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The functional morphology and attachment mechanism of pandarid adhesion pads (Crustacea: Copepoda: Pandaridae)

Abigail L. Ingram*, Andrew R. Parker

Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS

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Abstract

The attachment mechanism of pandarid adhesion pads is described from observations of their externally ridged structure and internal construction in three species; *Pandarus bicolor* Leach, 1816, *Dinemoura latifolia* (Steenstrup and Lutken, 1861) and *Echthrogaleus coleoptratus* (Guerin-Meneville, 1837). The host's external skin morphology was also examined, since parasite attachment mechanism and host surface can be considered as components of a single system.

The results emphasise the importance of the physical nature of the pad's surface. This is inferred from the compliance of the cuticle and subsurface structure, and the presence of cuticular ridging. The pads probably prevent pandarids from being dislodged by hydrodynamic drag, by increasing overall adhesion. It is proposed that this is achieved in different ways, by two types of adhesion pad identified here, distinguishable by their external structure and location. Type I pads are suggested to remove interfacial water and increase surface contact by one of two contrasting methods. The ridges may act as tyre treads, by channelling water from the contact surface. Alternatively, the channels between ridges may be hydrophobic and behave as dewetting structures, preventing water from entering in the same way that troughs between surface nodules function to produce superhydrophobicity on lotus leaves. Type I adhesion pads are also suggested to aid attachment by hindering the process of peeling, by which they are thought to be removed by hydrodynamic drag. Type II pads are more likely to function as one-way frictional attachments. Both types of pad appear to be attached passively, since they lack muscles inserting into them. The adhesive mechanism of each, which functions most effectively on hard surfaces, may explain why pads are absent or reduced on pandarids which parasitise the softer, unscaled surfaces of hosts.

Pandarids predominantly parasitise the skin and fins of fast-swimming sharks. This may be because the scales are characteristically smaller in these species and are more easily encircled by the primary attachment appendages, the maxillipeds.

This is thought to be the first published report to reveal frictional attachment structures from the Crustacea, which have convergently evolved in many terrestrial Arthropoda.

Keywords: Microstructures; Passive attachment; Friction

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*Corresponding author.

E-mail address: a.ingram@nhm.ac.uk (A.L. Ingram).

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1. Introduction

There are currently 12 recognised genera within the copepod family Pandaridae (Cressey 1967; Kabata 1979), of which almost all are exclusively ectoparasites of sharks and rays (Elasmobranchia). They are usually found on the outer skin and fins, and in the gill and nasal cavities (Cressey 1967; Kabata 1979), where they graze the epidermis and can cause infestations (Benz 1981).

The Pandaridae, along with other caligiforms, show a number of adaptations for reducing the effects of drag and lift, which are caused by water flow over the host and have the potential to remove parasites. Adaptations include dorsoventral flattening of the body, individuals tiling themselves over one another (Benz 1981), orientation of the body axis to face anteriorly into the flow (Cressey 1967; Kabata 1979) and streamlining the body to the genital complex.

In addition to lift and drag, elasmobranch ectoparasites encounter other problems associated with the external surfaces of the hosts, almost all of which are covered in protective, projecting placoid scales. This creates a surface roughness that prevents the Pandaridae from attaching like other caligiforms, by a water-tight suction seal beneath the dorsal cephalothoracic shield (Kabata 1979). Suction is further hindered by the relative lack of mucus on elasmobranch scales (Brown 1957), compared to those of teleosts where it is abundant and aids the formation of a seal by caligiforms found on these fish. These host factors have resulted in an alternative solution to attachment in the Pandaridae, which have instead adapted the maxillipeds and the antennae for this purpose. The morphology of the maxillipeds varies between genera and in those that parasitise the outer skin surfaces of the host, they are either spatulate or sharply hooked, allowing the parasite to clasp or hook individual scales (Cressey 1967; Benz 1992). By contrast, the gill-parasitic genera possess sharply hooked maxillipeds to pierce and anchor into the softer gill tissue (Cressey 1967). The maxillipeds of *Perissopus* Steenstrup and Lűtken, 1861 are different entirely, even though species parasitise the outer skin surface of their hosts (Cressey 1967). Here, the maxilliped claw is reduced and is cemented to the scales, presumably to substitute the diminished efficiency of the clasping attachment.

The antennae, which are generally hooked in all Pandaridae, are best developed in the gill-parasitic genera, *Gangliopus* Gerstaecker, 1854 and *Phyllothyreus* (Edwards, 1840), enveloping and piercing the gill filaments (Cressey 1967).

Together with the antennae and maxillipeds, the Pandaridae have evolved entirely new, secondary attachment structures termed adhesion pads, which function in an auxiliary capacity and are unique amongst the parasitic Copepoda (Kabata 1981). The pads, which are covered with transverse ridges (Cressey 1967), can be in one or more ventral locations; on the sympods (the double segments formed by the fused coxa and basis) of swimming legs 1–4 or at the base of the antennae, the antennules, the maxillipeds, the distal corners of the dorsal shield or on the postero-lateral plates of the first free thoracic segment (Kabata 1981). In general, pandarids that parasitise the outer host skin surfaces have more numerous pads than gill-parasitic genera, which usually have reduced numbers of pads or lack them completely (Cressey 1967).

While the detailed function of the adhesion pads is uncertain, it is agreed that they are most likely to increase friction and therefore grip, prompting the name adhesion pad (Wilson 1907). Frictional function was hypothesised because the ridges run transversely to the direction of force generated by the flow of water over the host (Cressey 1967; Kabata 1979, 1981; Benz 1992; Oldewage 1992). Benz (1992) gave a detailed description of the adhesion pads associated with the maxillipeds (= myxal pads) and examined how they are positioned during attachment. However, no description has been given of the function of the ridges, nor of the possible mechanism by which they may provide increased friction. This study addresses these gaps in our knowledge of pandarid attachment, by examining the structure of every pad on each of three species and also the skin of the host, since the substrate is likely to have played an important role in the evolution of the pad. This data was then interpreted within the context of the parasite's requirements for survival, and the environment surrounding the host.

2. Materials and methods

Pandarus bicolor was collected from around the dorsal fin of a recently killed female dusky shark, *Carcharhinus obscurus* (Leseur, 1818), at the Port Stephens Game Fishing Tournament (New South Wales, Australia) in 2002. *Dinemoura latifolia* was collected from the dorsal surfaces of two female shortfin mako sharks, *Isurus oxyrinchus* Rafinesque, 1809. *Echthrogaleus coleoptratus* was collected from the skin of its host, *I. oxyrinchus*, in the North Atlantic and was supplied by The Natural History Museum (London).

Host skin samples were dissected from the attachment sites of each parasite species. All samples were fixed in 70% ethanol.

2.1. Pad structure

For each parasite, body dimensions were recorded from two specimens. The adhesion pads were examined and described using the terminology of Cressey (1967)