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A PHYSIOLOGICAL COMPARISON OF ISOPODS IN THE TRANSITION FROM A MARINE TO A TERRESTRIAL HABITAT; WITH NOTES ON THEIR MORPHOLOGY AND BEHAVIOR

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Presented to
The Faculty of the Department of Biological Sciences
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In Partial Fulfillment
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Master of Arts

by
Gary John Brusca
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INTRODUCTION

The determination of the tolerance limits of organisms to various environmental factors is an active branch of comparative physiology known as environmental, or stress physiology. The importance of these studies is indicated by their use in explaining and illustrating distribution patterns, vertical zonation, environmental preferences and similar matters. The reasons influencing the ability of an organism to survive in a particular habitat are often found in studies of their physiology. The entire picture of any one population, however, is very complex and cannot be explained by one factor alone. The preference of an organism to a specific habitat usually involves the interaction of many physical and biological factors.

Organisms which are engaged in transitions from the sea to land are faced with great physiological stress. A common route from the sea is through estuaries. This transition involves adaptation to gradual changes in salinity, temperature fluctuations, and ionic composition. A more drastic transition is one which occurs through the intertidal zone, directly to land. Here the organisms encounter rapid temperature changes, immediate osmotic stress, and a great number of other problems. Animals living in the intertidal zone may be periodically exposed by the tides and must overcome such problems as desiccation, buoyancy, food source, etc. Such animals, in fact, represent a step toward land life for they have solved these terrestrial problems to the extent that they can survive short periods of exposure. Some of the conditions which may aid animals in this transition through the intertidal region are high humidity and moderate sunshine, both of which aid in preventing desiccation. A large tidal amplitude tends to make the transition more gradual by subjecting the animals to longer and longer periods of exposure as they move higher through the intertidal region. Moderate surf action is benificial in easing the physical aspect of the transition (Gislen, 1946).

The isopod crustaceans are excellent examples of animals making the transition from a marine to a terrestrial habitat, They may be found in completely marine situations, (e.g., Cirolana harfordi) fresh water, (e.g., Asellus sp.) and on land (e.g., Porcellio scaber). Even though the terrestrial species have no association with the sea they are not adjusted to very dry conditions as are some other arthropods. That is, they require more environmental moisture than the more terrestrial insects, arachnids, etc. None the less, a definite transition does exist and many intermediate stages are to be found between the extremes. Thus the isopods lend themselves very nicely to a study of the transition from the sea and the various environmental problems that are involved.

This study is of five species of isopods common to the Dillon Beach area, each of which represents a different level in the transition toward land life. Cirolana harfordi was used as a completly marine form. Idothea (Pentidotea) wosnesenskii represents a step toward land life as it inhabits an area uncovered by most low tides. Ligia occidentalis is found in the splash zone, receiving spray from the action of the surf. This illustrates another, higher, level in the transition. Alloniscus perconvexus was the fourth species studied. It is commonly found burrowed in the sand in the area of the berm, which is the nearly level portion of the beach formed by high tidal wave action. Finally, the terrestrial form, Porcellio (Porcellio) scaber, was used to illustrate those isopods best adapted to land life. The physiological data presented in this paper includes salinity tolerances and humidity tolerances. Some information on acclimating one species to lowered salinities is also presented. The results of these experiments are used to illustrate the degrees of adaptation to land life shown by the isopods in different areas of the transition. A discussion of the adaptive morphology and behavioral characteristics is also related to the environmental situations in which each animal is found.

A great deal of ecological and taxonomic work on the isopods illustrates and, in some cases, mentions the transition. Abbott (1940) discusses the transition and employs some physiological data. Abbott's work was concerned mainly with the family Lygididae. Some structural modifications were also considered in the study. Abbott places Ligia occidentalis nearly in the middle of the transition as it is considered in this present study. An interesting study concerning the terrestrial isopods of the San Francisco region was conducted by Miller (1938). Miller reports very high optimum humidities for all terrestrial forms, illustrating that the transition is still in a relatively early stage, compared to the more well adapted land arthropods. There have also been studies done on individual species in regards to their salt requirements, etc. (Barnes, 1932, 1935). These works are informative, but not actually comparative for use in illustrating the transition.

Some studies have been done relating generally physiological problems of different groups to their environment (Topping & Fuller, 1942; Smith, 1959; Robertson, 1949). Smith's work was concerned mainly with the problems of brackish water and may be involved in the transition to land through esturine conditions.

This paper is a consideration of some of the basic problems in the transition of isopods from a marine to a ~~terrestrial habitat. All organisms were collected in the~~ Dillon Beach area, Marin county, California (38^oN, 123^oW).

MATERIALS AND METHODS

Collection and maintenance of animals

Animals collected in the field were transported to the laboratory in glass containers. Conditions in the jars were made as close to the natural situation as possible. In the laboratory animals were maintained in a large water table. This table was 3 feet by 5 feet 11 inches, and was 11.5 inches deep. The water table was lined with fiber glass on the bottom and up the sides a few inches. Fresh water was placed in the table to a depth of about 5 inches and small dishes were placed in this water for the animals. A fairly constant temperature was maintained by the use of a thermostat-controlled refrigeration unit. The temperature ranged from about 13.5°C to 15.0°C throughout the entire study. Temperature changes of more than 1°C were not noted during any one experiment.

Salinity tolerance tests

The salinity tolerance tests were conducted in the above described water table. The summer tolerances were determined in July, 1960. Winter populations were tested in February, 1961. The salinities of experimental media and also of the field samples were determined by titration with silver nitrate and the following calculations.

$$\text{Molarity of Cl} = \frac{(\text{ml. AgNO}_3)\ (\text{norm. AgNO}_3)}{\text{ml. sample}}$$

$$\text{Chlorosity} = (\text{molar. Cl})\ (\text{at. wt. of Cl})$$

$$\text{Chlorinity} = \frac{\text{chlorosity}}{(\text{sp. den. at } 20^{\circ}\text{C})}$$

$$\text{Salinity} = .030 + (1.805 \times \text{chlorinity})$$

The animals were placed in 2oo ml. of each experimental solution and tests were conducted for 48 hour periods. Fifty percent death times were recorded during the experiments. Temperatures of experimental media were allowed to equalize with the temperature of the water table before introducing the animals. The water was not changed during the 48 hour period.

Humidity tolerance tests

These tests were also conducted in the water table. The tests were run in April, 1961. Experimental animals were placed in gallon jars in which various humidities had been established. The humidities were maintained throughout the 48 hour observation period by the use of various solutions of sulfuric acid. The following table is taken from Miller (1938) and gives the various concentrations for the different humidities.

Specific gravity	% H_2SO_4 in HOH	Approx. R.H.
1.00	0.00	100.0%
1.09	12.99	95.0%
1.14	19.61	90.0%
1.23	31.11	75.0%
1.27	35.71	66.0%
1.29	38.03	60.0%
1.340	43.60	50.0%
1.361	46.00	45.0%
1.417	52.40	33.0%
1.438	54.00	30.0%
1.459	56.00	25.0%
1.479	58.00	21.5%
1.524	62.00	15.0%
1.569	66.00	10.5%
1.840	100.00	00.0%

200 ml. of each solution used was placed in a flask and set in a gallon jar. The test animals were placed in beakers and set in the jar. The lids were sealed with tape and a small pin hole put in the top of the jar. This hole was covered with tape and was only opened to stimulate the animals with a small wire to establish death times. All test animals were considered dead when they no longer responded to mechanical stimulation of the body or the appendages. All humidities were checked after the experiments and found to have been maintained within 3% relative humidity of the prefered humidity.

Training experiment

This experiment was conducted in February and March of 1961. Specimens of Cirolana harfordi were placed in 200 ml. smaples of the test solutions. The temperature of each new solution was allowed to equalize before the specimens were transfered to a lower salinity. The experiment was carried out in the water table.

Removal of pleopods

The pleopods to be removed were grasped with fine-tipped forceps under a low power dissection microscope. The plepods were then simply pulled off the abdomen of the specimen. Animals were placed in small jars for observation.

The following salinities were used in interpretation of all test data involving various concentrations of sea water. There was no appreciable change in the salinity of 100% sea water in the summer and winter.

Medium	Salinity
100% sea water	32.25 °/oo
75% sea water	25.77 % oo
50% sea water	17.00 °/oo
25% sea water	8.32 °/oo
10% sea water	3.60 °/oo
fresh water	0.25 °/oo

ENVIRONMENT OF THE ISOPODS

Most of the specimens used in this study were collected in the Second Sled Road area, Dillon Beach. This region is of the sort described by Ricketts and Calvin (1956) as a protected outer coast. The intertidal zone is very rocky; in many places a sandy substrate underlies the rocks. The beach is sandy with numerous rock outcroppings, forming a splash, or spray zone. The entire area is backed by steep sandstone cliffs.

The area is well suited for studying the transition being considered. This section of the California coast is characterized by heavy fog and high humidities, lessening the problem of desiccation. There is an annual rainfall of 31.65 inches, and the mean air temperature of the region is 52.4°F (Johnson, et al.). A relatively large tidal amplitude (maximum=approximately 3.3m.) is observed and makes the transition somewhat more gradual.

Cirolana harfordi is commonly found in the mid-tide regions and lower. Individuals are apparently never exposed, even in their upper limits. Allaanimals in this study were taken from under rocks, usually in sandy tide pools. This is a very protected habitat and the animals here are not subjected to wave shock, large temperature fluctuations or drastic salinity changes. Several temperatures taken throughout the year (June, 1960 - June, 1961) under rocks where this species was collected ranged from 12.5°C to 16.0°C. Salinity changes were very slight, ranging from about 32.5°/oo to 33.0°/oo. These temperature and salinity changes represent gradual variations, not rapid fluctuations in a short period of time. This information suggests that Cirolana harfordi must accomodate only to the changes in the physical and chemical properties of the intertidal water itself. Taylor (1956) reports an abundance of C. harfordi in mussel beds. They are apparently confined to the lower tide zones where large amounts of water are retained during times when the general area is exposed by the tides.

Kaster and Lee (1959) report that Idothea (Pentidotea) wosnesenskii is concentrated along the band of Porphyra perforata which runs parallel to the beach. This is in Zone 3 according to Ricketts and Calvin (1956), and is described as an area below mean sea level, largely uncovered by most low tides and covered by most high tides. All specimens of I. wosnesenskii used in this study were collected from this red alga. These animals were subjected to quite regular periods of exposure and immersion by the tides. This presents a much greater stress than is faced by Cirolana harfordi. Temperatures ranging from 12.5°C to 15.0°C were recorded in the algal curtains where

I. wosnesenskii was collected. This represents rapid changes with tidal fluctuation rather than long-range changes during the seasons. Although exposed by tidal action I. wosnesenskii was always found in relatively moist situations, provided by Porphyra perforata. The problems of land life are presented to this animal alternately with periods of immersion by the tides.

Mid-way in the series is Ligia occidentalis. Franco (1958) discusses the distribution of this species in the Dillon Beach region, and describes the habitat as high in the spray zone, or the uppermost regions of Zone I, according to Ricketts and Calvin (1956). This is generally a bare rock area, inhabited by semi-terrestrial organisms. In the Second Sled Road area Ligia occidentalis is usually found in cracks in the rock outcroppings along the beach. Temperatures in these microclimates appear to be somewhat more stable than exposed air temperatures. With heavy wind, an air temperature of 15.0°C was recorded while in the cracks where the animals were found the temperatures ranged from 17.5°C to 19.0°C. These temperatures were recorded in June, 1961. Such higher temperatures may be considered benificial in that they maintain a higher humidity. Under less windy conditions, and thus a lessened problem of desiccation, this species was observed on the sand, on exposed rock surfaces, and submerged in small pools in the rocks. In these areas air temperatures ranged from 11.5°C to 21.0°C. The temperature in the water where *L. occidentalis* was found was 11.5°C. The air temperature immediately above the pool was 12.5°C. This species appears to be able to tolerate rather rapid fluctuations in temperature; the major problem seems to be a necessity of remaining in areas of high humidities.

Jamison (1951) reports the habitat of *Alloniscus perconvexus* as being in damp, loosely packed sand, above or slightly below the berm. Individuals were commonly found burrowed to a depth of three to six inches, depending on the amount of moisture in the sand. They were most abundant under masses of algae that had been washed up on the beach. It is quite probable that their entire moisture supply is attained from the interstitial water in the sand. They are not very active animals and were never found in either very wet or very dry sand. Temperatures recorded in the sand from which *Alloniscus perconvexus* was collected ranged from 14.2°C to 15.5°C. Moisture content of this sand during the summer of 1960 ranged from 2.89% to 5.50%. This appears to be a rather stable habitat, for the animals were observed to migrate and avoid extremely wet or dry sand. The problem of desiccation is minimized and temperatures are quite stable in this moist environment.

Porcellio (*Porcellio*) *scaber* is completely divorced from the sea and is the most terrestrial of the species studied. These animals were collected from under boards and rocks about a quarter of a mile from the beach. These isopods may be found much farther inland, but all specimens used in this study were taken near the beach. Temperatures taken under objects where *P. scaber* was collected ranged from 16.0°C to 20.8°C. Taylor (1956) reports a slightly higher temperature range in this same area: 18°C to 22°C. Retention of moisture seems to be the major problem in this habitat. The microclimate where these animals were found was less subject to factors of desiccation than exposed habitats in the same area. As soon as cover was removed from *P. scaber* they immediately moved toward protected areas. This activity was also reported by Taylor (1956).

Cirolana harfordi, *Alloniscus perconvexus* and *Porcellio* (*Porcellio*) *scaber* were usually found in aggregations. That is, in the case of *C. harfordi*, large numbers would be found under one rock, while under another rock in the same area they might have been completely absent. *A. perconvexus* were found to be congregated in groups in the sand under patches of algae while in the surrounding area they may not have been found at all. *P. scaber* exhibited the same type of grouping under boards and rocks. *Idothea* (*Pentidotea*) *wosnesenskii* appeared to be rather evenly distributed throughout the beds of Porphyra perforata. Groups of more than two or three individuals of Ligia occidentalis were rare and the animal was usually encountered singly.

ADAPTIVE MORPHOLOGY AND BEHAVIOR

There are several features of isopods which facilitate the transition from a marine to a terrestrial habitat (Figure 9, Appendix I). They are dorso-ventrally flattened, which allows the intermediate and terrestrial forms to locate themselves in narrow, moist areas, thus minimizing exposure to factors of desiccation. The respiratory appendages of most crustaceans are branches of the peraeopods; while in the isopods the gills are formed from the pleopods, or abdominal appendages. The ventral location of the gills allows for more protection of the respiratory surfaces from exposure and subsequent drying. The chitin of the pleopods is thin enough to allow diffusion of gases even in some of the more terrestrial forms. Most of the isopods which have become adapted to aerial respiration have pleopods equipped with thick outer branches, or exopodites, which serve as a protective covering over the thinner endopodites. The respiratory surfaces are kept moist by environmental moisture, aided by glandular secretions (Abbott, 1940). The chitin over the entire body aids in preventing water loss, and generally isolating the internal fluids from the environment. In the more terrestrial species the chitin is thicker than the marine forms. The legs of all isopods are relatively large and sturdy, enhancing their ability to adapt to walking on land. One very important characteristic of the isopods which has greatly aided their transition to land is their method of reproduction. Unlike many of the crustacean groups there are no free-swimming larval stages in the isopods. The young develop completely in the brood pouch formed by the oostegites along the abdomen of the female. Thus the isopods do not need the depending on the sea for any part of their life cycle.

Cirolana harfordi shows no adaptations to land other than those general characteristics displayed by all isopods. Its chitin is quite thin compared to the more terrestrial forms and the pleopods are thin and highly motile (Figure 1). Apparently both the exopodite and the endopodite serve in respiration. The first three pairs of legs are prehensile, and the last four pairs are ambulatory (Richardson, 1950). Due to this structural situation these animals are able to cling to rock surfaces and also move about with a gliding motion when water is present on the substrace. They find difficulty moving on dry surfaces, apparently due to the buoyancy problem. The pleopods are also well adapted to swimming. This species exhibits excellent protective coloration and blends as a mottled gray color with the substrate.

Idothea (Pentidotea) wosnesenskii shows some major adaptive characteristics in the transition toward land.

Its exoskeleton is much thicker than that of *Cirolana harfordi* tending to lessen the problem of desiccation. The exopodites of the pleopods are still quite thin and characteristic of the more marine forms (Figure 2a). The main modification is the respiratory structures in the form of pleopod covers formed by the margins of the valve-like uropods (Figure 2b). During periods of exposure by the tides these covers apparently form a small chamber in which water is retained for respiratory purposes. When the animals are covered by water the pleopod covers are opened and the gills beat in a similar manner as was described for *Cirolana harfordi*. This is theobnly species studied that possesses these covers. Although *I. wosnesenskii* is rather inactive the pleopods were observed to be used for swimming when the animals were submerged. The legs have terminal, hooked-shaped spines which aid in attachment to the thalli of *Porphyra perforata*. They tend to remain under the algal curtains when exposed, thus utilizing the moisture retained by the alga. Protective coloration is very common and the individuals tend toward the color of the algae upon which they are found. This is usually reddish-brown, borwn or green.

Considered mid-way in the transition is *Ligia occidentalis*. This species spends most of its time out of water and exposed to aerial conditions. The chitin is quite thick but very pliable which allows for rapid movement and aids in entering small cracks and crevices. The pleopods are suited to both aquatic and aerial respiration. Under water the gills beat in much the same manner as observed in the more marine forms, while on land the pleopods are held tight against the abdomen. The exopodite forms a rather thick, protective shield over the thinner endopodite. This reduces water loss from the respiratory surfaces (Figure 3). *L. occidentalis* is generally somewhat larger than the more marine forms and swimming by means of pleopodal action is not common. This isopod, however, is very active on land and rapid movement is easily observed. All seven pairs of legs are ambulatory (Richardson, 1905). It is necessary for the pleopods to be moist for respiration to be accomplished. In addition to glandular secretions the pleopods are moistened in a very interesting manner. This activity was observed during this study and has been also reported by several other investigators. Upon reaching water the animal first appears to "test" the water with its antennae, then reverses its position and immerses the tips of the uropods (not shown in Figure 3b). By bringing the spines together a capillary tube is formed which draws a droplet of water up and onto the pleopods. When an individual leaves the water after being completely submerged the abdomen is raised and lowered several times, apparently to remove excess water from the gills, for diffusion of atmospheric respiratory gases would be more efficient through a thin film of water than through a large drop of liquid. On warm days, with bright sun and low humidities, *L. occidentalis* tends to remain in shaded areas. Most of the specimens were found in cracks in rocks. Such behavior is most certainly a method of preventing desiccation. This species is reported bo be very active at night when desiccation is at a minimum (Abbott, 1940). Nocturnal activity enables the animals to feed on materials on the beach with little stress. Abbott (1940) reports *L. occidentalis* as displaying a positive hydrotaxis in that they may respond to low tides and move with the receding water. If, however, they are in an adequately moist place when low tide occurs they do not move with the water. The above mentioned behavioral features were all observed during this present study. The dipping of the uropods was also observed under laboratory conditions. The coloration of *L. occidentalis* is adaptive, varying from tan to dark gray and blending with the rocks.

Alloniscus perconvexus is a smaller isopod than *Ligia occidentalis* and is well adapted to its burrowing activity. They are less flattened than the other isopods studied and have a very thick chitin, giving them a robust appearance. Their legs are all ambulatory and are covered with stiff hair-like structures (Richardson, 1905). These appendages aid the animals in digging into the sand. They exopodites of the pleopods are quite thick and form a protective covering over the endopodites (Figure 4). Richardson

(1905) reports primitive air sacs on the pleopods of A. perconvexus used for aerial respiration; these structures are very inconspicuous and were not noted during this present study. Their tendency to remain in the sand under algal mats illustrates their attraction toward water. They do not ever remain in very wet sand, and apparently never enter the water. These animals are generally of a mottled coloration blending with the sand.

Porcellio (Porcellio) scaber was the most terrestrial species studied. Again the thickness of the chitin tends to aid the animal in preventing desiccation on land. Primitive tracheal organs, termed "white bodies" are developed on the exopodites of the first two pairs of pleopods (Figure 5). These "white bodies" are by no means as advanced as the tracheal organs of the insects. There is only one opening in the surface of each pleopod. It is necessary for the trachea of isopods to be bathed in a respiratory fluid for gaseous exchange to take place. The air passages do not extend into the body proper of the isopods, but terminate in the pleopods themselves. The remaining three pairs of pleopods are thinner and apparently serve very little, if any, respiratory function. Dependance of P. scaber on these tracheal organs was illustrated by removal of various pleopods and noting their survival times in a relatively low humidity (25-30% R.H.). Three groups of test animals and a control group were observed and the following data were obtained.

Group A. (six specimens) In this group the first two sets of pleopods were removed (all tracheal organs), and the last three left intact.

Group B. (six specimens) The last four pairs were removed and the first set of tracheal organs were left intact.

Group C. (six specimens) The last three pairs were removed leaving the first two (all tracheal organs) intact.

Group D. (ten specimens) No pleopods were removed

Group	50% death time
A	1 hr.
B	2.25 hr.
C	10 hrs.
D	12 hrs.

Similar results were published by Miller (1938). Some body fluid was lost in dissection, which may have lowered survival times to some extent in groups A, B and C.

All the legs of Porcellio scaber are ambulatory and facilitate rapid movement (Richardson, 1905). These animals tend to congregate under objects, reducing the effect of desiccation.

Figure 1. (a) Second right pleopod of <u>Cirolana harfordi</u> removed from the animal (exopodite and endopodite).

(b) Arrangement of pleopods of the abdomen of <u>Cirolana harfordi</u>.

Figure 2. (a) Second right pleopod of <u>Idothea wosnesenskii</u> removed from the animal (exopodite and endopodite)

(b) Arrangement of pleopods on the abdomen of <u>Idothea wosnesenskii</u>; one pleopod cover has been removed.

Figure 3. (a) Second right pleopod of <u>Ligia occidentalis</u> removed from the animal (exopodite and endopodite)

(b) Arrangement of pleopods on the abdomen of <u>Ligia occidentalis</u>.

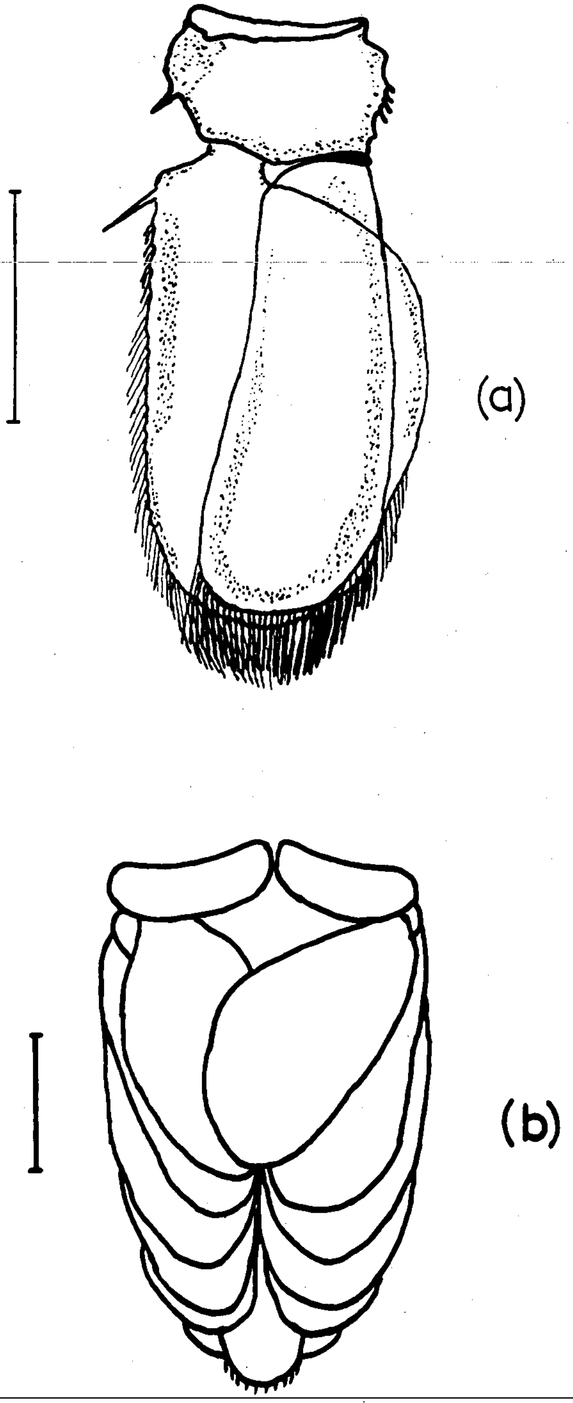
Figure 4. (a) Exopodite of second right pleopod of <u>Alloniscus perconvexus</u> removed from the animal.

(b) Arrangement of pleopods on the abdomen of <u>Alloniscus perconvexus</u>.

Figure 5. (a) Exopodite of second right pleopod of <u>Porcellio scaber</u> removed from the animal. Darkly stipled area represents tracheal organs.

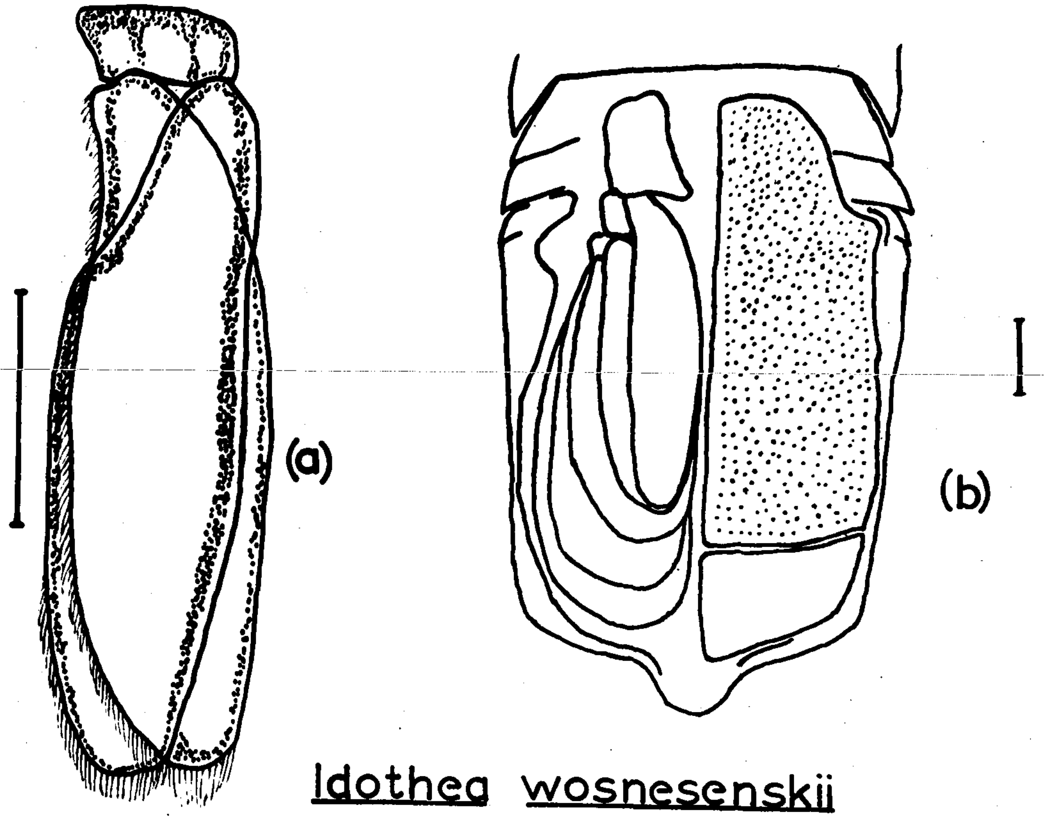
(b) Arrangement of pleopods on the abdomen of <u>Porcellio scaber</u> showing tracheal organs on first two pairs of pleopods.

Figure 1.

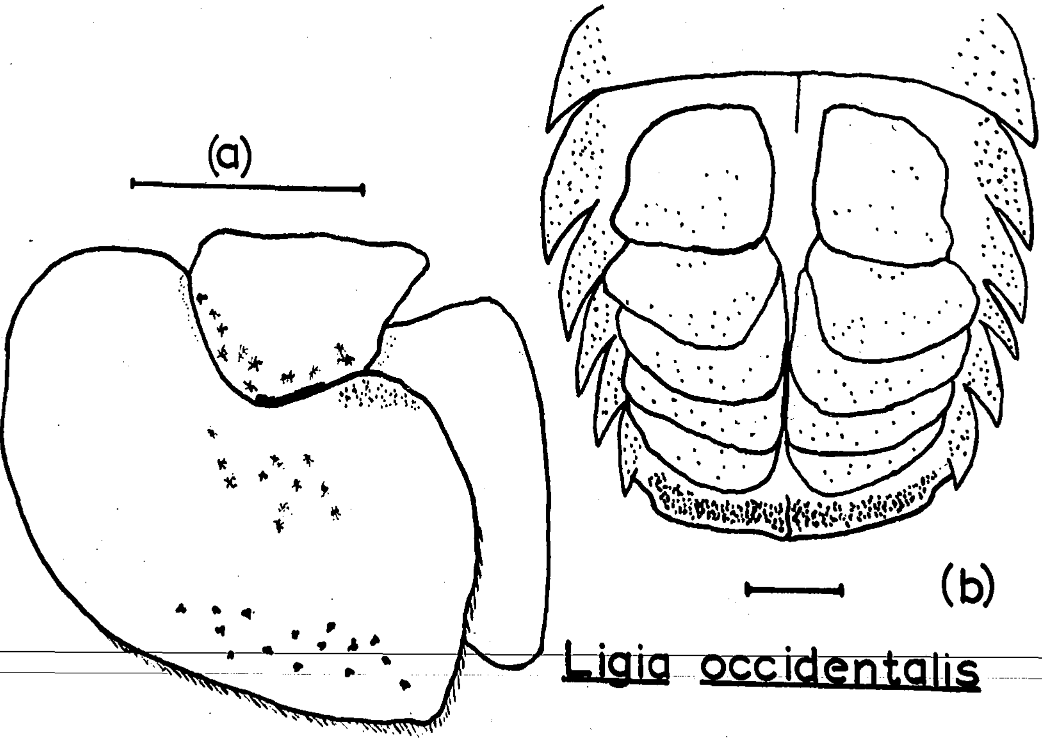


Cirolana harfordi

Figures 2&3

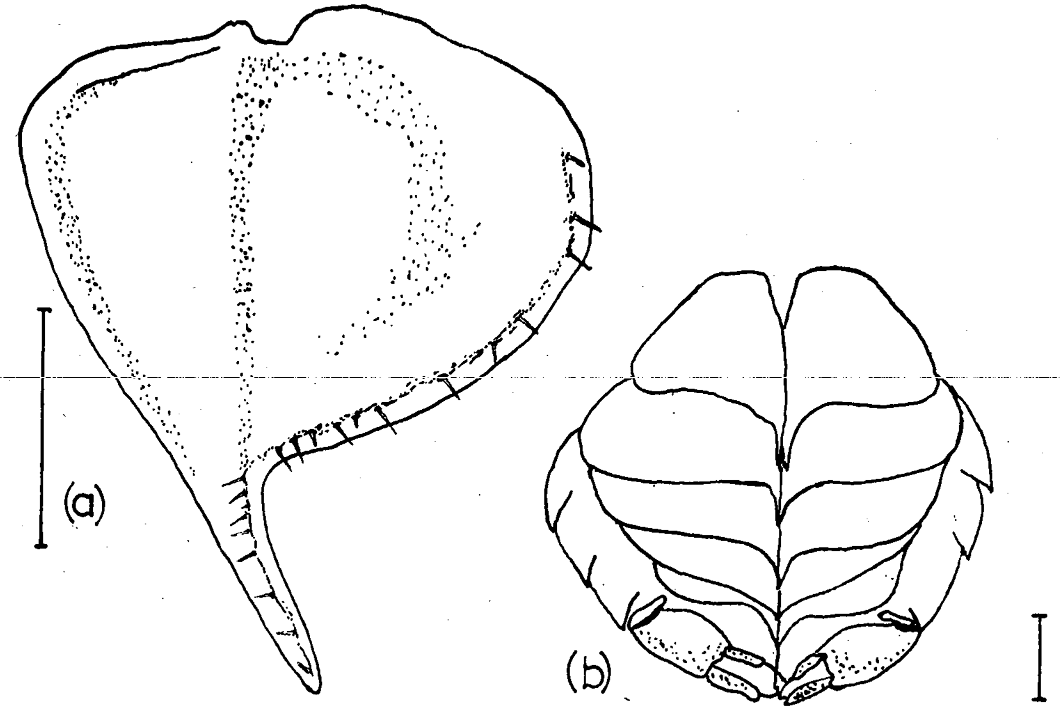


Idothea wosnesenskii

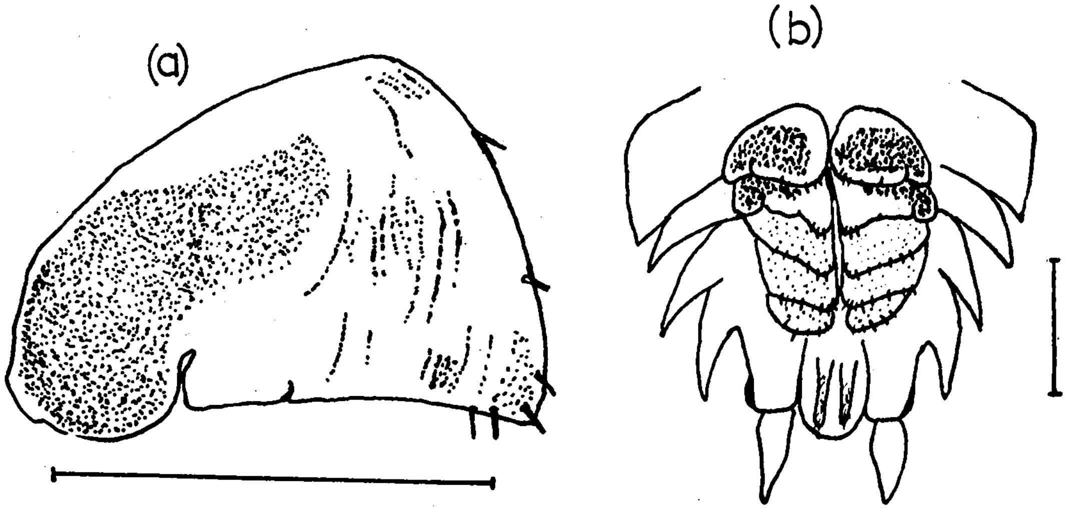


Ligia occidentalis

Figures 4&5



Alloniscus perconvexus



Porcellio (Porcellio) scaber

DISCUSSION OF PHYSIOLOGICAL DATA

There are many more factors involved in the physiological adaptations of isopods to land than are included in the experimental work of this study. Some of these problems are mentioned here as a basis for consideration of the whole problem of the transition from a marine to a terrestrial habitat.

In the more terrestrial arthropods such as insects, uricotelism is the main form of nitrogenous excretion. Most marine animals are ammonotelic. It is interesting to note that the isopods do not conform to this typical transformation of excretory products. Uricotelism is advantageous to life on land in that it aids in conserving water, but the isopods have remained ammonotelic. It is though by Dresel and Moyle (1950) that the main adaptation of the isopods to land, as far as excretion is concerned, may have taken the form of a general reduction in nitrogen metabolism, rather than a conversion to uricotelism. (Edney, 1957). They also report that the advanced terrestrial form Armadillidium sp. excretes nearly 10% of its nitrogenous wastes in the form of uric acid. Marine forms are considered not to excrete any appreciable amounts of uric acid. It should be considered that possibly the situation is one of a tolerance to ammonotelism during a period of slow transformation to uricotelism.

Cuticular permeability plays an important role in the rate of transpiration from body surfaces. Bursell (1955) found that terrestrial isopods have the ability to change the permeability of their cuticle when excess transpiration threatens. This is thought to be the reason for the absence of a "critical temperature" for isopods in regards to transpiration (Edney, 1957).

The problem of osmoregulation was studied in this work in the form of salinity and humidity tolerance determinations. Results of the experimental work is shown graphically in Figures 6, 7 and 8; tabular recorded data is presented in Appendix I.

In both summer and winter determinations of salinity tolerances, Cirolana harfordi and Idothea wosnesenskii are clearly defined as basically marine, aquatic forms. I. wosnesenskii did show somewhat higher tolerances to reduced salinities which may be a reflection of the fact that during periods of exposure by low tides this species must be adapted to lowered salinities in the form of rain and fog. Although summer and winter populations showed very similar relative survival times, some differences in the recorded death times can be seen. For example, C. harfordi showed slightly higher tolerances to lowered salinities in the summer than in the winter. Although these differences are rather constant within any one species, they may be a product of small sample size rather than any indication of seasonal changes in the enrivonment. It is the opinion of this investigator that I. wosnesenskii occupies the region of highest stress in the transition from sea to land. It is in this area that the major changes and adaptations to land life must be made in order to move any farther.

Ligia occidentalis displays an interesting, somewhat intermediate, set of salinity tolerances. They are commonly in contact with only 100% sea water and, accordingly, show a high tolerance to this situation. In salinities lower than 75% sea water their survival times drop rapidly. This suggests that this isopod is not leaving the sea through lowered salinities. That is, they are probably not leaving the sea via esturine conditions as is the common route in transitions from marine habitats.

Due to a lack of specimens during the winter months, Alloniscus perconvexus was only tested in the summer. Their highest survival times were obsered in the 50% and 75% sea water solutions. Heavy fog and fresh water runoff prevails in the Second Sled Road area where these animals were collected. The interstitial water is quite probably of a lower salinity than 100% sea water. Although a 50% death time was not noted in the 100% sea water test, two of the specimens had died at the end of the 48 hour observation period. Even in the 50% and 75% solutions the animals were not very responsive to stimulation at the end of the test, illustrating that this species is not adapted to complete submergence. Lowered survival times in very low salinities indicate, again, the non-esturine type of transition.

The low survival times of Porcellio (Porcellio) scaber in all aquatic situations illustrates the terrestrial habitation of this species. The highest tolerances for summer populations were observed in 50% and 75% sea water solutions, similar to the tolerances shown by Alloniscus perconvexus. Winter populations showed lowered survival times in all experimental solutions.

The training of Cirolana harfordi to lowered salinities was done in an attempt to illustrate the ability of the isopods, as a marine group, to adjust to new environmental conditions. With reference to Table IV, Appendix I, one sees that by slowly lowering the salinity of the water a much longer survival time was attained in 30% sea water than when the animals were placed directly from 100% to 30% sea water. When the animals were replaced into 100% sea water those that had been "trained" to the 30% solution died very quickly, while of those that were placed directly into 30%, two lived 10 hours and the third recovered completely. This may indicate that the animals not only gained the ability to survive in the normal situation. This suggests that re-invasion of the sea by terrestrial organisms might be as difficult as the original migration from the sea to land. It can be seen by comparing Groups A and B that a protracted "training period" is necessary for complete adaptation to lowered salinities. Migration to land, of course, involves a great deal more than the problem of osmotic stress.

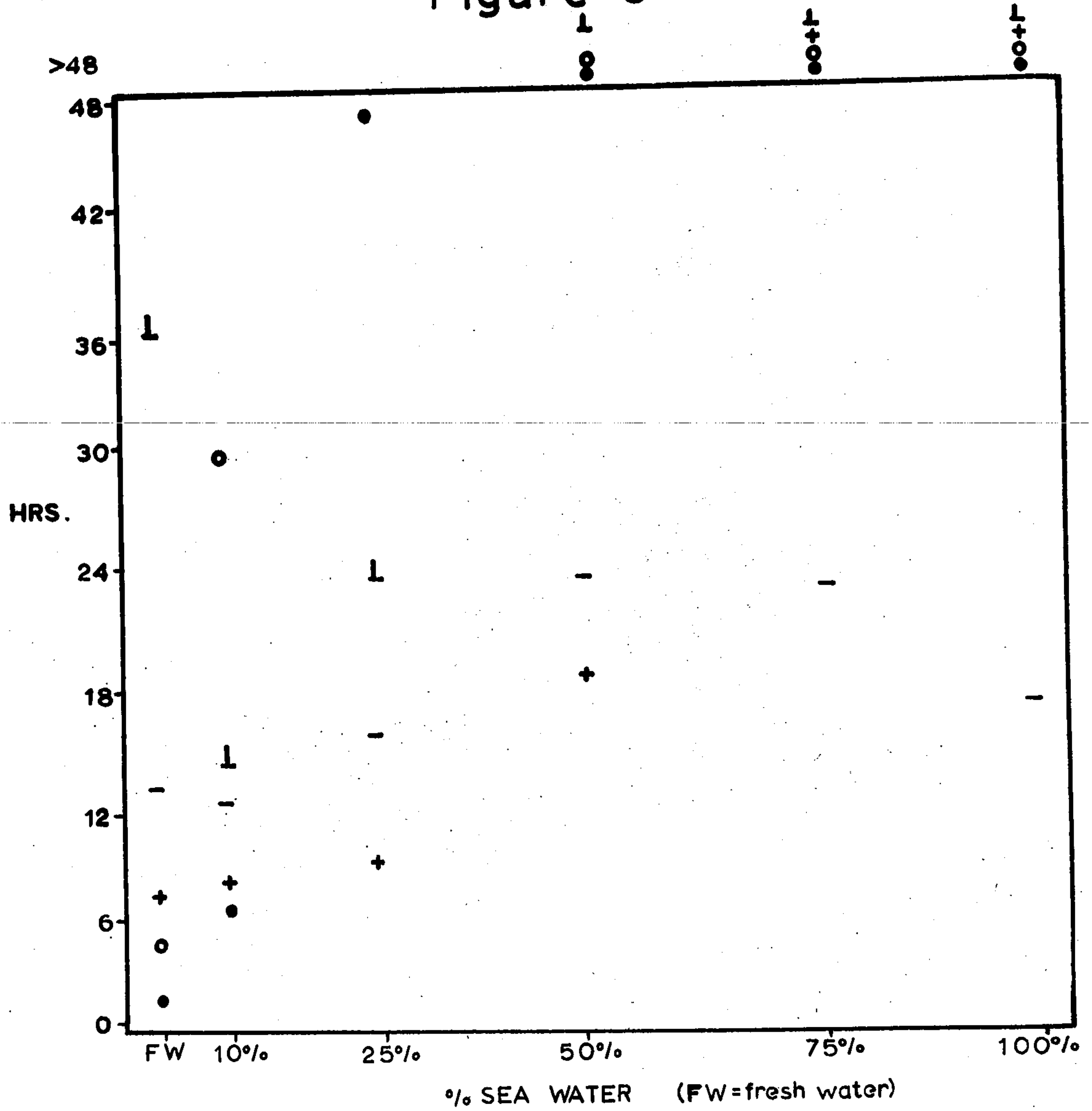
Table III, Appendix I is a record of the humidity tolerances of three of the isopods studied in this work. Cirolana harfordi, Ligia occidentalis and Porcellio (Porcellio) scaber were used to illustrate tolerances of isopods in three general areas of the transition. C. harfordi showed an expected range of tolerances, with very low survival times in the less humid situations and a steady increase in survival times with an increase in humidity. Abbott (1940) concluded that the intermediate forms in the transition show a controlling influence over the humidity. This is probably a tolerance to lowered humidities accomplished by changing the permeability of their cuticle. This present study indicates that this ability is limited to short periods of time, but that L. occidentalis does show fairly high survival times in all humidities. Porcellio scaber was the most terrestrial species subjected to the humidity tolerance tests. In its natural habitat it does, of course, encounter much lower humidities than the other species. From the data obtained it can be seen that P. scaber has adapted to such situations. Isopods are not capable of extracting water vapor from air that is not very near saturation (Edney, 1957). The increased survival times in higher humidities may, then, be due to an increased ability to retain body water, rather than a utilization of moisture from the air.

In these experiments size and sex were recorded for each animal than died during the first set of tests. No juvenile forms were used and size did not seem to be related to death times. Death was influenced by sex only in the case of gravid females which appeared less able to tolerate any adverse conditions than the others.

Contols were observed during the tests by placing a group of animals in a medium as near the natural situation as possible at the same temperature to which the test animals were being subjected. No deaths were noted in the controls during any of the experiments.

Another simple control method was employed in the form of a small "laboratory pool". An environment was prepared having water, exposed sand, Porphyra perforata at the edge of the water, and rocks in the sand. The purpose of this pool was to observe if the animals of each species would arrange themselves, under laboratory conditions, as they did in their natural environment. Two specimens of each species were placed in the pool. Both individuals of Cirolana harfordi immediately entered the water and burrowed in the sand, completely submerged. The specimens of Idothea wosnesenskii both ttached to the pieces of P. perforata at the edge of the water. Ligia occidentalis, which had been kept in a dry situation for a few hours, exhibited the process of dipping their uropods into the water after testing it with their antennae; then they retreated to the upper area of the sand and located themselves on the rocks. Both specimens of Alloniscus perconvexus burrowed about 15 inches into the sand in the driest area; they did not prefer the very wet sand. The specimens of Porcellio scaber continued to wander about at the upper edge of the pool area, apparently seeking drier conditions. Thus the animals did tend to arrange themselves in the laboratory as in their natural habitats.

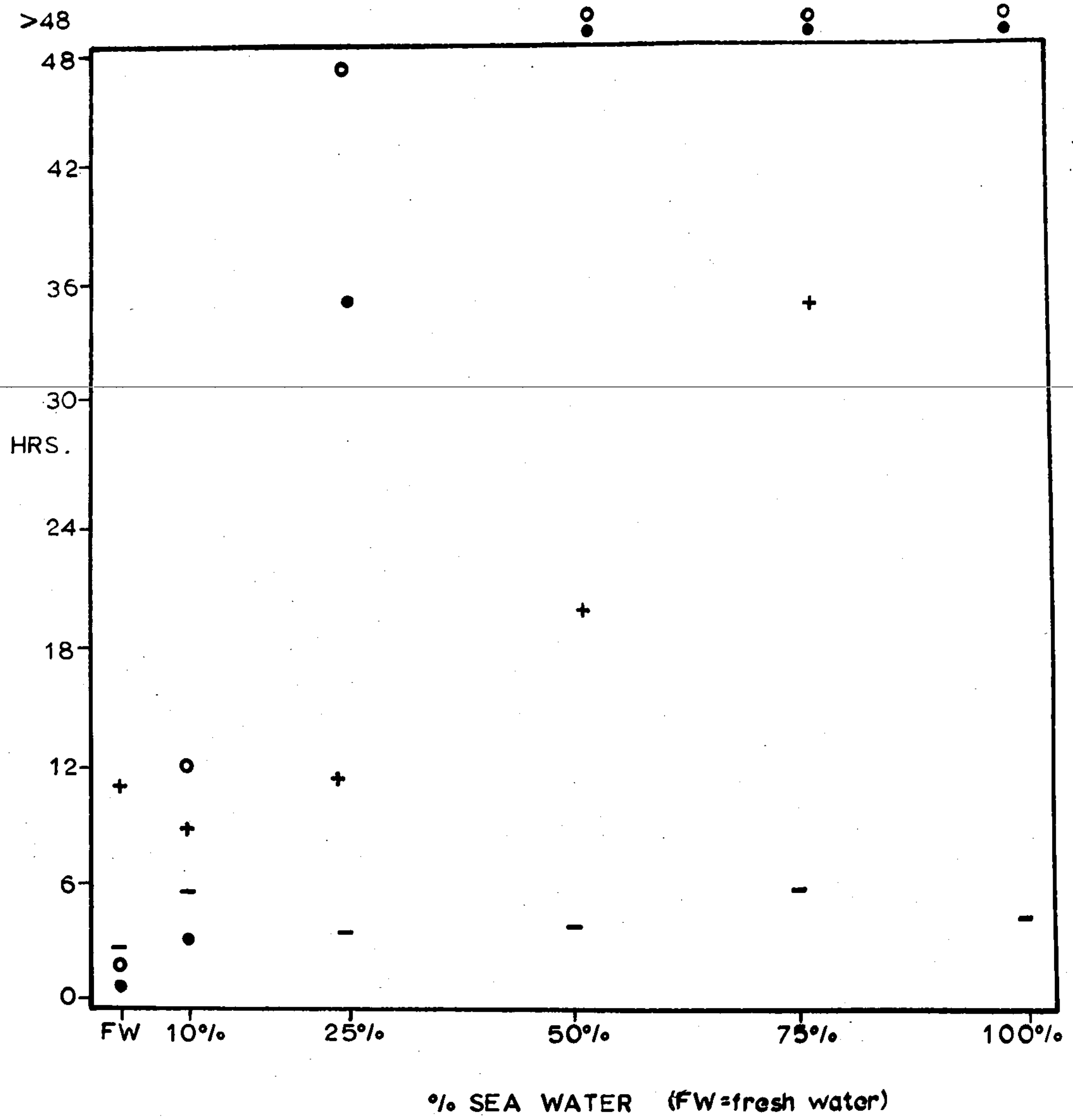
Figure 6



50% DEATH TIMES.
SALINITY TOLERANCES OF
SUMMER POPULATIONS

Cirolana harfordi ●
Idothea (Pentidotea) wosnesenskii ○
Ligia occidentalis +
Alloniscus perconvexus ⊥
Porcellio (Porcellio) scaber –

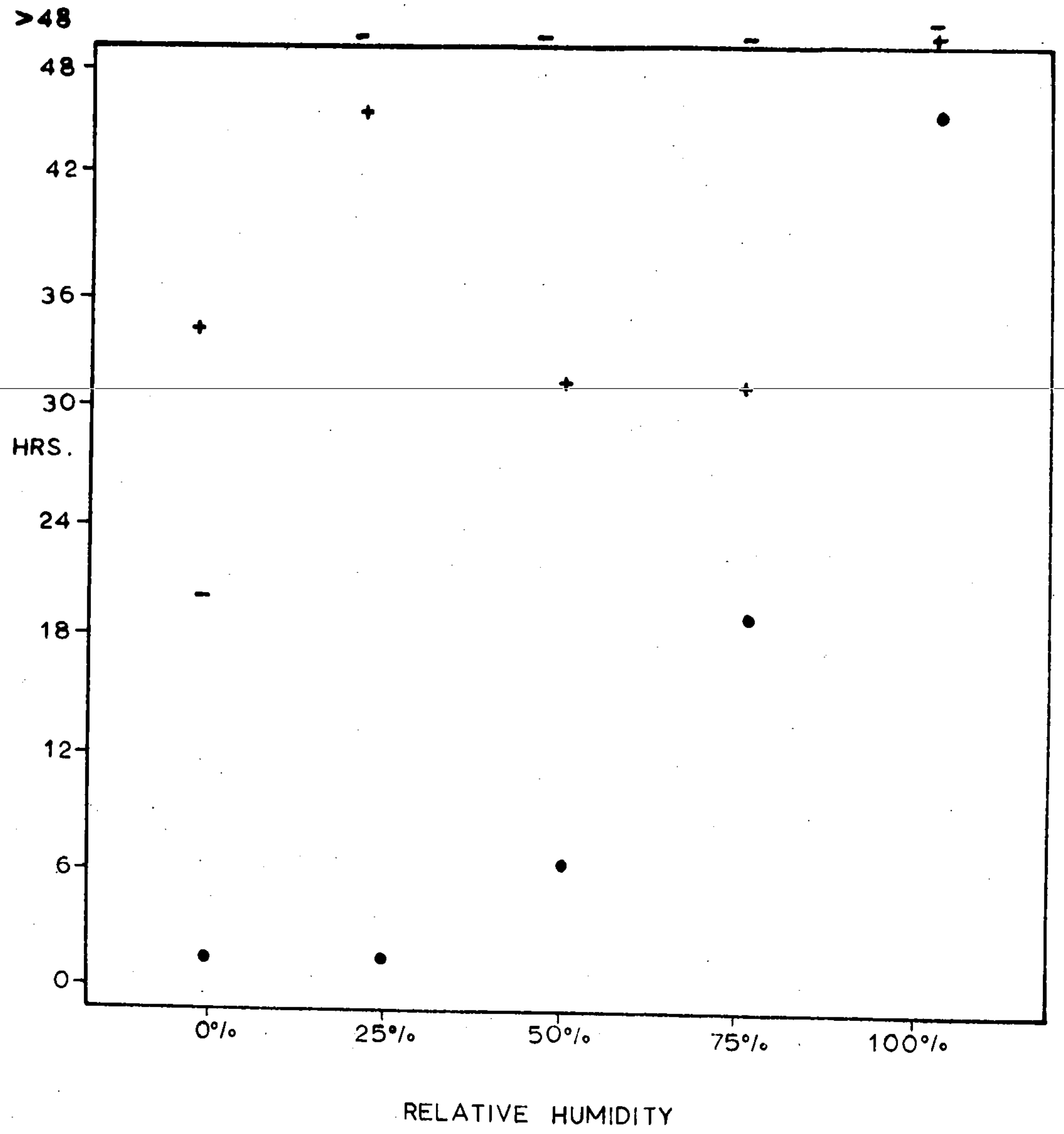
Figure 7



50% DEATH TIMES
SALINITY TOLERANCES OF
WINTER POPULATIONS

Cirolana harfordi ●
Idothea (Pentidotea) wosnesenskii ○
Ligia occidentalis +
Porcellio (Porcellio) scaber –

Figure 8



50% DEATH TIMES.
HUMIDITY TOLERANCES OF
SPRING POPULATIONS

Cirolana harfordi ●
Ligia occidentalis +
Porcellio (Porcellio) scaber –

SUMMARY

The purpose of this study is to illustrate the transition of isopod crustaceans from a marine to a terrestrial habitat. Of the many factors involved in such a transition a few were considered in this study. Five species of isopods were used representing different levels in the transition. A discussion of the ecology of each animal and the problems met in the various situations provides a basis for interpretation of the data presented. Morphological and behavioral adaptations are considered and related to the problems of the different habitats. Salinity tolerances and humidity tolerances were determined and used to illustrate the physiological adaptations to the problem of osmoregulation. The training of *Cirolana harfordi* to lowered salinities was attempted and illustrates the ability of the isopods, as a marine, aquatic group, to adapt physiologically to a long-range process of environmental change.

The information presented in this paper does define the isopods as a group which is engaged in the transition discussed. The species at different levels in the migration clearly display adaptations to their specific environmental problems.

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BIBLIOGRAPHY

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Appendix I

TABLE I

Recorded here are the salinity tolerances of summer populations. All experiments were conducted over a 48 hour period. (48+) indicates that a 50% death time was not observed during this period. Graphic representation is shown in Figure 6.

Organism	Number Individuals	Medium	50% Death Time
Cirolana harfordi	6	FW	1 hr.
	6	10% SW	7 hrs.
	6	25% SW	46 hrs.
	6	50% SW	(48+)
	6	75% SW	(48+)
	6	100% SW	(48+)
Idothea wosnesenskii	6	FW	4 hrs.
	6	10% SW	29 hrs.
	6	25% SW	(48+)
	6	50% SW	(48+)
	6	75% SW	(48+)
	6	100% SW	(48+)
Ligia occidentalis	6	FW	7 hrs.
	6	10% SW	8 hrs.
	6	25% SW	9 hrs.
	6	50% SW	19 hrs.
	6	75% SW	(48+) (2 dead)
	6	100% SW	(48+)
Alloniscus perconvexus	6	FW	37 hrs.
	6	10% SW	15 hrs.
	6	25% SW	24 hrs.
	6	50% SW	(48+)
	6	75% SW	(48+)
	6	100% SW	(48+) (2 dead)
Porcellio scaber	6	FW	14 hrs.
	6	10% SW	13 hrs.
	6	25% SW	16 hrs.
	6	50% SW	24 hrs.
	6	75% SW	23 hrs.
	6	100% SW	17 hrs.

FW = fresh water

SW = sea water

TABLE II

This table is a record of the salinity tolerances of winter populations, collected in the same area as those animals used in determining tolerances of summer populations. For a graphic interpretation of this data refer to Figure 7.

Organism	Number Individuals	Medium	50% Death Time
Cirolana 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.
	6	75%SW	5.5 hrs.
	6	100%SW	4 hrs.

Due to the lack of available specimens *Alloniscus perconvexus* was excluded from this series of determinations.

TABLE III

These are the humidity tolerances recorded for spring populations. Again, these animals were collected in the same area as those used in the other determinations. This data is presented in graphic form in Figure 8.

Organism	Number Individuals	Rel. hum.	50% Death Time
Cirolana harfordi	6	00.0%RH	2 hrs.
	6	25.0%RH	2 hrs.
	6	50.0%RH	6.5 hrs.
	6	75.0%RH	20 hrs.
	6	100.0%RH	45 hrs.
Ligia occidentalis	6	00.0%RH	34 hrs.
	6	25.0%RH	46 hrs.
	6	50.0%RH	32 hrs.
	6	75.0%RH	32 hrs.
	6	100.0%RH	(48+)
Porcellio scaber	6	00.0%RH	20 hrs.
	6	25.0%RH	(48+)
	6	50.0%RH	(48+)
	6	75.0%RH	(48+)
	48	100.0%RH	(48+)

Only the three above species were tested as to humidity tolerances. They are used to illustrate tolerances at the early, mid, and late stages of the transition.

TABLE IV

An attempt was made to train *Cirolana harfordi* to lowered salinities to illustrate the ability of the aquatic, marine isopods to adapt in a transition from one environment to another. Three groups were tested; below are the times each was left in various salinities in the training process.

Group A (5 individuals)

100% SW	24 hrs.
90% SW	25 hrs.
80% SW	23 hrs.
70% SW	65 hrs.
60% SW	28 hrs.
50% SW	84 hrs.
40% SW	175 hrs.
30% SW	93 hrs.

Group B (5 individuals)

100% SW	24 hrs.
75% SW	25 hrs.
50% SW	23 hrs.
25% SW	17 hrs.

Group C (6 individuals)

100% SW	24 hrs.
30% SW	30 Hrs.

Group A: Bunching or grouping of the animals was noted in the 50% sea water solution. In 40% sea water one gravid female died after 72 hours. After 93 hours in 30% sea water another gravid female died; the remaining three specimens were replaced directly into 100% sea water. These all died within 1 hour.

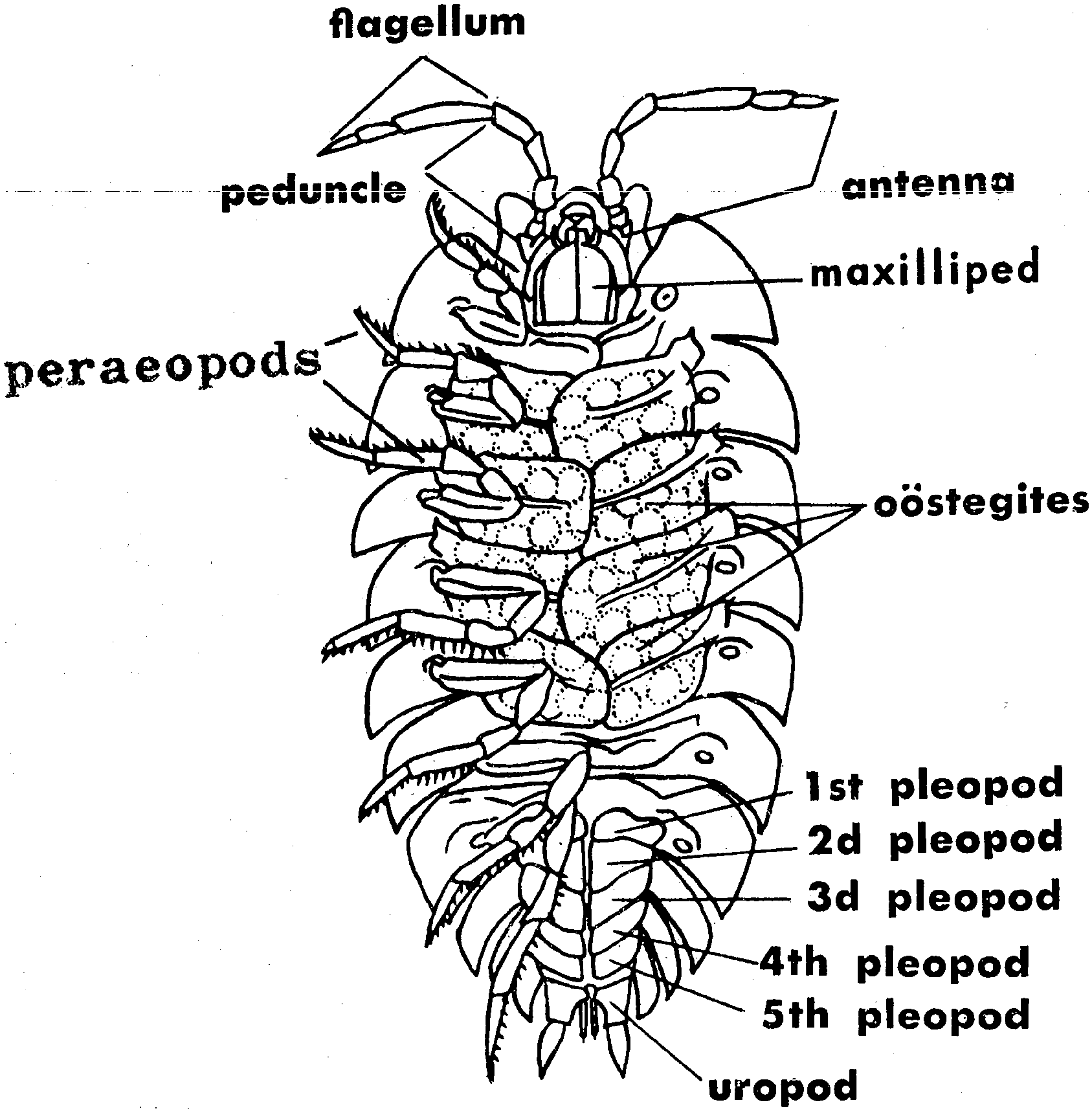
Group B: All individuals died after 17 hours in 25% sea water.

Group C: These animals were placed directly from 100% sea water into 30% sea water. A 50% death time was noted in 50 hours. The remaining animals were replaced directly into 100% sea water. Two of the specimens survived for 10 hours, the third recovered completely. All of the isopods used in the above experiment were collected at the same time and in the same area.

EXPLANATION OF FIGURE 9

This figure shows a ventral view of a female isopod (*Porcellio scaber*), modified from Light (1957).

Figure 9


flagellum
peduncle
antenna
maxilliped
peraeopods
oöstegites
1st pleopod
2d pleopod
3d pleopod
4th pleopod
5th pleopod
uropod