



Suitability of cuticular pores and sensilla for harpacticoid copepod species delineation and phylogenetic reconstruction



Tomislav Karanovic^{a, b, *}, Kichoon Kim^a

^a Hanyang University, Department of Life Sciences, Seoul 133-791, Republic of Korea

^b University of Tasmania, Institute for Marine and Antarctic Studies, Hobart, Tasmania 7001, Australia

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ABSTRACT

Cuticular organs have not been described systematically in harpacticoids until recently, and they have never been used as characters for reconstructing phylogenetic relationships in any crustacean group. We survey cuticular pores and sensilla on somites in ten Miraciidae species, belonging to six genera, from Korea, Australia, and Russia. Nine species belong to the subfamily Stenheliinae, while the outgroup belongs to the subfamily Diosaccinae. We aim to compare phylogenetic trees reconstructed for these harpacticoids based on: 1) cuticular organs (with 76 characters scored, 71% of them phylogenetically informative); 2) traditionally used macro-morphological characters (66 scored, 77% of them informative); and 3) mtCOI DNA data. All analyses suggest that cuticular organs are useful characters for harpacticoid species delineation, although not as sensitive as some fast-evolving molecular markers. Reconstructed cladograms based on all three datasets show very high bootstrap values for clades representing distinct genera, suggesting that cuticular organs are suitable characters for studying phylogenetic relationships. Bootstrap values for the more basal nodes differ among the different cladograms, as do the sister-group relationships they suggest, indicating that cuticular organs probably have different evolutionary constraints from macro-morphological characters. Cuticular organs could be quite useful in the study of old museum specimens and fossil crustaceans.

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1. Introduction

All arthropods have their bodies covered by a rigid cuticle, which protects their inner organs and tissues but at the same time impedes communication with the surrounding environment. A significant proportion of this communication is thus achieved through sensilla and pores, small cuticular organs which cover vast areas of their body (Hallberg and Hansson, 1999). Their very different size, structure, number, and function suggest that it would be difficult to homologize them in different arthropod groups (Keil, 1997; Crouau, 1997; Hallberg and Skog, 2011), although some researchers have implied this through common or analogous terminologies for insect and crustacean cuticular organs (Shelton and Laverack, 1968; Fleminger, 1973). Even within Crustacea their diversity is astonishing. A quick look through several complete or partial surveys of cuticular organs in some groups of decapods

(Mauchline et al., 1977), amphipods (Oshel et al., 1988; Zimmer et al., 2009), isopods (Powell and Halcrow, 1982; Khalaji-Pirbalouty, 2014), branchiopods (Cash-Clark and Martin, 1994; Olesen, 1996; Boudrias and Pires, 2002), cephalocaridans (Elofsson and Hessler, 1994), ostracods (Puri, 1974; Meisch and Wouters, 2004), and copepods (Von Vaupel Klein, 1982a) reveals a plethora of specialized sensilla and pores (and their terminology), some of which hold a potential to increase the number of recognized synapomorphies for certain taxa. According to Von Vaupel Klein (1982a) the total diversity of cuticular organs reported for copepods alone comprises at least some twenty distinct types. Unfortunately, there has never been a phylogenetic reconstruction of crustaceans, nor any groups thereof, based on cuticular organs, despite the fact that many studies have advocated this potential and proposed some groupings based on intuitive methods (Puri, 1974; Mauchline, 1988; Tsukagoshi, 1990; Olesen, 1996; Høeg and Kolbasov, 2002). This is in stark contrast with taxonomic and phylogenetic practices in some other groups of small animals with a rigid integument, such as, for example, insects (Bousquet and Goulet, 1984; Alarie, 1995, 1998; D'Haese, 2003; Fauchaux et al., 2006), tardigrades (Nichols et al., 2006), and kinorhynchans (Nebelsick, 1992; GaOrdóñez et al., 2000; Sørensen et al., 2012).

* Corresponding author. Hanyang University, Department of Life Sciences, Seoul 133-791, Republic of Korea. Tel.: +82 10 5787 0951.

E-mail addresses: Tomislav.Karanovic@utas.edu.au, tomislavkaranovic@hotmail.com (T. Karanovic).

The first comprehensive survey of cuticular organs in copepods was done by [Fleminger \(1973\)](#), who mapped and coded perforation sites of the dorsal and lateral parts of body tergites in the calanoid genus *Eucalanus* Dana, 1853, and demonstrated their taxonomic relevance. Additional data for calanoid copepods were supplied by [Strickler \(1975\)](#), [Mauchline \(1977\)](#), [Mauchline and Nemoto \(1977\)](#), [Von Vaupel Klein \(1982a,b\)](#), and [Malt \(1983\)](#), among other minor contributions. [Mauchline \(1988\)](#) examined the pattern of sensilla and pores in the five metasomal segments of 249 species belonging to 89 genera of calanoid copepods; this was the largest ever comparative study of this nature in any group of arthropods. Two major problems with this study were the absence of raw data for individual species (instead, a generalized pattern for genera was presented) and the abrasive nature of the chemicals employed for preparation and staining, which made it impossible to distinguish pores from sensilla. Although [Mauchline \(1988\)](#) concluded that the metasomal pattern of cuticular organs represents a species signature, the promised forthcoming publications that would deal with species and genera in more detail have never been published. Unfortunately, very few researchers continued to study this topic in calanoid copepods subsequently ([Koomen, 1992](#); [Koomen and Von Vaupel Klein, 1997, 1998](#)), and cuticular organs have not been used in recent taxonomic or phylogenetic studies ([Bradford-Grieve et al., 2010](#); [Blanco-Bercial et al., 2011](#)). Sensilla and pores have received even less attention among researchers working on cyclopoid copepods, although all studies undeniably showed their great potential ([Strickler, 1975](#); [Baribwegure and Dumont, 1999](#); [Baribwegure et al., 2001](#); [Baribwegure and Mirabdullayev, 2003](#); [Alekseev et al., 2006](#); [Karanovic and Krajcicek, 2012a](#); [Karanovic et al., 2013a](#)). [Karanovic and Krajcicek \(2012a\)](#), for example, were able to demonstrate that the cuticular pores on the urosomites of the cosmopolitan species *Macrocylops albidus* (Jurine, 1820) are equally suitable for distinguishing cryptic species as are some fast evolving molecular markers.

[Lang \(1965\)](#) was the first to pay special attention to somite ornamentation in harpacticoid copepods, and to use it as a diagnostic character in species descriptions and delineations, especially in regard to the spinule patterns on urosomites. Pores and sensilla on somites have not been used in harpacticoid taxonomy until very recently though. Occasional illustrations and photographs of various parts of the integument have shown cuticular organs in certain harpacticoid species (e.g., [Itô, 1985](#); [Galassi et al., 1998](#); [Karanovic, 2004, 2006](#); [Huys et al., 2005](#); [Karanovic and Hancock, 2009](#)), but usually no reference was made to them in the text, and they were omitted from phylogenetic analyses. This is not surprising, considering that some of the most cited contemporary reference works on copepod morphology either do not mention cuticular organs at all ([Huys and Boxshall, 1991](#); [Boxshall and Halsey, 2004](#)) or refer to them in a single passing sentence ([Huys et al., 1996](#), p. 4).

A combined molecular and morphological approach to harpacticoid taxonomy has brought these fine cuticular structures into attention in recent years. [Karanovic and Cooper \(2011a\)](#) showed in the freshwater family Parastenocarididae Chappuis, 1940 that the spinule ornamentation on urosomites can be used to distinguish closely related sister species; moreover, sensilla patterns seem to be extremely conservative within certain lineages ([Karanovic and Cooper, 2011a](#); [Karanovic et al., 2012](#); [Karanovic and Lee, 2012](#)), thus being potentially useful in reconstructing their phylogenetic relationships. Several examined species of the parastenocaridid genus *Proserpinicaris* Jakobi, 1972 have 45 pairs of sensilla on their body ([Karanovic et al., 2012](#)), while those of the genus *Parastenocaris* Kessler, 1913 have only 40 pairs of sensilla ([Karanovic and Lee, 2012](#)). A major conclusion of these studies was that

homologisation of cuticular organs seems to be relatively uncomplicated, and may prove useful in future revisions of this problematic family.

In the family Ameiridae Monard, 1927, a study of several marine species showed a greater diversity of sensillum and pore patterns even among closely related species ([Karanovic and Cho, 2012](#)), suggesting them as useful characters for species delineation; however, their homologisation proved to be somewhat more difficult. [Karanovic et al. \(2013b\)](#) showed how cuticular sensilla could be used (together with other characters) to distinguish between two subterranean Australian ameirids that were previously erroneously considered to belong to one variable species. [Karanovic and McRae \(2013\)](#) surveyed cuticular organs in an Australian species of the family Miraciidae Dana, 1846, and [Karanovic and Kim \(2014\)](#) and [Karanovic et al. \(2014\)](#) provided partial surveys of cuticular organs in several newly described or redescribed Korean and Russian species from the same family. Some of the species reported in the three last-mentioned taxonomic publications were used for the present study.

Our aim was to make a comparative examination of pores and sensilla on the somites (excluding the appendages), and to identify homologous structures, in nine species belonging to five genera of the subfamily Stenheiliinae Brady, 1880 (the ingroup): *Itostenhelia golikovi* ([Chislenko, 1978](#)); *Itostenhelia polyhymnia* [Karanovic and Kim, 2014](#); *Onychostenhelia bispinosa* [Huys and Mu, 2008](#); *Stenhelia pubescens* [Chislenko, 1978](#); *Stenhelia taiiae* [Mu and Huys, 2002](#); *Wellstenhelia calliope* [Karanovic and Kim, 2014](#); *Wellstenhelia clio* [Karanovic and Kim, 2014](#); *Wellstenhelia qingdaoensis* ([Ma, and Li, 2011](#)); and *Willenstenhelia thalia* [Karanovic and Kim, 2014](#). We aimed to compare the phylogenetic trees reconstructed for these harpacticoids based on: 1) cuticular pores and sensilla; 2) traditionally used macro-morphological characters; and 3) mtCOI DNA data. As an outgroup for all analyses we used the same species from the subfamily Diosaccinae Sars, 1906: *Schizopera cooperi* [Karanovic and McRae, 2013](#).

The subfamily Stenheiliinae is currently recognised as one of three well-defined suprageneric groups within the second largest harpacticoid family, the Miraciidae, beside the nominotypical subfamily and Diosaccinae (see [Willen, 2000](#); [Boxshall and Halsey, 2004](#); [Wells, 2007](#); [Huys and Mu, 2008](#)). Stenheiliines are common inhabitants of the marine benthos, and can be found from the deep sea ([Willen, 2003](#)) to shallow brackish waters ([Dussart and Defaye, 2001](#)). Although there is some disagreement about morphological synapomorphies defining this subfamily ([Willen, 2000, 2002](#); [Huys and Mu, 2008](#)), these six are undisputed for adults ([Karanovic and Kim, 2014](#)): laterally displaced genital apertures in females; a triangular and usually bifid rostrum, with a dorsal pair of sensilla inserted in deep anterior recesses; an elongated basis and endopod of the mandibula (often also with one extremely long and strong seta); the maxilliped with only 3 syncoxal setae, positioned close to one another, and with no setation on the ancestral second endopodal segment; the female fifth leg with a laterally directed exopod; and some form of sexual dimorphism in the second swimming leg (although probably secondarily lost in several species). Some additional synapomorphies have been postulated based on naupliar morphology ([Dahms et al., 2005](#)) but these need to be verified in a study with broader taxon sampling ([Huys and Mu, 2008](#)).

We have yet to see either a morphology-based or a molecular phylogenetic analysis of this subfamily, and nearly all discussions about their relationships have been purely intuitive. Ninety-three valid stenheiliine species ([Wells, 2007](#); [Karanovic and Kim, 2014](#); [Walter and Boxshall, 2014](#)) are currently classified into 12 genera: *Anisostenhelia* [Mu and Huys, 2002](#) (monospecific); *Beatricella* T. Scott, 1905 (monospecific); *Cladorostrata* Tai and Song, 1979 (two

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