Comparative microscopic anatomy of Schizomida − 2. The rostrosoma and the pharyngeal suction pump

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ABSTRACT

This paper tests hypotheses of independent parallel evolution of the rostrosoma among euchelicerate taxa by analyzing the microscopic anatomy and histology of the rostrosoma of Uropygi (Schizomida and Thelyphonida) and comparing it with the morphology of the snout region in other euchelicerates. The study employs analysis of multiple histological serial sections, μCT-imaging, and graphical as well as computer-based 3D reconstruction. Results of the study are that Thelyphonida and Schizomida share the same morphology of the rostrosoma. The rostrosoma of both groups contains a unique arrangement of musculature that is functionally interpreted as pre-oral suction pump. This is followed by a pharyngeal suction pump. The muscles of the pharyngeal suction pump attach to the epistome and the epipharyngeal sclerite. Neither Schizomida nor Thelyphonida possess a postcerebral suction pump as reported earlier. The microscopic anatomy of the rostrosoma of both taxa is unique and does not compare with any of the other euchelicerates, thus supporting the idea of independent evolutionary origin of the rostrosoma. Thelyphonida, Amblypygi and Scorpiones share the occurrence of a large epipharyngeal/epistomal sclerite with associated musculature, which is a feature that lines up with the Arachnopulmonata concept. A comparison with all Euchelicerata taxa shows that the snout region is formed by homologous morphological elements but the specific arrangement, additions and reductions shape the formation of the rostrosoma, so that parallel evolution of homologous parts of the arachnid ground pattern can be assumed that has formed those elements into convergent morphologies.

1. Introduction

Numerous arachnid taxa, e.g., Palpigradi, Solifugae, Acari, Thelyphonida, Schizomida, and Pseudoscorpiones, are characterized by a distinct rostrosoma, a snout-like anterior body region that is designed for the uptake of liquid, extra-intestinally digested prey. The rostrosoma is functionally linked to a pharyngeal suction pump, that creates the necessary negative pressure for food intake. The existence of a rostrosoma has been considered indicative of phylogenetic relationship (e.g., Bernard, 1896; van der Hammen, 1989; Dunlop, 2000) or, as resulting from multiple independent evolutionary events transforming the preoral structures into a channel through which the liquid food of euchelicerates is sucked into the mouth (e.g., Pocock, 1902; Snodgrass, 1948). Indeed, microscopic anatomical details of the appendicular and skeletal elements, the musculature, and the associated pharyngeal suction pump provide evidence for independent and parallel evolution of homologous parts resulting in the convergent formation of a rostrosoma (e.g., Palpigradi, Solifugae, Pseudoscorpiones, and Parasitiformes; Franz-Guess and Starck, 2020; Starck et al., 2022). This paper sets out to study the rostrosoma in Schizomida and Thelyphonida and compare it to the morphology of other chelicerate taxa.

The skeletal morphology of the rostrosoma of Uropygi (Schizomida and Thelyphonida) was, historically, described by Bernard (1896; pl 28, Figs. 11−14), Börner (1902, 1904), Kästner (1932) and Snodgrass (1948). Shultz (1993) gave a detailed account of the pharyngeal apparatus of *Mastigoproctus giganteus*. However, much of this information is based on manual dissection, and Schizomida have not been studied in sufficient detail. The aim of this study is, therefore, to document the microscopic anatomy of the feeding apparatus of two representative species of Schizomida, and compare it with Thelyphonida and other euchelicerates. The study is based on a detailed microscopic anatomical analysis of the

topographic configuration of skeletal elements (e.g., epistome, labrum, chelicerae, pedipalpal coxae, epipharyngeal sclerite), and pharyngeal muscles (e.g., dorsal and lateral pharyngeal dilator muscles). Complications are expected because simple homology of elements may not be informative if parallel evolution of homologous parts of the arachnid ground pattern has shaped those elements into convergent morphologies. Indeed, previous research documented morphological features evidencing independent evolutionary origin of the rostrosoma in various arachnid taxa (Starck et al., 2022). Also, the branching topology of recent molecular phylogeny (Ballesteros and Sharma, 2019; Ballesteros et al., 2019; Sharma et al., 2021; Ballesteros et al., 2022) requires the assumption of parallel and independent evolutionary origin of morphologically convergent structures in numerous arachnid taxa. In this framework of new phylogenetic hypotheses, rigorous tests of morphological similarity teasing apart the intricate similarities of morphological elements, are required to better understand the evolutionary morphology of similar phenotypes.

Always associated with the morphology of the rostrosoma is the formation of a suction pump. Because *Limulus* has traditionally been considered a basal branch of euchelicerates, its morphology comprising a pre- and a postcerebral muscular foregut, has been described as basal (e.g., Lankester et al., 1885; Shultz, 2001; Spotswood and Smith, 2007; Newman and Smith, 2021). Since recent phylogenies challenge the basal phylogenetic position of *Limulus* and place it among Arachnida (Ballesteros and Sharma, 2019; Ballesteros et al., 2019, 2022; Sharma et al., 2021; Sharma, 2023), it has also lost relevance as ancestral morphological reference point. Whatever its phylogenetic position is, *Limulus* is special, because of its morphology and feeding biology.

This paper is dedicated to the comparative and functional morphological analysis of the rostrosoma and the pharyngeal suction pump of two species of Schizomida and compares it to one representative species of Thelyphonida. Starting with the analysis of Thelyphonida, the study will proceed with a broader comparison of the rostrosoma, the formation of a preoral cavity and the modification of the pharyngeal suction pump of other arachnids and explores the idea that those elements evolved independently and multiple times. The study of serial histological sections through the rostrosoma of Schizomida allows to differentiate soft and sclerotized parts of the mouth parts, which offer new insights into the functional morphology of feeding. However, Thelyphonida are large, heavily sclerotized animals, that are almost impossible to section using histological methods. Therefore, I use series of μCT-images (with the known limitations in spatial resolution and tissue differentiation based on X-ray contrast) for documentation and comparison with Schizomida. Comparisons of those two taxa of Thelyphonida with other arachnids and the evolutionary interpretation of the morphology will be based on published data.

2. Materials and methods

Materials and methods are the same as those described in the Starck, 2024. Key elements are given here, for details I refer to the companion paper.

2.1. Material

Stenochrus portoricensis Chamberlin, 1922 (N = 15 histological series; Table 1 in Starck submitted). 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 in Starck submitted). 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 (Table 1 in Starck submitted). Micro-CT image stacks are deposited at (Morphosource; temporary access link: https://www.morphosource. org/projects/000561228/temporary_link/ ELHyNiFPeBMSR8ojDFk41Xm9?locale=en); samples remained in Vienna.

2.2. Histological methods

Specimens were washed in phosphate buffered saline (0.1 mol l^{-1}), postfixed in 1 % osmium tetroxide for 2 h and washed again to remove excess osmium tetroxide. Samples were dehydrated through graded series of acetone and then embedded in Glycidether 100 (Carl Roth GmbH + Co. KG, Karlsruhe, Germany). Series of histological semithin sections were cut at 1 μm thickness using an RMC MTXL ultra-microtome (Boeckeler Instruments, Inc., Tucson, Arizona, USA) equipped with a histo-Jumbo diamond knife (DiATOME Ltd, Biel, Switzerland). The sections were collected in water, attached to a glass slide, dried and 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 *M. 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 × 675 px.

Specimens of *S. 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-

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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
Glossary of anatomical terms.

	Term	description
Functional terms	Food canal	=> functional not a morphological term
	rostrosoma	snout-like anterior body region that is designed for the uptake of liquid => functional not a morphological term
	preoral channel	channel-like structure formed by preoral structures => functional not a morphological term
	Precerebral suction pump	= pharyngeal suction pump, muscle arrangement dilating the pharynx
	Postcerebral suction pump	Postesophageal and postcerebral, muscle arrangement around the anterior midgut

	Term	abbreviation	anatomical description		synonym	reference
Sclerites	rostrum	r	formed by epistome and labrum		epistomolabral plate, labrum-epistome	Dunlop (2000) Snodgrass (1948) Shultz (1993)
	epistome	eps	intensively sclerotized part of the frons (diagnostic feature attachment for dpda)			
	labrum		anterior part of the frons, forming the anterior part of the rostrum			
	coxoepistomal apodeme		large apodeme formed by fused parts of the epistome and the pedipalpal coxae		epistomal apodeme	Snodgrass (1948)
	intercheliceral septum					
	epipharyngeal sclerite	ephs	sclerotized extension of the intercheliceral septum		entosclerite epistomal complex epistomal apodeme	Lankester et al., 1885 Shultz (2007) [a] Snodgrass (1948)

	Muscle	abbreviation	origin	insertion	synonym	reference
muscles	anterior transversal muscle	atrm	horizontally between left and right side of the labrum		anterior transverse labral muscle (#1)	Shultz (1993), Fig. 3B
	anterior dorsoventral muscle	advm	anterior edge of the epistome	ventral side of the rostrum close to the apex	anterior dorsoventral labral muscle (#3)	Shultz (1993), Fig. 3B
	posterior transversal muscle	ptrm	horizontally between left and right shank of the epistome		posterior transverse labral muscle (#2)	Shultz (1993), Fig. 3B
	dorsal pharyngeal dilator muscle pars anterior	dpda	epistome	sclerotized roof of the pharynx	posterior dorsoventral labral muscle (#4)	Shultz (1993), Fig. 3B
	dorsal pharyngeal dilator muscle pars posterior	dpdp	ventral edge of epipharyngeal sclerite	posterior part of pharynx	muscle #98 dorsal extrinsic pharyngeal dilator muscle (#7)	Lankester et al. (1885) Shultz (1993), Fig. 3B
	lateral pharyngeal dilator muscles	ldm	coxoepistomal apodeme	lateral wall of pharynx	anterior/posterior extrinsic pharyngeal muscle (#5, 6)	Shultz (1993), Fig. 3B
	epipharyngeal muscles pars anterior	aepm	epipharyngeal sclerite	anterior propeltidium	muscle #62 anterior epipharyngeal muscle (#8)	Lankester et al. (1885) Shultz (1993), Fig. 3B
	epipharyngeal muscles pars posterior	pepm	epipharyngeal sclerite	propeltidium posterior region	posterior epipharyngeal muscle (#9)	Shultz (1993), Fig. 3B

[a] Shultz (2007) described internal skeletal structures of scorpions as "epistomal complex". Here, those structures are considered to be part of the epipharyngeal sclerite, i.e., an apodemal sclerotization of the intercheliceral septum (see text). Diagnostic feature of the epistome is the attachment of the dorsal pharyngeal depressor muscle pars anterior; the epipharyngeal sclerite is diagnosed by the posterior portion of that muscle (and the epipharyngeal muscle, where present). In scorpions, there is one muscle extending between a structure described as "entosclerite" by Lankester et al. (1885; Pl. 79, Fig. 12) and as "epistomal complex" by Shultz (2007) and the pharynx. I consider this muscle the dorsal pharyngeal dilator muscle pars posterior. Dorsal, in about that position, a muscle extends between the "entosclerite" and the dorsal shield, which I consider the epipharyngeal muscle. These assignments are base exclusively on topographic relationship and it will require developmental studies teasing apart the homologies, because the epistome and the intercheliceral septum are continuous as part of the frontal skeletal morphology.

imaging. For micro-computed tomography, an XRadia MicroXCT-200 x-ray microscope (Carl Zeiss Microscopy GmbH, Jena, Germany) equipped with scintillator-objective lens unit was used. The scan was performed with a 4 x 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 Zeiss Microscopy 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

3D-reconstructions from μCt-image stacks were prepared using the volume rendering function in 3D-slicer 5.0.3 (https://www.slicer.org/; Fedorov et al., 2012).

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. 9 are based on analysis of histological serial sections of intact specimens or μCT image stacks. Thus, the topography, the origin and insertion of muscles are documented as precisely as possible.

2.7. Terminology

I use a terminology of sclerites and muscles that is based on Shultz (1993) for Thelyphonida, the closest related taxon. The term "rostrosoma" as used here, is a topographic description of the anterior body region functionally related to food uptake. The term "rostrum" describes structure formed by the epistome and the labrum, that covers the mouth opening dorsally; the rostrum is part of the rostrosoma. — I use the term epipharyngeal sclerite (Shultz, 1993) for consistency with the literature, but it is synonymous with other existing terms, e.g., "interchelical septum" (Franz-Guess and Starck, 2020; Starck et al., 2022) or "epistomal apodeme" (Snodgrass, 1948). A comprehensive list of anatomical terms used here and synonyms found in published resources is provided in Table 1.

2.8. Data accessibility

All histological serial sections have been deposited at the Zoological State Collection, Munich (*Arthropoda varia*). µCT-image stacks are publicly available at Morphosource.com (for details see Table 1 in Starck, submitted).

3. Results

3.1. Rostrosoma of Schizomida

S. portoricensis and *Surazomus* sp. have been studied. No differences were found in their microsocpic anatomy. Therefore, the description and documentation are exclusively on *S. portoricensis*. The rostrosoma consist of an elongate and partially sclerotized rostrum (dorsally covered by the epistomo-labral plate), the chelicerae, and the large, medially merged coxae of the pedipalps. Dorsal, the propeltidium forms an anteriad pointing roof that is overarching the basis of the chelicerae (Fig. 1A). Lateral, the propeltidium fuses with the pedipalpal coxae, thus forming a space that contains part of the rostrum, part of the chelicerae, and the mouth opening.

Pedipalps: The pedipalpal coxae are large, horizontally oriented structures that contribute with three features to the feeding apparatus: (1) they merge medially, forming a trough-like structure, i.e., the preoral channel. This preoral channel houses the rostrum. (2) They carry a pair of free anterior lips; and (3) the pedipalpal coxae form, together with internalized parts of the epistome, a large apodeme (coxoepistomal apodeme) as attachment point for intrinsic coxal musculature (Figs. 1—3) and the lateral suspensor muscle the third prosoma segment (Starck,

submitted). - The distal articles of the pedipalps are palp-like structures.

ad 1: The thickness of the cuticle lining the preoral channel and its degree of sclerotization change from the anterior tip of the pedipalpal coxae to their more proximal parts. At the anterior tip of the preoral channel, the cuticle is thin and little sclerotized. It is internally lined by glandular tissue (Fig. 3C and D). Glandular canals through the cuticle are not distinct, but the number of pore canals penetrating the cuticle covering the glandular tissue is higher than in lateral regions, where no glandular tissue is found (mf, Fig. 3D). Little further proximal, the glandular tissue regresses and the cuticle lining of the preoral channel is more sclerotized, now covered by short bristles. In that position, the glandular tissue is found only on the inner medio-ventral face of the pedipalpal coxae (Fig. 3E and F). The bristles disappear at the mouth opening (Fig. 4A), where the preoral channel grades into the pharynx.

ad 2: The free anterior lips of the pedipalpal coxae are short and stout elements. However, the topographic differentiation of the cuticle covering the anterior lips has some functional implications (see discussion). The medial face of the lips consists of soft, non-sclerotized cuticle (procuticle; Figs. 2C and 3A, B). The lateral faces of the anterior lips, however, are intensively sclerotized as evidenced by a thick, layered exocuticle. The lumen of the lips contains a hemolymph space and subepidermal glandular tissue. Numerous pore canals penetrate the cuticle on the lateral face. No muscles have been found attaching at that anterior position in the anterior lips (Figs. 2C, 3A,B).

ad 3: At the basis of the rostrosoma, the lateral wall of the pedipalpal coxae, the propeltidium and parts of the rostrum merge, so that the chelicerae are enclosed in a dorsal compartment with the rostrum as bottom (Fig. 3E). Below this cheliceral compartment, the preoral channel becomes a food canal containing the mouth opening and pharynx (Fig. 3E and F). At that position, the cuticle of the dorso-medial face of the pedipalpal coxae is folded into an apodeme, which merges with an internalized part of the epistome (coxoepistomal apodeme; Fig. 3E and F; *epistomal apodeme* Snodgrass, 1948). The coxoepistomal apodeme is attachment site for intensively developed, intrinsic musculature of the coxae and, at its most posterior position, of the lateral suspensor muscle of the third prosoma segment.

Rostrum: The rostrum is a prominent element of the rostrosoma. It is formed by an anterior sclerotized extension of the frons of the propeltidium (epistomo-labral plate). It has the shape of an apically pointed rod that extends in the preoral channel between dorsal chelicerae and the ventral, trough-shaped coxae of the pedipalps. The rostrum cannot be seen in external examination. The apex of the rostrum reaches to the anterior end of the trough-shaped
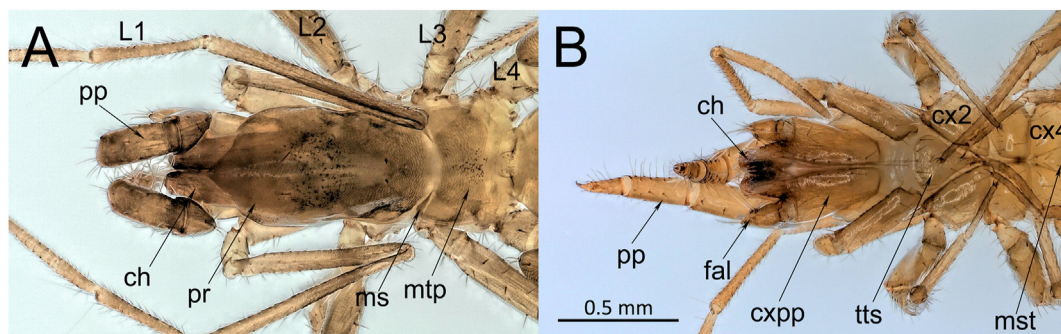
Fig. 1. *Stenochrus portoricensis*, microphotographs of the prosoma. **(A)** Dorsal view, documenting the tripartite dorsum. **(B)** Ventral view, documenting the coxae and sterna. **Abbreviations**: ch, chelicera; cxpp, coxa of pedipalp; cx2, cx4; coxae of walking legs two and four, respectively; fal, free anterior lips of pedipalpal coxae; L1-4, walking legs 1—4; ms, mesopeltidium; mst, metasternum; mtp, metapeltidium; pp, pedipalp; pr, propeltidium; tts, tritotetrasternum.

Fig. 2. *Stenochrus portoricensis*, serial horizontal longitudinal sections through the prosoma. The approximate position of the sections is given in the drawing on top of image. **(A)** Section on the level of the posterior endosternal bridge. **(B)** Mid-horizontal section; **(C)** section through the merged coxae of the pedipalps. **Abbreviations**: ch, chelicera; cx1, coxa of walking leg 1; cxpp, coxa of pedipalp;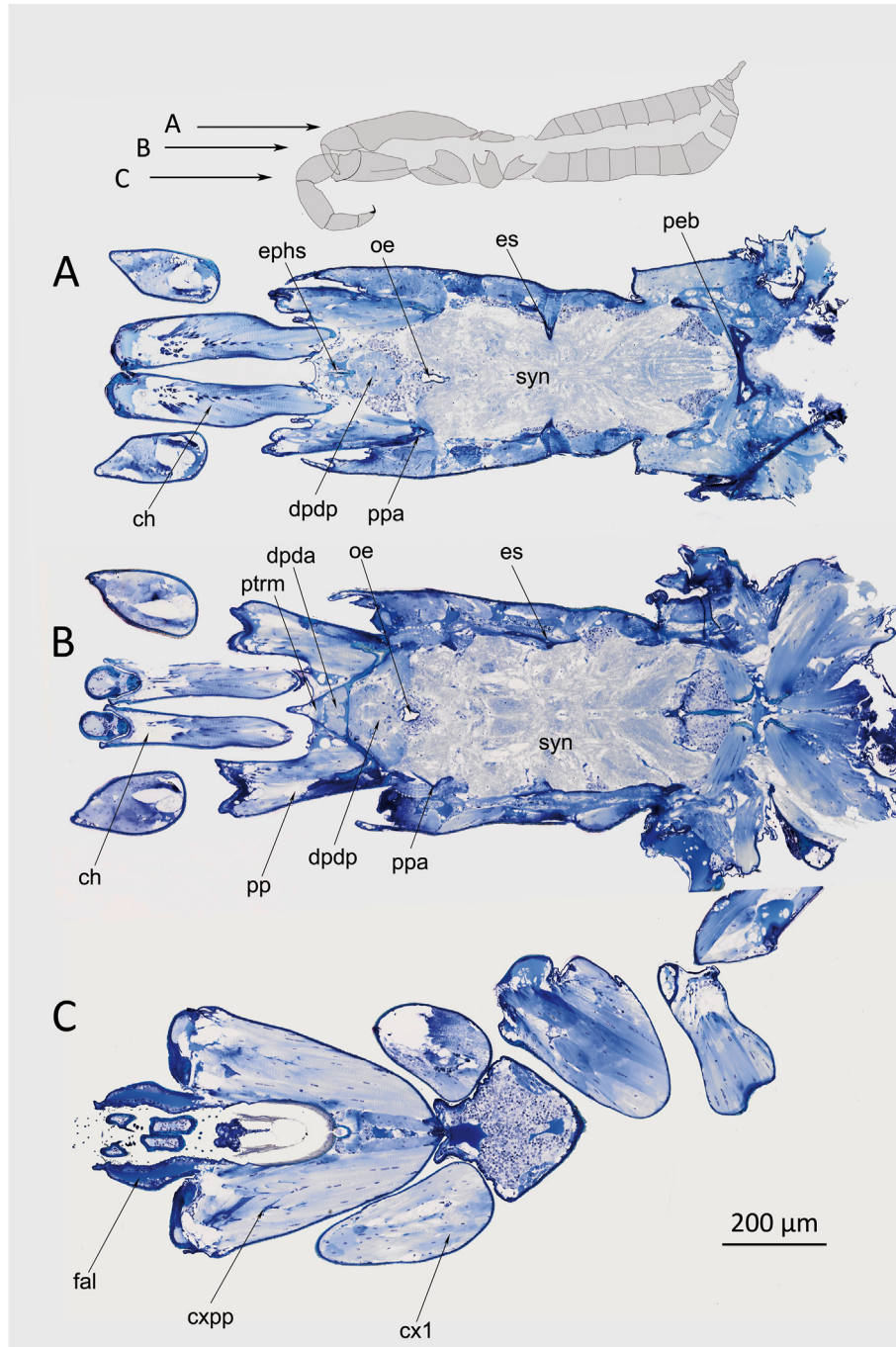 dpda, anterior dorsal dilator muscle; dpdp, posterior dorsal pharyngeal dilator muscle; ephs, epipharyngeal sclerite; es, endosternite; fal, free anterior lips of pedipalpal coxae; oe, oesophagus; peb, posterior endosternal bridge; pp, pedipalp; ppa, pedipalpal apodeme; ptrm, posterior transversal muscle of the rostrum; syn, synganglion.

channel, i.e., a position where the paired anterior lips emerge from the pedipalpal coxae. The apex of the rostrum is free (r, Fig. 3C and D). Rigid bristles form a filtering cage ventral to the tip of the rostrum.

Proximally, the dorsal cuticle of the rostrum is sclerotized as the epistome. Lateral, the epistome merges with the medial face of the pedipalps. The anterior part of the rostrum is the soft labrum. The ventral side of the labrum carries numerous bristles. They are arranged in a highly geometric order (Fig. 3D and E) forming a

filtering basket. The ventral side of the rostrum is soft and contributes to the formation of the preoral food canal, the mouth opening, and the roof of the pharynx.

The epistome, the coxoepistomal apodeme and the intercheliceral membrane form a continuous structure that extends internally as the epipharyngeal sclerite (ephs, Figs. 3F and 4A-E), i.e., sclerotized invagination of the intercheliceral septum (Shultz, 1993; syn. epistomal apodeme [Snodgrass, 1948]). The posterior edge of the epipharyngeal sclerite reaches far dorsal and deep into
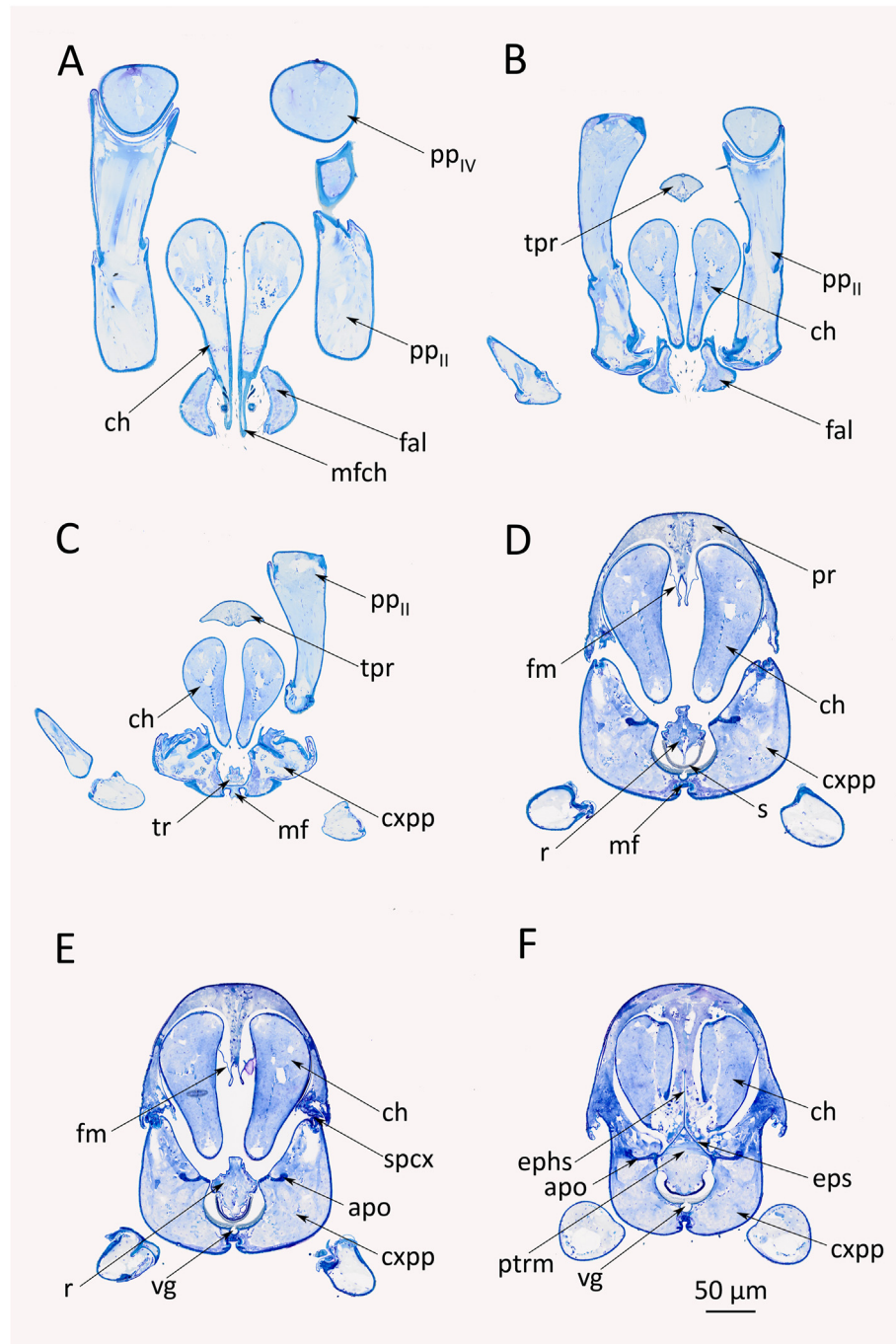
Fig. 3. *Stenochrus portoricensis*, serial cross-sections through the prosoma documenting the mouthparts and formation of the lower lip. **(A)** Section through free anterior lips of the pedipalpal coxae at the anterior part of the rostrosoma. **(B)** Section through the anterior part of the rostrosoma at the tip of the propeltidium and the free anterior lips of the pedipalpal coxae. **(C)** Section through the rostrosoma where the pedipalpal coxae merge and the soft tip of the rostrum is visible. **(D)** Section through the rostrosoma where the rostrum forms a bristle filtering basket. The medial side of the pedipalpal coxae form a distinct apodeme. **(E)** Section through the rostrosoma slightly basal to (D). Here the rostrum merges to the medial sides of the pedipalpal coxae. A strong pedipalpal apodeme is formed. The rostrosoma is divided into an upper floor for the chelicerae and a lower preoral food canal. **(F)** Oral regions transitioning between preoral canal and pharynx. Here, the posterior transversal muscle is sectioned. **Abbreviations:** apo, apodeme formed by basal article of the pedipalp; ch, chelicera; cxpp, coxa of pedipalp; ephs, epipharyngeal sclerite (= intercheliceral septum); eps, epistome; fal, free anterior lips of pedipalps; fm, frontal membrane; mf, merging fold of basal articles of pedipalps; mfch, movable finger of chelicera; spcx, seam between propeltidium and coxa of pedipalp; PP, pedipalp (roman numerals indicate articles); pr, propeltidium; ptrm, transversal muscle in rostrum; r, rostrum; s, setae (forming a basket beneath the rostrum); tpr, anterior tip of propeltidium; tr, tip of rostrum; vg, ventral groove.

the prosoma between the lobes of the syncerebrum (Fig. 4A–E, 8). The dorsal and anterior edge of the epipharyngeal sclerite is embedded in fibrous connective tissue, that histologically resembles the tendinous connection between muscles and the endosternite (Fig. 8A). It connects between the epipharyngeal sclerite, surrounding musculature and the inner face of the propeltidium.

Musculature of the rostrum: The apex of the rostrum contains the minute, anterior transversal muscle (atrm, Figs. 5A and B, 7B, 9); its fiber is only 2–3 sarcomeres thick. It extends horizontally through
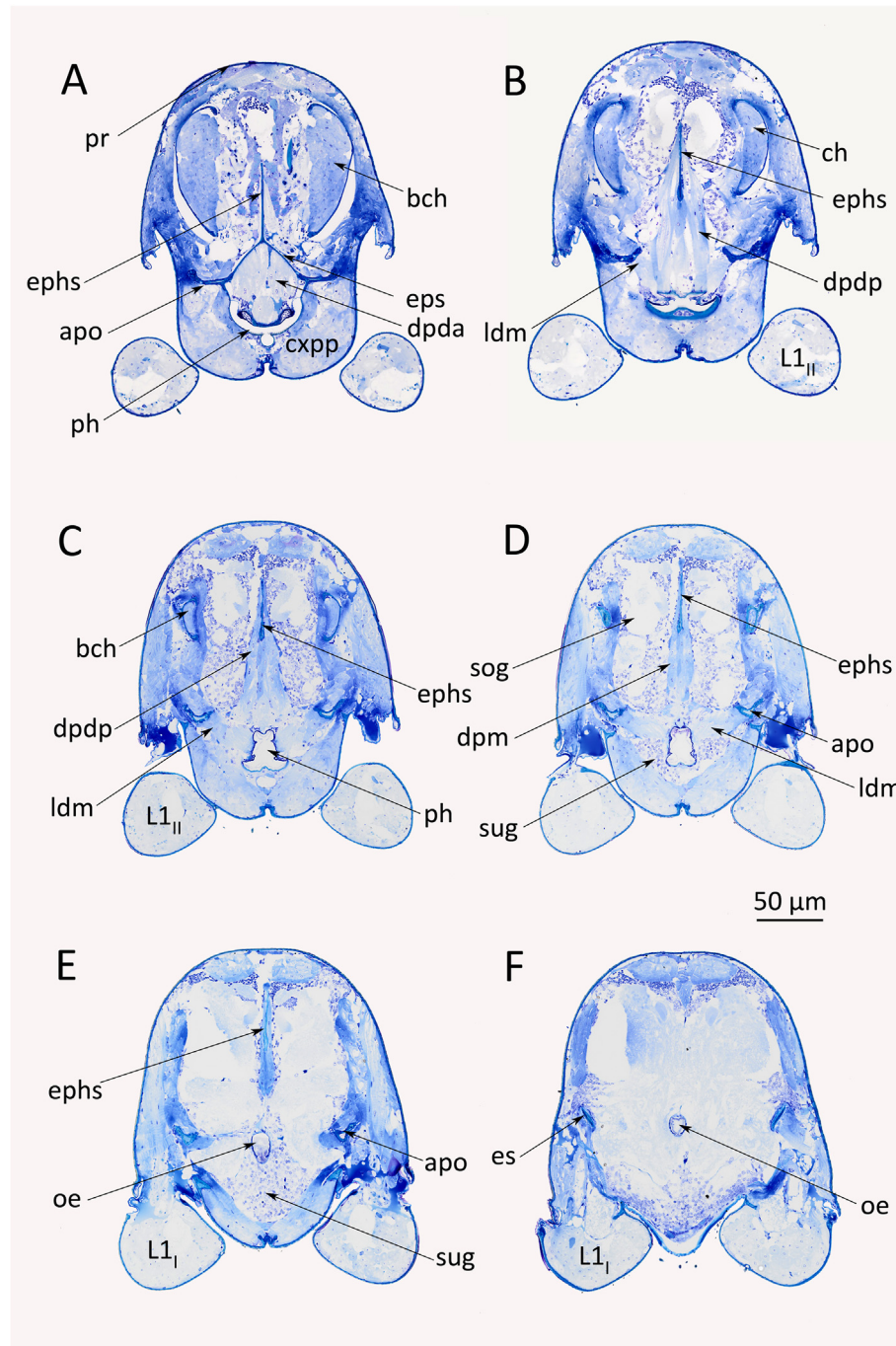
Fig. 4. *Stenochrus portoricensis*, serial cross-sections through the prosoma documenting the pharyngeal suction pump and the oesophagus. **(A)** Section through the epistome and the anterior portion of the dorsal pharyngeal dilator muscle. Note the sclerotized roof of the pharynx that supposedly is pulled dorsal by contractions of the dorsal pharyngeal dilator muscle. **(B)** Section through the posterior portion of the dorsal pharyngeal dilator muscles originating from the epipharyngeal sclerite and inserting to the sclerotized roof of the pharynx. Action like the anterior portion of the muscle. **(C)** Section through the lateral dilator muscles of the pharynx. **(D)** Section a little bit posterior to (C). **(E)** Section through the anterior part of the oesophagus. **(F)** Section through the middle region of the oesophagus. **Abbreviations:** apo, apodeme formed by coxa of the pedipalp; bch, basal article of chelicera; cxpp, coxa of pedipalp; dpda, anterior portion of the dorsal pharyngeal dilator muscle; dpdp, posterior portion of the dorsal pharyngeal dilator muscle; eps, epistome; ephs, epipharyngeal sclerite; es, endosternite; L1I, walking leg 1 first article (coxa); L1II, walking leg 1 s article (trochanter); ldm, lateral pharyngeal dilator muscle; ms, meso-peltidium; mtp, metapeltidium; oe, oesophagus; otI, opisthosoma tergite I; ph, pharynx; sog, supraoesophageal ganglion; sug, suboesophageal ganglion.

the tip of the rostrum and attaches to each side of the labrum. Dorsal and ventral to the anterior transversal muscle are small hemolymphatic spaces. The cuticle covering the tip of the rostrum (labrum) is thin and soft. Despite its minute size, the anterior transversal muscle of the rostrum has consistently been found in all individuals of both species. A little bit more proximal into the

rostrum follows the anterior dorsoventral muscle. Its fibers spans oblique between the anterior edge of the epistome and the soft, preoral part of the ventral side of the rostrum close to the apex (advm, Figs. 5C and D, 7B, 9). The anterior dorsoventral muscle is paired and surrounded by central and lateral hemolymphatic spaces.
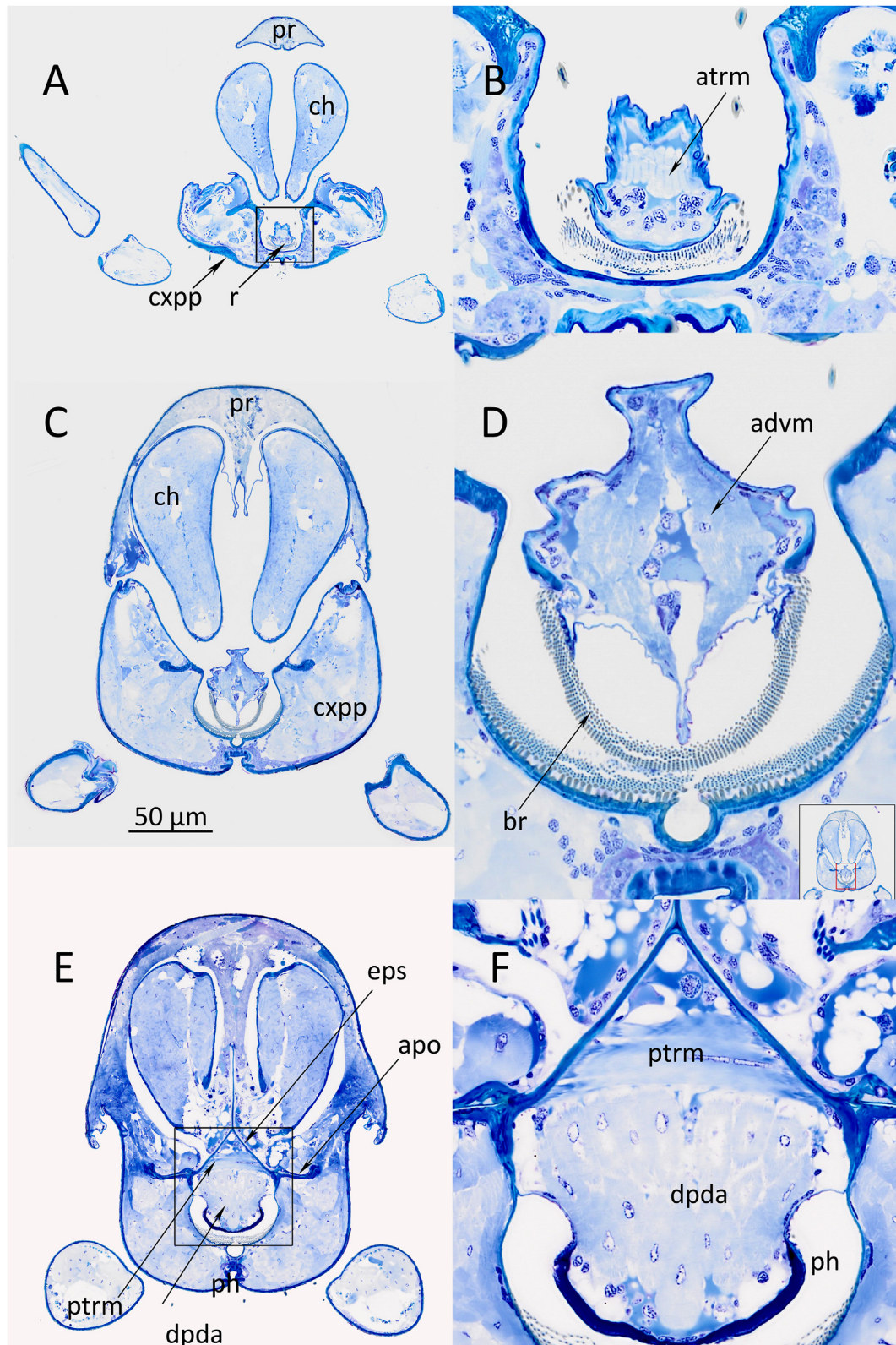
Fig. 5. *Stenochrus portoricensis*, muscles of the rostrum and the pharyngeal suction pump. **(A)** Cross-section through the rostrosoma where the coxae of the pedipalps are merging and through the tip of the rostrum. The frame indicates the area of interest shown in high-power magnification in (B). **(B)** High-power magnification of the anterior transversal muscle of the rostrum. The muscle is thin and, in this section, consists of only 4 sarcomeres. The cuticle of the tip of the rostrum is thin and soft. **(C)** Cross-section through the rostrum in the anterior region of the bristle basket and the anterior dorso-ventral muscle of the rostrum. Note that the muscle ventrally attaches to very thin cuticle, which is supposedly soft. Contractions of the muscle supposedly pull this cuticle up, thus creating negative pressure and suction into the bristle basket ventral to the rostrum. **(D)** High-power magnification of the rostrum and the anterior dorso-ventral muscle in (C). The exact position of the area of interest is shown in the inset in the lower right corner. **(E)** Section through the epistome and posterior transversal muscle of the rostrum. **(F)** High power magnification of the region framed in (E). **Abbreviations**: advm, anterior dorsoventral muscle of the rostrum; apo, apodeme of the pedipalpal coxae; atrm, anterior transversal muscle of the rostrum; br, basket of bristles; ch, cheliera; cxpp, coxa of pedipalpus; dpda, anterior portion of the dorsal pharyngeal dilator muscle; eps, epistome; pr, propeltidium, ptrm, posterior transversal muscle of the rostrum; r, rostrum.
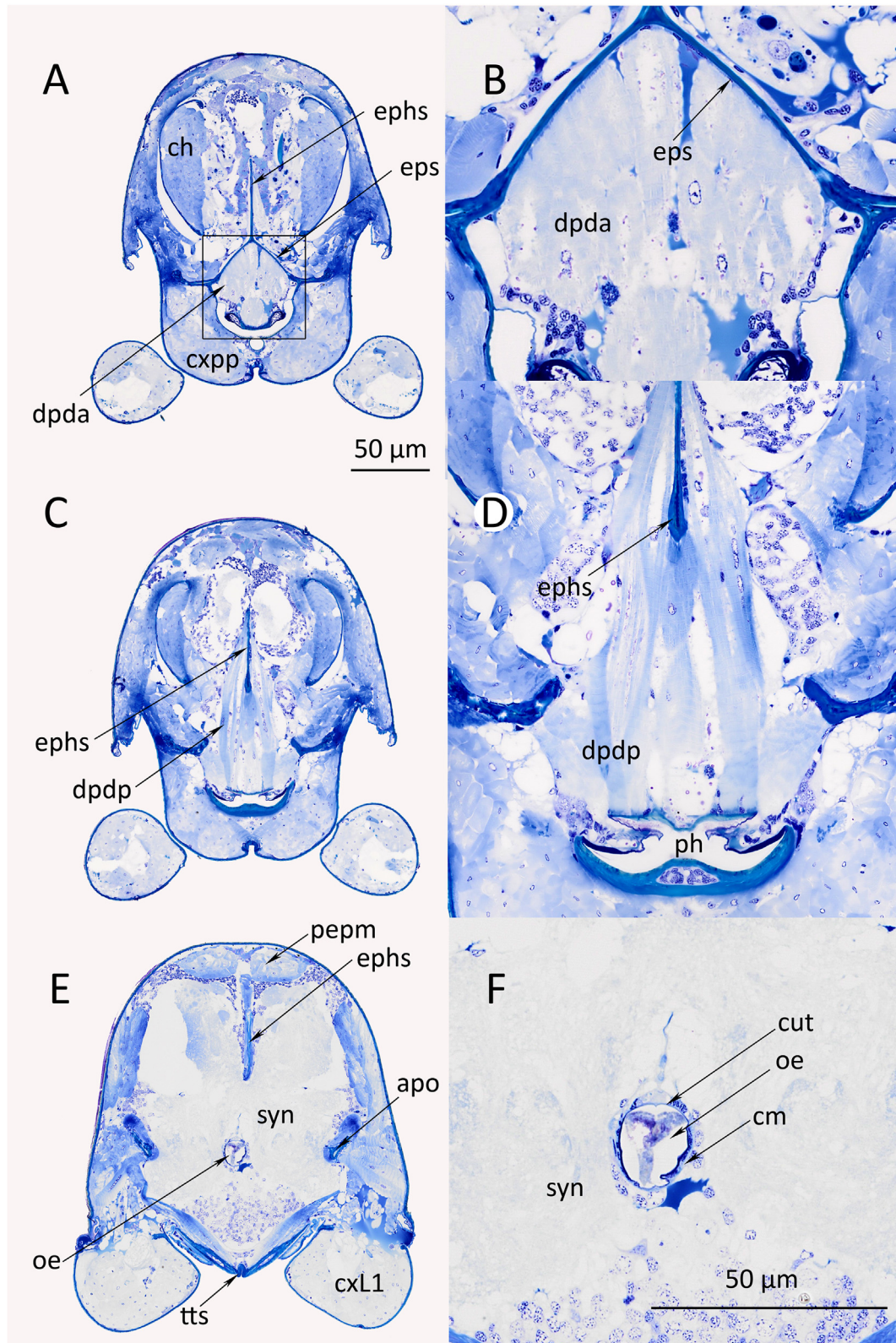
Fig. 6. *Stenochrus portoricensis*, muscles of the pharyngeal suction pump and the oesophagus. **(A)** Cross-section through the most anterior region of the pharynx at the level of the anterior portion of the dorsal pharyngeal dilator muscle. The frame indicates the area of interest shown in high-power magnification in (B). **(B)** Detail of the anterior dorsal pharyngeal dilator muscle as indicated in (A). Its attachment to the saddle-shape epistome is shown. **(C)** Cross-section through the pharyngeal region at the posterior portion of the dorsal pharyngeal dilator muscle. **(D)** High power magnification of the posterior portion of the dorsal pharyngeal dilator muscle, showing its origin from the epipharyngeal sclerite and insertion to the sclerotized roof of the pharynx. **(E)** Section through the syncerebrum with the oesophagus. The epipharyngeal sclerite is reaching deep into the syncerebrum. **(F)** High power magnification of the oesophagus, documenting the circular muscles surrounding the oesophagus in a thin layer. **Abbreviations**: apo, apodeme; ch, chelicera; cm, circular muscles around oesophagus; cut, cuticle lining the oesophagus internally; cxL1, coxa of first walking leg; cxpp, coxa of pedipalpus; dpda, anterior portion of the dorsal pharyngeal dilator muscle; dpdp, posterior portion of the dorsal pharyngeal dilator muscle; ephs, epipharyngeal sclerite; eps, epistome; oe, oesophagus; pepm, posterior epipharyngeal muscle; ph pharynx; syn, syncerebrum; tts, tritotetrasternum.
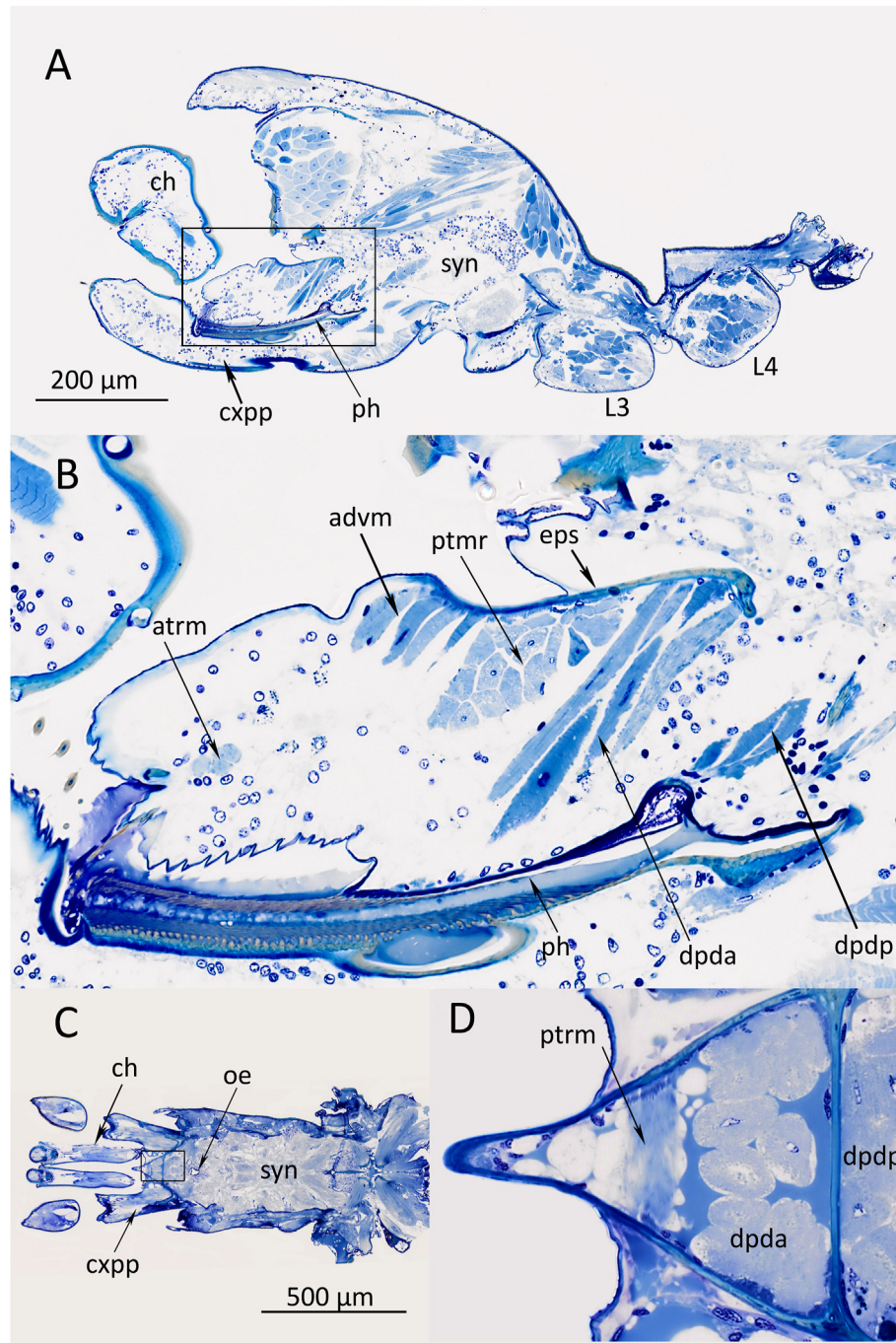
Fig. 7. *Stenochrus portoricensis*, parasagittal sections through the prosoma, documenting muscles of the rostrum and the pharyngeal suction pump (anterior is left). **(A)** Overview image of the prosoma. The frame indicates the area of interest shown in (B). **(B)** High power magnification of the rostrosoma showing sections through most of the muscles of the rostrum and the pharyngeal suction pump. **(C)** Horizontal section through the prosoma, overview. The frame indicates the area of interest shown in (D). **(D)** High power magnification of a horizontal section through the rostrum showing the posterior transversal muscle as well as the anterior and the posterior dorsal pharyngeal dilator muscles. **Abbreviations**: advm, anterior dorso-ventral muscle; atrm, anterior transversal muscle of the rostrum; ch, chelicera; cxpp, coxa of pedipalpus; dpda, anterior portion of the dorsal pharyngeal dilator muscle; dpdp, posterior portion of the dorsal pharyngeal dilator muscle; eps, epistome; L3, L4, coxae of third and fourth walking leg; oe, oesophagus; ph pharynx; ptrm, posterior transversal muscle of the rostrum; syn, synganglion.

More proximal on the rostrum, the epistome forms a saddleback roof-shaped sclerite and merges with the pedipalpal coxae on each side. Here, the posterior transversal muscle of the rostrum spans horizontally between left and right shank of the epistome (ptrm, Figs. 5E and F, 7B–D, 9). On cross-sections, a part of the anterior dorsal pharyngeal dilator muscle is also seen ventral to the posterior transversal muscle; it is attaching to the ventral face of the

rostrum (dpda, Fig. 5F). At that position the sclerotization of the cuticle surrounding the rostrum requires special attention. Dorsal, the cuticle is intensively sclerotized as the epistome, fixed to the pedipalpal coxae; lateral, the cuticle is thin. On its ventral face, the cuticle is thick and intensively sclerotized (Fig. 5F).

Mouth opening: The position of the mouth opening is difficult to determine because it apparently is a rather gradual transition from
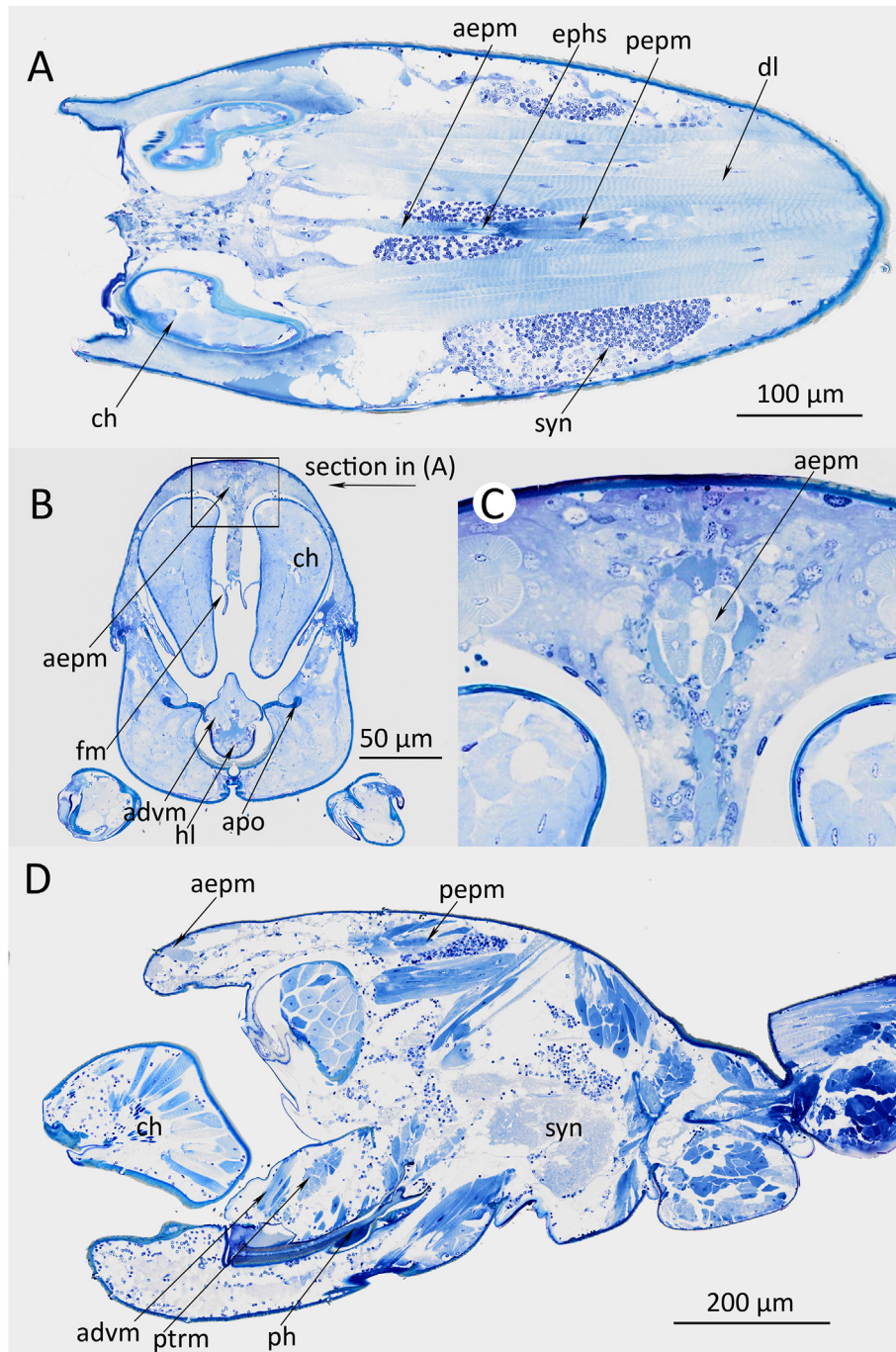
Fig. 8. *Stenochrus portoricensis*, documentation of the epipharyngeal muscles and dorsal longitudinal muscles. **(A)** Horizontal section through the propeltidium in a dorsal position (arrow in B indicates the approximate position of this section). This section shows the anterior and the posterior epipharyngeal muscles, with their origins from the epipharyngeal sclerite and their insertions at the anterior and posterior propeltidium, respectively. Anterior and posterior epipharyngeal muscles are unpaired medial muscles; lateral is the (paired) dorsal longitudinal muscle, which is part of the ancestral box truss system. **(B)** Anterior epipharyngeal muscle in cross section. The arrow indicates the approximate position of section in (A); the frame indicates the area of interest shown in (C). **(C)** High-power magnification of a cross-section of the anterior epipharyngeal muscle as framed in (B). At this position, the anterior epipharyngeal muscle consists of only four fibers. **(D)** Parasagittal section through the prosoma, showing attachments of the anterior and the posterior epipharyngeal muscles to the propeltidium. **Abbreviations**: advm, anterior dorso-ventral muscle of the rostrum; aepm, anterior epipharyngeal muscle; apo, pedipalpal apodeme; ch, chelicera; fm, frontal membrane; pepm, posterior epipharyngeal muscle; ph pharynx; ptrm, posterior transversal muscle of the rostrum; syn, synganglion.

the preoral food canal into the pharynx (ph, Fig. 7B); there are no constrictor muscles or valves that might close the mouth. Thus, the mouth opening can be described only by topographic landmarks: (i) the soft labrum transitions into the sclerotized epistome, (ii) the posterior transversal muscle of the rostrosoma spans between left and right, (iii) the roof of the pharynx changes from soft to intensively sclerotized, (iv) the filtering apparatus on the ventral side of the labrum ends, and (v) the rostrum laterally merges with the pedipalpal coxae.

Pharynx and pharyngeal suction pump: The pharynx is the most anterior part of the ectodermal foregut; it has no intrinsic circular constrictor muscles and no bristles. The pharynx is characterized by

Fig. 9. Schematic drawing of the pharyngeal musculature. See text for details. **(A)** Generalized drawing of the pharyngeal musculature of Schizomida, **(B)** Generalized drawing of the pharyngeal musculature of Thelyphonida. **Color code:** purple, epipharyngeal sclerite; red, musculature; blue, endosternite; yellow, central nervous system; 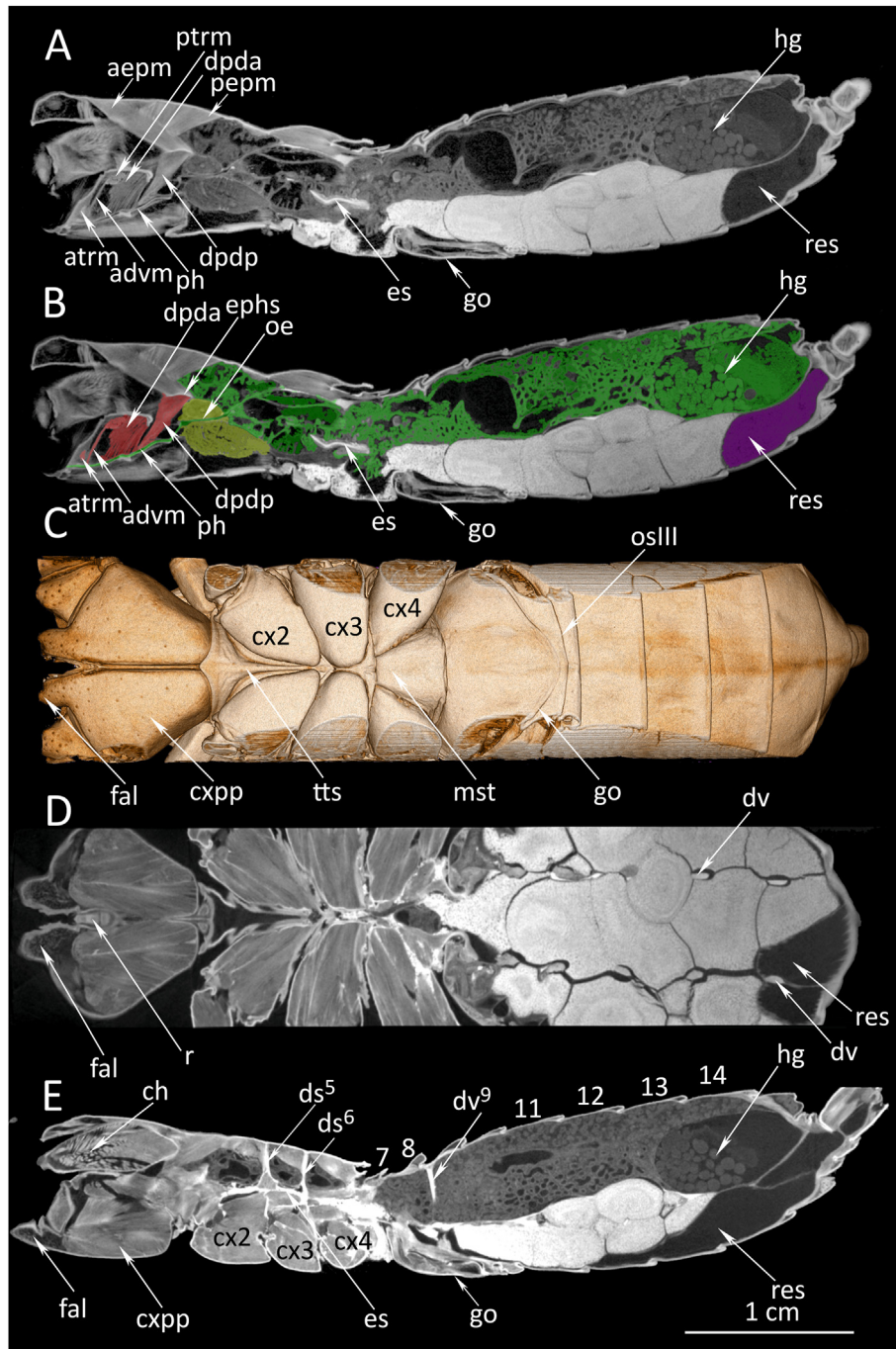green, midgut: **Abbreviations:** aepm, anterior epipharyngeal muscle; atrm, anterior transversal muscle of the rostrum; advm, anterior dorsoventral muscle of the rostrum; ch, chelicera; ci, circular muscles around oesophagus; dpda, anterior dorsal dilator muscle; dpdp, posterior dorsal dilator muscle; ds^3-ds^6, dorsal suspensor muscles of segments three to six; dvl, dorsoventral muscle of first opisthosoma segment; ec, endosterno-cheliceral muscle; ech, extrinsic cheliceral muscle; ephs, epipharyngeal sclerite; es, endosternite; et, endosternotergal muscle; lat, lateral muscle homolog to lateral suspensor 3; ldm, lateral pharyngeal dilator muscle; ls^4, ls^6 lateral suspensor muscles of segments four and six; mg, midgut; mpt, metapeltidium; ms, mesopeltidium; pepm, posterior epipharyngeal muscle; ot^7, tergite of first opisthosoma segment; ptrm, posterior transversal muscle of the rostrum; syn, synganglion; vs^5, vs^6, ventral suspensor muscles segments five and six.

a distinct muscle system attaching to the sclerotized regions of its cuticular lining. Muscles attachments to the pharynx as well as alternating areas of sclerotized and soft cuticle provide the morphological elements of a functional pharyngeal suction pump (= precerebral suction pump). The pharyngeal suction pump is driven by two main muscles, i.e., the dorsal pharyngeal dilator muscles and the lateral dilator muscles.

The dorsal pharyngeal dilator muscle has two parts, i.e., the anterior part of the dorsal pharyngeal dilator muscle and the posterior part of the dorsal pharyngeal dilator muscle. The anterior, dorsal pharyngeal dilator muscle originates from the entire internal face of the epistome and inserts on the intensively sclerotized roof of the pharynx (dpda, Figs. 4A, 5F, 6A,B, 7B,D, 9A); the fibers of this muscle take a steep inclination in their dorso-ventral course. The lateral wall of the pharynx is lined by a thin and soft cuticle, and the bottom is again sclerotized so that the contractions of the anterior dorsal pharyngeal dilator muscle supposedly move the sclerotized roof up and down like a piston in the pharynx. The posterior dorsal pharyngeal dilator muscle originates from the epipharyngeal sclerite and inserts on the posterior part of the pharynx (dpdp, Figs. 4C and D, 6C,D, 7B,D, 9A). Sclerotization of the cuticle in that part of the pharynx is highly differentiated; in cross-sections, the dorsal face of the pharynx with the insertion of the dilator muscle is sclerotized, it grades laterally into soft and sclerotizes cuticle so

that the lateral wall of the pharynx folds like a concertina; it is heavily sclerotized on the ventral face.

Posterior to the dorsal pharyngeal dilator muscles, lateral pharyngeal dilator muscles span between the coxoepistomal apodemes and the lateral wall of the pharynx (ldm, Fig. 4C and D). Its fibers extend in about 45°-angle from latero-dorsal to ventro-medial to attach on the pharynx (Fig. 4C and D, 9A). Here, the entire wall of the pharynx is lined by thin and soft cuticle. Behind the lateral pharyngeal dilator muscles, the pharynx grades into the oesophagus. — I did not find ventral dilator muscles or circular muscles around the pharynx.

Muscles originating from the epipharyngeal sclerite: The epipharyngeal sclerite is an apodeme originating from the intercheliceral membrane. It is an unpaired medial structure and serves as origin of the posterior dorsal pharyngeal dilator muscle and the anterior and posterior epipharyngeal muscles (aepm, pepm, Fig. 8A—D, 9A). The posterior epipharyngeal muscle originates from the dorsal edge of the epipharyngeal sclerite and reaches dorsal and posterior where it inserts on the propeltidium. The anterior epipharyngeal muscle is a minute muscle originating from the dorsal edge of the epipharyngeal sclerite and reaching anterior to the frontal membrane (Fig. 8A). It consists of only a few fibers (Fig. 8C and D).

Oesophagus: The oesophagus is, by definition, the part of the ectodermal foregut that is surrounded by syncerebrum. It has a thin internal cuticle lining, a thin epidermis and a thin layer of striated circular muscles, about as thick as the nuclei of the epidermis cells (c. 2 μm; Fig. 4E and F, 6E, F). Circular constrictor muscles were exclusively found around the oesophagus. The existence of a postcerebral suction pump in Thelyphonidae (including Schizomida) is controversial in the literature. Despite intensive search of multiple serial sections of both species of schizomids, I could not detect any structure that might be interpreted as a postcerebral suction pump as reported by Börner (1904); Kästner (1932) and Moritz (1993); instead, the oesophagus transitions directly into the midgut. — A schematic drawing (Fig. 9A) summarizes the muscle topography of the rostrosoma and the pharynx.

The mouthparts of *Surazomus* sp., musculature, cuticular differentiations and hemolymph spaces are identical to those described for *S. portoricensis*, therefore no description and documentation is repeated here. There appear to be minor differences in the dimensions of elements but this is difficult to assess without morphometric measurements and ultimately irrelevant for a comparative morphological approach.

3.2. Rostrosoma of M. manilanus (Thelyphonida)

The rostrosoma of *Minbosius* comprises the same elements as described for *Stenochrus* in detail, i.e., the chelicerae, the rostrum, and the fused pedipalpal coxae (Figs. 10—14).

The chelicerae are short and stout. Dorsally, they are covered by the overhanging shield of the prosoma (Fig. 10A and B). The lateral folds of the prosomal shield merge with the pedipalpal coxae, thus forming a short preoral canal that contains the chelicerae and the rostrum (Fig. 11E and F, 12A). The topology of these elements is the same as in Schizomida, however, they differ in dimensions. Especially the dorsal shield extends more to the anterior, but the chelicerae are shorter and stouter than in Schizomida.

Pedipalps: The coxae of the pedipalps fuse along almost their entire length, except for the free, anterior lips (fal, Fig. 10C and D). They constitute a distinct trough-like structure that houses the rostrum in a preoral channel (Fig. 11), like in Schizomida. The X-ray contrast of μCT is heterogenous; it is intermediate in the lumen of the free lips indicating that they contain hemolymph and possibly few scattered muscle fibers or connective tissue (Figs. 10D and 13A).

Fig. 10. *Minbosius manilanus*, µCT-images. **(A)** Mediosagittal section. **(B)** Same image but internal organs color coded; red = musculature of the preoral suction pump; yellow = syncerebrum; green = midgut and midgut diverticula; purple = defensive glands. **(C)** Volume rendering showing the ventrum. **(D)** Horizontal section (reconstructed) through the coxae of the pedipalps and the anterior lateral lips. The free lateral lips appear "empty", i.e., are hemolymph-filled and have no muscles inserting. **(E)** Parasagittal section, documenting the coxae of the pedipalps with the anterior, free anterior lips. **Abbreviations:** advm, anterior dorso-ventral muscle of the rostrum; aepm, anterior epipharyngeal muscle; atrm, anterior transversal muscle of the rostrum; cx2-4, coxae of walking legs two through four; cxpp, coxa of pedipalpus; dpda, anterior portion of the dorsal pharyngeal dilator muscle; dpdp, posterior portion of the dorsal pharyngeal dilator muscle; ds^5, ds^6, dorsal suspensor muscles of segments five and six, respectively; dv, dorsoventral muscles of opisthosoma, roman numerals indicate segment number; es, endosternite; go, genital operculum; hg, hindgut; mst, metasternum; oe, oesophagus; ph, pharynx; ptrm, posterior transversal muscle of the rostrosoma; res, reservoir of opisthosomal gland; tts, tritotetrasternum; Arabic numerals, opisthosoma segment numbers.

Their cuticle is differentiated in X-ray contrast with the lateral and ventral sides light (= higher X-ray density). The median face of the free lips is two to three times thicker than the ventral and lateral sides and darker, thus indicating a lower degree of sclerotization (Fig. 13A). — The coxae of the pedipalps contain intensively developed intrinsic musculature, which is not studied here. The distal articles of the pedipalps show the standard anatomy of palpal extremities.

Rostrum: The rostrum is relatively short and lies in the preoral (Figs. 11 and 12). On the dorsal side of the rostrum, the anterior part is recognized as the (soft) labrum, the more posterior, sclerotized part is recognized as the epistome. The (only) diagnostic features of
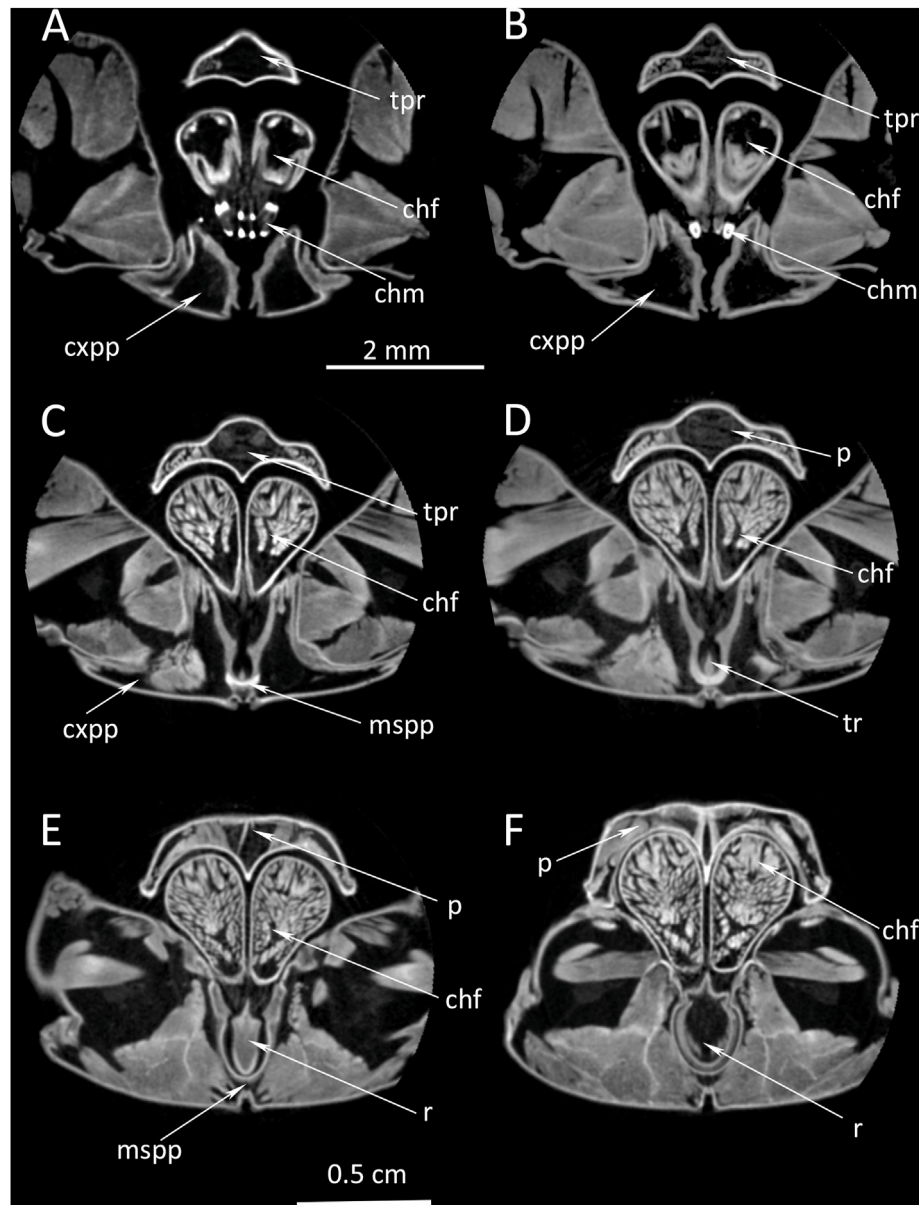
Fig. 11. *Minbosius manilanus*, serial μCT-images of cross-sections through the prosoma documenting the mouthparts and formation of the lower lip. Cross-sections have been computed from originally sagittal μCT-images. Positions have been selected that are largely equivalent to images of *Stenochrus portoricensis* shown in Fig. 3. **(A)** Cross-section through the anterior part of the rostrosoma anterior to the rostrum. **(B)** Section little bit posterior to (A). **(C)** Section at the level where the coxae of the pedipalps merge, thus forming the trough shaped preoral channel. **(D)** Section through the anterior tip of the rostrum. **(E)** Section through the anterior rostrum. **(F)** Section through the rostrum at the level of the attachment of the anterior dorsoventral muscles. **Abbreviations:** chf, fixed finger of chelicera; chm, mobile finger of chelicera; cxpp, coxa of pedipalp; mspp, median seam of merged pedipalpal coxae; p, prosoma shield; r, rostrum; tpr, anterior tip of prosoma shield; tr, tip of rostrum.

the epistome are the origin of the anterior dorsal pharyngeal dilator muscle and an increased X-ray contrast (sclerotization) as compared to the anteriorly sloping, soft labrum.

The musculature of the rostrum has a similar topographic arrangement as described for Schizomida though proportions differ. The apex of the rostrum, carries a small anterior transversal muscle that inserts to the lateral faces of the labrum (atrm, Fig. 13B). Posterior to this is a rather delicate anterior dorsoventral rostrum muscle. This muscle takes an oblique course, originating from the anterior margin of the epistome and inserts ventrally in the preoral region of the soft labrum (advm, Fig. 13C). A large posterior transverse muscle marks the transition between preoral channel and mouth opening. It spans horizontally between both sides of the saddle roof-shaped epistome (ptrm, Fig. 13D), similar to that

described for schizomids. Below the posterior transverse muscle is the ventral insertion of the anterior dorsal pharyngeal dilator muscle. It originates from the epistome and inserts on the ventral side of the rostrum where the cuticle has a distinctly higher X-ray absorbance (=sclerotized). This is also the position where the preoral channel grades into the mouth opening (Fig. 13D and E).

The posterior pharyngeal dilator muscle originates from the epipharyngeal sclerite and attaches to the dorsal wall of the pharynx. At about the same position, lateral pharyngeal dilator muscles span between the coxoepistomal apodemes and the pharynx (ldm, Figs. 12B and C, 13F,G). − Posterior to the lateral pharyngeal dilator muscles, the anterior ectodermal foregut continues as oesophagus and is surrounded by synganglion. The resolution of μCT does not allow recognizing possible circular muscles. When the oesophagus
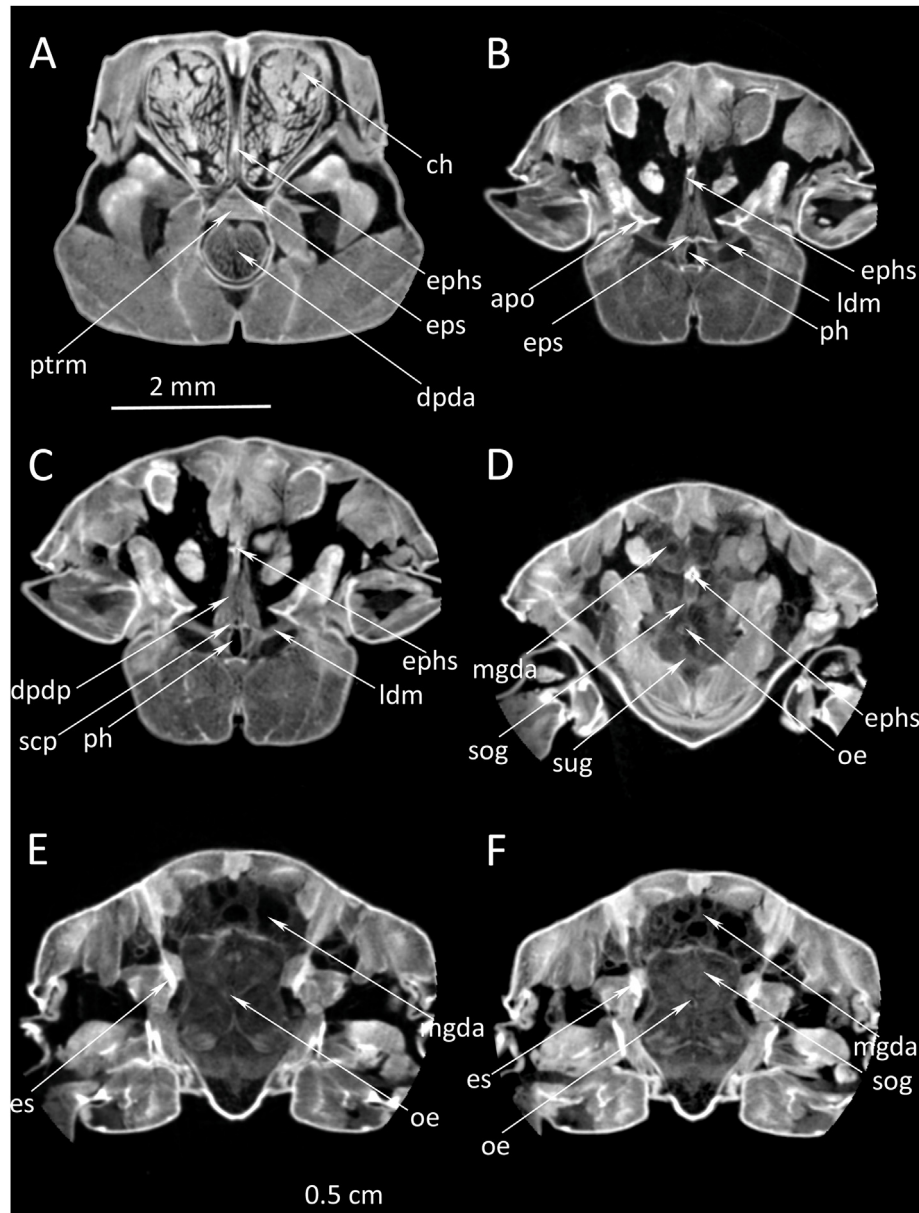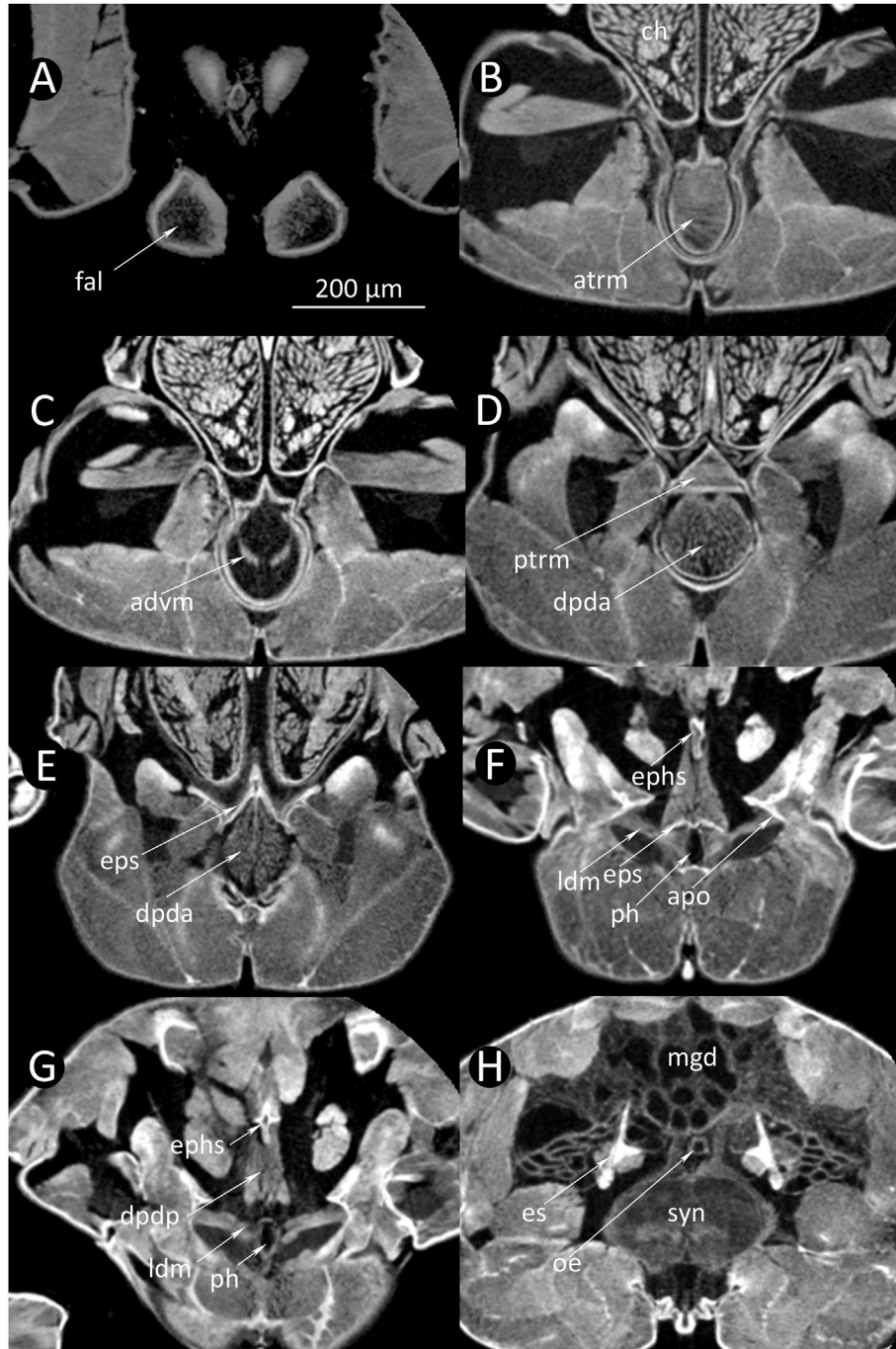
Fig. 12. *Minbosius manilanus*, serial μCT-images of cross-sections through the prosoma documenting the pharyngeal suction pump and the oesophagus Cross-sections have been computed from originally sagittal μCT-images. Positions have been selected that are largely equivalent to images of *Stenochrus portoricensis* shown in Fig. 4. **(A)** Section through the posterior transversal muscle of the rostrum. **(B)** Section through the lateral pharyngeal dilator muscle. **(C)** Section a bit more into the prosoma. **(D)** Section through the posterior end of the epipharyngeal sclerite, oesophagus in a middle position. **(E)** Section through the oesophagus, the endosternite with the most anterior dorsal suspensor muscle is visible. **(F)** Section a little bit posterior to (E). **Abbreviations:** apo, apodeme; ch, chelicera; dpda, anterior portion of the dorsal pharyngeal dilator muscle; dpdp, posterior portion of the dorsal pharyngeal dilator muscle; eps, epistome; ephs, epipharyngeal sclerite; es, endosternite; ldm, lateral pharyngeal dilator muscle; mgda, anterior midgut diverticle; oe, oesophagus; ph, pharynx; ptrm, posterior transversal muscle of the rostrum; scp, sclerotized dorsal wall of the pharynx; sog, supraoesophageal ganglion; sug, suboesophageal ganglion.

leaves the synganglion it immediately opens into the midgut (Figs. 13H, 14). No postcerebral suction pump or muscular parts of a postcerebral pharynx have been detected, despite descriptions of a postcerebral suction pump in the literature (see discussion).

Like Schizomida, Thelyphonida have a distinct epipharyngeal sclerite (ephs, Figs. 9B, 13 and 14). The epipharyngeal sclerite is a sclerotized part of the intercheliceral membrane. It is origin of the large anterior epipharyngeal muscle (#8 in Shultz, 1993; aepm in Fig. 14B). The anterior epipharyngeal muscle spans between the epipharyngeal sclerite and the inner side of the dorsal shield. The posterior epipharyngeal muscle (described as muscle #9 in Shultz,

1993; pepm in Fig. 14B) can be identified on μCT images as thin string of muscle that originates from the posterior dorsal edge of the epipharyngeal sclerite and insert on the dorsal shield (Figs. 9 and 14).

Pharynx and pharyngeal suction pump: the pharyngeal suction pump is composed by the anterior and posterior dorsal pharyngeal dilator muscles (Figs. 9B, 10A,B, 12C, 13E,F,G) and the lateral pharyngeal dilator muscles (Figs. 9B and 13F, G) together with specific regionalized sclerotizations of the bottom and the roof of the pharynx. The lateral walls of the pharynx remain soft. The degree of sclerotization can be differentiated by the x-ray contrast, i.e.,

Fig. 13. *Minbosius manilanus*, serial μCT-images of cross-sections through the rostrosoma documenting muscles of the rostrum and the pharyngeal suction pump. **(A)** Section through the free anterior lips of the pedipalpal coxae. **(B)** Section through the anterior transversal muscle of the rostrum. **(C)** Section through the anterior dorso-ventral muscle of the rostrum. **(D)** Section through the posterior transversal muscle of the rostrum and the anterior ventral insertion of the anterior portion of the dorsal pharyngeal dilator muscle. **(E)** Section through the anterior portion of the dorsal pharyngeal dilator muscle originating from the epistome. **(F)** Section through the lateral pharyngeal dilator muscles originating from the pedipalpal apodeme. **(G)** Section through the posterior part of the pharyngeal suction pump with the lateral and posterior dorsal pharyngeal dilator muscles. **(H)** Section through the oesophagus, just anterior to entering the midgut. **Abbreviations:** advm, anterior dorsoventral muscle of the rostrum; apo, apodeme formed by basal article of the pedipalp; atrm, anterior transversal muscle of the rostrum; dpda, anterior dorsal pharyngeal dilator muscle; ephs, epipharyngeal sclerite; es, endosternite; fal, free anterior lips of pedipalpal coxae; ldm, lateral pharyngeal dilator muscle; mgd, midgut diverticulum; oe, oesophagus; ph, pharynx; ptrm, posterior transversal muscle of the rostrum; syn, synganglion.

intensively sclerotized regions like roof and bottom of the pharynx have high X-ray contrast. - Like in schizomids, there is no evidence of a post-cerebral suction pump in Thelyphonida. Immediately post-cerebral, the oesophagus continues into the midgut.

Oesophagus: The resolution of μCT-imaging is not sufficient to recognize circular musculature in the oesophagus wall. The oesophagus is short, passes through the synganglion and opens directly into the midgut.
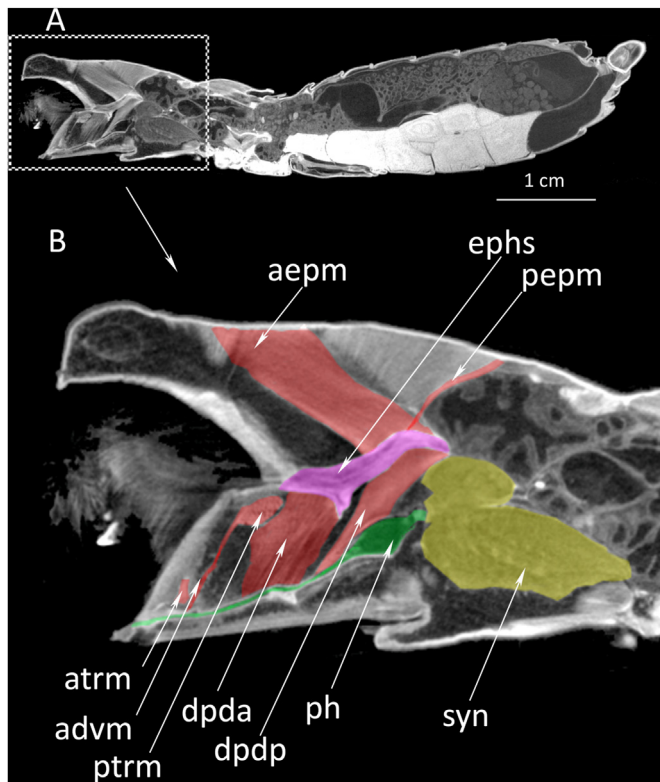
Fig. 14. *Minbosius manilanus*, mid-sagittal μCT-image. **(A)** Overview longitudinal image through the entire body to document muscles of the pharyngeal suction pump. **(B)** Detail of (A; framed box). Muscles of the pharyngeal suction pump and the epipharyngeal sclerite are marked with a transparent color overlay (red); the epipharyngeal sclerite is purple, the pharynx green, and the brain is labeled yellow. The image has been selected because it shows a topography that is similar to the schematic drawing presented by Shultz (1993; Fig. 3) for *Mastigoproctus giganteus.* **Abbreviations:** advm, anterior dorsoventral muscle of the rostrum; aepm, anterior epipharyngeal muscle; atrm, anterior transversal muscle of the rostrum; dpda, anterior dorsal pharyngeal dilator muscle; dpdp, posterior dorsal pharyngeal dilator muscle; ephs, epipharyngeal sclerite; pepm, posterior epipharyngeal muscle; ph, pharynx; ptrm, posterior transversal muscle of the rostrum; syn, synganglion.

4. Discussion

4.1. Morphology of the rostrosoma and pharyngeal suction pump in Thelyphonida

Börner (1902, 1904) described the cuticular elements and the muscle topography of Schizomida and Thelyphonida on the basis of dissections and some histology. His descriptions have been the basis for later work (and have been referenced intensively without adding new original data [Kästner, 1932; Weygoldt and Paulus, 1979; Moritz, 1993]). Studies by Shultz (1993, 1999, 2001, 2007) have been essential for establishing a modern understanding of the musculature of chelicerates. His work included careful and complete descriptions of the pharyngeal apparatus of Thelyphonida (Shultz, 1993), Amblypygi (Shultz, 1999), and Scorpiones (Shultz, 2007). Despite his work, the descriptions of the rostrosoma and pharyngeal suction pump as given here for Schizomida and Thelyphonida is novel and adds numerous details, which are important for an evolutionary comparison with other euchelicerate taxa.

The microscopic anatomy of the two species of Schizomida is identical. Also, the morphology of the rostrosoma of their putative sister group, i.e., Thelyphonida (here: *M. manilanus* Shultz, 1993: *M. giganteus*) has the same morphological elements in same

topographic relationship, but with different proportion. Despite using different methods, Shultz (1993) documented the same anatomy for rostrum muscles, skeletal elements and endosternal components as reported here. He did not consider the degree of sclerotization of the cuticle and did not present functional interpretations of the feeding apparatus.

The morphology of the rostrosoma comprises skeletal elements, i.e., epistome, labrum, pedipalpal coxae, and muscular elements, i.e., dorsal and lateral pharyngeal dilator muscles of the precerebral, pharyngeal suction pump and circular muscles of the oesophagus, that belong into the ancestral body plan of euchelicerates, if not arthropods. The specific transformation of those elements into the rostrosoma is considered a shared character of Thelyphonida and Schizomida, e.g., the elongate rostrum (formed by the ancestral elements epistome and labrum) and the trough-shaped preoral canal (formed by fusion of the elongated pedipalpal coxae). The rostrum of Thelyphonida and Schizomida is also characterized by the same set of muscles, i.e., anterior and posterior transverse muscles, an anterior dorsoventral muscle and two dorsal pharyngeal dilator muscles. Both taxa also possess a large epipharyngeal sclerite, which is a cuticular element contiguous with the intercheliceral membrane. The epipharyngeal sclerite is topographically associated with the epistome, but, Shultz (1993, p. 351) pointed out that epistome and epipharyngeal sclerite are two different elements. The epipharyngeal sclerite and its musculature are elements that are exclusive for Uropygi, Amblypygi (the putative sister group of Uropygi; Fig. 15G), and scorpions (Fig. 15K). In all groups, epipharyngeal musculature is spanning between the epipharyngeal sclerite and the dorsal shield.

The mouth opening is morphologically undefined and described as the transition zone between of preoral channel and the pharynx. This separates the rostrosoma muscles in two distinct topographic units, which supposedly represent two functionally independent suction pumps (see below): the preoral unit, composed of the transverse muscles and the dorsoventral rostrum muscle, and the pharyngeal suction pump, composed of the anterior and posterior pharyngeal dilator muscle and the lateral pharyngeal dilator muscle.

No post-cerebral suction pump has been found in the two taxa of Uropygi, despite earlier descriptions by Börner (1904), who reported a rudimentary post-cerebral suction pump ("hintere Schlundpumpe") for Uropygi and Palpigradi as consisting of lateral dilator muscles and circular muscles (Schizomida have not been studied). In his description, a dorsal dilator muscles of the postcerebral suction pump, as present in Amblypygi and Araneae, is lacking. However, Börner's (1904) description was based on Palpigradi[2] and was extended to Thelyphonida. His text Fig. 88 allows to identify the "postcerebral suction pump" as the anterior endosternal bridge and the lateral suspensor muscles of segment four. Obviously, he extrapolated the palpigrade morphology and its interpretation to Thelyphonida. This misinterpretation was discussed by Millot (1942) but obviously overlooked in other articles [Kästner (1932), Weygoldt and Paulus (1979), and Moritz (1993)], which referenced Börner (1904) without further verification. Snodgrass (1948), Millot (1949) and Shultz (1993) did not mention a post-cerebral suction pump in Thelyphonida, but they also did not discuss Börner (1904). Despite intensive search through multiple histological serial sections of schizomids and palpigrads *(Eukoenenia spelaea;* Franz-Guess and Starck, 2020), and multiple μCT series of *Minbosius,* I could not find a single muscle fiber in that topographic position of the claimed postcerebral suction pump. I

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[2] Börner himself was probably inspired by Rucker (1901) who described a post-cerebral suction pump in *Koenenia wheeleri.*
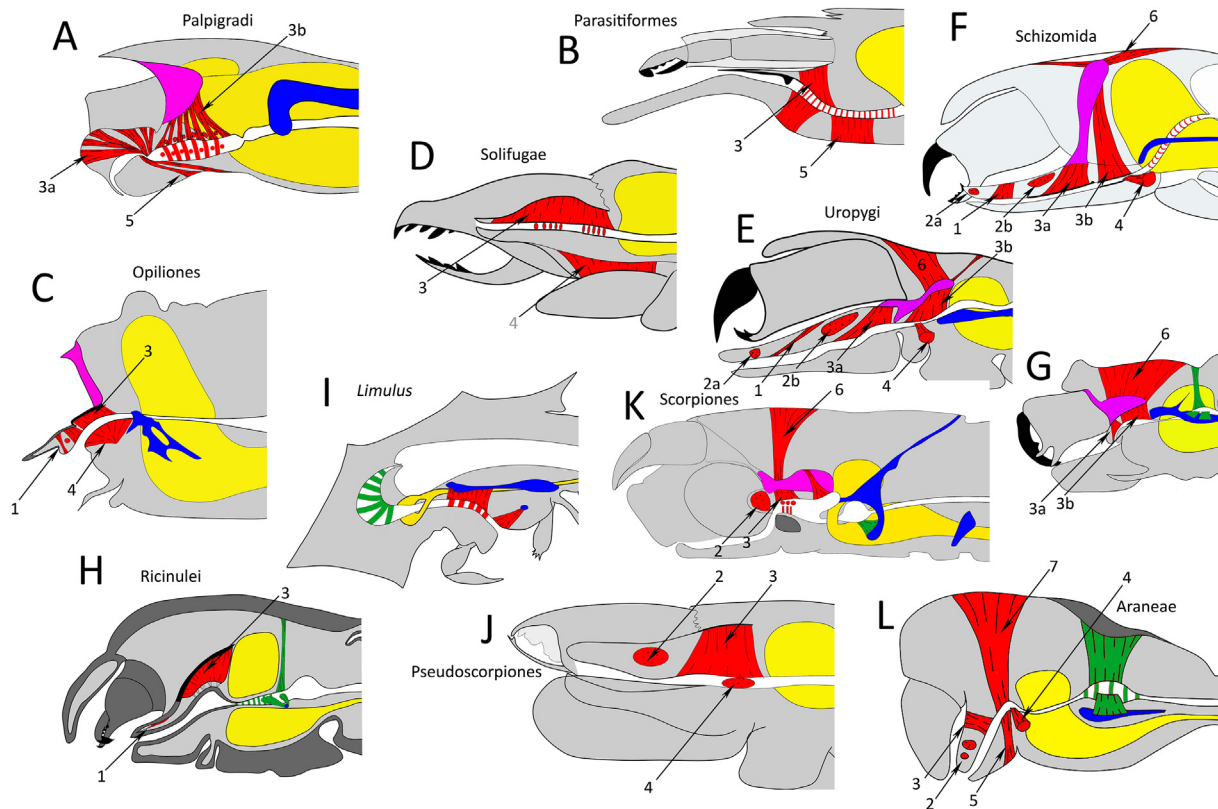
Fig. 15. Comparative morphology of the rostrosoma and pharyngeal suction pump of euchelicerates. Schematic drawings of the morphological key elements building the rostrosoma and the suction pump(s) in 11 euchelicerate taxa. **(A) Palpigradi** (based on Millot, 1943; Franz-Guess and Starck, 2020); The rostrosoma is a unique prominent tubular structure hosting the preoral cavity, the mouth opening, and anterior parts of the pharynx. The dorso-ventral muscle(s) associated with the anterior end of the pharynx (L. sup., Fig. 2 in Millot, 1942; P1, P2 in Franz-Guess and Starck, 2020) insert(s) on the upper lip. If the upper lip represents the epistomo-labral plate, then this muscle would be diagnosed as the anterior portion of the pharyngeal dilator muscle (Shultz, 1993). The intercheliceral septum extends deep into the prosoma and is origin of the posterior portion of the dorsal pharyngeal dilator muscle. The anterior dorsoventral rostrosoma muscles are missing, but a ventral dilator muscle is present. The pharynx is surrounded by circular muscles. **(B) Parasitiformes** (based on Starck et al., 2022); rostrum embedded in the gnathosoma, a unique acarine structure; no anterior rostrum muscles and only one dorsal pharyngeal dilator muscle (probably the anterior portion because it originates from the episteme) present. Ventral dilator muscles and a unique pharyngeal valve formed by parts of the labrum. **(C) Opiliones** (based on Shultz, 2000); ventral closure of the preoral chamber and the mouth formed by apophyses of the coxae of the pedipalps and leg 1 and a ventral sclerite (labium); anterior dorso-ventral rostrosoma muscle, posterior transversal rostrosoma muscle, and both portions of the dorsal pharyngeal dilator muscle present. The large lateral dilator muscles appear unique as compared to all other euchelicerates. Intercheliceral septum sclerotized (=epipharyngeal sclerite) but small. **(D) Solifugae** (based on Starck et al., 2022); the rostrum has a triangular upper lip and two lateral lips. The three lips merge at the mouth opening. The rostrum is free for most of its length but proximally fuses with the coxae of the pedipalps. The entire rostrum is dorsally covered by the enlarged episteme, labrum reduced. Anterior dorso-ventral muscle and transverse muscles missing. Intercheliceral septum soft, no muscle attachment. Unique morphology with extensive lateral pharynx muscles. **(E) Thelyphonida** (based on Shultz [1993] and described in detail in the text of this paper; medially merged, trough-shaped pedipalpal coxae form the ventral closure of the rostrosoma; complete set of rostrum muscles, epipharyngeal sclerite large and distinct; anterior and posterior epipharyngeal muscles. **(F) Schizomida**; detailed description in this paper; medially merged, trough shaped pedipalpal coxae form the ventral closure of the rostrosoma; complete set of rostrum muscles, epipharyngeal sclerite large and distinct; anterior and posterior epipharyngeal muscles. **(G) Amblypygi** (based on Shultz, 1999); similar to Thelyphonida but elongate rostrum and rostrosoma missing. Post-cerebral suction pump consisting of a dorso-ventral muscle. **(H) Ricinulei** (based on Hansen and Sørensen, 1904; Talarico et al., 2011); the pharyngeal suction pump has only dorsal dilator muscles probably representing the anterior dorsoventral muscle of the rostrosoma and the (anterior) dorsal pharyngeal dilator muscles but neither lateral, ventral dilator muscles, or constrictor muscles. The post-cerebral suction pump has a dorsal dilator muscle and pairs of anterior and posterior lateral dilator muscles spanning between the oesophagus and the endosternite; it has circum-oesophageal constrictor muscles. **(I) Limulus** (based on Lankester et al., 1885; Shultz, 2001); pharyngeal suction pump and postcerebral suction pump are unique and have no morphological equivalent among euchelicerates. The two muscles of the pharyngeal suction pump originate from the extensively developed endosternite. The post-cerebral suction pump consists of exclusively circular muscles of a stomach like extension of the oesophagus. Muscles have not been labeled because homologies are not known. **(J) Pseudoscorpiones** (based on Weygoldt, 1969; Starck et al., 2022); rostrum with dorsal, lateral and ventral lips, a preoral channel formed by the ventral interlocking of the pedipalpal coxae (lamina inferior); the pharyngeal suction pump is characterized by a single large transversal muscle in the rostrosoma and a large dorsal pharyngeal dilator muscle spanning between the (internalized episteme) and the pharynx. Lateral dilator muscles are present. **(K) Scorpiones** (based on Lankester et al., 1885; Snodgrass, 1948; Shultz, 2007); ventral closure of the preoral chamber by enlarged endites of the coxae of the pedipalps and the first two pairs of walking legs; the pharyngeal suction pump consists of a large transverse muscle in the labrum (camerostome: Lankester et al., 1885), dorsal dilator muscles (originating from the episteme) and lateral dilator muscles. The postcerebral suction pump has only lateral dilator muscles spanning between the oesophagus and the endosternite. Large epistomal/epipharyngeal sclerite with an epipharyngeal muscle. **(L) Araneae** (based on Brown, 1939; Meyer, 1981; Marples, 1983). Ventral closure of the preoral chamber by the labium (i.e., a sternal derivative). The epistome-labrum contains two transversal muscles (only in Brown 1939) and a dorsoventral muscle, probably the anterior portion of the dorsal pharyngeal dilator muscle, a large dorso-ventral muscle spanning from the pharynx to the dorsal shield appears to be unique to the Araneae. The pharyngeal suction pump also has lateral and ventral dilator muscles. The post-cerebral suction pump appears to be functionally dominant and consists of dorsal and lateral dilator muscles (attaching to the endosternite) and circular constrictor muscles. Meyer (1981) described some variability of the muscle morphology among families of the Araneae. **Color code:** blue = endosternite; purple = intercheliceral septum and epipharyngeal sclerite; red = muscles of the pharyngeal suction pump; green, muscles of the posterior foregut; yellow = central nervous system. **1**, dorsoventral muscle of rostrosoma; **2**, transverse muscles of rostrum (**2a**, anterior transverse muscle; **2b**, posterior transverse muscle); **3**, dorsal pharyngeal dilator muscle (**3a**, anterior portion; **3b** posterior portion); **4**, lateral pharyngeal dilator muscle; **5**, ventral pharyngeal dilator muscle; **6**, epipharyngeal muscle; **7**, aranean dorsal pharyngeal dilator muscle (no clear homology known).

conclude that Thelyphonida have no postcerebral suction pump and that its description was a misinterpretation of the anterior endosternal bridge and lateral suspensor muscles.

The unique topographic anatomy of the rostrosoma and the pharyngeal suction pump supports a phyletic relationship of Schizomida and Thelyphonida (which has never been questioned) and, in comparison to other arachnids, supports the view that their rostrosoma has been shaped by independent evolution. The epipharyngeal sclerite and its associated muscles are shared by Thelyphonida, Amblypygi and Scorpiones and fit into the Arachnopulmonata concept (Ballesteros et al., 2019, 2022; Ballesteros and Sharma, 2019; Sharma et al., 2021; Garwood and Dunlop, 2023; Sharma, 2023). However, Shultz (2007) consider the epipharyngeal structures in scorpions derived from the epistome, which is in distinct contrast to the interpretation presented here (as epipharyngeal sclerite). Whatever the correct interpretation is, other taxa of the Arachnopulmonata, i.e., Araneae (Fig. 15L) and Pseudoscorpiones (Fig. 15J), have no epipharyngeal sclerite and represent completely different morphologies. Further, Amblypygi have no transverse muscles (Shultz, 1999). Scorpions have one transverse muscle in the camerostome, which may be homologous to the transverse rostrum muscles of Thelyphonida. Their pharyngeal suction pump has additional circular pharyngeal muscles (Lankester et al., 1885). Pseudoscorpiones have a rostrosoma, but it differs substantially from that of Thelyphonida (Starck et al., 2022). Thus, morphology is diverse and phylogenetically not informative. The existence of the epipharyngeal sclerite fits into the context of the Arachnopulmonata concept. However, it should not be over-interpreted because it is an apodemic sclerotization of the interchelicheral septum which might evolutionarily occur or disappear relatively easily as a morphological feature. Ultimately, we see considerable morphological divergence, which, in the context of Arachnopulmonata, can be interpreted only as resulting from independent evolutionary diversification. Indeed, the morphology of the feeding apparatus supports a relationship between Schizomida and Thelyphonida, but fails to suggest or even support any other relationship because of the diversity of topographic arrangements observed.

4.2. Functional implications of the rostrosoma morphology

Given the close morphological similarity of the rostrosoma of Schizomida and Thelyphonida, functional implications are discussed for both groups together. The discussion of the functioning of the rostrosoma is based on the topographic anatomy of all mouthparts, their soft and sclerotized cuticle parts, muscles, muscle attachment sites, muscle fiber orientation, and hemolymphatic spaces. Basic assumptions are that muscles contract along their fiber orientation, hemolymphatic spaces allow for hemolymph volume displacement and force transmission, and the degree of sclerotization of the cuticle indicates its flexibility. Unfortunately, no observations or experimental data exist on the functioning of the rostrosoma of Schizomida or Thelyphonida.

Preoral suction pump: The rostrum, the epipharyngeal sclerite, the coxae of the pedipalps with the preoral channel and the muscles of the rostrum form a functional unit. The soft tip of the rostrum (i.e., the labrum) moves free in the preoral channel, while the proximal part (i.e., the sclerotized epistome) is firmly fused to the coxae of the pedipalps. The µCT-images of the *Minbosius*-rostrosoma show that, in relaxed condition, the rostrum almost completely fills the trough-shaped preoral channel of the pedipalpal coxae. The tip of the rostrum carries a ventral filtering basket of rigid bristles. The apical part of the rostrum supposedly is actuated by the anterior transverse rostrum muscle, the anterior

dorsoventral muscle, and hemolymph volume changes. Fibers of the anterior dorsoventral muscle originate from the anterior edge of the sclerotized epistome and insert on the soft cuticle of the ventral side of the anterior rostrum. Contractions of the dorsoventral rostrum-muscle may, therefore, lift the soft ventral side of the rostrum and, because of associated hemolymph volume displacement, may cause a thickening of the dorsal part of the rostrum, which is tightening-up the preoral channel. This may create a low pressure in the preoral channel, causing a flow liquid food through the through the filtering basket into the trough-like structure of the pedipalpal coxae. Antagonistic movement might be mediated by increasing hemolymph pressure caused by contractions of the anterior and posterior transverse muscles. The function of the posterior transverse muscle remains a bit unclear, as it attaches to two intensively sclerotized flanks of the epistome that are additionally merged to the pedipalpal coxae. The function of the muscle may therefore be found in increasing tension or hemolymph pressure in the rostrum. Mediated through hemolymph volume displacement, the action of the transverse muscles becomes antagonistic to the anterior dorsoventral muscles. This functional model is exclusively based on muscle and sclerite topography, but it suggests that the rostrum with its muscles functions as a "preoral" suction pump in the preoral channel. - The free anterior lips of pedipalps may form the flexible attachment to the prey, but their action is difficult to speculate and it requires live observations. However, there are two features that appear relevant for a functional interpretation: 1) the free anterior lips contain no distinct muscles, thus are probably actuated by hemolymph volume changes, and 2) the medial face of the free anterior lips is not sclerotized thus soft while the cuticle of the other sides is sclerotized. Thus, any hemolymph volume displacement may result in inflation of the free anterior lips resulting in outwards bulging medial surfaces.

Pharyngeal suction pump: the pharyngeal suction pump is formed by the soft and sclerotized wall of the pharynx, the anterior and posterior dorsal pharyngeal dilator muscles, and the lateral pharyngeal dilator muscles. The cuticle lining of the pharynx shows differentiated sclerotization, which may be the key for understanding the functional morphology. Just behind the mouth opening, the cuticular lining of the roof of the pharynx is intensively sclerotized while it is thin and soft on the lateral and ventral walls. The anterior portion of the dorsal pharyngeal dilator muscle attaches to the sclerotized roof of the pharynx, which can be moved like a piston creating low pressure in the anterior section of the pharynx when moved upwards, thus ultimately sucking liquid food from the preoral channel. — The attachment region of the posterior dorsal pharyngeal dilator muscle differs in sclerotization of the pharynx. Here, roof and bottom of the pharynx are intensively sclerotized and the side walls carry sclerotized plates, which are connected by soft cuticle. While roof and bottom may function like a piston pump, the sides accommodate up- and down-movements by folding like a concertina. The posterior region of the preoral suction pump is the attachment site of the lateral pharyngeal dilator muscles, which attach to a more or less thin cuticle lining, thus probably resulting in a more general expansion of the lumen of the pharynx. Anterior and posterior portion of the dorsal pharyngeal dilator muscles and the lateral dilator muscles contribute to an expansion of the pharynx volume, thus create low pressure in the pharynx. An antagonistic muscular system that reduces the pharynx-lumen has not been detected. Without circular constrictor muscles in place on can speculate only about a hemolymphatic system functioning as antagonist to the dilator muscles or about pharyngeal wall elasticity as functional component.

4.3. Multiple evolutionary pathways of the feeding apparatus in (eu)chelicerates

The homology of epistome, labrum and the dorsal pharyngeal dilator muscle has been established for arachnids (Snodgrass, 1948; Shultz, 1993, 1999; Dunlop, 2000; Bitsch and Bitsch, 2007; Starck et al., 2022). Indeed, these elements represent shared chelicerate (if not arthropod) features, but, their topographic association and relationship with musculature and the coxae of the pedipalps differ, so that evidence for independent evolutionary diversification of an ancestral pattern can be extracted (Fig. 15).

The rostrosoma of Thelyphonida and Schizomida (Fig. 15E and F) is largely identical. Both taxa possess a large rostrum that contains two transverse and one dorsoventral muscles; they have a distinct epistome and the intercheliceral septum extends as epipharyngeal sclerite deep into the prosoma. The dorsal pharyngeal dilator muscle has two portions, the anterior portion originates from the epistome, the posterior portion from the epipharyngeal sclerite. There is no postcerebral suction pump. A characteristic feature is the occurrence of an anterior and a posterior epipharyngeal muscle that originates on the dorsal edge of the epipharyngeal sclerite and inserts on the dorsal shield. While the function of these two muscles remains unknown it has been described exclusively from Thelyphonida (Figs. 9A and B, 15E,F), Amblypygi (Fig. 15G) and scorpions (Fig. 15K). The epipharyngeal sclerite as origin for two dorsal dilator muscles and as origin of the epipharyngeal muscles has been described for Amplypygi, Thelyphonida, Schizomida and scorpions (Fig. 15); it is in line with the Arachnopulmonata-hypothesis (Ballesteros and Sharma, 2019; Ballesteros et al., 2019; Sharma et al., 2021).

Shultz (1999) described and discussed the pharyngeal morphology of Amblypygi, i.e., the third taxon of Pedipalpi. Amblypygi do not possess a long rostrum, and thus miss some of the intrinsic muscles of the rostrum (transverse rostrosoma muscles are missing), they share with Thelyphonida the merged pedipalpal coxae, the large epipharyngeal sclerite, the dorsoventral muscle in the rostrum, a bipartite origin of the dorsal pharyngeal dilator muscle, and the epipharyngeal muscles with same origin and insertion. In addition, Amblypygi possess a postcerebral suction pump (Millot, 1949; Weygoldt and Paulus, 1979; Shultz, 1999), which has been considered a key element supporting a close relationship with Araneae (Weygoldt and Paulus, 1979). The postcerebral suction pump of Amblypygi has dorsal and lateral dilator muscles, originating on the stomach and inserting internally on the dorsal shield and the endosternite, respectively (Millot 1949; Shultz 1999, Fig. 15G). That of Araneae has additional circular muscle, thus differs in morphological complexity (Brown, 1939; Snodgrass, 1948; Meyer, 1981; Foelix, 1992, 2011, Fig. 15L). Assuming Araneae and Amblypygi share the postcerebral suction pumps as an apomorphic feature requires that either Amblypygi lost the constrictor muscles, or that Araneae added them.

The muscular details of the postcerebral suction pump in other taxa, add support for multiple evolutionary origins. The postcerebral muscular foregut of *Limulus* (Packard, 1880; Lankester et al., 1885; Fahrenbach, 1999; Shultz, 2001, Fig. 15I) has often been referenced as the ancestral archetype, i.e., the morphological substrate from which the postcerebral suction pump evolved in Scorpiones, Amblypygi, Thelyphonida (Börner, 1904; Kästner, 1932; Millot, 1949; Weygoldt and Paulus, 1979), Araneae and Ricinulei (Talarico et al., 2011). However, the postcerebral muscular stomach of *Limulus* consists of exclusively circular muscles and has no morphological equivalent among arachnids (like the pharyngeal suction pump; see above). In comparison, that of scorpions (Farley, 1999, Fig. 15K) has exclusively lateral muscles, that of Amblypygi only dorsal (see above), and that of Ricinulei has dorsal and lateral

dilator muscles as well as circular muscles (Talarico et al., 2011, Fig. 15H), like in Araneae. Given the divergence of morphological details, and the scattered distribution in a recent phylogenetic hypothesis (Ballesteros and Sharma, 2019; Ballesteros et al., 2019; Sharma et al., 2021; Ontano et al., 2021) it becomes highly probably that the postcerebral suction pump evolved several times and independently in the taxa discussed here.

5. Conclusions

The comparative morphological analysis of the rostrosoma, including the musculature of the pharyngeal suction pump allows for some relevant morphological conclusions: (1) Thelyphonida and Schizomida show almost the same morphology of the rostrosoma with a most complete set of pharyngeal muscles. This finding supports the unchallenged phylogenetic relationship of these two taxa. (2) Amblypygi and Scorpiones have no rostrosoma, thus miss the preoral suction pump, but they share with Schizomida and Thelyphonida an large epipharyngeal sclerite and the associated musculature. Amblypygi also possess the merged trough-shaped coxae of the pedipalps (not in Scorpiones). The exclusive similarity of the epipharyngeal morphology of Thelyphonida, Amblypygi and Scorpiones lines up with the Arachnopulmonata concept (Ballesteros and Sharma, 2019; Ballesteros et al., 2019; Sharma et al., 2021; Ontano et al., 2021) and adds to a growing body of morphological data in support of Arachnopulmonata (Klußmann-Fricke et al., 2014; Klußmann-Fricke and Wirkner, 2016; Lehmann and Melzer, 2018, 2019). (3) No consistent morphological pattern of the formation of the rostrosoma, its musculature and the suction pumps were found in comparison to all other euchelicerates (including *Limulus*). While certain elements (e.g., epistome, labrum, dorsal pharyngeal dilator muscle, lateral pharyngeal dilator muscle, transversal rostrosoma muscle) were diagnosed in almost all taxa (musculature different in *Limulus*; labrum reduced in Solifugae; Starck et al., 2022), their topographic relationship and the composition into a pharyngeal suction pump differs. Therefore, the divergent morphology of a snout region in euchelicerates is interpreted as originating from independent evolutionary pathways. (4) In a broad comparison, *Limulus* stands out because it does no align with any of the other taxa. The pharyngeal muscular foregut is unique with its origin from the endosternite; also, the postcerebral muscular foregut differs from that in other taxa as it consists exclusively of circular muscles. Looking at the microscopic anatomical detail and considering the (new) phylogenetic position of *Limulus* nested among Arachnida, the feeding apparatus of *Limulus* with two suction pumps must be considered an independent evolutionary acquisition.

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