Zoological Journal of the Linnean Society (2001), *131:* 251–307. With 38 figures
doi:10.1006/zils.2001.0246, available online at http://www.idealibrary.com on IDEAL®

The female abdomen of the viviparous earwig *Hemimerus vosseleri* (Insecta: Dermaptera: Hemimeridae), with a discussion of the postgenital abdomen of Insecta

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Received June 1999; accepted for publication January 2000

The viviparous, epizoic African earwigs of the genus *Hemimerus* are currently regarded as the sister taxon of the remaining Dermaptera (Forficulina). Exoskeleton, musculature, and part of the nervous system of the female abdomen, from segment IV on, are described. The morphological interpretation and homology relations of most components are discussed, using previous and original data on Forficulina, Zygentoma, Ephemeroptera, Orthoptera and Dictyoptera as a comparative framework. In the mid-abdominal segments some interesting similarities with Zygentoma are indicated. Focal issues in the postgenital abdomen are the terminal dorsal sclerites, the cercal muscles, and the paraprocts and associated muscles. Earlier hypotheses on the dermapteran postabdomen (opisthomere and pseudocercus hypotheses) and results from ontogenetic studies are scrutinized. Some interesting features detected in female *Hemimerus* are the immobilization of terga VIII–X by means of a thick internal cuticle layer, the lack of dorsal muscles on these terga, the shift of some insertions of cercal and rectal muscles from tergum X to tergum IX, and minute pits on the venters IX and X that could be spiracle vestiges. Some of these features occur also in other Dermaptera. Some abdominal characters suggest that *Hemimerus* is nested within the Forficulina. The lack of the clasper-shape in the cerci is not a strong argument against this.

ADDITIONAL KEY WORDS: cercus – genitalia – paraproct – postabdomen – Archaeognatha – Dictyoptera – Ephemeroptera – Zygentoma.

INTRODUCTION

The genus *Hemimerus* has long been of particular interest to entomologists, on the one hand for its viviparity and its habits as an epizoic on *Cricetomys* rats, on the other for the debate on its taxonomic rank either within or beside the Dermaptera (Popham, 1961; Giles, 1974). Hansen (1894), Verhoeff (1902), and Jordan (1909) were the first to give useful treatments on the external and internal morphology of *Hemimerus*. Deoras (1941a,b) gave some additions. Davies (1966) described changes in external morphology during nymphal development. Heymons (1912) studied the internal genitalia and early ontogeny in detail. Head and thorax morphology were exhaustively treated in some more recent contributions (Popham, 1962; Barlet, 1984, 1985). The knowledge of abdominal morphology, however, has remained very incomplete: extant descriptions of the exoskeleton are superficial, and data on the muscles and peripheral nerves are entirely absent. Information on these issues would be important for a convincing phylogenetic placement of *Hemimerus*.

The first to claim a close relationship of *Hemimerus* to the typical earwigs, Dermaptera Forficulina, was Hansen (1894). Verhoeff (1902) and Jordan (1909), finding further similarities, agreed with him. Popham (1961) proposed to exclude *Hemimerus* from Dermaptera, but Giles (1974) suggested reinstating it within Dermaptera. Nevertheless, both workers actually agreed that *Hemimerus* is the sister taxon of the (remaining) Dermaptera (i.e. Forficulina including *Arixenia*), their debate focusing on the 'importance' of certain characters and the taxonomic rank (order or suborder) of the groups in question. Popham (1985) re-examined the basal phylogeny of the Dermaptera

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at some length and affirmed that *Hemimerus* is the sister taxon of the remaining Dermaptera. Many of his arguments, however, are not very convincing. Alternatively, one might suspect that many of the features in which *Hemimerus* seems more primitive than the Forficulina could be due to secondary reduction, especially to paedomorphosis. Barlet (1985: 186) suspected such paedomorphic apomorphies in thorax morphology. Hence, it cannot be excluded that *Hemimerus* is nested within the Forficulina. More detailed morphological information is, however, obviously needed before reasonable conclusions can be drawn.

In the present study, the abdomen of female *Hemimerus* is described from segment IV on, thus including typical (mid-abdominal: IV–VI), genital *s.l.* (VII–IX), and postgenital segments (X, XI), and the telson. Exoskeleton and musculature are considered exhaustively; only setae, tracheae, and details of the hindgut are omitted. The nervous system is treated as far as possible with the material at hand. The homology and the morphological interpretation of the components under consideration are discussed in a wide systematic frame, using selected other lower-grade Insecta for comparison. Archaeognatha and Zygentoma are included because many components are present in a more plesiomorphic condition than in Dermaptera and other Pterygota, and because these more primitive conditions are important for the interpretation of many structures. Ephemeroptera, Dictyoptera, and Orthoptera are included because for these the literature contains the most elaborate data base on abdominal morphology. The highly controversial homologies and interpretations of the postgenital abdominal sclerites and muscles are a focal issue. Furthermore, the phylogenetic information content of a number of abdominal characters is examined, and their bearing on the phylogenetic placement of *Hemimerus* and on other inner-insect relationships is analysed.

MATERIAL AND METHODS

Of *Hemimerus vosseleri* Rehn & Rehn, 1935 (Hemimerina: Hemimeridae) five females preserved in 80% ethanol were available. Most structures were studied by dissection under a stereo microscope: dorsally, laterally, and anteriorly in 80% ethanol. For small muscles and some other structures the identity of the tissue was checked under a light microscope. For occasional comparison with *Hemimerus* and for the reinvestigation of certain characters, specimens were used of *Apachyus chartaceus* (de Haan, 1842) (Forficulina: Apachyidae), *Labidura riparia* (Pallas, 1773) (Forficulina: Labiduridae), *Forficula auricularia* Linnaeus, 1758 (Forficulina: Forficulidae), *Echinosoma yorkense* Dohrn, 1869 (Forficulina: Pygidicranidae), *Tagalina burri* Hincks, 1955 (Forficulina: Pygidicranidae), *Pygidicrana v-nigrum* Serville, 1831 (Forficulina: Pygidicranidae), *Diplatys* sp. indet. (Forficulina: Pygidicranidae), *Pyragra fuscata brasiliensis* (Gray, 1832) (Forficulina: Pygidicranidae), *Karschiella buettneri* (Karsch, 1886) (Forficulina: Pygidicranidae), and *Ctenolepisma lineata* (Fabricius, 1775) (Zygentoma: Lepismatidae). 'Forficulina' is used here *sensu* Popham (1985), i.e. as including the Arixeniidae. It should be noted that the Pygidicranidae as delimited herein (including Diplatyidae and Karschiellidae) are a paraphyletic assemblage comprising the lowest-grade Forficulina (see Haas, 1995); the phylogenetic relationships between their genera are largely unresolved. When data from previous studies are referred to, the names of the respective taxa, mostly species, are specified as (in)completely as in the original papers. After their first mention species are designated by the generic name alone.

TERMINOLOGIES, MORPHOLOGICAL INTERPRETATIONS AND ABBREVIATIONS

EXOSKELETON

The terminology follows essentially Snodgrass (1931, 1933, 1935b). However, the ventral (*s.l.*: sternal and pleural) abdominal sclerotizations are interpreted and designated based on more refined results on Archaeognatha (Bitsch, 1973, 1974a,b), Zygentoma (Rousset, 1973), and Dictyoptera (Klass, 1998). In Archaeognatha an abdominal segment has maximally five discrete ventral sclerites: the unpaired sternite and intersternite and the paired coxites (bearing the stylus), laterocoxites (= subcoxae in Smith, 1969), and precoxites (e.g. Bitsch, 1973: fig. 2, 1974a: fig. 1). A synthesis from Bitsch's findings in Archaeognatha, Rousset's results on Zygentoma, McKittrick's (1964) descriptions of nymphal Blattaria, and conditions in adult Dictyoptera led to an identification in these taxa of homologous sclerotization areas and muscle insertions on the venters of the female genital segments VIII and IX (Klass, 1998). Sclerites corresponding to coxite and laterocoxite of Archaeognatha, and, accordingly, also the division between them, could be determined in Dictyoptera (gonocoxa and laterogonocoxa in Klass, 1998; laterogonocoxa IX = gonangulum). Sclerites corresponding to sternite, intersternite, and precoxite, however, could not be identified because in Archaeognatha none of these sclerotizations bears muscle insertions that can be homologized with muscle insertions of Pterygota (compare Bitsch, 1973: e.g. fig. 8); nor is there a hypothesis for the demarcation of these sclerotizations in Zygentoma. Nevertheless, small unmuscled median sclerites in Dictyoptera were tentatively determined as homologues of sternite and/or intersternite and were referred to as the sternum. It is furthermore conceivable that the homologue of the archaeognathan precoxite is included in the anterior portion of what has been called in Dictyoptera and Zygentoma the laterogonocoxa.

Hence, the distinction of three major sclerotization areas is, as far as presently known, possible in the venters VIII and IX of female Dicondylia. These are called here coxa (=gonocoxa), laterocoxa (=laterogonocoxa), and sternum, and these terms are here more consistently applied than in Klass (1998). Coxa and laterocoxa are paired limb base sclerotizations designated here collectively as the coxopodium (pleural). Coxopodia and the unpaired sternum together constitute the coxosternum. Also the abdominal 'sterna' I–VII of Dicondylia are regarded as such coxosterna (see Heymons, 1895a: 27; Snodgrass, 1931; Smith, 1969). On the base of the abovementioned findings it is attempted here to trace the ventral sclerite components and hence the sclerite homologies with Archaeognatha, Zygentoma, and Dictyoptera also in the female genital segments VIII and IX of *Hemimerus* and, in part, other Dermaptera. It is moreover attempted to demarcate the homologous sclerotization areas in the mid-abdominal coxosterna and in the sclerotizations of the terminal segments X and XI.

It should be noted that, first, this demarcation of areas homologous with the genital coxae, laterocoxae, and sterna does not imply that the mid-abdominal coxosterna and Xth/XIth-segmental sclerotizations were ever actually divided into corresponding discrete sclerites, i.e. that such a division is ancestral for the abdominal segments of Insecta—though conditions in some Archaeognatha and Pterygota may indicate this. Second, the use of 'coxa' is not meant to indicate strict serial homology with the thoracic coxa, in particular because the serial homologue of the abdominal coxa-stylus border in the thoracic leg is unknown. Third, the interpretation of the archaeognathan sclerites in a wider arthropod context is largely unresolved (see Bitsch, 1973: 193f, 1994; Smith, 1969), and no reference is intended here, with the distinction between coxa and laterocoxa, to theories of limb base composition in a large-scale arthropod view. It is emphasized that the terminology as used herein is meant to indicate only inner-insect abdominal homologies and serial homologies, and only in this frame (serial) homologies are here traced. The problems in interpreting the archaeognathan sclerites have probably no impact on this comparison within the insect abdomen; only the terminology may have to be modified when these problems are solved.

Formative elements, established by an in- or outfolding or by a thickening of the cuticle, are considered herein as discrete structural components of the abdomen. Many of these are internal cuticular projections used for muscle attachment; they can be stout or delicate, hollow or massive, sclerotized to various extents or entirely membranous, shape shows much variation, and these attributes occur in many combinations. There is no consistent terminology for the various types. Moreover, as shown by corresponding muscles being attached to them, such internal projections of very different kinds can apparently be homologous or homodynamous (=serially homologous), and a terminological distinction appears thus not quite appropriate. The terms 'apodeme' and 'tendon' are used herein to designate sclerotized and membranous internal cuticular projections, respectively, and 'ridge' refers to an apodeme having this shape. These terms are more or less synonymous rather than meant as strict categories. 'Tendon' is not referred here to non-cuticular endoskeletal components. Of the latter some ventral ones of Archaeognatha and Zygentoma are considered herein, which are called 'endosternites'.

Sclerites, and also endosternites, are here designated by terms composed of two upper case letters. In the segments up to IX sclerite designations are based on the above explanations. Formative elements are designated by terms composed of two lower case letters. A number in the last position gives, if needed, the assignment of a sclerite, endosternite, or formative element to a segment. Exoskeletal structures not covered by these terms are designated by single lower case letters. It should be noted that generally in this paper the equal designation of components expresses the assumption of homology in different taxa or serial homology in different segments, with the restrictions given in the discussions in terms of the probability of (serial) homology.

MUSCULATURE

The muscles are numbered in sequence. In addition, many muscles are given descriptive names. The terminological principles followed, their inherent problems, and the terms used for characterizing the muscle shape are explained in Klass (1999: 5f). In the segments IV–VII insertions on a coxosternum and on the pleural membrane—most of both are probably pleural—are designated here as coxosternal. A distinction between tergal (*s.s.*) and paratergal insertions is attempted (but is tentative) in order to compare the results with those on Dictyoptera (Klass, 1999, 2000). Most muscles are present as a pair, and an unpaired condition is noted.

NERVOUS SYSTEM

All major components are designated by single upper case letters: ganglia, connectives, major nerves, and perisympathetic organs. A number in front gives, if needed, the assignment to a segment. Compound ganglia, composed of several segmental ganglia, are termed, for example **7–11G**. Primary branches of the major nerves are specified by numbers behind the letter; the numbers correspond to those of the homologous nerve branches of Dictyoptera (see Klass, 1999). The part of a nerve that continues beyond the origins of its branches is called its main part (definition arbitrary). Details of the terminological principles followed, and their inherent problems, are explained in Klass (1999: 6f).

SEGMENTAL ASSIGNMENT

For sclerites this is given with respect to secondary segmentation because the latter is established by the sclerites. For formative elements, muscles, and components of the nervous system assignment is given, as far as possible, with respect to primary segmentation. Components assumed to lie between two primary segments or to be of bisegmental origin (e.g. antecostae, alary muscles, anterior tergo-coxosternal muscles, endosternites) and the connectives, median nerves, and transverse nerves are formally assigned to the respective posterior segment (compare Klass, 1999: 7). In the segments up to VII, and partly in VIII and IX, the fact that most components belong to a certain primary segment is obvious from their positions. For many elements behind segment IX, however, the assignment to a certain segment is controversial; reasons are given, but firm conclusions cannot be drawn without further detailed ontogenetic studies.

ABBREVIATIONS

1 51	muscles
I IV	groups of cercal muscles
A (+number)	dorsal nerve (and its major branches)
a	desclerotized patch anterolaterally on tergum
ac (+number)	antecosta (number = segment following)
ag	accessory gland
an	anus
AP	anal plate (median part of paraproct)
at (+number)	tendon or apodeme anterolaterally on coxosternum = 'sternal' apophysis (number = segment following)
B (+number)	anterior ventral nerve (and its major branches)
b	fusion between terga IX and X
c	membranous stripe incompletely separating sclerites LC8 and CX8
C (+number)	posterior ventral nerve (and its major branches)
CE	sclerotization of cercus
ce	cercus
CP (+number)	coxopodium (number = segment)
CS (+number)	coxosternum (number = segment)
ct	tendons on cercal base
CX (+number)	coxa (number = segment)
df	dorsal fold of segment overlapping succeeding segment
dr	longitudinal dorsomedian cuticular ridge on tergum
DT	dorsal sclerite of telson
ec	line along which cuticle ends (mesoderm adjoining)
ei	inferior hind edge of subgenital fold
es	superior hind edge of subgenital fold
ES (+number)	endosternite (number = segment following)
G	ganglion
gl (+number)	projecting body of abdominal limb; gonoplac on segment IX (number = segment)
go	anterior border of definitive genital opening
gp (+number)	gonapophysis or corresponding area (number = segment)
il	posterior incision of subgenital fold
L	connective between ganglia
LC (+number)	laterocoxa (number = segment)
LP	lateral plate (lateral part of paraproct)
lt	lateral tendon beside coxosternum
M	median nerve
ma	median apodeme on cercal base
ms (+number)	manubrium of spiracle (number = segment)
mt (+number)	median tendon or ridge of coxosternum (part of antecosta; number = segment following)
oc	common oviduct
ol	lateral oviduct
P	perisympathetic organ
pc	transverse cuticular ridge on coxosternum or tergum behind antecosta
re	rectum
rp	rectal papilla
sb	subanal lobe
si (+number)	spiracle (number = segment)
sl (+number)	stylus area (number = segment)
so	spermathecal opening
sp	spermatheca
ST (+number)	sternum (number = segment)
T	transverse nerve
tf	terminal = caudal filament on tergum XI
TG (+number)	tergum (number = segment)
tl	lateral tubes (opening near accessory gland)
tr	transverse ridge on dorsal sclerite of telson
va	vagina

vf (+number)	ventral fold of segment overlapping succeeding segment (number = segment); subgenital fold on venter VII
vr	longitudinal ventromedian cuticular ridge on coxosternum

In addition, abbreviations, terms, and muscle numbers from other contributors are used in the comparisons between *Hemimerus* and other Insecta. In the text these are consistently marked with an asterisk, but not in the tables and illustrations. When used in the illustrations, these abbreviations are explained in the respective legends (Figs 25–38).

DESCRIPTION OF THE ABDOMEN OF *HEMIMERUS VOSSELERI*

EXOSKELETON OF *HEMIMERUS*

Condition of the cuticle

The cuticle was observed to have in many areas of the body wall two layers that are easily peeled apart. The external layer shows clearly the pattern of sclerotization (stiff, brown) and membrane (flexible, transparent). The internal layer, though brownish in some areas, is milky and has a rubber-like texture and flexibility. It is unclear in which way this 'mechanical' subdivision meets any biochemically or ultrastructurally defined layering of the cuticle (the delicate epicuticle being out of discussion). In the descriptions the relative contribution of the two layers to specific structures is only occasionally considered.

Cuticle thickness varies considerably along the body surface. A thickening of the cuticle can be due to a thickening of either or both of its two layers. Thickened areas, if sclerotized, usually appear darker. In some areas, thick cuticle is well delimited from the thinner surrounding cuticle. Information on the extension of these distinct thickenings, which form ridges or patches, is included where possible. Other cases where cuticular thickening is less strong, or where the areas of thickening are not well delimited, are not considered.

Exoskeleton of segments IV–VI

These mid-abdominal segments (Fig. 1) have, when observed in an undistorted condition, the tergum **TG** in a slightly more anterior position than the coxosternum **CS**. The lateral parts of a tergum gradually incline ventrad and mesad and overlap the lateral parts of the coxosternum, especially in the anterior part of the segment where the tergum is broader. Both terga and coxosterna broadly overlap their succeeding counterparts (folds **df**, **vf** in Figs 1, 2). Most of the cuticle bending forward from the sclerites' posterior edges is weakly sclerotized (Fig. 1, left margin), the sclerotization being regarded here as part of the respective tergum or coxosternum. The coxosternum forms at its anterolateral corner a strong apodeme **at** ('sternal apophysis'), whose external face is mostly membranous.

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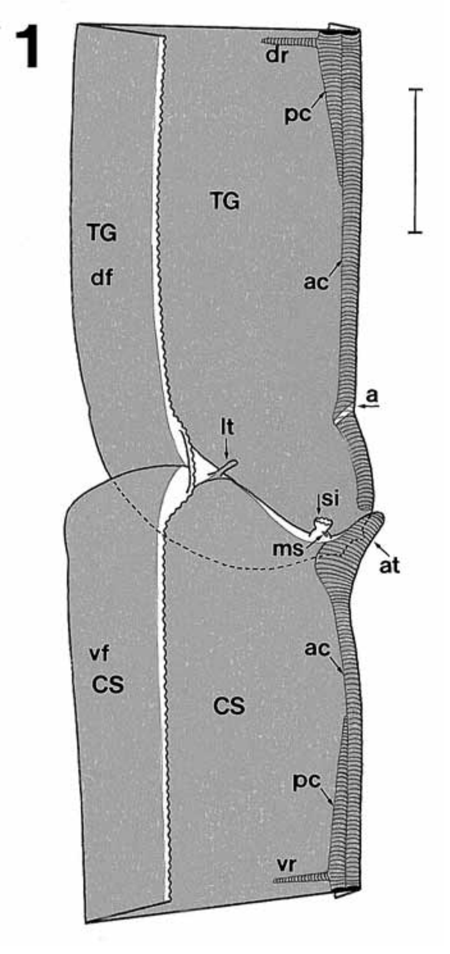


Figure 1. Exoskeleton of mid-abdominal segments. Left half of segment, internal view. Dorsal part bent, lying in same plane as ventral part. ↑ dorsomedian, ↓ ventromedian, → anterior. Ridges dr and vr located at dorsal and ventral midline. Sclerotization dark. Cuticular ridges/thickenings indicated by hatched stripes/areas. Dashed line: lateral edge of tergum. Scale bar = 0.5 mm.

A wide pleural membrane extends between the lateral margins of coxosternum and tergum. It bears, near the margin of the coxosternum, a small tendon **lt** and, more anteriorly, the spiracle **si**. The spiracle has a dish-shaped atrium, which is bordered internally by a neck-like constriction to the base of the trachea. Some details were observed (compare descriptions for Dictyoptera in Klass, 2000). The neck bears a tongue-shaped, anteromesad-directed apodeme, the manubrium **ms**. The tracheal base immediately internal to the neck has a narrow ring-shaped zone with anastomosing ridges that enclose circular or indistinctly

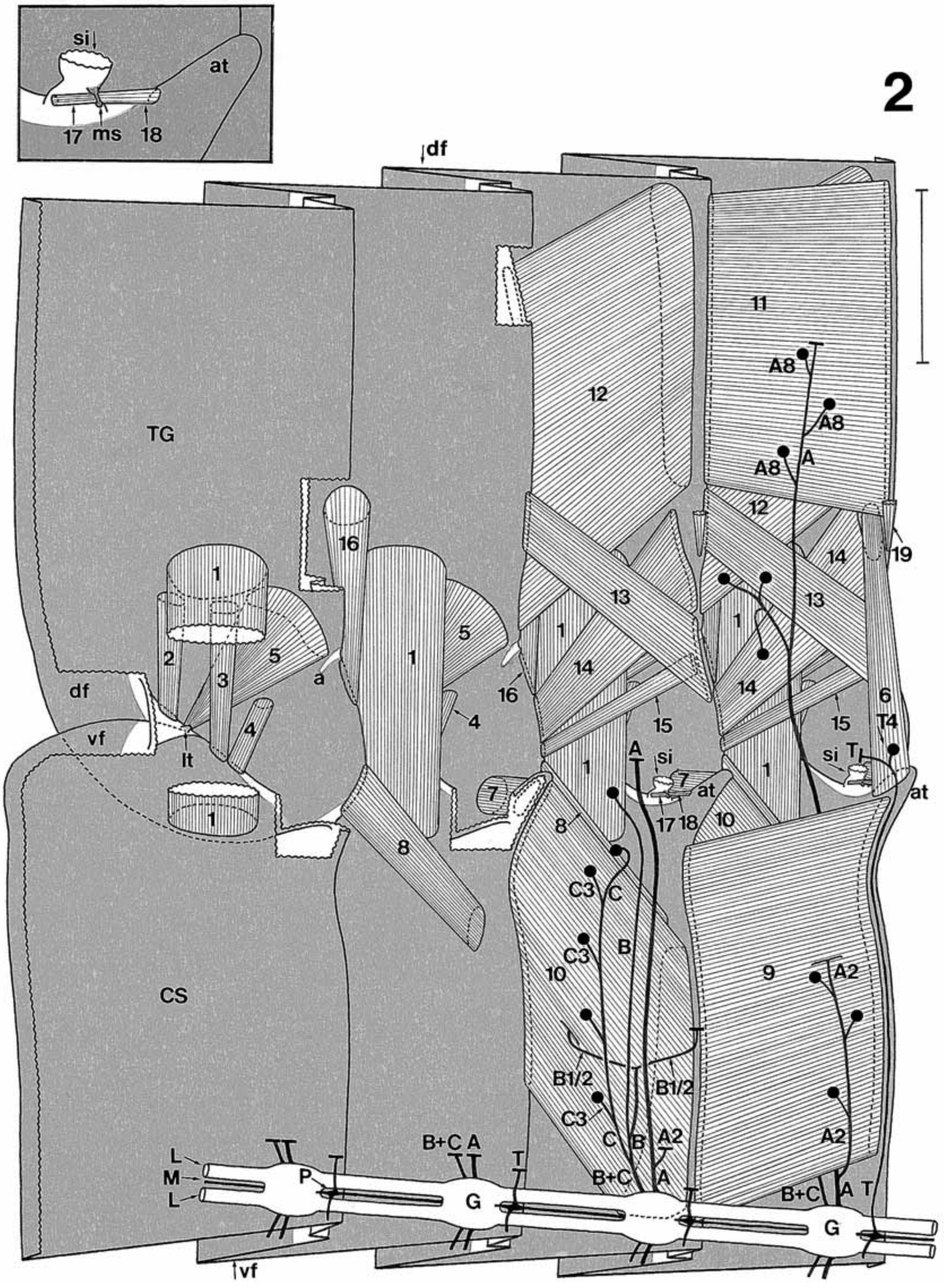


Figure 2. Musculature and nervous system of mid-abdominal segments. Left halves of segments, internal view. Four successive stages of dissection are shown, as would apply to segments IV to VI. From right to left, muscles and nerves are successively removed (left nerves cut by bars). Dorsal part bent, lying in same plane as ventral part. ↑ dorsomedian, ↓ ventromedian, → anterior. Sclerotization dark. Muscles striped according to course of fibres. Nerves black from their roots onward. Nerve branches supplying a muscle ending with a black dot. Cuticular ridges/thickenings not indicated (see Fig. 1). Dashed lines: lateral edge of tergum, hidden borderlines of muscles and their insertions. Scale bar = 0.5 mm. Spiracle area shown separately on upper left margin, 2.5 × enlarged.

polygonal craters (in Dictyoptera designated as zone **ZE***). Internal to this zone, and sharply delimited from it, the taenidial sculpture of the trachea begins (in Dictyoptera designated as zone **ZF***). The atrium has a sculpture resembling that in zone **ZE***. For the closing mechanism see Deoras (1941b; **mup*** therein = manubrium).

Both tergum and coxosternum have a strong antecosta **ac** along their entire anterior margins and, in the middle part, an accessory transverse ridge **pc** immediately behind the antecosta. From ridge **pc** arises, in the midline, a posteriad-directed ridge **vr** (ventral) or **dr** (dorsal). The coxosternal antecosta broadens laterally to occupy the entire apodeme **at**, rendering it very stout. The tergal antecosta has a small lateral area (**a** in Fig. 1) that lacks sclerotization but is as thick as the remaining antecosta; it works as an intrinsic articulation of the tergum. The part of the tergum lateral to point **a** is called here the paratergite (though there is no complete separation: see definition in Snodgrass, 1935b: 81; homology with sclerotizations called paratergites in other Insecta unresolved).

Exoskeleton of segment VII

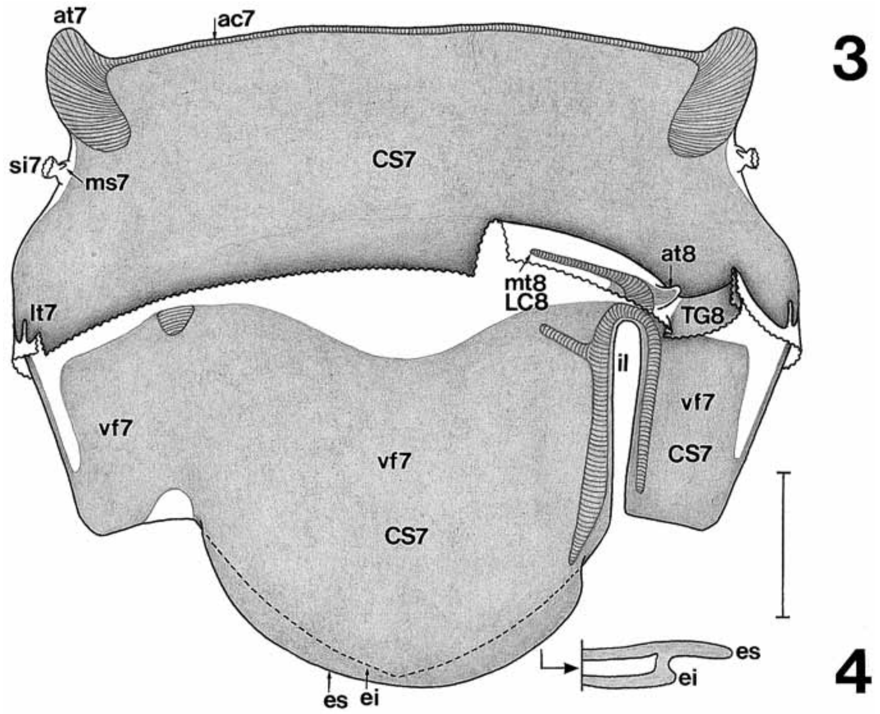
Tergum **TG7**, the pleural membrane with spiracle **si7** and tendon **lt7**, and the anterior part of coxosternum **CS7** are largely as in a mid-abdominal segment, though the ventral ridges **pc** and **vr** are wanting (or poorly indicated), and the broad lateral parts of the coxosternal antecosta extend farther to the posterior (Fig. 3). The posterior part of the venter, however, forms as in other Dermaptera a subgenital fold **vf7** (Fig. 3). This fold differs from its counterparts **vf** in the preceding segments (Fig. 1) by a much more extensive overlapping of the area posterior to it, and by a peculiar differentiation of its hind margin. The ventral wall of fold **vf7** is sclerotized by the posterior portion of **CS7**. Its dorsal wall is likewise sclerotized by **CS7** since as in the preceding segments the cuticle bending anteriad from the hind edge of the fold is sclerotized. The sclerotization is mostly continuous around the edges of the subgenital fold. In the middle part of fold **vf7** the dorsal and ventral sclerotizations stick quite firmly to each other, thus eliminating the body cavity between them.

The right side of the subgenital fold has a deep incision **il**, around which the cuticle is strongly thickened (**il** = proximo-lateral sulciform impression in Rehn & Rehn, 1935). On the left side cuticular thickenings occur in the corresponding area but are less extensive. The extension of the thickened areas shows on both sides some variation. The semicircular posteromedian part of fold **vf7** has two hind edges one above the other (**ei**, **es** in Figs 3, 4; **ei** = submarginal carina in Rehn & Rehn, 1935). The ventral anterior margin of the terminal sclerite **TG11 + DT** (Fig. 5) fits into the shallow groove in between (Fig. 4; submarginal sulciform impression in Rehn & Rehn, 1935). In this way the vestibulum (the chamber above the subgenital fold) can be closed. The left and the right side differ slightly in the outline of the edges **ei** and **es**.

Exoskeleton of segments VIII and IX

The terga **TG8** and **TG9** are very short (Figs 5, 6) and entirely covered by tergum VII (i.e. by **df7**). Both narrowly overlap their succeeding counterparts (by **df8**, **df9** in Figs 5, 6, 10). Distinct antecostae are wanting. In the literature it is claimed that the terga VIII, IX, and X are fused (e.g. Giles, 1963: 134). However, the relations are more complicated. Regarding only the external cuticular layer (Figs 5, 6), the three terga are all free from each other: the tergal sclerotizations are well-bordered; from their hind edges membrane bends anteriad towards the anterior edge of the following tergum. The unmelanized internal cuticular layer (shown together with the external layer in Fig. 10), however, fills the folds **df** between sclerites and membranes. The internal surface of the cuticle is thus an even plane all over the terga VIII–X. Hence, there is not a fusion (loss of membrane between sclerites) of terga VIII–X, but the thick internal cuticular layer holds all sclerites and membranes in a firm position (I call this tergal immobilization). Only the lateralmost parts of terga IX and X are actually fused, without membrane or overlapping between them (**b** in Figs 5, 6).

On the ventral side each segment bears a pair of conspicuous lateral sclerites, which are separated medially by the large genital opening (Figs 5, 6; sclerites usually called medially divided sterna, e.g. Jordan, 1909: 330). Each anterior sclerite **CP8** is, by the membranous line **c**, almost completely divided into a larger caudal portion **CX8** and a smaller cranial portion **LC8**. Each posterior sclerite **CX9** has a small sclerite **LC9** in front of it (Fig. 6), and both sclerites together are comprised here as sclerotization **CP9**. **CX8** articulates posterolaterally with **CX9** and extends medially onto a lobe **gp8** flanking the genital opening. Of **LC8** the lateral part extends onto an apodeme **at8**, and the median part constitutes a long ribbon-like sclerotization. Sclerite **CP8** has a 3-armed cuticular ridge. The posterolateral arm targets the articulation with **CX9**; the posteromedian arm supports lobe **gp8**; the anterior arm crosses the narrow membrane separating the sclerite portions **CX8** and **LC8** and strengthens the median ribbon-part of sclerotization **LC8**. This latter part of the ridge is called here **mt8**. Each sclerite **CX9** has a strong median part and a weak lateral extension fused to the ventromedian margins of terga



Figures 3, 4. Exoskeleton of venter VII. Fig. 3. Dorsal view of coxosternum VII and associated components. ↑ anterior. Sclerotization dark. Anteroventral parts of segment VIII included on right side. Cuticular ridges/thickenings indicated by hatched stripes/areas. Dashed line: inferior hind edge of subgenital fold. Undulate lines: cutting lines through cuticle. Scale bar = 0.5 mm. Fig. 4. Hind edge of subgenital fold. Left view of longitudinal section. Sclerotized cuticle dark; body cavity white. ↑ dorsal, → posterior. No scale.

IX and X (area **b** in Figs 5, 6). Cuticular thickening establishes an oblique ridge on the median part of sclerite **CX9** and occupies the entire lateral extension. The area median and posterior to **CX9** forms a broad lobe **gl9**. Between **CX8** and **CX9** originates an apodeme **at9**, which bears the small sclerite **LC9** in its dorsal wall.

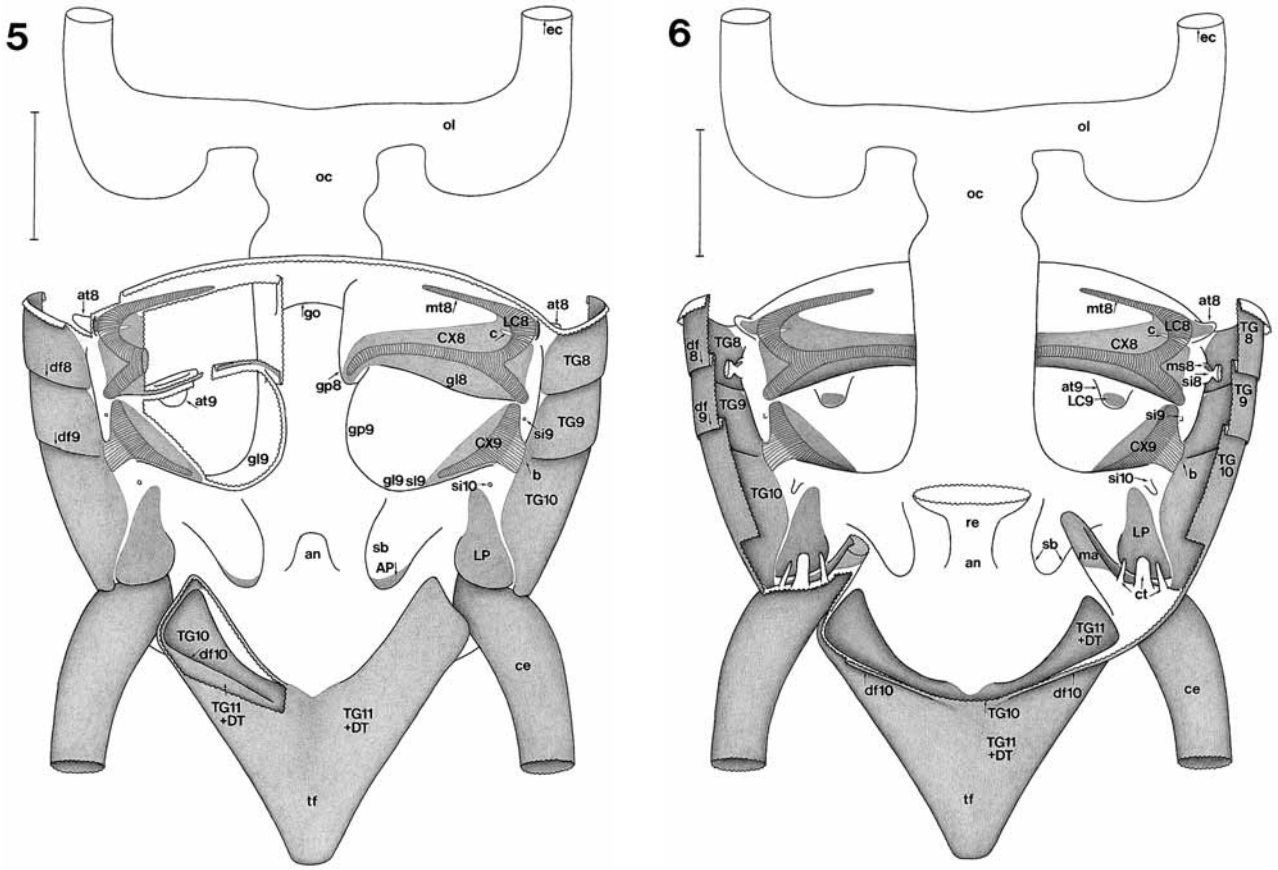
Spiracle VIII **si8** has the same structure and relative position as the more anterior spiracles (Fig. 6). Segment IX has, as in other insects, no spiracle. However, it has in the corresponding position, in the membrane between tergum and coxosternum, a minute brown spot **si9** (Fig. 5). This appears in cross-section as an invagination of the external layer of the cuticle, which is internally entirely embedded in the thick internal layer of the cuticle and thus not perceptible as an invagination from within (only external layer of this area depicted in Fig. 6).

The lateral and common oviducts (**ol**, **oc** in Figs 5, 6) are, due to the viviparity, very wide. Figures 5, 6 do not show that the oviduct walls are longitudinally folded all over, the folds being a reservoir for much further expansion of the ducts. The gonoduct opens between the lobes **gp8**, and the transverse fold **go** is the anterior border of the genital opening.

Exoskeleton of segments X and XI and telson

Tergum **TG10** is very long (Figs 6, 22). It is anteriorly overlapped by and immovably associated with **TG9** in the way explained above (Fig. 10). Posterior to the fusion area **b** of sclerites **TG9**, **TG10**, and **CX9** lies the triangular sclerite **LP**, which is separated from **TG10** by a narrow membrane (Figs 5, 6). Median to **LP** arises the subanal lobe **sb**, which bears a weak sclerite **AP** on its posterior face. The anus **an** lies between the two subanal lobes. The rectum **re** has a narrow terminal portion (Fig. 6) and widens internally into a bulb bearing the six rectal papillae **rp** (Fig. 12). Segment X has, like segment IX, on each side a brown spot **si10** near the ventromedian margin of the tergum (Fig. 5). It appears in cross-section as an invagination of both the external and internal layers of the cuticle (Fig. 11), thus being also from within perceptible as an invagination (Fig. 6).

The terminal sclerite **TG11 + DT** (Figs 5, 6), shaped like a posteriorly tapering bag, forms a massive process **tf**. This seems to be the posterior tip of the abdomen, which, however, is in the morphological sense constituted by the anus **an**. Sclerite **TG11 + DT** and process **tf** are thus entirely dorsal components. At its dorsal anterior margin (Figs 5, 12, 22) **TG11 + DT** is



Figures 5, 6. Exoskeleton of postabdomen, segments VIIIff. ↑ anterior. Sclerotization dark. All cuticular parts of lateral oviducts included; cerci cut; only external cuticle layer considered for terga VIII to X (compare Fig. 10). Cuticular ridges/thickenings indicated by hatched stripes/areas. Undulate lines: cutting lines through cuticle. Sclerites CX8 + LC8 = CP8; CX9 + LC9 = CP9. Scale bar = 0.5 mm. Fig. 5. Ventral, predominantly external view. On left side large parts of venters VIII and IX removed. Fig. 6. Dorsal, predominantly internal view. Rectum cut close to anus. Cercal apodeme ma cut on left side (cut through massive cuticle).

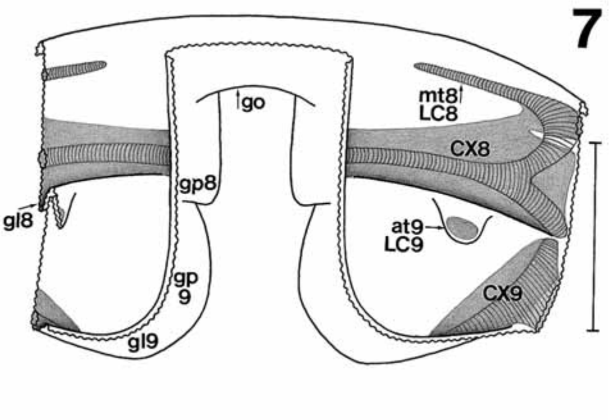
fused to and level with tergum **TG10** near the midline but free from **TG10** and narrowly overlapped by it more laterally (fold **df10** in Figs 5, 6, 8). At its ventral anterior margin (actually its posterior margin; Figs 5, 6) **TG11 + DT** has a wide semicircular recess, with the sclerite's rim somewhat overfolding the membrane in the recess. As mentioned above, this rim fits into the groove between the hind edges **es** and **ei** of the subgenital fold.

The bases of the cerci **ce** are located beneath the lateral hind margin of tergum **TG10** (Figs 6, 22); ventrally they are in contact with sclerites **LP** and **TG11 + DT** (Fig. 5). The cercal base is firmly held in between these three sclerites but has no distinct articulation with either of them. Basally the cercal walls project into the body cavity, forming a U-shaped infolding (U open laterally; Figs 6, 8, 9). Its median portion, projecting most deeply, is termed here apodeme **ma**. Only on the distal part of **ma** the cercal sclerotization **CE** enters the outer wall of the infolding. Dorsolaterally the cercal base bears three delicate cuticular tendons **ct**. The cerci are long and thread-like. I concur with Popham (1985: 204, fig. 8) that they may appear to be, but are not, divided into articles: the cuticle, very thick considering both external and internal layers, is uniformly weakly sclerotized all along the cerci, without annular membranes, and without complete annular grooves.

MUSCULATURE OF *HEMIMERUS*

Extent of muscle studies

Of the muscles present in the abdomen from segment IV on only the intrinsic muscles of the oviducts and of the rectum (except muscle **51**) are not considered here. The alary muscles were, due to the condition of the specimens, difficult to examine. Those of segments VIII–X were not found, probably overlooked. Nutting (1951: 530) indirectly reports these for *Hemimerus*



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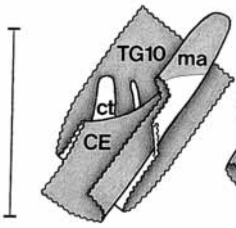

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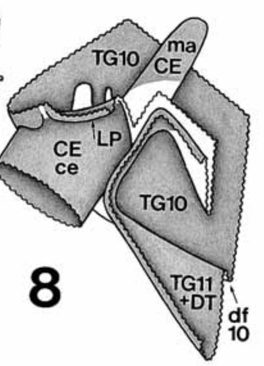

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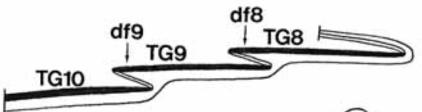

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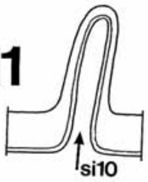

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Figures 7–11. Details of exoskeleton of postabdomen. Sclerotization dark. Fig. 7. Dorsal, predominantly internal view of area around genital opening. Representation as in Fig. 6 but many parts removed, in particular those of gonoducts. Scale bar = 0.5 mm. Figs 8, 9. Exoskeleton of cercal base area. Ventral view of right cercal base. ↑ anterior, → median. Cuticular thickenings not considered. Undulate lines: cutting lines through cuticle. Scale bar = 0.5 mm. Fig. 10. Terga VIII to X. Right view of longitudinal section near dorsal midline, schematic. ↑ dorsal, → anterior. External and internal layers of cuticle included. External layer: narrow interspace, partly melanized = filled black (TG8–10). Internal layer: broad interspace, entirely unmelanized. No scale. Fig. 11. 'Spiracle vestige' X si10. Section in median view, schematic. ↓ ventral, → posterior. External and internal layers of cuticle included. External layer: narrow interspace. Internal layer: broad interspace. No scale.

vosseleri, saying that all species he studied have 10 abdominal pairs.

Musculature of segments IV–VI

The musculature was found identical in these segments (Fig. 2). Homodynamous muscles are described and numbered together. Each insertion is assigned to the secondary segment it lies upon: 'N' designates the secondary segment, or a component of it, whose major part corresponds to the primary segment the muscle belongs to. 'N + 1' designates the succeeding secondary segment, or a component of it. Muscles having both insertions on 'N' are intrasegmental, muscles having one insertion on 'N + 1' are intersegmental relative to secondary segmentation.

1: Tergum N, lateral part↔Coxosternum N, lateral part. Intrasegmental tergo-coxosternal muscle. One strong, compact bundle. **2**: Tergum N, lateral part↔Pleural membrane above coxosternum N. Intrasegmental tergo-coxosternal muscle. One small, compact bundle. **3**: Tergum N, lateral part↔Coxosternum N, lateral margin. Intrasegmental tergo-coxosternal muscle. One small, compact bundle. **4**: Tergum N, far lateral part↔Coxosternum N, lateral margin. Intrasegmental (para)tergo-coxosternal muscle. One small, compact bundle. **5**: Tergum N, anterolateral part↔Tendon **lt** N. Intrasegmental tergo-coxosternal muscle. One strong, compact bundle. **6**: Tergum N, lateral anterior margin↔Coxosternum N, anterolateral corner, on apodeme **at**. Intrasegmental tergo-coxosternal muscle. One moderately strong, compact bundle. **7**: Tergum N, anterolateral corner↔Pleural membrane forming external face of apodeme **at** of coxosternum N. Intrasegmental (para)-tergo-coxosternal muscle. One moderately strong, compact bundle. **8**: Coxosternum N, lateral part↔Tergum N + 1, anterolateral corner; partly on adjacent membrane and on a small membranous tendon. Intersegmental coxosterno-(para)tergal muscle. One moderately strong, compact bundle.

9: Coxosternum N, anterior margin↔Coxosternum N + 1, anterior margin. Internal ventral muscle. One strong, compact sheet. **10**: Coxosternum N, anterior part↔Coxosternum N + 1, anterior margin, and intercoxosternal membrane. External ventral muscle. One strong, compact sheet. **11**: Tergum N, anterior margin↔Tergum N + 1, anterior margin. Internal dorsal muscle. One strong, compact sheet. **12**: Tergum N, anterior part↔Tergum N + 1, anterior margin, and, predominantly, intertergal membrane. External dorsal muscle. One strong, compact sheet. **13**: Tergum N, lateral anterior margin↔Tergum N + 1, anterior margin. External dorsal muscle. One moderately strong, compact sheet. **14**: Tergum N, anterior part↔Tergum N + 1, lateral anterior margin. External dorsal muscle.

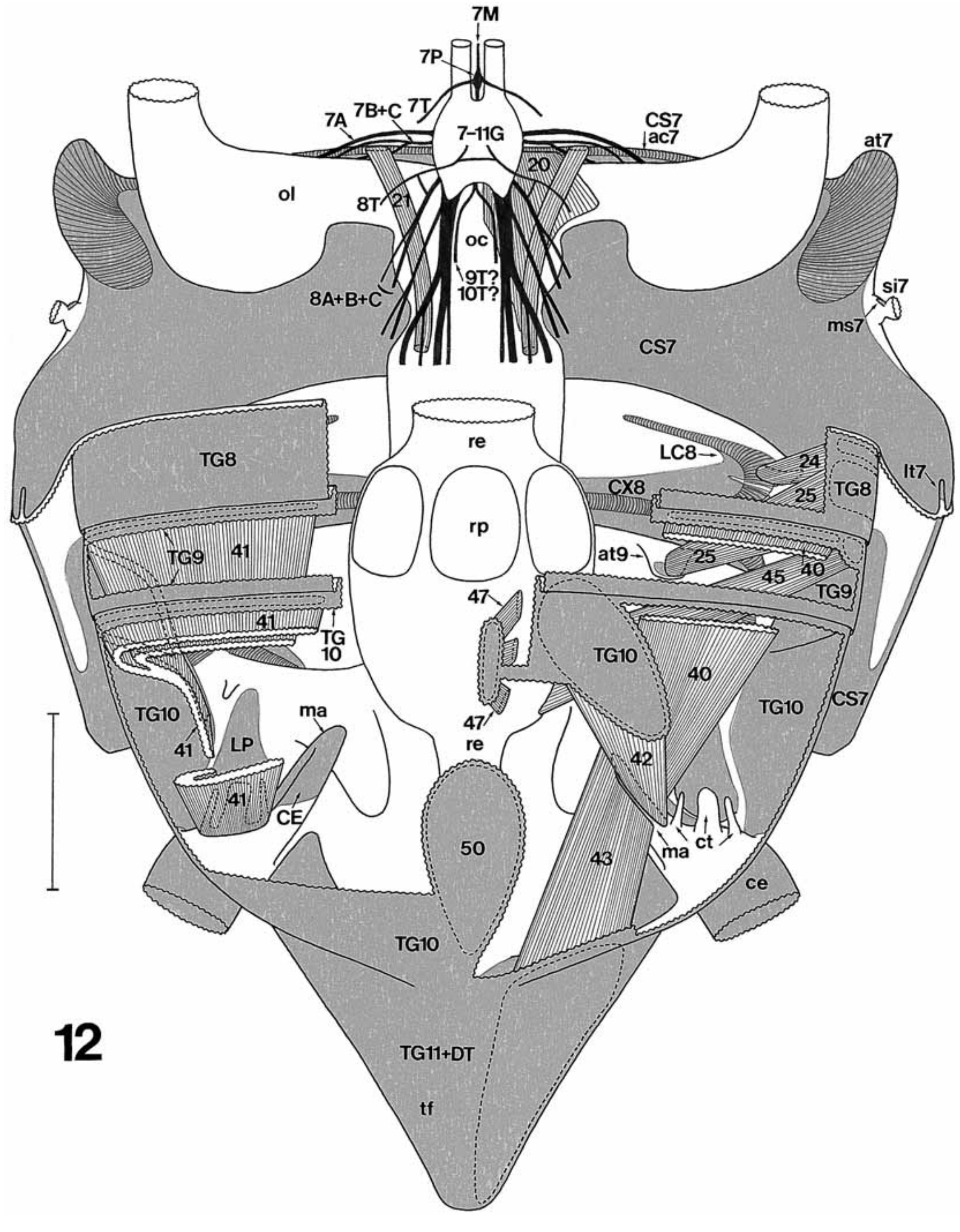

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Figure 12. Musculature and nervous system of postabdomen, segments VIIff. Focus on dorsally located muscles (those of segment VII not shown). Dorsal, predominantly internal view. ↑ anterior. Sclerotization dark. Cuticular ridges/thickenings indicated by hatched stripes/areas. Muscles striped according to course of fibres. Dashed lines: hidden borders of muscle insertions. Terminal compound ganglion 7–11G and bases of all nerves arising from it included; ganglion white, nerves black from their roots onward. Scale bar = 0.5 mm.

One moderately strong, compact sheet. **15**: Tergum N, anterolateral part↔Tergum N + 1, far lateral anterior margin. External dorsal muscle. One small, compact sheet. **16**: Tergum N, posterior part↔Tergum N + 1, lateral anterior margin. External dorsal muscle. One moderately strong, compact bundle.

17: Manubrium **ms** of spiracle N↔Posteromedian wall of atrium of spiracle N. Spiracle occlusor. One

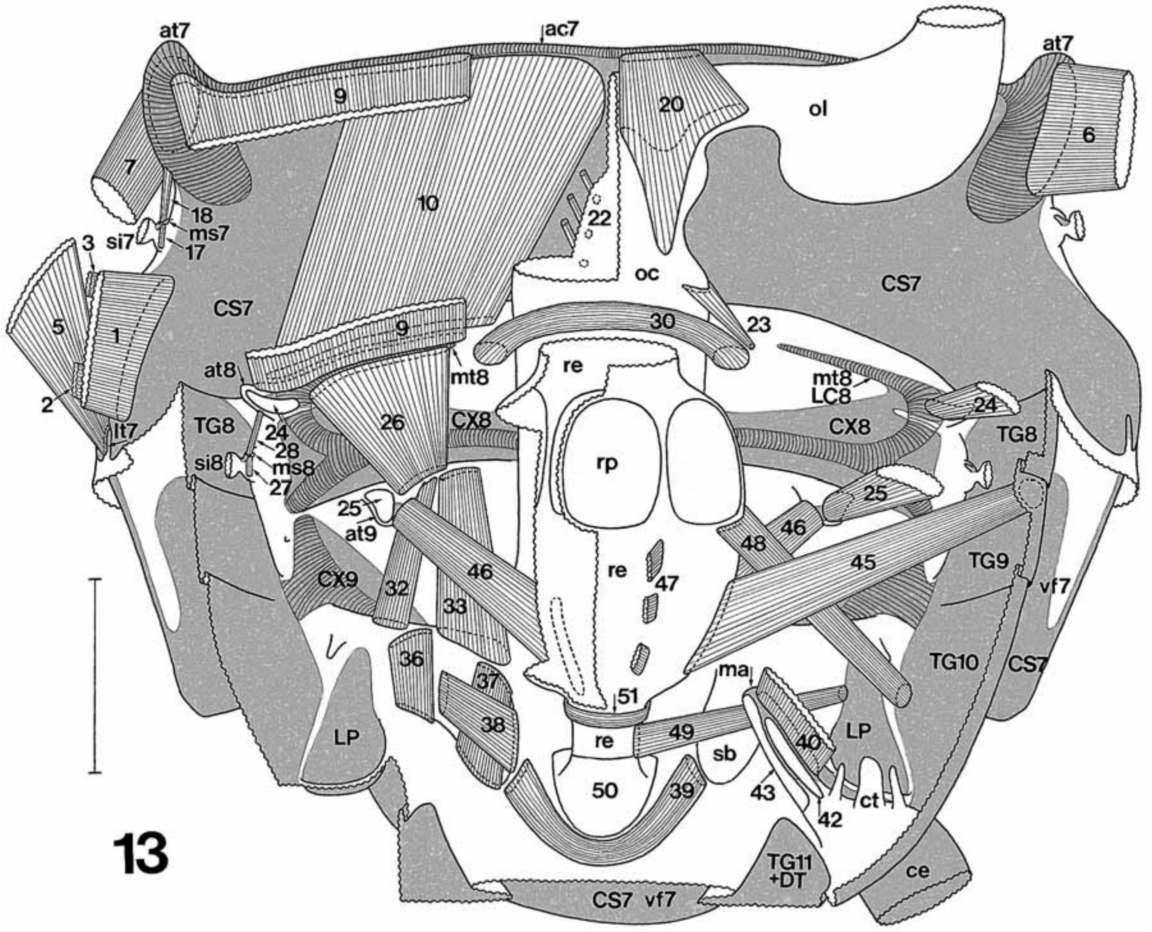


Figure 13. Musculature of postabdomen, segments VIIff. Focus on ventrally located muscles. Representation as in Fig. 12. Left parts of common and lateral oviducts and left wall of rectum removed. Scale bar = 0.5 mm.

small, compact bundle. **18**: Manubrium **ms** of spiracle N↔Coxosternum N, on lateral base of apodeme **at**. Spiracle dilator. One small, compact bundle. **19**: Tergum N, lateral anterior margin↔Extending towards dorsal midline. Alary muscle. It arises as a thin, compact bundle from the tergum, its fibres then spreading fanwise towards the dorsal midline (more details in Nutting, 1951).

Musculature of segment VII

Most muscles are serial homologues of and have the same courses as muscles of the segments IV–VI. They are designated by the same numbers and are not listed here (ventral and lateral muscles shown in Fig. 13). The differences are: (1) Intrasegmental (para)tergo-coxosternal muscle **4** and (2) intersegmental coxosterno-(para)tergal muscle **8** were not found. (3) Some additional muscles are present, all attached to the common oviduct **oc** (one of them, **23**, is assigned here to segment VIII): **20**: Coxosternum VII, median anterior margin↔Common oviduct, dorsal wall (Figs 12, 13). Delicate sheet, diffuse. **21**: Coxosternum VII, median anterior margin↔Common oviduct, posterior dorsal wall (Fig. 12). Internal to foregoing muscle, not always distinct from it. Delicate bundle, quite compact. **22**: Coxosternum VII, anteromedian part↔Common oviduct, ventral wall (Fig. 13). Diffuse group of fibres; only a few shown in figure.

Musculature of segment VIII

23: Common oviduct, lateral wall↔Membrane median to ridge **mt8** (Fig. 13). Quite compact near the latter insertion but becoming diffuse towards the former. **24**: Tergum VIII, anterolateral part↔Sclerite **CP8**, part **LC8** on dorsal face of apodeme **at8** (Figs 12, 13). Intrasegmental tergo-coxosternal muscle. One compact bundle. **25**: Tergum VIII, lateral part↔Sclerite **LC9** on apodeme **at9** (Figs 12, 13). Intersegmental tergo-coxosternal muscle VIII or intrasegmental tergo-coxosternal muscle IX. One compact bundle. **26**: Sclerite **CP8**, part **LC8** on ridge **mt8**↔Membrane posterior to sclerite **CP8** (Fig. 13). Internal (or external?) ventral

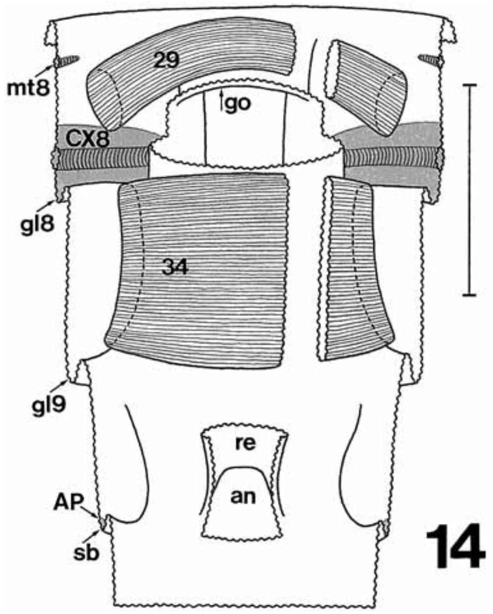


Figure 14. Ventral transverse muscles of postabdomen. Showing area between genital opening and anus; representation as in Fig. 12. Scale bar = 0.5 mm.

muscle. One compact sheet. **27**: Manubrium **ms** of spiracle VIII↔Posteromedian wall of atrium of spiracle VIII (Fig. 13). Spiracle occlusor. One small, compact bundle. **28**: Manubrium **ms** of spiracle VIII↔Sclerite **CP8**, part **LC8**, posterolaterally on apodeme **at8** (Fig. 13). Spiracle dilator. One small, compact bundle. **29**: Transversely on membranous venter VIII, crossing common oviduct (or vagina?) ventrally (Fig. 14). Unpaired. Slightly diffuse. **30**: Transversely on membranous venter VIII, crossing common oviduct (or vagina?) dorsally (Fig. 13). Unpaired. Slightly diffuse. **31**: Alary muscle VIII, see Nutting (1951).

Musculature of segment IX

32: Membrane posterior to sclerite **CP8**↔Membrane posterior to sclerite **CX9** (Fig. 13). Internal (or external?) ventral muscle (possibly a ventral muscle X). One compact sheet. **33**: Membrane posterior to sclerite **CP8**↔Membrane posteromedian to sclerite **CX9** (Fig. 13). Internal (or external?) ventral muscle (possibly a ventral muscle X). One compact sheet. **34**: Transversely on membranous venter IX (Fig. 14). It is unlikely but cannot be excluded that some fibres insert near the ventral midline. Unpaired. Slightly diffuse. **35**: Alary muscle IX, see Nutting (1951).

Musculature of segments X and XI and telson

36: Anterolateral base of subanal lobe **sb**↔Posterolateral base of subanal lobe **sb** (Fig. 13). One compact sheet. **37**: Anteromedian base of subanal lobe **sb**↔Posteromedian base of subanal lobe **sb** (Fig. 13). One compact sheet. **38**: Lateral part of subanal lobe **sb**↔Median base of subanal lobe **sb** (Fig. 13). One compact sheet. **39**: Transversely and U-shaped behind anus, insertions near posteromedian base of subanal lobe **sb** (Fig. 13). Unpaired. Median part compact, lateral parts diffuse. **40**: Tergum IX, anterior margin↔Median cercal base, anterior face of apodeme **ma** (Figs 12, 13). Cercal muscle (internal dorsal muscle X). One compact sheet. **41**: Complex anterior insertion: anterior margins of terga IX and X (occasionally some fibres inserted in between on body of tergum IX) and anterior ventromedian margin of tergum X↔Lateral cercal base, on tendons **ct** (Fig. 12). Cercal muscle (external dorsal muscle X). Anteromedially composed of two well-separated sheets. Ventromedially and posteriorly the sheets unite. **42**: Tergum X, anteromedian part↔Median cercal base, anterodorsal face of apodeme **ma** (Figs 12, 13). Cercal muscle (internal dorsal muscle X or intersegmental tergo-coxopodial muscle X). One strong, compact bundle. **43**: Sclerite **TG11 + DT**, entire dorsal wall↔Median cercal base, posterodorsal face of apodeme **ma** (Figs 12, 13). Cercal muscle (intrasegmental tergo-coxopodial muscle XI). One strong, compact bundle. **44**: Alary muscle X, see Nutting (1951).

Musculature of rectum

45: Tergum IX, lateral anterior margin↔A longitudinal line in lateral wall of rectum (Figs 12, 13). Lateral extrinsic rectal muscle. Compact near dorsolateral insertion but spreading fanwise and becoming diffuse towards rectal insertion. **46**: Sclerite **LC9** on apodeme **at9**, median face↔A longitudinal line in ventrolateral wall of rectum (Fig. 13). Ventral extrinsic rectal muscle. Compact near ventrolateral insertion but spreading fanwise and becoming diffuse towards rectal insertion. **47**: Tergum X, anteromedian part↔A longitudinal line in dorsolateral wall of rectum (Figs 12, 13). Dorsal extrinsic rectal muscle. Present as three slightly diffuse bundles. **48**: Tergum X, ventral margin↔A short vertical line in lateral wall of rectum, immediately anterior to rectal papillae (Fig. 13). One slightly diffuse bundle. **49**: Sclerite **LP**, median margin↔Posteriormost lateral wall of rectum (Fig. 13). One compact bundle. **50**: Tergum X, posteromedian part↔Anus, posterior side (Fig. 12: dorsal insertion area; Fig. 13: ventral insertion area). Unpaired. A diffuse group of fibres. **51**: Circular course around posterior part of rectum. Insertion of fibres unresolved. (Fig. 13). Unpaired. Rectal constrictor, a rather compact part of the rectal circular musculature.

NERVOUS SYSTEM OF *HEMIMERUS*

Central components

The neuromeres of segments IV–VI, **4G** to **6G**, form each a ganglion located in the anterior part of its segment (Fig. 2). The posterior neuromeres **7G** to (probably) **11G** form a terminal compound ganglion **7–11G** located at the segmental border VI/VII, in the fork between the lateral oviducts **ol** (Fig. 12). The composition of 5 neuromeres VII–XI is hypothetical: this is the set usually present when in the embryo all 11 abdominal segments are distinct (e.g. Heymons, 1895b: 38; Roonwal, 1937: fig. 102). However, in *Forficula* and probably in *Hemimerus talpoides* Walk., which is claimed by Heymons (1912: 167, 171) to conform in abdominal ontogeny with *Forficula*, the coelomic cavity and the neuromere anlage of segment XI are not distinct (Heymons, 1895b: 37).

The median nerve **M**, running in between the connectives **L**, is distinct between all ganglia (Fig. 2); the posteriormost is **7M** (Fig. 12). Paired transverse nerves **T** arise from all nerves **M**, the posteriormost of these being **7T**. A small swelling **P**, located where a pair of nerves **T** originates from a nerve **M**, is presumably the perisympathetic organ. Tentatively, these organs may represent the primitive median type, distal variant (see Grillot, 1983). A nerve pair arising from the dorsal wall of ganglion **7–11G** is probably **8T** (Fig. 12); the two **8T** are either transversely interconnected or have a short common stem (only two observations made). **8T** has a basal anastomosis with **8A + B + C**, the common stem of the dorsal and ventral nerves VIII, as in e.g. *Periplaneta americana* (L.) (**2A*** connecting **3A1*** and **2–VIII*** in Pipa, 1988: figs 6, 9). Another nerve pair arising with a common stem from the posterior face of ganglion **7–11G** may represent **9T** or **10T** (compare Pipa, 1988: fig. 8, **2–IX*** = **9T**, **2–X*** = **10T**; Seabrook, 1968: fig. 11, **8tv.n*** = **9T**, **9tv.n*** = **10T**).

From each ganglion **4G** to **6G** originate anteriorly the dorsal (**A**) and posteriorly the ventral nerve (**B + C**), the latter soon forking into the nerves **B** and **C** (Fig. 2). From ganglion **7–11G** originate several nerves, of which those of segments VII and VIII could be identified (**7A**, **7B + C**, **8A + B + C** in Fig. 12). The remaining nerves are those of the more posterior segments.

Peripheral components

Only the major nerves of the mid-abdominal segments and some of their branches and targets could be observed. Nerve **T** runs laterad between the ventral muscles **9** of successive segments (Fig. 2); this is a course along the primary segmental border. Having reached apodeme **at**, nerve **T** ascends shortly dorsad along muscle **6** and sends a branch **T4** into it. The main part of nerve **T** curves then posteriad towards the spiracle area. Nerve **A** produces a basal branch **A2** that runs laterad along the internal face of the internal ventral muscle **9** and sends rami into it. In the lateral third of muscle **9** branch **A2** dives into the muscle. The main part of nerve **A** runs laterad in between the internal and external ventral muscles **9** and **10**. Then it ascends dorsad and mesad internal to all lateral and dorsal muscles. Branches and rami of nerve **A** go, at least, into the dorsal muscles **11** (via several branches **A8**), **12**, **13**, and **14**. Both the nerves **B** and **C** likewise extend laterad between muscles **9** and **10**. Nerve **B** gives rise to a basal branch **B1/2** that targets with several rami the ventral body wall, partly by penetrating muscle **10**. **B1/2** is probably a ventral sensory branch. For the remainder of nerve **B** only the innervation of the tergo-coxosternal muscle **1** could be ascertained. Nerve **C** sends several branches **C3** into the external ventral muscle **10** before its distal part enters the coxosterno-(para)tergal muscle **8**.

DISCUSSION OF VENTRAL NERVE CORD

In *Hemimerus vosseleri* the posteriormost ganglion (**7–11G** in Fig. 12) clearly includes **7G** since its anteriormost nerves branch into segment VII. **4G**, **5G**, and **6G** are separate ganglia. Jordan (1909: 329) for *H. talpoides* and Deoras (1941b: 324) for *H. deceptus* report six discrete abdominal ganglia. Assuming correspondence between the three species, the two remaining ganglia are probably **2G** and **3G**, ganglion **1G** being then fused to the metathoracic ganglion (termed here **0G**) to form a compound ganglion **0–1G** (not counted as abdominal). The resulting ganglionic formula is 0–1/2/3/4/5/6/7–11, the same as in the investigated Forficulina (*Labidura riparia* in Khandekar, 1972; *Anisolabis maritima* [Géné] in Nesbitt, 1941) and in Blattaria and Isoptera (e.g. Nesbitt, 1941; Shankland, 1965). Mantodea have a formula derived from the aforementioned one, 0–3/4/5/6/7–11 (e.g. Kerry & Mill, 1987). The fusion of **7G** and **8–11G**, absent in many Neoptera (see e.g. Nesbitt, 1941), could be a synapomorphy of Dermaptera and Dictyoptera. On the other hand, there is much homoplasy in the fusion of abdominal ganglia. For instance, a formula derivable from 0–1/2/3/4/5/6/7–11 is also present in *Gryllus assimilis* Fabr. (Nesbitt, 1941: 0–2/3/4/5/6/7–11).

Deoras (1941b) reports for *H. deceptus* a different location of the ganglia in relation to their segments: all one segment more anteriorly (1st abdominal ganglion **2G** in abdominal segment I, etc.). The transverse band connecting the two connectives from **5G** to **6G** (Deoras, 1941b: **fu*** in fig. 11) probably corresponds to the roots of the transverse nerves **6T** from the median nerve **6M** (see Fig. 2; **T** and **M** not considered by Deoras).

DISCUSSION OF MID-ABDOMINAL SEGMENTS IV–VI

EXOSKELETON COMPARED IN *HEMIMERUS*, FORFICULINA, AND ZYGENTOMA

Similarities between the taxa

The mid-abdominal segments of *Hemimerus* (Fig. 1) resemble those of Forficulina and Zygentoma; *Ta-*

galina, Labidura, Forficula, and *Ctenolepisma* were used for a comparison. In all taxa the terga are slightly anterior to the corresponding coxosterna (most distinctly in *Ctenolepisma*), and their lateral parts broadly overlap the lateral parts of the coxosterna. 'Pleural' sclerites in the pleural membrane are lacking. The spiracles lie in the pleural membrane near the lateral margin of the coxosternum, thus hidden by the overlapping of the terga. The tergum has a distinct antecosta but no acrotergite. A point of weakness is present in the lateral anterior margin of the tergum (like **a** in Fig. 1; Rousset, 1973: 58, reports for the zygentoman *Thermobia domestica* [Packard, 1873] this weak point as "zone amincie", but only for segment IX; see **za*** in Fig. 28). In *Ctenolepisma* the antecosta forms in this point a small hook to the posterior and continues as a weak ridge slightly below the weak point, whereas in the Forficulina and in *Hemimerus* the sclerotization has a short gap but the antecosta continues straightly. The mentioned features shared by *Ctenolepisma, Hemimerus,* and the Forficulina could be plesiomorphies at the level of Dicondylia.

Two of Popham's (1959: 276) statements on *Forficula* have to be revised. (1) It is clearly incorrect that the spiracles lie on the terga, and Popham's conclusion that the terga therefore contain 'sclerotized pleural areas' has no base. (2) Terga and coxosterna do not alternate to the strong extent shown in Popham (1959: fig. 15), but the dorsal antecosta is only slightly anterior to the ventral antecosta. In a lateral view the impression of alternation is enhanced because each tergum is broadest (i.e. most strongly ventrad-projecting) anteriorly, overlapping the coxosternum much less in its posterior part. This results in a zig-zag line along the flanks of the abdomen. Conditions in *Hemimerus* and also in *Ctenolepisma* are in my view the same, and I cannot find a difference between Forficulina and *Hemimerus* in this respect as claimed by Popham (1961: 23; 1985: 204, 206, character 8).

Differences between the taxa

Ctenolepisma lacks apodemes **at**, tendons **lt**, and accessory ridges **pc**, **vr**, and **dr**; in its spiracles I found no trace of a manubrium **ms** and of the anastomosing ridges present in the tracheal base (zone **ZE***) and in the atrium of *Hemimerus*. The Forficulina have apodemes **at**, tendons **lt**, a manubrium **ms**, and anastomosing ridges in tracheal base (zone **ZE***) and atrium; ridges **vr** and **dr** are only in *Tagalina* distinct, but the other species have occasionally darker lines in the corresponding positions; ridges **pc** are absent.

The distribution of these components across the various pterygotan or dermapteran subgroups may give indications on the phylogeny of these taxa, but the currently available information does not allow unambiguous conclusions. (1) The manubrium **ms** is present in many Neoptera (see in Klass, 2000) but apparently not outside this taxon. (2) Anastomosing ridges in zone **ZE*** are present in Blattaria and Isoptera (Klass, 2000: figs 9, 12) but may be of wider occurrence. Both **ms** and **ZE*** could be autapomorphies of Neoptera or a subgroup thereof. (3) Apodemes resembling **at** are found in e.g. Odonata, Caelifera, and Hymenoptera; they bear, like in *Hemimerus*, the insertions of the spiracle dilator **18** (at the posterior base; muscle absent in Odonata) and of a muscle **7** to the ventrolateral part of the tergum (Odonata: posterior sternal apophyses, muscle **adv*** in Asahina, 1954: e.g. fig. E52; Caelifera: lateral apophyses **lAp***, muscles **177***, **180*** in Snodgrass, 1935a; Hymenoptera: apophyses **c***, muscles **159***, **160*** in Snodgrass, 1956: fig. 54). Nevertheless, the homology of the apodemes in these taxa is uncertain because of their absence in many other Pterygota. (4) Ridges **vr** and **dr** and (5) tendons **lt** are to my knowledge not reported for other Insecta and could be autapomorphies of Dermaptera or subgroups thereof.

MUSCULATURE COMPARED IN *HEMIMERUS* AND FORFICULINA

The mid-abdominal musculature of Dermaptera has so far been studied only by Ford (1923) and Popham (1959), who both treat *Forficula*. Their descriptions are very contradictory, and data on innervation are not available. This makes a comparison between *Forficula* and *Hemimerus* very difficult (results in Table 1).

In the lateral muscles (tergo-coxosternals) Ford's **qtg***, **ttg***, **stg***, and **tsm*** are very similar to **1**, **5**, **6**, and **7** of *Hemimerus* (Fig. 2). Homologues of the smaller intrasegmental tergo-coxosternals **2**, **3**, and **4**, and of the intersegmental coxosterno-(para)tergal **8** of *Hemimerus* are not reported. Instead, Ford finds in *Forficula* an additional anterior tergo-coxosternal **ptg***, which has a similar course as muscle **stg*** = **6** but inserts on the tergum more medially. Popham reports only two lateral muscles **DLM*** and **TSM***, which correspond to a fused muscle **6** + **7** and to muscle **1** of *Hemimerus*. In the ventral muscles Ford's **is*** and **os*** correspond with **9** and **10** of *Hemimerus*. Popham's muscle **MVM*** resembles the internal ventral **is*** = **9**; his **OVM*** may correspond to **os*** = **10** but is very unusual in extending posteromesad rather than posterolaterad from its anterior insertion.

In the dorsal muscles a counterpart of the far posterior muscle **16** of *Hemimerus* is not reported for *Forficula*. Popham, but not Ford, describes a muscle **LOM*** that extends posteromesad from its anterior insertion like muscle **13** of *Hemimerus*. Popham describes only one further dorsal muscle **RDOM/LDOM*** (defined as a pair), which may correspond to **11**, or **12**,

Table 1. Homology of muscles of mid-abdominal segments in Dermaptera and Dictyoptera. The first column gives the course of the muscle and its innervation by nerve A, B, C, or T; nerve in brackets: only known for Dictyoptera; nerve not in brackets: also known for *Hemimerus*. In the other columns the muscle terms used by the authors are entered (two terminologies used by Popham). NR = corresponding muscle not reported. AB = corresponding muscle clearly absent. * = muscle of Dictyoptera with more or less different course, thus possibly not homologous with muscle of Dermaptera

Muscle (-group)	*Hemimerus*	*Forficula*	*Forficula*	Dictyoptera
	This paper	Ford, 1923	Popham, 1959	Klass, 1999, 2000
lateral				
intrasegmental B	1	qtg	5 = TSM	1
intrasegmental ?	2, 3	NR	NR	1 ex parte (?)
intrasegmental ?	4	NR	NR	1 ex parte (?)
intrasegmental ?	5	ttg	NR	1 ex parte (?)
intrasegmental T	6	stg	3 = DLM ex parte	2
intrasegmental (T)	7	tsm	3 = DLM ex parte	3
intrasegmental ?	AB	ptg	NR	AB
intersegmental C	8	NR	NR	4, 5
intersegmental C	AB	NR	NR	6
ventral				
internal A	9	is	6 = MVM	7
external C	10	os	4 = OVM	8, 9
dorsal				
internal A	11	it	1 = R/LDOM	10
external A	12	ot median	1 = R/LDOM	11b
external A	13	NR	2 = LOM	AB
external A	14, 15	ot lateral	NR	12*
external (A)	16	NR	NR	11a
spiracle				
occlusor (T)	17	om	NR	13
dilator (T)	18	ant	NR	14*
transverse				
alary (A, T?)	19	NR	NR	15
hyperneural (A, T?)	AB	NR	NR	16

or both of *Hemimerus*; even if intended to represent two muscles of the same side they do not conform with the dorsal musculature as described in Ford. Ford's muscles **it*** and **ot***, the latter divided into two portions, resemble **11**, **12**, and **14** + **15** of *Hemimerus*. In addition, Ford describes two spiracle muscles (**ant***, **om***) in the same positions as in *Hemimerus*. The alary and ventral transverse muscles are not considered by Ford and Popham.

In sum, only the absence of the intersegmental coxosterno-(para)tergal **8** and of the external dorsal **16** in *Forficula* are differences to *Hemimerus* that result from both Ford's and Popham's studies. Since muscle **8** has homologues in Dictyoptera (see in next section) and other Pterygota, its absence in *Forficula* is, if true, probably the apomorphic state.

MUSCULATURE AND NERVOUS SYSTEM COMPARED IN *HEMIMERUS* AND DICTYOPTERA

Data on the mid-abdominal musculature and nervous system of Dictyoptera are available in the author's (Klass, 1999, 2000) studies of *Periplaneta americana* Linnaeus, 1758, *Sphodromantis viridis* Forskal, 1775, and *Mastotermes darwiniensis* Froggatt, 1896. In Dictyoptera the lateral muscles fall into three groups supplied by nerves **B**, **C**, and **T**, respectively (B-, C-, and T-muscles in Klass, 1999: e.g. fig. 41). The ventral muscles fall into internals and externals supplied by nerves **A** and **C**, respectively. The dorsal muscles are all supplied by nerve **A**. A comparison with some other Neoptera is included in Klass (1999). In the following, muscle numbers relating to taxa other than *Hemimerus* are marked with *; the nerve terminology corresponds in *Hemimerus* and Dictyoptera.

The lateral muscles fall also in *Hemimerus* (Fig. 2) into B-, C-, and T-muscles. Muscle **1** corresponds with muscle **1*** of Dictyoptera in its intrasegmental tergocoxosternal course near the middle of the segment and in its innervation by nerve **B**. Nerve **B** is further specified in both taxa by forming basal branches **B1/2** to the ventral body wall. The muscles **2–5** (innervation unresolved) could be subdivisions of muscle **1**. Muscle **6** is like muscle **2b*** of Dictyoptera intrasegmental, located at the anterior segmental border, attached dorsally next to the alary muscle **19** or **15***, and supplied by nerve **T**. The muscle is strong as in *Sphodromantis,* contrasting the degenerated condition in adult *Periplaneta.* Muscle **7** (innervation unresolved) may correspond to the intrasegmental T-muscle **3*** of *Periplaneta,* situated likewise near the anterior segmental border and inserted near the ventral margin of the tergum (paratergite). Muscle **3*** is degenerated in *Periplaneta* and absent in *Sphodromantis,* but a similar muscle in Caelifera is as strong as in *Hemimerus* (Klass, 1999: **3*** in fig. 42; see p. 265). Muscle **8** corresponds to muscle **4***, or **5***, or both of Dictyoptera. Like these it has an intersegmental course from the coxosternum to the anteroventral corner of the following tergum (paratergite) and is supplied by nerve **C**. Nerve **C** is further specified in both taxa by forming basal branches **C3** to the external ventral muscles (see below).

A homologue of the intersegmental tergo-coxosternal C-muscle **6*** of Dictyoptera (Klass 1999: figs 3, 4) is absent in *Hemimerus* and (probably) in *Forficula.* Since some Pterygota including Ephemeroptera have muscles in a similar position, their presence could be plesiomorphic within Neoptera, and absence in Dermaptera apomorphic. However, considering conditions in the closest outgroup taxa of Neoptera in detail, the support for this assumption is weak. (1) Homology of the ephemeropteran muscles with those of the respective Neoptera is doubtful because they are supplied not by nerve **C** but by nerve **A** (muscle **d*** in Fig. 27 and Birket-Smith, 1971), an innervation otherwise typical for dorsal muscles. (2) Similar muscles in Odonata insert on the pleural membrane rather than on the coxosternum (Asahina, 1954: **tp*** in fig. E52). This could indicate that the muscles in Odonata and possibly Ephemeroptera are genuine dorsal muscles that have shifted their posterior insertions to a more ventral area, similar as lateral IXth-segmental dorsal muscles have done in male Dictyoptera (Klass 1997: 269; 2000: 254, discussion of muscle **47***). (3) Intersegmental tergo-coxosternals are not at all reported for Zygentoma (Rousset, 1973; Birket-Smith, 1974). (4) For Archaeognatha only segment IX of the female is reported to have such a muscle, which is supplied by a nerve corresponding to **B** + **C** of Pterygota (muscle **d9*** and anterior somatic nerve **ns*** in Birket-Smith, 1974: 23). The interpretation of this muscle and of the sclerites it inserts upon, however, is very disputable. Other muscles of Archaeognatha from a tergum to an endosternite are, as the muscles of Ephemeroptera, supplied by the nerve corresponding to **A** of Pterygota, and they extend from segment N to segment N + 2 rather than to segment N + 1 (muscle **K*** and anterior intercalary nerve **IA*** in Birket-Smith, 1974: 15, 16, fig. 5; muscle **18*** in Bitsch, 1973: fig. 7). Hence, muscles like **6*** of Dictyoptera could as well be apomorphic within Neoptera and primitively absent in Dermaptera.

In the ventral muscles the innervation in *Hemimerus* of muscle **9** by one basal branch **A2** of nerve **A** and of muscle **10** by several basal branches **C3** of nerve **C** comply exactly with the conditions in the internal and external ventrals of Dictyoptera and some other Neoptera. Muscle **9** is thus an internal ventral, homologous with muscle **7*** of Dictyoptera. Muscle **10** is an external ventral, homologous with **8*** and **9*** of Dictyoptera but differing from these in being very large and undivided, and in inserting more anteriorly on the coxosternum.

For the dorsal muscles a detailed homologization is not possible because of their uniform course from one tergum to the following, because of their uniform innervation by nerve **A** in probably all Pterygota including *Hemimerus,* and because of the strong intraspecific and segmental variation of the branching sequence of nerve **A** as demonstrated, at least, for Dictyoptera (Klass, 1999: figs 10–21). The few nerve data obtained for *Hemimerus* are inadequate for a comparative analysis. Two points, however, are rather clear: the homology between the internal dorsals **11** of *Hemimerus* and **10*** of Dictyoptera, both supplied by several far distal branches **A8** of nerve **A**, and the absence in Dictyoptera of a muscle that runs like **13** of *Hemimerus* posteromesad from its anterior insertion. For the remaining dorsal muscles the homologies indicated in Table 1 are, though somewhat uncertain, the most plausible. The rich diversification of the dorsal muscles in *Hemimerus* is quite outstanding.

In the spiracle muscles the courses of the occlusor **17** and of the dilator **18** in *Hemimerus* from the manubrium to the atrium wall and to the anterolateral part of the coxosternum, respectively, are the same as in many Neoptera (survey in Klass, 2000). In Dictyoptera, however, the dilator **14*** connects the manubrium with the paratergite (Klass, 2000: fig. 5). The alary muscles **19** in *Hemimerus* conform with commonplace conditions in Pterygota (Nutting, 1951) in their small insertion areas anteriorly on the abdominal terga, their fan-shape, and their occurrence on the terga up to X. It is striking that no trace of ventral transverse muscles (see p. 271 for genital segments), or of a ventral diaphragm, or of something like the hyperneural muscle **16*** of Blattaria and Isoptera was found.

DISCUSSION OF FEMALE GENITAL SEGMENTS VII–IX

SEGMENT VII

Exoskeleton

Segment VII is in most Insecta peculiar by forming during nymphal ontogeny the oviduct anlage, a median cuticular invagination, on its hindmost part. Whether in *Hemimerus* the definitive genital opening of the adult retains this location or is shifted to segment VIII is discussed on p. 273. Otherwise segment VII of *Hemimerus* differs from the preceding segments mainly in the elongation of its ventral fold **vf**, which thus forms a subgenital fold **vf**7, and in some peculiar differentiations of this fold: two posterior edges **es** and **ei**, and incision **il** with surrounding cuticular thickenings. Also in Forficulina fold **vf7** is usually quite strongly elongated, but it shows otherwise no differentiations distinguishing it from the preceding folds **vf**. In some Forficulina, however, e.g. in *Echinosoma*, the elongation is not very distinct and **vf7** thus quite similar to the preceding **vf**. It is well-known that also in female Dictyoptera the area corresponding to **vf7** of Dermaptera forms a large subgenital fold (coxosternum VII **SVII*** in Klass, 1998: figs 1–4). Peculiar differentiations distinguishing it from the preceding folds **vf** are the paired terminal lobes **tl*** and, in Blattaria and *Mastotermes*, longitudinal folds **if*** on its dorsal face, hence components not found in Dermaptera. This is not surprising since both the lobes **tl*** and the folds **if*** are involved in ootheca formation and may thus be, like the oothecae, autapomorphies of Dictyoptera (or subgroups thereof; Klass, 1998: 76). Hennig (1969: 180) obviously suspects the elongation of **vf7**, and the resulting presence of a vestibulum above it ('Genitalkammer' therein), to be a potential synapomorphy of Dermaptera and Dictyoptera. This seems possible, but two things should be noted. (1) Regarding conditions in e.g. *Echinosoma*, **vf7** was possibly only slightly elongated in the ground plan of Dermaptera. (2) Bitsch (1973: 176, fig. 2B) reports also for Archaeognatha a slight elongation of the coxal lobes VII, the homologues of **vf7**, as compared to the preceding coxal lobes. (Such a condition is not reported for Zygentoma; Rousset, 1973: fig. 2.) It remains thus doubtful whether there is actually some potentially synapomorphic condition of fold **vf7** shared by Dermaptera and Dictyoptera.

Musculature

Segment VII of *Hemimerus* differs from the preceding segments in the absence of two lateral muscles (**4**, **8** in Fig. 2) and in the presence of the muscles **20**, **21**, **22** (Figs 12, 13) attached to the gonoducts. Only these extrinsic gonoduct muscles, under inclusion of the VIIIth-segmental **23**, are here commented on. Most of these originate on or near segmental borders, either VI/VII (**20**, **21**) or VII/VIII (**23**), as represented by ridges **ac7** and **mt8** (Fig. 13; see p. 269). Their insertions on the gonoducts are close together. A similar set of muscles is reported for Dictyoptera (muscles **C*** = **20** + **21**, **D*** = **23** in Klass, 1998: figs 20, 21). Muscles corresponding to **20** + **21** are reported for e.g. Ensifera (see Klass, 1998: 90) and Notoptera (muscle **200*** in Walker, 1943: fig. 8). For Zygentoma a muscle resembling **20** + **21** is reported by Birket-Smith (1974: muscle **j7*** in fig. 29), one resembling **23** by Rousset (1973: muscle **28*** in fig. 7; fig. 11; inserted on endosternite **E8*** near segmental border VII/VIII; Fig. 28). Hence, both muscles **20** + **21** and **23** could be groundplan components of Dicondylia.

The muscles **20**, **21** and their homologues, and possibly also the fiber group **22**, seem to be median portions of the external ventral muscles VII (**10** in Fig. 13), primarily inserted on the membranous hind margin of segment VII and then drawn internally by the invagination of the oviduct anlage. Muscle **28*** of Zygentoma is medially inserted on the antecosta of coxosternum VIII (on **sdovi*** in Fig. 28). If muscle **23** of *Hemimerus* is homologous with the latter muscle, its gonoduct insertion thus probably lies upon the segmental border VII/VIII. Muscle **23** and its homologues cannot be assigned to one of the major muscle groups defined by Snodgrass (1935b).

DORSAL COMPONENTS OF SEGMENTS VIII AND IX

In female *Hemimerus* terga VIII and IX are very short (Figs 21, 22), and terga VIII–X are immobilized by the internal cuticular layer (Fig. 10). Similar features occur in female Forficulina. Most species show the strong shortening of terga VIII and IX (Figs 23, 24), but some do not (e.g. *Arixenia*; Giles, 1963: 134). Terga VIII–X show several degrees of immobilization (original observations): (1) An interconnection between internal cuticular surfaces is entirely absent; the terga are freely movable. (2) Within the dorsal folds **df** small opposing areas on the internal face of the cuticle stick to each other; the movability of the terga is thus restricted. (3) The internal cuticular layer fills the folds **df** like in Fig. 10, thus causing immobilization of these terga, but only in a more or less broad dorsolateral area. (4) The filling of folds **df** and immobilization extend over the entire terga VIII–X except narrow (dorso)lateral and dorsomedian areas, thus approaching the condition in *Hemimerus*. This is true for e.g. *Forficula* (Figs 17, 18) and *Apachyus*.

A shortening of terga VIII and IX is outside Dermaptera found in Blattaria and Mantodea, but there it is less strong and both sexes are concerned (and the sclerites are not immobilized). Hence, the strong shortening of terga VIII and IX only in the female could be an autapomorphy of the Dermaptera, or of a subgroup thereof excluding e.g. *Arixenia*. Tergal immobilization is not reported for taxa outside Dermaptera. Its different degrees (2)–(4) appear thus straightforwardly as autapomorphies of hierarchically subordinate dermapteran subgroups, each including *Hemimerus*. Noteworthy is mainly that the immobilization includes only in case (4) the lateralmost parts of the terga (Figs 17, 19, right margins). This is an apomorphy shared by e.g. *Forficula, Apachyus,* and *Hemimerus,* but not by at least several Pygidicranidae, e.g. *Karschiella* (Fig. 15). Tergal immobilization thus indicates *Hemimerus* as nested within the Forficulina.

On the other hand, reversals could have occurred in these characters. Since tergal shortening (*Hemimerus*: Davies, 1966: 76; Forficulina: Günther & Herter, 1974: 136) and probably also tergal immobilization develop in late nymphs, reversals could be due to paedomorphosis. This is likely for e.g. *Arixenia* if it is actually nested within the Forficulina as claimed by Popham (1985), and it could be true also for other taxa.

It is a striking feature of the musculature of female *Hemimerus* that segments VIII and IX are completely devoid of dorsal muscles (tergo-tergal muscles), though this is not surprising in view of the immobilization of terga VIII–X. On the other hand, however, Popham (1965: fig. 6) shows dorsal muscles VIII (not IX) for female *Forficula* with likewise immobilized terga. The absence of dorsal muscles in segment IX and, possibly, their reduction in segment VIII could be autapomorphies of Dermaptera or a subgroup thereof. Paedomorphic reversals may occur as in the tergal characters. Further comparative investigations are needed, including the nymphs.

VENTRAL COMPONENTS OF SEGMENTS VIII AND IX

Major issues and problems of interpretation

Two basic issues in the interpretation of the components of venters VIII and IX in *Hemimerus* are discussed in this section: (1) the homologies with the components of venters VIII and IX of Insecta that have a well-developed, plesiomorphic ovipositor; (2) the serial homologies with the components of the mid-abdominal segments. For comparison with *Hemimerus* (Figs 19, 20) the genital area is illustrated for *Karschiella* and *Forficula* (Figs 15–18). Some aspects of the nymphal development of venters VIII and IX in Insecta provide an important viewpoint for interpretation and can contribute to a solution of these issues.

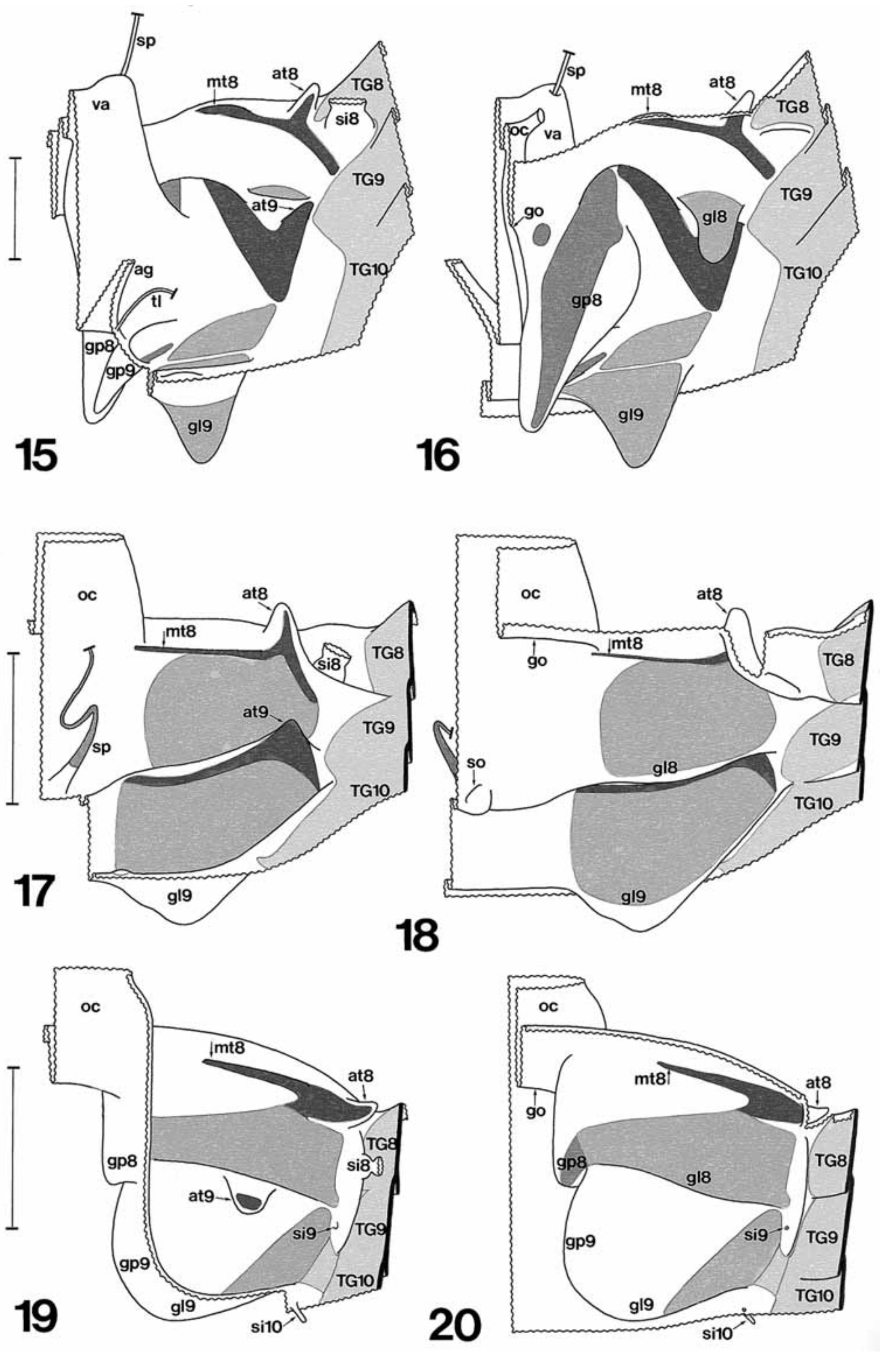
Nymphal development

In young nymphs of *Hemimerus vicinus* Rehn & Rehn the venters VIII and IX bear each an undivided transverse plate (Davies, 1966), which is probably a coxosternum, serially homologous with the mid-abdominal coxosterna. It is unknown whether the apodemes **at** and the cuticular ridges of the adult venters VIII and IX are already present. The plates become reduced in older nymphs and medially divided in the imagines. Undivided coxosterna on the venters VIII and IX of young nymphs are also described for e.g. Zygentoma (Heymons, 1897: fig. 9; Sahrhage, 1953: fig. 21c; styli not yet developed), Blattaria (McKittrick, 1964: figs 3A, 4A; styli IX already developed), and Notoptera (Nagashima, 1991: fig. 3; styli IX already developed). In Zygentoma the styli VIII and IX develop later from paired epidermal thickenings on the posterior margins of the coxosterna (Heymons, 1897: 599). Hence, the plesiomorphic condition in Dicondylia is probably that segments VIII and IX first develop, like the more anterior segments, undifferentiated coxosterna comprising the prospective sternal, coxal, and laterocoxal sclerotizations and still undeveloped styli, and that during nymphal development these components differentiate to form an ovipositor and associated structures.

This has two consequences. (1) Within the Dicondylia adult conditions in which an ovipositor is (secondarily) absent but entire or paired sclerites (coxosterna, coxopodia) are present on venters VIII and IX can represent paedomorphic conditions. Assumedly, similar such conditions could easily evolve independently in different taxa. A paedomorphic condition is suggested here for *Hemimerus* and *Forficula.* (2) Since the respective nymphal sclerites VIII and IX are probably complete serial homologues of the mid-abdominal coxosterna, moderately paedomorphic conditions as in *Hemimerus* could, like nymphal conditions, help in disclosing serial homologies between plesiomorphic, ovipositor-bearing genital segments and mid-abdominal segments. These two points should be kept in mind through the following discussions.

Ventral muscles and primary segmental borders

A basic step in the interpretation of the ventral components VIII and IX is the localization of the primary segmental borders. Parts of these are quite easily recognized in *Hemimerus.* (1) The lines of contact between the ventral muscles VII **9** and VIII **26**, and between the ventral muscles VIII **26** and IX **32** + **33** (Fig. 13) are part of the segmental borders VII/VIII and VIII/IX. There is, however, some doubt regarding the usefulness of the muscles in determining the border VIII/IX, which results from the uncertainty in the interpretation of both the ventral muscles VIII and IX (discussion on pp. 297–300). (2) The ridge **mt8** along which the muscles **9** and **26** meet is assumed to be a part of antecosta VIII **ac8** and to mark the border VII/VIII. (3) The apodemes **at8** and **at9** are located at the lateral ends of the lines of muscle contact, just as the apodemes **at** in the mid-abdominal segments (Fig. 2), and are assumed to be the serial homologues of these. For **at8** this is confirmed by the insertion of the spiracle dilator **28** (compare dilator **18** inserting on **at** in Fig. 2). For **at9** of *Hemimerus* this serial homology is less



Figures 15–20. Homology of sclerotizations and formative elements of female genital segments VIII and IX. Half of genital area shown, after cut along midline. Left column: dorsal, predominantly internal view. Right column: ventral, predominantly external view. ↑ anterior, → lateral. Sclerotizations darkened differently according to homology relations. Spermathecae and lateral tubes of accessory glands cut by bars. Scale bar = 0.5 mm. Figs 15, 16. *Karschiella buettneri*. Figs 17, 18. *Forficula auricularia*. Figs 19, 20. *Hemimerus vosseleri*.

■ Laterocoxa LC ▩ Gonapophyseal sclerotization ▨ Coxa CX □ Tergum TG obvious because **at9** is more median than **at** and **at8**, and its sclerotization **LC9** is separate from the ventral plates **CX9** (division of **CP9** into two sclerites). However, apodeme **at9** of *Forficula* (Fig. 17), probably the homologue of **at9** of *Hemimerus*, corresponds closely with **at** and **at8** in its far lateral position and in the connection of its sclerotization **LC9** with **CX9** (**CP9** undivided; compare also **at9** of *Karschiella*, Fig. 15). The mid-abdominal apodemes **at** bear part of the antecosta **ac** (Fig. 1) and are located at the segmental border; such a location is thus also assumed for **at8** and **at9**. (4) It has been explained above that probably also the median insertions of muscles **23** (Fig. 13) mark the border VII/VIII.

Lateral muscles

Only two are present in segments VIII and IX of *Hemimerus* (**24**, **25** in Figs 12, 13), both attached to tergum VIII. Their ventral insertions are on (probably) serially homologous areas, on **at8** and **at9**. Muscle **24** is obviously the VIIIth-segmental serial homologue of muscle **6** (Fig. 2), which is likewise located far anteriorly in its segment and inserted on apodeme **at**. Muscle **25** appears straightforwardly as an intersegmental tergo-coxosternal muscle VIII. However, such muscles from tergum N to coxosternum N + 1 are absent from the mid-abdominal segments (see p. 267). It seems unlikely that *Hemimerus* has retained or developed such a muscle only in the muscle-poor segment VIII. Muscle **25** is possibly better explained as a IXth-segmental serial homologue of muscles **6** and **24** whose dorsal insertion has shifted anteriad to tergum VIII. This seems plausible by analogy with the cercal muscles **40** and **41** (Fig. 12; see p. 278) and the lateral rectal muscles **45** (Fig. 13; see p. 301), for which there are reasons to postulate an expansion or shift of insertions in the same dorsolateral area from tergum X to tergum IX; thereby these could have displaced muscle **25** to tergum VIII.

Ventral transverse muscles

In segments VIII and IX muscles like **29**, **30**, and **34** of *Hemimerus*, which pass without a median insertion from one side to the other, are reported for only few Pterygota. Some Ensifera have an VIIIth-segmental muscle (Ford, 1923: 274, 277). In *Conocephalus fasciatus* DeGeer it is compact, while in *Gryllotalpa hexadactyla* Perty it is diffuse and forms the hindmost part of the ventral diaphragm. In both species the muscles are shaped like their counterparts in the preceding segments. *Grylloblatta campodeiformis* Walker, 1914 (Notoptera) also has an VIIIth-segmental muscle (**210*** in Walker, 1943) whose fibres predominantly traverse from one side to the other (pers. observ.). All these muscles cross the gonoducts dorsally like muscle **30** of *Hemimerus*. Odonata and Zygentoma have a compact IXth-segmental muscle in a similar position as **34** of *Hemimerus*. It interconnects the two coxae IX, i.e. the gonoplac bases (transverse sternal muscle in Asahina, 1954: plates 47, 48, 'lateral valvula' therein = coxa IX; muscle **IT9*** in Birket-Smith, 1974: fig. 29, 'hemisternite **sIX***' therein = coxa IX; muscle **33*** in Fig. 28 and Rousset, 1973: 68). Some Ensifera, e.g. *Conocephalus*, may also have a IXth-segmental muscle (**tb*** in Ford, 1923: fig. 22; assignment of **tb*** and **ttg8*** to segment VIII therein questionable).

The respective muscles are here tentatively homologized. Similar muscles may be of wider occurrence in Pterygota. They could be restricted to nymphal stages (as in some Ensifera; Ford, 1923: 273), and possible vestiges in the imagines could have been overlooked. In other cases the muscles may have become divided medially by having gained median insertion areas, as indicated by the presence in the *Grylloblatta* muscle of both traversing and medially inserted fibers. The transverse muscles **30** and **34** of *Hemimerus* could thus be plesiomorphic components, or paedomorphic components. It is, however, noteworthy that transverse muscles VIII crossing the gonoducts ventrally like **29** of *Hemimerus* are not so far reported from other Insecta.

Ventral sclerotizations and formative elements

CP8 and **CP9** of *Hemimerus* (Figs 19, 20) develop from undifferentiated coxosterna VIII and IX and never obtain many of the differentiations present in taxa that have a complete ovipositor. The resulting poorness of the structural pattern restricts the potential for homologization. The following interpretations are based on the comparison between Archaeognatha, Zygentoma, and nymphal and adult Dictyoptera in Klass (1998), and on conditions in the lower-grade dermapteran *Karschiella*, which resemble those in Dictyoptera and basal Insecta. The results of a comparison between *Hemimerus*, *Karschiella*, and *Forficula* are surveyed in Figures 15–20. The presence of sterna VIII and IX seems unlikely in these Dermaptera because sclerotizations near the midline of venters VIII and IX are absent. Only coxae and laterocoxae remain thus to be discussed (see p. 253).

The laterocoxae of *Hemimerus* can be determined by some specific features shared with the laterocoxae of other taxa. (1) In blattarian nymphs laterocoxae VIII and IX bear on their anterior margins the insertions of the internal ventral muscles VII, VIII, and IX (muscles **IS*** on laterosternites **ltst.a.VIII/IX*** in McKittrick, 1964: figs 6, 7). In Pterygota with differentiated female genital sclerotizations the anterior insertions of the internal ventrals IX are, if not on membrane, on laterocoxa IX (= gonangulum). This is documented at least for Blattaria ('intersternal muscles IX–X' in McKittrick, 1964: 50; 'laterosternite IX' = laterocoxa IX, see Klass, 1998: 95), Notoptera (muscle **219*** in Walker, 1943; 'valvifer' = laterocoxa IX, see Klass, 1998: 97), and several Ensifera (muscle **is9*** in Ford, 1923; posterior part of 'valvifer' bearing insertion = laterocoxa IX, compare Klass, 1998: fig. 26). In the zygentoman *Thermobia* the muscles insert on an endosternite, which is in turn attached to laterocoxa IX (endosternite **E9*** on sclerite **ga*** and muscles **62a**,**b*** in Fig. 28 and Rousset, 1973: 68; discussion of muscle homology, below). Hence, in *Hemimerus* the **LC8**-sclerotization of ridge **mt8** is considered as part of laterocoxa VIII, and the anterior insertion areas of muscles **32** and **33** (Fig. 13) as desclerotized parts of laterocoxa IX. (2) In blattarian nymphs the laterocoxae VIII and IX include the anterolateral parts of the coxosterna (**la*** in Klass, 1998: fig. 28), where in Dermaptera the apodemes **at** have their original positions (Figs 1, 15, 17). The **LC8**- and **LC9**-sclerotizations of **at8** and **at9** are thus indicated as laterocoxal. (3) The ventral extrinsic rectal muscles in at least *Gryllus assimilis* Fabr. (Ensifera) and *Mantis religiosa* (Mantodea) are attached to laterocoxa IX (see p. 301; muscle **vdr*** in Ford, 1923: 300, 'IXth-sternal valvifer' therein = laterocoxa IX, compare **gg*** in Klass, 1998: fig. 26; muscle **61*** in LaGreca & Rainone, 1949: 30, 'secundo valvifero' therein = laterocoxa IX; data for other Insecta not available). The attachment in *Hemimerus* of the ventral rectal muscle **46** (Fig. 13) to **at9** thus supports the assignment of sclerite **LC9** to laterocoxa IX. (4) Consequently, in *Hemimerus* the **LC8**-sclerotization of **at8** and **mt8** is assigned to laterocoxa VIII, and the **LC9**-sclerotization of **at9** is assumed to constitute the entire sclerotization of laterocoxa IX. The resulting demarcation of laterocoxae VIII and IX (Fig. 19) is supported by the fact that these **LC**-sclerotizations are partially (VIII) or entirely (IX) separated from the **CX**-sclerotizations, just as in e.g. blattarian nymphs the laterocoxae are separated from the coxae (**la*** and **ma*** in Klass, 1998: fig. 28). It should be noted that in *Karschiella* (Fig. 16) the separation is also in segment VIII complete. According to this result, the lateral muscles **24** and **25** as well as the spiracle dilator VIII **28** (Fig. 13) have their coxosternal insertions on the laterocoxa (compare tergo-laterocoxal muscle **22g*** of *Thermobia*, Fig. 28).

The coxae in *Hemimerus* (Figs 19, 20) are assumedly represented by the sclerotizations **CX8** and **CX9**, which are in the appropriate positions. However, there are no structural specifities present that could confirm this hypothesis. The paired lobes or folds **gl8** and **gl9** at the hind margins of venters VIII and IX are assumed to be what has remained of the projecting parts of the appendages. They correspond to the coxal lobes (Pterygota: gonoplacs IX; *Karschiella*: **gl8**, **gl9** in Figs 15, 16) of taxa with well-developed ovipositors. Styli are not differentiated. The stylus areas **sl** are probably located in the distal edges of **gl8** and **gl9** (**sl9** in Fig. 5) since in these positions the undifferentiated stylus 'material' is present in young nymphs of *Lepisma* (Heymons, 1897: 598). Distinct gonapophyses are also wanting. Vestiges would be located at the median margins of the lobes **gl8** and **gl9** (compare position of gonapophyses **gp8**, **gp9** in *Karschiella*, Figs 15, 16), and the small processes **gp8** and the median lobes **gp9** (Figs 19, 20) are thus probably what has remained of the gonapophyses.

Composition of mid-abdominal coxosterna and delimitation of laterocoxa

The mid-abdominal coxosterna of Dermaptera do not show any indication of a former subdivision into discrete sclerites. Conditions in Archaeognatha and certain Zygentoma suggest that a separation between sternum and coxopodia is ancestral for Insecta, but whether coxae and laterocoxae were ever separated in the mid-abdomen is unclear. Nevertheless, no matter whether these ever constituted discrete sclerites or not, sclerotization areas homologous with the coxae and laterocoxae VIII and IX should be present in the mid-abdominal coxosterna. Applying the above characteristics of laterocoxae VIII and IX, the laterocoxal areas should include here the anterolateral corners, with the apodemes **at** and the insertion areas of muscles **6** and **18** (and probably **7**), as well as most of the anterior margin, with the insertion areas of muscles **9** (see conclusions for muscles **24/25**, **28**, **26/32/33**). The coxal areas probably comprise large posterolateral parts of the coxosternum and may include the ventral insertions of some lateral muscles, mainly **1**. The sternum should comprise either only a narrow anteromedian part of the coxosternum, or a broader central part behind the laterocoxal anterior margin. Laterocoxa and coxa but not the sternum receive then muscles from the tergum as in Archaeognatha (see Bitsch 1974b: e.g. fig. 4). The ventral folds of the segments up to VII (**vf** in Fig. 1; **vf7** in Fig. 3) are probably the projecting part of the appendage, corresponding to the coxal lobes of Archaeognatha and to e.g. the ovipositor gonoplacs (**gl9** in Fig. 16; the terms **vf** and **gl** then being synonymous).

The delimitation of the laterocoxal area as applied herein includes a problem. The size and extension of the laterocoxa is similar in the mid-abdomen of *Hemimerus* and on venters VIII and IX of blattarian nymphs and of many adult Dicondylia (e.g. gonangulum = laterocoxa IX **ga*** in Fig. 28; **LC8**, **LC9** in Fig. 16). In Archaeognatha, however, the laterocoxite is much smaller and restricted to the anterolateral corner of the venter, and the lateral anterior margin of the venter is sclerotized by the precoxite (Bitsch, 1973: fig. 2, 1974b: fig. 1). It was noted above, p. 253 that the laterocoxa as defined herein for Dicondylia might include the homologue of this precoxite. In *Nicoletia* sp. (Zygentoma: Nicoletiidae; Rousset, 1973: fig. 9) suturae indicate the composition of the coxosternum. The coxae constitute the posterolateral parts, and the sternum a sizable central part. The parts identified as laterocoxae are, like in Archaeognatha, small and restricted to the anterolateral corners. An anterior transverse sclerotization (aire présternale in Rousset, 1973: 73) takes the same position as the precoxites of Archaeognatha. Bearing the endosternites, on which the internal ventral muscles insert, it also corresponds with the median part of the laterocoxa as defined above and with part of the endosternite-bearing laterocoxa IX of *Thermobia* (**E9*** and **ga*** in Fig. 28; Rousset, 1973: 68). Hence, it seems that Rousset's (1973) laterocoxa in *Nicoletia* is homologous with Bitsch's (1974a) laterocoxite in Archaeognatha, whereas the laterocoxa as addressed herein and Rousset's (1973) gonangulum in *Nicoletia* and *Thermobia* are homologous with the laterocoxite plus precoxite of Archaeognatha. This tentative hypothesis has to be tested by closer comparative investigations, of Zygentoma in particular.

Accessory gland and spermatheca

Both components are certainly present in the ground plan of Dermaptera (see *Karschiella* in Figs 15, 16). The lack of both in *Hemimerus* is not surprising since in other Insecta the spermatheca releases the sperm when the eggs pass its orifice, and the accessory gland provides glue for egg attachment or an outer envelope for the eggs. *Hemimerus* does not lay eggs! Fertilization must be assumed to take place within the ovaries, where also the embryos develop. It is unknown where, or whether, the sperm is stored prior to fertilization.

GONODUCTS AND GENITAL OPENING

Conditions in lower-grade Insecta

In nearly all Insecta the common oviduct anlage, and hence the primary gonopore, forms on the posteriormost part of venter VII. In many Insecta the gonopore is then translocated posteriad to segment VIII (or further) during development. It is then called here a secondary gonopore, and the channel extending the gonoducts is the extended oviduct. In addition, the area around the secondary gonopore can be invaginated anteriad to form a vagina, whose external opening is the vulva. The secondary gonopore lies then at the inner end of the vagina (details in e.g. Snodgrass, 1935b). A marker for the border between vagina and extended oviduct is the spermathecal opening, which is originally located at the hind margin of venter VIII but shifts away from it through the formation of the vagina.

The assignment of the definitive genital opening of the imago to segment VII or VIII is for many insect taxa strongly disputed in the literature. It must be based on an analysis of the spatial relations between the opening and the components marking the primary segmental border VII/VIII. The point is whether the anterior border of the opening (in *Hemimerus* fold **go** in Figs 5, 20) is physically formed by material of either venter VII or venter VIII, i.e. whether this anterior border is anterior or posterior to antecosta VIII, or to the corresponding line in case of its absence. Archaeognatha (Bitsch, 1974a: 105), Zygentoma (Fig. 28, **sdovi*** contains antecosta VIII; Rousset, 1973: 74), Dictyoptera, and Ensifera (Klass, 1998: 91) have the opening quite certainly on segment VII, thus retaining the primary gonopore. Archaeognatha have a longitudinal groove between coxae VIII that leads from the opening to the bases of gonapophyses VIII ('fente génitale' in Bitsch, 1974a: 105). Zygentoma, Dictyoptera, and Ensifera have a VIIth-segmental posteriad-directed lobe that arises immediately in front of the genital opening ('languette' **lang*** of Zygentoma in Fig. 28; Rousset, 1973: 74, fig. 9; subgenital lobe of Ensifera and laterosternal shelf fold of Dictyoptera in Klass, 1998: 90f). The anterior border of the genital opening, corresponding to the distal edge of the lobe, comes thus into a more posterior position and may appear VIIIth-segmental, though it is purely VIIth-segmental (as the entire lobe is VIIth-segmental). In e.g. Odonata, Notoptera, and Caelifera, however, the opening is quite clearly on segment VIII since it is separated from segment VII by a medially undivided coxosternal sclerite VIII with a more or less distinct antecosta along its anterior margin. The sclerite is identified as coxosternal by its musculature resembling that of the more anterior coxosterna (see Asahina, 1954; Walker, 1943; Snodgrass, 1935a). This condition could correspond to a closure of the coxal groove margins present in Archaeognatha. Accordingly, in the ontogeny of e.g. Caelifera a longitudinal groove forms on venter VIII, which is then closed (Qadri, 1940).

Conditions in Hemimerus

The genital opening lies medially between the lobes **gp8** (Figs 5, 6), as correctly described by Jordan (1909) and Deoras (1941a) (**CP8** = 'sternites VIII' in both). For its anterior border, fold **go**, there are three indications that it is VIIIth-segmental: (1) Fold **go** is located in between the VIIIth-segmental sclerites **CP8**. (2) The ridges **mt8**, which are part of antecosta **ac8** and mark the segmental border, have their inner tips distinctly anterior to fold **go**. (3) The transverse muscle VIII **29** crosses the gonoduct ventrally and the opening anteriorly (Fig. 14). However, all arguments are disputable. **CP8** and **mt8** are both restricted to lateral areas and give, in contrast to conditions in the abovementioned Pterygota with an VIIIth-segmental opening and Zygentoma with a VIIth-segmental opening, no criteria for localizing the segmental border VII/VIII near the midline. Muscle **29** seems to yield the strongest argument, but since potential homologues are not reported for any insects in which its insertions are located behind a clear segmental border, its interpretation as located at or behind the border VII/VIII (i.e. as VIIIth-segmental) remains tentative.

On the other hand, there is one indication that fold **go** is VIIth-segmental. If muscles **23** of *Hemimerus* (Fig. 13) and **28*** of *Thermobia* (Fig. 28) are homologous (see p. 268), the segmental border VII/VIII (the insertion of **23** on the gonoduct is then part of it) is in *Hemimerus* likely to cross the gonoduct dorsally, i.e. to pass the genital opening (morphologically) posteriorly. Then the fold **go** should belong to segment VII, being the distal edge of a VIIth-segmental lobe that protrudes into the area between the sclerites **CP8** and is potentially homologous with the abovementioned VIIth-segmental lobes of Zygentoma, Dictyoptera, and Ensifera. However, there remains a problem: after a translocation of the gonopore to the posterior by the ventral closure of a groove there would remain, beside a continuous transverse segmental border on the external side, somewhat like a segmental border ring around the gonoduct, and the insertions of muscles **23** = **28*** would still be located on this ring though fold **go** is then VIIIth-segmental. This is clearly not the case in *Thermobia*, where the antecosta continues from left to right across the oviduct, but it could be the case in *Hemimerus*. Hence, these insertions cannot lead to a clear decision. It should also be noted that the course of transverse muscle VIII **30**, crossing the gonoduct dorsally (Fig. 13), does not indicate a VIIth-segmental position of the opening. Also in *Grylloblatta*, with the opening on segment VIII, the transverse muscle VIII crosses the gonoduct dorsally. This makes sense because the muscle may well be present before the gonoducts develop, and, assuming then a gonopore translocation as in Caelifera, the muscle would cross the extended oviduct dorsally (ontogenetic data on *Grylloblatta* not available).

Hence, whether the genital opening is in *Hemimerus* on segment VII or VIII must be regarded as unresolved. Accordingly, whether the externalmost parts of the gonoducts belong to the common oviduct, to an extended oviduct, or to a vagina, and whether the opening is a VIIth-segmental primary gonopore, or an VIIIth-segmental secondary gonopore or a vulva remains unknown as well. Detailed studies of the nymphs are needed to resolve these questions.

Conditions compared in Hemimerus *and Forficulina*

Many Pygidicranidae have the anterior border **go** of the genital opening in the same relative position as *Hemimerus*, between the bases of gonapophyses VIII and behind the median tips of ridges **mt8** (original observations; see **go** in *Karschiella*, Fig. 16). *Forficula*, however, has **go** more anteriorly, distinctly anterior to the median tips of ridges **mt8** and thus more clearly on the posteriormost part of segment VII (compare **mt8** and **go** in Figs 18, 20). Nevertheless, in all these Dermaptera the course of the segmental border VII/VIII near the midline and hence the position of the gonopore relative to this border is uncertain because the median part of antecosta **ac8** is lacking.

Despite this problem in the interpretation of fold **go**, it is evident that in *Forficula* fold **go** is in the position where the oviduct anlage can be assumed to have invaginated, whereas in *Hemimerus* and the respective Pygidicranidae some shift of fold **go** to the posterior must occur during development—either through the growth of a VIIth-segmental lobe or through the closure of an VIIIth-segmental groove. Since in the immediate ovipositor-bearing outgroup taxa of Neoptera one finds either the VIIth-segmental lobe (Zygentoma) or the VIIIth-segmental channel (Odonata), it can reasonably be assumed that a location of fold **go** as in *Forficula* is apomorphic, due to simplification, possibly through paedomorphosis.

PAEDOMORPHIC AND OTHER APOMORPHIES

The venters VIII and IX of female *Hemimerus* (Figs 19, 20) and *Forficula* (Figs 17, 18) lack many of the structures present in the ground plan of the Dicondylia. Absences which in other Dicondylia are found in the nymphs can be reasonably interpreted as paedomorphic apomorphies of these species. This is true for the absence of elongate coxal lobes (gonoplacs), gonapophyses and styli, and, consequently, of many of the finer structures otherwise present in these basic components and of a stronger subdivision and differentiation of the sclerotizations. The well-developed and distinctly serial condition in *Hemimerus* of the ventral muscles VIII and IX, **26** and **32** + **33** (Fig. 13), might likewise be a paedomorphic condition since, for instance, in Blattaria the muscles are in a similar condition in the nymphs but more heterogenous and partly reduced in the imagines (McKittrick, 1964; but see below: these muscles are possibly not homodynamous).

Nevertheless, paedomorphic apomorphies are in *Hemimerus* less abundant than in *Forficula* (compare the more plesiomorphic conditions in *Karschiella*, Figs 15, 16). There is still a separation between laterocoxae and coxae (incomplete in VIII) and a vestigial gonapophysis **gp8**, and the genital opening undergoes a shift to the posterior. The paedomorphic apomorphies are in *Hemimerus* and *Forficula* restricted to the venters VIII and IX: the terga retain their shortening and immobilization as in the adult females of many other Dermaptera, and coxosternum VII (Fig. 3) is in *Hemimerus* even more elaborate than in most Dermaptera including *Forficula*. Some features of *Hemimerus* are, as far as known, found neither in the nymphs nor in the imagines of other species and are non-paedomorphic apomorphies: sclerites **CX8** and **CX9** are laterally articulated, **CX9** is connected with terga IX and X by a weak sclerotization, the sclerotization of laterocoxa **LC9** (gonangulum) is restricted to apodeme **at9**, and **at9** has shifted mesad.

DISCUSSION OF POSTGENITAL SEGMENTS X AND XI AND TELSON

PROBLEMS IN THE POSTGENITAL ABDOMEN

This area presents many morphological problems throughout the Insecta. First, the reduction of many components and the peculiar ontogenetic fate of the appendages in segments X and XI lead to problems in terms of serial homology and segmental assignment of components. Second, strong morphological differences lead to homology problems between taxa. A further problem is the sparse and mostly superficial knowledge on both the morphology and the ontogeny of the area. Accordingly, the interpretations of the postgenital components are strongly controversial. To illustrate the confusion, sclerite **LP** of *Hemimerus* (Figs 5, 6) and other Dermaptera has been regarded as sternum X (Hansen, 1894; Jordan, 1909; Deoras, 1941a), as sternum XI (Davies, 1966), as a ventral telson sclerite (Heymons, 1895a,b), as coxa X (Verhoeff, 1903), or as a lateral part of tergum X (Strenger, 1950). It should also be noted that the terms epiproct and, in particular, paraproct, frequently used to describe the ventral and dorsal terminal sclerites, are interpreted in a variety of ways by different authors. These terms as such can therefore not be regarded as having some concrete interpretative content, and in this neutral sense they are used herein.

In what follows, my aim is not to propose a comprehensive solution, but a survey of the problems and a scrutiny of the opinions; some new arguments are given which focus on Dermaptera. *Hemimerus* is first compared with Forficulina. Available ontogenetic and morphological information on Dermaptera and ensuing hypotheses on the postgenital components are then discussed. A detailed comparison between Dermaptera and Ephemeroptera follows. Finally, the components of the postgenital abdomen will be compared through a broader variety of lower-grade Insecta to find evidence for the morphological nature of components, homology relations, and character polarities; discussions will focus on taxa for which detailed information on postgenital abdominal morphology is available from the literature—mainly Zygentoma, Ephemeroptera, Orthoptera, and Dictyoptera.

POSTGENITAL ABDOMEN COMPARED IN *HEMIMERUS* AND FORFICULINA

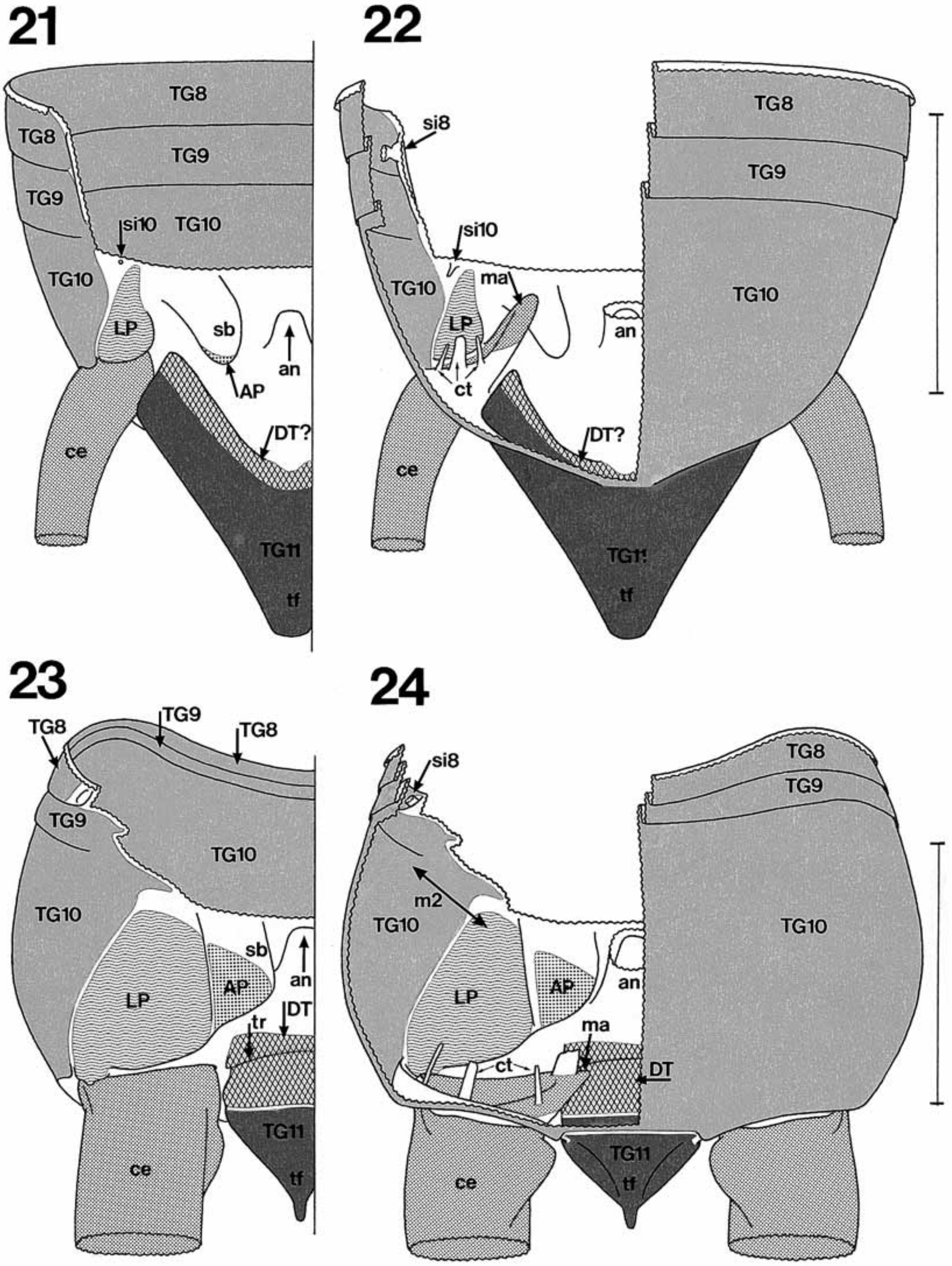
Similarities between the taxa

Strenger's (1950) descriptions of the postgenital abdomen and cercal musculature in various Forficulina (Forficulidae: *Forficula auricularia*, *Anechura bipunctata*, *Chelidura pyrenaica*, *C. acanthopygia*; Labiduridae: *Labidura riparia*) as well as original observations on Forficulina are used here for a comparison with *Hemimerus*. Tergum **TG10**, the terminal sclerotizations **TG11** and **DT**, process **tf**, the ventral sclerites **LP** and **AP** and their lobes **sb**, the bases and muscles of the cerci **ce**, and the anus **an** show in the Forficulina a similar configuration as in *Hemimerus* (Figs 21–24), but there are also some striking differences. A well-known difference is that the cerci are thread-like in *Hemimerus* but clasper-like in Forficulina. Yet the two taxa show some interesting similarities in the cercal base and musculature that should here be analysed.

(1) As in *Hemimerus*, an apodeme **ma** on the median cercal base is, though shorter, also present in Forficulina (**ma** in Figs 22, 24; area near **G3*** in Strenger, 1950: figs 3a, 4a, 7). It is also found in *Calopteryx splendens* (Harris, 1782) (Odonata; pers. observ.), *Grylloblatta campodeiformis* (Notoptera; pers. observ.), and, in a less distinct condition, in *Povilla adusta* Navas (Ephemeroptera; Birket-Smith, 1971; Fig. 26) and *Dissosteira carolina* (Caelifera; Snodgrass, 1935a: **b*** in fig. 7C; fig. 7D). Apodeme **ma** could thus be plesiomorphic within the Pterygota.

(2) *Hemimerus* and Forficulina have similar tendons **ct**. In *Echinosoma* three of them are located along the dorsal cercal base (**ct** in Figs 22, 24) like in *Hemimerus*. The arrangement in *Forficula* and *Labidura*, however, is quite different; considering muscle insertions (Table 2), only one narrow tendon on the lateral cercal base (**SAB1*** in Strenger, 1950: fig. 4a) is homologous with the **ct** of *Hemimerus*. I found similar tendons in *Calopteryx*, but potential homologies with the dermapteran tendons are not yet clear. For other Insecta such tendons are, to my knowledge, not reported, but they are certainly easily overlooked. It thus remains uncertain whether the **ct** and further cercal base tendons are autapomorphic for Dermaptera or plesiomorphic within the Pterygota.

(3) Cercal musculature in both *Hemimerus* and Forficulina is outstandingly heavy. Muscle homologies are given in Table 2. In both taxa three muscles (**40**, **42**,



Figures 21–26. Homology of components of female postgenital abdomen. Postgenital area, and terga VIII and IX in Figs 21–24, shown; cerci cut. Figs 21, 23, 25: ventral view of right half. Figs 22, 24, 26: dorsal view, most of terga VIII–X removed on left side. ↑ anterior. Sclerite shading indicating homologies. Scale bar = 1 mm (Figs 21–24) or 0.5 mm (Figs 25, 26). Double-headed arrows in Figs 24, 26 indicating position of muscles m2 and c10. Figs 21, 22. *Hemimerus vosseleri* (Dermaptera). Figs 23, 24. *Echinosoma yorkense* (Dermaptera). m2 = muscle described in Verhoeff (1903) for *Forficula auricularia*. Figs 25, 26. *Povilla adusta* (Ephemeroptera). Redrawn from Birket-Smith (1971), with his abbreviations predominantly used, indicating his interpretations: bc = basis cerci; cb = cercal base; c10 = muscle; pX = pleura X; pXI = pleura XI; sX = sternum X; sXI = sternum XI; tX = tergum X; tXI = tergum XI; tl + tf = terminal filament and its sclerotization. Remaining abbreviations (an, ce, ma) as defined in present paper.

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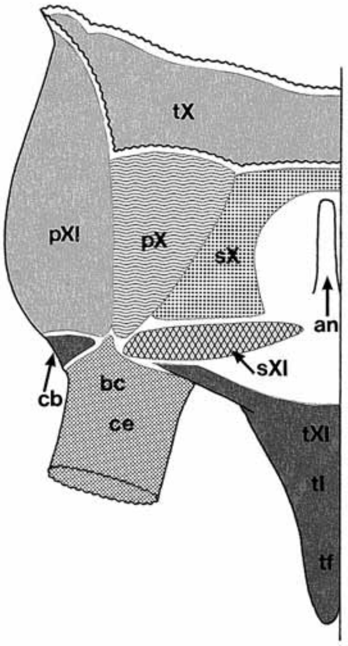

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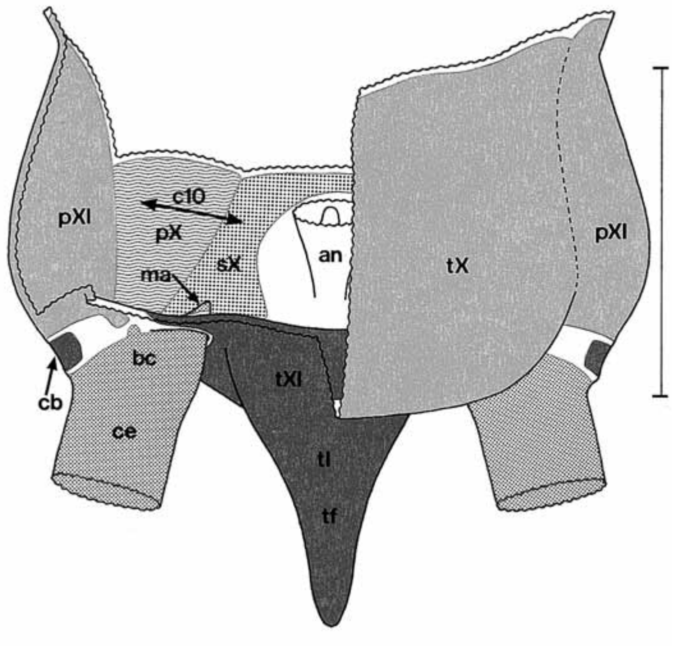

▒ Terga VIII, IX, X (TG8-10) ■ Tergum XI (TG11) ▩ Dorsal telson sclerite (DT) ▦ Cercal sclerotization (CE) ≋ Paraproct, lateral part (LP) ▦ Paraproct, median part (AP)

Table 2. Homology of cercal muscles in *Hemimerus* and Forficulina. The muscle terms used by the authors are entered. For specification of tergum* of Forficulina as tergum IX and/or X see pp. 277–278

Hemimerus This paper		Forficulina Strenger, 1950	
40	from median part of tergum IX to ventral margin of apodeme **ma**	MAD2	from median part of tergum* to tendon SAD2 originating ventromedially on cercal base, partly on apodeme **ma**
41	from lateral and ventromedian parts of terga IX and X to tendons **ct**	MAB1	from lateral and ventromedian parts of tergum* to tendon SAB1 originating laterally on cercal base
42	from median part of tergum X to middle part of apodeme **ma**	MAD1	from median part of tergum* to tendon SAD1 originating dorsomedially on cercal base, partly on apodeme **ma**
43	from tergum XI TG11+DT to dorsal margin of apodeme **ma**	MAB2	from tergum XI to tendon SAB2 originating far dorsomedially on cercal base, partly on apodeme **ma**

43) from the median cercal base go, in dorsoventral succession, to sclerite **TG11** (anterior **ZW***-sclerite in Strenger, 1950), to the median part of the tergum (IX and/or X, specification below), and to the lateral part of the tergum (IX/X); one muscle (**41**) from the lateral cercal base goes to the lateral and ventromedian parts of the tergum (IX/X). Strenger's (1950: figs 1, 9–12) illustrations show that in female *Anechura* and *Chelidura* spp., and possibly in female *Labidura*, the anterior insertions (except that of **MAB2***) extend onto tergum IX, whereas in female *Forficula* and in the males of all species these insertions are restricted to tergum X. The condition that cercal muscles insert on tergum IX is apparently not reported for any other insect. Though probably not true for *Forficula*, the extension of the insertions of muscles **40**=**MAD2***

and **41** = **MAB1*** onto tergum IX in the female may preliminarily be regarded as autapomorphies of the Dermaptera or a subgroup thereof.

Differences between the taxa

(4) As mentioned above, the cerci are thin threads in *Hemimerus* but stout claspers (forceps) in Forficulina.

(5) The sclerotization **TG11** is in *Hemimerus* dorsomedially connected with tergum **TG10** (Fig. 22) but in Forficulina separate from tergum **TG10** (Fig. 24). In *Hemimerus* the connection is even closer in 1st instar nymphs, which lack the lateral membranous sutures between **TG10** and **TG11** (Davies, 1966: 76). Forficulina show complete separation already in 1st instar nymphs (Verhoeff, 1903: 289), and probably even in late embryonic stages (Bhatnagar & Singh, 1965: 28).

(6) Forficulina have a discrete sclerite **DT** between **TG11** and the anus (Figs 23, 24; posterior **ZW***-sclerite in Strenger, 1950; the additional subdivision of **DT** claimed by Verhoeff, 1903: fig. 10, for some Forficulina is discussed on pp. 282–283). This condition is already found in 1st instar nymphs (Verhoeff, 1903: 289). *Hemimerus* lacks a discrete sclerite **DT**, and the sclerotization homologous with **DT** of Forficulina is thus either absent or firmly united with **TG11** (within sclerite **TG11** + **DT**, as suspected by Verhoeff, 1903: 270; Fig. 5). In Forficulina sclerite **TG11** (anterior **ZW***-sclerite in Strenger, 1950) frequently forms a stout terminal projection (**tf** in Figs 23, 24) and bears the entire insertion of the cercal muscle **MAB2***. Accordingly, in *Hemimerus* at least the entire sclerotization of process **tf** (Figs 21, 22) and insertion area of muscle **43** (Fig. 12) belong to **TG11**. The sclerotization **DT**, if present in *Hemimerus*, forms thus at most the ventral anterior marginal part of sclerite **TG11** + **DT** (Figs 21, 22, compare Figs 23, 24). Nevertheless, whether **DT** is absent or included in **TG11** + **DT** remains unresolved.

(7) *Hemimerus* lacks a distinct cercal articulation. In Forficulina the cercal base has a complex pattern of articulations, for which Strenger's (1950) descriptions reveal a great variability. This includes translocations of articulations to neighbouring areas: compare Strenger's figs 3, 4 **G2***, **GE***, **GZ***, and **Z*** of *Labidura* and *Forficula* with respect to their relation to groove **N*** (separating **TG10** and **LP**); the articulation is translocated from **TG10** to **LP** (the latter regarded therein as lateral part of tergum X). Furthermore, a condyle and a ginglymus can be present side by side on the same sclerite, thus establishing a double articulation, in the one but not in the other species: compare Strenger's figs 3, 4 **GG*** and **GG** + **HÖ***, which belong to articulation **G1*** between cercal base and hind margin of tergum X; this indicates some potential of condyle and ginglymus to exchange their positions in the course of evolution. Accordingly, the single cercal articulation of Dictyoptera (**A98*** in Klass, 1997: fig. 58), which probably corresponds to **G1*** of Forficulina, has the condyle on the margin of tergum X, whereas **G1*** in some Forficulina has the condyle on the cercal base. This variability calls for caution in the use of cercal articulations in the homologization of the surrounding sclerites.

(8) In contrast to *Hemimerus*, Forficulina (at least *Forficula*) have a muscle from the lateral part of **TG10** to sclerite **LP** (muscle **m2*** in Fig. 24 and Verhoeff, 1903: 272, fig. 11).

(9) In *Hemimerus* sclerite **AP** is small and weak and remote from sclerite **LP** (Fig. 21). In Forficulina **AP** is mostly larger and stronger, though always much weaker than **LP**, and it usually joins the median margin of **LP** quite closely (Figs 23, 24). Young *Hemimerus* nymphs have entire paraprocts extending from the flanks of the anus to the cercal base (Davies, 1966: 76), and **LP** and **AP** are probably subdivisions of these.

Interestingly, the clasper-bearing forficuline *Apachyus* conforms with *Hemimerus* in the connections between **TG10** and **TG11** and between **TG11** and **DT** (or in the absence of **DT**) as well as in the large size of sclerite **TG11** + **DT**. *Apachyus* shows, in addition, a connection between sclerites **TG11** + **DT** and **LP** (ventral to the cercal base, cf. Fig. 21). In some of the characters (4)–(9) the polarity of the states may seem quite obvious. Nevertheless, polarization needs outgroup comparison and, as a basis for this, well-founded hypotheses on homologies with other lower-grade Insecta and on the morphological nature of the various components—under consideration of morphological and ontogenetic data. These requirements are provided in the following sections, and conclusions are drawn, as far as possible, in 'Phylogenetic Implications', pp. 301–304.

HEYMONS' INTERPRETATION OF THE POSTGENITAL ABDOMEN

Heymons' results on the early ontogeny of Dermaptera and other lower-grade Insecta

Heymons (1895a,b) studies *Forficula auricularia* L. (Dermaptera), *Periplaneta orientalis* L. (= *Blatta orientalis* Linnaeus, 1758; in the following referred to as *Blatta*; Dictyoptera), *Gryllus campestris* L., *Gryllus domesticus* L., and *Gryllotalpa vulgaris* Latr. (Ensifera), claiming (Heymons, 1895a: 4) that all conform in the embryonic segmentation of the abdomen (with few exceptions, see below). It should be noted that Heymons' (1895a,b) 'Analstueck' or telson, bearing the anus, is by some authors called segment XII. 'Telson' is herein preferred because it lacks coelomic cavities (but not mesoderm), appendage buds, and a ganglion anlage (Heymons, 1895a: 6ff) and is thus not indicated to be or include a true segment.

Heymons' (1895a: 28ff) results on *Forficula* are the following. The posteriormost abdominal segments are X and XI, followed by the telson. Segment X forms a sternum, a tergum, coelomic cavities, appendage buds, and a ganglion anlage. Segment XI is claimed to be devoid of a discrete sternum and tergum (Heymons, 1895a: 28, 29), but there are contradictory statements (Heymons, 1895b: 22). It forms appendage buds, a mesodermal cell cluster lacking coelomic cavities, and no discrete ganglion anlage; the latter may be associated with ganglion anlage X from its beginning. As compared with *Blatta,* in which sternum XI (but not tergum XI), coelomic cavities XI, and a ganglion anlage XI are discrete, segment XI is somewhat reduced. The telson is a ring-wall around the anus. During later ontogenetic stages, regarding the body wall, segment XI disappears except its appendage buds, which develop into the cerci. Tergum X develops strongly (tergum XI might be included as its posterior marginal part); as in *Gryllotalpa,* but in contrast to *Blatta,* it does not fuse with the dorsal wall of the telson. The appendages X are leveled and integrated into sternum X, i.e. a coxosternum X is formed (1895b: 22); this becomes vestigial and fuses with the ventral wall of the telson. The telson divides into a dorsal lobe (lamina supraanalis) and a pair of ventrolateral lobes (laminae subanales). Heymons (1895a: 36) interprets both **TG11** and **DT** of adult *Forficula* as dorsal telson sclerites and **LP** (probably plus **AP**) as ventral telson sclerites (cf. Fig. 23; adult condition in *Forficula* very similar).

In *Lepisma saccharina* L. (Zygentoma) Heymons (1897) finds essentially the same development as in the above 'orthopteroids', with one striking difference: a distinct tergum XI develops and is retained in the imago; it forms a terminal filament. With respect to the other features, segment XI forms a discrete ganglion anlage, a mesoderm compartment without coelomic cavities, and appendage buds that develop into the cerci. Sterna X and XI disappear. The telson comprises a lamina supraanalis and a pair of laminae subanales surrounding the anus. The former lamina develops into the supraanal lobe (**lsa*** in Fig. 28). The latter laminae develop into the subanal lobes, which are occupied by the paraprocts (**ppct*** in Fig. 28). According to Heymons, the paraprocts are thus ventral telson sclerites and homologous with the similar paraprocts of Dermaptera (**LP**+**AP**), Dictyoptera, and Ensifera. With respect to tergum XI and the telson components, Larink (1969) in *Petrobius brevistylis* Carpenter (Archaeognatha) and Heymons (1896) in *Ephemera vulgata* L. (Ephemeroptera) come to the same results.

Scrutiny of Heymons' results

The most crucial point is the meaning of Heymons' frequent statements that certain terga or (coxo)sterna disappear during development or do not appear at all. Read critically, these statements are very ambiguous. It should be noted that the components to be discussed are probably the dorsum and the venter (not the tergum and the coxosternum) of the respective primary segments as bordered by the intersegmental grooves, though this is not clear from Heymons' wording. For simplicity, however, 'tergum' and 'coxosternum' are used in the following.

Disappearance of a tergum/coxosternum is true if the two intersegmental grooves bordering it anteriorly and posteriorly approach each other and unite; the area of the tergum/coxosternum in between is then entirely lost. However, disappearance as claimed by Heymons ("geht zu Grunde") probably means in most cases that the tergum/coxosternum becomes smaller, and then *one* of the intersegmental grooves is lost, the area of the tergum/coxosternum thus being fused with another area but still present as a vestige. This becomes especially clear, for example, in Heymons' description for coxosternum X of *Forficula* (1895a: 29): "Sehr bald darauf geht auch das nur einen schmalen Streifen bildende 10. Abdominalsternit zu Grunde, es schliesst sich eng an den hinten folgenden Analabschnitt an und kann an diesem als ein selbständiger Abschnitt nicht mehr nachgewiesen werden." (i.e. the narrow coxosternum X disappears *and* fuses with the succeeding telson area).

This distinction between (1) the reduction of an area plus its fusion to another area and (2) the complete disappearance of an area is of enormous importance. The same is true for the distinction between (3) the primary presence of an area in a state where it is not demarcated from another area and (4) the absolute primary absence of an area. In cases (1) and (3) a certain tergum or coxosternum is still present in a more or less vestigial condition and can bear muscle insertions or articulations, or develop some structure, or even undergo a secondary expansion. In cases (2) and (4) muscle insertions or articulations must be located elsewhere, and structures must originate from another area; a secondary expansion of a lost or primarily lacking area is, of course, impossible. Many of the problems in previous morphological interpretations of the postgenital abdomen are rooted in insufficient attention to these distinctions. Examples are found in e.g. Ford (1923) and Matsuda (1976), who frequently interpret 'disappearance' *sensu* Heymons as absolute absence in subsequent stages of development. In ontogenetic studies an observation of the body surface in its correlation with the underlying mesodermal compartments (mainly the anlagen of the musculature) might help to avoid such problems. In Heymons' contributions such correlation is never discussed when terga or (coxo)sterna are claimed to 'disappear'.

Two further problems concern the laminae supra- and subanales of the telson, which are supposed by Heymons to develop into the supraanal and subanal lobes of the nymphs and imagines. First, the developmental continuity of the three laminae into the respective lobes, or at least into their distal parts, was never actually demonstrated by Heymons. Second, it must be asked whether the laminae could belong to segment XI, the laminae subanales being, for instance, basal parts of the appendages XI (compare Bitsch, 1974b: 220, but see also comments on p. 293 on location of coxopodia XI). In ontogenetic studies I could not find any statement that the mesoderm portions of segment XI and of the telson lobes are separated. In contrast, Larink (1969: 137) reports that in Archaeognatha these are interconnected. Moreover, Heymons' observation that in some Insecta tergum XI and sternum XI are demarcated from the telson seems not very convincing from his illustrations (e.g. 1897: fig. 8). Hence, ontogenetic studies have not yet demonstrated conclusively that the subanal lobes of (some) adult Insecta, or their tips, correspond to ventral telson lobes, and that the paraprocts contain telson sclerotizations.

According to this scrutiny of Heymons' writings, his data permit quite different interpretations of the terminal components in Dermaptera and other lower-grade Insecta. While Heymons (1895a: 29) could not observe a separate tergum XI at any stage in *Forficula*, an area representing this tergum can well be present through all embryonic stages, connected either with tergum X (as suspected in Heymons, 1895a: 29) or with the dorsal part of the telson (as indicated in Heymons, 1895b: 22). The separation of sclerites **TG11** and **DT** as present in young nymphs or even in late embryos of Forficulina (see p. 278) could well be a division of Heymons' 'dorsal telson' into a true tergum XI and a dorsal telson sclerite. There is thus no objection that the dorsal telson *sensu* Heymons contains dorsal telson and tergum XI, that sclerite **TG11** of Dermaptera (Figs 22, 24) is a true tergum XI, homologous with that of Archaeognatha, Zygentoma (**TXI*** in Fig. 28), and Ephemeroptera (**tXI*** in Fig. 27), and that sclerite **DT** of Dermaptera (Figs 21, 23) is a true dorsal telson sclerite. This is here considered the most convincing interpretation, and it will be shown below that it is strongly supported by morphological data. A similar scrutiny is necessary for Heymons' assumptions on the terminal dorsal sclerotizations of other 'orthopteroids'.

Similarly, Heymons' (1895a: 28, 29) descriptions of the venters X and XI of *Forficula* can well mean that the area of (coxo)sternum XI does not become demarcated from the ventral telson but is included therein, and that the reduced coxosternum X fuses with this compound element. Heymons' (1895b: 22) wording even indicates that this is what he actually means. In addition, that the hindmost parts of this complex do actually belong to a telson is doubtful. Hence, according to Heymons' descriptions, the sclerites **LP** and **AP** are likely to include sclerotizations of segment X and segment XI, and possibly of the ventral telson, the extent and size ratios of the individual constituents within the imaginal sclerotizations being unknown. A corresponding composite nature can be true for the paraprocts of other Insecta, e.g. *Lepisma* and *Blatta*. Moreover, the division between **LP** and **AP**, and similar divisions in some other Insecta, could correspond to a delayed separation of some of the components.

SNODGRASS' INTERPRETATION OF THE POSTGENITAL ABDOMEN

Snodgrass (1931) considers a broad range of Insecta (though not Dermaptera), and his interpretations may be correct for some taxa and less so for others. Essentially, he regards the cerci as the entire appendages XI, i.e. as including the coxopodia XI, the serial homologues of coxal and laterocoxal parts. Most of the cercal muscles are suspected to be modified dorsal muscles X. The paraprocts represent sternum XI proper (not coxosternum XI), and the epiproct is tergum XI proper; this would also apply to **LP**+**AP** and **TG11**, respectively, of Dermaptera, though not mentioned therein. The three telson lobes (supraanal and subanal lobes) are only in few Insecta distinct and sclerite-bearing in postembryonic stages, e.g. in nymphs of Odonata (Snodgrass, 1931: fig. 12A; what is called subanal lobe herein, e.g. **sb** in Fig. 21, does not belong to this category and is not telsonal but XIth-segmental in the frame of Snodgrass' hypothesis). Snodgrass' interpretation thus contrasts with Heymons' in that tergum XI and sternum XI are well developed in the imagines, whereas telson components are minute or obsolete. This largely complies with the above scrutiny of Heymons' conclusions. Snodgrass' views of tergum XI, of the cerci and their muscles, and, to some extent, of the absence of ventral telson sclerites in the paraprocts will gain more support through the following discussions.

The interpretation of the paraprocts as sternum XI proper, however, is more disputable. It seems conclusive in the case of those Insecta which have, in addition to the paraprocts, sclerotizations on the ventral side of segment X (coxosternum X?) and lobes with sclerites ventrolateral to the anus (probably telson components). But there are two problems. First, it is not entirely clear whether the ventral sclerotizations X of e.g. Odonata and Notoptera (Walker, 1943: 688;

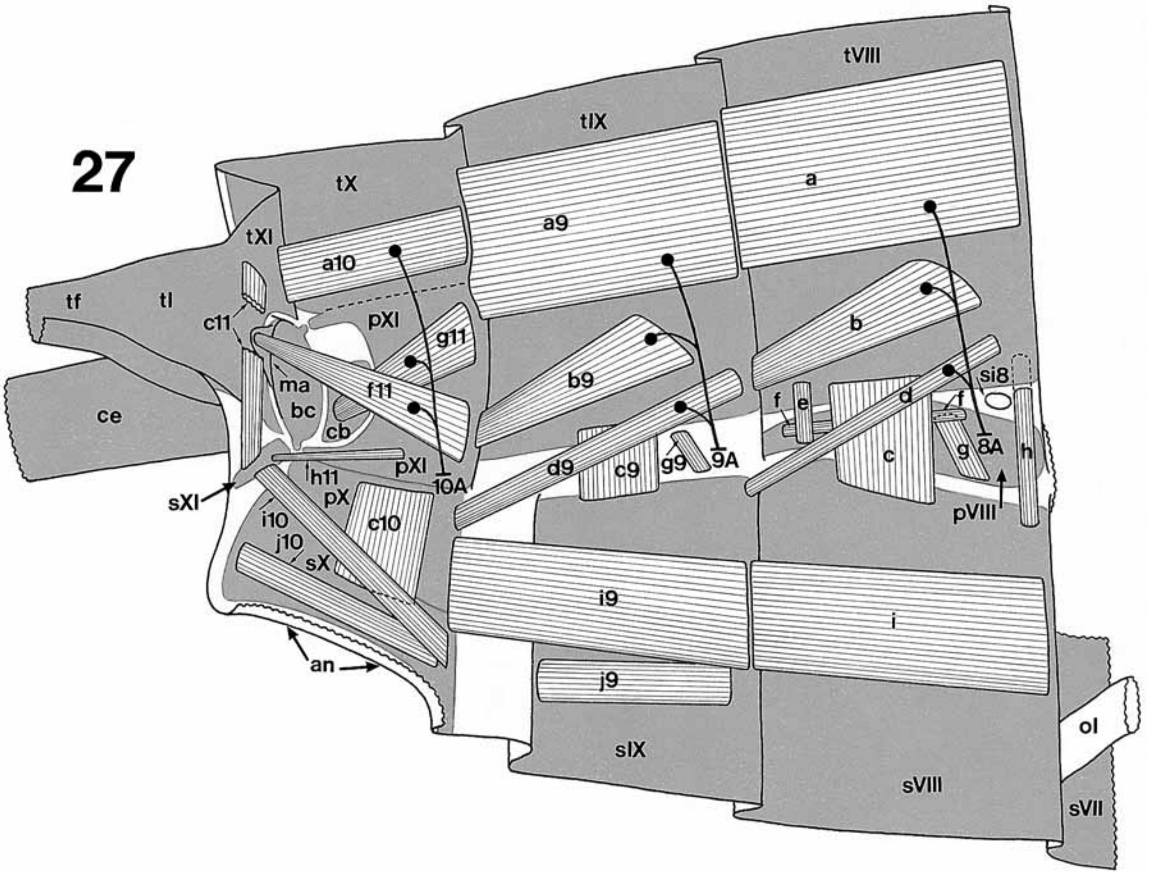

Figure 27. Female genital and postgenital abdomen in *Povilla adusta* (Ephemeroptera). Left halves of segments VIII–XI and telson shown semi-schematically; internal view; anteroventral parts of segment VII included (coxosternum, oviduct). Dorsal part bent, lying in same plane as ventral part. ↑ dorsomedian, ↓ ventromedian, → anterior. Sclerotization grey. Muscles striped according to course of fibres. Cerci and terminal filament cut. Not to scale. Redrawn from Birket-Smith (1971), with his abbreviations predominantly used, indicating his interpretations: single lower case letters (+numbers) = muscles (number gives segment); bc = basis cerci; cb = cercal base; ol = oviduct (paired); pVIII, X, XI = pleura VIII, X, XI; sVII–XI = sternum VII–XI; tVIII–XI = tergum VIII–XI; tl + tf = terminal filament and its sclerotization. Remaining abbreviations (an, ce, ma, si) as defined in present paper. Distal parts of dorsal nerves A of segments VIII, IX, and X included; black dots represent muscle innervation. Muscle f shown for segment VIII though present only in preceding segments. Muscle i10 included though present only in male. Relative widths of muscles only roughly indicated; most muscles actually broader.

Nagashima, 1991: 160) include the entire coxosternum X or even part of it. This topic needs detailed scrutiny, which will be given elsewhere. Second, in Insecta without such additional discrete sclerotizations, the homologues of these could well be included in the paraprocts. An inclusion of coxosternum X is even strongly indicated in taxa where the paraprocts receive muscles from coxosternum IX and tergum X (e.g. in Dictyoptera, muscles **48***, **60*** in Klass, 2000: fig. 20); the paraproctal insertions are likely to be coxopodial and Xth-segmental. This inclusion of coxosternum X, and, with the abovementioned restrictions, of ventral telson sclerotizations, is furthermore suggested for some of the relevant taxa by Heymons' descriptions. The paraprocts could thus also have a different composition in different taxa. The issue will be taken up again in 'Cerci and associated muscles', pp. 287–294.

MATSUDA'S INTERPRETATION OF THE POSTGENITAL ABDOMEN

Matsuda's hypotheses on Dermaptera

Matsuda (1976) proposes two perplexing hypotheses. (1) The cerci are components of segment XII, termed pseudocerci, and not homologous with the XIth-segmental cerci of other Insecta. (2) The area between tergum X and anus comprises three terminal segments XI, XII, and XIII (telson), termed the opisthomeres. Matsuda refers to Verhoeff (1903), Heymons (1895a, b), Burr (1915a), and Bhatnagar & Singh (1965). Of course, both the non-cercal origin of the dermapteran claspers and the putative extra abdominal segment in Dermaptera (12 + telson) as compared with other Insecta (maximum 11 + telson) are very unparsimonious hypotheses, which require good arguments to be accepted.

Scrutiny of the pseudocercus hypothesis

Heymons (1893, 1895a,b) claims unambiguously that the cerci develop in embryos of *Forficula,* as in those of other Insecta, from the 11th abdominal pair of a segmental series of outgrowths, which is thus likely to be homologous in the various taxa including *Forficula,* and to constitute the XIth-segmental appendage buds as well-demonstrated for other Insecta. In later stages of *Forficula* the cercal bases shift posterodorsad into their definitive position posterolateral to the paraprocts, like in other Insecta. Heymons' interpretation of the cerci in *Forficula* as appendages XI is reasonable considering the correspondence with other Insecta, but there are two points of uncertainty. First, illustrations showing these developments for *Forficula* are wanting. Second, *Forficula* embryos show no clear demarcation of segment XI on the body wall (connection probably with telson, see pp. 279–280) or in the mesoderm, and it would be impossible to identify the prospective cerci as XIth-segmental and non-telsonal by considering *Forficula* alone.

Bhatnagar & Singh (1965), studying the ontogeny of *Labidura riparia* (Pallas), mention the postgenital abdomen only in few sentences. The results comply with Heymons' on *Forficula*: 10 abdominal ganglion anlagen and pairs of coelomic cavities develop (fig. 36). No external border between segment XI and the telson is reported; both areas are comprised as the 'caudal segment' = 'segment XI', which develops the sclerites **TG11**, **DT**, and **LP** (and **AP**?), and the cerci. Regarding the origin of the cerci, the crucial point is that Bhatnagar & Singh (1965) only say that in the 69-hour embryo the 'paraprocts' (= laminae subanales) 'give rise' to the cerci. It remains unclear whether they have observed (1) that the cerci gradually grow out of the laminae subanales during successive stages, or only (2) that the laminae subanales bear the cerci in the 69-hour stage. If (2) is true, a previous shift of the cercal base into this position, conforming with Heymons' results, could have escaped their attention. If (1) is true, it should be noted that no border is present between venter XI and laminae subanales. Moreover, also in *Lepisma* the cerci and the laminae subanales develop in a close spatial relation (Heymons, 1897: 623, fig. 8). Such a condition can easily be misinterpreted as the cerci originating from the laminae subanales. Whatever is true, the descriptions of Bhatnagar & Singh (1965) are far from demonstrating that the cerci are in *Labidura* outgrowths of the laminae subanales and telson components.

Matsuda (1976: 221) makes some claims aimed at supporting the pseudocercus hypothesis. (1) Heymons' segment XI of *Forficula*, giving rise to the cerci, most probably refers to a segment XI plus 'segment' XII (= telson). (2) The cercal bases of adult Dermaptera are immediately behind the 'subanal lobes' (paraprocts), in contrast to other insects. (3) There is no sign of an ontogenetic shift of the cercal bases into this position. All claims are irrelevant or incorrect. (1) As explained above, Heymons' 'telson' probably includes segment XI, and, judging from this aspect alone, the origin of the cerci from segment XI or from the telson may be considered undecidable. Nevertheless, Heymons does clearly not have the view that the cerci originate from the laminae subanales. (2) In e.g. Ephemeroptera (Birket-Smith, 1971: fig. 1), Dictyoptera (Klass, 1997: figs 36, 293; Klass, 2000: fig. 4), and Zygentoma (Rousset, 1973: figs 3, 8) the cercal bases are in exactly the same relative position as in Dermaptera (cf. Figs 21–24 and 25, 26): behind the lateral parts of the paraprocts (not behind the far median subanal lobes, which is also not true for the Dermaptera; compare **sb** in Fig. 5). (3) Heymons (1895a: 28) in general claims a respective shift of the cercal bases and gives no exception for *Forficula*.

Matsuda's (1976) pseudocercus hypothesis is thus untenable. The works of Heymons (1895a,b) and Bhatnagar & Singh (1965) both have weak points, but Heymons seems more reliable because the process of cercus development is better documented and various Insecta are directly compared. In addition, the adult morphology of Dermaptera and other Insecta is, as will become clear in the following sections, entirely consistent with the assumption of the homology of the cerci.

Scrutiny of the opisthomere hypothesis

Verhoeff (1903) and Burr (1915a) claim the presence of three sclerites behind tergum X in some Forficulina: pygidium, metapygidium, and Analstueck (**Py***, **Mpy***, **A*** in Verhoeff's fig. 10; compare two sclerites **TG11**, **DT** in Figs 23, 24). I reinvestigated *Diplatys* and *Pyragra,* genera stated to clearly show the tripartition (Verhoeff, 1903: 269), as well as *Pygidicrana* and *Echinosoma* (Figs 23, 24). The results correspond with Verhoeff's (1903) fig. 10, but whereas **Py*** and **Mpy*** are clearly separated by a narrow membrane, **Mpy*** and **A*** are in all these taxa clearly not. Only two sclerites **Py*** = **TG11** and **Mpy** + **A*** = **DT** are present as in *Forficula*. Sclerite **DT** comprises areas of different appearance and a transverse ridge (**tr** in Fig. 23), which may correspond to the areas **Mpy*** and **A*** of Verhoeff and to the border between them.

Verhoeff's (1903: 269) hypothesis, uncritically accepted by Burr (1915a: 257) and Matsuda (1976: 219f), is that **Py***, **Mpy***, and **A*** are the terga of segments XI and XII and of the telson (segment XIII therein). For this hypothesis it is not so relevant whether **Mpy*** and **A*** are separated by a membrane or by a ridge **tr**, which could then be an antecosta between segment XII and telson. The hypothesis, however, has to be rejected because only postembryonic external morphology is considered, and because in both ontogenetic studies on Dermaptera only 11 segments plus telson were found. Furthermore, sclerite **DT** articulates in Forficulina with the cercal base (**h*** in Verhoeff, 1903: fig. 10) and is used as a median abutment for the movements of the cerci (Strenger, 1950). This articulation seems to be, within the lower-grade Insecta, peculiar to Forficulina, and ridge **tr** could be a secondary functional ridge for strengthening. Hence, there result no objections against the assumptions that these posterior sclerites are tergum XI (**Py*** = **TG11**) and a dorsal telson sclerite (**Mpy** + **A*** = **DT**), and that the postgenital abdomen has in Dermaptera the same segmental composition as in other lower-grade Insecta, but with segment XI showing some reduction in the embryo (see p. 279).

Though Verhoeff's findings on sclerite **DT** are not conclusive in this respect, it is well possible that in all Insecta the telson *sensu* Heymons includes vestigial segments that have lost all components characterizing a segment (demarcation by intersegmental grooves, discrete mesoderm, ganglion anlage, and appendage buds). Studies of gene expressions marking segmental borders might be more conclusive in this issue.

POSTGENITAL ABDOMEN COMPARED IN DERMAPTERA AND EPHEMEROPTERA

Similarities between the taxa

Birket-Smith's (1971) contribution on the ephemeropteran *Povilla adusta* Navas (Polymitarcidae) provides one of the most detailed morphological descriptions available for the abdomen of lower-grade Pterygota. Because *Povilla* also shows many interesting similarities with Dermaptera, a comprehensive comparison between the two taxa is given here (summarized in Table 3). The similarities are tentatively regarded here as homologies (plesiomorphies within the Pterygota), which can give also indications on the polarity of characters within the Dermaptera (see p. 278). It should be noted that in the interpretation of the postabdominal components the present author largely disagrees with Birket-Smith. The postgenital abdomen of *Povilla* has the following components.

(1) Sclerite **tXI*** (Figs 25, 26) closely resembles **TG11** of Forficulina, especially that of *Echinosoma* (Figs 23, 24): it joins the middle posterior margin of tergum X **tX***, lies as a vertically orientated, quadrangular plate between the cercal bases **bc***, and has a process arising from its centre (terminal filament **tf*** with cone-like base **tl***). As in Forficulina, but in contrast to *Hemimerus* (Fig. 22), separation from tergum X is complete. The terminal processes on **TG11** of Forficulina and on **TG11** + **DT** of *Hemimerus* (**tf** in Figs 21–24) are indicated as homologues of the terminal filament of Ephemeroptera (as suggested also by Verhoeff, 1903: 270).

(2) The medially divided transverse sclerite **sXI*** (Fig. 25) lies between the aforementioned sclerotization and the anus, in the same position as the medially undivided sclerite **DT** of Forficulina (Fig. 23). Hence, *Povilla* probably has a separation corresponding to that between **TG11** and **DT** in Forficulina, in contrast to *Hemimerus* (Fig. 21).

(3) The cercal base joins the lateral posterior margin of tergum X **tX***. The cercal walls are at the median cercal base folded into the body cavity (**ma** in Fig. 26) to form an apodeme like in Dermaptera (**ma** in Figs 22, 24). In these features *Povilla* conforms with both *Hemimerus* and Forficulina.

(4) Between the lateral margin of tergum X **tX*** and the ventral midline the plates **pXI***, **pX***, and **sX*** adjoin each other in succession (Figs 25, 26). Each is connected with its neighbor sclerite, the borderlines represented by 'seams'. Unfortunately, Birket-Smith (1971) does not specify 'seam' (line of weak sclerotization or internal ridge?). The most ventromedian of these sclerotizations, **sX***, flanks the anus **an** (Fig. 25), thus having the same position as sclerite **AP** of Dermaptera (Figs 21, 23). It is crossed by two longitudinal muscles (**i10***, **j10*** in Fig. 27) like **AP** in *Hemimerus* (**36**, **37** in Fig. 13), the muscles being more or less in line with the ventral muscles of the preceding segments. The transverse connection of the **sX*** = **AP** of the two sides (anterior to the anus; only in the female) in *Povilla* is in contrast to Dermaptera.

(5) The neighbouring sclerite **pX*** (Fig. 25) has the same position as sclerite **LP** of Dermaptera (Figs 21, 23). Its connection with **sX*** = **AP** (along a 'seam') in *Povilla* is in contrast to Dermaptera. Nevertheless, at least in *Hemimerus* **AP** and **LP** are connected in young nymphs (Davies, 1966).

(6) Sclerite **pXI*** (Figs 25, 26) takes the same position as the lateral part of tergum **TG10** of Dermaptera (Figs 21–24), occupying the lateral body wall anterior to the cercal base. **pXI*** is separated from **tX*** by a 'seam', completely so in the nymph but only posteriorly in the imago. Dermaptera lack such a borderline dividing **TG10**. **pXI*** is regarded here as the lateral part of tergum X; Birket-Smith's interpretation as pleura XI is discussed on pp. 289–293, below.

(7) *Povilla* has two cercal articulations, on the dorsal

Table 3. Homology and interpretation of components of postgenital abdomen. The first column gives the assignment to segment X or XI or to the telson. The next three columns give the components for the taxa considered, designated by the terms used by the respective authors; m. = muscle; NR = component not reported; trans. conn. = transverse interconnection between the pair of components named after. To the terms for the cercal muscles of Dermaptera the corresponding terms for Caelifera (Snodgrass, 1935a) are added. The last column gives the morphological interpretation resulting as the most probable from the discussions in the text. Cercal m. 42/287 is indicated as an intersegmental tergo-coxopodial X, but its specification as an internal dorsal X, together with cercal m. 40/288 may be more probable

Area	Dermaptera	Ephemeroptera	Zygentoma	Interpretation
	This paper Verhoeff, 1903*	Birket-Smith, 1971	Rousset, 1973	
X	TG10 median part	tX	TX median part	tergum X median part
	TG10 lateral parts	pXI	TX lateral parts	tergum X lateral parts
	LP	pX	ppct lateral parts	laterocoxa X (+coxa X?)
	AP	sX	ppct median parts	coxa X (?)
	NR	trans. conn. sX	trans. conn. ppct	sternum X
	cercal m. 40/288	dorsal m. a10	dorsal m. 1a	internal dorsal muscles X
	cercal m. 41/289	cercal m. g11	dorsal m. 4a,b,c	external dorsal muscles X
	cercal m. 42/287	cercal m. f11	NR	intersegmental tergo-coxopodial muscles X
	m. m2*	NR (m. c10?)	m. 63 (+m. 64?)	intrasegmental tergo-coxopodial muscles X
	m. 36	m. i10	m. 65 ex parte	?
	m. 37	m. j10	m. 65 ex parte	?
	m. 38	NR	m. 66d	?
	NR	NR	m. 66c	intersegmental coxopodio-tergal muscles X?
XI	TG11	tXI	TXI median part	tergum XI median part
	tendon ct area	sclerite cb	TXI stpz parts	tergum XI lateral parts
	process tf	process tl + tf	process ft	terminal filament XI = process of tergum XI
	cercus	cercus	cercus	entire appendage XI
	cercal base	cercal base bc	cercal base	coxopodium XI
	NR	m. c11	m. 68	dorsal muscles XI
	cercal m. 43/293	NR	cercal m. 67	intrasegmental tergo-coxopodial muscles XI
Telson	DT	sXI	sclerite per	dorsal telson sclerite
	NR	NR	lobe lsa	dorsal telson lobe

and on the ventral hind margin of **pXI***. Both have the condyle on the cercal base (Figs 25, 26). As described by Strenger (1950: fig. 3), the articulations **G1*** and **G2*** of certain Forficulina are similar: located on the dorsolateral and on the lateral hind margin of tergum **TG10**, with the condyles on the cercal base. However, for the lateral articulation **G2*** this position and orientation is probably apomorphic within the Forficulina. A condyle on sclerite **LP** seems here to be plesiomorphic (Fig. 23; Strenger, 1950: **Z*** and **GZ*** in fig. 5a, b), and a corresponding condyle on the paraproct is reported for Zygentoma (Fig. 28; Rousset, 1973: fig. 8). Altogether, cercal articulations do not seem to be very reliable as landmarks for homology analysis.

(8) *Povilla* has two cercal muscles, both coming from the lateral part of tergum X **pXI*** (Fig. 27). Muscle **g11*** inserts on the small sclerite **cb***, which lies in between **pXI*** and the lateral cercal base and is enclosed by the two cercal articulations (Figs 25, 26). **g11*** resembles muscle **41** of Dermaptera, which inserts on the unsclerotized lateral cercal base on the tendons **ct** (Fig. 12). The tendons **ct** and sclerite **cb*** are probably in homologous sites. Muscle **f11*** inserts on the apodeme **ma** of the median cercal base and resembles the **ma**-inserted muscles **40** and **42** of Dermaptera (Fig. 12; but the muscles are probably not homologous, see pp. 239–243, below).

Differences between the taxa

Some of the components that are overall similar in *Povilla* and Dermaptera show structural differences,

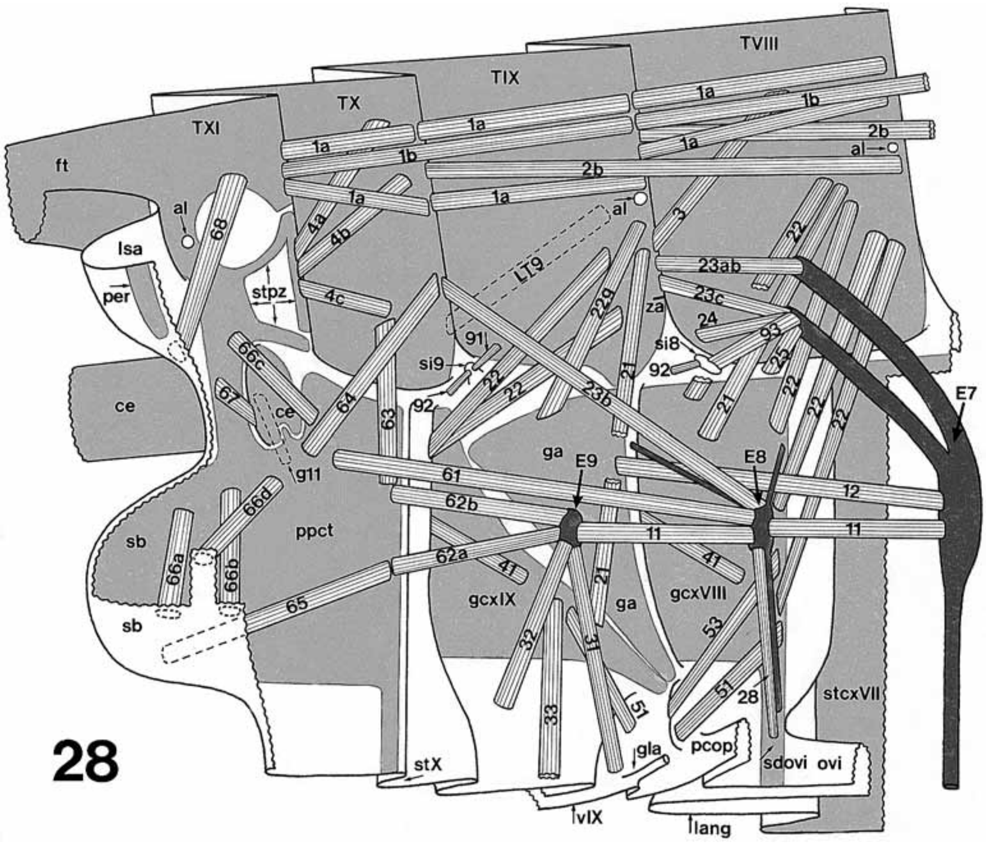

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Figure 28. Female genital and postgenital abdomen in *Thermobia domestica* (Zygentoma). Representation as in Fig. 27; in addition, endosternites dark grey. Redrawn from Rousset (1973), with his abbreviations predominantly used, indicating his interpretations: numbers (+lower case letters) = muscles; al = alary muscle insertion; E7–9 = endosternites; ft = terminal filament; ga = laterocoxa IX (gonangulum); gcxVIII = coxa + laterocoxa VIII (gonocoxite); gcxIX = coxa IX (gonocoxite); gla = accessory gland; lang = subgenital lobe VII (languette); lsa = supraanal lobe; ovi = median oviduct; pcop = spermatheca (copulatory pouch + seminal receptacle); per = dorsal telson sclerite (periproct); ppct = paraproct; sdovi = sternum VIII; stX = membranous area of coxosternum X; stcxVII = coxosternum VII; stpz = XIth-segmental sclerotizations surrounding trapezoidal membrane; TVIII–XI = terga VIII–XI; vIX = median interconnection of gonapophyses IX (valve); vVIII = gonapophyses VIII have their bases at the posteromedian insertions of muscles 51, 53; za = weak zone anterolaterally on tergum IX (zone amincie). Muscles 27 (from E8 to anteromedian margin of gcxVIII) and 52 (intrinsic gonapophyseal muscles) omitted. Two muscles described by Birket-Smith (1974) for *Lepisma saccharina* indicated by dashed lines: LT9, g11. Remaining abbreviations (ce, sb, si; si9 = vestigial spiracle IX) as defined in present paper. Muscle representation only reflecting arrangement, not relative widths of muscles, on which there is no information in Rousset (1973).

and there are components in each taxon that are not reported for the other.

(9) *Povilla* shows the following differences to Dermaptera. As mentioned above, **sXI*** = **DT** is medially divided, the two **sX*** = **AP** are interconnected anterior to the anus, **sX*** = **AP** and **pX*** = **LP** are connected, and there is a 'seam' between the dorsal and the lateral parts of tergum X, **tX*** and **pXI***. In addition, muscle **i10*** inserts in *Povilla* on sclerite **sXI*** (Fig. 27), whereas muscle **36** of *Hemimerus* does not reach **TG11** + **DT** posteriorly (Fig. 13). This makes the homology between **sXI*** and **DT** somewhat uncertain. On the other hand, **DT** could well be entirely absent in *Hemimerus* (see p. 278), and whether in Forficulina the homologous muscles insert on **DT** is unknown.

(10) Components restricted to *Povilla* are sclerite **cb*** (Figs 25, 26) and the muscles **a10***, **c10***, **c11***, and **h11*** (Fig. 27). Muscle **a10*** from tergum X **tX*** = **TG10** to tergum XI **tXI*** = **TG11** is clearly a dorsal muscle X (it has strongly modified homologues in Dermaptera, see p. 292). Muscle **c10*** from **pX*** = **LP** to **sX*** = **AP** is interpreted by Birket-Smith as an intrasegmental tergosternal X but has, according to his hypothesis, a pleural instead of a tergal insertion (compare the putatively homodynamous muscle **c*** in Fig. 27). The muscle connecting in *Forficula* the lateral

part of tergum X **TG10** = **pXI*** and sclerite **LP** = **pX*** has different insertions (compare **m2*** and **c10*** in Figs 24 and 26). Muscle **c11*** from tergum XI **tXI*** = **TG11** to sclerite **sXI*** = **DT** is interpreted by Birket-Smith as an intrasegmental tergosternal XI but is more probably a dorsal muscle XI (discussion on p. 287). Muscle **h11*** from the lateral part of tergum X **pXI*** = **TG10** to sclerite **sXI*** = **DT** is interpreted by Birket-Smith as an intrasegmental tergosternal XI but has, according to his hypothesis, a pleural instead of a tergal insertion (compare the putatively homodynamous muscle **h*** in Fig. 27). Muscles **c10*** and **h11*** fit neither into Birket-Smith's interpretation of the sclerotizations nor into mine. If their insertions are accurately described they are very exceptional for Insecta.

(11) *Hemimerus* has some muscles not reported for *Povilla*: muscle **38** crossing **AP** = **sX*** transversely (Fig. 13), muscle **43** from **TG11** = **tXI*** to the cercal base (Fig. 12), muscle **39** traversing behind the anus (Fig. 13), and the extrinsic rectal muscles **45–50** (Figs 12, 13). *Forficula* has the abovementioned muscle **m2*** (see Fig. 24; Verhoeff, 1903), which is absent in both *Hemimerus* and *Povilla*.

Conclusions on Dermaptera

In the dorsal terminal sclerites the similarity between **tXI*** of *Povilla*, bearing the terminal filament **tl** + **tf***, and **TG11** of Dermaptera, bearing the process **tf**, is noteworthy. Together with Heymons' (1896) finding that the corresponding area of *Ephemera* is tergum XI, it suggests that **TG11** of Dermaptera is actually tergum XI and that process **tf** of Dermaptera is a vestigial terminal filament. What Heymons (1895a,b) regards as the dorsal telson in *Forficula* is thus likely to include tergum XI, as described in 'Heymons' interpretation', above. The complete separation of terga **TG10** and **TG11** in Forficulina is then plesiomorphic, and their median fusion in *Hemimerus* and *Apachyus* is apomorphic (see p. 278). The similarity between **sXI*** of *Povilla* and **DT** of Forficulina suggests that the presence of a discrete sclerite **DT** in Forficulina is plesiomorphic, and that its lack or fusion with **TG11** in *Hemimerus* and *Apachyus* is apomorphic (see p. 278).

Regarding the cerci, *Povilla* and Dermaptera are similar in the location of the cercal base relative to tergum X (**tX** + **pXI***, **TG10**) and to the paraprocts (**pX** + **sX***, **LP** + **AP**), in the presence of an apodeme **ma** on the median cercal base, in the cercal articulations (with the restrictions given above), and in part of the cercal musculature (muscles **f11***, **g11***; **40**, **41**, **42**). This confirms the homology of the cerci of the two taxa contra Matsuda's (1976) pseudocercus hypothesis. The presence at least of the dorsal cercal articulation in Forficulina should be plesiomorphic, its absence in *Hemimerus* apomorphic (see p. 278).

The ventral terminal sclerites **sX*** and **pX*** of *Povilla* and **AP** and **LP** of Dermaptera extend together from the lateral margin of tergum X **tX** + **pXI*** = **TG10** onto lobes **sb** flanking the anus (Figs 21–26), just like the undivided paraprocts of e.g. Dictyoptera (Klass, 2000: fig. 4) and of *Hemimerus* nymphs. The far separation between **AP** and **LP** and reduction of **AP** in adult *Hemimerus* appears apomorphic (see p. 278). The division into **sX*** = **AP** and **pX*** = **LP** reminds of the division into coxa and laterocoxa in the genital segments. If **sX*** = **AP** are interpreted as coxae X and **pX*** = **LP** as laterocoxae X, the muscles **i10***, **j10*** of *Povilla* and **36**, **37** of *Hemimerus* could be ventral muscles spanning segment X. Muscle **m2*** of *Forficula* (cf. Fig. 24) could be an intrasegmental tergo-coxosternal X, inserted ventrally on the laterocoxa like muscles **6**, **7**, **24** of *Hemimerus* (Figs 2, 12) and the homologous muscles of *Forficula* (see Table 1) in the preceding segments. The subanal lobes (**sb** in Fig. 5) could from their position be coxal lobes X, serially homologous with e.g. the gonoplacs of segment IX (**gl9** in Figs 16, 18, 20). These interpretations, however, are equivocal since according to Heymons' results only a minor part of the paraprocts should be Xth-segmental (see pp. 279–280).

In the following sections the comparison of postgenital abdominal components is expanded to a wider systematic frame, under additional inclusion of Orthoptera, Dictyoptera, Archaeognatha, and, in particular, Zygentoma. It will be shown that especially conditions in Zygentoma lend further support to the homologies and polarities assumed above for tergum XI and dorsal telson sclerites, and to some of the last-mentioned interpretations in the ventral sclerotizations and muscles. Homologies between Dermaptera, Ephemeroptera, and Zygentoma are summarized in Table 3.

TERGUM XI, DORSAL TELSON SCLERITES, AND ASSOCIATED MUSCLES

Tergum XI

In the zygentoman *Thermobia* (Fig. 28; Rousset, 1973: fig. 8) tergum XI **TXI*** is larger than in Dermaptera and *Povilla*, arches far dorsally between the cercal bases, bears a long and filamentous terminal filament **ft***, and has a complex lateral part (**stpz*** in Fig. 28). Tergum XI receives several muscles from tergum X (**1a***, **4a**,**b**,**c*** in Fig. 28), i.e. dorsal muscles X having the original course from **TG10** to **TG11**; such muscles are poorer in *Povilla* (**a10*** in Fig. 27) and absent in *Hemimerus*. All these conditions in *Thermobia* are probably plesiomorphic as compared to those in Dermaptera and *Povilla*. Because the lateral parts of tergum

XI and the dorsal muscles X are deeply involved in the evolution of the cercal base and its muscles, these components and the respective anagenetic events are discussed in 'Cerci and associated muscles', below.

Dorsal telson sclerites

Thermobia has between the posterior base of the terminal filament and the anus a supraanal lobe **lsa*** with a transverse sclerite **per*** in its ventral wall (Fig. 28). Some nymphs of Odonata have a transverse sclerite in the same position (**sa*** in Snodgrass, 1931: fig. 12A). The position and the undivided condition of sclerites **per*** and **sa*** suggest their homology with sclerite **DT** of Forficulina. Homology between **per*** and the sclerite pair **sXI*** of *Povilla* is suggested by the similar position and by the musculature (Figs 27, 28): both *Thermobia* and *Povilla* have, besides the dorsal muscles X, only one muscle inserted on the dorsal part of tergum XI (**68***, **c11***), and this runs to the membrane near the lateral tips of **per*** and to **sXI***, respectively. For the zygentoman *Lepisma* two such muscles are reported (**DE11***, **DL11*** in Birket-Smith, 1974: fig. 25). Due to their location dorsal to (behind) the anus, the medially undivided **per***, **sa***, and **DT** are clearly not sternum XI as suggested for **sXI*** of *Povilla* by Birket-Smith (1971), and due to their probable homology and their separation from tergum XI, these sclerites are best all regarded as dorsal telson sclerites. The lack of a median division of the sclerite in Forficulina, *Thermobia,* and odonatan nymphs is plesiomorphic, and the division in *Povilla* apomorphic. The lack in *Hemimerus* of such a discrete dorsal telson sclerite **DT** is confirmed as apomorphic (see p. 286). Muscles **c11***, **68***, and **DE11/DL11*** are likely to be dorsal muscles XI (Rousset, 1973: 78; Birket-Smith, 1974: 51); their presence in Zygentoma and *Povilla* is plesiomorphic, and their absence in *Hemimerus* apomorphic.

CERCI AND ASSOCIATED MUSCLES

Major issues and problems of interpretation

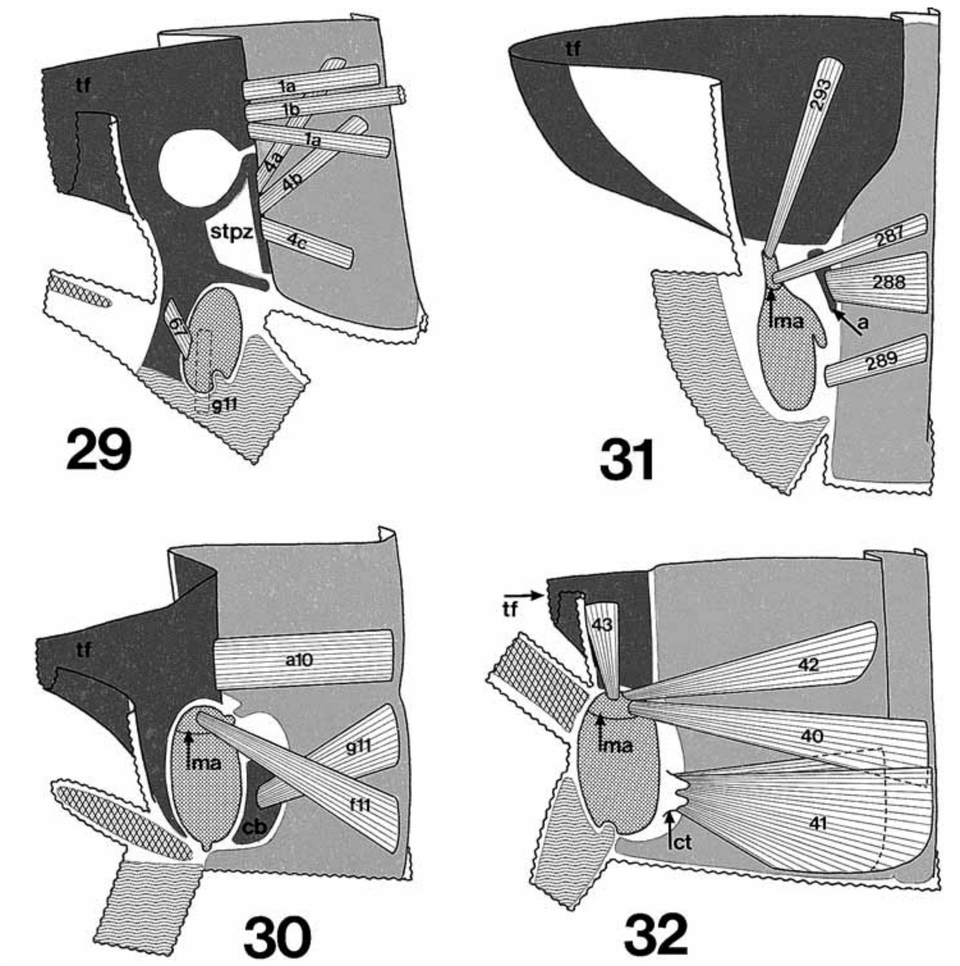
As explained above, the cerci of Insecta including Dermaptera are best regarded as the appendages XI. Two closely interrelated basic issues remain to be discussed.

(1) The morphological nature and anagenetic origin of the cercal muscles. Archaeognatha lack cercal muscles (Bitsch, 1974b: 220; Birket-Smith, 1974: 27). Zygentoma have one XIth-segmental cercal muscle (Rousset, 1973; Birket-Smith, 1974). Pterygota have often one XIth-segmental muscle (**43** of *Hemimerus,* Fig. 12), but predominant are some strong Xth-segmental cercal muscles from tergum X, or from tergum IX in female Dermaptera (**40**, **41**, **42** of *Hemimerus,* Fig. 12). The Xth-segmental muscles insert partly on the cercal base sclerotization, and partly on smaller sclerites or on the membrane around the cercal base (e.g. on sclerite **cb*** in *Povilla,* on tendons **ct** in *Hemimerus*). As mentioned on p. 280, Snodgrass (1931: 25) suspects their derivation from dorsal muscles X but does not go into details.

(2) The morphological nature of the cercal base. Snodgrass (1931: 25) assumes that the cercal base, and small surrounding sclerites if present, are formed by coxopodium XI (=laterocoxa+coxa XI); the major distal parts of the cerci correspond to abdominal styli, representing the distal part of appendage XI. Bitsch (1974b: 220) and Rousset (1973: 77), referring to Zygentoma, assume that the entire cerci correspond to abdominal styli, the coxopodia XI being represented by the paraprocts. Birket-Smith (1974) has the same view (coxopodium XI included in his 'sternum XI'). In the more anterior segments of Zygentoma and Archaeognatha the stylus base receives muscles only from the coxal area in front of it (muscle **60*** in Bitsch, 1973: fig. 8; muscles **f***, **g*** in Birket-Smith, 1974: figs 15, 25, 29; muscle **41*** in Fig. 28 and Rousset 1973: fig. 6), and the coxopodia receive muscles from the tergum of the same segment (**50–54*** in Bitsch, 1973: fig. 8; **c***, **h*** and **LA8***, **LP8***, **CC8*** in Birket-Smith, 1974: figs 15, 25; **21***, **22*** in Fig. 28). Hence, whether the cercal base is a coxopodium XI or a stylus base XI should be testable by the muscles inserted on it. In addition, of course, also the muscles inserted on the paraprocts have a bearing on this issue since they might indicate that coxopodium XI is included in these, hence not in the cercal base. The issue will therefore be taken up again in 'Paraprocts and associated muscles', below. A further point of interest is (3) the condition of the cerci in Diplura and the evidence it bears in terms of the morphological interpretation of the cerci and the related components of Insecta. This is discussed at the end of this section.

Cercal muscles XI

For the single cercal muscle of Zygentoma the origin is ascribed to rather different sites (Figs 28, 29): while muscle **g11*** of *Lepisma* inserts on the paraproct immediately anteromedian to the cercal base (Birket-Smith, 1974: fig. 29), muscle **67*** of *Thermobia* inserts on a sclerite bridge connecting paraproct and tergum XI posterior to the cercal base (Rousset, 1973: fig. 8). The *Lepisma* muscle **g11*** could be a typical coxo-stylar muscle and indicate that coxa XI is included in the paraprocts and that the cercal base is a stylus base. This muscle has then been lost in Pterygota, which never have muscles from the paraprocts to the cercal base (see Snodgrass, 1931: 25, 95; Bitsch, 1979: 329; Figs 30–32). The alternative proposal by Birket-Smith



Figures 29–32. Morphology of cercal base and neighbouring components. Terga X and XI, paraproct, dorsal telson sclerite, cercal base, and (prospective) cercal muscles of left side shown semi-schematically; internal view. ↑ dorsomedian, ↓ ventromedian, → anterior. Sclerite shading indicating homologies. Muscles striped according to course of fibres. Sclerotizations surrounding cercal base cut apart and spread out around cercal base. Abbreviations ma and tf as defined in present paper. No scale. Fig. 29. *Thermobia domestica* (Zygentoma). Redrawn from Rousset (1973), area stpz and muscles with his designations. Muscle g11 described by Birket-Smith (1974) for *Lepisma saccharina* indicated by dashed lines. Fig. 30. *Povilla adusta* (Ephemeroptera). Redrawn from Birket-Smith (1971), sclerite cb and muscles with his designations. Fig. 31. *Dissosteira carolina* (Caelifera). Redrawn from Snodgrass (1935a), sclerite a and muscles with his designations. Fig. 32. Dermaptera: essentially the condition in *Hemimerus*, but articulation between sclerite LP and cercal base, and separation between sclerites TG11 and DT shown as present in *Echinosoma*. Muscles designated as in *Hemimerus* (cf. Fig. 12).

░ Terga IX, X (TG9, TG10) █ Tergum XI (TG11) ▩ Dorsal telson sclerite (DT)

▒ Cercal sclerotization (CE) ≋ Paraproct, lateral part (LP)

(1971) that this muscle is retained, coxa XI (**pXI*** of *Povilla* in Fig. 27) integrated into tergum X, and the paraprocts of Zygentoma and Pterygota thus not strictly homologous is very unlikely (discussion below).

The *Thermobia* muscle **67***, however, can hardly be homodynamous with the usual coxo-stylar muscles (**41*** in Fig. 28), even if the bridge bearing its origin should belong to coxa XI as suspected by Rousset (1973). This bridge can as well belong to tergum XI, which also in *Povilla* (Figs 27, 30; Birket-Smith, 1971: fig. 1C) and in nymphs of Odonata (Snodgrass, 1931: fig. 12A) extends far ventrad posteromedian to the cercal base and closely approaches the paraproct, though remaining discrete. If the bridge is XIth-tergal, muscle **67*** can be homologous with the cercal muscles XI found in some Pterygota. Such muscles clearly originating on tergum XI are reported for Dermaptera (**43** in Figs 12, 32; Table 2), Caelifera (**293*** in Fig. 31 and Snodgrass, 1935a: fig. 14; **cs*** in Ford, 1923: 307), and Ensifera (**cs*** in Ford, 1923: 306f). Because coxopodia receive muscles from the tergum, while the styli do not, the muscles of *Thermobia* and these Pterygota connect tergum XI probably with coxopodium XI, being intrasegmental tergo-coxopodials XI, and the cercal base is thus likely to be formed by coxopodium XI. For Caelifera the report of a contribution from mesoderm XI to the cercal musculature (Roonwal, 1937: 184) confirms the segmental assignment of the muscles. Muscles **67*** of *Thermobia* and **43** of *Hemimerus* appear thus homodynamous with some of the intrasegmental tergo-coxosternals of the preceding segments (**21***, **22*** in Fig. 28; **1–7** in Fig. 2). The cercal muscles XI seem thus to be ancestral limb base muscles XI, whose absence may well be apomorphic in Archaeognatha and is quite certainly apomorphic in *Povilla* (Fig. 30) and respective other Pterygota. Nevertheless, these conclusions are tentative and in conflict with muscle **g11*** of *Lepisma*. Since this point is highly important, a reinvestigation of the cercal muscles in Zygentoma would be desirable.

It should be noted that Ford (1923: 305) interprets the cercal muscles XI **cs*** as "intersegmental dorsal muscles XI–XII", i.e. dorsal muscles XI from the XIth-segmental cercal base to a dorsal telson sclerite 'tergum XII'. This is purely based on her acceptance of Heymons' claims that segment XI is lost except the cerci and that the 'supra-anal plate' must therefore be 'tergum XII'. These claims, however, are for Orthoptera in the same way unreliable as for Dermaptera (see p. 280), and the 'supra-anal plate' is quite certainly tergum XI (**TG11** in Fig. 31). The presence of cercal muscles XI in some other Pterygota is disputable because the composition of what is called 'tergum X' (tergum X or terga X+XI?) and 'epiproct' (tergum XI or dorsal telson sclerite?) is unresolved and cercal muscles XI may thus arise from this 'tergum X'. This could be the case in e.g. Notoptera (muscle **230*** in Walker, 1943), and this could also be responsible for the ambiguous case of Phasmatodea: here the two cercal muscles **370*** and **371*** reported by Maki (1935: 261) for *Megacrania tsudai* Shiraki appear to be Xth-segmental since they do not arise from the well-developed epiproct (tergum XI?) but from tergum X (terga X+XI?); Leuzinger, Wiesmann & Lehmann (1926: 276), however, mention for *Carausius morosus* Br. an ontogenetic origin of the cercal muscles from mesoderm XI.

Cercal muscles X

The following hypothesis on the anagenetic origin of the cercal muscles X of Pterygota builds upon two assumptions. First, the anterior insertions are on genuine parts of tergum X (Birket-Smith's, 1971 abovementioned proposal that the insertions are on genuine coxae XI **pXI*** is discussed below). Second, these muscles have serial homologues in preceding segments or homologues in Zygentoma and Archaeognatha, i.e. they are not peculiar to segment X of Pterygota. Accordingly, it must be tested (1) whether some new abdominal muscles have developed in Pterygota that could be cercal muscles in segment X, and (2) whether Zygentoma and Archaeognatha have muscles in segment X that are indicated to have been modified into cercal muscles in Pterygota. There are then two groups of muscles that could potentially contribute to the cercal muscles X.

(1) Intersegmental tergo-coxosternal muscles (like **d*** in Fig. 27) are absent in Zygentoma and Archaeognatha (possibly except muscle **d9***; see p. 267) but present in the mid-abdomen of some Pterygota (though possibly not in the ground plan of Pterygota; see p. 267). Their ventral insertions are usually anterolaterally on a coxosternum, hence probably laterocoxal, less probably coxal (see p. 272). In segment X these muscles would connect tergum X and coxopodium XI. If the latter is included in the cercal base, as indicated by the cercal muscles XI (see above), some cercal muscles X could be the Xth-segmental representatives of these muscles. For such muscles an insertion directly on the cercal base (if coxopodium XI) is expected.

(2) Tergo-tergal muscles, i.e. typically located dorsal muscles, are in segment X as well-developed as in the preceding segments in Zygentoma and Archaeognatha but reduced or absent in Pterygota (see p. 286). Furthermore, in Pterygota the cercal muscles X connect the XIth-segmental cercal base area with the preceding tergum, and in Archaeognatha and Zygentoma only the terga have muscular connections with preceding terga, via the dorsal muscles, but not the coxosterna and styli (apart from **d9***, which is considered above). The dorsal muscles X of Zygentoma and Archaeognatha are thus the only potential progenitors of some cercal muscles X. If modified into cercal muscles, these are more likely to insert not directly upon but near the cercal base. Dorsal muscles X are **1a*** and **4a**,**b**,**c*** in Zygentoma (Fig. 28; Rousset, 1973: fig. 8) and **1***, **2***, **3***, **4*** in Archaeognatha (Bitsch, 1974a: fig. 3). In *Thermobia* the **1a*** bundles insert on the median main part of tergum XI and are probably internal dorsals. Muscles **4a**,**b**,**c*** are attached to a ribbon-like sclerite, which is part of the abovementioned complex lateral portion of tergum XI (**stpz*** in Fig. 28). The ribbon-sclerite is likely to be tergal, as indicated by its position

as compared to the preceding terga, as well as by the tergo-tergal course of the probable serial homologues of muscles **4a**,**b**,**c*** in the preceding segments (muscles **3***, **LT9*** in Fig. 28). Archaeognatha have similar muscles, also in segment X (muscles **3***, **4*** in Bitsch, 1974a: fig. 3). These muscles appear, due to their lateral position and oblique course, as external dorsals.

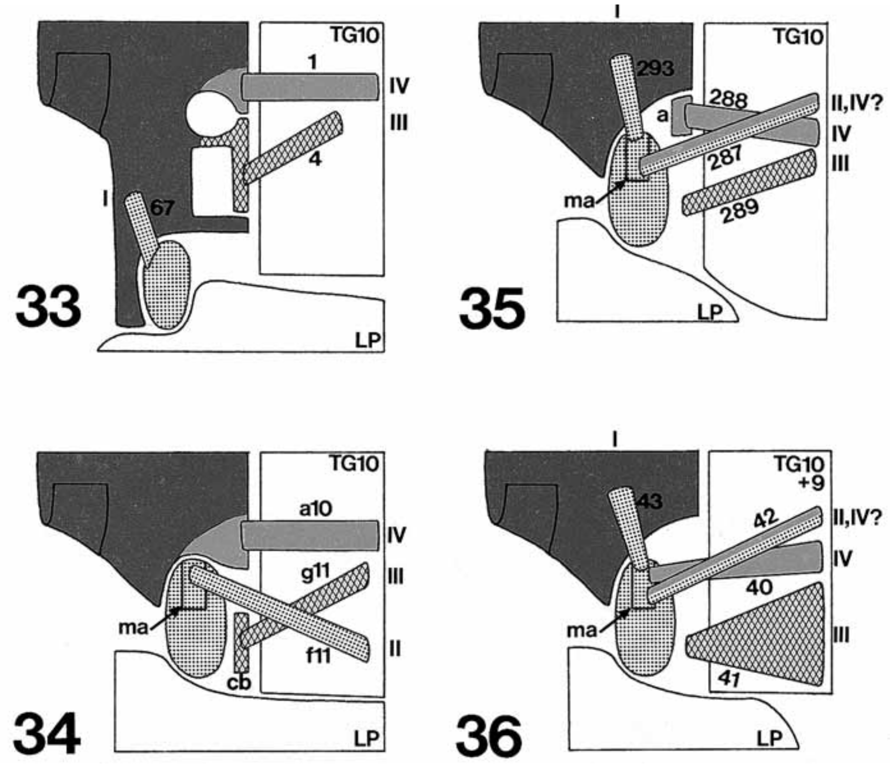
How can the two cercal muscles X and adjacent components in *Povilla* be interpreted in view of the facts and relations in points (1) and (2)? One cercal muscle X of *Povilla* (**g11*** in Fig. 27 and Birket-Smith, 1971: fig. 5B) has its 'cercal' insertion on the small sclerite **cb***, which is close to the cercal base like the ribbon-sclerite of *Thermobia*, though more ventral (Figs 27–30). It seems probable that **cb*** of *Povilla* and this sclerite of *Thermobia* are homologous lateral parts of tergum XI, more or less detached from its main part, and that muscles **g11*** and **4*** are homologous (Figs 33, 34). In *Povilla* muscle **g11*** has a similar course as the external dorsal muscles **b9*** of segment IX and **b*** of the mid-abdominal segments (Fig. 27) and seems to be their Xth-segmental serial homologue. The other cercal muscle X of *Povilla* (**f11*** in Fig. 27) is directly attached to the cercal base. One might suspect that part of the ribbon-sclerite of *Thermobia* (Fig. 28), with part of its muscle insertions **4***, has in *Povilla* been integrated into the cercal base, and that part of muscles **4*** is homologous with muscle **f11***. However, this demands a shift of the muscle insertion. It seems thus more parsimonious to assume that in *Povilla* muscle **f11*** is the Xth-segmental serial homologue of the intersegmental tergo-coxosternal (i.e. tergo-coxopodial) muscles **d*** of the preceding segments (Fig. 27), with no homologue in *Thermobia*. *Povilla* has, in addition, a typical internal dorsal muscle X **a10***, homodynamous with muscles **a9*** of segment IX and **a*** of the mid-abdominal segments (Fig. 27). Muscle **a10*** as well as the corresponding muscles **1a*** of *Thermobia* (Fig. 28) have the posterior insertion on the median main part of tergum XI and are located dorsomedian to the external dorsal muscles **g11*** and **4***.

In *Povilla* the nervous system has been studied. In the abdominal segments up to IX the intersegmental tergo-coxosternals **d***, the external dorsals **b***, and the internal dorsals **a*** are supplied by the distalmost branches of the dorsal nerve (**8A**, **9A** in Fig. 27; Birket-Smith, 1971: fig. 5A). In segment X the cercal muscles **g11*** and **f11*** and the internal dorsal **a10*** are likewise supplied by the distalmost branches of one single nerve (**10A** in Fig. 27; Birket-Smith, 1971: 151). Hence, the innervation is consistent with the serial homology of **d*** and **f11***, **b*** and **g11***, and **a*** and **a10*** as assumed above (but would also comply with the interpretation of **f11*** as another external dorsal muscle).

The caeliferan *Dissosteira* (Fig. 31; Snodgrass, 1935a: fig. 7) has, like *Povilla*, a discrete tergum XI and a small sclerite **a*** near the cercal base. Sclerite **a*** is located more dorsomedially than **cb*** of *Povilla* (Fig. 30), its median tip being almost in touch with the lateral tip of tergum XI. Cercal articulations are absent. *Dissosteira* has three cercal muscles X: **287***, inserted on the cercal base apodeme **ma**, might correspond to **f11*** of *Povilla* and might be an intersegmental tergo-coxopodial X (but see below for alternative interpretation). **288***, inserted on sclerite **a*** dorsomedian to the cercal base, and **289***, inserted on the membrane (dorso)lateral to the cercal base, are likely to be dorsal muscles. Judging from their positions, the median **288*** is the internal, and the lateral **289*** the external dorsal muscle, corresponding to **a10*** and **g11*** of *Povilla*, respectively. In contrast to *Povilla*, **287*** = **f11*** has its Xth-tergal insertion much more medially, a small sclerite that like **cb*** bears the external dorsal **289*** = **g11*** is absent, and the part of tergum XI bearing the internal dorsal **288*** = **a10*** has become detached from tergum XI to form sclerite **a***. The sclerites **cb*** of *Povilla* and **a*** of *Dissosteira* are thus probably not homologous but represent two 'generations' of sclerites detached from the main part of tergum XI (Figs 34, 35). This conforms with their different locations lateral (**cb***) and dorsal (**a***) to the cercal base. Many Ensifera also have three cercal muscles X (**ca***, **cd***, **ce*** in Ford, 1923: 306f), but the available descriptions are not very detailed. Ander (1957: 96) reports for some species two small sclerites ventral and dorsal to the cercal base, both bearing cercal muscle insertions. These sclerites may correspond to **cb*** of *Povilla* and **a*** of *Dissosteira* and support the non-homology of the latter sclerites.

Dermaptera (Fig. 32) also have a set of three cercal muscles X (**42**, **40**, **41** of *Hemimerus*, Fig. 13; Table 2). Disregarding the expansions/shifts to tergum IX in the female, the anterior and posterior insertions conform with those in *Dissosteira* (Fig. 31): **42** = **287***, **40** = **288***, **41** = **289***. The only difference is that **40** = **288***, probably the internal dorsal muscle X, is attached not to a separate XIth-tergal sclerite (**a*** in *Dissosteira*) but to the cercal base apodeme **ma**. An XIth-tergal area is thus assumed to have been integrated into the cercal base. The external dorsal muscle **41** inserts near the lateral cercal base like **289*** of *Dissosteira* and **g11*** of *Povilla*, and it is attached to membrane like the *Dissosteira* muscle. Hence, as suspected on p. 284, the tendons **ct** of Dermaptera are in a site homologous to that of sclerite **cb*** of *Povilla*.

The interpretation of most of the cercal muscles X as internal and external dorsals X seems conclusive, but the interpretation of others as intersegmental tergo-coxopodials X (**f11***, **287***, and **42*** in Figs 30–32) is partly problematic. The latter interpretation is convincing for **f11*** of *Povilla* (Fig. 34) because cor-



Figures 33–36. Anagenetic hypothesis for cercal muscles and their insertion areas. Representation and designations as in Figs 29–32 but more schematical, dorsal telson sclerites omitted, and different parts of tergum XI indicated. Each (prospective) cercal muscle shaded like the area of segment XI that originally bears the cercal insertion. Cercal muscles categorized as I = intrasegmental tergo-coxopodial XI; II = intersegmental tergo-coxopodial X; III = external dorsal X; IV = internal dorsal X; categorization of 287 (Fig. 35) and 42 (Fig. 36) as II or IV uncertain. Fig. 33. *Thermobia domestica* (Zygentoma). Fig. 34. *Povilla adusta* (Ephemeroptera). Fig. 35. *Dissosteira carolina* (Caelifera). Fig. 36. Dermaptera.

▓ Tergum XI (TG11), main part ▒ Tergum XI (TG11), anteromedian part, and internal dorsal muscles X inserted on it ▨ Tergum XI (TG11), anterolateral part, and external dorsal muscles X inserted on it

░ Cercal sclerotization (CE) and inter- and intrasegmental tergo-coxopodial muscles inserted on it

responding muscles **d*** are present in the preceding segments (Fig. 27) and **f11*** has like these a far lateral anterior insertion. Nevertheless, as explained on p. 267, the entire series of abdominal intersegmental tergo-coxopodials in *Povilla* may be derived from lateral dorsal muscles. In Dermaptera and *Dissosteira*, however, the interpretation of muscles **42** and **287*** (Figs 35, 36) as intersegmental tergo-coxopodials X faces two problems. First, the mid-abdominal segments lack corresponding muscles, and this could well be a primary absence (see p. 267; Klass, 1999: fig. 41; but compare also muscle **25** of *Hemimerus*, p. 281). Then it is unlikely that in these taxa intersegmental tergo-coxopodial muscles are present in segment X and contribute to the cercal musculature. Second, muscles **42** and **287*** have their Xth-tergal insertions much more dorsomedially than **f11*** of *Povilla* and than expected from an intersegmental tergo-coxopodial muscle (compare muscle **6*** of Dictyoptera in Klass, 1999: figs 3, 4). In addition, one reason to interpret muscles **42** and **287*** as intersegmental tergo-coxopodials X rather than as dorsal muscles X would be to explain their insertion directly on the cercal base. The cercal insertion of muscle **40** of Dermaptera, however, strongly indicates that the insertion area of a dorsal muscle can indeed shift onto the cercal base (compare Figs 35 and 36). Hence, muscles **42** and **287*** are probably better regarded as dorsal muscles—as part of the internal dorsals judging from their far median Xth-tergal insertion—and as non-homologous with **f11***, which is, then, a muscle peculiar to *Povilla.*

Birket-Smith's hypothesis on Povilla

According to Birket-Smith (1971) the anterior insertions of the cercal muscles X in *Povilla* are not on genuine parts of tergum X but on coxopodium XI (essentially what he calls pleura XI **pXI***; see Birket-Smith, 1974: 51), which has fused with tergum X (Fig. 27). His interpretation of the area **pXI*** as 'pleural XI' is based on two assumptions: (1) The appendage components of the abdominal segments up to VIII are represented by a pair of narrow pleural sclerites (**pVIII*** in Fig. 27) flanking a large true sternum. Each has two intrinsic muscles (**f***, **g*** in Fig. 27). (2) The cercus is the distal part of appendage XI, and some extra-cercal pleural area XI is the basal part. Then, because **f11*** and **g11*** (Fig. 27) are the only muscles inserting on or near the cercal base, the areas bearing their origins should represent the pleural area XI. This hypothesis implies homology between the cercal muscles X of Pterygota and the cercal muscle XI **g11*** of *Lepisma* (Fig. 28; see above), and the interpretation of all these muscles as XIth-segmental.

This interpretation entails serious problems, also within the framework of Birket-Smith's own homology hypothesis.

(1) Birket-Smith (1971: 149) considers muscles **f11*** and **g11*** *a priori* as intrinsic (±coxo-stylar) appendage muscles, and he *a priori* localizes coxopodium XI around the origins of **f11*** and **g11*** (sclerotization **pXI***) and excludes it from the cercal base. The possibility that the muscles are e.g. extrinsic appendage muscles or modified dorsal muscles is not considered.

(2) Muscle **b9*** (Fig. 27) from tergum IX **tIX*** to **pXI***, quite certainly homodynamous with the external dorsals **b*** of the preceding segments, strongly suggests that **pXI*** is a tergal area X rather than an area of segment XI.

(3) That the cercal muscles **g11*** and **f11*** and the internal dorsal X **a10*** are supplied by the distalmost branches of the same nerve (**10A*** in Fig. 27), just as the muscles **b***, **d***, **a*** in the preceding segments (**8A*** in Fig. 27), is more consistent with the interpretation advocated herein than with Birket-Smith's assumption that the muscles belong to different segments X and XI—though the nerve topography of the postgenital abdomen can certainly not yield strong arguments.

(4) As a consequence of Birket-Smith's hypothesis, large parts of what is apparently tergum X should also in other Pterygota actually be coxopodia XI. To my knowledge, however, there are no indications for such a relation, either from morphology or from ontogeny. For these reasons Birket-Smith's hypothesis is regarded here as improbable.

Conclusions on cercal muscles

In Pterygota four muscles can be regarded as cercal muscles, one XIth-segmental and three Xth-segmental (**I–IV** in Figs 33–36). **I** The intrasegmental tergo-coxopodial XI (absent in *Povilla,* **43** in *Hemimerus*) and **II** the intersegmental tergo-coxopodial X (**f11*** in *Povilla,* possibly **42** in *Hemimerus*) are primary cercal muscles inserted directly on the cercal base (coxopodium XI). **III** The external dorsal muscle X (**g11*** in *Povilla,* **41** in *Hemimerus*) is a secondary cercal muscle inserted on smaller sclerites or on membrane lateral to the cercal base. **IV** The internal dorsal muscle X (**a10*** in *Povilla,* **40** and probably **42** in *Hemimerus*) is not a cercal muscle in *Povilla* (Fig. 34) but becomes a secondary cercal muscle when tergum XI is further fragmented or reduced; it is then inserted on smaller sclerites (Fig. 35) or on membrane near the cercal base, or, in the most derived condition, directly on the cercal base (Fig. 36). In *Thermobia* **I**, **III**, and **IV** are present (Fig. 33), only **I** working as a cercal muscle. In *Povilla* **II**, **III**, and **IV** are present (Fig. 34), only **II** and **III** working as cercal muscles; **I** has been lost, **II** probably belongs to a muscle series peculiar to this taxon. In the Neoptera considered herein **I**, **III**, and **IV** are present, and either **II** is present in addition or **IV** has become subdivided (Figs 35, 36); all work as cercal muscles.

The intrasegmental tergo-coxopodials XI (**I**) are probably ancestral limb base muscles. The intersegmental tergo-coxopodials X (**II**) belong to an abdominal muscle series that has arisen in Ephemeroptera (or possibly in Pterygota), either *de novo,* or from lateral dorsal muscles through a shift of the posterior insertions to the coxopodium. The dorsal muscles X (**III**, **IV**) have developed into cercal muscles (Figs 33–36) by a stepwise detachment of their posterior insertion areas, the lateral parts of tergum XI around the dorsal and lateral cercal base, from the median main part of tergum XI, and by a subsequent desclerotization of these areas and development into a narrow membrane (bearing in Dermaptera the tendons **ct**). These muscles thus have originally maintained their insertion sites, but through the modifications of their insertion sites they have gained a new function as cercal muscles. A subsequent integration of the insertions into the cercal base is possible. After the reduction of the lateral parts of tergum XI, articulations between tergum X and the cercal base may have developed as an abutment for the functionally modified dorsal muscles X. The narrow membrane between the cercal base and tergum X, crossed by these articulations, is originally XIth-tergal, reduced and desclerotized but still bearing the insertions of the dorsal muscles. This scenario also explains the absence of 'true' dorsal muscles X, i.e. such inserted posteriorly upon a distinct tergum XI, in at least most Neoptera.

Autapomorphies of Dicondylia and subgroups thereof could be included in these developments. An incomplete subdivision of the lateral parts of tergum XI, found in *Thermobia* in the **stpz***-area (Fig. 29) but apparently not in Archaeognatha (Bitsch, 1974b: 219), could be autapomorphic for Dicondylia. The complete detachment of the posterior insertion areas of the external dorsals X (**III**) from tergum XI and possibly an articulation between cercal base and tergum X could be autapomorphic for Pterygota. A set of four cercal muscles as present in Dermaptera, Caelifera, and Ensifera could be a groundplan condition of Neoptera. Potential autapomorphies of Neoptera included in this pattern are the detachment of the posterior insertion areas of the internal dorsals X (**IV**) from the main part of tergum XI, i.e. the function of these muscles as cercal muscles, and either a dorsal shift of the intersegmental tergo-coxopodials X (**II**) or a specific subdivision of the internal dorsals X (**IV**). The integration of the cercal insertions of all internal dorsals X (**IV**) into the cercal base could be autapomorphic for Dermaptera or a more inclusive subgroup of Neoptera. These tentative proposals remain to be tested through an inclusion of further taxa into the comparison.

Conclusions on cercal base

Rousset's (1973) and Bitsch's (1974b) hypothesis that the cercal base is a stylus base is supported by two arguments. (1) The position of cercal muscle **g11*** of *Lepisma* (Fig. 28; Birket-Smith, 1974), which appears to be coxo-stylar XI. However, such a muscle was not found in *Thermobia* (Rousset, 1973: fig. 8) and Pterygota, and, as noted above, conditions in Zygentoma need re-examination. (2) The articulation between paraproct and cercal base, with the condyle on the paraproct, as present in *Thermobia* (Fig. 28; Rousset, 1973: fig. 8) and as the probably plesiomorphic condition in Forficulina (Fig. 32). It provides indirect support for this hypothesis through suggesting coxopodium XI to be included in the paraprocts. This articulation could be a groundplan component of Dicondylia. But regarding its absence in Archaeognatha (Bitsch, 1974b), in many Neoptera, and probably in *Povilla* (see p. 284), and also in view of the variability of cercal articulations in Dermaptera (see p. 278), it could as well have developed independently in Zygentoma and Dermaptera. In addition, whether a groundplan feature of Dicondylia or not, the articulation could well connect the cercal base and e.g. coxosternal sclerotizations X, as articulations have also developed between the cercal base and tergum X. It will be shown in 'Paraprocts and associated muscles', below that, furthermore, the paraproctal musculature does not indicate the inclusion of coxopodia XI within the paraprocts. Hence, the support of this first hypothesis is very weak.

Snodgrass' (1931) hypothesis that the cercal base is formed by coxopodium XI receives support from the cercal musculature. (1) The cercal muscles XI of Dicondylia (except **g11*** of *Lepisma*) are most reasonably interpreted as intrasegmental tergo-coxopodials XI. (2) The cercal muscle X **f11*** of *Povilla* is quite clearly the Xth-segmental serial homologue of intersegmental tergo-coxopodials of the preceding segments. None of the cercal muscles of Dicondylia can be interpreted as coxo-stylar (except **g11***). (3) The cercal muscles X of Pterygota certainly include dorsal muscles X, and the small sclerites (**cb*** of *Povilla*, **a*** of *Dissosteira*) or the membranous areas they insert upon are XIth-tergal areas. These enclose the cercal base dorsally and laterally, and also in *Thermobia* (Fig. 27) the cercal base is dorsally in contact with tergum XI. The first hypothesis has thus to assume a close spatial association of a stylus base to a tergal area, with the usually intervening coxopodium still well developed (paraproct); this is difficult to conceive. A close association of a coxopodium to a tergal area, on the other hand, as implied by the present hypothesis, is quite a usual condition. In this way, the cercal base is more likely to be constituted by coxopodium XI. If this is true, the cercal apodeme **ma** could be homodynamous with the coxosternal apodemes **at** of the preceding segments (Figs 1, 6), being **at11** and its sclerotization laterocoxal. Nevertheless, whereas apodeme **ma** is probably present in the ground plan of Pterygota, this is less probable for the apodemes **at**. Some of the small sclerites surrounding the cercal base in Pterygota may additionally belong to coxopodium XI, as assumed by Snodgrass (1931), but at least **cb*** of *Povilla* and **a*** of *Dissosteira* are better interpreted as lateral parts of tergum XI (Figs 34, 35), receiving dorsal muscles that are functionally modified into cercal muscles.

Conditions in Diplura

The Japygidae share in their cercal morphology and musculature as outlined by Verhoeff (1903) and Snodgrass (1931) some features with Pterygota and especially Forficulina (cf. Figs 24, 26). Tergum X is large, tergum XI a small terminal sclerite posterior to its median hind margin. The strong, forcipate cerci originate posterior to the lateral hind margin of tergum X and articulate with it. The cercal base bears some tendons resembling **ct** of Dermaptera, and it receives strong muscles from tergum X. Snodgrass (1931: 95) interprets these, like the cercal muscles X of Pterygota, as dorsal muscles X.

The above comparison within the Insecta (=Ectognatha) has suggested that the close neighborhood and articulation between cercal base and tergum X, the function of dorsal muscles X as cercal muscles, and the reduced and fragmented condition of tergum XI have gradually evolved within the Dicondylia (Figs 33–36). The similarities between Pterygota and Japygidae, however, permit the alternative hypothesis that all the respective conditions were already present in the ground plan of Diplura + Insecta (the probably smallest taxon comprising Japygidae and Pterygota). Since monophyly is well supported for Insecta and for Dicondylia (compare e.g. Kristensen, 1991: 129f), with Japygidae being clearly outside both taxa, the respective conditions are then secondarily absent in Archaeognatha and Zygentoma.

Nontheless, the above interpretation of the japygid postabdominal terga is probably incorrect, and the similarities to Pterygota thus only apparent. This is indicated by ontogenetic data, which, however, are available only for campodeid Diplura. Uzel (1898) studies the early ontogeny of *Campodea staphylinus* Westw., considering external morphology only (not the ganglia and the mesoderm). The last abdominal segment is the large segment X, followed by small laminae supra- and subanales. The cerci bud from the posterior two thirds of this segment X (Uzel, 1898: figs 67–75), indicating that the laminae supra- and subanales constitute the telson. Hence, as compared with Insecta, this 'segment X' either comprises segments X and XI, which are not differentiated from each other externally, and of which the latter forms the cerci and corresponds to the cercal segment XI of Insecta. Or, as suggested by the presence of only one pair of appendage buds on this 'segment X', there are only 10 abdominal segments instead of 11, and the entire 'segment X' corresponds to the cercal segment XI of Insecta. Whatever is true, Uzel's (1898) descriptions show no reduction of the cercus-forming segment during ontogeny. This segment is thus likely to form all or the posterior part of 'segment X' of the adult, and the small posterodorsal sclerite is probably a telson component.

Assuming that the ontogeny of Japygidae resembles that of *Campodea*, the adult tergum X either is or includes the tergum of the cercal segment. The cercal articulations with and the cercal muscles from tergum X link the cerci with the genuine cercal segment. This is in sharp contrast to Pterygota, where these links are between different segments, X and XI. The small dorsal sclerite that joins in Japygidae the posterior margin of the adult tergum X is probably a dorsal telson sclerite, and clearly not the tergum of the cercal segment as it is true for the superficially similar tergum XI of Pterygota. Hence, the strong cercal muscles of Japygidae appear as appendage muscles intrinsic to the cercal segment, like the cercal muscles XI of Dicondylia. The tergum of the cercal segment separates the cercal base from the preceding tergum as in Archaeognatha. Only within the Dicondylia this tergum becomes reduced, a contact between the cercal base and the preceding tergum becomes established, and dorsal muscles of the segment preceding the cercal segment develop into cercal muscles. In this context, the poorness in Dicondylia and absence in Archaeognatha of cercal muscles XI appear as apomorphic conditions. Nevertheless, a final assessment of the evidence from the japygid condition on the issues discussed here has to wait for a detailed study of this taxon.

PARAPROCTS AND ASSOCIATED MUSCLES

Major issues and problems of interpretation

The interpretation of the paraprocts is for several reasons very difficult: (1) In many contributions it is discussed whether the paraprocts are (coxo)sternum X *or* XI, *or* ventral telson sclerites. However, Heymons' (1895a,b) results, as read critically, indicate that the paraprocts may contain coxopodial and sternal sclerotizations X *and* XI, *and* ventral telson sclerotizations (see pp. 279–280). (2) The paraprocts of different taxa may differ in this composition, then not being strictly homologous. For instance, differences could be present between Pterygota that have a complete Xth-segmental sclerite annulus of uncertain configuration and well-developed paraprocts behind it (e.g. Odonata, Notoptera; see pp. 280–281) and Pterygota that have only the well-developed paraprocts (e.g. Dermaptera, Dictyoptera, Zygentoma). (3) Also the paraprocts of the two sexes are not necessarily identical in their composition (see Birket-Smith's, 1974 interpretation for male and female *Lepisma*).

Bitsch (1974b: 220) indicates that in Archaeognatha and Zygentoma ontogenetic and morphological results suggest different interpretations of the paraprocts, but for these and other Insecta there is still a confusing variety of morphology-based interpretations. The ontogenetic studies of Heymons (1895a,b, 1897), Woodland (1957), and Larink (1969) indicate, as concluded above in 'Heymons' interpretation', that much of the paraprocts is formed by coxosternum XI and possibly ventral telson sclerites, but also that coxosternum X is frequently included. Bitsch (1974b: 220) and Rousset (1973: 77) consider the paraprocts as coxosternum XI, based on the morphology of *Thermobia*. Snodgrass (1931) regards the paraprocts as sternum XI (*s.s.*; see p. 280). Ford (1923: 301) assumes for the paraprocts of Orthoptera a composition of Xth-segmental and telsonal sclerotizations; sternum XI is assumed to be lost, following Heymons' (1895a) misleading descriptions. A scrutiny of some hypotheses concerning Orthoptera is given by Ander (1957). Above (p 286) preliminary evidence was given that the divided paraprocts of Dermaptera and *Povilla* are the laterocoxae and coxae X, though they may include additional components. In this section the available morphological data on various Dicondylia are analysed in terms of which composition of the paraprocts they suggest, i.e. the extent to which coxopodia and sterna X and XI and ventral telson sclerites can be traced within the paraprocts, and how the muscles inserted on the paraprocts are to be interpreted. Conditions in Zygentoma are basic for this attempt.

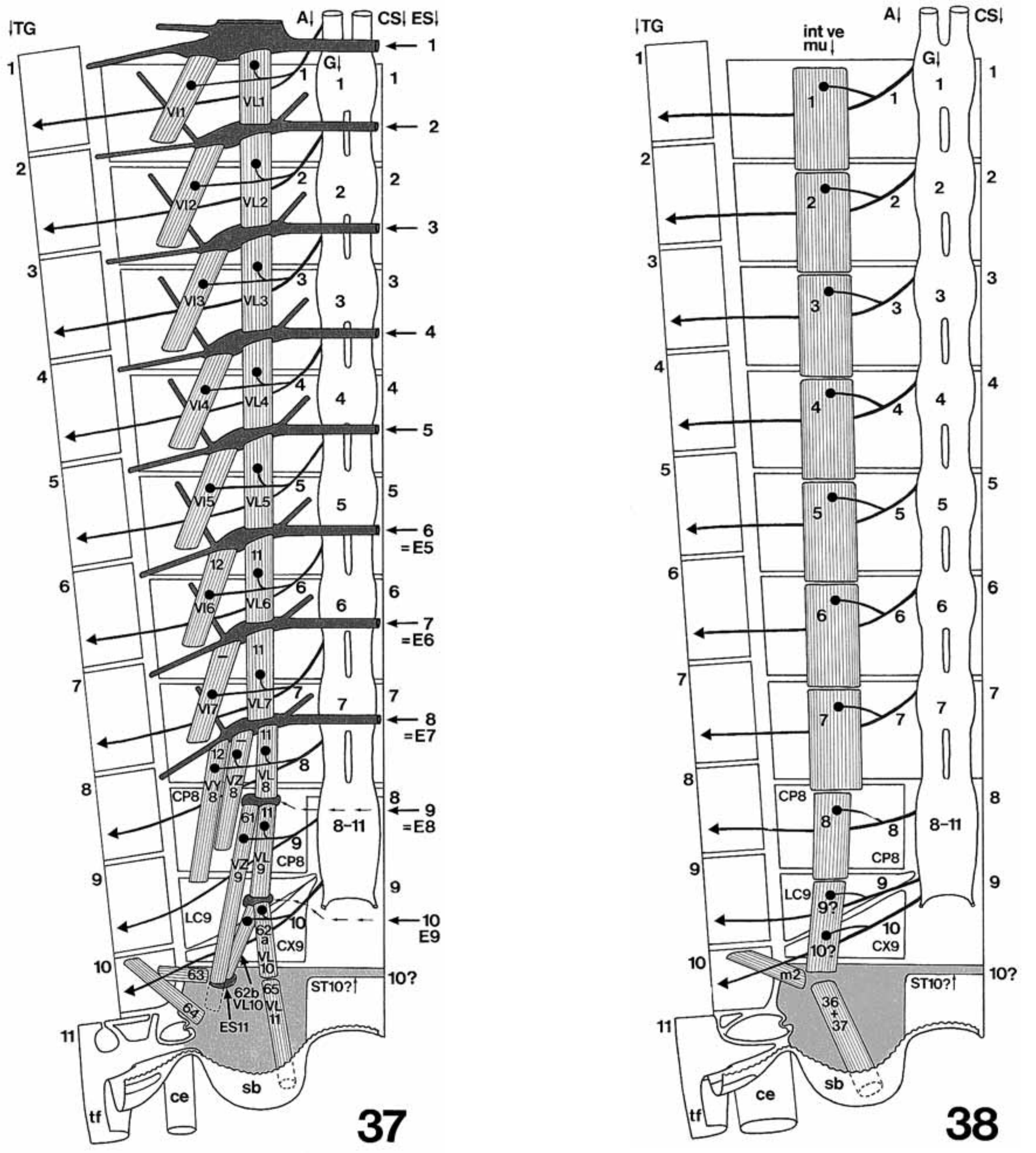
Conditions in Zygentoma

Rousset (1973: 76f) identifies in female *Thermobia* a membranous transverse fold anterior to the paraprocts as the reduced coxosternum X (**stX*** in Fig. 28). He and Bitsch (1974b: 220) consider the paraprocts (**ppct*** in Fig. 28), which are anteromedially interconnected as in *Povilla*, as coxosternum XI ('syncoxo-sternite' in Rousset): the anteromedian part is sternum XI ('sternite' in Rousset), the major posterolateral parts are the coxopodia XI (including coxal and laterocoxal sclerotizations XI; 'aires coxo-subcoxales' in Rousset). Their arguments are that the paraprocts provide the cercal articulation (rejected in 'Cerci and associated muscles') and bear some muscle insertions typical for coxopodia. The evidence from the musculature has thus to be tested. The paraprocts **ppct*** receive the following muscles (Figs 28, 37; data in Rousset, 1973): **61*** from endosternite 8 (**E8*** in Fig. 28; **ES9** in Fig. 37, following the different numbering of Birket-Smith, 1974; attached to the anterior part of coxopodium VIII **gcxVIII*** = **CP8**); Rousset considers it homodynamous with muscles **12*** of the preceding segments. **62a**,**b*** from endosternite 9 (**E9*** in Fig. 28; **ES10** in Fig. 37; attached to the central part of the gonangulum **ga*** = laterocoxa IX **LC9**), homodynamous with muscles **11***. **63*** and **64*** from tergum X, homodynamous with some tergo-coxosternals (**21***, **22*** in Fig. 28). **62a**,**b*** and **63*** insert on the anterior margin, **61*** and **64*** on the middle part of the paraprocts.

The muscles **11*** and **12*** of the preceding segments span only one segment and connect, for instance, endosternite 5 with coxosternum 6 and endosternite 6, respectively (from **ES6** = **E5*** to **CS6** and **ES7** = **E6*** in Fig. 37; Rousset, 1973: fig. 7). Only muscle **12*** from endosternite 7 **ES8** = **E7*** is one segment longer and goes to laterocoxa IX **LC9**. Hence, a muscle **11*** from endosternite 9 **ES10** = **E9*** on laterocoxa IX **LC9** (**62a**, **b***) should insert posteriorly on an endosternite 10 (**ES11** in Fig. 37, reported by Birket-Smith, 1974, but not by Rousset, 1973) on laterocoxa X. A muscle **12*** from endosternite 8 **ES9** = **E8*** (**61***) should likewise insert posteriorly on laterocoxa X, if as long as its immediately preceding serial homologue. The tergo-coxosternals and tergo-endosternals of the preceding segments are intrasegmental or connect tergum N with coxosternum/endosternite N-1 or N-2, but none of them connects tergum N with coxosternum/endosternite N + 1 (considering both ways of counting endosternites, **E*** and **ES** in Fig. 37; Rousset, 1973: figs 6, 7; Fig. 28). Hence, tergo-coxosternals originating from tergum X (**63***, **64***) should insert ventrally on coxosternal areas X (or IX). The ventral insertions of the intrasegmental tergo-coxosternals IX are on laterocoxa IX or coxa IX (**21***, **22*** on **ga*** and **gcxIX*** in Fig. 28). Muscle **63*** is in a position to be homodynamous with **22gIX*** inserted on laterocoxa IX. Muscle **64*** is in a position to be homodynamous with the two **22IX*** inserted on the posterolateral part of coxopodium IX, on the lateral base of the coxal lobe, i.e. on coxa IX. Muscles **63*** and **64*** should thus insert on laterocoxa and coxa X, respectively.

Muscles **61***, **62a**,**b***, **63***, and **64*** thus all suggest that coxosternum X, including its coxal and laterocoxal parts, contributes much of the paraprocts, but they give no indication for Rousset's (1973) and Bitsch's (1974b) assumption that coxosternum XI is included. The subanal lobes (**sb** in Figs 28, 37) are thus in the position to be coxal lobes X. The anterior transverse connection between the paraprocts is likely to be sternum X (**ST10?** in Fig. 37). Muscle **66c*** of *Thermobia* (Fig. 28) fits into this interpretation as an intersegmental coxosterno-tergal X, connecting coxosternum X with tergum XI and homodynamous with **22c*** of the pregenital segments (Rousset, 1973: figs 6, 8). Muscle **65*** from the anterior margin of the paraproct to the membranous posteromedian face of the subanal lobe (Fig. 28) cannot be reliably interpreted as a serial homologue of some muscles of the preceding segments because there is little structural differentiation around its posterior insertion area. The muscle could be (compare Fig. 28 and Rousset, 1973: figs 6–8): (1) A ventral muscle spanning segment X and homodynamous with **11*** and **62a**,**b*** (Birket-Smith's, 1974 interpretation for corresponding muscle **VL11*** of *Lepisma*). (2) A stylus muscle X homodynamous with **41***. (3) A gonapophyseal muscle X homodynamous with **51*** and **53***. (4) An anal or rectal muscle peculiar to segment X. If any of the cases (1)–(3) is true, most of the paraproct, as bridged by muscle **65***, is suggested to belong to segment X, and the subanal lobes **sb** are likely to be coxal lobes X. The muscles **66a**,**b**,**d*** from the posterior part of the paraproct to the membranous walls of the subanal lobe (Fig. 28) can neither be interpreted as serial homologues of muscles of the preceding segments.

Hence, in *Thermobia* the muscles clearly indicate that much of the paraprocts is formed by coxosternum X, including laterocoxae X and coxae X and a small sternum X. Sternum XI and ventral telson sclerites can generally not be determined by muscles, because muscle insertions are absent from the abdominal sterna of Archaeognatha (see e.g. Bitsch, 1973: fig. 8) and have never been reported for some unambiguous



Figures 37, 38. Ventral abdominal segmental components. Entire abdomen with selected segmental components shown schematically. ↑ anterior, ← dorsomedian, → ventromedian. Paraprocts grey, endosternites (Fig. 37) dark grey. Muscles striped according to course of fibres. Segmental components specified on top of figure and numbered serially below; from left to right: terga TG, internal ventral muscles int ve mu (only Fig. 38), dorsal nerves A, ganglia G, coxosterna CS, and endosternites ES (only Fig. 37). Endosternites numbered according to Birket-Smith (1974) (ES); for posterior ones numbering of Rousset (1973) given in addition (E). Dorsal nerves: black dots represent innervation of ventral muscles; arrowheads indicate innervation of the dorsal muscles spanning the respective tergum (cercal muscles X in Fig. 38 TG10). Not to scale. Fig. 37. Lepismatidae, female. Muscles designated according to Birket-Smith (1974; all segments: VI, VL, VY, VZ + number) and Rousset (1973; segments VIff: number + optional lower case letter; — = muscle not reported). Fig. 38. Pterygota, female, generalized condition. Muscles 36 + 37 and m2 designated as in Dermaptera (see Fig. 13 and Verhoeff, 1903); see p. 297 for other Pterygota.

ventral telson sclerite. Since the sternum in the pregenital and genital segments is a small anteromedian sclerotization, sternum XI is unlikely to contribute much to the paraprocts. Telson sclerites may or may not form distal parts of the paraprocts. Evidence from muscles, however, could be expected if the coxopodia

XI were included in the paraprocts. The absence of such evidence (except muscle **g11***, see pp. 287, 293) indicates that the coxopodia XI are not part of the paraprocts and conforms with the hypothesis advocated on p. 293 that they are included in the cercal bases. There are thus no objections from morphology to regard, furthermore, the paraprocts as exclusively Xth-segmental sclerites, and the subanal lobes **sb** as coxal lobes X, i.e. as **gl10** or **vf10** (see p. 272 for possible synonymy). The articulation between paraproct and cercal base then connects coxa X and coxa or laterocoxa XI. This is comparable to the articulation, or close association, or fusion between coxa VIII (valvifer VIII) and laterocoxa IX (gonangulum) in the genital segments (e.g. in Dictyoptera; Klass, 1998: figs 11–18).

Conditions in Dermaptera and other Pterygota

The result that probably most of the *Thermobia* paraprocts is contributed by laterocoxae and coxae X conforms with the tentative conclusion on p. 286 on the paraprocts of *Povilla* and Dermaptera (sclerites **pX*** + **sX*** and **LP** + **AP** in Figs 21–26). Can, furthermore, the above refined argumentation for *Thermobia* be applied also to Pterygota? Two of the *Thermobia* muscles crucial in this argumentation (Fig. 28) have counterparts in Pterygota (Figs 37, 38), e.g. in *Povilla*, Dermaptera, Dictyoptera (see male *Mastotermes* in Klass, 2000: figs 19–22), and some Ensifera (see female *Gryllotalpa hexadactyla* Perty in Ford, 1923).

(1) Homologues of muscle **63*** of *Thermobia* extend from tergum X to the anterior margin of the paraprocts (hypothetical laterocoxa X): **m2*** of *Forficula* in Verhoeff (1903), **60*** of *Mastotermes*, **tm10*** of *Gryllotalpa*, **m2*** in Fig. 38; muscle lost in *Povilla* and *Hemimerus*. These are categorized here as far anterior intrasegmental tergo-coxosternal muscles X.

(2) Homologues of muscles **62a**,**b*** of *Thermobia* span segment IX, have their posterior insertions on the anterior margin of the paraprocts (hypothetical laterocoxa X), and have their anterior insertions on laterocoxa IX, i.e. on the gonangulum in the females having this sclerite individualized: **i9*** of *Povilla*, **32** + **33** of *Hemimerus*, **48*** of *Mastotermes*, **is9*** of *Gryllotalpa*, **9?** + **10?** in Fig. 38. These are categorized here as internal ventral muscles spanning segment IX, or simply as ventral muscles IX in Pterygota.

Further *Thermobia* muscles (Fig. 28) are represented in some Pterygota, though the locations can differ in the details and the homologies are thus partly disputable.

(3) Homologues of muscle **65*** of *Thermobia* extend from (near) the anterior part of the paraproct to (near) the membranous posteromedian face of the subanal lobe: **i10** + **j10*** of *Povilla*, **36** + **37** of *Hemimerus*, **80** + **82*** of *Mastotermes*, **pam*** of *Gryllotalpa*, **36** + **37** in Fig. 38. They are more or less in line with the ventral muscles IX. Their interpretation is uncertain (see p. 295). In *Mastotermes* I classified them as extrinsic rectal muscles (Klass, 2000).

(4) Homologues of muscles **66a**,**b**,**d*** of *Thermobia* extend from the posterior part of the paraproct to the membranous posteromedian face of the subanal lobe: **38** of *Hemimerus*, **68** + **70*** of *Mastotermes*.

(5) Homologues of muscle **66c*** of *Thermobia* extend from the posterior part of the paraproct to tergum XI: **spm*** of *Gryllotalpa*. Assuming that in Dictyoptera terga X and XI are fused, as indicated by Heymons' (1895a,b) findings on *Blatta*, muscles **62** + **63*** of *Mastotermes* could likewise belong to this group. These could be intersegmental coxosterno-tergal muscles X.

Counterparts of muscles **61*** and **64*** of *Thermobia* are not represented in the pterygotan taxa considered here.

The overall similar pattern formed by these muscles (1)–(5) indicates that the composition of the paraprocts is identical in the taxa in question. In the respective Pterygota the intrasegmental tergo-coxosternal muscles X (1) and the ventral muscles spanning segment IX (2) do, if the above findings on *Thermobia* are correct, directly suggest the inclusion of laterocoxa X within the paraprocts. Nevertheless, muscles (1) and, in particular, (2) need further discussion because their morphological nature and evidence on paraproct composition in Pterygota have been strongly disputed in the literature.

Internal ventral muscles spanning segment IX and intrasegmental tergo-coxosternal muscles X of Dicondylia

In previous discussions involving these muscles focus lay on the Orthoptera, but the inherent problems concern Dicondylia as a whole. Ford's (1923) muscle interpretation conforms with that given herein, and she likewise concludes that the paraprocts contain the coxosterna X. Ander (1939, 1957), however, interprets both muscles differently, as inserting on the anterior margin of venter XI (not X), and he regards the paraprocts as XIth-segmental, not including Xth-segmental sclerotizations. His arguments are thus in conflict with the above findings and must be scrutinized.

Ander (1939: 196, 1957: 94ff) regards (1) the pterygotan *intra*segmental tergo-coxosternal X (**m2*** in Fig. 38) as an *inter*segmental tergo-coxosternal X, from tergum X to coxosternum XI (not X). This appears fairly reasonable since some Pterygota, e.g. *Povilla* (**d***, **d9*** in Fig. 27), have intersegmental tergo-coxosternals in the preceding segments (though many have not; see pp. 267, 291). However, in *Povilla* the muscle **d9*** of this series that arises from tergum IX (not that arising from tergum X) inserts on the anterior margin of the paraprocts, whereas the probable serial homologue **f11*** arising from tergum X is attached to the cercal base. In addition, since *Thermobia* lacks intersegmental tergo-coxosternals in the preceding segments, Ander would have to make one of the unparsimonious assumptions that the *Thermobia* muscle **63*** has either no homologue in Pterygota, or no serial homologues in the preceding segments, being peculiar to segment X. Hence, conditions in these lower-grade Insecta make Ander's muscle interpretation very unlikely and actually support the assignment of the paraprocts to segment X. Ander regards (2) the pterygotan ventral muscle spanning segment IX (**9?+10?** in Fig. 38) as composed of the ventral muscles IX and X (muscle **si9+10** in Ander, 1957: 94f, fig. 3; see p. 269). The two should have fused, with a loss of their attachments on the segmental border IX/X, and the resulting muscle should thus connect the anterior parts of the coxosterna IX and XI (not X). This interpretation needs a profound discussion because the issue is very complex and resolvable only within a consideration of the entire abdominal ventral musculature and nervous system. Ander's (1957) arguments that indicate a Xth-segmental muscle component will subsequently be accepted; however, it is further indicated that the entire muscle, not only part of it, is originally Xth-segmental. And it will also be shown that, still, this does not support Ander's XIth-segmental assignment of the paraprocts, whose Xth-segmental assignment remains probable.

Ander's (1957) first major argument for considering muscle (2) of Pterygota as fused ventral muscles IX and X concerns the relation to the vasa deferentia. In Archaeognatha the vasa deferentia pass mesad beneath internal ventral muscles X (m. stern. intern. 10 of Ander), i.e. beneath the 10th muscles of an abdominal series. Birket-Smith's (1974) data confirm this for both the archaeognathan *Petrobius lohmanderi* Agrell and the zygentoman *Lepisma* (ventral muscles X **62a**,**b***=**VL10*** in Fig. 37). In Ensifera and other Pterygota, however, the vasa deferentia pass beneath the ventral muscles spanning segment IX (**9?+10?** in Fig. 38), i.e. beneath the 9th muscles of an abdominal series. Ander therefore assumes a shift of the vasa deferentia to the anterior, and the insertions on the segmental border IX/X, blocking such a shift, should have been lost.

The ventral abdominal musculature of Archaeognatha and Zygentoma differs strongly from that of Pterygota. It is more complex, and many muscles insert on the segmental mesodermal endosternites (**ES** in Fig. 37; **lv*** in Birket-Smith, 1974; **E*** in Rousset, 1973). The ventral muscles of Zygentoma connect successive endosternites, or endosternites and coxosterna (muscles **VL***, **VI*** in Birket-Smith, 1974, included in Fig. 37), or different areas of the ventral body wall (muscles **j***, **i*** in Birket-Smith, 1974; not shown in Fig. 37). The endosterno-endosternal **VL*** are probably the homologues of the internal ventrals of Pterygota since they are, like these, supplied by the dorsal nerve (**IA*** in Birket-Smith, 1974; **A** in Figs 37, 38; for dorsal-nerve homology and the different locations of the nerve origins relative to their segmental ganglia compare Heckmann & Kutsch, 1995: e.g. fig. 15). The interrelations in Zygentoma between the relevant components (Fig. 37) are such that, for instance, endosternite **ES3** (=**lv3*** of Birket-Smith, 1974) is located above the posterior part of coxosternum II **CS2**, is connected by two pairs of anteriad-directed arms (frenula) with the anterior part of coxosternum II, and gives off the **VL3***, the 3rd ventral muscles of the abdomen, to the posterior. **VL3*** is supplied by the same dorsal nerve **3A** as the dorsal muscles spanning tergum III. Hence, **VL3*** should be a IIIrd-segmental muscle; **ES3** should represent the segmental border II/III; its arms connect it with the body wall just behind the segmental border I/II. The **VL3*** correspond to the internal ventrals III of Pterygota (**int ve mu 3** in Fig. 38), spanning segment III, which are likewise supplied by the same dorsal nerve **3A** as the dorsal muscles III.

Whereas in the anterior abdomen of *Lepisma* the endosternites are located just anterior to the segmental border they represent, they are closer to the anterior attachments of their arms in the posterior segments, especially in VIII and IX (Fig. 37). In this way endosternite **ES9** lies upon the anterior part of coxosternum VIII **CS8**; it gives off the backwards extending **VL9***, the 9th muscle of the abdominal series (Birket-Smith, 1974: 56; consider differences in muscle terminologies for males and females therein). Endosternite **ES10** is seated, without arms, upon the anterior part of coxosternum IX (in both sexes; Birket-Smith, 1974: figs 25, 29; on the gonangulum=laterocoxa IX in the female of *Thermobia*, **E9***=**ES10** in Fig. 28); it gives off the backwards extending **VL10***, the 10th muscle of the series beneath which the vasa deferentia pass. Hence, the puzzling condition results that the **VL9*** span essentially segment VIII; the **VL10*** span essentially segment IX (plus X?? see below) and have their posterior insertions on the paraproct. As expected from serial homology, the **VL10*** share the dorsal nerve **10A** with the dorsal muscles X (**IA10*** in Birket-Smith, 1974: 50). Hence, there is quite clearly a forward shift of muscles **VL9*** and **VL10*** by almost the length of one segment. Birket-Smith's (1974: fig. 22) observation of the condition near the thoracic-abdominal border agrees with that of Barlet (1953: fig. 1). For the mid-abdomen no other studies are available. The descriptions for the crucial posterior segments correspond with Rousset's (1973) for *Thermobia* (endosternites numbered differently: **E6*** = **ES7** = **lv7***, etc; Rousset's muscle numbers included in Fig. 37). The data base is thus fairly reliable.

Of the muscles in Pterygota (Fig. 38), which insert all directly on the body wall, the internal ventrals VIII **int ve mu 8** take the same position as the hindmost muscles **11*** = **VL9***, the internal ventrals IX **int ve mu 9?** + **10?** take the same position as **62a,b*** = **VL10***. Assuming that the same forward shift is present as in Zygentoma, the internal ventrals IX of Pterygota are originally internal ventrals X. Hence, whereas Ander assumes that in Pterygota the vasa deferentia have shifted in relation to the muscles and that muscles IX and X therefore had to fuse, one could alternatively assume that, like in Zygentoma, muscles and vasa deferentia together have shifted to the anterior, and that in all Insecta the vasa deferentia pass beneath the same muscles. This alternative hypothesis is more strongly supported by the actual presence of this muscle shift in Zygentoma. The question in terms of the interpretation of the paraprocts is then whether the posterior insertions of these ventral muscles on the paraprocts have been subjected to the same shift, i.e. are located on coxosternum X (instead of XI as assumed by Ander). The muscles discussed above under (1) support that they have. The Xth-segmental assignment of these ventral muscles can thus neither disprove the inclusion of coxosternum X in the paraprocts, nor does it prove the inclusion of coxosternum XI.

Ander's (1957: 97f) second major argument for considering muscle (2) of Pterygota as fused ventral muscles IX and X is that its anterior part is supplied by dorsal nerve IX **9A** but the posterior part by the same nerve as the cercal muscles X (= dorsal muscles X, see p. 292), i.e. by dorsal nerve X **10A** (Fig. 38). Straightforwardly the innervation through **10A** complies with the homology of the muscles with **VL10*** of Zygentoma (Fig. 37) and with a Xth-segmental origin and forward shift of these muscles. More surprising is then the contribution from dorsal nerve IX. However, the evidence from nerve supply in Pterygota is, in view of more recent findings, more ambiguous than recognized by Ander. First, such a bisegmental innervation of the muscle would comply also with its exclusive belonging to segment IX since in the chilopod *Lithobius forficatus* L. the endosterno-endosternal muscles (cf. muscles **VL*** in Fig. 37), the probable homologues of the pterygotan internal ventral muscles, are supplied by the dorsal nerve of their own segment but, in the posterior part, also by the dorsal nerve of the following segment (Rilling, 1960: nerve **VN8R*** in fig. 11). It should be noted that Rilling (1960) has analysed the nerve branches in much more detail than in the available contributions on lower-grade Insecta, and whether similar conditions occur in the latter is unknown. Second, however, there is apparently no uniform pattern of bisegmental innervation of the ventral muscles IX shared within lower-grade Pterygota, but the nerve supply is more diverse and, in addition, more complex. In *Periplaneta americana* L. (Pipa, 1988) the muscle is supplied from a plexus formed by connections between the dorsal nerve IX, the presumed dorsal nerve X, and the transverse nerve X (muscles **Q***, **T***, nerves **4A***, **5A***, **2-X*** of Pipa, 1988: figs 7, 8; for identification of components see in Klass, 2000: 251ff, table 1). Such a connection between a dorsal nerve and the succeeding transverse and dorsal nerves is peculiar to the postgenital abdomen and has no counterpart among the anastomoses in the mid-abdominal segments of *Periplaneta* (Klass, 1999: figs. 1, 3). The axon courses and therefore also the origin(s) of the muscle innervation are unknown. The corresponding muscle of Acrididae (**265*** in Snodgrass, 1935a: fig. 12) is supplied exclusively by the ventral nerve IX (**9v.n.*** and **265*** in Seabrook, 1968: fig. 5), hence through a very different path. Altogether, evidence from the nerve supply of the internal ventral muscles IX is thus very limited. A fusion of two muscles in Pterygota as compared with Zygentoma is not demonstrated. The different modes of IXth-segmental innervations in Pterygota could indicate that these are secondary, acquired several times independently. Also the peculiar IX/Xth-segmental anastomosis in *Periplaneta* might indicate some evolutionary change in the nerve supply. These relations and the Xth-segmental innervations, if actually present in *Periplaneta* on the axonal level, are consistent with (but do not strongly support) the above proposal that the pterygotan muscles are originally internal ventrals X that have shifted forward as in Zygentoma.

The homology in Zygentoma and Pterygota of the ventral muscles spanning segment IX is thus altogether quite strongly supported, by the corresponding locations of their attachments, by the vasa deferentia passing beneath them, and, to some extent, by the nerve supply. But in this homology hypothesis there is a very puzzling point. Zygentoma have, since eight muscle pairs **VL1–8*** span the segments I–VII (Fig. 37), one pair of internal ventral muscles more than Pterygota (Fig. 38). Assigning the ventral muscles to the same segments as the dorsal muscles with which they share innervation by the same dorsal nerve, in *Lepisma* the **VL***-muscles all belong to the segments they are assigned to by their numbers, though not for all segments the details are given in Birket-Smith (1974). In the Pterygota all internal ventral muscles belong to the segments they span; only in ventral muscle IX a combined innervation IX/X may occur. Hence, segments VIII and IX are suspected to be the crucial area for finding an explanation for the different numbers of ventral muscles, and from the currently available data there seems to be only one possible explanation. The muscles **VI*** (Birket-Smith, 1974) or **12*** (Rousset, 1973) of Zygentoma are, like the **VL***, supplied by the dorsal nerves **A** (Fig. 37). They connect an endosternite with the coxosternum behind it, thus not reaching the succeeding segmental border, and thus not likely to be homologous with the internal ventrals of Pterygota. As mentioned on p. 295, however, a similar VIIIth-segmental muscle **VY8*** (=posteriormost **12***) from endosternite **ES8*** (=**E7***) is longer and reaches coxosternum IX (gonangulum in female; Figs 28, 37; Rousset, 1973: fig. 7). It spans the same extension as **VL8*** and **VL9*** (=two muscles **11*** in Fig. 28) together. It could thus be assumed that Pterygota have lost **VL8*** and **VL9***, and that the ventral muscles VIII do not correspond to the posteriormost muscles **11***=**VL9*** of Zygentoma but to the posteriormost **12***=**VY8***. This would explain both that Pterygota have one muscle pair less than Zygentoma and that ventral muscle VIII is in Pterygota supplied by dorsal nerve VIII **A8** (Fig. 38). The ventral muscle IX of Pterygota is, again, a **VL***-muscle, **VL10***. In Pterygota all internal ventral muscles are then serial homologues, except ventral muscle VIII. Of course, this hypothesis is very preliminary. It should be noted in addition that tracing homologies in the internal ventral muscles is further complicated through the probable presence in some Pterygota of additional derivatives of the **VL***-muscles of Zygentoma, such as the hyperneural muscles in Dictyoptera (Klass, 1999: 38).

Conclusions on paraprocts and associated muscles

The foregoing discussion has demonstrated the difficulties in the interpretation of the paraprocts from the morphological viewpoint, and the dependence of a solution from a detailed consideration of the entire abdominal musculature and nervous system. A major problem is the insufficiently resolved muscle homologies between Archaeognatha, Zygentoma, and Pterygota, where many difficulties are due to the presence or absence of endosternites in the different taxa. The discussions in 'Heymons' interpretation', above, have shown that also from the ontogenetic viewpoint the interpretation of the paraprocts is very difficult, and the previous results are mostly ambiguous. In addition, the paraprocts may be composed differently in different taxa and, potentially, in the two sexes of a taxon. Much work on morphology and ontogeny has thus still to be done to arrive at firm conclusions, and gene expression patterns and axon mapping could be additional sources of evidence. The results achieved here are thus preliminary, and they also do not necessarily apply to taxa with separate sclerotizations on venter X.

For Dermaptera, Dictyoptera, Ensifera, Ephemeroptera, and Zygentoma the musculature indicates that at least much of the paraprocts is constituted by the coxae X and laterocoxae X, sternum X forming in (some) Zygentoma and Ephemeroptera an anterior transverse bridge. The division of the paraprocts in Dermaptera and Ephemeroptera could be serially homologous with that into coxae and laterocoxae in the genital segments, and the subanal lobes could be the coxal lobes X. The two latter assumptions, according to which also the posteromedian parts of the paraprocts and the subanal lobes are Xth-segmental, are proposed here very tentatively. Evidence for an inclusion of coxae XI, laterocoxae XI, sternum XI, and telson sclerites in the paraprocts cannot be found. The lateral muscles connecting tergum X and paraprocts are probably intrasegmental tergo-coxosternals X. The ventral muscles that have their posterior insertions on the paraprocts and cross the vasa deferentia are probably in all Dicondylia genuine internal ventrals X that have shifted their insertions forward by the length of one segment; their diverse IXth-segmental innervations in lower-grade Pterygota might be secondary. The internal ventrals VIII of Pterygota are possibly not serially homologous with the aforementioned muscles and the more anterior internal ventrals. Ander's (1957) arguments for different interpretations cannot be upheld. It should be noted that Heymons' results indicate, in contrast to some of the relations here advocated, that also in the taxa listed above coxosterna X should constitute only anterior parts of the paraprocts, and that ventral sclerotizations of segment XI and, possibly, of the telson are included in the paraprocts.

DISCUSSION OF SPIRACLE VESTIGES IX AND X

Insecta have a maximum of eight pairs of functional abdominal spiracles, belonging to segments I–VIII, but there are reports of vestigial spiracles or spiracle anlagen in segments IX and X. Cholodkowsky (1891, as cited in Snodgrass, 1935b: 429) reports a pair of IXth-segmental tracheal invaginations for the embryo of *Phyllodromia germanica* (=*Blattella germanica* [Linnaeus, 1767]; Blattaria: Blattellidae). Heymons (1897: 603, fig. 11) finds in the embryo of *Lepisma* distinct IXth-segmental spiracle anlagen and regards a paired cluster of epidermal cells ('Hypodermiszellen') taking the same relative position in segment X as the vestigial spiracle anlagen of this segment. Woodland (1957: 560), studying *Thermobia domestica* (Packard) and *Ctenolepisma lineata* Fabricius (both Zygentoma: Lepismatidae), however, finds no traces of spiracle anlagen on the segments behind VIII. Nonetheless, Heymons' (1897) findings are confirmed by Rousset's (1973: 70) report of IXth-segmental invaginations in adult *Thermobia* (**si9** in Fig. 28); these are in the same position as the spiracles in the preceding segments (**si8** in Fig. 28) and are associated with muscles (**91***, **92*** in Fig. 28 and Rousset, 1973) resembling the spiracle muscles of the preceding segments. The minute invaginations **si9** and **si10** of *Hemimerus* (Figs 5, 6) correspond in their position within the segment with the spiracles of the segments up to VIII. They are proposed here very tentatively to be vestigial spiracles IX and X. Female *Hemimerus* are then the only Pterygota in which traces of these components have been reported for the adults.

DISCUSSION OF EXTRINSIC RECTAL MUSCLES

The rectal muscles are only rarely considered in morphological studies, and there are no reports for Forficulina. Nevertheless, regarding the sparse information available, most Pterygota are likely to have a variety of muscles in the posterior abdomen that connect the rectum with peripheral parts of the exoskeleton. For members of several neopteran orders three pairs of usually large muscles have been reported that arise in a hexagonal pattern from the rectum (major extrinsic rectal muscles; see Klass, 2000: 256). These go from the dorsolateral rectal wall to the anteromedian part of tergum X, from the lateral rectal wall to the anterolateral part of tergum X, and from the ventrolateral rectal wall to the anterior margin of coxosternum IX (laterocoxa IX in females having this sclerite individualized; see p. 272). This set is reported for all major clades of Dictyoptera (muscles **74***, **75***, **76*** in Klass, 2000: fig. 21), for Orthoptera (muscles **ddr***, **ldr***, **vdr*** in Ford, 1923; muscles **264***, **286***, **290*** in Snodgrass, 1935a), for Plecoptera (muscles **A***, **B***, **D*** in Zwick, 1973: fig. 22), and for lepidopteran larvae (muscles **SR***, **PR***, **TR*** in Eaton, 1988: fig. 2.50). Phasmatodea have the two tergal muscles (muscles **378***, **379*** in Maki, 1935), but a pair from coxosternum IX is unknown. In *Hemimerus* (Figs 12, 13) the dorsal rectal muscle **47** conforms with the above pattern, though its Xth-tergal insertion is closer to the midline. The ventral rectal muscle **46**, inserted on the ventral anterior border of segment IX, also meets this pattern. The lateral rectal muscle **45**, however, has an aberrant insertion on tergum IX. This may be due to a shift of the insertion away from an original position on tergum X, as a consequence of the expansion of the cercal muscle insertions onto tergum IX. This probably apomorphic state constitutes the only strong difference to the typical arrangement of the major rectal muscles, and an examination of the insertion in other Dermaptera would be welcome.

Muscles resembling **50** of *Hemimerus* (Figs 12, 13), located posteromedially and inserted on the posterodorsal anal wall, are reported for Caelifera (**295*** in Snodgrass, 1935a) and Dictyoptera (**79*** in Klass, 2000: figs 19, 21). However, the homology is doubtful because the dorsal insertion seems to be in different positions. In *Hemimerus* it is on tergum X **TG10** proper, and anterior to that of the cercal muscle XI **43**. The same condition was found in the forficuline *Echinosoma* (pers. observ.). In Caelifera the insertion is on the epiproct (*sensu* Snodgrass, 1935a), which is tergum XI (**TG11** in Fig. 31) and may include a dorsal telson sclerite, but which does probably not include some part of tergum X; in addition, the muscle inserts posterior to the cercal muscles XI (**293*** in Fig. 31). In Dictyoptera the insertion is on 'tergum X' (muscle **79*** in Klass, 2000: fig. 19; pers. observ. in *Periplaneta americana*), which may include terga X and XI and a dorsal telson sclerite (Heymons, 1895a, b), and it could thus lie on either of the three sclerotizations. Hence, the segmental assignment and homology of these muscles remain unclear. Additional data could make the relations clearer, and the dorsal insertions could, in turn, yield evidence for the interpretation of the terminal dorsal sclerites.

Dictyoptera have like *Hemimerus* some additional rectal muscles from 'tergum X' and from the paraprocts (**77***, **78*** and **80***, **81***, **82*** in Klass, 2000: figs 21, 22; pers. observ.), all inserting near the anus. In the tergal group muscle **48** of *Hemimerus* differs from all muscles of Dictyoptera by its far anterior insertion on the rectum. In the paraproctal group muscle **49** of *Hemimerus* (Fig. 13) may correspond to the likewise strongly transverse muscle **81*** of Dictyoptera. The potential homology between muscles **36** and **37** of *Hemimerus* and **80*** and **82*** of Dictyoptera has been noted on p. 297.

PHYLOGENETIC IMPLICATIONS

The potential for phylogenetic conclusions from the data on *Hemimerus* abdominal morphology is presently, at all systematic levels, strongly restricted. One reason is that data on abdominal morphology are very poor in Dermaptera, and available to a useful extent for only a few species throughout the lower-grade Insecta. This is particularly true for the musculature and the nervous system, but partly also for the exoskeleton. There is thus, with some exceptions, too little information for reliably assessing features of *Hemimerus* in a broad comparative context. The second reason is that paedomorphosis in Dermaptera seems to play an important role in the evolution of several character systems, for instance in the female genital region (see p. 274). Homoplasious developments must here generally be suspected, and in some of the characters potentially concerned the polarity remains disputable even if sound outgroup comparison can be provided. Detailed morphological and ontogenetic studies of a variety of taxa within and outside Dermaptera are needed for firmer conclusions. Nevertheless, some preliminary hypotheses can be proposed for various systematic levels.

Some of the generally accepted major insect clades might receive additional support from several character systems. The absence of cercal muscles XI could be tested as an autapomorphy of the Archaeognatha, though many Pterygota also lack the muscles. The initial fragmentation of the lateral parts of tergum XI (as in Fig. 28) and the shift of the internal ventral muscles X to the IXth-segmental area are potential autapomorphies of the Dicondylia. The complete detachment of the lateralmost parts of tergum XI, with the functional change of external dorsals X into cercal muscles, the presence of a cercal base apodeme **ma**, the presence of a dorsal articulation between cercal base and tergum X, and the attachment of (most of) the abdominal internal ventral muscles directly to the body wall could be autapomorphies of the Pterygota. The detachment of further lateral parts of tergum XI, with the functional change of internal dorsals X into cercal muscles, the peculiar course of one of the cercal muscles X (**II**, **IV?** in Figs 35, 36; through either a division of muscle **IV** or a shift of muscle **II**), the lack of dorsal muscles XI, and the presence of a manubrium and of a zone **ZE*** of anastomosing ridges in the abdominal spiracles could be autapomorphies of Neoptera or rather inclusive subgroups thereof. Implications on inter-ordinal relationships within Neoptera are sparse; only the fusion of abdominal ganglia **7G** and **8–11G** and possibly a slight elongation of ventral fold **vf7** to form a female subgenital fold could be synapomorphic for Dermaptera and Dictyoptera. All these tentative proposals remain to be tested through the inclusion of further taxa into the comparison.

Abdominal characters that might bear evidence on the monophyly of the Dermaptera or on the placement of *Hemimerus* within this taxon are in the following referred to in more detail. The paedomorphic apomorphies shared between *Hemimerus* and e.g. *Forficula*, however (see p. 274), are not mentioned again. Some characters are included and scrutinized that were proposed previously to be autapomorphies of Dermaptera or Forficulina. The (putatively) apomorphic character states are listed, the respective plesiomorphic states are given in brackets. It should be noted that *Hemimerus* shows some features that appear at the present state of knowledge as autapomorphic for this taxon. For instance, the female genital sclerites **CX8** and **CX9** are articulated, **CX9** is fused with the medioventral margins of terga IX and X, apodeme **at9** has shifted mesad and the sclerotization of laterocoxa IX has become restricted to it, the cercal base lacks an articulation with tergum X, and the intrasegmental tergo-coxosternal X **m2*** is absent. The finding of these apomorphies in other Dermaptera could give further indications on the phylogenetic position of *Hemimerus*.

1. *Apodeme* **at** *in mid-abdominal segments: present (absent)*. This state is regarded as an autapomorphy of Dermaptera by Popham (1985: 200, character h). However, since apodemes in a similar position and with corresponding muscle insertions occur in Odonata, Caelifera, and some other Pterygota, these could as well be plesiomorphic within the Pterygota (see p. 265).

2. *Tendon* **lt** *in mid-abdominal segments: present (absent)*. This state is probably apomorphic within the Insecta, but reinvestigations are needed to test this assumption. It is shared by *Hemimerus* and at least several Forficulina including Pygidicranidae and might be an autapomorphy of Dermaptera (see p. 265).

3. *Ridges* **dr** *and* **vr** *in mid-abdominal segments: present (absent)*. This state is probably apomorphic within the Insecta, but reinvestigations are needed to test this assumption. It is shared by *Hemimerus* and *Tagalina*, but the ridges are indistinct in at least several other Forficulina. It might be an autapomorphy of Dermaptera or a subgroup thereof (see p. 265).

4. *Shortening of terga VIII and IX in female: strong (not strong)*. This state is certainly apomorphic within the Insecta. It is shared by *Hemimerus* and probably all Forficulina except *Arixenia* (Giles, 1963: fig. 63) and is proposed here to be an autapomorphy of Dermaptera. A paedomorphic reversal (in *Arixenia*?) is conceivable because shortening is established during late nymphal development (see p. 268).

5. *Immobilization of terga VIII–X in female by internal layer of cuticle: including lateralmost parts of terga (not including lateralmost parts of terga)*. This state is certainly apomorphic within the Insecta. It is shared by at least *Hemimerus*, *Apachyus*, and *Forficula* but not by some Pygidicranidae, and it is unlikely to be present in *Arixenia*; no data are available for other Dermaptera. It might be an autapomorphy of a subgroup of Dermaptera. Conditions with a less extensive tergal immobilization (see p. 268) might be autapomorphies of more inclusive subgroups of Dermaptera, including also at least some Pygidicranidae. On the other hand, however, a secondary stepwise reduction of tergal immobilization through paedomorphosis is also conceivable since, regarding the nymphal development of the terga, immobilization is likely to be absent in the nymphs.

6. *Dorsal muscles IX in female: absent (present)*. This state is certainly apomorphic within the Insecta. It is shared by at least *Hemimerus* and *Forficula*. In view

of the at least partial immobilization of terga VIII–X in many Dermaptera it can reasonably be hypothesized to be widespread in Dermaptera, though no muscle data are available for further genera. It might be an autapomorphy of Dermaptera or a subgroup thereof, but further studies are needed. A secondary presence of the muscles through paedomorphosis is conceivable since, regarding the nymphal development of the terga, the muscles could well be present in the nymphs. To which extent a reduction of the dorsal muscles VIII could be an autapomorphy of Dermaptera or a subgroup thereof remains to be investigated (see p. 269).

7. Manubrium of coxosternum IX in male: present (absent). The manubrium is an anterior sclerotization of coxosternum IX (male subgenital plate), which is laterally in close contact (*Hemimerus, Arixenia*) or connected (Forficulina; Giles, 1963: 133) with the posterior one, and which is more or less strongly invaginated as a median, anteriad-directed apodeme. Popham (1985: 200, character j) regards the manubrium as an autapomorphy of Dermaptera, but this is evidently not the case. First, a division of the male coxosternum IX into an anterior and a posterior sclerite is probably a groundplan condition of Dicondylia. Lateral connection of the sclerites, as in Forficulina, is present in Zygentoma (sclerites **sb***, **sc*** in Birket-Smith, 1974: 46) and many Dictyoptera (Klass, 1997: figs 62, 113, 147, 237, 265); complete separation, as in *Hemimerus* and *Arixenia*, is reported for Notoptera (Walker, 1943: 690). The anterior sclerite is probably not a sternum but a modified part of the coxopodia (Klass, 2000: 248). Second, the invagination of the anterior sclerite is due to its overlapping by coxosternum VIII (i.e. by the ventral fold **vf8**, cf. Fig. 1) as present in all the mentioned taxa. Its deeper, more distinctly apodemal invagination is also present, for instance, in many Dictyoptera but absent in some Dermaptera (see Burr, 1915b). Hence, the manubrium as specified above cannot be accepted as an autapomorphy of Dermaptera. Whether certain conditions of the manubrium, e.g. the extreme anterior extension of the invagination in some Forficulina (Burr, 1915b: figs 16–23), could provide autapomorphies for subgroups of Dermaptera remains to be reconsidered.

8. Terga X and XI: fused at least near midline (not fused). This state is certainly apomorphic within the Insecta, but cases of homoplasy probably occur (interpretation of sclerites uncertain in many Insecta). The state is shared by at least *Hemimerus* and *Apachyus* but not by at least most other Forficulina including *Arixenia*. It might be an autapomorphy of a subgroup of Dermaptera, but further studies are needed (see pp. 278, 286).

9. Dorsal telson sclerite **DT***: fused to tergum XI, or absent (present as a discrete sclerite)*. This state is certainly apomorphic within the Insecta, but cases of homoplasy probably occur (interpretation of sclerites uncertain in many Insecta). The state is shared by at least *Hemimerus* and *Apachyus* but not by at least most other Forficulina. It might be an autapomorphy of a subgroup of Dermaptera, but further studies are needed (see pp. 278, 286, 287).

10. Non-cercal insertions of cercal muscles X **40** *and* **41** *in female: expanded or shifted to tergum IX (restricted to tergum X)*. This state is certainly apomorphic within the Insecta. It is shared by *Hemimerus* and at least some Forficulina but not by *Forficula*. It might be an autapomorphy of Dermaptera or a subgroup thereof, but further studies are needed (see pp. 275–278).

11. Cercal insertions of internal dorsal muscles X **40***: integrated into the cercal base (located dorsomedian to cercal base)*. This state is certainly apomorphic within the Insecta. It is shared by *Hemimerus* and at least some Forficulina and might be an autapomorphy of Dermaptera or a subgroup thereof, though it cannot be excluded that the state occurs in some non-Dermaptera and is autapomorphic for a more inclusive taxon. Further studies are needed (see pp. 290, 293).

12. Shape of cerci: forcipate (not forcipate). Giles (1974: 192) regards this state as an autapomorphy of Dermaptera, secondarily lost in *Hemimerus*. Popham, though listing forcipate cerci as an autapomorphy of Dermaptera (1985: 200, character l), concludes that the cerci of *Hemimerus* are primarily non-forcipate (1985: 205). Some new arguments in favour of Giles' opinion are given here. A first point is that in the cercal musculature *Hemimerus* shares in several characters the apomorphic state with at least some Forficulina (see pp. 275–278, 290, 293): the cercal muscles are very large, their anterior insertions in the female are expanded onto tergum IX, and the posterior insertions of the internal dorsals X **40** are integrated into the cercal base. In addition, the cercal base has the tendons **ct**, which, however, might be plesiomorphic components of Pterygota. These features appear to be correlated with the presence of strong, forcefully working cerci, and the cerci in *Hemimerus* are thus likely to have been subjected to some kind of secondary reduction. This argument, however, is not very strong.

A second point concerns the function of the cerci. Forficulina use their claspers for unfolding the hindwings, for catching prey and holding it in front of the mouthparts, for defence, and for lifting the female abdomen in copulation (Günther & Herter, 1974: 48, 66, 116). *Hemimerus* has lost its wings, does not catch prey, and, living on *Cricetomys* rats, is perhaps unlikely to face situations necessitating defence by claspers. The copulation procedure of *Hemimerus* (male upon female, both facing the same direction; Ashford, 1970) is, according to Scudder's (1971: 390, 392) hypotheses, more derived than that of Forficulina, and it could well be derived from that of Forficulina. In addition, the cerci of *Hemimerus* grip the fur of the host (Popham, 1985: 205), and for this derived function thread-like but stiff cerci seem to be better suited than claspers. These drastic changes in the functional background make a secondary loss of the forcipate condition in *Hemimerus* quite plausible.

Popham (1985: 204, 205) discusses two of these functional aspects but comes to different conclusions. His argument regarding copulation, however, neglects the fact that the habits of *Hemimerus* are apomorphic and could be derived from those of Forficulina. In terms of feeding behaviour Popham notes that in Forficulina the abdominal terga are more anterior than the coxosterna (apomorphic), which makes the abdomen more flexible, enables the cerci to reach the mouthparts, and makes the forcipate condition useful. *Hemimerus* is said to have the terga perpendicularly above the coxosterna (plesiomorphic), and its cerci should thus be primarily non-forcipate. This, however, is not conclusive because the terga and coxosterna in *Hemimerus* and Forficulina actually show the same spatial relations, and a condition like in Zygentoma, with the terga still farther anteriorly, could well be plesiomorphic for Dicondylia (see p. 265).

A third point concerns the possibility of paedomorphosis. The *Hemimerus* cerci are not too different from those of young forficuline nymphs (see Caussanel, 1966: pl. 2). As *Hemimerus* probably has paedomorphic features in the thorax (Barlet, 1985: 186, 193) and in the female genital region (see p. 274), the thread-like shape of the cerci may also be due to paedomorphosis, and the potential functional advantage of this shape within the specific life habits of *Hemimerus* (see above) may have provided the respective selective pressure. Accordingly, also the absence of sexual dimorphism in the shape of the cerci is not necessarily a plesiomorphy of *Hemimerus* since the same is true for young forficuline nymphs (Caussanel, 1966). In addition, this dimorphism is not distinct in many Pygidicranidae (e.g. *Echinosoma*; F. Haas, pers. comm.). (See Popham, 1985: 206, character 16, fig. 14; there the presence of this dimorphism is regarded as an autapomorphy of Forficulina.)

In sum, these arguments do not prove that the non-forcipate condition in *Hemimerus* is derived from a forcipate condition, but they make it plausible. In the author's view the forcipate condition can therefore not support the monophyly of Forficulina.

Conclusions from character states 1–12 on the phylogenetic placement of Hemimerus

The presence of tendon **lt** (2), of ridges **dr** and **vr** (3), and, in the female, the shortening of terga VIII and IX (4), the immobilization of terga VIII–X (5), the absence of dorsal muscles IX (6), and the extension of cercal muscles to tergum IX (10) confirm the assignment of *Hemimerus* to Dermaptera. The insertion of the internal dorsals X on the cercal base (11) and the presence of tendons **ct** might be further arguments. The presence of coxosternal apodemes **at** (1) and of a manubrium (7), however, are no arguments for this relationship. The paedomorphic apomorphies in the female genital region shared with e.g. *Forficula* as well as the advanced immobilization of terga VIII–X (5) indicate that *Hemimerus* is nested within the Forficulina. In addition, the fusion between terga X and XI (8) and the absence of a discrete dorsal telson sclerite (9) provide weak support for a close relation of *Hemimerus* to *Apachyus*. None of the abdominal characters contradicts a subordinate placement of *Hemimerus* within the Forficulina, and this is also true for the non-forcipate condition and lacking sexual dimorphism of the cerci (12). The evidence from most of the respective characters, however, is preliminary due to the poor data on Forficulina and to the possible occurrence of reversals through paedomorphosis.

ACKNOWLEDGEMENTS

This work was sponsored by the Deutsche Forschungsgemeinschaft (Kl 1162/1-1). I wish to thank Dr F. Haas (Sektion für Biosystematische Dokumentation, Universität Ulm), Mr D. Matzke (Leipzig), and Dr M. Ohl (Museum für Naturkunde, Humboldt-Universität Berlin) for kindly providing specimens of *Labidura*, *Tagalina*, and *Karschiella*, respectively. I am also grateful to Prof. Dr Niels Peder Kristensen (Zoological Museum, University of Copenhagen) and to an anonymous referee for helpful comments on the manuscript.

REFERENCES

Ander K. 1939. Vergleichend-anatomische und phylogenetische Studien über die Ensifera (Saltatoria). *Opuscula Entomologica Supplementum* **2:** 1–306.

Ander K. 1957. Zur Morphologie des Hinterleibsendes der Ensiferen. *Entomologisk Tidskrift* **78:** 89–100.

Asahina S. 1954. *A morphological study of a relic dragonfly Epiophlebia superstes Selys (Odonata, Anisozygoptera).* Tokyo: The Japan Society for the Promotion of Science.

Ashford RW. 1970. Observations on the biology of *Hemimerus talpoides* (Insecta: Dermaptera). *Journal of Zoology, London* **162:** 413–418.

Barlet J. 1953. Morphologie du thorax de *Lepisma saccharina* L. (Aptérygote Thysanoure). II. Musculature, 1. partie. *Bulletin et Annales de la Société Royale d'Entomologie de Belgique* **89:** 214–236.

Barlet J. 1984. Précisions sur le squelette thoracique de quelques Dermaptères. *Bulletin et Annales de la Société Royale Belge d'Entomologie* **120:** 189–210.

Barlet J. 1985. La musculature thoracique d'*Hemimerus bouvieri* CHPD. (Dermaptères). *Bulletin et Annales de la Société Royale Belge d'Entomologie* **121:** 169–195.

Bhatnagar RDS, Singh KI. 1965. Studies on the embryonic development of the earwig *Labidura riparia* (Pallas) (Labiduridae: Dermaptera). *Research Bulletin of the Panjab University N.S.* **16:** 19–30.

Birket-Smith J. 1971. The abdominal morphology of *Povilla adusta* Navas (Polymitarcidae) and of Ephemeroptera in general. *Entomologica Scandinavica* **2:** 139–160.

Birket-Smith J. 1974. On the abdominal morphology of Thysanura (Archaeognatha and Thysanura s.str.). *Entomologica Scandinavica Supplementum* **6:** 1–67.

Bitsch J. 1973. Morphologie abdominale des machilides (Insecta Thysanura) I. Squelette et musculature des segments prégénitaux. *Annales des Sciences Naturelles Ser.12,* **15:** 173–200.

Bitsch J. 1974a. Morphologie abdominale des machilides (Thysanura) II. Squelette et musculature des segments génitaux femelles. *International Journal of Insect Morphology and Embryology* **3:** 101–120.

Bitsch J. 1974b. Morphologie abdominale des machilides (Thysanura) III. Squelette et musculature des segments génitaux males et des segments postgénitaux. *International Journal of Insect Morphology and Embryology* **3:** 203–224.

Bitsch J. 1979. Morphologie abdominale des insectes. In: Grassé PP, ed. *Traité de Zoologie,* VIII/ii. Paris: Masson, 291–578.

Bitsch J. 1994. The morphological groundplan of Hexapoda: critical review of recent concepts. *Annales de la Société Entomologique de France NS* **30:** 103–129.

Burr M. 1915a. The opisthomeres and the gonapophyses in the Dermaptera. *Transactions of the Entomological Society of London* **1915:** 257–268.

Burr M. 1915b. Note on the manubrium of the ninth sternite in the male earwig. *Transactions of the Entomological Society of London* **1915:** 269–272 + plates.

Caussanel C. 1966. Étude du développement larvaire de *Labidura riparia* (Derm. Labiduridae). *Annales de la Société Entomologique de France NS* **2:** 469–498.

Cholodkowsky N. 1891. Die Embryonalentwicklung von *Phyllodromia (Blatta) germanica. Mémoires de l'Académie Imperiale des Sciences de St. Petersbourg Ser. 7,* **38:** 1–120 + plates.

Davies RG. 1966. The postembryonic development of *Hemimerus vicinus* Rehn and Rehn (Dermaptera). *Proceedings of the Royal Entomological Society of London A* **41:** 67–77.

Deoras PJ. 1941a. Structure of *Hemimerus deceptus* Rehn var. *ovatus,* an external parasite of *Cricetomys gambiense. Parasitology* **33:** 172–185.

Deoras PJ. 1941b. The internal anatomy and description of *Hemimerus deceptus* var. *ovatus* Deoras (Dermaptera), with remarks on the systematic position of the Hemimeridae. *Indian Journal of Entomology* **3:** 321–333.

Eaton JL. 1988. *Lepidopteran anatomy.* New York: John Wiley & Sons.

Ford N. 1923. A comparative study of the abdominal musculature of orthopteroid insects. *Transactions of the Royal Canadian Institute* **14:** 207–319.

Giles ET. 1963. The comparative external morphology and affinities of the Dermaptera. *Transactions of the Royal Entomological Society of London* **115:** 95–164.

Giles ET. 1974. Relationships between the Hemimerina and other Dermaptera – a case for reinstating the Hemimerina in the Dermaptera based on numerical procedure. *Transactions of the Royal Entomological Society of London* **126:** 189–206.

Grillot JP. 1983. Morphology and evolution of perisympathetic organs in insects. In: Gupta AP, ed. *Neurohemal organs of arthropods.* Springfield Illinois: Charles C. Thomas Publisher, 481–512.

Günther K, Herter K. 1974. 11. Ordnung Dermaptera (Ohrwürmer). In: Helmcke JG, Starck D, Wermuth H, eds. *Handbuch der Zoologie* 4 (2) 2/11. Berlin: De Gruyter, 1–158.

Haas F. 1995. The phylogeny of the Forficulina, a suborder of the Dermaptera. *Systematic Entomology* **20:** 85–98.

Hansen HJ. 1894. Beiträge zur Kenntnis der Insektenfauna von Kamerun, 3. On the structure and habits of *Hemimerus talpoides* Walk. *Entomologisk Tidskrift* **15:** 65–93 + plates.

Heckmann R, Kutsch W. 1995. Motor supply of the dorsal longitudinal muscles II: comparison of motoneurone sets in Tracheata. *Zoomorphology* **115:** 197–211.

Hennig W. 1969. Die Stammesgeschichte der Insekten. Senckenbergbuch 49. Frankfurt/Main: W. Kramer.

Heymons R. 1893. Die Entwicklung des Ohrwurms (*Forficula auricularia* L.). *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin* **1893, 5:** 127–131.

Heymons R. 1895a. *Die Segmentirung des Insectenkoerpers.* Berlin: Verlag der Königlichen Akademie der Wissenschaften.

Heymons R. 1895b. *Die Embryonalentwicklung von Dermapteren und Orthopteren unter besonderer Berücksichtigung der Keimblätterbildung.* Jena: G. Fischer.

Heymons R. 1896. Grundzüge der Entwicklung und des Körperbaues von Odonaten und Ephemeriden. *Anhang zu den Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin* **1896:** 1–66 + plates.

Heymons R. 1897. Entwicklungsgeschichtliche Untersuchungen an *Lepisma saccharina* L. *Zeitschrift für Wissenschaftliche Zoologie* **62:** 583–631.

Heymons R. 1912. Über den Genitalapparat und die Entwicklung von *Hemimerus talpoides* Walk. *Zoologische Jahrbücher Supplementum* **15:** 141–184.

Jordan K. 1909. Notes on the anatomy of *Hemimerus talpoides. Novitates Zoologicae* **16:** 327–330.

Kerry CJ, Mill PJ. 1987. An anatomical study of the abdominal muscular, nervous and respiratory systems of the praying mantid, *Hierodula membranacea* (Burmeister). *Proceedings of the Royal Society of London B* **229:** 415–438.

Khandekar CD. 1972. Nervous system of *Labidura riparia* (Dermaptera). *Deutsche Entomologische Zeitschrift N.F.* **19:** 357–365.

Klass KD. 1997. The external male genitalia and the phylogeny of Blattaria and Mantodea. *Bonner Zoologische Monographien* **42:** 1–341.

Klass KD. 1998. The ovipositor of Dictyoptera (Insecta): homology and ground-plan of the main elements. *Zoologischer Anzeiger* **236:** 69–101.

Klass KD. 1999. The pregenital abdomen of a mantid and a cockroach: musculature and nerve topography, with comparative remarks on other Neoptera (Insecta: Dictyoptera). *Deutsche Entomologische Zeitschrift* **46:** 3–42.

Klass KD. 2000. The male abdomen of the relic termite *Mastotermes darwiniensis* (Insecta: Isoptera: Mastotermitidae). *Zoologischer Anzeiger* **239:** 231–262.

Kristensen NP. 1991. Phylogeny of extant hexapods. In: CSIRO, ed. *The Insects of Australia,* 2nd edn. Melbourne, 125–140.

LaGreca M, Rainone A. 1949. Il dermascheletro e la muscolatura dell'addome di *Mantis religiosa. Annuario dell' Istituto e Museo de Zoologia dell'Università di Napoli* **1:** 1–43.

Larink O. 1969. Zur Entwicklungsgeschichte von *Petrobius brevistylis* (Thysanura: Insecta). *Helgoländer Wissenschaftliche Meeresuntersuchungen* **19:** 111–155.

Leuzinger H, Wiesmann R, Lehmann FE. 1926. *Zur Kenntnis der Anatomie und Entwicklungsgeschichte der Stabheuschrecke* Carausius morosus *Br.* Jena: G. Fischer.

Maki T. 1935. A study of the musculature of the phasmid *Megacrania tsudai* Shiraki. *Memoirs of the Faculty of Science and Agriculture, Taihoku Imperial University* **12:** 117–243.

Matsuda R. 1976. *Morphology and evolution of the insect abdomen.* Oxford: Pergamon Press.

McKittrick FA. 1964. Evolutionary studies of cockroaches. *Memoirs of the Cornell University Agricultural Experimental Station* **389:** 1–197.

Nagashima T. 1991. Postembryonic development and homology of external genitalia in *Galloisiana nipponensis* (Caudell et King) (Notoptera: Grylloblattidae). *International Journal of Insect Morphology and Embryology* **20:** 157–168.

Nesbitt HHJ. 1941. A comparative morphological study of the nervous system of the Orthoptera and related orders. *Annals of the Entomological Society of America* **34:** 51–81.

Nutting WL. 1951. A comparative anatomical study of the heart and accessory structures of the orthopteroid insects. *Journal of Morphology* **89:** 501–597.

Pipa RL. 1988. Muscles and nerves of the posterior abdomen and genitalia of male *Periplaneta americana* (L.) (Dictyoptera: Blattidae). *International Journal of Insect Morphology and Embryology* **17:** 455–471.

Popham EJ. 1959. The anatomy in relation to feeding habits of *Forficula auricularia* L. and other Dermaptera. *Proceedings of the Zoological Society of London* **133:** 251–300.

Popham EJ. 1961. On the systematic position of *Hemimerus* Walker – a case for ordinal status. *Proceedings of the Royal Entomological Society of London B* **30:** 19–25.

Popham EJ. 1962. The anatomy related to the feeding habits of *Arixenia* and *Hemimerus* (Dermaptera). *Proceedings of the Zoological Society of London* **139:** 429–450.

Popham EJ. 1965. The functional morphology of the reproductive organs of the Common Earwig (*Forficula auricularia* L.) and other Dermaptera with reference to the natural classification of the order. *Journal of Zoology* **146:** 1–43.

Popham EJ. 1985. The mutual affinities of the major earwig taxa (Insecta, Dermaptera). *Zeitschrift für Zoologische Systematik und Evolutionsforschung* **23:** 199–214.

Qadri MAH. 1940. On the development of the genitalia and their ducts of orthopteroid insects. *Transactions of the Royal Entomological Society of London* **90:** 121–175.

Rehn AG, Rehn WH. 1935. A study of the genus *Hemimerus* (Dermaptera, Hemimerina, Hemimeridae). *Proceedings of the Academy of Natural Sciences of Philadelphia* **87:** 457–508.

Rilling G. 1960. Zur Anatomie des braunen Steinläufers *Lithobius forficatus* L. (Chilopoda). Skelettmuskelsystem, peripheres Nervensystem und Sinnesorgane des Rumpfes. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* **78:** 39–128.

Roonwal ML. 1937. Studies on the embryology of the African Migratory Locust, *Locusta migratoria migratorioides* Reiche and Frm. (Orthoptera, Acrididae). II Organogeny. *Philosophical Transactions of the Royal Society of London B* **227:** 175–244 + plates.

Rousset A. 1973. Squelette et musculature des regions génitales et postgénitales de la femelle de *Thermobia domestica* (Packard). Comparaison avec la region génitale de *Nicoletia* sp. (Insecta: Apterygota: Lepismatida). *International Journal of Insect Morphology and Embryology* **2:** 55–80.

Sahrhage D. 1953. Ökologische Untersuchungen an *Thermobia domestica* (Packard) und *Lepisma saccharina* L. *Zeitschrift für Wissenschaftliche Zoologie* **157:** 77–168.

Scudder GGE. 1971. Comparative morphology of insect genitalia. *Annual Review of Entomology* **16:** 379–406.

Seabrook WD. 1968. The innervation of the terminal abdominal segments (VIII–XI) of the desert locust, *Schistocerca gregaria. Canadian Entomologist* **100:** 693–715.

Shankland DL. 1965. Nerves and muscles of the pregenital abdominal segments of the American cockroach, *Periplaneta americana* (L.). *Journal of Morphology* **117:** 353–386.

Smith EL. 1969. Evolutionary morphology of external insect genitalia. – 1. Origin and relationships to other appendages. *Annals of the Entomological Society of America* **62:** 1051–1079.

Snodgrass RE. 1931. Morphology of the insect abdomen I: general structure of the abdomen and its appendages. *Smithsonian Miscellaneous Collections* **85:** 1–128.

Snodgrass RE. 1933. Morphology of the insect abdomen II: the genital ducts and the ovipositor. *Smithsonian Miscellaneous Collections* **89:** 1–148.

Snodgrass RE. 1935a. The abdominal mechanisms of a grasshopper. *Smithsonian Miscellaneous Collections* **94:** 1–89.

Snodgrass RE. 1935b. *Principles of insect morphology.* New York: McGraw-Hill.

Snodgrass RE. 1956. *Anatomy of the Honey Bee.* Ithaca: Cornell University Press.

Strenger A. 1950. Eine funktionsatomische Untersuchung einiger Dermapterencerci. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* **70:** 576–600.

Uzel H. 1898. *Studien über die Entwicklung der apterygoten Insecten.* Berlin: Friedländer & Sohn.

Verhoeff KW. 1902. Über die verwandtschaftliche Stellung von *Hemimerus. Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin* **1902**.

Verhoeff KW. 1903. Über die Endsegmente des Körpers der Chilopoden, Dermapteren und Japygiden und zur Systematik von *Japyx. Abhandlungen der kaiserlichen Leop.-Carol. Deutschen Akademie der Naturforscher, Halle* **81:** 257–298 + plates.

Walker EM. 1943. On the anatomy of *Grylloblatta campodeiformis* Walker 4: exoskeleton and musculature of the abdomen. *Annals of the Entomological Society of America* **46:** 681–706.

Woodland JT. 1957. A contribution to our knowledge of Lepismatid development. *Journal of Morphology* **101:** 523–563.

Zwick P. 1973. *Insecta: Plecoptera. Phylogenetisches System und Katalog. Das Tierreich 94.* Berlin: de Gruyter.