



Using controlled vocabularies in anatomical terminology: A case study with *Strumigenys* (Hymenoptera: Formicidae)

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ABSTRACT

Morphological studies of insects can help us to understand the concomitant or sequential functionality of complex structures and may be used to hypothesize distinct levels of phylogenetic relationship among groups. Traditional morphological works, generally, have encompassed a set of elements, including descriptions of structures and their respective conditions, literature references and images, all combined in a single document. Fast forward to the digital era, it is now possible to release this information simultaneously but also independently as data sets linked to the original publication in an external environment. In order to link data from various fields of knowledge, disseminating morphological information in an open environment, it is important to use tools that enhance interoperability. For example, semantic annotations facilitate the dissemination and retrieval of phenotypic data in digital environments. The integration of semantic (i.e. web-based) components with anatomic treatments can be used to generate a traditional description in natural language along with a set of semantic annotations.

The ant genus *Strumigenys* currently comprises about 840 described species distributed worldwide. In the Neotropical region, almost 200 species are currently known, but it is possible that much of the species' diversity there remains unexplored and undescribed. The morphological diversity in the genus is high, reflecting an extreme generic reclassification that occurred in the late 20th and early 21st centuries. Here we define the anatomical concepts in this highly diverse group of ants using semantic annotations to enrich the anatomical ontologies available online, focussing on the definition of terms through sub-jacent conceptualization.

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1. Introduction

In biology, morphology is used to describe or redescribe taxa (Fernandes et al., 2014; Pinheiro et al., 2016; Ulysséa and Brandão, 2012); to determine phenotypic traits linked to certain pathologies (Ortiz et al., 2017; Fiaz et al., 2018); to infer kinship among lineages in phylogenetic analyses (Fusari et al., 2014; Ramos and Melo, 2010; Zacca et al., 2016); to trace phenotypic variation during ontogenetic development (Thompson, 1999; Toyama et al., 2018); to investigate functional community organization (Gibb and Parr, 2013; Gibb et al., 2015; Silva and Brandão, 2014); to explore evolutionary hypotheses within anatomical groups (Kawada et al., 2015; Boudinot, 2013, 2018). The morphological terminology used by different

research groups for related organisms, however, may differ (Silva, 2017), making analyses of broader groups based on comparative morphology very difficult (Deans et al., 2012).

Morphology is the product of multiple factors. Some are intrinsic to individuals, such as the expression of differential traits through gene modularity and hormone variation throughout the ontogenetic development (Corona et al., 2016; Molet et al., 2012), while others are extrinsic, for instance climatic oscillations and environmental heterogeneity (Oms et al., 2017; Purcell et al., 2016). For this reason, morphological studies result in complex data sets that have been historically challenging in terms of referencing (Vogt et al., 2010).

Morphological works generally include descriptions of traits and their conditions, literature references, images and hypotheses about trait evolution. Morphologists establish connections between specimens and their anatomic features, using images and text to document what they see. They also make interpretations and advance hypotheses. In traditional morphological publications, all

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those elements are combined in a single document. In modern times, however, there is the possibility of releasing data sets in an external environment that is linked to the original publication and making them available to a broader scientific community (Deans et al., 2012; Godfray, 2002; Miller et al., 2012; Padial et al., 2010). In order to link data from various fields of knowledge in an open environment, tools such as semantic annotations can be used to enhance interoperability and to facilitate the dissemination and retrieval of phenotypic data in digital environments (Silva, 2017).

Semantic annotation is the process of attaching additional information to various concepts (e.g., terms, organisms etc) in a given text or any other content. These annotations link multiple concepts across different domains inside a digital environment and can be easily retrieved and used by machines. For example, they can be used in ontology-based information retrieval queries for efficient data mining, thus facilitating the spread of the current understanding of a specific concept to multiple domains (Silva, 2017). These annotations are possible because there are multi-species anatomic ontologies (i.e. data models which represent a set of concepts belonging to a specific domain, along with their relations), which contain definitions of anatomic concepts that are logically related (Dahdul et al., 2010). Annotations are logically composed using references to these anatomic concepts along with descriptive concepts from other ontologies. They make it possible, for example, to understand which processes are involved in the evolution of anatomic traits (Mabee et al., 2007).

The taxonomic and morphological diversity in Hymenoptera (ants, bees, and wasps), combined with various researchers focusing on projects in multiple domains, has led to the creation of several anatomical glossaries within the order (Yoder et al., 2010). The morphological terminology used for the group is, for the most part, family-specific (Seltmann et al., 2012), and it is not at all uncommon for a structure to be named differently across publications (e.g., “paramere” Yoder et al., 2010; see Boudinot, 2018 for a throughout discussion of genital terminology in Hexapoda) depending on the hymenopterists’ community the publication originated from (Yoder et al., 2010).

Despite the fact that anatomic studies in myrmecology have become less common with the advent of molecular endeavours and the development of robust analytic tools to understand variation at the molecular level (Keller, 2011), new-generation tools have become more popular in anatomical studies and have enabled the generation of fine-grained morphological data on the external and internal morphology of ants (Agavekar et al., 2017; Sarnat et al., 2016; Staab et al., 2018) in ways that are useful to other disciplines, such as biomechanics, ecology, behavioural and developmental biology (e.g., Gibb and Parr, 2013; Keller et al., 2014; Larabee and Suarez, 2014; Larabee et al., 2017; Molet et al., 2012; Silva and Brandão, 2014).

The ant genus *Strumigenys*, with 840 described species distributed worldwide, is most diverse in the tropics (Bolton, 2000, 2019). Their great morphological diversity (Baroni Urbani and de Andrade, 1994, 2007) reflects the fact that a number of genera that were historically kept separate have been synonymized with it in the late 20th and early 21st centuries (cf. Bolton, 2000 for a historical overview of the taxonomic history for the genus). New publications in the last fifteen years (Baroni Urbani and De Andrade, 2007; Bharti and Akbar, 2013; Lattke and Aguirre, 2015; Longino, 2006; Rigato and Scupola, 2008; Sosa-Calvo et al., 2010; Xu and Zhou, 2004; Zhou and Xu, 2003) have added approximately 30 valid names to the genus, indicating a crescent – although, seemingly slow – rate of new species discovery for this group, and the possibility that more species will be described in the future.

The present work defines anatomical concepts in *Strumigenys* using semantic annotations to enrich the anatomical ontologies available online, focussing on the definition of terms through subjacent conceptualization. For this, we perform a morphological investigation to substantiate previous definitions, and to establish structural correspondence between the studied group and other groups of ants and hymenopteran insects.

2. Material and methods

2.1. Sample information

The specimens used in this study were obtained from the following institutions:

CASC California Academy of Sciences, San Francisco, CA, USA.

DZUP Coleção Entomológica Padre Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, PR, Brazil.

MZSP Museu de Zoologia da Universidade de São Paulo, São Paulo, SP, Brazil.

UFES Universidade Federal do Espírito Santo, Vitória, ES, Brazil.

For the study of comparative morphology, 11 Formicidae subfamilies were studied, namely Agroecomyrmecinae, Amblyoponinae, Dolichoderinae, Dorylinae, Ectatomminae, Formicinae, Myrmicinae, Paraponerinae, Ponerinae, Proceratiinae, and Pseudomyrmecinae. At least one specimen of each subfamily, apart from Myrmicinae, was thoroughly studied in search of morphological characteristics (Table 1). In Myrmicinae, at least one specimen for three tribes (Crematogastrini, Pogonomyrmecini and Solenopsidini), apart from Attini, were studied in search of morphological characteristics (Table 1). In Attini, at least one specimen of the following genera, apart from *Strumigenys*, were studied: *Acromyrmex* Mayr, 1865, *Acanthognathus* Mayr 1887, *Basiceros* Schulz, 1906, *Octostruma* Forel, 1912, *Phalacromyrmex* Kempf, 1960, *Pheidole* Westwood 1839, and *Procrystocerus* Emery, 1887.

In *Strumigenys*, at least one specimen of each of the 74 species was observed (Table 1). Species belonging to this genus were arbitrarily chosen as to tentatively explore most of the morphological diversity present in the genus. Bolton (2000) recognizes several groups of species, using morphological traits to diagnose them. Since some representatives of those groups are not usually present in samples, and we opted to dissect and disarticulate most of the examined specimens, we used those species which were considered abundant in samples and were readily available for study. Other non-formicidae Hymenoptera were also examined, reflecting the most recent hypothesis of relationship among hymenopteran families, to encompass a wide range of morphological diversity within the order (Branstetter et al., 2017a; Peters et al., 2017) (Table 1).

2.2. Equipment

Morphological observations were made with a Leica S8APO stereomicroscope at 80× magnification. Scanning electron microscope images were obtained using an electronic microscope Tescan Vega3 LMU, under both low and high pressure. The method provided by Boudinot (2015) was used for mouthpart dissection and body disarticulation. The methods of Gibson (1985) and Vilhelmsen et al. (2010) were used in the study of the skeleton and musculature. The specimens were immersed in 100% alcohol one day prior to dissection for complete dehydration. After the dehydration process, the specimens were transferred to ethanol-immersed Bluetack, which allowed better handling. All the dissections were performed using a razor blade and size zero entomological pins.

Table 1

List containing all species studied (**Family, Subfamily, Tribe, Species**), sex of specimens studied, morphological form (apterous, brachypterous or macropterous), their collection of origin, their conservation medium (dry-mounted or ethanol) and their locality information (COUNTRY: Department/Province, Municipality).

Species	Sex	Form	Collection of origin	Conservation medium	Locality information
Apidae					
Apinae					
Meliponini					
<i>Melipona</i> sp.	Female	Macropterous	DZUP	Ethanol	BRAZIL: Paraná, Curitiba
Bethylidae					
Epyrinae					
Epyrinae sp.	Male	Macropterous	DZUP	Ethanol	FRENCH GUIANA: Saint-Laurent-du-Maroni, Saül
Pristocerinae					
Pristocerinae sp.	Female	Apterous	DZUP	Ethanol	BRAZIL: Paraná, Antonina
Ceraphronidae					
Ceraphronidae sp.1	Female	Macropterous	DZUP	Ethanol	BRAZIL: Paraná, Piraquara
Ceraphronidae sp.2	Female	Brachypterous	DZUP	Ethanol	BRAZIL: Paraná, Piraquara
Diapriidae					
Diapriinae					
Diapriinae sp.	Female	Macropterous	DZUP	Ethanol	BRAZIL: Paraná, Piraquara
Diapriini					
<i>Acanthopria</i> sp.	Female	Apterous	DZUP	Ethanol	BRAZIL: Paraná, Piraquara
Eucharitidae					
Eucharitinae					
Eucharitini					
<i>Kapala</i> sp.	Male	Macropterous	DZUP	Ethanol	BRAZIL: Paraná, Antonina
Evaniidae					
<i>Semaomyia</i> sp.	?	Macropterous	DZUP	Ethanol	BRAZIL: Santa Catarina, Blumenau
Ichneumonidae					
Ophioninae					
Ophioninae sp.	Male	Macropterous	DZUP	Ethanol	BRAZIL: Santa Catarina, Blumenau
Mutillidae					
Sphaerophthalminae					
Sphaerophthalminae sp.	Female	Apterous	DZUP	Ethanol	BRAZIL: Paraná, Curitiba
Pompilidae					
Pepsinae					
Pepsinae sp.	Female	Macropterous	DZUP	Ethanol	BRAZIL: Rio Grande do Sul, Gramado
Pteromalidae					
Cleonyminae					
Cleonyminae sp.	Male	Macropterous	DZUP	Ethanol	BRAZIL: Santa Catarina, Blumenau
Vespidae					
Polistinae					
Epiponini					
<i>Polybia</i> sp.	Female	Macropterous	DZUP	Ethanol	BRAZIL: Paraná, Curitiba
Formicidae					
Agroecomyrmecinae					
Agroecomyrmecini					
<i>Tatuidris tatusia</i>	Female	Apterous	DZUP	Dry-mounted	PERU: Madre de Dios, Puerto Maldonado
Amblyoponinae					
Amblyoponini					
<i>Fulakora armigera</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Rio de Janeiro, Itatiaia
Dolichoderinae					
Tapinomini					
<i>Tapinoma melanocephalum</i>	Female	Apterous	DZUP	Ethanol	BRAZIL: Paraná, Curitiba
Dorylinae					
<i>Labidus coecus</i>	Female	Apterous	DZUP	Ethanol	BRAZIL: Paraná, Antonina
Ectatomminae					
Ectatommini					
<i>Gnamptogenys</i> sp.	Female	Apterous	DZUP	Ethanol	BRAZIL: Rio Grande do Sul, Gramado
Formicinae					
Camponotini					
<i>Camponotus atriceps</i>	Female	Apterous	DZUP	Ethanol	BRAZIL: Santa Catarina, Blumenau
Paraponerinae					
Paraponerini					
<i>Paraponera clavata</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Mato Grosso, Chapada dos Guimarães
Ponerinae					
Ponerini					
<i>Pachycondyla striata</i>	Female	Apterous	DZUP	Ethanol	BRAZIL: Paraná, Curitiba
Proceratiinae					
Proceratiini					
<i>Discothyrea sexarticulata</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Paraná, Tibagi
Pseudomyrmecinae					
Pseudomyrmecini					
<i>Pseudomyrmex</i> sp.	Female	Apterous	DZUP	Ethanol	BRAZIL: Rio Grande do Sul, Gramado
Myrmicinae					
Crematogastrini					
<i>Crematogaster</i> sp.	Female	Apterous	DZUP	Ethanol	BRAZIL: Santa Catarina, Blumenau

(continued on next page)

Table 1 (continued)

Species	Sex	Form	Collection of origin	Conservation medium	Locality information
Pogonomyrmecini					
<i>Hylomyrma</i> sp.	Female	Apterous	DZUP	Ethanol	BRAZIL: Paraná, Antonina
Solenopsidini					
<i>Solenopsis</i> sp.	Female	Apterous	DZUP	Ethanol	BRAZIL: Paraná, Curitiba
Attini					
<i>Acromyrmex crassipisnus</i>	Female	Apterous	DZUP	Ethanol	BRAZIL: Paraná, Curitiba
<i>Acanthognathus</i> sp.	Female	Apterous	DZUP	Dry-mounted and ethanol	BRAZIL: Rondônia, Porto Velho
<i>Basicerus disciger</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Santa Catarina, Indaial
<i>Octostruma rugifera</i>	Female	Apterous	DZUP	Ethanol	BRAZIL: Paraná, Tunas
<i>Phalacromyrmex fugax</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Santa Catarina, Paniel
<i>Pheidole</i> sp.	Female	Apterous	DZUP	Ethanol	BRAZIL: Paraná, Curitiba
<i>Procryptocerus</i> sp.	Female	Apterous	DZUP	Ethanol	BRAZIL: Rio Grande do Sul, Gramado
<i>Strumigenys abditivata</i>	Female	Apterous	DZUP and MZSP	Dry-mounted	BRAZIL: Santa Catarina, Indaial
<i>Strumigenys alberti</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Maranhão, Açailândia
<i>Strumigenys appretiata</i>	Female	Apterous and macropterous	DZUP	Dry-mounted and ethanol	BRAZIL: São Paulo, Ribeirão Grande
<i>Strumigenys beebei</i>	Female	Apterous and macropterous	DZUP	Dry-mounted and ethanol	BRAZIL: Rio de Janeiro, Itatiaia
<i>Strumigenys borgmeieri</i>	Female	Apterous and macropterous	DZUP and MZSP	Dry-mounted	BRAZIL: Rondônia, Porto Velho
<i>Strumigenys carinithorax</i>	Female	Apterous	MZSP	Dry-mounted	BRAZIL: Sergipe, Areia Branca
<i>Strumigenys cincinatta</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Paraíba, João Pessoa
<i>Strumigenys comis</i>	Female	Apterous and macropterous	DZUP and MZSP	Dry-mounted	BRAZIL: Rondônia, Porto Velho
<i>Strumigenys conspersa</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Rio de Janeiro, Itatiaia
<i>Strumigenys cordovensisi</i>	Female	Apterous	DZUP and MZSP	Dry-mounted	BRAZIL: Santa Catarina, Canoinhas
<i>Strumigenys cosmostela</i>	Female	Apterous	MZSP	Dry-mounted	BRAZIL: Rondônia, Porto Velho
<i>Strumigenys crassicornis</i>	Female	Apterous and macropterous	DZUP	Dry-mounted and ethanol	BRAZIL: Pernambuco, Recife
<i>Strumigenys cultrigera</i>	Female	Apterous	MZSP	Dry-mounted	BRAZIL: São Paulo, Salesópolis
<i>Strumigenys dapsilis</i>	Female	Apterous	MZSP	Dry-mounted	BRAZIL: Rio de Janeiro, Itatiaia
<i>Strumigenys denticulata</i>	Female	Apterous and macropterous	DZUP	Dry-mounted and ethanol	BRAZIL: Rio de Janeiro, Itatiaia
<i>Strumigenys dentinasis</i>	Female	Apterous	DZUP and MZSP	Dry-mounted	BRAZIL: Rio Grande do Sul, Bom Jesus
<i>Strumigenys depressiceps</i>	Female	Macropterous	DZUP	Dry-mounted	BRAZIL: Santa Catarina, São Bento do Sul
<i>Strumigenys eggersi</i>	Female	Apterous	DZUP and MZSP	Dry-mounted and ethanol	BRAZIL: Paraná, Piraquara
<i>Strumigenys elongata</i>	Female	Apterous	DZUP	Dry-mounted and ethanol	BRAZIL: São Paulo, Ribeirão Grande
<i>Strumigenys emiliae</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Paraná, Bocaiúva do Sul
<i>Strumigenys emmae</i>	Female	Macropterous	UFES	Ethanol	FRENCH GUIANA: Saint-Laurent-du-Maroni, Saül
<i>Strumigenys epelys</i>	Female	Apterous	MZSP	Dry-mounted	BRAZIL: Minas Gerais, Boa Esperança
<i>Strumigenys epinotalis</i>	Female	Apterous	MZSP	Dry-mounted	BRAZIL: Bahia, Ilhéus
<i>Strumigenys fridericimuelleri</i>	Female	Apterous	MZSP	Dry-mounted	BRAZIL: Acre, Senador Guiomard
<i>Strumigenys glenognatha</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Maranhão, Estreito
<i>Strumigenys godmani</i>	Female	Macropterous	DZUP	Dry-mounted	BRAZIL: Santa Catarina, Indaial
<i>Strumigenys grytava</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Espírito Santo, Vitória
<i>Strumigenys gytha</i>	Female	Apterous	DZUP and MZSP	Dry-mounted	BRAZIL: Bahia, Mata São João
<i>Strumigenys hindenburgi</i>	Female	Apterous	MZSP	Dry-mounted	BRAZIL: Minas Gerais, Pedra Azul
<i>Strumigenys hyphata</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: São Paulo, Cananéia
<i>Strumigenys infidelis</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Rondônia, Porto Velho
<i>Strumigenys inusitata</i>	Female	Apterous	DZUP	Dry-mounted and ethanol	BRAZIL: Rondônia, Porto Velho
<i>Strumigenys kompsomala</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Rondônia, Porto Velho
<i>Strumigenys lanuginosa</i>	Female	Apterous and macropterous	DZUP	Dry-mounted	BRAZIL: Paraná, Piraquara
<i>Strumigenys lilloana</i>	Female	Apterous	MZSP	Dry-mounted and ethanol	BRAZIL: Rio de Janeiro, Itatiaia
<i>Strumigenys longimala</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Bahia, Milagres
<i>Strumigenys louisianae</i>	Female	Apterous	DZUP	Dry-mounted and ethanol	PERU: Madre de Dios, Puerto Maldonado
<i>Strumigenys</i> pr. <i>louisianae</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Paraná, Curitiba
<i>Strumigenys</i> pr. <i>louisianae</i>	Female	Apterous and macropterous	DZUP	Dry-mounted	BRAZIL: Rio de Janeiro, Ilha Grande
"bruchi complex"					BRAZIL: Santa Catarina, Indaial
<i>Strumigenys lygatrix</i>	Female	Apterous	MZSP	Dry-mounted	BRAZIL: Santa Catarina, Blumenau
<i>Strumigenys metopia</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Maranhão, Açailândia
<i>Strumigenys monstra</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Rondônia, Porto Velho
<i>Strumigenys minuscula</i>	Female	Apterous	MZSP	Dry-mounted	BRAZIL: Santa Catarina, Chapecó
<i>Strumigenys ogleblini</i>	Female	Apterous	MZSP	Dry-mounted	BRAZIL: São Paulo, Mirassol
<i>Strumigenys perparva</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Rondônia, Porto Velho
<i>Strumigenys planeti</i>	Female	Apterous	DZUP	Dry-mounted	PERU: Madre de Dios, Puerto Maldonado
<i>Strumigenys precava</i>	Female	Apterous	MZSP	Dry-mounted	BRAZIL: São Paulo, Tapiraí
<i>Strumigenys prospiciens</i>	Female	Macropterous	DZUP	Dry-mounted	FRENCH GUIANA: Saint-Laurent-du-Maroni, Saül

Table 1 (continued)

Species	Sex	Form	Collection of origin	Conservation medium	Locality information
<i>Strumigenys reticeps</i>	Female	Apterous	DZUP and MZSP	Dry-mounted	BRAZIL: São Paulo, Ribeirão Grande BRAZIL: São Paulo, Mogi das Cruzes
<i>Strumigenys rotogetis</i>	Female	Apterous	DZUP	Dry-mounted	MALAYSIA: Sabah, Maliau Basin
<i>Strumigenys rugithorax</i>	Female	Apterous	MZSP	Dry-mounted	BRAZIL: Santa Catarina, Blumenau
<i>Strumigenys saliens</i>	Female	Apterous	DZUP and MZSP	Dry-mounted and ethanol	BRAZIL: Santa Catarina, Blumenau BRAZIL: Paraná, São José dos Pinhais
<i>Strumigenys sanctipauli</i>	Female	Apterous	MZSP	Dry-mounted	BRAZIL: São Paulo, Salesópolis
<i>Strumigenys schmalzi</i>	Female	Apterous	DZUP and MZSP	Dry-mounted and ethanol	BRAZIL: Pará, Jari BRAZIL: Paraíba, João Pessoa
<i>Strumigenys schulzi</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: São Paulo, Sete Barras
<i>Strumigenys signae</i>	Female	Apterous	DZUP	Dry-mounted	MALAYSIA: Sabah, Maliau Basin
<i>Strumigenys smilax</i>	Female	Apterous	MZSP	Dry-mounted	BRAZIL: Rondônia, Porto Velho
<i>Strumigenys smithii</i>	Female	Apterous	DZUP	Dry-mounted and ethanol	BRAZIL: Rondônia, Porto Velho
<i>Strumigenys subdentata</i>	Female	Apterous	DZUP	Dry-mounted and ethanol	BRAZIL: Rio de Janeiro, Itatiaia
<i>Strumigenys</i> pr. <i>sublonga</i>	Female	Apterous	DZUP	Dry-mounted	PERU: Madre de Dios, Puerto Maldonado
<i>Strumigenys teratrix</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Sergipe, Nossa Senhora das Dores
<i>Strumigenys trinidadensis</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Rondônia, Porto Velho
<i>Strumigenys tridifera</i>	Female	Apterous	DZUP	Dry-mounted and ethanol	BRAZIL: Rondônia, Porto Velho
<i>Strumigenys urrhobia</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Santa Catarina, Paineel
<i>Strumigenys wheeleriana</i>	Female	Apterous	DZUP	Dry-mounted	VENEZUELA: Falcón, Cerro Los Caracoles
<i>Strumigenys villiersi</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Rondônia, Porto Velho
<i>Strumigenys xenochelyna</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Tocantins, Porto Nacional
<i>Strumigenys zeteki</i>	Female	Apterous	DZUP	Dry-mounted	BRAZIL: Rondônia, Porto Velho
<i>Strumigenys</i> sp.n.1 (fe)	Female	Apterous and m acropterous	MZSP	Dry-mounted	BRAZIL: Paraná, Tunas
<i>Strumigenys</i> sp.n.2 (ele)	Female	Apterous	MZSP	Dry-mounted	BRAZIL: Minas Gerais, Viçosa
<i>Strumigenys</i> sp.n.3 (fast)	Female	Apterous	MZSP	Dry-mounted	BRAZIL: Santa Catarina, Palhoça
<i>Strumigenys</i> sp.n.4 (gib)	Female	Apterous	MZSP and CASC	Dry-mounted	BRAZIL: São Paulo, Piedade
<i>Strumigenys</i> sp.n.5 (ro)	Female	Apterous	MZSP	Dry-mounted	BRAZIL: Paraná, Tunas
<i>Strumigenys</i> sp.n.6 (se)	Female	Apterous	MZSP	Dry-mounted	BRAZIL: Bahia, Mata São João

2.3. Morphological data

All morphological information presented in this work refer to morphemes (Richter and Wirkner, 2014) and are without functional or evolutionary implications. Morphemes are characterized as representations of the smallest morphological unit at a particular level of description and are useful to reference morphological characteristics as secondary data.

Each anatomical entity is represented by a class (i.e. concept), a definition, and class relationships (i.e. the record that links two concepts via a class relationship). Anatomical classes for Hymenoptera were recovered from the Hymenoptera Anatomy Ontology (Yoder et al., 2010; HAO version 26.iv.2018), while phenotypic quality classes are based on the Phenotypic Quality Ontology (PATO version 07.ii.2018). Class relationship types are based on the OBO Relations Ontology (OBOREL 2018; version 11.vii.2018) (Table 2). All ontologies are made available through the Open Biomedical Ontologies Foundry. The list of terms used in the current work and their definitions can be found in the Table 3.

Morphological definitions are constructed as *genus-differentia*, which are definitions structured to first describe a more inclusive class of concepts (*genus*) and then the characteristics differentiating (*differentia*) it from another subordinate of that same concept (Seltmann et al., 2012). Definitions in this format usually follow the pattern “The x that is y” (cf. Boudinot, 2018, Appendix A).

To refer to the distinct morphological forms commonly found in female ants we opted to use the terms apterous and macropterous rather than workers and queens/gynes, respectively. Since the last

two concepts are intrinsically related to colonial and reproductive function (Hölldobler and Wilson, 1990), we refrain from using them, based on the premise that the external morphology alone is not sufficient to infer reproductive aptitude (Silva and Feitosa, 2018). The recognition criterion applied in this study to determine the biological sex of the specimens is purely anatomical, through the observation of external elements of the genitalia; in our case, we observed the distal section of the modified ovipositor (i.e. tip of the sting apparatus).

2.4. Recovering classes from natural language statements

Each examined structure was described through natural language statements and variations found were discussed when pertinent. The description process was performed simultaneously by both authors in order to increase agreement during coding procedures. The descriptions were automatically parsed and concepts were recovered from each ontology using two tools: the *Analyze* tool from the Hymenoptera Anatomy Ontology portal (<http://portal.hymao.org/projects/32/public/ontology/analyze>) (Seltmann et al., 2013) for recognition of anatomical classes; and Bioportal's *Annotator* (<https://bioportal.bioontology.org/annotator>) (Shah et al., 2009) for recognition of phenotypic quality classes. Both tools recognize input natural language statements, parsing down textual data and recovering specific classes based on a defined set of dictionaries (in our case, ontologies). The output data are normally exported as CSV, JSON, or XML formats, and contains the classes recognized from the input text, along with their definitions and/or unique resource identifiers (URIs). Classes not

Table 2

Object (class relationship types) and annotation properties used in the annotation of anatomical classes.

Property	Definition
<i>is_a</i>	A subsumption object property. Represents a transitive, reflexive and anti-symmetric relation between two or more classes.
<i>part_of</i>	A composition object property. Represents a transitive, reflexive and anti-symmetric relation between two or more classes.
<i>has_related_synonym</i>	An aggregation annotation property. Represents a predicate between a class and a literal.

Table 3

List of terms, their definitions, and their respective ontology identifiers. To recover definitions of classes and annotations through the OBO Foundry, include <http://purl.obolibrary.org/obo/> before the identifier (e.g., http://purl.obolibrary.org/obo/PATO_0000402).

Term	Definition	Ontology identifier
acetabulum	The area that is concave and accommodates the base of a segment.	HAO_0000082
anatomical cluster	The anatomical group that has its parts adjacent to one another.	HAO_0000041
anatomical entity	Biological entity that is either an individual member of a biological species or constitutes the structural organization of an individual member of a biological species.	HAO_0000000
anatomical group	Anatomical structure consisting of at least two non-overlapping organs, multi-tissue aggregates or portion of tissues or cells of different types that does not constitute an organism, organ, multi-tissue aggregate, or portion of tissue.	HAO_0000054
anatomical structure	Material anatomical entity which has inherent 3D shape and is generated by coordinated expression of the organism's own genome.	HAO_0000003
angular	A shape quality inhering in a bearer by virtue of the bearer's having at least one salient angle on the margin.	PATO_0001977
anterior coxal fossa of the mesotrochanter	The fossa that is located on the anterior coxal articular process of the mesotrochanter and accommodates the anterior trochanteral condyle of the mesocoxa.	HAO_0001433
anterior coxal fossa of the metatrochanter	The fossa that is located anteriorly on the metatrochanter and accommodates the anterior trochanteral condyle of the metacoxa.	HAO_0001501
anterior coxal fossa of the protrochanter	The fossa that is located anteriorly on the proximal margin of the protrochanter accommodating the anterior trochanteral condyle of the procoxa.	HAO_0001500
antennal insertion	The foramen that is located on the head in which the radicle is positioned.	HAO_0001022
antennal scrobe	The scrobe that is located dorsally of the antennal foramen and is for the reception of the antenna.	HAO_0001432
area	The anatomical structure of the cuticle that is delimited by material or immaterial anatomical entities.	HAO_0000146
areolate	A surface feature shape inhering in a surface by virtue of the bearer's being divided by ridge-like structures into a number of small, irregular spaces.	PATO_0002295
articular process	The projection that bears the articular surface.	HAO_0000150
arolium	The lobe that is connected proximodorsally with the manubrium and proximoventrally with the planta.	HAO_0000148
basicostal suture	The sulcus that corresponds to the basicosta.	HAO_0000174
basicoxite	The area that is located on the coxa proximal to the basicostal suture.	HAO_0000175
basitarsus	The tarsomere that is the proximal most annulus of the tarsus, connected proximally with the tibia and distally with the second tarsomere via membranous conjunctivae.	HAO_0000178
coxal condyle of the pectus	The condyle that is located on the pectus and inserts into the pectal fossa of the coxa.	HAO_0001917
dilated	A size quality inhering in a bearer by virtue of the bearer's being made wider or larger in all dimensions.	PATO_0001571
femoro-tibial joint	The dicondylic joint that is composed of the femur and the tibia.	HAO_0001517
foramen	The anatomical space that is surrounded by sclerites and allows for the passage of haemolymph, nerves and tracheae.	HAO_0000345
frontal carina	The carina that extends along the lateral margin of the intertorular area towards the vertex.	HAO_0001533
joint	The anatomical cluster that is composed of two sclerites connected by at least one articulation and the articular membrane located connecting the two sclerite.	HAO_0001146
lateral pectal fossa of the coxa	The fossa that is located laterally on the proximal margin of the coxa and accommodates the lateral coxal condyle of the pectus.	HAO_0001913
malar area	The area that extends between the anterior eye margin and the anterolateral margin of the cranium, and its width is delimited by the width of the mandible.	HAO_0001393
mandibular acetabulum	The fossa that is located anteriorly on the proximolateral edge of the mandible and accommodates the pleurostomal coondyle.	/HAO_0001391
manubrium	The sclerite that is located proximodorsally on the pretarsus and connects the distodorsal margin of the telotarsus with the dorsal part of the arolium.	HAO_0000671
medial coxal articular process of the mesopectus	The articular process that is located on the ventral margin of the mesopectus medially of the mesocoxal foramen and bears the medial coxal condyle of the mesopectus.	HAO_0001389
medial coxal articular process of the metapectus	The articular process that is located on the ventral margin of the metapectus medially of the metacoxal foramen and bears the medial coxal condyle of the metapectus.	HAO_0001388
medial coxal condyle of the pectus	The coxal condyle of the pectus that inserts into the medial pectal fossa of the coxa.	HAO_0001918
medial pectal fossa of the coxa	The pectal fossa of the coxa that accommodates the median coxal condyle of the pectus.	HAO_0001916
mesodiscrimen	The discrimen that is located in the mesothorax and corresponds with the mesodiscrimenal lamella.	HAO_0000545
mesopectus	The sclerite that is U-shaped in cross section, connected anteriorly with the pronotum and the propectus, dorsally with the basalare, the mesonotum, the second axillary sclerite and the subalare, posteriorly with the metapectus and bears the mesodiscrimenal lamella and the mesofurca.	HAO_0000557
metapectus	The area that is located anteriorly of the metapleural sulcus and ridge.	HAO_0000605
orbicular	A shape quality inhering in a bearer by virtue of the bearer's being perfectly circular.	PATO_0001934
planta	The sclerite that is located proximoventrally on the pretarsus and is connected proximally with the unguitractor plate and distally with the arolium.	HAO_0000719
pleurostomal condyle	The condyle that is located on the anterior (dorsal) margin of the pleurostoma and inserts into the mandibular acetabulum.	HAO_0000731
posterior cranio-mandibular muscle	The mandibular muscle that arises posterodorsally from the cranium and inserts on the tendon attached anteroproximally on the mandible.	HAO_0000745
pretarsus	The anatomical cluster that is apical to the telotarsus and composed of the empodium, auxilia, planta, pulvillum, unguis, unguitractor plate, auxiliar sclerite and manubrium.	HAO_0000820
probasisternum	The basisternum that is located in the propectus.	HAO_0001317
pronotal carina	The carina that delimits posteriorly the pronotal neck.	HAO_0001031

Table 3 (continued)

Term	Definition	Ontology identifier
pronotal neck	The area of the pronotum that is delimited posterodorsally by an edge and that accommodates the posterior surface of the head.	HAO_0000837
protibial spur	The tibial spur that is located on the fore leg, is curved and together with the probasitarsus forms the strigil.	HAO_0000875
posterior coxal fossa of the mesotrochanter	The fossa that is located posteriorly on the proximal margin of the mesotrochanter accommodating the posterior trochanteral condyle of the mesocoxa.	HAO_0001348
posterior coxal fossa of the metatrochanter	The fossa that is located posteriorly on the proximal margin of the metatrochanter and accommodates the posterior trochanteral condyle of the metacoxa.	HAO_0001295
posterior coxal fossa of the protrochanter	The fossa that is located posteriorly on the proximal margin of the protrochanter accommodating the posterior trochanteral condyle of the procoxa.	HAO_0001297
sculpture	The area that is located on the sclerite and that is composed of repetitive anatomical structures.	HAO_0000913
setiferous patch	The patch that differs from the surrounding region by having denser setae.	HAO_0000936
spatulate	A shape quality inhering in a bearer by virtue of the bearer's being oblong, with the lower end very much attenuated.	PATO_0001937
strigil	The anatomical cluster that is composed of the probasitarsus and calcar.	HAO_0000102
subulate	A shape quality inhering in a bearer by virtue of the bearer's being linear, very narrow, tapering to a very fine point from a narrow base.	PATO_0001954
tarsal claw	The spur that is curved and projects from the apex of the last tarsal segment on either side of the arolium of the pretarsus.	HAO_0000989
trochantellus	The area that is located proximally on the femur and is delimited by a groove.	HAO_0001033
trochanter	The leg segment that is located proximal to the femur and distal to the coxa.	HAO_0001034
unguitractor plate	The sclerite that corresponds to the site of insertion of the flexor of the pretarsus.	HAO_0001043

recognized by those tools were manually annotated to the Hymenoptera Anatomy Ontology (Table 4).

2.5. Annotation development

Annotations were made following a four-step process: 1) Phenotypic and relational classes available in OWL (Web Ontology Language, <http://www.w3.org/TR/owl2-overview/>) were loaded into Protégé 4.1 (<http://protege.stanford.edu/>), an open-source ontology editor and a knowledge management system; 2) Annotations were manually added to anatomic entities within Protégé as OWL class expressions using the built-in Manchester syntax (www.w3.org/TR/owl2-manchester-syntax/) editor; 3) After annotation, we used the FaCT++ reasoner to determine if new annotations did not violate descriptions and axioms across the ontology; 4) Annotated entities were exported as OWL class expressions and individually added to mx (Mx., 2019), a collaborative open-source application that facilitates the construction of ontologies through a multi-feature environment. All phenotype statements in Manchester syntax are available in Table 4.

2.6. Images

Illustrations were made using Adobe Illustrator (version CS6), based on images available at AntWeb (2019) and personal observations of the studied material. Antweb images used to prepare the plates have their respective identifier explicitly indicated at the legend of the figure (in the form of CASENT0000000).

2.7. Data repository

All data obtained are available through an online open-access repository (<https://doi.org/10.6084/m9.figshare.7645400>) as .csv and .owl files. Annotations in Manchester syntax can be easily obtained through the 'annotations.csv' file. Novel anatomical classes were added to the most recent version of the 'hao.owl' file and are deposited as a 'hao-merged-strumigenys.owl' file.

3. Results and discussion

Terms and definitions for structures, along with their identifiers (i.e. persistent uniform resource locators; purl), which were used

throughout the text and figures, can be found in Table 3. Annotations for morphological terms discussed in the following sections, along with their definitions, can be found in Table 4.

We annotated 35 new anatomical classes based on the study of *Strumigenys*. From those, 12 were from structures found on the head and its appendages (i.e. mouthparts and antennae), nine were from the mesosoma and its appendages (i.e. legs), 13 were from the metasoma, and one refers to a structure that can occur in more than one body region (i.e. mesosoma and metasoma). Overall, six classes presented one synonym, with one class having two synonyms, totalling seven synonyms.

3.1. Head

Ants have the head oriented horizontally towards the longitudinal axis and mouthparts anteriorly-oriented. Hence, the spatial orientation terminology follows those of prognathous insects. The insect head has been divided into different areas (Snodgrass, 1993; Chapman, 1998): frons, vertex, temple, gena, postgena, malar space and occiput. However, these areas are difficult to establish, since their presence and dimensions depend on the presence and position of other structures, such as the compound eyes and ocelli. Most of those areas were named by Kirby and Spencer (1828), but their delimitations, for the most part, are elusive.

3.1.1. Fronto-vertexal area and complex

In Hymenoptera, the frons is the area between the epistomal line and the anterior ocellus and limited laterally by the inner margin of compound eye (Mikó, 2009/2019). Macropterous female and male ants generally retain all three ocelli, with the posterior limits of the frons and the anterior limits of the vertex being promptly determined. In apterous ant females, however, the posterior limits of the frons and anterior limits of the vertex cannot be externally defined in most groups, due to the loss of ocelli in this form. Another complex situation found in apterous females is the reduction or loss of the eyes in some groups, making the lateral delimitation of the frons and the dorsal delimitation of the gena somewhat ambiguous (discussed thoroughly in the section "Gena").

In Hymenoptera, the vertex is the area delimited by the intersection of the margin of the compound eyes, the interorbital plane, and the anatomical line tangential to the point on the margin of the

Table 4

List of terms, their definitions, and annotations expressed in Manchester syntax.

Term	Definition	Annotation
Antero-proximal process of the scape	The process that is located near the base on the anterior margin of the scape and is wider or larger in all dimensions	<i>is_a</i> some <u>process</u> and <u>part_of</u> some <u>sclerite</u> and <u>'bearer of'</u> some <u>dilated</u>
Antero-sclerite	The area that is located on an abdominal sclerite and is limited anteriorly by the antecostal sulcus and posteriorly by the transverse impression of the abdominal sclerite.	<i>is_a</i> some <u>area</u> and <u>part_of</u> some <u>metasoma</u> and <u>part_of</u> some <u>cuticle</u> and <u>has_related_synonym</u> <u>presclerite</u>
Antero-sternite	The antero-sclerite that is located ventrally.	<i>is_a</i> some <u>antero-sclerite</u> and <u>part_of</u> some <u>metasoma</u> and <u>part_of</u> some <u>cuticle</u> and <u>part_of</u> some <u>sternum</u>
Antero-tergite	The antero-sclerite that is located dorsally.	<i>is_a</i> some <u>antero-sclerite</u> and <u>part_of</u> some <u>metasoma</u> and <u>part_of</u> some <u>cuticle</u> and <u>part_of</u> some <u>tergum</u>
Antero-ventral notch of the mesopectus	The notch that is located anteriorly on the ventral margin of the mesopectus.	<i>is_a</i> some <u>notch</u> and <u>part_of</u> some <u>mesopectus</u> and <u>part_of</u> some <u>mesosoma</u> and <u>part_of</u> some <u>margin</u> and <u>part_of</u> some <u>sclerite</u>
Apical fork	The anatomical cluster that is consisted by the apicoventral tooth and the apicodorsal tooth.	<i>is_a</i> some <u>anatomical cluster</u> and <u>part_of</u> some <u>mandible</u> and <u>part_of</u> some <u>sclerite</u> and <u>part_of</u> some <u>cuticle</u>
Apico-dorsal tooth	The projection that is located distally on the mandible and limited ventrally by the intercalar tooth or by the apico-ventral tooth, forming the apical fork.	<i>is_a</i> some <u>tooth</u> and <u>part_of</u> some <u>mandible</u> and <u>part_of</u> some <u>sclerite</u> and <u>part_of</u> some <u>'apical fork'</u>
Apico-ventral tooth	The projection that is located distally on the mandible and limited dorsally by the intercalar tooth or by the apico-dorsal tooth, forming the apical fork.	<i>is_a</i> some <u>tooth</u> and <u>part_of</u> some <u>mandible</u> and <u>part_of</u> some <u>sclerite</u> and <u>part_of</u> some <u>'apical fork'</u>
Areolate process	The area of the sclerite that is raised and is divided by ridge-like structures into a number of small, irregular spaces.	<i>is_a</i> some <u>process</u> and <u>part_of</u> some <u>cuticle</u> and <u>part_of</u> some <u>sclerite</u> and <u>'bearer of'</u> some <u>areolate</u> and <u>has_related_synonym</u> <u>spongiform tissue</u>
Basicoxal foramen	The foramen that is located proximally on the basicoxite.	<i>is_a</i> some <u>foramen</u> and <u>part_of</u> some <u>basicoxite</u>
Disticoxal foramen	The foramen that is located distally on the disticoxite.	<i>is_a</i> some <u>foramen</u> and <u>part_of</u> some <u>disticoxite</u>
Disticoxite	The area that is located on the coxa distal to the basicostal suture.	<i>is_a</i> some <u>area</u> and <u>part_of</u> some <u>coxa</u>
Fronto-vertexal area	The area of the sclerite that is located between the epistomal line and the occipital carina and limited laterally by the inner margin of the compound eye.	<i>is_a</i> some <u>area</u> and <u>part_of</u> some <u>fronto-vertexal complex</u> <u>has_related_synonym</u> <u>fronto-vertex</u>
Fronto-vertexal complex	The sclerite that is between the epistomal line and the occipital carina and limited laterally by the inner margin of the compound eye.	<i>is_a</i> some <u>sclerite</u> and <u>part_of</u> some <u>frons</u> and <u>part_of</u> some <u>vertex</u> and <u>part_of</u> some <u>cuticle</u>
Intercalar tooth	The tooth that is located on the apical fork, limited ventrally by the apico-ventral tooth and dorsally by the apico-dorsal tooth.	<i>is_a</i> some <u>tooth</u> and <u>part_of</u> some <u>mandible</u> and <u>part_of</u> some <u>sclerite</u> and <u>part_of</u> some <u>cuticle</u> and <u>part_of</u> some <u>'apical fork'</u>
Lateral areolate process of the petiole	The areolate process that is located at the lateral margin of the petiole.	<i>is_a</i> some <u>'areolate process'</u> and <u>part_of</u> some <u>metasoma</u> and <u>part_of</u> some <u>'abdominal segment 2'</u> and <u>part_of</u> some <u>cuticle</u> and <u>part_of</u> some <u>sclerite</u>
Lateral areolate process of the abdominal tergum 3	The areolate process that is located at the lateral margin of the abdominal tergum 3.	<i>is_a</i> some <u>'areolate process'</u> and <u>part_of</u> some <u>metasoma</u> and <u>part_of</u> some <u>'abdominal segment 3'</u> and <u>part_of</u> some <u>cuticle</u> and <u>part_of</u> some <u>sclerite</u>
Lateral coxal condyle of the pectus	The coxal condyle of the pectus that inserts into the lateral pectal fossa of the coxa.	<i>is_a</i> some <u>'coxal condyle of the pectus'</u> and <u>part_of</u> some <u>pectus</u> and <u>part_of</u> some <u>sclerite</u> and <u>part_of</u> some <u>articulation</u>
Lateral mandibular articular process	The articular process that is located laterally on the proximal margin of the mandible.	<i>is_a</i> some <u>'articular process'</u> and <u>part_of</u> some <u>mandible</u> and <u>part_of</u> some <u>sclerite</u>
Lateral mandibular scrobe	The scrobe that is located proximally on the mandible and accommodates the anterolateral process of the head.	<i>is_a</i> some <u>scrobe</u> and <u>part_of</u> some <u>mandible</u> and <u>part_of</u> some <u>sclerite</u>
Metapleural gland	The gland that is located on the metapleuron and opens posteriorly near the propodeal foramen, on the orifice of the metapleural gland.	<i>is_a</i> some <u>gland</u> and <u>part_of</u> of and <u>part_of</u> some <u>metapleuron</u> and <u>part_of</u> some <u>body</u>
Orifice of the metapleural gland	The anatomical space that is situated posteriorly on the metapecto-propodeal complex, lateral to the propodeal foramen.	<i>is_a</i> some <u>'anatomical space'</u> and <u>part_of</u> some <u>'metapectal-propodeal complex'</u> and <u>part_of</u> some <u>metapleuron</u>
Postbuccal impression	The impression that is located posteriorly to the oral foramen.	<i>is_a</i> some <u>impression</u> and <u>part_of</u> some <u>sclerite</u> and <u>part_of</u> some <u>integument</u> and <u>part_of</u> some <u>'postgenal bridge'</u>
Postero-sclerite	The area of an abdominal sclerite limited anteriorly by the transverse impression of the abdominal sclerite and posteriorly by the posterior margin of the abdominal sclerite.	<i>is_a</i> some <u>area</u> and <u>part_of</u> some <u>metasoma</u> and <u>part_of</u> some <u>cuticle</u> and <u>has_related_synonym</u> <u>postsclerite</u>
Postero-sternite	The postero-sclerite that is located ventrally.	<i>is_a</i> some <u>postero-sclerite</u> and <u>part_of</u> some <u>metasoma</u> and <u>part_of</u> some <u>cuticle</u> and <u>part_of</u> some <u>sternum</u>
Postero-tergite	The postero-sclerite that is located dorsally.	<i>is_a</i> some <u>postero-sclerite</u> and <u>part_of</u> some <u>metasoma</u> and <u>part_of</u> some <u>cuticle</u> and <u>part_of</u> some <u>tergum</u>

Table 4 (continued)

Term	Definition	Annotation
Pronoto-mesonotal complex	The sclerite that is located dorsally to the propectus and mesopectus and is composed of the pronotum and mesonotum.	<i>is a</i> some <u>sclerite</u> and <i>part of</i> some <u>cuticle</u> and <i>part of</i> some <u>pronotum</u> and <i>part of</i> some <u>mesonotum</u>
Tibial scrobe	The scrobe that is located ventrally on the femur and accommodates the tibia.	<i>is a</i> some <u>scrobe</u> and <i>part of</i> some <u>sclerite</u> and <i>part of</i> some <u>femur</u>
Translucent patch of the frontal carina	The translucent patch that is located at the frontal carina.	<i>is a</i> some <u>'translucent patch'</u> and <i>part of</i> some <u>'frontal carina'</u> and <i>part of</i> some <u>integument</u> and <i>part of</i> some <u>cuticle</u>
Translucent patch of the metapleuron	The translucent patch that is located at the metapleuron.	<i>is a</i> some <u>'translucent patch'</u> and <i>part of</i> some <u>metapleuron</u> and <i>part of</i> some <u>integument</u>
Translucent patch of the ventral antennal scape	The translucent patch that is located at the ventral margin of the antennal scape.	<i>is a</i> some <u>'translucent patch'</u> and <i>part of</i> some <u>scape</u> and <i>part of</i> some <u>integument</u> and <i>part of</i> some <u>cuticle</u>
Transverse carina of the fourth postero-tergite	The carina that is located posteriorly to the impression of the fourth abdominal tergite, belonging to the fourth postero-tergite	<i>is a</i> some <u>carina</u> and <i>part of</i> some <u>sclerite</u> and <i>part of</i> some <u>postero-tergite</u> and <i>has related synonym</i> <u>limbus</u>
Transverse impression of the abdominal sclerite	The impression that is located on the external surface of an abdominal sclerite and does not correspond to a ridge.	<i>is a</i> some <u>impression</u> and <i>part of</i> some <u>metasoma</u> and <i>part of</i> some <u>sclerite</u> and <i>part of</i> some <u>integument</u> and <i>has related synonym</i> <u>'girdling constriction'</u>
Transverse patch of the abdominal sternum 4	The patch that is elongated and extends transversely along the anterior portion of the abdominal sternum 4.	<i>is a</i> some <u>patch</u> and <i>part of</i> some <u>'abdominal sternum 4'</u> and <i>part of</i> some <u>metasoma</u> and <i>part of</i> some <u>integument</u> and <i>part of</i> some <u>cuticle</u>
Ventral areolate process of the petiole	The areolate process that is located at the ventral margin of the petiole.	<i>is a</i> some <u>'areolate process'</u> and <i>part of</i> some <u>'abdominal segment 2'</u> and <i>part of</i> some <u>metasoma</u> and <i>part of</i> some <u>cuticle</u> and <i>part of</i> some <u>sclerite</u>
Ventral areolate process of the abdominal sternum 3	The areolate process that is located at the ventral margin of the abdominal sternum 3.	<i>is a</i> some <u>'areolate process'</u> and <i>part of</i> some <u>'abdominal sternum 3'</u> and <i>part of</i> some <u>metasoma</u> and <i>part of</i> some <u>cuticle</u> and <i>part of</i> some <u>sclerite</u>
Ventral notch of the propodeal foramen	The notch that is located medially on the ventral margin of the propodeal foramenal margin.	<i>is a</i> some <u>notch</u> and <i>part of</i> some <u>'propodeal foramen'</u> and <i>part of</i> some <u>'metapectal-propodeal complex'</u> and <i>part of</i> some <u>margin</u> and <i>part of</i> some <u>sclerite</u>

anterior ocellus which defines the minimum distance between the anterior ocellus and the oral foramen (Yoder, 2009). Similarly to the frons, the anterior margin of the vertex cannot be externally delimited in apterous females of ants, due to the lack of ocelli in most groups.

Muscular organization has been useful to establish structural equivalence in other groups of Hymenoptera (Kawada et al., 2015; Popovici et al., 2014; Zimmermann and Vilhelmsen, 2016) and in male ants (Boudinot, 2013). There have been several studies exploring the internal anatomy of the head of ants, especially in groups with drastic modifications in the cephalic appendages (Gronenberg, 1995, 1996; Gronenberg and Ehmer, 1996; Gronenberg et al., 1997, 1998a,b; Larabee et al., 2017, 2018; Paul and Gronenberg, 1999), high intraspecific morphological variation (Lilico-Ouachour et al., 2018) or novel appendage functionality (Khalife et al., 2018). Since these investigations are mainly focused on the mechanics and physiology of the muscular groups related to the mandibular motion, the cephalic muscular organization in different lineages of ants has remained relatively unexplored, hampering our understanding of the regionalization and sclerite fusion in this group.

Since we are not confident about the current understanding of the muscular arrangement in ants in a comparative context, and due to our inability to properly define the frons and vertex of apterous females both internally and externally, we opted to refer to them collectively as the *fronto-vertexal complex* when referring to the structure as an anatomical cluster, and *fronto-vertexal area* (or *fronto-vertex*) when referring to the externally observable area of the structure (Table 4).

The main distinction between both classes is how they are recognized. An *anatomical complex* is understood as being an *anatomical cluster*, which is defined as an *anatomical group that has its parts adjacent to one another* (Haendel et al., 2008). An *anatomical group* is understood as an *anatomical structure consisting of at least two non-overlapping organs, multi-tissue aggregates or portion of tissues or cells of different types that does not constitute an organism, organ, multi-tissue aggregate, or portion of tissue* (Haendel et al., 2008). On the other hand, an *anatomical area* can be understood as the *anatomical structure of the cuticle that is delimited by material or immaterial anatomical entities* (Mikó, 2009/2019). Therefore, an anatomical complex can be understood as an assembly of anatomical entities (including cuticle, muscles and apodemes), while an anatomical area can be understood as a two-dimensional anatomical entity (e.g., the cuticle) delimited by other anatomical entities (such as anatomical lines, anatomical spaces, or anatomical structures).

In *Strumigenys* the fronto-vertexal area can be easily delimited laterally even in species with reduced eyes (Fig. 1). Although variable in size and antero-posteriorly positioned, the compound eyes are rarely displaced in a dorso-ventral axis.

3.1.2. Gena

The gena in hymenopterans is the area delimited by the *intersection of the interorbital plane, the margin of the compound eye, the margin of the oral foramen, the occipital carina and the malar sulcus* (Yoder, 2009). It is divided into three other areas, namely the malar area, the gena s.s. and the temple (Fig. 1; ma, gn and tm, respectively) (Boudinot et al., 2013). Internally, it appears to not

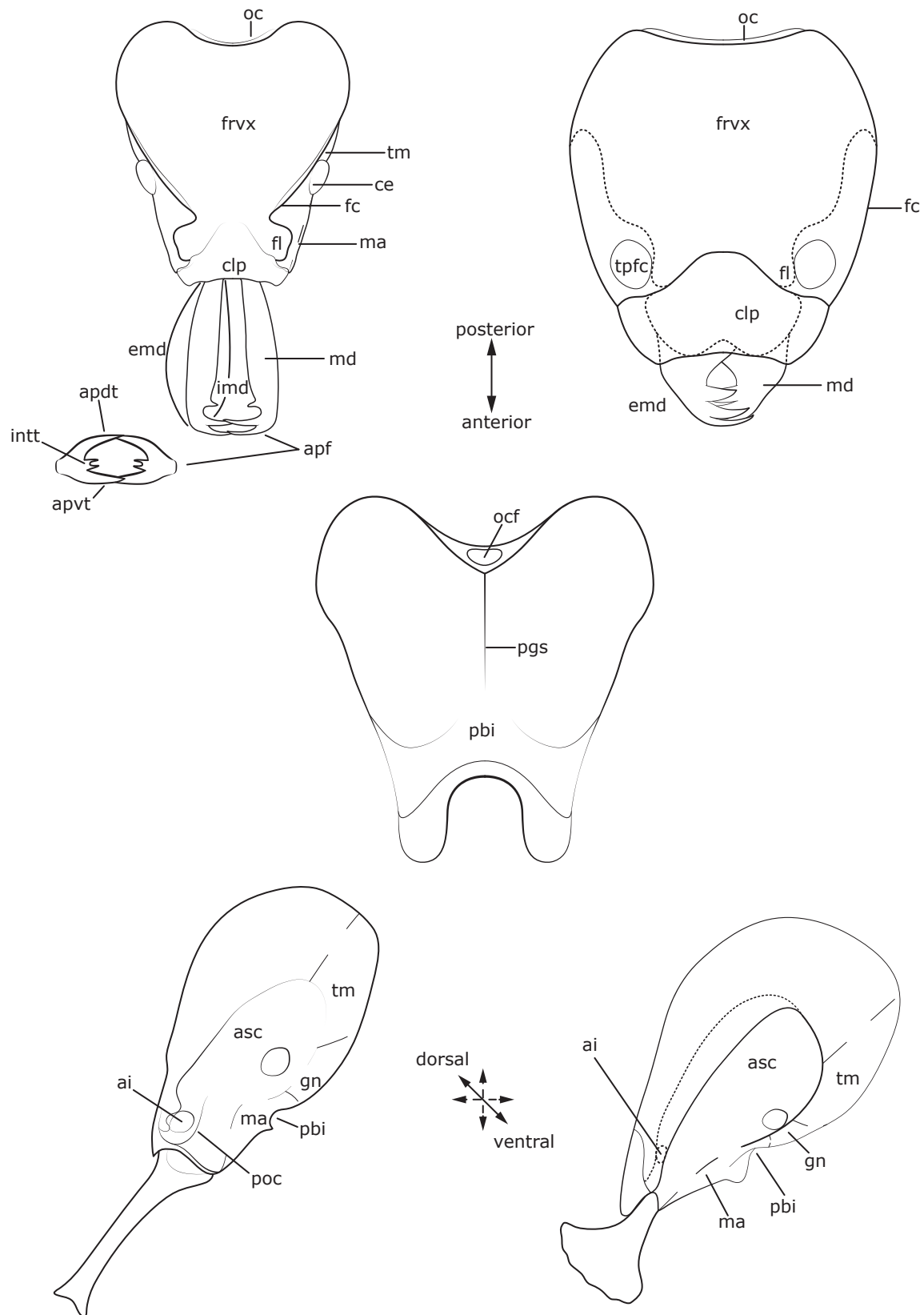


Fig. 1. Schematic illustration of the head and mandibles of apterous females of *Strumigenys*. Dotted lines indicate the limits of structures. Dashed lines indicate the limits of areas. Abbreviations: **ai**: antennal insertion; **apdt**: apicodorsal tooth; **apf**: apical fork; **apvt**: apicoventral tooth; **asc**: antennal scrobe; **ce**: compound eye; **clp**: clypeus; **emd**: external margin of the mandible; **fc**: frontal carina; **frvx**: fronto-vertex area; **gn**: gena; **imd**: internal margin of the mandible; **intt**: intercal teeth; **ma**: malar area; **md**: mandible; **oc**: occipital carina; **ocf**: occipital foramen; **pbi**: postbuccal impression; **pgs**: postgenal suture; **poc**: preocular carina; **tm**: temple; **tpfc**: translucent patch of frontal carina.

correspond precisely to any muscular group, although most of the crano-mandibular muscle group has its origins in this region. In Scelionidae (Mikó et al., 2007) and in Bethyridae (Lanes, 2013), this area corresponds to the origin sites of the median band of the anterior crano-mandibular muscle and of the posterior crano-mandibular muscle. This condition is similarly found in Formicidae, although there is major variation in muscle size, area of origin, apodeme length, and area of insertion in those muscles depending on the group (personal observation), age of individuals and task repertoire (Muscedere et al., 2011). Mandibular shape appears to be intrinsically related to the characteristics of those muscles, possibly affecting the characteristics of the gena, such as size and shape.

In Formicidae, there is a developed median longitudinal ridge that extends from the hypostomal margin to the occipital foramen, referred to by Khalife et al. (2018) as the ventromedial phragma, and appears to be the site of origin of a ventral band of the posterior crano-mandibular muscle (as in *Melissotarsus* Emery, 1877 and *Myrmoteras* Forel, 1893; Khalife et al., 2018 and Larabee et al., 2017, respectively). It varies greatly in height and degree of sclerotization and could probably represent an internal folding of the lateral margins of the postgenal bridge (cf. "Postgenal bridge and postgenal suture section"). In some observed specimens belonging to long mandibulate species of *Strumigenys* (e.g., *Strumigenys saliens* Mayr, 1887, *Strumigenys elongata* Roger, 1863, *Strumigenys* pr. *louisianae*), this ridge is reduced but still represents the site of origin of part of the posterior crano-mandibular muscle. However, this structure may vary in other species that possess distinct mandibular morphologies.

3.1.3. Postgenal bridge and postgenal suture

According to Burks and Heraty (2015), a lot of variation can be found on the subforaminal bridges in Aculeata, and the modifications in cephalic ventral elements in this group have not been properly studied. Internally, the putative lateral margins of the postgenal bridge are greatly expanded in some ants, acting as an attachment site for mandibular muscles (cf. discussion at the *Mandible* section). The modifications of the postgenal bridge and the reduction of the postgenal suture in various groups of ants are still poorly understood. In view of the high sexual polymorphism found in the family, comparative studies are needed to investigate the modifications in this region.

We observed, in *Strumigenys*, that the postgenal bridge is fused anteriorly. In some species, the postgenal suture (Fig. 1; pgs) is visible only from the occipital carina to the medial region of the ventral surface of the head. Internally, there is a reduced longitudinal ridge spanning from near the occipital foramen to the postgenal inflection anteriorly (in which the labiomaxillary complex rests). In some dissected specimens, part of the medial band of the posterior crano-mandibular muscle has its origins in this ridge. Compared with other groups that rely on mandibular strength to process resources (such as major females of *Pheidole*), the longitudinal ridge of *Strumigenys* is greatly reduced.

3.2. Antenna

3.2.1. Scape

Among the female ants observed, the basal antennal segment is usually extremely long when compared with other groups of Hymenoptera (Fig. 2). In most genera of ants, the scape may be as long as the flagellum (Fig. 2; scp and F1-4, respectively). Much of the variation in the scape of different ant groups has remained undocumented. For example, the muscular and glandular aspects of this particular structure in *Strumigenys* have been broadly overlooked by researchers.

One example of variation in the scape that might be informative in *Strumigenys* can be found on its ventral surface. While some species have an unsculptured patch there (e.g., *Strumigenys reticeps* (Kempf, 1969) and *Strumigenys thaxteri* (Wheeler, 1916); Lattke et al., 2018), others (e.g., *Strumigenys alberti* Forel, 1893, *Strumigenys appretiata* (Borgmeier, 1954), *Strumigenys borgmeieri* Brown, 1954) have this area mostly occupied by a translucent patch. The scape also varies in overall shape (from cylindrical to dorso-ventrally flattened) and presence of a dilated process near its base on the anterior margin (Fig. 2; scp) (such as in *Strumigenys crassicornis* Mayr, 1887). When the dilated process is present, it can be defined as "The process that is located near the base on the anterior margin of the scape and is wider or larger in all dimensions" and named as *antero-proximal process of the scape*. Rows of erect and decumbent setae on the anterior margin of the scape occur in several species and they can vary from subulate to orbicular.

3.2.2. Flagellum

In Hymenoptera, variation in the number of segments of the flagellum is significant, with various conditions of fusion or reduction of segments (Polaszek et al., 1992; Heraty, 2002). In Formicidae, the antennal segments of many groups seem to be fused. Some individuals of some species seem to have asymmetrical numbers of segments (Fischer et al., 2015). There is a slight variation in the number of segments of the flagellum in *Strumigenys* (Fig. 3A–E), ranging from two to four, possibly representing the more reduced number of flagellar segments in the entire family. In other genera of the tribe, the number varies from five (e.g., *Eurhopalothrix*) to ten segments (e.g., *Basicros*) (Fig. 9). Since we cannot easily trace fusion or reduction of segments in the flagellum based on structural equivalence, previous definitions based on this method are questionable.

3.3. Mouthparts

3.3.1. Labrum

In Hymenoptera, the labrum is defined as the sclerite that is situated along the distal margin of the clypeus and is connected along its proximal margin with the distal margin of the epipharyngeal wall (Vilhelmsen and Miko, 2010). In non-formicid hymenopterans it is connected posterodorsally to the clypeus by the clypeolabral articulation, contrasting with the anterior connection found in many other insects. In Formicidae, the position of the clypeolabral articulation varies among groups, but most often it is articulated lateroventrally with the clypeus.

In *Strumigenys*, the labrum is located posteroventrally in relation to the clypeus, as in most groups of ants. Most commonly, the apodeme of the posterior fronto-labral muscle is well-developed and sclerotized, bearing the site of attachment of the posterior fronto-labral muscle, which acts as the retractor of the labrum (Gronenberg, 1996). Since the shape of the labrum is extremely variable within the genus, the apodeme of the posterior fronto-labral muscle also appears extremely variable, especially in position, which, although appearing laterally in the sclerite, differs in distance from the clypeolabral articulation (Fig. 2; clbba). The setae located in the labral lobes (Fig. 2; lbl) vary among species, ranging from orbiculate to subulate. Most long-mandibulate species possess long subulate setae that are as long as the mandibles.

According to Bolton (1999) the labrum can be modified in two distinct conditions: (i) the labrum lacks lateral processes and the anterior labral lobes are large; and (ii) the labrum is T-shaped (*sic*), with lateral processes, and the anterior labral lobes are reduced or vestigial. However, J.C.M. Chaul and coworkers (pers. comm.) observed that there is immense variation in shape of the labrum within the genus, even within distinct types of Bolton's

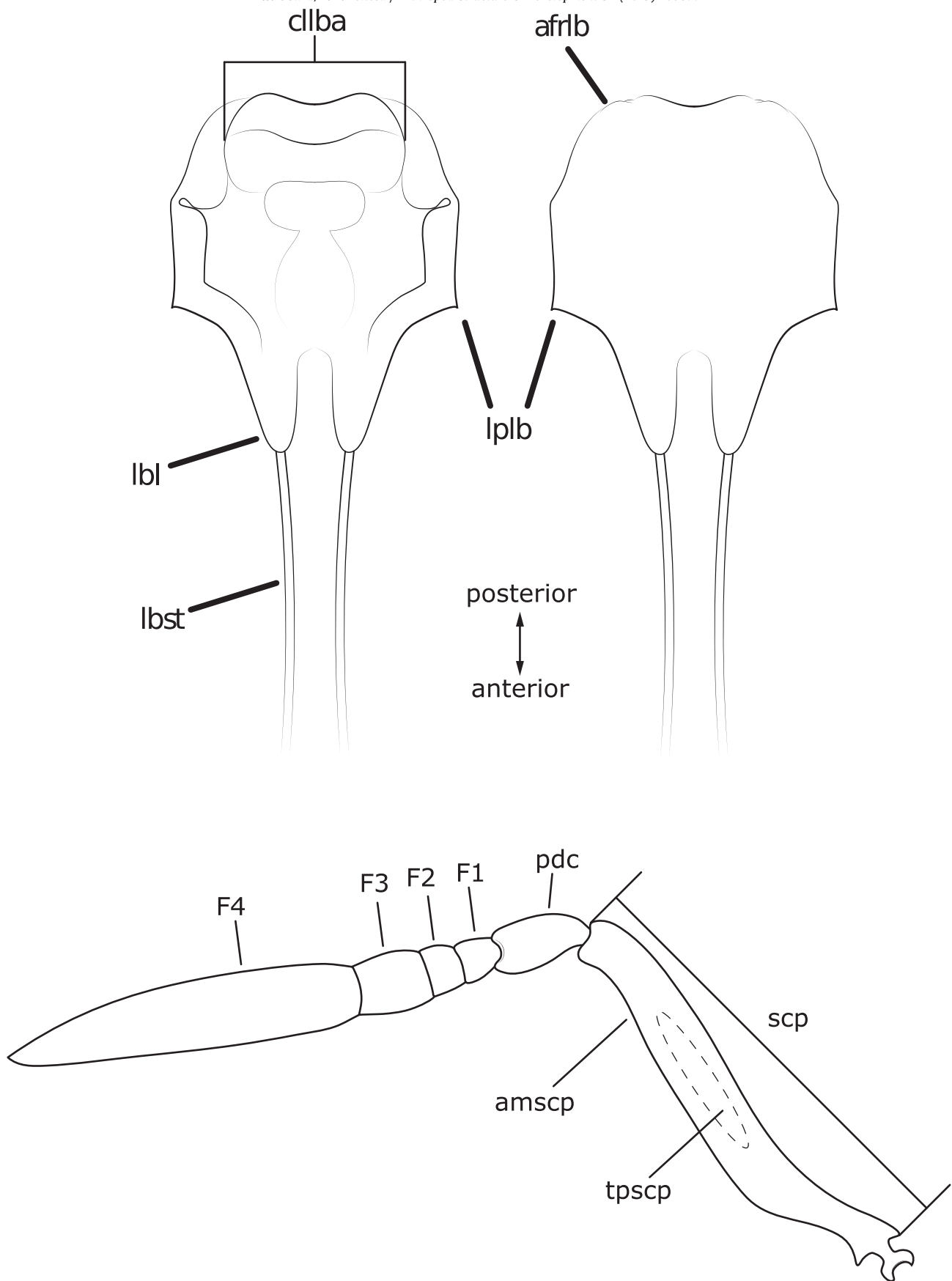


Fig. 2. Illustration of the labrum in dorsal (top left) and ventral (top right) views and of the antenna in ventral view (bottom) of apterous females of *Strumigenys*. Abbreviations: **afrlb**: apodeme of the posterior fronto-labral muscle; **amscp**: anterior margin of the scape; **clba**: clypeo-labral articulation; **F1**: first segment of the flagellum; **F2**: second segment of the flagellum; **F3**: third segment of the flagellum; **F4**: fourth segment of the flagellum; **lbl**: labral lobe; **lbst**: labral seta; **lplb**: lateral process of the labrum; **pdc**: pedicel; **scp**: antennal scape; **tpscp**: translucent patch of the antennal scape.

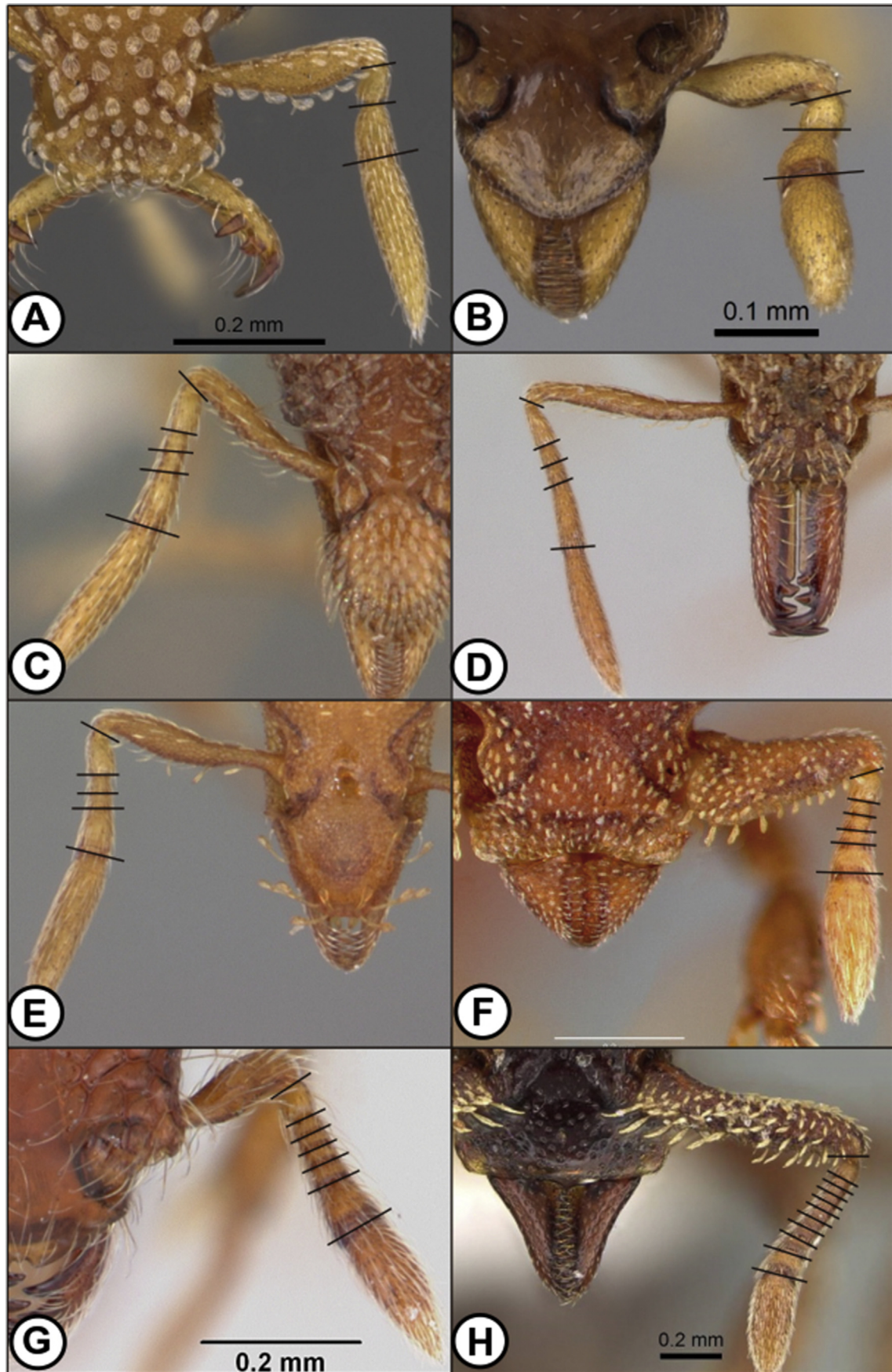


Fig. 3. Variation in the number of antennal segments in specimens of *Strumigenys* (A–E), *Eurhopalothrix* (F), *Pilotrochus* (G) and *Basiceros* (H). A: *Strumigenys anchis* CASENT0900916; B: *Strumigenys minuscula* CASENT0281948; C: *Strumigenys clypeata* CASENT0103000; D: *Strumigenys chroa* CASENT0436719; E: *Strumigenys ornata* CASENT0104478; F: *Eurhopalothrix floridana* CASENT0003195; G: *Pilotrochus besmerus* CASENT0047617; H: *Basiceros disciger* CASENT0914887.

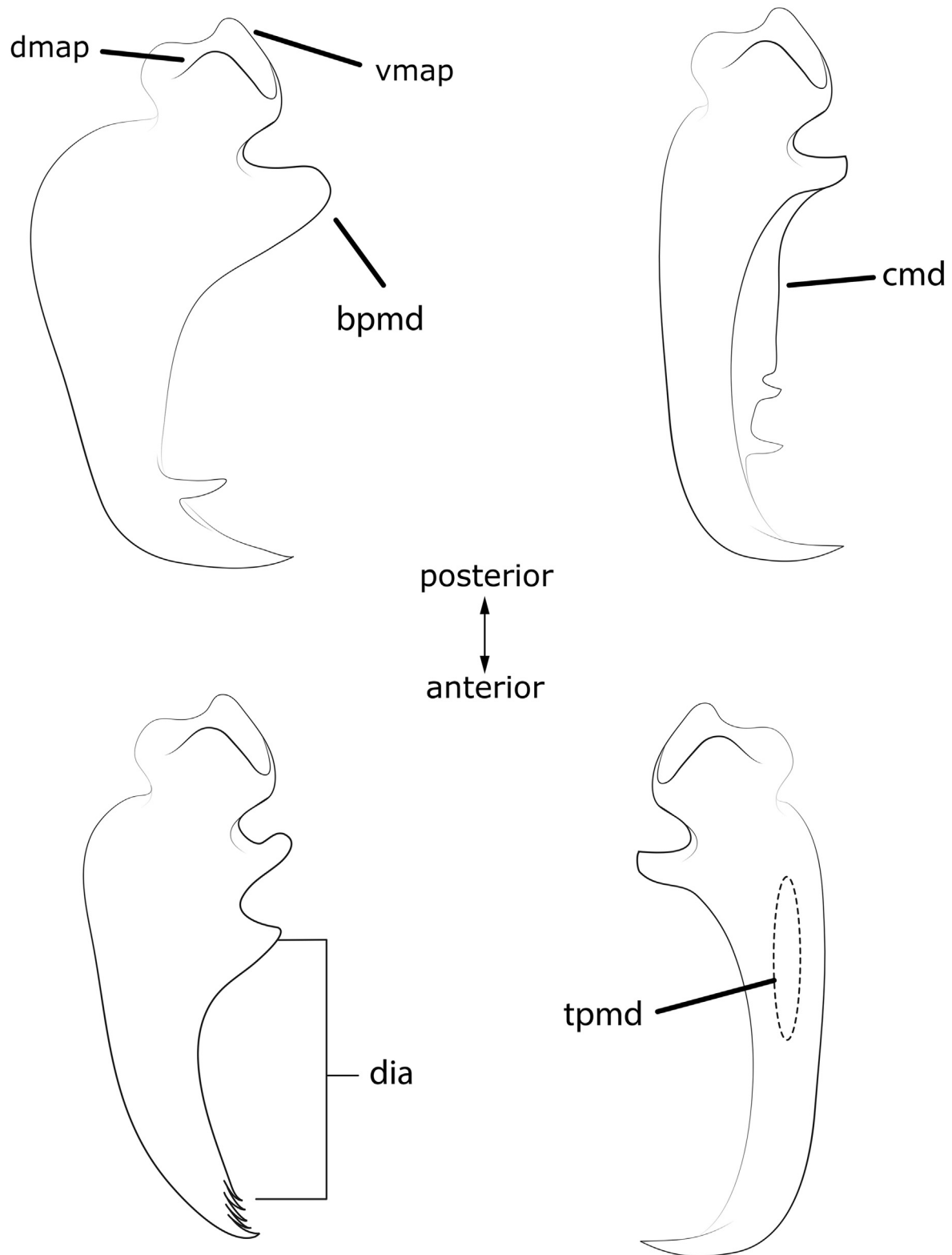


Fig. 4. Illustration of the mandible in dorsal (top left, top right, and bottom left) and ventral (bottom right) views of apterous females of *Strumigenys*. Abbreviations: **bpm**: basal process of the mandible; **cmd**: carina of the mandible; **dia**: diastema; **dmap**: dorsal articular process of the mandible; **tpmd**: translucent patch of the mandible; **vmap**: ventral articular process of the mandible.

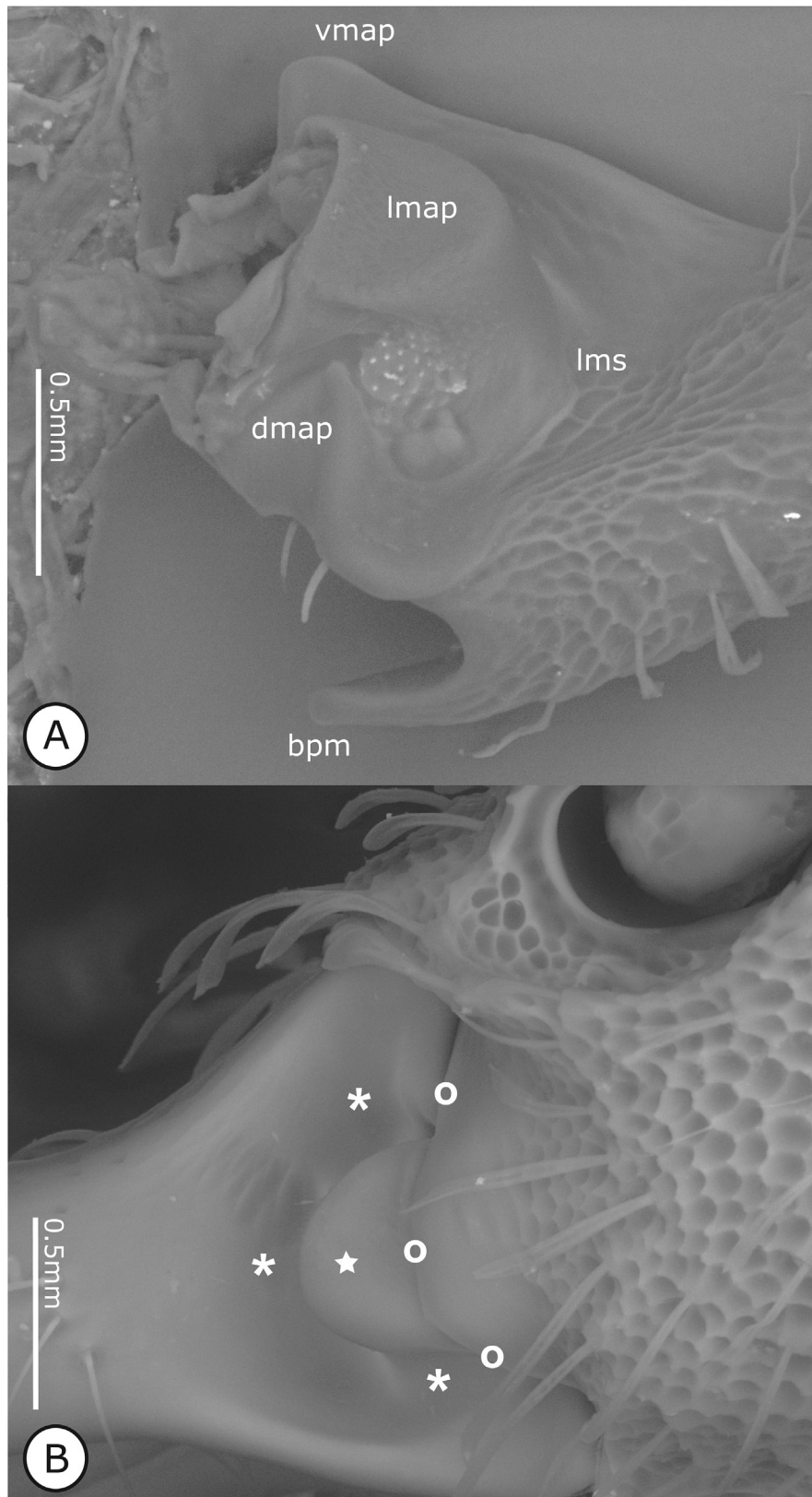


Fig. 5. Basal section of the external margin of the mandible of two apterous females of *Strumigenys*. A: Disarticulated mandible of *Strumigenys saliens*; B: Mandible inserted in the head of *Strumigenys planeti*, showing the points where the lateral scrobe of the mandible (marked by asterisks) would approximately contact the head capsule (marked by circles) when the mandible is open. The star indicates the surface of the lateral articular process of the mandible, which is concealed within the oral foramen when the mandible is open. Abbreviations: **bpm**: basal process of the mandible; **dmap**: dorsal articular process of the mandible; **lmap**: lateral articular process of the mandible; **lms**: lateral scrobe of the mandible; **vmap**: ventral articular process of the mandible.

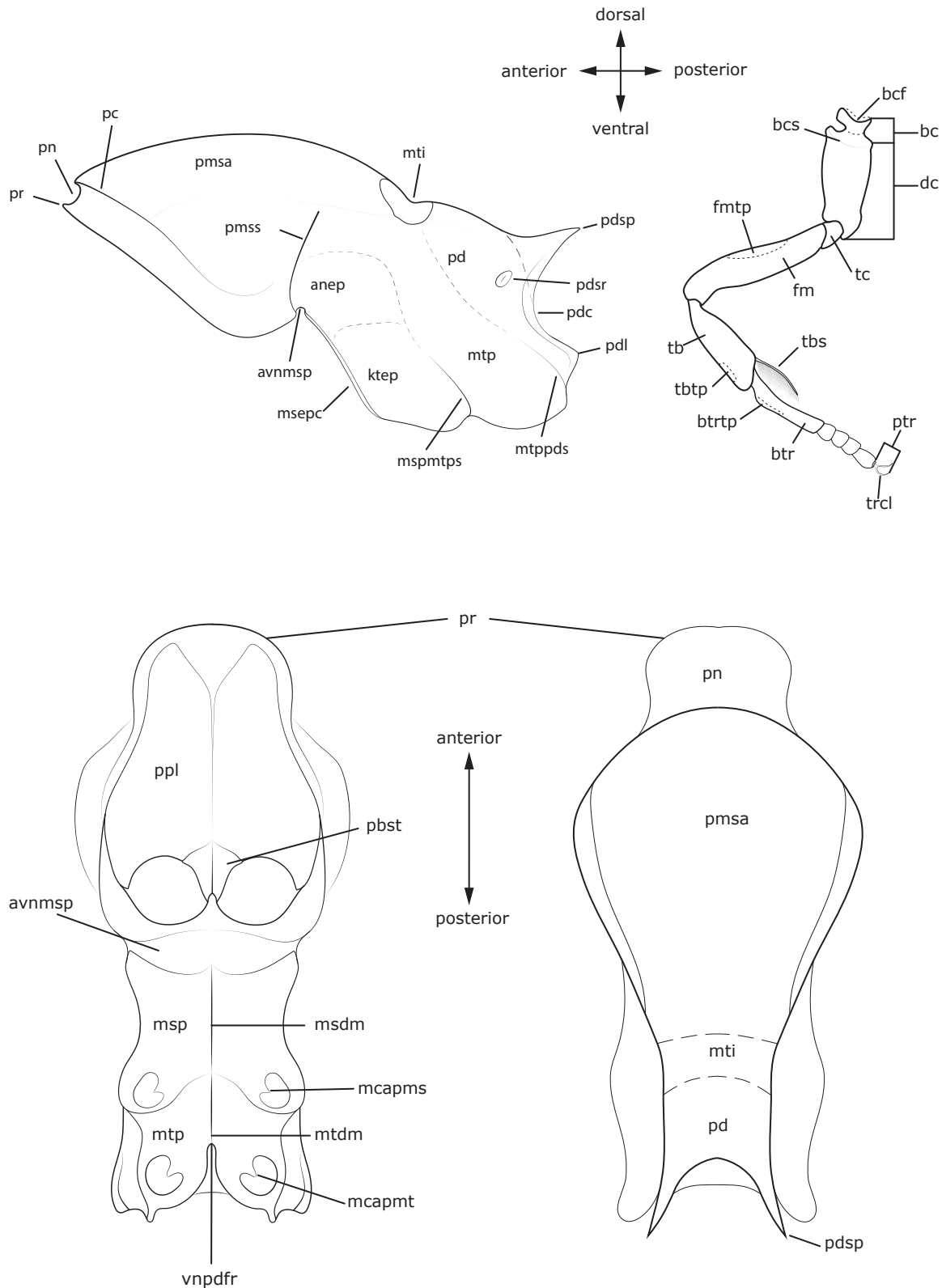


Fig. 6. Illustration of the mesosoma and fore leg of apterous females of *Strumigenys*. From top to bottom: lateral view, dorsal view and ventral view. Abbreviations: **anep**: anepisternum; **avnmosp**: antero-ventral notch of the mesopectus; **bc**: basicoxite; **bcf**: basicoxal foramen; **bcs**: basicostal suture; **btr**: basitarsus; **btrtp**: translucent patch of the basitarsus; **dc**: disticoxite; **fm**: femur; **fntp**: translucent patch of the femur; **ktep**: katepisternum; **mcapms**: medial coxal articular process of the mesopectus; **mcapmt**: medial coxal articular process of the metapectus; **msdm**: mesodiscrimen; **msep**: mesepisternal carina; **msep**: mesopectus; **msepmtps**: mesopecto-metapectal suture; **mtdm**: meta-discrimen; **mti**: metanotal impression; **mtp**: metapectus; **mtpdpds**: metapecto-propodeal suture; **pbst**: probasisternum; **pc**: pronotal carina; **pd**: propodeum; **pdc**: propodeal carina; **pdl**: propodeal lobe; **pdsp**: propodeal spine; **pdsr**: propodeal spiracle; **pms**: pronoto-mesonotal complex; **pmsa**: pronoto-mesonotal area; **pmss**: pronoto-mesonotal suture; **pn**: pronotal neck; **ppl**: propleura; **pr**: pronotal rim; **ptr**: pretarsus; **tb**: tibia; **tbs**: tibial spur; **tbtp**: translucent patch of the tibia; **tc**: trochanter; **trcl**: tarsal claw; **vnpdfr**: ventral notch of the propodeal foramen.

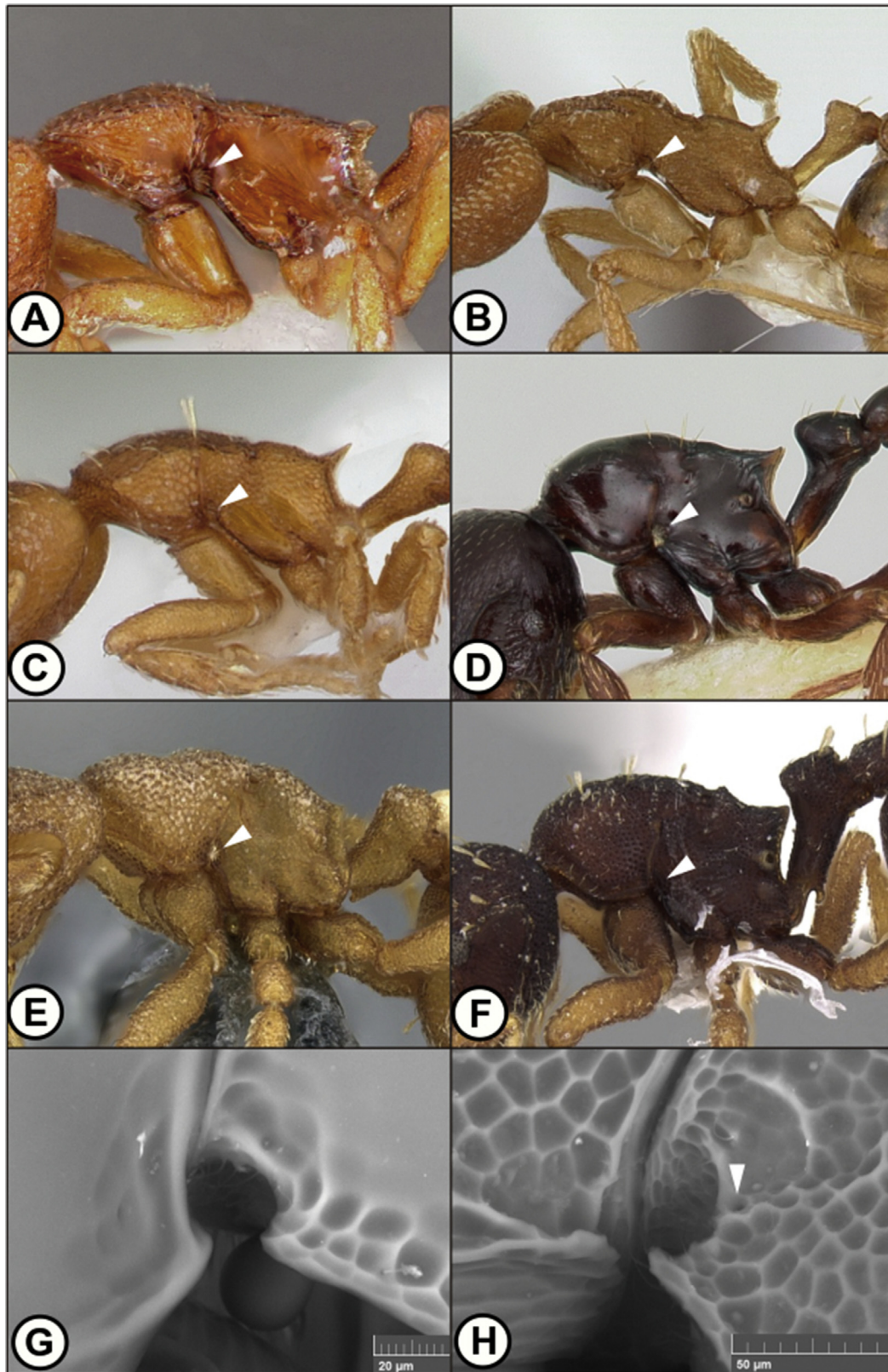


Fig. 7. Variation in the size of the anteroventral notch of the mesopectus in specimens of *Strumigenys* (A–C, G and H), *Phalacromyrmex* (D), *Rhopalothrix* (E) and *Octostruma* (H). A: *Strumigenys alperti* CASENT0003239; B: *Strumigenys actis* CASENT0005467; C: *Strumigenys denticulata* CASENT0178117; D: *Phalacromyrmex fugax* CASENT0103116; E: *Rhopalothrix ishtmica* CASENT0235905; F: *Octostruma stenognatha* CASENT0280761; G: *Strumigenys inusitata*; H: *Strumigenys saliens*. From A to F the white arrow indicates the position of the anteroventral notch of the mesopectus. In H, the white arrow indicates the position of a small circular impression adjacent to the anteroventral notch of the mesopectus.

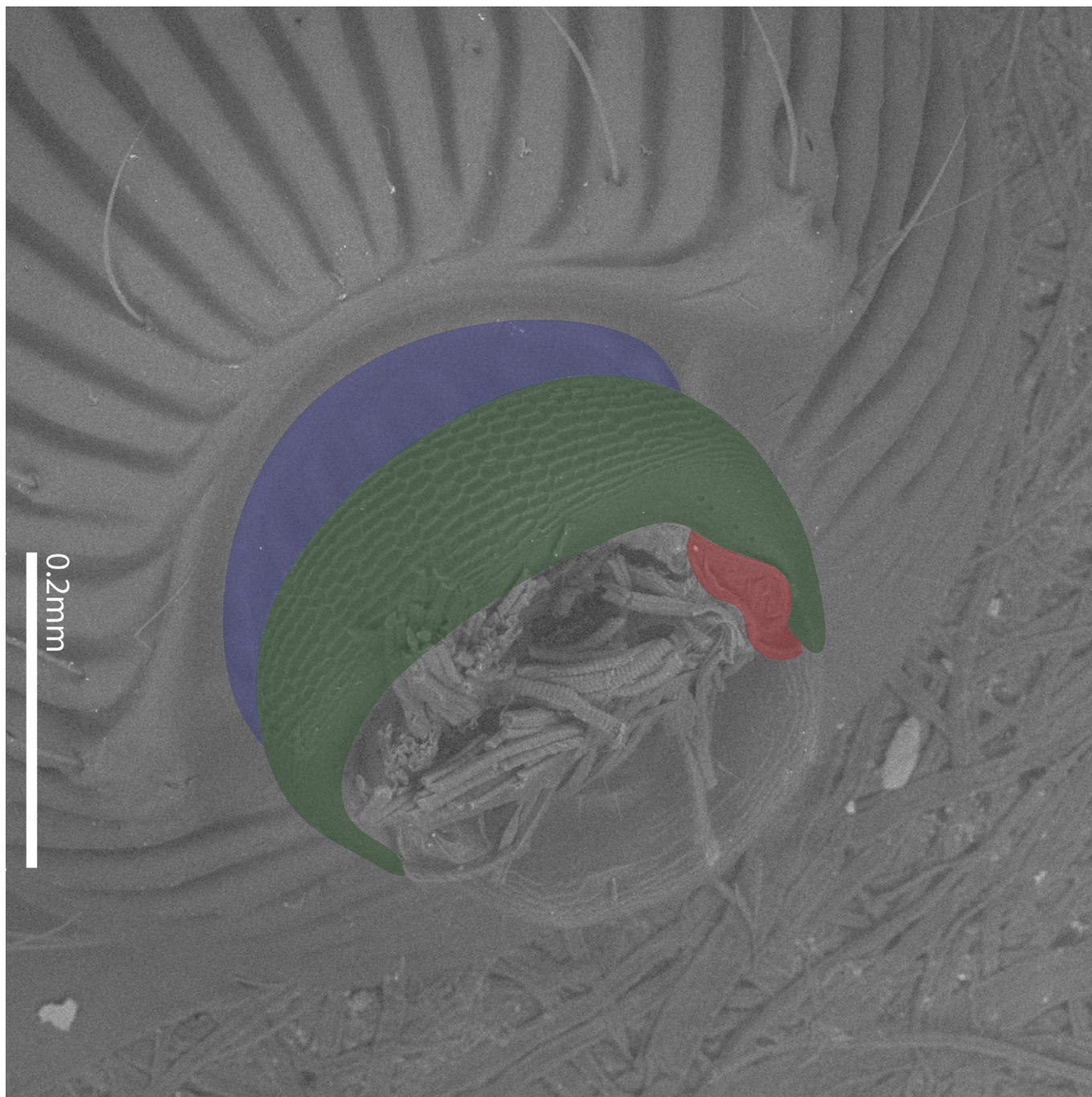


Fig. 8. Image representing the transverse impression of the third abdominal segment in a specimen of *Gnamptogenys striatula*. Blue: transverse impression of the third abdominal tergite; Green: anterior area of the third abdominal tergite; Red: antecosta of the third abdominal tergite. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

“mandibular mode of action” in *Strumigenys* (cf. “Mandible” section). A more in-depth exploration of labral variation has to be addressed as to properly establish structural correspondence of its instances in a broader scenario within the family, so as to enable accurate annotation within multi-species ontologies.

The labrum of *Strumigenys* commonly has setae on the anterior section of the sclerite (Fig. 2; lbst), which in some species appears to play a major role in prey recognition (Gronenberg, 1996). The setae can be orbicular, spatulate or linear, each type occurring alone or in combination with other types. In species in which the labral setae are not linear, several setae are disposed over the

anterior half of the labrum, most of them concentrated over the labral lobes. In these cases, we do not know which role they perform and if it is related to prey recognition. The lateral processes (Fig. 2; lplb) can be present or absent; when present, the lateral labral margin appears angular. The lateral processes in *Strumigenys* have been extensively studied and appear to function as part of the locking mechanism that holds the mandibles wide-open during hunting, interlocking with the proximal processes of the mandible (Brown and Wilson, 1959; Gronenberg, 1996). Similar to other groups of ants (Gotwald, 1969), the anterior fronto-labral muscle is absent, while the paired posterior fronto-

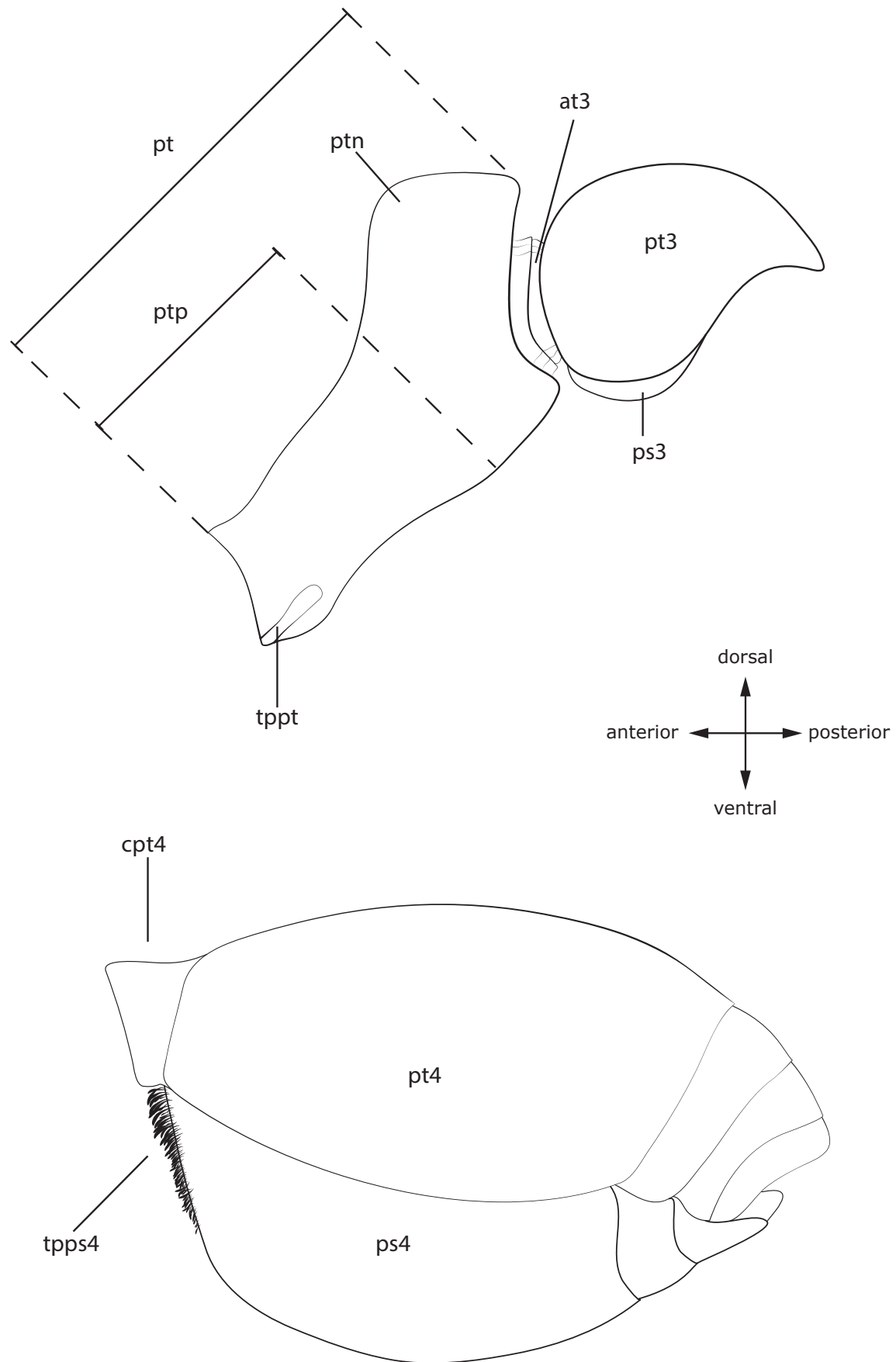


Fig. 9. Illustration of the metasoma in lateral view of apterous females of *Strumigenys*. Abbreviations: **at3**: third antero-tergite; **cpt4**: carina of the fourth postero-tergite; **ps3**: third postero-sternite; **ps4**: fourth postero-sternite; **pt3**: third postero-tergite; **pt4**: fourth postero-tergite; **pt**: petiole; **ptn**: petiolar node; **ptp**: petiolar peduncle; **tpps4**: transverse patch of the fourth postero-sternite; **tppt**: translucent patch of the petiole.

labral muscles are present and are solely responsible for the retraction of the sclerite.

3.3.2. Mandible

Overall, the mandible in Formicidae has three well-defined margins (Bolton, 1994): the masticatory margin, the basal margin and the external margin. The masticatory margin corresponds to the longitudinal margin of each mandibular blade near the anterior extension of the median line of the head. This margin, generally bearing one or more teeth, can be also called apical margin. The teeth can be well-developed or extremely reduced and both types can be found in the same specimen. Normally, the dentition occurs along all the masticatory margin (Bolton, 1994). When there is a space in the teeth row, it is called *diastema* (Bolton, 1994) (Fig. 4; dia).

The base of the masticatory margin finds a basal angle and turns into a transverse or oblique basal margin (Bolton, 1994). The external margin of each mandible can be straight, concave or convex (Bolton, 1994). In most species of ants, the external margins converge anteriorly and become triangular in dorsal view. In some cases, they project anteriorly, in an elongate-triangular shape (Bolton, 1994).

When the mandibles are slender and linear, the distinction between the masticatory and basal margins is absent, due to the loss of the basal angle (Bolton, 1999). In some lineages of Formicidae, the mandible is linear, with a long and slender blade and the masticatory and external margins approximately parallel or gradually converging anteriorly (Bolton, 1999). In groups with linear and elongate mandibles, the section with teeth is positioned at the apex of the mandible and is called *apical fork* (Fig. 1; apf) (Brown, 1948).

In their 1994 contribution, Baroni Urbani and de Andrade (1994) asserted that previous authors had never properly defined the apical fork. According to Bolton (2000), in most species with elongate and slender mandibles, the teeth at the apical section commonly form a fork of two or three vertically disposed teeth. Still according to the author, an apical fork is normally composed of two teeth, one dorsal and one ventral, called *apicodorsal* and *apicovertral* tooth, respectively (Fig. 1; apdt and apvt, respectively). The tooth that is located between those teeth is called *intercalar tooth* (Fig. 1; intt). According to Baroni Urbani and de Andrade (1994), one of the important characteristics of *Strumigenys* is that a pair of acute mandibular blades, dented or pointy, are opposed, but do not overlap. Still according to Baroni Urbani and de Andrade (*op. cit.*), a putative reduction occurred in the number and/or size of the median and basal teeth until their total loss, normally accompanied by the atrophy of one, or the formation of an apical fork with two or more distal teeth.

According to Bolton (*op. cit.*) the section that receives all teeth positioned apically would correspond to the masticatory margin (e.g. *Strumigenys fridericimuelleri* Forel, 1886) in species previously classified in *Pyramica* (a current synonym of *Strumigenys*), Schmidt and Shattuck (2014) mentioned that in the Ponerinae genera *Anochetus* Mayr, 1861 and *Odontomachus* Latreille, 1804, the masticatory margin corresponds to the internal margin of the mandible, in dorsal view. However, in *Strumigenys* the accurate delimitation of the distinct regions of the mandible can be difficult. The delimitation between the basal and masticatory margins is clear in some species (e.g., *Strumigenys alberti*, *Strumigenys schulzi* Emery, 1894, *Strumigenys urrhobia* (Bolton, 2000)) but not in others (e.g., *Strumigenys crassicornis*, *Strumigenys denticulata* Mayr, 1887, *Strumigenys elongata* Roger, 1863), especially in the case of the masticatory margin and the apical fork. Although this last can be easily observed, according to Bolton (2000), the variation in shape and presence sometimes leads to confusing interpretations. Hence, the term masticatory margin should be avoided, since the structural

equivalence in distinct groups of ants cannot be correctly established.

On the basal section of the internal margin of the mandible a cuticular process with variable shape and size is normally present, the *basal process of the mandible* (basimandibular process according to Bolton (2000)) (Fig. 4; bmd). In some species this structure connects with the dorsolateral margin of the labrum when the mandibles are open, thus locking them and preventing the torsion or displacement of the mandibles while they are open.

In some species, there is a translucent patch near the base of the mandible where a putative gland reservoir can be seen through transparency (Fig. 4; tmd).

Internally, the basal section of the mandible has two angled processes, one near the dorsoproximal margin and the other near the ventroproximal margin of each mandible, corresponding, respectively, to the *dorsal articular process of the mandible* and the *ventral articular process of the mandible* (Fig. 4; dmap and vmap, respectively). Both processes are responsible for maintaining the mandible in place during mandibular movement. In all observed formicide specimens, there is a lateral dilated process at the external margin of the basal section of the mandible; in *Wasmannia affinis*, it is understood as the process that bears the posterior cranio-mandibular muscle apodeme (Richter et al., 2019; see discussion below). In *Strumigenys*, this *lateral articular process* (abductor swelling in Richter et al., 2019; Fig. 5A, lms) can greatly vary in size (as in some long-mandibulate species, such as *Strumigenys godmani*, *Strumigenys saliens* and *Strumigenys planeti* Brown, 1953), and is limited anteriorly by a *lateral mandibular scrobe* (Fig. 5A; lms). It is uncertain if this scrobe is structurally equivalent to the *mandibular acetabulum* found in other hymenopteran groups (e.g., in *Opius dissitus* and in *Biosteres carbonarius*; Karlsson and Ronquist, 2012). In species, in which the lateral process is hypertrophied, its dorsal surface (Fig. 5B; star) possibly connects with an internal fossa at the head near the mandibular insertion during mandibular opening. The anterior margin of the mandibular scrobe (Fig. 5B; asterisks) would connect to an antero-lateral process at the head of the specimen (Fig. 5B; circles), near the mandibular insertion, holding the mandible into place, preventing its displacement from excessive opening. This lateral process of the head could be structurally equivalent to the *pleurostomal condyle* in other hymenopteran groups, although overall modification of *Strumigenys*' head hampers more accurate interpretations of structural equivalence. A similar mechanism has been observed in *Acanthognathus rudis* (Gronenberg et al., 1998b), although its morphology differs drastically.

Mandibular movement occurs by two muscles attached to the external articular margins of the mandibles via two apodemes: the *anterior cranio-mandibular muscle apodeme* and the *posterior cranio-mandibular muscle apodeme*. The anterior cranio-mandibular muscle apodeme receives the anterior cranio-mandibular muscle, which originates at the internal surface of the temple, in the posterodorsal section of the head and inserts on its respective short apodeme. The posterior cranio-mandibular muscle apodeme receives the posterior cranio-mandibular muscle, which originates at the ventromedian region of the head and on the postgenal ridge and inserts on its respective long apodeme. This apodeme is inserted in the lateral mandibular articular process through a membrane, similar to other genera (*W. affinis*; Richter et al., 2019). According to Gronenberg (1996), the first muscle is responsible for the adduction movement of the mandible, whilst the latter is responsible for the abduction movement of the same structure.

3.3.3. Labiomaxillary complex

In Hymenoptera, the labium and maxilla are united posteriorly by a membranous cuticle, forming the labiomaxillary complex

(Deans, 2009). In Formicidae, the maxillary palp is composed of 1–6 sclerites, being rarely absent, while the labial palp is composed of 1–4 sclerites (Fisher and Bolton, 2016).

According to Gotwald (1969), the galea and the lacinia are broadly joined in members of the family, and although the former is larger than the latter, the lacinia is still conspicuous in ants, compared to the reduced condition found in other families of Hymenoptera. According to Popovici et al. (2014), the anatomical complex comprised by the fusion of the galea and lacinia is termed as galeo-lacinal complex and can be defined as the area of the stipes that is delimited proximomedially by the stipito-premental conjunctiva, proximolaterally by the stipito-mandibular conjunctiva and posteroproximally by the margin of the posterior stipital sclerite (Mikó 2014).

Compared to other Hymenoptera and particularly to Formicidae, the labiomaxillary complex of *Strumigenys* presents reduction of several sclerites, especially the lacinia, which is poorly sclerotized and broadly joined to the proximolateral galeal sclerite. The lacinial lever, lacinial bar, lacinial lobe and lacinial setiferous patch could not be observed. Regarding the galeal sclerite, this structure is easily distinguished in *Strumigenys*, with both distolateral and proximolateral galeal setiferous patches well-developed. Although most sclerites of the labium appear fused, they are more sclerotized if compared to the maxilla, especially the prementum. Both the glossa and the prementum are well-developed. The number of palpi, both the maxillary and labial, are reduced, with most species having one segment each.

3.4. Mesosoma

3.4.1. Pronoto-mesonotal complex

In Hymenoptera and in most groups of Formicidae the pronotum is articulated posteriorly with the mesonotum. In Myrmicinae ants, however, the pronotum and mesonotum are externally fused in apterous females (Fernández, 2003) and represent an anatomical cluster. In some groups within the subfamily, an arched, transverse impression marks the section in which the putative areas representing the pronotum and the mesonotum might be located. Internally, the pronotal surface in apterous females of ants correspond to the site of origin of multiple muscles, such as the pronoto-laterocervical, pronoto-postoccipital, pronoto-profurcal, pronoto-propodeal, and pronoto-procoxal muscles. Other muscles normally observed in macropterous specimens have not been observed in apterous females belonging to the subfamily, possibly as a result of loss or fusion of several axillary sclerites. The same pattern of pronotal muscle organization was observed for apterous females of *Strumigenys*.

As in all specimens of Myrmicinae observed, the prophragma of apterous females of *Strumigenys* could not be observed. In fact, in other non-myrmicine ants (such as the formicine *Camponotus* Mayr, 1861 and the ponerine *Pachycondyla* Smith, 1858), a small anterior ridge can be observed on the mesonotum. However, there seems to be no muscles arising from it, suggesting the absence or reduction of the prophragma in apterous female ants. Although the reduction or absence of this structure can be intuitive when considering the loss of flight sclerites in apterous insects (since it is one of the main points of insertion of the indirect flight muscles; Snodgrass, 1993), a reduced prophragma can be observed in other species of apterous insects (Leubner et al., 2016) and may be related to the process of head movement. However, since the present study did not extensively focus on the muscular characteristics of the pronoto-mesonotal complex in Myrmicinae (and hence, in *Strumigenys*) and other subfamilies of ants, the skeleto-muscular features of this anatomical cluster remains poorly understood.

Externally, the shape and surface features of the dorsal area of the pronoto-mesonotal complex of *Strumigenys* (Fig. 6; pms)

greatly varies among species. However, all species of the genus have a distinct pronotal neck, delimited anteriorly by the pronotal rim and posteriorly by the transverse pronotal carina (Fig. 6; pn, pr and pc respectively). In some species (e.g., *Strumigenys nitens* Sanstchi, 1932 and *Strumigenys villiersi* (Perrault, 1986)), the transverse pronotal carina is absent.

3.4.2. Mesospectus

In Hymenoptera, the mesospectus can be defined as the sclerite that is U-shaped in cross section, connected anteriorly to the pronotum and the propectus, dorsally with the basalare, the mesonotum and the second axillary sclerite and the subalare, posteriorly with the metapectus and bears the mesodiscrimenal lamella and the mesofurca (Mikó 2014). Since this definition considers the presence of fully-developed flight sclerites, much of the structures in the definition cannot be observed in apterous specimens. Hence, in apterous females, the mesospectus can be roughly defined as the anatomical cluster composed of the mesopleura and mesosternum, connected anteriorly to the pronotum and the propectus, dorsally with the mesonotum, posteriorly with the metapecto-propodeal complex and bears the mesodiscrimenal lamella and the mesofurca. However, since there is a wide range of variation in this complex in ants, especially in Myrmicinae, throughout studies of skeleto-musculature of this specific complex have to be conducted, encompassing females and males, apterous and macropterous specimens, to properly define the limits of the mesospectus.

The anteroventral region of the mesospectus in females of *Strumigenys* has a transverse notch (Fig. 6; avnmsp) that is variously developed (Fig. 7A–C). In some species, there is a setiferous patch occurring throughout the ventral margin of the structure, with the shape of the setae varying among species. Bolton (1999) considered that the lateral margin of this structure would bear a glandular apparatus, although this could not be observed in the current work. Externally, a circular minute impression was observed in several specimens, positioned laterally to the notch (Fig. 7H). However, it was not possible to determine if the circular structure was an external indicative of the pleural apophyses, or the opening connected to a glandular duct. Although most common in *Strumigenys*, the anteroventral notch occurs in other groups of myrmicine ants, such as *Phalacromyrmex*, *Octostruma* and *Eurhopalothrix* (Fig. 7D–F).

3.4.3. Metapecto-propodeal complex

In Hymenoptera, the fusion of the first abdominal tergite with the third thoracic tergite is considered a diagnostic trait for the order. This anatomical complex has been studied in several hymenopterian lineages (Vilhelmsen et al., 2010; Kawada et al., 2015). It can be defined as the sclerite that is connected anteriorly with the mesospectus, dorsally with the metanotum, the metabasalar, the second axillary sclerite of the hind wing and the metasubalar and articulates with the metacoxae and the metasoma (Mikó 2014). In apterous female ants, it can be roughly defined as the sclerite that is connected anteriorly with the mesospectus and dorsally with the metanotal-propodeal sulcus and articulates with the metacoxae and the metasoma.

This anatomical complex varies greatly among different groups of ants, reflecting their variety of habits. This region accommodates the metapleural gland, metacoxae, and petiolar articulation. In *Strumigenys*, the propodeal foramen invaginates ventrally between the metacoxae, forming a medial notch (Fig. 6; vnpdfr). Some distinct pilosity can be found near the metacoxal foramina, and its shape varies from filiform to spatulate. Distinct types of processes can be found in the propodeal lobe, and some species lack any processes (e.g. *Strumigenys denticulata*, *Strumigenys elongata*, *Strumigenys eggersi* Emery, 1890). The same can be said regarding the

propodeal spine. Although this structure is present in most species, showing various degrees of development, it can be translucent in some species.

One of the main characteristics of ants is the presence of a gland located dorso-laterally to the coxal foramen and named as *metapleural gland*. It is composed of a reservoir (commonly known in myrmecology as *bulla*) and a duct that connects the reservoir to an orifice near the propodeal foramen. In most species of ants, the orifice is easily observed and varies greatly in shape and size. In some species, the reservoir can be observed externally through a *translucent patch of the metapleuron*, while in others the putative location of the reservoir can be inferred based on the presence of a dilated area of the cuticle, anterior to the *orifice of the metapleural gland*.

3.5. Legs

3.5.1. Coxa

Similar to the general coxal conformation of Formicidae, the coxa of *Strumigenys* is divided in a small *basicoxite*, separated from the larger *disticoxite* by a *basicostal suture* (Boudinot, 2015) (Fig. 6, *bc*, *dc* and *bcs*, respectively). In most female ants (both apterous and macropterous), the disticoxa of the fore leg is evidently enlarged if compared to the disticoxite of the other pairs of legs (such as in *Myrmecia nigrocincta*; Liu et al., 2019), and, according to Liu et al. (2019), it is possible that this could be considered as an apomorphic condition for the family, despite a similar condition occurring in other non-related hymenopteran families (Branstetter et al., 2017b). The disticoxite of the fore legs in *Strumigenys* follows the general elongated pattern occurring in ants.

According to Boudinot (2015), the basicoxite is limited proximally by the coxal articulation with the mesosoma consisting of a *basicoxal foramen* (Fig. 6; *bcf*), and *lateral* and *medial pectal fossae of the coxa*, which, in turn, articulate with the *lateral and medial coxal condyle of the pectus*, respectively. In *Strumigenys*, several muscles arise from distinct regions of the pronoto-mesonotal complex, propleuron and profurca and connect directly to the procoxal rim (anteriorly, mesally and laterally), similar to the condition observed in other species (*M. nigrocincta*; Liu et al., 2019). The disticoxa articulates distally with the *anterior and posterior trochanteral condyles* through the *anterior and posterior coxal fossae of the trochanter*, respectively (Boudinot, 2015). The *disticoxal foramen* of the fore leg is directed laterally, similar to other groups of ants (Boudinot, 2015; Liu et al., 2019).

Externally, the coxae of *Strumigenys* can be variously sculptured, ranging from areolate to totally smooth.

3.5.2. Trochanter

Studies on external and internal trochanteral anatomy in Hymenoptera are extremely scarce. Some studies superficially address this structure, when exploring adjacent structures (Boudinot, 2015; Johnson, 1988; Vilhelmsen et al., 2010); muscular organization and overall variation of said structure, however, are still poorly understood, especially in ants. Boudinot (2015) provided some commentaries on the trochanter for the family, whilst briefly discussing coxal variation in ants and Liu et al. (2019) briefly described and discussed trochanteral variations in *M. nigrocincta*.

The trochanter of *Strumigenys* is reduced in size (Fig. 6; *tc*), if compared to other hymenopteran specimens observed in this study (e.g. Diapriidae, Evaniidae), but has a size similar to some formicidae groups (e.g. *Camponotus*, *Pheidole*, *Octostruma*). The size and shape of this structure is somewhat variable in the genus and its variation deserves a more throughout exploration. However, all specimens of *Strumigenys* observed have the meso- and metatrochanters proximally slender and distally dilated, similarly to other ant groups

studied (e.g., *Octostruma* and *Pheidole*). The protrochanteral base is completely enclosed by the disticoxal foramen, providing additional support to the hypothesis of the apomorphic condition of this character for Formicidae (Boudinot, 2015; char. 6).

3.5.3. Femur

Trochantero-femoral joint is partly enclosed by the distal trochanteral foramen. The femur (Fig. 6; *fm*) in *Strumigenys* does not vary much apart from size and sculpture. As in all members of the family (Bolton, 2003), the *trochantellus* is absent. Translucent patches (Fig. 6; *fmtp*) are present on the dorsal area of the femur, mainly on the middle and distal section of the structure. Some species have a *tibial scrobe* on the ventral margin of the femur, which receives the tibia when it is pressed towards the femur.

3.5.4. Tibia

Femoro-tibial joint is enclosed by the distal femoral foramen. Although its sculpture pattern appears to be mainly smooth, in some species this region is completely areolate (e.g. *Strumigenys lilloana*), differing significantly from the remainder of the tibia (Fig. 6; *tb*). *Protibial spur* (Fig. 6; *tbs*) is similar to other ant groups, forming the proximal section of the *strigil*. Translucent patches are present on the dorsal area of the tibia, mainly on its dorsodistal margin, varying among species, being most common on the protibia.

3.5.5. Tarsus

The *basitarsus* (Fig. 6; *btr*) of *Strumigenys* varies considerably both in size and shape. The proximoventral margin of the probasitarsus is concave and bears a row of setae, forming the distal section of the *strigil*. In some species, the distodorsal margin of the basitarsus bears a translucent patch.

The *pretarsus* (Fig. 6; *ptr*) of *Strumigenys* is simplified, if compared to other hymenopteran and formicidae groups. The *tarsal claws* (Fig. 6; *trcl*) are structurally simple, varying in size, distance and curvature. The *arolium* is extremely reduced, which is a common condition within the family; the *manubrium* and the *unguitractor plate* are extremely reduced and the *planta* was not observed due to reduction, fusion or possible loss. The pretarsal anatomy is poorly studied in ants as a whole, despite their putative importance during exploration of structurally complex landscapes and their variation across different lineages in the family. Lattke et al. (2018) discussed the putative importance of pretarsal morphology (mainly size and shape of tarsal claws) during foraging in two species of *Strumigenys*.

3.6. Metasoma

The metasoma of ants is unique among other extant Hymenoptera families in having a transverse impression from the first metasomal segment (= petiole) to the second-third metasomal segment in female ants, varying in presence and size depending on the group. Internally, this impression does not correspond to the site of attachment of any muscular group. The metasomal acrosclerites are located laterally on their respective sclerites (Fig. 8 in red), followed posteriorly by a reduced antecostal sulcus. Posteriorly, a distinct plate follows (Fig. 8 in green) and, posterior to that, an arched impression occurs in all the sclerites (Fig. 8 in blue). Bolton (1994) refers to this impression as a girdling constriction, while Serna and Mackay (2010) refer to the same condition as *cinctus*. Nevertheless, Bolton (1990) mentioned that the region anterior to the impression, and posterior to the antecostal sulcus, should be referred to as *presclerites* and the region posterior to it should be referred to as *postsclerites*. However, according to Snodgrass (1993), the *postsclerites* (i.e. *posttergites* and

poststernites) correspond to the *postcostal lip of a definitive plate that includes the intersegmental sclerotization following*, with the anterior counterpart being the acrosclerites, both separated from each other by the antecostal sulcus. Since the transverse impression of the metasomal segment does not appear to be structurally equivalent to an antecostal sulcus, the pre- and postsclerites *sensu* Bolton (1990) are not structurally equivalent to the “pre-” and postsclerites of Snodgrass (1993). Hence, the most adequate term to refer to the region of the sclerites anterior and posterior to the transverse impression of the abdominal segment would be the antero- and postero-sclerites of the said segment. For the antero-sclerites, the definition would be *the area of the sclerite delimited anteriorly by the antecostal sulcus and posteriorly by the transverse impression of the abdominal segment* for the antero-sclerite (Fig. 9; aat3) and *the area of the sclerite delimited anteriorly by the transverse impression of the abdominal segment and posteriorly by the posterior margin of said sclerite* for the postero-sclerite (Fig. 9; pt3, ps3, pt4 and ps4).

3.6.1. Areolate processes (=spongiform tissue)

Several groups of ants possess a set of intricate shaped processes located in various regions of their metasoma, such as *Tetreamyrma* (Bolton, 1991), *Dacatinops* (Brown and Wilson, 1957) and, most commonly, *Strumigenys* (Bolton, 2000). These processes possess an overall areolate shape that superficially resembles a sponge and, historically, have been collectively referred as *spongiform tissues* (or *spongiform processes*) (Bolton, 2000). It is not clear when the term was first proposed and if an explicit definition was provided. For the best of our knowledge, a similar term (*spongy substance*; p. 149 under *Strumigenys lewisi* Cameron, 1886) was first used by Bingham (1903), while Forel (1886; p.5) described *Strumigenys fridericimuelleri* Forel, 1886 as having ‘a small foaming growth’ in the ventral margin of the petiole. In both cases, neither of the authors explicitly defines the concepts adopted. Since then, subsequent publications that dealt with the description of the *Strumigenys* fauna used some modifications of the term - *membranous appendices* (Emery, 1924), *spongiform processes* (Smith, 1931), *spongiform tissue* (Brown, 1953), *spongiform appendages* (Brown, 1954; Kempf, 1959; Bolton, 1972) - while not providing explicit definitions for the structure. Based on an etymological analysis, the possible definition of the concept could be ‘a structure that resembles a sponge’. The concept itself could also be understood as a “structural quality (...) resembling a sponge in elasticity, absorbency, or porosity” similar to the *spongy* class from PATO (http://purl.obolibrary.org/obo/PATO_0001480). Since we do not explicitly know which condition (i.e. shape, elasticity or permeability) a “spongiform” structure needs to possess to attain such quality, and, so far, we do not have documented observations that objectively describe other structural qualities of this structure (i.e. we do not know if it is elastic or permeable in live specimens), we opted to use a surface feature shape class to describe and define it. Hence, we also opted to use the term *areolate process*, in opposition to the traditional use of *spongiform tissue* to refer to this concept.

3.6.2. Second abdominal segment (=petiole)

The tergosternal fusion in the second abdominal segment (Fig. 9; pt) was observed in all Myrmicinae in the present work, although this is not the case in other subfamilies of ants. The tergosternal fusion of the second abdominal segment in *Strumigenys* is evident, and the lateral limits of the tergite and the sternite cannot be observed. In some species of *Strumigenys* there is a wide range of variation in the development of the areolate processes in the ventral margin of the petiole, when they are present. Apart from that, all studied specimens present a transverse carina in the

anteriormost region of the ventral margin of the petiole, near the articulation with the propodeal foramen.

3.6.3. Third abdominal segment (=postpetiole)

The tergosternal fusion of the third abdominal segment is universal in the Dorylinae females and almost universal among poneroid ants (Ward, 1994; Bolton, 2003; Keller, 2011). In Myrmicinae, however, it has only been documented for *Cataulacus* Smith, 1853, *Myrmecaria* Saunders, 1842, and *Cephalotes* Latreille, 1802 (Bolton, 2003). We did not observe the tergosternal fusion in any of the specimens of Myrmicinae available to us. On the other hand, we observed the tergosternal fusion of the third abdominal segment in all examined specimens of female *Strumigenys*. The segment is fused along its length and, although the putative tergosternal limits are present, the impression defining it is often hard to see as areolate processes covers it in many species.

3.6.4. Transverse carina on the fourth abdominal tergite (=limbus)

According to Bolton (2000), the *limbus* is an elevated cuticular rim that prolongs transversely in the entire anterior region of the fourth abdominal tergite, near its articulation with the third abdominal tergite. According to Bolton (*op. cit.*), this structure would be diagnostic for the genus, and, hence, exclusive to *Strumigenys*. However, Baroni Urbani and De Andrade (2007) mentioned that in some species belonging to other genera (e.g. *Octostruma stenognatha* Brown and Kempf 1980) there is a similar structure. Similar structures are also present in species of other attine genera, namely *Basicerus scambognathus* (Brown, 1964), *Colobostruma* sp. and *Ishakidris ascitaspis* Bolton, 1984.

In the description of *B. scambognathus*, Brown (1949) defined this structure as an “anterior border semicircularly excised to receive the postpetiole”. Later, Feitosa et al. (2007) described the structure similarly.

Besides the abovementioned works, there are no citations to similar structures in the groups mentioned. Although differing in size and shape, the position of the structure remains constant in the studied specimens. In *Strumigenys*, the structure has been found in the examined specimens, presenting drastic variation in shape and size. It can be described as a *transverse carina that is located posteriorly to the impression of the fourth abdominal tergite, belonging to the fourth postero-tergite* (Fig. 9; cpt4).

4. Conclusions

Previous studies on the morphology of *Strumigenys* were insufficient, in part due the great specific and morphological diversity of the genus. Also, in the past, it was difficult to exploit the minute and fragile structures or complexes of structures (such as the labio-maxillary complex). These structures can now be more easily addressed with the advent of new-generation tools. Specifically, for *Strumigenys*, some aspects related to skeleto-musculature of the head are currently being studied (D. Booher, pers. comm.) and collaborative efforts are being made to extensively explore the variation in the morphology of both males and females of *Strumigenys* J.C.M. Chaul, pers. comm. The use of ontologies to reference and to organize anatomical knowledge is extremely important to align anatomical terminology (and thus, anatomical data) with other groups of ants and families of Hymenoptera, aiming for an unambiguous referencing of morphological classes. However, one of the trade-offs for annotating anatomical classes is the need of in-depth exploration of anatomical parts and their instances. Therefore, the coarser the level of anatomical study, the more difficult it is to generate a fine-tuned class annotation. The ideal scenario would be to individually explore specific body regions (such as subforaminal bridges, or the legs and associated structures) and

provide the recognition criteria and conceptualization for those parts and their instances using an ontology framework. Under these circumstances, definitions construed on a *genus differentia* strategy promote a basis for unambiguous referencing and could possibly enhance annotation capability in ontologies, although lacking the qualities to define epistemological recognition criteria (Vogt and Bartholomeus, 2019).

Author contributions

TSRS and RMF designed the study and conducted the morphological documentation. TSRS recovered anatomical classes from natural language statements, developed the anatomical class annotations, performed the scanning electron microscopy, and prepared the figure plates. TSRS and RMF wrote the first version of the manuscript. All authors revised the manuscript and read and approved the final version.

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Appendix A. Supplementary data

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