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Previous volumes (2010-2016): 250 € / year (4 issues)
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The digitalization of Acarologia papers prior to 2000 was supported by Agropolis Fondation under the reference ID 1500-024 through the « Investissements d’avenir » programme (Labex Agro: ANR-10-LABX-0001-01)

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AMBULACRAL STRUCTURE IN
THE TERRESTRIAL MOIETY OF THE INTERTIDAL ACARI,
AND ITS RELATIONSHIP WITH THE LIFESTYLE OF THE ACARI

BY P. J. A. PUGH, P. E. KING and M. R. FORDY *

ABSTRACT : Ambulacral modifications among the terrestrial moiety of the intertidal Acari associated with maintenance of position reflect the lifestyles of these Acari. The Mesostigmata have strengthened or elongated pulvillar sclerites and long spatulate setae to aid adhesion. The claws of the genus Ameronothrus (Cryptostigmata) are proportionately longer in the intertidal compared with the supralittoral species. The claw mechanism of Hyadesia spp. (Astigmata) is unique; the mechanism and its mode of action are analysed. However, the Prostigmata show no unusual ambulacral modifications, with all structures having parallels among non-intertidal species.

RÉSUMÉ : Les modifications ambulacraires associées au maintien de la position, au sein de la partie terrestre des Acariens de la zone des marées, reflètent les modes de vie de ces Acariens. Les Mesostigmata ont renforcé ou allongé les sclérites pulvillaires et leurs longs poils spatulés pour aider l’adhésion. Dans le genre Ameronothrus (Cryptostigmata) les ongles sont proportionnellement plus longs chez les espèces de la zone des marées comparées à celles de la zone supralittorale. Le mécanisme de l’ongle des Hyadesia spp. (Astigmata) est unique ; mécanisme et mode d’action sont analysés. Toutefois, les Prostigmata montrent aucune modification ambulacraire inhabituelle et toutes les structures qu’ils possèdent ont leurs parallèles chez les espèces qui n’appartiennent pas à la zone des marées.

INTRODUCTION

One of the major factors determining the distribution of the fauna and flora in the intertidal zone is their ability to withstand mechanical stress resulting from wave action, and thus to maintain their position on the shore (BALLANTINE, 1961 ; NEWEL, 1979). The intertidal Acari may be divided into two groups; an aquatic moiety (the family Halacaridae) which are always submerged or at least wetted by a water film, and a terrestrial moiety, a mixed assemblage of species belonging to a number of families. These generally avoid wetting by retreating ahead of the tide, or withdraw to air pockets trapped in crevices (PUGH 1985 ; PUGH & KING, 1985b).

Many intertidal Acari have ambulacra which...
may help them to maintain their position on the shore. SCHUSTER (1962, 1965, 1979) described some ambulacral structures present among the Mesostigmata and Prostigmata. However, the different lifestyles described among the intertidal Acari (PUGH, 1985; PUGH & KING, 1985b), suggest that these may not be purely adaptations to submersion, but also to rapid locomotion, particularly in the Prostigmata. The evidence for these ideas is re-examined.

MATERIALS AND METHODS

Acari were collected from open rock surfaces and crevices in the intertidal zone, and from tidal debris in the supralittoral using an entomologist's aspirator. Specimens were extracted from intertidal algae, barnacles and lichens using a hypersaline flotation technique (PUGH, 1985; PUGH & KING, 1985a). Non-intertidal species were extracted from soil and leaf litter by means of Tullgren funnels (EVANS, et al., 1961), using live cells containing moist tissue paper instead of an alcohol based fixative.

Specimens for examination under the scanning electron microscope were fixed in alcoholic Bouin's fixative (GRIMSTONE & SKAER, 1972), cleaned in an ultrasonic wash, dehydrated in acetone, coated with gold under vacuum, viewed and photographed under a JEOL 35C SEM. Particular emphasis was placed upon claw structure. In some species which were not examined under the SEM, claw structure was analysed by light microscopy. The species studied are listed below:

MESOSTIGMATA

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macrocheles superbus</td>
<td>(Macrocheilidae)</td>
<td></td>
</tr>
<tr>
<td>Thinoecus fucicola</td>
<td>(Eiphiidae)</td>
<td></td>
</tr>
<tr>
<td>Onchodelus ressatus</td>
<td>(Pachyelaphidae)</td>
<td></td>
</tr>
<tr>
<td>Halolaelaps celticus</td>
<td>(Halolaelaphidaceae)</td>
<td></td>
</tr>
<tr>
<td>H. marinus (Brady)</td>
<td></td>
<td>(S)</td>
</tr>
<tr>
<td>Saprotagamasellus incisa</td>
<td></td>
<td>(S)</td>
</tr>
<tr>
<td>Arcosioiodes ibericus</td>
<td>(Asciidae)</td>
<td></td>
</tr>
<tr>
<td>Platysius neorniger</td>
<td>(Oudemansi)</td>
<td></td>
</tr>
</tbody>
</table>

Note: t: terrestrial non-intertidal/supralittoral species; S: examined in the stereoscan.

HYDROGAMASUS giardi (Berlese & Trouessart) (Crytolaephidae) (S)
H. salmus (Laboulsene) (Veigalidae) (S)

Validity

1. MESOSTIGMATA

Ambulacra II to IV of the free-living Mesostigmata consist of a basal pretarsus, paired distal claws, and a large lobate pulvillus, the lateral lobes of which are referred to as the pulvillar sclerites (Figs. 1G, 1H & 1I) (EVANS & TILL, 1979). Hydrogamasus salinus has modified ambulacra, the pulvillar sclerites are narrow and acuminate, reinforced by longitudinal ridges, and are orientated at 90° to the points of the claws (Figs. 1A & 1B). It is suggested that, if wetted, they would cause the claws to be pressed onto the substratum by water surface tension, and thus would increase the grip, while the renfor-
FIG. 1: Ambulacral Structure: Mesostigmata.

1A. *Hydrogamasus salinus*: ambulacrum II, lateral aspect. Note how the claws (c) may act antagonistically against the thumb-pad (tp) to provide grip. The pulvillar sclerites (ps) and spatulate setae (ss) are flattened to provide adhesion on wet surfaces. Scale: 10 μm; 1B. *H. salinus* ambulacrum II, dorsal aspect. Note the large ribbed pulvillar sclerites (ps). Scale: 10 μm; 1C. *H. giardi*: ambulacrum II, lateroventral aspect. Structure is similar to that of *H. salinus* (Figs. 1A & 1B), being equipped with large claws (c), pulvillar sclerites (ps), spatulate setae (ss), and thumb-pad (tp). Scale: 5 μm; 1D. *H. salinus*: spatulate seta shown in Fig. 1A. Note the reinforcing marginal ridge (r). Scale: 2 μm; 1E. *Cyrthydrolaelaps hirtus*: ambulacrum II, dorsolateral aspect. The claws (c), pulvillar sclerites (ps) and spatulate setae (ss) are very elongate, considerably more so than in *H. salinus* (Figs. 1A & 1B). Scale: 15 μm; 1F. *C. hirtus*: ambulacrum II, dorsal aspect. Note the very elongate claws (c), pulvillar sclerites (ps) and spatulate setae (ss). Scale: 20 μm; 1G, 1H & 1I *Pergamasus longicornis* (non-intertidal): ambulacrum II in lateral and ventral aspects. Note the short claws (c), broad and leaf-like pulvillar sclerites (ps); there are no prominent flattened or spatulate setae associated with maintenance of position under conditions of mechanical stress, contrasting with the intertidal species shown above. All scales: 10 μm.
cing ridges would prevent the sclerite bending. The ventral surface of tarsi II-IV have a central pad which may function as a fixed "thumb" against which the two moveable claws may act as "fingers", allowing the mite a better grip on irregular surfaces (Figs. 1A & 1B). A similar mechanism is present in Hydrogamasus giardi (Fig. 1C).

In contrast, the ambulacra of the mesostigmatic Cyrthydradaelaps hirtus Berlese, have flattened, spatulate pulvillar sclerites (Figs. 1E & 1F) which may aid in adhesion to wet surfaces, as suggested by Berlese (1905). However, their mode of action is different from those of Hydrogamasus salinus because, when wetted, they adhere to the substratum and increase their grip. Halolaelaps marinus has elaborate ambulacra similar to those of Hydrogamasus salinus (Halbert, 1915) but, in the related Halolaelaps celticus Halbert from tidal debris, they are not so well adapted. Here the ambulacra form an intermediate structure between those of Halolaelaps marinus (= H. glabriusculus) and "the typical gamasid" of terrestrial origin, for example P. coleoptratorum (Figs. 1G, 1H & 1I) (Hyatt, 1956).

Although the ambulacra of some intertidal Mesostigmata show adaptations associated with grip on wet surfaces, the legs are unmodified (Figs. 2 & 3). Legs of species occurring in the lower intertidal zone, namely Halolaelaps marinus, Hydrogamasus giardi, Hydrogamasus salinus and C. hirtus do not differ in relative lengths from those of the upper intertidal and supralittoral-zone dwelling species.

2. Prostigmata

The ambulacra of some intertidal Prostigmata are elaborate. Schuster (1962) suggested that the modified tarsi of Halotydeus albolineatus Halbert, (Penthaleidae) may prevent its dislodgement by wave action. However, the closely related H. hydrodromus collected extensively during the present study has similar tarsi (Fig. 4A), but is intolerant of submersion and is immobilised, or even damaged, by surf (Pugh, 1985; Pugh & King, 1985a). These ambulacra and the modified empodia of Bdella decipiens equipped with spatulate setae (Figs. 4B, 4D & 4F) may aid adhesion on to wet surfaces, but it is suggested that these tarsi are adapted for rapid locomotion, and that the spatulate setae increase adhesion on especially wet surfaces. However, such ambulacra are not unique to the intertidal fauna, and occur both intertidal and non-intertidal Acari from a number of different families e.g. the Bdellidae (Schweizer, 1951, Wallace & Mahon, 1972), and the Rhagidiidae (Zacharda, 1980).

Members of the genus Balaustium (Erythraeidae) have no empodia but, when running, both the claws and the setae on the ventral surfaces of the tarsi are brought into contact with the substratum to provide traction. These setae possibly function in a similar manner to the spatulate setae of the empodia of the species mentioned above. Those of the intertidal species, B. rubripes (Figs. 4C, 4E & 4G), are similar to those in the related non-intertidal B. murorum (Figs. 4H & 4I), providing furthur evidence in favour of this being an adaptation to rapid movement, rather than maintenance of position during submergence.

The majority of the terrestrial moiety of the intertidal Prostigmata are swift moving predators, whose elaborate ambulacral and tarsal structures presumably are adaptations for rapid locomotion, and not specifically for the maintenance of position when submerged. Field and laboratory data suggest not only that these mites avoid inundation, but that they are intolerant of it (Pugh, 1985; Pugh & King, 1985b). Thus, adaptations specific for the maintenance of position during submergence would hardly be useful in these mites.

3. Cryptostigmata

Schuster (1965) stated that there are no ambulacral modifications in the intertidal Cryptostigmata. However, Schubart (1975) demonstrated that the genus Ameronothrus, which has both intertidal and non-intertidal representatives, exhibits a correlation between the type of substratum and claw structure. The species occurring on hard substrata have three claws, and those on soft
Graphs showing the relative leg lengths of some intertidal Mesostigmata. Species occurring in the lower littoral zone are indicated by asterisks (*). The legs of these species do not differ significantly from the over upper intertidal and supralittoral species, as shown by the Mann-Whitney test (Meddis, 1975).

Graphs suggest a high correlation between leg and idiosomal length-regression line ‘r’ values calculated as follows:

Fig. 2A : $r = 0.968$

Fig. 2B : $r = 0.980$

3A : $r = 0.948$

3B : $r = 0.949$

Key:
- Al.: Arctoseiodes ibericus
- Ch.: Cytrohydrodegla hirtus
- Cl.: C. incisus
- Hc.: Halolaelaps celticus
- Hg.: Hydrogamasus giardi
- Hm.: Halolaelaps marinus
- Hs.: Hydrogamasus saffinus
- Ms.: Macrocheles superbus
- Ot.: Oncholaelaps tessellatus
- Pk.: Parasitus kempersi
- Ps.: Platynota necorniger
- Si.: Saprogamasel/us incisus
- Tf.: Thinositus fucicola
- Vi.: Vulgarogamasus immnans
- Vt.: V. trouessarti
FIG. 4: Ambulacral Structure: Prostigmata.

4A. Halodytes hydrodromus: ambulacrum II, lateral aspect. Scale: 10 µm; 4B. Bdella decipiens: ambulacrum II, lateral aspect, showing the prominent "haired" empodium (emp). Scale: 10 µm; 4C. Balaustium rubripes: ambulacrum II, lateral aspect. Note the dense mat of empodial processes on the ventral surface which acts as a "footssole" to increase traction. Scale: 5 µm; 4D. B. decipiens: ambulacrum II, lateral aspect of empodial processes shown in 3.2 Note that the tips of the processes are flattened to increase substrate adhesion. Scale: 2 µm; 4E. B. rubripes: tarsus III, detail of setae on the ventral surface, which give traction (compare with Fig. 4J). Scale: 5 µm; 4F. B. decipiens: ambulacrum II, dorsal aspect. Note the empodium (emp), and the setae claws (c). Scale: 10 µm; 4G. B. rubripes: tarsus IV, lateral aspect. Note the setae on the ventral surface used to provide traction (compare with Fig. 4E). Scale: 20 µm; 4H. Balaustium murreum (non-intertidal): tarsus IV, lateral aspect. Note the similarity with B. rubripes (compare with Figs. 4C & 4G). Scale 20 µm; 4I. Neotrombidium sp. (non-intertidal): tarsus IV, lateral aspect. Note the similarity with the tarsi of Balaustium spp. (compare with Figs. 4C, 4G & 4H). Scale: 20 µm; 4J. B. murreum (non-intertidal): tarsus II, detail of setae on the ventral surface of the tarsus, (compare with Fig. 4E). Scale: 5 µm.
substrata have only one. The claws of *A. marinus* are structurally unmodified, compared with those in related non-intertidal species (Schubart, 1975); in both groups the lateral claws are thin and serrated, while the medians are massive and simple (Figs. 5A & 5B), (Schubart, 1975). Although the claws of *A. marinus* are structurally similar to those of some of the non-intertidal Ameronothridae, they are larger both in absolute length, and in length relative to that of the whole animal, than are those of non-intertidal species. A second intertidal species, *A. lineatus*, also has relatively large claws (Fig. 6).

4. ASTIGMATA

*Hyadesia* is the only genus of the Astigmata normally encountered in the intertidal zone. The claws of this genus are of unusual structure, as shown by Michael (1901) and Benard (1961) (Figs. 7E & 7F). Benard gave a brief description of locomotion in *Hyadesia*. During the present study, additional observations were carried out on *H. furcillipes* to elucidate stepping sequence and claw function during locomotion.

The legs of *H. furcillipes* are relatively thick when compared to the empodial stalks (especially empodia I and II (Figs. 7D & 7E)), and probably function as compression members. The structure and position of the single heavy spine on tarsi I and II, and the smaller trio of spines on tarsi III and IV, suggest that they are points of contact with the substratum and that the animal “walks on tip toe”, and that the mite “stands” on the tarsal claws of legs I and II and the spines of tarsi III and IV. The pulvillar stalks are thinner and equipped with axially deflected hook-like claws, features suggesting that the stalks are tension members.

In the Halacaridae, the body is wetted and usually partially supported by water. The legs are used to pull the animal along, so that the claws function simply as hooks or grapnels. Thus legs I and II are thicker than III and IV (Fig. 7B) because they provide the majority of thrust (Pugh, 1985). In the terrestrial moiety, (excluding *Hyadesia*), because they move in air, legs III and IV are thicker and provide thrust. In some species of Mesostigmata, leg I is sensory, and may lose its ambulacrum and locomotor function to become antenniform, (most Macrocheilidae for example). In these cases legs II are heavier and may compensate for legs I in supporting the weight of the body. In many male Mesostigmata, legs II are thick and armed with heavy spurs, though this is a secondary sexual characteristic.

In *Hyadesia*, legs I and II are heavier than III and IV (Fig. 7C), suggesting that locomotion may involve pulling the body along in a manner similar to that described for the Halacaridae. This idea was supported by crushing individual tarsi with a pair of fine forceps; specimens with damaged tarsi I or II, showed greater difficulty in moving than those with damaged tarsi III or IV.

Locomotion in *H. furcillipes* was observed, and the sequence of leg movement was as follows:

1) Leg I on one side is extended and the empodial claw changes orientation from 90° to the axis of the leg, to it lying along the axis of the leg, which is then lowered until the tip of the tarsal claw is brought into contact with the substratum.

2) Leg II on the opposite side repeats this process almost simultaneously.

3) Legs III and IV also move in an alternate pattern, with the body supported on the terminal tarsal spines. Thus, the overall pattern of leg movement is: Left I and right II move together, followed by a short time lag, followed by left III and right IV together, time lag, right I and II together, time lag, right III and left IV together. The process then repeats itself (Fig. 7F). A similar pattern was noted in *Tyrophagus putrescentiae* (Schrank) (Acaridae) by Baker & Smith (1968).

If *H. furcillipes* is mechanically stimulated by water movement, the body is pulled forward on legs I and II, with the weight supported by the tips of the tarsal claws. Leaving the claws on tarsi III and IV hooked onto substratum irregularities, “leans forward”, applying downward pressure on tarsi I and II. This locks all 8 claws onto the substratum. The lock may be released by relaxing legs I and II.

The evidence presented here reinforces the
FIG. 5: Ambulacral Structure: Cryptostigma and Astigmata.

5A. Ameronothrus marinus: ambulacrum IV, lateroventral aspect. Note the serrated lateral claws (lc), and large smooth median claw (mc). Scale: 10 μm; 5B. A. marinus: ambulacrum II, lateroventral aspect. Scale: 10 μm; 5C. Euzetes seminulum (non-intertidal): ambulacrum III, lateral aspect. Scale: 10 μm; 5D. E. seminulum (non-intertidal): ambulacrum III, lateral aspect. Scale: 10 μm; 5E. Hyadesia furcillipes: tarsus II, lateral aspect. Note the empodial claw (ec), empodium (emp), tarsus (tar) and tarsal claw (tc). Scale: 10 μm; 5F. H. furcillipes: claw IV, lateral aspect. Scale: 5 μm.
Graph to show the relative median claw length among members of the genus *Ameronothrus* (*Ameronothridae: Cryptostigmata*). The "regression line" divides the species into two groups, and suggests that the intertidal species *A. lineatus* and *A. marinus* have proportionately larger claws. This is further supported by the Mann-Whitney test (Meddis, 1975), as shown below:

<table>
<thead>
<tr>
<th>Species</th>
<th>Length of Idiosoma (µm)</th>
<th>Claw Length (µm)</th>
<th>Claw Index (Id/Claw)</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. lineatus</em></td>
<td>769</td>
<td>50</td>
<td>15.38</td>
<td>Intertidal</td>
</tr>
<tr>
<td><em>A. marinus</em></td>
<td>784</td>
<td>45</td>
<td>17.42</td>
<td></td>
</tr>
<tr>
<td><em>A. maculatus</em></td>
<td>633</td>
<td>34</td>
<td>18.62</td>
<td>Supralittoral</td>
</tr>
<tr>
<td><em>A. bilineatus</em></td>
<td>682</td>
<td>36</td>
<td>18.94</td>
<td></td>
</tr>
<tr>
<td><em>A. schusteri</em></td>
<td>700</td>
<td>34</td>
<td>20.59</td>
<td>Terrestrial</td>
</tr>
<tr>
<td><em>A. schneideri</em></td>
<td>784</td>
<td>36.5</td>
<td>21.60</td>
<td></td>
</tr>
</tbody>
</table>

The claw index ratio values of the intertidal species are outside the range of those of the supralittoral and non-intertidal species, therefore there is a highly significant difference between the two groups.

*: additional data modified from Schubart (1975).
Locomotion in *Hyadesia furcillipes*.

Acari of the Terrestrial Moiety usually have legs III and IV thicker than I and II, e.g., *Bdella decipiens* (7A); compare with the aquatic moiety where legs I and II are the thickest, e.g., *Halacarellus basteri* (7B); *Hyadesia* spp. most resemble the aquatic moiety in this respect (7C); 7D. The grip mechanism of *H. furcillipes*. The tip of the tarsus is in contact with the substratum, with the pulvillar claw (pul) hooked over an irregularity in the substratum. A downward pressure on the leg (1), causes the point of the tarsus (2) to act antagonistically with the hook of the claw (3); 7E. Leg III of *H. furcillipes*. The body of the mite may be supported on the distal tarsal spines (1); the claw is used to grip onto irregularities (2); 7F Stepping sequence in *H. furcillipes*. Dots represent tarsi in contact with the substratum; direction of movement of legs not in contact with the substratum shown by the arrows.

(7C is modified after BENARD, 1961).
information regarding lifestyles observed among the Terrestrial Moiety of the intertidal Acari (PUGH, 1985; PUGH & KING, 1985b). The Mesostigma, and the genera Ameronothrus (Cryptostigmata) and Hyadesia (Astigmata), are tolerant of inundation, and have ambulacra adapted to increase adhesion on wet surfaces. However, the Prostigma, which are intolerant of wetting, show no such adaptations and rely upon speed to forage ahead of the tide. Their ambulacra are adapted to give maximum traction at speed, contrasting with the aquatic moiety (family Halacaridae), which show a range of adaptations to cope with the mechanical stresses resulting from wave action (PUGH, 1985; PUGH, et al. in press).

ACKNOWLEDGEMENTS

We would like to thanck Professors E. W. KNIGHT-JONES and J. S. RYLAND for providing research facilities, and one of us (P. J. A. P.) is grateful to the Natural Environment Research Council and the Gulf Oil Refining Company of Milford Haven for their financial support.

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