

# Comparative study of the functional morphology of antennae, pleopods and exoskeleton among five species of Amphipoda (Crustacea) living in different ecological zones: a gradual transition from marine to terrestrial environment

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The functional morphology of antennae, pleopods and exoskeleton of five amphipod species, living in different ecological zones was compared to investigate their possible adaptations from marine to terrestrial environment. The results of the present study showed that antenna 1 of the supralittoral species, i.e. *Talorchestia deshayesii* and *Talitrus saltator*, has the most reduced size compared to the terrestrial (*Arcitalitrus sylvaticus*) and the marine species (*Echinogammarus foxi* and *Hyale schmidtii*), collected from the midlittoral and the sublittoral zone, respectively; this was probably related to their limited chemosensory function on land. A gradual increase in the size of antenna 2 from marine to terrestrial environment was also detected, probably related to the need for strong antennae on land for burrowing and holding position during copulation. Both pairs of antennae appear to be the most robust in supralittoral species reflecting the harsh environmental conditions that occur in the semiterrestrial environment. A gradual increase in the pleopodal size was observed, from the sublittoral to the supralittoral species. The pleopodal size was much reduced in the terrestrial species, probably attributed to the decreased necessity for swimming on this habitat or other functions in different species of Talitridae. The thickness of the exoskeleton in the studied amphipods increased from marine to terrestrial environment; this fact can be regarded as a protective adaptation to the unfavorable conditions (high hydrodynamism mainly due to wave action, reduced humidity, exposure to high temperatures and solar radiation) that prevail on the ecological zone where each species lives.

**Key words:** *Hyale schmidtii*, *Echinogammarus foxi*, *Talorchestia deshayesii*, *Talitrus saltator*, *Arcitalitrus sylvaticus*.

## INTRODUCTION

Several authors have outlined the basic morphological and physiological trends in amphipod crustaceans that permitted their successful invasion to the terrestrial environment (Hurley, 1959, 1968; Bliss & Mantel, 1968; Bousfield, 1968; Friend & Richardson, 1986). Hurley (1959) noted that the distribution of the terrestrial species of amphipods is limited to countries bordering the Indian and Pacific Oceans and to the Pa-

cific islands, due to the humid mantle formed around the forests present in these areas. He also noted sufficient extent and variety of terrestrial amphipod fauna in Australia, New Zealand and South Africa, where attention was attracted to their ecology and physiology in order to understand the evolutionary process of their transition from the marine to the terrestrial environment. Friend & Richardson (1986) and Stock & Biernbaum (1994) mentioned the presence of terrestrial amphipods on islands of central Atlantic. They believe that talitrids are easily introduced, mostly with plant material, into foreign countries with tropical and warm-temperate climate. Several authors

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before had mentioned the occurrence of terrestrial species in the Azores, Madeira and the Canary islands (Andersson, 1963; Dahl, 1967) and in Britain (Richardson, 1980).

Among the different features used to determine the adaptation of amphipods in different environments, attention must be given to the antennae, the pleopods and the thickness of the exoskeleton. The second pair of antennae has generally been viewed mainly as the chemo- and mechano-receptor organs in aquatic Crustacea (Krång & Baden, 2004). According to Bliss (1968) marine decapods have larger antennae than the terrestrial species. Crane (1975) mentioned that both pairs of antennae of *Uca* (Ocypodidae) are smaller in size compared to the marine species and their function is limited. Spicer *et al.* (1987) reported that there has been a marked reduction in size of the first antennae in Talitridae associated with the colonization of land. The structure of the sensory setal groups of antennae 1 in Talitridae studied by Dahl (1973), suggested that the first antennae may still have an important role in chemoreception and in orientation behavior, although they are reduced in terrestrial environment (Bliss & Mantel, 1968). Dahl (1973) also suggested that in the semiterrestrial and terrestrial species both pairs of antennae, with their short terminal hair groups, play an important role in probing the surfaces of wrack beds and sand burrows where amphipods dwell. According to Williamson (1951), semiterrestrial and terrestrial species of the family Talitridae use their second antennae during mating in several ways; males use them to search for and grasp the female and for holding her in position during copulation, as well as to repulse the rivals that may try to capture the female.

Pleopods in aquatic species are used for swimming (Hurley, 1959; Bliss & Mantel, 1968; Friend & Richardson, 1986). The pleopods also draw a constant current of water over the gills; this current filtered by the gnathopods, serves as a food vehicle (Coelho & Rodrigues, 2001). According to the same authors, there is a trend with increasing terrestriality towards reduction or complete loss of pleopods except for vestigial triangular stumps. Though, there are terrestrial species that retain the marine pleopodal form. However all supralittoral species possess fully developed pleopods that are able to beat and probably use them when occasionally they are submerged (Friend & Richardson, 1986). Terrestrial species have lost their ability to swim and, when submerged, they walk or hop (Friend & Richardson, 1986). Moore &

Richardson (1992) suggested that pleopods of terrestrial amphipods are used to create air currents and to agitate water (exosomatic water) that is carried along the ventral surface of the body. As they beat, they transfer water from the urosome to the thoracic area. According to the same authors, terrestrial species that have reduced or lack pleopods, use the elongate posterior lobes of the last pair of gills for the same purpose. They suggested an inverse relationship between the size of pleopods and the length of the last pair of gills. Richardson (1998) mentioned that in terrestrial species the morphology of the last pair of gills correlates with the degree of reduction of the pleopods. Species with non-functional pleopods have elongated gills.

Until now, there was no available information about any possible changes of the thickness of the exoskeleton in amphipods living in different ecological zones. Chartosia (2010) compared the thickness of the carapace among four species of decapods that live in different ecological zones (sublittoral, midlittoral, supralittoral zones and the terrestrial environment) and reported a gradual increase in the carapace thickness from the marine to the terrestrial environment, which can be regarded as an adaptation of protection from the unfavorable conditions that prevail on the ecological zone where each species lives. Such conditions include a medium shift (from seawater to air), the exposure to high hydro-dynamism due to the wave action in midlittoral zone and the exposure to high temperatures and high levels of solar radiation in supralittoral zone and on land.

In this study, the functional morphology of the antennae, the pleopods and the thickness of the exoskeleton is described and compared among five species of Gammaridea amphipods: the sublittoral species *Hyale schmidtii* (Heller, 1860), the midlittoral species *Echinogammarus foxi* (Schellenberg, 1928), the lower supralittoral species *Talorchestia deshayesii* (Audouin, 1826), the higher supralittoral species *Talitrus saltator* (Montagu, 1808), and the terrestrial species *Arcitalitrus sylvaticus* (Haswell, 1879). Possible detected morphological differences among the above species were discussed to assess the features that permitted their adaptation to the different ecological zones.

## MATERIALS AND METHODS

Amphipods were collected from different coastal areas in the North Aegean Sea. Specimens of *Hyale schmidtii* (that lives usually in shallow waters among

the alga *Cystoseira* sp.) were collected from Agios Ioannis in Chalkidiki Peninsula. The midlittoral species *Echinogammarus foxi* lives usually on hard substratum coasts under or among gravels; specimens were

collected from Strymonikos Gulf. *Talorchestia deshayesii* usually is found in the soft substratum in lower supralittoral zone, but it occasionally moves to the midlittoral zone. *Talitrus saltator*, which lives in the

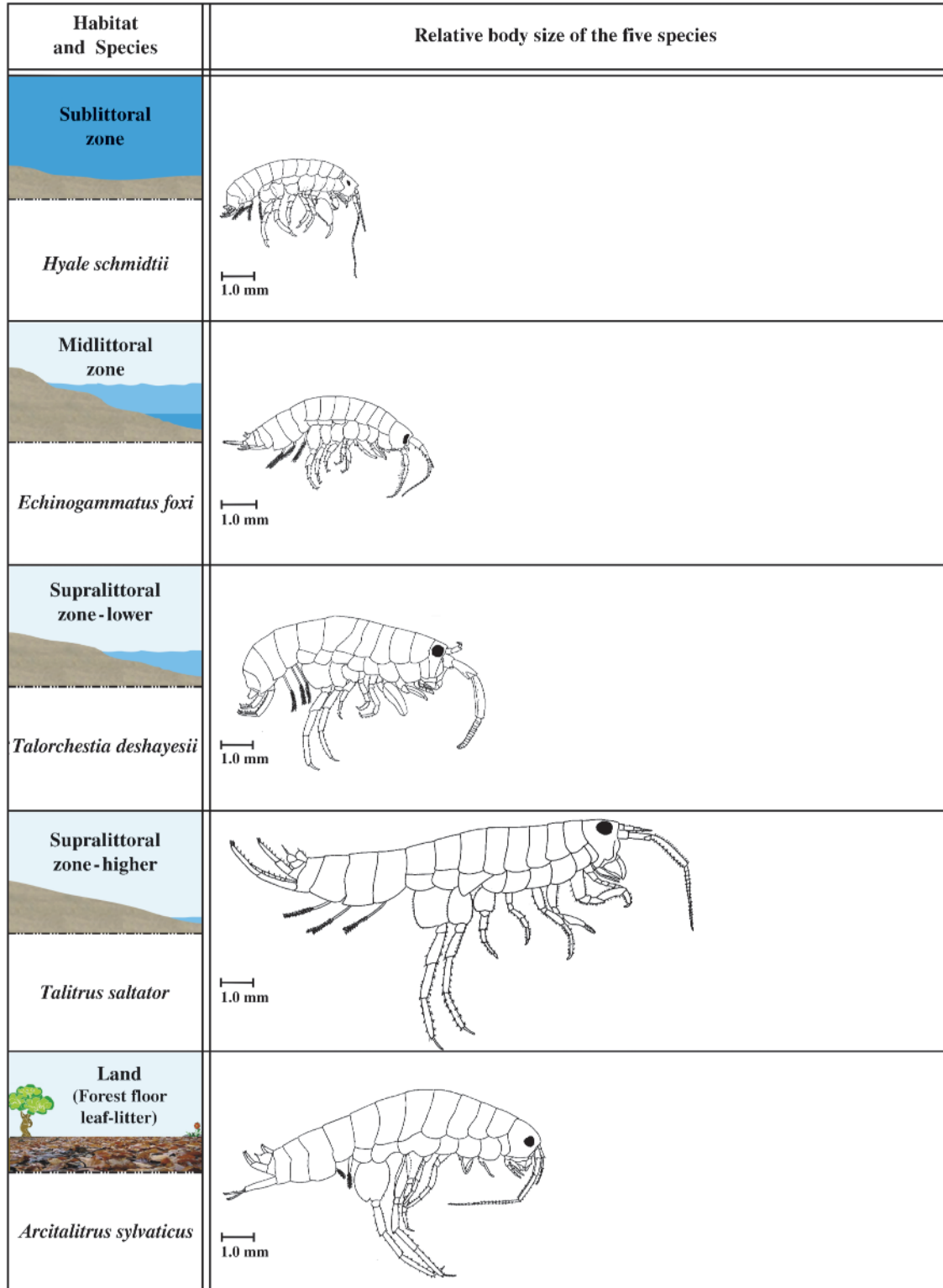


FIG. 1. Male individuals of the five species examined in this study and the different ecological zones where they live.

higher supralittoral zone, was found burrowing far from the tide line. Specimens of both species were collected from Korinos beach. Due to the absence of terrestrial amphipod species from Greece, specimens of *Arcitalitrus sylvaticus* were borrowed from the Victoria Museum of Melbourne, and from the Australian Museum of Sydney, Australia. This species inhabits the leaf litter and soil layer of deciduous woodlands. Peart & Lowry (2006) found this species in leaf litter under *Eucalyptus* trees. The relative body size and the ecological zone of each species are given in Figure 1.

All specimens examined were preserved in 90% alcohol. From each species, male mature individuals were examined and their appendages were removed with the use of dissecting tools and their morphology was examined in detail. Then a photo was taken from each one of them and drawn in detail.

For scanning electron microscopy study, the first pereon segment of the exoskeleton of each of the five species were removed and after a similar incision along the same position (medio-dorsal region), were mounted on metal discs and placed in a vacuum carbon evaporator. Then, after being carbon coated, they were observed with the use of a JEOL JSM 840A scanning electron microscope. The thickness of the incisions of their exoskeleton was measured and compared among the five selected species. From each of the four species the thickness was measured from ten male individuals, while from *Arcitalitrus sylvaticus* was measured from four male individuals. Data were checked for normality using Shapiro-Wilk test; results showed that the data were not normally distributed ( $p < 0.05$ ). For this reason, statistical analysis was performed using non-parametric tests (Kruskal-Wallis and Kolmogorov-Smirnov tests) in order to compare the exoskeleton thickness among male individuals of the five studied species (Statistica 6; StatSoft, Tulsa, Oklahoma, USA). Significance level was set at  $p = 0.05$  for all comparisons.

All the morphological features examined and compared among the selected species are shown in Figures 2-8.

## RESULTS

### *Hyale schmidtii* (Heller, 1860) ♂

The antenna 1 peduncle is shorter than the flagellum. Flagellum, with 13 articles, bearing tufts of simple setae on the distal margins of each article. Setae present on the ventral side are longer than those on the dorsal side. Few simple setae are also present on the

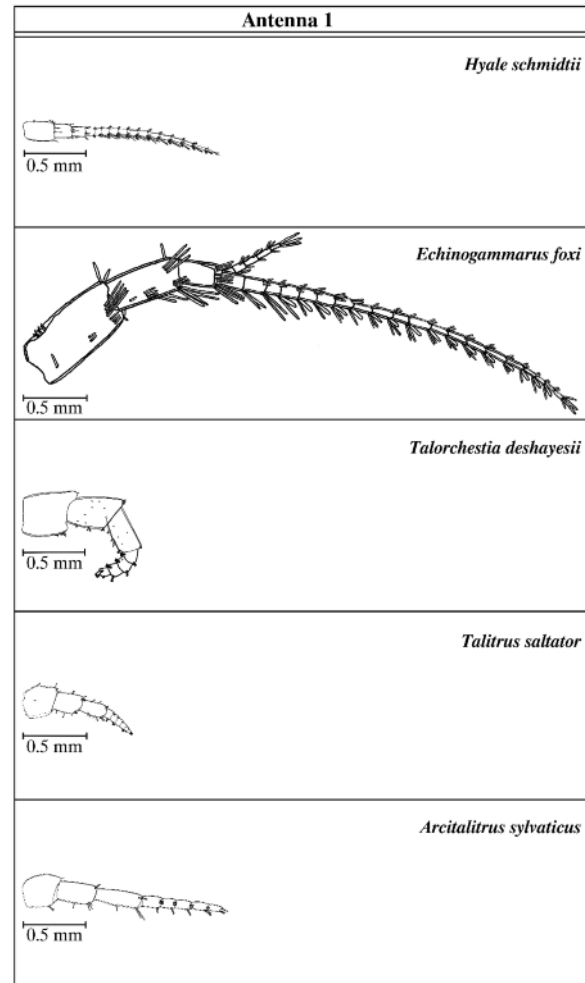


FIG. 2. Diagram of Antenna 1 of the five studied species.

lateral sides of the peduncle articles. Peduncle article 1 is longer than broad. Peduncle articles 2 and 3 almost as long as broad (Fig. 2).

The antenna 2 peduncle is shorter than the flagellum. Flagellum, with 24 articles, bearing tufts of simple setae on the distal margins of each article. Setae present on the ventral side are longer than those on the dorsal side. Setae are also present on the dorsal, ventral and lateral sides of the peduncle articles. Peduncle article 1 is broader than long. Peduncle articles 2 and 3 longer than broad (Fig. 3).

The external morphology of all three pairs of pleopods is the same. Pleopods are biramous and both rami are almost equal in length. Rami are longer than the peduncle. Outer ramus with 12 articles and inner ramus with 11 articles. Both rami bear plumose setae on the inner and outer margins of every article. Three plumose setae are also present on the inner margin of the peduncle (Figs 4-6).

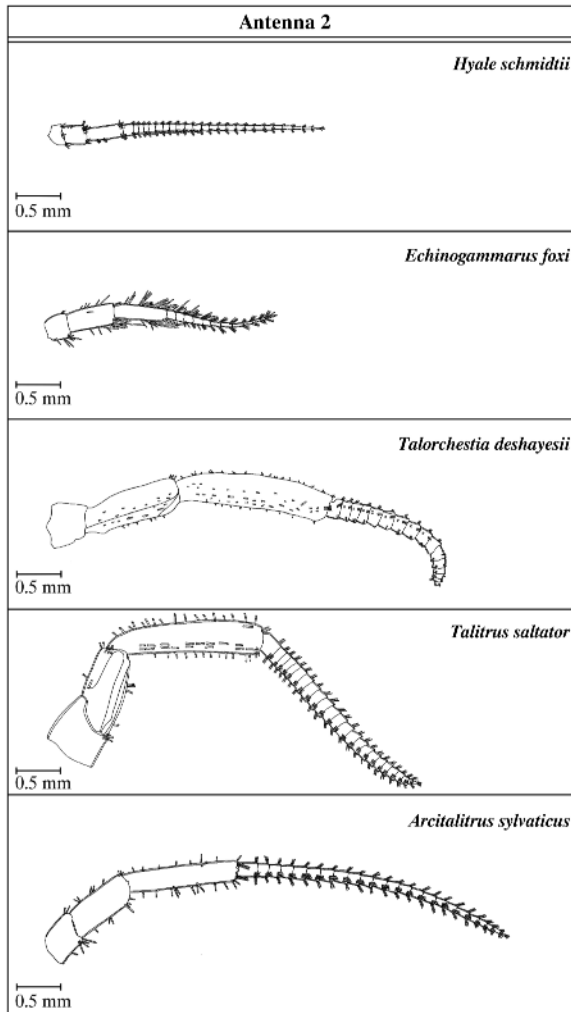


FIG. 3. Diagram of Antenna 2 from male individuals (sexually dimorphic) of the five studied species.

#### *Echinogammarus foxi* (Schellenberg, 1928) ♂

The antenna 1 peduncle is shorter than the flagellum. Flagellum with 20 articles. Accessory flagellum is present having 5 articles. Both flagella and accessory flagellum bear tufts of simple setae on the margins of each article on both dorsal and ventral sides. Setae on the ventral side are longer than those on the dorsal side. A few long simple setae are present on the terminal part of the accessory flagellum. Short and long simple setae are also present on the peduncle. Peduncle article 1 bears a few small plumose setae on the proximal dorsal margin. Peduncle articles are longer than broad (Fig. 2).

The antenna 2 peduncle is almost equal in length with the flagellum. Flagellum with 11 articles. Both peduncle and flagellum bear short and long simple setae throughout the dorsal and ventral sides. Pedun-

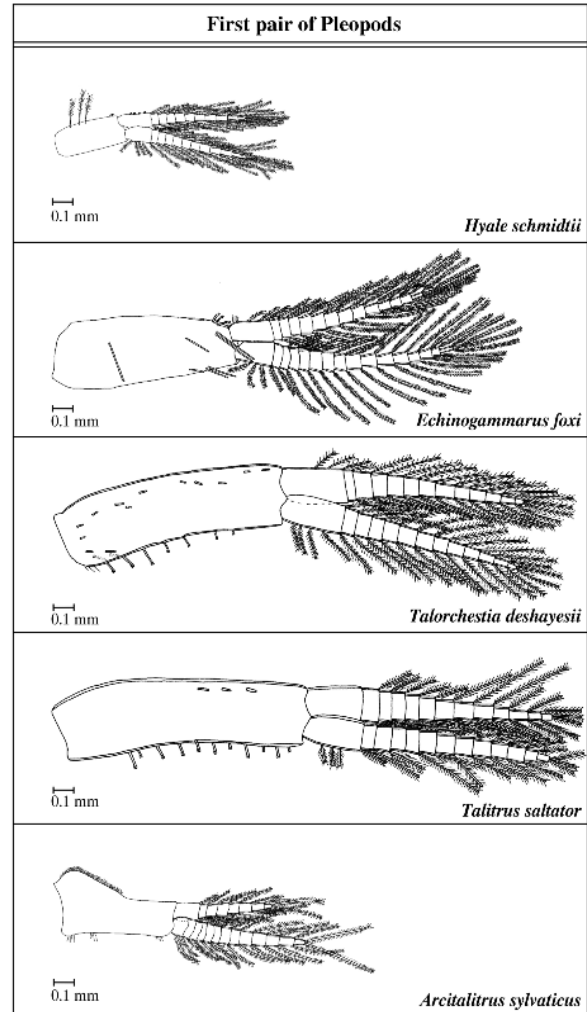


FIG. 4. Diagram of Pleopod 1 of the five studied species.

cle article 1 is almost as long as broad and peduncle articles 2 and 3 are longer than broad (Fig. 3).

The external morphology of all three pairs of pleopods is the same. Pleopods are biramous and both rami are almost equal in length. Rami are longer than the peduncle. Outer ramus with 17 articles and inner ramus with 15 articles. Both rami bear plumose setae on the inner and outer margins of every article. The peduncle bears a few simple setae dorsally and a few small serrate setae on the inner distal margin (Figs 4-6).

#### *Talorchestia deshayesii* (Audouin, 1826) ♂

The antenna 1 is short and stout not reaching the end of the antenna 2 peduncle. Flagellum having 5 articles is shorter than the peduncle. A few short simple setae are present on the ventral margins of the peduncle articles. Dorsal side almost with no setae. Fla-



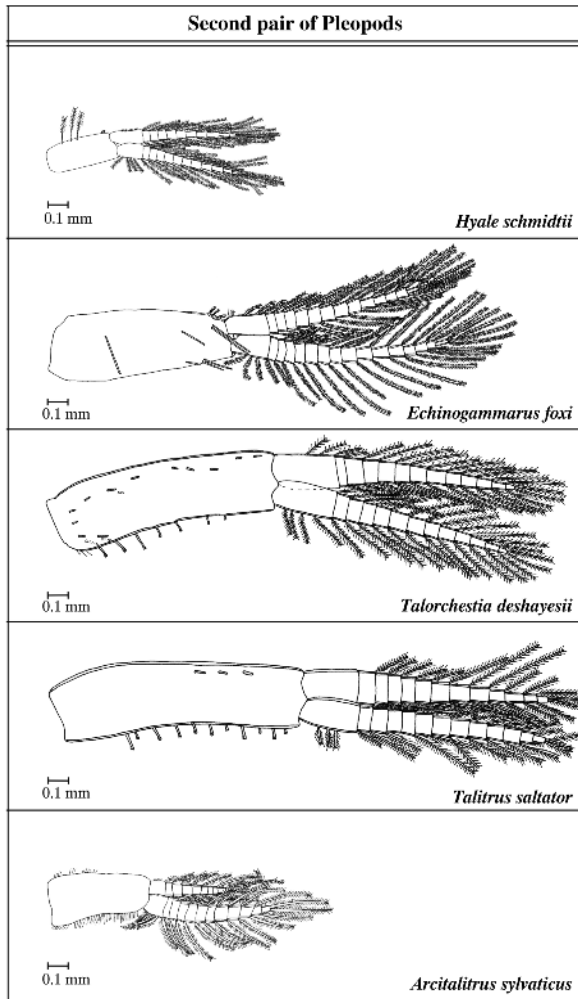


FIG. 5. Diagram of Pleopod 2 of the five studied species.

gellum bears on both dorsal and ventral margins tufts of short plumose setae. Peduncle article 1 is as long as broad. Peduncle articles 2 and 3 longer than broad (Fig. 2).

The antenna 2 is stout. Flagellum, with 16 articles is shorter than the peduncle. Peduncle article 2 bears a few short simple setae on the ventral margin. Dorsal margin with no setae except of the distal margin where a tuft of simple setae is present. Lateral side bears 3 rows of short simple setae. Peduncle article 3 bears short simple setae on both dorsal and ventral margins. Furthermore there are three rows of short simple setae on each lateral side. A pair of short plumose setae is present laterally and distally. Flagellum also bears short simple setae on the dorsal and ventral margins of each article. Also two rows of simple setae are present laterally along the flagellum. Peduncle article 1 is as long as broad. Peduncle articles 2 and 3 longer than broad (Fig. 3).

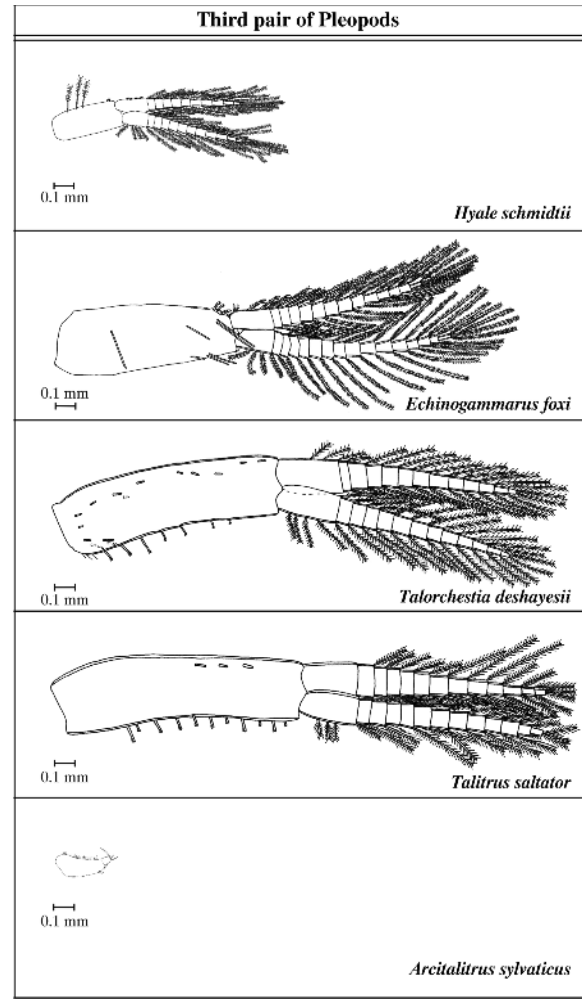


FIG. 6. Diagram of Pleopod 3 of the five studied species.

The external morphology of all three pairs of pleopods is the same. Pleopods are biramous and both rami are almost equal in length. Rami are almost as long as the peduncle. Both rami with 13 articles bearing plumose setae on the inner and outer margins of every article. A few short simple setae are present on the outer margin of the peduncle and one row is also present dorsally (Figs 4-6).

#### *Talitrus saltator* (Montagu, 1808) ♂

The antenna 1 is short and stout not reaching the end of the antenna 2 peduncle. Flagellum, with 6 articles, is shorter than the peduncle. A few short simple setae are present on the dorsal and ventral margins of the peduncle articles. Peduncle articles 2 and 3 bear two pairs of short plumose setae on the distal dorsal and ventral margins, respectively. Flagellum articles bear no setae dorsally but bear short plumose setae on the ventral margin. Laterally there are three rows of sim-

ple short setae along the flagellum. Peduncle article 1 is as long as broad. Peduncle articles 2 and 3 longer than broad (Fig. 2).

The antenna 2 is stout. Flagellum, with 24 articles, is shorter than the peduncle. Peduncle article 1 bears a tuft of short simple setae on the ventral distal margin. Dorsal margin with no setae. Peduncle article 2 bears a few tufts of short simple setae dorsally, ventrally and laterally. Peduncle article 3 bears short simple setae on both dorsal and ventral margins. Furthermore there are two rows of short simple setae on the lateral side. Flagellum bears short simple setae on the dorsal and ventral margins on each article. Also, three rows of simple setae are present laterally along the flagellum. Peduncle article 1 is broader than long. Peduncle articles 2 and 3 longer than broad (Fig. 3).

The external morphology of all three pairs of pleopods is the same. Pleopods are biramous and both rami are equal in length. Rami are almost as long as the peduncle. Both rami with 13 articles and bear plumose setae on the inner and outer margins of every article. A few short simple setae are present on the outer margin of the peduncle (Figs 4-6).

#### *Arcitalitrus sylvaticus* (Haswell, 1879) ♂

The antenna 1 is short not reaching the end of the antenna 2 peduncle. Flagellum, with 5 articles, shorter than the peduncle. Dorsal side of both peduncle and flagellum almost with no setae. A few simple short setae are present on the ventral margin of each peduncle article. Flagellum bears simple setae on the ventral margin and three rows of simple short setae laterally on each article. Peduncle article 1 is as long as broad. Peduncle articles 2 and 3 longer than broad (Fig. 2).

The antenna 2 peduncle is shorter than the flagellum. Flagellum with 23 articles. Peduncle and flagellum articles bear simple setae on both dorsal and ventral margins. Three rows of simple setae are also present along the flagellum laterally. Peduncle article 1 is as long as broad. Peduncle articles 2 and 3 longer than broad (Fig. 3).

The pleopod 1 is well developed, biramous, rami almost equal in size with the peduncle. Peduncle is broader proximally. Outer ramus with 13 articles and inner ramus with 8 articles. Both rami bear plumose setae on the inner and outer margins of every article. On the inner margin of the peduncle numerous setules are present and on the outer margin there are only some tufts (Fig. 4).

The pleopod 2 is well developed, biramous, rami almost equal in size with the peduncle. Outer ramus with 12 articles and inner ramus with 9 articles. Both rami bear plumose setae on the inner and outer margins of every article. On the outer margin of the peduncle numerous setules are present (Fig. 5).

The pleopod 3 is reduced and there are no rami. A few simple setae are present on the distal margin and numerous setules are present on the inner and outer margins (Fig. 6).

### Comparisons

#### Antennae

The size of antenna 1 of the semiterrestrial (*Talorchestia deshayesii*, *Talitrus saltator*) and terrestrial (*Arcitalitrus sylvaticus*) species appears to be reduced compared to the size of the marine (sublittoral and midlittoral) species (Fig. 2). A reduction also occurs on the corresponding numbers of the flagellum articles. From the marine to the terrestrial environment, setae become shorter and fewer, especially on the dorsal side of the antennae. Comparing among the semiterrestrial and the terrestrial species, the antennae of *Talorchestia deshayesii* and *Talitrus saltator* are shorter and stouter in relation to the longer and more delicate antennae of the terrestrial *Arcitalitrus sylvaticus*.

The size of antenna 2 of the semiterrestrial and terrestrial species appears to be increased compared to the size of the marine species (Fig. 3). *Hyale schmidtii* and *Echinogammarus foxi* have more delicate antennae compared to the strong and stout, poorly setosed antennae of the semiterrestrial species. On the other hand, the second antennae of the terrestrial *Arcitalitrus sylvaticus*, although the longest of all, appears to be more delicate compared to the antennae of the semiterrestrial *Talorchestia deshayesii* and *Talitrus saltator*.

#### Pleopods

From the marine to the semiterrestrial environment there is a tendency for increase of the pleopodal size (Figs 4-6). The three pairs of pleopods of each marine and semiterrestrial species are identical with the exception of the terrestrial species *Arcitalitrus sylvaticus*. Also, there are only slight differences between the pleopods of the semiterrestrial species *Talorchestia deshayesii* and *Talitrus saltator*. In contrast, the three pairs of the terrestrial species *Arcitalitrus sylvaticus* differ from each other significantly in comparison

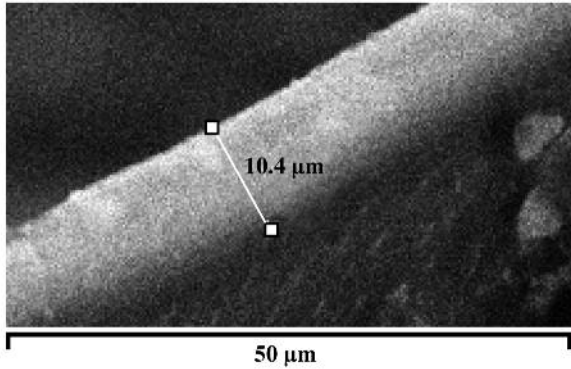


FIG. 7. Thickness of the pereon segment 1 of *Echinogammarus foxi* ( $\times 1000$ ).

to those of the four other species. Although the first two pairs of *Arcitalitrus sylvaticus* are smaller than the corresponding ones of the other species and well developed, the second pair is reduced compared to the first one and the third pair is a vestigial stump.

#### Thickness of first pereon segment

The thickness of the exoskeleton was measured in the same segment (first pereon segment behind the head), with a dorsal incision in all five selected species and under the same magnification (Fig. 7). Measurements showed that there is a tendency that the exoskeleton becomes thicker from the marine to the terrestrial environment ( $p < 0.05$ ), with the exception of the midlittoral species *Echinogammarus foxi*, which has a thickness greater than that of the lower-supralittoral *Talorchestia deshayesii* (Fig. 8). The mean value of thickness of the sublittoral *Hyale schmidtii* was  $7.75 \pm 0.24 \mu\text{m}$  and that of the midlittoral *Echinogammarus foxi*  $10.4 \pm 0.26 \mu\text{m}$ . The lower-supralittoral *Talorchestia*

*deshayesii* had a mean value of  $8.73 \pm 0.23 \mu\text{m}$  and that of the higher-supralittoral *Talitrus saltator*  $11.5 \pm 0.36 \mu\text{m}$ . The mean value of thickness of the terrestrial *Arcitalitrus sylvaticus* was  $36.7 \pm 3.39 \mu\text{m}$ .

## DISCUSSION

The five species selected in this study are characteristic inhabitants of the five different ecological zones. The differences in their morphological features allowed us to understand how each of the species has adapted and prevailed on its habitat. Regarding the size of antenna 1, the findings of this study seem to agree with the hypothesis that functions as a chemoreceptor organ (in order to recognize chemical signals in the water column) in marine species. Its reduced size in semiterrestrial and terrestrial species could be related to its limited function on land. The more delicate and longer pairs of antennae of the terrestrial species *A. sylvaticus* in comparison to the stout and short antennae of the supralittoral species *T. deshayesii* and *T. saltator* could be related to the different habitat that each of these species is adapted to live. Semiterrestrial species living on sandy beaches, where they burrow, require stronger antennae in order to prevent any injuries or damage caused, compared to the terrestrial species living under the relatively softer leaf litter.

The setae of the antennae also play an important role on the sensory functions of the antenna. In semiterrestrial and terrestrial species, antenna 1 bears only a few short setae while the accessory flagellum is absent. According to Friend & Richardson (1986), delicate structures such as accessory flagellum and se-

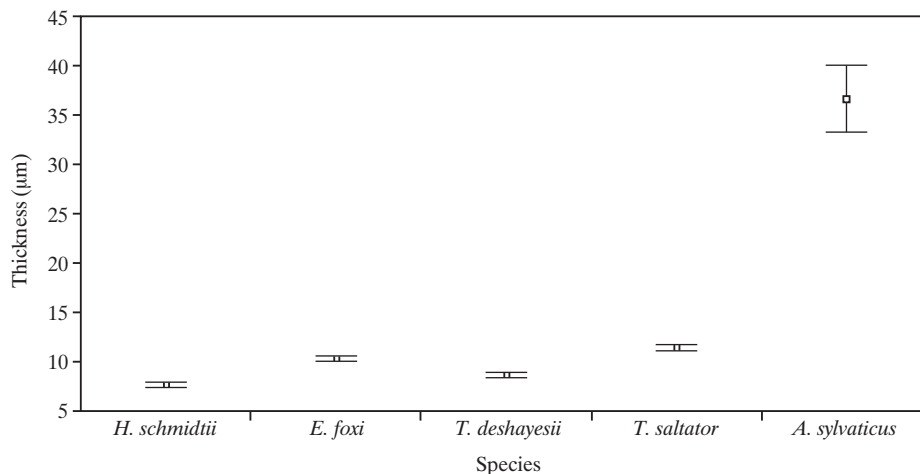


FIG. 8. Mean values ( $\pm$  standard deviation) of thickness of the pereon segment 1 of the five studied species.



tae are lost or shortened in order to be adapted to life in the high-energy littoral zone. Dahl (1973) mentioned that hairs are chemoreceptor organs. The two pairs of antennae in talitrids are used for probing the substrate and other objects and this means that the tips of the sensory hairs must come in contact with the surfaces investigated by the amphipod (Friend & Richardson, 1986). The short antenna 1 is used in probing the surface of the walls and roof of the burrows where the amphipods normally dwell. Semiterrestrial amphipods have been seen to burrow by bending the head in the sand keeping both antennae close to the ventral side of the body (personal observations).

Antenna 2 of semiterrestrial talitrids, play an important role in the holding position during copulation (Williamson, 1951). The holding position in marine amphipods is accomplished with the use of the gnathopods. *Talorchestia deshayesii* and many other semiterrestrial and terrestrial talitrids retain the large second gnathopod in the male, which is used for holding the female in copulation, so the changes in the second antenna cannot be solely due to their use in mating. The male is able to search for and hold the female with its antennae to facilitate copulation. During copulation, other males in the vicinity of the mating pair investigate the female with their antennae, and the mating male may hold off the rivals using the head and antennae. In the present study, the more delicate antennae 2 of the marine species can also be related to the increased chemosensory function required on the marine environment. In contrast, the increased size of antennae 2 in the semiterrestrial and terrestrial species may be related to their function in burrowing, in holding position during copulation and also in fighting and avoiding any rivals present. Comparing among the terrestrial and semiterrestrial species, the more delicate antennae of *Arcitalitrus sylvaticus* in relation to the stout and strong antennae of the semiterrestrial *Talorchestia deshayesii* and *Talitrus saltator* can be explained due to the different habitats, where they live (soft leaf litter forests and sandy beaches, respectively).

The results of this study support the previous reports that terrestrial species of amphipods have reduced pleopods. *Arcitalitrus sylvaticus* possesses the smallest pleopods, particularly pleopod 3 being a vestigial stump. It is the only species possessing unequal pleopods. According to Hurley (1959), the absence of pleopods in some terrestrial species suggests that sufficient air is available to the respiratory surfaces with-

out need of the current created by the pleopods over the gills. In contrast, Richardson (1998) mentioned that species with non-functional pleopods have enlarged and elongated the last pair of gills (via increased total gill surface) that serve to conduct water forward from the urosome to the other gills and ventral cavity. The semiterrestrial *Talorchestia deshayesii* and *Talitrus saltator* possess completely developed and functional pleopods which mean that there is not necessity for enlargement or elongation of the gills. All semiterrestrial species have reduced gill surface area in relation to the marine species (Moore & Taylor, 1984; Spicer & Taylor, 1986; Richardson, 1998). Occasionally, these species are submerged and by beating their pleopods they are able to move away from the sea line and thus surviving from drowning (personal observations). In contrast to the semiterrestrial species, which are able to swim, terrestrial species have lost this ability even though they may possess completely developed pleopods. Hurley (1959) also suggested that the retention of the pleopods in semiterrestrial and terrestrial species may function for the circulation of air in the burrows. This suggestion has also been made by Friend (1987) in his description of the burrowing terrestrial talitrid *Keratroides albidus*, which has plate-like pleopods that may be used to move air in the burrows that this species lives in. Further study of the pleopodal to gill relationships is required in order to investigate the morphological and physiological adaptations involved during the transition from the marine to the terrestrial environment.

The thickness of the first pereon segment was used in order to investigate any differences among the species of amphipods, living in different ecological zones. Chartosia (2010) studying the carapace thickness among four species of crabs, reported a gradual increase from the marine to the terrestrial environment. According to the findings of the present study there is a relatively slight, increasing trend of the pereon thickness in the four species; from the sublittoral until the higher supralittoral zone. Then the thickness of the first pereon segment in the terrestrial species is almost tripled. This increasing trend can be regarded as an adaptation for protection mainly from dehydration due to the gradual increase of the solar radiation from sea water to land. The thicker exoskeleton of the midlittoral species *Echinogammarus foxi* compared to that of the supralittoral species *Talorchestia deshayesii*, can be regarded as an adaptation to the conditions prevailing in the midlittoral zone. Although *Echinogammarus foxi* is less prone to desicca-

tion than *Talorchestia deshayesii*, it has to anticipate problems caused by high hydro-dynamism (mainly because of the wave action over gravels and rocks). The sublittoral species *Hyale schmidtii* has the thinnest exoskeleton compared to the other species because it lives in the milder conditions of the sublittoral zone, so there is no need for a thick exoskeleton. The relatively thin exoskeleton of *Hyale schmidtii* enhances the floating and swimming ability of this species. According to Hartnoll (1971) and Abelló *et al.* (1990) the thin carapace of Portunidae enables their swimming ability. In contrast, semiterrestrial and terrestrial species have thicker exoskeletons compared to the marine in order to resist desiccation and function as a protection from the harsh conditions of their habitats (sand and leaf-litter, respectively). Comparing *Talorchestia deshayesii* and *Talitrus saltator* to *Arcitalitrus sylvaticus*, the significantly thinner exoskeleton of the first two species can be related to the fact that they live in an environment without vegetation, where the lighter body enables them to move and jump faster in order to avoid their predators. On the other hand *Arcitalitrus sylvaticus* lives in an environment with thick vegetation where it is hidden from its predators but still requires a thick exoskeleton in order to be protected while walking or burrowing under the leaf litter. Thus, increase of the thickness of the exoskeleton from marine to terrestrial environment can be regarded as an adaptation towards unfavorable environmental conditions (mechanical as the wave action, high temperatures and solar radiation threatening with dehydration).

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