Notes on the Ecology and Environmental Adaptations of the Terrestrial Amphipoda[1]

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OF THE FEW CRUSTACEAN groups which have achieved some degree of freedom from the marine or freshwater environment, the Amphipoda have received least attention. The terrestrial Talitridae, to which family all of the terrestrial species belong, have been treated in various systematic papers but there is little else. The only nonsystematic work, to my knowledge, is contained in no more than four papers, those of Grimmett (1926), Birch and Clark (1953), Lawrence (1953), and Clark (1955).

Reasons for this neglect are not hard to find. The distribution of the terrestrial species is limited to countries bordering the Indian and Pacific oceans and to the Pacific islands (Fig. 1). In these countries development of zoological studies along other than descriptive lines is relatively recent. It would not be unreasonable to suggest that only South Africa, Australia, and New Zealand have a terrestrial amphipod fauna of sufficient extent and variety to attract attention to their ecology and physiology. And, as Dresel and Moyle (1950) have commented, and I can confirm, the mechanical problems involved in experimental work with the Talitridae are considerable, due in particular to their very great agility and to their susceptibility to dessication. This probably accounts for a general neglect of physiological work, even on littoral amphipods, when compared to the body of research on the closely related Isopoda.

Certainly, the difficulties in collecting terrestrial amphipods are reflected in the two or three species previously described from New Zealand, in contrast to some 40 species or more of terrestrial Isopoda. These difficulties have been overcome to some extent in recent years by modern methods of collecting, and many of the observations made in this paper have resulted from the study of Berlese Funnel material.

Considering the limited systematic work on terrestrial amphipods and the resultant lack of appreciation of their importance in the cryptozoic fauna, one might reasonably expect other research to be somewhat delayed. Nevertheless, there is an open field in Pacific countries for studies on the ecology and physiology of terrestrial amphipods, particularly in relation to soil formation. Such studies, in association with work on other cryptozoic groups, e.g., millipedes and isopods, would be of considerable value in understanding the conversion of leafmould and litter of Pacific forests into highly productive soil.

The abundance of the cryptozoic fauna is often not fully realised. In one particular instance, the animals in a bag of leafmould of less than one cubic foot capacity from Stephens Island, New Zealand, more than half filled a 2-ounce jar, the bulk of weight being made up of a relatively small amphipod, *Orchestia rubroannulata*. Similar large yields of *Talitrus sylvaticus* have been taken under hedges of African boxthorn and other plants in Taranaki, New Zealand.

The abundance of *Talitrus sylvaticus* has also been noted in Australia, where it is widespread in tropical and subtropical rainforests. "In some rain forests near Sydney we have

DISTRIBUTION OF
TERRESTRIAL AMPHIPODA
(CLASS CRUSTACEA :
FAMILY TALITRIDAE)
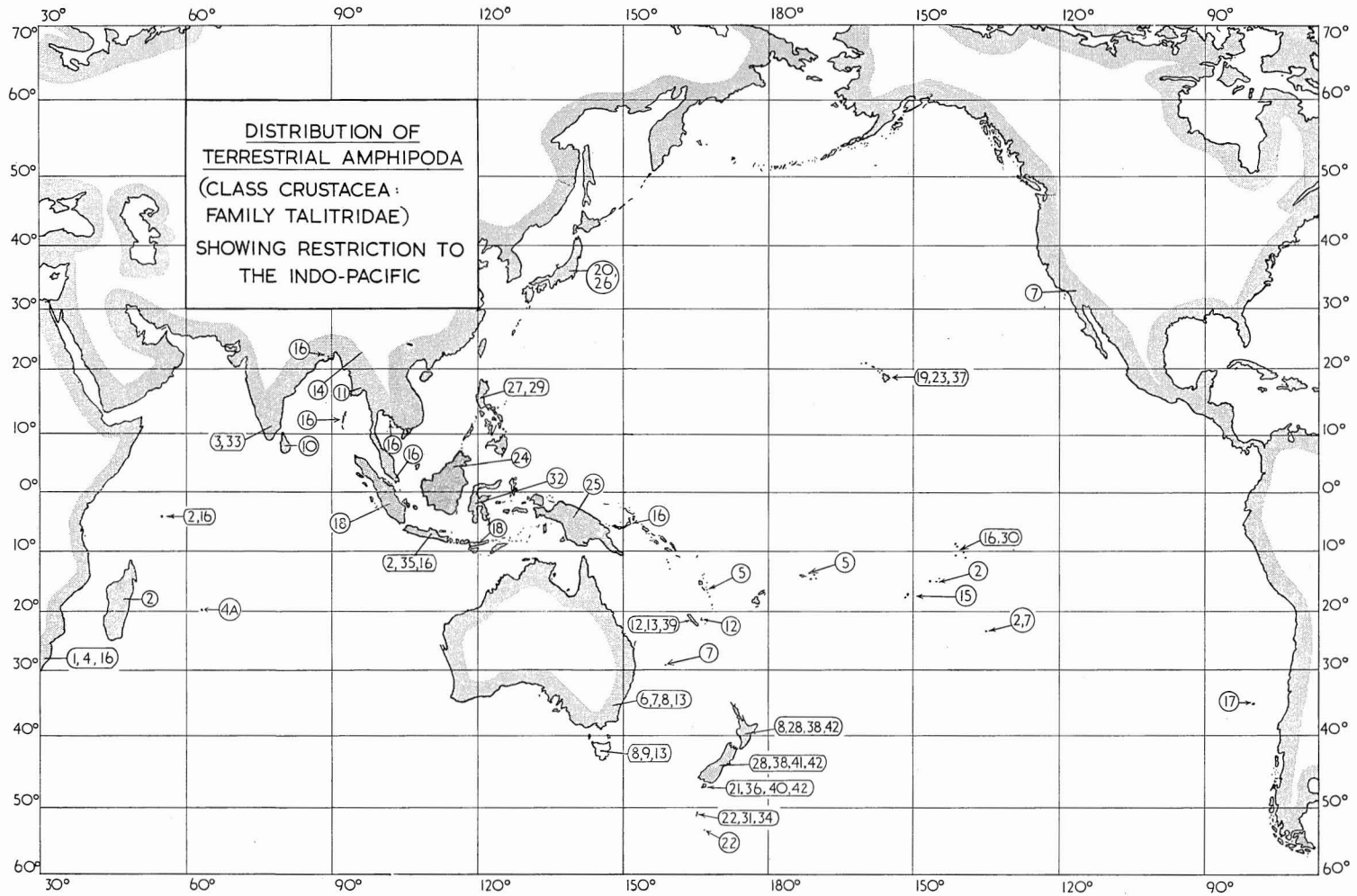SHOWING RESTRICTION TO
THE INDO-PACIFIC

FIG. 1. Distribution of terrestrial Talitridae. A general map based mainly on the literature to show their restriction to the Indo-Pacific. Misidentifications may contribute to the wide distribution of a few species, e.g., *Orchestia anomala* (16).

The literature references are to papers giving summary and more recent distributional data. This information is not necessarily complete.

1.	*Talitrus africanus*	South Africa (K. H. Barnard, 1940).
2.	*Talitrus alluaudi*	Seychelles, Madagascar, Java, Tuamotus, Gambier Archipelago, (Stephensen, 1935). Greenhouses and botanical gardens: Belgium, France, Monaco, Switzerland, Germany, Denmark, Hungary, British Isles, Sweden (Shoemaker, 1936; Stephensen, 1935); Czechoslovakia (Cerny and Straskraba, 1957?); U.S.A. (Shoemaker, 1936); U.S.A. and Canada (Medcof, 1939).
3.	*Talitrus decoratus*	Nilgiris, India (Carl, 1934).
4.	*Talitrus eastwoodae*	South Africa (K. H. Barnard, 1940).
4a.	*Talitrus gulliveri*	Annobon Island, Rodriguez Island (Ruffo, 1947).
5.	*Talitrus hortulanus*	Samoa, New Hebrides (Stephensen, 1943). Greenhouses: Kew Gardens.
6.	*Talitrus kershawi*	Australia (Stephensen, 1935).
7.	*Talitrus pacificus*	Australia, Marquesas, Norfolk Island (Hurley, 1955). Botanical gardens: U.S.A. (Shoemaker, 1936).
8.	*Talitrus sylvaticus*	Australia, New Zealand (Hurley, 1955); Tasmania (Ruffo, 1948). Botanical gardens: Scilly Isles, Ireland (Hurley, 1955).
9.	*Talitrus tasmaniae*	Tasmania (Ruffo, 1948).
10.	*Talitrus topitotum*	Ceylon (Burt, 1934).
11.	*Talitrus* sp.	Burma (K. H. Barnard, 1935).
12.	*Talorchestia antennulata*	New Caledonia, Loyalty Islands (Stephensen, 1935).
13.	*Talorchestia diemensis*	Australia, New Caledonia, Tasmania (Stephensen, 1935).
14.	*Talorchestia kempi*	Assam (Stephensen, 1935).
15.	*Talorchestia rectimana*	Tahiti (Stephensen, 1935).
16.	*Orchestia anomala*	Seychelles, Marquesas, ?Andaman Islands, Bismarck Archipelago, Gulf of Siam, Lower Bengal, Singapore, Java, Bali, Westflores, New Britain (Schellenberg, 1938); ?South Africa (K. H. Barnard—*Talorchestia malayensis*, 1955).
17.	*Orchestia chiliensis gracilis*	Juan Fernandez (Stephensen, 1935).
18.	*Orchestia floresiana*	Flores, Sumatra (Ruffo, 1948).
19.	*Orchestia hawaiiensis*	Hawaii (Stephensen, 1935; J. L. Barnard, 1955).
20.	*Orchestia humicola*	Japan (Stephensen, 1935).
21.	*Orchestia improvisa*	Snares and Stewart islands (Hurley, 1957).
22.	*Orchestia insularis*	Campbell and Auckland islands (Hurley, 1957).
23.	*Orchestia kaalensis*	Hawaii (J. L. Barnard, 1955).
24.	*Orchestia kinabaluensis*	North Borneo (Shoemaker, 1935).
25.	*Orchestia* sp. prope *kinabaluensis*	New Guinea (Ruffo, 1948).
26.	*Orchestia kokuboi*	Japan (Stephensen, 1935; Bulycheva, 1957).
27.	*Orchestia lagunae*	Philippines (Stephensen, 1935).
28.	*Orchestia lesliensis*	North and South islands of New Zealand, Stewart Island (Hurle, y1957).
29.	*Orchestia luzonensis*	Philippines (Stephensen, 1935).
30.	*Orchestia marquesana*	Marquesas (Stephensen, 1935*a*).
31.	*Orchestia maynei*	Auckland Islands (Hurley, 1957).
32.	*Orchestia montana*	South Celebes (Stephensen, 1935).
33.	*Orchestia notabilis*	Cochin State—India (K. H. Barnard, 1935).
34.	*Orchestia parva*	Auckland Islands (Hurley, 1957).
35.	*Orchestia parvispinosa*	Java (Stephensen, 1935).
36.	*Orchestia patersoni*	Snares and Stewart islands (Hurley, 1957).
37.	*Orchestia pickeringi*	Hawaii (J. L. Barnard, 1955).
38.	*Orchestia rubroannulata*	North Island and Stephens Island of New Zealand (Hurley, 1957).
39.	*Orchestia sarasini*	New Caledonia (Stephensen, 1935).
40.	*Orchestia simularis*	Snares Island (Hurley, 1957).
41.	*Orchestia sinbadensis*	South Island of New Zealand (Hurley, 1957).
42.	*Orchestia tenuis*	North and South islands of New Zealand, Stewart Island (Hurley, 1957).

recorded as many as 4000 amphipods per square meter. They are a very conspicuous part of the fauna, both because of their numbers and also because of their habit of jumping when the litter is disturbed. They eat fallen leaves, and there is little doubt that they play a major part in the disintegration of leaf litter in Australian rain forests" (Birch and Clark, 1953).

The observations which follow represent an attempt to piece together information acquired incidentally in systematic studies. They are almost entirely unsupported by experimental evidence, but are tentatively put forward to draw attention to the problems involved and to opportunities for future research.

DEFINITION

It is necessary to draw attention to past misuse of the term "terrestrial" in speaking of amphipods.

In each of the three talitrid genera, *Talitrus*, *Talorchestia*, and *Orchestia*, there are species of "sandhoppers," amphipods which live in the beach zone above low-tide level and often reach some distance above high-tide mark. These are quite distinct from the terrestrial Amphipoda which inhabit the forest floor of the Indo-Pacific region. In the European zone, where terrestrial species are not indigenous, there has been a tendency to speak of the littoral species as being "terrestrial"; for instance, Dahl (1946) speaks of *Talitrus saltator* as a terrestrial species, one "whose most important functions—eating, breeding, etc.

are performed on land." He remarks further that "their main distribution is passive and takes place in sea water." This conclusion points up one of the differences between the truly terrestrial species and those of which Dahl is speaking. The ecology of the terrestrial species is not sufficiently well known to assert in definition that their distribution is active, but it is clear that it does not take place in sea water. Those species of which Dahl speaks should be referred to, I propose, as "supralittoral" (cf., T. A. and Anne Stephenson, 1949). Those species which are essentially independent of sea water, that is, which may occur in leafmould at the water's edge but may equally as well occur in leafmould thousands of feet above sea level and miles away from the seashore, may then properly be referred to as "terrestrial."

The term "cryptozoic" is also used in this paper. It was first proposed by Dendy (1895) for "the assemblage of small terrestrial animals found dwelling in darkness beneath stones, rotten logs, and the bark of trees, and in other similar situations." Interestingly enough, Dendy specifically includes the amphipods, *Orchestia sylvicola*, from New Zealand, and *Talitrus sylvaticus* from Australia, in this fauna.

As an alternative, I have occasionally used the more colloquial term "leafmould species" which is both apt and accurate in describing the niche which these animals fill. It avoids confusion with the supralittoral species, but is of less universal application.

DISTRIBUTION

The most striking feature of the distribution of terrestrial Amphipoda is that they are domiciled essentially in the Indo-Pacific region, and especially in the Southern Hemisphere. Stephenson (1935) no doubt had this localisation in mind when he compiled his paper on "The Indo-Pacific Terrestrial Talitridae," but he did not elaborate any thesis beyond observing that the terrestrial species were characteristic of the Indo-Pacific Ocean,

TABLE 1
GEOGRAPHICAL DISTRIBUTION OF TERRESTRIAL AMPHIPODS
Based on arbitrary geographical regions

SPECIES	Africa–Madagascar	Bay of Bengal	Malay Peninsula	Japan	Philippines	Indonesia–Borneo	New Guinea–Bismarck Arch.	New Hebrides	Loyalty Isles	Australia–Tasmania–Norfolk Is.	New Zealand	Subantarctic Isles	Juan Fernandez	Tuamotu Group	Samoa	Hawaii	U.S.A.
Talitrus africanus	++																
Talitrus alluaudi	++					+								+			+
Talitrus decoratus		+															
Talitrus eastwoodae	+																
Talitrus gulliveri	+																
Talitrus hortulanus								+							+		
Talitrus kershawi										+++							
Talitrus pacificus										++++				+			
Talitrus sylvaticus											+						
Talitrus tasmaniae																	
Talitrus topitotum		+															
Talitrus sp.		+															
Talorchestia antennulata									++								
Talorchestia diemensis									++	+							
Talorchestia kempi		+															
Talorchestia rectimana														+			
Orchestia anomala	+	+	+			+	+										
Orchestia chiliensis gracilis													+				
Orchestia floresiana						+											
Orchestia hawaiiensis																+	
Orchestia humicola				+													
Orchestia improvisa											+						
Orchestia insularis												+					
Orchestia kaalensis																+	
Orchestia kinabaluensis						+											
Orchestia sp. prope *kinabaluensis*							+										
Orchestia kokuboi				+													
Orchestia lagunae					+												
Orchestia lesliensis											+						
Orchestia luzonensis					+												
Orchestia marquesana														+			
Orchestia maynei												+					
Orchestia montana						+											
Orchestia notabilis		+															
Orchestia parva												+					
Orchestia parvispinosa					+												
Orchestia patersoni										+							
Orchestia pickeringi										+						+	
Orchestia rubroannulata										+							
Orchestia sarasini									+								
Orchestia simularis										++							
Orchestia sinbadensis										++							
Orchestia tenuis										++							

and that "some species of Talitridae with truly terrestrial habits bear the impression of their terrestrial life." Figure 1, based on available records of distribution in the Pacific area, does not claim to be complete, but does give some idea of the extent of this fauna.

The distribution of species in the Indo-Pacific generally, as at present known, reveals little pattern, due mainly to the fact that most records are of one or two species from each of many island localities.

It is likewise practically impossible to make anything of distributional patterns in Polynesia and Micronesia, but it is interesting to speculate how much of this apparently chaotic distribution, making due allowance for misidentifications, is due to the voyages of the Polynesians. The custom of carrying ample stocks of fern root, taro, yam, gourds, and kumara on long journeys in the very humid and moist atmosphere of their canoes, makes them likely agents of distribution. When more is known of the amphipod distribution pattern, it may be interesting to attempt a reconciliation with ethnological theories of migration and botanical theories of plant distribution by natives in the Pacific.

One might predict an endemic fauna in each island or country where the terrestrial species occur, and where information is available this does seem to be the case. Chilton (1909) recorded five new species of *Orchestia* not found elsewhere from Auckland, Campbell, Snares, and Stewart Island. Stephenson (1938) described *Orchestia patersoni* (as *Talorchestia patersoni*) from Stewart Island. This has since been taken on Snares Island, Bench Island in Foveaux Strait, and Solander Island, all quite close to the original type locality, and there appear to be slight racial differences between some of these localities (Hurley, 1957). The New Zealand fauna includes six described species endemic to the mainland (Hurley, 1957) and at least two further species as yet undescribed, as well as the six species already mentioned from the outlying islands. Of these, only *Talitrus sylvaticus* is

known to occur elsewhere. If evidence can be produced to show that the Australian form of *T. sylvaticus* has not been introduced there in the last 200 years from New Zealand, then perhaps the solution to its distribution is to be looked for in the geological history of the two countries. It has been suggested that a New Zealand land mass was connected to Australia and farther north as late as Mid-Cretaceous time but probably not later, and had good connections much earlier which probably extended to take in various northern islands including New Guinea, New Britain, the Solomon Islands, and New Caledonia (Fleming, 1957).

One further possibility is that of transportation by birds, a theory of amphipod distribution for which Segerstrale, *et al.* (1954) has produced considerable geographical and experimental evidence. While there is evidence of considerable migration of bird populations between New Zealand and Australia, it must be said that the distances and the difficulties involved make this theory much less appealing in this instance than, for example, in explaining anomalous discontinuous distribution within New Zealand.

Certain affinities have been suggested in the past between the New Zealand and South African faunas. At present, the terrestrial amphipods of the two countries are considered specifically distinct, and the evidence, in my opinion, suggests parallel evolution from littoral ancestors in the two countries.

There is one surprising fact in this distributional pattern. It is the complete absence of any records from Central and South America, which is especially striking since the forest conditions there are just those which would be expected to support a large fauna of cryptozoic amphipods. Nor do any of the North American records suggest an indigenous fauna. This absence does not seem due to lack of collecting. Allee (1926a) in a comprehensive study of leafmould fauna of Barro Colorado Island, Panama Canal Zone, lists no amphipods whatsoever. Other papers I have

noted, including one on the rainforests of Mexico, similarly fail to note their presence. (Allee's paper, surprisingly, also fails to mention Collembola.) Strickland (1945) does not mention amphipods in a study of the soil and litter fauna of forest reserves and cacao estates in Trinidad, British West Indies, although his thorough sampling methods yielded Collembola and Isopoda.[3] The nearest to a South American report is Chilton's description of *Orchestia chiliensis* var. *gracilis* found under stones on Juan Fernandez Island, 590 metres above the sea shore (Chilton, 1920). The shorehopper, *Orchestia chiliensis* s.str., is found on the littoral zone of Juan Fernandez—as well as in Chile and New Zealand.

It is rather less surprising that terrestrial species should be absent from the European continent and the British Isles, especially when the type of forest found there is taken into consideration. It is indicative of this absence that as recently as 1956 a reputable British authority should say: "While the Isopoda have . . . successfully invaded the land, and woodlice lead a completely terrestrial existence, no Amphipoda occur right away from water, although some, like the sandhopper, live around the water's edge. . . . Failure to evolve suitable habits may have prevented the amphipods from becoming truly terrestrial" (Hynes, 1956). (In view of my definition already given of "terrestrial" Amphipoda, it is pertinent to note his reference to occurrence near water.)

Bornebusch (1930), in an extensive survey of the Danish leafmould fauna, failed to record any amphipods whatsoever, although he listed Isopoda, Collembola, Diplopoda, and all other major groups commonly found associated with amphipods in New Zealand

leafmoulds. All other accounts of similar collections from the European continent are similarly lacking in amphipods.

The only occurrences on the European continent or in the North American region are those recorded from botanical gardens or greenhouses where they have been accidentally introduced. In every case, the species concerned have since been tracked back to an endemic Pacific origin.

Talitrus alluadi Chevreux was first recorded from the "serres chaudes du Jardin des Plantes de Paris" (Chevreux, 1896). Considered identical with this species are *Orchestia senni*, described by Menzel (1911) from the botanical garden at Basel, and *Talitroides bonnieri* (the name proposed by Stebbing, 1906, for a species described by Bonnier, 1898) found in a conservatory at Ghent. This species, since found endemic in Seychelles, Madagascar, and Archipel de Gambier, Paumotu (Taumotu Islands) and Java, has also been found in greenhouses or botanical gardens in Copenhagen, Cambrai, Grenoble, several cities in Germany, Glasgow, and Norwich (Stephenson, *et al.*, 1924), and in New Jersey and Ohio, U.S.A. (Shoemaker, 1936).

Talitrus hortulanus (Calman, 1912) was described from the Royal Botanical Gardens, Kew, and has since been recorded from Samoa and the New Hebrides (Stephenson, 1943).

Talitrus sylvaticus (Haswell) was recorded as *Talitroides dorrieni* (Hunt, 1925) from Tresco Abbey Gardens in the Scilly Isles. This species, described originally from Australia, has since been found under conditions which suggest that it is endemic to New Zealand. It may also be endemic in Australia or it may have been introduced sufficiently long ago from New Zealand to have achieved a fairly wide distribution and to show minor differences in pleopod armature which possibly warrant subspecific rank (Hurley, 1955).

Talitrus pacificus Hurley, known in the Pacific from Norfolk Island and Australia (Hurley, 1955) and from the Marquesas (Stephenson, 1935, as *T. sylvaticus*) has also been

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[3] Since this paper was submitted, Dr. E. L. Bousfield has told me (personal communication) of a "*Talitriator* (sens. Methuen)" from 4,200 feet altitude in Jamaica, B. W. I., and says, "It seems closest to *T. eastwoodae* and may have been introduced, but its wide distribution remote from human habitation and at such altitudes suggests otherwise." I suspect this will prove an exotic species, probably from Africa, associated with plantation introductions. (D. E. H.)

recorded from the United States. Shoemaker (1936) has noted it from Louisiana, and from Balboa Park, San Diego, and Pasadena, California. "*Talitrus pacificus* (is) quite abundant around San Diego. Dr. Johnson used to find dead ones every morning at the east entrance to Ritter Hall. Apparently they had been attracted by the light over the entrance which was left on all night and killed by the insecticide there." (Dr. T. E. Bowman, personal communication.) It is hardly necessary to add that to the Australian or New Zealand visitor to Southern California, the most striking botanical feature there is the widespread cultivation of Australian trees and shrubs.

It has been recognised for many years that there is a considerable "hothouse" fauna. *Placocephalus kewensis* Mosley, a terricolous turbellarian found originally only in greenhouses, and later discovered endemic in a different part of the world, is a good example. Kraepelin (1900) lists a considerable number of introduced animals of different groups found in hothouses in Hamburg, whilst Hatch (1949) discusses Isopoda, Coleoptera, Dermaptera, Orthoptera, and Gasteropoda commonly found in greenhouses of the Pacific Northwest of the United States. Hatch cites the isopod, *Porcellio dilatatus*, as a "properly adapted species which can spread from greenhouse to greenhouse without being able to live in the surrounding situations." In speaking of a "properly adapted species," however, one is overlooking a rather essential feature of this fauna. The fact is that the species is properly adapted for forest floor conditions, but that few situations could be more to the liking of terrestrial amphipods and other cryptozoic fauna than the continuous humidity and the plentiful supply of leafmould for food and cover which most greenhouses provide. If the term "properly adapted" is to be used of anything in this context, it must be applied not to the animals but to the greenhouses.

On this point, Lawrence (1953) makes a most interesting comparison: "The great sur-face evaporation of the leaves creates a humid mantle around the [South African rain] forest while the foliage of the canopy blankets the substratum from the direct rays of the sun so that it keeps its moisture longer. The atmosphere . . . especially upon a hot day, often recalls that of a greenhouse."

ECOLOGY AND EVOLUTION

The most significant recorded fact in the literature of the terrestrial species is the repeated theme of habitat—"in damp soil in the forests," "among damp fallen leaves," "in burrows in soft damp soil under dead leaves," "on damp earth under logs," "under decaying leaves," and so on. The terrestrial species of amphipods are essentially inhabitants of the leafmould of the forests. They have evolved a habit of life which, while enabling them to colonise a sizable area of the Indo-Pacific land masses, yet imposes very great limitations. Or, bearing in mind the direction from which they have colonised the forests, and that taken by their more advanced relatives, the terrestrial isopods, it would be more correct perhaps to say that the terrestrial amphipods have not yet emerged from the limitations imposed by their cryptozoic environment to any more rigorous habitat.

The change to a terrestrial environment is a major one. There is a complete change of surrounding medium—air is substituted for water. There is a complete change in primary mode of progression, from swimming to jumping, and there is need for modification in most of the important functions of life: breeding, breathing, and excreting. The supralittoral species make the best of both environments. They live within easy reach of the sea, burrowing in wet sand or under stones; they feed on seaweed and animal matter washed up on the shore; they achieve distribution by means of the sea. Many species are able to swim to a certain extent and can survive immersion in sea water (Dahl, 1946).

Carter (1931) considers that the majority of terrestrial animals have reached the land by way of fresh water rather than directly from the sea. "The suggestion is made that this has been partly caused by the favourable series of intermediate environments between the fresh waters and the land, and that the evolution of many of the numerous adaptations necessary for terrestrial life has been induced in these environments serially and therefore with greater ease. The much greater variability of the fresh-water environments has undoubtedly been important in producing this result. The importance of the tide in maintaining the constancy of conditions on the marine littoral is emphasised."

Yet neither amphipods nor isopods fit this general pattern. Among the constituent groups of the cryptozoic fauna Dendy (1895) includes "isolated representatives of typically aquatic groups of animals which have as yet become little modified in accordance with their new life." He comments, "Every naturalist knows how many small animals swarm beneath half-dry stones on the seashore. Such species appear to me to be taking the first step towards a terrestrial life. Gradually, they will make their way inland, still keeping beneath logs and stones for the sake of moisture and coolness, until finally they accustom themselves to a thoroughly terrestrial existence. In this section of the cryptozoic fauna we must place the shrimplike Amphipoda and Isopoda which certainly look strangely out of place on land."

Edney (1954) speaks similarly of the isopods. "There is little doubt that the route to land was across the littoral zone rather than by way of estuaries and swamps (Pearse, 1929). Evidence for this is the existence today of littoral and halophilic forms such as *Ligia* sp. and *Halophiloscia*, which are undoubtedly primitive morphologically."

These views are further supported by the fact that the genera *Talorchestia*, *Talitrus*, and *Orchestia* all embrace supralittoral as well as terrestrial species, whilst the fresh-water species of the family Talitridae all belong to genera which are represented only in fresh water and are morphologically closer to the marine genera of Talitridae than to the supralittoral and terrestrial genera. The constancy of conditions on the marine littoral seems to have barred neither amphipods nor isopods from entering the terrestrial environment.

The forest floor was perhaps the most suitable place for a littoral animal to enter, especially considering that "animals crossing [the littoral] zone may well be subjected to extremely high temperatures" (Edney, 1954). In many lands, the forest reaches right to the water's edge or borders streams running down to the sea, and often beaches are the only barriers between sea and forest. In these places, the supralittoral zone is the beachhead for invasion by littoral species. And, in countries bordering the Pacific where the climate is relatively humid and the conditions of the forest floor are more or less uniform throughout the year, the leafmould zone is relatively moist and stable. Light intensity is considerably reduced by the nature of the zone itself, and by the strata of the forest canopy above. Humidity and temperature are relatively constant. "Forest temperatures are generally lower in summer and higher in winter than temperatures of adjacent areas. Similarly forests are cooler during the heat of the day and warmer during the night than areas external to them. Relative humidity is characteristically higher and evaporation rate lower within the forest than in adjacent, less dense terrestrial communities. Similarly, relative humidity is higher and evaporation rate lower within forests during the night than in daytime" (Allee, Emerson, Park, Park, Schmidt, 1949, references omitted). These tendencies towards a stable and more equable climate are intensified in the leafmould zone which, of its nature, has an insulating effect from the surrounding atmosphere. "The cryptozoa are not only sheltered by the growth of the forest and shrub which mitigates the extremes of light and temperature, but they are further covered

by the damp layer of humus which cuts off all light and movements of air, further reducing the comparatively small fluctuations of temperature and humidity that prevail throughout the forest" (Lawrence, 1953).

The microclimate may change a little but presumably the animals living therein can meet these changes by retreating a little farther and deeper into the leafmould and even into the soil beneath. The annual rhythm of adaptation to climate is then vertical and not horizontal as in the case of, say, the larger vertebrates. For smaller animals, this is an inestimable advantage. In unfavourable conditions their route of escape is not barred by large intractable areas of a biotype in which they cannot survive. In short, they can adjust themselves to seasonal changes without leaving their very specialised niche. When conditions do change abnormally, they may still survive in islands in the forest floor formed, for example, by deep pockets of leafmould, and by fallen and rotting logs which protect the ground beneath. This is well illustrated where forests have been felled or burned off. Under the remnant logs, there is usually a damp area with a relict cryptozoic fauna, absent in the immediately surrounding pasture or scrub. Examination will usually reveal isopods, millipedes, pseudoscorpions, opiliones, centipedes, endemic worms (found very rarely in New Zealand pastures, the pasture species being exotic ones), and, if the area is large and moist enough, amphipods. That land isopods tend to collect in such protected places has been recorded by Allee (1926) who has further shown that isopods will often conserve moisture still longer by aggregating together. This is of positive survival value since aggregated isopods lose moisture more slowly than isolated ones.

In areas of remnant native bush, often the only places where endemic terrestrial isopods are present in any numbers are the ecological islands provided by decaying trees and logs lying on the ground, an effect noted by Dendy (1895) for the cryptozoic fauna generally. "It is far easier to find cryptozoic animals in partially-cleared localities, where they are collected together under the remaining fallen logs, than in virgin forest, where there is so much cover that the animals are widely scattered, and the search becomes very laborious."

On the east coast of the North Island, New Zealand, where there are many such remnants, it is common to find the conglobating and relatively thick-skinned isopod, *Cubaris danae*, in the space between the log and the compact soil below, where there is a little but not a great deal more moisture than in the surrounding unprotected ground. The comparatively thin-skeletoned and nonconglobating *Styloniscus otakensis* is only found in the much moister, rotting wood of the log, associated with ants, peripatus, termites, millipedes, and other invertebrates with similar environmental preferences.

In Australian conditions, Birch and Clark (1953) have noted that amphipods occur in wet years "in the leaf litter of stands of timber in drier habitats such as *Casuarina*, *Eucalyptus*, and *Angophora* forests. But in most years the leaf litter in these forests is too dry for *Talitrus* to survive." However, the fact that repopulation occurs in wet years suggests a survival population in the "drier habitats" or in close proximity.

The fact that no great change in feeding is necessary would facilitate entry to the terrestrial environment. The decaying seaweed diet of supralittoral amphipods is not markedly different from the decaying leaf diet of the terrestrial ones. Birch and Clark (1953) include the amphipod *Talitrus sylvaticus* amongst the litter feeders or "decomposers," commenting that it feeds on leaves only after they have been on the ground for some months.

Terrestrial amphipods, like supralittoral ones, will turn cannibalistic and carnivorous in laboratory conditions when other food is not available, but in normal conditions they seem to be ectophagous rather than predatory. Lawrence (1953) remarks that "the intestine of *Talitrus* (*Talitroides*) *eastwoodae*

living in South African indigenous forests contains only the small fibrous particles of plants and other woody detritus."

Grimmett (1926) attempted to correlate the distribution of male talitrids with the nature of the forests in which they occurred and was led to this statement. "The males of [*Parorchestia sylvicola*] are known to be rather rare. All the specimens collected were therefore determined for sex, the large flattened front legs of the male being, on the suggestion of Dr. Chilton, used as a guide. It was found that in a total of 383 specimens from the beech-forest locality, 43, or 11.2 per cent were males, while in a total of 333 from the tawa forest no males were discovered, though each specimen was carefully examined with a dissecting lens. Moreover, the males in the former were fairly evenly distributed throughout all the samples. It would thus appear that males are extremely rare, or are not produced in the lower-altitude forest during this portion of the year. Temperature, dependent on altitude, is suggested as the environmental factor most likely to be involved."

Unfortunately, there is a simpler explanation which makes his conclusions of little value. Almost certainly he was dealing with two species, one an *Orchestia* with a large well-developed second gnathopod in the male, and the other a species of *Talitrus* with the feebly developed, femalelike second gnathopod in the male which is characteristic of that genus (cf. Fig. 3). It is worth noting that Forster (1954) finds no evidence of altitudinal speciation or correlation between distribution and type of forest cover in the opiliones, and I believe this finding applies equally well to the amphipods.

However, males are often absent from samples—Grimmett's figures suggest a normal proportion of one male in ten—but whether this is due to ecological factors is doubtful. When collecting by hand, there is possibly more chance of favouring one sex, due to such things as size and agility differences between sexes, or the possibility of sexual preferences for different depths in the leafmould. The season of the year, the biology of the species concerned, and location of the sample may affect the percentage of males. There is also no evidence that Grimmett's figures are the norm for all species.

SPECIATION

In spite of our relatively poor knowledge of the cryptozoic amphipods, the number of species already known is surprisingly high and past experience suggests that future work will reveal many more. From the New Zealand region alone, some 14 species are known, and the fauna is by no means intensively studied.

There are two lines of development towards the terrestrial environment, represented by *Talitrus* and *Orchestia* (and perhaps a third by *Talorchestia*). The supralittoral species of these genera form a basically compact group, varying generically only in combinations of gnathopod shape and other comparatively minor morphological variations—minor, that is, compared to generic distinctions in other families. There is, in fact, a tendency for *Talorchestia* and *Orchestia* to intergrade. However, the morphology of the terrestrial species of *Orchestia* and *Talitrus* suggests that they have arisen independently from supralittoral species.

It is also of interest that, whereas littoral species tend to be somewhat cosmopolitan, as may be seen by comparing the faunal lists for New Zealand and South Africa, the terrestrial species are noticeably localised.

It is not difficult to suggest reasons for the proliferation of species. The island nature of the Indo-Pacific provides textbook conditions for speciation due to reproductive isolation. The terrestrial fauna of the subantarctic islands, as recorded by Chilton (1909), suggests speciation through geographical isolation. With some exceptions, the terrestrial species of Polynesia and Melanesia also suggest geographical isolation.

Within New Zealand, Forster (1954) and Dell (1955) have suggested a possible cor-

relation of geographical speciation in leaf-mould animals with major events in past geological history, including glaciation. According to Forster (1954), the opilionid fauna of Stewart Island "suggests a series of invasions and reinvasions from the mainland following periods of isolation of sufficient time length to permit physiological isolation to be achieved." Further, "the distribution of the fauna of the West Coast of the South Island is strongly suggestive of bio-glacial control, paralleling as it does that of the *Paryphanta* snails for which Willett (1950) postulated a similar origin."

The formation of ecological islands, to which leafmould is particularly susceptible by the presence of such faunal barriers as rivers, mountain ranges, and valleys, also provides a marked stimulus to speciation. This has been noted for other leafmould animals. Speaking of the land molluscs of Fiordland, Dell (1955) comments ". . . such isolated pockets would form ideal localities in which speciation could proceed. The comparatively high number of forms of such a genus as *Ptychodon* could well be due to such a situation, coupled with subsequent invasions."

The mechanism of speciation is perhaps less obvious but I would suggest that the most probable is speciation by neotony—the retention of juvenile or embryonic characters in the adult.

In most species of *Orchestia*, including all of the supralittoral ones, the second gnathopod is large and subchelate in the male, and small and feebly chelate in the female. In *Talitrus* the male second gnathopod is small and feebly chelate, superficially indistinguishable from that of the female. Since the greatly developed male gnathopod in *Orchestia* is known to be used for grasping and even "carrying" the female *in coitu*, there is a strong likelihood that the large size of the male gnathopod is unnecessary in *Talitrus* because of changed sexual habits.

The terrestrial species of *Orchestia*, unlike the supralittoral ones, show gradations in size and type of male gnathopod from the typical *Orchestia* form to a form not far removed from the typical *Talitrus* gnathopod. These "intermediate" species show striking resemblances to the various stages in the development of the male second gnathopod in supralittoral species of Talitridae. A typical series is shown in Figures 2 and 3, where various adult male second gnathopods of "intermediate" forms are contrasted with growth stages of *Talorchestia bottae* (figured by Chilton, 1921, as *T. martensii*). The suspicion that these "intermediate" forms are no more than subadult is, I believe, unwarranted. All other evidence from morphology and distribution points to the animals being genuinely mature.

The other striking morphological feature of the terrestrial species is the trend to reduction of pleopods from the normal supralittoral and marine condition, with three pairs of fully-developed biramous pleopods, to the extreme in *O. patersoni*, a terrestrial species with three pairs of vestigial triangular stumps. The possibility that this trend is also an effect of species formation by neotony has been considered, but limited examination of supralittoral juveniles showed fully formed pleopods at an extremely early stage in development. While it is possible that pleopod formation passes through a bud stage similar to the vestigial stump, it would have to occur at a very early stage and would probably be revealed only by study of the late embryo. Nevertheless, the diagrammatic representation of pleopod structure in Figure 3 indicates that reduction of pleopods and reduction in size of male gnathopods occur more or less in phase and are not inconsistent with the process of neotony.

MORPHOLOGICAL AND
PHYSIOLOGICAL ADAPTATIONS

Work on the systematics of the terrestrial amphipods has revealed some interesting tendencies in adaptation. There are no morphological changes of any significance in the mouth parts, but in view of the similarity of
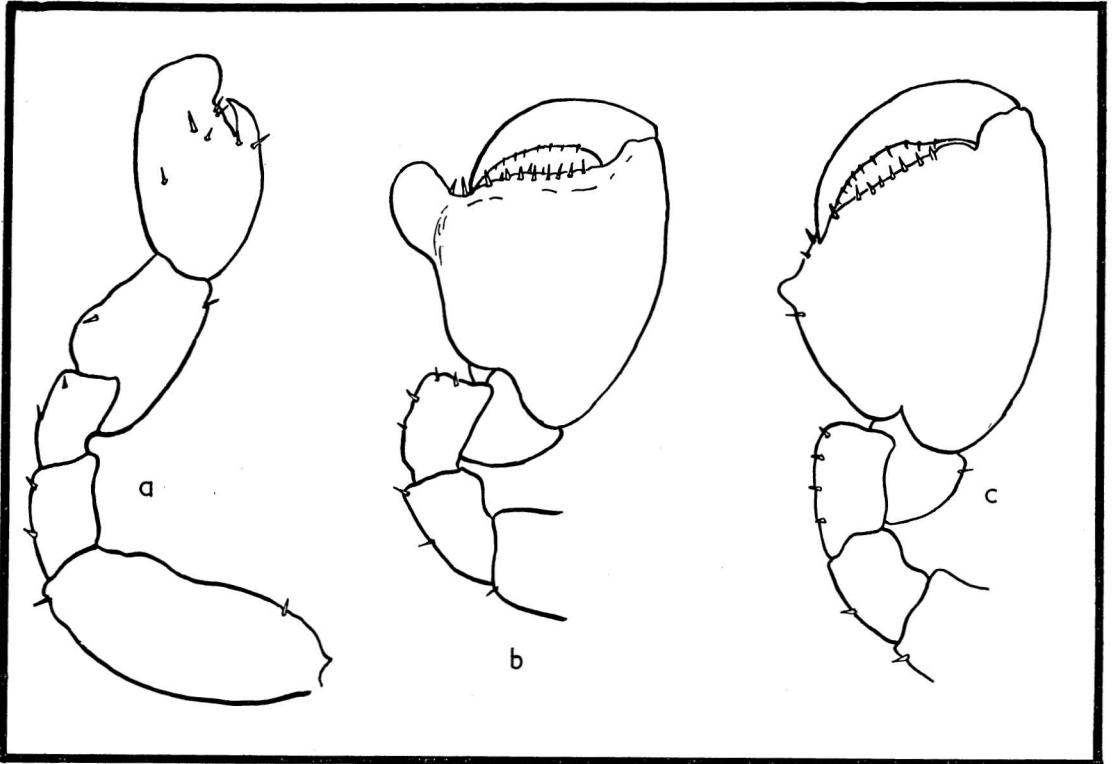
FIG. 2. *Talorchestia bottae*. Three successive stages in development of second gnathopod of male. (After Chilton, 1921.)

diet to that of the supralittoral species, this is not unexpected.

The gnathopod structure, however, does show certain modifications. Chilton, in an unpublished journal, writes of the "peculiar transparent portions of the merus, carpus, and propod" of the gnathopods of *Orchestia sylvicola* and asks, "What can be the function of these strange looking structures? In them, the integument appears semitransparent and usually more or less striated, and the joint bulges out at these places, but no muscles are to be seen in the enlargements."

Since these processes are absent from the male gnathopods in some species, it is unlikely that they are primarily connected with food or feeding habits; rather, reduction in size of the large second gnathopods from the condition found in marine and supralittoral species, and simultaneous development of processes in terrestrial species indicate changes in sexual habits as a primary cause. The most prominent features of the "pellucid lobes" are their lack of musculature, their transparency (partly due to the absence of muscle tissue), and their scabrous surface. They are situated on the lower margin of the limb which would scrape along the ground and be most exposed to external stimuli. These features all suggest to me a tactile sensory function. McIntyre, in an unpublished work, has described the value of the peculiarly twisted female second gnathopod, which is well supplied with these pellucid processes, in combing the broodplates.

In fact, it does seem likely that there has been a change in sexual habits. Williamson (1951) studied the mating and breeding of

some supralittoral or "semiterrestrial" amphipods, and found that in *Talitrus saltator* the female is held by the male with the aid of the stout antennae and the peraeopods, whereas "holding" in marine and supralittoral species is normally done with the aid of a greatly developed second gnathopod. *Talitrus saltator* is, however, the only species of *Talitrus* which shows this marked development of strong antennae. The other, more truly terrestrial, species of *Orchestia* and *Talitrus* have slender antennae. Since most of them also lack the large male "grasping hand" of the supralittoral species, it is likely that some further change in sexual habits has taken place. (A few terrestrial species retain the large "grasping hand.")

In the Gammaridae, the eggs are laid almost immediately after copulation, the time of laying in some species being determined by the time of copulation, in others by the time of moulting. In *T. saltator*, and probably in other talitrids, the time of laying is determined by the time of moulting. Laying takes place 4 days after moulting, but copulation may take place any time from 1 to 4 days before laying.

Williamson suggests that the eggs of the supralittoral Talitridae are fertilised in the brood pouch, and rules out both internal insemination and internal fertilisation. The spermatozoa, which are already present when laying takes place, are then most probably activated either by a secretion of the unfertilised egg or by a secretion which the female releases during laying. Spermatozoa of *T. saltator* can live at least 4 days in the brood pouch of the female, probably because of their inactivity and perhaps also because of their relatively large size (about 400 microns in length).

More tangible developments correlated with the terrestrial environment are evident. In aquatic species of Talitridae, the male normally carries the female around for some days before moulting, and copulation occurs immediately after moulting. "The carrying position adopted by . . . *Gammarus* . . . is obviously not suited to terrestrial conditions, . . . but it is probable that the aquatic ancestors of the Talitridae employed this form of carrying, and it is still found in the more aquatic members of the family (*Hyale* spp.)" (Williamson, 1951).

In the supralittoral species, there is no carrying before moulting. "Associated with the terrestrial habitat, therefore, we see not only modifications in the method of carrying, but also a great reduction in its duration" (Williamson, 1951).

From these facts, Williamson concludes that the delayed egg laying, associated with the longevity of the sperm, has an adaptive significance. Where the moult governs the time of laying, the delay increases the chances of mating by increasing the time, between moulting and laying, in which mating can take place; furthermore, the male does not have to carry the female. On the other hand, mating in aquatic forms "can take place over a period of several days before the moult, and the probability of mating would be very little increased if egg laying were delayed for a few hours, or even days, after the moult" (Williamson, 1951).

Correlated with the terrestrial environment, there is also a reduction in the number of eggs produced. In most species of terrestrial amphipods, I have found the number of eggs in the brood pouch ranges from 1 to 10, e.g., in *Talitrus sylvaticus* the average is between 3 and 4. Yet in marine genera of the same family, the number carried by an ovigerous female of similar size may be many times this. An *Allorchestes novizealandiae* female taken at random carried 161 eggs, the greater carrying capacity of the animal being in part due to the much smaller size of the eggs.

Sexton (1924) has shown a decrease in number of eggs produced by species of *Gammarus* from marine to pelagic species. *Gammarus locusta*, a marine species, has as many as 143 eggs in a brood. The brackish-water *G. chevreuxi* has 30–40 per brood; the fresh-
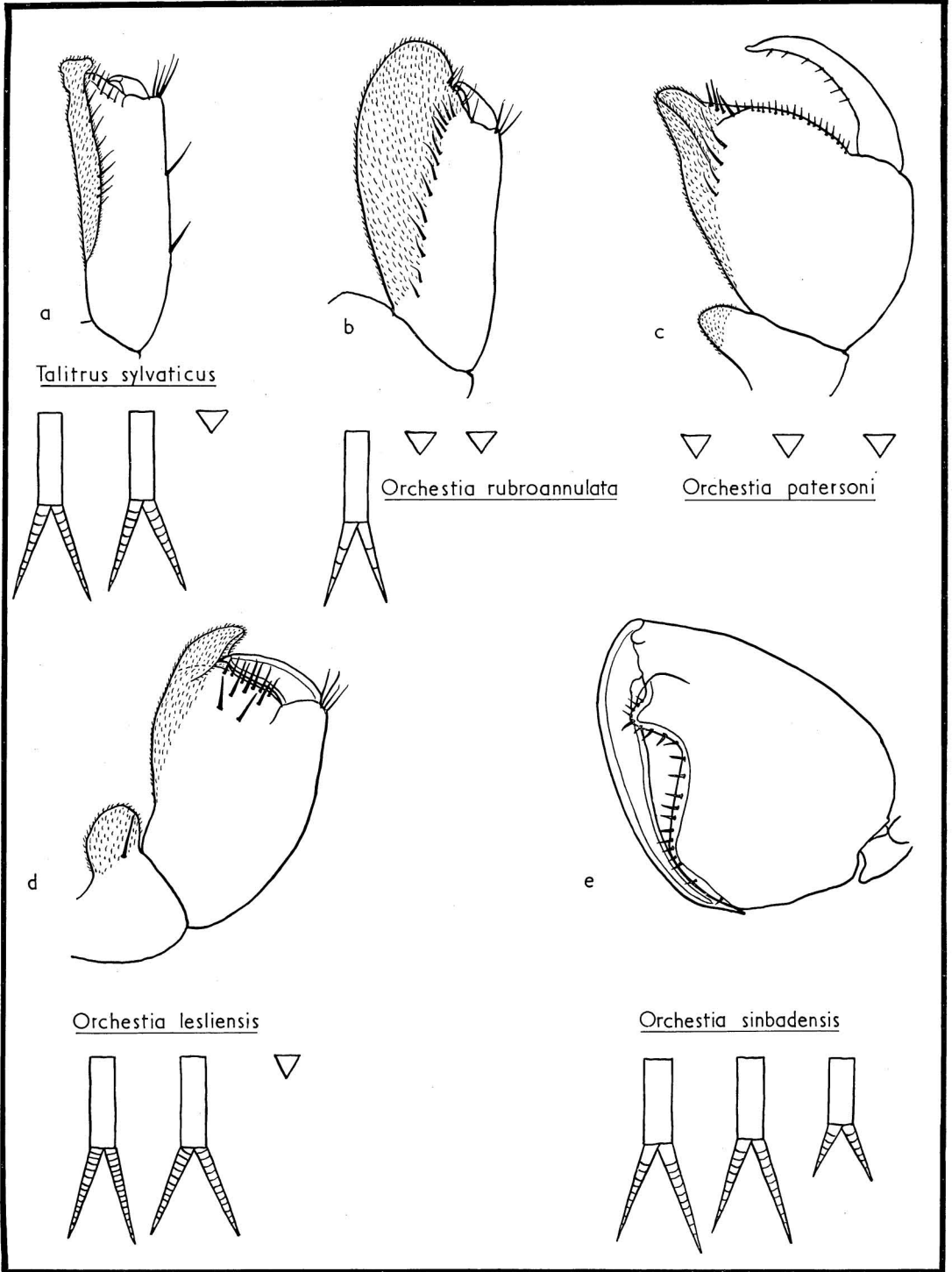
FIG. 3. Adult male second gnathopods of five species of terrestrial amphipods showing similarities to developmental stages of other species (cf. Fig. 2). Diagrammatic representations of the pleopods are given for each species. (The number of segments per ramus indicated corresponds to the number suggested by setation; in some species, actual segmentation appears superficial or incomplete.)

water *G. pulex*, 12–18; and a littoral species of *Gammarus*, 8–12. Lawrence (1953) gives a figure of 6–14 eggs for the terrestrial *Talitrus (Talitroides) eastwoodae*, "the average thus being almost identical with that of the littoral species quoted by Sexton." Lawrence further states that, as far as is known, there is only one annual brood in *T. eastwoodae*, whereas *G. chevreuxi* breeds all the year round. Sexton (1928) writes of one female *G. chevreuxi* which was known to have 29 broods in a lifetime—12 to 18 months is noted as the average breeding lifetime of a female *G. chevreuxi*—and Hynes (1955) says that *G. pulex* will breed five times in a year.

So, as in other groups of invertebrates which have adapted themselves to terrestrial or fresh-water life, the eggs tend to be larger and fewer, an example of the general tendency for the more advanced species of a group to be more sparing in the production of the young. It is reasonable to expect that, as in other advanced groups, the eggs and young will have a longer developmental period, but when launched from the protection of the parental brood pouch the young will be more mature than those of the marine species. It is significant that *Talitrus saltator* takes considerably longer to mature than the 2 to 2½ months required by the somewhat more hydrophilous *Orchestia gammarella* (Verwey, 1929, quoted by Williamson, 1951).

Thus, changes in sexual habits and breeding of the supralittoral species are directly advantageous in entering the terrestrial environment. The suggested trend in delaying of egg laying until after moulting is most significant, and one would expect the truly terrestrial species of *Talitrus* to have developed this trend even further, being limited ultimately only by the viability of the sperm.

MOISTURE REQUIREMENTS

Moisture requirements appear to have been met by the relatively stable nature of the environment. The nature of the leafmould zone itself does away with much of the necessity

for special adaptations. I have found that terrestrial amphipods in cultures uncontrolled for humidity vary specifically in resistance to changes of moisture, as would be expected from similar work on isopods (Edney, 1951) but that all species are extremely susceptible to dessication. Apart from these variations in resistance, no specific adaptations to moisture requirements have been observed. Edney's work on isopods (1951, 1954) suggests that adaptations to this environmental factor are to be found in behavioural and physiological rather than morphological factors. He believes that terrestrial isopods have not developed the waxes characteristic of insect cuticles "which have contributed largely to their success as terrestrial animals."

However, there is evidence that such water-conserving adaptations as impermeable cuticles are not the only way of meeting the hazards of at least a limited degree of terrestrial life. "The ability to evaporate water rapidly, and thus to cool the body, may be of survival value when woodlice are exposed to high temperatures for short periods, particularly in littoral forms which may well have been intermediate in the evolution of terricolous from maricolous isopods" (Edney, 1951*a*). This is supported by various measurements of transpiration rates in cryptozoic invertebrates quoted in Edney (1954), suggesting that "high transpiration rates are generally associated with cryptozoic arthropods."

Casual observations support the likelihood that the permeability of the exoskeleton of terrestrial amphipods is much greater even than that in isopods, and by inference, that transpiration rates may also be higher. Terrestrial amphipods, when placed in 70–95 per cent alcohol, immediately react vigorously, but in little more than 10 seconds show no further signs of life. Isopods, under the same conditions, have been observed to react for as long as 10 minutes before final quiescence. I have also noted a similar differential rate in susceptibility to dessication. Lawrence (1953) likewise notes that *Talitrus eastwoodae*

may survive as long as 9 days in fresh tap-water, but "on the other hand it is much more susceptible to dry air in which it succumbs very quickly," a statement which incidentally raises questions regarding control of osmotic pressure within the body.

These points further emphasise a very important aspect of the ecology of the cryptozoic fauna, that "the forest community, by its very nature, solves the problem of water conservation for a host of plants and animals, making unnecessary for them the specific adaptations to economy of water that may be essential in other terrestrial environments" (Allee, Emerson, et al., 1949).

EXCRETION

The excretory problems facing animals of marine origin which colonise the land are well known. Foremost amongst these is the retention of water, which requires the development of mechanisms for the resorption of water from excreta, and adaptation of the excretory end product. In most groups, this is expressed by a change in the major nitrogenous end product from the ammonia of marine groups to the urea or uric acid of terrestrial groups, with accompanying complexity of excretory organs.

Dresel and Moyle (1950) describe studies on nitrogenous excretion in amphipods and isopods, including a supralittoral species of *Orchestia*. They conclude that more than 50 per cent of the total soluble nonprotein nitrogen of the excreta is in the form of ammonia. "The level of nitrogen excretion is appreciably lower in the terrestrial species than in any of the others, indicating that, in this group, adaptation to terrestrial conditions has been attended by a general suppression of nitrogen metabolism rather than a transformation to other, less toxic products." Some excretion of uric acid, 5–10 per cent of the total soluble nonprotein nitrogen, took place in the terrestrial isopods. Associated with this excretion, "some retention of this insoluble compound usually occurs, and

it was found that among the terrestrial species the amount so stored parallels the degree of morphological and physiological adaptation to terrestrial conditions. . . . It seems more plausible, however, to attribute this increased uric acid retention in the more xerophilous species to a reduced rate of excretion rather than to a fundamental difference in metabolism."

Thus, they conclude that "adaptation to terrestrial conditions [in the Isopoda and Amphipoda] has been attended by a general suppression of nitrogen metabolism rather than by a transformation of ammonia to other, less toxic products."

Apart from this work of Dresel and Moyle, nothing is known of excretory processes or mechanisms in the terrestrial amphipods.

OXYGEN CONSUMPTION

The rate of oxygen consumption in *Talitrus sylvaticus* has been investigated by Clark (1955). Apart from a decrease in rate of respiration relative to increase of body weight, which is normal for Crustacea, he found that oxygen consumption was relatively higher in winter than in summer, the winter consumption corresponding to that at a temperature 2.5°C. higher in summer. "Of the factors influencing the rate of oxygen consumption . . . first order interactions occurred between temperature and body weight, temperature and season, and season and body weight. There was also a significant second order interaction between temperature, body weight and season. . . . Adaptation . . . to oxygen uptake by *Talitrus sylvaticus* to seasonal differences in temperature was not sufficient to enable it to maintain the same rate of output of energy in winter as in summer" (Clark, 1955).

The occurrence of a seasonal adaptation of rate of oxygen uptake has been found only infrequently in invertebrates, and the necessary physiological mechanism is unknown.

RESPIRATION AND PLEOPOD STRUCTURE

It is interesting to compare the relationship

of the pleopods to respiration in the Isopoda and the terrestrial Amphipoda.

In the Isopoda, the pleopods show a series of modifications for respiratory purposes. In marine species, the pleopods are used both in swimming and for respiration. In the terrestrial species, as in the amphipods, they are no longer of use in locomotion. In the primitive state, both exopodite and endopodite in all pleopods are respiratory. In the Ligiidae, the exopodite is the primary respiratory organ and the endopodite is a secondary one. In the more primitive terrestrial species, such as in the Oniscidae, the endopodites are transformed into branchial lamellae and take over most of the respiratory function. In *Porcellio* and other genera, the exopodites have completely lost their respiratory function and act as lamellae protecting the endopodites from dessication. However, in the most advanced terrestrial species, the endopodites again regress and are replaced by pseudotracheae ("white bodies" or "tracheal glands") on the inner side of the exopodites. It is these pseudotracheae which enable the desert-dwelling species to survive. The pseudotracheae have evolved in three independent lines comparable to and surpassing the development of a terrestrial mode of life in the amphipod genera, *Orchestia, Talorchestia,* and *Talitrus.*

In marine species of amphipods, the pleopods have three functions (Watkins, 1939, 1940). They are used for swimming, they draw a constant current of water over the gills, and the same current, filtered by the gnathopods, serves as a food vehicle.

With the development of extensive pleon muscles and the change to a supralittoral jumping habit, pleopods are no longer used in feeding. Food is obtained actively and the gnathopods are used to grasp and convey it to the mouth. However, all supralittoral species possess fully developed pleopods, suggesting that they are still used in respiration. Since supralittoral species have not lost the power to swim and occasionally need to swim

if they are to survive, their pleopods may fulfil two of these functions.

Among terrestrial species there is a trend towards reduction or complete loss of pleopods except for vestigial triangular stumps, but there are exceptions to this. New Zealand species from leafmould collected 2,000 to 3,000 feet above sea level have fully developed pleopods, e.g., *Orchestia sinbadensis* Hurley (1957).

A completely terrestrial habitat removes any need of pleopods for swimming. According to Lawrence (1953), *Talitrus eastwoodae* "never swims when placed in water and is evidently unable to raise itself above the bottom of a glass jar, moving round in it precisely the same way as if walking on dry land." The absence of pleopods in *O. patersoni* (Stephensen, 1938) implies that sufficient oxygen is available to the respiratory surfaces without need for a constant current of air created by the pleopods. As might be expected, there is in most species a considerable development of respiratory surfaces correlated with this loss. "The gills of the anterior pair of pereiopods are rather large, in the female especially so in pereiopod 2" (Stephensen, 1935). *Talitrus sylvaticus* is a good example of this marked development; it has the gills of the fourth peraeopod, as well as those of the second, much enlarged and elongated (Hurley, 1955). Possibly, the retention of pleopods in some terrestrial species depends on a burrowing habit, in which case the available air in the burrow might stagnate more rapidly were not the pleopods used to increase the circulation. A correlation has also been suggested between burrowing and reduction of eyes, or even loss of pigment, as in *Orchestia marquesana* (Stephensen, 1935), but evidence of this is very limited.

OTHER MODIFICATIONS

In the Isopoda, at the same time as the developments in the pleopods described above, other tendencies have appeared. The antennae have become reduced, probably with an as-

sociated loss of sensory perception; the body in many species has become capable of rolling into a ball, or "conglobating," thus giving the animal greater protection from desiccation and, presumably, from its natural enemies; and locomotory powers have been reduced by weakening of the peraeopods (Van Name, 1936:282,328). In the terrestrial Amphipoda, the antennae are much simpler than in most marine and littoral species; they are more slender; they lack calceoli and other similar sensory structures; but there does seem to be a development of fine setae of a tactile nature. Terrestrial species are extremely mobile. There is no morphological adaptation to protect the gills—if anything they are more exposed by reason of their greater length; nor is there any sign of structural adaptation like the "conglobating" power of isopods. However, with increase in gill size, as in *Talitrus sylvaticus*, it would not have been unreasonable to have expected some physiological or morphological modification analogous to the development of pseudotracheae in the terrestrial isopods. It is probably because of the lack of just such modifications that the terrestrial amphipods, seemingly well suited for the leafmould environment, have not occupied other, more stringent niches.

What has been said of the terrestrial isopods, also may be said of the amphipods: "Any success which the group enjoys on land is due, not so much to the development of characters conferring independence of the environment, but to behavioural mechanisms which keep them for the most part in moist, cool places. . . . The general picture which emerges is of a group of animals comparatively ill equipped for life on land. All the devices which permit such existence are in some degree makeshift. . . . And yet, despite these disadvantages, the animals are by no means uncommon, and there is little doubt that the success which they do enjoy is the result not so much of morphological or physiological adaptations as of behavioural mechanisms which restrict them to the cryptozoic

niche where the rigours of true terrestrial existence, as well as its opportunities, are avoided" (Edney, 1954).

SUMMARY

The term "supralittoral" is applied to Amphipoda of the seashore zone; "terrestrial" is restricted to those species which are entirely independent of sea water. Almost all of these are leafmould species which are characteristic of, and restricted to, the Indo-Pacific islands and land masses. The terrestrial amphipods have colonised the land directly from the littoral zone. The forest floor provides the relatively stable conditions which assist colonisation and provide considerable protection in unfavourable times. Drastic changes in feeding habits have not been necessary.

Adaptations which have taken place or seem most likely to have occurred are these:

1. Feebly chelate gnathopods in *Talitrus* and reduced male second gnathopods in *Orchestia* species are correlated with changes in sexual habits, the development of large second gnathopods in the male to hold the female during copulation having been lost. In *Talitrus saltator* stout antennae are used for this purpose, but in most terrestrial amphipods the antennae are long and slender, and there must have been a further, as yet undescribed, change in sexual habits. Scabrous pellucid areas on the male gnathopods, characteristic of terrestrial amphipods, are probably of tactile sensory nature and possibly correlated with feeding habits.

2. There is a tendency for the male second gnathopod in mature animals of some species to resemble the immature males in other, less terrestrial, species. It is suggested that species formation in terrestrial amphipods is correlated with neotony.

3. There is evidence that males are comparatively few in some terrestrial populations, although this may be true only of certain species and times of the year.

4. Fewer but larger eggs are produced by

terrestrial than by aquatic species of the same family, and there is a longer growth and breeding period. Carrying of the female by the male for long periods is obviated and may be entirely lacking, and the time after egg laying during which fertilisation is possible has been lengthened, thereby increasing the chances of mating. This would greatly facilitate entry into the terrestrial environment, especially since it appears first in supralittoral species.

5. There is a tendency for pleopods to be reduced to vestigial stumps, although species found high above sea level may have fully developed pleopods. Their absence in some species suggests that sufficient air is available to the respiratory surfaces without need of a pleopod-created current of air over the gills. In some species there is a marked development in size of gills.

6. The terrestrial species show strong evidence of endemism. This is probably due partly to the nature of their environment and partly to lack of available transport as compared with marine and littoral species, although the advent of man has complicated distribution patterns to some degree. In at least two genera, *Talitrus* and *Orchestia*, terrestrial species have arisen independently from littoral species.

7. Moisture requirements are met by the leafmould environment and behavioural patterns of the animals.

8. There is some evidence that excretory problems have been solved, not by a change in end products of excretion, but by a general slowing down and suppression of nitrogen metabolism.

9. The leafmould environment provides conditions most favourable to colonisation by a marine or littoral group of animals and requires a minimum of physiological or morphological adaptations.

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