Comparative microscopic anatomy of Schizomida − 1. Segmental axial musculature and body organization

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ABSTRACT

Schizomida is an enigmatic group of arachnids that is traditionally considered the dwarfed sister to Thelyphonida. Schizomids are of interest for evolutionary morphology, because they show a number of features like a tripartite prosoma dorsal shield (pro-, meso-, metapeltidium), formation of three sterna, a complex prosoma−opisthosoma transition and a metasoma. By analyzing the body organization of Schizomida and comparing it to Thelyphonida and other arachnids, this article provides evidence for independent evolution of some of these features in Schizomida. This supports the idea that, among arachnids, multiple and independent evolutionary pathways have resulted in similar morphologies, that conventionally have been considered shared similarities. − The analysis of serial microscopic sections and μCT-imaging of segmental indicator muscles of the prosoma evidences that the propeltidium covers prosoma segments 0−4, and the metapeltidium covers segments 5 and 6. The mesopeltidium is a dorsolateral sclerotization of the pleural membrane, not assigned to a segment, and therefore not a tergite. The topographic association of segmental musculature and sclerites of the tripartite dorsum of the prosoma differs from other taxa with such external body organization, e.g., Palpigradi and Solifugae, suggesting independent evolutionary origin. − The prosoma−opisthosoma transition integrates the first opisthosoma segment into the prosoma. The sternite of the first opisthosoma segment forms the metasternum between the coxae of the fourth pair of walking legs. The morphology of the prosoma−opisthosoma transition is similar to Uropygi and Amblypygi, but is less complex. − The morphology of the metasoma (opisthosoma segments X-XII) of Schizomida and Thelyphonida differs from that of all other arachnids carrying a metasoma, thus providing support for multiple independent evolutionary origins of metasomata.

1. Introduction

Schizomida Petrunkevitch, 1945 is an enigmatic group of tetrapulmonate arachnids. Two families, 34 genera and 205 species were recognized by Harvey (2002), but a considerable increase of new species descriptions has been recorded (i.e., 68 genera, 358 species in ITIS 2022; 71 genera, 372 species in the World Schizomida Catalog, 2022; see also Monjaraz Ruedas et al., 2020). A broad consensus exists that Schizomida are the sister-group to Thelyphonida Latreille 1804 (= Uropygi Thorell, 1882), with which they were united in a larger taxon Uropygi (Weygoldt and Paulus, 1979; Shultz, 1990; Wheeler and Hayashi, 1998; Shultz, 2007; Uropygi = Camarostomata Petrunkevitch, 1949; see also Giribet

et al. (2002). Recent recommendations of the International Arachnological Society reverse the taxonomic terminology and suggest Uropygi are sister to Schizomida and both belonging to a monophyletic taxon Thelyphonida (see Clouse et al., 2017; Giribet, 2018); however, I follow the classical use.

The microscopic anatomy and histology of Schizomida has not been investigated. The most comprehensive account that considered partial aspects of their microscopic anatomy was by Börner (1902, 1904). The comparative treatise of schizomids in the "Handbuch der Zoologie" by Kästner (1932) and "Traité de Zoologie" by Millot (1949) was based on those descriptions provided by Börner (1902, 1904). Firstman (1973) dissected one specimen of *Trithyreus pentapeltis* and provided new original information on the morphology of the endosternite and the arterial system. All later published comparisons and phylogenetic analyses are either based on external morphology or on molecular data. Numerous aspects of

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the comparative and evolutionary morphology of Schizomida may therefore benefit from an update using microscopic anatomical and histological methods. The aim of this study is documenting unprecedented histological detail of 2 species of schizomids, as well as analyzing, and answering questions from comparative and evolutionary morphology. In this first of a series of articles on the morphology of Schizomida, I investigate: (1) the morphology of the prosoma and the segment assignments of pro-, meso-, and metapeltidium; (2) the segmental origin of the ventral prosoma sclerites (sterna), (3) the prosoma—opisthosoma transition (pedicel) and (4) the morphology of the opisthosoma and its differentiation into meso- and metasoma. Two species of schizomids will be compared with a representative of their sister group, i.e., Thelyphonida, and discussed in the broader context of comparative morphology of euchelicerates.

Ad (1): All schizomids are characterized by a tripartite dorsal prosoma, recognized as pro-, meso- and metapeltidium. Pro-, meso- and metapeltidium have conventionally been considered tergites of their respective segments, i.e., the propeltidium covering segments 0—4, mesopeltidium covering segment 5, and metapeltidium covering segment 6 (Pocock, 1893; Börner, 1902, 1904; Dunlop and Lamsdell, 2017). Such partitioning of the prosoma into pro-, meso- and metapeltidium occurs in several, phylogenetically distant euchelicerate taxa (Solifugae, Palpigradi, Schizomida, Opiliones, and Acari) and has been interpreted either as ancestral or derived. If considered ancestral, the four segmented propeltidium is considered mirroring the ancestral head region of arthropods (Kraus, 1976; Dunlop and Arango, 2005), and the following two sclerites representing tergites of two ancestrally distinct segments. — Dunlop and Lamsdell (2017) were more careful and commented on the prosoma of schizomids as expressing "pseudotagmatization" with the propeltidium covering somites I-IV, and meso- and metapeltidium covering somites V and VI, respectively, but implicitly suggested that such "pseudotagmatization" represented the ancestral four-segmented head region of arthropods.

Alternatively, the tripartite dorsum was considered apomorphic (e.g., Weygoldt and Paulus, 1979; Shultz, 1990) and evolved independently in several lines, i.e., Solifugae, Palpigradi, Schizomida, Acari, as adaptation to improved maneuverability of the prosoma. Van der Hammen (1986) intuitively considered the propeltidium and the metapeltidium tergites of their respective segments and suggested the mesopeltidium were an "arthrodial sclerite", i.e., not representing a tergite of the fifth segment. His view remained speculative and isolated because he did not provide morphological evidence for this distinction; it was consequently neglected.

There is little doubt that the prosoma of euchelicerates includes segments of the ancestral arthropod head plus additional segments. Scholtz and Edgecombe (2006) reviewed ideas about the evolution of the arthropod head and briefly discussed the prosoma of euchelicerates. They concluded that *"it is likely that a head shield was present in the chelicerate stem species, but it is not clear to what extent it was fused to the head segments and the number of segments covered".* Scholtz (2016) presented a similar careful view on the head segmentation of arthropods.

Comparative morphology can answer two questions: (1) are the three dorsal sclerites of the dorsum of the schizomids prosoma true tergites, or are they de-novo sclerotizations that do not relate to original segments; (2) does the tripartite dorsum represents an ancestral pattern of body organization or is it of independent origin in several chelicerate taxa?

Testing for the segmental nature of externally visible sclerotizations requires independent morphological evidence. The "box truss axial muscular system" (BTAMS) as suggested by Shultz (1993, 1999, 2001, 2007) provides a hypothetical framework to test for segment assignments of body regions and individual sclerites

(Shultz, 2001, 2007; Mehnert et al., 2018; Franz-Guess and Starck, 2020). According to the BTAMS, each segment is characterized by a set of segmental axial muscles, i.e., dorsal and ventral suspensor muscles. The occurrence of lateral suspensor muscles is controversial (e.g., Börner, 1904; Firstman, 1973; Franz-Guess and Starck, 2020 vs. Shultz, 1993). The muscle arrangement of the arachnid BTAMS (different from Shultz by including lateral suspensor muscles), and three hypotheses about the segment assignment of pro-, meso-, and metapeltidium derived from this are laid out in Fig. 1. Documenting and analyzing the segmental axial musculature of the prosoma (i.e., dorsal and ventral suspensor muscles), their origin from the endosternite, and their insertion to the dorsal and ventral sclerites, respectively, will provide support for one of the hypotheses. Supposing a complete set of suspensor muscles, pro-, meso-, and metapeltidium may be assigned to segment numbers according to the indicator muscles attaching (Fig. 1B, C, D). The hypothesis of segmental nature of a sclerite can be rejected when no suspensor muscle inserts on it. In such case, an independent origin of the sclerite becomes probable (Van der Hammen's unsupported idea; Fig. 1C and D). Of course, using suspensor muscles as segment indicator muscles is only possible if segmental axial suspensor muscles can be explicitly identified. Recent work on Palpigradi has shown that in this taxon, pro- and metapeltidium represent tergites of their respective prosomal segments (propeltidium = merged tergites of segments 0—5; metapeltidium tergite of segment 6), while the mesopeltidium is a sclerotization of the pleural membrane and not a tergite *sensu strictu* (Franz-Guess and Starck, 2020, Fig. 1C).

Ad (2): The ventrum of the schizomid prosoma carries three sclerites that have traditional been recognized as tritotetrasternum, pentasternum and metasternum (Börner 1902, 1904; Kästner 1932) suggesting matching segmental borders with the dorsum. In particular, the segmental nature of the 'metasternum' is of interest. Earlier morphological analyses of schizomids (Börner 1902, 1904; Kästner 1932) considered it a sternite of the sixth prosoma segment. However, for closely related groups like Thelyphonida (Shultz 1993; for *Mastigoproctus*), Amblypygi (Shultz 1999, for *Phrynus*) and Scorpiones (Farley 1999; Shultz 2007) it was shown that the posterior sternum is morphologically derived from the first opisthosomal segment (i.e., post-oral segment seven). Therefore, I ask if the metasternum of Schizomida is a sternite of the last prosoma segment or the sternite of an anterior opisthosoma segment that has been shifted to the prosoma. Like for the dorsum, the analysis of the segmental axial musculature may provide an independent test for the segmental assignment of the ventral sclerites.

Ad (3) The opisthosoma of schizomids is differentiated into a meso- and a metasoma plus flagellum. By analyzing the segmental organization of the opisthosoma and compare it with Uropgyi as well as other arachnids the question can be answered if the metasoma of various euchelicerates is homologous or homoplastic across taxa.

2. Materials and methods

2.1. Material

Schizomid samples in appropriate fixation for histology are rare and the material was collected by colleagues in South America. The species selection, *Stenochrus portoricensis* and *Surazomus* sp., is therefore opportunistic. According to Clouse et al. (2017), both species are closely related members of the Hubbardiidae, with *Stenochrus portoricensis* showing a Central American and *Surazomus* sp. a South American center of distribution.

Stenochrus portoricensis Chamberlin, 1922 (N = 15 histological
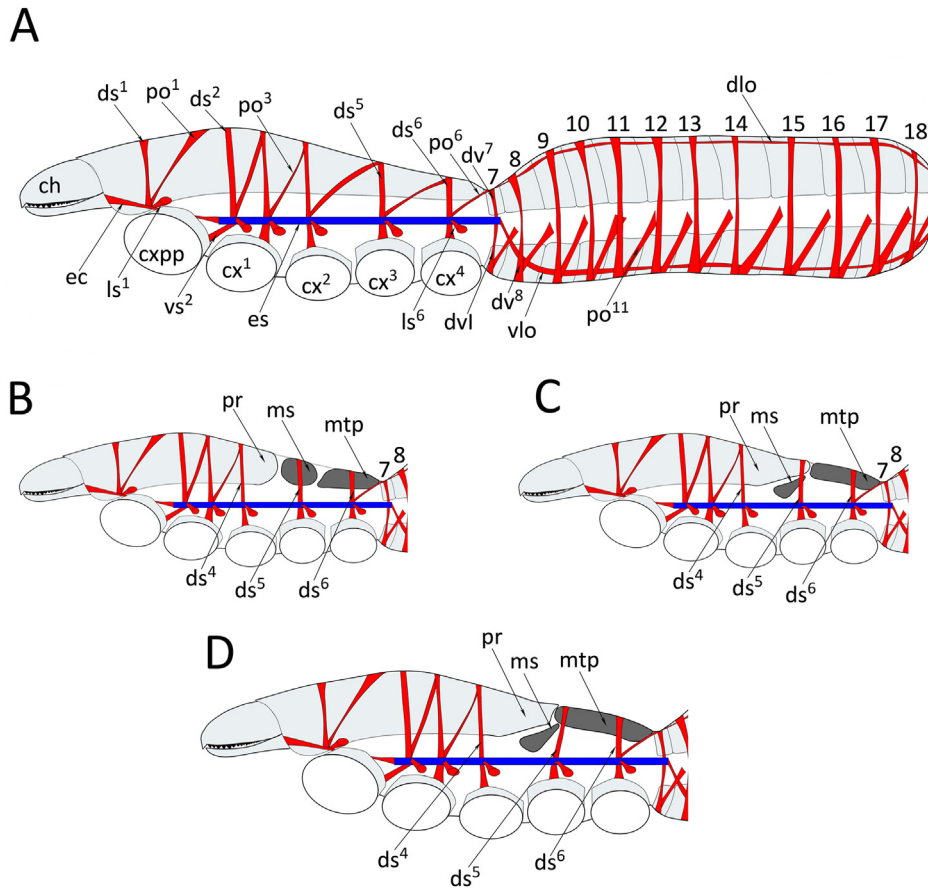
Fig. 1. The box truss axial muscle system (BTAMS) and predictions for segment assignment of pro-, meso-, and metapeltidium. **(A).** Schematic drawing of the hypothesized system of axial segmental muscles as suggested by the BTAMS ground pattern for arachnids (Shultz, 2001, 2007). In this model, the arachnid body is characterized by a system of dorsal and ventral longitudinal muscles, and segmental homonomous dorsoventral, transverse, and posterior oblique muscles. Shultz (2007) suggested that the ventral longitudinal and transverse elements of postoral segments 1–7 had "tendonized" and formed the endosternite, which is therefore considered part of BTAMS. The anterior endosterno-cheliceral muscle supposedly is a residual of the ancestral ventral longitudinal muscle. The dorsoventral muscles of the prosoma are divided into dorsal and ventral suspensor muscles. Dorsal suspensor muscles originate from the endosternite and insert to the segmental tergite. Ventral suspensor muscles originate from the endosternite and insert to the coxae of the appendage of their respective segments. Lateral suspensor muscles (not in the original model by Shultz), as residues of the transversal system, originate from the endosternite and insert to the lateral body wall. According to the hypothesized arachnid ground pattern developed by Shultz (2001, 2007) the posterior oblique muscles of the opisthosoma shift their attachment from tergites to pleural regions. Dorsal and ventral intersegmental muscles are not considered part of the BTAMS. **(B)** Schematic drawing of the tripartite dorsum and associated BTAMS-derived muscles following the concurrent paradigmatic view, i.e., propeltidium covering segments 0–4, the mesopeltidium is the tergite of segment five, and the metapeltidium it the tergite of segment six. **(C)** Schematic drawing of the pattern described for Palpigradi (Franz-Guess and Starck, 2020). The propeltidium covers segments 0–5, the mesopeltidium is a lateral sclerotization without segment assignment and the metapeltidium is the tergite of segment 6. **(D)** Schematic drawing of an alternate morphology in which the propeltidium covers segments 0–4, and dorsal suspensors of segments five and six attach to the metapeltidium. The mesopeltidium is without suspensor insertion and therefore considered a lateral sclerotization. Topologies shown in (C) and (D) represent alternate morphologies as suggested by van der Hammen's vision. Other muscle topographies are theoretically possible but not shown here. **Abbreviations:** ch, chelicera; cx, coxa of walking leg; cxpp, coxa of pedipalpus; dl, dorsal longitudinal muscle of the prosoma; dlo, dorsal longitudinal muscle of the opisthosoma; ds^{1-6}, dorsal suspensor muscles of prosoma segments 1 to 6; dv^{7-12}, dorso-ventral muscles of the opisthosoma (segments 7–12); ec, endosterno-cheliceral muscle (anterior, muscular extension of the endosternite); es, endosternite; ls^{1-6}, lateral suspensor muscles (=transverse connective in Shultz, 2001, 2007); ms, mesopeltidium; mtp, metapeltidium; po^6, posterior oblique muscle of segment 6 (=endosterno-tergal muscle); pr, propeltidium; vlo, ventral longitudinal muscle of the opisthosoma; po, posterior oblique muscles; Arabian numerals 1–12, segment numbers. Orientation of images: anterior is left, dorsal is up.

series; Table 1). Material collected in Rio de Janeiro by Prof. Babtista Renner, Museo National, Rio de Janeiro, Brazil and preserved in 5 % paraformaldehyde in 0.1 mol l^{-1} phosphate buffered saline or 2.5 % glutardialdehyde in 0.1 mol l^{-1} phosphate buffered saline. Material sent as donation to Zoological State Collection Munich (# MNRJ, 2017/08).

Surazomus Reddell and Cokendolpher, 1995 undetermined species[1] (N = 5 histological series; Table 1). Material collected 20.08.2016 by J.A. Moreno, Museo de Zoologia, Universidade de Sao Paulo, Brazil, in Colombia, Valle del Cauca, Aho Dapa, Bocatoma, Rio Dapa (03°34′15.4″N; 76°34′17.8″W) and preserved in 5 %

paraformaldehyde in 0.1 mol l^{-1} phosphate buffered saline or 2.5 % glutardialdehyde in 0.1 mol l^{-1} phosphate buffered saline. Material sent as donation to Zoological State Collection, Munich, Germany.

Minbosius manilanus (C.L. Koch, 1843), μCT image stacks of 4 ethanol preserved and iodine contrasted specimens. Micro-CT image stacks are deposited at Morphosource (Table 1; ww.morphosource.org); samples remained in Vienna.

2.2. Histological methods

Specimens were washed four times in phosphate buffered saline (0.1 mol l^{-1}) over a period of 20 min, postfixed in 1 % osmium tetroxide for 2 h and washed again (four times, 20 min each) in phosphate buffered saline to remove excess osmium tetroxide. Samples were dehydrated through graded series of acetone

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[1] The species was sent as *Surazomus andinus*, however *S. andinus* is an invalid species name or a not, yet, described species.

Table 1
List of Specimens

<u>*Surazomus* sp.:</u> Colombia, Valle del Cavca Yumbo, Alto Dapa, Bocatama rio Dapa, fecha:20.08.2016/1890 m, collected by Jairo A. Moreno, N 03° 34′15.4`´/W 76° 34′17.8`´
<u>*Stenochrus portoricensis:*</u> collected by Luiz Cerqueira Baptista Renner, 01.06.2016 in Rio de Janeiro state.
Minbosius manilanus: ethanol preserved collection material without numbers; original samples remained at Metscher lab in Vienna, μCt-image stacks deposited at Morphosource.com.

Species	Sex	Internal number	Type of material	ZSMA- Number
Stenochrus portoricensis	♀	I	Serial sections	ZSMA20240006
Stenochrus portoricensis	♀	III	Serial sections	ZSMA20240009
Stenochrus portoricensis	♀	IV	Serial sections	ZSMA202400018
Stenochrus portoricensis	♀	VI	Serial sections	ZSMA202400010
Stenochrus portoricensis	♀	VII	Serial sections	ZSMA202400014
Stenochrus portoricensis	♀	VIII	Serial sections	ZSMA202400019
Stenochrus portoricensis	♀	XI	Serial sections	ZSMA202400016
Stenochrus portoricensis	♀	XII	Serial sections	ZSMA202400015 a, b
Stenochrus portoricensis	♀	XV	Serial sections	ZSMA202400020
Stenochrus portoricensis	♀	XVI	Serial sections	ZSMA20240008
Stenochrus portoricensis	♀	XVIII	Serial sections	ZSMA202400017
Stenochrus portoricensis	♀	XX	Serial sections	ZSMA20240007
Stenochrus portoricensis	♀	XXII	Serial sections	ZSMA202400012
Stenochrus portoricensis	♀	XXIV	Serial sections	ZSMA202400011
Stenochrus portoricensis	♀	XXVIII	Serial sections	ZSMA202400013
Stenochrus portoricensis		2	μCT image stack	Morphosource ID 000620170
Stenochrus portoricensis		10	μCT image stack	Morphosource ID 000620175
Surazomus sp.		II	Serial sections	ZSMA20240001
Surazomus sp.		III	Serial sections	ZSMA20240002
Surazomus sp.		IV	Serial sections	ZSMA20240003
Surazomus sp.		V	Serial sections	ZSMA20240004
Surazomus sp.		VIII	Serial sections	ZSMA20240005
Surazomus sp.		4	μCT image stack	Morphosource ID 000620181
Surazomus sp.		10	μCT image stack	Morphosource ID 000620226
Minbosius manilanus		10	μCT image stack	Morphosource ID 000620113
Minbosius manilanus		13	μCT image stack	Morphosource ID 000620108
Minbosius manilanus		14	μCT image stack	Morphosource ID 000620103
Minbosius manilanus		15	μCT image stack	Morphosource ID 000620131

ZSMA = Zoological State Collection Munich, Arthropoda.

(30−100 %) and then embedded in Glycidether 100 (Carl Roth GmbH + Co. KG, Karlsruhe, Germany). Histological semithin sections were cut at 1 μm thickness using an RMC MTXL ultramicrotome (Boeckeler Instruments, Inc., Tucson, Arizona, USA) equipped with a histo-Jumbo diamond knife (DiATOME Ltd, Biel, Switzerland). In order to obtain serial sections, the ventral side of the trimmed specimen block was covered with a thin layer of ethyl acetate/methyl cyclohexane glue (Pattex Kraftkleber Classic, Henkel AG and Co. KGaA, Düsseldorf, Germany) mixed with xylene in a 1:1 mixing ratio. The section bands were then collected in water, attached to a glass slide and dried. Sections were stained using Rüdeberg-staining solution (Rüdeberg 1967).

2.3. Microscopy

Light microscopic images were taken with an automated Olympus BX61VS microscope and DotSlide software (Olympus, Hamburg, Germany). For images the extended focal imaging option was engaged to improve focal depth of images. Image analysis was done using OlyVIA (version 2.9, Build 13735, Olympus Soft Imaging Solutions GmbH, Münster, Germany). − Images of whole specimens were taken using a Keyence VHX-6000 microscope, either in fluorescent-light mode or in polarized light.

2.4. μCT-imaging

Specimens of *Minbosius manilanus* were μCT-scanned at University of Vienna. Before scanning all walking legs of all individuals were cut for better penetration of contrasting medium. Samples were transferred to 70 % and 95 % ethanol, and then contrasted in 1 % iodine solution (in 99.5 % ethanol; Metscher, 2009; Gignac and Kley, 2014) for a minimum of two weeks. Samples were scanned at University of Vienna; SkyScan 1174 (Bruker) with X-ray source setting at40 kV and 200 μA for 15 s exposure time. The scan was performed using Binning 2. The reconstruction resulted in system based calculated isotropic pixel size of 22.01 μm, 675 x 675 px. The complete sets of images are deposited with Morphosource # 000561228.

Specimens of *Stenochrus portoricensis* and *Surazomus* sp. were μCT-scanned at University of Greifswald. Specimens were dehydrated through graded series of EtoH (30 %, 50 %, 70 %, 90 %, 96 % and absolute) and transferred in 1 % iodine solution (in 99.5 % EtoH). Critical point drying of the specimens was performed using Leica EMCPD300 (Leica Mikrosysteme Vertrieb GmbH, Wetzlar, Germany). Only one specimen of each species was used for μCT-imaging. For micro-computed tomography, an XRadia MicroXCT-200×-ray microscope (Carl Zeiss Microscopy GmbH, Jena, Germany) equipped with scintillator-objective lens unit was used. The scan was performed with a 4× objective with X-ray source setting at40 kV and 8 W for 1 s acquisition time. The recorded 1600 projections per tomography were reconstructed with the XMReconstructor software (Carl ZeissMicroscopy GmbH, Jena, Germany), resulting in TIFF format image stacks. The scan was performed using Binning 2 and subsequently reconstructed using Binning 1 (full resolution) to avoid information loss. The reconstruction resulted in system based calculated pixel size of 3.13 μm, 1014 × 1014 px. Consequently, the spatial resolution of the images is optimally c. 6.5 μm for clear borders or c. 10 μm for individual structures. Image stacks of μCT-series and or individual μCT images were edited using Image J (Version 1.53c; Schindelin et al., 2012). The complete sets of images are deposited with Morphosource # 000561228.

2.5. 3D reconstruction

For the 3D-reconstruction of the endosternite, series of original images were imported into ImageJ (Schneider et al., 2012; RRID:SCR_003070) and an image stack was created. The image stack was cropped, optimized for brightness and contrast, and saved in tif-format. The tif-stack was then imported using Drishti Import v2.7 and structures of interest (endosternite, muscles, dorsal and ventral sclerites) were manually segmented in Drishti (Hu et al., 2010). Drishti files were imported in Meshlab_64bit_fp v2021.10 (Cignoni et al., 2008) and rendered as 3D-models.

Alternatively, 3D-reconstructions from µCt-image stacks were prepared using the volume rendering function in 3D-slicer 5.0.3 (https://www.slicer.org/; Kikinis et al., 2014).

2.6. Image processing

All images were adjusted for tonal range; background was removed, labels and scale bars were added using Adobe Photoshop CS2 Vers.09, 1990−2005 (RRID:SCR_014199). I used Inkscape 1.0.2−2 (2021) and SketchBook Version 8.7.1−2019 to create schematic drawings. Schematic drawings in Fig. 10 are based on analysis of histological serial sections of intact specimens. Thus, the topography, the origin and insertion of muscles are documented as precisely as possible.

2.7. Terminology

I use a simple descriptive language: the terms "sternite" and "tergite" refer to segmental sclerites on the ventral and dorsal side of a segment. Sternum refers to a ventral sclerite but does not have any segment implication. The descriptors apical − basal and distal − proximal is used interchangeably. For muscle descriptions, "origin" always refers to the attachment site to an unmovable, central element while "insertion" refers to the attachment site to a movable distal element. If origin and insertion cannot be differentiated by topographic anatomy, the neutral term "attachment" is used.

The term "segment" is used in a simple anatomical sense, i.e., what can be counted on a body (but see discussion in Minelli and Fusco, 2004; Dunlop and Lamsdell, 2017). Segment numbering follows conventions, i.e., a preoral segment is counted as zero, the cheliceral segment as one, and so on. A total of seven prosomal segments, i.e., segments 0−6, and 12 opisthosomal segments, i.e., segments 7−18 is recognized. In the figures, segment numbers, e.g. of segmental muscles, are indicated by superscript Arabic numerals.

Generally, the terminology of sclerites and muscles is leaned on Shultz (1993) for Thelyphonida, the closest related taxon. However, in some cases deviations in the terminology are necessary. Table 2 provides a glossary of muscle terminology including descriptions of origin and insertion of muscles as well as synonyms and references to related work.

2.8. Data accessibility

All histological serial sections (Table 1) have been deposited at the Zoological State Collection, Munich (*Arthropoda varia*). µCT-image stacks are publicly available at Morphosource # 000561228 (Table 1). High resolution scans of microscopic sections for virtual microscopy are available from the author on request.

3. Results

3.1. Schizomida − external morphology

The external morphology of schizomids is well described (Börner, 1902, 1904; Kästner, 1932). *Stenochrus portoricensis* and *Surazomus* sp. are eye-less species of the schizomids; faint "eye-spots" may be recognized as change in the carapace surface structure (Fig. 2A). Both species do not differ in microscopic anatomy. Therefore, all descriptions are provided for *Stenochrus portoricensis.* Reference material for the undescribed species of *Surazomus* is deposited at the Zoological State collection of Bavaria in Munich.

Prosoma dorsum: The dorsal shield of the prosoma is differentiated into three distinct sclerites, i.e., pro-, meso-, and metapeltidium. The propeltidium is large and covers all anterior segments including the segment of the second pair of walking legs. The "mesopeltidium" is a pair of small triangular sclerites topographically associated with the third pair of walking legs, and the metapeltidium is one large sclerite associated with the segment of the fourth pair of walking legs (Fig. 2A).

Prosoma ventrum: From anterior to posterior, the ventrum is characterized by the large coxae of the pedipalps, which are partially merged in the midline (Fig. 2C). The coxae of the first, palpiform pair of walking legs insert ventro-lateral, leaving a relatively large area between them. The coxae of the second pair of walking legs insert oblique (anterior more lateral, posterior they almost reach the midline). The area between the coxae of the first and the second walking legs is occupied by a large, triangular sclerite (i.e., the tritotetrasternum in the terminology of Börner 1902). A small and thin sclerite occupies the narrow space between the coxae of the third pair of walking legs (i.e., the pentasternum; ps, Fig. 2C). Posterior to that, is a broad sclerite between the fourth pair of walking legs (i.e., the metasternum). It grades into the pedicel, i.e., the narrow connection between prosoma and opisthosoma (mts, Fig. 2C). − The external topographic morphology is suggestive of segment assignments, but not conclusively informative. As highlighted above, it requires independent analysis of the segmental axial musculature for a segment assignment of the ventral sclerites (see below).

Opisthosoma dorsum: The opisthosoma has 9 + 3 (mesosoma and metasoma) segments and a flagellum. The first opisthosoma segment is narrow and small, forming the transition to the prosoma (pedicel). It carries a small, inconspicuous tergite (pd, Fig. 2A). Opisthosoma segments II-IX carry large tergites and sternites, that are connected by extensive pleural membranes (Fig. 2B). The terminal three segments X-XII have ring-shaped sclerites and form the metasoma ("postabdomen"). The last segment carries the flagellum, the anus and the openings of the opisthosoma glands.

Opisthosoma ventrum: following the paradigm that the genital opening of euchelicerates is on the second opisthosoma segment, the sclerite between the coxae of the fourth pair of walking legs (metasternum; Fig. 2C) must be assigned to the first opisthosomal segment. The ventrum of the following (second) opisthosoma segment functions as genital operculum. It is enlarged and covered by a sclerite that medially covers the genital opening and laterally covers the openings of the respiratory chambers. The sclerite of the third opisthosoma segment is (externally) somewhat thinner, while opisthosoma segments four through eight are almost equal. Opisthosoma segment nine tapers to the distinctly smaller opisthosoma segments X-XII, which form the metasoma. Those metasoma segments are small, narrow and each is surrounded by a continuous cuticular ring instead of distinct tergites and sternites. Cuticular impressions of the attachment sites of the dorso-ventral axial segmental musculature can be seen on the sternites of opisthosoma

Table 2
Glossary of anatomical terms.

muscle	abb.	origin	Insertion	synonyms/alternate identifications	reference	Notes
endosterno-cheliceral	ec	anterior end of endosternite	cheliceral membrane	endosterno-cheliceral muscle (#58)	Shultz (1993)	tentatively homologized with a muscular extension of the endosternite retractor of chelicerae, Fig. 5
lateral muscle	lat	coxal apodeme Anterior process of palpal coxa	lateral wall of dorsal shield/ propeltidium (palpal coxa)	seitl. Apophysenmuskel lateral palpal coxal (muscle #33)[a]	Börner (1904) Shultz (1993)	text Fig. 14, for *Schizomus cambridgei* *Mastigoproctus giganteus*, figs 5, 10
dorsal suspensor muscles	ds3	anterior end of endosternite	propeltidium	dorsale Apophysenmuskel a27 dorsale Apophysenmuskel a/f dorsal suspensor muscle dorsal endosternal suspensor (#13[b]) tergo-plastral muscle	Börner (1904) Börner (1904) Firstman (1973) Shultz (1993),[c] Lankester (1884)	*Thelyphonus caudatus,* text figs 15, 16 *Schizomus cambridgei*[d], text Fig. 14 *Hubbardia pentapeltis,* Fig. 17A *Mastigoproctus giganteus*, figs 2, 3, 5, 7, 10 *Euscorpio italicus,* Fig. 4
	ds4	dorsal on endosternite at aeb	propeltidium	dorsale Apophysenmuskel e29, e30 dorsale Apophysenmuskel e1, e2 dorsal suspensor muscle dorsal endosternal suspensor (#13[e])	Börner (1904) Börner (1904) Firstman (1973) Shultz (1993)	*Thelyphonus caudatus,* text figs 15, 16 *Schizomus cambridgei,* text Fig. 14 *Hubbardia pentapeltis*[f], Fig. 17A *Mastigoproctus giganteus*, figs 2, 5, 7
	ds5	middle position from endosternite	anterior edge of metapeltidium	dorsale Apophysenmuskel c30 dorsale Apophysenmuskel c dorsal suspensor muscle dorsal endosternal suspensor (#13)	Börner (1904) Börner (1904) Firstman (1973) Shultz (1993)	*Thelyphonus caudatus,* text figs 15, 16 *Schizomus cambridgei,* text Fig. 14 *Hubbardia pentapeltis,* Fig. 17A *Mastigoproctus giganteus*, figs 2, 5, 7
	ds6	endosternite at peb	metapeltidium	dorsale Apophysenmuskeld 31 dorsale Apophysenmuskel d dorsal suspensor muscle dorsal endosternal suspensor (#13)	Börner (1904) Börner (1904) Firstman (1973) Shultz (1993)	*Thelyphonus caudatus,* text figs 15, 16 *Schizomus cambridgei,* text Fig. 14 *Hubbardia pentapeltis,* Fig. 17A *Mastigoproctus giganteus*, figs 2, 5, 7
ventral suspensor muscles	vs3	anterior end of endosternite	coxa of walking leg 1	ventraler Apophysenmuskel f48 ventral suspensor	Börner (1904) Firstman (1973)	*Thelyphonus caudatus,* text figs 15, 16 *Hubbardia pentapeltis,* Fig. 17A
	vs4	endosternite at aeb	coxa of walking leg 2	ventraler Apophysenmuskel g50 ventral suspensor muscle #15	Börner (1904) Firstman (1973) Shultz (1993)	*Thelyphonus caudatus,* text figs 15, 16 *Hubbardia pentapeltis,* Fig. 17A *Mastigoproctus giganteus*, Fig. 2C
	vs5	middle part of endosternite	coxa of walking leg 3	ventraler Apophysenmuskel 54h ventral suspensor muscle #15	Börner (1904) Firstman (1973) Shultz (1993)	*Thelyphonus caudatus,* text figs 15, 16 *Hubbardia pentapeltis,* Fig. 17A *Mastigoproctus giganteus*, Fig. 2C
	vs6	endosternite at peb	coxa of walking leg 4	ventraler Apophysenmuskel i57 ventral suspensor muscle #15	Börner (1904) Firstman (1973) Shultz (1993)	*Thelyphonus caudatus,* text figs 15, 16 *Hubbardia pentapeltis,* Fig. 17A *Mastigoproctus giganteus*, Fig. 2C
lateral suspensor muscles	ls4	endosternite at peb	lateral wall of dorsal shield	pleuro-plastral muscle epimero-plastral muscles seitl. Apophysenmuskel b28 seitl. Apophysenmuskel g transverse suspensor dorsolateral endosternal muscle?	Lankester (1884) Lankester et al. (1885) Börner (1904) Börner (1904) Firstman (1973)	*Euscorpio italicus,* Fig. 4 *Heterometrus cyaneus;* Pl. 77, Fig. 1 muscles 79, 81, 83 15, 16, Pl.II Fig. 8 *Schizomus cambridgei,* text fig. 14 *Hubbardia pentapeltis,* Fig. 17A *Mastigoproctus giganteus*, fig. 5

Table 2 (*continued*)

muscle	abb.	origin	Insertion	synonyms/alternate identifications	reference	Notes
	ls5			seitl. Apophysenmuskel c30 endosternocoxal muscle (#25)	Shultz (1993),[g] Börner (1904) Shultz (1993)	*Thelyphonus caudatus*, figs 15, 16, Pl.II Fig. 8 *Mastigoproctus giganteus,* Fig. 5
	ls6	endosternite	coxa of walking leg 4	seitl. Apophysenmuskel d31 endosternocoxal muscle (#25)	Börner (1904) Shultz (1993)	*Thelyphonus caudatus*, figs 15, 16, Pl.II Fig. 8 *Mastigoproctus giganteus,* Fig. 5
endosternotergal muscle	et	posterior part of endosternite	tergite of first opisthosoma segment	5ter dorsaler Anhang 91 endosternotergal muscle (#16)	Börner (1904) Shultz (1993)	*Thelyphonus caudatus*, text figs 15, 16 *Mastigoproctus giganteus,* figs 2, 5, 7
dorsoventral opisthosoma muscle	dv	opisthosomal tergite	opisthosomal sternite (same segment as origin)	dorsoventral Muskeln dorsoventral Muskeln (#17)	Börner (1904) Börner (1904) Shultz (1993)	*Mastigoproctus giganteus*, Fig. 19 *Schizomus cambridgei*, text Fig. 20 *Mastigoproctus giganteus*, figs 7, 9
dorsal intersegmental	dis	tergite posterior edge	following tergite anterior edge	intertergal muscles (#64)	Börner (1904) Shultz (1993)	*Schizomus cambridgei*, text fig. 76,77, 79, 80 *Mastigoproctus giganteus*, figs 7, 8
ventral intersegmental	vis	sternite posterior edge	following sternite anterior edge	Intersternal muscles (#68)	Börner (1904) Shultz (1993)	*Schizomus cambridgei*, text figs 76,77, 79, 80 *Mastigoproctus giganteus*, figs 7, 8, 9
dorsal pygidial	dpy			dorsal pygidial muscles (#70−72)	Shultz (1993)	*Mastigoproctus giganteus,* figs 7, 8
ventral pygidial	vpy			ventral pygidial muscles (#73−75)	Shultz (1993)	*Mastigoproctus giganteus,* figs 7, 8

Figures references in this table refer to figures in the referenced papers

[a] "Migratory muscle" hypothesis in Shultz (1993) shifted origin from endosternite to pedipalpal process (=here: pedipalpal apodeme).

[b] Includes probably also muscles #14 which shares origin with #13 according to Shultz (1993

[c] According to Shultz (1993) assigned to somites II-VII, origin from pedipalpal apodeme in segment II, origin from endosternite in segments III- VII, insertion on dorsal shield (II-VI), tergite (VII).

[d] *Trithyreus cambridgei* (Thorell, 1889) = syn. *Schizomus cambridgei* Mello-Leitao, 1931.

[e] Includes probably also muscles #14 which shares origin with #13 according to Shultz (1993

[f] *Trithyreus pentapeltis* (Banks, 1900) = *Hubbardia pentapeltis* Cook, 1899.

[g] Shultz does not mention lateral suspensor muscles in chelicerates. See discussion in Shultz (1993) and in the discussion section of this paper. This muscle might be equivalent to his muscle #14, which Shultz tentatively homologized with muscle #83 described by Lankester et al. (1885).

segments four through seven. − Like for the prosoma, the external morphology of opisthosoma segments is suggestive but not conclusively informative about the segment assignment of the observed sclerites. Segment assignment requires an analysis of the axial musculature of the prosoma and the opisthosoma, and the morphology of the endosternite as origin of the prosoma suspensor muscle system.

3.2. Schizomida − endosternite

The endosternite extends as two lateral, chondroid bars in a horizontal midplane through the prosoma. In anterior-posterior direction, it extends from the level of the first pair of walking legs to the fourth pair of walking legs. Its anterior end has a distinct ventral bend; it also overlaps for a short distance with the posterior end of the pedipalpal apodeme (Figs. 3−7, 10). At the level of the coxae of the second pair of walking legs, the two lateral bars of the endosternite are connected by the anterior transverse bridge (Fig. 3). At that position, the endosternite has long dorso- and ventrolateral tendinous extensions. Histologically, it grades from the chondroidal endosternite through tendinous attachments into the dorsal and ventral suspensor muscles that originate at that position (see below). The endosternite extends to the posterior as a thin, tendinous rod along both sides of the syncerebrum. At the posterior end of the supraesophageal ganglion, the two lateral bars

of the endosternite thicken again and form a transverse bar, i.e., the posterior transverse bridge (Fig. 3C and D; 4E, F; 6C, D). − A comparatively prominent muscle originates from the anterior tip of the endosternite, and inserts to the cheliceral membrane (endo-sterno-cheliceral muscle; ec, Figs. 1, 3 and 4A, 10A).

The histological structure of the endosternite is cellular but heterogenous, with gradual transitions from a chondroidal, i.e., relatively large, ovoidal cells are surrounded by an extensive extracellular matrix, to a more tendinous structure, i.e., the cells are superficial to the matrix. However, the histology of the endosternite is always distinctly different from apodemes, i.e., infoldings of the cuticle (e.g., the epipharyngeal sclerite, the pedipalpal apodeme).

3.3. Schizomida − segmental axial musculature of the prosoma

Stenochrus portoricensis and *Surazomus* sp. possess four sets of suspensor muscles in the prosoma (Figs. 5−7, 10A) associated with the segments of the four walking legs. The most anterior suspensor muscle is a ventral suspensor muscle. It originates from the anterior edge of the endosternite and is associated with the first pair of walking legs, i.e., prosoma segment #3. This muscle has two portions, the median portion reaches from the endosternite to the inner side of the tritotetrasternum (vs3a, Figs. 5A and 7A), and the lateral portion inserts on the lateral edge of the coxa of the first walking leg (vs3b, Figs. 5B and 7B). The associated dorsal suspensor
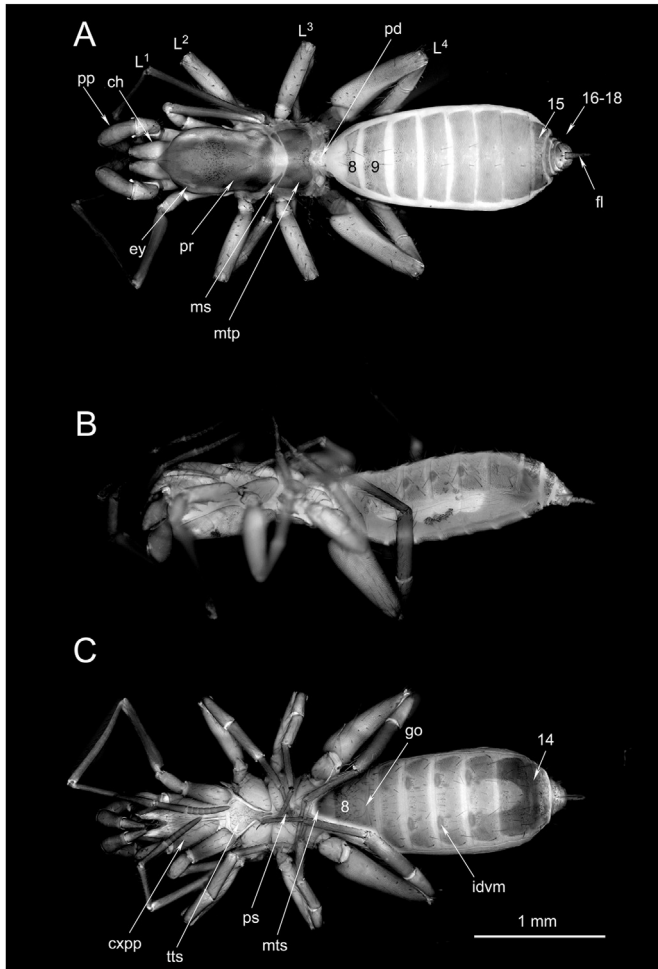
Fig. 2. *Stenochrus portoricensis*, external morphology of an adult individual. **(A)** Dorsal view, **(B)** lateral view, **(C)** ventral view. **Abbreviations:** ch, chelicerae; cxpp, coxa of pedipalp; ey, "eye spot"; fl, flagellum; go, genital operculum; idvm, impressions of dorso-ventral axial musculature; ms, mesopeltidium; mtp, metapeltidium; mts, metasternum; pd, pedicel; pp, pedipalp; pr, propeltidium; ps, pentasternum; tts, tritotetrasternum; L^1-4, walking legs 1–4; Arabic numerals, segment numbers. Scale bar in (C). Orientation of images: anterior is left.

muscles originate from the endosternite just a little bit posterior to the origin of the ventral suspensor (ds3, Figs. 5B and 7B). The dorsal suspensor of the third postoral segment is a delicate bundle of muscle fibers (c. 5 fibers) that reaches dorso-lateral and inserts on in inner side of the propeltidium. – A lateral suspensor was not found at that anterior position of the endosternite. However, a muscle taking the topographic position and orientation of a lateral suspensor originates from the posterior edge of the pedipalpal apodeme, which is in immediate proximity to the endosternite, and inserts to the lateral wall of the propeltidium (lat, Figs. 5A, 7A and 10).

The second group of suspensor muscles originates from the endosternite at the position of the anterior transverse bridge (Figs. 4–6, 7, 10A) and is associated with the second pair of walking legs (i.e., prosoma segment #4). The dorsal suspensor originates dorsal from the endosternite, reaches dorsal and inserts to the propeltidium (ds4, Fig. 5C and 7C). The lateral (transverse) suspensor muscles originate on the lateral side of the endosternite, and insert on the lateral wall of the propeltidium (ls4, Fig. 3C and D; 4C, G; 5C, D; 7D). The ventral suspensor muscles originate from the ventral side of the endosternite and insert on the medial edge of the

coxae of the second walking leg (vs4, Fig. 5C and 7C). At that position a thick nerve connects between the syncerebrum and the second walking leg. Therefore, the course of the ventral suspensor muscle is directed anterior and slightly bend circumventing the leg nerve. Histologically, dorsal and ventral suspensor muscles grade into the endosternite by long tendinous apodemes.

The propeltidium ends at a cross-sectional level between the second and the third pair of walking legs. A pair of small lateral dorsal sclerites (i.e., the "mesopeltidium") is located between the posterior margin of the propeltidium and the metapeltidium, that covers the prosoma over the third and fourth pair of legs (Fig. 2A). In this region, the endosternite is a pair of thin, tendinous rods extending left and right of the syncerebrum. There are no segmental axial muscles inserting on the mesopeltidium (Fig. 5E and F; 7E, F). Certainly, there are intrinsic prosoma muscles attached to the dorsolateral sclerite ("mesopeltidium"), but they are not associated with the endosternite or the segmental axial muscular system (Fig. 4B–D, F, H; 5E, F).

The third group of suspensor muscles originates from a middle position between the anterior and posterior transverse bridge of the endosternite and is associated with the third pair of walking legs (i.e., segment #5). The dorsal suspensor muscles insert at the anterior edge of the metapeltidium (ds5, Fig. 6A; 10). The ventral suspensors are short and inconspicuous. They insert on the dorsal edge of the coxa of the third walking leg (vs5, Fig. 6B; 10). Lateral suspensor muscles were not found at that position.

The fourth group of suspensor muscles originates at the level of the posterior transverse bridge of the endosternite, i.e., at the level of the fourth walking leg (prosoma segment #6). The fourth dorsal suspensor muscles reach around the midgut and insert dorsal on the metapeltidium (ds6, Fig. 6C, D, 10A). The ventral suspensor reaches ventral and inserts at median edge of the first article of the fourth walking leg. The insertion is close to but not at the edge of the ventral sclerite (vs6, Fig. 6C and D). The lateral suspensor muscles reach to an apodeme formed by a dorso-lateral infolding of the coxa of the fourth leg (ls6, Fig. 3D, 6D and 10A).

For comparative purpose (below), it should be highlighted here that the endosternite ends in the sixth postoral segment and does not extend into the opisthosoma. Also, the set of suspensor muscles associated with the sixth segment are the most posterior muscles attaching to the endosternite.

A ventral longitudinal muscle system as part of the BTAMS was not found; the endosterno-cheliceral muscle and the endosternite might represent residues of such a ventral longitudinal system (see discussion). Posterior oblique muscles, as hypothesized for the arachnid ground pattern (Shultz 2001, 2007) were not found. The topographic anatomy of the prosoma suspensor muscle system and the endosternite is schematically presented in Fig. 10A.

On the prosoma ventrum, the large anterior, triangular sclerite is associated with the first and second pair of ventral axial suspensor muscles as evidenced by the insertion of ventral suspensor muscles (vs3a,b, vs4; Fig. 5A–D, 6A-C). Thus, it can be associated with the third and fourth segment, i.e., is a tritotetrasternum. The segment of the third pair of walking legs is associated with the third group of suspensor muscles. Ventral is a small sclerotization between the coxae (pentasternum), however, no muscles attach to this sclerotization (pst, Fig. 6B). Therefore, an explicit segment assignment for this ventral sclerotizations cannot be given. The posterior group of suspensor muscles is associated with the fourth pair of walking legs. The ventral suspensors attach to the coxae of the fourth pair of walking legs, but not to the ventral metasternum (mst, Fig. 6C and 10A). The metasternum continues into the pedicel. In the posterior region of the pedicel, a pair of thin and delicate dorsoventral muscles spans between the ventral sclerite (metasternum) and the small tergite, which has been assigned to the first opisthosoma
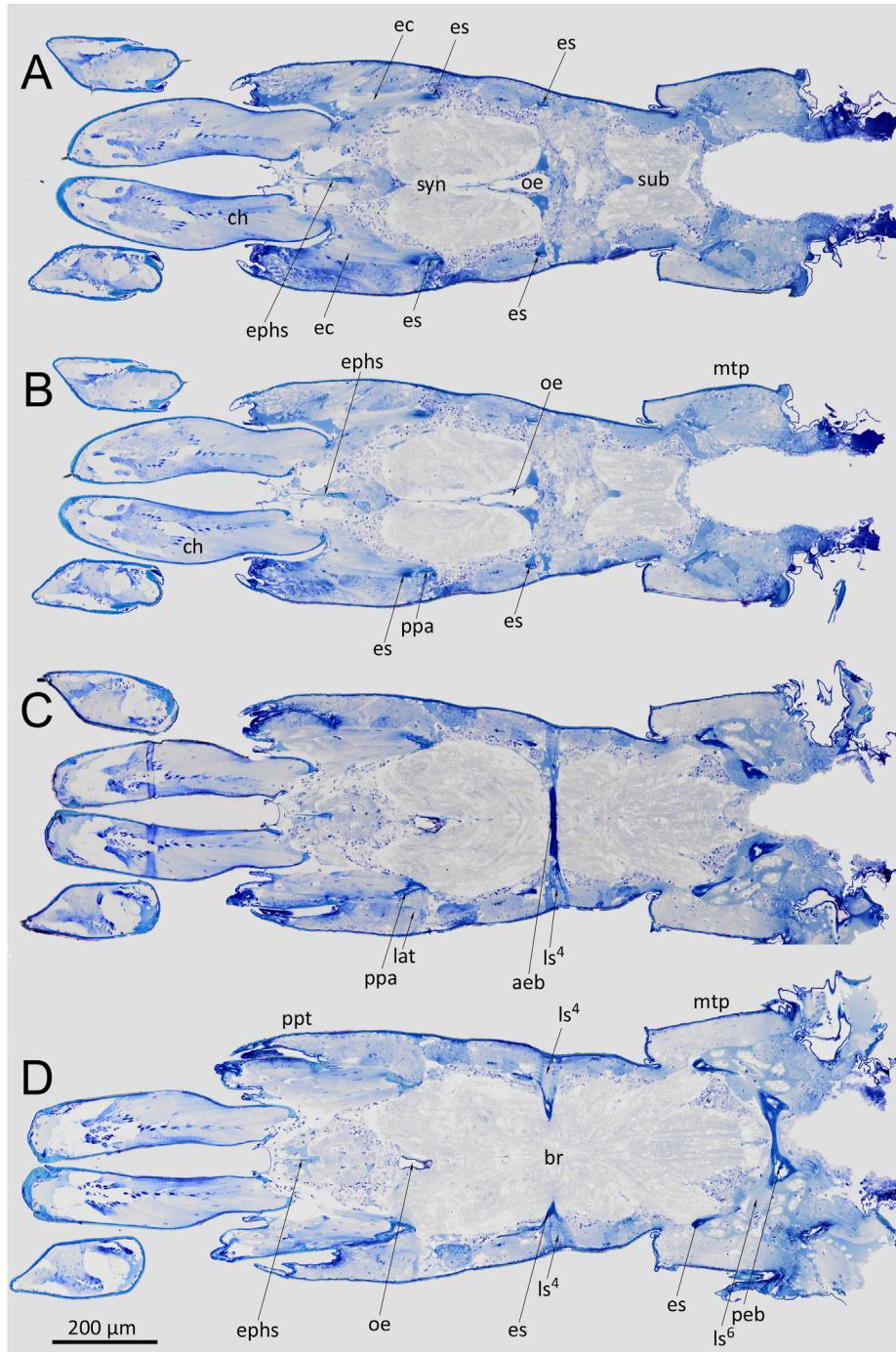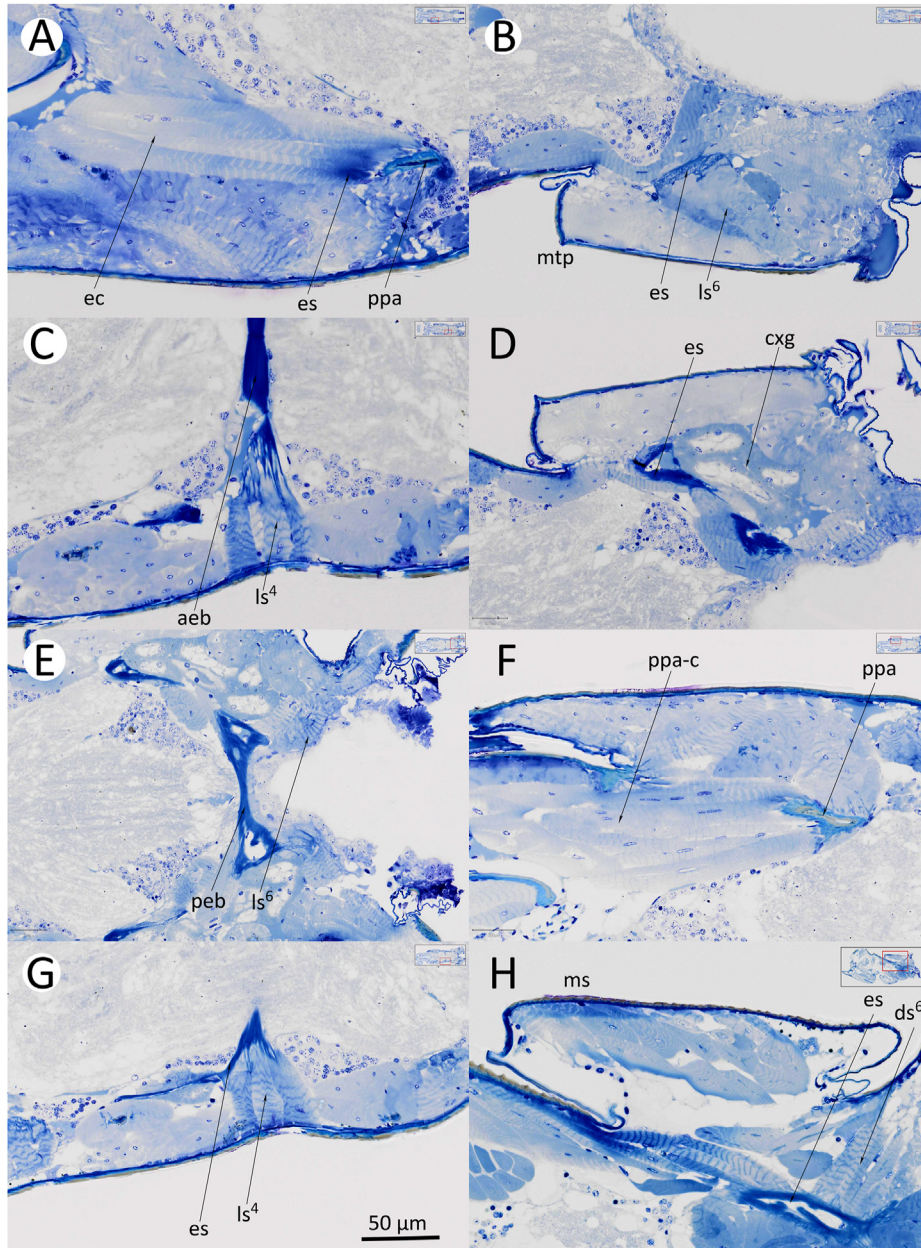
Fig. 3. *Stenochrus portoricensis*, serial horizontal sagittal sections through the prosoma documenting the endosternite and the axial suspensor muscle system in the prosoma. Sectioning planes in the Figs. proceed from more dorsal in (A) to more ventral in (D); anterior is left. **(A)** Relatively dorsal sectioning plane through the endosterno-cheliceral muscle and its origin from the endosternite. **(B)** Section ventral to A, showing the topographic relationship between the posterior end of the pedipalpal apodeme and the anterior end of the endosternite. **(C)** Section ventral to B, at the sectioning plane of the anterior endosternal bridge with the origin of the lateral suspensor 4; the posterior end of the pedipalpal apodeme is origin of a large lateral muscle, which is possibly the lateral suspensor of segment three that shifted its origin from the endosternite to the apodeme (see discussion for details). **(D)** Sectioning plane at the level of the posterior endosternal bridge with lateral suspensor six. **Abbreviations:** aeb, anterior endosternal bridge; br, brain; ch, chelicera; ec, endosterno-cheliceral muscle; ephs, epipharyngeal sclerite; es, endosternite; lat, lateral muscle originating from pedipalpal apodeme; ls^4, ls^6, lateral suspensor of prosoma segment four and six, respectively; mtp, metapeltidium; oe, oesophagus; peb, posterior endosternal bridge; ppa, pedipalpal apodeme; ppt, propeltidium; sub, suboesophageal ganglion; syn, syncerebrum (=supraoesophageal ganglion). Scale bar in (D).

segment. Also, dorsal and ventral intersegmental musculature originating from the metasternum and the tergite of the pedicel, respectively, reach into the next posterior opisthosoma segment and attach there (Fig. 8A, 9 and 10). Such pattern of intersegmental musculature does not occur in the prosoma but is typical for the opisthosoma (see below).

3.4. Schizomida — axial musculature of the opisthosoma

Segmental axial musculature of the opisthosoma consists of

Fig. 4. *Stenochrus portoricensis*, horizontal sagittal sections through the prosoma; high power magnification details from Fig. 2 documenting the origin of suspensor muscles from the endosternite. The Figs. insets at top of each image indicates the approximate positions of sections shown in A - H. **(A)** Endosterno-cheliceral muscle with origin from the endosternite (and partially from pedipalpal apodeme. **(B)** Lateral suspensor muscle of segment six, originating from the endosternite and inserting to the metapeltidium. **(C)** Anterior endosternal bridge with the lateral suspensor of prosoma segment four. Note the tendinous origin of the muscle its histological grading into the endosternite. **(D)** Endosternite in prosoma segment five, a prominent convolution of the coxal gland is lateral to the endosternite. **(E)** Posterior endosternal bridge with lateral suspensor of segment 6. **(F)** Sectioning plane somewhat deeper as compared to A, showing the origin of the muscle reaching to the cheliceral membrane from the pedipalpal apodeme. **(G)** Lateral suspensor muscle of segment four. **(H)** Detail of a longitudinal parasagittal section through the prosoma in the region of the dorsal lateral sclerite (="mesopeltidium"). No endosternal muscles span to the dorsal lateral sclerite, though intrinsic muscles are present. The endosternal origin of the dorsal suspensor muscle of the sixth segment is seen on the section. **Abbreviations:** aeb, anterior endosternal bridge; cxg, coxal gland; ds^6, dorsal suspensor muscle of prosoma segment 6; ec, endosterno-cheliceral muscle; es, endosternite, ls^4, ls^6, lateral suspensor muscles of segments four and six, respectively; ms, mesopeltidium; mtp, metapeltidium; ppa, pedipalpal apodeme, ppa-c, muscle spanning between pedipalpal apodeme and the cheliceral membrane. Scale bar in (G).

paired, dorso-ventral muscles, as well as dorsal and ventral intersegmental muscles (dv, dis, vis, Figs. 8 and 9A-D, 10A). *Stenochrus portoricensis* and *Surazomus* sp. have a pair of dorso-ventral muscles in opisthosoma segments one through seven. Segments eight to twelve do not possess dorsoventral muscles. All opisthosoma segments are connected by dorsal and ventral intersegmental muscles. These muscles are thin and delicate except for muscles connecting opisthosoma segments one and two, and those in opisthosoma segments VIII to XII, where they contribute to an extensive pygidial musculature (Fig. 9A and 10A). The opisthosoma does not have dorsal and ventral longitudinal muscles or posterior oblique muscles as hypothesized in the arachnid ground pattern (Shultz, 2001, 2007).

The first and the second opisthosoma segment are special. The first opisthosoma segment is small and thin, it functions as transitional segment between prosoma and opisthosoma (pedicel). The
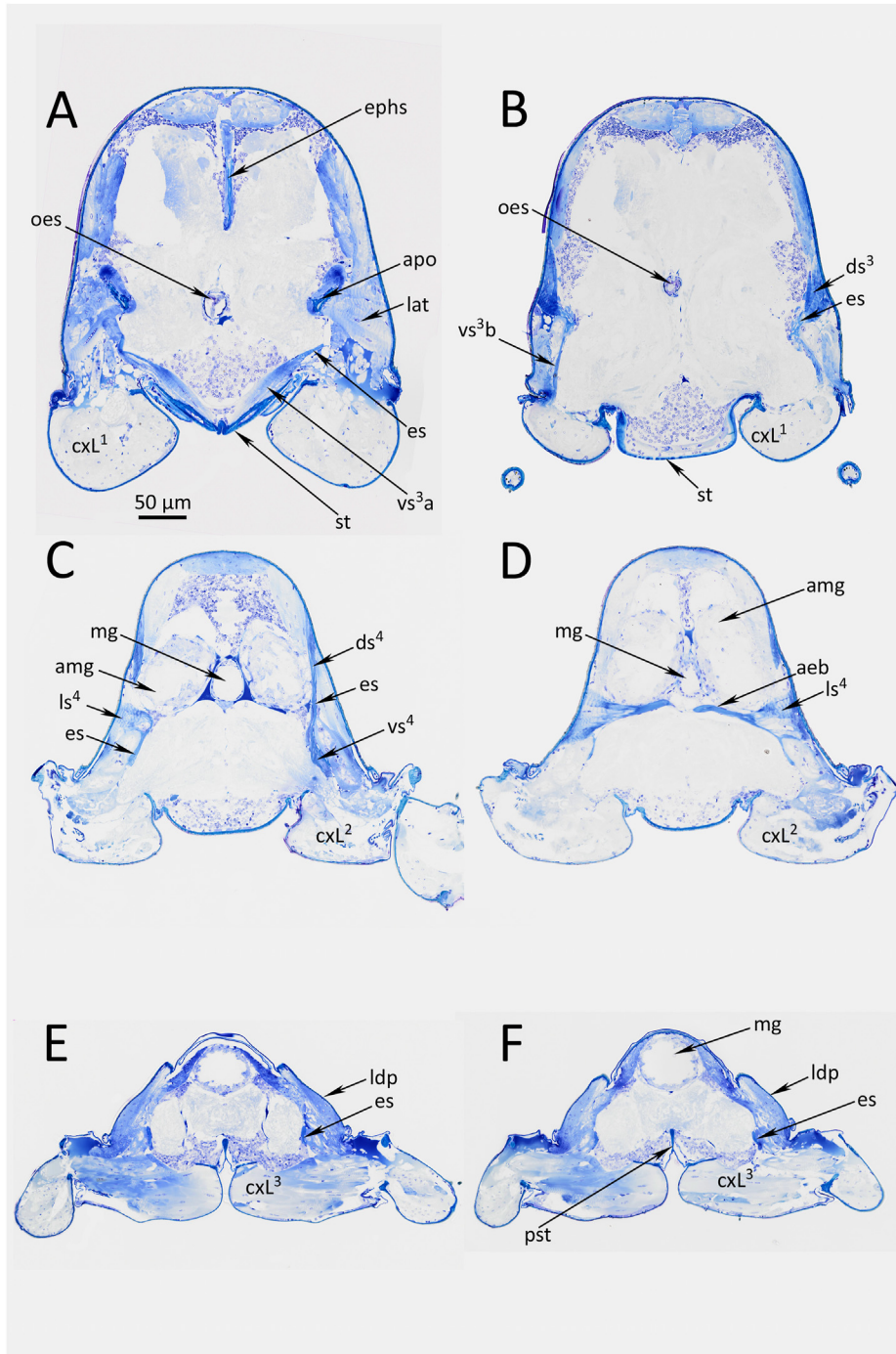
Fig. 5. *Stenochrus portoricensis*, serial cross-sections through the prosoma (from anterior in A to posterior in F) documenting details of the axial segmental muscles in the prosoma. **(A)** Section at the level of the coxae of the first walking leg. At this anterior end of the endosternite, the first ventral suspensor muscle (anterior portion) originates from the endosternite reaches ventral and inserts on the sternum. - Note that the posterior end of the intercheliceral septum and the posterior end of the apodeme of the pedipalpal coxae are still sectioned at that level. **(B)** Section a few microns posterior to (A) documenting the origin and insertion of the dorsal suspensor muscles 1 and the posterior portion of the ventral suspensor muscle inserting at the lateral internal edge of the coxa of the first walking leg. **(C)** Section at the level of the coxae of walking legs 2, just anterior to the anterior endosternal bridge. Here, a large hemolymph space surrounds the anterior midgut. **(D)** Section a few microns posterior to (C) at the level of the anterior bridge of the endosternite. The lateral suspensor muscles of segment four are documented. **(E)** Section at level of the coxae of the third pair of walking legs and the lateral dorsal plate. The endosternite is thin and no axial segmental muscles originate from here. **(F)** Section at the level of the coxae of the third pair of walking legs, lateral dorsal plate, and the pentasternum. **Abbreviations:** aeb, anterior bridge of endosternite; amg, anterior (lateral) midgut diverticle; apo, apodeme; cxL^{1-3}, coxa legs 1–3; dlm, dorsal longitudinal muscle of the prosoma; ds dorsal suspensor muscle (numbers indicate position 1–4); ephs, epipharyngeal sclerite; es, endosternite; ldp, lateral dorsal plate; ls, lateral suspensor muscle mg, midgut; ppt, propeltidium; pst, pentasternum; st, sternum (tritotetrasternum sensu Kästner); vs, ventral suspensor muscle (vs1a and vs1b indicate the anterior and posterior portion of the ventral suspensor muscle, respectively. Scale bar in (A).
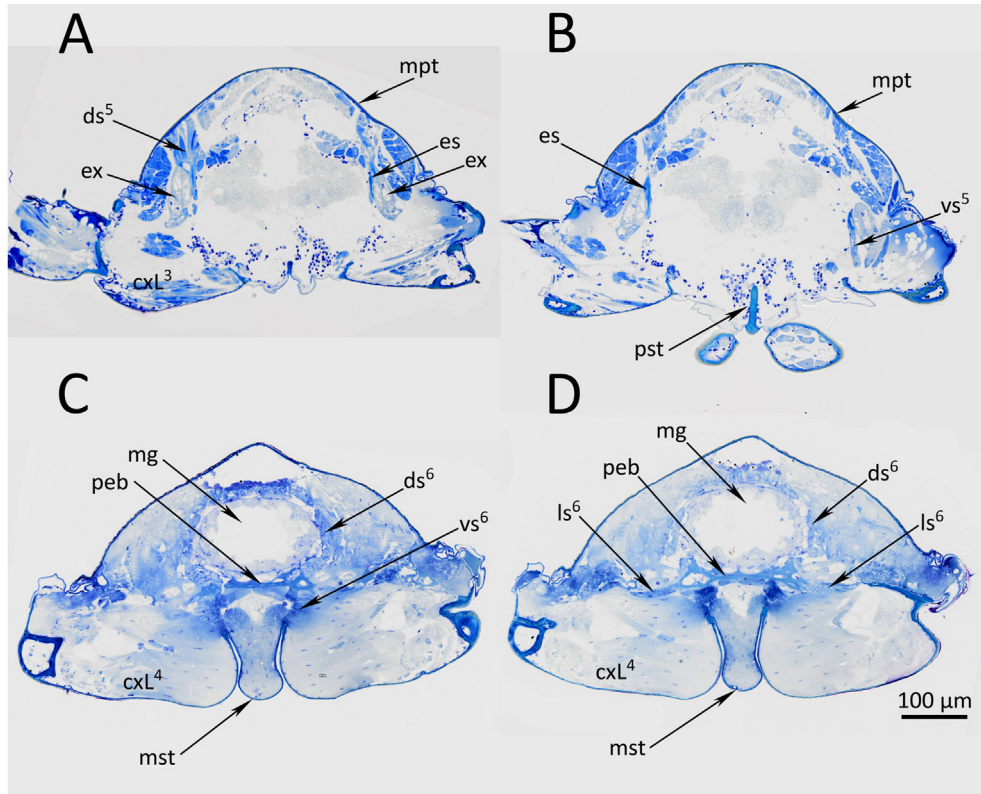
Fig. 6. *Stenochrus portoricensis*, serial cross-sections through the posterior part of the prosoma (metapeltidium) documenting details of origin and insertion of the axial segmental muscles in the prosoma. **(A)** Third dorsal suspensor muscle (segment five) originating from the endosternite and inserting on the metapeltidium. **(B)** Third ventral suspensor muscle originating from the endosternite. This muscle inserts on the inner edge of coxa 3 of the third walking leg (not shown). **(C)** Origin of the fourth suspensor muscles (segment six) from the posterior endosternal bridge. The origins of dorsal, transversal and ventral suspensor muscles are visible. The fourth dorsal suspensor inserts on the metapeltidium (not shown), the fourth ventral suspensor inserts on the medial edge of the coxae of the fourth pair of walking legs. **(D)** Fourth transverse suspensor muscle with origin and insertion to the coxa of the fourth pair of walking legs. **Abbreviations:** cxL^{3-4}, coxa of walking legs 3 and 4; ds^5, fifth dorsal suspensor muscle; ds^6, sixth dorsal suspensor muscle; es, endosternite; ex, tubular part of coxal gland (excretory system); ls^6, sixth lateral suspensor muscle; mg, midgut; mpt, metapeltidium; mst, metasternum; peb, posterior endosternal bridge; pst, pentasternum; vs^5, fifth ventral suspensor muscle; vs^6, sixth ventral suspensor muscle. Scale bar in (D).

cross-section of the first opisthosoma segment is occupied by the dorsal midgut, the ventral central nervous system, and strong dorsal and ventral intersegmental muscles connecting the tergites and sternites of the first and the second opisthosoma segment, respectively (Fig. 9A−D). The dorso-ventral muscles of the first opisthosoma segment are delicate fibers in the posterior half of the segment. They connect between the small tergite of opisthosoma segment one and the ventro-lateral body wall, where they have a tendinous attachment (dvI, Fig. 9B−D). Despite their delicate nature, the dorso-ventral muscles have consistently been found in all specimen of both species.

The second opisthosoma segment carries the lateral openings of the book lungs and the ventral genital aperture (Fig. 8C and 9E). It has a pair of thin but distinct dorso-ventral muscles (dvII, Fig. 8A and 10A). The dorsal attachment of this muscle is to the second opisthosomal tergite, and the ventral attachment of those muscles is at the posterior edge of a cuticular fold, that continues medial into the genital opening and lateral into the respiratory openings. This ventral attachment point of the dorso-ventral muscles is also attachment of the ventral intersegmental muscles from the 1st opisthosoma segment. It forms an extensive tendinous attachment, with considerable extracellular material. Histologically it resembles the endosternite.

3.5. Thelyphonida− external morphology

Prosoma dorsum: *Minbosius manilanus*, like all other

Thelyphonida, has a single, large dorsal sclerite that covers the entire prosoma. Thelyphonida possess eyes at the anterior margin of the prosoma (Fig. 11B−E).

Prosoma ventrum: The ventral side of the prosoma is characterized, from anterior to posterior, by the large and partially fused coxae of the pedipalps, small, almost lateral inserted coxae of the first pair of (palpiform) walking legs and the large coxae of the second to fourth pairs of walking legs (Fig. 11A). From anterior to posterior, the ventrum of *Minbosius manilanus* carries several sclerites (sterna). The most anterior ventral sclerite reaches from the posterior margin of the pedipalpal coxae to the end of the coxae of the second pair of walking legs. It is roughly triangular with the lateral tips extending to the coxae of the lateral inserted first pair of walking legs (Fig. 11A). The second sternum is a small sclerite between the third pair of walking legs. It is thin in its anterior part, but broadens at the posterior border of the coxae where it extends between the coxa of the third and fourth pair of walking legs. A large, posterior ventral sclerite extends between the coxae of the fourth pair of walking legs. It is directly followed by the genital operculum (= second opisthosoma segment). The external morphology and counting segment numbers suggests that this posterior sclerite between the coxae of the fourth pair of walking legs is the ventral sclerite (sternite) of the first opisthosomal segment. However, it requires analysis of the attaching axial segmental musculature for a detailed determination of the segmental nature of this sclerite (below).

Opisthosoma: The opisthosoma is broad and flattened in the
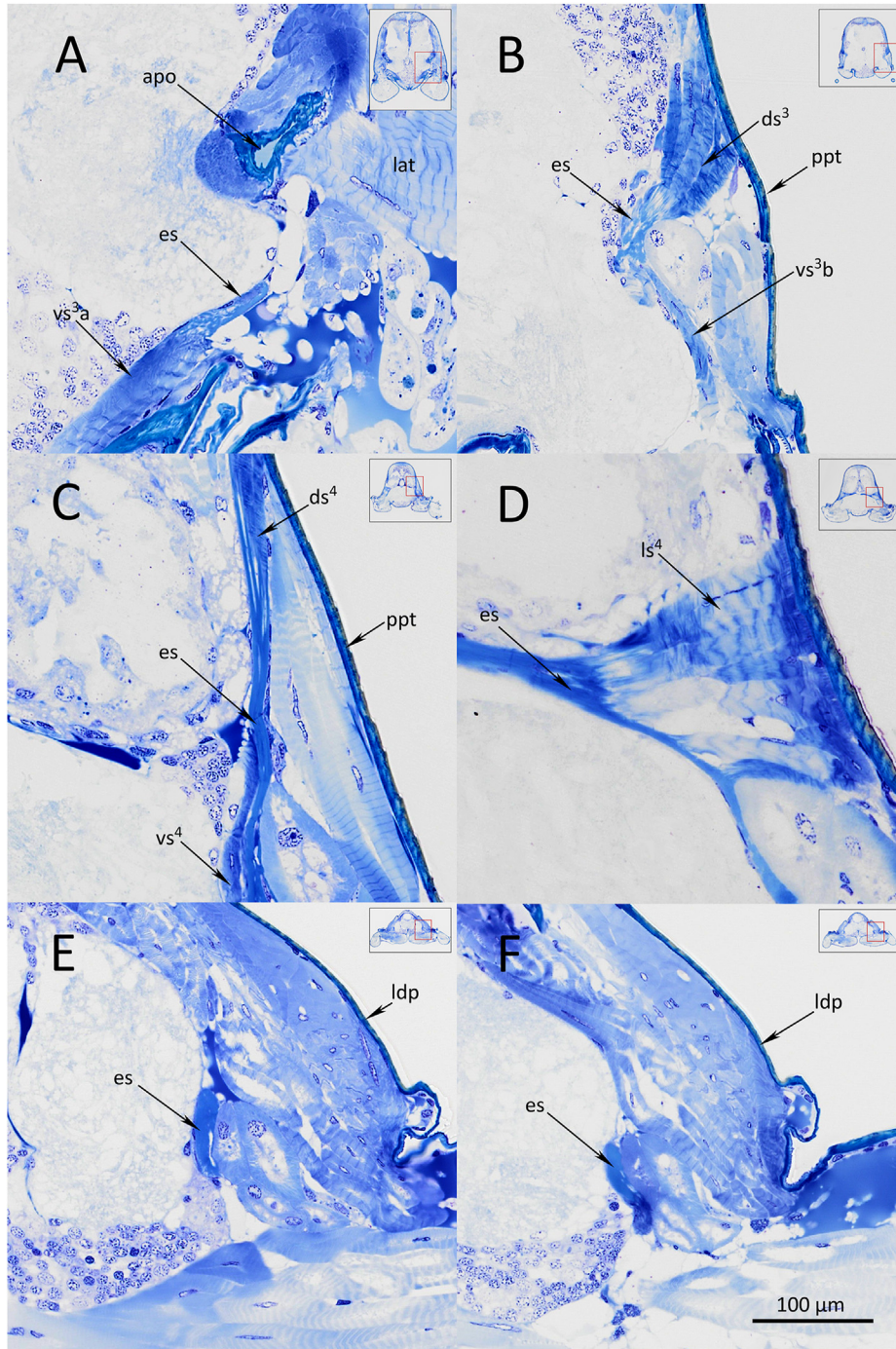
Fig. 7. *Stenochrus portoricensis*, serial cross-sections through the prosoma documenting details of origin and insertion of the axial segmental muscles in the prosoma (meta-peltidium). Images are details of Fig. 4A–F, as indicated by the respective insets in the right upper corner of each image. **(A)** Anterior end of the endosternite and the origin of the first ventral suspensor muscle. The posterior end of the apodeme formed by the coxa of the pedipalp is seen dorsal to the anterior end of the endosternite. A muscle stretching from the apodeme to the lateral wall of the propeltidium is homologized with lateral suspensor three (shifted origin from the endosternite to the apodeme). **(B)** Anterior end of endosternite with origin and insertion of the first dorsal suspensor muscle. **(C)** Dorsal and ventral suspensor 2 originating from the endosternite. **(D)** Transversal suspensor muscle 2 originating from the endosternite at the anterior commissure of the endosternite. **(E)** Endosternite in the region of the lateral dorsal plate (formerly "mesopeltidium"). No segmental muscle is attaching to the lateral dorsal plate. **(F)** More posterior position of the endosternite in the region of the lateral dorsal plate (formerly "mesopeltidium"). No segmental muscle is attaching to the lateral dorsal plate. **Abbreviations:** apo, apodeme; ds dorsal suspensor muscle (index numbers indicate segment numbers); es, endosternite; lat, lateral muscles between apodeme and propeltidium (shifted lateral suspensor); ldp, lateral dorsal sclerite; ppt, propeltidium; ls, transversal suspensor muscle; vs, ventral suspensor muscle. Scale bar in (F).

dorsoventral direction. It consists of 12 segments and a flagellum. In external examination, the first opisthosoma segment is small and forms the connection with the prosoma; its tergite is small and largely overarched by the posterior edge of the prosoma

(Fig. 11B–D) thus difficult to see from outside; its sternite is also small and shifted between the coxae of the fourth pair of walking legs (see above). The following eight segments are broad and carry dorsal tergites and ventral sternites, while the three terminal
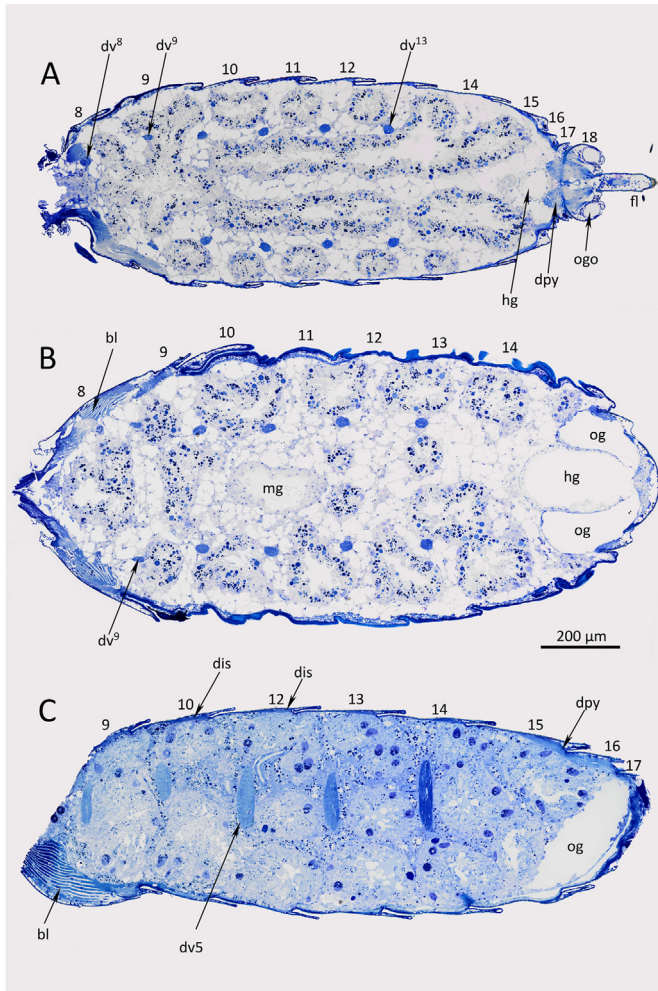
Fig. 8. *Stenochrus portoricensis*, horizontal and midsagittal serial sections through the opisthosoma; prosoma and opisthosoma were separated by cutting through the pedicel (left in images). **(A)** Horizontal longitudinal section through the opisthosoma from the second opisthosoma segment to the flagellum. Cross-sections through the dorso-ventral muscles from segment two trough seven are clearly seen. Dorsal inter-segmental muscles from the first opisthosoma segment (pedicel) reaching into segment two; dorsal pygidial muscles in the metasoma (segments 16–18) are distinct. **(B)** Horizontal longitudinal section through an equatorial level of the opisthosoma. Note that not all dorso-ventral muscles are seen because of the plane of sectioning. **(C)** Longitudinal section in a lateral position of the opisthosoma documenting the dorso-ventral muscle of segments three through seven. See Fig. 8 for a documentation of the small and delicate dorso-ventral muscles in opisthosoma segments one and two. **Abbreviations**: bl, book lung; dis, dorsal intersegmental muscle; dpy, dorsal pygidial muscles; dv^8-dv^{13}, dorso-ventral muscles of segments 8–13 (opisthosoma); fl, flagellum; hg, hindgut; mg, midgut; og, opisthosoma gland; ogo, opening of opisthosoma glands; Arabic numbers, segment numbers. Scale bar in (B).

segments are small and carry ring shaped sclerites ("postabdomen"; Dunlop and Lamsdell, 2017). The sternite of the second opisthosomal segment forms a broad cover of the genital opening. The opisthosoma carries a terminal flagellum. Respiratory openings are found at the ventro-lateral edges of the second and third opisthosomal sternites.

3.6. Thelyphonida — endosternite

The endosternite is a prominent structure that extends through the prosoma from the level of the pedipalpal apodeme into the first segment of the opisthosoma. In μCT, it is clearly distinguishable by its high X-ray absorbance, i.e., it is distinctly brighter than muscle

tissue (es; Figs. 11 and 12). The endosternite has two anterior horns that are origin of the first set of axial suspensor muscles (Fig. 13). The anterior endosternal bridge connects the left and right bar of the endosternite at the level of the first pair of walking legs. A large central window opens behind the anterior endosternal bridge. A second, posterior endosternal bridge connects left and right bars at the level of the second/third pair of walking legs. The posterior bridge of the endosternite continues into the posterior plate, i.e., an extension of the endosternite that reaches posterior into the first opisthosoma segment (Fig. 13).

3.7. Thelyphonida– axial musculature of the prosoma

The endosternite is origin of the axial segmental suspensor muscles. Four sets of suspensor muscles are associated with prosoma segments. The most anterior set of suspensor muscles originates at the anterior horns of the endosternite at the level of the coxae of the first pair of walking legs (prosoma segment #3). The anterior ventral suspensor muscles originate from the ventral side of the endosternite and reach to the sternum between the coxae of the first pair of walking legs (=tritotetrasternum). The first dorsal suspensor muscles originate from the endosternite immediately posterior the origin of the ventral suspensor muscles and insert on the inner side of the dorsal shield (ds3, Fig. 10B and 12A3, 13A, B). They are a rather delicate bundle of muscles. Lateral suspensor muscles were not found originating from the endosternite. However, a pair of anterior lateral muscles (lat, Fig. 10B and 12A3) originates from the posterior edge of the pedipalpal apodeme, reaches to the lateral side, and inserts on the lateral body wall. This pair of muscle takes the topographic position of an anterior lateral suspensor muscles, but has a different origin (compare to Schizomida, above).

The second set of suspensor muscles originates from the anterior endosternal bridge, i.e., at the level of the coxae of the second pair of walking legs. The muscles are not all on the same cross-sectional level and it requires screening through a stack of images to follow origin and insertion of all suspensors (ds4, vs4, ls4, Fig. 10B,12B). The second dorsal suspensor muscles (ds4) originate just posterior to the origin of the first dorsal suspensor and are characterized by a long tendinous origin. This tendon has the same x-ray contrast as the endosternite (Fig. 12) and has been reconstructed as part of the endosternite in Fig. 13A. From its origin, the second dorsal suspensor muscle (ds4) reaches to the posterior and inserts on the inner side of the dorsal shield, approximately at the topographic position of the insertion of the third dorsal suspensor muscle (ds5; Fig. 10B). The ventral suspensor muscles (vs4) originate from the endosternite and reach to the anterior edge of the coxae of the second pair of walking legs. The lateral suspensor muscles (ls4, Fig. 12B3) are well developed and originate with a strong tendon from the endosternite; at about half the distance to the lateral wall of the dorsal shield they fan out broadly and insert on the dorsal shield.

The third set of suspensor muscles (ds5) originates from the endosternite at the anterior level of the coxae of the third pair of walking legs (Fig. 10B, 11B and 12C, 13B,C). The dorsal suspensor muscles (ds5) are relatively strong muscle bundles. They reach straight dorsal and insert to the dorsal shield. Lateral suspensors (ls5) reach to the side to insert to the pleural body wall. The ventral suspensors (vs5) reach from the endosternite to the median edge (apodeme) of the coxae of the third walking legs.

The fourth set of suspensor muscles (ds6) originates from the posterior endosternal bridge, at the level of the posterior edge of the third pair of walking legs (Figs. 10, 11B, 12D). The fourth dorsal suspensor muscles (ds6) reach straight dorsal to the dorsal shield. The fourth ventral suspensor muscles (vs6) reach straight ventral to
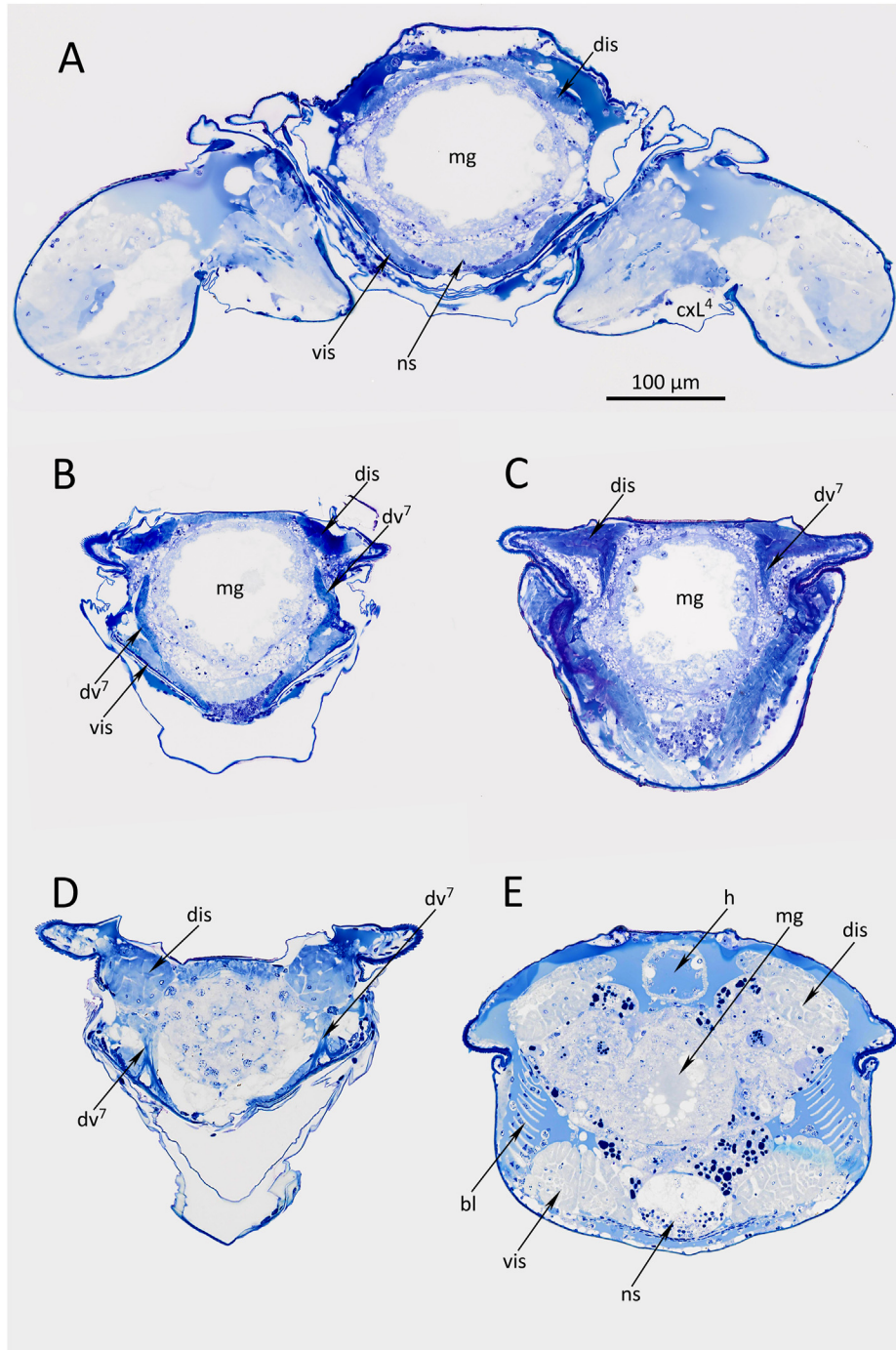
Fig. 9. *Stenochrus portoricensis*, microscopic anatomy of the serial axial muscle system in the pedicel, i.e., transition between prosoma and opisthosoma. Serial cross-sections documenting the microscopic anatomy of the pedicel (first opisthosoma segment) and the second opisthosoma segment. **(A)** Anterior part of the pedicel containing dorsal and ventral intersegmental muscles. **(B)** Pedicel, tendinous ventral insertion of the dorso-ventral muscles of opisthosoma segment one. **(C)** Cross-section through the posterior part of the pedicel, dorso-ventral muscles recognizable as thin muscle strings to both sides of the midgut. **(D)** Posterior part of the pedicel, close to the dorsal attachment of the dorso-ventral muscles. **(E)** Cross-section through the anterior part of the second opisthosoma segment documenting the book lungs. Large dorsal and ventral intersegmental muscles are seen, no dorso-ventral muscles in this section. **Abbreviations:** bl, book lung; cxL⁴, coxa of fourth walking leg; dis, dorsal intersegmental muscle; dv⁷, dorso-ventral muscles of the first opisthosoma segment (= segment 7); h, heart; mg, midgut; ns, nervous system; vis, ventral intersegmental muscle. Scale bar in (A).

the sternum between the fourth pair of walking legs. The lateral suspensor muscles are strong muscles that reach to the lateral body wall.

Additional muscles attaching to the endosternite are: (i) a pair of muscles originating from the anterior horns of the endosternite and inserting to the posterior edge of the chelicerae (i.e., the endosterno-cheliceral muscle), and (ii) a pair of dorsal and ventral muscles that originates from the posterior endosternal plate and inserts on dorsal and ventral sclerites of the first opisthosoma segment, respectively (dvI, Fig. 11D and 12E1, 13). The endosternite is also origin of (iii) the large oblique endosterno-tergal muscle (et, Fig. 11B–D, 13). This endosterno-tergal muscle is paired, originates

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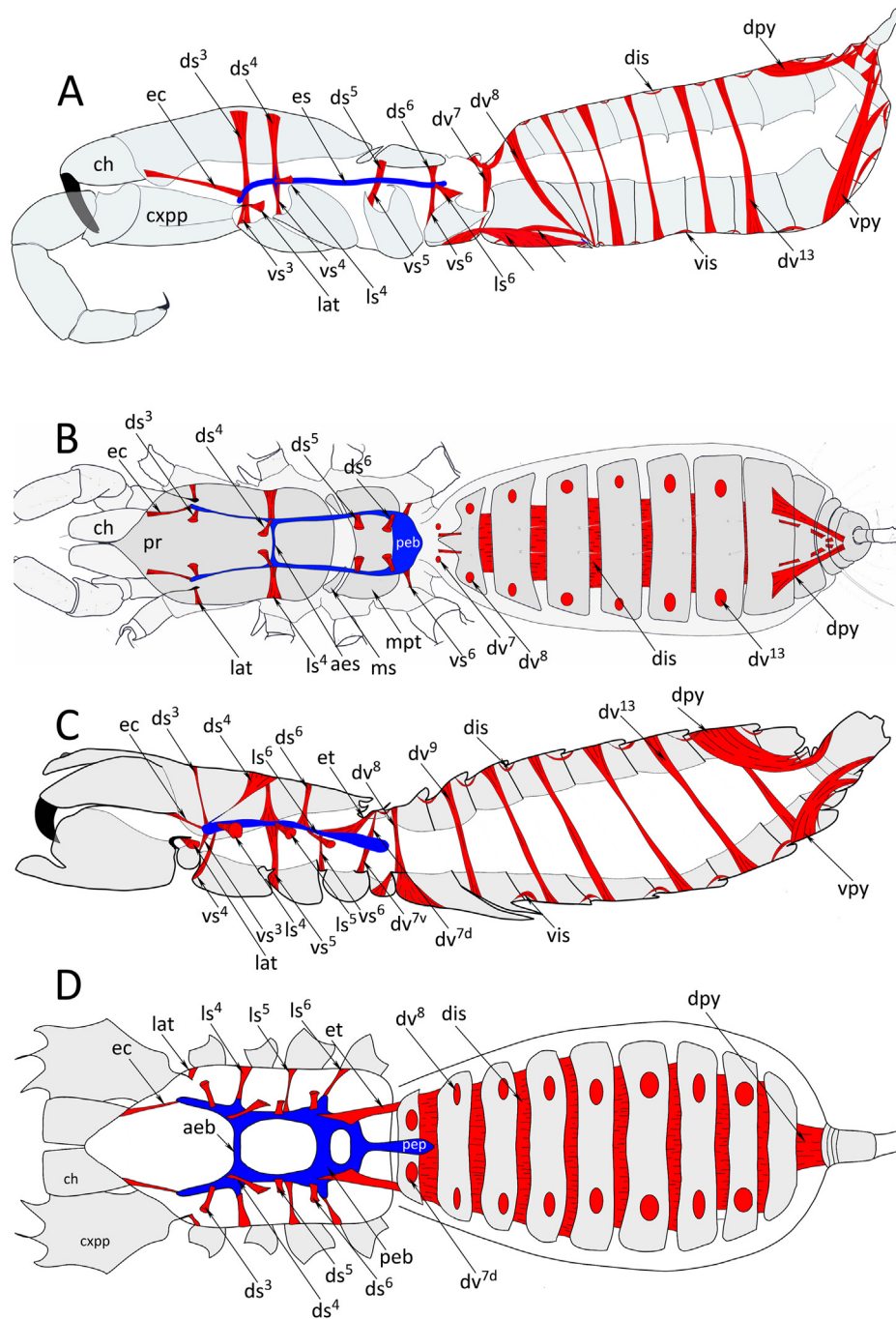
Fig. 10. Schematic drawings of the serial axial muscle system of a schizomid in (**A**) lateral view and (**B**) dorsal view. (C) Schematic drawing of a thelyphonid in lateral view and (d) in dorsal view. **Abbreviations:** ch, chelicera; cxpp, coxa of pedipalpus; dis, dorsal intersegmental muscle; dl, dorsal longitudinal muscle of the prosoma; ds$^{3-6}$, dorsal suspensor muscles of prosoma segments 3 to 6; dpy, dorsal pygidial muscles; dv$^{7-13}$, dorso-ventral muscles of segments 7−13 (opisthosoma); ec, endosterno-cheliceral muscle; es, endosternite; et, endosterno-tergal muscle; lat, lateral muscle originating from the pedipalpal apodem (probably homologous to the lateral suspensor of the third segment); ls$^{4-6}$, lateral suspensor muscles of prosoma segments 4−6; ppa, pedipalpal apodeme; stl, sternite of the first opisthosoma segment (="metasternum"); Arabic numbers, segment numbers. Orientation of images: anterior is left, dorsal is up.

from the posterior part of the endosternite, reaches posterior in a steep angle and inserts on the anterior edge of the tergite of the first opisthosoma segment.

There are two dorsal longitudinal muscles in the prosoma (dl, Figs. 10, 11C, 12A,B), that extend between the soft frontal membrane to a middle position on the dorsal shield and then from that middle position to the posterior edge of the dorsal shield. They, supposedly, represent the longitudinal dorsal muscles of the BTAMS.

3.8. Thelyphonida − axial musculature of the opisthosoma

The axial segmental musculature of the opisthosoma is dominated by the large dorsoventral muscles, that extend between the tergites and sternites of each segment, except opisthosoma segments IX through XII (Fig. 11B−E, 12E). The first opisthosoma segment is special, because it is small, forms the transition between prosoma and opisthosoma, is partially integrated into the prosoma,
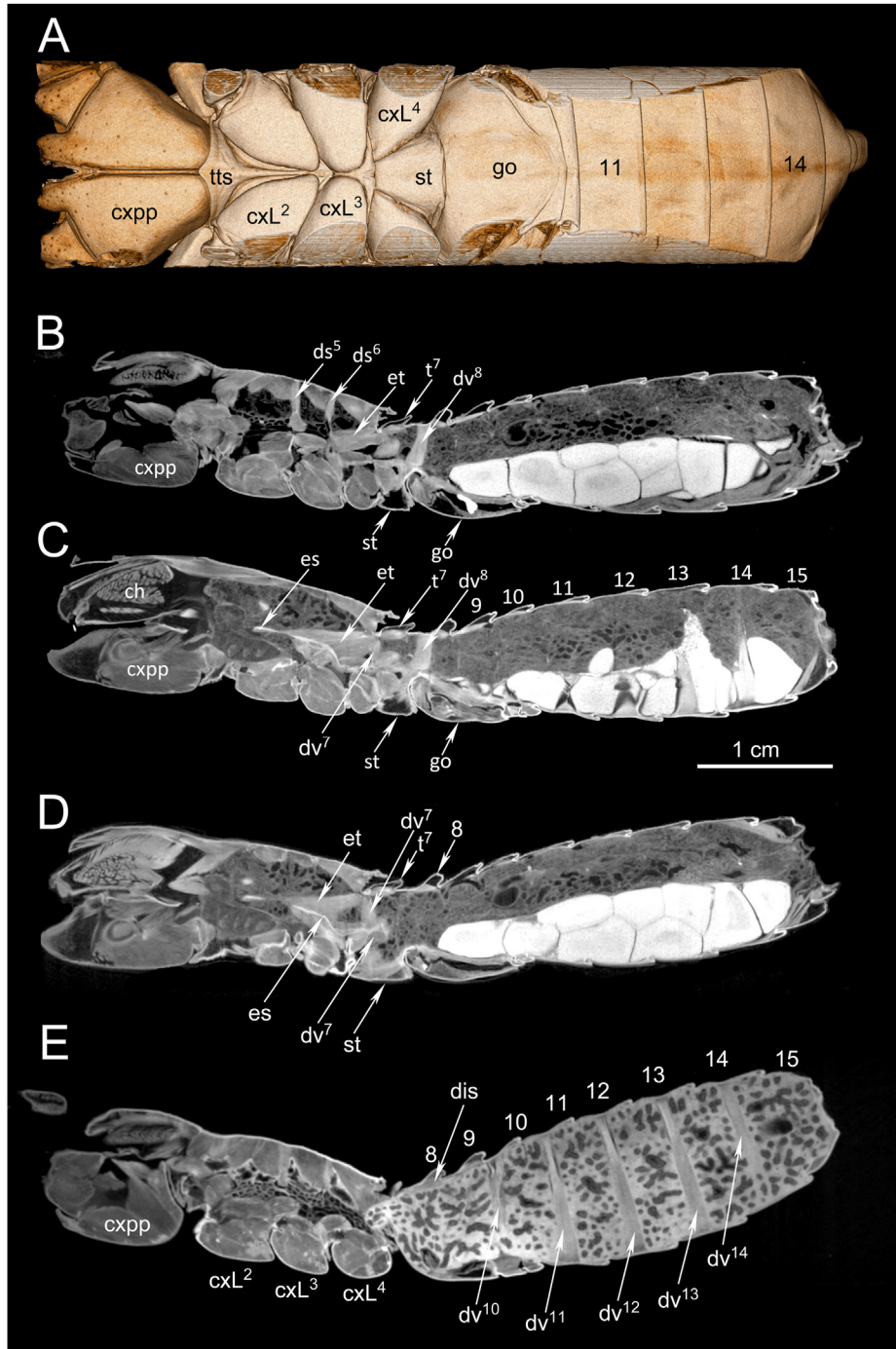
Fig. 11. *Minbosius manilanus,* microscopic anatomy of the serial axial musculature based on µCT-imaging. **(A)** 3D-reconstruction (volume rendering) of the ventral body surface (*Minbosius* #10); anterior is left. **(B)** Parasagittal µCT-image of the image stack of *Minbosius* #14 (image 129) documenting the prosomal axial segmental musculature and the transition to the opisthosoma. **(C)** Midsagittal µCT-image documenting the microscopic anatomy of the endosternite and the suspensor muscle system. **(D)** Midsagittal µCT-image documenting the microscopic anatomy of the prosoma−opisthosoma transition. Dorsoventral muscles of the first opisthosoma segment attach to the endosternite assimilating a prosoma muscle anatomy. **(E)** Parasagittal section through pro- and opisthosoma documenting the dorso-ventral muscles of the opisthosoma. **Abbreviations:** ch, chelicera; cxL$^{1-4}$, coxae of walking legs one to four; cxpp, coxa of pedipalpus; dis, dorsal intersegmental muscle; dl, dorsal longitudinal muscle of the prosoma; ds$^{5-6}$, dorsal suspensor muscles of prosoma segments five to six; dv$^{7-14}$, dorso-ventral muscles of the opisthosoma segments 7–14; es, endosternite; et, endosterno-tergal muscle; st, sternite of the first opisthosoma segment (="metasternum"); t^7, tergite of segment 7; tts, tritotetrasternum; Arabic numbers, segment numbers. Orientation of images (B−E): anterior is left, dorsal is up. Scale bar in (C).

and the dorso-ventral muscles have assumed a prosoma-muscle morphology. − The sternite of the first opisthosoma segment forms the metasternum. This is supported by the muscle topography. The first dorso-ventral muscle of the opisthosoma has assimilated a prosoma suspensor muscle morphology and is represented by dorsal and ventral suspensor muscles, each originating from the posterior plate of the endosternite and inserting on the tergite and sternite of the first opisthosoma segment, respectively (Figs. 11D and 12E1).

The second opisthosoma segment is the genital segment. Its
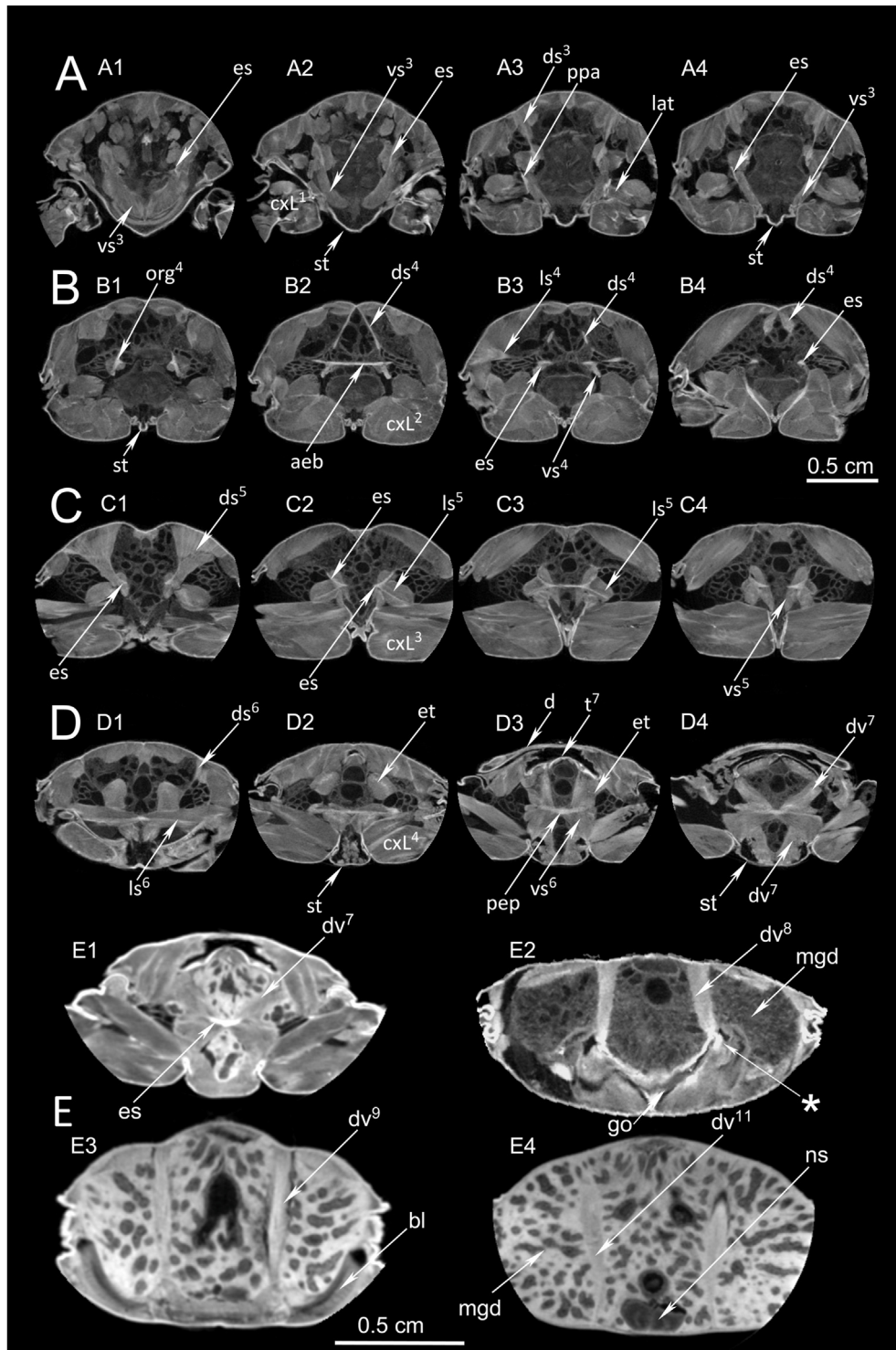
Fig. 12. *Minbosius manilanus.* Cross-sectional µCT-images through the prosoma and opisthosoma documenting all muscles of the axial segmental system. **(A₁₋₄)** Suspensor muscles of prosoma segment 3. **(B₁₋₄)** Prosoma segment four with the anterior endosternal bridge and the origin of suspensor muscles. **(C₁₋₄)** Prosoma segment five with the posterior endosternal bridge and the origin of the suspensor muscles. **(D₁₋₄)** Endosterno-tergal muscles and posterior group of suspensor muscles, originating from the endosternal plate, i.e., posterior extension of the endosternite that reaches into the opisthosoma, and inserting to tergite and sternite of the first opisthosoma segment, respectively. **(E₁₋₄)** First (E₁) second (E₂), third (E₃) and fifth (E₄) opisthosoma segment documenting the dorso-ventral muscles. In the first opisthosoma segment the dorso-ventral muscles attach to the endosternite assimilating a prosoma morphology (E₁). The asterisk in E₂ indicates a small sclerite just anterior to the genital operculum, which, according to Shultz (1993), may be homologized with the sternite of segment VIII. **Abbreviations:** aeb, anterior endosternal bridge; bl, book lung; es, endosternite, ds, dorsal suspensor muscle; dl, dorsal longitudinal muscle; dv, dorso-ventral muscle; go, genital operculum; lat, lateral muscle; ls, lateral suspensor; mgd, midgut diverticulum; ns, nervous system; pep, posterior endosternal plate; st, sternum; t⁷, tergite of segment 7 (= first opisthosoma segment); vs, ventral suspensor. Scale bar A-D in (B).
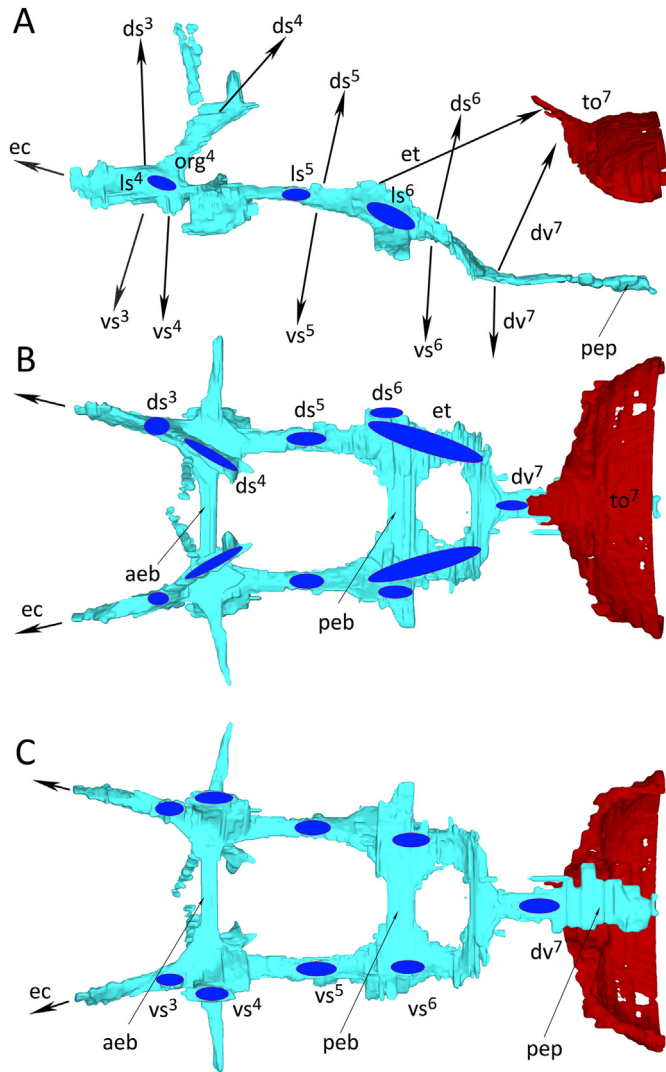
Fig. 13. *Minbosius manilanus*, endosternite and origin of suspensor muscles. Orthographic views of a 3D reconstruction from serial μCT-images, origins of suspensor muscles have been schematically inserted. **(A)** Lateral view; bold arrows indicated position and orientation of major muscles originating from the endosternite. Blue ellipses indicate place of origin of lateral suspensor muscles. Lateral suspensor 3 is not shown because it does not originate from the endosternite but, presumably, from the pedipalpal apodeme. **(B)** Dorsal view, and **(C)** ventral view of the endosternite. **Abbreviations:** aeb, anterior endosternal bridge; ds^{3-6}, dorsal suspensor muscles; dv^7, dorso-ventral muscle of the seventh segment (assimilating the prosoma muscle-phenotype and split into a dorsal and a ventral component); ec, endosterno-cheliceral muscle; et, endosterno-tergal muscle; ls, lateral suspensor muscles; org^4, origin of dorsal suspensor muscle 4; peb, posterior endosternal bridge; pep, posterior endosternal plate; t^7, tergite of segment 7 (= first opisthosoma segment).

tergite equals the large tergites on the following opisthosoma segments. However, its ventral sclerite is large and its posterior margin is deeply incorporated into the body, forming the anterior support for the genital operculum (anterior operculum according to Shulz, 1993). This sclerite and a very small sclerotization (marked * in Fig. 12E2) is attachment site for the dorso-ventral musculature. The third opisthosoma segment is regular on the dorsal side; on the ventral side, its sternite forms part of the internal lining of the genital duct (Fig. 11B and C) and the actual ventral sclerite is relatively narrow.

Short dorsal and ventral intersegmental muscles, i.e., intertergal and intersternal muscles, connect between the opisthosoma segments. In segments 15 through 18, they form strong pygidial muscles. The pygidial muscles are short, intermediate, and long, spanning between two, three or more segments, respectively. —Like in Schizomida, longitudinal dorsal and ventral muscles, as well as posterior oblique muscles have not been found in the opisthosoma of *Minbosus manilanus*.

4. Discussion

This paper aims at analyzing the segmental organization of the prosoma, i.e., segment assignment of pro-, meso-, and metapeltidium, the sterna, the prosoma—opisthosoma transition, and the mesosoma—metasoma transition in schizomids and compare it with Thelyphonida and other arachnids. The underlying idea is that the segmental axial musculature of the *box-truss axial muscular system* (Shultz, 2001, 2007) may serve as independent serial indicator for segment identity. This approach has been successfully applied by Shultz (1993, 1999, 2001, 2007), Mehnert et al. (2018), Franz-Guess and Starck (2020).

4.1. Segmental organization of the dorsum

As laid out in the introduction, the dorsal prosomal shield of schizomids is tripartite, with sclerites traditionally termed pro-, meso- and metapeltidium. It has been paradigmatically assumed that these three sclerites represent segmental tergites, i.e., propeltidium covering the first 5 segments (preoral segment, chericeral, pedipalpal, and segments of walking legs 1 and 2), the mesopeltidium supposedly were associated with the segment of the third walking leg, and the metapeltidium with the segment of the fourth pair of walking legs (Pocock, 1893; Börner, 1902, 1904; Kästner, 1932; Shultz, 1990; Dunlop and Lamsdell, 2017). Such segmental organization has either been interpreted as evolutionary ancestral (Pocock, 1893; Kraus, 1976) with the propeltidium representing the ancestral four-segmented arthropod head (for critical reviews of chelicerate head segmentation see Bitsch and Bitsch, 2007; Scholtz, 2016), or as derived (Weygoldt and Paulus, 1979), i.e., representing an adaptation for increased maneuverability in a highly structured habitat. Van der Hammen (1982, 1986) was, to my knowledge, the only who suggested, with reference to Grandejean (1965; not referenced here), that the sclerites of the mesopeltidium represent "pseudosclerites", i.e., independent local sclerotizations of the soft pleural membrane. However, he neither provided morphological evidence supporting this idea nor a functional interpretation.

The topographic morphology of the segmental axial muscles associated with the endosternite as presented here is (largely) consistent with the two original descriptions of the muscles of the endosternite in schizomids (Börner, 1904; Firstman, 1973) although they considered only the origin but not the insertion of the muscles to dorsal and ventral sclerites. Minor differences may be due to different tools of morphological analysis and species differences. I suppose, however, that serial sections of multiple individuals as studied here provide the most detailed information on the microscopic anatomical level.

The observed topography of axial segmental muscles in the prosoma is derived from the arachnid ground pattern as hypothesized in the box truss axial muscle system for arachnids (Shultz, 2001, 2007, Fig. 1). As compared to the hypothetical ground pattern, the number of dorsal and ventral suspensor muscles is reduced to four, one set associated with each segment of walking legs; suspensor muscles of the cheliceral and the pedipalpal segment have not been identified. Only two pairs of lateral suspensor muscles (segments 4, 6) have been found. The topography of an anterior lateral muscle (lat) extending between the pedipalpal apodeme and the coxa of the first walking leg is controversial,

because it does not originate from the endosternite but the pedipalpal apodeme. An identical muscle configuration is found in Thelyphonida (see discussion below) where Shultz (1993; muscle #33) suggested that an anterior endosternocoxal muscle had shifted its origin from the endosternite to the pedipalpal apodeme (see discussion below). Posterior oblique muscles are missing in schizomids. They are also missing in Thelyphonida except for the endosterno-tergal muscle, which might be a residual of the last posterior oblique muscles of the prosoma.

The pattern of insertions of the dorsal suspensor muscles to the dorsal sclerite(s) of the prosoma allows for a straightforward interpretation. The propeltidium covers segments 0—4, and the metapeltidium covers segments five and six, i.e., represents the merged tergites of those posterior two segments, while the "mesopeltidium" is not a tergite of a prosoma segment, but a local sclerotization of the otherwise soft pleural membrane (support for hypothesis D in Fig. 1). The analysis of segmental axial suspensor muscles provides morphological evidence for a so far neglected and unsupported suggestion by Van der Hammen (1982, 1986) that the mesopeltidium is not a tergite of prosomal segment five, but a dorso-lateral sclerotization of the pleural membrane.

A tripartite dorsum of the prosoma has also been found in Palpigradi, Solifugae, Opiliones and (some) Acari. For Palpigradi, Franz-Guess and Starck (2020) showed, that the "mesopeltidium" is not a tergite but a sclerotization of the pleural membrane and cannot be assigned to a certain segment. However, different from the pattern described here for Schizomida, Palpigradi have the dorsal suspensors of segments 3—5 associated with the propeltidium and dorsal suspensors 6 with the metapeltidium (schematic in Fig. 1C). Thus, their propeltidium is the common shield of segments 0—5 and the metapeltidium the tergite of segment 6. This different pattern of muscle insertions evidences an independent evolutionary origin of the tripartite dorsum in Palpigradi and Schizomida. An independent origin of the tripartite dorsum is in line with the idea that Schizomida are the dwarfed sister group to Thelyphonidai (i.e., derived from ancestors with a complete, undivided dorsal shield) and morphologically adapted to a highly structured environment in leaf litter (Weygoldt and Paulus, 1979), while Palpigradi are probably miniaturized sister to Acaromorpha with no relationship to tetrapulmonate arachnids (Franz-Guess and Starck, 2020).

Solifugae also have a tripartite dorsum of the prosoma, but, they do not have an endosternite (Firstman, 1973) and, compared to Palpigradi and Schizomida, their entire internal muscle anatomy is derived, with the ancestral suspensor muscle system reduced and locomotor muscles inserting to extensive apodemes (Bitsch and Bitsch, 2002; Runge and Wirkner, 2020). The different morphology of the suspensor muscle system in the three taxa with tripartite dorsum suggests that the tripartite prosoma of Schizomida, Palpigradi, and Solifugae, is neither a shared character nor an evolutionary residual of the ancestral arthropod head, but a derived condition that evolved independently in all three taxa. The topology of modern phylogenies of arachnids (e.g., Giribet, 2018; Ballesteros et al., 2022; Ballesteros and Sharma, 2019; Ballesteros et al., 2019; Sharma et al., 2021; Garwood and Dunlop, 2023) supports the conclusion that the tripartite dorsum evolved independently in those three groups, and, with reference to Schizomida, that the common ancestor of Schizomida and Thelyphonida possessed a single large dorsal shield.

In Opiliones, pro- (prodorsum), meso-, and metapeltidium have been assigned to prosoma segments 0—4, five, and six, respectively (Hansen and Sørensen, 1904; Winkler, 1957; van der Hammen, 1985; Shultz, 2000). Best support for such segmental assignments comes from developmental studies by Winkler (1957). Despite the apparent reduction of the axial suspensor muscle system of Opiliones and despite the remaining muscles are derived, the

(putative) identification of suspensor muscles of segments 3, 6 and 7 (Shultz, 2000) supports the interpretation that dorsal sclerites of the prosoma of Opiliones covers segments 0—4, 5, and 6. However, considerable but largely unexplored variability of the prosoma dorsum in Opiliones (i.e., not all Opiliones possess distinct pro-, meso-, and metapeltidium) suggests that the morphological differentiation of the dorsum represents evolutionary diversification within this taxon. If the interpretation of segment assignment is correct, Opiliones would represent, so far, the only group in which the mesopeltidium is a tergite of segment five — another case of independent evolution, here representing a prediction as derived from a topography as outlined in Fig. 1B.

4.2. Comparison with Thelyphonida

Thelyphonidaas the putative sister taxon to Schizomida have a complete dorsal shield of the prosoma. Compared to Schizomida, their endosternite and their segmental axial musculature of the prosoma show a mixture of similarities and differences. Like in schizomids, four sets of suspensor muscles originate from the endosternite, each set being associated with a segment of a pair of walking legs. A striking similarity of *Stenochrus* and *Surazomus* on the one side, and *Minbosius* and *Mastigoproctus* on the other side, is an anterior lateral muscle (segment #3) that originates from the posterior edge of the pedipalpal apodeme, which is close to the anterior end of the endosternite. Shultz (1993) described that topography for *Mastigoproctus giganteus* and suggested that the muscle is an endosternocoxal muscle (#33) that shifted origin from the endosternite to the pedipalpal apodeme. — The following lateral suspensor muscles are well developed in *Minbosius*, while the lateral suspensor ls5 is missing in schizomids (consistent with Firstman, 1973). Like in Schizomida, there are no posterior oblique muscles. However, by origin (endosternite) and insertion (tergite of the next following segment) the endosterno-tergal muscle might be interpreted as a residual of the posterior oblique muscles of segment six (an interpretation that has not been proposed by Shultz, 1993). It should be noted that Shultz (1993) did not describe lateral suspensor muscles but reported "dorsolateral endosternal suspensor muscles" (#14) and endosternocoxal muscles (#25), which are here considered equivalent to "lateral suspensor muscles" (Table 2).

Many details provided by Shultz (1993) for the topographic morphology of the axial segmental muscles in the prosoma of *Mastigoproctus giganteus* are consistent with the description given here for *Minbosius manilanus*. However, Shultz (1993) reported six dorsal (muscle #13 in his description) and ventral suspensor muscles (muscle #15), because he included the dorsoventral muscle of the first opisthosoma segment and anterior muscles as ventral suspensor muscles of the cheliceral and pedipalpal segments, that, in his interpretation, shifted origin. Thus, technically, his description of *Mastigoproctus* and the description of *Manilanus* provided here differ in the numbers of dorsal and ventral suspensor muscles and existence of lateral suspensor muscles (see Table 2 for a comparison). Minor differences in topographic anatomy may be due to species specific differences or be based on different resolution of methods, i.e., macroscopic dissection vs. μCT-imaging.

4.3. Prosoma ventrum

The ventrum of Schizomida carries 3 sclerites, that have traditionally been recognized as tritotetra-sternum, pentasternum and metasternum (Börner, 1902, 1904; Kästner, 1932). The large anterior sternum, between first and second pairs of walking legs is associated with the anterior pairs of ventral suspensor muscles. The analysis of the segmental muscles supports a segment assignment

of the anterior ventral sclerite to segments three and four, i.e., a tritotetrasternum. − The third pair of ventral suspensor muscles attaches to the coxae of the third pair of walking legs, but not to the ventral sclerite. Therefore, the interpretation of the minute pentasternum between the coxae of this pair of walking legs as a sternite of segment five (Börner, 1902, 1904; Kästner, 1932) can neither be supported nor rejected.

In a broader comparison, the ventrum of Schizomida, Thelyphonidaand Amblypygi appears to be organized in a similar manner. In all three taxa, the large anterior sclerite is the common sternum of the third and fourth segment. The following sclerite between the coxae of the third walking legs cannot be assigned to a segment except on accepts topographic position as indicator of its origin from sternite five (missing in Amblypygi). The sclerite between the fourth pair of walking legs is the sternite of the first opisthosoma segment that has shifted anterior. An anterior shift of the first opisthosoma sternite between the coxae of the fourth pair of walking legs is supported by origin and insertion of the first dorso-ventral muscle and intersegmental muscles of the opisthosoma. This is consistent with Shultz (1993) but in contrast to Börner (1902) and Kästner (1932, based on Börner) and later authors, who described a shift of the dorso-ventral muscle attachment from the second opisthosoma segment into the first and considered the metasternum the sternite of segment six.

4.4. Transition prosoma - opisthosoma

As discussed above, the transition between prosoma and opisthosoma is formed by integrating the first opisthosoma segment into the rear part of the prosoma. The muscle topography as described here for *Stenochrus portoricensis* and *Surazomus* sp. is similar to that found in *Minbosius manilanus* and *Mastigoproctus giganteus* (Shultz, 1993). Compared to schizomids, the two Thelyphonida, however, have a more intensive integration of the first opisthosoma segment into the last prosoma segment, as the prosomal endosternite extends into the first opisthosoma segment and the dorso-ventral muscle of that segment attach to the endosternite (Figs. 10D and 11E1). Based on the assumption that the dorsal and ventral suspensor muscles of the prosoma are (serial) homologues of the dorsoventral muscles of the opisthosoma (Shultz, 1993, 2007), the first dorso-ventral opisthosoma muscle has assimilated a prosoma-muscle phenotype.

In a broader comparison, Amblypygi, as sister to Uropygi (Thelyphonida + Schizomida) have been reported to have a similar morphological configuration of the prosoma−opisthosoma transition with the endosternite reaching into the opisthosoma as reported here for Thelyphonida (Shultz, 1999). The integration of the first opisthosoma segment into the prosoma of Schizomida and Thelyphonida has remarkable similarities with that described for Scorpions that also possess a large sternum behind the coxae of the last pair of walking legs (e.g., Shultz, 2007; Haug et al., 2019) but an even more advanced and more complex morphological integration of the first opisthosoma segment into the prosoma (Shultz, 2007). As convincingly reasoned by Shultz (2007), the sternum (and the internal musculature of the diaphragm) of scorpions evolved by the pregenital compression of the last prosoma segment and anterior movement of the first opisthosoma segment. This anterior movement the first opisthosoma segment was probably related to duplication events of hox-genes (Sharma et al., 2014a) causing a far-reaching assimilation of prosoma segment phenotype. Although this paper does not aim at a phylogenetic analysis of the morphological elements discussed here, the high similarity of the prosoma−opisthosoma transition lines up with a growing body of morphological evidence supporting the Arachnopulmonata-hypothesis (e.g., Scholtz and Kamenz, 2006; Regier et al., 2010;

Sharma et al., 2014b; Klußmann-Fricke and Wirkner, 2016; Giribet, 2018; Lehmann and Melzer, 2019; Ballesteros and Sharma, 2019; Ballesteros et al., 2019; Sharma et al., 2021).

4.5. Mesosoma and metasoma

Of the 12-segmented opisthosoma in schizomids and Thelyphonida, nine segments constitute the mesosoma and 3 segments (X-XII) the metasoma. Also, the formation of the dorsal and ventral pygidial muscles as derived from the intersegmental muscles is the same in both taxa. In both taxa, the terminal segment of the metasoma carries the anus and the openings of the opisthosomal glands. Although morphologically simple, this regionalization is identical in Schizomids and Thelyphonida, supporting their sister group relationship as Uropygida.

Other taxa with a mesosoma − metasoma distinction are Scorpions, Palpigradi and Ricinulei. In scorpions and Palpigradi, the metasoma consists of the four terminal segments IX- XII. In Ricinulei, it is formed by opisthosoma segments VIII-X. As already discussed by Franz-Guess and Starck (2020) all comparative morphological evidence as well as the phylogenetic positions of the taxa suggests that the metasoma evolved independently in Thelyphonida, Scorpionida, Palpigradi and Ricinulei.

4.6. Note on the endosternite

The idea that the chelicerate endosternite were derived from the tendons and muscles was published early (Lankester, 1884; Lankester et al., 1885; Simkewitsch, 1894; Pocock, 1902; Börner, 1902, 1904; reviewed in: Kästner, 1932; Bitsch and Bitsch, 2002). Shultz (2007) elaborated on this consensus and postulated a direct homology of the prosoma endosternite with ventral longitudinal suspensor muscles. He considered the endosternite a "tendonized" residue of the ventral longitudinal connectives spanning postoral segments 1−7. The histological gradient of the endosternite spanning between tissue structure of muscle − tendon − chondroid supports this idea. Also, the topography of the anterior endosterno-cheliceral muscles may be interpreted as residue of the ancestral longitudinal system. On its posterior end, the endosternite of Thelyphonida, Amblypygi, and Scorpiones, but not Schizomida, reaches into the seventh postoral segment (first opisthosomal segment). If one considers this extension of the endosternite into the first opisthosoma segment a feature of the arachnid ground pattern (Shultz, 2001), or rather a derived condition depends on the phylogeny used. However, since the extension into the opisthosoma is only known from those three taxa, it may rather be considered apomorphic related to the assimilation of the first opisthosoma segment into the prosoma (Sharma et al., 2014a) and supporting the Arachnopulmonata hypothesis. The prosoma−opisthosoma transition of Schizomida may then be considered as secondarily reduced from the condition seen in Thelyphonida.

4.7. Limitations

Critique that the arachnid ground pattern of the BTAMS is virtual and invokes an overly simplified archetypical pattern of the anterior segments of arthropods, as well as objections against the assumption of a strict homonomous post-oral organization (e.g., Richter et al., 2013) may be justified. Indeed, the complete BTAMS has never been described for any extant chelicerate taxon. However, the occurrence of segmental axial suspensor muscles, their origin from the endosternite and insertion to the tergite (dorsal) and coxae of the walking legs (ventral) is a common pattern in all euchelicerates and the BTAMS can be considered a reconstructed

ground pattern, that has been modified in the various lines of evolutionary diversification of euchelicerates, so that all extant taxa diverge more or less from the ground pattern. Therefore, I think the BTAMS functions well as a working hypothesis.

5. Conclusions

The tripartite dorsal shield of schizomids is derived from a single dorsal shield of the giant relatives, the Thelyphonida, and is supposedly related to increased maneuverability of the miniaturized forms in a highly structured habitat. The mesopeltidium is a dorsolateral sclerotization of the pleural membrane and not a tergite. Based on the analysis of segmental indicator muscles, the propeltidium is assigned to segments 0–4 and the metapeltidium to segments 5 and 6. When compared to Palpigradi or Solifugae, the different segment assignment and the well supported sister–group relationship to Thelyphonida are interpreted as evidences for an independent evolutionary origin of the tripartite dorsum of the prosoma.

The transition between prosoma and opisthosoma integrates the first opisthosoma segment into the prosoma. The sternite of the first opisthosoma segment forms the metasternum between the coxae of the fourth pair of walking legs. The integration of opisthosoma segment one into the prosoma is relatively simple (secondarily simplified) in schizomids and more complex in Thelyphonida, where the dorso-ventral musculature of the first opisthosoma segment attaches to the endosternite and assimilates a prosomal morphology of dorsal and ventral suspensor muscles.

The metasoma of Schizomida and Thelyphonidahas an identical morphology. However, it differs in number and position from metasomata in other arachnid taxa, documenting an independent evolutionary origin.

The morphological analyses presented here provide evidence for multiple evolutionary pathways in chelicerates resulting in convergent morphologies, that have conventionally been considered shared similarities. The study highlights the importance of microscopic anatomy to understand the evolutionary history of similarity of organisms. This is in particular important as molecular phylogenetic studies have challenged morphological phylogenetic hypotheses and questioned characters that had been considered autapomorphic for certain groups of chelicerates. This study contributes to the understanding that macroscopic similarity of chelicerates is rooted in considerable diversity of microscopic anatomy. It supports the idea that morphological similarity of chelicerates emerged from independent evolutionary pathways resulting in convergent phenotypes. This article also documents that microscopic anatomy has a remarkable explanatory power in evolutionary morphology. It contributes not only unpreceded morphological detail in chelicerate morphology but also uncovers plenty evidence for multiple evolutionary origins of similar morphologies and convergent evolution in arachnids.

The morphological analyses presented here provide evidence for multiple evolutionary pathways in chelicerates resulting in convergent morphologies, that have conventionally been considered shared similarities.

This study contributes to the understanding that macroscopic similarity of chelicerates is rooted in considerable diversity of microscopic anatomy. It supports the idea that morphological similarity of chelicerates emerged from independent evolutionary pathways resulting in convergent phenotypes.

CRediT authorship contribution statement

J. Matthias Starck: Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

I have no conflicts of interest to disclose.

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