

A general theory of genital homologies for the Hexapoda (Pancrustacea) derived from skeleto muscular correspondences, with emphasis on the Endopterygota

Brendon E. Boudinot

Department of Entomology & Nematology, University of California, Davis, One Shields Ave., Davis, CA 95616, USA



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ABSTRACT

No consensus exists for the homology and terminology of the male genitalia of the Hexapoda despite over a century of debate. Based on dissections and the literature, genital skeleto muscular correspondences were compared across the Hexapoda and contrasted with the Remipedia, the closest pancrustacean outgroup. The pattern of origin and insertion for extrinsic and intrinsic genitalic musculature was found to be consistent among the Ectognatha, Protura, and the Remipedia, allowing for the inference of homologies given recent phylogenomic studies. The penis of the Hexapoda is inferred to be derived from medially-fused primary gonopods (gonopore-bearing limbs), while the genitalia of the Ectognatha are inferred to include both the tenth-segmental penis and the ninth-segmental secondary gonopods, similar to the genitalia of female insects which comprise gonopods of the eighth and ninth segments. A new nomenclatural system for hexapodan genitalic musculature is presented and applied, and a general list of anatomical concepts is provided. Novel and refined homologies are proposed for all hexapodan orders, and a series of groundplans are postulated. Emphasis is placed on the Endopterygota, for which fine-grained transition series are hypothesized given observed skeleto muscular correspondences.

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1. Introduction

“Existe-t-il un plan unique dans la composition des oviscaptes et des verges des Insectes?” – Lacaze-Duthiers (1849, p. 354).

“This paper is an attempt to show the unity of ... structure that prevails throughout all ... orders of insects. It is hoped that it will be of special service to systematists in entomology and that it will meet with approval from students of morphology.” – Snodgrass (1909, p. 1).

The male genitalia of the Hexapoda have attained a resplendent degree of structural and functional diversity unparalleled in other groups of Arthropoda. As such, male genitalia have been and are recognized as a critical source of characters for taxonomy and systematics (Coleoptera, Sharp & Muir, 1912; Lepidoptera, Eyer, 1924; Diptera, Wood, 1952; Siphonaptera, Smit, 1957; Psocodea, New, 1974; Hymenoptera, Schulmeister, 2003; Auchenorrhyncha, Holzinger et al., 2003; overall, Song and Bucheli, 2010; Neuropterida, Liu et al., 2016; etc.). However, determining the homologies of these structures has remained a challenging evolutionary puzzle,

with thousands of terms (Tuxen, 1956; 1970a) applied with varying degrees of consistency across, and often within, the orders. Four primary theories have been developed to explain the homologies of the genitalia of the Hexapoda, here termed the (1) “coxopod”, (2) “penis-coxopod”, (3) “multi-coxopod”, and (4) “ontogenetic” hypotheses. The former three hypotheses postulate that the genitalia of the Hexapoda are homologous with a single or multiple pairs of abdominal appendages, while the latter hypothesis postulates *de novo* origin of genitalic structures given variation in the splitting of the genital *anlagen*, particularly in the Endopterygota, which display complex developmental patterns.

At a gross level, two structures are consistently observed across most ectognathian orders: a median unpaired “penis” and outer paired appendages which function as claspers in numerous lineages or which bear single-segmented apical styli. This observation is the basis for the coxopod hypothesis, which homologizes the intromittent organ and claspers with the penis and coxopods, respectively, of the Archaeognatha and Zygentoma, without assumptions of the origin of the penis. These two homologies, that of the claspers and penis, are agreed upon by a number of authorities. This hypothesis was assumed by several authorities, including

E-mail address: boudinob@gmail.com.

Crampton (1919, 1920, 1921, 1922), and expanded upon by Michener (1944a, b), Mackerras (1970), McAlpine (1981), among others. The female ovipositor system of pterygotes provides circumstantial support for the coxopod hypothesis, as the ovipositor has been satisfactorily homologized with the eighth and ninth abdominal appendages of the apterygote ectognaths (e.g., Scudder, 1961, 1971; Mickoleit, 1973b; Klass et al., 2012). However, the coxopod hypothesis is complicated by the supposition that the penis is derived from the tenth abdominal segment (Heymons, 1897; Qadri, 1940; Birket-Smith, 1974; “penis-coxopod hypothesis”), or from other elements (see section 3.1.4.2 below), and by a more recent extension of the theory: Aspöck (2002) and others (Aspöck and Aspöck, 2008; Liu et al., 2016) postulated that the sclerotic elements of the highly modified genitalia of Neuropterida are derived from appendages of the ninth, tenth, and eleventh segments, hereafter termed the “multi-coxopod hypothesis”.

Contrastingly, the “ontogenetic” hypothesis of Snodgrass (1931, 1935a, 1941, 1952, 1957, 1958) was based on the developmental observations of Zander (1900, 1901, 1903) and others (see references within Snodgrass’s work and the reviews of Matsuda, 1957, 1958, 1976). Snodgrass (1935a, pp. 586–592) proposed a model wherein the genitalia of Pterygota consist of “phallic” and “periphalllic” apparatus (hereafter termed the “phallic-periphalllic model”; see figures 299 and 300 of Snodgrass, 1935a). In *Principles of Insect Morphology*, Snodgrass (1935a) agreed with other authorities that the “periphalllic” structures, or claspers, were homologous with coxopods, but rejected the homology of any male structure with gonapophyses of Archaeognatha, which are the inner movable elements of the coxopods, medial to the gonostyli; later, Snodgrass (1957) completely rejected the coxopod hypothesis. Snodgrass considered phallic organs to include all structures produced by the fusion of a median pair of genitalic lobes during post-embryonic development. This meant, for example, that the erstwhile claspers of Hymenoptera (Crampton, 1919) are homologous with the “phallobase” of Coleoptera, which are variably armed with “parameres”. Given this and other ontogenetic observations, Snodgrass assumed that the phallic structures were *de novo* organs, without muscular homologies across the orders, and “bound by no phylogenetic influences to conform with the structure of any ancestral appendage” (Snodgrass, 1935a, p. 589). Due to the tremendously influential nature of Snodgrass’s work, his phallic-periphalllic model and terminology continue to be presented singly (e.g., Beutel et al., 2014) or side-by-side (e.g., Gullan and Cranston, 2010) with the coxopod hypothesis in entomology textbooks.

The objective of the present work is to test the coxopod, penis-coxopod, multi-coxopod, and *de novo* hypotheses based on direct observation of genitalic skeletomusculature of the Endopterygota (section 4) and via synthesis of the literature (section 3), particularly by comparison of the apterygote orders with the Remipedia, one of the closest pancrustean outgroups of the Hexapoda (Regier et al., 2010; Misof et al., 2014). From the skeletomuscular perspective, the coxopod and multi-coxopod hypotheses predict that the arrangement of muscular origin and insertion will be similar to that observed in Archaeognatha, and the penis-coxopod hypothesis predicts that the arrangement will be similar to that of appendages from multiple segments of the Remipedia. Specifically, the predictions are that structures identifiable as gonocoxae will bear extrinsic muscles originating from the tergum and ventral or sternal ligaments, with the abdominal-gonocoxal musculature repeated once or more than once for the coxopod and multi-coxopod hypotheses, respectively. Moreover, the coxopod hypotheses predicts that the genital appendages will have intrinsic musculature originating within the coxopodal sclerites and inserting on all mobile sub-elements, unless the origins have

shifted due to sclerite fusion. The “ontogenetic” or *de novo* hypothesis makes no *a priori* predictions except that the musculature will be unaccountable via comparison with the Archaeognatha and other apterygote lineages; for this reason, among others (see section 2.2), the *de novo* hypothesis is here treated as an alternative hypothesis, rather than the null. Skeletomusculature has previously been shown to be useful for homologizing both male and female genitalic structures (e.g., Hieke, 1966; Kristensen, 1984; Krell, 1996; Hünefeld et al., 2012), and is a largely untapped resource of characters for the male genitalia of the Endopterygota. No focused effort, to the author’s knowledge, has been made thus far to homologize male genitalic musculature across the Endopterygota, or between the Hexapoda and other Pancrustacea.

2. Materials and methods

2.1. Material and dissections

To make observations of genitalic skeletomusculature, one to several specimens of 10 of the 11 endopterygote orders were dissected: (1) Hymenoptera (Cimbicidae: *Cimbex rubida*), (2) Raphidioptera (Raphidiidae: *Agulla*), (3) Megaloptera (Corydalidae: *Corydalus*, Sialidae: *Sialis nevadensis*), (4) Neuroptera (Myrmeleontidae: ?*Dendroleon*), (5) Coleoptera (Cantharidae: *Cantharis* (*Cantharis*), Curculionidae: *Hypera* cf. *postica*, Dytiscidae: *Ilybius biguttulus*), (6) Strepsiptera (Elenchidae: *Elenchus koebeli*), (7) Mecoptera (Nannocharistidae: *Nannocharista andina*, Boreidae: *Boreus reductus*, Bittacidae: *Apterobittacus apterus*, *Harpobittacus phaeoscius*, Panorpidae: *Panorpa nuptialis*), (8) Diptera (Tipulidae: *Tipula* (*Hesperotipula*) *californica*), (9) Trichoptera (Limnephilidae: *Pycnopsyche antica*), (10) Lepidoptera (Noctuidae spp., Pyralidae: *Plodia interpunctella*). As the dissection of the strepsipteran, *Elenchus*, was inconclusive, micro-CT scans were evaluated (Hünefeld et al., 2011b). To include the final order of the Endopterygota, detailed comparative anatomies of Siphonaptera (Snodgrass, 1946; Günther, 1961) were studied. Additional skeletomuscular studies are cited as necessary in the taxon accounts, and a review of the literature is provided in section 3.

Specimens were from the author’s personal collection or were loaned from the Bohart Museum of Entomology (University of California, Davis) and the personal collection of Dr. Karl M. Kjer (unaffiliated). Specimens were preserved in varying concentrations of ethanol (unknown to 100%) and had been collected from a few days before dissection to over 50 years prior. After dissection, the vouchers were deposited in the UCDC preserved in 95% ethanol, except for *Panorpa nuptialis*, for which the genitalia were placed in a glycerin-filled microtube beneath the pinned specimen; specimen data, including unique specimen identifiers, are provided in Table S1. Identification resources used during this study are indicated as a note at the end of each taxon account; if there is no such note, the identification was made by a prior worker.

Dissections were carried out using size 5 forceps and minuteman pins in ethanol-filled dishes with a flattened disc of Blu-Tack (Bostik Ltd., Leicester, U.K.) at the bottom. A diffuse fluorescent lamp and strong fiber-optic Leica KL 1500 LCD illuminator were used. The dissection dish was situated on an X-Y mobile stage under a Leica MZ 16A with 115× maximum magnification and a 1.0× Planapo objective. Dissections were documented with a microscope-mounted JVC KY F75U digital camera. Montages were generated from stacked micrographs using Automontage (Synoptics Ltd., Cambridge, England) and figures were processed using Adobe Photoshop and Illustrator (Adobe Systems Inc., California, U.S.A.).

During dissections, sclerites were sequentially removed or chipped away, while muscles were removed strand-by-strand or by units. As copulatory structures may include the genitalic

appendages and sclerites of the surrounding abdominal segments, the abdominal segments were counted from anterior to posterior. Starting the abdominal segment count with the first tergum is preferable as the first and sometimes second abdominal sternum is reduced, fused, or absent in many orders; careful dissection is required in some cases to confirm segment count. Muscle and soft tissue were discarded after dissection, but sclerites along with the remainder of the specimen were preserved in 95% ethanol. Descriptions of the genital appendage skeletomusculature of the dissected taxa are provided below; description length varies based on modification complexity, and in most cases, does not include the pregenital abdominal sclerites.

2.2. Evolutionary morphology and anatomical assumptions

General. The comparative method, in the framework of evolutionary morphology (Richter and Wirkner, 2014), was employed in this study with specific reference to the phylogeny of the Pancrustacea as estimated by Regier et al. (2010), the Hexapoda by Misof et al. (2014), and for the Endopterygota by Peters et al. (2014). This study began with comparative study of the genitalic skeletomusculature of the Endopterygota, based on a series of dissections and available literature (section 2.1 above, chapter 4 below). The groundplan morphology of the Endopterygota (Fig. 1.F5) was established through a cycle of induction from comparative observations coupled with testing of deductive predictions of homology hypotheses for each muscle and sclerite (*i.e.*, the expectation that a given muscle with given topology occurs in a similar location and is similarly oriented). Once all muscles had been accounted for in this way, comparisons were made with the apterygote Ectognatha given the available literature on the skeletomusculature of the Archaeognatha and Zygentoma.

After establishing correspondences between the apterygote ectognaths and the Endopterygota, a concerted study of the literature on Palaeoptera, Polyneoptera, Condylognatha, and Psocodea was undertaken (section 3.2) to refine homologies and establish a transformation sequence from groundplan to groundplan (Fig. 1.B–F). A final layer of analysis was added via comparison of the skeletomuscular topologies of the abdomen and genitalia of the Hexapoda with the trunk musculature of the putative pancrustacean sistergroup, the Remipedia (section 3.1). In this context, the Protura proved to be particularly enlightening. Through repetition of the complete comparison cycle, a general theory was derived for the homologies of the male genitalia of the Hexapoda (see Fig. 1) and a nomenclature for abdominal musculature was developed and applied (Table 2). Results from these procedures are presented linearly, starting with the pancrustacean outgroup and proceeding through the hemimetabolous Ectognatha (chapter 3) to the Endopterygota (chapter 4). A number of homology problems remain, which may be addressed via morphological study at a finer level of detail, more holistic integration of skeletomuscular observations across the abdomen, with integration of innervation, and new dissections and analyses of groups for which only literature was available.

Practical. In the present work, I conceive of homology as the correspondence of spatial relationships of parts and their subparts contrasted across statistically-tested molecular phylogenies. Specifically, Remane's (1952) criteria of homology recognition were employed: In compared individuals, (I) parts correspond in their location relative to other parts, (II) subparts correspond in their location relative to other subparts, (III) intermediate forms connect disparate forms, and (IV) simple, corresponding structures are shared among closely related taxa. Homology hypotheses were almost exclusively considered for adult structures, regardless of

functionality or vestigiality, although developmental observations were references or interrogated where appropriate.

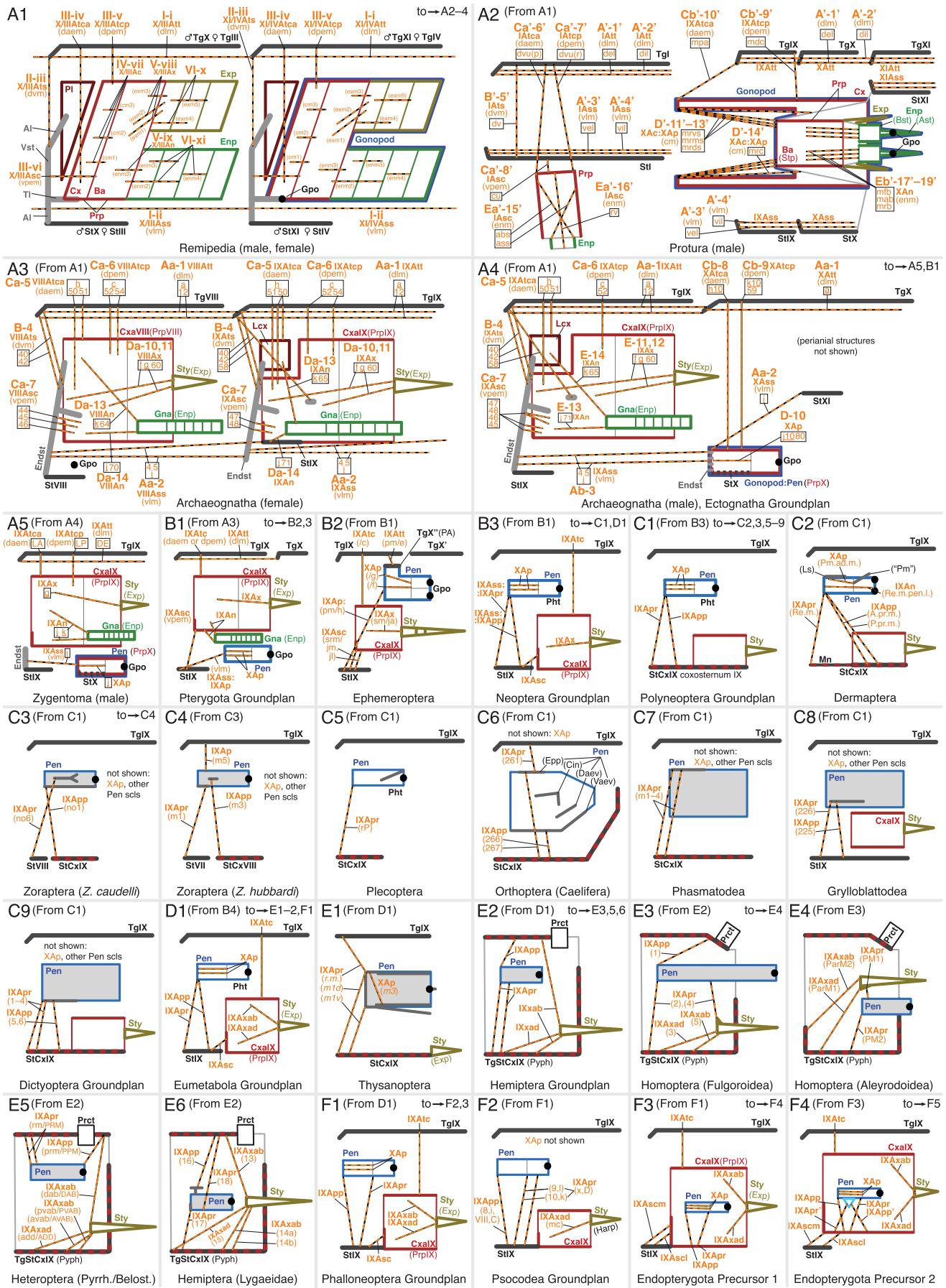
Four key assumptions were made when attempting to homologize muscles. (1) Muscles must be attached to both an origin and insertion site. Muscle attachments may not “jump” from sclerite to sclerite; they cannot spontaneously disappear from one sclerite and appear on another; shift of attachments across membrane is considered rare. (2) Change in the position of muscle attachments occurs primarily through shift across the sclerites or drift with sclerites as the sclerites are reorganized via fragmentation, fusion, reduction, expansion, and migration. (3) Muscle count changes through reduction (loss) and division (gain), *i.e.*, new muscles must be derived from previously existing musculature (examination of intermediate taxa clarifies muscle unit homology). (4) *De novo* appendage evolution must be supported by anatomical evidence, *i.e.*, *de novo* appendage evolution is a complex event and is therefore not the null hypothesis.

These assumptions require accounting for each muscle's respective origin and insertion, and comparison of these topological observations across all sampled lineages. This allows for sclerite homology to be logically parsed via hypothetical transformation series, including intermediates and groundplans for the most recent common ancestors of well-supported clades. While particular muscle units may be differentiated for functional reasons, accounting for muscle attachments allows the observer to recognize correspondences even when the anatomical detail (such as sclerite architecture) is highly divergent from previously encountered skeletomuscular conformations. Moreover, for any single muscle inserted on a sclerite there must be an origin, providing twice the amount of presence/absence information for tracking correspondences than just accounting for sclerite presence or absence relative to other sclerites. It should be noted that in the present work, sclerites are abstractly conceived of as elements of a continuous surface—that of the integument, which is like a balloon filled with liquid. Thus, in effect, tectonic-like migration of sclerites across the surface of the integument is observed across clades, with musculature providing consistent anchoring information about the sclerite identity, regardless the exact conformation of the genitalic structure under consideration.

3. Results: analysis of literature and synthesis with new observations

“There are no new facts of structure presented [in this section] that are not recorded elsewhere; but a mere lack of new information should not be held to lessen the value of a piece of work, or to make it unworthy of scientific consideration. Facts are the food of science, and, like all food, they do not contribute to the growth of the body until digested, distributed, and assimilated.” — Snodgrass (1926, p. 2).

In this chapter, two main sections are presented. Section 3.1 reviews the body plans and abdominal skeletomusculature of the Remipedia and the apterygote Hexapoda. Section 3.2 includes definition of a nomenclature for genitalic muscles and systematically treats the genitalic skeletomusculature non-endopterygote Hexapoda. Observed correspondences in sections 3.1 and 3.2 are inferred to be homologies given recent phylogenetic and phylogenomic results. Crucially, Hexapoda are now known to be nested within the “Crustacea” forming the clade Pancrustacea (e.g., Dunn et al., 2008; Philippe et al., 2009; Edgecombe et al. 2011; Nielsen, 2011; Legg et al., 2013; Edgecombe and Legg, 2014), and the Remipedia or Remipedia + Cephalocarida are supported as sister to the insects, forming the clade Miracrustacea (e.g., Regier et al., 2008, 2010; von Reumont et al., 2012; Oakley et al., 2012; Rota-Stabelli et al., 2013).



3.1. Comparison of Remipedia and apterygote Hexapoda

This section outlines the generalities of abdominal or trunk morphology for the Remipedia (subsection 3.1.1), the apterygote Ectognatha with emphasis on the Archaeognatha (subsection 3.1.2), and the Ellipura and Diplura with emphasis on the Protura (subsection 3.1.3). After defining the non-genitalic and genitalic skeletomusculature for these groups based on the literature, explicit comparisons are made in order to establish correspondences between non-genitalic and genitalic sclerites and muscles (subsection 3.1.4).

It should be noted that there is a “hard” terminological homonymy between the synonymous leg base structures called “protopodites” and “coxopodites” within the Pancrustacea (Bitsch, 2001; Boxshall, 2004): in crustaceomorphs, the basal segment is termed the “coxa”, the distal segment the “basis”; in hexapodans, the basal segment is the “subcoxa”, the distal segment the “coxa”. Here, the term “coxa” will be used for the distal segment. Additionally, and the suffix “-ite” has some confounding or unnecessary usages (Snodgrass, 1963, p. 9), and will only be used in this work to denote a smaller fragment of the coxa or other sclerotic part. Overall, leg parts will be referred to as follows (usage modified from Bitsch, 2001 and Boxshall, 2004): *Protopod* = primary proximal leg part, itself segmented into proximal *subcoxa* and distal *coxa*; *exopod* = lateral limb ramus situated distally on protopod; *endopod* (= *telopod*) = medial limb ramus situated distally on protopod, itself segmented from proximal to distal into the *trochanter*, *femur*, *tibia*, *tarsus*, and *pretarsus*. The term “coxopod” is used herein to refer to abdominal legs generally, in functional distinction to ambulatory thoracic or natatory trunk legs.

3.1.1. Remipedia

Body plan. Before addressing the skeletomusculature of the Remipedia, or “aquatic centipedes” (Yager via Schram and Jenner, 2001), it is first necessary to outline the general body plan of

these animals (see Yager, 1981) in a broader phylogenetic context, particularly in comparison with the “generalized” Pancrustacea, i.e., those pancrustaceans which are long-bodied and are not Branchiopoda or Hexapoda (McLaughlin, 1980; Schram, 2013). The head of remipedes, as derived in various other pancrustaceans (Schram, 2013), is a cephalothorax which comprises seven segments (Yager, 1981). These segments, from an integrated evolutionary perspective, are explicitly aligned as follows: (I) first segment, with eyes innervated by the protocerebrum—a “chimeric” entity derived from fusion of an apical, asegmental “archicerebrum” and first metamer “prosocerebrum” (Urbach and Technau, 2003a; Steinmetz et al., 2010); (II) second segment, with deutocerebrum which innervates the antennules (= antennae); (III) third segment, with tritocerebrum which innervates the second antennae (absent in Hexapoda), and associated with the labrum, which is developmentally and neurologically homologous with the frontal appendages of onychophores (Strausfeld, 2012; Ortega-Hernandez et al., 2017; although see Scholtz and Edgecombe, 2006; Richter et al., 2013); (IV–VI) fourth through sixth segments, with homonomous mandibles, maxillules (= maxillae), and maxillae (= unfused labium), all innervated by the gnathocerebrum (Urbach and Technau, 2003b); and (VII) seventh segment, with maxillipeds (= first thoracic limbs). Incorporation of the first thoracic legs into the head is likely an apomorphic state relative to the plesiomorphic condition of a 6-segmented cephalon, which is also observable in the Hexapoda and Myriapoda.

Unlike most other generalized pancrustaceans, remipedes do not have differentiated trunk and abdominal tagmata, rather they have up to 42 homonomous trunk segments (i.e., those following the maxillipeds), plus an “anal somite” or “telson” with a pair of unsegmented caudal rami (Yager, 1981; Koenemann et al., 2006, 2007a, b, 2009). The term “telson”, despite wide historical use, will be abandoned in the present work, as it assumes derivation of the arthropod body plan from an annelid ancestor; the term “anal somite” will be used in its place (Fusco and Minelli, 2013;

Fig. 1. Hypotheses of skeletomuscular homologies and evolutionary pathways here proposed based on topological and functional correspondences. Note that, for clarity, proportions and angles in these schemata have been distorted to varying degrees. Muscle names from the literature included in specific figures are either indicated in parentheses, (), or in black boxes (hence square brackets, []). Color coding as follows: Dark grey = tergum or sternum; light grey in (A) = tendon while light grey in (C) = penial sclerites; dark red = pleuron; red = protopod; barred red and grey = coxosternum or tergocoxosternum (= pygophore); dark yellow = exopod (= stylus); barred yellow and red = protopod-exopod composite; green = endopod; blue = gonopod, penis, or penial sclerite; light blue = lateropenite; barred blue and red = protopodal-penial composite. A1–5, transformation and homology from a pancrustacean groundplan represented by Remipedia (A1: Hessler and Yager, 1998) to Protura (A2: [François and Dallai, 1989; Berlese, 1910; Schädli, 2013]), Archaeognatha (A3, 4: alphabetical labels: Birket-Smith, 1974; numerical labels: Bitsch, 1973, 1974a, b]), and Zygentoma (A5: [Birket-Smith, 1974]). B1–3, transformation from ectognath groundplan represented by A4 to pterygote groundplan (B1: Hessler and Yager, 1998), the Ephemeroptera (B2: before slash: Brinck, 1957; after slash: Birket-Smith, 1971), and the inferred groundplan of the Neoptera (B3). C1–9, transformation from neopteran groundplan (B3) to polyneopteran groundplan (C1) through all polyneopteran orders (C2: Popham, 1965; C3: Matsumura et al., 2014; C4: Hünefeld, 2007; C5: Zwick, 1973; C6: Eades, 2000; C7: Helm et al., 2011; C8: Walker, 1943; C9: Klass, 1997). D1, groundplan inferred for Eumetabola. E1–6, transformation from eumetabolan groundplan (D1) to Thysanoptera (E1: Heming, 1970) and the hemipteran groundplan (E2); from this latter groundplan to Fulgoroidea (E3: Fennah, 1945), Aleyrodoidea (E4: Weber, 1935), Pyrrhocoridae and Belostomatidae (E5: before slash: Khanna, 1963; after slash: Bhargava, 1967), and Lygaeidae (E6: Bonhag and Wick, 1953). F1–5, transformation from phalloneopteran groundplan (F1) to psocodean groundplan (F2: Klier, 1956) and endopterygote groundplan (F5), the latter through precursors showing duplication of the penial protractors and retractors (F3 to F4) and splitting of the lateropenite from the penis (F4 to F5). G1–3, transformation from endopterygote groundplan to hymenopteran groundplan (G3: Schulmeister, 2001). H1–6, transformation from the neuropteridan groundplan, represented by Raphidioptera (H1), to Corydalidae (H4), Sialidae (H5), and Mymeleontidae (H6: Krivokhatsky, 2002) (note that, although the TgIX and GcxI are fused together in H4 and H5, they are still visually distinguishable, unlike in H6). H1–7, derivation of coleopteridan genital forms from an inferred precursor (H1), including the Strepsiptera (H8: Hünefeld et al., 2011b); inferred “trilobe” groundplan of the Coleoptera (I2), a trilobe form represented by Cantharidae (I3), cucujoid form represented by Curculionidae (I5), and an adephagan form represented by Dytiscidae (I7). J1–6, transformations inferred to derive a groundplan for the Euantiophora (J6) which accounts for all observed genital sclerites and muscles. J1–IV, transformations inferred for the Nannochoristidae (J1: Mickoleit, 2008), Bittacidae (JIII: Gao and Hua, 2015), and Panorpidae (JIV: Mickoleit, 2008). J1–viii, a transformation series inferred to explain the highly derived skeletomusculature of the Siphonaptera (Jviii: Günther, 1961). K1–2, representatives of the Diptera (K1: Spangenberg et al., 2012; K2: Paramonov, 2004). L1–3, Amphiesmenoptera, with Trichoptera—represented by Limnephilidae (L2)—and the lepidopteran groundplan (L3: Kristensen, 1984) derived from an approximated groundplan for the higher clade (L1). **Muscle abbreviations** indicated in Table 1. **Sclerite and other abbreviations:** **A1** = anchoring ligament; (Ars) = arcessus (see Aspöck, 2002); **Ba** = basis; **bp** = “basal piece” (sensu Crowson, 1955, 1981); (Cin) = cingulum; **Cx** = coxa (in the carcinological sense); **Cxa** = coxa (in entomological sense) or secondary gonocoxa (i.e., coxa IX in Ectognatha); (Cxp) = coxopenis; **Cxt** = coxite or gonocoxite (i.e., coxite of segment IX in Ectognatha); (Daev) = dorsal “aedeagal” valves; **Gna** = gonapophysis; (Gnr) = gonarcus (see Aspöck, 2002); **Endst** = endosternum; **Enp** = endopod; (Epp) = epiphallus; **Exp** = exopod; **Gpo** = gonopore; (Harp) = harpago (sensu Klier, 1956); (Ls) = lateral sclerite; (**ml55**) = “median lobe” (sensu Crowson, 1955); (Mn) = manubrium (sensu Popham, 1965); (PA) = “penial arm” (sensu Brinck, 1957); **Pen** = penis; (Phb) = phallobase (sensu Lawrence et al., 2010); **Pht** = phallotreme; **Pl** = pleuron; (pm1), (pm2) = “paramere” (Coleoptera, sensu Crowson, 1955, 1981; Lawrence et al., 2010); (“Pm”) = “paramere” (Dermaptera, sensu Popham, 1965); (pp81) = “penis proper” (sensu Crowson, 1981); **Prct** = proctiger; **Prp** = protopod (comprises Ba, Cx); (Pyph) = pygophore; **scls** = sclerites; **St** = sternum; **Sty** = stylus; **StCxIX** = coxosternum; **Tg** = tergum; (Tig) = tignum (see Aspöck, 2002); **Tl** = transverse ligament; (Vaev) = ventral “aedeagal” valves; **Vst** = ventral segmental tendon. **Sclerite abbreviations, Euantiophora (J1–6, I–IV, i–viii; see sections 4.5 and 4.5.4):** **aed. apod.** = aedeagal apodem; **aed. apod. prec.** = aedeagal apodem precursor; **aedt.** = aedeagal tasche; **bulb.** = bulbalis; **d. ps. par.** = dorsal pseudoparameren; **endot.** = endotendons; **ham.** = hamulus; **hypot.** = hypotendons; **inn. tub.** = innere tube; **kam.** = kammersklerit; **lun. skl.** = lunarsklerit; **mittelp.** = mittelpalte; **ostial.** = ostialsklerit; **param.** = “paramere”; **phb.** = “phallobasis”; **pistillt.** = pistillträger; **teg.** = tegimen; **telom.** = telomere; **virg. vent.** = virga ventralis; **Y-skl.** = Y-sklerit.

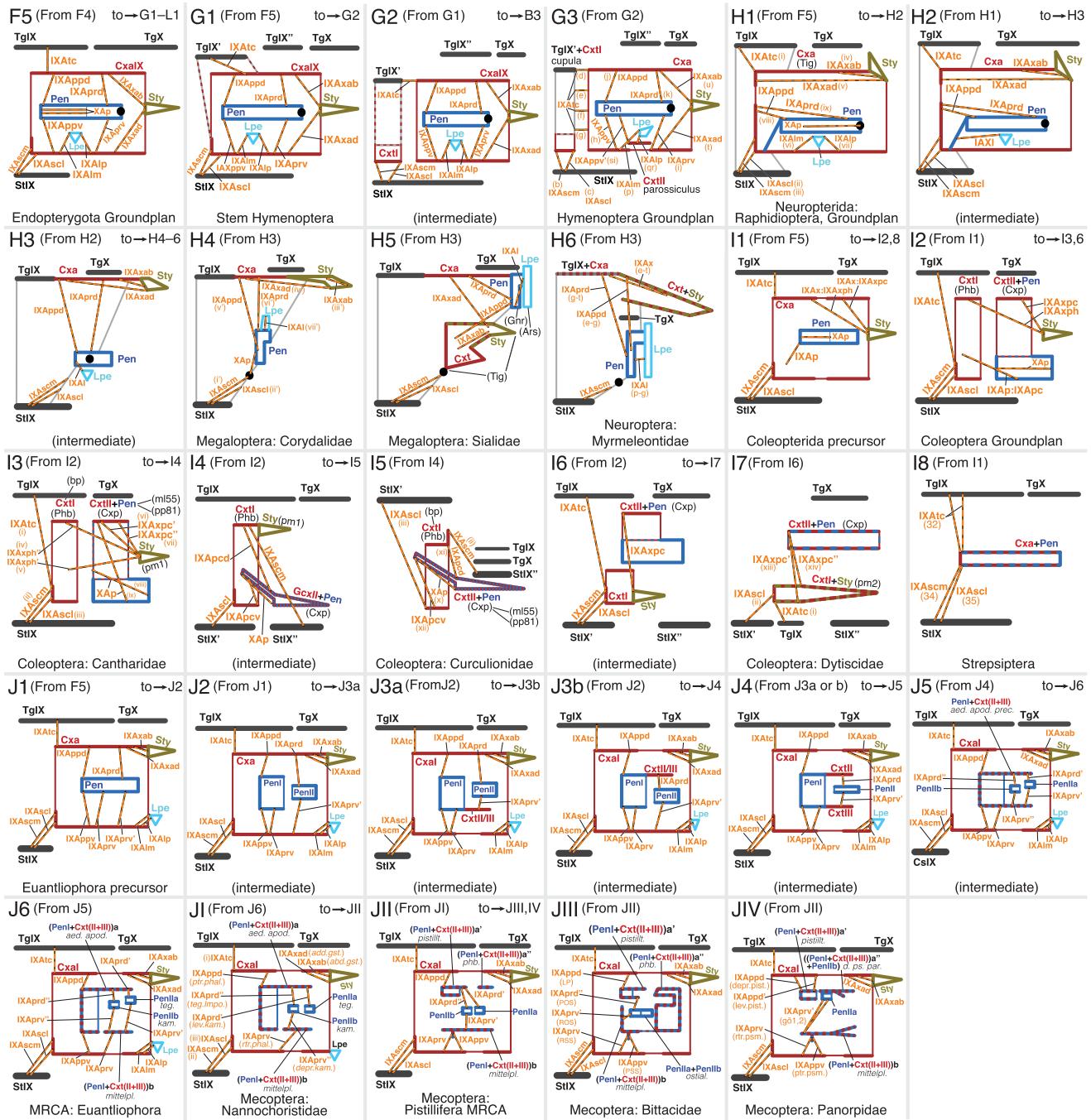


Fig. 1. (continued).

see also Schminke, 1976; Meisch, 2007). All but the last trunk appendages are biramous, consisting of a basal, two-segmented protopod (= subcoxa + coxa), a three-segmented exopod, and four segmented endopod (= telopod); no dactylus (= pretarsus), endites, or exites are expressed for these appendages (Yager, 1981; Hessler and Yager, 1998; limb terms modified from Boxshall, 2004; Wolff and Scholtz, 2008). The genital openings, or gonopores (*sensu* Snodgrass, 1936), are situated on the protopods of trunk segment XIV in males and segment VII in females (Koenemann et al., 2007b). From here forward, these and other gonopore-bearing limbs will be referred to as primary gonopods, allowing for reference to secondary gonopods (limbs modified for

copulation, gamete transfer, or egg laying) where appropriate (e.g., for Diplopoda: Snodgrass, 1952).

Trunk musculature. Hessler and Yager (1998) described and illustrated the trunk skeletomusculature of the species *Speleonectes tulumensis*. Each trunk segment of the remipede contains six **major** (I–VI) and eleven **minor** (i–xi) sets of muscles (Fig. 1,A1). The first two **major** (three **minor**) muscle sets do not attach to appendages, while the remaining four **major** (eight **minor**) sets are intra-segmental, inserting within elements of the appendages. **I. Longitudinal muscles:** (i) the “dorsal longitudinal trunk muscle” (dlm), attaching to the dorsal segmental tendons; (ii) the “ventral longitudinal trunk muscle” (vlm), attaching to the ventral segmental tendons.

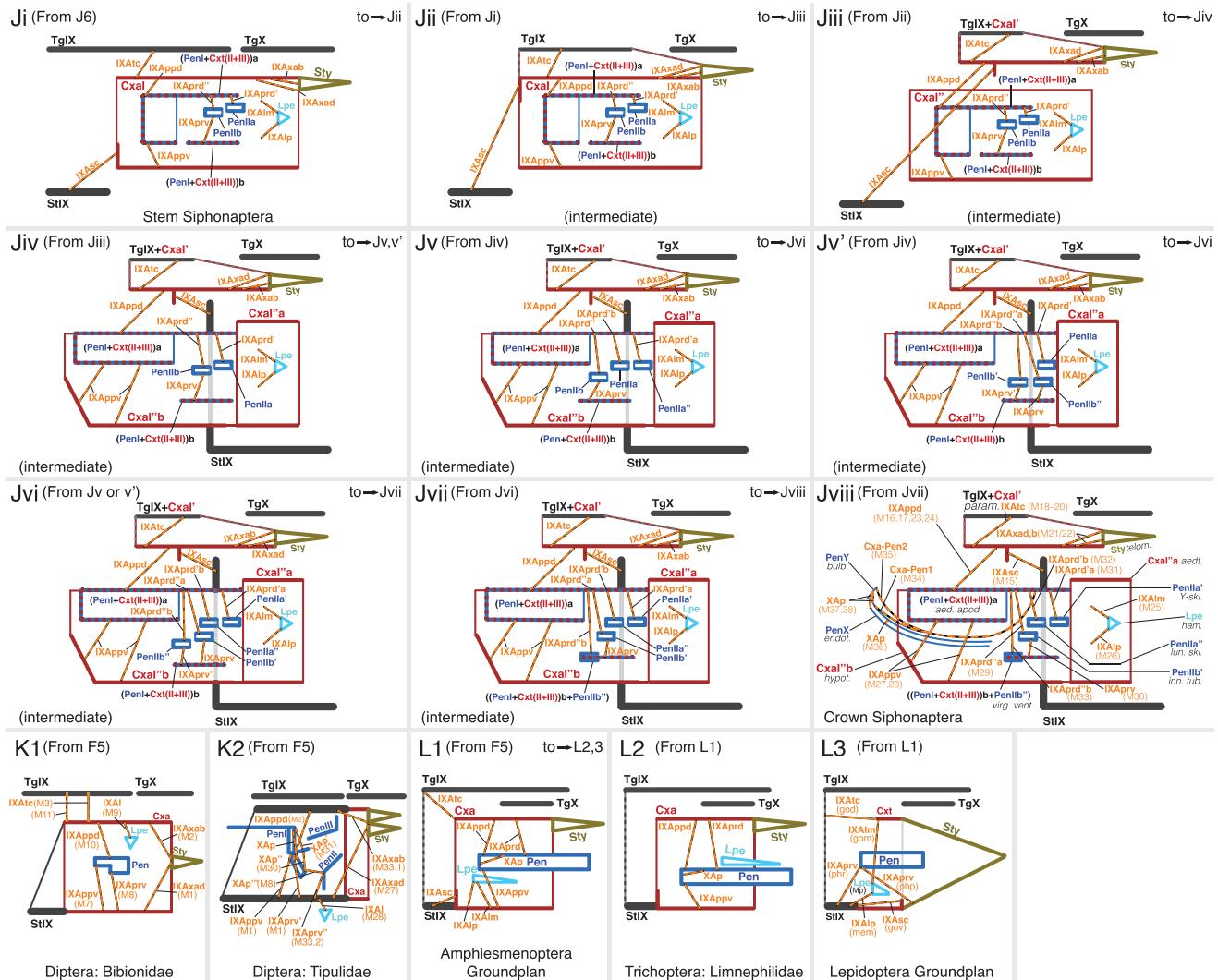


Fig. 1. (continued).

II. Dorsoventral muscles: (iii) the “dorsoventral trunk muscle” (dvm), originating on the *dlm* and tergum, and inserting on the ventral segmental tendons. **III. Extrinsic appendage muscles:** (iv) the “dorsoanterior extrinsic limb muscles” (daem), originating on the tergum and inserting on the ventral segmental tendon; (v) the “dorsoposterior extrinsic limb muscles” (dpem), originating on the tergum and inserting on the ventral segmental tendon; (vi) the “ventroposterior extrinsic limb muscle” (vpem), originating on the ventral longitudinal muscle (vlm) and inserting in the “coxa” and “basis” of the protopod. **IV. Intrinsic protopodal muscles:** (vii) the protopodal or “coxal muscles” (sensu Hessler and Yager, 1998) (cm1–3), originating within the “coxa” opposite the insertion of the dorsal extrinsic limb and inserting within the “basis”. **V. Extrinsic ramus muscles:** (viii) the extrinsic exopodal muscles (exm1–3), originating within the “basis” and inserting on the first exopodal segment; (ix) the extrinsic endopodal muscles (enm1–2), originating within the “basis” and inserting within the first and third exopodal segments, respectively. **VI. Intrinsic ramus muscles:** (x) the intrinsic exopodal muscles (exm4–5), originating within the first exopodal segment and inserting within the second and third exopodal segments, respectively; and (xi) the intrinsic endopodal muscles (enm3–4), originating within the first and third endopodal segments and inserting within the third and fourth segments, respectively.

3.1.2. Apterygote Ectognatha

Morphological overview. The Archaeognatha and Zygentoma together comprise the grade of apterygote ectognaths, and inform our understanding of the groundplan of the Ectognatha and Hexapoda as they are close to the phylogenetic root of insects, broadly speaking (Misof et al., 2014). From the entomological perspective, there is little that needs to be stated about the head capsule or thorax of these two orders here (e.g., cf. Snodgrass, 1935a; Sturm and Machida, 2001; Blanke et al., 2014). The abdomen of the apterygote ectognaths consists of 12 externally differentiated segments, with segment XI bearing the paired cerci, while the anal somite (= segment XII, “telson”) bears the median caudal filament (Snodgrass, 1935a; Machida, 1981; Kristensen, 1998; Klass, 2001; Klass and Matushkina, 2018).

The generalized abdominal segment of the Archaeognatha and Zygentoma have the following elements: a dorsal tergum, ventral sternum, paired coxopods, and an internal transverse ligament ("endosternum" of Bitsch, 1973, 1974a; 1974b) which attaches to both the sternum and coxopods (Bitsch, 1973, 1974a, 1974b; Klass and Matushkina, 2012, 2018). The sternum comprises up to four discrete elements (Klass, 2001; Klass and Matushkina, 2012, 2018): the large medial sternite, the smaller anteromedial intersternite, the paired anterolaterocoxites—situated anterolateral to the sternite—and the paired posterolaterocoxites, which are often incorporated with the

Table 1

Correspondences between major and minor muscle sets among the Remipedia, Archaeognatha, and Protura.

Remipedia		Archaeognatha		Protura	
Class	Name	Class	Name	Class	Name
I	Longitudinal muscles	A	Longitudinal muscles	A'	Longitudinal muscles
I-i	Dorsal longitudinal trunk muscle	Aa-1	Dorsal longitudinal muscle	A'-1'–2'	Dorsale externe, interne longitudinalmuskulatur
I-ii	Ventral longitudinal trunk muscle	Aa-2	Ventral longitudinal muscle	A'-3'–4'	Ventral externe, interne longitudinalmuskulatur
		Ab-3	Ventral extrinsic penial muscle	-	-
II	Dorsoventral muscles	B	Dorsoventral muscles	B'	Dorsoventral muscles
II-iii	Dorsoventral trunk muscle	B-4	Dorsal oblique muscle	B'-5'	Dorsoventral muskulatur
III	Extrinsic appendage muscles	C	Extrinsic appendage muscles	C'	Extrinsic appendage muscles
III-iv	Dorsoaterior extrinsic limb muscles	Ca-5	Anterior extrinsic appendage muscle	Ca'-6'	Dorsoventral protractor muscle
		Cb-8	Anterior extrinsic penial muscle	Cb'-10'	Muscle protracteur de l'apodème
III-v	Dorsoposterior extrinsic limb muscles	Ca-6	Posterior extrinsic appendage muscle	Ca'-7'	Dorsoventral retractor muscle
		Ca-9	Posterior extrinsic penial muscle	Ca'-9'	Muscle dilatateur de la chambre génitale
III-vi	Ventroposterior extrinsic limb muscle	Ca-7	Ventral extrinsic appendage muscle	Ca'-8'	Ventral adductor muscle
IV	Intrinsic protopodal muscles	D	Intrinsic penial muscles	D'	Intrinsic phallic muscles
IV-vii	Protopodal muscles	D-10	Penial intrinsic muscle	D'-11'–13'	Muscle rétracteur dorsal, médian, ventral du stipes
				D'-14'	Muscle rétracteur de la chambre génitale
V	Extrinsic ramus muscles	E	Intrinsic appendage muscle	E'	Extrinsic ramus muscles
V-viii	Extrinsic exopodal muscles	E-11–12	Stylar muscles	-	-
V-ix	Extrinsic endopodal muscles	E-13–14	Vesicular/gonapophyseal muscles	Ea'-15'–16'	Coxotrochanteral, coxovesicular muscles
				Eb'-17'–19'	Muscle fléchisseur, abducteur, releveur du basistylus
VI	Intrinsic ramus muscles	-	-	-	-
VI-x	Intrinsic exopodal muscles	-	-	-	-
VI-xi	Intrinsic endopodal muscles	-	-	-	-

coxae (note: “coxa” is used here over the prevailing term “coxite” for apterygote ectognaths, see exposition of section 3.1 above). In female Zygentoma and Pterygota, the anterolaterocoxites and postero-laterocoxites may be fused to form the gonangulum (Klass et al., 2012), a structure not observed in the Archaeognatha (Klass and Matushkina, 2018) or in male Pterygota (see below). The coxopods generally have two musculated elements, the posterolateral styli and posteromedial eversible vesicles; the vesicles are serially homologous with the multiannulate gonapophyses of segments VIII and IX of both females and males (Gustafson, 1950; Bitsch, 1974b; Birket-Smith, 1974; Klass and Matushkina, 2012, 2018).

The “genitalic segments” of the apterygote Ectognatha—segments 8 and 9 of females, segments 9 and 10 of males (see section 3.1.4 below)—differ from the pregenitalic segments in the form of the sclerites and in details of skeletomusculature (Bitsch, 1974b; Birket-Smith, 1974; Klass and Matushkina, 2018). In males, the ninth-segmental coxopods are anteroposteriorly elongated relative to the previous segments, and bear multiannulate gonapophyses as in segment VIII, unlike the coxal vesicles of the preceding segments (Klass and Matushkina, 2018). Due to modification of the ninth-segmental coxopods and styli for sexual purposes, these elements are here termed “gonopods” and “gonostyli”. Situated dorsomedially to the ninth-segmental gonapophyses is the unpaired “penis”, which bears the gonopore and is divided into the proximal and distal penial sclerites (Klass and Matushkina, 2018); these sclerites are traditionally known as the “phallobase” and “aedeagus”, respectively (Snodgrass, 1935a).

Abdominal musculature. Skeletomusculature of the abdomen and genitalia of Archaeognatha and Zygentoma have been described by Bitsch (1973, 1974a, b) and Birket-Smith (1974). Generally, the musculature of each pregenital segment of the apterygote ectognaths comprises four **major** (A–D) and fourteen **minor** (1–14) muscle sets (Fig. 1.A3–4). Where serial correspondence is observed between penial and non-penial muscles, the **major** muscle set is subdivided (e.g., Aa, Ab). Across all abdominal segments muscles attach either to ligament or directly to sclerite (Birket-Smith, 1974, p. 10); the muscular topology of most abdominal segments is as follows (note: alphabetical muscle names of Birket-Smith, 1974; numerical names of Bitsch, 1974b, italicized, with genital or pregenital association indicated, if

names differ). **Aa. Longitudinal muscles, non-penial:** (1) *dorsal*, attaching to tergal antecostae (DE, *a*, 1, 2); (2) *ventral*, originating and inserting on transverse ventral ligament (*j*, 5). **Ab. Longitudinal muscles, penial:** (3) *ventral*, originating on transverse ventral ligament of segment IX, inserting proximal ligament of penis (*i9*). **B. Dorsoventral muscles:** (4) *dorsal oblique*, attaching to tergal antecostae, descending posteriorly (*b*, 3). **Ca. Extrinsic appendage muscles, non-penial:** (5) *anterior*, originating on tergum, inserting on coxa and laterocoxite (LA, *h*, 50, 51, 53, 54); (6) *posterior*, originating on tergum, inserting on coxa (LP, *c*, 52); (7) *ventral*, originating on transverse ventral ligament, inserting on coxa (47 + 48). **Cb. Extrinsic appendage muscles, penial:** (8) *anterior*, originating on tergum X, inserting on coxa and laterocoxite or penis (LA, *h*, 50, 50 + 51); (9) *posterior*, originating on tergum X, inserting on penis (*k10*, 59). **D. Intrinsic penial muscles:** (10) *penial intrinsic*, originating at base of penis, inserting in distal portion (*j10*, 80). **E. Intrinsic appendage muscles:** (11) *longitudinal stylar*, originating on coxa, inserting within stylus (*f*, 60 [part]); (12) *oblique stylar*, originating on coxite, inserting within stylus (*g*, 60 [part]); (13) *longitudinal vesicular/gonapophyseal*, originating on coxa, inserting within vesicle or on gonapophysis (*j*, 62, 70, 71); (14) *oblique vesicular/gonapophyseal*, originating on element of transverse ventral ligament, inserting at base of vesicle (*k* [possibly], 43, 45, 46, 61, 65).

3.1.3. Ellipura and Diplura

Overview. To render complete the phylogenetic-comparative approach taken in the present study, it was necessary to review the literature on the Ellipura (Collembola, Protura) and the Diplura. Unfortunately, no studies were found which outline the skeletomuscular topology of the male genitalic somites of the Collembola or Diplura. The male (and female) genitalia of these two orders may be characterized as simple, comprising a single gonopore situated on a genital papilla which is of abdominal segment V in Collembola (Snodgrass, 1935a; Tuxen, 1970c; Dunger, 2003a) and just posterior to segment VIII in Diplura (Snodgrass, 1935a; Tuxen, 1970d; Dunger, 2003b). Notably, although appendages are absent from segment V in Collembola, stumpy “appendices genitales” occur on segment VIII of japygoid Diplura (Tuxen, 1970d); whether these putative coxae are muscled or not is uncertain. In contrast, the

Table 2

Generalized abdominal muscle nomenclature applicable to the trunk segments of Remipedia and the genitalic and non-genitalic segments of the Hexapoda. The symbol "#" stands for a Roman numeral indicating abdominal segment ("A") number. Preferred muscle names are **bolded** and specified synonyms are listed in square brackets, []. Where specific muscles are uniquely identified for a given clade, the clade name is indicated parenthetically. Note that additional names will need to be added as pre- and post-gonopodal abdominal segment muscles are enumerated (see, e.g., von Kéler, 1955).

Abbrev.	Name	Origin	Insertion
Non-appendicular muscles			
<i>Longitudinal muscles, general</i>			
#Att	M. tergo-tergalis [M. dorsales of Snodgrass, 1935]	the tergum of a given segment	the tergum of the succeeding segment
#Ass	M. sterno-sternalis [M. ventrales of Snodgrass, 1935]	the sternum of a given segment	"
<i>Dorsoventral muscles, general</i>			
#Ats	M. tergo-sternalis [M. laterales of Snodgrass, 1935]	a tergum	the isosegmental sternum
Appendicular muscles			
<i>Extrinsic, non-genital or genital (male or female); general or specific (indented)</i>			
#Asc	M. sterno-coxalis [M. sterno-gonopodalis]	a sternum	the isosegmental basal protopodal segment
#Ascm	M. sterno-coxalis medialis	the medial region of a sternum	"
#Ascl	M. sterno-coxalis lateralis	the lateral regions of a sternum	"
#Atc	M. tergo-coxalis [M. tergo-gonocoxitalis (Endopterygota)] [M. cupulo-gonocoxitalis (Hymenoptera)]	a tergum or the cupula	"
#Atca	M. tergo-coxalis anterior	the anterior region of a tergum	"
#Atcp	M. tergo-coxalis posterior	the posterior region of a tergum	"
<i>Extrinsic, penial (male); general or specific (indented)</i>			
IXAp	M. penialis [M. coxo-penialis] [M. coxosterno-penialis] [M. pygophoro-penialis] [M. gonocoxo-penialis]	sternum IX (Ephemeroptera), coxosternum IX (Polyneoptera), tergocoxosternum IX (= pygophore) (Hemiptera), or coxa IX (Endopterygota)	penis (Ectognatha)
IXApp	M. promotor penialis [M. penialis anterior]	posterior relative to insertion site when appendage in repose	anterior region of penis
IXAppv	M. promotor penialis ventralis [M. penialis anteroventralis] [M. penialis anteroventralis] [M. levator penialis anterioralis]	"	anteroventral region of penis
IXAppd	M. promotor penialis dorsalis [M. penialis anterodorsalis] [M. depressor penialis anterioralis]	"	anterodorsal region of penis
IXApr	M. remotor penialis [M. penialis posterior]	anterior relative to insertion site when appendage in repose	posterior region of penis
IXAprv	M. remotor penialis ventralis [M. penialis posteroventralis]	"	posteroventral region of penis
IXAprd	M. remotor penialis dorsalis [M. penialis posterodorsalis] [M. levator penialis posterioralis]	"	posterdorsal region of penis
IXApc	M. coxopenialis externus	phallobase (Coleoptera)	coxopenis (Coleoptera)
IXApcd	M. coxopenialis externus dorsalis	dorsal region of phallobase	"
IXApcv	M. coxopenialis externus ventralis	ventral region of phallobase	"
IXAl	M. lateropenitis [M. coxo-lateropenitis]	coxa IX (Endopterygota)	lateropenite (Endopterygota)
IXAlm	M. lateropenitis magnus	variable, often anterior or medial	lateropenital condyle
IXAlp	M. lateropenitis parvus	variable, often posterior or lateral	lateropenital condyle
<i>Intrinsic, non-genital or genital (male); general or specific (indented)</i>			
#Ac	M. coxalis	the basal protopodal segment	the distal protopodal segment
XAp	M. penialis internus	base of penis	distal portion of penis
#Ax	M. exopodalis [M. coxo-stylalis] [M. stylalis]	distal or sole protopodal segment	exterior ramus of appendage or stylus
#Axab	M. abductor exopodalis [M. abductor stylalis]	variable, often lateral, dorsal, or posterior	"
#Axad	M. adductor exopodalis [M. adductor stylalis]	variable, often medial, ventral, or anterior	"
#Axpc	M. coxopenialis-styialis	coxopenis (Coleoptera)	"
#Apxh	M. phallobasicus-styialis [M. coxitidis-styialis]	phallobase (Coleoptera)	"
#An	M. endopodalis [M. telopodalis]	distal or sole protopodal segment	interior ramus of appendage or endopod/telopod

male genitalia of the Protura are remarkable and deserve separate treatment, particularly as several studies on abdominal and genitalic skeleto muscular have been published. These studies allow for explicit—and informative—comparison to the Archaeognatha and Remipedia. Before proceeding, it should be noted that the proturan abdominal appendage, especially that of segment I, consists of basal and distal “podomeres” which correspond to the coxa and trochanter of thoracic legs (e.g., [Klass and Kristensen, 2001](#)).

Protura: External genitalia. The possibly intromittent (see [Pass and Szucsich, 2011](#); M. Fukui, pers. comm.) male genital structures of Protura, here termed the “phallic apparatus”, comprise two primary elements ([François and Dallai, 1989](#)): (1) a ring-like sclerite, termed “periphallus”, which bears a pair of long anterior apodemes (the “basal apodemes”); and (2) a “phallus” situated within the ring of the periphallus, and divided into a ring-like “stipes” basally and a pair of “styli” distally. Distal to the stipes and proximal to the styli are a pair of digitiform sclerites (“side plates”). The styli themselves are divided into cone-like “basistyli” and distal “acrostyli”; it is on the acrostyli that the gonopores occur. [Tuxen \(1970b\)](#) explicitly states that “no sternite is involved in [the] formation” of male or female proturan genital apparatus; the apparatus occur between sterna XI and XII ([Berlese, 1910, p. 160](#); [Snodgrass, 1935a, p. 583](#)) and form separately from the sterna during development ([Tuxen, 1949](#); [François, 1960](#)), first appearing in the preimago. Female genitalia ([Tuxen, 1970b](#)) are similar to those of the male in appearance and position, with the “perigynium” corresponding to the “periphallus”—including presence of “basal apodemes”—and the “styli” with the “phallus”. The primary difference between male and female proturan genitalia is the unpaired state of the female genital opening.

Protura: Abdominal musculature. Terms in English are derived from [Berlese \(1910\)](#), [François \(1996\)](#); terms in German, following [Snodgrass \(1935a, p. 260\)](#), are from [Schädl \(2013\)](#); and terms in French are from [François and Dallai \(1989\)](#). Overall, five **major** (A’–E’) and nineteen **minor** (1’–19’) muscle sets have been observed ([Fig. 1A2](#)). **A’. Longitudinal muscles:** (1–2’) “dorsale externe und interne longitudinalmuskulatur” (del, dil), attaching to tergal antecostae, transverse apodemes, or sagittal apodemes; (3–4’) “ventrale externe und interne longitudinalmuskulatur” (vel, vil), attaching to tergal structures as for previous muscle. **B’. Dorsoventral muscles:** (5) “dorsoventrale muskulatur” (dv), attaching terga and sterna. **Ca’.** **Extrinsic, non-genitalic appendage muscles:** (6’) “dorsoventral protractor muscle (dvu(p)) of [Berlese, 1910](#)”, originating on tergum, inserting anteriorly on coxa; (7) “dorsoventral retractor muscle (dvu(r))”, originating on tergum, inserting posteriorly on coxa; (8’) ventral adductor muscle (cu), originating on sternum, inserting medially on coxa. **Cb’.** **Extrinsic, genitalic appendage muscles:** (9) “muscle dilatateur de la chambre génitale” (mdc), originating posterolaterally on tergum IX, inserting on lateral (lumenal) surface of periphallus; (10) “muscle protracteur de l’apodème” (mpa), originating on antecosta of tergum IX, inserting on periphallitic apodeme. **D’.** **Intrinsic phallic muscles:** (11’–13’) “muscle rétracteur dorsal, médian, et ventral du stipes” (mrds, mrms, mrvs), originating on periphallitic (basal) apodeme, inserting on stipes; (14’) “muscle rétracteur de la chambre génitale” (mrc), originating in luminal surface of genital chamber, inserting on periphallitic (“basal”) apodeme. **Ea’.** **Extrinsic ramus muscles, non-genitalic:** (15) “coxotrochanteral muscles (abs, ass)”, originating in coxa, inserting on proximal margins of trochanter; (16) “coxovesicular muscle (rv)”, originating in coxa, inserting in apical vesicle. **Eb’.** **Extrinsic ramus muscles, genitalic:** (17’–19’) “muscle fléchisseur, abducteur, et releveur du basistylus” (mfb, mab, mrb), originating on stipes, inserting in basistylus.

3.1.4. Hexapoda—Remipedia correspondences

As there are numerous elements to contrast amongst the Remipedia, Archaeognatha, and Protura, this section is divided into three

subsections. The first subsection, **3.1.4.1**, addresses the correspondences and inferred homologies of non-genital structures and musculature (with reference to outgroup Ecdysozoa, *sensu* [Aguinaldo et al., 1997](#); [Dunn et al., 2014](#), others); the second subsection, **3.1.4.2**, addresses the gonopore-bearing structures; and the third subsection, **3.1.4.3**, summarizes the genitalic groundplans of the Hexapoda and Ectognatha given the observations in the prior to subsections.

3.1.4.1. Homology of non-genitalic structures. The identity of the thoracic and postthoracic tagmata of the Hexapoda and other Pancrustacea is necessary to address, as it is the fundamental correspondences between the Remipedia and Hexapoda which allow for the global homologization of hexapod genitalia. Therefore, the first concept to address is that of the hexapodan abdomen itself. Evolutionary developmental studies have demonstrated that the limbless or limb-rudiment-bearing “abdomen” of insects is equivalent to a “pleonized” (functionally differentiated) section of the trunk or “thorax” of other Pancrustacea, with the “true abdomen” of crustaceans being a region which completely lacks limbs and is posterior to the expression of *Abd-B*, which delimits the trunk ([Abzhanov and Kaufman, 2004](#); [Schram and Koenemann, 2004](#); [Schram, 2013](#); [Harzsch et al., 2015](#)). It is absurd, however, to accept the terminological recommendation of [Schram and Koenemann \(2004, p. 84\)](#) to replace “abdomen” with “pleon” for hexapods and to restrict the term “abdomen” to the post-*Hox* and appendageless segments of a subset of other Pancrustacea; rather, let that posterior region be a “posttrunk” and the differentiated section of the insect “trunk” be the abdomen. Note that the neologism “posttrunk” is suggested in order to avoid homonymy with the postgenital abdomen of insects known as the “postabdomen”, in distinction to the pregenital abdomen, or “preabdomen” (e.g., [von Kéler, 1955](#); [Fusco and Minelli, 2013](#), pp. 205–206).

Next, it is worthwhile to consider the terminal appendages of the abdomen—the cerci of Cercophora (Diplura + Ectognatha) and the median caudal filament of the Ectognatha. The median filament, which is lost in Odonata and Neoptera, is unique to the insects among the Pancrustacea, and as has been pointed out before ([Kristensen, 1991](#)) is probably an ectognath synapomorphy. Developmental observations ([Tojo and Machida, 1997](#)) indicate that the filament is derived from the absolute terminus of the body, thus is an appendicular structure of the anal somite. Cerci, on the other hand, roughly correspond to the “caudal rami” of the Remipedia, these latter structures being elements of the anal somite of that crustaceoform group; while the former have been recorded to lack direct muscular attachments ([Ford, 1923](#); [Snodgrass, 1935a, p. 225](#); [Birket-Smith, 1974](#); although see [Birket-Smith, 1971](#): p. 149, 156), comparable observations for the Remipedia are not in the literature. Given that these terminal structures exist alongside male and female hexapodan genitalia, however, the tentative homology of cerci with caudal rami is sufficient for the purposes of this work.

Focusing on skeleto muscular, correspondences between the **major** and **minor** muscle sets among the Remipedia, Archaeognatha, and Protura are presented in [Table 1](#) and schematized in [Fig. 1A](#). In brief, the key findings are: (1) **longitudinal** and **dorsoventral muscles** of all three groups match neatly (I:A’; II:B’); (2) **extrinsic appendage muscles** correspond categorically (III:C:C’); and specifically (III-iv: Cab-5/8: Cab-6/11’; III-v: Cab-6/9: Cab-7/10’; III-vi: Ca-7: Ca’-8’) in all three; (3) **intrinsic protopodal muscles** are only observed in the penis or phallus of Archaeognatha and Protura, respectively (IV:D-10:D-11’–14’); (4) **extrinsic expodal muscles** correspond to **stylar muscles** in Archaeognatha, but no similar muscle is observed in Protura (**V-viii:E-11–12:—**); (5) **extrinsic endopodal muscles** correspond to **vesicular/gonapophyseal**

muscles and coxotrochanteral plus coxovesicular muscles (**V-ix:E-13–14:Ea'-15'-16'**); and (6) **intrinsic ramus muscles** are absent in Archaeognatha and Protura (**VI:—**). Further correspondences of the remipedan **intrinsic protopodal muscles** (**IV**) and **intrinsic ramus muscles** (**VI**) are observed in the thorax, given that the telopod (trochanter–tarsus) and pretarsus of the leg form an endopod (thus *intrinsic endopodal muscles*, **VI-xi**), and assuming that the thoracic pleurae are derived from subcoxal sclerites (thus *intrinsic protopodal*, **IV-vii**) (e.g., Hasenfuss, 2002, 2008; Engel et al., 2013; Coulcher et al., 2015; Mashimo and Machida, 2017; Deuve, 2018).

What may be understood most broadly from these correspondences is that the *dorsal* and *ventral longitudinal trunk muscles* (**I-i:Aa-1:A'-1'; I-ii:Aa-2:A'-2'**) as well as *dorsoventral muscles* (**II-iii:B-4:B'-5'**) are probably plesiomorphic for the Arthropoda as a whole, as such muscles also occur in Onychophora (Snodgrass, 1938; Hoyle and Williams, 1980) and Tardigrada (e.g., Schmidt-Rhaesa and Kulessa, 2007; Halberg et al., 2009; Marchioro et al., 2013; references within these), as well as other major arthropodan groups (Manton, 1973a; Boudreux, 1979a,b). More-distant outgroup comparison within the Ecdysozoa (Nematoda: Schneider, 1866; Stretton, 1976; Bird and Bird, 1991; Nematomorpha: Schmidt-Rhaesa, 2013a; Priapulida: Schmidt-Rhaesa, 2013b; Kinorhyncha: Neuhaus, 2013; Loricifera: Bang-Bertelsen et al., 2013) indicates that gross division of the somatic musculature into *dorsal*, *lateral/dorsoventral*, and *ventral* units may be a synapomorphy of the Panarthropoda, as dorsoventral muscles are only observed in some kinorhynchs, while other muscle patterns vary. Critically, the *dorsoventral* and *ventral extrinsic limb muscles* (**III, C**) are another, certain, synapomorphy of the panarthropod clade; whether the **intrinsic appendage muscles** (**IV–VI, D–E, D'–E'**) are a synapomorphy of the Panarthropoda is uncertain, as such muscles occur in Tardigrada (e.g., Richters, 1926; Kristensen, 1978; Marchioro et al., 2013; contra Brusca et al., 2017) but not with Onychophora. Therefore, homology of the abdominal appendages of Archaeognatha and Zygentoma with trunk appendages of the Remipedia is strongly supported by the general (**III:C:C'**) and specific (**III-iv:Ca-5:Ca'-6'; III-v:Ca-6:Ca'-7'; III-vi:Ca-7:Ca'-8'**) correspondences of the prepenial **extrinsic appendage muscles**, as well as the extrinsic and intrinsic ramus muscles (points 4–8 in the preceding paragraph; see also Table 1, Fig. 1A). Further, these correspondences specifically indicate that the erstwhile “coxites” (Bitsch, 1973) or “coxopodites” (Snodgrass, 1935a) of the Hexapoda are homologs of the “protopodites” (Boxshall, 2004) or “basipods” (Waloszek et al., 2007) of the post-antennal limbs of other Arthropoda (see also Bitsch, 2001).

Although there has been considerable uncertainty about the homology of the abdominal vesicles and styli of the apterygote ectognaths (e.g., see Klass and Kristensen, 2001), the intrinsic appendage correspondences outlined above (**V-vii:E-11–12:—** and **V-ix:E-13–14:Ea'-15'-16'**) indicate that the abdominal appendages of the Hexapoda are indeed biramous, with the vesicles/gonapophyses and styli representing simplified derivatives of endo- and exopods, respectively. Multiple lines of circumstantial evidence favor the endopod/exopod interpretation: (1) The Hexapoda are *not* derived from nor are they sister to the Myriapoda, which also have eversible vesicles, rendering the assumption (e.g., Hennig, 1981; Manton, 1971, 1973a,b) or inference (e.g., Willmann, 2003) of homology between the clades inviable; (2) the sister group of the Hexapoda, the Remipedia, lack endites and exites on their trunk protopods (Yager, 1981); (3) the abdominal styli (putative exopods) do not have a respiratory or osmoregulatory function (Maas et al., 2009); (4) the distal vesicle of the uniramous abdominal appendages of Protura and Collembola are supported as modified telopods (= endopods) (Klass and Kristensen, 2001, references therein); and (5) presence of only two apical limb elements formed by division of

distally-developed limb *anlage*, as observed at the gross and molecular levels (Machida, 1981; Niwa et al., 2010; Jockusch and Smith, 2015), matches the developmental definition of endite and exites proposed by Wolff and Scholtz (2008), namely that endites and exites are derived from establishment of new axes relative to the proximo-distal clonal growth axis of the protopod and lateromedially divided rami (see also Boxshall, 2013). There is still some possibility that the vesicles/gonapophyses may be endites, and that the styli are exites, as the endites of the mouthparts (i.e., galeae, laciniae, glossa, and paraglossa) also bear the insertions of muscles originating in their respective coxopodites (Snodgrass, 1935a, ch. VII). However, based on the five points outlined above, the vesicle-endopod stylus-exopod homology is accepted here. Finer-grained evidence for this issue may be derived from additional molecular and cellular developmental (“evo-devo”) assays of Archaeognatha, Zygentoma, and Protura in the context of the Pancrustacea.

3.1.4.2. Homology of the gonopore-bearing structures. Central to the problem of the homologies of the male genitalia of the Hexapoda is the identity and origin of the penis of apterygote ectognaths. As a brief review, following the summary of Bitsch (1974b), several competing hypotheses have been proposed to explain the evolution of the penis: (1) *de novo* origin of the penis without homology to other orders (Snodgrass, 1957); (2) homology with medially-fused gonapophyses of segment VIII (Verhoeff, 1902); (3) homology with medially-fused secondary subdivisions of the ninth-segmental gonapophyses (see references in Bitsch, 1974b, p. 218); and (4) homology with appendages of abdominal segment X (Heymons, 1897). Hypothesis 4 has previously been supported by developmental and innervation patterns. With respect to ontogeny, Qadri (1940, p. 168) observed that the penis of Archaeognatha and Ephemeroptera develops from paired outgrowths of the genital chamber which is posterior to segment IX, *contra* Snodgrass (1935a, 1957), who reported but a single *anlage*. Regarding innervation, Birket-Smith (1974, pp. 17–18) observed that the apterygote penis is innervated by neurons of segment X (see also Niven et al., 2008), and indeed, so is the penis of the Ephemeroptera (Brinck, 1957).

At the risk of repetition, it is necessary to consider separately the skeletomuscular correspondences of the gonopore-bearing structures of the Remipedia, Archaeognatha, and Protura (see also Table 1, Fig. 1A): (1) the *ventral extrinsic penial muscle* of Archaeognatha corresponds to the *ventral longitudinal muscles* of preceding abdominal segments, and these muscles correspond to the *ventral longitudinal trunk muscles* of the Remipedia (**Ab-3:Aa-2:I-ii**); (2) the *anterior and posterior extrinsic penial muscles* of Archaeognatha correspond to the *anterior and posterior extrinsic appendage muscles* of preceding abdominal segments, these muscles correspond to the *doroanterior and dorsoposterior extrinsic limb muscles* of the Remipedia, and the *phallic protractor and dilator muscles* of the Protura, themselves corresponding with the *dorsoventral protractor and retractor muscles* (**Cb-8:Ca-5:III-iv:Cb'-11':Ca'-6'; Cb-9:Ca-6:III-v:Cb'-10':Ca'-7'**); (3) given 2, the *extrinsic penial muscles* of Archaeognatha correspond categorically to the *extrinsic phallus muscles* of the Protura (**Cb:Cb'**); (4) the **intrinsic penial muscle** of Archaeognatha correspond to the **intrinsic phallic muscles** of the Protura (**D:D'**); and (5) the *extrinsic endopodal muscles* of Remipedia correspond categorically to the *extrinsic basistylar muscles* of the Protura (**V-ix:Eb'-17'-19'**). These five primary correspondences strongly indicate that the penis of the Archaeognatha is homologous with the phallic complex of the Protura, and that these in turn are homologous with the gonopore-bearing appendages of the Remipedia. Hypothesis 4 for the origin of the penis—that of derivation from

modified appendages—is therefore supported, although the ancestral segmental identity is uncertain (see below).

Perhaps surprisingly, it is possible to reason out specific homologies of the remipedan gonopods, archaeognathan penis, and proturan phallic apparatus given the skeletomuscular correspondences observed among the focal taxa. The penis is here proposed to be the medially-united gonopodal protopods of the remipede-like hexapodan groundplan, with retention of *intrinsic penial muscles* (= *intrinsic protopodal muscles*). These muscles imply that the distal penial sclerite of Klass and Matushkina (2018) is homologous with the medially-fused “basis” of non-hexapodan Pancrustacea. With respect to the Protura, it is here proposed that the phallic apparatus is homologous with the paired biramous genital appendages of the Remipedia, with the following modifications (Fig. 1.A2): (1) the gonopodal protopods fused medially, forming the “periphallus” and “stipes”, these segments being the retained “coxa” and “basis”; (2) the proximal muscle insertion sites on the basal protopodal segment elongated into apodemes (“basal apodemes” of the “periphallus”); (3) exopods retained, but reduced to a single segment (“side plates”); (4) first two segments of endopods retained, forming “basistylus” and “acrostylus”; and (5) gonopores migrated distally from the protopod onto second endopodal segment (“acrostylus”). Moreover, comparison with the Archaeognatha reveals two synapomorphies for the Hexapoda and another for the Ectognatha: (6) hexapodan gonopodal protopods fused medially; (7) hexapodan primary gonopod (= phallic apparatus, penis) sunken into genital chamber; (8) ectognathan pre-gonopodal coxopods associated with reproduction, i.e., the paired condition of the genitalic appendages of females (VIII–IX) and males (IX–X) is a synapomorphy of the Ectognatha. Coxopods of segment IX in males may therefore be conceived of as secondary gonopods. The simple male genitalia of Collembola and Diplura are here inferred to be homoplastic reductions given the high degree of specific correspondence observed between the Protura and Archaeognatha.

The final principle feature of the genitalia to address in this section is the gonopore. Among the Hexapoda, the gonopore may be internal or external, single or paired (Snodgrass, 1935a). Remipedia, and other non-hexapodan Pancrustacea generally, bear gonopores on the protopods of paired gonopods. The gonopores of Remipedia occur on trunk segment XIV in males and segment VII in females (Koenemann et al., 2007a, b). Excluding the first three trunk segments which correspond to the hexapodan thorax, the gonopores of remipedes occur on segments XI in males and IV of females, or X and III if the maxillipedes are included in the count of thoracic segments. In contrast, the gonopore(s) of male and female hexapods occur on the same segment or two successive segments (Tuxen, 1970a). The closest correspondence with the Remipedia, whether incidental or inherited, is the genitalic opening after sternum XI in both sexes of the Protura (Tuxen, 1970b; François and Dallai, 1989). Briefly, the gonopore(s) of other Hexapoda open on: abdominal segment V in both sexes of Collembola; segment VIII in both sexes of Diplura; segments IX or X for female and male apterygote ectognaths, respectively; and segment IX or more-anterior segments in pterygotes. It is apparent, then, that the segmental identity of the genitalic opening is evolutionarily unstable, particularly near the root of the hexapod phylogeny. The process that leads to this instability has yet to be determined (Klass and Matushkina, 2018), but may relate to Hox-delimitation of segmentation, as, for example, the loss of abdominal segments in Collembola is analogous to the loss of the trunk and abdomen in Tardigrada (Maderspacher, 2016; Smith et al., 2016). It is plausible that such “deletion” of pregonopodal abdominal segments via mutation of Hox genes could render segmental count variable, while the primary and secondary gonopods remain homologous. In this context, it should also be recalled that non-hexapod Pancrustacea and Protura develop epimorphically (Chapman, 1982; Koenemann et al., 2006, 2009), i.e., by incrementally adding pre-anal segments during successive molts.

3.1.4.3. Groundplan and evolution of hexapod and ectognath genitalia. Integrating across the Archaeognatha, Protura, and Remipedia, the groundplans of both the Hexapoda (Fig. 1.A2) and Ectognatha (Fig. 1.A4) may be inferred. The ancestral hexapod plausibly had a single “genital segment” bearing multisegmented gonopods. The basal segments of the gonopods, the protopods, are inferred to have fused medially in the ancestor of extant Hexapoda, forming a phallic apparatus which was sunken into a genital chamber. Inferred to be borne on this apparatus were unisegmental (i.e., reduced) exopods, forming styli (“side pieces”), as well as multisegmented endopods (“basistylus”, “acrostyli”) which were situated at the apex the distal protopodal segment. The so-called “genital segment” of the hexapodan groundplan is uncertain due to differences in development between the Protura and Ectognatha, but it is clear that segment X bore the medially-fused primary gonopod (= penis) in the ancestral ectognathan. The female of this ancestral hexapod may have been similarly derived as that of the male, given the structural similarity of male and female Protura (e.g., Tuxen, 1970b).

From this inferred ancestral phallic apparatus may be derived the penis of the groundplan of the Ectognatha. The penis bears intrinsic musculature, suggesting that the “proximal” and “distal sclerites” of the penis observed in Archaeognatha (Snodgrass, 1935a; Klass and Matushkina, 2018) are homologs of the “coxa” and “basis” of the crustaceomorph ancestor. Additionally, the penis receives the insertion of longitudinal musculature originating on sternum IX and bears the origin of longitudinal musculature inserting on sternum XI, indicating that the penis is integrated with sternum X. Anterior to this penis were almost certainly the well-developed secondary gonopods, or coxopods of abdominal segment IX, which bear apically the gonostyli (= unisegmental exopod) and gonapophyses (= annulate, unisegmental endopod). This groundplan inference aligns with that which is understood for female ectognaths (Fig. 1.A3), namely, that the female genitalia of the insects comprise the paired appendages of abdominal segments VIII and IX, which together form the ovipositor complex (Snodgrass, 1933, 1935a; Scudder, 1961, 1971; Mickoleit, 1973a,b; Bitsch, 1974a; Hünefeld et al., 2012).

Evolution of the genitalia. What follows is a new evolutionary scenario for the abdomen and its appendages in the Hexapoda, which are complementary to the “aqueductal” and “sensorial” hypotheses of Klass and Matushkina (2018). During the transition from marine to terrestrial habitats, the crustaceoform ancestor of the Hexapoda was challenged by the need to conserve fresh water. This may have been done by a number of skeletomuscular remodelings: (1) increased coverage of the ventral membranous surfaces of the trunk by expanded sternites (as observed in Protura, Diplura); (2) rotation and flattening of the abdominal coxae to further conceal abdominal membrane (apterygote Ectognatha); (3) coxal vesicles, for water absorption (Weyda, 1974, 1998), derived from pre-gonopodal endopods (possibly transitioning through the non-segmented gonapophyseal form, Hädicke et al., 2014), being “stalked” on the coxae or protopods (Protura, collophore of Collembola) or flush with the abdomen because of modification 2 above; and (4) deposition of male gametes externally in spermatophore (Beutel et al., 2017), eased via medial fusion of gonopods basally, forming the “penis”. Weyda and Štys (1974) proposed that serially homologous sensorial structures on gonapophyses IX of male apterygote ectognaths were expressed on the penis, giving it increased sensorial function.

During these morphological transitions, some abdominal appendages may have been modified into the spring and locking mechanism of the Collembola and, in Cercopora, the abdominal exopods became modified as unisegmental styli for supporting the abdomen during stand-still and ambulation, while most of the

endopods expressed absorptive tissue. The endopods VII and VIII of females and VIII and IX of males in the apterygote Ectognatha retained more-or-less limb-like structure, being elongate and often multiannulate, although lacking intrinsic musculature. With increased tactile sensitivity (Weyda and Štys, 1974) and capacity for thread production from glandular setae (Klass and Matushkina, 2018), these “gonapophyses” function as part of the ovipositor complex of females and assist sperm-thread deposition in male apterygote ectognaths. A notable, possible exception is the genus *Petrobiellus* (Machilidae, Petrobiellinae), for which the elongate penis is hypothesized to be capable of depositing sperm almost directly into the female genital opening with help from gonapophyses IX, which may be modified for clasping the female's ovipositor (Klass and Matushkina, 2018).

In the greater context of the evolution of multicellular life, the transition from sea to land of the pancrustacean-hexapodan ancestor may be seen as one of the potentiating instances where there occurs decreased constraint on physical or mechanical activity (Vermeij, 2017; Glenner et al., 2006), and, for the Ectognatha, is probably the first event upon which the major trends of genitalic evolution is contingent. Without the constraint to use the abdominal limbs for swimming, these ancestrally biramous appendages were allowed to undergo structural change including fusion, reduction, and intersegmental integration, as well as major developmental and structural reorganizations. Another such event was almost certainly the invasion of the air via flight, wherein functional constraint on the abdominal appendages for water-absorption and support may have eased. This may have led to loss of the pregenital appendages, and allowed for new, copulation-specific adaptations of the secondary gonopods (coxopods IX) as in the Ephemeroptera and Neoptera (or synapomorphically for the “Chiastomyaria”) (see section 3.2.2 below). It is plausible that clasping itself may have arisen in parallel with intromittance of the primary gonopods.

3.2. Skeletomuscular patterns within the Hexapoda

This section has two main parts. First, subsection 3.2.1 presents a new nomenclature for the genitalic skeletomusculature of the Ectognatha for application throughout the remainder of the work. Second, subsection 3.2.2 outlines exoskeletal and muscular correspondences of all orders of non-endopterygote Pterygota in a step-wise, phylogenetic fashion. In other words, each successive internal node is compared with its sister group until all taxa have been addressed. The Endopterygota are addressed in detail in section 4.

3.2.1. Genital muscle nomenclature

After establishing the groundplan genitalic skeletomuscular topology for the Ectognatha, it is possible to trace evolutionary transformations of the gonopore-associated structures for the Pterygota. A new system of muscular nomenclature is here presented for uniform application across all orders of the Hexapoda (Table 2, above); this system is presented side-by-side well over a dozen taxon-specific muscle name sets in Fig. 1. One of the intents of the new nomenclatural system is to harmonize with the systems outlined in Beutel et al. (2014), i.e., with that of the cranium (Wipfler et al., 2011), the thorax (Friedrich and Beutel, 2008), and the abdomen (von Kéler, 1955), although the logical specifics of these four systems do not align perfectly. Some overlap in the homology-neutral labels from the above references and the new system are presented below for conceptual continuity. One of the major differences is that the new system here proposed accounts for correspondences despite the radical transformations observed in the genitalic skeletomusculature across the Pterygota; this is done via explicit definition of synonymous descriptive terms. In the

future, it may be possible to define the origins and insertions of the abdominal skeletomusculature of the genitalic and non-genitalic elements in as much detail as for the head and thorax, but this awaits subsequent documentation. For now, Table 2 indicates general classes of muscles, with subclasses indicated via indentation. Refinement on some level is almost certainly necessary, but awaits future study.

As applied throughout this work, terms for sclerites and muscles are used to indicate anatomical correspondence, with the inference of homology based on phylogenetic relationship among disparate taxa. An effort has been made to ensure that terminology employed in this work has the following four properties: (1) the terms indicate correspondence, with explicit synonyms used to recognize differing degrees of similarity (i.e., strict vs. loose homology); (2) the terminology is internally consistent linguistically and logically; (3) terms are used which have had minimal or no history of misuse; and (4) theoretical ties with the phallic-periphalllic concept of Snodgrass (1935a, 1938, 1957) are severed. The latter point is critical, as the implied homologies of the phallic-periphalllic model, derived from Snodgrass's recapitulation-based interpretation of genital development, are unsupported by skeletomusculature, are positively misleading, and are burdened by a century of misapplication and confusion—such as, for example, the noxious term “paramere” (see, e.g., the applications of this term in Hymenoptera reviewed in Schulmeister, 2001). Terms from Snodgrass's system are indicated in quotation marks parenthetically when appropriate. What follows are a series of sections addressing particulars of the skeletomusculature of the Pterygota, as well as inferred transformations up to, but not including the Endopterygota (for which, see chapter 4 below).

3.2.2. Male genital form across the Hexapoda

3.2.2.1. Pterygota. The pterygote groundplan. Derived from comparison among the Archaeognatha (Fig. 1.A4), Zygentoma (Fig. 1.A5), and all pterygote orders, the groundplan of the Pterygota inferred in the present work is presented in Fig. 1.B1. Three principle skeletomuscular states differentiate the genitalia of the Dicondylia from the Archaeognatha, and the Pterygota from the apterygote ectognaths: (1) the penises of the Zygentoma and Pterygota lack insertion of *dorsoventral extrinsic limb muscles* (**Cb-8:XAtca** and **Cb-9:XAtcp**); (2) extant Pterygota lack ninth-segmental gonapophyses, but retain musculated styli (= gonostyli); (3) the endosternal ligament of abdominal segment IX of pterygotes is absent, but the origin of the *ventral longitudinal muscle* (**Ab-3:IXAss:IXAp**) is retained, being on sternum IX itself. Ninth-segmental gonapophyses are presented in the pterygote groundplan (Fig. 1.B1) as these are observed to be present in early Carboniferous odonatopterans (Bechly et al., 2001).

3.2.2.2. Palaeoptera to Neoptera. Overview. The first three or four cladogenic events of the extant Pterygota are crucial for understanding the Neoptera, itself only comprehensible when subsequent splits — Polynooptera, Eumetabola, and their internal lineages — are compared. Whether the Odonata and Ephemeroptera form a clade, the Palaeoptera, is uncertain (Misof et al., 2014). However, a recent reanalysis of transcriptomic data (Simon et al., 2018) has rejected the Metapterygota hypothesis (Odonata + Neoptera), but found equivocal support for Palaeoptera or the Chiastomyaria (Ephemeroptera + Neoptera). Among the Palaeoptera, genital skeletomuscular and developmental observations have been recorded for the Ephemeroptera (Durken, 1907; Qadri, 1940; Brinck, 1957; Birket-Smith, 1971), but not for the Odonata, where virtually all work is on the secondary genitalia (e.g., Poonawalla, 1966; Pfau, 1971) or caudal appendages (e.g.,

Willkommen et al., 2015). As indicated by Simon et al. (2018), operationalizing non-cranial morphological characters, including genitalia and fossils, for both sexes of the “Palaeoptera” will be valuable for phylogenetic analysis, if not alone for understanding the evolutionary transformation of genitalia at the earliest splits of the Pterygota.

Odonata. The primary genitalia of odonates have been observed to consist of a pair of lobes covering the genital opening on segment IX (Fraser and Asahina, 1970). These lobes have been postulated to be the modified secondary gonopods (also termed “gonapophyses”) based on developmental observations (Van der Weele, 1906; Snodgrass, 1935a) as well as paleontological evidence (Brauckmann and Zessin, 1989; Whiting, 1996; Bechly et al., 2001). Presence of *tergocoaxal* (**IXAtc**) and/or *sternocoaxal* muscles (**IXAsc**) inserting on the gonopods is therefore predicted. Distal gonostyli, although apparently present in stem Odonata (e.g., Bechly et al., 2001), are absent from crown taxa (Van der Weele, 1906; Snodgrass, 1935a). The penis has been stated to be “obsolete” to the point of absence (Fraser and Asahina, 1970); this is contradicted by dissection of a male *Tanypteryx hageni* (Selys-Longchamps, 1879) (Anisoptera: Petaluridae) (Fig. S1), which revealed that the unpaired genital opening is borne on a saddle-horn-shaped protuberance of a triangular sclerite between the gonopods. This sclerite, also recorded in *Agrion* (Machotin, 1934), is inferred to be the penis or penis-gonapophysis composite, which appears to be completely integrated with segment IX, in contrast the penis of the Ephemeroptera (e.g., Brinck, 1957). Internally, a pair of flanged apodemes extending from the interior anterolateral margins of the gonopods; if these apodemes do receive the insertions of muscles, it will be valuable to determine if the origins are sternal. Although no gonapophyses IX (“parameres” *sensu* Verhoeff, 1893a, b, c; Nielsen, 1957) were observed in *Tanypteryx*, these are known from Odonatoptera (Bechly et al., 2001), indicating the absence of these structures is an independently-derived apomorphy relative to the “Chiastomyaria” (= Ephemeroptera + Neoptera).

Ephemeroptera. Based on the several descriptions of the male ephemeropteran genitalia (e.g., Verrier and Brinck, 1970; Kluge, 2004), the following generalizations may be drawn (Fig. 1.B2). The male genitalia of Ephemeroptera consist of multiannulate gonostyli situated on a transverse sclerite termed the “styliger plate”; the “styliger plate” corresponds to medially-fused gonocoxae IX given that it bears the insertions of *ventral extrinsic appendage muscles* (**Ca-7:IXAsc**), the origin of an *intrinsic appendage muscle*—that of the style (**E-11 + 12:IXAx**)—and the insertion of a *dorsovenital extrinsic appendage muscle* (**Ca-5/6:IXAtc**). Posterior to the medially fused gonocoxae occur the paired penes which are articulated posterolaterally to tergum IX by sclerotic “penial arms”; the penes bear *intrinsic penial muscles* (**D-10:XAp**), as well as the insertion of a muscle originating on tergum IX. The *intrinsic penial muscles* correspond to the *ninth-segmental dorsal longitudinal muscles* (**Aa-1:IXAtt**), which have probably been coopted via integration of abdominal acrotergite X (the “penial arm”). The alternative, that the dorsoventral tergo-penial muscle (*pm* of Brinck, 1957, *e9* of Birket-Smith, 1971) is derived from a posterior subunit of **IXAtc** is less likely, as presence this muscle (*pm/e9*) in the Ephemeroptera is unique among the Pterygota, and the penis is not completely developmentally integrated with segment IX (Qadri, 1940; Brinck, 1957). Note that paired penes are not universal in the Ephemeroptera, as unpaired penes are present in *Eatonigenia* (Kluge, 2004, p. 242) and “Cae-noptera” (Kluge, 2004, p. 277).

Neoptera. The most salient feature of the genitalia of the Neoptera (groundplan: Fig. 1.B3) relative to the Ephemeroptera is presence of two *ventral extrinsic penial muscles* (**Ab-3: XAss**).

Whereas the single extrinsic *penial muscle* (**IXAss:IXAp**) of the Ephemeroptera functions as a remotor, the two extrinsic penial muscles of Neoptera are generally antagonistic, and are thus referred to as the *penial promotors* (**IXApp**) and *penial remotors* (**IXApr**). These muscles are consistently present and originate on sternum IX in most orders, with a number of exceptions due to modification or loss. The neopteran groundplan includes differentiated coxae IX (secondary gonocoxae) receiving the insertions of *ventral* and *dorsovenital extrinsic appendicular muscles* (**Ca-5+6:IXAtc** and **Ca-7:IXAsc**) and retaining the *stylar muscle* (**E-11 + 12:IXAx**). This inference is based on the presence of corresponding extrinsic appendicular muscles in the Endopterygota (Fig. 1.F5) and stylar muscles in the Hemiptera (Fig. 1.E), Psocodea (Fig. 1.F2), and Endopterygota (Fig. 1.F5).

3.2.2.3. Polyneoptera. Overview. To date, no work is known which synthesizes observations of genitalic skeletomusculature across the Polyneoptera. For this reason, references and interpretations for each order are presented separately below. There are, however, a primary series of early-to mid-20th century references on the external genitalia of the polyneopteran orders: Crampton (1918), Walker (1922), Snodgrass (1937, 1957). Based on comparison of genitalic skeletomusculature within the Polyneoptera and among other clades—up or down the Linnaean hierarchy—the following generalities may be drawn (Fig. 1.C). Note that, for phylogenetic shorthand, the following unconventional clade names are used: Plecopteroptera (= Plecoptera + Orthopteroptera); Orthopteroptera (= Orthoptera + Phasmoblaettida); Phasmoblaettida (= Phasmatida + Dictyoptera); Phasmatida (= Eukinolabia + Xenonomia, these names *sensu* Terry and Whiting, 2005).

- (1) The “phalli” of the Polyneoptera are homologous not only amongst themselves, but with the penis of the Ephemeroptera, the apterygote ectognaths, and the Eumetabola. This conclusion is drawn from the observation that *penial promotor* (**IXApp**) and *remotor* (**IXApr**) muscles are present in all orders where descriptions are available; **IXApp** is observed to be absent only in the Plecoptera and Phasmatodea.
- (2) Despite lacking musculature, proximally-articulated styli of segment IX are present in Dermaptera, some Orthoptera (styli not illustrated), Grylloblaettodea, and the Dictyoptera. This observation, combined with lack of extrinsic appendicular musculature and flexible membrane indicates that coxae IX are undifferentiated from sternum IX, resulting in a “coxosternum IX” or “sternocoaxal-complex area” ventrad the penis. Remarkably, coxae IX are differentiated from sternum IX in the Grylloblaettodea, but this is almost certainly a secondarily derived state, given the deeply-nested relationship of this order. Without extrinsic or intrinsic musculature, the gonopods cannot clasp; this function is replaced in a number of orders by postgenitalic elements.
- (3) One of the major evolutionary trends in the Polyneoptera appears to be the evolution of increasingly complex penial sclerites and associated muscles. Indeed, parallel lines of derivation among the Dermaptera, Zoraptera, and core Polyneoptera (i.e., Orthopteroptera) from a simple groundplan are probably a root cause for the difficulties in homologizing the genitalic elements, beyond misinterpretation of genitalic development when the “biogenetic law” is assumed. Secondary simplification is observed in the Dictyoptera (Isoptera) (see Klass, 1997).
- (4) The second major trend is the evolution of asymmetrical genitalia, whether involving the penial (“phallic”) complex or postgenital sclerites. Asymmetrical genitalia are observed

in some Dermaptera, the Zoraptera, the Phasmatida (Eukinolabia + Xenonomia), and the Dictyoptera. Given that the dermpteran genital asymmetry is taxonomically restricted (Labiduroidea: Giles, 1963), the odd derivations of zorapteran penial sclerites (Hünefeld, 2007; Matsumura et al., 2014), as well as the symmetry of the Plecoptera (e.g., Zwick, 1973) and Orthoptera (e.g., Snodgrass, 1937), it seems probable that the asymmetry of the Phasmatida + Dictyoptera is a synapomorphy of the clade. This scenario was previously postulated by Helm et al. (2011), in contrast to Huber et al. (2007) who proposed asymmetry as a groundplan feature of the Polyneoptera. Explicit comparison of penial function and skeletomusculature of the Polyneoptera is a means of resolving this evolutionary question.

Dermoptera. Although the morphology of male dermpteran genitalia has been considered to be singular and uninformative at the ordinal level (Giles, 1963), among the Polyneoptera, the Dermaptera are most similar to the groundplan here inferred (Fig. 1.C2). Giles (1963) and Snodgrass (1957) recognized that the male genitalia of Dermaptera consist of sternum IX (lacking styli throughout development, Qadri, 1940, p. 132) and a phallic organ which comprises a pair of outer “parameres”, and inner “mesomeres” clonally derived from a single pair of phallic *anlagen* (Qadri, 1940). Two morphological “types” of penes are recognized in the order (Burr, 1915a, b, 1916a): “protodermapterous” genitalia, with a distally divided penis (resulting in “paired penes”), and “eudermapterous” with a single penis (see Kamimura, 2004b for subclassification). Historically, presence of paired penes was considered to be plesiomorphic for the order (Burr, 1915a, b, 1916a; Popham, 1965), a supposition which has been supported by molecular phylogenetic analyses (Kamimura, 2004a; Kocarek et al., 2013; Naegle et al., 2016). Based on Popham’s (1965) illustrations of genitalic skeletomusculature for three species (one with paired penes, two without), it is apparent that male Dermaptera have the following groundplan features (Fig. 1.C2): (1) duplicated *penial promotors* (IXApp), (2) a single pair of *penial remotors* (IXApr) originating on an anterior elongation of coxosternum IX (the “manubrium”; Burr, 1916b), and (3) simple *intrinsic penial muscles* (XAp). Intersex comparisons will be facilitated with reference to Schneider and Klass (2013) who treated female genitalia in great detail.

Zoraptera. Zorapteran genitalia have been coarsely categorized as “simple” and “complex” (Delamare-Deboutteville, 1970). The simple form, which is most taxonomically widespread, is typified for the purposes of the present work by *Zorotypus hubbardi* Caudell, whose genitalic skeletomusculature was studied by Hünefeld (2007), and the complex form is typified by *Zorotypus caudelli* Karny, studied by Matsumura et al. (2014). Both species have extrinsic *penial promotors* (IXApp) and *remotors* (IXApr), but there has been considerable shift of origin onto pregenitalic sterna (Fig. 1.C3, C4): the *remotor* of *Z. caudelli* and *promotor* of *Z. hubbardi* onto sternum VIII, and the *remotor* of *Z. hubbardi* onto sternum VII. Both species have a diverse array of penial sclerites with intrinsic musculature (not illustrated), and *Z. hubbardi* apparently lacks coxosternum IX altogether. Also in *Z. hubbardi*, the origin of an *extrinsic penial muscle* (IXAp, Fig. 1.C4) originates on tergum IX; this is unique among the Polyneoptera—and is analogous to IXAtt in the Ephemeroptera (Fig. 1.B2). The tergopenial *extrinsic penial muscle* (IXAp) of *Z. hubbardi* corresponds most reasonably a subunit of the phallic promotor and remotor with a dorsally-shifted origin. To better understand zorapteran genital homologies, including of the penial sclerites, further detailed anatomical study is required; emphasis on the pregenital segments will clarify the evolutionary transitions of the *extrinsic penial muscle* origins.

Plecoptera. According to Zwick (2009), the male genitalia of the Plecoptera “provide outstanding characters”, but are relatively

simplified (see, e.g., Crampton, 1918; Walker, 1922; Brinck, 1956, 1970; Snodgrass, 1957; Scudder, 1971). Studies including skeletomusculature have largely focused on postgenital sclerites, as muscles of the paraprocts and epiproct (= “proctiger” broadly speaking) are directly involved in copulation and display spectacular variation (Smith, 1917; Brinck, 1970; Nelson and Hanson, 1971; Zwick, 1973). Coxosternum IX bears the single *penial retractor muscle* (IXApr) (Fig. 1.C5) (“paramedian ventral longitudinal muscle of sternite 9”, Zwick, pers. comm., 2017 April 2). The penis itself a short, soft-skinned tube (Zwick, 1973, see particularly p. 76), which may bear sclerotic bars (Brinck, 1956) which Qadri (1940, p. 139) referred to as “penis valves”. Qadri (1940) further observed that the developing penis of the Plecoptera divides into dorsal and ventral parts, which corresponds in pattern to the Orthoptera and Blattodea (other clades were not studied); this may be a synapomorphy of the Plecoptera.

Orthoptera. In contrast to the other orders, numerous works incorporate skeletomuscular observations for the Orthoptera (e.g., Caelifera: Acridomorpha, Snodgrass, 1935b; Eades, 2000, Carbonell, 2000; Eumasticoidea, Blackith & Blackith, 1967; Pyrgomorphoidea, Wasti & Akbar, 1969; Ensifera: Gryllidae, DuPorte, 1920; Schizodactylidae, Khattar, 1965; Tettigoniidae, Mbata, 1985). Other studies address the penial sclerites, without reference to musculature (e.g., Roberts, 1941; Randell, 1964). No study has yet synthesized these observations across the order. The skeletal elements of orthopteran male genitalia are several and have complex spatial relationships, with numerous intrinsic muscles; these muscles will prove to be useful in aligning the penial sclerites. The penis itself, as evidenced by the Caelifera (Eades, 2000, Fig. 1.C6), bears the insertions of three extrinsic muscles, two of which are functional *penial promotors* (IXApp), and one being a *penial remotor* (IXApr). It should be noted that styli are observed at the apex of coxosternum IX in some, but not all Orthoptera (e.g., Tettigoniidae, Snodgrass, 1937). For finer comparison within the order, the phylogeny of Song et al. (2015) will be a valuable guide. Indeed, finer comparison is necessary if a groundplan of penial skeletomusculature is to be induced for the Orthoptera.

Eukinolabia: Phasmatodea. The male genitalia of Phasmatodea was described by Helm et al. (2011), representing an appealing foundation for homologizing the skeletomusculature of the Plecoptera and its constituent clades. From Helm et al. (2011), the genitalia of *Oxyartes* (Necrosceriinae; Bradler et al., 2011) consist of coxosternum IX (“subgenital plate”), a sclerotized process of the ventral surface of abdominal segment X (“vomer”), and a complicated “phallic organ” which comprises five phallic sclerites. This phallic complex corresponds to the penis of other Pterygota in retention of the *phallic remotor muscles* (IXApr) (Fig. 1.C7). The well-developed and asymmetrical genital appendages have been described for *Timema* by Tilgner et al. (1999), although this study did not address skeletomusculature. Specific study of the genitalic musculature of *Timema* may shed light on the correspondences of the penial sclerites of this and other core polyneopteran clades.

Eukinolabia: Embioptera. No studies, to my knowledge, address the genitalic skeletomusculature of this order, although Ross (1940) emphasized importance of external genitalia, and stated (p. 631) that “males [have] no prominent true phallic structures, [with] secondary development of the ninth and tenth segments and cerci apparently serving as substitutes.” This observation was buttressed by Hünefeld (2007), who recognized a complete lack of a copulatory organ and endophallus (p. 143). From Ross (1940), the genitalia consist of sternum IX (= “hypandrium”) plus the cerci and tergum X, all of which are asymmetrical and modified for clasping.

Xenonomia: Grylloblattodea. The external genitalia of the Grylloblattodea are asymmetrical, and have been regarded as both highly derived and apparently uninformative for interordinal phylogenetics (Wipfler et al., 2014). Walker (1919) and Crampton (1927, figures 2, 5, 7, 8) provide illustrations and descriptions of the grylloblattodean

external genitalia. Unique among the Polyneoptera, Grylloblattodea have well-developed ninth-segmental coxae—these also bear distinct styli. Above the coxites occur a pair of fleshy “phallic” lobes which bear the insertions of the *penial promotor* (**IXApp**) and *remotor* (**IXApr**) muscles (Walker, 1943, Fig. 1.C8).

Xenonomia: Mantophasmatodea. The external genitalia of this order have been described in great detail (Klass et al., 2003), but musculature has yet to be considered. Key observations of this group are that coxosternum IX is undivided, styli are absent, and the “phallic organ” comprises up to eight individual sclerites (PH1–8), which are probably penial sclerites, although this should be confirmed via enumeration of the musculature. In most Mantophasmatodea studied by Klass et al. (2003), the genitalia were asymmetrical, with one sclerotic element, PH1, possibly corresponding to the “right phallomere” of the Dictyoptera (p. 57). Although not mentioned by Klass et al. (2003), this “right phallomere” may be homologous with the “chitinous process … of the phallus” observed by Walker (1919) for the Grylloblattodea.

Dictyoptera. The male genitalia of the Dictyoptera, comprising Mantodea + Blattodea (the latter including Isoptera), have been exquisitely studied by Klass (1997). In addition to developing a highly structured and logical system of terminology for the genitalic elements, Klass (1997) reviews previous genitalic work, provides lucid discussion of controversies over homologies—with needed emphasis on postabdominal segments—and provides a groundplan hypothesis for the clade. Two key correspondences may be drawn based on skeletomusculature: (1) the “ninth sternum” corresponds to coxosternum IX, bearing styli apically, and the insertions of tergal muscles p1, p2, and p3 (Klass, 1997, Fig. 58); (2) the asymmetrical “phallic complex” corresponds to the penis, receiving the insertions of a series of *penial promotor* (**IXApp**) and *remotor* (**IXApr**) muscles. Regarding the correspondences of dictyopteran genitalia with other orders, Klass is decisive: “The homology relations between the phallomere elements of [Dictyoptera] … and the elements of the external genitalia of other ectognathian taxa … are completely unclear” (Klass, 1997, p. 19). This emphasizes, at the bottom line, the need to examine and contrast the genitalic and—particularly—penial skeletomusculature across the Polyneoptera.

3.2.2.4. Eumetabola. Overview. The key comparisons to make in order to understand the genitalic skeletomusculature of the Eumetabola (name used following Beutel et al., 2017) are among the Condylognatha, Psocodea, and Endopterygota, the latter two forming a clade (Misof et al., 2014) here termed the “Phallo-neoptera”, modifying the circumscription from Hamilton (1971) and Boudreaux (1979). The sole difference in inferred groundplan between the Neoptera collectively (Fig. 1.B3) and the Eumetabola specifically (Fig. 1.D1) is strengthening of the stylus via a *stylar abductor* (**IXAxab**) and *stylar adductor* (**IXAxad**). This modification is almost certainly related to the clasping function of coxopods IX (= secondary gonopods), and is probably a synapomorphy of the clade. Detailed skeletomuscular study of the Thysanoptera and explicit revisit of the Psocodea is necessary to confirm the clasping,-coxopod synapomorphy hypothesis.

Condylognatha: Thysanoptera. The external male genitalia of the Thysanoptera have been described by, e.g., Jordan (1888), de Gryse and Treherne (1924), Priesner (1926, 1960, 1970), Melis (1933), Doeksen (1941), and Jones (1953). Three studies make observational statements about genital skeletomusculature, albeit without clearly describing muscle origin and insertion (De Gryse and Treherne, 1924; Jones, 1953; Heming, 1970); among these three, however, a groundplan does appear. Morphology of the external genital structures, situated posterior to the ninth-sternal element, differ between the Tubulifera and Terebrantia (Priesner, 1970). Basic features shared between the two include a proximal

“periandrium” which is continuous with a pair of “parameres” situated ventral to a median unpaired “aedeagus”; a second pair of “parameres” occur dorsal to the “aedeagus” in the Terebrantia. A pair of apical “coxal lobes”—probably representing styli—are present in some taxa (Priesner, 1970) and may form a median, unpaired plate (Heming, 1970). Their presence indicates that the ninth-sternal element represents an “integrated” coxosternum IX, where the coxites are undifferentiated. The following muscles have been observed to occur in representatives of the two suborders, although not all together (Heming, 1970, Fig. 1.E1): (1) *extrinsic penial remotors* (**IXApr**) originating anteriorly on coxosternum IX and dorsally (tergum X?; unclear from literature), inserting on the ventral and dorsal apodemes of the “phallobase” or “periandrium”; (2) two sets of *intrinsic penial muscles* (**XAp**), one set surrounding the ejaculatory duct, the other (*m3* in Fig. 1.E1) originating within the “phallobase” and inserting on the internal, proximal surface of the “aedeagus”. De Gryse and Treherne (1924) reference a *promotor muscle* of the “genital apparatus”, but do not describe this muscle in greater detail and omit a label from their figures; it would be significant if this *promotor* was confirmed to be the *dorsal penial remotor* (*r.m.* in Fig. 1.E1), as such a muscle is observed in Hymenoptera. All-in-all, these observations indicate that the “periandrium”, “parameres”, and “aedeagus” comprise a single complex, and are homologous with the ectognathan penis. Further, refined study may shed light on specific penial homologies of the Hemiptera, Psocodea, and Endopterygota. Work solving questions of homology within the order will benefit from recent systematic studies (e.g., Buckman et al., 2013; Nel et al., 2014; Pereyra et al., 2018) although discretion should be used as no nuclear data have been employed for phylogenetic reconstruction.

Condylognatha: Hemiptera. The male genitalia of Hemiptera have received substantial attention (e.g., Singh-Pruthi, 1925, revised by Yang and Chang, 2000), although there remains disagreement over the inter- and intraordinal homology of part, particularly with respect to the phallic structures (e.g., Dupuis, 1970; see also the figures of Kahlow, 1962). Five studies on male genital skeletomusculature have been relied on in the present work: one for the Auchenorrhyncha (Fennah, 1945: Fulgoroidea), one for the Sternorrhyncha (Weber, 1935: Aleyrodoidea), and three for the Heteroptera (Khanna, 1963: Pyrrhocoridae; Bhargava, 1967: Belostomatidae; Bonhag and Wick, 1953: Lygaeidae). In brief, the Fulgoroidea and sampled Heteroptera share the following three derived states (Fig. 1.E2): (1) segment IX forms a capsule-like sclerite (“pygophore”) which bears muscle origins on the dorsal, lateral, and ventral surfaces; (2) the stylus has two functional *abductors* (**IXAxab**), one of which originates on the (internal) dorsal surface of the pygophore; (3) three *extrinsic penial muscles* (**IXAp**) are observed, with the *promotor* (**IXApp**) originating dorsally, and the *remotor* or *remotors* (**IXApr**) usually originating anteroventrally. The *dorsal penial promotor* (**IXApp**) is probably homologous with the *dorsal penial remotor* (**IXApr**) observed in the Thysanoptera (compare Fig. 1.E1, E2), therefore being a groundplan feature of the Condylognatha. Further derivations are also observed: (4) In Homoptera, the origin of one of the *penial muscles* (**IXApr**) has shifted onto the base of the style (Fig. 1.E3, E4); (5) in Heteroptera, the *stylus abductor* (**IXAxab**) is duplicated (Fig. 1.E5, E6). Besides the identity of individual penial sclerites (which is out of the scope of the present work), the two primary questions for the Hemiptera are whether or not the lateral clasping structures (“harpagones” of Snodgrass, 1935a; “parameres” of Snodgrass, 1957) are styli, and whether the phallic structures are homologous with other ectognaths. Consistent presence of *abductor* (**IXAxab**) and *adductor* (**IXAxad**) muscles strongly support the homology of the “harpagones” or “parameres” of Hemiptera with styli, and the varied *extrinsic penial muscles* (**IXAp**) indicate that the “phallus” or

“aedeagus” is indeed homologous with the penis of the Ectognatha generally. As styli are observed in Thysanoptera, but differentiated coxae are not, it is reasonable that formation of coxosternum IX is another groundplan feature of the Condylognatha. No study to my knowledge addresses the genital skeletomusculature of the Coleorrhyncha; given that this suborder is strongly supported as sister to the Auchenorrhyncha (Misof et al., 2014), a study enumerating musculature and genital sclerites will be of value for refining the groundplan of the Homoptera specifically, and the Hemiptera generally.

Phalloneoptera. Specific comparison between the Psocodea, Endopterygota, and Hemiptera indicates that the insertions of the *penial promotor* (**IXApp**) and *remotor* (**IXApr**) muscles have shifted, as represented in the inferred groundplan of the clade (Fig. 1.F1). Additionally, the coxae of segment IX are inferred to be closely associated with sternum IX, culminating in complete developmental integration of these appendages with the penis in Endopterygota (see section 4.1 below).

Phalloneoptera: Psocodea. Available literature on external male genitalia of the Psocodea overall is sparse, does not attempt interordinal comparison, and most studies only treat sclerite topology (Lyal, 1986; Yoshizawa, 2005; Yoshizawa and Johnson, 2006; Yoshizawa and Lienhard, 2010; Polilov, 2016). At least two works, however, address skeletomusculature (e.g., “Mallophaga”: Schmutz, 1955; “Pscoptera”: Klier, 1956). The current consensus is that male psocodean genitalia consist of a “basal plate/apodeme”, “parameres”, “mesomere”, and “ventral plates”, which together comprise the “phallosome”, abutted ventrally by a “hypandrium” (= “sternite” IX) (Yoshizawa, 2005; Yoshizawa and Johnson, 2006). Based on Klier (1956), the “phallosome” may be homologized with the penis, given that it bears extrinsic *remotor* (**IXApr**) and *promotor* (**IXApp**) muscles which originate on sternum IX (Fig. 1.F2). The identity of the individual penial sclerites (i.e., “parameres”, “mesomeres”, and “ventral plates”) relative to the Condylognatha and to the Endopterygota is uncertain due to lack of comparable skeletomuscular data. Klier (1956) describes a single muscle for the “harpago”, which acts as an *adductor* (**IXAxad**); for this reason, the psocodean “harpago” is inferred to be the stylus, as for the Hemiptera (above). Note that the psocomorphian *Stenopsocus* and *Lachesilla* have two pairs of *remotors* (9,l and 10,k in Fig. 1.F2), while *Philotarsus* (Psocomorpha) and *Trogium* (Trogiomorpha) have one pair (x,D in Fig. 1.F2). Despite low topological support in Yoshizawa and Johnson (2010), this does suggest that the state of having only one pair is ancestral. Revised and explicit skeletomuscular comparisons of the genitalia of the Psocodea may be very enlightening for the Eumetabola, given the possible ordinal relationships. Future studies will benefit from reference to the phylogenetic topologies of Yoshizawa and Johnson (2010) and Li et al. (2015a).

4. Results: observations and analysis of Endopterygota

This chapter addresses the skeletomusculature of the Endopterygota, for which direct observations of muscular topology were rendered via dissection. The first section addresses the groundplan of the Endopterygota (4.1), and the following sections (4.2 onwards) are taxon accounts for all taxonomic orders of the Endopterygota. These accounts are presented in a phylogenetic sequence, rather than in an order of derivation. The general organization used here is as follows: Hymenoptera (4.2), Neuropterida (4.3), Coleopterida (4.4), Euantliophora (4.5), Diptera (4.6), and Amphiesmenoptera (4.7).

To refer to the accounts from least to most derived, consider specific treatments in the following order: Raphidioptera (4.3.1) then other Neuropterida (4.3.2–4), Amphiesmenoptera (4.7),

Hymenoptera (4.2), Strepsiptera (4.4.4) then Coleoptera (4.4.1–3), and the Antliophora (Mecoptera, 4.5.1–3; Siphonaptera, 4.5.4; Diptera, 4.6). This linear arrangement, based on degree of derivation, is of course both arbitrary and artificial, and is thus not preferred as the main organizing scheme of the taxon accounts. For explanation of evidence for inferred homologies, refer to the most general section for each order (e.g., Hymenoptera 4.2 rather than *Cimbex rubidus* 4.2.1). These sections provide general background and specific reasoning for skeletomuscular interpretations reached for each treated subtaxon given the groundplans inferred for higher taxa (Fig. 1).

4.1. The endopterygote groundplan

Groundplan morphology. The abdominal organization of the Endopterygota is grossly similar to that of the apterygote Ectognatha. Differing from the apterygote Ectognatha, Palaeoptera, and Polyneoptera, however, the penis of the Endopterygota is developmentally and mechanically integrated with the coxopods of segment IX. Specifically, the gonopodal and penial *anlagen* arise together (Snodgrass, 1941, 1957), and the origins of the extrinsic penial muscles have migrated from their ancestral position on sternum IX to the inner surfaces of the gonocoxae. This transformation is indicated in Fig. 1.F, where the coxites become closely associated with sternum IX (Fig. 1.F1), allowing the extrinsic penial muscles to take “short steps” into the coxites (Fig. 1.F3). Once integrated into the gonocoxae, the *penial promotor* (**IXApp**) and *remotor* (**IXApr**) muscles duplicate laterally (Fig. 1.F4) and dorsally (Fig. 1.F5), with the sclerite of insertion for the lateral duplicates splitting off laterally, resulting in the *lateropenite* (= “parandrites” of Bechly et al., 2001; “volsella” of Michener, 1944b; and other, numerous terms).

In general, the coxopods of the Endopterygota function as claspers and receive the insertions of extrinsic muscles originating on tergum and sternum IX. Notably, the situation of developmental integration of the penis with the gonopods is paralleled in the Hemiptera, where the penis is internalized within the pygophore (Fig. 1.E2), which is rather the product of integration of the coxites with sternum and tergum X. As with other pterygotes, there is variable incorporation of pre- and postgenital sclerites in the collective male “copulatory apparatus”. To reiterate, skeletomuscular correspondences (Fig. 1) indicate that the sclerotic elements of endopterygote male genitalia comprise paired *coxopods of segment IX* (secondary gonopods), divided into basal coxae (gonocoxae) and distal styli (gonostyli); medial to the gonopods are the paired *lateropenites* and median *penis*.

To derive the homologies for the endopterygote orders, it is necessary to account for the five following muscle classes (Table 2) indicated in the groundplan (Fig. 1.F5): (1) *m. tergo-coxalis* (**IXAtc**); (2) *m. sterno-coxalis* (**IXAsc**); (3) *m. exopodalis* (**IXAx**) and its derivatives *m. adductor* and *abductor exopodalis* (**IXAad**, **IXAab**); (4) *m. lateropenitis* (**IXAI**) and its derivatives *m. lateropenitis magnus* and *parvus* (**IXAlm**, **IXAlp**); and (5) *m. penialis* (**IXAp**) and its derivatives, *m. promotor penialis ventralis* and *dorsalis* (**IXAppv**, **IXAppd**), *m. remotor penialis ventralis* and *dorsalis* (**IXAprv**, **IXAprd**). For this reason, the order treatments (section 4.2) are presented with a homology-neutral description followed by a “homology analysis” section, where correspondences are reasoned through. As well, the homology-explicit musculature descriptions are presented with the muscles organized by the five categories indicated above, with the distinction that **IXAtc** and **IXAsc** are extrinsic to the gonocoxa, and **IXAx**, **IXAlp**, and **IXAp** are intrinsic to the gonocoxa, i.e., the muscle origins are observed to be within the gonocoxae. A summary of observed muscles is presented in Table 3.

Table 3

Summary of observed muscles across the Endopterygota in the present study (see also Fig. 1G–L); muscle labels adapted from Table 2. Note the following: (1) For a given major muscle class, a blank cell indicates that subunits (minor classes) are undifferentiable; (2) extrinsic muscles may be present in Diptera and Trichoptera, as well as stylar muscles (IXAx) in the latter; (3) the origin of IXAI in Megaloptera and Neuroptera has shifted onto the penial sclerite; (4) the gonostylar and penial muscles of Coleoptera are highly derived with respect to function, thus precise minor-muscle-level correspondences are not possible to enumerate; (5) likewise, the penial extrinsic muscles of Siphonaptera are highly derived, thus correspondences may not be exact.

Muscle classes		Order										
Major	Minor	Hym.	Raph.	Megal.	Neur.	Col.	Strep.	Mec.	Siph.	Dip.	Trich.	Lep.
<i>Extrinsic to copulatory apparatus</i>												
IXAtc	-	1	1	0	0	1	1	1	1	1	0	1
IXAsc	m	1	1	1	1	1	1	1	1	0	0	1
I	l	1	1	1	0	1	1	1	1			
<i>Intrinsic to copulatory apparatus, non-penial</i>												
IXAx	ab	1	1	1	1	1'	0	1	1	1	0	0
	ad	1	1	1				1	1	1		1
IXAI	m	1	1	1	1	0	0	0	1	1	0	1
	p	1	1						1			
<i>Intrinsic to copulatory apparatus, penial</i>												
IXAp	pv	1	0	0	0	1'	0	1	1"	1	1	1
	rv	1						1	1"	1	0	0
	pd	1	1	1	1			1	1"	1	1	1
	rd	1	1	1	1			1	1"		1	0
XAp	-	0	1	1/0	0	1'	0	0	?	1	0	0

4.2. Hymenoptera

Homology-neutral description. The male genitalia of the Hymenoptera are best described generally based on representatives of the “Symphyta” or Eusymphyta (no consensus to date: contrast Peters et al., 2017 and Branstetter et al., 2017). The following homology-neutral description is provided for a representative of this group, *C. rubidus* (see below), with indication of deviation from the general genitalic organization of the order. The copulatory appendages are located posterior to sternum IX and ventral to a sclerotic pouch, which bears paired, digitate, unisegmental appendages, and the anus. Specifically, the copulatory appendages comprise five sclerites (Fig. 2; terms in quotations from Schulmeister, 2001; sclerite abbreviations from Fig. 1.G3 also indicated): (1) a sclerotic ring (“cupula”, TgIX+CtxI) which is situated at the anterior apex of the paired appendages; the paired appendages comprise clasping structures (“latimeres”), which themselves are divided into (2) a basal lamina (“gonostipes”, Cxa), which is petal-shaped in profile view and bears dorsomedian processes with their long axes oriented anteroposteriorly, and (3) an apical lobate structure (“harpe”, Sty); medial to the latimeres are two sets of paired sclerites: (4) a smaller clasping structure (“volsella”, CtxII plus Lpe), which is lateromedially narrow and with its length oriented along the anteroposterior axis; (5) medialmost to the volsellae are a pair of sclerites (“penisvalva”) with a conspicuous posterior lobe and anterior, longitudinally-oriented apodeme. Fourteen muscles are present (Fig. 1.G3, Fig. 2; muscle labels from Schulmeister, 2001, after Boulangé, 1924, indicated parenthetically in Fig. 1.G3): (1, 2) the cupula is attached to sternum IX via a pair of extrinsic muscles (*b*, *c*); (3–5) three muscles attach the cupula to the gonostipes (*e*, *f*, *g*); (6, 7) two muscles attach the gonostipites to the harpe (*t*, *u*); (8) one muscle attaches gonostipites to the volsella (*p*); (9) one muscle is intrinsic to the volsella (*qr*); (10–14) five muscles attach the gonostipites to the penisvalvae (*h*, *i*, *j*, *k*, *si*).

Homology analysis. In order to derive the musculature of *C. rubidus* from the inferred endopterygote groundplan (Fig. 1.F5) the following transformations must take place: (1) the lateral parts of tergum IX fragment off, bearing with them the origin of the *m. tergo-coxalis* (IXAtc) (Fig. 1.F5 to 1.G1); (2) the lateral tergites IX fuse with the gonocoxae at their anterior base (Fig. 1.G1); (3) along with the fused tergites IX, the ventral portion of the gonocoxae fragment off, bearing the insertions of the *m. sterno-coxalis* (IXAsc), thus forming the *cupula* (Fig. 1.G2); (4) the *m. tergo-coxalis* (IXAtc),

now intrinsic to the copulatory apparatus, divides into a series of subunits (*d*, *e*, *f*, *g*; Fig. 1.G2 to 1.G3); (5) the gonocoxae fragment a second time, with novel ventromedial fragments forming the *parossiculi*; and (6) the parossiculi fuse with the *lateropenite* to form the *volsella* (Fig. 1.G2 to 1.G3). Note also a muscle unique to the Hymenoptera (*si*; Fig. 1.G3) which originates on the anteromedial part of the parossiculus and inserts on the *penial sclerite* (= penisvalva). This seemingly bizarre muscular topology may be explained as a retention of origin of attachment via the fragmentation of the parossiculi from the coxites, bearing with them a subunit of the ancestral *m. promotor penialis ventralis* (IXAppv).

Explanation of homology analysis. Because much of the confusion over endopterygote genital homologies stems from apparent discord between developmental theory (Snodgrass, 1935a, 1941, 1957) and skeletal observations of the Hymenoptera (Crampton, 1920, 1938; Michener, 1944a), it is necessary to provide a detailed explanation of the hypothesis developed and proposed here. The first step in this dialectic is to recognize the historical terminology for hymenopteran genitalia. Traditionally (Schulmeister, 2001), the male genitalia of the Hymenoptera have been considered to comprise the “cupula” (or “lamina annularis”, “basal ring”; a sclerotic ring at the base of the appendages), the “parameres” (lateral clasping organs, each with a basal “basimere” and distal “telomere”, or “gonostipes” and “harpe” of Schulmeister, 2001), the volsellae (ventromedial appendages, each with an opposable “digitus” and “parossiculus”), and the “penisvalves” (intromittent penial sclerites). When the “basimeres” and “telomeres” are insensibly fused, the “parameres” are referred to as “gonoforceps” (Michener, 1944a, b; Schulmeister, 2001). Schulmeister (2001) proposed an alternative interpretation of the genitalia, wherein all structures are “phallic” in origin, rather than “phallic-peripheral”, thus she coined the term “latimere” to replace “paramere”.

Among the Hymenoptera, there are five recognizable sets of muscles (using traditional hymenopteran terminology for sclerites): sternal-cupular (*b*, *c*), cupular-basimeral (*d*, *e*, *f*, *g*), basimeral-telomeral (*t*, *u*), basimeral-volsellar (*p*, *qr*), basimeral-penisvalvar (*h*, *i*, *j*, *k*). Of the five primary muscle classes indicated in the endopterygote groundplan (section 4.1, Fig. 1.F5), the latter three muscle sets are neatly redefined based on clear topological correspondences as the *m. coxo-stylalii* (*u* + *t*:IXAx), the *m. coxo-lateropenitii* (*p* + *qr*:IXAI), and the *m. coxo-penialii* (*h* + *i* + *j* + *k*:IXAp) (for further reasoning on the coxal-lateropenital muscular homologies, see the following paragraph). That leaves

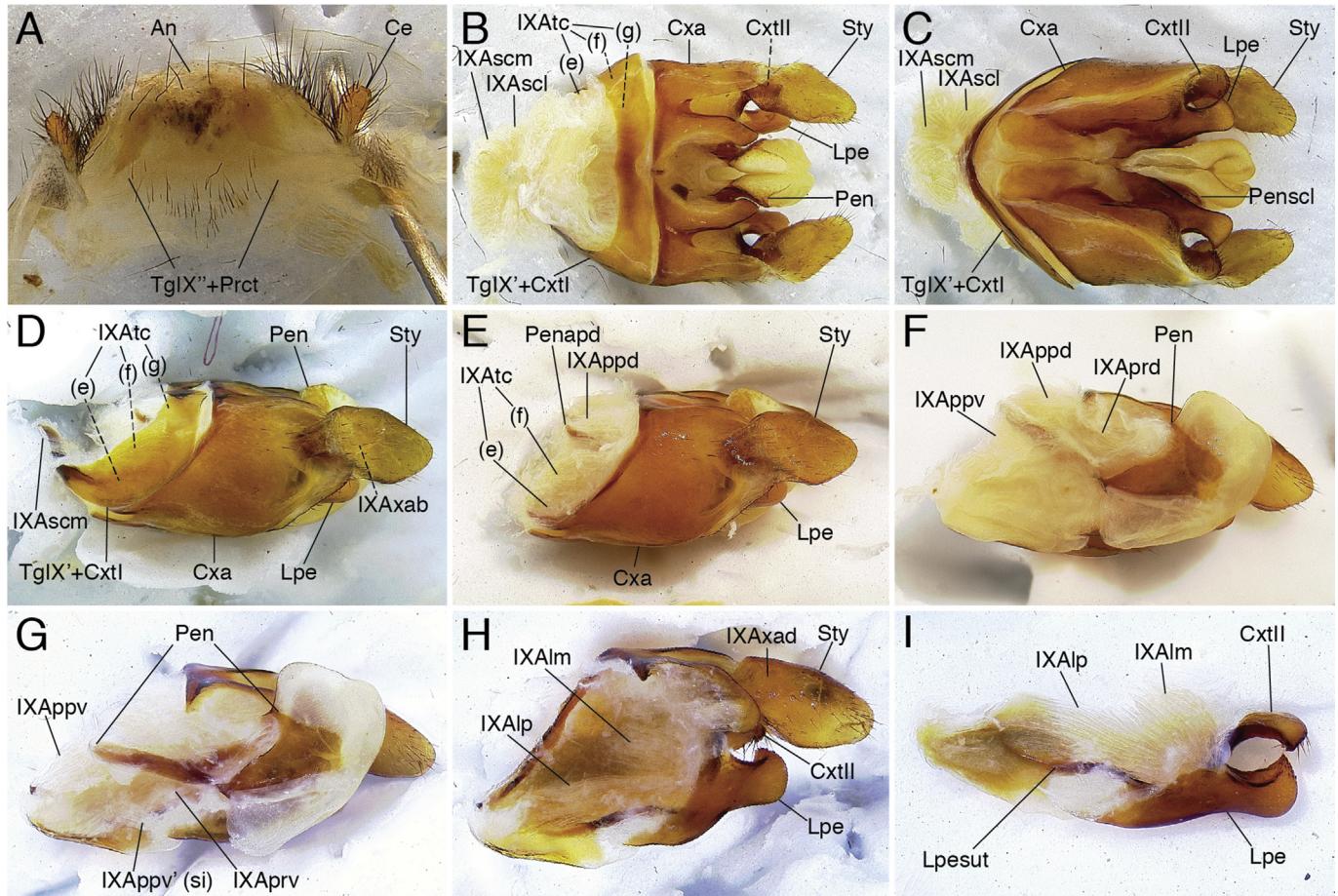


Fig. 2. Genital skeletomusculature of *Cimbex rubidus* (Hymenoptera: Cimbicidae). **A**, tergite IX and proctiger. **B–E**, genital capsule: **B**, dorsal; **C**, ventral; **D**, lateral; **E**, cupula removed, lateral. **F–G**, right coxopod and penial sclerite: **F**, mesal; **G**, penial conjunctiva and musculature partially removed, mesal. **H**, right gonopod, penial musculature removed, mesal. **I**, **1**, volsella, mesal (dorsal). **Abbreviations:** An = anus; Ce = cercus; Cxa = “basimere” (major part gonocoxa); CxtII = “parossiculus” (minor part of second gonocoxial fragment); Lpe = lateropenite; Lpesut = lateropinal suture with ventromedial gonocoxite; Pen = penis or penial sclerite; Penapd = penial apodeme (“valvula”); Prct = proctiger; StIX = sternum IX; Sty = stylus; TgIX' = tergite IX; TgIX'+Cxtl = “cupula” (composite sclerite of tergite IX plus basal/anterior fragment of gonocoxite). **Muscle abbreviations** indicated in Table 1.

the two extrinsic pairs of muscles which attach to the cupula to be homologized. The first muscle set, the sternal-basimeral muscles, originating on the sternum and inserting externally on the ventral surface of the cupula, indicate that the cupula is, in part, derived from the gonocoxae, and these muscles may be interpreted as the *m. sterno-coxalii* (*b + c:IXAsc*). With the “parameres” or “latimeres” homologized with the gonopods, the cupular-basimeral muscles (*d, e, f, g*) may be partially homologized as cupular-coxal. Two alternative hypotheses may be proposed to explain the homology of the muscular origins of the erstwhile cupular-coxal muscles: (1) the origins, which are on the internal surfaces of the cupula, may have arisen *de novo* with concomitant loss of the tergal-coxal muscles, or (2) they may be derived from the tergal-coxal (**IXAtc**) muscles themselves. Besides being more parsimonious, the latter hypothesis explains both the lack of other muscles originating on the paraproct complex situated above the copulatory apparatus, as well as the physical separation of the cupula from the remainder of the gonopods. Therefore it is here concluded that the “cupular-basimeral” muscles are the *m. tergo-coxalii* (*d + e + f + g:IXAtc*).

With the homologies of the cupula and lateral clasping appendages stabilized, the *digiti* may be homologized with the *lateropenites* of other groups, again a case supported by skeleto-muscular correspondences. The parossiculus, to which the *digiti* articulates, may be an anterior projection of the lateropenite

of the Hymenoptera, or may be a ventromedial fragment of the coxa. This latter scenario is more likely, as (1) the parossiculus is distinct from the *digiti* in some sawfly taxa (Schulmeister, 2003), (2) the parossiculus bears intrinsic musculature not present in the lateropenites of other orders (i.e., muscle *qr*, Fig. 1.G3), and (3) the penial sclerites (= penisvalvae) of most sawfly taxa, including Xyelidae, bear a penisvalvar-parossicular muscle, (*si*) (Schulmeister, 2003), which is reasonably derived from the *m. promotor penialis ventralis* (**IXAppv**) (see Homology analysis above). Indeed, the gonocoxal origin of the parossiculus was intimated by Michener (1956, p.135), who stated that the *volsella* “is a fragmentum” of the gonocoxa. With this nuanced understanding, the parossiculus, rather than the *volsellar complex* itself (Sharkey, 2007), may be considered a uniquely-derived apomorphy in the groundplan the Hymenoptera.

Genital evolution. The homology interpretations proposed here suggest the following autapomorphic modifications of the groundplan copulatory apparatus for the Hymenoptera (not necessarily in this sequence): (1) the lateral gonocoxal margins fold dorsomedially, forming a pair of half-pipes enclosed dorsally and ventrally, with the convex surface directed externally; (2) the ventromedial gonocoxal margins detached, these fragments (gonocoxites) form the parossiculi and bear one of the two coxal-lateropenital muscles and a coxal-penial muscle; and (3) the

anterior portion of tergum IX, bearing the tergal-coxal muscles, fused with the gonocoxae anterodorsally, and the tergital-coxital composite fragmented off anteriorly, forming the cupula. As paired penial sclerites also occur in the Raphidioptera, it is unclear whether paired penial sclerites are derived for the Hymenoptera or ancestral for the most recent common ancestor of the Endopterygota. The latter scenario would imply at least three independent origins of medially-fused penial sclerites within the Endopterygota: once in the neuropteroids, once in the most recent common ancestor of the Coleopterida, and once in the ancestor of the Amphiesmenoptera plus Antliophora. Based on study of the Formicidae, aculeate genital skeletomusculature generally appears to be reduced relative to the “Symphyta”, although expanded sampling is needed (Boudinot, 2013).

Comments. The *Hymenoptera Anatomy Ontology* follows Snodgrass's (1957) application of the phallic-periphalllic model. Specifically, according to the ontology, the phallus comprises the penial sclerites, and the periphalllic appendages comprise the volsella (= ventromedial gonocoxite plus lateropenite), the cupula (= anterior gonocoxite plus tergite IX), and “gonostipes” (= gonocoxae), all three of which represent divisions of a phallobase (see Table S2). Similarly, Schulmeister (2001, 2003) also applies the phallic-periphalllic model, but she interpreted the entire genital capsule or external genitalia as phallic, thus periphalllic structures were absent. The homologies drawn here from comparison of skeletomusculature across orders is thus more similar to Michener (1944a, b) and Smith (1970), as the two based their interpretations on the coxopodal hypothesis.

4.2.1. Hymenoptera: Cimbicidae, *Cimbex rubidus* Cresson, 1880

Note: Uniform Resource Identifiers (URIs) for each anatomical part, including musculature, from the *Hymenoptera Anatomy Ontology* (Yoder et al., 2010; HAO, 2016) are indicated in Table S2, as per the recommendations of Seltmann et al. (2012).

Sclerites. Abdomen. **Tergum IX** fragmented: (1) first/anterior fragment fused with a coxal fragment (Fig. 2B and C); (2) second/posterior fragment reduced, connected narrowly to sternum IX by conjunctiva (= membrane) and broadly joined to sac-like proctiger. **Sternum IX** large, shield shaped. Eleventh segment/proctiger insensibly fused with tergum IX, and tergite-proctiger complex bearing cerci laterally (Fig. 2A). **Genital appendages.** Genitalia strophandrous (rotated 180° around cephalocaudal axis within genital chamber). **Coxae** fragmented twice, resulting in three parts: (1) first (anterior) fragments fused together medially and dorsally with first/anterior fragment of tergum IX, forming ring-like sclerite abutting bases of second gonocoxal fragments (cupula = “basal ring”) (Fig. 2B and C); (2) gonocoxae (= “gonostipes”) with lateral margins folded dorsally and meeting medially, forming tube-like limb bases which are hemispherical in cross-section, and bearing origins of majority of genital musculature (Fig. 2B–H); (3) third fragments forming ventromedial splinters (parossiculi) which are partially fused to lateropenites forming the volsellar complex (Fig. 2B, C, H, I). **Styli** fused laterally with gonocoxae (Fig. 2D and E), gonocoxae without corresponding articulatory condyles. **Lateropenites** present as short digitate processes (“digitii”), fused laterally with third coxites (Fig. 2B–E, H, I), producing sinuate suture (Fig. 2I). **Penial sclerites** paired (Fig. 2B and C), distal portion of sclerite forming lobate blade in profile view (“valviceps”) which is sclerotized on lateral and medial surfaces, circumferences of these sclerotizations with broad membrane (Fig. 2B, C, F, G); penial apodeme (“valvura”) linear (Fig. 2G).

Musculature (Fig. 1G3). **Extrinsic coxal muscles.** **Tergo-coxal** muscles (**IXAtc**) present, originating within cupula on dorsal and lateral internal surfaces, inserting on anterior bases of gonocoxae (Fig. 2B, D, E). **Sterno-coxal:** lateral and medial muscles (**IXAscl**,

IXAscm) present, originating on anterior sternal margin and inserting on external ventral surface of cupula (Fig. 2B–D). **Intrinsic coxal muscles.** **Coxo-stylar:** stylar adductor (**IXAxad**) and abductor (**IXAxab**) muscles present (Fig. 2D, H), adductor originating on anterodorsal corner of gonocoxa, inserting in stylus via thin ligament. **Coxo-lateropenital:** two muscles present, small adductor (**IXAlp**) originating on broad inner, basal face of ventro-medial gonocoxite (parossiculus), and large abductor (**IXAlm**) originating within gonocoxa (Fig. 2H and I). **Coxo-penial:** penial depressors (**IXAppd**) and levators (**IXAppv**, **IXAppv'**, **IXAprv**) present: (**IXAppd**) originating on dorsomedial processes of gonocoxa (“parapenis”) medially, inserting on anterodorsal surface of penial apodeme (Fig. 2E and F); (**IXAprd**) originating on gonocoxa dorsally, medial to (**IXAppd**), inserting broadly on medial surface of penial apodeme base (Fig. 2F); (**IXAppv**) originating on anteromedial surface of gonocoxa, inserting on anteroventral surface of penial apodeme (Fig. 2F and G); (**IXAppv'**) originating broadly within basal region of parossiculus and inserted on penial sclerite near insertion of **IXAprv** (Fig. 2G); (**IXAprv**) originating on tough membrane attached to penis and inserted on ventrolateral surface of penial sclerite (Fig. 2G).

4.3. Neuropterida

Homology-neutral descriptions. To understand skeletomuscular correspondences among the Neuropterida, it is necessary to describe here two taxa with relatively generalized genitalic morphology. Among the Neuropterida collectively, the Raphidioptera represent the closest approximation to the groundplan morphology here inferred (Fig. 1H1). Four sclerites are observed (Fig. 3; labels indicated parenthetically): (1) a pair of large, petal-shaped sclerites (Cxa) which bear at their posterodorsal apices (2) small, claw-like sclerites (Sty), and encompass both (3) a pair of small, ventromedial, lobate sclerites (Lpe) and (4) a pair of medi-almost sclerites which are more-or less rod-shaped (Penscl); these rod-shaped sclerites are fused anteroventrally with the petal-shaped sclerites, and are somewhat lateromedially expanded. Musculature (Fig. 1H1; arbitrary muscle labels indicated parenthetically): three extrinsic muscle units are present: (1) one set attaching the petal-like sclerites (Cxa) to tergum IX (i), and (2, 3) two muscles attaching the petal-like sclerites (Cxa) to sternum IX (ii, iii), itself fused with the isosegmental tergum; six intrinsic muscles are present: (4, 5) two muscles attach the claw-like sclerites (Sty) to the petal-shaped sclerites (Cxa) (iv, v); (6, 7) two muscles attach the lobate sclerites (Lpe) to the petal-shaped sclerites (Cxa) (vi, vii); and (8, 9) two muscles attach the rod-shaped sclerites (Penscl) to the petal-shaped sclerites (viii, ix).

Between the Megaloptera and Neuroptera, the Corydalidae have the most-generalized genitalic morphology. Five sclerites are associated with abdominal segment IX (Fig. 4; labels indicated parenthetically): (1) sternum IX; (2) a large dorsal plate (Cxa, TgIX) which is divided anteriorly and medially by a T-shaped thinning of the cuticle corresponding to internal apodemes; (3) a pair of club-shaped sclerites (Cxa) articulating with the posterolateral apices of the dorsal plate; (4) a tiara-shaped sclerite (Penscl) which bears (5) a pair of digitate sclerites (Lpe). Seven muscles are directly associated with these sclerites (Fig. 1H4; arbitrary muscle labels indicated parenthetically): (1, 2) a pair of muscles attaching sternum IX to arthrodial membrane (corium) ventral to the tiara-shaped sclerite (i', ii'); (3) a muscle intrinsic to the club-shaped sclerite (iii'); (4) a muscle attaching the club-shaped sclerite to the dorsal plate (iv'); (5, 6) two muscles attaching the tiara-shaped sclerite to the dorsal sclerite (v', vi'); and (7) one muscle each inside of the lobate sclerites which attach to the tiara-shaped sclerite (vii'). Note that the T-shaped thinning is also observed in the Sialidae (Fig. 5).

Homology analysis. Comparison among the Raphidiidae, Corydalidae, and the endopterygote groundplan (Fig. 1.F5) shows that the ventral extrinsic muscles correspond to the *m. sterno-coxalii* (*ii + iii:i+ii':IXAsc*), and that the dorsal extrinsic muscles of the raphidiopteran correspond to the *m. tergo-coxalii* (*i:IXAtc*). Therefore, the “petal-shaped” sclerites may be homologized as the gonocoxae. The three remaining muscle sets in the examined raphidiopteran originate within the gonocoxae, and those of the corydalid within the “large dorsal plate”, which indicates that the dorsal plate is, at least in part, the gonocoxa, and that the sclerites onto which the three muscle sets insert are either penial, lateropenital, stylar, or derivatives thereof. With the identity of the gonocoxa established, the remaining skeleto muscular correspondences are straightforward: the “claw-like” and “club-shaped” sclerites are styli (*iv + v:iv':IXAx*), the “lobate sclerites” of both are lateropenites (*vi + vii:vii':IXAlp*), and the “rod-shaped” and “tiara-shaped” sclerites are penial sclerites (*viii + ix:v'+vi':IXAp*).

To derive the particular genital skeleto muscular topology of the Corydalidae from a neuropteridan groundplan resembling the Raphidioptera, the following transformations are inferred (Fig. 1.H1): (1) one of the coxo-lateropenital muscles (**IXAlp**) is lost

and the origin of the other migrates onto the base of the penial sclerite (which is ancestrally fused to the gonocoxa) (Fig. 1.H1 to 1.H2); (2) the gonocoxae migrate dorsally, fusing with tergum IX anteriorly and together medially, bearing the origins of the coxo-penial muscles (**IXAp**) (Fig. 1.H2 to 1.H3), resulting in the T-shaped suture observed on the “dorsal plate” of the Megaloptera, and leaving the genitalia unsclerotized ventrolaterally; (3) the lateropenites become articulated to the penial sclerite (Fig. 1.H3 to 1.H4); and (4) one of the coxo-stylar muscles becomes intrinsic to the stylus (Fig. 1.H3 to 1.H4). With this as a groundplan for the Megaloptera + Neuroptera (Fig. 1.H4), to derive the topology of the Sialidae (Fig. 1.H5), the dorsomedially-fused gonocoxae must fragment laterally, with the lateral fragments bearing the styli and the origin of one of the penial muscles (**IXAppd**), and the dorsal fragment bearing the origin of the remaining extrinsic stylar muscle (**IXAxad**); finally, the penial sclerite and lateropenites must migrate dorsomedially to become associated with the dorsomedially-situated gonocoxae. Finally, to derive the topology of the Myrmeleontidae (Fig. 1.H6) from the corydalid groundplan (Fig. 1.H4), the styli and tergum IX must become completely integrated with the dorsomedially-fused gonocoxae, the *sterno-coxal muscles* must be

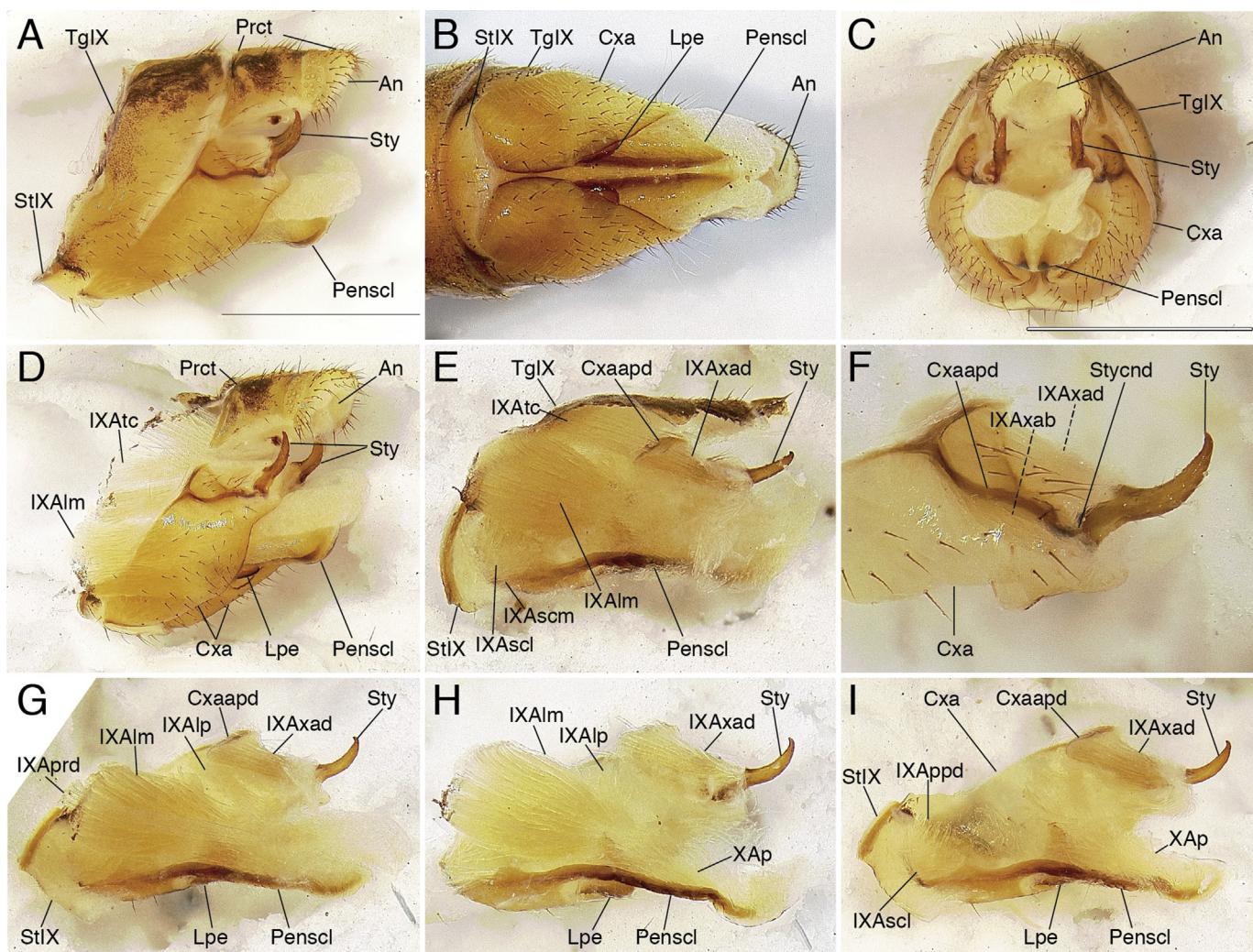


Fig. 3. Genital skeleto-musculature of *Agulla* sp. (Raphidioptera: Raphidiidae). **A–E**, segment IX, genital appendages, and proctiger: **A**, lateral; **B**, ventral; **C**, distal; **D**, tergum removed, lateral oblique; **E**, left half removed and proctiger partially removed, mesal. **F–I**, right coxopod and sternum part, mesal. **Abbreviations:** An = anus; Cxa = gonocoxa; Cxaapd = coxal apodeme; Lpe = lateropenite; Pen = penis; Penscl = penial sclerite; Prct = proctiger; StIX = sternum IX; Sty = stylus; Styapd = stylar apodeme; Stynd = stylar condyle; TgIX = tergum IX. **Muscle abbreviations** indicated in Table 1.

lost, and the proctiger must become associated with the penial sclerite and lateropenites.

Genital evolution. Observations of the skeletomusculature of these groups, in the context of the Endopterygota as a whole, suggests the following evolutionary sequence. Unlike other neuropteridan orders, the penial sclerites of the Raphidioptera are fused to the gonocoxae, which are themselves not markedly modified otherwise (Fig. 1.H1). This fusion may have allowed one unit of the coxo-lateropenital muscles to shift their origins onto the penial sclerites where these connect to the gonocoxae (Fig. 1.H2). With the reduction of the ovipositor in female Megaloptera and Neuroptera (Hünefeld et al., 2012), the female spermatheca became less concealed. Consequently, the requirement for fine

manipulation of ovipositor structures and intromission was lost. Without an intromittent organ, the clasping function of the gonopods was reinforced. In the process of optimization for non-intromittent or contact copulation, the gonocoxae migrated dorsad, eventually fusing together and effectively replacing tergum IX—a probable synapomorphy for the Megaloptera + Neuroptera (Fig. 1.H3). Functional modifications occurred to the gonocoxae, resulting in their subsequent fragmentation (Fig. 1.H5, 1.H6). Skeletomusculature suggests that the structure recognized as the “gonarcus” is in fact the medially-fused penial sclerites, which have drifted dorsad, becoming dissociated with the phallotreme, but retaining a tight relationship with the medially-fused lateropenites, and bearing the coxo-lateropenital muscles (Fig. 1.H).

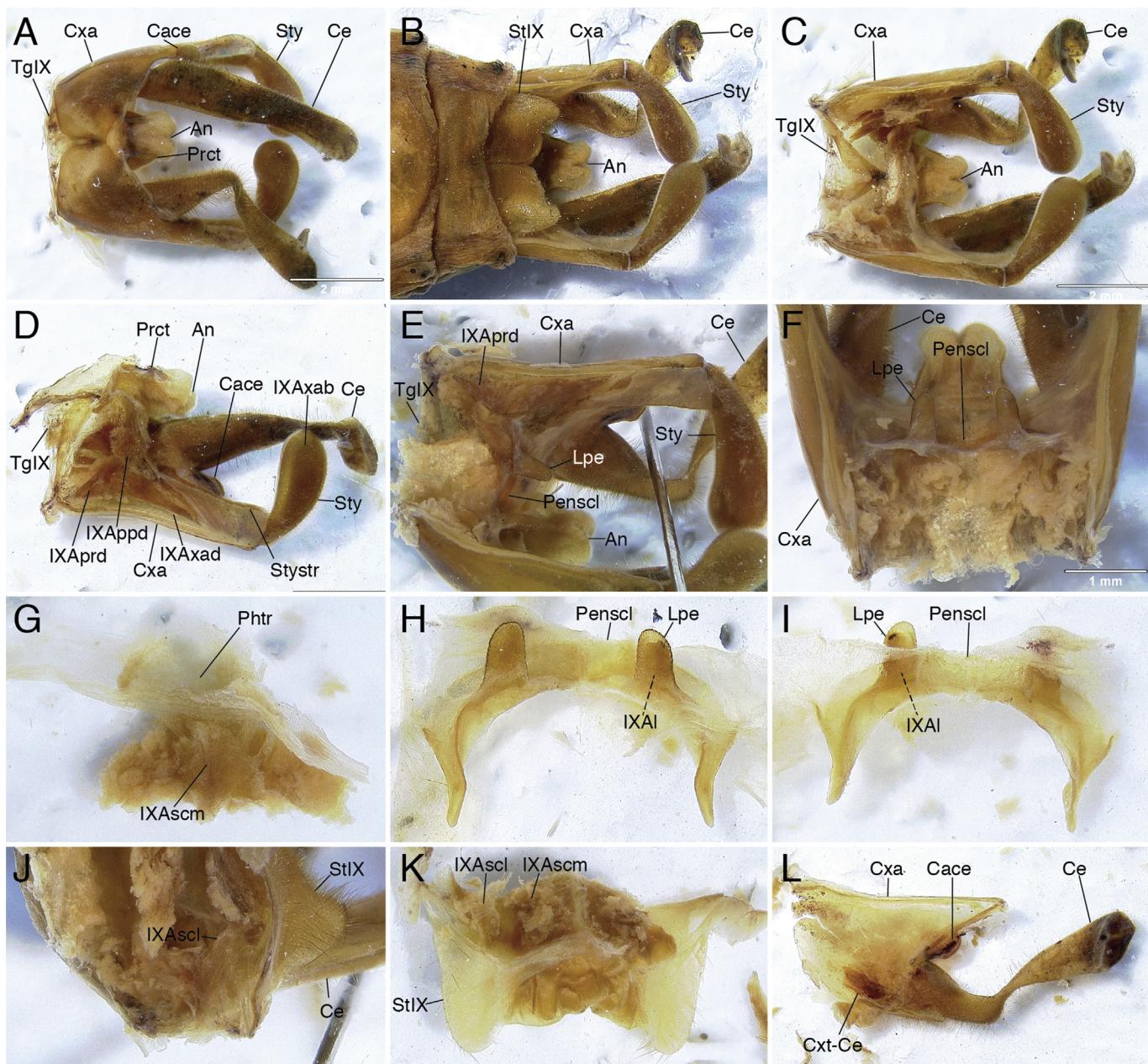


Fig. 4. Genital skeletomusculature of *Corydalus* sp. (Megaloptera: Corydalidae). **A**, genitalia, dorsal. **B**, genitalia *in situ*, ventral. **C**, **D**, genitalia, sternum and penial-lateropenital complex removed, mesal. **D** with part of left half removed. **E**, **F**, genitalia, sternum removed: **E**, mesal oblique; **F**, mesal. **G**, phallotreme and associated tissues. **H**, **I**, penial sclerite and lateropenite: **H**, ectal; **I**, mesal. **J**, left half of genitalia, anterior oblique. **K**, sternum, mesal oblique. **L**, left genital half, stylus, penis, and lateropenites removed, mesal. **Abbreviations:** An = anus; Cace = callus cercus; Ce = cercus; Cxa = gonocoxa; Lpe = lateropenite; Pen = penis; Penscl = penial sclerite; Phtr = phallotreme; Prct = proctiger; StlX = sternum IX; Sty = stylus; Stystr = stylar strut; TgIX = tergum IX. **Muscle abbreviations** indicated in Table 1.

General observations. Remarkably, in the Megaloptera and Neuroptera, the gonopore (*sensu lato*, see Snodgrass, 1936) is not associated with penial sclerite. This state is unique among the Endopterygota, and is probably a synapomorphy for the Megaloptera + Neuroptera clade, as noted above. To account for the attachments of two pairs of coxal-origin muscles (v', vi', Fig. 1.H4) which would otherwise have no homologs, the sclerotic arch dorsal to the lateropenites is here homologized as the penial sclerite. The penial sclerites of the examined (dissected) taxa have fused together medially, forming an arch (= “gonarcus” or “gonocoxites 11”, Aspöck, 2002) which has drifted dorsally in association with the lateropenites. Presence of both the cerci and callus cerci in *S. nevadensis* suggests that the appendages of abdominal segment X in *Corydalus* are cerci, and that the callus cerci are an evolutionary novelty, the origin or structural derivation of which is unclear. Given the convoluted history of morphological study of male neuropteridan genitalia and their application to phylogenetics (Aspöck, 2002; Aspöck and Aspöck, 2008; Aspöck et al., 2001, 2012), it will be of considerable value to reevaluate genitalic homologies across the clade employing skeletomuscular correspondences as

done herein, particularly with reference to the genomic phylogeny of the clade by Winterton et al. (2018). Note that homology interpretations provided in the present study disagree substantially with those of Aspöck and Liu et al. (2016); consequently, the “appendix-like” state of gonocoxae IX for the Megaloptera and Neuroptera (e.g., Aspöck, 2008; cited in Winterton et al. (2018)) is rejected.

4.3.1. Raphidioptera: Raphidiidae, Agulla sp.

Note: Examined specimens identified using Arnett (1985).

Sclerites. Abdomen. Tergum and sternum IX fused to bases of gonocoxae (Fig. 3A); tergocoaxal fusion broad, gonocoxae partially offset from tergum by apodeme bearing muscular attachments; sternocoaxal fusion narrow, anterolateral; tergum and sternum both articulating relatively freely with gonocoxae. **Genital appendages. Coxae** unmodified except for fusion with abdominal sternum and tergum X (Fig. 3A–D). **Styli** freely articulating with gonocoxae posterodorsally via single anterolateral condyle (Fig. 3F); gonocoaxal-gonostylar condyle supported by longitudinal apodeme connecting to anterior gonocoaxal margin (Fig. 3A, D, F).

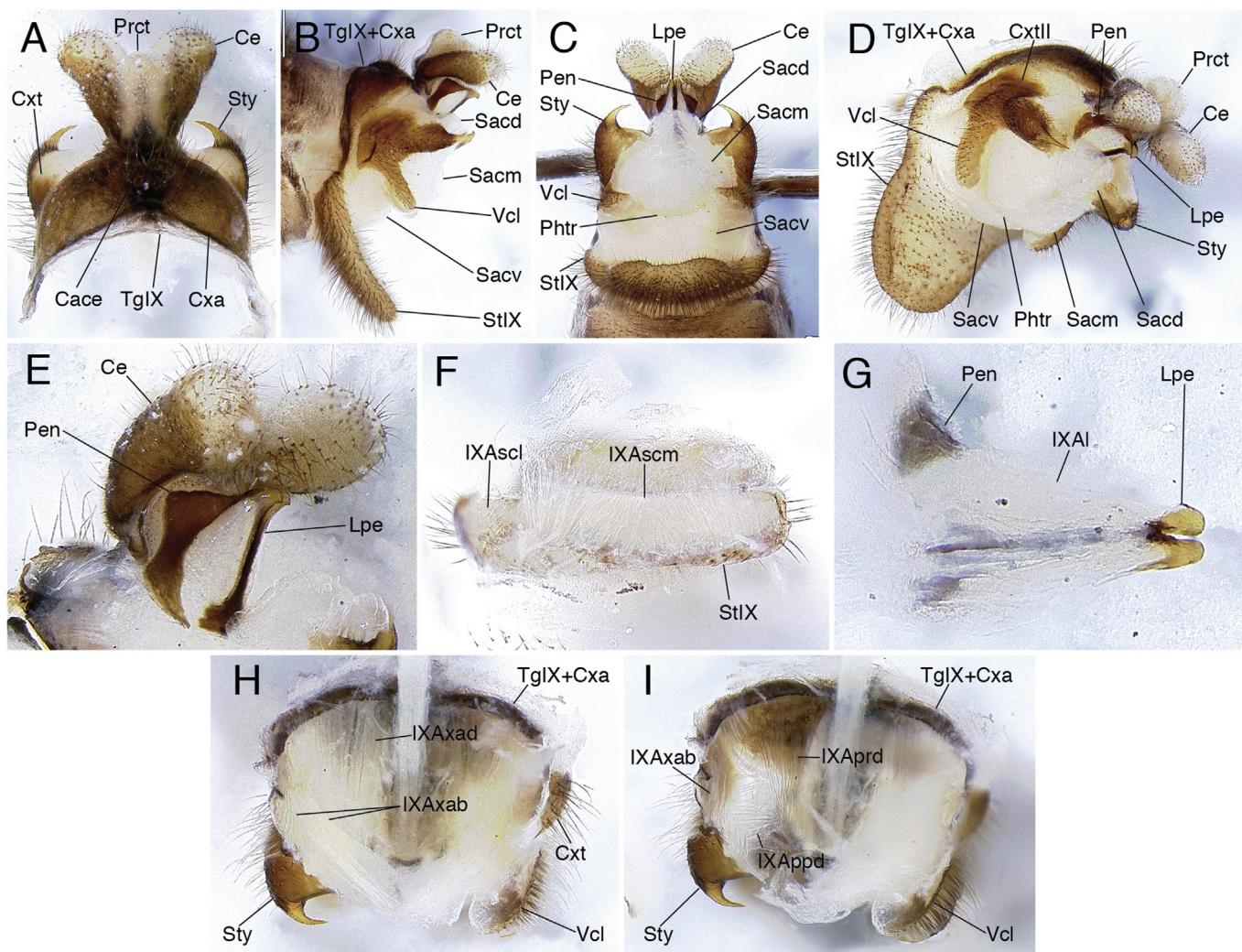


Fig. 5. Genital skeletomusculature of *Sialis nevadensis* (Megaloptera: Sialidae). **A–D**, genitalia and postgenital segments: **A**, dorsal; **B**, lateral; **C**, ventral; **D**, lateral oblique, genitalia rotated. **E**, penial sclerite, lateropenites, and cerci, lateral oblique. **F**, sternum, mesal. **G**, penial sclerite and lateropenites. **H, I**, genitalia and tergum IX with parts of second coxites and left stylus removed, mesal oblique. **Abbreviations:** An = anus; Cace = callus cercus; Ce = cercus; Cxa = gonoxoa (fused with tergum IX); Cxt = gonocoxite (fused with stylus); Cxt + Sty = coxostylar composite sclerite; Lpe = lateropenite; Pen = penial sclerite; Phtr = phallotreme; Prct = proctiger; Sacd = dorsal genital sac; Sacm = median genital sac; Sacv = ventral genital sac; StIX = sternum IX; Sty = gonostylus (fused with gonocoxite); TgIX = tergum IX (fused with gonocoxae) TgIX + Cxa = tergocoaxal composite sclerite; Vcl = ventral coxital lobe. **Muscle abbreviations** indicated in Table 1.

Lateropenites small, lobate (Fig. 3B–D, G–I). **Penial sclerites** fused anteroventrally with median margins of gonocoxae (Fig. 3G–I).

Musculature (Fig. 1.H1). **Extrinsic coxal muscles.** **Tergo-coxal:** muscle (IXAtc) present, originating laterally on tergum inserting on gonocoxal apodeme and opposing stylar adductor muscle origin (Fig. 3D and E). **Sterno-coxal:** two muscles present (IXAscm, IXAscl), originating on sternum and inserting on anteroventral gonocoxal margin (Fig. 3E, I). **Intrinsic coxal muscles.** **Coxo-stylar:** stylar adductor (IXAxad) and abductor (IXAxab) present, (IXAxad) originating on broad apodeme situated anterodorsally within gonocoxa (Fig. 3E–I), and (IXAxab) originating beneath longitudinal gonostyalar apodeme (Fig. 3F). **Coxo-lateropenital:** two muscles present (IXAlm, IXAlp), both inserting on narrowly-triangular mesal surface of lateropenite, (IXAlm) originating on anterolateral region of composite abdominal-coxal sclerite (Fig. 3D, E, G, H), (IXAlp) originating on gonocoxa ventral to stylar abductor muscle (Fig. 3H). **Coxo-penial:** muscles present: (1) small depressor (IXAppd) originating in anteroventral base of gonocoxa, inserting on penial sclerite anterodorsally (Fig. 3I); (2) narrow and longitudinal muscle (IXAprd) originating along anterior margin of coxal region, inserting in fleshy apex of penis (Fig. 3G). An intrinsic penial muscle (XAp) was observed, originating along posteromedial region of penis, inserting on fleshy penial apex (Fig. 3H and I).

4.3.2. Megaloptera: Corydalidae, *Corydalus* sp.

Sclerites. Abdomen. **Tergum IX** highly modified due to fusion with gonocoxae; tergum detectable along anterior gonocoxal margins as thin, differentiated sclerite which clearly extends posteriorly between gonocoxae (Fig. 4A, C–E). **Sternum IX** medially divided by longitudinal sulcus, articulating with tergum IX at anterolateral corners (Fig. 4B). Cerci forming long, limb-like appendages situated between proctiger and stylus (Fig. 4A–E, L); callus cerci, situated between cerci and styli on posterior tergocoaxal composite (Fig. 4A, D, L). Proctiger only sclerotized laterally (Fig. 4A–F). **Genital appendages.** **Coxae** fused dorsomedially (migrated dorsally from generalized ventral position) (Fig. 4A–F, L). **Styli** club-like, with long, thin strut projecting anteromedially (Fig. 4A–F, L) and ending ventrad cerci (Fig. 4D) (strut = apodeme of Liu et al., 2016). **Lateropenites** digitiform, situated dorsal to gonopore and ventral to proctiger (Fig. 4E and F), partially fused to penial sclerite (Fig. 4H and I). **Penial sclerite** dissociated from gonopore, migrated dorsally, and fused medially forming arch (“gonarcus”) (Fig. 4E, F, H, I).

Musculature (Fig. 1.H4). **Extrinsic coxal muscles.** **Tergo-coxal** muscles absent. **Sterno-coxal:** medial and lateral (IXAscm, IXAscl) muscles present: (IXAscm) inserting on ventral membrane of gonopore rather than gonocoxal sclerite (Fig. 4G, K); (IXAscl) inserting ventrolaterally on tergocoaxal complex (Fig. 4J). Cerci movable by muscles originating within tergocoaxal composite (Fig. 4L), inserting within base of cerci. Proctiger with one pair of intrinsic muscles. **Intrinsic coxal muscles.** **Coxo-stylar:** adductor and abductor present (IXAxad, IXAxab) (Fig. 4D); (IXAxad) long and narrow, originating within gonocoxa anterolaterally, (IXAxab) completely intrinsic to stylus. **Coxo-lateropenital:** single muscle present (IXAl) originating on penial sclerite (Fig. 4H). **Coxal-penial:** two muscle pairs present, one pair directed anterolaterally, another dorsally: (1) anterior pair (IXAppd) originating in gonocoxae near origin of (IXAxad) (Fig. 4D and E), (2) posterior pair (IXAprd) originating in posteromedial corner of gonocoxa (Fig. 4D). A penial intrinsic muscle (XAp) was observed, originating on penial sclerite, inserting on membrane dorsal to gonopore.

Comments on literature. Maki (1936) described the skeletal-muscular anatomy of another corydalid species, *Chaliodes formosanus* Petersen. Similar to *Corydalus*, *Sialis*, and the

examined myrmeleontid, the penial sclerite is dissociated from the gonopore (“genital aperture”, Maki). As with the other megalopterans, the gonopore is situated between a pair of membranous lobes ventrally and dorsally (“first and second male genital lobes”, Maki). Maki lists four muscles directly associated with the genitalia (his muscles 305–308): two of these muscles (307, 308) originate on the dorsally-migrated and fused gonocoxae (“tergum 9”, Maki) and insert laterally on the “penis hook” (also termed the “third genital lobe”) and the “posteriorlateral sclerite of the ninth abdominal sternum”, respectively; the third muscle (306) originates on the “penis hook” and inserts on the “second genital lobe”, while the fourth originates on the anterolateral portion of the “ninth abdominal sternal region” (305) and inserts on the dorsomedian base of the “second genital lobe”. Maki did not observe muscles originating on the rudiment of sternum IX. Based on positional correspondences with *Corydalus*, Maki’s muscle 307 may belong to the *m. coxo-penialis* class (IXAp), and 308 may belong to the *m. coxo-stylalis* class (IXAx); the identities of his muscles 305 and 306 are less uncertain. These interpretations suggest that the “penis hook” (= gonocoxites 9 in Liu et al., 2016) is the penial sclerite, and the “posteriorlateral ninth sternal sclerite” is a rudiment of the stylus.

4.3.3. Megaloptera: Sialidae, *Sialis nevadensis* Davis, 1903

Note: Examined specimens were identified using Ross and Frisson (1937).

Sclerites. Abdomen. **Tergum IX** integrated with gonocoxa, forming dorsal tergocoaxal composite (Fig. 5A, B, D, H, I). **Sternum IX** large, tongue-like, articulated anterolaterally with tergocoaxal composite (Fig. 5B–D, F). Proctiger sclerotized basally (Fig. 5A). Cerci appendage-like (Fig. 5A–E). Callus cercus present dorsomedially on tergocoaxal composite (Fig. 5A). **Genital appendages.** **Coxae** comprising the dorsal tergocoaxal composite (Fig. 5A, B, D, H, I), and a lateral fragment fused to and bearing the stylus, forming a coxostyler composite with ventrolateral lobe (Fig. 5A–D). **Styli** short and stout, each bearing single, sharp spine (Fig. 5A–D, H, I); styli fused to lateral gonocoxite, although coxostyler composite broadly articulated with tergocoaxal composite anteriorly (Fig. 5B, D, I). **Lateropenites** fused medially and tightly integrated with penial sclerite (“gonarcus”), penial-lateropenital complex migrated dorsally, subtending proctiger; lateropenites with long, thin, ventromedian strut (Fig. 5B–E, G). **Penial sclerites** dissociated from gonopore, fused together medially, and tightly associated with lateropenites (Fig. 5B–E, G). Three distinct membranous sacs are present (Fig. 5B–D), separated by two transverse impressions; ventral and medial sacs separated by impression formed by ventral lobe of coxostyler composite, impression with gonopore; medial sac broad, separated from dorsal sac by transverse impression between coxostyli.

Musculature (Fig. 1.H5). **Extrinsic coxal muscles.** **Tergo-coxal** muscles absent. **Sterno-coxal:** two muscles present: (1) medial muscle (IXAscm) short, inserting broadly on ventral membranous sac of genitalia (Fig. 5F), (2) lateral muscle (IXAscl) filling ventral lobe of coxostyler composite (Fig. 5B–D, F). **Intrinsic coxal muscles.** **Coxo-stylar:** two muscles present: (1) adductor muscle (IXAxad) originating medially in tergocoaxal composite lateral to dorsal coxo-penial muscle (IXAprd) (Fig. 5H), (2) abductor muscle (IXAxab) originating in dorsal membranous sac of genitalia and inserting on lateral surface of coxostyler composite (Fig. 5H and I). **Coxo-lateropenital:** single muscle (IXAl) present, originating on ventrolateral margins of penial sclerites (Fig. 5G). **Coxo-penial:** two muscles present: (1) lateral muscle (IXAppd) originating on lateral surface of coxostyler composite (Fig. 5I), (2) dorsal muscle (IXAprd) originating dorsomedially on tergocoaxal composite (Fig. 5I).

4.3.4. Neuroptera: Myrmeleontidae, Dendroleontinae, ?Dendroleon sp.

Note: Musculature of examined myrmeleontid and that of previously studied species (Krivokhatsky, 2002) is reduced relative to

the other Neuropterida here examined. Examined specimens were identified using Arnett (2000).

Sclerites. Abdomen. **Tergum IX** fused with anterior (first) fragments of gonocoxae (Fig. 6A, B, D). **Sternum IX** free, undivided

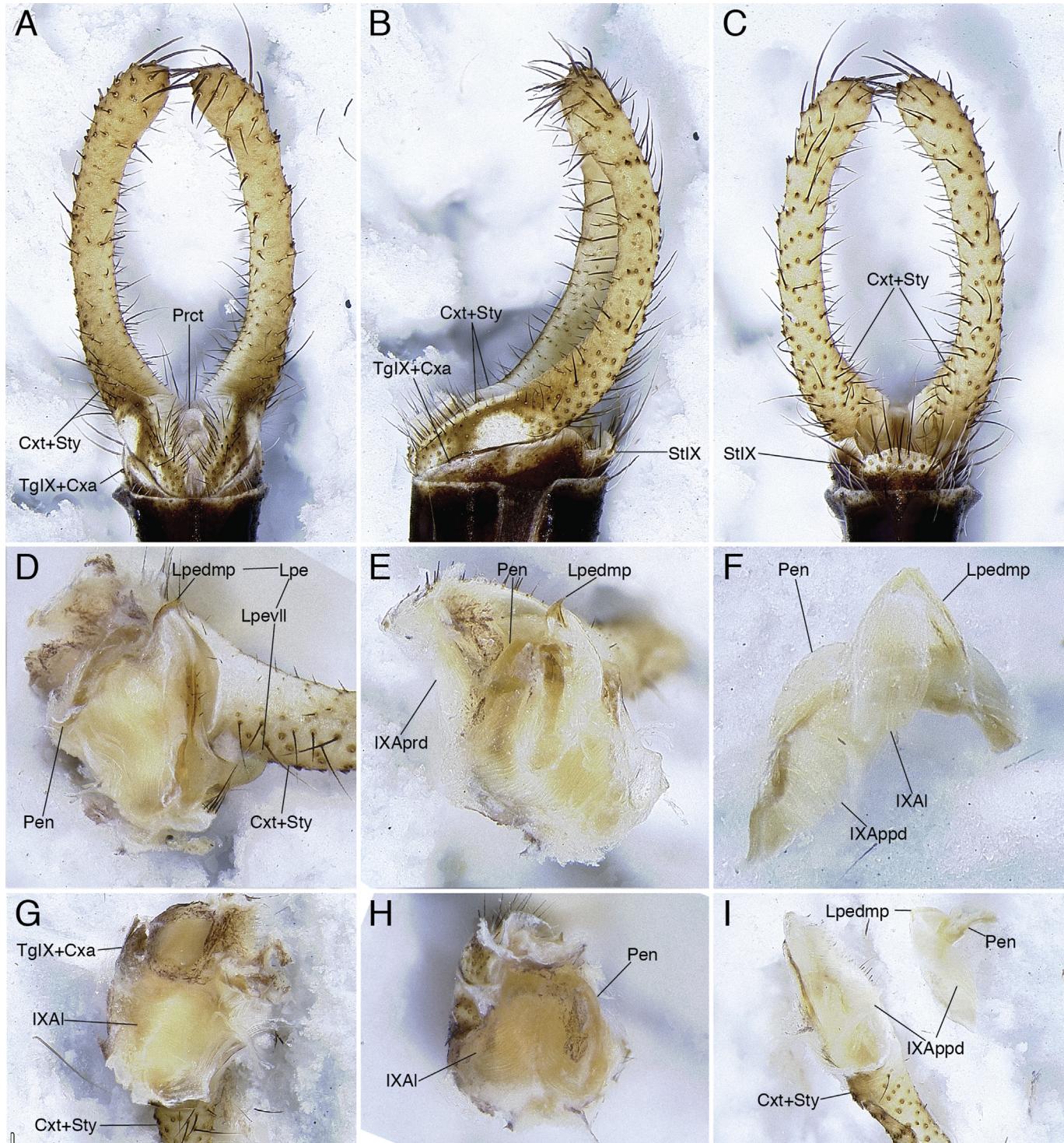


Fig. 6. Genital skeleto-musculature of ?Dendroleon sp. (Neuroptera: Myrmeleontidae). **A–C**, genitalia *in situ*: **A**, dorsal; **B**, lateral; **C**, ventral. **D, E**, right coxopod and penial-lateropenital complex, posterolateral oblique, **E** with lateropenites partially removed. **F**, part of penial-lateropenital complex, mesal (internal). **G**, right coxopod, mesal. **H**, genitalia with left coxopod removed, mesal; **I**, disarticulated right coxopod and penial-lateropenital complex, mesal. **Abbreviations:** An = anus; Cxt + Sty = coxostylar composite sclerite; Lpe = lateropenite; Lpedmp = lateropenital dorsomedian process; Lpevll = lateropenital ventrolateral lobe; Pen = penial sclerite; Prct = proctiger; StIX = sternum IX; Sty = gonostyli; TgIX + Cxa = tergocoxal composite. **Muscle abbreviations** indicated in Table 1.

(Fig. 6C). Proctiger desclerotized (Fig. 6A). Cerci and callus cerci absent. **Genital appendages.** **Coxae** migrated dorsally and fragmented: (1) anterior part of gonocoxa fused with tergum forming tergocoaxal composite, (2) posterior fragments fused with styli forming coxostylar composite (Fig. 6A, B, D, I). **Styli** (= “ectoprocts”, Krivokhatsky, 2002) long, trunk-like, fused with gonocoxites and articulated with tergocoaxal composite anteriorly (Fig. 6A–D). **Lateropenites** tightly integrated with penial sclerite (“gonarcus”), fused together medially forming dorsoventrally tall laminae which bear ventrolateral lobes and an acutely-pointed V-shaped process dorsomedially (Fig. 6D–F). **Penial sclerite** disassociated with gonopore, fused medially and migrated dorsally, forming inverted, U-shaped sclerite associated with lateropenites (Fig. 6D–F).

Musculature (Fig. 1.H6). **Extrinsic coxal muscles.** **Tergo-coxal** muscles absent. **Sterno-coxal:** muscles reduced apparently to one medial unit (**IXAscm**) inserted on ventral membrane of gonopore. **Intrinsic coxal muscles.** **Coxo-stylar:** one muscle present (**IXAx**), originating laterally on tergocoaxal composite and inserting within coxostylar composite (Fig. 6G). **Coxo-lateropenital:** lateropenite with massive pair of muscles (**IXAI**) originating on penial sclerite (Fig. 6D–F, H). **Coxo-penial:** two muscle pairs present: (1) first pair (**IXAppd**) originating dorsally in coxostylar composite and inserting dorsally on penial sclerite and (Fig. 6F, I), (2) second pair massive, (**IXAprd**) originating on tergocoaxal composite and inserting broadly on lateral arms of penial sclerite and (Fig. 8F, I).

4.4. Coleopterida

Note and overview. The higher taxonomy of the Coleoptera used here follows McKenna et al. (2015) and Zhang et al. (2018); Strepsiptera are treated in the Coleopterida given their sister-group relation to the Coleoptera (Misof et al., 2014; Beutel et al., 2018), and the relative simplicity of their copulatory apparatus. As is well known, the male genitalia of Coleoptera display astonishing diversity, and a variety of morphological forms, or “types”, have been recognized (e.g., Crowson, 1955, 1981). Of these forms, the sampling of the present study only evaluates three of Crowson’s types: “trilobate” (cantharid), phytophagan (curculionid, “chrysomeloid type”), and adephagan (dytiscid). Homologies of the additional forms, e.g., “sheath”, “cucujoid”, and “heteromeran” (Crowson, 1981), will need to be evaluated in future skeletomuscular studies. In particular, emphasis should be put on the Derodontidae and the scirtoid families (Clambidae, Decliniidae, Eucinetidae, Scirtidae) given that these represent offshoots of the first splits of the Polyphaga (Bocak et al., 2014; McKenna et al., 2015; Zhang et al., 2018). Focus on the Archostemata and Myxophaga will of course be critical for refining the groundplan of the order. A number of studies have already attempted to homologize the genital skeletomusculature within the Coleoptera; the results of several are presented in Table S4 along with a working hypothesis of correspondences from observations in the present study (the included studies are, namely: Burke, 1959; Cerezke, 1964; Hieke, 1966; Clark, 1977; Peschke, 1978; Kumar and Verma, 1980; Krell, 1996; Hünefeld et al., 2011a; Jałoszynski et al., 2014; Li et al., 2015b).

Homology-neutral description. The male genitalia of the Coleoptera are on the one hand simplified relative to other endopterygote orders, and on other the more complex due to the diversity of skeletomuscular modifications. Among the dissected taxa, the Cantharidae (Fig. 1.I3, 7) are the closest approximation to the inferred topological groundplan for the order (Fig. 1.I2); what follows is a homology-neutral description of this group. Four sclerites are present (Fig. 7): (1) a cup-shaped sclerite (Cxtl) which covers the anterior base of (2) a helmet-shaped sclerite (Cxtll), which bears a dorsal transverse carina and posterolateral spines; (3) situated posterolaterad the helmet-shaped sclerite is a pair of posteriorly-bifurcating sclerites

(Sty); and (4) ventral to the helmet-shaped sclerite is a half-pipe-shaped sclerite, which bears the gonopore (Pen). Musculature (Fig. 1.I3; arbitrary muscle labels indicated parenthetically): (I) three extrinsic muscles are present, all of which attach to an anteroventral median apodeme of the cup-shaped sclerite (Cxtl): (1) one attaching to tergum IX (i), and (2, 3) two attaching to sternum IX (ii, iii); (II) six intrinsic muscles are present: (4, 5) two muscles attach the cup-shaped sclerite (Cxtl) to the bifurcating sclerite (Sty) (iv, v); (6, 7) two muscles attach the helmet-shaped sclerite (Cxtll) to the bifurcating sclerite (Sty) (vi, vii); (8) one muscle attaches the half-pipe-shaped sclerite (Pen) to the helmet-shaped sclerite (Cxtll) (viii); and (9) one muscle inserts near the gonopore and attaches to the base of the half-pipe-shaped sclerite (Pen) (ix).

Homology analysis. The two sets of extrinsic copulatory apparatus muscles correspond to the *m. tergo-coxalii* (i:**IXAtc**) and *m. sterno-coxalii* (ii + iii:**IXAsc**), indicating that the “cup-shaped sclerite” (Cxtl) is a derivative of the gonocoxa; these muscles are consistently present in the other sampled Coleoptera (Fig. 1.I5, I7; Table S4). Within the copulatory apparatus, four of the remaining six observed muscles insert on the “bifurcating sclerite” (iv–vii), and two on the “half-pipe-shaped” sclerite (viii, ix), corroborating the identity of the cup-shaped sclerite as a gonocoxal derivative, and indicating that the “helmet-shaped” sclerite is gonocoxal as well. As the “half-pipe-shaped sclerite” bears the gonopore, this structure corresponds to the penial sclerite, and as it is integrated with the helmet-shaped gonocoxite, the composite sclerite is here termed a “coxopenis”. Across the sampled Coleoptera, there are muscles intrinsic to the coxopenis (x in Fig. 1.I5) and extrinsic to the coxopenis (xi, xii in Fig. 1.I5, xiii, xiv in Fig. 1.I7). The former may be considered the *m. penialis interni* (vii + ix + x:**XAp**), the latter *m. coxopenialis externi* (xi–xiv:**IXApc**). Given the strong musculature of the “bifurcating sclerite” originating in the anterior coxite and on the coxopenis, it is reasonable that these clasping structures correspond to the styli, rendering their muscles as *m. coxo-stylalii* (vi + v + vi + vii:**IXAx**). This is a categorical correspondence, however, as the functional differentiation of these muscles has obliterated the phylogenetic signal with respect to their relation to the *stylar adductors* (**IXAxad**) and *abductors* (**IXAxab**), thus these muscles are referred to as the *m. coxopenialis-stylalis* (iv + v:**IXApc**) and the *m. coxitalis-stylalis* (vi + vii:**IXAph**).

General observations. The copulatory apparatus was observed to be nestled within abdominal segment IX, which itself may be nestled in a genital chamber which may comprise segments VIII and VII (Wanat, 2007). The gonocoxae are consistently divided into two fragments: (1) first fragments, often fused medially, bearing insertions of the *coaxal extrinsic*, *coxo-stylar*, and *penial extrinsic muscles* (Cxtl, Fig. 1.I2); (2) second fragment, fused with the penis (forming coxopenis), bearing origins of the *coxo-stylar* and *penial intrinsic muscles* (Cxtll + Pen, Fig. 1.I2). Recognition of the first gonocoxites is certain, as the gonocoxae are the sole recipients of the *coaxal extrinsic* muscles across all Endopterygota which have unfused gonocoxae and abdominal sclerites IX. In the literature, the first gonocoxites are usually termed the “basal piece” or “phallobase” (Sharp and Muir, 1912; Wilson, 1930; Crowson, 1955; Lindroth and Palmén, 1970; Lawrence et al., 2010, 2011), although “phallobase” has also been used for a composite of the first gonocoxites and styli (Hieke, 1966; Harpalus, Liparis; Table S4), as well as a composite sclerite of the first and second gonocoxites plus the penial sclerite (Krell, 1996; Table S4). The first gonocoxites may be free, as in the sampled cantharid (Fig. 1.I3), or fused with the styli as in the dytiscid (Fig. 1.I7). When they are closely associated, the first gonocoxites and styli are sometimes together referred to as the “tegmen” (Lindroth and Palmén, 1970) or “gonoforceps” (Wood, 1952). The second gonocoxites, bearing the origins of the *coxo-stylar* and

coxo-penial muscles (when present, respectively), are inferred to be an element of the coxopenis (Fig. 1.I3, 1.I5, 1.I7). The identity of the stylus as such, rather than lateropenite, is uncertain to some degree, as two sets of paired movable elements of the gonocoxae are not observed in Coleoptera (this study, also e.g., Sharp and Muir, 1912; Crowson, 1981; Hünefeld, Marvaldi, et al., 2011a), except, apparently, in *Priacma* (Cupedidae, Edwards, 1953a, b). Notwithstanding the enigmatic *Priacma*, homology of the “parameres” (= “lateral lobes”, Beutel and Lawrence, 2005) of Coleoptera with the styli of other orders has already been proposed (Wood, 1952), and, circumstantially, no holometabolan order was observed in this study to bear lateropenites in the absence of styli.

Comments. Wanat (2007, pp. 166, 167) concluded that the “parameres” of Curculionoidea are not homologous with those observed in other groups of Coleoptera. Insofar as the “parameres” of Coleoptera are here understood to generally refer to styli, this conclusion is supported, at least for the Curculionoidea, as stylar musculature was not observed in lineages here sampled and literature studied (see Table S4 and section 4.4.2 below). The structure Wanat (2007) referred to as “parameral lobes” in curculionoids should be a focus of further study. Wanat (2007) also extended the conclusion of non-homology to the Chrysomeloidea and Cucujoidae, encouraging future workers to use the term “parameroids” for these structures. Among these groups, skeleтомuscular literature

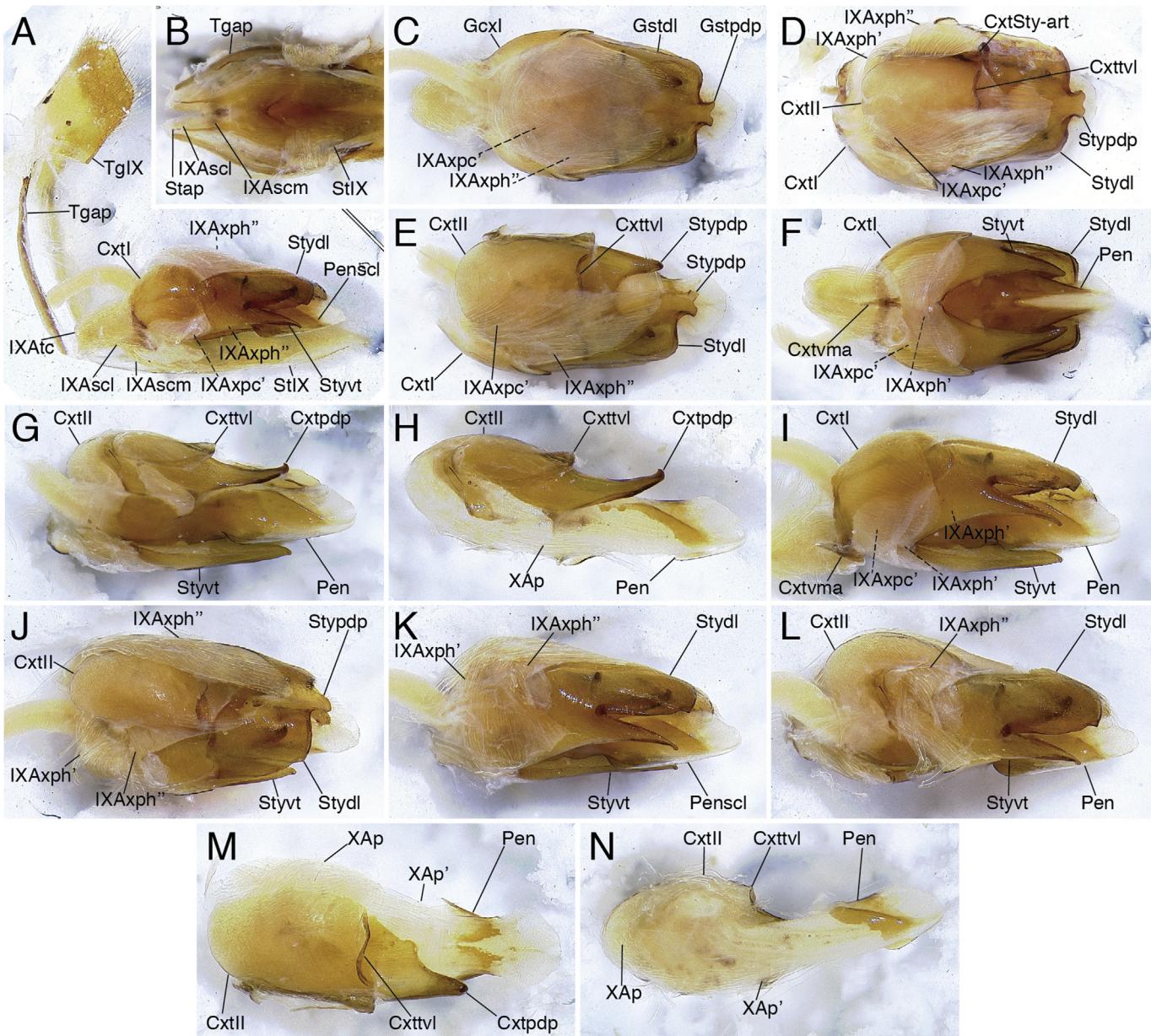


Fig. 7. Genital skeleton musculature of *Cantharis* (*Cantharis*) (Coleoptera: Cantharidae). **A, B**, genitalia *in situ*: **A**, lateral; **B**, ventral. **C–N**, genitalia various aspects and states of dissection: **C**, whole, dorsal; **D, E**, stylus and muscle partially removed, dorsal; **F**, whole, ventral; **G**, dorsal portion of stylus removed, lateral; **H**, full stylus and part of penile sclerite removed; **I**, whole, ventrolateral oblique; **J**, stylus and muscle partially removed, dorsal; **K, L**, stylus partially removed, with **K** in ventrolateral oblique view, **L** in lateral view; **M, N**, coxites II and penile sclerite, partially dissected, with **M** in dorsal view, **N** in mesal (lateral) view. **Abbreviations:** CxtSty-art = gonocoxite II–stylar articulation; Cxtdpd = gonocoxite II posterodorsal process; Cxtl = “phallobase” (first gonocoxites); CxtII = second gonocoxites (continuous with penis, forming “coxopenis” or CxtII + Pen); CxtvI = gonocoxite II transverse lamella; Cxtva = gonocoxite I ventromedial apodeme; Pen = penis and penile sclerite (continuous with CxtII, forming “coxopenis” or CxtII + Pen); StIX = sternum IX; Stap = sternal apophysis; Sty = genostylus; Stydl = genostylar dorsal lobe; Stydpd = genostylar prosterodorsal process; Styvt = genostylar ventral tine; TgIX = tergum IX; Tgap = tergal apophysis. **Muscle abbreviations** indicated in Table 1.

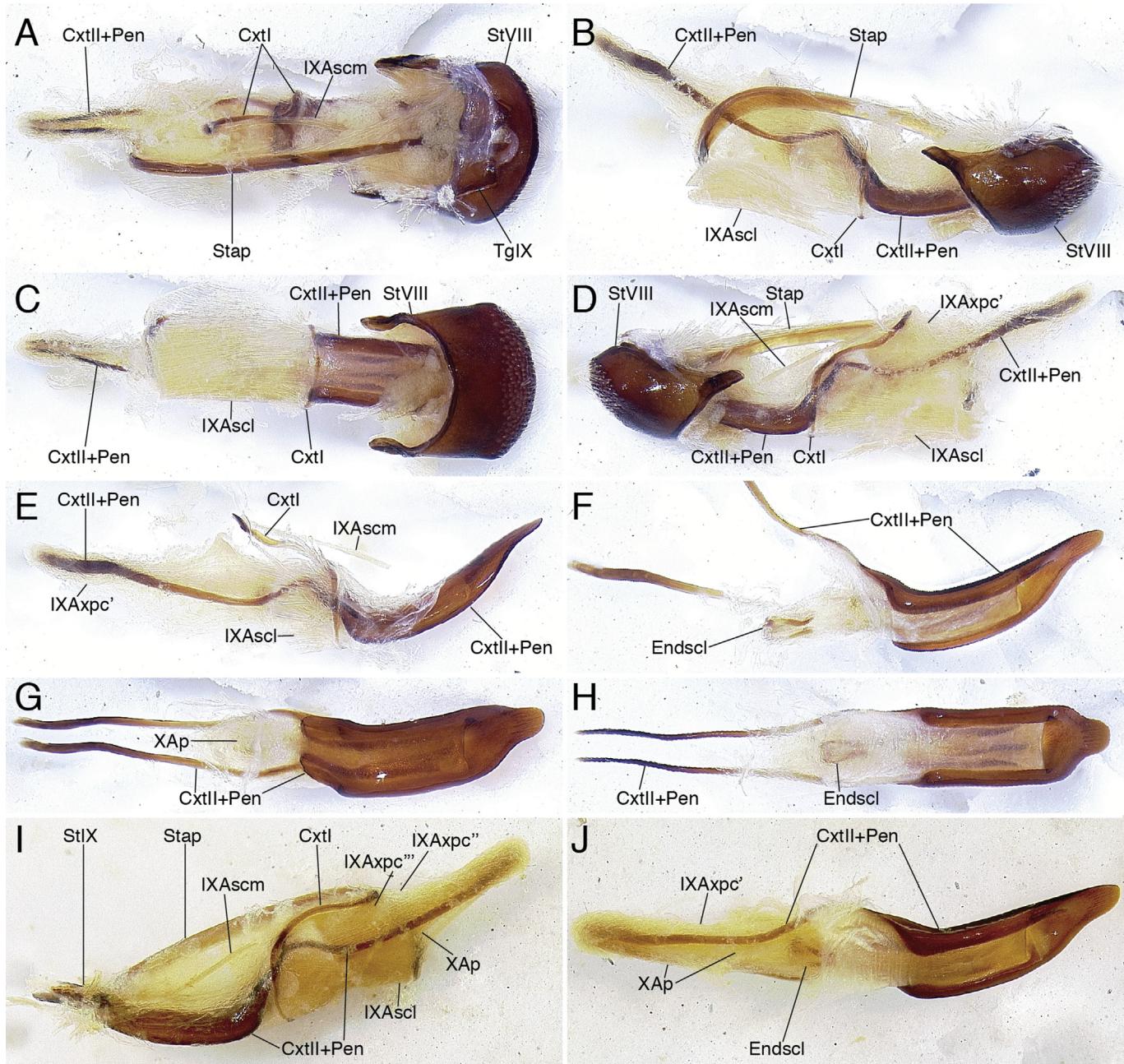


Fig. 8. Genital skeleto-musculature of *Hypera* cf. *postica* (Coleoptera: Curculionidae). **A–D**, genitalia *in situ* within terminal abdominal segments: **A**, dorsal; **B**, lateral, left side, sternal-coxital muscle partially removed; **C**, ventral; **D**, lateral, right side. **E, J**, coxites I encircling coxites II and stylar composite, lateral, with sternum removed in **E** which shows the left side. **F–J**, coxopenis (coxital-penial composite, CxtII + Pen): **F**, endophallus partially exerted, ventrolateral oblique; **G**, dorsal; **H**, ventral; **I**, sternum in place, right side; **J**, ventrolateral oblique. **Abbreviations:** Cxtl = “phallobase” (first gonocoxites); CxtII + Pen = coxopenial composite; Endscl = endophallic sclerite; StVIII = sternum VIII; StIX = sternum IX; Stap = sternal apophysis; TgIX = tergum IX. **Muscle abbreviations** indicated in Table 1.

was only found for the Cerambycidae (Chrysomeloidea), for which muscles corresponding with those of the stylus were described: “*m. urosterno-phallobasicus*” and “*tergapodemo-phallobasicus*” (*ustaphabas* and *m. trgapd phabas* in Table S4; Hieke, 1966; see General observations above).

All in all, the combination of skeleto-musculature observed here and the genital folds observed by Wanat (2007) suggest a complex history of morphological evolution, including sclerites and formative elements (*sensu* Klass, 1997). The morphological matrix of Lawrence et al. (2011) and the molecular phylogeny of McKenna et al. (2015),

complemented by traditional “type” classifications (viz., Sharp and Muir, 1912; Jeannel and Paulian, 1944; Jeannel, 1955; Lindroth and Palmén, 1970; Iablokoff-Khnzorian, 1980; Crowson, 1981; Wanat, 2007), will serve as valuable guides for future comparative study; it is beyond the scope of the present work to reconcile these systems. Given the skeleto-muscular system used herein, the genitalia of the Coleoptera may finally be understood within the framework of modified abdominal appendages (Fig. 1): As noted by Lawrence et al. (1991, p. 23) “the weight of probability still lies with the gonocoxite theory for the endopterygotes”.

4.4.1. Coleoptera (Polyphaga: Elateroidea): Cantharidae, Cantharis (Cantharis) sp.

Notes. Examined specimens were identified using Ramsdale (2002), in which the posterolateral horn-like processes of the second coxites are referred to as “laterophyses”.

Sclerites. Abdomen. Genitalia nestled within elongated abdominal **tergum** and **sternum IX** (Fig. 7A and B), each with linear, paired apophyses on anterior margin, apophyses wide-set on tergum and narrowly-approximated on sternum (Fig. 7A and B). Proctiger fused with tergum IX. Cerci absent. **Genital appendages. Coxae** fragmented into two portions: (1) first fragments situated anteriorly (Fig. 7A, C–E, F, I), fused together anteromedially and ventromedially, with broad lobe-like lateral regions cupping remainder of genitalia, and ventral portion with pronounced ventromedial apodeme (Fig. 7A, F, I); (2) second fragments situated posteriorly, fused dorsomedially, forming dome over penis (Fig. 7D, E, G, H, J, L–N), dome traversed by lamella near bases of posterolateral horn-like processes (Fig. 7D, E, G, H, J, M, N), lamella articulating with styli laterally (Fig. 7D). **Styli** divided into dorsal lobe and ventrolateral tines in lateral view (Fig. 7A, I, K, L); ventrolateral tines fused ventromedially (Fig. 7F), dorsal lobes fused dorsomedially, forming plate-like structure cupping dome of second gonocoxites and bearing bilobed posteromedian process (Fig. 7C, D, E, J); dorsal portion of styli articulating with second gonocoxite's dorsomedial dome (Fig. 7D). **Lateropenites** absent. **Penial sclerite** forming tube and appearing paired (Fig. 7F–H, M, N), bearing an anteroventral and posteroventral articulation with second gonocoxites (Fig. 7G).

Musculature (Fig. 1.I3). **Extrinsic coxal muscles. Tergo-coxal:** muscle (IXAtc) broadly inserted around ventrolateral margins of ring-like first (anterior) coxite, with thick, tough ligament joining muscle to origin (Fig. 7A and B). **Sterno-coxal:** medial (IXAscm) and lateral (IXAscl) muscles present: (IXAscm) originating within sternal plate, inserting on anteroventral portion of ventromedial apodeme (Fig. 7A); (IXAscl) originating on anterior sternal apodemes, integrated tightly with tergo-coxal muscle, inserting broadly on ventromedial apodeme of first (anterior) gonocoxite (Fig. 7A, B, F, I). **Intrinsic coxal muscles. Covo-stylar:** abductor (IXAxph:IXAxab?) and adductor (IXAxpc:IXAxad?) present, both divided into two units: (1) abductor (IXAxph) originating within first gonocoxite and divided into ventral and dorsal units: (1a) ventral unit (IXAxph') originating ventrolaterally within first gonocoxite and inserting medially on anteroventral surface of stylus (Fig. 7A, F, I), (1b) dorsal unit (IXAxph'') originating on dorsomedial surface of first gonocoxite, inserting broadly within stylus posteriorly, covering dome of second gonocoxite dorsally and joined medially by IXAxad' (Fig. 7A, C–E, J, K); (2) second muscle (IXAxpc) originating on second gonocoxite and divided into anterior and posterior units: (2a) posterior unit (IXAxpc') inserting posterolaterally in stylus (Fig. 7A, D, F, I, L); (2b) anterior unit (IXAxpc'') originating on anterolateral surface of second gonocoxite opposite origin of posterior muscle unit and inserting anteroventrally in stylus (Fig. 7D, I, K). **Covo-lateropenital** muscles absent. **Covo-penial:** two muscles present: (1) broad muscle (XAp(ix)) originating over most of second (posterior) gonocoxite's domed inner surface and inserting on penial membrane (Fig. 7M, N), and (2) narrow longitudinal muscle (XAp(viii)) originating on anteroventral surface of posterior gonocoxite's median dome and inserting within penial apex (Fig. 7H, M, N).

4.4.2. Coleoptera (Polyphaga: Curculionoidea): Curculionidae, Hyperinae, *Hypera* cf. *postica* (Gyllenhal, 1813)

Notes. (1) Examined specimens were identified using Blatchley and Leng (1916), Anderson (2002), and Titus (1911), with reference to an online glossary of weevil terminology (Lyal, 2016). (2) In other studies of the Phytophaga (Curculionoidea, Chrysomeloidea),

sternum IX has been termed the “spiculum gastrale” (Burke, 1959; Clark, 1977), the “spicule” (Cerezke, 1964), and the “second spiculum” (Kumar and Verma, 1980).

Sclerites. Abdomen. Tergum IX reduced, fitting into neat impression in abdominal sternum VIII (Fig. 8A). **Sternum IX** asymmetrical, with long, bow- or swoosh-like apodeme curving around symmetrical genital appendages on left-hand side (“gastral spiculum”, Fig. 8A, B, D, I). **Genital appendages. Coxae** fragmented into two portions: (1) first fragment forming thin ring around second gonocoxites and penis, and bearing rod-like dorsomedial apodeme (Fig. 8A–E, I); (2) second fragments fused with penis (forming “coxopenis”, Fig. 8A–J). **Styli** absent. **Lateropenites** absent. **Penial sclerite** indistinguishably integrated with second gonocoxites (Fig. 8F, H).

Musculature (Fig. 1.I5). Musculature much reduced. **Extrinsic coxal muscles. Tergo-coxal** muscles absent. **Sterno-coxal:** two muscles present: (1) medial muscle (IXAscm) originating on posterior lobe of sternum, inserting on dorsomedian apodeme of annular first gonocoxite (Fig. 8A, D, E, I); (2) lateral muscle (IXAscl) broadly originating in curved anteroventral portion of sternum and directed posteriorly as broad sheet to insertion on anterior left-hand surfaces of first gonocoxital ring (Fig. 8B–E, I). **Intrinsic coxal muscles. Covo-penial:** three muscle units present: (1) (IXApcl') originating on dorsomedial apodeme of first gonocoxites, inserting on apodemes of coxopenis (Fig. 8D, J); (2) (IXApcl'') originating on dorsomedian apodeme of first gonocoxites, inserting on main body of coxopenis (Fig. 8I); (IXApclv') originating on ring of first gonocoxites, inserting on apodemes of coxopenis (Fig. 8I). **Covo-lateropenital** muscles absent. **Penial intrinsic:** one muscle (XAp) present, originating on apodemes of coxopenis and inserting on endophallus (Fig. 8I and J).

4.4.3. Coleoptera (Adephaga: “Hydradephaga”): Dytiscidae, Colymbetinae, *Ilybius* biguttulus (Germar, 1824)

Notes. The examined specimens were identified using Larson et al. (2000). Specific interpretations contradict those of Li et al. (2015b). Hydradephaga is put in quotation marks, as its monophyly is uncertain (e.g., Baca et al., 2017; Zhang et al., 2018; Beutel et al., 2018).

Sclerites. Abdomen. Genitalia asymmetrical and nestled within abdominal tergum and sternum IX (Fig. 9A–D). Anterior apophyses of **tergum** fused medially, forming broad arc completely encircling sternum IX (Fig. 9C). **Sternum IX** divided in two, with right-hand apophysis forming broad anterior arm which contours tightly to genital appendages on ventral side (Fig. 9A–F); fragments of sternum IX joined by tough conjunctiva, which also covers part of genital appendages (Fig. 9F). Proctiger immovably fused to abdominal tergum IX. Cerci absent. **Genital appendages.** Taken together, genital appendages with claw-like silhouette (Fig. 9G). **Coxae** divided into two fragments: (1) first fragment pair, situated posteriorly, gnarled in form, unfused medially, and bearing elongate, horn-shaped lateropenites (Fig. 9D–H); (2) second fragment pair fused posteromedially, situated anteriorly, forming long claw-like structure sheathing endophallus, and with broad clamshell-like or wing-like apodemes directed anteriorly (Fig. 9D–I). **Styli** long and horn-shaped, tightly fitting to claw-like outgrowth of coxopenis (Fig. 9E–H), and fused to first gonocoxites via thin, stalk-like region (Fig. 9H). **Lateropenites** absent. **Penial sclerite** insensibly fused to second coxites; endophallus sclerotic, small and wishbone-shaped (Fig. 9I).

Musculature (Fig. 1.I7). **Extrinsic coxal muscles. Tergo-coxal:** muscle (IXAtc) originating on broad ventral arc encircling sternum, and inserting on internal surfaces of apodemes of first gonocoxites (= covo-styli), muscles extending from right-hand side of tergal arch wrap around genital appendages dorsally (Fig. 9A and B) (**tergo-sternal** muscles hypertrophied, inserting on thick sternal conjunctiva

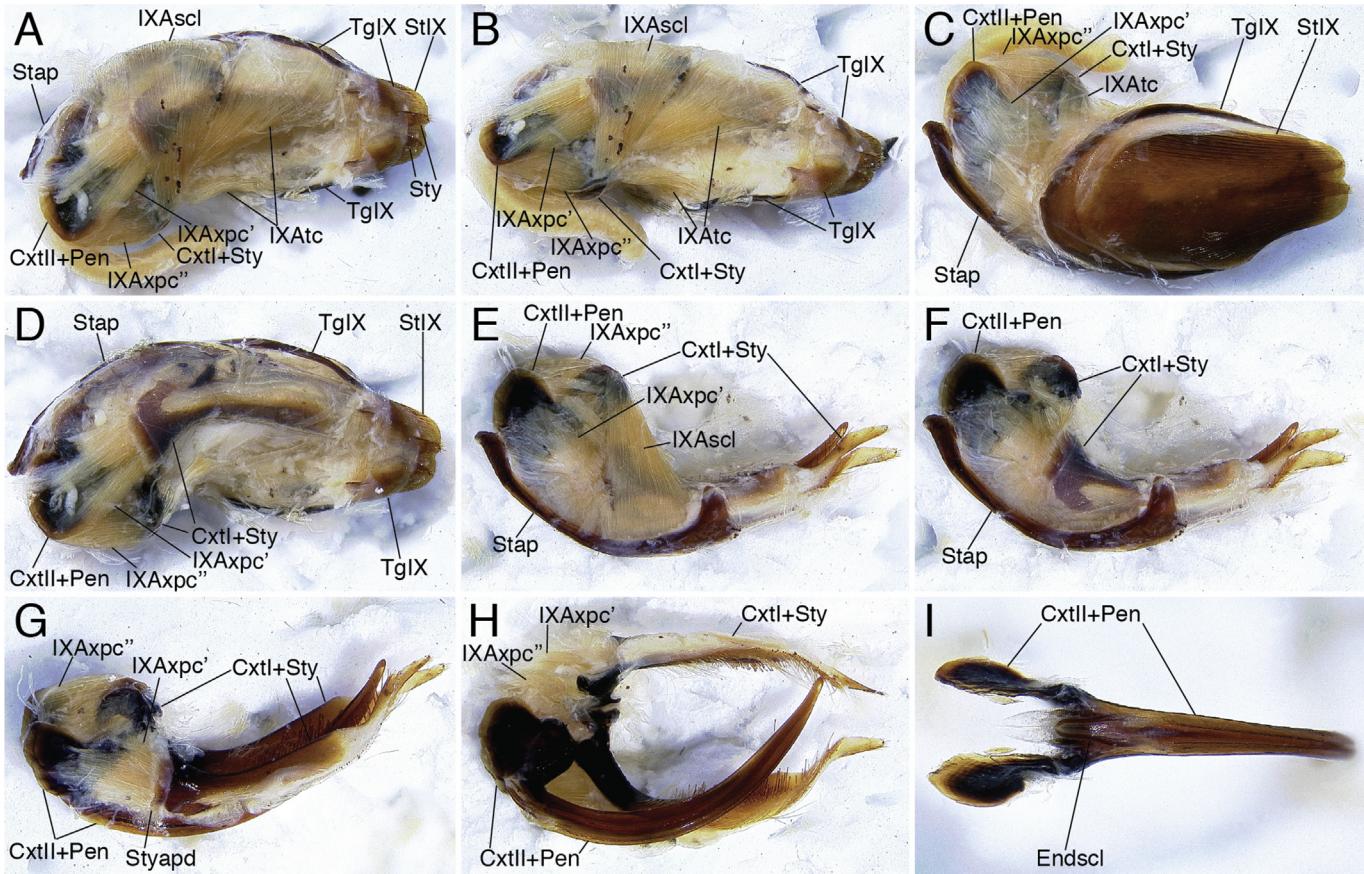


Fig. 9. Genital skeleтомusculature of *Ilybius biguttulus* (Coleoptera: Dytiscidae). **A–D**, genitalia *in situ*: **A**, dorsal; **B**, dorsolateral oblique; **C**, ventral; **D**, dorsal, tergal-coxital muscles removed. **E–G**, genitalia and anterior fragment of sternum IX (sternal apodeme): **E**, ventral; **F**, ventral, sternal muscle removed; **G**, dorsal. **H**, coxital-stylar composite sclerites spread away from coxopenis (composite of second coxites and penis, CxtII + Pen), dorsolateral oblique. **I**, coxopenis, left side, lateral. **Abbreviations:** CxtI + Sty = coxostylar composite sclerite; CstII + Pen = coxopenial composite; Endscl = endophalllic sclerite; StIX = sternum IX; Stap = sternal apodeme; Styapd = styalar apodeme; TgIX = tergum IX. **Muscle abbreviations** indicated in Table 1.

joining anterior and posterior sternal fragments). **Sterno-coxal**: only one muscle observed, although second may be present: lateral muscle (**IXAscl**) originating on anterior sternal fragment, inserting on apodemes of coxostyli (Fig. 9A–C, E). **Intrinsic coxal muscles**. **Coxo-stylar**: one muscle present (IXAxpc), originating on coxopenis and divided into external and internal units: (1) external unit (**IXAxpc'**) originating on external surfaces of clamshell-like apodemes of coxopenis, inserting on external apodemes of each stylus (Fig. 9A–H), (2) internal unit (**IXAxpc''**) originating on internal surfaces of coxopenial apodemes, inserting opposite insertions of sterno-coxal muscles on coxostylar apodemes (Fig. 9A–H). **Coxo-lateropenital** muscles absent. **Coxo-penial** muscles absent.

Comments on asymmetry. Beutel and Roughley (1988) postulated that rotated genitalia are a groundplan synapomorphy of the Adephaga. Assuming symmetrical genitalia in stem Adephaga, with a conformation similar to the examined cantharid, asymmetry may have evolved via rotation of the genitalic appendages around the longitudinal (cephalocaudal) axis, such that the ventral gonocoaxal margins were directed laterally to the left-hand side (as observed in the dytiscid), and the dorsal margins directed to the right-hand side. Subsequently, the second pair of gonocoaxal fragments, bearing the penis, would be produced anteriorly, and the left and right apophyses of tergum IX would fuse ventrally, forming a ring anteriorly around sternum IX. The sternum would then be divided into the anterior and posterior portions based on muscle function and location. Explicit study of the Gyrinidae may be revealing, as

they do not have rotated male genitalia (Beutel and Roughly, 1988), and they may be sister to the remainder of the Adephaga (Baca et al., 2017; Zhang et al., 2018; Beutel et al., 2018).

4.4.4. Strepsiptera

Genital homologies. The external male genitalia of Strepsiptera are highly simplified, being reduced to the intromittent organ (e.g., Beani et al., 2005; Pohl and Beutel, 2008). This organ consists solely of a tube- or scythe-like structure, which is neutrally referred to as the “penis” (Hünefeld, Pohl, et al., 2011b), although other terms have been applied (see Kinzelbach, 1971, 1978; Kathirithamby, 1989). This reduction is likely associated with modifications of female genitalic systems, at least for the ancestor of crown Strepsiptera (Pohl and Beutel, 2008). Apparently, two (138, 139, Hünefeld and Beutel, 2005) to four (32, 33, 34, and 35, Hünefeld, Pohl, et al., 2011b) muscle sets are associated with the intromittent organ, although the organ is maneuvered by abdominal torsion (Peinert et al., 2016). Given that these muscles originate on abdominal sternum and tergum IX, and the close association of the penis with the second gonocoxites in Coleoptera, it is here postulated that the “penis” of the Strepsiptera is a coxopenis, with complete loss of the gonostyli, lateropenites, and intrinsic musculature (Fig. 10; Hünefeld, Pohl, et al., 2011b).

Note. *Elenchus koebelei* (Pierce, 1908) of the family Elenchidae was dissected for this study. Unfortunately, this species is highly miniaturized and musculature could not be discerned.

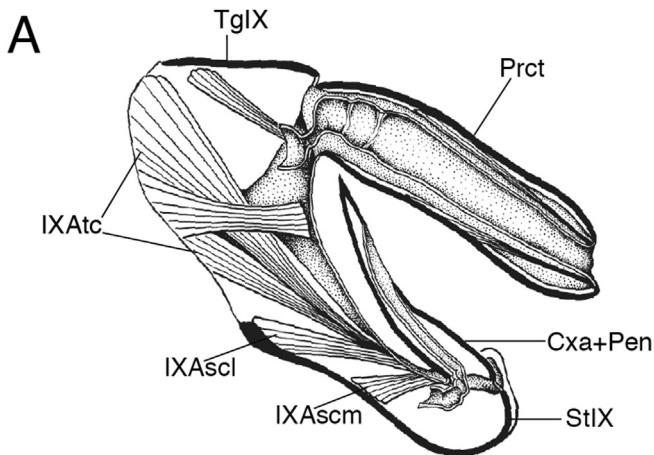


Fig. 10. Genital skeletomusculature of *Mengenilla* sp. (Strepsiptera: Mengenillidae), modified from Hünefeld, Pohl, et al. (2011b). **A**, abdominal segment IX and proctiger in cross-section. **Abbreviations:** Cxa = gonocoxa; Pen = penis; Prct = proctiger; StIX = sternum IX; Stap = sternal apodeme; TgIX = tergum IX. **Muscle abbreviations** indicated in Table 1.

4.5. Antliophora, Euantliophora

Overview. The Euantliophora, to coin a novel term, corresponds to the Mecoptera + Siphonaptera clade, recovered via transcriptomic analysis (Misof et al., 2014). The genitalic modifications of this clade, summarized in Fig. 1J (see also Tables S5 and S6), are fiendishly complex and require extended explanation. Unlike most genitalic conformations of the Endopterygota, those of the Euantliophora necessitate the postulation of multiple ancestral fragmentation and fusion events which are not observed in transitional forms. These events pertain particularly to the specialized sperm pumping complex, which is here homologized with fragments of the penial sclerite as well as with fragments of an unobserved ancestral coxital-penal composite sclerite. Fortunately, the task of homologizing the genitalia of the Euantliophora is eased by retention of some groundplan features which are shared between the Nannochoristidae and Siphonaptera (for a brief treatment of Boreidae, see *Homology analysis, detailed* below).

Homology-neutral description. As *Nannochorista* represents the closest approximation to the groundplan here inferred for the Euantliophora (Fig. 1J6), the structures of the male genitalia will here be described in a homology-neutral fashion. The male genitalia of *Nannochorista* comprise seven sclerites, which are as follows (Fig. 11; terms from Mickoleit, 2008; figure labels indicated parenthetically): (1) a large main body (*gonobasis*; Cxal), with an anterodorsal foramen and smaller posteromedial foramen from which the “sperm-pumping complex” is exserted; (2) articulated anterolaterally with the *gonobasis* are a pair of clasping elements (*gonostyli*; Sty), which bear denticles on the medial surfaces; within the *gonobasis* is a complex sperm-pumping complex, which comprises: (3) a bulbous structure (*phallobasis*; (PenI + Cxt(II + II))a), which extends posteriorly out of the lumen of the *gonobasis*, bearing lobate processes posteriorly, and a trilamellate structure anteriorly (*aedeagal apodem*; (PenI + Cxt(II + II))a), which is scruple-shaped in cross-section (3); (4) articulating ventrolaterally with the *phallobasis/aedeagal apodem* is an oval sclerite (*mittelplatte*; not figured, see Mickoleit, 2008), above which are (5) a chamber-like sclerite (*kammersklerit*; PenIIb) and (6) a complex sclerite (*tegimen*; PenIIa) above that; the *tegimen* articulates with the *aedeagal apodem* at a *fulcrum*, and projects posteriorly outside of the sperm-pumping complex; finally (7) a pair of unmusculated

triangular lobes (Lpe), which articulate at the *gonobasis* postero-medially, lateral to the posteromedial foramen. With respect to musculature, there are three extrinsic muscle units, and seven intrinsic muscle units (Fig. 2Jl; arbitrary muscle labels, and those from Mickoleit, 2008 indicated parenthetically): (1) one muscle unit connects the *gonobasis* to tergum IX (i), and (2, 3) two connect the *gonostyli* to the *gonobasis* (add.gst., abd.gst.); (6) one muscle connects the *aedeagal apodem* to the dorsal interior surface of the *gonobasis* (ptr.phal.), and (7) one muscle connects the *mittelplatte* to the ventral interior surface of the *gonobasis* (rtr.phal.); (8, 9) within the *aedeagal apodem* are attached two muscles which connect to the *tegimen* and *kammersklerit* (teg.lmpo., lev.kam.); (10) finally, there is one muscle which joins the *mittelplatte* to the *kammersklerit* (depr.kam.).

Homology analysis, outlined. Based on topological correspondences of the extrinsic muscles with other Endopterygota (i:**IXAtc**; ii + iii:**IXAsc**), the *gonobasis* may be homologized, at least in part, with the *gonocoxae*. Similarly, the *gonostyli* may be homologized with the *styli* of other endopterygote orders (add.gst.:**IXAxad**; abd.gst.:**IXAXab**). These constitute the two primary groundplan elements of the Euantliophora, with this pattern being shared among all sampled taxa of the Mecoptera and literature on the Siphonaptera. To derive the remaining homologies, i.e., those of the sperm-pumping complex, a series of transformations from the endopterygote groundplan (Fig. 1F5, 1J1) may be postulated. First, the penial sclerite must fragment (Fig. 1J1 to 1J2); to the anterior fragment fuse two *gonocoaxal* fragments, which bear with them the origins of the muscles which insert on the posterior penial sclerite fragment (Fig. 1J2 through 1J3a, b, to E4). This process results in the precursor sclerite to the *aedeagal apodem/phallobasis* (aed.apod. prec., Fig. 1J5). Next, in uncertain sequence, the second penial sclerite must fragment, resulting in the *tegimen* and *kammersklerit*, with each bearing a subunit of the dorsal muscle (Fig. 1J4 to 1J5), and the *aedeagal apodem* precursor must fragment, resulting in the *mittelplatte*, which bears the origin of the ventral muscle inserting on the *kammersklerit* (Fig. 1J5 to 1J6). To derive the skeletomuscular topology of *Nannochorista* from this groundplan, only four muscle subunits need to be lost (if ever gained; Fig. 1J6 to 1J1).

Homology analysis, detailed. The foremost groundplan elements of the genitalia of the Euantliophora are presence of the *styli* which articulate with the *gonocoxae* (Sty, Cxal in Fig. 1J6; Table S5). The *gonocoxae* bear the *styli* and the two *m. coxo-stylalii* muscles (**IXAxad**, **IXAxab**; M21, 22 of Günther, 1961), and are fused lateromedially via one or two bridges (first being the “genital jugum”, the second being the ventral surface of the *gonocoxae* in Mecoptera and “manubrium” of Siphonaptera). The identity of the *gonocoxae* is confirmed by the topology of the *m. tergo-coxalis* (**IXAtc**) and the *m. sterno-coxalii* (**IXAsc**), all of which attach to the basal/anterior apodeme of the *gonocoxae* in the Mecoptera. These muscles have a similar conformation in the Siphonaptera (**IXAsc** = M15; **IXAtc** = 18–20), despite the fact that the *gonocoxae* of the Siphonaptera are fragmented, with one part fused to abdominal tergum IX (Cxal' + TgIX in Fig. 1Jviii; Table S5), and that two additional *gonocoaxal* fragments are inferred to be present in the Siphonaptera, which are here labeled Cxal'a and Cxal'b (Fig. 1Jviii; Tables S5 and S6).

To understand the remaining sclerites — those of the sperm pumping complex — the morphology of the Nannochoristidae must be considered in detail, as this family bridges the morphological gap between the Siphonaptera and the remainder of the Mecoptera. The intermediate state of *Nannochorista* was previously noted by Mickoleit (2008), who observed that “the sperm pumps of the Siphonaptera and the Nannochoristidae are quite consistent ...

furthermore, it is not the sperm pump of the Pistillifera, but that of the Nannochoristidae which is closer to the basic plan of the Mecoptera" (Mickoleit, 2008, p. 214, here translated). The sperm pump of the Nannochoristidae comprises four sclerites, all of which are nestled within the gonocoxae (terms from Mickoleit, 2008): the (1) *aedeagal apodem* and *phallobasis*, (2) *mittelplatte*, (3) *tegimen*, and (4) *kammersklerit*. For clarity, these terms will be used throughout the remainder of this section. The *aedeagal apodem* and *mittelplatte* are inferred to be subfragments of an ancestral composite sclerite, which comprises two gonocoxal fragments and one penial sclerite fragment (*aed.apod.prec.*, PenI + Cxa(II, III); Fig. 1.J6; Table S5), while the *tegimen* and *kammersklerit* are inferred to be subfragments of a second penial sclerite (Pen II; transition: Fig. 1.J1 to 1.J2, 1.J4 to 1.J5; Table S5). Reasoning for these homologies plus a description of the sclerites follow (for a detailed explanation of correspondences with the Siphonaptera, see section 4.5.4 below).

In *Nannochorista*, five muscles are observed which attach to sclerites of the sperm pumping complex. All five muscles are inferred to belong to the *coxo-penial* class (IXAp), as the lateropenites are present as small, unmusculated sclerites situated ventrally between the sperm pumping complex and the styli. These muscles have the following attachments (muscle names from Mickoleit, 2008, italicized; Fig. 1.J1): (1) *protractor des phallosom*: origin: dorsomedial internal surface of first gonocoxites, insertion: anterior base of *aedeagal apodem* externally; (2) *retraktor des phallosom*: origin: ventromedial internal surface of first gonocoxites, insertion: anteromedial ventral surface of *mittelplatte*; (3) *depressor des kammersklerites*: origin: dorsomedial surface of *mittelplatte*, insertion: ventrolateral margins of *kammersklerit*; (4) *levator des kammersklerites*: origin: internal surfaces of *aedeagal apodem*, insertion: dorsolateral margins of *kammersklerit*; and (5) *tegimen-muskel*: origin: internal surface of *aedeagal apodem*, insertion: dorsal surface of *tegimen*.

The first muscle from above (1) is easily homologized with the *m. protractor penialis anterodorsalis* (IXAppd), which has a similar topology and function across the Mecoptera, Siphonaptera, and the rest of the Endopterygota, while the second muscle (2) is reasonably identified as the *m. retraktor penialis posteroventralis* (IXAprv), although the *mittelplatte* is a separate sclerite from the *aedeagal apodem*, indicating a fragmentation event (transition: Fig. 1.J1 to 1.J2). That these two sclerites are derived from an ancestral coxo-penial composite sclerite is evidenced by the origins of muscle (3) on the *mittelplatte* (depr.kam. Fig. 1.J1) and (4) and (5) (lev.kam., teg.lmpo. Fig. 1.J1) within the *aedeagal apodem* as the penial sclerites of other Endopterygota generally do not bear muscular attachments with free sclerites, except for the Megaloptera and Neuroptera, for which an ancestral muscle-shifting event is inferred (see section 4.3, above). Finally, the *kammersklerit* and *tegimen* are inferred to be subfragments of an ancestral penial sclerite fragment whose muscular origins on the gonocoxa are within the *aedeagal apodem*; the *kammersklerit* retains the insertions of two gonocoxal-penial muscles (lev.kam., depr.kam.) and the *tegimen* retains but one (teg.lmpo.).

A hypothetical evolutionary pathway demonstrating the requisite fusion and fragmentation events to form the *aedeagal apodem*, *mittelplatte*, *kammersklerit*, and *tegimen* is presented in Fig. 1.J. Given the inferred groundplan of the Euantliophora (Fig. 1.J6), only a few additional steps are required to model the genitalia of the Bittacidae and Panorpidae (for further explanation, see below): (1) fragmentation of the *pistillträger* anteriorly from the *aedeagal apodem* (ancestor of the Pistillifera; transition: 1.J1 to 1.JII); (2) retention of muscle IXAppv, resulting in an opposing retractor (IXAprv) and protractor (IXAppv) (transition: 1.J6 to 1.JII); (3) fusion of the *tegimen* and *kammersklerit* to form the *ostialsklerit* in the Bittacidae (transition: 1.JII to 1.JIII); and (4) integration of the

kammersklerit with the posterior fragment of the *aedeagal apodem* in the Panorpidae (*tegimen* retained as *pumpenkammer*) (transition: 1.JII to 1.JIV). These inferred modifications are summarized in Table S5.

With the sperm-pumping sclerites of the Euantliophora homologized via skeletomuscular evidence, the arrangement of these structures may be explained in greater detail. In the Nannochoristidae, the *aedeagal apodem* is a bulbous structure with three longitudinally-oriented lamellae, and which, in cross-section, resembles a scruple symbol (⌚) rotated counter-clockwise 90°, such that the free ends are facing downwards. This particular conformation corresponds to an unexpectedly high degree with the *aedeagal apodem* of the Siphonaptera, which has a similar construction and cross-section. Indeed, trilamellate cross-section is retained in *pistillträger* of the Bittacidae and Panorpidae, and the posterior *aedeagal apodem* fragment of the Bittacidae. Sandwiched between the *aedeagal apodem* dorsally and the *mittelplatte* ventrally are the *kammersklerit* and *tegimen*, with the latter fitting into a dorsal groove of the former.

The four sclerotic elements of the sperm pump are modified independently between the Siphonaptera and the remainder of the Mecoptera. Focusing on the Mecoptera, the Boreidae are found to be outliers, as their genitalia are highly simplified, with only four elements: the gonocoxae, the styli, and two "penial sclerites". The two "penial sclerites" are simple, flat ovals, one situated dorsally and the other posteriorly. The homology of these is uncertain and remains an open question, although the dorsal plate may be the *aedeagal apodem* and the posterior plate the *mittelplatte*. Mickoleit (1974) observed that *Boreus* sperm are transferred using a spermatophore — a significant reversal in the clade — which he hypothesized is a membranous elongation of the penis. No skeletomuscular evidence contradicts this hypothesis; other penial or gonocoxital composite or fragmented sclerites may have been present in stem boreids, which were eventually reduced to absence, or at the least insensibility with light microscopy. Conforming to Willmann (1981a), two muscles were observed in the dissected specimens, both muscles appearing to insert on the gonostylius. The Boreidae will not be considered further, as the reduced state of their genitalia were not found to provide information on sclerotic homology for the remainder of the order.

In the sampled Pistillifera (*sensu* Mickoleit, 2008, i.e., excluding the Boreidae, unlike Willmann, 1981b, 1987), the *aedeagal apodem* is divided into two fragments (Fig. 1.JII). In both the Bittacidae and Panorpidae, the anterior fragment of the *aedeagal apodem* is freely mobile, and is termed the *pistillträger*. Contrastingly, the posterior fragment of the *aedeagal apodem*, the "phallobasis", is without direct muscular attachments and has fused to a different sclerite between the two families (Fig. 1.JII–IV). In the Bittacidae, the posterior fragment of the *aedeagal apodem* ("phallobase" of Gao and Hua, 2015) is fused to the *mittelplatte* via a pair of ventrolateral sclerotic bridges (Fig. 1.JIII, 12G, I, L), while the *tegimen* and *kammersklerit* are fused together, forming the *ostialsklerit* (Fig. 1.JIII). In the Panorpidae (Fig. 1.JIV), the posterior fragment of the *aedeagal apodem* ("phallobasis") is fused with the *kammersklerit*, the *mittelplatte* is free, and the *tegimen* is retained as a minuscule sclerite tightly attached to the *pistillträger* by tendons, and is homologous with the unhomologized sclerite observed by Mickoleit (2008), which he termed the *pumpenkammer* (e.g., see Fig. 14 in Mickoleit, 2008).

These proposed homologies for the sperm pump complexes of the Mecoptera are supported by skeletomusculature (Fig. 1.JII–IV, 11–13). The simplest structure to homologize is the *pistillträger*, upon which muscle IXAppd is inserted, always with a similar topology, except for the Panorpidae, where IXAppd is divided into anterior and posterior subunits. Muscle IXAprv inserts on the

ventral surface of the *mittelplatte* in both the Bittacidae and Panorpidae, and opposes the protractor (**IXAppv**), while the dorsal surface of the *mittelplatte* bears the origin of muscle **IXAprv'** (Fig. 1.JII). Muscle **IXAprv'**, which inserts on the *kammersklerit* of the Nannochoristidae, is inserted on the *ostialsklerit* in the Bittacidae (Fig. 1.JIII) and on the *aedeagal apodem* plus *kammersklerit* composite in the Panorpidae (Fig. 1.JIV). Muscle **IXAprd'** is absent in the Panorpidae (Fig. 1.JIV), but is present in both the Nannochoristidae and Bittacidae (Fig. 1.JI, 1.JIII), connecting the *kammersklerit* to the *aedeagal apodem* in the former, and the *ostialsklerit* to the *pistillträger* in the latter. Note that, although lateropenites are present in *Nannochorista* (Fig. 1.JI, 1.JII), they are absent in the Bittacidae and Panorpidae.

Note: External genitalic morphology also examined for *Brachypanorpa*, *Panorpa*, *Merope*, *Notiothauma*, *Apterobittacus*, *Hylobittacus*, *Harpobittacus*. I identified the *Harpobittacus* as *H. phaeoscius* Riek using Tan and Hua (2009) and Lambkin (1994).

4.5.1. Mecoptera: Nannochoristidae, N. andina Byers, 1989

Notes: Terminology for *Nannochorista* skeleto-musculature in German from Mickoleit (2008) used for clarity, as applicable. The specimen dissected for the present study was dehydrated, thus musculature was poorly preserved. Therefore, refer to Figs. 1–11 in Mickoleit (2008) for clear demonstration of muscular topology.

Sclerites. Abdomen. **Tergum** and **sternum IX** fused, cupping genital appendages basally. Abdominal segment X, cerci, and anus all distinct, forming proctiger. **Genital appendages.** **Coxae** divided into three parts: (1) gonocoxa, bearing styli, massive, fused ventromedially (Fig. 11A–D), joined posterodorsally above sperm pumping complex by sclerotic bridge ("genital jugum") (Fig. 11C), with wide anterior apodeme for reception of tergo- and sternocoaxal muscles; (2) second gonocoxites fused with first penial sclerites, forming *aedeagal apodem* (Fig. 11A–I), *aedeagal apodem*

long and narrow (Fig. 11A–G), with median longitudinal lamina present internally (thus Ω-shaped in cross-section), internal and external portions of apodeme separated by transverse ridge (Fig. 11E–G), posterior apex with paired lobate processes which are directed posteriorly (Fig. 11C–H); (3) third gonocoxites fused with second penial fragment, forming *mittelplatte*, *mittelplatte* present as oval sclerite with bossed margins subtending third and fourth penial sclerites (see Mickoleit, 2008), all of which are situated within *aedeagal apodem*. **Styli** large, horn-like, with numerous peg-like teeth, and articulated with gonocoxae by pair of condyles, one dorsolateral and other ventrolateral (Fig. 11A–D). **Lateropenites** present as small lobe-like processes situated ventrolateral to sperm pumping complex and medial to styli (Fig. 11B–I). **Penial sclerite** divided into four fragments: (1) first fragment fused with second gonocoxites forming *aedeagal apodem* (see Coxae (2) above); (2) second fragment fused with third gonocoxites forming *mittelplatte* (see Coxae (3) above); (3) third fragment, *tegimen*, present as very small sclerite which is tightly associated with medial fulcrum of *aedeagal apodem*, and with narrow hairpin-shaped posteromedian process (Fig. 11B, C, E, G–I); (4) fourth fragment, *kammersklerit*, present between *mittelplatte* and *tegimen*, rimmed with apodeme (Fig. 11E, G–I).

Musculature (Fig. 1.JI). **Extrinsic coxal muscles.** **Tergo-coxal:** muscle (**IXAtc**) originating within tergum, inserting on dorsal apodemal margins of gonocoxae. **Sterno-coxal:** medial (**IXAscm**) and lateral (**IXAscl**) muscles present, both inserting on anterior region of gonocoxae. **Intrinsic coxal muscles.** **Coxo-stylar:** adductor (**IXAxad**) and abductor (**IXAxab**) present: (**IXAxad**) large, filling most of gonocoxa ventrally and laterally (*add. gonost.*, Fig. 2 of Mickoleit, 2008), inserting on ventral stylar apodeme; (**IXAxab**) originating on dorsal gonocoxal surface (*abd. gonost.*, Fig. 8 of Mickoleit, 2008), inserting on dorsal stylar apodeme. **Coxo-lateropenital:** absent. **Coxo-penial:** four muscle sets present: (1) (**IXAprv**, *retr. phal.*) originating in

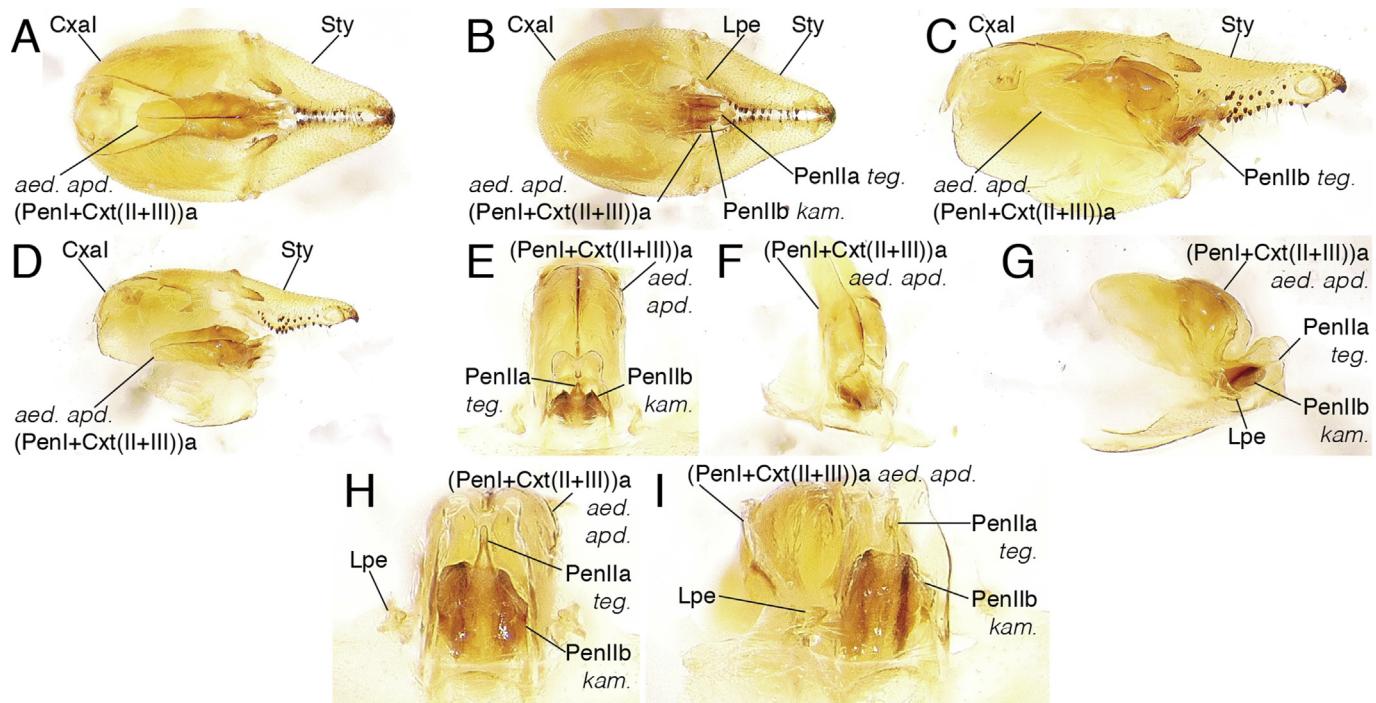


Fig. 11. Genital exoskeleton of *Nannochorista andina* (Mecoptera: Nannochoristidae); for musculature, refer to Mickoleit (2008) and see Fig. 1. **A**, genital appendages, dorsal view. **B**, genital appendages, ventral view. **C**, **D**, right coxopod and sperm pumping complex, dorsolateral oblique. **E–I**, sperm pumping complex: **E**, posterior view; **F**, dorsolateral oblique; **G**, lateral view; **H**, ventral view; **I**, ventrolateral oblique. **Abbreviations:** *aed. apod.* = *aedeagal apodem*; *Cxal* = gonocoxa or first gonocoxites; *kam.* = *kammersklerit*; *Lpe* = *lateropenite*; *Pen* = *penial sclerite*; *Sty* = *gonostylus*; *teg.* = *tegimen*. **Note:** Roman numerals indicate sclerite number; addition signs indicate sclerite fusion; italicized abbreviations indicate formal names for sclerites.

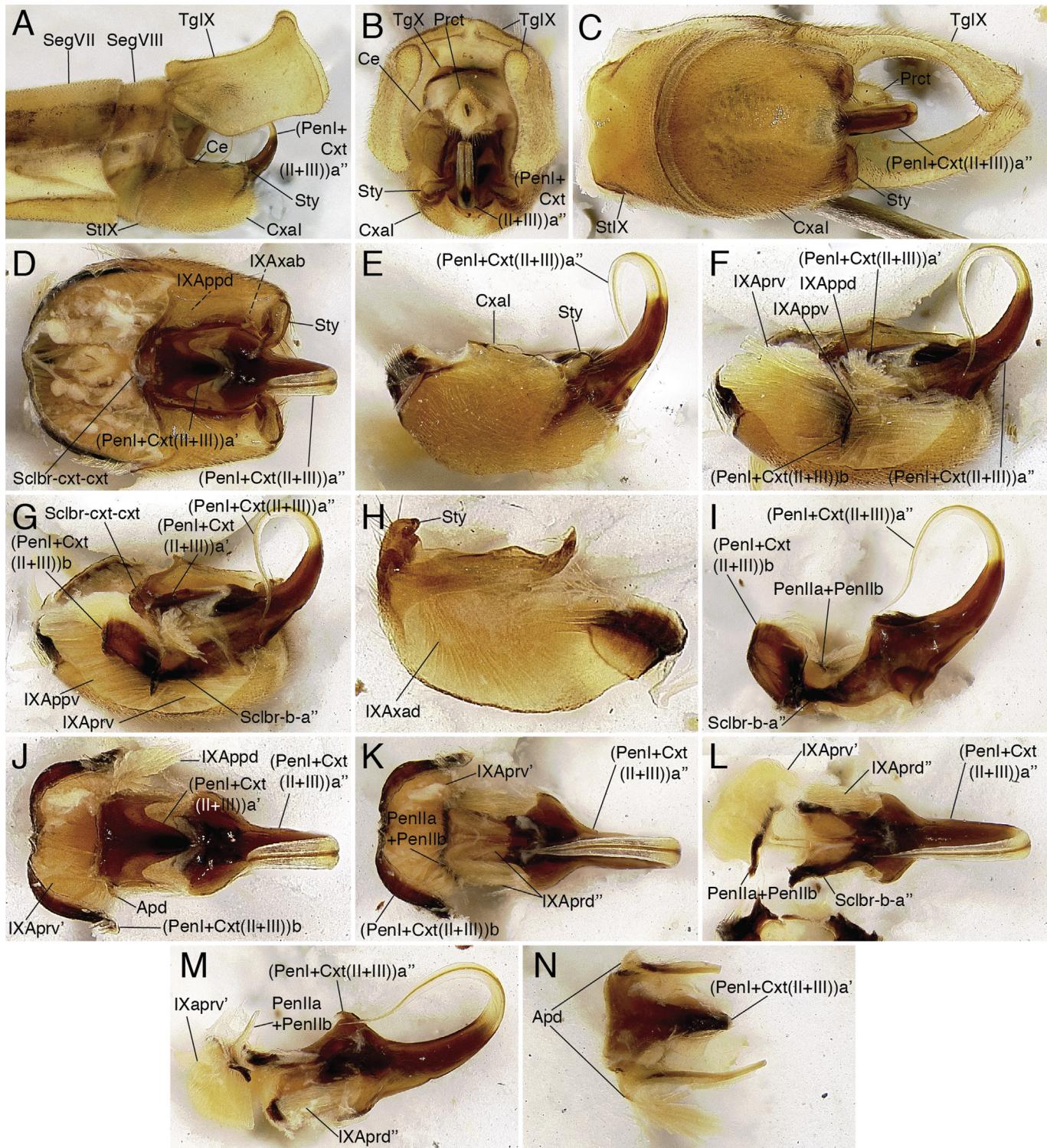


Fig. 12. Genital skeletemusculature of *Apterobittacus apterus* (Mecoptera: Bittacidae). **A–C**, genital and pregenital segments: **A**, lateral; **B**, distal; **C**, ventral. **D–G**, genital appendages and sternum IX: **D**, dorsal; **E**, lateral (partially dissected); **F**, lateral, left fragment of first coxite removed; **G**, same as **F**, with more muscle removed. **H**, left fragment of first coxite, mesal. **I–N**, complex of second coxite, lateropenite, and penial sclerite: **I**, lateral, first penial sclerite fragment removed; **J**, dorsal; **K**, dorsal, first penial sclerite fragment removed, dorsal. **L**, second coxites and first penial sclerite fragment removed, dorsal. **M**, same as **L**, dorsolateral oblique. **N**, first penial fragment, ventral (mesal), left and median tines partially broken. **Abbreviations:** Apd = apodeme; Ce = cercus; Cxa = gonocoxa or first gonocoxites; Cxt# = gonocoxite fragment; Lpe = lateropenite; Pen# = penial sclerite fragment; Prct = proctiger; Sclbr-b-a" = sclerotic bridge between *mittelplatte* and second fragment of *aedeagal apodeme*; Sclbr-cxt-cxt = sclerotic bridge between first gonocoxites; SegVII = seventh abdominal segment; Seg VIII = abdominal segment VIII; StIX = sternum IX; Sty = stylus; TgIX = tergum IX. **Muscle abbreviations** indicated in Table 1. **Note:** Sclerite fragment numbers indicated with Roman numerals; addition signs indicate sclerite fusion.

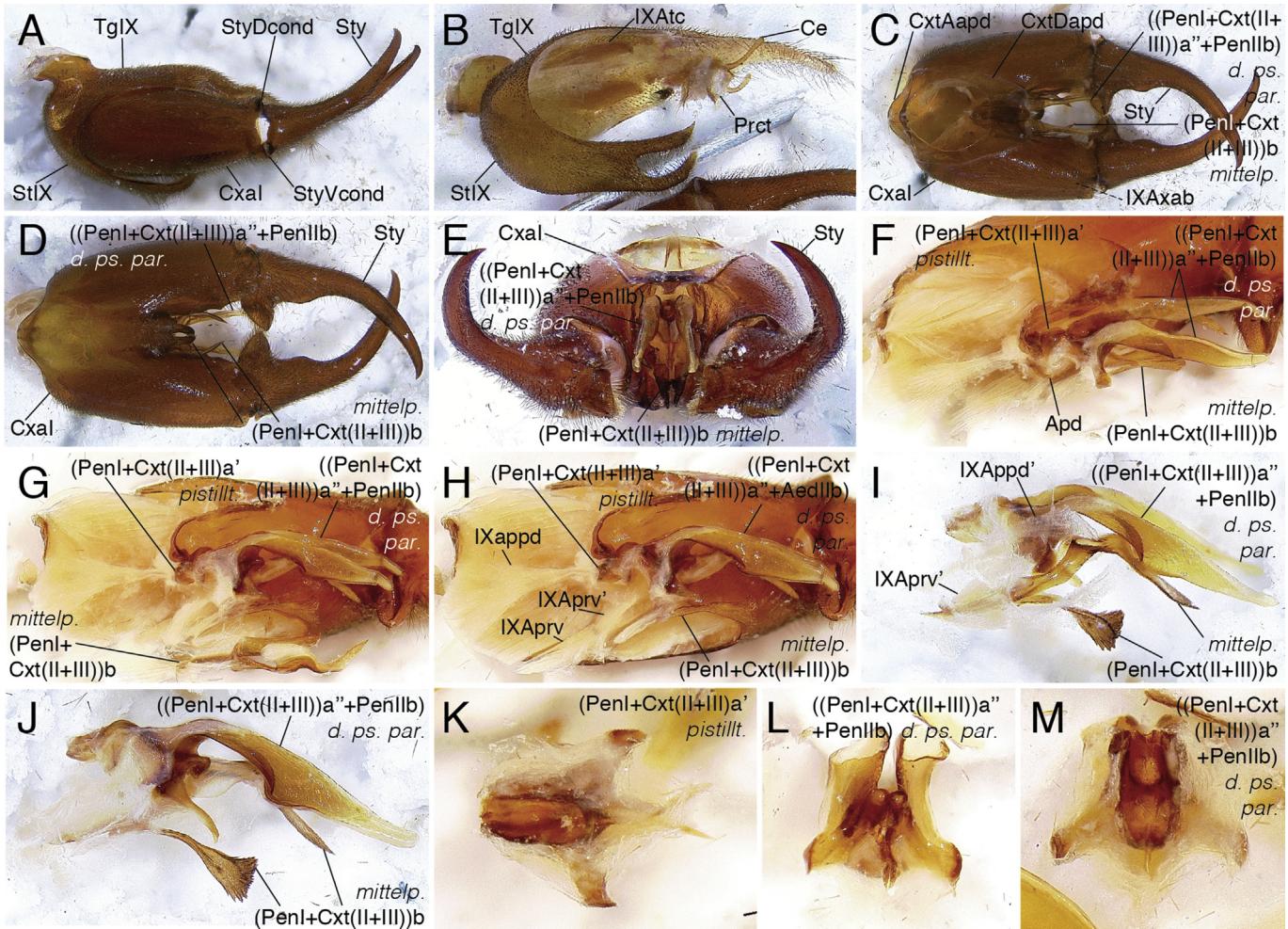


Fig. 13. Genital skeletomusculature of *Panorpa nuptialis* (Mecoptera: Panorpidae). **A**, genitalia *in situ*, lateral. **B**, composite sclerite of tergum and sternum IX. **C–E**, genital appendages: **C**, dorsal; **D**, ventral; **E**, distal. **F–H**, right half of genital appendages: **F**, dorsolateral oblique; **G**, lateral, paired appendages of sperm pumping complex intact; **H**, lateral, left half of sperm pumping complex removed. **I, J**, mittelplatte and dorsal pseudoparameres (= *kammersklerit* plus second fragment of *aedeagal apodeme*). **K**, *pistillträger*, ventrolateral oblique. **L**, base of dorsal pseudoparameres, posterior view. **M**, base of dorsal pseudoparameres, internal (anterior) view. **Abbreviations:** Apd = apodeme of *pistillträger*; Ce = cercus; d. ps. par. = dorsal pseudoparamere; Cxa = gonocoxa or first gonocoxites; Cxt = gonocoxite; CxtAapd = anterior apodeme of gonocoxite; CxtDapd = dorsal apodeme of gonocoxite; mittelp. = mittelplatte; pistillt. = *pistillträger*; Pen = penis or penial sclerite; Prct = proctiger; StlX = sternum IX; Sty = gonostylus; StyDcond = dorsal stylar condyle; StyVcond = ventral stylar condyle; TgIX = tergum IX. **Muscle abbreviations** indicated in Table 1. **Note:** Sclerite fragment numbers indicated with Roman numerals; addition signs indicate sclerite fusion.

posteroventral region of gonocoxae, directed posteromedially to anteroventral surface of *mittelplatte* (figures 2, 3 of Mickoleit (2008); (2) (**IXAprv'**), depr. kam.) originating on anterodorsal surface of *mittelplatte*, inserted on anteroventral surface of *kammersklerit* (Figs. 2–7, 9, 10 of Mickoleit, 2008); (3) muscle **IXAppd** subdivided: (3a) first subunit (**IXAppd'**, lev. kam.) originating within *aedeagal apodeme* between median longitudinal lamella and lateral surfaces, and inserting on dorsal surface of *kammersklerit* (figures 3, 7, 8, 10, 11 of Mickoleit, 2008); (3b) second subunit (**IXAppd''**, teg. lmpo.) originating on ventromedian apex of median longitudinal lamella of *aedeagal apodeme* and inserting on *tegimen* dorsally (figures 3, 7, 8, 11 of Mickoleit, 2008); (4) **IXAppd** (prot. phal.) originating within dorsomedian surface of gonocoxa, directed anteromedially to insertion on anterolateral surfaces of *aedeagal apodeme* (figures 2, 7, 8, 11 of Mickoleit, 2008).

4.5.2. Mecoptera: Bittacidae, *Apterobittacus apterus* (MacLachlan, 1871)

Notes. German terms from Mickoleit (2008) applicable to *A. apterus* used when necessary (see section 4.5 above); English terms

from Gao and Hua (2015), including muscle names, indicated in quotation marks. Species identification made by visual comparison with specimens, and confirmed based on distributional data in Penny (2006).

Sclerites. Abdomen. Tergum and sternum IX fused; tergum IX produced as massive clasping appendages (Fig. 12A–C), closure controlled by dorsomedial external muscles (*sensu* Snodgrass, 1935a). Tergum X forms sclerotic bridge encircling proctiger and cerci, and may be partially fused to gonocoxae anterolaterally (Fig. 12A and B). **Genital appendages. Coxae** divided into four parts: (1) gonocoxae, bearing styli, fused medially and forming bowl-shaped sclerite containing sperm pumping complex (Fig. 12E), gonocoxae joined anterodorsally by strap of sclerite bridging over penes ("genital jugum") (Fig. 12D, G); (2) second gonocoxites, fused with first penial sclerites (forming *aedeagal apodeme* composite sclerite), subdivided into two fragments: (2a) anterior fragment M-shaped, with each of the three posteriorly-directed points fitting into slots on posterior fragment (*pistillträger*) (Fig. 12D, G, J, N), (2b) posterior fragment fused with *mittelplatte* (composite of third gonocoxites and second penial sclerite), forming oil-lamp shaped

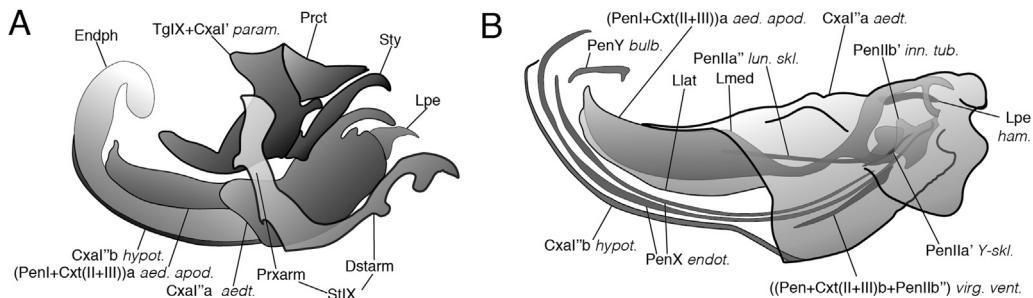


Fig. 14. Genital sclerites of *Hystrichopsylla talpae* (Siphonaptera: Hystrichopsyllidae), after Günther (1961); for musculature, see Fig. 1. **A**, genital appendages, sternum IX, tergum IX, and proctiger. **B**, genital appendages, excluding tergal-coxital composite. **Abbreviations:** *aed. apod.* = aedeagal apodem; *aedt.* = aedeagaltasche; *bulb.* = bulbalis; *Dstarm* = distal arm of sternum IX; *Endph* = endophallus; *endot.* = endotendons; *Cxa* = gonocoxa; *Cxt* = gonocoxite; *ham.* = hamulus; *hypot.* = hypotendon; *inn. tub.* = innere tube; *Llat* = lateral lamina of aedeagal apodem; *Lmed* = medial lamina of aedeagal apodem; *Lpe* = lateropenite; *lun. skl.* = lunarsklerit; *param.* = paramere; *Pen* = penial sclerite; *Prct* = proctiger; *Pxarm* = proximal arm of coxosternum IX; *StIX* = sternum IX; *Sty* = gonostylus; *TgIX* = tergum IX; *virg. vent.* = virga ventralis; *Y-skl.* = Y-sklerit. **Note:** Fragment numbers of gonocoxites and penites indicated with Roman numerals; addition signs indicate sclerite fusion.

structure, with long, curling, posterodorsal median process (“penisfilum”), and paired lateral sclerotic chambers (“lateral lumen of phallobase”) (Fig. 12A–G, I–M); (3) third gonocoxites fused with second penial sclerite forming *mittelplatte*, which is fused with posterior fragment of second gonocoxites plus first penial sclerite, *mittelplatte* forming thick dome (“dish-” or “spoon-shaped sclerite), dome connected to posterior *aedeagal apodem* fragment via pair of ventrolateral sclerotic bridges (“aedeagal apodeme”, Fig. 14I), convex surface of dome directed anteroventrally and concave surface directed posteroventrally (Fig. 12G, I, J, K). **Styli** present as small hooks at apices of gonocoxae, and bearing two condyles (Fig. 12A–E, H). **Lateropenites** absent. **Penial sclerites** divided into four fragments: (1) first fragment fused with second gonocoxites, forming *aedeagal apodem*, which itself is fragmented (see Coxae (2) above); (2) second fragment fused with third gonocoxites, forming *mittelplatte*, which is fused with posterior fragment of *aedeagal apodem*; (3, 4) third and fourth penial fragments (*tegimen* and *kammersklerit*) fused together, forming *ostialsklerit*, situated beneath M-shaped *pistillträger* and above composite of posterior *aedeagal apodem* plus *mittelplatte*, *ostialsklerit* with long posteromedian hairpin-like process associated with ejaculatory sac (Fig. 12K–M).

Musculature (Fig. 1JIII). **Extrinsic coxal muscles.** **Tergo-coxal** muscle (**IXAtc**) present, inserting on anterolateral corners of gonocoxae. **Sterno-coxal:** medial (**IXAscm**) and lateral (**IXAscl**) muscles present, inserting on anteroventral surface of gonocoxae. **Intrinsic coxal muscles.** **Coxo-stylocarp:** adductor (**IXAxad**) and abductor (**IXAxab**) present: (**IXAxad**) adductor originating broadly on ventrolateral surface of sterno-coxal composite (Fig. 12H); (**IXAxab**) abductor narrowly in medially-delimited region of gonocoxa (Fig. 12D). **Coxo-lateropenital** muscles absent. **Coxo-penital:** five muscle sets present: (1, 2) ventral retractor (**IXAprv**) and protractor (**IXAppv**) originating on internal ventral surface of gonocoxae, **IXAprv** (“retractor of spoon-shaped sclerite”, “RSS”), directed posteriorly to transverse apodeme on ventral surface of *mittelplatte* (Fig. 12F and G), **IXAppv** (“protractor of spoon-shaped sclerite”, “PSS”), directed anteriorly to broad insertion opposite that of **IXAprv** (Fig. 12F and G); (2) muscle **IXAprv'** (“retractor of ostial sclerite”, “ROS”) originating within dome of *mittelplatte* and inserting on anterior surface of penial sclerite III plus IV composite (*ostialsklerit*, Fig. 12J–M); (3) muscle **IXAprd'** (“protractor of ostial sclerite”, “POS”) originating on lateral arms of *ostialsklerit*, opposite insertion of **IXAprv'**, and inserting on apices of lateral arms of M-shaped *pistillträger* (anterior fragment of *aedeagal apodem*, Fig. 12K–M); (4) dorsal protractor (**IXAppd**: “levator of piston”, “LP”) originating within dorsomedial region of gonocoxae, inserting on anterolateral apodemes *pistillträger* (Fig. 12F, G, J, N).

4.5.3. Mecoptera: Panorpidae, *Panorpa nuptialis* Gerstaeker, 1853

Notes: Muscle names of sperm pumping complex from Mickoleit (2008, see his Fig. 18), all belonging to coxo-penital set, indicated in parentheses. Species-level identification rendered via comparison of the dissected specimen with previously identified museum material.

Sclerites. Abdomen. **Tergum** and **sternum IX** fused, cupping genital appendages basally (Fig. 13A and B). Proctiger and cerci borne within tergum (Fig. 13B). **Genital appendages.** **Coxae** divided into four parts: (1) gonocoxae, bearing styli, massive, fused ventromedially (Fig. 13C–E, J), joined posterodorsally above sperm pumping complex by sclerotic bridge (“genital jugum”) (Fig. 13C, E, J), and with wide apodeme which receives tergo- and sterno-coxal muscle insertions (Fig. 13C, J); (2) second gonocoxites, fused with first penial sclerites (forming *aedeagal apodem*), subdivided into two fragments: (2a) anterior fragment shell-shaped, with medial dome and lateral triangular processes which articulate with gonocoxae (*pistillträger*) (Fig. 13G), (2b) posterior fragment fused with fourth penial fragment (*kammersklerit*), forming *pseudoperameren* which bear paired, posteriorly-directed, tong-like processes, between which are two, smaller horn-like processes (Fig. 13F and G); (3) fourth gonocoxite fused with second penial sclerite (forming *mittelplatte*), this composite sclerite with posteriorly-produced ventral fan-like lobe and dorsal tine (Fig. 13A), apodemes of composite directed anteroventrally and joined medially (Fig. 13F). **Styli** large, horn-like, articulated with gonocoxae by pair of condyles, one dorsolateral and other ventrolateral (Fig. 13A, C–E). **Lateropenites** absent. **Penial sclerite** divided into four fragments: (1) first fragment fused with second gonocoxites (forming part of *aedeagal apodem*), *aedeagal apodem* itself divided into two subfragments (see 2a, 2b above); (2) second fragment fused with third gonocoxites (forming *mittelplatte*, see 3 above); (3) third fragment (*tegimen*) tightly connected to *pistillträger* by tendons (termed “*pumpenkammer*” by Mickoleit, 2008); (4) fourth fragment (*kammersklerit*) fused with second (posterior) subfragment of *aedeagal apodem* (thus forming *pseudoperameren*, see 2b above).

Musculature (Fig. 1JIV). **Extrinsic coxal muscles.** **Tergo-coxal:** muscle (**IXAtc**) originating within tergum, inserting on dorsal apodermal margins of gonocoxae (Fig. 13B and C). **Sterno-coxal:** medial (**IXAscm**) and lateral (**IXAscl**) muscles present, both inserting on anterior region of gonocoxae (Fig. 13J). **Intrinsic coxal muscles.** **Coxo-stylocarp:** adductor (**IXAxad**) and abductor (**IXAxab**) present: (**IXAxad**) large, filling most of gonocoxa ventrally and laterally, inserting on ventral stylocarp apodeme (Fig. 13I); (**IXAxab**) originating on dorsal gonocoxal surface, inserting on dorsal stylocarp apodeme (Fig. 13C). **Coxo-lateropenital:** absent. **Coxo-penital:** four muscle sets present: (1, 2) ventral retractors (**IXAprv**) and

protractors (IXAppv) originating on internal ventral surface of gonocoxae: **IXAprv** (*rtr. psm.*) directed posteriorly to transverse apodeme on ventral surface of *mittelplatte* (Fig. 13H), **IXAppv** (*ptr. psm.*), directed anteriorly to broad insertion opposite that of IXAprv (Fig. 13F, H); (2) muscle **IXAprv'** subdivided into two units, both originating on anterior apodemes of *mittelplatte*, first pair (*m. gö2, genitalfeldmuskel-2*) thin and inserting within main tines of *pseudoparameren*, second subunit (*m. gö1, genitalfeldmuskel-1*) broad and fan-like, inserting medial to *m.gö2* (Fig. 13F); (3) dorsal protractor (**IXAppd**) subdivided into two units, both subunits originating within dorsomedial surface of gonocoxa, anterior muscle pair (*depr. pist.*) inserting on anteromedian process of *pistillträger*, posterior muscle pair (*lev. pist.*) inserting on apices of posterolateral processes of *pistillträger* (Fig. 13F, H, I).

4.5.4. Siphonaptera

Because of the complexity of siphonapteran genitalia, this section is divided into a *Synthesis of observations* (4.5.4.1) and *Homology-explicit description of genital skeletomusculature* (4.5.4.2).

4.5.4.1. Synthesis of observations. The literature and skeletomuscular evidence. It is well appreciated that the male genitalia of the Siphonaptera are highly modified. Snodgrass (1946) remarked “[t]hroughout the skeletal anatomy of the flea ... there are numerous peculiarities that strain the imagination for a plausible explanation, and the complexity of the intromittent apparatus is almost beyond belief”. Snodgrass (1946) applied his ontogenetic hypothesis to homologize the clasping genitalia of fleas, with his interpretations refined by a detailed and thorough study of genital skeletomusculature by Günther (1961). Günther, using sclerite terms from Peus (1955), recognized 26 muscles in the genitalia of the Siphonaptera (M15–40), and provided useful abbreviations and formal names for them given their origins and insertions (Günther, 1961, p. 346). While Günther agreed with the phallic-origin hypothesis for most structures proposed by Snodgrass, he maintained that the “claspers” of the Siphonaptera were derived from gono-pods of abdominal segment X based on developmental observation. Developmental “origin” of the coxopods associated with abdominal segment X is here interpreted as an autapomorphic state. Based on the work of Günther (1961), Snodgrass (1946), and Cheetham (1987), the skeletomuscular homologies of the Siphonaptera are reinterpreted. Homologies drawn across these works are summarized in Table S6.

Homology-neutral description of genitalia. The genitalia of the Siphonaptera comprise thirteen sclerites (Fig. 14; terms from Günther, 1961): (1) tergum IX, bearing (2) clasping structures (“parameres”); (3) a sclerite within the endophallic bulb (*bulbalis*) which is situated at the anterior apex of the endophallus; (4) a sclerotic bag (*aedeagaltasche*) which encompasses multiple splinter-like sclerites, and which is produced anteriorly as a trilobate structure (*aedeagal apodem*) which is scutule-shaped (⌚) in cross-section; the *aedeagal apodem* comprises: (5) a median lamella which continues posteriorly into the *aedeagaltasche*, where it forks and articulates with other sclerites, and (6) paired lateral lamellae; within the *aedeagaltasche* are situated (7) a pair of clasping appendages (*hamuli*), and a series of splinter-like sclerites which are oriented along the anteroposterior axis: (8) ventralmost, along the median axis, is a thin rod (*hypotendon*) which may or may not be fused with the anteroventromedial margin of the *aedeagaltasche* or the anterodorsomedial margin of sternum IX; (9) dorsal to the *hypotendon* are a pair of similarly-shaped rods (*endotendons*) which are situated within the endophallus, and which extend from the endophallic bulb to nearly the posterior apex of the *aedeagaltasche*; (10) posteroventral to the *endotendons* is a thick rod-shaped sclerite (*virga ventralis*) which is closely

associated with the remaining sclerites; (11) dorsal to the posterior apices of the *endotendons* and *virga ventralis* is a sclerite (*lunarsklerit*) which bears a pair of probe-like apodemes which are directed anteriorly, and which meet posteriomedially forming a bulbous structure; (12) surrounding the *endotendons* near their posterior apices is a tube which has a Y-shape in dorsal or ventral view (*Y-sklerit*); and (13) finally, surrounding the posterior apices of the *endotendons* and *virga ventralis* is a sclerotic tube (*innere tube*).

The intricate musculature of the thirteen sclerites described above is best represented here in the form of the generalized topological schema in Fig. 1Jviii. Overall, there are 18 muscle units, which are comparable to the genitalic musculature of other endopterygotes for the purposes of this work (muscle names from Günther, 1961; note that the muscle units are partitioned differently here than in the original work): (1–3) three of these muscles are intrinsic to tergum IX and “parameres” (M18–20, M21, M22); (4, 5) two units attach the *aedeagal apodem* to the tergum and “parameres” (M16, 17, 23, 24, and M15); attached to the internal surfaces of the *aedeagal apodem* are eight muscles: (6, 7) two attach to the *hypotendon* (M27, 28), and (8–13) one each attach to the *virga ventralis*, the *innere tube*, the *lunarsklerit*, the *Y-sklerit*, the *endotendons*, and the *bulbalis* (M33, 29, 32, 31, 34, 35, respectively); (14) the *virga ventralis* and *innere tube* are connected by one muscle (M30); (15, 16) each *hamulus* is connected to the *aedeagaltasche* by two muscles (M25, 26); (17) one muscle unites the two *endotendons* (M36); and (18) a pair of muscles attach the *bulbalis* to the *endotendons* (M37, 38).

Reasoning for proposed homologies. Unlike *Nannochorista* which has five total coxo-penial muscles, which attach to five sclerites (including the gonocoxae), the Siphonaptera have 13 coxo-penial muscles, which attach to nine sclerites (including subfragments of first gonocoxites). This multiplication of muscles and sclerites may be explained by a series of fragmentation and fusion events, which can be untangled via comparison of skeletomuscular topologies between *Nannochorista* and the Siphonaptera (Fig. 1Ji–viii). Due to the complexity of siphonapteran genitalia and lack of micrographs (Fig. 14), readers are referred to Günther (1961), Snodgrass (1946), Cheetham (1987), and Fig. 1Jviii for illustrations of flea musculature; muscle names used below are drawn from Günther (1961). Terms in German from Mickoleit (2008) are used for logical continuity and ease of reference with explanation of euantliophoran homologies in section 4.5.

Table S5 summarizes the proposed genitalic homologies between the Siphonaptera with Mecoptera. Before continuing, there are four caveats for the following discussion: (1) the scenario proposed herein assumes few to no losses of muscles; (2) muscle shifts from sclerite to sclerite are not invoked to explain skeletomuscular topologies; (3) *Nannochorista* are assumed to have genitalia most similar to the most recent common ancestor of the Euantliophora; (4) after analysis, the sclerites of origin for the *endotendons* and *bulbalis* sclerites of the Siphonaptera remain uncertain and may be endophallic (although this would require muscle shift). Finally, note that hypothetical sclerites in this discussion are italicized, in addition to those of Mickoleit (2008). All inferences below may be treated as deductive hypotheses, predicting specific intermediate states, which may be tested via increased taxon sampling including both extant and extinct taxa. A simpler hypothesis may yet be derived.

The present explanation of homologies inferred from skeletomusculature for the Siphonaptera starts at J6 of the evolutionary pathway presented in Fig. 1. At stage J6, the ancestral penial sclerite is inferred to have fragmented, forming *aedeagal sclerites I* and *II* (transition: J1 to J2); sclerite *II* has fragmented, forming the *tegimen* and *kammersklerit* (*aedeagal sclerites IIIa* and *IIIb*) (transition: J4 to J5). Additionally, the gonocoxae have fragmented twice, with the

resultant gonocoxites bearing the origins of muscles *k* and *i*; these gonocoxites have fused with *aedeagal sclerite I*, forming the *aedeagal apodem precursor* (*gonocoxites II, III + aedeagal sclerite I*) (transition: **J2** through **J4**, with final label presented in **J5**). From this point, the *aedeagal apodem precursor* is inferred to have fragmented into the *aedeagal apodem* and the *mittelplatte* ((*PenI + Cx(I+II)*)*a* and *b*; transition: **J5** to **J6**). Fragmentation of the *aedeagal apodem precursor* is inferred to have been one of the final modifications to have occurred before the cladogenic event resulting in the MRCAs of the Mecoptera and Siphonaptera.

Continuing down the stem of the Siphonaptera, two series of changes are inferred to have occurred: (I) fragmentation of the *gonocoxae* (**J1–J4**), and (II) completion of the sperm pumping complex via further fragmentation and fusion of the penial sclerite and *mittelplatte* (**J4–Jviii**). Unfortunately, there is no evidence retained in intermediate taxa for whether the gonocoaxal modifications occurred before those of the sperm pumping complex, or whether both occurred concomitantly. The first series of changes (I) involves two fragmentation events of the *gonocoxae* which resulted in three fragments. The first fragments (*gonocoxae*) retained the styli and the *coxo-stylar* muscles (**IXAxad**:M21; **IXAxab**:M22) migrated dorsally and fused with abdominal tergum IX (**J1–Jiii**). The second fragment subdivided (*gonocoxae**a* and *b*) (transition: **Jiii** to **Jiv**); *gonocoxae**a* fused around the apex of the *aedeagal apodem*, forming the *aedeagaltasche*, which internally bears the origins of the *coxo-lateropenital* muscles (**IXAlm**:M25; **IXAlp**:M26), while *gonocoxae**b* is inferred to be the *hypotendon*, along which ventral muscles (**IXAppv**:M27 + 28) originate. Among the Siphonaptera, the *hypotendon* may be free, fused with the *aedeagaltasche*, or fused to sternum IX (Snodgrass, 1946; Günther, 1961).

The second series of changes (II) is invoked to explain the muscular topologies of the remaining sclerites of the sperm pumping complex, which include the *Y-sklerit* (= *virga dorsalis*), *lunarsklerit*, *innere tube*, *virga ventralis*, paired *endotendons*, and the *bulbalis*. Each of these sclerites receive the insertion of a muscle originating from the *penial apodem* (M29, 31–35, respectively). Among the first inferred steps is fragmentation of the *tegimen* into the *Y-sklerit* and *lunarsklerit* (*penial sclerites IIa'* and *a''*; transition: **Jiv** to **Jv**); both sclerites have but one muscular attachment, and the homology of the *tegimen* with the *Y-sklerit* has been previously proposed by Mickoleit (2008, p. 222). On the same page, Mickoleit speculates that the *lunarsklerit* is homologous with the *kammersklerit*. This could be true, and an alternative evolutionary pathway is presented (**Jv** and **Jv'**). To produce the *innere tube* and *virga ventralis*, the *kammersklerit* is inferred to have fragmented (transition: **Jv** to **Jvi**), with one fragment simply forming the *innere tube* (*penial sclerite IIb'*), while the other fragment fused to the *mittelplatte*, resulting in the *virga ventralis* (transition: **Jvi** to **Jvii**), which bears the origin of muscle **IXAprv** (M30), as well as the insertion of a subunit of **IXAprd** (M33). The *innere tube* is inferred to bear the insertions of both **IXAprv** and a subunit of **IXAprd** (M29). The final required modifications to the sperm pumping complex, producing the paired *endotendons* and *bulbalis* are uncertain (transition: **Jvii** to **Jviii**), as both have intrinsic musculature, and both receive the insertion of a *coxo-penial* muscle (M34, 35, respectively). These sclerites may be sclerotic developments of the endophallus or may be fragments of one or more elements of the *aedeagal apodem*, *tegimen*, or *kammersklerit*. Without further evidence for the origins of the *endotendons* and *bulbalis*, they are here referred to as *penial sclerites x* and *y*, respectively.

4.5.4.2. Homology-explicit description of genital skeletomusculature. **Sclerites. Abdomen.** **Tergum IX** fused with set of gonocoaxal fragments (see below) (Fig. 14A); tergum anteroposteriorly narrow. **Sternum IX** subtending sperm pumping complex, being more-or-

less T-shaped, with paired anterior arms ("proximal arms", Günther) and lateromedially narrow posteromedial lobe ("distal arm", Günther) (Fig. 14A). Segment ten comprising proctiger; eleventh segment insensible (Fig. 14A). **Genital appendages.** **Coxae** divided into several fragments: (1) first subfragments of gonocoxae (*Cxal'*), bearing styli, fused with tergum IX forming tergo-coxal fragment (Fig. 1.Ji–iv, 14A), with paired lateral apophyses which are directed anteriorly and joined together ventromedially by medially-sclerotized bridge, the bridge supported by struts ("rod in mesal wall of clasper", Snodgrass); (2) second subfragment of gonocoxa (*Cxal''a*; *aedeagaltasche*) forming sheath around sperm pumping complex (Fig. 1.Jiv–v, 14A, B) and bearing the lateropenites; (3) third subfragment of gonocoxa (*Cxal''b*; *hypotendon*) long and narrow, subtending endophallus within body (Fig. 1.Jiv–v, 14A, B), and either directly attached to posterior sternal fragment, free, or fused to second gonocoaxal fragments; (4) second and third gonocoaxites fused with first penial sclerite forming *aedeagal apodem precursor* (Fig. 1.J2–5), this composite itself subdivided: (4a) first *aedeagal apodem precursor* fragment (*Pen+Cxt(II+III)a*) forming the *aedeagal apodem*, which bears three longitudinal laminae (thus Ω-shaped in cross-section) and origins of coxo-penial muscles (Fig. 1.J5–6, 14A), and in some taxa may extend anteriorly as rod-like process closely associated with endophallus ("epitendon" of *Ceratophyllus*: Günther, 1961); (4b) second *aedeagal apodem precursor* fragment (*Pen+Cxa(II+III)b*) forming *mittelplatte* (Fig. 1.J5–6), which is further modified (see Penial sclerites (4) below); the *aedeagal apodem* and *coxo-tergal* composite are connected via membrane or suspensory sclerites. **Styli** (Fig. 1.Jviii, 14A) variable in shape, articulated with gonocoxa via single condyle. **Lateropenites** contained within *aedeagaltasche* (see *Coxae* (2) above) (Fig. 1.Jiii–iv, 14A, B; "hamulus", Günther). **Penial sclerites** highly complex, divided several times: (1) first fragment fused with second and third gonocoaxites, forming *aedeagal apodem precursor*, which divided to form the *aedeagal apodem* and *mittelplatte* (as described in *Coxae* (4) above); (2) second fragment ancestrally divided into *tegimen* and *kammersklerit* (*PenIIa, b*; Fig. 1.J4–5); (3) *tegimen* subdivided into (Fig. 1.Jiv–v): (3a) the *Y-sklerit* (*PenIIa'*), which articulates with the *aedeagal apodem* via the *fulcrum*; and (3b) the *lunarsklerit* (*PenIIa''*), which is closely associated with the *Y-sklerit* and the gonopore, forming a dome with paired, long, anteriorly-directed apophyses; (4) *kammersklerit* subdivided into (Fig. 1.Jv–vi): (4a) the *innere tube* (*PenIIb'*), which forms internal sclerotic wall of tube-like evagination of thick membrane/intima occurring within *aedeagaltasche*; (4b) a hypothetical intermediate sclerite, *PenIIb''*, which fused with the *mittelplatte*, forming the *virga ventralis* ((*PenI + Cxa(II + III)b*)*b* + *PenIIb''*; Fig. 1.Jv–vii), subtending the endophallus posteriorly, mostly within external section of *aedeagal apodem*; (5) fifth fragments (*endotendons*, *PenX*), from unknown antecedent sclerite(s), forming pair of long, thin rods embedded within tubular and coiled endophallus (Fig. 14B); (6) sixth fragments (*bulbalis*, *PenY*), from unknown antecedent sclerite(s), integrated with ejaculatory bulb at anterior end of endophallus.

Musculature (Fig. 1.Jviii). **Extrinsic coxal muscles. Tergo-coxal:** two to three muscles intrinsic to coxo-tergal composite present (**IXAtc**:M18 + 19+20; M19 unique to *Hystriopsylla*, Günther, 1961), originating on tergum IX, inserting on first subfragments of gonocoxae (stylar-bearing or clasping; *TgIX + Cxal'*; Fig. 1.Jviii). **Sterno-coxal:** single muscle present (**IXAsc**:M15), originating on proximal arm of posterior sternal fragment, inserting on apodemal apex of coxo-tergal composite (Fig. 1.Jviii). **Intrinsic coxal muscles.** **Coxo-stylar:** adductors and abductors present (**IXAxad**:M21; **IXAxab**:M22), originating on clasping coxotergum (*TgIX + Cxal'*), inserting within styli (Fig. 1.Jviii). **Coxo-lateropenital:** two muscles present (**IXAlm**:M25; **IXAlp**:M26), originating on lateral laminae of

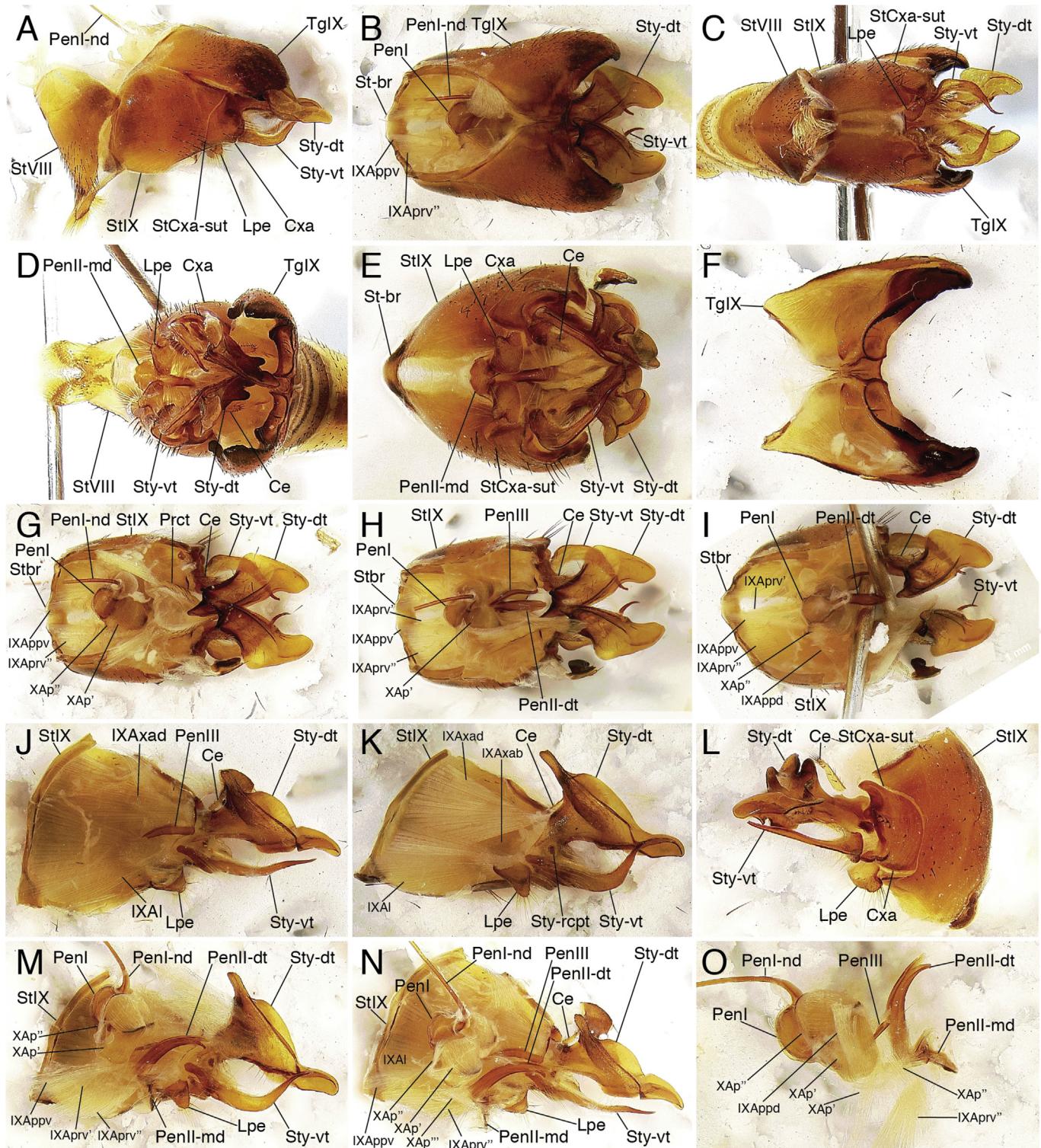


Fig. 15. Genital skeletemusculature of *Tipula (Hesperotipula) californica* (Diptera: Tipulidae). **A–E**, whole genitalia: **A**, lateral; **B**, dorsal; **C**, posteroventral oblique; **D**, distal; **E**, distal, tergum and sternum IX removed. **F**, tergum IX, mesal (ventral). **G–I**, genitalia with tergum IX and left gonopod removed, dorsolateral: **G**, with proctiger; **H**, proctiger partially removed; **I**, proctiger completely removed. **J–L**, right coxopod: **J**, **K**, mesal (medial); **L**, distal, oblique. **M**, genitalia with tergum IX and left coxopod removed, dorsolateral. **N**, right coxopod and penial sclerites, mesal. **O**, penial sclerites, lateral. **Abbreviations:** Ce = cercus; Cxa = gonocoxa; Lpe = lateropenite; Pen = penis; PenI = first penial sclerite; PenI-nd = penial needle; PenII = second penial sclerite; PenIIdt = dorsal tines of second penial sclerite; PenIImd = medial disc of second penial sclerite; PenIII = third penial sclerite; Prct = proctiger; StVIII = sternum VIII; StIX = sternum IX; St-br = sternal bridge; StCxa-sut = sternocoaxal suture; Sty = gonostylus; Sty-dt = dorsal tine of gonostylus; Sty-rcpt = stylar receptor; Sty-vt = ventral tine of gonostylus; TgIX = tergum IX. **Muscle abbreviations** indicated in Table 1.

aedeagal apodem, inserting on lateropenites (Fig. 1.Jviii). **Coxo-penial**: Six muscle sets present, representing 16 muscles total: (1) first muscle set (**IXAppd**:M16 + 17+23 + 24) originating on clasping coxotergum ($TgIX + Cxal'$; M16, 17 on *manubrium*, or anterior apodeme of tergo-penial composite, and M23, 24 on main body of tergal-gonocoxital composite), inserting on *aedeagal apodem* externally (Fig. 1.Jviii); (2) second muscle set (**IXAppv**:M27 + 28) originating along *hypotendon* (M27 externally, M28 internally), inserting on lateral lamellae of *aedeagal apodem* (Fig. 1.Jviii); (3) third muscle set (**IXAprd**:M29 + 31–35) originating on *aedeagal apodem*, inserting on penial fragments (Fig. 1.Jviii): M29 (**IXAprd'a**) inserts on *inner tube* ($PenIIb'$), M31 (**IXAprd'a**) on *Y-sklerit* ($PenIIa'$), M32 (**IXAprd'b**) on *lunarsklerit* ($PenIIa''$), M33 (**IXAprd'b**) on *virga ventralis* ($(PenI+Cxa(II+III)b+PenIIb')$, M34 ("Cxa-Pen1") on *endotendons* ($PenX$), M35 ("Cxa-Pen2") on *bulbalis* ($PenY$); (4) fourth muscle set consisting of single muscle (**IXAprb**:M30), originating on *virga ventralis* and inserting on *innere tube* (Fig. 1.Jviii); (5) fifth muscle set M36–38 (**XAp?**) intrinsic, joining *endotendons* and functioning as protractors and retractors of these sclerites (Fig. 1.Jviii); (6) sixth muscle set (**IXAprd'a**:M39) intrinsic to ejaculatory bulb, attaching to *bulbalis* sclerites; finally a muscle intrinsic to the ejaculatory duct (M40) is present.

4.6. Antliophora, Diptera

Comparison with the Euantliophora. The genitalia of Diptera demonstrate a spectacular range of elaboration, and have already been argued to be homologs of abdominal gonopods IX (McAlpine, 1981). Based on the homologies independently inferred for the Diptera and Euantliophora in the present work, the presence of a sperm pumping complex in the two clades appears to be the result of convergent or parallel evolution. This was previously concluded by Hünefeld and Beutel (2005), and more recently by Mickoleit (2008, pp. 223, 224), who noted that comparison between the groups was “sehr unbefriedigend”, or very unsatisfactory. Mickoleit contrasted the *aedeagal apodem*, *tegimen*, and *pistill* of the Mecoptera with the Diptera, and observed that the comparable structures in the Diptera have strikingly different topologies, and develop from different *anlagen* as well. These observations are supported by skeleto-musculature, for which muscular nomenclatures from Paramonov (2004) and Spangenberg et al. (2012) correspond much more neatly with the nomenclature employed here (see Table S7 for summary); note that all muscles for the genital appendages of *Tipula* sp. described by Paramonov (2004) were observed in the present study.

Taking the simpler genital skeleto-musculature of *Bibio marci* from Spangenberg et al. (2012, their Figs. 10–12), the penial sclerite comprises an “ejaculatory apodeme”, which is an anterior process of the “penis”. Three muscles insert on the penial sclerite, M7 (**IXAppv**), M8 (**IXAprv**), and M10 (**IXAppd**). M7 and M8 originate ventromedially from the fused region of the gonocoxae, while M10 originates anterodorsally on the gonocoxal apodeme (Fig. 1.K1). While M10 has a clear correspondence with the *m. tergo-coxalis* of *Nannochorista*, M7 and M8 only correspond to muscle **IXAppv** which inserts on the *mittelplatte* and as muscle **IXAprv'** originates instead on the *mittelplatte* and inserts on the *kammersklerit*. Likewise, even with the more complex skeleto-musculature of *Tipula californica* (described below), three coxo-penial muscles attach the “ejaculatory apodeme” to the sclerite situated ventrally (muscles **IXAppv**, **IXAprv'**, **IXAprv''**); again, a single muscle, **IXAppd**, connects the penial sclerite to the coxae dorsally, although the gonocoxae are replaced by sternum in *Tipula*. With the comparison of *Bibio* to *Tipula*, the pumping muscles of *Tipula* are best inferred as intrinsic to the penis (**XAp**, Fig. 1.K2), rather than as homologs with the pumping complex muscles of *Nannochorista*. Thus, to reiterate,

homology of the sperm pumping complexes of the Diptera and Euantliophora is not supported by comparison of musculature, and the *aedeagal apodem*, *tegimen*, and *kammersklerit* are autapomorphies attributable to the most recent common ancestor of the Euantliophora, and the *pistillträger* an autapomorphy of the Pissatillifera. Critical evaluation of the penial intrinsic muscles in the Antliophora is necessary.

4.6.1. *Tipulidae*, *Tipula* (*Hesperotipula*) *californica* (Doane, 1908)

Sclerites. Abdomen. The copulatory apparatus comprises abdominal tergum IX, genital appendages, and proctiger, all modified substantially (Fig. 15A). **Tergum IX** fused anterolaterally with base of sternum IX (Fig. 15A and B), forming pincer-like V-shaped complex dorsal to genital appendages (Fig. 15B, D, F); tergal complex with anteroposteriorly broad dorsal surface partially divided medially, posterolateral mesal (internal) surface of tergal complex elaborately modified structurally and bearing strongly-sclerotized lobe (Fig. 15F). **Sternum IX** replacing most of gonocoxa, the two of which are divided by an unsclerotized line (Fig. 15A, E, L); sternum desclerotized medially, except for anterior sclerotic bridge between left and right sides (Fig. 15B–E, G–I). Abdominal tergum X largely membranous, extending around dorsolateral region of genital appendages; cerci situated between styli ventrally and U-shaped lateral penial apodeme dorsally (Fig. 15D, E, G–J, L, N), cerci therefore situated slightly above level of lateropenite. **Genital appendages.** **Coxae** situated at posterior apices of sternum IX, about as third as long anteroposteriorly as sternum (Fig. 15A, C, E, L). **Styli** bifid, with horn-shaped ventrolateral tine and phylliform dorsomedial tine (Fig. 15A–E, G–N); dorsomedial tine with structural elaborations (Fig. 15J and K); patch of hypertrophied receptors present, situated between bases of ventrolateral and dorsomedial tines (possibly stretch detectors) (Fig. 15K); coxal condyle articulating with dorsomedial stylar tine, ventrolateral tine articulating with produced apical ventromedial margin of apical gonocoaxal section (Fig. 15L). **Lateropenites** small, lobate (Fig. 15A, C–E, J–N). **Penial sclerite** complex, divided into two distinct units, here referred to for convenience as “anterior” and “posterior penial sclerites”: (1) anterior penial sclerite consisting of bulb, bearing long needle dorsomedially (Fig. 15A, B, G–I, M–O); (1a) needle extending deep into abdomen before curving posteriorly and inserting through horn-shaped posterior penial sclerite (not figured in full extent); (1b) anterior penial sclerite with three apodemes, (1ba) first apodemes bearing origin of anterior pair of pumping muscles, (1bb) second apodemes bearing insertions of anterior pair of pumping muscles, and (1bc) third apodemes bearing origins of posterior pair of pumping muscles and a muscle joining the anterior and posterior penial parts (Fig. 15M–O); (1c) third apodemes with posterolateral extensions which end adjacent to cerci (Fig. 15H, I, J, M–O); (2) posterior penial sclerite with single disc- or plate-shaped apodeme nestled anteroventrally between lateropenites, and bearing paired horn-like processes which guide the penial needle (Fig. 15D, E, H, I, M–O).

Musculature (Fig. 1.K2). **Extrinsic coxal muscles. Tergo-coxal** muscle absent; additional intrinsic musculature of tergum IX retained (Fig. 15F). **Sterno-coxal** muscles absent. Intertergal muscle between segments IX and X present, originating near fusion of tergum IX with gonocoxa; this region of tergal-gonocoaxal fusion also bearing origins of intrinsic muscles of tergum X (and presumably XI). **Intrinsic coxal muscles. Coxo-stylar**: both muscles subdivided, with differing mechanical function and most origins shifted onto sternum IX: (1) adductor (**IXAxab**) originating in posteroventral region of sternum IX (Fig. 15J and K); (2) abductor (**IXAxad**) present, originating within both sternum IX and gonocoxa (Fig. 15K). **Coxo-lateropenital**: one muscle (**IXAI**) present, origin shifted into sternum IX where it is situated anteriorly,

insertion shifted partially onto apodeme of ventrolateral gonostylar tine (Fig. 15J and K), thus controlling movement of both elements. **Coxo-penial:** four muscle units present, with all origins shifted onto sternum IX: (1) paired muscle (**IXAppv**) originating on sternal bridge, inserting on second apodeme of anterior penial sclerite (Fig. 15B, G–I, M, N); (2, 3) muscle (**IXAprv**) divided once, resulting in two subunits: (2) (**IXAprv'**) thick, originating broadly on ventromedial sternal surface, inserting on medial surface of second apodeme of anterior penial sclerite (Fig. 15H, I, M, O); (3) (**IXAprv''**) originating ventromedially on sternum, inserting on basal apodeme of posterior penial sclerite (Fig. 15G–I, M–O); (4) dorsal coxopenial muscle (**IXAppd**) originating on dorsolateral sternal surface, inserting on second apodeme of anterior penial sclerite between pumping muscles (**XAp'**) and (**XAp**) (Fig. 15I, M, O). **Penial intrinsic:** penial intrinsic muscle (**XAp**) divided twice resulting in three subunits: (1) (**XAp'**) originating on posterior face of first apodeme of first penial sclerite, inserting on second apodeme (Fig. 15G, H, M–O); (2) (**XAp''**) originating on lateral margin of bulb of first apodeme of first penial sclerite, inserting laterally on second apodeme (Fig. 15H and I M–O); (3) (**XAp'''**) originating on second apodeme of anterior penial sclerite, inserting on basal apodeme of posterior penial sclerite (Fig. 15M, O);

Notes. Examined specimens identified using Alexander (1967). It is here hypothesized, as indicated by the terminology applied in the description above, that: (1) both the “adminiculum” and “semen pump” are derivatives of the penial sclerite(s) observed in other endopterygotan orders; and (2) the lateropenites (“parameres”) of *Tipula* are represented by the small triangular lobes situated between the gonostyli and penial sclerites (Fig. 15D, E, J–N). Previously, Frommer (1963), relying on ontogenetic recapitulation and the phallic-periphallid model, homologized the “anterior aedeagus” or “semen pump” with the endophallus, which is structurally consistent with the first hypothesis above. Contrastingly, Sinclair et al. (2013) — based on Paramonov (2004) — homologized part of the anterior aedeagus with the “paramere” (lateropenite). Musculature of the semen pump and adminiculum observed here is consistent with the origin of both structures from penial sclerites (including the possibility of endophallid sclerite). Moreover, skeleto-muscular correspondences are apparent between *Tipula californica* and *B. marci* (Bibionidae) (Table S7). Neither Frommer, Paramonov, nor Sinclair et al. have provided a postulate for the sclerotic origin of the “posterior aedeagus” or “adminiculum”, thus it appears that this structure is assumed to have evolved *de novo*.

With respect to the lateropenite, it is first necessary to address the coxo-stylar musculature. Paramonov (2004) interpreted the “outer” and “inner gonostyli” (*sensu* Ribeiro, 2006) variably across the Tipulidae, in some cases referring to one or the other as the “gonostylus”, “lobe of the gonocoxa”, or the “gonocoxa” itself; these applications are inconsistent with the musculature he observed, as the structures always bear the insertions of his M27 and M33¹, homologized here with (**IXAxad**) and (**IXAxab**), respectively (Table S7). With the stylar and penial musculature accounted for, the weak musculature of the small triangular lobes indicates correspondence with lateropenites. To compare this study to Paramonov (2004) the following synonyms are listed: first apodemes of anterior penial part = “lateral processes of semen pump”; second apodemes = “ejaculatory apodeme of semen pump”; third apodemes = “distal process of semen pump”.

Comments. The almost complete replacement of the gonocoxa by the sternum is as remarkable as the dorsal migration of the gonocoxae in the Neuroptera. Tipulid taxa with intermediate states of this replacement should be evaluated for the relative positions of the intrinsic coxal muscles: Do they remain relatively stable in position and orientation while the sclerites change proportions beneath them after the sternum and gonocoxae are rigidly fused,

thus maintaining their mechanical structure? Or have the muscles undergone some degree of reorganization, to return — in the presently sampled *Tipula* — to a layout similarly observed across most endopterygotes? The former is suggested by Paramonov's (2004) illustrations, but other forms of documentation are needed.

A simpler genitalic organization was observed in *Bibio* (Bibionidae) by Spangenberg et al. (2012). While *Bibio* also displays a state of fusion between sternum IX and gonocoxae similar to *Tipula*, the associated sclerites are less elaborate. Spangenberg et al. (2012) referred to the sterno-coxal composite simply as the gonopod, and recognized the lateropenites (“parameres”) as a fused plate which is dorsal to the penial sclerite (“penis”) and is ventral to the proctiger (“anal cone” with probable hypoproct, “subapical plate”). Unlike *Tipula*, it appears that the gonocoxae and sternum IX cannot be visually differentiated; therefore, there is some degree of uncertainty about whether muscular origins have shifted from one sclerite to another, or whether the sclerites have shifted beneath their relatively static origins. Correspondences of genitalic muscles observed by Spangenberg et al. (2012) are as follows: *tergo-coxal* : (**IXAtc**:M3+11), *coxo-stylar*: (**IXAxad**:M1; **IXAxab**:M2); *coxo-lateropenital*: (**IXAl**:M9); *coxo-penial*: (**IXAppv**:M7; **IXAprv**:M8; **IXAppd**:M10); *uncertain*: M12 (inter-gonocoxal muscle). These interpretations differ to some degree with respect to the homologies drawn between *Bibio* and the Tipulidae, as presented in table 4 of Spangenberg et al. (2012).

4.7. Amphiesmenoptera

Comments. Kristensen (1984) reviewed the evidence for interpretations of lepidopteran genitalic homologies in the light of anatomical observations of *Agathiphaga* (Agathiphagidae). Kristensen favored the hypothesis that abdominal tergum and sternum IX were ancestrally fused in the Amphiesmenoptera, to be divided secondarily into the “tegumen” and “vinculum”, respectively. Observations made here support this contention. In the Lepidoptera, however, two muscles of coxal origin — **IXAp1** and **IXAppv**, or “mem” and “phr” of Kristensen (1984) — originate on the “segment IX ring” sclerite. This suggests either that the segment IX ring is a composite of a gonocoxal fragment and tergum/sternum IX, or that the muscular origin shifted deep in the past. The coxa and stylus of the lepidopteran gonopod was parsimoniously interpreted as fused ancestrally, with subdivisions corresponding to these regions occurring subsequently in some cases. The “median plate” (or “juxta”) of the Lepidoptera is homologizable with the lateropenites, and likewise for the “parameres” (Nielsen, 1957; Schmid, 1980) of Trichoptera. The groundplan here inferred for the Amphiesmenoptera is presented schematically in Fig. 1L1.

4.7.1. Trichoptera: Limnephilidae, Limnephilinae, Pycnopsyche antica (Walker, 1852)

Note. Examined specimens were identified using Schmid (1980) and Wodjtowicz (1982); the lateropenites have previously been identified as “tillitators” in this genus (Betten, 1950).

Sclerites. Abdomen. Posterolateral margins of abdominal tergum VIII produced as subrectangular lobes (Fig. 16A). **Tergum** and **sternum IX** partially fused (Fig. 16B–D), tergum fused with proctiger, composite sclerite completely encircling anus (Fig. 16B–D), tergum IX bearing posterolateral lobes, similar to tergum VIII; sternum broadly fused with gonocoxae (Fig. 16A, D, E, H). Immobile paired processes (cerci?) situated dorsal to anus (Fig. 16B–D). **Genital appendages.** **Coxae** fused to sternum IX and fused together ventromedially (Fig. 16A, D, E, H). **Stylus** subrectangular, immovably fused to gonocoxa (Fig. 16B–D, H). **Lateropenites** present, in form of long, thin and flexible rods, situated dorsal to penial sclerite within invaginated membranous sheath (Fig. 16I–K). **Penial sclerite** tube-shaped, with thickened basal section, situated ventromedially

between gonocoxae in invaginated membranous sheath along with lateropenites (Fig. 16B, C, F, G, IeK).

Musculature (Fig. 1L1). **Extrinsic coxal muscles.** Muscle of tergal lobe IX attached to abdominal tergum VIII (Fig. 16F, G, H). Proctiger with strong lateral muscle connecting to anterior margin of sternum IX. **Tergo-coxal** and **sterno-coxal** muscles absent due to fusion of abdominal sternum IX. **Intrinsic coxal muscles.** **Coxo-stylar** muscles absent. **Coxo-lateropenital** muscles absent. **Coxopenital:** protractors (IXAppd, IXAppv), retractor (IXAprd); (IXAppv) originating ventrally in gonocoxa and directed anterodorsally to insertion on penis (Fig. 16F and G); (IXAprd) originating in gonocoxa, inserting on penial membrane (Fig. 16G); (IXAppd) origin shifted to anterolateral margin of abdominal sternum IX, directed anteroventrally to insertion on penis (Fig. 16F and G). **Penal intrinsic:** one intrinsic muscle present (XAp) originating within base of penial sclerite, inserting on endophallus (Fig. 16K).

Comments. Schmid (1980) referred to the gonopods as the “inferior appendages” of abdominal segment X. Based on the illustrations in Schmid (1980) it appears that the styli are mobile in other trichopteran taxa. The lateropenites of *P. antica* appear to be movable by the penial intrinsic muscle (XAp), as well as the muscles inserting on the penial sclerite base and sheath.

4.7.2. Lepidoptera

Note. Due to technical problems, specific dissections of lepidopteran genitalia are not described, nor are micrographs provided.

Except for recognizing the homology of the “median plate” of Kristensen (1984) with the lateropenites based on skeleto muscular deduction, the lepidopteran groundplan proposed by Kristensen was not here found to require further revision in light of musculature evidence. Kristensen's model has, therefore, been integrated with the observations made here based on dissections of a pantheine noctuid and several unidentified moths. Kristensen (1984) recognized eight groundplan muscles within the genitalia of Lepidoptera, plus nine non-genital muscles (table 1 and Fig. 46 of Kristensen, 1984); these ground plan muscles, and those identified in *Agathiphaga* (Kristensen, 1984), are parenthetically indicated below.

Sclerites. Abdomen. **Tergum IX** and **sternum IX** variably fused. Proctiger variable, borne on abdominal tergum IX, may be produced, narrow, and down-curved. **Genital appendages.** **Coxae** free or fused with tergal region of abdominal segment IX sclerite. **Stylos** fused with gonocoxa. **Lateropenites** fused ventromedially, forming vase- or ring-like structure which may be closely associated with gonopods or tergum IX. **Penial sclerite** forming tube.

Musculature (Fig. 1L2). **Extrinsic coxal muscles.** **Tergo-coxal** muscle (IXAtc: god:M8) present, originating dorsolaterally on segment IX sclerite, inserting on anterodorsal region of gonocoxa. **Sterno-coxal:** medial and lateral muscles (IXAsc:gov:M3) present, originating ventrally on segment IX sclerite, inserting on anterior and anteroventral margins of gonocoxae or “subgenital crypt”. **Intrinsic coxal muscles.** **Coxo-stylar:** absent (not recorded in

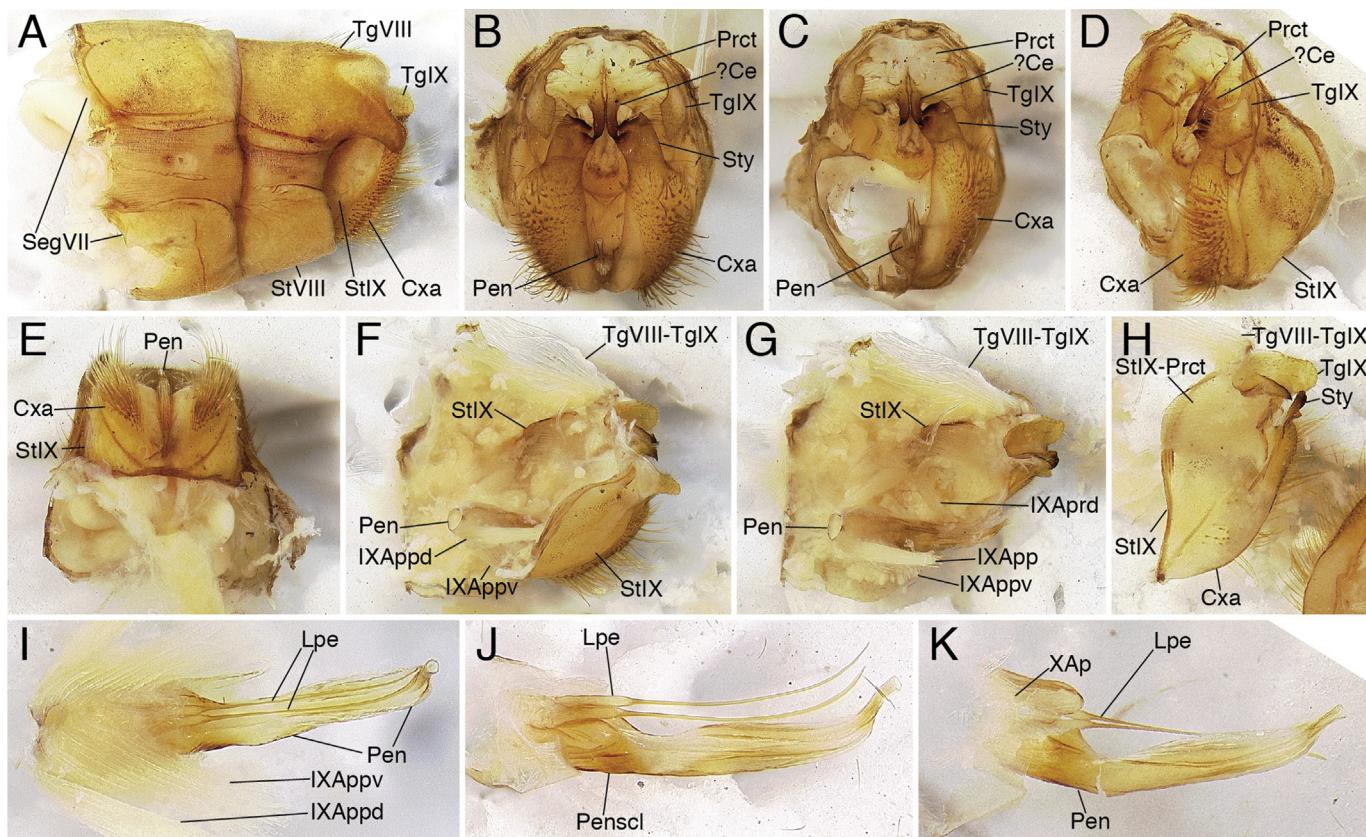


Fig. 16. Genital skeleto-musculature of *Pycnopsyche antica* (Trichoptera: Limnephilidae). **A**, genital and pregenital segments, lateral. **B**, genital and postgenital segments, posterior. **C**, same as **B**, left coxopod removed. **D**, same as **C**, lateral oblique. **E**, genital and postgenital segments, ventral. **F**, genital appendages, dorsolateral oblique. **G**, same as **F**, left gonopod removed. **H**, right gonopod and piece of postgenital complex, muscles removed, mesal (medial). **I–K**, penial sclerite and lateropenites: **I**, dorsolateral; **J**, dorsolateral, sheath membrane removed; **K**, ventrolateral, base of penial sclerite torn open. **Abbreviations:** ?Ce = structures possibly homologous with cerci; Cxa = gonocoxa; Lpe = lateropenite; Pen = penis or penial sclerite; Prct = proctiger; Seg = segment; St = sternum; Sty = gonostylus; Tg = tergum. **Muscle abbreviations** indicated in Table 1. **Note:** Segment numbers indicated with Roman numerals; addition signs indicate sclerite fusion.

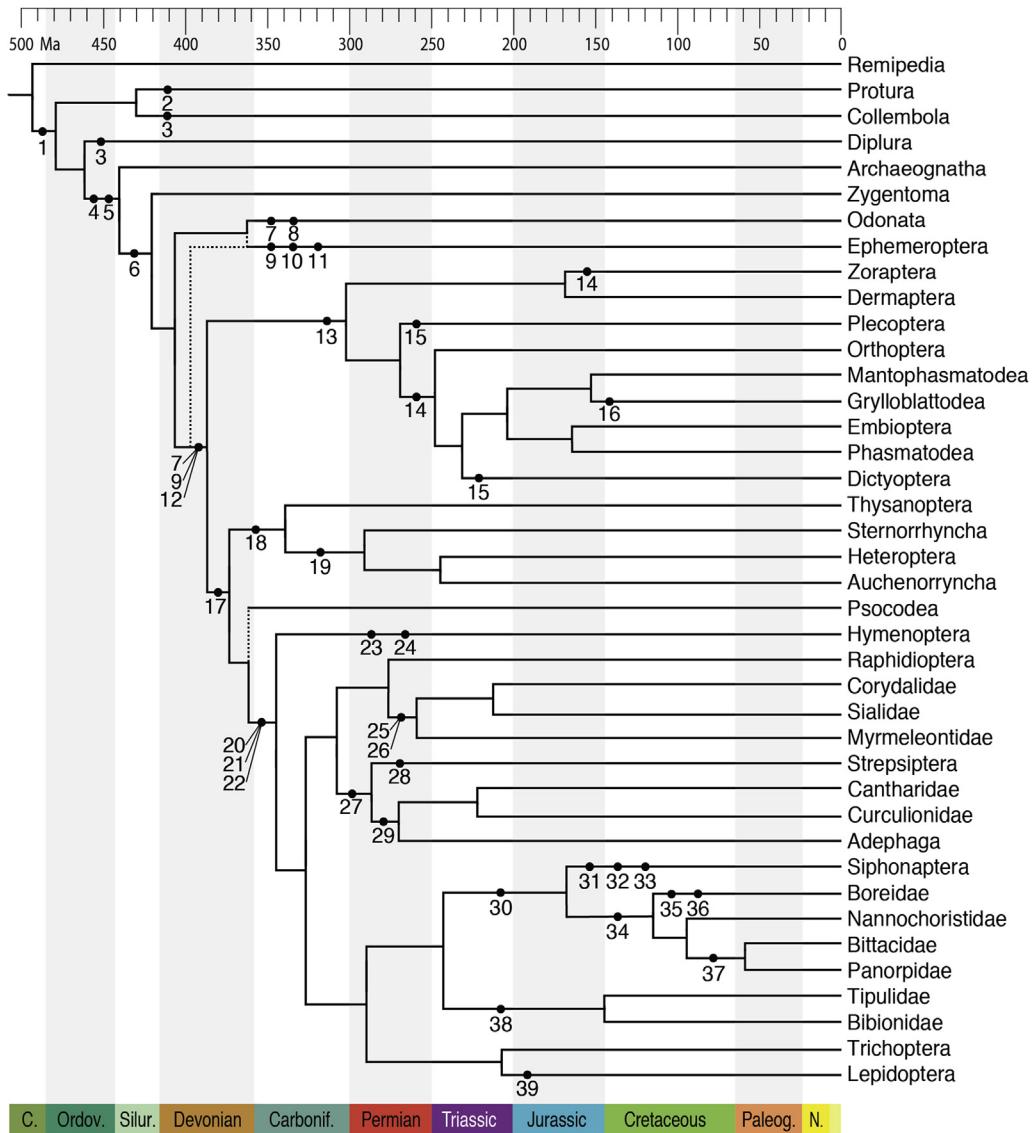


Fig. 17. Key skeleto-muscular morphological apomorphies of genitalia here inferred, mapped on the phylogenetic chronogram of the Hexapoda pruned to the specific terminals compared in the present study (tree modified from Misof et al., 2014). Bayesian analysis may provide estimates of rate and timing of inferred transformations. **1.** Hexapoda: male gonopore(s) situated on a lateromedially-undifferentiated gonopod (the penis). **2.** Protura: male gonopores situated on distal (second) endopodal segment. **3.** Collembola, Diplura: penes independently reduced to papillae. **4.** Ectognatha: male and female genitalia derived from appendages (primary and secondary gonopods) of two successive segments. **5.** Ectognatha: male phallic complex reduced to single, simple structure (the penis), modified from gonopores of abdominal segment X. **6.** Dicondyla: dorsoventral penial extrinsic muscle lost. **7.** Gonapophyses (endopods of coxopods IX) probably lost once in the Odonatoptera (along stem to Odonata) and once or twice in the Chiastomyaria. **8.** Odonata: plesiomorphic condition of gamete transfer via spermatophore retained, although the latter is deposited in the autapomorphic secondary genitalia. **9.** Ephemeroptera, Neoptera: sperm directly deposited in the female via intromission of the penis. **10.** Ephemeroptera: gonopods derive multiannulate styli. **11.** Ephemeroptera: penis laterally articulated with tergum IX, bearing derived tergal musculature. **12.** Neoptera: sternopenal muscle duplicated, resulting in novel penial promotor. **13.** Polyneoptera: secondary gonopods (coxopods IX) not incorporated into penial ("phallic") complex, being rather (usually) undifferentiated from sternum IX. **14.** Two independent lines of increasing complexity and disparity observed in the penial complex of Polyneoptera, once for the Zoraptera, the other for the Orthopterida (i.e., core Polyneoptera). **15.** Two independent lines of penial complex simplification observed in Polyneoptera, once for the Plecoptera, the other for the Dictyoptera (namely, reduction observed in Isoptera). **16.** Grylloblattodea: coxopods IX secondarily differentiated from sternum IX. **17.** Eumetabola: gonostyli strengthened for clasping, bearing differentiated abductor and adductor muscles. **18.** Condylognatha: dorsal extrinsic penial muscle gained. **19.** Hemiptera: gonopods undifferentiated from fused tergum and sternum IX, forming pygophore; pygophore also bearing origins of the penial extrinsic muscles. **20.** Endopterygota: penis completely integrated with gonopods developmentally and gonopods, as in Hemiptera, bear the origins of the penial extrinsic muscles. **21.** Endopterygota: penial musculature is duplicated dorsoventrally, resulting in greater functional potential of copulatory apparatus (penial-gonopodal complex). **22.** Endopterygota: lateropenite ("parandrite" or "paramere" sensu Verhoeff) uniquely derived from penial sclerite (skeletomusculature of Psocodea in need of renewed study). **23.** Hymenoptera: origin of cupula (= "basal ring"), which controls overall motion of gonopods. **24.** Hymenoptera: parossculus derived from ventromedial gonocoxa, forming volsellar complex with lateropenite ("digitus"). **25.** Sialida (sensu Bodreaux, 1979 modified from Handlirsch, 1908): gonocoxae migrated dorsally, fusing with tergum IX over the penis. **26.** Sialida: external gonopore dissociated from the penial sclerites (probably in correlation with female loss of ovipositor). **27.** Coleopterida: lateropenite lost. **28.** Strepsiptera: genitalia reduced, with only a penis (or coxopenis) expressed. **29.** Coleoptera: ancestral gonocoxa divided into two parts: the first or anterior gonocoxites ("phallobase") bearing the insertions of the extrinsic gonopodal musculature, the second or posterior gonocoxites incorporated to completely integrated with the penis (forming "coxopenis"); gonostyli variably associated with phallobase. **30.** Euantliophora: genitalic complexity increases to extreme degree, extant taxa inheriting an autapomorphic *aedeagal apodeme* (present in Siphonaptera and Nannochoristidae). **31.** Siphonaptera: gonopodites, bearing styli, fused with tergo-proctiger complex. **32.** Siphonaptera: sternum IX with lateral elongate arms. **33.** Siphonaptera: sperm-pumping complex significantly modified. **34.** Mecoptera: sperm-pumping complex with *mittelplatte* (note uncertainty of homology for boreid penial sclerites). **35.** Boreidae: sperm-pumping complex reduced, most sclerites lost. **36.** Boreidae: spermatophore regained. **37.** Pistillifera: *pistillträger* derived in sperm-pumping complex. **38.** Diptera: partial to complete integration of sternum IX with gonopods; increasing genitalic complexity observed. **39.** Amphiesmenoptera with relatively unmodified genitalia, although Lepidoptera with lateromedially fused lateropenites ("median plate") and enlarged and unmusculated gonostylus.

Kristensen, 1984). **Coxo-lateropenital:** muscles lacking or with a pair of muscles (**IXAlm:gom**; **IXAlp:mem**) originating on ventro-medial region of gonocoxae and inserting broadly within lateropenital structure. **Coxo-penial:** depressor/protractor (**IXAprv:php:M5**) and levator/retractor (**IXAprv:phr:M4**), originating in coxae or sternal region IX and inserting on penial sclerite. **Penial intrinsic** muscles may be present (= *adr*, *pht*, M6, 7).

Comments. Kristensen (1984) considered the penial protractor and retractor muscles (*php*, *phr*) as originating on the segment IX sclerite. Regarding the protractor, Kristensen remarked “it is very noteworthy that this muscle consistently originates in the gonopod in the lowest moths and this trait can therefore be ascribed to the ground plan of the Lepidoptera ... it is an autapomorphy of the order.” Based on the skeletomuscular correspondences observed in the present study, origin of the protractor in the gonocoxa could be plesiomorphic, and the origin of the retractor on segment IX sclerite may be an autapomorphy of the Amphiesmenoptera. It is here inferred that *m. protractor penialis ventralis* (= *m. penialis anteroventralis*) split, with the origin of the posterior subunit shifting drastically posterior into the gonopod resulting in a gain of a penial promotor muscle.

5. Conclusion

“There is nothing in taxonomic biology so hard to eradicate as a dead idea embalmed in a traditional nomenclature.” — Snodgrass (1957, p. 1).

5.1. Summary

The consistency of correspondence between the origins and insertions observed for the extrinsic and intrinsic musculature observed across the Hexapoda fail to support the multi-coxopod and ontogenetic hypotheses for the origin of male genitalia. It is here concluded that the male genitalia of insects are derived from reduced primary gonopods of the pancrustacean ancestor (single coxopod hypotheses), with incorporation of the preceding coxopods in the Ectognatha (penis-coxopod hypothesis), these forming the secondary gonopods which demonstrate significant variation across the Pterygota. With rejection of Snodgrass's ontogenetic hypothesis, it is consequently necessary to disabuse ourselves of the assumptions of the phallic-periphalllic nomenclatural model, including the term “paramere”. The muscular terminology employed in the present work is generalized based on categorical correspondences of origins and insertions, supported by comparisons across the Hexapoda, and a new vision of abdominal evolution is provided. A brief, general glossary of non-muscular terms for hexapod genitalia is provided in Appendix A.

In addition to the plesiomorphic retention of biramous trunk limbs in the abdomen of the apterygote hexapods and in the male and female genitalia of the Ectognatha, 39 morphological features here inferred to be apomorphic are summarized in Fig. 17. An evolutionary evaluation of the apterygote Ectognatha is provided above in section 3.1.4.3. From the groundplans inferred throughout the extant diversity of hexapodans, there are numerous paths to improving our understanding, including resolution of skeletomuscular correspondences of the “phallomeres” of Polyneoptera, inference of pattern and diversity in the Condylgnatha, phylogenetically-informed comparisons in the megadiverse Coleoptera, and revised study of the Psocodea given its putative sister relationship with the Endopterygota. Further gross and molecular studies — phylogenetic or developmental — are expected to provide rich insight, particularly with expanded ingroup sampling in the context of the Pancrustacea. Focus on non-muscular systems, such as endoskeleton, connective tissue, and innervation, will flesh out our understanding of genital

homologies, so to speak. Meaningful evolutionary context will be generated with functional morphological study of the skeletomuscular patterns of the abdomen and genitalia.

5.2. Coda

One of the basic objectives of comparative morphology in the 21st century — the era of “post-molecular systematics” (Pyron, 2015) — is the documentation of functional and developmental modifications of anatomy, whether at a gross-scale as observed herein, or at the molecular-level as practiced in the “evo-devo” school. Spanning the traditional (e.g., Huxley, 1878) to ultramodern (Friedrich et al., 2014), this documentation provides fundamental data for the process and mechanisms of morphogenesis and transformation across evolutionary timespans. Using phylogenetic methodology (e.g., Felsenstein, 1985, 2012; Lewis, 2001; O'Reilly et al., 2018), data from extant taxa generated via evolutionary morphological study (Wirkner and Richter, 2010; Richter and Wirkner, 2014) may be integrated with qualitative or quantitative observations of fossils (e.g., Ronquist et al., 2012) to make estimates of the tempo and mode of evolution (e.g., Lee et al., 2013; Klopstein et al., 2015) and to test hypotheses of homology (e.g., Hejnol and Lowe, 2015). The process of generating these phenotypic data from observations is greatly facilitated by ontologies (e.g., Yoder et al., 2010; HAO, 2016; Wirkner et al., 2017). Ontologies may further be useful for training a machine-learning program (e.g., Jones, 2014; Maxmen, 2017, others) to generate data from three-dimensional µ-CT models (e.g., Büsse et al., 2016; Polilov, 2011, 2015; see also Beutel et al., 2014, chapter 4). Beyond improving visual communication of morphological observations (e.g., Hendricks et al., 2018a, b), integration of the methodologies addressed above may allow us to critically watch as we replay life's tape in three dimensions.

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Appendix A. A brief, general glossary for the genitalia of Hexapoda

This appendix is intended as a pragmatic tool for the diagnosis and labeling of anatomical parts of the genitalia and associated structures for the Hexapoda. Each definition is made using the Aristotelian *genus differentia* formula employed by formal ontologies: “A” (specific class) is a “B” (general class) that/which “Cs” (differentiating features). Here, the *genus differentia* is formatted as “A. B that Cs.”. A minimum number of terms for elucidating the main text are supplied in this brief, general glossary.

For definition of taxon-specific genital sclerite terminology refer to Fig. 1 and the main text, and for muscle class definitions see Table 2. Terms specific to the female genitalia are excluded, as are terms from Snodgrass's phallic-periphallid model, including "aedeagus", "paramere", "harpe", and "harpago", due to their varied anatomical circumferences and epistemological foundation. Sources of terms are indicated in the main text; HAO refers to the Hymenoptera Anatomy Ontology; "purl" indicates an online permanent uniform resource identifier (URI).

Abdomen (= *pleon*). The region of the trunk that is functionally differentiated from and articulated to the posterior end of the thorax.

Anal somite (= *telson*). The segment that is posteriomost on the body.

Appendage. The integumentary evagination that is connected to the body via muscles. (Definition modified from purl HAO_0000144.)

Appendage segment. The anatomical structure that is part of the appendage, is metamerid, is connected to other metamerid subdivisions by muscles, and is delimited by sclerite. (Definition modified from purl HAO_0000145.)

Biramous appendage. The appendage that is branched distal to the coxopod.

Cercus. The appendage that is unsegmented, paired, and articulated to the postabdomen.

Coxa (= *basis* [carcinological sense]). The jointed part of the protopod that articulates with the ramus.

Coxopod. The appendage that is located on a postthoracic segment.

Endopod. The ramus of a biramous appendage that is located medially.

Eversible vesicle. The limb that is fleshy and invaginates via muscular contraction.

Exopod. The ramus of a biramous appendage that is located laterally.

Extrinsic muscle. The muscle that originates in one segment or anatomical complex and inserts in another.

Genitalia. The anatomical system that is involved in copulation, fertilization, and/or oviposition.

Genital chamber. The invagination of the trunk that accommodates the phallic apparatus.

Genital segment. The segment of the trunk that bears articulation with the gonopod or is connected by muscle to the gonopod.

Gonocoxa. The protopod that is part of the gonopod.

Gonocoxite. The sclerite that is part of the gonopod.

Gonopod. The appendage that is associated with gamete transfer or oviposition.

Gonapophysis. The ramus that is unisegmental, unsclerotized, and which corresponds in location with eversible vesicles, endopods.

Gonopore (= *phallotreme*). The genital duct opening that is distal to the testis or ovary. Used here in the broad sense.

Gonostylus. The stylus that is located on the gonopod.

Insertion. The area of muscle attachment that is on a relatively mobile structure.

Intrinsic muscle. A muscle that originates and inserts within a segment or anatomical complex.

Lateropenite (= *parandrite*). The sclerite that is lateral to the penis, medial to the secondary gonopod, and receives the insertion of muscle connected to the secondary gonopod.

Limb. The part of an appendage that is articulated proximally to an appendage segment.

Median caudal filament. The appendage that is unsegmented, unpaired, and articulated to the anal somite posterodorsally.

Origin. The area of muscle attachment that is on a relatively fixed structure.

Parandrite. See Lateropenite.

Penis. The primary gonopod that accommodates the vas deferens and the gonopore.

Penial sclerite (= *phallomere*). The sclerite that is part of the penis.

Phallic apparatus (= *genital complex*). The anatomical complex of sclerite and muscle that comprise the male genitalia.

Phallomere. See Penial sclerite.

Phallotreme. See Gonopore.

Postabdomen. The region of the abdomen that is posterior to the genitalia. The term *proctiger* is used in the present work in a broad sense which is approximately equal to postabdomen as here defined.

Posttrunk. The tagma of the body that is always limbless, is articulated to the posterior end of the trunk, and is posterior to expression of the *Hox* gene *Abd-B*.

Preabdomen. The region of the abdomen that is anterior to the genitalia.

Primary gonopod. The gonopod that accommodates the genital duct and bears the gonopore.

Proctiger. See Postabdomen.

Protopod (= *protopodite, coxopodite*). The coxopod segment that articulates with the body, which bears the insertions of muscles originating within the body, and which comprises the subcoxa and coxa.

Ramus. The limb of an appendage that is distal to the coxopod.

Secondary gonopod. The gonopod that does not accommodate the genital duct and gonopore.

Stylus. The ramus that is unisegmental and sclerotized.

Subcoxa (= *coxa* [carcinological sense]). The jointed part of the protopod that is most proximal and articulates distally with the coxa.

Thorax. The region of trunk that is functionally differentiated from the abdomen, and is articulated to the posterior end of the head and the anterior end of the abdomen.

Trunk. The tagma of the body that attaches to the head at its posterior end and bears limbs. The trunk is functionally differentiated into the thorax and abdomen, and differs from the posttrunk in *Hox* gene expression and by the state of bearing limbs.

Vas deferens. The genital duct that is connected to the testis.

Appendix B. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.asd.2018.11.001>.

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