

The ptychoid defensive mechanism in *Phthiracarus longulus* (Acari, Oribatida, Phthiracaroida): Exoskeletal and muscular elements

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Abstract

The most complex defensive mechanism in oribatid mites is ptychoity, a special body form allowing the animals to retract their legs and coxisternum into a secondary cavity in the idiosoma and to seal it off with the prodorsum. Many exoskeletal and muscular adaptations are required to enable the functionality of this mechanism, e.g. a soft and pliable podosoma. Its membranous part not only gives the coxisternum the ability to move independently from the rest of the hardened cuticular elements, but also builds up the ‘walls’ of the secondary cavity. Here, using scanning electron microscopy and synchrotron microtomography we present the first detailed study on ptychoity in a phthiracaroid mite, *Phthiracarus longulus*, and compare it to the Euphthiracaroida. Morphological differences regarding ptychoity between these groups are already noticeable from the outside: the ventral plates of *P. longulus* are embedded into the soft anogenital membrane, whereas euphthiracaroid mites connect the ventral plates to the notogaster through the hardened plicature plates. Internally, we discovered a not yet described coxisternal protractor muscle, which presumably assists haemolymph pressure during the deployment of the coxisternum during eptychosis.

Keywords: Synchrotron X-ray microtomography, *Phthiracarus longulus*, ptychoity, Phthiracaridae, box mite, convergent evolution, predator defence

1. Introduction

Particle feeding, the general mode of food ingestion in oribatid mites, is rare among the mostly fluid-feeding chelicerates (Heethoff & Norton 2009). The low digestive efficiency resulting from feeding on dead plant parts or saprophagous fungi leads to certain constraints: slow growth, relatively long generation time and low reproductive potential with an elongated adult life span (Norton 1994, Sanders & Norton 2004, Heethoff et al. 2007). These characteristics necessitate effective predator defence mechanisms, which evolved in various ways among oribatid mites. In general, there are two physically different strategies: chemical

defence through secretion of predator-repelling substances from the opisthonotal oil glands (e.g. Shimano et al. 2002, Raspotnig 2006, Saporito et al. 2007), and several mechanical defence mechanisms (e.g. prolongation of the body setae to form a hedgehog-like appearance, overhanging cuticular tecta concealing articulations; Grandjean 1934). Often these defensive mechanisms are combined with a mechanical hardening of exposed cuticle (Norton & Behan-Pelletier 1991, Alberti et al. 2001).

The most complex mechanical defensive mechanism in oribatid mites is ptychoidy, where the legs and the coxisternum can completely be withdrawn into a temporary cavity into the idiosoma (Sanders & Norton 2004, Schmelzle et al. 2008, 2009). In the encapsulated state the animals – commonly known as ‘box mites’ – then exhibit no soft membrane for a possible attack by predators (Figs. 1A, 2A, B). Rarely, this defensive mechanism can additionally be combined with an escape jump (Wauthy et al. 1998). Ptychoidy has probably evolved three times independently (Sanders & Norton 2004): in the Mixonomata (the monophylum Ptyctima containing the superfamilies Phthiracaroida and Euphthiracaroida; Grandjean 1954, Grandjean 1967, Balogh & Balogh 1992) and in two unrelated families of Enarthronota, Mesoplophoridae and Protoplophoridae (Grandjean 1969, Norton 1984). The special body form needs certain requirements, which accompany several exoskeletal and muscular adaptations: (i) the coxisternum must be isolated from all other hardened cuticle by a soft, pliable integument (ii) the opisthosomal cuticle must be hardened (iii) the coxisternum must be articulated and deformable and (iv) there must be a system that can manage the large internal volume changes.

Exoskeletal elements involved in ptychoidy can be divided into 5 groups. The *prodorsum* (*PR*) acts as an operculum-like seal for the encapsulated animal (Sanders & Norton 2004) and it bears several structures for insertion of muscles that are directly involved in ptychoidy, for instance the *manubrium* (*mn*) and the *inferior retractor process* (*irp*; Fig. 3; Schmelzle et al. 2008, 2009). The *opisthosomal venter* is the exoskeletal group that shows by far the most structural variation among the various ptychoid families and genera, and it is often used for identification. Only in Phthiracaroida, which is the focus of this paper, is the basic structure fixed. It always consists of two pairs of large plates: the genital valves (Wauthy 1984), consisting of the fused genital and aggenital plates, and the anal valves, consisting of the fused anal and adanal plates (Figs. 1A, 2A, B). Movements of the opisthosomal venter relative to the notogaster (see below), which are connected through a broad articulating membrane, the anogenital membrane (Wauthy 1984), are responsible for changes in haemocoel pressure that are required for ptychoidy. The *notogaster* – dorsal plate of the opisthosoma – is ovate to nearly spherical and hardened through mineralisation with calcium carbonate or calcium oxalate (Figs. 1A, 2A, B; Norton & Behan-Pelletier 1991, Alberti et al. 2001). For smaller predators (e.g. parasitiform mites) it presumably is an impenetrable and indestructible barrier. The *podosoma*, or leg-bearing region, comprises a supportive coxisternum, itself composed of four pairs of hardened epimeral plates (Sanders & Norton 2004), and a voluminous, pliable membranous part. The membranous part is one of the main adaptations to ptychoidy; it enables retraction of the legs into a secondary cavity built up by the membrane itself (Grandjean 1967). The *subcapitulum* – venter of the gnathosoma – has adaptations for ptychoidy that include a prominent capitular apodeme and an equally prominent projection of the mentum, as well as a fusion with the taenidiophore part of supracoxal sclerite 1 (Fig. 6A; Märkel 1964, Walker 1965, Sanders & Norton 2004).

Tab. 1 Abbreviations, origin and insertion of the muscular elements associated with ptychoidy in *Phthiracarus longulus*.

Muscle	Abbreviation	Origin	Insertion
Dorsoventral muscles of the Prosoma			
<i>DVP</i>			
coxisternal retractors	<i>csr</i>	notogaster, dorsal	apodeme 2 of the epimeres, apodemal shelves 3 and 4
coxisternal protractors	<i>csp</i>	notogaster, lateral	sejugal apodeme
inferior podosomal membrane adjustors	<i>ima</i>	anterior half of notogaster, ventrolateral	podosomal membrane
prodorsal dorsoventral muscles 1	<i>pdv1</i>	exobothridial field	lateral margin of apodemes 1
prodorsal dorsoventral muscles 2	<i>pdv2</i>	exobothridial field	lateral margin of apodemes 2
prodorsal dorsoventral muscles 3	<i>pdv3</i>	manubrium	sejugal apodeme
superior podosomal membrane adjustors	<i>sma</i>	notogaster, lateral	podosomal membrane
Endosternal Division of the Prosoma			
<i>EDP</i>			
anterior dorsal endosternal muscles	<i>ade</i>	manubrium	endosternum
posterior dorsal endosternal muscles	<i>pde</i>	notogaster, dorsolateral	endosternum
subcapitulum endosternal retractors	<i>ser</i>	endosternum	mentum of subcapitulum
taenidiphore endosternal retractors	<i>ter</i>	endosternum	taenidiphore
Longitudinal Division of the Prosoma			
<i>LDP</i>			
inferior prodorsal retractors	<i>ipr</i>	notogaster, dorsolateral	inferior retractor process, intercalary wall induration
prodorsum lateral adjustors	<i>pla</i>	notogaster, dorsolateral	manubrium
subcapitular retractors	<i>scr</i>	apodeme 1, 2 of the epimeres 1	anchoral process of subcapitular apodeme
superior prodorsal retractors	<i>spr</i>	notogaster, dorsal	basis of manubrium
Opisthosomal Compressor System			
<i>OCS</i>			
ventral plate adductors	<i>vpa</i>	preanal apodeme	genital valve
ventral plate compressors	<i>vpc</i>	preanal apodeme	lateral edge of genital valve
notogaster lateral compressors	<i>nlc</i>	notogaster, ventral curvature	anogenital membrane
cheliceral retractors	<i>chr</i>	posterior wall of prodorsum, sagittal apodeme	posterior surface of basal cheliceral segment
postanal muscles (= holovertral levators)	<i>poam</i>	terminal at posterior end of notogaster	postanal apodeme
trochanteral abductor	<i>tab</i>	endosternum	leg trochanter

Muscles that are directly involved in ptychoidity are grouped into four systems (Sanders & Norton 2004; Schmelzle et al. 2009; Tab. 1). Muscles not directly involved in ptychoidity (but nonetheless supporting the ptychoid process) are grouped together as 'additional muscles'. Those are the cheliceral retractor (*chr*), the trochanteral abductor (*tab*) and the postanal muscle (*poam*). These systems play different general roles in ptychoidity. (i) The *dorsoventral muscles of the prosoma* (DVP; Figs 4, 5) are responsible for retracting, protracting and correctly aligning the legs and the podosomal membrane in the idiosoma. (ii) The *endosternal division of the prosoma* (EDP; Fig. 6) comprises the muscles associated with the endosternum. Its main function is the retraction and correct alignment of the prodorsum in relation to the coxisternum and the subcapitulum. (iii) The *longitudinal division of the prosoma* (LDP; Fig. 7) is mainly responsible for retraction of the cheliceral and pedipalpal segments and the acron (epiprosoma) and for maintaining the encapsulated state. (iv) The function of the *opisthosomal compressor system* (OCS, Fig. 8) in ptychoidity is the build-up of sufficient haemocoel pressure for re-extension of the encapsulated animal. It is also responsible for building up pressure needed during the active state (extension of the legs, etc.).

The opisthosomal compressor system comprises three muscles according to Sanders and Norton (2004). The classification and nomenclature of the muscles involved is based on the morphology (associated muscle origin and insertion) of the euphthiracaroid mite *Euphthiracarus cooki* Norton et al. 2003.

To date, all detailed functional studies of ptychoidity are related to members of Euphthiracaroida (Akimov & Yastrebtsov 1991, Sanders & Norton 2004, Schmelzle et al. 2008, 2009, Yastrebtsov 1991) or cover only parts of the characteristics relevant to ptychoidity (e.g. the ano-genital system of *Phthiracarus nitens* in: Wauthy 1984). Here, we used the non-invasive technique of synchrotron X-ray microtomography to describe the morphology of exoskeletal and muscular elements in the phthiracaroid mite *Phthiracarus longulus* (C.L. Koch, 1841) (Phthiracaridae).

2. Materials and methods

Specimens

Phthiracarus longulus is a holarctic species of the family Phthiracaridae that has many synonyms (Niedbała 2008), of which the one most used in North American literature is *P. setosellus* (Jacot). It is common and abundant in temperate forest litter, where the non-ptychoid juvenile stages burrow within decaying woody substrates. Adults for our studies (mean total length about 540 µm) were collected from accumulated decaying needles and cone scales of introduced Norway spruce (*Picea abies*) in LaFayette, Onondaga Co., NY, USA.

Sample preparation

Specimens were killed and fixed in 1 % glutaraldehyde for 60 h and stored in 70 % ethanol. For the final preparation, specimens were dehydrated in an increasing ethanol series with steps of 70, 80, 90, 95 and 100 %, with three changes at each step and 10 min at each change. After storage in fresh 100 % ethanol they were critical-point dried in CO₂ (CPD 020, Balzers).

Scanning electron microscopy

Critical-point dried specimens were glued onto a T-section-like metal foil on a stub and then sputtered with a 20 nm thick layer of a gold-palladium mixture. Micrographs were taken on a Cambridge Stereoscan 250 Mk2 scanning electron microscope at 20 keV.

Synchrotron X-ray microtomography

Critical-point dried animals were fixed by the notogaster to the tip of a plastic pin (1.2 cm long; 3.0 mm diameter) using instant adhesive. For each specimen, typically 1500 radiographs under different projection angles were taken at the European Synchrotron Radiation Facility (ESRF) in Grenoble using beamline ID19 with a beam energy of 20.5 keV and using a sample-detector distance of 20 mm. A cooled 14-bit CCD-camera with a resolution of 2048 x 2048 pixels and an effective pixel size of 0.3 µm per pixel was used (a detailed description of the method is given in Betz et al. 2007, Heethoff & Cloetens 2008, Heethoff et al. 2008).

The data were visualised with the program VGStudio MAX 1.2.1 (Volume Graphics, Heidelberg, Germany) and three-dimensional modeling of muscles and cuticular elements was conducted with amira™ 4.0.1 (Mercury Computer Systems Inc., Chelmsford, MA). Muscle fibres were counted using the original phase contrast microtomography data or, if that was not possible, by the number of split ends in the resulting 3D model. Different portions of muscles are called muscle bands and subdivisions of muscle bands are called muscle fibres (Sanders & Norton 2004).

Terminology

Since phthiracaroid mites differ from euphthiracaroid mites in some morphological characteristics, some of the muscle names would in this case be misleading. For reasons of simplicity and comparability we will address the muscles of the opisthosomal compressor system according to Schmelzle et al. (2009) throughout the manuscript. We will address the issue of the muscles (origin, insertion and the therefore resulting name) in detail in the discussion (cf. Tab. 2).

Tab. 2 Comparison of muscle names of the Opisthosomal Compressor System (OCS) used in the literature.

Schmelzle et al. (2009)	Hoebel-Mävers (1967, in German) ¹	Sanders & Norton (2004)	Heethoff & Norton (2009) ²	origin	insertion in Euphthiracaroida	insertion in Phthiracaroida
ventral plate adductor (<i>vpa</i>)	<i>G.MU.</i>	holoventral adductor (<i>hva</i>)	muscles of the genital plate (<i>gm</i>)	preanal apodeme	genital region of the ventral plates	genital valve
ventral plate compressor (<i>vpc</i>)	<i>PR.A.MU.</i> ('Praeanale Spannmuskeln')	holoventral compressor (<i>hvc</i>)	preanal muscles (<i>pram</i>)	preanal apodeme	lateral edge of the genital plates	lateral edge of the genital valve
notogaster lateral compressor (<i>nlc</i>)	<i>NOT.MU.</i> ('Notogastrale Depressor-Muskelbänder')	notogaster lateral compressor (<i>nlc</i>)	outer anal muscles (<i>oam</i>)	ventral curvature of the notogaster	lateral edge of the ventral plates	anogenital membrane

¹ On the non-ptychoid mite *Nothrus palustris* KOCH.

² On the non-ptychoid mite *Archezogetes longisetosus* AOKI.

3. Results

3.1 Exoskeletal elements

Prodorsum

The interior surface of the prodorsum (*PR*) is uniformly textured (Figs. 2B, 3) and is differentiated into the solid, distal rostral limb (*rl*; Fig. 3B), the rosthrophragma and the tegulum (not shown). The inferior retractor process (*irp*), located at about mid-length of the prodorsum on the ventrolateral inner border, is broad, robust and long and is angled anteromedially at about 45° (Figs. 2B, 3). The manubrium (*mn*) at the posterolateral end of the prodorsum is rather short and slim (Figs. 2B, 3A, B). The sagittal apodeme (*sa*) is located medially on the posterior wall of the prodorsum and shows a triangular cross section (Figs. 2, 3B, D). The rounded bothridial scale (*bs*) overhanging the bothridium and base of the sensillus (*ss*) laterally on the prodorsum (Fig. 3A, D) is, in the encapsulated state, firmly anchored in the corresponding scale receptacle (*sr*) resting in the tectonotal notch (*tn*) on the anterior margin of the notogaster (Figs 3D, 4A). The short, medially thickened sensillus (= bothridial seta; *ss*) originates in the cup-like bothridium positioned below the bothridial scale (*bs*) and, in the encapsulated state, partly lies in a notogastral indentation – therefore pointing ventrally (Figs 1B, 3C). The bothridium is internally surrounded by a system of chambers (Figs 2B, 3C,D). A longitudinal carina (*car*) is present on each side of the prodorsum (Figs. 3A, 5). The carina originates at the bothridial scale and proceeds to the anterior tip of the prodorsum, where it gradually effaces. There is no evidence of a rostral notch (Fig. 3A).

Opisthosomal venter

The venter consists of two pairs of large compound plates, the genital (fused genital and a genital plates) and anal (fused anal and adanal plates) valves (*gv* and *av*, respectively), which are smooth and lack indication of the fusion between components. Collectively, the valves are broad, narrowing only slightly posteriorly, with the anal valves being rounded posteriorly (Fig. 1A; *av*). The valves are embedded in the pliable anogenital membrane that connects them with the notogaster (Figs. 2, 8; *mem*). The preanal apodeme (Fig. 2; *pra*) extends across the whole width of the ventral plates, whereas the postanal apodeme (*poa*) is relatively narrow and confined to the posterior end of the anal valves (Fig. 2; *av*). Each pair of valves is also connected transversely: the genital valves (*gv*) are integrally connected to each other anteriorly by the phragmatal bridge (Fig. 3C, D; *pbr*), whereas the anal valves (*av*) are only functionally connected at two locking points. The latter include the left-fitting or right-fitting anterior anal lock, consisting of two corresponding, interdigitating apophyses on each side (partly visible on the surface; Figs. 1A, D, 2B), and the posterior anal lock, consisting of 2–3 small corresponding lobes on each side (Fig. 2B). Among the 67 examined specimens, 40 individuals showed the right-fitting and 27 the left-fitting state. Hence the state of the anterior lock is uniformly distributed (LR $\chi^2 = 2.5385$, d.f. = 1, $P = 0.1111$). Each genital valve has a distinct transverse carina in the anterior region (Figs 1C, 2B; *car*) and a special notch at each anterolateral corner that enables some sort of articulation with a corresponding tooth of the notogaster (Fig. 1A, C).

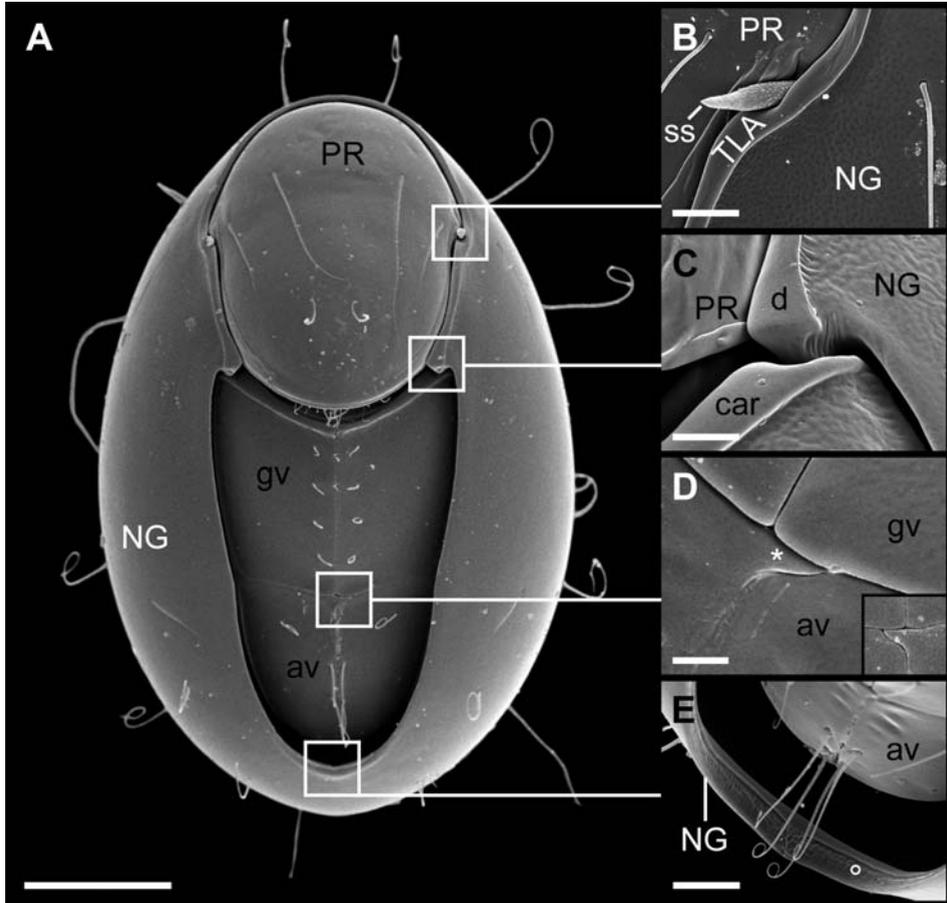


Fig. 1 *Phthiracarus longulus*. Scanning electron micrographs of 3 specimens (specimen 1: A, B, E; specimen 2: C; specimen 3: D). A: Ventral overview of encapsulated specimen (the withdrawn position of the ventral plates and the curled ends of notogastral setae are considered fixation artifacts; scale bar: 200 μ m); B: Detail of the bothridial scale, the sensillus and the tectonotal notch (scale bar: 20 μ m); C: Detail of the articulation of ventral plates and notogaster (scale bar: 10 μ m); D: Detail of the right-fitting (bottom right corner) and left-fitting state of the anterior anal lock (scale bar: 20 μ m); E: Detail of the simple U-shaped ventral margin of the notogaster (scale bar: 20 μ m). av: anal valve; car: carina; d: tooth; gv: genital valve; NG: notogaster; PR: prodorsum; TLA: lateral anterior tectum. Asterisk (*) indicates the left-fitting state of the anterior lock of the anal plates and degree (°) indicates the U-shaped plain lateral margin of the notogaster.

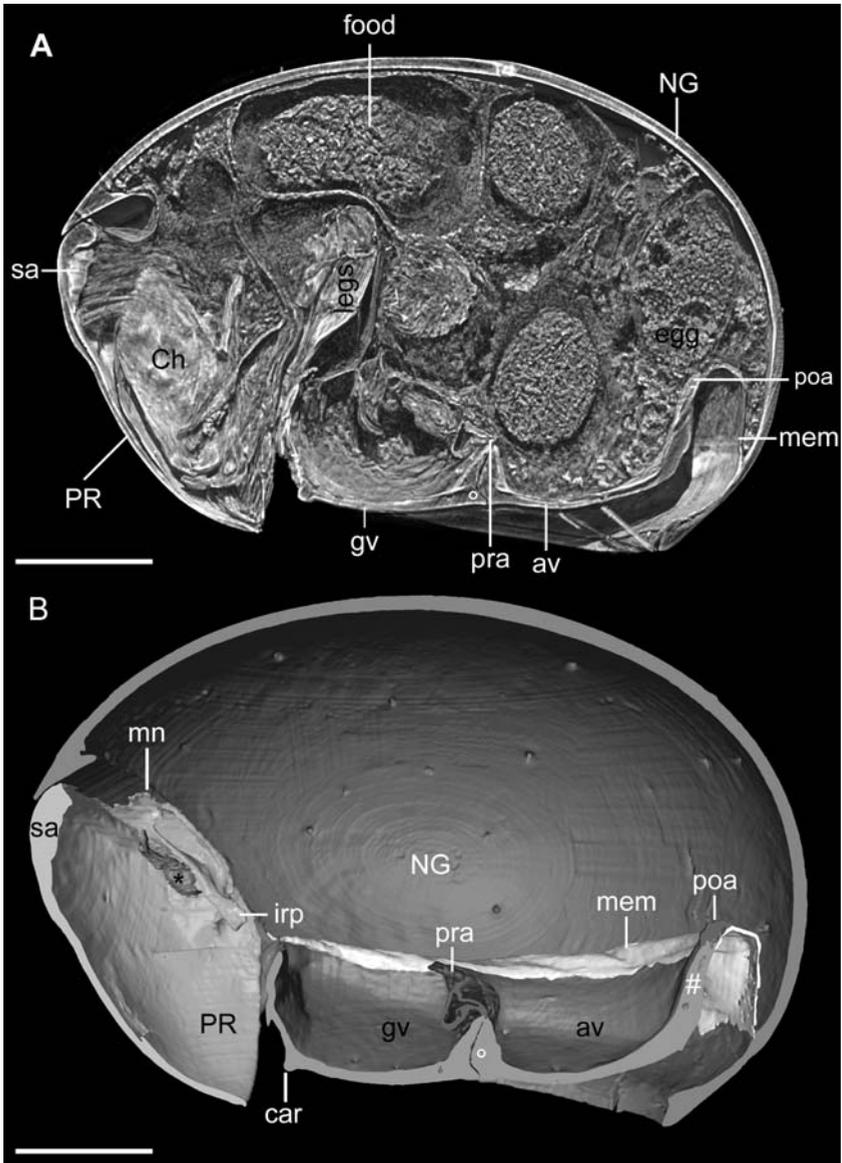


Fig. 2 *Phthiracarus longulus*, nearly encapsulated animal. A: Virtual sagittal section of a rendition of synchrotron X-ray microtomography data (scale bar: 100 μm); B: Virtual sagittal section of 3D-model of synchrotron X-ray microtomography data (scale bar: 100 μm). ap: anal plate; av: anal valve; car: carina; Ch: chelicera; food: food bolus; gp: genital plate; gv: genital valve; irp: inferior retractor process; mem: anogenital membrane; mn: manubrium; NG: notogaster; PR: prodorsum; pra: preanal apodeme; poa: postanal apodeme; sa: sagittal apodeme. Asterisk indicates the bothridium, degree indicates the anterior anal lock and pound indicates posterior anal lock.

Notogaster

The notogaster (*NG*) is hardened and quite thick (Fig. 2). Except anteriorly, the U-shaped ventral margin is more or less plain (Figs. 1A, E, 2), but at each anteroventral corner is a tooth (*d*) that articulates with the ventral plates, and that extends internally into a ridge (Fig. 1C). There is no terminal notogastral fissure (Fig. 1A). The border is provided with a tectum throughout, separated into two main parts, on either side of the corner tooth. The anterior tectum accommodates the prodorsum when encapsulated (Figs. 2B, 4A) and consists of the lateral anterior tectum (Fig. 1B; *TLA*), which encompasses the tectonotal notch (*tn*, Fig. 1A) and smoothly transitions into the pronotal tectum (*TPN*) at a point dorsally of the tectonotal notch. Posterior to the tooth the tectum (Fig. 4B) protects the articulation with the collective ventral plates. A scale receptacle (*sr*) inside the tectonotal notch is present (Figs. 1B, 3D).

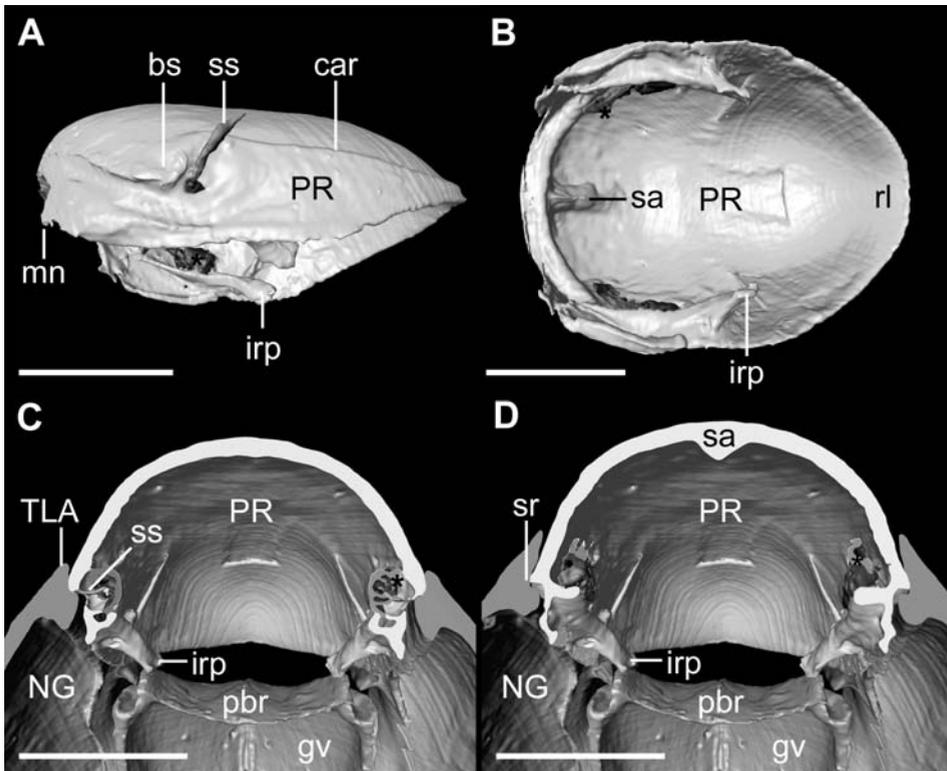


Fig. 3 *Phthiracarus longulus*, nearly encapsulated animal. Renderings of 3D-model of synchrotron X-ray microtomography data. A: Lateral view of the prodorsum (scale bar: 100 μ m); B: Ventral view of the prodorsum (scale bar: 100 μ m); C: Virtual frontal section in the region of the opening of the bothridium (scale bar: 100 μ m); D: Virtual frontal section in the region of the scale receptacle (scale bar: 100 μ m); bs: bothridial scale; car: carina; gv: genital valve; irp: inferior retractor process; mn: manubrium; NG: notogaster; pbr: phragmatal bridge; PR: prodorsum; rl: rostral limb; sa: sagittal apodeme; sr: scale receptacle; ss: sensillus; TLA: lateral anterior tectum. Asterisk (*) indicates the bothridium.

Podosoma

The coxisternum, forming the ventral center of the podosoma, encompasses the coxisternal umbilicus, a large area of membrane capable of compensating for the change of coxisternal form during ptychoid movement. Three articulations, or furrows, are present (not shown; compare Sanders & Norton 2004): the abjugal line (marking the intersection of podosomal membrane and the epiprosoma), the sejugal line (marking the intersection of hysterosoma and proterosoma) and the disjugal line (marking the intersection of podosomal membrane and opisthosoma). The areas of muscle insertion located in the membranous part of the podosoma do not seem to differ in any way from the rest of the podosomal membrane (Fig. 4B).

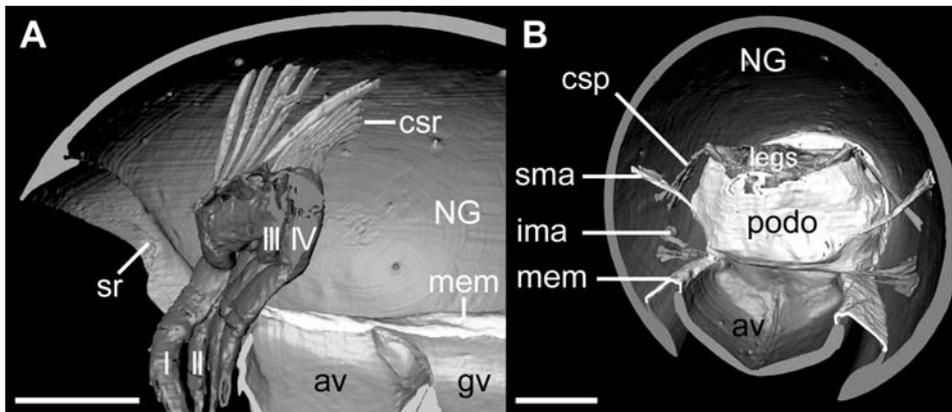


Fig. 4 *Phthiracarus longulus*, nearly encapsulated animal. DVP. Renderings of 3D-model of segmented synchrotron X-ray microtomography data. A: Virtual sagittal section showing the coxisternal retractor (csr) and its origin and insertion (scale bar: 100 μ m); B: Virtual cross section showing the inferior (ima) and superior (sma) membrane adjusters and the newly discovered coxisternal protractor (csp; scale bar: 100 μ m); I–IV: walking legs 1–4; av: anal valve; csp: coxisternal protractor; csr: coxisternal retractor; gv: genital valve; ima: inferior membrane adjuster; mem: anogenital membrane; NG: notogaster; podo: podosomal membrane; sma: superior membrane adjuster; sr: scale receptacle.

Subcapitulum

The capitular apodeme is developed as a large triangular, flat process with margins reinforced by a lemniscus (Figs. 6A, 7C). The mentum projects posteriorly in a shape similar to that of the capitular apodeme (Figs. 6A, 7C). The taenidiophore is located laterally between the base of the capitular apodeme and the projection of the mentum (Fig. 6A).

3.2 Muscular elements

Dorsoventral muscles of the prosoma (DVP)

The coxisternal retractor (csr) of *Phthiracarus longulus* consists of about 20 to 30 muscle fibres, originating dorsally on the notogaster and inserting on apodeme 2 and apodemal shelves 3 and 4 of the epimeres (Fig. 4A). The newly discovered coxisternal protractor (csp)

originates lateral on the notogaster and inserts directly onto the lateral margin of the sejugal apodeme (Fig. 4B). It consists of about 3 muscle fibres and is in encapsulated state directed dorsoposteriorly. The inferior and the superior podosomal membrane adjustors (*ima* and *sma*, respectively) both originate laterally on the notogaster and insert on the podosomal membrane (Fig. 4B).

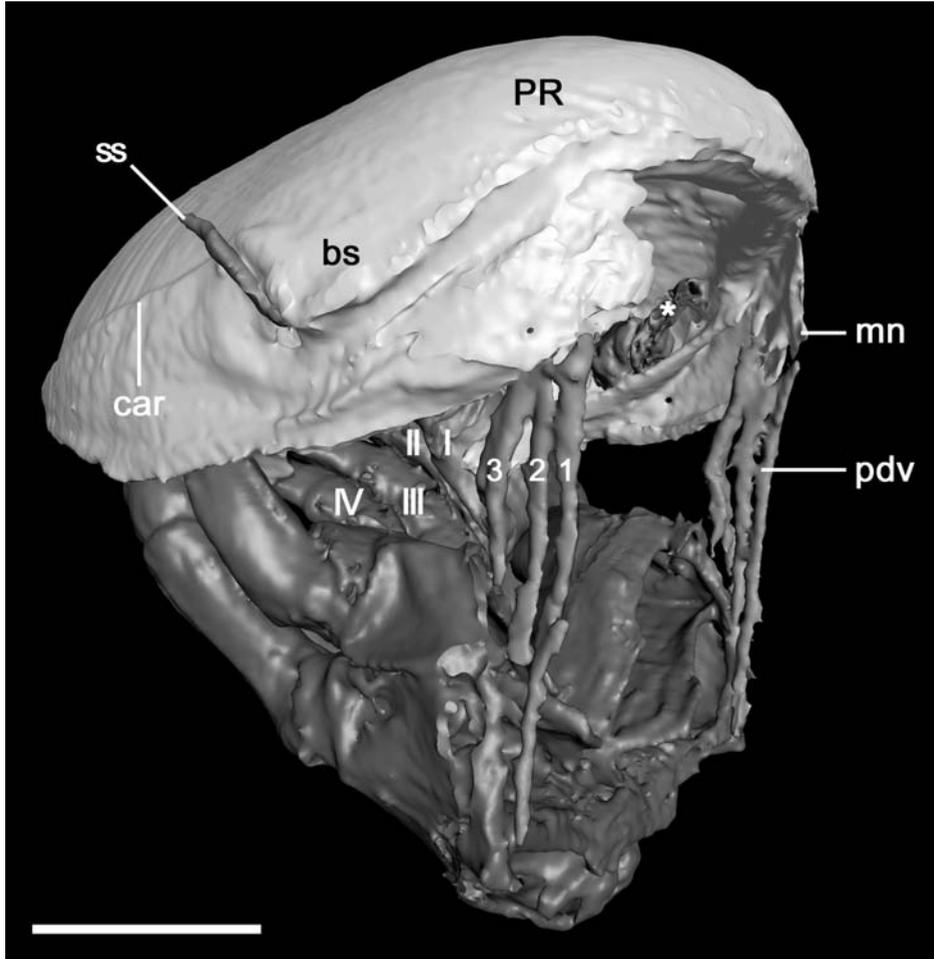


Fig. 5 *Phthiracarus longulus*, nearly encapsulated animal. Renderings of 3D-model of segmented synchrotron X-ray microtomography data of the prodorsum and podosoma, showing the prodorsal dorsoventral (DVP) muscle system (pdv1, pdv2 and pdv3), lateral view (scale bar: 50 μ m). I-IV: walking legs 1-4; bs: bothridial scale; car: carina (dorsal and ventral); irp: inferior retractor process; mn: manubrium; pdv1-3: prodorsal dorsoventral muscle 1-3; PR: prodorsum. Asterisk indicates the bothridium..

As the name implies, the inferior podosomal membrane adjustor (consisting of two muscle bands with 8 muscle fibres each) is situated more ventrally than the superior podosomal membrane adjustor (consisting of 2 muscle fibres) is. The *ima* inserts on the podosomal membrane via tendons, whilst the *sma* inserts directly. The prodorsal dorsoventral muscle (*pdv*) comprises three portions (Fig. 5; *pdv1*, *pdv2*, *pdv3*). *Pdv1* (two muscle fibres) and *pdv2* (one muscle fibre) originate on the exobothridial field and insert on the lateral margin of apodemes 1 and 2, respectively. *Pdv3* consists of only one muscle fibre; it originates ventrally on the manubrium and inserts on the sejugal apodeme.

Endosternal division of the prosoma (EDP)

The anterior and posterior dorsal endosternal muscles (*ade* and *pde*, respectively) each consists of at least two muscle fibres (Fig. 6B). Both muscles insert on the endosternum, but the *ade* originates on the tip of the manubrium, whilst the long, thin *pde* originates dorsolaterally on the notogaster at about its midlength. The subcapitulum endosternal retractor (*ser*) and the taenidiophore endosternal retractor (*ter*) both consist of two muscle fibres and have the endosternum as a common origin (Fig. 6A). The *ser* inserts on the mentum of the subcapitulum and the *ter* inserts on the tip of the taenidiophore (whether via a tendon or not was not determined).

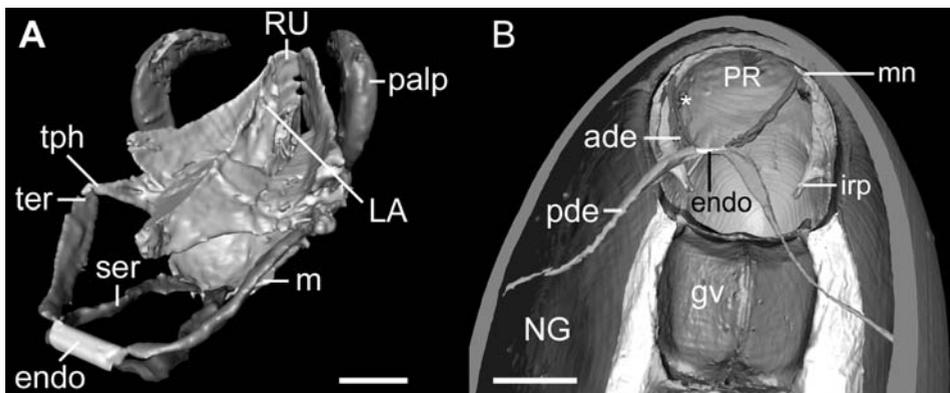


Fig. 6 *Phthiracarus longulus*, nearly encapsulated animal. EDP. Renderings of 3D-model of segmented synchrotron X-ray microtomography data. A: Subcapitulum (*ser*) and taenidiophore endosternal retractor (*ter*), dorsolateral view (scale bar: 50 μ m); B: Anterior (*ade*) and posterior dorsal endosternal muscle (*pde*), dorsal view of virtual frontal section (scale bar; 100 μ m); *ade*: anterior dorsal endosternal muscle; *av*: anal valve; *endo*: endosternum (in this form not visible in original data, but for reasons of clearness reconstructed this way); *gv*: genital valve; *irp*: inferior retractor process; *LA*: labrum; *m*: mentum of subcapitulum; *mem*: anogenital membrane; *NG*: notogaster; *palp*: palpus; *pde*: posterior dorsal endosternal muscle; *PR*: prodorsum; *RU*: rutellum; *ser*: subcapitulum endosternal retractor; *ter*: taenidiophore endosternal retractor; *tph*: taenidiophore. Asterisk (*) indicates the bothridium.

Longitudinal division of the prosoma (LDP)

The inferior prodorsal retractor (*ipr*) consists of about 20–25 muscle fibres (Fig. 7A). It originates dorsolaterally on the notogaster (at about the same level as the coxisternal retractor) and inserts via tendons on the inferior retractor process and the intercalary wall induration of the prodorsum. The prodorsum lateral adjustor (*pla*) comprises two muscle bands with two muscle fibres each (Fig. 7B). The origin is dorsal on the first quarter of the notogaster. The narrow insertion is via a tendon on the short manubrium. The subcapitular retractor (*scr*) also consists of two muscle bands with two muscle fibres (Fig. 7C).

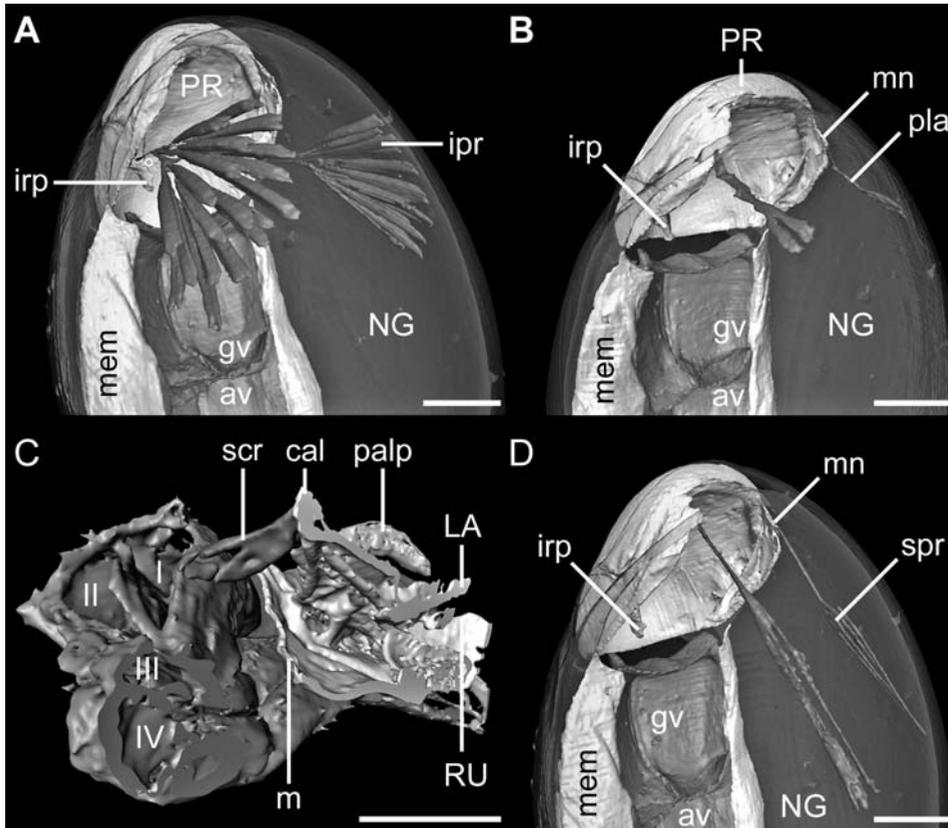


Fig. 7 *Phthiracarus longulus*, nearly encapsulated animal. LDP. Renderings of 3D-model of segmented synchrotron X-ray microtomography data. A: Dorsolateral view of anterior half with transparent notogaster, showing both sets of inferior prodorsal retractors (*ipr*, scale bar: 50 μ m); B: Same, showing prodorsum lateral adjustors (*pla*, scale bar: 50 μ m); C: Subcapitular retractor (*scr*), posterolateral view of virtual sagittal section of the reconstructed 3D-model of the legs and subcapitulum (scale bar: 100 μ m); D: Same as in A showing superior prodorsal retractors (*spr*, scale bar: 50 μ m). I–IV: walking legs 1–4; av: anal valve; cal: lemniscus of the capitular apodeme; gv: genital valve; ipr: inferior prodorsal retractor; irp: inferior retractor process; LA: labrum; m: mentum of subcapitulum; mem: anogenital membrane; mn: manubrium; NG: notogaster; palp: pedipalp; pla: prodorsum lateral adjustor; PR: prodorsum; RU: rutellum; spr: superior prodorsal retractor.

It originates on the first and second apodeme of the coxisternum and inserts directly on the anchoral process of the subcapitular apodeme. The superior prodorsal retractor (*spr*) originates as 2–4 muscle fibres dorsally on the notogaster at about half its length and inserts via a single tendon on the manubrium (Fig. 7D).

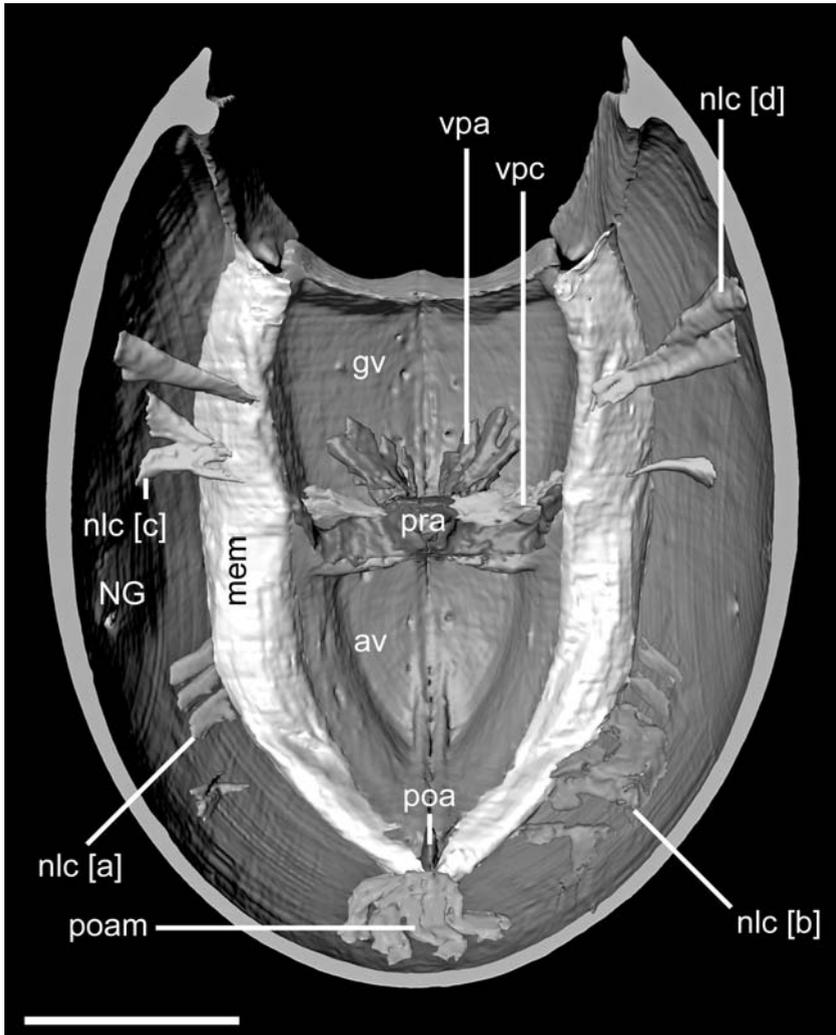


Fig. 8 *Phthiracarus longulus*, nearly encapsulated animal. OCS. Renderings of 3D-model of segmented synchrotron X-ray microtomography data, dorsal view of virtual frontal section (scale bar: 100 μ m). av: anal valve; gv: genital valve; mem: anogenital membrane; NG: notogaster; nlc [a]: portion a of notogaster lateral compressor; nlc [b]: portion b of notogaster lateral compressor; poa: postanal apodeme; poam: postanal muscle; pra: preanal apodeme; vpa: ventral plate adductor; vpc: ventral plate compressor..

Opisthosomal compressor system (OCS)

The ventral plate adductor (*vpa*) and the ventral plate compressor (*vpc*) both originate on the preanal apodeme (Fig. 8). The ventral plate adductor runs diagonally towards its more anterior insertion on the genital valves and consists of at least 12 muscle fibres, probably subdivided into six muscle bands with two muscle fibres each. The ventral plate compressor is directed laterally and inserts entirely on the genital valves and consists of five muscle bands with an unknown number of muscle fibres. The notogaster lateral compressor (*nlc*) originates on the ventral curvature of the notogaster and inserts on the anogenital membrane; it is probably divided into four portions (compare discussion): portion a (three muscle bands with two muscle fibres each) and b (at least five muscle fibres) are restricted to the last third of the animal, at the level of the anal valves (Fig. 8; *nlc [a]*, *nlc [b]*). Portions c (two muscle bands) and d (two muscle bands with a total of about three muscle fibres) are located in the first half of the animal (Fig. 8; *nlc [c]*, *nlc [d]*).

Additional muscles

The cheliceral retractor (*chr*) originates on the exobothridial field and the sagittal apodeme (not shown). It inserts directly onto the posterior surface of the basal cheliceral segment. The trochanteral abductor (*tab*) originates on the endosternum and inserts on the inner surface of the leg trochanter (not shown). The cheliceral retractor and the trochanteral abductor have not been studied in detail because their role in the ptychoid mechanism is only indirect. The postanal muscle (*poam*; also known as the ‘holoventral levator’, Sanders & Norton 2004), originates terminally on the notogaster and inserts directly on the postanal apodeme; it consists of 10–15 muscle fibres (Fig. 8).

4. Discussion

A significant functional aspect of ptychoidy relates to how the animal accommodates large changes in internal volume and hemocoel pressure that must accompany the closing and opening of the body, and a related issue is how legs that attach to a coxisternum surrounded by extensive soft cuticle are sufficiently supported (Sanders & Norton 2004). Mites of the two superfamilies of Ptyctima – Phthiracaroida and Euphthiracaroida – have many similarities, but the external differences are significant and probably affect how haemocoel pressure is controlled, as well as other ptychoid functions. However, muscles systems have until now not been studied in detail for the Phthiracaroida. Below, we compare the morphological adaptations to ptychoidy between the Phthiracaroida (*Phthiracarus longulus*) and the Euphthiracaroida (*Euphthiracarus cooki*, Sanders & Norton, 2004; and *Rhysotritia ardua* Koch, 1841 and *Oribotritia banksi* Oudemans, 1916, Schmelzle et al. 2008, 2009) and also inside the Phthiracaroida (*Phthiracarus nitens* Nicolet, 1855, in: Wauthy 1984).

4.1 Comparison of exoskeleton

Prodorsum

The inner texture of the prodorsum of *Phthiracarus longulus* is uniform (Fig. 3B) as it is in *Euphthiracarus cooki* and *Rhysotritia ardua*, but it is rough-textured in *Oribotritia banksi*. The rostraphragma is well differentiated in all four species. The manubrium of *P. longulus*

(Figs. 2B, 3A) and *O. banksi* is relatively shorter than the elongated manubrium of *E. cooki* and *R. ardua*. Also, in *P. longulus* it looks more delicate than in the euphthiracaroid species. The inferior retractor process of *P. longulus* (Figs. 2B, 3) is longer than in the euphthiracaroid species, but the angle at which it is directed is similar in all species. Except for *O. banksi* all species possess a sagittal apodeme (Fig. 3B, D). The bothridial scale covers the bothridium and base of the sensillus from above in all species except for *E. cooki*, although in *P. longulus* it is shifted slightly posterior (Figs 3A, 5). In the encapsulated state the very short sensillus of *P. longulus* lies in a ridge between the prodorsum and the notogaster (Fig. 1B), whereas it becomes pinched between prodorsum and notogaster in *O. banksi* and *R. ardua*; it stands free in *E. cooki* because its origin is dorsal to the bothridial scale. The internal system of chambers and short tracheae around the bothridium (not described here in detail) differs from that of euphthiracaroid mites but probably has a similar respiratory function (Figs 3C, D, 5; Grandjean 1967, Norton et al. 1997)

Opisthosomal venter

The opisthosomal venter of *Phthiracarus longulus*, and phthiracaroid mites in general, essentially differs from that of euphthiracaroid mites. Unlike the latter, there are no hardened plicature plates in phthiracaroid mites; instead in its place is the broad and pliable U-shaped anogenital membrane (Figs 2, 8). Unlike the rather simple, elongated ventral plates of euphthiracaroid mites, those of *P. longulus* are rather boat-shaped with a flat lateral margin (Figs 1A, 2, 8). In the encapsulated state the surrounding anogenital membrane is safely stored inside the notogaster (Figs 2, 8). The structure of the anterior and posterior anal lock of *P. longulus* (Fig. 1A, D) is similar to that of *Hoplophthiracarus* sp. (van der Hammen 1989), although both, right-fitting and left-fitting, locks have been found to be uniformly distributed in *P. longulus* (and also in: Wauthy 1984, about *Phthiracarus nitens*; Parry 1979, about the genus *Phthiracarus* Perty 1841). The state of right-fitting or left-fitting anterior locks thus is a matter of intraspecific variation and not, like van der Hammen (1989) stated, a specific character with taxonomical value.

Notogaster

The U-shaped ventral margin of the notogaster perfectly matches that of the ventral plates, ensuring a tight connection during ptychosis. The presence of a broad marginal tectum (Fig. 4B) covering the articulation ensures that no membrane (stored inside the notogaster) is exposed to possible attack by predators (Figs 1E, 2, 8). Except for some derived members of Synichotritiidae (e.g. Norton & Lions 1992), euphthiracaroid mites lack a marginal tectum along the ventral edge of the notogaster. The scale receptacle (Fig. 3D) present inside the tectonotal notch resembles those of *E. cooki* and *R. ardua*, but the problem of a pinched sensillus (in *R. ardua* and *O. banksi*) is solved in *P. longulus* by having a ridge along which the resting sensillus can lie during encapsulation (Figs 1B, 4A). *Oribotritia banksi* completely lacks a scale receptacle; instead, the bothridial scale rests on the tectonotal notch during encapsulation. Both *P. longulus* and *O. banksi* lack a terminal notogastral fissure (Fig. 1A), which is an adaptation present in *E. cooki* and *R. ardua*. This fissure probably allows slightly more flexing in the rather rigid cuticle during lateral compression events, which are not part of the ptychoid process in *P. longulus*. The tooth at the anteroventral corner of the notogastral

margin in *P. longulus* (Fig. 1C) is also present in *E. cooki*, but not in *O. banksi* or *R. ardua*. In contrast to *E. cooki* this tooth is prolonged internally as a ridge in *P. longulus* and forms an articulation for the ventral plates. The tectonotal notch separates the anterior notogastral tectum into two parts (pronotal and lateral anterior tecta) in euphthiracaroid species, but not in *P. longulus* (Fig. 1A, B).

Podosoma and subcapitulum

The principal morphology of muscular insertion points on these structures is similar among studied phthiracaroid and euphthiracaroid species.

4.2 Comparison of musculature

Dorsoventral muscles of the prosoma (DVP)

The coxisternal retractor of *P. longulus* consists of 20–30 fibres (Fig. 4A), which is an intermediate number between that of Oribotritiidae (*O. banksi* with 80 muscle fibres) and Euphthiracaridae (*R. ardua* with 17 muscle fibres, *E. cooki* with 12 muscle fibres). Since *P. longulus* (540 µm total length) is intermediate in size between *E. cooki* (300 µm) and *R. ardua* (900 µm), this contradicts the general correlation we suggested earlier (Schmelzle et al. 2009) that the number of *csr* muscle fibres increases with body size within the Ptyctima. The correlation still holds within the Euphthiracaroida, so perhaps there is a slight difference between these groups in the relationship of muscle fibres to body size; more data are needed for confirmation. The coxisternal protractor (*csp*) originates anteriorly to the superior membrane adjustor and inserts directly onto the lateral margin of the sejugal apodeme (Fig. 4B). In the encapsulated state its dorsoposteriorly directed course suggests a role as protractor for the coxisternum during reopening of the animal. We assume a change of its working direction when switching to the active state (when the legs and coxisternum are protracted). Then the *csp* should be directed anteroventrally and probably assumes a role as an auxiliary and adjusting retractor for the coxisternum. None of the studied euphthiracaroid mites show any evidence of this muscle (Schmelzle et al. 2008, 2009). The inferior membrane adjustors are quite similar among the species. Whilst *P. longulus* has two muscle bands with eight muscle fibres (Fig. 4B), *O. banksi* has two muscle bands with ten muscle fibres and *R. ardua* also has two muscle bands with nine muscle fibres (unknown for *E. cooki*). Regarding the superior membrane adjustors, *P. longulus* with two single muscle fibres (Fig. 4B) resembles *E. cooki* (3–4 muscle fibres), but differs strongly from *O. banksi* (nine muscle fibres) and *R. ardua* (two muscle bands with 1–3 fibres each). Regarding its origin and insertion there is no essential difference noticeable amongst these species. Portions 1 and 2 of the prodorsal dorsoventral muscle do not differ among *P. longulus* (Fig. 5), *O. banksi* and *R. ardua*, but the third portion (*pdv3*) of *P. longulus* (Fig. 5) shows only one muscle fibre, while the other species have two.

Endosternal division of the prosoma (EDP)

The numbers of muscle fibres in the 4 muscles of the EDP are the same in *P. longulus*, *O. banksi* and *R. ardua*. The only difference among the studied species is that the taenidiophore endosternal retractor of *E. cooki* has only one muscle fibre (two in other

species; Fig. 6A). The anterior dorsal endosternal muscle seems to be relatively longer in *P. longulus* (Fig. 6B) than in *O. banksi* and *R. ardua*; its insertion is more similar to *O. banksi* (a similar small area of insertion probably because of the relatively short manubrium) than to *R. ardua* (a large manubrium). The taenidiophore endosternal retractor seems to either insert directly or via a very short tendon ($< 1 \mu\text{m}$) on the taenidiophore in *P. longulus* (Fig. 6A), but via a prominent tendon in all of the studied euphthiracaroid mites.

Longitudinal division of the prosoma (LDP)

The number of muscle fibres (mf) of the inferior prodorsal retractors correlates roughly with body size: *E. cooki* (13 mf, 300 μm body length); *P. longulus* (20–25 mf, 540 μm body length; Fig. 7A); *R. ardua* (28–32 mf, 900 μm body length); *O. banksi* (90–100 mf, 1800 μm body length). In all species studied they insert via tendons onto both the inferior retractor process and the intercalary wall induration of the prodorsum. The prodorsum lateral adjustor of *P. longulus* (Fig. 7B) is similar to that of *O. banksi* regarding number of muscle bands (two), muscle fibres (two), and its insertion on the manubrium via tendons. The *pla* of *R. ardua* has two muscle bands with a maximum of five muscle fibres and inserts broadly and directly on the manubrium. The subcapitular retractor seems identical in *P. longulus* (Fig. 7C), *O. banksi* and *R. ardua*, originating on both apodemes 1 and 2; in contrast it originates only on apodeme 1 in *E. cooki*. The superior prodorsal retractor appears to insert onto the basal part of the manubrium via a tendon in *P. longulus* (Fig. 7D), *O. banksi* and *R. ardua*, but directly in *E. cooki*; it consists of 2–4, 4, 4 and 3 muscle fibres, respectively.

Opisthosomal compressor system (OCS)

Because of the great variation in the associated cuticular plates, the terminology of muscles in this system has varied. Herein we use a more generalised terminology, proposed previously (Schmelzle et al. 2009; cf. Tab. 2). The ventral plate adductor of *P. longulus* consists of at least twelve muscle fibres, probably subdivided into two muscle bands with six muscle fibres each; it originates on the preanal apodeme and runs anteriorly to insert on the genital valve (Fig. 8). Compared to the *vpa* of *E. cooki* and *R. ardua* (*O. banksi* lacks the *vpa*) the number of muscle fibres is noticeably smaller, but the area of insertion is more restricted (only the posterior half of the genital valve). The insertion of the ventral plate compressor of *P. longulus* (five muscle bands with an unknown number of muscle fibres) also is limited to the genital valve, probably due to the broad extension of the preanal apodeme (Fig. 8). In *E. cooki* (five muscle bands with an unknown number of muscle fibres), *O. banksi* (25 muscle fibres) and *R. ardua* (10–20 muscle fibres) the *vpc* inserts on both the genital and anal valves of the ventral plates. It appears, that Wauthy (1984) combined in his ‘anterior median muscles’ (*MMA*; in his figure 2B) our muscles *vpa* and *vpc*, but differentiated the tendons (*tam* and *tpm*, respectively; his figure 1C). However, in the text he wrote that the origin of the *MMA* is dorsally on the notogaster. We believe this to be a confusion with the ‘lateral rectal muscle’ of Heethoff & Norton (2009; *lrm*). The notogaster lateral compressor of *P. longulus* has a gap between an anterior and a posterior part (the anal region; Fig. 8), whereas in euphthiracaroid species it runs continuously along nearly the complete length of the ventral plates. Accordingly the number of muscle bands and fibres is very different. In *P. longulus* the *nlc* has probably four portions. Portion a (Fig. 8; *nlc [a]*) is clearly visible, whilst portion b is hard to detect. The reconstruction therefore could only be done for the right side of the animal.

Portion c and d of the *nlc* are difficult to distinguish from the genital papillae retractors (not shown), because they overlap with the *nlc* on nearly their whole length and their origin laterally on the notogaster and the direction they run to (median) are essentially the same. In contrast to Wauthy's research on *P. nitens* (1984) we found the genital papillae retractors (his *pga*, *pgm* and *pgp*) to originate laterally on the notogaster and not on the genital valves (cf. Fig. 2B of Wauthy 1984). Wauthy (1984) also described four portions of the *nlc* (his MF_1 , MF_2 , MF_3 , and MF_4). His MF_4 thereby corresponds to our portions a and b of the *nlc*, his MF_3 to our portion c and the MF_2 to portion d of the *nlc*. We believe his MF_1 to be our *ima*, which inserts on the podosomal membrane, close to but not on the anogenital membrane. It yet is not fully understood if portions c and d really are portions of the *nlc* (as in Wauthy 1984) with insertion on the anogenital membrane or if they are portions of the genital papillae retractor (which would mean that Wauthy 1984 was wrong). Unfortunately, the spatial resolution of our data meets its limit in this case.

This makes it difficult to compare the results with the studied euphthiracaroid mites. In *P. longulus* the *nlc* has at least three muscle bands with two muscle fibres each (portion a) and a separate second portion (b) with about five muscle fibres. Also there are two additional portions (c, d) with two muscle bands with an unknown number of muscle fibres and two muscle bands with a total of about three muscle fibres, respectively. In contrast, in *E. cooki* the *nlc* has 21 muscle bands with an unknown number of muscle fibres, in *O. banksi* it has 30–34 muscle bands with 2–6 muscle fibres and in *R. ardua* it has 25 muscle bands with 3–6 muscle fibres. In the euphthiracaroid species the notogaster lateral compressor originates ventrally on the notogaster and inserts on the medial edge of the ventral plates, whilst in *P. longulus* it originates laterally on the notogaster and inserts on the anogenital membrane.

Additional muscles

The cheliceral retractor originates on both the exobothridial field and the sagittal apodeme of the prodorsum of *P. longulus*. The same is true of *R. ardua* and *E. cooki*, but in *O. banksi* there is no sagittal apodeme. The trochanteral abductor of *P. longulus* is well developed and appears to be in a single frontal plane, unlike in the euphthiracaroid species studied. The postanal muscle seems similar in all species. It consists of 10–15 muscle fibres in *P. longulus* (Fig. 8), eight muscle bands with 4–5 fibres each in *O. banksi*, and two muscle bands with 10–20 fibres each in *R. ardua*. Only in *O. banksi* it inserts through tendons onto the postanal apodeme. Our *poam* probably corresponds with the 'posterior median muscles' of Wauthy (1984; *MMP*). The number of muscle fibres drawn in his Fig. 2B (four muscle fibres) for *Phthiracarus nitens* appears in comparison to our findings in *P. longulus* to be very low.

5. Conclusions

In this study we have shown that phthiracaroid and euphthiracaroid mites clearly differ in a number of characters that relate to functional aspects of ptychoidy. The most prominent differences are in the morphology of the ventral plates, the presence or absence of plicature plates and a posterior notogastral tectum, the number of muscle bands and fibres (e.g. the postanal muscle), the origin/insertion of the notogaster lateral compressor and the newly discovered coxisternal protractor muscle. However, the location of the taenidiophore and its connection to the subcapitulum as well as the shape of the capitular apodeme support the common origin of both groups.

While the morphological differences are clear, their functional importance remains to be elucidated in the future.

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