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'Ligia'

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Introduction

Adaptation to land from a water environment is a common topic in many textbooks. Most of the organisms discussed, though, have already adapted themselves to solve the most vital problems of water retention and temperature control. Animals such as mammals, reptiles, and birds have all developed outer coverings that are impermeable to water and allow these animals a great deal of independence from their water sources. Mammals and birds have physiological adaptations that allow them to regulate their body temperature, while reptiles have relied mostly on behavioral patterns to cope with this problem.

In this paper I would like to discuss the Isopod *Ligia* that is considered terrestrial in habitat, but is yet to evolve a complete independence from the sea.

Ligia belongs to the family Oniscoidae, which is the Family of Crustacea containing species living a completely terrestrial life. Within the Isopods there are species such as *Carolana harfordi* and *Idothea wasnesenskii* that live a marine existence and others such as *Porcellio* and *Amadillidium* that are completely terrestrial. *Ligia* represents an interesting point of study in that it appears to be an intermediate species in the transition from the sea to land.

I would like to discuss some of the physiological and morphological characteristics of *Ligia* that place it in the intermediate position and its general habitat and behavioral patterns that may help to give a fuller understanding of this unique genus.

Habitat

Ligia is a common inhabitant of the upper spray zone and has been reported in England, Meditteranean, Bermuda, and both coasts of North America. The "Sea Sister," as it is commonly called, spends most of its time hiding under rocks and in crevices above the high water line. Ligia is usually nocturnal and can be found on non-moonlite nights feeding in large numbers on Fucus, Ulva, and the scum and algea that cover the exposed areas at low tide.

Stevenson (29) reported Ligia oceanica (Dana) emerging in large numbers during the early morning hours at Cape Neddick, Maine. This daylight appearance is probably more the exception than the rule. Stevenson did mention finding varying amounts of these animals on his later visits to the same place. It is possible that he saw mostly young specimens for they show less of an aversion for light than the older and larger specimens. Also a high humidity in the air due to early morning fog or dew may have prompted this unusual appearance.

Ligia pallasii (Brandt) the common species found along the Oregon coast has been studied in three different habitats by the author: Winchester Bay, Pacific Mourage in Florence, and Devils Elbow.

The rocky beach areas at the base of the jetty's at

Winchester Bay have produced large groups of Ligia upon turning over large flat rock just above the high water line. They appear to occupy a similar niche as Ligia baudiniana (Edwards) in Bermuda (2). Barnes notices that the younger specimens were found closest to the water which is similar to my findings at Winchester Bay, but unlike Ligia baudiniana larger specimens of Ligia pallasii seem to be voluntarily submerged by the incoming tide.

At Winchester Bay Ligia appears to feed mostly on pieces of Ulva and Fucus left behind by the outgoing tides, but many smaller specimens have been found under the rocks at the waters edge where they would probably feed on living fucus and the scum on the rocks.

At Pacific Mourage in Florence Ligia pallasii occupies a similar niche as Ligia oceanica in the quays at Plymouth (20). Here they are found among the large crevices between the boards of the bulkade and behind those pilings that were not heavily covered with tar. At night they migrate 2 or 3 feet down the pilings or bulkade to graze on the sparse population of Ulva and the general scum left by the outgoing tide. Very definite clear areas with little Ulva growth can be seen along the bulkade where populations of Ligia are hiding. Although no Fucus can be found in the immediate area it has likely been grazed off for substantial growths are found in the unpopulated areas at the same tidal level.

The largest specimens were observed in the caves at Devils Elbow. They could be found scattered in small groups over the ceiling and in the moist crevices at the openings to the caves. Here males 35 by 22 mm were common, and females 26 by 12 could be found. These finds agree with Nicholl's (20) who found his largest specimens in the more rocky areas. The largest specimens were found in the darker reaches within the caves, with populations, intermediate in size, in the outer crevices. A large scattering of young could be found on the outer rocks in complete daylight. Most of the animals here were seen feeding at night on the green algae scum that would form on the face of the cliffs above the caves. This was caused by the constant seepage of ground water from the wooded areas above the caves. Only a very few animals were found to migrate toward the exposed tidal areas to feed on the *Ulva* and *Fucus*.

Physiological Adaptations

If *Ligia* is truly an intermediate animal in the transition from the sea to land you would expect it to show unusual physiological abilities when compared to the marine and terrestrial forms of Isopods.

Osmotic Regulation

All crustacea regulate ionic concentration and balance to some degree. There are two basic classes of crustacea to consider when discussing control of body fluids. One group has their body fluid concentration isotonic with their environment and consists mostly of marine forms. For this group the main problem is regulation of specific ionic balances. The other group which consists of all terrestrial forms, those that have left the sea for brackish or fresh water, and some that have left fresh for salt water and a few salt water forms. For this group the control of the concentration of body fluids and ionic regulation is necessary (28).

Ligia spends most of its life on land and would appear to belong to the second group discussed above, but on numerous occasions I have observed *Ligia pallasii* being submerged by the incoming tide. When chased they would retreat into the water with no apparent hesitation. Barnes (4) observed both young and adults submerged, but did indicate the young appeared much more at home in the water and were found there more often and for longer times.

Tait (29) tried a series of immersion experiments on *Ligia oceanica* to test its ability to withstand different concentrations of sea water and to shed possible light on whether *Ligia* inhabited land by a direct route from the sea or via a brackish estuary.

Table 1

Emersion Experiments

Concentration of sea water	Survival times
100% sea water	35,51,52,58,65,85 days
50% sea water	16,18,24,34,37,42 days
25% sea water	3,5,7 to 9, 15 days
Distilled water	8-9 hours, 36 hours

It is evident that *Ligia* is quite well adapted to live in sea water over prolonged periods of time. It can also be noted that a reduction in the concentration of sea water reduces survival time. These results lead Tait to the conclusion that *Ligia* is probably a direct descendent from the sea. Barnes (2) recorded similar results for *Ligia baudiniana* though the general survival time was much less than Tait's results with *Ligia oceanica*. Tait noticed that oedema was common in those dying in distilled water and indicated loss of essential salts to be a likely cause of death. This was confirmed by Barnes (2).

Brusca (6) compared Isopods of varying degrees of adaptibility to land in emmersion and humidity tests.

Carolina hartfordi - completely marine

Idothea occidentalis - Partial exposure at low tide

Ligia occidentalis - Upper spray zone

Porcelio scaber - completely terrestrial

Table 2

Humidity tolerance tests for spring populations of three species of isopods from Dillon Beach, California

Species	*No. individuals*	*Rel. hum.*	*50% death time*
Cirolana harfordi	6	00%	2 hrs.
	6	25%	2 hrs.
	6	50%	6.5 hrs.
	6	75%	20 hrs.
	6	100%	45 hrs.
Ligia occidentalis	6	00%	34 hrs.
	6	25%	46 hrs.
	6	50%	32 hrs.
	6	75%	32 hrs.
	6	100%	(48+)
Porcellio scaber	6	00%	20 hrs.
	6	25%	(48+)
	6	50%	(48+)
	6	75%	(48+)
	48	100%	(48+)

Table 3

Salinity tolerance tests for winter populations of four species of isopods from Dillon Beach, California.

Species	*No. individuals*	*Medium*	*50% death time*
Cirolani harfordi	6	FW	1 hr.
	6	10% SW	3 hrs.
	6	25% SW	34 hrs.
	6	50% SW	(48+)
	6	75% SW	(48+)
	6	100% SW	(48+)
Idothea wosnesenskii	6	FW	1.5 hrs.
	6	10% SW	12 hrs.
	6	25% SW	47.5 hrs.
	6	50% SW	(48+)
	6	75% SW	(48+)
	6	100% SW	(48+)
Ligia occidentalis	6	FW	10.5 hrs.
	6	10% SW	9 hrs.
	6	25% SW	11.5 hrs.
	6	50% SW	21.5 hrs.
	6	75% SW	34 hrs.
	6	100% SW	(48+)
Porcellio scaber	6	FW	2 hrs.
	6	10% SW	5 hrs.
	6	25% SW	3 hrs.
	6	50% SW	3.5 hrs.
	12	75% SW	5.5 hrs.
	12	100% SW	4 hrs.

Brusca's results showed as was expected that Ligia was slightly less adapted to the high salt concentration that the marine species but was more tolerant at the lower salinities. It was better adapted to immersion at all concentrations than the completely terrestrial *Porcellio*. *Ligia* showed a greater tolerance at all humidity readings than *Carolina*, but showed a lesser adaptation to all but one humidity reading than the terrestrial form. This one discrepancy is probably due to the larger size of *Ligia* and will be discussed later.

When comparing the normal osmotic pressure of the body fluids, using freezing point depression, *Ligia* was found to be higher 2.15° C than the marine species *Idothea* (1.96° C), which is usually isotonic to its environment (32). A comparison to the more terrestrial species also shows a much higher concentration for *Ligia* (Parry 1953).

Oniscus 1.04 C

Armadillidium 1.18 C

Porcellio 1.30 C

The osmoregulatory ability of *Ligia oceanica* and *Idothea granulosa* were compared (32). *Ligia* was found to remain osmotically steady between 75% and 100% sea water, but to slowly rise or fall at greater or lesser concentrations. *Idothea* dropped significantly throughout, something to be expected in an animal not normally concenred with maintenance of osmotic concentration. *Ligia* also appeared to have better regulatory control at the lesser concentrations showing a high degree of osmotic independence for short periods of time (5). Libia was able to maintain a freezing point depression of 1.65 C compared with 0.90 C for _Idothea_ at 25% sea water (0.48 C). The lethal point appeared to be 0.97 C and 1.16 C respectively for _Idothea_ and _Ligia_. _Ligia_ would remain hypotonic to high concentration and hypertonic to low concentrations (26).

Idothea and _Ligia_ do not show any corresponding increase in weight or volume with the lowering of internal osmotic concentrations (30). This would be expected if a passive influx of water was responsible for the lowering of osmotic pressure. Todd (32) proposed a possible controlled exchange of salts take place. Croghan (8) proposed that in _Artemia_ salts and water are absorbed through the gut and the excess salts excreted at the brachial plates. With the use of phenol red dye it was indicated that _Artemia_ swallows large amounts of water and allows it to pass through the gut wall. Oral drinking in small Crustacea has been assigned a strictly enema and food movement function by Fox (15), but he did indicate that the passage of water through the gut and out the excretory organs is likely.

Ligia pallasii was placed in a phenol red environment following Croghans method, and showed no signs of excessive uptake of water by oral drinking. To demonstrate the possible release of ions across the pleopod membranes in _Ligia_

Croghans method was used. Half a dozen Ligia were rinsed in distilled water for several hours to remove all external salts. They were then placed in a $AgNO_3$ solution for two minutes. Any chlorine ions being released from the body should combine with the silver to form a white precipitate. The animals were then rinsed for several hours in distilled water againto remove excess $AgNO_3$. The organisms were then placed in developing fluid for 1-2 minutes. This would cause any area of the body that showed a significant darkening was the median and posterior edges of the last four pleopods. The first pleopod usually showed little oedema and no significant darkening, which may indicate little if any ion or water exchange taking place at this point. Croghan did find that the eleventh branchae of Artemia showed no darkening from the developing fluid, which he interpreted similarly.

Resistance to Desiccation

The dry condition of air provides a very hostile environment for those organisms inhabiting land from the sea or fresh water. Prevention of rapid desiccation by the development of an impermeable integument is a problem already solved by most successful terrestrial forms. The Oniscoedea have not yet developed such a protective covering, although there are species that do show greater adaptation than others.

Table 4

Rate of Evaporation of Water in mg/cm^2/hr when exposed to dry air for an hour at various temperatures

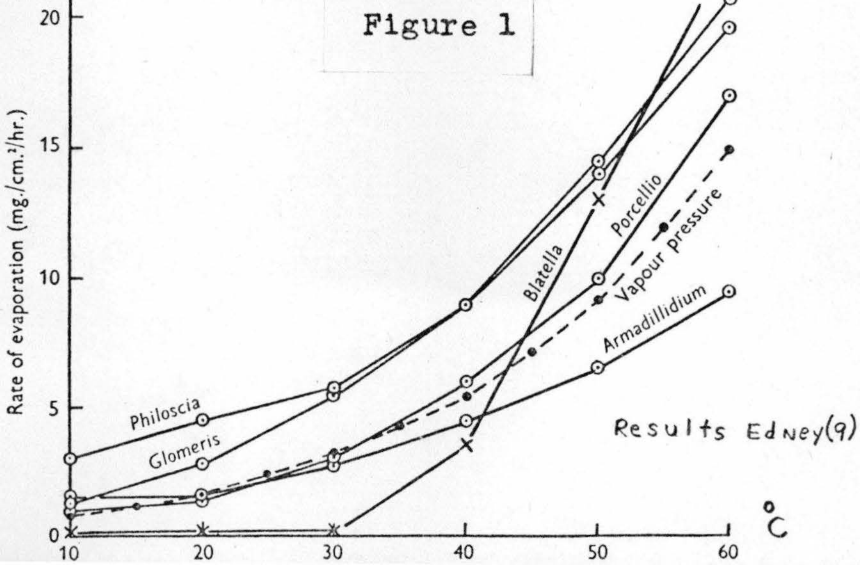
	10	20	30	40	50	60
Armadillidium	1.5	1.5	2.7	4.5	6.5	9.5
Porcellio	1.0	1.2	3.0	6.0	10.0	17.0
Cylisticus	1.0	3.5	7.0	9.0	13.0	18.5
Ligia	2.0	4.2	7.0	12.5	15.0	19.7

Results from Edney (9)

As would be expected Armadillidium the most terrestrial in habitat shows the least amount of water loss at all temperatures, while the inhabitant of the littoral zone, Ligia, shows the least resistance to desiccation. This difference in the permeability of Isopod cuticles by different amounts of lipoidi which impregnate the endocuticle. If the temperatures are raised above the melting-point a marked increase in permeability results (7).

Figure 1 shows the relationship between the vapour pressure and the rate of evaporation.

Figure 1



Note that there is a very close relationship between the increased vapour pressure and the rate of evaporation for the Oniscoidea, indicating little resistance to drying. Blatella (common cockroach) shows a comparative curve for insects. Note the great degree of resistance at the lower temperatures. The sudden rise for Blatella is to the breakdown of the waxy protective layer in the cuticle caused by the excessive temperature.

Porcellio, one of the better adapted Oniscoidea, was compared to other terrestrial forms (16).

Percent Weight Loss/Hour

Porcellio	4.0%	at	20 C
mealworm	0.05%	at	20 C
Cockroaches	1.14%	at	23 C
Earthworm	18.0 %	at	20 C

It appears that the terrestrial Isopods are not well enough adapted physiologically to survive a terrestrial existence without some type of behavioral pattern to compensate for their inability to resist drying.

Porcellio shows an increased activity when the humidity drops below 65%. This is believed to keep the organisms moving until it gets back into a suitably moist habitat (16). Ligia has been observed to group in various parts of the same cave, which would afford them greater protection from desiccation, but no formal study has been made to indicate that this may be a behavior similar to Porcellio's.

Table 5

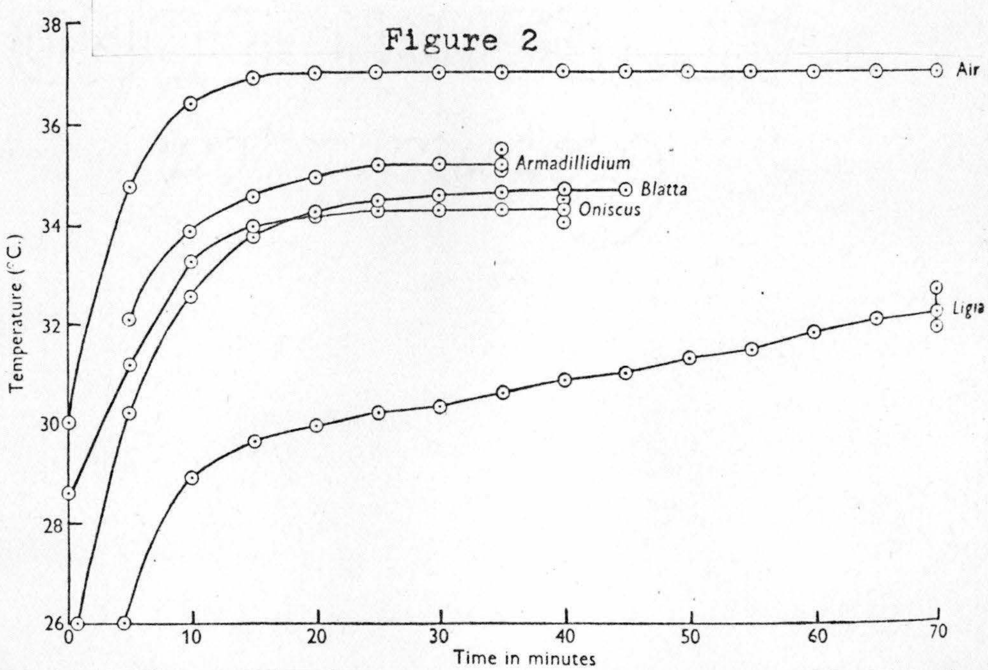
The highest temperature which various species of woodlice and other arthropods can tolerate at different humidity for various periods of time

Period of exposure ...	15 min.			1 hr.			24 hr.		
Relative humidity (%)...	0	50	100	0	50	100	0	50	100
Armadillidium vulgare	43	46·5	42	41	42	40	18	22	37·5
A. nasatum	42·5	45·5	41	41	41·5	40	11	17·5	37·5
Porcellio	42·5	43	38	39	39·5	37·5	13	17·5	36
Oniscus	40	41·5	37	34	36·5	33·5	9	15	31·5
Cylisticus	—	—	—	35·5	36	37·5	12·5	13·5	35
Philoscia	—	—	—	32·5	36·5	34	9	13	30·5
Ligia	41·5	40	34·5	39	35	32·5	9	—	29
Glomeris	—	—	—	42	42·5	42	27	33·5	38

Edney (9)

In Table 5 it can be seen that Ligia has the lowest temperature tolerance for all the arthropods tested. It is interesting to note that at lower humidities Ligia's temperature tolerance is much closer to the rest of the animals than at 100% relative humidity. It is probable that the true temperature tolerance is more accurately indicated at 100% relative humidity when the least amount of evaporation can take place.

Figure 2

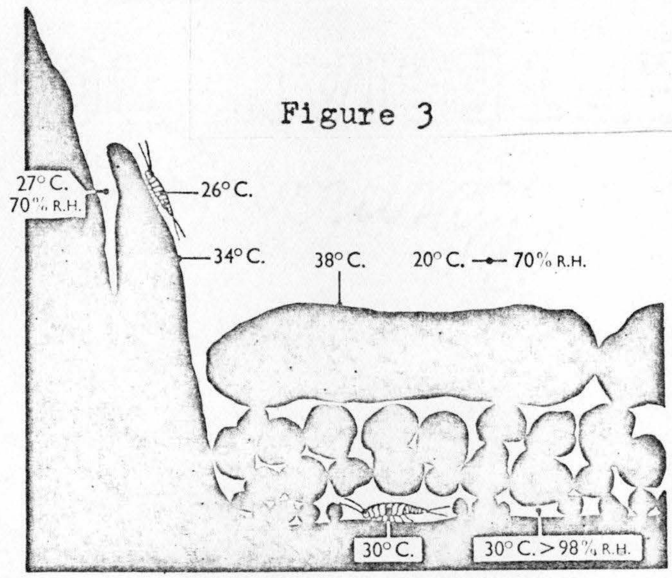


Temperature curves for various woodlice and the cockroach, Blatta, exposed to slowly moving air at 37° C. Edney (35).

Figure 2 demonstrates the cooling ability of evaporation on the body surface of woodlice. Note the amount of cooling obtained by Ligia, which has been shown earlier to have the greatest rate of evaporation. Ligia is able to maintain body temperatures up to 7° C below ambient temperature for up to 30 minutes.

Edney (12) was able to measure the body temperature of animals in the field to see if the temperature reducing effects of evaporation could be used by Ligia in its natural habitat.

Figure 3



Microclimatic conditions on verticle section of base of red sandstone cliff and shingle inhabitated by Ligia. Edney (10).

In Figure 3 Ligia has moved to a seemingly more hostile location with beneficial results. The protected rocky covering, which is the usual place of hiding during the day, has reached a lethal temperature level, and forced Ligia to make unusual daylight appearance in order to reduce its body temperature by rapid evaporation. It is likely that this behavioral pattern allows Ligia to range within a larger ecological habitat.

Miller (18) made the following comparisons:

On basis of moisture of habitat

Ligidium Ligia = Actoniscus Porcellio Armadillidium

Based on survival in suboptimum humidities

Ligidium Porcellio Armadillidium Ligia

Numanoi found that in a dry atmosphere Ligia could lose about 13% of its body weight before dying and about 7% in saturated conditions. These results are contrary to experiments performed on frogs, which would die quicker with a lower net loss when evaporation was faster. In Numanoi's experiments it is possible that animals living in saturated conditions may have died of partial starvation or metabolic disorders rather than water loss. The animals were kept at 25° C $\pm$ 2° with no way of cooling themselves due to the heavy humidity. Numanoi did show that there was definitely greater weight loss in living than dead animals which he attributed to metabolic activity. Ligia has been shown to gain weight in humidities of 98% at 15° C (9). The highest temperature Ligia can tolerate for even 24 hours is 29° C. Numanoi was working very close to the optimum temperature for Ligia and reported no deaths at 100% relative humidity until about 30 hours.

Respiration

In the sea respiration requires thin flat membranes of considerable surface area to facilitate the proper circulation of water and an adequate supply of oxygen. On land the great increase in partial pressure of oxygen and the less dense quality of the air allow for a reduced respiratory surface and a more closed system. The latter is especially important to eliminate excess loss of water from the gill areas.

Insects have developed small respiratory tubes, known as spiracles, that have the ability to close during severe drying conditions. In the Isopods species has developed respiratory organs as as those of the insects, but those, which are more terrestrial in habitat, do show definite adaptive changes in their respiratory structure. The aquatic Isopods such as Idothea have plate like abdominal appendages that serve as gills. The more terrestrial forms like Armadillidium have a tree-like branching system of tubules, bathed in blood, through each exopodite of the first two pleopods, or, sometime of all five pairs (33) (18). Table 6 compares some of the common Isopods by habitat and respiratory development.

Table 6

Name	Habitat	Respiratory Organ
Idothea	aquatic	thin gills
Asellus aquaticus	aquatic	thin gills
Ligia oceanica	high water line	gills, with stouter exopodites
Omiscus assellus	damp places	gills, with special air chambers at edge of exopodites
Porcellia scaber	drier places	trachea in first two pairs of exopodites
Armadillidium	dry places	same as above

It is evident that compared to other terrestrial forms *Ligia* has a very poorly adapted respiratory system. If you assume that in Isopods, the rate of evaporation at the respiratory sights is indicative of the permeability of the respiratory membranes, the following comparison can be made. If you compare the rate of weight loss per unit area of the total body weight lost from drying animals you receive values of 83 for *Armadillidium*, 97 for *Porcellio*, and 58 for *Ligia*. The lower rate of evaporation per unit area at the respiratory sights in *Ligia* atests to its thickened quality and only partial adaptation to land.

The sensitivity of marine Crustacea to decreased levels of O_2 was tested (14). The amphipods *Gammarus pulex*, and *G. locusta* showed increased gill movement when O_2 levels were dropped below the saturation level between air and water. Movements of the scaphogmathites of crayfish *Astacus* showed a similar increase. Though *Ligia* shows an increase pleopod beat with rising temperatures (20) (21), it did not show the sensitivity to change of O_2 level as in the other aquatic crustacea tested. Perhaps *Ligia's* relatively recent emergence from the sea has been long enough to allow it to lose some of its sensitivities to an aquatic life.

Behavioral Patterns

In this last section I would like to discuss some of my personal observations and shed some light on possible reasons why Ligia has not been able to advance much beyond the littoral area.

Eating Habits

Ligia is mostly herbivorous in its normal habitat, but has been observed in the laboratory to be quite capable of eating animal remains (31) (21). Those animals that were unable to adjust to laboratory conditions were usually devoured in two nights of feeding. Ligia showed a preference for the internal organs, but would eat the exoskeleton once the more choice areas were finished. When both plant and animal material was available they showed an equal liking for both.

A variety of foods were fed to the laboratory animals and yielded the following preference list. Mossy filamentous algae (in fresh water) = scum consisting of unicellular algaes, small filamentous algaes, diatoms, and small microscopic protozoa and crustacea = Fucus Ulva Alaria eel grass (more consumed). Moss capsules and parts of the syncytium of Vancheria were found in the gut contents of Ligia oceanica (20). The favorite food of some Ligia kept in a simulated seashore habitat was the synthetic cellulose sponge I had used as their hiding place. Although fresh Fucus was placed in the aquarium it was never consumed. Only the sponge and on several occasions the green scum covering the gravel made up the diet of this population.

It is apparent that Ligia has a very diversified appetite, which has no doubt helped it to take advantage of most of the suitable niches along the coast. In the three areas studied by the author Ligia appeared to be subsisting on different diets, with the largest animals feeding on fresh water algae forms.

Range and Grouping Patterns

Barnes (2) discussed how Ligia baudiniana would move with the incoming and outgoing tides, while feeding on the exposed plant life. I was never able to see such a clear example of orderly movement, although I did see some indication that this may be the case with the younger specimens at Winchester Bay.

For the most part I found that Ligia ranges very little from its normal hiding place. At Pacific Mourage in Florence this amounted to only about 2-3 feet in most cases. The most adventuresome animals may have travelled as far as five feet. During the day animals were marked with luminous paint. Up to 3 weeks later over half those marked could be found in the same approximate area behind the pilings. It's probable that a higher percentage waa continually returning but due to the difficulty in being able to see all individuals because of the closely packed populations and the occasional shedding of the paint observations were gross at best. At Winchester Bay the large adults would be found on or within a foot of the large rocks they would hide under. It seems almost essential that they would have to migrate closer to the water for enough food, but this was never observed.

At Winchester Bay I noticed that in the smaller rocks closer to the water there seemed to be a segregation of the sexes. If a rock waa overturned it would yield almost exclusively males or females. I don't know if this is a normal behavior pattern for the younger Ligia or is due to the inability for the larger males to get under many of the smaller rocks inhabited by females. At the other two places studied this separation was not so evident.

At Devils Elbow it was easiest to follow the movement of various individuals because they were often found on the roof of the caves in easy view. In one cave approximately 100 individuals found in a large gathering were marked. The next day only about 4 of the marked individuals could be found. The large gathering on the roof had scattered into the deeper crevices at the back of the cave. Continued markingsof individuals showed no consistant pattern of movement or that animals would return to the same approximate area after leaving on an evening feeding trip. This consisted of traveling 10-25 feet to the outside of the cave and up the face of the cliff. When animals migrated up the face of the cliff they would usually follow established routes of water seepage. When they would return to the cave with no specific guides to follow they appeared to wander randomly about toward the back of the cave until a suitable place could be found.

The animals kept in my 2' x 3' aquarium would always walk along the sides to get to the water and back. Their hiding place was about four inches from one corner and resulted in many missed attempts before they finally locate it.

Animals released near the waters edge would almost always orient themselves toward the rocks and begin moving. This was also observed by Barnes (4), who found inconsistent results when he tested his theory of possible geotaxic controls.

Ligia apparently has very poor navigational abilities and must rely on some type of natural barrier to guide its movements or else revert to random wandering.

Regulation of Moisture over Pleopods

Ligia has mostly been discussed as a terrestrial organism, but does on occasion submerge. It will exhibit a porpoise like swimming motion in deep water, until it is able to reach

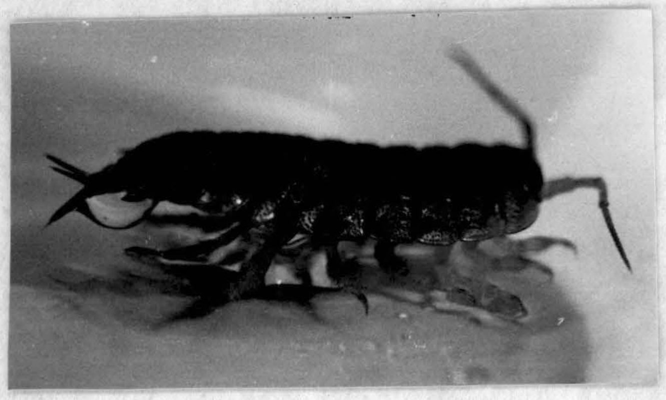


PLATE 1

PLATE 2

PLATE 3

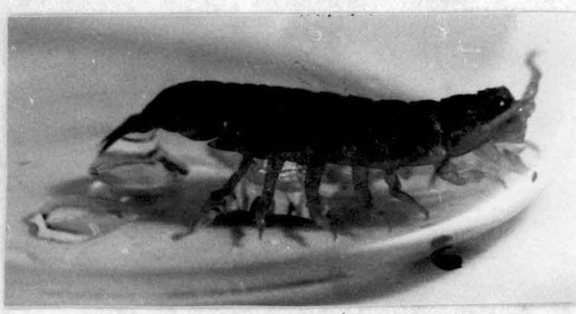


PLATE 4

PLATE 5

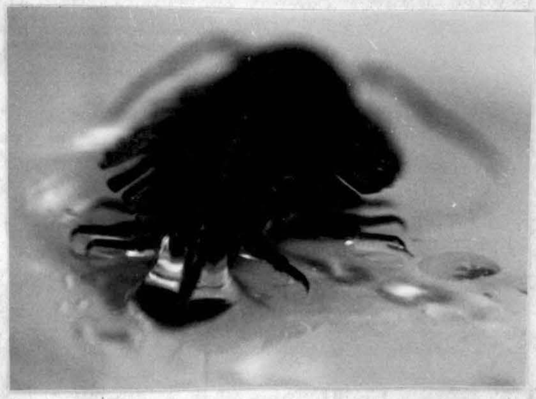


PLATE 6

PLATE 7

PLATE 8

a solid substrate. In the lab it has been seen to voluntarily submerge itself and graze on the algae coating covering the gravel. When *Ligia* does submerge the pleopods, that remain flat against the abdomen while on land, begin to beat. Warmer water or decreasing salinity will both cause an increase in the rate of beating (21) (20)probably due to a reduced O_2 concentration or increased asmatic work.

Some animals that have been observed grazing in water will elevate their abdomen to allow for aerial respiration (plate 8). Upon leaving the water *Ligia* will go through a series of movements to free the pleopods of excess water. This consists of flexing their pleopods with a raising and slight curling of the abdomen (plates 1-3). The result is the formation of a water droplet on the uropods. The animal will then lower the uropods to the substrate and deposit the excess water (plates 4-5). In plate 6 the uropods are seen to be held tightly together to facilitate the water release. Barnes (2) has observed this arrangement of the uropods to be also used for drawing water up to the pleopods by capillary action when additional moisture is needed. Plate 7 shows the common stance taken by animals that have finished depositing their excess water and apparently need some additional drying or increased respiration. This position is usually maintained for about 2-10 minutes probably depending on the dampness of the surroundings and the length of time submerged.

Limiting Factors of Land Inhabitation

While studying Ligia I have become aware of its relative abilities compared to other forms of more terrestrial wood-lice. Then considering its great mobility, its comparative ability to withstand drying conditions, and to vary unselective feeding habits I began to wonder why it has not been able to range farther into estuaries or up stream beds where it could still have an adequate water supply.

There appear to be two main possibilities that I see as restraining Ligia from further terrestrial adaptation.

First is the observations of Barnes (2) and Hewitt (17) that Ligia must return to the sea to release its young from the brood pouch. Very little research has been done on the young because of its possible affect on experimental results, so that specific weaknesses or needs of the newly liberated Ligia are not well known. In immersion experiments young Ligia have been shown to withstand rising temperatures in water as well or better than adults (20). Possibly the small size of the young and a high rate of evaporation necessitates an aquatic beginning.

The other area to consider in the unusually high osmotic concentration of Ligia's blood discussed earlier in this paper. The lethal level that Ligia can drop to and still survive is still higher than the more terrestrial forms normal osmotic concentration. _Ligia's_ poor ability to resist loss of essential salts in fresh water for prolonged periods of time would provide a serious problem during times of heavy rain.

This discussion brings up the problem of how _Ligia_ maintains its high salt concentration in areas like Devils Elbow, where most of the animals don't appear to go down to the salt water. Instead they spend the daylight hours in dry-cool caves and the evenings foraging on rocks bathed by fresh water. A simple study was carried out to see if _Ligia_ would be able to attain sufficient salt from its immediate surroundings. Samples from the rock faces were taken by scraping a 9 cm^2 area of all surface deposits and rock. Other samples were taken to correspond to the normal size of the scrapings. A sample of moist beach sand was used as an example of a salty substrate. All samples were soaked in distilled water for 4 hours and periodically mixed to allow time for the salts to dissolve. Samples were then titrated in Parts/Per/Million using 0.0141 $AgNO_3$ to determine the chloride ion content.

Table 7

Location	Conditions	a-content (parts/per/million)
Cave #1	at entrance	20.0
	inside	24.0
	18 ft. above ground	24.0
	40 ft. to right (no <u>Ligia</u> here)	0.8
Cave #2	at entrance	0.0
	at back wall	0.0
Cave #3	inside on top	4.0
	25 ft. above sand	20.0
	forage (several animals were grazing on)	0.0
Cave #4	Inside on top	0.0
Ground seepage	dripping off forage	100.0
Sand	moist	210.0
Measured sample	100/per/mil.	95.0
Sea water	35 0/00	35,000.0

Though the accuracy of the tests might be in question it appears that <u>Ligia</u> would have trouble getting a great deal of salt from its surroundings. This may indicate that periodic trips to the more salty tidal areas may be necessary. No indication of this was seen on four evening visits to this area. It is possible that under normal conditions <u>Ligia</u> is able to obtain enough salt from its food to compensate for any loss, but under severe conditions must return to the ocean for large amounts of salts.

Barnes (3) observed that <u>Ligia</u> would show a preference for being submerged in salt water over fresh water, but the opposite was the case if placed on damp filter paper.

Both ideas just discussed are mostly conjecture with available evidence very limited indeed. It is evident that more work has to be done on <u>Ligia</u> to gain a more knowledgeable understanding of its place in nature.

Summary

Ligia was found to be a common inhabitant of the upper-spray zone with the ability to occupy a wide ranging habitat.

When compared physiologically with other Isopods *Ligia* was found to be a superior osmoregulator to both the terrestrial and aquatic species. It exhibits a good ability to live submerged in salt water for prolonged periods of time, and was shown to be one of the most tolerant of the Isopods to severe drying conditions. *Ligia's* large size and rather permeable cuticle allow it to substantially cool itself when exposed to severe temperatures.

Ligia's respiratory mechanism shows very little adaptive change from that of the aquatic Isopods. Elaborate behavioral patterns have been established to free the pleopods of excess water after being submerged.

Ligia has a very omnivorous diet showing equal taste for plant or animal foods. *Ligia* has a very limited range and will only move far enough to find a meal or a place of suitable moisture. The range may be limited by very poor navigational abilities.

It was suggested that *Ligia's* continued advancement to a more terrestrial habitat may be hampered by the necessity of releasing the young in salt water or its unusually high salt requirements.

Ligia is definitely an intermediate Genus of Isopod in the transition from the sea to a terrestrial environment. Whether *Ligia's* present position is the result of a relatively recent ascent to land; some poorly adaptable characteristics; or a combination of the two, is difficult to say with the small amount of research that has thus far been done.

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