *isVII-VIII02*, **03** *isVII-VIII03* (site of origin is shifted dorsad), **04** *isVII-VIII04*, **05** *isVII-VIII05*, **06** *isVII-VIII06* (splits into 2 bundles before insertion on segment VIII), **14** *isVIII-IX01*, **15** *isVIII-IX02* (2 bundles), **25** *isIX-X01*, **26** *isIX-X02* (2bundles), **28** *isX-XI01* (site of origin shifted ventrad, below that of muscle 29), **29** *isX-XI02*, **30** *seX-ce01*, **36** *dvVII01*, **37** *dvVIII01*, **38** *dvVIII02*, **40** *dvIX01*, **41** *dvIX02*, **48** *tVIII01*, **55** *seVIII-gc01*, **57** *seVIII-gc03* (3 distinct portions), **58** *seIX-gc01*, **59** *seIX-gc02*.

Internal parts of the genital system (overview: Fig. 6A). The roof of the ***genital chamber*** of *Nannochorista* was described in detail by Mickoleit (1976). In *N. neotropica* the chamber

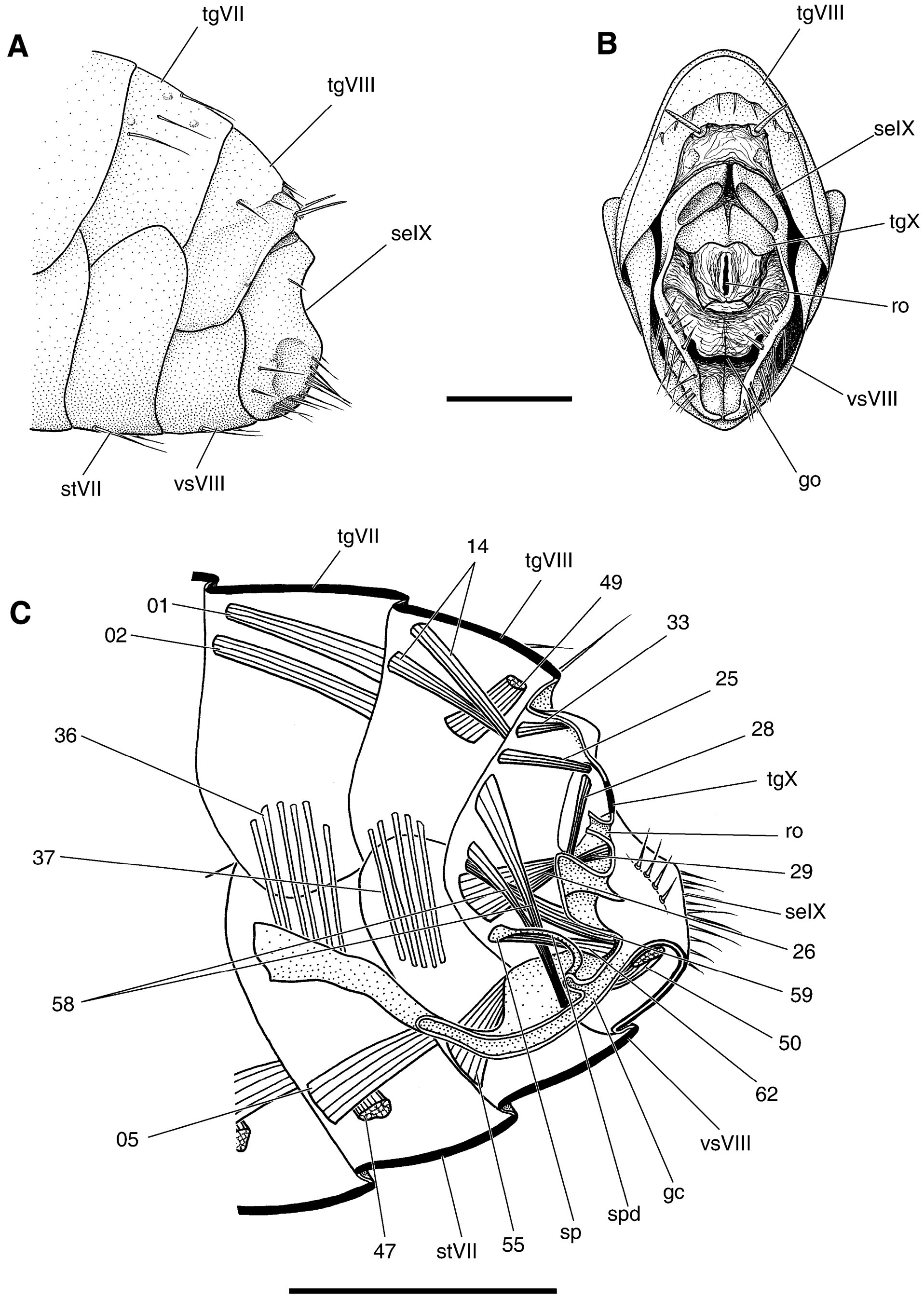

Fig. 5. *Archaeopsylla erinacei*, female postabdomen. (A,B) external morphology. (A) lateral view; (B) posterior view. (C) skeleto-muscular arrangement. Scale bar: 500 μm.

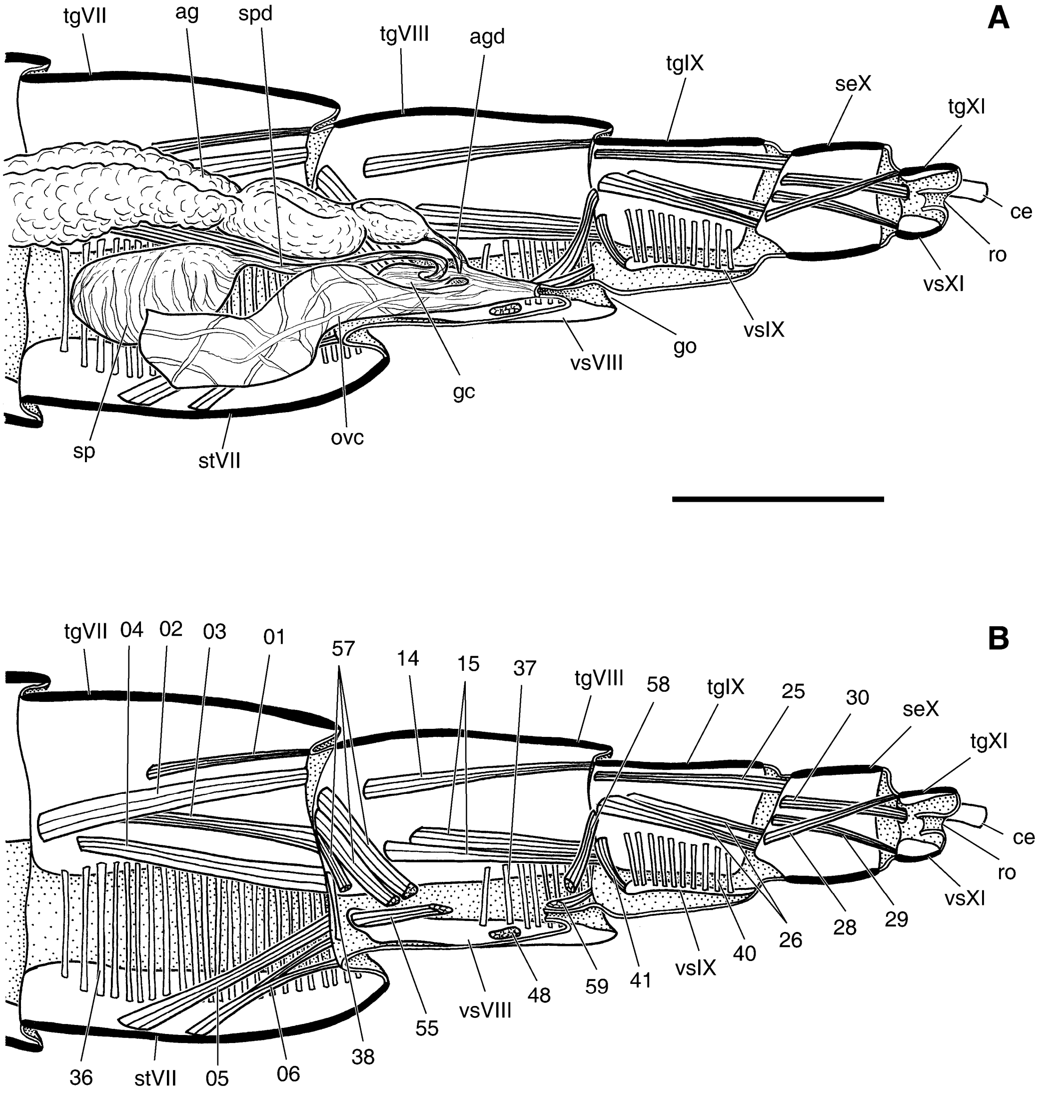

Fig. 6. *Nannochorista neotropica*, female postabdomen. (A) overview over the internal parts of the genital system; (B) skeleto-muscular arrangement. Scale bar: 500 µm.

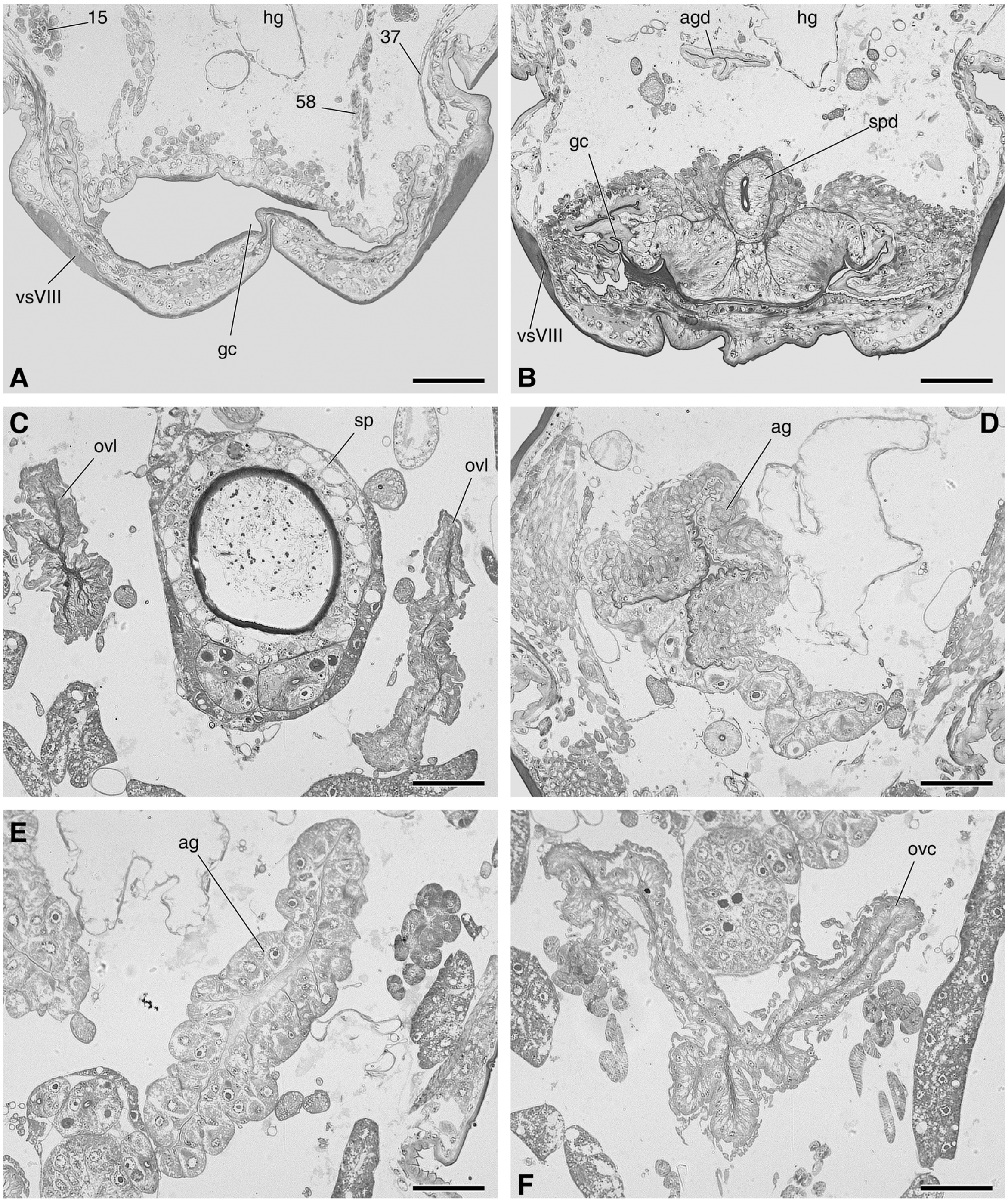

Fig. 7. *Nannochorista neotropica*, female postabdomen, histological cross sections. (A) segment VIII, posterior half; (B) segment VIII, anterior half; (C) segment VII, mid-length, spermatheca; (D) boundary region of segments VII and VIII, fused posterior parts of the accessory glands; (E) accessory gland, anterior part; (F) common oviduct. Scale bar: 50 µm.

forms a (superficially) sac-like forward extension in mid-length of segment VIII, into which the spermathecal duct opens from dorso-medially. The duct opening lies on the tip of a massive and conspicuously sclerotized papilla which fills out the lumen of the sac-like extension almost completely (Fig. 7B). The epithelium of the chamber is formed of cubic cells, and in the region of the spermathecal papilla of large prismatic cells (Fig. 7B). A conspicuous cuticular intima is present (Figs. 7A, B). The genital chamber is surrounded by a muscularis composed mainly of longitudinal fibres. A distinct bursa copulatrix is not developed.

The slender ***spermathecal duct*** (Fig. 7B) reaches the middle region of segment VII anteriorly. The epithelium is formed of large cubic cells with vesicles visible in the cytoplasm. An intima is present, as well as a weak muscular envelope composed of single longitudinal fibres. The ***spermatheca*** (Fig. 7C) has an oval shape in superficial appearance. Its epithelium is composed of extremely large cubic cells with numerous vesicles and huge storage vacuoles in the cytoplasm. A glandular function can be expected for both the spermatheca and the spermathecal duct. Namely the ventral half of the spermatheca is surrounded by single muscle fibres. A distinct spermathecal gland is lacking.

The short ***gland duct*** (Fig. 7B) evaginates from the genital chamber a short distance posterad of the spermathecal duct. The epithelium is squamose and displays no further specific features. An intima is well developed and the duct is surrounded by single longitudinal muscle fibres. The ***accessory glands*** (Figs. 7D, E) are paired, with their posterior regions fused. The epithelium of the fused gland region is formed of small cells with an irregular shape. The paired regions of the glands are surrounded by extremely enlarged epithelial cells with vesicles and storage vacuoles visible in the cytoplasm. A muscularis associated with the glands was not found.

The ***common oviduct*** (Fig. 7F) evaginates from the genital chamber ventro-medially, in opposite position to the gland duct. It is y-shaped in cross section. The common oviduct splits off into the paired ***lateral oviducts*** (Fig. 7C) in the boundary region of segments VII and VIII. Both the common oviduct and the lateral oviducts display an unspecialized epithelium. A cuticular outline of their strongly compressed lumina is not traceable. The oviducts are surrounded by a loose meshwork of scattered muscle fibres.

4.2.3. Neomecoptera

4.2.3.1. Boreidae: *Boreus hiemalis*

The external postabdominal morphology of *B. hiemalis* was described in detail by Mickoleit (1975); for the internal parts of the genitalia see Steiner (1936).

Musculature (Fig. 10B). A total of 15 muscles was found in the female postabdomen: **01** *isVII-VIII01*, **02** *isVII-VIII02*, **03** *isVII-VIII03*, **04** *isVII-VIII04* (site of origin shifted ventrad to sternum VII), **05** *isVII-VIII05*, **06** *isVII-VIII06*, **14** *isVIII-IX01*, **15** *isVIII-IX02* (2 large bundles), **16** *isVIII-IX03*, **25** *isIX-X01*, **26** *isIX-X02*, **28** *isX-XI01*, **30** *seX-ce01* (extremely large in *B. hiemalis*), **36** *dvVII01*, **37** *dvVIII01* (1 compact muscle), and **48** *tVIII01*.

4.2.4. Pistillifera

4.2.4.1. Bittacidae: *Anabittacus iridipennis*

The external parts of the female postabdomen of *A. iridipennis* were described by Willmann (1982). The musculature of the female postabdomen and the internal parts of the genital system are addressed here.

Musculature (Fig. 8B)**.** The muscle set of the female postabdomen is composed of 23 muscles: **01** *isVII-VIII01*, **03** *isVII-VIII03*, **04** *isVII-VIII04*, **14** *isVIII-IX01*, **15** *isVIII-IX02*, **25** *isIX-X01*, **26** *isIX-X02*, **28** *isX-XI01* (2 bundles), **29** *isX-XI02* (2 bundles), **30** *seX-ce01*, **31** *intraVIII01*, **36** *dvVII01*, **45** *dvXI01*, **46** *dvXI02*, **48** *tVIII01*, **54** *seVII-gc01*, **55** *seVIII-gc01*, **58** *seIX-gc01*, **59** *seIX-gc02*, **60** *seIX-gc03*, **61** *seX-gc01*, **62** *intra-gc01*, and **67** *rec/clo01*.

Internal parts of the genital system (overview: Fig. 8A)**.** The ***genital chamber*** reaches the boundary region of segments VII and VIII anteriorly. Two successive chamber regions can be distinguished. Around the posterior region, the epithelium is formed of small cubic cells ventrally, but of prismatic cells dorsally (Fig. 9B). The prismatic dorsal cells have the nuclei near the basal poles. In each cell 2 regions can be distinguished: a basal region containing the nucleus and a cytoplasm that seems granular due to the presence of numerous small vesicles, and an apical region with a huge, vacuole-like compartment. From these compartments dark violet- staining droplets are released into the chamber lumen. The wide lumen of the posterior chamber region is lined with a fine intima. Around the anterior region of the genital chamber, the epithelial cells are of an irregular shape ventrally, but prismatic dorsally (Figs. 9C, D). The prismatic dorsal cells seemingly have a glandular function (numerous vesicles in the cytoplasm), but unlike the dorsal cells of the posterior part they do not display the strict subdivision into 2 cell regions. The intima is much thicker in the anterior chamber region and contains sclerotized areas dorso-laterally (Figs. 9C, D). The lumen of the anterior region is slightly depressed dorso-ventrally and forms a pair of conspicuous, flattened evaginations in the anterior half of segment VIII (Fig. 9D). The epithelium of the evaginations has a glandular function: the epithelial cells are large and prismatic, with numerous secretory vesicles and storage compartments in the cytoplasm (Fig. 9F). The genital chamber is surrounded by a weak muscularis, consisting of single longitudinal fibres.

The ***spermathecal duct*** (Fig. 9C) leaves the genital chamber dorso-medially. The epithelium of the duct is fomed by cubic cells. The intima is heavily reinforced and the lumen extremely narrowed. The duct is rounded in cross section over its entire length and enclosed by a loose muscularis consisting of 1 layer of longitudinal fibres. The spermathecal duct leads into the ***spermatheca*** (Figs. 9D, E) in the boundary region of segments VIII and IX. Two compartments of the spermatheca can be distinguished. The proximal part is surrounded with a prismatic epithelium, with the nuclei almost in a central position; vesicles and a large storage vacuole are visible in the cells. An intima is clearly visible. The lumen is wide and rounded (cross section); it contains spermatozoans and secretion products from the epithelial cells. A loose meshwork of scattered muscle fibres is present around the proximal part of the

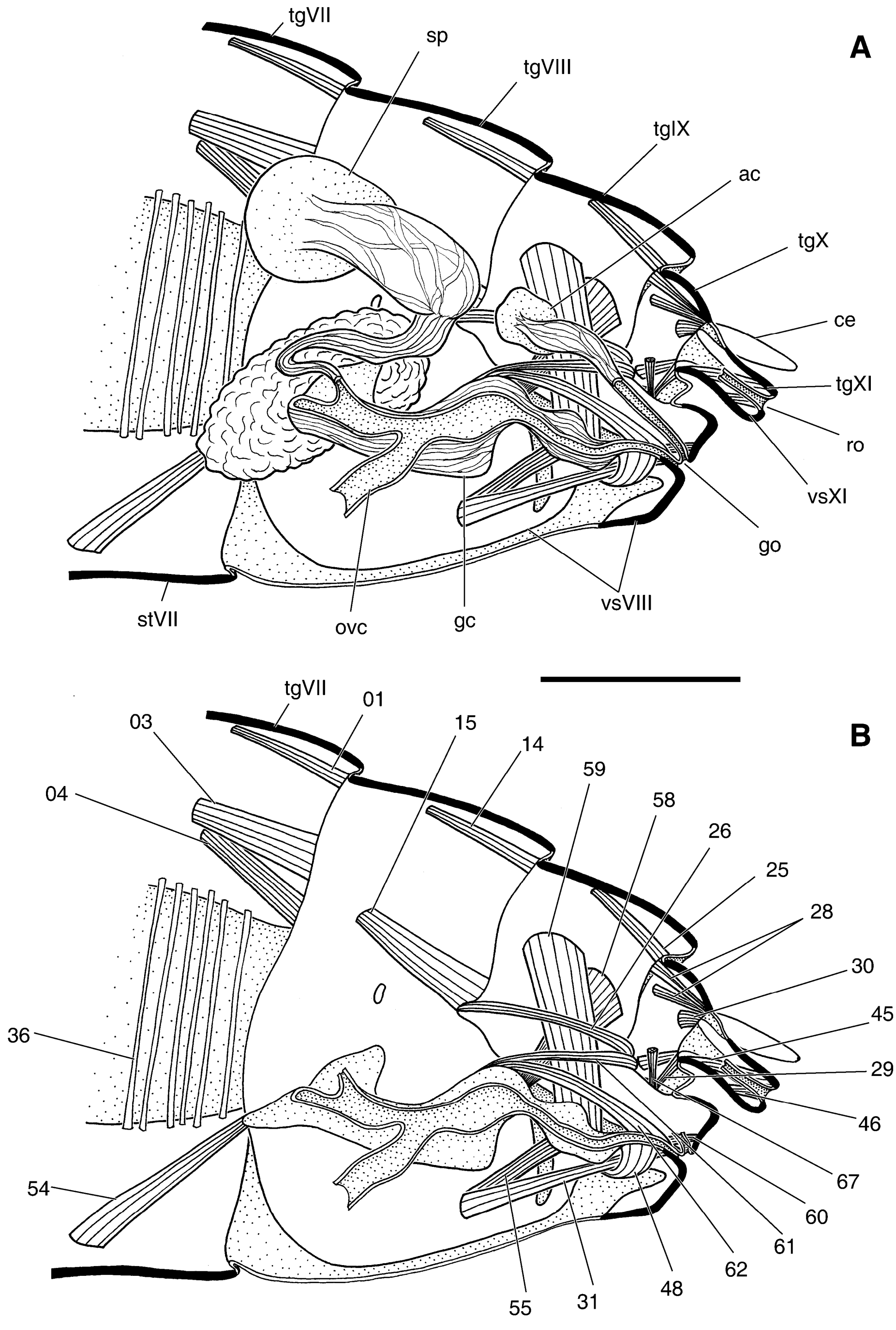

Fig. 8. *Anabittacus iridipennis*, female postabdomen. (A) overview over the internal parts of the genital system; (B) skeleto-muscular arrangement. Scale bar: 500 µm.

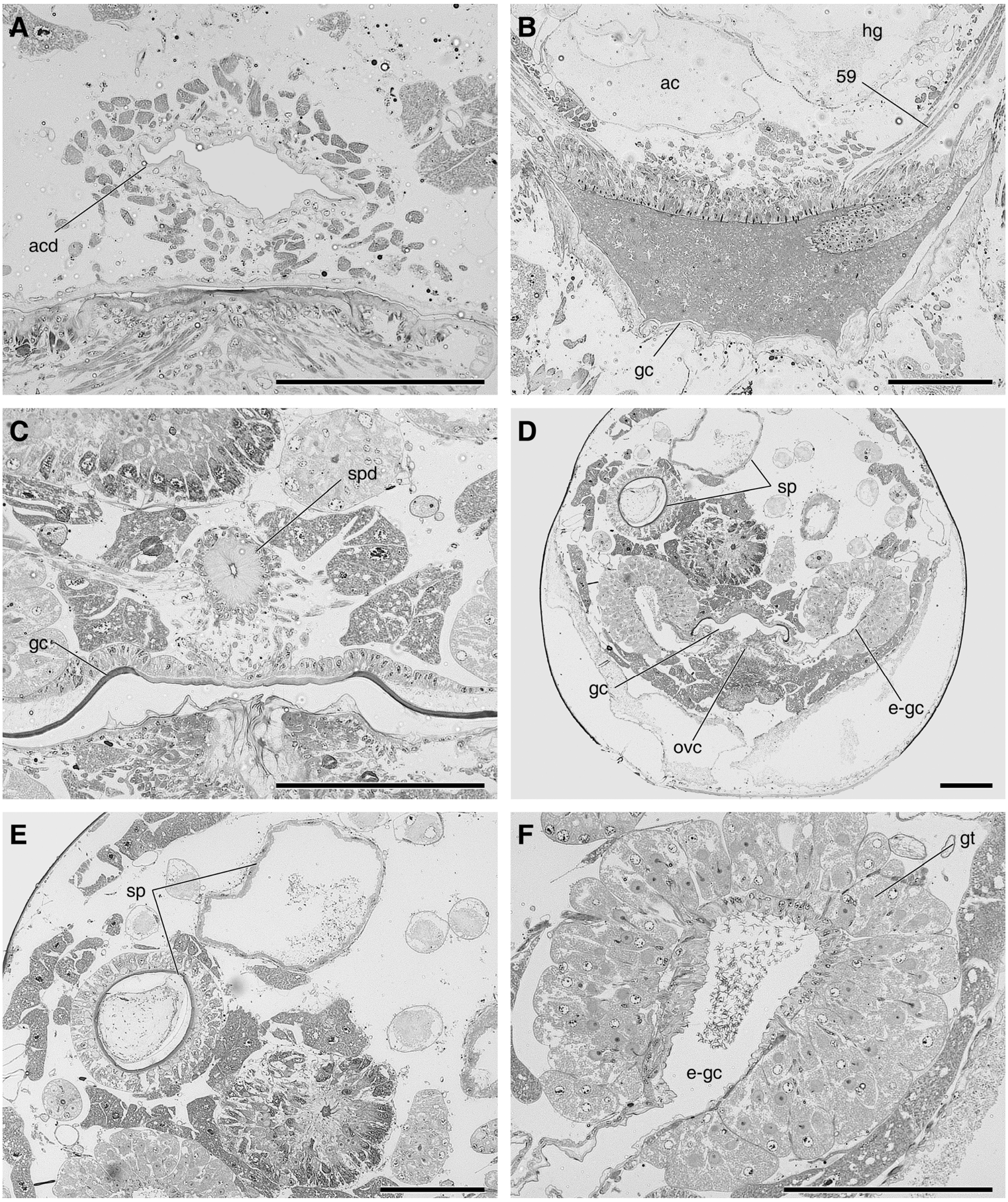

Fig. 9. *Anabittacus iridipennis*, female postabdomen, histological cross sections. (A) segment IX, duct leading to the chamber in a position as usually the accessory glands, ***acd*** – duct of additional chamber; (B) boundary region of segments VIII and IX, genital chamber; (C) segment VIII, anterior half; (D) segment VIII, anterior half, overview, ***e-gc*** – lateral evagination of genital chamber; (E) segment VIII, anterior half, spermatheca; (F) lateral evagination of the genital chamber in segment VIII with glandular tissue, ***gt***. Scale bar: 100 µm.

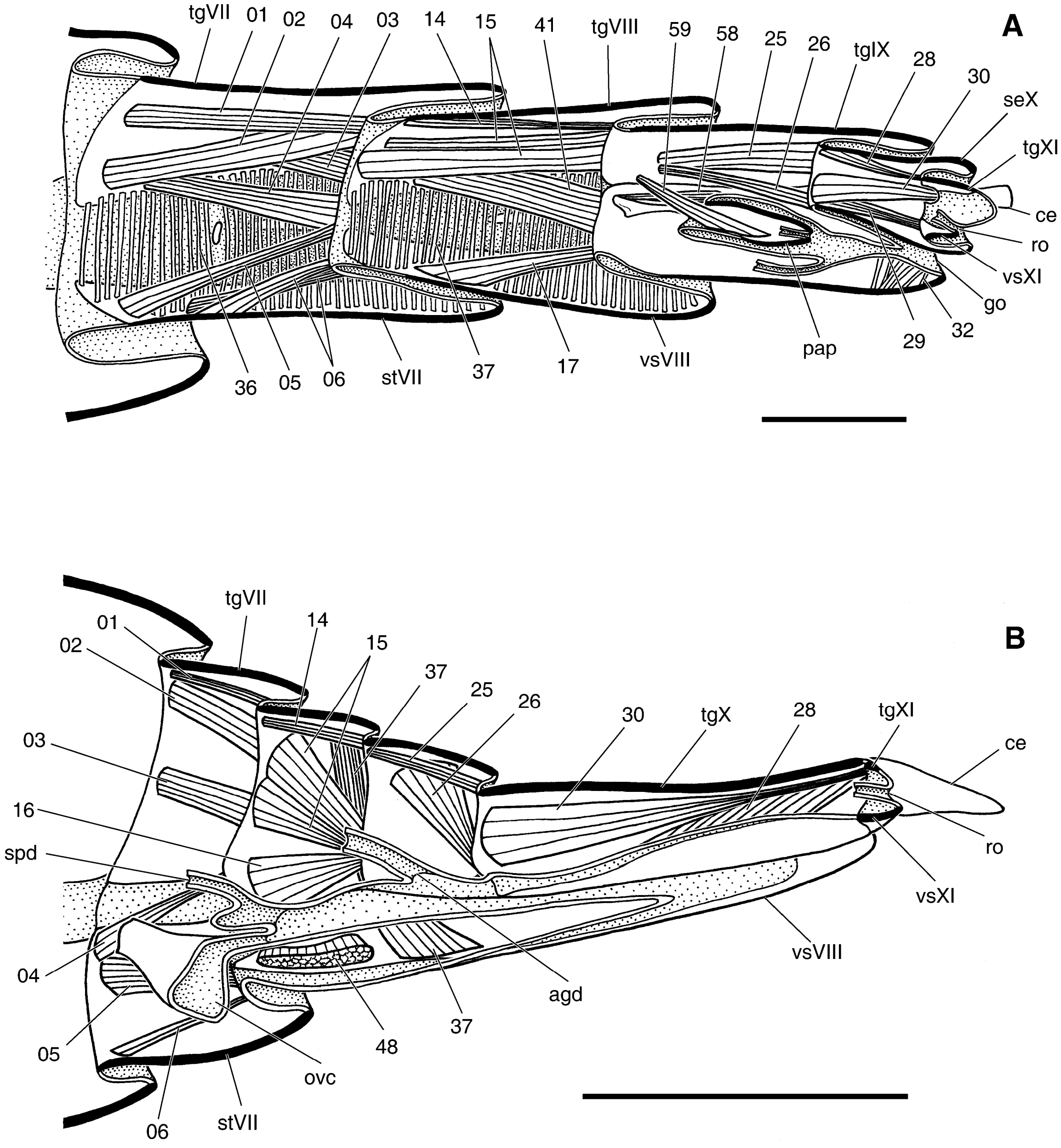

Fig. 10. Skeleto-muscular arrangement of the female postabdomen. (A) *Panorpa communis*, ***pap*** – papilla with the opening of the spermathecal duct on its tip; (B) *Boreus hiemalis*. Scale bar: 500 µm.

spermatheca. The epithelium of the distal part of the spermatheca is squamose. The lumen is even wider than the lumen of the proximal compartment and outlined with a well developed intima. A muscularis associated with the distal compartment of the spermatheca is lacking.

A ***bursa copulatrix*** and ***accessory glands*** are not developed. A duct with an epithelium composed of irregularely shaped cells evaginates from the chamber roof in a position, which is normally the location of the accessory gland duct opening (Fig. 9A, ***acd***). This duct is flattened dorso-ventrally; the lumen is lined with a well-developed intima. A muscularis is present (2-3 layers of longitudinal fibres). The duct leads into a wide, sac-like chamber that is equipped with an epithelium formed of extremely flattenend cells, which have definitively no secretory function (Fig. 9B, ***ac***). This chamber lacks an intima and associated muscle fibres.

The ***common oviduct*** (Fig. 9D) leaves the genital chamber ventro-medially, about at mid-length of segment VIII. Its epithelium is composed of cubic cells and forms regular folds. An intima is well developed. The lumen is extremely narrowed by the foldings of the epithelium and the intima. The common oviduct is surrounded by few layers of mainly longitudinal muscle fibres.

4.2.4.2. Panorpidae: *Panorpa communis*

A very detailed account on the external morphology and the internal parts of the genital system, including histological informations, was given by Grell (1942) (for information on the external morphology see also Ferris & Rees 1939, Mickoleit 1975).

Musculature (Fig. 10A)**.** The postabdominal muscle set of *P. communis* comprises 19 muscles: **01** *isVII-VIII01*, **02** *isVII-VIII02* (site of origin shifted ventrad), **03** *isVII-VIII03* (shortened; site of origin shifted dorsad, muscle crosses with muscle 02), **04** *isVII-VIII04*, **05** *isVII-VIII05*, **06** *isVII-VIII06* (2 distinct bundles), **14** *isVIII-IX01*, **15** *isVIII-IX02* (2 bundles), **17** *isVIII-IX04*, **25** *isIX-X01*, **26** *isIX-X02*, **28** *isX-XI01*, **29** *isX-XI02*, **30** *seX-ce01*, **32** *intraIX01* (scattered fibres), **36** *dvVII01*, **37** *dvVIII01*, **58** *seIX-gc01*, and **59** *seIX-gc02*.

4.2.5. Diptera

4.2.5.1. Limoniidae: *Limonia* sp.

Exoskeleton. The external morphology of the female postabdomen of *Limonia sciophila*, was described and depicted in detail by Rees & Ferris (1939). Most of the results presented there can be confirmed. However, a clear separation of a sclerite, designated with the term "coxopodite" in Rees & Ferris (1939), from ***tergum IX*** was not found in the investigated *Limonia*-species. Moreover, directly in front of the anterior apices of the ventral sclerotizations of segment IX a slender, rod-like sclerotization arises, pointing deep into the body cavity directly above the common oviduct. This sclerotized element clearly represents what is termed the "vaginal apodeme" of tipulids by Frommer (1963). The posteriormost portion of this sclerite is forked, the "arms" seem to articulate with the anterior apices of the ventral sclerotization of segment IX. As a "vagina" in the sense of Snodgrass´ definition is not developed, the term "vaginal apodeme" is omitted here and replaced by "rod-like sclerite" (***scl-rod***).

Musculature (Fig. 11B)**.** A total of 22 muscles were found in the female postabdomen of *Limonia*: **01** *isVII-VIII01*, **02** *isVII-VIII02*, **05** *isVII-VIII05*, **06** *isVII-VIII06* (fusion of the muscles of both body halves in the median line), **14** *isVIII-IX01*, **15** *isVIII-IX02*, **17** *isVIII-IX04*, **25** *isIX-X01*, **26** *isIX-X02*, **28** *isX-XI01*, **29** *isX-XI02*, **30** *seX-ce01* (muscles 28 – 30 are strongly elongated, as segment X), **36** *dvVII01*, **37** *dvVIII01* (2 compact bundles), ***38*** *dvVIII02*, **40** *dvIX01* (site of origin shifted posteriad to tergum X) , **41** *dvIX02*, **44** *dvX01* (2 distinct bundles), **48** *tVIII01* (2 large portions), **51** *tX01*, **53** *tXI01*, an **55** *seVIII-gc01*(inserts lateral on the anterior part of the rod-like sclerite ***scl-rod***, Fig. 12F).

Internal parts of the genital system (overview: Fig. 11A)**.** A closed ***genital chamber*** is not developed in *Limonia*. The oviduct system (common oviduct) opens directly behind the fused anterior parts of the ventral sclerotizations of segment VIII. A bursa copulatrix is lacking. The spermathecal duct and the paired gland ducts open immediately behind the common oviduct, from the ventral region of segment IX.

The ***spermathecal duct*** (Fig. 12B) opens directly behind the oviduct in the median line. Its epithelium is squamose. An intima is well developed. Following the duct in anterior direction, the lumen gradually widenes. A muscularis is present around the posterior parts of the spermathecal duct, composed of several layers of mainly longitudinal fibres. About mid-length of segment VIII the spermathecal duct leads into the ***spermatheca*** (Figs. 12 C, D), which branches off into two distinct lobes anteriorly. The epithelium of the spermathecal lobes is glandular, with vesicles and large storage vacuoles in the cell bodies. A cuticular outline is absent. The spermatheca lacks an associated muscularis and a spermathecal gland.

The paired ***gland ducts*** (Fig. 12A) open a short distance postero-lateral with regard to the spermathecal duct. The gland ducts are equipped with cubic epithelial cells. A strong cuticular intima is present. The ducts are surrounded by a muscularis composed of several layers of longitudinal fibres. The gland ducts are short and lead into the ***accessory glands*** in the boundary region of segments VIII and IX. Following the accessory glands in anterior direction, two successive regions can be distinguished. The epithelium of the posterior regions (Figs. 12B, C, D) is formed of large prismatic cells with numerous small vesicles and a large storage vacuole per cell. In the huge anterior regions of the glands (Fig. 12E), reaching segment V, the epithelial cells are of an irregular shape. The by far greatest compartment of each cell is a huge, balloon-like storage vacuole. Around the posterior gland regions a loose, one-layered arrangement of longitudinal muscle fibres is present. The anterior regions lack associated muscle fibres.

The ***common oviduct*** (Figs. 12 C, F) branches off into the ***lateral oviducts*** about mid-length of segment VII. The epithelium of both the common oviduct and the lateral oviducts is composed of small, irregularely shaped cells. A weak cuticular outline is present in the common oviduct. The oviducts are associated only with a few, scattered longitudinal muscle fibres.

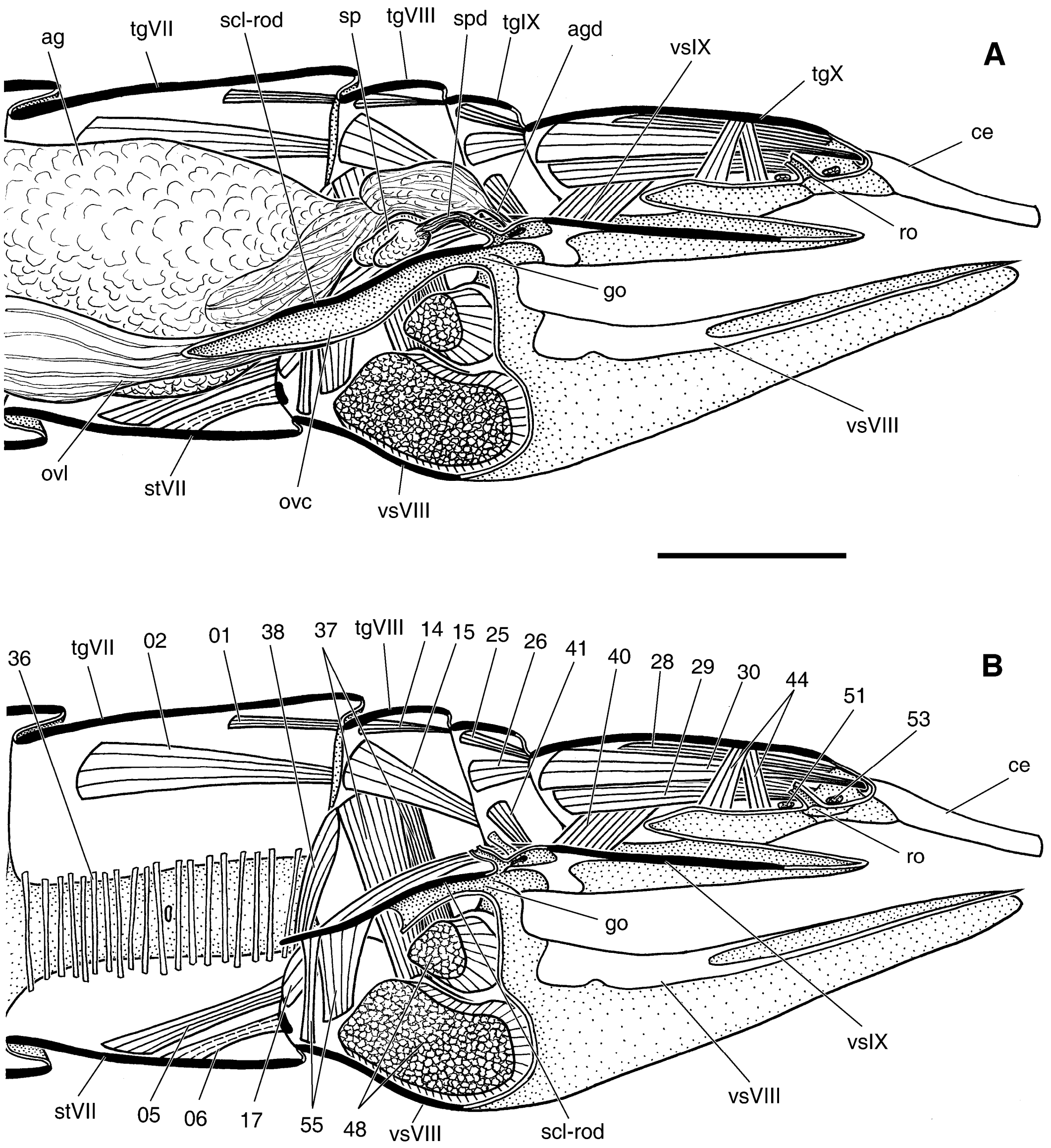

Fig. 11. *Limonia* sp., female postabdomen. (A) overview over the internal parts of the genital system; (B) skeleto-muscular arrangement. Scale bar: 500 µm.

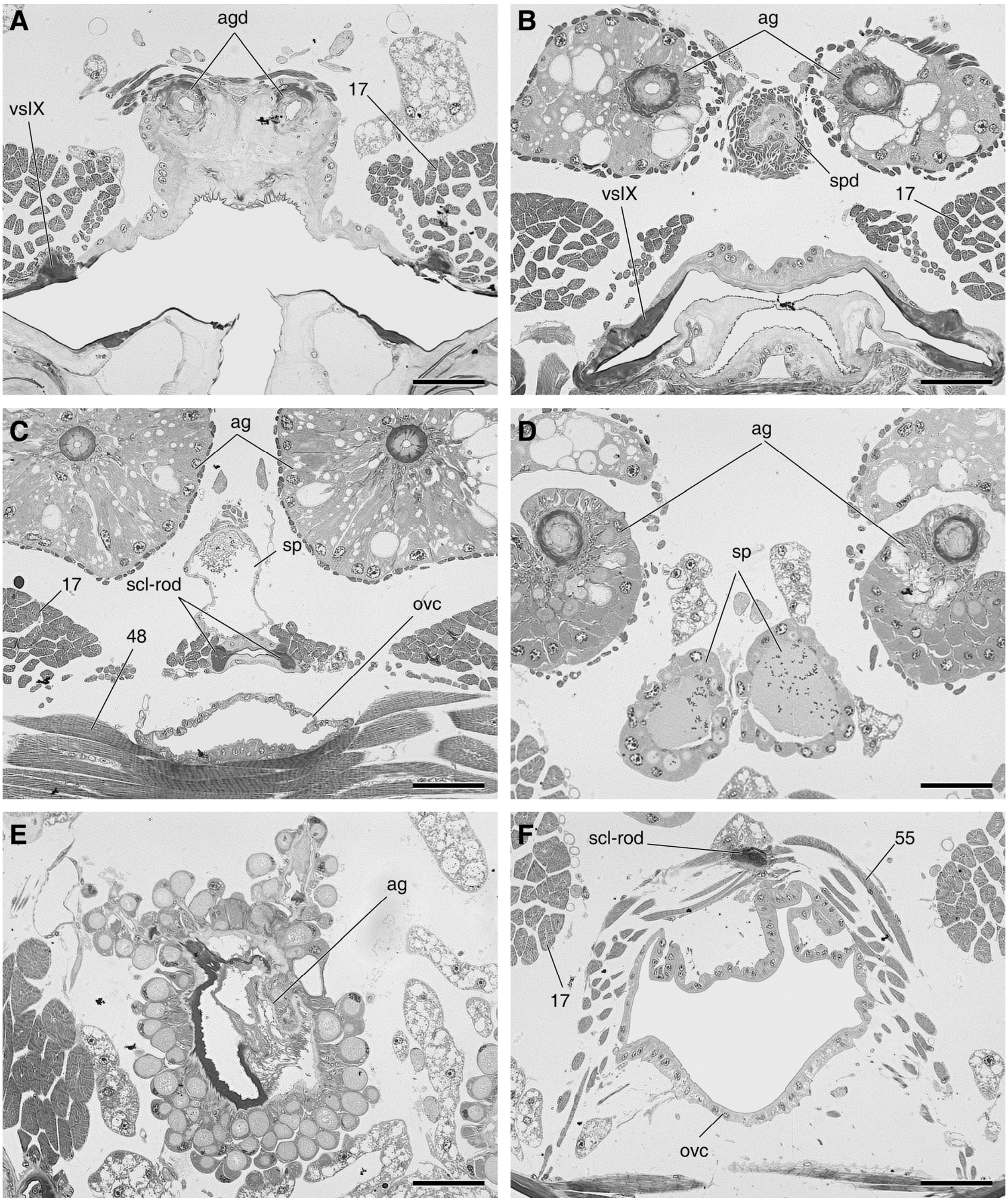

Fig. 12. *Limonia* sp., female postabdomen, histological cross sections. (A) boundary region of segments VIII and IX, paired gland ducts; (B) segment VIII, posterior parts of accessory glands, spermathecal duct, anterior arms of vsIX; (C) segment VIII, posterior region of spermatheca, posterior arms of the rod-like sclerite, ***scl-rod***; (D) segment VIII, anterior half, anterior lobes of spermatheca with glandular tissue; (E) segment VII, anterior part of accessory gland; (F) segment VIII, common oviduct, rod-like sclerite with muscle 55. Scale bar: 50 µm.

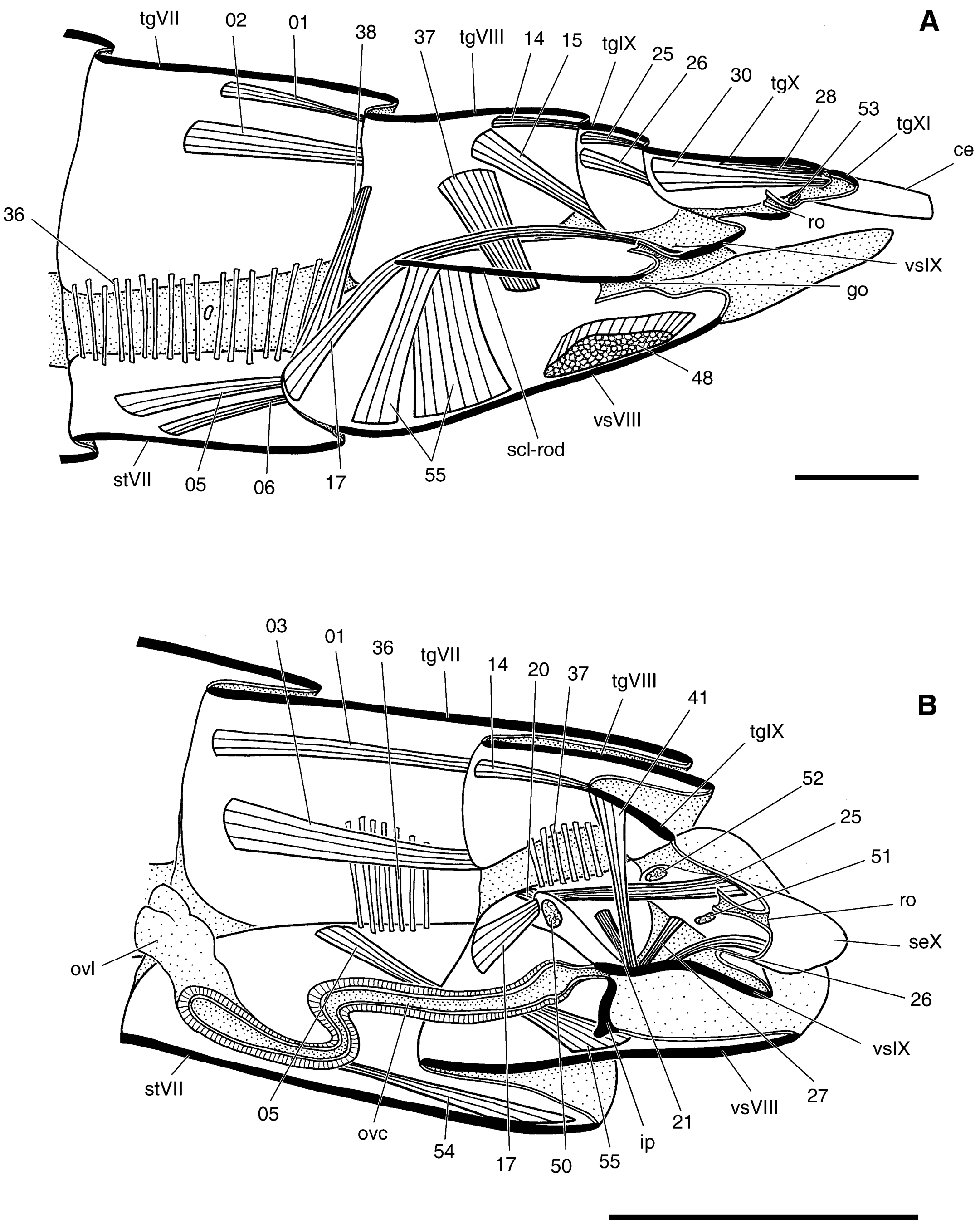

Fig. 13. Skeleto-muscular arrangement of the female postabdomen. (A) *Tipula* sp.; (B) *Aedes* sp., ***ip*** – insula plate. Scale bar: 500 μm.

4.2.5.2. Tipulidae: *Tipula* sp.

The external morphology as well as the internal components of the female genital system of tipulids are sufficiently described (see Frommer 1963, Rees & Ferris 1939). In the present study, the muscular equipment of the female postabdomen was addressed.

Musculature (Fig. 13A). The female postabdominal musculature of the *Tipula*-species studied here comprises 18 muscles: **01** *isVII-VIII01*, **02** *isVII-VIII02*, **05** *isVII-VIII05*, **06** *isVII-VIII06*, **14** *isVIII-IX01*, **15** *isVIII-IX02*, **17** *isVIII-IX04*, **25** *isIX-X01*, **26** *isIX-X02*, **28** *isX-XI01*, **29** *isX-XI02*, **30** *seX-ce01* (muscle 28 – 30 are elongated, as tergum X), **36** *dvVII01*, **37** *dvVIII01* (1 compact portion), **38** *dvVIII02*, **48** *tVIII01* (1 large portion), **53** *tXI01*, and **55** *seVIII-gc01* (inserts lateral on the rod-like sclerite ***scl-rod***).

4.2.5.3. Culicidae: *Aedes* sp.

Reliable contributions are available concerning the external morphology and the internal parts of the genital system of culicids, including representatives of the genus *Aedes* (see Brelje 1924, Christophers 1960). The musculature was subject to the present study.

Musculature (Fig. 13B). A total of 19 muscles are present in the female postabdomen of *Aedes*: **01** *isVII-VIII01*, **03** *isVII-VIII03*, **05** *isVII-VIII05*, **14** *isVIII-IX01*, **17** *isVIII-IX04*, **20** *isVIII-IX07*, **21** *isVIII-IX08*, **25** *isIX-X01* (origin shifted to the anterior parts of the ventral sclerotization of segment IX), **26** *isIX-X02* (muscle origin shifted to the midpart of the ventral sclerotization of segment IX), **27** *isIX-X03*, **36** *dvVII01*, **37** *dvVIII01*, **41** *dvIX01*, **50** *tIX01*, **51** *tX01*, **52** *tX02*, **54** *seVII-gc01*, **55** *seVIII-gc01*, and **71** *add04*.

4.2.6. Trichoptera

4.2.6.1. Rhyacophilidae: *Fansipangana vernalis*

F. vernalis was collected in the Fan-Si-Pan mountain area (Vietnam) and formally described by Mey in 1996. The habitus of an entire specimen is not depicted until now, so the female is shown here (Fig. 14 A).

Exoskeleton (Figs. 14 B-D). The last unmodified segment of the female postabdomen is ***segment VII***. Tergum and sternum of segment VII are equal sized and do not display distinct structural specifics. The ventral margins of tergum VII are strongly pigmented; a pair of conspicuous, dark-framed dorsal spots is present on it (as on the preceeding tergal plates). Along the dorsal mid-line the pigmentation is darker again, especially near the anterior segmental margin. Spiracle VII lies in the pleural membrane near the anterior segmental margin; it is the last abdominal spiracle.

Segment VIII is slightly elongated and strongly tapering towards its posterior margin. The tergum VIII – sclerotization is not closed in the dorsal midline, but its ventral margins are completely fused with the ventral sclerotizations of segment VIII. The latter are fused along the entire length of the segment. So segment VIII is enclosed by a sclerotized tube, with only a narrow dorso-median stripe of membranous cuticle. Behind the posterior margin of the segment VIII- sclerotization a collar of membranous cuticle remains unretracted. A pair of long apophyses invaginates from a ventral area of the anterior margin of the segment. These anterior apophyses reach up to the boundary region of segments VI and VII anteriorly. They are hollow over the greatest part of their length (Fig. 16E). A second pair of anterior apophyses (as it was proposed in the original description; Mey 1996) is absent.

In the ***terminal unit*** (segments IX – X [XI]) the tergum IX-sclerotization is present as a pair of dorsolateral sclerite-bands; anterior elongations of the latter are a pair of long, slender rods (posterior apophyses). The posterior apophyses reach the boundary region of abdominal segments VI and VII anteriorly. As the anterior apophyses, the posterior ones are hollow (Figs. 16B-E). A pair of small, oval dorsal plates is interpreted as vestiges of tergum X. Directly above the posterior apices of these plates each a minute, unsegmented, cercus rudiment articulates. In the ventral, membranous, region of the terminal unit the segmental margins are not traceable. Elements of a separate segment XI were not found.

The genital chamber and the rectum lead out by way of a common opening (cloaca). The cloacal aperture lies subapical, on the ventral side of the terminal unit.

Musculature (Fig. 15B)**.** A total of 16 muscles were found in the female postabdomen of *F. vernalis*: **01** *isVII-VIII01*(very short in *F. vernalis*), **02** *isVII-VIII02*, **05** *isVII-VIII05*, **08** *isVII-VIII08*, **11** *isVII-VIII11*, **13** *isVII-IX01*, **14** *isVIII-IX01*, **15** *isVIII-IX02* (muscle originates with 2 massive bundles; insertion site shifted to apical region of posterior apophysis), **17** *isVIII-IX04* (site of origin shifted to apex of anterior apophysis), **22** *isVIII-IX09*, **24** *isVIII-IX11*, **37** *dvVIII01* (restricted to the area of the membranous collar behind the segment VIII-sclerotization), **40** *dvIX01*, **55** *seVIII-gc01* (originates from the apical region of the anterior apophysis), **58** *seIX-gc01* (site of origin shifted to posterior apophysis), and **67** *rec/clo01.*

Internal parts of the genital system (overview: Fig. 15A)**.** The ***genital chamber*** is fused with the rectum just in front of the common opening of both (cloaca). The chamber reaches the anterior half of segment VIII anteriorly. Following the genital chamber in anterior direction, 2 successive regions can be distinguished. The posterior chamber region (Fig. 16A) stretches through the terminal unit as a slender tube, slightly flattened dorso-ventrally. The epithelial cells are extremely flattened. A fine cuticular outline is present. The posterior region is lacking a muscularis. Around the anterior region (Figs. 16B, C), the epithelium is squamose, but the cells are by far not as flat as in the posterior part of the chamber. The intima is conspicuously strengthened; its ventral part displays regular folds (Fig. 16B). A muscularis surrounding the anterior region is present, composed of a few (2-3) layers of mainly circular fibres. From the most anterior part of the chamber the ducts evaginate close to each other in the median line, the spermatecal duct on the tip of a heavily sclerotized spermathecal process (Fig. 16C).

The ***spermathecal duct*** (Figs. 16C, D, E) evaginates from the genital chamber anteriorly. Its epithelium is formed of cubic cells. The lumen of the duct is rounded in cross section and becomes gradually widened anteriorly. A strong intima is present, as well as a muscularis composed of 2-3 layers of circular fibres. Distinctive duct regions were not found. The

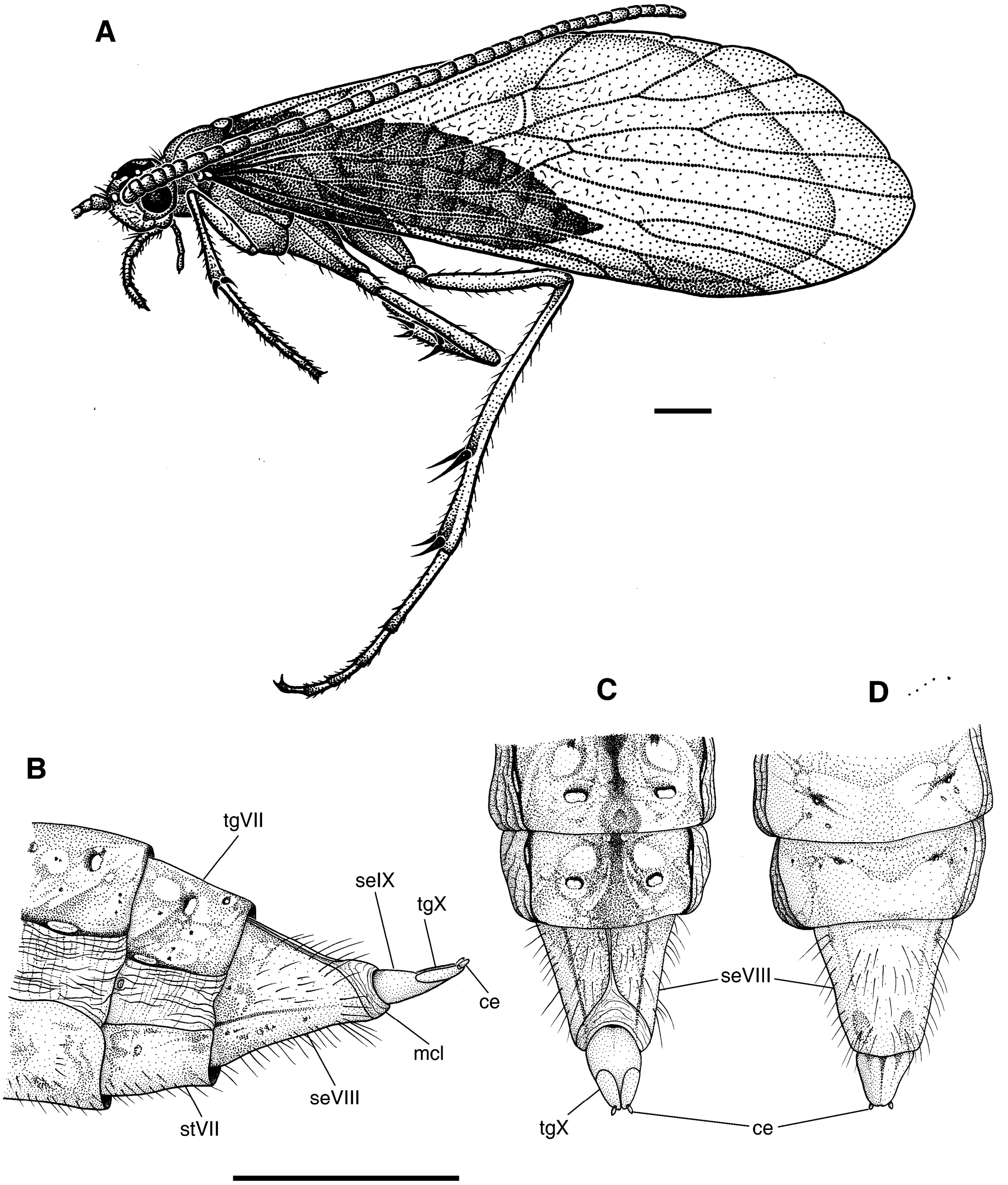

Fig. 14. *Fansipangana vernalis*, female. (A) habitus, lateral. (B-D) external morphology of the postabdomen; (B) lateral view; (C) dorsal view; (D) ventral view. Scale bar: 500 µm.

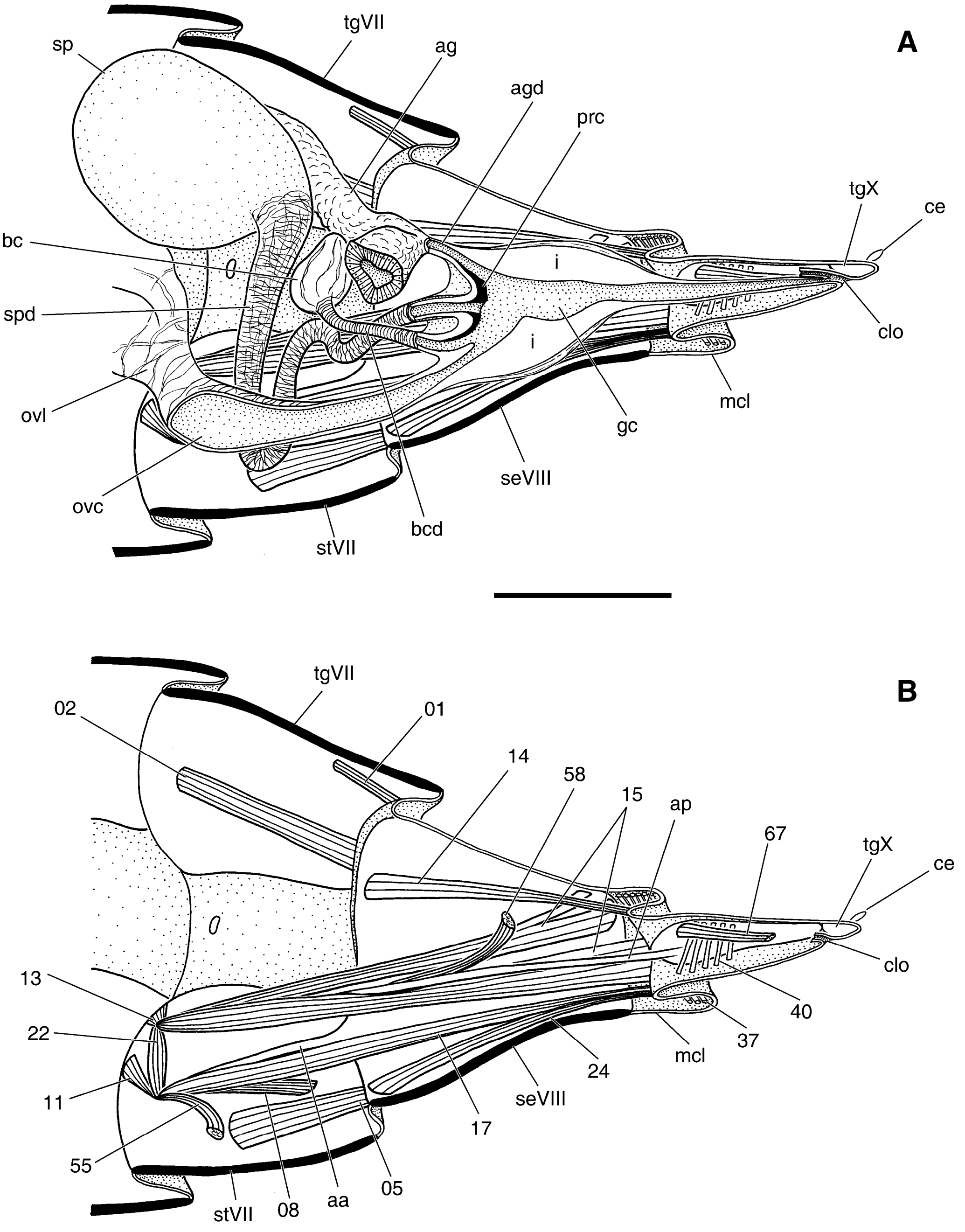

Fig. 15. *Fansipangana vernalis*, female postabdomen. (A) overview over the internal parts of the genital system; (B) skeleto-muscular arrangement. Scale bar: 200 µm.

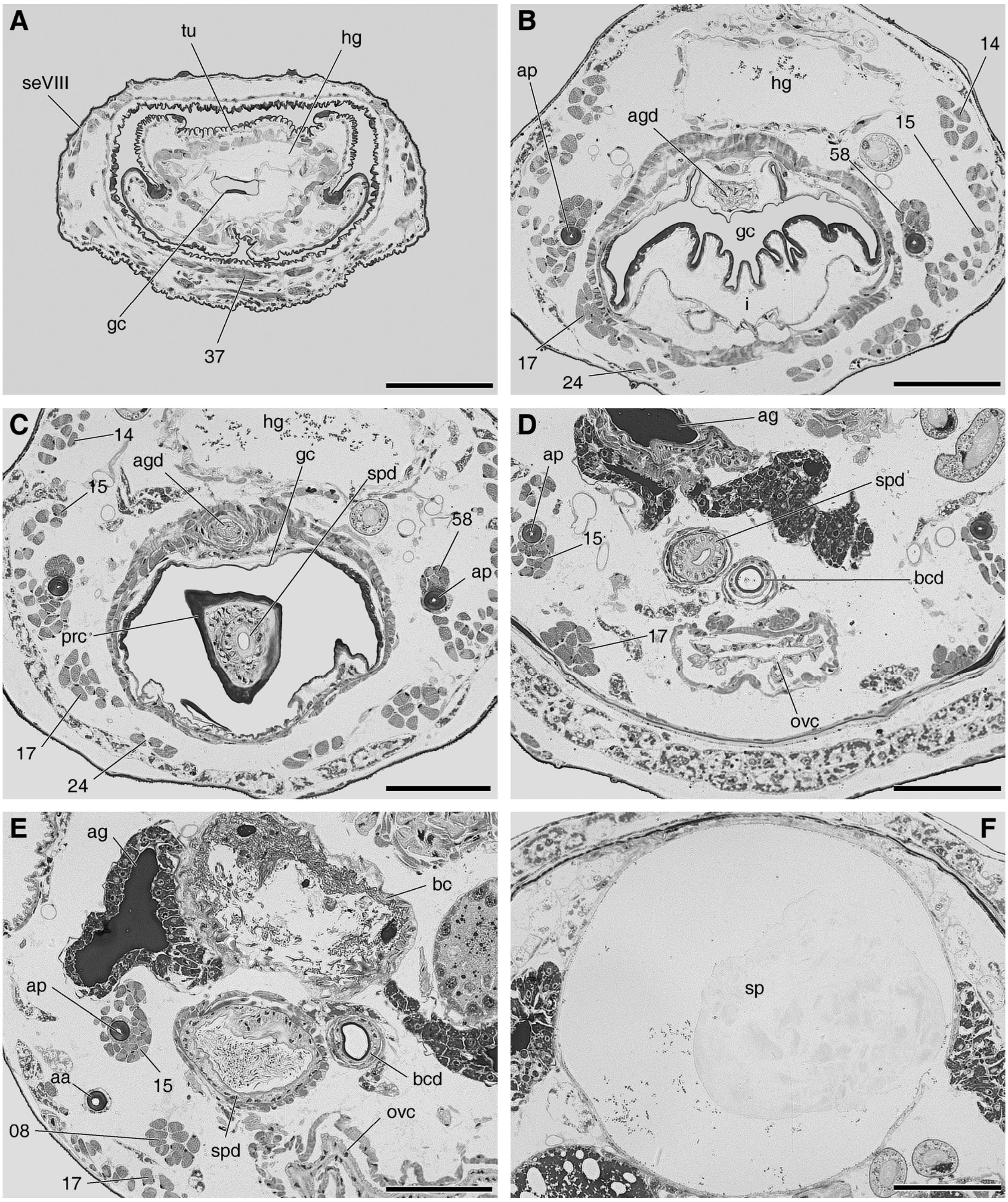

Fig. 16. *Fansipangana vernalis*, female postabdomen, histological cross sections. (A) segment VIII with the terminal unit partially retracted; (B) segment VIII, mid-length, gland duct and, note the strong intima of the genital chamber, ***i***; (C) segment VIII, anterior half, spermathecal process and spermathecal duct; (D) boundary region of segments VII and VIII, spermathecal duct, gland duct, common oviduct; (E) segment VII, anterior and posterior apophysis, bursa copulatrix, accessory gland; (F) segment VII, spermatheca. Scale bar: 50 µm.

spermathecal duct leads over into the ***spermatheca*** (Fig. 16F) in segment VII. The spermatheca is huge and balloon-like. The epithelial cells are strongly flattened. A delicate intima is noticeable, but not a muscularis. A small ***spermathecal gland*** is directly attached to the spermatheca in terminal position. The gland cells are irregularely shaped, with vesicles and storage vacuoles visible in the cytoplasm.

The ***ductus bursae*** (Figs. 16D, E) evaginates from the genital chamber directly below the ventral base of the spermathecal process. It is equipped with an epithelium composed of irregularely shaped cells. The lumen of the ductus is rounded (cross section). A strong intima is present. The ductus bursae is surrounded by a muscularis formed of 2-3 layers of circular fibres. The ductus leads into the ***bursa copulatrix*** (Fig. 16E) in the posterior half of segment VII. The bursa is of a simple, sac-like shape and moderately sized. The epithelial cells are of irregular shape. The bursa lumen is filled with spermatozoans and remnants of the spermatophore. The intima outlining the lumen is extremely weak. Just a few longitudinal muscle fibres are associated with the bursa copulatrix.

The unpaired ***gland duct*** (Fig. 16B, C) leaves the genital chamber in the median line postero-dorsad with regard to the spermathecal process. The gland duct is short, its epithelium is formed of irregularely shaped cells. An intima is present and also a muscular envelope, the latter composed of 1-2 layers of circular fibres. The ***accessory glands*** (Figs. 16D, E) are paired, with the most posterior parts fused directly in front of the gland duct. The glands are tube-like and stretch up into segment VI anteriorly. The glandular cells are prismatic, with vesicles and larger storage vacuoles visible in the cytoplasm. The gland lumen is densely filled with secretions. The glands are surrounded by a loose, one-layered arrangement of muscle fibres.

The ***common oviduct*** (Figs. 16D, E) evaginates from the genital chamber below the ductus bursae. It stretches through segment VII and splits off into the ***lateral oviducts*** in the boundary region of segments VI and VII. The epithelial cells of both the common oviduct and the lateral oviducts are irregularely shaped. The lumina of the oviducts are strongly depressed dorso-ventrally. In the common oviduct a weak intima is noticeable. The oviduct system is surrounded by 1-2 layers of mainly circular muscle fibres.

4.2.6.2. Rhyacophilidae: *Rhyacophila* sp.

The external morphology of the female postabdomen and the genital chamber of a large sample of trichopterans, including 2 species of *Rhyacophila*, were treated in great detail by Nielsen (1980).

Musculature (Fig. 17A)**.** The muscular arrangement of the female postabdomen of *Rhyacophila* is composed of 15 muscles: **01** *isVII-VIII01*, **02** *isVII-VIII02*, **05** *isVII-VIII05*, **08** *isVII-VIII08*, **10** *isVII-VIII10*, **11** *isVII-VIII11* (site of origin shifted anteriad to the anterior margin of segment VI), **13** *isVII-IX01* (origin shifted to anterolateral corner of tergum VI), **14** *isVIII-IX01*, **15** *isVIII-IX02* (insertion site shifted to apical region of posterior apophysis), **17** *isVIII-IX04* (site of origin shifted to apex of anterior apophysis), **22** *isVIII-IX09*, **24** *isVIII-*

IX11, **40** *dvIX01*, **55** *seVIII-gc01* (originates from the apical region of the anterior apophysis), and **58** *seIX-gc01* (site of origin shifted to posterior apophysis).

Internal parts of the genital system. The ***genital chamber*** and the rectum are fused in segment IX, leading out subterminal by way of a common opening (cloaca). The chamber stretches up into segment VII anteriorly. Two chamber regions can be distinguished. The epithelium covering the posterior region (Fig. 18A) is squamose. A weak intima is present. The lumen of the posterior region is strongly depressed dorso-ventrally. A muscularis is not developed. The epithelial cells of the second, anterior region (Fig. 18C) are irregularely shaped. The intima of this region is conspicuously strengthened and thrown into deep, regular folds. The lumen is wide and symmetrically shaped by the folds of the intima and the epithelium. From the anterior region the duct of the accessory glands, the spermathecal duct, the ductus bursae and the lateral oviducts evaginate. All ducts leave the chamber close to one another, in the boundary region of abdominal segments VII and VIII in the median line. The spermathecal duct opens through the chamber roof on the tip of a sclerotized papilla, the spermathecal process (Fig. 18C). Around the anterior chamber region a muscularis is present, composed of 1-2 inner layers of longitudinal fibres and 2-3 outer layers of circular and diagonal fibres.

The ***spermathecal duct*** (Figs. 18C, D) evaginates from the genital chamber dorso-medially, in the boundary region of segments VII and VIII. The duct has the shape of a simple tube. The epithelium of the spermathecal duct is composed of cubic cells. A cuticular intima is well developed, strengthened in the proximal part of the duct, and with annular thickenings in the more distal regions. The duct lumen is characteristically shaped by foldings of the intima (cross section images). The spermathecal duct is surrounded by a strong muscularis, composed of 5-6 layers of circular fibres. About mid-length of segment VII, the duct widenes into the ***spermatheca*** (Figs. 18E, F). The spermatheca is huge and stretches up into segment V anteriorly. The epithelial cells of the spermatheca are cubic. In the cell bodies, numerous vesicles and large storage vacuoles are visible. An intima is present, displaying annular thickenings in steady distances. The lumen is moderately sized and rounded in cross section; it contains cell remnants and spermatozoans. A muscularis associated with the spermatheca is lacking. The ***spermathecal gland*** is simple and tube-like. It opens into the spermatheca in segment VII, just some µm anteriorly with regard to the site where the spermatecal duct merges into the spermatheca. The epithelium of the spermathecal gland is formed of prismatic cells with the nuclei close to the basal poles. The gland cells are densely filled with small secretory vesicles. The lumen of the gland is narrow, but clearly visible, and filled with numerous vesicles, cell remnants, and single spermatozoans. A single layer of longitudinal and diagonal muscle fibres is associated with the spermathecal gland.

The ***ductus bursae*** evaginates from the genital chamber anteriorly, in terminal position. The epithelium of the ductus is squamose. An intima is well developed. The duct lumen is rounded in cross section. The ductus bursae is surrounded by a muscularis composed of 3-4 layers of circular fibres. The ductus leads over into the ***bursa copulatrix*** (Fig. 18E) in the boundary region of segments VI and VII. The bursa is moderately sized, sac-like, and shifted to the left body half.

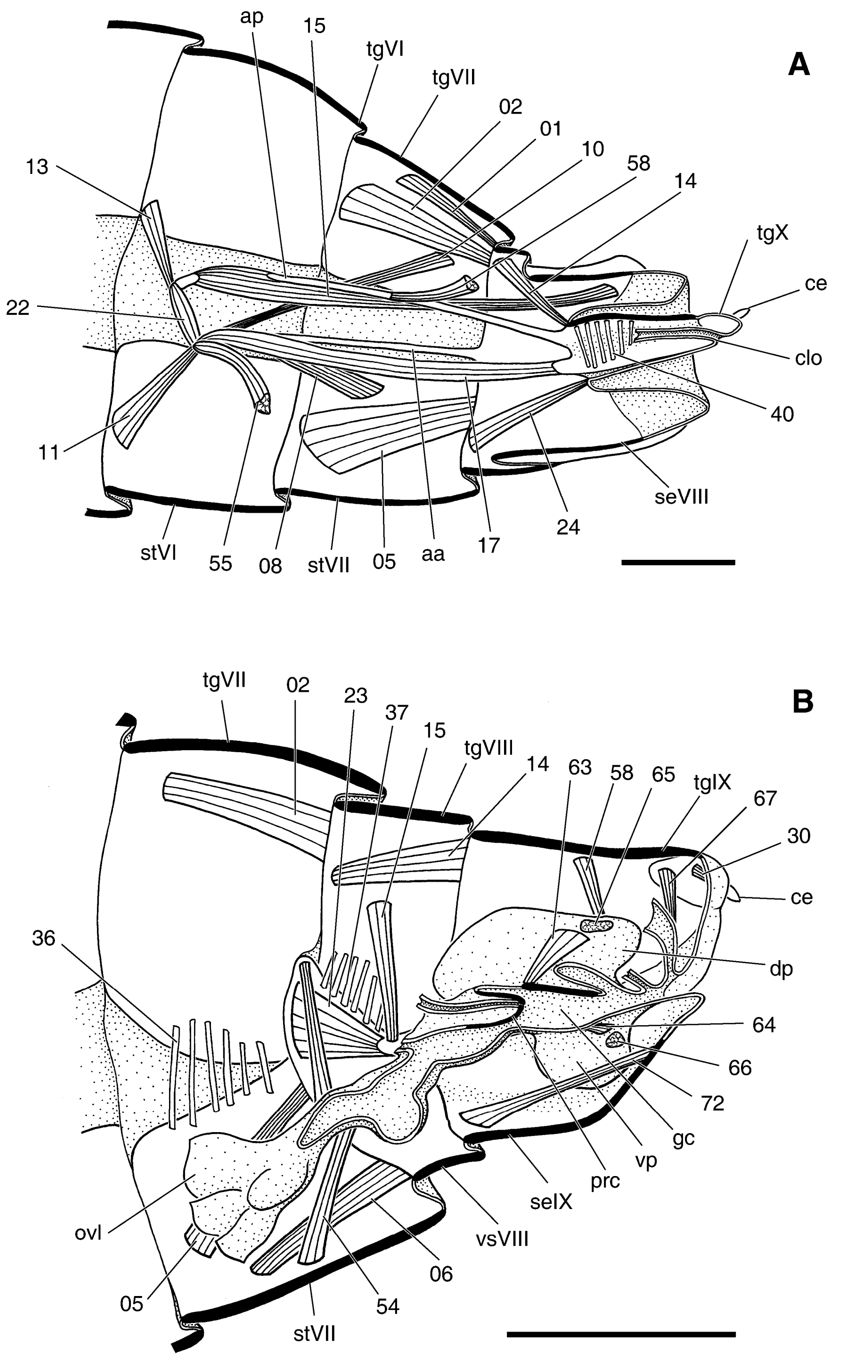

Fig. 17. Skeleto-muscular arrangement of the female postabdomen. (A) *Rhyacophila* sp.; (B) *Ulmerochorema* sp. Scale bar: 500 µm.

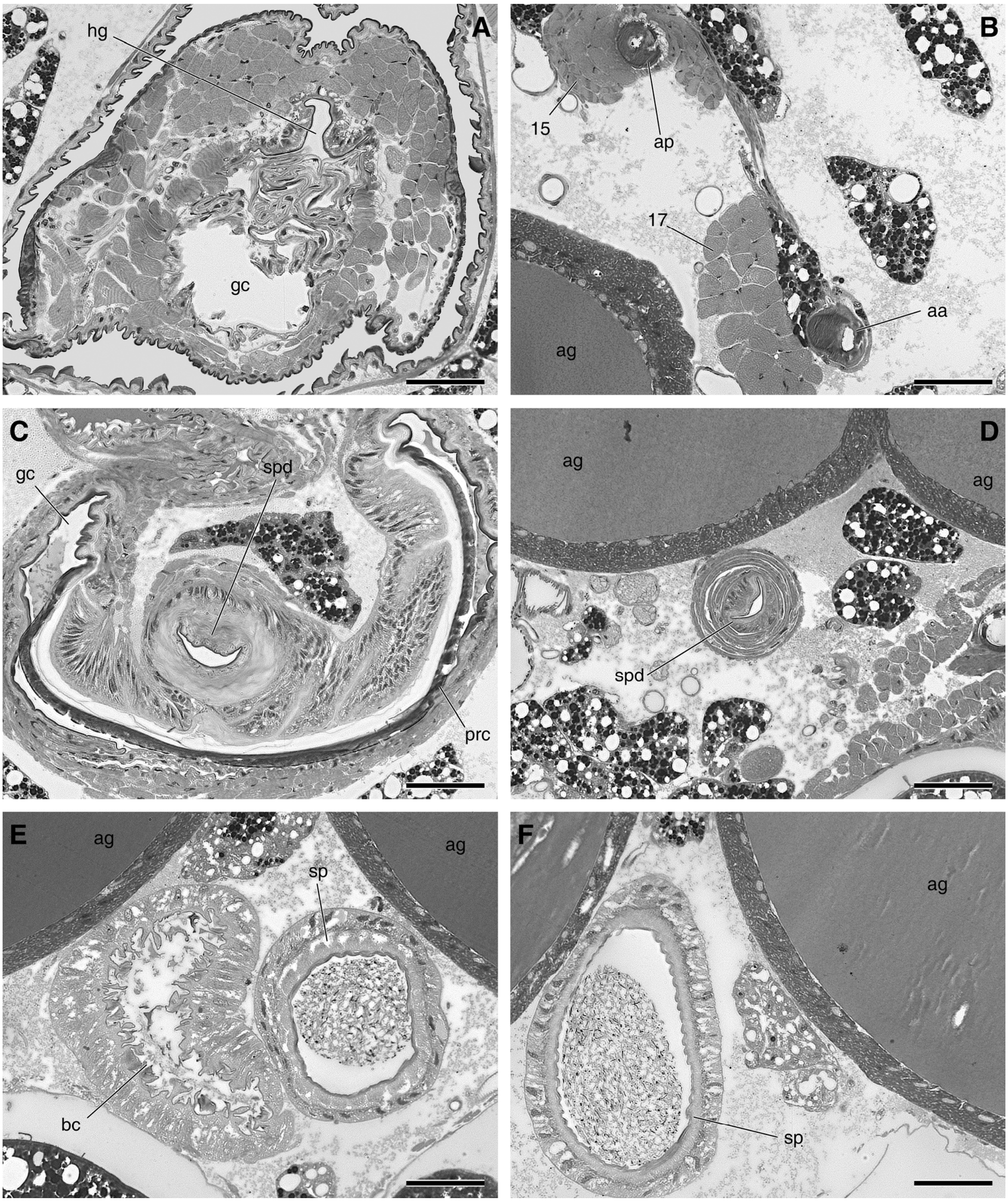

Fig. 18. *Rhyacophila* sp., female postabdomen, histological cross sections. (A) terminal unit; (B)segment VII, anterior and posterior apophysis; (C) segment VII, spermathecal process and spermathecal duct; (D) segment VII, anterior half, spermathecal duct, accessory glands; (E) segment VI, spermatheca, bursa copulatrix; (F) segment VI, spermatheca. Scale bar: 50 µm.

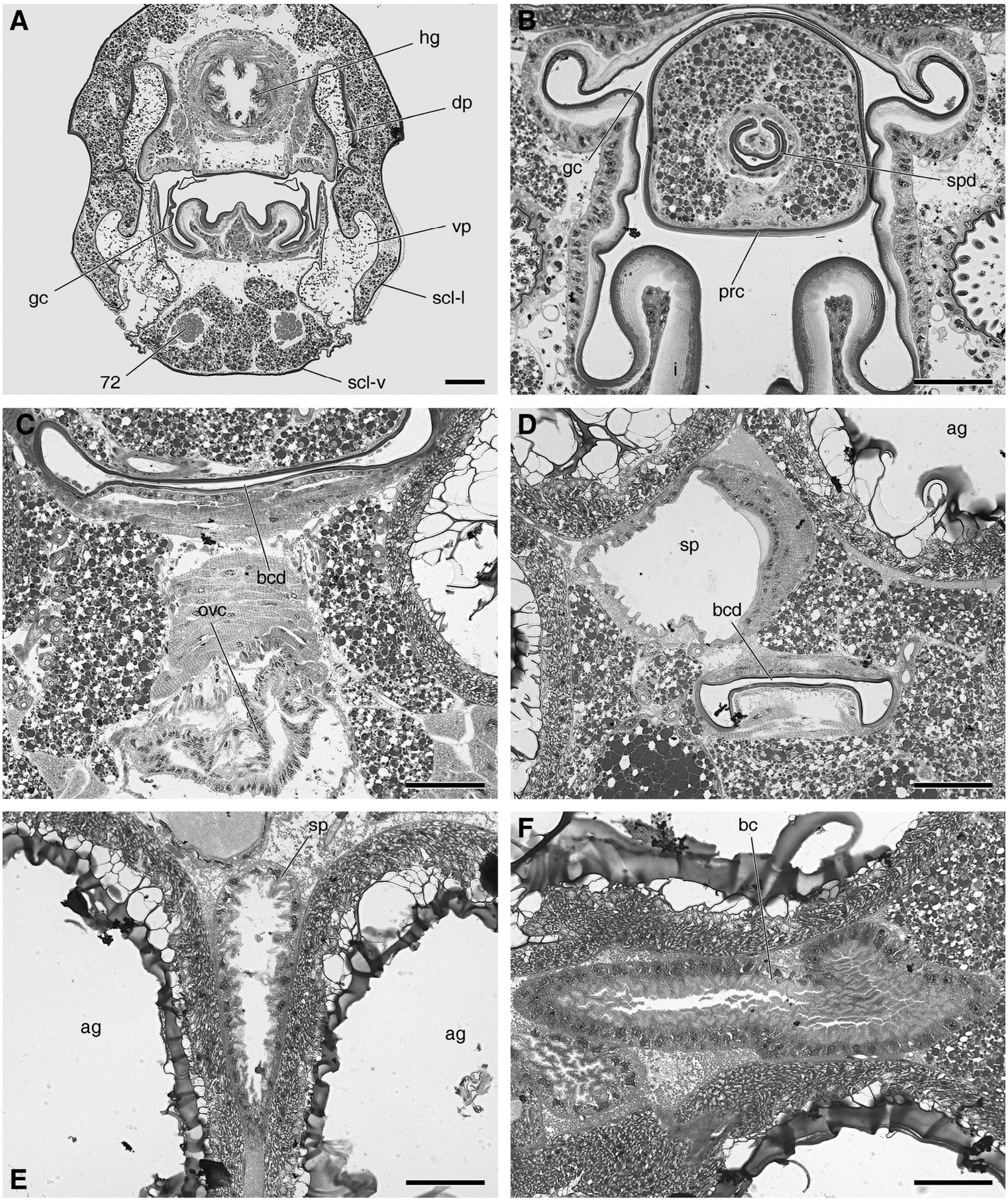

Fig. 19. *Ulmerochorema* sp., female postabdomen, histological cross sections. (A) terminal unit, note the paired lateral and unpaired ventral sclerite stripes, ***scl-l***, ***scl-v***, and the lateral evaginations of the genital chamber, ***dp***, ***vp***; (B) spermathecal process, spermathecal duct; (C) segment VIII, ductus bursae, common oviduct; (D) segment VIII, posterior part of spermatheca, ductus bursae; (E) segment VIII, anterior part of spermatheca, accessory gland; (F) segment VIII, bursa copulatrix. Scale bar: 50 μm.

The bursa epithelium is formed of prismatic cells with the nuclei near the basal poles. The cells are of a glandular appearance, with numerous vesicles visible in the cytoplasm. The cuticular intima of the bursa copulatrix is weak, with single spines projecting into the bursa lumen. The bursa lumen is triangular in cross section, and contains just a few cell remnants. A muscularis associated with the bursa copulatrix was not found.

The ***gland duct*** evaginates from the genital chamber dorso-medially in the boundary region of segments VII and VIII, just a minute distance posterior with regard to the spermathecal duct. The epithelial cells of the duct are irregularely shaped and flattened, with the nuclei recognizeable in widenings of the cell bodies. The intima of the gland duct is thick and heavily folded, giving the duct lumen a characteristic shape in cross section. The muscularis surrounding the gland duct consists of 3-4 layers of circular fibres. The gland duct is connected with the ***accessory glands*** (Figs. 18B, D, E, F) in the boundary region of segments VII and VIII. The glands are paired, just their most posterior parts are fused. The glands are huge and balloon-like and run up into segment V anterad. The glandular epithelium is cubic, with the nuclei in almost central position within the cells. There are numerous secretory vesicles visible in the cytoplasm, and in many cells a large "storage vacuole" near the apical cell pole. The gland lumen is densely filled with secretions.

A ***common oviduct*** is not developed. The ***lateral oviducts*** are directly connected to the genital chamber. The lateral oviducts are running up to mid-length of segment VII anterad, where the ovarioles are branching off. The epithelium of the oviducts is squamose. An intima is not developed – an indication that the oviducts are *true* lateral oviducts of mesodermal origin. The oviducts are surrounded by a one-layered network of muscle fibres.

4.2.6.3. Hydrobiosidae: *Ulmerochorema* sp.

Exoskeleton. The external morphology of the female postabdomen of hydrobiosids was described by Schmid (1989), and the putatively ancestral condition was depicted therein. However, some of the interpretations given by Schmid need critical evaluation. The last abdominal segment without strong modifications is segment VII. In ***segment VIII*** the tergum is only half in length than in the preceeding segment. The ventral sclerotizations of segment VIII are completely fused along the ventro-median line and of equal length as tergum VIII. The dorsal margins of the ventral sclerotizations of segment VIII are conspicuously prolonged. The ***terminal unit*** is almost completely covered dorsally by the large, saddle-shaped tergum IX, and there is no reason to assume absence of the entire segment IX, as it was stated by Schmid (1989). The antero-lateral corners of tergum IX are moderately elongated (rudimentary posterior apophyses). Tergum X is present as a pair of small plates of thickened cuticle, flanking the posterior apex of the terminal unit. Each of these plates bears a minute, one-segmented cercus. The membranous ventral half of the terminal unit is stiffened by a pair of ventro-lateral sclerite stripes. Moreover, a ventro-median sclerotization is present. The genital system and the rectum lead out separate, as stated by Dugdale (1974). Both open into a compartment which is enclosed by the dorsal and ventral parts of the terminal unit, but corresponds with the outside by ventro-lateral slits.

Musculature (Fig. 17B)**.** The postabdominal muscle equipment of *Ulmerochorema* comprises 18 muscles: **02** *isVII-VIII02*, **05** *isVII-VIII05*, **06** *isVII-VIII06*, **14** *isVIII-IX01*, **15** *isVIII-IX02*, **23** *isVIII-IX10*, **30** *seX-ce01*, **36** *dvVII01*, **37** *dvVIII01*, **54** *seVII-gc01*, **55** *seVIII-gc01*, **58** *seIX-gc01*, **63** *intra-gc02*, **64** *intra-gc03*, **65** *intra-gc04*, **66** *intra-gc05*, **67** *rec/clo01*, and **72** *add05*.

Internal parts of the genital system. The internal parts of the genital system of a hydrobiosid were depicted by Dugdale (1974). The "true", closed part of the ***genital chamber*** is short and restricted to the anterior half of the terminal unit. In the posterior half of the terminal unit the median lumen component of the genital system displays lateral evaginations, those branching off each in a dorsal and a ventral pouch (Fig. 19A; ***dp***, ***vp***). The ventral pouches communicate with the outside by way of long slits that open below the ventro-lateral sclerite stripes of the terminal unit. The epithelium of the chamber is composed of small, prismatic cells. A strong cuticular intima is present. The chamber lumen is characteristically shaped by deep, symmetric folds of the intima (Figs. 19A, B). Around the ventral part of the chamber a weak muscularis is developed, consisting of 2-3 layers of circular fibres. Anteriorly, the spermathecal duct, the ductus bursae and the common oviduct evaginate. The opening of the spermathecal duct is on the tip of a strongly sclerotized spermathecal process that points deep into the chamber lumen (Fig. 19B).

The ***spermathecal duct*** (Fig. 19B) is long and slender. The epithelial cells of the duct are irregularely shaped. An intima is well developed. The duct lumen is narrowed and U-shaped by a dorsal fold of the epithelium and the intima. A muscular envelope is present, composed of 1-2 layers of circular fibres. The spermathecal duct leads into the ***spermatheca*** in the boundary region of segments VI and VII. Regarding the spermatheca, 2 successive compartments can be easily distinguished. The posterior compartment (Fig. 19D) is tube-like. Its epithelium is formed of cubic cells. An intima is present, as well as a muscularis composed of 2-3 layers of circular fibres. The lumen is wide and rounded in cross section. The second, anterior compartment (Fig. 19E) lies between the huge accessory glands. The epithelial cells are of an irregular shape. The lumen is depressed laterally. The anterior compartment of the spermatheca lacks an intima and a muscularis. An unpaired ***spermathecal gland*** is directly attached to the spermatheca, in the region where the latter is connected with the spermathecal duct.

The ***ductus bursae*** (Figs. 19C, D) evaginates from the genital chamber directly below the base of the spermathecal process. The epithelium of the ductus is formed of flattened cells. The intima is strong, and a muscularis is present (1-2 layers of circular fibres). The ductus bursae is strongly compressed dorso-ventrally. The ductus leads over into the ***bursa copulatrix*** (Fig. 19F) in segment VI. The epithelial cells of the bursa are glandular (secretions in the lumen).

The unpaired ***gland duct*** is equipped with an epithelium formed of irregularely shaped cells. The intima is well developed. The duct is rounded in cross section. A strong muscularis is present (4-6 layers of circular and diagonal fibres). The paired ***accessory glands*** (Figs. 19D, E) are extremely huge and balloon-like, stretching up into segment V anterad. The posterior parts of the glands (in segment VIII) are fused. In segment VII each gland displays a conspicuous ventrad evagination. The cells of the glandular epithelium are irregular in shape, with the nuclei in various positions and numerous vesicles and storage vacuoles visible.

The ***common oviduct*** (Fig. 19C) leaves the genital chamber ventrad with regard to the ductus bursae. It splits off into the ***lateral oviducts*** in the boundary region of abdominal segments VII and VIII. The epithelium of the oviducts is formed of small, mainly cubic cells. A weak intima is present in the common oviduct. The muscular support of the oviduct system is restricted to a few scattered fibres.

4.2.7. Lepidoptera

4.2.7.1. Micropterigidae: *Micropterix calthella*

The external morphology of micropterigid moths, including *M. calthella*, is described and depicted in literature (e.g., Kristensen 1998, 2003b).

Musculature (Fig. 20)**.** In the female postabdomen of *M. calthella* a total of 17 muscles are present: **01** *isVII-VIII01*, **02** *isVII-VIII02*, **03** *isVII-VIII03*, **04** *isVII-VIII04*, **05** *isVII-VIII05*, **06** *isVII-VIII06* (site of insertion shifted to the anterolateral corner of the ventral sclerotization of segment VIII), **14** *isVIII-IX01*, **15** *isVIII-IX02*, **17** *isVIII-IX04*, **24** *isVIII-IX11*, **25** *isIX-X01*, **26** *isIX-X02*, **36** *dvVII01*, **37** *dvVIII01*, **51** *tX01*, **52** *tX02*, and **58** *seIX-gc01*.

Internal parts of the genital system. The ***genital chamber*** (Figs. 21A, B) stretches up to midlength of segment VII anteriorly. Two successive chamber regions can be distinguished. The epithelium of the posterior region is composed of irregular, flattened cells. An intima is present, but hardly noticeable in this part of the chamber. The narrow lumen of the posterior region becomes gradually widened anterad. The posterior chamber region is surrounded by a loose, single-layered arrangement of muscle fibres. The anterior region of the chamber is surrounded by cubic epithelial cells. The cuticular intima is much thicker than in the posterior part of the chamber. In the boundary region of segments VII and VIII, where the gland duct evaginates in dorso-median position, the intima is conspicuously strengthened and thrown into deep regular folds, giving the wide lumen of this region a characteristic shape (cross section). Midlength of segment VII, the spermathecal duct, the ductus bursae and the common oviduct evaginate from the genital chamber in the median line. The spermathecal duct leads out on the tip of a prominent spermathecal process (Fig. 21B). In this region also the lateral parts of the chamber intima are conspicuously strengthened. Around the anterior region a well developed muscularis is present, composed mainly of longitudinal fibres (2-3 layers around the ventral half, up to 6 layers dorsal). In addition, the ventral half is enveloped by 2-3 outer layers of circular fibres.

The ***spermathecal duct*** (Figs. 21B, C, D) evaginates from the genital chamber in antero-dorsal position, about mid-length of segment VII in the median line. Following the duct in anterior direction, two regions can be easily distinguished. The first region, extending just a short distance after the duct has left the genital chamber, is equipped with cubic epithelial cells. The intima is strong and sclerotized and the lumen narrow and rounded (in cross section). This proximal region is surrounded by a loose, one-layered network of muscle fibres. The epithelium of the second, distal section is composed of extremely flattened cells, with the nuclei in widenings of the cell bodies. A strong intima is present. The lumen is rounded in cross section and comparatively wide with regard to the proximal duct region. A muscularis surrounding the distal region is lacking. In the boundary region of segments VI and VII, the spermathecal duct opens into the ***spermatheca*** (Figs. 21D, F). The spermatheca has the shape of a huge, simple tube. The epithelium of the spermatheca is composed mainly of cubic cells. A well developed cuticular intima is present, displaying annular thickenings in steady distances. In the lumen of the spermatheca, a few spermatozoans and cell remnants are visible. A muscularis is not developed. The ***spermathecal gland*** (Fig. 21F) is bilobed and attached directly to the spermatheca in terminal position. The glandular epithelium is formed of prismatic cells with easily recognizeable nuclei, approximately in central position within the cells. Secretory vesicles are visible in the cytoplasm, as well as a large "storage vacuole" near the apical pole of each cell. The gland lumen is narrow. A muscularis surrounding the spermathecal gland is lacking.

The short ***ductus bursae*** (Fig. 21C) leads out from the genital chamber in terminal position, mid-length of segment VII. The epithelium of the ductus bursae is composed of irregularely shaped cells. The ductus is outlined with a delicate intima. A muscularis in a proper sense is not present, just a few single fibres. In anterior direction, the ductus widenes into the ***bursa copulatrix*** (Fig. 21E), approximately in the mid region of segment VII. The bursa is simply shaped and sac-like. The bursa reaches segment VI anteriorly. The epithelium of the bursa copulatrix is composed of irregularely shaped cells. A weak cuticular intima is present, but hardly noticeable. Inside the bursa lumen, remnants of a spermatophore are recognizeable. A muscularis is absent.

The ***gland duct*** branches off from the genital chamber in dorso-median position, in the boundary region of segments VII and VIII. The epithelium of the duct is composed of irregularely shaped cells. A weak cuticular intima is present. The gland duct is surrounded by a loose network of muscle fibres. The huge, balloon-shaped ***accessory glands*** (Figs. 21B-F) are paired, with their most posterior regions fused. The glands stretch through the dorsal half of the specimen up into segment III anteriorly. The cells of the glandular epithelium are prismatic, with numerous small vesicles in the cytoplasm. The gland lumen is filled with secretions. A muscularis is not developed.

The ***common oviduct*** (Figs. 21C, E) evaginates from the genital chamber in segment VII in ventro-median position. It is surrounded by an epithelium formed of irregularely shaped cells. An intima is absent; the duct lumen is depressed dorso-ventrally. The duct is enveloped by 1-2 layers of muscle fibres. The common oviduct branches off into the lateral oviducts in the anterior half of segment VII. The lateral oviducts run up to segment VI anteriorly. The epithelium of the lateral oviducts is composed of irregularely shaped cells. An intima is lacking. The lateral oviducts are surrounded by a one-layered, irregular arrangement of muscle fibres.

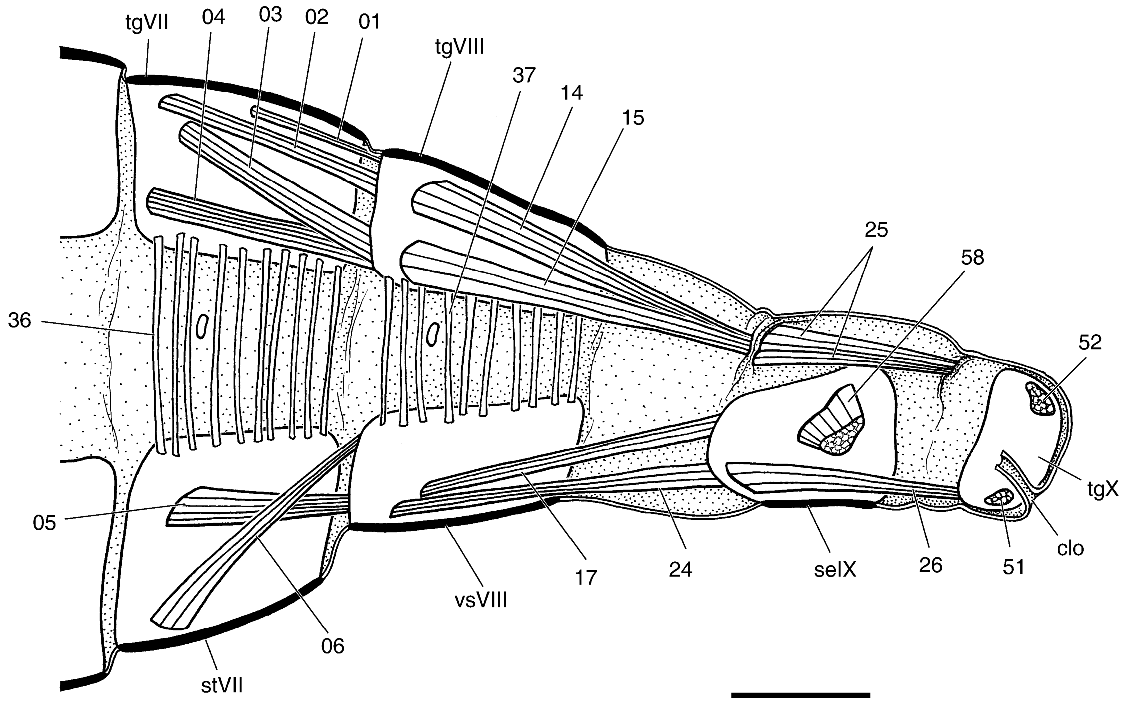

Fig. 20. *Micropterix calthella*, skeleto-muscular arrangement of the female postabdomen. Left body half, internal parts of the genitalia, soft tissue and fat body are not depicted. Scale bar: 100 µm.

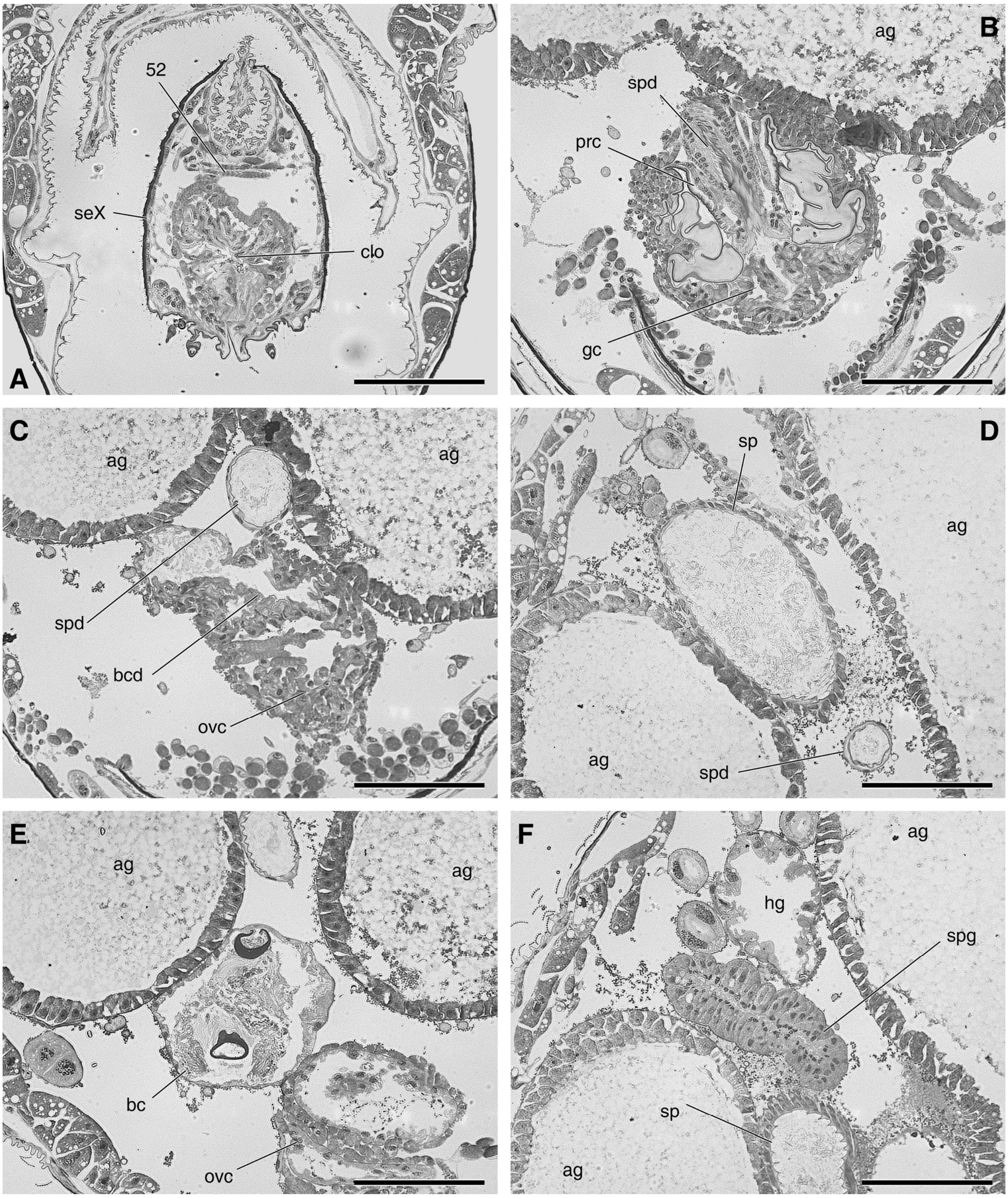

Fig. 21. *Micropterix calthella*, female postabdomen, histological cross sections. (A) segment X, note the lateral sclerotizations [dark staining]; (B) spermathecal process with spermathecal duct; (C) simple spermathecal duct, ductus bursae, accessory glands, common oviduct; (D) spermathecal duct and spermatheca; (E) bursa copulatrix, common oviduct; (F) spermatheca and spermathecal gland. Scale bar: 50 µm.

4.2.7.2. Agathiphagidae: *Agathiphaga vitiensis*

Exoskeleton (Fig. 22). Abdominal ***segment VIII*** is markedly lower and narrower than the preceeding segments. Tergum VIII and the ventral sclerotizations of segment VIII are not fused. From the anterior margin of tergum VIII a pair of long apophyses arises (Fig. 22D; ***aad***, dorsal anterior apophyses), reaching close to the anterior margin of tergum VII in repose. The ventral sclerotized elements of segment VIII are completely fused in the ventro-median line. The anterior margin of the resulting plate is almost straight, with a pair of ventral anterior apophyses arising from two areas of thickened cuticle (Fig. 22D; ***aav***). The ventral anterior apophyses are approximately 1,2 times as long as the dorsal anterior apophyses.

Abdominal ***segments IX - XI*** are fused, forming the oviscapt. In this region the segmental limits are impossible to trace. The oviscapt is partly retracted into segment VIII in repose, but a collar of soft cuticle behind tergum VIII and the venter VIII-plate always remains unretracted (Figs. 22A-C). The oviscapt walls are generally unsclerotized, but the dorsal side is strengthened by an Y-shaped sclerite (Fig. 22D). A pair of posterior apophyses arises from the anterodorsal oviscapt wall, just in front of the apices of the arms of the Y-shaped sclerite (Fig. 22D; ***ap***). These posterior apophyses are approximately 1,4 times as long as the dorsal anterior apophyses, similar in shape to the latter ones, but more slender.

The cloacal opening lies subapically on the lower surface of the oviscapt (Fig. 22C). The apical portion of the oviscapt bears a scarce coverage with scattered setae.

Musculature (Fig. 24). The postabdominal muscle set of *A. vitiensis* comprises 22 muscles: **01** *isVII-VIII01* (site of insertion shifted to apex of dorsal anterior apophysis), **02** *isVII-VIII02*, **03** *isVII-VIII03* (insertion site shifted to the base of dorsal anterior apophysis), **04** *isVII-VIII04* (site of origin shifted to the pleural membrane above spiracle, site of insertion to the base of dorsal anterior apophysis), **05** *isVII-VIII05*, **06** *isVII-VIII06*, **08** *isVII-VIII08* (insertion site shifted to ventral anterior apophysis), **09** isVII-VIII09, **11** *isVII-VIII11* (site of origin shifted dorsad to pleural membrane of segment VII above the spiracle; insertion site is on the ventral anterior apophysis), **12** *isVII-VIII12* (insertion on dorsal anterior apophysis), **14** *isVIII-IX01* (origin shifted to apical region of dorsal anterior apophysis, insertion site to the base of posterior apophysis), **15** *isVIII-IX02* (site of origin shifted to the posterior quarter of tergum VIII; insertion mid-length on the posterior apophysis), **17** *isVIII-IX04* (originates on ventral anterior apophysis), **22** *isVIII-IX09* (site of origin: apex of dorsal anterior apophysis), **23** *isVIII-IX10*, **37** *dvVIII01*, **38** *dvVIII02*, **39** *dvVIII03*, **40** *dvIX01*, **55** *seVIII-gc01*, **56** *seVIII-gc02*, and **67** *rec/clo01.*

Internal parts of the genital system (overview: Fig. 23). The ***genital chamber*** is fused with the rectum along a very short distance just in front of the cloacal opening. The chamber extends through the oviscapt as a narrow tube (Figs. 25B, C). In this region the epithelium is unspecialized and a simple cuticular intima is present. The chamber becomes conspicuously widened in segment VII, where the openings of the ducts are located. The chamber epithelium in this region is composed of cubic cells (Figs. 25D, E). A muscularis surrounding the genital chamber is well developed. It is composed of 1-2 fibre layers around the slender posterior region of the chamber, but becomes gradually much thicker around the anterior parts (in segment VII: 2-3 inner layers of longitudinal fibres, surrounded by 8-10 layers of circular and diagonal fibres; 2-4 outermost layers of longitudinal fibres, the latter not forming a closed coat in the dorso-median line) (Fig. 25E).

The ***spermathecal duct*** extends from the antero-dorsal end of the genital chamber. The intima in the region of the duct opening is thickened, but a conspicuous spermathecal process is not developed. Following the duct, three successive duct regions can be distinguished. The most posterior region (Fig. 26A) is kidney-shaped (cross section). The epithelial cells are prismatic with the nuclei clearly visible close to the basal poles. The lumen of this region is wide and outlined with a weak intima. In the second region (Fig. 26B) the intima is conspicuously strengthened, in particular the dorsal part. The epithelial cells are prismatic dorsally and ventrally, but smaller and of a cubic shape laterally. The lumen of the second region is flattened dorso-ventrally, and shaped by foldings of the intima. More anteriorly, from the second region the third region (Fig. 26C) starts as a dorsad evagination, with its lumen strongly depressed laterally. The epithelial cells in the third region are irregularely shaped. The narrow lumen of the third region is not fully subdivided into compartments, it is strongly structured by foldings of the intima and the epithelium (lumen with cross-like appearance in cross sections). A ventral component of mesocuticle is present in its intima (Fig. 26C, designated by arrow). The epithelial cells of the spermathecal duct in general appear to be glandular, with secretory vesicles visible in the cytoplasm. The entire spermathecal duct is surrounded by a muscularis (4-6 layers of circular and diagonal fibres). The spermathecal duct leads into the ***spermatheca*** (Fig. 26D) in the boundary region of segments VII and VI. The spermatheca extends in the narrow space between the accessory glands up to the middle of segment VI. The epithelial cells of the spermatheca are cubic, some groups of cells even slightly prismatic, with a glandular appearance (vesicles visible in the cytoplasm). The lumen of the spermatheca is characteristically shaped by several invaginations of the epithelium. The spermatheca is enveloped by a loose arrangement of a few scattered longitudinal muscle fibres. The terminal spermathecal gland is small and simple in shape, with a prismatic glandular epithelium. No muscularis is present around the gland. The gland lumen is densely filled with secretion.

The ***ductus bursae*** (Fig. 26E) extends forwards from the antero-ventral corner of the genital chamber. Its epithelium is composed of irregularely shaped cells and thrown into deep, regular folds. A weak cuticular intima is present, as well as a muscularis (one loose layer of inner longitudinal fibres, surrounded by two-three layers of circular and diagonal fibres; one layer of scattered outer longitudinal fibres). The ductus bursae gradually widenes into the sac-like ***bursa copulatrix*** (Fig. 26F). The bursa wall is formed of irregularly shaped epithelial cells, and the epithelium is thrown in regular longitudinal folds. The bursa lacks a compact muscularis, just a few scattered fibres are present.

The short ***gland duct*** evaginates from the roof of the genital chamber in segment VII. Its epithelium consists of cubic cells. The lumen of the duct is narrow and its cuticular intima hardly observable. The duct is enveloped by a muscular coat (1-3 layers of longitudinal and diagonal fibres) that is part of the inner longitudinal fibre layers of the genital chamber. The

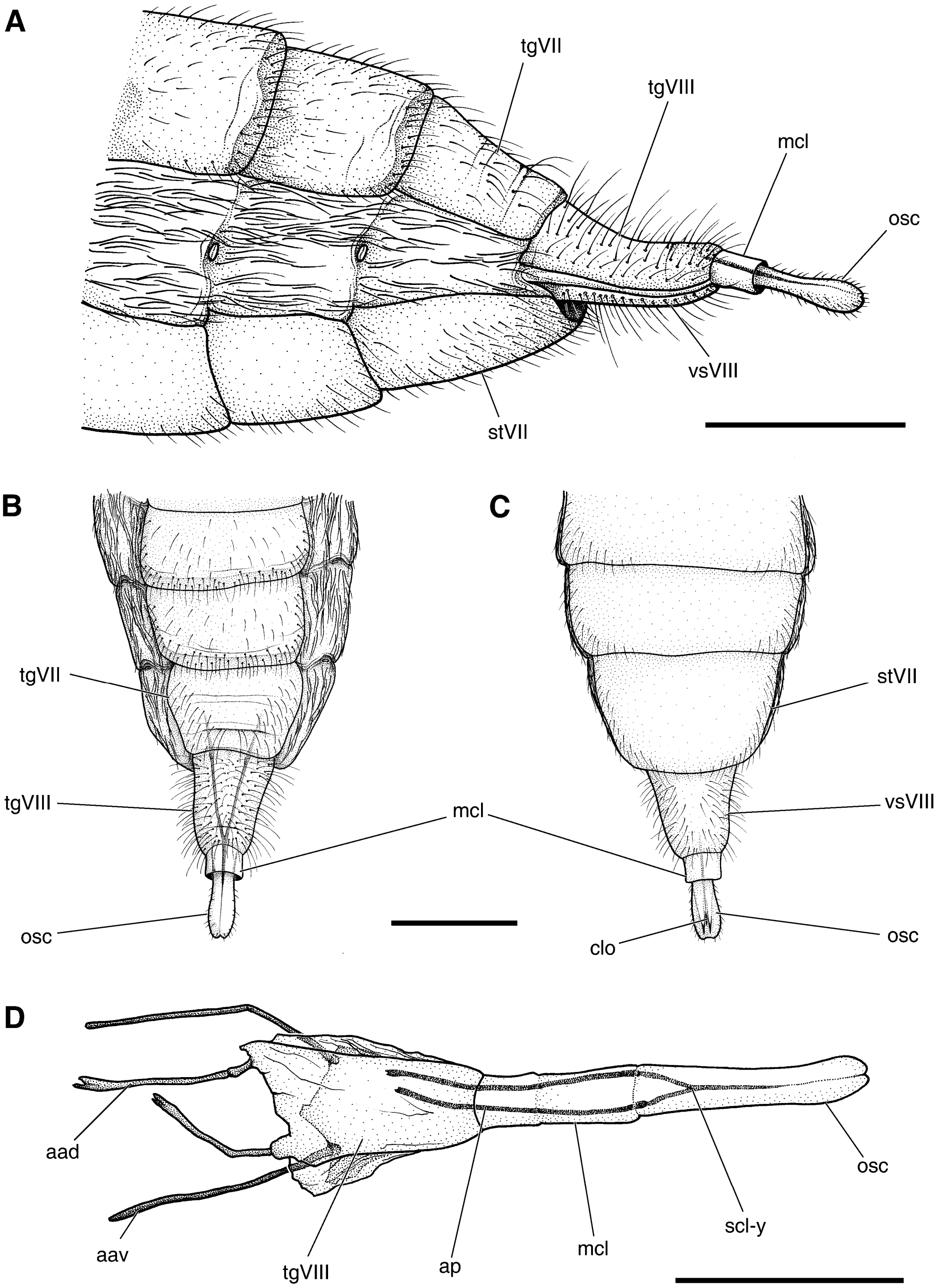

Fig. 22. *Agathiphaga vitiensis*, female postabdomen. (A-C) external morphology; (A) lateral view; (B) dorsal view; (C) ventral view. (D) segment VIII and oviscapt fully extruded, KOH-macerated preparation, note the three pairs of postabdominal apophyses. Scale bar: 1 mm.

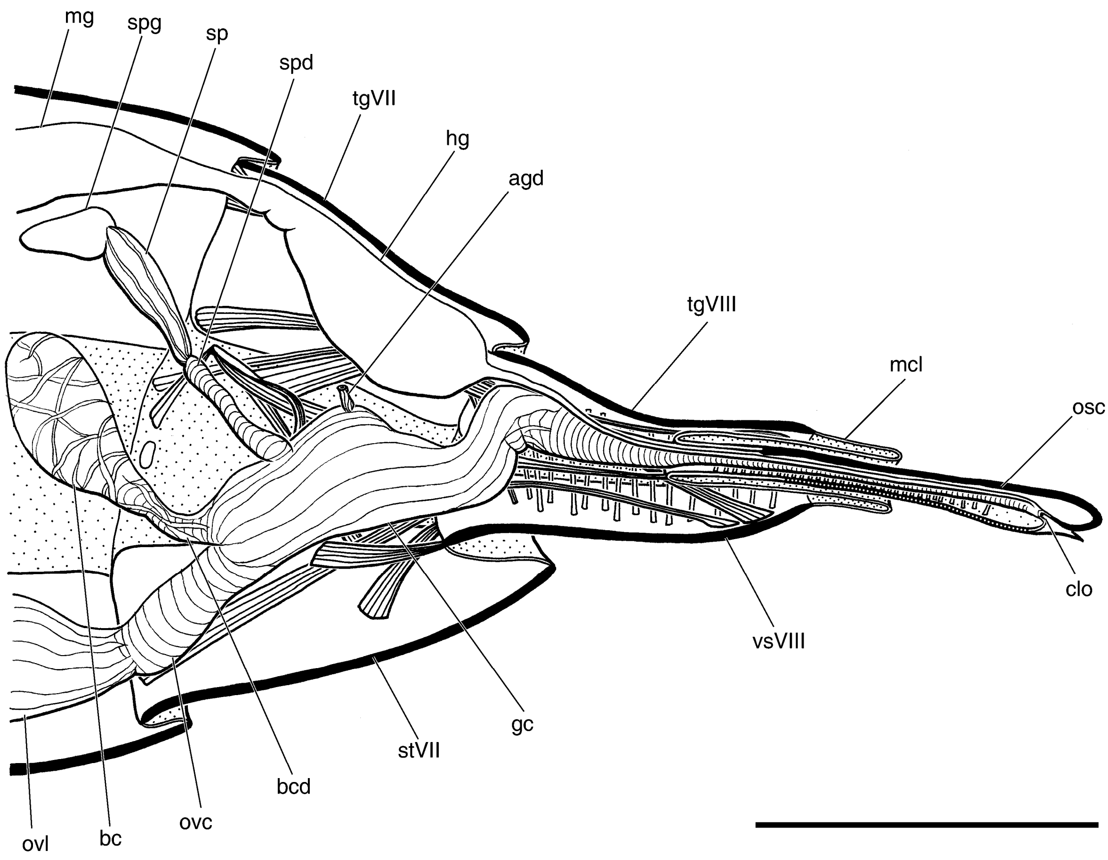

Fig. 23. *Agathiphaga vitiensis*, female postabdomen. Overview over the internal parts of the genital system. Scale bar: 1 mm.

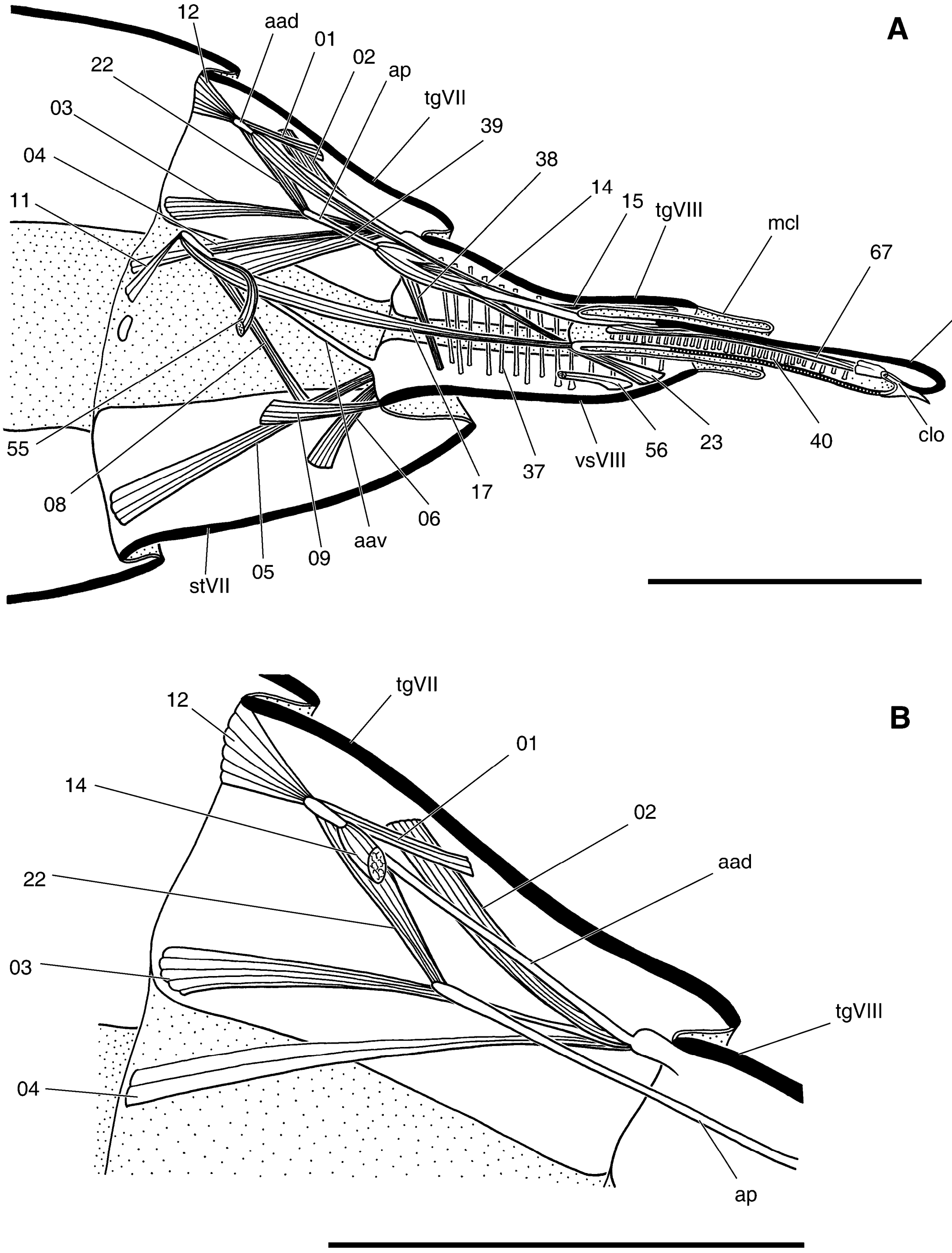

Fig. 24. *Agathiphaga vitiensis*, female postabdomen, skeleto-muscular arrangement. (A) overview; (B) detail, muscle 14 partially removed. Scale bar: 1 mm.

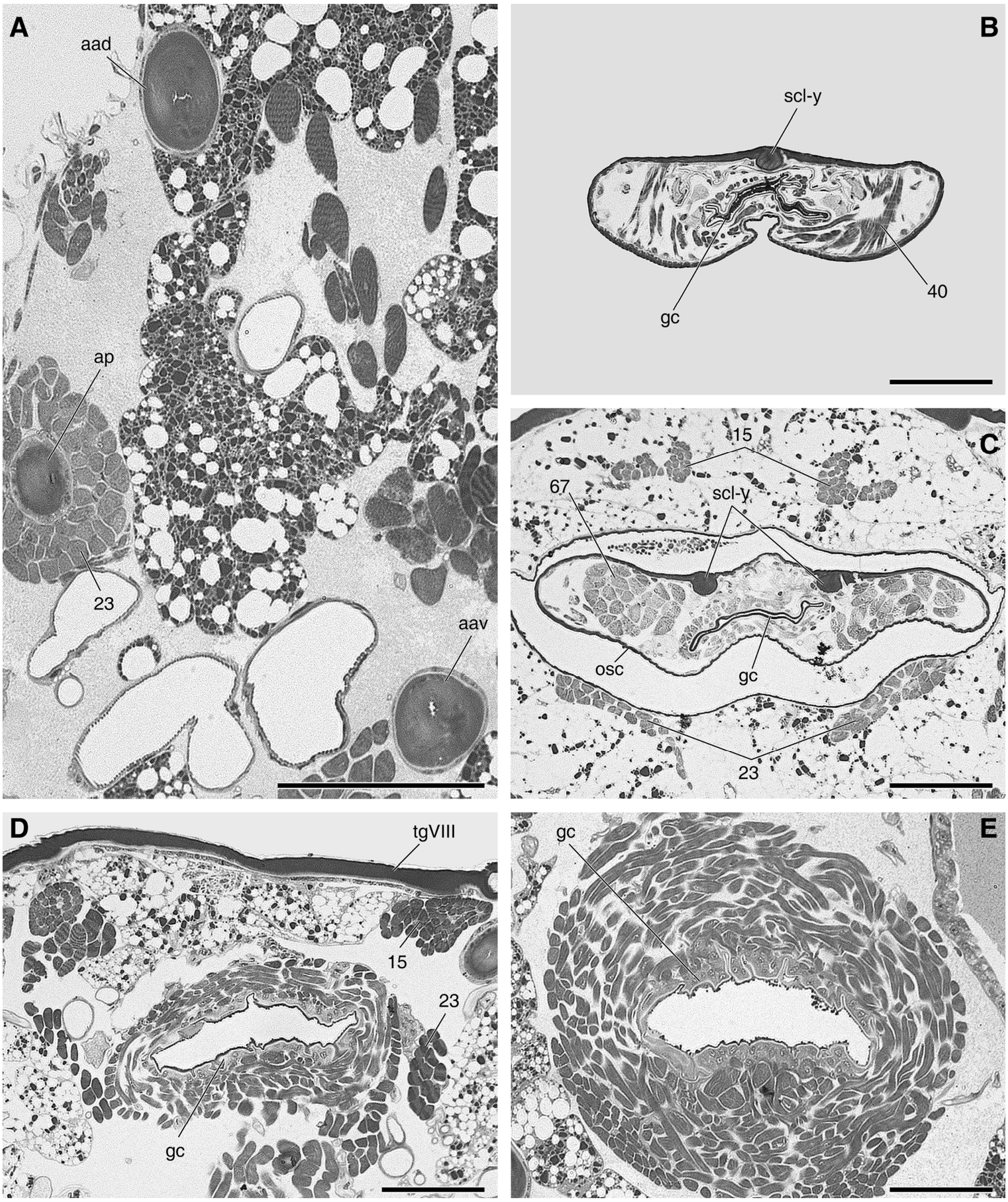

Fig. 25. *Agathiphaga vitiensis*, female postabdomen, histological cross sections. (A) the three pairs of apophyses; (B) oviscapt; (C) oviscapt, more anterior; (D) segment VIII, genital chamber; (E) segment VII, genital chamber, note the extremely developed chamber muscularis in this region. Scale bar: 100 µm.

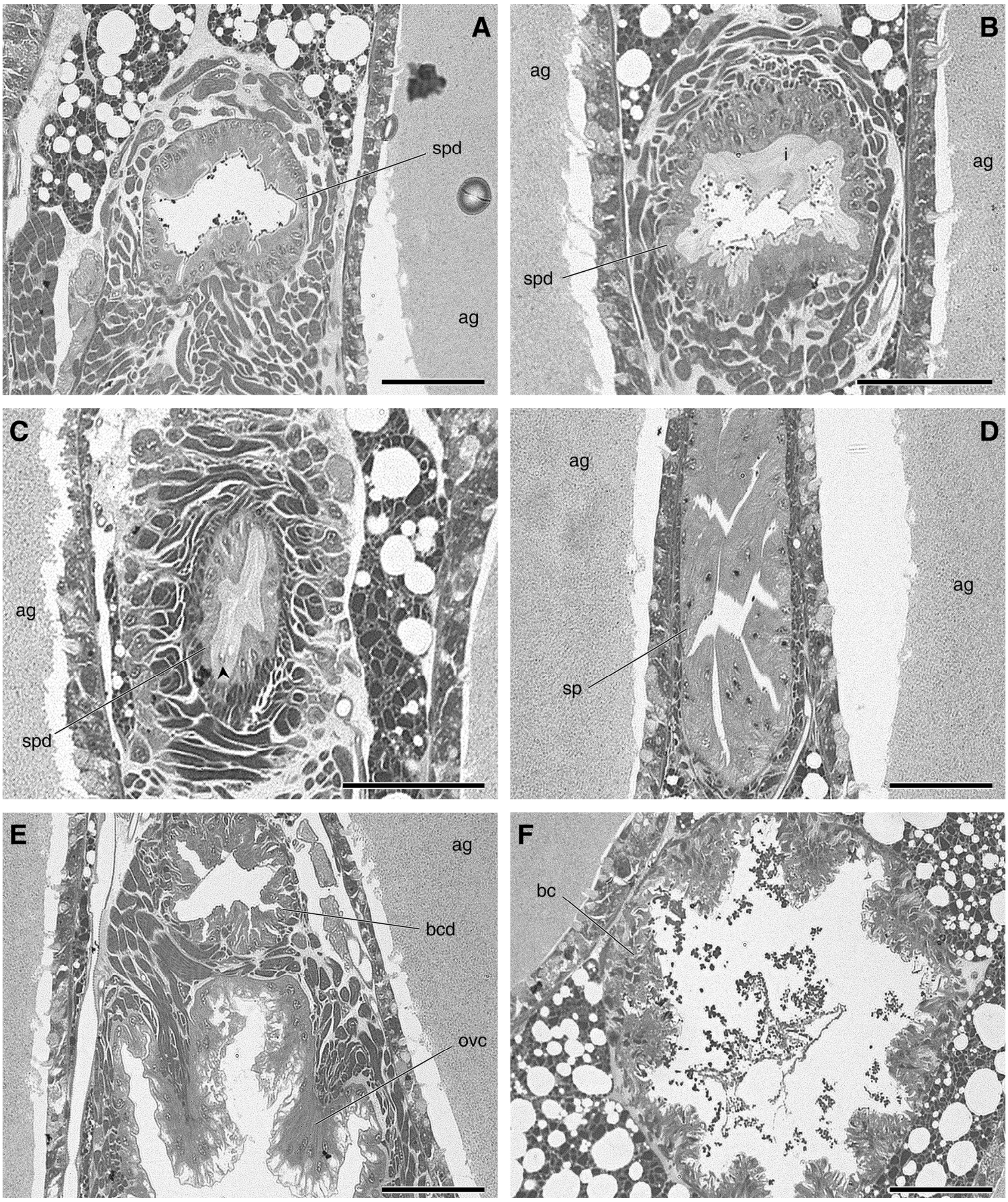

Fig. 26. *Agathiphaga vitiensis*, female postabdomen, histological cross sections. (A-C) spermathecal duct; (A) posterior region; (B) mid-region with strengthened intima; (C) anterior region, note the slightly darker staining in the ventral part of the intima that indicates a content of mesocuticle [red in trichrome-staining; Hünefeld & Kristensen in press.]; (D) segment VI, spermatheca, accessory glands; (E) segment VII, ductus bursae, common oviduct; (F) segment VI, bursa copulatrix. Scale bar: 50 µm.

accessory glands (Figs. 26A-F) are huge elongate sacs extending far forwards in the abdomen (almost up to segment IV); they have a pair of dorsal evaginations in the boundary region of segments VI and VII. The glandular epithelium consists of small, cubic cells which are densely packed with secretory vesicles. The gland lumen is filled with secretion, which is packed into extremely small, almost indiscernible globules. The mode of secretion is apparently merocrine. While the anterior parts of the accessory glands are paired and without any associated muscle fibres the posterior parts are fused and surrounded by a few scattered longitudinal and diagonal fibres.

The short ***common oviduct*** (Fig. 26E) extends forward from the genital chamber ventro-medially, below the bursa origin. Its epithelium is formed of irregularely shaped cells. The lumen of the common oviduct is lined with a weak cuticular intima and the epithelium thrown in several more or less symmetrical folds. The common oviduct is surrounded by a muscularis, composed of one layer of inner longitudinal fibres and 3 – 5 layers of outer circular and diagonal fibres; the most posterior section is enclosed by the complex muscularis of the genital chamber. The paired ***lateral oviducts*** merge into the common oviduct in segment VII. The lateral oviducts receive the eggs from the ovarioles in segment VI. In mature females the epithelium of the lateral oviduct system is composed of moderately flattened cells. A weak cuticular intima is present in the posteriormost portions of the lateral oviducts, just before they enter the common oviduct**,** hence they must have originated by an anterior bifurcation of the (ectodermal) common oviduct. The lumen of the lateral oviducts is narrow but becomes gradually widened towards the ovarioles. The distal branches of the lateral oviducts are surrounded by a loose, irregular meshwork of muscle fibres, while around the main portions a single layer of longitudinal fibres is present.

Despite the ***ovaries*** are not addressed in the present study, a short note is given to the situation found in Agathiphaga. Here the number of ovarioles per ovary is immensely high for a lepidopteran. A total of 45 ovarioles were counted in one ovariole; the exact number may be variable.

4.2.7.3. Heterobathmiidae: *Heterobathmia pseuderiocrania*

Exoskeleton. Segment VII is the posteriormost segment without noteworthy modifications. Tergum ***VIII*** is normally sized and slightly curved, like the preceeding ones. It is widely separated from the venter plate VIII by a large pleural membrane that includes the segmental spiracle. The venter plate VIII is enlarged, approximately 1,5 times as long as the corresponding tergum, and covers the anterior parts of the non-sclerotized ventral side of segment IX. While the dorsal midline of the postabdomen is nearly horizontal, the venter plates of segments VII and VIII are steeply inclined towards the abdominal apex. Apophyses as well as external appendages are absent on segment VIII.

In ***segment IX***, a true ventral sclerotization is not developed. Tergum IX is approximately 1,5 times as long as tergum VIII. It is saddle-shaped, with the ventral margins strongly prolonged, covering the lateral parts of the segment completely. A pair of short, anteriad directed processes (posterior apophyses) arises from the anterolateral corners of tergum IX. These apophyses function as muscle attachment areas. Distinctly developed terminal segments are absent. It is conceivable that paired "appendages" arising from the posterodorsal margin of tergum IX are vestiges of segment X and possibly also segment XI.

The openings of the genital system and the rectum are distinctly separated: the rectum opens terminally on the non-sclerotized apical area of the dorsal part of segment IX, whereas the genital chamber opens subapically on the non-sclerotized ventral side of segment IX.

Musculature (Fig. 28)**.** The postabdominal muscle set of *H. pseuderiocrania* comprises 14 muscles: **02** *isVII-VIII02*, **03** *isVII-VIII03*, **05** *isVII-VIII05* (short muscle), **13** *isVII-IX01* (site of origin on the anterolateral corner of tergum VIII), **14** *isVIII-IX01*, **15** *isVIII-IX02*, **23** *isVIII-IX10* (3 bundles), **25** *isIX-X01*, **52** *tX02*, **54** *seVII-gc01*, **55** *seVIII-gc01*, **56** *seVIII-gc02*, **58** *seIX-gc01*, and **67** *rec/clo01*.

Internal parts of the genital system (overview: Fig. 27A)**.** Three regions of the ***genital chamber*** can be easily distinguished. The posterior part (Fig. 29A) stretches through the entire segment IX and represents nearly half of the length of the chamber. Its epithelium is formed of irregularly shaped cells. The cuticular intima is extremely thick-walled. The ventral part of this intima strengthens the ventral side of segment IX thus compensating for the lack of the exoskeletal sclerotization. The lumen of the posterior genital chamber is strongly depressed dorso-ventrally. In the extremely thickened dorsal part of the intima, dorsally directed offshoots of the lumen form a strongly branched, symmetrical labyrinth. The external surface is surrounded by a weak muscularis, consisting of 1-2 layers of circular fibres. The muscularis is not closed ventrally in the posterior half of the posterior section. The middle region of the chamber runs ventrad, reaching mid-length of segment VIII anteriorly. The dorsal epithelial cells are cubic, whereas those of the ventral side are moderately flattened. The intima is thin in this part of the chamber. The lumen is extremely narrowed by more or less symmetrical folds of the epithelium (cross section), thus appearing strongly curved; it is scarcely recognizable on microtome sections. The duct of the accessory glands opens dorsomedially in the middle region and the common oviduct ventromedially. The muscularis is mainly composed of 4-5 layers of longitudinal fibres; between these, scattered circular fibres are present. The spermathecal duct and the ductus bursae originate medially in the anterior region (Fig. 29B) of the chamber, the former through the chamber roof in the anterior quarter of segment VIII, and the latter terminally, in the boundary region of abdominal segments VII and VIII. The opening region of the spermathecal duct does not show structural peculiarities. In contrast to this, the ductus bursae originates on the tip of a heavily thickened, cone-shaped papilla, which is a modification of the intima of the terminal part of the chamber (Figs. 27B, 29B; ***prc-bcd***). The ventral epithelium of the anterior region is squamose. The region of the spermathecal duct opening is characterized by prismatic cells with the nuclei near the basal poles. The intima of the anterior region is generally thin except for the cone-shaped papilla. The muscularis is composed of 3-5 layers of inner longitudinal and 1-2 layers of outer circular fibres.

The ***spermathecal duct*** (Figs. 29B, C) is composed of three regions. The posteriormost region is lined with an epithelium consisting of prismatic cells with a structure suggesting a secretory function: the nuclei are close to the basal poles, and numerous small vesicles are visible in the cytoplasm. The lumen of the posterior region of the spermathecal duct is flattened dorso-ventrally and outlined by an intima that is slightly strengthened, compared to the intima of the following mid-region. A muscularis is lacking. The epithelial cells of the middle region are cubic and the nuclei easily visible. The intima is thin and without noteworthy modifications. The lumen is rounded in cross-section. The weakly developed muscularis consists of 1-2 layers of circular fibres. The anteriormost region (Fig. 29C) of the duct is composed of 2 distinct compartments (a widened and a narrow lumen part). The epithelium surrounding the widened part is formed by comparatively small, more or less prismatic cells with the nuclei in a central position and numerous small vesicles in the cytoplasm. In contrast, the epithelial cells covering the narrow part are enlarged, almost cubic, with the nuclei near the basal poles, and comparatively fewer but larger vesicles. The intima of the widened part is well developed and formed by exocuticule, and even thicker and formed by mesocuticule in the narrow section. The muscularis surrounding the 2-compartment section is composed of 1-3 layers of circular and diagonal fibres. In the boundary region of segments VII and VIII, the spermathecal duct widenes into the ***spermatheca*** (Fig. 29C). After running a short distance antero-dorsad, the spermatheca describes a u-turn at approximately mid-length of segment VII, and runs back in postero-ventral direction, again reaching the boundary region of segments VII and VIII. In overall shape, the spermatheca is tube-like. The epithelium is exclusively composed of cubic cells. The intima is well developed and strengthened by regularly spaced annular thickenings. The lumen is moderately wide in the proximal section and is extended towards the distal part. It is filled with numerous vesicles, probably released by the spermathecal gland. The spermatheca is enclosed by a one-layered, dense network of muscle fibres. The ***spermathecal gland*** is connected with the spermatheca by a slender duct, which originates from the wide lumen of the spermatheca in a terminal position, approximately at mid-length of segment VII. It is connected with the gland in the anterior third of the same segment. The epithelium of the duct is formed by cubic cells with the nuclei and cell boundaries easily recognizable. A muscularis is present, consisting of a one-layered fibre network, similar to that of the spermatheca. Considering the cell morphology and the composition of the associated muscularis, the duct may be addressed as the anteriormost part of the spermatheca. The gland itself is simple and tube-like. The glandular epithelium is prismatic, with the nuclei close to the basal poles and numerous vesicles within the cell bodies. The narrow lumen of the gland is filled with secretions (larger vesicles). A muscularis surrounding the gland is not developed. The entire spermatheca / spermathecal gland complex is shifted to the right body half.

The ***ductus bursae*** (Fig. 29D) displays an epithelium composed of extremely flattened cells, with the nuclei in extensions of the cell bodies. The intima bears spines, projecting into the rounded lumen, which is filled with cell remnants and secretory vesicles. The ductus is surrounded by one layer of longitudinal and diagonal muscle fibres. The opening of the ductus bursae into the ***bursa***

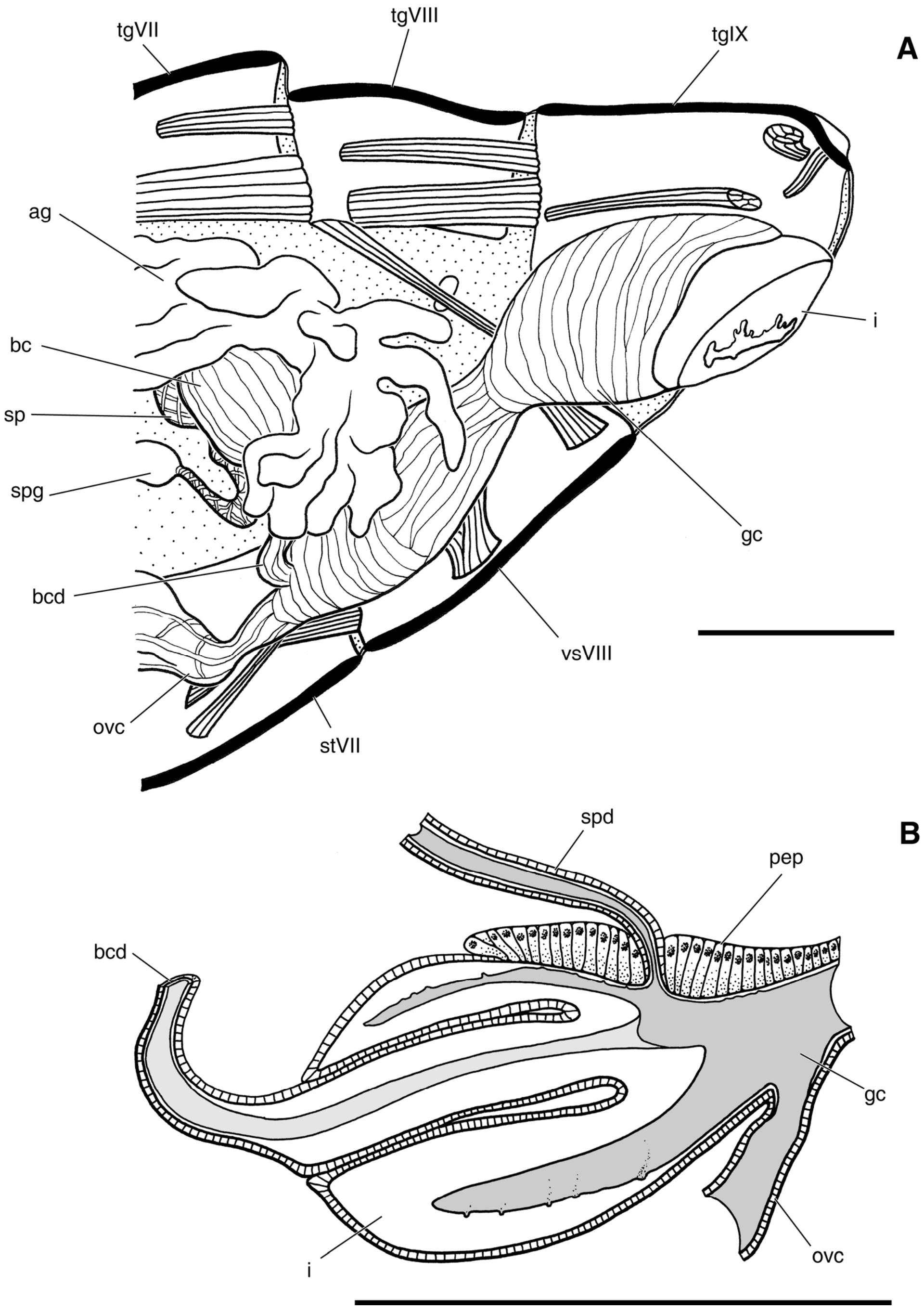

Fig. 27. *Heterobathmia pseuderiocrania*, female postabdomen, internal parts of the genital system. (A) overview; (B) detail: papilla with the opening of the ductus bursae on its tip, note the prismatic epithelium of the roof of the genital chamber in this region, ***pep***. Scale bar: 200 µm.

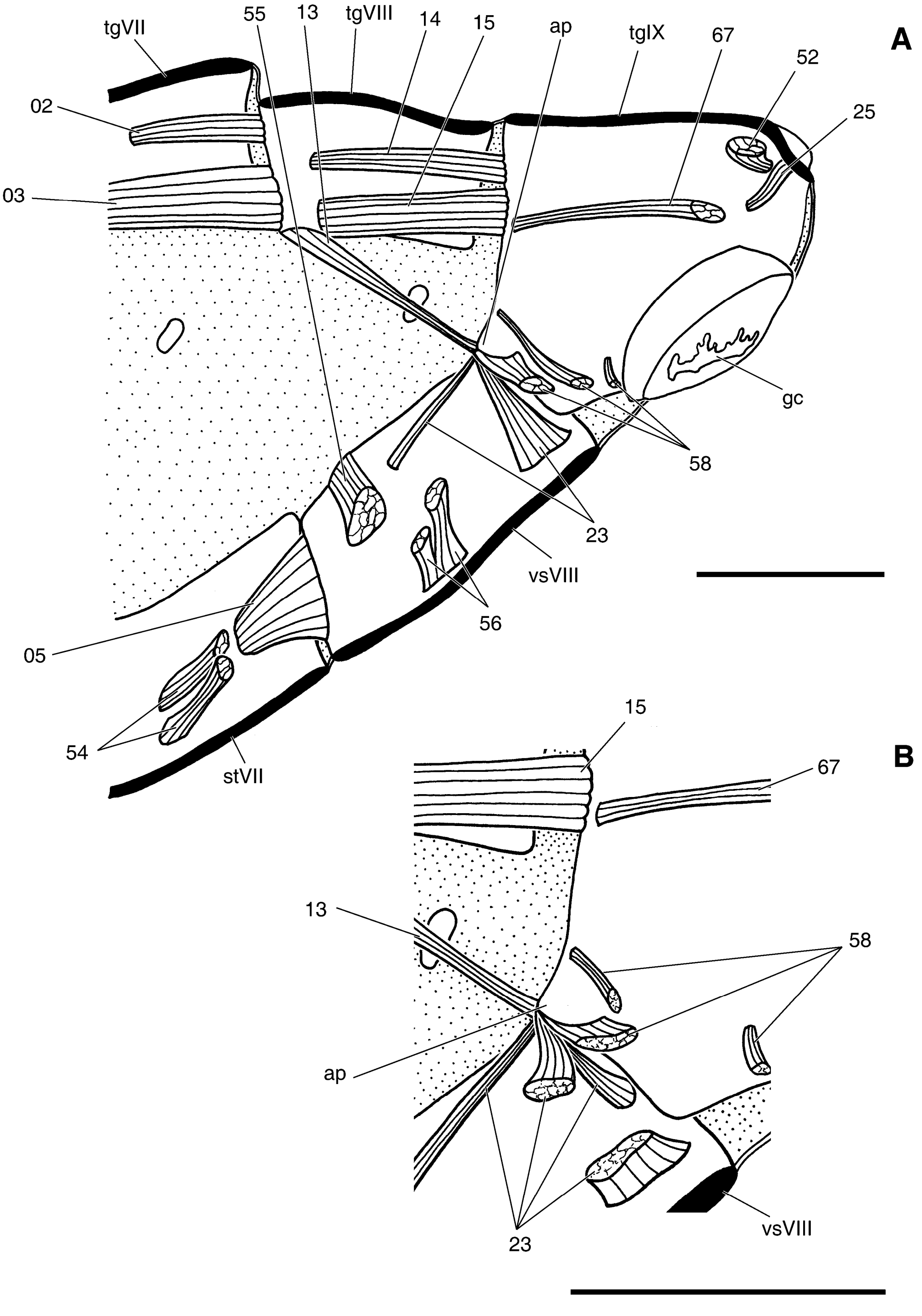

Fig. 28. *Heterobathmia pseuderiocrania*, female postabdomen, skeleto-muscular arrangement. (A) overview; (B) detail: short posterior apophysis and attached muscle portions. Scale bar: 200 μm.

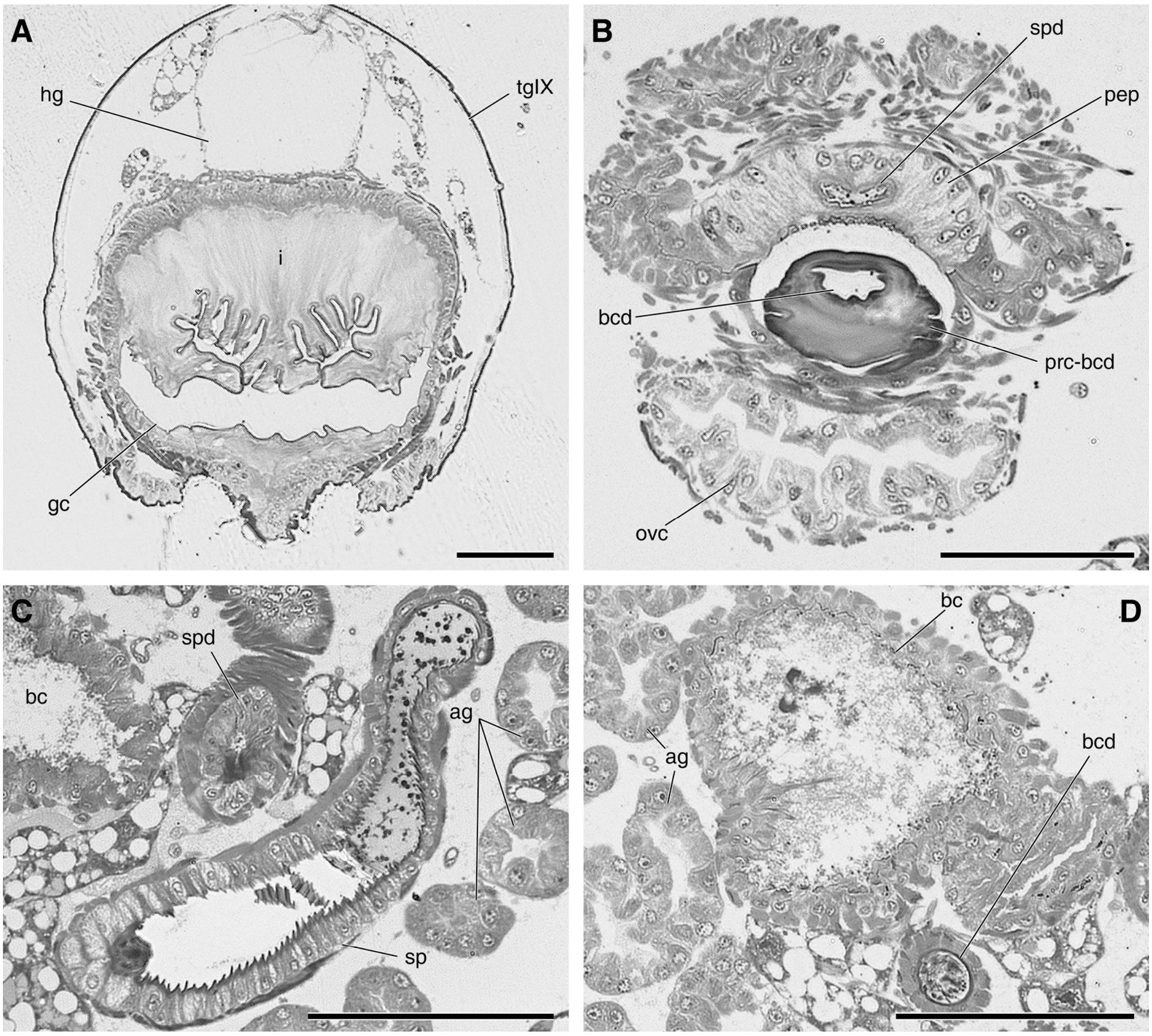

Fig. 29. *Heterobathmia pseuderiocrania*, female postabdomen, histological cross sections. (A) terminal unit, note the heavily strengthened intima of the genital chamber; (B) boundary region of segments VII and VIII, genital chamber: opening region of the spermathecal process, the ductus bursae and the common oviduct, note the sclerotized papilla an which the ductus bursae opens, ***prc-bcd***; (C) 2-compartment- section of the spermathecal duct, spermatheca; (D) segment VII, bursa copulatrix. Scale bar: 100 µm.

copulatrix (Figs. 29C, D) lies in the boundary region of abdominal segments VII and VIII. The simple sack-shaped bursa reaches the middle of segment VII anteriorly. The epithelial cells are of irregular shape, with nuclei and cell boundaries clearly recognizable. The epithelial cells have probably a secretory function, with vesicles in the cytoplasm (also in the lumen, near the cell apices). The cuticle is delicate, with spines projecting into the lumen in the proximal half. The lumen is filled with cell remnants, scattered particles of the spermatophore, and secretory vesicles. The one-layered muscularis is composed of longitudinal and diagonal fibres. The bursa copulatrix is slightly shifted to the left body half.

The ***gland duct*** branches off from the genital chamber in a dorso-median position, at about mid-length of segment VIII and some distance posterad of the spermathecal duct. Its epithelium is squamose; the cells are of a somewhat irregular shape, with the nuclei visible but the cell limits not recognizable. A thin intima is present, but scarcely invisible. The lumen of the slender duct is distinct. The muscularis is formed by scattered diagonal muscle fibres. The ***accessory glands*** (Figs. 29C, D) are paired, with the posterior parts fused. Each gland is composed of approximately 15 branched tubules. The glandular epithelium is formed of cubic cells with the nuclei near the basal lamina, and numerous secretory vesicles in the cytoplasm. The lumen is narrow but clearly visible. It contains few small vesicles. A muscularis is lacking.

The ***common oviduct*** (Fig. 29B) arises ventromedially from the genital chamber at mid-length of segment VIII. It reaches segment VII anteriorly. The epithelial cells are irregularely shaped, cubic or slightly flattened, with nuclei and cell boundaries clearly visible. An intima could not be identified. The lumen is extremely depressed dorso-ventrally, and not visible at all in some of the cross sections. The muscularis is formed by a one-layered, regular network of fibres. Approximately at mid-length of segment VII the common oviduct branches into the short ***lateral oviducts***, which reach the boundary region of segments VI and VII anteriorly, where the ovarioles branch off in one cluster. The epithelium of the lateral oviducts is formed of cubic cells. Nuclei as well as cell boundaries are visible. As in the common oviduct, an intima is not developed. The lumen of the lateral oviducts is also narrow and compressed dorso-ventrally. The muscularis is similar to that of the common oviduct.

4.2.7.4. Eriocraniidae: *Eriocrania cicatricella*

Exoskeleton. The external postabdominal morphology of eriocraniids is well studied (e.g., Davis 1978, Kristensen 1998, 2003b), so just a few additions are made. A pair of elongate sclerites is present in the membranous ventral oviscapt wall. These sclerites are strongly curved transversely. They are here referred to by the the neutral term “ventral rods” (Nielsen & Kristensen 1996). Between the sclerotizations of segments VIII and IX there is a large area of unsclerotized cuticle, forming a membranous collar behind the segment VIII – sclerotizations if the oviscapt is retracted. The cloaca opening is behind this collar, below the oviscapt (behind segment VIII).

Musculature (Fig. 31A)**.** The postabdominal muscle set of *E. cicatricella* comprises 13 muscles: **02** *isVII-VIII02*, **03** *isVII-VIII03*, **05** *isVII-VIII05*, **06** *isVII-VIII06*, **10** *isVII-VIII10* (site of origin on the pleural membrane of segment VII), **12** *isVII-VIII12* (origin shifted anteriad to tergum VI), **13** *isVII-IX01* (site of origin shifted anteriad to tergum VI), **14** *isVIII-IX01* (originates with 2 distinct bundles on tergum VIII; insertion on the apical region of the posterior apophysis), **15** *isVIII-IX02* (site of origin shifted to the apex of anterior apophysis), **17** *isVIII-IX04* (origin on the apex of anterior apophysis), **37** *dvVIII01* (compact muscle), **55** *seVIII-gc01* (originates from the apical region of anterior apophysis; insertion on the anterior side of the vaginal sclerite frame; vaginal sclerite retractor), and **56** *seVIII-gc02* (2 distinct bundles; insertion on the posterior side of the vaginal sclerite stem; vaginal sclerite protruder).

Internal parts of the genital system (overview: Fig. 30A)**.** The ***genital chamber*** (Figs. 30A, B, 32A) is short and compact, just reaching segment VII anteriorly. The chamber epithelium is composed of irregularely shaped cells. An intima is well developed and strengthened in the mid-region of the chamber where it displays a conspicuous modification: the vaginal sclerite (Figs. 30A, B, 32A). The vaginal sclerite is composed of a dorsal sclerite frame that encloses the canal for egg passage, and a ventral sclerite stem. A pair of posteriorly projecting processes of moderate length arises from the dorsal part of the sclerite frame, near the median line. A third, unpaired, long process pointing in posterior direction originates from the stem medially, directly below the opening of the sclerite frame. The chamber lumen is wide and characteristically shaped by foldings of the intima (Fig. 32A). A muscularis is present, consisting of dorsal circular fibres posterad from the vaginal sclerite. Anterad from the sclerite the muscularis is composed of 4-5 layers inner circular and 3-4 layers outer longitudinal fibres. The gland duct, the spermathecal duct, the ductus bursae and the common oviduct are evaginating from the chamber anterad with regard to the vaginal sclerite in the median line.

Along the ***spermathecal duct*** (Figs. 32C, D) three successive regions can be distinguished. The posterior region, extending only a short distance after evagination of the duct from the genital chamber, is surrounded by an epithelium formed of irregularely shaped cells. The intima is weak. The lumen of the posterior region is wide and rounded (cross section); a muscularis is present (2-3 layers of circular fibres). The epithelium of the mid-region is composed of irregularely shaped cells. The lumen is narrowed and displays a weak cuticular outline. The mid-region is surrounded by 1-2 layers of circular and diagonal muscle fibres. The third, most anterior region (Fig. 32D) represents the “2-compartment-section” observed in the vast majority of Lepidoptera (except Micropterigidae). The lumen of the distal region is divided into a wide and a narrow compartment by a zone of constriction. The narrow compartment is densely filled with spermatozoans, not so the wide part of the lumen. Around the wide compartment, the epithelium is formed of comparatively small prismatic cells, with the nuclei close to the basal poles and numerous small vesicles in the cytoplasm, whilst the narrow compartment is equipped by large cubic epithelial cells with the nuclei in a central position. The intima is conspicuously strengthened and with a certain content of mesocuticle in the narrow compartment. The “2-compartment- section” of the spermathecal duct is surrounded by a muscularis composed of 1-2 layers of circular and diagonal fibres. The spermathecal duct leads into the huge, balloon-like ***spermatheca*** (Fig. 32E) about mid-length of segment VII. The spermatheca is shifted to the right body half; it almost reaches segment V anteriorly. The epithelium of the spermatheca is composed of extremely flattened cells, with the nuclei visible in extensions of the cell bodies. A cuticular intima as well as a muscularis are not developed. The bilobed ***spermathecal gland*** (Fig. 32F) is directly attached to the spermatheca in terminal position. The glandular epithelium is composed of prismatic cells with easily recognizeable nuclei and numerous secretory vesicles in a separate cell compartment (storage vacuole). The gland lumen is filled with spermatozoans and vesicles. A muscularis associated with the spermathecal gland is absent.

The ***ductus bursae*** (Figs. 32C, D) evaginates from the anterior apex of the genital chamber medially. The epithelial cells of the ductus are irregularely shaped. The epithelium displays many foldings projecting into the lumen, giving the latter a regular and characteristic shape (cross section). A weak intima is present. The ductus bursae is surrounded by a muscular envelope, composed of 1-2 layers of circular fibres. The ductus bursae leads into the extremely huge, balloon-shaped ***bursa copulatrix*** in the boundary region of segments VI and VII. The bursa lies in the left body half. Its epithelium is composed of extremely flattened cells with the nuclei in conspicuous widenings of the cell bodies. The cuticular intima is weak, but with scattered minute spines projecting into the bursa lumen. The lumen is filled with remnants of the spermatophore. A muscularis is not present.

The ***gland duct*** evaginates from the genital chamber in front of the vaginal sclerite dorso-medially. Its epithelium is formed of irregularely shaped cells; the apical cell poles are bearing projections pointing into the duct lumen. An weak intima is present. The lumen is narrow. A muscularis composed of 1-2 layers of circular muscle fibres is present. There is just a single ***accessory gland*** (Figs. 32C, D) of moderate size in segment VII, shifted to the right body half. The glandular epithelium consists of large, prismatic cells, with numerous minute vesicles near the basal pole and per cell one large "storage vacuole" close to the apical pole. The nuclei are approximately in a central position. The basal poles of clusters of epithelial cells are projecting into the body cavity, giving the accessory gland a tubercular surface in superficial inspection. The gland lumen is densely filled with secretions. A muscularis is lacking.

The ***common oviduct*** (Figs. 32C, D) evaginates from the genital chamber directly below the ductus bursae. Two duct regions can be distinguished. In the proximal region, after evagination from the genital chamber, the epithelium is composed of cells of irregular shape. The intima is extremely weak in this region. The lumen of the proximal region of the common oviduct is characteristically shaped by foldings of the epithelium and slightly depressed dorsoventrally. The muscularis consists of 3-4 layers of circular fibres. Around the distal region of the common oviduct, the epithelium is squamose, with conspicuously depressed nuclei. The intima is extremely weak. The lumen of the distal region is widened and rounded in cross section. The muscularis becomes weaker coming more and more distal; around the most distal parts of the common oviduct it is composed of just one single layer of circular fibres. In the boundary region of abdominal segments VI and VII, the common oviduct splits into the paired ***lateral oviducts***. The lateral oviducts reach segment VI anteriorly, where the ovarioles are branching off. The

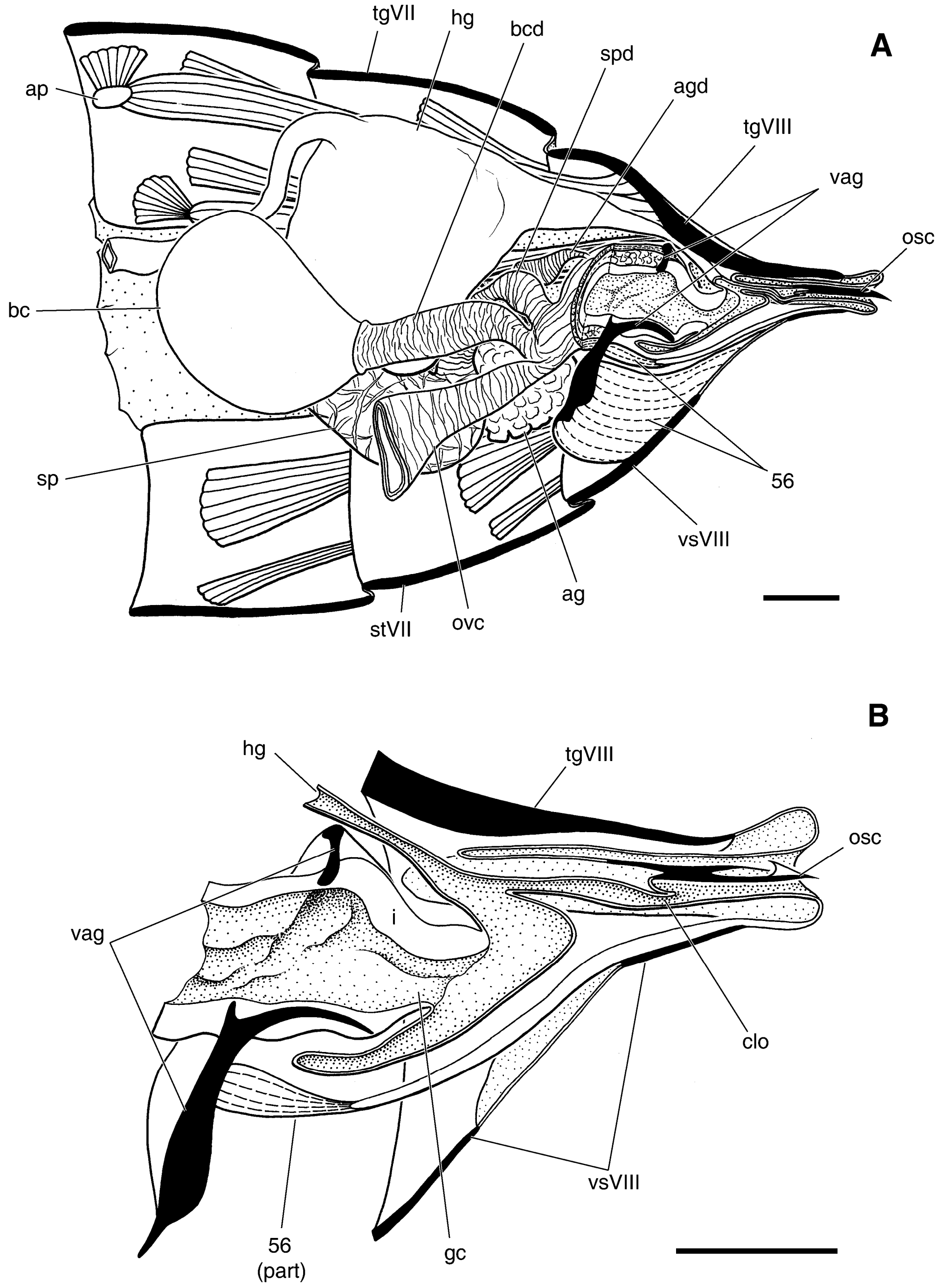

Fig. 30. *Eriocrania cicatricella*, female postabdomen, internal parts of the genital system. (A) overview; (B) detail, illustrating the fusion of the genital chamber with the hindgut and the position of the cloacal opening. Scale bar: 100 μm.

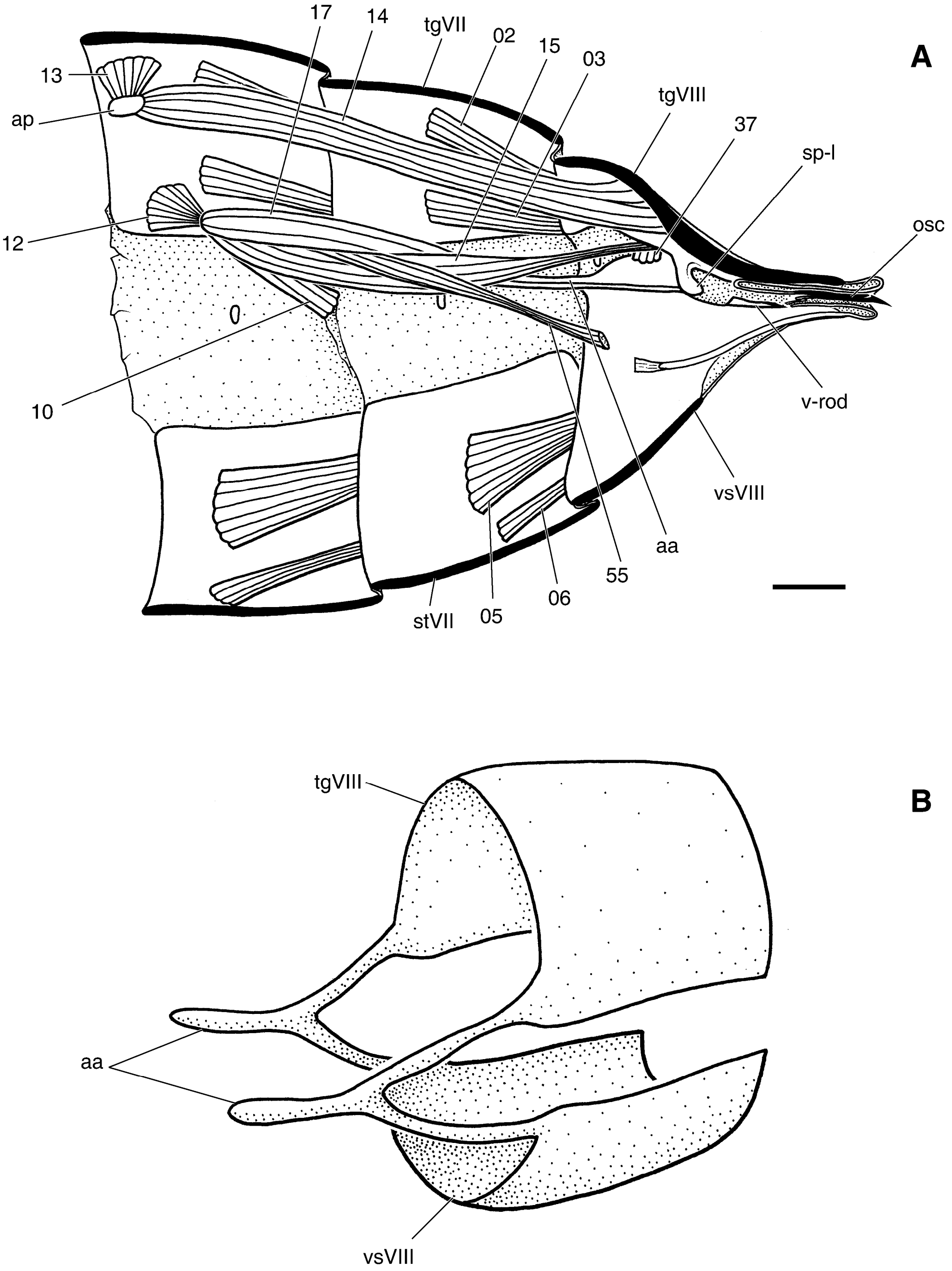

Fig. 31. (A) *Eriocrania cicatricella*, female postabdomen, overview over the skeleto-muscular arrangement, ***v-rod*** – ventral rod. Scale bar: 100 μm. (B) *Minoa* sp. (Geometridae): anterior apophyses basally forked, with connections to tergum VIII and the ventral plate of the segment; after Wood (1891), modified.

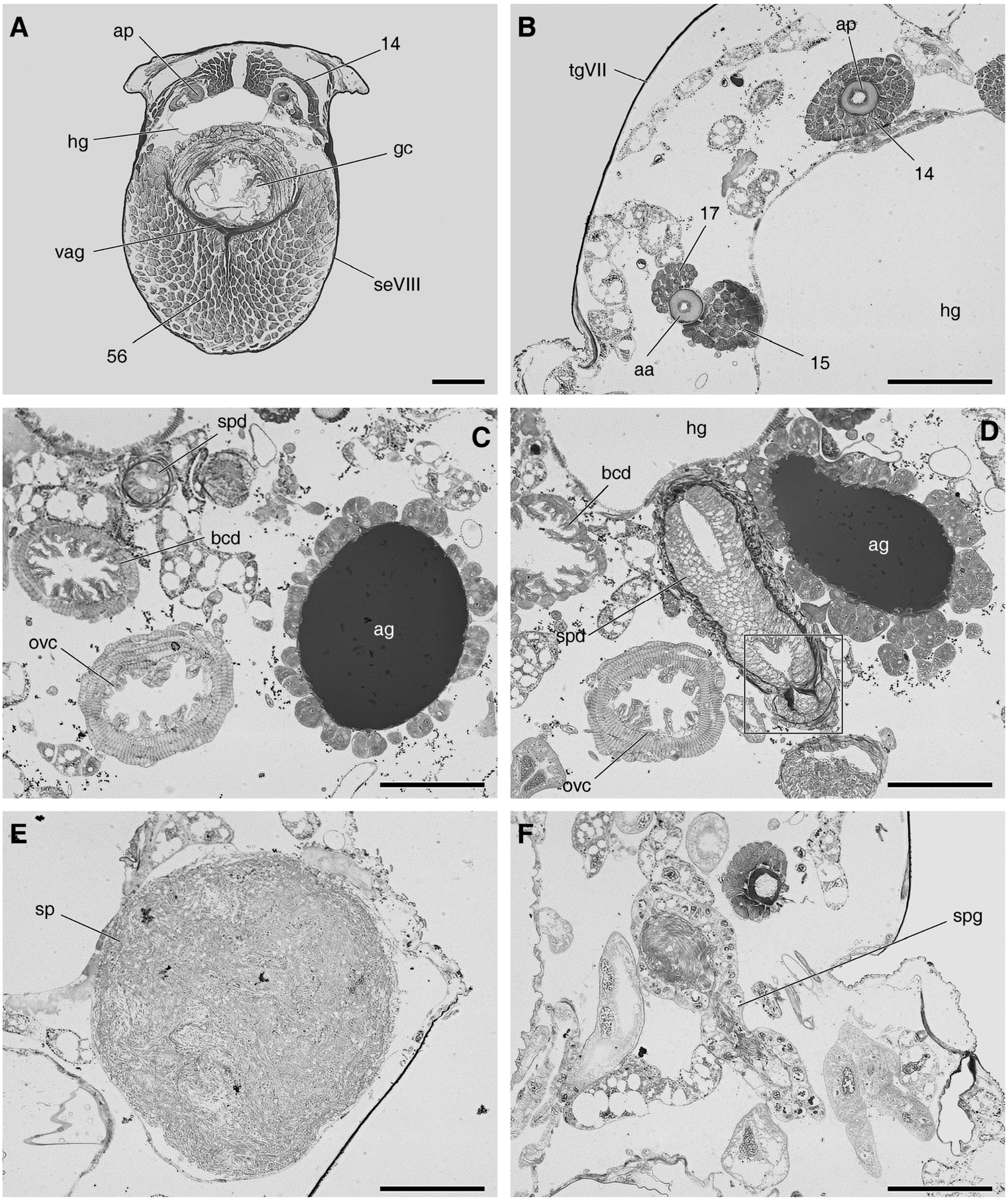

Fig. 32. *Eriocrania cicatricella*, female postabdomen, histological cross sections. (A) segment VIII, region with the dorsal and ventral external sclerotizations confluent; (B) anterior and posterior apophysis; (C) segment VII, spermathecal duct, ductus bursae, unpaired accessory gland, common oviduct; (D) segment VII, spermathecal duct, in a u-turn of the duct the 2-compartment- section is clearly visible [look at the square]; (E) segment VI, spermatheca; (F) segment VI, spermathecal gland. Scale bar: 50 µm.

lateral oviducts have a squamose epithelium with flattened nuclei. The lumen of the lateral oviducts is huge and rounded in cross section, with mature eggs inside.

4.3. The apophyses of Amphiesmenoptera

Following Ross (1967), the presence of paired rod-like apophyses, arising from the anterior margins of the female abdominal segment VIII and the terminal unit (segments IX – X [XI]), has been considered a potential synapomorphy of Trichoptera and Lepidoptera. It was already pointed out that the absence and / or reduction of the apophyses in some trichopteran lineages and in Micropterigidae and Heterobathmiidae are apomorphic traits of these families (e.g., Kristensen 1998, 2003b).

The assignment of the posterior apophyses to an area homologous to ***tergum IX*****,** especially in the four basal families of Lepidoptera-Glossata (Eriocraniidae, Acanthopteroctetidae, Lophocoronidae, Neopseustidae), was repeatedly doubted (Davis 1975, Davis & Nielsen 1980, Kristensen 2003b, Mutuura 1972). In Neopseustidae, the apophyses-bearing segment VIII is separated from the apophyses-bearing oviscapt saw by what appears to be a distinct segment (displaying both a distinct dorsal and a ventral sclerite plate). Assuming that this would be the true segment IX, the posterior apophyses consequently would originate from segment X. With regard to this, it remains a serious alternative that the posterior apophyses of Trichoptera and non-glossatan Lepidoptera (arising from the tergum IX- region) are not equivalent with the posterior apophyses in Lepidoptera-Glossata. However, the presence of the interjacent "segment" of Neopseustidae might rather be explained with a subdivision of the posterior part of segment VIII (and then considered as an autapomorphy of this family, see also Kristensen 2003b).

The situation is even more confusing, regarding the apophyses on ***segment VIII***. The condition with two pairs of apophyses VIII in Agathiphagidae may well be an autapomorphy of this family. However, an alternative interpretation would assign this situation to the ground plan of Lepidoptera, or even of Amphiesmenoptera. This is evidently related to the question, whether the segment VIII- apophyses in Lepidoptera-Glossata and Trichoptera are homologues of the dorsal or ventral pair in *Agathiphaga*, and whether the single anterior apophyses of Trichoptera and Lepidoptera-Glossata are really the same structure. In the families which arose in the first successive splitting events in Lepidoptera-Glossata (Eriocraniidae, Acanthopteroctetidae, Lophocoronidae) the invagination sites of the anterior apophyses on the anterior margin of segment VIII are variable, even within the family Eriocraniidae (see Davis 1978; Kristensen 1998, 2003b; Nielsen & Kristensen 1996; Stekolnikov 1967; Wood 1891). While tergum VIII and the ventral sclerite plate of segment VIII (***vsVIII***) are clearly separated in the non-glossatan lepidopteran families, these plates are more or less extensively fused in members of Glossata. So far the invagination site of the anterior apophyses has not been ascribed to either the dorsal or the ventral elements of segment VIII with certainty. A condition resembling that of "eriocraniid-grade" moths in having the dorsal and ventral sclerotizations of segment VIII fused, is found in

Trichoptera-Rhyacophilidae (Nielsen 1980). Here again, the origin of the single anterior apophyses (from the dorsal or ventral territory of segment VIII?) bears some uncertainty. However, in apophysis-bearing trichopterans which have tergum VIII and the ventral plate of segment VIII (***vsVIII***) separated (Philopotamidae, Stenopsychidae, Hydroptilidae–*Agraylea*), the apophyses always arise from the ventral plate (Nielsen 1980).

With 22 pairs of muscles (+ 2 single bundles each present only in one specimen) documented in this study, the female postabdominal musculature of *Agathiphaga* is by far the most complex reported from any amphiesmenopteran insect. Six of the muscles with attachment on the anterior apophyses of *Agathiphaga* have probable homologues in Rhyacophilidae and / or *Eriocrania* (**08**, **11**, **12**, **17**, **22**, **55)**. In *Agathiphaga*, muscles **08**, **11**, **17** and **55** are associated with the ventral anterior apophyses, and muscles **12** and **22** with the dorsal one. The rhyacophilid caddisflies possess muscles **08**, **11**, **17** and **55**, which are all associated with the ventral anterior apophyses in *Agathiphaga*. This and the ventrolateral position of the apophyse bases on the anterior segmental margin clearly suggest the homology of the anterior apophyses of Rhyacophilidae with the ***ventral*** one of *Agathiphaga*. However, an interapophyseal muscle (**22**) is present in both taxa, spanning between the apices of the posterior and the ***dorsal*** anterior apophyses in *Agathiphaga*. A shift of the site of origin from a ventral to a dorsal sclerite element would be one possible explanation, considering the identical insertion sites. However, the non-homology has to be considered as an alternative. Regarding *Eriocrania*, muscles **17** and **55** are certain homologues of their counterparts in *Agathiphaga*. Again, both support the homology of the single anterior apophyses in *Eriocrania* with the ***ventral*** ones in *Agathiphaga*. The problem here is muscle **12**, which is associated with the ***dorsal*** anterior apophysis of *Agathiphaga*. In case of a misinterpration of **12**, which may alternatively be equivalent with muscle **11** in *Eriocrania* (with the site of origin shifted far dorsad), this would corroborate support for the homology of the single *Eriocrania*- apophysis with the ventral one of *Agathiphaga*. If the homology of muscle **12** was correctly assessed for both taxa, this would be compatible with another interpretation of the anterior apophysis in Glossata, namely as a composite formation comprising homologues of both the dorsal and ventral anterior apophyses in *Agathiphaga*. This interpretation is ambiguous, but is arguably supported by a condition found in many heteroneurous moths: strengthening ridges extend from the bases of the anterior apophyses into both dorsal and ventral sclerotizations of segment VIII, giving the impression of the apophyses being basally "forked" (Fig. 31B; see also Dugdale 1974, Kristensen 2003b, Mutuura 1972, Wood 1891).

The following szenario for the ground plan condition in Amphiesmenoptera and the transformation series along the basal lineages of Trichoptera and Lepidoptera is suggested (under the premise of the correct homologization of muscles **12** and **22**). It is likely similar to what is found in Trichoptera-Rhyacophilidae, with one pair of anterior apophyses arising from a ventral area of segment VIII, with attachment of muscles **08**, **11**, **17**, **22** and **55**. This setup is retained in basal Trichoptera without noteworthy modifications, whereas in Lepidoptera a second, dorsal pair of anterior apophyses arises from tergum VIII, with attachment of muscle **12** (neo-formation), and the origin of the interapophyseal muscle **22** is shifted to the apex of this dorsal apophyses. At the base of Lepidoptera-Glossata the dorsal and ventral (ipsilateral!) anterior apophyses fused, involving also the muscle in the process, namely muscles **12** (dorsal), **17** and **55** (ventral). Losses or reductions of the apophyses with their muscles in subordinate lineages within Trichoptera and Lepidoptera are considered to be secondary events. However, an examination of the investigations of the musculature onto a broader sample of amphiesmenopteran taxa is urgently needed for further clarification.

4.4. Muscle table

Tab. 4 Muscles of the female postabdomen; taxa indicated by capital letters as follows: **A** *Gryllus*; **B** *Tettigonia*; **C** *Xyela*; **D** *Tenthredo*; **E** *Osmylus*; **F** *Archaeopsylla*; **G** *Nannochorista*; **H** *Boreus*; **I** *Anabittacus*; **J** *Panorpa*; **K** *Limonia*; **L** *Tipula*; **M** *Aedes*; **N** *Toxophora*; **O** *Fansipangana*; **P** *Rhyacophila*; **Q** *Ulmerochorema*; **R** *Micropterix*; **S** *Agathiphaga*; **T** *Heterobathmia*; **U** *Eriocrania*; **V** *Cydia.*

		A	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**	**O**	**P**	**Q**	**R**	**S**	**T**	**U**	**V**
01	*isVII-VIII01*	+	+	?	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	-	-	-
02	*isVII-VIII02*	+	+	?	+	+	+	+	+	-	+	+	+	-	-	+	+	+	+	+	+	+	+
03	*isVII-VIII03*	+	+	?	+	+	-	+	+	+	+	-	-	+	+	-	-	-	+	+	+	+	-
04	*isVII-VIII04*	+	+	?	+	+	-	+	+	+	+	-	-	-	-	-	-	-	+	+	-	-	-
05	*isVII-VIII05*	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+
06	*isVII-VIII06*	-	-	?	-	-	-	+	+	-	+	+	+	-	+	-	-	+	+	+	-	+	-
07	*isVII-VIII07*	+	+	?	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
08	*isVII-VIII08*	-	-	?	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	+	-	-	-
09	*isVII-VIII09*	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
10	*isVII-VIII10*	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	+
11	*isVII-VIII11*	-	-	?	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	+	-	-	-
12	*isVII-VIII12*	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	+
13	*isVII-IX01*	-	-	?	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	+	+	+
14	*isVIII-IX01*	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+
15	*isVIII-IX02*	+	+	+	+	+	-	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+
16	*isVIII-IX03*	+	+	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17	*isVIII-IX04*	-	-	-	-	+	-	-	-	-	+	+	+	+	+	+	+	-	+	+	-	+	-
18	*isVIII-IX05*	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19	*isVIII-IX06*	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20	*isVIII-IX07*	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
21	*isVIII-IX08*	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
22	*isVIII-IX09*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	+	-	-	-
23	*isVIII-IX10*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	+	-	-
24	*isVIII-IX11*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	+	-	-	-	+
25	*isIX-X01*	+	+	?	-	-	+	+	+	+	+	+	+	+	+	-	-	-	+	-	+	-	-
26	*isIX-X02*	+	+	?	-	+	+	+	+	+	+	+	+	+	+	-	-	-	+	-	-	-	-
27	*isIX-X03*	-	-	?	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
28	*isX-XI01*	+	+	?	+	-	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-
29	*isX-XI02*	-	-	?	-	-	+	+	-	+	+	+	+	-	-	-	-	-	-	-	-	-	-
30	*seX- ce01*	+	+	?	+	-	-	+	+	+	+	+	+	-	-	-	-	+	-	-	-	-	-
31	*intraVIII01*	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
32	*intraIX01*	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-

		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V
33	*intraIX02*	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
34	*intraIX03*	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
35	*intraIX04*	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
36	*dvVII01*	+	+	?	+	+	+	+	+	+	+	+	+	+	+	?	?	+	+	?	?	?	+
37	*dvVIII01*	-	-	-	-	+	+	+	+	-	+	+	+	+	+	+	-	+	+	+	-	+	-
38	*dvVIII02*	+	+	+	+	+	-	+	-	-	-	+	+	-	-	-	-	-	-	+	-	-	-
39	*dvVIII03*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
40	*dvIX01*	+	+	+	+	+	-	+	-	-	-	+	-	-	-	+	+	-	-	+	-	-	-
41	*dvIX02*	+	+	+	+	+	-	+	-	-	-	+	-	+	+	-	-	-	-	-	-	-	-
42	*dvIX03*	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
43	*dvIX04*	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
44	*dvX01*	-	-	?	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
45	*dvXI01*	-	-	?	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
46	*dvXI02*	-	-	?	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
47	*tVII01*	-	-	?	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
48	*tVIII01*	-	-	-	-	-	-	+	+	+	-	+	+	-	+	-	-	-	-	-	-	-	-
49	*tVIII02*	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
50	*tIX01*	-	-	-	-	+	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
51	*tX01*	-	-	?	-	-	-	-	-	-	-	+	-	+	-	-	-	-	+	-	-	-	-
52	*tX02*	-	-	?	-	-	-	-	-	-	-	-	-	+	+	-	-	-	+	-	+	-	-
53	*tXI01*	-	-	?	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-
54	*seVII-gc01*	-	-	-	-	-	-	-	-	+	?	-	-	+	?	-	-	+	-	-	+	-	?
55	*seVIII-gc01*	-	-	-	-	-	+	+	-	+	?	+	+	+	?	+	+	+	-	+	+	+	?
56	*seVIII-gc02*	-	-	-	-	-	-	-	-	-	?	-	-	-	?	-	-	-	-	+	+	+	?
57	*seVIII-gc03*	-	-	-	-	-	-	+	-	-	?	-	-	-	?	-	-	-	-	-	-	-	?
58	*seIX-gc01*	-	-	-	-	+	+	+	-	+	+	-	-	-	-	+	+	+	+	-	+	-	+
59	*seIX-gc02*	-	-	-	-	-	+	+	-	+	+	-	-	-	?	-	-	-	-	-	-	-	?
60	*seIX-gc03*	-	-	-	-	-	-	-	-	+	-	-	-	-	?	-	-	-	-	-	-	-	?
61	*seX-gc01*	-	-	-	-	-	-	-	-	+	?	-	-	-	?	-	-	-	-	-	-	-	?
62	*intra-gc01*	-	-	-	-	-	+	-	-	+	?	-	-	-	?	-	-	-	-	-	-	-	?
63	*intra-gc02*	-	-	-	-	-	-	-	-	-	?	-	-	-	?	-	-	+	-	-	-	-	?
64	*intra-gc03*	-	-	-	-	-	-	-	-	-	?	-	-	-	?	-	-	+	-	-	-	-	?
65	*intra-gc04*	-	-	-	-	-	-	-	-	-	?	-	-	-	?	-	-	+	-	-	-	-	?
66	*intra-gc05*	-	-	-	-	-	-	-	-	-	?	-	-	-	?	-	-	+	-	-	-	-	?
67	*rec/clo01*	?	?	?	?	+	-	-	-	+	?	-	-	-	?	+	-	+	-	+	+	-	?
68	*add01*	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
69	*add02*	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
70	*add03*	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
71	*add04*	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-
72	*add05*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-

5. List of phylogenetically relevant characters

Characters used in the cladistic analysis are listed in the following in a morphology based sequence (see **chapter 4**: Results). The different states are defined and coded. Characters are coded as inapplicable if the structure in question is missing (-). Missing data are coded as (?).

1. Tergum VII (tgVII), shape: (0) normally developed; (1) ventral margins enlarged, saddle-shaped. The ventral margins of tergum VII are distinctly enlarged and the tergum saddle-shaped in *Gryllus* (see also Snodgrass 1935), *Tettigonia*, *Xyela* (Vilhelmsen 2001), *Tenthredo*, *Archaeopsylla*, *Boreus* (see also Mickoleit 1975) and *Toxophora* (Mühlenberg 1971).

2. Tergum VIII (tgVIII), shape: (0) normally developed; (1) ventral margins enlarged, saddle-shaped. The ventral margins of tergum VIII are enlarged and the tergum saddle-shaped in *Gryllus* (see also Snodgrass 1935), *Tettigonia*, *Xyela* (Vilhelmsen 2001), *Tenthredo*, *Osmylus* (see also Aspöck & Aspöck 2008, Mickoleit 1973), *Archaeopsylla*, *Boreus* (see also Mickoleit 1975), *Limonia* , *Tipula* (see also Rees & Ferris 1939) and *Toxophora* (Mühlenberg 1971). The character is scored as inapplicable if tergum VIII is fused with ventral sclerotizations of segment VIII, as the definite margins of the "true" tergal area can not be identified in these cases.

3. Tergum VIII (tgVIII), length: (0) unmodified, about as long as tergum VII; (1) shortened, only +/- half length of tergum VII; (2) markedly longer than tergum VII. Tergum VIII is distinctly shorter than the preceeding tergum in *Limonia*, *Tipula* (see also Rees & Ferris 1939), *Aedes* (see also Christophers 1960), *Toxophora* (Mühlenberg 1971) and *Ulmerochorema* (see also Schmid 1989). The tergum is distinctly longer than the preceeding tergal plates in *Osmylus* (see also Aspöck & Aspöck 2008, Mickoleit 1973).

4. Tergum VIII (tgVIII), fusion with ventral sclerotization of segment VIII (vsVIII): (0) not fused with vsVIII; (1) fused with vsVIII over its entire length; (2) connected with vsVIII by a slender sclerotised stripe. Tergum VIII is fused with the ventral sclerotization of segment VIII over its entire length in *Anabittacus* (see Willmann 1982), *Fansipangana* and *Rhyacophila* (see Nielsen 1980). The sclerites are connected by a slender sclerotised stripe in *Eriocrania* (see also Davis 1978).

5. Ventral sclerotization of segment VIII (vsVIII), elements of right and left body half separate / fused: (0) paired, elements of right and left body half fully separated; (1) elements of right and left body half fused in the ventromedian line. The ventral sclerotizations of both body-halves of segment VIII are clearly separated in *Gryllus* (see also Snodgrass 1935), *Tettigonia*, *Xyela* (Vilhelmsen 2001), *Tenthredo*, *Nannochorista* and *Boreus* (see also Mickoleit 1975). State (0)/separated is also scored for *Anabittacus*, even though the posteriormost portions of the distal parts of the ventral segmental sclerotizations are connected by a sclerotised stripe (see Willmann 1982). In all other taxa under consideration the anterior parts or the entire length of the ventral sclerotizations are fused.

6. Ventral sclerotization of segment VIII (vsVIII), subordinate elements: (0) proximal and distal part (vsVIII-p and vsVIII-d) distinct, clearly separated; (1) vsVIII-p and vsVIII-d distinguishable, but fused; (2) no distinction of vsVIII-p and vsVIII-d possible. A clear separation of the proximal and distal part of the ventral sclerotization of segment VIII is recognizeable in the hymenopteran outgroup taxa. The proximal and distal parts are distinguishable, but firmly connected in *Gryllus* (see also Snodgrass 1935) and *Tettigonia*.

7. Ventral sclerotization of segment VIII (vsVIII), length: (0) unmodified, not markedly longer or shorter than tergum VIII; (1) moderately prolonged, ca. 1/3 longer than tergum VIII; (2) strongly prolonged caudally; (3) shortened. The ventral sclerotizations of segment VIII are moderately prolonged caudally in *Anabittacus* (see Willmann 1982), *Aedes* (see also Christophers 1960), *Toxophora* (Mühlenberg 1971) and *Heterobathmia* (see also Nielsen & Kristensen 1979). They are strongly elongated caudally in the orthopteran and hymenopteran outgroup taxa (see also Snodgrass 1935, Vilhelmsen 2001), and also in *Boreus* (see also Mickoleit 1975), *Limonia* and *Tipula* (see also Rees & Ferris 1939). In *Osmylus*, the ventral sclerotization of segment VIII is shortened (see also Aspöck & Aspöck 2008, Mickoleit 1973).

8. Additional (median) sclerotized plate in the venterVIII-region, close to anterior segmental margin: (0) absent; (1) present. An additional sclerotized plate without muscle insertions is found near the anterior margin of the venter-VIII – region in the orthopterans (see also Snodgrass 1935). The plate might represent a vestige of a "true" sternal sclerotization of segment VIII.

9. Tergum IX (tgIX), shape: (0) normally developed; (1) ventral margins enlarged, saddle-shaped. The ventral margins of tergum IX are distinctly enlarged and the tergum saddle-shaped in *Gryllus* (see also Snodgrass 1935), *Tettigonia*, *Xyela* (Vilhelmsen 2001), *Tenthredo*, *Osmylus* (see also Aspöck & Aspöck 2008, Mickoleit 1973), *Boreus* (see also Mickoleit 1975), *Limonia*, *Tipula* (see also Rees & Ferris 1939), *Toxophora* (Mühlenberg 1971), *Ulmerochorema* (see Schmid 1989) and *Heterobathmia* (see also Kristensen & Nielsen 1979). The character is scored as inapplicable if a sclerotized tergum IX is absent or fused with the ventral segmental sclerotization, or if segment IX is included in formation of the oviscapt.

10. Tergum IX (tgIX), length: (0) unmodified; (1) distinctly shorter (ca. ½) than preceeding tergal plates; (2) distinctly longer than tergum VIII. Tergum IX is markedly shortened in *Osmylus* (see also Aspöck & Aspöck 2008, Mickoleit 1973), *Nannochorista* (see also Mickoleit 1975), *Limonia*, *Tipula* (see also Rees & Ferris 1939), *Aedes* (see also Christophers 1960) and *Toxophora* (Mühlenberg 1971). It is distinctly longer than the tergum VIII in *Ulmerochorema* (see Schmid 1989) and *Heterobathmia* (see also Kristensen & Nielsen 1979). The character is scored as inapplicable if a sclerotized tergum IX is absent or fused with tergum X, or if segment IX is included in formation of the oviscapt.

11. Tergum IX (tgIX), internal cuticular ridge: (0) internal cuticular ridge present near anterior margin; (1) without internal cuticular ridge near anterior margin. An internal cuticular ridge near the anterior margin of tergum IX is present in *Gryllus* (see also Snodgrass 1935), *Tettigonia*, *Xyela* (Vilhelmsen 2001) and *Tenthredo*. The character is scored as inapplicable if a sclerotized tergum IX is absent or segment IX is included in formation of the oviscapt.

12. Tergum IX (tgIX), articulation or fusion with ventral sclerotized parts: (0) no articulation / fusion with ventral sclerites; (1) articulation with vsVIII-p; (2) articulation with vsIX-p(1); (3) fusion with vsIX. Tergum IX articulates with the ventral sclerotization of segment VIII in *Gryllus* (see also Snodgrass 1935), *Tettigonia*, *Xyela* (Vilhelmsen 2001) and *Tenthredo*. It articulates with the ventral sclerotization of segment IX in *Osmylus* (see also Aspöck & Aspöck 2008, Mickoleit 1973). It is fused with the ventral sclerotization of segment IX in *Anabittacus* (see also Willmann 1982). The character is scored as inapplicable if segment IX is part of the oviscapt.

13. Tergum IX (tgIX), presence of the posterior apophysis: (0) posterior apophysis absent; (1) posterior apophysis present, arising from the anterior margin of tgIX. The posterior apophysis is present in all examined trichopterans and lepidopterans with the exception of *Micropterix* (see also Kristensen 2003b, Nielsen 1980).

14. Tergum IX (tgIX), length of the posterior apophysis: (0) posterior apophysis long; (1) posterior apophysis short. The posterior apophysis is short or vestigial in *Ulmerochorema* and *Heterobathmia* (see also Kristensen 2003b, Kristensen & Nielsen 1979, 1998).

15. Ventral sclerotization of segment IX (vsIX), elements of right and left body half separate/ fused: (0) paired elements of right and left body half separated; (1) main elements, vsIX-p(1) of both body halfs ventromedially connected by additional sclerites, vsIX-p(2) / vsIX-p(3); (2) main elements, vsIX-p(1), of right and left body half fused in the ventromedian line, vsIX-p(2) and vsIX-p(3) not traceable. The ventral sclerotized parts of both body halves of segment IX are fully separated in *Xyela* (Vilhelmsen 2001), *Tenthredo*, *Osmylus* (see Aspöck & Aspöck 2008, Mickoleit 1973) and *Nannochorista* (see also Mickoleit 1975). They are connected by additional sclerites in the orthopteran outgroup taxa (see also Snodgrass 1935). The character is scored as inapplicable if vsIX is absent or segment IX is part of the oviscapt.

16. Ventral sclerotization of segment IX (vsIX), substructures: (0) proximal and distal part (vsIX-p and vsIX-d) distinct, clearly separated; (1) vsIX-p and vsIX-d distinguishable, but connected; (2) vsIX-p and vsIX-d not separable. The proximal and distal parts of the ventral sclerotizations of segment IX are clearly separated in the hymenopteran outgroup taxa (see also Vilhelmsen 2001). They are distinct, but connected in the orthopterans (see Snodgrass 1935) and *Osmylus* (see also Aspöck & Aspöck 2008, Mickoleit 1973). The character is scored as inapplicable if vsIX is absent or segment IX is part of the oviscapt.

17. Ventral sclerotization of segment IX (vsIX), length: (0) not markedly longer than tergum IX; (1) caudally strongly prolonged. The ventral sclerotizations of segment IX are elongated caudally in the orthopteran outgroup taxa (see Snodgrass 1935), in Hymenoptera (see also Vilhelmsen 2001), and also in *Osmylus* (see Aspöck & Aspöck 2008, Mickoleit 1973) and *Limonia* (see also Rees & Ferris 1939). The character is scored as inapplicable if vsIX is absent or segment IX is part of the oviscapt.

18. Tergum X (tgX), sclerotization: (0) closed in the dorsal midline; (1) not closed dorsomedially. The sclerotization of tergum X is not closed in the dorsal midline in *Osmylus* (see also Aspöck & aspöck 2008, Mickoleit 1973), *Aedes* (see also Christophers 1960), *Toxophora* (Mühlenberg 1971), the trichopteran representatives (see also Nielsen 1980, Schmid 1989), *Micropterix* and *Heterobathmia* (see also Kristensen 2003b). The character is scored as inapplicable if tergum X is fused with tergum IX or segment X is part of the oviscapt.

19. Tergum X (tgX), shape: (0) unmodified; (1) ventral margins strongly prolonged; (2) sclerotization not closed dorsomedially, tergum present as a pair of small dorsal or dorsolateral plates. The ventral margins of tergum X are enlarged in the orthopteran outgroup taxa (see also Snodgrass 1935), in *Osmylus* (see also Aspöck & Aspöck 2008, Mickoleit 1973), *Boreus* (see also Mickoleit 1975), *Anabittacus* (see Willmann 1982), *Aedes* (see Christophers 1960) and in *Toxophora* (Mühlenberg 1971). As the tergum-X – sclerotization is not closed dorsomedially in *Osmylus*, *Aedes*, *Toxophora* and *Micropterix*, the tergum appears in the shape of two lateral plates. In the trichopteran taxa and *Heterobathmia* the tergal halves are also separated dorsomedially and restricted to a pair of small dorsal or dorso-lateral plates (see also Kristensen 2003b, Nielsen 1980, Schmid 1989).The character is scored as inapplicable if tergum X is fused with tergum IX or with the ventral sclerotizations of segment X, or if segment X is part of the oviscapt.

20. Tergum X (tgX), length: (0) normal; (1) shortened; (2) strongly elongated. Tergum X is markedly shorter than tergum IX in *Nannochorista*, *Anabittacus*, *Panorpa* (see also Grell 1942, Mickoleit 1975, Willmann 1982), in the trichopterans examined (see also Nielsen 1980, Schmid 1989) and in *Heterobathmia* (see also Kristensen 2003b). It is extremely elongated in *Boreus* (see Mickoleit 1975), *Limonia* and *Tipula* (see also Rees & Ferris 1939). The character is scored as inapplicable if tergum X is fused with tergum IX or segment X is part of the oviscapt.

21. Tergum X (tgX), fusion with ventral sclerotized elements of the segment: (0) no fusion; (1) fully fused, forming a closed sclerite-ring around segment X. Tergum X forms a closed sclerotized ring around the segment together with the ventral sclerotizations in *Nannochorista* and *Panorpa* (see also Grell 1942, Mickoleit 1975). The character is scored as inapplicable if tergum X is fused with tergum IX or segment X is part of the oviscapt.

22. Ventral sclerotization of segment X (vsX), presence: (0) absent; (1) present. Absent in *Osmylus* (see Mickoleit 1973), *Boreus* (see Mickoleit 1975), *Anabittacus* (see Willmann 1982), *Limonia* (see also Rees & Ferris 1939), *Aedes* (see also Christophers 1960), *Toxophora*

(Mühlenberg 1971), *Micropterix*, *Heterobathmia* (see also Kristensen 2003b), and in the trichopterans examined (see also Nielsen 1980). The character is scored as inapplicable if segment X is fused with segment IX or part of the oviscapt.

23. TergumXI (tgXI), presence: (0) absent; (1) present. A distinct tergum XI is present in *Gryllus* (see also Snodgrass 1935), *Tettigonia*, *Osmylus* (see also Mickoleit 1975), *Nannochorista*, *Boreus*, *Anabittacus*, *Panorpa* (see also Mickoleit 1975, Willmann1982) and *Tipula* (see Rees & Ferris 1939). The tergal halves are unconnected medially in *Osmylus* and; the sclerite is vestigial in *Boreus*. The character is scored as inapplicable if an oviscapt is present or if segment XI is not recognizeable.

24. Ventral sclerotization of segment XI (vsXI), presence: (0) absent; (1) present. Present in *Nannochorista*, *Boreus*, *Anabittacus* and *Panorpa* (see Mickoleit 1975, Willmann 1982). The character is scored as inapplicable if an oviscapt is present or if segment XI is not recognizeable.

25. Cercus (ce), presence: (0) absent; (1) present. Absent in *Archaeopsylla*, *Aedes*, *Toxophora* (Mühlenberg 1971), and in the lepidopterans examined (see also Kristensen 2003b).

26. Cercus (ce), segmentation: (0) not subdivided in segments; (1) 3-segmented. 3-segmented in *Nannochorista* and *Panorpa* (see also Mickoleit 1975).

27. Cercus (ce), length: (0) short; (1) moderately long; (2) strongly elongated. Moderately long in *Tettigonia*, *Nannochorista*, *Anabittacus*, *Boreus* and *Panorpa* (see Mickoleit 1975, Willmann 1982). Strongly elongated in *Gryllus*, *Limonia* and *Tipula* (see also Rees & Ferris 1939).

28. Oviscapt (osc): (0) not developed; (1) developed. An oviscapt formed by complete fusion of the terminal segments (beginning with segment IX) is present in *Agathiphaga*, *Eriocrania* and *Cydia* (see also Kristensen 2003b).

29. Genital opening, position: (0) ventro-median, behind segment VIII; (1) ventro-median, behind segment IX; (2) subterminal. The genital ducts are opening ventrally behind segment IX in *Archaeopsylla*, *Panorpa* (see Mickoleit 1975), the trichopteran representatives examined and in *Heterobathmia*. The cloacal opening is shifted to a subterminal position in *Micropterix* and *Agathiphaga*.

30. Additional sclerotized plate below the genital opening, presence: (0) absent; (1) present. Present in *Aedes* and *Toxophora* (Mühlenberg 1971).

31. Muscle 01 *isVII-VIII01*, presence: (0) absent; (1) present. Absent in *Ulmerochorema*, *Heterobathmia*, *Eriocrania* and *Cydia* (see Kuznetzov & Stekolnikov 2001).

32. Muscle 01 *isVII-VIII01*, number of bundles: (0)1 bundle; (1) 2 bundles. Composed of 2 bundles in the orthopteran outgroup taxa.

33. Muscle 02 *isVII-VIII02*, presence: (0) absent; (1) present. Absent in *Anabittacus*, *Aedes* and *Toxophora* (see Mühlenberg 1971).

34. Muscle 02 ***isVII-VIII02*, number of bundles: (0) 1 bundle; (1) 2 bundles.** Composed of 2 bundles in orthopteran outgroup taxa and *Osmylus* (see Feuerstein 2008).

35. Muscle 03 ***isVII-VIII03*, presence: (0) absent; (1) present.** Absent in *Archaeopsylla*, *Limonia*, *Tipula*, the representatives of Trichoptera examined, and in *Cydia* (see Kuznetzov & Stekolnikov 2001).

36. Muscle 03 ***isVII-VIII03*, number of bundles: (0) 1 bundle; (1) 2 bundles.** Composed of 2 bundles in the orthopterans.

37. Muscle 03 ***isVII-VIII03*, site of origin: (0) tergum VII, lateral / ventral to isVII-VIII02; (1) shifted dorsal, median/dorsal to isVII-VIII02.** The site of origin is shifted dorsad in *Tenthredo*, *Osmylus* (see Feuerstein 2008), *Nannochorista* and *Panorpa*.

38. Muscle 04 ***isVII-VIII04*, presence: (0) absent; (1) present.** Absent in *Archaeopsylla*, in all examined representatives of Diptera (see also Mühlenberg 1971) and Trichoptera, and in *Heterobathmia*, *Eriocrania* and *Cydia* (see Kuznetzov & Stekolnikov 2001).

39. Muscle 04 ***isVII-VIII04*, number of bundles: (0) 1 bundle; (1) 2 bundles.** The muscle is composed of 2 bundles in the orthopteran outgroup taxa. The character is scored as inapplicable if the muscle is absent.

40. Muscle 06 ***isVII-VIII06*, presence: (0) absent; (1) present.** Absent in the orthopteran and hymenopteran outgroup taxa, in *Osmylus* (see Feuerstein 2008), *Archaeopsylla*, *Anabittacus*, *Aedes*, *Fansipangana*, *Rhyacophila*, *Heterobathmia*, and in *Cydia* (see Kuznetzov & Stekolnikov 2001).

41. Muscle 07 ***isVII-VIII07*, presence: (0) absent; (1) present.** Present in orthopterans, *Tenthredo*, and *Osmylus* (see Feuerstein 2008).

42. Muscle 07 ***isVII-VIII07*, number of bundles: (0) 1 bundle; (1) 2 bundles.** Composed of 2 bundles in the orthopteran outgroup taxa.

43. Muscle 08 ***isVII-VIII08*, presence: (0) absent; (1) present.** The muscle is present in *Fansipangana*, *Rhyacophila* and *Agathiphaga*.

44. Muscle 10 ***isVII-VIII10*, presence: (0) absent; (1) present.** Present in *Rhyacophila*, *Eriocrania* and *Cydia* (see Kuznetzov & Stekolnikov 2001).

45. Muscle 11 ***isVII-VIII11*, presence: (0) absent; (1) present.** Present in *Fansipangana*, *Rhyacophila* and *Agathiphaga*.

46. Muscle 12 ***isVII-VIII12*, presence: (0) absent; (1) present.** Present in *Agathiphaga*, *Eriocrania* and *Cydia* (see Kuznetzov & Stekolnikov 2001).

47. Muscle 13 ***isVII-IX01*, presence: (0) absent; (1) present.** Present in *Fansipangana*, *Rhyacophila*, *Heterobathmia*, *Eriocrania* and *Cydia* (see Kuznetzov & Stekolnikov 2001).

48. Muscle 14 ***isVIII-IX01*, number of bundles: (0) 1 bundle;(1) 2 bundles.** Composed of 2 bundles in the orthopteran outgroup taxa, in *Tenthredo*, *Archaeopsylla*, *Eriocrania* and *Cydia* (see Kuznetzov & Stekolnikov 2001).

49. Muscle 14 ***isVIII-IX01*****, site of insertion: (0) regular, anterior margin of tergum IX; (1) apical region of posterior apophysis.** The site of insertion is shifted to the posterior apophysis in *Eriocrania* and *Cydia* (see Kuznetzov & Stekolnikov 2001).

50. Muscle 15 ***isVIII-IX02*****, presence: (0) absent; (1) present.** Absent in *Archaeopsylla* and *Aedes*.

51. Muscle 15 ***isVIII-IX02*****, number of bundles: (0) 1 bundle; (1) 2 bundles.** Composed of 2 bundles in orthopterans, in *Tenthredo*, *Nannochorista*, *Boreus*, *Panorpa* and *Fansipangana*. The character is scored as inapplicable if the muscle is absent.

52. Muscle 15 ***isVIII-IX02*****, site of insertion: (0) anterior margin of tergumIX, lateral to** ***isVIII-IX01*****; (1) shifted to posterior apophysis.** The insertion site is shifted to the posterior apophysis in *Fansipangana*, *Rhyacophila*, *Ulmerochorema* and *Agathiphaga*. The character is scored as inapplicable if the muscle is absent.

53. Muscle 16 ***isVIII-IX03*****, presence: (0) absent; (1) present.** Present in the orthopterans and *Tenthredo*.

54. Muscle 16 ***isVIII-IX03*****, number of bundles: (0) 1 bundle; (1) 2 bundles.** Composed of 2 bundles in the orthopteran taxa. The character is scored as inapplicable if the muscle is absent.

55. Muscle 23 ***isVIII-IX10*****, presence: (0) absent; (1) present.** Present in *Ulmerochorema*, *Agathiphaga* and *Heterobathmia*.

56. Muscle 24 ***isVIII-IX11*****, presence: (0) absent; (1) present.** Present in *Fansipangana*, *Rhyacophila*, *Micropterix* and *Cydia* (see Kuznetzov & Stekolnikov 2001).

57. Muscle 25 ***isIX-X01*****, presence: (0) absent; (1) present.** Absent in *Tenthredo*, *Osmylus* (see Feuerstein 2008), *Agathiphaga*, *Eriocrania*, *Cydia* (see Kuznetzov & Stekolnikov 2001) and in the examined trichopterans.

58. Muscle 25 ***isIX-X01*****, number of bundles: (0) 1 bundle; (1) 2 bundles.** Composed of 2 bundles in the orthopterans. The character is scored as inapplicable if the muscle is absent.

59. Muscle 26 ***isIX-X02*****, presence: (0) absent; (1) present.** Absent in *Tenthredo* and in the trichopterans and lepidopterans examined with the exception of *Micropterix* (see also Kuznetzov & Stekolnikov 2001 [*Cydia*]).

60. Muscle 26 ***isIX-X02*****, number of bundles: (0) 1 bundle; (1) 2 bundles.** Composed of 2 bundles in the orthopterans, *Osmylus* (see Feuerstein 2008) and *Nannochorista*.

61. Muscle 28 isX-XI01, presence: (0) absent; (1) present. The muscle is absent in *Osmylus* (see Feuerstein 2008), *Aedes*, *Toxophora* (see Mühlenberg 1971) and in the amphiesmenopteran representatives (see also Kuznetzov & Stekolnikov).

62. Muscle 28 isX-XI01, number of bundles: (0) 1 bundle; (1) 2 bundles. The muscle is composed of 2 bundles in the orthopterans and in *Anabittacus*.

63. Muscle 29 isX-XI02, presence: (0) absent; (1) present. The muscle is present in *Archaeopsylla*, *Nannochorista*, *Anabittacus*, *Panorpa*, *Limonia* and *Tipula*.

64. Muscle 34 *intraIX03*, presence: (0) absent; (1) present. The muscle is present in the orthopterans (see also Snodgrass 1935) and hymenopterans (see also Vilhelmsen 2001).

65. Muscle 35 *intraIX04*, presence : (0) absent; (1) present. The muscle is present in the hymenopteran outgroup taxa (see also Vilhelmsen 2001).

66. Muscle 36 *dvVII01*, general shape: (0) 2 compact bundles; (1) sheet of single fibres; (2) 3 compact bundles. This muscle is composed of 2 compact bundles in the orthopteran outgroup taxa (see also Snodgrass 1935) and in *Tenthredo*, and of 3 bundles in *Cydia* (see Kuznetzov & Stekolnikov 2001).

67. Muscle 37 *dvVIII01*, presence: (0) absent; (1) present. The muscle is absent in orthopterans (see also Snodgrass 1935) and hymenopterans (see also Vilhelmsen 2001), also in *Anabittacus*, *Rhyacophila*, *Heterobathmia* and *Cydia* (see Kuznetzov & Stekolnikov 2001).

68. Muscle 38 *dvVIII02*, presence: (0) absent; (1) present. The muscle is absent in *Archaeopsylla*, *Boreus*, *Anabittacus*, *Panorpa*, *Aedes*, *Toxophora* (see Mühlenberg 1971), and in the amphiesmenopteran representatives except *Agathiphaga* (for the situation in *Cydia* see also Kuznetzov & Stekolnikov 2001).

69. Muscle 40 *dvIX01*, presence: (0) absent; (1) present. The muscle is absent in *Archaeopsylla*, *Boreus*, *Anabittacus*, *Panorpa*, *Tipula*, *Aedes*, *Toxophora* (see Mühlenberg 1971), *Ulmerochorema*, and in the lepidopterans except *Agathiphaga* (see also Kuznetzov & Stekolnikov 2001).

70. Muscle 40 *dvIX01*, general shape: (0) compact muscle; (1) thin layer of fibres. The muscle is a thin layer of fibres in *Nannochorista*, *Fansipangana*, *Rhyacophila* and *Agathiphaga.*

71. Muscle 41 *dvIX02*, presence: (0) absent; (1) present. Absent in *Archaeopsylla*, *Boreus*, *Anabittacus*, *Panorpa*, *Tipula*, and all examined representatives of Amphiesmenoptera (for the situation in *Cydia* see Kuznetzov & Stekolnikov 2001).

72. Muscle 42 *dvIX03*, presence: (0) absent; (1) present. Only present in the orthopteran outgroup taxa (see also Snodgrass 1935).

73. Muscle 43 *dvIX04*, presence: (0) absent; (1) present. Only present in the orthopteran outgroup taxa (see also Snodgrass 1935).

74. Muscle 48 *tVIII01*, presence: (0) absent; (1) present. Present in *Nannochorista*, *Boreus*, *Anabittacus*, *Limonia*, *Tipula* and *Toxophora* (see Mühlenberg 1971).

75. Muscle 48 *tVIII01*, shape: (0) 1 minute bundle; (1) 1 large bundle; (2) 2 large bundles. Extremely small single bundle in *Nannochorista* and *Anabittacus*. Represented by one large bundle in *Boreus*, *Tipula* and *Toxophora* (Mühlenberg 1971), and composed of 2 very large bundles in *Limonia.*

76. Muscle 50 *tIX01*, presence: (0) absent; (1) present. Present in *Osmylus* (see Feuerstein 2008), *Archaeopsylla* and *Aedes.*

77. Muscle 51 *tX01*, presence: (0) absent; (1) present. Present in *Limonia*, *Aedes* and *Micropterix.*

78. Muscle 52 *tX02*, presence: (0) absent; (1) present. Present in *Aedes*, *Toxophora* (Mühlenberg 1971), *Micropterix* and *Heterobathmia*.

79. Muscle 53 *tXI01*, presence: (0) absent; (1) present. Present in *Limonia* and *Tipula*.

80. Muscle 55 *seVIII-gc01*, presence: (0)absent; (1) present. Present in *Archaeopsylla*, *Nannochorista*, *Anabittacus*, and in all examined representatives of Diptera (see also Mühlenberg 1971) and Amphiesmenoptera (except for *Micropterix*) (see also Kuznetzov & Stekolnikov 2001).

81. Muscle 55 *seVIII-gc01*, number of bundles: (0) 1 bundle; (1) 2 bundles. Composed of 2 distinct bundles in *Limonia* and *Tipula*.

82. Muscle 56 *seVIII-gc02*, presence: (0) absent; (1) present. Present in *Agathiphaga*, *Heterobathmia* and *Eriocrania*.

83. Muscle 56 *seVIII-gc02*, number of bundles: (0) 1 bundle; (1) 2 bundles. Composed of 2 distinct bundles in *Heterobathmia* and *Eriocrania*..

84. Muscle 58 *seIX-gc01*, presence: (0) absent; (1) present. Absent in the orthopteran and hymenopteran outgroup taxa, and also also in *Boreus*, the dipteran taxa examined (see also Mühlenberg 1971), and in *Agathiphaga* and *Eriocrania*.

85. Muscle 58 *seIX-gc01*, site of origin: (0) regular, on tergum IX; (1) shifted to posterior apophysis. Shifted to the posterior apophysis in *Fansipangana* and *Rhyacophila*.

86. Muscle 59 *seIX-gc02*, presence: (0) absent; (1) present. Present in *Archaeopsylla*, *Nannochorista*, *Anabittacus* and *Panorpa*.

87. Muscle 62 *intra-gc01*, presence: (0) absent; (1) present. Present in *Archaeopsylla* and *Anabittacus*.

88. Muscle 68 *add01*, presence: (0) absent; (1) present. Present in the orthopteran (see also Snodgrass 1935) and hymenopteran outgroup taxa (see also Vilhelmsen 2001).

89. Muscle 69 *add02*, presence: (0) absent; (1) present. Present in the hymenopteran taxa examined (see also Vilhelmsen 2001).

90. Muscle 70 *add03*, presence: (0) absent; (1) present. Present in the hymenopteran taxa (see also Vilhelmsen 2001).

91. Muscle 71 *add04*, presence: (0) absent; (1) present. Present in *Aedes* and *Toxophora* (Mühlenberg1971).

92. Genital chamber, fusion with rectum (gc): (0) not fused, openings of chamber and rectum clearly separated; (1) fused, cloaca developed. A cloaca is developed in the amphiesmenopteran taxa examined (see also Kristensen 2003b).

93. Genital chamber (gc), muscularis: (0) simple, few layers of mainly longitudinal fibres; (1) simple, few layers of mainly circular fibres; (2) complex, composed of (inner) circular and (outer) longitudinal fibre layers. A simple muscularis consisting mainly of longitudinal fibres is found in *Osmylus*, *Nannochorista* and *Anabittacus*. The simple muscularis mainly consists of circular fibres in the trichopterans *Fansipangana* and *Rhyacophila* (in *Ulmerochorema* a muscularis was not found). In the examined members of

Lepidoptera the muscularis of the genital chamber is more complex, composed of multiple circular and longitudinal layers of fibres.

94. Genital chamber (gc), spermathecal process (prc): (0) process absent; (1) process present; (2) process present, with a pair of wing-like anterior apodemes. A sclerotized process with the opening of the spermathecal duct on its apex is developed in the trichopterans examined (see also Nielsen 1980) and in *Micropterix*. A structure superficially similar to these spermathecal processes was found in *Panorpa* (see Grell 1942). As it clearly differs structurally it was coded as a separate character state.

95. Spermathecal duct (spd), presence: (0) absent; (1) present. Absent in the hymenopteran outgroup taxa. The spermatheca is here a simple cylindrical or hemisphaerical evagination of the roof of the genital chamber (see Togashi 1970).

96. Spermathecal duct (spd), with "2-compartment-section"?: (0) no; (1) yes, precursor-structure developed; (2) yes, "2-compartment-section" fully developed. A duct section with a certain content of mesocuticle in its intima is present in the representatives of Lepidoptera, with the exception of *Micropterix* (see also Kristensen 2003b). The fully developed "2-compartment-section" with a content of mesocuticle in the intima and with a conspicuous separation of the duct lumen into 2 compartments is found in *Heterobathmia* and Lepidoptera-Glossata (*Eriocrania*, *Cydia*). Scored as inapplicable for the taxa without spermathecal duct.

97. Spermathecal duct (spd), muscularis: (0) no muscularis present; (1) muscularis present, mainly longitudinal fibres; (2) muscularis present, mainly circular fibres. A muscularis mainly consisting of longitudinal fibres is present in *Nannochorista*, *Anabittacus* and *Limonia*. The muscularis is mainly composed of circular fibres in the representatives of Amphiesmenoptera. The character is scored as inapplicable for taxa without spermathecal duct.

98. Spermatheca (sp), distinct spermathecal gland (spg): (0) gland absent; (1) gland present. A distinct spermathecal gland is present in the representatives of Amphiesmenoptera (see also Kristensen 2003b, Nielsen 1980). The epithelium of the spermatheca usually has a glandular function in the other groups under consideration.

99. Bursa copulatrix (bc), presence : (0) absent; (1) present. A well-developed bursa copulatrix, connected with the genital chamber by a distinct ductus bursae, is present in all examined representatives of Amphiesmenoptera (see also Kristensen 2003b, Nielsen 1980).

100. Bursa copulatrix (bc), size: (0) moderately sized; (1) enlarged, balloon-like. The bursa is conspicuously enlarged in the representatives of Lepidoptera. The character is scored as inapplicable for the taxa without a well developed bursa copulatrix.

101. Accessory glands (ag), degree of fusion: (0) glands of right and left body half fully separated, opening with 2 separated ducts; (1) posterior regions of glands fused, opening with a common duct; (2) no separated parts of right and left body half distinguishable, common gland duct. In the hymenopteran outgroup taxa the glands of both body halves are fully separated and open into the genital chamber with 2 separate ducts (into a bulb-like or hemisphaerical evagination of the roof of the genital chamber ["reservoir"], see Togashi 1970) and Diptera (see also Frommer 1960). A seemingly unpaired gland is present in *Osmylus* and *Eriocrania*.

102. Accessory glands (ag), shape and size: (0) tube-like, sometimes coiled, and mostly moderately sized; (1) rather compact and moderate in size; (2) composed of a couple of tubules which fuse some distance before the gland leads into the gland duct; (3) strongly enlarged, balloon-like; (4) enlarged, tube-like. Tube-like in the hymenopteran outgroup taxa (see Togashi 1970), *Nannochorista*, *Panorpa* (see Grell 1942), *Limonia* (conspicuously enlarged) and *Fansipangana*. Rather compact in *Osmylus*, *Boreus* (see Steiner 1936), *Tipula*, *Aedes* (see Brelje 1924, Christophers 1960), *Toxophora* (see Mühlenberg 1971) and *Eriocrania*. The glands are composed of several small tubules in *Heterobathmia*, and conspicuously enlarged and balloon-shaped in *Rhyacophila*, *Ulmerochorema*, *Micropterix* and *Agathiphaga*.

Apart from these morphological characters, the substrates of egg deposition were coded.

209. Oviposition in solid soil: (0) absent; (1) present. Oviposition into solid, rather dry soils takes place in Orthoptera and *Panorpa*.

210. Oviposition in wet soil and / or rotten plant material: (0) absent; (1) present. Oviposition into wet and therefore soft soils and / or rotten plant materials (often near water sides) takes place in *Nannochorista* and Diptera-Tipulomorpha.

211. Oviposition between bank vegetation / into water: (0) absent; (1) present. Oviposition into bank vegetation or in the water is observed in *Osmylus* and the trichopteran representatives.

212. Oviposition in mosses or liverwort masses: (0) absent; (1) present. Oviposition into moss or liverwort masses is reported from *Boreus* and *Micropterix*.

213. Oviposition between the cone-scales of Kauri-pines: (0) absent; (1) present. Oviposition between araucariacean cone-scales is present only in *Agathiphaga*.

214. Insertion of the egg into plant tissue: (0) absent; (1) present. The endophytic mode of oviposition is realized in Hymenoptera and in *Eriocrania*.

215. Egg deposition on plant surfaces: (0) absent; (1) present. The eggs are placed on plant surfaces in *Heterobathmia* and *Cydia*.

216. Eggs scattered randomly: (0) absent; (1) present. The eggs are scattered randomly in *Archaeopsylla* and *Anabittacus*.

For characters not related to the female postabdomen and oviposition (characters 103 – 205 in the matrix) see **Appendix B**, for the complete matrix and all trees yielded in the analysis the electronic supplement.

6. Results of the cladistic analysis

Characters 1 – 102 (structures of the female postabdomen and genitalia) were analyzed together with 106 characters concerning other structural complexes and developmental stages (103 – 108; see Appendix C: Additional characters used in the phylogenetic analysis) and 8 characters related to the modes and substrates of oviposition (109 – 116).
The cladistic analysis of the total data set yielded 7 alternative cladograms with the minimal number of 537 steps (CI = 0,49; RI = 0,64). While the basal branching patterns of Mecopterida and within Amphiesmenoptera are robust and well supported, the basal nodes within Antliophora are weakly supported (Bremer support values 2 – 3) and collapse in the strict consensus (except Pistillifera and Diptera which always come out as monophyletic groups; Fig. 33A). However, only a single of the 7 most parsimonious trees was yielded in all analyses (also with artificial data sets), thus proposing a clade (Nannomecoptera + (Siphonaptera + Diptera)) (Fig. 33B-D; Bremer support, Bootstrap values and Jackknife values shown at the nodes). For other trees and the strict consensus see the electronic supplement. *Tettigonia* (Orthoptera: Tettigoniidae), *Xyela* (Hymenoptera: Xyelidae), *Tenthredo* (Hymenoptera: Tenthredinidae) and *Osmylus* (Neuroptera: Osmylidae) were included as outgroups.

Endopterygota: tergum XI distinctly shorter than preceeding tergal plates (10.1, fast optimization).
Hymenoptera (Bremer support: 14): proximal and distal part of the ventral sclerotization of segment VIII distinct, clearly separable (6.0), proximal and distal part of the ventral sclerotization of segment IX distinct, clearly separable (16.0), presence of muscle **35** *intraIX04* (65.1), muscle **69** *add02* present (89.1), muscle **70** *add03* present (90.1), spermathecal duct absent (95.0)
Osmylus, **Mecopterida** (Bremer support: 6): tergum VII unmodified, normally shaped (1.0), ventral sclerotization of segment VIII: no distinction of proximal and distal parts possible (6.2), tergum IX distinctly shorter than preceeding tergal plates (10.1, slow optimization), tergum IX without internal cuticular ridge near anterior margin (11.1), muscle **34** *intraIX03* absent (64.0), muscle **36** *dvVII01* composed of single fibres (66.1), muscle **37** *dvVIII01* present (67.1, slow optimization), muscle **58** *seIX-gc01* present (84.1), muscle **68** *add01* absent (88.0), posterior regions of accessory glands fused (101.1, fast optimization / slow optimization)

Mecopterida (Bremer support: 14): ventral sclerotization of segment VIII not markedly different in length from tergum VIII (7.0/1), no articulation or fusion of tergum IX with ventral sclerites of segments VIII or IX (12.0), ventral sclerotizations of segment IX fused in the ventromedian line (15.2), no visible separation of ventral sclerotizations of segment

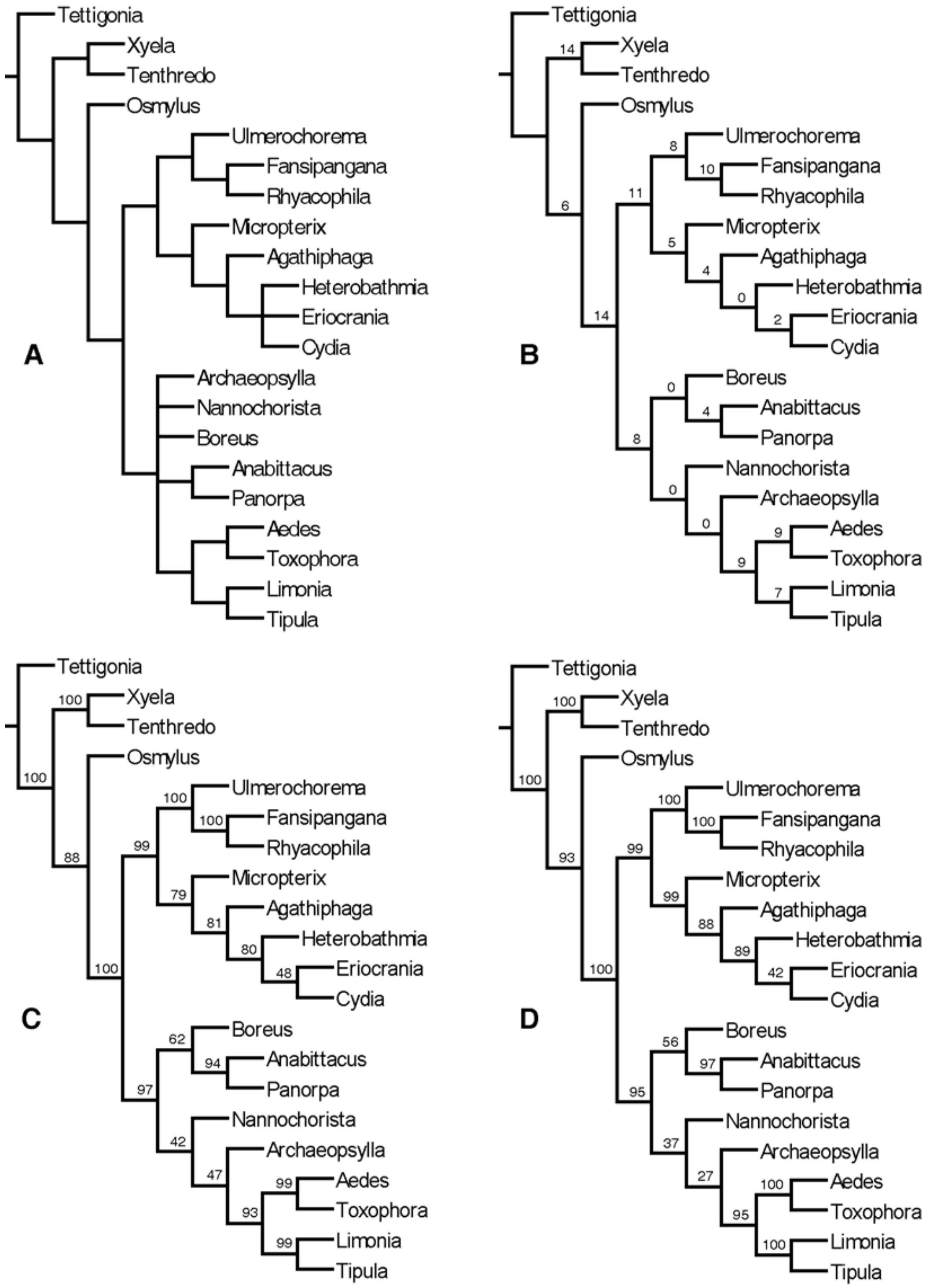

Fig. 33. Parsimony analysis of a data set of 216 morphological characters (see **chapter 5** of the present study). (A) strict consensus of 7 most parsimonious trees. (B-D) selected tree, support values shown at the nodes; (B) Bremer support values; (C) Bootstrap values; (D) Jackknife values. Note the basal position of Hymenoptera within Endopterygota, the monophyly of Mecopterida, Amphiesmenoptera and Antliophora, but also the weak support for basal splittings events within Antliophora (nodes collapse in the strict consensus).

IX into distinct proximal and distal part (16.2), ventral sclerotizations of segment IX not markedly longer than tergum IX (17.0), tergum X conspicuously shortened (20.1), ventral sclerotization of segment XI present (24.1, fast optimization), muscle **06** *isVII-VIII06* present (40.1, slow optimization), loss of muscle **07** *isVII-VIII07* (41.0), absence of muscle **38** *dvVIII02* (68.0), absence of muscle **40** *dvIX01* (69.0), muscle **40** *dvIX01* a thin layer of fibres (70.1, fast optimization), presence of muscle **55** *seVIII-gc01* (80.1), spermathecal duct with a muscularis composed of longitudinal fibres (97.1, fast optimization / slow optimization).

Amphiesmenoptera (Bremer support: 11): tergum IX distinctly longer than tergum VIII (10.2, fast optimization), posterior apophysis present, arising from the anterior margin of tergum IX (13.1), sclerotization of tergum X not closed dorso-medially, tergum present as a pair of small dorsal or dorso-lateral plates (19.2, fast optimization), fusion of genital chamber and rectum, cloaca (92.1), genital chamber with a simple muscularis, composed of a few layers of mainly circular fibres (93.1), spermathecal process developed (94.1, fast optimization), spermathecal duct with a muscularis composed of circular fibres (97.2), spermatheca with distinct spermathecal gland (98.1), well developed bursa copulatrix (99.1), accessory glands strongly enlarged, balloon-like (102.3).

Trichoptera (Bremer support: 8): no support from characters related to the female postabdomen and genital system.

Rhyacophilidae (Bremer support: 10): muscle **58** *seIX-gc01* originates on the posterior apophysis (85.1).

Lepidoptera (Bremer support: 5): genital/cloacal opening in subterminal position (29.2, fast optimization), genital chamber with complex muscularis, composed of circular and longitudinal fibre layers (93.2), bursa copulatrix enlarged, balloon-like (100.1, fast optimization).

Agathiphaga, ***Heterobathmia***, **Lepidoptera-Glossata** (Bremer support: 4): oviscapt developed (28.1, fast optimization), presence of muscle **12** *isVII-VIII12* (46.1, fast optimization), muscle **36** *dvVII01* composed of 3 compact bundles (66.2, fast optimization), muscle **56** *seVIII-gc02* present (82.1), spermathecal duct with "2-compartment-section" or precursor-structure (96.1).

Heterobathmia, **Lepidoptera-Glossata** (Bremer support: 0): muscle **56** *seVIII-gc02* composed of 2 distinct bundles (83.1, fast optimization / slow optimization), spermathecal duct with the "2-compartment-section" fully developed (96.2), accessory glands composed of a couple of tubules (102.2).

Lepidoptera-Glossata (Bremer support: 2): insertion site of muscle **14** *isVIII-IX01* shifted to apex of posterior apophysis (49.1).

Antliophora (Bremer support: 8): sclerotizations of segment X fully fused, forming a closed sclerite-ring (21.1, fast optimization), presence of muscle **29** *isX-XI02* (63.1, fast optimization), muscle **48** *tVIII01* present (74.1), presence of muscle **59** *seIX-gc02* (86.1, fast optimization).

Neomecoptera, **Pistillifera** (Bremer support: 0): no support from characters related to the female postabdomen and genital system.

Pistillifera (Bremer support: 4): no support from characters related to the female postabdomen and genital system.

Nannochorista, ***Archaeopsylla***, **Diptera** (Bremer support: 0): tergum X normally shaped, unmodified (19.0, fast optimization)

Archaeopsylla, **Diptera** (Bremer support: 0): cerci strongly elongated (27.2, fast optimization)

Diptera (Bremer support: 9): no support from characters related to the female postabdomen and genital system.

Diptera-Tipulomorpha (Bremer support: 7): cerci strongly elongated (27.2, slow optimization), presence of muscle **53** *tXI01* (79.1), muscle **55** *seVIII-gc01* composed of 2 distinct bundles (81.1).

Aedes, ***Toxophora*** (Bremer support: 9): additional sclerotized plate below genital opening (30.1), presence of muscle **71** *add04* (91.1).

7. Discussion

A typical and complete orthopteroid ovipositor is present in Ensifera (Orthoptera), comprising the first valvifers and the first valvulae (***vsVIII-d***, ***vsVIII-p***) on segment VIII, the second valvifers, second valvulae, and the third valvulae on segment IX (***vsIX-p(1)***, ***vsIX-d(1)***, ***vsIX-d(2)***). Additionally, two sclerites are present connecting the second valvifers of both body halves, the anterior and posterior intervalvulae (***vsIX-p(2)***, ***vsIX-p(3)***).

The detailed investigation of the postabdominal musculature allows the hitherto highly problematic homologization of ventral sclerites of the female genital segments of mecopterid taxa with the elements of the orthopteroid ovipositor. Two muscles are particularly important in this context. The intersegmental muscle **05** *isVII-VIII05* can be used as a landmark for the genital appendages of segment VIII, the dorsoventral muscle **41** *dvIX02* for the appendages of segment IX or their derivatives or vestiges. Muscle **05** originates on the anterior half of sternum VII and inserts on the anterior margin of the genital appendage of segment VIII. The origin of muscle **41** is near the anterior margin of tergum IX in paralateral position, with the site of insertion always on the genital appendage of segment IX (***vsIX***). This muscle is lost in all representatives of Amphiesmenoptera – and ventral sclerotized elements that can be ascribed to segment IX with certainty are not present in this group (fusion of the terminal segments; clear segmental limits are not traceable).

Evidence from musculature shows that the ventral sclerites present on segments VIII and IX in Mecopterida are derived from elements of the genuine orthopteroid ovipositor. True sternal sclerotizations on segments VIII and IX are absent in mecopterid females.

A sistergroup relationship between Hymenoptera and Mecopterida was discussed by Hennig (1969) and this was the prevalent hypothesis for several decades (see e.g., Kristensen 1999; Beutel & Gorb 2001; Castro & Dowton 2005; Grimaldi & Engel 2005). However, a basal position of this megadiverse order and all the remaining endopterygote lineages was already suggested by Ross (1965), and later by Rasnitsyn & Quicke (2002) and Kukalová-Peck & Lawrence (2004). Recent investigations of large morphological and molecular data sets confirm this placement of Hymenoptera (Hünefeld & Kjer unpubl. Results, see Fig. 1; Beutel pers. comm.; Misof pers. comm.), and this is also supported by the preliminary results of the cladistic analyses carried out with a limited endopterygote taxon sampling in the framework of this study (Fig. 33; see also **chapter 6.**).

In the following discussion, it is assumed that Hymenoptera are indeed a basal lineage of Endopterygota, displaying among other ancestral character states (e.g., high number of Malpighian tubules, well developed glossae and paraglossae) uniquely plesiomorphic features of the female postabdomen. One of the ground-plan apomorphies of Ectognatha (Insecta s. str.) is the orthopteroid ovipositor (e.g., Matsuda 1972), and basal hymenopteran lineages ("Symphyta": Xyelidae, Tenthredinidae and related groups) are the only endopterygotes where it is preserved in its typical form (e.g., Vilhelmsen 2001). Conspicuous transformations of the female postabdomen took place with the splitting event dividing Endopterygota into Hymenoptera on one hand and the (Mecopterida + (Coleoptera + Neuropterida) [+Strepsiptera]) clade on the other. They include reductions, fusions, and losses or changes of function of the primary ovipositor elements. On segment IX, the second valvulae (= gonapophyses IX) are totally lost and the third valvulae (= gonostyli IX) are at most present as minute vestiges (e.g., Mickoleit 1975). A neo-formation at the base of the clade is an intersegmental muscle (**06** *isVII-VIII06*), which inserts on the genital appendage of segment VIII. This was not recovered as apomorphy in the analyses presented here, as the muscle is present throughout Mecopterida, but absent in *Osmylus*. However, its presence in Raphidioptera (Achtelig 1977, Matsuda 1957) suggests that it belongs to the ground plan of Endopterygota excl. Hymenoptera, with parallel loss in Osmylidae, and possibly in other groups of Neuroptera.

In the context of structural modifications of the female postabdomen, especially the ovipositor, the primary mode and substrate where eggs are deposited play a crucial role. However, an unambiguos assessment of the groundplan condition in Endopterygota is not possible. Basal hymenopterans insert their eggs with the well developed orthopteroid ovipositor into living plant tissues. This is also common in non-endopterygote insects with a well-developed ovipositor, but oviposition into soil as an alternative is also reported from many representatives of the same groups (Orthoptera, Acercaria [= Paraneoptera]; e.g., Deckert & Göllner-Scheiding 2003, Groll & Günther 2003, Strümpel 2003). Therefore it remains ambiguous whether egg insertion in plant tissues is a plesiomorphic ground-plan feature of Endopterygota (retained in Hymenoptera) or an autapomorphy of Hymenoptera. In the (Coleoptera + Neuropterida) clade, oviposition takes place primarily under bark in Coleoptera (Archostemata) and Raphidioptera, but on vegetation in moist or even semi-aquatic habitats in Neuroptera and Megaloptera. As a consequence the reductions of ovipositor-elements are more advanced in the latter two groups of Neuropterida (see Mickoleit 1973). Oviposition in soil is found in several groups of Endopterygota, such as for instance in Carabidae and Scarabaeoidea (Coleoptera), and Mecoptera (major part).

The results of the cladistic analysis clearly confirm the monophyly of **Mecopterida**, which was hitherto only supported by weak evidence (e.g., veins A1 and CuP of hind wing partly fused; see e.g., Kristensen 1975, 1999). A conspicuous and characteristic feature very distinctly different from the neuropterid and coleopteran condition is that the postabdominal segments (VIII-XI) are tapering towards the posterior end and are therefore retractible in a telescope-like manner (see also Mickoleit 1973, 1975). Separate distal parts of the genital appendages of segment VIII (= first valvulae) are no longer discernable in Mecopterida. The entire ventral sclerotizations of segement VIII are therefore shortened; the remaining proximal parts of the genital appendages VIII are not directly involved in the oviposition. The strongly prolonged (and functional) ventral sclerotizations of segment VIII of *Boreus* (Mecoptera, Boreidae) and the tipulomorph dipterans have very likely evolved secondarily, considering the isolated systematic position of these groups, and therefore represent character reversals. While the genital appendages of segment IX are still longer than tergum IX in Raphidioptera and some Neuroptera, they are generally shortened in Mecopterida (see Aspöck & Aspöck 2008, Ferris & Pennebaker 1939, Matsuda 1957, Mickoleit 1973). A subdivision of the ventral sclerotisations of segment IX is not recognisable any more. Furthermore, the appendages of segment IX are not fused or articulated with tergum IX as it has to be assumed for the endopterygote ground-plan. An exception is found in *Anabittacus* (Pistillifera-Bittacidae), but considering the systematic position of this taxon, the fusion is very likely a genus-specific autapomorphic trait. In Orthoptera and Hymenoptera, the elongated anteroventral edges of tergum IX articulate with the appendages of segment-VIII (see also Snodgrass 1935), but with the appendages of segment IX in the Coleoptera-Neuropterida-lineage (see Aspöck & Aspöck 2008, Mickoleit 1975). Tergum X is conspicuously shortened in Mecopterida compared to the preceeding tergal plates. Only in *Boreus* and tipulomorph dipterans the entire segment X is secondarily elongated and forms a functional, secondary egg-depositioning device together with segment IX, the elongated genital appendages of segment VIII (***vsVIII***) and the cerci. This is clearly an autapomorphic condition in both cases as a close relationship between both taxa is extremely unlikely (e.g., strongly supported monophyly of Diptera). More potential autapomorphies of Mecopterida are the acquisition of a muscle spanning between the ventral sclerotizations of segment VIII and the genital chamber (**55**), the losses of an intersegmental muscle between segments VII and VIII (**07**) and two dorsoventral muscles (**38** and **40**), and a muscularis composed of longitudinal fibres around the spermathecal duct. Considering all this,

this large lineage of endopterygote insects appears strongly supported by characters of the female postabdomen. Among 11 apomorphic features of the female postabdomen, 9 turned out as unambiguous autapomorphies in the cladistic analysis (see **chapter 6**).

Nannomecoptera is very likely closest to the ancestral mecopterid condition. It was already pointed out by Evans (1942), that "…the female genitalia of *Nannochorista* are more complete and less specialized than those of […] other Mecoptera…". This statement can be extended onto the whole Mecopterida. The largely uniform nannomecopteran female postabdomen (Evans 1942, Mickoleit 1975) is telescoping and paired genital appendages are present on segments VIII and IX (***vsVIII***, ***vsIX***). They are simply-shaped, not fused in the ventro-median line, and are not directly involved in the oviposition. Moreover, most of the postabdominal muscles present in the outgroups are retained. Unfortunately, no informations on the egg depositing substrates are available. The larvae are aquatic, and therefore it appears likely that oviposition takes place in moist soil, or rotten plant materials (or possibly moss) in the riparian zone (oviposition in similar substrates is documented from other groups with aquatic and semi-aquatic larvae: Limoniidae part., Tipulidae part.). In any case, the telescoping postabdomen is well suited for oviposition in soft, moist substrates, and in the following it is assumed as a working hypothesis that such egg-laying habits are ancestral for Mecopterida. This is in agreement with Kristensen´s statement that the larvae at the origin of Mecopterida might be best characterized as "soil animals" (Kristensen 1997).

The monophyly of **Amphiesmenoptera**, comprising Trichoptera and the megadiverse Lepidoptera is exceptionally well supported by morphological and molecular evidence (see e.g., Hennig 1969; Kristensen 1999; Wheeler et al. 2001; Hünefeld & Kjer, unpublished). The present study adds a remarkable number of new autapomorphies of the female postabdomen. As mentioned above the female posterior segments are telescoping in the ground plan of Mecopterida, and this is maintained in the two amphiesmenopteran orders. Striking neoformations are 2 pairs of rod-like apophyses, an anterior one arising from the anterior margin of segment VIII (very likely from the ventral sclerotization of segment VIII), and a posterior one from the terminal unit, i.e. the tergum IX- region (e.g., see Kristensen 2003b). Closely linked to this is another apomorphic trait: the extrusion of the terminal unit is now effected by muscle force, and not by hemolymph pressure as it is the case in Antliophora, and in the mecopterid groundplan. Three of the muscles effecting extrusion of the terminal unit in Amphiesmenoptera (**01**, **14**, **15**) are also generally present in non-amphiesmenopteran insects. However, their insertion sites are shifted far anterad to the apical parts of the apophyses in females of Trichoptera and Lepidoptera. Four other muscles involved in the extrusion (**08**, **10**, **17**, **23**) are apparently neo-formations and their presence therefore autapomorphic for Amphiesmenoptera. Further autapomorphies of the lineage are the dorso-median separation of the tergum X- sclerotization into a pair of dorso-lateral plates (see Kristensen & Nielsen 1979, Nielsen 1980, Schmid 1989), the fusion of the posteriormost region of the genital chamber with the rectum (cloaca), a simple muscularis surrounding the genital chamber (few layers of mainly circular fibres), a conspicuous sclerotized papilla arising from the roof of the genital chamber with the opening of the spermathecal duct on its tip (spermathecal process), a spermathecal duct with a muscularis composed of circular fibres, a distinct spermathecal gland (in the other taxa under comparison the spermathecal epithelium itself has a glandular function), a well developed bursa copulatrix separated from the genital chamber by a distinct ductus bursae, and strongly enlarged, balloon-like accessory glands. In many trichopterans, the females embed the eggs into a mucose substance (spumalin), which protects the eggs and serves as nutrition for the newly hatched larvae (see Mey 2003). Spumalin is produced in the accessory glands. It can be hypothetized that the increase in gland-size is linked to the need for large amounts of mucose secretion products at the base of Amphiesmenoptera.

The monophyly of **Trichoptera** is supported by the complete data set presented here (e.g., rostrum and reduced paired mouthparts of adults, terminal abdominal hooks in larvae), but no apomorphies related to the female postabdomen turned out in the analysis. The entire complex of autapomorphies described above for Mecopterida is retained in the rhyacophilid representatives (and throughout many other trichopteran families; e.g., Nielsen 1980). In 1996, an enigmatic caddisfly was described from the Fan-Si-Pan mountain area in North Vietnam: *Fansipangana vernalis* (Mey 1996). In the brief original decription it is pointed out that *Fansipangana* represents an "old evolutionary line" (M-cell of the forewing closed, male genitalia extremely simple; Mey 1996). Furthermore, Mey (1996) described 3 pairs of apophyses on the female postabdomen, a condition that is known only from Lepidoptera-Agathiphagidae. The postabdomen of a female of the paratype-series of *Fansipangana vernalis* was examined in great detail and reconstructed 3-dimensionally in the framework of the present study. The presence of a third apophyses pair must be rejected as an erroneous observation; the female postabdomen of *Fansipangana* is overall similar to the postabdomen of *Rhyacophila*, with only 2 pairs of apophyses, and an almost identical muscle equipment. In agreement with the preliminary assignment of *Fansipangana* to Rhyacophilidae by Mey (1996) both taxa group together in the analysis presented here. However, the trichopteran taxon sampling is too limited for a reliable clarification of the position of the genus.

Features related to the female postabdomen that support the monophyly of **Lepidoptera** are a complex muscularis around the genital chamber (multiple circular and longitudinal fibre layers), and a strongly enlarged bursa copulatrix, where compounds of the spermatophore are stored after mating. Whereas the monophly of Lepidoptera is no matter of discussion, controversies prevail concerning the question of the basal splitting events within the order. Micropterigidae and Agathiphagidae both have been proposed as the basalmost lineage of Lepidoptera, and both phylogenetic hypotheses require *ad hoc* explanations for a suite of homoplasies (see Kristensen 1984, 1998, 2003a, Kristensen & Nielsen 1998). The sister-group relationship between Agathiphagidae and all other Lepidoptera was favoured by Shields (1993), but the time-honoured option of a sister-group relationship between Micropterigidae and all other groups is better supported by morphological data, and is also suggested by the available molecular evidence (Hünefeld & Kjer, unpublished; Kristensen 1998, 2003a, 2003b; Wiegmann et al. 2002; Kristensen et al. 2007). In the present analysis a clade **(*Agathiphaga* +**

(*Heterobathmia* + Lepidoptera-Glossata)) is clearly supported, thus rendering Micropterigidae basal within the order. The strongest support for this grouping probably comes from a specific condition of the spermathecal duct: a clearly discerneable duct region with a certain content of mesocuticle and differentiations in cell morphology is present in all Lepidoptera except Micropterigidae (Hünefeld & Kristensen, in press.). Other possible synapomorphies are neoformations of an intersegmental muscle (**12**) and a muscle inserting on the genital chamber (**56**), and loss of the spermathecal process (present throughout Trichoptera and in Micropterigidae). Furthermore, it is assumed here, that acquisition of a second pair of anterior apophyses (from tergum VIII) is a neoformation at the base of this clade. Monophyly of **(*Heterobathmia* + Lepidoptera-Glossata)** is strongly supported by presence of a fully developed "2-compartment- section" of the spermathecal duct (e.g.; Hünefeld & Kristensen, in press.; Kristensen 2003b). Besides this, the accessory glands are not longer balloon-like but composed of a couple of tubules, and muscle **56** is split into 2 distinct bundles. **Lepidoptera-Glossata** are supported by a single apomorphic trait related to the female postabdomen: the insertion site of the intersegmental muscle **14** is shifted to the apex of the posterior apophysis. Another possible synapomorphy might be fusion of the ipsilateral dorsal and ventral anterior apophyses.

It is not possible to reconstruct the ovipositing habits in the ground plan of Amphiesmenoptera due to the secondarily acquired aquatic habits of trichopteran larvae and high variation in the basal lepidopteran lineages. However, considering the structural features and functional peculiarities, notably the advanced extrusion mechanism, it appears likely that females of the common ancestor of Trichoptera and Lepidoptera deposited their eggs in crevices, rather than in moist substrates. Correlated with the aquatic habits of the larvae, Trichoptera have adopted oviposition in a more or less moist or aquatic environment, between floated parts of the riparian vegetation or into the free water. This did apparently not affect the structures involved in the process. They largely retained the presumably ancestral amphiesmenopteran condition of the postabdomen.

Females of Micropterigidae, the most basal lineage of Lepidoptera, oviposit into liverwort masses or rotten plant materials (Kristensen 1997). Remarkably, the postabdomen of females of this family is highly modified, completely devoid of apophyses and associated muscles present in the amphiesmenopteran groundplan. Like in Antliophora, it is extruded by hemolymph pressure. The analyses clearly confirm, that this is by no means an ancestral condition, but a secondarily acquired autapomorphic trait of the family. It is conceivable that this is an adaptation to the easy-to-penetrate substrates, i.e. liver mosses, which are used by these moths for oviposition.

In Agathiphagidae, probably the second branch in Lepidoptera, an exceptional situation with three pairs of apophyses is present and the terminal unit is telescoping to a higher degree than in most groups of Lepidoptera. This can be best explained as an adaptation to oviposition directly on the seeds deep between the crevices formed by the cone-scales of Kauri-pines (Araucariaceae: *Agathis* spp.) (see Kristensen 1997). The specific deposition site may be autapomorphic for the family. However, the ovipositon in crevices as such may be ancestral as pointed out above. The possession of three pairs of apophyses renders Agathiphagidae a group of particular interest for clarification of the ground-plan condition in Lepidoptera and even Amphiesmenoptera (see also **4.3.**).

Heterobathmiidae are the first lepidopteran family with the larvae feeding on eudicot angiosperms (Fagaceae: deciduous *Nothofagus* spp.) (Kristensen 1998, Kristensen & Nielsen 1979). In the following, angiosperm-feeding will be established as the predominant life-style of the larvae of all "higher Lepidoptera". The heterobathmiid postabdomen displays a series of autapomorphies of the group. It lacks the anterior apophyses, and the posterior ones are reduced to various degrees within the family. Heterobathmiid females place their eggs exposed on the leaf surfaces of the larval host plants; retractability of the terminal unit is therefore not necessary. Instead the postabdominal segments carry out nodding movements while tipping the eggs onto the leaf surfaces. Muscle **13** induces the nodding, while muscle **23** is the antagonist (Hünefeld, in prep.).

In the basal families within Lepidoptera-Glossata, the eggs are inserted into living angiosperm tissue by use of an "oviscapt saw" (formed by the serrated, sclerotized lateral edges of the posteriormost section of the terminal unit) (e.g., Kristensen 2003b). This is a similar egg laying mode as it is observed close to the base of Endopterygota, in basal Hymenoptera. However, considering the subordinate systematic position of Glossata within Lepidoptera, it is evident that this habit has evolved secondarily. The construction principles of the female postabdomen within Lepidoptera-Ditrysia (which comprise 99% of the extant Lepidoptera) vary only in minor features (e.g., Dugdale 1974, Kristensen 2003b, Mutuura 1972), and the mode of oviposition (on plant surfaces) is maintained in most groups. The extreme diversification of this group was probably correlated with the rapid evolution of eudicot angiosperms (see also Kristensen 1997).

Summarizing, the habits of ovipositon are variable throughout the basal lineages of Amphiesmenoptera, but more conservative within Trichoptera and Lepidoptera-Ditrysia.

Antliophora (e.g., Hennig 1969, Kristensen 1999, Wheeler et al. 2001), i.e. a clade comprising the three traditional orders Mecoptera, Siphonaptera and Diptera, were introduced by Hennig (1969), and named after the most conspicuous presumptive apomorphy, the sperm pump of males (Antliophora = "pump bearers"). The support for the monophyly was substantially weakened when it turned out that the sperm pump had at least evolved two times independently and is completely absent in Boreidae (Hünefeld & Beutel 2005, Mickoleit 2009). In the present study, the monophyly of Antliophora is supported by a single unambiguous apomorphy of the female postabdomen, the neo-formation of a transverse muscle spanning between the genital appendages of segment VIII (**48**). Its absence in some antliophoran taxa is likely due to secondary loss. Other possible autapomorphies (all accelerated optimization) are the acquisition of muscles **29** and **59**, and a ring-like fusion of the sclerotizations of segment X. Absence of ventral sclerotizations on segment X in basal groups of Diptera (Limoniidae, Culicidae), in Siphonaptera, and in two non-related groups of the traditional Mecoptera

(Bittacidae, Boreidae) suggest that this derived condition may have evolved several times independently. The alternative interpretation would imply several reversals.

The Mecoptera in the traditional sense, i.e. including Neomecoptera (=Boreidae) and Nannomecoptera (=Nannochoristidae) are not supported as a clade by characters presented here, which is in agreement with other studies suggesting the non-monophyly of the group (e.g., Whiting 2002; Beutel & Baum 2008). **Pistillifera**, which are strongly supported by a specific type of the male sperm pump (Hünefeld & Beutel 2005, Mickoleit 2009, Willmann 1981) and also by the complete data set analysed here, are not characterised by autapomorphies of the female postabdomen. Within Pistillifera, paired and unsegmented genital appendages of segments VIII and IX, as they are observed in *Nannochorista*, are widespread. In Panorpidae the ventral sclerites of both body halves are fused, forming plate-like sclerotizations that cover the ventral regions of segments VIII and IX (e.g., Ferris & Rees 1939, Grell 1942, Mickoleit 1975). In Bittacidae, which possibly might represent the most basal lineage within Pistillifera (Beutel & Friedrich, subm. for publ; see also Willmann 1989), the situation is more complicated. In most bittacid genera the genital appendages of segment VIII are clearly separated along the ventromedian line (Mickoleit 1975). In *Thyridates chilensis* these sclerotized elements of both body halves can be completely separated, or even fused ventro-medially over more than half of their lengths (Willmann 1982). Within Bittacidae, ventro-medially fused appendages IX are only reported from *Anabittacus iridipennis*, which possibly represents the most basal species within the family (see Byers 1965, Penny 1975, Willmann 1981, 1982).

In contrast to recent hypotheses suggesting a sistergroup relationship between Neomecoptera and Siphonaptera, the present analyses yielded a clade comprising **Neomecoptera and Pistillifera**. However, like in the case of Pistillifera, autapomorphies of the female postabdomen were not recovered.

A clade comprising ***Nannochorista*, *Archaeopsylla*** and **Diptera**, in agreement with Beutel & Baum (2008), is recovered in some of the minimum length trees obtained in the analyses carried out in this study. It is supported by 7 potential autapomorphies, all of these unrelated to the female postabdomen. In alternative trees, a sistergroup relationship between **Siphonaptera (*Archaeopsylla*)** and **Diptera**, as suggested in earlier studies (e.g., Hennig 1953), is supported only by 1 unambiguous autapomorphy (absence of larval legs). A derived feature shared by Siphonaptera and Diptera, the loss of an intersegmental muscle (**04**), was not recovered as a synapomorphy in the analysis (but see Tab. 4 for character distribution). The monophyly of **Diptera** is undisputed. It was clearly confirmed in the analyses, but not by unambiguous autapomorphies of the female postabdomen. However, the character state distribution suggests that losses of muscles **58** and **59** are likely autapomorphies of the order (see Tab. 4). A monophylum **(*Aedes* + *Toxophora*)** obtained in the analyses would be conform with a basal position of Tipulomorpha within Diptera (e.g., Hennig 1973, Sinclair 1992, Wood & Borkent 1989, Wood et al. 1991). Two autapomorphies (both unambiguous) support the above mentioned sister-group- relationship: presence of a median sclerotized plate below the genital opening (“insula plate” of mosquitos; Gerry 1932, see also Mühlenberg 1971

[*Toxophora*]), and acquisition of a muscle that inserts on this plate (**71**). Considering the very limited dipteran taxon sampling, it is evident that these character interpretations have to be considered as working hypotheses at best.

The substrates and habits of egg deposition are very heterogenous in Antliophora, and consequently also the adaptations of the female postabdomen. It is assumed here that oviposition in moist soil or similar substrates, as well as a telescoping postabdomen, represent the ground-plan conditions (as in Mecopterida). These are fully retained in Nannomecoptera (see above). In Pistillifera, oviposition primarily takes place into crevices in dryer, more solid types of soil; the telescoping postabdomen is retained in principal outline, but the genital opening is shifted caudad behind segment IX and the genital appendages of segments VIII and IX tend to fuse ventro-medially (see Mickoleit 1975). Bittacidae are exceptional within Pistillifera in scattering their eggs to the ground randomly during flight. Arguably in correlation with that, the bittacid postabdomen is strongly modified and has lost the telescopic retractability. In Boreidae, oviposition takes place into bryophyte masses in moist habitats. The females strongly differ in the possession (*Boreus*, *Hesperoboreus*) or lack (*Caurinus*) of a secondary ovipositor (Mickoleit 1975, Willmann 2003b). Apparently the presence is a synapomorphy of the former 2 genera. The monophyly of the family and a basal position of *Caurinus* are strongly suggested by features of the adult head (Beutel et al. 2008). In Diptera-Tipulomorpha (comprising the families Trichoceridae, Limoniidae, Pediciidae, Tipulidae and Cylindrotomidae) the substrates of oviposition are moist soils and rotten plant materials, often close to watersides. The females possess a secondary ovipositor. In Culicomorpha-Culicidae the eggs are usually deposited directly on the water surface; consequently, specialized structures for oviposition are not developed. In general, the "nematoceran-grade" families within Diptera ("lower Diptera") are all closely associated with moist or even (semi-) aquatic habitats, at least in the pre-adult stages (see Ziegler 2003). In Siphonaptera the eggs are layed randomly in the nests of the hosts, in adaptation to the adults ectoparasitic life-style (Kinzelbach 2003). As a consequence, the siphonapteran female postabdomen is devoid of any specialized features for oviposition.

8. Summary

8.1. Summary

The monophyly of the following groups is confirmed in the phylogenetic analysis presented here: Mecopterida, Amphiesmenoptera, Trichoptera, Lepidoptera, (Agathiphagidae + (Heterobathmiidae + Lepidoptera-Glossata)), Antliophora, Pistillifera, Diptera and (*Aedes* + *Toxophora*).

The groundplan of the endopterygote female postabdomen and apomorphies resulting from the major evolutionary steps are summarized in the following (see also **Fig. 34**). The numbers of the subsequent paragraphs correspond to the numbers of the squares in Fig. 34.

(1) Endopterygota (groundplan). Orthopteroid ovipositor fully preserved in basal hymenopterans, but sternum VIII reduced. Genital opening on ventral side, behind segment VIII (plesiomorphy).
The primary mode and substrate of oviposition at the base of Endopterygota remain ambiguous. The alternatives are either in living plant tissue or in soil.

(2) Mecopterida. Female postabdomen posteriorly tapering, with telescopic retractability. (nannochoristid type). Paired genital appendages on segments VIII and IX (ovipositor homologues) preserved, but proximal and distal parts (i. e., valvifers and valvulae) not longer distinguishable.
Oviposition takes place in moist soil, in rotten plant materials or in moss.

(3) Amphiesmenoptera. Genital appendages on segment VIII fused ventro-medially, forming a solid plate. Loss of the genital appendages on segment IX and of an associated muscle (**41**). Fusion of the terminal segments (IX – X [XI]), forming a terminal unit. Genital opening shifted posterad to a subapical position on the terminal unit. Neoformation of two pairs of apophyses (anterior pair ventral on segment VIII, posterior pair on the terminal unit). Extrusion of the terminal unit effected by muscle force; neoformation of four muscles performing extrusion (**08**, **10**, **17**, **23**). Fusion of rectum and posterior part of genital chamber (cloaca). Presence of a sclerotized papilla with the opening of the spermathecal duct on its tip (spermathecal process). Neoformation of spermathecal gland and bursa copulatrix. Accessory glands enlarged, balloon-shaped (production of secretions for egg protection and nutrition of newly hatched larvae).
Structural and functional features, notably the ability to extrude the postabdomen by muscle activity, suggest that the primary oviposition sites may be crevices. However, the oviposition habits vary widely within the group.

(4) Trichoptera. The entire complex of characters described for Amphiesmenoptera is retained in Trichoptera-Rhyacophilidae. The larvae are secondarily aquatic. Apparently the structural features of the female postabdomen are not affected by the deposition of eggs in the free water or between floating parts of the riparian vegetation.

(5) Lepidoptera. Complex muscularis of the genital chamber; bursa copulatrix strongly enlarged.
Primary mode of oviposition like in the groundplan of Amphiesmenoptera.

(6) Micropterigidae. Total reduction of the anterior and posterior apophyses and associated muscles. Terminal segments (IX and X) secondarily separated; extrusion by hemolymph pressure.
These features are closely linked to the oviposition in soft substrates, such as liverwort masses or rotting plant materials.

(7) (Agathiphagidae + (Heterobathmiidae + Lepidoptera-Glossata)). Presence of a region of the spermathecal duct with a content of mesocuticle in the intima. Neoformation of a third pair of apophyses (on tergum VIII) (with secondary loss in different lineages). Loss of the spermathecal process.
This configuration is retained in Agathiphagidae. The agathiphagid postabdomen is extremely telescoping. Eggs are deposited exclusively between cone scales of Kauri pines (*Agathis* sp.), directly on the seeds. This may be close to the ancestral condition in Amphiemenoptera and Lepidoptera.

(8) (Heterobathmiidae + Lepidoptera-Glossata). Fully developed "2-compartment-section" of the spermathecal duct. Accessory glands secondarily reduced in size.

(9) Heterobathmiidae. Loss of the anterior and strong reduction of the posterior apophyses; loss of the telescopic retractability of the female postabdomen.
These derived features are probably correlated with the habits of oviposition on exposed leaf surfaces of the host plants.

(10) Lepidoptera-Glossata. The fusion of the ipsilateral dorsal and ventral anterior apophyses is a possible autapomorphy of this clade.
The eggs are inserted in living plant tissues by females of the 3 basal glossatan lineages, but usually on plant surfaces by other members of the group.

(11) Antliophora. Neoformation of a transverse muscle spanning between the genital appendages of segment VIII (**48**).
The configuration of the female postabdomen and the primary habits of oviposition of Antliophora are likely as postulated for the ground plan of Mecopterida (nannochoristid type).

(12) Neomecoptera: Boreidae. Loss of the genital appendages of segment IX and muscle **41**. Oviposition takes place in bryophyte masses. Females of *Boreus* and *Hesperoboreus* possess a secondary ovipositor (formed of genital appendages of segment VIII, the terminal segments and the cerci). This device is missing in *Caurinus*, and therefore probably in the ground plan of Boreidae.

(13) Pistillifera. The group is not characterised by apomorphic features of the female postabdomen.
Eggs are primarily deposited into crevices in dryer, more solid soils. Bittacidae disperse their eggs at random and are arguably plesiomorphic in displaying the genital opening behind segment VIII (shifted behind segment IX in all other pistilliferan groups).

(14) Nannomecoptera: Nannochoristidae. The entire complex of autapomorphies listed for Mecopterida is retained in Nannochoristidae.
The larvae are secondarily aquatic. Eggs are likely deposited between riparian vegetation. Like in Trichoptera, structural features are apparently not affected.

(15) Siphonaptera. Loss of the telescopic retractability; potential loss of the genital appendages of segment IX and muscle **41**.
The eggs are scattered randomly in the nests of the hosts.

(16) Diptera. Possibly supported by the loss of two muscles associated with the genital chamber (**58**, **59**).
Oviposition takes place in moist or semi-aquatic habitats throughout the basal lineages.

(17) Diptera-Tipulomorpha: Limoniidae. Secondary ovipositor formed of genital appendages of segment VIII, the terminal segments and the cerci.
Oviposition takes place in moist soils and rotten plant materials.

(18) Diptera-Culicomorpha: Culicidae. Possibly supported by a median plate below the genital opening ("insula plate") and a muscle associated with this (**71**) Both are also reported from brachyceran representatives (Bombyliidae).

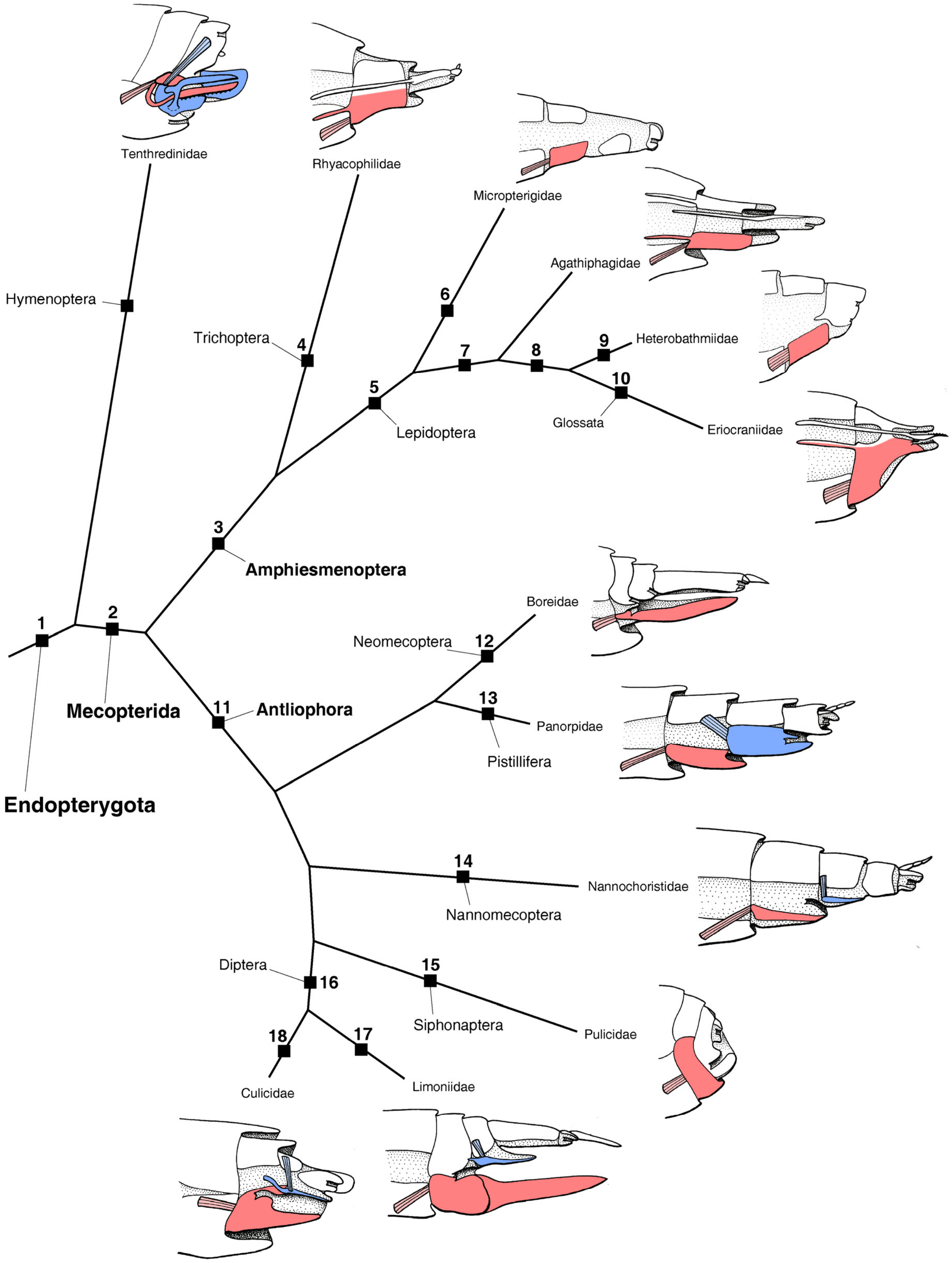

Fig. 34. Diagrammatic scheme showing the evolution of the female postabdomen throughout the major lineages of Mecopterida, with emphasis on the elements of the orthopteroid ovipositor. Square numbers correspond to the paragraph numbers in the summary (**chapter 8**). Colour code: red: genital appendage of segment VIII and homologues; light red: muscle 05; blue: genital appendage of segment IX and homologues; light blue: muscle 41.

8.2. Zusammenfassung

Die Monophylie folgender Gruppen wurde durch die Ergebnisse der im Rahmen dieser Arbeit durchgeführten phylogenetischen Analyse bestätigt: Mecopterida, Amphiesmenoptera, Trichoptera, Lepidoptera, (Agathiphagidae + (Heterobathmiidae + Lepidoptera-Glossata)), Antliophora, Pistillifera, Diptera sowie (*Aedes* + *Toxophora*).

Die Zusammenfassung gibt einen Überblick über die Konstruktion des weiblichen Postabdomen im Grundmuster der Endopterygota und über die aus den wesentlichsten evolutiven Schritten resultierenden Apomorphien (siehe auch **Fig. 34**). Die Nummerierung der folgenden Absätze entspricht den Nummern in Fig. 34.

(1) Endopterygota. Ein voll ausgebildeter Orthopteroider Ovipositor ist noch bei ursprünglichen Hymenopteren erhalten. Verlust von Sternit VIII. Genitalöffnung ventral, hinter dem Hinterrand von Segment VIII (Plesiomorphie).
Über den primären Eiablagemodus sowie das primäre Ablagesubstrat besteht nach wie vor Unklarheit. Alternativen sind Insertion der Eier in lebendes Pflanzengewebe, oder Ablage in den Boden.

(2) Mecopterida. Das weibliche Postabdomen entspricht dem Konstruktionsprinzip, welches bei Nannochoristidae vorzufinden ist: es verjüngt sich zum Hinterende hin; die terminalen Segmente sind teleskopartig ineinander einziehbar. Die Genitalanhänge der Segmente VIII und IX sind erhalten, jedoch nicht länger in proximale und distale Elemente unterteilt (*Nannochorista*- artig).
Die Eiablage erfolgt wahrscheinlich in feuchte Böden, verrottende Pflanzenreste oder in Moospolster.

(3) Amphiesmenoptera. Ventro-mediane Verschmelzung der Genitalanhänge von Segment VIII zu einer soliden Platte. Verlust der Genitalanhänge von Segment IX und eines an diesen ansetzenden Muskels (**41**). Verschmelzung der terminalen Segmente (IX – X [XI]). Verlagerung der Genitalöffnung weit zum Körperende hin (subterminal). Neuentstehung von 2 Apophysenpaaren (ein vorderes an Segment VIII, ein hinteres am Vorderrand der verschmolzenen Segmente IX-XI). Ausstülpen der terminalen Segemnte durch Muskelkraft; damit verbunden Neubildung einiger Muskeln (**08**, **10**, **17**, **23**). Verschmelzung von Enddarm und hinterstem Abschnitt der Genitalkammer (Kloake). Der Ductus spermathecae mündet auf einer sklerotisierten Papille (Processus spermathecae) in die Genitalkammer. Neuentstehung von Spermathecaldrüse und Bursa copulatrix. Anhangsdrüsen stark vergrößert; ballonartig aufgetrieben (Produktion großer Sekretmengen zum Schutz der Eier und Ernährung schlüpfender Larven).

Strukturelle und funktionelle Merkmale, insbesondere die starke Ausstülpbarkeit des Postabdomen durch Muskelkraft, legen nahe, dass die Eiablage primär in Spalträume erfolgte. Insgesamt sind die Ablagegewohnheiten innerhalb der Gruppe sehr variabel.

(4) Trichoptera. Der gesamte für Amphiesmenoptera beschriebene Merkmalskomplex ist bei Trichoptera-Rhyacophilidae erhalten.
Trichopterenlarven sind sekundär aquatisch. Die strukturellen Eigenheiten des Postabdomen erfuhren keine Veränderung im Zusammenhang mit der Eiablage in freies Wasser oder zwischen Uferpflanzen.

(5) Lepidoptera. Komplexer Aufbau der Muskelhülle der Genitalkammer; starke Vergrößerung der Bursa copulatrix.
Primärer Eiablagemodus vermutlich wie für das Grundmuster der Amphiesmenoptera angenommen.

(6) Micropterigidae. Die postabdominalen Apophysenpaare und ansetzende Muskulatur sind vollständig reduziert. Segmente IX und X sind sekundär wieder klar getrennt; ihre Ausstülpung erfolgt durch Haemolymphdruck.
Beides ist im Zusammenhang zu sehen mit der Eiablage in weiche Substrate (Lebermoospolster oder zersetzende Pflanzenreste).

(7) (Agathiphagidae + (Heterobathmiidae + Lepidoptera-Glossata)). Abschnitt des Ductus spermathecae mit einem Anteil von Mesocuticula in der Intima. Neuentstehung eines drittes Apophysenpaares (an Tergit VIII). Verlust des Processus spermathecae.
Dieses Konstruktionsprinzip ist so bei den Agathiphagidae vorzufinden. Die teleskopartige Einzieh- und Ausstülpbarkeit des weiblichen Postabdomen ist bei Agathiphagidae extrem stark ausgeprägt. Die Eier werden ausschließlich zwischen die Zapfenschuppen von Kauri-Kiefern (*Agathis* sp.) direkt an die Samen abgelegt. Möglicherweise kommt diese Art und Weise der Eiablage dem Grundmusterzustand der Amphiesmenoptera und Lepidoptera sehr nahe (in Spalträume).

(8) (Heterobathmiidae + Lepidoptera-Glossata). Vollständig ausgebildete „2-compartment- section“ des Ductus spermathecae. Sekundäre Größenreduktion der Anhangsdrüsen.

(9) Heterobathmiidae. Vordere Apophysen vollständig reduziert, hintere stark verkürzt. Verlust der telsekopartigen Einziehbarkeit.
Diese Reduktionserscheinungen sind in engem Zusammenhang zu betrachten mit der Art und Weise der Eiablage (frei auf die Blattoberflächen der Raupennährpflanzen).

(10) Lepidoptera-Glossata. Eine mögliche Autapomorphie dieser Gruppe stellt die Verschmelzung der dorsalen und ventralen vorderen Apophysen (jeweils derselben Körperseite) dar.
Die Eiablage erfolgt bei den drei ursprünglichsten Familien durch Insertion in lebendes Pflanzengewebe, bei den übrigen Angehörigen dieser Gruppe jedoch gewöhnlich auf die Oberflächen der Raupennährpflanzen.

(11) Antliophora. Neuentstehung eines Transversalmuskels (**48**), welcher sich zwischen den Genitalanhängen des achten Segmentes spannt.
Der Aufbau des weiblichen Postabdomen und die primären Eiablagegewohnheiten entsprechen wahrscheinlich den Zuständen im Grundmuster der Mecopterida (*Nannochorista*- artig).

(12) Neomecoptera: Boreidae. Verlust der Genitalanhänge von Segment IX und Muskel **41**. Eiablage in Moospolster. Ein sekundärer Ovipositor, an dessen Bildung die Genitalanhänge von Segment VIII, die Segmente IX-XI sowie die Cerci beteiligt sind, ist bei *Boreus* und *Hesperoboreus* ausgebildet, nicht jedoch bei *Caurinus*. Die Zugehörigkeit einer solchen Vorrichtung zum Grundmuster der Gruppe ist daher fraglich.

(13) Pistillifera. Die Gruppe ist nicht durch apomorphe Merkmale des weiblichen Postabdomen charakterisiert.
Die Eiablage erfolgt in Spalträume in trockeneren und festeren Böden. Lediglich die Weibchen der Bittacidae verstreuen ihre Eier frei im Flug; bei ihnen liegt die Genitalöffnung noch hinter dem achten Segment (bei allen übrigen Pistillifera hinter Segment IX).

(14) Nannomecoptera: Nannochoristidae. Der gesamte für Mecopterida angegebene Merkmalskomplex ist bei den Nannochoristidae erhalten.
Die Larven sind sekundär aquatische Organismen. Die Eiablage erfolgt wahrscheinlich zwischen Ufervegetation. Wie bereits bei den Trichopteren hat jedoch die Konstruktion des Postabdomen keine im Zusammenhang mit dem Eiablagemodus stehenden Veränderungen erfahren.

(15) Siphonaptera. Verlust der teleskopartigen Einziehbarkeit der terminalen Segmente; wahrscheinlich Verlust der Genitalanhänge von Segment IX und von Muskel **41**.
Die Eier werden ungeordnet in die Lagerstätten der Wirtstiere fallen gelassen.

(16) Diptera. Mögliche Autapomorphien der Ordnung sind der Verlust zweier Muskeln, welche beide mit der Genitalkammer in Verbindung stehen (**58**, **59**).
Die Eiablage erfolgt in den basal abzweigenden Familien durchweg in feuchten oder halbaquatischen Lebensräumen.

(17) Diptera-Tipulomorpha: Limoniidae. Die Weibchen besitzen einen sekundären Ovipositor, welcher aus den verlängerten Genitalanhängen von Segment VIII, den Segmenten IX-XI und den verlängerten Cerci aufgebaut ist.
Die Eiablage erfolgt in feuchte Böden und verrottende Planzenreste.

(18) Diptera-Culicomorpha: Culicidae. Weibchen der Culicidae besitzen eine Skleritplatte unterhalb der Genitalöffnung, sowie einen daran ansetzenden Muskel (**71**). Beide, die Platte und der Muskel, sind auch von Vertretern der höheren Fliegen (Brachycera) bekannt.

9. References

Achtelig, M., 1977. Skelet und Muskulatur des Abdomens weiblicher Raphidioptera (Insecta, Neuropteroidea). Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere 98, 137 – 167.

Aspöck, U., Aspöck, H., 2008. Phylogenetic relevance of the genital sclerites of Neuropterida (Insecta: Holometabola). Systematic Entomology 33, 97 – 127.

Beutel, R. G., Baum, E., 2008. A longstanding entomological problem finally solved? Head morphology of *Nannochorista* (Mecoptera, Insecta) and possible phylogenetic implications. J. Zool. Syst. Evol. Res. 46, 346 – 367.

Beutel, R. G., Friedrich, F., Whiting, M. F., 2008. Head morphology of Caurinus (Boreidae, Mecoptera) and ist phylogenetic implications. Arthropod Structure & Development 37 (5), 418 – 433.

Beutel, R. G., Gorb, S., 2001. Ultrastructure of attachment specializations of hexapods (Arthropoda): evolutionary patterns inferred from a revised ordinal phylogeny. J. Zool. Syst. Evol. Res. 39, 177 – 207.

Beutel, R. G., Gorb, S., 2006. A revised interpretation of the evolution of attachment structures in Hexapoda (Arthropoda), with special emphasis on Mantophasmatodea. Arthropod Systematics & Phylogeny 64, 3 – 25.

Beutel, R. G., Pohl, H.-W., 2006. Endopterygote systematics – where do we stand and what is the goal (Hexapoda, Arthropoda). Systematic Entomology 31, 202 – 219.

Bonneton, F., Brunet, F. G., Kathirithamby, J., Laudet, V., 2006. The rapid divergence of the ecdysone receptor is a synapomorphy for Mecopterida that clarifies the Strepsiptera problem. Insect Molecular Biology 15 (3), 351 – 362.

Brelje, R. v. d., 1924. Die Anhangsorgane des weiblichen Geschlechtsganges der Stechmücken (Culicidae). Zool. Anz. 61, 63 – 80.

Byers, G. E., 1965. New and uncommon neotropical Mecoptera. J. Kansas ent. Soc. 38, 135 – 144.

Castro, L. R., Dowton, M., 2005. The position of the Hymenoptera within the Holometabola as inferred from the mitochondrial genome of Perga condei (Hymenoptera: Symphyta: Pergidae). Mol. Phylogenet. Evol. 34, 469 – 479.

Chalwatzis, N., Hauf, J., Perr, Y., Kinzelbach, R., Zimmermann, F. K., 1996. 18S ribosomal RNA genes of insects: Primary structure of the genes and molecular phylogeny of the Holometabola. Ann. Ent. Soc. Amer. 89, 788 – 803.

Christophers, S. R., 1960. *Aedes aegypti* (L.) the Yellow Fever Mosquito. Its Life History, Bionomics and Structure. Cambridge.

Common, I. F. B., 1975. Evolution and classification of the Lepidoptera. Annual Review of Entomology 20, 193 – 203.

Davis, D. R., 1975. Systematics and zoogeography of the family Neopseustidae with the proposal of a new superfamily (Lepidoptera: Neopseustoidea). Smithson. Cont. Zool. 188, 1 – 66.

Davis, D. R., 1978. A revision of the North American Moths of the superfamily Eriocranioidea with the proposal of a new family, Acanthopteroctetidae (Lepidoptera). Smithson. Cont. Zool. 251, 1 – 131.

Davis, D. R., Nielsen, E. S., 1980. Description of a new genus and two new species of Neopseustidae from South America, with discussion of phylogeny and biological observations (Lepidoptera: Neopseustoidea). Steenstrupia 6, 253 – 289.

Deckert, J., Göllner-Scheiding, U., 2003. 24. Ordnung Heteroptera, Wanzen. p. 402 – 423 in: Dathe, H. H. (ed.): Lehrbuch der Speziellen Zoologie, begründet von A. Kästner, Band I, 5. Teil: Insecta. 2. Auflage. Spektrum Akademischer Verlag; Heidelberg, Berlin.

Dugdale, J. S., 1974. Female genital configuration in the classification of Lepidoptera. New Zealand Journal of Zoology 1, 127 – 146.

Evans, J. W., 1942. The morphology of *Nannochorista maculipennis* Tillyard (Mecoptera). Trans. Roy. Soc. S. A. 66 (2), 218 – 225.

Ferris, G. F., Pennebaker, P., 1939. The morphology of *Agulla adnixa* (Hagen) (Neuroptera: Raphidiidae). Microentomology 4 (5), 121 – 142.

Ferris, G. F., Rees, B. E., 1939. The morphology of *Panorpa nuptialis* Gerstaecker (Mecoptera: Panorpidae). Microentomology 4 (3), 79 – 108.

Feuerstein, V., 2008. Musculature of the female terminalia of *Osmylus fulvicephalus* (Scopoli, 1763) – a contribution to the understanding of the female genitalia of Neuropterida (Insecta: Holometabola). Poster, presented at Systematics 2008, Göttingen, April 09 – 12, 2008.

Friedrich, F., Pohl, H., Hünefeld, F., Beckmann, F., Herzen, J., Beutel, R. G., 2008. SRµCT-based study of external and internal structures of adults and larvae of Endopterygota (Hexapoda). Hasylab Annual Report 2007, 1527-1528.

Frommer, S. I., 1963. Gross Morphological Studies of the Reproductive System in Representative North American Crane Flies (Diptera: Tipulidae) The University of Kansas Science Bulletin XLIV (12), 535 – 626.

Gerry, B. I., 1932. Morphological studies of the female genitalia of Cuban Mosquitoes. Ann. Ent. Soc. Amer. 25 (1), 31 – 75.

Goloboff, P., 1999. NONA, Version 2.0. Fundacion e Instituto Miguel Lillo, Tucuman, Argentina.

Grell, K. G., 1942. Der Genitalapparat von *Panorpa communis* L. Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere 67, 513 – 588.

Grimaldi, D., Engel, M. S., 2005. Evolution of the Insects. Cambridge University Press; Cambridge.

Groll, E. K., Günther, K. K., 2003. 17. Ordnung Saltatoria (Orthoptera), Heuschrecken, Springschrecken. p. 261 – 290 in: Dathe, H. H. (ed.): Lehrbuch der Speziellen Zoologie, begründet von A. Kästner, Band I, 5. Teil: Insecta. 2. Auflage. Spektrum Akademischer Verlag; Heidelberg, Berlin.

Hennig, W., 1953. Kritische Bemerkungen zum phylogenetischen System der Insekten. Beiträge zur Entomologie 3, 1 – 85.

Hennig, W., 1969. Die Stammesgeschichte der Insekten. Frankfurt am Main. W. Kramer Verlag.

Hennig, W., 1973. Diptera (Zweiflügler). Handbuch der Zoologie IV. Insecta. Lieferung 20.

Herting, B., 1957. Das weibliche Postabdomen der calyptraten Fliegen und sein Merkmalswert für die Systematik der Gruppe. Zeitschr. Morph. Ökol. Tiere 45, 429 – 461.

Hünefeld, F., Beutel, R. G., 2005. The sperm pumps of Strepsiptera and Antliophora (Hexapoda). J. Zool. Syst. Evol. Res. 43 (4), 297 – 306.

Hünefeld, F., Kristensen, N. P. (in press.). The female postabdomen and internal genitalia of the basal moth genus *Agathiphaga* (Insecta: Lepidoptera: Agathiphagidae): morphology and phylogenetic implications. Zoological Journal of the Linnean Society.

Kéler, S. v., 1963. Entomologisches Wörterbuch. Akademieverlag Berlin, Berlin.

Kinzelbach, R., 2003. 34. Ordnung Siphonaptera (Aphaniptera), Flöhe. p. 734 – 745 in: Dathe, H. H. (ed.): Lehrbuch der Speziellen Zoologie, begründet von A. Kästner, Band I, 5. Teil: Insecta. 2. Auflage. Spektrum Akademischer Verlag; Heidelberg, Berlin.

Klass, K.-D., (ed., 2003). Proceedings of the 1st Dresden Meeting on Insect Phylogeny: Phylogenetic Relationships within the Insect Orders (Dresden, September 19-23, 2003). Entomologische Abhandlungen 61, 119 – 172.

Klaus, A. V., Kulasekera, V. L., Schawaroch, V., 2003. Three-dimensional visualization of insect morphology using confocal laser scanning microscopy. J. Microsc. 212 (2), 107 – 121.

Kristensen, N. P., 1975. The phylogeny of hexapod "orders". A critical review of recent accounts. Z. zool. Syst. Evolut.-forsch. 13, 1 – 44.

Kristensen, N. P., 1984. Studies on the morphology and systematics of primitive Lepidoptera (Insecta). Steenstrupia 10, 141 – 191.

Kristensen, N. P., 1997. Early evolution of the Lepidoptera + Trichoptera Lineage: Phylogeny and the Ecological Scenario. In: Grandcolas, P. (ed.), The Origin of Biodiversity in Insects: Phylogenetic Tests of Evolutionary Scenarios. Mém. Mus. Natn. Hist. nat. 173, 253 – 271.

Kristensen, N. P. (ed.), 1998. Lepidoptera: Moths and Butterflies 1. Handbuch der Zoologie / Handbook of Zoology IV / 35. Walter de Gruyter; Berlin, New York.

Kristensen, N. P., 1999. Phylogeny of endopterygote insects, the most successful lineage of living organisms. Eur. J. Entomol. 96, 237 – 253.

Kristensen, N. P., 2003a. Resolving the basal phylogeny of Lepidoptera: morphological evidence. Entomologische Abhandlungen 61, 167 – 169.

Kristensen, N. P. (ed.), 2003b. Lepidoptera: Moths and Butterflies 2. Handbuch der Zoologie / Handbook of Zoology IV / 36. Walter de Gruyter; Berlin, New York.

Kristensen, N. P., Nielsen, E. S., 1979. A new subfamily of micropterigid moths from South America. A contribution to the morphology and phylogeny of the Micropterigidae, with a generic catalogue of the family (Lepidoptera: Zeugloptera). Steenstrupia 5, 69 – 147.

Kristensen, N. P., Nielsen, E. S., 1998. *Heterobathmia valvifer* n. sp.: A moth with large apparent "ovipositor valves"(Lepidoptera, Heterobathmiidae). Steenstrupia 24, 141 – 156.

Kristensen, N. P., Scoble, M. J., Karsholt, O., 2007. Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. Zootaxa 1668, 699 – 747.

Kukalová-Peck, J., Lawrence, J. F., 2004. Use of hind wing characters in assessing relationships among Coleopteran suborders and major endoneopteran lineages. European Journal of Entomology 101, 95 – 144.

Kuznetzov, V. I., Stekolnikov, A. A., 2001. New Approaches to the System of Lepidoptera of World Fauna (On the base of the Functional Morphology of Abdomen). Nauka; St. Petersburg [in Russian].

Matsuda, R., 1957. Comparative morphology of the Abdomen of a Machilid and a Raphidiid. Trans. amer. Ent. Soc. 83, 39 – 63.

Matsuda, R., 1976. Morphology and Evolution of the Insect Abdomen. Pergamon Press; Oxford, New York, Toronto, Sydney, Paris, Frankfurt.

Mey, W., 1996. The caddisfly fauna of the Fan Si Pan mountain range in North Vietnam. 1. Descriptions of new and endemic species of the suborders Spicipalpia and Annulipalpia (Trichoptera). Beiträge zur Entomologie 46 (1), 39 – 68.

Mey, W., 2003: 32. Ordnung Trichoptera, Köcherfliegen. p. 652 – 672 in: Dathe, H. H. (ed.): Lehrbuch der Speziellen Zoologie, begründet von A. Kästner, Band I, 5. Teil: Insecta. 2. Auflage. Spektrum Akademischer Verlag; Heidelberg, Berlin.

Mickoleit, G., 1973. Über den Ovipositor der Neuropteroidea und Coleoptera und seine phylogenetische Bedeutung (Insecta, Holometabola). Z. Morph. Tiere 74, 37 – 64.

Mickoleit, G., 1975. Die Genital- und Postgenitalsegmente der Mecoptera-Weibchen (Insecta, Holometabola). I. das Exoskelet. Z. Morph. Tiere 80, 97 – 135.

Mickoleit, G. 1976. Die Genital- und Postgenitalsegmente der Mecoptera-Weibchen (Insecta, Holometabola). II. das Dach der Genitalkammer. Zoomorphologie 85, 133 – 156.

Mickoleit, G., 2009. Die Sperma-Ausspreßvorrichtung der Nannochoristidae (Insecta: Mecoptera). Entomol. Gen. 31 (2), 193 – 226.

Mühlenberg, M., 1971. Die Abwandlung des Eilegeapparates der Bombyliidae (Diptera). Eine funktionsmorphologische Studie. Z. Morph. Tiere 70, 1 – 72.

Mutuura, A., 1972. Morphology of the female terminalia in Lepidoptera and its taxonomic significance. Canadian Entomologist 104, 1055 – 1070.

Nielsen, A., 1980. A comparative study of the genital segments and the genital chamber in female Trichoptera. Biologiske Skrifter 23 (1), 1 – 200.

Nielsen, E. S., Kristensen, N. P., 1996. The Australian moth family Lophocoronidae and the basal phylogeny of the Lepidoptera-Glossata. Invertebrate Taxonomy 10, 1199 – 1302.

Oosterbroek, P., Courtney, G., 1995. Phylogeny of the nematocerous families of Diptera (Insecta). Zoological Journal of the Linnean Society 115, 267 – 311.

Penny, N., 1975. Evolution of the extant Mecoptera. J. Kansas ent. Soc. 48, 331 – 350.

Rasnitsyn, A. P., Quicke, D. L. J., 2002. History of Insects. Kluwer Academic Publishers; Dordrecht, Boston, London.

Rees, B. E., Ferris, G. F., 1939. The morphology of *Tipula resii* Alexander (Diptera: Tipulidae). Microentomology 4 (6), 143 – 178.

Ross, H. H., 1965. A Textbook of Entomology. 3rd Edition. Wiley; New York.

Ross, H. H., 1967. The evolution and past dispersal of the Trichoptera. Annual Review of Entomology 12, 169 – 206.

Schmid, F., 1989. Les Hydrobiosides. Bulletin de l´Institut Royal des Sciences naturelles de Belgique 59, Supplement, 1 – 154.

Shields, O., 1993. Is Micropterigidae or Agathiphagidae the most primitive lepidopteran family? Tyo to Ga 44, 152 – 156.

Sinclair, B. J., 1992. A phylogenetic interpretation of the Brachycera (Diptera) based on the larval mandible and associated mouthpart structures. Systematic Entomology 17, 133 – 252.

Snodgrass, R. E., 1935. Principles of Insect Morphology. McGraw-Hill Publications in the Zoological Sciences.

Stekolnikov, A. A., 1967. Functional morphology of the copulative organ in archaic moths and the general directions of the evolution of genitalia in Lepidoptera. Entomological Review 3, 400 – 409. [Translation of Entomologicheskoe Obozrenie 3, 670 - 688].

Steiner, P., 1936. Beitrag zur Fortpflanzungsbiologie und Morphologie des Genitalapparates von Boreus hiemalis L. Z. Morph. Ökol. Tiere 32, 276 – 288.

Strümpel, H., 2003. 22. Ordnung Auchenorrhyncha, Zikaden. p. 346 – 365 in: Dathe, H. H. (ed.): Lehrbuch der Speziellen Zoologie, begründet von A. Kästner, Band I, 5. Teil: Insecta. 2. Auflage. Spektrum Akademischer Verlag; Heidelberg, Berlin.

Togashi, I., 1970. The comparative morphology of the internal reproductive organs of the Symphyta (Hymenoptera). Mushi 43 (suppl.), 1 – 114.

Vilhelmsen, L., 2001. The ovipositor apparatus of basal Hymenoptera (Insecta): phylogenetic implications and functional morphology. Zoologica Scripta 29, 319 – 345.

Wheeler, W. C., Whiting, M. F., Wheeler, Q. D., Carpenter, J. M., 2001. The phylogeny of the extant hexapod orders. Cladistics 17, 113 – 169.

Whiting, M. F., 1998. Phylogenetic position of the Strepsiptera: review of molecular and morphological evidence. International Journal of Insect Morphology and Embryology 27, 53 – 60.

Whiting, M. F., 2002a. Phylogeny of the holometabolous insect orders: molecular evidence. Zoologica Scripta 31 (1), 3 – 15.

Whiting, M. F., 2002b. Mecoptera is paraphyletic: multiple genes and phylogeny of Mecoptera and Siphonaptera. Zoologica Scripta 31, 93 – 104.

Whiting, M. F., Carpenter, J. C., Wheeler, Q. D., Wheeler, W. C., 1997. The Strepsiptera Problem: Phylogeny of the Holometabolous Insect Orders inferred from 18S and 28S ribosomal DNA Sequences and Morphology. Syst. Biol. 46 (1), 1 – 68.

Wiegmann, B. M., Regier, J. C., Mitter, C., 2002. Combined molecular and morphological evidence on phylogeny of the earliest lepidopteran lineages. Zoologica Scripta 31, 67 – 81.

Willmann, R., 1981. das Exoskelett der männlichen Genitalien der Mecoptera (Insecta. I. Morphologie, II. Die phylogenetischen Beziehungen der Schnabelfliegenfamilien. Z. zool. Syst. Evolut.-forsch. 19, 96 – 150, 153 – 174.

Willmann, R., 1982. Die phylogenetischen Beziehungen unter den südamerikanischen Bittacidae (Insecta : Mecoptera). Zoologische Beiträge, Neue Folge 28, 47 – 65.

Willmann, R., 1989. Evolution und Phylogenetisches System der Mecoptera (Insecta: Holometabola). Abh. Senckenbergischen Naturforsch. Ges. 544, 1 – 153.

Willmann, R., 2003b. 35. Ordnung Mecoptera, Schnabelfliegen. p. 746 – 755 in: Dathe, H. H. (ed.): Lehrbuch der Speziellen Zoologie, begründet von A. Kästner, Band I, 5. Teil: Insecta. 2. Auflage. Spektrum Akademischer Verlag; Heidelberg, Berlin.

Wood, J. H., 1891. On oviposition, and the ovipositor, in certain Lepidoptera. Entomologists Monthly Magazine 26, 175 – 185, 212 – 215, 253 – 259.

Wood, D. M., Borkent, A., 1989. Phylogeny and classification of the Nematocera. Manual of Nearctic Diptera 3, 1333 – 1370.

Wood, D. M., Weismann, L., Orszagh, I., Pont, A. C., 1991. Homology and phylogenetic implications of male genitalia in Diptera. The ground plan. Proceedings of the 2nd International Congress of Dipterology; Bratislava, Czechoslovakia, August 27 – September 1, 1990, 255 – 271.

Yeates, D. K., Meier, R., Wiegmann, B. M., 2003. Phylogeny of true flies (Diptera): a 250 million year old success story in terrestrial diversification. Entomologische Abhandlungen 61, 170 – 172.

Yeates, D. K., Wiegmann, B. M., 1999. Congruence and controversy: toward a higher-level phylogeny of Diptera. Annual Review of Entomology 44, 397 – 428.

Ziegler, J., 2003. 35. Ordnung Diptera, Zweiflügler (Fliegen und Mücken). p. 756 – 860 in: Dathe, H. H. (ed.): Lehrbuch der Speziellen Zoologie, begründet von A. Kästner, Band I, 5. Teil: Insecta. 2. Auflage. Spektrum Akademischer Verlag; Heidelberg, Berlin.

10. List of abbreviations used in the figures

aa	anterior apophysis	***ro***	rectal opening
aad	dorsal anterior apophysis	***scl-rod***	rod-like sclerite
aav	ventral anterior apophysis	***scl-y***	y-shaped sclerite
ag	accessory gland	***se***	segment
agd	gland duct	***sp***	spermatheca
ap	posterior apophysis	***spd***	spermathecal duct
bc	bursa copulatrix	***st VII***	sternum VII
bcd	ductus bursae	***tg***	tergum
ce	circus	***vag***	vaginal sclerite
clo	cloacal opening	***vs***	ventral sclerotization
gc	genital chamber	***vsVIII***	genital appendage VIII
go	genital opening	***vsVIII-d***	first valvula
hg	hindgut	***vsVIII-p***	first valvifer
i	intima	***vsIX***	genital appendage IX
mcl	membranous collar	***vsIX-d(1)***	second valvula
ovl	lateral oviduct	***vsIX-d(2)***	third valvula
ovc	common oviduct	***vsIX-p(1)***	second valvifer
osc	oviscapt	***vsIX-p(2)***	anterior intervalvula
prc	spermathecal process	***vsIX-p(3)***	posterior intervalvula

In addition to the abbreviations listed above, a few more are used only for a single taxon in one or two figures. These abbreviations are explained directly in the corresponding figure legends.

The muscles are numbered as listed in **Tab. 4** and **Appendix A**.

Appendix A. Generalized list of muscle origins and insertions following the proposed nomenclature (with notes on function)

The following abbreviations are used in the muscle descriptions: O – origin; I – insertion; F – function (observed or assumed).

Intersegmental muscles

01 ***isVII-VIII01*** O: tergumVII, sometimes with 2 bundles, paramedian (*Nannochorista*: shifted to paralateral area of tergumVII); I: anterior margin of tergumVIII and/or adjacent intersegmental membrane, paramedian (*Agathiphaga*: shifted to apex of dorsal anterior apophysis); F: retractor of segmentVIII (*Agathiphaga*: protractor of segmentVIII)
02 ***isVII-VIII02*** O: tergumVII, laterad of *isVII-VIII01*, sometimes composed of two bundles; I: anterior margin of tergumVIII and/or adjacent intersegmental membrane, laterad of *isVII-VIII01* on the dorsal parts of the tergum; F: segmentVIII-retractor
03 ***isVII-VIII03*** O: tergumVII, paralateral, laterad of/below *isVII-VIII02*; I: anterior margin of tergumVIII and/or adjacent intersegmental membrane, laterad of *isVII-VIII02* (*Agathiphaga*: base of dorsal anterior apophysis); F: retractor of segmentVIII
04 ***isVII-VIII04*** O: tergumVII, laterad of *isVII-VIII03*, often near the anterolateral corner of the tergum (*Boreus*: shifted to anterolateral corner of sternumVII; *Agathiphaga*: shifted ventrally to pleural membrane, above spiracleVII); I: laterad/ventrad of *isVII-VIII03*, often near the anterolateral corner of tergumVIII and/or adjacent intersegmental membrane (*Agathiphaga*: shifted to base of dorsal anterior apophysis); F: segmentVIII-retractor
05 ***isVII-VIII05*** O: sternumVII, in various positions on the anterior half of the sternum (*Heterobathmia*: muscle shortened, origin paralaterally on the posterior third of sternumVII); I: anterior part of the ventral sclerotizations of segmentVIII and/or adjacent membranes, paralateral (*Osmylus*: shifted dorsally to tergumVIII); F: retractor of segmentVIII
06 ***isVII-VIII06*** O: sternumVII, mediad of *isVII-VIII05*; I: anterior margin of the ventral sclerotizations of segmentVIII and/or adjacent membranes, median to *isVII-VIII05* (*Micropterix*: laterad of *isVII-VIII05*, muscles cross before insertion); F: segmentVIII-retractor
07 ***isVII-VIII07*** O: tergumVII, laterad of isVII-VIII04 (*Osmylus*: shifted ventrally to the pleural membrane of segmentVII); I: tergumVIII, laterad of *isVII-VIII04*; F: segmentVIII-retractor
08 ***isVII-VIII08*** O: sternumVII, paralaterally around midlength of the sternum; I: apex of anterior apophysis (*Agathiphaga*: ventral anterior apophysis); F: segmentVIII-protractor

09 ***isVII-VIII09*** O: midlength of sternumVII, paralateral; I: anterior margin of the ventral sclerotization of segmentVIII, median to isVII-VIII06; F: segmentVIII-retractor

10 ***isVII-VIII10*** O: posterior part of tergumVII, paralateral (*Eriocrania*: shifted ventrally on the pleural membrane of segmentVII); I: apex of anterior apophysis; F: segmentVIII-protractor

11 ***isVII-VIII11*** O: anterior margin of sternumVII, paralateral (*Rhyacophila*: shifted anteriorly to anterior margin of segmentVI; *Agathiphaga*: shifted dorsally to pleural membrane of segmentVII, directly above spiracleVII); I: apex of anterior apophysis (*Agathiphaga*: ventral anterior apophysis); F: segmentVIII-retractor

12 ***isVII-VIII12*** O: anterior margin of tergumVII in various positions (*Eriocrania*: shifted to anterior half of tergumVI); I: apex of anterior apophysis (*Agathiphaga*: dorsal anterior apophysis); F: segmentVIII-retractor

13 ***isVII-IX01*** O: anterior margin of tergumVII (shifted to various positions due to relative length and position of the posterior apophysis; *Fansipangana*: anterolateral corner of sternumVII; *Rhyacophila*: anterolateral corner of tergumVI; *Heterobathmia*: anterolateral corner of tergumVIII; *Eriocrania*: anterior quarter of tergumVI, paramedially); I: apex of posterior apophysis; F: retractor of the terminal unit (segments IX-X[XI]); in *Heterobathmia* probably involved in nodding movements of the terminal unit during oviposition

14 ***isVIII-IX01*** O: anterior half of tergumVIII, sometimes with two bundles, paramedially (*Tipula*: shifted to posterior half of tergumVIII; *Agathiphaga*: shifted to apical region of dorsal anterior apophysis); I: anterior margin of tergumIX (*Agathiphaga*: base of posterior apophysis; Lepidoptera-Glossata: apical region of posterior apophysis); F: retractor of the terminal unit (oviscapt protractor in Lepidoptera-Glossata)

15 ***isVIII-IX02*** O: tergumVIII, at or before midlength of the tergum, sometimes with 2-3 bundles, paralateral (*Agathiphaga*: shifted to posterior quarter of tergumVIII; *Eriocrania*: apex of anterior apophysis); I: anterior margin of tergumIX, laterad of *isVIII-IX01* (*Fansipangana, Rhyacophila, Agathiphaga*: shifted to various regions of posterior apophysis); F: retractor of the terminal unit (*Fansipangana, Rhyacophila, Agathiphaga*: oviscapt protractor)

16 ***isVIII-IX03*** O: tergumVIII, laterad of *isVIII-IX02*, with 2 bundles; I: tergumIX, anterolateral corner; F: retractor of the terminal unit

17 ***isVIII-IX04*** O: anterior parts of ventral sclerotization of segmentVIII (*Fansipangana, Rhyacophila, Eriocrania*: apex of anterior apophysis; *Agathiphaga*: ventral anterior apophysis); I: anterior margin of ventral sclerotization of segmentIX and/or adjacent membranes; F: retractor of the terminal unit

18 ***isVIII-IX05*** O: anterolateral part of tergumVIII; I: lower process of tergumIX; F: unclear

19 ***isVIII-IX06*** O: posterolateral part of tergumVIII; I: upper process of tergumIX; F: unclear

20 ***isVIII-IX07*** O: anterolateral corner of ventral sclerotization of segmentVIII; I: ventral sclerotization of segmentIX, lateral side of anterolateral arm; F: retractor of segmentIX

21 ***isVIII-IX08*** O: midlength of ventral sclerotization of segmentVIII, paralateral; I: lateral on the ventral sclerotization of segmentIX; F: retractor of segmentIX

22 ***isVIII-IX09*** O: apex of anterior apophysis (*Agathiphaga*: dorsal anterior apophysis); I: apex of posterior apophysis; F: probably adjusts the relative position of the apophyses to each other

23 ***isVIII-IX10*** O: ventral sclerotization of segmentVIII in various positions, in *Heterobathmia* with 3 bundles; I: apical region of posterior apophysis; F: in *Agathiphaga* protractor of the oviscapt; in *Ulmerochorema* and *Heterobathmia* probably involved in nodding movements of the terminal unit during oviposition

24 ***isVIII-IX11*** O: anterior half of ventral sclerotization of segmentVIII, paramedian; I: paramedially at the ventral anterior margin of segmentIX; F: oviscapt retractor

25 ***isIX-X01*** O: anterior half of tergumIX, paramedian (*Micropterix*: equivalent membranous area; *Aedes*: shifted to lateral arm of ventral sclerotization of segmentIX), sometimes with 2 bundles; I: paramedially on anterior margin of tergumX and/or adjacent membranes; F: segmentX-retractor

26 ***isIX-X02*** O: anterior half of tergumIX, laterad of isIX-X01 (*Micropterix*: equivalent membranous area; *Aedes*: shifted to the mid-part of ventral sclerotization of segmenIX), sometimes with 2 bundles; I: anterior margin of tergumX and/or adjacent membranes, paralateral or ventral areas; F: retractor of segmentX

27 ***isIX-X03*** O: mid-part of ventral sclerotization of segmentIX, in front of origin of isVIII-IX02; I: ventral edge of tergumX; F: unclear

28 ***isX-XI01*** O: paramedially on anterior part of tergumX (Nannochorista: shifted to lateral position); I: paramedially on anterior margin of tergumXI; F: seXI-retractor

29 ***isX-XI02*** O: anterior part of tergumX, lateral parts; I: anterior margin of segmentXI, lateral and ventral areas; F: retractor of seXI

Cercal muscle

30 ***seX-ce01*** O: tergumX, in various positions; I: cercus ; F: moves the cercus

Intrasegmental muscles

31 ***intraVIII01*** ventrally from anterior to posterior part of ventral sclerotization of segmentVIII, in Ulmerochorema with 2 bundles; F: unclear

32 ***intraIX01*** scattered fibres between ventral sclerotization of segmentIX and bottom of the genital chamber; F: unclear
33 ***intraIX02*** running dorsal from anterior to posterior part of tergumIX; F: unclear
34 ***intraIX03*** O: vsIX-p(1), anterior part; I: vsIX-p(3) (Tenthredo: vsIX-p(?), not exactly to define due to possible fusion or reduction of parts of the vsIX-p – group); F: unclear
35 ***intraIX04*** O: vsIX-p(1), posterior part; I: vsIX-p(?); F: unclear

Dorso-ventral muscles

36 ***dvVII01*** connecting tergumVII and sternumVII, scattered fibres (*Toxophora*: Mühlenberg, 1971 depicts a compact muscle; *Cydia*: Kuznetzov & Stekolnikov, 2001 depict 3 compact muscle bundles); F: dorso-ventral compressor of segmentVII

37 ***dvVIII01*** connecting tergumVIII and ventral sclerotization of segmentVIII, scattered fibres (*Boreus, Tipula, Eriocrania*: compact muscle; *Osmylus, Limonia*: 2 compact bundles); F: dorso-ventral compressor of segmentVIII
38 ***dvVIII02*** O: paralaterally on anterior margin of tergumVIII; I: paralaterally on anterior 1/4 of ventral sclerotization of segmentVIII; F: dorso-ventral compressor of segmentVIII
39 ***dvVIII03*** O: base of dorsal anterior apophysis; I: mid-part of ventral anterior apophysis; F: probably plays a role in adjusting the position of both anterior apophyses of *Agathiphaga* relative to each other

40 ***dvIX01*** connecting tergumIX and the ventral part of the segment, scattered fibres (*Orthoptera, Osmylus*: compact muscle; *Xyela*: 2 compact bundles; *Limonia*: compact muscle with the dorsal attachment shifted to tergumX); F: dorso-ventral compressor of segmentIX
41 ***dvIX02*** O: laterally of anterior margin of tergumIX (*Panorpa*: shifted anteriorly to anterior part of tergumVIII); I: anterior part of ventral sclerotization of segmentIX; F: likely involved in the movements of the ventral sclerotization of segmentIX
42 ***dvIX03*** O: tergumIX, near anterolateral corner; I: dorsal lobe of scl-vIX-p(A); F: unclear
43 ***dvIX04*** O: tergumIX, below *dvIX02*; I: scl-vIX-p(B); F: unclear

44 ***dvX01*** O: tergumX, paramedian, 2 bundles; I: ventral membrane of segmentX; F: dorsoventral segmentX-compressor

45 ***dvXI01*** O: tergumXI, posterior part; I: scl-vXI, near anterior margin; F: dorsoventral compressor of segmentXI
46 ***dvXI02*** O: tergumXI, behind dvXI01; I: scl-vXI, mid-region; F: dorsoventral compressor of segmentXI

Transverse muscles

47 ***tVII01*** connecting the lateral areas of sternumVII; F: lateral compressor of segmentVII

48 ***tVIII01*** connecting the right and left ventral sclerotizations of segmentVIII, if both are fused ventromedially between the lateral parts of the combined sclerite (*Limonia*: 2 large distinct portions); F: adjusting the distance between the ventral sclerotizations of segmentVIII of both body halves
49 ***tVIII02*** connecting the lateral areas of tergumVIII; F: lateral compressor of segmentVIII

50 ***tIX01*** running between right and left ventral sclerotization of segmentIX, if both are fused between lateral parts of the combined structure; F: adjusts distance between the right and left part of the ventral sclerotization of segmentIX

51 ***tX01*** connecting ventrolateral areas of tergumX; F: lateral compressor of segmentX
52 ***tX02*** connecting dorsolateral areas of tergumX; F: lateral compressor of segmentX

53 ***tXI01*** running ventrally between both sides of segmentXI; F: lateral compressor of segmentXI

Muscles of the genital chamber (with site of origin on external segmental sclerotizations or adjacent membranous parts)

54 ***seVII-gc01*** O: sternumVII, at or behind mid-length, paramedially, sometimes with 2 bundles; I: lateral or ventrolateral areas of the genital chamber in segmentsVII/VIII; F: dilator of the genital chamber
55 ***seVIII-gc01*** O: anterior parts of the ventral sclerotization of segmentVIII, sometimes with 2 bundles (*Fansipangana, Rhyacophila, Eriocrania*: apical region of anterior apophysis; *Agathiphaga*: apex of ventral anterior apophysis); I: lateral areas of the genital chamber in segmentVII/VIII (*Limonia, Tipula*: laterally on the median sclerotization of the chamber roof in segmentVIII; *Eriocrania*: frame of the vaginal sclerite); F: dilator of the genital chamber (*Eriocrania*: retractor of the vaginal sclerite)

56 ***seVIII-gc02*** O: ventral sclerotization of segmentVIII, sometimes with 2 portions; I: ventral or ventrolateral areas of the genital chamber in segmentVIII(*Eriocrania*: posteriorly on the stem of the vaginal sclerite and its lateral extensions); F: dilator of the genital chamber (*Eriocrania*: protractor of the vaginal sclerite)
57 ***seVIII-gc03*** O: anterior margin of tergumVIII, 3 bundles; I: laterally on the genital chamber in segmentVIII; F: dilator of the genital chamber

58 ***seIX-gc01*** O: laterally on tergumIX, from mid-length or anterior part of the tergum (*Fansipangana, Rhyacophila*: shifted to posterior apophysis); I: laterally on the genital chamber in segmentsVIII/IX (*Panorpa*: laterally on the lateral arms of the spermathecal process); F: dilator of the genital chamber (*Panorpa*: protractor of the spermathecal process)
59 ***seIX-gc02*** O: laterally on segmentIX, near seIX-gc01; I: posterior section of the roof of the chamber (*Panorpa*: inside the spermathecal process); F: probably dilator of the genital aperture (*Panorpa*: retractor of the spermathecal process)
60 ***seIX-gc03*** O: ventral sclerotization of segmentIX; I: posteriormost region of the roof of the chamber; F: probably dilator of the genital aperture

61 ***seX-gc01*** O: anterolateral corner of tergumX; I: dorsolaterally on the genital chamber; F: protractor of the chamber

Muscles of the genital chamber (running between parts of the genital chamber)

62 ***intra-gc01*** *Archaeopsylla*: between spermatheca and most posterior part of the chamber roof; *Anabittacus*: between the dorsolateral area of the genital chamber in segmentVIII and the posteriormost part of its roof; F: unclear
63 ***intra-gc02*** present only in *Ulmerochorema*: connects the dorsolateral sac of the genital chamber and the chamber roof; F: unclear
64 ***intra-gc03*** present only in *Ulmerochorema*: connects the right and left dorsolateral sac of the genital chamber; F: unclear
65 ***intra-gc04*** present only in *Ulmerochorema*: connects the right and left ventrolateral sac of the genital chamber; F: unclear
66 ***intra-gc05*** present only in *Ulmerochorema*: connects the right and left ventrolateral sac of the genital chamber; F: unclear

Muscles of the rectal/cloacal aperture

67 *rec/clo01* O: tergum IX or X, position variable; I: near the opening of the rectum or cloaca; F: probably a retractorof the rectal/cloacal opening

Muscles that can not be ascribed to one of the above mentioned groups

68 *add01* O: vsVIII-p, dorsal part; I: vsIX-p(3); F: unclear

69 *add02* O: dorsal sclerotization of segments IX/X, posterior part; I: genital membrane; F: unclear

70 *add03* O: dorsal sclerotization of segments IX/X, anterior part; I: genital membrane; F: unclear

71 *add04* O: paralaterally on ventral sclerotization of segmentVIII; I: laterally on sclerite below genital opening; F: unclear

72 *add05* O: anterior fourth of the ventro-median sclerotization of the terminal unit; I: posterior part of the same sclerotized element; F: unclear

Appendix B. Additional characters used in the phylogenetic analysis

The following additional characters used in the phylogenetic analysis presented here were worked out, defined and coded by R.G. Beutel and H. Pohl (both University of Jena). Submission of the character matrices and character definitions for use in the present study is gratefully acknowledged.

For more detailed explanations and illustrations see Beutel and Ge (2008), Beutel et al. (2008a), Beutel & Friedrich (in press), Beutel et al. (subm., in prep.) for larval characters, and Beutel et al. (2007), Beutel and Vilhelmsen (2007), Beutel et al. (2008b) and Beutel and Baum (in press) for characters of adults.

Larval head

103. (*ori*) Orientation of head: (0) orthognathous; (1) prognathous or slightly inclined

104. (*cey*) Compound eyes: (0) well developed; (1) present, simplified, lacking crystalline cone; (2) absent

105. (*ste*) Stemmata: (0) absent; (1) several distinctly separated stemmata; (2) stemmata closely aggregated, with or without single cornea lense; (3) strongly reduced, 1-2 stemma or single eyespot

106. (*oce*) Paired ocelli: (0) present; (1) absent

107. (*fcl*) Transverse facial strengthening line (frontoclypeal suture): (0) present and distinct; (1) absent or only vaguely indicated (Beutel et al., in prep.)

108. (*acl*) Division of clypeal area into anteclyepus (tranparent, without muscle attachment) and postclypeus: (0) absent; (1) present

109. (*cls*) Shape of clypeal part anterad of transverse strengthening line: (0) broader than long; (1) longer than wide, trapezoid, anteriorly converging

110. (*afr*) Anterior ('adfrontal') cranial strengthening lines: (0) absent; (1) present; (2) present, strongly developed

111. (*occ*) Occipital furrow: (0) absent; (1) present

112. (*hys*) Hypostomal/postgenal bridge: (0) absent; (1) present, not sperated from genal area; (2) present, distinctly separated from genal area

113. (*ptg*) Posterior tentorial grooves: (0) close to hind margin of head capsule; (1) shifted anterad

114. *(dta)* Dorsal tentorial arm: (0) present; (1) vestigial

115. (*ten*) Shape of tentorium in cranial view: (0) not X-shaped, without distinct constriction between anterior and posterior arms; (1) X-shaped, with distinct constriction between anterior and posterior arms; (2) largely or completely reduced

116. (*8*) M. frontolabralis with attachment to external wall of labrum (M. 8): (0) present; (1) absent

117. (*mmu*) Messorial muscles: (0) absent; (1) present

118. (*9*) M. frontoepipharyngalis with insertion on tormae or posterolaterally on epipharynx (M. 9): (0) present; (1) absent

119. (*ase*) Antennal segmentation: (0) multisegmented, antennomeres distinctly separated; (1) pseudo-multisegmented, with mid-segment subdivided; (2) 5-7 antennomeres; (3) 4 antennomeres; (4) 3 antennomeres; (5) less than 3 antennomeres

120. (*1-4*) Number of extrinsic antennal muscles: (0) 4; (1) 3; (2) 2; (3) 1; (4) absent

121. (*iam*) Intrinsic antennal muscles (Mm. scapopedicellaris): (0) present; (1) absent

122. *(lmo)* **Articulated lacinia mobilis:** (0) absent; (1) present

123. *(pmx)* **Position of maxilla:** (0) retracted; (1) protracted, cardines at level of prementum, maxillary groove absent

124. (*mxl*) Maxillolabial complex: (0) absent; (1) present

125. (*smx*) Shape of the proximal parts of the maxilla: (0) not 'transverse'; (1) 'transverse' (i.e., distinctly wider than long)

126. (*mpr*) Posteromesal process of cardo/proximal element of the maxilla: (0) absent; (1) present

127. (*lob*) Galea and lacinia: (0) present as discrete structures; (1) extensively united, but separate origins clearly discernible; (2) completely united, composite formation without clear indication of double origin

128. (*sfm*) Stipital flexor muscles of lacinia and galea: (0) both present; (1) only a single muscle present; (2) no stipital lobe muscles present

129. (*15*) M. craniocardinalis (M. 15): (0) well developed; (1) absent

130. (*19*) M. craniolacinialis: (0) well developed; (1) absent

131. (*mdi*) 'M. craniodististipitalis': (0) present; (1) absent

132. (*28*) M. submentopraementalis: (0) present; (1) absent

133. (*31l*) M. praementoparaglossalis: (0) present; (1) absent

134. (*32l*) M. praementoglossalis: (0) present; (1) absent

135. (*ppr*) Apical prelabial region: (0) without process or extension or with short unsclerotised ligula; (1) together with hypopharynx foming compact lobe with salivary (silk) orifice on apex

136. (*spi*) spinneret: (0) absent; (1) present

Larval thorax

137. (*leg*) Legs: (0) present; (1) absent

138. (*cla*) Claws: (0) double; (1) single; (2) absent

Larval abdomen

139. (*sXI*) Segment XI: (0) present; (1) absent

140. (*pro*) Retractile prolegs: (0) absent; (1) present on segments II-VII; (2) present on segments III-VI and X

141. (*con*) Conical ventral protuberances on segments I-VIII: (0) absent; (1) present

142. (*cer*) Cerci: (0) present; (1) absent

143. (*hoo*) Terminal hooks: (0) absent; (1) single hook on fleshy lobes of segment X; (2) single hook on subdivided prolegs with scerotised elements

144. (*lha*) Larval (or nymphal) habitat: (0) terrestrial; (1) semiaquatic; (2) aquatic

Adult head

145. Rostrum (*rst*): (0) absent or extremely short; (1) elongated, not including parts of maxillae and labium; (2) elongated, including parts of maxillae and labium

146. (*fap*) Median internal frontal apodeme: (0) absent; (1) present

147. (*con*) Shape of posterior side of head (con): (0) not concave; (1) concave

148. (*pgb*) Postgenal bridge: (0) absent; (1) present, not delimited laterally; (2) laterally delimited sclerite

149. (*cif*) Clypeus: (0) not inflected; (1) inflected

150. (*col*) Shape of posterior tentorium: (0) not collar-like; (1) strongly developed, collar-like; (2) absent

151. (*mlb*) Movability of labrum: (0) present; (1) absent

152. (*fch*) Labro-epipharyngeal food canal: (0) absent; (1) present

153. (*8*) M. frontolabralis: (0) present, origin on frons; (1) origin on clypeus; (2) absent

154. (*9*) M. frontoepipharyngalis: (0) present; (1) absent

155. (*ics*) Intercalary sclerite in the lateral scapo-pedicellar membrane: (0) present; (1) absent

156. (*shm*) Shape and size of mandible: (0) not elongated and blade-like or lamelliform; (1) elongated, flattened and lamelliform or blade-like

157. (*mol*) Mandibular mola: (0) distinctly developed; (1) strongly reduced or absent

158. (*hau*) Haustellum including labial and hypopharyngeal parts: (0) absent; (1) present

159. (*lmc*) Labio-maxillary complex: (0) absent; (1) present

160. (*cal*) Dorsal concavity of the anterior labium for reception of elements of the paired mouthparts: (0) absent; (1) present

161. (*gal*) Galea: (0) distinctly developed; (1) vestigial or absent

162. (*gen*) Galea enfolds lateral part of labrum and lateral mandibular base: (0) absent; (1) present

163. (*lac*) Shape of lacinia: (0) not elongated and blade-like; (1) elongated and blade-like

164. (*sch*) Salivary channel formed by laciniae: (0) absent; (1) present

165. (*15*) M. craniocardinalis: (0) absent; (1) present

166. (*o17*) Origin of M. tentoriocardinalis and M. tentoriostipitalis: (0) tentorium; (1) frontoclypeal region

167. (*flx*) Flexion points between maxillary palpomeres 1 and 2 and 3and 4: (0) absent; (1) present

168. (*asc*) Arched sclerite with long piliform scales formed by postlabium: (0) absent; (1) present

169. (*npm*) Number of labial palpomeres: (0) three; (1) five; (2) two or less

170. (*pgl*) Paraglossae: (0) present; (1) absent or vestigial, without muscles

171. (*31*) M. praementoparaglossalis: (0) absent; (1) present

172. (*32*) M. praementoglossalis: (0) absent; (1) present

173. (*34/5*) Size of Mm. praementopalpales: (0) not enlarged; (1) enlarged

174. (*sit*) Sclerotised sitophore plate: (0) absent; (1) present

175. (*epl*) Epipharyngopharyngeal lobe with spines reaching into pharynx posteriorly: (0) absent; (1) present

176. (*43*) Size of M. clypeopalatalis: (0) not enlarged; (1) enlarged, two major subcomponents and multiple bundles; (2) arranged as a long series of bundles

177. (*tme*) Transverse muscles of the epipharynx: (0) absent; (1) present

178. (*pum*) Postcerebral pharyngeal pumping apparatus: (0) absent; (1) present

179. (*ims*) Strongly developed intrinsic muscle of salivarium: (0) absent; (1) present

180. (*cbs*) Configuration of brain and suboesophageal complex: (0) both parts of central nervous system distinctly separated by the circumoesophageal connectives; (1) forming a compact mass around the pharynx

Adults, thorax

181. (*met*) Size reduction of metathorax: (0) not distinctly reduced in size, than 20% smaller than mesothorax or both segments equally sized; (1) distinctly reduced

182. (*tie*) Movable 'epiphysis' of fore tibia: (0) absent; (1) present

183. (*win*) Wings: (0) normally developed; (1) distinctly reduced; (2) absent

184. (*srw*) Size relation of wings: (0) about equally sized, size difference below 10%; (1) forewings larger; (2) hindwings larger

185. (*tfm*) Transverse interprofurcal muscle: (0) absent; (1) present

186. (*pax*) Pleural muscle attached to to Axillary 1 (plr2-1ax2/sc2 (Kristensen 2003): (0) absent; (1) present

187. (*pnp*) Pleural muscle attached posterior notal wing process: (0) absent; (1) present

188. (*ocr*) Outer tergocoxal remotor muscle (Larsén, 1966: M. 76): (0) absent; (1) present

189. (*ha3*) Hind wings transformed into halteres: (0) absent; (1) present

190. (*ccv*) Number of costal cross veins: (0) more than 5; (1) less than 5

191. (*sca*) Dense vestiture of scales on wings: (0) absent; (1) present

192. (*ham*) Hamuli: (0) absent; (1) present, connecting fore wings and hind wings

193. **(*aro*) Arolium:** (0) present; (1) absent

194. **(*pul*) Hairy pulvilli:** (0) absent; (1) present

Adults, abdomen

195. **(*abI*) Fusion of abdominal segment I and abdomen:** (0) absent; (1) present

196. **(*cap*) Genitalic capsule formed by dorsal and ventral fusion of basistyli:** (0) absent; (1) present

197. **(*aca*) Acanthae of proventriculus present and with close-set prominently elongated:** (0) absent; (1) present

198. **(*nmt*) Number of Malpighian tubules:** (0) more than 20; (1) 8 or less

199. **(*spp*) Sperm pump with genital folds enclosing the pumping chamber with pistill and pistillifer:** (0) absent; (1) present

200. **(*spe*) Sperm pump formed by modified endophallus:** (0) absent; (1) present

201. **(*ov1*) Ovarioles:** (0) panoistic; (1) meroistic

Developmental characters

202. **(*sex*) Male sex chromosomes:** (0) not homogametic; (1) homogametic

Pupal characters

203. **Movability of pupal mandible:** (0) present; (1) absent

204. **Size of pupal mandible:** (0) not hypertrophied; (1) hypertrophied

205. **Muscle foramen**

Additions (Mickoleit 2009)

206. **(*spp*) Sperm pump with genital folds enclosing the pumping chamber with pistil and pistillifer:** (0) absent; (1) present, with longitudinal tegimen formed by roof of endophallus; (2) present, with pistil formed by roof of endophallus; (3) present, pistil formed by median lobe arising from fulcrum

207. **(*aed*) Aedeagus apodeme with median longitudinal lamella:** (0) absent; (1) well developed; (2) vestigial, serving as lever of the pistil levator

208. **(*ful*) Fulcrum:** (0) absent; (1) present, well developed; (2) present, fused with pistil