SENCKENBERG
world of biodiversity

Comparative morphology of male genital skeletomusculature in the Leptanillinae (Hymenoptera: Formicidae), with a standardized muscular terminology for the male genitalia of Hymenoptera

Zachary H. Griebenow[1,2], Adrian Richter[3,4], Thomas van de Kamp[5,6], Evan P. Economo[4], Ziv E. Lieberman[1]

1 *Department of Entomology & Nematology, University of California, Davis, CA, USA*
2 *Department of Agricultural Biology, Colorado State University, Fort Collins, CO, USA*
3 *Friedrich-Schiller-Universität Jena, Institut für Zoologie und Evolutionsforschung, Entomologie Gruppe, Jena, Germany*
4 *Biodiversity and Biocomplexity Unit, Okinawa Institute of Science and Technology Graduate University, 1919–1 Tancha, Onna-son 904–0495, Japan*
5 *Institute for Photon Science and Synchrotron Radiation (IPS), Karlsruhe Institute of Technology (KIT), Eggenstein-Leopoldshafen, Germany*
6 *Laboratory for Applications of Synchrotron Radiation (LAS), Karlsruhe Institute of Technology (KIT), Karlsruhe, Germany*

https://zoobank.org/42506B80-3683-4CF4-A3A4-FBD40F6DE277

Corresponding author: Zachary H. Griebenow (zachary.griebenow@colostate.edu)

Received 20 April 2023
Accepted 15 September 2023
Published 13 December 2023

Academic Editors Michael Schmitt, Klaus-Dieter Klass

Citation: Griebenow ZH, Richter A, van de Kamp T, Economo EP, Lieberman ZE (2023) Comparative morphology of male genital skeletomusculature in the Leptanillinae (Hymenoptera: Formicidae), with a standardized muscular terminology for the male genitalia of Hymenoptera. Arthropod Systematics & Phylogeny 81: 945–1018. https://doi.org/10.3897/asp.81.e104810

Abstract

The male genitalia of the Insecta are famed for structural and functional diversity. Variation in this anatomical region shows ample phylogenetic signal, and this variation has proven indispensable for classification across the insects at multiple taxonomic ranks. However, in the ants (Hymenoptera: Formicidae) the male genital phenotype is ancillary to the morphology of the worker caste for systematic purposes. Ants of the enigmatic subfamily Leptanillinae are an exception, as males are easier to collect than workers. Ongoing systematic revision of the Leptanillinae must therefore rely upon the male phenotype – particularly the spectacular morphological profusion of the male genitalia. To thoroughly illuminate this anatomical region and aid comparative morphological research on ant male genitalia, we present a comparative morphological study of the male genitalia in nine exemplar lineages spanning the Leptanillinae, plus three outgroups representing other major clades of the Formicidae. We use micro-computed tomography (micro-CT) to generate 3D volumetric reconstructions of male genital skeletomusculature in these specimens. Our descriptions use new muscular terminology compatible with topographic main-group systems for the rest of the pterygote soma, and applicable to all Hymenoptera. We find that male genitalia in the Leptanillinae show an overall trend towards skeletomuscular simplification, with muscular reduction in some cases being unprecedented in ants, or even hymenopterans in general. In several lineages of the Leptanillinae we describe derivations of the male genitalia that are bizarre and unparalleled among the Hymenoptera. We conclude by discussing the functional implications of the often-extreme morphologies here observed.

Keywords

Anatomy, evolutionary morphology, homology, micro-CT, pregenital abdomen, suicidal mating

1. Introduction

"… *Auteurs ne s'accordaient ni entre eux, ni avec eux-mêmes: autant de formes diverses, autant de noms différens.*" –

"… *Authors agreed neither among themselves, nor with themselves: so many varied forms, so many different names.*"

Pierre A. Latreille, in Audouin (1821: 287).

The structural diversity of the male genitalia in insects (Hexapoda: Ectognatha) is famously diverse. Snodgrass (1957: 11) referred to this diversity as being a dialectical "delight of taxonomists, [and] despair of morphologists". Empirical studies indicate that the genital variety observed in metazoans with internal fertilization, including insects, is attributable to sexual selection (Hosken and Stockley 2004). Being intimately involved in pre-zygotic reproductive isolation, this anatomical region is regarded as a rich source of discrete characters for taxon delimitation (Tuxen 1970), useful at a broad span of taxonomic ranks, and is consequently used for classification and phylogenetic inference in myriad insect taxa (Dirsh 1956; Yoshizawa and Johnson 2006; Clarke 2011; Tarasov and Solodovnikov 2011; Buenaventura and Pape 2018; Chiquetto-Machado and Cancello 2021; Girón et al. 2022). Allaying concerns that the putative rapidity of male genital evolution in insects erases phylogenetic signal in this character set, a review of morphological cladistic analyses across the Insecta by Song and Bucheli (2010) indicated that male genitalia display phylogenetic signal comparable to other anatomical regions. Even in cases where no discrete character state differences can be found, male insect genitalia are of morphometric utility as a source of continuous measurements that show negative hypoallometry (Dreyer and Shingleton 2011; Mikó et al. 2013). Male insect genitalia are therefore unavoidably "an everlasting temptation" (Aspöck 2002: 161) to entomologists interested in classifying insects.

Compared to the general utility of male genitalia in insect taxonomy, ant classification has traditionally incorporated few male genitalic characters. Systematic myrmecology has overwhelmingly focused upon the female worker caste: workers are numerically more abundant than their reproductive counterparts, and males are short-lived, with rare exceptions (Boomsma et al. 2005; Fuessl et al. 2015). Nonetheless, male ant genitalia have seen study and description for taxonomic purposes at the species level (Schmidt and Heinze 2017) and above (e.g., Yoshimura and Fisher 2011; Ward and Boudinot 2021).

In Formicidae, attention on the male genitalia has historically been nearly exclusively limited to sclerites. Prior to the 21st century, only three studies described ant genital musculature. Kempf (1956) described the skeletomusculature of *Cephalotes pusillus* (Klug, 1824) (Myrmicinae), following the homologies and terms of Snodgrass (1941). Birket-Smith (1981) described the skeletomusculature of the male abdomen, including genitalia, of the doryline ants *Eciton* and *Labidus* using an eclectic synthesis of terminology. Birket-Smith (1981) considered all insect genitalia homologous – but asserted no more specific homologies at the interordinal scale, although he did discuss homologies between Dorylinae and other Hymenoptera. Ogata (1991) described the genitalia of *Myrmica kotokui* Forel, 1911 (Myrmicinae), also using the numeral designations of Snodgrass (1941), but without any explicit homology statements. The comparative study of Boudinot (2013) was therefore instrumental in connecting male genital skeletomusculature in Formicidae with other Hymenoptera, increasing the total sampled ant taxa from four to 25, re-interpreting Birket-Smith (1981) and Ogata (1991), and providing a new level of detail, while also considering muscular function.

In some lineages, male morphology, including that of the genitalia, provides phylogenetic signal absent from the phenotype of corresponding workers (Kempf 1954; Ward and Downie 2005; Eguchi et al. 2006; Lapolla et al. 2012; Barden et al. 2017; Boudinot et al. 2021). This is the case for the Old World ant subfamily Leptanillinae Emery, with male morphology therefore being integral to leptanilline taxonomy rather than supplemental to worker morphology. Leptanilline ants are minute, with the worker caste appearing to be strictly subterranean in biology (Masuko 1990; Yamada et al. 2020; Ito et al. 2021), although colonies have been also reported from dead wood (Hsu et al. 2017) and lone workers of *Protanilla lini* Terayama, 2009 were collected in SLAM (Sea, Land and Air Malaise) traps (Griebenow 2020: 244). Male specimens are more abundant in collections than females, due to the ease with which they are collected by passive means, and a variety of species and even several genera have been described based solely upon males unassociated with workers (Brues 1925; Petersen 1968; Kugler 1986). The classification of the Leptanillinae must therefore rely upon a firm understanding of male morphology. Comprehensive description of male genitalia in the Leptanillinae is indispensable to systematic revision of the clade, with the aim of devising a classification that integrates both sexes and acknowledges evolutionary relationships.

The largely undescribed morphological derivation of male genital skeletomusculature seen within the Leptanillinae relative to the remaining Formicidae is of broader scientific interest, as is the conspicuous morphological disparity of the male phenotype in the Leptanillinae (Fig. 1), and of the genitalia in particular. This disparity has not been scrutinized, beyond the use of discrete external skeletal characters of the male leptanilline genitalia in phylogenetic inference (Griebenow 2021), but has been emphasized in the literature: Boudinot (2015: 29) noted that "some [leptanilline] males are so derived as to be difficult to intuitively ascribe to the Formicidae", with reference to the whole of leptanilline male morphology; while Bolton (1990b: 271) remarked that male genitalia in the Leptanillinae are "often bizarre", without further elaboration.

In the present study, we elucidate this "bizarre" quality by describing male genital skeletomusculature across all major subclades of the Leptanillinae for which males are known. We study male genital skeletomusculature here according to the comparative method set out by evolutionary morphology sensu Richter and Wirkner (2014). To facilitate comprehensive comparison of tiny, often rare or unique specimens, we nondestructively generate high-resolution, three-dimensional (3D) anatomical data via micro-computed tomography (micro-CT). Where necessary and feasible, we supplement these 3D reconstructions, or "virtual dissections", with 2D imaging, including photomicrography and scanning electron microscopy (SEM). Scans of 22 specimens are published for future comparative study.

We report spectacular modifications to the male genitalia in certain lineages of the Leptanillinae relative to homologous skeletomusculature observed in other Formicidae, some apparently unique not just among ants but among the Hymenoptera as a whole. We observe numerous striking autapomorphies of the posterior pregenital segments and the genital apparatus, in clades at the tribal, generic, and lower ranks. We discuss the degree of consilience of male genital morphology with the phylogeny of the Leptanillinae, as inferred by Borowiec et al. (2019)

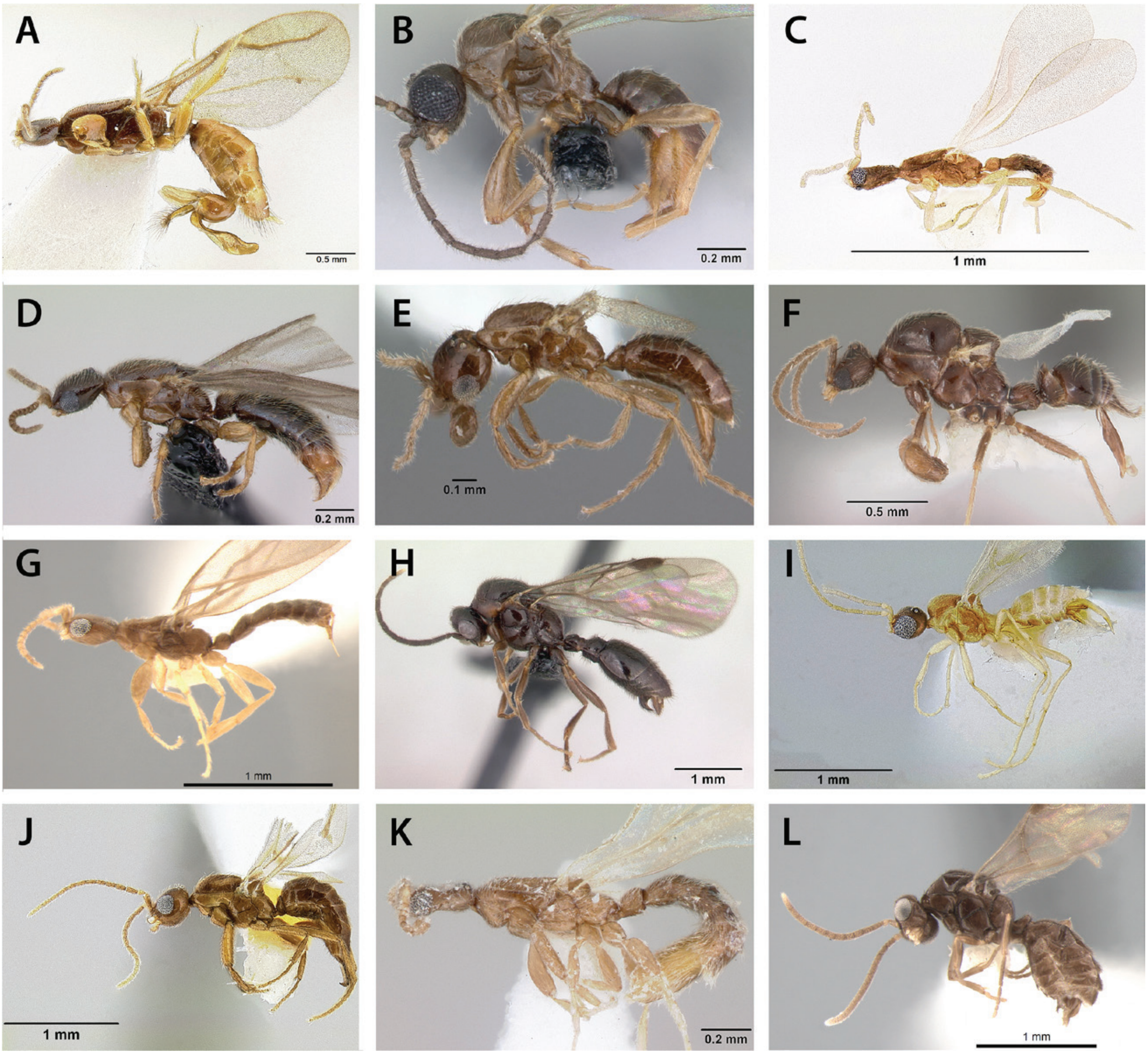

Figure 1. Variety of male habitus across the Leptanillinae, profile view; images from AntWeb.org. **A** *Leptanilla* zhg-my05 (CASENT042571; Zachary Griebenow). **B** *Yavnella* TH02 (CASENT0119531; April Nobile). **C** *Leptanilla* zhg-bt02 (CASENT0842612; Zachary Griebenow). **D** *Leptanilla* TH01 (CASENT0119792; April Nobile). **E** *Scyphodon* cf. *anomalum* (CASENT0106168; April Nobile). **F** *Leptanilla* ci01 (CASENT0102373; April Nobile). **G** *Leptanilla* zhg-mm01 (CASENT0842788; Zachary Griebenow). **H** *Protanilla* TH03 (CASENT0119791; Erin Prado). **I** *Yavnella* nr. *indica* (CASENT0106380; Zachary Griebenow). **J** *Noonilla* zhg-my06 (CASENT0106372; Zachary Griebenow). **K** *Leptanilla* indet. (CASENT0104306; April Nobile). **L** *Protanilla* zhg-my01 (CASENT0842734; Zachary Griebenow).

and Griebenow (2020, 2021), and compare with that documented in other ants, contrasting macroevolutionary tendencies across the entire genitalia and details thereof.

To connect the previous status quo for ant and Hymenopteran skeletomusculature with interordinal homology, contextualize the Leptanillinae, facilitate comparison, and link genitalic terminology to that of other anatomical regions, we provide a new muscular terminology. This system synthesizes interordinal holometabolan homologies (Boudinot 2018) and the terminology for the neopteran thorax (Friedrich and Beutel 2008) and worker ant abdomen (Lieberman et al. 2022). Finally, though our approach is motivated by phenomenology rather than mechanism (Rodrigue and Philippe 2010), we speculate on the functional and evolutionary implications of the highly derived male genital modifications here described, and summarize overall trends observed in the evolution of male genitalia in Leptanillinae, ants, and Hymenoptera.

2. Methods

2.1. Material examined

2.1.1. Institutional deposition

Specimens are deposited at the following institutions, with abbreviations following Evenhuis (2022) unless enclosed in brackets: **CAS** = California Academy of Sciences, San Francisco, USA; **CSCA** = California State Collection of Arthropods, Sacramento, USA; [**JMGDC**] = personal collection of José María Gómez-Durán; **MZLU** = Lund University, Lund, Sweden; **PMJ** = Phyletisches Museum, Friedrich-Schiller-Universität, Jena, Germany; **UCDC** = R. M. Bohart Museum of Entomology, University of California, Davis, USA; **NHMD** = Natural History Museum of Denmark, Copenhagen, Denmark.

2.1.2. Examined specimens

Collection data for all male specimens examined in this study, and the modality with which each was examined, is presented in Table S1. All image data are publicly available on Zenodo (10.5281/zenodo.7647890). All specimens are deposited as vouchers in their respective collections. Putative morphospecies are designated with numerical codes relating to their country of origin, following the generic assignments of Griebenow (2020) where relevant.

2.2. Methods

2.2.1. X-Ray microtomography

X-ray microtomography was performed using the following equipment and facilities: (1) Beamline 8.3.2 with a LuAD:CE scintillator and PCO.edge CMOS detector at the Lawrence Berkeley National Laboratory Advanced Light Source (ALS), University of California, Berkeley; (2) KIT Light Source of Karlsruhe Institute for Technology (KIT) using a 12-µm LSO:Tb scintillator and a 12-bit PCO.dimax detector. Laboratory X-ray microscopes used for this study were as follows: (1) a ZEISS Xradia 510 Versa 3D X-ray microscope, with the ZEISS Scout & Scan Control System (ZEISS, Oberkochen, Germany), at the Okinawa Institute of Science & Technology; (2) an XRadia 620 Versa at ZEISS X-ray Microscopy Inc., Dublin, CA; and (3) a Skyscan 2211 (Bruker, Belgium) at the Max Planck Institut for the Science of Human History Jena, equipped with a high resolution (4000 × 2600 pixel) X-ray sensitive CCD camera. Metadata for all scans published herein and relevant information on scan settings for all facilities are included in Table S2.

Segmentation of micro-CT data was performed manually with Dragonfly v.2021.1–2. Microtomographic sequences were imported as stacks of .tif or DICOM images, the latter reconstructed using XMReconstructor (v. 10.7.2936). If unwieldy for system RAM, scan data were cropped upon import into Dragonfly to include only structures that were relevant to the study. See Lieberman et al. (2022) for detailed explanation of manual tissue segmentation using Dragonfly. Segmentation labels were exported as image series for volume rendering using a custom code (K. Jandausch, pers. comm.). These series were cropped to the label extent, then imported to VG Studio Max 3.4.5 (Volume Graphics GmBH, Heidelberg, Germany) for volume rendering, with Phong interpolation shading. Scale for perspective renders was obtained from equivalent orthographic projections using Rendering > Parallel.

The minute size of most specimens belonging to the Leptanillinae largely prevented their suspension in fluid for imaging, therefore prohibiting iodine staining, except for *Yavnella* zhg-bt01. Therefore, leptanilline specimens were scanned dry on the end of cardstock points; if originally obtained in ethanol, these were treated with hexamethyldisilane (HMDS), preceded by two washes in absolute ethanol, to diminish distortion of muscles by desiccation. Outgroups were stained with iodine (PMJ:Hex:2205, CASENT0844684) or left unstained in conjunction with phase contrast (CASENT0842842), and scanned in ethanol.

2.2.2. Photomicrography and scanning electron microscopy

Photomicrographs were acquired as focus stacks, either (1) using a JVC KY-F75 digital camera (JVC, Yokohama, Japan), with manual z-stepping; or (2) 3.1-megapixel Leica DMC2900 camera (Leica Microsystems, Wetzlar, Germany) mounted on a Leica MZ16A stereomicroscope, with automated *z*-stepping via the Leica Application Suite software (v. 4.13.0). Image stacks were combined into full-focus montages and manually retouched using the Syncroscopy AutoMontage Program (v. 5.02.0096) (Synoptics Ltd., Cambridge, UK) or Helicon Focus (Helicon Soft. Ltd., Kharkiv, Ukraine). Additional photomicrographs were obtained from AntWeb (Version 8.68.7, California Academy of Sciences) and are attributed in figure captions. Scanning electron microscopy (SEM) was performed on uncoated specimens using a Hitachi TM4000.

2.2.3. Ancestral state reconstruction

We referred to Table S3 in illustrating tip states and reconstructing ancestral node states under maximum parsimony across the Hymenoptera included in that table. When multiple terminals belonging to the same family were included, they were either (1) collapsed into polymorphic tip states; (2) treated individually; or (3) omitted prior to parsimony analysis. The choice of collapsing, expanding, or omitting a terminal depended on whether its inclusion led to polymorphism including uncertainty or inapplicability, thereby precluding parsimony analysis; and whether a reliable internal topology was available for that family.

Topology was assembled manually in Newick format using cladograms from the literature (Wang et al. 2016, Romiguier et al. 2022, Blaimer et al. 2023). Athaliidae was treated as a family (Niu et al. 2022). When a family included only two terminals, they were left as sister taxa. We implemented parsimony analysis in Mesquite 3.81 (Maddison and Maddison 2023) using the Mesquite_Starter_E4 executable. The character matrix and topology in a combined Nexus-format file were used as input. We used Tree Block > View Trees, then Analysis:Tree > Trace All Characters > Parsimony Ancestral States.

2.3. Terminology

2.3.1. Scope

The male pregenital metasomal segments of Formicidae are abdominal segments II–VIII. The genitalia are composed by parts of abdominal segments IX–X, specifically abdominal sternite IX and its appendages and derivative structures, and the fused appendages of abdominal segment X (primary gonopods, i.e., the penis). Following prior convention, we do not consider abdominal tergites IX–XI to be part of the genital apparatus. In Formicidae, tergites X–XI cannot be clearly distinguished from one another. To describe the extreme derivations of the genitalia in certain lineages of Leptanillinae, we include the skeletomusculature of (pregenital) abdominal segment VIII if (1) the tergite and sternite are fused to one another, or (2) when musculature of segment VIII is extrinsic and connects to genital sclerites. Visceral muscles, which have at least one non-skeletal attachment, were excluded from consideration in this study.

We caution that the muscular terminology introduced here is solely applicable to the male genitalia of Hymenoptera. For comparison of male genital skeletomusculature across the Hexapoda, we suggest retaining the system of Boudinot (2018), with which our terminology is congruent. We also caution that terminological correspondence with terms used in topographic main-group terminology of female hymenopteran genitalia in the Hymenoptera is not intended to indicate homology between the sexes.

2.3.2. Genital terminology

The terminology used for sclerites of male genitalia in the Formicidae is highly variable (Table 1), recapitulating the longstanding profusion of genital terms across the Insecta as a whole (>5,400 listed by Kaestner and Wetzel 1972) and resulting in redundancy and confusion. Most publications make no theoretical justification for terminology, but may implicitly follow either the coxopodal (Michener 1944) or phallic-periphallic (Snodgrass 1935b, 1957) hypotheses of male genital evolution in the insects. Conversely, this study follows the skeletomuscular homology hypotheses of Boudinot (2018). This model is preferred to the coxopodal and phallic-periphallic models in that it homologizes male genital skeletomusculature across the entire Hexapoda with reference to the Remipedia (Pancrustacea: Allotriocarida), the sister taxon of the Hexapoda (von Reumont et al. 2012; Misof et al. 2014). By contrast, the coxopodal and phallic-periphallic hypotheses of male genital skeletomuscular homology assumed the falsified view promulgated by Snodgrass and others that the Myriapoda are sister to the Hexapoda. Terminological correspondences with selected previous descriptions of male ant genitalia are summarized in Tables 1, 2.

The genital appendages of males in the Ectognatha (Insecta s.str.) are derived from abdominal limbs, or coxopods, of abdominal segments IX–X, which constitute secondary and primary gonopods respectively; the protopods of gonopods X (i.e., gonocoxae) are medially fused to form the penis (Boudinot 2018). In the Endopterygota, the penis is developmentally integrated with gonopods IX, such that extrinsic penial musculature originates within gonocoxae IX, rather than on sternite IX. Additionally, in the endopterygote ancestor, bilateral portions of the penis split off, forming the paired "lateropenites". The Hymenoptera are further derived relative to the endopterygote groundplan by 1) the fusion of fragments of abdominal tergite IX and the (ninth) gonocoxae to form the cupula; and 2) the fusion of the lateropenite with the "parossiculus", a ventromedial fragment of the gonocoxite (gonocoxal sclerite IX), the parossiculus and lateropenite together forming a paired appendage called the "volsella".

2.3.3. General definitions

We consider homology of anatomical structures to refer to the phenomenon of morphological character states that are shared between individual organisms due to inheritance from a common ancestor. We recognize homologous structures according to the criteria presented by Remane (1952), chiefly the first three: (1) parts correspond in location relative to other parts; (2) components of given parts correspond in location relative to other compo-

Table 1. Terminological equivalencies in hymenopteran male genital sclerites across a selection of morphological studies. HAO URIs are unique reference identifiers; the associated webpage can be accessed by appending the URI to the URL https://purl.obolibrary.org.

HAO URI		HAO_0000238	HAO_0000383		HAO_0000328	HAO_0000091	HAO_0001084		HAO_0000047	HAO_0000191
			HAO_0000386	HAO_0000395			HAO_0000703	HAO_0000385		
Source	Focal Taxon									
1°	Leptanillinae	cupula	gonopodite		endophallic sclerite	penial sclerites	volsella		abdominal sternite IX	cercus
			gonocoxite	gonostylus			parossiculus	lateropenite		
Boudinot (2013)	Formicidae	cupula	basimere	telomere	—	penisvalva	cuspis	digitus	abdominal sternite IX	—
Yoshimura & Fisher (2011)	Proceratiinae	basal ring	basimere	harpago	—	aedeagus	cuspis	digitus	abdominal sternum IX	pygostyle
Hymenoptera Anatomy Ontology (Yoder et al. 2010)	Hymenoptera	cupula	gonopod		—	aedeagus	volsella		abdominal sternum IX	cercus
			gonostipes	harpe			parossiculus	digitus		
Prins (1982)	*Anoplolepis*	gonocardo/lamina annularis	gonostipes		—	penis cuspis	volsella		—	—
							digitus			
Birket-Smith (1981)	*Dorylus*	cupula	stipes	harpide	flap valve	aedeagus/thrysos	cuspis	digitus	sternum IX	pygostyle
Watkins (1976)	Dorylinae *sensu* Ashmead	—	stipites		—	sagitta	volsella		—	—
Kempf (1956)	*Paracryptocerus* (= *Cephalotes*)	basal ring	parameral plate	paramere	—	penial valve	cuspis volsellaris	digitus volsellaris	subgenital plate	—
Boulangé (1924)	Hymenoptera	sclérite accessoire	pièce principale	palette	—	valve du pénis	pièce complementaire	pièce en trébuchet	plaque sous-génitale	cerque
Michener (1944)	Insecta	gonobase	gonocoxite	gonostylus	—	penis valve	volsella		sternum IX	cercus

nents of those given parts; and (3) parts that are disparate in appearance are related by intermediate forms.

The integument is here regarded as a continuous exoskeletal surface enclosing the fluid-filled haemocoel. Features situated on the exterior of this surface are called "ectal"; those within, "mesal". For internalized sclerites which do not enclose a lumen, ectal indicates the outer surface (towards the body wall), and mesal indicates the inner surface (towards the anteroposterior axis). Along the transverse axis, features are referred to in mediolateral order.

Anatomically, sclerites are regions of the cuticle that are reinforced with exocuticle and separated by flexible conjunctivae, which consist only of endocuticle. A much more general definition is provided by the Anatomy of the Insect Skeleto-Muscular System (AISM; Girón et al. 2022), which considers a sclerite (AISM:0000003) to be a region of cuticle (AISM:0000174) that is less flexible than the neighboring, conjunctival cuticle (AISM:0000004). Because we neither examined the integument histologically or by physical manipulation, we recognize sclerites by a combination of their higher contrast and thickness in micro-CT images, as well as visually by degree of melanization and opacity, relative to adjacent membrane.

For orientation of parts within the male genitalia, we divide this region into axial and appendicular anatomical categories. These categories are informed both by genital homologies across the Hymenoptera and the phenotype of genital components in the Leptanillinae. Abdominal sternite IX and the cupula are considered axial (unpaired and derived in whole or in part from segmental sclerites); the gonopodites, volsellae and penial sclerites are considered appendicular (paired and derived in whole from appendages). Axial structures are oriented along the craniocaudal axis, even when fused completely to components of the appendicular genitalia. Appendicular structures are oriented along a proximodistal axis relative to the body, with abdominal sternite IX and cupula (when present) being the collective proximal point of reference. When skeletomuscular features could not be resolved due to limitations of the dataset, these features are referred to as "not discernible".

2.3.4. Skeletal terminology (Fig. 2)

Abdominal segments are abbreviated **A** and numbered in an anteroposterior direction using Roman numerals, with AII being the petiole, and AIII–XI comprising the gaster (in some outgroup subfamilies, AIII comprises the postpetiole and AIV–XI the gaster). Abdominal tergites and sternites are abbreviated **T** and **S**, respectively. Abdominal tergite IX may be a continuous, unpaired sclerite, as in the unmodified pregenital segments, or it may be fully divided into disjunct lateral fragments, or hemitergites. In species with undivided ATIX, the distinction between ATIX and ATX is usually unclear, due to weak sclerotization and continuity of the membranous surfaces between the tergites confusing the intersegmental boundary; Richards (1934) contended that ATIX–ATX are indistinct in all male Aculeata. However, as pointed out by Peck (1937), the insertions of the longitudinal intertergal muscles IX–X, and the extrinsic

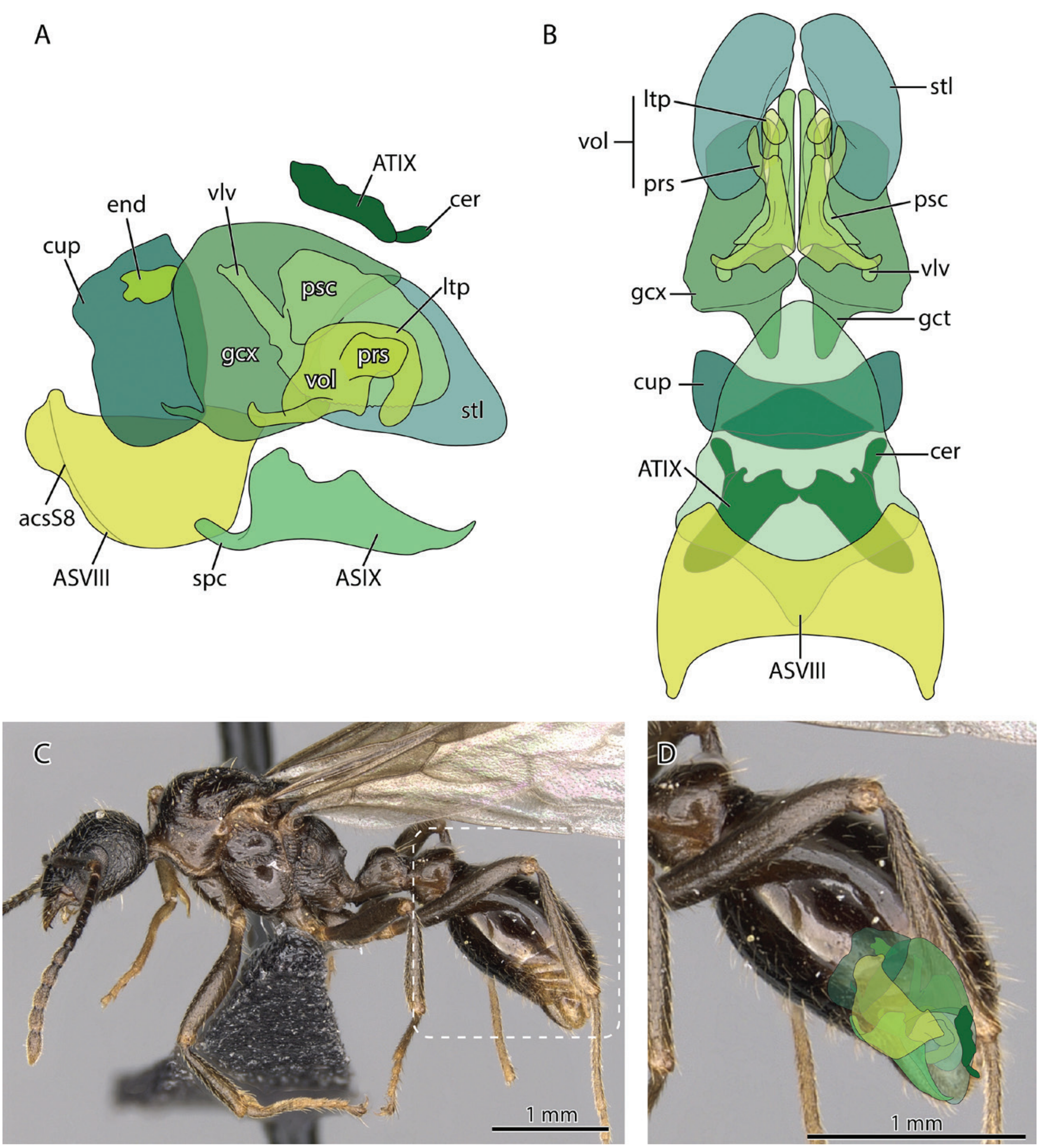

Figure 2. Diagrammatic summary of ♂ genital and pregenital sclerites in the Formicidae considered in the scope of this study, using *Myrmica ruginodis* Nylander as template. Mediolateral arrangement of overlapping sclerites in Figure 2A is not true to life, for visual clarity. **A** profile view of considered male genital and pregenital sclerites, exploded. **B** ventral view of male genital and pregenital sclerites, exploded. **C** Habitus of male *Myrmica ruginodis*, profile view (CASENT0902305; from AntWeb.org, Ziv Lieberman). **D** inset of same profile view, with included genital and pregenital sclerites diagrammed in situ. Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; ATIX = abdominal tergite IX; acsS8 = antecosta of abdominal sternite VIII; cer = cercus; cup = cupula; gct = gonocoxital arm; gcx = gonocoxite; ltp = lateropenite; prs = parossiculus; psc = penial sclerite; spc = spiculum; stl = gonostylus; vlv = valvura; vol = volsella.

proctiger muscles (cf. Lieberman et al. 2022) may serve as landmarks. Since the anatomy of ATX is beyond the scope of the present study, we did not investigate these traits in detail.

We follow the skeletal terminology of Boudinot (2018), with the following extensions. The sclerotized portion of the endophallus called the wedge sclerite (e.g., Forbes and Do-Van-Quy 1965) or sperrkeil (Clausen 1938) in the Formicidae, or endophallite more generally (Génier 2019), is here termed the endophallic sclerite (Fig. 2A, D) as in other taxa described by Boudinot (2018). The term "mulceator" is hereby coined to describe posterolateral filiform processes of the male abdominal sternite IX, a character state that is an autapomorphy of the Bornean morphospecies-group within *Leptanilla* s.l. Mulceators are observed nowhere else in the order Hymenoptera. The name derives from the Latin "mulceō", meaning "I caress".

External cuticular processes which do not enclose apparent haemocoelic lumina and are compressed enough to result in transparency to visible light are termed laminae. The gonopodites are considered "inarticulate" if there is no trace of a conjunctiva separating the gonocoxite and gonostylus, and the gonostylus is not reflexed relative to the gonocoxite, which in deceased specimens implies articulation of the gonopodite (Ward and Sumnicht 2012). In any instance in which conjunctiva is present along only part of the gonopodite, the articles of the gonopodite are segmented separately, with parts of their boundary being approximate. When the gonopodite is inarticulate but with an internal transverse ridge, or shows some distal differentiation suggestive of a gonostylus, the gonostylus was assumed to be present but was not distinguished from the gonocoxite during segmentation.

Table 1 provides an abbreviated list of synonyms in skeletal terminology from a selection of the literature on male genitalia in the Formicidae, along with respective Uniform Resource Identifiers (URIs) from the Hymenoptera Anatomy Ontology (HAO; Yoder et al. 2010, Seltmann et al. 2012) when available. For more extensive comparisons of genital terms across Hymenoptera, see Boulangé (1924, table 1 and chapter 3) and especially Schulmeister (2001, fig. 3).

2.3.5. Muscular terminology

An abdominal muscle is extrinsic if it attaches two different body segments, two true segments of an appendage, or connects an appendage to the body; it is intrinsic if both attachments are within the same body segment or segment of an appendage. The origin (**O**) of an extrinsic muscle is the attachment on the cephalad segment of the body, the proximad segment of an appendage, or the body segment if it attaches an appendage to the body; its insertion (**I**) is the attachment on the caudad body segment, distad appendage segment, or the appendage if the muscle attaches an appendage to the body. For intrinsic muscles, the origin is point of putatively fixed attachment, while the insertion is the point of mobile attachment (von Kéler 1955). Certain muscles that attach to two putatively mobile elements, present in outgroups to the Leptanillinae, are assigned origin and insertion based on their form and most likely function. We also designate muscles originating and inserting within the volsella as intrinsic, indicated in the Latin name by the descriptor interior, while those that originate on the gonopod and insert in the volsella are considered extrinsic (exterior). We choose not to use the term tendon in reference to insertions, as we did not examine myotendinous junctions histologically (Chapman et al. 2013).

In our extension of Boudinot (2018) to include all known male Hymenopteran genital muscles (see following section), we in part apply the topographic main-group approach of Friedrich and Beutel (2008) for the thorax in the Neoptera and Lieberman et al. (2022) for the worker ant abdomen. Topographic main groups refer to the general spatial position and orientation of muscle origins and insertions, providing a framework for recognizing subdivisions. Where possible, we align our main groups with interordinal homologies and use topography to distinguish within such homology classes. A "homology class" in this context is a set of structures which can be reasonably inferred to derive from the same ancestral structure, and are variably expressed among the considered exemplars.

Terminology and enumeration for pregenital musculature follows Lieberman et al. (2022). Although these authors described a worker ant (Amblyoponinae: *Amblyopone australis* Erichson, 1842), in which the genital segments are AVIII and AIX and lack sternites, homonymy is clear between the muscles of the male eighth segment and the serial homologues in the female pregenital abdomen, as additionally supported by descriptions of the posterior pregenital musculature by Boulangé (1924), Peck (1937), Snodgrass (1942), and Youssef (1969).

Genital musculature and context of other systems

We introduce an expansion of the homology inferences of Boudinot (2018), providing designations both for subdivisions of the neopteran groundplan muscles occurring in male Hymenoptera, and for main groups which cannot be decisively homologized with those of outgroup neopterans. We note that the recognition of subdivisions as separate muscles is somewhat subjective; see Sections 4.3.2.–3. for discussion of our approach to identifying homologies and recognizing subdivisions.

While the system applied here generally refers to muscle groups plesiomorphic for the Hexapoda, the numeration and descriptors of muscles apply strictly to male Hymenoptera. That is, the system used here is not intended to apply across insect orders and does not inherently imply intersexual homology with female Hymenoptera. We are aware of potential drawbacks in introducing new terminology, especially of limited scope and in systems rife with historical synonymy and terminological homonymy. Nevertheless, we consider the application of the system justifiable. We submit that considering interordinal homologies in terminology (see Section 2.3.2., and below), and constructing that terminology congruently with terms used for extralimital anatomical systems and clades, is valuable in moving towards a unified and comprehensive schema with the broadest possible taxonomic applicability. To the latter end, we explicitly orient term construction to congruent systems for the hymenopteran head (Beutel and Vilhelmsen 2007; Richter et al. 2019, 2020, 2021, 2023; Boudinot et al. 2021), the Neopteran thorax (Friedrich and Beutel 2008; cf. Polilov 2016; Liu et al. 2019; Peeters et al. 2020; Aibekova et al. 2022; Khalife et al. 2022), and the pregenital ant abdomen (Lieberman et al. 2022). Achieving a unified, global system of terms for hymenopteran and hexapod anatomy is necessarily iterative, but the above studies are a promising foundation for such a system, in both morphological and orthographic senses.

The commonly used existing schema for male genital terminology in Hymenoptera is the homology-neutral alphabetic system of Boulangé (1924) with occasional modification (e.g., Schulmeister 2001, 2003). We avoid this system for practical and epistemological reasons. Operationally, the Boulangé names only provide very coarse and approximate spatial information (with lettering broadly proceeding cephalad to caudad) and are inconsistently constructed. For instance, the compound name qr implies the close association of subgroups q and r, while si refers to an intermediate position between s and i on the transverse axis (Boulangé 1924). Our epistemology holds that homology-oriented terms are preferable to purely anatomical (descriptive) terms, when the homology adduced is robust and consistent across the focal taxa, although we do appreciate the value of neutral morpheme-based terminology in some systems (Richter and Wirkner 2014). As explained in Section 2.3.2. (and see below) our preferred framework is that of Boudinot (2018). For these reasons, we also elect not to use HAO terms (Yoder et al. 2010), which combine the phallic-periphallic hypothesis and homology-neutral descriptions. HAO muscle terms are therefore based on sclerite terms that may cause confusion when incorporated into our understanding of interordinal skeletal homology (Section 2.3.2.). For example, the "gonostyle" (HAO0000389) is not equivalent to the gonostylus as used here, for which the HAO preferred term is "harpe" (HAO0000395), although the harpe is homologous with the gonostylus of other hexapods. Our system and the HAO approximate two different but complementary approaches to comparative morphology (homology-explicit and homology-neutral), each providing value to the other in the progression and refinement of insect morphology.

Because most muscles of the male genitalia can be confidently identified as subsets of these homology classes, we adopt these groups where applicable. However, we make certain modifications to both convey evolutionary-anatomical information and provide an intuitive and usable shorthand for communicating spatial information. To these ends, we combine the homologies of Boudinot (2018) with the topographical main-group approach. Where relevant, we prioritize the homological class of muscles with plastic or secondarily modified topography with respect to origin or insertion. In general, attachments tend to be plastic with respect to fused or closely associated sclerites, especially those that derive from the same ancestral structure. Specifically, origins may drift to a limited degree between the gonocoxites and gonostyli, and insertions between the parossiculus and lateropenite. For clarity, we list here the cases where observed topography may be apparently incongruent with the homological class designation. (1) The anterior coxo-stylar muscle (9csm1) is secondarily intrinsic to the gonocoxite, and the intrinsic coxo-stylar muscle (9csm4, v) in outgroups is secondarily intrinsic to the gonostylus; (2) the coxo-lateropenital muscles are frequently labile in insertion, and in ants generally insert on the parossiculus, or at the proximal junction of parossiculus and lateropenite; and (3) the dorsal coxo-penial muscles may originate at or distad the coxo-stylar articulation.

We enact the following additions or modifications to Boudinot (2018): (1) we designate the remotors and promotors of the penial sclerites as "coxo-penial" to explicitly reference the origin; (2) we recognize subsets of the coxo-penial muscles (9cppv1–2) and the coxo-lateropenital muscles (9clm1, –4, s, o) not addressed in Boudinot (2018); (3) we interpret the muscle si to be derived from the ventral coxo-penial remotors, rather than promotors (9cprv1); (4) we recognize the pene-lateropenital muscles (10plm1–2, m, n); (5) we designate the muscles attaching the gonocoxite to the gonostylus as coxo-stylar muscles (9csm1–3, t, w, u, v) rather than adductors and abductors of the exopod; and (6) we recognize the intrinsic penial and coxal muscles (10ppm1–2, 9ccim; x, z, y), and the ninth intrinsic sterno-sternal muscle (9vvim), which are autapomorphies of particular families or genera (Schulmeister 2001, 2003). We also provide new abbreviations and modified Latinized names for readability and congruence with analogous systems.

Relative transverse position is stabler at deeper nodes than anteroposterior or dorsoventral position, as in the worker abdomen (Lieberman et al. 2022). Therefore, for sequential numbering of muscles in the same group, we order origins from medial to lateral, anterior to posterior (proximal to distal), and dorsal to ventral, in that sequence.

We recognize thirteen homological-topographic groups in male Hymenoptera, of which eight are known in ants. Table 2 lists the full complement of muscles with terminological equivalencies; for ease of comparison, the Boulangé (1924) labels are provided throughout and HAO preferred terms below. Not all groups designated here have equivalent alphabetic labels. Groups known in ants and outgroups are: (1) **sterno-coxal muscles** (**9vcm1–3**; a, b, c; medial S9-cupulal, mediolateral 9th sterno-cupular, lateral S9-cupulal muscles) which originate on ASIX and insert on the cupula; (2) **tergo-coxal muscles** (**9dcm1–4**; g, f, e, d; dorsomedial, dorsolateral, ventrolateral, ventromedial cupulo-gonostyle/volsella complex muscles), which originate on the cupula and insert on the gonocoxite; (3) **dorsal coxo-penial promotors** (**9cppd**; j; distodorsal gonostyle/volsella complex-penisvalval muscle) which originate dorsally on the gonocoxite and insert api-

Table 2. Muscular terminology used in this study and equivalencies with selected systems. The Boulangé (1924) names are supplemented by the additions of Schulmeister (2001; 2003) and Boudinot (2013). HAO URIs are unique reference identifiers; the associated webpage can be accessed by appending the URI to the URL https://purl.obolibrary.org.

Boulangé 1924	**Snodgrass 1941**	**Boudinot 2018**	**HAO**	**HAO URI**	**Abbreviation**	**Homological/topographic main group**	**Descriptors**
a	1	IXAscm*	medial S9-cupular muscle	HAO_0000516	**9vcm1**	sterno-coxalis	anteromedialis
b	2	IXAscm	mediolateral 9th sterno-cupular muscle	HAO_0000533	**9vcm2**	sterno-coxalis	posteromedialis
c	3	IXAscl	lateral S9-cupular muscle	HAO_0000464	**9vcm3**	sterno-coxalis	lateralis
g	6	IXAtc	dorsomedial cupulo-gonostyle/volsella complex muscle	HAO_0000279	**9dcm1**	tergo-coxalis	dorsalis
f	7	IXAtc	dorsolateral cupulo-gonostyle/volsella complex muscle	HAO_0000278	**9dcm2**	tergo-coxalis	dorsolateralis
e	5	IXAtc	ventrolateral cupulo-gonostyle/volsella complex muscle	HAO_0001074	**9dcm3**	tergo-coxalis	ventrolateralis
d	4	IXAtc	ventromedial cupulo-gonostyle/volsella complex muscle	HAO_0001075	**9dcm4**	tergo-coxalis	ventralis
j	10	IXAppd	distodorsal gonostyle/volsella complex-penisvalval muscle	HAO_0000250	**9cppd**	coxo-penialis promotor dorsalis	—
h	8	IXAppv	proximoventral gonostyle/volsella complex-penisvalval muscle	HAO_0000879	**9cppv1**	coxo-penialis promotor ventralis	anterior
h’	—	—	—	—	**9cppv2**	coxo-penialis promotor ventralis	posterior
k	11	IXAprd	proximodorsal gonostyle/volsella complex-penisvalval muscle	HAO_0000877	**9cprd1**	coxo-penialis remotor dorsalis	medialis
l	12	—	lateral gonostyle/volsella complex-penisvalval muscle	HAO_0000472	**9cprd2**	coxo-penialis remotor dorsalis	lateralis
si	—	IXAppv†	parossiculo-penisvalval muscle	HAO_0000701	**9cprv1**	coxo-penialis remotor ventralis	medialis
i	9	IXAprv	distoventral gonostyle/volsella complex-penisvalval muscle	HAO_0000251	**9cprv2**	coxo-penialis remotor ventralis	lateralis
m	22	—	lateral penisvalvo-gonossicular muscle	HAO_0002579	**10plm1**	pene-lateropenitalis	medialis
n	24	—	penisvalvo-phallotremal muscle	HAO_0000710	**10plm2**	pene-lateropenitalis	lateralis
s	23	—	gonostyle/volsella complex-gonossiculus muscle	HAO_0000517	**9clm1**	coxo-lateropenitalis	interior medialis
qr	21	IXAlp	median gonostyle/volsella complex-volsella muscle	HAO_0000473	**9clm2**	coxo-lateropenitalis	interior lateralis
p	19	IXAlm	lateral gonostyle/volsella complex-volsella muscle	HAO_0002580	**9clm3**	coxo-lateropenitalis	exterior medialis
o	18	—	gonostyle/volsella complex-parossicular muscle	HAO_0002041	**9clm4**	coxo-lateropenitalis	exterior lateralis
—	—	—	—	—	**9csm1**	coxo-stylalis	anterior
w, *t*	16, 15	IXAxad	intrinsic muscle of the gonostipes; gonostyle/volsella complex-harpal muscle	HAO_0000443; HAO_0002043	**9csm2**	coxo-stylalis	intermedius
u	—	IXAxab	apical gonostyle/volsella complex-harpal muscle	HAO_0000246	**9csm3**	coxo-stylalis	posterior
v	17	—	harpo-gonomacular muscle	HAO_0000396	**9csm4**	coxo-stylalis	interior
x	13	—	interpenisvalval muscle	HAO_0000433	**10ppm1**	pene-penialis	traversus
z	14	—	penisvalvo-median sclerotized style muscle	HAO_0002582	**10ppm2**	pene-penialis	medialis
y	—	—	intervolsellal muscle	HAO_0000441	**9ccm**	coxo-coxalis	interior
—	—	—	—	—	**9vvim**	sterno-sternalis	interior

*Erroneously omitted from Boudinot 2018.

†Interpreted as a penial promotor by Boudinot 2018; here considered a penial remotor; see Sections 2.3.5.2 and 4.5.2.

cally on the valvura; (4) **dorsal coxo-penial remotors (9cprd1–2**; k, l; proximodorsal, lateral gonostyle/volsella complex-penisvalval muscles) which originate dorsally on the gonocoxite and insert basally on the penial sclerite; (5) **ventral coxo-penial promotors** (**9cppv1–2**; h, h'; proximoventral gonostyle/volsella-complex-penisvalval muscle) which originate ventrally on the gonocoxite and insert apically on the valvura; (6) **ventral coxo-penial remotors (9cprv1–2**; si, I; parossiculo-penisvalval muscle, distoventral gonostyle/volsella complex-penisvalval muscle) which originate ventrally on the gonocoxite and insert basally on the penial sclerite, usually on a lateral apodeme; (7) **coxo-stylar muscles (9csm1–4**; t, u, v; intrinsic muscle of the gonostipes and gonostyle/volsella complex harpal muscle, apical gonostyle/volsella complex-harpal muscle, harpo-gonomacular muscle), which originate on the gonocoxite and insert on the gonostylus (or are secondarily intrinsic to the gonocoxite in 9csm1, or the stylus in 9csm4, v); and **(8) coxo-lateropenital muscles** (**9clm1–4**; s, qr, p, o; gonostyle/volsella complex-penisvalval, median gonostyle/volsella complex-volsella, lateral gonostyle/volsella complex-volsella, gonostyle/volsella complex-parossiculal muscles), which originate on the gonocoxite or parossiculus (both of which are gonocoxal fragments; Boudinot 2018) and insert on the lateropenite or secondarily on the parossiculus. Groups present in outgroup Hymenoptera are: **(9) pene-lateropenital muscles (10plm1–2**; m, n; lateral penisvalva-gonossiculal, penisvalva-phallotremal muscles) which originate on the valvura and insert on the lateropenite, sometimes associated with the membranes of the endophallus; (10**) pene-penial muscles (10ppm1–2**; x, z; interpenisvalval, penisvalva-median sclerotized style muscles) which are intrinsic to the penial sclerites; (11) **coxo-coxal muscles (9ccim**; y; intervolsellal muscle) which connect the left and right parossiculi; and finally (12) **sterno-sternal intrinsic muscles** (**9vvim**) which are intrinsic to ASIX.

For the coxo-penial muscles, the names "promotor" and "remotor" are used to indicate homology with other Neoptera, although in the Hymenoptera these muscles may not protrude or retract the genitalia. The heuristic definition of these terms is that promotors insert apically on the valvurae while remotors insert at the base of the valvurae on the mesal surface or a lateral apodeme on the ectal surface. In some cases, the insertions are secondarily expanded, as in 9cprd1 (k) which may insert broadly on the mesal surfaces of the penial sclerites, both distally, and on parts of the valvurae. Functionally, the dorsal and ventral promotors are usually antagonists of one another.

We use Latinized names to take advantage of differences in grammatical word order between Latin and English, allowing the presentation of information hierarchically while also providing cogent English names. Latin names give homological, spatial, and orientational information in order from general to specific (origin-insertion, main descriptor, detailed descriptors) and parallel the construction of abbreviations (segment of origin, origin-insertion, numeration of subsets). An English term can be derived by reading the Latin name in reverse. For example, 9clm2, Musculus coxo-lateropenitalis interior lateralis is the "lateral intrinsic coxo-lateropenital muscle [of AIX]", while 9cprd1, M. coxo-penialis remotor dorsalis medialis is the medial dorsal coxo-penial remotor [of AIX]".

2.4. Taxonomy and phylogeny

2.4.1. Taxonomy

The tribal, generic, and species-group phylogeny of the exemplars used here is provided in Fig. 3. This paper follows the treatment of leptanilline taxonomy in Boudinot et al. (2022), which erected the monobasic tribe Opamyrmini and synonymized the Anomalomyrmini under Leptanillini. Thus, Leptanillini = Anomalomyrmini + Leptanillini s.str. The generic limits of *Leptanilla* follow Griebenow (2021), with Leptanilla s.l. encompassing both *Scyphodon* Brues and *Noonilla* Petersen. The phylogenetic position of the monotypic *Scyphodon* relative to the multiple sequenced exemplars of *Noonilla* remains unclear, but *Scyphodon* + *Noonilla* exhibit many synapomorphies; therefore, this clade is here conservatively referred to as *Scyphodon* s.l. according to the principle of priority. A depauperate clade that we here term the Indochinese morphospecies-group is sister to *Scyphodon* s.l. + the Bornean morphospecies-group (Griebenow 2021); these three groups comprise the "Indomalayan clade". Males of *Anomalomyrma* remain unknown, and so the taxonomic problem presented by the paraphyly of *Protanilla* with respect to *Anomalomyrma* (Borowiec et al. 2019; Griebenow 2020; Griebenow et al. 2022) is moot for the purposes of this study.

2.4.2. Taxon sampling

Except for *Noonilla* zhg-my03, *Leptanilla* zhg-my06, and *Leptanilla* zhg-id04, all leptanilline morphospecies for which micro-CT data were obtained in this study have been sequenced using ultraconserved elements (UCEs; Griebenow 2020, Griebenow et al. 2022). Morphospecies for which UCEs are not yet available can be confidently situated in one of the major leptanilline subclades based upon morphology alone, since this morphology is contextualized by robust molecular or total-evidence phylogenies (Griebenow 2020, 2021; Griebenow et al. 2022).

Scans are hereby published for all major subclades of the Leptanillini, with at least two morphospecies being scanned per subclade. Males of three outgroups to the Leptanillinae were scanned and described in full (Sections 3.1.2., 3.2.2.), representing both major ant clades: the "poneroids" (Ponerinae: Ponerini: *Odontomachus* indet.) and the "core formicoids" (Myrmicinae: Myrmicini: *Myrmica ruginodis* Nylander, 1846), and the latter's comparatively minor sister lineage, the Dorylinae (*Lioponera* indet.; Branstetter et al. 2017).

Descriptive sampling within the Leptanillinae in this study focuses largely on the tribe Leptanillini s.str., with a single exemplar (*Protanilla* zhg-vn01) of their sister clade, the former Anomalomyrmini. The only conspicuous lacuna in the phylogenetic distribution of our volumetric reconstructions of male genital skeletomusculature in the Leptanillini s.str. is the Indochinese morphospecies-group, known only from undescribed male morphospecies and was represented in previous studies by *Leptanilla* TH01, –7, and *Leptanilla* zhg-th01 (Borowiec et al. 2019; Griebenow 2020, 2021; Griebenow et al. 2022). *Leptanilla* zhg-mm03 is the only representative of the Indochinese morphospecies-group for which micro-CT scans are published here. Preliminary observations of this morphospecies are referred to when necessary, but it is not included in ancestral-state reconstructions.

The former Anomalomyrmini are less speciose than the Leptanillini s.str., and variation in the external morphology of all available male specimens is so limited as to obviate any apparent need for description of multiple morphospecies, with the following exceptions. *Protanilla* TH03 (CASENT0119791) differs from all other known males of the former Anomalomyrmini in several conspicuous morphological characters (Griebenow 2020: 240), as does *Protanilla* zhg-th02 (CASENT0842645), but neither of these morphospecies nor any related ones were available for micro-CT scanning or dissection. Phylogenetic inference confidently recovers both these morphospecies distantly from one another and outside the subclade of the former Anomalomyrmini which contains both *Protanilla* sampled in this study (Griebenow, in prep.).

Males of the monotypic genus *Opamyrma*, which is sister to the remaining Leptanillinae (Ward and Fisher 2016), were unavailable for micro-CT scanning; however, the skeletal morphology of the male genitalia in *Opamyrma* was thoroughly described by Yamada et al. (2020) using manual dissection. The male genital musculature of this lineage remains unknown and will require the collection of fresh specimens. Likewise, description of the male genital musculature of *Martialis heureka* Rabeling and Verhaagh (Martialinae), the sister taxon of the Leptanillinae, will require collection of fresh material. The genital skeleton of the putative male of *M. heureka* was described by Boudinot (2015).

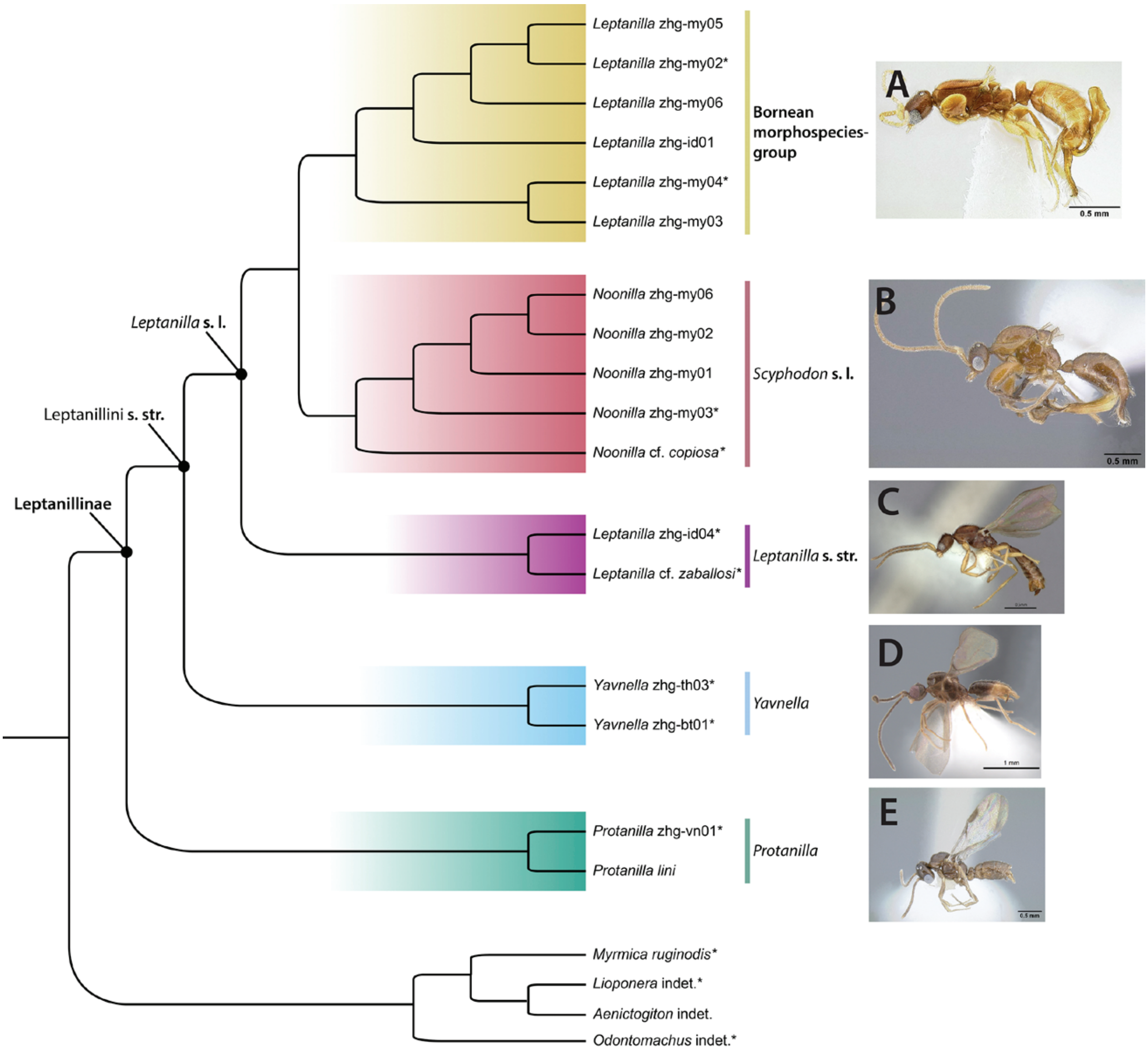

Figure 3. Cladogram of exemplars for which scan data are published in this study. Terminals with full genital skeletomuscular descriptions here are marked with an asterisk. Leptanillini s.str. = Leptanillini sensu Bolton (1990b).

3. Results

3.1. Integument

3.1.1. Summary

The following is a coarse summary of the totality of variation observed in the male genital sclerites of the Formicidae, supplementing findings described in the present paper with previous literature as necessary (cited throughout Section 3.1.1.). This summary cannot be construed as representative of the ancestral condition of the male genital sclerites for the Formicidae.

The terminal pregenital segment is abdominal segment VIII (**AVIII**), which comprises the dorsal tergite VIII (**ATVIII**), and ventral sternite VIII (**ASVIII**), which lacks limbs. Both these sclerites bear an anterior marginal invaginated ridge, the antecosta (**acs**) which represents the apparent segmental boundary (i.e., secondary segmentation; Snodgrass 1935a) and serves as a point for muscle attachment. The anterior margin of abdominal sternite VIII is entire but may be produced into diverging anterolateral apodemes homologous with those in the female metasoma (Lieberman et al. 2022). The remnant of abdominal tergite IX (**ATIX**) is situated dorsal to the genitalia and is fused to the fused remnants of abdominal tergites X and XI, which bear the median proctiger, here defined as the area of cuticle surrounding the anus, and lateral cerci (also known as pygostyles; Table 1) (**cer**); abdominal tergite IX may be divided into hemitergites, i.e., incontiguous lateral sclerites.

The genital skeleton comprises abdominal sternite IX (**ASIX**, Fig. 2A, B) and its appendages, and the fused remnants of the appendages of abdominal sternite X. ASIX is variably integrated with the copulatory appendages; its main body variably bears an antecosta (**acsS9**) and diverging anterolateral processes (**atpS9**) which may be serially homologous to the anterolateral apodemes of the pregenital segments. ASIX is often produced anteriorly into a median spiculum (**spc**, Fig. 2A, B), a “spiniform apodeme” (MacGown et al. 2014); rarely, two to three spicula are present, or the spiculum is absent (Barden et al. 2017). The cupula (**cup**, Fig. 2A, B) is usually annular in shape, forming a complete ring that outlines the foramen genitale (**fog**; Fig. 4A–E), through which the paired ducti ejaculatorii or unpaired endophallus run; or the cupula is reduced to a slat ventrad the gonopodites (Boudinot et al. 2022). The anteroventral margin of the cupula may be produced into a median process called the gonocondyle (**gcy**, Fig. 4C). The paired gonopodites (**gpd**) are distal to the cupula and each comprise a proximal gonocoxite (**gcx**, Fig. 2A, B) (equivalent to the gonocoxa of Griebenow [2021]) and distal gonostylus (**stl**, Fig. 2A, B), with the gonostylus being sometimes articulated with a mesal condyle, or rarely absent; the ventromedial margin of the gonocoxite may be extended into a gonocoxital arm (**gct**, Figs 2B, 7D) (equivalent to the “gonostipital arm” of Boudinot [2013]). The paired volsellae (**vol**, Fig. 2A, B) originate medially on the gonocoxites, and each consist of a lateral parossiculus (**prs**, Fig. 2A, B) and distomedial lateropenite (**ltp**, Fig. 2A, B). The proximoventral surface of the volsella may bear a basivolsellar process (Boudinot, 2015; Barden et al., 2017). The parossiculus may bear recurved medial processes (**prp**). Medial to the volsellae are the paired penial sclerites (**psc**, Fig. 2A, B), which are proximally produced into paired apodemes called valvurae (**vlv**, Fig. 2A, B), serving as the origin or insertion of much of the penial musculature; in some cases, the penial sclerites bear proximal apodemes that are not homologous with valvurae, and so these are here agnostically designated as posterior penial processes (**ppp**; Figs 15D, 16D, 21D). Posterior penial processes are not to be confused with the “penisvalva lateral apodeme[s]” (Boudinot 2013: 39) or lower oblique carinae (Ward 2001), both of which are variably present on the proximolateral surfaces of the penial sclerites in the Formicidae. The portion of the penial sclerites distal to the penial sclerite base may be produced into lateral penial condyles. The penial sclerites are medially separated by dorsal thickened conjunctiva, or medially conjoined by a proximodorsal “sclerotic bridge” of cuticle (Boudinot et al. 2016) or are medially fused along the entire length of the penial sclerites. If medially fused, the penial sclerites may be perforated proximally by a proximomedian foramen, which admits the endophallus to the penial sclerites. A small, unpaired endophallic sclerite (**end**, Fig. 2A, B**)** may be situated at the proximal end of the endophallus. The distal opening of the endophallus is the phallotreme (**pht**; Figs 17B, 18A, 19A), which is surrounded by the penial sclerites when the latter are medially fused.

3.1.2. Outgroup taxa (Figs 5–11)

The following summarizes the scleritic condition across all three outgroup exemplars for which we undertook volumetric reconstruction of male genital skeletomusculature.

Abdominal sternite VIII (**ASVIII**) shallowly convex, not recurved dorsally, anteroposteriorly prolonged; posteriorly separate from abdominal sternite IX; without lateral fusion to abdominal tergite VIII. Abdominal sternite IX (**ASIX**) present, shallowly convex, anteroposterior length greater than that of abdominal sternite VIII; spiculum (**spc**) present; mulceators absent; antecosta present. Abdominal tergite IX (**ATIX**) present, either medially divided into hemitergites (*Lioponera* indet.) or not; cerci present or not (*Lioponera* indet.). Cupula (**cup**) present, annular. Gonopodites (**gpd**) articulated, or not (*Lioponera* indet.); if articulated, then so by ventral conjunctiva. Gonocoxites (**gcx**) medially articulated, sometimes (*Myrmica ruginodis*) with anteromedial gonocoxital arm (**gct**) extending from margin. Gonostyli (**stl**) present, apices entire, medially separated. Volsellae (**vol**) present, fully articulated with gonocoxites; medially separated; parossiculus (**prs**) and lateropenite (**ltp**) distinct, or indistinguishably fused (*Lioponera* indet.). Penial sclerites (**psc**) medially joined by dorsal conjunctiva along some to most proximodistal length, ventro-apical margins serrated or hooked; ventromesal septa (**mes**) present (*M. ruginodis*), arising by conjunctival connection with the ventral penial margins and sclerotic connection by a distal bridge; valvurae (**vlv**) present, anterior apices curving dorsally; endophallic sclerite (**end**) present or absent (*Odontomachus* sp.), dorsal outline divaricate, dorsum concave.

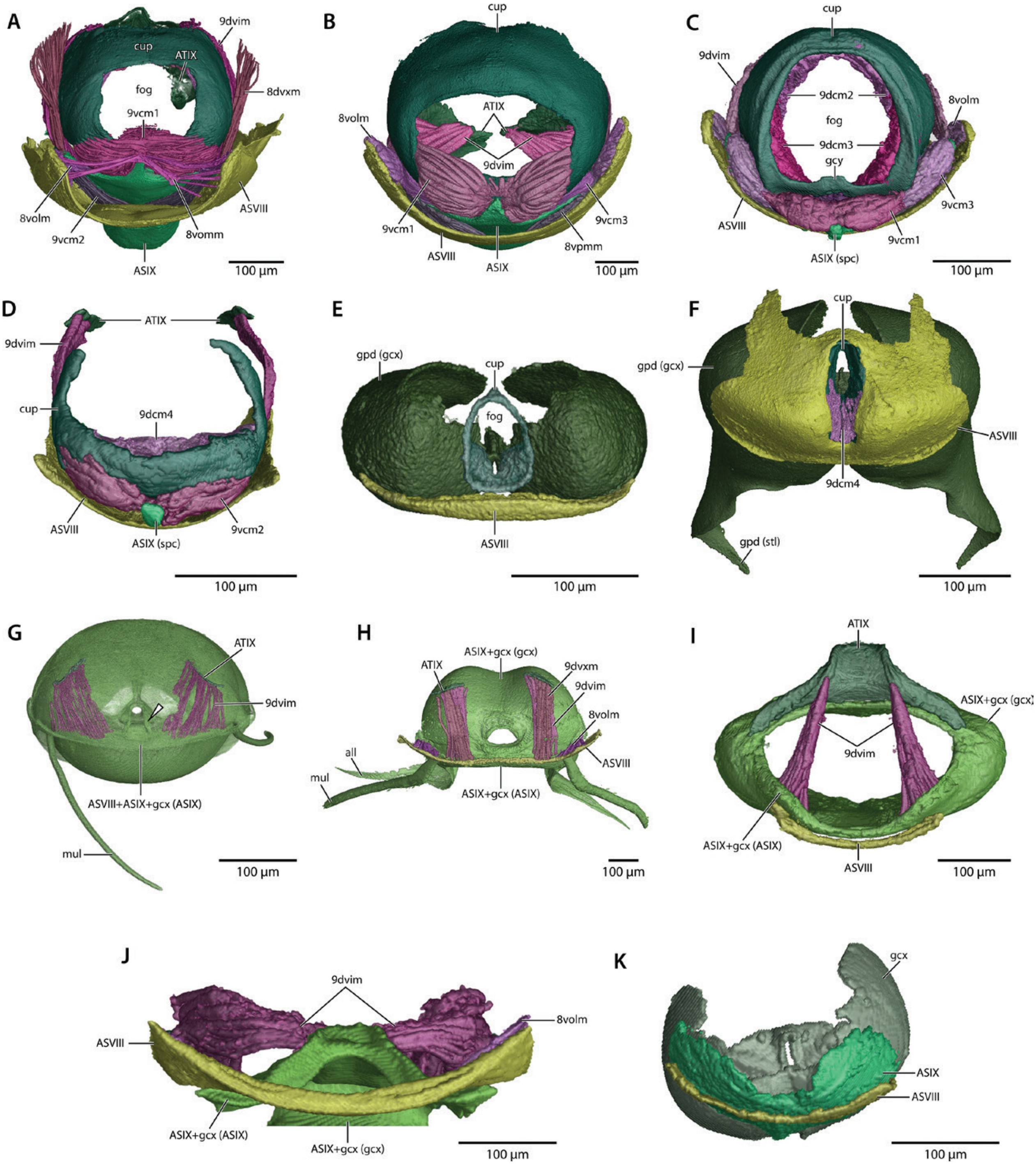

Figure 4. Axial sclerites and gonocoxites, 3D reconstructions in anterior view. **A** *Odontomachus* indet. **B** *Myrmica ruginodis*. **C** *Lioponera* indet. **D** *Protanilla* zhg-vn01. **E** *Yavnella* zhg-bt0.1 **F** *Yavnella* zhg-th03. **G** *Leptanilla* zhg-my04. **H** *Leptanilla* zhg-my02. **I** *Noonilla* zhg-my03. **J** *Noonilla* cf. *copiosa*. **K** *Leptanilla* zhg-id04. White arrowhead in G indicates possible cupular remnant. Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; ATIX = abdominal tergite IX; cup = cupula; fog = foramen genitale; gcx = gonocoxite; gcy = gonocondyle; spc = spiculum; stl = gonostylus; 8volm = ventral ortholateral muscles VIII-IX; 8vpmm = ventral paramedial muscles VIII-IX; 9dvim = dorsoventral intrinsic muscles IX; 9vcm1 = anteromedial sterno-coxal muscles; 9vcm2 = posteromedial sterno-coxal muscles; 9vcm3 = lateral sterno-coxal muscles; 9dcm2 = dorsolateral tergo-coxal muscles; 9dcm3 = ventrolateral tergo-coxal muscles; 9dcm4 = ventral tergo-coxal muscles.

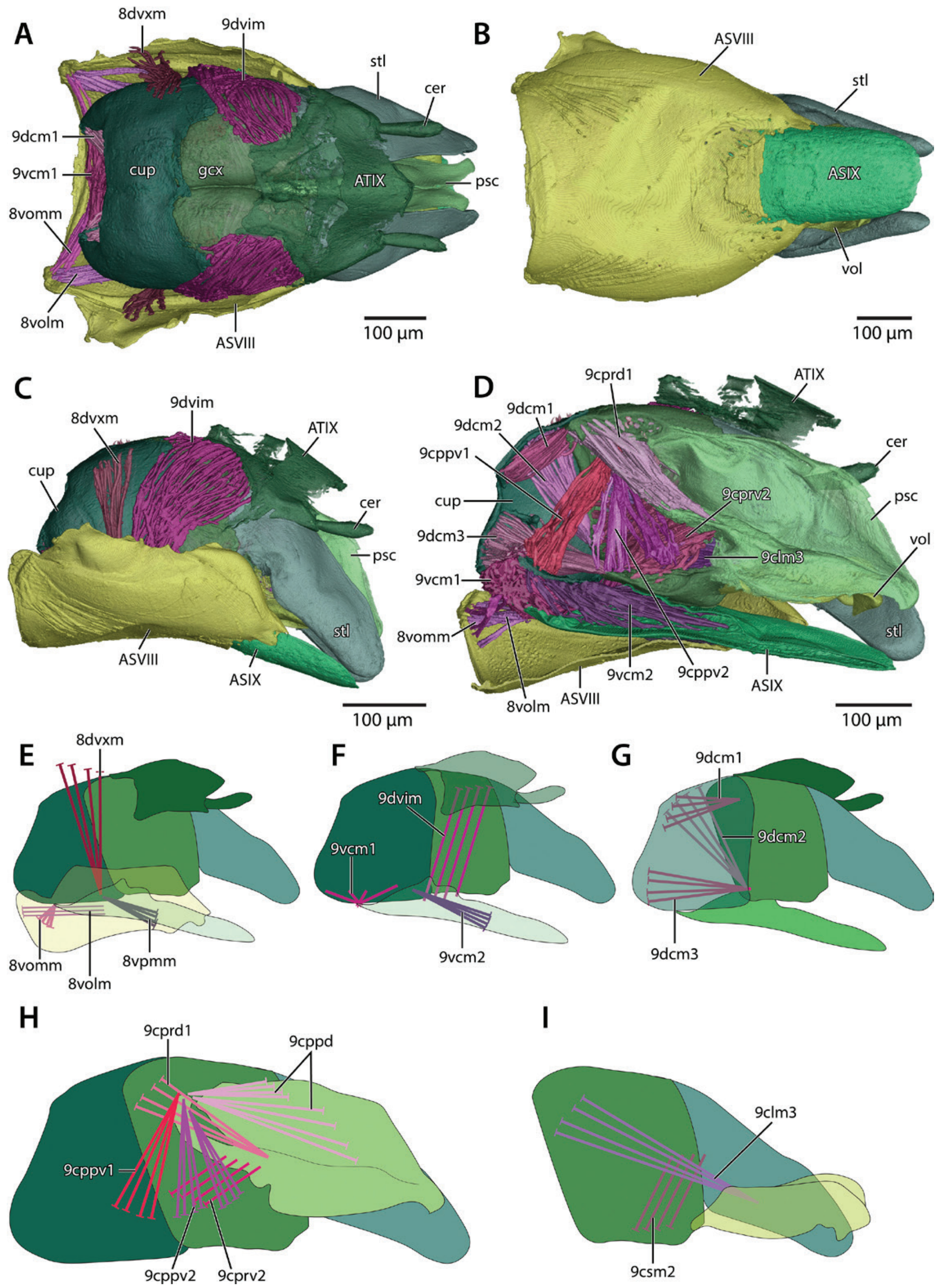

Figure 5. ♂ genitalia of *Odontomachus* indet. (CASENT0842842), 3D reconstructions (A–D) and summary diagrams (E–H). Orthogonal caps at end of diagrammatic muscle lines signify origin; lack of caps, insertion. **A** dorsal view. **B** ventral view. **C** profile view. **D** sagittal cross-section. **E** ventral longitudinal muscles VIII–IX and dorsoventral extrinsic muscles VIII–IX, profile view. **F** intrinsic dorsoventral muscles IX and sterno-coxal muscles IX, profile view. **G** tergo-coxal muscles IX, profile view. **H** coxo-penial muscles sagittal cross-section. **I** coxo-stylar and coxo-lateropenital muscles, profile view. Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; ATIX = abdominal tergite IX; cer = cercus; cup = cupula; gcx = gonocoxite; psc = penial sclerite; stl = gonostylus; vol = volsella; 8vomm = ventral orthomedial muscles VIII-IX; 8vpmm = ventral paramedial muscles VIII-IX; 8volm = ventral ortholateral muscles VIII-IX; 8dvxm = dorsoventral extrinsic muscles VIII-IX; 9dvim = dorsoventral intrinsic muscles IX; 9vcm1 = anteromedial sterno-coxal muscles; 9vcm2 = posteromedial sterno-coxal muscles; 9dcm1 = dorsal tergo-coxal muscles; 9dcm2 = dorsolateral tergo-coxal muscles; 9dcm3 = ventrolateral tergo-coxal muscles; 9dcm4 = ventral tergo-coxal muscles; 9csm2 = intermediate coxo-stylar muscles; 9clm3 = medial extrinsic coxo-lateropenital muscles; 9cppd = dorsal coxo-penial promotors; 9cprd1 = dorsal coxo-penial remotors; 9cppv1 = anterior ventral coxo-penial promotors; 9cppv2 = posterior ventral coxo-penial promotors; 9cprv2 = lateral ventral coxo-penial remotors.

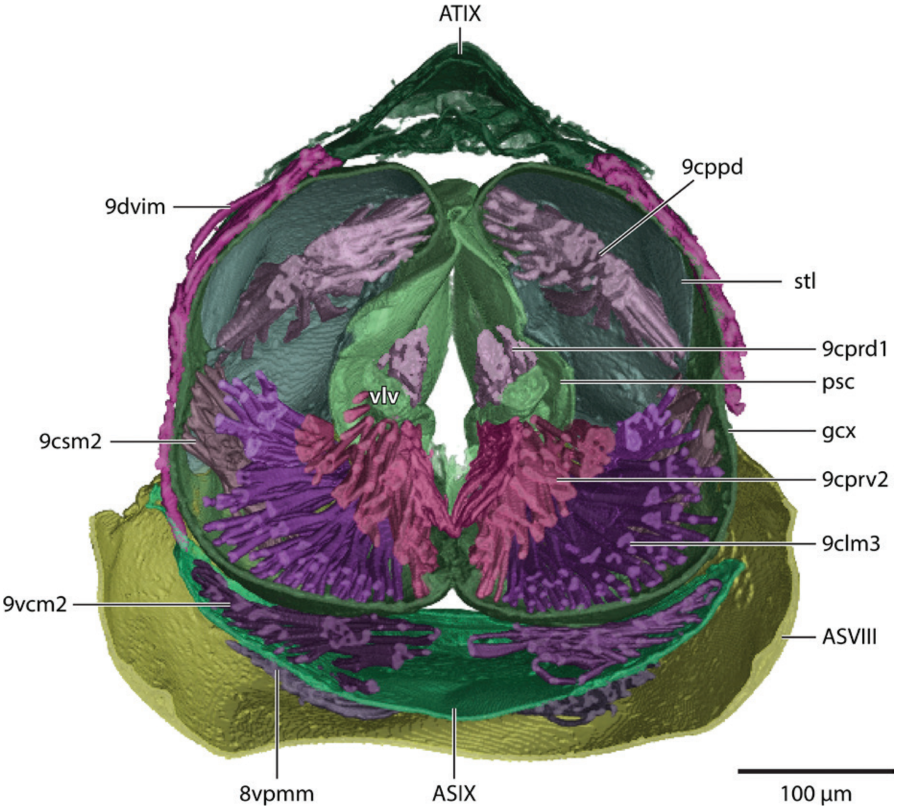

Figure 6. ♂ genitalia of *Odontomachus* indet. (CASENT0842842), 3D reconstruction in transverse cross-section. Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; ATIX = gcx = gonocoxite; psc = penial sclerite; stl = gonostylus; vlv = valvura; vol = volsella; 8vpmm = ventral paramedial muscles VIII-IX; 9dvim = dorsoventral intrinsic muscles IX; 9vcm2 = posteromedial sterno-coxal muscles; 9csm2 = intermediate coxo-stylar muscles; 9cppd = dorsal coxo-penial promotors; 9clm3 = medial extrinsic coxo-lateropenital muscles; 9cprd1 = dorsal coxo-penial remotors; 9cprv2 = lateral ventral coxo-penial remotors.

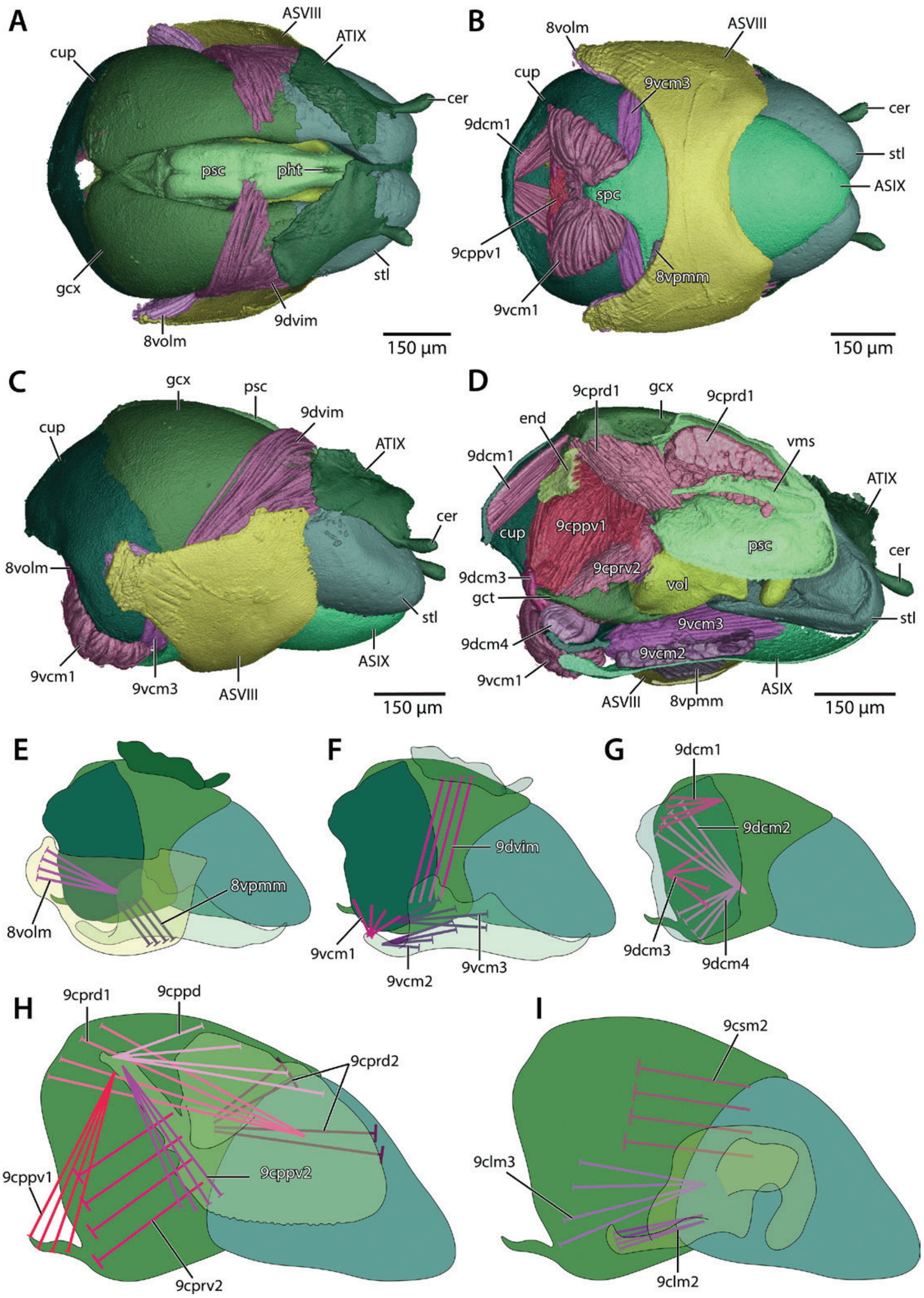

Figure 7. ♂ genitalia of *Myrmica ruginodis* (PMJ:Hex:2205), 3D reconstructions (A–D) and summary diagrams (E–H). Orthogonal caps at end of diagrammatic muscle lines signify origin; lack of caps, insertion. **A** dorsal view. **B** ventral view. **C** profile view. **D** sagittal cross-section. **E** ventral longitudinal muscles, profile view IX. **F** intrinsic dorsoventral muscles IX and sterno-coxal muscles IX, profile view. **G** tergo-coxal muscles IX, profile view. **H** coxo-penial muscles, sagittal cross-section. **I** coxo-stylar and coxo-lateropenital muscles, profile view. Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; ATIX = abdominal tergite IX; cer = cercus; cup = cupula; end = endophallic sclerite; gct = gonocoxital arm; gcx = gonocoxite; psc = penial sclerite; stl = gonostylus; vol = volsella; 8vpmm = ventral paramedial muscles VIII–IX; 8volm = ventral ortholateral muscles VIII–IX; 9dvim = dorsoventral intrinsic muscles IX; 9vcm1 = anteromedial sterno-coxal muscles; 9vcm2 = posteromedial sterno-coxal muscles; 9vcm3 = lateral sterno-coxal muscles; 9dcm1 = dorsal tergo-coxal muscles; 9dcm2 = dorsolateral tergo-coxal muscles; 9dcm3 = ventrolateral tergo-coxal muscles; 9dcm4 = ventral tergo-coxal muscles; 9csm2 = intermediate coxo-stylar muscles; 9clm2 = lateral intrinsic coxo-lateropenital muscles; 9clm3 = medial extrinsic coxo-lateropenital muscles; 9cppd = dorsal coxo-penial promotors; 9cprd1 = medial dorsal coxo-penial remotors; 9cprd2 = lateral dorsal coxo-penial remotors; 9cppv1 = anterior ventral coxo-penial promotors; 9cppv2 = posterior ventral coxo-penial promotors; 9cprv2 = lateral ventral coxo-penial remotors.

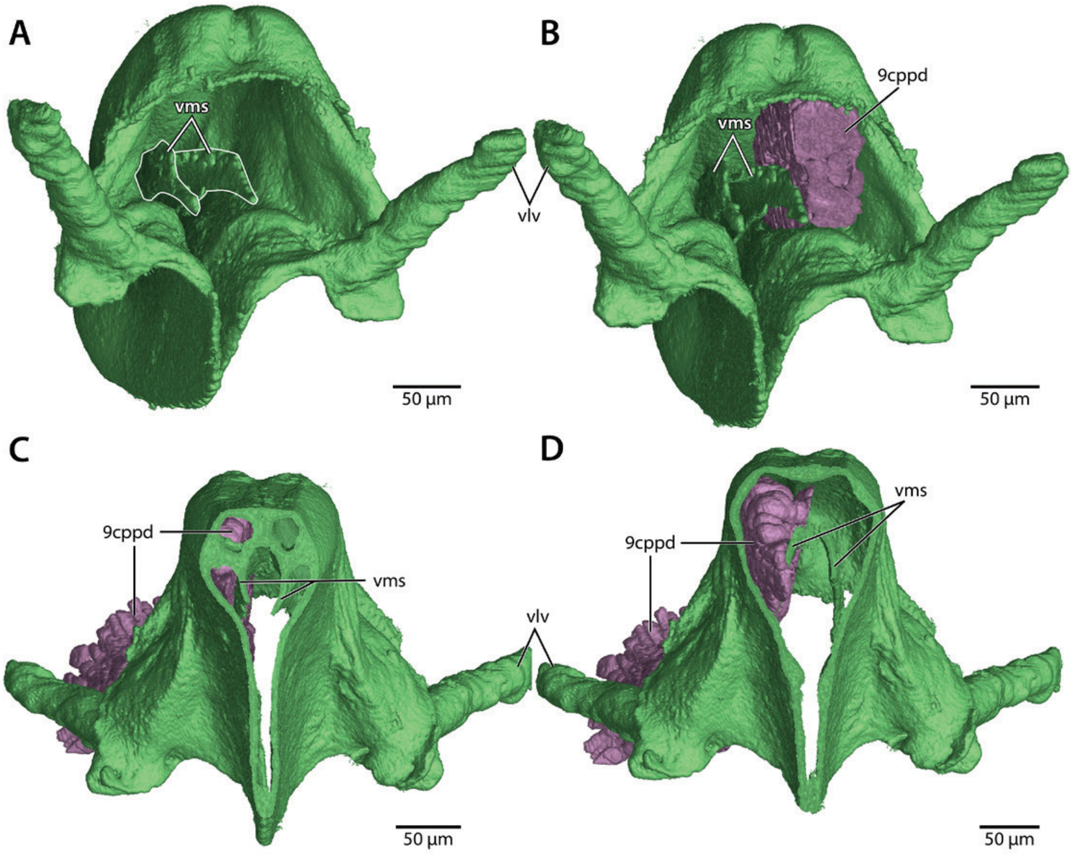

Figure 8. Penial sclerites of *Myrmica ruginodis*, 3D reconstruction in anterior oblique view (A–B) and posterior transverse section (C–D). Section plane in C is slightly caudad that in D. Left half of 9ppcd hidden. Abbreviations: vlv = valvura; vms = ventromesal septum; 9cppd = dorsal coxo-penial promotor.

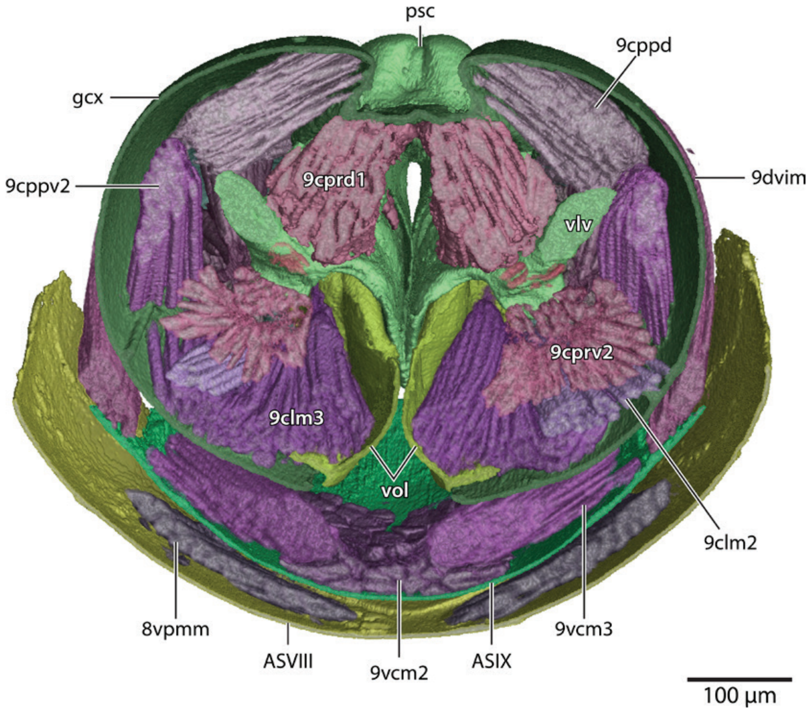

Figure 9. ♂ genitalia of *Myrmica ruginodis* (PMJ:Hex:2205), 3D reconstruction in transverse cross-section. Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; gcx = gonocoxite; psc = penial sclerite; vlv = valvura; vol = volsella; 8vpmm = ventral paramedial muscles VIII–IX; 9dvim = dorsoventral intrinsic muscles IX; 9vcm2 = posteromedial sterno-coxal muscles; 9vcm3 = lateral sterno-coxal muscles; 9clm2 = lateral intrinsic coxo-lateropenital muscles; 9clm3 = medial extrinsic coxo-lateropenital muscles; 9cppd = dorsal coxo-penial promotors; 9cprd1 = medial dorsal coxo-penial remotors; 9cppv2 = posterior ventral coxo-penial promotors; 9cprv2 = lateral ventral coxo-penial remotors.

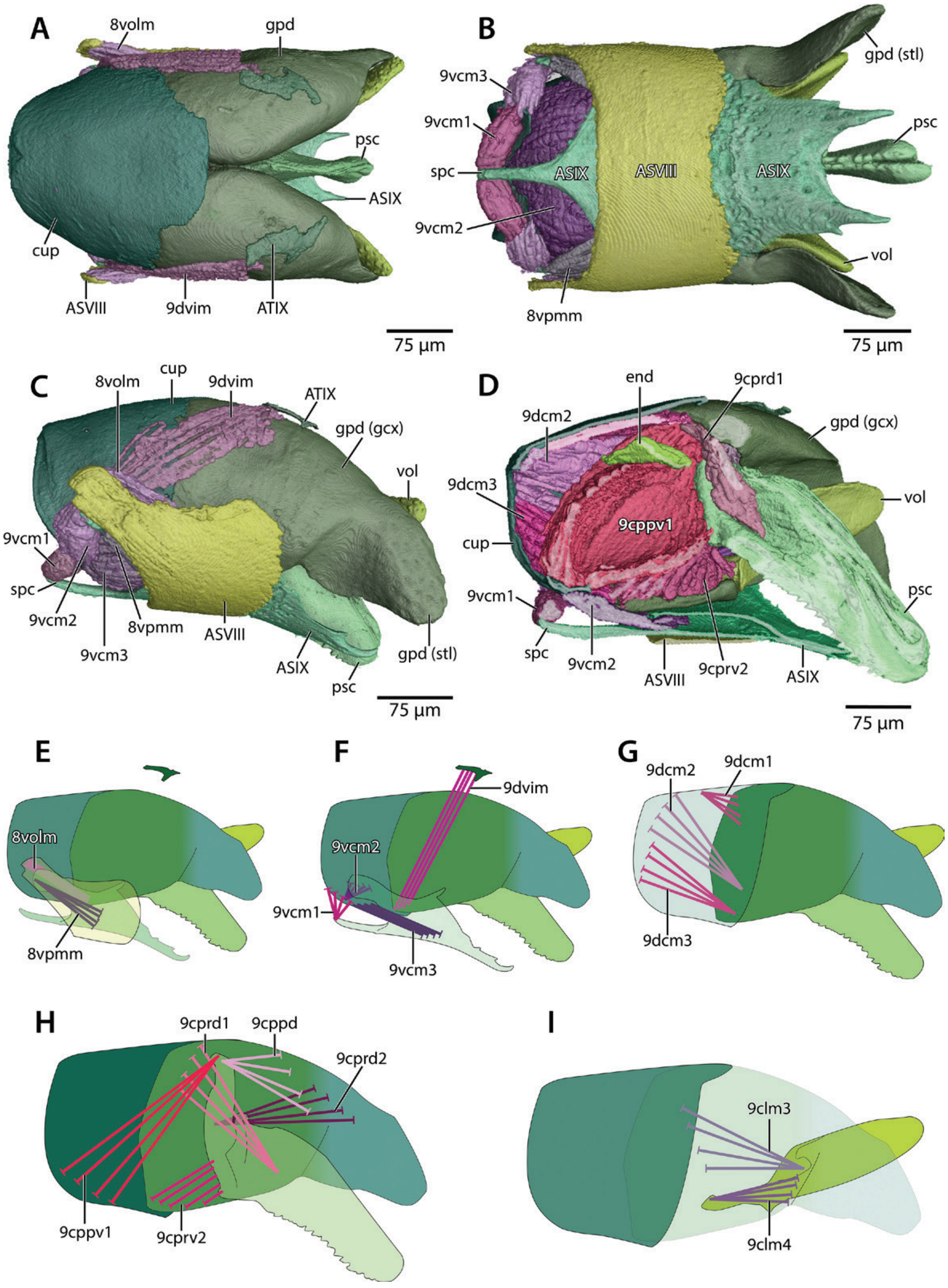

Figure 10. ♂ genitalia of *Lioponera* indet. (CASENT0844684), 3D reconstructions (A–D) and summary diagrams (E–H). Orthogonal caps at end of diagrammatic muscle lines signify origin; lack of caps, insertion. **A** dorsal view. **B** ventral view. **C** profile view. **D** sagittal cross-section. **E** ventral longitudinal muscles IX, profile view. **F** intrinsic dorsoventral muscles IX and sterno-coxal muscles, profile view. IX **G** tergo-coxal muscles IX, profile view. **H** coxo-penial muscles, sagittal cross-section. **I** coxo-lateropenital muscles, profile view. Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; ATIX = abdominal tergite IX; cup = cupula; gcx = gonocoxite; gpd = gonopodite; psc = penial sclerite; spc = spiculum; stl = gonostylus; vol = volsella; 8vpmm = ventral paramedial muscles VIII–IX; 8volm = ventral ortholateral muscles VIII–IX; 9dvim = dorsoventral intrinsic muscles IX; 9vcm1 = anteromedial sterno-coxal muscles; 9vcm2 = posteromedial sterno-coxal muscles; 9dcm1 = dorsal tergo-coxal muscles; 9dcm2 = dorsolateral tergo-coxal muscles; 9dcm3 = ventrolateral tergo-coxal muscles; 9clm3 = medial extrinsic coxo-lateropenital muscles; 9clm4 = lateral extrinsic coxo-lateropenital muscles; 9cppd = dorsal coxo-penial promotors; 9cprd1 = medial dorsal coxo-penial remotors; 9cprd2 = lateral dorsal coxo-penial remotors; 9cppv1 = anterior ventral coxo-penial promotors; 9cprv2 = lateral ventral coxo-penial remotors.

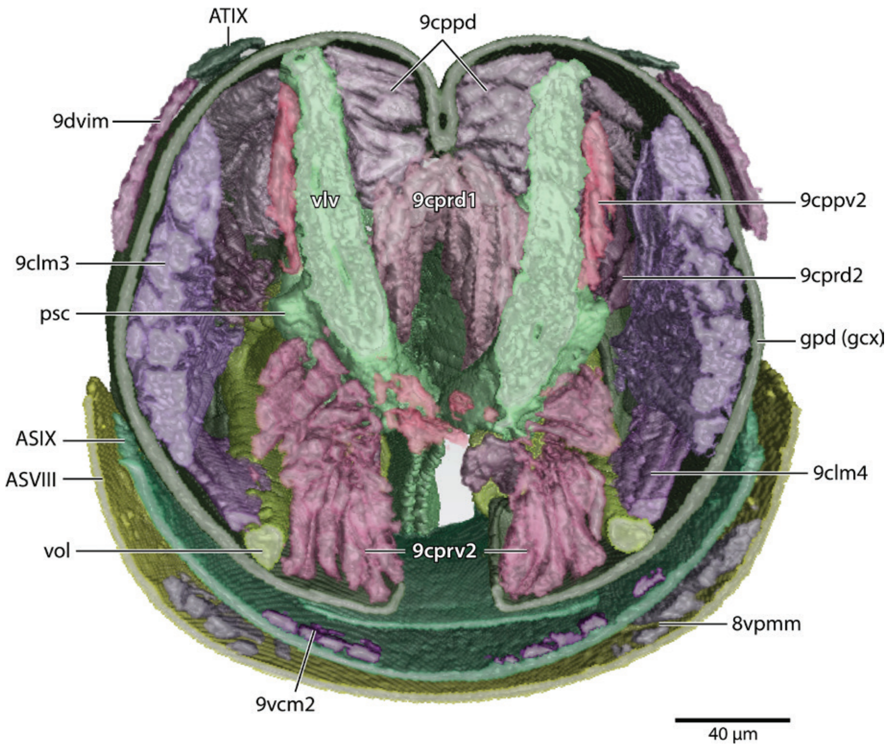

Figure 11. ♂ genitalia of *Lioponera* indet. (CASENT0844684), 3D reconstruction in transverse cross-section. Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; ATIX = abdominal tergite IX; gcx = gonocoxite; gpd = gonopodite; psc = penial sclerite; vlv = valvura; vol = volsella; 9dvim = dorsoventral intrinsic muscles IX; 9vcm2 = posteromedial sterno-coxal muscles; 9clm3 = medial extrinsic coxo-lateropenital muscles; 9clm4 = lateral extrinsic coxo-lateropenital muscles; 9cprd2 = lateral dorsal coxo-penial remotors; 9cppv2 = posterior ventral coxo-penial promotors.

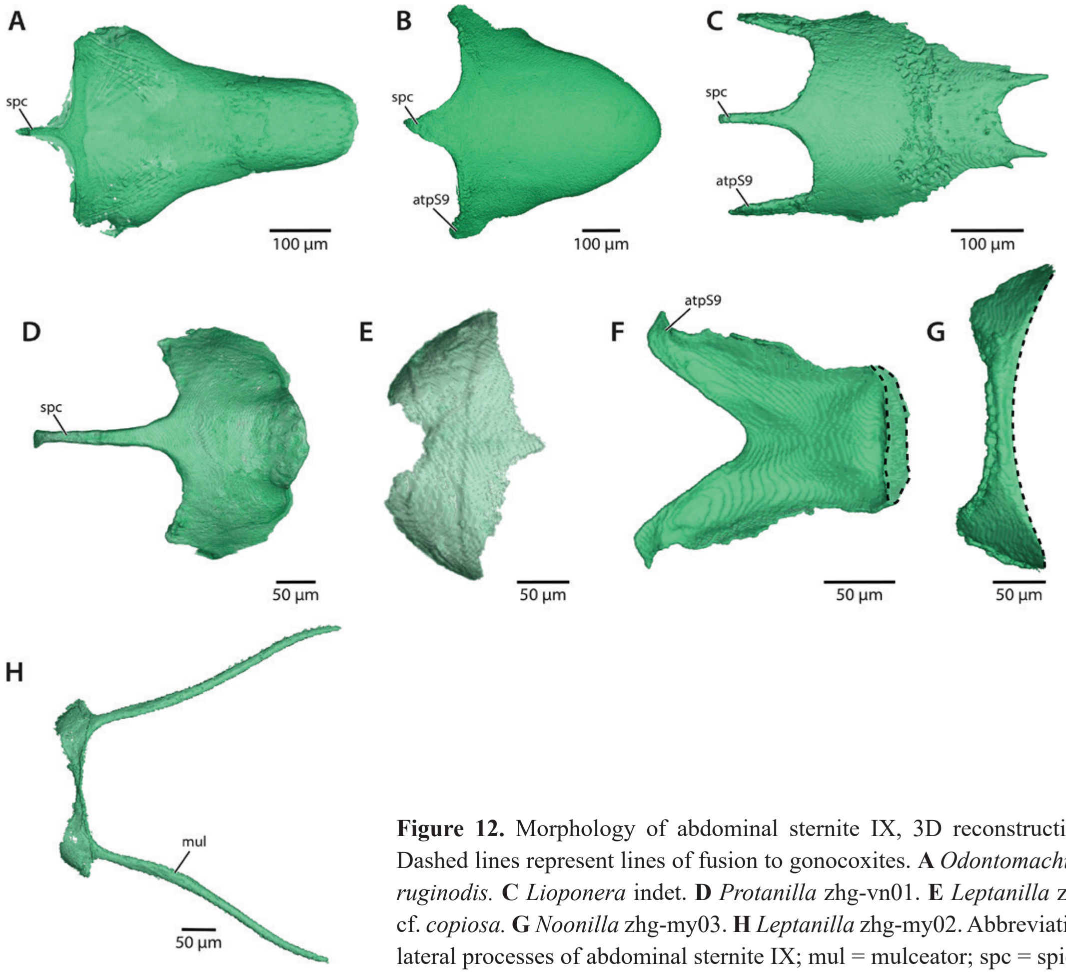

Figure 12. Morphology of abdominal sternite IX, 3D reconstructions in dorsal view. Dashed lines represent lines of fusion to gonocoxites. **A** *Odontomachus* indet. **B** *Myrmica ruginodis*. **C** *Lioponera* indet. **D** *Protanilla* zhg-vn01. **E** *Leptanilla* zhg-id04. **F** *Noonilla* cf. *copiosa*. **G** *Noonilla* zhg-my03. **H** *Leptanilla* zhg-my02. Abbreviations: atpS9 = anterolateral processes of abdominal sternite IX; mul = mulceator; spc = spiculum.

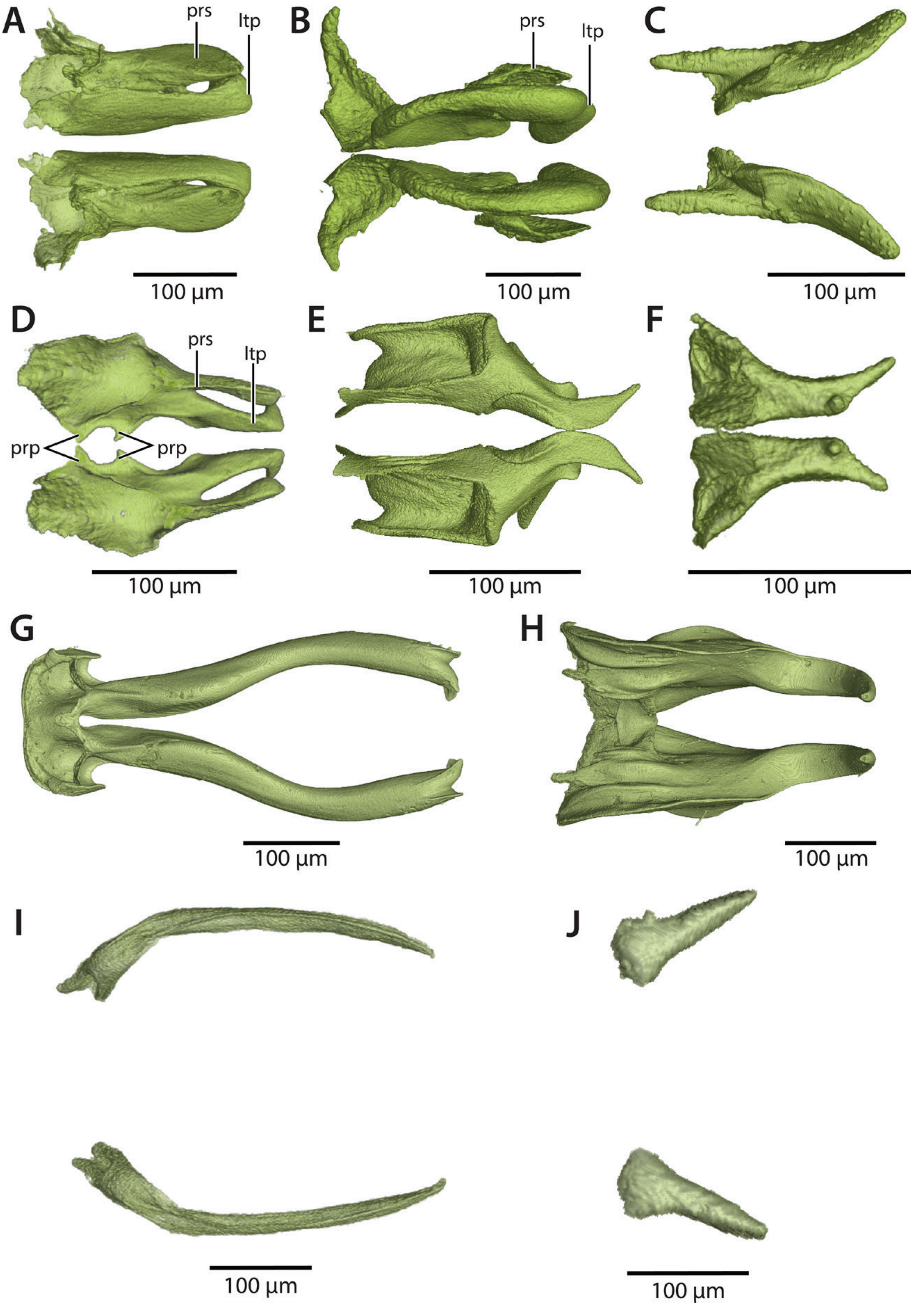

Figure 13. Morphology of the volsella, 3D reconstructions in dorsal view. **A** *Odontomachus* indet. **B** *Myrmica ruginodis.* **C** *Lioponera* indet. **D** *Protanilla* zhg-vn01. **E** *Yavnella* zhg-th03. **F** *Yavnella* zhg-bt01. **G** *Leptanilla* zhg-my02. **H** *Leptanilla* zhg-my04. **I** *Leptanilla* cf. *zaballosi.* **J** *Leptanilla* zhg-id04. Abbreviations: ltp = lateropenite; prp = lateropenital recurved processes; prs = parossiculus.

3.1.3. *Protanilla*

3.1.3.1. *Protanilla* zhg-vn01 (Fig. 14)

Abdominal sternite VIII (**ASVIII**; Fig. 14A–E) with length equivalent across lateromedial span; antecosta of abdominal sternite VIII not discernible; diverging anterolateral apodemes of abdominal sternite VIII present, triangular, truncate; laterally separate from abdominal tergite VIII; posteriorly separate from abdominal sternite IX. Abdominal sternite IX (**ASIX**; Fig. 14B–D) elongate, hull-shaped, not narrowing laterally along anteroposterior axis; anterolateral corners angular, not produced into diverging anterolateral processes; diverging anterolateral processes absent; spiculum (**spc**; Fig. 14B–D) present, anterior apex narrowly truncate, lateromedial breadth constant along most of anteroposterior length; abdominal sternite IX produced posteriorly into triangular, truncate posteromedian process, delimited anteriorly by transverse carina (Fig. 14D, arrowhead); separate posteriorly from gonopodites. Mulceators absent. Antecosta of abdominal sternite IX present. Abdominal tergite IX (**ATIX**; Fig. 14A, C–E) divided into hemitergites; outline sigmoidal in dorsolateral profile view, tapering medially and laterally. Cerci absent. Cupula (**cup**; Fig. 14A–D) present; non-annular and crescentiform, situated ventral to proximodistal axis of genitalia, tapering laterally. Gonocondyle absent. Gonopodites proximally separated from abdominal sternite IX, articulate. Gonocoxites (**gcx**; Fig. 14A, C, E) separated along dorsum; along venter, medially fused along apical 1/3 of length; dorsum proximally enclosed by, and separated from, penial sclerites; apicolateral laminae absent; gonocoxites with ventrolateral mesal carinae running to ventral bases of gonostyli, ventrally articulated with gonostyli. Gonostyli (**stl**; Fig. 14A–D) present, separated from gonocoxites by ventral conjunctiva, but not distinguishable from gonocoxites dorsal to conjunctiva; outline of gonostyli bluntly cuneiform in dorsolateral view, anteroposterior length subequal to that of the gonocoxites. Volsellae (**vol**; Fig. 14A–E) present, proximally indistinct from gonopodites; not medially fused; lateropenite (**ltp**; Fig. 14B, D) and parossiculus (**prs**; Fig. 14B, D) present, proximally indistinct; two recurved, dorsoventrally compressed medial processes present (**prp**; Fig. 14D), placed successively along medioventral margin. Penial sclerites (**psc**; Fig. 14A–E) medially joined by dorsal conjunctiva along proximal 4/7 of length, medially separated at apex; not dorsoventrally or lateromedially compressed, unsculptured; valvurae present, lamellate proximolateral processes, proximal apices of valvurae not directed dorsally; posterior penial processes absent; endophallic sclerite absent; phallotreme distodorsal, situated at apex of penial conjunctiva, not surrounded by sclerotized portions of the penial sclerites, not recessed; penial sclerites distad phallotreme produced ventrally, dorsolateral margins bowed outwards.

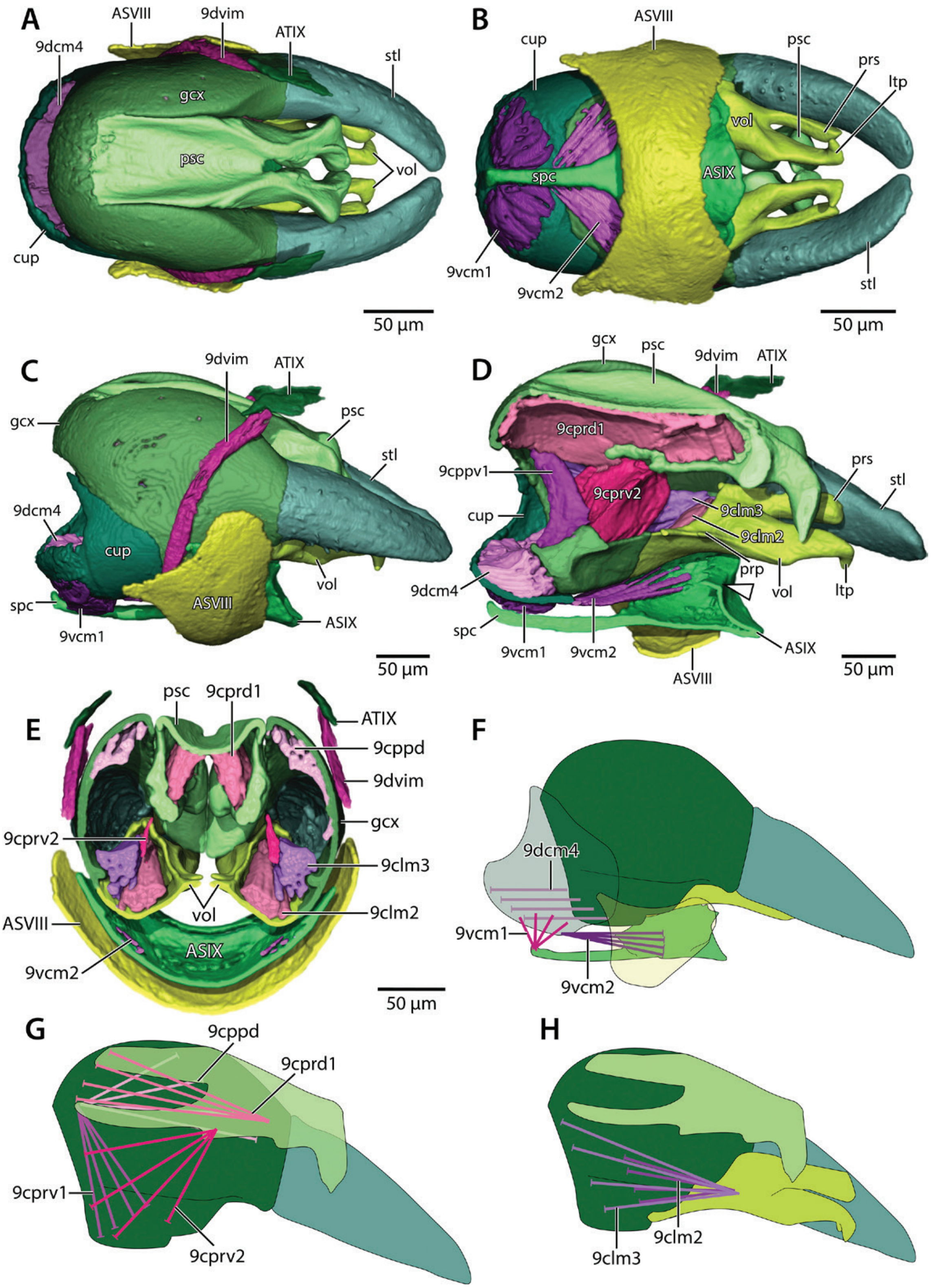

Figure 14. ♂ genitalia in *Protanilla* zhg-vn01 (CASENT0106408), 3D reconstructions (A–E) and summary diagrams (F–H). Orthogonal caps at end of diagrammatic muscle lines signify origin; lack of caps, insertion. White arrowhead in Fig. 14D indicates posterior transverse carina. **A** dorsal view. **B** ventral view. **C** profile view. **D** sagittal cross-section. **E** transverse cross-section. **F** sterno-coxal and tergo-coxal muscles, profile view. **G** coxo-penial muscles, sagittal cross-section. **H** coxo-lateropenital muscles, profile view. Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; ATIX = abdominal tergite IX; cup = cupula; gcx = gonocoxite; lateropenite = ltp; prp = lateropenital recurved processes; prs = parossiculus; prp = lateropenital recurved processes; psc = penial sclerites; spc = spiculum; stl = gonostylus; vol = volsella; 9dvim = dorsoventral intrinsic muscles IX; 9vcm1 = anteromedial sterno-coxal muscles; 9vcm2 = posteromedial sterno-coxal muscles; 9dcm4 = ventral tergo-coxal muscles; 9clm2 = lateral intrinsic coxo-lateropenital muscles; 9clm3 = medial extrinsic coxo-lateropenital muscles; 9cppd = dorsal coxo-penial promotors; 9cprd1 = medial dorsal coxo-penial remotors; 9cppv1 = anterior ventral coxo-penial promotors; 9cprv2 = lateral ventral coxo-penial remotors

3.1.4. *Yavnella*

Yavnella zhg-bt01 (Fig. 15)

Abdominal sternite VIII (**ASVIII**; Fig. 15B–D) anteroposteriorly compressed laterally, anteroposteriorly expanded medially, posteromedian margin produced into paired obtuse processes; antecosta of abdominal sternite VIII absent; laterally separate from abdominal tergite VIII; posteriorly separate from abdominal sternite IX. Abdominal sternite and tergite IX not discernible. Mulceators absent. Cerci absent. Cupula (**cup**; Fig. 15D) present, venter anteroposteriorly expanded, dorsum anteroposteriorly compressed, forming a narrow ring surrounding a broad, circular foramen genitale. Gonopodites (**gpd**; Fig. 15A–E) proximally separate from abdominal sternite IX, inarticulate. Gonocoxites (**gcx**; Fig. 15A–D) present, not externally distinct from gonostyli, separated along dorsum; along venter, medially fused along proximal ¼ of length; dorsum proximally enclosed by penial sclerites, fused with penial sclerites along proximodorsal margin; apicolateral laminae absent. Gonostyli (**stl**; 15A–E) present, not articulated to gonocoxites, internally delimited from gonocoxites by mesal carinae; outline rounded in profile view, length less than that of the gonocoxites. Volsellae (**vol**; Fig. 15A–E) present, proximally distinct from gonopodites; medially separate; parossiculus and lateropenite not distinct; recurved medial processes absent; volsella bifid. Penial sclerites (**psc**; Fig. 15A, C–E) completely medially fused, proximally separate from gonopodites; dorsoventrally compressed, unsculptured; valvurae absent; posterior penial processes absent; endophallic sclerite absent; phallotreme distal, situated at penial apex; penial apex dorsoventrally compressed, not laminate, margins convergent.

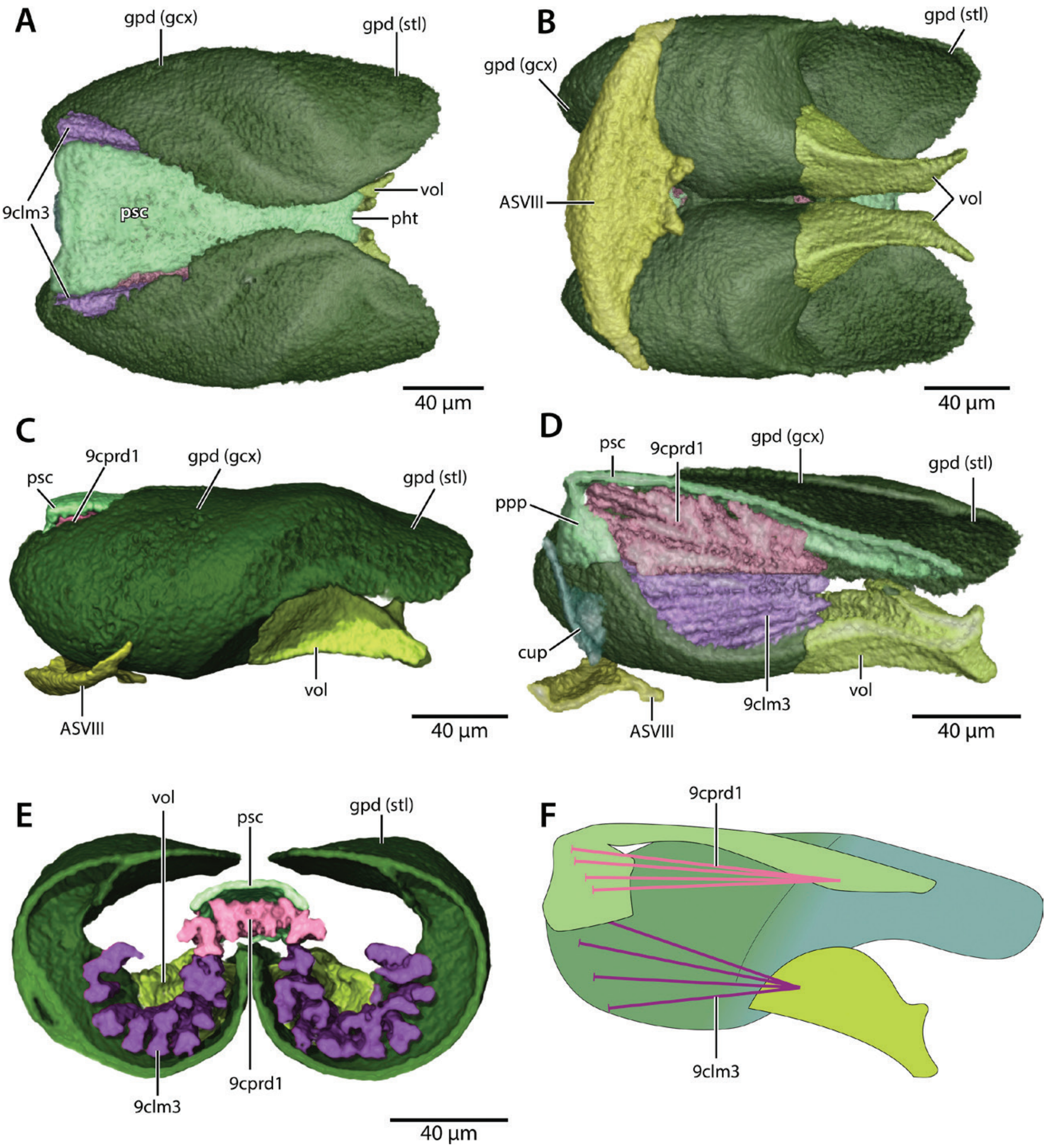

Figure 15. ♂ genitalia of *Yavnella* zhg-bt01 (CASENT0842743), 3D reconstructions (A–E) and summary diagram (F). Orthogonal caps at end of diagrammatic muscle lines signify origin; lack of caps, insertion. **A** dorsal view. **B** ventral view. **C** profile view. **D** sagittal cross-section. **E** transverse cross-section. **F** genital musculature, sagittal cross-section. Abbreviations: ASVIII = abdominal sternite VIII; cup = cupula; gcx = gonocoxite; gpd = gonopodites; pht = phallotreme; ppp = posterior penial process; psc = penial sclerite; stl = gonostylus; vol = volsella; 9clm3 = medial extrinsic coxo-lateropenital muscles; 9cprd1 = medial dorsal coxo-penial remotors.

Yavnella zhg-th03 (Fig. 16)

Abdominal sternite VIII (**ASVIII**; Fig. 16A–D) expansive, enclosing dorsal base of genitalia; antecosta of abdominal sternite VIII present laterally, absent medially, where present rotated and projecting ventrad; diverging anterolateral apodemes present, tapering dorsally, recurved posteriorly; posteromedially fused to cupula (Fig. 35B) (Section 4.4.1.). Abdominal sternite IX absent. Mulceators absent. Abdominal tergite IX absent. Cupula **(cup**; Fig. 16A–D) present**,** anteriorly fused to abdominal sternites VIII–IX (Fig. 35B) (Sections 4.2., 4.4.1.–4.4.2.); lateromedially compressed, anteroposteriorly prolonged, with foramen genitale lateromedially compressed. Cerci absent. Gonopodites (**gpd**; Fig. 16A–E) proximally separate from abdominal sternite IX, inarticulate. Gonocoxites (**gpd** (gcx); Fig. 16A–D) present, not externally distinct from gonostyli, separated along dorsum; along venter, medially fused along proximal 1/3 of length; dorsum proximally enclosed by penial sclerites; fused with penial sclerites along ventromedial face; apicolateral laminae absent. Gonostyli (**gpd** (stl); Fig. 16A–D) present; tapering, apices medially recurved. Volsellae (**vol**; Fig. 16B–E) present, not medially fused; fully articulated to gonopodites; basal ½ of volsella subcylindrical in cross-section, with ectal longitudinal costae on medial face; apical ½ of volsella produced into dorsal linear process and ventral hook-like process, with latter process proximally recurved, surface of processes unsculptured. Penial sclerites (**psc**; Fig. 16A–E) completely medially fused, fused to gonocoxites along proximal 1/3 of length, subtriangular proximomedian notch present; proximal longitudinal carinae present on penial dorsum, absent medially and laterally; valvurae absent; ventral longitudinal posterior penial processes (**ppp**; Fig. 16D) present at base, insensibly fused with gonocoxites; endophallic sclerite absent; phallotreme posterodorsal, not recessed, outline teardrop-like, narrowing distally; narrow linear apicomedian slit present, distal to phallotreme; penial apex dorsoventrally compressed, laminate, with linear lateral margins.

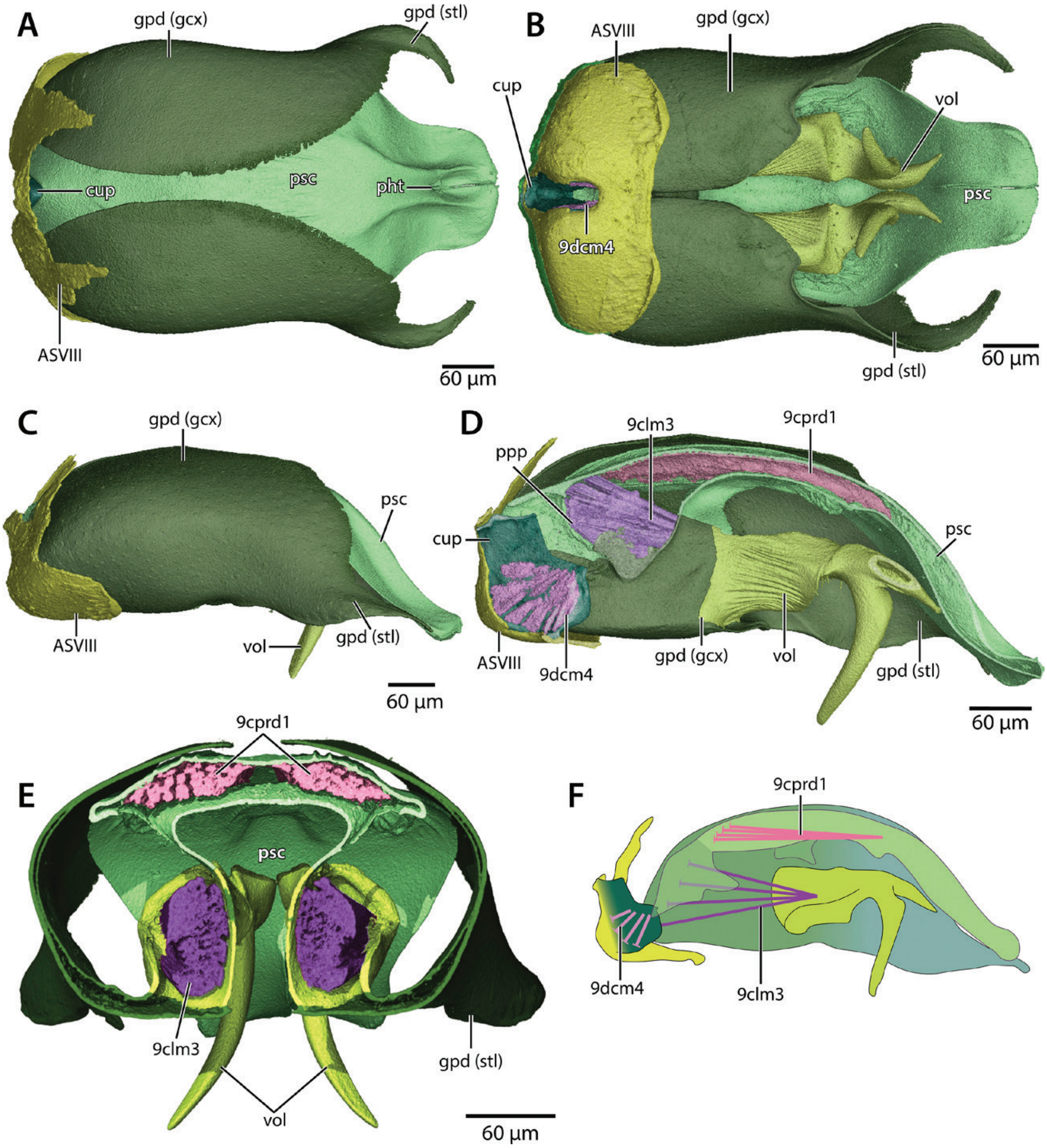

Figure 16. ♂ genitalia of *Yavnella* zhg-th03 (CASENT0842741), 3D reconstructions (A-E) and summary diagram (F). Orthogonal caps at end of diagrammatic muscle lines signify origin; lack of caps, insertion. **A** dorsal view. **B** ventral view. **C** profile view. **D** sagittal cross-section. **E** transverse cross-section. **F** genital musculature, sagittal cross-section. Abbreviations: ASVIII = abdominal sternite VIII; cup = cupula; gcx = gonocoxite; gpd = gonopodite; pht = phallotreme; psc = penial sclerite; stl = gonostylus; vol = volsella; 9clm3 = medial extrinsic coxo-lateropenital muscles; 9dcm4 = ventral tergo-coxal muscles; 9cprd1 = medial dorsal coxo-penial remotors.

3.1.5. *Scyphodon* s.l.

Noonilla zhg-my03 (Fig. 17)

Abdominal sternite VIII (**ASVIII**; Fig. 17A–D) anteroposteriorly compressed, bar-like, with anteroposterior breadth equivalent across lateromedial span; antecosta present, weakly developed; diverging anterolateral apodemes absent; abdominal sternite VIII laterally separate from abdominal tergite VIII; posteriorly separate from abdominal sternite IX. Abdominal sternite IX (**ASIX**; Fig. 17A–C) anteroposteriorly compressed medially; antecosta present, not hypertrophied, abdominal sternite IX not reduced to antecosta; spiculum absent; diverging anterolateral processes absent; posteromedian process absent, abdominal sternite IX fused to gonocoxites posteriorly, intersecting with gonocoxites at obtuse angle in profile view, delimited from gonocoxites by mesal transverse carina (Section 4.1.1.); mulceators absent. Abdominal tergite IX (**ATIX**; Fig. 17A, C, D) with posteromedian fusion, insensibly blending posteriorly into proctiger, expanded into apodemes anterolaterad median fusion; abdominal tergite IX anteroposteriorly narrowing laterad apodemes. Cerci absent. Cupula absent (Fig. 4I). Gonopodites proximally fused to abdominal sternite IX, articulate. Gonocoxites (**gcx**; Fig. 17A–E) present, proximally fused to abdominal sternite IX (Section 4.4.2.), distinct from gonostyli; with complete medial fusion along dorsum and venter, delimited by ventromedian carina; dorsum not proximally enclosed by, and indistinguishably fused with, penial sclerites; apicolateral laminae absent. Gonostyli (**stl**; Fig. 17A–E) present, separated dorsally from gonocoxites by invaginated conjunctiva, ventrally fused to gonocoxites along proximal ½ of length; medially fused at base, delimited by shallow median sulcus, unfused distally; each gonostylus distally produced into paired lobate, medially recurved processes, subequal in length. Volsellae absent (Section 4.1.1.). Penial sclerites (**psc**; Fig. 17A–E) with complete median fusion, indistinguishably fused with gonocoxites at base, proximal margin entire, dorsum intersecting that of the gonocoxites at a 90° angle; unsculptured; valvurae absent; posterior penial processes absent; endophallic sclerite absent; phallotreme (**pht**; Fig. 17B) posterodorsal, outline elliptical, slightly narrowing proximally, not recessed; penial apex not dorsoventrally compressed, dorsal surface concave, not laminate, distal margin entire, lateral margins converging.

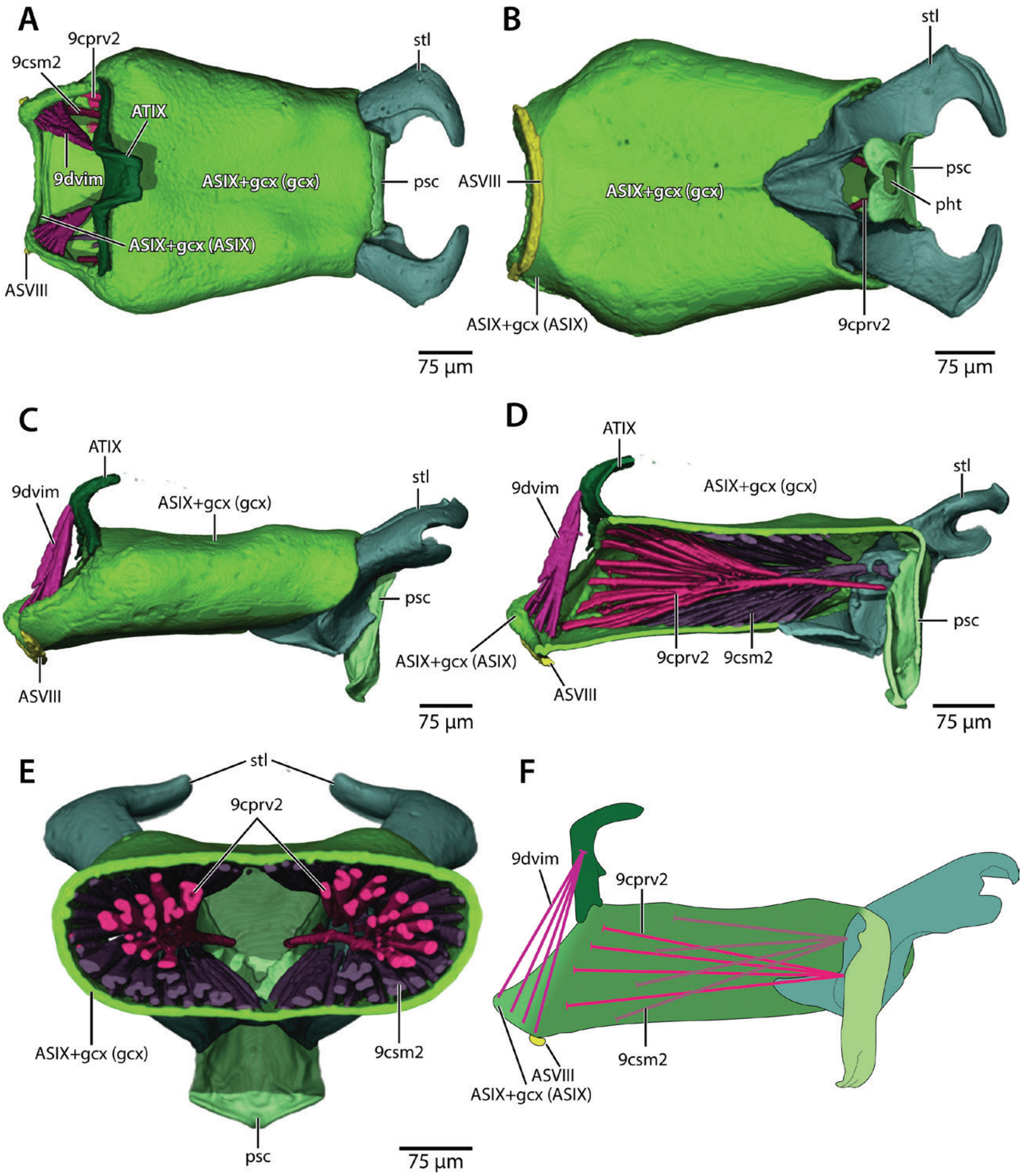

Figure 17. ♂ genitalia of *Noonilla* zhg-my03 (CASENT0842609), 3D reconstructions (A-E) and summary diagram (F). Orthogonal caps at end of diagrammatic muscle lines signify origin; lack of caps, insertion. **A** dorsal view. **B** ventral view. **C** profile view. **D** sagittal cross-section. **E** transverse cross-section. **F** genital musculature, sagittal cross-section. Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; ATIX = abdominal tergite IX; gcx = gonocoxite; pht = phallotreme; psc = penial sclerite; stl = gonostylus; 9dvim = dorsoventral intrinsic muscles IX; 9csm2 = intermediate coxo-stylar muscles; 9cprv2 = lateral ventral coxo-penial remotors.

***Noonilla* cf. *copiosa* (Fig. 18)**

Abdominal sternite VIII (**ASVIII**; Fig. 18A–D) anteroposteriorly compressed, bar-like, with anteroposterior length equivalent across lateromedial span; antecosta (**acsS8**; Fig. 18B, D) present, well-developed; diverging anterolateral apodemes absent; laterally fused to abdominal tergite VIII (Sections 4.1.1., 4.4.1.); not posteriorly fused to abdominal sternite IX. Abdominal sternite IX (**ASIX**; Fig. 18B, C) anteroposteriorly extended, posteriorly constricted along lateromedial axis; antecosta (**acsS9**; Fig. 18B) hypertrophied, extending along median faces of diverging anterolateral processes, medially prolonged into recurved triangular process, abdominal sternite IX not reduced to antecosta; diverging anterolateral processes (**atpS9**; Fig. 18B) present, outline of abdominal sternite IX being yoke-shaped (Fig. 12F); posteromedian process absent, abdominal sternite IX indistinguishably fused with gonocoxites posteriorly (Section 4.4.2.), intersecting with gonocoxites at 45° angle in profile view; mulceators absent. Abdominal tergite IX (**ATIX**; Fig. 18) divided into hemitergites; hemitergites anteroposteriorly compressed, tapering laterally. Cerci absent. Cupula absent (Fig. 4J). Gonopodites proximally fused to abdominal sternite IX, articulate. Gonocoxites (**gcx**; Fig. 18A–E) with narrow proximal fusion to abdominal sternite IX, distinct from gonostyli; with complete medial fusion along dorsum and venter, delimited by shallow ectal ventromedian sulcus and dorsomedian mesal carina; dorsum not proximally enclosed by, and indistinguishably fused with, penial sclerites; apicolateral laminae absent. Gonostyli (**stl**; Fig. 18A–E) present, articulated dorsally with gonocoxites, indistinguishably fused with gonocoxites ventrally; without medial fusion; apex of each gonostylus entire, medially recurved. Volsellae absent (Section 4.1.1.). Penial sclerites (**psc**; Fig. 18A–E) completely medially fused; indistinguishably fused with gonocoxites at base, proximal margin absent, dorsum at same dorsoventral level as that of the gonocoxites; ventromedian margin irregularly serrated, sculpturation otherwise absent; lateromedially compressed, valvurae absent; posterior penial processes absent; endophallic sclerite absent; phallotreme (**pht**; Fig. 18A) posterodorsal, recessed, outline teardrop-shaped; penial apex lateromedially compressed, rounded, outline entire, subapically produced into ventromedian “trigger”, consisting of a proximal, proximally recurved process and apical proximally recurved process with length ~130% that of proximal process.

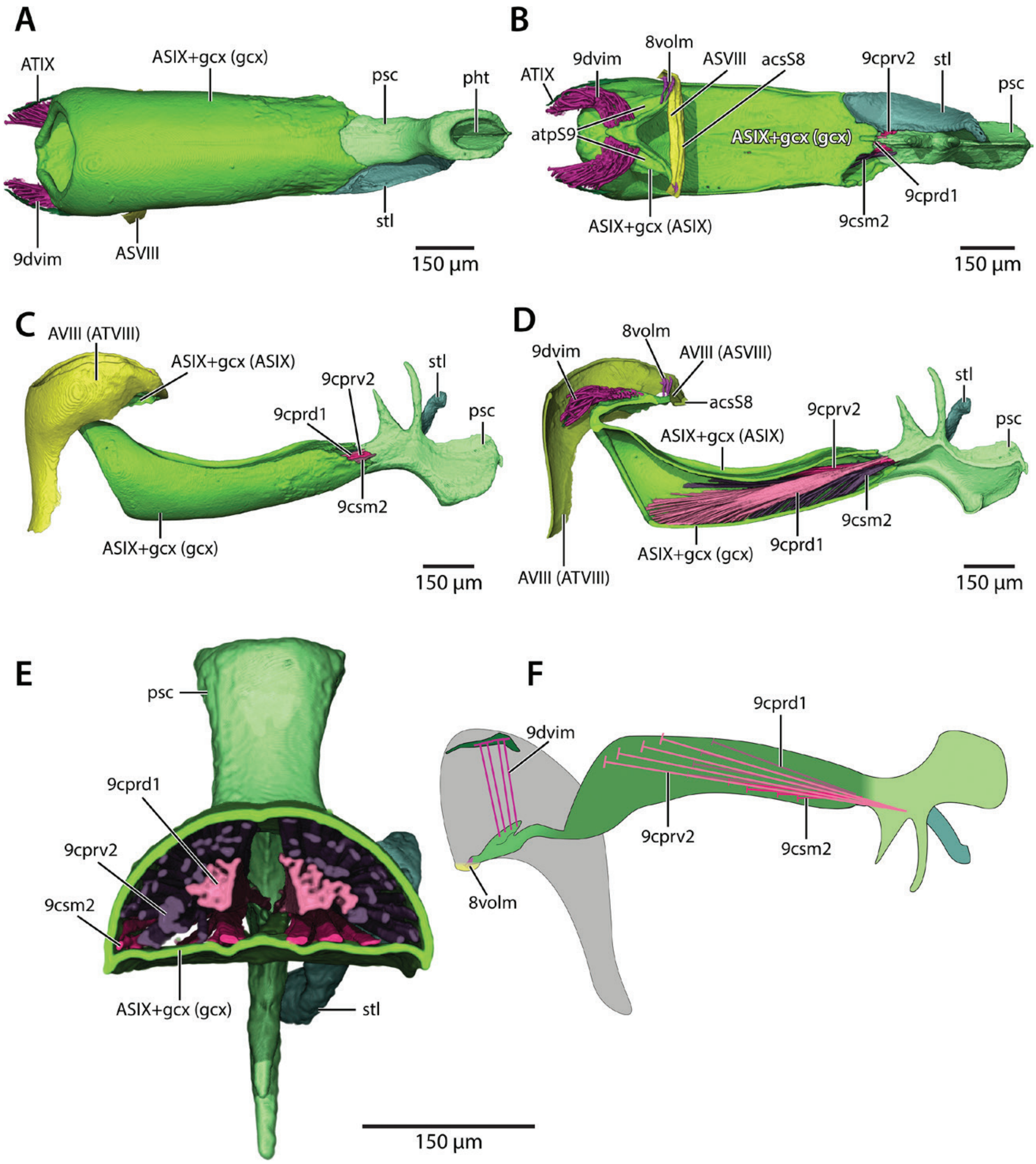

Figure 18. ♂ genitalia of *Noonilla* cf. *copiosa* (CASENT0842844), 3D reconstructions (A–E) and summary diagram (F). Orthogonal caps at end of diagrammatic muscle lines signify origin; lack of caps, insertion. **A** dorsal view. **B** ventral view. **C** profile view. **D** sagittal cross-section. **E** transverse cross-section. **F** genital musculature, sagittal cross-section; abdominal segments VIII–IX are shown rotated 180° relative to its position in situ. Abdominal sternite VIII is shown without sagittal cross-section. Abbreviations: AVIII = abdominal segment VIII; ASVIII = abdominal sternite VIII; ATVIII = abdominal tergite VIII; ASIX = abdominal sternite IX; ATIX = abdominal tergite IX; atpS9 = anterolateral processes of abdominal sternite IX; gcx = gonocoxite; pht = phallotreme; psc = penial sclerite; stl = gonostylus; 8volm = ventral ortholateral muscles VIII-IX; 9dvim = dorsoventral intrinsic muscles IX; 9csm2 = intermediate coxo-stylar muscles; 9cprd1 = medial dorsal coxo-penial remotors; 9cprv2 = lateral ventral coxo-penial remotors.

3.1.6. The Bornean morphospecies-group

Leptanilla zhg-my02 (Fig. 19)

Abdominal sternite VIII (**ASVIII**; Fig. 19A–D) anteroposteriorly compressed; antecosta present, not well-developed, abdominal sternite VIII medially reduced to antecosta; diverging anterolateral apodemes absent; laterally separate from abdominal tergite VIII; posteriorly separate from abdominal sternite IX (Sections 4.1.1.3., 4.4.1.). Abdominal sternite IX (**ASIX**; Fig. 19A–D) anteroposteriorly compressed, strap-like with posterolateral corners expanded and rounded, narrowing medially along anteroposterior axis; antecosta absent medially, not produced into recurved lateral apodemes; diverging anterolateral processes absent; spiculum absent; posteromedian process absent, abdominal sternite IX with posteromedian fusion to gonocoxites (Section 4.4.2.), ventral to gonocoxital foramen (Fig. 35F); mulceator (**mul**; Fig. 19A–E) present, subcircular in cross-section towards apex. Abdominal tergite IX (**ATIX**; Fig. 19A–D) divided into hemitergites; hemitergites anteroposteriorly compressed, lozenge-shaped in outline. Cerci absent. Cupula absent (Fig. 4H). Gonopodites with narrow proximomedian fusion to abdominal sternite IX. Gonocoxites (**gcx**; Fig. 19A–E) present, with medial fusion complete, not medially delimited by sulcus, carina, or both; circular gonocoxital foramen present; dorsum enclosing, and separate from, penial sclerites; apicolateral laminae (**all**; Fig. 19A–C, E) present, outline subulate. Gonostyli absent (Griebenow 2021; Section 4.1.1.). Volsellae (**vol**; Fig. 19A–E) present, fully articulated to gonocoxites at base, medially fused by narrow bridge of cuticle at base; lateropenite indistinguishably fused with parossiculus; recurved medial processes absent; lateral faces of volsellar apices produced into dorsally recurved hook. Penial sclerites (**psc**; Fig. 19A–E) completely medially fused, fully articulated to gonocoxites along proximodorsal margin, subcircular in proximal cross-section, dorsally recurved, unsculptured; penial condyles present; valvurae absent; posterior penial processes absent; endophallic sclerite absent; phallotreme (**pht**; Fig. 19A) distoventral, subapical, recessed, on platform-like ventromedian process, outline elliptical; penial apex produced into median ventral carina distad phallotreme, with lateral margins produced into ventral carinae that converge apically.

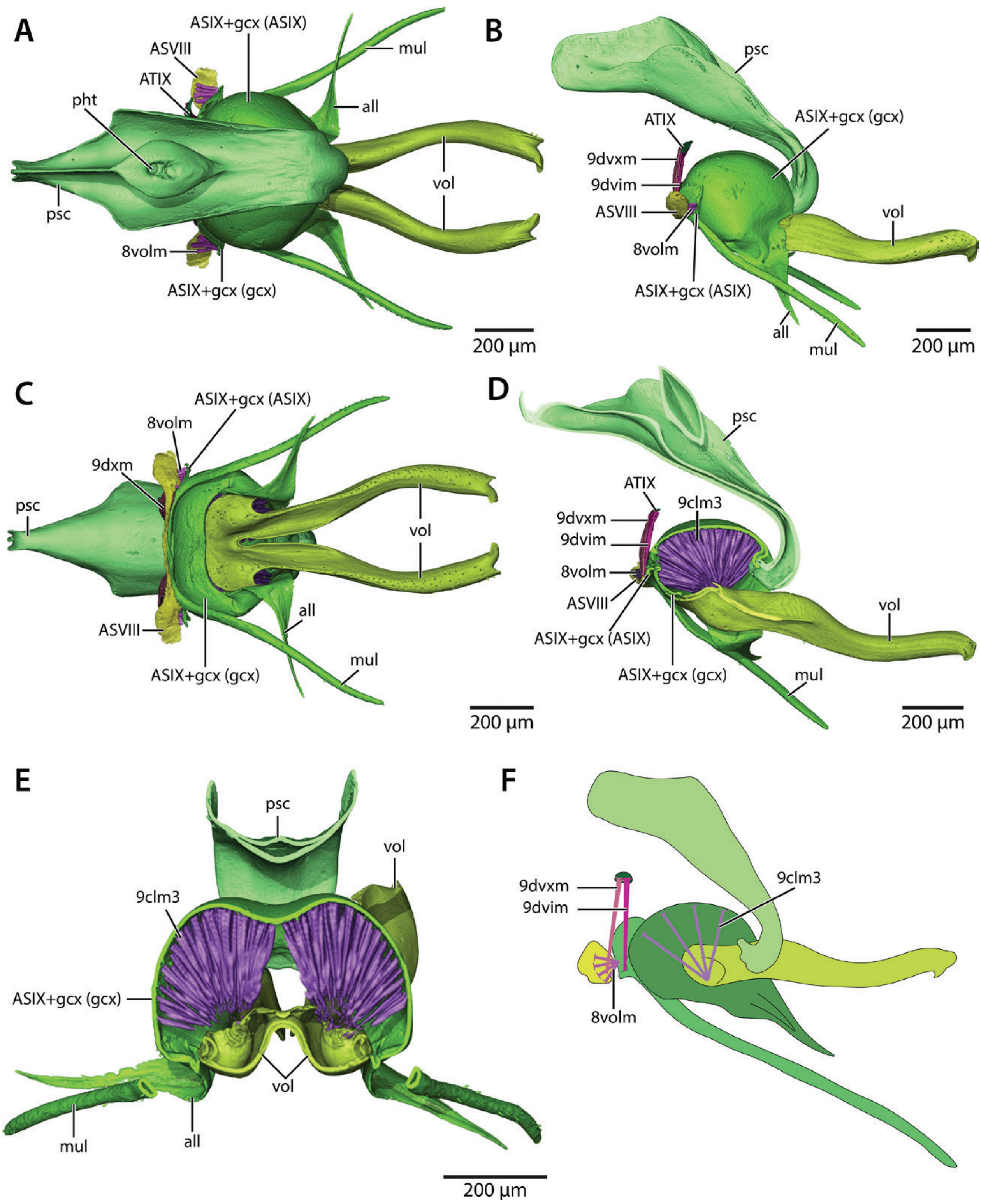

Figure 19. ♂ genitalia of *Leptanilla* zhg-my02 (CASENT0106416), 3D reconstructions (A–E) and summary diagram (F). Orthogonal caps at end of diagrammatic muscle lines signify origin; lack of caps, insertion. **A** dorsal view. **B** ventral view. **C** profile view. **D** sagittal cross-section. **E** transverse cross-section. **F** genital musculature, sagittal cross-section. Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; mul = mulceator; ATIX = abdominal tergite IX; gcx = gonocoxite; all = apicolateral lamina; vol = volsella; psc = penial sclerites; pht = phallotreme; 8volm = ventral ortholateral muscles VIII–IX; 9dvxm = dorsoventral extrinsic muscles IX–VIII; 9dvim = dorsoventral intrinsic muscles IX; 9clm3 = medial extrinsic coxo-lateropenital muscles.

Leptanilla zhg-my04 (Fig. 20)

Abdominal sternite VIII (**ASVIII**; Fig. 20A–D) anteroposteriorly compressed medially; antecosta present, not well-developed, abdominal sternite VIII not reduced to antecosta; diverging anterolateral apodemes absent; laterally separate from abdominal tergite VIII; broadly fused to abdominal sternite IX posteriorly (Section 4.4.1.), delimited from abdominal sternite IX by mesal transverse apodeme. Abdominal sternite IX (**ASIX**; Fig. 20A–D) anteroposteriorly compressed, strap-like with posterolateral corners expanded and rounded, narrowing medially along anteroposterior axis; antecosta present medially; antecosta of abdominal sternite IX produced into recurved lateral apodemes; spiculum absent; anterolateral processes absent; posteromedian process absent, abdominal sternite IX with insensible posteromedian fusion to gonocoxites (Section 4.4.2.), fusion forming hairpin-like outline surrounding gonocoxital foramen (possibly cupular; Fig. 4G, Section 4.1.1.); mulceators (**mul**; Fig. 20A–E) present, originating medially to lateral apodeme, lateromedially compressed towards apex. Abdominal tergite IX (**ATIX**; Fig. 20A, C) divided into hemitergites; hemitergites anteroposteriorly compressed. Cerci absent. Cupular condition ambiguous (Section 4.1.1.). Gonopodites with narrow proximomedian fusion to abdominal sternite IX. Gonocoxites (**gcx**; Fig. 20A–E) present, with medial fusion complete, not medially delimited by sulcus, carina, or both; circular gonocoxital foramen present; dorsum enclosing penial sclerites, which are fused to the gonocoxites surrounding the gonocoxital foramen; apicolateral laminae absent. Gonostyli absent (Griebenow, 2021: p. 617) (Section 4.1.1.). Volsellae present, fully articulated to gonocoxites, medially fused by narrow bridge of cuticle 1/3 of length from base; parossiculus and lateropenite insensibly fused; recurved medial processes absent; volsellar apex produced into large, dorsally recurved hook, penial sclerites supported by proximomedial volsellar condyles. Penial sclerites (**psc**; Fig. 20A–E) completely medially fused, with insensible proximal fusion to gonocoxites, fusion surrounding gonocoxital foramen, proximal margin entire, unsculptured, lateromedially compressed along entire length; penial condyles absent; posterior penial processes absent; valvurae absent; endophallic sclerite absent; phallotreme situated apically, not recessed, outline slit-like; penial apex lateromedially compressed, lacking distinct lateral margins, dorsomedian carina present; apical margin entire.

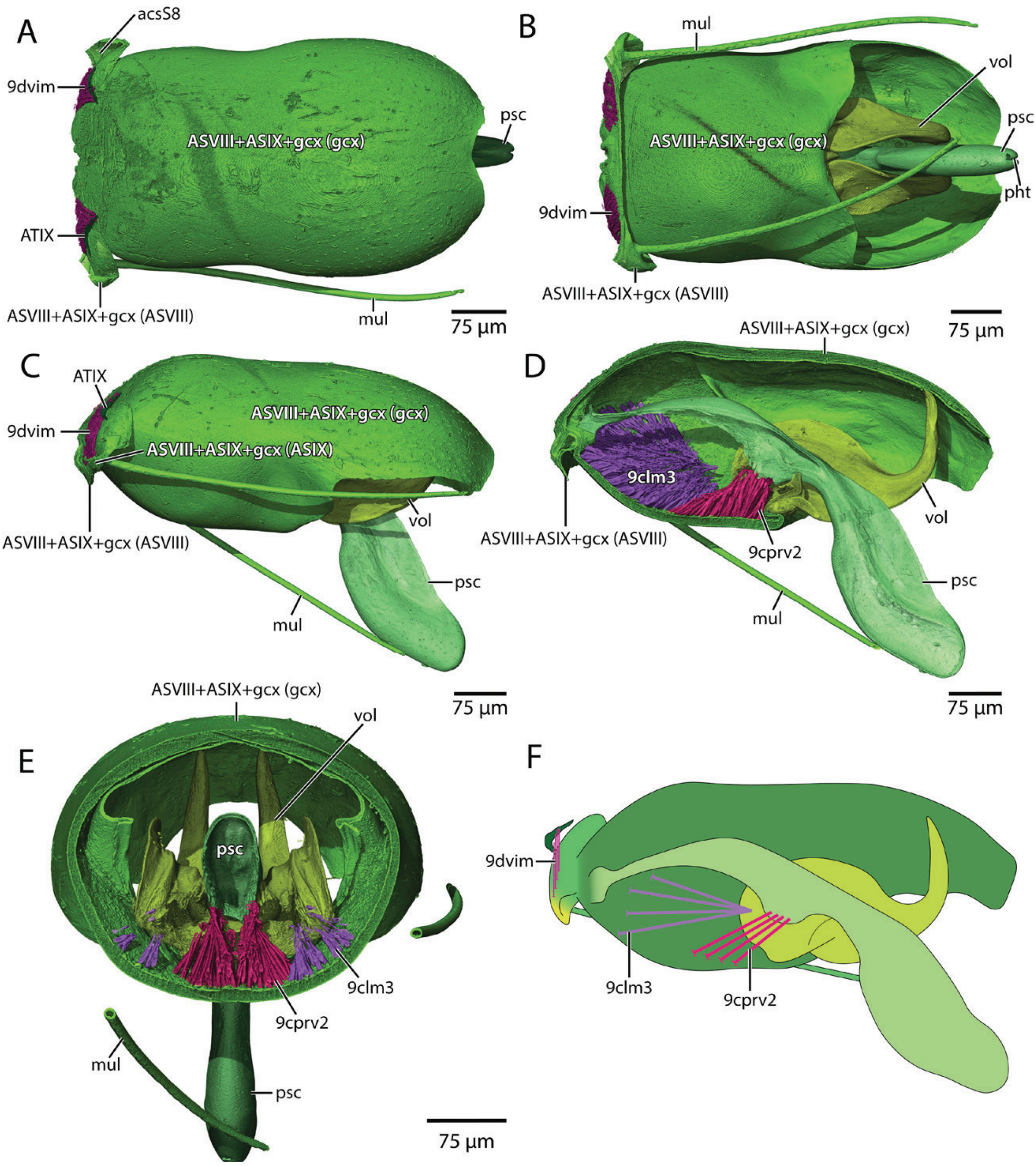

Figure 20. ♂ genitalia of *Leptanilla* zhg-my04 (CASENT0842565), 3D reconstructions (A–E) and summary profile diagram (F). Orthogonal caps at end of diagrammatic muscle lines signify origin; lack of caps, insertion. **A** dorsal view. **B** ventral view. **C** profile view. **D** sagittal cross-section. **E** transverse cross-section. **F** genital musculature, sagittal cross-section. Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; ATIX = abdominal tergite IX; gcx = gonocoxite; mul = mulceator; pht = phallotreme; psc = penial sclerites; vol = volsella; 9dvim = intrinsic dorsoventral muscles IX; 9clm = medial extrinsic coxo-latero-penital muscles; 9cprv2 = lateral ventral coxo-penial remotors.

3.1.7. *Leptanilla* s.str.

Leptanilla zhg-id04 (Fig. 21)

Abdominal sternite VIII (**ASVIII**; Fig. 21A–D) anteroposteriorly compressed, narrowest medially; antecosta not discernible; diverging anterolateral apodemes absent; laterally separate from abdominal tergite VIII; posteriorly separate from abdominal sternite IX. Abdominal sternite IX (**ASIX**; Fig. 21A–D) elongate, moderately narrowing laterally along anteroposterior axis; antecosta not discernible; spiculum absent; diverging anterolateral processes absent; small, obtuse posteromedian process present, not delimited from anterior mesal surface of abdominal sternite IX by transverse carina, separate posteriorly from gonocoxites; mulceators absent. Abdominal tergite IX not discernible. Cerci absent. Cupula absent (Fig. 4K). Gonopodites proximally separate from abdominal sternite IX, articulate. Gonocoxites (**gcx**; Fig. 21A–E) present, with narrow proximal ventromedian fusion (Fig. 29E), otherwise with complete medial articulation; dorsum proximally enclosed by penial sclerites; narrowly fused with penial sclerites along proximal ventromedian face; apicolateral laminae absent. Gonostyli (**stl**; Fig. 21A–E) present, fully articulated to dorsomedial apex of the gonocoxites; not medially fused; apex of each gonostylus bifid, not medially recurved, apical teeth truncate. Volsellae (**vol**; Fig. 21E) present, proximally articulated to gonocoxites; completely medially separate; parossiculus and lateropenite insensibly fused; lamellate, unsculptured, not medially recurved; recurved medial processes absent. Penial sclerites (**psc**; Fig. 21A–E) medially fused, without ventromedian carina; narrowly fused to gonocoxites at proximal margin, proximal margin entire, with a proximomedian foramen; dorsoventrally compressed at base, unsculptured; penial condyles absent; posterior penial processes present distolaterad proximal margin, obtusely rounded; valvurae absent; endophallic sclerite absent; phallotreme distodorsal, not recessed, outline subcircular; penial apex dorsoventrally compressed, laminate, unsculptured, margin entire, lateral margins converging.

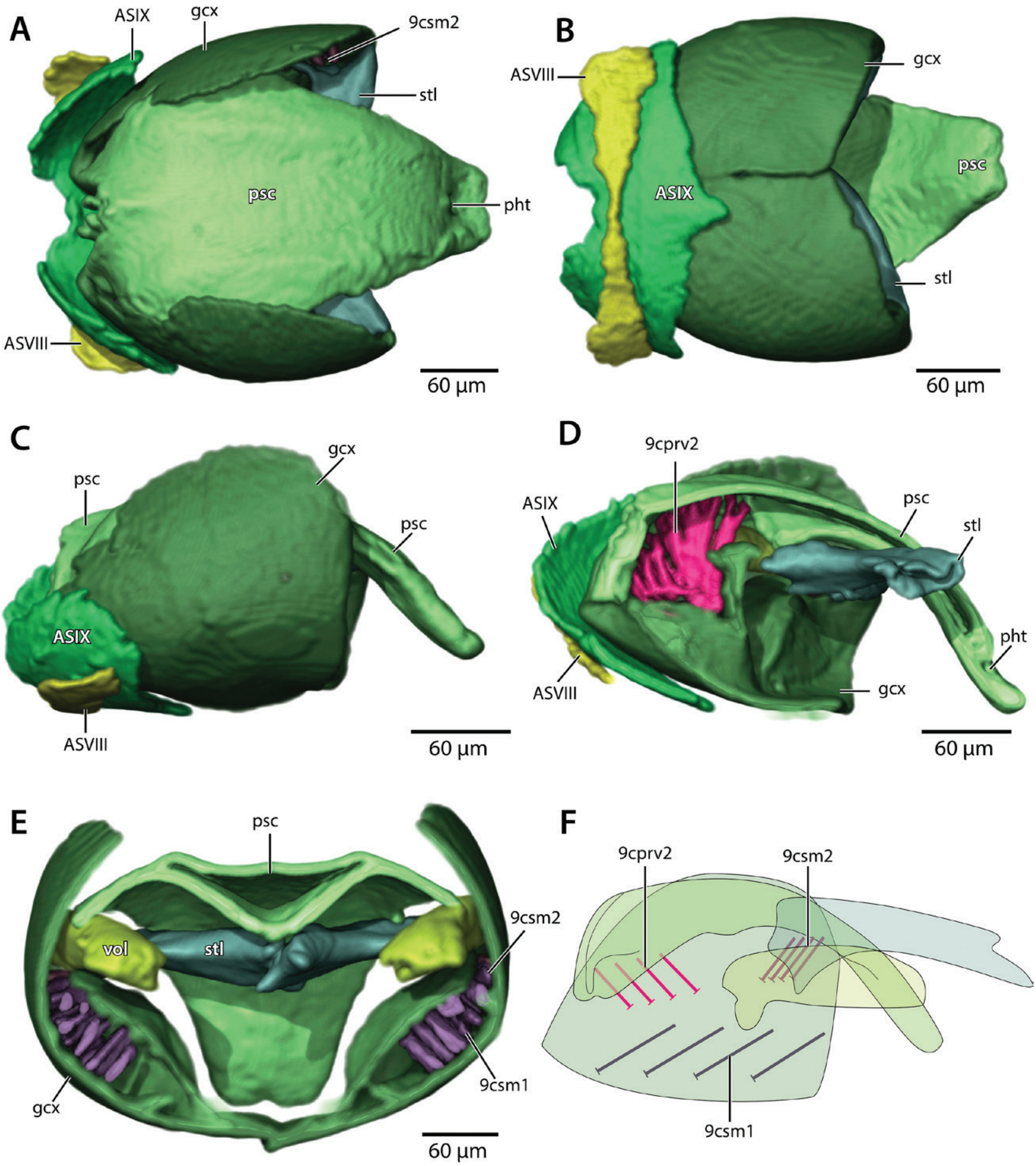

Figure 21. ♂ genitalia of *Leptanilla* zhg-id04 (CASENT0106357), 3D reconstructions (A–E) and summary diagram (F). Orthogonal caps at end of diagrammatic muscle lines signify origin; lack of caps, insertion. **A** dorsal view. **B** ventral view. **C** profile view. **D** sagittal cross-section. **E** transverse cross-section. **F** genital musculature, external profile view. Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; gcx = gonocoxite; pht = phallotreme; psc = penial sclerites; stl = gonostylus; vol = volsella; 9csm1 = anterior coxo-stylar muscle; 9csm2 = intermediate coxo-stylar muscle; 9cprv2 = lateral ventral coxo-penial remotors.

***Leptanilla* cf. *zaballosi* (Fig. 22)**

Abdominal sternite VIII present, posteriorly separate from abdominal sternite IX, but not discernible *in toto*. Abdominal sternite IX (**ASIX**; Fig. 22A–D) elongate, moderately narrowing laterally along anteroposterior axis; antecosta absent; spiculum absent; diverging anterolateral processes absent; small, obtuse posteromedian process present, not delimited from anterior mesal surface of abdominal sternite IX by transverse carina, posteriorly distinct from gonocoxites; mulceators absent. Abdominal tergite IX not discernible. Cerci absent. Cupula absent. Gonopodites proximally separate from abdominal sternite IX, articulate. Gonocoxites (**gcx**; Fig. 22A–E) present, without median fusion; dorsum proximally enclosing penial sclerites; fully articulated to penial sclerites (**psc**; Fig. 22A–E); apicolateral laminae absent from gonocoxites. Gonostyli (**stl**; Fig. 22B–E) present, fully articulating with dorsomedial apices of the gonocoxites; not medially fused; apex of each gonostylus entire, tapering, somewhat medially recurved. Volsellae (**vol**; Fig. 22D, E) present, proximally articulated to gonocoxites; completely medially separate; parossiculus and lateropenite insensibly fused; falcate, not dorsoventrally compressed, proximal 1/6 of length recurved ventrolaterad relative to proximodistal axis of genitalia; recurved medial processes absent. Penial sclerites (**psc**; Fig. 22A–D) medially fused, with ventromedian carina; posterior penial processes (**ppp**; Fig. 22D) present, broad, and dicondylic, articulating narrowly with gonocoxites; proximal condyle obtuse; distal condyle (**ppp2**; Fig. 22D) tapering; proximal margin entire, without proximomedian foramen; dorsoventrally compressed at base, unsculptured; valvurae absent; endophallic sclerite absent; phallotreme distodorsal, not recessed, outline elliptical; penial apex dorsoventrally compressed, laminate, margin entire, lateral margins converging.

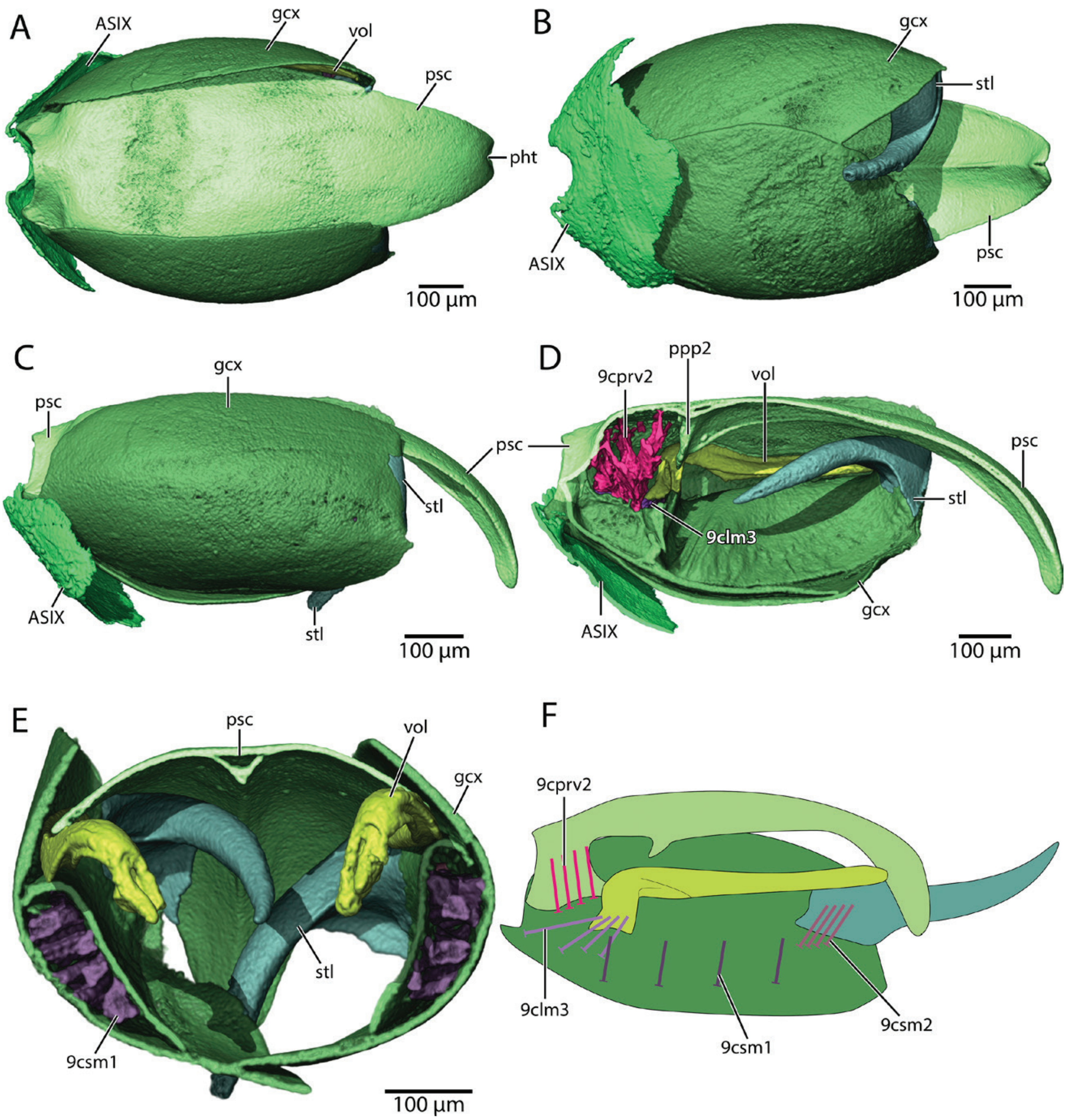

Figure 22. ♂ genitalia of *Leptanilla* cf. *zaballosi* (CASENT0842782), 3D reconstructions (A–E) and summary diagram (F). Orthogonal caps at end of diagrammatic muscle lines signify origin; lack of caps, insertion. **A** dorsal view. **B** ventral view. **C** profile view. **D** sagittal cross-section. **E** transverse cross-section. **F** genital musculature, sagittal cross-section. Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; gcx = gonocoxite; pht = phallotreme; ppp = posterior penial process; psc = penial sclerites; stl = gonostylus; vol = volsella; 9csm1 = anterior coxo-stylar muscles; 9csm2 = intermediate coxo-stylar muscles; 9clm3 = medial extrinsic lateropenital muscles; 9cprv2 = lateral ventral coxo-penial remotors

3.2. Musculature

3.2.1. Summary

As in Section 3.1.1., the following summarizes the totality of muscular variation in the male genitalia of the Formicidae, based upon previous literature (Boudinot 2013) and the findings described in the present study. This summary of genital musculature includes the intrinsic dorsoventral muscles IX, extrinsic dorsoventral muscles VIII–IX and ventral longitudinal muscles VIII–IX but excludes dorsal longitudinal muscles VIII–IX and intrinsic dorsoventral muscles VIII.

Ventral longitudinal muscles VIII–IX (8vlm) originate on abdominal sternite VIII and insert on abdominal sternite IX. These include the ventral longitudinal orthomedial (**8vomm)**, paramedial (**8vpmm**) and ortholateral (**8volm**) muscles. The ventral paramedial muscles VIII–IX (**8vpmm**) originate on abdominal sternite VIII posterior to their insertion on abdominal sternite IX and are therefore reversed in position relative to the orthomedial and -lateral ventral longitudinal muscles**.** In many cases sampled in this study, these subsets of 8vlm cannot be distinguished. Intrinsic dorsoventral muscles IX (**9dvim**) originate on abdominal tergite IX (**ATIX**) and insert on abdominal sternite IX; extrinsic dorsoventral muscles IX–VIII (**9dvxm**) originate on abdominal tergite IX and insert on abdominal sternite VIII. Median sterno-coxal muscles (**9vcm1–2**; a, b; M. sterno-coxalis antero-, posteromedialis) and lateral sterno-coxal muscles (**9vcm3**; c; M. sterno-coxalis lateralis) originate on abdominal sternite IX and insert on the cupula (**cup**); 9vcm1 (a) are paired, originating on the anterior end of the spiculum (**spc**) and inserting on the anteroventral margin of the cupula (**cup**); 9vcm2 (b) is unpaired, originating posteriorly or around the longitudinal midpoint of abdominal sternite IX, sometimes on a transverse carina or lamella ("cranial apodeme", Boudinot 2013: 38), and inserting on the ventromedian margin of the cupula (**cup**); 9vcm3 (c) are paired, originating on anterolateral projections of abdominal sternite IX, inserting on the anteroventral margin of the cupula (cup), anterad the insertions of 9vcm1. Tergo-coxal muscles (**9dcm1**–**4**; g, f, e, d; M. tergo-coxalis dorsalis, dorsolateralis, ventrolateralis, and ventralis) originate on the cupula (**cup**) and insert on the gonocoxites (**gcx**), of which 9dcm1–3 (g, e, f) are paired; 9dcm4 may be paired or unpaired. The coxo-stylar muscles (**9csm**, M. coxo-stylalis) originate within the gonocoxite (**gcx**) and insert within the gonostylus (**stl**); these are rarely divided into a proximal, intrinsic (**9csm1**, M. coxo-stylalis anterior) and intermediate, extrinsic (**9csm2**; t; M. coxo-stylalis intermedialis) subsets, with the anterior subset inserting on the mesomedial surfaces of the gonocoxites; note that 9csm2 (t) is termed intermediate due to the presence of a third, distal coxo-stylar muscle in outgroup taxa (9csm3, u). Lateral intrinsic coxo-lateropenital muscles (**9clm2**, M. coxo-lateropenitalis interior lateralis; qr) and medial extrinsic coxo-lateropenitals (**9clm3**, M. coxo-lateropenitalis exterior medialis; p) originate on the medial surfaces of the parossiculus (**prs**) and gonocoxites, respectively. 9clm2 always insert on the mesal surfaces of the volsellae, while 9clm3 may insert mesally or ectally on the parossiculus; very rarely the origin of 9clm3 shifts in part to the penial sclerites (**psc**). Lateral extrinsic coxo-lateropenital muscles (**9clm4**, M. coxo-lateropenitalis exterior lateralis) originate distally on the gonocoxite and insert anterad their origin on the proximal part of the volsella; these muscles are only rarely present. Dorsal coxo-penial promotors (**9cppd**, j; M. coxo-penialis promotor dorsalis) originate on the mesal distodorsal surfaces of the gonocoxites, inserting on anterodorsal surfaces of the valvurae, anterad their origin. Medial dorsal coxo-penial remotors (**9cprd1**, k; M. coxo-penialis remotor dorsalis medialis) originate on the gonocoxites (**gcx**) medial to origin of 9cppd, and insert distally on mesal surfaces of the penial sclerites (**psc**); lateral dorsal coxo-penial remotors (**9cprd2**, l; M. coxo-penialis remotor dorsalis lateralis) originate distomesally on the gonocoxite near the gonostylar articulation, or on the dorsomedial mesal surfaces of the gonostyli at the proximal margin, inserting distad the insertions of 9cprv2 (i), sometimes on a penial apodeme resembling the ergot of symphytan Hymenoptera (e.g., Schulmeister 2001). Ventral coxo-penial promotors (**9cppv1**, h, **–2**; M. coxo-penialis promotor ventralis anterior, posterior) insert on the proximoventral surfaces of the valvurae; **9cppv1** originate on the ventromesal surface of the cupula (cup), while **9cppv2** originate on the ventromesal surfaces of the gonocoxites (**gcx**). Ventral coxo-penial remotors (**9cprv2**, i; *M. coxo-penialis remotor ventralis lateralis*) originate on the proximoventral mesal surfaces of the gonocoxites (**gcx**), and insert on the proximolateral surfaces of the penial sclerites.

3.2.2. Outgroup taxa (Figs 5–11)

Ventral longitudinal muscles AVIII–IX: 8vomm, ventral orthomedial muscles. Present (*Odontomachus* indet.) or absent. **O**: narrowly on ASVIII, anteromediad O: 8vpmm. **I**: narrowly on ASIX at the anterior apex of the spiculum. **8vpmm**, ventral paramedial muscles. **O**: broadly on median or lateral surface of ASVIII. **I**: narrowly or broadly on ventral surfaces of anterolateral extremities of ASIX. **8volm**, ventral ortholateral muscles. **O**: broadly or narrowly on mesal surfaces of anterolateral margins or apodemes of ASVIII. **I**: broadly on anterolateral margins of ASIX, posterad anterolateral apodemes of ASIX, if present (*Lioponera* indet.).

Dorsoventral muscles AVIII: 8dvxm, dorsoventral extrinsic muscles VIII–IX. Present (*Odontomachus* indet.) or absent. **O**: broadly on dorsolateral margins of ATVIII. **I**: narrowly on anterolateral corners of ASIX.

Dorsoventral muscles AIX: 9dvim, dorsoventral intrinsic muscles IX. **O**: narrowly or broadly on anterolateral margin of ATIX. **I**: narrowly or broadly on mesal surfaces of anterolateral processes of ASIX.

Sterno-coxal muscles IX: **9vcm1** (a), anteromedial sterno-coxal muscles. **O**: narrowly on anterior apex of spiculum, or along lateral edges of spiculum (*Myrmica ruginodis*). **I**: broadly on anteroventral surfaces of cupula, or narrowly on anteroventral rim of cupula. **9vcm2** (b), **O**:

broadly on posteromesal surface of ASIX, or on mesal surface of ASIX near middle of anteroposterior length (*M. ruginodis*). **I**: narrowly or broadly on the ectal ventral surface of the cupula, or posterior margin of spiculum and antecosta of ASIX laterad spiculum (*M. ruginodis*). **9vcm3** (c), present or absent (*Odontomachus* indet.). **O**: broadly on lateromesal surface of ASIX (*Odontomachus* indet.), or on anterior margins of diverging anterolateral processes of abdominal sternite IX (*Lioponera* indet.). **I**: broadly on anteroventral rim of cupula.

Tergo-coxal muscles IX: 9dcm1 (g), dorsal tergo-coxal muscles. **O**: broadly on posterodorsal margin of cupula (*Odontomachus* indet.) or dorsomedian mesal surface of cupula. **I**: broadly on posterodorsal surfaces of the gonocoxites, or narrowly on anterodorsal edge of the anterior gonocoxital margin (*Myrmica ruginodis*). **9dcm2** (f), dorsolateral tergo-coxal muscles. **O**: broadly on mesal dorsolateral or anterior (*Lioponera* indet.) surface of cupula, in *Myrmica ruginodis* partially overlapping O:9dcm1. **I**: narrowly or broadly on proximal margins of the gonocoxites. **9dcm3**), ventrolateral tergo-coxal muscles. **O**: broadly on anteromesal or ventrolateral (*Myrmica ruginodis*) mesal surfaces of the cupula. **I**: broadly on ventro-ectal margins of the gonocoxites, or (*Myrmica ruginodis*) more narrowly on the anterodorsal edges of the proximal processes of the gonocoxites, thus muscles triangular and transverse in orientation. **9dcm4** (d), ventral tergo-coxal muscles. Absent or present (*Myrmica ruginodis*). **O**: ventromedially on the cupula, ventromediad O:9dcm3, **I**: on the anterior surfaces of the proximal processes of the gonocoxites, ventromediad 9dcm3.

Coxo-stylar muscles: 9csm2 (t), intermediate coxo-stylar muscles. Present or absent (*Lioponera* indet.) **O**: broadly on distal margins of the gonocoxites, or partly slightly beyond (*Myrmica ruginodis*). **I**: narrowly on anterior mesal surface of the gonocoxites (*Odontomachus* indet.) or (*Myrmica ruginodis*) distodorsally on the mesomedial surfaces of the gonostyli.

Coxo-lateropenital muscles: **9clm2** (qr), lateral intrinsic coxo-lateropenital muscles. Absent or present (*Myrmica ruginodis*). **O**: at the junctions of the distoventral gonocoxites and the proximoventral parossiculi, **I**: on the mesal surfaces of the parossiculi, slightly distad (and mesad) I:9clm3. **9clm3** (p), medial extrinsic coxo-lateropenital muscles. **O**: one bundle, broadly on ventromesal or (*Lioponera* indet.) dorsomesal surfaces of the gonocoxites **I**: on parossiculi or (*Lioponera* indet.) narrowly on ectal surface of volsellae. **9clm4** (o), lateral extrinsic coxo-lateropenital muscles. Present or absent (*Lioponera* indet.). **O:** broadly on ventral dorsal surfaces of the gonopodites. **I:** narrowly on ectal surfaces of the proximal volsellar apices.

Dorsal coxo-penial promotors: **9cppd** (j). **O**: broadly on the dorsomesal surfaces of the gonopodites **I**: narrowly on posterior apices of the valvurae.

Dorsal coxo-penial remotors: **9cprd1** (k), medial dorsal coxo-penial remotors. **O**: on proximodorsal surfaces of gonocoxites. **I**: broadly on mesal surfaces of the penial sclerites, sometimes (*Myrmica ruginodis*) bundles located intrinsic to penial sclerites, divided by medial sclerotic septum. **9cprd2** (l), lateral dorsal coxo-penial remotors. Present or absent (*Odontomachus* indet.) **O**: broadly on dorsomesal surfaces of the gonopodites. **I**: narrowly on the ventro-ectal surfaces of the penial sclerites.

Ventral coxo-penial promotors: **9cppv1** (h), anterior ventral coxo-penial promotors. **O**: broadly on mesal ventromedian surface of the cupula, or (*Myrmica ruginodis*) on the gonocoxital arms. **I**: at apices of the valvurae. **9cppv2**, posterior ventral coxo-penial promotors. Present or absent (*Lioponera* indet.). **O**: broadly on mesal ventral surfaces of the gonocoxites. **I**: narrowly distad I: 9cppv1. **I**: apically on the ectal surfaces of the valvurae, laterad apical parts of I:9cppv1.

Ventral coxo-penial remotors: **9cprv2** (i), lateral ventral coxo-penial remotors. **O**: broadly on mesal surfaces or (*Odontomachus* indet.) proximolateral margins of the gonocoxites. **I**: broadly on the bases of the valvurae, or (*Lioponera* indet.) broadly along margin of the lateral posterior penial processes, proximad and ventrad I: 9cprd2.

3.2.3. *Protanilla*

Protanilla zhg-vn01 (Fig. 14)

Dorsoventral muscles AIX: **9dvim**, dorsoventral intrinsic muscles. **O**: narrowly on anterior margin of abdominal hemitergites IX. **I**: narrowly on anterolateral corners of ASIX.

Sterno-coxal muscles: **9vcm1** (a), anteromedial sterno-coxal muscles. **O**: on anterior half of spiculum. **I**: posterolaterally on cupula. **9vcm2** (*b*), posteromedial sterno-coxal muscles. **O**: on posterior margin of cupula. **I**: posterolaterally on disc of ASIX.

Tergo-coxal muscles: **9dcm4** (d), ventral tergo-coxal muscles. Unpaired. **O**: widely on cupula, **I**: on the ectal anteroventral surfaces of the gonocoxites.

Coxo-lateropenital muscles: **9clm2** (qr), lateral intrinsic coxo-lateropenital muscles. **O**: at base of parossiculi. **I**: narrowly basad the base of the lateropenite. **9clm3** (p), medial extrinsic coxo-lateropenital muscles. **O**: broadly on posterolateral mesal surfaces of the gonocoxites. **I**: narrowly basad the base of the lateropenites, adjacent to I: 9clm2.

Dorsal coxo-penial promotors: **9cppd** (j). **O**: on the mesal anterodorsal surfaces of the gonocoxites. **I**: broadly on anterodorsal surfaces of valvurae.

Dorsal coxo-penial remotors: **9cprd1** (k), medial dorsal coxo-penial remotors. **O**: on gonocoxites, mediad O: 9cppd. **I**: broadly on mesal surfaces of the penial sclerites.

Ventral coxo-penial promotors: **9cppv1** (h), anterior ventral coxo-penial promotors. **O**: on mesal proximoventral surfaces of the gonocoxites, proximomediad O:9cprv2. **I**: narrowly on ventral surfaces of the proximal apices of the valvurae.

Ventral coxo-penial remotors: **9cprv2** (i), lateral ventral coxo-penial remotors. **O**: on the mesal proximoventral surfaces of the gonocoxites, **I**: broadly on ectal ventral surfaces of the penial sclerites, at and distal to the base of valvurae.

3.2.4. *Yavnella*

Yavnella zhg-bt01 (Fig. 15)

Coxo-lateropenital muscles: **9clm3** (p), medial extrinsic coxo-lateropenital muscles. **O:** broadly on posterior and medial mesal surfaces of the gonocoxites. **I**: narrowly at proximoventral margins of the volsellae.
Dorsal coxo-penial remotors: 9cprd1 (k), medial dorsal coxo-penial remotors. **O:** narrowly on the proximodorsal mesal margin of the penial sclerites. **I**: narrowly on proximodorsal margins and distodorsal mesal surfaces of the penial sclerites.

Yavnella zhg-th03 (Fig. 16)

Tergo-coxal muscles: **9dcm4** (d), ventral tergo-coxal muscles. Paired. **O**: narrowly along dorsoventral length of anterior cupular rim (Fig. 27B) (Sections 4.4.1.–4.4.2.). **I**: broadly along mesal surface of cupula.
Coxo-lateropenital muscles: **9clm3** (p), medial extrinsic coxo-lateropenital muscles: **O**: broadly on posterior and medial mesal surfaces of the gonocoxites, along with proximoventral surfaces of the penial sclerites. **I**: narrowly within the volsellae.
Dorsal coxo-penial remotors: **9cprd1** (k), medial dorsal coxo-penial remotors: **O**: on proximodorsal mesal surfaces of the penial sclerites, apical to ventral posterior penial processes. **I**: broadly on distodorsal mesal surfaces of the penial sclerites.

3.2.5. *Scyphodon* s.l.

Noonilla zhg-my03 (Fig. 17)

Dorsoventral muscles AIX: **9dvim**, dorsoventral intrinsic muscles. **O**: narrowly on ATIX. **I**: broadly on most anterior ventral surface of the sterno-gonocoxital complex (ASIX+gcx+psc), anterior to antecosta of ASIX.
Coxo-stylar muscles: **9csm2** (t), intermediate coxo-stylar muscles. **O**: broadly on mesal gonocoxital surface, both dorsally and ventrally. **I**: along median edge of gonostyli.
Ventral coxo-penial remotors: 9cprv2 (i), lateral ventral coxo-penial remotors (Section 4.1.2.). **O**: broadly on mesal proximal surfaces of the gonocoxites, origin forming dorsoventral parabola proximad O: 9csm2. **I**: narrowly on anatomical venter of posterior penial processes.

Noonilla cf. *copiosa* (Fig. 18)

Ventral longitudinal muscles AVIII–AIX: One pair of 8vlm present and extremely reduced, identity uncertain (Section 4.1.2.), here identified as **8volm**, ventral ortholateral muscles. **O**: on medial apodemes of ASVIII. **I**: on apodeme of ASIX near most proximolateral extent of anterolateral processes.
Dorsoventral muscles AIX: **9dvim**, dorsoventral intrinsic muscles. **O**: narrowly on abdominal hemitergites IX. **I**: narrowly on anteromedian region of antecosta ASIX.
Coxo-stylar muscles: 9csm2 (t), intermediate coxo-stylar muscles. **O**: broadly on mesal dorsal surface of sterno-gonocoxital complex, along entire length of sterno-gonocoxital complex. **I**: along median edge of gonostyli.
Dorsal coxo-penial remotors: 9cprd1 (k), medial dorsal coxo-penial remotors (Section 4.1.2.). **O**: broadly on mesal dorsal surface of the sterno-gonocoxital complex, proximomediad O: 9csm2. **I**: narrowly along mesal ventral surfaces of the penial sclerites, at base of ventromedian “trigger.”
Ventral coxo-penial remotors: 9cprv2 (i), lateral ventral coxo-penial remotors (Section 4.1.2.). **O**: broadly along distal third of the mesal ventral surfaces of the gonocoxites. **I**: on the penial sclerites. Medial to bases of gonostyli.

3.2.6. Bornean morphospecies-group

Leptanilla zhg-my02 (Fig. 19)

Ventral longitudinal muscles AVIII–AIX: **8volm**, ventral ortholateral muscles. **O**: on ASVIII and **I:** on ASIX dorsal to bases of mulceators.
Dorsoventral muscles AIX: **9dvim**, dorsoventral intrinsic muscles. **O**: on abdominal hemitergites IX. **I**: mediad I: 8volm. **9dvxm**, dorsoventral extrinsic reversed muscles: **O**: on abdominal hemitergites IX. **I**: on dorsal surfaces of ASVIII.
Coxo-lateropenital muscles: **9clm3** (p), medial extrinsic coxo-lateropenital muscles. **O**: broadly on dorsomesal surfaces of the gonocoxites. **I**: broadly on apical margin of proximal volsellar aperture.

Leptanilla zhg-my04 (Fig. 20)

Dorsoventral muscles AIX: **9dvim**, dorsoventral intrinsic muscles. **O**: along entire lateromedial lengths of abdominal hemitergites IX. **I**: narrowly posterior to antecosta of ASIX, medial to bases of mulceators.
Coxo-lateropenital muscles: **9clm3** (p), medial extrinsic coxo-lateropenital muscles. **O**: broadly on mesal ventral surfaces of the gonocoxites. **I**: narrowly on proximomedian processes of the volsellae.
Ventral coxo-penial remotors: **9cprv2** (i), lateral ventral coxo-penial remotors. **O**: broadly on distomedian mesal surfaces of the gonocoxites. **I**: narrowly on the ventrolateral margins of the penial sclerites, proximad the proximomedial volsellar condyles.

3.2.7. *Leptanilla* s.str.

Leptanilla zhg-id04 (Fig. 21)

Ventral longitudinal muscles AVIII–IX and **dorsoventral intrinsic muscles AIX** not discernible.
Coxo-stylar muscles: **9csm1**, intrinsic coxo-stylar muscles. **O**: broadly on mesolateral surfaces of the gonocoxites. **I**: broadly on mesomedial surfaces of the gonocoxites. **9csm2** (*t*), intermediate coxo-stylar muscles. **O**: on the distal mesolateral surfaces of the gonocoxites. **I**: narrowly at proximoventral margins of gonostyli.

Ventral coxo-penial remotors: **9cprv2** (i), lateral ventral coxo-penial remotors. **O**: narrowly on mesal proximomedian apodemes of the gonocoxites. **I**: broadly on mesal proximal surfaces of the penial sclerites.

Leptanilla cf. *zaballosi* (Fig. 22)

Ventral longitudinal muscles AVIII–IX: One pair of 8vlm present, identity indeterminate between 8vomm, 8vpmm, 8volm, but likely not 8vpmm.
Dorsoventral intrinsic muscles AIX not discernible.
Coxo-stylar muscles: **9csm1**, intrinsic coxo-stylar muscles. **O**: broadly on mesolateral surfaces of the gonocoxites. **I**: broadly on mesomedial surfaces of the gonocoxites. **9csm2** (t), intermediate coxo-stylar muscles. **O**: on the distal mesolateral surfaces of the gonocoxite. **I**: narrowly at proximomedial margins of gonostyli.
Coxo-lateropenital muscles: **9clm3** (p), medial extrinsic coxo-lateropenital muscles. **O**; broadly on ventral proximomesal surfaces of the gonocoxites and on proximoventral surfaces of the penial sclerites. **I**: narrowly on medial surfaces of proximomedial condyles of the volsellae.
Ventral coxo-penial remotors: **9cprv2** (i), lateral ventral coxo-penial remotors. **O**; narrowly on ventromedian apodemes of the gonocoxites. **I**: broadly on mesal proximoventral surfaces of the penial sclerites.

4. Discussion

4.1. Ambiguities

The extremely small size of many of the structures described herein, and the inability to confirm some observations based on micro-CT using manual dissection or SEM, means that the interpretation of these primary observations is sometimes uncertain. Moreover, extreme derivation of male genital skeletomusculature in certain lineages of the Leptanillinae means that assertion of primary homology (de Pinna 1991) can be debatable. While Section 3 described the male genital skeletomusculature of 12 exemplar ants according to what appeared to be the most likely interpretation of these ambiguous aspects, with the awareness that these conclusions are provisional, the following is a list of observations that must be regarded as in need of further study.

4.1.1. Skeletal ambiguity

Axial sclerites. The transverse posterior mesal carina of abdominal sternite IX in *Scyphodon* s.l. may not correspond to the antecosta of abdominal sternite IX, rather being an invagination of abdominal sternite IX derived in *Scyphodon* s.l. independently from the antecosta of abdominal sternite IX that is plesiomorphic for the Formicidae, which appears to have been ancestrally lost in male Leptanillinae. This reasoning assumes that the antecosta of abdominal sternite IX is sufficiently complex to not be regained once lost (Simpson 1953). Nonetheless, the transverse posterior mesal carina of abdominal sternite IX in *Scyphodon* s.l. is positionally and functionally equivalent to the antecosta of abdominal sternite IX.

While the cupula appears unambiguously present, albeit heavily reduced and fused to adjacent sclerites, in *Leptanilla* zhg-id01 (not fully described; Table 1; Fig. 3), a cupular remnant may also be present in *Leptanilla* zhg-my03 and -my04 in the form of a robust cuticular ridge wrapping around the dorsum of the gonocoxital foramen, and spanning the median fusion between abdominal sternite IX and the gonocoxites (Fig. 4G). In the absence of any sterno-coxal or tergo-coxal musculature with which to confirm this hypothesis, such a homology must be regarded as tentative.

Appendicular sclerites. 1. Petersen (1968) interpreted the paired, articulated distal appendages in *Noonilla copiosa* Petersen, 1968 as volsellae, an interpretation that we contest based upon micro-CT scans from across a broad sampling of *Scyphodon* s.l. The ambiguity arises from the fact that gonostyli and volsellae do not co-occur in any *Scyphodon* s.l. scanned in this study or observed by Petersen. The origins of the coxo-lateropenital and coxo-stylar muscles also have very little utility in identifying these appendages, as a single muscle attaches the gonocoxite to the mesal surface of the appendage, running laterad to the coxo-penial remotors, which, absent other landmarks, could reasonably be either 9clm3 (p) or 9csm2 (t). The mesal insertion on the appendage is also of little use as both 9clm3 (p) and 9csm2 (t) can insert ectally or mesally on the volsella or gonostylus respectively. One suggestive analogy to other leptanillines is that the muscle originates extensively on the mesal surfaces of the gonocoxite, including the ventral, lateral, and dorsal surfaces, a condition observed for 9csm2 (t) in *Leptanilla* s.str. but never for 9clm3 (p). Nevertheless, we observe that these appendages articulate at the distolateral margins of the gonocoxites, a positioning contrary to that observed for the volsellae, which in this study and available literature always articulate medially with the gonocoxites and proximad the distal gonocoxital margins.

2. In *Leptanilla* zhg-my03 and -04, which together are the sister clade to the remainder of the Bornean morphospecies-group, confirmation of gonostylar condition is unfeasible. The gonopodites are completely fused along their entire proximodistal length, forming a capsule without suture. Given the precedent of gonostylar absence in *Leptanilla* zhg-my02 and -my05 established by Griebenow (2021), we here treat the gonostyli as absent in *Leptanilla* zhg-my03 and -my04 but admit the conceivability of the presence of gonostyli in these morphospecies, indistinguishably fused to the gonocoxites. The discovery of morphospecies that present morphological intermediates between the gonopodital condition in *Leptanilla* zhg-my03 + *L.* zhg-my04 and that in exemplars of the Bornean morphospecies-group in which the gonostylus is clearly present (i.e., *Leptanilla* zhg-id01) could disambiguate the condition of the gonopodites in the former lineage.

Conjunctival ambiguity. Relative contrast between sclerite and conjunctiva in micro-CT data is sometimes insufficient to discriminate these forms of the integument from each other. At the gonostylar base, this could sometimes (e.g., *Protanilla*) be disambiguated by external examination (Griebenow 2020: fig. 19D). In many cases, however, such examination or manual dissection was inadvisable, resulting in the following points of interpretive ambiguity:

1. The tergosternal fusion of abdominal segment VIII in *Noonilla* cf. *copiosa* (Fig. 18C, D) can only be assessed with certainty by manual dissection or histology, and since Petersen (1968) did not mention the tergosternal condition of this segment in the description of *N. copiosa*, it is possible that the tergosternal fusion here inferred from micro-CT scans of *Noonilla* cf. *copiosa* is erroneous. Alternatively, this fusion may simply be more pronounced than in the type series of *N. copiosa*.

2. Abdominal sternites VIII–IX may be sternosternally fused in *Leptanilla* zhg-my02 and -my05. The extreme median anteroposterior compression of abdominal sternites VIII-IX, and their adjacency (Fig. 19D), makes it difficult to be certain that the intervening cuticle is conjunctival in form.

3. It is uncertain if the endophallic sclerite is indeed absent in *Odontomachus* indet., as opposed to present but weakly developed. The endophallic sclerite is widely reported in the Formicidae (Marcus 1953; Forbes 1954; Hagopian 1963; Trakimas 1967; Shyamalanath and Forbes 1983; Ball and Vinson 1984) and appears evolutionarily labile, but has not been included in any comprehensive anatomical or morphological survey of male ant genitalia. To our knowledge, the condition of the endophallic sclerite has never been examined in the Ponerinae or even the “poneroids” sensu Moreau and Bell (2013). Therefore, the condition in *Odontomachus* cannot be predicted based upon other, more readily observable characters, nor extrapolated from observations of related poneroids. It is possible that this sclerite is present in *Odontomachus* but poorly developed, such that contrast of the micro-CT scans was insufficient to differentiate it from the adjacent membranous endophallus.

4.1.2. Muscular ambiguity

The homology of the penial muscles present in *Scyphodon* s.l. is open to debate since the reduction of the penial sclerites in this clade removes topological points of reference necessary for the assertion of primary homology. This is likewise the case for the ventral longitudinal muscles VIII–IX in *Noonilla* cf. *copiosa*. In both instances, homologies were inferred based on our best judgment given the limited information available.

4.2. Overview and phylogenetic context

A pronounced tendency towards skeletomuscular simplification is apparent in the Leptanillinae relative to the remainder of the Formicidae (Figs 23–27; Table 3). This trend is most striking in the Leptanillini s.str. but is also applicable to *Protanilla* zhg-vn01, in which the coxo-stylar muscles and three out of four tergo-coxal muscles are absent.

Several of these skeletal or muscular simplifications are homoplasious. The intermediate coxo-stylar muscles (9csm2, t) are lost in *Protanilla* zhg-vn01, the Bornean morphospecies-group and *Yavnella*; concomitantly, the gonopodite is fully to partly inarticulate in all these lineages, while in the remaining sampled lineages the presence of the intermediate coxo-stylar muscles is always associated with articulated gonopodites. It can be inferred that the intermediate coxo-stylar muscles are absent in all *Yavnella* and members of the Bornean morphospecies-group, and may be absent in many, if not all, male *Protanilla*. The gonostyli themselves have been lost on four different occasions in the tribe Leptanillini s.str.: once in *Yavnella* (*Yavnella* TH03), twice in the Bornean morphospecies-group (*Leptanilla* zhg-my03 + *L.* zhg-my04 and *L.* zhg-my02 + *L.* zhg-my05), and in *Leptanilla santschii* Wheeler and Wheeler (Wheeler and Wheeler 1930; Petersen 1968). The extrinsic medial coxo-lateropenital muscles (9clm3, p) were lost at least twice within the Leptanillini s.str., while the medial dorsal coxo-penial remotors (9cprd1, k) are retained within the sampled Leptanillini s.str. in *Noonilla* cf. *copiosa*, implying independent losses of this muscle pair in *Leptanilla* s.str. and the Bornean morphospecies-group.

In terms of scleritic simplification, there is a tendency towards median fusion of paired structures. In addition to the synapomorphic fusion of the penial sclerites in Leptanillini s.str., the gonocoxites are medially fused along their entire anteroposterior length in the Bornean morphospecies-group and *Scyphodon* s.l., and partial gonocoxital fusion is observed in *Yavnella*; while the complete medial fusion of the volsellae is an autapomorphy of the Bornean morphospecies-group, observed nowhere else in male Formicidae. The medial fusion of the gonostyli in *Noonilla* zhg-my03 is apparently unique to that morphospecies throughout the entire Hymenoptera, providing a serial parallel to the medial fusion of the volsellae in the Bornean morphospecies-group. The apparent tergosternal fusion of abdominal segment VIII in *Noonilla* cf. *copiosa* (see Section 4.4.1.) is unique among the Hymenoptera.

Anteroposterior fusion of sclerites is also a notable tendency. Abdominal sternite IX is at least partly fused to the gonocoxites in all sampled representatives of *Scyphodon* s.l. and the Bornean morphospecies-group, with this fusion probably being homoplasious between the two clades (Section 4.4.2.). The fusion of abdominal sternite IX to the gonocoxites was confirmed by manual dissection only in *N. copiosa* (Petersen 1968) but is unambiguous based on micro-CT scans obtained among *Scyphodon* s.l. and the Bornean morphospecies-group. Complete posterior fusion of abdominal sternite VIII to abdominal sternite IX has evolved at least twice in the Leptanillini s.str. (Sections 4.1.1., 4.4.1.). Another case of homoplasy is the partial fusion of the penial sclerites to the gonocoxites in *Opamyrma hungvuong* Yamane et

Table 3. Muscular observations across the 12 exemplars described in detail in this study. 1 = presence; 0 = absence; — = inapplicable (sclerite hosting muscle origin or insertion absent).

1°			**8vomm**	**8vpmm**	**8volm**	**8dvxm**	**9dvim**	**9dvxm**	**9vcm1**	**9vcm2**	**9vcm3**	**9dcm1**	**9dcm2**	**9dcm3**	**9dcm4**	**9csm1**	**9csm2**	**9clm2**	**9clm3**	**9clm4**	**9cppd**	**9cppv1**	**9cppv2**	**9cprd1**	**9cprd2**	**9cprv2**
Boulangé (1924); Schulmeister (2001, 2003)			—	—	—	—	—	—	*a*	*b*	*c*	**g**	**f**	**e**	**d**	—	**t–w**	**qr**	**p**	**o**	**j**	**h**	**h'**	**k**	**l**	**i**
Subfamily	**Specimen**	**Exemplar**																								
Dorylinae	CASENT0844684	*Lioponera* indet.	0	1	1	0	1	0	1	1	1	1	1	1	0	0	0	0	1	1	1	1	0	1	1	1
Myrmicinae	PMJ:Hex:2205	*Myrmica ruginodis*	0	1	1	0	1	0	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1
Ponerinae	CASENT0842842	*Odontomachus* indet.	1	1	1	1	1	0	1	1	0	1	1	1	0	0	1	0	1	0	1	1	1	1	0	1
Leptanillinae	CASENT0842782	*Leptanilla* cf. *zaballosi*	?	?	?	?	?	?	—	—	—	—	—	—	—	1	1	0	1	0	0	0	0	0	0	1
Leptanillinae	CASENT0106357	*Leptanilla* zhg-id04	?	?	?	?	?	0	—	—	—	—	—	—	—	1	1	0	0	0	0	0	0	0	0	1
Leptanillinae	CASENT0106416	*Leptanilla* zhg-my02	0	0	1	0	1	1	—	—	—	—	—	—	—	0	—	0	1	0	0	0	0	0	0	0
Leptanillinae	CASENT0842565	*Leptanilla* zhg-my04	0	0	0	0	1	0	—	—	—	—	—	—	—	0	—	0	1	0	0	0	0	0	0	1
Leptanillinae	CASENT0842844	*Noonilla* cf. *copiosa*	0	0	1	0	1	0	—	—	—	—	—	—	—	0	1	—	—	—	0*	0*	0*	1*	0*	1*
Leptanillinae	CASENT0842609	*Noonilla* zhg-my03	0	0	0	0	1	0	—	—	—	—	—	—	—	0	1	—	—	—	0*	0*	0*	0*	0*	1*
Leptanillinae	CASENT0106408	*Protanilla* zhg-vn01	?	?	?	0	1	0	1	1	0	0	0	0	1	0	0	1	1	0	1	1	0	1	0	1
Leptanillinae	CASENT0842743	*Yavnella* zhg-bt01	?	?	?	0	0	0	?	?	?	?	?	?	?	0	0	1	1	0	0	0	0	1	0	0
Leptanillinae	CASENT0842741	*Yavnella* zhg-th03	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0

*Homology of the coxo-penial muscles (9cpm) present in *Scyphodon* s. l. tentative (Section 4.1.2).

al., 2008 (Yamada et al. 2020), *Protanilla* zhg-vn01 (Fig. 14), and both sampled *Yavnella* (Figs 15, 16), with complete fusion of the gonocoxites and penial sclerites being observed in *Leptanilla* zhg-my03, -my04 and all sampled *Scyphodon* s.l. (see Section 4.4.5.) (Figs 17–20).

Although these homoplasies appear straightforward at a coarse comparative scale, further examination may show noteworthy functional differences. An example is the parallel fusion of the penial sclerites to the gonocoxites in *Scyphodon* s.l. and the clade comprising *Leptanilla* zhg-my03 and -4. In both cases, the penial sclerites are musculated by a single muscle pair. In *Leptanilla* zhg-my03 and -my04, the penial sclerites are narrowly but firmly fused to the medially fused gonocoxites at the most proximal penial extremity (Fig. 19D, F), surrounding the gonocoxital foramen (and, perhaps, the foramen genitale; Section 4.4.3.); contraction of the lateral ventral coxo-penial remotors (9cprv2, i) affords limited motion of the penial sclerites relative to the rigid gonocoxital capsule. Conversely, the anterior and venter of the penial sclerites in *Scyphodon* s.l. are broadly fused to the medially fused gonocoxites, forming an inarticulate gonocoxital complex (Figs 17D, F, 18D, F); in these cases, the medial dorsal coxo-penial remotors (9cprd1, k) or lateral ventral coxo-penial remotors (9cprv2, i) move the entire gonocoxital complex relative to the gonostyli.

Based upon the micro-CT data for the 22 exemplars for which micro-CT scans are here published, and physical examination of additional specimens, along with the published description of male *Opamyrma hungvuong* (Yamada et al. 2020), the following synapomorphies can be asserted (Fig. 28). Loss of the spiculum and valvurae, and complete medial fusion of the penial sclerites, are synapomorphies of the Leptanillini s.str. The loss of the spiculum is also observed in some *Leptomyrmex* spp. (Dolichoderinae: Leptomyrmecini) (Barden et al. 2017) and is widespread among symphytan hymenopterans (Schulmeister 2003: fig. 14). The absence of the lateropenites was suggested to be a synapomorphy of the Leptanillinae excluding the former Anomalomyrmini by Boudinot (2015: 33), by which was meant the clade here referred to as the Leptanillini s.str. (*Opamyrma* was at the time still classified in the Amblyoponinae; Yamane et al. 2008); if the distal volsella of the Leptanillini s.str. is indeed homologous with the apex of the parossiculus, this hypothesis is correct, although tests are not possible with present sampling. Loss of the anterior ventral and dorsal coxo-penial promotors (9cppv1, h; 9cppd, j) is also synapomorphic for the Leptanillini s.str., while the loss of the medial coxo-lateropenital muscles is a synapomorphy of *Leptanilla* s.l. Finally, the

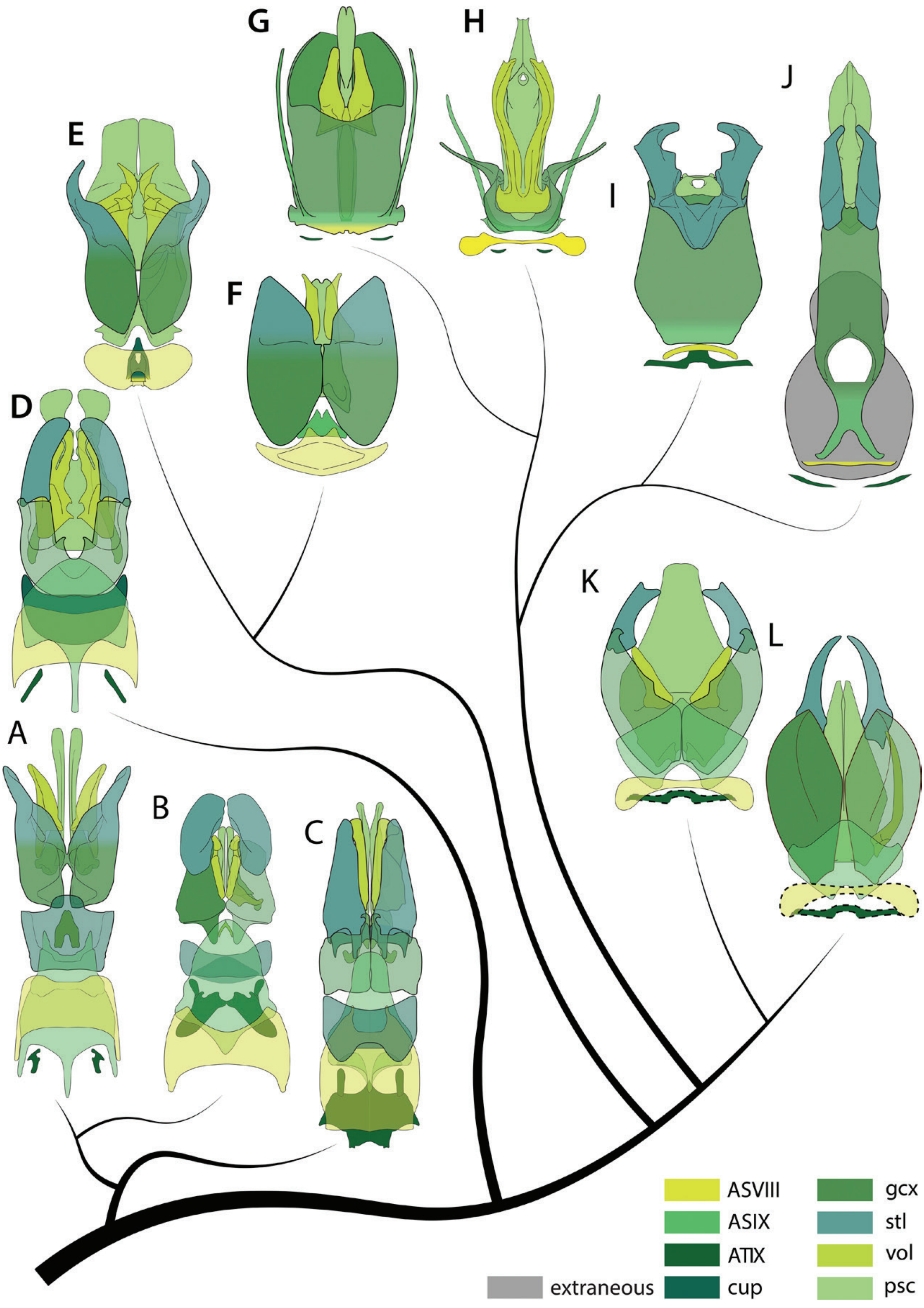

Figure 23. Diagrammatic cladogram of genital and pregenital sclerites, ventral view. Sclerites bounded by dotted lines were indiscernible; those bounded with dotted lines were discernible, but not fully segmented. Extraneous sclerites were beyond the scope of this study. **A** *Lioponera* indet. **B** *Myrmica ruginodis*. **C** *Odontomachus* indet. **D** *Protanilla* zhg-vn01. **E** *Yavnella* zhg-th03. **F** *Yavnella* zhg-bt01. **G** *Leptanilla* zhg-my04. **H** *Leptanilla* zhg-my02. **I** *Noonilla* zhg-my03. **J** *Noonilla* cf. *copiosa*. **K** *Leptanilla* zhg-id04. **L** *Leptanilla* cf. *zaballosi*. Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; ATIX = abdominal tergite IX; cup = cupula; gcx = gonocoxite; psc = penial sclerite; stl = gonostylus; vol = volsella.

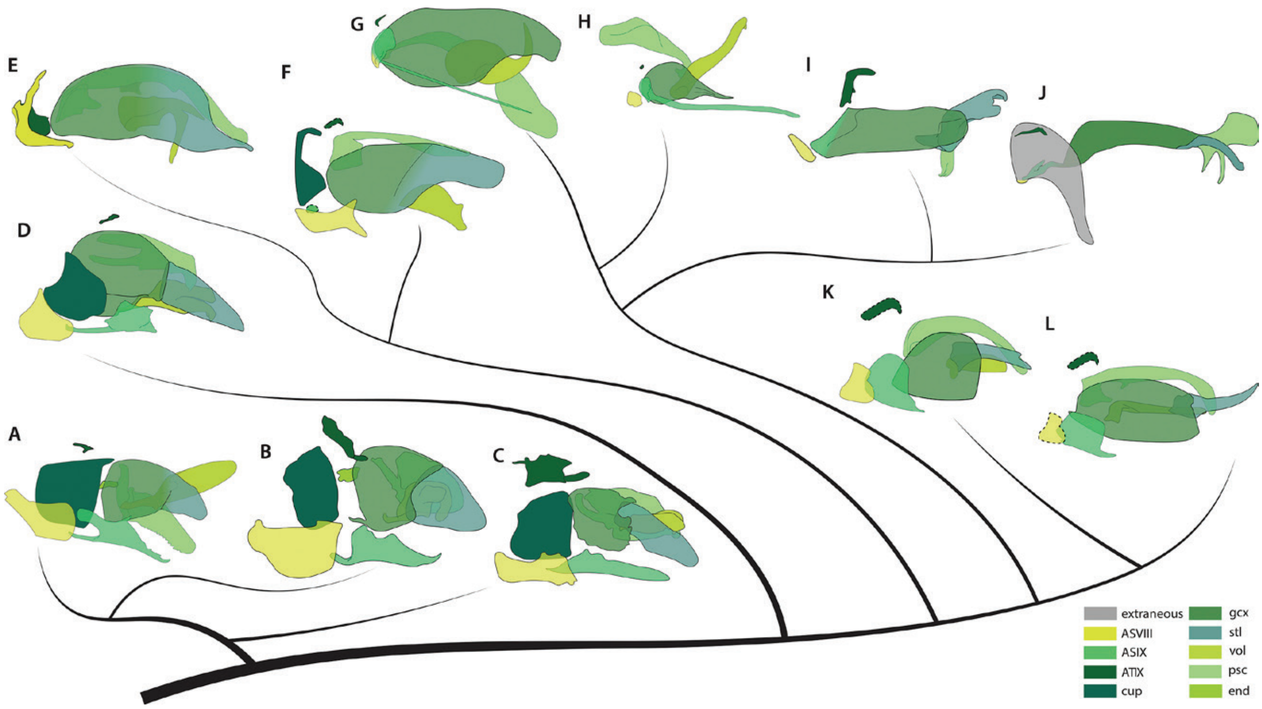

Figure 24. Diagrammatic cladogram of genital and pregenital sclerites of exemplars, profile view. Sclerites bounded by dotted lines were indiscernible; those bounded with dotted lines were discernible, but not fully segmented. Extraneous sclerites were beyond the scope of this study. Abdominal sternite IX of *Noonilla* cf. *copiosa* is rotated 180° relative to in situ position. **A** *Lioponera* indet. **B** *Myrmica ruginodis.* **C** *Odontomachus* indet. **D** *Protanilla* zhg-vn01. **E** *Yavnella* zhg-th03. **F** *Yavnella* zhg-bt01. **G** *Leptanilla* zhg-my04. **H** *Leptanilla* zhg-my02. **I** *Noonilla* zhg-my03. **J** *Noonilla* cf. *copiosa.* **K** *Leptanilla* zhg-id04. **L** *Leptanilla* cf. *zaballosi*. Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; ATIX = abdominal tergite IX; cup = cupula; end = endophallic sclerite; gcx = gonocoxite; psc = penial sclerite; stl = gonostylus; vol = volsella.

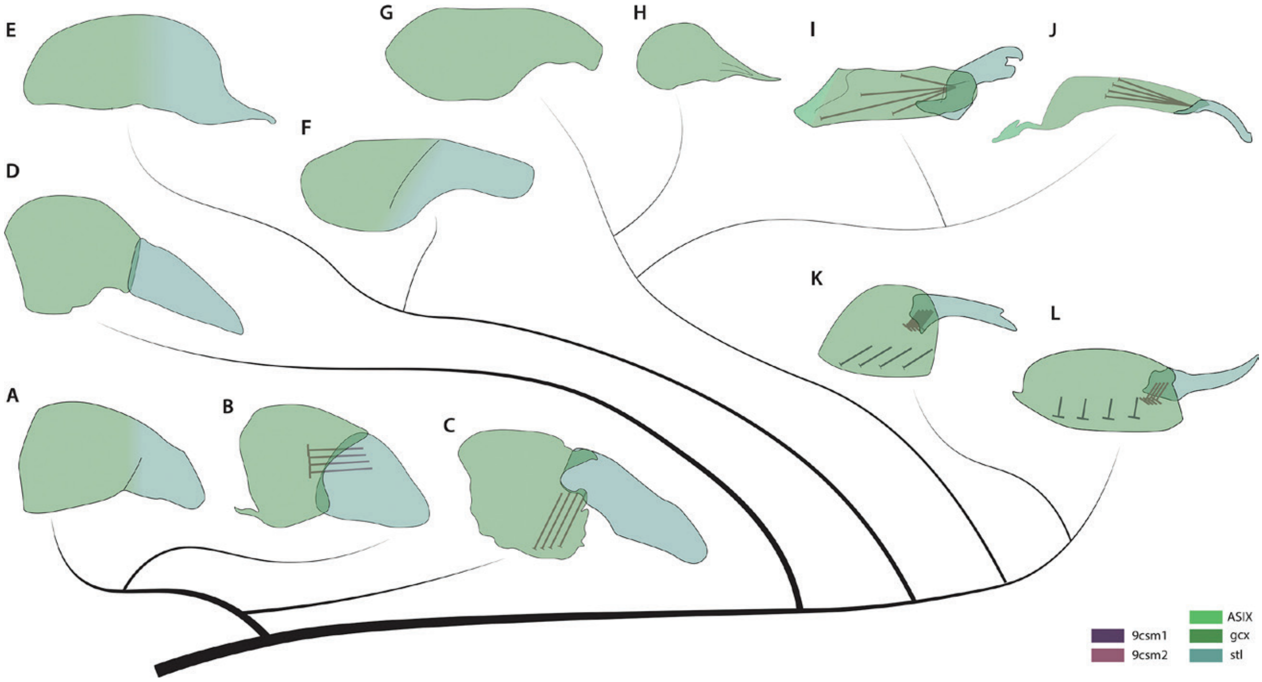

Figure 25. Diagrammatic cladogram of coxo-stylar skeletomusculature, profile view. Abdominal sternite IX of *Noonilla* cf. *copiosa* is rotated 180° relative to in situ position. Orthogonal caps at end of diagrammatic muscle lines signify origin; lack of caps, insertion. **A** *Lioponera* indet. **B** *Myrmica ruginodis.* **C** *Odontomachus* indet. **D** *Protanilla* zhg-vn01. **E** *Yavnella* zhg-th03. **F** *Yavnella* zhg-bt01. **G** *Leptanilla* zhg-my04. **H** *Leptanilla* zhg-my02. **I** *Noonilla* zhg-my03. **J** *Noonilla* cf. *copiosa.* **K** *Leptanilla* zhg-id04. **L** *Leptanilla* cf. *zaballosi*. Abbreviations: ASIX = abdominal sternite IX; gcx = gonocoxite; stl = gonostylus; 9csm1 = anterior coxo-stylar muscles; 9csm2 = intermediate coxo-stylar muscles.

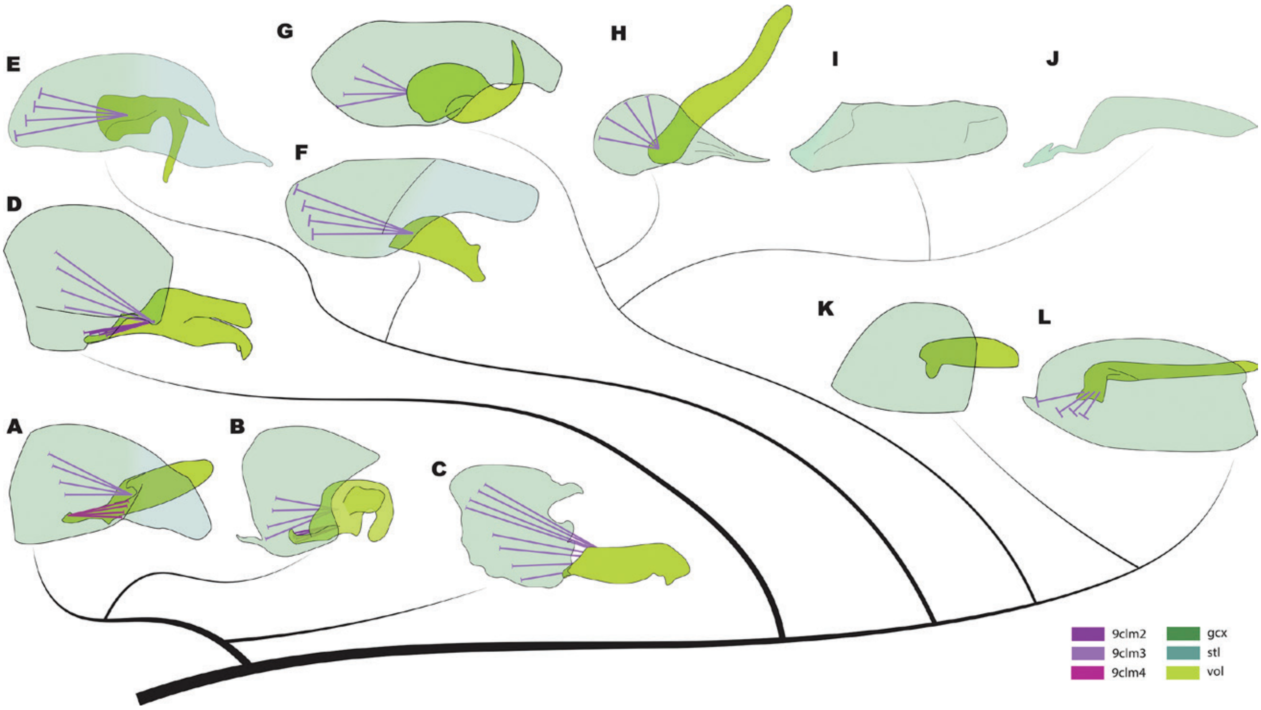

Figure 26. Diagrammatic cladogram of coxo-lateropenital skeletomusculature, profile view. Orthogonal caps at end of diagrammatic muscle lines signify origin; lack of caps, insertion. **A** *Lioponera* indet. **B** *Myrmica ruginodis*. **C** *Odontomachus* indet. **D** *Protanilla* zhg-vn01. **E** *Yavnella* zhg-th03. **F** *Yavnella* zhg-bt01. **G** *Leptanilla* zhg-my04. **H** *Leptanilla* zhg-my02. **I** *Noonilla* zhg-my03. **J** *Noonilla* cf. *copiosa*. **K** *Leptanilla* zhg-id04. **L** *Leptanilla* cf. *zaballosi*. Abbreviations: gcx = gonocoxite; stl = gonostylus; vol = volsella; 9clm2 = lateral intrinsic coxo-lateropenital muscles; 9clm3 = medial extrinsic coxo-lateropenital muscles; 9clm4 = lateral extrinsic coxo-lateropenital muscles.

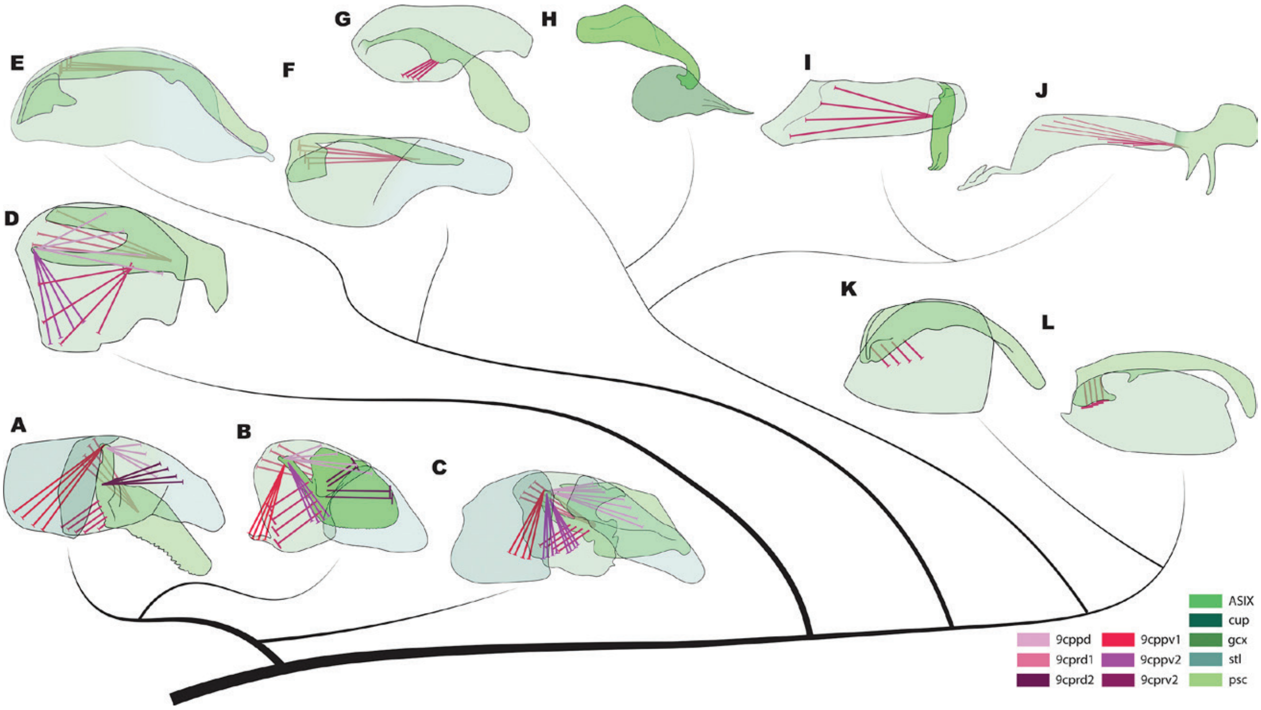

Figure 27. Diagrammatic cladogram of coxo-penial skeletomusculature, profile view. Abdominal sternite IX of *Noonilla* cf. *copiosa* is rotated 180° relative to in situ position. Orthogonal caps at end of diagrammatic muscle lines signify origin; lack of caps, insertion. **A** *Lioponera* indet. **B** *Myrmica ruginodis.* **C** *Odontomachus* indet. **D** *Protanilla* zhg-vn01. **E** *Yavnella* zhg-th03. **F** *Yavnella* zhg-bt01. **G** *Leptanilla* zhg-my04. **H** *Leptanilla* zhg-my02. **I** *Noonilla* zhg-my03. **J** *Noonilla* cf. *copiosa.* **K** *Leptanilla* zhg-id04. **L** *Leptanilla* cf. *zaballosi*. Abbreviations: ASIX = abdominal sternite IX; cup = cupula; gcx = gonocoxite; psc = penial sclerite; stl = gonostylus; 9cppd = dorsal coxo-penial promotors; 9cprd1 = medial dorsal coxo-penial remotors; 9cprd2 = lateral dorsal coxo-penial remotors; 9cppv1 = anterior ventral coxo-penial promotors; 9cppv2 = posterior ventral coxo-penial promotors; 9cprv2 = lateral ventral coxo-penial remotors.

Table 4. Scleritic character state definitions used in Figure 28.

State (semi-ordered)	ASVIII	ASIX	Spiculum	Cupula	Gonopodites	Gonocoxites	Volsellae	Penial sclerites
0	ASVIII separate from ASIX.	ASIX unfused to distal sclerites.	Spiculum absent.	Cupula present, separate from gonocoxites, annular.	Gonopodites articulated.	Gonocoxites demarcated medially.	Volsellae present, parossiculus and lateropenite distinct.	Penial sclerites medially articulated, proximally articulated to gonocoxites.
1	ASVIII fused with ASIX.	ASIX fused to cupula.	Spiculum present.	Cupula present, separate from gonocoxites, anteriorly fused to ASVIII, annular.	Gonopodites inarticulate.	Gonocoxites not demarcated medially.	Volsellae present, parossiculus and lateropenite not distinct, basivolsella and distivolsella not distinct.	Penial sclerites medially fused, proximally articulated to gonocoxites.
2	N/A	ASIX fused to gonocoxites.	N/A	Cupula present, separate from gonocoxites, non-annular.	Gonostyli absent.	N/A	Volsellae present, parossiculus and lateropenite not distinct, basivolsella and distivolsella not distinct, volsellae fused medially.	Penial sclerites medially fused, proximally fused to gonopodites.
3	N/A	ASIX absent.	N/A	Cupula present, annular, fused to gonocoxites.	Gonostyli present, articulate, medially fused.	N/A	Volsellae absent.	N/A
4	N/A	N/A	N/A	Cupula absent.	N/A	N/A	N/A	N/A

complete medial fusion of the gonocoxites (Fig. 29G–I) is a synapomorphy of *Scyphodon* s.l. + the Bornean morphospecies-group.

Although the phylogeny of the Leptanillini s.str. is well-resolved, with subclades readily diagnosed by multiple non-genital male morphological characters (Griebenow 2020, 2021), this internal phylogeny is not always reflected by male genital skeletomusculature with plain fidelity. For example, we may speculate that the posterior fusion of abdominal sternite IX to the gonocoxites in *Scyphodon* s.l. and the Bornean morphospecies-group (or to a cupular-gonocoxital complex, as in *Leptanilla* zhg-id01) is homoplasious due to differences in Remanean “special qualities,” despite these being sister clades, but this hypothesis is untestable with available taxon sampling. Nor can we propose definitive male genital synapomorphies for the Indomalayan clade within *Leptanilla* s.l. Members of this clade that do not belong to *Scyphodon* s.l. or the Bornean morphospecies-group, i.e., the Indochinese morphospecies-group, have medially separated gonocoxites, unlike *Scyphodon* s.l. and the Bornean morphospecies-group.

4.3. Male genital musculature in the Leptanillinae compared to other Hymenoptera

4.3.1. Historical précis

The male genitalia of Hymenoptera have been studied from anatomical and comparative morphological perspectives for at least 300 years, since the early microscopist and seminal entomologist Jan Swammerdam (1637–1680) examined the dissected genitalia of bees (Swammerdam 1775). The great advances that attended improvements in imaging and communication technologies, the introduction of Linnaean taxonomy, and the rise in collections and descriptions were also accompanied by the proliferation of parallel systems of terminology and homology hypotheses or comparative models (cf. epigraph). In the 20th century, the exhaustive studies of Boulangé (1924) and Snodgrass (1941) formed the foundation for contemporary treatments of the male genitalia. These works are distinguished by their treatments of musculature in addition to sclerite morphology; as discussed previously, the former remains one of the most prevalent terminological schema for muscle terms today. The works of Schulmeister (e.g., 2001, 2003) refined and expanded the characterization of “symphytan” genitalia and brought analysis thereof into the cladistic era. In the last two decades, descriptive and comparative power have again leapt forward, with studies such as Mikó et al. (2013) incorporating “next-generation” imaging techniques, while the Hymenoptera Anatomy Ontology (Yoder et al. 2010; Seltmann et al. 2012) has provided novel access to curated anatomical resources.

Homology hypotheses have simultaneously developed over the last century, from unstructured observations of correspondence of parts, to the concepts of Snodgrass (1936, 1941), Michener (1944, 1956), Gustafson (1950) and Smith (1969, 1970, 1971) (and cf. Matsuda 1958). The advent and establishment of phylogenomic methods has enabled interpretation of morphology in phylogenetic context from an independent data source. Significantly, Boudinot (2018) demonstrated male genitalic muscular homologies across hexapods, providing a new basis for studying derivations in insect subclades. However, the wide scope of that work precluded extensive sampling within Hymenoptera, leaving apomorphic subdivisions and reorganizations largely unaddressed. Similarly, the last (and first) node-spanning sampling of ant genitalia, Boudinot (2013) still used the neutral Boulangé (1924) terminology, motivating our approach to terminology here (see also Introduction and Sections 2.3.5., 4.3.3.).

4.3.2. Framework of muscle evolution

Our understanding of muscle evolution is generally based in a modification of the inferential guidelines of Boudinot (2018: 565): (1) evolutionary sequences of muscle movement occur in steps of local movement, without spontaneous "leaps" from sclerite to sclerite; (2) shifts of attachment across conjunctiva, and transverse translation across other muscles, are rare; (3) topographic reorganization is usually due to local plasticity within a sclerite or to "vicariant" drift of attachments concomitant with scleritic modification; and (4) new muscles are derived from fission (gain) or fusion (loss) of existing muscles rather than de novo innovation. Relative probability of transformation series is guided by the principle of parsimony.

4.3.3. Muscle subdivisions and terminology

While insect muscles are frequently arranged in discrete groups, they lack an epimysial sheath like that of vertebrates, such that recognition of specific bundles of fibers as separate sets is somewhat subjective. Here, we consider both the degree of separation at both origin and insertion, and implied transformations, as evidence to discern subsets of the homological-topographic main groups, but acknowledge that there is no solid, global criterion for recognizing individual subgroups. In terms of subdivisions within a main group, we consider that distinct lack of overlap of attachments of bundles within a main group indicates a mechanical reorganization, implying a semi-independent ontogenetic and therefore evolutionary program, which may be captured through terminology.

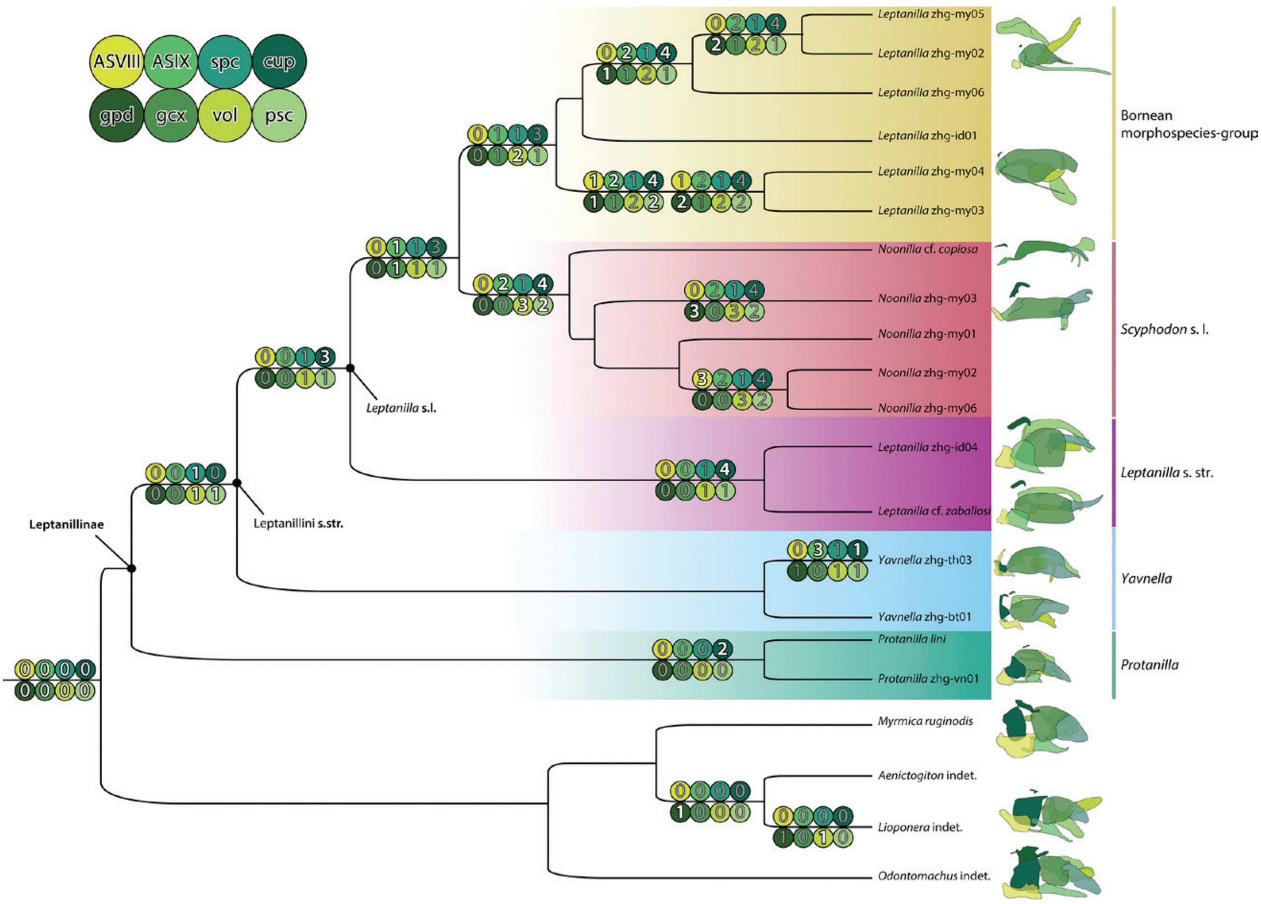

Figure 28. Sclerite character states for primarily observed taxa as inferred transformations. Circles and fill colors correspond to characters as shown in legend at top left. Characters in left-to right order: (top row) ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; spc = spiculum; cup = cupula; (bottom row) gpd = gonopodite; gcx = gonocoxite; vol = volsella; psc = penial sclerite. Numbers correspond to states in Table 4. State numbers with white fill indicate changes from inferred preceding character state. Multiple state summaries on the same branch indicate inferred transformation series due to character ordering. Diagrams at right, top-to-bottom: *Leptanilla* zhg-my02; *Leptanilla* zhg-my04; *Noonilla* cf. *copiosa*; *Noonilla* zhg-my03; *Leptanilla* zhg-id04; *Leptanilla* cf. *zaballosi*; *Yavnella* zhg-th03; *Yavnella* zhg-bt01; *Protanilla lini*; *Protanilla* zhg-vn01.

Part of our aim in designing the numeration is that future authors may further expand our schema by addition of numbers, if necessary, based on additional splits in particular taxa. Nevertheless, we performed an exhaustive review of the literature (Kluge 1895; Beck 1933; Peck 1937; Snodgrass 1941, 1942; Alam 1952; Kempf 1956; Smith 1969, 1970, 1972; Youssef 1969; Chiappini and Mazzoni 2000; Schulmeister 2001, 2003; Boudinot 2013; Mikó et al. 2013) to identify stable designations for all major muscles observed in male Hymenoptera.

In two cases, we observe partial differentiation of dorsal coxo-penial muscles into anterior and posterior partitions, which we do not designate separately. In *M. ruginodis*, the origins of 9cprd2 (l) are widely separated, with the anterior partition originating in the gonocoxite and the posterior part in the gonostylus; however, the partitions coalesce into unified insertions (Fig. 9H). In *Odontomachus* indet., the origins of 9ppd (j) are similarly partially on the gonocoxite and partially the gonostylus, but both partitions are closely approximated otherwise over their entire length (Fig. 5H). Potential subdivisions of 10plm2 (n) and 9clm4 (o) discussed by Schulmeister (2001, 2003) are not designated individually due to uncertainty on the part of Schulmeister (2001, 2003), and because we did not primarily observe 10plm2, while our observations of 9clm4 are limited. We do note that if parts of 10plm2, 9clm4, and 9prd2 are formally recognized in the future, such a modification could append names to our schema without altering the existing terminology.

4.3.4. Potential ant apomorphies

Most muscles named here are clearly homologous across Hymenoptera. Specifically, the sterno-coxal, tergo-coxal,

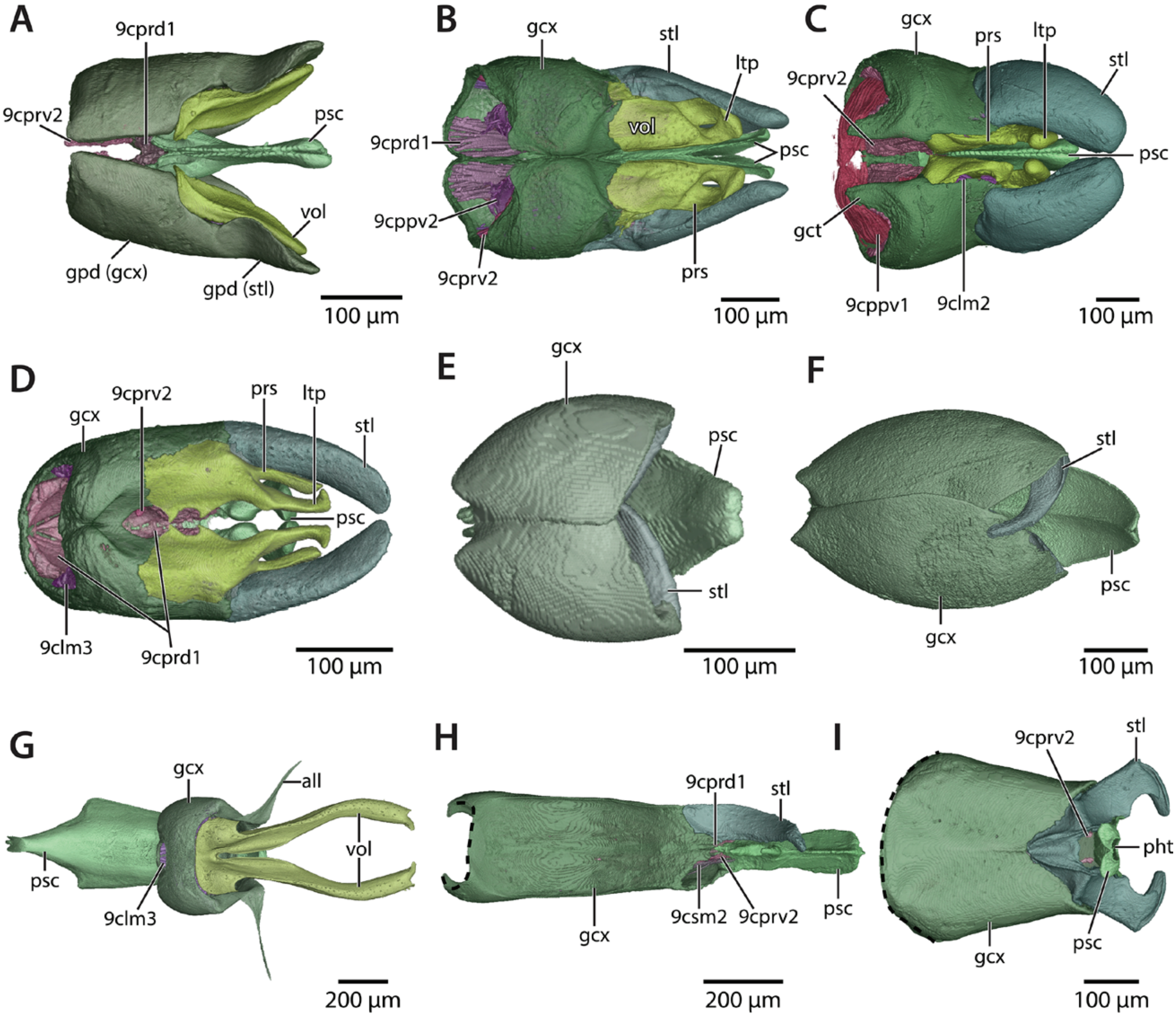

Figure 29. Morphology of the genitalia, abdominal sternite IX hidden, 3D reconstructions in ventral view. Dashed lines represent lines of fusion to abdominal sternite IX. **A** *Lioponera* indet. **B** *Odontomachus* indet. **C** *Protanilla* zhg-vn01. **D** *Myrmica ruginodis.* **E** *Leptanilla* zhg-id04. **F** *Leptanilla* cf. *zaballosi.* **G** *Leptanilla* zhg-my09. **H** *Noonilla* cf. *copiosa.* **I** *Noonilla* zhg-my03. Abbreviations: all = apicolateral lamina; gct = gonocoxital arm; gcx = gonocoxite; gpd = gonopodite; ltp = lateropenite; pht = phallotreme; psc = penial sclerite; prs = parossiculus; stl = gonostylus; vol = volsella; 9csm2 = intermediate coxo-stylar muscles; 9clm2 = lateral intrinsic coxo-lateropenital muscles; 9clm3 = medial extrinsic coxo-lateropenital muscles; 9cprd1 = medial dorsal coxo-lateropenital remotors; 9cppv2 = posterior ventral coxo-penial promotors; 9cprv2 = lateral ventral coxo-penial remotors.

and most coxo-lateropenital and coxo-penial muscles are most certainly homologous. However, some exceptions can be postulated in which topographic correspondence does not indicate homology. The most probable such case is the exact correspondences of the coxo-stylar muscles 9csm1 and 9csm2 (t). Three main states of these muscles are observed in various hymenopteran lineages: (1) in the plesiomorphic condition, there is a single 9csm2 (which may be bifid distally) which connects the gonocoxite to the gonostylus; (2) in a few taxa, there is a single muscle intrinsic to the gonocoxite; and (3) there may be both an intrinsic (anterior) gonocoxital muscle and extrinsic

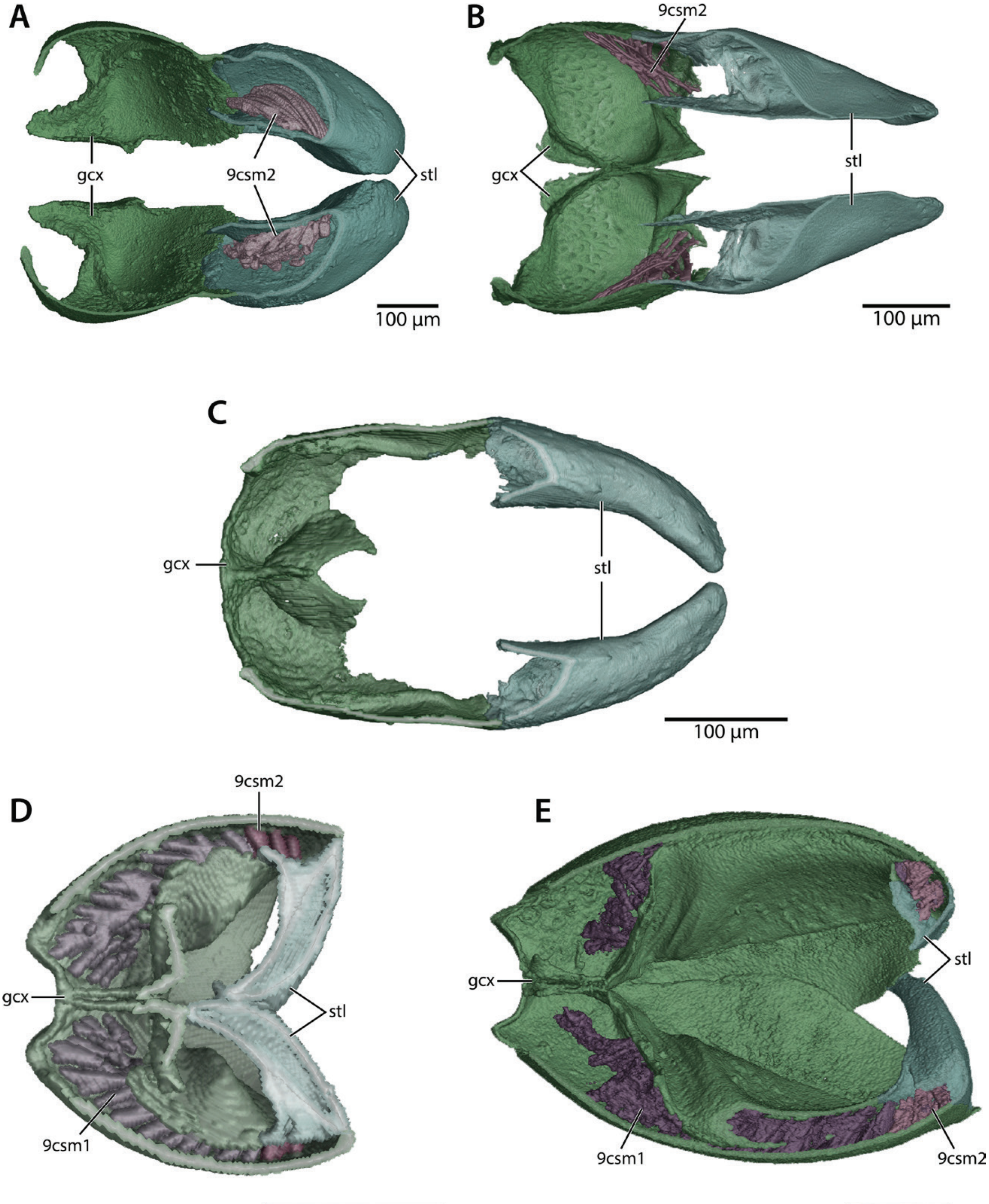

Figure 30. Coxo-stylar skeletomusculature, 3D reconstructions in coronal cross-section. **A** *Myrmica ruginodis.* **B** *Odontomachus* indet. **C** *Protanilla* zhg-vn01. **D** *Leptanilla* zhg-id04. **E** *Leptanilla* cf. *zaballosi*. Abbreviations: gcx = gonocoxite; stl = gonostylus; 9csm1 = anterior coxo-stylar muscles; 9csm2 = intermediate coxo-stylar muscles.

coxo-stylar muscle. Schulmeister (2003) observed state (2) in Vespidae and termed the single muscle w. On the other hand, following the principle of parsimony, we hypothesize that in state (2) the muscle is truly 9csm2 (t), having shifted its insertion proximally. In state (3), we designate the intrinsic muscle 9csm1 as different from the extrinsic 9csm2. The orientation of muscle w in *Dolichovespula* spp. and *Odontomachus* indet., as described here (Fig. 25B), is dorsoventral; while the intrinsic coxo-stylar muscle (9csm1) here observed only in *Leptanilla* s.str. and *Leptanilla* zhg-mm03 is transverse in orientation, spanning the medial and lateral surfaces of the gonocoxite (Figs 21E, 22E, 30D, E). Therefore, we do not equate 9csm1 with w. We do caution that many possible transformation series could lead to the observed topographies of the coxo-stylar muscles and emphasize that the present hypothesis is based on limited information, given the infrequent presence of an intrinsic coxo-stylar muscle in Hymenoptera.

For two other muscles (9cppv2, 9clm4; h', o), our primary observations were too limited to confidently assert homology at the ordinal scale. The posterior subdivision of the ventral coxo-penial promotors, 9cppv2, occurs in a few ant taxa and in at least *Stenobracon deesae* (Cameron, 1902) (Braconidae; Alam, 1952), most probably having derived independently from 9cppv1 (h) in Formicidae and Braconidae, and perhaps multiply within ants. It is also probable that the lateral extrinsic coxo-lateropenital muscle 9clm4 (o), which we observe in *Lioponera* (Figs 10I, 11) and that was previously reported in *Cephalotes pusillus* by Kempf (1956), derive independently from a subdivision of 9clm3 (p), rather than corresponding to the putatively homoplasious 9clm4 in non-ant taxa.

4.3.5. Muscle evolution and variation in Hymenoptera

Based on the evolutionary sequence inferred by Boudinot (2018), informed by the phylogenetic analysis of Schulmeister (2003) and our recoding of muscle presence and absence across Hymenoptera (Figs 31–33; Supplementary Tables S3, S4), some hypotheses may be made regarding the evolution of the male genital musculature in this clade.

We interpret muscles both muscles 9cprd1 (k) and 9cprd2 (l) to be dorsal coxo-penial remotors derived from a single pair of ancestral muscles (IXAprd in Boudinot 2018). As expected for coxo-penial remotors, both muscles insert basally on the penial sclerites, rather than apically on the valvura as in the coxo-penial promotors. It seems probable that this subdivision occurred in stem Hymenoptera via a split of the ancestral holometabolan IXAprd. The origin of IXAprd likely had little overlap with that of the ancestral holometabolan coxo-penial promotor (IXAppd in Boudinot, 2018), and was located dorsomediad IXAppd, when IXAprd subdivided into medial and lateral groups. Subsequent drift of the origin of the lateral group 9cprd2 (l) led to the conformation observed in many symphytan hymenopterans, in which the two dorsal coxo-penial remotors "straddle" the coxo-penial promotor (e.g., Schulmeister 2001: figs 7E–G). In ants, expansion of the gonocoxital area relative to the condition of that area in symphytans drew the origin of the medial dorsal remotor 9cprd1 (k) anteriorly. This movement resulted in the observed topography in the Formicidae: the orientation of 9cprd1 (k), which inserts posterad its origin, is opposite to that of 9cprd2 (l) and 9ppd (j). That this subdivision of IXAprd is a hymenopteran autapomorphy is suggested by the single pair of dorsal coxo-penial remotors in most other neopteran orders. While two or more subdivisions of IXAprd do occur sporadically in other Holometabola, it seems clear that these are homoplasious (Boudinot 2018).

The main difference between our muscular interpretations and those of Schulmeister (2003) regards the evolution of muscle 9clm1 (s) with respect to muscles 9cprv1 (si) and 9clm2 (qr). We consider 9cprv1 (si) to be a coxo-penial muscle since it originates on the parossiculus (gonocoxal fragment) or on the gonocoxite itself and inserts on the penial sclerite. This is also the suggestion of Boudinot (2018), although we infer 9cprv1 (si) is a remotor, rather than a promotor due to its basal insertion. In this interpretation, 9cprv1 (si) derives from a split of 9cprv2 (i) into a lateral and medial group, followed by limited movement of origin and insertion on the anteroposterior axis. We hypothesize that muscle 9clm1 (s) similarly derived from a simple subdivision of the plesiomorphic intrinsic coxo-lateropenital muscle 9clm2 (qr) into a medial and lateral group, with 9clm1 shifting its insertion to the base of the lateropenite. By contrast, Schulmeister (2003) infers that s derives from si by splitting followed by a transition in insertion of s to the lateropenite and the origin to a more definitively parossicular location. We consider the latter interpretation less parsimonious because it involves migration of insertions across disparate, unfused sclerites. The partial differentiability of 9clm2 into portions labeled q and r in some taxa may additionally support our hypothesis, though we here consider 9clm2 to constitute a single muscle group, as in Snodgrass (1941) and Schulmeister (2001, 2003).

The pene-lateropenital (10plm1–1; m, n) and pene-penial muscles (10ppm1–2; x, z) are considered muscles of AX, since they originate on the penial sclerites, which derive from the tenth gonocoxae. Both groups can be considered intrinsic to the penis, since the lateropenite is a penial fragment. However, the homology of these muscles cannot be definitely asserted based on our review of the literature or our primary observations (these muscles are absent in ants), so it is possible, though unparsimonious, that they truly derive from ninth segmental muscles, having moved their origin during the evolution of ontogenetic integration of gonopods X with gonopods IX in the endopterygote ancestor (Boudinot 2018). In general, the homologies of intrinsic penial muscles are obscure in the Endopterygota, given their apparent lability and distribution of occurrence among holometabolan orders. The groundplan of the Phalloneoptera includes two intrinsic penial muscles, which are inferred to have been retained in the Endopterygota groundplan and which frequently have their distal attachment on membranes of the penis or the primary gonopore specifically (XAp, Boudinot 2018). One or more intrinsic penial muscles are variably present in Neuropteroidea and Antliophora, where they may participate in the semen pumping apparatus; they are known in Trichoptera, but not Lepidoptera (Boudinot 2018). That these muscles are homologous across orders, having been variously lost or modified in taxa that lack them, seems probable, but primary homology cannot be definitively asserted. The evolutionary origin of 10plm (m, n) and 10ppm (x, z) in Hymenoptera may therefore be of broader significance, given the sister-group relationship of Hymenoptera with the remaining Endopterygota.

Within Hymenoptera, the pene-lateropenital muscles occur much more frequently than the pene-penials, the latter being mostly restricted to Siricidae and Cephidae (Table S3, Fig. S1). The most commonly retained muscle, 10plm2 (n), often inserts partially or entirely on the membranes of the primary gonopore (nb, nd, Schulmeister 2003), suggesting that if 10plm are not homologous with XAp in outgroup orders, they have both functionally and topographically converged. The major difference between 10plm and XAp as described by Boudinot (2018) is that 10plm may also insert on the lateropenite, a penial derivative which became discrete in the endopterygote ancestor. This suggests that if XAp and 10plm are homologous, then 10plm moved their insertion to the lateropenite in the stem Hymenoptera, prior to the integration of the lateropenite with the parossiculus in the crown Hymenoptera (Boudinot 2018). Our preferred, though largely speculative, inference is that 10plm correspond to XAp, with 10ppm deriving from 10plm to connect the valvurae of Ichneumonidae (10ppm1, x) or the "median sclerotized style" (Ross 1937), a ventromedian interpenial sclerite which may be a fragment of the penial sclerites, or a secondary sclerotization of the ventromedian penial membrane (10ppm2, z). The muscle connecting the proximal aedeagal apodemes and another set of longitudinally-oriented penial apodemes in *Anagrus* (Mymaridae) is likely an independent derivation, possibly of 10plm1, but cannot be decisively identified based on the description or figures of Chiappini and Mazzoni (2000). Multiple losses would account for the scattered presence of the pene-lateropenital muscles across Hymenoptera. Under this interpretation, the coxo-coxal intrinsic muscle, here conservatively termed 9ccim (y), could also reasonably derive from 10ppm1, shifting anteriorly in origin from the valvurae to the parossiculi.

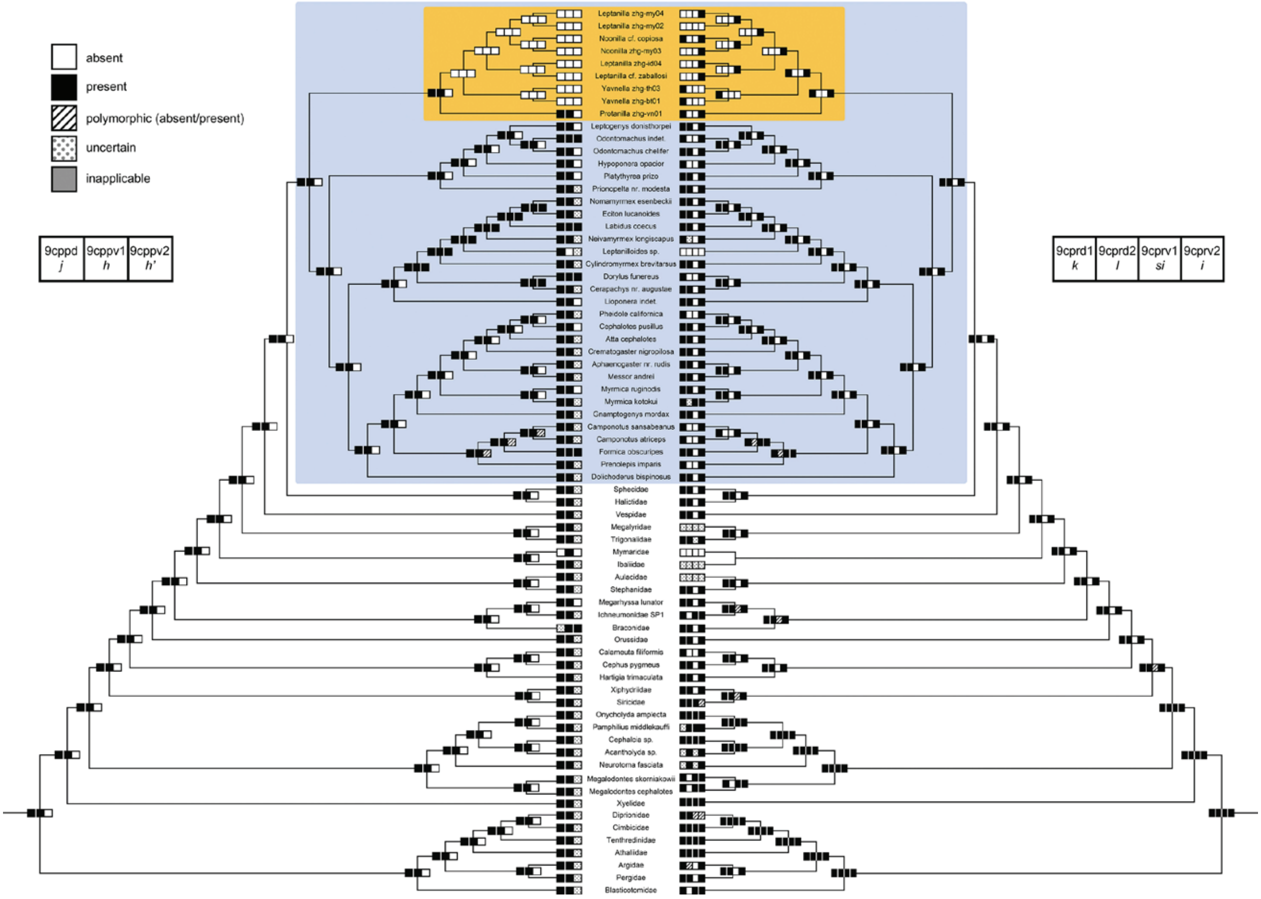

Figure 31. Ancestral state reconstruction and sampled tip states of coxo-penial musculature across the Hymenoptera. Blue = Formicidae; yellow = Leptanillinae Left and right topologies are identical. Node reconstructions not shown when all sampled descendants were scored as uncertain or inapplicable. See Supplementary Document 1 for explanation of inapplicability and additional notes. Cells represent characters. Cell fill represents character states: white = absent; black = present; diagonal lines = polymorphic absent/present; grey dots = uncertain; solid grey = inapplicable. Left tree: coxo-penial promotors; cells in left-to-right order: 9cppd (j), 9cppv1 (h), 9cppv2 (h'). Right tree: coxo-penial remotors; cells in left-to-right order: 9cprd1 (k), 9cprd2 (l), 9cprv1 (si), 9cprv2 (i).

4.3.6. Trends of skeletomuscular simplification of male genitalia in the Formicidae

Of the 28 species of Formicidae for which the genital muscles have been completely described or coded (Kempf 1956; Birket-Smith 1981; Ogata 1991; Boudinot 2013), in only *Leptanilloides* sp. (Dorylinae) is muscular reduction comparable to that observed in the Leptanillinae. To wit, all coxo-penial muscles except the dorsal promotor (9cppd, j) are absent in *Leptanilloides* sp. (Fig. 31, Table S3; Boudinot 2013: table 3), with some or all these penial muscles being absent in sampled exemplars of Leptanillini s.str. At least four coxo-penial muscles (9cppd, 9ppv1, 9prd1, 9cprv2; j, h, k, i) are present in all other studied male ants, and in some taxa up to six (9cppv2, 9cprd2; h’, l) (Fig. 31, Table S3). Reduction of male genital musculature is quantitatively more extreme in the Leptanillini s.str. than in *Leptanilloides* sp., since the posteromedial sterno-coxal muscles (9vcm2, b), ventrolateral tergo-coxal muscles (9dcm3, e) (Fig. 32, Table S3), and dorsal coxo-penial promotors are present in the latter taxon but are absent in the former; further, the extrinsic lateral coxo-lateropenital muscles (9clm3, p) and intermediate coxo-stylar muscles remain in the unidentified *Leptanilloides* species sampled by Boudinot (2013), but have been lost in multiple lineages within the Leptanillini s.str. and in *Lioponera* indet. (Fig. 33, Table S3).

Leptanilloides males are unusual among the Formicidae in equaling the small size of certain leptanilline males. Skeletomuscular simplification of the male genitalia in the Leptanillinae and across the Formicidae as a whole may therefore correlate with miniaturization. Male genital skeletomuscular simplification as correlate of miniaturization in the Leptanillinae could be corroborated by the extreme scleritic simplification observed in male genitalia throughout the Chalcidoidea (Snodgrass 1941; Hansson 1996), which are for the most part miniaturized relative to other Hymenoptera, with a distinct cupula being universally lost in that superfamily (Domenichini 1953; Viggiani 1973), and also absent in the similarly minute Mymarommatoidea (Gibson et al. 2007). Parallel losses of the gonostyli within the Leptanillini s.str. are also paralleled by extreme reduction of the gonostyli in *Anagrus* (Chalcidoidea: Mymaridae) (Viggiani 1988; Chiappini and Mazzoni 2000) and some *Perditorulus* spp. (Chalcidoidea: Eulophidae) (Hansson 1996). All members of the Leptanillini s.str. sampled herein equal or surpass the degree of muscular reduction

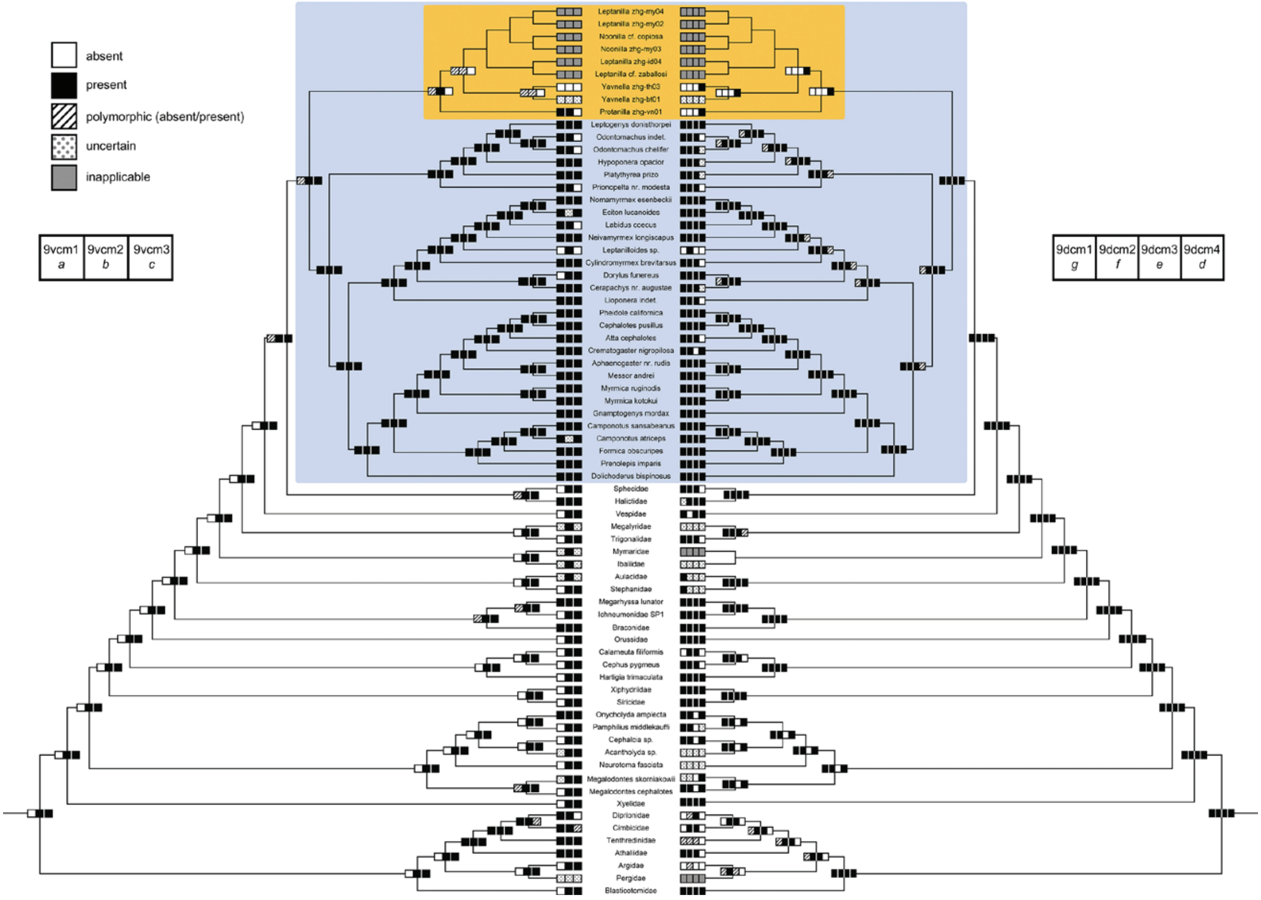

Figure 32. Ancestral state reconstruction and sampled tip states of sterno-coxal and tergo-coxal musculature across the Hymenoptera. Blue = Formicidae; yellow = Leptanillinae. Left and right topologies are identical. Node reconstructions not shown when all sampled descendants were scored as uncertain or inapplicable. See Supplementary Document 1 for explanation of inapplicability and additional notes. Cells represent characters. Cell fill represents character states: white = absent; black = present; diagonal lines = polymorphic absent/present; grey dots = uncertain; solid grey = inapplicable. Left tree: sterno-coxal muscles; cells in left-to-right order: 9vcm1 (a), 9vcm2 (b), 9vcm3 (c). Right tree: tergo-coxal muscles; cells in left-to-right order: 9dcm1 (g), 9dcm2 (f), 9dcm3), 9dcm4 (d).

observed in *Anagrus* spp., as four muscles or less are associated with the appendicular sclerites, although the identity of these muscles differs somewhat between *Anagrus* and the Leptanillini s.str. (Chiappini and Mazzoni 2000).

Male genitalia in *Leptanilloides* show far less morphological derivation than the Leptanillini s.str., meaning that the skeletomuscular simplification of leptanilline male genitalia cannot be attributed to miniaturization per se. Trends of skeletomuscular simplification paralleled in multiple anatomical regions across the phylogeny of the Endopterygota also coincide with evolutionary factors beyond miniaturization (Beutel et al. 2022). Any hypotheses concerning the evolutionary impetus behind male genital skeletomuscular simplification in the Leptanillinae are tentative, and must be tested further.

4.4. Comparative discussion of male genital sclerites of interest across the Leptanillinae

4.4.1. Abdominal sternite VIII

The pregenital abdominal sternite VIII is peculiarly modified in some lineages of the Leptanillinae, associated with derivation of abdominal sternite IX (see Section 4.4.2.). Yamada et al. (2020) did not describe or figure abdominal sternite VIII for *O. hungvuong*. In *Protanilla* zhg-vn01, sampled *Leptanilla* s.str., and *Leptanilla* zhg-mm03, abdominal sternite VIII is unmodified relative to the ancestral condition of homonomy with immediately preceding abdominal sternites. There is a tendency towards anteroposterior reduction of abdominal sternite VIII observed in sampled *Scyphodon* s.l. and the Bornean morphospecies-group, with median loss of post-antecostal sternite VIII in *Leptanilla* zhg-my02 and complete loss of post-antecostal sternite VIII in *Noonilla* zhg-my03. In *Leptanilla* zhg-my03, -4 and *Noonilla* zhg-my02 and -6, abdominal sternite VIII is completely fused to abdominal sternite IX to form an inarticulate ASVIII+ASIX+gcx+psc (Fig. 20). This interpretation is confirmed by serial numeration of the abdominal sternites, and definitive identification of abdominal sternite IX (Section 4.4.2.), in these exemplars.

Abdominal sternite VIII is completely fused to the cupula in *Yavnella* zhg-th01, -th03, zhg-my02, and *Yavnella* nr. *indica*, encircling the entire foramen genitale (Fig. 4F). This condition is unique among the Hymenoptera. This expanded fusion of abdominal sternite VIII to the cupula corresponds to the hypertrophied condition

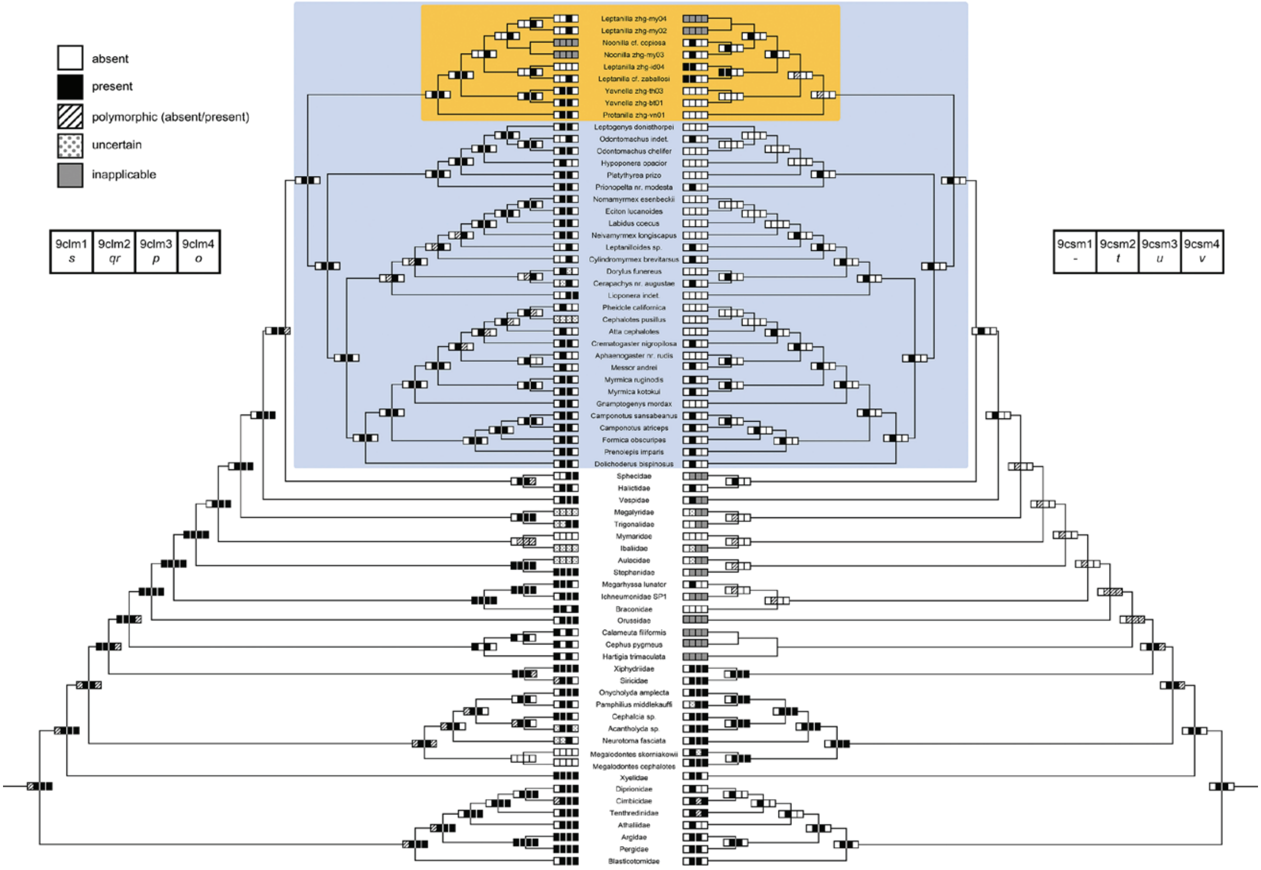

Figure 33. Ancestral state reconstruction and sampled tip states of coxo-lateropenital and coxo-stylar musculature across the Hymenoptera. Blue = Formicidae; yellow = Leptanillinae. Left and right topologies are identical. Node reconstructions not shown when all sampled descendants were scored as uncertain or inapplicable. See Supplementary Document 1 for explanation of inapplicability and additional notes. Cells represent characters. Cell fill represents character states: white = absent; black = present; diagonal lines = polymorphic absent/present; grey dots = uncertain; solid grey = inapplicable. Left tree: coxo-lateropenital muscles; cells in left-to-right order: 9clm1 (s), 9clm2 (qr), 9clm3 (p*)*, 9clm4 (o). Right tree: coxo-stylar muscles; cells in left-to-right order: 9csm1, 9cms2 (t), 9csm3 (u), 9csm4 (v).

of the former sclerite in these morphospecies, forming a dorsally recurved "dish" surrounding the base of the appendicular genitalia, seemingly a sclerotized analog to the genital pouch referred to by Boulangé (1924), which is absent in *Yavnella*. Conversely, abdominal sternite VIII is only moderately expanded medially in *Yavnella* zhg-bt01, in which it is posteriorly separate from the cupula: the fusion of abdominal sternite VIII to the cupula may therefore be a synapomorphy of *Yavnella* exclusive of *Yavnella* zhg-bt01.

Posterior fusion of abdominal sternite VIII to abdominal sternite IX has evolved at least once in *Scyphodon* s.l., and the Bornean morphospecies-group, respectively. This is comparable to the condition observed in *Dolichovespula maculata* (Linn., 1763) and *Dolichovespula adulterina* (du Buysson, 1905) (Vespidae: Vespinae), in which AS-VIII–ASIX are fused, but remain distinguishable by the retention of antecostae (Fig. 34; Peck 1937: figs 36, 37; Schulmeister 2003: fig. 14W).

In *Yavnella* zhg-bt01, abdominal sternite VIII is medially bifurcated (Fig. 15B), recalling derivation of the male abdominal sternite IX elsewhere among the Formicidae (Section 4.4.2.) and the median emargination of the male abdominal sternite VII in *Ooceraea* (Dorylinae) (Borowiec 2016). This serial analogy between abdominal sternites VIII and IX may apply to *Yavnella* TH03, meaning that it is conceivable that this posteromedian sternal process observed in *Yavnella* TH03 is in fact anatomically derived from abdominal sternite VIII. Further specimens of *Yavnella* TH03 would be required to assess this possibility.

We speculate that the structural reinforcement afforded by tergosternal fusion of abdominal segment VIII in *Noonilla* cf. *copiosa* aids the maneuverability of the genital capsule. This maneuverability is presumably greater in *Noonilla* cf. *copiosa* relative to other *Scyphodon* s.l. included in this study, which have lost all ventral longitudinal muscles VIII–IX, and thus the capacity for movement of the genital capsule along the craniocaudal or transverse axes.

4.4.2. Abdominal sternite IX

The modification of abdominal sternite IX is diverse across the Leptanillinae sampled herein (Fig. 12), and structural integration of this sclerite with the appendicular genitalia is variable (Fig. 35). In *Protanilla* zhg-vn01 and *O. hungvuong*, abdominal sternite IX is separate from all adjacent pregenital and genital sclerites and ventrally vaulted, with an anteromedian spiculum and posteromedian triangular process. This posteromedian process is visible without dissection in *O. hungvuong* (Yamada et al. 2020: fig. 13C) and all available *Protanilla*, implying that this condition of abdominal sternite IX is plesiomorphic for the Leptanillinae. The spiculum is lost in the Leptanillini s.str., almost always along with the sterno-coxal muscles, which are retained only in *Leptanilla* zhg-mm03. In the Leptanillini s.str. the posteromedian process of abdominal sternite IX, if present, is broadly triangular or filiform, as in *Yavnella* TH03 (Griebenow 2021: 616).

In *Leptanilla* s.str., abdominal sternite IX is unmodified relative to the ancestral condition for Leptanillini s.str. (Fig. 12E) or is reduced to an anteroposteriorly narrow strip. The posterior margin may be entire; bear a truncate posteromedian process; be medially incised (Petersen 1968: fig. 13); or be shallowly emarginate (Griebenow 2021: fig. 23A). Further derivation of abdominal sternite IX is observed in other subclades of *Leptanilla* s.l., as follows.

In most examined *Yavnella* abdominal sternite IX is judged to be absent, in what is perhaps the most extreme derivation of this sclerite among the Leptanillinae. This conclusion is drawn from *Yavnella* zhg-th03, using the proctiger as topographical reference, and considering the absence both of dorsoventral intrinsic muscles IX and sterno-coxal muscles. No putative trace of abdominal sternite IX whatsoever can be argued in this exemplar (Figs 24F, 35B). The anterior fusion of the cupula to abdominal sternite VIII, a corollary of the absence of abdominal sternite IX, is confirmed by manual dissection in all other sampled *Yavnella*, save *Yavnella* zhg-bt01, in which the cupula is anteriorly separated from abdominal sternite VIII. Due to limitations of available scan data, we could not assess the condition of abdominal segment IX in *Yavnella* zhg-bt01.

In the Bornean morphospecies-group, abdominal sternite IX is reduced to an anteroposteriorly narrow strip and posterolaterally produced into mulceators (Figs 19, 20), which are an unequivocal autapomorphy of this clade. The neologism "mulceator" aids concision. Since the term describes a structure that is unique among the Hymenoptera, this terminological addition does not overturn preexisting conventions. Among ants excluding the Leptanillinae, paired posterior processes of the male abdominal sternite IX occur in *Paraponera clavata* (Fab., 1775) (Paraponerinae) (Boudinot 2015), *Nothomyrmecia macrops* Clark, 1934 (Myrmeciinae: Prionomyrmecini) (Taylor 1978), and are present in the Dorylinae (Bolton 2003), but these processes are not elongate and filiform. Furthermore, in contrast with the Bornean morphospecies-group, abdominal sternite IX in male *P. clavata*, *N. macrops* and the Dorylinae is anteroposteriorly prolonged and robust, rather than exhibiting median compression along the anteroposterior axis to form a ductile strap, as in the Bornean morphospecies-group. Abdominal sternite IX in the Bornean morphospecies-group also shows median fusion to the gonocoxites, in *Leptanilla* zhg-id01 via a reduced cupula. The narrow posteromedian fusion of abdominal sternite IX in *Leptanilla* zhg-my02, -my05, -my06, and -id01 to distal genital sclerites anchors this sternite medially, allowing differential motion of the lateral portions of abdominal sternite IX and thus of the mulceators, mediated by the ventral ortholateral muscles VIII–IX (Fig. 35C, F).

In sampled *Scyphodon* s.l., abdominal sternite IX is indistinguishably fused with the medially fused gonocoxites along the ventral gonocoxital margin, with abdominal sternite IX being definitively identified by the origin of unambiguous dorsoventral intrinsic muscles IX thereon. The "reversed *v*-shaped, strongly sclerotized structure in firm connection with the genitalia" described by Petersen (1968: 584) for *N. copiosa* is here identified as abdominal sternite IX (Fig. 12F, Fig. 35C), as suggested by Petersen (1968). The posteromedian fusion of abdominal sternite IX to the gonocoxites in the Bornean morphospecies-group is much less pronounced than that in *Scyphodon* s.l. and is functionally different in the presence of mulceators. We therefore regard the posterior fusion of ASIX to the appendicular genitalia as homoplasious between *Scyphodon* s.l. and the Bornean morphospecies-group.

4.4.3. Cupula

In most ants, the cupula forms a "basal ring" (sensu Crampton 1919) proximad the remainder of the genital capsule (Fig. 4A–C), a condition retained among the Leptanillinae included in this study only in *Yavnella*. The non-annularity of the cupula in *Protanilla* and *Opamyrma* by absence of the dorsum is unique among the ants and homoplasious between these lineages, outside the Formicidae paralleled by *Gasteruption* and *Pseudofoenus* (Evanioidea: Gasteruptiidae) (Mikó et al. 2013). *Leptanilla* zhg-mm03 – and perhaps the whole Indochinese morphospecies-group – retains an annular cupula, as does *Leptanilla astylina* Petersen, 1968 (Ogata et al. 1995), the phylogenetic position of which is unclear; in *Leptanilla* zhg-id01, within the Bornean morphospecies-group, the cupula is fused anteriorly to abdominal sternite IX and posteriorly to the gonocoxites. A possible cupular remnant is also discernible in *Leptanilla* zhg-my03 and -4, but less evidently so (Fig. 4G; Section 4.1.1.).

Otherwise, we infer that the cupula is absent in almost all sampled exemplars of *Leptanilla* s.l. (Fig. 4E–K). The obvious absence in *Leptanilla* s.str., *Scyphodon* s.l. and the Bornean morphospecies-group of sterno-coxal and tergo-coxal muscles IX obviates using these muscles to adduce the presence or condition of the cupula. Except for *Leptanilla* zhg-id01, -my03, and -04, any features of the male genital sclerites in sampled members of these clades that could conceivably represent a cupular remnant are readily explicable as proximal apodemes of the gonocoxites (Fig. 36A, G), or sutures between ASIX and the gonocoxites (Fig. 36D). These homologies are intuitive given the definitive presence of abdominal sternite IX in all *Leptanilla* s.l. Therefore, the cupula was independently lost in *Leptanilla* s.str., *Scyphodon* s.l., and twice in the Bornean morphospecies-group.

As noted in Section 4.2., the reduction or total absence of the cupula averred here for most *Leptanilla* s.l. is associated with the absence of tergo-coxal and sterno-coxal muscles IX. In *Yavnella* zhg-th03, and by extension the Southeast Asian radiation of *Yavnella* that comprises most of the species-level diversity in this genus, the cupula and 9dcm4 are present, but this muscle is intrinsic to the cupula. (Resolution in the scan data for *Yavnella* zhg-bt03 was insufficient to discern the condition of tergo-coxal or sterno-coxal muscles IX.) Meanwhile, the cupula and sterno-coxal muscles IX are observed in *Leptanilla* zhg-mm03, but the tergo-coxal muscles IX are absent in that morphospecies. In most Leptanillini s.str., therefore, the genitalia are not musculated from abdominal segment IX. Taxon sampling within *Yavnella* is here insufficient to determine if this is a synapomorphy of the Leptanillini s.str., or evolved separately within *Yavnella* and in *Leptanilla* s.l. Although the cupula is extremely reduced in other ant lineages, e.g., the Old World army ants (Dorylinae:

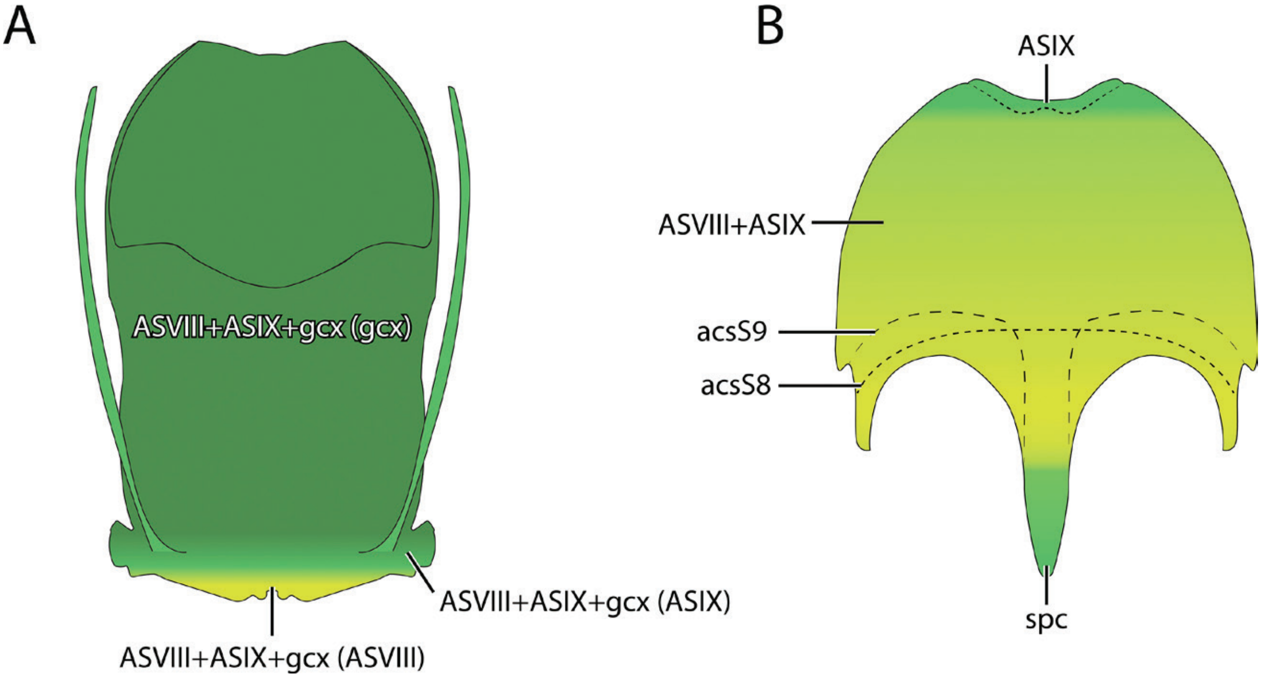

Figure 34. Diagrammatic comparison of fusion of male abdominal sternites VIII-IX in the Hymenoptera, ventral view. Figure 34B redrawn from Peck (1937: fig. 37). **A** *Leptanilla* zhg-my04. **B** *Dolichovespula maculata* (Linn.). Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; acsS8 = antecosta of abdominal sternite VIII; acsS9 = antecosta of abdominal sternite IX; spc = spiculum; gcx = gonocoxite.

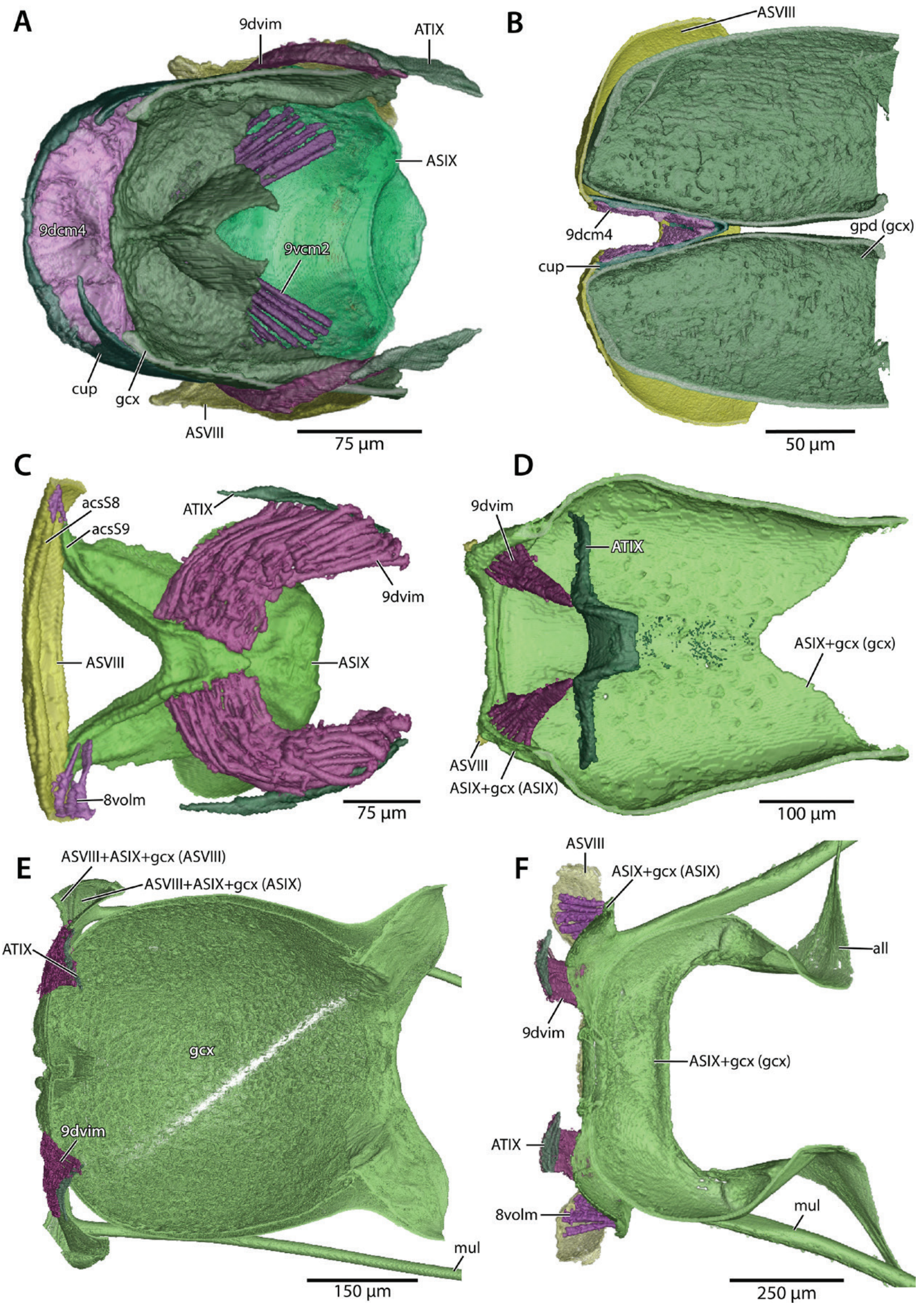

Figure 35. Morphology of the axial sclerites, gonopodites, and associated musculature, 3D reconstructions, coronal cross-sections in dorsal view. **A** *Protanilla* zhg-vn01. **B** *Yavnella* zhg-th03. **C** *Noonilla* cf. *copiosa*. **D** *Noonilla* zhg-my03. **E** *Leptanilla* zhg-my04. **F** *Leptanilla* zhg-my02. Abbreviations: ASVIII = abdominal sternite VIII; acsS8 = antecosta of abdominal sternite VIII; ASIX = abdominal sternite IX; ATIX = abdominal tergite IX; all = apicolateral lamina; acsS9 = antecosta of abdominal sternite IX; cup = cupula; gpd = gonopodite; gcx = gonocoxite; mul = mulceator; stl = gonostylus; 8volm = ventral ortholateral muscles VIII–IX; 9dvim = dorsoventral intrinsic muscles IX; 9vcm2 = posteromedial sterno-coxal muscles; 9dcm4 = ventral tergo-coxal muscles.

Aenictogiton, *Aenictus*, *Dorylus*; Bolton 1990a) the absence of extrinsic male genital musculation from the metasoma is unique to the Leptanillini s.str. among the Formicidae. Extrinsic musculation is derived secondarily in *Scyphodon* s.l. and the Bornean morphospecies-group by fusion of abdominal sternite IX to the gonocoxites, in *Leptanilla* zhg-id01 with an intervening cupula, with the movement of the genitalia thus being mediated by ventral longitudinal muscles VIII–IX, intrinsic dorsoventral muscles IX, both, or in the case of *Leptanilla* zhg-my02 and -my05, the autapomorphic extrinsic dorsoventral muscles IX–VIII in addition (Fig. 15B, D, F).

4.4.4. Volsellae

The variation observed in volsellar anatomy across the Leptanillinae is dramatic, ranging from presence and complete articulation of the parossiculus and lateropenite in *O. hungvuong* to complete absence of the volsella in *Scyphodon* s.l. (Fig. 26) and *Leptanilla* zhg-mm03. The loss of distinction between the parossiculus and lateropenite is a synapomorphy of the Leptanillini s.str. As noted above, due to a lack of intermediates in volsellar form between the former Anomalomyrmini and Leptanillini s.str., it is not externally evident if the volsellar sclerite observed in the latter clade is homologous with the parossiculus or with the lateropenite. The proximal insertion of the extrinsic medial coxo-lateropenital muscles on the volsellae would identify at least the proximal portion of that sclerite as parossicular, implying that the whole of the sclerite perhaps corresponds to the parossiculus rather than to the lateropenite in part.

The volsella in the Leptanillini s.str. therefore consists of a single article (Fig. 13E–J), which in many *Yavnella* is divided into proximal and distal sections (cf. Kugler 1986: figs 18, 22) by an ectal transverse sulcus on the medial face. This division is not observed in *Yavnella* zhg-bt01 or *Yavnella* TH03, and so may be synapomorphic for the speciose radiation within *Yavnella* to which *Yavnella* zhg-bt01 and *Yavnella* TH03 do not belong (Griebenow et al. 2022). These proximodistal volsellar sections are not respectively homologous with the basi- and distivolsella observed in symphytan Hymenoptera, since the distinction between proximodistal articles was apparently lost in the most recent common ancestor of the Leptanillini s.str.; the proximodistal division described here for some *Yavnella* spp. is a secondary derivation.

In the remainder of the Leptanillini s.str. the volsella (if present) exhibits no trace of a transverse sulcus (Fig. 13G, H). As mentioned above, the medial fusion of the volsellae, synapomorphic for the Bornean morphospecies-group, is unique among the Formicidae but paralleled in *Sceliphron caementarium* (Drury, 1773) (Sphecidae: Sceliphrini) in the form of a "basivolsellar bridge" (Schulmeister 2003: fig. 11C). The shape and proportions of the volsellae in the Bornean morphospecies-group differ markedly on the morphospecies level, particularly when considering the clade comprising *Leptanilla* zhg-my03 and -4 contrasted with their sister-group (which constitutes the remainder of the Bornean morphospecies-group), but are always large and prominent. The shape of the volsellae appears to be less variable in *Leptanilla* s.str., in which these sclerites are reduced proportionally to the gonopodites and largely concealed by the latter appendages in situ. *Leptanilla* zhg-id04 shows an odd juxtaposition of character states in that the volsellae are present and seemingly articulated to the gonocoxites yet are unmusculated (Fig. 21). This interpretation is not artifactual, and such a condition is paralleled outside the Formicidae by *Megalodontes* (Pamphilioidea: Megalodontesidae) (Table S3; Schulmeister 2003). No trace of volsellae could be discerned in *Leptanilla* zhg-mm03, nor in any *Scyphodon* s.l. examined with micro-CT: it appears that what Petersen (1968) identified as volsellae in *N. copiosa* are in fact gonostyli (see Section 4.1.1.), as previously argued by Ogata et al. (1995). However, Ogata et al. (1995: 32) also claimed that the volsellae were indeed present in "a congeneric species" to *N. copiosa*, with the lateropenite being visible "between the paramere [gonostylus] and aedeagus [penial sclerites] and has an elongate acuminate apex": this presumably refers to the recurved ventromedian process of the penial sclerites known in *N. copiosa*. Neither Petersen (1968) nor Ogata et al. (1995) considered the possibility that the volsellae are completely absent in *Noonilla*, and understandably so: the loss of volsellar musculature has never been previously observed in the ants (Table S3; Boudinot 2013: table 2), nor has the loss of the volsellae homoplasious between *Scyphodon* s.l. and the Indochinese morphospecies-group.

4.4.5. Penial sclerites

The complete medial fusion of the penial sclerites is a synapomorphy of the Leptanillini s.str. (Fig. 27), here inferred to be homoplasious with the condition observed in *M. heureka* (Boudinot 2015). In *Protanilla* zhg-vn01, and all known *Protanilla* by extension, the penial sclerites are not medially fused, as is reported for *O. hungvuong* (Yamada et al. 2020), instead being separated by a medial conjunctiva. Within the Leptanillinae, the medial fusion of the penial sclerites is associated with the loss of the posteromedial dorsal coxo-penial muscles and valvura – conditions that are synapomorphic for the Leptanillini s.str. as well. The penial sclerites in *Yavnella* TH03 and *Leptanilla astylina* appear to be medially separated, at least in part, but dissection would be required to determine the penial condition of these lineages.

Despite the tendency towards fusion of the penial sclerites with the gonocoxites in scanned exemplars of the Leptanillini s.str., at least one pair of coxo-penial muscles is retained in those scanned specimens in which partial (*Yavnella* zhg-th03) to complete fusion (*Scyphodon* s.l., *Leptanilla* zhg-my03, -4) is observed. Complete loss of penial musculature is observed among scanned male Leptanillinae in certain members of the Bornean morphospecies-group (*Leptanilla* zhg-my02, -my05, -my06, and *Leptanilla* zhg-id01), which display remarkable modification of the penial sclerites: these are proximally recurved (less so in *Leptanilla* zhg-id01 than the others), with paired penial condyles articulating to the gonocoxites, and the recessed phallotreme situated on the anatomical venter proximal to the penial apex.

Certain outgroup taxa exhibit sclerotized structures mediad the penial sclerites, which are almost certainly non-homologous with the fused penial sclerites in Leptanillini s.str. but may provide informative comparative data. Birket-Smith (1981: 385) notes that a proximodorsal, interpenial sclerite, which he terms the "patella intermediare", occurs "in several species" of Dorylinae, but unfortunately does not list these species by name. Among the Apoidea, and in *Sceliphron caementarium* (Drury), the dorsal membranes are variably sclerotized (Snodgrass 1941); the sclerites in these cases are unmusculated. In Cephidae and Siricidae, the median sclerotized style is a ventral strip of sclerite, proximally fused to the gonocoxite in cephids (Schulmeister 2003). Smith (1970), who posited intersexual genital homology, interpreted the median sclerotized style to be the detached ninth gonapophyseal rhachies; this could be broadly brought into alignment with our understanding of sclerite homologies as a fragment of the penial sclerites. Alternately, the style could be a secondary sclerotization of the penial conjunctiva. In cephids and siricids this sclerite may bear the insertion of 10ppm2 (z, Schulmeister, 2001). We note that the term "median rod" has been variably used to refer to either the dorsal (e.g., Snodgrass, 1941) or ventral

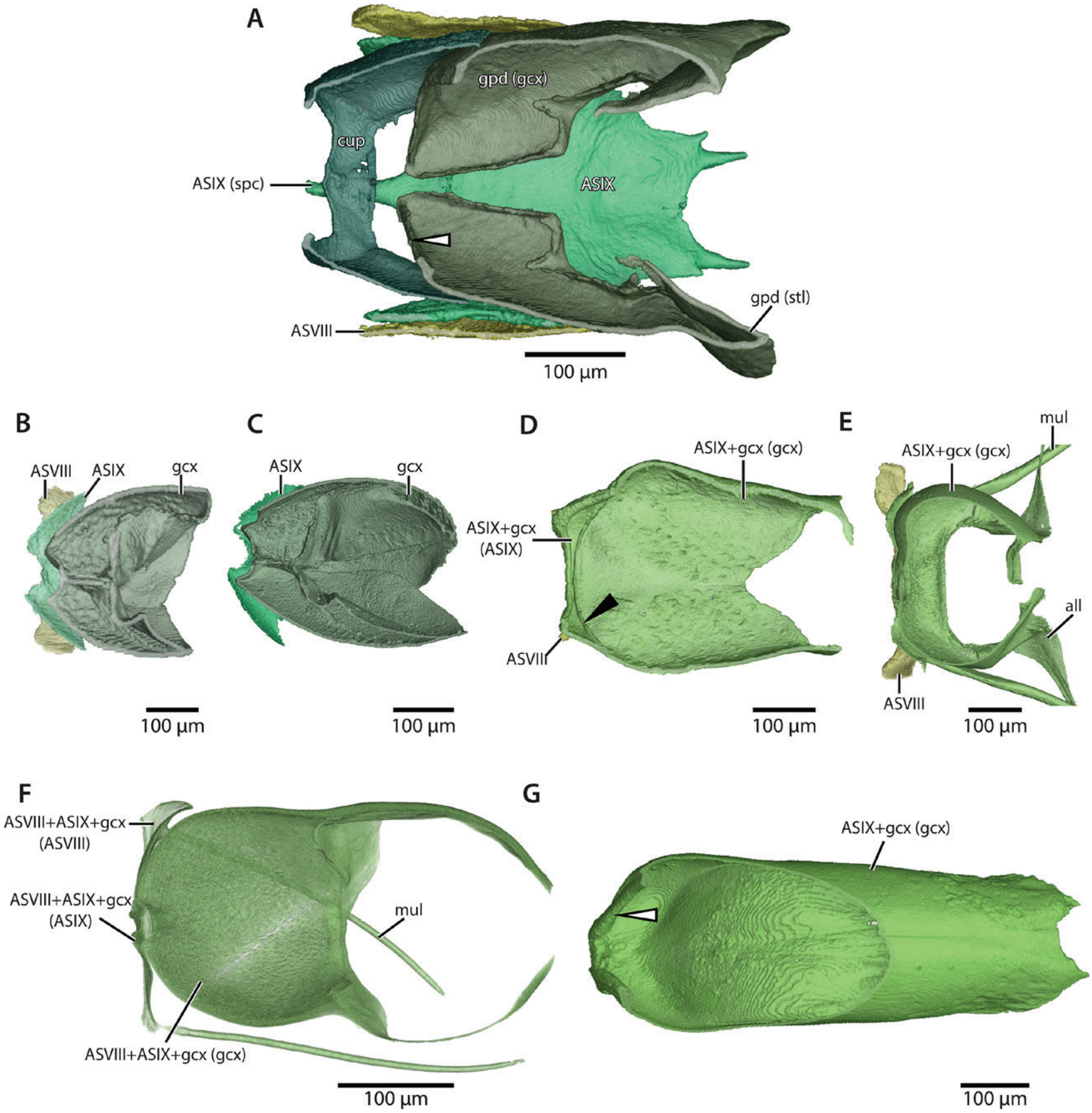

Figure 36. Morphology of the terminal sternites, cupula, and gonopodites, 3D reconstructions in slightly oblique dorsal view. **A** *Lioponera* indet. **B** *Leptanilla* zhg-id04. **C** *Leptanilla* cf. *zaballosi.* **D** *Noonilla* zhg-my03. **E** *Leptanilla* zhg-my02. **F** *Leptanilla* zhg-my04. **G** *Noonilla* cf. *copiosa*. Arrowheads with white fill in A, G indicate anterior boundary of gonocoxites; arrow with black fill in D indicates mesal transverse carina (Section 4.1.1.). Abbreviations: ASVIII = abdominal sternite VIII; ASIX = abdominal sternite IX; cup = cupula; gcx = gonocoxite; gpd = gonopodite; mul = mulceator, stl = gonostylus.

interpenial sclerite (Schulmeister 2001), while “spatha” has been applied to both sclerotizations of the dorsal and ventral interpenial membranes, as well as to parts of the gonocoxites (Audouin 1821).

4.5. Comparative discussion of muscles of interest across the Leptanillinae

Musculation of abdominal sternites VIII–IX is diverse among those lineages in which these sclerites have derived morphologies. Ventral longitudinal muscles VIII–IX are absent in *Noonilla* zhg-my03, *Yavnella* zhg-th03, *Leptanilla* zhg-my03, and -my04, concomitant with the anteroposterior fusion of abdominal sternites VIII–IX. This is unlike *Dolichovespula*, in which abdominal sternites VIII–IX are anteroposteriorly fused and sternosternal musculature is retained (Peck 1937). Intrinsic dorsoventral muscles IX are uniquely lost in *Yavnella* concomitant with the reduction of abdominal segment IX. Ventral longitudinal muscles VIII–IX are retained in *Noonilla* cf. *copiosa* and *Leptanilla* zhg-my02, -my05 as ventral ortholateral muscles VIII–IX.

Based on outgroup sampling, the ancestral insertion of the dorsoventral intrinsic muscles IX in Formicidae is at the anterolateral corners of abdominal sternite IX, and this condition is retained in *Protanilla* zhg-vn01. Dorsoventral intrinsic muscles IX are indiscernible in sampled *Leptanilla* s.str. and absent in *Yavnella*, but where discernible in the Leptanillini s.str. show varying degrees of derivation, in conjunction with often extreme modifications to abdominal sternite IX. In *Noonilla* zhg-my01, -my02, -my03, and -my06 the insertions of the dorsoventral intrinsic muscles IX retain their ancestral position (Fig. 17A), whereas in all examined members of the Bornean morphospecies-group these insertions are well mediad the lateral extremities of abdominal sternite IX (Fig. 35E, F). In *Noonilla* cf. *copiosa* this tendency is developed still further, with the insertions of the dorsoventral intrinsic muscles IX being closely approximated medially (Fig. 35C). These insertions are restricted to the anterior margins of the antecosta of abdominal sternite IX, which forms an anteriorly directed triangle in dorsal view.

Leptanilla zhg-my02 and -my05 exhibit unique extrinsic dorsoventral muscles IX that insert on abdominal sternite VIII from origins on abdominal hemitergites IX (9dvxm) (Fig. 19D, F). Extrinsic muscles are expected to insert on the segment caudad the segment of origin, as observed across the insects. Both intrinsic and extrinsic dorsoventral muscles in the Hymenoptera almost always originate on the tergite and insert on the sternite. The one notable exception to the orientation of origins and insertions in extrinsic muscles cited above is the muscle 7vdxm (M. sterno-tergalis exterior) in female Aculeata, which is clearly homologous among the lineages in which it is present but cannot be serially homologized (Lieberman et al. 2022) and certainly does not correspond to the male 9dvxm. Therefore, the two possibilities for the correspondence of 9dvxm are as follows. First, these muscles properly belong to AVIII, potentially being sterno-sternal longitudinal muscles which shifted their insertion to the tergite, possibly through a series of local translations beginning with movement from the sternite to the ventral tergite. This seems unlikely given the reduction of ATIX to hemitergites in those lineages in which 9dvxm is observed, and a lack of correlates to 9dvxm in species with ATIX not so divided. Second, 9dvxm corresponds to the external intrinsic dorsoventral muscles of AIX, having shifted their insertion to ASVIII during extreme reduction and modification of both ATIX and ASVIII. We here tentatively infer the latter with according terminological designation, but the identity of this ludicrous muscle deserves further investigation.

The orientation of the dorsoventral muscles that are here termed 9dvxm is confounding, and the lack of descriptions of pregenital musculature in male Hymenoptera further obscures evolutionary derivation. We therefore emphasize the importance of descriptions of at least some of the muscles of AVIII–AIX in treatments of the male genitalia. These are largely absent from the literature, with a few notable exceptions (Birket-Smith, 1981; Boulangé, 1924; Kempf, 1956; Youssef, 1969) and occasional mention of 9dvim.

4.6. Functional and evolutionary-biological speculation

4.6.1. Part-wise overview of putative mechanics

Leptanilline ants are rarely observed alive, and only the males of *Leptanilla japonica* Baroni Urbani (Ogata et al. 1995) and *O. hungvuong* (Yamada et al., 2020) have been collected in association with conspecific females. Therefore, we have no direct observations of male ethology in the Leptanillinae and can only speculate on the functional implications of the disproportionately diverse male genital morphology here described from that clade. The sheer novelty of some of the morphological character states observed herein, both among the ants and among the Hymenoptera, makes extrapolation of mechanical function difficult. Nonetheless, the mechanical functions of some conditions can be reasonably inferred.

Any case of recurved serration, or recurved processes, presumably serves an anchoring function, extrapolating from Kamimura (2008). This condition is observed in all three of the non-leptanilline outgroups included in this study, and in other formicids (Forbes and Hagopian 1965: fig. 5; Boudinot 2013: fig. 13), despite the phylogenetic distance of these taxa from one another. When coincident with medial articulation of the penial sclerites, such serration can be inferred to gain purchase on the female genital tract “via a motion analogous to mastication” (Boudinot 2013: 41), mediated by the medial dorsal coxo-penial remotors, 9cprd1, and perhaps aided by the lateral ventral coxo-penial remotors (Boudinot, 2013). Concomitant with the medial fusion of the penial sclerites in the Leptanillini s.str. is the loss of 9cprd1 in all exemplars except *Noonilla* cf. *copiosa*, precluding masticatory motion of the penial sclerites in this tribe. Nonetheless, the recurved process at the penial apex, ventrad the phallotreme, observed in some *Scyphodon* s.l. (Griebenow 2020: fig. 13A) would serve an anchoring function analogous to the penial serration observed in many other male ants, as would the ventromedian genital "trigger" unique to *N. copiosa*, with the longitudinal pairing of proximal and distal ventromedian penial processes here described in *Noonilla* cf. *copiosa* granting opposability (Fig. 18C, D). An obvious anchoring function is otherwise only observed for the penial sclerites among the Leptanillinae in sampled *Protanilla*, in which the penial sclerites exhibit plesiomorphic medial separation.

An anchoring function is inferred for the volsellae of examined *Protanilla* and *Yavnella* zhg-th03, in which ventral penial serration is not observed: this is indicated in both *Protanilla* sampled in this study by recurved medial processes of the parossiculus (Fig. 37E), which in *P. lini* would work in concert with shagreened cuticular denticles on the penial sclerites (Griebenow 2020: figs 19A, C). An anchoring function of the volsellae in *Yavnella* zhg-th03 is indicated by dorsal volsellar serration, analogous to that observed in the penial sclerites across the Formicidae. Recurved spines with a similar putative function are observed on the volsellae in *Anagrus* spp., although these are distal, and laterally rather than medially recurved (Chiappini and Mazzoni 2000).

It can be surmised that the ancestral function of the volsellae for the Hymenoptera was a pincing one (Snodgrass 1941; Smith 1970; Schulmeister 2001, 2003). Loss of the medial ventral coxo-penial remotors (9cprv1, si) and intrinsic medial coxo-lateropenital muscles (9clm1, s) in the Formicidae prevents opening of the parossiculus and lateropenite relative to the resting position of the volsella, a function probably ancestral in the Hymenoptera given the wide distribution of these muscles among symphytan Hymenoptera (Table S3; Schulmeister 2001). The synapomorphic loss of distinction between the parossiculus and lateropenite in the Leptanillini s.str. is therefore associated with loss of the plesiomorphic grasping function of the volsellae, a transformation paralleled among the ants by the Dorylinae (e.g., Boudinot 2013; this study) and elsewhere in the Hymenoptera by the Ceraphronoidea and some Proctotrupomorpha (Mikó et al. 2013). Furcation of the volsellar apices is prevalent in the Southeast Asian clade constituting almost all known *Yavnella* and is somewhat correlated with the secondary proximodistal articulation of the volsella in that clade. It is tempting to infer that the volsella here anchors the genitalia, with contraction of the coxo-lateropenital muscles facilitating a grasping function not accomplished by the gonopodites, which in *Yavnella* are always firmly inarticulate.

The medial fusion of the volsellae in the Bornean morphospecies-group is intriguing from a functional standpoint. In *Leptanilla* zhg-my03 and -my04, the volsellar apices are dorsally recurved (Fig. 38G), and therefore would function analogously to furcated or falcate volsellae observed in most *Yavnella*. In the remainder of the Bornean morphospecies-group sampled here (which constitute a monophyletic group), the volsellae are elongated, and fit into slots in the penial sclerites laterad the elevated, recessed phallotreme. Uniquely among hymenopterans, so far as is known, coxo-penial muscles are here found to be absent in *Leptanilla* zhg-id01, zhg-my02, -my05, and -my06. Movement of the penial sclerites along the dorsoventral axis in this clade is therefore mediated by retraction of the basomedially fused volsellae, musculated by lateral coxo-lateropenital muscles, with the penial sclerites articulating with the gonocoxites via penial condyles. Recurved teeth at the volsellar apices in *Leptanilla* zhg-my02, -my05, and -my06 (Figs 37F, 38H) imply that the volsellae serve an anchoring function in these morphospecies, concurrent with indirect movement of the penial sclerites by way of the volsellae; no such function is implied for *Leptanilla* zhg-id01, since in this morphospecies the volsellar apices are entire. Rather, such a function is obviously served in *Leptanilla* zhg-id01 by a small falcate hook, at the penial apex, dorsally recurved (Griebenow 2020: fig. 13C).

The absence of the volsellae in *Scyphodon* s.l. is associated among the exemplars of that clade sampled in this study with irregular ventral serration or a recurved process proximoventrad the penial apex, as noted above. *Noonilla* zhg-my03 is an exception, with a penial venter that is unsculptured and lacks any recurved processes proximad the apex. Notably, the gonostylar apex in *Noonilla* zhg-my03 is unique among known *Scyphodon* s.l. in its bifurcation into recurved lobes; we infer that in the absence of penial serration, the gonostyli in this morphospecies act in an anchoring capacity, unlike the clasping observed in other ants. Moreover, the exceptional medial fusion of the gonostyli in *Noonilla* zhg-my03 constitutes serial parallelism with the volsellae of the Bornean morphospecies-group, suggesting a similar function. Curiously, the complete absence of the volsellae in *Leptanilla* zhg-mm03 is not concurrent with any penial serration.

Although we do not examine membranous structures in detail here, a few observations of apparently derived skeletomusculature likely relate to the function of the endophallus through direct or indirect muscular action. First is the presence and expression of the endophallic sclerite, which is located within the ejaculatory duct at or near the primary gonopore, i.e., the point at which the paired ducti ejaculatorii merge to form the endophallus. This sclerite may or may not be homologous in the various ants in which it occurs, or with the endophallic sclerite in other orders, including Coleoptera (see, e.g., Boudinot 2018, Génier 2019 and references therein), or the anterior sclerite in the endophallic bulbalis of Siphonaptera (Günther 1961). Possible homology has also been questioned between the formicid endophallic sclerite and the fibula ducti in symphytan Hymenoptera or even the musculated "Ostialsklerit" of some Mecoptera (Schulmeister 2001). The term "fibula ducti" has been applied to two dissimilar forms: a small, unpaired sclerite within the endophallus or ductus ejaculatorius of various sawflies; and, in Pergidae and Argidae, a larger pair of plates on the ectodorsal and ectoventral surfaces of the ducti ejaculatorii, connected to one another by a sclerotic bridge in "the median plane"

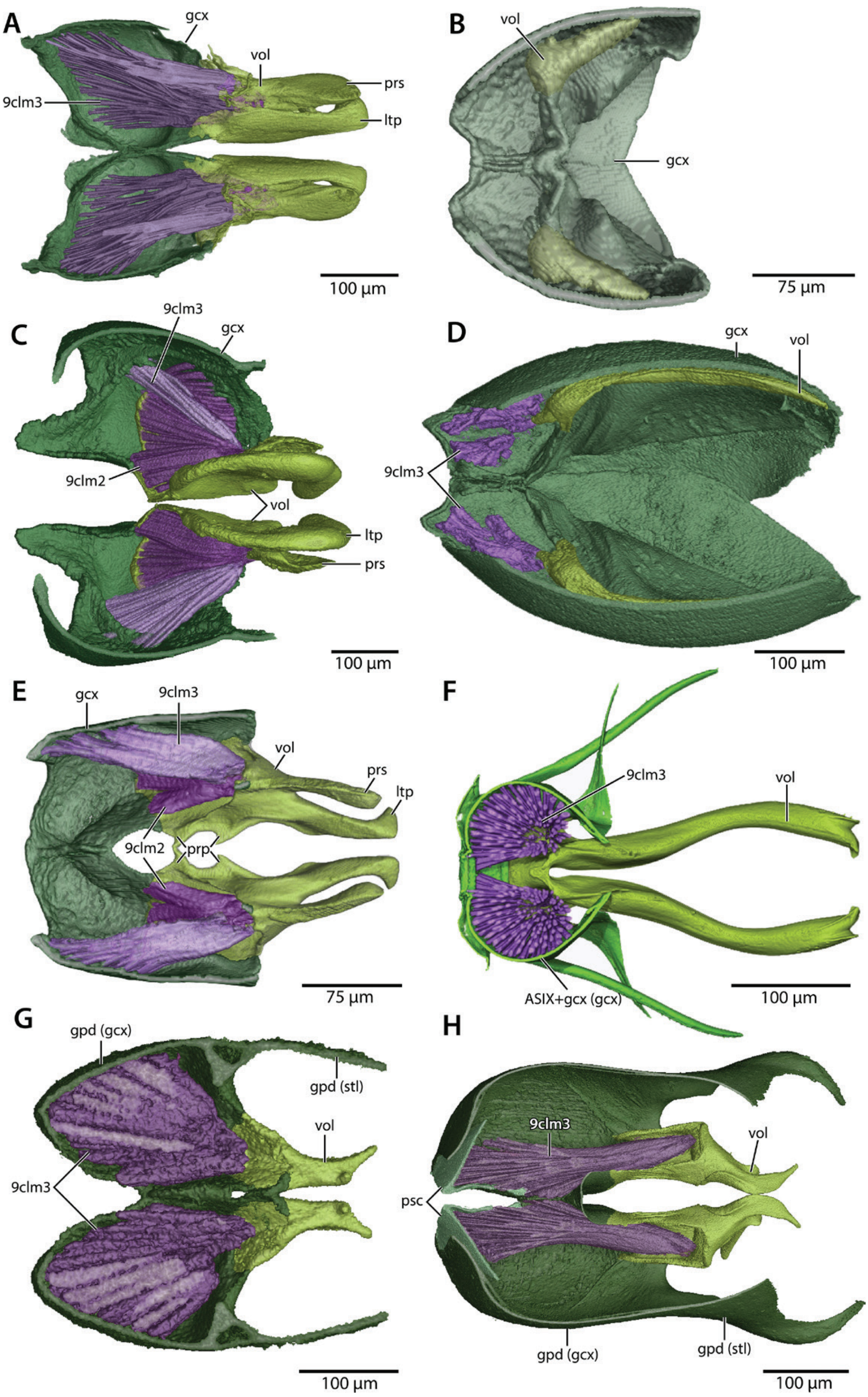

Figure 37. Morphology of the coxo-lateropenital musculature and associated sclerites, 3D reconstructions, coronal cross-sections in dorsal view. **A** *Odontomachus* indet. **B** *Leptanilla* zhg-id04. **C** *Myrmica ruginodis.* **D** *Leptanilla* cf. *zaballosi.* **E** *Protanilla* zhg-vn01. **F** *Leptanilla* zhg-my02. **G** *Yavnella* zhg-bt01. **H** *Yavnella* zhg-th03. Abbreviations: gpd = gonopodite; gcx = gonocoxite; ltp = lateropenite; prp = lateropenital recurved processes; prs = parossiculus; psc = penial sclerite; stl = gonostylus; vol = volsella; 9clm2 = lateral intrinsic coxo-lateropenital muscles; 9clm3 = medial extrinsic coxo-lateropenital muscles.

(Schulmeister 2001:339, 2003). It seems likely that the endophallic sclerite corresponds to the former, internal form, while homology with the external sclerites is more doubtful, although the two forms may indeed be homologous, as suggested by the presence of the median bridge. In Mecoptera, the Ostialsklerit is unpaired, and approximates the form of the formicid endophallic sclerite; however, the term has been applied both to an ectal sclerite, as in *Bittacus*, and to an internal sclerite at the distal end of the endophallus as in *Apteropanorpa* (Willmann 1981).

Inferring the evolutionary origin of the endophallic sclerite is complicated by the lack of intermediate forms

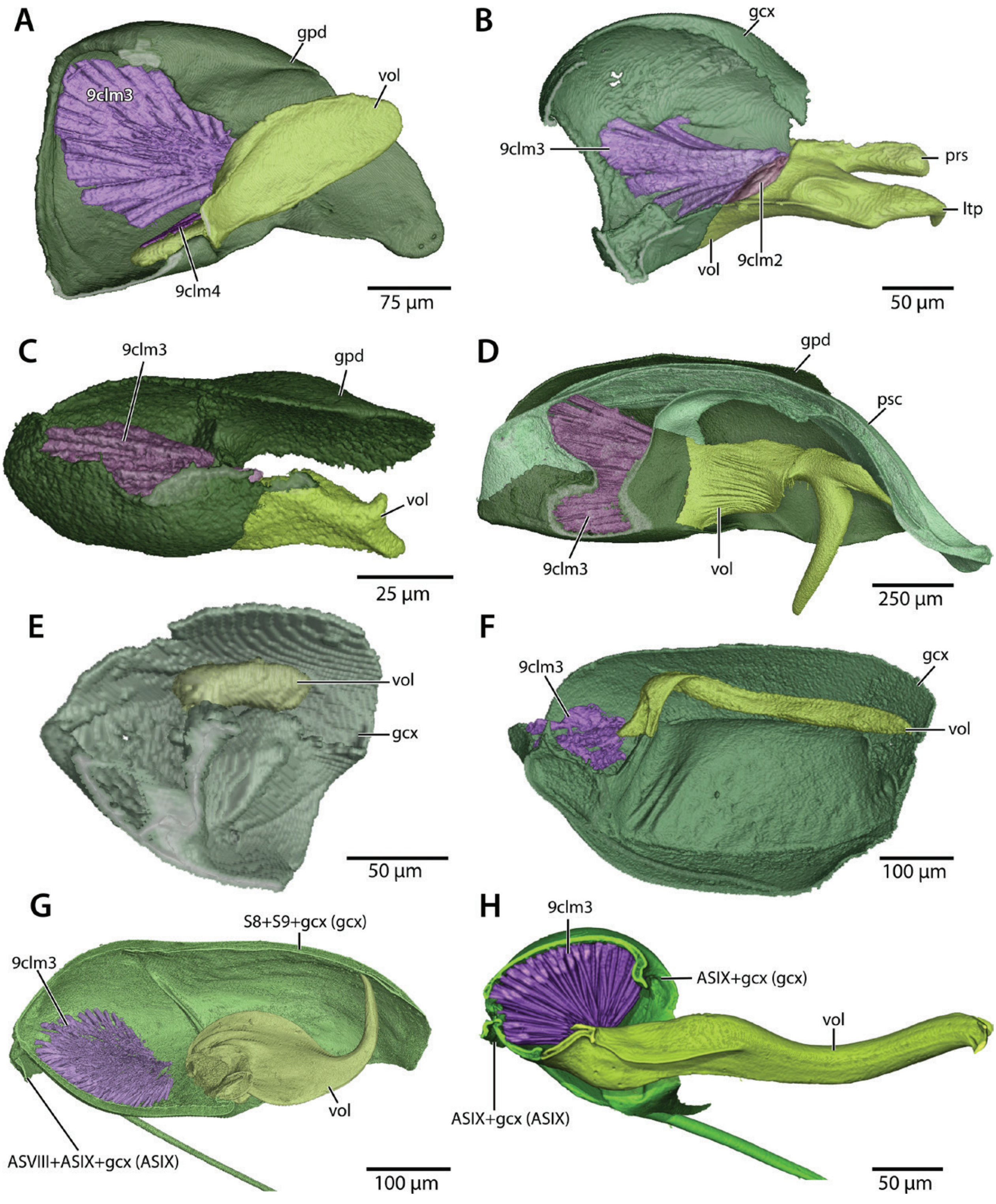

Figure 38. Morphology of the coxo-lateropenital musculature and associated sclerites, 3D reconstructions in sagittal cross-section. **A** *Lioponera* indet. **B** *Protanilla* zhg-vn01. **C** *Yavnella* zhg-bt01. **D** *Yavnella* zhg-th03. **E** *Leptanilla* zhg-id04. **F** *Leptanilla* cf. *zaballosi.* **G** *Leptanilla* zhg-my04. **H** *Leptanilla* zhg-my02. Abbreviations: ASIX = abdominal sternite IX; gcx = gonocoxite; gpd = gonopodite; ltp = lateropenite; prs = parossiculus; psc = penial sclerites; vol = volsella; 9clm2 = lateral intrinsic coxo-lateropenital muscles; 9clm3 = medial extrinsic coxo-lateropenital muscles; 9clm4 = lateral extrinsic coxo-lateropenital muscles.

indicating that it is, e.g., derived by fragmentation and internalization of an existing penial sclerite, or represents a novel sclerotization of the endophallus itself. The ducti ejaculatorii and endophallus are ectodermal organs with cuticular surfaces and thus may be expected to display ontogenetic plasticity between conjunctiva and sclerite as in exoskeletal surfaces, albeit within a different set of constraints, for example, of optimum flexibility and space-filling.

The endophallic sclerite is not directly musculated in any known ants, and therefore likely functions through indirect action of muscles associated ectally with the endophallus. Contraction of 9cppv1 (h) in *Myrmica ruginodis*, for example, close the endophallus and allow accumulation of potential energy through pressure on the endophallic sclerite, the release of which could increase the velocity of ejaculation. An alternate hypothesis is that the endophallic sclerite serves as simple reinforcing structure against pressure during ejaculation, or more specifically as a stent to keep the endophallus dilated during contractions of other powerful genital muscles, a situation which may be more probable in lineages that lack muscles near the primary gonopore.

In many sawflies, the lateral pene-lateropenital muscles 10plm2 (n) are frequently associated medially with the endophallic membrane, probably playing a role in closing or opening the genital tract (Schulmeister 2001). A compelling preliminary observation is that in some ants, which lack pene-lateropenital muscles, other muscles appear to be partially or totally associated with the endophallus. In *M. ruginodis*, some partially differentiated fibers of 9cppv1 (h) wrap ventromedially around the endophallus in its proximal region, near the primary gonopore, and may serve to compress the duct dorsoventrally. Similarly, 9cppv2 (h') in *Dorylus funereus* Emery, 1895 "embrace the vesica ejaculatorius" and "cause a powerful contraction ... presumably essential for the ejaculation of sperm" (Birket-Smith 1981: 385). In at least *Aenictogiton* (Dorylinae), there is a massive, approximately toroidal "knot" of muscles surrounding the endophallus, which appears to comprise at least 9cppv1 and likely includes other coxo-penial muscles. Contraction of this effectively circular muscle group might cause forceful ejaculation or extension of the membranous elements of the genitalia. A dedicated comparative study of the structure and function of the endophallic sclerite and muscles acting on the genital tract is merited, preferably histological.

4.6.2. "Detachable Penis": implications of putative suicidal mating in the Leptanillinae

As noted above, copulation in the Leptanillinae has never been observed. Given that the queens of *Opamyrma*, *Protanilla*, and *Anomalomyrma* are usually alate (Bolton 1990b; Baroni Urbani and de Andrade 2006; Chen et al. 2017; Ito et al. 2021) it is theoretically feasible for queens and males of these taxa to be observed in copula, but all known queens within the tribe Leptanillini s.str. are wingless, with reduced eyes (e.g., Kutter 1948; Ito and Yamane 2020): this dichthadiiform phenotype would suggest that copulation is subterranean in the Leptanillini s.str., and so it is extremely improbable that mating behaviors will ever be observed in this clade. This limitation is disappointing from a biomechanical perspective, since all leptanilline lineages in which the male genitalia are most extreme in derivation and interspecific variation belong to the Leptanillini s.str. Due to these limitations, the biological implications of the skeletomusculature and macroevolutionary trends described herein are for now only the subjects of well-informed speculation.

The loss of extrinsic genital musculature in the Leptanillini s.str., whether due to the remaining tergo-coxal muscles IX becoming intrinsic to the cupula (e.g., *Yavnella* zhg-th03), the loss of tergo-coxal muscles (*Leptanilla* zhg-mm03), or the complete loss of the cupula by fusion to adjacent sclerites (*Leptanilla* s.l. except for the Indochinese morphospecies-group), is presumably associated with suicidal mating – manifesting male-male competition for mating time. This is analogous to copulation in *Apis* (Apidae: Apinae: Apini), in which suicidal mating by detachment of the male genital capsule (Koeniger and Koeniger 1991) is enabled by the absence of the cupula and associated musculature, with there being extrinsic musculation by a single pair of muscles that proceed from abdominal sternite VIII to the gonocoxites (Snodgrass 1942). The corollary of this hypothesis is that suicidal mating does not occur in *Scyphodon* s.l. and the Bornean morphospecies-group, since in these clades sterno-sternal and dorsoventral tergosternal musculature connects the male genital capsule to the remainder of the metasoma. Such a conclusion is contradicted by the common occurrence of suicidal mating in *Dinoponera* and *Diacamma* (Ponerinae: Ponerini) (Monnin and Peeters 1998; Allard et al. 2002), neither of which show reduction or loss of the cupula and associated musculature (Tozetto and Lattke 2020; this study).

In metazoans that use internal fertilization, genital morphology is often conspicuously varied relative to other anatomical regions, with the male genitalia having received more descriptive study than the female counterparts (Sloan and Simmons 2019). Empirical studies continue to indicate that sexual selection is the primary evolutionary force behind this phenomenon (Hosken and Stockley 2004) rather than pleiotropic effects (Mayr 1963) or the lock-and-key hypothesis (Dufour 1844), but the mechanisms that are at play in sexual selection, and their proportional significance in the evolution of a given lineage, often cannot be discriminated experimentally. Under the theoretical synthesis of Eberhard (1985), one would hypothesize that the diversity of male genitalia in the Leptanillinae results from Fisherian sexual selection (Fisher 1930) and is therefore driven by female choice. Other hypothesized selective mechanisms, such as sexual antagonism, that would give rise to observed morphological divergence which is disproportionate in genitalia relative to other anatomical regions, are not mutually exclusive with female choice (Simmons 2014). These may operate on male genitalia in the Leptanillinae as well.

Qualitatively, the male genitalia of *Scyphodon* s.l. and the Bornean morphospecies-group show increased morphological disparity relative to that observed in *Leptanilla* s.str. or the Indochinese morphospecies-group. This could indicate that posterior fusion of abdominal sternite IX to the genital capsule is associated with an increased tempo of morphological evolution in the genitalia – an observation that invites macroevolutionary scrutiny. Quantitative tests of this hypothesis would require phylogenetic comparative analyses utilizing landmark-based geometric morphometrics, applied to scleritic structures. Such an enterprise is conceivable given the scan data published here but may be theoretically challenging, due to operational obstacles and analytical conundrums presented by phylogenetic variance in articulation of adjacent sclerites (Vidal-García et al. 2018), and the absence of definitively homologous landmarks in certain leptanilline lineages (cf. Borgard et al. 2020).

5. Conclusion

Male genitalia in the insects are diverse in morphology and corresponding function, with this profusion of form often covarying with phylogenetic structure. The male genitalia are therefore of enduring functional, evolutionary, and taxonomic interest. Despite the ecological prevalence and diversity of the Formicidae, little comparative work has focused on the male genitalia of this clade for either classificatory or comparative morphological purposes, compared to the scientific attention that the male genitalia in other insect taxa have received. The ant subfamily Leptanillinae deserves further scrutiny in this regard, since the male genitalia in this clade show high morphological disparity and sometimes spectacular derivation, which have hitherto received only piecemeal description (e.g., Santschi 1907, 1908; Wheeler and Wheeler 1930; Petersen 1968).

In this study we provide the first descriptions of male genital skeletomusculature within the Leptanillinae, from the perspective of comparative morphology. These descriptions are guided by phylogeny, as inferred from molecular and morphological data (Griebenow 2020, 2021; in prep; Griebenow et al. 2022). Our observations are facilitated by virtual dissection of male genital skeletomuscular components, as reconstructed from scans acquired with micro-CT, or directly derived from these scans without segmentation. To describe the range of muscular modifications relative to the putative ancestral condition for the Hymenoptera that are observed across sampled leptanilline lineages, we present a new synthetic terminology for male genital musculature, using interordinal genital homologies inferred by Boudinot (2018) for the Endopterygota, and designed to be practically extensible across the whole of the order Hymenoptera. While this terminology is designed specifically for hymenopteran male genitalia, the notational conventions of this terminology are deliberately congruent with that used for other insect anatomical regions (e.g., Friedrich and Beutel 2008), adding to a comprehensive and consistent schema for morphological study across the entire hymenopteran soma. We identify equivalencies with the HAO (Yoder et al., 2010) and consider the two approaches complementary, though based on different homology hypotheses.

Taxonomy in the Leptanillinae relies on male morphological characters, especially those of the genitalia, due to the scarcity of female specimens and lack of phylogenetic signal from worker morphology; our observations clarify and expand our understanding of male genital morphology in the Leptanillinae, therefore aiding future systematic revision of this clade. We find that male genital skeletomusculature in the Leptanillinae is characterized by an overall trend of skeletomuscular reduction relative to the remainder of the Formicidae, in some lineages to an extreme otherwise not observed among ants. Many apomorphic scleritic fusions and muscular losses are homoplasious amongst different lineages of the Leptanillinae and are therefore examples of evolutionary parallelism sensu Futuyma (1998) but have no known morphological parallels in other ant lineages, and few known parallels across the Hymenoptera as a whole. Other modifications are autapomorphies of certain leptanilline subclades, relative to the remainder of the Formicidae: particularly striking among these is the fusion of the cupula to abdominal sternite VIII in most *Yavnella*, and the proximomedian fusion of the gonostyli in *Noonilla* zhg-my03.

Despite our inability to observe copulation in most leptanilline ants, and the complete absence to date of such observations, we extrapolate the function of some derived skeletomuscular character states observed in this study. Noteworthy among these in its behavioral implications is the lack of extrinsic musculation to the male genitalia that is synapomorphic for the Leptanillini s.str., to our knowledge unique among the ants. The loss of extrinsic musculation of the genital capsule would mechanically oblige detachment of the genitalia during copulation. Certain subclades of the Leptanillini s.str. are here found to exhibit posterior fusion of abdominal sternite IX to the genital capsule; by consequence, the genital capsule is extrinsically musculated in these clades by ventral longitudinal and dorsoventral abdominal muscles, with this musculation therefore being a secondary derivation of these subclades.

While provincial in scope – focusing upon a species-poor clade of ants, sister to nearly all other members of the formicid crown-group (Borowiec et al. 2019; Romiguier et al. 2022) – this comparative study is the first to address the male genitalia of any ant clade in such descriptive detail, explicitly grounded in phylogeny, and with a mind towards an evolutionary-morphological research program (Richter and Wirkner 2014). It is on account of this perspective that, so far as is possible given the cryptic biology of our study system, we address the functional and evolutionary implications of our findings; further, we communicate our findings with terminology that incorporates hypothesized homology and accommodates male genital variation not just in the Leptanillinae but the Hymenoptera as a whole. This establishes a foundation for a synthetic view of male genital evolution in the Leptanillinae, and indeed to the whole of the ants.

6. Author Contributions

Zachary Griebenow: Conceptualization, Methodology, Data Curation, Writing – Original Draft, Writing – Review and Editing, Visualization **Adrian Richter:** Investigation, Resources, Data Curation, Writing – Review and Editing, Visualization **Thomas van de Kamp:** Investigation **Evan Economo:** Data Curation, Funding Acquisition, Writing – Review and Editing **Ziv Lieberman:** Conceptualization, Writing – Original Draft, Writing – Review and Editing, Visualization

7. Acknowledgements

We thank Dilworth Parkinson, Douglas Rowland and Georg Fischer for their help in obtaining additional scan data for ingroup exemplars, despite the perpetually challenging minuteness of these specimens. We thank Lars Vilhelmsen and an anonymous reviewer for their insightful critiques of an initial draft of this manuscript. We also thank Phil Ward for advice and enduring support throughout the course of this project. We are grateful to Elias Hamann and Mathias Hurst for their assistance during the tomographic measurements at KIT and thank Tomáš Faragó for tomographic raw data reconstruction. Lastly, we thank all who provided specimens included in this study: Bonnie Blaimer (ZMHB), José María Gómez-Durán, Brian Fisher (CASC), Jadranka Rota (MZLU), Lars Vilhelmsen (NHMD), Kevin Williams (CSCA), Masashi Yoshimura, and the staff of Flora & Fauna International (Myanmar). This research used resources of the Advanced Light Source, which is a DOE Office of Science User Facility under contract no. DE-AC02-05CH11231. This research was supported by the UC Davis Dept. of Entomology & Nematology, UC Davis Jastro-Shields, NSF grant DEB-1932405 to P. S. Ward, Helmsley Charitable Trust, and Smithsonian Institution Global Genome Initiative. We gratefully acknowledge the data storage service SDS@hd supported by the Ministry of Science, Research and the Arts Baden-Württemberg (MWK) and the German Research Foundation (DFG) through grant INST 35/1503-1 FUGG. Further, we acknowledge the KIT Light Source for provision of instruments at their beamlines and we would like to thank the Institute for Beam Physics and Technology (IBPT) for the operation of the storage ring, the Karlsruhe Research Accelerator (KARA).

8. References

Aibekova L, Boudinot Be, Beutel RG, Richter A, Keller RA, Hita Garcia F, Economo EP (2022) The skeletomuscular system of the mesosoma of *Formica rufa* workers (Hymenoptera: Formicidae). Insect Systematics and Diversity 6(2): 1–26. https://doi.org/https://doi.org/10.1093/isd/ixac002

Alam SM (1952) Studies on "skeleto-muscular mechanism" of the male genitalia in *Stenobracon deesae* Cam. (Hymenoptera: Braconidae). Beiträge zur Entomologie, Band 2 2(6): 620–634.

Allard D, Gobin B, Ito F, Billen J, Tsuji K (2002) Sperm transfer in the Japanese queenless ant *Diacamma* sp. (Hymenoptera: Formicidae). Netherlands Journal of Zoology 52(1): 77–86. https://doi.org/10.1163/156854202760405203

Aspöck U (2002) Male genital sclerites of Neuropterida: An attempt at homologisation (Insecta: Holometabola). Zoologischer Anzeiger 241(2): 161–171. https://doi.org/10.1078/S0044-5231(04)70071-6

Audouin JV (1821) Observations sur les organs copulateursâles des Bourdons. Rapport lit par Latreille en lundi 9 avril. Annales géné rales des sciences physiques 8: 285–289.

Ball DE, Vinson SB (1984) Anatomy and histology of the male reproductive system of the fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae). International Journal of Insect Morphology and Embryology 13: 283–294.

Barden P, Boudinot BE, Lucky A (2017) Where fossils dare and males matter: combined morphological and molecular analysis untangles the evolutionary history of the spider ant genus *Leptomyrmex* Mayr (Hymenoptera: Dolichoderinae). Invertebrate Systematics 31(6): 765–780. https://doi.org/10.1071/IS16067

Baroni Urbani C, de Andrade ML (2006) A new *Protanilla* Taylor, 1990 (Hymenoptera: Formicidae: Leptanillinae) from Sri Lanka. Myrmecologische Nachrichten 8: 45–47.

Beck DE (1933) A morphological study of the male genitalia of various genera of bees. Doctor of Philosophy, Iowa State University, Digital Repository, Ames, 77 pp. https://doi.org/10.31274/rtd-180813-14568

Beutel RG, Vilhelmsen L (2007) Head anatomy of Xyelidae (Hexapoda: Hymenoptera) and phylogenetic implications. Organisms Diversity & Evolution 7(3): 207–230. https://doi.org/10.1016/j.ode.2006.06.003

Beutel RG, Friedrich F, Economo EP (2022) Patterns of morphological simplification and innovation in the megadiverse Holometabola (Insecta). Cladistics 38: 227–245. https://doi.org/10.1111/cla.12483

Birket-Smith J (1981) Male genitalia of Hymenoptera – a review based on morphology in Dorylidae (Hymenoptera: Formicoidea). Entomologia Scandinavica Supplement 15: 377–397.

Blaimer BB, Santos BF, Cruaud A, Gates MW, Kula RR, Mikó I, Rasplus J-V, Smith DR, Talamas EJ, Brady SG, Buffington ML (2023) Key innovations and the diversification of Hymenoptera. Nature Communications 14: 1212. https://doi.org/10.1038/s41467-023-36868-4

Bolton B (1990a) Abdominal characters and status of the cerapachyine ants (Hymenoptera, Formicidae). Journal of Natural History 24(1): 53–68. https://doi.org/10.1080/00222939000770051

Bolton B (1990b) The higher classification of the ant subfamily Leptanillinae (Hymenoptera: Formicidae). Systematic Entomology 15: 262–282.

Bolton B (2003) Synopsis and classification of the Formicidae. Memoirs of the American Entomological Institute 71: 1–370

Boomsma JJ, Baer B, Heinze J (2005) The evolution of male traits in social insects. Annual Review of Entomology 50(1): 395–420. https://doi.org/10.1146/annurev.ento.50.071803.130416

Borgard HL, Baab K, Pasch B, Riede T (2020) The shape of sound: A geometric morphometrics approach to laryngeal functional morphology. Journal of Mammalian Evolution 27(3): 577–590. https://doi.org/10.1007/s10914-019-09466-9

Borowiec ML (2016) Generic revision of the ant subfamily Dorylinae (Hymenoptera, Formicidae). ZooKeys 608: 1–280. https://doi.org/10.3897/zookeys.608.9427

Borowiec ML, Rabeling C, Brady SG, Fisher BL, Schultz TR, Ward PS (2019) Compositional heterogeneity and outgroup choice influence the internal phylogeny of the ants. Molecular Phylogenetics and Evolution 134: 111–121. https://doi.org/10.1016/j.ympev.2019.01.024

Boudinot BE (2013) The male genitalia of ants: Musculature, homology, and functional morphology (Hymenoptera, Aculeata, Formicidae). Journal of Hymenoptera Research 30: 29–49. https://doi.org/10.3897/jhr.30.3535

Boudinot BE (2015) Contributions to the knowledge of Formicidae (Hymenoptera, Aculeata): A new diagnosis of the family, the first global male-based key to subfamilies, and a treatment of early branching lineages. European Journal of Taxonomy (120). https://doi.org/10.5852/ejt.2015.120

Boudinot BE (2018) A general theory of genital homologies for the Hexapoda (Pancrustacea) derived from skeletomuscular correspondences, with emphasis on the Endopterygota. Arthropod Structure & Development 47(6): 563–613. https://doi.org/10.1016/j.asd.2018.11.001

Boudinot BE, Probst RS, Brandão CRF, Feitosa RM, Ward PS (2016) Out of the Neotropics: newly discovered relictual species sheds light on the biogeographical history of spider ants (Leptomyrmex, Dolichoderinae, Formicidae). Systematic Entomology 41(3): 658–671. https://doi.org/10.1111/syen.12181

Boudinot BE, Moosdorf OTD, Beutel RG, Richter A (2021) Anatomy and evolution of the head of *Dorylus helvolus* (Formicidae: Dorylinae): Patterns of sex- and caste-limited traits in the sausagefly and the driver ant. Journal of Morphology: jmor.21410. https://doi.org/10.1002/jmor.21410

Boudinot BE, Khouri Z, Richter A, Griebenow ZH, van de Kamp T, Perrichot V, Barden P (2022) Evolution and systematics of the Aculeata and kin (Hymenoptera), with emphasis on the ants (Formicoidea: †@@@idae fam. nov., Formicidae). https://doi.org/10.1101/2022.02.20.480183

Boulangé H (1924) Recherces sur l'áppareil copulateur des Hyménopterès et spécialement des Chalastogastres. Mémoires et Travaux de la Faculté Catholique de Lille 28: 1–444.

Branstetter MG, Longino JT, Ward PS, Faircloth BC (2017) Enriching the ant tree of life: Enhanced UCE bait set for genome-scale phylogenetics of ants and other Hymenoptera. Methods in Ecology and Evolution 8(6): 768–776. https://doi.org/10.1111/2041-210X.12742

Brues CT (1925) *Scyphodon*, an anomalous genus of Hymenoptera of doubtful affinities. Treubia 6: 93–96.

Buenaventura E, Pape T (2018) Phylogeny, evolution and male terminalia functionality of Sarcophaginae (Diptera: Sarcophagidae). Zoological Journal of the Linnean Society 183(4): 808–906. https://doi.org/10.1093/zoolinnean/zlx070

Chapman RF, Simpson SJ, Douglas AE (2013) The insects: Structure and function. Fifth edition. Cambridge University Press, New York, 929 pp.

Chen Z-L, Shi F-M, Zhou S-Y (2017) First record of the monotypic genus *Opamyrma* (Hymenoptera: Formicidae) from China. Far Eastern Entomologist 335: 7–11.

Chiappini E, Mazzoni E (2000) Differing morphology and ultrastructure of the male copulatory apparatus in species-groups of *Anagrus* Haliday (Hymenoptera: Mymaridae). Journal of Natural History 34(8): 1661–1676. https://doi.org/10.1080/00222930050117549

Chiquetto-Machado PI, Cancello EM (2021) Cladistic analysis of *Paraphasma* (Phasmatodea: Pseudophasmatidae) highlights the importance of the phallic organ for phasmid systematics. Zoological Journal of the Linnean Society 193(1): 158–198. https://doi.org/10.1093/zoolinnean/zlab004

Clarke DJ (2011) Testing the phylogenetic utility of morphological character systems, with a revision of *Creophilus* Leach (Coleoptera: Staphylinidae). Zoological Journal of the Linnean Society 163(3): 723–812. https://doi.org/10.1111/j.1096-3642.2011.00725.x

Clausen R (1938) Untersuchungen über den männlichen Copulationsapparat der Ameisen, speziell der Formicinae. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 17: 233–346.

Crampton GG (1919) The genitalia and terminal abdominal structures of males, and the terminal structures of the larvae of "chalastogastrous" Hymenoptera. Proceedings of the Entomological Society of Washington 21: 129–151.

Dirsh VM (1956) The phallic complex in Acridoidea (Orthoptera) in relation to taxonomy. Transactions of the Royal Entomological Society of London 108(7): 223–270. https://doi.org/10.1111/j.1365-2311.1956.tb02270.x

Domenichini G (1953) Studio sulla morfologia dell'addome degli Hymenoptera Chalcidoidea. Bollettino di Zoologia Agraria e Bachicultura, Milano 19: 183–298.

Dreyer AP, Shingleton AW (2011) The effect of genetic and environmental variation on genital size in male *Drosophila*: canalized but developmentally unstable. PLOS ONE 6(12): e28278. https://doi.org/10.1371/journal.pone.0028278

Dufour L (1844) Anatomie générale des Dipteres. Annales des Sciences Naturelles 1: 244–264.

Eberhard WG (1985) Sexual Selection and Animal Genitalia. Harvard University Press, Cambridge, Mass. Available from: http://www.degruyter.com/search?f_0=isbnissn&q_0=9780674330702&searchTitles=true (April 8, 2022).

Eguchi K, Yoshimura M, Yamane S (2006) The Oriental species of the ant genus *Probolomyrmex* (Insecta: Hymenoptera: Formicidae: Proceratiinae). Zootaxa 1376(1): 1. https://doi.org/10.11646/zootaxa.1376.1.1

Evenhuis NL (2022) The insect and spider collections of the world website. Available from: http://hbs.bishopmuseum.org/codens.

Fisher RA (1930) The genetical theory of natural selection. Oxford Clarendon Press, 306 pp. Available from: http://archive.org/details/geneticaltheoryo00fishuoft (April 8, 2022).

Forbes J (1954) The anatomy and histology of the male reproductive system of *Camponotus pennsylvanicus* DeGeer (Formicidae, Hymenoptera). Journal of Morphology 95: 523–555.

Forbes J, Do-Van-Quy D (1965) The anatomy and histology of the male reproductive system of the legionary ant, *Neivamyrmex harrisi* (Haldeman) (Hymenoptera: Formicidae). Journal of the New York Entomological Society 73: 95–111. https://doi.org/10.25849/myrmecol.news_030:229

Forbes J, Hagopian M (1965) The male genitalia and terminal segments of the ponerine ant *Rhytidoponera metallica* F. Smith (Hymenoptera: Formicidae). Journal of the New York Entomological Society 73(4): 190–194.

Friedrich F, Beutel RG (2008) The thorax of *Zorotypus* (Hexapoda, Zoraptera) and a new nomenclature for the musculature of Neoptera. Arthropod Structure & Development 37(1): 29–54. https://doi.org/10.1016/j.asd.2007.04.003

Fuessl M, Heinze J, Schrempf A (2015) Queen and male longevity in the Southeast Asian ant *Cardiocondyla tjibodana* Karavaiev, 1935. Asian Myrmecology 7: 137–141.

Futuyma DJ (1998) Evolutionary Biolog$^{y.}$ 3rd ed. Sinauer Associates Inc., Massachusetts.

Génier F (2019) Endophallites: a proposed neologism for naming the sclerotized elements of the insect endophallus (Arthropoda: Insecta). Annales de la Société entomologique de France (N.S.) 55(6): 482–484. https://doi.org/10.1080/00379271.2019.1685907

Gibson GAP (1986) Evidence for monophyly and relationships of Chalcidoidea, Mymaridae, and Mymarommatidae (Hymenoptera: Terebrantes). The Canadian Entomologist 118(3): 205–240. https://doi.org/10.4039/Ent118205-3

Gibson GAP, Read J, Huber JT (2007) Diversity, classification and higher relationships of Mymarommatoidea (Hymenoptera). Journal of Hymenoptera Research 16(1): 51–146.

Girón JC, Tarasov S, González Montaña LA, Matentzoglu N, Smith AD, Koch M, Boudinot BE, Bouchard P, Burks R, Vogt L, Yoder M, Osumi-Sutherland D, Friedrich F, Beutel R, Mikó I (2022) Formalizing insect morphological data: A model-based, extensible insect anatomy ontology and its potential applications in biodiversity research and informatics. https://doi.org/10.20944/preprints202201.0254.v1

Griebenow ZH (2020) Delimitation of tribes in the subfamily Leptanillinae (Hymenoptera: Formicidae), with a description of the male of *Protanilla lini* Terayama, 2009. Myrmecological News 30: 229–250. https://doi.org/10.25849/myrmecol.news_030:229

Griebenow ZH (2021) Synonymisation of the male-based ant genus *Phaulomyrma* (Hymenoptera: Formicidae) with *Leptanilla* based upon Bayesian total-evidence phylogenetic inference. Invertebrate Systematics 35: 603–636. https://doi.org/10.1071/IS20059

Griebenow ZH, Isaia M, Moradmand M (2022) A remarkable troglomorphic ant, *Yavnella laventa* sp. nov. (Hymenoptera: Formicidae: Leptanillinae), identified as the first known worker of *Yavnella* Kugler by phylogenomic inference. Invertebrate Systematics 36(12): 1118–1138. https://doi.org/10.1071/IS22035

Günther KK (1961) Funktionell-anatomische Untersuchung des männlichen Kopulationsapparates der Flöhe unter Berücksichtung seiner postembryonalen Entwicklung (Siphonaptera). Deutsche Entomologische Zeitschrift 8: 258–349.

Gustafson, JF (1950) The origin and evolution of the genitalia of the Insecta. Microentomology 15: 35–67.

Hagopian M (1963) An anatomical and histological study of the male ponerine ant, *Rhytidoponera metallica* F. Smith (Formicidae, Hymenoptera). Doctor of Philosophy, Fordham University, New York, 110 pp.

Hansson CT (1996) A new genus of Eulophidae (Hymenoptera: Chalcidoidea) with remarkable male genitalia. Systematic Entomology 21(1): 39–62. https://doi.org/10.1111/j.1365-3113.1996.tb00598.x

Hosken DJ, Stockley P (2004) Sexual selection and genital evolution. Trends in Ecology & Evolution 19(2): 87–93. https://doi.org/10.1016/j.tree.2003.11.012

Hsu P-W, Hsu F-C, Hsiao Y, Lin C-C (2017) Taxonomic notes on the genus *Protanilla* (Hymenoptera: Formicidae: Leptanillinae) from Taiwan. Zootaxa 4268(1): 117–130. https://doi.org/10.11646/zootaxa.4268.1.7

Ito F, Yamane S (2020) Behavior of the queen of *Leptanilla clypeata* Yamane et Ito collected in the Bogor Botanical Gardens, West Java, Indonesia (Hymenoptera; Formicidae), with a note on colony composition and a description of the ergatoid queen. Asian Myrmecology 12: e012004. https://doi.org/10.20362/AM.012004

Ito F, Hashim R, Mizuno R, Billen J (2021) Notes on the biology of *Protanilla* sp. (Hymenoptera, Formicidae) collected in Ulu Gombak, Peninsular Malaysia. Insectes Sociaux 69(1): 13–18. https://doi.org/10.1007/s00040-021-00839-z

Kaestner A, Wetzel A (1972) Lehrbuch der Speziellen Zoologie: Band 1: Wirbellose: 3. Teil: Insecta: A. Algemeiner Teil. Fischer Verlag.

Kamimura Y (2008) Copulatory wounds in the monandrous ant species *Formica japonica* (Hymenoptera, Formicidae). Insectes Sociaux 55(1): 51–53. https://doi.org/10.1007/s00040-007-0968-z

von Kéler S (1955) Entomologisches Worterbuch. Akademie-Verlag, Berlin, 679 pp.

Kempf WW (1954) A descoberta do primeiro macho do gênero *Thaumatomyrmex* Mayr (Hymenoptera: Formicidae). Revista Brasileira de Entomologia 1: 47–52.

Kempf WW (1956) A morphological study on the male genitalia of *Paracryptocerus* (*P.*) *pusillus* (Hymenoptera: Formicidae). Revista Brasileira de Entomologia 5: 101–110.

Khalife A, Peeters C, Economo EP (2022) Minute workers and large soldiers in the subterranean ant *Carebara perpusilla*: Musculoskeletal consequences of Haller's rule in the thorax. Arthropod Structure & Development 69: 101188. https://doi.org/10.1016/j.asd.2022.101188

Kluge MHE (1895) Das männliche Geschlechtsorgan von *Vespa germanica*. Archiv für Naturgeschichte 61(a): 159–168.

Koeniger N, Koeniger G (1991) An evolutionary approach to mating behaviour and drone copulatory organs in *Apis*. Apidologie 22(6): 581–590. https://doi.org/10.1051/apido:19910602

Kugler J (1986) The Leptanillinae (Hymenoptera: Formicidae) of Israel and a description of a new species from India. Israel Journal of Entomology 20: 45–57.

Kutter H (1948) Beitrag zur Kenntnis der Leptanillinae (Hym. Formicidae). Eine neue Ameisengattung aus Süd-Indien. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 21: 286–295.

Lapolla JS, Kallal RJ, Brady SG (2012) A new ant genus from the Greater Antilles and Central America, *Zatania* (Hymenoptera: Formicidae), exemplifies the utility of male and molecular character systems. Systematic Entomology 37(1): 200–214. https://doi.org/10.1111/j.1365-3113.2011.00605.x

Lieberman ZE, Billen J, van de Kamp T, Boudinot BE (2022) The ant abdomen: The skeletomuscular and soft tissue anatomy of *Amblyopone australis* workers (Hymenoptera: Formicidae). Journal of Morphology 283(6): 693–770. https://doi.org/10.1002/jmor.21471

Liu S-P, Richter A, Stoessel A, Beutel RG (2019) The mesosomal anatomy of *Myrmecia nigrocincta* workers and evolutionary transformations in Formicidae (Hymenoptera). Arthropod Systematics and Phylogeny 77: 1–19. https://doi.org/10.26049/ASP77-1-2019-01

MacGown JA, Boudinot BE, Deyrup M, Sorger DM (2014) A review of the Nearctic *Odontomachus* (Hymenoptera: Formicidae: Ponerinae) with a treatment of the males. Zootaxa 3802(4): 515. https://doi.org/10.11646/zootaxa.3802.4.6

Maddison WP, Maddison DR (2023) Mesquite: a modular system for evolutionary analysis. Version 3.81. http://mesquiteproject.org

Marcus H (1953) Estudios mirmecológicos. Folia Universitaria Cochabamba 6: 14–68.

Masuko K (1990) Behavior and ecology of the enigmatic ant *Leptanilla japonica* Baroni Urbani (Hymenoptera: Formicidae: Leptanillinae). Insectes Sociaux 37(1): 31–57.

Matusda R (1958) On the origin of the external genitalia of insects. Annals of the Entomological Society of America 51(1): 84–94. https://doi.org/10.1093/aesa/51.1.84

Mayr E (1963) Animal Species and Evolution. Harvard University Press. Available from: https://doi.org/10.4159/harvard.9780674865327 (April 8, 2022).

Michener CD (1944) A comparative study of the appendages of the eighth and ninth abdominal segments of insects. Annals of the Entomological Society of America 37(3): 336–351. https://doi.org/10.1093/aesa/37.3.336

Michener CD (1956) Hymenoptera. In: Tuxen SL (Ed.), Taxonomist's Glossary of Genitalia in Insects (first ed.), Eljnar Munksgaard, Copenhagen, 131–140.

Mikó I, Masner L, Johannes E, Yoder MJ, Deans AR (2013) Male terminalia of Ceraphronoidea: morphological diversity in an otherwise monotonous taxon. Insect Systematics & Evolution 44(3–4): 261–347. https://doi.org/10.1163/1876312X-04402002

Misof B, Liu S, Meusemann K, Peters RS, Donath A, Mayer C, Frandsen PB, Ware J, Flouri T, Beutel RG, Niehuis O, Petersen M, Izquierdo-Carrasco F, Wappler T, Rust J, Aberer AJ, Aspöck U, Aspock H, Bartel D, Blanke A, Berger S, Bohm A, Buckley TR, Calcott B, Chen J, Friedrich F, Fukui M, Fujita M, Greve C, Grobe P, Gu S, Huang Y, Jermiin LS, Kawahara AY, Krogmann L, Kubiak M, Lanfear R, Letsch H, Li Y, Li Z, Li J, Lu H, Machida R, Mashimo Y, Kapli P, McKenna DD, Meng G, Nakagaki Y, Navarrete-Heredia JL, Ott M, Ou Y, Pass G, Podsiadlowski L, Pohl H, von Reumont BM, Schutte K, Sekiya K, Shimizu S, Slipinski A, Stamatakis A, Song W, Su X, Szucsich NU, Tan M, Tan X, Tang M, Tang J, Timelthaler G, Tomizuka S, Trautwein M, Tong X, Uchifune T, Walzl MG, Wiegmann BM, Wilbrandt J, Wipfler B, Wong TKF, Wu Q, Wu G, Xie Y, Yang S, Yang Q, Yeates DK, Yoshizawa K, Zhang Q, Zhang R, Zhang W, Zhang Y, Zhao J, Zhou C, Zhou L, Ziesmann T, Zou S, Li Y, Xu X, Zhang Y, Yang H, Wang J, Wang J, Kjer KM, Zhou X (2014) Phylogenomics resolves the timing and pattern of insect evolution. Science 346(6210): 763–767. https://doi.org/10.1126/science.1257570

Monnin T, Peeters C (1998) Monogyny and regulation of worker mating in the queenless ant *Dinoponera quadriceps*. Animal Behaviour 55(2): 299–306. https://doi.org/10.1006/anbe.1997.0601

Moreau CS, Bell CD (2013) Testing the museum versus cradle tropical biological diversity hypothesis: Phylogeny, diversification, and ancestral biogeographic range evolution of the ants. Evolution 67(8): 2240–2257. https://doi.org/10.1111/evo.12105

Niu G, Budak M, Korkmaz EM, Doğan Ö, Nel A, Wan S, Cai C, Jouault C, Li M, Wei M (2022) Phylogenomic analyses of the Tenthredinoidea support the familial rank of Athaliidae (Insecta, Tenthredinoidea). Insects 13: 858. ttps://doi.org/10.3390/insects13100858

Ogata K (1991) A generic synopsis of the poneroid complex of the family Formicidae (Hymenoptera). Part II. Subfamily Myrmicinae. Bulletin of the Institute of Tropical Agriculture Kyushu University 14: 61–149.

Ogata K, Terayama M, Masuko K (1995) The ant genus *Leptanilla*: Discovery of the worker-associated male of *L. japonica*, and a description of a new species from Taiwan (Hymenoptera: Formicidae: Leptanillinae). Systematic Entomology 20: 27–34.

Peck O (1937) The male genitalia in the Hymenoptera (Insecta), especially the family Ichneumonidae: I. Comparative morphology. Canadian Journal of Research 15d(11): 221–252. https://doi.org/10.1139/cjr37d-018

Peeters C, Keller RA, Khalife A, Fischer G, Katzke J, Blanke A, Economo EP (2020) The loss of flight in ant workers enabled an evolutionary redesign of the thorax for ground labour. Frontiers in Zoology 17: 33. https://doi.org/10.1186/s12983-020-00375-9

Petersen B (1968) Some novelties in presumed males of Leptanillinae (Hym., Formicidae). Entomologiske Meddelelser 36: 577–598.

de Pinna MCC (1991) Concepts and tests of homology in the cladistic paradigm. Cladistics 7(4): 367–394. https://doi.org/10.1111/j.1096-0031.1991.tb00045.x

Polilov AA (2016) Features of the structure of hymenoptera associated with miniaturization: 2. Anatomy of *Trichogramma evanescens* (Hymenoptera: Trichogrammatidae). Entomological Review 96: 419–431. https://doi.org/10.1134/S0013873816040047

Remane A (1952) Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik. Geest & Portig K.-G., Leipzig, 400 pp.

von Reumont BM, Jenner RA, Wills MA, Dell'Ampio E, Pass G, Ebersberger I, Meyer B, Koenemann S, Iliffe TM, Stamatakis A, Niehuis O, Meusemann K, Misof B (2012) Pancrustacean phylogeny in the light of new phylogenomic data: Support for Remipedia as the possible sister group of Hexapoda. Molecular Biology and Evolution 29(3): 1031–1045. https://doi.org/10.1093/molbev/msr270

Richter A, Keller RA, Rosumek FB, Economo EP, Hita Garcia F, Beutel RG (2019) The cephalic anatomy of workers of the ant species *Wasmannia affinis* (Formicidae, Hymenoptera, Insecta) and its evolutionary implications. Arthropod Structure & Development 49: 26–49. https://doi.org/10.1016/j.asd.2019-02-002

Richter A, Hita Garcia F, Keller RA, Billen J, Economo EP, Beutel RG (2020) Comparative analysis of worker head anatomy of *Formica* and *Brachyponera* (Hymenoptera: Formicidae). Arthropod Systematics and Phylogeny 78: 133–170. https://doi.org/10.26049/ASP78-1-2020-06

Richter A, Hita Garcia F, Roberto K, Billen J, Katzke J, Boudinot BE, Economo EP, Beutel RG (2021) The head anatomy of Protanilla lini (Hymenoptera: Formicidae: Leptanillinae), with a hypothesis of their mandibular movement. Myrmecological News 31: 85–114. https://doi.org/10.25849/myrmecol.news_031:085

Richter A, Boudinot BE, Yamamoto S, Katzke J, Beutel RG (2022) The first reconstruction of the head anatomy of a Cretaceous insect, †*Gerontoformica gracilis* (Hymenoptera: Formicidae), and the early evolution of ants. Insect Systematics and Diversity 6(5): 4. https://doi.org/10.1093/isd/ixac013

Richter A, Boudinot BE, Hita Garcia F, Billen J, Economo EP, Beutel RG (2023) Wonderfully weird: the head anatomy of the armadillo ant, *Tatuidris tatusia* (Hymenoptera: Formicidae: Agroecomyrmecinae), with evolutionary implications. Myrmecological News 33: 35–75. https://doi.org/10.25849/myrmecol.news_033:035

Richter S, Wirkner CS (2014) A research program for evolutionary morphology. Journal of Zoological Systematics and Evolutionary Research 52(4): 338–350. https://doi.org/10.1111/jzs.12061

Rodrigue N, Philippe H (2010) Mechanistic revisions of phenomenological modeling strategies in molecular evolution. Trends in Genetics 26(6): 248–252. https://doi.org/10.1016/j.tig.2010.04.001

Romiguier J, Borowiec ML, Weyna A, Helleu Q, Loire E, La Mendola C, Rabeling C, Fisher BL, Ward PS, Keller L (2022) Ant phylogenomics reveals a natural selection hotspot preceding the origin of complex eusociality. Current Biology: S0960982222007606. https://doi.org/10.1016/j.cub.2022.05.001

Ross HH (1937) A generic classification of the Nearctic sawflies (Hymenoptera, Symphyta). Illinois Biological Monographs 15(2): 1–173.

Santschi F (1907) Fourmis de Tunisie capturées en 1906. Revue Suisse de Zoologie 15: 305–334.

Santschi F (1908) Nouvelles fourmis de l'Afrique du Nord (Égypte, Canaries, Tunisie). Annales de la Société Entomologique de France 77: 517–534.

Schmidt CV, Heinze J (2017) Genital morphology of winged and wingless males in the ant genus *Cardiocondyla* (Formicidae, Myrmicinae). Insect Systematics & Evolution 49(1): 59–80. https://doi.org/10.1163/1876312X-48022163

Schulmeister S (2001) Functional morphology of the male genitalia and copulation in lower Hymenoptera, with special emphasis on the Tenthredinoidea s. str. (Insecta, Hymenoptera, 'Symphyta'). Acta

Zoologica 82(4): 331–349. https://doi.org/10.1046/j.1463-6395.2001.00094.x

Schulmeister S (2003) Genitalia and terminal abdominal segments of male basal Hymenoptera (Insecta): morphology and evolution. Organisms Diversity & Evolution 3(4): 253–279. https://doi.org/10.1078/1439-6092-00078

Seltmann K, Yoder M, Mikó I, Forshage M, Bertone M, Agosti D, Austin A, Balhoff J, Borowiec M, Brady SG, Broad G, Brothers D, Burks R, Buffington M, Campbell H, Dew K, Ernst A, Fernández-Triana J, Gates M, Gibson G, Jennings J, Johnson N, Karlsson D, Kawada R, Krogmann L, Kula R, Mullins P, Ohl M, Rasmussen C, Ronquist F, Schulmeister S, Sharkey M, Talamas E, Tucker E, Vilhelmsen L, Ward PS, Wharton R, Deans A (2012) A hymenopterists' guide to the Hymenoptera Anatomy Ontology: utility, clarification, and future directions. Journal of Hymenoptera Research 27: 67–88. https://doi.org/10.3897/jhr.27.2961

Shyamalanath S, Forbes J (1983) Anatomy and histology of the male reproductive system in the adult and pupa of the doryline ant, *Aenictus gracilis* Emery (Hymenoptera: Formicidae). Journal of the New York Entomological Society 91(4): 377–393.

Simmons LW (2014) Sexual selection and genital evolution. Austral Entomology 53(1): 1–17. https://doi.org/10.1111/aen.12053

Simpson GG (1953) The Major Features of Evolution. Columbia University Press, New York Chichester, West Sussex, 436 pp. Available from https://doi.org/10.7312/simp93764.

Sloan NS, Simmons LW (2019) The evolution of female genitalia. Journal of Evolutionary Biology 32(9): 882–899. https://doi.org/10.1111/jeb.13503

Smith EL (1969) Evolutionary morphology of external insect genitalia. 1. Origin and relationships to other appendages. Annals of the Entomological Society of America 62(5): 1051–1079.

Smith EL (1970) Evolutionary morphology of the external insect genitalia. 2. Hymenoptera. Annals of the Entomological Society of America 63(1): 1–27. https://doi.org/10.1093/aesa/63.1.1

Smith EL (1972) Biosystematics and morphology of Symphyta – III. External genitalia of *Euura* (Hymenoptera: Tenthredinidae): Sclerites, sensilla, musculature, development and oviposition behavior. International Journal of Insect Morphology and Embryology 1(4): 321–365. https://doi.org/10.1016/0020-7322(72)90016-5

Snodgrass RE (1935a) Principles of Insect Morphology. McGraw-Hill Book Company, Inc.

Snodgrass RE (1935b) The abdominal mechanisms of a grasshopper. Smithsonian Miscellaneous Collections 94(6).

Snodgrass RE (1941) The male genitalia of Hymenoptera. Smithsonian Miscellaneous Collections 99(14): 123.

Snodgrass RE (1942) The skeleto-muscular mechanisms of the honey bee. Smithsonian Miscellaneous Collections 103(2): 124.

Snodgrass RE (1957) A revised interpretation of the external reproductive organs of male insects. Smithsonian Miscellaneous Collections 135(6): 64.

Song H, Bucheli SR (2010) Comparison of phylogenetic signal between male genitalia and non-genital characters in insect systematics. Cladistics 26(1): 23–35. https://doi.org/10.1111/j.1096-0031.2009.00273.x

Swammerdam J (1758) The book of nature, or, The history of insects: reduced to distinct classes, confirmed by particular instances, displayed in the anatomical analysis of many species: and illustrated with copper-plates: including the generation of the frog, the history of the ephemerus, the changes of flies, butterflies, and beetles: with the original discovery of the milk-vessels of the cuttle-fish, and many other curious particulars. Printed for C.G. Seyffert. London. 153 pp.

Tarasov SI, Solodovnikov AY (2011) Phylogenetic analyses reveal reliable morphological markers to classify mega-diversity in Onthophagini dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). Cladistics 27(5): 490–528. https://doi.org/10.1111/j.1096-0031.2011.00351.x

Taylor RW (1978) *Nothomyrmecia macrops*: A living-fossil ant rediscovered: The most primitive living ant, previously an enigma, rediscovered and the subject of international study. Science 201(4360): 979–985. https://doi.org/10.1126/science.201.4360.979

Tozetto L, Lattke JE (2020) Revealing male genital morphology in the giant ant genus *Dinoponera* with geometric morphometrics. Arthropod Structure & Development 57: 100943. https://doi.org/10.1016/j.asd.2020.100943

Trakimas WB (1967) An anatomical and histological study of the male myrmicine ant, *Myrmica rubra*, L. (Hymenoptera: Formicidae). Doctor of Philosophy, Fordham University, New York, 125 pp.

Tuxen SL (Ed.) (1970) Taxonomist's glossary of genitalia in insect[s.] 2nd ed. Munksgaard, Copenhagen, 362 pp. Available from: http://antbase.org/ants/publications/21060/21060.pdf (April 8, 2022).

Vidal-García M, Bandara L, Keogh JS (2018) ShapeRotator: An R tool for standardized rigid rotations of articulated three-dimensional structures with application for geometric morphometrics. Ecology and Evolution 8(9): 4669–4675. https://doi.org/10.1002/ece3.4018

Viggiani G (1973) Osservazioni morfobiologiche sull'*Azotus pulcherrimus* Merc. (Hymenoptera: Aphelinidae). Bollettino del Laboratorio di Entomologia Agraria "Filippo Silvestri", Portici 30: 300–311.

Wang M, Rasnitsyn AP, Li H, Shih C, Sharkey MJ, Ren D (2016) Phylogenetic analyses elucidate the inter-relationships of Pamphiloidea (Hymenoptera, Symphyta). Cladistics 32: 239–260. https://doi.org/10.1111/cla.12129

Ward PS (2001) Taxonomy, phylogeny and biogeography of the ant genus *Tetraponera* (Hymenoptera: Formicidae) in the Oriental and Australian regions. Invertebrate Taxonomy 15: 589–665.

Ward PS (2007) The ant genus *Leptanilloides*: Discovery of the male and evaluation of phylogenetic relationships based on DNA sequence data. Memoirs of the American Entomological Institute 80: 637–649.

Ward PS, Downie DA (2005) The ant subfamily Pseudomyrmecinae (Hymenoptera: Formicidae): Phylogeny and evolution of big-eyed arboreal ants. Systematic Entomology 30(2): 310–335. https://doi.org/10.1111/j.1365-3113.2004.00281.x

Ward PS, Sumnicht TP (2012) Molecular and morphological evidence for three sympatric species of *Leptanilla* (Hymenoptera: Formicidae) on the Greek island of Rhodes. Myrmecological News 17: 5–11.

Ward PS, Fisher BL (2016) Tales of dracula ants: the evolutionary history of the ant subfamily Amblyoponinae (Hymenoptera: Formicidae). Systematic Entomology 41(3): 683–693. https://doi.org/10.1111/syen.12186

Ward PS, Boudinot BE (2021) Grappling with homoplasy: Taxonomic refinements and reassignments in the ant genera *Camponotus* and *Colobopsis* (Hymenoptera: Formicidae). Arthropod Systematics & Phylogeny 79: 37–56. https://doi.org/10.3897/asp.79.e66978

Wheeler GC, Wheeler EW (1930) Two new ants from Java. Psyche (Cambridge) 37: 193–201.

Willmann VR (1981) Das Exoskelett der männlichen Genitalien der Mecoptera (Insecta): I. Morphologie. Journal of Zoological Systematics and Evolutionary Research 19(2): 96–150. https://doi.org/10.1111/j.1439-0469.1981.tb00235.x

Yamada A, Nguyen D, Eguchi K (2020) Unveiling the morphology of the Oriental rare monotypic ant genus *Opamyrma* Yamane, Bui & Eguchi, 2008 (Hymenoptera: Formicidae: Leptanillinae) and its evolutionary implications, with first descriptions of the male, larva, tentorium, and sting apparatus. Myrmecological News 30: 27–52. https://doi.org/10.25849/myrmecol.news_030:027

Yamane S, Bui TV, Eguchi K (2008) *Opamyrma hungvuong*, a new genus and species of ant related to *Apomyrma* (Hymenoptera: Formicidae: Amblyoponinae). Zootaxa 1767(1): 55. https://doi.org/10.11646/zootaxa.1767.1.3

Yoder MJ, Mikó I, Seltmann KC, Bertone MA, Deans AR (2010) A gross anatomy ontology for Hymenoptera. PLOS ONE 5(12): e15991. https://doi.org/10.1371/journal.pone.0015991

Yoshizawa K, Johnson KP (2006) Morphology of male genitalia in lice and their relatives and phylogenetic implications. Systematic Entomology 31(2): 350–361. https://doi.org/10.1111/j.1365-3113.2005.00323.x

Youssef NN (1969) Musculature, nervous system and glands of metasomal abdominal segments of the male of *Nomia melanderi* Ckll. (Hymenoptera, Apoidea). Journal of Morphology 129(1): 59–79. https://doi.org/10.1002/jmor.1051290105

Yoshimura M, Fisher BL (2011) A revision of male ants of the Malagasy region (Hymenoptera: Formicidae): Key to genera of the subfamily Dolichoderinae. Zootaxa 2794: 1–34. https://doi.org/10.11646/zootaxa.2794.1.1

Supplementary Material 1

Tables S1–S4

Authors: Griebenow ZH, Richter A, van de Kamp T, Economo EP, Lieberman ZE (2023)
Data type: .zip
Explanation note: Table S1. Collection data for the specimens included in this study. Micro-CT data are published for the specimens highlighted in green; those in yellow were not examined with that method. Skeletomuscular descriptions are provided for specimens highlighted in dark green. — **Table S2.** Scan settings for all 22 datasets here published. Fundamental differences in modality between X-ray microscopes and synchrotrons result in reciprocal inapplicability of some scan parameters here reported. — **Table S3.** Presence and absence of male genital musculature across Hymenoptera. See Supplementary Document 1 for explanation of coding schema. — **Table S4.** Recoding of characters from Schulmeister (2003). **Character** column – Text character number, followed by Boulangé name of muscle treated; in some cases one character number corresponds to multiple muscles; **From** – original code; **To** – new code; **Meaning** – new character state meaning. **nr** = not recoded. Character 267 includes 9vcm2 (b), which is always present, hence not included in recoding. Character 277 was invariant for all taxa (9cppd, j, always present). Character 291 (w) was combined with character 287 (9csm2, t) but otherwise not recoded.

Link: https://doi.org/asp.81.e104810.suppl1

Supplementary Material 2

Supplementary Document 1

Authors: Griebenow ZH, Richter A, van de Kamp T, Economo EP, Lieberman ZE (2023)
Data type: .docx
Explanation note: Extended description of coding schema for Table S3.

Link: https://doi.org/asp.81.e104810.suppl2

Supplementary Material 3

Figure S1

Authors: Griebenow ZH, Richter A, van de Kamp T, Economo EP, Lieberman ZE (2023)
Data type: .tif
Explanation note: Ancestral state reconstruction and sampled tip states of pene-lateropenital and pene-penial musculature across the Hymenoptera. See Supplementary Document 1 for explanation of inapplicability and additional notes. Cells represent characters. Cell fill represents character states: white=absent; black=present; diagonal lines=polymorphic absent/present; gray dots=uncertain; solid gray=inapplicable. Cells in left-to-right order: 10plm1 (m), 10plm2 (n), 10ppm1 (x), 10ppm2 (z).

Link: https://doi.org/asp.81.e104810.suppl3

Zeitschrift/Journal: Arthropod Systematics and Phylogeny

Jahr/Year: 2023

Band/Volume: 81

Autor(en)/Author(s): Griebenow Zachary H., Richter Adrian, van de Kamp Thomas, Economo Evan P., Lieberman Ziv E.

Artikel/Article: Comparative morphology of male genital skeletomusculature in the Leptanillinae (Hymenoptera: Formicidae), with a standardized muscular terminology for the male genitalia of Hymenoptera 945-1018