

The female genitalic region and gonoducts of Embioptera (Insecta), with general discussions on female genitalia in insects

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Abstract

The exoskeleton of the female postabdomen, including the external genitalia and ectodermal gonoducts, was studied in five phylogenetically distant species of Embioptera from the genera *Metoligotoma* (Austrolembiidae), *Clothoda* (Clothodidae), *Aposthonia* (Oligotomidae), *Biguembia* (Archembiidae), and *Enveja* (without family assignment). The morphological interpretation of the embiopteran postabdominal sclerites and gonoduct components is discussed in a wider context of Insecta. This includes some issues of general importance, such as effects of the translocation of the gonopore from venter 7 to venter 8, the definition of gonopore location, and the definition of the vagina. We then compare the five study species regarding their postabdominal morphology, and define characters that can be used for future phylogenetic and taxonomic work on Embioptera; the corresponding character states are presented in a matrix. Important results on Embioptera are as follows. (1) The gonopore appears to lie in the posterior part of venter 8, but this apparent location probably only results from the median parts of venter 8 having been formed from an extension of venter 7. (2) The ectodermal gonoducts consist of a common oviduct and an extended oviduct, while there is either no vagina or only a very short and wide one. (3) In contrast to earlier reports, accessory glands are absent from venter 9 (although there may be vestiges in *Enveja*). (4) No support was found in female genital characters for the conventional view that the Clothodidae are the sister group of the remaining Embioptera; instead, we report several character states suggesting *Metoligotoma* as sister to the remaining Embioptera.

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Introduction

Diversity and taxonomy of Embioptera

The order Embioptera (web-spinners) currently comprises about 300 described (valid) species (Ross 2009; close to 400 according to Szumik et al. 2008), while

surely hundreds of additional species remain undescribed (Ross 2000, p. 1). According to recent classifications (Szumik 1996, 2004; Ross 2009; Szumik et al. 2008), Embioptera is divided in eight major extant families: Clothodidae, Anisembiidae, Embiidae, Archembiidae, Oligotomidae, Teratembiidae, Notoligotomidae, and Austrolembiidae. In addition, there are three small and somewhat obscure ‘families’, Embonychidae, Andesembiidae, and Paedembiidae, all erected or reinstalled by E.S. Ross (e.g. Ross 2003).

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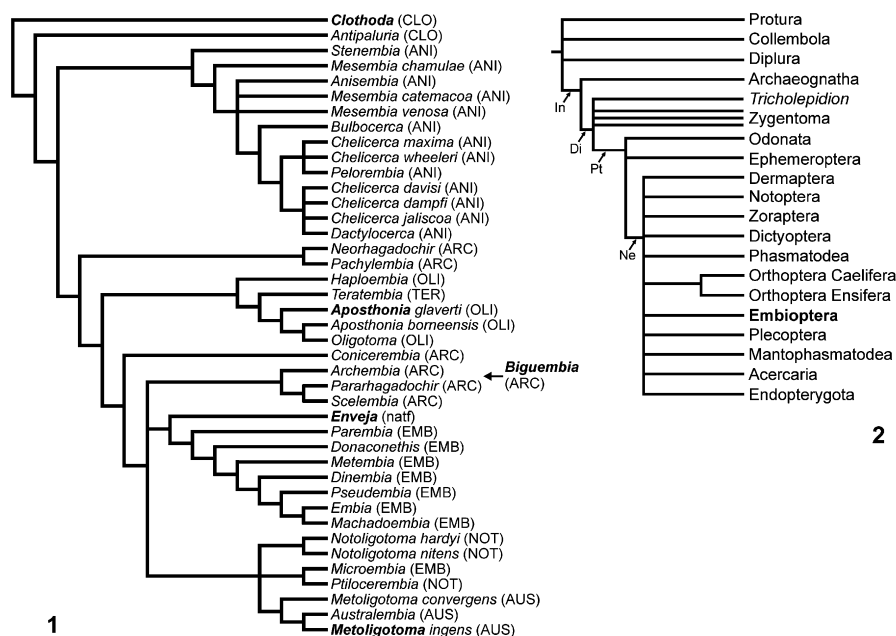
The structures most important for taxonomic work in Embioptera are those of the terminal abdominal segments of the males which are used for copulation and are usually asymmetrical and highly differentiated (the phallic organs, however, are highly reduced). The male terminalia are usually shown in great detail in contemporary taxonomic contributions (e.g. Ross 1987, 2001; Szumik 2001). In contrast, elements of the female genitalic region are hardly ever used for taxonomic purposes; in the rare cases where they have been described or illustrated, the text is brief and figures are crude (e.g. Ross 1987, 2001; Szumik 2001, fig. 31). Identification keys mostly focus on males, while females can usually be identified to genus or family only (e.g. Ross 1987, p. 13, 20, 27; Ross 2001, p. 25). Thus, increased knowledge of the female genitalic region is likely to improve taxonomic work in Embioptera.

Phylogeny of Embioptera

Phylogenetic relationships within Embioptera had long remained understudied. Until recently, the most outstanding contribution was the morphology-based cladistic analysis by Szumik (1996), which included 36 characters and 41 terminal taxa (genera or species). It was later supplemented by a phylogenetic study of the New World Archembiidae (Szumik 2004; family defined

therein). A much more extensive phylogenetic work was eventually published by Szumik et al. (2008), based on 186 morphological characters for 157 species and on molecular sequence data for 22 species (2672 aligned positions from 16S, 18S, and 28S rDNA, and from COI). While some of the ‘families’ were obtained as monophyletic in those papers (present Fig. 1, based on Szumik 1996), others were not, such as the grossly polyphyletic Embiidae (Szumik et al. 2008, fig. 1). It might be considered a problem in both Szumik (1996) and Szumik et al. (2008) that no outgroup taxa were included, and that for the phylogenetic analyses Clothodidae was presumed as the sister group of the remaining Embioptera. While this assumption was based on the weak degree of asymmetry in the male terminalia and on plesiomorphic conditions in some wing, thorax, and head characters of Clothodidae, the structure of the female genitalia may contradict that hypothesis.

The only other phylogenetic study that included a decent sample of embiopteran species was Terry and Whiting (2005). This predominantly molecular work included taxa from all lower neopteran orders, whereby its (limited) results on embiopteran phylogeny were based on broad outgroup comparison. The 9 embiopterans in that study represent all families except Embiidae (the included ‘embiid’ belongs to Archembiidae in the current classification). Terry and Whiting’s (2005)



Figs. 1 and 2. (1) Morphology-based phylogenetic tree of Embioptera after Szumik (1996), but assignment of taxa to Archembiidae after Szumik (2004). Names of genera in present study shown in boldface. Basal position of *Clothoda* assumed a priori; location of tree root thus predefined. For *Biguembia*, not included in Szumik (1996), position among Archembiidae indicated after Szumik et al. (2008, fig. 16). *Enveja* had been obtained by Szumik et al. (2008, fig. 1) in a trichotomy with Oligotomidae and Teratembidae. ANI = Anisembiidae; ARC = Archembiidae; AUS = Austrelembidae; CLO = Clothodidae; EMB = Embiidae; natf = not assigned to family; NOT = Notoligotomidae; OLI = Oligotomidae; TER = Teratembidae. (2) Phylogenetic tree of Hexapoda after Klass (2007). Di = Dicondylia; In = Insecta (= Ectognatha sensu Hennig 1969, 1981); Ne = Neoptera; Pt = Pterygota.

results were ambiguous concerning the basal position of Clothodidae (represented by *Antipaluria*): it was confirmed by Bayesian methodology, but *Antipaluria* was more deeply nested in Embioptera when direct optimisation was used.

Embioptera surely belongs to the Neoptera, as shown by molecular analyses (Terry and Whiting 2005; Kjer et al. 2006) and by the wing flexion of males (Ross 2000, p. 2, fig. B; females are wingless). The Neoptera comprise 11 principal lineages; besides Embioptera, these are the Plecoptera, Dictyoptera, Notoptera (= Grylloblattodea), Dermaptera, Orthoptera, Phasmatodea, Zoraptera, Acercaria (= hemipteroid orders), Endopterygota (= Holometabola) (Kristensen 1991, 1995), and Mantophasmatodea (Klass et al. 2002, 2003; Damgaard et al. 2008). Based on morphological data, Haas and Kukalová-Peck (2001) proposed a clade Embioptera + Plecoptera; Grimaldi and Engel (2005) considered Zoraptera as the sister group of Embioptera (Plecoptera being the next-closest branch); and in the cladistic analysis of Beutel and Gorb (2006) Embioptera were sister to all other Neoptera except Plecoptera. Molecular data yielded a clade Embioptera + Phasmatodea (Terry and Whiting 2005; Kjer et al. 2006; based on different analytical methods), which in some analyses was strongly supported. Rähle (1970) had found the same relationship supported by a particular muscle in the mouthparts. In general, however, recent morphology-based hypotheses on neopteran relationships (Haas and Kukalová-Peck 2001; Grimaldi and Engel 2005; Willmann 2005; Beutel and Gorb 2006) were all supported by some characters but incompatible with others, and in the sole numerical analysis (Beutel and Gorb 2006) all nodes inside Neoptera are weakly supported. The molecular evidence is also conflicting; neopteran relationships vary depending on the data sets and analytical methods used (Terry and Whiting 2005; Cameron et al. 2006a, 2006b; Kjer et al. 2006).

The state of science regarding insect phylogeny has recently been surveyed by Klass (2007), who suggests that a basal polytomy of 11 clades is still the most adequate representation for Neoptera (Fig. 2). The main problems in the morphology-based reconstruction of neopteran relationships are the vast incompleteness of the morphological data and the frequent incongruence between different characters. Detailed comparative studies on further character systems are badly needed, and one promising character system is the female genitalic region. Thus, also from the perspective of neopteran phylogenetics, a study of female genitalia in Embioptera is desirable.

The female genitalic region in Insecta

Hereafter, particular abdominal segments are often referred to simply by Arabic numerals. For instance,

‘coxal lobe 9’ denotes the coxal lobe of abdominal segment 9.

In the basic pattern of Insecta the female genitalic region comprises the ventral sides (= venters) of abdominal segments 8 and 9 and the hind part of venter 7, and it forms a classical ovipositor composed of valves. This region is fairly complex, with much structural differentiation in the sclerites, formative elements (projections and invaginations of the body wall and thickenings of the cuticle), and musculature (see Bitsch 1974 for Archaeognatha; Rousset 1973 for Zygentoma; Birket-Smith 1974 for both; Klass 2003, p. 195 for a summary). Major formative elements are the paired coxal lobes 8 and 9 (gonoplags; gonoplag 9 = 3rd valve), each of which gives rise to a gonapophysis mesobasally (modified coxal vesicles; 1st and 2nd valves) and to a stylus distally (distal part of appendage). The gonapophyses 8 and 9 and gonoplags 9 together form the ovipositor, but only in many Pterygota the gonoplags 9 actually ensheath the two pairs of gonapophyses (while coxal lobes 8 are usually absent in Pterygota). Sclerotisations of the female genitalic region include the large coxites 8 and 9 (paired; 1st and 2nd valvifers), the smaller, anteriorly located postlaterocoxites and antelaterocoxites (paired), and unpaired remnants of the true (eu)sternite. In addition, the gonapophyses have their own sclerotisations, which also form the olistheter (sliding interlock) between gonapophyses 8 and 9. In most Dicondylia the post- and the antelaterocoxite of segment 9 are fused into a gonangulum (Klass 2003, 2008).

The female genitalic region usually comprises three unpaired ectodermal invaginations on the ventral hind margins of segments 7 (common oviduct), 8 (spermatheca), and 9 (accessory glands) (Snodgrass 1933, 1935a); all these ducts bear a cuticular intima. The common oviduct has an open connection with the mesodermal internal genitalia, and thus is the primary outlet channel for the eggs. The spermatheca is an organ for sperm storage, whereas the accessory glands add secretions to the eggs.

In the Pterygota the female genitalic region has undergone enormous structural diversification. While in many groups this part of the body is specialised to some particular mode of egg laying, in others some or all parts of the female external genitalia have become simplified. In the most extreme cases the ventral side of the genitalic segments bears even, undifferentiated coxosterna 8 and 9 resembling those of the pregenital abdominal segments; examples are the Ephemeroptera and Plecoptera. In most pterygotan subgroups, the gonopore has been translocated to the hind part of segment 8 by the formation of an extended oviduct, and then is located immediately in front of the spermathecal opening. Furthermore, the area containing these two openings can become invaginated in anterior direction,

whereby a vagina is formed (Klass 2003, p. 211; Klass 2008, section 6.3.1; found in, e.g., Odonata, Notoptera, Mantophasmatodea, and many Dermaptera and Plecoptera).

Its high original complexity and great extent of variation makes the female genitalic region a very interesting character system for phylogeny reconstruction in Insecta and its subgroups.

The female genitalic region in Embioptera

While the Embioptera are among the taxa with a strongly simplified female genitalic region, the diversity of this body part in web-spinners is particularly poorly known. The most informative contribution is given by Ross (2000, p. 40, figs. 37, 38). According to him, the female genitalia are most complete in *Metoligotoma ingens* (Austrolembiidae), where the sclerotisations of venter 8 show subdivisions that appear to represent a median (eu)sternite, lateral coxites, and distal gonapophyseal sclerites; the latter are located on paired lobes that likely represent short gonapophyses 8. This entire complex is flanked by a pair of pleurites. Venter 9 bears an undivided coxosternum 9, which shows a large anteromedian recess of membranous cuticle. In front of it there is a short, slightly bilobate, membranous fold interpreted as a vestige of gonapophyses 9. In contrast, in *Oligotoma nigra* (Oligotomidae) coxosternum 8 is an undivided plate with a weakened median part; there are no evident vestiges of gonapophyses 8, while a very short transverse fold might represent gonapophyses 9 even more reduced than in *M. ingens* (coxosternum 9 resembles that in *M. ingens*). Ross (2000) indicates for both species a transverse gonopore on the hind part of venter 8 and an “accessory gland aperture” anteromedially on venter 9. However, there is no information on the internal arrangement of the genitalic invaginations (oviduct, spermatheca, accessory glands, and vagina), and a spermatheca is not mentioned at all.

Melander (1903) and Mukerji (1927) focally treat the internal, mesodermal genitalia of female Embioptera, but also provide fragmentary data on the ectodermal invaginations. Melander, in his few sentences and a crude illustration (Melander 1903, fig. 4) on “*Embia texana*” (= *Anisembia texana* (Melander, 1902); Anisembidae), mentions a short vagina, into whose dorsal wall opens a tortuous spermathecal duct terminating in a large spermathecal bulb in the interior of the body. For *Embia minor* Mukerji, 1927 (Embiidae), Mukerji (1927) also mentions a vagina, which opens through a transverse gonopore on the hind part of venter 8; a large, elongate spermathecal bulb is said to be present, the innermost parts of which extend anteriorly to the 2nd or 3rd abdominal segment, and which opens into the dorsal wall of the vagina via a spermathecal

duct. Verhoeff (1904, p. 186) mentioned the female genitalic region in Embioptera only very briefly, noting that there is no ovipositor and that the genital opening is located behind coxosternum 8. The brief notes by Grassi (1889) conform with those in the aforementioned papers. Nothing seems to be known about the embryonic and nymphal development of the female gonoducts and external genitalia.

In phylogenetic studies on Embioptera, the female genitalia have been used to a very limited extent. Szumik (1996, character 3; 2004, character 47) only defined a single female genital character, which refers to the subdivision of the sclerotisations on abdominal venter 8. Szumik et al. (2008, p. 996) claimed that “the female terminalia has a low variation within Embioptera”. They found only five (out of 186!) characters from this body part to be useful for inclusion in their character matrix (their characters 85–89). Unfortunately, the definitions of characters and states in that paper are very brief (in many cases even cryptic), with only very few accompanying illustrations or references.

In contrast to Szumik et al.’s (2008) cited statement, the inter-specific differences in the female genitalic region, especially as evident from Ross’ (2000) illustrations of *Oligotoma* and *Metoligotoma* species, indicate that this body part in Embioptera should contain much information both on phylogenetic relationships and for the identification of taxa.

Scope of present study

In summary, the previously published data on the external female genitalia and gonoducts in Embioptera were very sparse, and the few descriptions did not provide a coherent picture, as they referred to either the external or the internal parts. Our contribution aims at providing a more complete picture of embiopteran female genitalia by means of a coherent study of the exoskeleton, including the ectodermal gonoducts, in a sample of five species from five of the principal embiopteran lineages as identified by Szumik (1996; present Fig. 1) and Szumik et al. (2008). We will also consider characters from other parts of the female postabdomen, compare our morphological results with previous descriptions, discuss the interpretation and homologies of the components of the embiopteran female genitalia in a wider systematic context, and compare conditions in the various Embioptera studied by us. Lastly, we will compose a list of characters and their states based on our study of five species (which, however, is liable to modification when further species become included). All this should provide a sound framework for future studies on female genitalia in a broader embiopteran taxon sample. We thus hope that our results will facilitate the inclusion of female genitalic

characters in phylogenetic studies of Embioptera, and will also promote consideration of the female genitalia (including the gonoducts) in webspinner taxonomy.

Material, methods, and terminology

Material and methods

Species and specimens

The five species studied by us are listed in Table 1; in the text these species are referred to by genus names only. The systematic assignment follows Szumik (1996, 2004) and Szumik et al. (2008). From each species, two specimens were examined. All specimens had been kindly donated to the first author by E.S. Ross, and were stored in c. 70% ethanol.

Morphological studies

The abdomen was cut off in the middle of abdominal segment 5, and macerated at room temperature for several hours using c. 5% KOH solution. Macerated abdomina were examined and dissected in 70% ethanol under a stereo-microscope, using 20x–60x magnification.

Illustrations

Illustrations were first drawn on paper, then scanned and completed using the computer graphics programmes CorelPhotoPaint ver. 12 (for processing individual illustrations) and CorelDraw ver. 12 (for composing plates and labelling).

Sclerotisation is represented by shades of grey (lighter for weaker sclerotisation), while membranes are shown in white (only in sagittal sections the interior of the body is also shaded in very light grey). Undulate lines represent cuts through the cuticle, except for “ec” (e.g. in Figs. 4, 11), which is not a cutting line but represents the internal end of the cuticular intima inside the gonoduct.

Many illustrations show parts of the ventral wall of the abdomen (in either dorsal or ventral view), and often lateral and dorsolateral parts in addition (e.g. Figs. 3–5

vs. Figs. 6–9). In all such illustrations all included parts of the abdominal wall are shown spread out on a plane and flattened.

Morphological terminology

Generalities

As a general rule, when identical terms are applied to different species below, this means that homology is assumed for the respective structures, sclerotisations, or areas – though with limitations depending on the respective extent to which homology is supported by evidence. The only exception concerns the term “gonopore” (go), which is meant in a functional sense.

The shapes of body areas depend on whether the body wall forms concavities or convexities; both categories are here generally referred to as “formative elements”. Wherever the body wall is bulging towards the (tissue-containing) interior of the body, this is considered as an invagination (e.g. membranous or sclerotised apodemes, tendons, pouches, and inwardly directed folds or ridges); wherever the body wall is bulging away from the interior of the body, this is considered as an evagination (e.g. membranous or sclerotised processes or outwardly directed folds or ridges).

Ventral sclerites

We use the terminology explained in Klass (2003, p. 176; 2008, p. 50), which is derived from Bitsch’s (1973, 1974) contributions on the abdomen of Archaeognatha.

In Archaeognatha the venter of an abdominal segment bears several sclerites (Bitsch 1973, fig. 2; Bitsch 1974, fig. 1; Klass 2003, fig. 64; Klass 2008, fig. 71): the median intersternite (at the anterior segmental border) and sternite s.str. (behind the border), which together constitute the (eu)sternum s.l.; the large, paired coxites; the small, paired postlaterocoxites (“laterocoxites” of Bitsch; anterolateral to the coxites, and often fused to these) and the small, paired antelaterocoxites (“pre-coxites” of Bitsch; anterior to the coxites), which together constitute the laterocoxa; the sclerotisations of the styli and (in the genitalic segments) of the gonapophyses. This

Table 1. Species of Embioptera studied, their systematic assignment (Szumik 1996, 2004), numbers of specimens examined (N), and geographic provenance.

Species	Systematic assignment	N	Provenance
<i>Clothoda nobilis</i> (Gerstaecker, 1888)	Clothodidae	2 ♀	Brazil (Rondonia)
<i>Metoligotoma ingens</i> Davis, 1936	Australembiididae	2 ♀	Australia
<i>Aposthonia thoracica</i> Davis, 1940	Oligotomidae	2 ♀	Burma
<i>Enveja bequaerti</i> Navás, 1916*	not assigned to family	2 ♀	Zaire
<i>Biguembia multivenosa</i> Ross, 2001	Archembiidae	2 ♀	Brazil (Piauí)

All species identifications by E.S. Ross; * = identification uncertain, Ross’ label reads “*Enveja prob. bequaerti* [sic] Navas”.

pattern is considered to represent, or at least approximate, the insect groundplan condition.

In the pregenital abdomen of Pterygota, the sternal (s.l.), coxal, and postlaterocoxal sclerotisations are usually combined to a uniform coxosternite (often simply called “sternite” in the literature; see [Klass 2001, p. 272](#)); the antelaterocoxal and perhaps the stylar sclerotisations may also be included, or they may have become lost. In the female genital segments (8 and 9) of Pterygota, the separation between the original sclerites is more persistent (especially in taxa having retained a complete ovipositor), though fusions do also frequently occur there (especially when the ovipositor becomes reduced). Due to the wide potential range of different combinations of sclerite fusions, subdivisions and losses, and to the additional possibility of new sclerites appearing, it is hardly possible to consistently use a terminology that correctly reflects the detailed composition of any compound sclerite of the abdominal venter. Moreover, with regard to a particular abdominal segment in a particular pterygotan, it is often very difficult, and sometimes impossible, to say which part of the sclerotisation is homologous with which sclerite in the Archaeognatha, and which fusions, divisions, losses or de-novo formations of sclerites have occurred. This is true even if the musculature is known, because in Archaeognatha only the coxite and postlaterocoxite as well as the gonapophyses bear muscle insertions ([Bitsch 1973, 1974; Klass 2008, fig. 71](#)).

In the present paper, it is attempted to distinguish between sternal (s.l.), coxal, laterocoxal, and gonapophyseal sclerotisations. It is not attempted to differentiate laterocoxal sclerotisations into ante- and postlaterocoxal parts, as there is no basis for this in embiopteran morphology, where in addition the identification of laterocoxal sclerotisations as such will be tentative. It may be noted, however, that what we identify as laterocoxal below more probably represents postlaterocoxal than antelaterocoxal portions. We will furthermore consider sclerites traditionally termed pleurites and laterotergites (e.g. by [Ross 2000](#)), which are located lateral to the aforementioned sclerites and beneath the tergites, and are both unknown in Archaeognatha (and many other insects); the laterotergites and perhaps also the pleurites fall into the category of epipleural sclerotisations as defined by [Deuve \(e.g. 2001\)](#).

If the sternite and coxites are fused, the resulting compound sclerite is called coxosternite s.str.; if the laterocoxites additionally join this plate, this is called coxosternite s.l.. In addition, the term coxosternum s.str. or s.l. is used to comprise the respective sclerites, regardless of whether they are fused or not. In Embioptera, however, in abdominal segment 8 the gonapophyseal sclerotisations can also be included in the coxosternite (s.l. or s.str.); the ventral plates of both segments 8 and 9 probably lack a sternal component, yet

we call them coxosternites; and in cases of absence of discrete laterocoxites it is often disputable whether laterocoxal sclerotisations are absent or included in the coxosternite, and how large this portion is. All these uncertainties should be kept in mind in the following, and we emphasise that our application of this terminology is preliminary and has to be adapted as soon as uncertainties in the interpretation are overcome.

Genital invaginations, gonoducts, and genital openings

As “ectodermal genital invaginations” we define here **(1)** the total of the derivatives of the three primary ectodermal median invaginations on venters 7 (common oviduct, often plus adjacent parts of the lateral oviducts if these are intima-bearing), 8 (spermatheca), and 9 (accessory glands); plus **(2)** secondary invaginations causing the orifices of the primary ones to sink even more deeply into the body (as in the case of extended oviduct and vagina). The term “ectodermal gonoducts” here comprises those parts of the ectodermal genital invaginations through which the eggs actually pass: the common oviduct (plus often parts of lateral oviducts), extended oviduct, and vagina (spermatheca and accessory glands excluded).

The definitive genital opening (= gonopore) is called **(A)** a “primary oviducal opening”, if it is the opening of the common oviduct on the hind margin of venter 7 (widely separated from the spermathecal opening); **(B)** a “secondary oviducal opening”, if it is the opening of an extended oviduct on the hind part of venter 8 (separated from but close to the spermathecal opening); **(C)** a “vulva”, if it is the opening of a vagina on the hind part of venter 8 (a chamber receiving internally both the oviducal and spermathecal openings).

Abbreviations

The following abbreviations are used for morphological structures both in the illustrations and the text, and emphasised by boldface lettering in the text. Abbreviations from other contributions are occasionally used in the text, for clear reference; these are marked with an asterisk and explained, where necessary, but are not included in the following list.

c	lateral end of hind edge of subgenital lobe
CB	sclerite at ventral base of cercus (in ventral wall of subanal lobe)
CD	sclerite at dorsal base of cercus (in dorsal wall of subanal lobe)
ce	cercus
CS (+ number)	coxosternite (number = segment)
CX (+ number)	coxite (number = segment; genitalic segments: valvifer)

do	dorsal fold of (extended?) oviduct, including lateral and median parts
ec	line along which cuticle ends (mesodermal gonoducts adjoining)
gl (+ number)	gonoplac = coxal lobe (number = segment)
go	genital opening = gonopore
gp (+ number)	gonapophysis (number = segment)
GP (+ number)	sclerotisation of gonapophysis (number = segment)
gp8i	internalised part of gonapophysis 8
gpf	fold transversely connecting the two gonapophyses 8
gpl	median lobe formed by fold gpf
LC (+ number)	laterocoxite (number = segment)
LG7	'languette' sclerite of venter 7
LT (+ number)	laterotergite (number = segment)
mf	'membranous field' anteromedially on venter 9
MF	sclerite within 'membranous field' mf
mfi	membranous invagination on 'membranous field' mf
oc	common oviduct (intima-bearing)
oe	extended oviduct (intima-bearing)
PL (+ number)	pleurite (number = segment)
PP	paraproct
psc	prespermathecal chamber (space above fold gpf)
re	rectum
sbl	subanal lobe
sbo	spongiose cuticular body on extended oviduct
sgl	subgenital lobe
si (+ number)	spiracle (number = segment)
sp	spermatheca in general (all parts derived from spermathecal invagination)
spb	spermathecal bulb
spd	spermathecal duct
spl	supraanal lobe
ST (+ number)	(eu)sternite (number = segment)
tf	transverse fold in border region of abdominal venters 8 and 9
TG (+ number)	tergite (number = segment)
TG11	epiproct = median part of tergite 11
va	vagina
vlg	ventral lip of gonopore = hind edge of lobe sgl
xx	infolding along hind margin of coxosternum 9, above vestigial gonoplacs 9
yy	cuticular invagination between hind margin of coxosternum 9 and anteromesal corners of lobes sbl

Descriptions of female postabdomina

Metoligotoma ingens (Austrolembiidae) (Figs. 3–9)

Segments 6 and 7

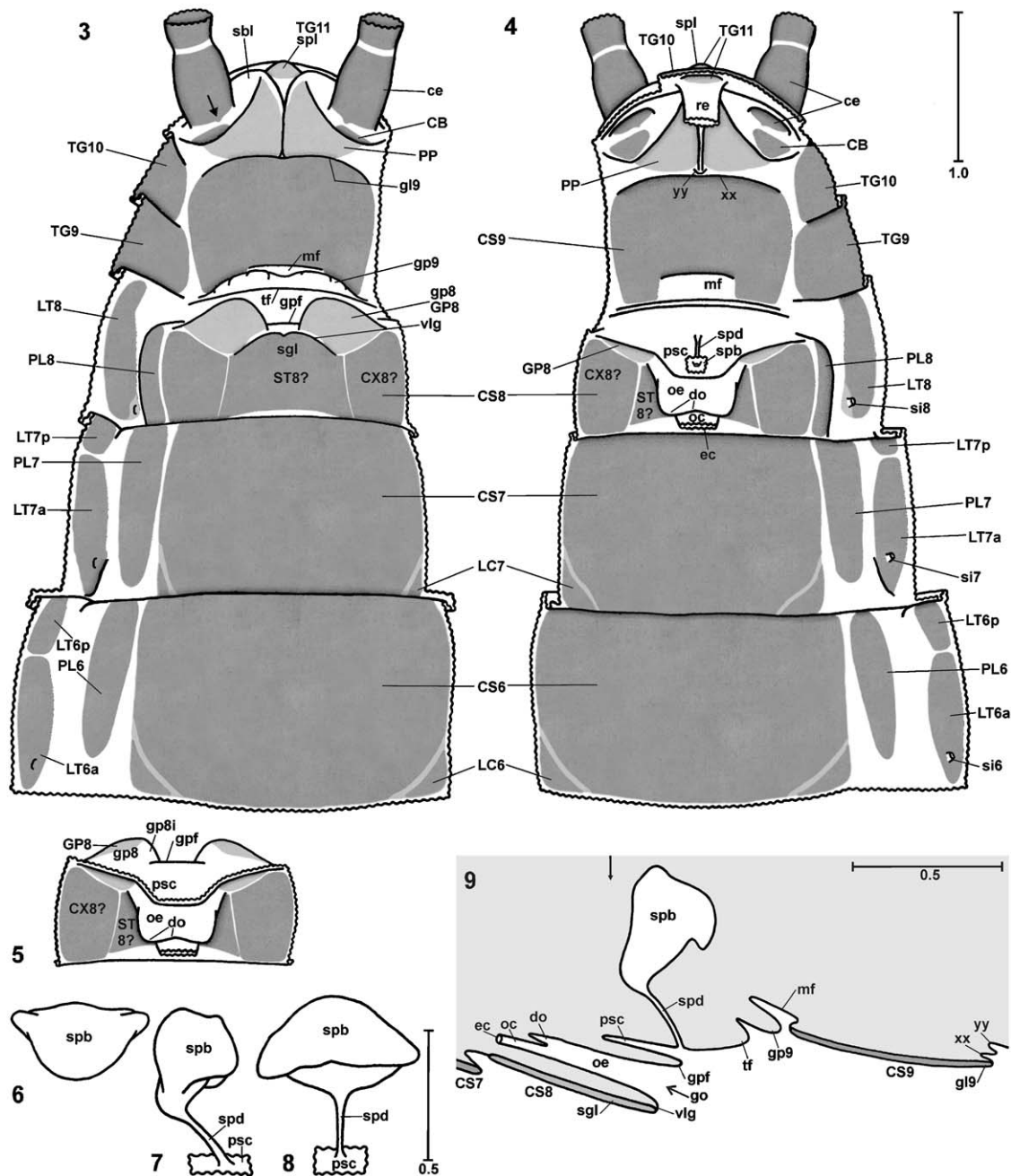
The coxosterna s.l. (Figs. 3, 4) are each composed of a large unpaired posterior plate, which is the coxosternite s.str., **CS6** and **CS7**, and a pair of very small anterolateral sclerites, the laterocoxites **LC6** and **LC7**. The **LC** are either set off from the **CS** by a ribbon of weaker sclerotisation (specimen 2: Fig. 3) or almost confluent with the **CS** (specimen 1). The hind rims of venters 6 and 7 narrowly overfold the ventral areas behind them. The long-oval pleurites **PL6** and **PL7** extend alongside the **CS**, only narrowly separated from them, and each forming a lateroventrally projecting longitudinal bulge (flattened out in Figs. 3, 4).

The laterotergites **LT6** and **LT7** are located lateral to the pleurites. Each **LT** is fully divided into a large anterior sclerite (c. 2/3 of its length; **LT6a** and **LT7a**) and a small posterior one (c. 1/3; **LT6p** and **LT7p**); in both segments this separation is effected by a distinct ribbon of membrane. The two parts of the **LT** sclerites together are slightly longer than the pleurites. Each anterior **LT** sclerite bears a spiracle (**si6** and **si7**) in its anteroventral part.

Segment 8

Coxosternum 8 s.l. **CS8** consists of a median plate (**ST8?** in Figs. 3–5) and a pair of lateral plates (**CX8?** in Figs. 3–5), the latter being somewhat more heavily sclerotised. The separation between these plates is due to a narrow but distinct membranous ribbon in the posterior part, whereas more anteriorly the plates are more confluent. Laterocoxal sclerotisations detached from the main part of the coxosternum, in the anterolateral corners of venter 8, were not found. As in the preceding segments there are distinct pleurites **PL8** flanking the coxosternum on both sides; each forms a lateroventrally projecting longitudinal bulge. The laterotergites **LT8** differ from those of the more anterior segments by the lack of a subdivision; each **LT8** bears a spiracle (**si8**) in its weaker anteroventral part.

The hind part of venter 8 forms three distinct lobes, which are sclerotised ventrally (Fig. 3) but mostly membranous dorsally (Fig. 5): the unpaired median lobe **sgl** (subgenital lobe) behind the weaker median plate of **CS8**, and the paired lateral lobes **gp8** (gonapophyses 8) behind the heavier lateral plates of **CS8**. While the sclerotisation of lobe **sgl** is part of **CS8** (i.e. of **ST8?**), that of each lobe **gp8** forms an independent sclerite, the gonapophyseal sclerite **GP8**. At its anterior margin, sclerite **GP8** is hinged to the plate **CX8?** for its larger lateral part, but the anteromesal



Figs. 3–9. Female postabdomen in *Metoligotoma ingens* (Austrolembiidae), specimen 2 (see text for different conditions in specimen 1). (3, 4) Segments 6 ff., dorsalmost and lateral parts of right body side removed; (3) ventral view; (4) dorsal view, spermathecal bulb removed except for small part of bulb wall around opening of duct. (5) Ventral parts of segment 8, dorsal view; sclerites PL8, spermatheca, and dorsal wall of prespermathecal chamber removed. (6–8) Spermathecal bulb and duct; (6) dorsal view, spermathecal duct hidden; (7), left-lateral view; (8) posterior view. (9) Mediosagittal section of ventral parts of segments 8 and 9; light grey = interior of specimen; simple black lines = membranous cuticle; double black lines filled with dark grey = sclerotised cuticle; arrow at top = posterior end of ectodermal gonoducts with lateral closure. Scales in mm; scale in Fig. 4 valid for Figs. 3–5, scale in Fig. 8 valid for Figs. 6–8.

corner of **GP8** touches the posterolateral corner of the median **ST8?**. The mesal bases of lobes **gp8** are transversely connected by a membranous fold (**gpf** in

Figs. 3, 5, 9). The membranous border region between venters 8 and 9 is bulged outward, and in a ventral view this is seen as a transverse fold **tf** (Figs. 3, 9).

Segment 9

The most anterior element of venter 9 is another (but more pronounced) membranous transverse fold following immediately behind fold **tf**: fold **gp9**, which is more (specimen 1) or less (specimen 2: Fig. 3) bilobed at its hind edge; it likely represents the strongly reduced gonapophyses 9, which are fused medially to a varied extent. Coxosternite **CS9** is a large undivided plate. At its anterior margin it has a wide, transversely rectangular notch, the ‘membranous field’ **mf**; the cuticle of **mf** is membranous, yet conspicuously different from other membranes (apparently somewhat thickened). Along its hind margin, field **mf** is sunken inward and somewhat to posterior (Fig. 9) as compared to the level of **CS9**, and its posterior margin is thus slightly overfolded by **CS9**. The posterior rim of **CS9**, which is more (specimen 1) or less (specimen 2: Fig. 3) bilobed, shortly overfolds the membrane behind it; this fold **gl9** is tentatively considered as the remains of the gonoplares 9 (coxal lobes). The depth of the infolding above the hind rim of **CS9** is labelled **xx** in Figs. 4, 9. Closely behind the infolding **xx** there is a tiny median cuticular invagination **yy** arising from the anteromesal bases of the two subanal lobes. The ventrally curved lateral parts of the tergites **TG9** and **TG10** closely approach the lateral margin of **CS9**. There are no sclerites in between that could correspond to the pleurites **PL** and laterotergites **LT** of the preceding segments.

Ectodermal genital invaginations

The genital opening (or gonopore **go**) is located immediately above the median posterior lobe of venter 8, the subgenital lobe **sgl** (Figs. 3, 9); i.e., the hind edge of lobe **sgl** is the ventral lip of the gonopore, **vlg**. Internally the gonopore continues into a wide, flat, membranous invagination here interpreted as the extended oviduct **oe**; this, in turn, continues anteriorly into a narrower channel, the common oviduct **oc**, whose posterior portion is overfolded by the dorsal wall of **oe** (dorsal fold of extended oviduct, **do**, Figs. 4, 9, an invagination whose lateral parts are more deeply infolded than the median part). The ectodermal gonoduct formed by **oe** and **oc** reaches anteriorly to about the border between venters 7 and 8, where the lining of the duct walls with cuticle ends (**ec**) and a wide opening is found in the macerated preparation (the mesodermal parts of the gonoducts would likely follow beyond **ec**).

The spermathecal invagination is composed of a long, narrow spermathecal duct **spd** (Figs. 4, 9), and, internal to it, a roughly globular spermathecal bulb **spb**, which does not show any bilobation (Figs. 6–9; mostly removed in Fig. 4, where only the bulb wall next to the inner end of the spermathecal duct is retained). The spermathecal duct opens externally into the far posterior part of a wide, flat, membranous chamber with a blind

anterior end (Figs. 4, 9); this is the space above the transverse fold **gpf** connecting the left and right **gp8** lobes, and is here called the prespermathecal chamber **psc**.

As evident from Fig. 9, the orifices of the oviducal and spermathecal invaginations are fully separated by the lobes **gp8** and their interconnecting fold **gpf**, without a shared distal duct that could be considered a vagina; this was clearly the condition in specimen 2. In specimen 1 we found the fold **gpf** extending somewhat less posteriorly (and being fully covered ventrally by the subgenital lobe **sgl** – in contrast to Fig. 3, where **gpf** is exposed behind the hind edge of **sgl**); this would agree with the presence of a very short, indistinct vagina. Nevertheless, the two conditions very likely reflect the range of movements possible in the genitalic region.

There is no discrete invagination in the area of venter 9 that could represent the accessory glands. On the anterior part (on field **mf**) neither an external aperture nor any internal invagination (as proposed by Ross 2000, fig. 38, for *Metoligotoma ingens*) was detected. The invagination **yy** behind **CS9** (Figs. 4, 9), due to its small size, can be a vestigial accessory gland at most, and is anyway more likely to be a tendon for muscle attachment.

Terminal abdomen

The posteriormost (postgenitalic) part of the abdomen (Figs. 3, 4) is dominated by tergite 10 **TG10**, which is a simple, posteriorly rounded plate that covers most of the dorsal wall and whose anterolateral parts bend far ventrally and closely approach coxosternum **CS9**. The most conspicuous elements of the ventral wall are the subanal lobes **sbl**, in whose ventral walls lie the (fairly weak) paraprocts **PP**. Further laterally the ventral wall of each lobe **sbl** bears another, smaller sclerite **CB**. The **sbl** walls around **CB** can be folded inside (specimen 2), **CB** then lying in the dorsal wall of the infolding and being partly hidden (as shown in Figs. 3, 4); or they can be fully expanded without a trace of infolding (specimen 1), sclerite **CB** then being fully exposed in ventral view. These two conditions appear to represent the range of potential movements in the terminal abdomen. The cerci **ce** have their bases laterally between tergite 10 and the subanal lobe. Each cercus is composed of two elongate cercomeres separated by a distinct ring of membrane. The sclerotised base of the cercus bears, at its ventral margin, a tiny, tongue-like anteromesal extension (arrow in Fig. 3), which articulates upon sclerite **CB**. The small supraanal lobe **spl** is located medially beneath the downcurved hind margin of **TG10**. Tergite 11 **TG11** (epiproct) extends over the dorsal and ventral walls of **spl**. The opposed margins of **TG10** and **TG11** are only narrowly separated. The supraanal lobe and the two subanal lobes together surround the anus, which leads

into the membranous rectum **re** (cut next to the anus in Fig. 4).

Clothoda nobilis (Clothodidae) (Figs. 10–16)

Segments 6 and 7

The coxosterna s.l. (Figs. 10, 11) are each composed of a large unpaired posterior plate, which is the coxosternite s.str., **CS6** and **CS7**, and a pair of very small anterolateral sclerites, the laterocoxites **LC6** and **LC7**. The sclerotisation of both **CS6** and **CS7** is weakened in the posterior third. The laterocoxites **LC** are either fully separated from the coxosternite, or connected to it by a bridge of weaker sclerotisation (only segment 7 of specimen 1). The hind rims of venters 6 and 7 very narrowly overfold the ventral areas behind them. The long-oval pleurites **PL6** and **PL7** extend alongside the **CS**, quite widely separated from them, and each forming a lateroventrally projecting longitudinal bulge (flattened out in Figs. 10, 11).

The laterotergites **LT6** and **LT7** are located lateral to the pleurites. They are slightly shorter than the latter, and undivided; each bears a spiracle (**si6** and **si7**) in its weaker anteroventral part.

Segment 8

Coxosternum 8 s.l. (Figs. 10, 11) consists of a large posterior plate, which is the coxosternite s.str., **CS8**, and of a pair of fully detached small anterolateral laterocoxites **LC8**. In specimen 1 the lateral fourths of **CS8** were more strongly sclerotised than the larger median part, whereas in specimen 2 such a differentiation was not indicated. On each side **CS8** forms a small lateral expansion. Discrete pleurites **PL8** were not found. The laterotergites **LT8** resemble those of the more anterior segments; each bears a spiracle (**si8**) in its weaker anteroventral part.

The hind part of venter 8 forms a single, very wide lobe, which is considered to be composed of a median subgenital lobe (**sgl**; the respective part of the lobe's hind edge is called **vlg** in Figs. 10, 12, 16) and a pair of lateral gonapophyses 8 (**gp8**) that have lost their demarcation from each other. The entire lobe is sclerotised ventrally (part of **CS8**, without any particular differentiation; Fig. 10) but membranous dorsally (Fig. 12). The membranous border region between venters 8 and 9 is essentially level.

Segment 9

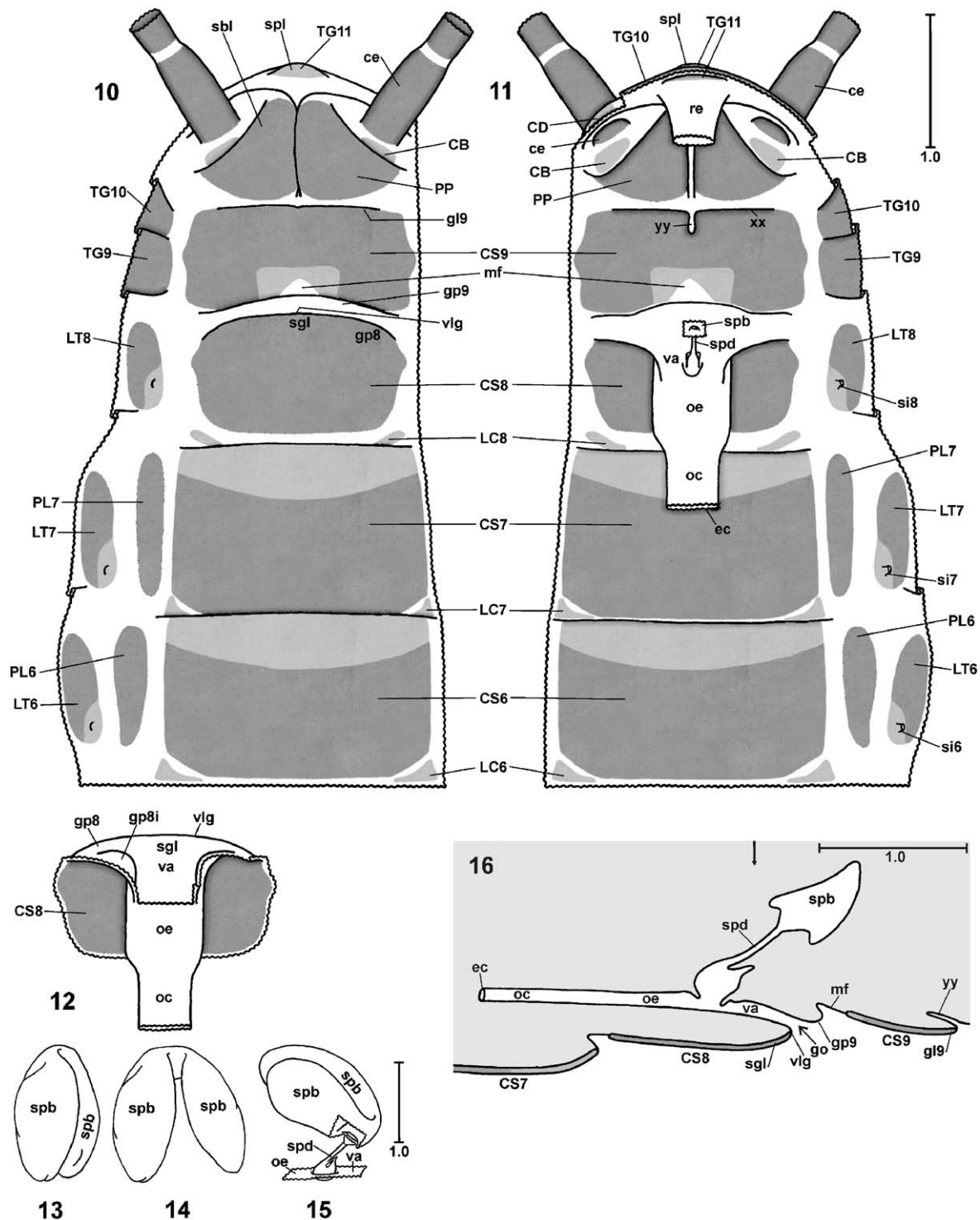
The most anterior element of venter 9 is the weakly pronounced membranous transverse fold **gp9**, whose hind edge is not at all bilobate; it likely represents the extremely reduced and medially fused gonapophyses 9. Coxosternite **CS9** is a large undivided plate. At its

anterior margin it has a wide, transversely rectangular, but indistinctly bordered area of somewhat weaker sclerotisation. Inside this area there is a triangular notch, the 'membranous field' **mf**; the cuticle of **mf** is membranous, resembling other membranes; no thickening is evident. The posterior rim of **CS9**, which shows a very slight trace of a bilobation (inconspicuous median notch), very narrowly overfolds the membrane behind it; this fold **gl9** is tentatively considered as the last remains of the gonoplas 9. The depth of the infolding above the hind rim of **CS9** is labelled **xx** in Fig. 11. The median part of the infolding **xx** is additionally deepened into a long, tongue-shaped cuticular invagination **yy**. The ventrally curved lateral parts of the tergites **TG9** and **TG10** quite closely approach the lateral margin of **CS9**. There are no sclerites in between that could correspond to the pleurites **PL** and laterotergites **LT** of the preceding segments.

Ectodermal genital invaginations

The very wide genital opening (gonopore **go**) is located immediately above the posterior lobe of venter 8 (composed of **sgl** medially and **gp8** laterally; Figs. 10, 16); i.e., the hind edge **vlg** of the **sgl** part is the median part of the ventral lip of the gonopore. Internally the gonopore continues into a wide, flat, membranous invagination here interpreted as the combined vagina **va** (short, wide posterior part) and extended oviduct **oe** (long, narrow anterior part); the latter, in turn, continues anteriorly into a still somewhat narrower channel (though the shape of the ducts is indistinct in this area), the common oviduct **oc**. Oviduct **oc** reaches anteriorly to about midlength of **CS7**, where the lining of the duct walls with cuticle ends (**ec**) and a wide opening is found in the macerated preparation (the mesodermal parts of the gonoducts would likely follow beyond **ec**). The parts **va**, **oe**, and **oc** together are here called the ectodermal gonoduct. A pair of small, rounded, membranous lobes **gp8i** originate from the lateral walls of the vagina and extended oviduct (Fig. 12) and divide the most lateral parts of these dorsoventrally; the **gp8i** lobes are not connected with each other across the midline.

The spermathecal invagination is composed of a long, narrow spermathecal duct **spd**, and, internal to it, a large spermathecal bulb **spb** (Figs. 11, 15, 16). Its external opening lies in the dorsal wall of the ectodermal gonoduct (Figs. 11, 16) and is considered (by definition) to mark the border between the vagina **va** and the extended oviduct **oe**. Near its opening into the ectodermal gonoduct, the duct **spd** is altogether widened, and there is in addition a particular, discrete widening at the posterior face of the duct (Figs. 15, 16). Also internally, where it opens into the spermathecal bulb **spb**, the duct **spd** is somewhat widened, and its orifice is bulged into the bulb lumen (Fig. 15). The



Figs. 10–16. Female postabdomen in *Clothoda nobilis* (Clothodidae), specimen 2 (see text for different conditions in specimen 1). (10, 11) Segments 6 ff., dorsalmost and lateral parts of right body side removed; (10) ventral view; (11) dorsal view, spermathecal bulb removed except for small part of bulb wall around opening of duct. (12) Ventral parts of segment 8, dorsal view; sclerites LC8 removed; dorsal walls of ectodermal gonoducts (together with spermatheca) and of left lobe gp8i partly removed. (13–15) Spermathecal bulb, dorsal view; (13) situated as in specimen; (14) with the two arms spread apart; (15) left-lateral view, spermathecal duct visible and window cut into left wall of bulb to show junction with duct. (16) Mediosagittal section of ventral parts of segments 8 and 9; graphical representation as in Fig. 9. Scales in mm; scale in Fig. 11 valid for Figs. 10–12, scale in Fig. 15 valid for Figs. 13–15.

spermathecal bulb **spb** consists of two similar, sac-like arms (Figs. 13–15; removed in Fig. 11, where only the bulb walls next to the inner end of the spermathecal duct are retained); the two arms were found closely appressed to each other, partly overlapping (Fig. 13), but they are easily spread apart (Fig. 14). A prespermathecal chamber **psc** is absent – in accordance with the absence of a transverse fold **gpf** in *Clothoda*.

As mentioned above, behind the point where the spermatheca opens into the dorsal wall of the ectodermal gonoducts, there still follows a shared distal part of the ectodermal gonoducts that has to be regarded as a vagina (by definition; see Fig. 16). Nonetheless, one has to consider that the hind part of what appears to be a vagina in the mediosagittal section (Fig. 16) is actually open laterally (due to the curvature of the hind edge of the lobe composed of the subgenital lobe **sgl** and gonapophyses **gp8**; see Figs. 10, 12); the posterior end of lateral closure of the gonoducts is marked by the vertical arrow in Fig. 16. In addition, the more internal, laterally closed part of the ‘vagina’ is very wide (see strong widening of gonoduct posterior to spermatheca in Fig. 11). Thus, this vagina is nothing but a very short, strongly widened terminal part of the ectodermal gonoducts (not a long, discrete duct or chamber as one would expect from a vagina).

There is no discrete invagination in the area of venter 9 that could represent the accessory glands. On the anterior part neither an external aperture nor any internal invagination was detected. For the invagination **yy** behind **CS9** (Figs. 11, 16) the same applies as said above for **yy** of *Metoligotoma*.

Terminal abdomen

The posteriormost part of the abdomen (Figs. 10, 11) corresponds with the description for *Metoligotoma*, with two exceptions: First, the opposing margins of sclerite **CB** and the cercal sclerotisation lack any articulation-like differentiations; second, there is an additional (weak) sclerite **CD** between the dorsal base of the cercus and the margin of tergite 10.

Biguembia multivenosa (Archembiidae) (Figs. 17–20)

Segments 6 and 7 (not illustrated)

The coxosterna s.l. are each composed of a large unpaired posterior plate, which is the coxosternite s.str., **CS6** and **CS7**, and of a pair of small, weak anterolateral sclerites, the laterocoxites **LC6** and **LC7**. The sclerotisation of both **CS6** and **CS7** is somewhat weakened in the posterior fifth. The laterocoxites **LC** appear to be fully separated from the coxosternite by a ribbon of membrane (alternatively, this ribbon might consist of weakened sclerotisation). The hind rims of venters 6

and 7 very narrowly overfold the ventral areas behind them. The long-oval, posteriorly hardly widened pleurites **PL6** and **PL7** extend alongside the **CS**, quite widely separated from them, and each forms a low, lateroventrally projecting longitudinal bulge.

The laterotergites **LT6** and **LT7** are located lateral to the pleurites. Each **LT** is fully divided into a large anterior sclerite (c. 2/3 of its length; **LT6a** and **LT7a**) and a small posterior one (c. 1/3; **LT6p** and **LT7p**); in both segments this separation is effected by a very fine hinge line; thus the two sclerites touch each other. The two parts of the **LT** sclerites together are of the same length as the pleurites. Each anterior **LT** sclerite bears a spiracle (**si6** and **si7**) in its weaker anteroventral part.

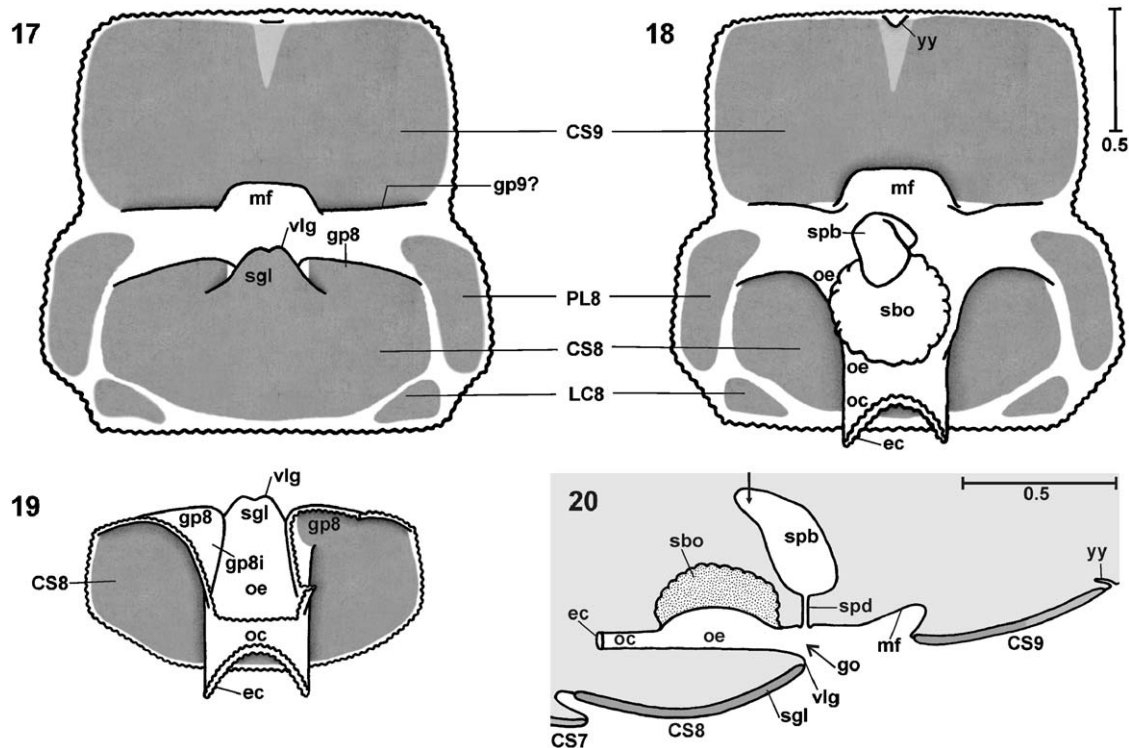
Segment 8

Coxosternum 8 s.l. (Figs. 17, 18) consists of a large posterior plate, which is the coxosternite s.str., **CS8**, and of a pair of fully detached, small anterolateral laterocoxites **LC8**. The sclerotisation of **CS8** is uniformly strong. Beside the coxosternite there are distinct pleurites **PL8** on both sides, which are located far posteriorly, only their anterior 2/3 flanking **CS8**; each **PL8** forms a low, lateroventrally projecting longitudinal bulge. The laterotergites **LT8** resemble those of the more anterior segments and are divided and hinged in the same way; however, the posterior sclerite **LT8p** is relatively smaller (c. 1/4 of entire length). Each anterior sclerite **LT8a** bears a spiracle (**si8**) in its weaker anteroventral part.

The hind part of venter 8 forms three distinct lobes, which are sclerotised ventrally by parts of **CS8** (Fig. 17) but membranous dorsally (Fig. 19): the unpaired median lobe **sgl** (subgenital lobe, with a slight median notch; its hind edge is **vlg**) and the paired lateral lobes **gp8** (gonapophyses 8). The mesal parts of the lobes **gp8** are located in the lateral walls of the ectodermal gonoduct; due to this internal location they are called the internalised mesal parts of **gp8**: **gp8i**. The two **gp8** are not transversely connected by a fold (no **gpf** in Fig. 19 as there is in Fig. 5). The membranous border region between venters 8 and 9 is level and does not show any conspicuous structures.

Segment 9

Most anteriorly on venter 9 there is a very short and shallow membranous transverse fold **gp9**, which shortly overfolds the anterior rim of sclerite **CS9** and in the middle is interrupted by the membranous field **mf** (Fig. 17); it may represent extremely reduced gonapophyses 9. Coxosternite **CS9** is a large undivided plate (Figs. 17, 18). At its anterior margin it has a wide rectangular notch, the ‘membranous field’ **mf**, whose cuticle is membranous but considerably thickened. The posterior part of field **mf** is sunken inward and slightly overfolded by the surrounding parts of **CS9** (Fig. 20).



Figs. 17–20. Female genitalic region in *Biguembia multivenosa* (Archemiidae), specimen 1 (specimen 2 virtually identical). (17, 18) Ventral parts of segments 8 and 9; (17) ventral view; (18) dorsal view. (19) Ventral parts of segment 8, dorsal view; sclerites PL8 and LC8 removed; dorsal walls of ectodermal gonoducts (together with spermatheca) and of left lobe gp8 partly removed. (20) Mediosagittal section of ventral parts of segments 8 and 9; graphical representation as in Fig. 9, except widely separated double black lines filled with dots = strongly thickened, spongiöse cuticle. Scales in mm; scale in Fig. 18 valid for Figs. 17–19.

The posterior rim of CS9 shows no trace of a bilobation and does not overfold the area behind it. Yet, the most posteromedian parts of CS9 are less heavily sclerotised than the remainder. The left and right parts of the hind margin of CS9 are particularly closely associated with the paraprocts PP (not illustrated; Fig. 10 shows much less close contact), so that the sclerites are almost hinged upon each other. Closely behind the posterior rim of CS9 there is a tiny median cuticular invagination yy arising from the anteromesal bases of the two subanal lobes (Figs. 18, 20; smaller in specimen 2). The ventrally curved lateral parts of tergites TG9 and TG10 approach the lateral margin of CS9, but not very closely. There are no sclerites in between that could correspond to the pleurites PL and laterotergites LT of the preceding segments.

Ectodermal genital invaginations

The genital opening (or gonopore, go) is a wide transverse slit immediately above the three posterior lobes of venter 8 (sgl medially and gp8 laterally; Figs. 17, 19, 20); i.e., the hind edge vlg of lobe sgl is the median part of the ventral lip of the gonopore. Internally the gonopore continues into a wide, flat, membranous invagination here interpreted as the extended oviduct oe, which without demarcation continues anteriorly into

the common oviduct oc. The ectodermal gonoduct formed by oe and oc reaches anteriorly to about the border between venters 7 and 8, where the lining of the duct walls with cuticle ends (ec) and a wide opening is found in the macerated preparation (the mesodermal parts of the gonoducts would likely follow beyond ec). The mesal parts of the lobes gp8 (the membranous gp8i) have their bases in the lateral walls of the extended oviduct and divide its most lateral lumen dorsoventrally (Fig. 19). The dorsal wall of the extended oviduct bears a conspicuous bulge, which consists of strongly thickened, somewhat spongiöse cuticle (sbo in Figs. 18, 20) and might have a glandular function.

The spermathecal invagination is composed of a spermathecal duct spd, and, internal to it, a moderately sized spermathecal bulb spb (Figs. 18, 20). Its external opening lies immediately above and behind the gonopore go, at the same vertical level as the posterior tip of the subgenital lobe sgl (Fig. 20). The spermathecal duct (spd in Fig. 20) is straight, narrow, and moderately long; it is very rigid, and its posterior wall is grooved (a cross section through the duct would be U-shaped). Around the small external opening of duct spd the cuticle is elevated to form a low ring wall. The roughly oval spermathecal bulb (spb) shows no trace of a bilobation; its cuticle is delicate and flexible. A prespermathecal

chamber **psc** is absent (compare Figs. 9 and 20) – in accordance with the absence of a transverse fold **gpf** in *Biguembia*.

As evident from Fig. 20, the oviducal and spermathecal invaginations open separately, without a shared distal duct that could be considered a vagina.

There is no discrete invagination in the area of venter 9 that could represent the accessory glands. On the anterior part neither an external aperture nor any internal invagination was detected (apart from the fact that the membranous field **mf** is sunken inward; Fig. 20). The invagination **yy** behind **CS9** (Figs. 18, 20) is more likely to be a tendon for muscle attachment.

Terminal abdomen (not illustrated)

The posteriormost part of the abdomen corresponds with the description for *Metoligotoma*: as in that species, no sclerite **CD** between the dorsal base of the cercus and the margin of tergite 10 was found (for **CD**, see Fig. 11). On the other hand, there is no particular articulation between sclerite **CB** and the ventral base of the cercus (but the two sclerites altogether appear to be closely hinged to each other), and **TG11** is more closely associated with the hind margin of **TG10** than in *Metoligotoma* (appearing as fused). The abovementioned especially close association (hinge) of the paraprocts **PP** with the hind rim of coxosternite **CS9** is also peculiar to this species.

Enveja bequaerti (not assigned to family) (Figs. 21–25)

Segments 6 and 7 (not illustrated)

The coxosterna s.l. are each composed of a large, unpaired posterior plate, which is the coxosternite s.str., **CS6** and **CS7**, and of a pair of very small, very weak anterolateral sclerites, the laterocoxites **LC6** and **LC7**. The sclerotisation of both **CS6** and **CS7** is somewhat weakened in the posterior third. The laterocoxites **LC** are fully separated from the coxosternite. The hind rims of venters 6 and 7 very narrowly overfold the ventral areas behind them. The long-oval, posteriorly strongly widened pleurites **PL6** and **PL7** extend alongside the **CS**, quite widely separated from them, and each forms a lateroventrally projecting longitudinal bulge.

The laterotergites **LT6** and **LT7** are located lateral to the pleurites. Each **LT** is fully divided into a large anterior sclerite (c. 2/3 of its length; **LT6a** and **LT7a**) and a small posterior one (c. 1/3; **LT6p** and **LT7p**); the two almost touch each other, and the contact is closer (almost hinge-like) in segment 7 than in segment 6. The two parts of the **LT** sclerites together are slightly longer than the pleurites. Each anterior **LT** sclerite bears a spiracle (**si6** and **si7**) in its weaker anteroventral part.

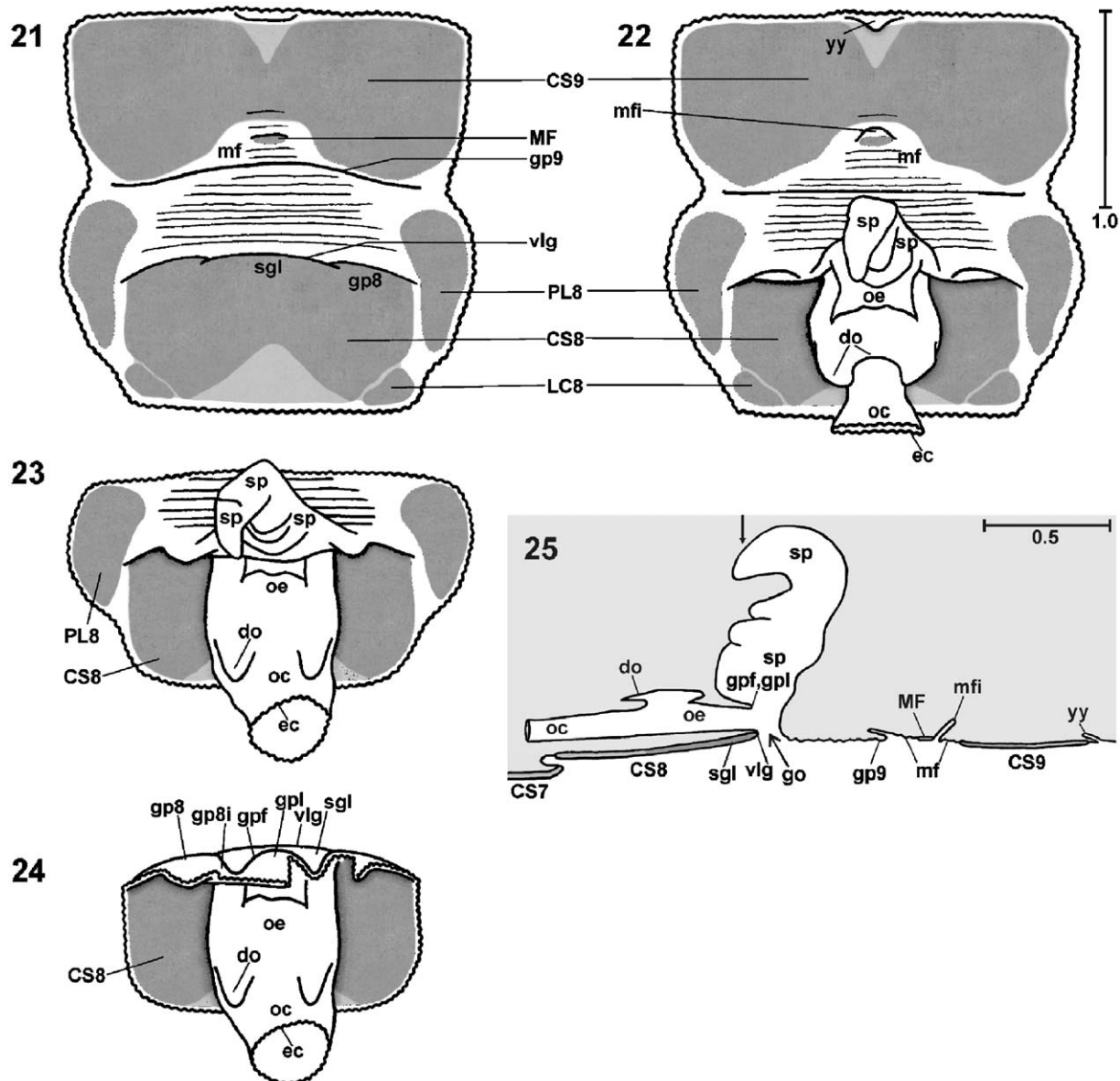
Segment 8

Coxosternum 8 s.l. consists of a large posterior plate, which is the coxosternite s.str., **CS8**, and (in specimen 1) of a pair of small anterolateral laterocoxites **LC8**, which are set off from the main part by a ribbon of weaker sclerotisation (Figs. 21, 22). However, in specimen 2 no such set-off **LC8** areas were found (Fig. 23). A triangular anteromedian part of **CS8** is less heavily sclerotised than the rest of **CS8**. Beside the coxosternum there are distinct pleurites **PL8** on both sides, which are located far posteriorly, only their anterior halves flanking **CS8**; each **PL8** forms a lateroventrally projecting longitudinal bulge. The laterotergites **LT8** resemble those of the more anterior segments, but the detached posterior parts **LT8p** are relatively smaller (hardly identifiable on left side of specimen 2), and their contact to the anterior sclerite is even closer than in segment 7. Each anterior sclerite **LT8a** bears a spiracle (**si8**) in its weaker anteroventral part.

The hind part of venter 8 forms three shallow lobes, which are sclerotised ventrally (Fig. 21) but membranous dorsally (Fig. 24): the unpaired median lobe **sgl** (subgenital lobe; its hind edge is **vlg**) and the paired lateral lobes **gp8** (gonapophyses 8). The three lobes are hardly demarcated from each other, i.e. their hind edges are almost continuous (Fig. 21 for specimen 1; demarcation even less distinct in specimen 2). The mesal parts of the lobes **gp8**, located above the dorsal face of lobe **sgl**, however, are fairly discrete and purely membranous (these internalised mesal parts of the **gp8** lobes are called **gp8i** in Fig. 24). These mesal parts **gp8i** are transversely connected by a membranous fold (**gpf** in Fig. 24), which itself forms a posteriorly directed membranous lobe **gpl** lying above the subgenital lobe **sgl**. The membranous border region between venters 8 and 9 forms a series of fine transverse folds.

Segment 9

The most anterior element of venter 9 is a membranous transverse fold (more pronounced than the fine surrounding folds): fold **gp9**, which is not at all bilobate at its hind edge (Figs. 21, 25); it likely represents the strongly reduced gonapophyses 9, which are fully fused medially. Coxosternite **CS9** is a large undivided plate. At its anterior margin it has a wide notch, the 'membranous field' **mf**, whose cuticle is membranous and weakly thickened, and throughout which the fine transverse folds continue. In its centre field **mf** bears a minute, weak sclerite **MF** (Figs. 21, 22). Immediately behind **MF** the membrane is invaginated, forming a small semicircular pouch **mfi** (Figs. 22, 25). The cuticle immediately around **MF** and **mfi** is thickened more strongly than in the remainder of field **mf**. The posterior margin of **CS9** shows no trace of a bilobation and does not overfold the area behind it. However, the posteromedian part of **CS9** is less heavily sclerotised than the



Figs. 21–25. Female genitalic region in *Enveja bequaerti* (not assigned to family), specimen 1 (21, 22, 25) and specimen 2 (23, 24); see text for differences. (21, 22) Ventral parts of segments 8 and 9; (21) ventral view; (22) dorsal view. (23) Ventral parts of segment 8 in specimen 2, dorsal view; preparation as in Fig. 22, except elements of venter 9 removed. (24) Ventral parts of segment 8 in specimen 2, dorsal view; sclerites PL8 removed, spermathecal invagination and dorsal wall of left lobe gp8 partly removed. (25) Mediosagittal section of ventral parts of segments 8 and 9; graphical representation as in Fig. 9. Scales in mm; scale in in Fig. 22 valid for Figs. 21–24.

rest. Closely behind the posterior rim of CS9 there is a small median cuticular invagination yy arising from the anteromesal bases of the two subanal lobes. The ventrally curved lateral parts of tergites TG9 and TG10 approach the lateral margin of CS9, but less closely so than in the preceding species. There are no sclerites in between that could correspond to the pleurites PL and laterotergites LT of the preceding segments.

Ectodermal genital invaginations

The genital opening (or gonopore go) is located immediately above the median posterior lobe of venter 8, the subgenital lobe sgl (Figs. 21, 24, 25); i.e., the hind edge of lobe sgl, vlg, is the entire ventral lip of the gonopore. Internally the gonopore continues into a wide, flat, membranous invagination here interpreted as the extended oviduct oe, which continues anteriorly into the common oviduct oc. In specimen 1 the posterior

portion of **oc** was completely overfolded by the membranous dorsal wall of **oe** (dorsal fold of extended oviduct, **do**; Figs. 22, 25), the lateral parts of fold **do** were expanded into tongue-like invaginations (possibly tendons for muscle attachment); in specimen 2 only these lateral ‘tongues’ of fold **do** were found (Figs. 23, 24); this difference might reflect potential movements of the gonoducts and adjacent areas. The posterolateral and central portions of the dorsal wall of **oe** are somewhat elevated as compared to the posteromedian portion, and they somewhat overfold that area (shown in Figs. 22–24 by two vertical and a transverse line; in Fig. 25 median part of overfolding represented by fold above label “oe”). The ectodermal gonoduct formed by **oe** and **oc** reaches anteriorly to the posteriormost part of venter 7, where the lining of the duct walls with cuticle ends (**ec**) and a wide opening is found in the macerated preparation (the mesodermal parts of the gonoducts would likely follow beyond **ec**; in specimen 2 the cuticle reached further anteriorly on the ventral side than on the dorsal side of the gonoduct; see Fig. 23 vs. specimen 1 in Fig. 22).

The spermathecal invagination is sac-like and does not show any structuring into an external duct and an internal bulb (thus all parts together are collectively termed the spermatheca, **sp**; Figs. 22, 23, 25). The spermatheca is very wide near its external opening, but continuously narrows transversely towards the interior, its walls being intensively folded. As the ventral border of the spermatheca, as labeled in Fig. 25, is formed by the transverse fold constituted by **gpf** and its lobe **gpl** (medially) and **gp8i** (laterally) (Figs. 24, 25), its most external portion additionally includes a space corresponding to the prespermathecal chamber **psc** of *Metoligotoma* (compare parts **psc**, **spd**, **spb** in Fig. 9). In theory, the true ‘opening’ of the spermathecal invagination thus is located somewhere in the external portion of the sac-like cavity **sp** in Fig. 25 (but is not represented by any discrete constriction).

As evident from Fig. 25, the orifices of the oviducal and spermathecal invaginations are separated by the lobes **gp8i** and their interconnecting fold **gpf**, without a shared distal duct that could be considered a vagina.

There is no discrete invagination in the area of venter 9 that could represent functional accessory glands. However, the tiny invagination **mfi** on the anterior part (on field **mf**; Figs. 22, 25) could be a vestige, though regarding its thickened condition it rather appears to be a tendon for muscle attachment. The invagination **yy** behind **CS9** (Figs. 22, 25) is also more likely to be a tendon.

Terminal abdomen (not illustrated)

The posteriormost part of the abdomen corresponds with the description for *Metoligotoma*: As in that species, there is an articulation between sclerite **CB**

and the base of the cercus (but it is located further mesally, at the mesal extreme of the cercal base; see Fig. 3), and a sclerite **CD** between the dorsal base of the cercus and the margin of tergite 10 was not found (Fig. 11). On the other hand, **TG11** seems to be more closely associated with the hind margin of **TG10** than in *Metoligotoma* (almost fused).

Aposthonia thoracica (Oligotomidae) (Figs. 26–29)

Segments 6 and 7 (not illustrated)

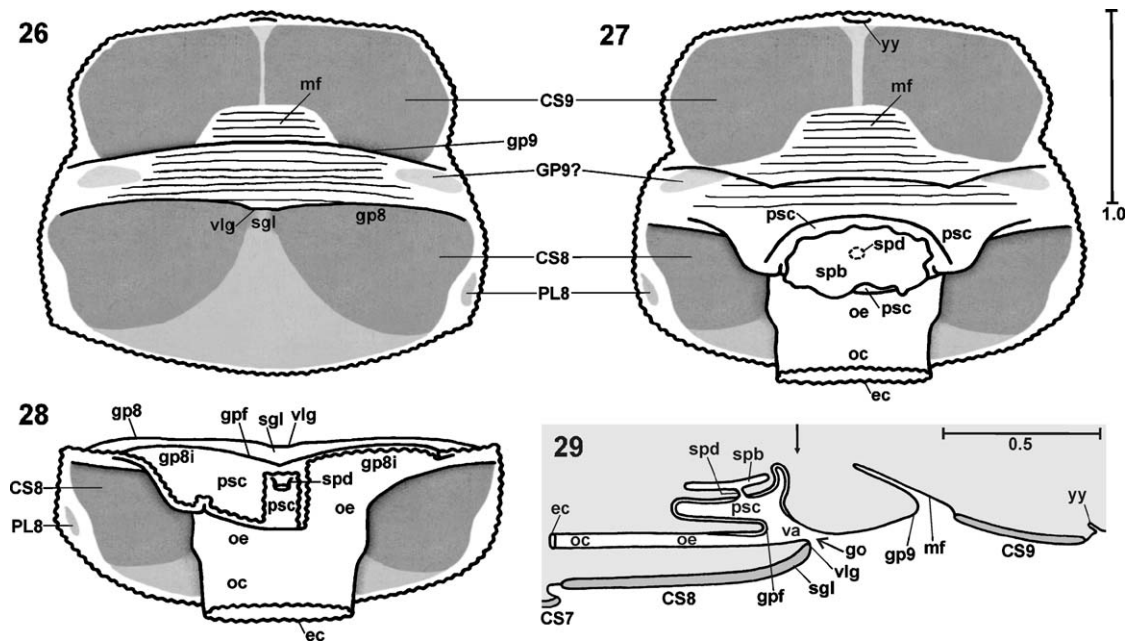
The coxosterna s.l. are each composed of a large unpaired posterior plate, which is the coxosternite s.str., **CS6** and **CS7**, and of a pair of very small, very weak anterolateral sclerites, the laterocoxites **LC6** and **LC7**. The sclerotisation of both **CS6** and **CS7** is somewhat weakened in the posterior fifth. The laterocoxites **LC** appear to be fully separated from the coxosternite (or perhaps there is a connection by very weak sclerotisation). The hind rims of venters 6 and 7 very narrowly overfold the ventral areas behind them. The long-oval, posteriorly slightly widened pleurites **PL6** and **PL7** extend alongside the **CS**, quite widely separated from them, and each forms a lateroventrally projecting longitudinal bulge.

The laterotergites **LT6** and **LT7** are located lateral to the pleurites. Each **LT** is fully divided into a large anterior (c. 3/4 of its length; **LT6a** and **LT7a**) and a small posterior sclerite (c. 1/4; **LT6p** and **LT7p**); the two are quite widely separated by membrane (c. 1/5 of length of posterior sclerite) in both segments. The two parts of the **LT** sclerites together are roughly of the same length as the pleurites. Each anterior **LT** sclerite bears a spiracle (**si6** and **si7**) in its weaker anteroventral part.

Segment 8

Coxosternum 8 s.l. consists of a single large plate, coxosternite **CS8** (Figs. 26, 27); a roughly triangular part of it, comprising its anterior and median portions, is less heavily sclerotised than the rest. Laterocoxal sclerotisations detached from the main part of the coxosternum, in the anterolateral corners of venter 8, were not found. Pleurites **PL8** beside the coxosternum are usually lacking; only on the right side of specimen 1 a minute sclerite was found that is likely a vestigial **PL8** (or perhaps a posteriorly shifted **LC8**; Figs. 26, 27). The laterotergites **LT8** are distinct, broad-oval; in contrast to the **LT** sclerites of the more anterior segments, they are undivided (no trace of a small posterior sclerite was found). Each **LT8** bears a spiracle (**si8**) in its weaker anteroventral part.

The hind part of venter 8 forms a short, wide lobe (**gp8** + **sgl** in Fig. 26), with slightly produced lateral parts and a shallow notch in between. The lobe is interpreted



Figs. 26–29. Female genitalic region in *Aposthonia thoracica* (Oligotomidae), specimen 1 (specimen 2 virtually identical). (26, 27) Ventral parts of segments 8 and 9; (26) ventral view; (27) dorsal view. (28) Ventral parts of segment 8, dorsal view; spermathecal invagination (including dorsal wall of prespermathecal chamber psc) and dorsal wall of left lobe gp8i partly removed. (29) Mediosagittal section of ventral parts of segments 8 and 9; graphical representation as in Fig. 9, except double black lines filled with white = thickened but unsclerotised cuticle. Scales in mm; scale in Fig. 27 valid for Figs. 26–28.

as being composed of a median subgenital lobe (**sgl**) and a pair of lateral gonapophyses 8 (**gp8**). Unless the **sgl** part is limited to the notch area (then being very narrow), the three parts have lost their demarcation from each other. The entire lobe is sclerotised ventrally by **CS8** (Fig. 26), but membranous dorsally (Fig. 28). Above the **gp8** + **sgl** lobe (and completely covered by it in ventral view), another short but wide transverse lobe is found, which is labeled **gp8i** (lateral parts) and **gpf** (median part) in Figs. 28, 29; it is slightly notched at the midline. The cuticle of this lobe is membranous but thickened, thus the lobe is fairly stiff. The membranous border region between venters 8 and 9 forms a series of fine transverse folds.

Segment 9

The most anterior element of venter 9 is a fairly pronounced membranous transverse fold (much more pronounced than the fine surrounding folds): fold **gp9**, which is not at all bilobate at its hind edge (Figs. 26, 29); it likely represents the strongly reduced gonapophyses 9, which are fully fused medially. In its far lateral ventral wall fold **gp9** has a pair of very weak sclerites, which are here tentatively interpreted as gonapophyseal sclerites **GP9** (but could alternatively be other anterior sclerotisations of venter 9 or even posteriorly shifted hind portions of **PL8**; Figs. 26, 27). Coxosternite **CS9** is a large, essentially undivided plate (Figs. 26, 27).

However, the sclerotisation is weakened along the entire midline of **CS9**. At its anterior margin **CS9** has a wide notch, the ‘membranous field’ **mf**, whose cuticle is membranous and very weakly thickened throughout. The fine transverse folds continue throughout field **mf**. The posterior rim of **CS9** shows no trace of a bilobation and does not overfold the area behind it. Closely behind the posterior rim of **CS9** there is a small median invagination **yy** arising from the anteromesal bases of the two subanal lobes (Figs. 27, 29). The ventrally curved lateral parts of the tergites **TG9** and **TG10** approach the lateral margin of **CS9**, but not very closely (to the same extent as in *Enveja*). There are no sclerites in between that could correspond to the pleurites **PL** and laterotergites **LT** of the preceding segments.

Ectodermal genital invaginations

The genital opening (or gonopore **go**) is located immediately above the wide posterior lobe **gp8** + **sgl** of venter 8 (Figs. 26, 28, 29); i.e., the entire hind edge of this lobe is the ventral lip of the gonopore, while the hind edge of the **sgl** lobe, **vlg**, is only the median part of it. Internally the gonopore continues into a wide, flat, membranous invagination here interpreted as the extended oviduct **oe**, which continues anteriorly into the common oviduct **oc** without any evident demarcation. An overfolding of **oc** by the dorsal wall of **oe** was not observed (Figs. 28, 29). The ectodermal

gonoduct formed by **oe** and **oc** reaches anteriorly to the posteriormost part of venter 7, where the lining of the duct walls with cuticle ends (**ec**) and a wide opening is found in the macerated preparation (the mesodermal parts of the gonoducts would likely follow beyond **ec**).

The spermathecal invagination is composed of a very short and narrow spermathecal duct **spd**, and, internal to it, a moderately sized, very flat spermathecal bulb **spb**, which does not show any bilobation and whose cuticle is extremely delicate (Figs. 27, 29). The spermathecal duct opens externally into a wide, flat prespermathecal chamber (**psc**) with a blind anterior end, and with an upcurved, likewise blind posterior end (Figs. 27, 29). The anterior part of chamber **psc** is the space above the transverse lobe composed of **gp8i** (lateral parts) and **gpf** (median part; Figs. 28, 29). The cuticle of chamber **psc** is membranous but thickened to the same extent as on lobe **gp8i** + **gpf**, and thus fairly stiff.

As evident from Fig. 29, the orifices of the oviducal and spermathecal invaginations are essentially separated from each other by the lobe **gp8i** + **gpf** (**gpf** in Fig. 29). Yet, behind the junction of the oviducal invagination and chamber **psc** in Fig. 29, there still follows a very short shared distal part of the ectodermal gonoducts that could formally be regarded as a vagina (**va** in Fig. 29). Nonetheless, the hindmost part of what appears to be a vagina in Fig. 29 is actually open laterally (due to the weakly curved hind edge of the lobe **sgl** + **gp8**; see Figs. 26, 27, and vertical arrow in Fig. 29). In addition, the more internal, laterally closed part is very wide (Fig. 27). Thus, this ‘vagina’ is an extremely short and wide terminal part of the ectodermal gonoduct. The situation is similar to the one in specimen 1 of *Metoligotoma* in which fold **gpf** was somewhat retracted.

There is no discrete invagination in the area of venter 9 that could represent accessory glands. The invagination **yy** behind **CS9** (Figs. 27, 29) is more likely to be a tendon for muscle attachment.

Terminal abdomen (not illustrated)

The posteriormost part of the abdomen corresponds with the description for *Metoligotoma*. As in that species, there is an articulation between sclerite **CB** and the base of the cercus (located a bit further mesally; compare Fig. 3). On the other hand, a sclerite **CD** between the dorsal base of the cercus and the margin of tergite 10 is also present, as in *Clothoda* (compare Fig. 11).

Comparison with earlier descriptions

The only previous detailed descriptions of the female postabdomen in embiopterans were those by Ross (2000,

figs. 37, 38) for *Metoligotoma ingens* and *Oligotoma nigra*, where abdominal segments 7ff. were considered. The former species was also included in our study; thus the results can be compared directly. *Oligotoma* is phylogenetically close to *Aposthonia* (Fig. 1; Szumik 1996; Szumik et al. 2008, fig. 6); the two genus names have sometimes been considered as synonyms (Davis 1940; Ross 1943; Szumik 1996, p. 54). *Aposthonia* was included in our study; the results on the two genera can also be compared, though with limitations. The study by Ross (2000) was limited to an external examination of specimens; gonoducts and other internal features, included in our study, were not considered.

Metoligotoma ingens

Our results on this species (Figs. 3–9) agree in most aspects with those in Ross (2000, fig. 38). However, there are some exceptions. In general, we found many sclerites considerably larger than shown by Ross (2000; Ross might have studied either a female whose abdomen was filled with mature eggs, or a fairly young adult female with the sclerites still incompletely matured). Regarding venter 7, we found coxosternite **CS7** to reach further posteriorly, and the membrane between venters 7 and 8 to be shorter. In addition we found (weak) laterocoxites **LC7**, which were not reported by Ross (2000). The sclerotisation of the subdivided laterotergites **LT7** was also found to be larger, and the anterior and posterior **LT7** sclerites to be much closer in touch. For segment 8, we did not find the division of the laterotergites **LT8** as indicated by Ross (2000). We observed the same set of discrete ventral sclerites as reported by Ross (2000): sternum **ST8?**, coxites **CX8?** (labeled as basal sclerite of “1st valvula” = gonapophysis 8 by Ross), pleurites **PL8**, and gonapophyseal sclerites **GP8** (labeled as distal sclerite of “1st valvula” by Ross). However, while according to Ross (2000) these sclerites are mostly small and separated by wide membranes, we observed them to be larger and all quite closely in contact with each other. Moreover, Ross (2000) did not report the transverse fold **gpf** connecting the mesal bases of the gonapophyses **gp8**; he even contradicted its presence by the way he figured the mesal bases of the **gp8** (hidden and shown by dashes in his fig. 38). For segment 9 we found the ‘membranous field’ **mf** to be smaller, and, most importantly, we did not find on it any external aperture (or internal invagination) that could represent the “accessory gland aperture” indicated by Ross to be located anteriorly on field **mf**. For the terminal abdomen, we observed the paraprocts **PP** to approach the hind margin of coxosternite 9 **CS9** more closely, and we additionally found a sclerite **CB** located between the paraproct and the base of the cercus.

Aposthonia/Oligotoma

Our results on *Aposthonia* (Figs. 26–29) largely agree with those on *Oligotoma* in Ross (2000, fig. 37). Yet, besides the many differences in proportions (which may well reflect differences between the two species), some more fundamental differences are noteworthy: Ross showed well-developed pleurites of segment 8 **PL8**, whereas we found at most tiny vestiges of **PL8**; as large **PL8** are present in many other Embioptera, this is likely to be a difference between species. While Ross showed laterotergite 7 **LT7** to be undivided, we found it divided in a larger anterior and a smaller posterior sclerite; since both conditions occur in Embioptera, this could be another difference between species. (Descriptions agree with regard to the undivided laterotergite **LT8**.) In addition, we found a sclerite **CB** between the paraprocts and the cercal base in *Aposthonia*, which was not reported by Ross; as we found this sclerite in all Embioptera studied by us, and Ross apparently missed it in *Metoligotoma* (see above), it appears not unlikely that Ross also overlooked it in *Oligotoma*. (Descriptions agree with regard to the presence of a sclerite **CD** at the dorsal base of the cercus: “cercus-basipodite” in Ross.)

Other contributions

The brief descriptions by Melander (1903) and Mukerji (1927) on the internal anatomy of embiopterans are plausible, as they are within the range of the overall conditions found for Embioptera in this study. Since these papers deal with species of the families Anisembiiidae (*Anisembia texana*) and Embiidae (*Embia minor*), respectively, neither of which was represented in our study, they cannot be evaluated in more detail here.

Discussion: homologies, interpretations, and characters

In this chapter the various major areas of the posterior abdomen will be discussed separately.

First, conditions in Embioptera are compared with those in other insects in order to obtain hypotheses on the homology of sclerites and other elements, and thus on their morphological interpretation in Embioptera. These hypotheses will be the basis for polarity assumptions with regard to characters that vary among the embiopterans. However, this comparison will be limited for two reasons: (1) It is far beyond the scope of this contribution to compare structures between Embioptera and all other order-level subgroups of Insecta; comparisons will rather be punctual. (2) There are no data on postabdominal muscles in Embioptera; consequently an important landmark system for the assessment of

sclerite homologies is missing. (The most complete contribution so far is that on the mid-abdomen of *Antipaluria* in Klug and Klass 2007, fig. 3, which is still quite insufficient.)

The structural differences among our five study species will then be discussed. The above descriptions have shown that there is fundamental diversity in the female genitalic region, especially regarding venter 8 and the ectodermal genital invaginations. While these two areas are major sources of characters, other parts of the postabdomen also include a few useful characters.

Lastly, characters and their states will be formulated and a character matrix (Table 2) will be presented.

Elements of pregenital venters 6 and 7

Comparison with other insects and interpretations

In Archaeognatha the venter of a pregenital abdominal segment bears the unpaired intersternite and sternite s.str. (together forming the sternite s.l.), and the paired coxites, postlaterocoxites (often fused to the coxites), and antelaterocoxites, plus the sclerotisations of the styli (Bitsch 1973); the tergite is undivided, and there are no pleural sclerites. This pattern is considered to represent, or at least approximate, the insect groundplan condition. In many Zygentoma and Pterygota the tergite is also undivided and pleural sclerotisations are absent, but there is a single major ventral plate per segment, the coxosternite (s.l.; usually simply called “sternite”). This is composed of coxal (laterally), postlaterocoxal (anterolaterally), and sternal (anteromedially) sclerotisations (e.g. Rousset 1973 for Zygentoma; Klass 2001 for Dermaptera; Klug and Klass 2007), whereas the inclusion of antelaterocoxal and styler components is unclear. The coxal and postlaterocoxal components are identified by the attachment of dorsoventral muscles on the coxosternite (Klass 2001, p. 272). In many other Pterygota, however, a variety of discrete sclerites occur in the lateral walls of a segment; these variously belong to the coxosternum, tergum, or pleural region (Klug and Klass 2007, p. 76). In addition, Deuve (e.g. 2001) defined an epipleural region immediately beneath the tergum.

The Embioptera studied here generally have a large coxosternite **CS**, small anterolateral laterocoxites **LC** that are set off from the coxosternite to a varied extent, fully discrete pleurites **PL** flanking the coxosternite, and discrete laterotergites **LT** in between the pleurites and the tergites (Figs. 3, 4, 10, 11).

For the coxosternites **CS** of Embioptera it can be assumed that they include sternal and coxal components, as they do in other Dicondylia. The coxal component is identified by the insertion of dorsoventral muscles in the embiopteran *Antipaluria* (Klug and Klass 2007, fig. 3).

The laterocoxal sclerites **LC** of Embioptera are essentially in the same position as the postlaterocoxites of Archaeognatha, but the narrow mesal parts of **LC** often reach a position more typical for the antelaterocoxites. In Archaeognatha, postlaterocoxites discrete from the coxosternite occur in some species (but not in others; Bitsch 1973, “laterocoxite” on p. 193; see also references therein), and discrete antelaterocoxites occur quite regularly in this group (Bitsch 1973, “precoxite” in fig. 2). However, such discrete laterocoxal sclerites are certainly absent in most Pterygota (though their separation from the coxosternite might have been overlooked in some taxa). Therefore it is doubtful whether the (semi-)detached condition of the laterocoxal sclerotisation could be homologous between Archaeognatha and Embioptera.

The pleurites and laterotergites of Embioptera (**PL** and **LT** in Figs. 3, 10) are difficult to assess regarding their homology with sclerotisations in other insects and their general interpretation. Discrete sclerites in between the lateral margins of the tergites and coxosternites are absent in, e.g., Archaeognatha (Bitsch 1973, 1974), Zygentoma (Rousset 1973), Dictyoptera (Klass 1999, 2000), Dermaptera, Phasmatodea, and Plecoptera (Klug and Klass 2007, p. 76). Many Pterygota have one sclerite in that position, such as the fairly large ‘laterosternites’ of many Ensifera (ventral to the spiracles and bearing lateral muscle insertions; e.g. Ford 1923; Klug and Klass 2007, fig. 6) and the small ‘pleural sclerites’ of Odonata (Asahina 1954; Klass 2008, **SI*** in figs. 1, 16; spiracle-bearing and \pm above the lateral muscle insertions). Others have two or more small sclerites in the area concerned: some Ensifera, and probably Mantophasmatodea and Notoptera, where these sclerites are very weak (Klug and Klass 2007, p. 77). There is much variation in this regard, also within orders (see Snodgrass 1935b for Orthoptera-Caelifera).

The problem with the embiopteran pleurites and laterotergites is part of the more general problem of the division of the arthropod body surface into longitudinal fields. Four such fields are widely accepted: 1 sternal, 1 tergal s.l. (= 1 tergal s.str. + 2 tergopleural), and 2 appendicular in between. Deuve (2001) additionally defines a paired epipleural field between the tergal (better: tergopleural) and appendicular fields; in hexapods it is marked by the spiracles. Thus, the spiracle-bearing laterotergite **LT** (Figs. 4, 11) of Embioptera would be an epipleural sclerite sensu Deuve. The pleurite **PL** should then be either another epipleural sclerite (located ventral to the spiracle as **epl*** in Deuve 2001, fig. 16), or a sclerite originally belonging to the appendage base. However, there are two limitations to Deuve’s hypothesis. (1) While abdominal spiracles surely are important landmarks for the interpretation of sclerites, the evidence from them can sometimes

appear as conjectural. For instance, Zygentoma have the spiracles in the pleural membrane, whereas Archaeognatha have them on the lateralmost part of the tergite (Bitsch 1973; Rousset 1973; Klug and Klass 2007, p. 76), while otherwise the lateral areas of the abdominal segments are of a similar structure. (2) Deuve’s (2001) discussions do not include evidence from the musculature. Therefore, this important landmark system cannot yet be used for the identification of epipleural sclerites, and potential conflicts between the muscular pattern and Deuve’s identification of epipleural sclerites in different taxa would also remain undetected.

Antipaluria has a muscle connecting the laterotergite and pleurite (Klug and Klass 2007, fig. 3). However, since (besides tergo-coxosternal muscles) both pleuro-coxosternal and tergo-pleural muscles occur in Insecta (Klug and Klass 2007), this allows for the interpretation of the laterotergite as a pleural (perhaps epipleural) or (detached) tergal sclerite, and of the pleurite as a pleural (perhaps epipleural) or (detached) coxosternal sclerite.

Altogether, homologising the embiopteran pleurites and laterotergites with sclerotisations in other Insecta requires a detailed comparison of the lateral parts of the abdominal segments (considering all available landmarks including muscle attachments) across the major lineages of the Insecta.

Variation in Embioptera

Our five embiopteran species differ with regard to the degree of separation of the laterocoxites **LC** from the coxosternite **CS** (by membrane or weaker sclerotisation; Figs. 3, 10). However, this feature is difficult to assess, mainly because the laterocoxal sclerotisations are often quite weak and not well-bordered. Thus it is problematic to use this for taxonomic or phylogenetic purposes; consequently no character is formulated here. In addition, since the comparison with other Insecta is ambiguous, the polarity of such a character would be unclear.

The presence or absence of a subdivision of laterotergites **LT6** (in **LT6a** and **LT6p**) and **LT7** (in **LT7a** and **LT7p**) seems to be a more useful character (**Ch 01** in the character list below). We found such a division in *Metoligotoma* (Fig. 3), *Biguembia* (hinge line), *Enveja*, and *Aposthonia*, but not in *Clothoda* (Fig. 10). The division is easily recognised even where the dividing membrane is very narrow and the sclerites are hinged to each other (as in *Biguembia*). Experimental movement of the area in macerated specimens is useful to support the evaluation of a separation of the sclerites. However, the polarity of characters related to the laterotergites is presently unclear due to the unclarified homology of the laterotergites with sclerotisations in other Insecta.

Elements of venter 8

Comparison with other insects and interpretation

In ovipositor-bearing Insecta, major formative elements of venter 8 are the gonoplags 8 (coxal lobes; usually absent in Pterygota) and the gonapophyses 8; sclerotisations include the originally large coxites 8 (1st valvifers), the originally smaller, anteriorly located postlaterocoxites and antelaterocoxites (combined in the laterocoxa), the gonapophyseal sclerites, and unpaired remnants of the sternite (Klass 2003, p. 195). Such a complicated structure of venter 8, which contributes to a well-developed ovipositor, and a gonopore located on the hind rim of venter 7 are likely groundplan conditions of Insecta. This configuration is found in both Archaeognatha and Zygentoma (e.g. Bitsch 1974; Rousset 1973) as well as in Dictyoptera and Ensifera (Klass 1998). However, most ovipositor-bearing Pterygota have the gonopore translocated to the hind part of venter 8, e.g. Odonata (Klass 2008), ‘basal’ Dermaptera (Klass 2003), Mantophasmatodea (Klass et al. 2003), Caelifera (Snodgrass 1935b), Notoptera (Walker 1943; Klass 2005), and Phasmatodea (Kalusche 1972). That translocation has a strong influence on the structure of venter 8. This mainly concerns the anterior part, where laterocoxal plus perhaps sternal sclerotisations can form a large subgenital plate (often referred to as “sternite 8”; see Klass 2008, figs. 63–65 for several taxa), and the median part along which the gonopore has been ‘shifted’ (see below); the posterolateral portions bearing the coxites and gonapophyses are less affected by these changes. Many other Pterygota have a strongly simplified venter 8, with the ovipositor reduced to a varied extent; their gonopore is either located on venter 7, e.g. as in ‘higher’ Dermaptera (secondary shift to venter 7; Klass 2001, 2003) and in Ephemeroptera, or it lies on venter 8, as in Plecoptera (Zwick 1980).

In the embiopterans studied by us the gonopore is also consistently located on the hind part of venter 8, and venter 8 ranges from moderately complicated with distinct ovipositor vestiges (as in *Metoligotoma*; Figs. 3, 30) to very simply structured with the ovipositor being entirely absent (as in *Clothoda*; Figs. 10, 34).

Metoligotoma (Figs. 30, 35) shows a structural pattern quite similar to ovipositor-bearing Insecta: it has a discrete gonapophyseal sclerite **GP8** on each side, and this sclerite is located on a distinctly projecting gonapophysis **gp8**, with the largest part of **GP8** lying in the ventral wall of the gonapophysis. Basally, sclerite **GP8** is ± closely in touch with discrete lateral plates **CX8**, which agrees with the usual relationship to plate-like coxites (e.g. as in Odonata; Klass 2008, fig. 4).

In addition, *Metoligotoma* has large pleurites **PL8** and laterotergites **LT8** (Figs. 3, 35). Such sclerites lateral to coxites 8 are absent in most ovipositor-bearing Insecta, but present in some Pterygota, though with varying

characteristics (concerning spiracle position and muscle attachments). At present, neither **PL8** nor **LT8** can be interpreted with much confidence, while a categorisation of **LT8** and perhaps also **PL8** as epipleural sclerites appears feasible; the problems are similar to those with the **PL** and **LT** of the pregenital segments.

Furthermore, *Metoligotoma* (Figs. 3, 30, 35) has a large median sclerite **ST8?** reminiscent of a sternite 8 (as compared to, e.g., conditions in Archaeognatha; **ste*** in Klass 2003, fig. 64; posterior **ST8*** sclerite in Klass 2008, fig. 71). *Metoligotoma* lacks discrete laterocoxal sclerites **LC8**, which are present, however, in other embiopterans (Figs. 36, 37, 39); based on positional comparison, laterocoxal sclerotisations of *Metoligotoma* should either be fused to the coxites **CX8?** (interpretation in Fig. 35), or absent. Concerning the laterocoxal and (surmised) sternal sclerotisations, things are very complicated.

First, in other Pterygota with an 8th-segmental gonopore the size of and connection between these sclerotisations varies. In Mantophasmatodea (Klass et al. 2003, figs. 7, 8), Odonata, Caelifera, and Notoptera (Klass 2008, figs. 4, 7–9, 63–65), laterocoxal and sternal sclerites of venter 8 (but not the coxites 8) seem to have fused and enlarged to form a large, unpaired sclerite occupying the anterior part of venter 8: a laterocoxosternite **LS8**, usually acting as a subgenital plate; nonetheless, only the (post)laterocoxal portion can be identified clearly based on insertions of anterior dorsoventral muscles, while the delimitation of the sternal component is conjectural (it might even be absent from the sclerite). In contrast, ‘basal’ Dermaptera (Klass 2003, figs. 67–74) have small laterocoxites 8, which are usually discrete but in some taxa fused with coxite 8; a sternite 8 is apparently entirely absent. Embioptera thus resemble Dermaptera in the condition of the laterocoxites 8, but the other taxa in the large size of the surmised sternal sclerite.

Second, the sternal nature of the median sclerotisation of venter 8 in Embioptera (sclerite “**ST8?**” or median part of coxosternite **CS8**; Figs. 35–39) and the other abovementioned taxa with an 8th-segmental gonopore is debatable if one pays attention to gonoduct formation. In taxa with a 7th-segmental gonopore, such as Archaeognatha and Zygentoma, the median sclerite of venter 8 can be interpreted as a true sternite 8 without conflict (Bitsch 1974, p. 113; Rousset 1973). In contrast, in taxa having an 8th-segmental gonopore and an extended oviduct, both the fate of the original median part of venter 8 (bearing the true sternite 8) and the interpretation of the definitive median part of venter 8 obviously depend on the way the extended oviduct (a) was formed during evolution, and (b) is formed during ontogeny. Hypotheses derived with regard to (a) and (b) are potentially conflicting, since ontogeny does not necessarily repeat evolution; the latter is especially

evident from the very different modes of gonoduct formation in various Cicadomorpha that lead to virtually identical conditions in the adults (see below; summary in Klass 2008, section 6.3.1.). Nonetheless, since there are no relevant data from fossils, discussions can be based only on ontogenetic development, or on adult structures in Archaeognatha and Zygentoma that may appear as evolutionary precursor structures to an extended oviduct. In the case of Embioptera, there are no data on gonoduct ontogeny; therefore, one must consider all possibilities that are evident from gonoduct formation in other Insecta with an 8th-segmental gonopore. There are essentially three possibilities for the interpretation of the middle part of venter 8.

(1), shown in Fig. 41. The extended oviduct originates from a median longitudinal groove on venter 8 that eventually becomes closed to a channel by the fusion of the left and right margins of the groove; only the most posterior part of the groove remains open to form the gonopore (secondary oviducal opening). Such an ontogenetic process has been reported for Caelifera (Nel 1929; Gupta 1948; Roonwal 1937, 1962) and some Cicadomorpha (George 1929). In the adult, the true sternal area 8 will then be located in the dorsal and lateral walls of the extended oviduct; the definitive middle part of venter 8 (including **ST8?** in *Metoligotoma*) will correspond to (originally) more lateral parts of venter 8 that flanked the groove at an earlier stage. The median sclerotisation of venter 8 in Embioptera would then likely represent mesal parts of coxites 8 (as in Fig. 41). However, this would not explain why in the otherwise most plesiomorphic embiopteran condition (as found in *Metoligotoma*; Figs. 30, 35) **ST8?** is separated from **CX8?** by a ribbon of membrane.

The adult condition in Archaeognatha includes a potential evolutionary precursor structure, the “fente génitale” (Bitsch 1974, p. 105, figs. 1A, 2B, C): The groove-like median part of venter 8 is overfolded by the mesal edges of the coxites 8 flanking it (see also Klass 2008, fig. 71, with the mesal edges of the coxal lobes 8 – basal to the origins of the gonapophyses 8 – being contiguous). However, this condition only starts behind the level of the short sternite 8.

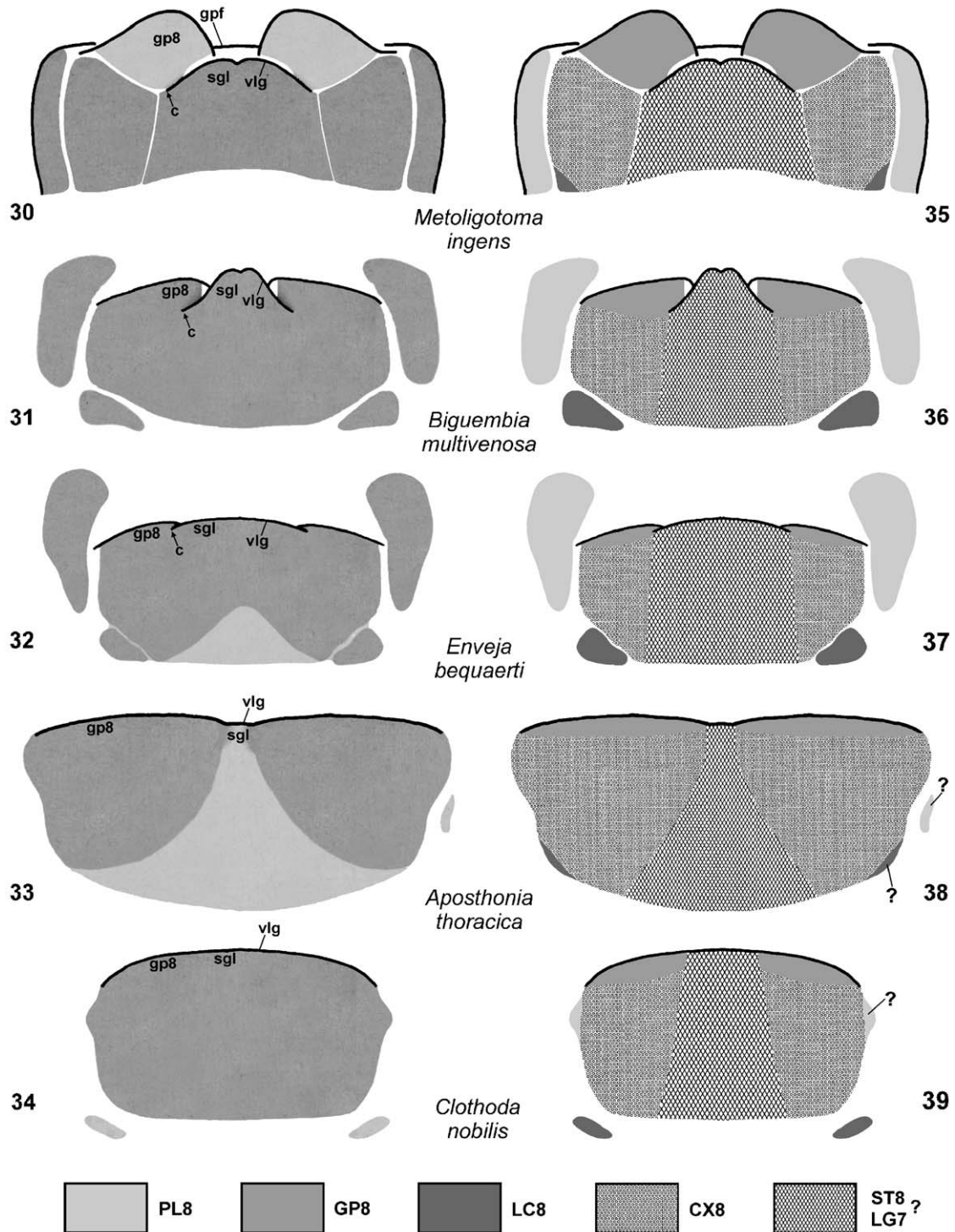
(2), shown in Fig. 42. The extended oviduct is formed in the way that a median lobe originating from the hind rim of venter 7 (but in front of the common-oviduct opening) grows posteriorly to cover the median parts of venter 8; the lateral edges of the lobe fuse, in antero-posterior direction, with the opposing parts of venter 8, whereby the extended oviduct becomes a laterally closed tube that continues the common oviduct; only the posteriormost edges of the 7th-segmental lobe do not fuse with venter 8, so that a posterior gonopore is left open (secondary oviducal opening). Such an ontogenetic process has been reported for Phasmatodea (Cavallin 1970; Kalusche 1972). As with mode (1), in the adult the

true sternal area 8 will then be located in the dorsal and lateral walls of the extended oviduct. However, the definitive middle part of venter 8 (including **ST8?** in *Metoligotoma*) will actually correspond to (originally) posteromedian parts of venter 7 (the parts from which the lobe proliferates; Fig. 42). The median sclerotisation of venter 8 in Embioptera would then be a 7th-segmental sclerite that has overgrown venter 8. This would explain the membranous separation between **ST8?** and **CX8?** in *Metoligotoma* (while a fusion of the sclerites into an undivided plate, **CS8**, in other embiopterans is not contradictory).

The adult condition in many Zygentoma includes a potential precursor structure, the “languette” (Rousset 1973, **lang*** in figs. 5, 9–11; Koch 2003). This is a median lobe originating from the hindmost median part of venter 7, immediately in front of the common-oviduct opening (primary oviducal opening), and concealing the median parts of venter 8 from below. In several Zygentoma the ventral wall of the ‘languette’ bears a sclerite (Klass 2008, fig. 70, lobe **gf*** and sclerite **LG7***). A corresponding sclerotised lobe is also present in Dictyoptera and Ensifera (Klass 1998). In an ongoing study by K.-D. Klass and N. Matushkina, a similar (but short) lobe with a feeble sclerotisation was also found in an archaeognathan (genus *Petrobiellus*) – in addition to the ‘fente génitale’.

It should be noted that for Caelifera Roonwal (1962) mentioned that the formation of the extended oviduct is partly due to a “backward extension of the vaginal tissue”, which in the framework of his descriptions is likely to refer to tissue of what is here called ‘common oviduct’, hence 7th-segmental. Thus, Caelifera may actually show a mixed type of extended-oviduct formation, including both a median 7th-segmental lobe and lateral 8th-segmental folds, whose edges all fuse to form the extended oviduct above them (as in Fig. 43).

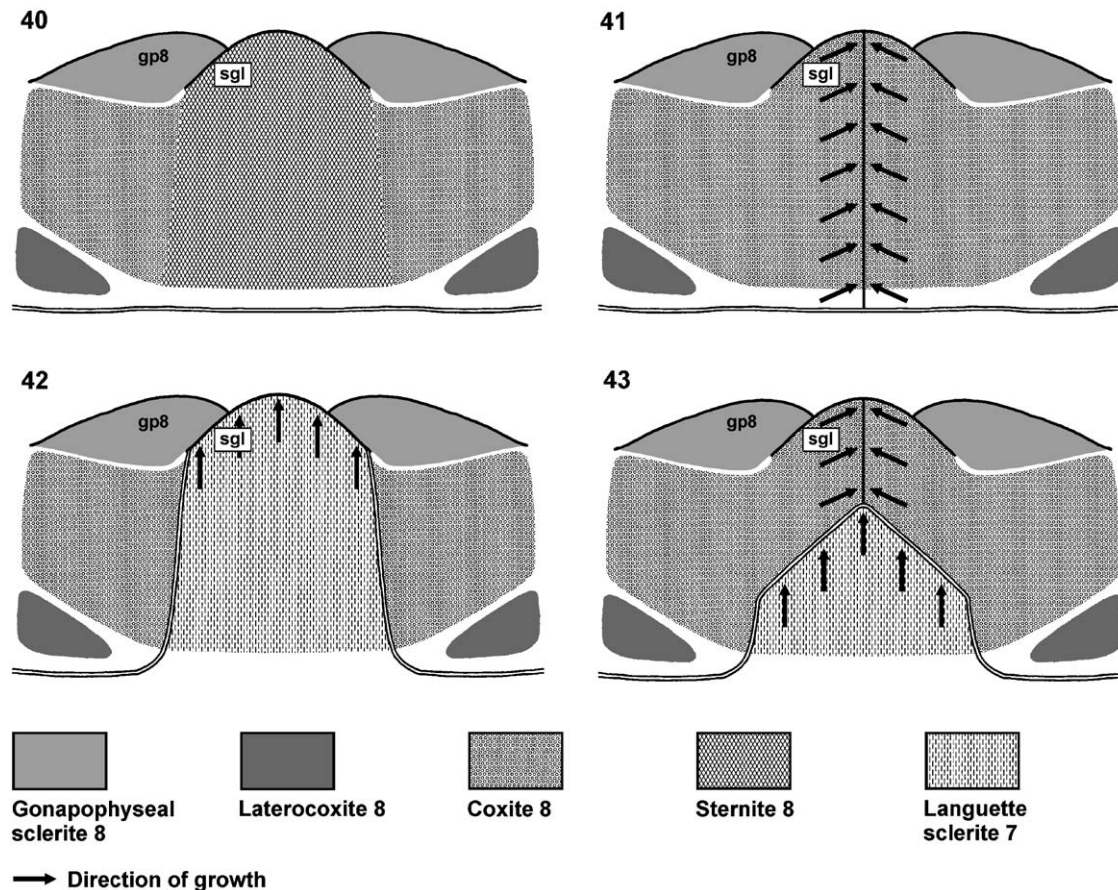
(3), shown in Fig. 40. The extended oviduct originates from a posterior invagination on venter 8 that grows antierad internally and eventually connects with the common oviduct, whose external opening then becomes closed. Such an ontogenetic process has been reported for some Cicadomorpha (Metcalf 1932), where, however, the 8th-segmental invagination not only yields the extended oviduct but, in addition, the spermatheca and a vagina. A zygopteran odonatan studied shows a similar mode, but probably no invagination (and thus no common-oviduct opening) is formed on venter 7, and the invagination from the hind part of venter 8 directly contacts the mesodermal oviducts and forms the extended oviduct, spermatheca, and vagina (George 1929). With these modes, the sternal area 8 would remain unchanged, and the median sclerotisation of venter 8 in Embioptera would fully correspond to sternal sclerotisations in Archaeognatha and Zygentoma.



Figs. 30–39. Female venter 8 in five species of Embioptera, natural condition (at left) and homology interpretation (at right). (30–34) Natural condition; dark grey = strong sclerotisation, light grey = weak sclerotisation, black lines = edges where cuticle bends out of plane of view (mainly hind edges of gonapophyses gp8 and subgenital lobe sgl). (35–39) Hypothesised extensions of sclerotisation components: pleural (PL8), gonapophyseal (GP8), laterocoxal (LC8), coxal (CX8), and a sclerotisation that either represents (eu)sternite of venter 8 (ST8) or the languette sclerite of venter 7 (LG7); particularly questionable interpretations indicated by “?”.

In overview, however, mode (3) seems to be highly derived and also co-occurs with mode (1) in the same insect order, the Cicadomorpha. Mode (2) appears to be

best demonstrated by morphological data, and it may also contribute to gonoduct formation in (some?) taxa in which otherwise mode (1) was observed. With regard to



Figs. 40–43. Semi-diagrammatic representations of female venter 8 area in Embioptera, showing four different interpretations of its median part (compare to Figs. 30–39). (40) Sternite 8 (median part of venter 8 not overgrown). (41) Mesal parts of coxites 8 (median part of venter 8 overgrown from lateral). (42) Languette sclerite of segment 7 (median part of venter 8 overgrown from anterior). (43) Languette sclerite (anteriorly) and mesal parts of coxites 8 (posteriorly) (median part of venter 8 overgrown from lateral in posterior part, and from anterior in anterior part); interpretation mixes those in Figs. 41 and 42. Arrows indicate directions of overgrowth. Double line = border between abdominal segments 7 and 8.

Embioptera one should note that molecular-based phylogenetic analyses suggest a sister-group relationship to Phasmatodea (Terry and Whiting 2005), as do some morphological characters (special muscle of paraglossa as proposed by Rähle 1970, operculum of egg; see Klass 2007). As the studied phasmatodean shows mode (2), it is perhaps the most likely hypothesis that this mode also applies to Embioptera (interpretation in Fig. 42). With this interpretation the name ‘coxosternite 8 CS8’ for the compound 8th-segmental sclerite of most Embioptera would be inaccurate.

Deuve (2001, fig. 24) suggested a further evolutionary hypothesis for taxa that have the gonopore on venter 8. In this scenario, the ventral elements of segment 8, i.e. the coxites 8 together with the gonapophyses 8 and gonoplacs 8 (laterocoxal and sternal elements not considered), have become condensed to the hind rim of venter 8. The originally far lateral epipleural sclerites have expanded to the ventral midline to take the area

from where the former elements had retreated; then the left and right epipleurites have fused medially, thus forming the subgenital plate (the sclerite called LS8 above) as well as the extended oviduct above their median portions. This hypothesis has been discussed in Klass (2008, p. 117), and rejected because it is inconsistent with the pattern of the musculature. In addition, in the insect orders here in question, there is probably no mode of ontogenetic development of the genitalic region to support this hypothesis – in contrast to the possibilities (1) and (2).

In summary, the gonapophyses 8 (gp8), the gonapophyseal sclerites 8 (GP8), and the coxites 8 (CX8?) are easily identified in *Metoligotoma* (Figs. 30, 35); the separation of the sclerites and the projecting condition of the gonapophyses appear to be plesiomorphic. The median sclerotisation of ‘venter 8’ (ST8?) is probably the 7th-segmental ventral sclerite of the ‘languette’ lobe; its separation from coxites 8 appears as plesiomorphic. The

subgenital lobe (**sgl**) is the free distal part of the ‘languette’ lobe, and then also belongs to segment 7. If this hypothesis is true, the extended oviduct is composed of 7th- (ventral parts) and 8th-segmental (dorsal parts) components. In the strict sense, the genital opening in Embioptera (and Phasmatodea, and perhaps other Pterygota with an ‘8th-segmental’ gonopore) would then still be 7th-segmental. The sclerites **PL8** and **LT8** of Embioptera might be epipleurites sense Deuve (2001), but a reliable interpretation would require data on the musculature.

Variation in Embioptera

As in the preceding segments, embiopterans vary with regard to the subdivision of laterotergites, **LT8** (**Ch 02**): in *Clothoda* (Fig. 10), *Metoligotoma* (Fig. 3), and *Aposthonia* they are undivided, whereas *Enveja* and *Biguembia* show a clear, hinge-like subdivision in a large anterior (**LT8a**) and a small posterior sclerite (**LT8p**). Regarding character polarity the same applies as said for the pregenital laterotergites.

Another character relates to the presence of pleurites **PL8** (Figs. 30–39). *Metoligotoma* (Figs. 30, 35), *Enveja* (Figs. 32, 37), and *Biguembia* (Figs. 31, 36) have large, discrete pleurites. Only in *Clothoda* (Figs. 10, 34, 39) individualised **PL8** were always found to be completely absent; their sclerotisation is either actually absent, or included in coxosternite **CS8** – then perhaps very small and represented by lateral extensions of the **CS8** (as shown in Fig. 39). In *Aposthonia* well-developed **PL8** are also clearly absent, but otherwise the interpretation is conjectural for this taxon: The small sclerite on the right side of one individual is in the right place to be a reduced **PL8** (Figs. 26, 33, 38), and this interpretation is here advocated (Fig. 38). Alternatively, however, this sclerite could perhaps be a posteriorly shifted laterocoxite **LC8**; the **PL8** could then be either absent throughout in *Aposthonia*, or integrated into the large sclerite **CS8** (then represented by the lateral expansions of **CS8**, similar to *Clothoda*; Fig. 39); furthermore, the enigmatic sclerite **GP9?** (Fig. 26; see below under “Comparison with other insects and interpretation” concerning elements of venter 9) could perhaps be a posterior fragment of a reduced **PL8** that, in addition, has shifted posteriorly (though not very far compared to the hind part of **PL8** in taxa with posteriorly located **PL8**, such as *Enveja*; compare Figs. 21 and 26). A study of muscle attachments could perhaps clarify this issue for *Clothoda* and *Aposthonia*. Despite the variation and uncertainty in *Aposthonia*, a character (**Ch 03**) can be defined in which a large, discrete condition of **PL8** is opposed to a reduced condition or absence. However, it should be noted that the latter state has to be used with caution, because the way of reduction of **PL8** is unclear and could be different in *Clothoda* and *Aposthonia*. Since homologues of **PL8** cannot be reliably identified in other

Insecta at this time, we consider the polarity of this character as unclear.

The discreteness of gonapophyseal sclerites **GP8** from the lateral parts of coxosternite **CS8** (or from coxites **CX8?** if these are separated from a median **ST8?**; Fig. 3) also varies (**Ch 04**). Only in *Metoligotoma* (Figs. 3, 30, 35) are the **GP8** and **CX8?** separated by a narrow ribbon of membrane. In the other species the sclerotisations showing positional correspondence with the **GP8** of *Metoligotoma* (located ventrally along the hind edges of lobes **gp8** in Figs. 10, 17, 21, 26) are fully included in sclerite **CS8** (Figs. 31–34, 36–39). Comparison with ovipositor-bearing insects suggests that the discreteness of **GP8** is plesiomorphic.

A separation between lateral coxites **CX8?** and a median ‘sternite’ **ST8?** (likely the languette sclerotisation of segment 7; **Ch 05**) is also only found in *Metoligotoma* (Figs. 3, 30, 35; by a very narrow membrane). In the other four species the sclerotisations showing positional correspondence are combined within a single undivided plate **CS8** (Figs. 10, 17, 21, 26, 31–39). We regard separation of the sclerites as plesiomorphic; this is in accord with the interpretation of the median sclerotisation as either the languette sclerite **LG7** (most likely; Fig. 42) or the true sternite 8 **ST8** (Fig. 40). But we note that with the interpretation as the mesal parts of the coxites 8 **CX8** (Fig. 41) the polarity would rather be the reverse.

The embiopterans differ with regard to the presence of small laterocoxites **LC8** discrete from **CS8** (or **CX8?**; Figs. 30–39). *Metoligotoma* (Fig. 3) and *Aposthonia* (Fig. 26) show no trace of free **LC8**; the respective sclerotisation may be either absent or integrated into **CS8**; however, it cannot be excluded that in *Aposthonia* the small sclerite beside the large coxosternum 8 is **LC8** (whereas it is interpreted as **PL8** here). In *Enveja* specimen 2 shows the same condition (Fig. 23), while specimen 1 (Figs. 21, 22) has distinct **LC8** sclerotisations that are connected with **CS8** by a ribbon of weaker sclerotisation. Only *Biguembia* (Fig. 17) and *Clothoda* (Fig. 10) have fully discrete, unambiguous **LC8**. We define a character (**Ch 06**) that distinguishes between complete discreteness of the **LC8** and conditions where **LC8** is not completely or not at all separated from the other sclerites of venter 8. Character polarity is considered ambiguous, and the scoring of *Aposthonia* as state [0] is uncertain.

A further difference relates to whether the (antero) median parts of **CS8** (or **ST8?** in *Metoligotoma*) are more weakly sclerotised than the (postero)lateral parts (or **CX8?** in *Metoligotoma*). While in *Aposthonia* (Fig. 26) and *Enveja* (Fig. 21) these parts are distinctly weaker, they are only slightly weaker in *Metoligotoma* (Fig. 3), and the sclerotisation is of uniform strength in *Biguembia* (Fig. 17). In *Clothoda* (Fig. 10) the condition varied between the two specimens examined. We did not

formulate a character for this trait. We additionally note that in taxa with a **CS8** plate the borders of weaker median sclerotisation cannot be considered ad hoc as the borders of the sclerotisation derived from the median sclerite **ST8?**.

Some further differences among the embiopteran species concern the relationships between the lateral lobes **gp8** (their mesal, internalised parts **gp8i** included), the median lobe **sgl**, and the transverse fold **gpf**, which connects the left and right **gp8** across the midline.

One issue is the separation of the lobes **gp8** from lobe **sgl** (disregarding for the moment the mesal parts **gp8i**) (**Ch 07**). In *Clothoda* (Figs. 10, 34) there is no separation at all, as the hind edges of the lobes **gp8** and **sgl** together form a single continuous edge along the entire hind margin of sclerite **CS8** (therefore the exact border between the three lobes cannot be determined). *Aposthonia* (Figs. 26, 33) shows the same condition, but the continuous edge along the hind margin of **CS8** has a median recess; the part of the edge along the bottom of the recess may represent either the entire **sgl** portion or a median notch of the **sgl** lobe (as in *Biguembia*; Fig. 31). In *Enveja* (Figs. 21, 32) the **gp8** lobes are slightly set off from the **sgl** lobe, as the hind edges of the lateral and median lobes are not continuous (i.e. the hind edge of the **sgl** lobe has a lateral end, at point **c** in Fig. 32). This is also true for *Biguembia* (Figs. 17, 31, point **c**), though here the **gp8** and **sgl** lobes are set off from each other much more distinctly. The most distinct separation of the three lobes is found in *Metoligotoma* (Figs. 3, 30). A clear separation of the lobes would appear as plesiomorphic, but this is actually ambiguous, because a comparison of the transition area between the subgenital lobe and the bases of the gonapophyses 8 with that in other insects is difficult. We note that only comparison with insects that have an ‘8th-segmental’ gonopore will be admissible for this character.

The extent of development of the lobes **gp8** (or, rather, of the lateral parts of these) varies in parallel with the preceding character (Figs. 30–34, where both characters can be seen). Lobes **gp8** are especially long, projecting, and distinct in *Metoligotoma* (Figs. 3, 30), where also lobes **gp8** and **sgl** are most distinctly separated. In *Biguembia* (Figs. 17, 31) the **gp8** are much less distinct (i.e. shorter and wider); in *Enveja* (Figs. 21, 32), *Aposthonia* (Figs. 26, 33), and *Clothoda* (Figs. 10, 34) the **gp8** are even less prominent. We define a character (**Ch 08**) where an extraordinarily elongate condition (such as in *Metoligotoma*) is defined as a state opposed to another that comprises all conditions showing wider and shorter lobes **gp8**. The former state is plesiomorphic, since in ovipositor-bearing insects the **gp8** are even more prominent.

The mesal parts of the lobes **gp8** (**gp8i** in Figs. 5, 12, 19, 24, 28 and Figs. 44–49) are located above the subgenital lobe **sgl**, and their bases extend \pm far into the

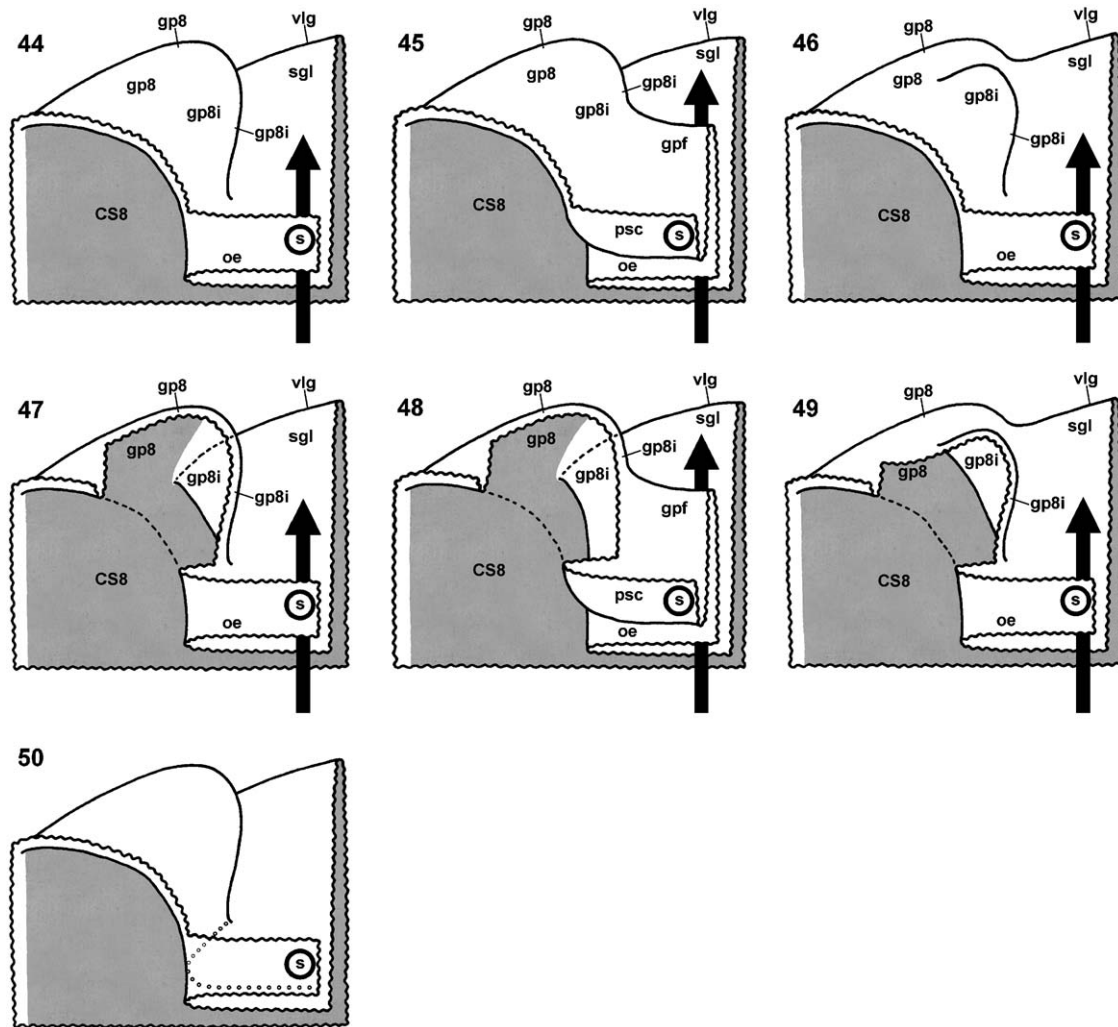
ectodermal gonoducts (hence the **gp8i** are termed “internalised” parts of **gp8** here). The mesal bases of the left and right **gp8i** are either connected by a transverse fold **gpf** (Figs. 5, 24, 28; as in Figs. 45, 48), or they end freely in the gonoduct walls (Figs. 12, 19; as in Figs. 44, 47). *Clothoda* (Fig. 12) and *Biguembia* (Fig. 19) lack a transverse fold **gpf**. *Metoligotoma* (Figs. 3, 5) has a straight fold **gpf**, in *Aposthonia* (Fig. 28) fold **gpf** is medially notched, and in *Enveja* the median part of fold **gpf** is convex and projects as a lobe (termed **gpl** in Fig. 24). The difference between the two conditions with and without fold **gpf** is emphasised in the schematic Figs. 44, 47 (without **gpf**) and Figs. 45, 48 (with **gpf**). A condition with a fold **gpf** can be reached from a condition without **gpf** by an outfolding of the body wall along the line marked with ringlets in Fig. 50. This line traverses between the mesal bases of the **gp8** lobes along the dorsal gonoduct wall, where it passes the opening of the spermathecal duct (circle in Fig. 50) internally. Accordingly, the formation of a fold **gpf** goes along with the formation of a prespermathecal chamber **psc** (compare Figs. 9, 29, both with a fold **gpf**, to Fig. 20, without fold **gpf**), and the fold separates the spermathecal opening from the oviducal opening. Thus, a particularly long fold **gpf** shifts the junction of the gonoduct and the spermathecal invaginations to the posterior. We define two characters, one related to the presence of fold **gpf** (**Ch 09**) and one related to the formation of a lobe **gpl** by this fold (**Ch 10**).

In *Metoligotoma* (Figs. 3, 5), *Biguembia* (Figs. 17, 19), and *Enveja* (Figs. 21, 24) the mesal part of each lobe **gp8** (**gp8i**) is not set off from the lateral part of **gp8**, i.e. the edges of the mesal and lateral parts are continuous (this can be recognised by comparing dorsal and ventral views of the respective area, i.e. Figs. 3, 17, 21 with Figs. 5, 19, 24). Thus, this condition is found in the same taxa in which lobes **gp8** are set off from lobe **sgl** (see above). In contrast, in *Aposthonia* (Figs. 26, 28) and *Clothoda* (Figs. 10, 12) the mesal part of each **gp8** (**gp8i**) is set off from the lateral part as an individualised lobe (i.e. the edges of the two parts are discontinuous) (compare Figs. 10, 26 with Figs. 12, 28). These are the same taxa where lobes **gp8** are not set off from lobe **sgl**. The difference is emphasised in the schematic Figs. 44, 47 (**gp8i** as simple mesal parts of lobes **gp8**) and Figs. 46, 49 (**gp8i** as individualised lobes separate from **gp8**). We define a character for this difference (**Ch 11**); polarity is difficult to establish, for the same reason as stated above for character **Ch 07**.

Elements of venter 9

Comparison with other insects and interpretation

In ovipositor-bearing Insecta, major formative elements of venter 9 are the gonoplares 9 (coxal lobes) and



Figs. 44–50. Semi-diagrammatic representations of area of female genital opening on hind part of venter 8; right half of venter 8 in a dorsal view, posterior end at top (compare to Figs. 5, 12, 19, 24, 28). Three basic structural types shown. (44, 47) Type with gonapophyses 8 (gp8) undivided and not connected by a transverse fold. (45, 48) Type with gp8 undivided and connected by a transverse fold (gpf) that delimits a prespermathecal chamber (psc) above it. (46, 49) Type with gp8 divided (detachment of internalised mesal part gp8i as a separate lobe from lateral main part). In Figs. 44–46 the dorsal wall of gp8 is retained, in Figs. 47–49 it is largely removed. Undulating lines intersect cuticle. Open circle labelled “s” = external opening of spermathecal duct (see, e.g., spd in Fig. 9). Large arrows indicate pathway of eggs. (50) Type as in Fig. 44; series of small ringlets indicates line along which cuticle had to be folded posteriorly (and outwardly) to form a fold gpf (i.e. reach the condition in Fig. 45).

the gonapophyses 9; sclerotisations include the large coxites 9 (2nd valvifers), the smaller, anteriorly located postlaterocoxites and antelaterocoxites (together forming the gonangulum), the gonapophyseal sclerites, and unpaired remnants of the sternite (Klass 2003, p. 195). Such a complicated structure of venter 9, which contributes to a well-developed ovipositor, likely is a groundplan condition of Insecta, as it is found in Archaeognatha (without a sternite 9; Bitsch 1974), Zygentoma, and many Pterygota. Across the Insecta venter 9 varies to the same extent as venter 8, including simplification and reduction in a number of taxa. In contrast to venter 8, however, it is not influenced by

posterior shifts of the genital opening (with the exception of some endopterygotan taxa).

In all Embioptera studied by us, venter 9 is strongly simplified (i.e. in a highly apomorphic condition). In contrast to venter 8, however, the structural pattern is fairly uniform.

The most anterior element of venter 9 in Embioptera is the transverse fold **gp9** (Figs. 3, 10, 21, 26), which is interpreted as the vestiges of gonapophyses 9 (as in Ross 2000). On venter 9 of Insecta the bases of the gonapophyses are generally located further anteriorly than on venter 8, because the eggs exit the gonoducts in front of venter 9. A position of the bases of

gonapophyses 8 on the hind part of venter 8, and of gonapophyses 9 on the frontal part of venter 9, is common in taxa with the gonopore located on the posterior part of venter 8, and is especially evident in taxa where these venters are fairly long (Odonata in Klass 2008, fig. 4). In addition, in many Insecta with well-developed ovipositors the left and right **gp9** are fused for some distance from their bases; examples are many Zygentoma and the odonatan *Epiophlebia* (survey in Klass 2008, p. 125). Both the far anterior location of fold **gp9** in the embiopterans and its continuation across the midline are thus in agreement with its interpretation as the gonapophyses 9.

In insects, a true sternite **ST9** should be located medially in front of the bases of gonapophyses **gp9**. Postlaterocoxites and antelaterocoxites (or a gonangulum) as well as anterior parts of the coxites **CX9** also lie anterior and lateral to the gonapophyseal bases. In some insects anterior portions of the coxites are detached from the main parts and fused medially (sclerite **Scs*** in Archaeognatha, Bitsch 1974; anterior intervalvula of Dictyoptera and Orthoptera, Klass 1998). Furthermore, the gonapophyses 9 themselves often bear a sclerotisation, **GP9**. Since in the embiopterans the areas anterior and lateral to fold **gp9** as well as the fold itself are completely membranous, the sternal, postlaterocoxal, antelaterocoxal, and gonapophyseal sclerotisations as well as the anteriormost parts of the coxal sclerotisations are probably all absent. There is also no trace of the olistheter (rhachis+aulax), which in the insect ground plan constitutes a sliding interlock between the gonapophyses 8 and 9 of one body side. All these are apomorphic reductions. A noteworthy exception might be the weak sclerite **GP9?** of *Aposthonia* (Figs. 26, 27) at the lateral ventral base of fold **gp9**. If this does not constitute a secondary formation, it could be a gonapophyseal (**GP9**), laterocoxal (**LC9**), or anterior coxal (**CX9**-part) sclerite. On the other hand, it might be a sclerite of venter 8, representing the posterior part of the strongly reduced **PL8** (which then would have been in a far posterior position prior to its reduction – even a bit further than in *Enveja*, Fig. 21; see the above section “Variation in Embioptera” concerning elements of venter 8). Finding a muscular connection of sclerite **GP9?** might allow a clearer interpretation.

The large ventral plate **CS9** of Embioptera thus likely only represents the larger posterior parts of the coxites of venter 9, which are fused along the midline (thus, the term ‘coxosternite’ is inaccurate; see the section on “Terminology of ventral sclerites”). The weaker midline sclerotisation of **CS9** in most embiopterans (often limited to the posterior part; Figs. 17, 21, 26) can be considered an incomplete fusion, and hence as plesiomorphic. The posterior parts of the coxal sclerotisations 9 in ovipositor-bearing Insecta are located on paired, posteriorly projecting coxal lobes (= gonoplace **gl9**).

Therefore, conditions in Embioptera in which the hind rim of **CS9** overlaps the area behind (**gl9** in Figs. 3, 10) can be tentatively interpreted as vestiges of the gonoplace, and thus as plesiomorphic. A bilobation of the hind margin of **CS9** (as in Fig. 3) also appears as plesiomorphic, reminiscent of the paired nature of the coxal lobes. This interpretation appears plausible for *Metoligotoma* with its fairly distinct overfolding and bilobation and its altogether plesiomorphic female genitalic region; but it may be less convincing for *Clothoda*, where this body region is generally more apomorphic and the overfolding and bilobation less distinct.

The area where in the embiopterans the ‘membranous field’ (**mf** in Figs. 3, 10, 17, 21, 26) is located is usually also membranous in ovipositor-bearing Insecta (anterior membrane between left and right coxites 9). In Insecta with a reduced ovipositor the same is true if the coxites 9 remain separated (e.g. Klass 2001, fig. 18 for a derived dermapteran), but not if a uniform ventral plate is formed. Embioptera are peculiar by the width and discreteness of their membranous field **mf**, which is evident despite the median fusion of the coxites. In this way, field **mf** appears not only as some membranous area, but as a particular structural component of the genitalic region, and thus perhaps as an embiopteran autapomorphy. *Stenoperla* species among the Plecoptera have a membranous field of somewhat similar appearance on venter 9 (Zwick 1980, fig. 58f); however, this bears the posteriorly shifted opening of the spermatheca, thus likely is a posterior part of venter 8 expanded into venter 9, and surely not homologous with field **mf** in Embioptera.

Variation in Embioptera

Some differences on venter 9 relate to the degree of sclerotisation of parts of coxosternite **CS9**. Only *Metoligotoma* (Fig. 3) shows **CS9** sclerotised uniformly throughout. In *Clothoda* (Fig. 10) only the sclerotisations surrounding the membranous field **mf** are weakened, but not those along the midline. In *Biguembia* (Fig. 17), *Enveja* (Fig. 21), and *Aposthonia* (Fig. 26) the posteromedian part of **CS9** is more weakly sclerotised. In *Aposthonia* the more anterior median parts of **CS9** are also weakened, so that a midline ribbon of weak sclerotisation almost divides **CS9** in two halves and functions as a midline hinge. However, all these differences are not very distinct. In addition, also in the taxa where a midline weakening of **CS9** is not evident in the form of a reduced degree of melanisation, **CS9** can be folded somewhat along the midline by experimental manipulation, at least in the posterior part, which is indicative of some midline weakness being present. We define characters for these differences (**Ch 12**, **Ch 13**), but advise caution in using them. A midline weakness along the entire **CS9** appears to be

plesiomorphic, as it reflects the separation between the two coxites.

In *Metoligotoma* (Figs. 3, 4) the hind margin of **CS9** narrowly overfolds the area behind it, and to a lesser extent this is also true for *Clothoda* (Figs. 10, 11). In *Biguembia* (Figs. 17, 18), *Enveja* (Figs. 21, 22), and *Aposthonia* (Figs. 26, 27) no such overfolding was found. Furthermore, in *Metoligotoma* (Fig. 3) the hind margin of **CS9** is somewhat bilobate. The weak median notch in the hind margin of **CS9** in *Clothoda* (Fig. 10) may be seen as a very slight indication of a bilobation. In *Biguembia* (Fig. 17), *Enveja* (Fig. 21), and *Aposthonia* (Fig. 26) the hind margin of **CS9** is straight. Both the overfolding (**Ch 15**) and the bilobation (**Ch 14**) reflect original conditions of the gonopods and are considered as plesiomorphic. Concerning *Clothoda*, however, this interpretation is very tentative for both characters.

All embiopterans studied here have a membranous field **mf** located in an anteromedian notch of sclerite **CS9** (Figs. 3, 4, 10, 11, 17, 18, 21, 22, 26, 27). Field **mf** shows some variation in shape: in *Metoligotoma* (Fig. 3), *Aposthonia* (Fig. 26), *Enveja* (Fig. 21), and *Biguembia* (Fig. 17) it is rectangular or trapezoidal (with a long posterior margin), whereas in *Clothoda* (Fig. 10) it is roughly triangular (pointed posteriorly). We formulate a character (**Ch 16**), but note that in *Clothoda* field **mf** is surrounded by weaker sclerotisation and thus indistinctly bordered, and if one regards the weaker sclerotisation as part of **mf**, this **mf** would be rectangular as in the other species. In *Aposthonia* (Figs. 26, 27, 29), *Enveja* (Figs. 21, 22, 25), and *Clothoda* (Figs. 10, 11, 16) field **mf** is at the same level as sclerite **CS9** behind it. In *Metoligotoma* (Figs. 3, 4, 9) and *Biguembia* (Figs. 17, 18, 20), however, the posterior part of field **mf** is sunken inward and thus overfolded by the parts of **CS9** behind it (**Ch 17**). *Enveja* has two additional elements on its field **mf** (Figs. 21, 22, 25): the small, weak sclerite **MF** (**Ch 18**) and the small pouch **mfi** (**Ch 19**); both are absent in the other four embiopterans. Since a discrete field **mf** likely is an autapomorphy of Embioptera, the polarity of the characters referring to it is unclear.

The transverse fold **gp9** in front of sclerite **CS9** is interpreted as the vestiges of gonapophyses 9. In *Metoligotoma* (Fig. 3) fold **gp9** is longer than in all other embiopterans studied here, and it is quite distinctly bilobate. In *Enveja* (Fig. 21), *Aposthonia* (Fig. 26), and *Clothoda* (Fig. 10) fold **gp9** also traverses the entire width of venter 9, but it is much shorter and not at all bilobate. In *Biguembia* (Fig. 18) fold **gp9** is similarly short, and it is interrupted around the midline (by field **mf**), thus actually paired. Here we only define a character that reflects the particularly strong development in *Metoligotoma* (**Ch 20**), which is considered as plesiomorphic. Only in *Metoligotoma* (Figs. 3, 9) there is an additional transverse fold **tf** anterior to **gp9**; a polarity is not assumed for this character (**Ch 21**).

Only *Aposthonia* (Figs. 26, 27) has a pair of small, weak sclerites **GP9?** in the basal ventral wall of fold **gp9** (**Ch 22**). Although their interpretation is ambiguous, these sclerites are in the right position to represent some plesiomorphic sclerotisation of venter 9 (see above); in this interpretation their presence would be plesiomorphic. However, if these sclerites proved to be fragments of sclerites **PL8** (see above), this character would have to be reformulated, and an especially strong posterior shift of these sclerotisations in *Aposthonia* would then represent an apomorphic condition. Due to this ambiguity we leave the polarity for **Ch 22** open.

Ectodermal genital invaginations

Comparison with other insects and interpretation

General pattern of ectodermal genital invaginations in female Insecta. According to Snodgrass (1933, 1935a), there is a general pattern with three median ectodermal invaginations developed at the posterior margins of venters 7 (prospective common oviduct), 8 (prospective spermatheca), and 9 (prospective accessory glands). All invaginations bear a cuticular intima. The common oviduct obtains an open connection with the mesodermal internal genitalia and becomes the primary outlet channel for the eggs. The adult spermatheca is an organ for sperm storage. The accessory glands add secretions to the eggs that serve various purposes. The structural pattern of these genital invaginations is of major importance to insect morphology and systematics.

Archaeognatha have a short ectodermal common oviduct that opens at the hind margin of venter 7; this is the definitive gonopore and is here called the primary oviducal opening. Otherwise, however, they have several spermathecal vesicles per side around midlength of venter 8, and a pair of non-invaginated glandular epidermal stripes on venter 9 (Bitsch 1974, **rs***, **glg*** in figs. 1, 2c,f; Klass 2008, section 6.3.2). The respective homology of these latter structures with the spermatheca and accessory glands in Dicondylia is unclear.

Like Archaeognatha, Zygentoma and a few subgroups of Pterygota (e.g. Dictyoptera, Ensifera; Klass 1998) have an ectodermal common oviduct that opens at the hind margin of venter 7 as the definitive gonopore (primary oviducal opening); however, there is a single median spermatheca. In most Pterygota the gonopore has been translocated to the hind part of venter 8 by the formation of an extended oviduct, which continues the common oviduct and extends through segment 8; its orifice is called a secondary oviducal opening and is located immediately in front of the spermathecal opening (the relevance of this to the structure of venter 8 was discussed above under “Comparison with other insects and interpretation” concerning elements of

venter 8). As a further evolutionary step the area containing the secondary oviducal and spermathecal openings can become invaginated to the anterior. This is the formation of a vagina, which eventually receives the spermatheca in its dorsal wall and the extended oviduct in its anterior or anteroventral wall; the gonopore then is the opening of the vagina and is called a vulva (Klass 2003, p. 211). Regarding the accessory glands of venter 9, there apparently are two different, non-homologous types in the dicondylarian insects (see below).

Extension of cuticle inside gonoducts. Insects show variation with regard to how far the cuticular intima extends internally along the gonoduct walls. The main point is whether or not the cuticle reaches beyond the fork of the common oviduct into the lateral oviducts, which is a major landmark. An example of an animal in which a considerable part of the lateral oviducts bears a cuticular intima is the ovoviviparous dermapteran *Hemimerus* (Klass 2001, fig. 6). The other end of the range is found in the archaeognathan *Trigoniophthalmus* (Bitsch 1974), in which only the extremely short common oviduct bears an intima. Details on conditions in other insect taxa are given in Klass (1998, 2003, 2008 for Dictyoptera, Dermaptera, Odonata) and Matsuda (1976 for a variety of insect taxa). In all the embiopterans studied here the circular line where the cuticle ends internally (**ec** in Figs. 4, 11, 18, 22, 27; as assessed from what has remained after clearing by KOH) is in the area external to the fork: in the cleared specimens we never found any trace of intima-bearing lateral oviducts.

Location of gonopore. All embiopterans studied here have the gonopore on the posterior part of venter 8 (while the ventral lip of the gonopore is probably 7th-segmental; see “Comparison with other insects and interpretation” concerning elements of venter 8). However, as in many insects, a closer definition of the location of the gonopore is problematic, and this becomes especially evident when different taxa are to be compared in this regard. In general, the location of the gonopore can be defined only by the location of its ventral lip, where the body wall is sharply bent from outside to inside the gonoducts (see bend at **vlg** in Figs. 20, 29), whereas at the dorsal rim of the gonopore the body walls in- and outside of the gonoducts may just form a smooth continuum without any demarcation (see Figs. 20, 29). Furthermore, it must be considered that the ventral lip of the gonopore possesses some (or even considerable) width, along which structural differentiations may occur, and that these differentiations may differ among related taxa. This can make exact determination of ‘gonopore location’ complicated and partly subjective, and it can be difficult to apply uniform criteria even to closely related taxa.

The ventral lip of the gonopore in Embioptera is located along the hind edge of the subgenital lobe **sgl** (this part being defined here as “**vlg**”), or perhaps along

the combined hind edges of **sgl** and the lobes **gp8** lateral to it. The choice is somewhat subjective, and it depends both on the extent of structural demarcation between the three lobes and on the presence of a fold **gpf** connecting the mesal bases of the **gp8** lobes. For instance, in *Clothoda* there is no fold **gpf**, and lobes **gp8** are not externally demarcated from lobe **sgl**, i.e. the hind edges of the lobes form a continuous line (Figs. 10, 34). Along this entire edge the cuticle bends inward into the walls of the gonoducts (compare Figs. 10, 11, 12, and 16). In contrast, in *Metoligotoma* the **gp8** lobes are transversely connected by a fold **gpf**, and there is a distinct structural demarcation between lobes **gp8** and **sgl** (Figs. 3, 30). While along the hind edge of **sgl** the cuticle bends inward into the walls of the gonoducts (compare Figs. 3, 4, 5, and 9), it bends into the prespermathecal chamber **psc** along the hind edges of the **gp8** lobes (and **gpf** fold; Figs. 5, 9). Thus, it would appear reasonable to equate the ventral lip of the gonopore with only the hind edge of the **sgl** lobe in *Metoligotoma*, but with the combined (and continuous) hind edges of **sgl** and **gp8** in *Clothoda*. Then, however, what is considered the ventral lip of the gonopore would not be homologous between the two taxa. Yet, in the following we consider the entire edge along which the cuticle bends into the ectodermal gonoducts as the ventral lip of the gonopore – either the edge of lobe **sgl** alone (*Metoligotoma*, *Enveja*) or the combined edges of lobes **sgl** and **gp8** (*Clothoda*, *Biguembia*, *Aposthonia*).

Another major issue regarding the location of the gonopore concerns its segmental assignment, as evident from discussions under “Comparison with other insects and interpretation” concerning elements of venter 8 and from Figs. 40–43. Ontogenetic studies indicate that in some Pterygota with an ‘8th-segmental gonopore’ the subgenital lobe (**sgl**) and its terminal edge (ventral lip of gonopore **vlg**; see Fig. 30) – i.e. the only useful landmark for gonopore location – indeed is a posterior formation of venter 7 (Fig. 42). Edge **vlg** in these taxa is likely homologous with the apical edge of a clearly 7th-segmental lobe in, e.g., Zygentoma (languette lobe); in this taxon the entire edges would constitute the ventral lip of the gonopore. From this one could legitimately conclude that in both groups of taxa the gonopore is in the same (7th-segmental) position. The only principal difference lies in the extension of the free edges **vlg** to the anterior: In Zygentoma they reach the hind part of venter 7, whereas in the Pterygota with an ‘8th-segmental gonopore’ they end at various longitudinal levels of venter 8 (due to the fusion of the former anterior parts of the edges to venter 8). In order to maintain the practical distinction between 7th- and 8th-segmental locations of the gonopore, the anterior extension of the edges **vlg** would thus appear as the most appropriate criterion.

Presence of a vagina. In insects one speaks of a vagina when a chamber immediately inside the functional gonopore bears the spermathecal opening on its roof (Snodgrass 1933, 1935a). Accordingly, a vagina is clearly present wherever the spermatheca joins the extended oviduct and external to this junction there still follows a chamber or tube of considerable length, and closed all around, before the gonopore (vulva) is reached. There are many insects that clearly fulfil this criterion. Examples are Mantophasmatodea (Klass et al. 2003, fig. 8), Notoptera (Walker 1943; Klass 2005, Fig. 9.3), many Plecoptera (Zwick 1980, fig. 58a, b), some basal Dermaptera (Klass 2003, figs. 10–16), and ovipositor-bearing Odonata (Klass 2008, figs. 7, 8, 30, 31, 34, 35). It is unclear whether a distinct vagina is a groundplan element of Pterygota (or of a clade Odonata + Neoptera): The lack of a vagina and even of an extended oviduct in Dictyoptera and Ensifera (Klass 1998) suggests frequent parallel evolution of a vagina. On the other hand, the similar structure of vaginae in Odonata and the mentioned Neoptera, as well as clear cases of secondary reduction (subgroups of Dermaptera, Klass 2003; and Plecoptera, Zwick 1980), make homology across Pterygota appear plausible.

In Embioptera things are less clear. With respect to the external border of the gonoducts, it is important to note that the ventral lip of the gonopore is curved to a varied extent, the median part reaching farthest posteriorly (except in *Aposthonia*; Fig. 26). Between the vertical levels marked by the posterior tip of the lobe **sgl** and the arrow on top in the mediosagittal sections (Figs. 9, 16, 20, 25, 29), the gonoduct is laterally open due to the curvature of the hind edge of **sgl** (or hind edges of **sgl** plus **gp8**); only in front of the arrow (to its left in the illustrations) there is a gonoduct closed all around. Only these parts could theoretically contribute to a vagina. Internally, the opening of the spermathecal duct into the gonoducts is the decisive landmark for the presence of a vagina. Therefore, among the Embioptera studied here a vagina is clearly absent in those taxa that have the spermathecal opening posterior to (i.e. to the right of) the vertical level indicated by the arrow: *Metoligotoma* (Fig. 9; but see the above description of this species for movements), *Biquembia* (Fig. 20), and *Enveja* (Fig. 25). Only in *Clothoda* (Fig. 16) and *Aposthonia* (Fig. 29) there is a gonoduct portion, closed all around, external to the area where the spermathecal duct joins the extended oviduct. However, in both taxa this portion is very short, and also very wide. The formal criterion for a ‘vagina’ thus is fulfilled (as in the case of *Metoligotoma* with fold **gpf** withdrawn inward). Nonetheless, this is not a discrete chamber or tube as in the other pterygotan taxa mentioned above, and one would hesitate to apply the term ‘vagina’.

Mukerji (1927) claimed a vagina to be present in *Embia minor*. However, the term was not used in the sense of Snodgrass. Mukerji (1927) claimed the ‘vagina’ to begin in the area where the paired lateral oviducts unite into a median channel. This also includes the intima-bearing gonoduct portions here called the common oviduct (**oc**) and extended oviduct (**oe**). It is difficult to judge from Mukerji’s (1927) data and fig. 8B whether there is a closed ectodermal gonoduct portion distal to where the spermatheca joins the extended oviduct, hence whether or not a vagina in the sense of Snodgrass is present.

The preceding discussions on the vagina are based on the idea that the spermathecal opening is retained in the position in which it has formed ontogenetically, i.e. on the hind margin of venter 8. This requires first the formation of an extended oviduct to bring the opening of the ectodermal gonoducts into close proximity with the spermathecal opening. Only after that can an invagination of the hind part of venter 8 (which bears both openings) lead to the formation of a vagina, i.e. a terminal part of the gonoduct that bears the spermathecal opening on its roof. On the other hand, perhaps something resembling a vagina can also originate by the formation of an extended oviduct alone – if the spermathecal opening is located, or shifts, further anteriorly on venter 8. This is indicated by conditions in Archaeognatha: The ventral closure of the ‘fente génitale’ (see above) would yield an extended oviduct (as in Fig. 41). By the same process, however, the vesicles for sperm storage, located at midlength of venter 8, would come to lie in the walls of this extended oviduct. On this basis, Bitsch (1974) interpreted the (hypothetical) closure of the archaeognathan ‘fente génitale’ as the formation of a vagina (while, as mentioned above, the homology of the archaeognathan vesicles with the dicondylarian spermatheca is conjectural). We would advocate to interpret the result of such a development as an extended oviduct, perhaps additionally specified as a ‘pseudovagina’. In morphological practice, however, it will often be difficult to distinguish this case from a true vagina.

Accessory glands. Accessory glands that open on venter 9 are a basic feature of the female genitalia in Dicondylia. However, there seem to be two different types of such glands (Klass 2003, p. 215; Klass 2008, section 6.3.2): paired ones with a somewhat more anterior location, and unpaired median ones with a more posterior location. The former occur, at least, in Zygentoma-Lepismatidae (Rousset 1973) and in ovipositor-bearing Odonata (Asahina 1954; Klass 2008, figs. 3, 7). The latter are found in Zygentoma-Nicoletiidae (Rousset 1973) and many Neoptera, such as Dictyoptera (Klass 1998), basal Dermaptera (Klass 2003), and Notoptera (Walker 1943). Homology relations between the two types of glands appear unlikely,

especially due to the possible co-occurrence of both in Cicadomorpha. The paired glands might be derived from the glandular stripes found in Archaeognatha (Klass 2008, section 6.3.2). In some other groups of Pterygota both types of glands are missing, e.g. in most Orthoptera (Beier 1972), Mantophasmatodea (Klass et al. 2003), and higher Dermaptera (Klass 2003).

The accessory glands of insects are usually very large and conspicuous, as seen in macerated preparations viewed internally. In basal Dermaptera, for instance, they consist of a wide outlet duct (which can be expanded into a sac-like reservoir) that more internally branches into a number of tubes (Klass 2003, figs. 19, 24, 28, 43). Nonetheless, accessory glands can become reduced to small, internally unbranched invaginations (such as in *Diplatys* among basal Dermaptera; Klass 2003, **ag*** in fig. 38); it is unknown whether such vestiges still have a (considerable) glandular function, or may serve for other purposes.

Ross (2000, figs. 37, 38) indicated that in *Oligotoma* and *Metoligotoma* there is a median opening of accessory glands on the anterior part of venter 9 (on the anterior part of the membranous field **mf**; compare Figs. 3, 4). In our study of Embioptera, which in contrast to Ross' study also included an internal view of the exoskeleton, we did not find any conspicuous accessory gland opening on venter 9, and there clearly is no opening or internal invagination on or around field **mf** in *Metoligotoma* or *Aposthonia* (a close relative of *Oligotoma*; see "Comparison with earlier descriptions" above).

However, there are two small median invaginations on venter 9 that might represent strongly reduced accessory glands (though with low probability). One is pouch **mfi** on field **mf** in *Enveja* (Figs. 22, 25), the other is the invagination **yy** behind the posterior rim of coxosternum **CS9**, which occurs in all Embioptera examined here. Both structures are candidates, because accessory glands usually develop on the posterior rim of venter 9 (the location of **yy**) but at a later stage can shift further anteriorly (the location of **mfi**). Considering their simple structure, neither pouch **mfi** nor invagination **yy** appear to have a glandular function, but this must be examined further by serial sectioning in adequately preserved specimens. Pouch **mfi** is unique to *Enveja*, and comparison with other insects does not provide indications as to its nature or evolutionary origin. Invagination **yy**, however, is in the same place as a tendon in Odonata, which bears the posterior insertions of a pair of muscles from venter 9 (Klass 2008, tendon **rt*** and muscle **66*** in figs. 15, 62). These structures in Embioptera thus are more plausibly interpreted as tendons than as vestiges of accessory glands. This will have to be tested by a study of the postabdominal musculature in embiopterans.

Variation in Embioptera

Clothoda and *Aposthonia* have a very short terminal part of the gonoducts that formally fulfils the criterion for a 'vagina', whereas *Biguembia* and *Enveja* do not. Nevertheless, we did not define a character for this trait, because it depends on minor shifts in the proportions of the gonoducts (or the entire ectodermal genital invaginations), and parts of such shifts could be due to movements within a specimen (as clearly indicated by the situation in the two specimens of *Metoligotoma*).

Some embiopterans have a special cavity around the external opening of the spermatheca, the prespermathecal chamber **psc**. In *Metoligotoma* (Figs. 4, 5, 9) this is only invaginated anteriorly, whereas in *Aposthonia* (Figs. 27–29) there is an additional invagination to the posterior. The anteriorly invaginated part is correlated with the presence of a transverse fold **gpf** between the gonapophyses **gp8** (i.e. this part of **psc** is simply the space above fold **gpf**; see "Variation in Embioptera" concerning elements of venter 8), and thus is covered by character **Ch 09**. In theory, this anterior part of chamber **psc** is also present in *Enveja*, which likewise has a fold **gpf** (Figs. 24, 25), but the chamber is not discrete because there is no differentiation of a spermathecal duct and thus no internal border (the most external part of cavity **sp** in Fig. 25 can be considered as representing chamber **psc**). On the other hand, the posterior part of chamber **psc** in *Aposthonia* (Fig. 29) is an independent structure, for which we formulate a separate character (**Ch 23**); we consider presence of that structure as apomorphic, since apparently no similar feature has been described for any other insect. Along the entire **psc** walls in *Aposthonia* the cuticle is fairly thick and stiff, and this might provide physical support for the very delicate spermathecal bulb **spb** (Fig. 29). *Biguembia* (Fig. 20) and *Clothoda* (Fig. 16) clearly lack a prespermathecal chamber. While in the sagittal section for *Clothoda* (Fig. 16) the widened most external portion of the spermathecal duct may appear to resemble a prespermathecal chamber (see Fig. 29), it should be noted that the respective folds in Fig. 16 are not transverse folds (like **gpf** in Fig. 29) but folds embracing the spermathecal duct or its opening.

As mentioned above, *Enveja* (Figs. 22, 25) differs from the other four embiopterans in the lack of a clearly defined, narrow spermathecal duct (compare duct **spd** in Figs. 9, 16, 20, and 29; **Ch 24**). Among the other taxa, *Aposthonia* (Figs. 28, 29) is peculiar by its extremely short spermathecal duct, whereas duct **spd** is much longer in *Metoligotoma* (Figs. 7–9), *Clothoda* (Figs. 15, 16), and *Biguembia* (Fig. 20) (**Ch 25**). We consider the absence of a duct and, in case of its presence, a very short condition as apomorphies, since in other Pterygota and Zygentoma there is usually a relatively long spermathecal duct. However, this polarity assumption is tentative.

The shape of the spermathecal bulb **spb** varies considerably. Still, in *Metoligotoma* (Figs. 6–9), *Biguembia* (Figs. 18, 20), and *Aposthonia* (Figs. 27, 29) it is somewhat irregularly globular or oval, and undivided, whereas only in *Clothoda* it is deeply divided in two symmetrical lobes (Figs. 13, 15). In *Enveja* the innermost part of the spermathecal invagination (**sp** in Fig. 25) can be considered as homologous with bulb **spb** in the other species, and this part is not at all bilobed. Thus, the character we define for the shape of the spermathecal bulb (**Ch 26**) is applicable to all five species. We leave character polarity open, because spermathecal shape in insects varies a lot on a low systematic level, and undivided and symmetrically divided conditions of the innermost parts of the spermathecae co-occur in several pterygotan orders (Klass 2003, p. 214).

Further differences relate to special formations in the dorsal wall of the extended oviduct **oe**. *Metoligotoma* and *Enveja* have a pair of flat, anteriorly directed invaginations consisting of normal membranous cuticle (lateral parts of fold **do**, labeled **do** in Figs. 4, 5, 9, and 22–25); they may be connected across the midline by a lower infolding (median part of fold **do**; Figs. 4, 22), or they may not (Fig. 23; intraspecific variation in *Enveja*, though perhaps only reflecting movements). The lateral parts of **do** likely are tendons for muscle attachment – perhaps for muscles to the anterior margin of coxosternite 7, as they are known for, e.g., Dermaptera (Klass 2003, 3* in fig. 22). *Clothoda*, *Biguembia*, and *Aposthonia* lack such tendons (Figs. 11, 18, 27). We leave the polarity of the character (**Ch 27**) open, because there are only scattered data for other insects. The expansion of the dorsal wall of the extended oviduct in *Biguembia* (**sbo** in Figs. 18, 20) is of a very different kind: The enormously thickened, spongy cuticle might indicate a glandular function. This structure is unique for *Biguembia* (**Ch 28**). Since nothing comparable appears to have been described from other insect taxa, we suggest the absence of **sbo** to be plesiomorphic.

Elements of the postgenital abdomen

Comparison with other insects and interpretation

The exoskeletal structure of the postgenital abdomen in female Embioptera (Figs. 3, 4, 10, 11) complies with that in many other lower Neoptera. This includes the condition and location of tergite **TG10**, of the supraanal lobe **spl** and its sclerite, tergite **TG11** (epiproct), of the subanal lobes **sbl** and their sclerites, the paraprocts **PP**, of the bases of the cerci **ce** and associated small sclerites, and of the rectum and anus.

The interpretation of lobes **sbl** and paraprocts **PP**, of lobe **spl** and epiproct **TG11**, and of sclerites around the cercal base (like **CB** and **CD** in Embioptera; Fig. 11) was discussed in Klass (2001, 2008) for a variety of insect

taxa. For lobes **sbl** and sclerites **PP** the evidence is highly conflicting; their interpretation as coxal lobes and coxites of segment 10 appears likely, but 11th-segmental components may be included in addition. Tergite 11 has undergone a fragmentation at the base of Pterygota that continued at the base of Neoptera. The epiproct is the median part of tergite 11 (this also applies to the epiproct of Embioptera; **TG11** in Figs. 3, 4, 10, 11), while several sclerites at the dorsal and lateral base of the cerci represent its lateral parts.

Sclerite **CD** of Embioptera is most likely such a lateral sclerite derived from tergite 11, corresponding to similar sclerites in, e.g., the caeliferan *Dissosteira* (Klass 2001, **a*** in figs. 31, 35) and the blattodean *Eurycotis* (Klass 1997, **Cc*** in fig. 58). Sclerite **CB** of Embioptera may be another, further lateral 11th-tergal sclerite perhaps homologous with sclerites in the ephemeropteran *Povilla* (Klass 2001, **cb*** in figs. 30, 34) and various Ensifera (Klass 2001, p. 290). Alternatively, **CB** could be interpreted as the homologue of the lateral plates **LP*** of Dermaptera (Klass 2001, figs. 21–24) – although size ratios are very different – and then perhaps represent laterocoxites of segment 10 (sclerotisations that are included in the paraprocts in at least some other Neoptera). The interpretation of sclerites **CB** is important with regard to the articulations between **CB** and the cercal base in some Embioptera (arrow in fig. 3), and to related character polarities. While data on cercal articulations are sparse in the literature, in at least some zygentomans, ephemeropterans, and dermapterans articulations occur between the cercal base and lateral parts of the paraprocts (or sclerites like **LP***; Klass 2001, figs. 23, 25, 29; Klass 2003, p. 180), whereas articulations between the cercal base and lateral 11th-tergal sclerites are apparently unknown. Thus, articulations in Embioptera would likely be plesiomorphic based on the former interpretation, but apomorphic based on the latter. This issue remains unclear, however, because the exact homologies of sclerites **CD** and especially of **CB** in Embioptera can only be ascertained based on muscle data. Without such data, yet another alternative must be kept in mind, namely that sclerites **CB** (and perhaps **CD**) could be vestiges of basal cercomeres.

Variation in Embioptera

The invagination **yy** behind sclerite **CS9** (discussed above under “Comparison with other insects and interpretation” concerning ectodermal genital invaginations) shows some variation in size and shape (Figs. 4, 11, 18, 22, 27). The only noteworthy condition, however, is the strong elongation and internal widening of **yy** in *Clothoda*, and we define a character on this basis (**Ch 29**). Tendon **rt*** in the Odonata studied by Klass (2008, fig. 15) is long as in *Clothoda*, but as this apparently is the only other case of such a tendon being reported among insects, we leave character polarity open.

Most striking is the presence or absence of a sclerite **CD** between the dorsal base of the cercus and the margin of tergite 10. **CD** was found in *Clothoda* (Fig. 11) and *Aposthonia* but not in *Metoligotoma* (Fig. 4), *Biguembia*, and *Enveja*. However, as the sclerite is generally quite weak, and may be difficult to recognise in some taxa where it is particularly weak though present, this character (**Ch 30**) should be used with caution. We consider presence of sclerite **CD** as plesiomorphic, but note that this depends on the correctness of the interpretation of **CD** as a lateral 11th-tergal sclerite.

A sclerite **CB** between the ventral base of the cercus and the margin of the paraproct was found in all embiopterans. However, a discrete articulation between that sclerite and the cercal base was only found in *Metoligotoma* (arrow in Fig. 3), *Enveja*, and *Aposthonia*; it consists of a tongue- or knob-like basal extension of the cercal sclerotisation that approaches the margin of sclerite **CB**. *Clothoda* (Fig. 10) and *Biguembia* lack the articulation, i.e. the opposed sclerite margins are both straight. In the character we defined (**Ch 31**) we leave the polarity open due to the unresolved interpretation of sclerite **CB**. In *Biguembia* sclerite **CB** is particularly closely hinged to the sclerite margin of the cercus as compared to the other embiopterans, but this character is difficult to use, because the differences are not very conspicuous.

There are also differences in the closeness of the association between the epiproct **TG11** and the median hind margin of tergite **TG10**, and the sclerites may even

appear as fused (in *Biguembia*). However, also in this character caution is advisable, due to the weak condition and indistinct borders of **TG11** which makes the character very difficult to assess.

The closeness of the association between the hind margin of coxosternite **CS9** and the anterior margins of the paraprocts **PP** may be a useful character in the way that the very close, hinge-like association in *Biguembia* is striking within our embiopteran sample (**Ch 32**). We tentatively suggest the close hinge to be apomorphic, as such a condition apparently is unreported from other insects (though it may have been overlooked). In addition, such a close hinge can hardly be present in cases where the hind margin of **CS9** overfolds the area behind it and, thus, vestigial gonopods **gl9** are present. Since the latter condition is plesiomorphic and probably has been retained in *Metoligotoma* and perhaps *Clothoda* (see **Ch 15**), the above polarity assumption may appear supported.

List of characters

Here we formulate characters from the female abdomen that appear useful for phylogenetic (and taxonomic) work in Embioptera. The list results from the considerations in the preceding discussion sections.

(Ch 01) Subdivision of laterotergites LT6 and LT7: [0] undivided; [1] divided into anterior and posterior sclerite.

Table 2. Character state matrix for characters of the female postabdomen in the five embiopteran species studied.

Character	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16
Proposed plesiomorphic state	?	?	?	0	0	?	?	0	?	?	?	0	0	0	0	?
<i>Metoligotoma ingens</i>	1	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0
<i>Clothoda nobilis</i>	0	0	0	1	1	1	1	1	0	–	1	1	1	1	0	1
<i>Biguembia multivenosa</i>	1	1	1	1	1	1	0	1	0	–	0	0	1	2	1	0
<i>Enveja bequaerti</i>	1	1	1	1	1	0	0	1	1	1	0	0	1	2	1	0
<i>Aposthonia thoracica</i>	1	0	0	1	1	0	1	1	1	0	1	0	0	2	1	0
Character	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Proposed plesiomorphic state	?	?	?	0	?	?	?	0	0	?	?	0	?	0	?	0
<i>Metoligotoma ingens</i>	1	0	0	0	1	1	0	0	0	1	1	0	0	1	1	0
<i>Clothoda nobilis</i>	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
<i>Biguembia multivenosa</i>	1	0	0	1	0	1	0	0	0	1	0	1	0	1	0	1
<i>Enveja bequaerti</i>	0	1	1	1	0	1	0	1	–	1	1	0	0	1	1	0
<i>Aposthonia thoracica</i>	0	0	0	1	0	0	1	0	1	1	0	0	0	0	1	0

For reasoning behind the tentative proposal of plesiomorphic character states, see the Discussion chapter in the text.

“–” = not applicable.

(Ch 02) Subdivision of laterotergites LT8: [0] undivided; [1] divided into anterior and posterior sclerite.

(Ch 03) Condition of pleurites PL8: [0] reduced (small and weak), or absent, or perhaps fused to coxosternite CS8; [1] large and discrete.

(Ch 04) Discreteness of gonapophyseal sclerotisation GP8 from other sclerotisations of venter 8: [0] GP8 as a pair of separate sclerites; [1] GP8 not separated from other sclerotisations of venter 8 (included in CS8).

(Ch 05) Separation of lateral sclerites CX8? and median sclerite ST8? on venter 8: [0] CX8? and ST8? separated by membrane; [1] sclerotisations of CX8? and ST8? combined in a single plate CS8. (ST8? is either a true sternite 8, ST8, or, more likely, a languette sclerite, LG7.)

(Ch 06) Discreteness of laterocoxites LC8 from CS8 or CX8?: [0] LC8 not at all discrete (it is unclear whether the sclerotisation of LC8 is absent or included in CS8), or LC8 not fully discrete (connected with CS8 by a ribbon of weaker sclerotisation); [1] LC8 separated from CS8 by membrane.

(Ch 07) Presence of delimitation of lateral parts of lobes gp8 from median lobe sgl (mesal parts gp8i of gp8 not considered here): [0] delimitation present: the hind edge of lobe sgl has a lateral end; [1] delimitation absent: the edge behind CS8 is fully continuous from left to right.

(Ch 08) Distinctness of lobes gp8 (gonapophyses 8): [0] elongate, thus very distinct; [1] short and wide, thus quite indistinct.

(Ch 09) Presence of a fold gpf transversely connecting the left and right lobes gp8 (i.e. the mesal portions gp8i of these): [0] absent; [1] present.

(Ch 10) Presence of a distinct lobe gpl formed by median part of transverse fold gpf: [0] absent; [1] present. Character not applicable to taxa that lack a fold gpf (see Ch 09).

(Ch 11) Delimitation of mesal (internalised) portions of lobes gp8 (gp8i) as individualised lobes from the lateral (external) portions: [0] delimitation absent: gp8i included in gp8 without delimitation; [1] delimitation present: gp8i forming separate lobes.

(Ch 12) Degree of sclerotisation of posteromedian parts of CS9: [0] weaker than other parts of CS9; [1] same as other parts of CS9.

(Ch 13) Degree of sclerotisation of anteromedian parts of CS9 (immediately behind field mf): [0] weaker than other parts of CS9; [1] same as other parts of CS9.

(Ch 14) Shape of hind margin of CS9: [0] distinctly bilobate; [1] slightly bilobate; [2] straight.

(Ch 15) Overfolding of anterior part of venter 10 by posterior rim of venter 9: [0] present (vestiges of gonoplares?); [1] absent.

(Ch 16) Shape of membranous field mf: [0] roughly rectangular or trapezoidal, i.e. with a long posterior margin; [1] roughly triangular, i.e. pointed posteriorly (but additionally surrounded by a rectangular weaker sclerotisation of CS9).

(Ch 17) Immersion of posterior part of membranous field mf: [0] absent, the entire mf at the same level as the surrounding parts of sclerite CS9; [1] present, posterior parts of mf overfolded by surrounding parts of CS9.

(Ch 18) Presence of sclerite MF on membranous field mf: [0] absent; [1] present.

(Ch 19) Presence of a transverse infolding mfi on membranous field mf: [0] absent; [1] present.

(Ch 20) Distinctness of transverse fold gp9 (gonapophyses 9): [0] very distinct and prominent, fold of considerable length; [1] less distinct, fold very short or virtually absent.

(Ch 21) Presence of transverse fold tf anterior to fold gp9: [0] absent; [1] present.

(Ch 22) Presence of sclerites GP9? in lateral ventral wall of fold gp9: [0] present; [1] absent. (The definition and polarity of this character depend on the ambiguous interpretation of GP9?.)

(Ch 23) Presence of a posterior part of a prespermathecal chamber psc: [0] absent; [1] present.

(Ch 24) Distinctness of spermathecal duct: [0] spermathecal duct distinct; [1] no spermathecal duct differentiated in spermathecal invagination.

(Ch 25) Length of spermathecal duct: [0] spermathecal duct long; [1] spermathecal duct very short. Character not applicable to taxa in which a spermathecal duct is not differentiated (see Ch 24).

(Ch 26) Shape of spermathecal bulb spb: [0] deeply divided in two symmetrical lobes; [1] no indication of a division in two lobes.

(Ch 27) Presence of anteriorly directed lateral parts of fold do in dorsal wall of extended oviduct (consisting of normal cuticle): [0] absent; [1] present (either the lateral parts form a pair of isolated invaginations, or there is also a median part of fold do that transversely connects the lateral parts).

(Ch 28) Presence of bulged cuticular body sbo in dorsal wall of extended oviduct (consisting of very thick, spongy cuticle): [0] absent; [1] present.

(Ch 29) Shape of cuticular invagination yy: [0] not or hardly longer than wide; [1] much longer than wide.

(Ch 30) Presence of sclerite CD dorsal to base of cercus: [0] present; [1] absent.

(Ch 31) Presence of a distinct articulation between sclerite CB and ventral base of cercus, consisting of a tongue- or knob-like basal extension of the cercal sclerotisation: [0] absent; [1] present.

(Ch 32) Presence of a very close, hinge-like contact between coxosternite CS9 and paraprocts PP: [0] absent; [1] present.

Phylogenetic implications and conclusions

The purpose of this contribution was to describe the external and internal structure of the female postabdominal exoskeleton in a few phylogenetically distant Embioptera, to discuss the interpretation and homology of the structural components in a wider context of Insecta, and to discuss differences between the sampled embiopteran species. This and the compiled list of characters and character matrix should provide a sound basis and guideline for forthcoming phylogenetic studies in Embioptera using larger taxon samples, and for including female genitalic features in descriptions of embiopteran taxa; furthermore, it should also improve the database for phylogenetic work on neopteran relationships.

Summary of female abdominal morphology of Embioptera

In the pregenital abdomen, the embiopterans are peculiar by the delimitation of laterocoxites **LC** from the coxosternite – a feature that among insects is otherwise known only from some Archaeognatha. The pleurites **PL** and laterotergites **LT** regularly present in embiopterans, flanking the coxosternite **CS**, cannot be homologised with sclerites in other Insecta at this time; while the spiracles suggest a general interpretation of **LT** and perhaps also **PL** as epipleural sclerites, muscle data are required for further evidence.

In the female genitalic region of Embioptera, venter 8 shows a wide range of variation, whereas venter 9 is relatively uniform. One major issue of variation is the degree of reduction of the elements of the ovipositor: gonapophyses **gp8** (including their sclerites) and **gp9**, and gonoplace **gl9**. These elements are strongly reduced in all Embioptera, but by far most well-developed in *Metoligotoma*. Other characters of venter 8 concern the separation of median and lateral sclerites, **ST8?** and **CX8?**, and the presence of discrete laterocoxites **LC** and pleurites **PL**. It is difficult to give a uniform definition of the gonopore valid for all embiopterans (a problem applying to many insects). The gonopore is consistently located on the hind part of venter 8. However, the median part of venter 8, including the subgenital lobe and ventral lip of the gonopore, likely is formed by a posterior extension of segment 7 (homologous to the ‘languette’ lobe in *Zygentoma*). If this is true, the median sclerotisation of venter 8 should be called **LG7** rather than **ST8**; the genital opening could then be considered as still 7th-segmental, but probably is preferably defined as 8th-segmental based on the limited anterior extension of edges **vlg**. The same may be true for several (or all) other pterygotan taxa with an 8th-segmental gonopore. On venter 9 all Embioptera

have an undivided sclerite plate **CS9**, which likely consists only of medially fused coxal sclerotisations. In contrast to venter 8, pleurites and laterotergites are consistently absent. The membranous field **mf** located in an anterior notch of **CS9** appears as a particular structural element of Embioptera.

Besides venter 8, the ectodermal genital invaginations are another area in which Embioptera show much structural diversity. Differences concern the presence of special structures in the dorsal wall of the extended oviduct (dorsal fold **do**, or only its lateral parts; spongiose cuticular body **sbo**), in the shape of the spermathecal bulb **spb** and differentiation of a spermathecal duct **spd**, and in the formation of a prespermathecal chamber **psc**. The presence or absence of a fold **gpf** that transversely connects the bases of the two gonapophyses **gp8**, and the segregation of the mesal parts **gp8i** of the **gp8** as individualised lobes also strongly effect the design of the terminal part of the ectodermal gonoducts. A true vagina (in the sense of a discrete chamber or tube bearing the spermatheca) is absent in all Embioptera studied here. Webspinners also lack 9th-segmental accessory glands that are large and could have a considerable glandular function; yet, the infolding **mfi** on venter 9 of *Enveja* might be a vestige.

The postgenital abdomen resembles that in many other lower Neoptera. Small sclerites **CD** and **CB** at the dorsal and ventral bases of the cercus are likely lateral fragments of tergite 11 (the epiproct **TG11** being the median main part), but especially for **CB** alternative interpretations seem plausible.

For a more comprehensive understanding of the embiopteran postabdomen, data on the musculature and on the ontogenetic development (especially of the ectodermal genital invaginations) are urgently needed.

Implications on embiopteran phylogeny

Since only five embiopteran species were sampled for this basic study, a cladistic analysis of the character matrix in Table 2 would appear premature. However, some preliminary implications from these data on the phylogeny of Embioptera should be mentioned.

For 19 of the 32 characters included in Table 2, we did not propose a character polarity. This is for two reasons: First, because the phylogenetic relationships among the 11 principal lineages of Neoptera are unresolved, the choice of outgroup taxa for Embioptera is problematic. Considering all other neopteran lineages would be a daunting task, and there would be considerable ambiguity in the polarity of many characters. Second, many of the character-bearing structures of Embioptera either do not occur in other Neoptera, or topographic homologies are unclear. In the following we only consider those 13 characters with a well-supported

statement of polarity. Of these, 9 are phylogenetically informative in our sample.

(1) Characters 04, 05, 08, 14 (states 1 and 2 versus 0), and 20 support a clade *Clothoda* + *Biguembia* + *Enveja* + *Aposthonia*, i.e. suggest *Metoligotoma* as the sister group of the remaining Embioptera: the fusion of lateral sclerites **CX8?** and median sclerite **ST8?** on venter 8, the additional fusion of the gonapophyseal sclerotisations **GP8** with this compound sclerite, the short and wide (i.e. reduced) condition of gonapophyses **gp8**, the reduction of the bilobation of the hind margin of coxosternite **CS9**, and the short, reduced condition of gonapophyses **gp9**.

(2) Character 13 supports a clade *Metoligotoma* + *Clothoda* + *Biguembia* + *Enveja*, i.e. *Aposthonia* as sister to the remaining Embioptera: the absence of a midline weakness in the anterior part of coxosternite **CS9**. Character 22, i.e. the absence of sclerites **GP9?** in the lateral ventral wall of fold **gp9**, supports the same relationship if the **GP9?** are actually 9th-segmental sclerites rather than fragments of **PL8**.

(3) Characters 14 (state 2 versus 0 and 1) and 15 support a clade *Biguembia* + *Enveja* + *Aposthonia*: the complete loss of the bilobation of the hind margin of coxosternite **CS9**, and the lack of an overfolding of the anterior part of venter 10 by the posterior rim of venter 9 (i.e. lack of gonoplac vestiges). However, neither of these characters appears very meaningful.

(4) Character 30 supports a clade *Metoligotoma* + *Biguembia* + *Enveja*: the absence of sclerite **CD** dorsal to the base of the cercus.

(5) Character 12 supports a clade *Clothoda* + *Metoligotoma*: the absence of a midline weakness in the posterior (and anterior) part of coxosternite **CS9** – surely not a very striking character.

Regarding the female genitalia, *Metoligotoma* is clearly closest to what can be considered as plesiomorphic for Embioptera, and this concerns mainly the elements of the ovipositor: The gonapophyses **gp8** are the best-developed ones among the Embioptera studied here; they show a much more elongate shape than in other embiopterans, and a particularly strong demarcation from the subgenital lobe **sgl**; also their sclerotisations **GP8** are discrete from other sclerites of venter 8. Similarly, both the vestigial gonapophyses **gp9** and gonoplacs **gl9** are the longest among the embiopterans, and the ones with the most distinct distal bilobation. All these conditions correspond with those in insect taxa that possess a complete ovipositor. Furthermore, the clear separation between sclerites **CX8?** and **ST8?** on venter 8 also appears as plesiomorphic if either the interpretation of **ST8?** as a sclerite of the 7th-segmental languette lobe (**LG7**), or that of **ST8?** as representing sternite 8 is correct. All this would suggest that *Metoligotoma* is the sister taxon of a clade comprising all other embiopteran species studied here.

This scenario must compete with the usually advocated hypothesis that Clothodidae (including *Clothoda*) is the sister group of all other Embioptera. While in our study we found no support for such a relationship, that basal dichotomy was presumed in Szumik's (1996; morphology only) and Szumik et al.'s (2008; morphology and molecules) cladistic analyses of Embioptera. It was based on the weak degree of asymmetry in the male terminalia and on plesiomorphic conditions in some wing, thorax, and head characters of Clothodidae (while no particular characters are named in either of the two contributions). Thus, regarding the basal dichotomy in Embioptera there is clearly a conflict between different character systems.

Szumik et al. (2008, p. 996) support a (probably misunderstood) statement by Ross (2000) that the seemingly plesiomorphic condition of the female genitalia in *Metoligotoma* (and the closely related *Austrolembia*) is actually apomorphic and due to neoteny – correlated with neotenic trends in male austrolembiids. While one could imagine that a character reversal has taken place in this taxon (this seems to be the actual meaning of the statement in Ross 2000, p. 39), this hypothesis of neoteny would require that in other Embioptera the female genitalia are more strongly differentiated and ovipositor-like in the nymphs than in the adults, and that these structures undergo regressive development during the last ontogenetic stage. To our knowledge, nothing like this has been shown in Embioptera (a group in which hardly anything is known about nymphal genitalic morphology). Considering the increasing differentiation of female genitalia during nymphal development in other insects, such a course of development would appear highly unlikely.

In the molecular-based phylogeny reconstruction in Terry and Whiting (2005), Bayesian analyses yielded the sampled clothodid as the sister group of the remaining Embioptera, but analyses using parsimony or direct optimisation did not. Consequently, a basal position of *Metoligotoma* (or Austrolembiidae altogether) appears as a plausible alternative to a basal position of Clothodidae. However, one should also note that a reduction of the ovipositor has occurred frequently in Pterygota, and this might also be the case within Embioptera with their limited functional requirements for egg deposition. Thus, the characters of this compound structure might not be very meaningful.

Phylogenetic aspects at the superordinal level

Discussing phylogenetic relationships in Pterygota would require a much wider scope than intended for this paper. Nevertheless, two general aspects should be mentioned here.

In phylogenetic work on the basal levels of the insect tree, characters are sometimes used that in a very general way refer to a reduction of the ovipositor (Beutel and Gorb 2006, character 72 state [2]; Wheeler et al. 2001, character 47 state [2] “vestigial”). This is inadequate, first because characters should refer to particular structural elements, in this case the individual valve pairs. Second, it is important that the structural pattern of the female genitalic segments is often very different in taxa with a strongly reduced ovipositor. This is evident, for instance, from a comparison of the female genitalic venters in derived Dermaptera (Klass 2001, figs. 17–20) and Embioptera (present paper). These differ, for example, with regard to the location of the gonopore, the median fusion of the coxal sclerotisations, and the discreteness of the laterocoxites, and also concerning the shape, position, median fusion, and extent of retention of the vestiges of gonapophyses and gonoplags. Such very different reductive structural patterns also indicate that the general reduction of female genitalia has occurred independently (as is demonstrated also by the well-developed ovipositor in many basal Dermaptera; Klass 2003). Evidently, too simplistic coding of characters leads to the inclusion of potentially misleading information in cladistic analyses. Of course, for a refined coding more refined morphological data than presently available are needed for many taxa.

The interpretation of the median part of venter 8 in taxa with an 8th-segmental gonopore (Figs. 40–43) is of major importance for phylogeny reconstruction in Pterygota. As explained in the respective discussion sections entitled “Comparison with other insects and interpretation” concerning elements of venter 8 and concerning ectodermal genital invaginations, a 7th-segmental gonopore (primary oviducal opening) combined with a languette lobe projecting from the hind part of venter 7 is found in Archaeognatha, Zygentoma, Dictyoptera, and Ensifera. On the other hand, an 8th-segmental gonopore (secondary oviducal opening or, due to further modification, vulva) without an evident languette lobe is found in Odonata and many Neoptera. Either condition would appear as homologous among the taxa listed, but as the relationships are likely Archaeognatha + (Zygentoma + (Odonata + (Dictyoptera, Ensifera, and other neopteran taxa))), only one of the two conditions can be homologous.

Based on the hypothesis that the translocation of the gonopore to venter 8 (i.e. the formation of the extended oviduct) has occurred by an overfolding of the median parts of venter 8 by lateral parts of venter 8 (as in Fig. 41), the choice between the two following alternatives would appear difficult. (A) The condition with a languette lobe and a 7th-segmental gonopore was retained throughout much of the basal neopteran phylogeny (and has been retained until today in Dictyoptera and Ensifera), and the overfolding originated and the lobe became lost

independently in Odonata and many neopteran taxa. (B) The overfolding originated and the languette lobe became lost at the base of Odonata + Neoptera; thereafter, probably independently in Dictyoptera and Ensifera (given the monophyly of Caelifera + Ensifera), the overfolding became lost again, but in addition a structure resembling the languette lobe (re)appeared. Both alternatives require considerable homoplasy.

However, based on the hypothesis that the translocation to venter 8 occurred by a fusion of the edges of the languette lobe to venter 8 (as in Fig. 42), the decision appears easier. Then, either (C) the languette lobe remained unfused throughout much of the basal neopteran phylogeny (and has remained so until today in Dictyoptera and Ensifera), and the fusion originated independently in Odonata and many neopteran taxa; or (D) the fusion of the lobe edges to venter 8 originated at the base of Odonata + Neoptera, and was then suppressed again independently in Dictyoptera and Ensifera. Two points make hypothesis C/D more plausible than A/B. (1) The presence/absence of an entirely free lobe and of the overfolding here are two aspects of the same structural transformation (whereas for hypothesis A/B two parallel transformations must be assumed). (2) According to (D), the free lobe and location of the gonopore at the hind margin of venter 7 can be explained as secondary by an arrested ontogenetic development of the languette lobe: the fusion of its edges to venter 8 is abandoned. This means that the gonopore can be shifted back to venter 7 and that a free languette lobe can reappear by a single, simple transformation. Consequently, it now appears more plausible that the shift of the gonopore to venter 8 occurred at the base of Pterygota already.

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References

- Asahina, S., 1954. A Morphological Study of a Relic Dragonfly *Epiophlebia superstes* Selys (Odonata, Anisozygoptera). Japan Society for the Promotion of Science, Tokyo.

- Beier, M., 1972. 9. Ordnung Saltatoria (Grillen und Heuschrecken). In: Helmcke, J.G., Starck, D., Wermuth, H. (Eds.), *Handbuch der Zoologie*, Vol. 4 (2) 2/9. De Gruyter, Berlin, New York.
- Beutel, R.G., Gorb, S., 2006. A revised interpretation of the evolution of attachment structures in Hexapoda (Arthropoda), with special emphasis on Mantophasmatodea. *Arthrop. Syst. Phyl.* 64, 3–25.
- Birket-Smith, J., 1974. On the abdominal morphology of Thysanura (Archaeognatha and Thysanura s.str.). *Entomol. Scand. Suppl.* 6, 1–67.
- Bitsch, J., 1973. Morphologie abdominale des machilides (Insecta Thysanura) – I. Squelette et musculature des segments prégénitaux. *Ann. Sci. Nat., Sér.* 12 (15), 173–200.
- Bitsch, J., 1974. Morphologie abdominale des machilides (Thysanura) – II. Squelette et musculature des segments génitaux femelles. *Int. J. Insect Morphol. Embryol.* 3, 101–120.
- Cameron, S.L., Barker, S.C., Whiting, M.F., 2006a. Mitochondrial genomics and the new insect order Mantophasmatodea. *Mol. Phyl. Evol.* 38, 274–279.
- Cameron, S.L., Beckenbach, A.T., Dowton, M.A., Whiting, M.F., 2006b. Evidence from mitochondrial genomics on interordinal relationships in insects. *Arthrop. Syst. Phyl.* 64, 27–34.
- Cavallin, M., 1970. Développement embryonnaire de l'appareil génital chez le phasme *Carausius morosus* Br. *Rev. Bull. Biol.* 104, 343–366.
- Damgaard, J., Klass, K.-D., Picker, M.D., Buder, G., 2008. Phylogeny of the heelwalkers (Insecta: Mantophasmatodea) based on mtDNA sequences, with evidence for additional taxa in South Africa. *Mol. Phyl. Evol.* 47, 443–462.
- Davis, C., 1940. Taxonomic notes on the order Embioptera. XVIII. The genus *Oligotoma* Westwood. *Proc. Linn. Soc. N.S. Wales* 65, 362–387.
- Deuve, T., 2001. The epipleural field in hexapods. *Ann. Soc. Entomol. Fr.* 37, 195–231.
- Ford, N.B.A., 1923. A comparative study of the abdominal musculature of orthopteroid insects. *Trans. R. Can. Inst.* 14, 207–319.
- George, C.J., 1929. The morphology and development of the genitalia and genital ducts of Homoptera and Zygotera as shown in the life histories of *Philaenus* and *Agrion*. *Quart. J. Microsc. Sci.* 72, 447–485 + pls.
- Grassi, G.B., 1889. Intorno al gen. *Embia*. *Bull. Mensile Sedute Accad. Gioenia Sci. Nat. Catania* 9, 6–8.
- Grimaldi, D., Engel, M.S., 2005. *Evolution of the Insects*. Cambridge University Press, Cambridge, NY.
- Gupta, P.D., 1948. On the structure, development and homology of the female reproductive organs in orthopteroid insects. *Indian J. Entomol.* 10, 75–123.
- Haas, F., Kukalová-Peck, J., 2001. Dermaptera hindwing structure and folding: new evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta). *Eur. J. Entomol.* 98, 445–509.
- Hennig, W., 1969. *Die Stammesgeschichte der Insekten*. Waldemar Kramer, Frankfurt/Main.
- Hennig, W., 1981. *Insect Phylogeny* [translated and edited by Pont, A.C.; revisionary notes by Schlee, D., with 9 collaborators]. John Wiley & Sons, New York.
- Kalusche, D., 1972. Wirkungen der Exstirpation und Transplantation der Corpora allata auf die Entwicklung des Geschlechtsapparates der Stabheuschrecke *Carausius morosus* Br. *Zool. Jb. Anat. Ont.* 89, 117–165.
- Kjer, K.M., Carle, F.L., Litman, J., Ware, J., 2006. A molecular phylogeny of Insecta. *Arthrop. Syst. Phyl.* 64, 35–44.
- Klass, K.-D., 1997. The external male genitalia and the phylogeny of Blattaria and Mantodea. *Bonn. Zool. Monogr.* 42, 1–341.
- Klass, K.-D., 1998. The ovipositor of Dictyoptera (Insecta): homology and ground-plan of the main elements. *Zool. Anz.* 236, 69–101.
- Klass, K.-D., 1999. The pregenital abdomen of a mantid and a cockroach: musculature and nerve topography, with comparative remarks on other Neoptera (Insecta: Dictyoptera). *Dt. Entomol. Z.* 46, 3–42.
- Klass, K.-D., 2000. The male abdomen of the relic termite *Mastotermes darwiniensis* (Insecta: Isoptera: Mastotermitidae). *Zool. Anz.* 239, 231–262.
- Klass, K.-D., 2001. The female abdomen of the viviparous earwig *Hemimerus vosseleri* (Insecta: Dermaptera: Hemimeridae), with a discussion of the postgenital abdomen of Insecta. *Zool. J. Linn. Soc. Lond.* 131, 251–307.
- Klass, K.-D., 2003. The female genitalic region in basal earwigs (Insecta: Dermaptera: Pygidicranidae s.l.). *Entomol. Abh.* 61, 173–225.
- Klass, K.-D., 2005. 9. Ordnung Notoptera (Grylloblattodea). In: Dathe, H.H. (Ed.), *Lehrbuch der Speziellen Zoologie*, Bd. I: Wirbellose, 2. Aufl., 5. Teil: Insecta. Spektrum Akademischer Verlag, Heidelberg, Berlin, pp. 155–161.
- Klass, K.-D., 2007. Die Stammesgeschichte der Hexapoden: eine kritische Diskussion neuerer Daten und Hypothesen. *Denisia* 20, 413–450.
- Klass, K.-D., 2008. The female abdomen of ovipositor-bearing Odonata (Insecta). *Arthrop. Syst. Phyl.* 66, 45–142.
- Klass, K.-D., Picker, M.D., Damgaard, J., van Noort, S., Tojo, K., 2003. The taxonomy, genitalic morphology, and phylogenetic relationships of southern African Mantophasmatodea. *Entomol. Abh.* 61, 3–67.
- Klass, K.-D., Zompro, O., Kristensen, N.P., Adis, J., 2002. Mantophasmatodea: a new insect order with extant members in the Afrotropics. *Science* 296, 1456–1459.
- Klug, R., Klass, K.-D., 2007. The potential value of the pregenital abdominal musculature and nervous system in the reconstruction of interordinal relationships in lower Neoptera. *Arthrop. Syst. Phyl.* 65, 73–100.
- Koch, M., 2003. Towards a phylogenetic system of the Zygentoma. *Entomol. Abh.* 61, 122–125.
- Kristensen, N.P., 1991. Phylogeny of extant hexapods. In: CSIRO (Ed.), *The Insects of Australia*, 2nd ed. Melbourne University Press, pp. 125–140.
- Kristensen, N.P., 1995. Forty years' insect phylogenetic systematics: Hennig's "Kritische Bemerkungen..." and subsequent developments. *Zool. Beitr. N.F.* 36, 83–124.
- Matsuda, R., 1976. *Morphology and Evolution of the Insect Abdomen with Special Reference to Developmental*

- Patterns and their Bearings upon Systematics. Pergamon, Oxford.
- Melander, A.L., 1903. Notes on the structure and development of *Embia texana*. Biol. Bull. (Woods Hole) 4, 99–118.
- Metcalf, M.E., 1932. Notes on the structure and development of the reproductive organs in *Philaenus spumarius* L. Quart. J. Microsc. Sci. 75, 467–481.
- Mukerji, S., 1927. On the morphology and bionomics of *Embia minor*, sp. nov., with reference to its spinning organ. Rec. Indian Mus. 29, 253–282 + 1 pl.
- Nel, R.I., 1929. Studies on the development of the genitalia and the genital ducts in insects. I. Female of Orthoptera and Dermaptera. Quart. J. Microsc. Sci. 73, 25–85.
- Rähle, W., 1970. Untersuchungen an Kopf und Prothorax von *Embia ramburi* Rimsky-Korsakow 1906 (Embioptera, Embiididae). Zool. Jb. Anat. Ont. 87, 248–330.
- Roonwal, M.L., 1937. Studies on the embryology of the African Migratory Locust, *Locusta migratoria migratorioides* Reiche and Frm. (Orthoptera, Acrididae). II Organogeny. Phil. Trans. R. Soc. B 227, 175–244 + pls.
- Roonwal, M.L., 1962. Structure and postembryonic development of female reproductive organs in the desert locust, *Schistocerca gregaria*. Rec. Indian Mus. 60, 95–120 + pls.
- Ross, E.S., 1943. Two new Indian Embioptera and the lectotype of *Oligotoma borneensis* Hagen. Psyche 50, 100–108.
- Ross, E.S., 1987. Studies in the insect order Embiidina: a revision of the family Clothodidae. Proc. Calif. Acad. Sci. 45, 9–34.
- Ross, E.S., 2000. EMBIA: Contributions to the biosystematics of the insect order Embiidina, part 1. Occas. Pap. Calif. Acad. Sci. 149, 1–53.
- Ross, E.S., 2001. EMBIA: Contributions to the biosystematics of the insect order Embiidina, part 3: The Embiididae of the Americas (order Embiidina). Occas. Pap. Calif. Acad. Sci. 150, 1–86.
- Ross, E.S., 2003. EMBIA: Contributions to the biosystematics of the insect order Embiidina, part 4: Andesembiididae, a new Andean family of Embiidina. Occas. Pap. Calif. Acad. Sci. 153, 1–13.
- Ross, E.S., 2009. World List of Extant and Fossil Embiidina (= Embioptera). Available at: http://research.calacademy.org/research/entomology/Entomology_Resources/embiilist/index.htm.
- Rousset, A., 1973. Squelette et musculature des régions génitales et postgénitales de la femelle de *Thermobia domestica* (Packard). Comparaison avec la région génitale de *Nicoletia* sp. (Insecta: Apterygota: Lepismatida). Int. J. Insect Morphol. Embryol. 2, 55–80.
- Snodgrass, R.E., 1933. Morphology of the insect abdomen. Part II. The genital ducts and ovipositor. Smithson. Misc. Coll. 89/8, 1–148.
- Snodgrass, R.E., 1935a. Principles of Insect Morphology. McGraw-Hill, New York.
- Snodgrass, R.E., 1935b. The abdominal mechanisms of a grasshopper. Smithson. Misc. Coll. 94, 1–89.
- Szumik, C., 1996. The higher classification of the order Embioptera: a cladistic analysis. Cladistics 12, 41–64.
- Szumik, C., 2001. Nuevos embiópteros de América del Sur. Rev. Soc. Entomol. Arg. 60, 257–272.
- Szumik, C., 2004. Phylogenetic systematics of Archembiididae (Embiidina, Insecta). Syst. Entomol. 29, 215–237.
- Szumik, C., Edgerly, J.S., Hayashi, C.Y., 2008. Phylogeny of embiopterans (Insecta). Cladistics 24, 993–1005.
- Terry, M.D., Whiting, M.F., 2005. Mantophasmatodea and phylogeny of the lower neopterous insects. Cladistics 21, 240–257.
- Verhoeff, K.W., 1904. Zur vergleichenden Morphologie und Systematik der Embiiden. Abh. Kaiserl. Leopold.-Carol. Dt. Akad. Naturforscher (Halle) 82, 141–204 + pls.
- Walker, E.M., 1943. On the anatomy of *Grylloblatta campodeiformis* Walker: 4. Exoskeleton and musculature of the abdomen. Ann. Entomol. Soc. Am. 36, 681–706.
- Wheeler, W.C., Whiting, M., Wheeler, Q.D., Carpenter, J.M., 2001. The phylogeny of the extant hexapod orders. Cladistics 17, 113–169.
- Willmann, R., 2005. Phylogenese und System der Insecta. In: Dathe, H.H. (Ed.), Lehrbuch der Speziellen Zoologie, Bd. I: Wirbellose, 5. Teil: Insecta, 2. Aufl. Spektrum Akademischer Verlag, Heidelberg, Berlin, pp. 1–65.
- Zwick, P., 1980. 7. Ordnung Plecoptera (Sternfliegen [sic!]). In: Helmcke, J.G., Starck, D., Wermuth, H. (Eds.), Handbuch der Zoologie, Vol. 4 (2) 2/7. De Gruyter, Berlin, New York.