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Mechanics of the ptychoid defense mechanism in Ptyctima (Acari, Oribatida): One problem, two solutions

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ABSTRACT

The most complex mechanical defense of oribatid mites is ptychoidy, in which the animals can retract their legs and gnathosoma into the idiosoma and encapsulate by deflecting the prodorsum. Since Acari lack most antagonistic musculature, extension of appendages is facilitated through hemolymph pressure that in mites mostly is generated by dorso-ventral compression of the opisthosoma. The hardened notogaster of box mites requires a different system of pressure generation that is also able to accommodate huge hemolymph movement accompanying ptychoidy. We compared the functional morphology of ptychoidy in one model species from each of the two ptyctime superfamilies, Euphthiracaroidea and Phthiracaroidea, using synchrotron X-ray microtomography and high-speed videography. We show that the two groups evolved very different functional modes of hydrostatic pressure control. While euphthiracaroids employ a lateral compression of the notogaster using all muscles of the opisthosomal compressor system, phthiracaroids employ a dorsoventral compression generated by only the notogaster lateral compressor and additionally the postanal muscle; these retract the temporarily unified ventral plates into the idiosoma, revealing the *poam* as an integral part of the opisthosomal compressor system in this group. The primitive mode of operation for generating hemolymph pressure in the Ptyctima probably was lateral compression, as molecular studies indicate that Phthiracaroidea evolved within Euphthiracaroidea. In this hypothesis, dorsoventral compression evolved secondarily in phthiracaroid mites, but whether the immediate ancestors of Ptyctima used lateral or dorsoventral compression remains to be determined.

1. Introduction

1.1. General

Oribatid mites are a speciose (9000 described species; Schatz, 2002) and old group of Devonian, Silurian or even Precambrian origin (Schaefer et al., 2010, and references therein). Reaching high densities of up to 400,000 individuals/m^2, they represent an important part of soil decomposer systems, and should also be a significant resource for soil predators (Heethoff et al., 2009). Their feeding mode (particle feeding; Norton, 2007; Heethoff and Norton, 2009a,b) and use of relatively low quality food are unusual for chelicerates and have been considered constraints that resulted – for most species – in comparatively slow movement, low reproductive potential and prolonged generation time (Norton, 1994; Sanders and Norton, 2004; Heethoff et al., 2007).

To achieve the long adult life necessary for reproduction, oribatid mites evolved various defensive strategies including mechanical, chemical and behavioral mechanisms. Chemical defense is based on the secretion of allomones from a pair of opisthonotal exocrine glands, and can be effective even against larger predators like rove beetles (Heethoff et al., 2011; Heethoff and Raspotnig, 2012; Heethoff, 2012). Mechanical defensive mechanisms include elongated setae that in some cases can also be erected (Norton, 2001), and cuticular hardening by sclerotization or additionally biomineralization using calcium carbonate, calcium oxalate or calcium phosphate (Norton and Behan-Pelletier, 1991a,b; Alberti et al., 2001). Behavioral defenses often go along with either chemical and/or mechanical mechanisms, *e.g.* flight behavior upon perception of alarm-pheromones, thanatosis (‘playing dead’) in combination with a turtle like “retraction” of the legs within protective cavities or under overhanging tecta (Schmid, 1988; Norton, 2001, 2007) or the ability to jump (Krisper, 1990; Wauthy et al., 1998).

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Table 1
Glossary of terms.

Term	Definition
Ptychoidy	The mechanism/body form/ability to encapsulate
Ptychosis	The process of changing between states/the process 'enabled' by the ptychoid body form
Enptychosis	The process of encapsulation
Ecptychosis	The process of extension/re-opening
Extended	The state of being extended/open. 'Active' mode of operation, *i.e.* walking, feeding, *etc.*
Encapsulated	The state of being encapsulated/closed. 'Inactive' mode of operation

The most complex mechanical defensive mechanism is ptychoidy (Sanders and Norton, 2004), in which the animals can effectively deflate the rather soft podosoma, retract their legs and gnathosoma into the idiosoma and encapsulate themselves (Fig. 1). This seems always to be combined with biomineralization (Pachl et al., 2012) and can in some species also be combined with chemical defense by secretion of repellents (*e.g.* chrysomelidial as shown for the euphthiracaroid mite genus *Oribotritia*; Raspotnig et al., 2008; Raspotnig, 2010) and rarely – as a mechanical and behavioral addition – also an escape-jump (Wauthy et al., 1998).

Ptychoidy probably evolved three times independently: one time each in the Ptyctima, the Mesoplophoridae and the Protoplophoridae (Grandjean, 1932, 1969; Norton, 1984, 2001; Sanders and Norton, 2004; Pachl et al., 2012). The Ptyctima consist of the two ptychoid superfamilies Euphthiracaroidea (comprising the families Euphthiracaridae, Oribotritiidae and Synichotritiidae) and Phthiracaroidea (comprising only one family, the Phthiracaridae) (Fig. 2). Ptychoidy is enabled through a system of exoskeletal and muscular elements and has four different systems of muscles that are actively involved in enptychosis, the process of encapsulation (Sanders and Norton, 2004; *cf.* Table 1). It seems to be highly effective: rove beetles of the genus *Stenus* are not able to crack the cuticle of *Euphthiracarus cribrarius* (Berlese, 1904) (own unpublished observations). Interestingly, ptychoidy is ineffective against *Euconnus pubicollis* (Müller and Kunze, 1822), a rove beetle of the sub-family Scydmaeninae, who given a choice of heavily protected oribatid mites prefers species of the family Phthiracaridae to others (Jałoszyński and Olszanowski, 2013).

So far the morphology associated with ptychoidy has been well studied within Euphthiracaroidea and Phthiracaroidea (Sanders and Norton, 2004; Schmelzle et al., 2008, 2009, 2010, 2012), but the mechanics behind it have been studied only by Sanders and Norton (2004) for *Euphthiracarus cooki* (Norton, Sanders and Minor, 2003). Like Acari in general, both groups lack most antagonistic musculature (except *e.g.* in the claws and chelicerae; Heethoff and Koerner, 2007; Heethoff and Norton, 2009b), such that movements of appendages, *e.g.* the straightening of a flexed leg segment, require a hydraulic system. This system becomes especially important in ptychoidy, as ecptychosis is also achieved through hydraulic pressure. This process of reopening requires forced displacement of the relatively large volumes of fluid needed to re-inflate the podosoma and protrude the legs and gnathosoma. In species of Euphthiracaroidea, this hydraulic action seems to be facilitated by only one active system, the so-called opisthosomal compressor system (OCS; Sanders and Norton, 2004; Fig. 3). This muscle system exists in species of the other superfamily, Phthiracaroidea, as well (Schmelzle et al., 2010, 2012), but the morphology of the ventral plates (*cf.* Schmelzle et al., 2008, 2010) and at least one of the muscles of the OCS suggest a different mode of operation that also involves the postanal muscle (*poam*), so far not included in the OCS.

Another morphological peculiarity is the coxisternal protractor (*csp*) so far found only within the genus *Phthiracarus* (Schmelzle et al., 2010, 2012) but none of the euphthiracaroid species. Its position indicates a direct involvement and a unique mode of operation in ptychoidy.

To investigate and compare these subjects in both ptyctime superfamilies, we used synchrotron X-ray microtomography and high-speed videography. Before proceeding and going into detail, it is necessary to summarize and compare some morphological details of the two superfamilies.

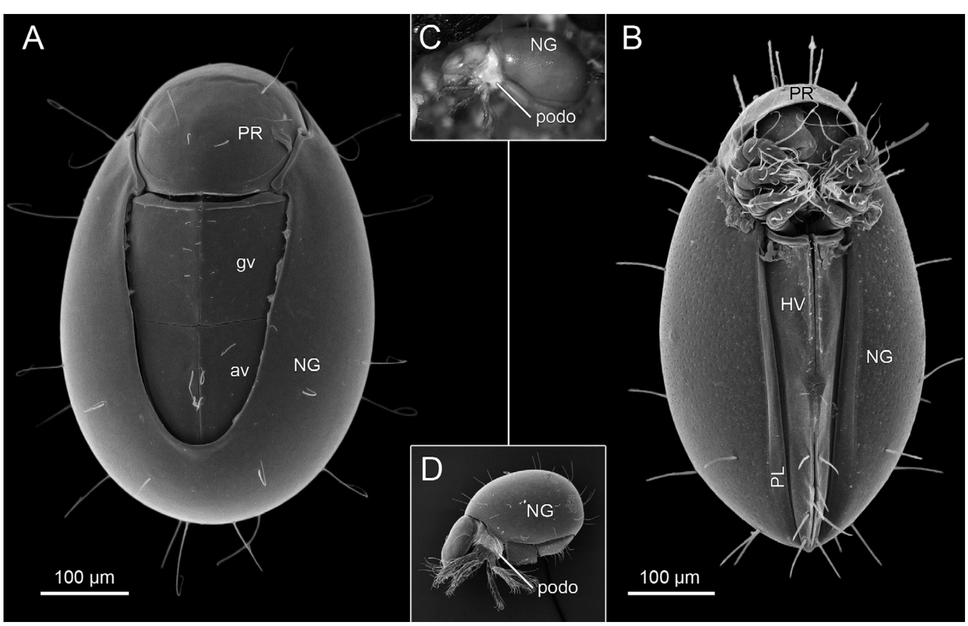

Fig. 1. Scanning electron micrographs of (A) phthiracaroid species *Phthiracarus longulus* in encapsulated state and (B) euphthiracaroid species *Acrotritia ardua* in partially encapsulated state, ventral view. Lateral view of phthiracaroid species (C) *Hoplophthiracarus* sp. (light microscopic image) and (D) *Phthiracarus* sp. (scanning electron micrograph). (C–D) In the extended state the soft podosomal membrane (highlighted) connecting the notogaster, coxisternum, gnathosoma and prodorsum is visible. av, anal valves; gv, genital valves; HV, holoventral plates; NG, notogaster; PL, plicature plates; podo, podosomal membrane; PR, Prodorsum. Source of (D): Marilyn Clayton, Natural Resources Canada, Canadian Forest Service, 2013.