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The exoskeleton of the male genitalic region in Archaeognatha, with hypotheses on the early evolution and the morphological interpretation of genitalia in insects

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Abstract. The ventral exoskeleton of abdominal segments 7–9, including the phallic organs (belonging to segment 9 or 10), is described for five archaeognathan species: *Machilis hrabei* and *Lepismachilis notata* (Machilidae-Machilinae), *Pedetontus unimaculatus* (Machilidae-Petrobiinae), *Petrobiellus takunagae* (Machilidae-Petrobiellinae), and *Machilinus* sp. (Meinertellidae). In the focus are the segmental patterns of sclerites and formative elements, and fine structures of the cuticular surface. The results are compared with earlier descriptions of these body parts in Archaeognatha. Hypotheses of homonomy (transsegmental and male-female) and homology at the level of Ectognatha (= Insecta) are proposed and insect-wide terminologies applied. Morphological interpretations are revised, if required, with a focus on the segmental assignment and other aspects of the male genital opening and phallic organs. A data matrix of 39 male genitalic characters is composed as a source of information for subsequent phylogenetic and taxonomic work on Archaeognatha. Some discussions on character evolution are given; few apomorphies agree with previous molecular results of a clade Petrobiellinae + Meinertellidae, but phylogenetic conclusions remain limited due to poor data for outgroup comparison (mainly for Zygentoma). We compare and discuss the occurrence of genitalic specialities (= structural differences compared to pregenital segments) on segments 7–9 in both sexes. The new data shows that male Archaeognatha exhibit many genitalic specialities on segment 9 and few on segment 8, whereas females show many on segments 9 and 8 and on the posterior part of segment 7; the male specialities are largely a subset of the female ones, except for structures categorised as phallic in the male being largely absent in the female (with possible exceptions). Based mainly on the genitalic specialities common to both sexes, we discuss two discrete scenarios for the early sex-shared evolution of the genitalic region in stem-Insecta: (1) The 'aquaeductal hypothesis' proposes that water-uptake from crevices was the initial driving force of structural specialities that today mainly serve for genitalic functions. (2) The 'sensorial hypothesis' proposes that improving the sensorial exploration of the substrate was the driving force.

Key words. Genitalia, penis, phallic organs, gonapophysis, paramere, morphology, homology, evolution, taxonomy, SEM.

1. Introduction

In Insecta (= Archaeognatha + Zygentoma + Pterygota) the males bear external genitalia, i.e. the phallic organs, on the ventral side of the posterior part of the abdomen. Together with the genital opening upon or close to them, the genitalia either belong to abdominal segment 9 or 10, being either derivatives of (parts of) the 9th- or 10th-segmental limbs or formations independent of limbs. Hypotheses on the morphological interpretation of the phallic organs are highly diverse, with many questionable arguments but also conflicting evidence (e.g. Snodgrass 1936, 1957; Becker 1966: p. 264; Bitsch 1974b: p. 218; Birket-Smith 1974; Rohdendorf & Rasnitsyn 1980: p. 22; see Appendix chapter 8 for a preliminary discussion). The phallic organs range from being very simple (e.g. Embioptera: Ross 2000) to highly complicated (e.g. Dictyoptera: Klass 1997) in their structure. Complicated structuring includes the presence of many sclerites, many formative elements (such as processes, apodemes, and ridges), and a rich musculature. The symmetry of the phallic organs ranges from fully bilateral (e.g. many Orthoptera: Snodgrass 1937) to asymmetrical in a way that the homonomy of elements of the two sides has re-

mained obscure (e.g. Dictyoptera: Klass 1997; Phasmatodea: Helm et al. 2011). The ontogenetic development of the phallic organs (e.g. Snodgrass 1936, 1957; Matsuda 1976 and references therein) starts with a pair of primary phallic lobes. These either fuse medially to form an unpaired penis (Archaeognatha, Zygentoma); or each forms one penis of a pair (Ephemeroptera); or each lobe divides (typial for Neoptera), usually in a mesal mesomere and a lateral paramere, and the two mesomeres often fuse to form a median aedeagus. The phallic organs as such are likely – though not with certainty – homologous across the Insecta, but their morphology is so diverse that the homology of their elements in different order-level taxa is widely unknown (see Snodgrass 1957). This is especially evident when comparing taxa with highly complicated phallic organs, such as Dictyoptera and Phasmatodea (see Klass 1997 and Helm et al. 2011, respectively). Homologies may even partly not exist, as both the structural complexity and the asymmetry could well have been acquired independently in different major lineages. The starting point of phallic evolution in insects may have resembled the simple, more or less cylindrical median penes of Archaeognatha (Bitsch 1974b) and Zygentoma (Birket-Smith 1974), but there are competing hypotheses of paired penes like those of Ephemeroptera being ancestral (e.g. Snodgrass 1936). The females seem to consistently lack projections potentially homonomous with the phallic organs (e.g. Bitsch 1974a,b for Archaeognatha). However, whether females possess projecting or non-projecting elements isosegmentally homonomous with particular phallic elements depends strongly on the morphological interpretation of the male phallic organs and other postabdominal structures of both sexes, which is widely unclarified.

Many of the non-phallic parts of the posterior abdomen of male insects can show differentiations more or less strongly involved in genitalic functions. Most usually the ventral side of abdominal segment 9 (= venter 9) shows differentiations correlated with the placement of the phallic organs on or immediately behind it. This mainly concerns an elongation of its limb vestiges (coxal lobes) and often their median fusion to form a subgenital lobe (the likewise fused coxal sclerotisations forming a subgenital plate), thus providing a cavity (genital chamber) where the phallic organs are harboured. In addition, further parts of venter 9 and even parts of dorsum 9 can be modified, and a various number of the preceding segments as well as the two following segments (10, 11) can also show differentiations related to genitalic functions (e.g. Ross 2000 for Embioptera; Zwick 1980 for Plecoptera). The ventral and laterodorsal parts of the abdomen that show genitalic differentiations can be informally comprised as the 'male genitalic region'. Archaeognatha males show extra-phallic genitalic specialities on venter 9 and to a lower extent on venter 8 ('specialities' meaning structural differences compared to the preceding mid-abdominal segments), and some of these resemble genitalic specialities of the females (Bitsch 1974a,b). Examples of sex-shared specialities are the elongate condition of the coxal lobes on venter 9 and the presence on venters 8 and 9 of long, sclerotised gonapophyses (often called 'parameres' in the males) instead of coxal vesicles (Bitsch 1994). In the males, both pairs of gonapophyses can be present or absent; those of venter 9 are, if present, intimately associated with the penis.

Archaeognatha is most likely the sister group of the remaining Insecta, the Dicondylia, which comprise Zygentoma and Pterygota (e.g. Beutel & Gorb 2006; Kjer et al. 2006; Klass 2009; Misof et al. 2014). Therefore, the morphology of the male genitalic region in Archaeognatha is important for conclusions on the early evolution of this body part in Insecta and for the use of it as a character system for phylogenetic work. In addition, among the insects with well differentiated male and female genitalic regions, the archaeognathans are the ones where male and female genitalic morphologies as well as the morphologies of genitalic and pregenitalic abdominal segments are most similar, with the homonomies between sexes and among segments being largely resolved (Bitsch 1974a,b). The abdominal morphology of Archaeognatha is thus also of great significance in tracing the origin of insect genitalia *under consideration of both sexes*. This matter was never analysed in detail.

The numerous illustrations of archaeognathan male genitalia in taxonomic contributions are mostly sketches focused on the shape and surface structures (e.g. setation) of the projecting parts: coxal lobes, penis, and gonapophyses (e.g. Sturm & Machida 2001: figs. 4.3., 8.26, 8.27; Bach de Roca et al. 2013). Contributions considering the other exoskeletal parts of the male genitalic region are scarce. Most of them only treat selected parts (Smith 1969, 1970) or are very sketchy (Snodgrass 1935, 1936). Gustafson (1950) studied several archaeognathan species in order to conclude on the origin of insect genitalia, but his work lacks detailed descriptions and illustrations. Matsuda's (1957) investigation of the archaeognathan *Neomachilis halophila* Silvestri, 1911 is focused on the abdominal musculature; he only provides a brief textual description and diagrammatic drawings of the male genitalic exoskeleton. Becker (1966) conducted comparative studies of adult and developing female and male morphologies of several apterygote hexapods, including the archaeognathans *Praemachiloides* and *Mesomachilis*. His interest is focused on revealing homologous regions of the exoskeleton via the musculature, but the ligamentous endoskeletal elements are poorly considered.

However, there are two outstanding morphological treatments of the entire abdomen of Archaeognatha, considering both sexes: Bitsch (1973, 1974a,b) and Birket-Smith (1974). Bitsch (1974b) provides a detailed documentation of the exoskeleton, ligamentous endoskeleton, and musculature of the male genitalic region focally of *Machilis* species. The musculature revealed to be important for tracing transsegmental homonomies of sclerites. Regarding the exoskeleton, there is a clear distinction between various ventral sclerites; yet the illustrations are quite sketchy, leaving many structural details open. Birket-Smith (1974) provides very detailed data on

the musculature, ligamentous endoskeleton, and nerve topography of *Petrobius lohmanderi* Agrell, 1944. In contrast, the configuration of sclerites and formative elements is mostly not clearly illustrated; in particular, there is no consideration of the pattern of ventral sclerotisations, which are altogether comprised as the "sternum". Consequently, the main gap in the knowledge of the male genitalic region of Archaeognatha is the lack of a detailed and coherent description of the exoskeleton in a selection of species from the major subgroups.

The current classification of the ca. 500 extant species of Archaeognatha (Sturm & Machida 2001) distinguishes two families plus three genera not assigned to family, assuming the relationships *Mesomachilis* (*Charimachilis* (*Ditrigoniophthalmus* (Machilidae, Meinertellidae))) (fig. 4.4b therein). However, the origin of the three isolated genera from the most basal dichotomies is very poorly supported (if at all: see Koch 2003). Meinertellidae is overall quite uniform, shows a few (almost) consistently present apomorphies (Sturm & Machida 2001: fig. 4.4b), and is thus supported as a monophyletic taxon. In contrast, the diverse, heterogeneous Machilidae is mainly characterised by obvious plesiomorphies and thus potentially paraphyletic with regard to Meinertellidae. Machilidae is classified in Machilinae, Petrobiinae (both including many genera), and Petrobiellinae (only *Petrobiellus*), following Kaplin (1985). Machilinae is further divided in seven genus groups, and Petrobiinae in four. Most of the characters regularly used in taxonomic work on Archaeognatha vary in an incongruent manner within the subfamilies, genus groups or even genera, showing that there is a high degree of homoplasious character evolution. Ma et al. (2015) presented the so far only molecular-based analyses with a significant archaeognathan taxon sample. Sequences of 13 mitochondrial protein-coding genes were analysed for one meinertellid and machilids from seven genera representing all three subfamilies. The results varied with analytical methods and with full versus reduced datasets (figs. 1, 2 therein): Bayesian Inference yielded clades Machilinae + Petrobiinae and Petrobiellinae + Meinertellidae with high node supports, while Maximum Parsimony and Maximum Likelihood yielded either the same or monophyletic Machilidae (with at most moderate support). All analyses found a clade Machilinae + Petrobiinae, with Machilinae never monophyletic and Petrobiinae variously monophyletic or not. The limited taxon sampling restricts the interpretive power of the topologies found. In sum, Koch's (2003: fig. 1C) representation of our knowledge of archaeognathan phylogeny as a rich basal polytomy giving rise to a meinertellid tree is still up to date.

The morphology-based classification of Archaeognatha suffers from (1) the focus on easily visible characters that are useful for taxonomic purposes but mostly show a high degree of homoplasy; (2) the mixed foundation of taxa by apomorphic and plesiomorphic features; and (3) the absence of both coherent studies of character systems and comprehensive phylogenetic analyses of morphological data sets. Among others, genitalic structures of both sexes were traditionally considered as important for Archaeognatha systematics, but the exposed parts so far in the focus of the considerations (penis, gonapophyses, coxal lobes) are quite variable at most taxonomic levels down to genera (Sturm & Machida 2001). To what extent the remaining genitalic parts could be useful for taxonomic and phylogenetic work remains to be examined based on datasets yet to be established. A great relevance of the genitalic region to Archaeognatha systematics would conform with the situation in many other insect orders, where detailed studies of the genitalia of both sexes have greatly improved morphology-based systematics (e.g. in Blattodea, see McKittrick 1964 and Klass 1997).

We present here a comparative study of the exoskeleton of the male abdominal venters 7–9 and the phallic region in five species of Archaeognatha representing all families and subfamilies, thus providing a coherent study of a character system that could be highly relevant for the systematics of both Archaeognatha and Insecta. Via SEM micrographs we also show numerous details of the cuticular surface for the first time. This work has four major goals: First, based on the comparison of the male genitalic region in the study taxa, we derive a list of characters and a character matrix, which can be used as a basis for forthcoming phylogenetic work on Archaeognatha (with increased taxon samples) and as a guideline for the use of this body part in taxonomic work. Second, we use the data from the studied males to search for functional-morphological correlations between genitalic morphology and male reproductive behaviour (production of sperm threads or spermatophore, or copulation). Third, we compare venters 7–9 of the male with the same body part of the female (where these three venters form the genitalic region; based on Klass & Matushkina 2012) and analyse the distribution of structural specialities compared to pregenital venters in the two sexes (also considering interspecific differences with regard to males). Fourth, in context with the latter comparison between sexes and under inclusion of relevant data from the literature, we derive and discuss two discrete hypotheses on the origin and early evolution of genitalia in insects, including many functional considerations. For having a sound frame for our morphological comparisons and functional hypotheses, we additionally discuss the segmental assignment and morphological interpretation of the phallic organs and gonopores in insects, including comparison with Diplura (in an Appendix: chapter 8) – as far as this is possible with currently available data.

2. Material and methods

Specimens. Four adult males of *Lepismachilis notata* Stach, 1919 (Machilidae: Machilinae), collected by NM (05 July 2007; near Kaniv Nature Reserve, 49°43′29″N 31°31′55″E, Ukraine), identified by Carmen Bach. Three adult males of *Machilis hrabei* Kratochvil, 1945

(Machilidae: Machilinae), collected by Nikolaus Szucsich (09 September 2009; Leopoldsberg, Nasenweg, 48°16′36–40″N 16°21′00–05″E, 315–335 m a.s.l., Wien, Austria). Two adult males of *Pedetontus unimaculatus* Machida, 1980 (Machilidae: Petrobiinae) and two adult males of *Petrobiellus takunagae* Silvestri, 1943 (Machilidae: Petrobiellinae), collected by Yasutaka Nakagaki and provided by Ryuichiro Machida (22 June 2005; Shiroyama, Shimoda, Shizuoka Prefecture, Japan). Three adult males of *Machilinus* sp. (Meinertellidae), collected by Alex Gumovsky (01 June 2008; nr. Muğla, "waterfall-valley", Turkey), identified by Luis Mendes. All samples were preserved in 70–80% ethanol.

Preparation, dissection and light microscopy. The posterior abdomen was cut off through segment 5. Observations were first made on this unmacerated postabdomen. Then the postabdomen was macerated for 10–12 h at room temperature with proteinase solution (proteinase K : ATL tissue lysis buffer = 1 : 9). The macerated preparations were thoroughly washed in distilled water, and then examined in 70% ethanol under a stereo-microscope and gradually dissected into smaller pieces. All cuticular parts were examined both from inside and outside, using different angles of incident light as well as transmitted light. Many parts were manipulated with forceps to examine their flexibility and moveability and to localise sclerite borders.

Scanning electron microscopy. Various parts of the macerated postabdomina were cut out, dehydrated in a graded ethanol series and acetone, and critical-point dried (OM CPD 7501). Scales were removed from dried preparations by cautiously stroking the integument with a pin. Then preparations were mounted on holders, sputtered with gold-palladium (OM-SC7640), and examined with a Zeiss EVO-50 SEM.

3. Terminologies and abbreviations

Elements of the male abdomen of Archaeognatha are similar to those of the female abdomen (described in Klass & Matushkina 2012); this also applies to many parts of the genitalic regions (Bitsch 1974a,b). We thus name the male elements according to the female-focused terminology developed by K.-D. Klass and coworkers, and supplement names for male-specific elements according to the same terminological principles (see Klass 2003, 2008 for essentials and Klass & Ulbricht 2009, Matushkina & Klass 2011, Klass et al. 2012, Klass & Matushkina 2012, and Schneider & Klass 2013 for further details and background information on the terminology and inherent interpretations). This terminology is largely based on conditions reported for various archaeognathans by Bitsch (1973, 1974a,b) and is widely congruent with Bitsch's terminology. Apart from full names for structures, the terminology comprises a system of standardised abbreviations, which are also used in the text (in boldface).

This study considers two kinds of exoskeletal elements: **(1)** Sclerotisations: Full names can traditionally either end in -ite (e.g. coxite, tergite) or in -a/-um (e.g. coxa, tergum). Terms ending in -ite are only used when the addressed sclerotisation forms a discrete and undivided sclerite (used herein when emphasis is put on this aspect), while terms ending in -a/-um are also applicable when the addressed sclerotisation is fused with another or is subdivided. Abbreviations are composed of two uppercase letters (e.g. **ST**, **CX**, **GP**); subdivisions are specified by a lowercase letter in the third position (e.g. **STt**, **STi**). **(2)** Formative elements: These comprise all in- and evaginations of the cuticle (or body wall) and distinct thickenings of the cuticle, such as processes, pouches, apodemes, tendons, and ridges. Abbreviations are composed of 2–4 lowercase letters (e.g. **cx**, **gp**, **mvh**; these abbreviations were previously limited to 2 lowercase letters, which proved to be too restrictive). The same 2-letter combinations are often used for sclerotisations and formative elements that are approximately co-extensive or otherwise closely associated (e.g. **gp** for the gonapophysis and **GP** for its sclerotisation(s)).

Both the terms for sclerotisations and formative elements can have a number in the last position, which specifies the abdominal segment to which the element belongs (e.g. **STt7**, **CX7**, **cx8**). Segmental assignment of structures consistently refers to position relative to the primary segmental borders (i.e. to the embryonic segmentation and intersegmental grooves). Accordingly, "intersegmental" refers to a position upon such a segmental border, in contrast to the frequent use of this term for membranes spanning between sclerites establishing secondary segmentation. Structures upon the segmental border (e.g. putative parts of antecostae) are formally assigned to the segment following posteriorly (e.g. antecosta **ac8** is a structure of the border between abdominal segments 7 and 8).

The use of identical terms for elements of different abdominal segments (then with different numbers in the last position), of different sexes, or of different taxa represents the hypothesis of these elements being homonomous or homologous, respectively. In doubtful cases, "?" is added to the term.

Our usage of terms implies only homologies and homonomies within the insect abdomen, but not strict transsegmental homonomy with parts of the thorax or head, and no reference is intended to theories of limb base composition in a large-scale arthropod view. This includes the interpretations and the terminology of abdominal (and thoracic) sclerites suggested by Deuve (2018), which is focussed on the identification of sclerites of the (partly overlapping) categories epipleural / precoxal / subcoxal. The hypotheses in that work are surely widely plausible, while some conflicts regarding homologies and transsegmental homonomies (Klass 2008; response in Deuve 2018) remain to be clarified, and an integration of muscular data in the discussions would be desirable. Further development of Deuve's concepts might eventually lead to a more holistic (all-arthropod and all-tagma-

ta) terminology, but we consider it premature to follow this pathway herein.

In addition, we use single lowercase letters to label special parts of the cuticular surface that are not covered by the above terminology. The use of the same letter indicates a hypothesis of homology or homonomy only if explicitly stated.

Abbreviations: **ac** (+ number) = antecosta or part of it (mostly ventromedian parts) (belonging to segmental border; number = segment following); **al** = aulax (part of olistheter: groove on gonapophysis 8); **bpt** = basal penial tendon; **BS** (+ number) = basal sclerite of coxal vesicle (number = segment) (= 'operculum' in Becker 1966); **cn** (+ number) = midline notch between left and right coxal lobe (number = segment); **CS** (+ number) = coxosternum / -ite (compound sclerite including at least coxal and eusternal elements) (number = segment); **cx** (+ number) = coxal lobe, i.e. projecting body of abdominal limb (without stylus and gonapophysis, see st and gp) (number = segment); **CX** (+ number) = coxa / -ite (= 'coxite' in Bitsch) (number = segment); **CXp9** = larger posterior sclerite of coxa 9; **CXt9** = transverse anteromedian sclerite of coxa 9, including medially fused left and right elements ('sclerite scS' of females in Bitsch); **d** = mesal edge of coxal lobe 8; **df** (+ number) = dorsal fold of segment overlapping succeeding segment (number = segment); **dpa** = dorsal penial apodeme; **e** = medially fused anteromesal extensions of coxae 9 (forming a transverse coxal bridge, and a sclerite CXt9 if detached from remainder of CX9); **f** = distal end of transverse fusion of left and right gonapophyses 9; **g** = dorsal mesal edge of coxal lobe 9 (gonoplac 9); **gf** = genital lobe or fold of female, at hind margin of venter 7; **gl9** = coxal lobe 9 = gonoplac 9 (= '3rd valve of ovipositor'); **gp** (+ number) = gonapophysis (number = segment) (= '1st and 2nd valves of ovipositor'); **GP** (+ number) = sclerotisation of gonapophysis (number = segment); **h** = ventral mesal edge of coxal lobe 9 (gonoplac 9); **k** = paired anterolaterally directed extension of basal part of gonapophyseal or penial sclerite, GP9 or PEp (interpretation unresolved); **LCa** (+ number) = antelaterocoxa / -ite (= 'precoxite' in Bitsch) (number = segment); **LCp** (+ number) = postlaterocoxa / -ite (= 'laterocoxite' in Bitsch) (number = segment); **LG7** = genital plate of female (= 'languette sclerite' in Rousset 1973) at hind margin of venter 7; **li** (+ number) = laterocoxal inflexion (lateral apodeme of postlaterocoxa) (number = segment); **lic** (+ number) = infracoxal lobe (outward directed fold anterior to intersternite) (number = segment); **me** (+ number) = mesal expansion of coxal lobe (number = segment); **mic** (+ number) = intercoxal membrane (membrane between left and right coxae) (number = segment); **mvh** = midventral hollow on transverse coxal bridge (e) of venter 9; **oc** = part of common oviduct bearing intima; **pe** = penis; **PE** = sclerite(s) of penis; **PEd** = distal sclerite of penis; **PEp** = proximal sclerite of penis; **pn** (+ number) = paranotal lobe (number = segment); **PS** (+ number) = posterosternite at ventral hind margin of a segment (a loosely defined group of sclerites; number = segment); **PS9** (**PSp9**) = posterosternite (or its posterior part) ventrally on posterior margin of segment 9, or sternite (plus other elements?) on anterior margin of segment 10 (interpretation unresolved); **ptr** = phallotrema (genital opening in male Archaeognatha); **rh** = rhachis (part of olistheter: ridge on gonapophysis 9); **sbs** (+ number) = stylus-base spine (number = segment); **si** (+ number) = spiracle (number = segment); **sl** (+ number) = stylus (number = segment); **SL** (+ number) = sclerotisation of stylus (number = segment); **sn** (+ number) = spina (belonging to segmental border; number = segment following); **sp** = spermatheca of female; **ST** (+ number) = eusternum / -ite, including intersternite and sternite (number = segment); **STi** (+ number) = intersternum / -ite ('intersternite' in Bitsch) (belonging to segmental border; number = segment following); **STt** (+ number) = ('true') sternum / -ite ('sternite' in Bitsch) (number = segment); **TG** (+ number) = tergum / -ite (number = segment); **tr** (+ number) = part of trachea near spiracle (number = segment); **vf** (+ number) = ventral fold of segment overlapping succeeding segment (number = segment); **vs** (+ number) = coxal vesicle (number = segment).

There are several cases of (clear or possible) synonymy in this list, which mainly concern (potentially) homonomous elements of different segments (see Klass & Matushkina 2012): **(1) cx** (coxal lobe) is synonymous with **gl** (gonoplac), the latter is a coxal lobe with a specialised genitalic function; **cx** is also synonymous with **vf** (ventral fold), as the latter is the product of the (at least basal) fusion of the left and right coxal lobes of a segment. **(2) vs** (coxal vesicle) is synonymous with **gp** (gonapophysis), as the two are most likely different structural variants of transsegmentally homonomous elements. **(3) BS** (basal sclerite of coxal vesicle) is probably synonymous with **GP**, as sclerites **BS** are likely transsegmentally homonomous with some proximal parts of the gonapophyseal sclerotisations **GP**. **(4)** The specific sclerite categories **LG** (female) and **PE** (male; if 9th-segmental) may in some way be subsets of the wider category **PS** ('posterosternites'); alternatively, **PE** (male; if 10th-segmental) might include synonymy with **ST** and perhaps **GP**; however, homonomies, homologies, and partly the segmental assignment of the sclerotisations concerned are vastly unclear (see chapter 8).

Morphological terms and abbreviations from other publications (used herein for clear cross-reference) are marked with an asterisk – except for the terms from previous publications of K.-D. Klass & coworkers that follow the same terminology as used herein.

We distinguish different types of surface structuring of the cuticle: types 1–6 (with transitions), which are characterised in Klass & Matushkina (2012: p. 578). These types correlate with the degree of sclerotisation as observed by stiffness (strongest in type 1), but the correlation is not perfect.

There is an old debate about the term 'paramere'. We follow Snodgrass (1957: p. 2) in using it for lateral branches of the penis, i.e. for the parts of the phallic complex that together with the mesomeres originate from a longitudinal division of the primary phallic lobes. Parameres do then not exist in Archaeognatha, as the phallic lobes remain undivided. The term has also been frequently used (e.g. Sturm & Machida 2001) for 8th- and 9th-segmental ventroabdominal appendages of male Archaeognatha that are homonomous with the isosegmental gonapophyses of the female and with coxal vesicles of the preceding segments. These are outgrowths of the bases of the 8th- and 9th-segmental limbs, i.e., of the coxal lobes (coxal endites according to Bitsch 1974b), and we call them gonapophyses in both sexes. The penis is usually intimately associated with the 9th-segmental gonapophyses of the male; this we term the phallogonapophyseal complex.

Essentially following Snodgrass (various papers cited herein), we use the term 'genital opening' for all openings in male and female insects where the genital products (germ cells, as sperm or eggs) leave the body. In contrast, we use the term 'gonopore' for the external end(s) of the tube(s) that have originated by invagination of the body wall and guide sperm or eggs towards the outside but do not necessarily reach the outside; this is

the external end(s) of the ejaculatory duct(s) in the male and of the common oviduct(s) in the female insects. The genital opening can be a gonopore, as in, e.g., female Archaeognatha. However, projecting elements flanking the gonopore can fuse to form a fully closed channel, the opening of this channel then being the genital opening. This occurs in males by the median fusion of phallic lobes, which includes the formation of an endophallus between them, whose external opening is the 'phallotrema'; this is likely the situation in, e.g., male Archaeognatha. In females various morphogenetic processes (details of which remain to be studied) can lead to the formation of a vagina, whose external opening is the 'vulva'. The border between ejaculatory duct and endophallus and between common oviduct and vagina ranges from very distinct to not at all distinct, and the identification of the border in an adult insect is always hypothetical to some extent.

4. Results

We present a comparative description of the males of all five studied archaeognathan species, which covers abdominal venters 7, 8, and 9 and the phallic area. We include the phallic area (penis and associated structures) in the description of segment 9 but submit that it more likely belongs to segment 10 (see chapter 8). All differences among the species are mentioned explicitly, except for minor differences in proportion (see illustrations) and setation. After the description we present a list of characters that can be drawn from it and survey morphological differences in a character matrix (Table 1).

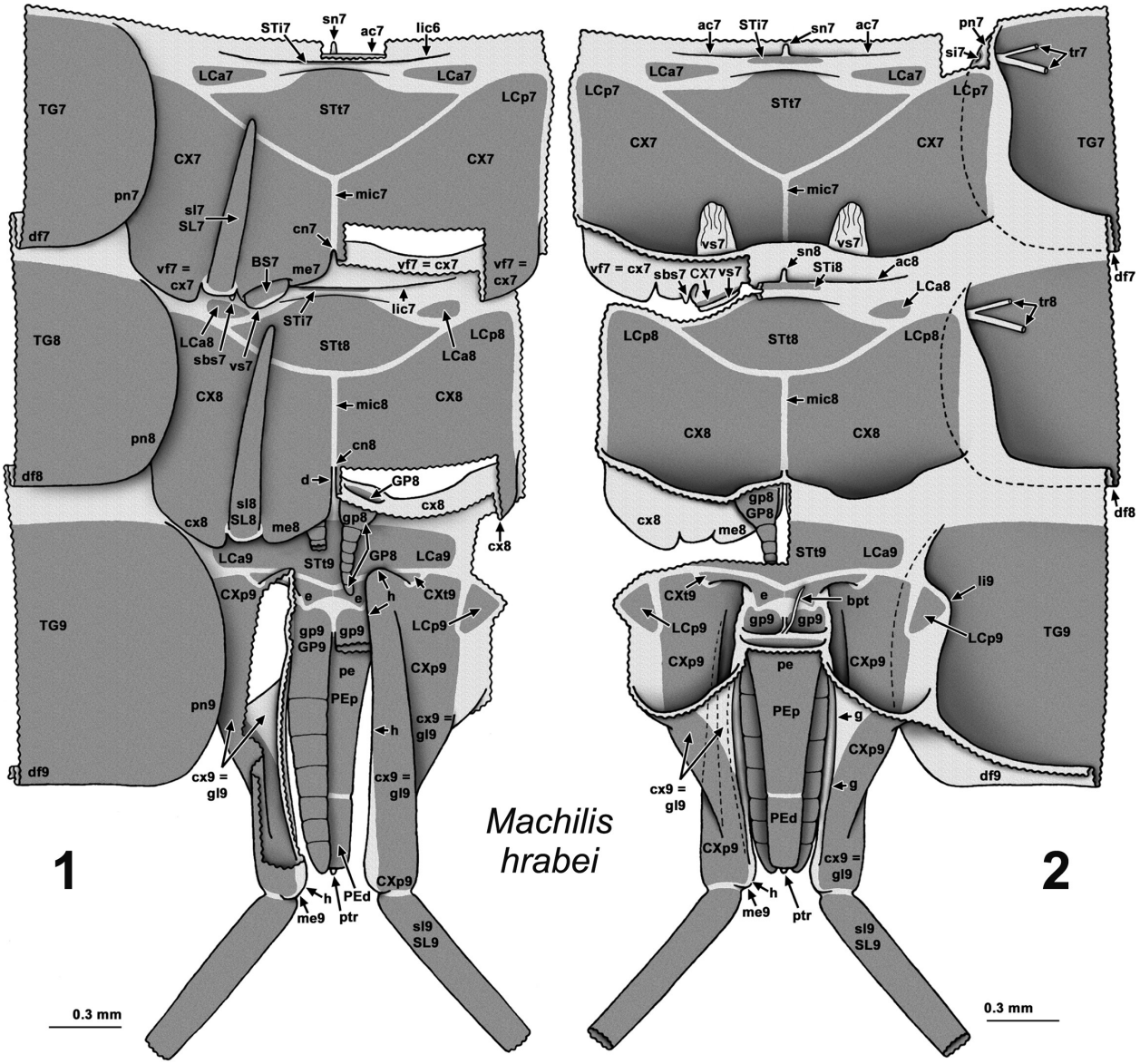
4.1. Segment 7

In all examined species, male venter 7 (Figs. 1–11) is dominated by a pair of large coxae (**CX7**) and a large median sternite (**STt7**). **STt7** (type 1 cuticle) has a more or less convex anterior margin, which in *Machilis* forms a wide, tongue-like anteromedian expansion (Figs. 1, 2). While the overall size, the lateral extension, and the triangular, posteriorly pointed shape of **STt7** is similar in *Machilis*, *Lepismachilis*, *Pedetontus* and *Petrobiellus*, **STt7** of *Machilinus* is much smaller by reaching less far laterally and posteriorly, and thus also more rhomboid (Figs. 10, 11). Sternite **STt7** and the two coxites **CX7** are entirely separated by very narrow stripes of membrane (between left and right coxites: intercoxal membrane **mic7**, showing type 6 cuticle). The apparent anterolateral parts of the coxal sclerites (labeled **LCp7**) represent the paired postlaterocoxae **LCp7**. In most species these are fully connected with the coxae **CX7**; only in *Pedetontus* a narrow stripe of membrane separates **LCp7** from **CX7** (Figs. 5, 6).

Anteriad of sclerites **STt7** and **CX7**, there are three smaller, very short sclerites, which are poorly bordered but can be easily traced both by their reduced flexibility (compared to surrounding membrane) and using SEM: a pair of weak lateral antelaterocoxites (**LCa7**; type 4 cuticle) and a stronger median intersternite (**STi7**; type 2 cuticle). In most species the cuticle of the area bearing sclerite **STi7** and the membrane laterad of it forms a transverse groove, which is here interpreted as the ventromedian part of the antecosta of venter 7 (**ac7**). The groove fades out long before it reaches the lateral margin of venter 7; its median part is especially deep and at the midline forms a small discrete internal projection (spina **sn7**, upon **STi7** if this is present). Sclerite **STi7**, groove **ac7**, and spina **sn7** are formally assigned to venter 7, but groove **ac7** most likely marks the border between segments 6 and 7. The entire set of anterior elements of venter 7 is fully present in all species, with the exception of *Machilinus*, which has distinct sclerites **LCa7** but lacks sclerite **STi7**, groove **ac7**, and spina **sn7** (Figs. 10, 11). Spina **sn7** has a wide base and a rounded triangular shape in *Pedetontus* and *Petrobiellus* (Figs. 6, 8), but a very narrow base and a cylindrical shape in *Machilis* and *Lepismachilis* (Figs. 2, 4). Sclerites **LCa7** show much variation in their width (very narrow in *Machilis*, very wide in *Pedetontus*), but always include the area in front of the membranous stripe separating sclerites **STt7** and **CX7**.

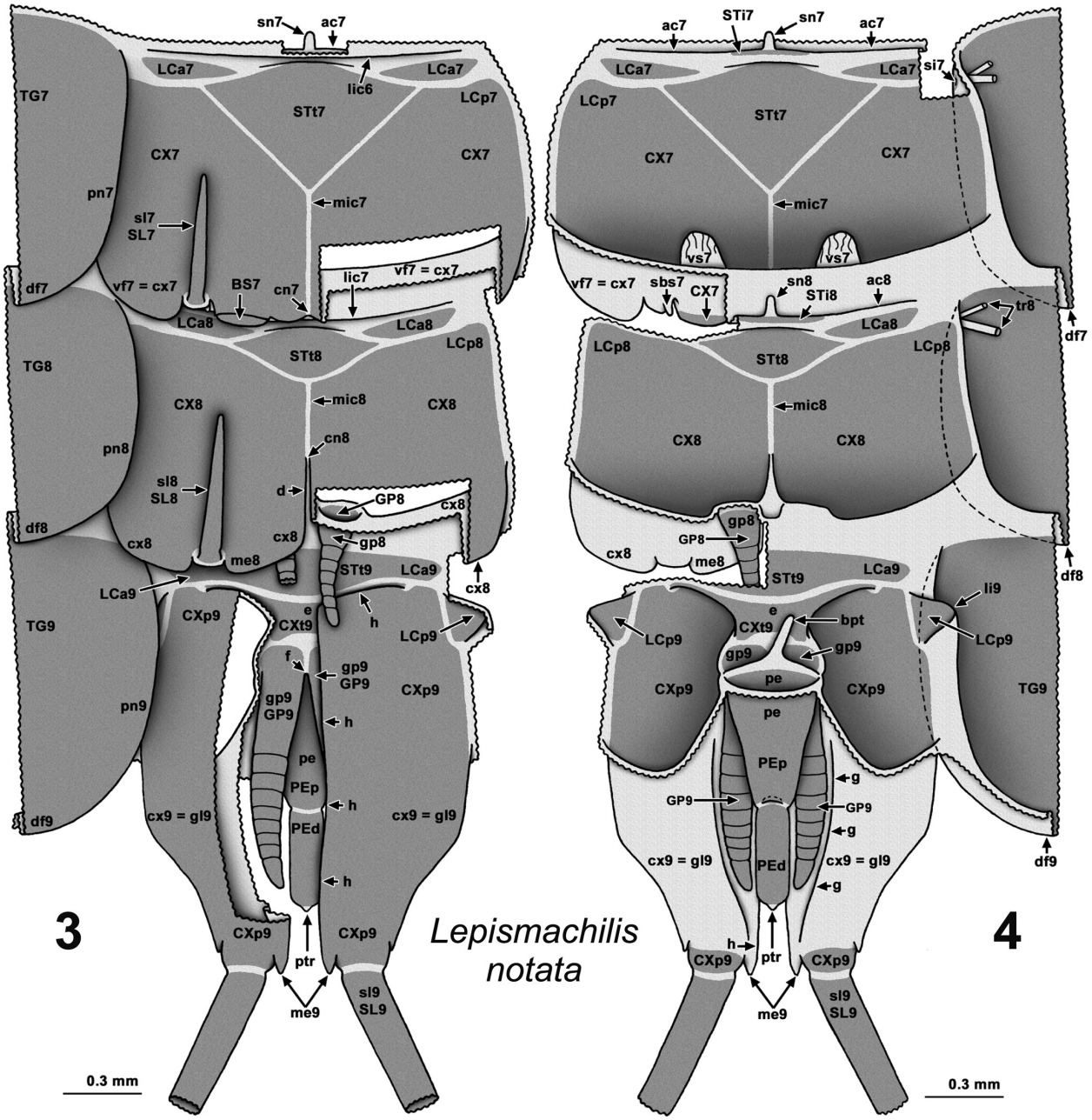
The posterior part of venter 7 forms a depressed posteriorly-directed fold, the ventral fold **vf7**, which covers the anterior part of venter 8 ventrally. The ventral wall of fold **vf7** is sclerotised by the posterior parts of coxae **CX7**, the dorsal wall is membranous (type 5 cuticle). Fold **vf7** is composed of the left and right coxal lobes of the segment (**cx7**). These are fused in their proximal parts, but separated by a midline notch (**cn7**) in their distal parts. (Note that the left and right coxal sclerites **CX7** remain entirely separated by membrane **mic7**.) In *Lepismachilis* notch **cn7** (Fig. 3) is much shallower than in the other species. In the species having a deep notch **cn7**, the transverse fusion of the coxal lobes **cx7** is still long anteriad of the notch; only in *Machilis* the fusion area is very short (no character is drawn from this feature, as the differences may partly depend on movement).

The distal edge of each coxal lobe **cx7** bears a stylus (**sl7**; further laterally) and a coxal vesicle (**vs7**; further mesally); the mesal-most part can be expanded posteriorly to a varied extent (expansion **me7** of coxal lobe in Figs. 1, 3, 5, 7, 10, ranging from virtually absent in *Machilinus* to strongly projecting in *Pedetontus*). Stylus **sl7** has an elongate-conical shape, is entirely sclerotised (sclerite **SL7**; type 1 cuticle), and apially bears a slender, basally articulated process appearing as a large seta or spine (not shown in Figs. 1–11; compare apial process of stylus 9 shown in Fig. 16B). At the stylus base the distal edge of the coxal lobe is quite deeply notched (in *Machilinus* less than in the other taxa). The sclerotisations of the stylus (**SL7**) and of the coxal lobe (**CX7**) are clearly separated by a narrow ring of membrane (type 6 cuticle). A stylus can swing along the sagittal plane of the



Figs. 1, 2. Ventral exoskeleton of male abdominal segments 7–9 (including penis) in *Machilis hrabei*, semi-diagrammatic, (**1**) ventral (essentially external) view, (**2**) dorsal (essentially internal) view. — Lowest parts of tergites included on animal's right side; some parts cut away on either side to give view to hidden areas. Sclerotised areas in dark gray (strong sclerotisation) or medium gray (weak sclerotisation); membranous areas in light gray. Waved lines are cutting lines. Continuous black lines are freely visible edges (= lines along which the cuticle bends away from the observer's view). Dashed black lines are (parts of) edges hidden beneath other cuticle. Terms used for labeling explained in text chapter 3.

animal, as the lateral basal parts of its sclerotisation are most closely in contact with the adjacent coxal sclerotisation, forming an undifferentiated articulation. A short spine **sbs7** (**sbs** in Fig. 12D,E,G) is situated at the mesodorsal base of the stylus **sl7**. Evidence on its structure is conflicting: in some pictures it appears to originate from the membrane at the mesal stylus base and to be movable at its base (compare procumbent and erected conditions in Fig. 12D and E), but in other pictures it appears to have an unarticulated, stiff or perhaps flexible base upon coxal sclerotisation (Fig. 12G). The coxal vesicle **vs7** (shown invaginated in Figs. 2, 4, 6, 8, 11, evaginated in Fig. 12E) has its base immediately mesad of the notch bearing the stylus. At its base, the coxal sclerotisation **CX7** also extends into the dorsal wall of ventral fold **vf7** (Figs. 2, 4, 6, 8, 11), so that **CX7** forms a narrow bridge along the dorsal base of the vesicle and thus surrounds it entirely. The ventral base of vesicle **vs7** bears a weak sclerite (**BS7** in Figs. 1, 3, 5, 7, 10; type 3 cuticle), which is fully separated from **CX7** by membrane of type 6 cuticle (separation not visible in Figs. 1, 3, because the distal rim of the coxal lobe projects beyond the vesicle base). The much larger distal part of the vesicle as well as its dorsal base are membranous, with three distinct regions of different cuticular microsculpture (Fig. 12E–H): In the proximal collar region of the vesicle, the ventrolateral part is of type 5 cuticle, while all other parts are of (likely somewhat softer) type 6 cuticle. The further distal part of the vesicle consists of plicate smooth cuticle (Fig. 12H), which is strongly folded in the retracted condition but be-



Figs. 3, 4. Ventral exoskeleton of male abdominal segments 7–9 (including penis) in *Lepismachilis notata*, semi-diagrammatic, (**3**) ventral (essentially external) view, (**4**) dorsal (essentially internal) view. — Lowest parts of tergites included on animal's right side; some parts cut away on either side to give view to hidden areas. For meaning of shading and lines see legend Figs. 1, 2. Terms used for labeling explained in text chapter 3.

comes greatly expanded during eversion of the vesicle. In all species, the surface of the coxal lobe along the dorsal base of vesicle **vs** bears a coxal setal organ consisting of a transverse row of basally articulated (likely tactile) setae and, immediately ventrad of the former, a transverse row of microtrichia (as in Fig. 12E,G).

The posterior-most part of venter 7 – behind the bases of coxal lobes **cx7** – bears no structural elements up to the segmental border 7/8, i.e., in contrast to the female there is no median lobe (genital fold **gf**) bearing a weak sclerotisation (genital plate **LG7**) and associated pouches (compare KLASS & MATUSHKINA 2012: figs. 1, 2). Only *Petrobiellus* has kind of a very weak median sclerotisation in this area, the posterosternite **PS7** (possibly homonomous with the female **LG7**), which is very smooth and can be distinguished from surrounding membrane by a peculiar light reflection and by slightly greater stiffness (both **PS7** and surrounding membrane are type 6 cuticle of KLASS & MATUSHKINA 2012, and **PS7** is a sclerite only in a very wide sense). Such a posterosternite was in *Petrobiellus* also found in the corresponding areas of other segments, the 6th (**PS6**) and the 8th (**PS8**) (Figs. 7, 8, 19A).

The tergite of segment 7 (**TG7**; type 1 cuticle) is entire and is placed slightly further anteriorly than the ventral sclerotisations. The lateral parts of **TG7** strongly

overlap the lateral parts of the venter; this outfolding is the paranotal lobe **pn7** (Bitsch 1973: p. 175). The posterior parts of **TG7** overlap the succeeding tergite **TG8**; this outfolding is here called 'dorsal fold' of segment 7, **df7**. The dorsal fold continues into the paranotal lobes around the rounded posterolateral corners of tergite **TG7**. While the outward-facing walls of folds **pn7** and **df7** are strongly sclerotised by **TG7**, the inward-facing walls are membranous and smooth (type 5 cuticle).

The spiracle (**si7**) is slit-like and tiny, and located far anteriorly either on the mesally facing wall of the paranotal lobe **pn7** (Figs. 2, 4, 6, 8), or on the laterally facing wall (Fig. 10), though in both cases very close to the distal edge of the lobe. In the taxa bearing the spiracle on the mesal wall of the lobe, tergite **TG7** bends in the spiracle area around the distal edge of the paranotal lobe to enclose the spiracle. The spiracle is thus in all taxa placed on the morphologically most ventrolateral part of tergite **TG7**.

4.2. Segment 8

In all species, venter 8 (Figs. 1–11) is quite similar to venter 7 concerning both its sclerites and formative elements. The degree of similarity and occurrence of differences is partly congruent among the studied species, but there are also cases of incongruence among the species. Only differences to venter 7 are described in the following.

Sternite **STt8** (type 1 cuticle) is usually less far expanded to the posterior and is posteriorly more truncated than **STt7**, and the membranous stripes (type 6 cuticle) separating it from the coxites **CX8** are thus less angled at the midline. This is very distinct in *Machilis* and *Lepismachilis*, where the membranous stripes are not angled at all (Figs. 1–4). The difference is also present but less distinct in *Machilinus* (as the stripes are also poorly angled on venter 7; Figs. 10, 11) and *Pedetontus* (as the stripes are slightly angled on venter 8; Figs. 5, 6). Only *Petrobiellus* shows no difference in this regard between venters 7 and 8: sternites are of similar outline and the stripes well angled on both venters (Figs. 7, 8).

A separation between coxite **CX8** and postlaterocoxite **LCp8** (both type 1 cuticle) is found in *Pedetontus* (as for venter 7; by membrane of type 6 cuticle) and in *Petrobiellus* (in contrast to venter 7; by very weak sclerotisation); the other taxa have these sclerotisations firmly connected. *Petrobiellus* is thus the only taxon showing an intersegmental difference in this feature.

Regarding the occurrence of an intersternite **STi8**, the same is true as for **STi7** of venter 7. Correspondence of venter 8 with venter 7 also largely applies to the presence of an antecostal groove **ac8** and to the presence and the shape of the spina **sn8**, but there are two exceptions: First, the absence of **ac8** and **sn8** in *Machilinus* is not so clear-cut as for **ac7** and **sn7** of venter 7, since there is a shallow but distinct invagination around the midline, which may either represent a vestigial **ac8** groove or a wide spina **sn8** (or both together; Fig. 11). Second, in *Pedetontus* spina **sn8** is narrower than **sn7**, whereby the distinction between wide and narrow spinae is not as clear-cut for venter 8 as for venter 7 (Fig. 6). In *Machilinus* the membrane (type 6 cuticle) in front of **STt8** bears a few orifices of glands (no data for the other taxa).

In *Pedetontus*, *Petrobiellus*, and *Machilinus* the left and right coxal lobes **cx8** show a basal fusion, thus forming together a ventral fold **vf8** that continues across the midline (Figs. 5–8, 10, 11); the distal parts of the coxal lobes are separated by a midline notch **cn8**. *Machilis* and *Lepismachilis*, in contrast, lack a basal fusion of lobes **cx8**, which are free from each other down to their bases (i.e., each **cx8** has a free-ending mesal edge, labeled **d** on left sides of Figs. 1, 3; and the posterior 'notch' **cn8** has an open anterior end); the ventral fold **vf8** is thus interrupted at the midline.

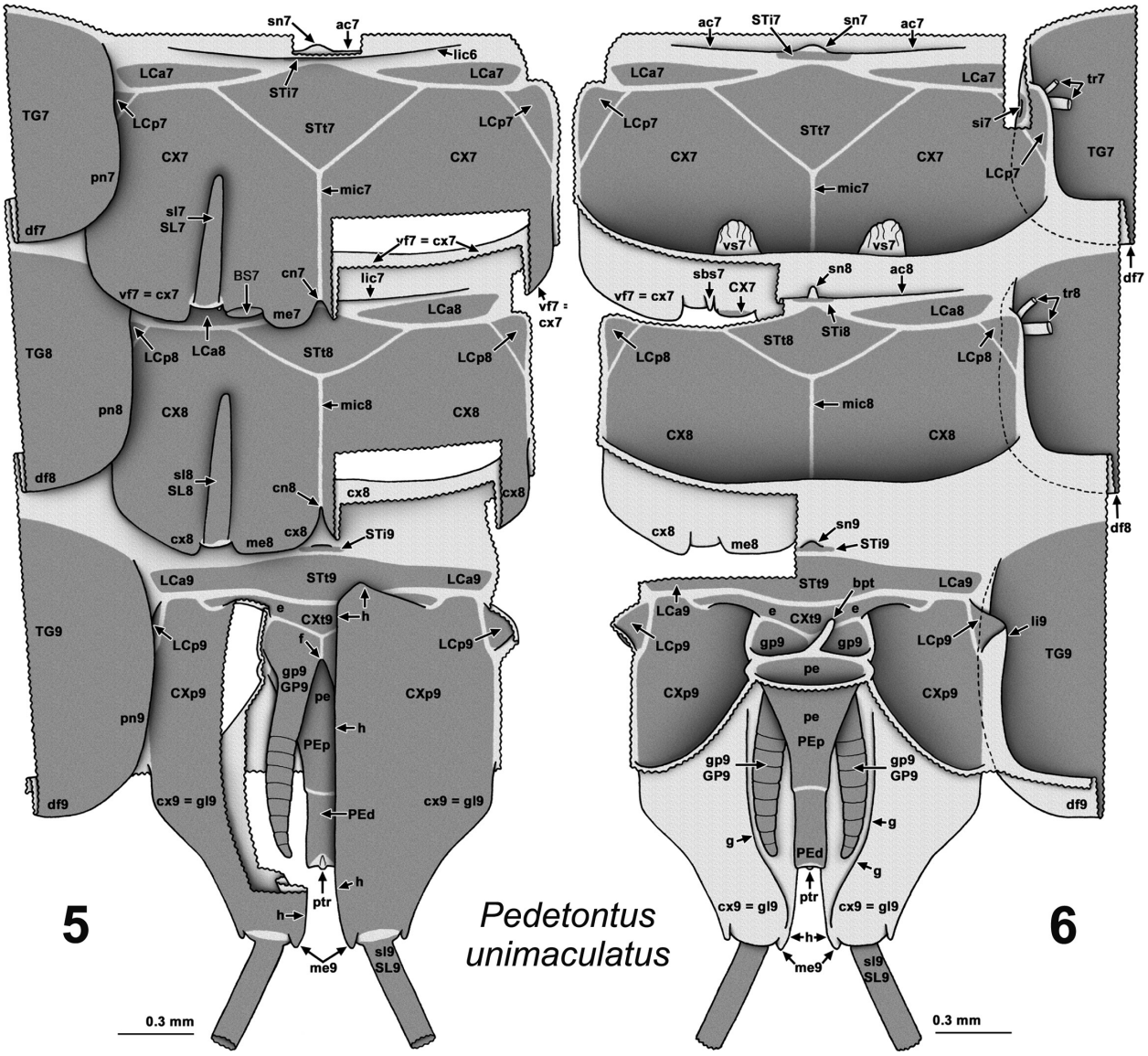
The stylus **sl8** is in all species very similar to that on venter 7, but a bit longer or shorter. A spine **sbs** at the mesal base of stylus **sl8** is absent.

The most significant difference compared to venter 7 concerns the 'coxal vesicles': in none of the species there is any trace of a typial coxal vesicle on coxal lobe **cx8**. However, in *Machilis* and *Lepismachilis* there is on each side an elongate, non-retractable gonapophysis (**gp8** = **vs8** = 'paramere' 8) (Figs. 1–4, 13A, 14A). The bases of the **gp8** are situated a bit further mesally and much further anteriorly than the bases of the vesicles **vs7** of segment 7, on the anteromesal part of the membranous dorsal wall of the coxal lobe **cx8** (Figs. 1–4). They thus appear (like vesicles **vs**) as projections of the coxal lobes, and their basal parts are hidden by the coxal lobes. The gonapophyses **gp8** are almost entirely but weakly sclerotised (sclerite **GP8**; type 3 cuticle), and the sclerotisation is distinctly annulated: a long and wide basal-most annulus is followed by six (both taxa) or five (some *Lepismachilis*) shorter and narrower annuli, whose borders are partly difficult to recognise (Figs. 13A, 14A,B). Annuli are separated by narrow stripes of membrane (type 6 cuticle; Fig. 14A–C). It is noteworthy that gonapophyses **gp8** are found in the same two species that lack a basal median fusion of the coxal lobes **cx8**. The other taxa, *Pedetontus*, *Petrobiellus*, and *Machilinus*, show no traces either of gonapophyses or coxal vesicles on venter 8 (Figs. 5–8, 10, 11).

4.3. Segment 9

In all species, venter 9 (Figs. 1–11) differs strongly from both venters 7 and 8 concerning both its sclerites and formative elements. While the distinctions of venter 9 are mostly quite similar in the various species, there are also striking interspecific differences.

The anterior part of venter 9 bears distinct sclerotisations (type 2 cuticle) that most likely represent the sternite **STt9** and the antelaterocoxites **LCa9**. In *Petrobiellus* (Figs. 7–9) there is an unpaired median sternite **STt9** and a lateral pair of antelaterocoxites **LCa9** (the latter with a near-membranous mesal region of type 4 cuticle),



Figs. 5, 6. Ventral exoskeleton of male abdominal segments 7–9 (including penis) in *Pedetontus unimaculatus*, semi-diagrammatic, (**5**) ventral (essentially external) view, (**6**) dorsal (essentially internal) view. — Lowest parts of tergites included on animal's right side; some parts cut away on either side to give view to hidden areas. For meaning of shading and lines see legend Figs. 1, 2. Terms used for labeling explained in text chapter 3.

i.e. three independent sclerites – a pattern allowing for a clear identification of these parts. *Machilis* (Figs. 1, 2), *Lepismachilis* (Figs. 3, 4), and *Pedetontus* (Figs. 5, 6) have a single very wide sclerite, which, however, covers the same area as the three sclerites in the foregoing taxa and thus likely comprises firmly connected **STt9** and **LCa9**; in all three taxa the sclerotisation between the putative **STt9** and **LCa9** parts is weaker. *Machilinus* (Figs. 10, 11) has a single sclerite of type 2 cuticle that, however, covers only the median area and thus likely only represents sternite **STt9**; the pair of **LCa9** is most likely represented by anterior extensions of the coxal sclerites **CX9** (i.e. the **LCa9** are fused to **CX9**). An intersternite **STi9** is present as an isolated sclerite only in *Pedetontus* (Figs. 5, 6), and also only this species has a median invagination (on **STi9**) that might represent a spina **sn9** or a narrow vestige of the antecostal groove **ac9**. In the other species the intersternite **STi9** may either be absent or constitute the anterior part of what is called sternite **STt9**; the latter interpretation is supported only in *Petrobiellus*, where the anterior margin of this median sclerite is folded inward – a possible vestige of an antecostal groove **ac9** (its sclerotisation then being intersternal).

The **STt9** sclerotisation has in most species a straight or slightly convex hind margin. Only in *Petrobiellus* this sclerotisation is strongly expanded posteriorly around the midline, forming a long tongue (Figs. 7–9). It is noteworthy that this unique condition is found in the only taxon in which the sternite is not more truncated on venter 8 than on venter 7. *Machilinus* shows another unique condition of the **STt9** sclerotisation: the heavy median part is elevated relative to the small lateral parts (semimembranous: type 4 cuticle) along a discrete step on each side (Figs. 10, 11). In all other species **STt9** is even along its flanks.

Venter 9 bears large coxae **CX9** (type 1 cuticle), which are longer and narrower than **CX7** and **CX8** of the preceding venters. *Machilis*, *Lepismachilis*, and *Pedetontus* have a small, fairly heavy, roughly triangular discrete sclerite located laterad of the anterior part of **CX9**, the postlaterocoxite **LCp9** (Figs. 1–6). **LCp9** is separated from **CX9** by a stripe of membrane, which is especially narrow in the posterior part. **LCp9** is dorsally more or less concave and has its lateral part slightly invaginated dorsolaterally, thus forming a rounded-triangular internal apodeme (laterocoxal inflexion **li9** in Figs. 2, 4, 6). *Petrobiellus* has a similarly shaped and inward-folded (**li9**) sclerotisation in the same position, which thus most likely represents the **LCp9**, but this is fully connected with the coxal sclerotisation **CX9** (Fig. 8), appearing as a triangular expansion of it. In *Machilinus* there is only a very small lateral expansion of the coxal sclerotisation in the same area, which also shows an inward-folded lateral part (**li9**); we interpret this as a small **LCp9**, fused to **CX9** as in *Petrobiellus* (Fig. 11). In all taxa, **LCp9** is widely separated from the lateral margin of tergite **TG9** (by the entire membranous mesal wall of the paranotal lobe **pn9**).

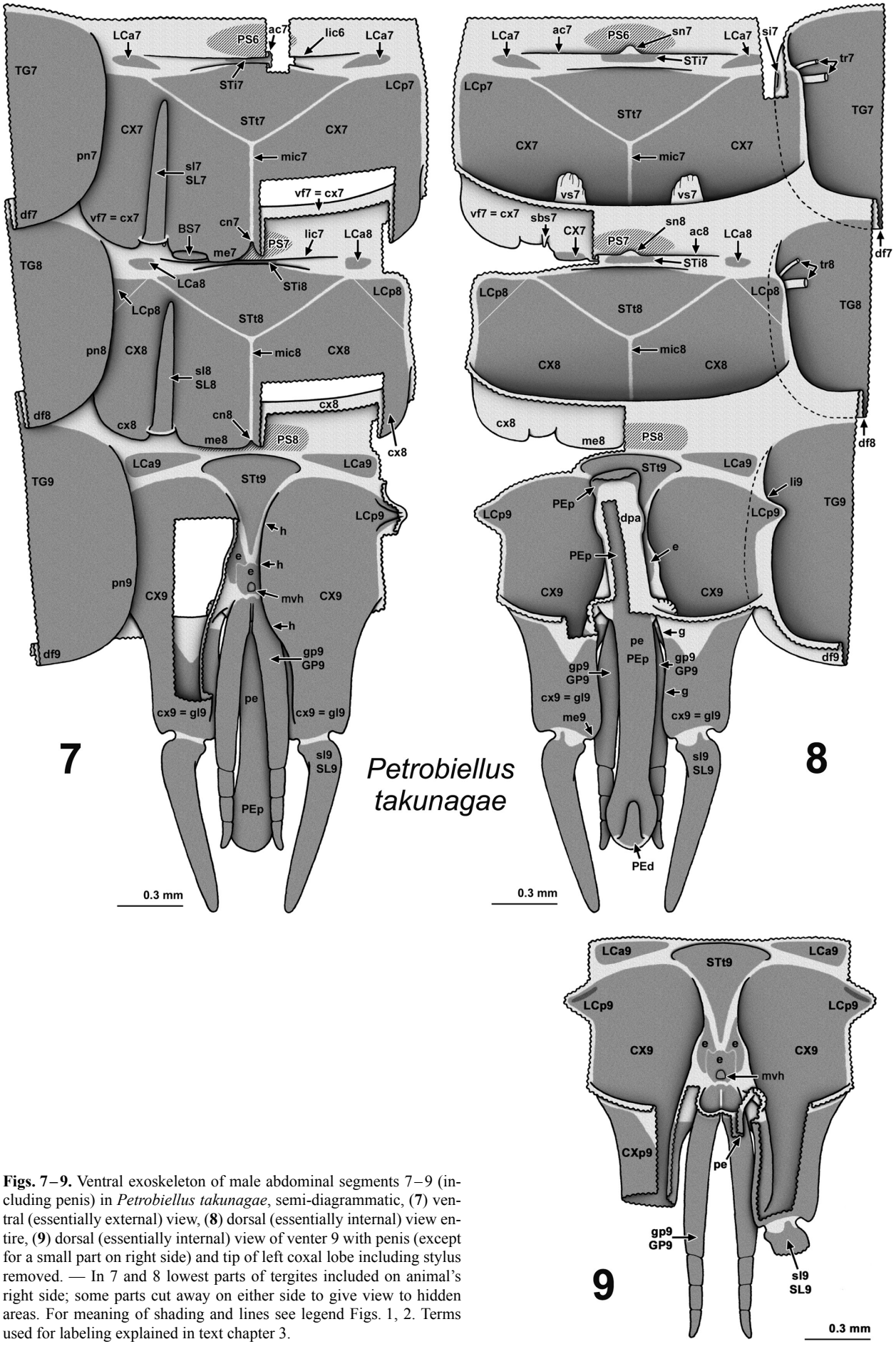
Most anteriorly the left and right coxae **CX9** are in all species transversely connected by a strong sclerite bridge (**e** in Figs. 1–11; type 2 cuticle); the bridge is part of **CX9**, i.e. mesal extensions of the left and right coxae **CX9** are fused to each other across the midline. In *Machilis* (Figs. 1, 2), *Lepismachilis* (Figs. 3, 4), and *Pedetontus* (Figs. 5, 6) the bridge is laterally separated from the larger remainder of **CX9** by a stripe of membrane (type 6 cuticle), whereby coxa **CX9** is divided in an unpaired anteromedian sclerite (**CXt9**, the bridge part, including **CX9** portions from the left and right body sides) and a pair of larger posterolateral sclerites (**CXp9**, each comprised of portions from only one body side). The separation is established in a way that the resulting sclerites are firmly articulated upon each other in the area of their separation (the membrane forming a syndesis, which is always a bit curved). In *Petrobiellus* (Figs. 7–9) and *Machilinus* (Figs. 10, 11), in contrast, the bridge part **e** is firmly connected with the remainder of **CX9** (no membranous stripe establishing a syndesis; accordingly, the entire sclerite is simply called **CX9**). It is noteworthy that a fused transverse sclerite **STt9**+**LCa9** occurs in the species that show a separation between **CXp9** and **CXt9**.

In all species the bridge part **e** of **CX9** has a slightly concave anterior margin (almost straight in *Machilinus*) and thus altogether bends a bit to the posterior around the midline. This correlates with the slightly convex shape of the hind margin of **STt9**, which is paralleled by the margin of the bridge part of **CX9**. *Petrobiellus* shows the same correlation, but the bridge part bends much more strongly to the posterior, paralleling the margin of the posteriorly expanded **STt9**.

The lateral portions of the bridge part **e** of **CX9** are narrow in all species (no matter whether separated from or connected with the remainder of **CX9**). The median portion of the bridge, however, is expanded posteriorly to a varied extent (in addition to its posterior bending) and shows various differentiations. The hind margin is always in contact with the gonapophyseal sclerotisations **GP9**. In *Machilis* (Figs. 1, 2), *Lepismachilis* (Figs. 3, 4), *Petrobiellus* (Figs. 7, 9), and *Machilinus* (Figs. 10, 11) the margin forms a pair of posterior expansions (tiny and hardly distinct in *Petrobiellus*), which establish especially close contact with the gonapophyseal sclerotisations **GP9**. In contrast, in *Pedetontus* (Figs. 5, 6, 15A) the margin is almost straight on each side and is altogether in close contact with the sclerotisations **GP9**. Two further differentiations are unique for *Petrobiellus* (Figs. 7, 9, 16A–C): The posteromedian part of the bridge (of type 2 cuticle) is demarcated from the remainder by a feeble line of membrane (type 6 cuticle; details and movability could not be observed), and in the center of this part lies a small but discrete hollow (**mvh** in Figs. 7, 16B,C; a duct or tendon that continues internally could not be detected). Another differentiation is only distinct in *Machilis* (Figs. 10, 11): Bridge **e** (sclerite **CXt9**) shows a feeble longitudinal line at midline (not discernible in SEM), which is immovable but might be a reminiscence of the fusion of formerly separated left and right **CX9** sclerotisations (then being a true suture).

The posterior part of venter 9 forms a pair of long posteriorly directed coxal lobes **cx9** (= gonoplacs **gl9**), which are laterally depressed (as the entire **cx** lobes in the preceding segments) but are raised fairly high mesally (in contrast to **cx** lobes of preceding segments). In *Lepismachilis* (Fig. 3), *Pedetontus* (Fig. 5), *Petrobiellus* (Fig. 7), and *Machilinus* (Fig. 10) the ventral wall of the coxal lobe ascends quite gradually to the higher mesal part (the coxal lobe thus having a fairly triangular cross section). In *Machilis* (Fig. 1), however, it runs mesad and then abruptly bends ventrad (the coxal lobe thus having a more Γ-shaped cross section), and the vertical mesal part bends a bit laterally over the lateral part.

The high mesal walls of the coxal lobes **cx9** form mesally projecting edges most dorsally (**g**, Figs. 2, 4, 6, 8, 11) and most ventrally (**h**, Figs. 1–8, 10, 11). In between these edges, the mesal **cx9** walls form a concavity, which harbours the longer distal part of gonapophysis **gp9** (not of the **gp8**, which, if present, is too short to reach this area). The left and right lobes **cx9** are not fused at all but free from each other down to their bases (i.e. both the dorsal and ventral mesal edges, **g** and **h**, have free ends and are completely separate from their counterparts of the opposite side). Venter 9 thus consistently lacks a transversely continuous ventral fold **vf9**. The ventral mesal edge **h** of **cx9** extends further to the anterior than the dorsal edge **g**; the concavity above edge **h** continues the concavity between edges **g** and **h** to the anterior and harbours the basal parts of gonapophyses **gp9** and, if **gp8** are present, the apial parts of gonapophyses **gp8** in addition (**gp8** in Fig. 3 dragged out of the concavity). In *Machilinus* (Fig. 10) and *Petrobiellus* (Fig. 7), the ventral mesal edge **h** of **cx9** has its anterior end near the lateral flank of sternum **STt9**. In contrast, in *Lepismachilis* (Fig. 3), *Pedetontus* (Fig. 5), and *Machilis* (Fig. 1), edge **h** of **cx9**



Figs. 7–9. Ventral exoskeleton of male abdominal segments 7–9 (including penis) in *Petrobiellus takunagae*, semi-diagrammatic, (**7**) ventral (essentially external) view, (**8**) dorsal (essentially internal) view entire, (**9**) dorsal (essentially internal) view of venter 9 with penis (except for a small part on right side) and tip of left coxal lobe including stylus removed. — In 7 and 8 lowest parts of tergites included on animal's right side; some parts cut away on either side to give view to hidden areas. For meaning of shading and lines see legend Figs. 1, 2. Terms used for labeling explained in text chapter 3.

continues much further anteriad and then laterad, whereby the coxal lobes **cx9** have a far anterior part that projects anteromesally.

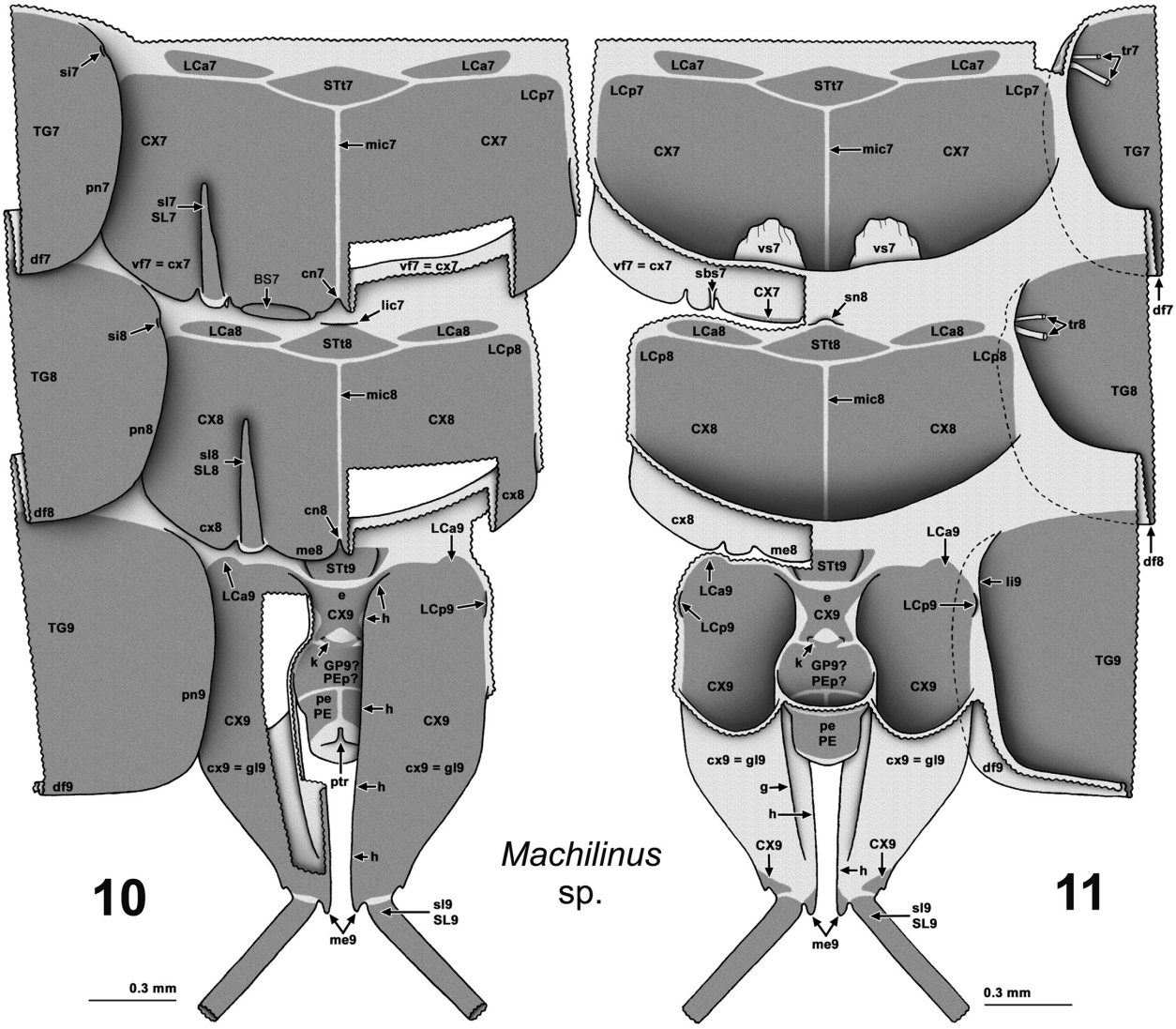
The coxal sclerite **CX9** (or **CXp9**, if **CX9** is divided; type 1 cuticle) extends in all species over the entire ventral wall of the coxal lobe **cx9** (Figs. 1–11). The concave mesal wall of lobe **cx9** usually remains membranous; only in *Petrobiellus* it is weakly sclerotised in its distal part. The extent to which **CX9** extends into the dorsal wall of lobe **cx9** varies more strongly: In *Pedetontus* (Fig. 6) the dorsal wall is entirely membranous, including the area of the stylus (**sl9**) base; in *Machilinus* (Fig. 11) and *Lepismachilis* (Fig. 4) the sclerotisation ascends into the dorsal wall only next to the stylus base, where it is dorsally closed only in *Lepismachilis*; in *Petrobiellus* (Figs. 8, 9) and *Machilis* (Figs. 1, 2) the stylus base area plus much of the remaining dorsal wall are sclerotised, only the proximo-mesal parts being membranous. We did not code characters referring to the sclerotisation of the coxal lobes **cx9**, as the degree of hardening varies gradually over the lobe walls and sclerite borders are not very clear.

The apex of each coxal lobe **cx9** bears a stylus **sl9**, which is similar to **sl7** and **sl8** (but longer to a varied extent), and usually straight. In *Petrobiellus* (Figs. 7–9, 16A,D), however, stylus **sl9** has a sharp laterally directed bend next to its base. Since the stylus base is located on the vertically oriented mesal part of the coxal lobe, the plane of movement of **sl9** is in all species a bit rotated compared to that of the preceding styli: it predominantly swings from mediodorsal to lateroventral, and nearly dorsoventrally in *Petrobiellus*. A spine **sbs** at the mesal base of stylus **sl9** is absent. Mesad of the stylus base, lobe **cx9** forms an expansion (mesal expansion **me9**), which in *Machilinus* (Figs. 10, 11), *Pedetontus* (Figs. 5, 6), and *Lepismachilis* (Figs. 3, 4) is a distinct posteriorly directed process, whereas in *Machilis* (Figs. 1, 2) and *Petrobiellus* (Figs. 7, 8) it is a hardly projecting bulge. There is no trace of a typial coxal vesicle on coxal lobe **cx9** (as expected if the **gp9** – see below – are homonomous with the **vs**).

In front of the dorsal base of the coxal lobes **cx9**, the cuticle between the left and right coxae **CX9** is, in contrast to venters 7 and 8 (**mic7**, **mic8**), very wide and strongly arched dorsally, thus forming a wide midline concavity along venter 9 (called 'gouttière génitale' in Bitsch 1974b; Figs. 2, 4, 6, 8, 11). In the female of *Petrobiellus* this concave area was called 'intercoxal membrane **mic9**' (see Klass & Matushkina 2012: fig. 2). We also call the area **mic9** in the males here studied, where, however, only small parts of this area are membranous. The concavity is partly covered ventrally by the mesally projecting ventromesal edges **h** of the coxal lobes **cx9**. The lateral portions of the concavity are thus the above-mentioned concavities above the edge **h** and continue posteriorly into the concavities of the mesal faces of the coxal lobes **cx9**. The upper walls of the large concavity give rise to a pair of projections (further anteriorly: gonapophyses **gp9**) and to an unpaired projection (further posteriorly: penis **pe**), which are of similar length, have densely spaced bases, and together form the phallogonapophyseal complex. The part of the concavity posteriad of the origins of these processes harbours the proximal parts of these three processes. Posteriad of the bases of the gonapophyses **gp9** and the penis **pe** (area cut away in Figs. 2, 4, 6, 8), there is a very weak, indistinctly bordered median sclerotisation **PSp9** (type 4 cuticle) surrounded by membrane (type 6 cuticle); it is clearly present in *Lepismachilis* and *Machilinus* (Figs. 12A–C) but could not be demonstrated for the other taxa (presence unclear).

The base of each gonapophysis **gp9** (Figs. 1–9) in the **mic9** concavity is located at the level of the anterior parts of the **CX9** sclerites (and far from the apial parts of the **cx9** lobes), and outside of the dorsal wall of the coxal lobe **cx9**. The **gp9** do thus, straightforwardly, not appear as projections of the coxal lobes. Each gonapophysis **gp9** is almost entirely sclerotised (sclerite **GP9**). The gonapophyses **gp9** are well developed in all species, with the exception of *Machilinus*, where no traces of projections are present in the respective area. However, in *Machilinus* this area bears a transverse sclerite plate (**GP9?** in Figs. 10, 11, 17A–E), which we tentatively interpret as the levelled and medially fused pair of **GP9** sclerites (see below for an alternative interpretation), mainly based on its articulations with the **CX9** bridge anterior to it; the transverse **GP9?** plate forms a pair of anterolaterally directed extensions **k** (Figs. 10, 17C,D). In *Petrobiellus* (Figs. 7–9, 16A) the **gp9** bases are located further posteriorly than in the other species; this is correlated with the strong posterior expansion of sternite **STt9** and of the median bridge **e** of coxa **CX9**.

The bases of the left and right gonapophyses **gp9** are close together at the midline. In *Machilis* (Fig. 1) and *Petrobiellus* (Fig. 7) the bodies of the left and right **gp9** are fully separated from each other down to the very base (as seen by the free anterior ends of their mesal edges). In *Lepismachilis* (Fig. 3) and *Pedetontus* (Fig. 5), however, the left and right **gp9** show a very short basal fusion (as seen by their mesal edges bending into each other, at **f** in Figs. 3, 5). The left and right gonapophyseal sclerites **GP9**, on the other hand, are fully separated (by membranous type 5 cuticle) in *Machilis* (Fig. 1), *Lepismachilis* (Fig. 3), and *Pedetontus* (Fig. 5), whereas in *Petrobiellus* (Figs. 7, 9, 16C) they show a very short connection across the midline at their ventral anterior margins. A more extensive transverse connection of the two **GP9** is present in *Machilinus* if the above identification of **GP9** is true (Fig. 10). The ventral anterior margins of the **GP9** sclerites are straight in *Lepismachilis* (Figs. 3, 4) and *Pedetontus* (Figs. 5, 6), and the **GP9** base is hinged upon the **CX9** bridge (by a syndesis). In contrast, in *Machilis* (Figs. 1, 2) and *Petrobiellus* (Figs. 7, 9) there is a notch on each side that receives the posterior end of the expansion of the **CX9** bridge, whereby a simple, narrow articulation is present between each **GP9** and the **CX9** bridge. In *Machilinus*, the **GP9** margin forms a pair of oblique extensions (**k** in Figs. 11, 17D); their tips meet the tips of



Figs. 10, 11. Ventral exoskeleton of male abdominal segments 7–9 (including penis) in *Machilinus* sp., semi-diagrammatic, (**10**) ventral (essentially external) view, (**11**) dorsal (essentially internal) view. — Lowest parts of tergites included on animal's right side; some parts cut away on either side to give view to hidden areas. For meaning of shading and lines see legend Figs. 1, 2. Terms used for labeling explained in text chapter 3.

the extensions of the **CX9** bridge and merge a bit beneath these to form a small hollow on each side.

Sclerite **GP9** is distinctly annulated all around in all taxa having gonapophyses **gp9**, and the basal-most annulus is always by far the longest (but not wider than the following ones). In *Machilis* (Figs. 1, 2) the basal annulus is ca. 1/3 the length of **gp9**, and 6 annuli follow; in *Lepismachilis* (Figs. 3, 4) and *Pedetontus* (Figs. 5, 6, 15A) the basal annulus is ca. 1/2 the length of **gp9**, and 8 annuli follow; in *Petrobiellus* (Figs. 7–9, 16A) the basal annulus is well 2/3 the length of the slender **gp9**, and 3 annuli follow.

The penis **pe** is at its base as wide as the two gonapophyses **gp9** together (if these are present) and most parts of its walls are sclerotised (sclerite(s) **PE**). *Machilis* (Figs. 1, 2, 13C,F), *Lepismachilis* (Figs. 3, 4, 14E–H), and *Pedetontus* (Figs. 5, 6, 15A) have similarly structured penes: the penis is elongate, the walls are covered by a proximal (**PEp**) and a distal (**PEd**) cylindrical sclerite separated by a narrow annular membrane (type 6 cuticle); this membrane is wider ventrally, allowing for in- and outfolding mainly in this area and thus for a ventral bending of the **PEd**-bearing part (Fig. 13D); sclerite **PEp** appears to be weaker along the ventral midline; the proximal part of the penis gradually narrows, while the distal part is essentially parallel-sided; the phallotrema (**ptr**) is placed on a small membranous field upon the more or less truncated apex and is surrounded by scattered non-articulated and articulated setae (Figs. 13D,F,G, 14C–H, 15C–F); the ventral base of the penis (at the same time the dorsal base of the gonapophyses **gp9**) bears a slender, membranous, soft median invagination, the basal penial tendon **bpt** (Figs. 2, 4, 6). The penis of *Machilinus* (Figs. 10, 11, 17A–E) is much shorter and a bit wider; it has only one cylindrical sclerite (**PE**), which, however, is ventrally open by a longitudinal stripe of membrane; the phallotrema (**ptr**) is placed on a large membranous field in a ventro-subapial position; the ventral base of the

penis lacks a tendon **bpt**. Regarding the sclerotisation, the sclerite labeled **GP9?** in *Machilinus* could alternatively be the proximal penial sclerite (**PEp**, the above-mentioned '**PE**' then being the distal penial sclerite **PEd**), or a fusion product of **PEp** and **GP9**. The penis of *Petrobiellus* (Figs. 7, 8, 21A,B) is elongate, for most of its length parallel-sided, but swollen subapially, and then dorsally hooked, with a somewhat pointed apex; the walls are covered by a very long cylindrical proximal sclerite (**PEp**), which reaches beyond the swollen part, and a short distal sclerite (**PEd**) upon the apial hook, the two being separated by a narrow annular membrane (both penial sclerites show type 2 cuticle); the phallotrema (**ptr**) is likely placed on the apial hook but its position could not be clearly identified; the ventral base of the penis lacks a tendon **bpt**; as a unique structure, the dorsal base of the penis is invaginated to form a long and wide apodeme, the dorsal penial apodeme **dpa**, with a sclerotised ventral wall (an anterior continuation of sclerite **PEp**) and a membranous dorsal wall; the inner end of apodeme **dpa** bends posterodorsally and is a bit scoop-shaped.

The cuticulised terminal part of the male gonoduct was only observed in *Machilis*, where it does not reach the level of the base of the penis. The duct is likely composed of an ectal endophallus (derived from part of the former mesal walls of the phallic lobes) and an ental ejaculatory duct (derived from the invagination between the phallic lobes), but we could not see a border in our preparations (which were not aimed at observing this).

The posterior extension of the phallogonapophyseal complex or of the penis (if gonapophyses 9 are absent) varies strongly among the taxa: it reaches far beyond the apices of the coxal lobes **cx9** in *Petrobiellus* (Figs. 7, 8), just reaches the **cx9** apices in *Machilis* (Figs. 1, 2), ends well proximad of the **cx9** apices in *Lepismachilis* (Figs. 3, 4) and *Pedetontus* (Figs. 5, 6), and does not extend beyond the proximal parts of the **cx9** lobes in *Machilinus* (Figs. 10, 11). This observed variation in length can hardly depend on movement, since both the stretches from the anterior **CX9** bridge to the apices of the **cx9** lobes and from the **CX9** bridge to the apices of the phallogonapophyseal complex are almost fully sclerotised (without membrane that could be expanded or shortened by folding), and the **CX9** bridge is too strong to become bent to a significant extent.

The tergite of segment 9 (**TG9**) and its associated formative elements (paranotal lobes **pn9**, dorsal fold **df9**) show the same condition as described above for segment 7 (and 8). However, there is no trace of a spiracle.

4.4. Setation and glandular equipment of selected parts

We consider fine-structural cuticular elements present on the penis (**pe**), gonapophyses (**gp8**, **gp9**), and styli (**sl9**). There are five main morphotypes of such elements in the studied species:

(1) Articulated setae without visible pores (e.g. Fig. 13E: grey arrowheads) are more or less slender, have a finely extended apex, and are finely grooved oblique-longitudinally; the base is countersunk into an articulatory socket, which is surrounded by a collar; their length varies. Randomly distributed on gonapophyses 8 and 9, penis, and styli, usually being more numerous on distal parts; present in all species. Taxonomists call the longest articulated setae 'macrochaetae', and the smaller ones 'microchaetae'. Macrochaetae (= sensilla chaetica) on the antenna have been considered mechanoreceptors in Archaeognatha (Berg & Schmidt 1996; Sturm & Machida 2001: p. 146 and references therein); they superficially resemble sensilla chaetica B recorded from the antennae in e.g. Mantophasmatodea (see Drilling & Klass 2010: fig. 4A,B,F). Microchaetae (= sensilla trichodea, S-shaped sensilla) have been considered to have a mechanosensory function and/or a contact chemosensory function based on their external morphology (Missbach et al. 2011: p. 327 and references therein). Articulated setae without visible pores are the most abundant sensillar morphotype on the female gonapophyses in Archaeognatha (Matushkina 2017).

(2) Articulated thorns (Fig. 16B,C) show the same structural characteristics as mentioned above for the articulated setae, but are much stouter and less pointed; their length varies. They might be thickened articulated setae (then likely also sensilla chaetica B). Only found on styli **sl9** and neighboring parts of coxal lobes of *Petrobiellus*.

(3) Non-articulated setae (e.g. Fig. 15E: black arrowhead) are moderately slender and pointed to a varied extent, and have a slightly corrugated apex; the base is not countersunk, and no basal articulation is evident. While we have not examined structural details, we note their resemblance to sensilla trichodea and basiconica (as specified in Drilling & Klass 2010: fig. 4D,E). Only found on distal part of penis; present in all species. [Note: in the previous literature, 'sensilla trichodea' has been applied to quite different types of setae, including articulated and non-articulated ones, hence the conflicting references to this term in (1) and (3).]

(4) Articulated tubular setae (Figs. 13A,B,C,E, 14A–D, 15B) are thick and straight, have a fairly blunt, partly scoop-shaped or even upcurved apex, bear a large slit-like or round orifice usually at one flank of the apex, and are finely grooved oblique-longitudinally; the base is countersunk into an articulatory socket, which is or is not surrounded by an indistinct collar. These setae are connected with unicellular glands and provide the secretion for the carrier thread during mating (Sturm & Machida 2001; see section 5.3.). Only found on gonapophyses; absent in *Machilinus* and *Petrobiellus*.

(5) Orifices of hypodermal glands ('rosette-like structures' of Matushkina 2010; see also Fröhlich & Lu 2013; Figs. 13E, 14F) usually possess several small peg-like cuticular protrusions of different shape and length around a central orifice. The distribution pattern of these glands on

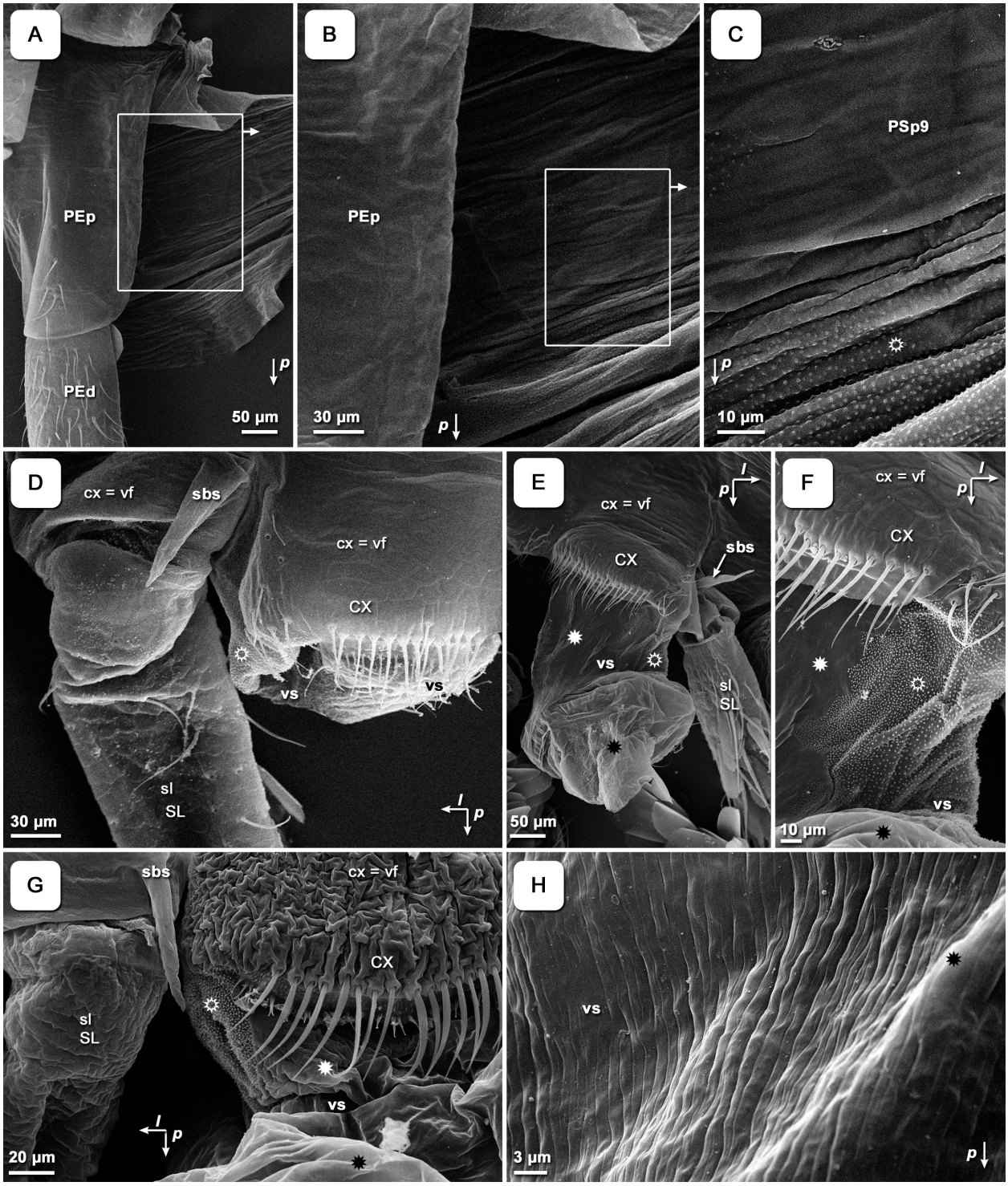


Fig. 12. SE micrographs of the male abdominal venters in *Lepismachilis notata* (A–F) and *Machilinus* sp. (G,H). **A**–**C**: Postpenial region in *L. notata* showing sclerotisation PSp9 posterior to penis base, enlarged stepwise from A to C. **D**: Posterior edge of a left pregenital coxal lobe in *L. notata* showing base of stylus (sl), stylus-base spine (sbs), and coxal vesicle (vs), dorsal view. **E**: The same but of right side and with partly everted coxal vesicle and erected spine sbs. **F**: Microsculpture of cuticle of coxal vesicle in *L. notata* (enlarged from E). **G**: Posterior edge of a left pregenital coxal lobe in *Machilinus* showing base of stylus (sl), stylus-base spine (sbs) and partly everted coxal vesicle (vs), dorsal view. **H**: Microsculpture of cuticle of extensible part of coxal vesicle in *Machilinus*. — ***Symbols, arrows, and terms***: Stars indicate membranous regions of coxal vesicle of different microsculpture (see Klass & Matushkina 2012: p. 578): white filled = type 5 cuticle; white empty = type 6 cuticle; black filled = highly elastic plicate cuticle. Arrows give directions: l = lateral, p = posterior. Terms used for labeling explained in text chapter 3.

the insect body and gland morphology suggest that these glands release aggregation pheromones for marking shelters, trails and/or conspecifics (Matushkina 2010; Fröhlich & Lu 2013). Scattered over gonapophyses, penial sclerites, and styli; not found in *Machilinus* and *Petrobiellus* (where not all parts of the cuticular surface were examined).

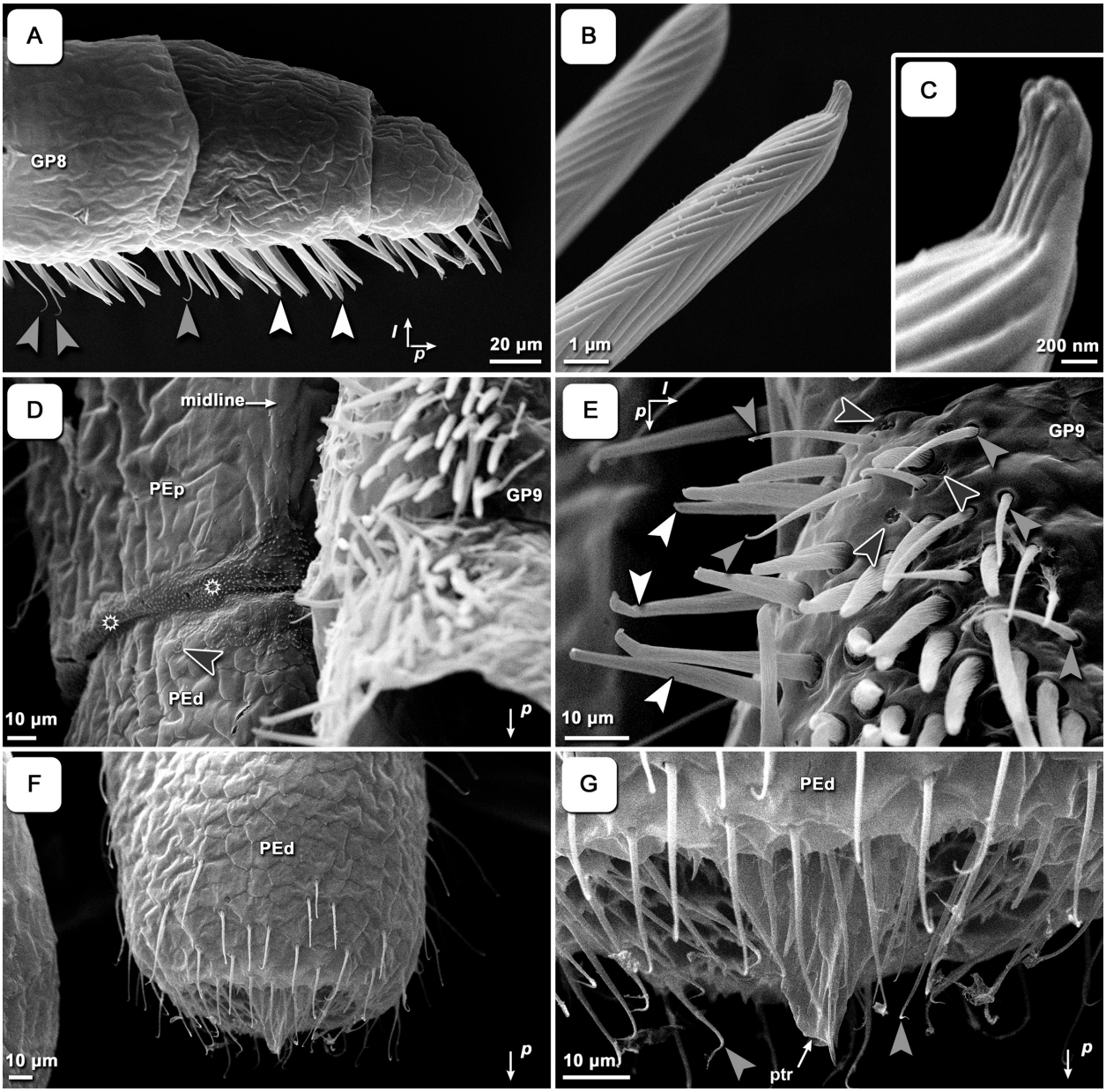


Fig. 13. SE micrographs of male genitalic structures in *Machilis hrabei*. **A**: Apial part of left gonapophysis gp8, ventral view. **B**: Tubular setae on gonapophysis gp8. **C**: Apex of a tubular seta. **D**: Midlength part of penis, ventral view (including border between proximal and distal sclerites PEp and PEd, indicated by type 6 cuticle). **E**: Setation of gonapophysis gp9 on its distal ventromesal surface. **F**: Apial part of penis, ventral view. **G**: Apex of penis, ventral view, showing setation. — ***Symbols, arrows, and terms***: Dark gray arrowheads indicate orifices of hypodermal glands; light gray arrowheads indicate slender articulated setae; white arrowheads indicate tubular setae; white empty stars indicate membranous region of type 6 cuticle. Arrows give directions: l = lateral, p = posterior. Terms used for labeling explained in text chapter 3.

Gonapophyseal equipment. In *Machilinus*, which lacks gonapophyses, the putative gonapophyseal sclerite **GP9?** bears sparse slender articulated setae of different length (Fig. 17C,D), but no other elements. In *Petrobiellus* (with **gp9** only), gonapophyses **gp9** only bear articulated setae, which are numerous on almost the entire surface (Fig. 16A,B). *Machilis*, *Lepismachilis* (with **gp8** and **gp9**), and *Pedetontus* (with **gp9** only) also bear articulated setae along the entire gonapophyses; these are more numerous on the surface facing the penis, and much more numerous on **gp9** than on **gp8**. These three taxa additionally have tubular setae, which also focally occur on the mesal surface and are limited to the distal gonapophyseal annuli: on the **gp8**, 3 distal annuli in *Machilis* and 6 in *Lepismachilis* (Figs. 13A,B, 14A,B); on the **gp9**, 6 distal annuli in *Machilis* and 8 in *Lepismachilis* and *Pedetontus* (Figs. 13E, 14C,D, 15B); except for **gp8** of *Machilis* this is all annuli except the basal-most. In *Machilis*, *Lepismachilis*, and *Pedetontus* orifices of hypodermal glands are scattered among the setae, mainly on the mesal gonapophyseal walls.

Penial equipment. The sclerites **PEp** and **PEd** of *Petrobiellus* lack all of the cuticular elements here consid-

Table 1. Character matrix for the Archaeognatha species herein studied. Only characters of the male genitalic region are included. Characters and their states are defined in section 4.5. Character numbers are written vertically in the first two lines. –: character not applicable.

Character	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
Machilis hrabei	0	1	0	0	0	0	0	0	1	0	0	2	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	1	1	0	0	1	1	1
Lepismachilis notata	0	1	0	0	0	0	1	0	1	0	0	2	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	1
Pedetontus unimaculatus	0	0	0	0	1	0	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1	1	–	0	0	0	1
Petrobiellus takunagae	0	1	0	0	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	1	0	0	0	1	0	0	0	1	1	0	0	1	1	0	–	1	1	1	0
Machilinus sp.	1	1	1	1	–	1	0	0	1	1	0	2	1	1	1	0	1	0	1	1	1	0	0	0	1	0	0	0	0	1	–	1	0	2	–	–	1	1	1

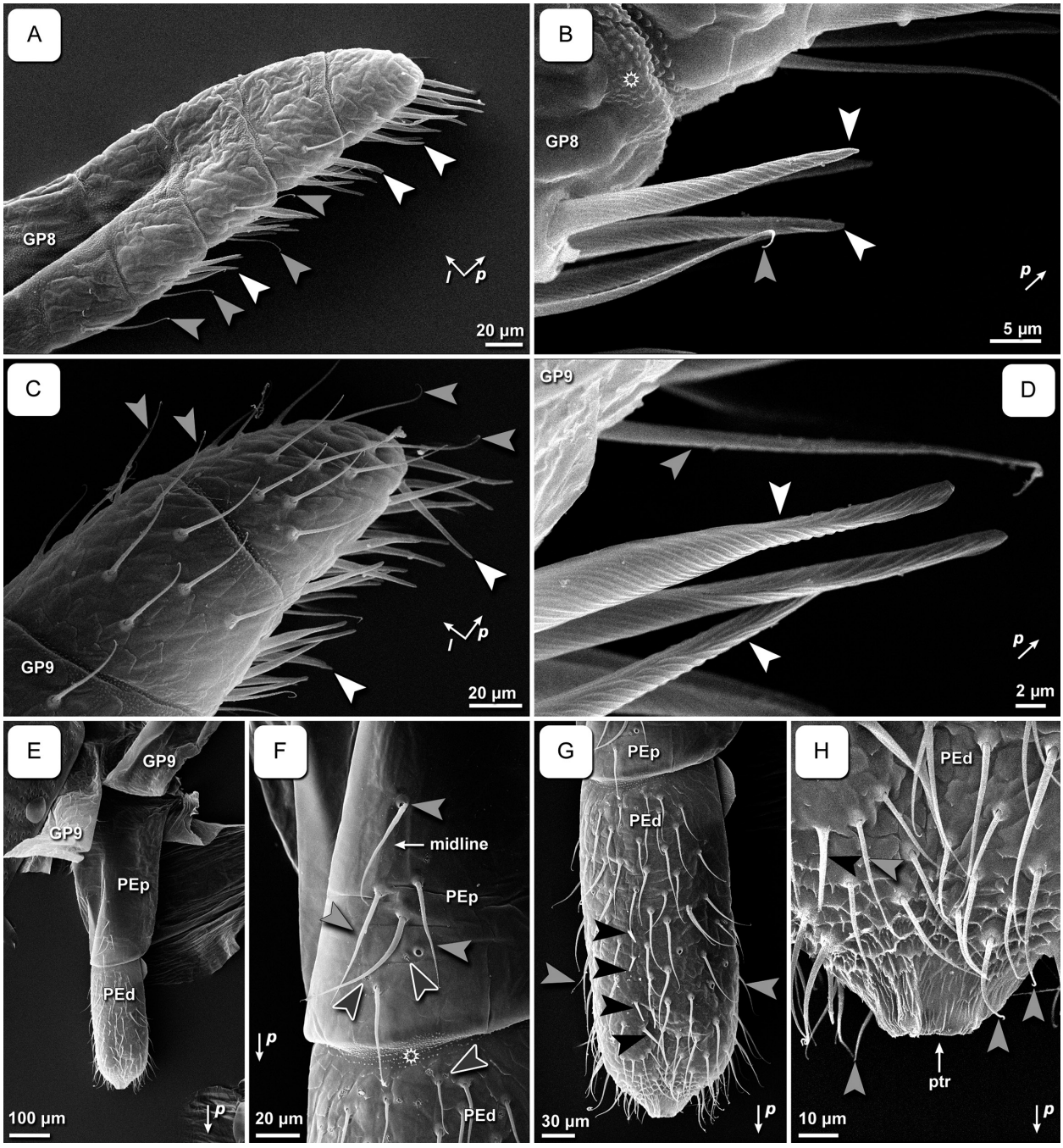


Fig. 14. SE micrographs of male genitalic structures in *Lepismachilis notata*. **A**: Apial part of left gonapophysis gp8, ventral view. **B**: Setae on gonapophysis gp8. **C**: Apial part of left gonapophysis gp9, lateral view. **D**: Setae on gonapophysis gp9. **E**: Penis, ventral view. **F**: Midlength part of penis, ventral view (including border between proximal and distal sclerites PEp and PEd, indicated by type 6 cuticle). **G**: Apial part of penis, ventral view. **H**: Apex of penis, ventral view, showing setation and phallotrema. — ***Symbols, arrows, and terms***: Dark grey arrowheads indicate orifices of hypodermal glands; white arrowheads indicate tubular setae on gonapophyses; light grey arrowheads indicate slender articulated setae; black arrowheads indicate thick unarticulated setae on penis; white empty stars indicate membranous regions of type 6 cuticle. Arrows give directions: l = lateral, p = posterior. Terms used for labeling explained in text chapter 3.

ered. In *Machilinus* sclerite **PE** (and **GP9?**) only bears short articulated setae (Fig. 17D,E). In *Machilis*, *Lepismachilis*, and *Pedetontus* sclerites **PEp** and **PEd** bear articulated setae of varied length and thickness, which are more numerous apially, and placed more densely in *Lepismachilis* and *Pedetontus*. Orifices of hypodermal glands additionally occur in *Machilis* and *Lepismachilis* (Figs. 13D–G, 14E–H). Only in *Lepismachilis* and *Pedetontus* the distal sclerite **PEd** bears a few non-articulated setae (Figs. 14G,H, 15C). The membranous region around the phallotrema bears articulated and non-articulated setae in all species (Fig. 15D,F), probably except *Petrobiellus*.

Stylar equipment. The equipment of **sl8** and **sl9** is in all species similar to that of pregenital styli (except for **sl9** of *Petrobiellus*). Styli are scaled (*Machilis*, *Lepismachilis*, and *Pedetontus*) or unscaled (*Petrobiellus* and *Machilinus*), and densely covered with long, thin to fairly stout articulated setae, apial ones being distinctly stouter; few orifices of hypodermal glands are scattered over the stylus. Stylus **sl9** of *Petrobiellus* (Fig. 16A,D,E) is special by bearing articulated thorns, which form a group on the dorsal surface of **sl9**; such thorns also occur on the distal mesal and ventral surfaces of the coxal lobe **cx9** (Fig. 16D).

4.5. List of characters

The intention of the following list and the character matrix (Table 1) is to document and categorise the differences found among the archaeognathan species here studied. The matrix is too small to yield convincing phylogenetic results, but by addition of further taxa it can easily be expanded into a dataset for analysing phylogenetic relationships in Archaeognatha. We therefore also include many characters that with the current sample are not informative on phylogeny, but appear promising with an expanded taxon sample.

Homonomous elements of different abdominal segments can in each single sampled taxon show the same structuring across all these segments; the homonomous elements then also consistently show the same differences among different taxa. In such cases, for any occurring interspecific difference one would not code a separate character for each segment, but code one character valid for all segments concerned. This often applies, for instance, to elements of the fairly homogeneous midabdominal segments. However, if selected taxa differ with regard to homonomous elements showing identical versus different conditions in a particular character, the character must be coded separately for certain (groups of) segments. In segments 7 and 8 of male Archaeognatha, many characters show serial identity in structure; these characters are coded only once, being valid for both segments. In other structural characteristics the segments differ (in at least one species); then characters are coded separately for segments 7 and 8. The decision for either serial (polysegmental) or separate (monosegmental) coding is to some extent subjective, and a change from poly- to monosegmental coding can be required as soon as a taxon is newly included that shows an intersegmental difference not present in the previously included taxa. In each single character here coded for both segments 7 and 8, we name the elements of both segments, separated by '//'.

01 Length of sternite **STt7** at midline: **[0]** ≥ 1/3 of length of venter 7; **[1]** < 1/4 of length of venter 7. — Length of venter 7 measured from anterior margin of **STt7** to anterior end of notch **cn7**.

02 Connection between coxa **CX7** and postlaterocoxa **LCp7**: **[0]** Absent: separated by a stripe of membrane; **[1]** Present: connected by equally strong sclerotisation.

03 Presence of an independent intersternum **STi7** // **STi8**: **[0]** Present; **[1]** Absent. — In the taxa with state [1], **STi7** // **STi8** is likely entirely absent, but its fusion with **STt7** // **STt8** combined with a reduction of its anterior part cannot be fully excluded; therefore, "independent" was included in the character definition.

04 Presence of spina **sn7**: **[0]** Present; **[1]** Absent.

05 Shape of spina **sn7**: **[0]** Narrow base, cylindrical (apex rounded); **[1]** Wide base, rounded triangular. — Not applicable to taxa with state [1] in character 04.

06 Presence of antecostal groove **ac7**: **[0]** Present; **[1]** Absent.

07 Depth of midline notch **cn7** between coxal lobes **cx7**: **[0]** Deep; **[1]** Very shallow. — This character is partly correlated with the degree of development of the expansions **me7**, which flank the notch **cn7** (see character 08).

08 Degree of projecting of mesal part of hind edge of coxal lobe **cx7** (expansion **me7**): **[0]** Not or hardly projecting beyond part of hind edge further laterally; **[1]** Significantly projecting beyond part of hind edge further laterally. — See remark on character 07.

09 Presence of posterosternite **PS7** // **PS8**: **[0]** Present; **[1]** Absent. — A posterosternite, **PS6**, can also be present in segment 6 (and possibly further pregential sclerites; not considered here in character coding).

10 Location of spiracle **si7** // **si8** on paranotal lobe **pn7** // **pn8**: **[0]** On the mesally facing wall; **[1]** On the laterally facing wall. — The position is in both states close to the apial edge of lobe **pn** and upon tergal sclerotisation **TG7** // **TG8**.

11 Difference between venters 7 and 8 regarding the distinctness of a midline angle between the left and right membranous stripes separating the sternite (**ST**) from the coxites (**CX**): **[0]** Angle much less distinct on venter 8 than on venter 7; **[1]** Angle similarly distinct or indistinct on venters 7 and 8. — The character is correlated with the posterior extension and truncatedness of the sternite.

12 Connection between coxa **CX8** and postlaterocoxa **LCp8**: **[0]** Absent: fully separated by a stripe

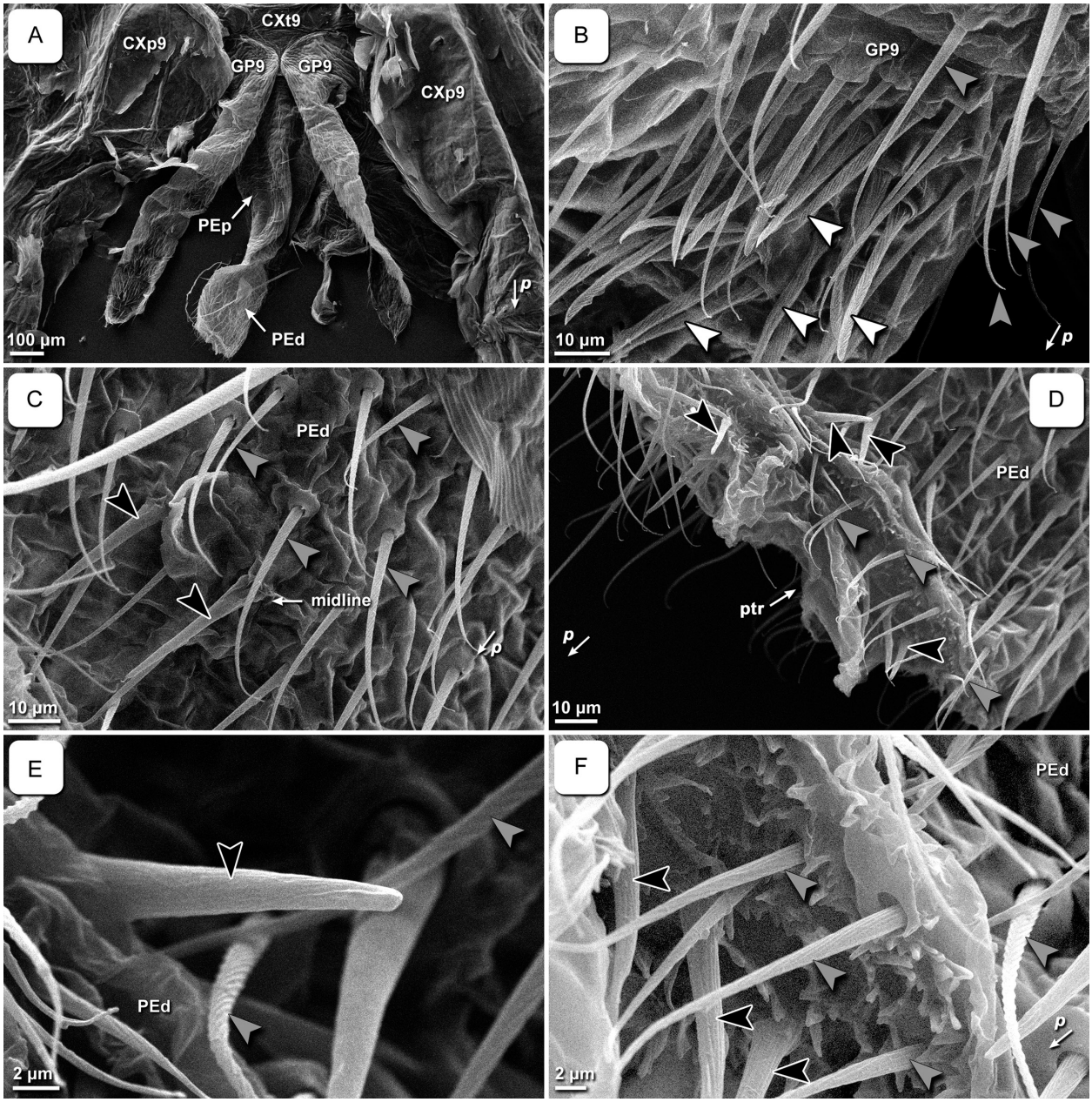


Fig. 15. SE micrographs of male genitalic structures in *Pedetontus unimaculatus* (specimen distinctly deformed during preparation). **A**: Venter of 9th abdominal segment, ventral view. **B**: Setation of gonapophysis gp9 on its distal ventromesal surface. **C**: Setation of ventral apial part of penis. **D**: Apex of penis, ventral view, showing setation and phallotrema. **E**: Close view on thick unarticulated seta on penis. **F**: Apex of penis, membranous region around phallotrema with setae. — ***Symbols, arrows, and terms***: White arrowheads indicate tubular setae on gonapophyses; light grey arrowheads indicate slender articulated setae; black arrowheads indicate thick unarticulated setae on penis. Arrows give direction: p = posterior. Terms used for labeling explained in text chapter 3.

of membrane; **[1]** Present: connected by distinctly weaker sclerotisation. **[2]** Present: connected by equally strong sclerotisation. — The character is best treated as ordered.

13 Presence of basal fusion of left and right coxal lobes **cx8** (formation of ventral fold **vf8**): **[0]** Absent; **[1]** Present.

14 Presence of gonapophyses **gp8**: **[0]** Present; **[1]** Absent.

15 Connection between coxa **CX9** and antelaterocoxa **LCa9**: **[0]** Absent: separated by membrane; **[1]** Present: connected by equally strong sclerotisation.

16 Connection between sternum **STt9** and antelaterocoxa **LCa9**: **[0]** Absent: separated by membrane (type 6 cuticle); **[1]** Present: connected by sclerotisation of varied strength.

17 Presence of an independent intersternite **STi9**: **[0]** Present; **[1]** Absent. — See below for alternative coding: character 17'.

18 Shape of posterior margin of sternum **STt9**: **[0]** Straightly transverse to slightly convex; **[1]** Strongly expanded posteriorly, tongue-shaped. — As the anterior margin of the median part of the coxal sclerotisations **CX9** (or **CXt9**) quite closely fits the hind mar-

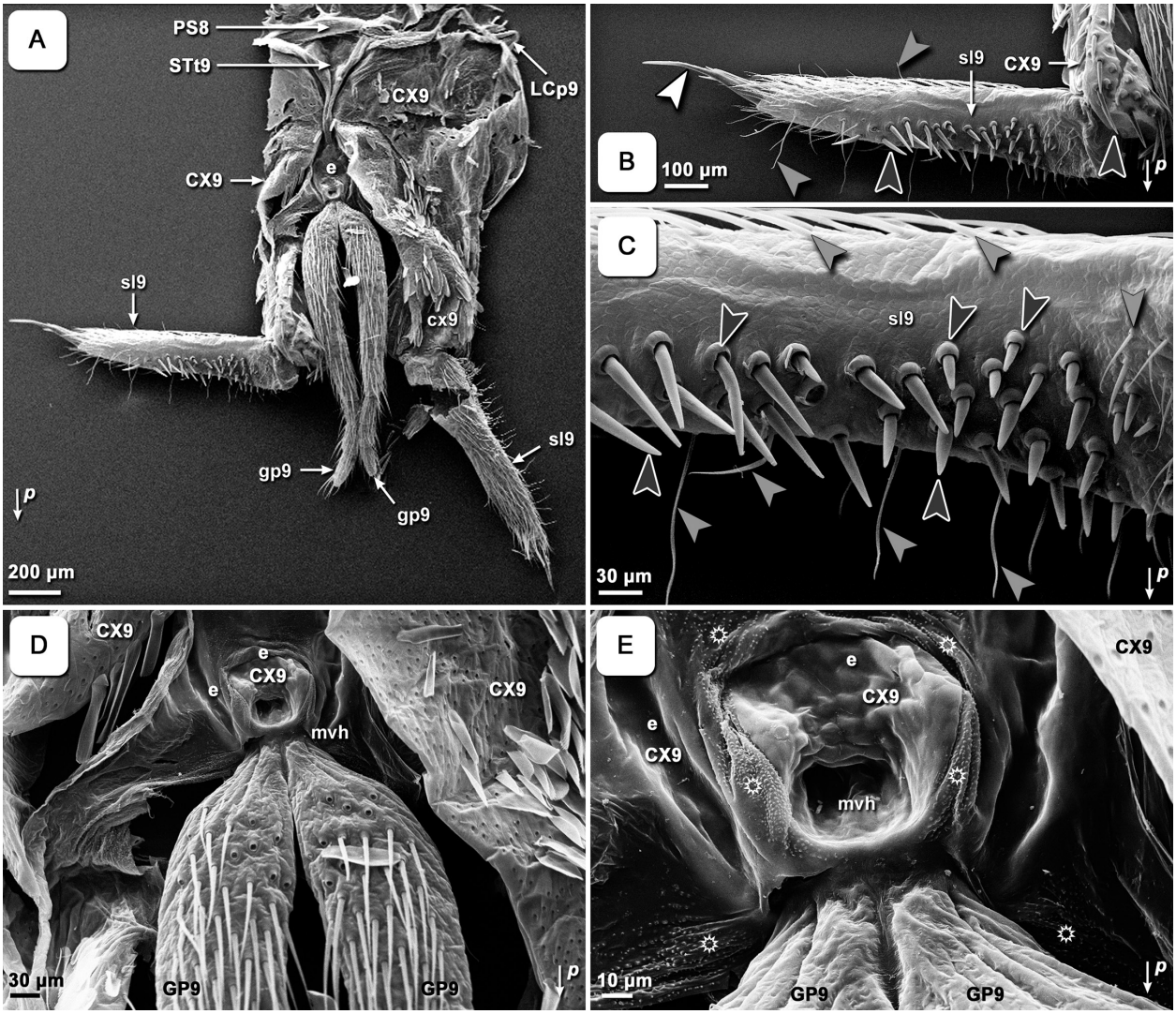


Fig. 16. SE micrographs of male genitalic structures in *Petrobiellus takunagae* (penis and lateral region of right coxal lobe cx9 removed). **A**: Venter of 9th abdominal segment, essentially ventral view but right stylus twisted to a mesal view. **B**: Right stylus sl9 and apial part of coxal lobe cx9, mesal view, showing articulated setae and thorns. **C**: Close-up of slender articulated setae and thorns on stylus sl9 (enlarged from B). **D**: Bases of gonapophyses gp9 and median sclerite bridge e of coxa CX9, ventral view. **E**: Articulation between ventrobasal sclerotisation GP9 of gonapophyses gp9 and median sclerite bridge e of coxa CX9. — ***Symbols, arrows, and terms***: Dark grey arrowheads indicate thorns; light grey arrowheads indicate slender articulated setae; white arrowhead indicates apial spine of stylus 9; white empty stars indicate membranous region of type 6 cuticle. Arrows give direction: p = posterior. Terms used for labeling explained in text chapter 3.

gin of **STt9**, the **CX9** margin is straight to slightly concave in case of state [0], and deeply notched in case of state [1]. This is not coded as a separate character, but it could be coded if species are detected that show a less parallel course of the opposing **STt9** and **CX9** margins.

19 Elevation of median part of sternum **STt9** relative to lateral parts: **[0]** Absent: sternum overall flat or slightly convex; **[1]** Present by a discrete step on each side.

20 Connection between coxa **CX9** and postlaterocoxa **LCp9**: **[0]** Absent: separated by membrane; **[1]** Present: connected by equally strong sclerotisation.

21 Size of postlaterocoxa **LCp9**: **[0]** Large, far and distinctly projecting from lateral margin of coxa **CX9**; **[1]** Small, hardly projecting from lateral margin of coxa **CX9**.

22 Division of coxa **CX9** into sclerites **CXt9** (bridge part **e**) and **CXp9** (posterolateral parts) by membrane: **[0]** Absent; **[1]** Present.

23 Presence of a pair of posterior expansions on median posterior margin of bridge part **e** of **CX9**: **[0]** Present; **[1]** Absent. — With the current taxon sample, in all cases of state [0] the expansions establish especially close contact with the gonapophyseal sclerotisations **GP9**.

24 Presence of a deep median hollow **mvh** on bridge part **e** of **CX9**: **[0]** Absent; **[1]** Present.

25 Presence of a pair of shallow holes where sclerite(s) **GP9** (or their extensions **k**) contact the posterior margin of **CX9**: **[0]** Absent; **[1]** Present.

26 Shape of ventral wall of coxal lobe **cx9**: **[0]** Fairly even, i.e. gradually ascending (to a varied extent) towards the higher mesal part of lobe **cx9**; **[1]** Strongly

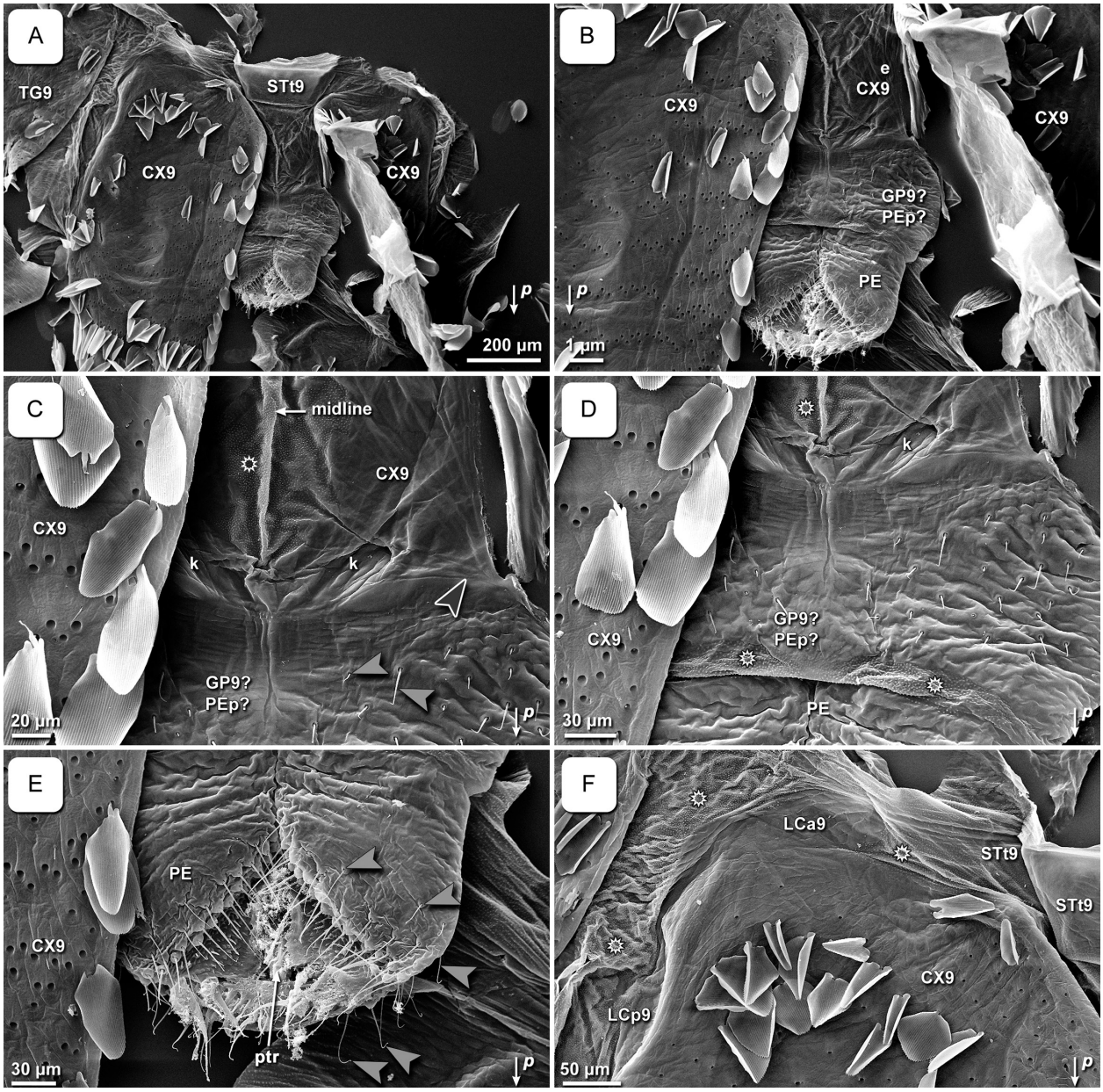


Fig. 17. SE micrographs of male genitalic structures in *Machilinus* sp. **A**: Venter of 9th abdominal segment, ventral view. **B**: Phallogonapophyseal complex and surrounding parts, ventral view. **C**: Close-up of articulation between coxa CX9 and sclerite GP9?. **D**: Sclerite GP9?, ventral view, showing midventral pattern of microsculpture and setation. **E**: Apex of penis, ventral view, showing setation and phallotrema. **F**: Anterolateral region of coxa CX9 fused with antelaterocoxa LCa9 and postlaterocoxa LCp9. — ***Symbols, arrows, and terms***: Dark grey arrowhead indicates articulation between coxa CX9 and sclerite GP9?; light grey arrowheads indicate slender articulated setae; white empty stars indicate membranous regions of type 6 cuticle. Arrows give direction: p = posterior. Terms used for labeling explained in text chapter 3.

bent, i.e. first running mesad and then abruptly bending ventrad to form the higher mesal part of lobe **cx9**.

27 Extension of ventral mesal edge **h** of coxal lobe **cx9**: **[0]** Ending near the lateral flank of sternum **STt9** and not extending laterally, coxal lobe **cx9** thus without an anteriorly projecting basal part; **[1]** Continuing far laterally from near the lateral flank of sternum **STt9**, coxal lobe **cx9** thus with an anteriorly projecting basal part. — The projecting of lobe **cx9** to the anterior is strongly pronounced in *Machilis* and *Pedetontus*, but less in *Lepismachilis*.

28 Shape of stylus **sl9**: **[0]** Straight; **[1]** With a laterally directed bend near the base.

29 Development of mesal expansion **me9** of coxal lobe **cx9**: **[0]** A distinct posteriorly projecting process; **[1]** An indistinct bulge hardly projecting posteriorly.

30 Presence of gonapophyses **gp9**: **[0]** Present; **[1]** Absent.

31 Presence of basal fusion of left and right gonapophyses **gp9**: **[0]** Absent; **[1]** Present. — Not applicable to taxa with state [1] in character 30.

32 Presence of basal fusion of left and right gonapophyseal sclerites **GP9**: **[0]** Absent; **[1]** Present. — The

basal penial sclerite of *Machilinus* is interpreted either as the medially fused **GP9** alone, or as a combination of medially fused **GP9** and sclerite **PEb**. The ambiguous interpretation makes no difference for *Machilinus* with the character definition here given.

33 Number of (near-)cylindrical sclerites along penis: **[0]** 1 (**PE**); **[1]** 2 (**PEp**, **PEd**). — See below for alternative coding: character 33'.

34 Posterior extension of penis (**pe**) relative to coxal lobes **cx9**: **[0]** Far beyond apices of lobes **cx9**; **[1]** To distal parts or apices of lobes **cx9**; **[2]** Not beyond proximal part of lobes **cx9**. The character is best treated as ordered.

35 Presence of tubular setae on gonapophysis **gp8**: **[0]** Present; **[1]** Absent. — While in taxa lacking gonapophyses **gp8** a level cuticular area homologous with gonapophyses **gp8** can be assumed to be present, we consider the formation of projecting gonapophyses **gp8** as required for scoring this character; the character is thus not applicable to taxa with state [1] in character 14.

36 Presence of tubular setae on gonapophysis **gp9**: **[0]** Present; **[1]** Absent. — Not applicable to taxa with state [1] in character 30 (for the same reason as given for gonapophysis **gp8** in character 35).

37 Presence of articulated setae on penial sclerite(s) **PE**: **[0]** Present; **[1]** Absent.

38 Presence of non-articulated setae on penial sclerite(s) **PE**: **[0]** Present (at least on distal part of **PE**); **[1]** Absent.

39 Presence of articulated thorns on vertical mesal region of coxal lobe **cx9** and mesal surface of stylus **sl9**: **[0]** Present; **[1]** Absent.

The two following characters represent alternative codings for the above characters 17 and 33; they reflect alternative interpretations of the structures concerned by the characters.

17' Connection between sternum **STt9** and intersternum **STi9**: **[0]** Absent: separated by membrane; **[1]** Present: connected by equally strong sclerotisation. — The two alternative codings in characters 17 and 17' refer to the competing hypotheses of whether **STi9** is (17) absent or is (17') integrated into '**STt9**' (which then is **STt9+STi9**) when it is not present as a discrete sclerite. The scoring is for all taxa identical for 17 and 17'. If with an expanded taxon sample both hypotheses prove to be true (in different taxa), both 17 and 17' should be used, as separate characters.

33' Condition of proximal penial sclerite **PEp**: **[0]** Plate-like: only in basal ventral wall of penis, not ascending dorsally and not closed to a cylinder; **[1]** (Near-) cylindrical: Surrounding the entire base of the penis, closed to a cylinder dorsally (but potentially open or weak along ventral midline). — The two alternative codings in characters 33 and 33' refer to the competing hypotheses of whether in *Machilinus* the sclerite anteriad of the ventral base of the penis is (33) purely gonapophyseal (**GP9**) or is (33') fused gonapophyseal (**GP9**) + penial (**PEp**). The scoring is for all taxa identical for 33 and 33'.

5. Discussion

5.1. Comparison with morphological results from previous publications

It makes little sense to compare our morphologhical results with data and illustrations in Snodgrass (1931, 1935, 1936), Gustafson (1950), Matsuda (1957), Becker (1966), and Hädicke et al. (2014), where the majority of the skeletal features is not considered. Only the work of Bitsch (1968 on *Machilinus*; 1974b on species of *Machilis*, *Lepismachilis*, and *Dilta*) and some of the drawings in Birket-Smith (1974 on *Petrobius lohmanderi*) are here relevant, and there are only few differences or points of variation to be pointed out.

Bitsch's (1974b) data on the exoskeleton are not very detailed, and many positional relationships are not evident from his simple line drawings. In addition, it is often not specified whether some character was observed in all examined species or only in some. As far as data are clear, they agree with our findings in *Machilis hrabei* and *Lepismachilis notata* – with the following exceptions:

(1) Bitsch (1974b: p. 205, figs. 1B, 4) reports that the left and right parts of the anterior coxal bridge (his **scS*** sclerites, **CXt9** herein) are not connected across the midline. We clearly found **CXt9** to be continuous across the midline in all studied species. The only potential reminiscence of a median separation we detected is an immovable suture in *Machilis* (the genus to which Bitsch's figs. 1B, 4 refer).

(2) Bitsch (1974b: p. 207) writes that the two gonapophyses **gp9** show a basal median fusion; we confirm this for *Lepismachilis* (for which Bitsch's result is supported by serial cross sections: fig. 2B therein), but note that in *Machilis* the **gp9** are entirely free from each other (character 31 in section 4.5.).

(3) Bitsch (1974b: p. 205) writes that the lateral end of postlaterocoxite **LCp9** (his 'laterocoxite') is in contact with tergite **TG9**; we found a wide separation between the two sclerites, which is established by the membrane forming the mesal face of the paranotal lobe **pn9**.

(4) Birket-Smith (1974) reports paired, cuticular ventral tendons (**vt***) that arise on the anterior margin of each abdominal venter, presumably on the primary segmental border. He also reports a median cuticular tendon (**vt10***) arising from the ventral base of the penis, which he interprets as medially fused **vt*** tendons (Fig. 23A,B, yellow). Bitsch (1973, 1974a,b) did not report any of these tendons. We found a distinct basipenial tendon (**bpt** = **vt10***) in three of our species (Figs. 2, 4, 6), but in none

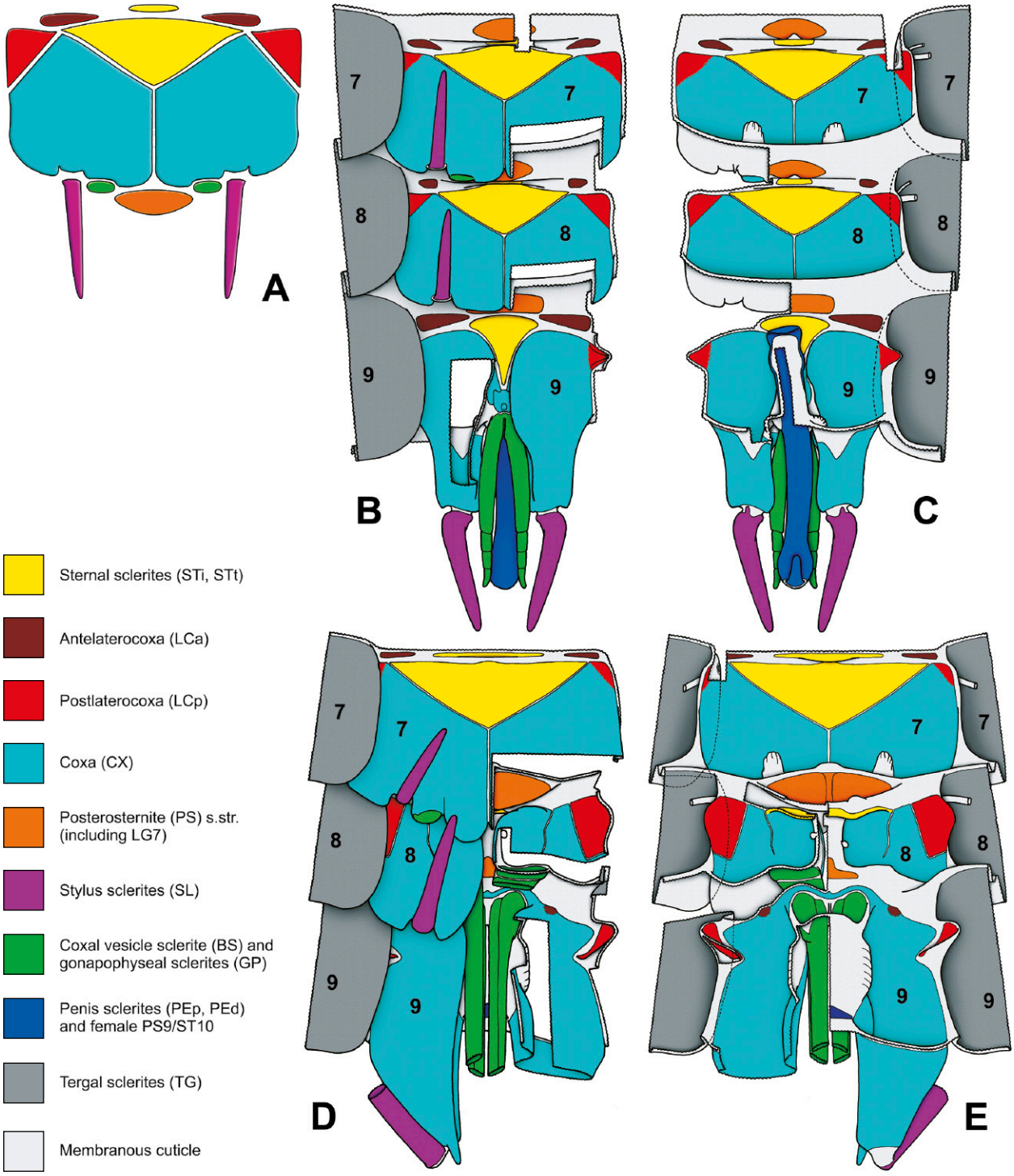


Fig. 18. Survey of interpretation and homonomy relations (between sexes and segments) of sclerotisations in the archaeognathan abdomen, exemplified by *Petrobiellus takunagae*. **A**: Generalised pregenital abdominal venter as present in both sexes. **B**,**C**: Male postabdomen, essentially venters 7–9, ventral (B) and dorsal (C) views. **D**,**E**: Female postabdomen, essentially venters 7–9 (based on Klass & Matushkina 2012), ventral (D) and dorsal (E) views. — Numbers 7, 8, 9 upon the terga TG and coxae CX indicate abdominal segments. Sclerite PS9/ST10 of female and sclerite PE (penial) of male could belong to the PS sclerotisations (then 9th-segmental) or be anterior 10th-segmental sclerotisations (see Figs. 19 and 23); if 10th-segmental, PE potentially includes eusternal (ST10), coxal (CX10), and especially gonapophyseal (GP10) sclerotisations, PS9/ST10 may be limited to eusternal (ST10) and coxal (CX10) components (chapter 8).

we found a trace of paired **vt*** tendons in the preceding segments (if cuticular, they should have been visible in macerated specimens).

Our results on *Machilinus* fully agree with Bitsch's (1968) work on this genus, which is focussed on the soft internal genitalia. The condition of the ectodermal gonoduct (likely composed of endophallus and ejaculatory duct) as not reaching beyond the penis lumen, which we found in *Machilis*, is also reported for *Machilinus* by Bitsch (1968: p. 109).

5.2. Interpretation of structures

Our interpretation of sclerotisations in male and female Archaeognatha is surveyed in Fig. 18, based on *Petrobiellus*; for formative elements please refer to Figs. 1–11. These interpretations and our application of a standardised terminology to the included elements only refer to homonomies and homologies in the abdomen of Archaeognatha and other insects, including both sexes. We neither refer to homonomies between the abdomen and other tagmata nor to homologies between Insecta and other arthropod taxa. However, we generally consider the abdominal coxal lobes, styli, and coxal vesicles / gonapophyses as representing parts of the segmental limbs, leaving open whether coxal vesicles / gonapophyses are endites of a proximal podomere (Bitsch 1994) or endopods (Hädicke et al. 2014). Within this frame, our interpretations for the elements of the male (and female) genitalic region of Archaeognatha largely agree with those of Bitsch (1968, 1973, 1974a,b, 1994). We detailed most of this with regard to the female genitalic region in Klass & Matushkina (2012); and as our terminology reflects hypotheses of homology and homonomy, these hypotheses are evident from the naming of elements in Klass & Matushkina (2012) and herein.

Most homonomies among segments and between sexes are trivial due to great overall similarity, and we only discuss here the few differences compared to Bitsch and cases that we find more ambiguous than he did. There are, however, two highly problematic issues of interpretation, which are intercorrelated and which will be addressed here separately: The first concerns the phallic organs, whose interpretation at the insect level has been extensively discussed in the literature but has remained conflictual. The second concerns the **PS** group of sclerotisations ('posterosternites'), to which the penial sclerites **PE** as well as the female genital plate **LG7** (languette sclerite) may also belong, and which have hardly ever been considered in the literature.

Non-phallic elements. Bitsch (1974b: p. 204, figs. 1B, 4), likely based on the configurations in *Machilis* and *Lepismachilis*, interprets the entire anterior sclerite of venter 9 (**STt9**+**LCa9** in Figs. 1–4) as the sternite **STt9**, antelaterocoxae **LCa9** ('precoxites' in Bitsch 1974b) being absent on venter 9. In contrast, we interpret the lateral parts of this sclerite as the **LCa9**, because they are semi-detached from **STt9** by broad sublateral weak zones in *Machilis*, *Lepismachilis*, and *Pedetontus*, and the positionally corresponding sclerotisations are fully separated from a median **STt9** by membrane in *Petrobiellus* (Figs. 7–9). Our interpretation also agrees with the position of these **LCa9** sclerotisations compared to **LCa** sclerites on preceding venters (in the identification of these we agree with Bitsch 1973, 1974a,b). The identification of **LCa9** sclerotisations cannot be further substantiated by muscle attachments, as such are absent on **LCa** sclerites (Bitsch 1973, 1974a,b).

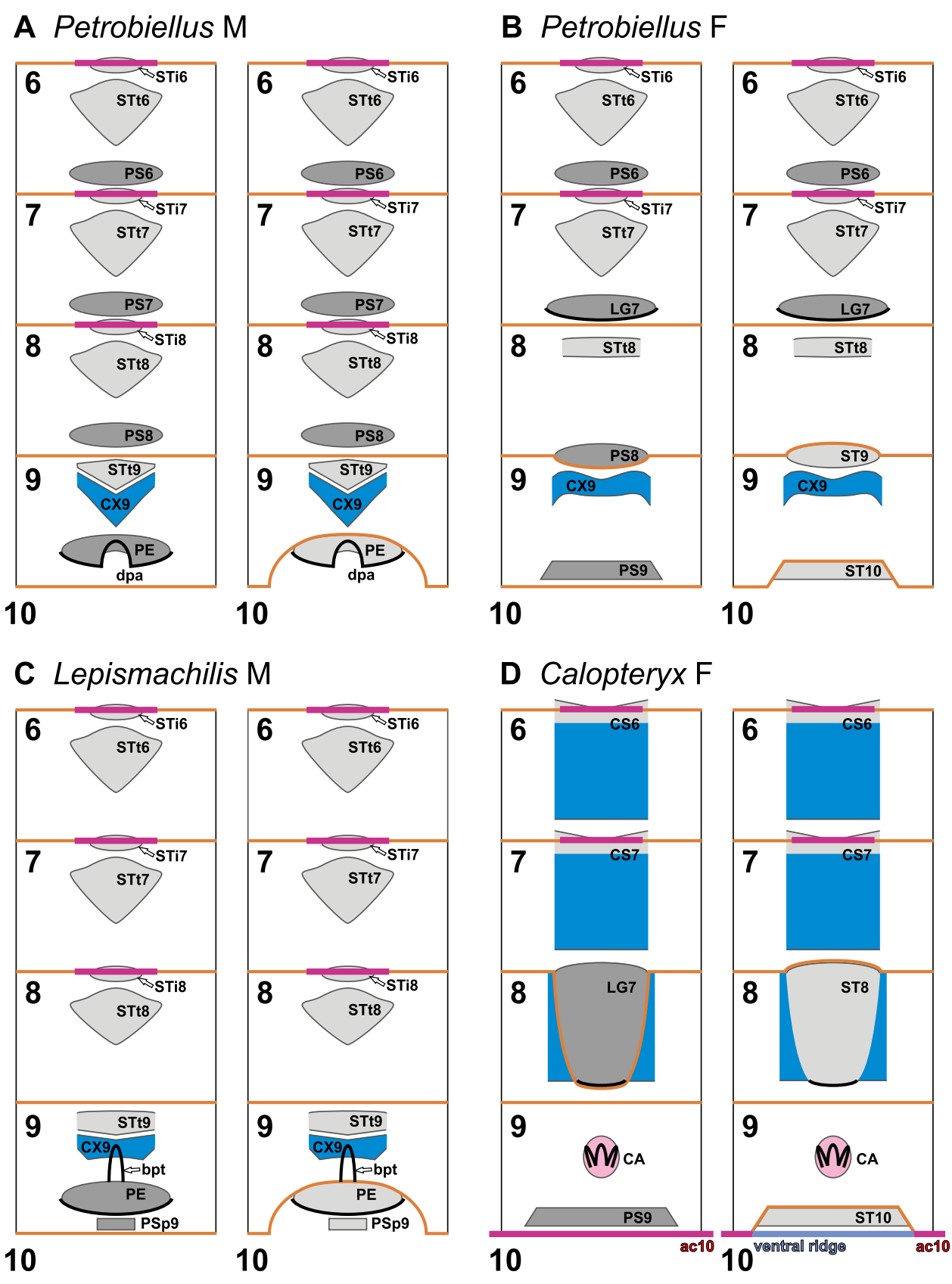
Bitsch (1968) interprets the **GP9?** sclerite of *Machilinus* (Figs. 10, 11, 17) as a genuine basal sclerite of the penis (**sbp*** therein, **PEp** herein). We consider this as one option, but find it more likely that **GP9?** is derived from the gonapophyseal sclerites **GP9** (fused at midline) or is a fusion product **PEp+GP9** (see characters 33 versus 33' in section 4.5.). More evidence is needed for a solution. The course of (latero)coxogonapophyseal muscles and of intrinsic penial muscles, if present in *Machilinus*, could perhaps resolve the problem. Penial muscles connect the proximal and distal penis sclerites (**PEp**, **PEd**) in *Machilis* (**80*** in Bitsch 1974b: fig. 4), but are not reported for *Machilinus* in Bitsch (1968). The point could also be clarified by meinertellids that show a penis base morphology as *Machilinus*, but have in addition a tendon **bpt** (marking the ventral penis base and the basal rim of **PE** sclerotisations).

Hädicke et al. (2014) refer to the female morphology of Archaeognatha, but interpretations would in the same way affect male structures. While we agree with the representation of the stylus of venter 9 (**sl9**) compared to styli of the preceding segments in their schematic fig. 8, we do not agree with it in their fig. 6B (marked in blue). In the latter, stylus 9 is claimed to comprise the process interpreted as stylus **sl9** herein (e.g. Fig. 1) and in Klass & Matushkina (2012: fig. 1) plus the mesal part of the coxal lobe **cx9** down to its base. This is at odds with all serial similarities between abdominal venter 9 and preceding venters, including the musculature (see Bitsch 1974a, e.g. posterior insertions of stylus muscles **60*** in figs. 5, 6). The authors' claim of "coxopodites of abdominal metamere 9" (coxal lobes **cx9**) not being visible in their fossil (p. 174 therein) is incorrect; it is a result of their misinterpretation of the stylus **sl9** (in their fig. 6B).

We additionally note that the newly reported spine **sbs** (Fig. 12D,E,G), which is placed laterally on the dorsal face of the coxal lobe and close to the stylus base, might contribute to a long-standing dispute: whether the abdominal styli **sl** are possibly homonomous with small articulated processes on the thoracic coxae. Like e.g. Bitsch (1994: p. 121) we contradict this homonomy, but note that the abdominal spines **sbs** might be plausibly homonomous with the processes on the thoracic coxae (though this is difficult to test).

PS sclerites and phallic organs. The sclerites called **PS** herein and in Klass & Matushkina (2012) and Klass (2008) form a quite heterogeneous group (survey in Fig. 19: dark grey). Here we define sclerotisations **PS** based on those present on abdominal venters 6 and 7 in male *Petrobiellus* (**PS6**, **PS7** in Figs. 7, 8), i.e. each sclerotisation being homonomous (in female or other segments) or homologous (in other taxa) with such a **PS6** or **PS7** is a true **PS** sclerotisation. In this sense, **PS** sclerites should typially be unpaired and located posteromedially on a venter (hence **PS** = 'posterosternite'), but these characteristics might vary. It is unclear whether such **PS** sclerites are muscled, since pregenital **PS** sclerites were reported neither by Bitsch (1973, 1974a,b) nor by Birket-Smith (1974).

In the abdominal segments up to 7 of Archaeognatha, the posteromedian location on a venter can be deter-


A Petrobiellus M
B Petrobiellus F
C Lepismachilis M
D Calopteryx F
6
7
8
9
10
STi6
STt6
PS6
STi7
STt7
PS7
STi8
STt8
PS8
STt9
CX9
PE
dpa
LG7
PS9
ST9
ST10
CS6
CS7
ST8
CA
bpt
PSp9
ac10
ventral ridge
Sclerotisations
(only those at midline):
eusternal
ST
posterosternal
PS
coxal
CX
CA

mined by structures clearly representing the segmental border following (antecosta **ac**, spina **sn**; e.g. Figs. 2, 8, 19A–C). In our sampled male archaeognathans we could detect (very weak) **PS6** and **PS7** sclerites only in *Petrobiellus*. Female *Petrobiellus* also have weak pregenital **PS** sclerites up to **PS6**, which resemble those in the males. In addition, the (likewise weak) languette sclerite **LG7** reported for female *Petrobiellus* (Klass & Matushkina 2012: figs. 1, 2) takes the same position on venter 7 as **PS7** in male *Petrobiellus* and is thus likely a strongly outwardly folded (by the genital fold/lobe **gf**), enlarged **PS7** (Fig. 19A,B). It is closely associated with the female gonopore, which lies apially on fold **gf**. The female **LG7** = **PS7** is also the only unambiguous **PS** sclerite for which a wider occurrence across Insecta is supported: it forms the female genital plate (= primary subgenital plate) in zygentomans (e.g. *Nicoletia*, Rousset 1973: **lang*** in figs. 9, 10) and Dictyoptera (Klass 1998: **ls*** in figs. 1–10), and likely in many other Pterygota, where **LG7** has probably fused with lateroventral 8th-segmental sclerites (in the way indicated in Fig. 19D left picture of an odonatan and in Klass & Ulbricht 2009: fig. 42; similar to Deuve's 2018, e.g. fig. 4, configuration of the 'sympleural I' type of female genitalia, which, however involves only lateroventral 8th-segmental sclerites, but no 7th-segmental languette lobe).

Abdominal segments 8 and 9 of both sexes of Archaeognatha are usually not posteriorly bordered by antecostae and/or spinae. Therefore, it is difficult to determine whether a midventral sclerite lies on the posterior part of segment 8 resp. 9 (then being a potential **PS**) or on the anterior part of the following segment 9 resp. 10 (then not being a **PS**, but likely a eusternal sclerite, **ST**). **PS** candidate sclerites in Archaeognatha are those labeled **ST9?** (possibly **PS8**?) and **PS9** (a true **PS9**?) in female *Petrobiellus* (Klass & Matushkina 2012: figs. 1, 2; **PS9** also reported for *Petrobius* in Birket-Smith 1974, as **sX***; females of no other taxa studied for this detail), and the sclerites labeled **PS8** (Figs. 7, 8; a true **PS8**?), **PSp9** (Fig. 12A–C; a posterior part of **PS9**?), and **PE** (the penial sclerite(s); an anterior part of **PS9**?) in the various males (see Fig. 19A,B,C). Regarding venter 8, the identification of male **PS8** as a **PS** sclerite is clearcut, as a eusternal sclerite **ST9** is present behind it, and as this extra **PS8** sclerite in front of **ST9** occurs only in *Petrobiellus*, which is also special in having distinct **PS** sclerites in the preceding segments. This may support the alternative interpretation of the female **ST9?** as a **PS8**, while there are no direct arguments for the identification of this sclerite as either **PS8** or **ST9**. Regarding venter 9, the identification of sclerites as posterior 9th-segmental ones (**PS**) or as anterior 10th-segmental ones (**ST**?) is intimately correlated with the problem of the segmental assignment of the phallic organs.

The phallic organs are represented by an undivided median penis (**pe**) in Archaeognatha, Zygentoma, and some Pterygota, and by a phallic complex composed of several lobes in most Pterygota (see Introduction). The problems in their morphological interpretation in Archaeognatha and other Insecta group around three questions: **(i)** Do phallic organs and the gonopore (opening of ejaculatory duct) belong to the venter of abdominal segment 9 or 10 or are they of some bisegmental origin? **(ii)** Are the phallic organs structures independent of limbs or are they (partly or entirely) derived from parts of the 9th- or 10th-segmental limbs; if the latter is true: from which parts of the limbs? An origin from limbs is more likely in case of a 10th-segmental or bisegmental origin. **(iii)** Are the male phallic organs and gonopore isosegmentally homonomous with any structures of the female postabdomen? The Appendix (chapter 8) provides a preliminary discussion of questions i–iii, but current morphological knowledge does not allow for clear answers (see section 8.6. for a plausible working hypothesis).

Here we only exemplify the situation by one specific conflict. It concerns the penial sclerotisation **PE** (especially the ventral part of the proximal sclerite **PEp**) as well as the small, weak post-penial sclerite **PSp9** of male Archaeognatha (e.g. Figs. 4, 12A–C; **PE** and **PSp9** in Fig. 19A,C) and sclerite **PS9** of female *Petrobiellus* and *Petrobius* (**PS9** and **ST10**, reflecting different interpretations, in Fig. 19B; **sX*** in Birket-Smith 1974: figs. 9, 10). There are three relevant pieces of evidence:

(1) On the one hand, female **PS9**/**ST10** and male **PEp** appear as isosegmentally homonomous based on identical relative position (though the male **PEp** is located a bit further anteriorly) and on muscle attachments reported in Birket-Smith (1974: muscle series **i***; see Fig. 23A,B) for a *Petrobius*. Furthermore, **PS9**/**ST10** and **PEp** belong to venter 10 according to these muscle con-

← **Fig. 19.** Diagrammatic representation of abdominal venters 6–10 of archaeognathan males and females and an odonatan female. **A**: *Petrobiellus* male (this paper, compare Figs. 8, 9). **B**: *Petrobiellus* female (based on Klass & Matushkina 2012 e.g. fig. 2). **C**: *Lepismachilis* male (this paper, compare Fig. 4). **D**: *Calopteryx* female, Odonata-Zygoptera (based on Klass 2008 e.g. figs. 1, 7). — ***Representation***: For each taxon/sex (i.e., in each panel A, B, C, D) the two pictures show the range of plausible hypotheses: the left picture shows the maximum identification of sclerites as posterosternal (dark grey); the right picture shows alternative non-posterosternal interpretations if such are feasible. All pictures are based on an internal view (i.e., dorsal view of ventral exoskeleton). Of venter 10 only (anterior) elements included that potentially belong to venter 9. Of the segmental sclerites only those shown that traverse the midline, i.e. parts of the eusternum (intersternite STi and true sternite STt if distinguishable; in light grey), candidate sclerites for assignment to the series PS (= 'posterosternites'; in dark grey), medially fused parts of the coxae (CX, in Archaeognatha bridges 'e'; in blue), and the CA sclerotisation (only *Calopteryx*, bearing tendons ft and ca; in pink). Sclerotisations with dark margin where they end, without margin where they continue (as the same or as nominally different sclerotisations). Thin orange lines represent hypothesised course of primary segmental borders; thick violet lines represent parts of a segmental border that are distinctly marked (by e.g. antecostae ac or spinae sn); thick blue lines represent non-antecostal transverse ridges. — ***Morphological terms*** used for labeling explained in text chapter 3.

nections: Muscles **i*** of the preceding segments are attached to cuticular tendons (**vt*** in BIRKET-SMITH 1974: figs. 4, 5; partly mislabeled as **iv***, e.g. in figs. 10B, 15B; tendons yellow in Fig. 23A,B) arising from the abdominal segmental borders (from the "antecosta of the sternum"). The internal tips of tendons **vt*** are attached to the segmental ligamentous endosternites (green in Fig. 23A,B). The tendon(s) **vt10*** arising from the anterior margin of **PEp** in the male (**vt10***, medially fused = tendon **bpt** in e.g. Fig. 4) and from the anterior margin of sclerite **PS9**/**ST10** in the female (**vt10***, paired), which give attachment to **i9*** (posterior end) and **i10*** (anterior end), would then mark the anterior border of venter 10. Since **PS9**/**ST10** and **PEp** follow behind the origins of the **vt*** tendons, they should belong to venter 10. Male **PSp9**, located even further posteriorly (Fig. 19C),would then also be 10th-segmental. If this is true, 'PS9' and 'PSp9' would be misnomers regarding both the posterosternal specification (PS) and the segmental assignment (9). The median fusion of left and right tendons **vt*** in the male could be correlated with the median fusion of the primary phallic lobes into the penis. A hypothethical median spina **sn10** may or may not be included in the fusion product. The 10th-segmental eusternal region is then in the male likely included in the ventral penis base, either contributing a **ST** component to the **PE** sclerotisations or being membranous; in the female it is represented by the area bearing **PS9**/**ST10**, which is thus likely to be or include a **ST** sclerotisation. (We note that except **vt10*** = **bpt** we did not observe cuticular tendons **vt*** in the species we studied.)

(2) On the other hand, the same muscles as described in BITSCH (1973, 1974a,b: muscle series **5***, see Fig. 23C) provide no evidence for the segmental assignment of sclerotisations **PEp** and **PS9**/**ST10**. The point is that BIRKET-SMITH (1974) finds the muscles (**i***) attached to cuticle (**vt***-tendons), which allows for conclusions on exoskeletal segmental borders. BITSCH (1974b), however, does not report any cuticular tendons like **vt*** (in agreement with our results, except for **vt10*** = **bpt**), and he finds the muscles (**5***) attached to the ligaments (endosternites). Neither ligaments nor muscle attachments upon them can be referred to specific areas of the cuticular surface, which prevents conclusions on exoskeletal segmental borders. (Note that each ligament is connected to the body wall in various places, as shown in Fig. 23A–C, and this includes areas at, or near, two successive segmental borders; see also KLASS 2001 for problems of interpretation with muscle attachments on ligaments.)

(3) Sclerite **PS9** of some female Odonata (KLASS 2008: fig. 7; bare of muscle attachments and tendons) closely resembles **PS9**/**ST10** of female Archaeognatha (KLASS & MATUSHKINA 2012: p. 587). This odonatan **PS9** lies anteriad of a strong ventral transverse ridge that is continuous with the tergal antecosta **ac10** and thus appears as a veritable ventral part of antecosta **ac10** (Fig. 19D left picture). This suggests a 9th-segmental position for this **PS9**. In case of homology this is then also true for the archaeognathan female **PS9**/**ST10**, and in case of isosegmental homonomy also for the archaeognathan male **PEp** and perhaps **PSp9**. Interpreting the odonatan **PS9** as 10th-segmental (± **ST10**; Fig. 19D right picture) would require that the ventral part of 'antecosta **ac10'** is not part of the antecosta but a secondary ventral ridge located further posteriorly, deeply within venter 10.

Points (1)–(3) perfectly illustrate the problems with the segmental assignment of sclerites **PS9**/**ST10** and **PE** (and thus also of the entire phallic organs) based on current morphological evidence. The assignment and interpretation of these structures remains unresolved, though a 10th-segmental assignment appears more likely (as in right pictures of Fig. 19A–D; see chapter 8).

5.3. Functioning of phallogonapophyseal complex in Archaeognatha and in insect ground plan

The current knowledge of the function of male genitalic structures in Archaeognatha is essentially limited to three facts: the penis (**pe**) releases sperm through the phallotrema near its apex; in some species it also releases secretions for the production of a spermatophore; in many species the gonapophyses (**gp8**, **gp9**) use their tubular glandular setae to produce threads, on which sperm is deposited for transfer to the female. The sparse knowledge on this topic is summarised in STURM & MACHIDA (2001: pp. 42ff), from where we have drawn the data on mating briefly surveyed below. Our morphological data can contribute to understanding some functional aspects. We structure this section according to methods of sperm transfer to the female, which appear to be strongly correlated with male genitalic morphology. Three methods of sperm transfer have been observed in Archaeognatha (1, 3, 4 below); two additional ones can be suspected based on a specific divergent male genitalic morphology (5) or other observations (2).

(1) Indirect transfer of fluid sperm using carrier thread(s) is the most wide-spread method and is unique for Archaeognatha. The male secretes a thread from the gonapophyseal tubular setae (Fig. 14A–D). He draws the thread out and attaches it to a substrate using his gonapophyses (it is unclear to what extent this depends on movement of the gonapophyses or of the entire postabdomen). Then he secretes one or more uncoated sperm droplets onto the thread using his penis. The female takes the droplets up using her ovipositor for transport towards the body. It is likely – but not demonstrated – that this involves capillary forces of the ovipositor channel. Among the taxa here studied this behaviour occurs in *Machilis*, *Lepismachilis*, and *Pedetontus* (STURM & MACHIDA 2001). The male genitalia of these species share several structural features (Figs. 1–6): One or two pairs of gonapophyses bearing tubular setae are present. The phallogonapophyseal complex is relatively long; gonapophyses **gp9** and the penis **pe** are of similar length and bear numerous articulated setae on the apial parts, which implies a high

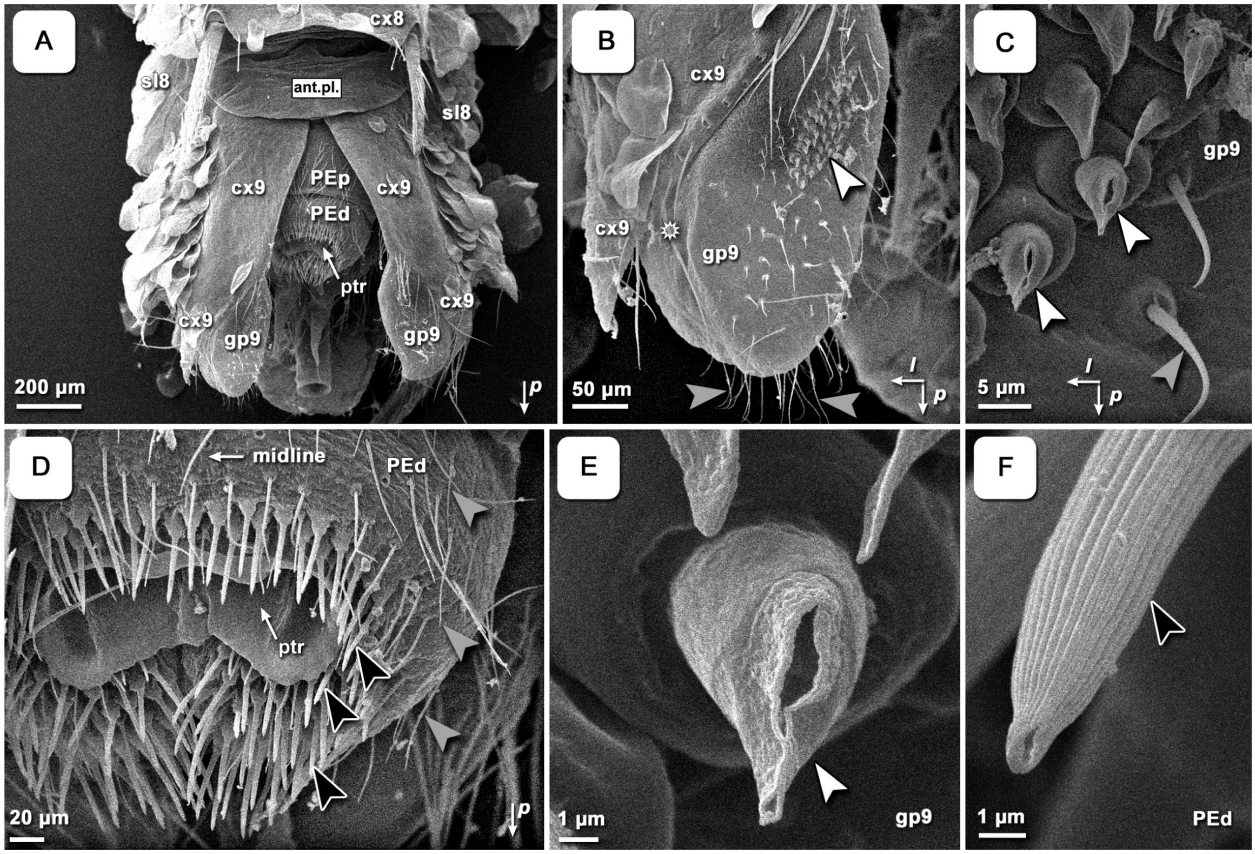


Fig. 20. SE micrographs of male genitalic structures in *Lepisma saccharina*, with focus on venter 9. **A**: Entire venter 9 and neighbouring parts, ventral view. **B**: Right gonapophysis gp9, ventral view (enlarged from A). **C**: Tubular setae and slender articulated setae on ventromesal surface of right gonapophysis gp9, ventral view (enlarged from B). **D**: Apex of penis, ventral view, showing setation and phallotrema. **E**: One of the tubular setae on gonapophysis gp9 shown in C, ventral view (enlarged from C). **F**: Apex of one of the tubular setae on penis shown in D, ventral view (enlarged from D). — ***Symbols, arrows, and terms:*** Light grey arrowheads indicate slender articulated setae; white arrowheads indicate tubular setae on gonapophysis gp9; black arrowheads indicate tubular setae on penis; white empty stars indicate membranous regions of type 6 cuticle. Arrows give directions: l = lateral, p = posterior. Terms used for labeling explained in text chapter 3; in addition: ant.pl. = anterior plate of venter 9, the composition of which is unresolved (likely including true sternum STt9, antelaterocoxae LCa9, and perhaps postlaterocoxae LCp9).

tactile capacity. On venter 9 the anterior sclerotisations – sternum **STt9** and antelaterocoxae **LCa9** – are connected into an unpaired transverse sclerite, which provides some stabilisation for this area. In contrast, the remaining 9th-ventral sclerotisations show a high degree of movability: The anterior coxal bridge **e** is on each side articulated with the main coxal sclerotisation, whereby separate sclerites **CXt9** and **CXp9** are present. Postlaterocoxae **LCp9** are large and fully separated from the main coxal sclerite **CXp9**. The left and right gonapophyseal sclerites **GP9** are not fused at the gonapophyseal base. The distal part of the penis (with sclerite **PEd**) can be moved relative to the proximal part (with **PEp**). Altogether, venter 9 appears to be optimised for a great extrinsic and intrinsic movability of the phallogonapophyseal complex.

(2) Indirect transfer of a spermatophore using carrier threads was never observed directly in Archaeognatha. However, its occurrence is suggested by the finding of a spermatophore associated with threads upon the ovipositor of a preserved *Mesomachilis* female (Sturm & Machida 2001: p. 49). This is relevant, as this method (2) was found in all of the very few examined Zygentoma (Sturm 1997; Sturm & Machida 2001: p. 52, fig. 5.8e). In *Lepisma saccharina* (Lepismatidae), according to Sturm (1997), glands upon the gonapophyses **gp9** produce the threads and the web into which the spermatophore is packed. We found tubular setae on the **gp9** (Fig. 20B,C,E) and additionally on the penis (Fig. 20D,F) of *Lepisma*, which resemble those in Archaeognatha. *Thermobia domestica* (Lepismatidae) and *Tricholepidion gertschi* (Lepidotrichidae) likely use glands on the penis only (Sturm 1997).

(3) Indirect transfer of a spermatophore without carrier thread(s) was observed in several Meinertellidae (while no other methods have been reported for this taxon). The male deposits a stalked spermatophore on the substrate using his short penis and secretions from glands opening into the vasa deferentia (Bitsch 1968). Then he pushes the female onto the spermatophore, and she picks it up with her ovipositor. Meinertellidae males consistently lack gonapophyses (Sturm & Machida 2001: p. 32), which may correlate with the loss of their thread-producing function, and they have a short penis, which appears to suffice for depositing a spermatophore

(STURM & MACHIDA 2001: p. 49). In the 9th-ventral sclerotisations of *Machilinus* we found characteristics quite opposite to the carrier thread producing species (Figs. 10, 11): There is no anterior transverse compound sclerite, but a free, heavy median sternite **STt9**. Regarding the remaining sclerotisations, both ante- and postlateral coxae, **LCa9** and **LCp9**, are fused to coxa **CX9**, and in **CX9** the median bridge **e** is firmly connected with the lateral main parts; the left and right **GP9** sclerotisations are fused with each other and possibly, in addition, with the proximal penial sclerite **PEp**. The movability of the articulation between proximal and distal phallic elements is limited to the sagittal plane, hence restricted compared to the other studied species. Setation of the phallogonapophyseal complex is sparse and uniform. On the whole, venter 9 of *Machilinus* revealed low movability essentially restricted to near the penis base (**GP9?/PEp?-CX9** articulation in Fig. 11).

(4) Seemingly direct transfer of fluid sperm is known from *Petrobius* (STURM & MACHIDA 2001: pp. 31, 35f, fig. 4.3b). The male deposits a sperm droplet onto the proximal half of the female ovipositor by means of its long, movable, pipette-like penis, whose strong setosity indicates a high tactile capacity. The sperm likely reaches the base of the ovipositor by capillary forces. (Sperm transfer *into* the ovipositor or closer to the spermathecae would be classified as 'truely direct'.) Male gonapophyses **gp9** are moderately long and indistinctly annulated, and may thus provide mechanical support for the extruded penis; they lack tubular setae. A detailed study of the exoskeleton of the male genitalia of *Petrobius* species is wanting (skeletal details difficult to see in BIRKET-SMITH 1974).

(5) (Seemingly?) direct sperm transfer with male clasping was never observed in Archaeognatha, but has been suspected for *Petrobiellus* (STURM & MACHIDA 2001: p. 31). In *Petrobiellus takunagae* (Figs. 7–9, 16) we found no tubular setae on the gonapophyses or elsewhere in the genitalic region, sperm transfer involving carrier thread(s) is thus unlikely. On the other hand, parts of male venter 9 are uniquely modified in a way that grasping the female during mating appears likely. The very long penis is bent dorsally, hook-like, and strongly sclerotised, stiff, and bare of setae; the styli are distinctly curved (Fig. 21). The dorsal base of the penis forms a unique, huge apodeme (**dpa** in Fig. 8), which likely serves for muscle attachment (muscles not examined). The muscles of styli **sl9** appear to be enlarged (STURM & MACHIDA 2001: fig. 4.3c; but we did not find a tendon or apodeme on the stylus base that could increase the attachment area). The base of the phallogonapophyseal complex is located further posteriorly compared to other archaeognathans (Figs. 2, 9) and its tips reach beyond tergite **TG10** (Fig. 21A,E). Gonapophyses **gp8** are absent, and gonapophyses **gp9** are apparently tactile devices, as articulated setae are present all around. We view two possibilities for the clasping posture:

(a) To reach the posture, the gonapophyses **gp9** could use their tactile capacity for finding the ovipositor between the female coxal lobes **cx9** and bringing the penis and styli **sl9** into the right position approximately perpendicular to it. In the completed posture, the female ovipositor lies perpendicular to the male genitalia, at the level of the proximal third of the styli **sl9**, passing beneath the styli and above the penis (Fig. 21C). The styli clasp by a mesoventral movement, thus bending the ovipositor over the penis. The penis clasps by a dorsal movement depending on muscles pulling its **dpa** apodeme anteroventrally, using the close association of the penis base with the **gp9** bases and of the latter with the coxal bridge **e** (Fig. 9) as an abutment. Where the ovipositor is in contact with a stylus, it is harboured within the mesal concavity of the stylus (Fig. 21C), and the thorns in this area both prevent the ovipositor from escaping and perceive whether the grip is appropriate. The thorns on the coxal apices additionally prevent the ovipositor from slipping too far to the male's anterior. The upcurved distal part of the penis prevents the ovipositor from escaping caudally, and the penial apex would lie in close proximity of the surface of the ovipositor. Depending on whether, and to what extent, the dorsoventral axis of the male is rotated compared to that of the female, the penial apex faces the slit between the two **gp9** (no rotation) or between the two **gp8** (180° rotation), or between the **gp8** and the **gp9** of one side (90° or 270° rotation; this requires a slight local opening of the tongue-and-groove connection of the female olistheter). Through such a slit the penial apex could be inserted into the ovipositor channel by further activity of the muscles on **dpa**. According to the different directions of clasping forces of penis and styli (Fig. 21C), we call this the 'up-and-down hypothesis'. Shortcomings of this hypothesis are that the thorns on the stylus are in a position that might appear too far dorsal for holding the ovipositor, and that the ovipositor must experience bending to a perhaps unlikely extent.

(b) This differs from (a) in that the styli **sl9** clasp upward (like the penis) and in cooperation with the penis press the ovipositor against male venter 10 and the ventrally projecting paranotal lobes **pn10** (Fig. 21D). The stylar and coxal thorns prevent the ovipositor from slipping too far to the male's anterior, and the penis prevents it from escaping caudally. According to the uniformly upward direction of clasping forces of penis and styli (Fig. 21D), we call this the 'all-up hypothesis'. A shortcoming of this hypothesis is that no counter-clasping structures on venter 10 and lobes **pn10** are known.

With both hypotheses (a) and (b), fluid sperm could be released or a spermatophore be built either into the female ovipositor (direct sperm transfer) or upon the ovipositor (seemingly direct sperm transfer).

In *Tricholepidion* the male grips the anterior part of the female body using its terminal filament and cerci (STURM 1997: fig. 1), though these processes lack evident structural differentiations for this activity (WYGODZINSKY 1961). The male then guides the female to his spermatophore. We submit that the male clasping structures of *Petrobiellus* do not appear suited for such a frontal grip. Styli **sl9** clasping in interaction with the phallic or-

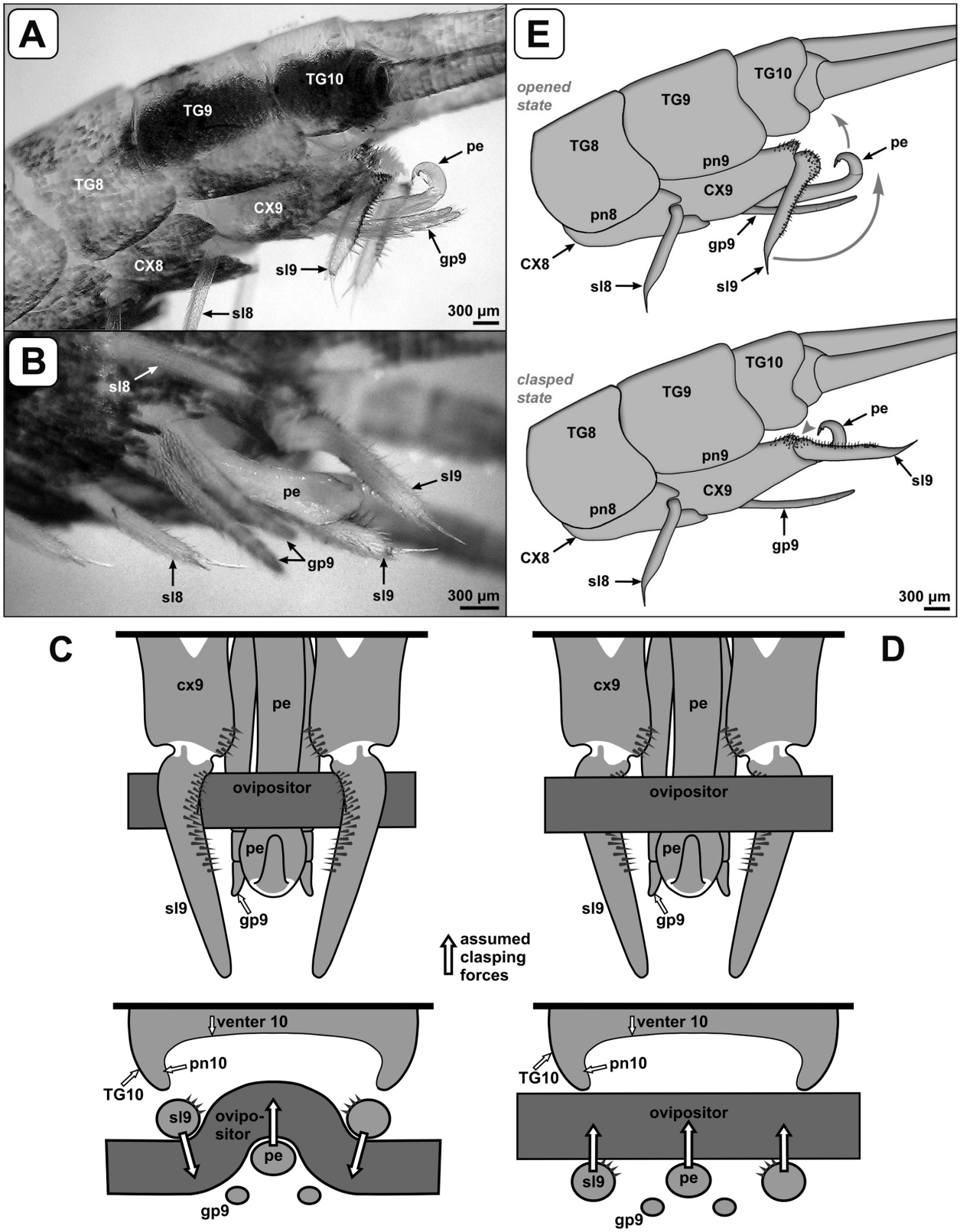


Fig. 21. Functional hypotheses for the male postabdomen of *Petrobiellus takunagae*. **A**: Macerated postabdomen, lateral view (light microscopy). **B**: Ventral side of unmacerated postabdomen, ventrolateral view (light microscopy). **C**,**D**: Schemata illustrating the hypothesised up-and-down mechanism (C) and all-up mechanism (D) of male clasping; upper picture is a dorsal view (with postgenital abdomen removed), lower picture is a transversal section through the area where the ovipositor is held during clasping (with ventral side of postgenital abdomen included); sclerotised elements of male in medium grey; female ovipositor in dark grey; large arrows indicate direction of forces applied during clasping. **E**: Diagrams derived from A, illustrating the suggested all-up clasping mechanism (shown in (D)), lateral view: styli 9 and penis move in a dorsoventral plane; thorned surfaces on styli and coxal lobes 9 may provide firm and precise fixation of a female body part (ovipositor?) above the penis, which may suggest direct sperm transfer (i.e. true copulation); grey arrows indicate directions of movement of penis and styli 9 in clasping process; grey arrowhead indicates male thorn-bearing region presumably holding female body parts during clasping.

gans occurs in Ephemeroptera, but this is regarded as an apomorphy of this group (e.g. Kluge 2003), in which females consistently lack an ovipositor.

Ground-plan functions of penis in Insecta. The primary function of the penis, sperm release, is indispensible for reproduction and, accordingly, highly conserved in Archaeognatha and other Insecta (including Odonata). However, a secretional function for the formation of a spermatophore usually adds to this (Matsuda 1976 and references therein). It may be a ground-plan function in Insecta, then lost in the archaeognathan taxa transferring only fluid sperm. Yet, this needs further comparative studies for assessing the possible homology of the respective glands and secretions, especially in Meinertellidae and Zygentoma.

Ground-plan functions of gonapophyses in Insecta. The role of the **gp8** and **gp9** is of particular evolutionary interest, especially because their functions as well as their degree of conservation are very different in the two sexes. At least in Archaeognatha and Zygentoma, the gonapophyses of both sexes are always generously equipped with articulated setae of different length (e.g. Klass & Matushkina 2012: fig. 4D and Matushkina 2017 for female Archaeognatha). This and the associated tactile capacity thus appear as insect ground-plan features shared by both sexes. Moreover, there is morphological evidence of olfactory receptors in female Archaeognatha (Matushkina 2017).

Regarding the ***male sex***, in Archaeognatha the gonapophyses usually produce carrier threads using tubular setae ((1) above). This function is only known to be absent in Meinertellidae, where both pairs of gonapophyses have become lost ((3) above), and in a few likely specialised Machilidae. In the latter, gonapophyses **gp9** are retained (not the **gp8**), they might support the penis ((4) above) or might have focused on a guiding tactile function ((5) above). Gonapophyses **gp8** are only known from carrier thread producing taxa, where they co-occur with always larger **gp9** and have become lost many times (as evident from their distribution over taxa as given in Sturm & Machida 2001: pp. 25ff, with both presence and absence of **gp8** found in several genus groups). In Pterygota, gonapophyses **gp8** are absent, and gonapophyses **gp9** are probably also absent (e.g. Snodgrass 1957) – at least, the presence of **gp9** could not be convincingly demonstrated (e.g. in Smith 1969, whose writings appear as a long series of mostly unsupported statements). If in Pterygota gonapophyses **gp9** are yet present in a modified and/or obscured way, i.e. either as parts of the phallic organs (which then rather form a phallogonapophyseal complex) or amalgamated with the subgenital lobe (**vf9** = medially fused coxal lobes **cx9**), their function is different from those known for Archaeognatha (except for a potential tactile function). Among Zygentoma, small gonapophyses **gp8** have been reported only for *Tricholepidion* (Wygodzinsky 1961: fig. 38; therein categorised as non-functional coxal vesicles; Smith 1970: p. 214). Gonapophyses **gp9** occur more widely; in *Lepisma* they produce carrier threads using tubular setae ((2) above). Thus, the production of threads for placing sperm (as drops or spermatophores) is likely the ground-plan function of gonapophyses in male Insecta. Gonapophyses can become lost when thread production is abandoned either in favour of direct sperm transfer (Pterygota) or of threadless indirect sperm transfer (Meinertellidae). However, in some such cases the **gp9** have been retained and acquired a new function (possibly different ones in *Petrobius* and *Petrobiellus*). The cases of the zygentomans *Thermobia* and *Tricholepidion* are odd, as gonapophyses have been retained (with unknown function), while the function of thread production has apparently become limited to the penis (compare (2) above).

This multilayered evolutionary picture for the male gonapophyses is in stark contrast to the more clearly defined and more widely uniform function of the gonapophyses in the ***female sex***: in all Archaeognatha and Zygentoma and in many subgroups of Pterygota both pairs **gp8** and **gp9** together form an ovipositor functioning in egg deposition. Sperm uptake is a second function in the female, as long as sperm transfer is indirect, but also in cases of (seemingly) direct sperm transfer where sperm is placed onto or into the ovipositor. Both egg deposition and sperm uptake were thus likely functions of the female gonapophyses present in the ground plan of Insecta. It appears most plausible that in the groundplan condition egg deposition involved insertion of the gonapophyses in crevices, and sperm uptake involved capillary forces of the gonapophyseal channel. We note, however, that neither of these two modes of operation (use of capillary forces, pushing of gonapophyses into crevices) has been clearly demonstrated for archaeognathans and zygentomans.

In sum, gonapophyses **gp8** and **gp9** of the two sexes have entirely different sets of functions in the ground plan of Insecta, i.e. in the latest stem-Insecta. In the following we will discuss whether in view of the overall structural similarity of the male and female genital regions of Archaeognatha the functions of the gonapophyses and other genitalic structures could have been more similar between sexes in earlier stem-Insecta. This requires, first, a detailed comparison of the genitalic region in male and female Archaeognatha.

5.4. Genitalic region compared in male and female Archaeognatha

In Archaeognatha the pregenital, 'typcial' abdominal segments show the same structural pattern in the two sexes (e.g. Bitsch 1973; Fig. 18A). The morphology of the genitalic segments differs in both males and females (Fig. 18B–E) from that of the pregenital segments mainly by specialities that clearly are, or at least could be, useful for genitalic functions; only for a few specialities a genitalic function is unlikely ('speciality' meaning any structural difference compared to the pregenital segments, irrespective of its evolutionary polarity). In

female Archaeognatha, abdominal venters 7, 8, and 9 can be considered as the genitalic region, as they bear the gonopore and genital fold (7) and the ovipositor built of gonapophyses (8, 9) (Bitsch 1974a; Klass & Matushkina 2012). In males, venter 9 and perhaps 10 and to a limited extent venter 8 represent the genitalic region, as they bear the gonopore and penis (9 or 10) and the gonapophyses (9, in some species 8). (In the following discussions, the penis, its **PE** sclerites, and the gonopore and phallotrema of the male as well as sclerite **PS9**/**ST10** of the female are treated as 9th-segmental elements, while their assignment to venter 9 or 10 is unclear, see section 5.2., chapter 8, and Fig. 19.)

The differences between the various genitalic segments and the pregenitalic segments in each sex, and those between particular genitalic segments of males and females are moderate in Archaeognatha (compared to Zygentoma and especially Pterygota that have well-developed genitalia). Therefore, both the transsegmental homonomy of structures in each sex and the homonomy of isosegmental structures between the sexes are mostly quite obvious (Fig. 18), as is the presence of particular structures or special conditions (i.e., specialities) in both sexes, or in the one sex but not in the other. All this is evident from Bitsch (1973, 1974a,b) and additions in Klass & Matushkina (2012) and herein (section 5.2.). By showing this situation and by their phylogenetic position (being one of the two branches from the basal-most dichotomy within Insecta: Misof et al. 2014), Archaeognatha is the most useful taxon for analysing the evolutionary origin of genitalia in insects with regard to structure and function.

Structural specialities in the genitalic region of Archaeognatha differ between the various segments of each sex, between the same segments of the two sexes, and between the same segment and sex in different species. We here analyse these occurrence of these specialities using detailed data so far accumulated. The kind and distribution (over sexes, segments, and species) of genitalic specialities are summarised in Table 2, referring to the five species studied herein regarding the male sex, but to *Petrobiellus takunagae* alone with regard to the female sex (data from Klass & Matushkina 2012). We code structural specialities of the genitalic segments (compared to pregenitalic segments) using terms like "G13-8". G stands for "genitalic speciality", i.e. a difference to pregenitalic segments. The first number (here 13) specifies the different specialities, the same number being given to corresponding specialities of different segments. The second number (here 8) names the abdominal segment concerned (i.e., G13-8 and G13-9 address corresponding genitalic specialities in segments 8 resp. 9). A $^{+}$ is added to specialities that are here assigned to segment 9 but could belong to segment 10 (e.g. G35-9^{+}).

Likely due to the further anterior location of the gonopore in the female (venter 7) compared to the male (venter 9 or 10), genitalic specialities start further anteriorly in the female (Table 2). On venter 7, the female shows several specialities, but only in the posterior part (as this is the area where eggs are released), while the male shows no specialities (as venter 7 is not involved in genitalic functions). On venter 8, the female shows numerous specialities across the entire venter (as this area is involved in oviposition), while, in some species only, the male shows two intercorrelated specialities in the posterior part, both of which are also present in the female (as this male area contributes to genitalic functions focally taking place in the following segment). On venter 9 numerous specialities across the entire venter are present both in the female (as this area is involved in oviposition) and in the male (as this is the area where sperm is released and manipulated); the 9th-segmental specialities of the two sexes are partly very different, but mostly very similar. For comparing the sets of genitalic specialities in males and females, and for discussing their possible original functional context in section 5.5., we loosely classify the majority of the specialities in 5 Groups, I–V (the functional relevance of this grouping will become clear in section 5.5.; specialities not grouped – see Table 2 – are of no relevance in that discussion). Specialities of Groups I and II are shared between the sexes (at least in some species); those of Groups III, IV, and V are limited to one sex (though with a few possible exceptions).

Group I specialities. This is a large set of features (see Table 2) of venters 8 and 9 that are *shared between males and females* and that are suspected to have been *part of the same original functional context* (as detailed in section 5.5.). In the focus are the gonapophyses and surrounding elements. Therefore, males that have, like females, both **gp8** and **gp9** are here of special relevance (*Machilis* and *Lepismachilis* herein, Figs. 1–4).

In both sexes, the homonomous counterparts of the coxal vesicles are on both venters 8 and 9 shaped as largely sclerotised, non-retractable, and annulated gonapophyses **gp8** (G26-8) and **gp9** (G26-9). The base of these **gp** processes is not located at the mesal distal edge of the coxal lobe **cx** (where coxal vesicles are typially placed). Instead, on venter 8 the **gp8** base is located in the mesal dorsal wall of lobe **cx8** (G28-8). On venter 9 the **gp9** base is located even more divergent from pregenitalic segments: in an area outside the walls of the coxal lobes **cx9** and both close to the midline and far anteriorly (G29-9). On both venters 8 and 9, the left and right coxal lobes **cx8** resp. **cx9** show no basal fusion across the midline (G17-8, G17-9). This allows for a close grouping of the gonapophyses **gp8** and **gp9** (G17-9; as there is no fold at the midline to keep them apart) and for their greater vertical movability (G17-8; as there is no fold at the midline to hinder their ventral bending). On venter 9, the body wall area between the left and right coxae **CX9** and from the **gp9** bases to the posterior is strongly arched dorsally (**mic9** area; G24-9), and the mesal flanks of the coxal lobes **cx9** are very high and concave (G20-9). This results in a midventrally open cylinder by which the gonapophyses **gp9** are ensheathed (together with the **gp8** in females and with the penis **pe** in males). The presence of an anteromesally projecting anterior part of the

Table 2. The distribution of genitalic specialities (= morphological differences compared to pregenitalic abdominal segments) over the abdominal venters 7–9(10) in female (one species: *Pbl*. = *Petrobiellus takunagae*) and male Archaeognatha (five species: *Lema*. = *Lepismachilis notata*; *Mach*. = *Machilis hrabei*; *Ped*. = *Pedetontus unimaculatus*; *Pbl*. = *Petrobiellus takunagae*; *Man*. = *Machilinus* sp.). For the coding of the specialities (as e.g. G03-7) see text section 5.4. The code for a speciality is inserted if it is present; – is inserted if the speciality is absent; na (not applicable) is inserted if presence or absence cannot be assessed due to the lack of the speciality-bearing element. + is added to specialities that may not belong to venter 9 but to venter 10. [1] in G12-8: only partly separated, by weaker sclerotisation, in *Petrobiellus*. [2] in G29-9: while both coxal vesicles and gonapophyses are absent on venter 9 in *Machilinus*, the structural configuration of the median part of venter 9 shows that the area bearing gonapophyses gp9 in other taxa has undergone the shift here in question. The last column "Gr" specifies the assignment of a genitalic speciality to a Group (I–V) as discussed in section 5.4.

Segmental speciality	***Pbl.***	***Mach.***	***Lema.***	***Ped.***	***Pbl.***	***Man.***	**Gr**
	♀	♂	♂	♂	♂	♂	
Venter 7							
genital opening **go** present (gonopore, opening of comm. oviduct)	G01-7	–	–	–	–	–	**V**
genital lobe or fold **gf** present (enlarged infracoxal lobe)	G02-7	–	–	–	–	–	**V**
genital plate **LG7** = **PS7** present (or: enlarged)	G03-7	–	–	–	–	–	**V**
median pouch at anteroventral base of **gf** present	G04-7	–	–	–	–	–	
paired pouches at posterodorsal base of **gf** present	G05-7	–	–	–	–	–	
parts **me7** of coxal lobes **cx7** extended	G06-7	–	–	–	–	–	
Venter 8							
intersternite **STi8** absent	G07-8	–	–	–	–	–	**III**
sternite **STt8** short, strong, folded inward, fused to the **CX8**	G08-8	–	–	–	–	–	**III**
antelaterocoxites **LCa8** absent	G10-8	–	–	–	–	–	
postlaterocoxites **LCp8** separated from coxites **CX8**	G12-8	–	–	G12-8	G12-8 [1]	–	
laterocoxal inflexion **li8** present on **LCp8**	G13-8	–	–	–	–	–	
coxa **CX8** incompletely divided by membranous stripe	G14-8	–	–	–	–	–	
left and right coxal lobes **cx8** without basal fusion	G17-8	G17-8	G17-8	–	–	–	**I**
coxal lobes **cx8** with anteromesally projecting anterior part	G18-8	–	–	–	–	–	**III**
intercoxal area **mic8** wide and arched dorsally	G24-8	–	–	–	–	–	**III**
spermathecae **sp** present on lateral parts of **mic8** membrane	G25-8	–	–	–	–	–	**III**
coxal vesicles **vs8** as sclerotised, annulated gonapophyses **gp8**	G26-8	G26-8	G26-8	na	na	na	**I**
coxal vesicles **vs8** (or gonapophyses **gp8**) absent	–	–	–	G27-8	G27-8	G27-8	
base of coxal vesicles / gonapophyses **gp8** in dorsal **cx8** wall	G28-8	G28-8	G28-8	na	na	na	**I**
dorsal aulax groove **al** present on **gp8** (**gp9** interlock)	G33-8	–	–	na	na	na	**III**
Venter 9							
intersternite **STi9** absent (or fused to sternite **STt9**)	G07-9	G07-9	G07-9	–	G07-9	G07-9	**II**
sternite **STt9** small and weak	G09-9	–	–	–	–	–	
antelaterocoxites **LCa9** fused to **CX9**	G10-9	–	–	–	–	G10-9	
antelaterocoxites **LCa9** connected with sternite **STt9**	–	G11-9	G11-9	G11-9	–	na	
postlaterocoxites **LCp9** separated from coxites **CX9**	G12-9	G12-9	G12-9	G12-9	–	–	**II**
laterocoxal inflexion **li9** present on **LCp9**	G13-9	G13-9	G13-9	G13-9	G13-9	G13-9	**II**
coxae **CX9** forming anterior transverse bridge (**e**)	G15-9	G15-9	G15-9	G15-9	G15-9	G15-9	**I**
coxal transverse bridge detached from **CX9** main parts	–	G16-9	G16-9	G16-9	–	–	
left and right coxal lobes **cx9** without basal fusion	G17-9	G17-9	G17-9	G17-9	G17-9	G17-9	**I**
coxal lobes **cx9** with anteromesally projecting anterior part	G18-9	G18-9	G18-9	G18-9	–	–	**I**
coxal lobes **cx9** strongly elongated	G19-9	G19-9	G19-9	G19-9	G19-9	G19-9	**I**
coxal lobes **cx9** with high, concave mesal flanks	G20-9	G20-9	G20-9	G20-9	G20-9	G20-9	**I**
coxal lobes **cx9** with dorsal walls largely sclerotised	G21-9	G21-9	–	–	G21-9	–	
styli **sl9** distinctly elongated	G22-9	G22-9	G22-9	G22-9	G22-9	G22-9	**II**
styli **sl9** with proximal lateral bend	–	–	–	–	G23-9	–	
intercoxal area **mic9** wide and arched dorsally	G24-9	G24-9	G24-9	G24-9	G24-9	G24-9	**I**
coxal vesicles **vs9** as sclerotised, annulated gonapophyses **gp9**	G26-9	G26-9	G26-9	G26-9	G26-9	na	**I**
coxal vesicles **vs9** (or gonapophyses **gp9**) absent	–	–	–	–	–	G27-9	
base of coxal vesicles / gonapophyses **gp9** mesad of **cx9** wall	G29-9	G29-9	G29-9	G29-9	G29-9	G29-9 [2]	**I**
left and right gonapophyses **gp9** with short basal fusion	G30-9	–	G30-9	G30-9	–	na	
left and right gonapophyseal sclerites **GP9** with basal fusion	–	–	–	–	G31-9	G31-9	
midventral hollow **mvh** on transverse coxal bridge	–	–	–	–	G32-9	–	
ventral rhachis ridge **rh** present on **gp9** (**gp8** interlock)	G33-9	–	–	–	–	na	**III**
Venter 9 or 10							
transverse sclerite **PS9** (female) or **PSp9** (male) present	G34-9+	?	G34-9+	?	?	G34-9+	
genital opening **go** present (phallotreme, opening of endophallus)	–	G35-9+	G35-9+	G35-9+	G35-9+	G35-9+	**IV**
penis **pe** present	–	G36-9+	G36-9+	G36-9+	G36-9+	G36-9+	**IV**
sclerotisation **PE** of penis present	–	G37-9+	G37-9+	G37-9+	G37-9+	G37-9+	**IV**
basal penial tendon **bpt** present (at ventral base of penis)	–	G38-9+	G38-9+	G38-9+	–	–	**IV**
dorsal penial apodeme **dpa** present (at dorsal base of penis)	–	–	–	–	G39-9+	–	**IV**

coxal lobes **cx9** (G18-9) increases the concavity in its anterior part, perhaps with the purpose of a better ensheathing of the gonapophyses **gp8**, which extend here from their farther anterior origin (especially in the female, but also in the male: **gp8** dragged out of concavity in Figs. 1, 3). A strong elongation of the coxal lobes **cx9** (G19-9) extends the ensheathing of the gonapophyses and penis posteriorly. The bases of the gonapophyses **gp9** receive a firm abutment from the anterior, which in both sexes is provided by the anteromedian transverse fusion of the coxae **CX9** (bridge **e**, G15-9).

In the males where gonapophyses **gp8** (*Pedetontus*, *Petrobiellus*) or both **gp8** and **gp9** (*Machilinus*) are absent (G27-8, G27-9), there are neither coxal vesicles on the consegmental coxal lobes nor any other projections potentially corresponding with these structures; in addition, the left and right coxal lobes **cx8** are fused medially as in the pregenital segments (G17-8 absent). We assume that this configuration is derived from one where both pairs of processes were present as gonapophyses and the coxal lobes **cx8** fully separate (i.e., showing specialities G26-8, G26-9, and G17-8). This is difficult to demonstrate with regard to the **gp8** but is suggested for the **gp9** in *Machilinus* by the structural context of neighbouring elements (especially by the anteromedian position and the articulation of the putative **GP9** sclerotisations, Fig. 11).

Group II specialities. These are further specialities of venter 9 that are *shared by males and females*, but are *not evidently correlated with the same functional context as those of group I* (and do not occur consistently at least in males). First, the intersternite **STi9** is absent (or possibly fused with sternite **STt9**; G07-9, not in *Pedetontus*). The functional relevance of this feature is unclear. Second, the styli **sl9** are very long (G22-9). This may simply be because they are the last in the abdominal series of styli, no matter whether they predominantly function in sensory perception or in supporting the abdomen above ground (or even have some ambulatory function).

The characteristics of the postlaterocoxal sclerotisations **LCp** are here also assigned to Group II (but might alternatively be classified in Group I, i.e. may have played a role in the functional context there addressed). **LCp** gives attachment to dorso-ventral (tergo-laterocoxal) muscles and to muscles running to coxal vesicles and gonapophyses (Bitsch 1973, 1974a,b). Both a greater movability of **LCp** (depending on the degree of its separation from coxa **CX9**) and its larger size (depending on the degree of its lateral expansion forming infolding **li**) may reflect a higher workload on it, but functional details are unclear. The segmental distribution of **LCp** characteristics is partly inconsistent: Infoldings **li** tend to be more distinct in more posterior segments. The separation of **LCp** from **CX** increases in more posterior segments in some cases (*Petrobiellus* female: Klass & Matushkina 2012: fig. 2), but varies in a different way in other cases (*Petrobiellus* male: compare venters 8 and 9 in Figs. 8, 9), or does not vary over segments (*Pedetontus* male: compare venters 7–9 in Figs. 5, 6). However, males and females share the trends that postlaterocoxites **LCp9** are separated from coxites **CX9** (G12-9; only in males producing sperm threads) and form a distinct lateral infolding **li9** (G13-9; in all males).

Group III specialities. These are specialities seen *on venter 8 or on venters 8 and 9 of the females but not of the males*. Some of the 8th-ventral female specialities are of the same kind as 9th-ventral specialities shared by both sexes (those of Group I or II).

Regarding the 8th-ventral female-only specialities, the intercoxal area **mic8** is strongly arched dorsally (G24-8), and the coxal lobes **cx8** have an anterior anteromesally projecting part (G18-8) – both as on venter 9 (see G24-9, G18-9); spermathecae **sp** are present on the lateral parts of the **mic8** membrane (G25-8). By these features, a ventrally open passage is established which can guide an egg from the genital opening to the ovipositor base, and on this way the egg can be fertilised (Klass & Matushkina 2012). The intersternite **STi8** is absent (or possibly fused with sternite **STt8**; G07-8), as usually on venter 9 (see G07-9). Note that the spermatheca (G25-8) has no corresponding, homonomous speciality in segment 9 in Archaeognatha (thus no 'G25-9' in Table 2), but in other insects this is likely represented by the 9th-segmental female accessory glands (see section 8.3.).

Another important 8th-ventral female-only speciality has no homonomous counterpart on venter 9: An anterior transverse stabilisation is provided by sternite **STt8**, which is strengthened, folded, and laterally fused with the coxae **CX8** (G08-8). The resulting anterior transverse bridge resembles that of venter 9 (bridge **e**, G15-9), which, however, is formed by anteromesal arms of the coxae **CX9** (Bitsch 1974a; Klass & Matushkina 2012). In contrast to the 9th-ventral bridge of both sexes, the 8th-ventral bridge of the female does not provide abutment to the bases of the consegmental gonapophyses **gp8**. The different way of forming an anterior bridge may have a functional reason concerning the muscles moving the gonapophyses (coxo-gonapophyseal muscles **70*** and **71*** in Bitsch 1974a: figs. 5, 6): The derived anteromedian location of the **gp9** bases on venter 9 may have required an anteromedian shift of the coxal insertion of the muscle, therefore the bridge is formed by the coxae **CX9**. This constraint is absent on venter 8.

Two further, functionally correlated female-only Group III specialities concern both segments 8 and 9: the presence of an aulax groove **al** on the **gp8** (G33-8) and a rhachis ridge **rh** on the **gp9** (G33-9), which together form the olistheter interlocking gonapophyses **gp8** and **gp9**. (The assumption of a transsegmental homonomy of **al** and **rh**, as expressed by use of the same number, 33, is tentative. It is based on Smith 1969, who accordingly proposes a rotation of the gonapophyses **gp9** along their longitudinal axis. Bitsch 1973, 1974a, however, did not find any evidence for this.)

Group IV specialities. These are the *male genitalic specialities on venter 9* (*or 10*) *which are absent on venter 9*

(*or 10*) *of the female* (though with possible exceptions): In the males of all species studied herein, there is a genital opening (phallotrema; G35-9$^+$), which is located on an unpaired projection (**pe**, with a paired ontogenetic origin; G36-9$^+$), and the projection is sclerotised in a partly (near-)cylindrical fashion (sclerite(s) **PE**; G37-9$^+$). Males of some species have a ventral membranous tendon **bpt** (G38-9$^+$) or a dorsal apodeme **dpa** (G39-9$^+$) at the base of the penis, and at least some (possibly all) have a poorly developed transverse sclerite **PSp9** posterior to the penis base (G34-9$^+$).

Regarding the male sclerites **PE** and **PSp9** there are some uncertainties, as discussed in section 5.2.: **(1)** If **PE** and/or **PSp9** are homonomous with true pregenital **PS** sclerites (only found in *Petrobiellus*, Fig. 8), addressing them as segmental specialities (G34-9$^+$, G37-9$^+$) would be problematic for *Petrobiellus*. Yet, at least for the penial **PE** a condition very different from a **PS** sclerite could then be counted. **(2)** One of the specialities here listed likely also occurs in the female, either G34-9$^+$ or G37-9$^+$, depending on whether the female sclerite **PS9**/**ST10** (G34-9$^+$) is isosegmentally homonomous with the ventroproximal part of the penis sclerotisation **PE** or with the postpenial sclerite **PSp9**. **(3)** The same limitation as specified in (1) for sclerite(s) **PE** also applies to the female sclerite **PS9**/**ST10**. As a preliminary solution with regard to (1)–(3), in Table 2 we specify presence of **PS9** (female) and of **PSp9** (at least some males) as the same genitalic speciality (G34-9$^+$), but we note that having a sclerotisation **PS9** (female) and a sclerotisation **PE** (male) may represent the same speciality (i.e., G34-9$^+$ = G37-9$^+$).

The nature of all the Group IV specialities compared to the pregenital venters is unclear and depends much on whether the elements concerned belong to venter 9 or 10. If they belong to venter 9, the speciality quite likely consists for each element in its exclusive presence on male venter 9 (corresponding with the view of insect male genitalia being newly formed structures), though homonomy with the occasionally occurring pregenital **PS** sclerites is an option. If they belong to venter 10, the speciality consists for each element in its shift to the anterior, plus some structural transformation that can only be specified when the interpretation of the elements – as, e.g., particular parts of the 10th-segmental limbs – becomes clarified (which is not the case, see sections 8.4. and 8.6.).

Group V specialities. These are the *female genitalic specialities on venter 7, which are absent on venter 7 of the male*; they are partly comparable with male-only specialities on venter 9 (or 10; see Group IV): There is a genital opening (gonopore = opening of common oviduct; G01-7), which is located on an unpaired projection (**gf**; G02-7), and the projection is weakly sclerotised (**LG7** = **PS7**; G03-7). These, of course, are very unspecific similarities. As **LG7** is likely homonomous with true pregenital **PS** sclerites (only found in *Petrobiellus*, including male venter 7), addressing it as a segmental speciality (G03-7) would be problematic for *Petrobiellus*. Yet, at least an enlarged condition of **LG7** compared to normal **PS** sclerites could then be counted.

The dorsum. Lastly, it is noteworthy that in both sexes of Archaeognatha the dorsum is not at all involved in the genitalic specialities: All tergites 7–9 resemble pregenital tergites and have undifferentiated lateral margins, which remain widely separated from the elements of the genitalic venters (by the membranes forming the mesal faces of the paranotal lobes **pn**).

5.5. Hypotheses on the evolutionary origin of insect genitalia

5.5.1. Setting the scene

The basic genitalic functions in insects are sperm release, sperm manipulation (including transfer to female), and usually spermatophore production in the males; and sperm uptake and storage as well as oviposition in the females. The male and the female functions should have quite different morphological requirements. Structural specialities in the genitalic region that were dedicated to these genitalic functions from the beginning should thus have been fairly different between the two sexes even at an initial evolutionary stage. This is especially true if at this initial stage the female genital opening was placed on the posterior part of venter 7 (as in Archaeognatha, Zygentoma, and various Pterygota: e.g. BITSCH 1974a; ROUSSET 1973; KLASS & ULBRICHT 2009), contrasting the position of the male genital opening on venter 9 or 10. The presence of a large set of identical specialities in the genital region that are shared by both sexes (Group I in section 5.4. and Table 2, with a central role of the gonapophyses) thus indicates that these specialities originally evolved in a functional context other than genitalic and shared by both sexes.

We here propose that this functional context could have been ***water uptake***. This appears especially plausible because water uptake is a genuine function of coxal vesicles (WEYDA 1998), with which gonapophyses are homonomous. This possibility is detailed below as the "***aquaeductal hypothesis***" on the origin of insect genitalia. We also discuss the possibility of an explicitly ***sensorial context*** having preceded either the functional context of water uptake or directly a genitalic functional context, assuming that elongate sensilla-bearing gonapophyses initially developed for the sake of a tactile, gustatory, and olfactory exploration of the substrate or medium within their reach. This possibility is detailed in second place as the "***sensorial hypothesis***" on the origin of insect genitalia.

These two hypotheses attempt to reconstruct the morphological and functional pattern of insect genitalic specialities from an evolutionary stage onward where the genitalic and pregenital segments showed (nearly) the same morphology. As a background for this, some corner points of the possible span of morphological evolution

of some relevant structures prior to the phylogenetic dichotomy separating Archaeognatha and Dicondylia must be outlined. This concerns, first, the span from early to late members of the insect stem-lineage: Conditions in late members can largely be reconstructed based on conditions shared among Archaeognatha, Zygentoma, and some Pterygota. Conditions in early members, however, depend more strongly on a comparison with the sister taxon of Insecta, which most likely is Diplura (e.g. Misof et al. 2014). Relevant aspects of this comparison between Insecta and Diplura are discussed in section 8.5., but many aspects remain unclear, mainly because knowledge of the postabdomen of Diplura is sparse and data are ambiguous. It is one out of several possibilities that many of the genitalic specialities in question have undergone secondary reduction in Diplura (as they have in many Pterygota). Accordingly, the evolutionary transformations addressed in the aquaeductal and sensorial hypotheses have likely occurred in the stem-lineage of Insecta; but they may have alternatively occurred (partly or entirely) in the stem-lineage of Insecta + Diplura. In the latter case, all that is referred below to the stem lineage of Insecta would rather refer to this stem lineage plus the stem lineage of Diplura + Insecta.

For the time when the genitalic specialities of Insecta started to emerge, the discussion in chapter 8. (see therein for references) leads to the following corner points and uncertainties: **(i)** The male gonopore (opening of ejaculatory duct; likely median but possibly paired) was most likely located in the segmental border region 9/10 (i.e., either posteriorly on venter 9 or anteriorly on venter 10, see section 5.2.) throughout the insect stem-lineage. The presence of phallic organs is uncertain for early members of the insect stem-lineage but is clear for late members, which likely had a simple tubular penis bearing the genital opening (sub-)apially, as in Archaeognatha and Zygentoma (paired penes appear less likely). **(ii)** The female gonopore (opening of common oviduct) was located posteriorly on venter 7 in late members of the stem-lineage, as it is in this position in Archaeognatha, Zygentoma, and various Pterygota; in early members it was either in the same position or in the border region 9/10. The presence of a partly sclerotised 7th-segmental genital fold is clear for late members of the stem-lineage, as such a fold is present in Archaeognatha, Zygentoma, and various Pterygota; for early members of the stem-lineage its presence is uncertain. The opening(s) of the female accessory glands is clearly 9th-segmental and a good candidate to have been the original female genital opening if this was located in the border region 9/10. The accessory gland opening, however, is unlikely to be homonomous with the male ejaculatory duct opening (even if the latter is 9th-segmental), as the openings show a different (anterior versus posterior) position relative to the bases of the gonapophyses **gp9** when these are medially fused. **(iii)** From (i) and (ii) follows that the genitalic specialities including the gonapophyses have likely evolved in association with a 9/10th-segmental male gonopore and either with a 9/10th-segmental or with a 7th-segmental female gonopore. In addition, **(iv)** typial coxal vesicles on abdominal segments 1 – 7 were most likely already present in the stem-lineage of Diplura + Insecta, as these structures are wide-spread in Diplura (Pagés 1989), Archaeognatha, and Zygentoma. This indicates (but does not at all prove) that the design of these processes as coxal vesicles is older than that as gonapophyses, i.e. that gonapophyses are derived from quite typial coxal vesicles. The following discussions follow this assumption (but see section 5.5.4. for a discussion of other possibilities for the evolution of vesicles and gonapophyses and their effect on the aquaeductal hypothesis).

5.5.2. The aquaeductal hypothesis

The proposed original function of structures in water uptake. We propose the following Group I specialities (sex-shared) to represent together an early stage of the evolution of insect "genitalia" that is shared by both sexes, showing little sexual dimorphism: A lengthening, narrowing, and stiffening of coxal vesicles **vs8** (prospective gonapophyses **gp8**; G26-8 in Table 2) and **vs9** (prospective **gp9**; G26-9) may have allowed these processes to enter deeper and narrower crevices (where water is retained for a longer time) than the coxal vesicles of the preceding segments. With the inflation of a balloon-like coxal vesicle expanding in all directions, water can be absorbed from a level or hollowed moist surface, but the bottom of a crevice is difficult to reach. In contrast, a bundled group of stiffened, slender processes can be gradually pushed into a crevice, and water can be extracted from the crevice using the capillary forces of the channel enclosed by the processes (if the centrally facing surfaces are hydrophilic). The proximal ensheathing of the gonapophyses by the coxal lobes **cx9** and the intercoxal **mic9** area (set of specialities G18-9, G19-9, G20-9, G24-9) may have developed for bundling the two pairs of gonapophyses and inserting them together into a target crevice. The lacking basal fusion of the left and right coxal lobes **cx9** (G17-9) is required to allow for a close grouping of the gonapophyses of both segments. The lacking basal fusion of the left and right coxal lobes **cx8** (G17-8) likely had the effect that gonapophyses **gp8** and **gp9** could together be angled ventrally relative to the abdominal trunk; this might have been required to advance deeper into a crevice when the ensheathing by coxal lobes **cx9** starts to be hindering. The presence of articulated setae (likely tactile) on the gonapophyses could have enabled them to find a crevice and the way deeper into it. Chemosensitive setae on the gonapophyses might have tested the presence and quality of the water. The annulation of the gonapophyses of both sexes (included in G26-8 and G26-9) might have eased bending in irregular crevices. The anteromesal shift of the **gp9** bases (G29-9) likely was the most substantial part of the close spatial association of the gonapophyses. The fact that in both sexes of Archaeognatha a firm basal abutment is only present for the gonapophyses **gp9** (but not for the **gp8**), established by the anterior coxal bridge (**e**; G15-9), sug-

gests that the **gp9** played the leading role in the steering and forward-pushing of the water-uptake apparatus, while the **gp8** were mainly with them to form a channel and perhaps to stabilise the proximal part. Capillary water uptake via the gonapophyses could initially have focally supplied the genital products or the process of their release with humidity. We submit that the only Group I speciality that cannot be explained with this functional context of water uptake (but does not contradict it) is the anterior shift of the bases of gonapophyses **gp8** (G28-8) in both sexes.

Transformation of vesicles into gonapophyses. A coxal vesicle **vs** of Archaeognatha bears the semicircular, setose ventrobasal sclerite **BS** (Klass & Matushkina 2012; 'operculum' in Becker 1966) and a much larger membranous eversible distal part bare of setae. The eversible part consists of two functionally different surface regions: The dorsal side is hydrophobic, the ventral side is hydrophilic (Weyda 1974). These sides are internally separated by the vesicular diaphragm, which enables circulation of haemolymph in the vesicle lumen (Weyda 1974; a similar diaphragm was found in each female gonapophysis **gp8** and **gp9** of *Gryllus*: Hustert et al. 2014). A vesicle is everted by an increase of haemolymph pressure, and inverted by muscles attached between the dorsal and ventral sides of the membranous parts of the vesicle walls. There are two ± plausible scenarios of how such coxal vesicles could have transformed into gonapophyses while the function of water uptake was maintained.

According to a first scenario **(Sc1)**, the larger distal part of a gonapophysis originated from the membranous part of the vesicle. Then the ventral side of a gonapophysis was initially hydrophilic, and the dorsal side hydrophobic, and especially the latter became sclerotised to support the gonapophysis. With the spatial association of the four gonapophyses (the **gp8** and **gp9** pairs), capillary water uptake through the channel enclosed by them became possible; the water was either absorbed along the channel-facing walls of the gonapophyses or at the bases of the gonapophyses. For this sake, the gonapophyses rotated so that their hydrophilic surfaces faced the channel. This requires stronger rotation for the **gp8** (hydrophilic surface from ventral to dorsomesal) than for the **gp9** (from ventral to ventromesal). This scenario is possibly supported by muscle attachments being positioned on the membranous distal parts of vesicles and on proximal to distal parts of gonapophyses (e.g. Bitsch 1973, 1974a,b, but data are not very clear).

A second scenario of transformation **(Sc2)** is suggested by Becker's (1966: p. 251, fig. 100) report of an eversible vesicle on the apex of the male **gp9** (= 'paramera') of a nicoletiid zygentoman (*Lepidospora*; documented therein by a drawing), which could either represent an atavistic condition or a stabilised reversal. Based on this, the larger proximal part of a gonapophysis originated from the **BS**-bearing vesicle base, sclerite **BS** having lengthened and subdivided; this led to a stalked vesicle. Only the distal part of the process corresponds with the membranous part of the vesicle; this part was still shaped as an eversible vesicle, part of whose walls were hydrophilic and able to take up water. With this scenario, the transformation of two pairs of vesicles into gonapophyses and the close association of them only served for penetration into crevices, but the channel enclosed by the gonapophyses was not used for capillary water uptake. Becker's observation has apparently not been repeated since, but, if indeed true, it is relevant even if it refers to an atavistic condition in an exceptional specimen. We note that stalked abdominal vesicles occur on anterior abdominal segments of Collembola and Protura, but their homology with vesicles in Diplura and Insecta is not very likely (Klass & Kristensen 2001: pp. 277f).

The transition to genitalic functions. In addition to the primary function of water uptake, the Group I specialities, with the gonapophyses in the focus, could have sooner or later become functional in the genitalic activities presumably performed by the gonapophyses in the latest stem-insects. This especially concerns **(1)** the manipulation of sperm and **(2)** the production of sperm threads in males, and **(3)** sperm or spermatophore uptake and **(4)** oviposition in the females (see section 5.3.). Not all these functions were necessarily acquired at the same time. We propose that in the late stem-lineage of insects the genitalic functions (1)–(4) became predominant, which led to an increase of sexual dimorphism in the genitalic segments – approximately to the limited extent seen in Archaeognatha. Since in no extant insect male gonapophyses are shaped in a way suited for water uptake via capillarity, we propose that in the male sex this function was abandoned in the late insect stem-lineage. We note, however, that for the female sex a continuation of capillary water uptake up to the present is an option, since for Archaeognatha and Zygentoma reports that could exclude (or confirm) such an activity are absent.

There are two possible conflicts at this stage of reasoning: First, at the evolutionary stage when in the female the uptake of water and of fluid sperm co-occurred (a stage possibly still persisting today), water and sperm would go the same way along the gonapophyses (although not at the same time), i.e. along parts of the body wall adapted to water absorption (following the above scenario Sc1). On the coxal vesicles, water is actively transported through the vesicle wall (see Sturm & Machida 2001: p. 111); this had then also to be assumed for gonapophyses functioning in water uptake. Yet, the sperm was probably quite safe from exsiccation along this way by having a similar osmotic potential as the absorbing tissue (see Houlihan 1976 for strongly reduced intensity of water absorption of coxal vesicles for solutions with high osmotic potential compared to pure water). In addition, the sperm might have been safe by being coated with spermatophore material on its way up the ovipositor.(We submit that with the above scenario Sc2, the issue of desiccating sperm has no relevance.) Second, why was such a useful gonapophyseal function of water uptake given up? Its loss is plausible when tak-

ing the evolution of the water-absorbing coxal vesicles in Diplura, Archaeognatha, and Zygentoma into account: Compared to the apparently plesiomorphic set of vesicles on abdominal segments 1 – 7 in all three orders, there is multiple parallel reduction in the equipment with vesicles up to complete loss (data in Pagés 1989; Matsuda 1976: pp. 69, 120, 124; Wygodzinsky 1961); complete loss is also likely for Pterygota. This suggests an increasing independence from water uptake of this kind, achieved in parallel in several lineages (perhaps by optimisation of structures reducing loss of water, e.g. the epicuticle). Structures that had additional functions for which they could be optimised, such as the genitalic functions in case of the gonapophyses of both sexes, would have plausibly been the first to lose the function of water uptake.

In Archaeognatha the modes of operation of the gonapophyses in both female genitalic activities (3) and (4) are potentially very similar to those postulated above as the original modes of operation in both sexes: uptake of fluid by capillary forces (either water – according to the above scenario Sc1 – or sperm fluid) and entering crevices (either for reaching water or for depositing eggs; see Sturm & Machida 2001: p. 52 for oviposition) (but see section 5.3. for lacking demonstration in Archaeognatha of the use of capillary forces and of an insertion of the gonapophyses into crevices). In contrast, the modes of operation of the gonapophyses in the male genitalic activities are very different from the hypothesised original modes of operation and also require some male-specific morphological differentiation of the gonapophyses, such as the tubular setae producing sperm threads (Fig. 13B,C,E). It is thus plausible that the morphology of the female gonapophyses is closer to the original morphology shared by the two sexes, while the male gonapophyses may also have undergone some reduction along with their specialisation for new, genitalic functions. The female gonapophyses acquired genitalic functions that require a channel (sperm uptake, oviposition), which has apparently stabilised an equally strong development of the two gonapophyseal pairs as long as one of these functions is maintained (oviposition). In contrast, the functions that the gonapophyses acquired in the males do not depend on the formation of a channel (sperm manipulation, sperm thread production), but the gonapophyses can contribute to these individually or pairwise. These functions can thus be focused on a single pair, preferrably on the one closer to the place of sperm release (apex of penis), which is the **gp9** pair. The second pair, **gp8**, may easily undergo reduction. This agrees with the fact that in male Archaeognatha (and Zygentoma, as far as known) gonapophyses **gp8** are consistently more weakly developed than gonapophyses **gp9** and have been lost multiple times (indicating their dispensability), and that the 8th-segmental laterocoxo-gonapophyseal muscle has been lost (at least in *Machilis*, Bitsch 1974b: p. 209, fig. 3). Indeed, our hypothesis of an original function of the gonapophyses in water-uptake in both sexes and of the known present function of sperm thread production in the males being secondary provides an explanation of this multiple loss in Archaeognatha. A purely genitalic context of genitalia evolution can hardly explain why gonapophyses **gp8** are present in many Archaeognatha but simultaneously show a strong trend of parallel reduction.

Did males initially possess additional, female-specific genitalic specialities? Based on the foregoing paragraph, one might tentatively suspect that some of the genitalic specialities present in Archaeognatha only in the female could have been shared by both sexes in stem-lineage insects, as long as water uptake was the predominant function, and were reduced in the male when genitalic functions began to prevail. This concerns the specialities of Group III (see section 5.4. and Table 2) that are potentially useful in capillary water uptake from crevices. In each sex the gonapophyses **gp8** and **gp9** should have been of similar length to form a channel. Then it is also plausible that a strongly arched intercoxal area **mic8** (G24-8) and coxal lobes **cx8** with an anteromesally projecting part (G18-8) were present in both sexes for ensheathing the well-developed proximal parts of the **gp8**. For advancing into crevices, a sliding interlock between gonapophyses **gp8** and **gp9** is plausibly useful (olistheter with aulax **al** on **gp8** and rhachis **rh** on **gp9**; G33-8, G33-9). This structure was then retained only in the female for the sake of oviposition.

However, whereas in case of all Group I specialities an early presence in both sexes is suggested by direct morphological evidence from extant taxa, such presence is only functionally plausible and thus highly speculative in case of these Group III specialities. Yet, the far anterior position of the bases of gonapophyses **gp8** (G28-8 of Group I) and the lacking transverse fusion of coxal lobes **cx8** (G17-8 of Group I), both present in the female and in **gp8**-possessing males of Archaeognatha, could indeed be reminiscences of males formerly having had a genitalic structural pattern nearly as complete as in the female.

The role of the gonopores. The location of the male and especially the female genital opening during the evolution of the sex-shared genitalic specialities of Group I (in the stem lineage of Insecta or perhaps Insecta + Diplura) is highly significant when we ask how exactly genitalic functions could have been taken over by the gonapophyseal apparatus. We submit that the location of the openings is also significant if one rejects the aquaeductal hypothesis and assumes genitalic functions having been the original purpose of the sex-shared genitalic specialities.

The location of the ***female gonopore*** is crucial because depending on its various possible locations on venters 9/10 or 7 (see (ii) in section 5.5.1.) either the Group I specialities alone may have sufficed for oviposition, or various additional genitalic specialities are required. There are essentially three possibilities:

(A) *Female genital opening was located posteriorly on venter 7* (*represented by what is the common oviduct opening = gonopore in extant insects*). In this case, the acquisition of the function of oviposition by the gon-

apophyses likely required the evolution of some 7th- and 8th-segmental female specialities to establish a connection between gonopore and gonapophyseal channel: an arched intercoxal area **mic8** (G24-8 of Group III), coxal lobes **cx8** with an anteromesally projecting part (G18-8 of Group III), and a 7th-segmental genital fold **gf** (G02-7 of Group V). In female Archaeognatha these structures allow the eggs to enter the gonapophyseal channel (Klass & Matushkina 2012; see also female 'gouttière génitale' in Bitsch 1974b). The presence of a strong sternite **STt8** fused with coxae **CX8** (G08-8 of Group III), perhaps correlated with the absence of an independent intersternite **STi8** (G07-8 of Group III), could have evolved for stabilising the concavity of the anterior-most part of the egg passage. In contrast, regarding the function of storage of uptaken sperm, the 8th-segmental spermatheca(e) would have been in reach from within the gonapophyseal channel without further genitalic specialities beyond the sex-shared ones of Group I. We submit that an initial presence in both sexes of an arched **mic8** area (G24-8) and anteromesally projecting **cx8** lobes (G18-8), as suspected in the previous paragraph in context with the function of water uptake, would more easily explain the connection of the gonapophyseal apparatus to the 7th-segmental female genital opening and its use for oviposition. In this case only fold **gf** and the strengthened **STt8** bridge had to be additionally developed in the female.

(B) *Female genital opening was located on venter 9 anterior to the median contact area of left and right gonapophyses **gp9*** (*represented by what is the accessory gland opening in extant insects*). The position of the accessory gland opening(s) anterior to the **gp9** contact is exemplified by female insects that both have accessory glands and show a basal midline fusion of the **gp9** (see section 8.4.(H)). Eggs released through such an opening would be immediately guided into the channel enclosed by the gonapophyses **gp8** and **gp9**. In this case, oviposition could have been taken over by the gonapophyses without an arched **mic8**, anteromesally projecting **cx8**, a fold **gf**, and a **STt8** bridge having been present. These apomorphic specialities could then have evolved later in the female, when her gonopore was translocated to venter 7. We submit that in this case an arched **mic8** and anteromesally projecting **cx8** were likely never present in the male. In this case, however, there is no evident reason why at some later point in the insect stem lineage the female gonopore was transferred to venter 7.

(C) *Female genital opening was located on venter 9 posterior to the median contact area of left and right gonapophyses **gp9**, or on venter 10* (*isosegmentally homonomous with ejaculatory duct opening of male, opening not existing in females of extant insects*). The position of such an opening posterior to the **gp9** contact is directly evident from the position of the male gonopore in Archaeognatha (Figs. 1 – 11; see also section 8.4.(H)). In this case, the close median association of gonapophyses **gp9** (included in G29-9), found in both sexes, would likely have prevented eggs from entering the gonapophyseal channel, thus excluding oviposition through this channel. On the other hand, outgroup comparison with Diplura may indeed suggest such a position of the genital opening, identical in the two sexes, for early stem-lineage insects (see sections 8.5. and 8.6.). Then such an ancestral position could have been the (or one) reason for a translocation of the female gonopore to venter 7 in later stem-lineage insects. The possible preceding presence of an arched **mic8** area and anteromesally projecting coxal lobes **cx8** – in both sexes as part of the water-uptake system – would have eased such a translocation, or even made the hind margin of venter 7 the proper new place for the female genital opening. Then only the female genital fold **gf** and the **STt8** bridge had to evolve in addition.

The ***male gonopore*** has likely constantly maintained its location in the 9/10th-segmental border area (posterior to the **gp9** contact, as in (C)) throughout the evolution of genitalic specialities (see (i) in section 5.5.1.). However, the midventral area bearing it has probably shifted to the anterior, as indicated by ontogenetic studies on a few insects (e.g. Wheeler 1893; see section 8.4.(A,B)). In the frame of the aquaeductal hypothesis, this shift has plausibly occurred when the gonapophyses started to take over genitalic functions, to achieve a closer spatial association of the penis with gonapophyses **gp9**. Alternatively, however, this could have occurred earlier, when the gonapophyses still served for water uptake: the ensheathing shelter between coxal lobes **cx9** that had evolved for accomodating the gonapophyses could have been used to shelter the penis as well, and in this position the genital products or their release may have gained an improved supply with humidity. Even in very close association with gonapophyses **gp9**, the penis was unlikely to hinder a gonapophyseal function of water uptake. On the other hand, however, the gonapophyseal apparatus, if too long, may have hindered the function of the penis.

Conclusions on aquaeductal hypothesis. The aquaeductal hypothesis proposes that water uptake via capillary forces of a gonapophyseal apparatus was the original purpose of most of the sex-shared structural specialities in the genitalic segments of stem-lineage insects, with little or no sexual dimorphism having been present in the postabdomen as long as this function prevailed. At a later stage, the same structural specialities came to serve for genitalic functions. Eventually, genitalic functions became predominant, while the function of water uptake was abandoned (completely at least in the male), and new, sex-specific genitalic specialities arose; this was the basis for increasing sexual dimorphism in the genitalic region. All this occurred in the stem lineage of Insecta, or (less likely) in part already in the stem lineage of Diplura + Insecta.

We consider this hypothesis especially attractive for the following reasons: **(1)** It explains why many structural specialities of the genitalic segments are very similar in both sexes of Archaeognatha; due to the different requirements of male and female genitalic functions, these similarities should not occur if genitalic functions had prevailed from the beginning. **(2)** Nearly all struc-

tural specialities shared by the two sexes in the genitalic segments can be explained by the function of capillary water uptake via grouped gonapophyses. **(3)** The proposed subsequent absorption of water (likely along the centrally facing gonapophyseal walls) corresponds with the known function of the homonomous structures of the pregenitalic segments, the coxal vesicles. **(4)** The proposed function of capillary water uptake by the gonapophyses is additionally very similar to one likely (although not demonstrated) function of the gonapophyses in the females of many Archaeognatha, the uptake of sperm fluid by capillary forces. **(5)** The proposed initial activity of the gonapophyses, entering narrow crevices to reach water, corresponds with a likely (although not clearly demonstrated) activity of the gonapophyses in the female, namely entering such crevices for egg deposition. **(6)** The aquaeductal hypothesis is independent of the original location of the female genital opening; or, in the reverse, it can explain why the gonapophyseal apparatus developed in a position that is not immediately in reach for a 7th-segmental female genital opening and also unpractical for a 9th- or 10th-segmental one posterior to the median junction of gonapophyses **gp9**. **(7)** If a translocation of the female genital opening from venter 9 or 10 to venter 7 occurred in the insect stem-lineage (quite likely by comparison with Diplura), the hypothesis might yield the explanation why the hind margin of venter 7 was a proper place for the new position of the opening. **(8)** The aquaeductal hypothesis also explains the odd situation in Archaeognatha where male gonapophyses **gp8** are present in many taxa but simultaneously show a strong trend of parallel reduction.

5.5.3. Origin of insect genitalia in a purely genitalic functional context?

Emeljanov (2014: pp. 373, 376) suggests that female genital functions, i.e. taking up fluid sperm or spermatophores and releasing the eggs, were the original purposes for the transformation of coxal vesicles **vs8** and **vs9** into longer, sclerotised, non-retractile gonapophyses **gp8** and **gp9** enclosing a channel. We see two shortcomings in this hypothesis:

Most importantly, Emeljanov's (2014) hypothesis does not consider the male sex. It is not explanatory with regard to the large set of Group I specialities that are shared by the two sexes in Archaeognatha (which above was the starting point for exploring a possible non-genitalic context of 'genitalia' origin), and not with regard to the presence and frequent loss of gonapophyses **gp8** in male Archaeognatha (compare (1) and (7) in foregoing paragraph).

Even when considering the female sex alone, Emeljanov's (2014) hypothesis is not unproblematic: With this hypothesis, the female gonopore(s) should have been located on venter 9 at an early evolutionary stage, because an opening on venter 7 would have been out of reach for the gonapophyseal channel without further structural differentiations (see paragraph on gonopores in 5.5.2.). Emeljanov (2014) adequately assumes this: location likely upon the vesicles / gonapophyses of venter 9, i.e., paired. This is also quite plausible, if the openings that in extant insects form the accessory glands openings are regarded as the original gonopores (the above alternative (B) for the location of the female genital opening). In insects, accessory glands with paired openings and with unpaired openings occur (see section 8.2.3.). The paired glands of Odonata, for instance, open at the anteromesal bases of the gonapophyses **gp9** (Klass 2008: figs. 5, 7). This agrees with Emeljanov's (2014) assumption – though an unpaired opening would appear as likely. However, a later translocation of the female genital opening to venter 7, where it is placed in e.g. Archaeognatha and Zygentoma (and in the insect ground plan), is then difficult to explain.

5.5.4. Evolutionary correlation between coxal vesicles and gonapophyses

The transsegmental homonomy of the mesal processes of the abdominal coxal lobes – the pregenital coxal vesicles and the genital gonapophyses – is uncontested (e.g. Bitsch 1994; see sections 8.4.(B,F) and 8.6. for homonomous 10th-segmental processes possibly forming the insect penis). The water-absorbing vesicular morphotype upon abdominal segments 1 – 7 is found in diplurans, archaeognathans, and zygentomans, and this morphotype plausibly evolved in the stem lineage of Diplura + Insecta (or even of Hexapoda) in the context of terrestrialisation to secure water supply. The gonapophyseal morphotype is only found on abdominal segments 8 and 9 of Insecta. It is unclear how the shared precursor structure of the two morphotypes looked like, and, accordingly, which transformations took place to shape typial vesicles and gonapophyses. Hypotheses on the condition of the precursor structure depend in part on the morphological interpretation of all these elements either as endites of some proximal podomere (then likely of the coxa, e.g. Bitsch 1994), which are typially short and non-annulated, or as endopods (Hädicke et al. 2014), which are typially long and annulated. There are three basic possibilities:

(A) *The precursor structure was vesicle-like*. The water-absorbing vesicular morphotype was originally present on abdominal venters 1 – 9 (or even 1 – 10), and the gonapophyseal morphotype of venters 8 and 9 is derived from it. This is one possibility complying with the interpretation of these structures as endites, and it was assumed above in the context of the aquaeductal hypothesis (see Sc1 and Sc2 in 5.5.2. for two plausible pathways of transformation).

(B) *The precursor structure was neither vesicle-like nor gonapophysis-like*. The water-absorbing vesicular morphotype of abdominal venters 1 – 7 and the gonapophyseal morphotype of venters 8 and 9 were derived by different modifications from a more primitive type of endite of obscure structure and function.

(C) *The precursor structure was gonapophysis-like*. The gonapophyseal morphotype was originally present

on abdominal venters 1–9 (or even 1–10), and the water-absorbing vesicular morphotype of venters 1–7 is derived from it. In this sense, Hädicke et al. (2014: view of J.T. Haug on pp. 180f) propose that the long, slender, sclerotised-annulated condition of the gonapophyses represents the older morphotype. This interpretation is based on their hypothesis that gonapophyses and vesicles represent the endopod (fig. 8 therein), i.e. the limb part transsegmentally homonomous with the thoracic legs from the trochanter onward; it involves comparison with Crustacea. All this is supported by the authors neither via a detailed consideration of skeletal morphology nor via a comparative analysis of limb musculature. As we consider a detailed consideration of the skeletomuscular morphology as essential in discussions on podomere homologies and homonomies in arthropod limbs, and as this would overcharge the present article, we do not further discuss Hädicke et al.'s (2014) interpretation herein – but include it as one possible option. We submit that with this option, gonapophysis-like appendages on venters 8 and 9 were most likely also present in the early stem lineage of Diplura, where they may or may not have had genitalic functions.

Options (A)–(C) leave us with a wide range of possibilities for the original condition of "vesicles" and "gonapophyses" and their transformational relationships. Possibility (A) is the functionally most plausible in the context of the aquaeductal hypothesis, as (A) clearly goes along with an original presence of a water-absorbing capacity of part of the gonapophyseal walls (important for the putative function of water uptake), and as the transformation from vesicle to gonapophysis can be explained by the aquaeductal hypothesis. An original presence of a water-absorbing capacity of the gonapophyses is not inherent in possibilities (B) and (C), as the gonapophyses had never been vesicle-like. However, with both (B) and (C), the gonapophyses could well have acquired a water-absorbing capacity together with their pregenital counterparts (prospective vesicles), as these structures are homonomous and thus may have shared evolutionary changes in gene expression. Consequently, possibilities (B) and (C) do not seriously challenge the aquaeductal hypothesis. We note that with (B) and (C) the genitalic specialities G26-8 and G26-9 either include or altogether represent primitive rather than derived characteristics of venters 8 and 9.

5.5.5. Sensorial capacity of coxal vesicles and gonapophyses and the sensorial hypothesis

Functional contexts for having sensilla. Insects have many motivations to use body appendages for a sensorial exploration of their surroundings: localisation of food, water, enemies, or conspecifics, and exploring conditions of the substrate or medium. Perception is partly mediated by the surrounding air (e.g. olfactory perception and airflow-related mechanoperception), and partly it needs contact with a specific part of the surroundings (e.g. gustatory perception and object-related, tactile mechanoperception). Contact with the surroundings occurs in two different categories of functional context: **(i)** Some body appendages extend away from the trunk to perform specific, focally non-sensorial activities at some distance to it; they bear sensilla to guide their activity and/or to perceive the conditions they meet during their activity (e.g. the tarsi). **(ii)** Other body appendages extend away from the trunk with sensorial perception being the main purpose; they may perform sweeping movements (e.g. the antennae). There are also body appendages combining (i) and (ii) (e.g. the palps). Accordingly, most appendages of the insect body are equipped with sensilla of various sensorial capacities.

Sensilla and sensorial capacities on coxal vesicles and gonapophyses. These appendages show a variously rich equipment with sensilla in extant Archaeognatha and other insects. The gonapophyses overall appear to include a greater diversity of sensilla types and sensorial capacities in the females (see e.g. Matushkina 2017 for various Archaeognatha; Matushkina 2011 for *Tricholepidion*; Matushkina 2008, Matushkina & Lambret 2011, Matushkina & Klass 2011, and Rebora et al. 2013 for Odonata) than in the males (data given herein); however, the sensilla on male gonapophyses have also received much less attention so far. Unfortunately, with the present limited degree of histological and experimental studies of sensilla, it is largely impossible in many insects to assign specific sensorial capacities to the various sensilla present on vesicles, gonapophyses, and other body parts. There has been recent progress in the study of archaeognathan sensilla, but this mainly concerns the antennae (e.g. Missbach et al. 2011).

Coxal vesicles: The ventrobasal sclerite **BS** bears numerous presumably sensory microchaetae (Edwards 1992), likely including S-shaped sensilla trichodea (Klass & Matushkina 2012: fig. 3B), which probably have a mechanosensory and/or chemosensory function (Missbach et al. 2011). No sensilla have been reported for the membranous part of the vesicle. When an everted vesicle touches dry substrate, it is withdrawn whithin seconds (Weyda 1974). This suggests that sclerite **BS** is also hygroreceptive (perhaps based on one type of its microchaetae), since the coxal setal organ at the dorsal base of the vesicle cannot touch the substrate when the vesicle is everted. This organ, which is present in Archaeognatha (Fig. 12E,G) and *Tricholepidion* (Wygodzinsky 1961), likely registers the eversion and retraction of the vesicle (Weyda & Stys 1974).

Gonapophyses: Both male and female Archaeognatha (and Zygentoma) bear numerous mechanosensory sensilla chaetica ('macrochaetae') and S-shaped sensilla trichodea ('microchaetae'). Female Archaeognatha additionally have articulated grooved type I sensilla basiconica ('sensory rod' and probably 'spine') of likely gustatory or gustatory + mechanoreceptive function; and non-articulated porous type II sensilla basiconica ('conule' or 'sensory cones'), whose external morpho-

logy suggests an olfactory function (Matushkina 2017 and references therein).

This means that, compared to vesicles, gonapophyses additionally show olfactory perception (at least in females), and tactile as well as gustatory perception are present all over instead of only being present basally. The additional olfactory perception may initially have also been present in male gonapophyses and have undergone reduction later on, concomitant with functional changes. Chemoreception can have a variety of targets, such as the detection of food, of unfavourable chemical conditions, or of conspecifics or their trails. Aggregation behaviour is common in Archaeognatha and Zygentoma (Wertheim et al. 2005); it was shown to be pheromone-mediated in some zygentomans (Tremblay 2002; Tremblay & Gries 2003; Woodbury & Gries 2007), which has also been suggested for *Petrobius brevistylis* (Frohlich & Lu 2013). Pheromones are likely non-volatile, produced by adults and nymphs, and probably released by hypodermal glands distributed all over the body (Fröhlich & Lu 2013).

A sensorial or a non-sensorial functional context for the origin of gonapophyses? We discuss here whether the gonapophyseal sensillar equipment is more likely present due to a focally non-sensorial functional context (**i** above) or due to an explicitly sensorial context (**ii** above).

(i) A tactile, gustatory, and olfactory sensillar equipment of the gonapophyses is fully explainable within context (i), i.e., with the gonapophyses initially having been processes of the body that mainly served for a specific non-sensorial activity but had the sensilla equipment that was useful for this activity. This is plausible within the frame of the aquaeductal hypothesis: tactile setae allow the bundled gonapophyses to search for a crevice and guide them deeper into it; gustatory and olfactory sensilla test the quality of the water contained in the crevice and whether the crevice was previously exploited by a conspecific or is inhabited by an enemy.

(ii) Yet, one might suspect that on venters 8 and 9 the gonapophyseal morphotype has specifically developed (in case of (A) or (B) in section 5.5.4.) or been retained (in case of (C)) for a sensorial function, i.e. for the sake of a more sweeping tactile, gustatory, and olfactory exploration of the substrate and air within the reach of the highly, especially horizontally movable gonapophyses. This might have been a useful addition to the sensorial activity of the cerci and terminal filament, whose 'territories' of perception are located further behind. The gonapophyses may have specifically served adults of both sexes for finding a proper place for deposition of genital products, or adults and nymphs for tracing pheromones from conspecifics.

When considering this ***sensorial hypothesis*** of the gonapophyses, with context (ii), there are two options: This sensorial function can either be assumed to have been immediately followed by genitalic functions (pure sensorial hypothesis). Or it can be assumed to have been followed by functions according to the aquaeductal hypothesis, which only then were gradually supplemented and replaced by genitalic functions (combined sensorial-aquaeductal hypothesis). We start with discussing the former option.

For this it is relevant to examine the extent to which the ***pure sensorial hypothesis*** is explanatory in terms of the sex-shared genitalic specialities, i.e. those of Groups I and perhaps II (Table 2). Out of the 11 Group I specialities, 2 can be explained by a sweeping sensorial function of the gonapophyses: the condition as long, sclerotised, annulated gonapophyses **gp8** and **gp9** (G26-8, G26-9). 4 further specialities are indifferent in this regard (i.e. neither explainable nor contradictory): the lacking fusion between left and right coxal lobes **cx8** and **cx9** (G17-8, G17-9), the elongated condition of coxal lobes **cx9** (G19-9), and coxae **CX9** forming an anterior transverse bridge (**e**; G15-9). The 5 remaining Group I specialities, however, would have been obstructive to a sweeping sensorial function by limiting the degree of movability of the gonapophyses and thus the area they could explore. These are specialities that effect the gonapophyses to be ensheathed or their bases to be hidden: The location of the base of the gonapophyses **gp8** in the dorsal **cx8** wall (G28-8), the location of the base of the gonapophyses **gp9** mesad of the **cx9** wall (G29-9), the presence of an anteromesally projecting anterior part of coxal lobes **cx9** (G18-9), the high, concave mesal flanks of coxal lobes **cx9** (G20-9), and the strongly arched intercoxal **mic9** area (G24-9). The 4 Group II specialities would all appear indifferent: Intersternite **STi9** absent (or fused to sternite **STt9**; G07-9), postlaterocoxites **LCp9** separated from coxites **CX9** (G12-9), laterocoxal inflexion **li9** present on **LCp9** (G13-9), and styli **sl9** distinctly elongated (G22-9). In sum, the assumption of sweeping sensorial gonapophyses explains 2, is likely indifferent for 8, and is contradictory for 5 of the sex-shared genitalic specialities of Groups I and II. The 5 contradictory specialities and perhaps some of the indifferent ones should thus have evolved later, when the sweeping sensorial function was replaced by genitalic functions. This, however, leads to the problem that the shared presence of these numerous genitalic specialities in both sexes needs to be explained based on genitalic functions, while the genitalic functions in the two sexes are very different (see section 5.5.1.).

In contrast, the aquaeductal hypothesis has a much greater explanatory power: it explains 10 and is indifferent for 5 (G28-8 of Group I and all of Group II) of the sex-shared genitalic specialities (see section 5.5.2.), while there are no sex-shared specialities contradicting this hypothesis. Thus, one possible explanation for the 5 sex-shared specialities in conflict with the pure sensorial hypothesis and for several of the specialities indifferent with it is yielded by the ***combined sensorial-aquaeductal hypothesis***: The sensorial function of the gonapophyses was followed by an aquaeductal function, for the sake of which these specialities have evolved in both sexes; only at a later stage genitalic functions followed.

One might submit that a transition from the sensorial to the aquaeductal function could involve problems, but these appear, at most, minor: **(1)** A sweeping sensorial

activity of the gonapophyses of two successive segments probably makes only sense if these work in different directions (such as antero- vs. posterolaterally). While this is a clear constraint to such gonapophyses, they could in the same specimen have the option of swinging mesad to take a longitudinal parallel orientation. The latter positioning could have gradually come to prevail, followed by a tube-like design of the group of gonapophyses and the development (for the purpose of water uptake) of the abovementioned specialities that appear problematic in the frame of the sensorial hypothesis. **(2)** A sweeping movement of individual gonapophyses over the substrate can likely be achieved by the same muscular activities as required for gradually pushing grouped gonapophyses into a crevice (for reaching water): muscles targeting the gonapophyseal base can contract alternately for the former movement and simultaneously for the latter. **(3)** It is not evident why a sweeping sensorial activity of the gonapophyses should have been given up: If a sensorial exploration of the respective part of the substrate was advantageous in stem-insects, why shouldn't this still be the case in extant Archaeognatha and Zygentoma? Yet, water supply may have been the more important challenge for some time in the evolution of stem-insects. The transformations according to (1)–(3) do thus appear possible. We submit that with the aquaeductal hypothesis these issues (1)–(3) do not appear: The gonapophyses are assumed to show a parallel orientation (1) and a back-and-forth movement relative to each other (for entering crevices; (2)) from the beginning, and the abandoning of the original function, water uptake, parallels the multiple reduction of other organs of water uptake (abdominal vesicles) in different lineages (see section 5.5.2.).

Conclusions on pure sensorial, combined sensorial-aquaeductal, and aquaeductal hypotheses. According to the discussions on **(i)** and **(ii)** in the foregoing paragraphs, we favour the aquaeductal hypothesis, i.e. that water uptake was the original non-genitalic purpose of the early evolution of genitalic specialities in stem-insects and explains the presence of many of the structural similarities in the male and female genitalic segments as presently still found in Archaeognatha. However, the combined sensorial-aquaeductal hypothesis, meaning that the aquaeductal function was preceded by an explicitly sensorial function of the gonapophyses, is also plausible. It appears especially attractive if the precursor structures of vesicles and gonapophyses indeed showed the gonapophyseal morphotype (case of (C) in section 5.5.4.). Such an initial sensorial function may then have been true for all abdominal appendages of the vesicle-gonapophysis-series.

5.6. Phylogenetic evaluation of male genitalic characters in Archaeognatha

A phylogenetic evaluation of our morphological data (Table 1) is difficult for several reasons: **(1)** The possibilities for outgroup comparison are strongly limited, with regard to Diplura, Zygentoma, and Pterygota. In Diplura the male genitalic region is very simply structured (see Pagés 1989 and section 8.5.), most of the characters in Table 1 are not applicable. Zygentoma would be useful for outgroup comparison, as their male genitalic structures appear to be overall similar to those of Archaeognatha. However, detailed descriptions of their male genitalia are lacking, and only few of the characters in Table 1 could currently be reliably scored for some member of this taxon. Among the Pterygota, Ephemeroptera appears as the most useful outgroup taxon with regard to archaeognathan male genitalia. However, their male genitalia are structurally diverse, and several issues of morphological interpretation and homology need to be clarified (see e.g. Snodgrass 1957: pp. 14ff). **(2)** Our archaeognathan taxon sample is still small, and the majority of the few features that could reasonably be considered as apomorphies are only present in a single taxon and thus not phylogeny-informative (such as the lack of gonapophyses **gp9** only in *Machilinus*, character 30). The information content will likely increase with the addition of further archaeognathan taxa. As expected from (1) and (2), a phylogenetic analysis of the data in Table 1 yielded no result worth being presented here. In the following we only mention a few characters whose polarity is quite clear and which thereby can group species of our sample.

Two characters support a clade *Petrobiellus* + *Machilinus*: The connection of postlaterocoxa **LCp9** and coxa **CX9** (character 20); this is likely an apomorphy, but one that could perhaps easily arise by paedomorphosis (as in the females of many Dicondylia: Klass et al. 2012). The presence of a basal fusion of left and right gonapophyseal sclerites **GP9** (character 31); this could be an apomorphy, as paired elements are concerned. Zygentoma is the only other taxon with representatives having unambiguous gonapophyses **gp9** in the male. The **gp9** of *Lepisma* (Fig. 20) are not shifted as far anteromesally as in Archaeognatha, they take a position intermediate between coxal vesicles and archaeognathan **gp9**; thus they as well as their sclerotisations **GP9** are clearly medially separated and support the above character polarity. At least one character in Sturm & Machida (2001: fig. 4.4, p. 19) may also support this clade: The absence of scales on the scapus and pedicellus of the antenna (evidence from their characters 12, 15, 20). Two other characters support a clade *Machilis* + *Lepismachilis* + *Pedetontus*: The division of coxa **CX9** into sclerites **CXt9** (bridge part) and **CXp9** (posterolateral parts) (character 22); and the at least weak connection between sternum **STt9** and antelaterocoxa **LCa9** (character 16). Both are likely apomorphies, but the polarity is not entirely clear. This should not yet be considered as support for a clade Machilinae + Petrobiinae, because both subfamilies are too diverse for such an extrapolation. Yet, both clades *Petrobiellus* + *Machilinus* and *Machilis* + *Lepismachilis* + *Pedetontus* tentatively agree with the phylogenetic evidence predominant in Ma et al.'s (2015) analyses, i.e. Petrobiellinae + Meinertellidae being sister to Machilinae + Petrobiinae.

We additionally note that a study of the three genera *Mesomachilis*, *Charimachilis*, and *Ditrigoniophthalmus*, considered as basal offshoots of the archaeognathan tree in Sturm & Machida (2001; see Introduction), could be of considerable interest. To us these taxa were not available.

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8. Appendix: Interpretation and segmental position of phallic elements and genital openings in insects

8.1. Frame of discussion

We discuss this topic in a wider frame, including both sexes, due to its fundamental importance for insect (and hexapod) morphology. The position of the genital opening(s) is highly variable across the Arthropoda, and both paired and unpaired openings occur (e.g., Snodgrass 1936). Hexapods are consistently opisthogoneate, i.e., genital openings are located ventrally on the posterior part of the abdomen. In **Protura** and **Collembola** the opening is, straightforwardly seen, in both sexes placed posteriorly on the venter of the 11th and 5th abdominal segment, respectively (e.g., Snodgrass 1936: pp. 57ff, 1957). This is in both taxa the last segment, which precedes the well-developed, likely non-segmental telson (often called segment 12 or 6, respectively). However, the matter may be more complicated, especially in the Protura. Protura and Collembola contribute little to understanding the morphology of genitalia in Insecta and will not be considered in detail. **Diplura** is either the sister group of Insecta (e.g., Misof et al. 2014; more likely) or part of its sister group (in case of monophyletic Entognatha as in, e.g., Kjer et al. 2006); the genital openings are said to be located on abdominal segments 8 or 9 (e.g., Pagés 1989; Snodgrass 1936, 1957), similar to many Insecta. Dipluran genitalic morphology is thus of great relevance when reconstructing ancestral conditions in Insecta, and it will be considered herein.

8.2. General issues in the morphological interpretation of insect genitalia

There are five major general issues that are relevant in the morphological interpretation of insect male genitalia and contribute to the multiple inherent problems: the numbering and homologising of abdominal segments, the segmental assignment of structures, the paired versus unpaired condition of genitalia, the origin of genitalia from limb parts versus de-novo formation, and the homology of genitalia across Insecta. Most of these topics are also relevant to the female genitalia. A general discussion of these topics is here provided in first place.

8.2.1. Numbering and homologising abdominal segments

The major lineages of Hexapoda have different numbers of abdominal segments: 11 in Protura and Insecta could be the plesiomorphic number; 10 in Diplura and 5 in Collembola are likely apomorphic. Protura and Collembola, however, have a well-developed terminal telson, which cannot be excluded to include another true segment, the 12th resp. 6th (the true telson then only being its terminal portion). The question is whether segments can be homologised among these taxa only by their numbering from the anterior, or partly by their numbering from the posterior (e.g., could the forelast segments be homologous as such?), or whether there is a sound basis at all for homologising individual segments.

Snodgrass (1936: pp. 57, 65) does not accept homologising segments by a count from the posterior end. For instance, he rejects the idea of genital openings being on homologous segments in Collembola (on 5th = last segment) and Protura (on 11th = last segment). His point is that segments newly added during development originate just in front of the telson, i.e. posterior to the segment later forming the genital opening. This point, however, is flawed: It relies on the assumption that if in, e.g., a collembolan abdominal segments were added to reach the number of 11, the genital opening would still be shaped

on segment 5. However, the opening could then as well be shaped on segment 11, i.e. on the last of the additionally formed segments. The 'solution' of this virtual case would depend on the mode of operation of the gradients in the abdomen that induce particular segments to form a genital equipment (or other structures). Beyond this, however, it may not even make sense to postulate homology for any particular segments in case of series of different lengths. As a conclusion, both directions of counting appear justified to us, but in case of different numbers of abdominal segments, counting and homologising from either end loses safe ground very soon.

This issue is highly relevant when comparing the postabdomen between Insecta and Diplura. Diplura have 10 abdominal segments (cerci belonging to the 10th), whereas Insecta have 11 in their ground plan (cerci belonging to the 11th; terminal segments poorly developed in many pterygote subgroups) (Uzel 1898; Ikeda & Machida 1998; Klass 2001: pp. 293f). The cercus-bearing segment can probably be considered homologous between Diplura and Insecta (as the terminal segment with its structural peculiarities, such as cercus-like appendages), as can probably be the 1st abdominal segment (if segment-specific shared conditions can be demonstrated for the two taxa, such as the lack of styli: Ikeda & Machida 1998: p. 114). However, the homology of particular segments in the series in between is unclear: With which segment of Insecta should a segment of Diplura be compared – with that of same number or of same number plus 1 when counting from the anterior? For the present, we consider both alternatives justifiable – having the general flawedness of a 1-to-1 homologisation of segments in abdomina with different segment numbers in mind.

8.2.2. Segmental assignment

Statements on the segmental assignment of structures only make sense if they refer to the primary, embryonic segmental borders. These are in all ontogenetic stages up to the adult represented by the lines derived from the depths of the early-embryonic intersegmental grooves. With ongoing development, however, the grooves usually obliterate at least in part, and segmental borders thus become increasingly obscure or even purely hypothetical and need careful reconstruction based on other available morphological 'landmarks'. With this concept, there is not really a 'between segments' (e.g., no 'intersegmental membranes'), except for the narrow depths of antecostae and their ontogenetic derivatives. Referring segmental assignment to secondary segmentation (based on seemingly segmental sclerite portions of the adult or a nymphal/larval stage) is meaningless, especially as it does not allow for referring a structure to an embryonic segment and thus a priori prevents a sound morphological interpretation (i.e., such reference ignores the main point of the question). In addition, the ventral side of a postabdomen with well-developed male or female genitalia rarely shows an evident pattern of secondary segmentation. Most insect morphologists refer to primary segmental borders when discussing the segmental assignment of structures, though often not consistently. Others refer to secondary segmentation, such as Matsuda (1976: p. 72) in his list of the sites of origin of primary phallic lobes in various insect groups (which is thus of little use in a discussion of the morphological interpretation of genitalia).

Identifying the segmental assignment (relative to primary segmentation) of a gonopore, a genital opening (see chapter 3. for the distinction of these terms), or any genitalic structure can be complicated and conjectural. There are several relevant points:

(i) The midventral areas of segments are crucial, because they bear the openings of the various gonoducts (s.lat.) and elements immediately associated with them, whose segmental assignment is the most relevant issue.

(ii) During ontogenetic development, parts of the body wall of the genitalic region can be subjected to shifts, expansions, and overgrowth both in anteroposterior and lateromesal directions. These can lead to a considerable interdigitation of ventral segmental territories, i.e., segmental borders are often not straight, and occasionally have a complex course. Most relevant is an anteromesal shift and anterior expansion of abdominal venter 10 (the area suspected to bear the phallic organs and gonopore in the male), which eventually projects like a tongue into a recess of venter 9 (e.g., Wheeler 1893 for both sexes of an ensiferan; details in section 8.4.(B)).

(iii) The localisation of segmental borders on the ventral side thus needs landmarks, the most important ones being (remains of) the antecostae (including spinae). However, in the adults these are often obsolete, or other internal ridges or projections may have developed that might be mistaken as antecostae or spinae.

(iv) Certain muscle attachments can also serve as landmarks for the location of segmental borders (e.g., the internal ventral longitudinal muscles, see section 8.4.(C)), as do certain sclerites (which, in turn, are often identified by their position relative to particular muscle attachments). However, evidence on this is often ambiguous, since identifying the right muscles can be problematic, or these have been reduced or their attachments been shifted in the course of development.

(v) In pre-imaginal stages, expansions and mutual overgrowth of parts of the body wall may not yet have taken place, and structures marking segmental borders (e.g., antecostae and muscles) can be more completely present than in adults. Ontogenetic studies are thus of great relevance to issues of segmental assignment (though they can as well be misleading in case of developmental shortcuts, see, e.g., Klass 2008: section 6.3.1.). This, however, requires a careful consideration of the location of primary segmental borders and of structures marking them throughout the developmental stages. Unfortunately, in many papers on the ontogenetic development of the postabdomen this consideration is insufficient (e.g., in Qadri 1940), whereby conclusions on the segmental assignment of structures are often limited.

8.2.3. Paired versus unpaired

It has long been disputed whether the male phallic organs and/or genital openings were originally paired or unpaired in (adult) stem-Insecta, and whether the paired condition of both in Ephemeroptera (and possibly other, extinct palaeopteran taxa) and Dermaptera (Snodgrass 1957: pp. 16–19) are primary or secondary. We will not discuss this multilayered topic in detail, as its bearing on the segmental assignment is limited, but we provide some notes. First, pairedness has to be evaluated separately for the phallic organs and for the genital openings and their exit ducts (ejaculatory duct(s) and endophallus/-i).

The ***phallic organs*** of insects undoubtedly have a paired ontogenetic origin (as primary phallic lobes; e.g., Matsuda 1976). Their median fusion into a penis or aedeagus, present in many insects, occurs at a later developmental stage. In the adults of some insect taxa, especially in Ephemeroptera and some polyneopteran orders, a median fusion of phallic lobes is absent or limited to the base. This could be plesiomorphic for Insecta or a paedomorphic apomorphy. Based on parsimony, the latter appears much more likely in view of the complete median fusion into a penis in Archaeognatha and Zygentoma (e.g., Snodgrass 1957: fig. 2).

Regarding the ***genital opening(s)***, it is important that many of the polyneopteran taxa lacking a significant median fusion of the phallic lobes yet have an unpaired genital opening between the lobes (e.g., Dictyoptera; Klass 1997), which is likely a true gonopore and is an unpaired median invagination from its first ontogenetic appearance (e.g., Nel 1929; Qadri 1940). Ephemeroptera and Dermaptera are the only high-rank insect taxa with paired genital openings (and ejaculatory ducts). Based on parsimony, the paired condition appears apomorphic in view of the unpaired condition in Archaeognatha, Zygentoma, and most Pterygota. In addition, one may ask whether paired and unpaired openings or ducts can be homologous and, if yes, how significant a transformation between paired and unpaired is.

Cases of transformation between paired and unpaired conditions of genitalic ducts (s.lat.) and their openings are known from female insects. One example is the 9th-segmental accessory glands in Odonata, which are paired and widely separated in Zygoptera and Aeshnidae (Klass 2008: **ag*** in figs. 3, 7, 39, 40), paired and close together near the midline in *Epiophlebia* (Klass 2008: **ag*** in fig. 41), and unpaired with an internal dichotomy in the petalurid *Phenes* (Matushkina & Klass 2011: p. 204). The female spermathecae of Dermaptera yield another example: in most species the opening is unpaired, either without (e.g., *Dacnodes caffra*) or with (e.g., *Tagalina burri*) an internal dichotomy; in diplatyids, however, openings are paired, with the left and right ones either close together near the midline (*Diplatys macrocephalus*) or widely separated and even placed on a pair of deep pouches (*Haplodiplatys orientalis*) (Klass 2003: figs. 24, 28, 38, 43, 81–89). These examples suggest that an evolutionary transformation between paired and unpaired openings is not necessarily a striking one. On the one hand, an unpaired condition can be derived from a paired one by a gradual mesal shift of the openings until their invagination areas become confluent; this has probably occurred in the above example from Odonata. On the other hand, the ejaculatory duct of some male insects is internally forked (i.e., the terminal parts of the 'vasa deferentia' are lined with cuticle; Snodgrass 1935: p. 572). A paired condition can then easily be derived from an unpaired one by the dichotomy shifting to the external surface; this is what we tentatively assume for male genital openings in Ephemeroptera and Dermaptera.

However, there are also cases in the females where consegmental organs with unpaired versus paired openings are not homologous, but a replacement has occurred, as shown by the presence of both kinds of structures in some taxa. For instance, blaberoid Blattodea have replaced the unpaired spermatheca on venter 8 by paired ones on venter 7 or 8 (assignment not clarified), as shown by the presence of all three spermathecae in some members of the genus *Anaplecta* (McKittrick 1964). Or, on venter 9, unpaired and paired tubular ectodermal glands co-occur in some Dermaptera (accessory glands **ag** and lateral tubes **tl** in Klass 2003; see discussion in Klass 2008: section 6.3.2.).

8.2.4. Origin from (parts of) limbs or not

Segmental limbs of Pan-Crustacea (including Hexapoda) outside of the hexapodan clade have a wealth of branches and processes that could be hypothesised to form or contribute to the phallic organs in insects. The reduced abdominal limbs of insects include the coxal lobe and, arising from it, the stylus and one or two coxal vesicles / gonapophyses, which form a basic set of candidate phallic precursors (see, e.g., Sturm & Machida 2001: fig. 8.30a for the occasional occurrence in Archaeognatha of two vesicles per abdominal limb). As the phallic organs might have developed when abdominal limbs were still less reduced, limb parts that are additionally present in various crustacean lineages could, with varied plausibility, be taken into account as further candidate structures. Furthermore, with the phallic organs being potentially 9th-, 10th-, or 9+10th-segmental, limb elements of either or of both these segments could be involved. This opens a wide range of possibilities for the interpretation of insect phallic structures. Only those limb parts can be excluded that are 'occupied' by well-secured non-phallic interpretations (such as the coxal lobes, styli, and – with limitations – gonapophyses of venter 9, which in Archaeognatha and various other insects are most clearly present beside the phallic organs). Two hypotheses illustrating the possible range are those of Becker (1966: p. 264), who proposes an origin of the phallic organs from a lateral pair of eversible vesicles of segment 9, and of Birket-Smith (1974) and Rohdendorf & Rasnitsyn (1980: p. 22), who suggest an origin from gonapophyses or coxal vesicles of segment 10. Both hypotheses deal with structures potentially occurring in ancient hexapods,

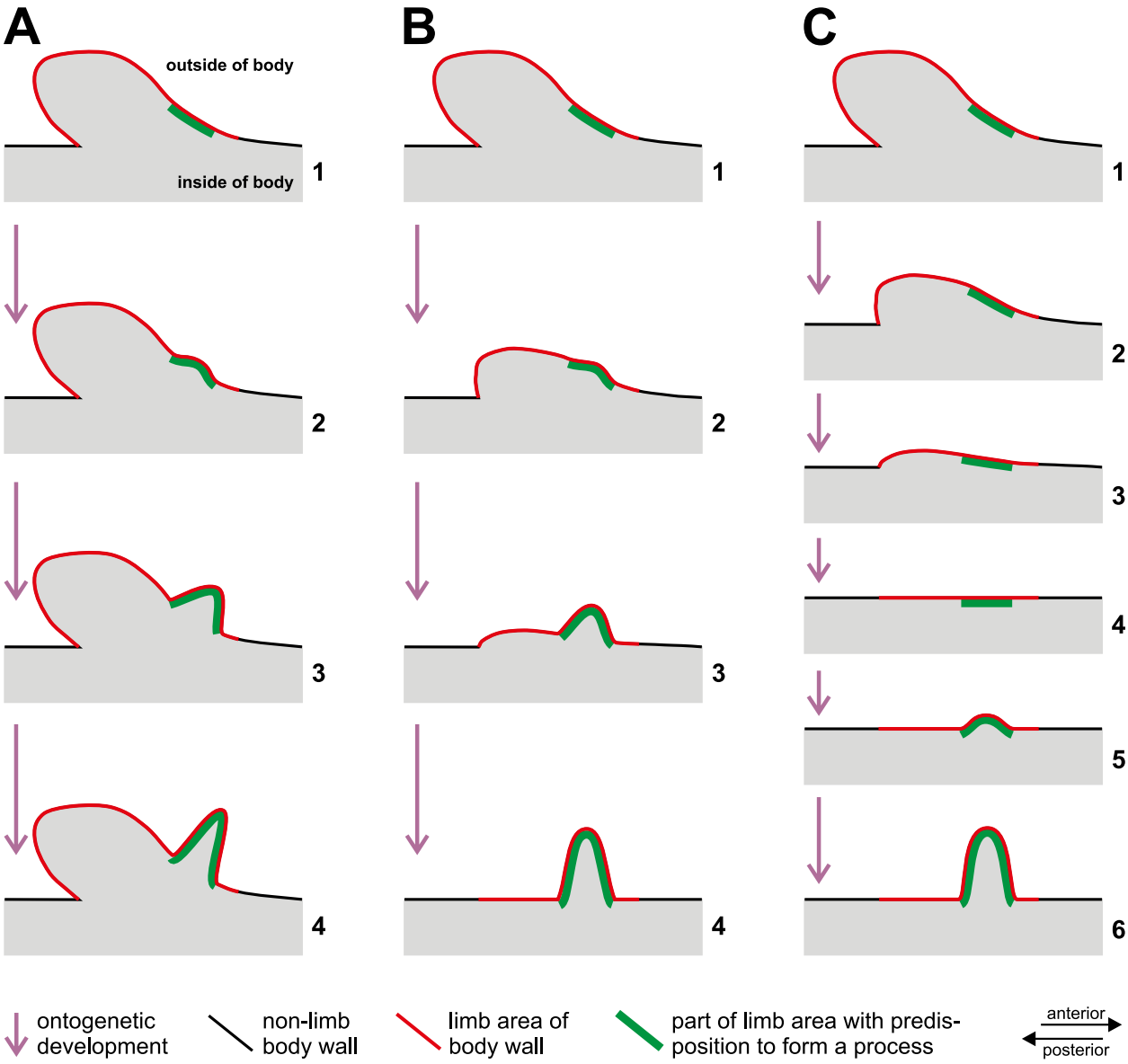

Fig. 22. Diagrammatic representation of ontogenetic development of embryonic/nymphal limb bud and a limb-borne process from its base. Three hypothetical cases are shown that differ in the development of the limb-base process relative to the development and leveling of the entire limb. **A**: Limb-base process develops while the entire limb is retained as a projection. **B**: Limb-base process develops while the entire limb is becoming leveled. **C**: Limb-base process develops long after the entire limb has become leveled.

without taking additional crustacean elements in account. The major alternative to a limb-based origin is a de-novo formation of insect phallic organs independent of limbs, as proposed by, e.g., SNODGRASS (various papers).

A substantial discussion of the numerous alternatives is not possible at present due to the strong structural divergence between venter 10 and the preceding abdominal venters in extant insects (making interpretations based on transsegmental comparison difficult) combined with the sparsity of detailed data on the postabdominal segments and conflicts among such data (see, e.g., KLASS 2001).

However, we address here one important general issue (Fig. 22): In the course of ontogeny, limb buds develop, and subordinate processes (e.g., endites) arise from them; in this, the limb buds can either be retained to develop further side by side with their subordinate processes (Fig. 22A), or they become leveled, only their subordinate processes remaining (Fig. 22B). In both cases the belonging of the process to the limb is quite clear. However, cases that include a stage of complete leveling (Fig. 22C) are problematic. Segmental limbs are usually considered to be 'absent' as soon as their buds become leveled in the course of ontogeny (as in Fig. 22C4). This kind of 'absence' is occasionally taken as the basis to deny the body area concerned the ability to form any limb-borne processes later on during development. We submit, however, that the limb bud material (e.g. its epidermis) is still present in the leveled limb bud area (red in Fig. 22C), and there is no reason to believe that a predisposition of part of the limb bud wall (e.g., to form a process; green in Fig. 22C) cannot survive the leveling of a limb bud area. In this way we consider it reasonable to

interpret a process arising from a long-leveled limb bud area (as in Fig. 22C5,6) as a limb-borne process, if such a hypothesis is in agreement with the spatial relationships and not in conflict with significant evidence.

8.2.5. Insect-wide homology

Male gonopores, the ejaculatory ducts leading to them, and phallic organs are not necessarily in the same position and of the same morphogenetic origin or composition in different insect lineages, i.e., not necessarily homologous throughout (irrespective of their paired or unpaired condition). Regarding the composition, one question is the fate of male gonapophyses **gp9** in the Pterygota. In Archaeognatha and (many) Zygentoma the **gp9** are distinct structures beside the phallic ones, the penis **pe**. In the various lineages of Pterygota, however, it is unclear whether the **gp9** have either been lost, or have become completely amalgamated with phallic structures, or have been retained as part of the 9th-segmental coxal (**cx9**) or (if medially fused) subgenital lobes (ventral fold **vf9**; see, e.g., Matsuda 1976 on the hymenopteran volsella, contra Snodgrass 1957: p. 49ff). It may thus be an option that phallic organs in (part of) Pterygota are **pe+gp9**, then not strictly homologous with the **pe**-only phallic organ in Archaeognatha and Zygentoma. Considering that the discussion of the segmental position and morphological interpretation of the phallic structures must rely on fragmentary data from a variety of insect taxa (both due to the sporadic occurrence of certain structures across insect taxa and to the limited availability of sophisticated data), possible non-homology of male genitalia is a general background uncertainty plaguing any insect-wide discussion of the topic. We base our discussions on the plausible assumption of insect-wide homology of male genitalia (which remains to be tested).

8.3. Female genital openings (s.lat.) in Archaeognatha and other Insecta

This issue is here discussed for the sake of comparison of the conditions in the two sexes, e.g., for assessing whether the male gonopore could be isosegmentally homonomous with any female opening. The female configuration is understood better than the male one.

Openings on 3 successive segments. In the ontogenetic development of female insects there is a widespread set of three ventromedian ectodermal genitalic invaginations being located on the posterior margins of venters 7 (prospective common oviduct; opening = gonopore), 8 (spermatheca), and 9 (accessory glands) (e.g., Snodgrass 1933: pp. 32ff, fig. 8A; Nel 1929; Qadri 1940). The condition in, e.g., young nymphs of *Locusta* (Roonwal 1937: fig. 138d, **vg.i.***, **sr.i.***, **ac.i.***) indicates that all three invaginations originate well anterior to the segmental border following, i.e., they are unlikely structures of the segmental borders.

Regarding adults, the genital opening (s.str., where the eggs leave the body) is clearly located on the posterior part of venter 7 in Archaeognatha (Bitsch 1974a; Birket-Smith 1974) and Zygentoma (Rousset 1973; Birket-Smith 1974), as shown by retained midventral parts of the segmental border 7/8 (intersternite and its transverse antecostal infolding and spina in Bitsch 1974a: fig. 1A; Klass & Matushkina 2012: p. 589); this opening is unpaired and likely represents the true gonopore (opening of common oviduct). The same configuration is thus probably true for the ground plan of Insecta. In the pterygote insects, however, problems in the interpretation of the genital opening (as a true gonopore, a vulva, or else) and in its segmental assignment (to venter 7 or 8) abound (see Klass 2003, 2008; Klass & Ulbricht 2009).

Besides the common oviduct, the spermatheca and the accessory glands are most likely also present as discrete median invaginations in the ground plan of adult Dicondylia (Zygentoma + Pterygota). In Archaeognatha, the spermathecae are small and have paired openings, and the accessory glands are only represented by a pair of glandular stripes upon level body wall (Bitsch 1974a; Klass & Matushkina 2012). It is unclear whether this is a primary condition or a result of secondary simplification. Regarding the accessory glands, a discrete invagination (and possibly the entire glands) is also absent in some Pterygota (e.g., Mantophasmatodea: Klass et al. 2003), most likely by secondary loss.

For the common oviduct an unpaired opening appears to be plesiomorphic for Insecta based on its occurrence in Archaeognatha and Zygentoma. For the spermathecae and accessory glands it is unclear whether the opening was originally paired or unpaired due to the divergent conditions in Archaeognatha and Zygentoma (and Odonata: Klass 2008). The examples given in section 8.2., however, let appear differences with regard to pairedness less striking.

Mesodermal parts. The development of the mesodermal internal genitalia in the embryo and nymph is here of interest, especially regarding the ampullae (or diverticula), which are segmental widened parts of the strands later forming the lateral oviducts. In insects of both sexes, ampullae are formed in several abdominal segments. In females those of segment 7 project into the 7th-segmental appendage buds and usually contact the ectodermal common oviduct invagination of venter 7, thereby establishing the connection between ectodermal external and mesodermal internal genitalia (e.g., Heymons 1897: p. 606 for the ampullae in the zygentoman *Lepisma*; Wheeler 1893: pp. 119ff for the ensiferan *Conocephalus* [as *Xiphidium*]). Roonwal's (1937: pp. 233, 234) results on the caeliferan *Locusta* show an initial presence of female internal genitalia anlagen (partly with segmental ampullae) up to segment 10, and Wheeler (1893: p. 120) also reports transient ampullae in segment 10; then the parts behind segment 7 degenerate. In *Lepisma* Heymons (1897: p. 607) observes a vestigial, discontinuous strand of tissue that seems to

continue the mesodermal strand shaping the internal genitalia at least up to segment 9.

Conclusions on female insects. The presence of an oviduct invagination (unpaired) for egg release on venter 7 and of a spermathecal invagination (paired?) on venter 8 of females are surely features of the insect ground plan, and an accessory gland invagination (paired?) on venter 9 may add to this. This configuration might date back throughout the stem-lineage of Insecta or even Insecta + Diplura (see possibility (A) in section 5.5.2. 'The role of the gonopores'). On the other hand, the presence in female insects of genitalic invaginations on venters 7, 8, and 9 and of a transient extension of internal genitalia into segment 10 would also be in agreement with (but does not support) the following hypothesis: Early stem-Insecta perhaps released their eggs through the opening on venter 9 (accessory gland opening of extant insects having been the genital opening) or perhaps through a hypothetical opening on venter 10 (if 10th-segmental ampullae are taken as indicating the former presence of a consegmental opening); the 7th- and 8th-segmental (and perhaps the 9th-segmental) invaginations have then been newly acquired later on in the stem lineage of Insecta, and the one on venter 7 has taken over the function of an outlet duct for the eggs. Either the opening on venter 9 (accessory glands; unlikely) or that on venter 10 (hypothetical; more likely) could then be isosegmentally homonomous with the male gonopore (see possibilities (B) and (C) in section 5.5.2.). The decision will depend on comparisons with male Insecta (see section 8.4.) and with Diplura (see section 8.5.), if these yield sufficient evidence.

8.4. Male genital openings and phallic elements in Archaeognatha and other Insecta

The gross morphology of adult male insects is suggestive of the phallic organs and the genital opening being placed on the posterior part of venter 9, between the bases of the coxal lobes **cx9** (Archaeognatha: Figs. 1–11), or, if the **cx9** lobes are medially fused to form a subgenital lobe (ventral fold **vf9**), at the posterior base of this lobe (e.g., Dictyoptera in KLASS 1997: figs. 58, 60, 62). It is tempting to assign the phallic organs to segment 9 and to consider the male genital opening isosegmentally homonomous with the accessory gland opening of the female (SNODGRASS 1935: p. 567). However, SNODGRASS (1936: pp. 57ff; 1957: pp. 6ff) lists several arguments suggesting the phallic organs and the ejaculatory duct to pertain to venter 10, which we would then consider to apply as well to the male genital opening. Later morphological studies on Archaeognatha (BIRKET-SMITH 1974; BITSCH 1974b) and ontogenetic studies on various insects (e.g., WHEELER 1893; ELSE 1934) appear to largely confirm this view, but there is also contradictory evidence. Here we briefly survey Snodgrass' views and then discuss the various relevant points ((A)–(I) below), starting with those from ontogeny and including a new one from the present work.

Snodgrass' hypotheses. Snodgrass is the most prominent authority in the discussion of the segmental position of the gonopore and phallic organs in insects. Over the years he changed his preference regarding the position, but details are not very clear, as the relevant phrasing is partly unclear and contradictory. Three structural elements are essential in his hypotheses: **(i)** The phallic organs. **(ii)** Ectodermal male accessory glands on the posterior part of venter 9. **(iii)** The embryonic to nymphal mesodermal terminal ampullae: These are the widened posterior-most parts of the mesodermal strands later forming the vasa deferentia, and they develop in abdominal segment 10. In the adults the ampullae form the terminal parts of the vasa deferentia and often seminal vesicles and mesodermal accessory glands, and they also obtain an open connection with the ejaculatory duct (e.g., SNODGRASS 1937).

SNODGRASS (1935: pp. 582, 583) assumes that originally in adult male insects the 10th-segmental ampullae had a pair of external openings on venter 10, located at the base of the 10th-segmental limbs, as the ampullae are closely associated with the embryonic 10th-segmental limb buds (SNODGRASS 1936: p. 8). The male accessory glands had a (paired?) opening posteriorly on venter 9. Then the openings of the ampullae migrated anteromesally to near the accessory gland opening(s), and an ejaculatory duct formed anew and carried all the aforementioned openings to the interior. The ejaculatory duct would then be an intersegmental (or rather bisegmental) structure with a 9th-segmental anterior wall (bearing the original opening(s) of the accessory glands) and a 10th-segmental posterior wall (bearing the original openings of the ampullae). The phallic organs are entirely assigned to venter 9 in SNODGRASS (1935: pp. 582, 586, 587). As the phallic organs can fuse transversely both behind and in front of the gonopore, this leads to the odd assumption that a 9th-ventral area (phallic organs) entirely encloses a part of venter 10 (posterior wall of ejaculatory duct).

SNODGRASS (1936: pp. 57, 58) is undecided between a 9/10th-inter-/bisegmental or a purely 10th-segmental position of the ejaculatory duct (the latter hypothesis being based on the duct's innervation, see 8.4.(G)). He tentatively assumes that the ejaculatory duct is the original outlet duct of the accessory glands, which is in conflict with his view of 1935 (newly formed duct) and, in case of a 10th-segmental duct, with his assignment of the accessory glands to segment 9. SNODGRASS (1936: p. 59) still ascribes the phallic organs to venter 9 (to the "ventral membrane between the ninth and tenth abdominal segments", which in 1935: p. 582 he assigns to venter 9; we note that the cited phrase implies reference to secondary segmentation, which is inappropriate in the discussion of the segmental assignment of a structure).

SNODGRASS (1957: pp. 6, 14), however, clearly assigns the phallic organs to venter 10. His assignment of the

ejaculatory duct has apparently remained unchanged; if it is considered 9/10th-inter-/bisegmental, this leads to the odd assumption that a 10th-ventral area (phallic organs) entirely encloses a part of venter 9 (anterior wall of ejaculatory duct).

Besides the various unclarities in the interpretations, we see two problems in Snodgrass' views: First, ectodermal male accessory glands only occur in subgroups of the hemipteroid clade and of Endopterygota, while in the remaining insects accessory glands are either absent or mesodermal accessory glands are present (formed by the 10th-segmental ampullae, as far as known; e.g., Matsuda 1976: pp. 92–96, 140). We thus see no evidence for the respective 9th-segmental outlet duct in male stem-insects; only the 9th- or 10th-segmental duct(s) for the ampullae (ejaculatory duct(s)) was likely present, and only this we will consider in the following. Second, as the primary phallic lobes fuse medially both on the anterior and the posterior flank of the gonopore (ejaculatory duct opening), Snodgrass' hypotheses have, in various ways, the abovementioned problem that an isolated island of one segment is completely enclosed by a neighbouring segment. In our opinion a gonopore and a projection surrounding or bearing it do necessarily either belong to the same segment or are in the same way inter- or bisegmental – unless there is strong ontogenetic evidence to the contrary (which we cannot see).

(A) 10th-segmental mesodermal ampullae. One argument in favour of the male gonopore being 10th-segmental (e.g., Snodgrass 1936, 1957) is the ontogenetic origin of the abovementioned terminal ampullae in segment 10. Later the ampullae move anteromesally, seemingly to the hind part of segment 9 (but see (B) below), and contact the inner end of the ectodermal ejaculatory duct rudiment to establish the open connection between ectodermal external and mesodermal internal genitalia. These procedures have been found in several ontogenetic studies (e.g., Heymons 1897 on the zygentoman *Lepisma*; Else 1934 and Roonwal 1937 on caeliferans; Wheeler 1893: pp. 116ff, figs. 42–44 on the ensiferan *Conocephalus*). The ontogenetic shift of the ampullae can also be recognised in adult morphology (i.e., without ontogenetic studies) by a looping spatial relationship between cercal nerves and vasa deferentia (Snodgrass 1936: fig. 21); this has been reported for a wider selection of insects.

However, all this only shows that the terminal parts of the internal genitalia are 10th-segmental, while the ectodermal ejaculatory duct contacting the internal genitalia as well as the phallic organs surrounding the duct's opening could still be 9th-segmental. In the examined female insects the common oviduct and the mesodermal ampullae contacting it belong to the same segment, the 7th (see section 8.3.); but it is not clear whether this is sufficient reason for hypothesising consegmentality also for the ejaculatory duct and the ampullae of the male.

(B) Ontogeny of 10th-segmental venter and limbs. The male terminal ampullae, when still located in segment 10, are closely associated with the 10th-segmental embryonic limb buds and also extend into their lumina. Then the limb buds together with the ampullae migrate anteromesally for some distance (e.g., Snodgrass 1937: p. 8; Else 1934: pp. 593f on *Locusta*; Wheeler 1893: pp. 118, 121 on *Conocephalus*); this is a substantial part of the abovementioned (section 8.2.) anterior expansion of the median part of venter 10 into a recess of venter 9. This process suggests that in the adult the area bearing the phallic organs and the gonopore, which straightforwardly appears to represent the posteromedian part of venter 9, rather represents the anterior part of venter 10. It also suggests that there is no migration of the ampullae alone into segment 9 (compare (A)), but an anterior expansion of part of segment 10 that also involves the ampullae and by which posteromedian parts of segment 9 are displaced.

According to most of the relevant ontogenetic studies, the 10th-segmental limb buds become leveled after some anteromesal migration (as in Fig. 22C1–4; e.g., Wheeler 1893); the primary phallic lobes arise newly further anteromesally in the nymph (comparable to Fig. 22C5,6; e.g., Matsuda 1976: p. 73). The leveling of the limb buds makes it difficult to observe potential later stages of the anteromesal shift of part of venter 10, as there are no buds marking it. Else (1934: pp. 591, 594), however, found in the caeliferan *Melanoplus* that the 10th-segmental limb buds persist as bulges, that they migrate far anteromesally together with the ampullae, and that they develop into the primary phallic lobes (i.e., 10th-segmental limb buds, or parts of them, and phallic lobes are developmentally continuous; similar in Roonwal 1937: p. 233 for the caeliferan *Locusta*; similar to Fig. 22B). Else (1934) consequently considers the phallic organs as being derived from the 10th-segmental limbs. The true ejaculatory duct seems to invaginate from the area surrounded by the phallic lobes after their median fusion anterior and posterior to this area; the duct would thus also be 10th-segmental. (Note that in Else 1934 the "ejaculatory duct" is essentially the endophallus of Snodgrass' terminology, and phallic organs are called "internal genitalia".)

Based on the lack of developmental continuity in all studied insects except the caeliferans, Snodgrass (1936, 1957) rejected the idea of the phallic organs being derived from (parts of) the 10th-segmental limbs, and he interpreted the phallic organs as de-novo formations. Matsuda (1976: p. 73) interprets the case of Caelifera in the way that phallic lobes (basically considered 9th-segmental) appear very early (already in the embryo) and 'take the opportunity' to use the material of the not yet disappeared 10th-segmental limb buds. We would not see any basis for this far-fetched hypothesis, and we would not feel able to distinguish whether in Caelifera the limb buds persist longer or the phallic lobes appear earlier than in other insects.

Contra Snodgrass and Matsuda, we submit that a leveling of the 10th-segmental limb buds does not contradict the use of persisting 'limb material' in the later formation of the phallic lobes and the interpretation of the latter as outgrowths of 10th-segmental limbs (e.g., as endites; as

in Fig. 22C). The developmental step occurring between figs. 43 and 44 in WHEELER (1893), for instance, can well be interpreted in the way that 'material' of the leveling 10th-segmental limb buds (**ap10*** therein) expands to the anterior, together with the internal terminal ampullae, into the area where later the primary phallic lobes arise. Furthermore, this view is indeed supported by the finding of developmental continuity of the processes in caeliferan ontogeny (similar to Fig. 22B), which we consider a strong piece of evidence in favour of phallic organs being derived from and homologous with (part of) the 10th-segmental limbs. This agrees, for instance, with BIRKET-SMITH's (1974) and ROHDENDORF & RASNITSYN's (1980: p. 22) interpretation of phallic organs as the 10th-segmental gonapophyses resp. coxal vesicles (i.e., **gp10** or **vs10**, which refer to the same elements). The anterior shift of these elements in segment 10 could be homonomous with the anterior shift of the bases of the gonapophyses in segments 8 and 9 (see section 5.4.: group I specialities for both sexes of Archaeognatha), which then increases from segment 8 to 10. Eventually, with this interpretation the ectodermal outlet duct and the mesodermal ampullae contacting it would be consegmental in the male (segment 10), as they are in the female (segment 7) (compare (A)).

(C) Ventral longitudinal muscles in Pterygota. Most pterygotes have ventral longitudinal muscles of segment 9 (originating from the anterior part of coxosternite 9, the subgenital plate) that have their posterior attachments on the phallic organs. SNODGRASS (1957) took this as a possible argument supporting the phallic organs to pertain to venter 10. However, there is actually no clear evidence from these muscles.

In typical pregenital abdominal segments of pterygotes, the ventral longitudinal musculature is comprised of two groups, both being intrasegmental with regard to the primary segmentation: **(i)** Internal ventral muscles usually reach (but do not go beyond) the primary segmental border following, their posterior insertions mark this border (together with parts of the antecosta, if this is retained; e.g., KLASS 1999). Since the primary segmental border is usually included in the anterior part of the following coxosternite, internal ventral muscles appear as intersegmental with regard to the secondary (sclerotisation-based) segmentation. **(ii)** External ventral muscles do not usually reach the following primary segmental border; they insert on the 'intersegmental' membrane or on the anterior rim of the following coxosternum.

In segment 9 of, e.g., Dictyoptera, some of these ventral muscles originating from coxosternite 9 cross the phallic organs lengthwise to insert, quite far laterally, on sclerotisations belonging to the paraprocts (KLASS 1997: muscles **p1*** and sclerotisations **Pv*** in figs. 1, 58). These muscles appear straightforwardly as internal ventral muscles of segment 9. Then the segmental border 9/10 is located well behind the base of the phallic organs. However, this is only valid for the ventrolateral areas, not for the ventromedian part, where the phallic organs are focally located and which has likely undergone an expansion to the anterior (compare (B)). In addition, there are muscles running from coxosternite 9 to the phallic organs, i.e., to areas located anterior to the insertions of the aforementioned muscles targeting **Pv*** (KLASS 1997: muscles s + number in figs. 1, 2, 58, 59); these are the muscles mainly referred to by SNODGRASS (1957). If these are further, more mesal parts of the internal ventral musculature of segment 9, they suggest that a small anteroventral part of the phallic organs belongs to segment 9, but the larger posterior part to segment 10; the presumably 9th-segmental portion might then be considered as derived from the gonapophyses **gp9** (compare section 8.2.5.), not being truly phallic. Alternatively, however, these could be external ventral muscles; then the entire phallic organs could well be formations of venter 9. The evidence from the musculature is thus ambiguous even if comparability with pregenital abdominal segments is assumed.

Furthermore, however, this genitalic-pregenitalic comparability appears questionable when the diverse ventral musculature of Archaeognatha and Zygentoma is taken into consideration. Part of this musculature is attached to ventral ligaments (Fig. 23), whose segmental assignment is partly conflicting (see section 5.2. and KLASS 2001). In female Pterygota, by comparison with the zygentoman *Thermobia* (based on ROUSSET 1973), the apparent internal and external ventral muscles of the genitalic segments (especially the 9th) may not all be homonomous with those in the preceding segments, and originally bisegmental muscles might be involved (KLASS 2001: figs. 37, 38, pp. 295ff). There is no reason to believe that the situation in the males is more uniform among segments. The ventral musculature is thus altogether highly ambiguous with regard to the segmental assignment of the phallic organs. It is also ambiguous with regard to the inclusion of gonapophyses **gp9** in these phallic organs.

(D) Ventral longitudinal muscles in Archaeognatha. Yet, there is evidence from one group of abdominal muscles in Archaeognatha, for which both the seriality throughout the abdomen and the segmental assignment are quite clear. As discussed in section 5.2., BIRKET-SMITH (1974) reports ventral longitudinal muscles (series **i***) that in *Petrobius* connect successive ventral tendons (**vt***) arising from the segmental borders (Fig. 23A,B). The location of the origin of the posterior-most tendons **vt*** (**vt10*** = **bpt** herein) suggests that the penis and its sclerite(s) **PE** in the male as well as sclerite **PS9**/**ST10** in the female belong to segment 10. This would appear as a strong argument in favour of a 10th-segmental position of male genitalia and gonopore. However, BITSCH (1973, 1974a,b) found the same muscles (his series **5***) to insert on the successive ligaments (Fig. 23C), which allows no conclusion on the location of segmental borders on the exoskeleton.

The positions of tendons **vt10*** in female (paired) and male (medially fused: **bpt**) *Petrobius* as reported

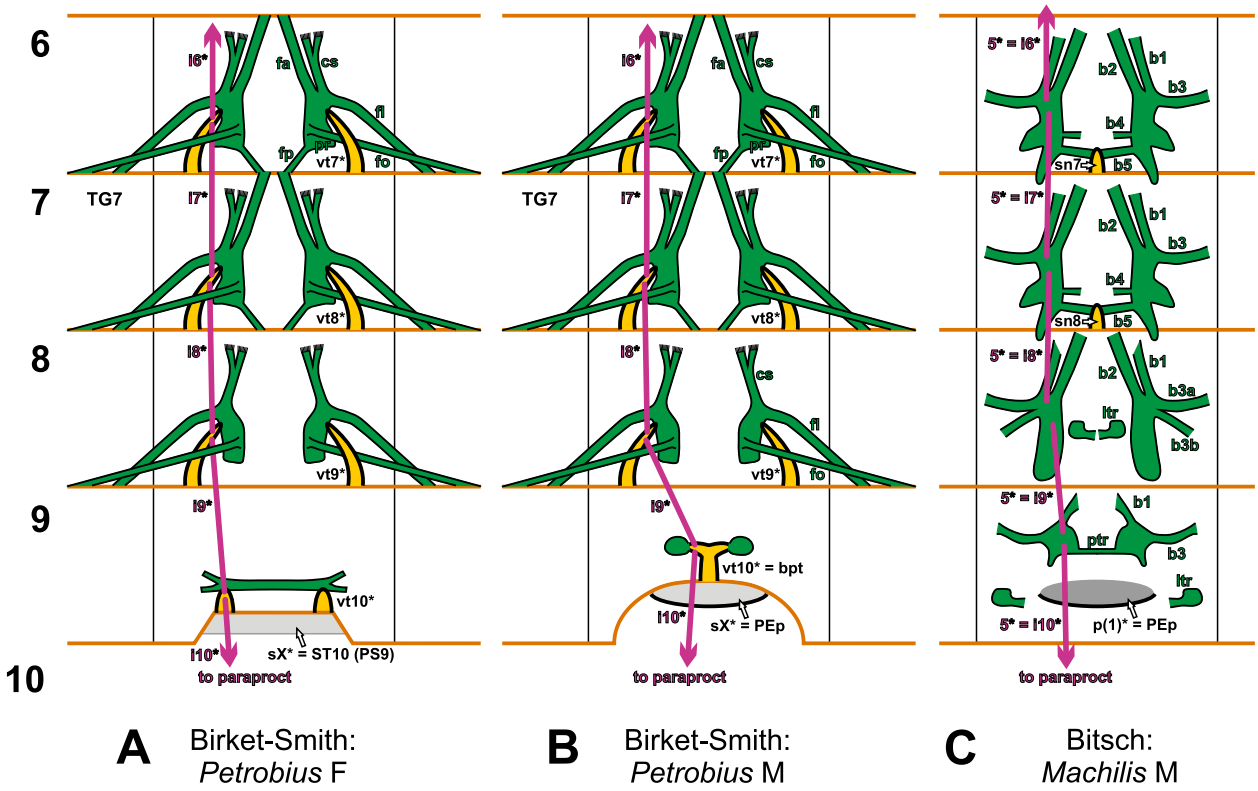

Fig. 23. Diagrammatic representation of abdominal venters 6–10 of archaeognathan males and females, with selected structures relevant for the segmental assignment of sclerites PS9/ST10 and PE. **A**: *Petrobius* female (based on Birket-Smith 1974). **B**: *Petrobius* male (based on Birket-Smith 1974). **C**: *Machilis* (supplemented with data from other Archaeognatha) male (based on Bitsch 1973, 1974a,b). — ***Representation***: Only the following elements are included (as described by the authors): **(1)** Ligamentous endosternites (in ***green***); fa, fl, fo, fp, and cs (Birket-Smith) as well as b1, b2, b3, b4, and b5 (Bitsch) are branches of endosternites that are fixed to the body wall, either to cuticle (end of branch open, no black line) or to subdermal adipose tissue (end of branch fringed, only cs); remainder of endosternites without contact to body wall (with black marginal line). **(2)** Cuticular tendons and apodemes (in ***yellow***), i.e. paired ventral tendons vt* (Birket-Smith; male vt10* medially fused) and unpaired spinae sn (Bitsch), both putatively arising from segmental borders. **(3)** The ventral sclerites that are disputed to be either 9th- or 10th-segmental, i.e. the candidate sclerites for identification as PS9 (male: penial sclerotisation PE); these are shown in ***dark grey*** if potentially 9th-segmental, and in ***light grey*** if there is evidence for them to be 10th-segmental. **(4)** The series of the likely corresponding muscles i* (Birket-Smith) and 5* (Bitsch) shown in ***violet***, attached either to ventral tendons (i*, Birket-Smith) or to endosternites (5*, Bitsch). Thin orange lines represent hypothesised course of primary segmental border. Vertical black lines mark border between venter and dorsum. — Further ***morphological terms*** used for labeling explained in text chapter 3.

by Birket-Smith (1974) also indicate that sclerites **PS9**/**ST10** of the female (Klass & Matushkina 2012: figs. 1, 2) and the ventrobasal part of sclerite(s) **PE** of the male are isosegmentally homonomous (Fig. 23A,B; we submit that tendons **vt10*** are absent in female *Petrobiellus*, see Klass & Matushkina 2012: fig. 2, as tendon **bpt** is absent in male *Petrobiellus*, see Figs. 8, 9). If this is true, males and females share the proximal sclerotisation (**PS9**/**ST10**, ventrobasal part of **PE**), which may more or less represent eusternum 10; but the female lacks a projection homonomous with the male penis as well as the associated more distal **PE** sclerotisations. The female sclerite **PS9** is placed further posteriorly than the male **PE**, quite far remote from the bases of the gonapophyses **gp9** (compare Figs. 2, 4, 6 with Klass & Matushkina 2012: fig. 2). This does not necessarily contradict their homonomy: The anteromesal expansion of venter 10, which Wheeler (1893: pp. 118, 121) reported for *Conocephalus*, occurs in both sexes and may well be stronger in the male than in the female; the same may apply to Archaeognatha.

(E) Female sclerite PS9/ST10 and antecosta ac10. A sclerite resembling **PS9** of female Archaeognatha, but lacking tendons (like **vt10***) and muscle attachments (like muscles **i***), is also present in some ovipositor-bearing Odonata-Zygoptera (Klass & Matushkina 2012: p. 587; Klass 2008: **PS9** in fig. 7; schematised in Fig. 19B,D). The **PS9**-homologous sclerotisations in ovipositor-bearing polyneopteran insects are likely represented by the posterior part of what is usually called the posterior intervalvula (Klass 2008: section 6.5.7.). These sclerotisations would then likely be isosegmentally homonomous with proximal ventral sclerotisations of the phallic organs in the males of the same polyneopterans. However, there are many uncertainties in this topic.

As discussed in section 5.2., there is a conflict arising from the situation in female Zygoptera: All examined zygopterans have a complete circumferential internal ridge (Klass 2008: character 65, fig. 7), whose tergal part is a typial dorsal portion of antecosta **ac10**, and whose ventral part was consequently interpreted in Klass (2008) as the ventral portion of antecosta **ac10** and thus

as representing the segmental border 9/10 (Fig. 19D left picture). The ventral **ac10**, however, is located posterior to sclerite **PS9**. This would assign **PS9** and all its homologues in male and female insects (possibly also including the penial sclerites **PE** of Archaeognatha) to venter 9. Alternatively, if the latter structures are considered to pertain to venter 10, the ventral part of the zygopteran **ac10** must be a secondary ridge located deep within segment 10 (Fig. 19D right picture).

(F) Phallic muscles of Archaeognatha. The evidence from the extrinsic 'phallic muscles' reported in Bitsch (1974b) and Birket-Smith (1974) is ambiguous, mainly because these are either inserted on membrane near the penis base, or it is not clear whether this or an insertion on penial sclerites applies (examples are **k10*** and **c10*** in Birket-Smith 1974: pp. 32f and **59*** in Bitsch 1974b, which all originate from tergite 10). Considering the abovementioned anteromesal expansion of venter 10 (see (B)), membrane next to the penis base may well belong to segment 9 even if the penis belongs to segment 10.

In addition, both Bitsch (1974b: **80*** on p. 211) and Birket-Smith (1974: **j10*** on pp. 32f) report a pair of intrinsic muscles of the penis, which connect the proximal and the distal penial sclerites (**PEp**, **PEd**) ventrolaterally. Bitsch (1974b: p. 219) concludes that the presence of two (near-)cylindrical sclerites interconnected by muscles – a situation resembling podomeres of limbs – agrees with the hypothesis of the penis being derived from (parts of) 10th-segmental limbs. We find this quite convincing, but submit that an identification of particular limb parts by comparison with preceding segments is difficult based on the anatomical data. The interpretation of muscles **80*** and **j10*** as coxo-gonapophyseal muscles 10, as in Birket-Smith (1974; sterno-gonapophyseal therein, but 'sternal' in his sense includes coxal), is one option – the one in accord with the interpretation of the penis as the medially fused gonapophyses 10 in Birket-Smith (1974) and Rohdendorf & Rasnitsyn (1980) (see (B)). If this interpretation is followed, sclerite **PEp** should also include a coxal component of segment 10.

(G) Innervation of ejaculatory duct. Snodgrass (1936: p. 58) puts forward that "the ductus ejaculatorius derives its innervation from nerve trunks that pertain to the tenth segment", suggesting its 10th-segmental origin (see above in section 8.4.). However, such an observation of the topography of nerves can hardly support a 10th-segmental assignment. First, in insects the bundling of particular axons into nerves generally appears to show considerable variation, as seen from the fact that in different specimens of a species the same targets can be reached along very different nerve pathways (e.g., Klass 1999: figs. 10–21, 22–32). Second, in the postabdomen nerves leaving the terminal compound ganglion are combined in few nerve roots. The fact that nerve branches targeting the ejaculatory duct are included in the same main nerve with branches targeting clearly 10th-segmental structures is thus not very meaningful. Innervation-based morphological interpretation of a particular body wall area of the terminal segments needs a tracing of axons from the target area to a subset of the central nervous system, plus comparison with innervation in preceding segments for identifying transsegmentally homonomous areas.

(H) Spatial relation between gonopore and gonapophyses 9. One argument tentatively favouring a 10th-segmental position of the genital opening in male insects can be derived from our results. In male Archaeognatha the close median contact or fusion of the bodies of the gonapophyses **gp9** (Figs. 3–6) takes place anterior to the phallic organs and gonopore (male **gp9** not clearly identified in pterygote insects). In contrast, in female insects that both have 9th-segmental accessory glands and show a basal midline fusion of the **gp9** (e.g., *Nicoletia* in Rousset 1973: **gli*** in fig. 10; *Epiophlebia* in Klass 2008: fig. 41; *Sphodromantis* in Brannoch et al. 2017), the fusion is located posterior to the opening of the accessory glands (female accessory glands not discrete in Archaeognatha). The different spatial relationships of the male genital opening and of the female accessory gland opening relative to the median contact of gonapophyses **gp9** indicate that the two openings are not isosegmentally homonomous (contra Snodgrass 1935: p. 567; compare section 8.3. above and possibilities (B) and (C) in section 5.5.2. 'The role of the gonopores'), but that the male opening is in a further posterior position than the female opening. As the female opening is located quite far posteriorly on venter 9 (Snodgrass 1933: **AcGl*** in fig. 8A), the male opening could well lie on venter 10.

(I) What about further posterior structures? Lastly, it should be noted that assuming 10th-segmental sternal and limb-related sclerotisations to be included in the phallic organs leaves an 'explanatory gap' for other sclerotised structures in a few insect taxa that appear to be in a 10th-ventral position and are located posterior to the phallic organs; examples are the vomer of Phasmatodea (Bradler 1999) and the vomeroid of Mantophasmatodea (Klass et al. 2003). Nonetheless, as no such structures are known from Archaeognatha and Zygentoma, these structures rather appear as de-novo formations of some subgroup(s) of Polyneoptera.

Conclusions on male insects. Points (A)–(I) have shown the great complexity, the considerable ambiguity, and the incompleteness of relevant data regarding the segmental localisation and morphological interpretation of the male gonopore and phallic organs of insects. Our critical review of the relevant anatomical facts shows that some of the arguments previously put forward in favour of a 10th-segmental position do not hold (10th-segmental origin of ampullae contacting ejaculatory duct; targets of 9th-segmental ventral muscles of Pterygota; innervation of ejaculatory duct) – or, at least, much more structural detail is required to test their validity; one feature remains to contradict a 10th-segmental position (apparent ventral antecosta **ac10** in female Zygoptera). On the other hand, there is significant evidence supporting a 10th-segmental position (ontogenetic anteromesal expansion

of venter 10 with occasional developmental continuity of 10th-segmental limb buds and phallic lobes; tendons **vt10*** and attachments of muscles **i*** in Archaeognatha; intrinsic penial muscles in Archaeognatha), and a new feature may point in the same direction (position of male gonopore posterior to gonapophyses **gp9**). Some arguments suggest an interpretation of the penis as medially fused parts of the 10th-segmental limbs, the 10th-segmental gonapophyses / coxal vesicles being especially plausible candidates, but coxal and eusternal components may then additionally be included. Female insects likely have a sclerotisation homonomous with the ventrobasal part of the phallic / penial **PE**, viz. **PS9** and its homologues. In case of a 10th-segmental assignment of sclerites **PE**, this **PS9** is better called sternite **ST10** (or possibly coxosternite **CS10**, as anterior coxal elements might be included). However, females lack both a process homonomous with the penis **pe** and the distal **PE** sclerotisations. The works by Birket-Smith (1974) on adult morphology and Else (1934) on embryology yielded the most instructive evidence on the topic.

These results do not represent a final solution of the issue. However, the discussions in section 8.4. also provide a guideline which targeted studies could lead towards a solution. Indeed, the extensive data on the archaeognathan and zygentoman abdomen in Bitsch (1973, 1974a,b), Birket-Smith (1974), and Rousset (1973) may include additional 'hidden' information relevant for the morphological interpretation of the phallic organs (and other postabdominal structures). These works require a comprehensive comparative evaluation. This will be a daunting task, as Archaeognatha and Zygentoma have a highly complex abdominal musculature and ligamentous endoskeleton, and because data in these papers lack clarity in many relevant details. Such a critical conspectus could not be accomplished herein.

8.5. Genital openings and associated elements in Diplura and comparison with Insecta

Sophisticated data on the postabdomen of Diplura is poor, and virtually absent for the musculature and mesodermal ampullae; interpretations of elements in the literature are partly contradictory.

Similarity between males and females. Pagés (1989) studied the abdominal exoskeleton of diplurans of various subgroups. According to his descriptions, the configuration of venters 8 and 9 appears to be overall very similar in the two sexes (sexes not differentiated in Pages' 1989 descriptions), including internal ridges (potential antecostae). Only some small structures immediately surrounding the genital opening differ between sexes (elements of genital papilla, e.g., structures **aa***, **ap***, **ag*** below). This similarity indicates that the male and female genital openings are in the same morphological position.

8th-segmental openings? Pagés (1989: p. 537) locates the genital opening for both sexes on a papilla "between the 8th and 9th urites" (translated from French; urite = abdominal segment). This localisation based on secondary segmentation is of little morphological use. However, at least in some taxa (including japygids) the ventral side of the postabdomen has a transversely continuous internal ridge (Pagés 1989: p. 519, figs. 12, 13) that appears to be an antecosta demarcating venters 8 and 9. As it traverses the genital opening posteriorly, it suggests the genital opening to lie on the posterior part of venter 8 (as also stated by Matsuda 1976: p. 120) rather than on the anterior part of venter 9. However, caution is advised in view of the ventral 'antecosta' **ac10** of female Zygoptera (see section 8.4.(E)): This dipluran ventral ridge could be non-antecostal, located further posteriorly on venter 9, and the genital opening could then be located on the anterior part of venter 9 (see below).

9th-segmental openings? Snodgrass (1936: p. 70, not referring to a particular taxon) locates the genital opening "between the 8th and 9th segments" in female Diplura (like Pagés 1989), but "between the 9th and 10th segments" in male ones (unlike Pagés 1989). For the males, Snodgrass (1957: p. 11) confirms this referring to a *Heterojapyx* (Japygidae): male opening behind "a small plate, apparently the ninth sternum, bearing a pair of styluslike processes". This might be a misinterpretation (or a valid alternative interpretation?) of the configuration described for Japygidae by Pagés (1989: pp. 519, 538, figs. 12, 13, 49): Venter 9 lacks a coxosternal sclerite and styli in both sexes; but the genital opening in front of it is, in the male, anteriorly (and posteriorly) adjoined by a scaled (and darkened?) area (**aa*** and **ap*** in Pagés 1989: fig. 49), from whose flanks arise a pair of genital appendages (**ag*** in Pagés 1989: fig. 49). Snodgrass (1957) might have (mis?)taken structures **aa*** and **ag*** as a strongly reduced (coxo)sternite and its styli; these structures would then have undergone a considerable shift to the anterior relative to further lateral parts of venter 9.

An 8th-segmental position of the male opening (contra Snodgrass) is supported by the course of the abovementioned ridge, which, if an antecosta, marks the border 8/9. The following observations may be taken as further support for this, though their relevance to the point here in question is limited: For Campodeidae, Uzel (1898: p. 39) and Ikeda & Machida (1998: figs. 7–11) report that limb buds of venters 8 and 9 show no differentiation of styli and vesicles and eventually become levelled; there is also no expansion of the median part of venter 9 to the anterior evident. Both in Campodeidae and Japygidae a backward looping of the vasa deferentia appears to be absent (Grassi 1888: figs. 39, 40), which suggests an ontogenetic shift of mesodermal ampullae to the anterior not to have occurred (compare section 8.4.(A)).

In female Japygidae (Pagés 1989: fig. 46), the scaled areas (**aa***, **ap***) seem to be absent, but venter 9 apparently shows the same configuration as in the male (see above). Then, if one yet follows Snodgrass (1957), a 9th-

segmental location of the genital opening must not only be taken in account for the male, but likely also for the female, in combination with a complete reduction of the putative 9th-segmental (coxo)sternite. With this interpretation the abovementioned dipluran transverse ridge is not considered an antecosta but traverses within venter 9.

7th-segmental openings? Marten (1939: fig. 22) studied the female of *Campodea*; he agrees with Pagés (1989) in the position of the genital opening on the posterior part of venter 8. However, *Campodea* has a vagina ('bursa copulatrix' therein) receiving both the common oviduct and a spermatheca. The same configuration is shown by Grassi (1888: p. 569, figs. 53, 67, 'borsa copulatrice' = spermatheca) for a campodeid and a japygid (the latter with a shorter vagina and with unclear location of the opening = 'vulva'); vagina and spermatheca are claimed to have a cuticular intima. Similar female morphologies in at least some Pterygota result from a posterior growth of the 7th-segmental genital fold (likely the homologue of fold **gf** of Archaeognatha: Klass & Matushkina 2012: figs. 1, 2), the genital opening actually being 7th-segmental (but seemingly 8th-segmental; see Klass & Ulbricht 2009: fig. 42). This might also apply to Diplura. However, since a fundamental difference between sexes in the configuration of venter 8 appears unlikely in view of the lack of significant structural differences (Pages 1989: pp. 518, 523), the genital opening of the males should then be in the same 7th-segmental (only seemingly 8th-segmental) position.

Comparing Diplura and Insecta. According to the foregoing, when straightforwardly numbering segments in Diplura from the anterior, a position of the genital opening on venter 8 appears quite likely for both sexes, but venters 7 and 9 are alternative options. Posterior abdominal segments of Diplura can be homologised with segments of Insecta that either have the same number counting from the anterior, or the same number counting from the posterior (see section 8.2.), the latter equaling the same number plus 1 when counting from the anterior. Considering both options, abdominal venters 7–10 of insects are to be taken into account when comparing the location of genital openings between Diplura and Insecta.

Despite this confusing situation, there are two especially plausible possibilities of how positions of genital openings could compare between Insecta and Diplura: one from the insect perspective (a), and one from a (more reasonable) insect & dipluran perspective (b).

(a) Could the configuration in Diplura agree with the one present in the ground plan of Insecta? The possible range of genital opening locations in Diplura formally indeed includes a 7th-segmental (seemingly 8th-segmental) genital opening combined with a (truly) 8th-segmental spermathecal opening in the female, and a 9th-segmental genital opening in the male (for which a 10th-segmental position, however, is not suggested by any evidence). With homology assumed between segments of same number (not 'plus 1'), this would comply with insects if these had a 9th-segmental male opening (which is less likely than 10th-segmental). This pattern shared between Diplura and Insecta could be present in the ground plan of Diplura + Insecta.

The genital papilla of male diplurans (Pagés 1989: figs. 49–51) could then either be homologous with the penis of Archaeognatha and Zygentoma, if the latter is a formation of venter 9, or with medially fused gonapophyses 9. It would be tempting to interpret the short processes of the genital papilla of female Diplura (**va*** resp. **vp*** in Pagés 1989: figs. 46–48; 'papille' in Grassi 1888: figs. 50, 52) as the gonapophyses of venters 8 and 9, those of venter 9 having shifted even farther to the anterior than in Archaeognatha and thus having their bases closely associated with those of gonapophyses 8 (yet with the segmental border 8/9 traversing between them). These interpretations would also comply with the fact that venters 8 and 9 of Diplura otherwise lack coxal vesicles, as in Archaeognatha (though in contrast to Archaeognatha they also lack styli; Pagés 1989). However, the similarity with gonapophyses is very unspecific due to the poor structuring of the dipluran processes, the interpretation is in conflict with the course of the abovementioned putative antecosta 8/9 (but see in (b)), and according to Ikeda & Machida (1998: figs. 7–11) the lack of styli and vesicles on venters 8 and 9 is likely due to their lacking differentiation (while, however, their delayed differentiation, as in Fig. 22C, would be an option).

Altogether, however, this entire segmental context of hypothesis (a) appears highly unlikely in view of the inherent extreme segmental divergence between sexes. This is in stark contrast to the hardly divergent male and female morphologies of Diplura, a fact suggesting genital openings of the sexes to be isosegmental in this taxon.

(b) In Diplura the genital openings of both sexes could lie on the anterior part of venter 9 (on the forelast segment; following Snodgrass' 1936, 1957 male-based hypothesis). With dipluran-insect homology assumed between segments of same number plus 1, this would comply with a location on the anterior part of venter 10 (on the forelast segment) in insects, which is likely true for male insects. In view of the female genital opening of Diplura likely being in the same morphological position as in the male, the female genital opening could have also been placed anteriorly on venter 10 (on the forelast segment) in the stem lineage of Diplura + Insecta. It was translocated anteriorly to venter 7 in the stem lineage of Insecta; in Diplura it remained on its segment, which, however, became segment 9 by the reduction of abdominal segments by one. A plesiomorphic location of the genital opening on venter 10 in female insects is plausible considering the ontogenetic development of the female set of mesodermal ampullae (reaching segment 10; compare section 8.3.). The advantage of its translocation from venter 10 to venter 7 could have been that from there eggs could en-

ter the channel enclosed by gonapophyses / vesicles **gp8** and **gp9** (which is not possible from venter 10 because due to their anteromesal shift the **gp9** bases are medially in touch, see section 5.5.2.). Furthermore, male and female genital openings being isosegmental in Diplura and (initially) in Insecta would also comply with the situation in Protura and Collembola. As a difference, the latter taxa likely bear the genital openings on the last segment – though possibly this is the forelast segment, if their 'telson' includes another true segment (see section 8.2.).

The sole argument in conflict with this interpretation is the abovementioned putative antecosta of the segmental border 8/9, which favours an 8th-segmental location of the genital openings in Diplura. However, this is exactly the same kind of evidence as the one suggesting a 9th-segmental location and contradicting a 10th-segmental location in Insecta (putative ventral antecosta **ac10** on segmental border 9/10 in female Zygoptera; see section 8.4.(E)), while a 10th-segmental position appears more likely based on other evidence. The ventromedian part of the transverse ridge may thus be non-antecostal in both Diplura and Zygoptera. With homology assumed between segments of same number plus 1, as done in this hypothesis (b), these 'antecostae' could be isotopic in Diplura and Zygoptera. Their homology, however, is not very likely as no such ridge has been reported from Archaeognatha and Zygentoma.

In the context of hypothesis (b), a homology between the genital papilla of male Diplura (Pagés 1989: figs. 49–51) and the penis of Archaeognatha and Zygentoma (as suggested by Snodgrass 1935: p. 585) is difficult to judge and depends on hypotheses on the origin of the insect penis. Yet, as it is an option for the insect penis that it is formed by gonapophyses / vesicles 10 of otherwise leveled limbs 10 (see section 8.4.(B)), it is an option for the dipluran papilla that it is formed by gonapophyses / vesicles 9 of otherwise undifferentiated limbs 9 (Ikeda & Machida 1998: figs. 7–11) – i.e. by the gonapophyses / vesicles of the forelast segment in both cases. The same origin might then apply to the isosegmental female genital papilla of Diplura (Pagés 1989: figs. 46–48); this, however, clearly has no homologue in insects, where it has plausibly been lost when the female genital opening was translocated to the anterior. Furthermore, in female Diplura the 'vulva' would represent the original gonopore of the forelast venter (9); this is divided internally into a common oviduct and a spermatheca (see above). None of the female openings of insects (on venters 7, 8, and 9) is then present in Diplura.

Conclusions on Insecta vs. Diplura. Using Diplura as an outgroup taxon for Insecta in order to infer the primitive locations of male and female genital openings in early members of the insect stem-lineage would be of great interest, e.g., for conclusions on original functions of genitalic elements in Insecta. With the current state of knowledge, however, such comparison necessarily includes numerous ambiguities. Yet, whereas the above hypothesis (a) appears very unlikely, hypothesis (b) appears as a quite plausible working hypothesis. Progress in this issue requires sophisticated morphological and ontogenetic studies in diplurans.

8.6. Conclusion on Insecta

According to the foregoing discussions, the following scenario appears to us as the most plausible: In Protura, Collembola, and likely Diplura (the putative sister group of Insecta) the male and female genital openings are isosegmental; this is then also likely for the hexapod ground plan and for early stem-lineage Insecta. The original location of the openings in Hexapoda could have been the forelast true segment, if the segmental assignment to venters 9 in Diplura and 10 in Insecta is correct, and if the large telson of Protura and Collembola includes another true (perhaps ± reduced), 12th segment. The ventromedian area of the forelast segment including the genital opening has undergone a shift to the anterior already in the ground plan of Diplura + Insecta. In the stem lineage of Insecta (preceding the split into Archaeognatha and Dicondylia), the females abandoned the opening on venter 10 but developed two (or three) new segmental openings on abdominal venters 7 and 8 (and perhaps 9). These took over the functions of the gonopore (7; by acquiring a connection with the 7th-segmental ampullae, i.e., with the internal genitalia), a spermatheca (8), and accessory glands (9). None of these openings is present in the males, which have maintained the genital opening on the forelast venter 10; yet the 9th-segmental ectodermal accessory glands in the males of some insects could be a feature transferred from the female to the male sex (which remains to be tested). The 7th-segmental genital fold of female insects is a newly evolved structure. In view of the consistently unpaired condition of both the male and the female genital opening in Diplura, Archaeognatha, and Zygentoma, this condition is also likely for the ground plans of Diplura + Insecta and of Insecta. Processes homonomous with coxal vesicles are either absent on the posterior segments of Diplura, or those of the 9th (forelast) venter form the genital papilla in the male and perhaps also in the female. In the insect stem lineage those of the 8th and 9th venters have instead obtained the shape of long gonapophyses; those of the 10th (forelast) venter have likely come to form (part of) the phallic organs in the male (which might be homologous with the dipluran genital papilla), while in the female they have become lost. The relative timing of the evolution of the 8th- and 9th segmental gonapophyses and the translocation of the female genital opening to the anterior is unclear. This means that in the stem-lineage of Insecta the gonapophyses could have evolved in association either with a 10th-segmental or with a 7th-segmental female genital opening; they have evolved most likely in association with a 10th-segmental male genital opening. However, the segmental translocation in the female could have been plausibly correlated with the anteromesal shift of the bases of the vesicles or gonapophyses of venter 9.

This is a tentative but viable working hypothesis that needs to be tested and refined based on new morphological and ontogenetic evidence. At present there are numerous ambiguities concerning most of the included elements.