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Morphological diversity of setae on the grooming legs in Anomala (Decapoda: Reptantia) revealed by scanning electron microscopy

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Abstract

The fifth pereiopods (P5) in Anomala are specialized appendages used mainly for grooming. We studied the articulated cuticular outgrowths, setae, on the distal segments of the P5 in 40 species from 18 Anomala families using light and scanning electron microscopy. Five general classes of setae can be found on the P5: serrate, serrulate and simple setae which all appear bristle-like, and tooth-like and scale-like cuspidate setae. We classified the bristle-like setae according to criteria of shape and the arrangement of distinct outgrowths – denticles and setules – on the shaft of the seta. In this way we were able to distinguish eleven mainly serrate and serrulate types of seta. Some setal types imply homology due to their distinctness and could thus help to solve problematic phylogenetic questions. One setal type, for example, is only present in pagurid hermit crabs and king crabs, which corroborates the theory that these two morphologically very dissimilar groups are, in fact, closely related.

Keywords: Anomala; Homology; Phylogeny; Seta; Seta classification; Scanning electron microscopy

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1. Introduction

The advanced use of the fifth pereiopods as a grooming apparatus is described as an apomorphy of reptant decapods (Scholtz and Richter, 1995). Gill grooming with specialized setose fifth pereiopods, however, is restricted to Anomala and some Thalassinida.

Anomala comprise quite disparate taxa, e.g., hermit crabs, squat lobsters, mole crabs and king crabs. Their grooming limbs are carried under the carapace in the branchial cavities or behind the carapace. The distal segments of the grooming limbs possess tufts of bristle-like setae (Bauer, 1981; Förster and Baeza, 2001). As well as getting rid of debris, the grooming legs are able to selectively remove epibionts and parasites thanks to the chela at the end of the leg (e.g. Bauer, 1981; Martin and Felgenhauer, 1986; Fleischer et al., 1992). Aside from active gill and body cleaning, the fifth pereiopods are used for egg grooming (Bauer, 1981; Martin and Felgenhauer, 1986; Pohle, 1989; Fleischer et al., 1992; Förster and Baeza, 2001) and in some taxa also for spermatophore transfer (Brandes, 1897; R. Baxter pers. comm. in Pohle, 1989; Bliss, 1990).

In other decapod taxa (e.g. Caridea, Brachyura, Astacida, Thalassinida), other setal systems located in the branchial cavities, e.g. epipodal setobranch setae, branchiostegite setae and scaphognathite setae (Bauer, 1981, 1989, 1998; Suzuki and McLay, 1998; Batang et al., 2001; Batang and Suzuki, 1999, 2000) are used to prevent gill fouling. Setae, specialized outgrowths of the cuticle which are mostly bristle-like in shape, appear to be both chemosensory and mechanosensory (bimodal) in function in most aquatic crustaceans (Garm et al., 2004) and are normally present on structures

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responsible for grooming (Bauer, 1989). Most morphological studies into crustacean setae, however, concentrate on feeding or grooming structures on mouthparts (Bauer, 1977; Factor, 1978; Schembri, 1982; Nickell et al., 1998; Garm and Hoeg, 2000; Coelho and Rodrigues, 2001; Garm et al., 2003; Garm, 2004a,b, 2005; Horn and Buckup, 2004). Bauer (1981) provided an overview of grooming behavior and morphology in decapod crustaceans.

Crustacean setae are composed of an articulated socket and a shaft with an annulus on the lower half. In most cases they bear outgrowths in the form of articulated setules and non-articulated denticles (Pohle and Telford, 1981; Watling, 1989; Garm, 2004a). Ultrastructurally, a seta is defined as having a continuous lumen with a semicircular arrangement of sheath cells basally (Garm, 2004a). Furthermore, a terminal pore is often present on the tip of the seta, connecting the lumen with the environment.

Martin and Felgenhauer (1986) provided the first detailed morphological information about the setae on the grooming legs of Anomala which they obtained via scanning electron microscopy (SEM). This study of the South American freshwater anomalans Aeglidae (exemplified by *Aegla platensis* Schmitt, 1942 and *A. uruguayana* Schmitt, 1942) was followed by those by Pohle (1989) on king crabs (Lithodidae and Hapalogastridae), Holmquist (1989) on the terrestrial hermit crab *Coenobita clypeatus* (Fabricius, 1787) (Coenobitidae) and Fleischer et al. (1992) on porcellanid crab species of *Petrolisthes* and *Pachycheles* (Porcellanidae; see also Bauer, 1989 who did some work on the fifth pereiopods of *Petrolisthes galathinus* (Bosc, 1802)). Other morphological analyses have been carried out on the grooming legs of Thalassinida, several taxa of which use their fifth pereiopods for gill grooming, as Anomala do, or at least for general body grooming (Batang et al., 2001; Batang and Suzuki, 2003a).

However, there is still a serious lack of detailed information on the morphology and function of the fifth pereiopods in most anomalan taxa.

Furthermore, contradictory conclusions have been drawn about the relevance of setal morphology for phylogenetic reconstructions. Garm (2004a) suggested that different setal types “reflect mechanical functions and not evolutionary history”, while for other authors it is “likely that grooming setae will be of considerable systematic value in the study of crustacean phylogeny” (Pohle, 1989) or at least serve as an indicator of phylogenetic affinity (Bauer, 1981; Martin and Felgenhauer, 1986).

In this paper, we describe the morphological diversity of setae on the grooming limbs in Anomala through scanning electron microscopy and provide a classification of these setae, based mainly on shape and the arrangement of outgrowths on the shaft. The grooming limbs and their setae have been proven to be distinct character complexes, and these might be helpful in solving taxonomic or phylogenetic problems, especially since the phylogeny of this disparate group is still controversial (Lemaitre and McLaughlin, 2009).

2. Materials and methods

The fifth pereiopods of animals were obtained from several zoological collections (MNB – Museum für Naturkunde Berlin; MTD – Museum für Tierkunde Dresden; SMF – Senckenberg Naturmuseum Frankfurt; ZMUC – Zoological Museum Copenhagen; ZSRO – Zoologische Sammlung Rostock), including our own (no collection abbreviation) and dissected (Table 1). All specimens were stored in 70–100% ethanol. For microscopy, the fifth pereiopods were cut off at the proximal segments. The distal parts were cleaned mechanically with fine forceps under a stereomicroscope and subsequently treated briefly (approx. five seconds) in an ultrasonicator while immersed in ethanol. Light microscope images were taken through a stereomicroscope (ZEISS Discovery V12) with a digital camera (ZEISS ICc3). For scanning electron microscopy (SEM), specimens were dehydrated in a graded series of acetone baths and then critical point dried (EMITECH K850, UK).

We used a SEM specimen holder introduced by Pohl (2010) that incorporates an electron trap to produce images with an evenly black background. Each single dried pereiopod was mounted on a small steel pin with conducting silver glue (ACHESON Silver DAG by Plano) and coated with gold-palladium (EMITECH K500, UK). The specimens then were fixed with plastic conductive carbon cement (Leit-C-Plast by Plano) on the SEM specimen holder, allowing them to be viewed from various angles. The SEM used was a DSM 960A (ZEISS, Oberkochen). Subsequent image processing was carried out using the software Corel Draw 13 (Corel, Ottawa).

3. Results

3.1. Gross morphology of the grooming legs

The fifth pereiopods (P5) of the Anomala are stenopodous legs segmentally composed (proximally to distally) of a coxa, basis, ischium, merus, carpus, propodus and a dactylus. In contrast to most other reptant decapods, these legs are not used for any mode of locomotion in Anomala. They are much smaller than the first to fourth pereiopods (P1–4) and carried below or behind the carapace. In non-shell-bearing Anomala these legs are only visible in representatives of Galatheidae, Munididae (Fig. 1B), Mundopsidae and Porcellanidae, while in Chirostylidae, Eumunididae, Hippidae, Albuneidae, Lomisidae, Aeglidae (Fig. 1A), Hapalogastridae and Lithodidae the last pair of pereiopods is carried under the carapace and more or less hidden in the branchial chambers.

In all investigated species the proximal end of the carpus is markedly bent towards the merus, as in P1–4, and has a hinged articulation which permits a relatively tight fold between carpus and merus. In Porcellanidae, Galatheidae, Munididae and Munidopsidae the carpus is relatively