BEHAVIOR OF JANIROIDEAN ISOPODS (ASELLOTA), WITH SPECIAL REFERENCE TO DEEP-SEA GENERA

ROBERT R. HESSLER & JARL-OVE STRÖMBERG

Knowledge about the behavior of deep-sea isopods is sparse, in spite of their importance (as judged from faunal diversity and numerical abundance) in deep-sea communities. Yet an understanding of the ecology of those communities ultimately requires information on where and how component species live. Many deep-sea isopod families and genera have shallow-water representatives at northern and southern high latitudes. Basic behavioral features of these taxa have been revealed through study of these shallow-waters forms.

This report describes behavior seen in aquaria of species within the Janiridae, Munnidae, Paramunnidae, Ischnomesidae, Desmosomatidae, Eurycopidae, and Ilyarachnidae. Observations cover locomotion (walking, swimming, burrowing), feeding, grooming, respiration, brooding, and interindividual behavior. Several activities, particularly concerning grooming and respiration, characterize many of the taxa. Locomotory habits are strongly correlated with morphology, but borrowing is more common than has been predicted from body design, and taxa with natatory conformation were surprisingly reluctant to swim.

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INTRODUCTION

One aspect of the deep sea that has stimulated our facination is the fact that so many of its animals are different from those found in shallow water. While this is a source of delight for systematists, it presents serious difficulties for other investigators, such as ecologists or functional morphologists, because there is usually little way of knowing what these animals do except at a very general level. This is particularly evident with deep-sea isopods.

Isopods are among the most abundant and diverse macrofaunal taxa in the deep sea (HESSLER & SANDERS 1967; HESSLER & al. 1979). This is almost entirely due to the asellote superfamily Janiroidea, which has undergone an extensive radiation in the deep sea that resulted in the evolution of diverse and often bizarre morphologies (HESSLER & THISTLE 1975). It is not unusual to see the majority of these morphologies in a single sample, and the question of how they live in order to allow this coexistence is often raised.

It has long been known that many families and even genera of deep-sea janiroideans emerge into relatively shallow water at high latitudes (WOLFF 1962), probably because the temperatures there are relatively cold throughout the year and do not exhibit substantial seasonal fluctuation (HESSLER 1970). For example, at 150 m in Kosterfjorden along the Swedish west coast, thermal range is only 2.1° C. Such shallow distribution provides an oppor-

tunity to obtain living individuals for study of the behavior of deep-sea taxa, yet this opportunity has barely been tapped. Short sections in SARS (1899) and HULT (1941) are the only published observations of which we are aware.

The present paper recounts observations we have made, both by accident and design, over a period of several years. The observations are qualitative; no attempt was made to quantify the proportion of time spent at different activities. Nor can we evaluate the degree to which the behavior was affected by artificial conditions, but we hope what is described here is basic enough to transcend such influences.

MATERIAL AND METHODS

Four laboratories served as bases during this study: Kristinebergs Marinbiologiska Station, Sweden (Winter, 1978; Autumn, Winter, 1987–88), Tjärnö Marinbiologiska Laboratorium, Sweden (Winter, 1978), Friday Harbor Laboratories, San Juan Islands, Washington, U.S.A. (Hessler only; Summer, 1980), and McMurdo Base, Antarctica (Hessler only; Austral summer, 1976). Specimens were collected from the following regions: Skagerrak west of Lysekil, Sweden, 153–210 m; Gullmarsfjorden, Sweden, near north end of Skaftö, 60 m; Kosterfjorden, Sweden, west of Tjärnö, 140–200 m; San Juan Islands, Washington, U.S.A.; 45–110 m; New Harbor, McMurdo Sound, Antarctica, 26 m. The substrates were soft muds at all localities except the San Juan Islands, where they where much coarser, principally shell gravel and water-logged wood chips.

The species that were collected at these localities are listed in Table 1.

Table 1. Collecting localities of specimens used in this study.

Skagerrak, 153–210 m, 58°10' N, 11° E
 Pleurogonium rubicundum (G.O. SARS, 1864)
 Paramunna bilobata G.O. SARS, 1866
 Ischnomesus bispinosus (G.O. Sars, 1868)
 Whoia angusta (G.O. SARS, 1899)
 Eugerda tenuimana (G.O. SARS, 1868)
 Eugerda filipes (HULT, 1936)
 Desmosoma lineare (G.O. SARS, 1864)
 Echinopleura aculeata (G.O. SARS, 1864)
 Eugerdella coarctata (G.O. SARS, 1899)
 Eugerdella armata (G.O. SARS, 1864)
 Prochelator lateralis (G.O. SARS, 1899)
 Macrostylis spinifera G.O. SARS, 1899
 Eurycope cornuta G.O. SARS, 1864
 Pseudarachna hirsuta G.O. SARS, 1899

Gullmarsfjorden, 60 m, 58°16.5' N, 11°29.5' E
 Pleurogonium rubicundum (G.O. SARS, 1864)
 Baeonectes muticus (G.O. SARS, 1864)

Kosterfjorden, 140–200 m, 58°52–53' N, 11°6' E
 Pleurogonium rubicundum (G.O. SARS, 1864)
 Ischnomesus bispinosus G.O. SARS, 1868)
 Whoia angusta (G.O. SARS, 1899)
 Eugerda tenuimanna (G.O. SARS, 1868)
 Eugerda filipes (HULT, 1936)
 Eugerda intermedia (HULT, 1936)
 Desmosoma lineare (G.O. SARS, 1864)
 Echinopleura aculeata (G.O. SARS, 1864)
 Eugerdella coarctata (G.O. SARS, 1899)
 Prochelator lateralis (G.O. SARS, 1899)
 Macrostylis spinifera G.O. SARS, 1899
 Eurycope cornuta G.O. SARS, 1864
 Ilyarachna longicornis (G.O. SARS, 1836)
 Pseudarachna hirsuta G.O. SARS, 1899

San Juan Islands, 45–110 m, 48° N, 123' W
 Janiralata occidentalis WALKER, 1898
 Janiralata solasteri HATCH, 1947
 Munna fernaldi GEORGE & STRÖMBERG, 1968
 Uromunna ubiquita (MENZIES, 1952)
 Munnogonium waldronense GEORGE & STRÖMBERG, 1968

McMurdo Sound, 26 m, 79° S, 165° W
 Echinozone sp

In Sweden and the San Juan Islands, animals were collected with a dredge; the Warén dredge proved to be very effective at the Swedish localities. The soft mud samples at Sweden were processed with care to avoid damaging the more delicate species. The mud was slid out of the dredge without letting it drop into the bucket. Washing the mud out of the samples was delayed until return to the laboratory, in order to avoid using the less saline surface water. We employed the elutriation technique, and animals were collected on a 0.5 mm screen. At the San Juan Islands, the animals were found trough visual inspection of the surfaces of wood chips, or large epifauna, or were shaken free of these substrates in a bucket of water, which was subsequently screened. At McMurdo, both animals were found in hand cores collected by divers.

Specimens were stored and studied on hard substrates or on mud in small dishes that would easily fit under a dissection microscope. In the latter case, initial studies were made on reconstituted bottoms, that is, bottoms formed by allowing sediment to settle out of suspension.

This was done in order to obtain a homogeneous substrate that was free of other macrofauna. However, this technique was soon abandoned because the resulting substrate was unrealistically loose. Instead, the natural mud from the same samples was used. Whenever other macrofauna were seen and judged to interfere with our animal subjects, they were removed. Unless indicated otherwise below, a natural mud bottom was used.

To minimize thermal stress, our work in Sweden was done during the cold months, when the surface water and air were similar to that of the environment we were sampling. Obviously, this was not a problem in Antarctica. The genera that were sampled at the San Juan Islands are shallow-water ones (HESSLER & THISTLE 1975) and required no such precautions. Except for the San Juan material, the observation aquaria were stored in a refrigerator at 5–7° C. Their water was changed once a week. Observations with a stereomicroscope were either made in an unheated room or were brief in order to minimize warming up. A fiber optic light source also minimized heating.

From time to time, the animals were offered food: finely chopped, frozen spinach, live baker's yeast or small pieces of freshly-broken, living mussel (*Mytilus edulis*). The yeast is a finely divided substance which immediately settled into a thick puddle upon the sediment.

To study the movement of animals when they were underground, we constructed aquaria of drawn-out capillary tubing to simulate the confined space of a burrow. These were unsatisfactory except for some observations of *Pseudarachna*.

No attempt was made to visually document the postures of living animals. At Friday Harbor, clove oil was used successfully to immobilize *Janiralata* and *Munna* in natural stances prior to fixation. These specimens are illustrated in Figs 1 and 2. All the other illustrations are from the literature. They are provided to refresh the reader about the animal's appearance and some of the nomenclature used in text. Only one representative of each family is illustrated.

OBSERVATIONS

Janiridae G.O. SARS, 1899

(Fig. 1)

Janiralata MENZIES, 1951

Janiralata occidentalis (WALKER, 1898), was found at the San Juan Islands on a variety of hard objects, but particularly waterlogged bark and wood. HATCH (1947) found *Janiralata solasteri* abundant on the asteroid *Solaster stimpsoni*, but in aquaria, it was kept on bark, as with the other species, and it did not behave noticably differently. The descriptions given here are of *J. occidentalis*. A detailed analysis of the mechanics of locomotion was given in HESSLER (1982).

When at rest, the animal stands with pereopods II–VII radiating like spokes on a wheel. Pereopod I is usually under the body and may not be touching the bottom. Nor do pereopods VI–VII neces-

Fig. 1. Janiridae: *Janira-lata occidentalis* (WAL-KER, 1898). Oblique view, from rear. Abbreviations: A I, first antenna; A II, second antenna; Per II, second pereopod; Per VII, seventh pereopod; Ur, uropod.
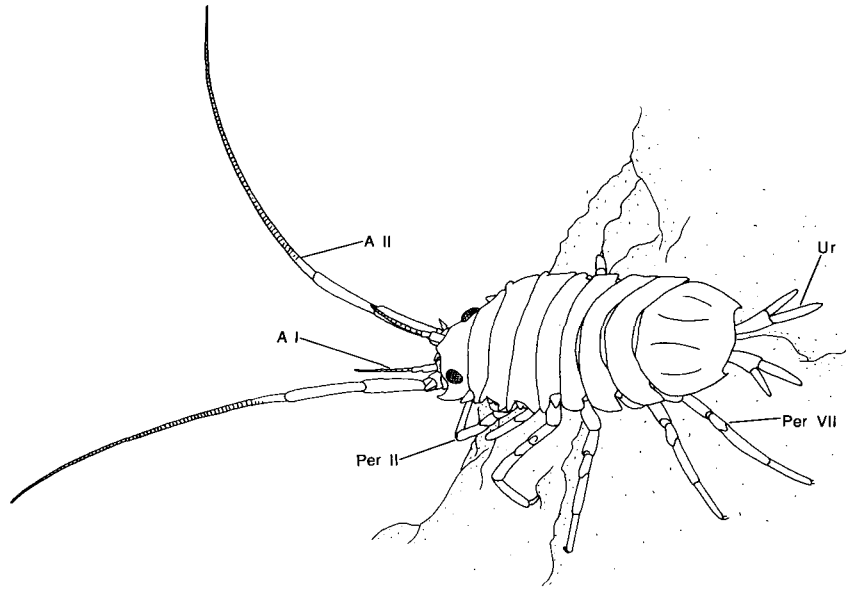
sarily give active support. The basis of the pereopods angles inward, but the pereopods are acutely flexed at the articulation of basis and ischium, so that the rest of the limb extends outward, arcing up and then down to the substrate. Thus, the body is suspended between the arching limbs. If threatened, the animal may crouch closer to the bottom than in its relaxed stance. The antennae I are held up into the water and move little. The antennae II extend outward and are actively moved about, most frequently with their tips just above the bottom.

Janiralata walks rapidly, both forward and backward, and even to the side for short distances. Even pereopods I are sometimes used. The trailing limbs do not seem to engage in active forward propulsion, although often they passively keep in step. This was verified by seeing one accidentally hook into the bottom with its dactylus, which was then briefly dragged along. These observations suggest that the principal motive force is flextion of the leading limbs. Corroboration came from an individual that had molted improperly, so that its anterior pereopods could not be used in walking. It was not able to walk forward, but could move backward quite rapidly.

Not surprisingly, these animals are strongly thigmotactic. Even when the substrate upon which they are standing is lifted from the water, they will cling to it rather than fall off. A probe was used to test their sensitivity to disturbance. When the body was touched, the animal would run away. Only some

of the time did touching the antennae II yield the same response, although the antennae would usually be pulled back. Touching the uropods caused them to flick, but did not stimulate escape. Generally, *Janiralata* preferred to flee forward, but would also move backward or even sideways. Moving the probe in front of the eyes without touching the animal elicited no response.

Janiralata would feed by bending down to the substrate and biting off a chunk of detritus. More than once, an individual was seen digging through the loose detritus with pereopods I, much as a dog digs with its front legs, presumably searching for food. Defecation was seen twice. Pereopods VII helped to pull the feces clear of the anus, after which, these limbs were cleaned by rubbing the distal podomeres together.

The tergum of the body can become lightly fouled, but except for the uropods, the limbs are kept clean. The flagellum of antenna II is groomed particularly often. The animal catches the antenna in the crook of pereopod I and passes it to the mandibular palp, which has bent laterally to receive it. The antenna is engaged by the groove of the distal palp segment, whose setae face into the groove to form a brush. The antenna then pulls through, leaving its foulings behind. These are passed to the mouthfields, where they are treated like food.

Pereopods can be cleaned in two ways. Often they are simply rubbed together to dislodge particles. They may also be extended into the mouthfields; as they are pulled back out, the setae on the
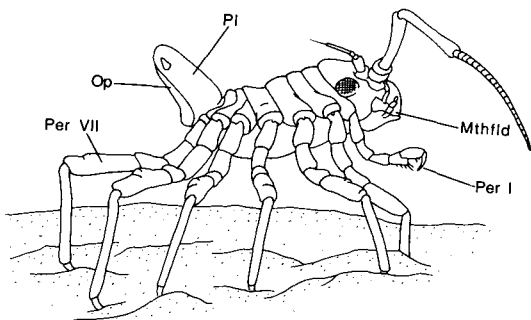
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Fig. 2. Munnidae: *Munna fernaldi* GEORGE & STRÖMBERG, 1968. Lateral view. Abbreviations: Mthfld, mouthfield; Op, operculum; Per I, first pereopod; Per VII, seventh pereopod; Pl, pleon.

vigorously active mouthparts brush them off. Posterior pereopods must be stretched to the extreme under the body, but at the same time, the animal may flex the anterior half of the trunk downward so that the head is facing down toward the limb. Attempts to clean the tergum were not seen.

Respiration is sporadic. The operculum (pleopods I and II in the male, and the fused pleopods II in the female) to the branchial chamber opens, and the branchial pleopods (III–V) beat. The resulting water current enters the branchial chamber laterally and leaves posteriorly. When the branchiae stop beating, the operculum closes.

The marsupium of brooding females extends for most of the length of the thorax, beginning at its anterior end. This chamber is rhythmically expanded and contracted with a motion that is reminiscent of vertebrate breathing. It can even be detected in dorsal view because the bases of pereopods I–IV oscillate mediolaterally. This movement, which serves to ventilate the eggs, is probably generated by slight ab- and adduction of the pereopodal coxae, to which the oostegites (brood plates) are rigidly attached. Prebrooding females do not make this motion. One female which had shed its eggs, but still retained the marsupium, continued the ventilatory motion, but when she molted again to a preparatory condition, in which the oostegites are again simple anlagen, the motion was discontinued. One brooding female was observed to 'punch' back against the anterior end of the marsupium with the basis of the first pereopod. This movement was violent enough to realign the eggs.

Munnidae G.O. SARS, 1899

(Fig. 2)

Two species, *Munna fernaldi* GEORGE & STRÖMBERG, 1968, and *Uromunna ubiquita* (MENZIES, 1952),

were obtained in the State of Washington from subtidal dredgings south of Pear Point, San Juan Island (55–80 m), and southeast of Iceberg Point, Lopez Island (75 m). The bottom was a shell gravel with waterlogged wood and a fauna that included echinoids, pectinids and large sessile barnacles. The distinction between the two taxa was not appreciated at the time of observation. Therefore they will be treated together.

The animal stands on pereopods II–VII, although II and III are frequently lifted off the bottom. The posture is different from that of the other asellotes we observed. Here, there is less flexure between the basis and ischium; the major flexure is between ischium and merus. The basis and ischium form a column below the animal, those of the different pereopods being rather close together. From there, the merus and carpus extend flatly outward, and the propodus and dactylus arc down to the substrate. Thus, the animal's body is high off the bottom, being more above the legs than suspended between them.

It was difficult to capture munnids from the aquaria. To avoid damaging an animal, attempts were made to blow it free from the bottom using a jet of water from a pipette. The technique did not work well because the animal would hunch down against the substrate with its pereopodal dactyls hooked into the bottom until the jet of water ceased. Then it scurried away.

Munnids walk using pereopods II–VII with a greater springiness than was seen with other asellotes. They can move well on flat surfaces and complex arborescences alike. As an example of their agility on complex terrains, when one individual reached the edge of a crack, instead of descending into it and climbing up the other side, as *Janiralata* would have done, it reached over with pereopods II and III until it contacted the other side, and then stepped across, one limb at a time. Another individual that had scrambled to the tip of a thin filament, balanced on no more than three of its pereopods while it reached around to find another substrate.

The dorsal surface of the body is rather fouled except for the eyes and perhaps the forehead. One specimen put detritus on its back, using pereopods II–IV. It was able to reach up so far that it could pat the detritus down. All three limbs could be used simultaneously.

The tip of antenna I and all of antenna II are clean. Antenna II is groomed frequently. The antenna flexes so that the flagellum is in the mouthfield. Then the antenna pulls through the field. Pereopods I and II may help hold it. Occasionally,

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one individual would lift pereopod II and brush its propodus past antenna I or the flagellum of antenna II. A male holding a female in amplexis (wherein a male holds onto a female for an extended period prior to copulation) lowered its antenna II flagellum so that it could be held between the propodi of pereopods I while the pereopods were held ventrally. The flagellum was then pulled through. Pereopods are cleaned in two ways. Often they are briefly brushed together, even brushing a limb against one on the opposite side of the body. The animal might also bend its head down a little, so that a posterior pereopod could be extended forward into the mouthfield to be cleaned as in *Janiralata*. The male in amplexis brushed its pleon with pereopod VII.

The animal respires sporadically. As with *Janiralata,* the operculum is opened widely and the branchial pleopods beat vigorously. Then the operculum closes again. One individual was seen respiring in an unusual way. It rhythmically flexed its pleon up and down, respiring on the upstroke. At the same time its antennae II, which were flexed in a transverse plane, and antennae I were moved forward and backward. At other times, this individual simply held the pleon vertically and respired in the usual way.

Brooding females intermittently ventilate the marsupium by moving at least pereopods II–IV in the fashion described for *Janiralata.*

Feeding is accomplished in several ways. The animal may apply the mouthfield to the bottom and bite off some detritus. Or the subchelate pereopod I may nip off a piece of detritus and lift it to the mouthfield. On one occasion, an animal held an arborescent mass with one or both pereopods I while it bit into it. At times, pereopods II were also used. When walking, the animal might repeatedly poke the tip of pereopod II into the substrate as though testing it.

Amplexis was observed twice. In both cases, the female was much smaller than the male; one proved to be a manca. He clasped her between the distal portions of pereopods II and held her under the thorax. At times she would walk when the male walked, or feed. When disturbed, the male would quickly bring the female up against his ventral surface so that her pereopods were clear of the bottom. When the male is feeding, he positions the female more posteriorly. He can even move the female to the side so that he can bring a pereopod forward for cleaning.

Twice, we observed munnids meeting another species – a caprellid and a *Janiralata*. In neither case did the munnid pay any attention, although in
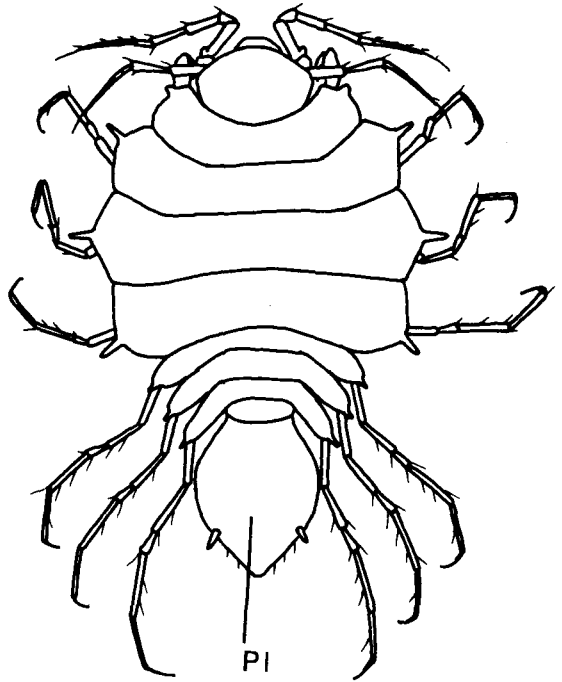

Fig. 3. Paramunnidae: *Pleurogonium rubicundum* (G.O. SARS, 1864). Dorsal view, after G.O. SARS (1899). Abbreviation: Pl, pleon.

the former encounter, the caprellid reared back and lunged forward to strike it. One individual, as it walked along, became wary of something in front of it. Having stopped, it streched forward as if to investigate it, with its posterior pereopods completely extended, and its body close to the bottom. Then it suddenly pulled back and ran away.

Because munnids were only observed on hard surfaces, it is not known whether they would dig or burrow.

Paramunnidae VANHÖFFEN, 1914

(Fig. 3)

Pleurogonium rubicundum (G.O. SARS, 1864)

This species is sturdily built and therefore easy to obtain in good condition. It lives on or in the surface of the sediment. The animal is frequently active, and walks rapidly. If the sediment is soft, it may also plow within the uppermost layers, making a furrow as it goes, but this is not common. When stationary, it may stand on the surface or be buried in a shallow pit of its own making. Here, it can either be fully covered with loose sediment or dorsally exposed. It digs these pits by alternately extending its limbs away from the body and flexing them inward. In this way, it pushes sediment out from under the body into piles along its margin, and the

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animal settles down horizontally until the animal is just below the surface. Some surrounding sediment may then collapse over it, or it may actively shovel sediment on top of itself with its pereopods. When buried, its position is marked by the disturbance of the sediment or by the tip of the pleon, which pokes up through the bottom when respiring. Sometimes, when it is standing on the surface, its body is strongly arched, concave upward, and the pereopods are partially flexed up over the back; the function of this is not obvious.

Typically, the animal is covered with a loose layer of sediment, even when living on the surface. We have seen individuals piling this sediment on their backs with their pereopods. Yet they may be free of sediment as well. Grooming is not common. Once an individual was observed to extend and flex its pereopods so that they rubbed against each other, perhaps in order to clean them.

Respiration is sporadic. Animals do not seem to respire when moving about. Typically, they stop other activity, point the pleon upward, open the operculum and oscillate the branchial pleopods. A few moments later, branchial activity stops, and the pleon assumes its normal configuration.

Pleurogonium ate the spinach, fresh mussel and yeast. For spinach and mussel, the behavior was the same. Animals seemed to sense the food from a distance; they found it more quikly than they would have by accident. The food was grasped by pereopods I and II, which pulled it toward the mouthfield, allowing the mouthparts to work it. Sometimes an animal would push the food away so that some of it was torn off by the grasping mouthparts. At the same time, it would dig into the bottom with its remaining pereopods. Gradually, the animal and at least the part of the food it was holding disappeared from view. One could tell that the animal continued to work on the food by the fact that the visible portion continued to quiver. With yeast, the animal either shoved its head into the puddle or pushed the yeast against the mouthparts with pereopods I. With this food, it did not burrow.

This is the only asellote we observed that displayed frequent inter- and intraspecies behavior. Once, while observing a gravid *Paramunna bilobata*, a *Pleurogonium* that was only slightly larger approached it and immediately attacked it. It grasped the *Paramunna* with its anterior pereopods and tipped the *Paramunna* over, exposing its underside. The *Pleurogonium* nipped at the pereopods and oostegites, displacing one of them. Then the *Pleurogonium* backed off. The *Paramunna*, which had defended itself only feebly, did not seem to be seriously injured. On another occasion, a *Pleurogonium*

pounced on an *Ischnomesus bispinosus* and bit it at least once. At that point, the *Ischnomesus* rapidly backed off to safety and burrowed into the mud. Yet another time, a stationary *Pleurogonium* was approached by another. As soon as they touched, the former individual jumped on the back of the intruder, its head facing the posterior end of the other, and quietly held on while the other bucked and squirmed. Then after a bit, it got off and walked away. However, in another intraspecific encounter, the two individuals paid no attention to each other. Agonistic behavior with other species is not inevitable. A tube-dwelling amphipod was feeding on a piece of mussel, up off the bottom at the entrance to its tube. A *Pleurogonium* climbed the tube and immediately joined the amphipod in feeding, with no abrasive interaction.

Munnogonium waldronense GEORGE & STRÖMBERG, 1968

Little time was spent on this species. The animal walks awkwardly, with each leg being lifted high off the bottom as it steps forward. Pereopod I is not used.

The body is always covered with fine, flocculent detritus. At times, only the tip of the pleon, appendages and mouthfield are free of it. The animal actively maintains this cover. Once, an individual fell off its wood chip and lost much of its detritus during the time it lay on the clean bottom of the beaker. As soon as it was placed back on the chip, it bent down and bit off a piece of aufwuchs. It manipulated this material with the mouthparts and pereopods I, then lifted it up to its forehead. There, antennae II, acting as forceps, moved the material onto the top of the head and anterior pereonites. The animal does clean the face, however, by frequently wiping it with pereopods I.

One brooding female was seen as young were leaving her marsupium. She was holding onto a branch using pereopods VI and VII. The body, which was covered with detritus as usual, was strongly arched so that the anterior end pointed almost vertically upward. While in this position, she expanded the marsupium deeply, and many active young could be seen inside. None hatched during observation, but two newborn were already out. One was standing on the same branch. The other minute individual was standing on the detritus that was on the female's head. When first seen, this manca was completely clean, but a minute or so later, it too was covered with detritus. Then the female walked away, with the manca still on her head, but leaving one young behind.

In this species, the pleon is held vertically up-

ward. As with other asellotes, it respires sporadically by briefly opening the operculum and rapidly beating the branchial pleopods.

Two individuals were seen to come into contact with a harpacticoid copepod and the tentacular crown of a tube-dwelling polychaete, respectively, but took no notice of them. When disturbed with a probe, the animal would crouch down, but then run away if disturbed further.

Ischnomesidae HANSEN, 1916

(Fig. 4)

Ischnomesus bispinosus (G.O. SARS, 1868)

Not surprisingly, *Ischnomesus bispinosus* is an excellent walker, on jumbled surfaces as well as smooth mud. The pereopods are oriented primarily anteroposteriorly, with II–IV angling forward and V–VII directed backward. The massive pereopod I is not used; it serves more for feeding and burrowing. While the pace of walking does not seem particularly fast, the animal moves rapidly and smoothly because of its long legs.

This species also burrows. On unprocessed sediment, some animals remain on the surface; others make permanent burrows which did not seem to extend too deeply below the sediment surface. In the initial stage of burrowing, leg movements seem little different from that of walking; animals can disappear completely from view in this way. Although sometimes an open burrow remains behind, we saw no activity especially designed to make it so; the sediment is simply pushed aside. In one case, after a night's activity, the entrance to the burrow was a shallow depression with a hole in the side extending downward. With time, the entrance depression became deeper. Once, an animal appeared at the entrance of its burrow with mud piled up in the fork formed by the bases of the antennae, then knocked the sediment free with pereopods I. On one occasion, it subsequently patted the sediment down. With the Skagerrak specimens, many individuals never fully buried themselves, but remained on the surface in the half-buried configuration for all the weeks of the study; these may not have been healthy.

On reconstituted mud, the animal angles its body downward and walks forward, immersing its anterior end in the mud as it does so. It either continues to walk, plowing a furrow, or stops and remains motionless in a partially burried position. When left long enough, it might bury itself completely. During one observation, the animal scooped up mud with pereopods I and placed it on its head. Attempts to burrow on reconstituted mud may have
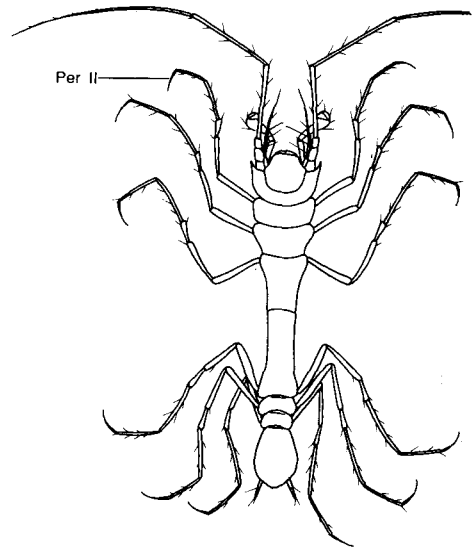

Fig. 4. Ischnomesidae: *Ischnomesus bispinosus* (G.O. SARS, 1868). Dorsal view, modified from G.O. SARS (1899). Abbreviation: Per II, second pereopod.

been less effective because of the looseness of the sediment.

The burrow's diameter is larger than the animal's body, but not so large as the span of fully extended limbs. An animal might appear at the entrance anterior or posterior end first, sometimes exiting either way. This species is capable of substantial ventral flexure, particularly at the junction of pereonites 4 and 5, such that the mouthparts can reach the ventral surface of the pleon. It is therefore possible that they reverse themselves in the tube by rolling over, as stomatopods do. However, breaking open one burrow revealed a chamber that was large enough to allow turning around without extreme flexure. On one occasion, an individual started a burrow, but only penetrated part of a body length before stopping. It backed out of the opening and stood at the entrance, now facing away from it. When surprised, it quickly backed into it; this happened more than once. Finally it turned around and entered the hole head first, whereupon it continued to dig until it disappeared, and the hole collapsed behind it. On another occasion, an individual entered the burrow of another; it did not reappeared during the period of observation.

We never saw *I. bispinosus* feed in a serious way, although they showed some interest in mussel meat. On a single occasion, one individual took the meat with pereopods I and pressed it against its
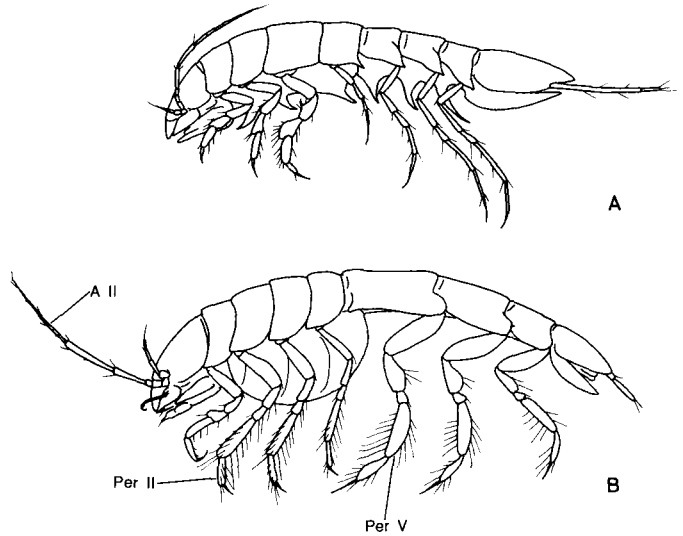
Fig 5. A. Macrostylidae: *Macrostylis spinifera* G.O. SARS, 1899. Lateral view, after G.O. SARS (1899). B. Desmosomatidae: *Desmosoma lineare* G.O. SARS, 1864. Lateral view of female with marsupium, after G.O. SARS (1899). Abbreviations: A II, second antenna; Per II, second pereopod; Per V, fifth pereopod.

mouthfields. Then it let it go. Another individual came up, and both grasped the meat, but they dropped it shortly thereafter. We do not think they fed.

Desmosomatidae G.O. SARS, 1899

(Fig. 5B)

Desmosomatids are diversely represented in Scandinavian waters (HULT 1941; HESSLER 1970); the majority of known species live together at the localities we sampled (Table 1). Unfortunately, it was difficult to identify individuals while they were alive, and therefore we cannot associate all observations with species. Still, at the level being considered here, all individuals behaved in sufficiently similar ways that this inadequacy does not seem serious. Observed exceptions will be noted.

All species prefer to burrow rather than remain on the surface. They burrow anteriorly, using the first four pereopods, particularly pereopods II and III. These limbs make a breaststroke-like motion, first extending forward, then rotating to the side as they are drawn back. Pereopods V–VII participate little in burrowing. The burrow cavity did not necessarily remain open during the initial excavation, but after some days, there were a number of small, round, permanent openings to the surface. While not all of these could definitely be attributed to desmosomatids, we did see desmosomatids entering or leaving some of them, and on one occasion, we saw one in a tunnel we had exposed. An individual of *Eugerda filipes* (HULT, 1936) that was standing on the surface turned around using an enrol-

ling technique that is typical of tube-dwelling animals. It flexed ventrally so that the anterior part of the body was under the posterior, then followed through with the posterior part of the body, so that it was straightened out again, but upside down and facing in the opposite direction. Then it righted itself. All of this was a single, fluid motion.

All species except *Echinopleura aculeata* (G.O. SARS, 1864) were seen to swim, mostly as an escape reaction. The animal swims backward, using pereopods V–VII. The direction of movement did not seem deliberate. Typically, the animal swam up into the water with a flurry of backstrokes, then stopped and settled to the bottom. Swimming progression was smooth because limb movement was not synchronous. Pereopods V and VII of either side were in phase with each other, but about 180° out of phase with pereopod VI; left and right limbs of their pair were 180° out of phase. During swimming, anterior pereopods were tucked under the body in flexed position.

Walking is normal, although in at least one case, pereopods II and III rotated more toward the side on the power stroke than is typical; this rotation was reminiscent of the burrowing movement. In walking backward to retreat from our probe, the posterior pereopods moved much as they would in swimming.

A *Prochelator lateralis* (G.O. SARS, 1899) that was surprised on the surface curled ventrally into a tight, motionless coil, with the antennae pressed back over the head. *Eugerda* sp. did the same when lying in a sedimentless collecting dish.

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In grooming itself, an adult male *Whoia angusta* (G.O. SARS, 1899) hooked antenna I or II with the propodus of an anterior pereopod and combed it clean. The distal parts of the anterior pereopods are cleaned by rubbing them together while they are all next to each other in an anteroposterior orientation. Posterior pereopods are extended forward to be cleaned by the mouthparts.

No information on feeding was obtained.

Macrostylidae HANSEN, 1916
(Fig. 5A)

Macrostylis spinifera G.O. SARS, 1899

The species behaves much like the Desmosomatidae, but it does not swim. Accordingly, its pereopods V–VII are not modified in any way for swimming. When placed on mud, *Macrostylis* might walk a bit in a normal fashion, but soon will burrow steeply downward into the sediment. The animal burrows anteriorly, using pereopods II–IV in the way described for desmosomatids. The macrostylid tendency for pereopods I–III to be bent laterally at the merocarpal articulation enhances their effectiveness. We are not sure whether pereopod I is employed in burrowing. Pereopods V–VII are not used actively during initial burrowing.

Once having burrowed, individuals were never seen on the surface again. However, they may have come to the surface to feed. We washed one aquarium's sediment through a screen after it had not been disturbed for more than two weeks. One adult *Macrostylis* and some mancas had chlorophyll in their foreguts. This could only have come from spinach that had been lying on the surface.

In the one case where attention was paid to respiration, it was continuous during initial burrowing.

Eurycopidae HANSEN, 1916
(Fig. 6)

Eurycope cornuta G.O. SARS, 1864

Eurycope cornuta was the least satisfactory species for observation because captured individuals were invariably damaged. Nevertheless, a couple of individuals were sufficiently healthy to reveal some basic activities. Both walking and swimming were observed. Pereopods II–IV are used for standing. The arc of deployment is almost as wide as that of all seven pereopods on an unspecialized janirid. Pereopods V–VII are flexed up under the body. When walking, pereopods II–IV dominate, although pereopod I may also participate. The ampli-
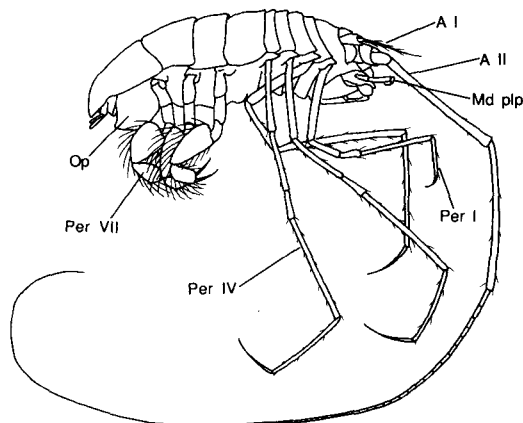

Fig. 6. Eurycopidae: *Eurycope cornuta* G.O. SARS, 1864. Lateral view, Modified from WILSON & HESSLER (1981). Abbreviations: A I, first antenna; A II, second antenna; Md plp, mandibular palp; Op, operculum; Per I, first pereopod; Per IV, fourth pereopod; Per VII, seventh pereopod.

tude of motion of each limb is much larger than on other asellotes. One manca larva employed pereopods V and VI when walking backward. This species swims backward, using pereopods V–VII. The progression is jerky. Burrowing was not seen. A brooding female sporadically dilated and contracted the marsupium, presumably to ventilate it.

Baeonectes muticus (G.O. SARS, 1864)

Many of the animals were undamaged, but some had lost an antenna II or an anterior pereopod on one or both sides.

While the animals were still in the initial collecting dish (without mud), they were able to stand only with difficulty on the smooth, hard bottom. When disturbed, for instance when attempts were made to capture them in order to transfer them to the mud aquaria, many attempted escape by swimming away. They would dart backward into the water with a jerky progression, but on a constant course. The motion was too fast to analyze in detail, but it was obvious that it is caused by the beating of pereopods V–VII, which are shaped like paddles and have numerous marginal swimming setae. They appear to beat in synchrony, which fits well with the jerky progression. At the same time, antennae II and more anterior pereopods extend anteriorly and therefore trail behind the animal as it moves. When an animal stops swimming, it settles slowly to the bottom, with antennae II and pereopods II–IV spread out anteriorly or to the sides in a posture similar to that when standing. In this

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way, they settle in a horizontal, upright posture. When residing in the mud aquaria, *B. muticus* is extremely reluctant to swim. Only considerable provocation elicits this form of escape, and one brooding female would never do it. Adult animals touched with a probe from in front might dart a short distance backward, most frequently just above the bottom. We only saw spontaneous swimming on the part of manca larvae, and when these did swim, they often rose higher into the water than adults did.

The swimming limbs, pereopods V–VII, are ordinarily tucked under the posterior half of the thorax and not easily visible. They do not move routinely except in swimming; they do not participate in walking. Occasionally, some of these limbs are extended posteriorly or rubbed against the ventrolateral surface of the body; perhaps this is grooming.

Pereopods II–IV are employed to stand on the bottom. The first extends anterolaterally, the middle pair laterally, and the last pair posterolaterally, much as with an insect. The posture is a little like that of members of the Munnidae, where the basis is directed strongly ventrally, rather than having a strong mediad slope. Distal to the basis, the leg bends laterally; the long carpus has a horizontal orientation, and the two more distal podomeres slope increasingly downward. Where the substrate was firm, the body was held well off the bottom, but where it was loose, the animal might sink in up to the supporting surface formed by the carpi.

Adults walking on firm surfaces are rapid and agile. The animal would spontaneously walk forward or sideways. When disturbed from the front, it could retreat backward. However, in general, animals tend not to move around much. There was no obvious choice of substrate; one was as likely to see them on soft as hard portions of the bottom, and sometimes they would stand on the vertical surface of a worm tube. Mancas seemed less adept at walking, in that their motion was more jerky.

In the first day after capture, many of the animals were found with their bodies pressed against the substrate, or even in small, self-made depressions, so that their bodies were even with the surrounding surface. They dig their way down using all the anterior pereopods, which clutch at the bottom in their normal standing orientations and thus loosen the particles and at the same time pull the body downward. After the animals became well-established in the aquaria, this posture was uncommon. This behavior was also evident when we attempted to pick an animal up with forceps or a pipette. It would clutch at the bottom to prevent its being displaced. This was the normal first response. Only after that did not work would they walk away, or even swim. Thus, this posture might have been defensive.

It was typical for animals to be stationary, but with antennae II in motion. These are extended in a smooth downward arc and are continuously swept forward and backward through a range that extends from directly in front of the head to directly behind the body. On the foresweep, when the antenna is brushing the bottom, movement is slower than on the backsweep. Many times the antenna is held well up in the water during all of its oscillation. When we touched the antenna, the animal pulled it away immediately. Persistent contact made the animal move away. Apparently antenna II is the principal structure used in sensing larger features of the animal's environment and potential sources of harm.

The short antenna I is always held erect and has not been seen to move.

The flagellum of antenna II is often partially covered with detritus. Frequently, the animal flexes the antenna at its base to bring the shaft close to the head, whereupon pereopod I lifts up and hooks over it in order to bring it close to the mouthfield. Here, the antenna is engaged by the mandibular palp, and the animal pulls the antenna through in a posterior direction. Sometimes the antenna is hooked by the palp without the aid of pereopod I. The detritus is transferred to the tips of the masticatory appendages (mandible, maxillae I and II, maxilliped), which then actively work on the material.

Sometimes a pereopod is extended forward under the body and into the mouthfield for grooming. The mandibles are held apart so that the shaft of the pereopod passes directly between the incisor processes. Then the pereopod is drawn out of the field, and the detritus on the limb is left on the mouthparts, which work actively upon it for a few moments. These grooming motions may be repeated several times during a few minutes' period, even though the animal had not moved otherwise and no additional detritus had accumulated on the limb. We were not sure whether subsequent movements of the mouthparts signified processing the detritus for nourishment.

Pereopods I do not appear to be used routinely in locomotion. They are frequently used as sensory probes. The animal might be stationary or moving slowly forward. While doing so, the tips of the dactyls constantly touch the bottom, sometimes penetrating it very slightly, then lift up and move to another spot to probe again. It is very likely that

this is a chemosensory activity and is related to the search for food.

After the animals had been in the aquaria for a week, we attempted to feed them. While some animals showed no interest, several fed.

The spinach was placed within reach of antennae II of one adult. As soon as an antenna touched, it pulled back. Then it touched again and proceeded to palpate the food at different points. The animal then approached it and touched it with the tips of pereopods I. Finally, it placed its mouthfields against the spinach, picked a small chunk out of the mass and worked it with its mouthparts. It did not take a second bite.

Several animals responded positively to mussel meat. The behavior was much the same, but was distinctly less hesitant. When feeding, the animal gripped and manipulated the meat with pereopods I and II. At times, it seemed to be pushing the mass of meat away as it bit into it, as though trying to tear a piece off. Once it had a manageable piece, its mouthparts worked for several moments. Sometimes an individual interrupted feeding in order to groom an appendage. Several animals seemed jittery while feeding on mussel meat. On three occasions, the animal darted suddenly backward for several body lengths when the dish was jarred so slightly that normally it would not have elicited a reaction. In two of these cases, the animal carried the meat with it; one piece was much larger than the animal.

When yeast was put into the aquarium, once again, the animal touched it with antenna II, which was immediately pulled back. Then it approached it and touched with the tip of pereopod I in several places. It finally bent down so that its mouthfields was slightly immersed in the yeast and worked with its mouthparts. As it did so, pereopods IV, which were angled posterolaterally, hooked into the bottom to aid in balance. The animal then straightened up and continued to work on what it had in its mouthfield. On these occasions, we noticed that pereopod II is also used to sense the food, much like pereopod I. Yeast that was placed in front of an individual which lacked antenna II caused no reaction until the tip of pereopod II touched it; then it immediately began to feed.

Natural feeding was observed at least once. An animal that had been probing the bottom with pereopods I bent down and took a bit of sediment off the bottom with its mouthparts. It then straightened up and masticated it. The meaning of some other observations is more equivocal. Once, an animal dropped a fecal pellet from its mouthfield

as we brought it into view. Sometimes, animals would be inclined anteriorly downward, with the head pressed into the substrate. When getting into this position, pereopods I would be employed in digging; on one occasion, the animal may have used one of the swimming pereopods briefly. More often than not, the animal was motionless in this posture, but occasionally the mouthparts moved. Rarely was more than the head buried in the sediment. It is possible the animals were feeding on these occasions.

Respiration is sporadic. For periods, the branchial pleopods do not move (one can see through the body wall). Then the operculum opens, and the branchial pleopods begin to beat. When they stop, the operculum closes again.

Brooding females were common. On one, the thorax was observed to rhythmically move as though expanding and contracting, as described for *Janiralata*. On expanding, the head was lifted up somewhat, and the bases of pereopods II–IV moved laterally. This was clearly an act of ventilating the eggs. One of the females came to full term in the mud aquarium. Three mancas were seen. These moved about far more actively than adults did, and as already mentioned, were the only animals we saw swim spontaneously. Six days later, the mancas were distinctly larger, indicating they had surely moulted. The common exuviae of larger animals attested to active moulting for the population in general.

The body of this species is more flexible than would appear from preserved specimens. It can flex somewhat dorsally and ventrally, and can even bend slightly laterally.

Interactions with other individuals were rare. Occasionally, two individuals might be near each other. If their antennae touched, they pulled them apart, but did not move away from each other. Once a small ciliated creature swam under a motionless individual whose body was nearly contacting the bottom. A moment after the animal disappeared under it, one of the swimming pereopods flicked to the side, and the small animal was suddenly thrown clear of the *B. muticus*.
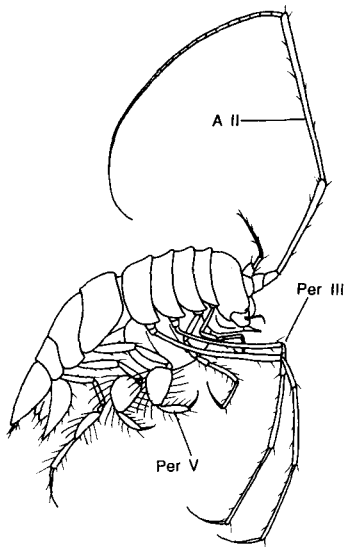
Fig. 7. Ilyarachnidae: *Ilyarachna longicornis* G.O. SARS, 1863. Lateral view of female with marsupium, modified from G.O. SARS (1899). Abbreviations: A II, second antenna; Per III, third pereopod; Per V, fifth pereopod.

Ilyarachnidae HANSEN, 1916

(Fig. 7)

Echinozone G.O. SARS, 1899

Because they were hand-collected in cores, the two specimens of *Echinozone* sp. from McMurdo Sound were in exceptionally good condition. Both were first seen to be buried in shallow pits that were open so that the dorsal portion of the body was visible. The head and anterior portion of the thorax were in a nearly horizontal position a short distance below the surface, but the remainder of the body was bent downward and burried below. Pereopods III and IV, which are distinctly longer than the rest, extended up out of the hole, and the distal halves were flexed outward so that they were resting on the surface in a radial pattern. The long antennae II also extended out and arced down to the sediment surface toward their tips. The pereopods were motionless, but the antennae occasionally waved back and forth as though sensing the surroundings.

When prodded from in front, the animals became more deeply entrenched, but when disturbed from behind, they came out of the burrows and walked a short distance before reburying themselves. Pereopods III and IV are the primary walking limbs. Pereopods II may have been used a little, but per-

haps were only probing the bottom, as with pereopods I of *Baeonectes*. As might be expected where only two pairs of limbs are used, walking seems jerky. The body is held well up off the bottom. When at rest, pereopods III and IV angle anterolaterally and posterolaterally, respectively. The proximal half slopes upward and the distal half downward, so that the body is suspended within them, with the anterior half of the body being horizontal and the posterior half bent somewhat downward. Pereopods V–VII are tucked up under the posterior half of the thorax.

The animal burrows backward, with the tip of the abdomen entering the bottom first. Pereopods V–VII play the most important role. These are extended posteriorly into the bottom, with their tips arcing laterally at the same time. They then swing the limbs forward, thus pulling the animal down.

These animals could swim, but were reluctant to do so and required persistent prodding. They swim backward, using pereopods V–VII. The progression is jerky because the limbs beat synchronously; during the recovery stroke, the animal settles a little through the water. The anterior pereopods and antennae II are extended anteriorly and thus trail behind the moving animal, as in *Baeonectes*. When it stops swimming, pereopods III and IV are spread out, and the animal falls to the bottom like a parachute.

Ilyarachna longicornis G.O. SARS, 1863

Only one of the collected specimens was undamaged. It walked as with *Echinozone*, except that pereopods V–VII participated weakly. The animal burrowed as soon as it could, in the same fashion as *Echinozone;* its resting orientation, with the distal portions of antennae II and pereopods III and IV radiating outward from the opening, was also the same.

Pseudarachna hirsuta G.O. SARS, 1899

In contrast to all the other species examined, *P. hirsuta* would neither walk nor swim. When placed on a surface, it may initially curl up with the antennae pressed back over the head, but after a few moments, it begins to burrow. Often it burrows immediately and so rapidly that once it disappears below the surface, it is difficult to retrieve. When it begins to burrow, the body is strongly flexed, with anterior and posterior halves at right angles to each other and the anterior half in a horizontal position. As with *Ilyarachna*, this species burrows backward using pereopods V–VII in a nearly synchronous motion resembling the swimming stroke

of *Ilyarachna* or *Baeonectes*. Once the body is below the surface, the animal may stop for a bit, with antennae II still protruding, before it disappears entirely.

Pereopods III and IV are much shorter than on *Ilyarachna*. Pereopod III is held out to the side, but IV extends up over the back. As seen during initial burrowing and in the capillary tube aquaria, these limbs are used to gain purchase to the side and above. Pereopods II are large and robust. They are used to thrust the animal backward. We never saw *P. hirsuta* go forward, but pereopod II appears to be excellently designed for this as well. When completely buried (as seen in the capillary aquarium), the body is still flexed, but not as much as during initial burial. Antennae II are held up over the head more than in *Ilyarachna*.

Once we saw one of the posterior pereopods (V–VII) cleaned as it was extended forward into the mouthfields and pulled it back through.

DISCUSSION

The only other observations on living individuals of deep-sea janiroidean taxa are found in G.O. SARS (1899) and HULT (1941) (partially summarized in THISTLE & WILSON 1987). They too did their work in Scandinavian waters, with many of the species observed by us. Only two genera observed by them, *Munnidopsis* and *Aspidarachna*, are not covered here. HULT goes into greater detail on some points. He examined burrowing ability of desmosomatids on substrates of different grain size. Most interestingly, *Eugerda tenuimana* could burrow more effectively than *Eugerdella armata* in coarser mud, but neither could burrow in sand.

Most of our findings agree with theirs, but there are a few discrepancies with HULT's observations. He found *Pleurogonium rubicundum* unwilling to burrow, whereas we saw it burrow in the way he described for *P. spinosissimum*. HULT gives the impression he saw desmosomatids swim spontaneously more than we did.

Our observation that *Ischnomesus bispinosus* burrows is concordant with several findings of specimens of the same family in cavities and crevices in plant material dredged from the deep sea (WOLFF 1979; GEORGE & HIGGINS 1979; GOODAY 1984).

In the present study, many different taxa showed common behavior:

Respiration is sporadic in all the species we studied. The respiration chamber is opened by lowering the operculum, after which the respiratory pleopods beat rapidly. Afterward, the chamber is closed again. In certain cases, as in *Pleurogonium*, the abdomen may be bent vertically, but usually no change in abdominal position accompanies the bursts of respiratory activity.

Brooding females also need to ventilate the marsupium. This is done by rhythmic expansion and contraction of the brood chamber by means of movements of the oostegites, or rather the pereopodal coxae to which they are firmly attached. This movement has the dual function of exchanging the water in the marsupium and redistributing the embryos within it. JANCKE (1926) claimed that beating of maxillipedal coxae, whose posterior borders were fringed with feathered setae pointing in many directions, were not causing a ventilatory current into the marsupium as was argued by EMDEN (1922) for *Asellus aquaticus* and *Idothea viridis* (now *Idotea chelipes*). JANCKE argued that its major function is brushing the embryos clean of bacteria, fungi and various particles, while the principal respiratory movement is that of the oostegites. This seems plausible for asellotes, but is hard to explain for other isopods whose pereopodal coxae are fused to the body. JANCKE (l.c.) also studied *Jaera albifrons* and found two ways in which the marsupium could be ventilated. One was the normal way of moving the coxae, and the other by bending the head and anterior thorax ventrally and then straightening again. The latter way was the most continuously used method with this species. Janiroideans do not have posterior, lobe-shaped maxillipedal coxae that could serve a ventilatory purpose.

Most of the nonburrowing species we studied allow or encourage their bodies to become fouled; *Baeonectes* is an exception to this, but we never learned how cleaning of the body is accomplished. In contrast, burrowing species generally show a clean body surface when extracted from the sediment. This might well be because of lack of setae on most of its surfaces, but the abrasion against the walls of the burrow could also play a role.

All our janiroideans seemed to be particularly active in keeping the flagellum of the second antenna clean. This was achieved by combing or brushing it with the mandibular palp, mouthpart endites, or even pereopods I or II. The main objective of this activity is obvious – to keep the major source of environmental information free of disturbing objects. Additional benefits might come from tasting the material sticking to the antennae to gain more chemical information, or simply feeding on the material. Most species, except the Munnidae mentioned above, also managed to keep their pereopods clean of detritus. This was accomplished by pulling these limbs through the mouth field. The

material thus collected by the mouth appendages was tasted and probably used as a food source.

In all cases of swimming (Desmosomatidae, Eurycopidae, Ilyarachnidae), movement was in a backward direction and powered by use of pereopods V–VII. These observations agree with those of G.O. SARS (1899) and HULT (1941) on *Desmosoma lineare, Eugerdella armata, Eugerda tenuimana, Baeonectes muticus, Ilyarachna longicornis, Aspidarachna clypeata,* and *Munnopsis typica*. This ability results from modification of pereopods V–VII into paddles fringed with swimming setae and the enhancement of the extrinsic muscles, whose origins are in the corresponding body segments. To accomodate this increased muscle mass, those body segments are often enlarged, remarkably so in more advanced forms, i.e. the Eurycopidae and Ilyarachnidae (HESSLER 1981). Finally, the shape of the posterior end of the body is streamlined for backward movement.

Thus, a substantial evolution has resulted in a major investment of the body for this specific purpose. Therefore, it is interesting to observe that virtually all of the animals we watched were reluctant to swim. Only the mancas of *Baeonectes muticus* swam spontaneously. In all other cases, swimming served only for escape; walking or burrowing were preferred methods of moving about. This situation is not unique. The caridoid form of the abdomen of the lower Eucarida functions primarily for escape, and a significant fraction of the body is modified for this purpose, but only rarely (*Pleuroncodes,* for example) does it supplant the pleopods for routine swimming.

Two very different ways of burrowing were observed: forward, through use of the anterior pereopods (Ischnomesidae, Macrostylidae, Desmosomatidae), and backward, by using pereopods V–VII (Ilyarachnidae). Our observations are consistent with those of HULT (1941) on *Eugerdella armata* and *Eugerda tenuimana*. Note that posteriad digging is employed by a taxon that swims posteriorly, indeed, it involves a limb motion not unlike that used for swimming. Because the Ilyarachnidae evolved from a eurycopid-like ancestor (THISTLE & HESSLER 1976), and that eurycopids have not been observed to burrow and are not well designed to do so, it is probable that backward burrowing in ilyarachnids is a secondary development. Interestingly, some ilyarachnids (*Pseudarachna*) subsequently abandoned swimming entirely. The Desmosomatidae, which is the least modified of all the swimmers, still employs the primitive anteriad method of burrowing.

We believe many of the behaviors we have observed are also characteristic of janiroideans living in the deep sea. The fact that different families exhibit similar behaviors indicate that those behaviors are fundamental to much of the Janiroidea. Further, most of the genera we studied are also found in the deep sea. This applies to almost the full range of desmosomatid genera (*Whoia, Eugerda, Desmosoma, Echinopleura, Eugerdella, Prochelator*), the monogeneric family Macrostylidae (*Macrostylis*), our single ischnomesid (*Ischnomesus*), one of our eurycopids (*Eurycope*), and one of our ilyarachnids (*Ilyarachna*). Common attributes with deep-sea species should include grooming behavior, respiratory movements, ability to burrow and general mobility. Conceivably, feeding behavior may be different because of different availability of various food sources. Finally, even when a genus is not represented in the deep sea (e.g. *Baeonectes,* 9–223 m (SVAVARSSON 1987), the similarity in basic morphological features of the family gives good ground for believing similar or identical behavior within most genera of the family. The swimming behavior of eurycopid species and the digging of ilyaracynids are examples of this.

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