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Countershading by Physiological Colour Change in the Fish Louse *Anilocra physodes* L. (Crustacea: Isopoda)

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Summary. Specimens of the fish louse *Anilocra physodes* L. from the Mediterranean Sea exhibited a striking colour asymmetry in their dorsal pigmentation: one longitudinal half of their back was dark, the opposite half was light-coloured. The dark side corresponded with the physiological upper side when the fish louse was attached to the flank of a host fish.

The colour pattern derives from the different shape (stellate/punctate) of chromatophores, which lie immediately beneath the epidermis. The appearance and distribution of the chromatophore stages indicate the possibility of physiological colour change in *Anilocra*. In this way the fish louse probably achieves adaptive countershading and thus additional protection from predators, advantageous for both parasite and host.

Introduction

There are various strategies of adaptation that can protect a species from its predators. One of them is camouflage by means of a certain form and/or colour, giving the animal's body a reduced three-dimensional appearance. This can take place both by the body being flattened laterally and thus casting less shadow, and also by means of so-called countershading, also known as the Thayer Principle (Portmann 1956) after Thayer, who first described it. Countershading means that the side of the body facing the sun is darker and the side of the body away from the sun is of a lighter colour. This pattern results in less colour contrast and in the body giving an optically flattened impression, thus making the animal much more difficult to see for prospective predators. This protective effect of countershading is an explanation of the well-known fact that the upper side of many vertebrates (also some species of insects) is darker than the ventral side.

Many fishes, particularly those which live in the well-lit surface waters have a dark, often bluish- or greenish-toned back and silvery flanks like the herring. Thus, they are not only camouflaged from the glances of airborne predators against the dark-coloured deeper water but also protected from the eyes of predatory fish glancing up at the light sparkling surface of the sea. An additional camouflage effect is produced by the optical flattening of the body resulting from the simultaneous countershading. There is striking evidence of the adaptive value of countershading, for instance in the tropical African upside-down catfishes (Mochokidae), which habitually swim on their backs in order to glean algae from the undersides of floating lily-pads (Wheeler 1977), or the common water-bug *Notonecta glauca*, which also swims on its back. In both cases the ventral side of the body is dark and the back is light-coloured.

Results

While examining the catch on 24 September 1981 off the coast of Banyuls-sur-Mer in southern France, in a drag-rat which contained an exceptionally large number of pandoras (*Pagellus erythrinus* L.), I noticed a fish that had been attacked by a fish louse. The fish louse, *Anilocra physodes* L., had attached itself to the *right* side of the porgy at the beginning of the caudal third of the body; just above this spot there was a severe skin wound (Fig. 1). The direction taken by the parasite was clearly adapted to the current of the water, in other words, parallel to the longitudinal axis of the body of the host fish an with its head pointing forward. A closer examination revealed the asymmetry in the colour pattern of the dorsal side of the fish louse: the left half of its back was dark-coloured, the right half seemed to be almost without pigment. The dark side was uppermost when the parasite was attached to the fish. A thorough examination of the entire catch in the net revealed another specimen, which had also attached itself to the right side of a pandora. This had the same colour asymmetry as the first specimen found. The third specimen, which had come on board in the same net, had attached itself to the *left* side of a pandora, also head-first and parallel to the longitu-

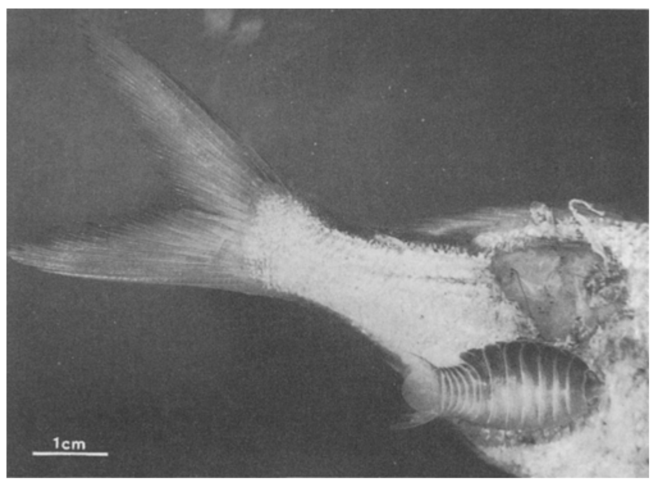

Fig. 1. *Anilocra physodes* L. attached to the right side of a pandora (*Pagellus erythrinus* L.); above: a skin wound. (Photo taken from a living specimen)

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dinal axis of the fish. This fish louse also had deep grey-brown pigmentation on the half of its dorsal side which turned uppermost and was practically colourless on the opposite half of its back, but in this case the anatomically right half of its dorsal side was the pigmented one (Fig. 2). Exactly the same colour pattern was found on a specimen caught off the coast of Rovinj (Yugoslavia) in 1967; the side on which this fish louse had attached itself to the host fish is, however, understandably no longer known.

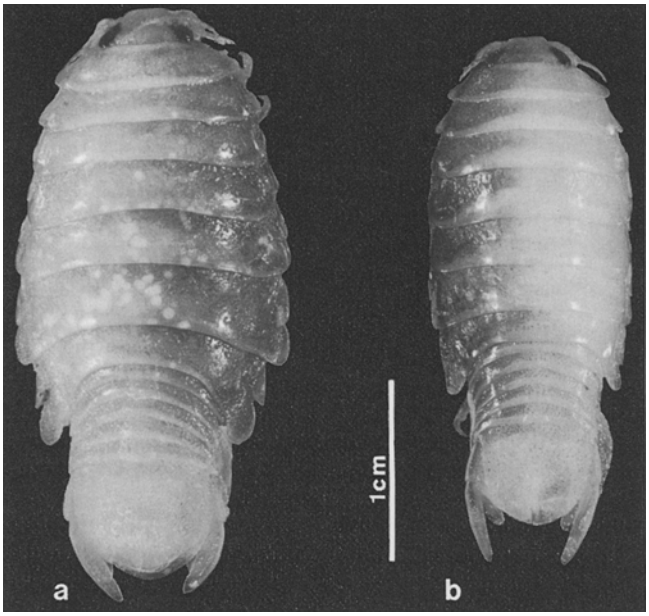

Fig. 2a, b. Asymmetric colour pattern of the dorsal side of *Anilocra*. **a** Specimen from the left side, **b** specimen from the right side of a host fish (*Pagellus erythrinus* L.). (Fixed specimens)

Laboratory investigations were first carried out to establish the location of the colour pattern. A possible deposition of pigment in the exoskeleton was excluded; the tergites were completely transparent. In whole mounts of the dorsal integument it was possible (after removal of the tergites) to recognise chromatophores in the undermost layers of the integument, which contained brownish to blackish pigment. The degree of dispersion of the pigment within the chromatophores varied considerably: on the dark half of the dorsal side of *Anilocra* stellate chromatophores were found, starting from the middle of the back, which then eventually changed into reticulate chromatophores laterally (Fig. 3a). In the reverse direction, going from the middle of the back to the light half of the dorsal side, the stellate chromatophores decreased and the punctate ones occurred more frequently (Fig. 3b), representing the typical stage in the light region (stages after Hogben and Slome 1931). Thus, in the dorsal skin of *Anilocra* within a thoracic or pleon segment transverse to the axis of the body, it was possible to find a graduated arrangement of the various stages of chromatophores.

Histological cross-sections of the dorsal integument supplied more exact information on the position of the chromatophores and confirmed the findings from the whole mounts of varying distribution of pigment. The chromatophores lay immediately beneath the single layer of the epidermis, adjacent to the dermis. The dark brown pigment granules (melanosomes?) in the cells were just visible near the resolution limit of the light microscope. In the region of the dark side of the back, where the stellate and reticulate chromatophores could be observed to occur most frequently (Fig. 3a), a thin but continual pigment layer was seen under the epidermis, with only occasional light interruptions (Fig. 3c). The corresponding region on the light side of the back looked quite different. Here, chromatophores occurred only sporadically in niches between the dermis and

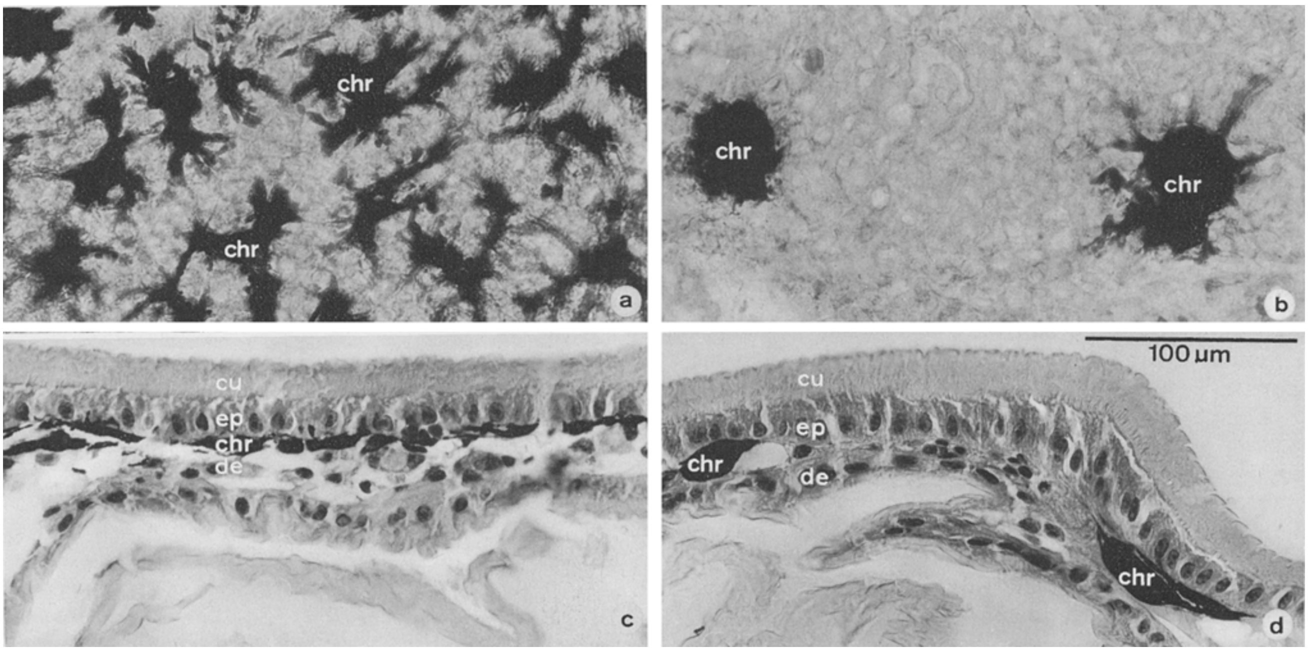

Fig. 3a–d. Chromatophore stages from the dark and from the light halves of the dorsal side of *Anilocra*. **a** Reticulate chromatophores (dark). **b** Punctate chromatophores (light). Whole mounts. **c** Nearly continual pigment layer (dark). **d** Pigment concentrated around the nucleus (light). Cross sections. Note: Equal scale. chr = chromatophore(s), cu = cuticle (tergite), de = dermis, ep = epidermis

the epidermis. The pigment of these chromatophores, which appeared nearly punctate in shape (Fig. 3b), was closely concentrated around the nucleus of the cell (Fig. 3d).

The appearance and distribution of the chromatophore stages closely resembled cases of physiological colour change described by Fingerman (1963, 1969). The asymmetry of the colouring of the dorsal side in connection with the side-specific attachment to the host fish indicated the principle of countershading in the fish louse *Anilocra physodes* L.

Discussion

Anilocra lives as a stationary parasite on various species of marine fish. Having swum up to a host fish, the fish louse clings with the needle-like claws of its peraeopods to the skin of the fish and feeds on the host's blood by means of its piercing and sucking mouth parts. As soon as *Anilocra* has attached itself head-first along the side of the body of a fish, its body lies parallel to that of the fish, but turned at an angle of about 90°, i.e. swimming on its side. Depending on which side the fish louse has attached itself, either the left or the right side of its body is now physiologically the upper side. It seems unlikely that an adaptation of countershading to the corresponding side of the host fish would occur genetically through dimorphism. The microscopic observations on the chromatophores indicate that the countershading in *Anilocra* is probably achieved by means of a physiological colour change.

The ability to change colour physiologically is widespread amongst certain groups of Crustacea. Experiments have been carried out chiefly on shrimps, prawns and marine isopods (Bauer 1929; Brown 1973). In the case of the fish louse *Anilocra* it is, however, remarkable that no colour adaptation to the direct environment of the animal occurs, but that a countershading results which is adapted to the left or right side of the host's body. It should be emphasised that the cases which are known to be examples of the Thayer Principle are based on stable colour patterns. As far as *Anilocra* is concerned, there is much evidence that it achieves an *adaptive* countershading by physiological colour change.

The dangers which a fish faces from its predators are the same for parasites living either on or inside the fish. Thus, it can be expected that *Anilocra* has also developed protective mechanisms which prevent it from being plucked off by a cleaner fish as soon as it has reached its host, or from being a prey to some predator together with its host. First of all the flatly appressed body, which reduces the pressure of the water, is at the same time advantageous to the camouflage achieved by a diminished three-dimensional effect. In addition, the countershading increases the optical illusion of a flattening of the attached fish louse, as it is the direct opposite of the natural body shading. At present it cannot be stated definitely whether *Anilocra* makes use of its ability to produce countershading in every case. One may well suppose that a connection between the colouring of the host (*Anilocra* is also a parasite on fish which have no countershading) and the colour adaptation of the fish louse exists; this would be an explanation for the different data on the colouring of *Anilocra* in usual reference books (e.g. Luther and Fiedler 1967; Riedl 1970).

The closely related species *Nerocila bivittata* (Risso) apparently succeeds in camouflaging itself in a different manner when on the host fish. The dorsal side of this fish louse is dark brown, broken up by two light lines running along the back (Fig. 4). This colour pattern, which gives the species its name (*bivittata*) was described in 1901 by Gerstaecker and Ortmann and also in 1970 by Riedl. The ability to produce side-specific countershading by physiological colour change probably does not exist in this species. *Nerocila bivittata* probably camouflages itself for both possible sites of attachment to the host fish by a stable bilateral symmetrical pigment distribution supported by the somatolytic effect of both its longitudinal lines.

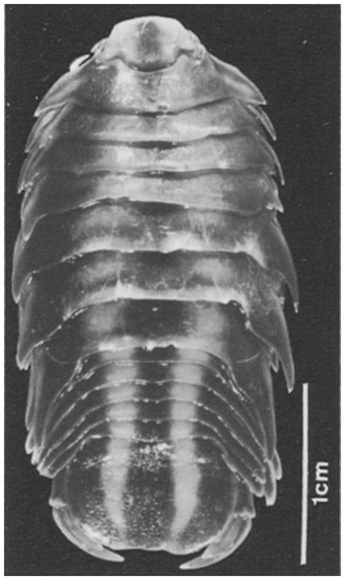

Fig. 4. Bilaterally symmetrical colour pattern of the dorsal side of *Nerocila bivittata* (Risso). (Fixed specimen from Rovinj 1967)

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