POSSIBLE SIGNIFICANCE OF THE CLAW STRUCTURE IN THE RHOMBOGNATHINAE (HALACARIDAE : PROSTIGMATA : ACARI)

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

ETHOLOGY
HALACARIDAE
INTERTIDAL ZONE

ABSTRACT : The vertical distribution of the Rhombognathinae in the intertidal zone and hence their tolerance to wave action, is correlated with the structure of the ambulacrum. Lateral claw structure, and in particular the development of combs, is an important factor, with heavy multidentate combs providing most grip, and therefore greater tolerance to wave action. The median claw is of secondary importance because it provides less grip than the combs which present a greater number of points of contact with the substratum.

ÉTHOLOGIE
HALACARIENS
ZONE RECOUVERTE
PAR LES MARÉES

RÉSUMÉ : La répartition verticale des Rhombognathinae dans la zone recouverte par les marées, et par conséquent leur tolérance à la pression des vagues, sont en corrélation avec la structure de l'ambulacre. La structure de l'ongle latéral, et en particulier la formation de peignes, sont un facteur important, comportant l'accroissement de l'adhérence apporté par les peignes fortement pluridentés, et donc une plus grande tolérance à l'action des vagues. L'ongle médian est d'une importance secondaire parce qu'il fournit moins d'adhérence que les peignes qui présentent des points de contact plus nombreux avec le substratum.

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 maintain their position on the shore (BALLANTINE, 1961 ; NEWELL, 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 are generally exposed to these stresses ; and a terrestrial moiety, a mixed assemblage of species belonging to a number of families which avoid wetting by retreating ahead of the tide, or withdraw into air pockets trapped in crevices, and thus do not experience these stresses (PUGH, 1985 ; PUGH & KING, 1985b).

Among the Halacaridae, a variety of claw structures has been described by previous workers ; and in the present study, a possible relationship between claw structure and position on the shore is considered in the Rhombognathinae.

MATERIALS AND METHODS

Halacaridae were extracted in the laboratory from samples of intertidal algae and barnacles using a hypersaline flotation technique (PUGH, 1985 ; PUGH & KING, 1985a), or by hand sorting of material.

*. Marine Biology Research Group, School of Biological Sciences, University College of Swansea, Singleton Park, Swansea, West Glam. SA2 8PP Great Britain.

Macroalgae on open rock surfaces of rocky shores form a vertical stratification pattern (LEWIS, 1964) ; correlation between these algae and Halacaridae allows accurate estimations of the vertical distribution of these Acari (PUGH, 1985 ; PUGH & KING, 1985a). In the present study, eight species of macroalgae were examined which form a stratified system on the shores of the South Wales coast with a Ballantine exposure rating of 4 + (BALLANTINE, 1961). These algae were *Laminaria digitata* (Hudson), *Ascophyllum nodosum* (L.) [and its associated epiphyte *Polysiphonia lanosa* (L.)], *Pelvetia canaliculata* (L.), *Fucus serratus* (L.), *Fucus spiralis* L., *Fucus vesiculosus* L. (Phaeophyceae) ; *Gigartina stellata* Stackhouse and *Laurencia pinnatifida* (Hudson) (Rhodophyceae). Ten species of Rhombognathinae were shown to have positive correlations with these algae, based on the 0.05 P level of the Yates corrected Chi-squared analysis (YATES, 1934).

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, and viewed in a JEOL 35C SEM. Claw structure in the following species was studied :

Rhombognathus lionyx Trouessart * ; *R. notops* (Gosse) (S) ; *Rhombognathides merrimani needleri* Newell ; *R. mucronatus* (Viets) * ; *R. pascens* (Lohmann) * (S) ; *R. seahami* (Hodge) * (S) ; *R. spinipes* (Viets) * (S) ; *Metarhombognathus armatus* (Lohmann) *(S) ; *Isobactrus levis* (Viets) * (S) ; *I. setosus* (Lohmann) * (S) ; *I. ungulatus* Bartsch (S) ; *I. uniscutatus* (Viets).

Note : * : indicates species correlated with the intertidal algae (Fig. 1) (S) : examined in the stereoscan (Fig. 2).

OBSERVATIONS & DISCUSSION

The association between some Acari and algae, combined with the algal zonation pattern, suggests a vertical stratification of these Acari (PUGH, 1985 ; PUGH & KING, 1985a) (Fig. 1). The Rhombognathinae have ambulacra bearing paired hardened lateral claws each of which may be simple and smooth (Fig. 2 A), ornamented with a dorsal accessory tooth and fine comb (Figs. 2 B & 2 C), or its distal edge is expanded laterally to become scythe-like and armed with a broad comb along the entire distal edge of the claw (Figs. 2 D, 2 E & 2 F). A simple median claw may also be present (Fig. 2 F). *I. levis, I. uniscutatus, R. lionyx* and *R. spinipes*, all of which occur among the algae of the upper intertidal zone which includes *P. canaliculata* and *F. spiralis* (Fig. 1), have two smooth claws on each tarsus (Fig. 2 A). *M. armatus* from both upper and mid-intertidal algae down to the *F. serratus* zone has three simple but massive claws on each tarsus (Fig. 1). *I. setosus* with the same vertical range as *M. armatus* (Fig. 1), has only two claws which are armed with a comb consisting of few long slender tines, subequal in length to the main claw point (Fig. 2 C & Table 1). In contrast, the lateral claws of *R. mucronatus, R. pascens* and *R. seahami*, which occur among algae at all shore levels including the more exposed lower intertidal zone (Fig. 1) are more elaborate, being expanded distally to become scythe-shaped, and armed with a broad comb of many narrow tines with each tine being level with the main claw point (Figs. 2 E, 2 F & Table I). These species have an additional simple median claw on tarsi I and II as in *R. pascens* (Fig. 2 E), or on all tarsi as in *R. mucronatus* and *R. seahami* (Fig. 2 F). This suggests that species with comparatively simple ambulacra, consisting of two smooth claws, are found in the upper intertidal zone, whilst other species with more elaborate ambulacra including the development of fine combs on the lateral claws, occur in the upper and mid-intertidal. Species in which each of the lateral claws are distally expanded, scythe-shaped and armed with a broad multidentate heavy comb, occur in the upper and lower intertidal zones (Fig. 1). This distribution may be related to a number of factors, but it is probable that the elaborate ambulacra equipped with heavy multidentate claw combs are important for the maintenance of position among Rhombognathinae occuring in conditions where prolonged submergence may cause extended exposure to mechanical stress generated by increased wave action, for

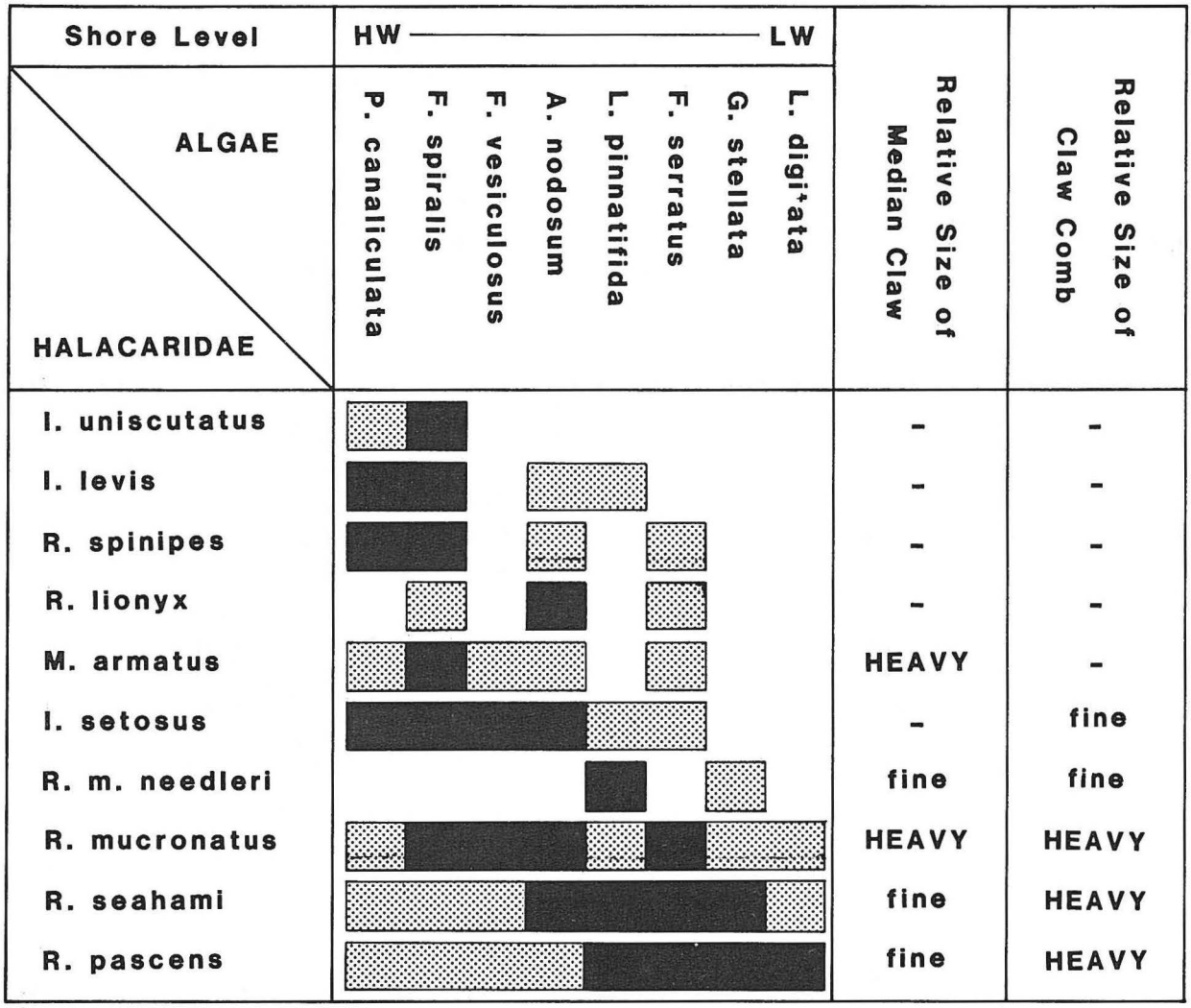

FIG. 1 : The relationship between level on shore and claw structure among the Rhombognathinae. The levels on the shore are determined using the common littoral macroalgae, and both Acari and algae are ranked according to level, ranging from high water (HW) to low water (LW) in the intertidal zone. The bars represent the occurence of Acari among the algae, with solid bars representing a positive association between Acari and algae at the .05P level, determined by the Yates corrected Chi squared analysis (YATES, 1934). Stippled bars represent records not significant at the .05P level. Association data derived from PUGH (1985), PUGH & KING (1985a).

example in the lower intertidal zone of moderately exposed shores (NEWELL, 1979).

I. ungulatus occurs almost exclusively amongst mid-intertidal barnacles, particularly *S. balanoides* (PUGH, 1985 ; PUGH & KING, 1985a) on moderately exposed shores (BALLANTINE, 1961), and is subjected to conditions of greater mechanical stress than any of the species associated with intertidal algae (PUGH, 1985). It has massive, broad adze-shaped claws, each armed with a distal comb of relatively few very long, stout tines (Fig. 2 D & Table I) ; by contrast, *R. notops* is confined to calm pools, and has two relatively thin claws each armed with short, fine dorsal combs associated with the accessory tooth (Fig. 2 B & Table I).

The function of Rhombognathine claw ornamentation is open to question. The elaborate expanded combs of *I. ungulatus, R. pascens* and *R. seahami* in which the comb tines are the same length as, and form a continuous series with the main claw point

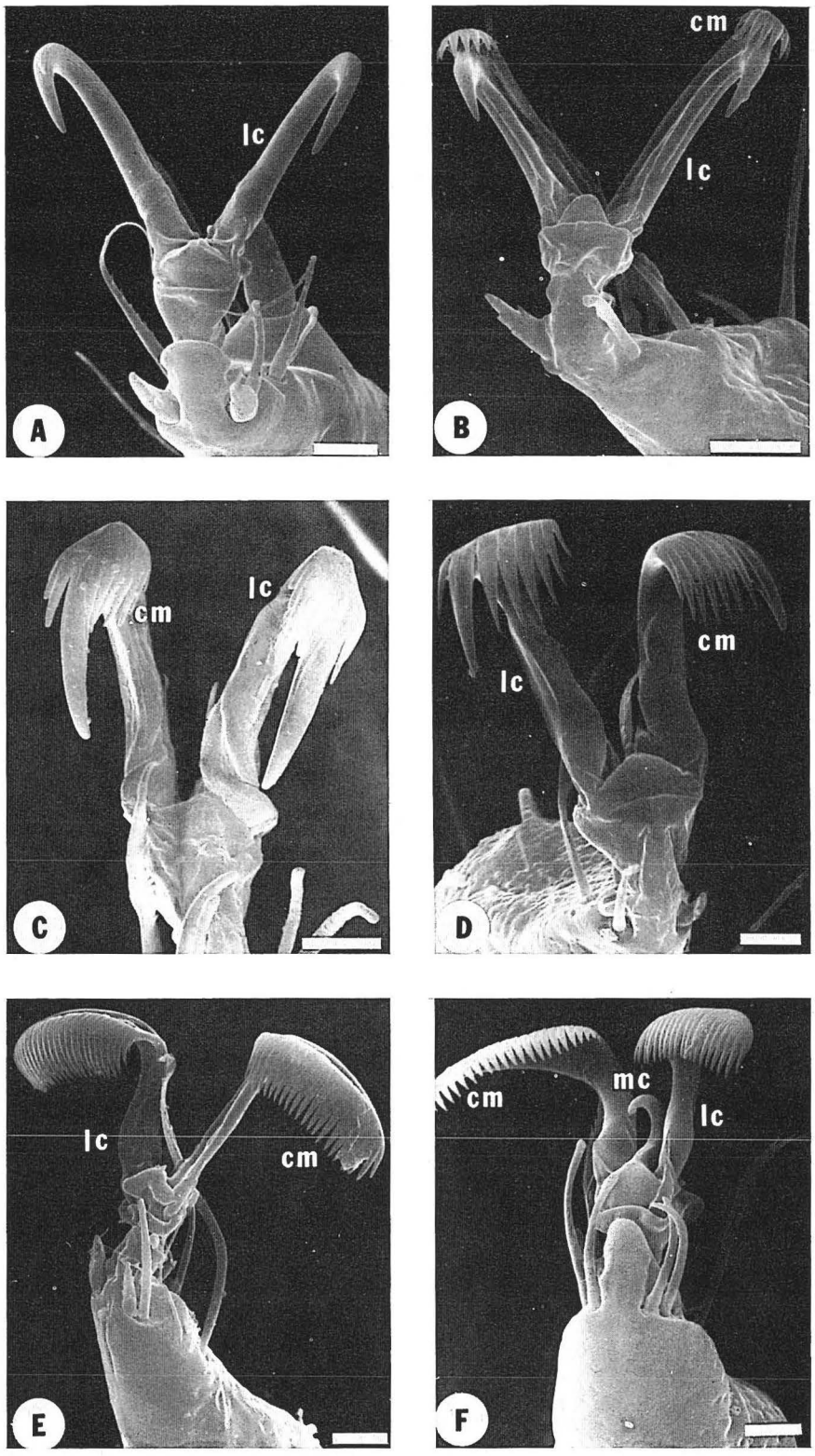

FIG. 2 : Claw morphology in the Rhombognathinae.

2 A. — *Rhombognathides spinipes* : ambulacrum II, ventral aspect. The large simple lateral claws (lc), lack combs (compare with 2 B *et seq.*). Scale : 5 µm. 2 B. — *Rhombognathus notops* : ambulacrum II, ventral aspect. The thin lateral claw (lc), are equipped with very fine combs (cm) which are associated with the dorsal accessory tooth. Scale : 5 µm. 2 C. — *Isobactrus setosus* : ambulacrum II, ventral aspect. The lateral claws (lc), are equipped with fine combs (cm). Scale : 5 µm. 2 D. — *Isobactrus ungulatus* : ambulacrum II, ventral aspect. The broad adze-shaped lateral claws (lc), are equipped with massive combs (cm). Scale 5 µm. 2 E. — *Rhombognathides pascens* : ambulacrum I, ventral aspect. The lateral claws (lc) are distally expanded, scythe-shaped and equipped with broad multidentate combs (cm). Scale : 5 µm. 2 F. — *Rhombognathides seahami* : ambulacrum II, ventral aspect. The lateral claws (lc) and combs (cm) are very similar to those of *R. pascens* (compare with 2 E), but with the addition of a small median claw (mc). Scale : 5 µm.

TABLE I : Claw comb morphology in some Rhombognathinae

Species	Maximum Tine length * (µm)	Maximum (basal) Tine diameter (µm)	Length/ Diameter Ratio (ranked)	Number of Tines *
R. notops	1.78	0.42	4.23	7-8
I. ungulatus	8.8	1.8	4.88	7-8
I. setosus	9.6	1.76	5.45	7-9
R. pascens	5.0	0.62	8.06	18-22
R. seahami	5.2	0.62	8.37	18-23

* : excluding the main claw point.

obviously increase grip onto the substratum by providing a greater number of points of contact with it. Whether those of *R. pascens* and *R. seahami* which are associated with intertidal algae actually pierce their algal substrates, or merely hook onto minute surface irregularities is not at present known. However, in *I. setosus* and *R. notops* the combs do not reach the tips of the main claw points ; the dorsal position of the combs and accessory teeth, combined with the fact that these species are largely confined to sheltered pools and algae, suggests that they provide minimal grip and have little use in maintenance of position.

The evidence suggests that species in which the lateral claws are distally expanded and armed with multidentate heavy combs are better adapted to cope with conditions of mechanical stress generated by wave action, and are able to penetrate lower down the intertidal zone. The presence of combs and the relative size of the comb teeth are of primary importance ; the distally expanded combs with numerous tines provide more points of contact with, and hence give a better grip onto, the substratum. The presence and relative development of the median claw is of only secondary importance, because it only provides one point of contact with the substratum. Species occuring under conditions of extreme mechanical stress, have relatively fewer tines on the combs, but these are much stouter and longer than those of the species confined to the algae. This parallels the adaptations of the terrestrial moiety of the intertidal Acari, where species exposed to wave action have particularly adapted ambulacra (PUGH, 1985 ; PUGH *et al.* 1987).

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