

# The Female Abdomen of Ovipositor-bearing Odonata (Insecta: Pterygota)

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## > Abstract

The exoskeleton and musculature of the middle and posterior abdomen in female *Calopteryx virgo* are described (segments IVff), including parts of the midabdominal nervous system. Based on a sample of 16 species of Odonata with a plesiomorphic morphology of the ovipositor (various Zygoptera, *Epiophlebia*, and Aeshnidae) the range of variation in the abdominal exoskeleton is documented, and a preliminary list and table of 79 characters are assembled. Abdominal muscles in Odonata are surveyed based on data from the literature. Topographic homologies between Odonata and other Insecta are discussed, with a focus on the female genitalic region and the terminal abdomen, and with consideration of previous ontogenetic studies. The results are used for including outgroup scorings into the character list for Odonata. Odonata conform with many Neoptera (e.g., Notoptera, pygidicranid Dermaptera) in the location of the female genital opening between or behind the gonapophyses VIII bases, contrasting with the VIIth-segmental openings in other Neoptera (e.g., Dictyoptera, Ensifera, 'advanced' Dermaptera), Archaeognatha, and Zygentoma. The gonangulum in most Odonata consists, like in Archaeognatha and some Dermaptera, of two separate sclerites; this contrasts with the one-piece condition of the gonangulum in other Dicondylia and *Epiophlebia*. The interpretation of terminal appendages in Odonata as the true cerci is supported by musculature data, and it is shown that previous counter-arguments are invalid. While *Epiophlebia* is in many characters highly peculiar among Odonata, the abdominal characters provide no resolution for the relationships between *Epiophlebia*, Zygoptera, and Anisoptera. The monophyly of Zygoptera receives considerable support.

## > Key words

Cercus, characters, female genitalia, gonangulum, gonapophysis, homology, musculature, ovipositor, phylogeny.

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## 1. Introduction

### 1.1. Phylogenetic relationships of Odonata

The taxon Odonata is characterized by many unique morphological specializations, which convincingly support its monophyly. Examples are the highly derived structure of the thorax and its flight device (e.g., PFAU 1986, 1991) and the unique secondary male genitalia on the anterior part of the abdomen (treated excellently in PFAU 1971). Beside the Ephemeroptera and the Neoptera, the Odonata represent one of the three principal lineages of the Pterygota and are thus of par-

ticular relevance in attempts to reconstruct the basal phylogeny and diversification of the entire winged insects. In addition, the Odonata are a meaningful out-group taxon for studies on interordinal phylogenetic relationships in Neoptera, and this is especially true with regard to parts of the body that have undergone strong reduction in the Ephemeroptera. One example is the female genitalic region, which in many Odonata forms a complicated plesiomorphic ovipositor (like in Archaeognatha and Zygentoma), while no trace of this structure has been retained in ephemeropterans. The relationships between Odonata, Ephemeroptera, and Neoptera are still ambiguous (see KRISTENSEN 1991; WILLMANN 2003, 2005; BEUTEL & GORB 2001, 2006; KJER 2004; KJER et al. 2006; HOVMÖLLER et al. 2002; OGDEN & WHITING 2003; TERRY & WHITING 2005; summary in KLASS 2007), and the relationships among the principal lineages of the Neoptera are also widely unresolved (KLASS 2007). Due to this situation a continued exploration of morphological (as well as molecular) character systems would appear desirable, including Odonata.

Odonata comprises the three subgroups Zygoptera (damselflies), Anisozygoptera (with *Epiophlebia* as the sole extant genus), and Anisoptera (dragonflies). Phylogenetic work on the order (see reviews in, e.g., REHN 2003; MISOF 2004; CARLE et al. 2008) has been dominated by the question whether the Zygoptera are monophyletic, or paraphyletic with respect to a clade comprising Anisozygoptera and Anisoptera (which together may form a monophylum, called Epiprocta by LOHMANN 1996; see also PFAU 1991; BECHLY 1995, 1996; REHN 2003). This long-standing question has been addressed in a number of recent phylogenetic studies. On the morphological side, the phylogenetic discussions of CARLE (1982) and BECHLY (1995, 1996) as well as the cladistic analyses of REHN (2003) have arrived at the conclusion that Zygoptera is monophyletic, while the cladistic analysis of TRUEMAN (1996) finds strongly paraphyletic Zygoptera (but see comments in BECHLY 1996: 10 on problems with that analysis). PFAU (2002), based on the structure and musculature of male caudal appendages, also favours paraphyletic Zygoptera. Among the molecular studies with a decent sample of Odonata, OGDEN & WHITING (2003) state that in their analyses Zygoptera consistently appear as monophyletic, whereas in their fig. 2 (a POY-analysis) they show strongly paraphyletic Zygoptera. SAUX et al. (2003) using one mitochondrial gene (12S rDNA) and HASEGAWA & KASUYA (2006) using one gene each from the mitochondria and nucleus (16S and 28S rDNA), both with a fairly limited taxon sample (16 resp. 19 genera; the latter including *Epiophlebia*), obtain paraphyletic Zygoptera. However, CARLE et al. (2008) using five nuclear and mitochondrial genes (EF-1 $\alpha$  and various rDNAs) and a much larger sample (66 genera

including *Epiophlebia*) find considerable support for monophyletic Zygoptera. (See also MISOF et al. 2001 for molecular-based phylogenetic work focused on Anisoptera and MISOF & FLECK 2003 for the use of 16S rRNA secondary structure in phylogeny reconstruction of Odonata.)

Apart from the “Zygoptera problem”, the basal relationships in both the Zygoptera and the Anisoptera are not well resolved, and hypotheses vary among contributions. In Zygoptera this mainly concerns the relationships among the major lineages Calopterygoidea, Coenagrionoidea (Coenagrionoidea), and Lestoidea (Lestinoidea) as well as the placement of a few smaller (sub)families and crucial genera (such as *Philoganga*, *Diphlebia*, and *Hemiphlebia*) in the one or the other lineage, or outside all of them (see differences in hypotheses of BECHLY 1996, REHN 2003, and CARLE et al. 2008). In Anisoptera a major problem in the basal dichotomies is whether the Aeshnidae alone (e.g., PFAU 1991; LOHMANN 1996) or together with Austropteralidae (CARLE et al. 2008), or perhaps the Petaluridae (TRUEMAN 1996; BECHLY 1996; REHN 2003) are sister to the remaining groups. In addition, the placement of *Epiophlebia* as sister group to Anisoptera is perhaps also not completely settled. In the major morphological contributions (BECHLY 1995, 1996; REHN 2003) this relationship is supported. However, in the so far most extensive molecular analysis of Odonata (CARLE et al. 2008), Zygoptera, *Epiophlebia*, and Anisoptera form an unresolved basal trichotomy, and in HASEGAWA & KASUYA (2006) the position of the genus varies among different analyses.

All the large morphology-based phylogenetic studies of Odonata are strongly focused on wing characters (venation and articulation; TRUEMAN 1996; BECHLY 1995, 1996; REHN 2003: 78 out of 122 characters) – the character system on which the classification of Odonata has been based traditionally. One reason for this choice is that for Odonata and their extinct relatives there is a good fossil record, including some of the oldest known pterygote fossils from the early Upper Carboniferous (e.g., RIEK & KUKALOVÁ-PECK 1984; BECHLY et al. 2001; GRIMALDI & ENGEL 2005) – and most fossils are only represented by wings. The study of REHN (2003) also includes many characters from other parts of the body. However, none of the phylogenetic studies has so far included characters of the female genitalia to some noteworthy extent (not a single female genitalic character represented in REHN 2003! Two characters used in CARLE 1995), and except for the secondary genitalia and terminal claspers of the males, other parts of the abdomen are also poorly represented. It is thus obvious that detailed comparative studies on the abdomen are very likely to improve the data base for phylogenetic studies in Odonata, and this may be especially true for the female genitalia.

## 1.2. Abdominal morphology in Odonata

The female genitalia in many Odonata and many other insects, including their musculature, are highly complicated, and they show much structural diversity. They are thus among the most interesting character systems with regard to phylogeny reconstruction among and within high rank insect taxa. Some further character systems of the abdomen can also be useful with regard to phylogenetic work, such as the midabdominal and terminal segments with their muscles, and the pattern of extrinsic rectal muscles. The author has previously studied the abdomen in some ‘lower-grade’ Neoptera, with a focus on Dictyoptera (KLASS 1995, 1997, 1998, 1999, 2000; KLASS et al. 2000), Dermaptera (KLASS 2001a, 2003), Notoptera (KLASS 2005), Mantophasmatodea (KLASS et al. 2003), and Embioptera (K.-D. Klass & J. Ulbricht submitted); the midabdominal musculature and nervous system were surveyed across the “lower” Neoptera in KLUG & KLASS (2007). It has been one objective of this work to find characters phylogenetically informative at the inter- or intraordinal levels. Therefore, there was extensive comparison included with Archaeognatha, Zygentoma, and Ephemeroptera – mainly based on the treatments by BITSCH (1973, 1974a,b), ROUSSET (1973), and BIRKET-SMITH (1971, 1974). However, the information available on the abdominal morphology of the Odonata has so far been too sparse for including this taxon into the comparative discussions.

Among the older studies on the abdomen of Odonata, ASAHINA’s (1954) work is most prominent, in which the exoskeleton and musculature are described for several species, with a focus on *Epiophlebia*. WHEDON’s (1918) study of the nymphal abdominal musculature of segments up to IX is a useful supplement to the latter work. VAN DER WEELE (1906) contributed an extensive study of the female genitalic region, with consideration of both adult morphology and nymphal development. ST. QUENTIN (1962) and PFAU (1991) have also treated some aspects of ovipositor morphology comparatively, though with a focus on function. DUNCAN (1933) has outlined some muscles and nerves of the female genitalia in the anisopteran *Anax*, and HAKIM (1964) has given a comparative account on the female genitalic musculature in several Odonata. CHAO (1953) has described the imaginal exoskeleton of a gomphid, and WINKELMANN (1973) much of the nymphal and imaginal morphologies of a libellulid (with many remarks on other Odonata). Some information on the abdominal spiracles is given in TILLYARD (1917) and POONAWALLA (1966). SNODGRASS’ (1954) treatment of abdominal morphology in the nymphs is focused on the respiratory devices. For aeshnid nymphs, ZAWARZIN (1911) has given a detailed

account on the heart, while ROGOSINA (1928), WHEDON (1929), and, more comprehensively, MILL (1964) have described the musculature and nervous system. TILLYARD (1917) has summarized the morphological results then available, adding also many original observations. A more recent survey of the abdominal exoskeletal structure and ontogeny is given in MATSUDA (1976). Further morphological data on the abdomen are dispersed in the taxonomic literature (e.g., CALVERT 1927). In recent years Nataly Matushkina has begun with an in-depth study of female genitalia in Odonata (and a cooperation with the author has been established in 2007). While much of her work is focused on the function and the sensory equipment of the ovipositor (MATUSHKINA & GORB 2002, 2004, 2007), there are also important contributions on the exoskeleton and musculature of the female genitalia (MATUSHKINA & GORB 1997; MATUSHKINA 2004, 2008a,b).

HEYMONS (1896, 1904) was the first to study particular aspects of the embryonic and nymphal development in Odonata in some detail. He claimed that the projections that in adult Odonata resemble the cerci of other insects are not the true cerci and called them 'cercoids'; this led to the famous controversy between him and HANDLIRSCH (e.g., 1904) about the nature of these structures. Though many have later contributed their opinion – WALKER (1922), SCHMIDT (1933), SNODGRASS (1954), ASAHINA (1954), and MATSUDA (1976) are only a few of them – some of HEYMONS' arguments have remained uncontested. With respect to embryological work on Odonata ANDO'S (1962) contribution is as prominent as ASAHINA'S (1954) is for comparative morphology, and it is likewise focused on *Epiophlebia*. Yet, some of ANDO'S conclusions appear disputable, and the cercus problem is not touched. The development of the female gonoducts, on which little information is found in the aforementioned contributions, has been studied by GEORGE (1929) – together with gonoduct development in the auchenorrhynchan *Philaenus*. Many of his findings on the latter taxon, however, have been rejected by METCALFE (1932) after her study of *Philaenus*, and GUPTA (1948) doubts GEORGE'S (1929) results on Odonata – though not on the basis of own original work.

Due to the strong differences between their nymphal and imaginal life-styles and morphologies, odonatans undergo a metamorphosis that in the extent of body reorganization far exceeds that in 'lower-grade' Neoptera. The exoskeleton, musculature, tracheal system, and fat body become extensively restructured during imaginalization (e.g., WOLF 1935; WHEDON 1918, 1929; FORD 1923). The degeneration of nymphal muscles and growth of imaginal muscles are still in full swing in teneral imagines, and changes in muscle proportions as well as losses of muscles even continue in mature imagines (ASAHINA 1954: 54). Eventually,

mature odonatans are devoid of some of the muscles predominant in the abdomen of other Pterygota, e.g., of the long internal (= inner) dorsal and ventral muscles (e.g., FORD 1923). These ontogenetic changes have been extensively explored in an aeshnid by MATUSHKINA (2008a). This all makes comparative morphological work difficult, because not a standard set of imaginal abdominal muscles can be ascribed to a certain taxon; differences found between specimens of two taxa may be interspecific, but may as well purely depend on the age of the specimens, and heterochrony may additionally be involved.

Although much has been written on the abdomen of imaginal Odonata, the information so far available is quite insufficient. For instance, there is no study of the peripheral nervous system in the midabdominal segments of the imago. In the terminal abdomen (segments Xff) many small muscles and extrinsic rectal muscles have remained undescribed, and for others the insertions are inadequately determined. For the female genitalia the previous studies have shown that an ovipositor is present in *Zygoptera*, *Epiophlebia*, and *Aeshnidae* (herein comprised as the ovipositor-bearing Odonata), and with some modification in *Petaluridae* (VAN DER WEELE 1906: 171f; PFAU 1991), whereas this structure is strongly modified or reduced in the remaining Anisoptera. However, the finer structure and exact interrelations of the elements around the ovipositor base as well as the inconspicuous muscles have been neglected. Previous comparison of female genitalic morphology among ovipositor-bearing Odonata has rarely gone beyond the statement of general uniformity (e.g., ASAHINA 1954: 68; PFAU 1991: 135), and the only characters mentioned as distinguishing certain subgroups are those easily visible externally or relating to proportions (e.g., ST. QUENTIN 1962). The limited knowledge on abdominal morphology in Odonata is presently impeding (1) a reliable homologization of structural elements between Odonata and other Insecta and (2) the use of abdominal morphology as a source of characters for phylogenetic analyses among insect orders and within Odonata.

The work of recent years by N. Matushkina and S.N. Gorb has already contributed much to an improvement of the knowledge on female genitalia in Odonata. They have been mainly exploring the function and major muscular connections as well as the sensory equipment and development of the odonatan ovipositor (MATUSHKINA 2004, 2008a,b; MATUSHKINA & GORB 1997, 2002, 2004, 2007).

### 1.3. Scope of present study

In contrast to the work of N. Matushkina & S.N. Gorb, the present study is focused on the comparison of structural details throughout the abdomen of ovipositor-bearing Odonata, and on related morphological interpretations on both the inter- and intraordinal levels. Both strands of research together are currently closing the major gaps in the knowledge on odonatan abdominal morphology.

Herein, *Calopteryx virgo* has been chosen for a complete study of the posterior half of the abdomen, including the musculature. 15 additional species of ovipositor-bearing Odonata have been sampled for a comparative study of exoskeletal characters; this sample predominantly comprises zygopterans, but also *Epiophlebia superstes* and two species from Aeshnidae. Further data on the musculature has been compiled from the literature. Based on the morphological data and comparisons, abdominal characters of Odonata are listed in order to provide a basis and guideline for the use of abdominal morphology in forthcoming phylogenetic studies. Topographic homologies (see KLAS 2001b: identification of corresponding parts) between Odonata and other Insecta are also discussed in order to provide outgroup comparison for the characters in Odonata and to increase the availability of abdominal characters for phylogenetic studies across the insects. Phylogenetic implications of the characters here studied are discussed to some extent, but conclusions will be preliminary.

## 2. Material and methods

The nomenclature at the genus and species levels follows STEINMANN (1997a,b). The classification at the (super)family level is given according to PFAU (1991), but in the following list the synonyms used in STEINMANN (1997a,b) are placed in front. (The classification has been chosen for practical reasons and does not imply the acceptance of a particular phylogenetic hypothesis.) When data from previous studies are referred to, the names of the respective taxa, mostly species, are specified as (in)completely as in the original papers. After their first mention species are designated by the genus name alone whenever this is unambiguous.

Of *Calopteryx virgo* (Linnaeus, 1758) (Zygoptera: Calopterygoidea = Agrioidea: Calopterygidae = Agriidae) 7 females and 4 males preserved in 80% ethanol

were used. Most structures were studied by dissection under a stereo microscope, done from various directions in 80% ethanol. For small muscles and some other structures the identity of the tissue was checked under a light microscope. The exoskeleton was additionally studied in KOH-macerated specimens. (The specimens were misnamed as “*Calopteryx splendens*” in KLAS 2003: e.g., fig. 76.)

For comparison with *Calopteryx*, KOH-macerated specimens were used of the following species:

#### (1) Zygoptera

*Hetaerina americana* (Fabricius, 1798) (Calopterygoidea: Hetaerinaidae), *Epallage fatime* (Charpentier, 1840) (Calopterygoidea: Euphaeidae = Epallagidae), *Platycypha caligata* (Selys, 1853) (Calopterygoidea: Chlorocyphidae), *Diphlebia lestoides* (Selys, 1853) (Calopterygoidea?: Diphlebiidae? not included in PFAU 1991), *Chlorocnemis* Selys, 1863 sp. indet. (Coenagrionoidea = Coenagrionoidea: Protoneuridae), *Drepanosticta fontinalis* Lieftinck, 1937 and *Drepanosticta* Laidlaw, 1917 sp. indet. (Coenagrionoidea: Platystictidae), *Pyrrhosoma nymphula* (Sulzer, 1776) (Coenagrionoidea: Coenagrionidae = Coenagriidae), *Platycnemis pennipes* (Pallas, 1771) (Coenagrionoidea: Platycnemididae), *Mecistogaster lucretia* (Drury, 1773) (Coenagrionoidea: Pseudostigmatidae), *Lestes elatus* Hagen, 1862 (Lestinoidea: Lestidae), *Rhipidolestes* Ris, 1912 sp. indet. ([no superfamily assignment] Pseudolestidae), *Argiolestes aurantiacus* Ris, 1898 (*A. aurentiacus*; [no superfamily assignment] Megapodagrionidae = Megapodagriidae).

#### (2) Anisozygoptera

*Epiophlebia superstes* (Selys, 1889) ([no superfamily assignment] Epiophlebiidae).

#### (3) Anisoptera

*Aeshna cyanea* (Müller, 1764) (Aeshnoidea: Aeshnidae: Aeshninae), *Caliaeshna microstigma* (Schneider, 1845) (Aeshnoidea: Aeshnidae: Brachytroninae), and *Cordulegaster brevistigma* (Selys, 1854) (Cordulegasteroidea: Cordulegasteridae = Cordulegastridae).

Three specimens were used in most species, but only two specimens were available of *Mecistogaster* and *Epiophlebia*, and only a single one each of *Diphlebia*, *Cordulegaster*, and the two *Drepanosticta* species. Of the *Epiophlebia* specimens one was caught fairly young, the other one is likely fully matured (observed during oviposition; Ryuichiro Machida, pers. comm.).

Supplementary examinations on non-odonatan taxa were conducted for *Magicycada septendecim* (Linnaeus, 1758) (Auchenorrhyncha: Tibicinidae) and *Grylloblatta campodeiformis* Walker, 1914 (Notoptera = Grylloblattodea).

### 3. Terminologies, morphological interpretations, and abbreviations

#### 3.1. Elements studied and their interpretation

This study includes muscles, parts of the nervous system, and two categories of exoskeletal elements, namely the sclerites and the formative elements. The latter comprise all in- and evaginations and thickenings of the body wall, such as processes, apodemes, and ridges (for the usage of ‘apodeme’, ‘ridge’, and ‘tendon’ see KLASS 2001a: 253). The interpretation of many elements will be discussed below, but some generalities from previous work on the terminal abdomen and female genitalic region should be noted in advance. The designation and interpretation of the elements of the terminal abdomen is based on the discussions in KLASS (2001a), which refer to the nature of the epiproct, paraprocts, and cercus bases. The designation and interpretation of the ventral (s.l.: sternal plus pleural) elements of the female genitalic segments VIII and IX is based on SCUDDER (1961a,b), but some modifications are applied according to more refined contributions on Archaeognatha (BITSCH 1973, 1974a,b), Zygentoma (ROUSSET 1973), Dictyoptera (KLASS 1998), and Dermaptera (KLASS 2003), and in view of new findings in the present study. Detailed explanations in terms of the female genitalic components are given in KLASS (2003), and only the essentials are here repeated.

For the ventral sclerites of the female genitalic region the terminology is largely based on conditions in Archaeognatha as described by BITSCH (1973, 1974a). Five sclerotization areas are distinguished: the paired coxae (‘coxites’ in BITSCH), antelaterocoxae (‘precoxites’), postlaterocoxae (‘laterocoxites’), and gonapophyseal sclerotizations, and the unpaired sternum (‘sternite’ plus ‘intersternite’). Ante- and postlaterocoxa together constitute the laterocoxa (gonangulum in segment IX). Laterocoxa and coxa are comprised as the coxopodium. A pair of coxopodia and the sternum together constitute the coxosternum (the pregenital abdominal ‘sterna’ of Dicondylia are regarded as such coxosterna; see KLASS 2001a: 272). A sclerite composed of the laterocoxae and the sternum is called a laterocoxosternum. The usage of these terms implies only inner-insect abdominal homology and homonymy, but not strict homonymy with parts of the thoracic limbs, and no reference is intended to theories of limb base composition in a large-scale arthropod view. Major projections of the female genitalic region are the coxal lobes (= gonoplacs), the styli

located upon them, and the gonapophyses. The coxal lobe is presumably the projecting body of a limb, corresponding to the coxal and possibly more distal parts of the thoracic leg, while the stylus likely represents further distal podomeres (KLASS & KRISTENSEN 2001: 274). The gonapophyses are likely homonomous with the eversible vesicles (BITSCH 1994).

The interpretation of the female gonoducts largely follows the scheme of SNODGRASS (1933: 16ff). As a basic pattern, in the development of insects each of the abdominal segments VII, VIII, and IX forms a median invagination at its hind margin; these are the rudiments of the common oviduct, spermatheca, and accessory gland. The common oviduct later acquires contact with the mesodermal lateral oviducts and their ampullae. In cases where the common oviduct opening develops directly into the definitive genital opening, the intima-bearing median gonoduct in the adult is exclusively constituted by the common oviduct, whose opening is a primary oviducal opening (primary gonopore) on the hind margin of venter VII. In cases where a groove forms behind the common oviduct opening and becomes closed ventrally, the resulting extension of the duct is called the extended oviduct, the intima-bearing (ectodermal) median gonoduct in the adult is constituted by the common plus the extended oviducts, and the opening is a secondary oviducal opening (secondary gonopore) located on segment VIII. In cases where additionally the VIIIth-segmental area bearing the secondary oviducal opening and the spermathecal opening becomes invaginated anteriorly, the terminal part of the intima-bearing median gonoduct is a vagina (or a genital chamber if it is not a discrete tube), whose opening is the vulva located on the posterior part of venter VIII (see SNODGRASS 1933: fig. 4A–D; median oviduct **Odc**’ = common oviduct; median oviduct **Odc** = common + extended oviduct). Problems with this scheme are discussed below. The term ‘spermatheca’ is here used in a morphological sense, comprising all surmised derivatives of the embryonic or nymphal spermathecal invagination.

#### 3.2. Segmental assignment

For sclerites it is given with respect to secondary segmentation because the latter is established by the sclerites. For formative elements, muscles, and components of the nervous system, assignment is given, as far as possible, with respect to primary segmentation. Elements assumed to lie at the border between two primary segments or to be of bisegmental origin (e.g., antecostae, alary muscles, anterior tergo-coxosternal

muscles) as well as the median and transverse nerves are formally assigned to the respective posterior segment (see KLASS 1999: 7). In the abdominal segments up to IX the belonging of most elements to a certain primary segment is obvious from their positions. For many elements behind segment IX, however, the segmental assignment is controversial; discussions are given, building on the results of KLASS (2001a) on other insects.

### 3.3. Terminologies

The terms for sclerites and formative elements are the same as used in KLASS (2001a, 2003). Sclerites receive names composed of two upper case letters; their subdivisions are specified by a lower case letter in the third position. A term of the same kind (ES) is also used for the segmental subsets of the mesodermal endoskeleton ('endosternites', only in Archaeognatha and Zygentoma). Formative elements are given terms composed of two lower case letters; those of the tendon-apodeme category have a, t, u, v, w, or x in the second position, while the front letter is arbitrary (though it expresses a characteristic in many cases). Internal ridges have r, and external ridges have y or z in the second position. A number in the last position gives, if needed, the assignment of a sclerite or formative element to a segment. Single lower case letters are used to mark some particular locations in the exoskeleton that are referred to in the descriptions (mostly specific extensions or areas of sclerites).

The muscles are numbered in sequence. In addition, many are given descriptive names. The terminological principles followed and their inherent problems are explained in KLASS (1999: 5f). In segments IV–IX insertions on the coxosternum and on the pleural membrane – most of both are probably pleural – are designated as coxosternal (coxal, laterocoxal, or laterocoxosternal in case of corresponding subdivisions of the coxosternum). Unless otherwise noted, muscles are present as a pair.

For parts of the nervous system the terminology previously applied to Dictyoptera, Dermaptera, and other taxa in KLASS (1999, 2001a) and KLUG & KLASS (2007) is used, according to the presumed homologies. The principal components – ganglia, connectives, and major nerves – are given single upper case letters. Primary branches of the major nerves are specified by numbers behind the letter. A number in front gives, if needed, the assignment to a segment. Compound ganglia including several segmental ganglia (neuromeres) are termed, e.g., '8–11G'. Designating the major

nerves and their branches includes problems because branching patterns are quite different in Odonata and the neopteran taxa. Compound major nerves, comprising tracts that are entirely separated in Dictyoptera and Dermaptera, are called, e.g., B+C; their branches, however, are designated as their homologues in Dictyoptera and Dermaptera (e.g., branch C3 of nerve B+C in Odonata corresponds with branch C3 of nerve C in Dictyoptera). Anastomoses connecting major nerves are called, e.g., 'C–T' (= anastomosis between nerves C and T).

Generally in this paper the identical designation of elements expresses the assumption of homology between taxa or homonymy between segments – with the limitations given in the discussions with regard to the probability of such relations.

Morphological terms and abbreviations from other publications are marked with an asterisk – with the exception of the terms for sclerites and formative elements in KLASS (2001a, 2003), which fit into the scheme of homologization here proposed.

### 3.4. Abbreviations

The following abbreviations are used both in the illustrations and in the text:

1 ... 89	muscles
I ... IV	groups of cercal muscles
a	extension of tergum at its anteroventral corner, supporting tendon et
A (+ number)	dorsal nerve (and its major branches) (number = segment)
ac (+ number)	antecosta (= anterior transverse carina in midabdomen) (number = segment following)
ag	accessory gland
al	aulax (part of olistheter: groove on gonapophysis VIII)
an	anus
ap	patch of thick, flexible cuticle at intertergal articulation
AP	surmised (postero)median sclerite of 'paraproct'
at (+ number)	apodeme on anterolateral corner of (latero)coxosternum = anterior 'sternal' apophysis (number = segment following)
b	extension of tergum VIII at its posteroventral corner
B + number	some of the primary branches of the ventral nerve B+C
ba (+ number)	lateral apodeme of (latero)coxosternum, behind spiracle (number = segment)
B+C	ventral nerve
bt (+ number)	tendon of pleural membrane on anterior segmental border (number = segment)

C + number	some of the primary branches of the ventral nerve B+C	h	narrow ribbon of heavy sclerotization connecting TG9 and LCa9
c	extension of tergum IX at its anteroventral corner	hrt ht	heart tendon lateral to cercal base, in front of sclerite AP dorsal anterior margin
ca	central apodeme between coxae IX		
CA	sclerite of central apodeme	i	posteriad-directed extension of basal part of sclerite GP9
ce	cercus		
CE	sclerotization of cercus	it	tendon in front of sclerite AP lateral anterior margin
cr	collar-shaped (soft) 'ridge' of vagina		
CS (+ number)	coxosternum (number = segment)	IT9	ventral sclerite (or vestiges of it) interconnecting posteroventral corners of tergum IX
ct	tendon next to dorsal cercus base		
CX (+ number)	coxa (number = segment)		
d	extension of sclerite CX8 that articulates with sclerite LCa9	jt	tendon in front of sclerite AP ventral anterior margin
da	anterodorsal apodeme of tergum IX, on anterior segmental border	L la	connective between successive ganglia posterolateral apodeme of coxa IX
df (+ number)	dorsal fold of segment overlapping succeeding segment (number = segment)	lc (+ number)	longitudinal external ridge on lateral part of tergum (= supplementary lateral carina) (number = segment)
dh (+ number)	longitudinal dorsomedian hinge line on tergum (= middorsal carina) (number = segment)	LC (+ number) LG7	laterocoxa (number = segment) genital plate (= languette sclerite) at hind margin of venter VII
dl	dorsal lobe of gonoplac IX		
dp	dorsomedian process on hind margin of tergum X	LP	surmised (antero)lateral sclerite of 'paraproct'
dps	dorsal protraction sensor	ls	membranous lobe on mesal part of spiracle
dt (+ number)	dorsomedian tendon in front of tergum, on anterior segmental border (number = segment)	LS (+ number) M	laterocoxosternum (number = segment) median nerve
DT	dorsal sclerite of telson	ma	median apodeme of cercal base (partly membranous)
e	anterolateral extension of sclerite GP8, articulating with CX8 and LCa9	mr	midventral (soft) 'ridge' of vagina
ec	line along which cuticle ends (mesoderm adjoining)	MS	sclerite at anterior end of cleft between gonapophyses VIII
ES	endosternite (mesodermal)	oc	part of common oviduct bearing intima
et (+ number)	ventrolateral tendon in front of tergum, on anterior segmental border (number = segment)	oe oco ol	extended oviduct part of common oviduct lacking intima part of lateral oviduct bearing intima
f	anterodorsal extension of sclerite GP8, bearing anterior end of aulax	ola pa (+ number)	part of lateral oviduct lacking intima apodeme on anterior lateral margin of coxosternum, in front of spiracle = posterior 'sternal' apophysis (number = segment following)
fa	anterolateral apodeme of coxa IX		
fg	longitudinal fold along dorsal face of gonapophysis VIII		
ft	tendons flanking central apodeme, between coxae IX	pp (+ number)	unpaired process on posterior margin of laterocoxosternum (number = segment)
g	anteroventral extension of sclerite GP9, bearing anterior end of rhachis	PP	'paraproct', as a collective term for sclerites AP plus LP
G	ganglion	PS9	'poststernum' at ventral hind margin of segment IX (interpretation unresolved)
ga	anterior apodeme of coxa VIII		
gf	genital fold or lobe at hind rim of venter VII	re rh	rectum rhachis (part of olistheter: ridge on gonapophysis IX)
gl (+ number)	projecting body of abdominal limb (without stylus) = coxal lobe; gonoplac on segment IX (number = segment)	rt	median tendon beneath posterior end of rectum
gp (+ number)	gonapophysis (number = segment)	sa	spine on antelaterocoxa IX
GP (+ number)	sclerite of gonapophysis (number = segment)	sb	subanal lobe
gt	anterior tendon of coxa VIII, median to apodeme ga	si (+ number) SI (+ number)	spiracle (number = segment) spiracle sclerite (number = segment)
gy	rounded external ridges on ventromesal edge of gonapophysis VIII	sl (+ number) SL (+ number)	stylus (number = segment) stylus sclerotization (number = segment)
gz (+ number)	oblique external ridges distally on gonapophysis (number = segment)	sp SP ST (+ number)	spermatheca sclerotization of spermatheca sternum (number = segment)

T	transverse nerve
tc (+ number)	transverse internal ridge on anterior part of tergum (= supplementary transverse carina) (number = segment)
tf	terminal = caudal projection/filament on tergum XI
TG (+ number)	tergum (number = segment)
tm (+ number)	teeth on distal lateral edge of gonapophysis (number = segment)
tt	cap-like tendon arising from tip of terminal "filament" tf
ty (+ number)	transverse external ridge on posterior part of tergum (= posterior transverse carina) (number = segment)
ut	cap-like tendon arising from posterior tip of subanal lobe
v	shallow groove probably bordering the fused sclerotizations LCa9 and LCp9
va	vagina
vb	anterior bulb-like portion of vagina (bursa copulatrix)
VB	sclerite in basal lateral wall of vagina
vc (+ number)	longitudinal external ridge on lateral margin of tergum (= ventral carina) (number = segment)
vf (+ number)	ventral fold of segment overlapping succeeding segment (number = segment)
vk (+ number)	longitudinal ventromedian external ridge/keel on (latero)coxosternum (number = segment)
vl	lobes flanking vaginal opening
VL	sclerite upon lobe vl
vt	tendon ventromedially on vagina
xl	'x-lobe' (SCHMIDT 1933) on mesal base of subanal lobe
xr	circular internal ridge near hind margin of segment IX
yl	'y-lobe' (SCHMIDT 1933) on ventral base of terminal 'filament'

## 4. Female abdominal morphology of *Calopteryx*

### 4.1. Exoskeleton of female *Calopteryx*

#### 4.1.1. Condition of the cuticle

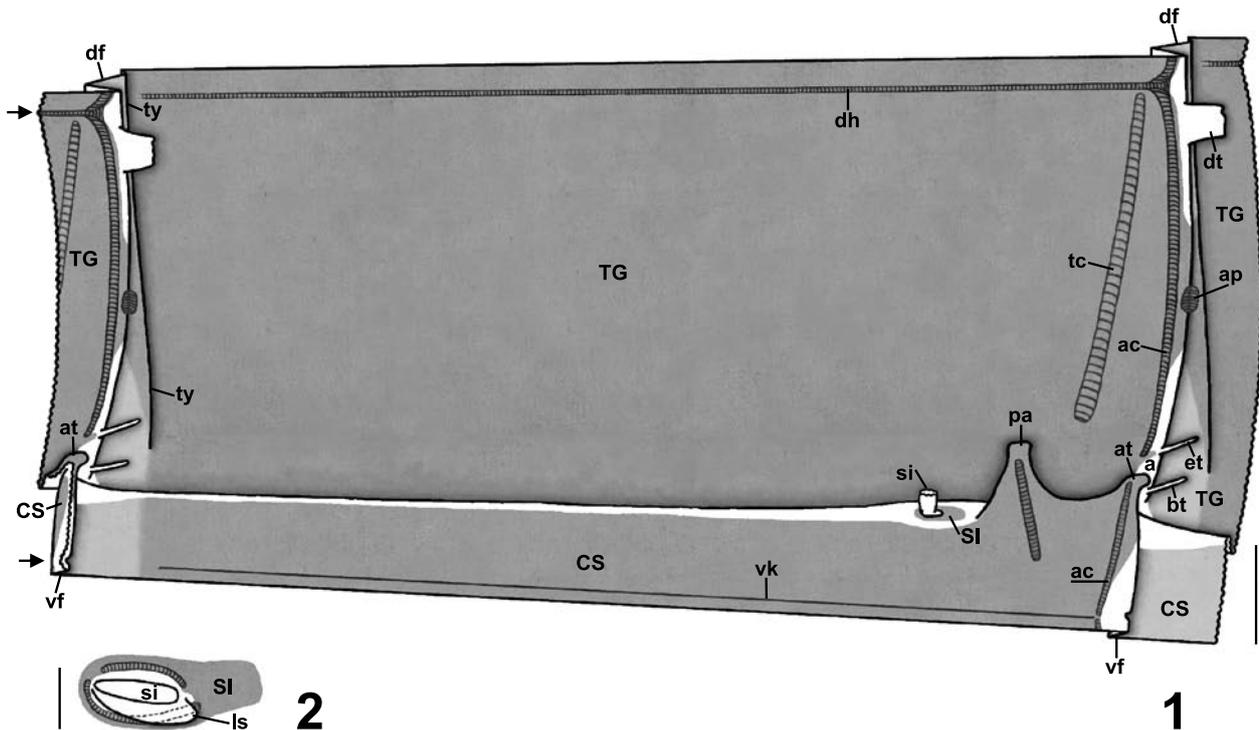
In many areas of the body wall the cuticle has two layers that are easily peeled apart. The external layer shows clearly the pattern of sclerotization (stiff, brown) and membrane (flexible, transparent), while the internal one is milky, flexible, and of a rubber-like texture, with occasional melanization (for the same condition

in Dermaptera see KLASS 2001a: 255). Cuticle thickness varies strongly along the body surface, and either layer, or both, can contribute to a thickening of the cuticle. In some areas thick cuticle is well delimited from the thinner surrounding cuticle. It is attempted to include information on such distinct thickenings, which form ridges or patches. It should be noted that in young imagines many of the structures that depend on cuticular thickening (ridges, tendons, etc.) are much less developed than in fully matured ones. In addition, fusions between particular sclerites are often more extensive in mature imagines than in teneral ones.

#### 4.1.2. Exoskeleton of segments IV–VII

The very wide, transversely arched terga **TG** and the narrow coxosterna **CS** (Fig. 1) of the approximately cylindrical midabdominal segments are very long. The lateral parts of a tergum considerably overlap the lateral parts of the corresponding coxosternum, and both terga and coxosterna very narrowly overlap their succeeding counterparts (folds **df**, **vf**). The narrow cuticle bending forward from the sclerites' posterior margins is largely membranous. On the macerated terga and coxosterna many muscle insertions are recognizable as whitish, slightly swollen areas internally, and as bright, polished areas externally.

The tergum **TG** (Figs. 1, 24) has a distinct antecosta **ac** (= anterior transverse carina of TILLYARD 1917), which becomes narrower towards the lateral margins and eventually obliterates; around the dorsal midline **ac** is weakly developed. An acrotergite (in front of **ac**) is indistinct along the dorsomedian and far lateral anterior tergal margins, but very distinct in the dorso-lateral area, where it even bends back posteriad into the fold **df** and thus almost contacts the hind margin of the preceding tergum. Shortly behind the antecosta a very shallow, inconspicuous internal ridge **tc** (= supplementary transverse carina), which is more heavily sclerotized than its surroundings, separates a fairly smooth anterior area of the tergum from the larger posterior part that bears a sculpture of transverse ribs. A transverse external ridge **ty** (= posterior transverse carina) delimits a narrow, largely very weakly sclerotized posterior portion of the tergum from the heavier anterior main part. Neither **tc** nor **ty** reach the lateral tergal margin, and both are weakly developed around the dorsal midline. In a roughly triangular area (Figs. 1, 24) the sclerotization behind **ty** is as strong as that in front of it. The hind tip of the triangle is opposed to the broadest part of the acrotergite of the following tergum. In this area where heavy sclerotizations of successive terga almost meet and the flexible cuticle between them is very narrow, the cuticle of the dorsal fold **df** is strongly thickened to form a soft, flexible



**Figs. 1, 2. *Calopteryx virgo*, exoskeleton of midabdominal segments.** Sclerotization grey, weak sclerotization shown lighter. Cuticular ridges/thickenings indicated by ladder-shaped patches or ribbons. **1:** Left half of segment and adjacent parts of neighbouring segments, internal view. Dorsal part bent, lying in same plane as ventral part. Undulate lines are cuts through cuticle. Orientation: ↑ dorsomesal, ↓ ventromesal, → anterior. Large arrows at left side indicating dorsal and ventral midline. Longitudinal line on coxosternum indicating extension of ventral keel vk. Scale 0.5 mm. **2:** Left spiracle, dorsal internal view. Orientation: ↑ lateral, ↓ mesal, → anterior. Opening of spiracle represented by slit si in center. Scale 0.1 mm.

patch **ap** that fills fold **df** and restricts its extensibility. The area of patch **ap** thus constitutes an articulation between successive terga. When the abdominal segments are bent vertically, the intertergal membranes (and partly the weak sclerotization behind ridge **ty**) above and below patch **ap** fold in and out, **ap** constituting the point of rotation. The left and right patches **ap** of a segment thus constitute kind of a dicondylic articulation between successive segments (intertergal articulations). Along the dorsal midline of the tergum runs a narrow whitish line **dh** (= middorsal carina) with slightly inwardly thickened cuticle but fairly thin sclerotization; it establishes a middorsal hinge line, i.e., if the lateral parts of a tergum are artificially forced towards each other, the tergum properly folds along **dh**. Line **dh** reaches the anterior tergal margin, where it divides the antecosta into two articulated halves. Posteriorly **dh** obliterates shortly in front of ridge **ty**. Three delicate membranous tendons arise in front of the anterior tergal margin: the broad **dt** near the dorsal midline, and the slender **et** and **bt** at and shortly ventral to the lateral end of the antecosta. A small anterior extension **a** of the tergum supports the base of tendon **et**.

The coxosternum **CS** (Fig. 1) bears far anteriorly two pairs of apodemes **at** and **pa** ('sternal apophyses'),

whose internal faces are sclerotized (by parts of **CS**) but whose external faces are largely membranous. Both are supported by weak internal ridges, the anterior of which, **ac**, almost meet in the midline and may together constitute the ventral part of the antecosta. In its far posterior part the coxosternum quite abruptly becomes narrower, weaker, and very flexible, and frequently it is here divided medially by very weak melanization or membrane (not shown in Fig. 1). At its hind margin, where it curves anterodorsally around the ventral fold **vf**, **CS** becomes distinctly broader and heavier again (though also this part is fairly flexible); it extends laterad into the external walls of the apodemes **at** (Fig. 1 left side), thus establishing a close contact between successive coxosterna. The ventral midline of the coxosternum bears a narrow external ridge **vk** (Fig. 1), which in an internal view appears as a narrow whitish groove; in contrast to the dorsal midline **dh** the sclerotization is not weakened along **vk**. Yet, in weakly sclerotized (young?) specimens **vk** acts, as seen in artificial movement, as a hinge line, but such a function is hardly recognizable in more heavily sclerotized individuals. Ridge **vk** obliterates posteriorly where the coxosternum becomes weaker.

The moderately wide pleural membrane bears a small oval sclerite **SI** upon whose posterior half the

spiracle **si** opens (Figs. 1, 2). The opening (**si** in Fig. 2) is associated with a membranous internal lobe **ls** on its mesal face. Opening and lobe together are embraced by two curved ridges on the **SI**-sclerite (Fig. 2). The tracheal base immediately internal to these has a narrow ring-shaped zone with anastomosing ridges that enclose polygonal craters (zone **ZE** in K<sub>CLASS</sub> 2000: figs. 8–13, 2001a; so far reported for Dictyoptera, Dermaptera, and Orthoptera); the ring is much broader in the posterior two thirds of the tracheal base. Internal to zone **ZE**, and apparently sharply delimited from it, the taenial sculpture of the trachea begins (zone **ZF** in K<sub>CLASS</sub> 2000: figs. 8, 9). There is nothing like an atrium external to zone **ZE**.

It is noteworthy that segment VII in *Calopteryx* largely corresponds in the abovementioned structural features with the preceding segments; the only difference is that the posterior rim of coxosternum VII is neither broadened nor strengthened (according to the absence of apodemes **at** on the following laterocoxosternum VIII, Fig. 3). This contrasts with conditions in many other ‘lower-grade’ Insecta (e.g., Zygoptera, Ephemeroptera, Dictyoptera), where the posteroventral part of segment VII is more or less strongly modified due to genitalic functions, forming various kinds of subgenital lobes and occasionally bearing the primary gonopore (ROUSSET 1973; K<sub>CLASS</sub> 1998).

#### 4.1.3. Exoskeleton of segment VIII

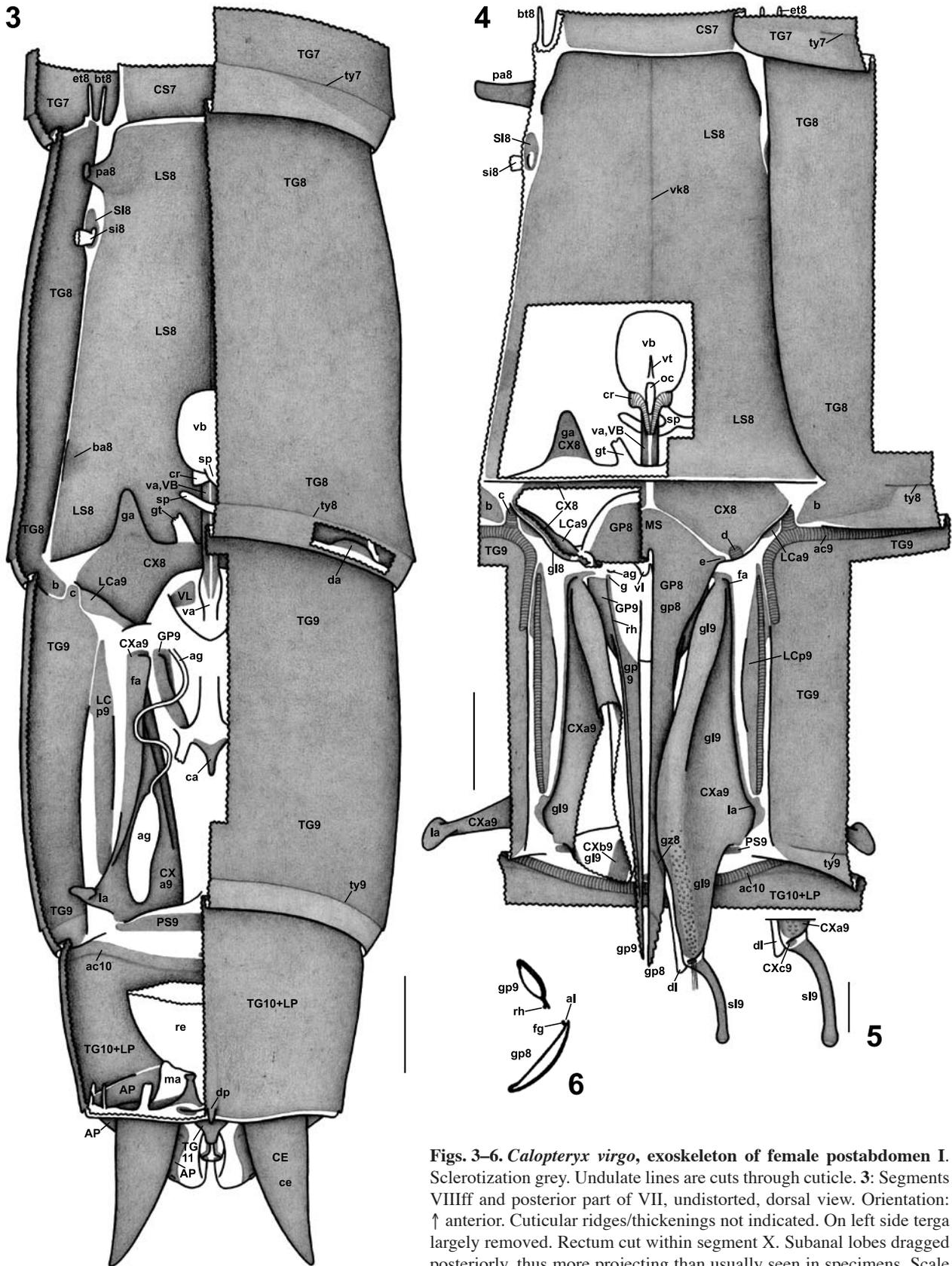
Tergum **TG8** and the pleural membrane with spiracle **si8** (Figs. 3, 4, 7) are much shorter than their preceding counterparts but conform with them – with the following exceptions: The middorsal hinge **dh** is, especially in its posterior part, less clear-cut and less functional (antecosta **ac** is dorsomedially divided as in the preceding segments). The hind margin of **TG8** lacks the triangular heavy sclerotization and patch **ap**, and hence a typical intertergal articulation with **TG9**. Instead, **TG8** forms at its posterolateral corner a strongly sclerotized extension **b**, which closely approaches the articulation between the IXth-segmental tergum **TG9** and antelaterocoxa **LCa9** (see below).

Laterocoxosternum **LS8** (Figs. 4, 7) resembles the preceding coxosterna **CS**, but it has only one pair of anterior apodemes (probably **pa8**), and in the posterior third of its lateral margin it bears an indistinct internal fold **ba8** upon a small heavily sclerotized area. The posterior rim of **LS8** is broad but not strengthened. The ventral ridge **vk8** obliterates in the posterior part of **LS8**; regarding its function the same is true as for the preceding **vk**.

The posteroventral part of segment VIII, which bears the gonapophyses **gp8** and the genital opening, shows a complicated architecture (Figs. 4, 7, 9). Paired

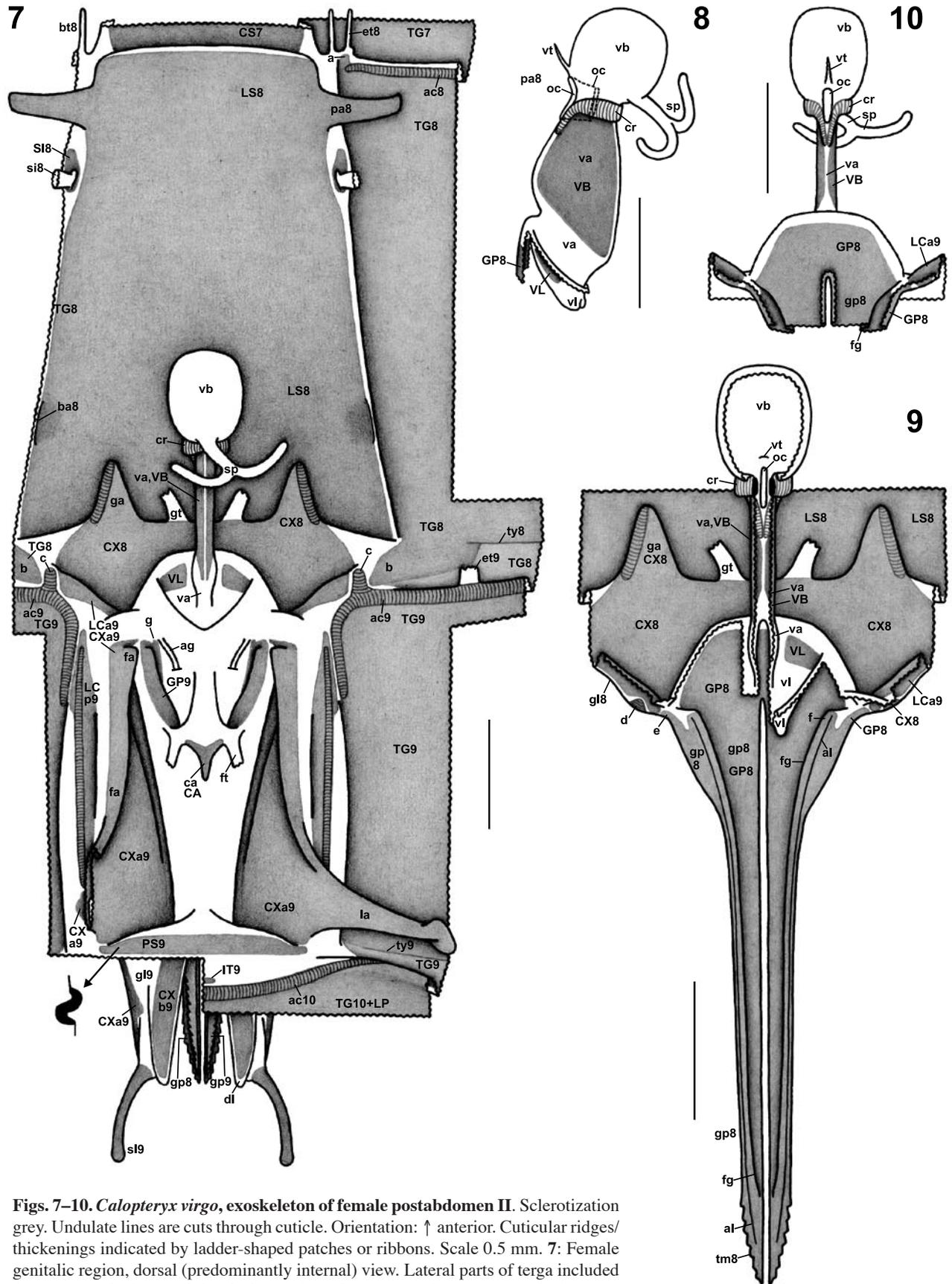
plates **CX8**, immediately behind **LS8**, bear on the anterior margin a stout lateral apodeme **ga** (with a dorsal internal ridge) and a membranous mesal tendon **gt**. The posterolateral margin of **CX8** lies on a broad, short outfolding **gl8**, which overlaps much of the antelaterocoxa IX **LCa9** following behind **CX8**. Along the posterior edge of **gl8** the sclerotization of **CX8** largely terminates and is separated from **LCa9** by a narrow membrane. Far mesally, however, a discrete thickened extension **d** of sclerite **CX8** bends around the edge to articulate with **LCa9** (Fig. 9). Within this narrow articulation area **CX8** and **LCa9** are connected by very weak sclerotization; a very incomplete fusion between the sclerites is thus indicated (Figs. 4, 9; area unfolded and schematized in Fig. 26). The posteromesal margin of **CX8** meets the sclerotization **GP8** of the gonapophyses **gp8**; the contact is particularly tight immediately mesal to the extension **d**, where the **GP8**-base forms a lateral extension **e** that joins the articulation between **CX8** and **LCa9** (Figs. 4, 9).

The sclerites **GP8** occupy the entire gonapophyses **gp8** and are basally broadly interconnected along the midline (Figs. 4, 9, 26, 28). The **GP8**-sclerotization at the ventral **gp8**-base shows a pair of oblique lines of increased flexibility (Fig. 26, lines flanking ‘**MS**’; recognizable when the **gp8** are forced apart by pressing them from ventrally against a firm ground). For reasons given below the median sclerotization in between the two lines is considered a sclerite of its own, **MS**. At the dorsal **gp8**-base the fused **GP8** occupy the ventral wall of a wide invagination (Figs. 9, 10). The dorsal wall of this invagination receives anteromedially a laterally compressed tube, the vagina **va** (Figs. 7–9), and posterolaterally it forms a pair of small lobes **vl**, which thus guard the entrance to the vagina, and which bear small sclerites **VL** at their bases. The compressed posterior portion of the vagina is strengthened by a pair of lateral plates **VB**; the bulb-like anterior (further internal) portion **vb** (often called the spermatheca in the literature; ‘bursa copulatrix’ in HAYASHI & TSUCHIYA 2005) is membranous and bears posterodorsally a forked spermatheca **sp** (often called the spermathecal gland; ‘spermatheca’ in HAYASHI & TSUCHIYA 2005). The border between the anterior and posterior portions of the vagina is marked by a soft, collar-shaped cuticular thickening **cr**, between whose ventral arms the vagina receives the common oviduct **oc** (which theoretically should also include an extended oviduct **oe**). In all KOH-macerated specimens the retained, i.e., intima-bearing **oc** was very short and evaginated into the vaginal lumen (which is external space; Fig. 8, artificially invaginated in Fig. 30). Apparently, most of the common oviduct, the part here called **oco**, and the entire lateral oviducts **ola** (both shown in Fig. 19) lack an intima. In front of the **oc**-opening the vaginal bulb **vb** bears a midventral tendon **vt**.



**Figs. 3–6. *Calopteryx virgo*, exoskeleton of female postabdomen I.** Sclerotization grey. Undulate lines are cuts through cuticle. **3:** Segments VIIIff and posterior part of VII, undistorted, dorsal view. Orientation: ↑ anterior. Cuticular ridges/thickenings not indicated. On left side terga largely removed. Rectum cut within segment X. Subanal lobes dragged posteriorly, thus more projecting than usually seen in specimens. Scale 0.5 mm. **4:** Female genitalic region, ventral (predominantly external) view. Lateral parts of terga included (more extensively on right side) and bent into same plane as ventral elements; apodemes la bent sideward. Orientation: ↑ anterior. Cuticular ridges/thickenings indicated by ladder-shaped patches or ribbons. On left side gonapophysis VIII and gonoplac IX cut basally. Window cut into laterocoxosternum VIII to show intima-bearing parts of internal genitalia (gonoducts). Scale 0.5 mm. **5:** Stylus and its base, shown as in Fig. 4 but without setae. Scale 0.2 mm. **6:** Gonapophyses VIII and IX, schematic transverse section at about midlength. Orientation: ↑ dorsal, ↓ ventral, → lateral. Thickness of line indicating strength of sclerotization. No scale.

and bent into same plane as ventral elements; apodemes la bent sideward. Orientation: ↑ anterior. Cuticular ridges/thickenings indicated by ladder-shaped patches or ribbons. On left side gonapophysis VIII and gonoplac IX cut basally. Window cut into laterocoxosternum VIII to show intima-bearing parts of internal genitalia (gonoducts). Scale 0.5 mm. **5:** Stylus and its base, shown as in Fig. 4 but without setae. Scale 0.2 mm. **6:** Gonapophyses VIII and IX, schematic transverse section at about midlength. Orientation: ↑ dorsal, ↓ ventral, → lateral. Thickness of line indicating strength of sclerotization. No scale.



**Figs. 7–10.** *Calopteryx virgo*, exoskeleton of female postabdomen II. Sclerotization grey. Undulate lines are cuts through cuticle. Orientation: ↑ anterior. Cuticular ridges/thickenings indicated by ladder-shaped patches or ribbons. Scale 0.5 mm. **7:** Female genitalic region, dorsal (predominantly internal) view. Lateral parts of terga included (more extensively on right side) and bent into same plane as ventral elements; apodemes la bent sideward (but left one cut near base). Longitudinal section through sclerite PS9 given at left bottom (arrow), with epidermal surface to the left. **8:** Vagina with spermatheca and intima-bearing oviduct (natural position, i.e., evaginated into vagina lumen), left view. **9:** Posterior midventral area of segment VIII, dorsal (predominantly internal) view. In vulva area some more parts removed on left side. Dorsal wall of internal genitalia (gonoducts) removed. **10:** Vagina and gonapophyses VIII bases, ventral (predominantly internal) view.

The gonapophyses **gp8** (Figs. 4, 9) are entirely sclerotized, though **GP8** is weaker along the dorsomesal face, which lines the egg channel enclosed by the gonapophyses VIII and IX (section Fig. 6). A mesally directed fold **fg** runs along most of the dorsal gonapophysis wall (Figs. 9, 10). It bears the aulax **al**, a longitudinal groove into which a ridge of gonapophysis IX, the rhachis **rh**, is inserted (Fig. 6) in order to interlock **gp8** and **gp9** in a way that the two can slide upon each other (**al** and **rh** together form the olistheter). The anterior end of the aulax lies on a small extension **f** of sclerite **GP8** (Fig. 9). Distally the **gp8** bear a series of lateral saw-teeth **tm8**, which are directed laterodistad, and three oblique ventral ridges **gz8** (two of them visible in Fig. 4).

#### 4.1.4. Exoskeleton of segment IX

Tergum **TG9** (Figs. 3, 4, 7), which is slightly shorter than **TG8**, differs strongly from the preceding terga. Antecosta **ac9** is generally more massive; it traverses the dorsal midline as a heavy ridge, and also its lateral parts, which articulate with the laterocoxa IX sclerites **LCa9** and **LCp9**, are much heavier. Nevertheless, **ac9** has a middorsal point of weakness, which constitutes an indistinct articulation. A middorsal hinge **dh9** behind it is only poorly indicated. An intertergal articulation with the following tergum **TG10** and a patch **ap** are absent. The posterior transverse carina **ty9** almost reaches the lateral tergal margin. Tendon **et9** is located further dorsally than in the preceding segments, tendon **dt9** is weakly developed, and a tendon **bt** is absent. Between **et9** and **dt9** the anterior tergal margin forms a lobe-like apodeme **da** (Fig. 3). The pleural membrane lacks a spiracle and a sclerite **SI**.

On the ventral side (Figs. 4, 7) the anteriormost IXth-segmental sclerites are the abovementioned antelaterocoxae **LCa9**, whose lateral and mesal tips articulate with a small extension **c** of **TG9** and with extension **e** of **GP8**. A heavy internal ridge on **LCa9** (Fig. 26), which is continuous with the tergal antecosta **ac9** and may be a ventral part of antecosta **ac9**, strengthens **LCa9** between these articulations. **TG9** and **LCa9**, though distinctly hinged upon each other when artificial movement is observed, are partly synsclerotic: They are largely separated by stripes of weak melanization (external view) or absent melanization (internal view; the cuticle is very thick within the articulation!), which altogether constitute the hinge; especially in fully sclerotized specimens, however, in both views one notices a narrow, conspicuous black stripe (**h** in Fig. 26) that traverses the articulation near the posterior rim of the internal ridge.

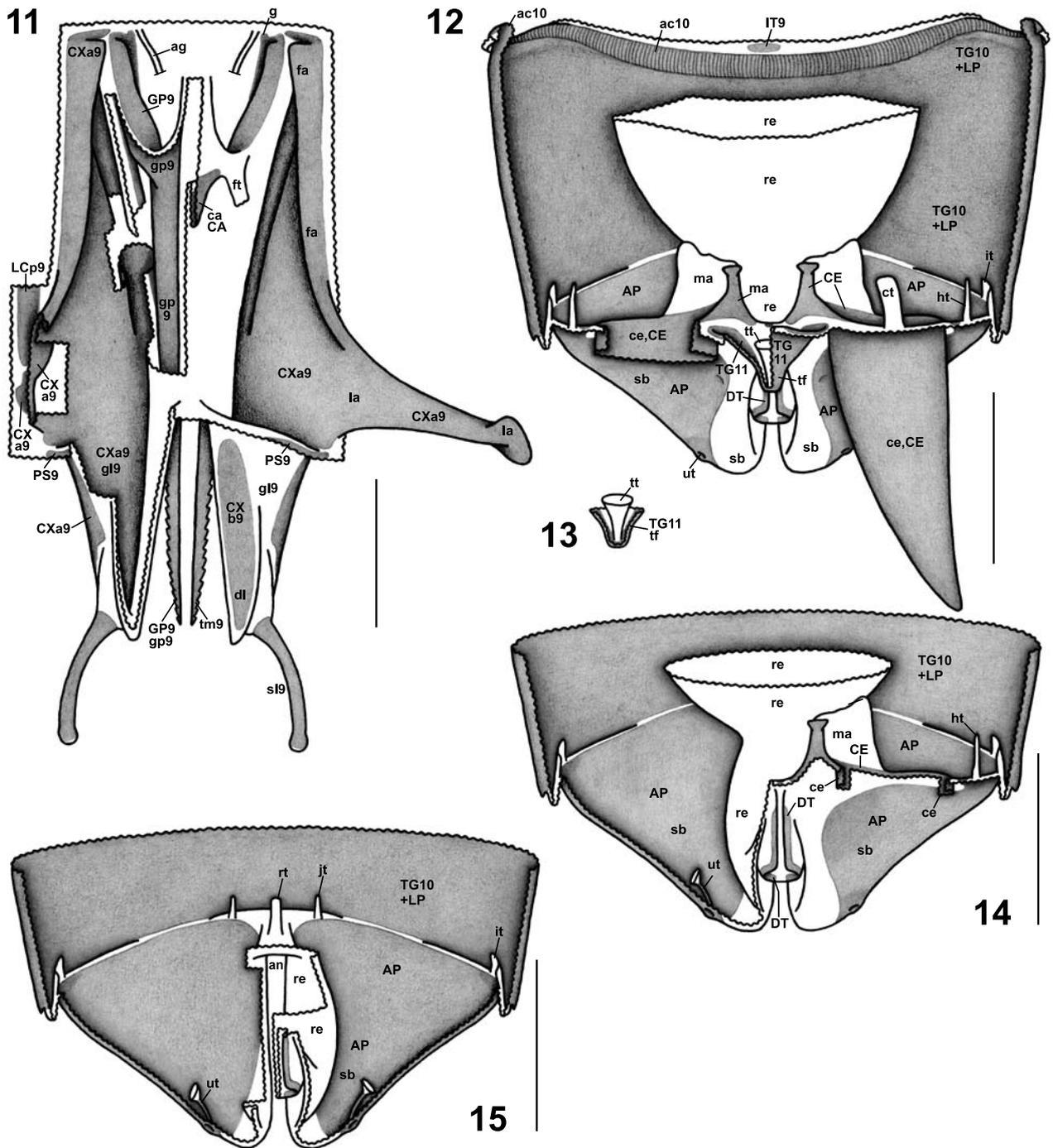
The ribbon-like sclerite **LCp9** (Figs. 4, 7), likewise strengthened by an internal ridge, extends along

the lateral margin of **TG9**. Its anterior part joins **TG9** particularly closely to form a hinge-like articulation, and in fully sclerotized specimens it is connected with **TG9** by a wide bridge of weak sclerotization. The posterior tip of **LCp9** articulates with coxa IX **CXa9** (Fig. 4).

The gonoplares **gl9** are large ventral projections (Figs. 4, 39) that somewhat ensheath the two pairs of gonapophyses, **gp8** and **gp9**. The lateral face and ventral edge of **gl9** are heavily sclerotized by the main gonoplares sclerite **CXa9**. On the lateral gonoplares base **CXa9** forms a deeply invaginated posterior apodeme **la** and a ridge-like, mesally directed anterior apodeme **fa** (Figs. 3, 7, 11). The distal part of the gonoplares bears a tubercular sculpture along its ventral edge (Figs. 4, 39), a tuft of long setae distal to these tubercles, a sclerotized stylus **sl9** (with sclerite **SL9**, which is weakened at the tip of the stylus; Fig. 5), and a minute oval sclerite **CXc9** at the ventral base of the stylus (Fig. 5). The dorsal gonoplares wall forms a lobe-like element **dl**, which bears a ribbon-shaped sclerite **CXb9** (Figs. 11, 39).

The gonapophyses **gp9** (Figs. 4, 11) originate between the anterior gonoplares bases and are, apart from their basal-most mesal walls, entirely sclerotized by **GP9**. Neither the gonapophyses **gp9** nor the sclerotizations **GP9** of the two sides are basally interconnected. The abovementioned rhachis **rh**, a fine external ridge (Figs. 4, 6), runs along most of the ventral side of **gp9** and terminates basally on a small extension **g** of sclerite **GP9** (Figs. 11, 39). In the undistorted ovipositor the extensions **f** (of sclerite **GP8**, Fig. 9) and **g** (of sclerite **GP9**, Fig. 11), and thus the anterior ends of the aulax **al** and rhachis **rh**, are at the same vertical level, exactly opposing each other. Distally the **gp9** bear a series of lateral saw-teeth **tm9**, which are directed laterobasad (Fig. 11). The series of **tm9** extends farther basally than the series of **tm8** on **gp8**. Furthermore, the dorsolateral face of the **gp9** bears a series of oblique ridges **gz9**, which are much more numerous than the **gz8**, and which, in contrast to the latter, are associated with the **tm9**-teeth: each **tm9** is the strongly projecting ventrolateral end of a ridge **gz9**. Immediately anteromesal to extension **g** of **GP9** opens on each side an accessory gland **ag**, which is composed of a thin outlet duct and an oval reservoir lying above the gonoplares bases (Figs. 3, 11). Shortly behind the **gp9**-bases, within the membrane arching over the gonapophyses VIII and IX, originates the central apodeme **ca**, which is sclerotized (sclerite **CA**; Figs. 3, 7, 11), in a lateral view has the outline of a cockscomb, and is flanked by a pair of membranous tendons **ft**.

A strong transverse sclerite here preliminarily called the poststernum IX **PS9** extends between the posterior gonoplares bases; its lateral tips are articulated upon the **CXa9** (Figs. 7, 61). While in weakly



**Figs. 11–15.** *Calopteryx virgo*, exoskeleton of female postabdomen III. Sclerotization grey. Undulate lines are cuts through cuticle. Orientation: ↑ anterior. Cuticular ridges indicated by ladder-shaped patches or ribbons. Scale 0.5 mm. **11:** Midventral area of segment IX, dorsal (predominantly internal) view. On left side parts of gonoplac IX and neighboring elements removed; on right side apodeme la bent sideward. **12:** Segments Xff, dorsal view. Dorsal part of sclerite ring X and left-dorsal part of tergum XI removed. Left cercus and rectum cut basally. **13:** Tip of terminal projection tf with cap-tendon tt. **14, 15:** The same as in Fig. 12 but further parts removed.

sclerotized individuals **PS9** and **CXa9** are separated by a narrow articulation membrane, they are narrowly synsclerotic in more heavily sclerotized specimens; also in the latter, however, a discrete hinge between the sclerites can be recognized when these are moved. The posterodorsal part of **PS9** is folded inward, the anteroventral part folded outward, and the cuticle along

these transverse folds is distinctly thickened. A sagittal section through **PS9** is thus S-shaped (Fig. 7, left bottom, epidermal side of cuticle to the left), and the sclerite is thus fairly stiff in a transverse direction. A minute midventral sclerite **IT9** is situated shortly behind **PS9** (Figs. 7, 12, 61).

#### 4.1.5. Exoskeleton of segments X and XI and telson

Segment X is, apart from a narrow seam along its dorsal hind margin, entirely sclerotized by a ring called here sclerite ring X, **TG10+LP** (Figs. 3, 12). The front margin of **TG10+LP** (Fig. 12) is shaped as an inwardly directed groove in the dorsal and lateral areas, and as a strong internal transverse ridge in the ventral area, which together are here regarded as antecosta **ac10**. Along the dorsal midline **TG10+LP** is weakened and forms a low external ridge, which posteriorly terminates in a small process **dp** (Fig. 3).

Tergum XI **TG11** joins the dorsomedian hind margin of **TG10+LP** (Figs. 3, 12) and altogether forms a blunt projection **tf**. From the tip of **tf** a funnel-shaped, tendon-like cuticular structure **tt** (Fig. 13) projects inwardly, leaving an externally visible scar at the point of its invagination.

The bases of the cerci **ce** join the dorsolateral hind margin of **TG10+LP**. The cerci show neither any articulations with neighboring sclerites nor any indication of a subdivision into cercomeres (annuli or "segments"). The mesal base of the cercus is folded inward to form an apodeme **ma**, which is composed of a membranous, lobe-like ventral part and a stout, heavily sclerotized dorsal part (Fig. 12); the sclerotization of the latter is firmly connected with the cercal sclerotization **CE**. A minute median sclerite is usually present between the **ma**-bases of the two sides. A membranous tendon **ct** originates in the membrane immediately above the dorsal base of the cercus (Fig. 12).

The broad subanal lobes **sb** arise from the area beneath the cercal bases (Figs. 12, 14) and are largely sclerotized by the paraproctal sclerites **AP** (whose borders are less discrete than shown in the illustrations). The ventral and lateral anterior margins of the sclerites **AP** closely join the hind margin of the **TG10+LP** ring (Figs. 12, 14) and give rise to tendons **ht** and **it**, around the origins of which the sclerites **AP** are particularly heavy. Tendons **jt** originate from the membrane near the anteroventral corners of the sclerites **AP** (Fig. 15). The dorsal anterior margins of the sclerites **AP** approach the base of the cercus, but there is no contact between sclerites **AP** and **CE**. Distally each subanal lobe forms a tendon **ut** with a narrow sclerotized stalk and a widened or distinctly funnel-shaped membranous apex. The point of origin of **ut** is visible as a scar externally, around which the sclerites **AP** are particularly heavy (like tendon **tt**, the **ut** remind of the cap-tendons found in the thorax of Odonata, see, e.g., ASAHINA 1954: pl. 31 D29). The tips and mesal walls of the subanal lobes are membranous and continue inwardly into the walls of the rec-

tum **re** (Figs. 14, 15), thus bordering the anus **an** laterally. Where the dorsal subanal lobe walls meet in the midline, a curved posteriorly directed fold is formed (Fig. 14), which is U-shaped as viewed from behind (U open dorsally), which protrudes into the anus from dorsally, and whose edges are weakly sclerotized (paired sclerite **DT**, which is less discretely bordered than shown in the illustrations).

## 4.2. Musculature of female *Calopteryx*

### 4.2.1. Extent of muscle studies

Of the musculature present in the abdomen from segment IV onward only the intrinsic muscles of the internal genitalia (except muscle **22**), heart, and rectum are herein not considered. Some formations are included that lack transverse striation but may be degenerated (nymphal) muscles. One should keep in mind the age-dependent condition of many muscles, which only in some cases is particularly mentioned though not studied in detail. Unless otherwise noted a muscle is present as a pair.

### 4.2.2. Musculature of segments IV–VII

The musculature in these segments is identical (Figs. 16–18) – except for proportions and the presence of muscle **12** only in segment VII (Fig. 19). Homonomous muscles are given the same number. Each insertion is assigned to the secondary segment it lies upon: 'N' designates the secondary segment, or a component of it, whose major part corresponds to the primary segment the muscle belongs to. 'N+1' designates the succeeding secondary segment, or a component of it. Muscles having both insertions on 'N' are intrasegmental, muscles having one insertion on 'N+1' are intersegmental relative to secondary segmentation.

**1**: Tergum N, anterolateral part ↔ Coxosternum N, anterior edge of apodeme **pa**. Intrasegmental tergo-coxosternal muscle. One strong, compact sheet. — **2**: Tergum N, anterior lateral margin ↔ Coxosternum N, anterior lateral margin on external face of apodeme **pa**. Intrasegmental tergo-coxosternal muscle. One moderately strong, compact sheet (shown separately at bottom of Fig. 16). — **3, 4**: Tergum N, lateral part ↔ Coxosternum N, lateral margin, and pleural membrane beside it (especially in case of **3**). Intrasegmental tergo-coxosternal muscles. Each a short, broad sheet that in the used alcohol material consisted of several small, compact bundles. — **5**: Tergum N, posterolateral part ↔ Pleural membrane near anterolateral cor-

ner of coxosternum N+1, on tendon **bt**. Intersegmental tergo-coxosternal muscle. One slender, compact bundle. — **6**: Coxosternum N, posterior part ↔ Coxosternum N+1, anterior margin. External ventral muscle. One moderately strong, compact sheet. — **7**: Tergum N, posterolateral part ↔ Tergum N+1, lateral anterior margin, including tendon **et**. Lateral external dorsal muscle. One strong, compact sheet. — **8**: Tergum N, posteromesal part ↔ Tergum N+1, mesal anterior margin, including tendon **dt**. Median external dorsal muscle. One strong, compact sheet.

**9**: A delicate sheet of connective tissue and embedded fibers (Fig. 18) that continues through the abdomen up to the anterior part of segment VIII. Ventral diaphragm; unpaired, entirely above the CNS. It has insertions on all apodemes **at** and **pa** (Fig. 16; hence two insertions per side in segments up to VII, but only one insertion per side in segment VIII, on **pa8**, Fig. 19). From each insertion stout, striated muscle fibers, usually grouped into 4 or 5 discrete bundles, fan out towards the midline. The posterior portion of the fibers inserted on **pa**, however, continues into a strand along the flank of the diaphragm, which reaches the **at** of the following segment (a continuity of the included fibers, however, could not be demonstrated); no longitudinal fibers were observed that in a similar way connect **at** and **pa** of the same segment (Fig. 18). In many places along the flanks of the diaphragm dense bunches of fibers originate from the lateral strands, where they seem to be firmly rooted; their fibers spread towards the midline, most of them showing a transverse to moderately oblique course. In some instances it appeared as if fiber bundles continued from one flank of the diaphragm to the other. In between the bundles inserted on **pa** and **at**, and in between the fiber bunches originating along its flanks, the diaphragm has a series of perforations (left white in Fig. 18). A distinct striation of the fibers of the diaphragm was found only in the bundles near the insertions on **pa** and **at** (i.e., in the parts labeled **9** in Fig. 16).

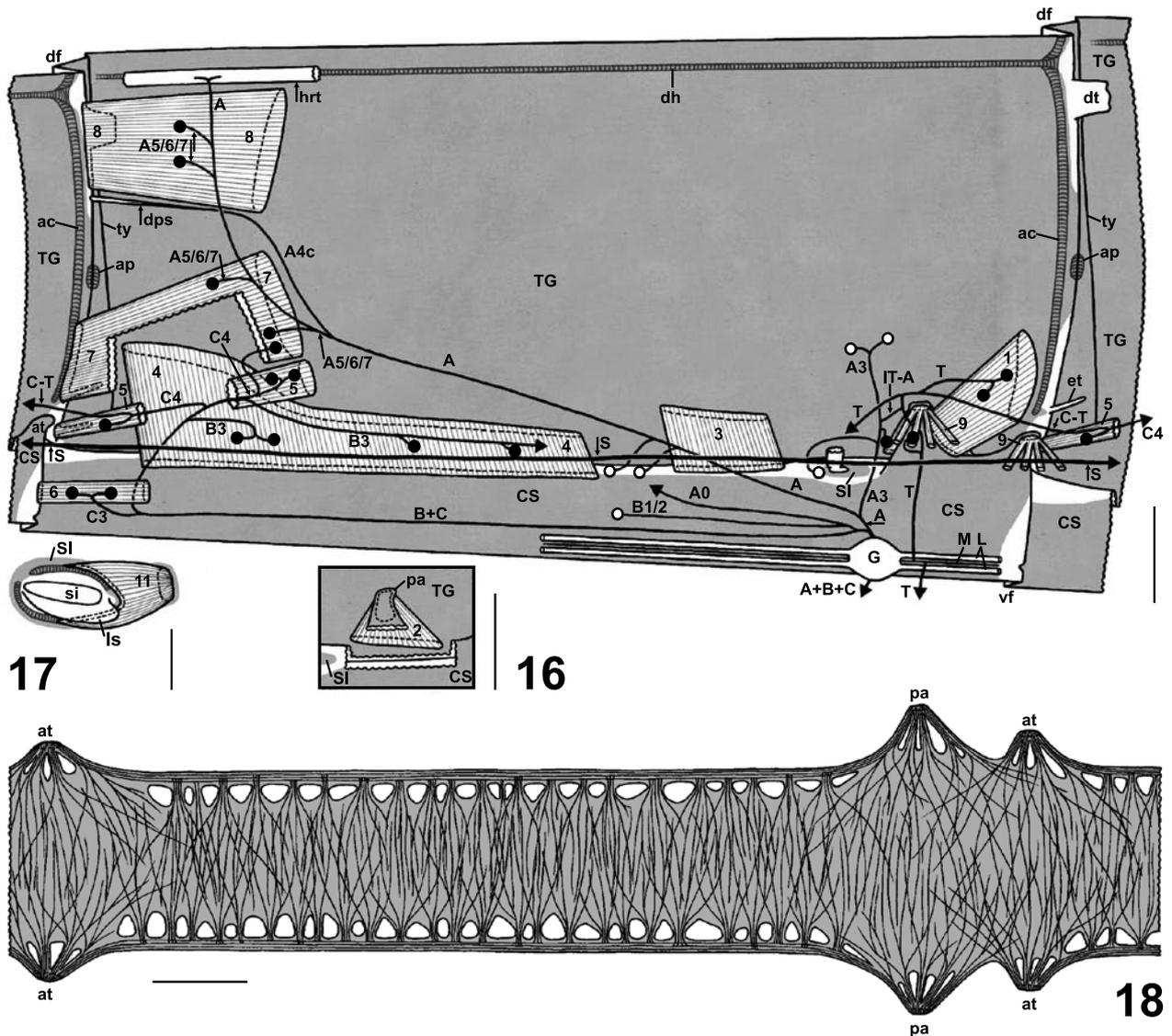
**10**: Striated fibers were occasionally found embedded in a dorsal septum that middorsally contacts the heart wall; discrete tergal insertions were not detected, and closer observation was impossible with the alcohol material available. The fibers (not illustrated) could be vestiges of alary muscles, which are otherwise absent in segments up to VII. — **11**: Spiracle sclerite **SI**, anterior part ↔ Spiracle sclerite **SI**, middle part, on the ridges embracing the spiracle opening (**si**; Fig. 17). Spiracle occlusor. One minute, compact sheet. — **12**: Coxosternum VII, posterior part ↔ Anteromedian ventral wall of vagina, on tendon **vt** (Figs. 19, 20). This muscle peculiar to segment VII is apparently a mesal portion of the external ventral muscle VII (muscle **6**), with which it shares its innervation (see below). One slender, compact sheet.

#### 4.2.3. Musculature of segment VIII

The VIIIth-segmental muscles are shown in Figs. 19, 20. — **13**: Tergum VIII, anterior lateral margin ↔ Laterocoxosternum VIII, anterior lateral margin on external face of apodeme **pa8**. Intrasegmental tergo-laterocoxosternal muscle, homonomous with muscle **2**. One moderately strong, compact sheet. — **14, 15**: Tergum VIII, lateral part ↔ Laterocoxosternum VIII, lateral margin including fold **ba8**, and pleural membrane beside it. Intrasegmental tergo-laterocoxosternal muscles, homonomous with muscles **3, 4** and showing the same condition. — **16**: Tergum VIII, midlength lateral part ↔ Coxa VIII, infolded anterior margin, on tendon **gt**. Intrasegmental tergo-coxal muscle. One strong, compact bundle. — **17**: Tergum VIII, posterolateral corner ↔ Coxa VIII, anterior lateral margin, on lateral edge of apodeme **ga**. Intrasegmental tergo-coxal muscle. One strong, compact bundle. — **18**: Laterocoxosternum VIII, posterior lateral margin, on fold **ba8** ↔ Vagina, midlength lateral wall, on sclerite **VB**. One strong, compact sheet. — **19**: Coxa VIII, lateral part ↔ Vagina, posterior lateral wall, on sclerite **VB**. One strong, compact bundle. — **20**: Coxa VIII, anteromesal part ↔ Vagina, midlength lateral wall, on sclerite **VB**. One strong, compact sheet. — **21**: Coxa VIII, anteromesal part ↔ Vagina, lateral wall, on collar-shaped thickening **cr**. One slender, fairly compact bundle. — **22**: Vagina, lateral wall, on anterodorsal corner of sclerite **VB** ↔ Vagina, lateral wall, on ventral part of thickening **cr**. One moderately strong, compact bundle. — **23**: Coxa VIII, central part ↔ Area around dorsal base of gonapophysis VIII, including sclerite **VL**. Coxo-gonapophyseal muscle. One broad, compact sheet. — **24**: Tergum VIII, midlength lateral part ↔ Tergum IX, lateral anterior margin, on tendon **et9**. Lateral external dorsal muscle, homonomous with muscle **7**. One strong, compact sheet. — **25**: Tergum VIII, midlength mesal part ↔ Tergum IX, mesal anterior margin. Median external dorsal muscle, homonomous with muscle **8**. One strong, compact sheet. — **26**: See remarks for muscle **10**. — **27**: Spiracle muscle VIII, homonomous with muscle **11** and showing the same condition (not shown; cf. Fig. 17).

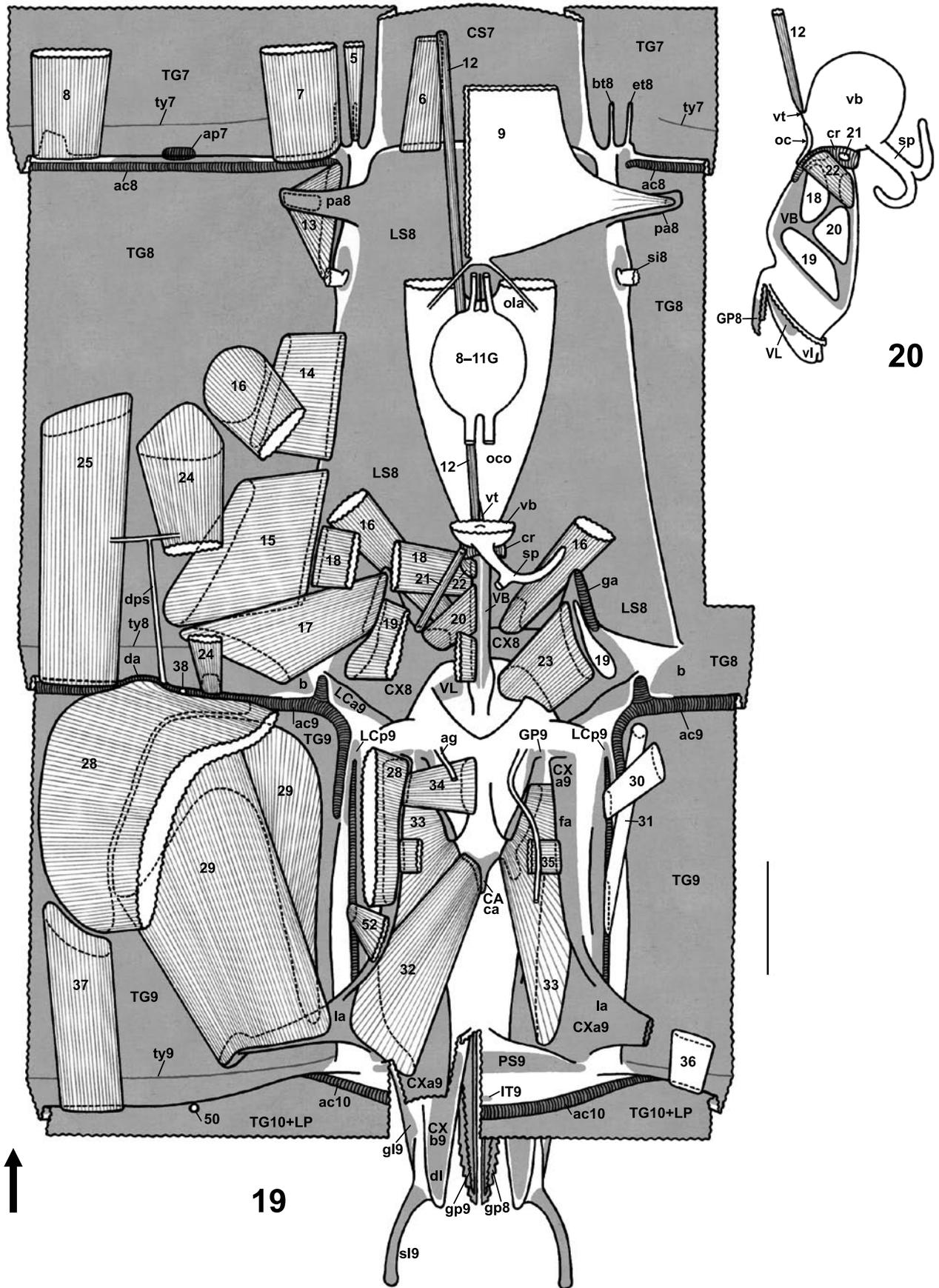
#### 4.2.4. Musculature of segment IX

The IXth-segmental muscles are shown in Fig. 19. — **28**: Tergum IX, mesal part and anterior margin ↔ Coxa IX **CXa9**, anterior part, on apodeme **fa**. Intrasegmental tergo-coxal muscle. One enormously strong, compact bundle. — **29**: Tergum IX, lateral part, with U-shaped insertion area ↔ Coxa IX **CXa9**, posterior part, on apodeme **la**. Intrasegmental tergo-coxal mus-



**Figs. 16–18. *Calopteryx virgo*, musculature and nervous system of midabdominal segments.** Sclerotization grey. Muscles striped according to course of fibers. Undulate lines are cuts through cuticle or ventral diaphragm, or surround cut surfaces of muscles. Dashed lines are hidden borderlines of muscle insertions. **16:** Left half of segment, and adjacent parts of neighbouring segments, internal view. Dorsal part bent into same plane as ventral part. Orientation: ↑ dorsomesal, ↓ ventromesal, → anterior. Only some cuticular ridges/thickenings indicated by ladder-shaped patches or ribbons (cf. Fig. 1). Nerves black from their roots onward. Nerve branches supplying a muscle ending with a black dot, sensory branches ending with a ring; arrowheads upon nerve ends indicate that the nerve continues. Short piece of heart included schematically. CNS, with elements G, L, and M, cut near anterior border of segment and in middle of segment. Muscle 2 and apodeme pa (with basal part cut out) shown separately at bottom of main figure. Scale 0.5 mm. **17:** Left spiracle with its muscle, dorsal internal view. Orientation: ↑ lateral, ↓ mesal, → anterior. Ladder-shaped ribbons representing thickened spiracle bars. Scale 0.1 mm. **18:** Ventral diaphragm (= muscle 9), dorsal view. Orientation: ↑ ↓ lateral, → anterior. Black lines inside diaphragm represent muscle fibers. 'pa' and 'at' mark insertions on respective apodemes (cf. Fig. 16). Area filled with connective tissue shaded in grey, perforations left white. Scale 0.5 mm.

**Figs. 19, 20. *Calopteryx virgo*, musculature of female genitalic region.** Sclerotization grey. Cuticular ridges/thickenings indicated by ladder-shaped patches or ribbons. Muscles striped according to course of fibers. Undulate lines are cuts through cuticle or surround cut surfaces of muscles. Dashed lines are hidden borderlines of muscles and their insertions. Orientation: ↑ anterior. Scale 0.5 mm (for both figures). **19:** Entire female genitalic region, dorsal (predominantly internal) view. Parts of terga included (almost completely on left side: position of dorsal midline of segment IX indicated by large arrow) and bent into same plane as ventral elements; apodemes la bent sideward, right la cut. Alary muscles (38, 50) not shown, but insertions represented by small white areas. Unstripped ribbons 30, 31, 36 represent groups of unstriated fibers, probably degenerated muscles. Mesodermal parts of common oviduct and lateral oviducts (oco, ola), and terminal abdominal ganglion (8–11G) included. **20:** Vagina with spermatheca, left view. Muscles 18–21 not shown, but insertions represented by white areas.



cle. One enormously strong, compact bundle. — **30**, **31**: Tergum IX, anterolateral corner ↔ Postlaterocoxa IX. Intrasegmental tergo-laterocoxal ‘muscles’. Delicate, fairly diffuse sheets of fibers lacking striation. — **32**: Coxa IX **CXa9**, basal lateral wall around base of apodeme **la** ↔ Sclerite **CA** of central apodeme **ca**. One strong, compact bundle. — **33**: Coxa IX **CXa9**, distal lateral wall of anterior half ↔ Tendons **ft** lateral to apodeme **ca**, and basal sclerotization **GP9** of gonapophysis IX. Coxo-gonapophyseal muscle. One strong, compact bundle. — **34**: Coxa IX **CXa9**, most anterior basal lateral wall, on apodeme **fa** ↔ Membrane between bases of gonapophyses IX **gp9**. One moderately strong, compact bundle. — **35**: Transversely between apodemes **fa** of coxae IX **CXa9**. Coxal transverse muscle. One moderately strong, compact sheet; unpaired. — **36**: Tergum IX, posterolateral part ↔ Sclerite ring X **TG10+LP**, lateral anterior margin. Lateral external dorsal ‘muscle’; or perhaps intersegmental tergo-coxosternal ‘muscle’. One delicate, fairly diffuse sheet of fibers lacking striation; found only in some specimens. — **37**: Tergum IX, midlength mesal part ↔ Sclerite ring X **TG10+LP**, dorsomesal anterior margin. Median external dorsal muscle. One moderately strong, compact sheet. — **38**: Tergum IX, anterior margin ↔ Extending towards dorsal midline. Alary muscle IX. It arises as a thin, compact bundle from the tergum, its fibers then spreading fanwise towards the dorsal midline, on which way the striation becomes lost; very delicate.

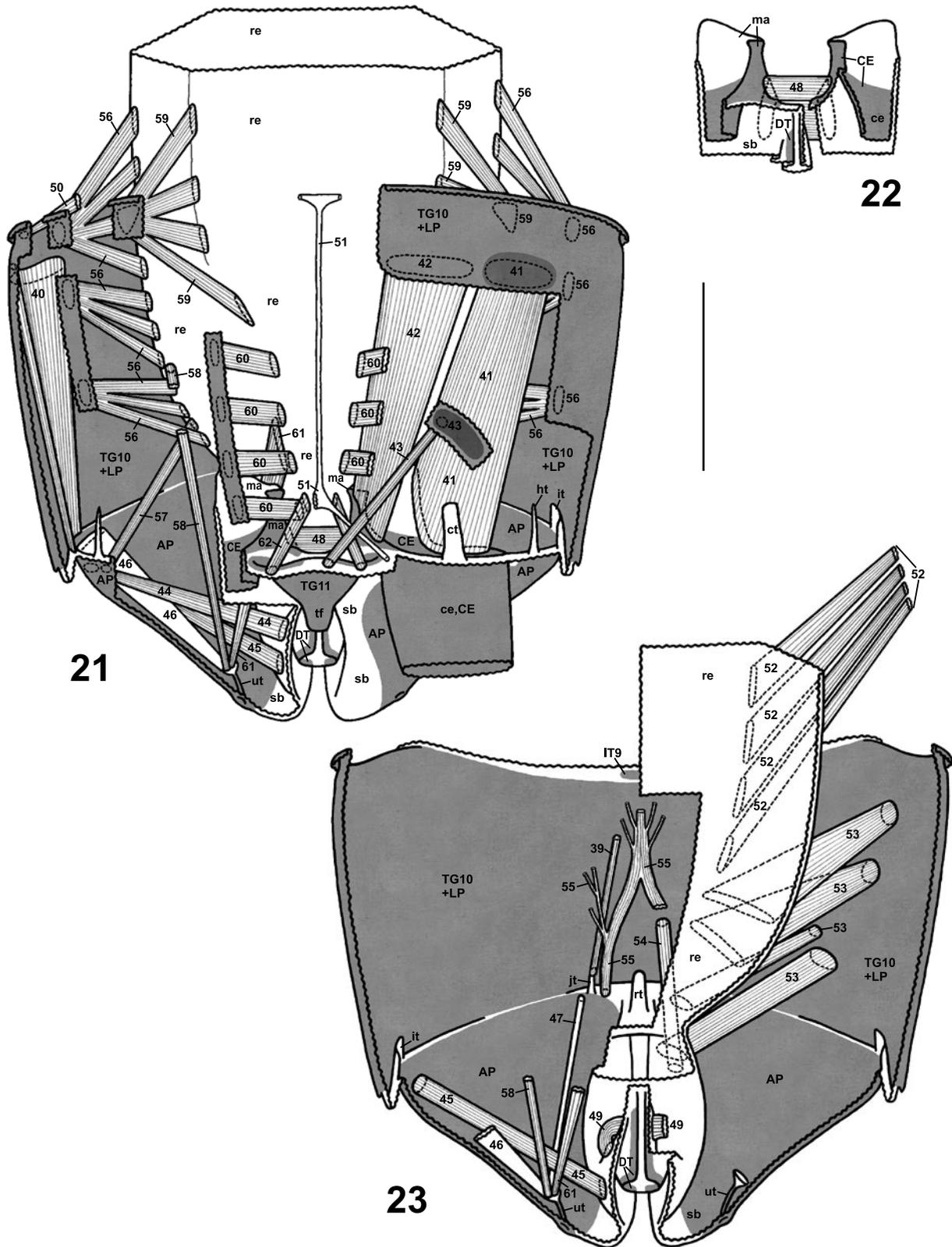
#### 4.2.5. Musculature of segments X and XI and telson

The muscles of the terminal abdomen are shown in Figs. 21–23. — **39**: Sclerite ring X **TG10+LP**, anterior ventromedian part ↔ Tendon **jt** near ventromedian anterior margin of sclerite **AP**. One very slender, compact bundle, which was distinct only in one specimen, while no trace of it was found in some others. — **40**: Sclerite ring X **TG10+LP**, lateral anterior margin ↔ Tendon **it** at lateral anterior margin of sclerite **AP**. One strong, compact sheet. — **41**: Sclerite ring X **TG10+LP**, dorsolateral anterior part (on an externally visible muscle scar) ↔ Ventral base of cercus, on ventrolateral edge of membranous lobe of apodeme **ma**, and lateral to it. One strong, compact sheet. — **42**: Sclerite ring X **TG10+LP**, dorsomedian anterior part ↔ Mesal base of cercus, on dorsolateral edge of apodeme **ma**. One strong, compact sheet. — **43**: Sclerite ring X **TG10+LP**, central dorsal part (on an externally visible muscle scar, which is much larger than the insertion area) ↔ Tergum XI, anterior margin near midline. One slender, compact bundle, which in some specimens was very indistinct. — **44**: Sclerite **AP**, dor-

solateral anterior margin ↔ Membranous mesal wall of subanal lobe **sl**. One moderately strong, compact sheet. — **45**: Sclerite **AP**, ventrolateral anterior margin ↔ Membranous mesal wall of subanal lobe **sl**. One moderately strong, compact sheet. — **46**: Sclerite **AP**, ventrolateral anterior margin ↔ Cap-tendon **ut** of sclerite **AP**. A broad sheet that was distinct only in some specimens (and consistently absent after KOH-maceration), is indistinctly fibrous, and lacks striation; its nature as a degenerated muscle is uncertain. — **47**: Sclerite **AP**, ventral anterior margin ↔ Cap-tendon **ut** of sclerite **AP**. A very slender, unstriated strand that was distinct in most specimens; its posterior insertion could be observed only once. — **48**: Transversely between the mesal cercal bases, the insertion lying on the mesal face of apodeme **ma** and on the membranous dorsal subanal lobe wall immediately behind it (Fig. 22). One strong, compact sheet; unpaired. — **49**: Connecting areas within the membranous mesal walls of the subanal lobes **sl**. One moderately strong, fairly compact bundle. — **50**: Sclerite ring X **TG10+LP**, lateral anterior margin ↔ Extending towards dorsal midline. Alary muscle X, homonomous with and similar to muscle **38**. — **51**: Membrane immediately lateral to anterior margin of tergum XI ↔ Posterior end of heart (located at segmental border IX/X), ventrally. Probably an alary ‘muscle’ XI, homonomous with **38** and **50**. Composed of very thin strands, which are distinctly fibrous but apparently non-striated. The strands of the paired posterior part usually unite in the midline to target the heart as an unpaired strand, which is accompanied by a trachea (length ratio between paired and unpaired parts variable). Near the posterior heart wall the strand forks and its fibers disperse. The posterior insertion beside tergum XI, observed twice, is difficult to find because posteriorly the strands of muscle **51** pass through a dense meshwork of fibers of muscle **60**.

#### 4.2.6. Musculature of rectum

The rectal muscles are shown in Figs. 21, 23. Only the extrinsic ones are here considered, most of which have their insertions on three pairs of longitudinal lines along the rectal walls, located ventrolateral, lateral, and dorsolateral (see corners of anteriorly cut rectum in Fig. 21). Muscles **53**, **56**, **60** are composed of several bundles, the number of which varies; the condition found most typical is illustrated. — **52**: Postlaterocoxa IX ↔ Longitudinal line in anterior ventrolateral wall of rectum (see also Fig. 19). Major ventral extrinsic rectal muscle. Fairly compact near ventral insertion but spreading fanwise and becoming diffuse towards rectal insertion. — **53**: Longitudinal line in ventrolateral part of sclerite ring X ↔ Longitudinal line in



**Figs. 21–23.** *Calopteryx virgo*, musculature of female terminal abdomen. Sclerotization grey, externally visible muscle scars darker (at insertions of muscles 41, 43). Cuticular ridges/thickenings not indicated. Muscles striped according to course of fibers. Unstriped ribbons 46, 47, 51 represent groups of unstriated fibers or non-fibrous strands, probably degenerated muscles (46, 47), or alary muscle XI (51). The extrinsic rectal muscles are usually more diffuse than here depicted. Undulate lines are cuts through cuticle or surround cut surfaces of muscles. Dashed lines are hidden borderlines of muscles and their insertions. Orientation: ↑ anterior. Scale 0.5 mm (for all figures). **21:** Segments Xff, dorsal view. Dorsal part of sclerite ring X removed except for the parts bearing muscle insertions. **22:** Mesal bases of cerci (mainly apodemes ma) and adjacent areas, with unpaired muscle 48. **23:** Segments Xff, dorsal view. Dorsal parts and most of rectum removed.

posterior ventrolateral wall of rectum. Constituted by several bundles, which are all fairly compact near the ventrolateral insertion but spread fanwise towards the rectal insertion. — **54**: Sclerite ring X, posteromedian ventral part ↔ Posteriormost ventrolateral wall of rectum. One fairly compact bundle; observed only once. — **55**: Membrane near ventromedian anterior margin of sclerite **AP** ↔ Ventromedian wall of rectum. One thin, fairly compact sheet. The muscles of the pair give off lateral fibers to the rectal wall, while their main bodies unite medially beneath the rectum; only one successful observation of the latter part of the muscle. — **56**: Longitudinal line in dorsolateral part of sclerite ring X ↔ Longitudinal line in lateral wall of rectum. Major lateral extrinsic rectal muscle. Constituted by several bundles, which are all fairly compact near the lateral insertion but spread fanwise towards the rectal insertion. — **57**: Sclerite **AP**, dorsolateral anterior margin ↔ Posterior lateral wall of rectum. One or several groups of fibers, which are usually diffuse and were not found in some specimens. — **58**: Cap-tendon **ut** of sclerite **AP** ↔ Posterior lateral wall of rectum. One slender, compact bundle. — **59**: Sclerite ring X, dorsomedian anterior margin ↔ Longitudinal line in anterior dorsolateral wall of rectum, posterior parts inserted further medially. Major dorsal extrinsic rectal muscle. Fairly compact near dorsal insertion but spreading fanwise and becoming diffuse towards rectal insertion. — **60**: Longitudinal line in posterior dorsomedian part of sclerite ring X ↔ Longitudinal line in posterior dorsomedian wall of rectum. Constituted by several bundles, which are all fairly compact near the dorsolateral insertion but spread somewhat towards the rectal insertion. — **61**: Cap-tendon **ut** of sclerite **AP** ↔ Posterior dorsolateral wall of rectum. One slender, compact bundle, which becomes diffuse near the rectal insertion. — **62**: Tergum XI, anterior margin ↔ Posteriormost dorsomedian wall of rectum (farther posteriorly than shown in Fig. 21). One moderately strong, fairly compact bundle.

### 4.3. Nervous system of female *Calopteryx*

In the abdominal CNS, each of the neuromeres of segments II–VII, **2G–7G**, forms a ganglion of its own. **4G–7G** lie in the anterior part of their segments (Fig. 16), **3G** is close to the anterior segmental border, and **2G** lies within the preceding segment I. **1G** is fused with the metathoracic ganglion. The posterior neuromeres **8G–11G** form a terminal compound ganglion **8–11G** located within segment VIII, above and shortly behind the fork between the lateral ovi-

ducts **ola** (Fig. 19; for the composition of four neuromeres VIII–XI see ANDO's 1962 data on other Odonata). The connectives **L** are closely appressed to each other medially. A thin median nerve **M** runs between them, one such nerve connecting each two successive individualized abdominal ganglia (Fig. 16). Nerve **M** can be freed from the connectives by teasing the paired transverse nerves **T**, which arise from **M** shortly in front of a ganglion, usually at slightly different levels. A swelling of nerves **M** or **T** near their junctions, i.e., a discrete perisymphatic organ, was not observed (for details of neurohemal tissue distribution see GRILLOT 1983). From each ganglion originates one pair of stout nerve stems, which soon divide into several nerves; these are here categorized into (branches of) the dorsal nerve **A** and the ventral nerve **B+C**, according to supposed homologies with nerve branches in Dictyoptera and other Neoptera (KLASS 1999, 2001a; KLUG & KLASS 2007).

The following data, which apply to segments IV–VII (shown in Fig. 16), are partly preliminary because many details could not be clearly observed in the available alcohol material. Nevertheless, the observations seem worth to be reported since there are so far no such data for imaginal Odonata, and since they allow some conclusions.

Nerve **T** runs from its origin on **M** straightly laterad beneath the ventral diaphragm **9**. Near the diaphragmal insertion on apodeme **pa** it gives off some rami that seem to innervate the lateral bundles of the diaphragm. **T** then passes dorsad between these bundles to fork – lateral to **pa** – into a posterior and an anterior branch, either of which can form rami into muscle **1**. The posterior branch **T** continues towards the spiracle area, where it could be traced no longer. The anterior branch **C–T** crosses to the preceding segment and enters muscle **5**. In the two attempts to trace it further, it was found to join a branch of nerve **B+C** (posterior **C4** in Fig. 16) within muscle **5**, thus forming an anastomosis **C–T** (see KLASS 1999: e.g., fig. 3). Near its lateral fork nerve **T** was once observed to form a very thin ramus that joins branch **A3** of nerve **A**; if consistently present, this likely constitutes an anastomosis **IT–A** (see KLASS 1999: e.g., figs. 3, 4; with the limitation that the respective branch is not unambiguously a true **A**-branch).

Nerve **A**, while forming several branches, targets the dorsomedian area of the segment. The basalmost branch **A3** produces assumedly sensory rami upon the pleural membrane and the spiracle area, and upon the anterolateral part of the tergum, and it probably also innervates muscle **2**. However, because nerves **T** and **A** probably anastomose in this area (via **IT–A**), the origin of the innervation of muscle **2** actually remains unclear. The following branches of nerve **A** approach the pleural membrane, where they probably form sensory

rami. Where nerve **A** approaches muscle **7** it gives rise to a branch **A4c** that curves posteriad and continues into a glossy ribbon **dps** attached to the body wall at the anterior margin of the following tergum. This formation evidently constitutes a dorsal protraction sensor (stretch receptor; see KLASS 1999: **ps\*** in figs. 5, 6; FINLAYSON & LOWENSTEIN 1958). Nerve **A** continues along the internal faces of muscles **7** and **8** and sends branches into both of them, which here are collectively called **A5/6/7**. It finally targets the heart wall, where, apparently via a short fork, it may join the lateral heart nerve as in the *Aeshna* nymph (ZAWARZIN 1911: nerve **mhn\***).

Nerve **B+C** runs, closely alongside the connectives, to the posterior part of the segment. On this way it gives off some apparently sensory branches **B1/2** to the ventral body wall. **B+C** targets the external ventral muscle **6**, gives off a branch **C3** supplying it, and crosses beneath it to turn anterolaterad. On the internal face of muscle **5** nerve **B+C** gives rise to branches **C4** and **B3**, which enter the latter muscle (and form the anastomosis **C-T**) and the posterior part of muscle **4**, respectively. Some further branches here assigned to **B3** extend far anteriad to supply the other parts of muscle **4**; it remains unclear whether they reach muscle **3**. Some of the **C4**-rami within muscle **5** continue into ventral fibers of muscle **7**, which thus likely shows a double innervation through **A** and **B+C**.

One more nerve to arise from the ganglionic stem is the one here called **A0**. It extends, probably without branching, posteriad to join the ventral diaphragm **9** above it. Along each flank of the ventral diaphragm, throughout segments IV–VIII and crossing the insertions on **at** and **pa** dorsally, runs a white, fairly stiff and thick strand **S**. It forms some rami that mostly run within the diaphragm. Connections with other nerves were not found (possibly overlooked), but in segment IV strand **S** was observed to arise from the nerve stem originating from **4G**. It seems possible that the segmental nerves **A0** join **S**, and that they are homonomous with the root of **S** in segment IV. If **S** actually is a nerve, as suggested by its origin, it constitutes a paramedian nerve.

#### 4.4. Observations on the terminal abdomen of male *Calopteryx*

In the male the exoskeleton and some muscles of segments X and XI were studied; the following list of differences to the female is incomplete in terms of the muscles. Additional muscles found, as compared to the female, are all included in Fig. 62, which shows all muscles of the terminal abdomen ever reported for

nymphal or imaginal Odonata – projected upon the female imago of *Calopteryx* (rectal muscles not included).

The subanal lobes **sb** and cerci **ce** of the male (compare female in Figs. 12–15) have, due to their copulatory function, a shape very different from that in the female. The lobes **sb** and their sclerites **AP** bear long processes (inferior appendages), and sclerites **AP** are very heavily sclerotized. Tendon **ut** originates from the mesal base of the process, which is thus formed by the lateral part of the subanal lobe (see Fig. 15). The sclerotization along the dorsal hind rim of sclerite ring **TG10+LP** is stronger than in the female and reaches the fold where the cuticle bends anteriad (compare membranous seam in Fig. 3). Tergum **TG11** is largely obliterated; only the tip of the terminal projection **tf**, around the **tt**-origin, and the far lateral parts are distinctly sclerotized. The lateral parts are closely in touch with (but not fused to) the **CE**-sclerotization of the mesal base of the cercus (see Fig. 12). Apodeme **ma** is larger and more elaborate than in the female; its sclerotization extends onto the ventral lobe-like part (insertion area of muscle **41**, see Fig. 21) and is separated from **CE** (compare connection in Fig. 12). The ventral part of antecosta **ac10** is much less thickened than in the female.

The musculature is somewhat richer than in the female (see Fig. 62). The cercal muscles **41** and **42** are much more massive (corresponding to the elaboration of apodeme **ma**), and an additional cercal muscle **63**, a fairly thin sheet, goes from sclerite ring **TG10+LP** to tendon **ct**. The dorsal muscle **43** is much stronger than in the female and inserts farther laterally on tergum **TG11**. A further muscle **64**, from sclerite ring **TG10+LP** to tendon **ht**, was found in a degenerated condition. Muscle **39**, inserted posteriorly on tendon **jt**, was found more distinct in the male, though still very small. In addition, distinct fibers **65**, which in a light microscopic view are clearly independent of the **39**-fibers, run along tendon **jt** to connect its tip with its base. The basal insertion of muscle **65** is in touch with the anterior attachment of strand **47**, which also in the male was found non-striated. A further pair of very slender muscles **66** extend from ventral sclerotizations IX to the median tendon **rt**. Hence, in the male all the tendons that are bare of muscle insertions in the female (**ct**, **ht**, **rt** in Figs. 21, 23) are occupied by muscles, at least by vestigial ones.

## 5. Range of female abdominal morphology in ovipositor-bearing Odonata

### 5.1. Generalities

This chapter surveys the structural variation in the female abdominal exoskeleton (own studies) and musculature (literature data) for those Odonata that bear an ovipositor resembling that in *Calopteryx* and, accordingly, exhibit an altogether plesiomorphic architecture of the posterior abdomen. The respective (extant) taxa are the various subgroups of Zygoptera, the monogeneric Epiophlebiidae (*Epiophlebia*), and, among the Anisoptera, the Aeshnidae. The Petaluridae, whose ovipositor shows an initial stage of reduction/modification (PFAU 1991) will only occasionally be considered. Muscle data are partly included also for the remaining Anisoptera (Exophytica sensu BECHLY 1996).

#### 5.1.1. Exoskeleton

It was studied in a sample of Zygoptera in which the various superfamilies and most families are represented, in *Epiophlebia*, and in one member each of the two subfamilies of Aeshnidae (as defined by STEINMANN 1997b). First, the selected Aeshnidae (*Aeshna*, *Caliaeshna*) and *Epiophlebia* will be compared with *Calopteryx* by listing all differences; then for the sampled Zygoptera the peculiarities as compared to *Calopteryx* will be explained. Literature data will additionally be included if they are of particular interest (e.g., those from MATUSHKINA 2008b for *Epiophlebia*). Most of the differences observed will be formulated as states of characters (character list in 5.6.) and summarized in a character table (Tab. 1, with character states indicated by abbreviations to improve readability; this can be easily transformed into a character matrix for cladistic analysis just by replacing different abbreviations by 0, 1, etc.). A cladistic analysis is not attempted at this stage, because the taxon sample is currently being expanded. One should note that there is no reliable outgroup comparison for many characters (see last column in Tab. 1), and many characters are not phylogenetically informative within the small taxon sample here used (while many of these characters may be informative at a lower systematic level).

In many characters morphological transitions are fluent. This is particularly true for relations between neighboring sclerites, which in different taxa

can show all stages between complete separation by membrane and complete fusion. Intermediates may vary in the breadth of a fusion, in the heaviness of the connecting sclerotization as compared to that of the two sclerites, or, if all sclerotization is similarly heavy, in the degree of flexibility retained within the fusion area. Similarly, in terms of the presence of sclerites all intermediates between heavy sclerotization and absence can occur. Features of these kinds were observed to vary also between conspecific imagines that have the sclerotizations altogether relatively bright and flexible, or dark and stiff, respectively. This variation is presumably age-dependent: With proceeding maturity sclerotizations darken and harden, articulation membranes may become sclerotized, sclerites thus appearing separated in young imagines but connected in older ones (though flexibility remains focused to the articulation); cuticular thickenings, apodemes, and tendons can apparently become much more expressed during maturation, and sclerites that are weak, but recognizable, in fully matured individuals can be invisible in younger ones. Therefore, in many characters states are hardly definable due to fluent transitions between taxa and the frequent additional overlap between the structural range found across the taxa and the age-dependent spectrum of variation. Some characters that are mentioned in the text but show disturbing problems of this kind were thus excluded from the character list. Dark individuals were here preferably assessed; the single available specimen of *Diphlebia*, however, was fairly bright, and the weak development of many tendons and apodemes, and of the intertergal articulations, may be due to young age. The two included species of *Drepanosticta* (*D.* sp. indet. and *D. fontinalis*) correspond in all characters here considered, except that in *D. fontinalis* sclerite **CXb9** (see Fig. 11) was much less distinct (as the entire abdominal sclerotization was much brighter).

#### 5.1.2. Musculature

Literature data for comparison with *Calopteryx virgo* are available for only very few species, and for different ones regarding the various parts of the abdomen.

(1) The midabdomen has been studied in the Calopterygidae *Mnais strigata* Selys (ASAHINA 1954) and *Calopteryx maculata* Beauvois (WHEDON 1918), in *Epiophlebia superstes* Selys (ASAHINA 1954), in the Aeshnidae *Anax junius* (WHEDON 1918), in the Gomphidae *Davidius nanus* Selys (ASAHINA 1954), and in some Libellulidae (WHEDON 1918). The spiracle and alary muscles and the ventral diaphragm (9, 10, 11 in Figs. 16–18), not considered in the aforementioned contributions, are treated in POONAWALLA (1966), in

ZAWARZIN (1911; nymph), and in FORD (1923) and RICHARDS (1964), respectively.

(2) Muscles of the female genitalic segments have been examined in the Coenagrionidae *Pseudagrion decorum* (Rambur) (HAKIM 1964), in *Mnais strigata* (ASAHINA 1954), in *Epiophlebia superstes* (ASAHINA 1954), in the Aeshnidae *Gynacantha japonica* Bartenef (ASAHINA 1954) and *Anax junius* (DUNCAN 1933; PFAU 1991, with *Anax* sp. indet.), and in the Petaluridae *Petalura* sp. indet. (PFAU 1991). DUNCAN'S (1933) contribution is difficult to evaluate because the locations of insertions are not adequately specified. WHEDON'S (1918) descriptions, which are fairly superficial and evidently include incorrect data, are considered only if additional information is given as compared to the other authors. Most important are the recent studies of MATUSHKINA & GORB (1997) and MATUSHKINA (2004, 2008a,b) on the major muscles of the female genitalia in a variety of ovipositor-bearing Odonata; this includes the zygopterans *Calopteryx splendens*, *Lestes barbarus*, *Enallagma cyathigerum*, *Bayadera melanopteryx* Ris, 1912, *Chalcolestes parvidens* (Artobolevsky, 1929), *Heteragrion alienum* Williamson, 1919, *Platycnemis pennipes* (Pallas, 1771), and *Palaemnema domina* Calvert, 1903; *Epiophlebia superstes* and the anisopterans *Aeshna mixta* and *Anax imperator* Leach, 1815 are also treated.

(3) Muscle data on the terminal female abdomen are provided only by ASAHINA (1954), but only a minor part of the muscles are therein considered, and the insertions are mostly not discretely indicated. For the terminal abdomen ASAHINA'S (1954) and CALVERT'S (1927) data on the nymphal musculature are here considered (see Fig. 62) because of their importance for the interpretation of the exoskeletal elements.

The musculature of the midabdomen is quite uniform throughout the Odonata, and that of the female genitalic segments and terminal abdomen is fairly uniform throughout the ovipositor-bearing Odonata; differences lie mainly in the occasional absence or subdivision of particular muscles. There are thus hardly any problems in the topographic homologization of muscles within Odonata, which is summarized in Tabs. 2 and 3. However, as noted in the Introduction, the musculature in a species can differ considerably between teneral and mature individuals, the former exhibiting many degenerating nymphal muscles (e.g., WHEDON 1929; FORD 1923: fig. 18; MATUSHKINA 2008a), and even between mature specimens of different age (ASAHINA 1954: 54; MATUSHKINA 2008a). For many muscle characters the use in phylogenetic analyses is thus problematic.

## 5.2. Exoskeleton of female Aeshnidae

### 5.2.1. Exoskeleton of segments V–VII

The midabdominal segments are relatively much shorter than in *Calopteryx*. On the terga (Fig. 25) the lateral parts of the posterior transverse carina **ty** bend anteriorly to continue into a longitudinal external ridge **vc** near the lateral tergal margin (= ventral carina in TILLYARD 1917); **vc** gradually obliterates anteriorly. Another longitudinal external ridge **lc** (= supplementary lateral carina) joins **ty** posteriorly and closely approaches the antecosta **ac** anteriorly. The supplementary transverse carina **tc** is more conspicuous than in *Calopteryx*; while in *Aeshna* it is a ribbon of heavy sclerotization, **tc** in *Caliaeshna* is weaker than the tergum around it and appears to work as a hinge line. The **tc** are likely the insertion areas of the internal dorsal muscles, which degenerate in teneral individuals (compare Fig. 25 and WHEDON 1929: figs. 5–8). The intertergal articulations are constructed as in *Calopteryx* (**ap**-areas in Figs. 24, 25); articulation VII/VIII is well developed in *Caliaeshna*, but in *Aeshna* it is virtually absent: there is no patch **ap**, the 'triangular' sclerotization is reduced to a narrow ribbon behind carina **ty**, and the breadth of the intertergal membrane is fairly uniform all along the hind margin of **TG7**. Dorsomedian tendons **dt** are poorly developed in *Aeshna* (hardly projecting from the surrounding membrane) and absent in *Caliaeshna*.

The coxosterna in Aeshnidae bear a further pair of apodemes **ba** on their lateral margins, two thirds backward from the spiracle to the coxosternal hind margin; these long, shallow, and weakly sclerotized infoldings are in *Caliaeshna* more discrete than in *Aeshna*, and in segments V and VI more strongly developed than in VII. The posterior part of the coxosterna is narrow and weak as in *Calopteryx*, and the far posterior portion is somewhat broader again; however, the hind margin is by far not as heavy as in *Calopteryx*, and not as broad as to extend into the apodemes **at**. Of the midventral keel **vk** in *Caliaeshna* only the hindmost part is present in the narrowed area of the coxosternum (indistinct in VII); *Aeshna* has such a remnant only in segment V. In the Aeshnidae midventral 'caudal processes' (ASAHINA 1954; see PFAU 1971: 341f for distribution over taxa) arise on some of the segments preceding V from the area where otherwise the **vk** terminate posteriorly; apparently they are strongly projecting hind tips of these keels. Accordingly, the hind end of **vk5** in *Caliaeshna* is, as compared to that in *Calopteryx*, which gradually fades out, slightly raised from the surrounding coxosternum.

### 5.2.2. Exoskeleton of segment VIII

Tergal carinae **lc8** and **vc8** are poorly developed, or absent as in *Calopteryx*. The middorsal hinge **dh8** in *Caliaeshna* is, as in *Calopteryx*, clear-cut throughout tergum **TG8**, but in *Aeshna* it is distinct only on the anteriormost part of **TG8**. The posteroventral corner of **TG8** is neither strengthened nor expanded towards sclerite **LCa9**, i.e., extension **b** is absent (compare Figs. 26 and 27). The midventral **vk8** of laterocoxosternum **LS8** is present as a line, but only indistinctly keel-shaped in *Caliaeshna* and not at all so in *Aeshna*; it clearly works as a hinge line. The apodeme **ba8** (see Fig. 7) on the post-spiracular lateral **LS8**-margin is in both aeshnids much more discrete than in *Calopteryx*.

The tendon **gt** originates from the membrane mesal to coxa **CX8** rather than from the anterior **CX8**-margin (Figs. 26, 28 vs. 27, 29). As in *Calopteryx* the posterolateral margin of **CX8** lies on a short outfolding **gl8**, which overlaps much of **LCa9** (area unfolded and schematized in Figs. 26, 27). However, the sclerite extension **d** of **CX8** is broad, short, and thus hardly discrete, and it lacks cuticular thickening. Extension **d** furthermore does not join **LCa9** very closely, and also in this ‘articulation’ area **CX8** and **LCa9** are distinctly separated by membrane; a fusion between the sclerites is thus not at all indicated.

The cleft between the left and right gonapophyses **gp8** extends much farther anteriorly in the aeshnids than in *Calopteryx*, to the area between the **CX8** (Figs. 26, 28 vs. 27, 29). The two **gp8** as well as their sclerotizations **GP8** are thus free from each other at their bases, ventrally (Fig. 27) as well as dorsally (Fig. 29). *Aeshna*, but not *Caliaeshna*, has a minute median sclerite **MS** at the anterior end of the **gp8**-cleft (Fig. 27). The **GP8**-sclerotization at the dorsal base of **gp8** does not form an anteriorly-directed plate as in *Calopteryx* (Figs. 28, 29). In *Aeshna* it is subdivided into three lobes (**x**, **y**, **z** in Fig. 29) by membranous stripes: The median lobe (**x**) and the major part of the lateral lobe (**z**), which bear some oblique external ridges **gy** (along the mesal face of the **gp8**) and the anterior end of the aulax **al**, respectively (Fig. 29), are very heavy; these sclerotizations are also present in *Caliaeshna*. The aulax-bearing lobe has, in addition, a very weak mesad-directed extension (**z<sup>m</sup>**), which is narrowly separated from the moderately heavy middle lobe (**y**); the two latter sclerotizations (**z<sup>m</sup>**, **y**) are absent in *Caliaeshna*, where the corresponding areas are membranous. Regarding the ridges **gy** on the sclerotization **x**, in both aeshnids three stout, roughly semi-circular basal **gy** per side are followed distally by ca. five much more delicate **gy** (the latter are indistinct in *Caliaeshna*). The series of **gy**-ridges reaches the distal third of the **gp8**. The **gy** are arranged asymmetricaly; those of the two sides fit between each other and

likely establish a transverse interlock between the two **gp8** (traces of such ridges were also found in some individuals of *Calopteryx*; see below). The distal part of **gp8** in both aeshnids lacks saw-teeth **tm8** (Fig. 44) and oblique ridges **gz8** (see Figs. 4, 9).

In the vaginal area (Figs. 30, 31) of the aeshnids the lobes **vl** are distinct, but very short, and lack sclerites **VL**. The probable homologue of the vaginal sclerite **VB** of *Calopteryx* is restricted to the far posterior part of the vagina. In *Aeshna* **VB** is, apart from a small central part, fairly weak; in *Caliaeshna* the entire **VB** is very weak. The anterior end of the vagina forms in both aeshnids a bulb-like expansion, as in *Calopteryx* (**vb** in Figs. 30, 31). The spermatheca **sp** originates from the ventral vaginal wall, rather than from the dorsal wall as in *Calopteryx*, and the common stem of its two branches is very short. Of course, according to their reversed positions, either the vaginal bulbs **vb** or the spermathecae **sp** (or both elements) are non-homologous in *Calopteryx* and Aeshnidae (discussion below). The Aeshnidae lack a complete collar-shaped ridge **cr**, but paired cuticular thickenings in the anterior and posterior lateral vaginal wall may be remnants (**cr?** in Fig. 31). A long, rigid, and partly melanized midventral thickening **mr** (Fig. 31), absent in *Calopteryx* (Fig. 30), extends anteriorly onto the common oviduct **oc**, which, accordingly, was never found evaginated into the vagina lumen as in *Calopteryx* (Fig. 8). Also the tendon **vt** in Aeshnidae is seated upon a strong midventral thickening, whereas in *Calopteryx* a thickening of this area is, at most, indistinct.

### 5.2.3. Exoskeleton of segment IX

*Caliaeshna* is peculiar in that antecosta **ac9** obliterates middorsally and is divided into two articulated halves; this articulation is part of the middorsal abdominal hinge line. In *Aeshna* **ac9** continues through the midline as a heavy ridge (though not as heavy as in *Calopteryx*), without a trace of an articulation.

In the Aeshnidae both the antelaterocoxa **LCa9** and the postlaterocoxa **LCp9** are more extensively synsclerotic with tergum **TG9** than in *Calopteryx* (Figs. 26, 27), but as in *Calopteryx* **LCa9** and **LCp9** are entirely separated from each other. The relation between **TG9** and **LCa9** differs from that in *Calopteryx* in that in an external view, as well as in an internal view of the anterior part of the borderline, the melanization continues more uniformly across the articulation, without a distinct weakening. In an internal view of the posterior part of the borderline one notices the black stripe **h**, which like in *Calopteryx* traverses the articulation at the hind rim of the internal ridge **ac9** and is on both sides flanked by the

unmelanized inner cuticle of the ridge. Through this structure the border between **TG9** and **LCa9** is also in Aeshnidae very clear-cut in its posterior part. Another difference to *Calopteryx* is that cuticular flexibility is less strongly focused to the borderline between **TG9** and **LCa9**, i.e., the articulation is less sharply defined. In the relation between **TG9** and **LCp9** the Aeshnidae differ from *Calopteryx* in that **LCp9** extends much farther anteriorly and closely approaches the **TG9-LCa9** articulation, and in that the anterior part of **LCp9** is extensively synsclerotic with **TG9** immediately behind the **TG9-LCa9** articulation, without any separation by weak sclerotization.

On the gonapophyseal sclerite **GP9** of Aeshnidae the extension **g**, bearing the anterior end of the rhachis **rh**, is located farther posteriorly than in *Calopteryx* (Figs. 39, 40). Tendons **ft**, which in *Calopteryx* flank apodeme **ca**, are absent. The articulation between **LCp9** and the major gonoplac sclerite **CXa9** is much farther anteriorly than in *Calopteryx*, in front of apodeme **la** rather than at its base. The gonoplacs **g19** lack tubercles on their distal ventral edge as well as the tuft of setae on the tip of sclerite **CXa9** (VAN DER WEELE 1906: 159 mentions some vestigial tubercles for *Aeshna grandis* L.). Instead, the tip of the stylus **sl9** bears a setal tuft (in both aeshnids the tuft was absent in some specimens but distinct in others; in the former the setae have presumably been rubbed off). The styli are straight and cylindrical rather than curved and clubbed as in *Calopteryx*. The small sclerite **CXc9** beside the stylus base is discrete in *Caliaeshna*; in *Aeshna* it is indistinct but probably represented by a small basal extension of the stylus sclerotization **SL9** (Fig. 40). Sclerite **CXb9** on the dorsal gonoplac lobe **dl** is absent in *Aeshna*; in *Caliaeshna* it is well developed but distally fused with **CXa9** (Figs. 46, 47, 61).

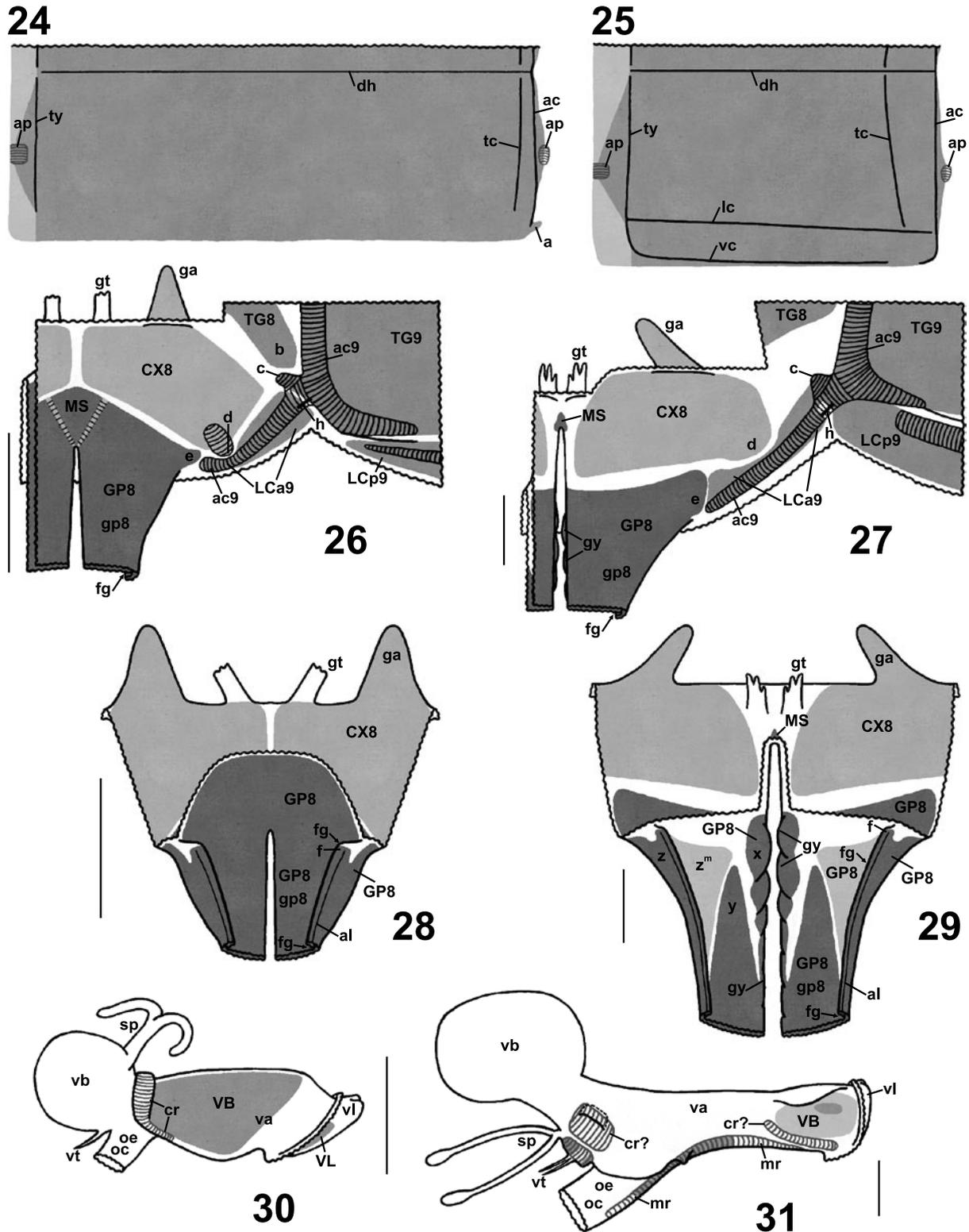
In the area around the posterior gonoplac bases *Aeshna* differs strongly from *Calopteryx* (Figs. 46, 61): Sclerite **PS9** (for homology see section 6.5.7.) is much weaker, is on each side broadly expanded towards the gonoplac lobe **dl**, and is interrupted in the midline, where its two halves hinge upon each other. The lateral tips of **PS9** are, as in some *Calopteryx*, narrowly and flexibly synsclerotic with the gonoplac sclerite **CXa9**, but the sclerites are, in addition, broadly connected by very weak sclerotization. **PS9** in *Aeshna* furthermore lacks the transverse folds that stiffen **PS9** in *Calopteryx* (see section at bottom of Fig. 7). Since, moreover, the anteroventral part of sclerite ring X **TG10+LP** is very weak and lacks any trace of an antecosta **ac10** (see next section), the posterior gonoplac bases in *Aeshna* are easily movable relative to each other in a transverse direction, whereas the strong transverse stiffening through **PS9** and **ac10** puts much resistance to such a movement

in *Calopteryx* (see Fig. 7). Behind **PS9** *Aeshna* has a very weak transverse sclerotization **IT9** (Fig. 46), which extends laterally beyond the **CXa9** (to near the posteroventral corners of tergum **TG9**) and forms on each side a low bulge; no trace of this structure is present in *Calopteryx*, if not the small median sclerite **IT9** is a homologue (Fig. 61). The respective area in *Caliaeshna* (Fig. 47) forms only some weak, diffuse melanization; since it extends far laterad it is likely homologous with **IT9** of *Aeshna* rather than with **PS9**. **PS9** is then completely absent in *Caliaeshna*. In the aeshnid *Anax*, MATUSHKINA (2008a: fig. 5B,C) has apparently found a more strongly sclerotized **IT9** that has the shape of a transverse ribbon and is laterally fused with the posterolateral corners of tergum **TG9**, like in *Epiophlebia* (compare Fig. 48).

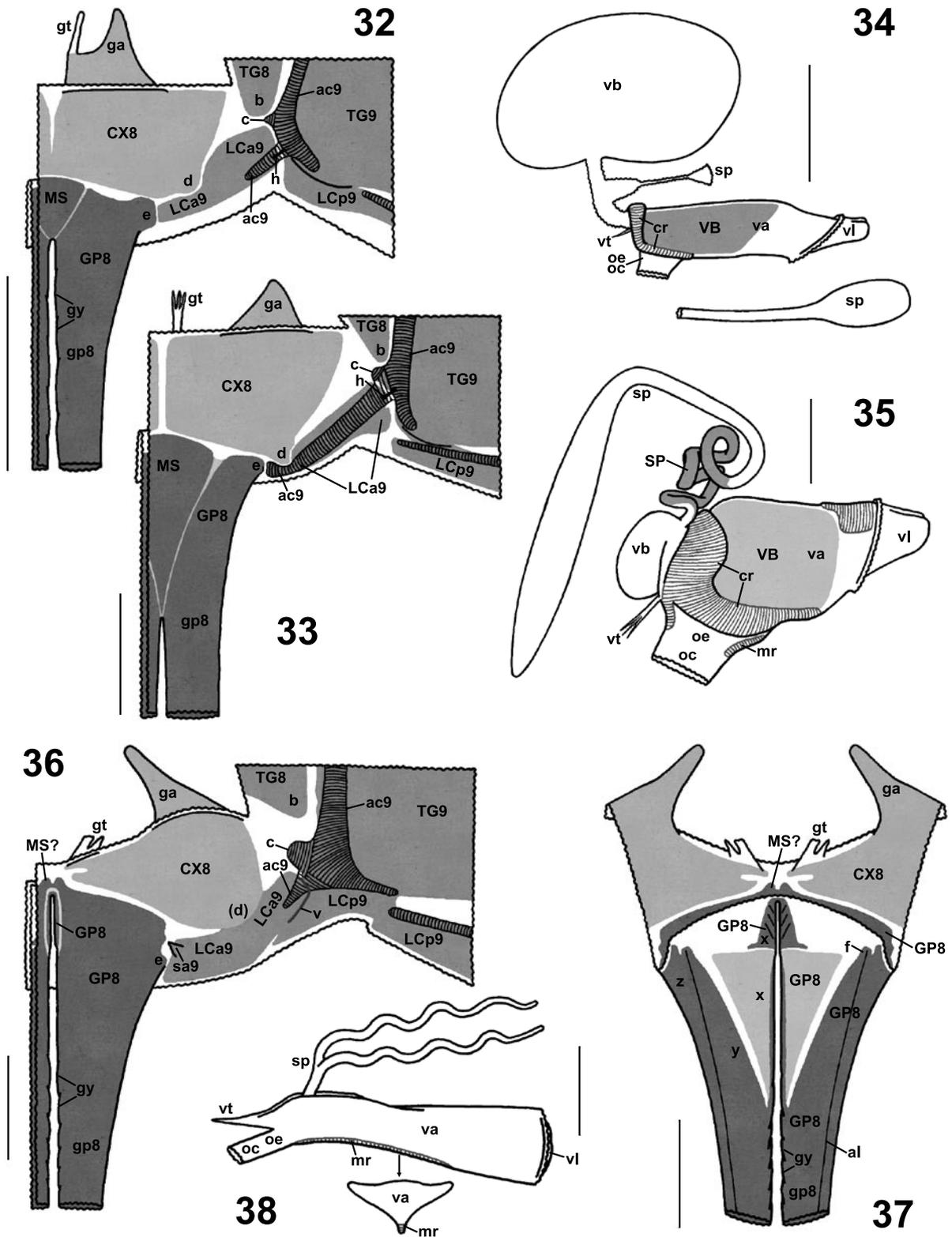
#### 5.2.4. Exoskeleton of segments X and XI and telson

Whereas the ventral part of sclerite ring X **TG10+LP** in *Calopteryx* is heavy throughout and supplied with a thick and continuous antecosta **ac10** (Figs. 7, 12), in *Caliaeshna* the left and right parts are entirely separated by a midventral membrane, and **ac10** is absent ventrally (a condition also found in *Cordulegaster*). In *Aeshna* the anteroventral part of sclerite ring X is very weak and likewise devoid of an **ac10**, but the posteroventral part is well sclerotized and forms a transverse bulge that projects beneath the subanal lobe bases and bears strong tubercles (the bulge works as an abutment for ovipositor movements, see ST. QUENTIN 1962: figs. 6–8; see the same contribution and VAN DER WEELE 1906: 165f for variation within Aeshnidae).

The posterior middorsal process **dp** (see Fig. 3) is missing in the Aeshnidae. Tendon **ht** on the lateral anterior margin of sclerite **AP** (see Figs. 12, 14) is very small or absent in *Caliaeshna* but well developed in *Aeshna*. The tendons **jt** at the anteroventral corners of the sclerites **AP** are in both Aeshnidae located much farther medially than in *Calopteryx*, in front of the tendon **rt**, their bases being close together. The sclerotization of the cercal base apodeme **ma** in *Aeshna* is separated from the cercal sclerotization **CE** (as in *Calopteryx* males) and connected with the lateral tip of tergum **TG11**. In *Caliaeshna* the **ma**-sclerotization is very indistinct (flexible and hardly melanized), but at least its separation from **CE** is evident. The anterior margin of **TG11** in the Aeshnidae bears, quite close to the midline, a pair of tendons **dt11** tentatively considered here homonomous with the dorsal tendons **dt** of the preceding segments. The terminal projection **tf** and the subanal lobes **sb** each bear on their anus-flanking face a weakly sclerotized, triangular lobe called here **yl** (unpaired) and **xl** (paired), respectively



**Figs. 24–38. Details of abdominal structure in Odonata.** **24:** *Calopteryx virgo*, and **25:** *Aeshna cyanea*: Midabdominal tergum, entire right half and dorsomedian part of left half (cut along undulate line), diagrammatically, showing tergal ridges and articulations. External view. Orientation: → anterior, dorsal midline along dh. Sclerotization grey, weak sclerotization lighter. Areas ap are the cuticular patches of the intertergal articulations. **26:** *Calopteryx virgo*, **27:** *Aeshna cyanea*, **32:** *Lestes elatus*, **33:** *Rhipidolestes* sp., and **36:** *Epiophlebia superstes*: Segmental border area VIII/IX of left side, with bases of gonapophyses gp8 and tergal-laterocoxal articulations IX, diagrammatically and unfolded (area thus not in its natural appearance, but components with original spatial interrelations and largely with original proportions). Ventral view. Orientation: for median parts ↓ posterior, → lateral; for lateral parts → posterior, ↑ dorsal. Right gonapophyses cut longitudinally. Sclerotizations light grey (coxae CX8) or dark grey (gonapophyseal sclerites GP8, and MS, but weak sclerotization shown lighter), or medium grey (remaining ones). Undulate lines are cuts through the cuticle. Ladder-shaped areas or ribbons are cuticular thickenings. Series of transverse dashes are lines of increased flexibility (Fig. 26). In the area of articulation between TG9, LCa9, and LCp9 sclerotizations connecting



these sclerites are not considered if distinctly weaker than the sclerites (i.e., membranous separations are then shown; see text). Though the view is generally external, articulation TG9-LCa9 is shown as viewed internally, the black bar h (absent in *Epiophlebia*) representing the stripe of internal sclerotization traversing the articulation. Scale 0.5 mm. **28:** *Calopteryx virgo*, **29:** *Aeshna cyanea*, and **37:** *Epiophlebia superstes*: Coxae CX8 and bases of gonapophyses gp8, diagrammatically. Dorsal view. Orientation: ↓ posterior. Sclerotizations light grey (CX8) or dark grey (GP8 and MS, but very weak sclerotization shown lighter). Undulate lines are cuts through the cuticle. Scale 0.5 mm. **30:** *Calopteryx virgo*, **31:** *Aeshna cyanea*, **34:** *Chlorocnemis* sp., **35:** *Mecistogaster lucretia*, and **38:** *Epiophlebia superstes*: Vaginal area. Left view. Orientation: ↑ dorsal, → posterior. Sclerotization grey (two categories: darker = heavier). Undulate lines are cuts through the cuticle. Ladder-shaped areas or ribbons are cuticular thickenings. Intima-bearing oviduct oc+oe artificially invaginated in Figs. 30, 34, 35 (natural position as in Fig. 8) but being in natural position in Figs. 31, 38. Fig. 34 with the (cut) spermatheca additionally shown in expanded condition. Fig. 38 with transverse section through vagina additionally shown. Scale 0.5 mm.

(lobes **y\*** and **x\*** in SCHMIDT 1933). The lobes arise from approximately the same areas (though slightly further anad) where in *Calopteryx* tendons **tt** and **ut** originate (see Figs. 12–15). Tendons **tt** and **ut** are entirely lacking in the Aeshnidae.

### 5.3. Exoskeleton of female *Epiophlebia*

#### 5.3.1. Exoskeleton of segments V–VII

The midabdominal segments show similar proportions as in the Aeshnidae (see Fig. 25). On the terga the transverse carina **ty** is fairly weak. Its lateral parts bend anteriorly like in the Aeshnidae but do not continue beyond the area of the posterolateral corner of the tergum; a longitudinal ridge **vc** is thus only slightly indicated. The longitudinal ridge **lc** is absent. The supplementary transverse carina **tc** is a conspicuous ribbon of heavy sclerotization as in *Aeshna*, but is located farther posteriorly, in the middle of the segment. The intertergal articulations are constructed as in the foregoing taxa: patches **ap** are weakly developed but distinct; though the entire sclerotization behind ridge **ty** is rather dark, the ‘triangular’ sclerotization is distinguishable from the remainder by its stiffer condition. Articulation VII/VIII is well developed. Dorsomedian tendons **dt** as well as dorsolateral tendons **et** were not found, while tendons **bt** are well developed (see Fig. 1).

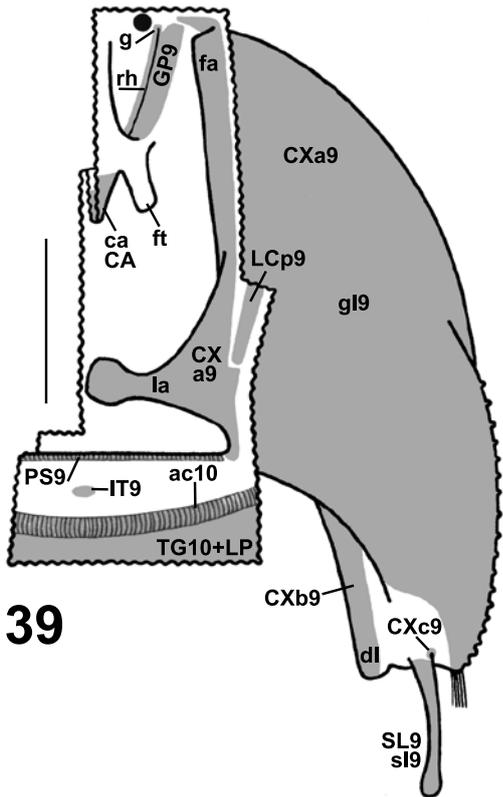
The coxosterna in *Epiophlebia* lack, like in *Calopteryx*, the posterior apodemes **ba**. Their posterior part gradually narrows, is as strong as the anterior part, and is set off from the latter by a transverse stripe of membrane (sclerotized longitudinal connections are retained most laterally). From the hind margin of this small posterior plate of the coxosternum arises a long, slender process (caudal process **pp**), which is sclerotized ventrally and membraneous dorsally, and whose tip forks into two small membraneous lobes; it is slightly up-curved, as if to support the anterior portion of the succeeding coxosternum from below. A caudal process is well developed on coxosterna V and VI but absent on coxosternum VII. There is no sclerotization behind the base of the process, and the (sometimes medially divided) weak sclerotization as well as the broadened portion of the coxosternum that contacts the succeeding apodemes **at** in *Calopteryx* (see Fig. 1 left side) are all absent; there is thus a fairly long membraneous area present between successive coxosterna. Of the midventral keel **vk** no trace was found.

#### 5.3.2. Exoskeleton of segment VIII

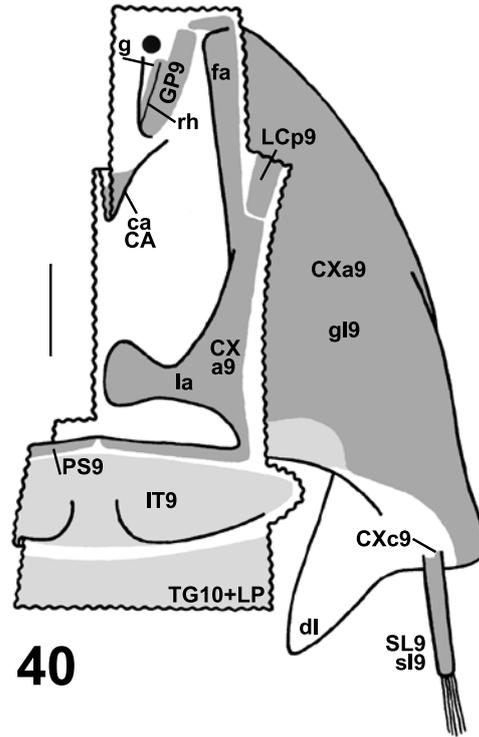
The middorsal hinge **dh8** in *Epiophlebia* is virtually absent (no discrete line of folding during artificial movement). Though antecosta **ac8** completely obliterates middorsally, there is no articulation either in this anterior part of **TG8**. The posteroventral corner of **TG8** is somewhat strengthened and expanded towards sclerite **LCa9**, i.e., extension **b** is present (Fig. 36); however, **b** is not as clear-cut as in *Calopteryx* (Fig. 26), and it does not reach the articulation between **TG9** and **LCa9**. Laterocoxosternum **LS8** lacks a midventral keel **vk8**. The apodeme **ba8** on the postspiracular lateral **LS8**-margin is as discrete as in the Aeshnidae (but was fairly indistinct in the surmisedly younger specimen). A peculiarity in *Epiophlebia* is the presence of a median posterior process on the hind margin of **LS8**, which is terminally bilobate, sclerotized dorsally and ventrally (continuous with **LS8**), and appears to serve as an abutment for the ventromedian part of the gonapophyseal sclerotization **GP8** (or better: **MS**, see below; compare Fig. 4 for spatial relationship of elements). This **pp8** may be homonomous with the coxosternal caudal processes occurring in the preceding segments except for VII.

The tendon **gt** originates partly from membrane (lateral portion) and partly from a narrow anteromesal arm of coxa **CX8** (median portion; Figs. 36, 37); the arm was only weakly connected with **CX8** in the surmisedly more mature specimen. On the hind margin of **CX8** and lobe **gl8** (area unfolded and schematized in Fig. 36) the part of **CX8** that corresponds to extension **d** in *Aeshna* (see Fig. 27) is broadly connected with sclerite **LCa9** by a sclerotization that is somewhat weaker than that of **CX8** and **LCa9** (in one individual the connection was broader than shown in Fig. 36, and the sclerotization weakened less distinctly than in the other specimen). The fusion between **CX8** and **LCa9** is thus more complete than in *Calopteryx* (no connection at all in Aeshnidae). As in Aeshnidae, cuticular thickening in the **CX8-LCa9** contact area is absent.

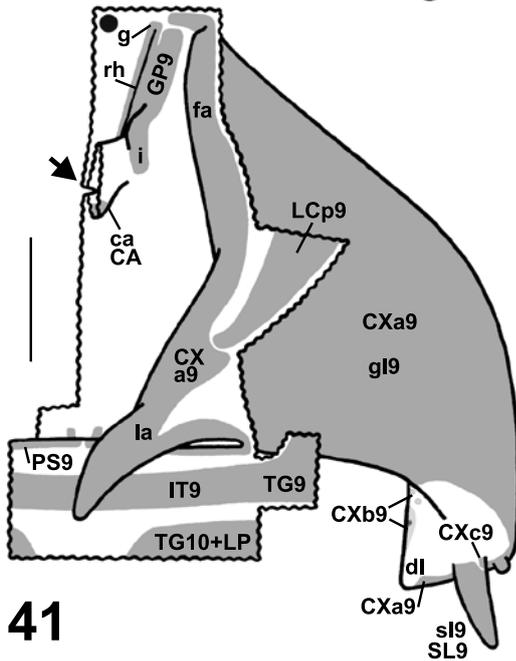
The cleft between the left and right gonapophyses **gp8** (Figs. 36, 37) ends anteriorly in a position intermediate between *Calopteryx* and Aeshnidae (Figs. 26–29). Anterior to the cleft, the left and right gonapophyseal sclerotizations **GP8** are fused for a very short distance at the ventral (Fig. 36) and dorsal **gp8** bases (Fig. 37). The ventral fusion area (**MS?** in Fig. 36) forms two small bulges, which rest upon the tip of process **pp8** of laterocoxosternum **LS8**. The **GP8**-sclerotization at the dorsal base of **gp8** (Fig. 37) shows, similar to *Aeshna* (Fig. 29), a subdivision by a membraneous stripe. The part mesal to the stripe (**x**) is mostly very weak, but along the mesal face of **gp8** the strong sclerotization continues to the base of **gp8**, where it is, like in Aeshnidae, widened. These widened parts, however, differ



39



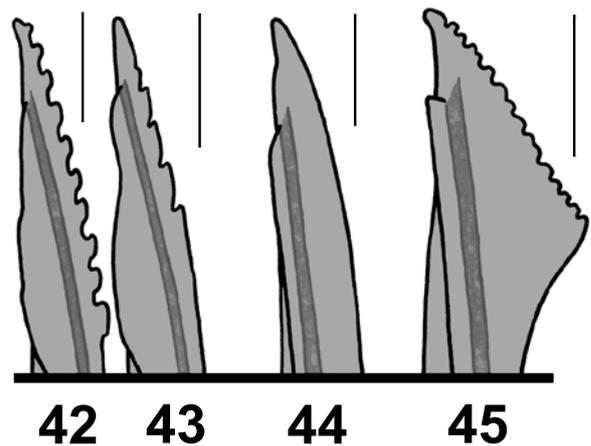
40



41

**Figs. 39–41. Gonoplacs and elements around their bases.** 39: *Calopteryx virgo*, 40: *Aeshna cyanea*, and 41: *Epiophlebia superstes*. Gonoplac base area of right side viewed dorsally (largely internally), right gonoplac forced dorsolaterad (and apodeme la forced mesad) and thus viewed laterally. Semi-diagrammatical. Sclerotization grey (two categories: darker = heavier). Undulate lines are cuts through the cuticle. Orifice of right accessory gland indicated by black dot. Of gonapophysis gp9 only base shown internally; course of rhachis on opposite (external) face of cuticle indicated by line on sclerite GP9. Of the setae only those included that together form a discrete tuft. The arrow in Fig. 41 shows the membranous transverse fold (cut at midline) that constitutes a very basal transverse connection of the bodies of the two gonapophyses gp9. Scale 0.5 mm.

**Figs. 42–45. Tips of gonapophysis VIII.** 42: *Lestes elatus*, 43: *Hetaerina amazonica*, 44: *Aeshna cyanea*, and 45: *Epiophlebia superstes*. Tip of left gonapophysis VIII viewed dorsally (and slightly laterally), with series of teeth tm8 along right edge. Orientation: ↑ posterior, → lateral. Sclerotization grey, aulax groove dark grey. Scale 0.1 mm.



42 43 44 45

strongly from those in the Aeshnidae: First, they are connected with the remaining **GP8** (around the mesal edge of the gonapophysis, compare Figs. 36 and 37) only through a very weak sclerotization, thus almost constituting separate sclerites. Second, the left and right widened parts are connected basally to establish a very short dorsal fusion between the left and right **GP8**. Third, the widened parts bear only some very fine folds (Fig. 37), which in contrast to ridges **gy** in Aeshnidae run from anterodorsally to posteroventrally; since in the undisturbed ovipositor the widened basal parts of **GP8**, which bear these ridges, are tightly appressed to each other medially, these ridges probably also establish a transverse interlock. Interlock ridges having the same orientation as the **gy** of Aeshnidae are present more distally (**gy** in Figs. 36, 37; see also MATUSHKINA 2008b: 73), in the area from the distal part of the membrane stripe to roughly the middle of the **gp8**; they cannot be counted properly because the distal **gy** become gradually weaker and obliterate (six per side are distinct at least). The extension **f**, bearing the anterior end of the aulax **al**, is inconspicuous. The **gp8** bear saw-teeth **tm8**, which, however, are finer and more numerous than in *Calopteryx*, and restricted to a shorter distal area, which is especially widened (Fig. 45; more structural details, including sensilla, are shown in MATUSHKINA 2008b: fig. 3e–g). Oblique ridges **gz8** on the **gp8** are as distinct as in *Calopteryx* (ca. five per side; see Fig. 4).

In the vaginal area (Fig. 38) lobes **vl** are represented by two very indistinct vertical folds, which are hardly elevated from the surrounding membrane. Sclerites **VL** upon them as well as vaginal sclerotizations **VB** are lacking. The vagina is dorsoventrally compressed, though with a ventral keel (cross section in Fig. 38). The mid-ventral edge of the keel is formed by a very delicate cuticular thickening **mr**. As in the Aeshnidae the oviduct (**oc+oe**) is not evaginated into the vaginal lumen. The spermatheca **sp** originates from the anterior dorsal vaginal wall and is forked upon a common stem. A vaginal bulb **vb** is not developed, and any potential vestiges of a collar-shaped ridge **cr** are likewise absent. Tendon **vt** originates from the anterior tip of the vagina, and the vaginal wall around its origin is neither thickened nor melanized.

### 5.3.3. Exoskeleton of segment IX

In *Epiophlebia* antecosta **ac9** becomes slightly weaker middorsally, where a very narrow articulation can be observed during artificial movement.

Both the antelaterocoxa **LCa9** and the postlaterocoxa **LCp9** are as extensively synsclerotic with tergum **TG9** (Fig. 36) as in Aeshnidae (Fig. 27). **LCa9** is even in the internal aspect fully fused with **TG9**, with

no unmelanized patch and black stripe **h** recognized in the posterior part (see Fig. 27); the anterolateral part of a shallow groove (curved line **v** in Fig. 36) likely represents the border between **TG9** and **LCa9**. As in the Aeshnidae **LCp9** extends far anteriorly to approach **LCa9**. In contrast to both *Calopteryx* and Aeshnidae, however, the anteriormost part of **LCp9** is expanded mesad and fused to the lateral hind margin of **LCa9**; a one-piece gonangulum is thus present (it is defined by the fusion of these two sclerites). The posteromedian part of the shallow groove **v** may represent the border between **LCa9** and **LCp9**. In the contact area of **TG9**, **LCa9**, and **LCp9** there are no discrete articulations (in the sense of focal lines of cuticular flexibility), but the entire area is somewhat flexible. **LCa9** bears near its articulation with **GP8** a small backward-directed spine **sa** (directed anteriorly in Fig. 36, due to unfolding of area).

The bases of the gonapophyses **gp9** and gonapophyseal sclerites **GP9** in *Epiophlebia* (Fig. 41) show several peculiarities as compared to both *Calopteryx* and Aeshnidae (Figs. 39, 40). Each sclerite **GP9** forms a conspicuous posterior extension **i** of thick sclerotization, which flanks the apodeme **ca** (Fig. 41; though best distinguished in an external view by forcing the **gp9** anteriorly; see ‘posteriorly-directed process’ in MATUSHKINA 2008b: 73). The two **gp9** are fused basally for a short distance, as seen from the median longitudinal section in Fig. 41 (arrow: a transverse membrane fold connects the two **gp9**, which also in the midline is distinctly elevated posteroventrad from the surrounding membrane). *Epiophlebia* furthermore has a long row of strong saw-teeth **tm9** (compare Fig. 11) upon the dorsal edge of the **gp9**, which extends basally into the basal third of the **gp9**; this is in contrast to all other odonatanans here studied, where the row **tm9** reaches at most halfway down the **gp9**. MATUSHKINA (2008b: fig. 3a–d) provides structural details of the gonapophyses **gp9** and their saw-teeth, including the equipment with sensilla. The basal extension **g** of sclerite **GP9**, bearing the anterior end of the rhachis **rh**, is located even a bit farther anteriorly than in *Calopteryx*. The openings of the accessory glands **ag** (black dots in Figs. 39–41) are, in contrast to *Calopteryx* and aeshnids, close to each other near the midline, thus far remote from the anterior end of the rhachis. Apodeme **ca** (‘posterior intervalvula’ **piv\*** in MATUSHKINA 2008b: 73) is poorly developed, and tendons **ft** are absent like in the Aeshnidae.

The articulation between **LCp9** and the gonoplac sclerite **CXa9** is almost as far posteriorly as in *Calopteryx*. The anterior apodemes **fa** are ridge-like as in *Calopteryx*, the posterior apodemes **la** are strongly inclined posteriorly (Fig. 41; see also apodemes **aAp\*** = **fa** and **pAp\*** = **la** in MATUSHKINA 2008b: 74). The gonoplacs **gl9** lack tubercles on their distal ventral

edge; only a small but discrete bulge close to the stylus base (Fig. 41; MATUSHKINA 2008b: fig. 4c,g, ‘sclerotized protuberance’) is likely a far distal representative of these tubercles. Both setal tufts on the tip of sclerite **CXa9** and on the stylus tip (see Figs. 39, 40) are absent (in confirmation of VAN DER WEELE 1906: 157; ASAHINA 1954: pl. 45). The styli are short, stout, conical, and somewhat compressed (Fig. 41), thus differing from those of all foregoing taxa; further details of the stylus are shown in MATUSHKINA (2008b: fig. 4). The small sclerite **CXc9** at the stylus base is present but partly connected with the stylus sclerotization **SL9**. Sclerite **CXa9** is peculiar by extending far dorsally mesal to the stylus base; it reaches the tip of the gonoplastic lobe **dl** (Figs. 41, 48). Sclerite **CXb9** on the lobe **dl** is represented only by some brown spots bearing setae, some of which are confluent by very weak sclerotization (Figs. 41, 48).

In the area around the posterior gonoplastic bases (Figs. 41, 48) sclerite **PS9** in *Epiophlebia* resembles that in *Aeshna* (Fig. 46), but it is stronger, the mesal margins of the two **PS9** approach each other along a long median hinge, and the lateral connection with sclerite **CXa9** is more extensive (in particular, the stripe of weakened sclerotization separating the two is narrower, is heavier than in *Aeshna*, and was absent in the surmisedly young specimen; yet it is categorized as ‘weak’ in Fig. 48). As in *Aeshna* **PS9** lacks stiffening transverse folds (and a ventral antecosta **ac10** is absent as well, see next section). Nevertheless, the posterior gonoplastic bases in *Epiophlebia* are hardly movable relative to each other in a transverse direction, because a ribbon-like transverse sclerite **IT9** behind the **PS9** is strongly developed. **IT9** is laterally firmly connected with the posteroventral corners of tergum **TG9**.

#### 5.3.4. Exoskeleton of segments X and XI and telson

The sclerite ring X **TG10+LP** is, similar to *Caliaeshna*, ventrally open: the ventral wall of segment X is, though not entirely membranous, only very weakly sclerotized. A ventral antecosta **ac10** is absent. Like in *Aeshna* the posteroventral parts of segment X form a transverse, spiny bulge that projects beneath the subanal lobe bases, but the sclerotization of this bulge in *Epiophlebia* is divided medially by the (almost) membranous venter, and the bulge itself has a median notch (see MATUSHKINA 2008b for further details: ‘bearing edge’). The posterior middorsal process **dp** (see Fig. 3) is missing in *Epiophlebia*. Dorsal tendons **dt10** on the anterior margin of sclerite ring X are strongly developed in *Epiophlebia*, though corresponding tendons are lacking in the preceding segments (the reverse configuration is true for *Calopteryx*

and Aeshnidae). Tendon **ct** at the dorsal base of the cercus (see Fig. 12) is very short and thin, while tendon **ht** is well developed. The tendons **jt** at the anteroventral corners of the sclerites **AP** are remote from each other like in *Calopteryx*; these and tendon **rt** are particularly long. The cercal base ‘apodeme’ **ma** in *Epiophlebia* is devoid of sclerotization. The tendons **dt11** on the anterior margin of **TG11** are, in contrast to the Aeshnidae, very short (not found in the surmisedly young specimen) and located far laterally. The terminal triangular lobes **yl** (unpaired) and **xl** (paired) are more strongly developed than in the Aeshnidae; **yl** is a straight continuation of projection **tf** (i.e., its dorsal wall is level with **TG11**), and the **xl** are less distinctly set off from the tips of the subanal lobes **sb** than in Aeshnidae. Terminal tendons **tt** and **ut** as well as the associated external scars (see Figs. 12, 14) are, like in the Aeshnidae, absent in *Epiophlebia*.

### 5.4. Exoskeleton of female Zygoptera

#### 5.4.1. Exoskeleton of segments V–VII

The midabdominal segments (see Figs. 24, 25) show a wide range of width/length ratios; they are very long in most Zygoptera, particularly so in, e.g., *Lestes*, but in *Platycypha* they are even shorter than in the Aeshnidae. Their structural features are fairly uniform throughout the Zygoptera, resembling those in *Calopteryx*.

On the terga the longitudinal carinae **vc** and **lc** are consistently absent. The posterior transverse carina **ty** is always recognizable, though fairly indistinct in *Pyrrhosoma*, *Platycnemis*, *Chlorocnemis*, and *Mecistogaster*. Dorsal tendons **dt** are always present (but were not found in the single, likely teneral *Diphlebia* specimen, for which this character is considered in-assessable). They range from a very broad and short shape (e.g., *Epallage*, *Platycypha*) to a very long and narrow one (e.g., *Lestes*). In *Mecistogaster* each **dt** is seated upon a small and weak sclerite plate that lies within the intertergal membrane, and the **dt** also show some melanization. Intertergal articulations including patches **ap** and triangular heavier sclerotizations are always well developed at the segmental borders V–VI and VI–VII. Only in the single available *Diphlebia* specimen these articulations were poorly developed, with small patches **ap** and the triangular sclerotizations having a narrow base upon carina **ty**; this may be due to a not fully mature condition. Intertergal articulation VII–VIII is usually less distinctly developed than its preceding counterparts (especially in *Mecistogaster* and *Pyrrhosoma*), but the triangular sclerotization and patches **ap** are in all Zygoptera

distinct (the *Diphlebia* specimen considered inassessable).

The coxosterna always have keels **vk** along most of their midline. The **vk** act to a varied extent as hinge lines, and this function apparently depends on the heaviness of the sclerotization. Median caudal processes upon the posterior part of the coxosternum (found in *Epiophlebia*) are consistently absent. The median division of the weak posterior part of the coxosternum is frequently more discrete than in *Calopteryx*, e.g., in *Pyrrhosoma* and *Rhipidolestes*. The strengthening and lateral expansion into apodemes **at** of the coxosternal hind margin are in *Hetaerina*, *Mecistogaster*, *Chlorocnemis*, and *Lestes* as clear-cut as in *Calopteryx* (see Fig. 1), only vaguely indicated in *Epallage* and *Diphlebia*, and absent in the remaining zygopterans. In *Mecistogaster*, *Platycypha*, and especially *Pyrrhosoma* the coxosternal apodemes **at** and **pa** (see Fig. 1) are poorly developed in the segments up to VII (while **pa8** is well developed, as in Fig. 7). Only *Lestes* and *Rhipidolestes* show shallow, weakly sclerotized infoldings upon the posterior lateral margin of the coxosternum – possibly homologues of the **ba**-apodemes in *Caliaeshna*.

#### 5.4.2. Exoskeleton of segment VIII

The middorsal hinge of tergum **TG8** shows much variation. In most Zygoptera, as in *Calopteryx*, antecosta **ac8** obliterates middorsally and is divided into two articulated halves by the hinge **dh8**, which continues throughout **TG8**, though it is always less developed than the **dh** of the preceding segments. In *Platycypha*, however, as in *Aeshna*, **dh8** is very indistinct in the larger posterior part of **TG8**. In *Mecistogaster*, though **ac8** obliterates middorsally and a whitish line runs along the tergal midline, the sclerotization is hardly weakened middorsally, and the function of **dh8** as a hinge is very poor; this condition most closely resembles that in *Epiophlebia*, where, however, the whitish line is absent and the sclerotization is less heavy. In *Hetaerina* **ac8** continues across the middorsal area as a heavy, undivided ridge, but a middorsal weakening of its sclerotization establishes an indistinct articulation, and a well-functioning hinge **dh8** runs along most of the posterior part of **TG8**. *Drepanosticta* shows the poorest condition of the hinge: **ac8** is particularly stout and heavily sclerotized in the middorsal area and lacks a point of weakened sclerotization (a condition found in other Odonata, if at all, only on terga **TG9** and **TG10**), and a hinge line **dh8** behind it is entirely absent.

The posterolateral corner of **TG8** is in all Zygoptera developed as a conspicuously heavy sclerotization **b** that at least slightly projects ventrad beyond the

lateral margin of **TG8** immediately in front of it (see Fig. 7). While in most zygopterans extension **b** closely approaches the articulation between tergum **TG9** and antelaterocoxa **LCa9** (as in Figs. 26, 32, 33), it remains far remote from this area in *Drepanosticta* and *Platycypha*. These taxa as well as *Epiophlebia* (with a less clear-cut **b**) are thus intermediate between the other Zygoptera and the Aeshnidae: in the latter the posterolateral part of **TG8** is likewise far remote from the **TG9-LCa9** articulation, but it is altogether not particularly heavy and not at all expanded towards the articulation.

On the laterocoxosternum **LS8** (see Fig. 7) the postspiracular apodeme **ba8** is in *Drepanosticta*, *Mecistogaster*, *Platycnemis*, and *Chlorocnemis* as strongly developed as in Aeshnidae and *Epiophlebia*, while in other Zygoptera there is only a poor infolding as in *Calopteryx* or no differentiation of this area at all. The midventral **vk8** (see Fig. 4) is in all Zygoptera developed as a keel. A posteromedian process **pp8**, found in *Epiophlebia*, is always absent.

*Lestes* shows two special features of the coxae **CX8** (Fig. 32): their hindmost parts are medially fused, and the bases of their apodemes **ga** are expanded mesad to bear the origins of the tendons **gt**. The latter condition is closely approached in *Drepanosticta* and *Epallage* in the way that apodeme **ga** extends mesad exactly to the area where **gt** originates. While the origin of tendon **gt** in these and some other Zygoptera is distinctly on sclerite **CX8**, it is on weak marginal parts of **CX8** in *Diphlebia* and *Argiolestes*, and, like in Aeshnidae, on the membrane (antero)median to **CX8** in *Pyrrhosoma*, *Platycnemis*, and *Chlorocnemis*.

The relation between sclerites **CX8** and **LCa9** is in most Zygoptera the same as in *Calopteryx* (Figs. 4, 26), with a (almost) membranous separation and an articulation through a discrete extension **d** (the sclerites are rarely connected by very weak sclerotization in the articulation area). In *Drepanosticta*, *Lestes* (Fig. 32), and *Mecistogaster*, however, extension **d** and thus the articulation are less distinctly set off from the outline of sclerite **CX8**, like in Aeshnidae (Fig. 27; the membrane separating the sclerites is narrower than in Aeshnidae).

The structure of the area around the bases of the gonapophyses **gp8**, with its sclerotizations **GP8** (basal parts) and **MS**, is particularly interesting (see Figs. 26–29). Major differences among the odonatans here studied lie in the extent of the basal fusion or separation between the bodies of the left and right **gp8**, in the discreteness of **MS** at the ventral base of gonapophyses **gp8**, and in the condition of the **GP8**-sclerotizations at the dorsal base of gonapophyses **gp8**.

In the Aeshnidae (Figs. 27, 29) the cleft between the two **gp8** separates these down to the area in between the coxae **CX8**; this condition is here catego-

alized as the absence of a fusion between the **gp8**, or as the presence of a very long cleft. As compared to this condition, *Epiophlebia* shows a very short basal fusion (Figs. 36, 37). In all Zygoptera (Figs. 26, 28, 32, 33) the cleft between the two **gp8** is much shorter, reaching basad at most to the level where more laterally the sclerites **GP8** articulate with the antelatero-coxae **LCa9**; this condition is categorized as an extensive basal fusion between the gonapophyses **gp8**. While in most Zygoptera the cleft reaches the level of that articulation (e.g., *Calopteryx*, Figs. 4, 9, 26, and *Lestes*, Fig. 32), it is much shorter in *Chlorocnemis* and *Platycypha*, and especially in *Rhipidolestes* (Fig. 33), *Argiolestes*, and *Drepanosticta*, which thus have the **gp8** more extensively fused basally than the other Odonata here studied.

Along with the basal fusion of the bodies of the two gonapophyses **gp8**, their sclerites **GP8** in *Calopteryx* appear to be firmly fused as well, both at the dorsal and at the ventral base of the **gp8** (Figs. 4, 9, 10), and a corresponding but much shorter fusion of the **GP8** appears to be present in *Epiophlebia* (Figs. 36, 37), contrasting with the full separation of the left and right **GP8** in Aeshnidae (Figs. 27, 29). However, structural variations in Zygoptera show that conditions at the ventral **gp8**-base are more complicated (Figs. 26, 27, 32, 33, 36). *Rhipidolestes* (Fig. 33), *Argiolestes*, *Lestes* (Fig. 32), and *Drepanosticta* have a discrete midventral sclerite **MS**, which posteriorly reaches the anterior end of the **gp8**-cleft and thus completely separates the left and right **GP8** sclerites at the ventral **gp8**-base. **MS** is delimited from the **GP8** by narrow stripes of very weak sclerotization, which in an artificial movement of the gonapophyses are observed to act as hinge lines. The weak lines in *Lestes* are located farther anteromedially than in the other taxa – partly because the anterior end of the **gp8**-cleft, their point of origin, is farther anteriorly (compare Figs. 32 and 33) – and **MS** in *Lestes* is thus much smaller. *Chlorocnemis* and *Pyrrhosoma* have discrete hinge lines of slightly weakened sclerotization in the corresponding position. *Epallage*, whose **MS**-area is fairly weak and very small (the borderlines are located far medially), is difficult to assess, but the sclerotization appears somewhat weakened in between **MS** and **GP8**. The remaining Zygoptera lack obvious stripes of weaker sclerotization, but in *Platycypha* and *Diphlebia*, and to a lower extent in *Hetaerina* and in moderately sclerotized *Calopteryx*, an **MS**-area is bordered by discrete hinge lines in the same position, which are observable during movement (forcing the gonapophyses apart). In *Platycnemis*, *Mecistogaster*, and fully sclerotized *Calopteryx* the **MS**-area is, if at all, indistinctly delimited from **GP8** through somewhat wider ribbons of increased flexibility (position indicated in Fig. 26) rather than through discrete, very narrow hinge lines.

In *Epiophlebia* there is no **MS**-area that in some way is discrete from the **GP8** sclerites (Fig. 36). In sum, there is not in any zygopteran a ventral connection between the left and right sclerites **GP8** (as it would seem from conditions in *Calopteryx*), but the **GP8** in some Zygoptera are both fused with a median sclerite **MS**, whereas in others **MS** remains discrete. Because the extent of separation/connection of **MS** and **GP8** varies gradually among the Zygoptera and in part apparently also depends on the developmental stage of the imaginal cuticle (as apparent from *Calopteryx*), it is difficult to define and score states in this character (suggestions in Tab. 1 are preliminary). Since **MS** of *Rhipidolestes*, *Argiolestes*, *Lestes*, and *Drepanosticta* is like **MS** of *Aeshna* (Figs. 27, 32, 33) a discrete sclerite at the anterior end of the **gp8**-cleft, and since the size of **MS** ranges in the Zygoptera from very large (*Rhipidolestes*, Fig. 33) to very small (*Epallage*) as in *Aeshna*, it appears parsimonious to homologize the **MS** of *Aeshna* and the Zygoptera and to consider **MS** a basic component of the odonatan female genitalia. The presence of an **MS**-sclerotization in *Epiophlebia*, however, remains unresolved; the anterior transverse bridge between the **GP8** could be a small **MS**-area (**MS?** in Fig. 36; scoring in Tab. 1 tentative). There are indications that **MS** is originally a pair of sclerites: In *Drepanosticta* **MS** has a membranous midline stripe through its posterior third, and in *Mecistogaster* and some specimens of other taxa it is yellowish along the midline. In tearing the two **gp8** in *Rhipidolestes* apart along the midline (i.e., in extending the **gp8**-cleft forcefully basad along the supposed median fusion line of the **gp8**-bases), **MS** was observed to divide properly into two symmetrical halves.

At the dorsal base of the gonapophyses **gp8** (Fig. 28) a connection between the **GP8** sclerites of the two sides is to some extent present in all Zygoptera, and it seems to be direct, not mediated by some other sclerite. In *Argiolestes* the midline sclerotization is very weak and flexible, thus almost constituting a separation between left and right **GP8**. Also *Lestes* shows a distinct midline weakness. In the remaining Zygoptera the sclerotization is not obviously weaker along the midline than more laterally, though it frequently bears here a whitish seam, shows increased flexibility, and quite easily breaks when some force is applied. The fused anteriormost part of **GP8** is in, e.g., *Hetaerina* and *Mecistogaster*, as in *Calopteryx* (Figs. 9, 28), strongly expanded anteriorly to form a semicircular plate that underlies the vaginal opening. *Chlorocnemis* and *Pyrrhosoma* show a similar condition, but the anterior portion of the plate is very weak. In *Rhipidolestes*, *Argiolestes*, and *Platycypha* the plate is less expanded and **GP8** more or less truncated anteriorly. These differences in the basal extension of **GP8** can hardly be formulated as states of a character. The main

problem is the reasonable definition of a point of reference in comparison to which the anterior extension of sclerite **GP8** is measured: the potentially useful points, i.e., the anterior tip of the aulax-bearing extension **f**, the articulation between sclerites **GP8** and **LCa9**, and the anterior end of the **gp8**-cleft vary with regard to their spatial interrelations, and it is hardly possible to tell whether in a certain case **GP8** has expanded or the chosen point of reference has shifted. Only conditions in *Aeshna* and *Epiophlebia* (with membraneous stripes subdividing the dorsal sclerotization of the **gp8**-base; Figs. 29, 37: 'lobes' **x**, **y**, **z**), and *Caliaeshna* (with extensive areas being membraneous) are sufficiently distinct from the condition shared between all Zygoptera (with **gp8** completely sclerotized down to the very base) for being defined as different states related to the basal extension of sclerites **GP8**.

The asymmetrical interlock ridges **gy**, of which the basal ones are very prominent in the Aeshnidae (Fig. 29), are among the Zygoptera fairly distinct in *Mecistogaster* (five counted per side), *Platycypha* (about ten per side), *Lestes* (Fig. 32), *Chlorocnemis*, *Platycnemis*, and *Pyrrhosoma*. However, the basal ridges are as fine as the distal ones, and thus much less conspicuous than in the Aeshnidae. The entire **gy**-series usually extends far distally as in the Aeshnidae and *Epiophlebia* (into the distal third of the **gp8** in *Platycypha*). The ridges appear more discretely in very strongly melanized individuals than in weakly melanized ones (but are still difficult to see; a median view of a cut gonapophysis, with changing angles of light, is most instructive). Whereas ridges of the same kind are slightly indicated in *Diphlebia* and *Hetaerina*, and traces of them were observed also in some *Calopteryx*, no trace of them was found in *Rhipidolestes*, *Argiolestes*, *Drepanosticta* (the taxa with the most extensively fused gonapophyses **gp8**), and *Epallage*.

A series of lateral saw-teeth **tm8** on gonapophysis **gp8** is present in most Zygoptera – restricted to roughly the same distal area as in *Calopteryx* (Fig. 9; the range is indicated by Figs. 42, 43). However, **tm8** are lacking in *Platycypha*, *Mecistogaster*, and *Argiolestes*, where the tip of the **gp8** resembles that in *Aeshna* (Fig. 44). Oblique ridges **gz8** (see Fig. 4) are likewise present in most Zygoptera – though occasionally they are fairly indistinct – but there is no trace of them in *Argiolestes*. Some variation occurs in the number of the **gz8** and in their arrangement upon the distal half of gonapophyses **gp8**.

The vaginal area in all Zygoptera here studied essentially conforms with that in *Calopteryx* (Figs. 7–10, 30; Fig. 34 for *Chlorocnemis*, Fig. 35 for *Mecistogaster*). The lobes **vl** at the vaginal opening are always more strongly developed than in the aeshnids and *Epiophlebia* (Figs. 31, 38). However, distinct sclerites **VL** were found only in *Calopteryx* (Fig. 9), *Platy-*

*cnemis*, and *Pyrrhosoma*, and there is some weak, diffuse melanization of the respective area in *Hetaerina*. The vaginal sclerite **VB** is usually strong, fairly weak only in *Mecistogaster* (Fig. 35); it always extends anteriorly to near the oviduct opening. In front of **VB** all Zygoptera have a complete collar-shaped ridge **cr** also crossing the dorsal midline (Figs. 30, 34, 35), though in *Lestes* the posteroventral arms alongside the oviduct opening are poorly developed. Only *Mecistogaster* (Fig. 35) has a very short, partly melanized midventral thickening **mr** at the posterior base of the common oviduct **oc**. In contrast to the much longer ridge **mr** in Aeshnidae and *Epiophlebia* (Figs. 31, 38), however, it does not prevent the evagination of the oviduct into the vagina. In all Odonata here studied the intima-bearing (presumably ectodermal) part of the oviduct (common oviduct **oc** plus extended oviduct **oe**) is very short, and in all Zygoptera it is evaginated and thus not visible upon a macerated vagina. Tendon **vt** is present in all Zygoptera. The median thickening around the base of tendon **vt** (see Fig. 31) is in some Zygoptera considerably heavier than in *Calopteryx* (where it is virtually absent and not included in Fig. 30), especially in *Mecistogaster* (Fig. 35). In *Pyrrhosoma* and, to a lower extent, in *Lestes* the **vt**-base was found melanized. The vaginal bulb **vb** is large and conspicuous in nearly all Zygoptera here studied; it is very small only in *Mecistogaster* (Fig. 35) and *Diphlebia*, but never completely absent as in *Epiophlebia* (Fig. 38).

The spermatheca **sp** is distinctly forked in *Calopteryx* (Fig. 30), *Diphlebia*, *Drepanosticta*, and *Rhipidolestes*, only terminally bilobed (and very thick) in *Argiolestes*, and entirely unforked in some other taxa: It is an oblong bulb in *Epallage*, and a short sac in *Pyrrhosoma*. In *Platycnemis* **sp** consists of a basal tube and a terminal oblong bulb and is seated leftdorsally upon the vaginal bulb, whereas in all other Zygoptera it is in a middorsal position (all other elements of the vaginal area in *Platycnemis* are bilaterally symmetrical). In *Chlorocnemis* (Fig. 34) the spermatheca-bearing posterior part of the vaginal bulb forms a long, narrow neck from which arises a dorsomedian sac that receives the unforked but distally widened spermatheca; the cuticle of the neck and of the spermatheca is strongly folded, but in one specimen the spermatheca was found in an expanded condition (both conditions shown in Fig. 34). The unforked spermatheca in *Mecistogaster* (Fig. 35) is peculiar in being heavily sclerotized (sclerite **SP**) and coiled in its basal part. In *Platycypha* the vagina in front of ridge **cr** and tendon **vt** consists only of one unpaired oblong bulb; this is tentatively identified as the vaginal bulb, while the spermatheca is considered absent. Also *Lestes* appears to lack a spermatheca, though a large posterodorsad-directed extension of the vaginal bulb may be a spermatheca that has become indiscretely bordered against

the bulb. Similarly, in *Hetaerina* a small lobe-like infolding seated posterodorsally upon the vaginal bulb may be the vestige of a spermatheca. Nevertheless, spermathecal characters are here not scored for *Lestes* and *Hetaerina*.

#### 5.4.3. Exoskeleton of segment IX

The middorsal hinge line continues in many Zygoptera to tergum **TG9**. Its antecostal midline articulation, however, is never as discrete as in *Caliaeshna*. Whereas in *Lestes* **ac9** distinctly obliterates middorsally, **ac9** crosses the midline as a heavy ridge in the remaining Zygoptera. While in *Lestes* as well as in *Epallage* and some other taxa with a heavy **ac9** a narrow middorsal part of **ac9** is clearly the focal area of flexibility and thus constitutes an indistinct articulation (as in *Epiophlebia*), other Zygoptera lack, like *Calopteryx*, a middorsal antecostal articulation, albeit a hinge line is frequently present farther behind.

The area where tergum **TG9** meets the ante- and postlaterocoxae **LCa9** and **LCp9** (Figs. 26, 27, 32, 33, 36) is morphologically highly important, because the two latter sclerites together constitute the gonangulum. Whereas in *Calopteryx* all three sclerites are quite distinctly bordered, with membrane (or very weak sclerotization) and clear hinge lines in between, in Aeshnidae and especially *Epiophlebia* sclerotizations are strongly confluent and hinge lines much less discrete (Figs. 26, 27, 36); certain Zygoptera show intermediate conditions. In view of this structural range one would expect that some characters could be drawn from this area. However, the treatment of most of the potential characters is very difficult: First, the definition of states and assignment of these to taxa is difficult because in the distribution and extent of sclerotization a gradual variation through the taxa is combined with some intraspecific variation (in part surely age-dependent). Second, assessment of specimens is difficult due to the frequently fluent transitions between sclerotization/melanization of different degree, due to differences with respect to melanization between the external and the internal aspect of the cuticle (especially along thickening **ac9** crossing from **TG9** to **LCa9**, see Figs. 26, 27), and due to the occasional indistinctness of hinge lines between the sclerites concerned (these are often themselves quite flexible, and lines of focal flexibility, i.e., obvious seams of sclerite fusion, can be virtually absent; this is partly a consequence of the strong cuticular thickening). The treatment of the respective characters as herein proposed is thus to some extent tentative.

The contact between **TG9** and **LCa9** is in most Zygoptera shaped as in *Calopteryx* (Fig. 26), but in some it is, approaching aeshnid/epiophlebian conditions,

more extensively synsclerotic. Nevertheless, in all Zygoptera **TG9** and **LCa9** are in front of stripe **h** and the flanking membranes separated by an internally visible line of lacking melanization (compare Figs. 27, 36 and 26, 32, 33). The differences, however, are considered too vague for defining states.

**TG9** and the anterior part of **LCp9** are in some Zygoptera separated, or connected only via a narrow or weak sclerotization, as it is true for *Calopteryx*. In others, however, and most distinctly in *Platycypha*, *Lestes* (Fig. 32), *Rhipidolestes* (Fig. 33), and *Mecistogaster*, the connection is more similar to that in Aeshnidae and *Epiophlebia*, including (almost) the entire anterior part of **LCp9** and being established by sclerotization (almost) as heavy as that of the original sclerites. The anterior tip of **LCp9** remains in *Calopteryx* (Fig. 26), *Chlorocnemis*, *Pyrrhosoma*, *Platynemis*, and *Mecistogaster* far remote from **LCa9**, while in *Hetaerina*, *Epallage*, *Diphlebia*, *Drepanosticta*, and *Rhipidolestes* (Fig. 33) the gap is smaller. In *Platycypha* (with a very weak **LCp9**), *Argiolestes*, and *Lestes* (Fig. 32) **LCp9** approaches **LCa9** as closely as in Aeshnidae and *Epiophlebia* (Figs. 27, 36), i.e., it reaches the articulation between **LCa9** and **TG9** as marked by the area of the stripe **h** (though in *Lestes* the border between **TG9** and **LCp9** cannot be clearly identified due to the intimate connection of the sclerites). Since in *Lestes* **LCp9** both extends far anteriorly and shows a very extensive connection with **TG9**, in this taxon the contact area of **TG9**, **LCa9**, and **LCp9** approaches conditions in the Aeshnidae most closely (the same is possibly true for *Platycypha*, but **LCp9** in this taxon is too weak for permitting such a definite assessment). The only somewhat discrete difference to Aeshnidae is that in *Lestes*, like in other Zygoptera, **TG9** and **LCa9** are internally separated in front of stripe **h** (see above).

In all Zygoptera, even in *Lestes*, as well as in Aeshnidae (Figs. 26, 27, 32, 33) **LCp9** is clearly not synsclerotic with **LCa9** (i.e., with the sclerotization median to stripe **h** and the internal membrane flanking it), and the two sclerites do thus not form a one-piece gonangulum as in *Epiophlebia* (Fig. 36). A spine **sa** upon the median part of **LCa9**, as found in *Epiophlebia* (Fig. 36), is absent in the Zygoptera, but *Diphlebia* has a small bulge in the respective position.

The accessory glands **ag** are paired in all Odonata here studied. Nearly always their openings are far separated medially and lie in the immediate neighborhood of (usually shortly anteromedian to) the anterior end of the rhachis **rh** (as in Figs. 7, 39, 40). Among the zygopterans only *Lestes* has the openings of the two sides close to each other in the midline (like *Epiophlebia*, Fig. 41); the openings lie – far medially and distinctly posterior to the end of the rhachis **rh** – upon a transverse membranous groove, which may lead the secretions laterad towards the rhachis.

The rhachis reaches in many Zygoptera, like in *Calopteryx* and *Epiophlebia* (Figs. 4, 39, 41), the anterior tip of the gonapophyseal sclerite **GP9**, but in others it is shortened like in the Aeshnidae (Fig. 40). This correlates with the anterior extension of the small sclerotization **g**, which bears the anterior end of the rhachis. All Zygoptera have well-developed tendons **ft** on each side of the **ca**-apodeme (as in Fig. 39) – in contrast to Aeshnidae and *Epiophlebia* (Figs. 40, 41).

Like in Aeshnidae, but in contrast to *Epiophlebia*, none of the zygopterans showed any trace of a basal fusion between the bodies of the two gonapophyses **gp9**, and the gonapophyseal sclerite **GP9** had never an extension like **i** of *Epiophlebia* (see Figs. 39, 40 vs. 41). The saw-teeth **tm9** dorsally on gonapophyses **gp9** (see Fig. 11) are more or less distinct in all Zygoptera, but like in Aeshnidae and in contrast to *Epiophlebia* the series of **tm9** was never found to extend further basally than halfway down the **gp9**. The only exception was *Lestes*, in which **tm9** are distinct in the two distal thirds of **gp9**, but (in contrast to *Epiophlebia*) indistinct in the basal third.

The gonoplacs **gl9** bear in all Zygoptera some kind of tubercles on their distal ventral edge; with some variation in tubercle shape and distribution, many uniform tubercles are usually present along much of this edge (as in Figs. 4, 39). *Lestes* also has a long row of small tubercles, but the distalmost is much bigger than the others. This approaches conditions in *Drepanosticta*, which has only one strong, claw-shaped projection far distally on the gonoplac – much like *Epiophlebia* (Fig. 41), whose single distal tubercle, however, is much smaller.

The styli **sl9** show in many Zygoptera the shape described for *Calopteryx* (Fig. 5), with a strong curvature and a clubbed tip. In *Lestes* the club, and in *Epallage*, *Platycypha*, *Pyrrosoma*, and *Drepanosticta* both the club and the curvature are less distinct. In *Argiolestes* and *Mecistogaster* the styli are neither clubbed nor curved, but cylindrical as in the Aeshnidae (Fig. 40). The small sclerite **CXc9** at the stylus base (see Fig. 5) is present in most Zygoptera, but it is poorly melanized in *Chlorocnemis* and connected with the weak basal part of the stylus sclerotization **SL9** in *Lestes*, thus indistinct in both taxa. The dorsal

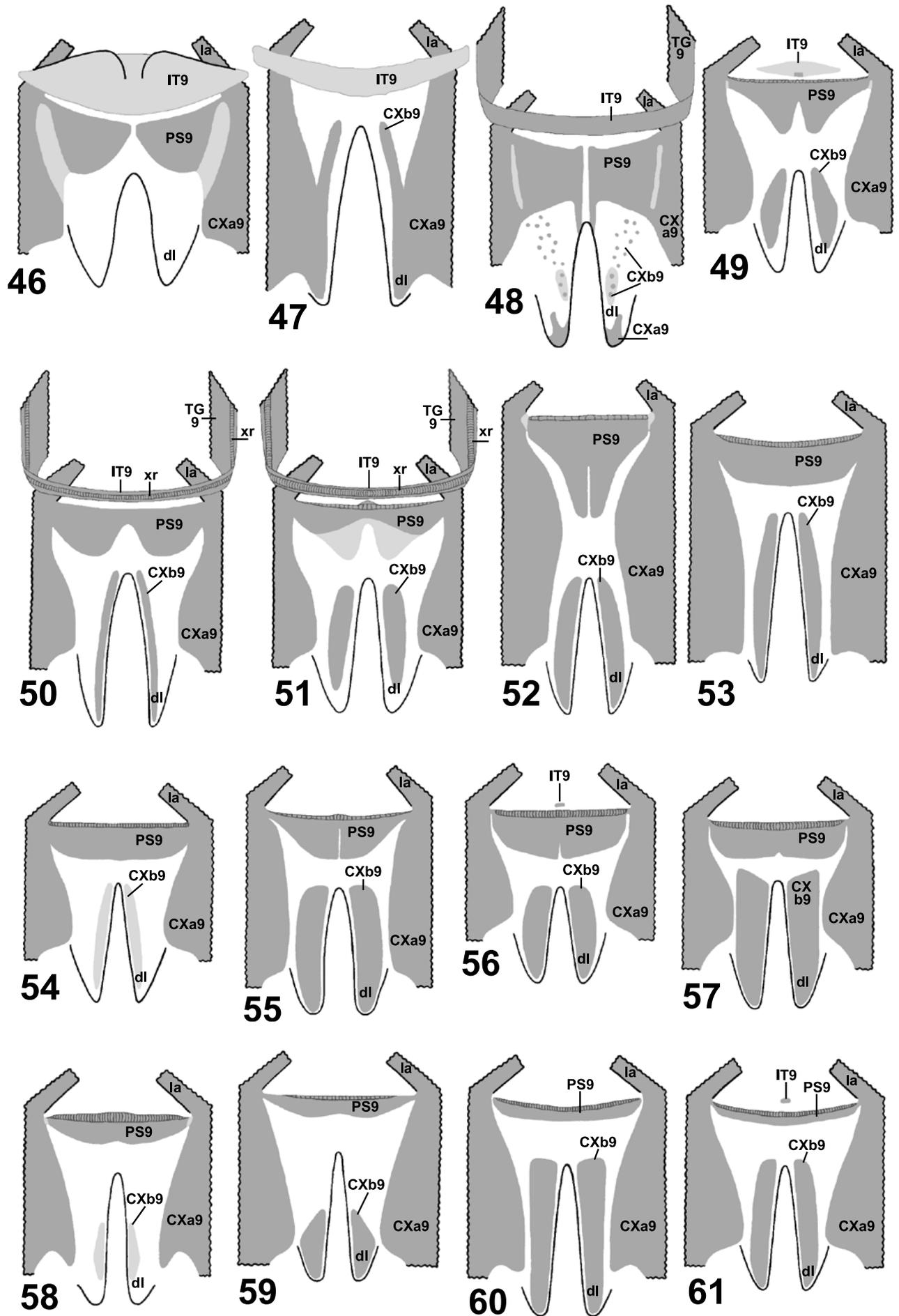
gonoplac sclerites **CXb9** were observed in all Zygoptera (Figs. 49–61), but they were found very weak in *Platycypha* and *Mecistogaster* (Figs. 54, 58) and in one specimen of *Drepanosticta*. A connection between **CXb9** and **CXa9**, as in *Caliaeshna* (Fig. 47), was never observed.

Setal tufts were clearly observed distally on the main gonoplac sclerite **CXa9** in *Calopteryx* (Figs. 4, 39) and on the stylus tip in the aeshnids (Fig. 40). The tuft on **CXa9** is in *Hetaerina* as discrete as in *Calopteryx*. Some other Zygoptera bear long setae in the same area, but these are less clearly distinguished (e.g., by their length) from the setae along the distal ventral gonoplac edge, and not spaced as closely as in *Hetaerina* and *Calopteryx*. Similar tufts are reported for several Zygoptera in ST. QUENTIN (1962) and for an *Aeshna* in VAN DER WEELE (1906: **H2\*** in fig. 28) (see also MATUSHKINA & GORB 2002). A discrete tuft of long setae upon the stylus was among Zygoptera only found in *Argiolestes*. Finding absence of setal tufts in a particular specimen, however, does not necessarily indicate their general absence in the species, because the setae are apparently easily rubbed off during oviposition activities (see MATUSHKINA & GORB 2002: e.g. fig. 1). This character clearly needs an SEM study in larger samples per species.

The sclerotizations around the posterior gonoplac bases are particularly variable and interesting (Figs. 46–61). All Zygoptera have a clear homologue of the *Calopteryx* sclerite **PS9**, as identified by the close contact (articulation or fusion) of its posterolateral tips with the margins of **CXa9** immediately behind the bases of the apodemes **la** (see Fig. 7). **PS9** shows variation in the kind of the latter contacts, in its length (= extension along longitudinal axis of animal), in the shape of its anteroventral margin (lower margin in Figs. 46–61), and in the distinctness of transverse folds or thickenings that stiffen it. Because in all **PS9** characters transitions are gradual, the definition of states and the scoring here proposed are necessarily tentative.

**PS9** and **CXa9** in *Calopteryx* (Figs. 7, 61) are either separated by an articulation membrane or narrowly synsclerotic (with or without an obvious weakness, but always with a discrete functional hinge). The

**Figs. 46–61. Area of posterior gonoplac bases.** 46: *Aeshna cyanea*, 47: *Caliaeshna microstigma*, 48: *Epiophlebia superstes*, 49: *Epallage fatime*, 50: *Lestes elatus*, 51: *Drepanosticta fontinalis*, 52: *Rhipidolestes* sp., 53: *Argiolestes aurantiacus*, 54: *Platycypha caligata*, 55: *Diphlebia lestoides*, 56: *Hetaerina americana*, 57: *Platycnemis pennipes*, 58: *Mecistogaster lucretia*, 59: *Pyrrosoma nymphula*, 60: *Chlorocnemis* sp., 61: *Calopteryx virgo*. Posterior view of posterior gonoplac base, diagrammatically. Included are sclerotizations **CXa9** (partly), **CXb9**, **CXc9**, **PS9**, **IT9** (if **IT9** is connected with **TG9** the posterolateral corners of **TG9** are additionally shown), and, of the formative elements, dorsal gonoplac lobes **dl**, apodemes **la** (partly), and internal ridges/thickenings. Elements posterior to (= above in illustrations) the line connecting the left and right contacts between **CXa9** and **PS9** are forced anterodorsad, components anterior to (= below in illustrations) this line are forced anteroventrad (gonoplacs thus viewed dorsally). Sclerotization grey (two categories: darker = heavier). Undulate lines are cuts through the cuticle. Ladder-shaped ribbons are cuticular thickenings (spacing of hatches roughly indicating extent of thickening).



former condition was found in *Chlorocnemis* (Fig. 60), the latter in *Hetaerina*, *Pyrrhosoma*, *Platycnemis*, *Diphlebia*, and *Mecistogaster* (Figs. 55–59), but the occurrence of the respectively alternative condition in these taxa cannot be excluded after the examination of only few specimens. In *Argiolestes*, *Platycypha*, *Drepanosticta*, and *Lestes* (Figs. 50, 51, 53, 54) the seam along which **PS9** is synsclerotic with **CXa9** is obviously longer than in the aforementioned taxa, thus approaching conditions in *Aeshna* and *Epiophlebia* (where, however, the major anteroventral part of the connection is weakened; Figs. 46, 48). *Epallage* and *Rhipidolestes* are intermediate in this respect (Figs. 49, 52).

The posterodorsal margin of **PS9** (upper margin in Figs. 46–61), in between the contacts with **CXa9**, is in all Zygoptera fully sclerotized, without a midline weakening or division by membrane as found in *Aeshna* and *Epiophlebia* (Figs. 46, 48; **PS9** in *Mecistogaster*, Fig. 58, is brighter in the midline but not evidently weaker or more flexible than farther laterally). This margin usually forms, as in *Calopteryx* (Fig. 61), a strong transverse infolding or internal thickening, but this is only slightly indicated in *Epallage*, *Diphlebia*, *Drepanosticta*, *Pyrrhosoma*, and *Rhipidolestes* (Figs. 49, 51, 52, 55, 59), and entirely absent in *Lestes* (Fig. 50). The part of **PS9** anteroventral to the former fold is in most Zygoptera bulged outward to some extent; in *Chlorocnemis*, as in *Calopteryx*, this transverse bulge is condensed to form a narrow, discrete outward-directed fold (as in the section in Fig. 7).

The length of **PS9** varies enormously; *Calopteryx*, *Chlorocnemis*, and *Pyrrhosoma* have the shortest **PS9** (Figs. 59–61), *Rhipidolestes* (Fig. 52) has the longest. Usually, the longer the **PS9**, the more distinctly is its anteroventral margin (lower margin in Figs. 46–61) bilobed through a median membranous incision, which ranges from a broad tongue (e.g., in *Epallage*, Fig. 49) to a narrow line (which acts as a hinge line; e.g., in *Rhipidolestes* and *Diphlebia*, Figs. 52, 55). The length and bilobation of **PS9** appear thus essentially correlated, and the extent of bilobation is used here as a character. *Drepanosticta*, with a very weak anteroventral part of **PS9** (Fig. 51), constitutes an intermediate between conditions of strong and weak bilobation (its **PS9** is here considered strongly bilobed and long; it should be noted that also in some other taxa with long or moderately long **PS9** the sclerotization becomes weaker in the anteroventral part of **PS9**). Nevertheless, the correspondence between length and bilobation is not complete, as shown by a comparison of, e.g., *Argiolestes* and *Pyrrhosoma* (Figs. 53, 59).

Some Zygoptera have sclerotizations in between **PS9** and the anterior margin of sclerite ring X **TG10+LP** (see Figs. 39–41); these are here collectively called **IT9**, but as they vary considerably,

homologies are partly uncertain. *Epallage* (Fig. 49) has a weak transverse **IT9**, which may well be the homologue of **IT9** in *Aeshna* and *Caliaeshna* (Figs. 46, 47). Since the *Epallage* sclerite has a median spot of heavy sclerotization, the minute median sclerite **IT9** that apart from *Calopteryx* (Figs. 4, 7, 61) is also distinct in *Hetaerina* (Fig. 56) may as well be a strongly reduced homologue of the aeshmid **IT9**. Homology between all the **IT9** mentioned so far appears thus conceivable. *Lestes* and *Drepanosticta* (Figs. 50, 51) have, like *Epiophlebia* (Figs. 41, 48), a strongly sclerotized, narrow transverse bridge **IT9** that is firmly connected laterally with the posterolateral corners of tergum **TG9**, which in these taxa are heavily sclerotized. Both *Lestes* and *Drepanosticta* have, moreover, an internal ridge **xr** near the hind margin of **TG9** (immediately in front of the posterior transverse carina **ty9** – see Figs. 3, 4 – and thus clearly on primary segment IX). Ridge **xr**, which is particularly strong in *Drepanosticta*, continues ventrally throughout **IT9** and thus encircles the entire segment. It forms a hinge either within the patch of heavy **TG9**-sclerotization (*Lestes*) or shortly mesal to it (*Drepanosticta*). Possibly in correlation with the transverse strengthening through **IT9** and **xr**, antecosta **ac10** is poorly developed (*Lestes*) or absent (*Drepanosticta*). No trace of a ridge **xr** was found in the other Odonata here studied, not even in *Epiophlebia* with its similar **IT9** (Fig. 48). The homology of the **IT9** of *Lestes*, *Drepanosticta*, and *Epiophlebia* with the aforementioned **IT9** is here tentatively assumed. The remaining Zygoptera here studied – *Rhipidolestes*, *Argiolestes*, *Platycypha*, *Diphlebia*, *Platycnemis*, *Mecistogaster*, *Pyrrhosoma*, and *Chlorocnemis* (Figs. 52–55, 57–60) – lack any sclerites that could be interpreted as **IT9**.

#### 5.4.4. Exoskeleton of segments X and XI and telson

Sclerite ring X **TG10+LP** (see Figs. 3, 12) is in all Zygoptera ventrally closed. Its posteroventral part is in several taxa weaker than the remainder of the ring (e.g., in *Epallage*), but only in *Hetaerina* this area forms a discrete membranous field. *Mecistogaster* shows a hinge line along the ventral midline of **TG10+LP**, though the sclerotization is not recognizably weakened. A strong, transversely continuous ventral antecosta **ac10** is present in all Zygoptera except *Lestes* and *Drepanosticta* (see section 5.4.3.). It likely contributes to a transverse stabilization of the posterior gonoplac bases. Anterodorsal tendons **dt10** upon **TG10+LP** are absent in all Zygoptera; they occur only in *Epiophlebia*. The posterior dorsomedian process **dp** of **TG10+LP** is distinct only in *Calopteryx* (Fig. 3); in *Hetaerina*, however, some small tubercles

are agglomerated in the same area in order to form an indistinct process **dp**.

The set of tendons present in the terminal abdomen (see Figs. 12–15) is, like in the preceding segments, very uniform throughout the Zygoptera. However, *Lestes* lacks the cercal base tendons **ct**, and in *Drepanosticta* the tendons **ht** on the anterior margin of sclerites **AP** are missing. The ventral tendons **jt** are, in contrast to Aeshnidae but like in *Epiophlebia*, always far remote from each other (as in Fig. 15); in some taxa they are seated upon the sclerites **AP** rather than on the adjacent membrane as in *Calopteryx*. The Zygoptera differ consistently from Aeshnidae and *Epiophlebia* by the presence of tendons **ut** and **tt**, which usually resemble those in *Calopteryx*, and by the absence of the terminal lobes **xl** and **yl** on the subanal lobes **sl** and on the terminal projection **tf**. Nevertheless, either **ut** (in *Drepanosticta*) or **tt** (in *Platycypha* and *Diphlebia*) can be reduced to tiny, purely membranous ribbons – with some intraspecific variation. A sclerotization of the cercal base apodeme **ma** is present only in *Calopteryx* (Fig. 12) and *Hetaerina*, where it is firmly connected with the cercal sclerotization **CE**, and in *Epallage* and *Drepanosticta*, where it forms a small plate at the mesal base of the otherwise membranous ‘apodeme’ **ma**. In the remaining Zygoptera **ma** is a purely membranous lobe. The anterior margin of tergum **TG11** (see Fig. 12) is in many Zygoptera folded inside to form an internal ridge, which can be distinctly bilobed. *Mecistogaster* has very short, and *Chlorocnemis* has fairly long membranous tendons **dt11** seated upon the lobes, approaching the aeshnid condition with very long **dt11** (these tendons likely serve for the attachment of muscles **43**, see Fig. 21).

### 5.5. Additional remarks and differences to previous descriptions

The findings on the midabdomen essentially comply with SCHMIDT’s (1915: 95ff, textfigs. B, C) descriptions, which are the so far most elaborate and likewise focus on *Calopteryx* and *Aeshna*. Some differences and additions are noteworthy (Figs. 1, 24, 25): The dorsal midline (**m\*** in SCHMIDT) forms a hinge **dh**. Patches **ap** of thick, soft cuticle are present in the intertergal articulations. Also in *Calopteryx* the tergum has around the patches **ap** a clear acrotergal portion anteriorly and, though less distinctly than in *Aeshna*, a triangular heavy sclerotization posteriorly (**x\*** and **y\*/y1\*** in SCHMIDT). The anterior ventrolateral ridges starting from apodemes **at** (**ac** in Fig. 1, ventral antecosta? **sp1\*** in SCHMIDT) were never found to continue through the ventral midline. The broad and

heavy condition of the posterior coxosternal margin in *Calopteryx* is not mentioned by SCHMIDT. Whether the ventral carina **vc** is absent in *Calopteryx* (and the other Zygoptera here studied), or almost unrecognizable as categorized by ASAHINA (1954: 57) for *Mnais*, may be a matter of taste (the character is tentatively retained in Tab. 1).

The spiracles in all Odonata here studied are in a position corresponding to that in *Calopteryx* (Fig. 1) and are seated on the posterior part of a small oval sclerite **SI** (Fig. 2); spiracles are similar in at least segments IV–VIII, and that of VIII is by far the largest (spiracles probably similar throughout segments II–VIII, see POONAWALLA 1966: 809, fig. 1K, peritreme = **SI**). POONAWALLA (1966) notes that Aeshnidae, in contrast to Coenagrionidae and Lestidae, have a short atrium. Further details of the spiracles were not consistently studied in the taxa here sampled and have apparently not been described in the literature. In preliminary studies of *Aeshna* and *Caliaeshna* a zone **ZE** of anastomosing ridges internal to the closing bars, as present in *Calopteryx*, was not found; an internal lobe resembling **ls** (Fig. 2) is present but arises from the anterior part of the median bar rather than from the inner flank of this bar. Spiracle structure may thus contain characters worth a comparative SEM-study.

Some of VAN DER WEELE’S (1906) data on the female genitalic segments are in conflict with my findings. In *Coenagrion pulchellum* L. (*Agrion p.* therein; Zygoptera: Coenagrionidae) coxae **CX8** (basalia **b\*** of gonapophyses anteriores in VAN DER WEELE 1906: 103, fig. 1) are reported to be connected with the gonapophyseal sclerites **GP8** (though sutures are mentioned on p. 133 therein), while in all taxa here studied sclerites **CX8** and **GP8** are fully separated (Figs. 26, 27, 32, 33, 36). Furthermore, VAN DER WEELE’S (1906: 152f, 158) claims that the **CX8** in *Calopteryx virgo* L. and *Aeshna grandis* L. lack apodemes (compare **ga** in Figs. 26, 27), and that ridges **gz8** (‘Feilenrippen’ therein) are absent in *Calopteryx* (compare **gz8** in Fig. 4) are incorrect.

HAKIM (1964: 578) claims that in all Zygoptera the left and right sclerites **CX8** (larger anterior part of valvifer I therein, e.g., fig. A) are transversely fused, and the **CX8** fused with the **LCa9** (smaller posterior part of valvifer I). In the present study the former fusion was found in *Lestes* (Fig. 32; see above) but not in the other Zygoptera, and the latter fusion is present in none of the Zygoptera. Further inaccuracies in HAKIM’S descriptions concern the relations between **LCa9** and **TG9**, and between **LCp9** and **TG9**, and the structure of the **CX9** and gonoplaes (especially in terms of his comparison between Zygoptera and Aeshnidae, Figs. A, B, D, E).

GEORGE (1929: 453, fig. 14) in *Coenagrion* reports a ridge-and-groove interlock between the left

and right gonapophyses **gp8**; but what is seen in his transverse section is likely one of the ridges **gy** (as in Fig. 32), which may provide some interlock but do not form continuous ridges or grooves along the **gp8**.

SCUDDER (1961b: 32, fig. 6) describes for an *Aeshna* a sclerite (gonangulum **Ga\*** therein) that evidently comprises sclerites **LCa9** and **LCp9** (Fig. 27). These together are the homologues of the gonangulum in other insects; however, these sclerites were found entirely separated in nearly all taxa here studied, including *Aeshna* (Figs. 4, 7, 26, 27, 32, 33); only *Epiophlebia* (Fig. 36) has **LCa9** and **LCp9** connected. Since the structure and articulations of the area are not very clear in SCUDDER's illustration, one may assume that the extensive synsclerotism in *Aeshna* (Fig. 27) between tergum **TG9** and both **LCa9** and **LCp9** may have misled him. PFAU's illustrations (1991: fig. 20a,b) indicate for the aeshnid *Anax* separated **LCa9** (the ribbon-shaped middle sclerite of **Vf1\*** that articulates with **V1\*** = **GP8**) and **LCp9** (the posterior **Vf1\***-sclerite articulating with **Vf2\*** = the part of **CXa9** forming apodemes **la** and **fa**). The same is evident from MATUSHKINA's (2008a) study of *Anax imperator*.

The different spatial relationships between the spermatheca **sp** and the vaginal bulb **vb** in Zygoptera (Figs. 30, 34, 35) and Aeshnidae (Fig. 31) is one of the few problems of topographic and primary homology in ovipositor-bearing Odonata. Either the spermatheca or the bulb (or both) should be non-homologous (if not a ventral shift of the spermatheca origin, with a dorsolateral position as in *Platycnemis* being an intermediate, is assumed). Since the similarity between the spermathecae **sp** may appear more specific (usually a narrow, forked tube; Figs. 30, 31) than that between the bulbs **vb**, and since *Epiophlebia* (Fig. 38) also has a narrow, forked tube upon the vagina but lacks a bulb like **vb**, a homologization of the forked spermatheca in Zygoptera, *Epiophlebia*, and Aeshnidae seems most parsimonious; **vb** in Zygoptera and Aeshnidae is then topographically non-homologous (i.e., formed by different parts of the vagina). However, this issue will additionally require consideration of homologies in the male genitalia of the taxa concerned, as these enter the female gonoducts and have substructures entering the spermatheca and vaginal bulb (e.g., HAYASHI & TSUCHIYA 2005 for Calopterygidae, WAAGE 1986, and references cited therein).

## 5.6. List of characters of abdominal exoskeleton in female Odonata

Characters are numbered in sequence. The abbreviations used for character states are explained in the leg-

end of Tab. 1 (for cladistic analysis abbreviations can be replaced by 0, 1, 2 etc.). In presence/absence characters, states are distinguished in which a structure is clearly present ('distinct'), in which some trace of it is present ('indistinct'), and in which it is entirely absent ('absent'). This is preferred to a distinction of only 'present' and 'absent' because more information is retained. Similarly, in some other characters intermediate conditions are defined as states. For the characters concerned an ordered treatment is recommended, which does not need assumptions on evolution in addition to those on which the delimitation of the character states is based. Conditions categorized as 'indistinct' or 'intermediate' in some way are, if necessary, explained in sections 5.2.–5.4. or in the following list. In some of the respective characters 'indistinct' conditions were not found within the sample here used, but because they may be observed in an expanded sample, clear presence is still categorized here as 'distinct'. Midabdominal characters are assessed for segments V–VII, or for V–VI if VII differs. Peculiarities of the segments up to IV remain thus unconsidered (e.g., medio-caudal coxosternal processes).

The formulation of many characters is to be considered preliminary, because: (1) Characters referring to homonomous structures of different segments (mostly V–VII) may have to be split in case taxa are found in which the segments show different conditions. (2) Characters including two or more assessed attributes, whose variation across taxa is consistently correlated in the sample here used, may have to be split in case taxa are found for which the correlation is not true. (3) With the addition of further taxa refined definitions of states may be required. In addition, many characters will need further pictorial documentation. In this way the character list and table should rather be seen as a survey of structural conditions in ovipositor-bearing Odonata that will be elaborated further under inclusion of more taxa.

(1) Presence of ventral carina **vc** (V–VII) (see Fig. 25): [dst] distinct at least throughout posterior third of tergum; [ids] present only at posterolateral corner of tergum, as the lateral tips of ridge **ty** bend anteriorly; [abs] absent.

(2) Presence of supplementary lateral carina **lc** (V–VII) (see Fig. 25): [dst] distinct; [abs] absent.

(3) Presence of dorsal tendon **dt** (V–VII) (see Fig. 1): [dst] distinct; [ids] indistinct; [abs] absent. Considered inassessable in *Diphlebia*.

(4) Presence of post-spiracular coxosternal apodeme **ba** (V–VI): [dst] distinct: an infolding discretely elevated from lateral margin of coxosternum; [ids] indistinct: an infolding hardly elevated from lateral margin of coxosternum (similar to **ba8** in Fig. 3); [abs] absent (as in Fig. 1).

(5) Extension of midventral coxosternal keel **vk** (V–VI) (see Fig. 1): [lon] long: extending along entire coxosternum except anteriormost and narrow/weak posteriormost parts; [sho] short: restricted to area shortly in front of narrow/weak posteriormost part; [abs] absent.

(6) Presence of broad and heavy posterior margin of coxosternum **CS** (V–VI) (see Fig. 1, left end): [dst] distinct: marginal sclerotization much heavier and broader, extending into wall of apodeme **at** (as in Fig. 1); [ids] indistinct: marginal sclerotization somewhat heavier and broader but not extending into wall of **at**; [abs] absent.

(7) Presence of intertergal articulation between terga **TG7** and **TG8** (see Figs. 1, 24, 25): [dst] distinct: triangular heavy sclerotization and patch **ap** discrete (as in Figs. 1, 24, 25); [abs] absent: triangular heavy sclerotization not discrete and patch **ap** lacking. Considered inassessable in *Diphlebia*.

(8) Condition of middorsal hinge **dh8** and antecosta **ac8** (area not illustrated): [ent] **ac8** obliterated and well-articulated middorsally, with a distinct hinge line **dh8** behind it that continues throughout **TG8**; [ant] **ac8** obliterated and well-articulated middorsally, with a hinge line **dh8** behind it that is distinct only in the anteriormost part of **TG8**; [ids] **ac8** obliterated middorsally, but not articulated and without a distinct hinge line **dh8** behind it; [pos] **ac8** heavy and poorly articulated middorsally, but a distinct hinge line **dh8** behind it that continues throughout **TG8**; [abs] **ac8** heavy and not articulated middorsally, without a distinct hinge line **dh8** behind it.

(9) Presence of extension **b** on posteroventral corner of tergum **TG8** (see Figs. 4, 7): [lon] distinct and long: posterolateral corner of **TG8** heavy and projecting beyond lateral **TG8**-margin in front of it, reaching articulation **TG9-LCa9** (as in Figs. 4, 7, 26, 32, 33); [sho] distinct and short: posterolateral corner of **TG8** heavy and projecting beyond lateral **TG8**-margin in front of it, by far not reaching articulation **TG9-LCa9** (as in Fig. 36); [abs] absent: posterolateral corner of **TG8** neither particularly heavy nor projecting beyond lateral **TG8**-margin in front of it, by far not reaching articulation **TG9-LCa9** (as in Fig. 27).

(10) Presence of post-spiracular apodeme **ba8** on lateral margin of laterocoxosternum **LS8** (see Fig. 7): [dst] distinct: a discrete, sclerotized internal projection present; [ids] indistinct: some shallow but clearly elevated internal fold or ridge with strengthened sclerotization present (as in Fig. 7); [abs] absent.

(11) Presence of median process **pp8** on posterior margin of laterocoxosternum **LS8** (see Fig. 4): [dst] distinct; [abs] absent (as in Fig. 4).

(12) Location of origin of tendon **gt** (see Fig. 7): [sct] arising from distinct sclerotization on anterior margin or anteromesal corner of coxa **CX8** (as in Figs. 28,

32); [ime] arising from weak marginal parts of an indiscretely bordered **CX8**, on anterior margin or anteromesal corner of **CX8** (as in Fig. 37); [meb] arising from membrane median to **CX8** (as in Fig. 29).

(13) Extension of base of apodeme **ga** of **CX8** towards midline (see Fig. 7): [sho] not reaching area of origin of tendon **gt**, which thus does not originate from **ga** (as in Figs. 26, 27, 33, 37); [ime] just reaching area of origin of **gt**, which thus originates from mesal base of **ga**; [lon] reaching and continuing through area of origin of **gt**, which thus originates from mesal part of **ga** (as in Fig. 32).

(14) Interrelation between coxae **CX8** of the two sides (see Fig. 7): [cnt] connected in the posterior part (as in Fig. 32); [sep] entirely separated by membrane (as in Figs. 26, 27, 33, 36).

(15) Interrelation between coxae **CX8** and antelaterocoxae **LCa9** (see Figs. 4, 9): [cnt] extensively connected by uniform or only slightly weakened sclerotization, presence of extension **d** thus not assessable, and no articulation present (as in Fig. 36); [art] articulated upon each other through distinct extension **d**, narrowly separated by membrane or connected by very weak sclerotization in articulation area, separated by membrane outside articulation area (as in Figs. 26, 33); [sep] widely (Aeshnidae) or narrowly (Zygoptera concerned) separated by membrane, not articulated upon each other, extension **d** indistinct (as in Figs. 27, 32). Considered inassessable in *Diphlebia*.

(16) Extension to the anterior of cleft between gonapophyses **gp8** of the two sides (see Fig. 9; reciprocally corresponding to the extent of basal fusion between the two **gp8**): [vlo] anterior end of cleft in between coxae **CX8**, far anterior to level of articulation **GP8-LCa9** (as in Figs. 27, 29); [lon] anterior end of cleft not reaching area in between coxae **CX8**, but far anterior to level of articulation **GP8-LCa9** (as in Figs. 36, 37); [ime] anterior end roughly at the level of articulation **GP8-LCa9** (as in Figs. 26, 28, 32); [sho] anterior end far posterior to level of articulation **GP8-LCa9** (as in Fig. 33).

(17) Size of sclerite **MS** at ventral **gp8**-bases: [lar] large (as in Fig. 33); [ime] intermediate (as in Fig. 26, 32); [sml] small (as in Fig. 27); [abs] absent.

(18) Interrelation between sclerites **MS** and **GP8** at ventral **gp8**-bases (see Fig. 4): [sep] separated by narrow stripe (as in Figs. 32, 33) or wider area (as in Fig. 27) of membrane or very weak sclerotization, with a discrete hinge line between them in case the separation is narrow; [ime] not separated by membrane or distinctly weakened sclerotization, but with a discrete hinge line between them; [cnt] not in some way separated, and only some wider, diffuse ribbons of increased flexibility present between them (or not), but not a narrow hinge line (as in Fig. 26). Not applicable to taxa lacking **MS**.

(19) Interrelation between sclerites **GP8** of the two sides at dorsal **gp8**-bases (see Fig. 10): [cnt] connected, sclerotization not distinctly weakened along midline (as in Fig. 28, and Fig. 37 with a very short connection); [ime] connected, but with distinctly weakened midline; [sep] separated by membrane (as in Fig. 29).

(20) Condition of **GP8** sclerotization at dorsal **gp8**-bases (see Fig. 10): [ent] entire, with a convex or straight anterior margin (as in Fig. 28); [div] divided into several lobes by stripes of membrane (as in Figs. 29, 37); [mes] with a deep, broad membranous notch.

(21) Presence of oblique ridges **gy** on mesal face of **gp8** (see Fig. 32): [dst] distinct (as in Figs. 27, 32, 36); [ids] indistinct; [abs] absent (as in Fig. 33).

(22) Condition of ridges **gy** on basal mesal face of **gp8**: [lar] conspicuously large, much larger than distal **gy** (as in Fig. 29); [sml] not or at most indistinctly larger than distal **gy** (as in Fig. 37). Not applicable to taxa lacking **gy**.

(23) Presence of saw-teeth **tm8** distolaterally on **gp8** (see Fig. 9): [dst] several distinct, regularly shaped teeth (as in Figs. 42, 43); [ids] numerous minute, fairly irregular teeth (as in Fig. 45); [abs] absent (as in Fig. 44).

(24) Presence of ridges **gz8** distoventrally on **gp8** (see Fig. 4): [dst] distinct; [ids] indistinct; [abs] absent.

(25) Presence of lobes **vl** beside vaginal opening (see Fig. 8): [lon] long (as in Figs. 30, 34, 35); [sho] short (as in Fig. 31); [ids] indistinct (as in Fig. 38).

(26) Presence of sclerite **VL** beside vaginal opening (see Figs. 7, 8): [dst] distinct: discrete sclerite (as in Fig. 30); [ids] indistinct: diffuse melanization; [abs] absent (as in Figs. 31, 34, 35, 38).

(27) Presence of lateral vaginal sclerite **VB** (see Figs. 8, 10): [dst] distinct: discrete sclerite (as in Figs. 30, 31, 34, 35); [ids] indistinct: very weak melanization; [abs] absent (as in Fig. 38).

(28) Extension of sclerite **VB** to the anterior (see Figs. 8, 10): [lon] reaching level of oviduct opening into vagina (as in Figs. 30, 34, 35); [sho] by far not reaching level of oviduct opening (as in Fig. 31). Not applicable to taxa lacking **VB**.

(29) Presence of collar-shaped soft ridge **cr** of vagina (see Figs. 8, 10): [cpl] complete: forming a complete collar (as in Figs. 30, 34, 35); [frg] fragmentary: only isolated thickenings in lateral walls of vagina present, not connected dorsally (as in Fig. 31); [abs] absent (as in Fig. 38).

(30) Presence of midventral thickening **mr** of vagina (see Fig. 31): [lon] present, extending from opening of oviduct **oc+oe** into the posterior part of the vagina (as in Figs. 31, 38); [sho] present, restricted to posterior base of oviduct opening (as in Fig. 35); [abs] absent (as in Figs. 30, 34).

(31) Presence of spermatheca **sp** (see Fig. 8): [dst] distinct: a tube clearly demarcated from the vagina (as

in Figs. 30, 31, 34, 35, 38); [ids] indistinct: a pouch or expansion not clearly demarcated from the outline of the vagina; [abs] absent.

(32) Presence of vaginal bulb 'vb' (surely not in all cases homologous) anteroventral, anteromesal, or anterodorsal to spermatheca **sp** (see Fig. 8): [dor] distinct vaginal bulb formed from the vaginal walls anterodorsal to the spermathecal orifice into the vagina (as in Fig. 31); [lat] distinct vaginal bulb formed from the vaginal walls anteromesal to the spermathecal orifice into the vagina (the spermatheca originates from the left-dorsal base of **vb**, the area being asymmetrical); [ven] distinct vaginal bulb formed from the vaginal walls anteroventral to the spermathecal orifice into the vagina (as in Figs. 30, 34, 35); [abs] no vaginal bulb present (as in Fig. 38). Not applicable to taxa lacking a spermatheca or having an indistinct spermatheca.

(33) Shape of spermatheca **sp**: [for] distinctly forked (as in Figs. 30, 31, 38); [ime] not distinctly forked but terminally bilobed; [nfo] neither forked nor bilobed but occasionally terminally widened (as in Figs. 34, 35). Not applicable to taxa lacking **sp** or having **sp** indistinct.

(34) Presence of spermathecal sclerotization **SP**: [dst] distinct (as in Fig. 35); [abs] absent (as in Figs. 30, 31, 34, 38). Not applicable to taxa lacking **sp** or having **sp** indistinct.

(35) Condition of middle part of vagina **va**, which bears the spermatheca (if present) and the tendon **vt** (see Fig. 8): [tub] narrowed to a long tubular neck, with a sac receiving the spermatheca (as in Fig. 34); [ntu] not narrowed to a long tubular neck, orifice of spermatheca (if present) not upon a sac (as in Figs. 30, 31, 35, 38).

(36) Condition of ectodermal oviduct **oc+oe**: [iva] not evaginated, extending directly into body cavity (as in Fig. 31); [eva] evaginated, extending into lumen of vagina (as in Fig. 8).

(37) Condition of antecosta **ac9** around dorsal midline (area not illustrated): [div] distinctly articulated (very narrow area of flexibility) and obliterated middorsally; [obl] indistinctly articulated (very narrow area of flexibility) and somewhat weakened middorsally; [art] indistinctly articulated (moderately narrow area of flexibility) but particularly heavy middorsally; [hvy] not articulated and particularly heavy middorsally.

(38) Presence of spine **sa** on antelaterocoxa **Lca9** near its articulation with sclerite **GP8**: [dst] a strong spine present (as in Fig. 36); [ids] a low bulge present; [abs] absent (as in Figs. 26, 27, 32, 33).

(39) Extension of postlaterocoxa **Lcp9** to the anterior (see Fig. 4): [sho] by far not reaching articulation between tergum **TG9** and antelaterocoxa **Lca9** (as in Fig. 26); [ime] approaching this articulation more closely than in the foregoing state but clearly not

reaching it (as in Fig. 33); [lon] reaching this articulation (as in Figs. 27, 32, 36). In illustrations compare extension of **LCp9** towards stripe **h** (which is only lacking in *Epiophlebia*, Fig. 36).

(40) Interrelation between tergum **TG9** and anterior part of postlaterocoxa **LCp9** (see Fig. 4): [cnt] more or less broadly connected by sclerotization that is (almost) as heavy as that of the two sclerites in this area (as in Figs. 27, 32, 33, 36); [sep] separated by very weak sclerotization or membrane (as in Fig. 26).

(41) Interrelation between ante- and postlaterocoxa, **LCa9** and **LCp9** (see Figs. 4, 7): [cnt] connected, one-piece gonangulum (as in Fig. 36); [sep] separated by membrane, two-piece 'gonangulum' (as in Figs. 26, 27, 32, 33).

(42) Interrelation between gonapophyses **gp9** of the two sides (see Fig. 11): [cnt] fused basally: a transverse, posteriad-directed membraneous fold connects the basal parts of the two **gp9** across the midline (arrow in Fig. 41); [sep] free from each other down to the very base: no such transverse fold present (as in Figs. 39, 40).

(43) Extension of row of saw-teeth **tm9** along dorsal edge of gonapophysis **gp9** (see Fig. 11): [lon] row of discrete saw-teeth **tm9** extending into basal third of **gp9**; [ime] only indistinct teeth in basal third of **gp9**, discrete teeth in middle and distal thirds; [sho] row of saw-teeth **tm9** not reaching basal half of **gp9**.

(44) Location on gonapophyseal sclerite **GP9** of extension **g** bearing anterior end of rhachis **rh** (see Fig. 7): [ant] at or near anterior tip of **GP9** (as in Figs. 39, 41); [pos] distinctly farther posteriorly than anterior tip of **GP9** (as in Fig. 40).

(45) Presence of tendons **ft** flanking apodeme **ca** (see Fig. 7): [dst] distinct (as in Fig. 39); [abs] absent (as in Figs. 40, 41).

(46) Presence of posteriad-directed extension **i** at base of sclerite **GP9**: [dst] distinct (as in Fig. 41); [abs] absent (as in Figs. 39, 40).

(47) Location of openings of accessory glands **ag** of the two sides (see Fig. 3): [rem] far remote from each other, usually shortly anteromesal to anterior end of rhachis **rh** (as in Figs. 39, 40); [adj] closely adjacent to each other near the midline, far (postero)mesal to anterior end of **rh** (as in Fig. 41).

(48) Location of articulation between sclerites **CXa9** and **LCp9** (see Fig. 4): [pos] at lateral base of apodeme **la** (as in Figs. 39, 41); [ant] distinctly anterior to lateral base of **la** (as in Fig. 40).

(49) Presence of dorsal gonoplac sclerite **CXb9** (see Figs. 7, 11): [dst] distinct: very discrete from surrounding membrane (as in, e.g., Figs. 47, 49–53); [ids] indistinct: hardly discrete from surrounding membrane (as in Figs. 48, 54, 58); [abs] absent (as in Fig. 46).

(50) Interrelation between distal parts of sclerites **CXa9** and **CXb9** (see Figs. 7, 11): [sep] separated (as

in Figs. 48–61); [cnt] connected (as in Fig. 47). Not applicable to taxa lacking **CXb9**.

(51) Presence of sclerite **CXc9** beside base of stylus **sl9** (see Fig. 5): [dst] distinct: at least moderately distinct and discrete from surrounding membrane as well as from stylus sclerotization **SL9** (as in Figs. 39, 41); [ids] indistinct: weak, hardly discrete from surrounding membrane and potentially connected with **SL9** (as in Fig. 40).

(52) Shape of stylus **sl9** (see Figs. 4, 5): [clu] curved, narrower in middle part, tip clubbed (as in Fig. 39); [ime] intermediate between **clu** and **cyl** in listed attributes; [cyl] straight, cylindrical, tip not widened (as in Fig. 40); [con] conical (as in Fig. 41).

(53) Presence of tubercles/projections on distal ventral edge of gonoplac **gl9** (see Fig. 4): [dst] present at least on distalmost part of this edge (as in Figs. 39, 41); [abs] absent (as in Fig. 40).

(54) Condition of tubercles/projections on distal ventral edge of gonoplac **gl9**: [tbr] many small tubercles or spines along gonoplac edge, all of similar size (as in Fig. 39); [ime] many small tubercles or spines along gonoplac edge, but the distalmost considerably larger, forming a small prong; [prg] only one prong distally on gonoplac edge (as in Fig. 41). Not applicable to taxa lacking tubercles/projections on **gl9** altogether.

(55) Presence of setal tuft on tip of stylus **sl9**: [dst] distinct: setae on tip of stylus much longer than those potentially occurring along stylus flanks, and forming a well-defined group (as in Fig. 40); [abs] absent: setae on tip of stylus not different from those along stylus flanks or altogether absent. The scoring [abs] of this character in Tab. 1 should be viewed with caution and rather be based on SEM-studies.

(56) Presence of sclerite **PS9** (see Fig. 7): [dst] distinct (as in Figs. 46, 48–61); [abs] absent (as in Fig. 47).

(57) Condition of midline of sclerite **PS9** in its posterodorsal part: [scl] sclerotized (almost) as strongly as more laterally, **PS9** thus undivided (as in Figs. 49–61); [mes] membraneous, **PS9** thus divided into two articulated halves (as in Figs. 46, 48). Not applicable to taxa lacking **PS9**.

(58) Presence of posterodorsal, inward-directed transverse fold on sclerite **PS9**: [dst] distinct; [ids] indistinct; [abs] absent. Not applicable to taxa lacking **PS9**.

(59) Shape of anteroventral margin of **PS9**: [stt] straight (sclerite usually short) (as in Figs. 53, 57–61); [ime] with shallow median recess, thus slightly bilobed (sclerite usually moderately long) (as in Figs. 57–59); [bil] with deep median incision, thus distinctly bilobed (sclerite usually long) (as in Figs. 49, 55). Not applicable to taxa lacking **PS9**.

(60) Extension of connection between lateral part of **PS9** and gonoplac sclerite **CXa9** (considering also weak sclerotization) (see Fig. 7): [nrw] very narrow, or

**Tab. 1. Distribution of abdominal exoskeletal characters in ovipositor-bearing Odonata.** Taxa: CP = Calopterygoidea: Cp = *Calopteryx*, Ha = *Hetaerina*, Eg = *Epallage*, Py = *Platycypha*, Dp = *Diphlebia*; LT = Lestinoidea: Lt = *Lestes*; MP = Megapodagriidae: Al = *Argiolestes*; PL = Pseudolestidae: Rl = *Rhipidolestes*; CA = Coenagriidea: Ds = *Drepanosticta*, Mg = *Mecistogaster*, Ps = *Pyrrosoma*, Pc = *Platycnemis*, Cc = *Chlorocnemis*; AZ = Anisozygoptera: Ep = *Epiophlebia*; AP = Anisoptera: Ae = *Aeshna*, Cl = *Caliaeshna*.

Column of characters (full definition of characters in section 5.6.). Abbreviations for assessed attributes: cod = condition, ext = extension, ire = interrelation, loc = location, pre = presence, shp = shape, siz = size. Other abbreviations and symbols (unless included in the morphological terminology here used, see section 3.4.): dsbp = dorsal basal part, midl = midline, pstp = posterior transverse part, ptfd = posterior transverse fold, pvbu = tuberculized posteroventral bulge of sclerite ring X, scler = sclerotization, tbcl = tubercles, / between two sclerites = articulation, // between two sclerites = fusion.

Columns of taxa and their character states (full definition of character states in section 5.6.). Abbreviations for character states: abs = absent, adj = adjacent, ant = anterior, art = articulated, bil = bilobate, brd = broad, cls = closed, clu = clubbed, cnt = connected, con = conical, cpl = complete, cyl = cylindrical, div = divided, dor = dorsal, dst = distinct, ent = entire, eva = evaginated, for = forked, frg = fragmentary, hvy = heavy, ids = indistinct, ime = intermediate, iva = invaginated, lar = large, lat = lateral, lon = the longer condition of the specified element, meb = on membrane, mes = membranous, nfo = not forked, nrw = narrow, ntu = not tubular, obl = obliterated, opn = open, pos = posterior, prg = prong, rem = remote, scl = sclerotized, sct = on sclerite, sep = separate, sho = the shorter condition of the specified element, sml = small, stt = straight, tbr = tubercles, tub = tubular, ven = ventral, vlo = very long, wan = weak anteriorly, wpo = weak posteriorly, --- inapplicable or inassessable due to lack or indistinctness of the respective elements.

Column OG. Outgroup comparison for Odonata based on conditions in Archaeognatha, Zygentoma, and a variety of (mainly 'lower') Pterygota (with fairly sparse data in many characters), discussions in chapter 6. Reasonably certain conditions given in normal print, doubtful ones in italics. ??? marks ambiguous outgroup comparison or lacking evidence. --- marks the inapplicability of a character to the outgroup (characters relating to elements peculiar to [some] Odonata).

Characters	CP	CP	CP	CP	CP	LT	MP	PL	CA	CA	CA	CA	CA	AZ	AP	AP	OG
	Cp	Ha	Eg	Py	Dp	Lt	Al	Rl	Ds	Mg	Ps	Pc	Cc	Ep	Ae	Cl	
1 pre vc5-7	abs	ids	dst	dst	abs												
2 pre lc5-7	abs	dst	dst	abs													
3 pre dt5-7	dst	dst	dst	dst	---	dst	abs	ids	abs	???							
4 pre ba5-6	abs	abs	abs	abs	abs	ids	abs	ids	abs	abs	abs	abs	abs	abs	ids	dst	abs
5 ext vk5-6	lon	abs	sho	sho	abs												
6 pre pstp CS5-6	dst	dst	ids	abs	ids	dst	abs	abs	abs	dst	abs	abs	dst	abs	abs	abs	abs
7 pre TG7/TG8	dst	dst	dst	dst	---	dst	abs	dst	---								
8 cod dh8	ent	pos	ent	ant	ent	ent	ent	ent	abs	ids	ent	ent	ent	ids	ant	ent	---
9 pre b (TG8)	lon	lon	lon	sho	lon	lon	lon	lon	sho	lon	lon	lon	lon	sho	abs	abs	???
10 pre ba8	ids	abs	ids	abs	abs	ids	ids	ids	dst	dst	abs	dst	dst	dst	dst	dst	abs
11 pre pp8	abs	dst	abs	abs	abs												
12 loc gt	sct	sct	sct	sct	ime	sct	ime	sct	sct	sct	meb	meb	meb	ime	meb	meb	---
13 ext ga	sho	sho	ime	sho	sho	lon	sho	sho	ime	sho	---						
14 ire CX8-CX8	sep	sep	sep	sep	sep	cnt	sep										
15 ire CX8-LCa9	art	art	art	art	---	sep	art	art	sep	sep	art	art	art	cnt	sep	sep	<i>sep</i>
16 ext gp8 cleft	ime	ime	ime	sho	ime	ime	sho	sho	sho	ime	ime	ime	sho	lon	vlo	vlo	<i>vlo</i>
17 siz MS	ime	ime	sml	ime	ime	ime	lar	lar	lar	ime	ime	ime	ime	sml	sml	abs	---
18 ire MS-GP8	cnt	cnt	ime	ime	ime	sep	sep	sep	sep	cnt	ime	cnt	ime	cnt	sep	---	---
19 ire GP8-GP8	cnt	cnt	cnt	cnt	cnt	ime	ime	cnt	sep	sep	sep						
20 cod dsbp GP8	ent	div	div	mes	???												
21 pre gy	ids	ids	abs	dst	ids	dst	abs	abs	abs	dst	???						
22 cod gy	sml	sml	---	sml	sml	sml	---	---	---	sml	sml	sml	sml	sml	lar	lar	???
23 pre tm8	dst	dst	dst	abs	dst	dst	abs	dst	dst	abs	dst	dst	dst	ids	abs	abs	<i>dst</i>
24 pre gz8	dst	dst	dst	ids	dst	dst	abs	dst	dst	dst	dst	dst	ids	dst	abs	abs	<i>dst</i>
25 pre vl	lon	ids	sho	sho	???												
26 pre VL	dst	ids	abs	dst	dst	abs	abs	abs	abs	???							
27 pre VB	dst	abs	dst	ids	???												
28 ext VB	lon	---	sho	sho	---												
29 pre cr	cpl	abs	frg	frg	abs												
30 pre mr	abs	sho	abs	abs	abs	lon	lon	lon	abs								
31 pre sp	dst	ids	dst	abs	dst	ids	dst										
32 pre vb	ven	---	ven	---	ven	---	ven	ven	ven	ven	ven	lat	ven	abs	dor	dor	abs
33 shp sp	for	---	nfo	---	for	---	ime	for	for	nfo	nfo	nfo	nfo	for	for	for	???
34 pre SP	abs	---	abs	---	abs	---	abs	abs	abs	dst	abs	abs	abs	abs	abs	abs	???
35 cod va	ntu	tub	ntu	ntu	ntu	ntu											
36 cod oc	eva	iva	iva	iva	iva												
37 cod ac9	hvy	hvy	art	hvy	art	obl	art	art	hvy	hvy	art	art	hvy	obl	hvy	div	---

Characters	CP	CP	CP	CP	CP	LT	MP	PL	CA	CA	CA	CA	CA	AZ	AP	AP	OG
	Cp	Ha	Eg	Py	Dp	Lt	Al	Rl	Ds	Mg	Ps	Pc	Cc	Ep	Ae	Cl	
38 pre sa	abs	abs	abs	abs	ids	abs	dst	abs	abs	abs							
39 ext LCp9	sho	ime	ime	lon	ime	lon	lon	ime	ime	sho	sho	sho	sho	lon	lon	lon	???
40 ire TG9-LCp9	sep	cnt	sep	sep	sep	cnt	cnt	cnt	sep								
41 ire LCa9-LCp9	sep	cnt	sep	sep	???												
42 ire gp9-gp9	sep	cnt	sep	sep	???												
43 ext tm9	sho	sho	sho	sho	sho	ime	sho	lon	sho	sho	lon						
44 loc g (GP9)	ant	ant	ant	pos	ant	ant	pos	pos	pos	pos	ant	ant	ant	ant	pos	pos	???
45 pre ft	dst	abs	abs	abs	abs												
46 pre i (GP9)	abs	dst	abs	abs	???												
47 loc ag	rem	rem	rem	rem	rem	adj	rem	adj	rem	rem	???						
48 loc CXa9/LCp9	pos	ant	ant	ant													
49 pre CXb9	dst	dst	dst	ids	dst	dst	dst	dst	dst	ids	dst	dst	dst	ids	abs	dst	???
50 ire CXa9-CXb9	sep	---	cnt	---													
51 pre CXc9	dst	dst	dst	dst	dst	ids	dst	dst	dst	dst	dst	dst	ids	ids	ids	dst	???
52 shp sl9	clu	clu	ime	ime	clu	ime	cyl	clu	ime	cyl	ime	clu	clu	con	cyl	cyl	???
53 pre tbcl gl9	dst	abs	abs	abs													
54 cod tbcl gl9	tbr	tbr	tbr	tbr	tbr	ime	tbr	tbr	prg	tbr	tbr	tbr	tbr	prg	---	---	---
55 pre setae sl9	abs	abs	abs	abs	abs	abs	dst	abs	dst	dst	abs						
56 pre PS9	dst	abs	???														
57 cod midl PS9	scl	mes	mes	---	???												
58 pre ptfd PS9	dst	dst	ids	dst	ids	abs	dst	ids	ids	dst	ids	dst	dst	abs	abs	---	???
59 shp PS9	stt	bil	bil	stt	bil	bil	stt	bil	bil	ime	ime	ime	stt	bil	bil	---	???
60 ext PS9//CXa9	nrw	nrw	ime	brd	nrw	brd	brd	ime	brd	nrw	nrw	nrw	nrw	brd	brd	---	???
61 pre IT9	dst	dst	dst	abs	abs	dst	abs	abs	dst	abs	abs	abs	abs	dst	dst	ids	abs
62 ire TG9-IT9	sep	sep	sep	---	---	cnt	---	---	cnt	---	---	---	---	cnt	sep	sep	???
63 pre xr	abs	abs	abs	abs	abs	dst	abs	abs	dst	abs							
64 cod ring X	cls	wpo	cls	opn	wan	opn	???										
65 pre ac10	dst	dst	dst	dst	dst	ids	dst	dst	abs	dst	dst	dst	dst	abs	abs	abs	abs
66 pre dt10	abs	dst	abs	abs	???												
67 pre pvbu X	abs	dst	dst	abs	---												
68 pre dp	dst	ids	abs	???													
69 pre ct	dst	dst	dst	dst	dst	abs	dst	ids	dst	dst	dst						
70 pre ht	dst	abs	dst	dst	dst	dst	dst	dst	ids	???							
71 loc jt	rem	adj	adj	???													
72 pre scler ma	dst	dst	dst	abs	abs	abs	abs	abs	dst	abs	abs	abs	abs	abs	dst	ids	???
73 ire ma-CE	cnt	cnt	sep	---	---	---	---	---	sep	---	---	---	---	---	sep	sep	???
74 ire ma-TG11	sep	sep	sep	---	---	---	---	---	sep	---	---	---	---	---	cnt	---	???
75 pre dt11	abs	ids	abs	abs	dst	ids	dst	dst	???								
76 pre xl	abs	dst	dst	dst	abs												
77 pre yl	abs	dst	dst	dst	abs												
78 pre ut	dst	ids	dst	dst	dst	dst	abs	abs	abs	abs							
79 pre tt	dst	dst	dst	ids	ids	dst	abs	abs	abs	abs							

connection entirely absent (as in Figs. 55–61); [ime] moderately broad (as in Figs. 49, 52); [brd] very broad (as in Figs. 46, 48, 50, 51, 53, 54). Not applicable to taxa lacking **PS9**.

**(61)** Presence of sclerite **IT9** between sclerite **PS9** and sclerite ring X **TG10+LP** (see Figs. 7, 39–41): [dst] distinct, but potentially very weak (but then still discrete from surrounding membrane by its stiffness), and with wide range of size (as in Figs. 46, 48–51, 56, 61); [ids] indistinct: only some diffuse melanization present, not distinguished from surrounding membrane in stiffness (as in Fig. 47, but actually more diffuse along margins); [abs] absent (as in Figs. 52–55, 57–60).

**(62)** Interrelation between sclerite **IT9** and posteroventral corners of tergum **TG9** (see Figs. 7, 39–41): [cnt] firmly connected (as in Figs. 48, 50, 51); [sep] separated by membrane (as in Figs. 7, 46, 47, 49, 56, 61). Not applicable to taxa lacking **IT9**.

**(63)** Presence of circumferential internal ridge **xr** on posterior part of segment IX, on **TG9** and **IT9**: [dst] distinct (as in Figs. 50, 51); [abs] absent.

**(64)** Condition of sclerite ring X **TG10+LP** with regard to its ventral part (see Figs. 4, 12, 14, 15): [cls] ring closed by heavy sclerotization throughout (as in Figs. 4, 12, 14, 15), though the ventral part may be slightly weaker than the lateral parts, and the posteroventral part may be slightly weaker than the antero-

ventral part; [wpo] ring closed but with membrane or very weak sclerotization in posteromedian ventral part; [wan] ring closed but with very weak sclerotization in anteromedian ventral part; [opn] ring open ventrally through a continuous longitudinal ribbon of membrane or very weak sclerotization.

(65) Presence of ventral antecostal ridge **ac10** on sclerite ring X **TG10+LP** (see Figs. 4, 12): [dst] distinct; [ids] indistinct; [abs] absent.

(66) Presence of dorsal tendon **dt10** on sclerite ring X **TG10+LP** (area not illustrated): [dst] distinct; [abs] absent.

(67) Presence of bulged outfolding and tubercles or of more massive/elaborate projections on posteroventral part of sclerite ring X **TG10+LP**: [dst] distinct; [abs] absent.

(68) Presence of posteromedian dorsal process **dp** on sclerite ring X **TG10+LP** (see Fig. 3): [dst] distinct: one discrete process (as in Fig. 3); [ids] indistinct: agglomeration of some smaller tubercles; [abs] absent.

(69) Presence of tendon **ct** at dorsal base of cercus (see Fig. 12): [dst] distinct; [ids] very short and delicate; [abs] absent.

(70) Presence of tendon **ht** on dorsolateral anterior margin of sclerite **AP** (see Fig. 12): [dst] distinct; [ids] indistinct; [abs] absent.

(71) Location of bases of tendons **jt** of the two sides (see Fig. 15): [rem] far remote from each other (as in Fig. 15); [adj] closely adjacent to each other next to the midline.

(72) Presence of sclerotization on cercal base apodeme **ma** (see Fig. 12): [dst] distinct (as in Fig. 12); [ids] indistinct: flexible and hardly melanized; [abs] absent.

(73) Interrelation between sclerotization of apodeme **ma** and cercal sclerotization **CE**: [cnt] distinctly connected; [sep] distinctly separated. Not applicable to taxa lacking sclerotization on **ma**.

(74) Interrelation between sclerotization of apodeme **ma** and lateral parts of tergum **TG11**: [cnt] distinctly connected; [sep] distinctly separated. Not applicable to taxa lacking sclerotization on **ma** and considered inassessable in *Caliaeshna*.

(75) Presence of tendon **dt11** on anterior margin of tergum **TG11** (see Fig. 12 for **TG11**): [dst] distinct; [ids] indistinct; [abs] absent.

(76) Presence of lobe **xl** on anus-flanking face of subanal lobe **sl** (see Fig. 12 for lobe **sl**): [dst] distinct; [abs] absent.

(77) Presence of lobe **yl** on anus-flanking face of terminal projection **tf** (see Fig. 12 for **tf**): [dst] distinct; [abs] absent.

(78) Presence of tendon **ut** on subanal lobe **sl** (see Fig. 15): [dst] distinct (as in Fig. 15); [ids] indistinct; [abs] absent.

(79) Presence of tendon **tt** on terminal projection **tf** (see Fig. 12): [dst] distinct (as in Figs. 12, 13); [ids] indistinct; [abs] absent.

## 5.7. Musculature of female Odonata

### 5.7.1. Musculature of segments V–VII

The muscles of the midabdominal segments described in previous contributions are compiled in Tab. 2 (upper part).

The musculature as described for Calopteryginae in WHEDON (1918: figs. 20–23, *Calopteryx maculata*) and ASAHINA (1954: pl. 35 M32, *Mnais strigata*) corresponds with that in *Calopteryx virgo* (Fig. 16) in the arrangement of muscles **6**, **7**, and **8** (**ls\***, **inlt\***, **sult\***; WHEDON and ASAHINA use the same terminology; see Tab. 2). The treatment by these authors of muscles **1** and **2** appears incomplete: WHEDON's **adv\*** surely corresponds to muscle **1**, while muscle **2** is only vaguely indicated by stripes upon apodeme **pa** and remains unnamed. ASAHINA shows only one muscle **adv\***, which more likely represents **1** than **2**. ASAHINA's (1954: pl. 35 E52) **adv\*** in *Epiophlebia*, however, fully complies with muscle **2**. Hence, **adv\*** as previously used refers to two different muscles. Neither WHEDON nor ASAHINA indicate for Calopteryginae farther posterior tergo-coxosternal muscles that would correspond with the intrasegmental **3** and **4** and the intersegmental **5** of *Calopteryx* (Fig. 16) – with the exception of counterparts of muscles **4** and **5** in segment VII (**pdv7\***, **tp7\*** in ASAHINA 1954: pl. 47 M42). However, muscles taking also in segments preceding VII the same position as **5** and the posterior part of **4** are described by WHEDON (1918: fig. 31) and ASAHINA (1954: pl. 35 E52, D33) as **tp\*** and **pdv\***, respectively, for Aeshnidae and *Epiophlebia*; ASAHINA (1954: pl. 35 E52) in *Epiophlebia* shows an additional muscle **mdv\***, which likely is the homologue of **3** in *Calopteryx*.

Thus, in contrast to previous studies, the present findings show that Zygoptera imagines do not consistently lack dorsoventral muscles in the posterior (**4** = **pdv\***) and middle parts (**3** = **mdv\***) of the midabdominal segments, and muscles **3** are not unique to *Epiophlebia* (see notes in ASAHINA 1954: 59f, 140): both muscles were here found in *Calopteryx*. The differences in the findings on muscles **3–5** in Calopteryginae may be due to different taxa studied, or to the study of mature adults of different age, with some muscles more strongly degenerated in WHEDON's and ASAHINA's specimens.

The contribution by MATUSHKINA (2008a) on the aeshnid *Anax imperator* is of particular value as it

shows the full set of muscles for segment VII of the nymph and explains which muscle of the imago is derived from which nymphal muscle, and which muscles degenerate during maturation. The muscle set reported for segment VII of the mature female (tab. 2 therein) largely complies with the muscles here found for *Calopteryx* (Fig. 16, Tab. 2): muscles **1** (**dva\***), **3** (**dvm\***), **4** (**dvp\***), **5** (**dvo\***), **6** (**pls\***; but see below), **7** (**qnl\***), and **8** (**tl\***+**qlt\***). Only muscle **2**, located beside apodeme **pa** in *Calopteryx*, is not reported; it may be actually absent in *Anax* as it was neither found in that genus by WHEDON (1918) (see Tab. 2). In the teneral imago, MATUSHKINA (2008a: tab. 2) found several additional muscles, retained from the nymphal stage and partly with signs of degeneration: There is still a muscle **dvo\*** showing a similar course as muscle **5** (**dvo\***) as well as an ascending intersegmental lateral muscle **lpsp\*** ('sternopleural' muscle). Furthermore, long internal dorsal muscles (**plt\***, **slt\***) are still present as well as an additional external dorsal muscle (**sxlt\***), but all these show signs of degeneration. A full set of two long internal ventral muscles (**pls\***, **sls\***) and three short external ventral muscles (**itls\***, **tls\***, **qls\***) is also retained. The identification of the only ventral muscle found in the mature female of *Anax* as an internal ventral **pls\*** in MATUSHKINA (2008a; muscle not illustrated) appears problematic, since in *Calopteryx* the sole ventral muscle (**6** in Fig. 16) is short and innervated by the ventral nerve (**C3** in Fig. 16), both suggesting its interpretation as an external ventral muscle; this also complies with the findings of FORD (1923: muscle **os\*** in Fig. 18) in a *Libellula*. Yet, the ventral muscles retained in mature females are perhaps not strictly homologous in all Odonata, since according to ASAHINA (1954: **ls\*** in tab. 9) they can be derived from different bundles or differently inclusive portions of the nymphal external ventral muscles **tls\***, **qls\***, and **itls\***. However, MATUSHKINA's (2008a) report of **pls\*** would probably be the first of an internal ventral muscle in a mature female odonatan.

As compared to the set of midabdominal muscles herein reported for *Calopteryx* (Fig. 16) there has so far probably only one further muscle been described for mature Odonata: the short external dorsal muscle **mlt\*** (in between **7** and **8**, see Fig. 16) in Gomphidae and Cordulegastridae, and in segment VII of *Epiophlebia* (ASAHINA 1954: 56, pl. 35 D33, pl. 47 E69). Though not depicting it, ASAHINA (1954: tab. 9) indicates **mlt\*** also for imaginal *Mnais*. This **mlt\*** is one of the muscles that MATUSHKINA (2008a: **sxlt\*** in fig. 3) has reported for teneral *Anax*, and it is also regularly present in odonatan nymphs (ASAHINA 1954: **sxlt\*** in tab. 9). Thus, either in the aforementioned taxa the results were obtained from teneral specimens, or there is heterochrony involved in the evolution of this muscle.

Muscle **12** from coxosternum VII to the tendon **vt** of the vagina has so far been reported only by ASAHINA (1954: 'anterior spermathecal muscle' in pls. 47, 48; **ast\*** in Tab. 2 lower part).

In the abdominal spiracles, an oclucor muscle (see MILLER 1962: 516 for function) in the same position as in *Calopteryx* (**11** in Fig. 17) has been observed in a number of Anisoptera, but so far not in Zygoptera, though members of Lestidae and Coenagrionidae were examined (POONAWALLA 1966: 809). In *Aeshna* I observed, apart from a spiracle muscle resembling **11** in Fig. 17, a strand (muscle?) from an internal projection of the spiracle to apodeme **pa**; such a muscle, if confirmed in adequately preserved specimens, would conform with the coxosternal spiracle dilator present in many Neoptera (see KLASS 2000).

### 5.7.2. Musculature of segments VIII and IX

The muscles of the genitalic segments described in previous contributions are compiled in Tab. 2 (lower part).

ASAHINA (1954: pl. 47 M42) reports for *Mnais* most of the muscles that in the present study were found in *Calopteryx* (Figs. 19, 20). For segment VIII muscles **13** (**adv8\***), **15** (**pdv8\***), **16** (**1\***), **17** (**3\***), **18** (lateral spermathecal muscle **lst\***, see ASAHINA 1954: pl. 48 G8), **24** (**inlt8\***), and **25** (**sult8\***) are shown in the same condition that I observed in *Calopteryx*. Muscles **19** and **20**, however, are represented by a single, unnamed bundle of fibers. The midlength tergo-laterocoxosternal muscle **14** (it would be **mdv8\*** in ASAHINA's terminology), the coxo-gonapophyseal muscle **23**, the intrinsic vaginal muscle **22**, as well as the few fibers **21** from coxa **CX8** to the collar-shaped ridge **cr** are not reported. For segment IX muscles **28** (**6\***), **29** (**7\***), **32** (**10\***), **35** (transverse sternal muscle **tv\***), and **37** (**sult9\***) correspond with those in *Calopteryx*. The coxo-gonapophyseal muscle **33** and muscle **34** from coxa **CX9** to the membrane in between the **gp9**-bases, as well as the tergo-laterocoxal bundles **30** and **31** of unstriated fibers are not indicated. With the exceptions mentioned below, according to ASAHINA (1954) *Epiophlebia* and *Gynacantha* fully correspond with *Mnais*.

Of the muscles not reported by ASAHINA (1954), **23** and **34** are indicated for *Anax* by PFAU (1991: fig. 20a; **23** = the muscle inserted on **Vf1\*** behind muscles **1\*** and **3\***, **34** = the muscle running beneath muscle **6\***) and probably by DUNCAN (1933; **23** = **LSP\***, **34** = **ING\***), whose descriptions of muscles and insertions, however, are quite unclear. HAKIM's (1964: fig. K) muscle **vl2m\*** of *Pseudagrion* likely corresponds to **34** of this study. The portion of muscle **LSP\*** that DUNCAN (1933: 149) mentions to form a ring around

**Tab. 2. Abdominal muscles in Odonata I: midabdomen and female genitalic segments.** Muscles of midabdominal segments V–VII and muscles of female genitalic segments VIII and IX (including muscle 12 of segment VII) are treated separately because data are available for different sets of taxa. First column: Muscles of female *Calopteryx virgo* as found in present study; in blocks for segments VIII and IX numbers on the right side indicate homonomous muscles of segments V–VII. Remaining columns: Muscles of various Odonata as reported by WHEDON (1918), FORD (1923), DUNCAN (1933), ASAHINA (1954), HAKIM (1964), PFAU (1991), MATUSHKINA & GORB (1997), and MATUSHKINA (2004, 2008a,b). The four latter contributions are comprised as ‘MATUSHKINA’, data on midabdominal segments are therein limited to segment VII (or absent). For muscles not labeled in the original illustration, either the corresponding name (if evident from illustrations of other species) or [ulb] (‘unlabeled’; if for none of the studied species a name is offered) is given in square brackets; muscles only found in teneral females (only columns ‘MATUSHKINA’) or found degenerated in mature females (only column ‘THIS PAPER’) are enclosed in round brackets; ast = anterior spermathecal muscle; pst = posterior spermathecal muscle; remaining terms as used by original authors. --- = muscle not reported despite study of respective area. Muscles present only in segment VII of V–VII are indicated as, e.g., ‘---, mlt7’. Questionable identifications are indicated by question marks. pp = pro parte indicates that the homology of a muscle with part of a muscle as (inadequately) described by DUNCAN (1933) appears likely.

<i>Calopteryx virgo</i> THIS PAPER	<i>Calopteryx maculata</i> WHEDON	<i>Mnais strigata</i> ASAHINA	<i>Epiophlebia superstes</i> ASAHINA	<i>Anax junius</i> WHEDON	<i>Davidius nanus</i> ASAHINA	<i>Libellula 4-maculata</i> FORD	<i>Anax imperator</i> MATUSHKINA
Segments V–VII							
1	adv	adv?	---	adv	---	adv?	dva
2	[ulb]	---	adv	---	adv	[ulb]?	---
3	---	---	mdv	---	---	stg	dvm
4	---	---, pdv7	pdv	pdv	pdv	ttg	dvp
5	---	---, tp7	tp	tp	tp	---	dvo'
6	ls	ls	ls	ls	ls	os	pls
7	inlt	inlt	inlt	inlt	inlt	ot	qnlt
---	---	---	---, mlt7	---	mlt	---	(sxt)
8	[sult]	sult	sult	sult	sult	ot	tlt+qtl
9	---	---	---	---	---	ts	---
10	---	---	---	---	---	---	---
11	---	---	---	---	---	---	---

<i>Calopteryx virgo</i> THIS PAPER	<i>Mnais strigata</i> ASAHINA	<i>Pseudagrion decorum</i> HAKIM	<i>Epiophlebia superstes</i> ASAHINA	<i>Gynacantha japonica</i> ASAHINA	<i>Anax junius</i> DUNCAN	<i>Anax sp. indet.</i> PFAU	Zygoptera, <i>Aeshna</i> & <i>Anax</i> , <i>Epiophlebia</i> MATUSHKINA
Segment VII (addition)							
12	ast		ast	ast			
Segment VIII							
---	1	---	[ulb]	---			dva
13	2	adv8	adv8	adv8			---
14	3	---	---	---			dvm
15	4	pdv8	pdv8	pdv8			dvp
16	1	v1m1	1	1	---	1	M1
17	4??	v1m2	3	3	TSG pp?	3	M2
18	[lst]		[lst]	lst	LSA pp		---
19	[ulb]		[ulb]	[ulb] + pst?	LSA pp?		---
20	[ulb]		[ulb]	[ulb] + pst?	LSA pp?		---
21	---		---	---	---		---
22	---		---	---	LSA-ring		---
23	---		---	---	LSP	[ulb]	---
24	7	v1m (VIII)	[inlt8]	inlt8			M3=qnlt
25	8	mlm	sult8	sult8			tlt+qtl
26	10	---	---	---			---
27	11	---	---	---			---
Segment IX							
28	6	v2m1	6	6	TSG pp	6	M4
29	7	v2m2	7	7 + 8	TSG pp	7 + 8	M5
(30)	---	---	---	---	---		(dvm)
(31)	---	---	---	---	---		(dvm?)
32	10	v2m3	10	10	LS	10	M8
33	---	---	---	---	?		M6 part
34	---	v12m	---	---	ING?	[ulb]	M6 part
35	---	tvS	tvS	tvS	TRS	[ulb]	M7
(36)	5?	v1m (IX)	tp9?	inlt9			dvo'
37	sult9	[ulb]	sult9	sult9			plt'
38	---	---	---	---			---

**Tab. 3. Abdominal muscles in Odonata II: terminal abdomen.** Columns for taxa divided into subcolumns for female (fe), male (ma), and nymph (ny). Muscles grouped according to similarity in position. Non-striated strands and very weakly developed striated muscles put in round brackets. First column: Muscles of *Calopteryx virgo* as found in present study. Remaining columns: Muscles of various Odonata as reported by CALVERT (1927), ASAHINA (1954), and MATUSHKINA (2008a), with their terms used; [ulb] = muscle/strand indicated in illustration but not labeled or mentioned; ~ = no illustration provided; --- = muscle not reported despite study of respective area; " = two bundles present that correspond to the two muscles herein distinguished; ^ = one bundle present that may correspond to either or to both of the two muscles herein distinguished. *Anax parthenope* nymph: muscle 42 = adc\* has been mislabeled ada\* in ASAHINA's (1954) pl. 44 Ax1.

<i>Calopteryx virgo</i> THIS PAPER		<i>Mnais strigata</i> ASAHINA			<i>Lestes forficula</i> CALVERT	<i>Epiophlebia superstes</i> ASAHINA			<i>Gynacantha japonica</i> ASAHINA		<i>Anax parthen.</i> ASAHINA	<i>Anax imperator</i> MATUSHKINA
fe	ma	fe~	ma	ny	ny	fe	ma	ny	fe	ma	ny	ny
Cercal muscles												
41	41	abc?	adc"	adc"	abc	adc^	adc^	adc^	abc	---	abc	ada"
42	42	adc	adc"	adc"	adc	adc^	adc^	adc^	adc	adc	adc	ada"
---	63	?	abc	abc	---	---	---	---	---	---	---	---
48	48	---	---	---	---	---	---	---	---	---	---	---
Muscles sclerite ring X ↔ tergum XI												
(43)	43	---	---	ada	ada	ada	ada	ada	---	---	ada	abc
Muscles sclerite ring X ↔ AP-sclerite/subanal lobe												
(39)	39	---	---	---	---	---	---	---	---	---	---	---
40	40	advg	advg	advg	advg	advg	advg	advg	advg	advg	advg	advg
---	64	(ala)	---	ala	ala	---	ala?	ala	---	---	ala	ala
---	---	---	---	---	---	---	---	adpp	---	---	---	---
Muscles within AP-sclerite/subanal lobe												
44	44	ppra	ppra	ppra	---	ppra	ppra	ppra	ppra	ppra"	ppra"	---
45	45	---	---	---	---	---	---	---	---	---	---	---
(46)	(46)	---	---	---	---	---	---	---	---	ppra"	ppra"	---
(47)	(47)	---	---	[ulb]	---	[ulb]	---	---	---	---	[ulb]	---
---	65	---	---	---	---	---	---	---	---	---	[ulb]	---
Muscles tergum XI ↔ anus												
62	62	---	---	---	---	epra	epra	epra	epra	epra	epra	---
Muscles venter IX ↔ AP-sclerite/anal area												
---	66	---	---	vra	vra	---	(vra)	vra	---	---	vra	vra
---	---	---	---	vad	vad	---	---	vad	---	---	vad	vad

the vagina may be the homologue of **22** in *Calopteryx* (Fig. 20), which, however, is a pair of vertical muscles rather than a ring. The muscle that VAN DER WEELE (1906: 105) mentions to insert at the base of gonapophysis **gp9** is likely muscle **33**.

As compared to the findings on *Calopteryx* in the present study, only two further VIIIth-segmental muscles have been described for mature ovipositor-bearing Odonata: First, an VIIIth-segmental counterpart of the midabdominal muscle **1** (see Fig. 16) has been reported for *Epiophlebia* (ASAHINA 1954: pl. 47 E69, unlabeled muscle in front of **adv8\***; muscle **67** in Fig. 63); this muscle is absent in Calopterygidae and *Gynacantha* (muscle **13** of *Calopteryx* is clearly homonomous with muscle **2** of the preceding segments; Figs. 16, 19). Second, ASAHINA (1954: 67) furthermore mentions, but does not depict, an **mlt8\*** ('**mult8\***'; a mid-level external dorsal muscle, see section 5.7.1.) for segment VIII of *Epiophlebia* (not included in Tab. 2).

MATUSHKINA & GORB (1997) and MATUSHKINA (2004, 2008a,b) describe the major muscles of the female genitalia that are of primary importance for the movements of the ovipositor; the four contributions

together include a variety of zygopterans, the aeshnids *Aeshna mixta* and *Anax imperator*, and *Epiophlebia superstes*. For all taxa studied they consistently report muscles **16** (**M1\***), **17** (**M2\***), and **24** (**M3\*** = **qnl1**) of segment VIII as well as muscles **28** (**M4\***), **29** (**M5\***), **32** (**M8\***), **33/34** (**M6\***), and **35** (**M7\***) of segment IX. The only exception is the lack of the coxo-gonapophyseal muscles IX **33/34** in the two Aeshnidae. For muscles **29** (**M5\***), **32** (**M8\***), and **33/34** (**M6\***) they describe specific subdivisions into bundles that are limited to particular species of their sample and could be phylogenetically informative. The subdivision of muscle **29** (**M5\***) into two bundles, which MATUSHKINA & GORB (1997: fig. 11) and MATUSHKINA (2008a: fig. 4) report for *Aeshna* and *Anax*, had been described before for various Aeshnidae and Petaluridae (muscles **7\***, **8\*** in ASAHINA 1954: 67, pl. 48 G8 and in PFAU 1991: figs. 20a, 22); this division is absent in *Epiophlebia*.

For *Anax* MATUSHKINA (2008a) gives a more comprehensive description of muscles in segments VIII and IX. The set of muscles she reports for mature females (tab. 2 therein) includes the ovipositor muscles listed above – with the aforementioned exception that

muscle **33/34 (M6\*)** is absent (also at earlier stages). Segment VIII additionally has external dorsal muscles corresponding to **25 (tlt\*+qlt\*)**, tergo-laterocoxosternal muscles corresponding to **14** and **15 (dvm\* and dvp\*)**, and an anterior tergo-coxosternal muscle **dva\***. The latter may correspond to muscle **13** (Fig. 19), or could be an VIIIth-segmental counterpart of muscle **1** as described for *Epiophlebia* (which is absent in *Calopteryx*, see above). The two only additional muscles reported for segment IX are the dorsal muscle **plt'?**\* and the intersegmental tergo-coxosternal muscle **dvo'**\*.

The interpretation of the dorsal muscle **plt'?**\*, which reaches the anterior rim of tergum IX, as an internal one would appear adequate, while the dorsal muscle of *Calopteryx* (**37** in Fig. 19) is much shorter and thus likely an external dorsal muscle. In this case the only dorsal muscles IX retained in the mature females would not be homologous between these two taxa. ASAHINA (1954: pls. 47, 48), on the other hand, considers the longer and shorter muscles as homologous (muscles **sult9\***).

Muscle **dvo'**\* clearly corresponds to the unstriated bundle **36** (Fig. 19) of *Calopteryx*, which is thus confirmed as a degenerated muscle. Similar muscles have been reported for various Odonata but have been interpreted in different ways. In *Gynacantha* this is the strong muscle **inlt9\*** (ASAHINA 1954: pl. 48 G8; interpreted as an external dorsal muscle), and also *Pseudagrion* is shown as having a strong muscle in the same position (**vlm\*** of segment IX in HAKIM 1964: fig. K). *Epiophlebia* has a similarly located muscle, which according to ASAHINA, however, targets the intersegmental membrane IX/X instead of the anterior margin of sclerite ring X and has thus been categorized (ASAHINA 1954: pl. 47 E69) as a tergopleural **tp9\***; according to my own examination of an *Epiophlebia*, however, the muscle reaches sclerite ring X as in *Gynacantha*.

Also WHEDON (1918: **tp\***, **ls\*** in fig. 31) indicates for *Anax* some IXth-segmental muscles to insert posteriorly on sclerite ring X, but these muscles are probably all attached to apodeme **la** instead: The two bundles of **tp\*** might correspond to ASAHINA's **inlt9\*** and **tp9\***, but they are more likely muscles **7\*** and **8\*** of ASAHINA (1954: pl. 48 G8) and PFAU (1991: fig. 20a) (muscle **29** in Fig. 19) since these are otherwise not indicated by WHEDON. WHEDON's **ls\*** of segment IX is clearly muscle **10\*** of the other mentioned authors (muscle **32** in Fig. 19), not an external ventral muscle reaching segment X as categorized by WHEDON.

According to MATUSHKINA (2008a: tab. 2), teneral *Anax* females have retained some additional muscles from the nymphal stage. In segment VIII, all internal and external dorsal muscles of the nymph are still recognizable (same as for segment VII), as well as the two internal ventral muscles (**pls\*** and **sls\***; external

ventral muscles VIII are also absent in the nymph), and also a muscle **dvo'**\* corresponding to **5** (Fig. 1) of the pregenital segments (see Fig. 63). Muscles **pls\*** and **dvo'**\* have their posterior insertions on sclerite **LCa9**. In segment IX, the tergo-coxosternal muscles **dva\***, **dvm\***, and **dvp\*** are still seen, as well as the external dorsal muscle **qnlt\*** – but all in some state of degeneration. The bundles **30** and perhaps **31** of *Calopteryx* (Fig. 19) are likely to represent degenerated parts of the **dvm\***. The abovementioned muscle **mlt8\*** of *Epiophlebia* is likely a homologue of **qnlt\*** and may be retained longer in that taxon.

MATUSHKINA (2008a: 324) notes that neither in nymphs nor in adult females of *Anax* there are any ventral muscles. However, these are likely represented by the muscles **vra\*** and **vad\*** (see Tab. 3 herein, and muscles **66** and **68** in Tab. 4 for comparison across Insecta) of the nymph and teneral imago studied by her (figs. 1A, 3A therein). They run from the anterior part of venter IX to tendons **rt** and **jt** next to the paraproctal sclerite **AP** (see Fig. 62; muscle **vra\*** = **66** was found herein in male *Calopteryx*). In the teneral imago, MATUSHKINA (2008a: fig. 5D) found the anterior insertions on sclerites **LCa9 (vad\*)** and **LCp9 (vra\*)**. ASAHINA (1954) also notes vestiges of these muscles in the imagines (Tab. 3), while WHEDON (1918: figs. 1, 8) found them only in nymphs.

### 5.7.3. Musculature of segments Xff

The musculature of the terminal abdomen is difficult to treat comparatively because for this area previous descriptions are especially superficial; as in the preceding segments, vestiges of nymphal muscles can be present to very different degrees in the imagines. Fig. 62 is used as an explanatory basis; it shows the full set of muscles so far described for nymphal and imaginal (male and female) Odonata – projected on the terminal abdomen of a female *Calopteryx* imago (the illustration is thus schematical). The muscles found herein and in the studies of ASAHINA (1954), MATUSHKINA (2008a; only *Anax* nymph treated), and CALVERT (1927, only *Lestes* nymph treated) are also listed in Tab. 3, which shows the synonymy of terms (WHEDON's 1918 fragmentary data are negligible).

The author agrees with the muscle homologies between taxa/stages proposed by ASAHINA (1954), though with some uncertainty due to the frequently very superficial indication of the insertion areas in the illustrations. The latter is particularly true for the posterior insertions of the cercal muscles in ASAHINA's illustrations, and homologization with *Calopteryx* cercal muscles (Tab. 3) is thus partly tentative (especially between *Calopteryx* and Aeshnidae). ASAHINA's application of **abc\*** to certain cercal muscles evidently in-



male by the additional presence of muscles **63**, **64**, **65**, and **66** (Fig. 62), and by the heavier condition of cercal muscles **41** and **42** and dorsal muscle X **43**. Since muscles **63**, **64**, **66**, and **43** are well-developed in *Mnais* nymphs (Tab. 3; ASAHINA 1954: pl. 43 M40), this seems to be largely due to a more extensive retention of muscles present in the nymphs; the excessive development of muscles **41** and **42**, which appear moderately sized in the nymph, is more likely a male imaginal characteristic, probably correlated with the use of the cerci as claspers. The development of tendons **ct**, **ht**, and **rt** in the female to the same extent as in the male, albeit they are bare of muscle insertions, may indicate that in teneral females muscles **63** (on **ct**), **64** (on **ht**), and **66** (on **rt**) have not yet degenerated; regarding muscle **66** (**vad\***; on **rt**), and also **vra\*** (on **jt**), this would be in accord with the stout condition of the homologous muscles reported by MATUSHKINA (2008a: fig. 3A) for teneral *Anax* females; the same might be true for teneral females of other odonatan. Tendons **ct** and **ht** are consistently present in all Odonata here studied (with very few exceptions: Tab. 1, characters 69, 70), though muscle **64** (on **ht**) has only sporadically been observed in the imagines, and muscle **63** (on **ct**) has not been found in Odonata other than Calopterygidae, neither in nymphs nor imagines.

Tendons **ut** of the subanal lobes **sb** (Fig. 62) were found in *Calopteryx* to bear the attachment of unstriated strands **46** and **47**, both coming from the anterior margin of the paraproctal sclerite **AP**. Fully developed muscles in corresponding positions are reported very sporadically from Odonata (see Tab. 2), so that the **ut** likely act as tendons. However, there has never been a muscle reported for any stage or sex that could be inserted on 'tendon' **tt** of the terminal projection **tf** (Figs. 12, 13); this structure may thus well have some other, unknown function.

#### 5.7.4. Rectal and alary muscles and ventral diaphragm

The extrinsic rectal muscles have so far hardly been considered in descriptions, but there are two exceptions: The first is muscle **62** (**epra\***), which according to its far posterior rectal insertion (Fig. 62) can as well be categorized as an anal muscle and is included in ASAHINA's (1954) treatment (Tab. 3). In contrast to ASAHINA's results in *Mnais*, muscle **62** (**epra\***) was here found in *Calopteryx*. The second exception is probably the ventral extrinsic rectal muscle **52** from postlaterocoxa **LCp9** (Figs. 19, 23), which is illustrated for *Lestes* and *Aeshna* nymphs in WHEDON (1918: **vdrt\*** in figs. 1, 8); interestingly, in these nymphs the anterior insertions lie on the front margin of venter IX.

The muscles related to the heart in *Aeshna* nymphs are described by ZAWARZIN (1911: 484f, pl. XXIV fig. 6; see also TILLYARD 1917: fig. 71). While most 'lower-grade' Pterygota have standard alary muscles throughout the abdomen up to segment X (with their lateral insertions on the anterior margin of the terga up to X; e.g., NUTTING 1951), *Aeshna* has only the two hindmost pairs (inserted on terga IX and X) and, in addition, anterior and posterior non-striated ligaments in front of and behind them. The anterior ligaments are attached to the anterior margin of tergum VIII, the posterior ones to the "wall of the tenth segment above the anus" (TILLYARD 1917: 159). The alary muscles of the segments in front of VIII are reduced to poor formations of few, diffuse fibers embedded in a septum (ZAWARZIN 1911: 485; comprised herein as 'muscle' **10**, see section 4.2.2.). Though not all parts could herein be traced with certainty, conditions in imaginal *Calopteryx* conform with this description. The extensive median fusion of the left and right posterior ligaments (**51** in Fig. 21), however, is in contrast to *Aeshna* nymphs, though *Calopteryx* shows some variation in the extent of this fusion. The posterior insertion of ligaments **51** immediately lateral to the anterior margin of the reduced tergum **TG11** (also ZAWARZIN 1911 and TILLYARD 1917 may well mean this position) is on XIth-segmental territory (discussion below) and thus in a position potentially homonomous with the usual location of the alary muscle insertions of the preceding segments. Hence, the posterior ligament **51** in Odonata may be a reduced alary muscle XI. Such a muscle has apparently not been reported for any other Pterygota but has been found in the zygantom *Thermobia* (ROUSSET 1973: **al\*** in fig. 8), where its insertion is further posteriorly on tergum XI. This difference complies with the membranization and fragmentation of the lateral parts of tergum 11 in Pterygota as compared to apterygote Insecta (discussed in section 6.9.1.).

The ventral diaphragm in Odonata (apart from the highly specialized components in anisopteran nymphs; ASAHINA 1954: pl. 70) has been treated only by FORD (1923: **ts\*** in fig. 18) for a teneral libellulid and by RICHARDS (1964: figs. 9, 32). FORD's illustration agrees with my findings in *Calopteryx* (Fig. 18), with the exception that I found the perforations distributed more regularly along the margins and not so extensive in the areas near the apodemes **at** and **pa**. RICHARDS (1964: tab. 1) reports the diaphragm also for a zygopteran, but does not provide much detail.

## 6. Discussion of abdominal elements and characters

### 6.1. Generalities

In this chapter the abdomen is compared between Odonata and other Insecta. The major goals are to reach hypotheses on the topographic homology (identification of corresponding parts) and the morphological interpretation of structural elements, and to find outgroup evidence for the polarity of the characters defined in 5.6. (results summarized in Tab. 1, column OG). Furthermore, characters for the phylogenetic reconstruction of the Pterygota are traced. However, the data on the insect abdomen that are available from the literature are in many issues too sparse for reaching here well-founded conclusions. Only some selected subjects can therefore be treated in sufficient detail. The outgroup entries in the character table (Tab. 1) correspond to the scoring of a 'hypothetical ancestor' that is combined from evidence on a variety of (or often only a few) insect taxa.

The morphological comparisons will focus on Archaeognatha, Zygentoma, and the non-endopterygote Pterygota with a completely developed ovipositor (mainly Notoptera, pygidicranid Dermaptera, Orthoptera, Phasmatodea, Mantophasmatodea, Dictyoptera, and Auchenorrhyncha). The Notoptera are particularly interesting because they resemble the Odonata in several aspects of female abdominal architecture: in the location of the genital opening behind and between the gonapophyses **gp8**, in the condition of the ventral sclerites VIII, **LS8** and **CX8**, and in the presence of a sclerite ring on segment X. The Ephemeroptera, which have lost the ovipositor, are considered with regard to the terminal abdomen, and data on Carboniferous (Eo)Meganisoptera (BECHLY et al. 2001) and Diaphanopterodea (KUKALOVÁ-PECK 1992) are also occasionally included.

Data on the development in embryos and nymphs are used as additional evidence in the discussion of the components of the gonoducts (s.l.: lateral, common, and extended oviduct, vagina, spermatheca, accessory glands), ovipositor (gonapophyses, gonoplasts), and terminal abdomen (sclerite ring X, paraproctal sclerites, tergum XI and its terminal projection, cerci). Ontogenetic studies of these areas in Odonata have been conducted by HEYMONS (1896; Coenagrionidae: '*Agrion*' = *Coenagrion*; Corduliidae: *Epithea*; Libellulidae: *Sympetrum*, *Libellula*), VAN DER WEELE (1906; several Zygoptera and Anisoptera), GEORGE (1929; Coenagrionidae: '*Agrion*'

= *Coenagrion*), and ANDO (1962; *Epiophlebia* and many Zygoptera and Anisoptera, but not all fully studied).

### 6.2. The elements of the midabdominal segments

#### 6.2.1. Midabdominal exoskeleton

It is not intended to discuss here all midabdominal characters in detail across all Insecta; only some notes on (apparent) structural peculiarities in Odonata (shown in Figs. 1, 24, 25) should be made, which must be seen in the context of the altogether highly peculiar midabdominal architecture found in this taxon.

Some of these structural peculiarities occur in (nearly) all Odonata here examined but have apparently not been reported for Archaeognatha, Zygentoma, and other Pterygota; they could thus be autapomorphic for Odonata: the posterior transverse carina **ty** and the presence of weakened sclerotization behind it, the intertergal articulations with patches **ap** and triangular heavy sclerotizations, the dorsal hinge lines **dh**, and possibly the ventral keels **vk**. In terms of **vk** (see character 5) the complete lack in *Epiophlebia* but also the very long condition in Libellulidae and the only slightly shorter condition in the cordulegasterid *Chlorogomphus* (both Anisoptera; SCHMIDT 1915: 99) should be noted; the **vk** might thus rather be synapomorphic for a clade Zygoptera + Anisoptera, excluding *Epiophlebia*. Midline ridges somewhat reminiscent of **vk** and **dh** occur in some Dermaptera (KLASS 2001a: **dr\*** and **vr\*** in fig. 1), but these are restricted to the anterior-most parts of the terga resp. coxosterna and do not act as hinges, whereby homology with the structures in Odonata appears unlikely.

The consistent occurrence of two pairs of anterior coxosternal apodemes, **at** and **pa**, in Odonata is also noteworthy, but this character is not unique among insects. For instance, two pairs of apodemes are also present in Caelifera (SNODGRASS 1935a: **aAp\***, **lAp\*** in figs. 4, 10, 12) and Megaloptera (MAKI 1936: fig. 58). Homology of the caeliferan condition with that in Odonata receives support with regard to the posterior apodemes (**pa**), as in both taxa these bear tergo-coxosternal muscles with reversed orientation (compare muscle **2** in Fig. 16, lower picture, and muscle **3\*** in KLUG & KLASS 2007: fig. 5). A homology between the apodemes in Odonata and Megaloptera is supported by the corresponding insertions of the ventral diaphragm (see section 6.2.3.). Nevertheless, these similarities could also be parallelisms due to similar functional requirements.

The longitudinal tergal ridges **lc** and **vc**, the posterior coxosternal apodemes **ba**, and the extension of the coxosternal hind-margins into the apodemes **at** (characters 1, 2, 4, 6) are also features that seem to be limited to Odonata, but they only occur sporadically in the used odonatan sample and are perhaps apomorphies developed in subgroups of Odonata. Dorsal tendons **dt** and an intertergal articulation VII/VIII are also restricted to part of the odonatan sample (see characters 3, 7); however, for these structures there is no outgroup comparison possible due to the lack of data for outgroup taxa (**dt**) or the non-applicability of the character to outgroup taxa (articulation).

### 6.2.2. Midabdominal musculature and nervous system

In these systems the Odonata (Fig. 16) by and large resemble the Neoptera (surveys in KLASS 1999 and KLUG & KLASS 2007). However, there are also some differences in both systems.

One striking difference concerns the lack in mature female Odonata of long internal dorsal and ventral muscles. These muscles degenerate during maturation in teneral females (see FORD 1923: fig. 18, WHEDON 1929, and MATUSHKINA 2008a for the anisopterans *Libellula* and *Anax*). The short muscles **6**, **7**, and **8** retained in mature *Calopteryx* (and **mlt\*** in ASAHINA 1954: pl. 35 D33) are all external ventral and dorsal muscles. For muscle **6** the innervation confirms this: In its supply through a branch (**C3** of **B+C** in Fig. 16) that continues to an intersegmental tergo-coxosternal muscle (**5**; **C4** in Fig. 16), muscle **6** fully complies with the external ventral muscles in, e.g., Dictyoptera, whereas the internal ventral muscles in probably all Neoptera are supplied by the branch of a nerve that furthermore innervates all dorsal muscles (KLASS 1999: nerves **C\*** resp. **A\*** in figs. 3, 4). The lack of internal ventral muscles in Odonata is shared with Phasmatodea except for the genus *Timema* (see KLASS 1999: 35; KLUG & BRADLER 2006), which likewise have comparatively long abdominal segments.

The continuation of the nerve supplying muscles **5** and **6** to the intrasegmental tergo-coxosternal muscle **4** (and possibly **3**; branch **B3** in Fig. 16) conforms with conditions previously found in some Ensifera (SCHMITT 1954, 1964; see KLASS 1999: 36). It corresponds to the combination of the ventral nerves **B** and **C** within one tract and is in sharp contrast to conditions in other Neoptera, where nerves **B** and **C** separate near the ganglion (as in KLASS 1999: figs. 3, 4; see KLUG & KLASS 2007: 81). The contribution of a branch of nerve **C** (upper part of **C4** in Fig. 16) to the supply of a dorsal (i.e., distinctly tergo-tergal) muscle is very peculiar, contrasting the strict separation of the innervation of

dorsal muscles and posterior tergo-coxosternal muscles in Neoptera. (The finding in *Periplaneta americana* L. of such a relation by SCHMITT 1954 could not be confirmed by the more detailed studies of the same species in SHANKLAND 1965 and KLASS 1999: 17.) The nerve anastomoses **C-T** and **IT-A** (Fig. 16), though both constituted by very thin branches, are probably consistently present in *Calopteryx*. These anastomoses are typically present in the Neoptera (KLASS 1999; KLUG & KLASS 2007: 81f), but both were not found in *Povilla* (Ephemeroptera; BIRKET-SMITH 1971). An anastomosis corresponding with **IT-A**, however, has also been reported for *Lepisma* (BIRKET-SMITH 1974; see KLASS & KRISTENSEN 2001: **IT-A** in figs. 14, 15; KLUG & KLASS 2007: 82).

Muscle **12** of segment VII (Fig. 19) is, regarding its supply through nerve **C** of segment VII (shared with muscle **6** of that segment, compare Figs. 16, 19), likely an external ventral muscle, and possibly a modified mesal part of muscle **6**. The area of its posterior insertion, the vaginal tendon **vt** (Figs. 19, 20), should thus be a far posterior part of segment VII, or perhaps be part of the segmental border VII/VIII (though external ventral muscles do usually not reach the succeeding primary segmental border). However, this is not in agreement with the evidence on the morphological interpretation of the gonoducts, according to which the vagina should be purely VIIIth-segmental (see remark 9 in legend of Tab. 4, and below).

### 6.2.3. Ventral transverse muscles and related components

The abdominal ‘ventral transverse muscles’ in Pterygota are a very heterogeneous group of structures composed of muscle fibers and connective tissue. They can be shaped **(1)** as compact transverse muscles lying in the anterior part of each segment (many Ensifera; e.g., FORD 1923: figs. 9–13); **(2)** as paired longitudinal muscles that extend through most of the abdomen, are attached only to coxosterna II and IX, and form either a chiasma or a transverse plate of connective tissue in each segment (hyperneural muscles of Blattaria and Isoptera; KLASS 1999: fig. 1, 2000: fig. 19); or **(3)** as a sheet-like ventral diaphragm, in which muscle fibers of varied orientation are embedded in a sheet of connective tissue, and which extends continuously through most of the abdomen (Odonata, muscle **9** in Figs. 16, 18; Caelifera, SNODGRASS 1935a: fig. 15C, FORD 1923: fig. 6, and BLACKITH & BLACKITH 1967: fig. 9; Megaloptera, MAKI 1936: fig. 58 and SELMAN 1965: 521, figs. 38, 39; several other Endopterygota, RICHARDS 1964). Due to the limited data on these muscles there is no clear picture about their structure in many taxa, and about their evolution. Nevertheless, all the

said structures are likely to some extent homologous and derived from a subset of the ventral muscle-tendon system of Archaeognatha and Zygentoma (see BIRKET-SMITH 1974; KCLASS 2001a). A discussion on the 'ventral transverse muscles' across Insecta is given in KLUG & KCLASS (2007: 87f).

That discussion revealed a close similarity of the ventral diaphragmata in *Calopteryx* (and the few other Odonata studied) and the examined Megaloptera (*Chauliodes* in MAKI 1936; *Sialis* in SELMAN 1965). This concerns both the location of the insertions and the particular pattern of fibers. In both Odonata and Megaloptera the diaphragm is attached to two pairs of coxosternal apodemes in each abdominal segment up to VII (in contrast to Caelifera, which have insertions distributed along much of the segment). In segment VIII the diaphragm has in both *Chauliodes* and *Calopteryx* (at least in the females) only one insertion (**9** on **pa8** in Fig. 19; **261\*** in MAKI 1936: fig. 59). However, the diaphragm in *Chauliodes* reaches only to the middle of segment VII (compare Fig. 19), from where the strands **261\*** extend posteriad as narrow, compact bundles, and likely form the posterior end of the diaphragm. In *Calopteryx* the delicate strands arising from the hind margin of the diaphragm (Fig. 19) likely establish an additional insertion farther posteriorly, but this was not found in the present study. The details of the diaphragm shown for *Sialis* in SELMAN (1965: figs. 38, 39) also comply closely with conditions in *Calopteryx*: Muscle fibers arise in dense bundles from the insertions and spread into the diaphragm. The insertions of successive segments (**pa** and left **at** in Fig. 18; area around **e\*** in SELMAN's fig. 38) are probably also in *Sialis* connected by continuous longitudinal fibers along the lateral margin of the diaphragm (in contrast to Caelifera, which lack lateral longitudinal fibers) – though this portion seems to be poorly developed in *Sialis*. Furthermore, in both *Sialis* and *Calopteryx* these longitudinal fibers give rise to bunches of fibers that extend into the diaphragm (SELMAN's fig. 39). The connective tissue between the muscle fibers is in *Sialis* more poorly developed than in *Calopteryx*, and the entire diaphragm is thus much more extensively perforated (as also indicated in MAKI's fig. 58 of *Chauliodes*). The phylogenetic implications of these similarities between Odonata and Megaloptera, most of which are likely apomorphic within the Pterygota, remain unclear.

#### 6.2.4. Abdominal spiracles and their muscles

The location of the abdominal spiracles in Insecta varies strongly. They can be situated anywhere between the anterior and the posterior rim of their segments, and either in the pleural membrane (Figs. 65–69), on

isolated sclerites within the pleural membrane (Fig. 63), or on the lateral parts of the terga (Figs. 64, 71) or coxosterna. In the latter cases it is tempting to assume that some isolated spiracle-bearing sclerites have become fused to the terga or coxosterna and spiracle location upon these major sclerotizations is thus only apparent. Ideas of this kind are covered by DEUVE's (e.g., 2001) hypothetization of an epipleural field as a basic lateral component of the hexapod segment; this epipleura includes the spiracles and the surrounding sclerotization (if present). While DEUVE's (2001: e.g., figs. 28–31) delimitation of epipleurites in the female genitalic region of many insects is problematic (see section 6.4.2. for sclerite **LS8** in Odonata, which DEUVE considers a medially fused pair of epipleurites VIII), the epipleural-field hypothesis as such may well prove valuable in searching for a solid interpretation of the spiracle area. A well-founded hypothesis, however, needs a comparative analysis of the musculature, innervation pattern, and ontogeny of the lateral parts of the abdominal segments in a rich sample of insects, which is not yet available.

The location of the spiracles in Odonata within the pleural membrane (Fig. 1) resembles that in, for instance, Zygentoma (ROUSSET 1973: fig. 5), Dermaptera (KCLASS 2001a: figs. 1, 3), and certain Caelifera (Morabinae in BLACKITH & BLACKITH 1966: fig. 28; *Paratettix* in FORD 1923: fig. 19). But in contrast to these taxa Odonata have spiracle sclerites **SI**, which, moreover, are the remainder of much larger sclerites that in the nymphs flank the coxosternum ('laterosternites' in SNODGRASS 1954: 26; 'spiracular plates' in ASAHINA 1954: pl. 67 E123; 'pleuron' in MILL 1964). This location on sclerites **SI**, which could be considered epipleurites sensu DEUVE (2001), does not exclude positional correspondence with the former taxa. Nevertheless, similarity is closer to, e.g., Embioptera and certain Ephemeroptera, which likewise have the spiracles seated upon sclerites of varied size and heaviness that are located between tergum and coxosternum (ROSS 2000: figs. 37, 38, as laterotergites; BIRKET-SMITH 1971: figs. 1A, 5A).

Comparing the odonatan spiracles (Fig. 2) with those in other insects is difficult. The two ridge-like closing bars may be homologous with those in many Neoptera (for condition in Dictyoptera see KCLASS 2000: **K\***, **M\*** in figs. 5–7), but the similarities are very unspecific. The internal spiracle lobe **ls** as located in *Aeshna* (upon the anterior part of the mesal closing bar) reminds of the posteroventral spiracle apodeme in many Neoptera (KCLASS 2000: **ks\*** in figs. 5, 7); **ls** in *Calopteryx*, however, is located internal to the bar and does not bear the insertion of a spiracle muscle, all in contrast to apodeme **ks\*** in Neoptera. An anterodorsal spiracle apodeme, present in many Neoptera (manubrium; KCLASS 2000: **ms\*** in figs. 5, 7), is absent in the

Odonata and probably in the Zygentoma as well (pers. obs. in *Ctenolepisma* sp.). The manubrium is thus a potential autapomorphy of the Neoptera or a subgroup thereof (see KLASS 2001a: 265). A zone **ZE** of anastomosing ridges internal to the spiracle closing bars, found in *Calopteryx* but not in *Aeshna*, has otherwise been reported for Dictyoptera, Dermaptera, and Orthoptera, while the zygentoman *Ctenolepisma* lacks it (KLASS 2000: figs. 9–13, 247, 2001a: 265).

The metathoracic spiracle muscles in Odonata are supplied by axons that come from the preceding (mesothoracic) neuromere via the median and transverse nerves, **M** and **T** (MILLER 1962: 517; cf. Fig. 16); the same supply route is true for thoracic and abdominal spiracles in Blattaria (CASE 1957), and also in the chilopod *Lithobius* spiracle muscles probably show a corresponding nerve supply (KLASS & KRISTENSEN 2001: figs. 13, 15). It seems thus likely that in Odonata nerves **M** and **T** supply the abdominal spiracle muscles as well, though the innervation of spiracle muscle **11** (Fig. 17) could not be observed in the present study. Nevertheless, the homology of muscle **11** with muscles in other Insecta seems presently doubtful, because its location differs distinctly from all spiracle muscles found in other Pterygota and in Zygentoma (KLASS & KRISTENSEN 2001: **13\***, **14\***, **X\*** in fig. 15 and **91\***, **92\***, **93\*** in fig. 14).

### 6.3. The gonoducts: ontogenetic development and adult structure

#### 6.3.1. Common and extended oviducts, spermatheca, and vagina

The structure and development of the gonoducts in Odonata present some problems with regard to the morphological interpretation of their components, which also influence conclusions on some other elements of the segments VIII and IX. In addition, the presence of an VIIIth-segmental gonopore in Odonata raises the question about the position of the gonopore (on segment VII or VIII) and the composition of the gonoducts (with or without a vagina) in the ground plan of the Pterygota. Therefore, some issues of gonoduct structure and development are here discussed for some selected insects.

In the late embryos and nymphs of most insects abdominal segments VII–IX each form a median ectodermal invagination near the hind margin, which develops into the common oviduct (VII), spermatheca (VIII), and accessory glands (IX), respectively (SNODGRASS 1933: 16ff, 32ff; NEL 1929) (see section 3.1. for general explanations). In the simplest way of

further development the oviducal invagination VII contacts the mesodermal oviducts internally and retains its position as well as its opening externally, thus forming in the imago a common oviduct that opens on the posterior rim of segment VII (primary oviducal opening); invagination VIII grows, remaining independent, to form a spermatheca (see section 6.3.2. for accessory glands). Such conditions are found in, e.g., Ensifera, Blattaria, ‘higher’ Dermaptera (NEL 1929; GUPTA 1948: 111), and Archaeognatha (NEL 1929: 60; BITSCH 1974a), and in at least those Zygentoma for which the imaginal genital opening has been shown to lie at the hind margin of segment VII (*Thermobia* and *Nicoletia* in ROUSSET 1973). On the other hand, several other modes of development lead to imaginal conditions where an opening on segment VII is (usually) absent due to a secondary closure or posterior shift, and the definitive genital opening lies upon segment VIII, in front or behind the bases of the gonapophyses VIII and closely associated with the spermathecal opening. Among ovipositor-bearing insects this is found in, e.g., Odonata, Auchenorrhyncha, Caelifera (taxa with the ontogeny studied), Notoptera, Mantophasmatodea, and ‘lower’ Dermaptera (most Pygidicranidae).

In Odonata the most striking aspect is that an invagination VII is not reported at all for any ontogenetic stage. According to GEORGE (1929), in *Coenagrion* nymphs the posteriorly fused mesodermal oviducts reach into segment VIII. A midventral invagination develops on the hind part of segment VIII, between the bases of the gonapophyses VIII rudiments, and grows anteriorly to lie above the end of the mesodermal oviduct; this invagination shows positional correspondence with the spermathecal invagination of the generalized pattern. The anterior part of the invagination VIII forms an outgrowth, the rudiment of the vaginal bulb (‘spermatheca’ in GEORGE), which in turn gives rise to the spermatheca (‘spermathecal gland’ in GEORGE; see Fig. 30). The fused part of the mesodermal oviducts acquires an opening into the ventral wall of the invagination VIII behind the vaginal bulb. The main body of the invagination VIII apparently develops into the vagina **va** of the imago, and its external aperture becomes the vaginal opening (vulva, between lobes **vl** in Figs. 8, 9, 30, 63); the contact between invagination VIII and the mesodermal oviduct is in the imago likely represented by the duct **oc+oe** (Fig. 30). Based on HEYMONS’ (1896) finding that in young *Coenagrion* nymphs the mesodermal oviducts terminate in segment VII, NEL (1929: 53f) doubts GEORGE’s observation that these ducts reach deeply into segment VIII. One may furthermore object that GEORGE’s (1929) studies leave open whether in *Coenagrion* an invagination VII develops, contacts the mesodermal oviducts, and becomes externally closed in embryonic stages, thus already constituting in the

nymphs (studied by GEORGE) part of the fused oviduct portion (i.e., an externally closed ectodermal common oviduct; see also GUPTA 1948: 117). However, the finding in the present study that in imaginal Odonata only a short basal part of the oviduct bears an intima (the part **oc+oe** shown in Figs. 30, 31, 34, 35), while extensive mesodermal parts of the oviducts lie within segment VIII (**ola** and **oco** in Fig. 19) is in agreement with GEORGE's proposal of posteriorly fused mesodermal oviducts lying within segment VIII in the nymph. The formation of an invagination VII in the embryo may appear unlikely also from the fact that ANDO (1962) does not report anything like this. According to VAN DER WEELE (1906: 102, 162f, 188) the female gonopore in *Aeshna* is, like the male one, invaginated from the central part of venter IX and then shifted anteriorly to near the dorsal bases of the gonapophyses VIII by the growth and anterior shift of the gonapophyses IX bases. GEORGE (1929: 470), however, claims that even in young nymphs the duct arises from in between the gonapophyses VIII bases (unfortunately he does not show longitudinal sections). VAN DER WEELE (1906) may have observed the accessory gland rudiment, for which then, however, the unpaired condition is surprising (see below).

Auchenorrhyncha show a striking diversity with regard to gonoduct development. In *Philaenus leucophthalmus* (Cicadomorpha: Cercopidae), according to GEORGE (1929), the mesodermal oviducts, which are not fused posteriorly, reach into segment VII. An oviducal invagination on the hind part of segment VII grows anterodorsad to lie above the ends of the mesodermal oviducts, with which it connects. A groove develops from the hind margin of venter VII to the bases of the gonapophyses VIII rudiments, which then becomes closed by the fusion of its margins. By this formation of an VIIIth-segmental tube (extended oviduct) the gonopore is translocated from segment VII to VIII. The spermatheca develops from the anterior portion of the invagination VII, thus being VIIIth-segmental in origin unless tissue has shifted from segment VIII to this area along the groove walls. In *Philaenus spumarius*, however, METCALFE (1932) found very different origins of the VIIIth-segmental tube and spermatheca: a discrete VIIIth-segmental invagination is formed, which grows anteriorly internally to overlie the VIIth-segmental invagination, obtains an open connection with the latter, and develops a spermatheca from its free anterior end; the invagination VII becomes closed externally. The imaginal genital opening in *Philaenus* lies, like in Odonata, posterodorsal to the gonapophyses VIII bases. (It may be noted that the two genital openings reported for *Magicicada septendecim*, Cicadomorpha-Tibicinidae, in SNODGRASS 1933: 97ff might represent the invaginations VII and VIII, the former remaining open in this taxon.) In *Em-*

*poasca fabae* (Cicadomorpha: Cicadellidae), studied by HELMS (1968), the mesodermal oviducts reach into segment VIII. A hollow mass of ectodermal tissue is present either posterodorsal or anteroventral to the gonapophyses VIII bases (conflicting locations in HELMS 1968: **APL\*** in figs. 19, 21A). The genital ducts are reported to develop from this mass, and an invagination VII is apparently absent like in *Coenagrion*.

In the various Acrididae (Caelifera) studied by NEL (1929), QADRI (1940), GUPTA (1948), and ROONWAL (1937, 1962), the mesodermal oviducts, which are not fused posteriorly, reach the border area between segments VII and VIII. The oviducal invagination ('vaginal' in ROONWAL), develops in late embryos on the hind margin of segment VII and lies far anteriorly on segment VIII in freshly hatched nymphs; it later connects with the mesodermal oviducts. The spermathecal invagination develops on the hind margin of segment VIII. The oviducal invagination then shifts further posteriorly, not to the hind margin of segment VIII as claimed by some (ROONWAL 1962: 111, 114; NEL 1929: 38f), but only to somewhat beyond its middle, as coxosternum VIII has become transversely divided before and only the membrane behind the anterior plate is reached (GUPTA 1948: 99; confusion results from the inadequate application by the former authors of 'sternum', i.e., 'coxosternum' VIII to the larger anterior plate only). The shift is described as a "backward extension of the vaginal tissue", though the exact mechanism is unknown (ROONWAL 1962), or as the formation of a groove along the midline of segment VIII, whose margins eventually fuse to form an internal tube (extended oviduct). Both descriptions probably mean the same: the formation of the groove and the fusion of its margins proceed from anteriorly to posteriorly, the latter closely following up the former (see NEL 1929: 38; GUPTA 1948: 101f). The shifted oviducal opening (secondary oviducal opening) has thus closely approached the spermathecal aperture, but because the membrane between them – that separating the anterior and the posterior plate VIII ('intersegmental membrane VIII–IX' in ROONWAL 1962: 111; compare usage of 'sternum' above) – strongly expands and folds inward to form a genital pouch/chamber (vagina, its opening being the vulva), the two openings become again far separated on the hind part of venter VIII, and lie ventrally resp. dorsally in the walls of the chamber (Fig. 64; NEL 1929: fig. 45; SNODGRASS 1935a: fig. 20A).

The configuration thus reached in adult Acrididae resembles that in Odonata (compare Figs. 63 and 64). Yet it shows one seemingly fundamental difference: The vagina opens farther anteriorly, in front of the gonapophyses VIII bases (see also NEL 1929: 62). This would correspond to a deep infolding of the membrane between the laterocoxosternum **LS8** and the coxae **CX8** in Odonata (Figs. 4, 7, 63) – if one considers the

divisions of coxosternum VIII into the anterior and the medially divided posterior plates in Acrididae, and into **LS8** and **CX8** in Odonata homologous (as done in Figs. 63, 64). The vulva position found in Odonata would be reached if either the groove/tube formation in Acrididae additionally continued posteriad to pass between the two halves of the posterior plate, the secondary genital opening then lying posterodorsal to the gonapophyses VIII, and if the vagina was formed in this area instead; or, more parsimoniously, if the vulva undergoes a posterior shift to the area behind the gonapophyses VIII bases.

The Notoptera (Fig. 65; gonoduct ontogeny unknown) bridge the gap between the imaginal conditions in Odonata and Acrididae (Figs. 63, 64) – in the sense of a shift of the vulva. In Notoptera coxosternum VIII is, like in the two other taxa, composed of an unpaired (though almost medially divided) anterior plate **LS8** and paired posterior plates **CX8** between the former and the gonapophyses VIII bases (see also WALKER 1943: **st8\***, **bv\*** in fig. 5; KLASS 2005: **S8\***, **Vf8\*** in fig. 9.3.A,B). A deep vagina is present, into which the median oviduct opens ventrally, and a spermathecal tube dorsally. The vulva extends from the hind margin of the anterior plate to the area posterodorsal to the gonapophyses VIII bases; accordingly, the lateralmost parts of the vagina are divided into a lower and an upper floor by the inner basal parts of the gonapophyses VIII, which project somewhat into the vagina (Fig. 65).

Considering the intermediate conditions in Notoptera, vaginae in Acrididae, Notoptera, and Odonata are potentially homologous as far as imaginal structure is concerned (in contrast to NEL 1929). Those Pygidicranidae that show the most plesiomorphic condition of the ovipositor found in Dermaptera (e.g., species of *Dacnodes*, Fig. 66, and *Tagalina*; KLASS 2003: figs. 18–29) have a long vagina, which receives the median oviduct and spermathecal tube in the same positions as the vaginae in the aforementioned taxa, and whose opening is, like in Odonata, restricted to the area posterodorsal to the gonapophyses VIII bases. In Acrididae, Notoptera, and Pygidicranidae the spermatheca is a tube opening dorsally into the vagina, and the vagina extends somewhat anteriorly beyond the spermathecal and oviducal openings (Figs. 64–66). Because Zygoptera and *Epiophlebia* (Figs. 30, 34, 35, 38) show the same configuration, the structure frequently called the spermathecal gland is here called the spermatheca **sp** (used as a purely morphological term), and the bulb frequently called the spermatheca is here designated the vaginal bulb **vb** (Fig. 8) (see HAYASHI & TSUCHIYA 2005 for alternative terminology and function).

Besides the exoskeletal structure, also the musculature of the gonoducts in Odonata, Notoptera, Pygidicranidae, and Caelifera (Figs. 63–66, Tab. 4) appears

similar enough to support the homology of the vaginae in these taxa. A muscle from coxosternum VII to the anterior tip or dorsal wall of the vagina, like **12** of *Calopteryx*, is almost consistently present; it is only lacking in Acrididae but is found in Caelifera-Acrydiidae (and included in Fig. 64). Muscle **12** is likely a modified external ventral muscle VII (see section 6.2.2.). A muscle from the anterior ventral sclerites VIII **LS8** (laterocoxosternum mainly composed of laterocoxae) or **LC8** (laterocoxae), like **18** of *Calopteryx*, is also found in all these taxa (see section 6.4.1. for the identification and different sizes of **LS8/LC8**). Notoptera, however, are probably exceptional, since all fibers of the muscle seem to continue from one side of the **LS8** to the other (fibers inserted medially on the vagina were not identified with certainty). Muscles like **20+21** and **19** in *Calopteryx* run from the coxae **CX8** (or from the membrane immediately in front of these: Fig. 65) to the middle resp. posterior part of the vagina. However, in Caelifera only one of these muscles is present (likely the anterior one, **20+21**), and *Dacnodes* lacks both. In *Calopteryx* and *Grylloblatta* the **CX8**-insertion of the posterior muscle **19** is close to that of the coxo-gonapophyseal muscle VIII **23**. A muscle **70**, which originates on **LS8** close to muscle **18** but goes to a median infolding in between the dorsal bases of the gonapophyses VIII, is peculiar to Caelifera and Notoptera (Figs. 64, 65). The intrinsic vaginal muscle **22** (Fig. 20) appears to occur only in *Calopteryx* (and possibly other Odonata).

One may argue that VIIIth-segmental vaginae in at least Odonata and Acrididae are, after all, likely non-homologous regarding their different modes of gonoduct development, and the difference with regard to a contribution by an invagination of venter VII in particular. However, the high plasticity of gonoduct development in Auchenorrhyncha (see above), where *Empoasca* probably also lacks a VIIth-segmental contribution to the gonoducts and shows an extension of the mesodermal oviducts into segment VIII, would indicate that hypothesizing homology is reasonable despite different developmental pathways (see MATSUDA 1976: 296 for even more aberrant modes of development in Hemiptera). There are surely many examples where elements are rightfully considered homologous in different taxa though they are borne by different developmental processes from different precursor structures or tissues. Thus, also on grounds of ontogenetic development the homology of the vaginae in the taxa here considered can hardly be rejected.

Nevertheless, due to the developmental differences there remains much uncertainty in the explicit application of homology hypotheses: can one homologize cuticular elements (e.g., sclerites) that are formed upon VIIth-segmental epidermis in the one taxon but upon VIIIth-segmental epidermis in an other one, and can

an element originating from VIIIth-segmental tissue be considered VIIth-segmental? Consequently, the interpretation and designation of the gonoduct components and their comparison between taxa is very difficult. With regard to Odonata and *Empoasca*, for instance, it remains open whether the median oviduct (**oc+oe** in Fig. 30) should be regarded as a pure common oviduct, or as a common plus extended oviduct as in the Acrididae, its opening into the vagina either being a 'VIIth-segmental' primary or an VIIIth-segmental secondary oviducal opening. Also the distinction between the spermathecal duct and the vagina is often problematic in view of this developmental background. This is not so in Acrididae, where two successive invaginations occur on the hind part of segment VIII: a discrete ingrowth of a spermatheca is observed before the area that bears the spermatheca, and has meanwhile also been reached by the median oviduct, invaginates to form the vagina. In *Coenagrion* and *Philaenus spumarius*, however, a single VIIIth-segmental invagination continuously grows inward to obtain an open internal connection with invagination VII (*Philaenus*) or with the mesodermal oviducts (*Coenagrion*), and to form a spermatheca from its internal portions. Should then the principal invagination be regarded as the spermathecal one (as in, e.g., METCALFE 1932: 475) or as the vaginal one, i.e., is the spermathecal duct seated internally upon a vagina, or does the external portion of the spermathecal duct acquire the function of a vagina by its connection with invagination VII? It seems reasonable to assume that in such cases the formation of the spermatheca and that of the vagina are combined within a single invagination process, and that a spermatheca is seated upon a vagina; yet, a refined interpretation could consider to which part(s) of invagination VIII growth is focused (two separate growth zones might reflect two different invagination procedures). More evidence on these issues is clearly needed.

In sum, the presence of a fairly similar vagina posteriorly on segment VIII is potentially homologous in Odonata, Notoptera, Caelifera, (many) Dermaptera-Pygidicranidae, and Auchenorrhyncha – and perhaps some further Neoptera. The exoskeletal architecture of the gonoducts in Mantophasmatodea (KLASS et al. 2003: figs. 7, 8) corresponds with that in the aforementioned taxa – with Notoptera in particular, as the vulva extends from the area in front of the gonapophyses VIII bases to behind them. However, the musculature has not yet been studied in this taxon. Among the Neoptera with reduced ovipositors similar vaginae are found in most Plecoptera (ZWICK 1980: 73) and probably the Zoraptera (GURNEY 1938: fig. 1) (while a vagina is absent in Embioptera, as shown by current work of K.-D. Klass & J. Ulbricht). Hence, one might ask whether such a vagina could be a groundplan element

of the Pterygota (or Odonata + Neoptera, or Insecta) – instead of a VIIth-segmental primary gonopore as present in, e.g., Archaeognatha, (at least some) Zygentoma, Ensifera, and Dictyoptera. This question is highly important because the interpretation of much of the female genitalic region in Insecta as well as the polarization of many genitalic characters and thus phylogenetic conclusions depend on it.

The 'higher' Dermaptera, where in contrast to the 'primitive' Pygidicranidae the invagination VII retains its position to become the definitive genital opening (see KLASS 2003), constitute one example where a VIIth-segmental gonopore is very likely secondary. This position of the opening has been considered paedomorphic by KLASS (2001a; in contrast to NEL 1929: 57) because also the remainder of the female genitalic region in these insects shows strong paedomorphic features. One could assume paedomorphosis also for VIIth-segmental gonopores in other Neoptera (or even Insecta) – possibly even when ovipositors are well developed. However, Zygentoma, Dictyoptera, and Ensifera with their VIIth-segmental openings share, in addition, the presence of a genital fold, which arises from the posterior part of venter VII, immediately in front of the gonopore, and is usually sclerotized: 'subgenital plate' in Ensifera, 'laterosternal shelf' in Dictyoptera (e.g., KLASS 1998), 'languette' in Zygentoma (ROUSSET 1973); these are the lobe **gf** and the yellow sclerite **LG7** in Figs. 69, 70. Yet, a secondary re-appearance of this element can perhaps be explained in the framework of a paedomorphosis hypothesis. The way the genital opening is translocated from venter VII to venter VIII in the ontogeny of the phasmatodean *Carausius morosus* (CAVALLIN 1970; KALUSCHE 1972) appears to be crucial in this regard: In this taxon a tongue-like lobe from the hind margin of venter VII (immediately in front of the common oviduct opening) grows posteriorly, and its lateral margins fuse with the opposing walls of venter VIII (the result is the operculum = lamina subgenitalis, previously misinterpreted as the 'sternum VIII' by, e.g., GÜNTHER 1956). The median part of what appears to be venter VIII in the imago is thus actually part of venter VII. At an early ontogenetic stage the lobe corresponds with the genital fold; in the framework of a paedomorphic scenario the fusion of its margins with venter VIII would be abandoned, and a free genital fold and VIIth-segmental genital opening would remain. This hypothesis, and alternative ones, will be elaborated and discussed in a subsequent paper (K.-D. Klass & J. Ulbricht in prep.).

Unfortunately, the structural range of gonoducts in Zygentoma is still unclear. ROUSSET (1973) in *Thermobia* and *Nicoletia* found in the adults a VIIth-segmental position of the gonopore, as indicated by the course of antecosta VIII (along the sternal sclerotization VIII in

Fig. 70). In the so far only relevant ontogenetic study, however, HEYMONS (1897: 610) mentions for *Lepisma* an VIIIth-segmental invagination that contacts the mesodermal oviducts and produces also the spermatheca – like in Odonata. Nevertheless, HEYMONS' short explanations are not very clear. One should further note the conditions reported for campodeid and japygid Diplura (GRASSI 1888; MARTEN 1939; MATSUDA 1976: fig. 14C), where the female genital opening lies on the posterior part of venter VIII, and where something like a vagina is present ('bursa copulatrix' of MARTEN 1939) that receives the common oviduct anteriorly and a median spermatheca ('borsa copulatrice' of GRASSI 1888) dorsally. For resolving the important question of the location of the genital opening and the composition of the gonoducts in the ground plans of Insecta and Pterygota, detailed studies of gonoduct development in Diplura, Archaeognatha, and various Zygentoma and Odonata are urgently needed.

For assessing the polarity of vagina characters in Odonata, outgroup reference to conditions in Notoptera, Caelifera, and Pygidicranidae (Figs. 64–67), and also Mantophasmatodea (KLASS et al. 2003: figs. 7, 8) appears presently as the only feasible possibility. This is also justified based on the potential homology of vaginae among these taxa, but one should keep in mind that this homology is not well ascertained.

Vaginal 'ridges' like **cr** and **mr** are absent in the said outgroup taxa (see characters 29, 30; Figs. 30, 31, 34, 35, 38). Lateral vaginal sclerites like **VB** (see character 27) are present in (some?) Caelifera, where they closely approach the coxae **CX8** posteriorly (Fig. 64; **c\*** in SNODGRASS 1935a: fig. 17C); in the pygidicranid *Echinosoma*, where they are basal extensions of the gonapophyseal sclerites **GP8** (**GPb8\*** in KLASS 2003: fig. 15); and in Mantophasmatodea-Mantophasmatidae, where they are not in contact with other sclerites (**VS\*** in KLASS et al. 2003: figs. 21, 23). Because **VB**-like sclerites are absent in the remaining examined Pygidicranidae and Mantophasmatodea, and in Notoptera (Fig. 65), outgroup evidence is here considered ambiguous. Character 28 of the extension of sclerite **VB** along the vagina is not applicable to the outgroup due to that ambiguity, and also because the proportions of the vaginae possessing sclerotizations are quite different from those in Odonata. The spermatheca in the outgroup taxa is discretely set off from the vagina (Figs. 64–67) as in most Odonata (see character 31) – if the identification of the spermatheca in Odonata (**sp** in Fig. 63) as given herein is correct. Vaginal bulbs **vb** (see character 32) are not found in the outgroup taxa, neither in the zygopteran nor in the aeshnid position, but a **vb**-less condition like in *Epiophlebia* is present (Figs. 30, 31, 38). A tubular neck of the vagina (as in *Chlorocnemis*, Fig. 34; see character 35) is likewise absent from all outgroup taxa. Like in *Epiophle-*

*bia* and Aeshnidae, the median oviduct **oc+oe** in the outgroup taxa is not evaginated into the vaginal lumen (see character 36).

For spermathecal characters of Odonata most Dicondylia can be used as outgroups. Outgroup comparison for the spermathecal sclerotization **SP** (found in *Mecistogaster*, Fig. 35; see character 34) is ambiguous, because many Dicondylia lack sclerotizations within the spermatheca, whereas others have very different kinds of sclerotizations, which are likely not all homologous: examples are a sclerotized knob at the spermathecal opening (*Grylloblatta*, Fig. 65), a dorsal and a ventral sclerite near the external base of the spermatheca (Acrididae, Fig. 64), or only a ventral one (*Thermobia*, Fig. 70). Also for the forking of the spermatheca (see character 33) outgroup evidence is best considered ambiguous, because both forked and unforked spermathecae are found in many insect orders (e.g., Dictyoptera: MCKITTRICK 1964; KLASS 1998; Dermaptera: KLASS 2003). The asymmetrical left-side origin of the spermatheca from the vagina in *Platycnemis* (character 32: 'lat') is surely apomorphic within the Odonata.

### 6.3.2. Accessory glands

The standard female accessory glands found in many insects develop, as mentioned above, from a midventral invagination on the hind part of venter IX, which is often bilobate internally (SNODGRASS 1933; NEL 1929). In some taxa, however, different accessory glands occur. In *Philaenus* GEORGE (1929) found, in addition to the standard glands, paired invaginations anterolaterally upon segment IX (not mentioned in METCALFE 1932). These develop into the imaginal lateral accessory glands (GEORGE 1929: **Pacg\*** in fig. 23 for *Philaenus*; SNODGRASS 1933: **e\*** in fig. 32A for *Magicicada*), which open beside the vaginal opening and distinctly in front of the posteromedian accessory gland. In many basal Dermaptera there are paired (glandular?) tubes in addition to a median accessory gland (**tl\*** in KLASS 2003: e.g., figs. 11, 19, 24), but these are located behind the median gland.

The accessory glands in *Coenagrion* (GEORGE 1929) originate as paired, backward growing ectodermal invaginations from the anterior part of venter IX. It is tempting to homologize these with the paired glands in Auchenorrhyncha, the unpaired posterior accessory gland being absent in Odonata (but compare in section 6.3.1. the note on VAN DER WEELE's 1906 observation of an unpaired, quite far posteriorly located potential accessory gland rudiment).

ROUSSET's (1973: 60) observations in adult Zygentoma are furthermore particularly interesting: *Thermobia* has paired accessory glands (bent posteriad as to

lie within segment IX like the glands of Odonata, Fig. 3), but *Nicoletia* has an unpaired gland. Both types of glands open near the gonapophyses IX bases, but the paired ones are distinctly farther in front as related to the opening of the spermatheca ('receptaculum seminis + bursa copulatrix' in ROUSSET 1973: figs. 5, 10). *Lepisma* likewise has the paired anterior glands (GUSTAFSON 1950: fig. 27B).

Consequently, both paired anterior and unpaired posterior glands may have been present in the ground plan of Dicondylia, and the posteromedian one may have been lost in the Odonata. It is not clear from ROUSSET's (1973) fig. 3 of *Thermobia* whether the gland openings are close to the midline (as in *Epiophlebia* and *Lestes*) or farther laterally and in close association with the rhachis of the olistheter (as in the other Odonata here sampled; see Figs. 39–41). Out-group comparison in character 47 is thus considered unclear.

BITSCH (1974a: 107) reports for Archaeognatha a pair of glandular stripes (**glg\*** in fig. 2f therein) located in the lateral walls of the wide midventral groove above the mesal rims of the coxal lobes IX, which ensheath the gonapophyses VIII and IX. The corresponding areas in Odonata are the lateral parts of the membrane bulged over the gonapophyses VIII and IX, on both flanks of the apodeme **ca** (Fig. 11). Though the relative position of the glands is not exactly the same, because in Odonata the bases of the **gp9** intervene between the said membranous areas and the openings of the glands **ag**, homology may not appear impossible. One may then tentatively suggest that the glands in Dicondylia have become restricted to the anterior-most part of the area along which the glandular stripes extend in Archaeognatha (to the anterior base of the rhachis of the olistheter) and have become strongly enlarged in this area. The presence of discrete paired anterior accessory glands and the presence of an unpaired posterior gland may thus be synapomorphies of Zygentoma (or part of this taxon) and Pterygota. A study of the accessory glands in *Tricholepidion*, an enigmatic 'primitive' zygentoman (see KRISTENSEN 1991; STANICZEK 2000; BEUTEL & GORB 2006; KJER et al. 2006; KLASS 2007), would be desirable in this regard.

There seem to be no data on the function of the accessory glands in the Odonata. According to the position of their apertures close to the anterior end of the rhachis (which in the interlocked gonapophyses **gp8** and **gp9** opposes the anterior end of the aulax on the **gp8**), and according to the presence in *Lestes* (with apertures close to the midline) of laterad-directed grooves that extend from the apertures to near the basal end of the rhachis, the secretions might act as a grease that enters the olistheter anteriorly and creeps along it by adhesive forces. For the **glg\***-glands in Archaeognatha BITSCH (1974a: 107) also suggests a grease-like func-

tion of the secretions. On the other hand, it also appears conceivable that secretions intended to cover the eggs are transported distally along the olistheter and the internal faces of the gonapophyses.

## 6.4. Ventral sclerotizations VIII and their muscles

### 6.4.1. Basic ventral sclerotizations VIII and their identification and variation

The sclerotizations of venter VIII vary strongly among ovipositor-bearing insects. This is in part due to the position of the genital opening either in front of these sclerotizations or behind them (VIIth- or VIIIth-segmental gonopore). Homologizing sclerotizations and muscles between different high-rank insect taxa is thus a difficult task.

Archaeognatha (according to BITSCH 1973, 1974a) is used here for defining the basic sclerotizations (as in KLASS 2003). Venter VIII (Fig. 71) bears, as a maximum set of sclerites, paired coxae (**CX8**; 'coxite' in BITSCH), postlaterocoxae (**LCp8**; 'laterocoxite'), and antelaterocoxae (**LCa8**; 'precoxite'), and an unpaired median sternum ('sternite', posteriorly) and intersternum ('intersternite', anteriorly); gonapophyseal sclerotizations (**GP8**) are not clearly reported, but the gonapophyses are known to bear an aulax groove (**al**). Sternum and intersternum are comprised as the eusternum (**ST8**). While the coxae are very large and extend onto large coxal lobes (gonoplacs **gl8**) posteriorly, the remaining sclerites are restricted to the anterior marginal area of the segment. The sclerite pattern and the size ratios are much the same in the pregenital segments, though losses and fusions of sclerites can be found.

In the Zygentoma *Thermobia* and *Nicoletia* (ROUSSET 1973) the basic sclerites are all fused to form one large coxosternum. This is true for segment VIII (Fig. 70) as well as for the pregenital segments, but in segment VIII the left and right parts are transversely connected only by a narrow anterior bridge (**ST8**-part). Furthermore, for these zygentomans gonapophyseal sclerites **GP8** are reported, which comprise a ribbon each in the dorsal and in the ventral gonapophyseal wall, the dorsal ribbon bearing the aulax **al**.

In most Pterygota with well developed ovipositors, sclerotizations VIII differ strongly from those in the preceding segments, because on the one hand the basic sclerotizations in the pregenital segments are usually united within large undifferentiated coxosterna (though with possible exceptions, see KLUG & KLASS 2007), and on the other hand the basic sclerotiza-

tions VIII have partly remained separated or become reduced or modified. Most strikingly, coxae VIII are usually reduced in size, which usually goes along with a vestigial condition of their coxal lobes (= gonoplares VIII, **g18**). Accordingly, in some groups of ovipositor-bearing Pterygota only several small sclerites are present on venter VIII, contrasting the large coxosterna in the preceding segments. Such conditions are found in the Dictyoptera (Fig. 69) and Ensifera with their

VIIIth-segmental genital openings, but also in some of the taxa having an VIIIth-segmental vulva (e.g., the pygidicranid *Dacnodes*, Fig. 66). However, in other groups of ovipositor-bearing Pterygota – in most of those that have a vulva on venter VIII – the anterior part of venter VIII bears a large unpaired sclerite.

This is, for instance, true for Odonata with their large sclerite **LS8** (Fig. 7): With regard to its sclerotization and musculature the long anterior part of venter

**Figs. 63–71. Venter VIII and gonangulum area in various insects.** Entire venter VIII and gonangulum area (laterocoxa) of venter IX of female genitalic region shown, dorsal (predominantly internal) view. Lateral parts of terga VIII and IX included on right side, bent downward, thus lying in same plane as ventral elements. Orientation: ↑ anterior. Sclerotization coloured differently according to hypotheses of topographic homology. Undulate lines are cuts through cuticle and embrace cut surfaces of muscles. Dashed lines show hidden borderlines of muscles and their insertions. Right side showing all muscles inserted on venter VIII, laterocoxa IX, and ectodermal gonoducts; muscles from coxosternum VII or endosternite ES8 cut anteriorly; muscles running posteriad from laterocoxa IX cut posteriorly; insertions of ventral diaphragm (on laterocoxa VIII: muscle 9, see Fig. 19) and ventral extrinsic rectal muscle (on laterocoxa IX: muscle 52, see Figs. 19, 23) only represented by insertion areas, if present. Muscles in non-Odonata (Figs. 64–71) numbered like their homologues in Odonata (Fig. 63); muscles having no homologues in Odonata given other numbers in arbitrary sequence (see Tab. 4 for muscle names used in original contributions). Of the oviducts only the intima-bearing ectodermal parts are included; these parts continue further internally than shown when the lateral oviducts are terminated by undulate lines. The illustrations focus on showing spatial relationships between the components; thus, the exoskeletal components are partly distorted and not in all respects to proportion (therefore no scale), and the muscle representation reflects the spatial arrangement but not consistently the relative width of muscles.

**63:** Scheme of Odonata. Gonapophyses VIII cut, basal dorsal wall removed on left side. Vaginal walls partly removed on left side. Spermatheca complete. Muscle 67 included (reported for *Epiophlebia* but not labeled in ASAHINA 1954: pl. 47 E69); muscles only found in teneral females of *Anax* (MATUSHKINA 2008a) but not in mature females included as bars in lighter grey.

**64:** Scheme of Acrididae (Orthoptera-Caelifera), according to SNODGRASS (1935a: *Dissosteira*) and own studies of exoskeleton in *Locusta*. Gonapophyses VIII entire, but most of dorsal wall removed on left side. Vaginal walls partly removed on left side. Spermatheca cut. Muscle 12 of *Paratettix* (Caelifera: Acrydiidae) included (FORD 1923: part of os6\* in fig. 19; absent in Acrididae). Posterior insertions of muscles 16? and 20/21 on coxa VIII, which is visible on the left side.

**65:** Scheme of *Grylloblatta* (Notoptera), according to own studies. Gonapophyses VIII cut, basal dorsal wall removed on left side. Vaginal walls partly removed on left side. Spermatheca entire. The area ‘ST8 or LG7’ is weakly sclerotized. Muscles 18 and 20/21 traverse to the same positions of the opposite side.

**66:** Scheme of *Dacnodes* (Dermaptera), according to KLASS (2003). Gonapophyses VIII cut, most of dorsal wall removed on left side. Vaginal walls largely removed on left side. Spermatheca cut. Muscle 78 traverses to the same position of the opposite side (ventral transverse muscle IX).

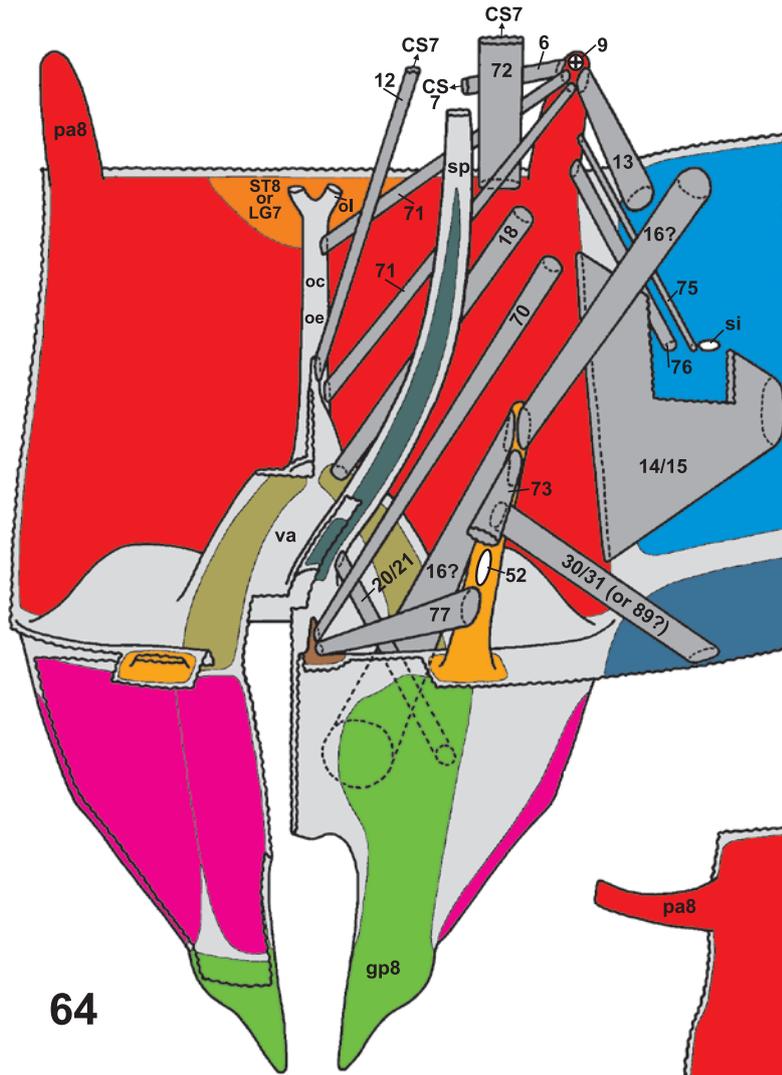
**67:** Scheme of *Karschiella* (Dermaptera), according to KLASS (2003); muscles not studied. Gonapophyses VIII entire, but basal dorsal wall removed on left side. Vaginal walls removed on left side. Right spermatheca included, cut. Most of laterocoxa IX removed on left side to show gonoplares VIII.

**68:** Scheme of *Hemimerus* (Dermaptera, viviparous), according to KLASS (2001a). The vestigial gonapophyses VIII entire, dorsal wall removed on left side. Dorsal vaginal (or oviducal?) wall largely removed on left side. Spermatheca absent. The posterior bundle of muscle 18 traverses to the same position of the opposite side (ventral transverse muscle VIII).

**69:** Scheme of Dictyoptera, according to own studies (KLASS 1998 and unpublished). Left illustration: gonopore area shown in an artificially extended condition, with area anterior to front margin of venter VIII dragged forward and thus levelled; gonapophyses VIII cut; spermatheca entire; some muscles are variable in Dictyoptera; coxa VIII is in most Blattaria divided into two sclerites (gonocoxa VIII s.str. and basivalvula VIII in KLASS 1998: figs. 11–19); fine line on tergum VIII shows borderline between tergite and paratergite. Right illustration: gonopore area shown in natural condition, with gonopore upon genital fold VII (laterosternal shelf); left parts of venters VIII and IX removed; spermatheca not cut.

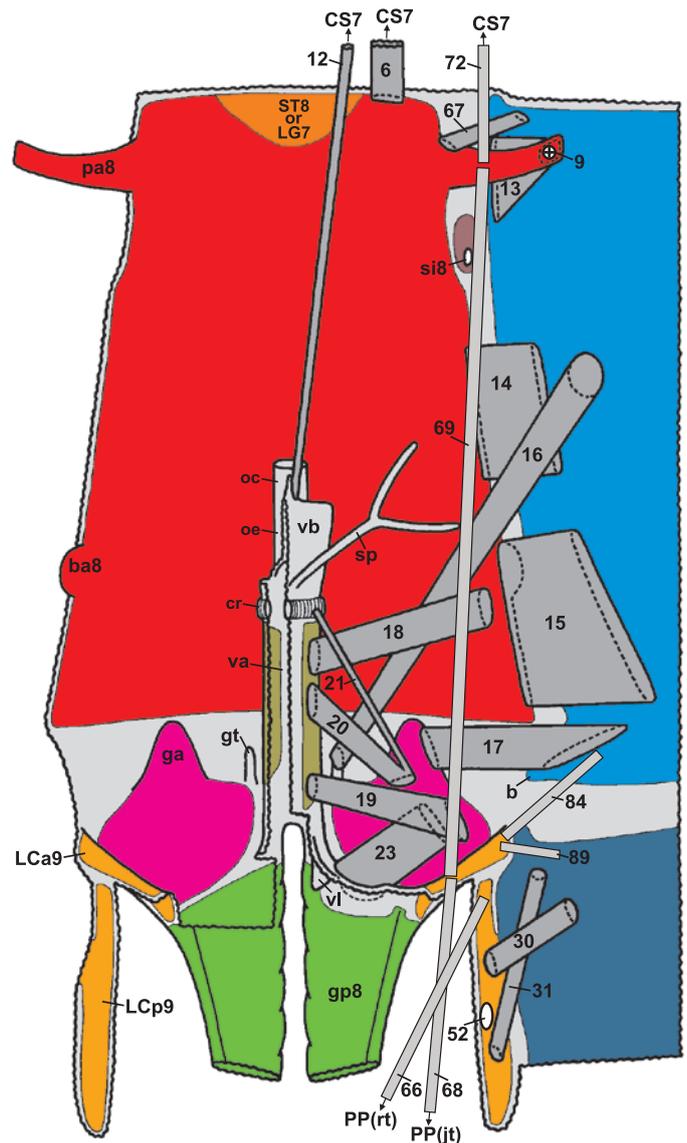
**70:** Scheme of *Thermobia* (Zygentoma: Lepismatidae), according to ROUSSET (1973). Right illustration: gonopore area shown in an artificially extended condition, with area anterior to front margin of venter VIII dragged forward and thus levelled; gonapophyses VIII cut; spermatheca (bursa copulatrix + receptaculum seminis in ROUSSET) entire but dorsal wall partly removed. Muscle 6 and the posterior transverse portion of muscle 18 as well as sclerite LG7 (languette sclerite) of *Nicoletia* (Zygentoma: Nicoletiidae) included (ROUSSET 1973, see Tab. 4 for muscle names used therein; all absent in *Thermobia*). The anterior, medially inserted portion of muscle 18 is labelled ‘28’ for *Thermobia* but ‘29?’ for *Nicoletia* in ROUSSET (1973: figs. 7, 11). Left illustration: gonopore area shown in natural condition, with gonopore upon genital fold VII (gf, languette); left parts of venters VIII and IX removed; spermatheca cut longitudinally.

**71:** Scheme of *Trigoniophthalmus* (Archaeognatha), according to BITSCH (1974a). Right illustration: gonopore area shown in an artificially extended condition, with area anterior to front margin of venter VIII dragged forward and thus levelled; gonapophyses VIII cut, data on gonapophyseal sclerotizations not available; typical insect spermatheca absent, but several smaller spermathecae present. Left illustration: gonopore area shown in natural condition, with gonopore upon intercoxal lobe (= genital fold gf?); left parts of venters VIII and IX removed.

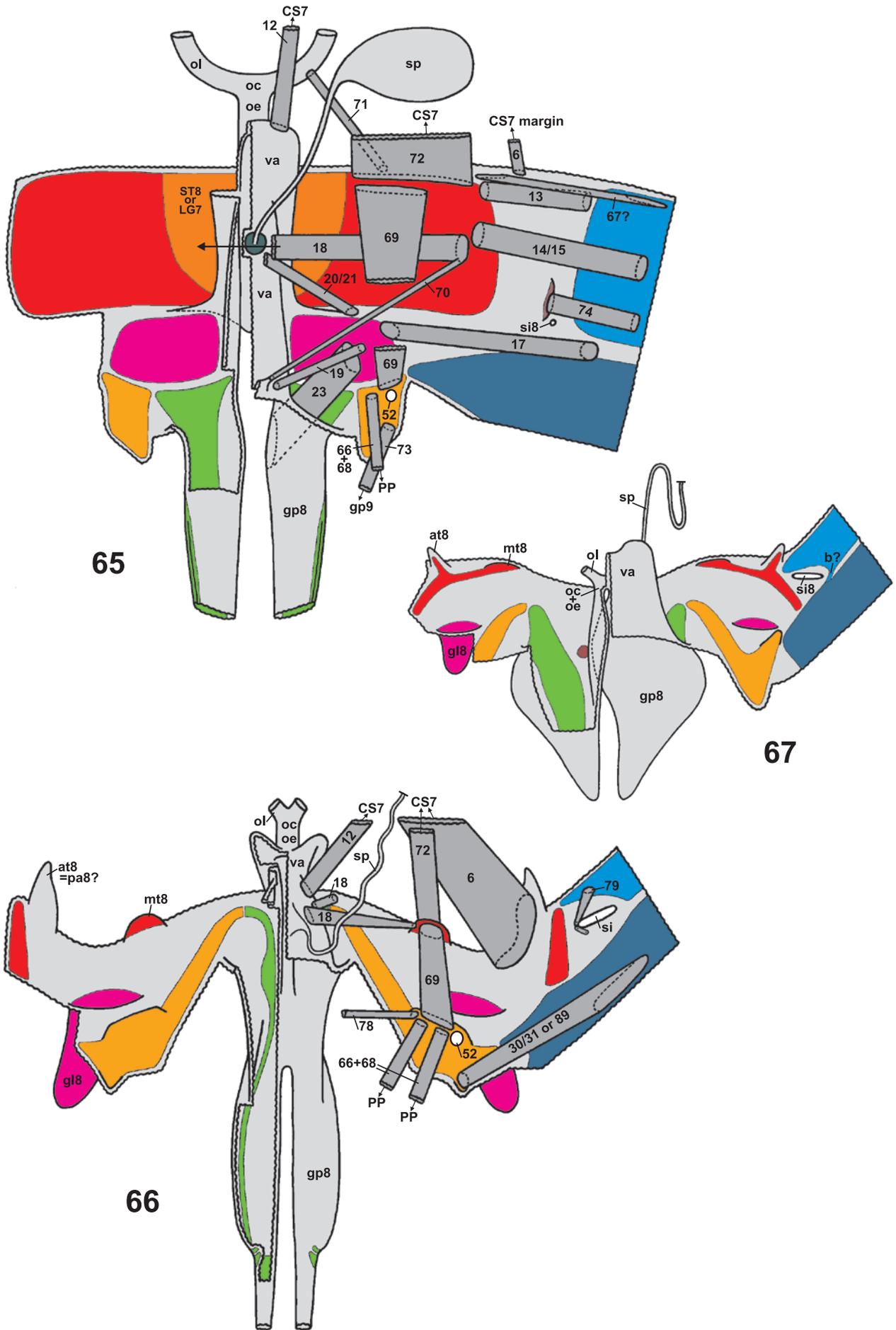


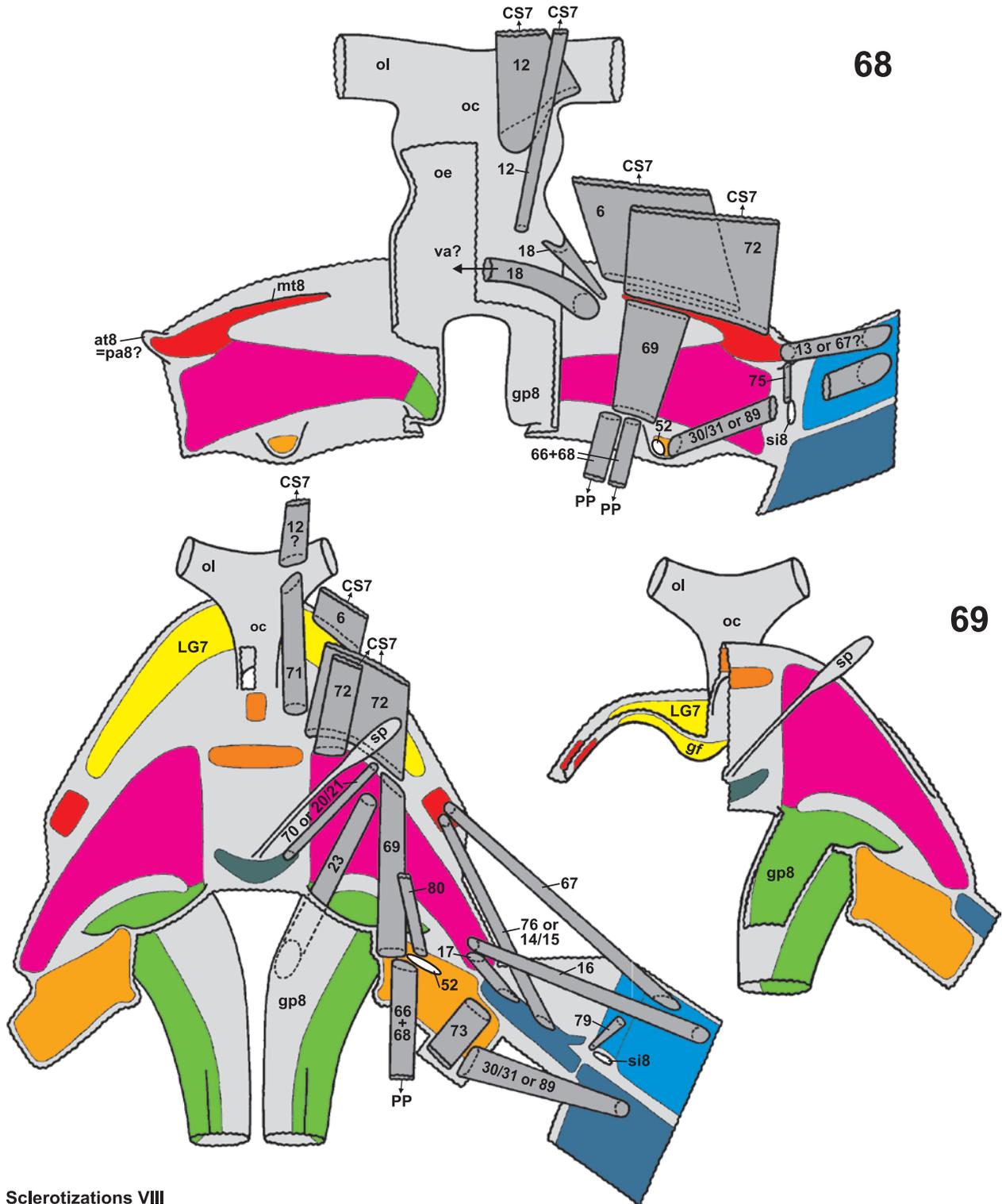
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- Sclerotizations VII**
- Sclerite of genital lobe – LG7
- Sclerotizations VIII**
- (Eu-)Sternal sclerites VIII – ST8
  - Laterocoxa VIII – LC8
  - Coxa VIII – CX8
  - Gonapophyseal sclerite VIII – GP8
  - Tergum VIII – TG8
  - Sclerites in vagina – VB
  - Sclerites in/around spermatheca – SP
  - Sclerites in pleural membrane
  - Other sclerites
- Sclerotizations IX**
- Laterocoxa IX – LC9
  - Tergum IX – TG9
- Other Elements**
- Membraneous cuticle
  - Muscles
  - Endoskeleton – ES



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**Sclerotizations VIII**

- (Eu-)Sternal sclerites VIII – ST8
- Laterocoxa VIII – LC8
- Coxa VIII – CX8
- Gonapophyseal sclerite VIII – GP8
- Tergum VIII – TG8
- Sclerites in vagina – VB
- Sclerites in/around spermatheca – SP
- Sclerites in pleural membrane
- Other sclerites

**Sclerotizations VII**

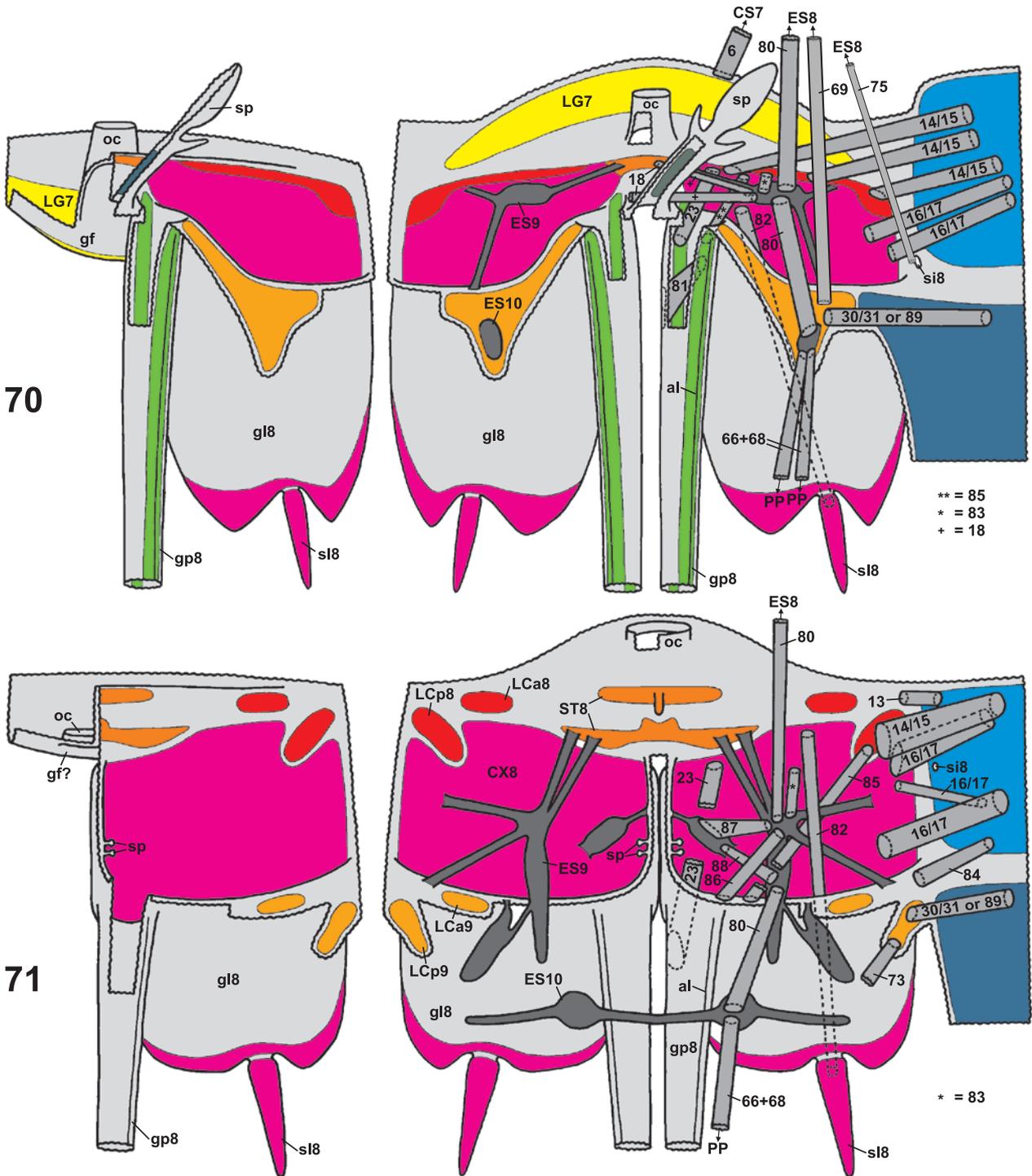
- Sclerite of genital lobe – LG7

**Sclerotizations IX**

- Laterocoxa IX – LC9
- Tergum IX – TG9

**Other Elements**

- Membraneous cuticle
- Muscles
- Endoskeleton – ES



\*\* = 85  
\* = 83  
+ = 18

\* = 83

- Sclerotizations VIII**
- (Eu-)Sternal sclerites VIII – ST8
  - Laterocoxa VIII – LC8
  - Coxa VIII – CX8
  - Gonapophyseal sclerite VIII – GP8
  - Tergum VIII – TG8
  - Sclerites in vagina – VB
  - Sclerites in/around spermatheca – SP
  - Sclerites in pleural membrane
  - Other sclerites

- Sclerotizations VII**
- Sclerite of genital lobe – LG7
- Sclerotizations IX**
- Laterocoxa IX – LC9
  - Tergum IX – TG9
- Other Elements**
- Membraneous cuticle
  - Muscles
  - Endoskeleton – ES

VIII bearing **LS8** strongly resembles the preceding venters, which also have a large, undivided ventral plate **CS** (compare Figs. 16 and 19); however, there are some additional sclerites in the posteriormost part of venter VIII (especially the paired **CX8**; Figs. 3, 4, 7, 63). The same is true for Caelifera and Notoptera (Figs. 64, 65), and also Mantophasmatodea (muscles unknown). One might thus suppose that plate **LS8** in Odonata, Caelifera, and Notoptera is homonomous with the midabdominal coxosterna **CS**, and that the paired sclerites **CX8** are possibly basal sclerotizations of the gonapophyses **gp8**, as it has been suggested by VAN DER WEELE (1906), ST. QUENTIN (1962: 166), SNODGRASS (1935a: 39), and WALKER (1943: 686). Accordingly, the **LS8** have usually been called ‘sterna’ like the ventral plates of the preceding segments, while the **CX8** have been referred to as the ‘basivalvulae’ (SNODGRASS 1935a: figs. 1, 4; WALKER 1943: fig. 5).

However, the musculature of the **CX8** suggests a different interpretation: the **CX8** represent the coxal sclerotization of their segment, and **CX8** plus **LS8** are homonomous with the pregenital coxosterna **CS**. In Archaeognatha the coxal (**CX8**) and the postlaterocoxal (**LCp8**) sclerites receive muscles from tergum **TG8** (**14/15** and **16/17** in Fig. 71; for muscle synonymy with the original description by BITSCH 1974a see Tab. 4), but the bases of the gonapophyses **gp8** do not; the latter receive muscles from the coxa **CX8** (**23** in Fig. 71). The same basic arrangement is true for the Zygentoma (muscles **14/15** and **16/17** resp. **23** in Fig. 70), though the fairly different arrangement of the lateral muscles and the fused ventral sclerotizations impede with homologizing elements in detail between Archaeognatha and Zygentoma. In Odonata both **LS8** and **CX8** receive muscles from tergum **TG8** (**13–15**, **67** resp. **16**, **17** in Fig. 63), and the gonapophyses **gp8** receive muscles from **CX8** (**23** in Fig. 63). The **CX8** are thus clearly coxae VIII (or at least parts of these). The same arguments hold for the identification of **CX8** as the coxae VIII in Notoptera (see muscles **13**, **67**, **14+15**, **17**, and **23** in Fig. 65).

In turn, the anterior plate **LS8** in Odonata and Notoptera, as it bears the anterior muscles from the tergum and is placed in front of the coxae **CX8**, likely includes the laterocoxal sclerotizations VIII; and as it extends through the median part of the venter it may also include sternal sclerotizations VIII (compare Figs. 63 and 65 with 71). The resulting identification of the plate as a laterocoxosternum **LS8** is supported by comparison with Dermaptera, for which the medially separated laterocoxae VIII **LC8** have been identified in KLASS (2001a, 2003). Like **LC8** in Dermaptera, **LS8** in Notoptera and teneral-adult Odonata gives origin to the internal ventral muscles anteriorly as well as to muscles targeting the vagina (or traversing the vagina; muscles **72**, **69** resp. **18** in Figs. 63, 65, 66,

68). In Odonata muscle **18** is inserted upon the vagina like in *Dacnodes*; the internal ventral muscles **72** and **69** degenerate during maturation (like the internal ventrals of the preceding segments; MATUSHKINA 2008a).

In sum, it appears as the most parsimonious hypothesis that in Odonata and Notoptera, as compared to Archaeognatha, the basic sclerites antelaterocoxa, postlaterocoxa, sternum, and intersternum have all become fused to form a laterocoxosternum **LS8**, and that only the coxae have remained discrete. Nonetheless, it is doubtful whether the (antero)median part of **LS8** is actually a ‘sternal’ component VIII (**ST8**) or perhaps a posterior VIIth-segmental sclerite (**LG7**); this topic will be discussed in 6.4.2.

That the separation between **CX8** and **LS8** in Odonata and Notoptera is homologous with the separation of **CX8** from the remaining sclerites in Archaeognatha is in accord with the musculature, but it requires that the anterior sclerites contained in **LS8** have become strongly lengthened, and that the coxae **CX8** have become strongly shortened (compare proportions in Figs. 63, 65, and 71). Nevertheless, the former requirement is consistent with the much shorter condition of the laterocoxae **LC8** in, e.g., the Dermaptera (i.e., for Notoptera and Odonata such a lengthening must be assumed anyway by comparison with dermapterans); the latter requirement is consistent with the strong reduction of the coxal lobes **gl8** in Odonata and Notoptera (and other Pterygota, as compared to Archaeognatha and Zygentoma), which are either only represented by very short folds along the hind margins of the coxae **CX8** (see **gl8** in Figs. 4, 9 for Odonata) or entirely absent.

In Acrididae venter VIII also has an unpaired anterior and paired posterior plates (Fig. 64), which are reasonably considered homologous with sclerites **LS8** and **CX8** of Odonata and Notoptera. Then, several tergo-laterocoxal muscles (**13**, **14/15** in Fig. 64) and the usual laterocoxal insertion of the internal ventral muscle VII (**72** in Fig. 64, compare Figs. 65, 66, 68) are present in Acrididae, but tergo-coxal muscles (like **16**, **17**) and coxo-gonapophyseal muscles (like **23**) are absent. Nevertheless, the two muscles labelled **16?** in Fig. 64 might represent a subdivided muscle **16** (compare Fig. 63) that has developed new insertions on the long gonangulum (**LC9**) apodeme that is peculiar to the Caelifera. This would be in agreement with the fact that muscles from tergum **TG8** to the gonangulum **LC9** and from the latter to a sclerite in front of the ventral base of the **gp8**, as constituted by the two muscles **16?** in Acrididae, are otherwise very unusual (see Figs. 63, 65, 66; yet, a muscle connecting **TG8** and **LC9** is found in Odonata and Archaeognatha: **84** in Figs. 63, 71). Furthermore, muscles **20+21** from **CX8** to the vagina (Figs. 63–65) also indicate **CX8** of Acrididae to be the homologue of coxa **CX8** of Odo-

**Tab. 4. Homology of muscles of abdominal segments VIII and IX in various Insecta.**

Muscles inserted on venter VIII, on the hind rim of venter VII, on the laterocoxa of venter IX, and on the gonoducts are categorized into ten groups. Within each group individual muscles are distinguished. Placement of muscles in the same line across columns indicates a homology hypothesis. The hypotheses are tentative because positional variation of muscles in some groups is strong, positional criteria are partly sparse (especially for the lateral muscles), and data on nerve supply are lacking for most of the taxa. The muscles here considered are shown in Figs. 63–71.

The muscle groups are: (1) Lateral muscles, with tergo-laterocoxals, tergo-coxals, and ‘tergo-epipleurals’, mostly intrasegmental but some intersegmental. ‘Epipleural’ is used in an informal way, comprising muscles with the ventral insertion lateral to the sclerotizations identified as coxal or laterocoxal, either on membrane or on isolated sclerites (tentatively considered epipleurites sensu DEUVE 2001). Tergo-endosternal muscles, occurring in Zygentoma and Archaeognatha, are not included but may constitute additional homologues of the muscles of the Pterygota here listed. — (2) Internal (inner) ventral muscles VII–IX including hyperneural muscles. The anagenetic relationships of these muscles between Archaeognatha and Zygentoma on the one side and Pterygota on the other are highly complicated, partly due to the location of insertions either on endosternites or on cuticle. The homologies here suggested are based on the discussions in KLASS (2000: 256, 2001a: 297ff); see remarks 4–7 below. — (3) External (outer) ventral muscles VII–IX including extrinsic gonapophyseal (= vesicular) muscles. In the mid-abdominal venters of Zygentoma and Archaeognatha the coxopodial sclerotizations give rise to muscles to the eversible vesicles and to the posterodorsal base of the coxal lobe. Mid-abdominal external ventrals in Pterygota (lacking the vesicles) may be derived from both these muscle groups. In segments VIII and IX the vesicles have become modified into the gonapophyses (BITSCH 1994), whose extrinsic muscles are thus vesicular muscles. Nevertheless, the detailed relationships between the various external ventral and extrinsic vesicular/gonapophyseal muscles are unknown. The mid-abdominal vesicular muscles can comprise median coxo-vesiculars and lateral laterocoxo-vesiculars (see e.g. BITSCH 1973: 61\* resp. 62\* in fig. 8), and the extrinsic gonapophyseal muscles likely fall into corresponding groups (see also BITSCH 1974a: 113). While the coxo-gonapophyseals are, if present, consistently attached to the gonapophysis base, this is usually not the case for the muscles here categorized as laterocoxo-gonapophyseals (exception: Zygentoma, 85 in Fig. 70). Of segment IX only the laterocoxo-gonapophyseals are here considered since only the laterocoxa is included (not the coxa). The muscles listed as ‘12’ are likely specialized parts of the external ventrals VII but are here grouped with the other muscles attached to the gonoducts. — (4) Intrinsic gonapophyseal muscles VIII, which have been reported only for Zygentoma. — (5) Muscles inserted on the gonoducts (a heterogeneous group). The muscles listed as ‘70’ and ‘77’ are here tentatively included though they insert behind the vaginal area. For taxa lacking a vagina (Dictyoptera, Zygentoma, Archaeognatha) the potentially homologous muscles are listed in the same lines; the insertions are not on a part of a vagina but assumedly upon a corresponding area. — (6) Transverse muscles. — (7) Spiracle muscles VIII, with only the dilators included (laterocoxal and tergal ones), but not the occlusors. Endosternal dilators (Zygentoma) are homologized with laterocoxal dilators (many Pterygota; see KLASS & KRISTENSEN 2001: 93\* and X\* in figs. 14, 15). — (8) Rectal muscles, with only the major ventral extrinsic rectal muscle included, which originates from postlaterocoxa IX. — (9) Stylus muscles, all coxo-stylar. — (10) Remaining endosternal muscles: muscles that have one

or both insertions upon an endosternite (ES in Figs. 71, 72) and cannot be assigned to any of the foregoing categories.

Column 1 gives the muscle number used herein for all taxa (see Figs. 63–71). Column 2 gives a descriptive name of the muscle or outlines its course by indicating the two insertions. In columns 3–10 the muscle numbers/terms used in the original treatments of the respective taxa are indicated. — Odon = Odonata: numbers from this paper, based on *Calopteryx virgo*, but muscle 67 of *Epiophlebia superstes* included (ASAHINA 1954); if muscles are absent in matured-adult Odonata but have been reported for teneral-adult *Anax imperator* (MATUSHKINA 2008a), this is indicated by terms in brackets. — Noto = Notoptera: numbers from WALKER’s (1943) study of *Grylloblatta campodeiformis*, but additional muscles found in own studies of *Grylloblatta campodeiformis* included as ++. — Cael = Caelifera: terms from SNODGRASS’ (1935a) study of *Dissosteira carolina* (all numbers) and FORD’s (1923) study of *Paratettix cucullatus* and *Melanoplus bivittatus* (only os6\* and ts7\*). — Pygi = Pygidicranidae (Dermaptera): numbers from KLASS’ (2003) study of *Dacnodes* sp. — Hemi = Hemimeridae (Dermaptera): numbers from KLASS’ (2001a) study of *Hemimerus vosseleri*. — Dict = Dictyoptera: terms from MCKITTRICK’s (1964) study of various Blattaria (but modified as in KLASS’ 1998 treatment of Dictyoptera) and KLASS’ (2000) study of male *Mastotermes darwiniensis* (only 14\*, 38\*, 76\*); data from these contributions were supplemented by own studies in *Ergaula capucina* (Polyphagidae), *Periplaneta americana* (Blattidae), and *Mantis religiosa* (Mantidae). Each occurring muscle has here been included if a potential homologue is present in another taxon, and in case of variation the likely plesiomorphic position of the insertion (as resulting from comparison with the other taxa) is shown in Fig. 69; newly found muscles are indicated as ++. — Zege = Zygentoma: numbers from ROUSSET (1973), based on *Thermobia domestica*, but muscle 6 (13\*) and posterior transverse portion of muscle 18 (*ulb*) of *Nicoletia* sp. included (*ulb* = unlabeled in ROUSSET 1973); the anterior portion of muscle 18 has been variously labeled 28\* or 29\* in ROUSSET (1973). — Arch = Archaeognatha: numbers from BITSCH’s (1973, 1974a) study of *Trigoniophthalmus alternatus*.

Symbols and abbreviations used (in addition to those listed in section 3.4.): ↔ = from...to...; --- = muscle not reported or clearly absent; ++number = muscle not previously reported but found in own studies (numbers arbitrarily assigned in sequence); + between muscle terms = two or more muscles together are considered the homologue of the muscle named in first column. // between muscle terms = an insertion has developed that transversely divided a forerunner muscle; muscles with *italicized name* have one or both insertions on endosternites; ant. = anterior; ins. = intersegmental; its. = intrasegmental; post. = posterior; pt = part of respective muscle; tv = traversing muscle.

Remarks: <sup>1</sup> The three anterior bundles of muscle 22\* of segment VIII in ROUSSET (1973: fig. 6) are grouped as tergo-laterocoxals, but 21\* and the posterior bundle of 22\* as tergo-coxals. — <sup>2</sup> Muscle 76 is peculiar by its insertion ventral to the spiracle level. The newly reported muscle ‘++6’ of Dictyoptera might belong here rather than being a muscle 14+15. — <sup>3</sup> Dorsal insertion likely shifted from TG9 to TG8 (see KLASS 2001a: 271 and compare Figs. 66 and 68). — <sup>4</sup> Probably the internal ventral muscle VII, 72, is represented in Zygentoma by part of muscle VI<sub>lm</sub>-11\* from E6\* to E7\* in ROUSSET (1973: fig. 7) and in Archaeognatha by part of muscle VII-5\* from endVI\* to endVII\* in BITSCH (1973: fig. 3) (E6\* = endVI\* = ES7, and E7\* = endVII\* = ES8; see KLASS 2001a: fig. 37 for different numbering systems); muscle 72 is not shown in Figs. 70, 71 and is, like ES8, located slightly anterior to all shown elements. — <sup>5</sup> The hyperneural muscle 80 is represented in Zygentoma and Archaeognatha by the remainder of the former muscles (not



nata and Notoptera. Like in fully mature Odonata the internal ventral muscles **69** are lacking in Acrididae.

In contrast to Odonata, Notoptera, and Caelifera, the anterior sclerotizations VIII in pygidicranid and hemimerid Dermaptera (KLASS 2001a, 2003) are very short, have the left and right laterocoxae **LC8** separated, and clearly lack median (potentially sternal) sclerotizations (Figs. 66–68). Whether the occasional subdivision of the laterocoxae (*Dacnodes*, Fig. 66) is homologous with that into ante- and postlaterocoxae in Archaeognatha (Fig. 71) is unclear (KLASS 2003: 203). Dictyoptera (Fig. 69) also have short left and right laterocoxae, but possible sternal sclerotizations (**ST8**, not **LG7**) have also been retained (KLASS 1998). *Zygentoma* (Fig. 70) show a fusion between all ventral sclerotizations VIII (formation of a coxosternum), with the anteromedian sternal part being present in *Thermobia* but not in *Nicoletia* (ROUSSET 1973). Since the insertions of the (coxo-?)gonapophyseal muscles (**23** in Fig. 70) are located far anteriorly on the coxosternum, the laterocoxal and sternal sclerotizations are likely very short as in Archaeognatha (compare Figs. 70 and 71).

Odonata, Caelifera, and Notoptera thus share a likely apomorphic transverse fusion of left and right laterocoxae VIII (with additional inclusion of sternum VIII **ST8** or a posterior VIIIth-segmental sclerotization **LG7** in the median part) into a laterocoxosternum (also found in *Thermobia*, Fig. 70), and they additionally share an apomorphic lengthening of these anterior sclerotizations, which is particularly prominent in Odonata. The same conditions may be present in some further neopteran taxa (e.g., Mantophasmatodea). In taxa with functional ovipositors used as egg channels, these transformations are surely dependent on a location of the genital opening on the hind part of segment VIII, because with a VIIIth-segmental opening the distance between it and the entrance into the egg channel (at the bases of the gonapophyses **gp8**) would be too long.

Additional evidence on the evolution of the anterior ventral sclerotizations VIII in Pterygota may come from BECHLY et al.'s (2001: fig. 5) reconstruction of the Carboniferous odonatopteran *Erasipteroides valentini*. In this taxon venter VIII is very short, with only one (paired?) plate **GCXVIII\***. Judging from its relation to laterocoxa **LC9** (gonangulum **GA\***) and to the base of the gonapophysis **GAPVIII\***, this plate surely includes coxa **CX8**. Hence, the **LS8**-parts are either fused with the **CX8** or are restricted to the anterior margin of venter VIII, where they are covered by the expanded hind margin of venter VII (this either being a genital fold VII **gf**, see Figs. 69, 70, or the expanded hind part of coxosternum VII). Whatever is true, **LS8** seems to be much shorter than in Odonata, and, if this part of the fossil has been reconstructed correctly, this would in-

dicate homoplasies in the lengthening of **LS8** in the respective Pterygota.

#### 6.4.2. Alternative interpretations

As mentioned above, with regard to the taxa having an VIIIth-segmental genital opening, there are several competing interpretations for the (antero)median part of sclerite **LS8** (and for the corresponding membranous area in taxa with medially separate **LC8**). The matter depends on the mode in which the extended oviduct has formed during evolution; this can be discussed based on the mode in which the extended oviduct forms during ontogeny (as mentioned in section 6.3.1.), but one must keep in mind the great plasticity of this process, which surely cannot in each case be considered to reflect the evolutionary transformation of structure.

(1) This area could be the (eu)sternum VIII **ST8** and thus a true part of venter VIII, as implied in the foregoing section and by the orange colour in Figs. 63–65 (compare **ST8** in Fig. 71). This interpretation requires that the median part of venter VIII has not been overgrown during the evolutionary formation of the extended oviduct (as reflected by the type of ontogenetic formation as reported for Odonata and some other taxa).

(2) This area could represent mesal parts of the coxae VIII **CX8**. This would correspond with an evolutionary formation of the extended oviduct by a median fusion of the mesal edges of the coxal lobes VIII (as reflected by the ontogenetic formation of a groove on venter VIII, and its eventual median closure, as reported for *Philaenus leucophthalmus* and Caelifera).

(3) Alternatively, this area could indeed be VIIIth-segmental, corresponding with the ventral wall of the genital lobe **gf** and its sclerite **LG7** of the taxa having a VIIIth-segmental genital opening – as implied by the label '**LG7**' in Figs. 63–65 (compare **LG7** in 69–71). This would correspond with an evolutionary formation of the extended oviduct by a posterior growth of a **gf**-lobe of venter VII and the fusion of its lateral edges to venter VIII (as reflected by the ontogenetic development of such a lobe in the phasmid *Carausius*).

With the alternatives (2) and (3), the sternal area VIII would be displaced into the dorsal and lateral walls of the extended oviduct. Therefore, internalized parts of sternum VIII are legitimately searched for within the gonoduct walls internal to the opening of the spermatheca. While an identification of the (antero)median part of sclerite **LS8** as sclerotization **LG7** might appear most plausible (due to the potential secondary re-appearance of genital lobe **gf**, see 6.3.1.), the matter remains ambiguous. Unfortunately, the sternum and intersternum in Archaeognatha (**ST8**-scler-

ites in Fig. 71) bear no muscle insertions that could provide further criteria for tracing the true sternal sclerites (or area) in other insects.

DEUVE (2001: figs. 29–31) suggests another interpretation of sclerite **LS8** in Odonata, Notoptera, and Caelifera, regarding it as the medially fused epipleurites VIII. This interpretation, however, faces many problems. In the framework of DEUVE's (2001: e.g., figs. 23–25) hypothesis the epipleurite and the coxosternum in the insect abdomen are mutually exclusive areas. Thus, the ventral plates VII (**CS7**) and VIII (**LS8**) in DEUVE's (2001) fig. 31 of a zygopteran, which are interpreted as a coxosternum VII (**cxstVII\***) resp. medially fused epipleurites VIII (**epIVIII\***), are considered exclusively non-homonomous. This is strongly contradicted by the musculature, since **LS8** closely resembles **CS4–7** in all of its muscle insertions (also considering those reported for teneral *Anax* females by MATUSHKINA 2008a; compare Figs. 16 and 19). DEUVE's interpretation is thus highly unparsimonious, because it would demand a complete rearrangement of the lateral and ventral muscles in segment VIII.

#### 6.4.3. Venter VIII characters in Odonata

Using the above homology hypotheses of sclerites **LS8** (or their subsets) and **CX8** (Figs. 63–71), the posterior laterocoxal apodemes **ba8** and the coxal apodemes **ga** and coxal tendons **gt** occur only in Odonata (compare Figs. 7, 63 and 64–71). Regarding apodemes **ba8**, absence should thus be plesiomorphic within Odonata (see character 10). Apodeme **ga** and tendon **gt** have been found in all Odonata here studied and are thus likely autapomorphies of this taxon; characters 12 and 13 of the location of **gt** and the mesal extension of **ga** are not applicable to the outgroup taxa.

The anterior laterocoxal apodemes in Odonata (**pa8** in Fig. 63), Acrididae (**pa8** in Fig. 64), and Dermaptera (**at8\*** in Figs. 66–68) are positionally identical: they bear the insertions of a muscle from the anteroventral corner of tergum **TG8** and of the ventral diaphragm in Odonata and Acrididae (**13** and **9** in Figs. 63, 64), and the insertion of a coxosternal spiracle dilator in Acrididae and *Hemimerus* (**75** in Figs. 64, 68; muscle absent in Odonata). The internal ventral muscles VII (**72**) and VIII (**69**) are variously inserted on the apodemes or median to these (on apodeme **mt8** in *Dacnodes*); however, this inconsistency could be due to the variable width of these muscles as demonstrated by comparing muscles **72** in Figs. 66 (*Dacnodes*) and 68 (*Hemimerus*). Altogether, homology of apodemes **pa8** in Odonata, Caelifera, and Dermaptera (= **at8\***) appears conceivable.

A mediocaudal process of **LS8**, like **pp8** of *Epiophlebia* (see character 11), is also found in some Acrididae

(SNODGRASS 1935a: egg guide **eg\*** in fig. 20A), but since this is likely a specialization within the Caelifera, the outgroup is here scored 'absent', and **pp8** appears as an autapomorphy of *Epiophlebia*.

The two coxae **CX8** are in all outgroup taxa here considered (Figs. 64–71) fully separated medially, and their median fusion thus appears as autapomorphic for *Lestes* (see character 14 and Fig. 32).

A sclerite that like **MS** is located at the anterior end of the cleft between the gonapophyses **gp8** (Figs. 26, 27, 32, 33) has apparently been reported only for few pygidicranid Dermaptera (KLASS 2003: fig. 23). **MS** is thus tentatively considered absent in the outgroup, and characters 17 and 18 of the size of **MS** and of its fusion with sclerites **GP8** in Odonata are regarded as inapplicable to the outgroup. Due to its far posterior position on venter VIII **MS** in Odonata is unlikely to be a sternal element VIII.

### 6.5. Ventral sclerotizations IX and their muscles

#### 6.5.1. Basic ventral sclerotizations IX

The sclerotizations of venter IX in ovipositor-bearing Insecta show much variation, but this is less extensive than for venter VIII. In contrast to venter VIII, sternal sclerotizations (see Figs. 63–65, 69–71) are absent in Archaeognatha, Zygentoma, Odonata, and probably all Neoptera. According to BITSCH (1973a), in Archaeognatha separate coxae (**CX9**; 'coxite'), postlaterocoxae (**LCp9** in Fig. 71; 'laterocoxite'), and antelaterocoxae (**LCa9** in Fig. 71; 'precoxite' in BITSCH) are present (see also KLASS 2003: fig. 64), which thus constitute the basic sclerotizations of venter IX; gonapophyseal sclerites (**GP9**) are not clearly reported. In the coxae IX the Archaeognatha show a modification as compared to the preceding segments: small antero-medial parts (those bearing the coxo-gonapophyseal muscles; compare **23** in Fig. 71) have segregated and fused medially to form a sternum-like sclerite (**scS\*** in BITSCH 1974a: fig. 6). Since this modification is absent in Zygentoma and Pterygota (where similar but non-homologous modifications occur in some groups: KLASS 2003: 203ff), it is not considered as part of the basic pattern.

In Zygentoma and Pterygota ante- and postlaterocoxae are usually fused to form a one-piece laterocoxa IX (gonangulum **LC9**; Fig. 70), and rarely the laterocoxae IX and coxae IX are additionally fused (as in the zygentoman *Nicoletia*; ROUSSET 1973: 71). Furthermore, several additional sclerites can be present on the posterior part of venter IX, such as the median sclerites **CA**, **PS9**, and **IT9** in *Calopteryx* (Fig. 7).

In the following, laterocoxae IX, coxae IX, and supplementary posterior sclerotizations of segment IX are discussed separately (laterocoxae IX and their muscles included in Figs. 63–71 and Tab. 4).

### 6.5.2. Identification and variation of laterocoxae IX (gonangulum)

The gonangulum (**LC9**) has played a major role in establishing a monophyletic clade Dicondylia (= Zygentoma + Pterygota; SCUDDER 1961a,b; HENNIG 1969: 106). SCUDDER's (1961b: 26) term 'gonangulum' means a paired one-piece sclerite that lies anterolaterally upon venter IX and articulates with the anterolateral corner of tergum **TG9**, with the lateral margin of coxa **CX9**, and with the basal sclerotization of gonapophysis **gp8** (i.e., with **GP8**). Furthermore, the anterior margin of the gonangulum is often in contact with the hind margin of coxa **CX8** (SCUDDER 1961b: **Ga\*** and **1Gx\*** in figs. 2, 5) and occasionally articulates upon it (e.g., in Mantodea; KLASS 1998: **A4\*** in fig. 11).

BITSCH (1974a: 115, 118, fig. 1b) reported for Archaeognatha a small sclerite ('laterocoxite IX' = post-laterocoxa IX **LCp9** in Fig. 71) that corresponds with the posterior part of the dicondylial gonangulum in its position and articulation upon tergum **TG9** and coxa **CX9**, and which he therefore considered a gonangulum precursor. Consequently, a one-piece gonangulum that extends anteriorly to articulate additionally with **GP8** and to approach **CX8** has then been regarded as autapomorphic for the Dicondylia (KRISTENSEN 1991: 130). Such a gonangulum is actually present in Zygentoma (Fig. 70; ROUSSET 1973: **ga\*** in figs. 3, 9) and most ovipositor-bearing Pterygota (Figs. 65, 66, 67, 69; SCUDDER 1961b; latero(gono)coxa IX in KLASS 1998, 2003). It has been explicitly described also for an *Aeshna* (SCUDDER 1961b: 32, fig. 6), but the structure and articulations of the area are not depicted very clearly.

KLASS (2003: 202), however, claimed that in Archaeognatha (according to the data in BITSCH 1974a) the gonangulum is actually represented by two precursor sclerites: the 'laterocoxite IX' and the 'precoxite IX' (**LCp9** and **LCa9** in Fig. 71), the latter being located in the area over which the sclerite had been considered to expand only in Dicondylia. KLASS (2003: 202) furthermore claimed a similar two-sclerite condition for ovipositor-bearing Odonata (except for *Epiophlebia*, and according to own data), which thus lack a one-piece gonangulum. MATUSHKINA (2008a), who studied the relevant sclerotizations in nymphal, teneral-adult, and mature-adult *Anax* (Aeshnidae) arrived at the same conclusion. Due to its great phylogenetic importance, this issue will here be discussed in some detail.

The maximum set of criteria for identifying laterocoxa **LC9** is discussed in KLASS (2003: 198ff). Apart from the abovementioned articulations with **TG9**, **CX9**, and **GP8** and its position immediately behind **CX8**, **LC9** bears the insertions of the ventral major extrinsic rectal muscles and internal ventral muscles VIII and IX (muscles **52**, **69**, **66+68** in Figs. 64, 66, 69, 70), it furthermore receives tergo-laterocoxal muscles from **TG9** (**30/31** or **89** in Figs. 64, 66, 69, 70), and it bears some characteristic internal ridges between the articulations. (Of course, in many taxa some of the respective characteristics have become reduced or lost.) In the Odonata here studied the sclerites homologous with the gonangulum are easily identified by these criteria (Fig. 63; compare Figs. 65, 66–70).

(1) A posterior sclerite **LCp9** fully complies with the posterior part of the dicondylial gonangulum and with the postlaterocoxa IX in Archaeognatha in articulating with the anterolateral corner of **TG9** and the lateral margin of coxa **CX9**, and in bearing a ridge in between these articulations (Figs. 4, 7, 26, 27, 32, 33, 38, 39–41; BITSCH 1974a: laterocoxite **lax\*** in fig. 1B, with ridge; KLASS 1998: gonangulum in figs. 11, 12, 14, 15, 16, with ridge connecting articulations **A1\*** and **A2\***; KLASS 2003: figs. 10, 23, 27, 32, 36, 41, 46, 52). **LCp9** is furthermore identified as a part of the gonangulum by the insertion of the ventral rectal muscle **52** (Figs. 19, 63). MATUSHKINA (2008a: fig. 5D), for teneral *Anax*, furthermore reports the insertion of one internal ventral muscle IX to be located on **LCp9** (muscle **vra\*** on 'elongated sclerite' = muscle **66** in Fig. 63) – the homologue of (part of) muscles **66+68** inserted on the gonangulum in the taxa shown in Figs. 65–70. In addition, she also found the insertions of tergo-laterocoxal muscles on that sclerite (**dvm\*** and **dvp\*** in fig. 5B therein), of which only degenerated strands were found in *Calopteryx* (**30** and **31** in Figs. 19, 63).

(2) An anterior sclerite **LCa9** complies with the anterior part of the dicondylial gonangulum in articulating with the anterolateral corner of **TG9** and with the basis of the gonapophyseal sclerite **GP8** (at **h** resp. **e** in Figs. 4, 9, 26, 27), in bearing an internal ridge in between these articulations (likely a ventral part of antecosta **ac9**; Figs. 26, 27; KLASS 1998: gonangulum in figs. 11, 12, 14, 15, 16, with ridge connecting articulations **A1\*** and **A3\***; KLASS 2003: figs. 10, 23, 27, 32, 36, 41, 46, 52), and in lying immediately behind coxa **CX8**. **LCa9** is furthermore identified as a part of the gonangulum by several typical muscle insertions that in Odonata are only found in teneral females (MATUSHKINA 2008a: fig. 5D; see Fig. 63): Muscle **68** (**vad\***) is another bundle of the internal ventral muscle IX (**66+68** in other taxa, Figs. 65–70); muscle **69** (**pls\***) represents the internal ventral muscle VIII; muscle **89** (**dva\***) is a typical tergo-laterocoxal. The intersegmen-

tal tergo-laterocoxal muscle **84** (**dvo**'\*) is not found in the other Dicondylia illustrated herein, but it could be homologous with muscle **84** of Archaeognatha (Fig. 71), which is attached to membrane near the **LC**-sclerites (and perhaps to the anterior muscle **16**? of Caelifera, Fig. 64; see above). A muscle of the dermapteran *Hemimerus* (**30/31** or **89** in Fig. 68) is another potential homologue, but is more likely a shifted intrasegmental tergo-laterocoxal muscle IX (homologous with muscle **30/31** or **89** in Fig. 66 of *Dacnodes*; see KLASS 2003: 271). Furthermore, **LCa9** appears homologous with the antelaterocoxa IX in Archaeognatha (Fig. 71; BITTSCH 1974a: precoxite **precx**\* in fig. 1B), which takes the same position in between tergum IX and the gonapophysis VIII basis, but reaches neither of these elements and is very weak. This sclerite in Archaeognatha lacks muscle insertions (Figs. 63, 71): As compared to Odonata, the attachment of the internal ventral muscles IX (**66+68** in Fig. 71) is still on an endosternite **ES10**, which in addition is still far remote from the gonangulum (but **ES10** is seated on the gonangulum in *Zygentoma*, Fig. 70); the attachment of the abovementioned muscle **84** is on membrane; and homologues of both muscles **69** (see Tab. 4 and its legend, remark 6) and **89** are absent.

In sum, the entire articulations or other contacts, the ridges, and the musculature of the odonatan **LCa9** and **LCp9** together are all typical of a gonangulum.

All Odonata here studied, with the sole exception of *Epiophlebia* (but including *Aeshna*), show one important feature in which they differ from other Dicondylia and from SCUDDER's description of *Aeshna*, but in which they resemble Archaeognatha: Like the 'laterocoxite' and 'precoxite' in Archaeognatha (**LCp9** and **LCa9** in Fig. 71), but in contrast to the two portions of the dicondylia one-piece gonangulum, **LCp9** and **LCa9** are entirely separated from each other (Figs. 26, 27, 32, 33). Both parts, however, can be extensively synsclerotic with tergum **TG9** (such as in *Aeshna*, Fig. 27), and this may have misled SCUDDER to ascribing a one-piece gonangulum to *Aeshna*. As mentioned above, PFAU's (1991: fig. 20A,B) illustrations indicate the same separation for the aeshnid *Anax*, and MATUSHKINA (2008a) explicitly states it for that taxon. The division between **LCp9** and **LCa9** may be, as it is present in Archaeognatha, all Zygoptera, and Aeshnidae among Anisoptera + Anisozygoptera, a groundplan condition of Odonata and possibly of Pterygota. Gonangula divided in a similar manner are also present in some (but not all) of those Pygidicranidae that show the most plesiomorphic condition of the ovipositor within the Dermaptera (KLASS 2003: fig. 27).

On the other hand, in *Epiophlebia* (Fig. 36) **LCp9** extends further anteromesad than in the other Odonata, and most of its anterior margin is fused with the

lateral portion of **LCa9**; a one-piece gonangulum is thus present. *Epiophlebia* shows, in addition, a fusion between **LCa9** and coxa VIII **CX8** that is much more extensive than in all other Odonata examined herein. Both fusions also occur in lineages of Anisoptera that show a modified structure of the female genitalia. For the moderately modified ovipositor of *Petalura* (Anisoptera: Petaluridae), fused **LCa9** and **LCp9** are indicated by an illustration in PFAU (1991: **Vf1**\* in fig. 22); as shown by the attachments of muscles **1**\* and **3**\* therein, this compound sclerite additionally includes **CX8** (see muscles **16** and **17** in Figs. 19, 63; compare figs. 20a and 22 in PFAU; in PFAU's illustrations of *Anax* **CX8** is the plate-like anterior sclerite of **Vf1**\*). In *Cordulegaster* (Anisoptera: Cordulegasteridae), with the ovipositor modified more strongly than in *Petalura*, PFAU's (1991: fig. 21) sclerite **Vf1**\* is the vestige of the gonangulum. According to my own studies this is a narrow ribbon extending from the anterior lateral margin of **TG9** to near the gonapophysis **gp9** basis. As it has no contact with **CX8** and **GP8**, it may be the postlaterocoxa **LCp9** alone; however, a short, very weak extension directed towards **CX8** may be a vestigial anterolaterocoxal **LCa9**-portion, fused to **LCp9**. Fusions between **LCa9**, **LCp9**, and partly **CX8** could thus be autapomorphic for subgroups of Anisoptera. Alternatively, since a one-piece gonangulum is present in (all?) *Zygentoma*, *Epiophlebia*, and Petaluridae, the traditional assumption that this condition was present in the ground-plans of Odonata, Pterygota, and Dicondylia still appears as a sound alternative to the hypothesis that in the ground-plans of all these taxa the 'gonangulum' was still bipartite.

Although the gonangula (**LCp9** + **LCa9**) in Archaeognatha and most Odonata show the same bipartition, they also differ in some important aspects, namely by the presence in the Odonata of close contacts of **LCa9** with the neighboring sclerites **TG9**, **GP8**, and **CX8**, as well as by a much heavier condition of **LCa9** in Odonata (compare Figs. 63 and 71). What about these characters in other Dicondylia? The contact with **TG9** in the bipartite gonangulum of the respective Pygidicranidae is established by **LCp9**, while **LCa9** lacks a contact with **TG9**; in taxa with one-piece gonangula (**LC9**) the contact with **TG9** may well correspond to that established in Archaeognatha, Odonata, and Pygidicranidae by the **LCp9**. The contact with **CX8** appears in *Zygentoma* and some Neoptera (e.g., many Pygidicranidae) not closer than in Archaeognatha. The contact with **GP8** and also the heavy condition of the **LCa9**-part, however, are differences to Archaeognatha that besides in Odonata are rather consistently present in *Zygentoma* and ovipositor-bearing Neoptera.

### 6.5.3. Laterocoxa IX characters and the principal lineages of Insecta

Which potential autapomorphies of principal insect lineages are inherent in gonangulum morphology after these revisions? Regarding the heaviness of **LCa9** and its close contact with **GP8** it is difficult to tell whether these are apomorphic for Dicondylia or plesiomorphic within Insecta (then lost in Archaeognatha) – mainly because no ovipositor-bearing outgroup exists. The small, weak, and non-articulated condition in Archaeognatha of both antelaterocoxae VIII and IX (BITSCH 1974a: **prex\*** in fig. 1A,B; **LCa8** and **LCa9** in Fig. 71) may, since homonomous elements are here similar, indicate the weakness of the sclerite and the lack of the **GP8**-contact as plesiomorphic. However, this argument is weak because in all Insecta only antelaterocoxa IX **LCa9** has a gonapophysis base (**GP8**) to articulate with, but not antelaterocoxa VIII **LCa8**.

Thus, only a fusion of **LCa9** and **LCp9** may still be regarded as an autapomorphy of the Dicondylia, with a reversal having occurred in the Odonata, but the alternative that the fusion has been acquired several times within the Dicondylia appears as parsimonious.

The former hypothesis receives support from the report of one-piece gonangula in Carboniferous Palaeodictyopteroidea (e.g., KUKALOVÁ-PECK 1992: figs. 27–37) and Odonoptera (BECHLY et al. 2001: fig. 5), though one might doubt whether the structure in these fossils can be observed in sufficient detail (compare discussion in 5.4.3. of stripe **h** and the surrounding internal membrane, which in many Odonata are needed for delimiting **LCa9**; Figs. 26, 27).

In contrast, the latter hypothesis may be supported as there is possibly a mechanism leading to a frequent homoplastic formation of a one-piece gonangulum. In *Zygentoma* (HEYMONS 1897: fig. 9; SAHRHAGE 1953: fig. 21c) and in at least some ovipositor-bearing Pterygota as well (e.g., NAGASHIMA 1991: fig. 3; GUPTA 1948: fig. 9; VAN DER WEELE 1906: 140; SCUDDER 1964: figs. 1, 2), and hence probably in the ground plan of the Dicondylia, female venters VIII and IX in young nymphs each bear a single undifferentiated plate, which appears fully homonomous with the coxosterna of the preceding segments, and which during development segregates into the sclerites present in the adult (coxae, laterocoxae, and occasionally a sternum). This is also true for Odonata, as shown by MATUSHKINA (2008a) for *Anax*. It has been proposed in KLASS (2001a: 269) that the presence of undifferentiated or only medially divided coxosterna VIII and IX in many adult Pterygota with a reduced ovipositor (e.g., many ‘higher’ Dermaptera, Embioptera, and Plecoptera) is due to paedomorphosis, i.e., to a retention of the nymphal condition. An abandoning of a segregation into

**LCa9** and **LCp9**, and thus the constitution of a one-piece gonangulum, could be an early step in such a paedomorphic character evolution. As it is true for the advanced paedomorphosis of female venters VIII and IX, also such an initial paedomorphic transformation could bear a high potential of homoplasy. This hypothesis would be supported if in the nymphal development or imaginal maturation of Odonata and Archaeognatha the **LCa9** and **LCp9** are separated very late; unfortunately, however, nothing seems to be known about the timing of these developmental steps.

It should further be noted that the additional fusion between the gonangulum and (subsets of) coxa **CX8**, as found in *Epiophlebia* (Fig. 36) and *Petalura* (see above), has occurred independently in several pterygotan lineages (see in 6.5.4.).

### 6.5.4. Laterocoxa IX characters in Odonata

According to the above discussions the outgroup evidence concerning a separation or connection between **LCa9** and **LCp9**, and the extension of **LCp9** to the anterior (characters 39, 41) is considered ambiguous.

With regard to the relations between **LCa9** and **TG9** and between **LCp9** and **TG9** (character 40), Archaeognatha, *Zygentoma*, and most subgroups of the Neoptera show a clear separation. The various fusions found within the Odonata (Figs. 27, 32, 36) appear thus as apomorphies. Nonetheless, tergal-gonangular fusions are also present in many Acercaria and Emdopterygota (MICKOLEIT 1973; KRISTENSEN 1991: 135, 137), and in *Polyphaga* among the Dictyoptera (KLASS 1998: fig. 16a).

For the relation between **LCa9** (or **LC9**) and **CX8** (see character 15) ‘separated’ (which includes the absence of an articulation) is here tentatively scored for the outgroup. A fusion between **LCa9** and **CX8**, as found in *Epiophlebia* and *Petalura*, is absent in Archaeognatha, *Zygentoma*, Pygidicranidae, Notoptera, and Caelifera (Figs. 64–71), and in most Dictyoptera (KLASS 1998: figs. 11, 12, 14, 15, 17, 18), where separation is the plesiomorphic condition. The connection is present, however, in some Dictyoptera (KLASS 1998: figs. 13, 16) and many Ensifera (see KLASS 1998: connection between **gg\*** and **vf\*** in fig. 26). A discrete articulation between **LCa9** and **CX8**, as present in many Zygoptera, has apparently been reported only for Mantodea (KLASS 1998: **A4\*** in fig. 11), where, however, the condyle is located on **LC9**, not on **CX8** as in Odonata (**d** in Fig. 26).

A spiny projection **sa** on the **LCa9**-portion of the gonangulum (Fig. 36; character 38) is not reported from any of the outgroup taxa here considered and is thus likely apomorphic for *Epiophlebia* (and possibly *Diphlebia*).

The articulation **LCp9-CXa9** (character 48; Figs. 4, 7, 39) is, as related to the base of apodeme **la**, located far anteriorly in Aeshnidae (Fig. 40) and also Petaluridae (PFAU 1991: fig. 22) but far posteriorly in *Epiophlebia* (Fig. 41) and in all Zygoptera (Fig. 39). As in Aeshnidae, in, e.g., the phasmid *Timema* (TILGNER et al. 1999: fig. 30), Archaeognatha (BITSCH 1974a: fig. 1B), and some Zygentoma (ROUSSET 1973: fig. 3) **LCp9** or **LC9** articulates upon the anterior part of coxa **CX9** (in other Zygentoma **LC9** extends farther posteriorly, but instead of being articulated upon **CX9**, **LC9** is likely fused with **CX9**; ROUSSET 1973: 71, fig. 9). In many other Neoptera character 48 is difficult to assess due to modified proportions: **CX9** shortened in, e.g., Ensifera and Dictyoptera; anterior part of **CX9** reduced and shifted in Pygidicranidae (see KLASS 2003). Reconstructions of female genitalia in the diaphanopterodean *Uralia* (KUKALOVÁ-PECK 1992: figs. 27–39) are particularly interesting since some elements around the gonoplac base closely resemble those in Odonata: shape and arrangement of **LCp9**, gonoplacs **gl9**, apodeme **la**, and gonapophyses **gp9**; the muscle strands shown in fig. 27 therein resemble parts of the tergo-coxal muscles **28** and **29** in *Calopteryx* (Fig. 19). Also in *Uralia* the articulation **LCp9-CXa9** is in a position as in the Aeshnidae. Thus, altogether the posterior position of the articulation as found in Zygoptera and *Epiophlebia* can tentatively be considered apomorphic.

#### 6.5.5. Identification and variation of coxae IX and gonoplacs IX

Like the laterocoxae **LC9**, the coxae **CX9** also bear a great potential for analysing the phylogenetic relationships among the principal lineages of Insecta and Pterygota. The identification of **CX9**-sclerotizations, the major variations in Insecta, and some phylogenetic implications are discussed in KLASS (2003: 203ff). The main characteristics for identifying coxae **CX9** as compared to Archaeognatha and Zygentoma are a lateral articulation with laterocoxa **LCp9**, an anteromedian contact with the basal sclerotization of gonapophysis **gp9** (i.e., with **GP9**), the insertion of muscles from tergum **TG9** (tergo-coxal muscles) and to gonapophysis **gp9** (coxo-gonapophyseal muscles), and the location of much of their sclerotization upon lobes (coxal lobes = gonoplacs **gl9**). The presence of small, articulated distal projections (styli **sl9**) upon these lobes is a criterion for their identification as the gonoplacs.

All these characteristics apply to the sclerotizations **CX9** in Odonata, which beside the large sclerite **CXa9** also include the small sclerites **CXb9** and **CXc9** (Figs. 4, 5, 7, 39–41).

The gonoplacs **gl9** in Odonata and the slender styli **sl9** situated upon them resemble those in Archaeognatha and Zygentoma (Fig. 4; GUSTAFSON 1950; for the occurrence of styli **sl9** in a few other extant adult Pterygota see KLASS 2003: 207, and for occurrence in Hymenoptera see VILHELMESEN 2000). In the Odonata, however, the bases of the gonoplacs are more explicitly longitudinally orientated than in Archaeognatha and Zygentoma, and they show thus an orientation more suitable to ensheath the two pairs of gonapophyses, **gp8** and **gp9** (Fig. 4).

Of the characteristic articulations of **CX9**, the one with **LCp9** has been discussed in section 6.5.2. For the articulation with **GP9**, which in both Zygentoma and Odonata is mediated by the anteromesal tip of **CX9**, compare Fig. 4 (left side) and KLASS (2003: e.g., figs. 23, 46, 63) (see below for Archaeognatha).

In Archaeognatha, Zygentoma, and Odonata the **CX9** receive muscles from tergum **TG9** (see KLASS 2001a: fig. 28 and ROUSSET 1973: figs. 6, 7 for muscles in *Thermobia*): the very heavy muscles **28** and **29** in Odonata (Fig. 19) show positional correspondence with muscles **21\*** and **22\*** in *Thermobia*.

In both Zygentoma and Odonata the gonapophyseal muscles are inserted on **CX9** (on **CXa9** in Odonata; on segregated coxal sclerite in Archaeognatha: see 6.5.1., and muscle **71\*** and sclerite **scS\*** in BITSCH 1974a: fig. 6); among these, muscle **33** in Odonata has, though it is much broader, the same position as muscle **51\*** in *Thermobia*.

Muscles **32** and **34** of Odonata show the same mesal insertions as **32\*** and **31\***, respectively, of *Thermobia*: in the wide midline membrane between the **CX9**, distinctly behind the **gp9**-bases in case of **32/32\***, and at the ventral **gp9**-base and near the accessory gland openings in case of **34/31\*** (which may, like muscle **33**, be considered gonapophyseal muscles). However, the lateral insertions of both muscles lie on the **CX9** in Odonata, whereas in *Thermobia* they are located on the small endosternite that is fixed to the gonangulum **LC9** (see **ES10** in Fig. 70). Due to the general similarity of the musculature of this area between Odonata and *Thermobia*, it is here assumed that muscles **32** and **34** have obtained coxal insertions in Odonata after the loss of the endosternite. This, however, is a peculiarity of Odonata, since gonangular insertions of corresponding muscles are also found among, at least, Auchenorrhyncha and Hymenoptera (muscles **26\*** in KLASS 2003: figs. 77, 78). The two latter taxa thus resemble Zygentoma more closely in this aspect.

A homologue of the coxal transverse muscle **35** in Odonata is also present in *Thermobia* (**33\*** in ROUSSET 1973: 68, fig. 7 and in KLASS 2001a: fig. 28). Such a muscle has been found also in the pygidicranid *Dacnodes* (KLASS 2003: muscle **16\*** in fig. 22) and, with some doubt in terms of its homology, in *Hemimerus*

(34\* in KLASS 2001a: fig. 14) and in Orthoptera (discussion in KLASS 2001a).

Altogether, the muscle pattern on venter IX of Odonata is much like in Zygentoma, hence fairly plesiomorphic within the Pterygota. However, as probably in all other Pterygota, coxo-stylar muscles IX and muscles of vestigial spiracles of abdominal segment IX, all found in *Thermobia* (muscles 41\*, 91\*, 92\* in ROUSSET 1973), are absent in Odonata.

In Archaeognatha as well as in Orthoptera, Dictyoptera, and possibly Phasmatodea among the Neoptera the anteromedian parts of the CX9, which give rise to the coxo-gonapophyseal muscles, have segregated from the main part of CX9 and fused medially. This coxal transverse sclerite located in front of the bases of gonapophyses gp9 has been called scS\* (Archaeognatha; BITSCH 1974a: fig. 6) or anterior intervalvula (neopteran groups; e.g. KLASS 1998). Regarding the different position of the anterior tergo-coxal muscles IX either on the main part of CX9 (Archaeognatha) or on the segregated sclerite (neopteran taxa), this division is likely not homologous between Archaeognatha and the said neopteran groups (discussion in KLASS 2003: 206). Accordingly, the condition in Zygentoma, Odonata, and many Neoptera (e.g., Dermaptera, Auchenorrhyncha, and Hymenoptera), in which such a division and such a sclerite bridge are absent and the gonapophyseal muscles arise from the main part of the coxa (like in segment VIII), likely represents the plesiomorphic condition of Insecta.

In the taxa that lack the latter division and sclerite bridge there is usually a close contact between the opposed margins of the most anterior parts of sclerite CX9 and the gonapophyseal sclerite IX GP9. This is very distinct in ovipositor-bearing Odonata (Figs. 11, 39–41), also found in Zygentoma (ROUSSET 1973: 60, gcxIX\* and sclI\* in fig. 4A), and also present in Auchenorrhyncha and Hymenoptera (KLASS 2003: figs. 77, 78). This kind of contact thus appears to be plesiomorphic at least at the level of Dicondylia. In pygidicranid Dermaptera the bases of the gonapophyses have shifted posteriad, so that the point of contact (in the taxa where it is retained) on CX9 is also located further posteriorly (KLASS 2003: fig. 79); only in *Diplatys* this shift is not so extensive (KLASS 2003: fig. 80). A small finger-like mesal extension of sclerite CX9 in the contact area CX9-GP9, as present in Odonata (Figs. 39–41), is also found in at least some Pygidicranidae and Hymenoptera (KLASS 2003: p\* in Figs. 76, 78, 80) and may be a plesiomorphic element of Pterygota (not shown for Zygentoma in ROUSSET 1973: fig. 4A). In Archaeognatha, Orthoptera, and Dictyoptera – the taxa having a segregated transverse sclerite – this is likely to act as an anterior abutment for gonapophyseal sclerites GP9 (see BITSCH 1974a: fig. 6). Unfortunately, for Archaeognatha BITSCH (1974a) does not explicitly

describe the gonapophyseal sclerites, so that further details are not known for this taxon.

The coxal apodemes fa and la, of which the latter is particularly dominant in Odonata (Figs. 11, 39–41), give attachment to the strong anterior resp. posterior tergo-coxal muscles 28 and 29 (Fig. 19). Their coxal attachments are located anterior resp. posterior to the articulation CXa9-LCp9 with the postlaterocoxa (posterior part of gonangulum). All this constitutes a mechanism by which CX9 is rocked upon articulation CXa9-LCp9. This is a basic functional aspect of the insect ovipositor and is found in many ovipositor-bearing insect taxa (see KLASS 2003: 204), though coxal apodemes are often absent. The latter is apparently true for Archaeognatha and Zygentoma (apodemes not indicated in BITSCH 1974a and ROUSSET 1973). Among the Neoptera, the dermapteran, auchenorrhynchan, and hymenopteran shown in KLASS (2003: figs. 76–79, muscles 14\* and 25\*) have an internal ridge along coxa CX9 that also bears the muscle insertions concerned and likely represents the homologue of both apodemes fa and la. A strong development of the posterior part of the ridge (corresponding to apodeme la), however, is not found in these taxa; in contrast, in the auchenorrhynchan and the hymenopteran the insertion area of the anterior tergo-coxal muscle is strongly invaginated (pouch cp\* in KLASS 2003: figs. 77, 78). In Notoptera the part of CX9 that bears the posterior muscle and is located behind the articulation with the gonangulum forms an apodeme (KLASS 2005: fig. 9.3.B, left above “Vf9\*”); this, however, is by far not as heavy as la in Odonata. Altogether, apodemes or ridges like fa and la could be autapomorphies of Pterygota (or Metapterygota), providing increased stabilization and surface for muscle attachment for a more forceful rocking mechanism; an excessive development of the posterior apodeme la could be tentatively viewed as an autapomorphy of Odonata.

The dorsal lobe dl of the gonoplac gl9 in Odonata may correspond to the projection of the coxal lobe IX gl9 that in Zygentoma arises mesal to the stylus base (ROUSSET 1973: fig. 2). An individualized sclerite CXb9 in the dorsal wall of this lobe dl (Figs. 11, 47–61), however, is not reported for Zygentoma. A homologue of CXb9 may also be absent in the other ovipositor-bearing Pterygota, unless sclerites occasionally found on the mesal face of the gonoplac are such homologues (e.g., sclerite labeled CXb9 for an auchenorrhynchan in KLASS 2003: fig. 77).

#### 6.5.6. Coxa IX and gonoplac IX characters in Odonata

Outgroup evidence for character 49 of the presence of CXb9 is here regarded as ambiguous, because some-

what similar sclerites are found in a few other Insecta (though homology is unclear), while many other Insecta clearly lack such sclerites. Nonetheless, since absence of **CXb9** was here only found for *Caliaeshna*, this is very likely an autapomorphy of this taxon. Character 50 of **CXa9** and **CXb9** being connected or separated is regarded as inapplicable to the outgroup.

The styli **sl9** of Odonata, which are an essential element of the sensory equipment of the gonoplags **gl9** (used during endophytic egg deposition: MATUSHKINA & GORB 2002), show much variation in shape and in the occurrence of various sensilla (see also MATUSHKINA & GORB 2002; MATUSHKINA 2004: fig. 10, 2008b). The shape of the styli in Archaeognatha and Zygentoma varies from spindle- to cone-shaped, but long cylindrical styli do also occur (BITSCH 1974a: fig. 1; ROUSSET 1973: figs. 3, 9); the outgroup condition in character 52 of stylus shape is thus considered ambiguous. Though in Archaeognatha and Zygentoma the stylus bears setae of different size and shape, and apical ones are often longer and stouter than those along the stylus flanks, a discrete setal tuft on the stylus tip (see character 55: present in *Argiolestes* and Aeshnidae) has apparently not been reported; the outgroup is thus scored 'absent' in character 55. However, variation of this character in Odonata needs more refined study by SEM, as demonstrated by the presence of a subapical tuft of fairly short setae in *Epiophlebia* (MATUSHKINA 2008b: fig. 4f), which may constitute a transitory condition between states 'absent' and 'present' in this study.

Small sclerites **CXc9** at the bases of the styli have likewise not been reported previously for Archaeognatha and Zygentoma, but they are surely easily overlooked; the outgroup condition is thus considered as unknown in character 51.

Conditions with a series of tubercles along the ventral edge of the gonoplag **gl9** (as in Fig. 39), or with at least a single large distal tubercle (as in Fig. 41) have apparently not been reported for other Insecta. Therefore, in character 53 absence of tubercles is scored for the outgroup, and character 54 on the condition of the series of tubercles is considered inapplicable to the outgroup. Outgroup scoring is done tentatively, because the vast taxonomic literature may well include reports of such tubercles in some non-odonatan insects.

#### 6.5.7. Midventral sclerotizations IX and associated elements

The structural elements located between the mesal margins of the two coxae **CX9** and behind the bases of the gonapophyses **gp9** in Odonata are difficult to compare with other insects. This concerns the median apodeme **ca** with its sclerite **CA** and the paired tendons **ft**

in the anterior part, as well as two categories of sclerites located at the posterior base of the gonoplags **gl9**, called here **PS9** and **IT9**, both highly variable (Figs. 7, 11, 39–41, 46–61). Apodeme **ca** gives attachment to muscles **32** from **CX9** (base of apodeme **la**), while tendons **ft** receive the posterior parts of the gonapophyseal muscles **33** from **CX9** (Fig. 19). Sclerites **PS9** and **IT9** are bare of muscle insertions; this is true for *Calopteryx* (Fig. 19) and probably all Odonata studied by ASAHINA (1954), and also for general adults of at least *Anax* (MATUSHKINA 2008a: fig. 5B). Both **PS9** and **IT9** (Figs. 46–61) probably belong to segment IX, since in Zygoptera they are located in front of the ventral ridge along the anterior margin of sclerite ring X (**ac10** in Fig. 7), which is likely the ventral antecosta X; since, in addition, the posterior sclerite **IT9** is in some taxa fused to tergum **TG9** (Figs. 48, 50, 51); and since the circumferential ridge **xr** (Figs. 50, 51), which in *Lestes* and *Drepanosticta* traverses along **IT9** ventrally, is clearly on segment IX dorsally (in front of ridge **ty** of **TG9**, cf. Figs. 3, 7).

For the studied Archaeognatha and Zygentoma (BITSCH 1974a,b; ROUSSET 1973) discrete sclerites and tendons between the bases of the two coxites **CX9** are not reported; the sclerites following the **CX9** to the posterior are the 'paraprocts', which likely represent coxosternum X (KLASS 2001a). Thus, none of the cuticular elements here in question seems to occur in these taxa. Nevertheless, a (membraneous?) transverse fold between the gonoplag bases and 'paraprocts' in Zygentoma (ROUSSET 1973: **stX\*** in fig. 5) could perhaps be a forerunner structure of the transverse fold that in many Odonata is found on sclerite **PS9**. At least in Zygentoma muscles homologous with **32** and **33** are present – though the homologue of muscle **32** originates from **LC9** rather than **CX9** (see section 6.5.5.).

The area in between the two **CX9** shows similar proportions in Odonata and in the auchenorrhynchan and hymenopteran illustrated in KLASS (2003: figs. 77, 78). The two latter taxa have a sclerite in the same position as **CA** of Odonata. The muscle inserted upon it (KLASS 2003: **26\*** in figs. 77, 78) originates from the **LC9** as in Zygentoma (and is thus likely muscle **32**; this is in contrast to the assumption of non-homology for the coxal and laterocoxal muscles labeled **27\*** resp. **26\*** in KLASS 2003: figs. 76–78). Since the coxal origin of the muscle in Odonata is likely due to an evolutionary shift (see section 6.5.5.), sclerites **CA** in Odonata and in auchenorrhynchans and hymenopterans can well be considered homologous. In contrast to Odonata, in the two latter taxa neither an apodeme **ca** nor tendons **ft** were found, and there are no sclerites around the posterior gonoplag bases like **PS9** and **IT9**. The gonapophyseal muscle **33** is only represented in the hymenopteran (**17\*** in KLASS 2003: figs. 76, 78) but not in the auchenorrhynchan.

In many ovipositor-bearing 'lower' Neoptera (Orthoptera, Dictyoptera, Notoptera, Mantophasmatodea) the identification of elements corresponding to **CA**, **ca**, and **ft**, and to **PS9** and **IT9** is difficult, because the hind part of venter IX (together with the gonoplac bases) is much shorter and spatial relationships thus quite difficult to compare; this even includes difficulties in the distinction between potential homologues of the anterior sclerites **CA** and of the posterior ones **PS9** and **IT9**, which are widely separated in Odonata (Figs. 39–41). Further difficulties result from the fact that both **PS9** and **IT9** are highly variable within the Odonata, so that even homologies within this order (as proposed in Figs. 46–61) are partly questionable. In addition, potential homologues in lower neopteran taxa (the so-called posterior intervalvulae, among other structures) also show a great extent of structural variation. In the attempt to trace homologies between Odonata and lower neopterans, following muscles that extend from **LC9** or **CX9** into the intercoxal area IX is a good starting point (identification of **CA**, **ca**, and **ft** by homologues of muscles **32** and **33**).

Ensifera have a median sclerite that bears an internal midline ridge and receives muscles from both **LC9** and **CX9** (KLASS 1998: general scheme for Ensifera fig. 26: sclerite **pm\*** = posterior intervalvula and muscles **9\*** resp. **10\***). This resembles the configuration of sclerite **CA** and apodeme **ca** in Odonata – while muscle **9\*** comes from **LC9** as in *Zygentoma* (and thus likely corresponds to muscle **32**), and both muscles are inserted medially upon the **ca**-like ridge (no tendons like **ft** present). On the other hand, sclerite **pm\*** is laterally articulated with the coxae **CX9** near the posterior bases of the gonoplacs **gl9**; in this aspect **pm\*** rather resembles sclerite **PS9** of Odonata (Fig. 7); **PS9**, however, has no muscles attached to it. Therefore, it appears reasonable to assume that in Ensifera during the shortening of the area homologues of **CA** and **PS9** have come into contact and fused to form the posterior intervalvula **pm\***; this would explain all features of that sclerite (which is then a sclerite **CA+PS9**).

Dictyoptera show a similar condition as Ensifera: a transverse sclerotization connects the left and right coxae **CX9** behind the gonoplac bases (but the sclerotizations are fused rather than articulated), has a median apodeme, and receives muscles from both **LC9** and **CX9** (KLASS 1998: general scheme for Dictyoptera fig. 25: sclerotization **pm\*** with bilobate apodeme, and muscles **gpl9\*** resp. **cm\***). Muscle **cm\*** from **CX9** is considered the homologue of muscle **33**; muscle **gpl9\*** from **LC9** is – again by comparison with *Zygentoma* – considered the homologue of muscle **32**. Medially, muscle **cm\*** (**33**) is inserted on the apodeme, while muscle **gpl9\*** (**32**) is attached to the sclerite more laterally (without tendons). This is the opposite relation as in Odonata (Fig. 19). Yet, also the sclerotization

in Dictyoptera might be tentatively considered to be composed of **CA** and **PS9**.

Nonetheless, there is another problem with this interpretation for Ensifera and Dictyoptera: Some members of both taxa have gonapophyseal muscles IX (**ivm\*** resp. **vv9\*** in KLASS 1998: figs. 25, 26, 29) that also originate from coxal sclerotizations IX. It must therefore be assumed that in both taxa the homologue of muscle **33** has divided into two muscles (**10\*** and **ivm\*** resp. **cm\*** and **vv9\***).

Mantophasmatodea adds an interesting aspect to the discussion (KLASS et al. 2003: fig. 7): These insects have a sclerite **IP\*** with an apodeme **ai\*** in between the coxae **CX9**, and additionally another small sclerite **PS9\*** with an apodeme **ps\*** between the posterior bases of the **CX9**. Based on positional criteria, the former could be homologous with **CA** and **ca** of Odonata, and the latter with **PS9** or perhaps **IT9** of Odonata. With this interpretation, a fusion of the anterior and posterior intercoxal sclerites would be absent – in contrast to Ensifera and Dictyoptera. Unfortunately, the musculature has remained unknown for Mantophasmatodea.

The posterior intervalvulae of Ensifera and Dictyoptera as well as sclerites **IP\*** and **PS9\*** of Mantophasmatodea are median sclerites firmly sclerotized across the midline. Assuming their (partial) homology with **PS9** in Odonata would require that in Odonata the type of **PS9** that is undivided at the midline and only articulated (not broadly fused) with **CX9** (as in, e.g., Figs. 58, 61) is plesiomorphic. On the other hand, **PS9** shows a wide structural range from the latter condition to another where **PS9** shows a complete median division and is extensively fused with **CX9** (as in Figs. 46, 48). The lastmentioned condition could be the basis for an alternative hypothesis of **PS9** having evolved within Odonata, as a derivative of posteromesal parts of sclerite **CX9**.

In none of the non-odonatan insect taxa here considered there seems to be a sclerite that can with some good reason be homologized with **IT9** of Odonata. And a condition where a IXth-segmental sclerite behind the **CX9** is laterally fused with the corners of tergum IX (like **IT9** in Figs. 48, 50, 51) seems to be unknown in insects.

In sum, none of the exoskeletal elements here discussed (**CA**, **ca**, **ft**, **PS9**, **IT9**) appears to occur in Archaeognatha and *Zygentoma*. Only sclerite **CA** is found in auchenorrhynchans and hymenopterans. Mantophasmatodea may have homologues of both **CA** (with apodeme **ca**) and **PS9**. A compound sclerite **CA+PS9** with an apodeme **ca** may occur in Ensifera and Dictyoptera (and perhaps some other 'orthopteroïd' insects), but the identification is ambiguous. There is no indication that the posterior sclerite **IT9** of Odonata has a homologue in any other insect, and

tendons like **ft** have apparently not been reported for any insects other than Odonata.

#### 6.5.8. Characters of midventral sclerotizations IX and associated elements in Odonata

Due to all the uncertainties with regard to the identification of homologues of elements **CA**, **ca**, **ft**, **PS9**, and **IT9**, it is here preferred to omit outgroup scoring for characters of Odonata that concern attributes of these elements (characters 56–60, 62). Only with regard to the general presence of tendons **ft**, sclerites **IT9**, and the circular ridge **xr** (characters 45, 61, 63), absence is tentatively scored for the outgroup, as these elements have apparently not been reported for any other insect. However, one should note that tendons like **ft** and a ridge like **xr** are, if very delicate, surely easily overlooked. Concerning the transversely folded condition of **PS9** (character 58), the abovementioned fold in *Zygentoma* (**stX\*** in ROUSSET 1973) could be homologous, but that would appear too vaguely supported.

### 6.6. Gonapophyses VIII and IX and their substructures

In the various Insecta, on both segments VIII and IX the bodies of the left and right gonapophyses (**gp**) as well as their sclerotizations (**GP**) show very different degrees of transverse interconnection.

On segment VIII, there is a functional correlation to be considered: A fusion of the **gp8** or **GP8** is generally unlikely in taxa having a VIIth-segmental gonopore or an VIIIth-segmental gonopore located in front of the **gp8**-bases, because the eggs have to enter the egg channel above the two **gp8** from below. Accordingly, the two gonapophyses **gp8** as well as their sclerotizations **GP8** are free from each other down to their very base in Archaeognatha (Fig. 71; BITSCH 1974a: fig. 1A), *Zygentoma* (*Thermobia* and *Nicoletia*; Fig. 70; ROUSSET 1973: 58, **vVIII\*** in figs. 5, 9, 10), Dictyoptera (Fig. 69; KLASS 1998: figs. 2–4), Ensifera (ANDER 1939), and Phasmatodea (*Timema*: TILGNER et al. 2000: fig. 32). In Caelifera, however, the two **gp8** are extensively fused behind the genital opening (Fig. 64; SNODGRASS 1935a: 37ff); this is functionally possible because the ovipositor is used for burrowing rather than for providing an egg channel. A complete lack of a connection of the two **gp8** and **GP8** is also true for Notoptera (Fig. 65) and Mantophasmatodea (KLASS et al. 2003: fig. 7A) with their genital opening (vulva) between and behind the **gp8**-bases; in Notoptera, as

in the Aeshnidae (Fig. 29), the cleft between the **gp8** extends far basally to separate the coxae **CX8**. Some pygidicranid Dermaptera and Auchenorrhyncha show a distinct basal fusion of the **gp8**, but the sclerotizations **GP8** are separated (Fig. 66; KLASS 2003; own observations in *Magiccada*). In sum, a far basally reaching disconnection of the left and right **gp8** and a complete disconnection of the **GP8** like in Aeshnidae appears plesiomorphic for Odonata, and the more extensive basal fusion in *Epiophlebia* (Fig. 37) and, in particular, Zygoptera (e.g., Fig. 28) appears apomorphic (see characters 16, 19). Nevertheless, the scoring of entirely separated **gp8** for the outgroup is tentative, as it might appear disputable in view of the basal fusions in Caelifera, some Pygidicranidae, and (at least) some Auchenorrhyncha. In terms of the extension and subdivision of the sclerotization **GP8** at the dorsal bases of the gonapophyses **gp8** (Figs. 28, 29, 37; see character 20) outgroup comparison is ambiguous, because the sclerotization in this area varies to strongly among outgroup taxa (Figs. 64–71).

In segment IX, the bodies of the left and right gonapophyses **gp9** are transversely fused in several *Zygentoma*. The fusion extends far distally in *Lepisma* and *Thermobia* (POHL 1957: 359, fig. 10a; ROUSSET 1973: fig. 4) but is restricted to the base of the **gp9** in *Nicoletia* (ROUSSET 1973: fig. 10). The latter condition is also found in Archaeognatha (BITSCH 1974a: 106, fig. 1B). It is not quite clear from the literature whether the sclerotizations **GP9** are fused as well in the taxa mentioned so far. In other *Zygentoma*, however, the two **gp9** (and thus necessarily also the **GP9**) seem to be entirely free from each other (*Atelura*; POHL 1957: fig. 10b). An at least basal fusion of the **gp9** is present, for instance, in Ensifera (ANDER 1956), Auchenorrhyncha (own observations in *Magiccada*; SMITH 1969: fig. 3J), and Hymenoptera (SMITH 1970), but complete disconnection is found in Dictyoptera (KLASS 1998: figs. 2–4), Phasmatodea (*Timema*: TILGNER et al. 1999: fig. 32), and pygidicranid Dermaptera (KLASS 2003); conditions in Notoptera are difficult to assess. The support for SMITH's (1969: 1059f, fig. 3E) assumption of a (basal?) transverse fusion of the **gp9** and of the **GP9** as plesiomorphic for (at least) the Pterygota appears thus ambiguous. If SMITH is correct, the absence of a fusion of sclerites **GP9** in all Odonata here studied (as in Figs. 4, 11), and the lack of a fusion of the **gp9**-bodies in all Odonata except *Epiophlebia* (which has a basal **gp9**-fusion; see character 42 and compare Figs. 41 and 39, 40) would be apomorphic. However, due to the ambiguous outgroup evidence the outgroup is here scored as ambiguous.

In terms of the presence (*Epiophlebia*, Fig. 41) or absence (other Odonata, Figs. 39, 40) of a sclerite extension **i** at the dorsal **gp9**-base (character 46), outgroup data are quite insufficient, but at least in the

examined Pygidicranidae (KLASS 2003) and Dictyoptera (KLASS 1998) such a sclerotization is absent; yet, the outgroup is scored as ambiguous due to the limited data.

An olistheter with an aulax **al** (groove) on the **gp8** and a rhachis **rh** (ridge) on the **gp9** (Figs. 4, 6, 9) is present in many ovipositor-bearing Insecta, such as Archaeognatha (BITSCH 1974a: 106), Zygentoma (POHL 1957: fig. 10; ROUSSET 1973: 58, fig. 4), Orthoptera (ANDER 1939: figs. 120–123), Notoptera (KLASS 2005: fig. 9.3.B), Hymenoptera (SMITH 1970: figs. 5, 6), and all Odonata here studied, and it is likely an autapomorphy of Insecta. However, with the currently available data on the various Insecta the polarity in character 44 of the basal extension of the rhachis, which is correlated with the position of extension **g** at the base of sclerite **GP9** (compare Figs. 39 and 40), cannot be assessed.

Ridges **gy** (Figs. 29, 32, 37) have apparently not been clearly recorded from insects other than Odonata, and they are surely absent in many insects. In illustrations showing cross sections of the ovipositor, ridges and grooves on the ventromesal edges of the left and right gonapophyses **gp8** are reported for a number of insects. However, such illustrations leave open whether straight, continuous ridges and grooves are present or a series of short, oblique ridges like **gy**. The former is true for, e.g., Auchenorrhyncha (personal observations in *Magiccada*; cross section in SMITH 1969: fig. 3J). The latter is true for GEORGE'S (1929) cross section illustrations of an odonatan. In the case of the Zygentoma that show such a structure the issue is apparently not clarified (e.g., POHL 1957: cross section fig. 10b of *Atelura*, with mesal tongues and grooves on both **gp8** and **gp9**; these are absent in *Lepisma* and *Thermobia*: POHL 1957: fig. 10a; ROUSSET 1973: fig. 4). There is thus no clear outgroup comparison available for characters 21 and 22.

The various sculptural components of the **gp8** and **gp9** that appear as adaptations for sawing into the substrate, i.e., the teeth **tm8** and **tm9**, ridges **gz8** (Fig. 4; see also Figs. 42–45), and dorsal **gp9**-teeth in *Lestes* and, particularly, *Epiophlebia*, are likely all plesiomorphic elements. They appear to be remnants or derivatives of the sculpture present in, e.g., the zygentoman *Tricholepidion* (WYGODZINSKI 1961: figs. 47–50), various Diaphanopteroidea (KUKALOVÁ-PECK 1992: figs. 27ff), and Hymenoptera (SMITH 1970; VILHELMSSEN 2000) – though the exact structural relationships are currently difficult to assess, and much homoplasy is to be expected for these functionally exposed parts. The outgroup scorings given for characters 23, 24, and 43 in Tab. 1 are thus tentative. Further discussions must await detailed studies by SEM (such as in MATUSHKINA 2008b or VILHELMSSEN 2000) in a broad selection of taxa.

With regard to the ontogenetic development of the gonapophyses in Odonata, it is noteworthy that in *Coenagrion* a small lobe (GEORGE 1929: **rpaol\***, **paol\*** in figs. 15–17) arises from the mesal base of each **gp8**-rudiment; it flanks the vaginal opening and is evidently the rudiment of lobe **vl** of the imago (Figs. 8, 9). Similar lobes have been reported for nymphs of Blattaria and Acrididae, but here they become leveled into the mesal bases of the **gp8** and are absent in the adults (GUPTA 1948: 87, 90, 99, figs. 10, 11). Such lobes have apparently not been reported for Zygentoma and Archaeognatha, neither for the adults nor for earlier ontogenetic stages; however, in these taxa this ontogenetic aspect has not yet been studied in detail. It is thus difficult to say whether the **vl**-lobes could be autapomorphic elements of the Pterygota, whether their presence in the adults is plesiomorphic within the Pterygota (or perhaps a paedomorphism of the Odonata), and whether they were originally long or short, and sclerotized (sclerite **VL**) or membraneous. In characters 25 and 26 the outgroup is thus scored ambiguous due to insufficient data.

## 6.7. Composition of pregenital coxosterna

The above results on the interpretation of the ventral sclerotizations VIII **CX8** and **LS8** (Figs. 4, 7, 63) allow conclusions on the composition of the midabdominal coxosterna **CS** in Odonata. Comparing the lateral muscles inserted on **LS8** and **CS** (Figs. 16, 19), homonomy is quite obvious for muscles **1** and **67** (see Fig. 63), **2** and **13**, **3** and **14**, as well as **4** and **15**, which are then all tergo-laterocoxal. Tergo-coxal muscles (**16** and **17** in segment VIII) are probably lacking in the midabdomen. While muscle **5** cannot be completely excluded as homonomous with muscle **16**, MATUSHKINA'S (2008a: tab. 2) studies on the nymphal, teneral, and mature musculature in *Anax* females strongly supports the idea that muscles **16** (**M1\***) and **17** (**M2\***) have no homonomous muscles in the preceding segments, as these develop only in segment VIII and only in adults, without nymphal precursor muscles.

Consequently, the strong lengthening of the segments in the midabdomen is like in segment VIII due to a lengthening of the anterior (laterocoxal and likely sternal) components of the coxosternum **CS**. Only the posteriormost part of a coxosternum **CS**, which in most Odonata is weaker than the anterior part, remains to represent the coxal sclerotizations. This interpretation of a large anterior part of the **CS** as laterocoxal complies with the positions of the segmental medio-caudal processes in *Epiophlebia*: these arise from the hind margin of **LS8** in segment VIII (**pp8**) and from

the posterior part of the venter in the preceding segments. The coxal area has then become desclerotized in this taxon (compare section 5.3.1.).

## 6.8. Dorsal sclerotizations VIII and IX

As in the terga of the preceding abdominal segments (see section 6.2.1.), in segments VIII and IX mid-dorsal hinge lines **dh** are apparently not reported for insects other than Odonata; however, clear outgroup data are sparse. In terms of the various conditions of **dh** and of the antecosta **ac** in the middorsal area (see characters 8, 37), outgroup comparison for Odonata is best considered as impossible (characters not applicable to outgroup), even if **dh** and the dorsal weakness of **ac** are entirely absent (as in segment VIII of *Drepanosticta*), which is likely also true for most outgroup taxa.

In terms of the sclerite extension **b** of tergum **TG8** (Fig. 4; see character 9), which is present in *Epiophlebia* and all Zygoptera, and which reaches extension **c** of tergum **TG9** (i.e., the articulation **TG9-LCa9**) in most Zygoptera (Figs. 26, 27, 32, 33, 36), outgroup evidence is conflicting (see KLAS 1998: 83f): An extension like **b** is absent in, e.g., the studied Zygentoma (Fig. 70; ROUSSET 1973: figs. 5, 9, 10), Notoptera (Fig. 65; WALKER 1943: fig. 8), Caelifera (Fig. 64), and Pygidicranidae (Fig. 66; with possible exceptions, **b?** in Fig. 67). However, in some Dictyoptera (dorsal part of tergal extension VIII **tg\*** in KLAS 1998: 83f, **Z\*** in figs. 13, 17, fig. 11), in at least some Ensifera (SNODGRASS 1933: fig. 18), and apparently in the phasmid *Timema* (TILGNER et al. 1999: fig. 30) the posterolateral corner of **TG8** is ventrally extended towards the articulation between tergum **TG9** and laterocoxa **LC9** (and can be fused with **TG9**).

## 6.9. The elements of the terminal abdomen

### 6.9.1. Cerci and dorsal sclerotizations of the terminal abdomen

**Findings and interpretations of Heymons.** There is a widely known controversy that concerns the nature of the projections called herein, like in most other recent contributions, the cerci (**ce** in Figs. 3, 12). HEYMONS (1896, 1904) refuted the cercal nature of these based on his ontogenetic observations in a variety of Odonata. He found in late embryos and freshly hatched nymphs 11 discrete abdominal segments. Those up to

X appear as complete rings, each with a tergum and a ‘sternum’ (coxosternum at least in segments up to IX), and each possibly with a pair of transitory limb buds (note in TILLYARD 1917: 238). Segment XI is well developed, well demarcated from segment X by a circular groove, and, from late embryonic stages onwards, divided into three lobes down to near its anterior margin. The lobes grow to form three caudal appendages (anglicized form of HEYMONS’ ‘appendices’, not meant as ‘limb’): a dorsal appendage arising from tergum XI and a pair of lateral appendages arising from the medially divided sternum XI. These develop into the three caudal (tracheal) gills in zygopteran nymphs and the three flaps of the anal pyramid in anisopteran nymphs. Since in the imaginal molt the epidermis retreats from the distal parts of these appendages, only the bases are retained in the adults as short bulges (subanal lobes **sl** and terminal projection **tf** in Figs. 12–15). HEYMONS consequently interprets the sclerotizations of these bulges (paraproctal sclerites **AP** and tergum **TG11** in Figs. 12–15) as the medially divided sternum XI and the tergum XI. In adult males, however, a stout projection is said to be retained in Zygoptera from each lateral appendage (the subanal lobe projection mentioned in section 4.4.), and in Anisoptera from the dorsal appendage (occasionally bifid); both kinds of projections, though not considered homologous, are called inferior appendages by TILLYARD (1917: e.g., fig. 12). The telson behind segment XI forms in late embryos three lobes (anal laminae), one at the inner base of each XIth-segmental appendage, which together surround the anus: a dorsal supraanal lamina and a pair of ventrolateral subanal laminae. These are retained throughout the nymphal stages but may become fairly inconspicuous. While adult Zygoptera possibly retain the supraanal lamina (U-shaped fold with sclerite **DT** in Figs. 12, 14) but show no trace of the subanal laminae, in many adult Anisoptera all three laminae remain conspicuous (lobes **xl**, **yl** in characters 76, 77). During nymphal life the paired cercoids (= caudal processes) gradually grow out of the interspaces between the dorsal and lateral appendages. In adult Odonata the cercoids are always well developed (cerci **ce** in Fig. 3), and they are used in copulation by the males (superior appendages in TILLYARD 1917: fig. 12) together with the inferior appendages.

HEYMONS considers the cercoids as newly acquired Xth-segmental elements. The lateral appendages are regarded as the homologues of the cerci in other Insecta, which according to their reduction during the last molt are virtually absent in imaginal Odonata (well developed only in male Zygoptera). This makes sense considering that the dorsal and lateral appendages develop in the embryo as a group of three similar projections, apparently all from the same segment XI, and remain similar in the larvae, just as the terminal

projection/filament and the cerci do in the *Zygentoma* and Ephemeroptera (compare HEYMONS 1897: figs. 8, 18 and 1896: figs. 2, 3; see also HEYMONS 1904: 22). HEYMONS' interpretation was accepted by many later authors, e.g., TILLYARD (1917: 90ff), HENNIG (1969: 323), and WINKELMANN (1973: 49).

**Findings and interpretations of subsequent authors.** SCHMIDT (1933) and especially ASAHINA (1954: 69f) have demonstrated that, in contrast to HEYMONS' findings, the lobes **xl** and **yl** (**x\*** and **y\*** therein) of Anisoptera emerge in late last-instar nymphs from the shed cuticle of the lateral and dorsal appendages (anal pyramid) rather than from that of the anal laminae; strongly reduced anal laminae are additionally present on the adanal faces of **xl** and **yl** but disappear soon after. The imaginal inferior appendages (of all male Odonata) are thus not derived from the projecting bodies of the nymphal lateral and dorsal appendages but are secondary outgrowths from the abanal parts of the subanal lobes and terminal projection. Following HEYMONS in the interpretation of the lateral appendages, SCHMIDT consequently regards the lobes **xl** as the cerci (see below for ASAHINA), which are then virtually absent in Zygoptera but more or less strongly developed in Anisoptera.

HANDLIRSCH (1904), after some dispute with HEYMONS, accepted the lateral appendages as the cerci. However, he legitimately doubted the validity of HEYMONS' arguments for a Xth-segmental origin of the cercoids, albeit he does not discuss them in some detail. He proposed that also the cercoids are true XIth-segmental cerci, which substitute (being the imaginal cerci) the lateral appendages (nymphal cerci) like structures in endopterygotes are substituted from imaginal disc tissue during metamorphosis.

The latter hypothesis is rightfully criticized by MATSUDA (1976: 133), due to the presence of both generations of cerci side by side for some time inherent in it, which constitutes a fundamental difference to conditions in endopterygotes. Otherwise MATSUDA's (1976: 56, 133) conclusions are confused: He sensibly regards (only) the cercoids as the true cerci whose appearance in ontogeny has become delayed, and notes that the cercoid base in adult Odonata is in the same relative position as the cercal base in many other Pterygota (a 'similarity' in the location had also been admitted by HEYMONS 1904: 31). On the other hand, he also accepts HEYMONS' (1904) hypothesis of a Xth-segmental origin of the cercoids. This homologization with cerci of projections that allegedly originate from segment X in an insect with eleven discrete abdominal segments appears puzzling (for the different case of a Xth-segmental origin of the cerci in *Diplura* see KLASS 2001a: 293f).

SNODGRASS (1931: 107; 1935b: 256, 1954: 33ff) likewise regards the cercoids as the true cerci and the

lateral appendages as projections of the paraprocts (i.e., of the subanal lobes). He explains that the cercoids of the adults are in the right position to be cerci, whereas the subanal lobes and their mesal projections in Anisoptera (lobes **xl**, see SCHMIDT 1933) are not, but neither does he go into the details, nor does he consider most of HEYMONS' arguments.

Also WALKER (1922: 52) only generally notes that regarding adult exoskeletal structure the cercoids should be the cerci; he further relies on muscle data by N. Ford, which, however, have apparently remained unpublished (no contribution in FORD 1923).

ASAHINA (1954: 114) likewise considers the caudal processes ('cercoids') as the true cerci and the lateral appendages as seated on the paraprocts, but he also claims there is "no positive morphological evidence, for example, of the muscle insertion from the eleventh segment".

The multi-segmented condition in Carboniferous Odonoptera, as shown by, e.g., BECHLY et al. (2001: fig. 10) may be considered an argument for the cercal nature of the odonatan 'cercoids'. However, also non-limb body projections, as 'cercoids' would be, can be annulated, as exemplified by the terminal filament in Archaeognatha and *Zygentoma*.

ANDO's (1962) results on the embryology of the terminal abdomen in Odonata comply with HEYMONS', but there are differences in the interpretation of the three XIth-segmental lobes (paraprocts and epiproct in ANDO). (1) ANDO (1962: 56, 167, 169) regards not only the bases of the lateral appendages (gills, pyramid flaps) as the paraprocts (= 'sternum' XI), but also their distal projecting parts, thus negating HEYMONS' (1904) hypothesis of the cercal nature of the latter. Nevertheless, there are neither 'cerci' mentioned in ANDO's discussion, nor is there any argument given for the non-cercal and exclusively paraproctal nature of the lateral appendages. (2) ANDO (1962: 159) notes that segments X and XI become combined at some stage, but it is unclear which kind of process he means, because mesoderms and the intersegmental groove are said and shown (figs. 24/7, 29 therein) to remain distinct afterwards. ANDO (1962: 107, 159, fig. 45/1) furthermore finds a double set of dorsal exuvial glands on the apparent tergum X and assigns the posterior ones to segment XI; this lends some support to his suggestion of segment X actually being a 'synsegment' X+XI, the epiproct (**TG11** in Fig. 12) then being only the posterior part of tergum XI (HEYMONS regards the epiproct as the entire tergum XI). Yet, this hypothesis seems unlikely because what appears to be the intersegmental groove X/XI traverses behind the glands, and because it is in conflict with imaginal structure: muscle **43** (Fig. 21) is most parsimoniously interpreted as a dorsal muscle X and is properly attached to the anterior margin of **TG11** (compare KLASS

2001a: figs. 29, 30 for *Zygentoma* and Ephemeroptera). It should further be noted that, apart from the pleuropodia of abdomen I, abdominal limb buds are neither mentioned nor depicted by ANDO (1962).

Thus, apart from pointing out the positional correspondence between the cercoids in Odonata and cerci in other Pterygota, previous contributions to the cercus issue do neither give conclusive arguments in favour of the cercoids being the cerci, nor have HEYMONS' arguments for the secondary and Xth-segmental nature of the cercoids been disproved.

**Scrutiny of Heymons' arguments.** For a scrutiny of HEYMONS' view, in the first place the exact location of the cercoid origin and its morphologically correct assignment must be known. In 2.5-mm-nymphs of Zygoptera, the youngest for which HEYMONS (1904: 26) clearly explains the location, the buds (epidermal thickenings) are "etwas unter dem vorstehenden Hinterrande des 10. Tergits" (= slightly beneath the posteriorly projecting hind margin of tergum X); for 5-mm-nymphs HEYMONS (1904: 27) states the cercoid to be seated upon the area slightly *behind* tergum X. Corresponding conditions are indicated for Anisoptera (HEYMONS 1904: 35, 38). The crucial point is that the area concerned, immediately behind the Xth tergal margin and between the dorsal and lateral appendages, can, contrary to HEYMONS's assignment to segment X, well be regarded as XIth-segmental: As noted by SNODGRASS (1954), in exactly this area many Pterygota, adults as well as nymphs, have situated the base of the cercus (e.g., Blattaria, Dermaptera, with XIth-segmental cerci according to HEYMONS 1895a,b). The close contact of the XIth-segmental cercal base in Pterygota to the hind margin of tergum X, often with articulations between them, has probably become established during evolution through a fragmentation and membranization of the lateral parts of tergum XI (which in the plesiomorphic condition are intercalated between the cercal base and tergum X: Archaeognatha and *Zygentoma*; KLASS 2001a: 293, fig. 29). Thus, if a delay of the ontogenetic formation of the cerci is assumed, the cerci in Odonata should appear exactly in the place where the cercoids arise.

HEYMONS' (1904: 27) further arguments for the cercoids being Xth-segmental are (1) the undisturbed continuation in the nymphs of the epidermis from tergum X to the cercoid walls (probably meaning that there is no segmental borderline X/XI differentiated in this area), (2) the continuation of a trachea from segment X into the cercoid, and (3) the insertion of a muscle from tergum X on the ventral base of the cercoid (HEYMONS 1904: muscle **Mus\***, considered a dorsal muscle X).

(1) However, the lack of any segmental borderline structure in the epidermis in front of the cercoid base tells nothing. Only the demonstration of such a border-

line to traverse behind the cercoid base would suggest that the cercoids belong to segment X.

(2) In the zygentoman *Lepisma* a trachea from spiracle VIII continues, after some branching, beneath terga X and XI into the cercus (BARNHART 1961: fig. 2); after an extreme shortening of the XIth-tergal territory in front of the cercal base, as present in Pterygota (KLASS 2001a: figs. 29–32), a trachea would enter a cercus immediately after having passed beneath tergum X, just as it enters the cercoid in Odonata according to HEYMONS (1904: pl. 1 fig. 8; the same would be true for the cercal nerve).

(3) Though muscle **Mus\*** in HEYMONS is correctly described (probably muscle **41** in Fig. 21) and interpreted (dorsal muscle X), HEYMONS' conclusion is untenable: **Mus\*** corresponds in its posterior insertion on the ventromesal cercal base with, e.g., muscle **40\*** in the dermapteran *Hemimerus* (KLASS 2001a: figs. 12, 13; note that in female Dermaptera the anterior insertion has become translocated to tergum IX), which has been interpreted as an internal dorsal muscle X; though this is probably not the homologue of muscle **41** in Odonata (where an internal dorsal muscle has probably retained its plesiomorphic posterior insertion on XIth-tergal sclerotizations: **43** in Fig. 21), the location of the *Hemimerus* muscle clearly shows the invalidity of HEYMONS' argument (note that HEYMONS 1895a,b, 1912, like KLASS 2001a, identifies the cerci/claspers in Dermaptera as the true cerci). **Mus\*** also resembles muscle **f11\*** in the ephemeropteran *Povilla* (KLASS 2001a: figs. 30, 34; original data from BIRKET-SMITH 1971), which has been considered an intersegmental tergo-coxosternal muscle X (from tergum X to limb base XI; see below for interpretation of cercal muscles); if **Mus\*** is such a muscle, its position would strongly contradict HEYMONS' conclusion.

The cercoids in Odonata are thus unlikely formations of Xth-segmental territory, but they very likely originate from XIth-segmental ground. It is here proposed that the 'cercoids' are the true cerci, whose formation is delayed to a nymphal stage; this delay appears autapomorphic for the Odonata.

**Evidence from the cercal musculature.** Contrary to ASAHINA's (1954: 114) statement, the musculature of the cercal base and its neighborhood clearly indicates the 'cercoids' of Odonata to be true cerci. Relevant data on the cercal musculature in some Insecta (especially *Zygentoma*, Ephemeroptera, Caelifera, and Dermaptera) are analysed in KLASS (2001a: figs. 29–36, based on data from various previous authors). Therein, four morphological groups of cercal muscles were distinguished, **I–IV**. The main conclusion was that in Pterygota the external (group **III**) and internal (group **IV**) dorsal muscles X have become cercal muscles. While in Archaeognatha and *Zygentoma* muscles of both groups have their posterior insertions still on

the anterior margin of a wide tergum XI, in Pterygota a fragmentation and reduction (membranization) of the lateral parts of tergum XI occurred, by which the posterior insertions have come to lie on small sclerites or membrane around the cercal bases (initially without a shift of insertions). This is true for muscles of groups **III** and **IV** in the examined Neoptera, but only for group **III** in Ephemeroptera (KLASS 2001a: figs. 33–36). In addition, intersegmental tergo-coxosternal muscles X (group **II**; but see below) and intrasegmental tergo-coxosternal muscles XI (group **I**) can occur in Insecta, but the latter have become lost in many Pterygota (retained in, e.g., Dermaptera and Caelifera: KLASS 2001a: **43\*** and **293\*** in figs. 31, 32).

All muscles to (near) the cercal base that can occur in Odonata are shown in Fig. 62: From tergum X, muscle **42** runs to the mesal cercal base on apodeme **ma**, muscle **41** runs to the ventral cercal base (partly on apodeme **ma**), and muscle **63** runs to the area between the hind margin of tergum X and the dorsal and lateral cercal base (to tendon **ct**). In addition, muscle **43** connects tergum X with the anterior margin of tergum XI **TG11**, and muscle **48** transversely connects the left and right apodemes **ma** (Figs. 21, 22).

Group **I** muscles: Cercal muscles from **TG11** have not been reported for Odonata; their absence is shared with Ephemeroptera and many Neoptera, but since the muscles are still present in, e.g., Dermaptera and Caelifera, there is clearly homoplastic evolution in this regard. In addition, it should be noted that transverse muscles like **48** of Odonata (Figs. 21, 22) have not been reported for any other insect; rather than regarding it as a muscle newly evolved in Odonata, one could assume that this muscle has been derived from the former pair of group **I** muscles by a loss of the insertion on **TG11**.

Group **IV** muscles: Odonata share with the Ephemeroptera the plesiomorphic condition that one dorsal muscle X has retained its posterior insertion on the median main part of tergum **TG11** (**43** in Fig. 21 and **a10\*** in KLASS 2001a: fig. 30); this is not true for the examined Neoptera (see KLASS 2001a: figs. 31, 32), where the homologous muscle inserts on a lateral fragment of **TG11**, or on membrane, or directly on the cercal base. By comparison with Ephemeroptera muscle **43** of Odonata should be, despite its far posterior insertion on tergum X, an internal dorsal muscle, representing group **IV**. These muscles have become cercal muscles only in the Neoptera (by a further fragmentation of **TG11**) – perhaps an autapomorphy of that group (see KLASS 2001a: 302).

Group **III** muscles: Muscle **63** of Odonata likely represents the external dorsal muscles, which in the other insects studied are also inserted on membrane or small sclerites (**TG11**-fragments) around the dorsal and lateral cercal base, occasionally upon tendons (Dermaptera: KLASS 2001a: figs. 22, 24).

Group **II** muscles: Muscles **41** and **42** of Odonata are directly attached to the cercal base, at least partly to apodeme **ma**. This conforms with muscle **f11\*** of the ephemeropteran *Povilla* (which is the muscle for which this group **II** has been defined) and muscles **287\*** and **42\*** of Caelifera resp. Dermaptera (which were tentatively assigned to group **II**, but could alternatively belong to group **IV**) (see KLASS 2001a: figs. 34–36). The interpretation of these muscles needs closer discussion:

In KLASS (2001a) the presence of muscles that run from tergum X directly to the basal sclerotization of the cercus in Pterygota raised a problem; the point is that it had to be hypothesized either that a group of cercal muscles is present in Pterygota (intersegmental tergo-coxosternal muscles, group **II**) that is absent in Zygentoma; or that in Pterygota a fragment of tergum XI has become integrated into the cercal base; or that a translocation of a muscle insertion from XIth-tergal territory to the cercal base has occurred. The muscles concerned are inserted on an apodeme at the mesal cercal base in many Pterygota, e.g., Ephemeroptera, Dermaptera, Ensifera (apodeme **ma** and muscles **42\*/287\*** in KLASS 2001a: figs. 30–32), Notoptera, and Odonata (*Calopteryx*: apodeme **ma** in Fig. 12, muscles **41** and **42**; KLASS 2001a: 275); KLASS (2001a) considers the presence of this apodeme as an apomorphy of Pterygota. The present study on Odonata provides an important additional aspect on the interpretation of these muscles and the sclerotization (of **ma**) to which they are attached. Among the Odonata the **ma**-sclerotization is only in *Calopteryx* and the closely related *Hetaerina* fused with the cercal sclerotization **CE** (as in the abovementioned other Pterygota); but it is clearly detached from **CE** and, instead, connected with the lateral tip of tergum **TG11** in *Aeshna*; in the other Odonata here studied the **ma**-sclerotization is isolated or absent (characters 72–74). This now indicates the possibility that **ma**, its sclerotization, and the insertion area of the respective muscle do possibly not genuinely belong to the cercal base, but could be parts of tergum XI that have become integrated into the cercal base. This seems to have occurred independently in Ephemeroptera, a subordinate clade of Odonata (including *Calopteryx* and *Hetaerina*), and at least some Neoptera; *Aeshna*, on the other hand, would show the plesiomorphic condition. Accordingly, the interpretation in Pterygota of the **ma**-inserted muscles, previously categorized as a separate group **II**, as further internal dorsal muscles X (of group **IV**) seems now feasible.

### 6.9.2. Ventral sclerotizations of the terminal abdomen

The nature of the ventral sclerotizations of the insect terminal abdomen (essentially the ‘paraprocts’) is generally a highly controversial and difficult issue. A discussion focused on Zygentoma, Ephemeroptera, Dermaptera, and Dictyoptera is given in K<sub>L</sub>ASS (2001a), including evidence from the musculature and (as far as available) nerve topography. The paraprocts in these taxa are likely composed of the coxae X (posteromesal parts) and laterocoxae X (anterolateral parts), which are (still?) separated in Ephemeroptera and Dermaptera; in addition, a sternum X seems to be present anteromedially in Zygentoma and Ephemeroptera. The subanal lobes are then possibly coxal lobes X, homonomous with, e.g., the gonoplags **gl9**. However, these hypotheses have remained very tentative, mainly because the structure of segments X and XI is strongly modified and reduced as compared to the preceding abdominal segments, and because complete data on the musculature of this part of the body are extremely sparse. It was additionally noted in K<sub>L</sub>ASS (2001a) that the results on the aforementioned taxa are not directly applicable to taxa that, like Odonata and (female) Notoptera, have a circumferential sclerite ring X (**TG10+LP** in Figs. 3, 12) with apparently ‘normal paraprocts’ (sclerites **AP**) behind it. The crucial point is the interpretation of the ventral part of this sclerite ring.

HEYMONS’ (1896, 1904) illustrations show that segment X in Odonata is ring-shaped and fairly long at least from the earliest nymphal stage onwards, and according to ANDO’S (1962) figures this condition can apparently be traced back to the embryonic origin of the posterior abdomen. HEYMONS indicates that segment X possesses a tergum and a ‘sternum’. It is thus likely that all parts of sclerite ring X actually belong to segment X (see section 6.9.1. for ANDO’S 1962 interpretation of dorsum X). Evidently, an extensive dorsal part of sclerite ring **TG10+LP** represents tergum X, as indicated by the origin on it of the cercal muscles X **41**, **42**, and **63**, and of the tergo-tergal muscle X **43** as compared to other Insecta (compare K<sub>L</sub>ASS 2001a: figs. 29–36).

For the ventral parts of sclerite ring X and the paraproctal sclerites **AP** the hypotheses (1)–(3) presented below appear possible. In the following the interpretation of the ‘paraprocts’ in insects according to K<sub>L</sub>ASS (2001a) is adopted, and homologies between Odonata and other insects are searched for. If the interpretations of K<sub>L</sub>ASS (2001a) will have to be revised for insects in general, only the names for structures will have to be exchanged in what follows, but comparison between Odonata and the other taxa as such will remain the same.

(1) The entire sclerite ring X **TG10+LP** is formed by tergum X, which extends far ventrally in all Odonata and is medially fused in Zygoptera and *Aeshna* (see character 64). The paraproctal sclerites **AP** then likely include the fused laterocoxae X and coxae X, the subanal lobes are the coxal lobes X. Sternum X, which would then transversely connect sclerites **AP** in the area of tendons **jt**, has been lost. With this hypothesis the membranous seam separating sclerites **AP** from sclerite ring X in Odonata would be homologous with the border between **pX\*** and **pXI\*** in Ephemeroptera and **LP\*** and **TG10\*** in Dermaptera (see K<sub>L</sub>ASS 2001a: figs. 23–26). Muscles **40** and **64** (Fig. 62) are intrasegmental tergo-coxal and/or tergo-laterocoxal muscles X. If it is legitimate to assume any homonomy for muscles (or unstriated strands) **44–47** with muscles in preceding segments, they could be considered Xth-segmental muscles that run from the laterocoxa and coxa to the (undifferentiated) vesicles/gonapophyses or styli.

(2) Sclerite ring X **TG10+LP** is composed of tergum X and laterocoxae X (as expressed by ‘**TG10+LP**’): the latter have fused with tergum X laterally, and with each other medially in Zygoptera and *Aeshna*, and they have lengthened as in the preceding segments. The paraproctal sclerites **AP** are then likely constituted by the coxae X alone, the subanal lobes are the coxal lobes X. Sternum X, which would then form the ventral anteromedian part of sclerite ring X, could be present in taxa with an anteriorly closed ring. With this hypothesis the membranous seam separating sclerites **AP** from sclerite ring X would be homologous with the border between **sX\*** and **pX\*** in Ephemeroptera and **AP\*** and **LP\*** in Dermaptera (see K<sub>L</sub>ASS 2001a: figs. 23–26). Muscles **40** and **64** (Fig. 62) are intrasegmental tergo-coxal muscles X, intrasegmental tergo-laterocoxal muscles X being absent. Muscles/strands **44–47** could be Xth-segmental muscles from the coxa to the (undifferentiated) vesicles/gonapophyses or styli.

(3) Sclerite ring X **TG10+LP** is composed of tergum X, laterocoxae X, and coxae X, which are all fused to each other. Sternum X would then form, as in the foregoing hypothesis, the ventral anteromedian part of sclerite ring X. The paraproctal sclerites **AP** are ventral sclerotizations XI, the subanal lobes are projections XI. With this hypothesis the membranous seam separating sclerites **AP** from sclerite ring X would be the ventral segmental border X/XI, homologous with the border between **sXI\*** (paired) and **sX\*** in Ephemeroptera and **DT\*** (unpaired) and **AP\*** in Dermaptera (see K<sub>L</sub>ASS 2001a: figs. 23–26). Muscles **40** and **64** are intersegmental dorsoventral muscles. Muscles/strands **44–47** are some intrinsic XIth-segmental muscles, for which further specification would hardly be possible.

These hypotheses could be evaluated using muscle data for different insect taxa, but such data are sparse,

and only a single piece of evidence appears to be relevant: The ventral muscles that insert anteriorly on venter IX (laterocoxa IX if differentiated; muscles **66+68** in Figs. 63, 65, 66, 68–70; KLASS 2003: **11\***, **12\*** in fig. 23 for Dermaptera; KLASS 2001a: **i9\*** in fig. 27 for Ephemeroptera, **62a,b\*** in fig. 28 for Zygentoma; KLASS 2000: **48\*** in fig. 20 for male dictyopteran *Mastotermes*) have their posterior attachments around the frontal margins of plates **sX\*** and **pX\*** in Ephemeroptera and **AP\*** and **LP\*** in Dermaptera, or on the frontal margin of the ‘paraprocts’ in taxa lacking this separation (e.g., Zygentoma and Dictyoptera). In Odonata the posterior insertion is medially at the frontal margin of plates **AP** (Fig. 62). This allows for hypotheses (1) and (2), but is incompatible with hypothesis (3).

This means that sclerites **AP** of Odonata include the coxae X, and only the location of the laterocoxae X either within **AP** or within **TG10+LP** remains questionable. Unfortunately, muscular connections of the area in Ephemeroptera and Dermaptera (the only insect taxa in which a separation of surmised coxal and laterocoxal sclerites appears to be distinct) are very different, while the musculature is poorer than in Odonata. Thus, there is no further evidence available on this issue.

It should additionally be noted that the musculature in Odonata bears some close resemblance with that in the zygentoman *Thermobia* (compare Fig. 62 and KLASS 2001a: fig. 28 derived from data in ROUSSET 1973): Muscle **40** could be homologous with muscles **63\*** and/or **64\*** in *Thermobia*, muscles **44**, **45**, and **46** with the muscle group **66\*** of *Thermobia*, and strand **47** perhaps with muscle **65\*** (no further muscles are documented for *Thermobia*).

HEYMONS (1904: 31f, fig. 3) recognized in female zygopterans the small external bulges (‘Knöpfe’) bearing the external origins of tendons **ut**, and the scar around the origin of tendon **tt** (see Figs. 12–15). He regarded them as vestiges of the tracheal gills (i.e., of the ‘cerci’ and the terminal filament), a view followed by ASAHINA (1954). However, this is not quite correct because the bulges and scars are the points of invagination of the tendons that partly bear muscle insertions (neither author mentions tendons or muscles associated with these scars). Of the muscles or strands inserted on **ut** (**46**, **47**, **58**, **61** in Figs. 21, 23) only those to the rectum were found striated in imaginal female *Calopteryx*, whereas those to sclerite **AP** are degenerated (if they are muscles at all). It seems conceivable that in the nymphs the latter are striated and move the gills. Then the external origin of the **ut**-tendon should in the nymph be located at the gill base – possibly at the mesal base, as the homologous flaps of the anal pyramid in Anisoptera are closed together by muscles (HEYMONS 1904: 36). This issue needs a detailed study of the nymphal terminal abdomen.

### 6.9.3. Characters of the terminal abdomen in Odonata

Two of the characters herein defined refer to the ventral part of sclerite ring X: character 65 of the condition of the ventral part of antecosta **ac10**, and character 64 of an open, weakened, or closed condition of the ventromedian part of sclerite ring X (see Fig. 12).

The ventral parts of sclerite ring X probably represent either the ventromesally expanded lateral parts of the tergum, or the laterocoxae X. A median fusion would be apomorphic if the former is true; if the latter is true, the median fusion would be plesiomorphic if a sternum X is additionally present, but apomorphic if there is no sternum X. Both the morphological interpretation of this area and the outgroup comparison are too ambiguous for outgroup scoring. The outgroup is thus scored ambiguous in character 64.

Nearly all Zygoptera have a massive ventral antecosta **ac10** (as in Figs. 7, 12; character 65); only *Drepanosticta* lacks it, and in *Lestes* it is weak. Such a strong ventral **ac10** is apparently absent in other Insecta, though the respective area is usually not described in sufficient detail; absence is clearly true for Notoptera females (K.-D. Klass unpubl. observations on *Grylloblatta campodeiformis*), which have a circumferential sclerite ring X resembling that in Zygoptera. With some low probability, however, **ac10** could be represented by the fold **stX\*** in *Thermobia* (ROUSSET 1973: fig. 4C; mentioned alternatively as a potential forerunner structure of **PS9** in section 6.5.7.). Accordingly, the outgroup is only tentatively scored ‘absent’ in character 65. The massive condition of the ventral **ac10** could thus be autapomorphic for Zygoptera or a subgroup thereof. Its weak development in *Drepanosticta* and *Lestes* may be due to its functional replacement by a strong ventral transverse bridge **IT9** (also found in *Epiophlebia*), which in these taxa is connected with the hind corners of tergum **TG9** and bears a ridge **xr** (Figs. 50, 51).

Three further characters refer to the presence of sclerotization on the apodeme or tendon **ma** (Figs. 12, 14) at the mesal cercal base (character 72) and to the connection of this sclerotization with either the cercal sclerotization **CE** (character 73) or tergum XI **TG11** (character 74); the two latter characters are not applicable to taxa in which **ma** is entirely membranous. Because the homology of the **ma**-area of Odonata with particular XIth-segmental areas in other insects as well as the homology of muscles inserted to this area is only tentatively resolved (see section 6.9.1.), the outgroup is here scored ambiguous for all three characters.

The very uniform pattern of cuticular tendons in the terminal abdomen of the Odonata (**ct**, **ht**, **it**, **jt**, **rt**; additionally **ut** and **tt** in Zygoptera; see Figs. 12–15) is

remarkable, the more so as the tendons are frequently present even if the muscles attached to them are degenerated or absent in the (mature) imago. Only in exceptional cases tendons are reduced or absent (see characters 69, 70, 78, 79) or show minor positional shifts (see character 71). In morphological studies such tendons are rarely considered, and outgroup comparison for Odonata is thus not on safe grounds. Hence, it is uncertain whether some of the tendons could be autapomorphic for Odonata, and in characters 70 (presence of **ht**) and 71 (location of **jt**) outgroup evidence is considered too sparse for scoring. In character 69 the outgroup is tentatively scored 'distinct' because tendons like **ct** are present in Pygidicranidae (KLASS 2003: **ct** in figs. 1–4). In characters 78 and 79 the outgroup is tentatively scored 'absent' because tendons **ut** and **tt** are more conspicuous than the others, yet such structures have apparently not been reported for other insects, and in the Dermaptera and Dictyoptera examined by the author such tendons are clearly absent (K.-D. Klass unpubl. observations on taxa included in KLASS 2003 and 1998).

The tendons **dt10** and **dt11** (characters 66 and 75) were only found in a few of the sampled Odonata: **dt10** only in *Epiophlebia*; **dt11** in the latter taxon (though 'indistinct') as well as in aeshnids and the zygopterans *Chlorocnemis* and *Mecistogaster*. Also for these tendons outgroup data are practically non-existing, and the outgroup is scored ambiguous for both characters. Yet, due to their potential homonymy with tendons in the preceding segments (**dt** in Fig. 1), both **dt10** and **dt11** might be plesiomorphic elements, especially the more widely distributed **dt11**.

Large lobes like **xl** and **yl** of *Epiophlebia* and Aeshnidae (see characters 76, 77), the remainders of the nymphal anal pyramid, have apparently not been reported for insects other than Odonata, and the outgroup is tentatively scored 'absent' for both characters. A distinct Xth-tergal process **dp** (character 68; Fig. 3) has been found only in *Calopteryx* among the Odonata here sampled; the outgroup is scored ambiguous as no own comparative studies were done. With regard to the bulge (or other projections) upon the posteroven-tral part of sclerite ring X (character 67), the outgroup is considered 'inapplicable', since (apart from female Notoptera) there is no sclerite ring X in other Insecta. Alternatively, the outgroup could be scored 'absent', since a bulge of this kind is apparently unknown in other Insecta.

## 7. Phylogenetic implications

It is not intended to use the list of characters compiled in this paper for a cladistic analysis; such analyses should wait for a larger taxon sample. However, a preliminary evaluation of the character data in Tab. 1 with regard to odonatan phylogeny will be given in this chapter.

### 7.1. Monophyly of Odonata

The abdominal characters herein examined provide some further potential autapomorphies of Odonata, confirming its monophyly (which is beyond doubt anyway). In the midabdominal segments (and partly in the genitalic segments) the terga possess a posterior transverse carina **ty**, a dorsal hinge line **dh**, and intertergal articulations with patches **ap** and triangular heavy sclerotizations behind **ty** (Fig. 1). The coxae of segment VIII, **CX8**, form anteriorly directed apodemes **ga** and tendons **gt** (Fig. 7). Doubtful odonatan autapomorphies are, among others, the ventral coxosternal keels **vk**, the vaginal sclerites **VB** (both absent in *Epiophlebia*; see section 7.2. for alternative interpretation), and some of the tendons in the terminal abdomen (**ht**, **it**, **jt**, **rt**; poor outgroup data).

### 7.2. Special role of *Epiophlebia* and clade Zygoptera + Anisoptera

*Epiophlebia* (Anisozygoptera) is in several characters highly peculiar among all the odonatan taxa here studied: It is the only sampled taxon that shows a basal fusion between the two gonapophyses IX **gp9** (Fig. 41; character 42), a row of saw-teeth **tm9** on **gp9** that reaches far basally (character 43), a tongue-like extension **i** of the gonapophyseal sclerite IX **GP9** (Fig. 41; character 46), a fusion between ante- and postlaterocoxa IX **LCa9** and **LCp9** (Fig. 36; formation of one-piece gonangulum; character 41), a further fusion of **LCa9** with coxa VIII **CX8** (Fig. 36; character 15), a median process **pp8** on the hind margin of laterocoxosternum VIII **LS8** (character 11), a unique conical, somewhat compressed shape of the stylus **sl9** (character 52; see also MATUSHKINA 2008b: 79), a distinct Xth-segmental tendon **dt10** (character 66), a complete lack of the ventromedian ridge **vk** on the pregenital

coxosterna (character 5), and, in the vagina, of a collar-shaped ridge **cr** (Fig. 38; character 29), of the vaginal sclerite **VB** (Fig. 38; character 27), and of a vaginal bulb **vb** (Fig. 38; character 32; while **vb** is likely non-homologous in Zygoptera and Aeshnidae).

Furthermore, *Epiophlebia* has a spine **sa** on **LCa9**, of which there is otherwise only a trace in the zygopteran *Diphlebia* (Fig. 36; character 38), and it shows a far median location of the accessory gland **ag** opening (Fig. 41; character 47), which is otherwise only found in *Lestes*.

For most of the characters listed above there is no clear outgroup comparison possible, so that phylogenetic implications are not clear. Of the few characters that can be reasonably polarized, however, some support a sistergroup relationship between *Epiophlebia* and a clade Zygoptera + Anisoptera; potential apomorphies of the latter clade are: (1) the presence of a ventromedian ridge **vk** on the pregenital coxosterna (at least of a short one; character 5; indeed, e.g., SCHMIDT 1915: 99 reports long **vk** for some Anisoptera other than Aeshnidae); (2) the presence of a collar-shaped ridge **cr** on the vagina (at least a fragmentary one; character 29); and (3) a loss of saw-teeth **tm9** in the basal parts of gonapophysis **gp9** (character 43).

This altogether does surely not provide strong evidence for a monophyletic Zygoptera + Anisoptera. In addition, some other characters variously point to a relationship of *Epiophlebia* either to Zygoptera or Anisoptera (i.e., Aeshnidae in the sample here used).

### 7.3. Clade *Epiophlebia* + Zygoptera

This hypothesis is supported by the following apomorphies shared between *Epiophlebia* and the zygopterans here sampled: (1) the basal connection of the gonapophyseal sclerites **GP8** of the two sides (Figs. 28, 37; character 19); (2) the far posterior location of the articulation between postlaterocoxa IX **LCp9** and coxa IX **CXa9** (Figs. 39, 41 versus Fig. 40; character 48); (3) the presence of tubercles on the distal part of the ventral gonoplac edge (character 53); in *Epiophlebia* as well as some Zygoptera this is a single far distal tubercle (Fig. 41), while most Zygoptera have a greater number of tubercles; however, vestigial tubercles have also been reported for aeshnids. Altogether, the evidence for this relationship is not very strong.

### 7.4. Clade *Epiophlebia* + Anisoptera

This traditional view is supported by the following apomorphies shared between *Epiophlebia* and Aeshnidae (partly also reported for other Anisoptera in the literature): (1) the presence of a longitudinal external ridge on the lateral margin of the pregenital terga (= ventral carina **vc**; Fig. 25; character 1), which, however, is only very short in *Epiophlebia* (limited to the posterolateral corner of the tergum); (2, 3) the presence in the imago of lobes **xl** and **yl** in the anus area. The evidence for this relationship appears even weaker than that for *Epiophlebia* + Zygoptera.

### 7.5. Monophyly of Zygoptera

The mono- or paraphyly of Zygoptera has been the most-disputed issue with regard to odonatan phylogeny. Monophyly of the group is supported by a few female postabdominal characters: (1) In all Zygoptera the bodies of the gonapophyses **gp8** of the two sides are basally more extensively fused than in *Epiophlebia* and Aeshnidae (i.e., the cleft between the two **gp8** is shorter; Figs. 26, 32, 33 versus 27, 36; character 16). (2) An evagination of the intima-bearing common oviduct **oc** into the vagina lumen (as in Fig. 8) is present in all Zygoptera but absent in Aeshnidae and *Epiophlebia* (character 36). (3) The tendons **ft** behind the bases of the gonapophyses **gp9** were found in all Zygoptera, but not in Aeshnidae and *Epiophlebia* (Fig. 39 versus 40, 41; character 45). (4) With the exception of *Drepanosticta* and, to some extent, *Lestes*, all Zygoptera have a massive ventral antecosta **ac10** (as in Figs. 7, 12; character 65), which is entirely absent in *Epiophlebia* and Aeshnidae. (5, 6) All Zygoptera have tendons **ut** and **tt** in the terminal abdomen (Figs. 12–15; characters 78, 79), though these are somewhat reduced in *Drepanosticta* (**ut**), *Platycypha*, and *Diphlebia* (**tt**). The evidence in favour of monophyletic Zygoptera is thus quite considerable.

### 7.6. Paraphyly of Zygoptera

There are also several likely apomorphic conditions that are shared between certain Zygoptera and either Anisoptera or *Epiophlebia* + Anisoptera (i.e., Aeshnidae resp. *Epiophlebia* + Aeshnidae in the present study). Importantly, however, the various apomorphies of this kind occur in different (sets of) zygopterans and

do thus not add up to some significant evidence in favour of paraphyletic Zygoptera. Such apomorphies are, for instance: (1) The fusion between postlaterocoxa IX **LCp9** and tergum IX **TG9** (character 40) is in some Zygoptera, e.g., *Lestes*, more extensive than in others (Figs. 26, 32, 33), thus approaching conditions in *Epiophlebia* and Aeshnidae (Figs. 27, 36). (2) *Mecistogaster* shares with *Epiophlebia* and Aeshnidae the presence of a midventral cuticular thickening **mr** on the vagina, around the posterior base of the oviduct **oc+oe** (Figs. 31, 35, 38; character 30). (3) *Argiolestes* is peculiar among the Zygoptera here sampled in having, like Aeshnidae (see above and PFAU 1991: fig. 20a; ASAHINA 1954: pl. 46 G7; TILLYARD 1917: 223) and Petaluridae (PFAU 1991: fig. 22; ST. QUENTIN 1962: figs. 4, 5), a discrete tuft of long setae on the tip of the stylus **sl9** (character 55). ST. QUENTIN (1962: 172) reports such tufts also for a few other Zygoptera: Chlorocyphidae in general (but no tuft was found here in *Platycypha*), and some Lestidae (*Sympetma*, with short setae). This character should be studied by SEM, as setae could be of very different length in related taxa, only the long ones recognized as a tuft by light microscopy. (4) Some Zygoptera, such as *Drepanosticta*, *Mecistogaster*, and *Chlorocnemis*, have, like *Epiophlebia* and Aeshnidae, distinct posterior apodemes **ba8** on laterocoxosternum **LS8** (see Fig. 7 for indistinct **ba8**; character 10). (5, 6) Like Aeshnidae (but unlike *Epiophlebia*), *Platycypha*, *Argiolestes*, and *Mecistogaster* among the Zygoptera show no traces of distal teeth **tm8** on the gonapophyses **gp8**, and **gp8**-ridges **gz** are absent in *Argiolestes* and indistinct in *Platycypha* (characters 23, 24). Altogether, indications for zygopteran paraphyly can surely not compete with the support for monophyletic Zygoptera listed in 7.5.

### 7.7. A functional aspect: transverse stiffening between gonoplastic bases

With regard to function, the perhaps most interesting result of the present study relates to the several sclerites effecting a transverse stiffening between the posterior bases of the left and right gonoplastic **gl9**. There are altogether three different sclerotizations that in different taxa can contribute to the stiffening, and these are located densely one behind the other: **PS9**, **IT9**, and the ventral anterior margin of **TG10+LP** (Figs. 46–61, compare Figs. 7, 39–41 for a less schematic view):

(1) The most anterior sclerite is **PS9**, which in *Calopteryx* and several other Zygoptera (especially those in Figs. 58–61) is optimized for transverse stiffen-

ing, as it shows a double transverse folding (S-shaped cross section in Fig. 7, left bottom) and its sclerotization is fully continuous across the midline. In the other extreme, represented by *Aeshna* and *Epiophlebia*, the **PS9** sclerotizations lack transverse folds and are medially completely divided (and furthermore fused laterally with coxa **CX9**; Figs. 46, 48).

(2) Immediately behind **PS9** sclerite **IT9** follows. This cannot effect any transverse stiffening in most Zygoptera, where it is tiny or absent (Figs. 52–61) or somewhat larger but weak (*Epallage*, Fig. 49), and in Aeshnidae, where it is large but very weak (Figs. 46, 47). In *Epiophlebia*, the zygopterans *Lestes* and *Drepanosticta* (Figs. 48, 50, 51), and perhaps the aeshnid *Anax* (MATUSHKINA 2008a: fig. 5B,C), however, **IT9** is strong and is laterally fused with the posterolateral corners of tergum **TG9**; *Lestes* and *Drepanosticta* additionally have the circumferential ridge **xr**, which further increases transverse stiffening.

(3) In nearly all Zygoptera, but not in *Epiophlebia* and Aeshnidae, the ventral anterior margin of **TG10+LP** is folded inward (**ac10**) and strongly sclerotized; the two only exceptions are *Drepanosticta* (absent) and *Lestes* (indistinct), i.e., the taxa with a strong, laterally connected **IT9**.

The transverse stiffening in that area is thus accomplished mainly by **IT9** in *Epiophlebia*, *Lestes*, and *Drepanosticta*, and mainly by **ac10** in all other Zygoptera, where it is supplemented by **PS9** to a varied extent (especially in *Calopteryx*, *Chlorocnemis*, and *Pyrrosoma*). In the Aeshnidae none of these sclerotizations appear to be suited for effectuating much transverse stiffening, only **PS9** in *Aeshna* may contribute a bit (while **PS9** is absent in *Caliaeshna*). In sum, there seems to be a strong functional need for such transverse stiffening in *Epiophlebia* and Zygoptera, but there is much evolutionary change with regard to the elements that contribute to it.

## 8. Conclusions

The present study has provided a complete description of the exoskeleton and musculature of the female *Calopteryx* abdomen from segment IV onwards, and parts of the nervous system have also been included. The exoskeleton has been studied in members of 15 further genera of Odonata that show a plesiomorphic design of the female genitalic region ('ovipositor-bearing Odonata') as compared to other Odonata (non-aeshnid Anisoptera); members of *Epiophlebia*, of Aeshnidae, and of a variety of zygopteran families

represent the three suborders Anisozygoptera, Anisoptera, and Zygoptera. The muscle data on *Calopteryx* have been compared with muscle data from previous studies on Odonata, and tables of homology and synonymy are presented. A list of 79 characters and a character table have been compiled for the female abdominal exoskeleton of Odonata; these characters can be used in forthcoming phylogenetic studies on Odonata. In order to provide outgroup comparison the comparative discussion of abdominal morphology has been done with an all-insect framework – as far as data are available.

The structure of the abdomen is fairly similar in all Odonata here studied, while it is clear from the previous literature that in the anisopteran families here not included the female genitalic region has undergone more or less drastic modification. Most of the variation in the taxon sample here used concerns minor changes that yield phylogenetically informative characters but do not lead to problems in terms of topographic homology (i.e., in the identification of corresponding parts). Some problems of this kind do only occur in the few areas that show particularly strong variation: the bases of the gonapophyses **gp8** (problems resulting from different degrees of basal fusion), the contact area of tergum, ante-, and postlaterocoxa IX (difficult identification of borders between sclerites **TG9**, **LCa9**, and **LCp9**) and the border area of venters IX and X (with sclerites **PS9** and **IT9**). Most striking is the very consistent presence of all the small, membranous tendons distributed across the abdomen (the terminal abdomen in particular), and especially the presence of the tendons in the cases where the associated muscles were found absent in the imago. This indicates that the muscles might still be present and functional in teneral individuals, which, in turn, is in agreement with previous findings that the degeneration of abdominal muscles in Odonata continues during the imaginal stage. This also causes problems in the use of many muscle characters in phylogeny reconstruction.

The exoskeleton of the midabdominal segments in Odonata shows a design unique among insects. This is due to the presence of a tergal transverse carina **ty**, of a middorsal hinge line **dh**, of a midventral keel **vk** (present to a varied extent), of two pairs of anterior coxosternal apodemes **at** and **pa**, and, in particular, of intertergal articulations with soft cuticular patches **ap** and triangular heavy sclerotizations in front of them. The latter feature appears to be a mechanical adaptation for an elaborate dorsoventral bending of the abdominal segments with respect to each other, as it occurs, for instance, during mating. The strong upper and lower external dorsal muscles (**7**, **8**), which are situated above and below the intertergal articulations, likely play the main role in this movement. In the midabdominal musculature of (adult) Odonata the detailed

similarities to Megaloptera in the ventral diaphragm and the complete absence of internal ventral and dorsal muscles, reminiscent of Phasmatodea, are further striking aspects. The abdominal spiracles of Odonata lack, in contrast to many Neoptera, a manubrium apodeme; like in many Neoptera, however, a zone **ZE** of anastomosing ridges is present immediately internal to the closing bars. For the abdominal spiracle muscles found in some Odonata the homology with spiracle muscles in Zygentoma and Neoptera remains unclear due to positional differences. The midabdominal nervous system in Odonata resembles that in Neoptera, including the presence of anastomoses **IT–A** and **C–T**. However, the two major ventral nerves (**B** and **C**) are combined in one tract (**B+C**), like in some Ensifera but in contrast to the remaining Neoptera studied.

With regard to the female genitalic region the composition of the ectodermal gonoducts has here been discussed for a broad range of Insecta, with consideration of previous results on gonoduct ontogeny. A VIIth-segmental genital opening (primary gonopore) covered ventrally by a genital fold VII (occasionally sclerotized), as found in Archaeognatha (vestigial fold), Zygentoma, Dictyoptera, and Ensifera, appeared previously as the likely groundplan condition of the Pterygota. However, it has been demonstrated herein that Odonata and at least several other orders of the 'lower' Pterygota (e.g., Notoptera, Mantophasmatodea, Caelifera, basal Dermaptera) have similar vaginae that open on the hind part of segment VIII, receive the spermatheca dorsally and the median oviduct ventrally, and also receive corresponding muscles. In terms of the potential homology of these vaginae between the taxa, differences in the position of the vaginal openings (vulvae) and in the pathways of gonoduct development have been shown to be of limited relevance (while these differences lead to problems in the terminology of the gonoducts). Consequently, an VIIIth-segmental vulva now appears as likely for the pterygote ground plan as does a VIIth-segmental primary gonopore.

The presence of discrete accessory glands of segment IX is likely an autapomorphy of the Dicondylia. Due to the varied occurrence in Dicondylia of paired or unpaired glands and the potential co-occurrence of both in Auchenorrhyncha, however, a plesiomorphic presence of two different sets of glands must probably be assumed. Odonata have the paired glands. Their openings are closely associated with the anterior ends of the olisthetes of the two sides, and they may produce a grease-like substance supporting the gliding activity in this groove-and-tongue system.

The sclerites and muscles of the female genitalic region in Odonata and some groups of Neoptera have been traced back to elements in Archaeognatha and Zygentoma; one major issue was the identification of

laterocoxal, coxal, and sternal sclerotizations. Odonata, Notoptera, Mantophasmatodea, and Caelifera, all with an VIIIth-segmental vulva, share a striking modification of the VIIIth-segmental sclerites: the laterocoxae **LC8** have become strongly lengthened and – under inclusion of either sternum **ST8** or a VIIth-segmental languette sclerite **LG7** – medially fused to form one large plate, the laterocoxosternum **LS8**. This **LS8** resembles the coxosterna of the preceding segments, but in contrast to these the coxae **CX8** are not included; the latter have remained discrete, heavy sclerites at the bases of the gonapophyses **gp8**. In taxa with a functional ovipositor such a lengthening of venter VIII, by which the hind rim of venter VII and the bases of gonapophyses **gp8** become far separated, is likely only possible in combination with a genital opening on the hind part of venter VIII.

In segment IX the presence in nearly all ovipositor-bearing Odonata of a bipartite laterocoxa **LC9** (two-piece gonangulum: sclerites **LCa9** and **LCp9**) is most striking. The bipartition corresponds with that in Archaeognatha, but like in most other Dicondylia the anterior sclerotization (**LCa9**-part) is heavy and articulated upon the basal sclerotization of gonapophysis **gp8**. Only *Epiophlebia* among the Odonata was found to have **LCa9** and **LCp9** fused. Therefore, it is ambiguous whether a one-piece or a two-piece gonangulum was present in the ground plan of the Dicondylia. The coxae **CX9** in Odonata show plesiomorphic correspondence with those in Zygentoma, Dermaptera, Mantophasmatodea, Acercaria, and Endopterygota by the lack of a detached anteromedian transverse sclerite (anterior intervalvula); in contrast, such a discrete sclerite is found in Archaeognatha and, with a different composition, in Orthoptera and Dictyoptera.

The area behind the posterior bases of the gonoplares is interesting from both the morphological and the functional point of view, because there are three different sclerotizations that can transversely stiffen the area between the posterior gonoplares bases. Sclerite **PS9** fulfils this function in many Zygoptera, but (due to a median division) much less so in other Zygoptera, *Aeshna*, and *Epiophlebia*. Sclerite **IT9**, which is very weak in Aeshnidae and very small or absent in most Zygoptera forms a firm transverse bridge between the posteroventral corners of tergum **TG9** in *Epiophlebia*, *Lestes*, and *Drepanosticta*. In all Zygoptera except for *Lestes* and *Drepanosticta* a heavily sclerotized ventral antecosta **ac10** additionally keeps the gonoplares bases apart.

The gonapophyses **gp8** and **gp9** of Odonata show, despite the strong modification of the ventral sclerotizations VIII, a fairly plesiomorphic condition with a complete olistheter, but they are completely and particularly heavily sclerotized. While in the insect ground plan the gonapophyses **gp8** are likely entirely

free and the **gp9** either free or basally fused, in Odonata the **gp8** have become basally fused in all Zygoptera, and a basal fusion of the **gp9** has been found only in *Epiophlebia*. Small lobes **vl** at the mesal bases of the gonapophyses **gp8** are consistently present in Odonata and guard the vulva. Among insects such processes have been reported only for Caelifera and Dictyoptera, where, however, they are reduced during nymphal development. The consistent presence of styli on the gonoplares **gl9** of Odonata contrasts with most but not all Neoptera.

With regard to the terminal abdomen of Odonata the re-evaluation of previous arguments and a discussion of muscular connections clearly showed that some pair of terminal appendages are the true cerci; this may settle an old dispute. The cercal musculature largely corresponds with that in Ephemeroptera and Neoptera; like in many (but not all) other members of these taxa, cercal muscles XI are absent. The retention of the attachment of one internal dorsal muscle X on the unfragmented median part of tergum XI is a plesiomorphy shared between Odonata and Ephemeroptera. The composition of the sclerite ring X, which is ventrally continuous in most Zygoptera but  $\pm$  incomplete in *Epiophlebia* and Aeshnidae, remains enigmatic. It may be entirely formed by the ventrally expanded tergum X, or the laterocoxae X are additionally included; the coxae X are likely represented by the plates **AP** ('paraprocts'), which may additionally include the laterocoxae X; the presence of a sternum X is generally unclear. Striking aspects of the musculature in *Calopteryx* are the presence of an alary muscle XI (**51**); apart from Odonata only known for the zygentoman *Thermobia* and of a transverse muscle connecting the left and right cercal bases (**48**; so far not reported for Insecta).

The data on the female exoskeleton of the 16 species of Odonata here studied have been used to build a character list and character table comprising 79 abdominal characters. However, age-dependent variation (e.g., in the degree of fusion between sclerites) frequently causes problems in the assignment of character states to taxa. The use of many characters in phylogeny reconstruction is difficult due to insufficiently supported polarity assumptions, which either result from an extensive lack of data for many insect taxa, or, if data are sufficient, from ambiguous outgroup comparison. Phylogenetic implications of the characters studied have been discussed but must be considered preliminary.

The (undoubted) monophyly of the Odonata is confirmed by several abdominal apomorphies, such as the presence of a tergal carina **ty**, a middorsal hinge **dh**, and intertergal articulations in the midabdominal segments, and the occurrence of anterior apodemes **ga** and tendons **gt** on the coxae **CX8**. The abdomi-

nal characters here defined underline the special role of *Epiophlebia* among extant Odonata, as this taxon shows many unique features. Evidence on the relationships between the three odonatan suborders is ambiguous. A few characters agree with the traditional view of a clade *Epiophlebia* + Anisoptera (very short ventral carina **vc** present, anal lobes **xl** and **yl** present), while others favour either *Epiophlebia* + Zygoptera (basal connection of gonapophyseal sclerites **GP8**, far posterior location of articulation **LCp9-CXa9**, tubercle(s) on distal part of ventral gonoplac edge present) or Zygoptera + Anisoptera (ventromedian ridge **vk** on pregenital coxosterna present, fragmentary collar-shaped ridge **cr** on vagina present, loss of saw-teeth **tm9** in basal parts of gonapophysis **gp9**). The monophyly of Zygoptera is considerably supported by a variety of abdominal characters (gonapophyses **gp8** basally fused, oviduct **oc+oe** evaginated into vagina, tendons **ft** present, massive ventral antecosta **ac10**; tendons **ut** and **tt** present). On the other hand, evidence in favor of zygopteran paraphyly is scattered, with the various characters suggesting different (groups of) zygopterans to be related to *Epiophlebia* and Anisoptera. In sum, apart from considerable support for monophyletic Zygoptera, phylogenetic implications based on female abdominal characters are widely ambiguous. Improving the morphological data base for outgroup taxa would probably help, as such data might clarify the polarity of many characters within Odonata.

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