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SYSTEMATICS AND PHYLOGENY OF THE LANDHOPPERS
(CRUSTACEA: AMPHIPODA: TALITRIDAE)
OF MÉXICO AND CENTRAL AMERICA

By
Dorothy H. Lindeman

A dissertation submitted to
the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements
for the degree of
Doctor of Philosophy

Department of Biology

Carleton University
Ottawa, Ontario
November, 1988

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OF MÉXICO AND CENTRAL AMERICA

submitted by
Dorothy H. Lindeman, HBSc., MSc.

in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

Chairman, Department of Biology

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January 10, 1989

Abstract

Five new species of terrestrial amphipods from the rain and cloud forests of México, Costa Rica, and Panamá are described: *Caribitroides tuztlensis* n. sp., *Caribitroides newtoni* n. sp., *Meritroides pecki* n. gen. n. sp., *Meritroides chiapensis* n. sp., and *Cerrochestia hyloraina* n. gen. n. sp. Keys to common genera of sea shore and forest leaf litter talitrid amphipods and to the known species of forest leaf litter landhoppers of México and Central America are provided. Notes on the biology of *Caribitroides tuztlensis* and *Cerrochestia hyloraina* are included. To establish the taxa most closely related to *Caribitroides*, *Meritroides*, and *Cerrochestia*, a phylogenetic analysis of 22 taxa within the family Talitridae was performed, using phenetic and cladistic methods. From these results, two genera of Old World landhoppers (*Talitroides* and *Talitriator*) and two genera of beachfleas (*Floresorchestia* and *Tethorchestia*) were chosen for inclusion in the phylogenetic analysis of the New World landhopper species. The results of this analysis indicated that the Old World landhoppers were probably less closely related to the New World landhoppers than the palustral taxon *Chelorchestia*, and the Old World landhoppers were excluded from the final analysis. From these results, a phylogeny of the known New World landhopper species was constructed, showing that *Cerrochestia* was apparently derived directly from *Chelorchestia*, and that *Caribitroides* shared a common ancestor with *Chelorchestia*. The zoogeography of New World landhoppers is discussed in relation to this phylogeny, and a hypothesis explaining the present distribution of species is offered. A discussion of terrestriality in talitrid landhoppers is included.

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Chapter 1 INTRODUCTION

1.1 Terrestrial Amphipods

Amphipods of the family Talitridae Bulycheva 1957 are one of the few groups of crustaceans that have achieved some degree of freedom from the aquatic environment (Hurley, 1959). Some species have become completely terrestrial, living in the leaf litter of forests, well away from the supralittoral zone (Friend, 1980). Terrestrial amphipods are known from Australia, New Zealand, South Africa, Madagascar, India, Ceylon, Burma, Malaysia, Indonesia, the Phillipines, Japan, most major Pacific and Indian Ocean island groups, the Azores, Madeira, Canary Is., Annobon Is., Jamaica, Haiti, and Central America (Bousfield, 1982; Friend, 1980). Several synanthropic species have spread from greenhouses and introduced tropical vegetation, into England (Richardson, 1980), Florida, Louisiana, South Carolina, California, Brazil, Australia, New Zealand, and Hawaii (Bousfield, 1982; Friend and Richardson, 1986).

Bousfield (1982) proposed that talitrid amphipods can be conveniently placed in four loose and overlapping ecological groups:

- 1. Palustral species, which occur in estuaries and salt marshes, and show many primitive morphological characters;
- 2. Beachfleas, which are usually sexually dimorphic, and occur on sandy and rocky beaches, under wrack, seaweed, and other beach drift;
- 3. Sandhoppers, which are heavy bodied, often very spinose talitrids which burrow in sand beaches, and have appendages specialized for digging;
- 4. Landhoppers, which are truly terrestrial talitrids that live in forest leaf litter, and may or may not be sexually dimorphic.

Both beachfleas and sandhoppers are referred to as supralittoral, semiterrestrial¹, or strand species. Terrestrial amphipods are referred to as landhoppers, or as euterrestrial species (Bousfield, 1982, 1984; Friend, 1980; Friend and Richardson, 1986).

¹an ecologically meaningless term which should be avoided (Wildish, pers. comm.)

Hurley (1959, 1968) defined "terrestrial" as being independent of the sea or standing bodies of water for breeding, feeding and distribution. He separated the supralittoral species from those that he regarded as fully terrestrial, to prevent confusion when dealing with sandhoppers such as *Talitrus saltator* (Montagu), and beachfleas such as *Orchestia gammarillus* (Pallas). Unfortunately, the precision of these separations is questionable, and each of the above four categories contains taxa which violate the definitions. Several species of "beach-flea", for example, occur well inland, in terrestrial habitats (for example, see Bousfield, 1982; Morino, 1978). *Orchestia cavimana* (Heller), a species common in estuaries (Wildish, pers. comm.) has been recorded from altitudes of 1500 m on Mount Olympus, Greece (Spicer, Moore and Taylor, 1987). These ecological divisions can thus be used for general purposes, but must not be applied too rigidly.

The earliest reference to amphipods in localities well away from the ocean was by J.D. Dana (1853), who collected landhoppers from forest leaf litter in Tahiti and New Zealand. Early amphipod systematists tended to describe species on the basis of gnathopod configuration alone, causing unrelated taxa to be lumped under the same generic and/or specific names. The limitations of this approach were overcome by workers such as Bousfield (1971, 1982, 1984), Hurley (1975), and Friend (1980), who recognized the two basic morphological types of talitrid, (species with sexual dimorphism of the gnathopods, and species with sexually similar gnathopods) and used a broader basis of comparison, with characters from all body regions. The history of terrestrial amphipod systematics, including an account of the biological and ecological publications concerning landhoppers, is summarized by Friend (1980).

The New World landhoppers are a relatively recent discovery. Prior to 1959, terrestrial amphipods had not been recorded in Central or South America (Hurley, 1959). A few unidentified specimens were subsequently collected. Hurley (1968) cited unpublished records of forest dwelling amphipods from Jamaica, Haiti and Panamá. Bousfield (1978) mentioned landhoppers from Jamaica, and mountainous areas of Central America. Friend (1980) mentioned a personal communication from Bousfield regarding a Mexican record. Ecological works on Central American forest leaf litter faunas (Anderson, 1982; Buskirk and Buskirk, 1976; Levings and Windsor, 1982; and Mitchell and Peck, 1977) have mentioned unidentified terrestrial amphipods. In a discussion of evolutionary relationships within the Talitridae, Bousfield (1984) referred to a sexually dimorphic talitrid from Costa Rica and Panamá as "Parorchestia", and described the genus *Caribitroides* (type species *C. jamaicensis* Bousfield

1984) from Jamaica, noting that several undescribed species occur in material from Central America. Apart from these reports, no other information is available on New World species.

1.2 Adaptation to Land

Hurley (1959) suggested that terrestrial amphipods were independently derived from "supra littoral ancestors", and that "the [most probable] mechanism of speciation is speciation by neoteny — the retention of juvenile or embryonic characters in the adult." A discussion of adaptation to the terrestrial environment (Hurley, 1959, 1968) included four major categories of change: locomotion (from swimming, in aquatic species, to jumping [sic. normal locomotion is walking] in terrestrial ones), breeding, breathing, and excretion. Tendencies toward smaller brood size, larger egg size, and larger and more complex gills were noted as forming a gradient of terrestriality, from beachfleas to landhoppers. Excretory changes apparently involve simply a suppression of nitrogen metabolism, rather than transformation of ammonia to other less toxic products (Spicer, Moore and Taylor, 1987).

Morphological tendencies observed in terrestrial species (Bousfield, 1981, 1982, 1984; Friend and Richardson, 1986; Hurley, 1959, 1968) include:

- 1. reduction of subchelate male gnathopods to a "juvenile" or "feminized" state, in which gnathopod 1 is simple (or only weakly subchelate), and may lack pellucid lobes entirely, and gnathopod 2 retains the mitten shaped propod, and merus/carpus pellucid lobes seen in juveniles and females;
- 2. reduction and loss of pleopods, from a simple shortening of pleopod 3, to reduction of one or more pleopods (or their rami) to vestigial stumps;
- 3. enlargement of gills, folding of the gill surfaces, and proliferation of convolutions and/or secondary lobes (the increased surface area obviously has some effect on gas exchange, but the purpose or benefit of this remains unknown);
- 4. elongation and slimming of the body and appendages, and reduction of spines and processes thereon;
- 5. reduction in brood plate size and setation;
- 6. enlargement of the eye

The most obvious adaptation to a terrestrial existence is a cryptozoic, moisture-seeking behaviour, which was deemed a universal characteristic of terrestrial species (Hurley, 1959). A physiologically important feature which was noted, but the potential of which was not explored, was the tolerance of landhoppers to immersion in fresh water. Lawrence (1953) noted that *Talitrus* (= *Talitriator*) *eastwoodae* Methuen could survive for up to 9 days in fresh tap water. Moisture requirements of the animals were considered to be met by the humidity inherent in the leaf litter habitat, and dessication was avoided through moisture seeking behaviour (Hurley, 1968).

Feeding was considered to require no great change between the aquatic and terrestrial environments, because the decaying seaweed diet of supralittoral beach amphipods was deemed to be little different from the decaying leaf diet of landhoppers (Hurley, 1959). This point is debatable, since the biochemical and cellular makeup of seaweed, driftwood and leaf litter may be very different to the organisms which feed upon them.

Wildish (1979, 1982a) listed the basic adaptations to a terrestrial existence as the adoption of cryptozoic habits, and reduced growth rate and adult body size (with consequent reductions in brood size and number of broods per year). He also noted tendencies toward: a sex ratio bias in favour of females, female body size being larger than male, and biogeographic endemism. The freshwater littoral was proposed as a route for colonization of land, with evolution proceeding from estuarine species, toward terrestrial species. A second hypothesis proposed by Wildish (1982b) explored the evolutionary implications of the supralittoral driftwood ecological niche. The adaptations required for colonization of this niche were suggested as logical preadaptations for a leaf litter environment.

Matsuda (1982) discussed genetic assimilation as a possible mechanism of evolution in talitrid amphipods. He noted that it is the physiology of animals, including their hormonal activity, which is first affected by environmental changes. The gland which produces an androgenic hormone necessary for spermatogenesis, and the production of secondary male sexual characters, is controlled by a hormone from the light-sensitive X organ/sinus gland, which also affects the production of ecdysone (the moult hormone). Matsuda hypothesized that the lower light levels in a leaf litter habitat would reduce the titre of the androgenic gland- controlling hormone. Deinhhibition of the androgenic gland would increase androgenic hormone levels, and result in precocious male maturity. Females have no comparable mechanism to accelerate oogenesis, hence the tendency toward large females, and small males. Slower moulting associated with the terrestrial habitat can also be explained by inhibition

of the Y organ by a hormone from the X organ/sinus gland (Matsuda, 1982).

The tendency to fewer, larger eggs in terrestrial talitrids may be associated with low salinity (Matsuda, 1982). Production of yolk-rich eggs in brackish water and fresh water habitats occurs in some other groups of invertebrates (Matsuda, 1982). The low light conditions of the leaf litter enhances secretion of vitellogenin- stimulating ovarian hormone, which results in large amounts of yolk per egg. Several terrestrial adaptations can therefore be explained by the effect of environment on pre-existing physiological/ hormonal mechanisms (genetic assimilation) (Matsuda, 1982).

Matsuda's hypotheses were challenged by Duncan (1985). His measurements of light intensities in supralittoral and forest leaf litter habitats showed great variation in light intensities within habitats, but no significant difference between habitats. Duncan also pointed out that there is no evidence that the amount of androgenic hormone released in talitrids diminishes with diminishing light intensity. In temperate North America, the moult frequency of the talitroidean amphipod *Hyalomma azteca* (Saussure) is controlled by photoperiod and temperature (de March, 1977, 1978). Whether these factors are relevant in rain forest landhoppers living near the equator is unknown.

Duncan (1985) proposed an hypothesis for the evolution of landhoppers in which primitive estuarine supralittoral species were isolated by geological uplift, and forced into adjacent terrestrial environments. These estuarine species would have been preadapted by having a lowered haemolymph osmotic pressure and an ability to cope with rain or river soaked litter. After isolation through a geological/geographic event, gene flow with the parent estuarine species would cease, and the new species would proceed with further adaptations to the terrestrial environment. Duncan felt that these adaptive changes were probably made through "traditional" genetic mechanisms, rather than genetic assimilation. He also pointed out that the majority of supralittoral species are not appropriate ancestors for landhoppers because they are adapted to hypertonic environments, whereas terrestrial habitats are strongly hypotonic.

Lazo-Wasem (1984) studied aspects of the physiology and behaviour of *Arcitalitrus sylvaticus* (Haswell). He found that acclimation temperature affected upper lethal temperature. Animals accustomed to higher normal temperatures survived exposure to higher extremes than cool-acclimated animals. Water loss through transpiration was higher in dry air than in moist air. In dry air there was a pronounced temperature effect, which was

negligible in moist air at temperatures below 30 °C. Survival times in various temperature/humidity combinations increased with greater humidity and lower temperature. All individuals showed strong hygrokinesis, moving along moisture gradients toward the highest humidity (Lazo-Wasem, 1984). Positive orientation to moist air has also been established for beachfleas (Williamson, 1951).

Spicer, Moore and Taylor (1987) presented a comprehensive review of talitrid physiology, discussing water relations, ionic and osmotic regulation, respiration, temperature tolerance, activity, locomotion and rhythmicity, sensory apparatus and cuticular microstructures, and feeding. They noted that, although experiments on transpiration were difficult to compare due to varying experimental methods, the following generalities were evident: beachfleas and landhoppers apparently lose water from the whole body surface; smaller animals lose water faster than larger ones; and dead animals lose water at an equivalent rate to live ones (ie, no active water conservation mechanisms). Differences in humidity tolerances and transpiration rates were thought also to be a function of size, since landhoppers tend to be smaller than the more heavy bodied beachfleas and sandhoppers. It was also noted that although beach species tend to show reductions in gill size and surface area (long assumed to be an adaptation to reduce water loss), landhoppers usually have a greater gill area than beachfleas. The assumption that talitrids require chloride ion as an environmental factor, thought by Bousfield (1982, 1984) to limit distribution, was refuted (Spicer *et al*, 1987).

These workers reported that two species of *Orchestia* Leach can remain alive indefinitely in well aerated sea water, but landhoppers are unable to survive prolonged immersion. The tolerance of beachfleas for fresh water and landhoppers for salt water was not documented. Available data on the oxygen transporting properties of the haemolymph indicate the presence of a pigment with high oxygen-affinity, unlike the low oxygen-affinity pigment present in other terrestrial and supralittoral crustaceans. Several other examples of unique talitrid physiology were cited, indicating that extrapolation from other crustacea, including isopods, is rarely applicable to talitrids (Spicer, *et al*, 1987).

1.3 Phylogenetic relationships

Talitrid amphipods are taxonomically difficult (Bousfield, 1984), and relatively few biologists are familiar with even the existence of terrestrial amphipods (Friend and Richardson, 1986). It is not surprising that little work has been done on the phylogeny of this group. An early attempt at an evolutionary classification for talitrid amphipods was by Bulychева

(1957), who proposed a phylogeny of the superfamily Talitroidea Bulycheva based mainly on gnathopod form. She considered the ancestral stock to be within the family Hyalidae Bulycheva, which was itself derived from a gammaridean ancestor. Littoral zone hyalids invaded the beach (supralittoral) habitat, then proceeded inland after further development of the jumping apparatus. It was proposed that the family Hyaellidae Bulycheva was secondarily aquatic, derived from beachflea/terrestrial ancestors, and geologically old (the only non-marine representatives in the superfamily Talitroidea are the supralittoral and terrestrial Talitridae, and the freshwater Hyaellidae). The genus *Talitrus* Latreille was proposed to be the oldest of the Talitridae, and close to the ancestral root (see Figure 1).

Friend (1980) thought that both sexually dimorphic and sexually similar talitrids were polyphyletic, and that terrestrial adaptations produced convergent morphologies in unrelated lineages. A table of characters with plesiomorphic and apomorphic states, which showed the morphological progression from a (primitive) beachflea, *Orchestia*, through what Friend considered plesiomorphic landhoppers, to apomorphic landhoppers, was presented. The progression away from the beachflea facies to landhoppers did not occur as a smooth cline, but showed evidence of mosaic evolution (*sensu* Schram, 1982). Different groups (which may or may not constitute discreet clades) may share parallel changes in some characters, while other characters remain unchanged in one group, but not in another. The tendency of apomorphic terrestrial species to have sexually similar gnathopods was considered an indication that sexual dimorphism of gnathopods had been lost a number of times, in different phyletic lines (Friend, 1980).

Bousfield (1981) stated that the most primitive talitroidean family was the Hyalidae. The family Hyaellidae Bulycheva was considered closely related to the hyalids (refuting Bulycheva's phylogeny). The actual relationship of supralittoral (beach) and terrestrial amphipods of the family Talitridae to the marine littoral Hyalidae was not explored. Within the Talitridae, certain beachfleas were noted to have many primitive characters, while sandhoppers were considered very specialized, and highly advanced.

Although not presented as a phylogeny, a phenogram (see Figure 2) constructed by Bousfield (1982) inferred evolutionary trends within subgroups of the family Talitridae, and was used to "suggest new insights into their evolutionary history". A table of morphological characters (Bousfield, 1982 Table IV) was used in a "simplified two-stage average linkage" cluster analysis to produce the phenogram. The dentition of the left mandibular lacinia mobilis, and the presence or absence of cusps on the dactyls were considered to be

two characters of "transcending significance". The same phenogram was presented in a later publication (Bousfield, 1984) to illustrate that beachfleas and sandhoppers constitute distinct groups, and that landhoppers are morphologically remote from sandhoppers.

Bousfield (1984) divided landhoppers into two phyletic types: (1) a non-cusate (lacking small teeth on the dactyl bases at the dactyl/unguis suture), "ancient" group, probably derived from palustral (estuarine/semiterrestrial) ancestors in southern (Gondwanaland) regions; and (2) a cusate (bearing dactyl cusps) "modern" group, of tropical and warm temperate coastal regions of both hemispheres, derived from beachflea ancestors (specifically those with 4 teeth on the left lacinia mobilis). Both of these groups contain sexually dimorphic and sexually non-dimorphic representatives; the latter "were apparently derived independently and convergently within each phyletic group as a result of neotenic loss of the ancestral 'amplexing' male gnathopod 2". Regarding the Caribbean landhoppers, he stated that "the relatively primitive shore-dwelling *Tethorchestia* Bousfield subgroup [of the four-dentate *Orchestia* group of beachfleas] apparently gave rise to the more advanced, non-sexually dimorphic species of the *Caribbitoides* landhopper group" (Bousfield, 1984).

In a recent attempt to address the phylogeny of the Talitridae, Bousfield (1984) presented a diagram of hypothetical relationships among groups of talitrids (Figure 3). This diagram was apparently based on arbitrary groupings of talitrids into palustral amphipods, beachfleas, sandhoppers, and landhoppers (no supporting data was included). Each group was further subdivided by lacinia mobilis dentition and dactyl cusps. In comparison, the phenogram (Figure 2) presented earlier (Bousfield, 1982) does not support the large phyletic distance hypothesized between cusate and non-cusate landhoppers.

1.4 Biogeography

Landhoppers are generally believed to have low vagility (Bousfield, 1984; Friend, 1980; Wildish, 1982b), and may therefore pose interesting questions in biogeography. The tendency to local endemism is well documented (Bousfield, 1984; Friend, 1980, 1987; Hurley, 1959; Wildish, 1982b). Hurley (1968) suggested four hypotheses to account, in whole or in part, for the world distribution of landhoppers:

- (a) continental drift
- (b) distribution along continental margins and island arcs

- (c) local origins from littoral species
- (d) distribution by man.

In his generic subdivision of sexually similar landhoppers, Hurley (1975) noted affinities which corresponded to geographic areas, and postulated a single origin for the group, in Gondwanaland.

Friend (1980) suggested a Gondwanaland origin for the supralittoral (beach) Talitridae, but proposed that the modern world landhopper (terrestrial) fauna is the result of a limited number of different invasions of the land, occurring from before the breakup of Gondwanaland until the present. The tendency toward endemism in landhopper faunas was suggested to be evidence either for previous land connections with a source area, or local evolution of terrestrial species from (more vagile) supralittoral ancestors. Lack of landhopper faunas in areas which apparently possess suitable climates may indicate extinctions of terrestrial lines. It may also be notable that few areas of former Laurasia have native landhoppers (Friend, 1980).

Bousfield (1982) commented on the lack of native terrestrial amphipods in North America, despite their presence in Central America, Cocos Island, the Galápagos Islands, Hawaii, and Japan. In the last three cases, the antecedents of the terrestrial taxa are quite clear. The Japanese species *Platorchestia japonica* (Tattersall) is closely related to the common beach-flea *Platorchestia platensis* (Kroyer). *Floresorchestia pickeringi* (Dana) is closely related to *Floresorchestia floresiana* (Weber), in Hawaii and other south sea islands. *Chelorchestia vaggalla* (Bowman) of the Galápagos is related to the palustral *Chelorchestia costaricana* (Stebbing). Bousfield implied in his paper that many derivations of terrestrial taxa from local ancestors is a preferable hypothesis to the idea of a single origin, and subsequent continental drift dispersal.

In a later attempt to explain the world distribution of landhoppers, Bousfield (1984) discussed the origin and evolution of the family Talitridae. The initial radiation of this group was attributed to the breakup of the Pangaea supercontinent. Two phyletic lines of landhoppers were postulated, the non-cusate type having been derived from estuarine "palustral" ancestors in Gondwanaland, and the cusate type having been derived from four-dentate beachflea ancestors along Tethyan shorelines of both hemispheres. Both of these phyletic lines contained sexually dimorphic, and sexually non-dimorphic genera, the

latter derived independently and convergently, through neoteny. Sexually dimorphic landhoppers tend to be ecologically restricted, occurring near the coast and/or in areas of heavy precipitation, but retain some marine dispersal capability, and can populate offshore islands, including geologically young volcanic islands. Non-dimorphic landhoppers are more eurytopic, existing in much drier and colder continental regions, but have almost no marine dispersal ability, and rarely occur naturally on volcanic islands (although synanthropic introductions are common). Estuarine and beach dwelling amphipods retain a much greater capacity for marine dispersal than any landhopper (Bousfield, 1984).

Several anomalies are apparent in the distribution of Middle American landhoppers, as known at present. No landhoppers have been reported from Cuba or Puerto Rico, despite their presence on Jamaica and Hispaniola (Bousfield, 1984). It is unknown whether or not any landhoppers occur between southern México and Costa Rica, or in South America; lack of records (as in the case of the Central American landhoppers) is not conclusive proof of absence. Bousfield (1984) stated that the sexually dimorphic form in Costa Rica/Panamá ("Parorchestia") was not the same as the sexually similar genus of Jamaica and southern México (*Caribitroides*), but did not offer an explanation of how they might be related.

1.5 Thesis objectives

Within the framework presented above, I undertook a study of the systematics of available collections of terrestrial amphipods from México and Central America.

- 1. The available landhopper material from México and Central America was described, figured and keyed.
- 2. Field studies of the biology of local landhoppers were undertaken at two sites where field station facilities were available. Studies of quantitative and qualitative distribution, observations on feeding and behaviour, size frequency analysis of preserved specimens, and experiments on immersion tolerance in both salt and fresh water were included. This work was intended to develop baseline information on the biology of New World landhoppers, compare representatives of two different genera, and speculate on how biological parameters relate to distribution and zoogeography of these animals.
- 3. An analysis of talitrid genera was undertaken, based on the generic characters, character states and data of Bousfield (1982). The objectives of this analysis were

to establish which genera may be most closely related to, and the possible phyletic derivation of, the New World landhoppers. The hypothesis being tested was that the New World landhoppers were derived from local *Tethorchestia* group (beachflea) ancestors, as proposed by Bousfield (1984).

- 4. Using a character set specifically constructed for the New World landhoppers, a species analysis was undertaken, including those taxa that the generic analysis indicated might be most closely related to the American landhoppers.
- 5. A phylogeny was constructed for the New World landhopper species.
- 6. The affinities indicated by the phylogeny, and the local geological history, were used to construct a biogeographic scenario offering an explanation of the present distribution of terrestrial amphipods in México and Central America.
- 7. A discussion of terrestriality in talitrid amphipods explored adaptation to the leaf litter habitat, and the effects on morphology, reproduction, behaviour and physiology. Mechanisms of evolution and speciation within the group were considered.

Figure 1: An early hypothesis of talitroidean phylogeny (including genera known at that time), proposing that a gammaridean ancestor gave rise to the family Hyalidae. The family Talitridae then evolved from a hyalid ancestor. The Hyaletidae were considered secondarily aquatic. Bulycheva (1957, page 55).

Figure 2: A phenogram showing similarities among talitrid genera, and used in a preliminary discussion of talitrid evolution. Bousfield (1982, Figure 28).

Figure 3: An hypothesis of talitrid phylogeny with a proposed time scale, showing the derivations of principal ecological/evolutionary groupings. The presence or absence of dactyl cusps and the number of teeth on the left mandibular lacinia mobilis (dentition) were considered very important. After Bousfield (1984, Figure 9).

Chapter 2 MATERIALS AND METHODS

Specimens for taxonomic study were collected by Dr. S. B. Peck, Dr. H. F. Howden, Dr. L. Masner, Dr. A. Newton, and the author, and were borrowed from the collections of the National Museum of Natural Sciences, National Museums of Canada (NMC), Ottawa, the Smithsonian Institution (USNM), Washington, and the Museum of Comparative Zoology (MCZ), Harvard University.

2.1 Collection and Preservation

Forest habitats examined by the author include the leaf litter, the overburden (moss, ferns and epiphytes growing on trees), fallen logs, bromeliads and tree fern axils. Beach habitats included the sand above and below high tide line, drift and wrack piles, and estuarine and mangrove mudflats.

Field methods used to collect specimens included the following:

- 1. baited and unbaited pit traps, in most ground level habitats, including beaches and mudflats above high tide line;
- 2. beating of vegetation, using an entomologist's stick and sheet;
- 3. leaf litter and wrack sifting and processing in Berlese funnels (used for collecting live specimens as well as preserved ones);
- 4. hand collecting with an aspirator in leaf litter, and on beaches at night when amphipods are active on top of the sand and wrack;
- 5. quantitative box sampling and processing in Berlese funnels.

Preservation was in 70 % ethanol with 2 % propylene glycol. In some cases, field preservation was in whatever preservative was available, with subsequent transfer to ethanol.

2.2 Field Biology

Field studies were undertaken at two sites at which field station facilities and organizational support were available:

- 1. the Monteverde Cloud Forest Reserve, Monteverde, Puntarenas Province, which is administered by the Tropical Science Centre, San José, Costa Rica; and
- 2. the Estación de Biología de Los Tuxtlas, 33 kilometers north of Catemaco, Veracruz State, administered by the Universidad Autónoma de México, México, D.F.

The vulnerability of landhoppers to pit traps was established by a series of simultaneous transects of 5 traps each in similar habitats, with dung, fruit, and no bait; propylene glycol, and salt water preservatives; and moss for live trapping. The pits were large plastic beer cups set into the soil such that the rims were flush with the soil surface. Normally a section of *Heliconia* leaf was placed over each trap as a rain roof. Since there were no significant differences among catches, it was concluded that bait and preservative have no effect on pit trap efficiency.

Initial experiments on quantitative distribution and methodology were made by scooping measured areas of leaf litter into the sifter, processing the siftate in Berlese funnels and hand sorting the residues afterward. The most efficient heat source for the Berleses was a 60 watt light bulb (100 watts killed the animals in the leaf litter). A twelve hour Berlese run was 95 to 100 % efficient in driving all amphipods in the sample down into the collection cup. Initial estimates of amphipod density were applied to the table of density versus sampler size provided by Downing (1979) to establish an appropriate number of replicates. The replicates were taken in a random distribution within a five meter square of any given habitat.

At each quantitative sample site, temperature was taken just above the leaf litter, at the soil surface, and in the soil at a depth of 7 cm. A maximum-minimum thermometer was placed at the site to record overnight temperature fluctuations. Leaf litter depth was recorded for each replicate, and a separate series of unsifted samples taken to determine leaf litter water content for the site. A standard method of drying was used for each water content sample. Although the crude drying apparatus probably did not dry the samples completely, the values are at least comparable estimates of relative moisture content within each sample set. Precipitation values were obtained from local meteorological records. Relative humidity of the air was recorded, but Friend (1980) showed that the relative humidity in the leaf litter is much higher than that of the air, and even in the dry season returns to maximum values overnight.

Live animals were captured by hand aspirating leaf litter scooped onto a ground sheet, and by Berlese processing of sifted litter with damp moss in the collection cups rather than preservative. Live pit trapping was rather ineffective due to high mortality among captured individuals from heat and ant predation.

Pit traps were used in habitat and movement studies. They were placed in transects parallel and perpendicular to streams, large fallen logs, ravine slopes, light gaps, large forest clearings, and man made clear-cut areas. The traps were inspected daily in 5 day experiments, to establish where animals were active. Two replicates of each transect were performed. Traps were closed between replicates by placing another cup full of soil into the emptied trap cup, to reduce perturbation of the area. Diurnal activity was tested using pit trap transects, which were inspected every six hours, at 6 AM, 12 noon, 6 PM and 12 midnight. Four replicates of this 24 hour experiment were run in two habitat types, with the traps opened at a different time for each replicate to reduce any time or opening bias.

Limited mark and recapture experiments, and movement experiments with Tanglefoot (a sticky substance designed to trap insects that try to cross it) applied to logs and trees were also attempted.

Live amphipods were held in petrie dish habitats for daily observation, to try to establish intermolt intervals, mating periodicity and behaviour, care and hatching interval of eggs, and for general observations of feeding, locomotion and behaviour. Animals were held singly, through male-female pairs, to groups of various sizes, sexes and ages. Each petrie dish was furnished with sufficient leaf litter to provide food and cover, yet allow observation. Water was introduced daily by eye dropper. The petrie dishes were not sealed. The studies were performed at field stations which lacked temperature control, so the experimental temperatures were simply the ambient temperatures inside the buildings (often much hotter than the forest leaf litter). Attempts were made to bring landhoppers back to Canada for further experimentation, but all failed. The animals died in transit.

Feeding was observed in the petrie dish habitats and in separate experimental dishes. Food choice experiments in clean dishes tested starved animals' preferences with fresh and aged leaves, and aged leaves of different species. Leaves were aged two weeks on the forest floor in gauze bags.

Adult specimens were held in jars of earth with and without leaf litter, to observe whether or not they would attempt to construct burrows.

Drowning experiments were performed in clean high sided petrie dishes 8.7 cm in diameter and 2.3 cm deep. Seawater collected from the ocean and freshwater from clear forest streams were placed in the dishes to a depth of approximately 1 cm. It was felt that the large surface area of these petrie dishes would provide sufficient oxygen to the water so that agitation (a procedure difficult to quantify) was not necessary. Attempts were made to place 10 adults of both sexes and 15 juveniles of various sizes in each dish. Due to handling difficulties and escapes, these numbers varied. Food portions were very difficult to quantify under field conditions, so the animals were fed very little.

In these drowning experiments, a replicate consisted of one petrie dish and its contents (water and test animals). Three replicates of adults and three replicates of juveniles were performed with salt water and freshwater respectively. The dishes were observed as much as possible for 96 hours (4 days). Amphipods were considered dead when they did not respond to a light squeeze from soft forceps. Time of death was noted. If less than 50 % of any trial's test animals were dead at the 96 hour point, the experiment was continued to 192 hours (8 days).

Analysis of drowning data and estimates of lethal exposure (immersion) for 50 % of the sample (hereinafter called LI50) were performed using standard bioassay procedures as outlined by Sprague (1973, and pers. comm.). The toxicant concentration in this case was taken to be the time to death. Cumulative per cent mortality was converted to probits using the tables in Hubert (1980), and graphed against time to death on log (base 10)-probit paper. The immersion tolerance curves were calculated by linear regression. The LI50 was taken as the point where the line crossed 50 % mortality (which equals the probit 5.0). The mean of each three-replicate experiment was calculated, and compared.

Body lengths of preserved specimens were measured from rostrum to telson tip with a dissecting microscope, using a finely divided ruler mounted on a piece of plexiglass in which appropriate width slots were cut, such that the animals could be straightened and held steady within the slot (Lindeman, 1982). Antennal segment counts were taken at the same time, for size frequency analysis.

Sufficient specimens were available from field work to allow a limited size frequency analysis. Several hundred specimens were measured. Lengths were grouped into length intervals and bar graphs constructed to see if instar sizes would manifest as distinct peaks. Since the peduncular segments of both antennae were constant from hatching, flagellar antennal segment numbers (for A1, A2 and A1 + A2) were graphed against total length

for males, females, juveniles, and all specimens. Only graphs of $A1 = A2$ are included, although the other data were taken into consideration in instar analysis.

2.3 Study, Preparation, and Illustration

Specimens were examined, sorted, and dissected in alcohol under a dissecting microscope. The method outlined by Barnard (1969) was used to dissect specimens. Mouthparts, telson and third uropod were mounted under one coverslip, and the antennae, pereopods, pleopods, epimera, and uropods 1 and 2 were mounted under another coverslip on the same slide as is the convention (Bousfield, pers. comm.). The mounting medium, for permanent mounts, was polyvinyl lactophenol with lignin pink stain.

A representative series of slides was made for each population; 10 males and 10 females where the number of specimens allowed. When few specimens were available, or the material was from a museum, temporary slide mounts in glycerin were used, or the undissected specimens were carefully examined under very high power. Dry mounts of gnathopods and maxillipeds were made on insect pins with paper "points". These were examined under high power using dissecting microscopes and a scanning electron microscope at Carleton University to determine fine detail in cases where slide preparations did not permit sufficient detail to be resolved (particularly in cases of three dimensional structures such as the maxilliped palp). A full SEM investigation was, however, beyond the scope of this study.

Drawings of most appendages were made from the permanent, or in some cases, temporary slide mounts, using a Nikon binocular compound microscope fitted with a Wild camera lucida. Habitus outlines were drawn from specimens in alcohol, using a Wild M5A dissecting microscope with a camera lucida. Details of the appendages on the habitus illustration were drawn from slides projected onto the habitus outline using a microprojector, and corrected if necessary by comparison with specimens, and the higher magnification appendage drawings.

2.4 Descriptions of new taxa

Each lot of specimens collected at one time and in one place was assumed to be of the same species unless morphological differences were distinct. A species was defined as those lots of specimens which were morphologically indistinguishable from the type lot.

Descriptions were based on examination of slide mounts and preserved material, under

high power on a Zeiss compound microscope, and a dissecting microscope. Types were chosen from the most representative and best preserved lot. A female holotype (usually an ovigerous female) and a male allotype were selected from the same lot if possible. In most cases, slide mounts were prepared from these specimens; when this was not done, very careful examination under high power was performed with a dissecting microscope, in order to preserve the types in an undamaged state.

In the species descriptions, spine (setal) counts are given first for the holotype, then the range observed is given in square brackets. Spine counts on anterior and posterior margins of pereopod segments omit the setal cluster at the anterior and posterior distal angles, and spine counts on the dorsal margins of uropod rami exclude the terminal cluster, unless otherwise stated.

2.5 Evolutionary analysis

The character tables and phenogram constructed by Bousfield (1982) was used as a starting point for this study. Bousfield chose 39 characters of a possible 60 (Bousfield, 1982, Table I), and scored 16 taxa for those characters (Bousfield, 1982, Table IV). These data were checked by the author against available specimens and/or literature, as completely as possible. *Talitrus* character 15 was corrected from the apomorphic state to the alternate apomorphic state.

Ten taxa were added to Bousfield's table, scored as closely as possible by the same criteria (Bousfield, 1982, Table 1). Characters were obtained directly from specimens for the taxa *Caribitroides*, *Mexitroides*, and *Cerrorchestia* (landhoppers), and the Caribbean beachflea *Tethorchestia*. Data for the South African landhopper *Talitriator* were drawn partly from literature (Methuen, 1913), and partly from available specimens. *Floresorchestia* was scored partly from literature (Bousfield, 1971), and partly from specimens. *Parorchestia gowerensis* was scored from the original description (Bousfield, 1976). Data for *Parorchestia tenuis* were obtained from Hurley (1957), although the identity of the species described may be in question (Friend, 1980). The taxa *Agilestia* and *Austrotroides* were scored from the original descriptions (Friend, 1982). These latter five taxa were judged to be reasonably representative of the world landhopper fauna.

Initially, an attempt was made to incorporate all the qualifiers shown in Bousfield's Table IV (1982) into a complete character matrix. However, these multiple state characters badly obscured the results of the initial analyses. As the information content of the +

and - qualifiers was questionable, and since Bousfield had himself "slotted [characters] into either the primitive or advanced category" (Bousfield, 1982), qualifiers were omitted, and the characters scored as either plesiomorphic (0) or apomorphic (1). Characters with alternate apomorphic states were each broken into two binary characters; the plesiomorphic state codes as 00, the apomorphic state as 10 and the alternate apomorphic state as 01, as suggested by Dr. J. McNeill (pers. comm.)

Phenetic analysis was performed with the CLUSTRIT package (written by L. P. Lefkovitch, Biosystematics Research Institute) using simple matching and Jaccard coefficients, in Average Linkage, Flexible Sort, Steiner tree, and Incremental Sum of Squares algorithms. Principal components and principal coordinates analyses were run using the SAS statistical package (SAS Institute). Cladistic analyses were performed using the PHYLIP package (written by J. Felsenstein, University of Washington), using parsimony (MIX) and compatibility (CLIQUE) programs. Three variations of MIX were used; Camin-Sokal parsimony, which allows no character reversions, Wagner parsimony, which allows characters to revert to the plesiotypic state, and mixed parsimony, in which the parsimony method is chosen for each character. The Wagner trees were rooted using the "ancestor" option, which gives direction to the character states. All computer analyses were run on the Amdahl mainframe at the Université d' Ottawa. In the interests of brevity, only the results from the principal components, average linkage (both simple matching and Jaccard coefficients), and parsimony (Camin-Sokal, Wagner, and mixed methods) analyses are reported, although the results from the other analyses were taken into consideration.

The first generic analysis, using the full character set as in Bousfield (1982 Table IV), gave unsatisfactory and inconsistent results. In several subsequent analyses, attempts were made to identify and delete characters which contributed little information to the analysis, or contributed to instability of the results (extremely high step number in the cladograms, for example). A total of eight characters (characters 18, 25, 27, 34, 41, 42, 50 and 52) were deleted from Bousfield's original data set. To simplify analysis further, four taxa whose relationships were well established (Bousfield, 1982, 1984) (a beachflea and three sandhoppers) were deleted. The final data set used here consisted of 22 taxa and 34 characters. The results of these analyses were used to judge which species were most closely related to the New World landhoppers, and to interpret general trends of evolution within the talitrid amphipods.

The species character set was composed of some characters from the generic matrix, and

new characters drawn from the species descriptions. All characters in the species matrix were obtained from the examination of specimens. The taxa scored for this character set included the New World terrestrial species and those species deemed most closely related to them, based on the results of the generic analyses. The same series of phenetic and cladistic analyses as above were performed. The results were compared, and integrated with biogeographic literature and biological information, in order to construct a phylogeny and to assist with interpretation of the zoogeography of Central American landhoppers.

Chapter 3 IDENTIFICATION OF TALITRID AMPHIPODS FROM MÉXICO AND CENTRAL AMERICA

The following key is designed to allow identification by non-specialists of common genera of seashore and inland talitrid amphipods of Middle America, without the need for slide mounts. Characters requiring slide mounts are used, as far as is possible, for verification only. Since many important characters are on the gnathopods, and sexual dimorphism or lack of it is the most convenient way to separate genera, users of this key must be able to determine the sex of a specimen.

The general morphology of a female talitrid amphipod (or either sex of non-sexually dimorphic, terrestrial species) is shown in Figure 4. The peduncle of antenna 2 is slender, and the pleopods short, as is typical of terrestrial species. Body parts useful in identification, with labels defining segments and features of note, are diagrammed in Figure 5 and Figure 6 (after Bousfield, 1973, 1982; Holsinger, 1976; McLaughlin, 1980).

Landhoppers generally show no sexual characters until the animals are quite large. In contrast, beach fleas may acquire some secondary sexual characters at a fairly small size, but not develop all characters until several instars later (Wildish, 1972). For example, *Tethorchestia* males develop the powerfully subchelate propod of gnathopod 2 at a fairly small size, but the distinctive setal brushes on the inner distal angles of P7 propod are evident only on the largest males. The best way to begin identification of specimens is to choose the largest individuals available in the sample.

The easiest way to sex an amphipod is to look for eggs in the brood pouch. Gravid females are often evident in profile. If no eggs are present the animals must be turned to expose the venter, and the coxae of pereopods 2 to 5 examined for oöstegites (see Figure 5). Oöstegites are thin, flat plates which occur on gnathopod 2 and pereopods 3, 4, and 5 of females only. They are distinct from the gills, which occur on the coxae of gnathopod 2, and pereopods 3, 4, 5, and 6. The gills are soft flap-like or sac-like structures much thicker than the oöstegites, and often bear lobes and convolutions (see Figure 15). If the animal is in breeding condition, long setae are visible on the oöstegites. If the animal is not in breeding condition the oöstegites lack setae but are still visible, except when the individual is very young. Gonopores are not visible in all species. They occur on P5 in females.

Intersex individuals are not uncommon among talitrid amphipods (see Wildish, 1987). When individuals which are difficult to sex are encountered, all of the secondary sexual characteristics must be checked. In sexually dimorphic species the adult males bear a large, powerfully subchelate propod on gnathopod 2 (see Figure 8 and Figure 11), which is visible even to the naked eye. The propod of gnathopod 1 is also enlarged, but not to the same extent (see Figure 11). Another characteristic is enlarged peduncular segments of antenna 2 or, in some species, elongation of the flagellae. If an individual is of large size, but has no oostegites, the venter of pereon segment 7 must be examined for penil papillae. These occur as short, fleshy cylinders between or slightly behind the coxae of pereopods 7. In poorly preserved specimens, the penil papillae can be very difficult to see.

If adults are lacking in the sample, slide mounts of the largest specimens may be made to attempt identification; however, immature amphipods frequently lack diagnostic characters, and are often of limited use in taxonomy.

The following is a list of abbreviations used in illustrations and the key.

sex	f.	female
	m.	male
antennae	A1	antenna 1 (antennule)
	A2	antenna 2
	ped	peduncle (also in pleopods, uropods)
	flag	flagellum (also in pleopods)
mouthparts:	UL	upper lip
	LL	lower lip
	MXPD	maxilliped
	ip	inner plate of maxilliped
	op	outer plate of maxilliped
	MX1	maxilla 1
	MX2	maxilla 2
	LMD	left mandible
pereopods:	CX	coxa (leg segment 1, proximal to body)
	BA	basis (leg segment 2)
	BA7	pereopod 7 basis
	IS	ischium (segment 3)

	MER	merus (segment 4)
	CARP	carpus (segment 5)
	PRO	propod (segment 6)
	DA	dactyl (segment 7)
	DA (#)	pereopod (#) dactyl
	GN1	gnathopod 1
	GN2	gnathopod 2
	P (#)	pereopod (3,4,5,6, or 7)
gills:	G1	gill 1, on gnathopod 2
	G2	gill 2, on pereopod 3
	G3	gill 3, on pereopod 4
	G4	gill 4, on pereopod 5
	G5	gill 5, on pereopod 6
oöstegites:	O1	oöstegite 1, on gnathopod 2
	O2	oöstegite 2, on pereopod 3
	O3	oöstegite 3, on pereopod 4
	O4	oöstegite 4, on pereopod 5
pleon appendages:	EP (#)	epimeron, or abdominal side plate 1, 2, or 3
	U (#)	uropod 1, 2, or 3
	PL (#)	pleopod 1, 2, or 3
	ir	inner ramus of uropod or pleopod
	or	outer ramus of uropod or pleopod
	T	telson

Key to Genera of leaf litter and seashore talitrid amphipods of Central America

- 1.(a) Coxal plate 1 anterodistally subacute (Figure 7h); pereopod 5 very short, usually not exceeding merus of P6; P5 dactyl short and swollen, with unguis small or vestigial (Figure 7g); uropod 3 ramus long, cylindrical (Figure 7i); eyes very large, up to 2/3 head length, and nearly contiguous dorsally; antenna 2 sexually dimorphic, flagellum extremely long, may be longer than body in male;

- sandhopper *Pseudorchestoidea* Bousfield 1982
- 1.(b) Coxal plate 1 subtriangular, anterodistally rounded (Figure 7b); P5 equal to or exceeding merus of P6 (Figure 12); P5 dactyl not swollen, unguis not vestigial; uropod 3 ramus conical (Figure 13); eyes normal to small; A2 flagellum no more than 1/2 body length 2
 - 2.(a) Adults sexually dimorphic; male with large, subovate, powerfully subchelate propod of gnathopod 2 (Figure 7i, Figure 11); female with GN2 propod slim, mitten-like (Figure 7c). Terrestrial and semiterrestrial 3
 - 2.(b) Adults not sexually dimorphic; male and female both with mitten-like propod of GN2 (Figure 7c). Fully terrestrial, forest leaf litter inhabitants (landhoppers) 6
 - 3.(a) Male GN1 with pellucid lobes on carpus and propod (segments 5, 6) only (Figure 7b); female GN2 basis anterior margin broadly convex (Figure 7c); U3 peduncle with 3 or more lateral spines, ramus with 1 or more marginal spine in addition to terminal cluster (Figure 7a) U2 inner ramus with double spine row (Figure 7e) 4
 - 3.(b) Male GN1 with pellucid lobes on merus, carpus and propod (segments 4, 5, 6) (Figure 11); female GN2 basis anterior margin sinuous or almost linear (Figure 10); U2 inner ramus with single row of dorsal marginal spines; U3 peduncle with 1 or 2 lateral spines, ramus with terminal cluster only, no marginal spines (Figure 10) 5
 - 4.(a) Female GN2 pellucid lobe on merus very small or lacking; coxal plate 6 anterodistal angle right-angled (Figure 8f); A2 peduncle and P7 carpus sexually dimorphic, incrassate (swollen) in male; U1 lacking inter-ramal spine, inner ramus may have double spine row (Figure 8g), obscure or lacking in immature specimens; P4 carpus very short, little longer than wide; left mandible lacinia mobilis 5 dentate; beachflea *Platorchestia* Bousfield 1982
 - 4.(b) Female GN2 with distinct pellucid lobe on merus; Coxal plate 6 anterodistal angle rounded, carina pronounced (Figure 7f); A2 peduncle and P7 not incrassate in male; U1 with large interramal spine, inner ramus with one spine row

(Figure 7d), and single small proximal lateral spine in males of some species; P4 carpus length more than twice width; left lacinia mobilis 4 dentate; beachflea *Tethorchestia* Bousfield 1982

- 5.(a) Female GN1 propod linear (Figure 8h); male GN2 propod strongly chelate, dactyl toothed, posterior margin sinuous (Figure 8i); P3 and P4 dactyls similar, lacking cusps (Figure 8k); P7 basis posterior margin sexually dimorphic, expanded in female (Figure 8j); gills small, flap-like, weakly convoluted, except G5, which is larger and bears one secondary lobe; antenna 1 much shorter than A2 peduncular segment 4; pleopods long, third little reduced, rami equal to peduncles; palustral, usually found in salt marshes and estuaries *Chelorchestia* Bousfield 1984
- 5.(b) Female GN1 propod short, sublinear (Figure 10); male GN2 propod subchelate, dactyl smoothly arcuate (Figure 11); P3 and P4 dactyls dissimilar, with distinct cusps (see Figure 18); P7 basis not sexually dimorphic; gills large, flap-like, convoluted; G1 large, with secondary lobe; A1 equal to or exceeding A2 peduncular segment 4; pleopod rami distinctly shorter than peduncles, PL3 much shorter than PL1 and PL2 (Figure 11); terrestrial, found in wet forest leaf litter *Cerrorchestia* n. gen.
- 6.(a) A1 peduncular segments elongate, segment 3 very long (Figure 8e); PL3 rami vestigial, reduced to small buds (Figure 8b); U3 peduncle with 3 or more lateral spines (Figure 8c); U1 interramal spine very large, with upturned "spade" tip (Figure 8a); U2 outer ramus lacking dorsal marginal spines (Figure 8d); terrestrial *Talitroides* Bonnier 1898
- 6.(b) A1 peduncular segments short, segment 3 no longer than segment 2 (Figure 12); PL3 with multisegmented rami; U3 peduncle with 1-2 lateral spines (Figure 13); U1 inter-ramal spine normal, without spade tip; U2 outer ramus with dorsal marginal spines (Figure 14); terrestrial 7
- 7.(a) U1 outer ramus unarmed (Figure 14); gill 1 with one or no secondary lobes .. *Caribitroides* Bousfield 1984
- 7.(b) U1 outer ramus spinose (Figure 17); gill 1 with 2 secondary lobes (Figure 18) *Mezitroides* n. gen.

A key to talitrid genera of Pacific shores of North America is available in Bousfield (1982). Included in this work are generic diagnoses for *Platorchestia* and *Pseudorchestoides*, with descriptions of the species of *Pseudorchestoides* which occur on the shores of México and Central America. Although this genus is therein stated to occur only on Pacific shores, the material containing *P. biolleyi* includes an entry from Airport Beach, Limón, which is on the Caribbean coast. Specimens of *P. biolleyi* have also been taken by the author at Cahuita National Park, south of Limón.

Several genera which have not yet been collected from Central America but have representatives on the Pacific shores of northern México or South America are: *Protorchestia* Bousfield (Chile), *Paciforchestia* Bousfield (N. México), *Traskorchestia* Bousfield (N. México), *Transorchestia* Bousfield (Chile), *Megalorchestia* Brandt (N. México), and *Orchestoides* Nicolet (Chile, Peru). These taxa are described, figured and keyed by Bousfield (1982). This publication, and Bousfield (1973) should be consulted by workers desiring an in-depth reference for seashore talitrids, and extensive illustrations of character states. The genera *Tethorchestia*, and *Chelorchestia* are briefly described, but not figured, in Bousfield (1984).

Key to Species of Terrestrial (forest leaf litter) Amphipods in México and Central America

- 1.(a) Female GN2 basis almost linear (Figure 10); GN2 oöstegite (ovigerous female) usually with more than 15 marginal setae; maxilliped apical spine teeth small (Figure 10); male GN1 with pellucid lobes on merus, carpus and propod, propod subchelate (Figure 11); male GN2 lacking pellucid lobes, propod powerfully subchelate; found in moist forests of Costa Rica and Panama *Cerrorchestia hyloraina* n. sp.
- 1.(b) Female GN2 basis anterior margin sinuous (Figure 17); GN2 oöstegite (ovigerous female) with less than 14 setae; maxilliped apical spine teeth lacking (Figure 13) or robust (Figure 17); Adults not sexually dimorphic, male and female both with simple GN1 lacking pellucid lobes (Figure 12) and GN2 with pellucid lobes on merus, carpus and propod; found in moist forests of México 2

- 2.(a) Antenna 1 peduncular segments elongate, segment 3 very long (Figure 8e); U2 outer ramus lacking dorsal spines (Figure 8d); U3 peduncle with 3 strong lateral spines (Figure 8c); pleopod 3 rami vestigial (Figure 8b); U1 interramal spine with hooked, spade-like tip (Figure 8a); known to occur in Oaxaca, introduced *Talitroides topitotum* (Burt)
- 2.(b) Antenna 1 peduncular segments short (Figure 12); U2 outer ramus with dorsal spines; U3 peduncle with 1-2 lateral spines (Figure 15); PL3 rami multisegmented; U1 interramal spine with simple tip 3
- 3.(a) U1 outer ramus smooth; gill 1 with 1 or no secondary lobes (Figure 15) 4
- 3.(b) U1 outer ramus with dorsal marginal spines; gill 1 with 2 secondary lobes (Figure 19) 5
- 4.(a) Coxal plate 6 with spine at sulcus only (Figure 14); rami of each pleopod distinctly unequal in length, PL3 very short compared to PL2; gill 5 lacking secondary lobes; maxilliped inner plate setose, with apical spines teeth very small or lacking (Figure 13); from the Los Tuxtlas upland, state of Veracruz, México *Caribitroides turtle-crisis* n. sp.
- 4.(b) Coxal plate 6 with spines at carina and behind (Figure 15); rami of each pleopod approximately equal, PL3 comparable in length to PL2; gill 5 bearing a secondary lobe; maxilliped inner plate sparsely setose, with apical spine teeth distinct (Figure 15); known from Oaxaca uplands *Caribitroides newtoni* n. sp.
- 5.(a) Epimeron 3 with distinct recurved shape (Figure 18), epimera rear margins with less than 5 setae; coxal plate 6 with spines anterior and posterior to carina (Figure 17); maxilliped palp segment 2 narrow, without large inner lobe (Figure 17), MXPD palp segment 4 conical, distinct, known from Oaxaca uplands *Mezitroides pecki* n. sp.
- 5.(b) EP3 quadrate, epimera rear margins with 5 or more setae (Figure 19); coxal plate 6 without spines anterior to carina; maxilliped palp segment 2 wide, with large inner lobe (Figure 19), MXPD palp segment 4 small, inconspicuous; known from Chiapas uplands *Mezitroides chiapensis* n. sp.

Two specimens of *Talitroides topitotum* were recently collected in the city of Oaxaca by Dr. H. F. Howden. This species is well known to be synanthropic, having been introduced into several areas of North America including Florida (Bousfield, 1984; Biernbaum, 1980). The México occurrence is probably also an introduction, although if populations are discovered well away from possible introduction sites, this assumption will have to be reconsidered.

Figure 4: Talitrid amphipod body plan (lateral view), with appendage and body segment terms (after Bousfield, 1973, 1982; Holsinger, 1976; McLaughlin, 1980). See text for abbreviation codes. For scale, see Figure 9.

Figure 5: Talitrid amphipod appendages (not to scale). Gnathopods are inner lateral view, coxal plate of pereopod 6 is outer lateral view. Leg segments are identified by name (abbreviations as in text), and segment number (coxa is segment 1). Other abbreviations: cx.plt.-coxal plate; b.setae-brood setae; pl.lobe- pellucid lobe; cari. -carina; s.ant.cari.-spines anterior to carina; s.a.cari.-spine at carina; s.post.cari.-spines posterior to carina

Figure 6: Talitrid amphipod appendages (not to scale). Abbreviations: il.-inner lobe; ast.- apical setulose spines; t.set.-terminal setulose spines; subt set.(dor.)-subterminal setulose spines (dorsal); subt.set.(vent.)- subterminal setulose spines (ventral); set. -setulose spine ; memb.- membranous centre (of maxilliped); ret.-retinacula; t.setae-terminal setae; dor.marg.s.-dorsal marginal spines; t.s.clust.-terminal spine cluster; irs.-inter-ramal spine.

Figure 7: Appendages showing key characters for *Tethorchestia* and *Pseudorchestoides* (g,h,i) (not to scale). *Tethorchestia* shows typical beach flea characteristics, including the anteriorly expanded basis of f. gnathopod 2, and subchelate propod of m. GN 1.

Figure 8: Appendages showing key characters for *Talitroides* (a,b,c,d,e), *Platorchestia* (f,g), and *Chelorchestia* (h,i,j,k,l) (not to scale).

Chapter 4 NEW LANDHOPPERS OF MÉXICO AND CENTRAL AMERICA

Cerrorchestia n. gen.

"Parorchestia" Bousfield 1984

Sexually dimorphic landhoppers of the cloud and rain forests of Costa Rica and Panamá, characterized by:

Eyes large, subovate tending to dorsal contiguity. Appendages slender, long, not heavily spinose. Antenna 1 short, little longer than A2 peduncle segment 4. Antenna 2 slender, not sexually dimorphic, geniculate at flagellum, peduncle not incrassate, flagellum longer than peduncle. Mandibular left lacinia mobilis 4-dentate. Maxilla 1: inner plate narrow, linear, with a few scattered fine long hairs proximally; outer plate subquadrate, outer margin convex; palp vestige minutely 2 segmented. Maxilliped: palp short, stout, fourth segment very small, button-like, may be partially masked by terminal setae of segment 3; outer plate slightly arcuate, with subterminal pellucid lobe on inner corner, masked by a comb of stout setae; inner plate subquadrate, with 3 small blunt apical spine teeth (innermost smallest). Pereopod dactyls cusped. Gnathopod 1 sexually dimorphic: female lacking pellucid lobes, propod simple; male bearing pellucid lobes on merus, carpus, and propod; male propod short, subchelate (dactyl not exceeding palm). Gnathopod 2 sexually dimorphic: female GN2 basis little expanded, almost linear; merus, carpus and propod bearing pellucid lobes; propod long, minutely subchelate, mitten-like, pellucid lobe extended well beyond dactyl, dactyl short, unguis very short with hooked tip. Male GN2 basis distally expanded; ischium bearing anterior wing-like processes; propod powerfully subchelate, subovate, palm slightly oblique, and bearing a raised cushion of spines; dactyl long, exceeding palm attenuated at nail, posterior margin bearing a row of short spines. Merus, carpus and propod longer in P3 than in P4; dactyl posterior margin sinuous, notched. P5-7 heteropodous, P5 much shorter. P6-7 long and slender. Pleopods slender, third shortest; peduncles sublinear, with occasional tiny setae and with 2 retinacula; rami shorter than peduncles, unequal (inner distinctly longer). Uropod 1 peduncle robust; interramal spine large; outer ramus lanceolate, lacking marginal spines; U2 rami subequal, outer slightly shorter. U3 short,

peduncle bearing 1-2 lateral distal spines; ramus conical, shorter than peduncle, with 3-4 terminal spines. Telson short, triangular, narrowing distally, apex slightly notched, with apical and dorsal spines. Gills large, flap-like, convoluted; G1 and 5 large, with lateral secondary lobes, G5 largest, G2-4 smaller, subequal. Oostegites long, sublinear (except O4 which is short, broadly subovate); distal marginal setae simple.

Type species: *Cerrorchestia hyloraina* n. sp.

REMARKS: *Cerrorchestia* belongs to the cuspidactylate, 4-dentate (left lacinia mobilis) group of talitrids (Bousfield 1984). Bousfield (1984) lists this taxon as "Parorchestia" species A and species B. However, *Parorchestia tenuis* differs from *Cerrorchestia* in the following characters: maxilliped palp segment 4 is distinct; male gnathopod 1 carpus long; female gnathopod 1 subchelation strong; male gnathopod 2 propod palm sinuous, slightly concave; pereopod 4 dactyl similar to P3, not notched; pleopod rami not shorter than peduncles; telson bearing apical spines only; oostegite setae bear hooked tips.

Central American 4-dentate talitrid genera include *Caribitroides* and *Tethorchestia*. *Caribitroides* is distinguished by its narrower maxilliped palp, larger and sharper inner plate apical spine teeth and the lack of sexual dimorphism in the gnathopods. *Tethorchestia* differs from *Cerrorchestia* in that GN1 (female) is weakly subchelate, GN1 (male) bears a pellucid lobe on the merus (rather than merus, carpus and propod, as in *Cerrorchestia*) and in pereopods 3 and 4, the carpus is not unequal.

Two other genera with which *Cerrorchestia* might be compared are *Orchestia* and *Talitroides*, both 4-dentate. *Orchestia*, a beach flea, differs from *Cerrorchestia* in lacking or almost lacking a fourth segment on the maxilliped palp, GN1 subchelate in the female, P3 and P4 dactyls similar, pleopods subequal, U1 outer ramus marginally spinose, and larger, more heavily setose oostegites. *Talitroides*, a landhopper, is distinct from *Cerrorchestia* in the following: maxilliped palp 3 segmented, P3 to P7 short, pleopod 3 vestigial.

The range of *Cerrorchestia* as presently known is from El Llano, Panamá, to Volcán Rincón de la Vieja, in the Cordillera de Guanacaste, Costa Rica. The lowest elevation from which specimens have been taken is 80 meters, on Barro Colorado Island, Gatun Lake, Panamá. Usually they are found in upland wet forest, and cannot tolerate drier conditions. The lack of specimens from lower elevations may be related more to habitat destruction than a true altitudinal limitation; further collecting in remaining lowland forests could provide more information.

ETYMOLOGY: Cerro, Spanish for hill or mountain, the usual collection site (eg, Cerro

Campana, Cerros Sentinelas) and *Orchestia* Gr., original name given to most talitrids. Feminine, adaptation of "Parorchestia" (first literature reference to these landhoppers).

Cerrorestia hyloraina n. sp.

Figure 9. Figure 10. Figure 11

HOLOTYPE female 12.6 mm, adult female range 7.4-12.6 mm.

A2 flagellum 18 [12-19] segments, each segment bearing 4 very fine terminal setae (each of the four is actually 3 setae fitted closely together in a common socket, visible under SEM). Maxilliped: inner plate with 4 [3-6] terminal and 8 [4-10] subterminal setulose spines, apical spine teeth small, blunt (innermost smallest); median margin with 3 plumose setae; palp segment 2 inner lobe broad. Gnathopod 1 basis anterior margin with 3 [2-5] small spines, posterior margin with 0 [1-2] larger spines, 1 [0-2] lateral spine distally on inner face; carpus wider than merus; propod posterior margin with 4 [4-5] clusters of spines, inner face with 2 [2-3] large spines, outer face with 5 [3-6] small spines. Gnathopod 2 basis anterior margin with 6 [5-7] small spines, posterior margin with 1 [0-2] tiny spines; propod outer face bearing 10 [9-13] setae, inner face bearing 22 [17-24] setae along lobe base. Pereopod 6 coxal plate ventral margin scalloped, with 1 spine at carina and 2 [2-3] posteriorly. Pereopod 7 coxal plate subovate, ventral margin with 2 [2-3] tiny spines. Oostegite setation: 19 [15-19], 13 [12-14], 11 [10-12], and 4 [3-5]. Gills: G1 long, with broad base and small secondary lobe approximately half way along length, narrower distally; G2-4 no more than two thirds as long as G1; G4 slightly shorter and thicker; G5 largest, similar in form to G1 except broader above secondary lobe. Epimera: EP1 broadly subtriangular, lacking posterior tooth, 1 [1-3] setae on posterior margin; EP2 subquadrate, posterior distal angle somewhat produced, but lacking distinct tooth, with 1 [1-3] posterior marginal setae; EP3 subquadrate, posterior distal angle rarely produced, with 2 [2-4] posterior marginal setae. Pleopods: rami shorter than peduncles, inner ramus only slightly longer than outer; PL1 inner and outer rami with 7 [6-8] and 8 [6-8] segments; PL2 peduncle with 1-2 tiny distal setae and a few fine hairs along outer margin; inner ramus with 7 [6-7] segments, outer with 8 [7-8]; PL3 shortest, peduncle with 1-3 small distal setae, rami very short, inner with 5 [3-6] segments, outer with 6 [5-7]. Uropod 1 peduncle with 2 rows of 4 dorsal spines, inner ramus with 4 [3-4] dorsal marginal spines. Uropod 2 peduncle with 3 [3-5] dorsal spines, inner ramus with 4 [3-4] dorsal spines, outer ramus with 3 [2-3]. Uropod 3 peduncle with 1 [1-2] spines; ramus slightly arcuate, with 4 [3-4] apical spines.

ALLOTYPE male 11.0 mm, adult male range 7.2 to 11.8 mm.

As female except for: Antenna 2 flagellum with 9 [12-20] segments. Gnathopod 1 basis slightly expanded postero-distally, 1 [0-2] proximal facial spine, 2 [1-3] spines on anterior margin, 2 large spines on posterior margin; propod short, stout, wider distally, pellucid lobe extending slightly beyond palm; inner face bearing 4-6 spines along lobe base and 5-7 anteriorly; outer face with 4-6 along lobe base and 1 [0-2] anteriorly. In fully adult males: gnathopod 2 basis anterior margin with 2 [2-3] small proximal spines, posterior margin with 1 [1-2] spines, propod palm "cushion" bearing 24 [20-28] short stout spines and 7 [4-16] tiny facial spines proximally; propod posterior margin grooved; dactyl posterior margin bearing 17 [16-18] tiny spines. Pereopods 3 and 4, coxal plates slightly more quadrate than in female.

REMARKS: Males are extremely variable in the appearance of gnathopod 2. Fully adult males usually have the powerfully subchelate form, but a small proportion of full size males have GN2 identical to the female form. Subadult males may have an appearance intermediate between adult female and adult male, with partial development of the large propod, and retention of pellucid lobes on propod, carpus, and/or merus.

Geographic Variation

Variations noted between Costa Rican and Panamánian populations form a gradient, and thus are not considered sufficiently distinctive to warrant erection of separate species. Of note are the following differences in Panamánian specimens as compared to the Monteverde population: left lacinia mobilis teeth raked at a sharper angle; antenna 2 may have 2-3 more segments in adults; maxilliped inner plate apical spine teeth sharper, with a more pronounced size difference between smallest and largest; GN1 female, coxal plate apex sharper; GN1 male, propod palm spine rows less regular, with fewer spines; GN2 female, coxal plate ventral margin with 16-21 spines (the Monteverde population has 13-15), oöstegite 2 has fewer setae; P4 coxal plate very quadrate; P5 basis posterior margin with 11 spines (7 in Monteverde).

ETYMOLOGY: The species name, *hyloraina*, meaning "forester" (Gr.), was considered appropriate for an organism which inhabits untouched forests.

MATERIAL EXAMINED

Unless otherwise noted, the following material was collected by the author.

Type Locality:

COSTA RICA, PUNTARENAS, MONTEVERDE: Cerro Roble 22 Feb 1983, 1690 m,

cloud forest leaf litter, D. Lindeman, HOLOTYPE female 12.6 mm (ovigerous, 6 eggs) NMC-C-1988-0012, PARATYPES 2 f. NMC-C-1988-0014. Cerro Roble 23 June 1983, 1650m, cloud forest leaf litter, sifter sample, D. Lindeman, ALLOTYPE male 11.0 mm NMC-C-1988-0013, PARATYPES 34 f., 21 m., 78 juv NMC-C-1988-0015.

Other Material:

COSTA RICA:

PUNTARENAS PROVINCE, MONTEVERDE: 21-23 Feb 1983, 1500m, cloud forest, pit traps, 3 f., 10 m.; 24 Feb 1983, 1500 m, cloud forest, pit traps, 3 f., 13 m.; 13-15 June 1983, 1550 m. cloud forest, pit traps, 7 f., 8 m., 3 juv; Cerro Roble 17 June 1983, 1650 m. cloud forest, pit traps, 7 f., 16 m., 6 juv; 07 July 1983, elfin forest, sifter sample, 19 f., 7 m., 22 juv; Campbell farm ridge 7 July 1983, 1475 m, sifter sample, 14 f., 2 m., 33 juv; Stuckey farm 12 July 1983, 1350 m, spring bottom leaf litter, pit traps, 5 f., 10 m., 25 juv; 11-18 July 1983, 1500 m, cloud forest, fruit baited pit traps, 16 f., 18 m., 12 juv; 15 July 1983, 1500 m, cloud forest, 6 hr. pit traps, 5 f., 21 m., 9 juv; Cerro Roble 19 July 1983, 1680 m, cloud forest, 6 hr. pit traps, 6 f., 15 m., 9 juv; 17-21 July 1983, 1600 m, elfin forest, dung traps, 10 f., 25 m., 4 juv; Cerro Roble 28 July 1983, 1680 m, cloud forest leaf litter, sifter sample, 31 f., 3 m., 81 juv; Stuckey farm 27-31 July 1983, 1350 m. spring bottom, pit traps, 6 f., 16 m., 5 juv; Cloud Forest Reserve 1 June 1979, 1500 m, H. and A. Howden, NMC-C-1983-1278, 2 f., 1 m.; Cambell's Woods March 1982, 1540 m, M. D. Hayes, NMC-C-1983-1274, 5 f.; 24 May 1979, 1500 m, H. and A. Howden, NMC-C-1983-1272, 1 f.; 23 May 1979, 1500 m, H. and A. Howden, NMC-C-1983-1275, 9 f., 6 m.; 1 June 1979, 1500 m, H. and A. Howden, NMC-C-1983-1279, 1 m..

Several hundred other specimens were examined during the course of this study, but were retained for biological studies, and so are not listed here.

GUANACASTE: Rincón de la Vieja National Park 9 Aug 1983, 1830 m, humid forest, 3 f., 1 m., 5 juv.

HEREDIA: Braulio Carillo National Park 20 km N Moravia 11 Aug 1984, 20 f., 12 m., 44 juv.

CARTAGO: Cartago-Limón border 40 km NE Turrialba 18 May 1979, H. and A. Howden, NMC-C-1983-1271, 1 m., 3 juv.

PANAMÁ

CANAL ZONE: Gatun Lake, Barro Colorado Island 7-14 June 1983, 80 m, wet forest, B. Gill, 3 f., 7 m.; Barro Colorado Island June 1981, B. Gill, 1 f.; Rio Agua Salud 19.3 km NW

Gamboa 19 Feb 1976, wet leaves and flood debris along river, Berlese, A. Newton. MCZ, 1 f., 1 m.; Barro Colorado Island 12 Feb 1976, wet leaves and flood debris by forest stream. Berlese, A. Newton, MCZ, 1 f., 1 m., 42 juv.

CHIRIQUI: La Fortuna Dam 15-21 June 1982, 1200 m, wet forest, B. Gill, 10 f., 21 m., 7 juv; Cerro Hornito 15 km NW Gualaca Aug 1982, 1200 m, B. Gill, 3 f., 1 m.; 2 km W Cerro Punta, 20 May 1977, 1700 m, S. Peck, NMC-C-1983-1280, 49 f., 13 m., 13 juv; 2 km W Cerro Punta 22 May 1977, cup traps, H. Howden, NMC-C-1983-1266, 4 f., 3 m.; 2km W Cerro Punta, 27 May 1977, 1300 m. cup traps, H. Howden, NMC-C-1983-1267, 4 f., 1 m., 2 juv; El Mirador, Finca Collins near Boquete 25 June 1976, 2800 m. cloud forest leaf litter. Berlese, A. Newton, MCZ, 1 m..

PANAMÁ: El Llano, Carti Road July 1982, 400 m, B. Gill, 1f., 3m., 1juv; Cerro Campana 30 July 1970, H. and A. Howden, NMC-C-1984-777, 4 f., 1 m., 1 juv; Cerro Campana 17 June 1976, 1000 m. cloud forest leaf litter, Berlese, A. Newton, MCZ, 1 f., 1 m., 18 juv; Cerro Campana 14-23 Feb 1976, 1000 m, cloud forest leaf litter, A. Newton, MCZ, 4 f., 6 m., 11juv; Cerro Campana 23 Feb 1976, 1000 m. wet debris by forest stream, A. Newton, MCZ, 4 m., 5 juv.

Figure 9: *Cerrorchestia hyloraina* n. gen., n. sp. Holotype female, from the Monteverde Cloud Forest Reserve, Monteverde, Puntarenas Province, Costa Rica. Arrows indicate locations of key characters: maxilliped, gnathopod 2, pleopods, outer ramus of uropod 1.

Figure 10: Appendages of *Cerrorchestia hyloraina* n. gen. n. sp. Gnathopods and CX6 to scale line a; UL, LL, MX1, MX2, LMD, T, U3 to scale line b; MXP and GN1 propod to scale line c.

Figure 11: Appendages of *Cerrorchestia hyloraina*. GN1 propod to scale line b; all others to scale line a.

Caribitroides Bousfield 1984

The genus *Caribitroides* was originally only briefly diagnosed (Bousfield, 1984). An expanded description based on the Mexican species, and Jamaican material examined by the author at the National Museum of Natural Sciences, Ottawa, is provided below.

Non-sexually dimorphic landhoppers of the cloud and rain forests of México and Jamaica, characterized by:

Eyes large, subovate, tending to dorsal contiguity. Appendages slender, long, not heavily spinose. Antenna 1 short, slightly longer than antenna 2 peduncle segment 4. Antenna 2 slender, not sexually dimorphic, geniculate at flagellum, peduncle not incrassate, flagellum longer than peduncle. Mandibular lacinia mobilis 4-dentate. Maxilla 1: inner plate narrow, linear, with a few scattered fine long hairs proximally; outer plate subquadrate, outer margin convex; palp vestige minutely 2 segmented. Maxilliped: palp short, very stout, fourth segment very small and inconspicuous, may be masked by terminal setae of segment 3; outer plate slightly arcuate, with terminal pellucid lobe; inner plate subquadrate, apical spine teeth usually large, sharp (except for *C. tuztlensis*). Pereopod dactyls bearing cusps at the posterior dactyl-unguis suture. Gnathopod 1 not sexually dimorphic; lacking pellucid lobes; propod simple, lacking palm; carpus and propod short. Gnathopod 2 not sexually dimorphic; basis anterior margin proximally expanded or sinuous; ischium elongate; merus, carpus and propod bearing posterior pellucid lobe; propod minutely subchelate, mitten-like, pellucid lobe large, extending well beyond dactyl; dactyl short, unguis very short, with hooked tip. Merus, carpus and propod longer in P3 than in P4; dactyl notched behind on P4 (see Figure 18). P5-7 weakly heteropodous; P5 much the shortest, P6-7 long and slender. Dactyls long (unguis greater than one half the dactyl base length). Pleopods slender, reduced, third shortest; peduncles sublinear, lacking setae, bearing 2 retinacula, rami of approximately equal lengths (except *C. tuztlensis*). Uropod 1 prepeduncle robust, interramal (disto-lateral) spine large; outer ramus lanceolate, lacking dorsal marginal spines. U2 rami subequal, outer slightly shorter. Uropod 3 short, broad; peduncle with 1-2 lateral spines, distal ramus conical, shorter than peduncle, with 1-4 terminal spines. Telson short, triangular, narrowing distally, apex slightly notched, with apical and dorsal spines. Gills large, flap-like, convoluted, G1, G5 large, with lateral secondary lobes, G5 largest, G2-3 smaller, subequal, G4 broader. Oostegites long, sublinear (except O4 which is short, broadly subovate); distal marginal setae sparse, simple.

Type species: *Caribitroides jamaicensis* Bousfield 1984

REMARKS: Central American talitrid genera include *Cerrorchestia* n. gen., *Orchestia* Leach and *Tethorchestia* Bousfield 1984. *Cerrorchestia* is distinguished from *Caribitroides* by its broader maxilliped palp, sexual dimorphism of the gnathopods, less elaborate gills, and more setose oöstegites. *Tethorchestia* differs from *Caribitroides* in that GN1 (male) is fully subchelate and bears a small pellucid lobe; GN2 is sexually dimorphic; in the female the GN2 basis anterior margin is arcuate; and the inner ramus of uropod 2 bears two rows of dorsal marginal spines. *Orchestia* differs from *Caribitroides* in the following: GN1 is subchelate in the female; P3 and P4 dactyls are similar; all pleopods are subequal; U1 outer ramus is marginally spinose; and the oöstegites are larger and more heavily setose. *Talitroides* Bonnier, an Old World landhopper, is distinct from *Caribitroides* in the following: maxilliped palp 3 segmented, P3 to P7 short, pleopod 3 vestigial. The genus most similar to *Caribitroides* is its sister genus *Mexitroides* n. gen., distinguished by a marginally spinose outer ramus of uropod 1, the distinctively bilobed first gill, and pleopod rami equal to peduncles.

Caribitroides is presently known from Jamaica and southeastern México. It is usually found in moist upland forest; however, this may reflect habitat destruction rather than a true altitudinal limitation, since *C. tuztlensis* is found down to very low altitudes at the Los Tuxtlas Biology Station. Distributional patterns known so far suggest that these amphipods occur in undisturbed moist tropical forests which are contiguous with an upland area (of at least 1000 meters) which typically includes cloud forest. Dr. S. B. Peck recently sampled (1983) in the Yucatán Peninsula, but did not capture any landhoppers.

Several species in material from Jamaica await description. Dr. E. L. Bousfield (National Museum of Natural Sciences, Ottawa) is working on this material (Bousfield, 1984, and pers. comm.), and it is therefore not described here.

Caribitroides tuztlensis n. sp.

Figure 12, Figure 13, Figure 14

Landhoppers of the Los Tuxtlas upland in Veracruz State, México.

HOLOTYPE female 9.7 mm, adult female range 6.3-9.9 mm.

Antenna 2 flagellum with 15 [12-15] segments. Lower lip occasionally with setulose

spines on inner lobes. Maxilliped inner plate heavily setose, with 7 terminal and 5 [4-8] subterminal setulose spines, apical spine teeth completely lacking; median margin with 2 plumose setae per side; palp segment 4 minute, segment 2 inner lobe large. Gnathopod 1 basis anterior margin with 3 [2-6] spines, posterior margin with 3 spines; carpus no wider than merus; propod posterior margin with 5 irregular clusters of spines, inner face with 8 [6-9] small spines, outer face with 3 large spines. Gnathopod 2 basis anterior margin expanded but not sinuous, with 6 [4-7] spines, posterior margin unarmed; propod outer face with 22 [17-26] setae, inner face with 8 [6-11] setae. Pereopod 6 coxal plate ventral margin with 1 spine at carina. P7 coxal plate ventral margin with 3 [2-4] spines. Oöstegite setation: 12 [10-12]; 13 [10-13]; 10 [7-11]; 6 [4-6]. Gills: G1 with anterior proximal broadened region, posterior secondary lobe small; G4 distally broad, G2-4 not highly convoluted; G5 lacking complete development of the posterior secondary lobe posterior margin with 1 seta; EP2 posterior distal angle toothed, posterior margin with 1 [0-1] seta; EP3 subquadrate, posterior distal angle toothed, produced, posterior margin with 1 [0-1] seta. Pleopods: rami distinctly unequal, outer shorter; inner rami of PL1 and PL2 greater than or equal to peduncle length. PL1 inner and outer rami with 11 [9-12] and 12 [10-15] segments; PL2 rami with 10 [8-10] and 12 [9-12] segments; PL3 reduced, rami shorter than peduncles, rami with 7 [5-8] and 8 [6-9] segments. Uropod 1 peduncle with 2 rows of 4 dorsal spines, inner ramus with 6 [3-6] dorsal spines. U2 peduncle with 5 [4-6] dorsal spines; rami each with 3 [2-3] dorsal spines. U3 peduncle with 1 lateral spine; ramus with 1 terminal spine. One specimen also had a lateral spine on the ramus, as in *C. jamaicensis*. Telson armature 1 apical and 4 [3-5] dorsal spines per lobe.

ALLOTYPE male 8.5 mm, adult male range 6.0-8.5 mm.

As female, except for: Antenna 2 with 16 [12-17] flagellar segments. Gnathopod 2 basis with 1 [0-1] small spines on anterior margin. U1 inner ramus with 5 [3-5] dorsal spines. U2 rami with 2 [2-3] dorsal spines.

ETYMOLOGY: This species is named for the Los Tuxtlas region of México, the type locality.

REMARKS: *C. tuxtensis* has been collected only in the Sierra de Los Tuxtlas in Veracruz State. Without further sampling both north and south of this highland region (particularly the Tehuantepec lowland around the Coatzacoalcos River) it is not possible to establish the full extent of its range. The morphological differences between *C. newtoni* n. sp. and *C. tuxtensis* (the latter's lack of maxilliped inner plate apical spine teeth, unequal pleopod rami

and lack of secondary lobe on gill 5) suggest considerable separation between the amphipod populations of the Sierra Madre de Oaxaca, and the Los Tuxtlas volcanic highland.

MATERIAL EXAMINED

Type Locality:

MEXICO, VERACRUZ: Los Tuxtlas Biological Station 33 km NE Catemaco 25 July 1984, 160 m, rain forest leaf litter, quantitative samples, D. Lindeman. HOLOTYPE female 10mm NMC-C-1988-0010; ALLOTYPE male 9 mm NMC-C-1988-0011; PARATYPES 18 f., 7 m., 132 juv.

Other Material:

MEXICO, VERACRUZ: 13 km NNW Sontecomapan 29 July-4 Aug 1970, rain forest, stn 137, carrion trap, A. Newton, NMC-C-1983-1862, 3 f., 3 m., 8 juv; 13 km NNW Sontecomapan 31 July-1 Aug 1970, rain forest, stn 140, dung trap, A. Newton, NMC-C-1983-1863, 1 m., 2 juv; 13 km NNW Sontecomapan 31 July-4 Aug 1970, rain forest, stn 139, dung trap, A. Newton, NMC-C-1983-1865, 4 f., 2 m., 5 juv; 3 km NNW Sontecomapan 31 July-4 Aug 1970, rain forest, stn 140, carrion trap, A. Newton, NMC-C-1983-1866, 1 f., 10 juv; 13 km NW Sontecomapan 2-7 Aug 1970, A. Newton, NMC-C-1984-846, 2 f., 2 m.; 8 km E Catemaco 31 June-4 Aug 1970, 366 m, stn 136, carrion traps, A. Newton, NMC-C-1984-842, 2 f., 5 juv; 13 km NW Sontecomapan 4 Aug 1971, 120 m, stn 324, rain forest leaf litter, A. Newton, MCZ, 3 f., 2 m., 2 juv; 33 km NE Catemaco, Los Tuxtlas Biol Stn 9 June 1984, rain forest leaf litter, D. Lindeman, 3 f., 4 m., 6 juv; 33 km NE Catemaco, Los Tuxtlas Biol Stn 21 July 1984, 160 m, climax rain forest, quantitative samples, D. Lindeman, 13 f., 11 m., 592 juv; Los Tuxtlas Biol Stn, 33 km NE Catemaco 25 July 1984, rain forest leaf litter, D. Lindeman, 14 f., 1 m., 11 juv; Los Tuxtlas Biol Stn, 33 km NE Catemaco 7 June 1984, leaf litter, D. Lindeman, 22 f., 1 m., 41 juv; 33 km NE Catemaco, Los Tuxtlas Biol Stn, 1 July-1 Aug 1983, 160 m, stn 83-51, FIT ravine rain forest, S. and J. Peck, 94 f., 42 m., 22 juv; 33 km NE Catemaco Los Tuxtlas Biol Stn 1 July-1 Aug 1983, 160 m, M. Kaulbars, 20 f., 10 m..

Several hundred other specimens captured by the author during field work at the Los Tuxtlas Biology Station in June and July of 1984 were examined during the course of the study, but were retained for biological studies, and are therefore not listed here.

Caribitroides newtoni n. sp.

Figure 15

HOLOTYPE female 11 mm, adult female range 9-12 mm.

Antenna 2 flagellum 15 [14-16] segments. Maxilliped inner plate sparsely setose, with 3 terminal and 3 [3-4] subterminal setulose spines, apical spine teeth very unequal; median margin with 3 plumose setae per side; palp segment 4 vestigial, segment 2 inner lobe narrow. Gnathopod 1 basis anterior margin with 4 [3-5] spines, posterior margin with 3 [3-4]; carpus no wider than merus; propod posterior margin bearing 4 irregular clusters of spines, inner face with 5 [4-5] small spines, outer face with 1 [1-2] large spines. Gnathopod 2 basis at anterior margin sinuous, bearing 7 [5-9] small spines, posterior margin unarmed; propod long, outer face with 19 [14-19] setae, inner face with 11 [8-12] setae. Pereopod 6 coxal plate ventral margin with 1 spine at carina and 2 [0-2] spines posterior to carina. P7 coxal plate ventral margin with 4 [2-4] spines. Oöstegite setation: 7 [7-9]; 9 [8-11]; 7 [7-9]; and 4 [4-5]. Gills: G1 with anterior proximal broadened region (approaching secondary lobe distinction), posterior secondary lobe small, distal region of gill narrow; G4 wider than G2, G3, but of comparable length, all highly convoluted; G5 very long, wider distally than G1, posterior secondary lobe small, proximal. Epimera: EP1 posterior distal angle not toothed, posterior margin with 1 seta; EP2 posterior distal angle not toothed or produced, posterior margin with 1 [1-2] seta; EP3 subquadrate, posterior distal angle not produced, posterior margin with 1 [1-2] seta. Pleopods: rami subequal, outer slightly shorter; rami equal in length to peduncles, or only slightly shorter. PL1 outer ramus with 16 [12-16] segments; inner ramus with 15 [11-15] segments; PL2 outer ramus with 15 [11-15] segments; inner with 13 [10-13]; PL3 slightly reduced, outer ramus with 11 [10-13] segments; inner with 10 [9-11]. Uropod 1 peduncle with 2 rows of 4 [4-6] dorsal spines, inner ramus with 4 [3-4] dorsal spines. U2 peduncle with 3 [2-3] dorsal spines; rami approximately equal, outer with 3 [3-4] dorsal spines, inner with 3. U3 peduncle with 1 lateral spine, ramus with terminal cluster of 4 [3-4] apical spines. Telson armature 2 [1-2] apical and 3 [2-3] dorsal spines on each lobe.

ALLOTYPE male 9 mm, adult male range 8-10 mm.

As female, except for: Gnathopod 2 basis anterior margin less sinuous than female, with 1-2 spines. U1 inner ramus with 3 [2-3] dorsal spines. U2 inner ramus with 2 [2-3] dorsal spines, outer ramus with 3 dorsal spines.

ETYMOLOGY: *C. newtoni*, named after Dr. A. F. Newton Jr., who collected all 47

known specimens.

REMARKS: *Caribitroides newtoni* has so far been collected only near Valle Nacional in Oaxaca State, México. At one site it was captured with *Meritroides pecki* n. gen. n. sp. Much more collecting is needed before the range or biology of these amphipods can be described with accuracy. *C. newtoni* is very similar to *C. turtlensis*, but is identifiable by: pleopod 3 comparable in length to PL2, gill 5 with secondary lobe, maxilliped inner plate apical spine teeth distinct, and coxal plate 6 with spines at, and posterior to, the sulcus.

MATERIAL EXAMINED

Type Locality:

MÉXICO, OAXACA: 30 km S Valle Nacional 22-31 July 1971, 1550 m, stn 305, dung trap, A. Newton. HOLOTYPE female 11 mm NMC-C-1988-0016; ALLOTYPE male 9 mm NMC-C-1988-0017; PARATYPES 25 f., 12 m. NMC-C-1983-1858.

Other Material:

MÉXICO, OAXACA: 29 km S Valle Nacional 22-31 July 1971, 1460 m, forest, stn 304, dung trap, A. Newton, NMC-C-1983-1859, 2 f., 3 m.; Valle Nacional 9-12 Aug 1970, A. Newton, NMC-C-1984-847, 1 f., 1 m., 1 juv.

Figure 12: *Caribitroides tuxtlenensis* n. sp., holotype female, from the Los Tuxtlas Biological Station forest leaf litter, 33 km north of Catemaco, Veracruz State, México. Arrows indicate locations of key characters: maxilliped, pleopods, uropod 1 outer ramus.

Figure 13: Appendages of *Caribitroides tuxtlensis* n. sp. Gnathopods are to scale line a; UL, LL, LMD, MX1, MX2, U3, and T to scale line b; MXPd and gnathopod propod detail are to scale line c.

Figure 14: Appendages of *Caribitroides tuxtlensis* n. sp. All parts to scale line a.

Figure 15: Appendages of *Caribitroides newtoni* n. sp. Oostegites, pleopods, epimera, gills, gnathopods, coxa 6, U1 and U2 to scale line a. Telson and U3 to scale line b. MXP1 and GN1 propod to scale line c.

Meritroides n. gen.

Non-sexually dimorphic landhoppers of the cloud and rain forests of southeastern México, characterized by:

Eyes large, subovate, tending to dorsal contiguity. Appendages slender, long, not heavily spinose. Antenna 1 slightly longer than A2 peduncle segment 4. Antenna 2 slender, not sexually dimorphic, geniculate at flagellum, peduncle not incrassate; flagellum longer than peduncle. Mandibular left lacinia mobilis 4-dentate. Maxilla 1: inner plate narrow, linear, with a few scattered fine long hairs proximally; outer plate subquadrate, outer margin convex; palp vestige minutely 2 segmented. Maxilliped: palp short, stout, fourth segment very small, conical, may be masked by terminal setae of segment 3; outer plate slightly arcuate, with terminal pellucid lobe; inner plate subquadrate, apical spine teeth large, sharp. Pereopod dactyls with cusps. Gnathopod 1 not sexually dimorphic, simple, lacking palm on propod; lacking pellucid lobes. Gnathopod 2 not sexually dimorphic; basis slightly expanded proximally, ischium elongate, merus, carpus and propod bearing posterior pellucid lobe; propod long, minutely subchelate, mitten-like, pellucid lobe large, extending well beyond dactyl; dactyl very small, with hooked tip. Basis, merus, carpus, propod and dactyl longer in P3 than in P4; dactyl notched behind in P4. Pereopods 5-7 weakly heteropodous, P5 much shorter. Pleopods slender, third shortest; peduncles sublinear, lacking setae, bearing 2 retinacula, rami equal to or longer than peduncles, inner slightly longer than outer. Uropod 1 prepeduncle long, robust; interramal (disto-lateral) spine large; outer ramus lanceolate, with marginal spines. U2 rami subequal, outer slightly shorter. U3 short, broad; peduncle with 1-2 lateral spines, ramus conical, shorter than peduncle, with 2-4 apical spines. Telson short, triangular, narrowing distally, apex slightly notched, with apical and dorsal spines. Gills large, flap-like, convoluted; G1 with 2 large secondary lobes (see Figure 19), one anterior and one posterior; G5 with lateral secondary lobe; G2 and 3 smallest, subequal; G4 broader. Oostegites long, sublinear (except O4 which is short, broadly subovate); distal marginal setae sparse, simple.

Type species: *Meritroides pecki* n. sp.

REMARKS: *Meritroides* belongs among the cuspidactylate, 4-dentate (left lacinia mobilis) group of talitrids (see Bousfield's 1984 groupings of world talitrid fauna). It is very similar to the genus *Caribitroides*, to which it is closely related, but differs from it in the following ways: the maxilliped palp segment 4 is larger and more distinct, the outer ramus of uropod 1 bears spines, the first gill is distinctively trilobed, and pleopod rami are longer

than the peduncles.

Meatroides is presently known from southeastern México, in Oaxaca and Chiapas States. It is usually found in moist upland forest, however, much further collecting is required to establish the range.

ETYMOLOGY: *Meatroides*, a combination of México, the location of occurrence, and *Caribitroides* Bousfield 1984, the most closely related genus. Gender: feminine.

Meatroides pecki n. sp.

Figure 16, Figure 17 and Figure 18

HOLOTYPE female 12 mm, adult female range 9-12 mm.

Antenna 2 flagellum 17 [15-19] segments. Maxilliped: palp segment 2 with narrow inner lobe; inner plate sparsely setose, with 4 [4-6] terminal and 3 [3-4] subterminal setulose spines; apical spine teeth large, sharp, (innermost smaller, but occasionally almost the same length as the outer two); median margin with 3 large plumose setae per side, distalmost smallest. Gnathopod 1 basis sublinear, narrower proximally, with 5 [5-7] anterior and 3 [2-3] posterior marginal spines; carpus not wider than merus; propod posterior margin bearing 1 irregular spine clusters, inner face with 3 large spines almost at posterior margin, outer face with 4 [4-6] small spines. G2 basis anterior margin sinuous, with 7 [5-10] small spines, posterior margin slightly concave, with 0 [0-2] tiny spines; propod outer face bearing 7 [6-13] inner face bearing 15 [14-28] setae. Pereopod 6 coxal plate ventral margin scalloped, with 2 [1-2] spines anterior to carina, 1 [0-1] spine on ventral margin at carina, and 2 spines on ventral margin posterior to carina. P7 coxal plate ventral margin with 3 small spines. Oostegite setation: 5 [4-9], 8 [5-9], 8 [5-9], and 2 [2-5]. Gills: G1 long, with large secondary lobe posteriorly, and small secondary lobe anteriorly on main axis; G2-4 highly convoluted, wide, broadened posteriorly (see Figure 13); G4 slightly wider than G2 and 3; G5 longest, wider than G1 above secondary lobe. Epimera: EP1 weakly subquadrate, with distal margin broadly convex, posterior margin stepped, with 5 [1-5] setae, posterior distal angle lacking tooth. EP2 subquadrate, posterior distal tooth produced, 3 [2-5] posterior marginal setae. EP3 with distinctive "recurved" shape, posterior distal tooth small, 3 [2-4] posterior marginal setae. Pleopods: rami equal to or slightly longer than peduncles. PL1 inner ramus with 13 [11-13] and outer with 14 [13-14] segments (annulation incomplete near base); PL2 peduncle with 1 [1-2] tiny setae, inner ramus with 13 [11-13] and outer

with 14 [11-14] segments; PL3 reduced, rami slightly shorter than peduncle, peduncle with 1 [0-3] tiny setae, inner ramus with 11 [9-11] and outer with 12 [10-12] segments. Uropod 1 peduncle with 4 [3-4] pairs of dorsal spines, inner ramus with 4 (very occasionally 3) dorsal spines; outer ramus with 3 dorsal spines. U2 peduncle with 4 dorsal spines, rami subequal, inner ramus with 4 [3-4] dorsal spines, outer ramus with 4 [2-4] dorsal spines. U3 peduncle with 1 [1-2] spine; ramus with 2 terminal spines. Telson armature 2 [2-3] apical, and 3 [2-3] dorso-lateral spines per lobe.

ALLOTYPE male 10 mm adult male range 8-10 mm.

As female, except for: Antenna 2 flagellum 18 [16-20] segments. Gnathopod 2 basis: anterior margin with 2 [2-4] spines, more linear than female, occasionally lacking antero-proximal expansion, posterior margin without spines. P3:P4 length difference more pronounced in male than in female; P3 longer in almost all segments. P6 and P7 longer in male than female. P6 coxal plate margin with 3 [1-4, usually 3] spines anterior to carina, 1 [0-1] spine at carina, and 2 [1-2] posterior to carina.

REMARKS: *Meritroides pecki* has been collected only in the eastern part of the state of Oaxaca, near Valle Nacional. In one collection (Newton stn 305) it occurred in the same sample with *Caribitroides newtoni* n. sp., which indicates that the ranges of the two species overlap at least at this site. The actual distribution of these species is very poorly known.

Meritroides pecki is distinguished from species of *Caribitroides* by the spinose outer ramus of uropod 1, and the trilobed first gill. It is distinct from *M. chiapensis* n. sp. in the distinctive shape of the third epimeron, and the presence of spines anterior to the carina of coxal plate 6.

ETYMOLOGY: *M. pecki* is named after Dr. S. B. Peck, who collected most of the material of this species.

MATERIAL EXAMINED

Type Locality:

MÉXICO, OAXACA: Scorpion Gap, 26 km E Valle Nacional 25 June-2 Aug 1983, 1220 m, montane tropical forest, FIT, S. Peck. HOLOTYPE female 12mm NMC-C-1988-008; ALLOTYPE male 10 mm NMC-C-1988-009; PARATYPES 16 f., 29 m., 6 juv.

Other Material:

MÉXICO, OAXACA: 24 km S Valle Nacional 21 May 1971, 1216 m, leaf litter, Ber 204, S. Peck, 87 f., 37 m., 14 juv; km 140 on Hwy 175 22 May 1969, 1216 m, H. Howden, 1 f.;

30 km S Valle Nacional 22-31 July 1971, 1550 m, Stn 305, dung trap, A. Newton, NMC-C-1983-1856, 6 f., 2 m.(subadult); 21 km S Valle Nacional 22-30 July 1970, 1094 m, forest, stn 143, carrion trap, A. Newton, NMC-C-1983-1848, 5 f., 2 m.; 24 km S Valle Nacional 22-31 July 1971, 1307 m, forest, stn 303, dung trap, A. Newton, NMC-C-1983-1850, 4 f., 3 m.; 21 km S Valle Nacional 12-15 Aug 1973, 1125 m, tropical evergreen forest, stn 522G, fish trap, A. Newton, NMC-C-1983-1851, 3 f., 1 m.

Meritroides chiapensis n. sp.

Figure 19

HOLOTYPE female 13 mm, adult female range 10-13 mm.

A2 flagellum 20 [18-21] segments. Maxilliped: palp segment 2 with broad inner lobe; inner plate with 5 [4-6] terminal and 3 subterminal setulose spines; apical spine teeth large, blunt, innermost much smaller; median margin with 4 [2-4] plumose setae, distalmost smallest. Gnathopod 1 basis with 7 [3-7] anterior and 4 [2-4] posterior marginal spines; carpus not wider than merus; propod posterior margin bearing 5 irregular clusters, inner face bearing 7 [6-8] small setae, outer face with 4 [4-6] small spines. G2 basis anterior margin sinuous with 10 [7-10] small spines, posterior margin unarmed; propod more setose than *M. pecki*, outer face bearing 23 [15-30], inner face bearing 37 [23-37] setae. Pereopod 6 coxal plate with 1 spine on ventral margin at carina, and 4 [2-6] spines posterior to carina (some specimens have 1 spine anterior to carina). P7 coxal plate ventral margin with 4 [4-5] small spines. Oöstegite setation: 11 [9-11], 9 [9-13], 10 [10-13], 2 [2-3]. Gills similar to *M. pecki*, except G2 more elaborate. Epimera: EP1 subtriangular, posterior distal angle not toothed, posterior margin with 2 [1-4] setae; EP2 subquadrate, posterior distal tooth small, and 4 [3-6] posterior marginal setae; EP3 quadrate, lacking distinctive "recurve" shape of *M. pecki*, posterior distal tooth lacking, and 5 [3-6] posterior marginal setae. Pleopods: rami equal to or longer than peduncles; PL1 inner ramus with 16 [13-16] and outer with 17 [13-17] segments; PL2 slightly longer than PL1, inner ramus with 13 [11-14] and outer with 14 [12-15] segments; PL3 shorter, inner ramus with 13 [9-13] and outer with 14 [10-14] segments. Uropod 1 peduncle with 8 scattered dorsal spines, inner ramus with 5 [4-5] dorsal spines, outer ramus with 4 [3-4]. U2 inner ramus with 4 and outer with 3 dorsal spines U3 peduncle with 2 [1-2] lateral spines, ramus with 4 [3-4] apical spines. Telson armature 2 apical and 3 dorso-lateral spines per lobe.

ALLOTYPE male 11 mm, adult male range 8-11 mm.

As female, except for: Antenna 2 flagellum with 20 [18-21] segments. Gnathopod 2 basis with 3 [2-3] spines on anterior margin. P6 coxal plate margin with 5 [usually 2-3] spines posterior to carina (females usually have 5-6). Uropod 1 outer ramus with 3 [3-4] dorsal spines.

ETYMOLOGY: *M. chiapensis* is named after Chiapas State, México, the type locality.

REMARKS: *Mezitroides chiapensis* has been collected only in montane areas of Chiapas State, México. No collection sites contained any other amphipod species, suggesting that the Tehuantepec lowland is a barrier between *M. chiapensis* and *M. packi*. These two species are closely related, but are easily distinguishable by the differences in oöstegites, pleopods, uropod armature, and the shape of epimera 1 and 3.

MATERIAL EXAMINED

Type Locality:

MÉXICO, CHIAPAS: 11 km W El Bosque 25-29 Aug 1973, 1460 m, cloud forest, stn 542, A. Newton. HOLOTYPE female 13 mm, slide mount, NMC-C-1988-0018; ALLOTYPE male 11 mm, slide mount, NMC-C-1988-0019; PARATYPES 18 f., 12 m., 2 juv NMC-C-1983-1854.

Other Material:

MÉXICO, CHIAPAS: 19 km NW Ocozocoautla 19-25 Aug 1971, 1031 m, tropical evergreen forest and oaks, stn 362, A. Newton, NMC-C-1983-1849, 1 f.; 13 km N Pueblo Nuevo Solistahuacan 26-27 Aug 1973, 1824 m, cloud forest leaf litter, stn 511, Berlesate, A. Newton, NMC-C-1983-1852, 2 f., 2 m., NMC-C-1983-1853, 1 f., 1 m., NMC-C-1983-1857, 1 f., 2 m., 12 juv; 19 km NW Ocozocoautla 4 Sept 1973, 973 m, oak and tropical evergreen forest litter, Berlesate, A. Newton, NMC-C-1983-1855, 1 m.; 11 km W El Bosque 29 Aug 1973, 1460 m, cloud forest and pine litter, Berlesate, A. Newton, NMC-C-1983-1867, 1 f. (partial), 1 m., 31 juv; El Bosque 25-29 Aug 1973, A. Newton, NMC-C-1983-1860, 1 m.

Figure 16: *Mezitroides pecki* n. gen. n. sp., holotype female, from Scorpion Gap, north of Valle Nacional, Oaxaca State, México.

Figure 17: Appendages of *Mezitroides pecki* n. gen. n. sp. Gnathopods, CX6, U1, and U2 to scale line a; UL, LL, LMD, MX1, MX2, U3 and T to scale line b; MXPd and GN1 propod to scale line c.

Figure 18: Appendages of *Mezitroides pecki* n. gen. n. sp. Dactyls 3 and 4 to scale line b;
all others to scale line a.

Figure 19: Appendages of *Mezitroides chiapensis* n. sp. Epimera, pleopods, gills, oostegites, gnathopods, CX6, U1 and U2 to scale line a; T and U3 to scale line b; MXPd and GN1 propod to scale line c.

Chapter 5 DISTRIBUTION AND FIELD BIOLOGY OF A MEXICAN AND A COSTA RICAN LANDHOPPER

5.1 Biology of *Cerrorchestia hyloraina*

5.1.1 Geographic Distribution

Cerrorchestia inhabits moist leaf litter in undisturbed tropical wet forests, or areas contiguous with such forest. In northern Costa Rica, the distribution of landhoppers seems closely related to the occurrence of tropical wet forest, premontane, lower montane and montane rain forest (Holdridge, 1967; Tosi, 1969). In the Cordillera de Tilarán, a very wet climate is maintained on the eastern slopes all the way from the Caribbean coast, by the movement of moist air west toward the mountains. The continental divide tends to have a belt of very wet elfin forest on the windward side, and cloud forest on the leeward side (Lawton and Dryer, 1980). The leeward cloud forest ends at the lower limit of the cloud spill over, and a much drier forest type exists from that altitude, down to the Pacific lowlands. Landhoppers occur well down the lower slopes of the Cordillera de Tilarán on the Caribbean (moist) side, but only occur below the lower limits of cloud forest on the drier Pacific side in moist refugia such as stream beds and spring bottoms.

No landhoppers have been captured in the tropical moist forest and tropical dry forest of the Guanacaste lowlands. No landhoppers were captured in the cold wet forest at the summit of Volcán Poás (2560 m). It may be that the conditions near the summits of volcanoes are not favourable for landhopper populations. It is also likely that landhoppers do not live in páramo (high altitude tundra-like vegetation; see Tosi, 1969), as none were found in the dwarf bamboo forests near the summit of Cerro de la Muerte.

It may be speculated that landhoppers probably occur at lower elevations in the Cordillera de Talamanca than the Cordillera de Tilarán, since the former has a less rigorous rain shadow on the Pacific side (Holdridge, 1967; Lawton and Dryer, 1980) than the latter. Little sampling has been done in the Talamanca range. There are apparently no landhoppers on the Osa Peninsula, despite its undisturbed tropical wet forest, but further sampling is needed inland from the coast.

In Panamá, *Cerrorchestia* has been collected in elevations and forest types similar to

the collection locations in Costa Rica, with the notable exception of the Gatún Lake area. According to Porter (1973), the natural vegetation of the region is tropical moist forest. The El Llano collection site in eastern Panamá province is near Cerro Jefe, and the higher elevation (approximately 980 m at the summit) of the formation may provide a moist refugium during dry periods. It is notable that in eastern Panamá, cloud forest can occur at only 750 meters, while in western Panamá it usually occurs at much higher elevations (Myers, 1969). The apparent lack of landhoppers in lowland forest in Costa Rica may be an artifact of inadequate sampling, of habitat destruction (since *Cerromachia* disappears when forest is cleared), of marginally drier forests at lower elevations which provides poor quality landhopper habitat, or all of the above. The population on Barro Colorado Island experiences large fluctuations in density, with high abundance in wet or normal years, and very low abundance in drier years (B. Gill, pers. comm.). This may indicate that this is a marginal habitat for landhoppers.

5.1.2 Previous Studies

In an extensive study of seasonal variation in litter arthropod populations, Levings and Windsor (1982) found that amphipod numbers fluctuated from low densities in the dry and early wet seasons, to high densities in the late wet season. Juvenile amphipods appeared during the wet season, comprising a greater percentage of the total numbers captured over the course of the wet season. The proportion of small individuals dropped from about 10 % of the total captured during the late wet season, to 0-11 % of the total sample during the dry season. Densities ranged from 0-84 animals per square meter in the dry season through 0-20 animals per square meter in the early wet season to 0-264 animals per square meter in the late wet season. No mean densities were reported. Litter moisture was generally estimated at between 50 and 70 % in the wet season, dropping to around 20 % in the dry season, although brief moisture peaks of up to 50 % could occur during the dry season as well. Most litter fell during the dry season, but most decomposition appeared to occur during the wet season. Amphipods constituted an important fraction of arthropod biomass (Levings and Windsor, 1982).

The pattern of abundance of large and small amphipods encountered in the above study suggests that little or no reproduction occurs during the dry season. The start of the wet season may be the beginning of breeding, although without extensive size frequency sampling the details of life history remain vague. In the 7-8 months from the early wet

2

season to the dry season, it is possible that most young attain adult size, which explains the low numbers of small animals during the dry season.

In a study of deermice food sources, Anderson (1982) used pit trapping to capture leaf litter arthropods at Monteverde, Costa Rica. In the three test sites, amphipods were common at 1540 m, just at the lower edge of the cloud forest, rare at 1420 m, and absent at 1400 m in a much drier forest area. The relative abundance of amphipods in the upper grids rose steadily from August to December but, unfortunately, the sampling was terminated at this time, and no other data are available from this study. Numerically, amphipods were the most abundant animals trapped in the cloud forest site. This may partially be due to high pit trap vulnerability compared to other arthropods, but may still indicate that amphipods are an extremely abundant leaf litter group. Buskirk and Buskirk (1976) also captured amphipods, but obtained such low numbers that they did not report on seasonal changes.

5.1.3 Climate and Characteristics of the Field Study Site

Seasonal weather patterns in the Monteverde region usually include four phases: dry season (January through April), early wet season (May through June), veranillo, the "little summer" (July and/or August), and the late wet season (August through December). Rainfall is less than 100 mm/month in the dry season, rises to about 500 mm in the early wet season, drops to 200-300 mm in the veranillo, and peaks at about 600 mm in the late wet season. Temperatures rarely rise above 25 °C and, in the cloud forest, usually range between 16 and 20 °C (Buskirk and Buskirk, 1976; John Campbell, local meteorologist, pers. comm.). Relative humidity of the air at the leeward edge of the cloud forest may drop to 70 % during the day, but almost invariably rises to 100 % at night, even in the dry season (J. Campbell, pers. comm.).

Lawton and Dryer (1980) mapped and characterized the vegetation of the Monteverde Cloud Forest Reserve. They noted that the density of epiphytes and number of growth forms increase with increasing trade wind exposure. Forest stature and the continuity of the canopy decrease with increased exposure. Lawton and Dryer (1980) described six subdivisions of cloud forest within the Reserve, which are determined by exposure to the cloudbearing winds. These were: Cove Forest, an association with a relatively high canopy and clear understory; Leeward Cloud Forest, with a lower, more open canopy, more understory shrubs and heavier epiphyte development; Oak Ridge Forest, with oaks forming a

high canopy, diverse and dense lower canopy and shrub layers, and dense epiphytes; Windward Cloud Forest, with a multi-story broken canopy, luxuriant epiphyte growth, common light gaps and dense understory shrubs; Swamp Forest, an association similar to Windward Cloud Forest, occurring in a poorly drained plateau with year-round standing pools of water, but arranged in a mosaic of low thickets and patches of taller forest; and Elfin Forest, a very dense, wet forest of short gnarled trees and very dense epiphyte growth. These last four types fall within the Holdridge (1967) definition of Lower Montane Rain Forests.

In the cloud forest, condensation plays an important part in determining leaf litter moisture, since the heavily saturated air and constant drip from the vegetation ensures very wet conditions, particularly on the windward side of the continental divide (Lawton and Dwyer, 1980; Myers, 1969). Rainfall is, therefore, a poor indicator of leaf litter moisture. Myers (1969) indicated that cloud forest is more a topographic phenomenon than a meteorological one, as this forest type can occur on ridgetops which receive no more rain than the adjacent lowlands.

A section of land recently added to the Reserve contains a young secondary growth forest (approximately 20-25 years) with fairly dry leaf litter. Below the Reserve on the Pacific side of the continental divide were the Campbell and Guindon farms, on the approximate lower edge of cloud forest conditions. Further down the mountain, near a steep altitudinal gradient known as "Cliff Edge" which drops steeply away to the Guanacaste lowlands, the Stuckey and Rockwell farms contained stands of forest with very dry leaf litter, and much different vegetation.

5.1.4 Habitat Distribution

Within the cloud forest, landhoppers were found primarily in the leaf litter. Streams and pools yielded only the ubiquitous aquatic hyalellid *Hyalella azteca*. The interior of rotting logs, tree fern leaf base rosettes, and bromeliads did not yield any amphipods. Beating of the moss and overburden on trees dislodged some amphipods, particularly in the elfin forest. Tanglefoot traps girdling large trees in the cloud forest did not capture amphipods, although there is a report of amphipods being encountered in low numbers in the branch axils of some trees in the lower edge of the cloud forest (Anderson, pers. comm.).

Pit trapping transects in a small man-made clearing near the lower edge of the cloud forest, but still surrounded by woods, showed that amphipods did not venture far from the forest edge. A notable exception to this was along very large rotten logs. Somewhat

lusher ground vegetation near these logs suggests that they provided a moister corridor along which leaf litter invertebrates could move. Amphipods were captured beside logs, but none were trapped more than 4 meters away from them into the pasture. Trap results showed that after heavy rains the amphipods would move farther out into the clearing (up to 20 meters) but retreated to the forest edge or the undersides of logs directly as conditions became drier.

Four of the six subdivisions of cloud forest were sampled quantitatively for landhoppers. These were Cove Forest, Leeward Cloud Forest, Oak Ridge Forest and Elfin Forest. The secondary growth area and Campbell, Guindon, Stuckey and Rockwell farm woods were also sampled quantitatively. The pH, measured by pH hydrion paper, was 4.5 at the soil surface in almost all sites.

Amphipods were captured in pit traps in all of these sites except the Rockwell farm. The forest on the Stuckey farm was comparatively dry, but a single male amphipod was captured near a rotten log. A stream in a shallow ravine on the Stuckey land yielded amphipods; however, pit trap transects up the ravine sides and into the forest captured no amphipods away from the wet leaf litter on the ravine bottom. In the same ravine closer to Cliff Edge, where there was little leaf litter on the ravine bottom, no amphipods were found.

The results of quantitative sampling in these forest sites in dry season and wet season are shown in Table 1. Sampling on the Stuckey farm was performed in the forest, not on the ravine bottom where landhoppers were encountered in high numbers. The highest landhopper densities of any site in Monteverde occurred in the elfin forest in both wet and dry seasons. The anomalously high concentration of amphipods on the Guindon farm in the dry season may be related to the relatively moist pocket in which samples were taken. Leaf litter a few meters from this spot was noticeably drier. It may be that the Guindon farm site was, by chance, a local refugium for the amphipods from the general vicinity.

In simple linear regressions of amphipod density against elevation, leaf litter depth, and leaf litter water content, the best correlation coefficient ($r^2 = 0.76$) was obtained for moisture content. (the other r^2 values were less than half of the water content value). These three factors are interrelated to a certain extent (drier conditions, lower elevation and deeper leaf litter generally coincide, at least on the Pacific side of the continental divide). However, the complicated air movements around the ridges and valleys of the Monteverde area may affect forest type and leaf litter factors in unpredictable ways. For example, on the Campbell farm, one ridge exhibits conditions comparable to cloud forest, yet less than 200 meters away, in

Table 1: Quantitative distribution of *Cerrorchestia hylorina* in various habitats of the Monteverde Cloud Forest Reserve, on the Pacific (leeward) side of the continental divide. Habitat forest types in brackets are as defined by Lawton and Dryer (1980). Each average represents the mean of 8 replicates. LL - leaf litter; SE - standard error.

Habitat Type	Elevation (meters)	Av. No. per square meter	SE	Av. LL depth (cm)	SE	Av. LL % water content	SE
A: Dry Season February 1983							
Cloud Forest site I (Cove Forest)	1520	108.8	56.2	2.5	0.3	63.4	1.5
second growth forest	1540	99.7	49.5	5.0	0.8	58.2	1.3
Bosque Enano (Elfin Forest)	1600	226.6	81.2	1.9	0.2	80.1	1.0
Guindon farm woods	1500	202.9	19.9	3.2	0.2	58.4	2.0
Stuckey farm woods	1380	0.0	0.0	4.0	0.4	32.3	1.4
Rockwell farm woods	1340	0.0	0.0	4.0	0.3	28.1	1.2
B: Wet season June 1984							
Cloud Forest site I (Cove Forest)	1520	95.2	22.4	3.6	0.3	80.6	0.5
second growth forest	1540	68.0	17.0	3.0	0.4	76.2	1.1
Cloud Forest site II (Leeward Forest)	1530	74.8	35.5	4.4	0.5	76.5	0.7
Cerro Roble (Oak Ridge Forest)	1650	136.0	39.8	3.8	0.3	77.9	2.0
Bosque Enano (Elfin Forest)	1600	265.2	89.3	2.5	0.2	83.8	1.1
Campbell farm woods	1540	54.4	25.2	3.9	0.4	68.7	1.4
Stuckey farm woods	1380	0.0	0.0	5.5	0.3	61.1	1.0
Rockwell farm woods	1340	0.0	0.0	3.1	0.2	51.5	1.1

the "cloud shadow" of this ridge, is a drier forest type similar to that on the Stuckey land at lower elevation. Measurements of relative humidity of the air are of limited use. Below the cloud forest conditions can range from clear, with a relative humidity of about 80 % to fog, with an RH of 99 %, within a few minutes. Depending on location relevant to the Brillante Gap and Quebrada Cuecha ravine (through which most of the cloud-bearing air masses pour), the lee edge of cloud can vary from 1300 m to 1600 m (Lawton and Dryer, 1980).

Amphipods were the dominant arthropod in the elfin forest. Even baited traps captured little besides amphipods in this habitat. The high degree of saturation of the leaf litter may be unfavourable for many of the leaf litter arthropods found in abundance in slightly drier conditions, resulting in a depauperate fauna. In the cloud forest, amphipods generally outnumbered other arthropods (excluding mites) by about 2 to 1, except in cases where ant columns filled the traps.

The Atlantic side of the continental divide is much different from the Pacific side. Down the valley of the Río Penas Blancas toward the Llanura de San Carlos, cloud forest merges gradually into premontane wet forest (*sensu* Holdridge, 1967). Amphipods have been captured at 700 m, in moist forest near the river. Evidently the forest receives sufficient moisture to maintain amphipod populations at a relatively low elevation. This is unsurprising, as the air masses that give rise to the Monteverde Cloud Forest flow mainly from the Caribbean side of the mountains (Lawton and Dryer, 1980). Unfortunately, due to difficulty of access, no quantitative samples are available from the Penas Blancas valley.

5.1.5 Immersion Tolerance

Drowning experiments yielded lethal immersion for 50 % of the sample (LI50) as given in Figure 20 and Figure 21, and in Table 2. Over the 8 day test, temperatures in the field station varied from 18 to 23 °C, which may have affected the results. The salt water was seawater collected from the Gulf of Nicoya at Puntarenas. Fresh water was collected from Quebrada Cuecha in the Cloud Forest Reserve. Salinity meters were not available to record water chemistry data.

There were notable differences between response to fresh water and salt water in both adults and juveniles. Juveniles had greater LI50 values.

Table 2: Lethal immersion time in hours for 50 % of sample, for *Cerrorchestia hyloraina* adults and juveniles tested in salt water and freshwater. The LI50 values are the point where the linear regressions cross the 50 % mortality level, for each replicate of salt and fresh water (see immersion tolerance figures). SE - standard error.

Taxon	Division	Trial	Salt water	Fresh water
<i>Cerrorchestia hyloraina</i>	Adults	A	6.2	45.5
		B	4.5	28.4
		C	5.2	68.3
		average	5.3	47.4
		SE	0.5	11.6
<i>Cerrorchestia hyloraina</i>	Juveniles	A	12.6	117.2
		B	34.3	169.9
		C	47.7	93.1
		average	31.5	126.7
		SE	10.2	22.7

5.1.6 Feeding

Food choice experiments, although plagued with subject mortality, indicated that amphipods preferred aged leaves to fresh ones. Eighty per cent of observed feeding took place on aged leaves. Tough, dry leaves of *Cecropia* and thick, waxy-coated leaves of *Clusia* were avoided in preference to more tender forms such as *Centronia*, *Eleagia*, *Didymopanax*, and *Ficus*. In initial experiments, the amphipods ignored the leaf sections and ate paper napkin sections placed in the dishes to provide moisture and cover. In other situations, amphipods ate paper labels, pencil lettering and all. Fruit, bark and insect or mammal flesh were not touched, and no cannibalism was observed.

The normal feeding mode of *Cerrorchestia hyloraina* was to scrape the surfaces of leaves, although some biting of leaf edges (like caterpillars) was observed. Leaves left in the petrie dish habitats were skeletonized in 5-15 days. There was no apparent difference in diet between young and adult; however, observational difficulties may have masked this. Young released from the pouch were translucent, and were observed to rapidly acquire gut contents, but active feeding in such small individuals was very difficult to observe. They may have fed upon the fecal pellets of the adults, or upon leaf litter. Slides of amphipod gut contents were uninformative, showing fragmented plant material and amorphous detritus.

5.1.7 Movement and Behavioural Observations

Six-hour pit trapping established that movement normally occurred between 6 PM and 6 AM. There was no significant difference between numbers of amphipods captured before and after midnight. The few times amphipods were captured between 6 AM and noon were always during or after heavy rain and fog. No amphipods were captured between noon and 6 PM.

The trough of a flight intercept trap, cleaned weekly, captured a remarkably regular number of amphipods each week. This suggests that the amphipods move about a great deal, since it might be expected that a large stationary trap would yield fewer animals with time if the species were sedentary or territorial. Pit traps cleared daily often showed unusually large catches of amphipods after heavy rains, indicating that the animals must have been particularly active at such times.

Attempts to mark individual *Cerrodontia* with nail polish failed, because the animals convulsed and died upon application, even if the polish was only brushed lightly on the uropods. Lasting marks were achieved with water based typewriter correction fluid. Mark and recapture experiments failed to obtain any recaptures.

When walking, pereopod 6 was normally held up over the animal's back and was used for pushing against whatever was above it. Gnathopod 1 was used in walking (although not always), but GN2 was always held tucked up under the body in both male and female. The vertical orientation of P6 was particularly useful in the crevices of leaf litter; animals often turned somersaults in place by pushing on material above them with P6 and on the substrate with P5 and P7. Within the litter, the animals did not maintain a particular body orientation, moving and resting sideways or upside-down as much as right side up. If a covering leaf was gently lifted off an amphipod, the animal would actively search for it with P6, before moving off to other cover. No burrowing was observed.

Walking was the normal mode of locomotion. Jumping only occurred when the animals were abruptly disturbed by abrupt vibration or sudden movements near their containers. Agitated animals would jump 3-4 times, then freeze against the substrate. Jumping was accomplished by spreading and bracing P5 and P7, then snapping the abdomen (normally carried curled under the body) down and back to fling the animal into the air. Jumps reached up to 30 cm in height, covered up to 60 cm distance, and were apparently random. Animals could be touched gently without eliciting an escape jump.

The second antennae were crooked at the flagellum so that the tips touched the substrate.

When moving about the antennae were tapped on the substrate in front of the animal, each antenna moving independently, in a manner remarkably reminiscent of ants. Under the scanning electron microscope, a spray of very fine tendrils was visible at the tip of antenna 2. These are probably chemosensory and tactile organs.

Individual *Cerrochestia* readily entered water droplets within their habitats. In water, they would occasionally turn on their sides and proceed with the pereopods of one side only; similar to the "sidling" gait of freshwater amphipods such as *Hyalella*. In water the pleopods beat rapidly, although the animals never swam. Pleopods did not normally beat when the animal was in air, although distressed animals would sometimes lie on their sides with pleopods beating. Landhopper young would often leave their mother's pouch and walk about if she entered water, or lay on her side. They were occasionally seen to reenter, if the female did not move away. Beachflea young were also observed to leave the mother's pouch in fresh water, but actively swam away using their pleopods, and did not appear to reenter.

Females with eggs or young in the pouch carried GN2 crossed across the venter while moving. Pouch contents were easily lost, particularly during violent movements. Females used the first and second gnathopods and mouthparts to groom the body and appendages, in movements very similar to those described for *Talitroides alluaudi* by Holmquist (1985). The second antennae were groomed by drawing them through the maxillipeds. Females were observed to scrub their legs with the propod of GN2, possibly using the scale fields on the pellucid lobe, as suggested by Holmquist (1982, 1985). Males groomed almost exclusively with GN1. They were not observed to use the second gnathopods for any manipulation, and usually carried them tucked up against the venter.

5.1.8 Reproduction

The appearance of oostegites as small flaps of tissue was taken as an indication of female sexual maturity. This occurred in females between the lengths of 7.4 and 8.8 mm. Males were more difficult to characterize due to the occurrence of "feminized" gnathopods. Enlargement of the propods of both gnathopods was used as an indication of male sexual maturity, since the penil papillae were not always evident. The smallest recognizable male was 7.1 mm. It is not known how many moults compose the subadult stage.

In quantitative samples, the sex ratio averaged 1.5 females to 1 male, but varied a great deal among samples. Pit traps tended to catch more males than females, averaging a ratio of 2 males to 1 female.

Fecundity of females was relatively low, with an average egg count of 7 (ranging from 3 to 12). Loss of eggs over the development time was apparently normal, as the smallest eggs (newly laid) were most numerous, and the largest (ready to hatch) tended to be fewer. The average count of young in the pouch was 5 (ranging from 1 to 9). These estimates may be low, since females may have lost brood pouch contents in struggling to escape traps and sampling. Minimum egg length was 0.63 mm long, maximum length was 1.1 mm, and the average 0.74 mm.

Despite many hours of observation of male/female pairs, only one interaction was seen. A male reached toward a passing female with both pairs of gnathopods, but the female used its limbs and abdomen to break free. No further interaction was observed. It may be that mating behaviour was disturbed by light, or that some factor to elicit courtship was missing from the experimental habitats.

Seasonal samples obtained by local helpers, while too small to analyze for size frequency distributions, showed that ovigerous females and very small juveniles could be encountered at any time of year. There was no indication of especially high numbers of juveniles in any one season. In Monteverde, breeding may be continuous. In contrast, the Barro Colorado population apparently breeds only during the wet season (Levings and Windsor, 1982). Populations at lower elevations in Costa Rica where seasonality is more pronounced, may have breeding periods more comparable to the BCI population.

5.1.9 Growth

To moult, the animals usually lie on their sides. The break point of the old exoskeleton is between the first and second thoracic segments. The posterior portion of the exoskeleton is shed first, then the head capsule. Movements are slow, compared to the violence with which the freshwater amphipod *Hyaletta* kicks free of the moult. Also in contrast to freshwater amphipods, *Cerriorchestia* individuals always eat the shed exoskeleton. Their feces are bright red for 24 hours afterward.

Mortality during moulting among the captive individuals in Monteverde became very high when temperatures rose over 20 °C.

Average female size was 9.9 mm ($n = 74$, S.E. = 0.12) ranging from 7.4 to 12.6 mm. Average male size was 9.6 mm ($n = 71$, S.E. = 0.12) ranging from 7.2 to 11.8 mm. The two means were significantly different at the 95 % level.

Newly hatched (first instar) juveniles taken from female brood pouches were from 2.9

to 3.2 mm. First instar antennal segment counts were as follows: antenna 1 had 3 peduncle and 2 flagellar segments; antenna 2 had 5 peduncle and 5 flagellar segments. Since the peduncular segments are fixed from birth, antennal segment counts are reported as flagellar counts only. The first instar had very small eyes with only 10-14 facets, and there were no visible gut contents.

Instar sizes were difficult to establish from the available size frequency data. Size ranges and antennal segment counts overlapped a great deal, resulting in a continuum of data, within which discreet groups (instars) were not readily distinguishable (see Figure 22). Using graphs and frequency tables, initial estimates of juvenile moult statistics were obtained (Table 3). The average moult increment was 0.5 mm, and the animals apparently did not add one flagellar podomere to antenna 2 with each moult.

The overlap among adults was even more pronounced than among juveniles (see Figure 22). Reliable determinations of adult moult statistics could not be made from available data, but the moult increment may have been larger for adults than for juveniles. The maximum podomere count for A1 was 5, but the largest specimens measured had 4. The maximum A2 flagellar count was 20 podomeres in males and 18 in females. Males tended to have two more A2 flagellar podomeres than females in all adult size classes. Identifiable size frequency peaks were at comparable sizes for both sexes, suggesting that moult increment is not subject to sexual differences.

The relationship between antennal segment number and total length (Figure 22) can be described by the linear equation

$$(A1 + A2) = 1.34 + 0.18(TL)$$

where $(A1 + A2)$ is the total number of flagellar segments on antenna 1 and antenna 2 (right side only), and TL is total length (mm). The r^2 statistic for this relationship was 0.94.

Rearing experiments failed to establish moult interval (time between moults), because no individuals were successfully held through two moults. The longest holding periods were 26 and 32 days without moulting, with subsequent death of the animals. It is probable that the high temperatures within the field building were responsible for the mortality, although inadequate diet and/or habitat may also have contributed.

The duration of life cycle for these amphipods is still unknown. The limited evidence available for infrequent moulting suggests that in the cloud forest these animals may well live more than one year.

Table 3: Average length and flagellar antennal segment counts from size frequency analysis of field samples of juvenile *Cerrorchestia hyloraina* from the Monteverde Cloud Forest Reserve in Costa Rica. Length is total body length from rostrum to telson tip. Instar 10 may overlap with sexually mature adults.

size category (instar)	mean length mm	A1 flagellar segments	A2 flagellar segments	A1 + A2 flagellar segments
1	3.1	2	5	7
2	3.4	2	6	8
3	3.9	2	6-7	8-9
4	4.4	2	7	9
5	4.9	2	8-9	10-11
6	5.6	2	9	11
7	6.0	2	9-10	11-12
8	6.4	3	10	13
9	7.0	3	11	14
10	7.6	3	12	15

Figure 20: Immersion tolerance data from experiments in fresh and salt water using adult *Cirrorchestia hyloraina*. Each datum represents the percent of the test animals of that replicate which had expired by that time. The regression lines were calculated by linear regressions of the base 10 logarithm of time to death (in hours) on the probit equivalents of percent mortality, for each replicate. Lethal immersion time for 50 % of the population is where the regression line crosses the 50 % mortality level of the vertical axis. The experiment included 6 replicates: salt water and fresh water trials A, B, and C.

Adult
Cerrorestia hyloraina

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Figure 21: Immersion tolerance data from experiments in fresh and salt water using juvenile *Cerrorchestia hyloraina*. Each datum represents the percent of the test animals of that replicate which had expired by the given time. The experiment included 6 replicates: fresh water and salt water trials A, B, and C. The regression lines were calculated by linear regressions of the base 10 logarithm of time to death (in hours) on the probit equivalents of percent mortality, for each replicate.

Juvenile
Cerrorchestia hyloraina

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Figure 22: Relationship of the number of flagellar segments on both antennae to total body length (rostrum to telson tip) for *Cerrorchestia hyloraina*, in the Monteverde Cloud Forest Reserve, Monteverde, Costa Rica. Numbers indicate multiple individuals for that size and segment count. See text for linear regression equation. n = 312

5.2 Biology of *Caribitroides tuxtlenis*

5.2.1 Geographic Distribution

Caribitroides tuxtlenis inhabits tropical rain forest in the Sierra de Los Tuxtlas, Veracruz State. It apparently can not survive clearing of the forest, although it may be able to persist in relatively small relict forest patches. None have been captured in the Gulf Coastal Plain, the Tehuantepec lowlands nor in the Yucatán. The highland which includes Mt. Orizaba (5747 m) may be too cold to harbour landhoppers, since even the city of Córdoba (at 1000 m) experiences occasional frost (Gómez-Pompa, 1973). The highlands in Oaxaca and Chiapas have yielded other landhopper species but specimens of *C. tuxtlenis* have not been captured outside of the Los Tuxtlas area.

5.2.2 Climate and Characteristics of the Field Study Site

The climate of the Sierra de Los Tuxtlas is affected by the Gulf of México and local relief. Cooling and ascension of the humid northeast trade winds from the Gulf, upon contact with highlands, produces heavy precipitation on the windward side, and a semi-arid zone on the northwest (leeward) side. The average annual temperature at Coyame, near Lago Catemaco in the central basin of the Sierra, is approximately 24 °C, and total annual rainfall is over 4400 mm. The rainy season begins in June and continues into November, with a short period of dry warm weather called *canícula*, in mid-rainy season (usually August). The dry season is usually from February to May. During the dry season, rain is not brought by trade winds but by polar air masses called *nortes*. Fairly cool temperatures may occur during *nortes* (the city of Veracruz is occasionally affected by frost). The severity of the dry season is greater at lower elevations and on the leeward side of Los Tuxtlas (Andrie, 1964; Gómez-Pompa, 1973).

A vegetational transect from the summit of Volcán San Martín Tuxtla to the ocean showed an altitudinal front gradient (Gómez-Pompa, 1973) as follows:

- 1500 m elfin forest/cloud forest
- app 1000-900 m *Liquidambar* forest
- 900-700 m high semi-evergreen montane forest
- 700 to app 100 m high evergreen forest

- app 100-0 m coastal scrub

Small patches of elfin forest occur on both San Martín and Santa Marta volcano summits (windward sides only) and patches of cloud forest (*sensu* Lawton and Dryer, 1980) occur on both main volcanoes and two lower volcano summits above 1000 to 1200 meters. Volcanic eruptions may have had important effects on the biota, as there are historical records of the destruction of fairly large areas of forest. Clearing of forest by humans is also a recent factor. The existence of endemic species of bird, reptile, and amphibian indicate the relative isolation and importance as a refugium of this Sierra (Andrle, 1964).

The Los Tuxtlas Tropical Biology Station is located 33 km northeast of Catemaco, 4.5 km from the Gulf Coast, and comprises 700 hectares of evergreen rain forest, mostly between 160 and 530 m elevation. Mean annual rainfall is 4600 mm, and no month has less than 40 mm of rain (Estrada and Coates-Estrada, 1983). The majority of leaf fall in the reserve is during the dry season. The least decomposition occurs during the dry season, resulting in a buildup of litter during this time. The major leaf litter components, comprising 50 % of leaves on the forest floor, are *Nectandra ambigua*, *Pseudolmedia oxyphyllaria*, *Vatairea lundelli*, *Poulsenia armata* and *Ficus glabrada* (Alvarez, 1982).

5.2.3 Habitat Distribution

Caribitroides tuxtlenis was found only in the leaf litter. Searches of streams and pools, the interior of rotten logs, tree branch axils and bromeliads did not disclose any landhoppers.

Pit trapping transects captured slightly more landhoppers near large rotten logs than in standard forest floor leaf litter. No amphipods were captured on cleared land. Watercourse tests did not indicate higher landhopper numbers near streams. Several forest transects did not show clear patterns of distribution, although sifting of leaf litter tended to capture more landhoppers in pockets of noticeably moister leaf litter than the surrounding areas. These pockets seemed to be randomly distributed, and may have been artifacts of topography. The pit traps captured more animals in July than in June, although there was slightly less rain in July. This may be due to a relatively long dry season in 1984 (R. Coates-Estrada, pers. comm.), which may have delayed movement of amphipods, and reduced their vulnerability to trapping until after the rainy season was established. The leaf litter seemed very dry, and amphipods very scarce by all sampling methods until after a week of heavy rains in mid-June.

The results of quantitative sampling are shown in Table 4. Since the research area of the station lacks significant altitudinal or forest type gradients, an attempt was made to study differences in amphipod density between climax forest and light gap situations.

Light gaps are areas of major canopy breaks, usually caused by the collapse of large trees. Immediately after the light gap is opened, secondary growth begins to develop, and proceeds through a succession of understory growth, development of trees specialized to colonize light gaps, and regrowth of primary forest species (Lawton and Dryer, 1980). Light gaps in the Los Tuxtlas forest are characterized by deeper leaf litter, and secondary growth understory (including young *Cecropia* trees, which are gap colonizers). A peculiar feature of these light gaps are chocho palms (*Astrocaryum mexicanum*) with 90 degree elbows in their trunks from being crushed by treefalls (Miguel Martínez, pers. comm.). Lacking suitable quantification techniques, the differentiation of light gaps from primary forest (which had a high canopy and relatively thin leaf litter) was somewhat arbitrary. Gaps pointed out by M. Martínez (pers. comm. 1984) were sampled.

Amphipod density was extremely patchy, and mean densities for each sample were highly variable. Leaf litter water content apparently varied little among sample sites, although this may have been an artifact of crude techniques and the regular heavy rains. Dry season comparisons would probably be more informative. The leaf litter from climax forest, while slightly shallower than that of gaps, was apparently slightly moister, and tended to have more amphipods, but correlations for each variable were very weak.

The results seem to indicate that percent water content was apparently not the primary factor affecting distribution. It may be that amphipods clustered in areas which maintained a certain moisture level all year round, or perhaps of a certain minimum size or topographic configuration. Amphipods may be capable of sensing details of microhabitat that are not readily evident to humans, and may be impossible for us to quantify. Much further sampling with sophisticated habitat quantification is necessary to establish further details.

Further sampling over a major altitudinal gradient may reveal a macrohabitat distribution similar to that of Monteverde, Costa Rica. It is possible that the Los Tuxtlas Station forest is the lower limit of the landhopper range in the Sierra de Los Tuxtlas in terms of leaf litter moisture and altitude. A transect from the summit of San Martín volcano to the ocean, through the forest types documented by Gómez-Pompa (1973) would provide more informative data. Such a transect was impossible within the limitations of this study, due to the difficulty in reaching the windward side of the volcano. An attempt to sample the

area near Coyame was unsuccessful due to the inaccessibility of uncut forest.

Sampling established that *Caribitroides tuztlensis* does not survive destruction of the forest. On one side of the Los Tuxtlas protected area, the forest has been cut right to the property line, and a fence separates climax rain forest from clear-cut. At this site no amphipods were seen more than four meters away from the forest edge, and quantitative sampling 10 meters from the forest edge yielded no amphipods.

Amphipods were also absent from coastal woods. On ravines behind Playa Escondida and Montepío, in coastal scrub, no amphipods were captured by any trapping method. Although more sampling is necessary, it appears (see also the immersion tolerance study) that landhoppers may be intolerant of salt to the point where they cannot maintain populations within a kilometer or two of the ocean. Correlations of soil salinity with amphipod presence and density, and lab studies of amphipod growth on substances with varying amounts of salt, would establish hard data on this subject.

5.2.4 Immersion Tolerance

Simultaneous drowning experiments were run with *Caribitroides tuztlensis* and a colony of *Platorchestia* sp. collected from Gulf shore beach wrack by the mouth of the Río Máquina at Montepío. These beachfleas, while resembling the description of *Platorchestia platensis*, varied in several characters so that they are not assignable to that species. The salt water used in the experiments was seawater from the Gulf of México, collected at Montepío near the mouth of the Río Máquina. The freshwater was collected from a forest stream near the Los Tuxtlas Biological Station. No equipment was available to determine water chemistry accurately.

The immersion tolerance data are shown in Figure 23, Figure 24, Figure 25, Figure 26, and in Table 5. The temperature in the field station was 25–27 °C over the test period. Cannibalism of dead animals was observed among *Platorchestia* but not *Caribitroides*.

Landhoppers showed significant differences between freshwater and saltwater LI50s for both adults and juveniles. *C. tuztlensis* juveniles died in salt water at much the same rate as did adults, although their fresh water immersion tolerance was slightly higher.

In contrast, *Platorchestia* adults were more tolerant of submersion in salt water than were the juveniles, but less tolerant of fresh water. Immersion tolerances for both fresh and salt water were significantly different from *C. tuztlensis*.

Table 4: Quantitative distribution of *Caribitroides tuztlensis* in habitats near the Los Tuxtlas Biology Station, 33 km northeast of Catemaco, Veracruz State, México. These samples were taken during the early wet season, July 1984. Each average represents the mean of 5 replicates. LL - leaf litter; SE - standard error.

Habitat Type	Elevation (meters)	Av. No. per square meter	SE	Av. LL depth (cm)	SE	Av. LL % water content	SE
Site I climax forest	160	144.5	17.4	2.1	0.1	38.1	1.2
Site II climax forest	160	99.7	49.5	2.5	0.3	42.0	1.9
Site III climax forest	160	4.5	1.7	2.2	0.2	43.6	2.4
Site IV climax forest	250	108.8	28.1	1.9	0.2	48.5	1.6
Site V climax forest	190	79.2	23.9	2.5	0.2	39.7	2.0
Site VI light gap	160	40.5	6.6	3.5	0.3	30.2	1.6
Site VII light gap	160	8.6	2.9	3.9	0.4	35.9	3.2
Site VIII light gap	160	39.8	17.6	3.2	0.2	38.9	1.5
Site IX light gap	190	120.3	52.8	4.4	0.5	40.1	2.2
Site X light gap	200	18.5	6.9	3.3	0.4	35.6	1.3
Pasture near forest	150	0.0	0.0	0.5	0.1	22.9	2.6
Playa Escondida coastal scrub	50	0.0	0.0	3.4	0.2	29.1	1.7
Montepío coastal scrub	25	0.0	0.0	2.3	0.2	33.4	2.6

5.2.5 Feeding

The results of feeding experiments and observations were very similar to those of *Cerrorchestia hyloraina*. Aged leaves of *Psychotria*, *Turpinia*, *Poulsenia* and *Faramea* were readily eaten. *Cecropia* was taken more rarely. *Clusia* and *Astrocaryum* were not fed upon. Feeding modes were as in *Cerrorchestia*, with both surface scraping and edge biting.

5.2.6 Movement and Behavioural Observations

Pit trapping at six hour intervals established that all movement was between 6 pm and 6 am. There was no significant difference between numbers of amphipods captured before and after midnight. Amphipods were not captured between 6 am and noon. Higher numbers of

Table 5: Lethal immersion time in hours for 50 % of sample, for *Caribitroides turtlensis*, a landhopper and *Platorchestia* sp., a beachflea, in salt water and freshwater. The L150 values are the point where the linear regressions cross the 50 % mortality level for each replicate of salt and fresh water (see immersion tolerance figures). SE - standard error.

Taxon	Division	Trial	Salt water	Fresh water
<i>Caribitroides turtlensis</i>	adults	A	1.4	29.6
		B	1.9	20.0
		C	1.2	27.6
		average	1.5	25.7
		SE	0.2	2.9
<i>Caribitroides turtlensis</i>	juveniles	A	1.2	38.9
		B	2.1	38.1
		C	1.4	64.7
		average	1.6	47.2
		SE	0.3	8.7
<i>Platorchestia</i> sp.	adults	A	24.2	18.7
		B	19.2	17.1
		C	18.0	23.0
		average	20.5	19.6
		SE	1.9	1.8
<i>Platorchestia</i> sp.	juveniles	A	13.0	17.2
		B	10.8	8.3
		C	11.9	14.3
		average	11.9	13.3
		SE	0.6	2.6

amphipods were captured after heavy rains (which usually occurred at night).

Locomotion was the same as in *Cerrorchestia hyloraina*, with P6 held vertically and A2 testing the substrate. Jumping sometimes occurred with no obvious disturbance stimulus. No burrowing was observed in jars of soil with or without leaf litter. Animals in petrie dish habitats moved very little during the day unless disturbed, but were very active at night. This nocturnal activity did not seem to be affected by artificial light. Controlled daylight laboratory studies could be used to establish whether the diel activity patterns are innate or are affected by daylength and/or light intensity.

No burrowing was observed among *C. tuztlensis* colonies or individuals held in terraria and jars with and without leaf litter. When leaf litter was available, the landhoppers stayed within it. When no leaf litter was available, they pressed themselves against the substrate or tried to crawl under small clods of soil.

In contrast, *Platorchestia* could not be kept alive if not allowed to burrow. In petrie dishes, whether sand or leaf litter was supplied as cover, the animals engaged in constant attempts to burrow, and died within 48 hours. Colonies kept in bags or terraria with six inches of sand persisted for months. Evidently *Platorchestia* requires a minimum depth of sand in which to burrow. *Tethorchestia* collected at Playa Escondida did not construct burrows, but hid under driftwood and wrack where the sand was visibly damp. Mortality was also high for these beachfleas in petrie dishes, but not terraria.

Individuals of *Caribitroides* did not readily enter water. When immersed, they occasionally walked or tried to jump, but usually clung tenaciously to any solid object with all pereopods. In water the pleopods beat, although the abdomen was carried curled under the body as in normal activity. The pleopods were not observed to beat in air. No attempts to swim were observed in adults or juveniles.

In contrast, most *Platorchestia*, particularly juveniles, readily entered water and swam effectively by extending the abdomen and beating the pleopods rapidly, as in aquatic species. Animals in distress from prolonged immersion lay on their sides or back with pleopods beating. In a terrarium partially filled with beach sand, *Platorchestia* females were observed to enter a dish of fresh water to release the young, which swam actively about until exiting the dish 0.25 to 1 hour later.

As in *Cerrorchestia hyloraina*, females of *Caribitroides tuztlensis* carried GN2 crossed across the brood pouch when eggs or young were occupying it. The first gnathopods were used far less than GN2 and the mouthparts as grooming tools. Male grooming was identical

to that of females. Gills were appressed to the body and leg coxae in a noticeable film of water on the venter between the coxal plates.

5.2.7 Reproduction

No mating or behaviour attributable to courtship was observed. Mating is probably very brief. Mating behaviour, recognition between sexes, and courtship remain unknown. Also unknown is if males will compete for females. Although amphipod density in the Tuxtlas forest was extremely patchy, groups of amphipods held together in petrie dishes and terraria did not cluster closely together, but seemed randomly distributed in available leaf litter space. If encounters between individuals are random, then some recognition signals must be present to allow receptive females to be mated.

Female mean total length was 8.3 mm [SE 0.1]. Females with visible oöstegites ranged from 6.7 to 10.5 mm. Male mean length was 7.0 mm [SE 0.1], ranging from 5.9 to 8.4 mm. Sex ratios averaged 2 females to 1 male in all sampling types, although there was considerable variation between samples.

Female fecundity averaged 6.8 eggs, ranging from 1 to 10. The average count of young in the pouch was 5 (range 1 to 7). Average egg length was 0.83 mm, with a range of 0.63 mm to a maximum of 1.10 mm in eggs apparently about to hatch. Fecundity counts may be low due to loss of pouch contents with handling.

A full year of regular sampling would be necessary to establish breeding seasonality. From the limited field data available, it appears that the proportion of juveniles in the population increases shortly after the rainy season begins. It is possible that *Caribitroides tuxtlenensis* breeds primarily during the wet season at the low elevation of the Los Tuxtlas Biology Station. A seasonal series of comparative samples taken in the cloud or elfin forests near the highest elevations in the Sierra, and at the Los Tuxtlas Station near the lowest occurrence of *C. tuxtlenensis* would establish whether there were differences in seasonality between low elevation and high elevation demes, and thus give an indication of the importance of moisture variations to reproductive activity.

5.2.8 Growth

Female mean total length was 8.3 mm ($n = 64$, S.E. = 0.12) ranging from 6.3 to 10.5 mm. Male mean total length was 7.0 mm ($n = 38$, S.E. = 0.13) ranging from 5.9 to 8.4 mm. These means were significantly different at the 95 % level.

Young taken from the females pouch were between 2.2 and 2.4 mm total length, with 1 flagellar segment on A1 and 3 flagellar segments on A2. Antennal segment addition occurred at the first segment of the flagellum, which elongated to twice the length of a normal flagellar segment, then formed the crosswall of the new segment approximately halfway down the elongation. This often occurred in one antenna before the other, so that the segmental counts differed from left to right.

Bar graphs and cross tabulation of size categories and antennal segment counts were used to construct an estimate of juvenile instar statistics at approximately 27 °C (Table 6). In some cases, antennal segment counts varied by one or two above and below the recorded averages. Particularly variable A2 counts occurred in instars 2, 4, 6, 8, 9 and 10. A segment was added to antennae 1 approximately every 3 instars. About one segment per instar was added to A2 for the first 6 instars, then less regularly. The average size increment per moult was approximately 0.5 mm.

As in *Cerrochestia*, adult instar overlap was much more pronounced than that of juveniles (see Figure 27). The apparent moult increment was about the same as for juveniles. The maximum podomere count for the flagellum of A1 was 4. The maximum A2 flagellar count was 15 for both males and females. The relationship between antennal segment number and total length (Figure 27) can be described by the linear equation

$$(A1 + A2) = -0.25 + 2.12(TL)$$

where (A1+A2) is the total number of flagellar segments on antenna 1 and antenna 2 (right side), and TL is total length (mm). The r^2 statistic for this relationship was 0.93.

No data on moult rates were obtained in this study, because no individual was successfully held through more than 1 moult. Some individuals were held 23 days without moulting, which suggests a fairly slow growth rate. Controlled laboratory studies could determine both the frequency of moulting at given temperatures, and the moult increments of length and antennal segments.

Table 6: Estimated instar statistics from size frequency analysis of field samples of juvenile *Caribitroides tuxtensis* from the Los Tuxtlas Biology Station in México. Length is total body length from rostrum to telson tip. Instars 9 and 10 overlap with sexually mature adults.

size category (instar)	mean length mm	A1 flagellar segments	A2 flagellar segments	A1 + A2 flagellar segments
1	2.5	1	3	4
2	2.8	1	4	5
3	3.2	1	5	6
4	3.7	1-2	6	7-8
5	4.2	2	7	9
6	4.6	2	8	10
7	5.0	2	8-9	10-11
8	5.5	2-3	9	11-12
9	6.0	3	9-10	12
10	6.7	3	10-11	13-14

Figure 23: Immersion tolerance data from experiments in fresh and salt water using adult *Caribitroides turtlensis*. Each datum represents the percent of the test animals of that replicate which had expired by that time. The experiment included 6 replicates: salt and fresh water trials A, B and C. The regression lines were calculated by linear regressions of the base 10 logarithm of time to death (in hours) on the probit equivalents of percent mortality, for each replicate. Lethal immersion time for 50 % of population is where the regression line crosses the 50 % mortality level of the vertical axis.

Adult
Caribitroides tuxtlensis

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Figure 24: Immersion tolerance data from experiments in fresh and salt water using juvenile *Caribitroides tuxtlensis*. Each datum represents the percent of the test animals of that replicate which had expired by that time. The experiment included 6 replicates: fresh water and salt water trials A, B, and C. The regression lines were calculated by linear regressions of the base 10 logarithm of time to death (in hours) on the probit equivalents of percent mortality, for each replicate.

Juvenile
Caribbitroides tuxtlensis

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Figure 25: Immersion tolerance data from experiments in fresh and salt water using adult *Platorchestia* sp. Each datum represents the percent of the test animals of that replicate which had expired by that time. The experiment included 6 replicates: fresh water and salt water trials A, B, and C. The regression lines were calculated by linear regressions of the base 10 logarithm of time to death (in hours) on the probit equivalents of percent mortality, for each replicate.

Adult
Platorchestia sp.

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Figure 26: Immersion tolerance data from experiments in fresh and salt water using juvenile *Plutorchestia* sp. Each datum represents the percent of the test animals of that replicate which had expired by that time. The experiment included 6 replicates: fresh water and salt water trials A, B, and C. The regression lines were calculated by linear regressions of the base 10 logarithm of time to death (in hours) on the probit equivalents of percent mortality, for each replicate.

Juvenile
Platorchestia sp.

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Figure 27: Relationship of the number of flagellar segments on both antennae to total body length (rostrum to telson tip) for *Caribitroides tuxtensis*, in Los Tuxtlas Biological Station forest, Veracruz State, México. n = 241

Flügeljar Antennal Segments

5.3 Discussion

5.3.1 Distribution

The combination of high rainfall on the windward side of elevations of about 1000 m seem to be the prerequisites for a sufficiently wet forest to support landhoppers. In México, Costa Rica and the West Indies, this pattern holds reasonably true (with the notable exception of Barro Colorado Island). Landhoppers can occur down to very low elevations on the windward side of such highlands, but little below the lower edge of cloud forest on the leeward side.

Within wet forests, the New World landhoppers occur within the leaf litter, and can also climb trees, particularly where a luxuriant epiphyte layer is available from the ground up (producing, in effect, an unbroken habitat from the leaf litter to the tree branch axils). In very wet conditions such as elfin forest, the microdistribution and population density are less patchy and irregular than in drier forests. At lower elevations, where the effects of dry season are more pronounced, landhoppers seek out the moistest patches of habitat (such as springs and ravine bottoms). These form local refugia during the driest periods, from which the animals may spread out during wetter conditions. The lowest population densities and most patchy distributions are in these drier areas. Moisture content is apparently the most important factor in determining local distribution.

5.3.2 Immersion Tolerance

The results of the petrie dish experiments suggest that beachfleas can tolerate extended immersion in salt water but landhoppers cannot. Unfortunately, the biological oxygen demand of the subjects may have exceeded the rate of re-aeration across the air-water interface. This could ensure that higher biomass of amphipods (with higher biological oxygen demand) would expire before lower biomass. This means that the larger differences in LI50 between adults and juveniles may be at least partially an artifact. Lack of aeration may or may not be responsible for some of the apparent differences between landhoppers and beachfleas, as well¹.

Further studies under controlled laboratory conditions (with replicable food portions) on these taxa and other species of talitrids (including palustral species) would provide more

¹Dr. D. Wildish believes these experiments are invalid, since the amphipods died of combined anoxia/ion problems.

information on a poorly understood aspect of talitrid biology. High salinity tolerances are quite different between essentially marine versus freshwater *Orchestia* (Spicer *et al.* 1987; Wildish, 1970).

5.3.3 Feeding

The diet of New World landhoppers is relatively unspecialized, although they seem to avoid animal tissue (with the notable exception of their own cast exoskeletons). Most landhoppers seem to share this diet of decaying plant material (Friend and Richardson, 1986; Lawrence, 1953). Leaves that have undergone some microbial conditioning are preferred to fresh ones, but it is apparently the chemical and physical effects of fungi and bacteria, rather than their actual presence, which makes the aged leaves attractive (Morton and Richardson, 1984).

Friend (1980) found that leaves tended to lie on the forest floor in Tasmania for one or two months before attack by amphipods. He concluded that the palatability of leaves was increased by leaching and fungal attack. The main tree species in Friend's study site were *Olearia*, *Acacia* and *Eucalyptus*. In Central American forests with greater species diversity, and greater potential variability in the timing of leaf fall, the ageing time for optimum palatability may vary among species, depending on the tenderness of the leaf, quantities of tannins and other defensive or noxious chemicals, and the timing of leaf fall in relation to precipitation and litter moisture.

It is probable that landhoppers have a gut flora to aid in digestion of plant material. This flora may be mostly bacterial in nature. Trichomycete gut fungi may not be significant, since infestation by these fungi often is relatively low in amphipods (R. W. Lichtwardt, pers. comm.), probably due to moulting of the hindgut cuticle (where the fungi are attached by holdfasts). Re-inoculation of adults between moults, and initial inoculation of newly hatched young may be accomplished by coprophagy. Young *Hyalella azteca* graze extensively on the feces of adults (Lindeman, unpublished). This may serve a dual purpose; providing flora inoculation, and allowing the young a source of partially digested food.

5.3.4 Movement and Behaviour

The field studies showed that both *Cerrochestia hyloraina* and *Caribitroides tuxtlensis* were most active at night and during heavy rains. These data indicate that in the field as well as in captive colonies, landhopper activity increases at low light levels. Similar behaviour among Tasmanian landhoppers was noted by Friend (1980), who proposed that since diurnal

activity rhythms were evident under conditions of almost constant high humidity in the leaf litter, light intensity and temperature must be important factors affecting activity. The high activity levels observed during heavy rains may be partially due to lowering of temperature/moisture constraints, but may also be partially due to avoidance of immersion.

In the cloud forest, landhoppers move freely about, and seem to be quite active. This is probably due to the low levels of light and temperature normal for this habitat. In lowlands, these factors are probably much more powerful constraints. It is likely that lowland landhoppers move about freely during the rainy season, but during the dry season remain in moist microhabitats, and are much less active.

5.3.5 Reproduction

The brood sizes noted for *Cerrorchestia hyloraina* and *Caribitroides tuztlensis* are relatively low in comparison with those recorded for *Platorchestia* (Morino, 1978; Tamura and Koseki, 1974). They are comparable to brood counts for other terrestrial species (Friend, 1980). The tendency toward reduced brood size in terrestrial species is apparent in the New World landhoppers; however, loss of eggs out of the brood pouch during capture and handling may have given misleadingly low counts.

In the aquatic amphipod *Hyaella azteca*, eggs are laid by breeding females even if males are not present, but these unfertilized eggs break down after a day or two (Lindeman, unpublished). The appearance and subsequent breakdown of unfertilized eggs was observed for *Caribitroides tuztlensis*, and probably also occurs in *Cerrorchestia*. In *Hyaella azteca*, and some supralittoral talitrids, the number of eggs per brood increases with the size of the female (Lindeman, 1982; Morino, 1978; Wildish, 1982a), although this relationship seems to be less linear in beachfleas and landhoppers (Friend, 1980; Wildish, 1982a).

Females generally carried the second gnathopods "crossed" across the venter of the brood pouch. This may be a mechanism to help hold the eggs in the pouch while moving about. The loss of eggs during development, when egg volume exceeds the capacity of the brood pouch, has been documented for other amphipods (Duncan, 1969; Friend, 1980; Morino, 1978). As well, Friend (1980) also noted that the low counts of newly hatched young in the pouch may be the result of the exit of the young over a period of time rather than simultaneously. These tendencies are shared by New World landhoppers.

Reproductive activity in Canadian populations of *Hyaella* is regulated by the correspondence of thresholds of temperature (minimum 20 °C) and photoperiod (12 hour

daylength)(de March, 1977; 1978). Photoperiod was less important to more southerly populations of *H. azteca* (Strong, 1972).

Moisture and temperature may determine breeding seasonality in tropical landhoppers (since photoperiod variations are minimal close to the equator). In the cloud forest, where these factors vary very little, breeding is constant, whereas in lowland forests which are seasonally dry and hot, breeding is mostly restricted to the rainy season.

Mating in landhoppers has yet to be described, but may well involve recognition and courtship behaviour. In *Hyaella azteca*, males always amplex females upon contact during the breeding season and carry them until they moult, whereupon egg laying and mating occurs (Geisler, 1944). Extended carrying of the female (grasped in the male's gnathopods) is obviously impractical in a terrestrial environment. *Platorchestia* has a form of amplexus in which the male carries the female grasped in the second antennae (Lindeman, unpublished). However, the gnathopods are used in manipulating the females during and after mating (see Williamson, 1951). In most full sized adult beachfleas, the males are larger than the females. Antennal carrying would not be effective in *Caribitroides*, since the males are smaller than the females.

Of great importance to potential mating behaviour is whether only freshly moulted females can lay eggs. If the female gonopores are sufficiently elastic to allow a longer "window" for egg laying, then the precise timing for encountering a male is lessened. Another alternative is that females may store sperm in the brood pouch until needed. This has been documented by Friend (1979) for a Tasmanian landhopper.

Morino (1978) proposed that the following generalization could be made: low latitude species are apt to have a long life span and breed in a restricted season. The life history data accumulated in this study, while sparse, seem to indicate that this is not true. Lowland landhoppers apparently have breeding periods restricted to the favourable temperature/moisture conditions of the rainy season. The life cycle may be one year or less, but could be longer. Highland (cloud forest) landhopper populations may breed year round, but may have very slow growth (under the cool temperature regimes), and may live several years. These life history variations may also occur in different populations of the same species. Therefore not only latitude, but altitude and climate must be taken into consideration when attempting generalizations. Temperature may be the single most important factor governing amphipod life histories, just as moisture is the key factor in distribution.

5.3.6 Growth

In studies of amphipod growth, most species have been reported to add one podomere to the A2 flagellum per moult. *Hyaella azteca* (Cooper, 1965; Geisler, 1944; Wilder, 1940), *Orchestia* [*Platorchestia*] *platensis* (Morino, 1978), *Platorchestia platensis japonica* (Tamura and Koseki, 1974), *Orchestia hurleyi* and *Orchestia patersoni* (Duncan, 1969) were reported to follow this pattern. In an excellent study of *Orchestia* [*Traskorchestia*] *traskiana*, Page (1979) studied males and females separately, and discovered that as females approached maximum size, the frequency of podomere addition on moulting decreased. The majority (83 %) of juvenile and young adult females added one podomere per moult, but only a minority (35 %) of older adult females (with 13 A2 flagellar segments or more) added one podomere. Males generally (78 %) added one podomere per moult at all sizes. Occasionally, two podomeres were added in one moult (this occurred oftener in males than in females). Page proposed that individuals which experience a small moult increment might not add an antennal segment, and that seasonal changes in moult increment might be accompanied by a change in the frequency of podomere addition, as well.

A growth pattern such as the above could explain the greater number of A2 podomeres seen in *Cerrorchestia* males. Failure to add a podomere during moults of small size increment, and the occasional addition of two podomeres in one moult could explain the overlap in antennal segment counts among adults of both *Cerrorchestia* and *Caribitroides tuzienseis*, although the latter species apparently has no difference in A2 podomere counts between the sexes.

Adult total lengths in *Hyaella azteca* are inversely proportional to early development temperatures, with large individuals developing under cool temperature regimes, and smaller individuals developing in warmer temperatures (de Marche, 1977, 1978). Moult rate varied directly with temperature in *Hyaella* (Bovee, 1950; Cooper, 1965; de March, 1977; Mathias, 1971) and in *Orchestia gammarellus* (Wildish, 1972).

Temperatures at Coyame rarely exceed 30 °C or drop below 15 °C as an average monthly maximum and minimum (Andrie, 1964), but if the breeding period of *Caribitroides tuzienseis* extends over a sufficient part of the year, some temperature effects on the size of individuals may occur. Temperatures at Monteverde vary little, so the cloud forest *Cerrorchestia* population may not experience variations in adult sizes caused by the above temperature effects, but lowland populations such as that on Barro Colorado Island, Panamá, may well be affected.

Another factor which may affect individual size is nutrition. Wilder (1940) noted that lack of food or oxygen can have negative effects on reproduction and growth in *Hyalella azteca* when photoperiod and temperature are otherwise favourable. Venables (1981a) stated that increases in reproduction in *Talorchestia margaritae*, a beachflea of Venezuela coasts, coincide with the arrival of fresh vegetation on the beach. He also noted that variability in the growth rate of *T. margaritae* increased with size/age (Venables, 1981b). In a comparison of growth rates among four species of *Orchestia*, Wildish (1972) noted that the relatively slow growth of *O. remyi roffensis* was caused by a decrease in moulting frequency rather than a reduction in length increment at each moult. He proposed that slow growth may be related to the low nutrient value of driftwood as a diet.

The high variability in antennal segment count and length in landhoppers may be partially due to individual variation in growth increment due to the effects of developmental temperature and nutrition. Moisture could affect growth indirectly, by affecting how much an individual moves about in search of optimal habitat, or in avoidance of immersion during heavy rains.

5.3.7 Summary

Cerrorchestia hyloraina and *Caribitroides tuztlensis* both show the characteristics of small brood size, large egg size, large, complex gills, reduced pleopods, slim, smooth body and appendages, small oöstegites with few setae, large eyes, slow growth rate, and cryptozoic moisture seeking behaviour typical of terrestrial species. In addition, these taxa exhibit a marked difference between salt and fresh water lethal immersion exposures (unlike the beachflea *Platorchestia* sp.).

Cerrorchestia hyloraina is apparently not as advanced in terrestrial adaptation (and may therefore be phylogenetically younger) as *Caribitroides tuztlensis*. *Cerrorchestia* retains dimorphism of the gnathopods and a greater ability to survive immersion, both of which may be primitive conditions.

As important members of the leaf litter fauna, and possible major detritivores in tropical forest energy cycles, New World landhoppers merit considerable further attention.

Chapter 6 ANALYSIS OF TALITRID GENERA

The objectives of this section were to establish which talitrid genera are most closely related to the target genera *Cerriorchestia* and *Caribitroides*, and to attempt to ascertain whether the American landhoppers are derived from other landhoppers, beach fleas, or palustral ancestors. Table 7 lists the taxa included in this generic analysis.

6.1 Generic Character Polarity

Bousfield (1982) gave a table of 60 talitrid characters with his interpretations of their plesiomorphic and apomorphic states (Bousfield, 1982 Table 1). The polarities of these characters "were derived by comparison with related outgroups in presumed ancestral families Hyalidae, Hyaellidae, Najnidae, and palustral Talitridae". It is unclear whether or not the tenets of outgroup analysis, as defined by Watrous and Wheeler (1981), were used by Bousfield. The specific outgroup taxa used to establish polarity were not listed, nor was there a discussion of individual characters. Confirmation of character polarity would require a complete character analysis of talitroidean amphipods, which is beyond the scope of this study. The character polarities given by Bousfield are therefore accepted, pending a fully documented character analysis.

6.2 Phenetics

A representation of the values in Table 10 for the first three principal axes is shown in Figure 28. *Mezitroides* and *Caribitroides*, which have high positive values in principal axes 2 and 3, and negative values in principal axis 1, occur in the upper left quadrant.

Table 7: Genera and species included in the talitrid fauna analysis, showing distribution, Bousfield designation, sexual dimorphism (SD), dactyl cusps, and dentition of the left mandible lacinia mobilis (Dent) (after Bousfield, 1982; 1984). Synanthropic introductions are not included. N.Am. - North America, S.Am. - South America

Taxon	Author	Distribution	Designation	SD	Cusps	Dent.
<i>Protorchestia</i>	Bousfield	South S.Am., New Zealand	beachflea	yes	no	5
<i>Paciforchestia</i>	Bousfield	N.Pacific Rim	beachflea	yes	yes	5
<i>Chelorchestia</i> <i>vagalla</i>	(Bowman)	Galapagos Is.	palustral/ terrestrial	yes	trace	4
<i>Chelorchestia</i> <i>costaricana</i>	(Stebbing)	Florida to Brazil, Argentina, Galapagos	palustral	yes	trace	4
<i>Transorchestia</i>	Bousfield	E.Australia, New Zealand, Southern S. Am.	beachflea	yes	yes	4
<i>Platorchestia</i>	Bousfield	Cosmopolitan	beachflea	yes	yes	5
<i>Orchestia</i>	Leach	N.Atlantic, Mediterranean	b.flea (1sp terr)	yes	yes	4
<i>Talitrus</i>	Latreille	N.Atlantic coasts, Kamchatka	sandhopper	no	yes	5
<i>Pseudorchestoidea</i>	Bousfield	Middle America, Mediterranean	sandhopper	yes	yes	4 (weak 5)
<i>Megalorchestia</i>	Brandt	N.Am. Pacific Coast	sandhopper	yes	yes	6
<i>Caribitroides</i>	Bousfield	Mexico, Jamaica	landhopper	no	yes	4
<i>Mexitroides</i>	Lindeman	Mexico	landhopper	no	yes	4
<i>Cerrorchestia</i>	Lindeman	Costa Rica/Panama	landhopper	yes	yes	4
<i>Tethorchestia</i>	Bousfield	Florida to Brazil	beachflea	yes	yes	4
<i>Floresorchestia</i>	Bousfield	Indo-Pacific, Hawaii, S.Africa, Venezuela	beachflea 1sp terr.	yes	yes	4
<i>Austrotroides</i>	Friend	Tasmania, Australia	landhopper	no	no	4
<i>Talitriator</i>	Methuen	S.Africa	landhopper	no	no	4
<i>Arcitalitrus</i>	Hurley	SE Australia	landhopper	no	no	4
<i>Agilestia</i>	Friend	SE Australia	landhopper	yes	yes	4
<i>Parorchestia</i> <i>gowerensis</i>	Bousfield	Lord Howe Islands, Australia	landhopper	yes	yes	4
<i>Parorchestia</i> <i>tenuis</i>	(Dana)	New Zealand	landhopper	yes	yes	4
<i>Talitroides</i>	Bonnier	Madagascar, India, New Caledonia	landhopper	no	yes	4

Table 8: Phyletic characters and character polarity after Bousfield (1982) for talitrid amphipod genera. The first character number refers to the data in this study. The character numbers in brackets are the original character numbers given by Bousfield (1982, Table 1).

Char. No.	BOUSFIELD CHARACTER	PLESIOTYPIC STATE	APOTYPIC STATE
1 (1)	Eye: size and position	Medium, lateral	large, dorsally contiguous
2 (2)	A1: length	Equal to or exceeding A2 peduncle seg. 4	short, not equal to A2 ped. 4
3 (4)	A2: sexual dimorphism	lacking or slight	strong, peduncle incrassate
4 (7)	Left mandible lacinia mobilis	5 dentate	4 dentate
5 (8)	Maxilliped palp	short, broad	tall, seg 3 subconical
6 (9)	MXPDP palp segment 4	present; distinct or masked by spines	fused to 3 or lacking
7 (10)	MXPDP palp segment 2	lacking inner lobe	with inner lobe
8 (11)	Coxal plate 1	rounded anterodistal angle	acute antero-distal angle
9, 10 (15)	m. GN1 subchelation	strong, dactyl not exceeding palm	weak, dactyl exceeding palm Alternate apotypic state: simple, no palm
11 (16)	m. GN1 merus (segment 4)	pellucid lobe present	pellucid lobe absent
12 (17)	m. GN1 carpus (segment 5)	short; posterior margin 1/2 anterior margin	long; posterior margin 3/4 anterior margin
13 (20)	f. GN1 subchelation	strong, dactyl not exceeding palm	weak or simple
14, 15 (24)	m. GN2 propod palm	smoothly convex	toothed, incised Alternate apotypic state: as in f.
16 (26)	f. GN2 basis	margins subparallel	anterior margin arcuate
17 (28)	Pereopods 3- 4	similar in size and form	P4 shorter
18 (30)	P3- P4 dactyls	similar in shape	P4 dactyl stout and pinched
19 (31)	P3- P7 dactyls	lacking cusps	with cusps
20 (33)	f. P5- P7 bases	bases similar	bases unlike
21 (36)	P6- P7 length	P7 longer	P6 longer
22 (37)	P6- P7 sexual dimorphism	lacking	present, P7 merus incrassate
23 (40)	Pleopod rami length	not or little shorter than peduncle	rami much shorter than peduncle
24 (43)	Uropod 1 prepeduncle	short, depth greater than length	long, length greater than depth
25 (45)	U1 peduncle armature	large inter- ramal spine	inter- ramal spine small or lacking
26 (46)	U1 outer ramus armature	unarmed	spinose
27 (47)	U2 rami length	almost equal	outer ramus much shorter
28 (48)	U2 inner ramus armature	single row of spines	double row of spines
29 (55)	Telson apex shape	variously cleft	lobes distally fused
30 (56)	Telson armature	apical and/or lateral spines only	dorsal, apical and lateral spines
31 (58)	Oostegite 4 (on P5)	large, little smaller than O1- O3	much smaller than O1- O3
32 (59)	Oostegite setae	tips hooked	tips simple
33, 34 (60)	Gill size and shape	plate- like or sac- like, size and shape similar	reduced or very small Alternate apotypic state: enlarged, convoluted and/or lobed

Table 9: Binary character data for selected talitrid genera and species, using characters and polarity established by Bousfield (1982).

CODE	TAXON	CHARACTER			
*		1 1234567890	111111112 1234567890	222222223 1234567890	3333 1234
A	<i>Pseudorchestoidea</i>	1101111110	1111011111	0001100101	1110
B	<i>Megalorchestia</i>	1111111110	1111011111	1010111111	1110
C	<i>Orchestia</i>	0111011000	1010011110	0110110101	1110
D	<i>Florcsorchestia</i>	1101011000	0011001111	0010100101	1111
E	<i>Platorchestia</i>	0110011000	1011011111	0100101100	1110
F	<i>Caribitroides</i>	1001001001	1010101111	0011000001	1111
G	<i>Cerrorchestia</i>	1001011000	0010001111	0011000001	1111
H	<i>Meritroides</i>	1001001001	1010101111	0001010001	1111
I	<i>Tethorchestia</i>	0001011000	0010011111	0010000101	1100
J	<i>Talitroides</i>	0001010010	1010101011	0010000010	1111
K	<i>Talitrus</i>	0110111101	1110111110	1000111110	0100
L	<i>Talitriator</i>	0001000001	1010101001	0011000101	1111
M	<i>Transorchestia</i>	0011001000	0001011111	0100110100	0000
N	<i>Parorchestia</i>				
	<i>gowerensis</i>	1001011000	0000001011	0010010001	0100
O	<i>Austrotroides</i>	0101011001	0010100001	0010000001	0111
P	<i>Agilestia</i>	0001001000	0001001010	0001001100	1100
Q	<i>Parorchestia</i>				
	<i>tenuis</i>	1001001000	0101001011	1000000000	0011
R	<i>Chelorchestia</i>				
	<i>vaggala</i>	0101010000	0011000001	0000000000	1100
S	<i>Paciforchestia</i>	0000001000	0000001010	0010010000	0100
T	<i>Chelorchestia</i>				
	<i>costaricana</i>	0001010000	0011000001	0000010000	1100
U	<i>Arcitalitrus</i>	0001000010	1100100001	0010000010	1111
V	<i>Protorchestia</i>	0000000000	0000000000	0000000000	0000

Talitriator, *Talitroides* and *Austrotroides* are relatively close, but have negative third axis values. *Cerrorchestia* has a higher third axis value than *Caribitroides* and *Mexitroides*, but is closer to them than is *Talitriator*. *Arcitalitrus* is relatively remote. The apparent closest neighbours to the landhoppers are the two species of *Chelorchestia* although these taxa have negative values in all axes. *Floresorchestia* and *Parorchestia tenuis* are also relatively close.

The eigenvectors for each character in the first three principal axes are given in Table 11. In axis 1, characters 3, 5, 8, 16, 18, 25, and 28 have particularly high positive values. With the exception of character 25, these are beachflea distinguishing characters. In axis 2, characters 13, 30, 31, 32, 33, and 34 have high positive eigenvectors. These are characters of female GN1 subchelation, telson, oostegites and gills; involving finer distinctions, but still distinguishing landhoppers from beachfleas/sandhoppers. Axis 3 has high negative loading in characters 9, 12, 15, 17, and 29, which involve sexual dimorphism and the telson. This arrangement of eigenvectors suggests that the data will readily show groupings of beachfleas, sandhoppers and "other".

In the average linkage (simple matching coefficient) phenogram (Figure 29) *Caribitroides* and *Mexitroides* are clustered with *Cerrorchestia*, *Talitriator* and *Austrotroides*, while *Tethorchestia* and *Floresorchestia* constitute the nearest group. *Arcitalitrus* and *Talitroides* are also associated with these taxa, but at a distance of 0.75. The intrusion of two beachfleas into a cluster of landhoppers is explicable only if *Floresorchestia* and *Tethorchestia* are more closely related to the primitive *Paciforchestia* and *Protorchestia* than to the other beachfleas. Average linkage using the Jaccard coefficient (Figure 30) gave fairly similar results, although distances between clusters were larger. *Cerrorchestia* again occurred next to *Caribitroides* and *Mexitroides*, but no beachfleas were included in the cluster.

6.3 Cladistics

The Camin-Sokal cladogram (Figure 31) grouped *Caribitroides* and *Mexitroides* with other non-sexually dimorphic landhoppers. *Chelorchestia* and *Cerrorchestia* were grouped with *Floresorchestia* and *Tethorchestia* within the beachfleas. This tree required 130 steps, with multiple separate derivations of the apotypic state in almost all characters.

A 122 step phenogram (Figure 32), obtained using mixed Wagner and Camin-Sokal parsimony, showed a similar grouping of the non-dimorphic landhoppers with *Chelorchestia*. The beachfleas and non-dimorphic landhoppers were broken into two fairly distinct

Table 10: Generic principal components analysis eigenvalues for each taxon.

EIGENVALUES				
CODE	TAXON	PRIN 1	PRIN 2	PRIN 3
A	<i>Pseudorchestoidea</i>	4.24	2.10	-0.19
B	<i>Megalorchestia</i>	6.51	1.34	-2.21
C	<i>Orchestia</i>	2.98	-0.39	2.47
D	<i>Floresorchestia</i>	0.71	1.61	2.39
E	<i>Platorchestia</i>	3.60	-1.66	1.61
F	<i>Caribitroides</i>	-1.36	3.72	1.16
G	<i>Cerrorchestia</i>	-1.21	2.46	2.21
H	<i>Mexitroides</i>	-1.02	3.03	1.10
I	<i>Tethorchestia</i>	0.06	0.09	2.12
J	<i>Talitroides</i>	-1.49	2.21	-2.34
K	<i>Talitrus</i>	5.78	-1.52	-3.62
L	<i>Talitriator</i>	-2.28	2.91	-0.42
M	<i>Transorchestia</i>	1.42	-4.10	2.21
N	<i>Parorchestia</i>	-1.53	-0.79	1.34
	<i>gowerensis</i>			
O	<i>Austrotroides</i>	-2.36	1.54	-0.71
P	<i>Agilestia</i>	-0.80	-2.15	0.86
Q	<i>Parorchestia</i>	-1.26	-1.39	-0.63
	<i>tenuis</i>			
R	<i>Chelorchestia</i>	-2.09	-1.42	-0.84
	<i>vaggala</i>			
S	<i>Paciforchestia</i>	-1.81	-3.03	0.17
R	<i>Chelorchestia</i>	-2.32	-1.74	-0.74
	<i>costaricana</i>			
U	<i>Arcitalitrus</i>	-2.45	1.36	-4.32
V	<i>Protorchestia</i>	-3.32	-4.18	-1.64
eigenvalue		8.10	5.54	3.86
cumulative proportion		0.24	0.40	0.51

Table 11: Character coefficients for each character in the eigenvectors of the first three principal axes of the generic principal components analysis. Asterisks indicate particularly high loading for that axis.

Character	Eigenvectors		
	principal axis 1	principal axis 2	principal axis 3
01	0.06	0.21	0.12
02	0.23	0.03	-0.02
03	0.28 *	-0.13	0.01
04	-0.06	0.23	0.10
05	0.28 *	0.04	-0.21
06	0.15	0.06	0.04
07	0.18	0.02	0.28 *
08	0.28 *	0.04	-0.21
09	0.10	0.15	-0.28 *
10	-0.02	0.19	-0.07
11	0.17	0.22	-0.16
12	0.17	0.04	-0.32 *
13	0.12	0.26 *	0.05
14	0.12	-0.12	0.06
15	-0.06	0.24 *	-0.24 *
16	0.30 *	-0.07	0.06
17	0.17	0.09	0.24 *
18	0.25 *	0.11	0.22
19	0.19	0.02	0.23
20	-0.04	0.22	0.05
21	0.18	-0.04	-0.23
22	0.13	-0.15	0.22
23	-0.05	0.22	0.04
24	-0.03	0.23	0.12
25	0.31 *	-0.04	0.06
26	0.12	-0.12	0.02
27	0.22	-0.08	-0.10
28	0.26 *	-0.03	0.12
29	0.12	0.07	-0.09 *
30	0.05	0.30 *	0.22
31	0.04	0.24 *	0.07
32	0.05	0.24 *	0.00
33	0.05	0.32 *	0.00
34	-0.15	0.30 *	-0.04

lineages: *Parorchestia tenuis* and *Agilestia* were represented as early offshoots of the beachflea/ sandhopper group, while *Parorchestia gowerensis* and *Cerrorechestia* were contained in a separate branch of beachfleas including *Paciforchestia*, *Tethorchestia* and *Florsorchestia*.

A tree of 114 steps was obtained using Wagner parsimony. The non-dimorphic landhoppers are shown as a sister group to the main beachflea/ sandhopper lineage in Figure 33. Sexually dimorphic landhoppers were scattered among the beachfleas.

6.4 Discussion

Many talitrid characters are dependent upon one another. This violates the ideal situation (for phylogenetic analysis) of characters which have evolved independently (see Felsenstien, 1978). For example, there are no intermediate states between sexually dimorphic gnathopods (Figure 9) and sexually similar gnathopods (Figure 16) among the taxa under study. A taxon which has a simple female GN1 will lack a pellucid lobe on the merus, without exception. The merus pellucid lobe is sometimes absent in sexually dimorphic forms, which makes it a useful and independent character for beachfleas and/or sandhoppers, but it is a dependent, and therefore less useful character for landhoppers. Although the "total body approach" (Bousfield, 1982) may help reduce the effect of dependent characters (by allowing the inclusion of more characters from all body regions), it may also introduce more dependent characters.

Another difficulty of choosing and analyzing talitrid characters is the strong tendency for losses and reductions rather than the acquisition of new apomorphic structures. This tendency leaves any attempt to polarize characters open to unresolvable problems of homoplasy. A loss or reduction may be apomorphic, but there is no way to tell if the loss is independent in different phyletic lines or common to members of the same phyletic line, without pre-existing knowledge of the relationships among the phyletic lines in question (see discussion of characters in Wiley, 1981). Talitrid amphipods may represent a case where inclusion of more characters actually decreases the effectiveness and stability of the analysis. Dependent characters, parallelism, and mosaic evolution will all act to obscure phyletic relationships.

Principal components analysis is a method of data reduction designed to clarify the relationships between characters, and to divide the total variance of all characters into a limited number of uncorrelated new variables, termed "principal components". The first principal component summarizes more of the variability than any other component. The

second summarizes more of the variability not summarized by (and uncorrelated with) the first, and so on. Because the new variables are not correlated, they may be interpreted independently. Each component may be interpreted to signify something about the size, shape, or other quantitative aspect of the members of the group (Wiley, 1981).

When the first three principal axes are responsible for most of the variance (for example 75 %), a satisfactory model of similarities can be obtained (Sneath and Sokal, 1973). In Table 10 the cumulative percentage of the first three axes was 51 %. This indicates that about half the total variance of the data is explained by the first three principal axes. By the above criterion, this analysis provides a less satisfactory model than could be desired. Sexual dimorphism and consequences thereof are apparently the main factors in spatial distribution of the taxa, indicating that these data will not be effective in distinguishing non-sexually dimorphic taxa from one another.

The principal components analysis (Figure 28) shows that sandhoppers, apomorphic beachfleas, and non-sexually dimorphic landhoppers are reasonably natural groups (for this data set). Primitive beachfleas, sexually dimorphic landhoppers and *Chelorchestia* seem near each other. Although principal components analysis is simply a representation of the relative positions of taxa (as determined by their characters), it has the advantage of not distorting these spatial relationships by manipulating the distances between them, and hence is useful as an unbiased indicator of groups, or shared character sets (McNeill, pers. comm.). In this case, Figure 28 shows that non-sexually dimorphic landhoppers are remote from apomorphic beach fleas and sandhoppers.

In the Jaccard coefficient phenogram, the landhoppers, except for two taxa, are clustered with the palustral *Chelorchestia*, suggesting that landhoppers are an offshoot of estuarine forms. The two terrestrial taxa that fall outside the main group of landhoppers are *Agilestia* and *Parorchestia gowerensis*. It may be that these two taxa are derived directly from beachflea ancestors, or that convergence obscures the actual phyletic relationship.

In both phenograms, the apomorphic (*sensu* Bousfield, 1982) beachfleas form a group connected to the sandhoppers. These are sister groups in the simple matching phenogram, and a less coherent single group in the Jaccard phenogram. Neither phenogram supports the hypothesis that the American landhoppers are more closely related to *Tethorchestia* than to other landhoppers. Both phenograms indicate a greater similarity between New World landhoppers and Old World landhoppers than between New World landhoppers and beachfleas.

The lack of concordance among the results suggests several problems with the data. Three possibilities are:

- (a) characters have been polarized incorrectly,
- (b) the real relationships are still being obscured by phyletically meaningless characters (despite elimination of some), or
- (c) there are so many homoplasies that true relationships cannot be determined.

The large number of steps in the cladograms suggests a large degree of homoplasy among the characters. It may also reflect the fact that some characters violate the assumption inherent in the algorithm, that different characters evolve independently (Felsenstein 1973, 1978, 1979, 1981). The dentition of the left lacinia mobilis and dactyl cusps, considered by Bousfield (1982, 1984) to be of major importance in phyletic relationships, are examples of two of the less stable characters in the generic analysis, and show high step numbers (reversions, in Wagner parsimony, and/or independent derivations of the apotypic state, in Camin-Sokal parsimony).

Particularly high numbers of steps occurred in all cladograms for the following Bousfield characters: 1 (eye size and position), 4 (left mandible lacinia mobilis), 13 (female GN1 subchelation), 14 (male GN2 propod palm convexity), 20 (P5-7 bases form), 23 (pleopod rami length), 26 (U1 outer ramus armature), 28 (U2 inner ramus armature), 31 (oöstegite 4 relative size), and 33 (gill reduction). Reductions in gnathopod subchelation, pleopod length, oöstegite size, and gill size seem common among apomorphic talitrids, and are difficult to resolve as homoplasies or true synapomorphies.

Variations in uropod ramus armature are exemplified by *Pseudorchestoidea*, in which the presence or absence of dorsal spines on the outer ramus of U1, and the number of rows of spines on the inner ramus of U1 and U2 vary from one species to another within the genus. This suggests that uropod armature may be of limited use in phyletic analysis. An in-depth, species by species search for similar variable characters would be required to establish the reliability of each character in this set. Such an undertaking is beyond the scope of this study, but is needed before an accurate and reliable phylogeny can be provided for all talitrid amphipods.

All of the cladograms agree in grouping *Caribitroides* and *Mezitroides* with the Old World sexually similar landhoppers. The base of the lineage seems to be an ancestor similar to the palustral taxon *Chelorchestia*. The non-dimorphic landhoppers may have been

derived from a common palustral ancestor, as was suggested by Bousfield (1984). However, Bousfield also stated that *Caribitroides* was derived from the lineage of *Tethorchestia*. This view is not supported by these cladograms, because the non-dimorphic landhopper lineage was consistently remote from the beachfleas.

The sandhopper *Talitrus saltator* is non-sexually dimorphic, and in early talitrid taxonomy, was considered congeneric with the landhoppers (Friend, 1980). The generic analysis clearly shows that it is a sandhopper. *Talitrus* still inhabits the upper strand habitat, and has not moved inland into the leaf litter. It is therefore not truly terrestrial (in the usage of this work). In this case, lack of sexual dimorphism has not affected the characters that define *Talitrus* as a sandhopper. It might be speculated that a landhopper derived from a beachflea should still be recognizable as a beachflea. The results of this analysis do not seem to support this speculation, since the relationships between sexually dimorphic landhoppers and beachfleas are not clearly defined.

Another pertinent fact is the low frequency occurrence of feminized (non-sexually dimorphic) males among collections of *Cerrorchestia*. The physical manifestation of this can range from a powerfully subchelate GN2 propod which has retained a trace of pellucid lobe to a GN2 identical with that of the female, in specimens which bear penil papillae and are of a comparable size to normal males. If these specimens represent a low frequency of fertile neotenic males which may be, under certain conditions, selected for, then it is possible that *Cerrorchestia* may eventually give rise to a non-sexually dimorphic species. If this speculation is correct, then this is evidence for the possibility of multiple, separately derived phyletic lines of sexually similar landhoppers. The problem would then be to determine the nearest relatives of these sexually dimorphic species.

According to the cluster analysis results, there have been three derivations of terrestrial amphipods. The first group includes all non-sexually dimorphic species plus *Cerrorchestia* and *Parorchestia tenuis*. This group supposedly shares a common ancestor with *Chelorchestia*, and is therefore probably derived from palustral ancestors. Two other taxa which are terrestrial (Bousfield, 1984; Friend, 1982), *Parorchestia gowerensis* and the genus *Agilestia* are apparently derived from beachflea ancestors.

The results of parsimony methods are similar to the above, in that the main group of non-sexually dimorphic landhoppers is apparently derived from palustral ancestors. However, all non-sexually dimorphic landhoppers are grouped with the beachfleas, and the nearest relatives differ. The large number of character reversions (some of which seem implausible)

make the Wagner parsimony results less convincing than those of the other algorithms.

All methods agree in indicating that the majority of (non-sexually dimorphic) landhoppers seem to have arisen from palustral ancestors, while some sexually dimorphic taxa have apparently arisen independently from beachflea ancestors. This is in contrast to the hypothesis proposed by Bousfield (1984), in which he stated that only primitive, non-cusate landhoppers were derived from palustral ancestors. The results of this analysis suggest that cusate landhoppers also may have been derived from palustral ancestors.

A question of great importance to landhopper evolution is the significance of the dactyl cusp traces present in *Chelorchestia*. Bousfield's (1984) argument that palustral taxa cannot have given rise to cusate landhoppers seems to be based on the assumption that no palustral taxa have dactyl cusps. It is not certain whether the cusp traces on the dactyls of *Chelorchestia* represent the remnants of structures which have been lost, or the first indication of structures that are being developed. If the former is true, then the assumption that palustral taxa are non-cusate must be reconsidered, and the possibility of palustral taxa giving rise to cusate landhoppers is a viable hypothesis. If *Chelorchestia* is developing cusps, then the derivation of Old World cusate landhoppers is brought into question, but the possibility of several parallel acquisitions of dactyl cusps must be considered. Either way, dactyl cusps constitute a character subject to parallel loss or gain, and contribute to analysis instability.

The clustering of sexually similar landhoppers in this analysis may be at least partially an artifact of an extremely homoplastic character set, and not a reflection of true phyletic relationships. The principal components analysis showed that the data set used here would not clearly distinguish between sexually similar landhoppers. Felsenstein (1978) showed that when parallel character changes exceed informative, non-parallel changes, both parsimony and compatibility methods will fail to converge to the true phylogeny. Jensen and Barbour (1981) also noted that increasing numbers of homoplasies decrease the concordance between cladistic methods.

On the basis of the above results, it was decided to include *Talitriator*, *Talitroides*, *Tethorchestia*, *Floresorchestia*, and *Chelorchestia* in the species analysis. *Platorchestia* was also included as a convenient outgroup, since it was consistently remote from the American landhopper taxa. *Austrotroides* and *Arcitalitrus*, although appearing closely related to *Caribitroides* in some results, were omitted due to unavailability of specimens, and because it was believed that *Talitriator* and *Talitroides* adequately represented the Old World

landhoppers. The relationship of Old World to New World landhoppers was less than entirely clear from the generic results. Inclusion of *Talitriator* and *Talitroides* in a preliminary species analysis, using different characters and fewer taxa, was considered necessary to establish how closely related these taxa are to the New World species.

6.5 Conclusions

It has already been noted that in talitrid amphipods, the tendency is to loss of structures (which can easily occur as parallel changes in different lineages), rather than the acquisition of novel new structures. When parallel changes are more probable than unique and unreversed change, parsimony methods will experience consistency failure (Felsenstein, 1978). Under these conditions, the disagreement among cladograms regarding the position of *Cerriorchestia* and the relationship of American taxa to other landhoppers (and to the beachfleas) suggests that the generic results should be interpreted as a general framework only, and not as a working hypothesis of phylogeny.

The conclusions which can be drawn from this generic analysis are:

- 1. A more efficient character set, with fewer convergent characters, must be constructed. More stable results and better concordance between methods are required, before a satisfactory phylogeny can be constructed for talitrid genera.
- 2. More palustral taxa should be included in the analysis to provide better information on how palustral taxa are related to beachfleas and landhoppers.
- 3. Terrestriality may have arisen several times among the Talitridae, including species derived from beachfleas, as well as terrestrial clades derived from palustral ancestors. This could indicate that some of the characteristics of the family Talitridae may be preadaptations for terrestrial existence.

Figure 28: Relative positions of talitrid taxa in a three dimensional space representing the first three axes of a principal components analysis. The scale on the right represents the first principal axis, the vertical scale the second and the scale on the left the third. The largest and darkest objects are closest to the viewer, and the smallest and faintest are farthest away. The key on the right lists the taxa in order of their distance from the viewer. *P.*–*Parorchestia*, *C.*–*Chelorchestia*

A: Pseudorchestoidea
B: Megalorchestia
C: Orchestia
D: Floresorchestia
E: Platorchestia
F: Caribbitroides
G: Cerrorchestia
H: Mexitroides
I: Tethorchestia
J: Talitroides
K: Talitrus saltator
L: Talitriator
M: Transorchestia
N: P. gowerensis
O: Austrotroides
P: Agilestia
Q: P. tenuis
R: C. vaggala
S: Paciforchestia
T: C. costaricana
U: Arcitalitrus
V: Protorchestia

Figure 29: Cluster analysis of talitrid taxa, using the simple matching coefficient.

Figure 30: Cluster analysis of talitrid taxa using the Jaccard coefficient.

Figure 31: Cladogram of talitrid taxa using Camin-Sokal parsimony. Numbers are characters, and their placement on the tree indicates a change from plesiotypic to apotypic state. Letter codes indicate branches with large numbers of changes, listed below.

- (A) 3 18 10 22 25 26 28
- (B) 3 21 23 26 27 29

Figure 32: Cladogram of talitrid taxa using mixed Camin-Sokal and Wagner parsimony. Numbers indicate the change of that character from plesiotypic to apotypic state. Bracketed numbers indicate a reversion of that character. Letter codes indicate branches with large numbers of changes, listed below.

- (A) 24 25 27
- (B) 2 6 11 13 32 33
- (C) 4 10 14 15 20 21 29 33

Figure 33: Cladogram of talitrid taxa using Wagner parsimony, rooted by defining the ancestral character states. Numbers indicate the change of that character from plesiotypic to apotypic state. Bracketed numbers indicate a reversion of that character. Letter codes indicate branches with large numbers of changes, listed below the tree.

④ 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87 88 89 90 91 92 93 94 95 96 97 98 99 100

Chapter 7 ANALYSIS OF NEW WORLD LANDHOPPERS

7.1 Species Character Polarity

The method of out-group comparison for polarizing characters, as discussed by Stevens (1980), and outlined by Watrous and Wheeler (1981), is followed here. The group under study is the Taxonomic In-Group (TIG), and the taxa with which they are compared constitute the Taxonomic Out-Group (TOG) (which need not be a monophyletic assemblage). The simplest situation to polarize is that of a binary character, of which one state occurs only in the TIG, and the other state occurs in both the TIG and TOG. This latter, general state is inferred to be the plesiomorphic state. If neither state of a character occurs in the TOG, the character must be examined within sub-groups of the TIG (established by other characters). If both states occur in the TOG, the character must be shown to be non-homologous, or else the TOG must be narrowed such that only one of the states is present (Watrous and Wheeler, 1981).

Stevens (1980) states that the outgroup should include a sister group to the TIG, and at least one cladistically primitive taxon. For the species character set (Table 12), the taxonomic out-group consisted of *Orchestia gammarella* (*sensu* Bousfield, 1973), *O. grillus*, *Protorchestia nitida*, *Hyale nilssoni*, *Hyale plumulosa*, and *Hyalella azteca*. These choices were based on the availability of adequate descriptions, illustrations and literature on talitrid evolution.

Bousfield (1984) argued that talitrid amphipods have arisen from the Hyalidae, with the family Hyalellidae as an early offshoot (see Figure 3). Friend (1987) considered the Hyalidae to be an appropriate outgroup for determining character state polarity within the Talitridae. *Protorchestia* is presumed to be little changed from a hyalid ancestor (Bousfield, 1982). The genus *Orchestia* is included as a potential sister group to *Tethorchestia* (Bousfield, 1984), although it may be argued that since the TIG includes beachfleas (*Tethorchestia*, *Platorchestia* and *Floresorchestia*), it might not be valid to have another in the outgroup.

In cases where a character cannot be resolved by outgroup, the TIG is subdivided into functional groupings (Watrous and Wheeler 1981). The functional in-group (FIG) was composed of *Caribitroides* and *Mezitroides*. The functional out-group was composed of

Tethorchestia, *Floricorhestia*, *Platorchestia*, *Chelorchestia* and *Cerrorechestia*. Comparison proceeded using functional groupings in the same way as for taxonomic groupings. In cases where the character was unresolvable by either outgroup comparison or functional comparison, the plesiomorphic state was considered to be the state exhibited in *Hyale* and *Protorechestia*. If these two taxa did not agree, the example of *Hyale* was followed. The choice of in-group and out-group representatives may have caused errors in polarity, if the assumptions made in assigning taxa to these groupings were incorrect.

Character polarity: Character -

- 1: As far as can be determined, *Hyale*, *Hyalella* and *O. grillus* do not exhibit sexual dimorphism of antenna 2. *O. gammarella* is questionable, but no dimorphism is mentioned by Bousfield (1973). The plesiomorphic state is considered to be: male A2 peduncle linear, not incrassate.
- 2: *Hyalella* and *Hyale plumulosa* have long peduncular segments in A1, but these segments are all about the same length. The other taxa of the outgroup have short A1 peduncular segments, and this state is considered plesiomorphic.
- 3: The maxilliped palp segment 2 inner lobe is visible in *Hyale*, *Protorechestia* and *Hyalella*, although not to the extent that it is developed in *Orchestia*. A very narrow palp segment 2 is only visible within the TIG (and even then, only within the FIG), so by the rules set out by Watrous and Wheeler (1981) it must be considered apomorphic. (In contrast, Bousfield, 1982 considers the narrow palp segment 2 to be a plesiomorphic state.)
- 4: Maxilliped palp segment 4 is present and distinct in *Protorechestia*, *Hyale*, and *Hyalella*. The available illustrations show that in *Orchestia* it is tiny or lacking. Within the TIG, even the largest palp segment 4 is small, compared with that of *Protorechestia* or *Hyale*. For this analysis, the loss of segment 4 is considered apomorphic. It is acknowledged that the loss of a small structure may occur separately several times within a lineage, and that many characters in this set, including this one, may be subject to homoplasy.
- 5: The state of the maxilliped outer plate pellucid lobe is not illustrated clearly enough in most of the TOG to establish polarity. Using functional groupings, the large pellucid lobe is restricted to members of the FOG, and is considered plesiomorphic.

- 6: Large maxilliped inner plate spine teeth occur in *Protorchestia*, *Hyale*, and *Orchestia*. Large apical spine teeth are scored as plesiomorphic.
- 7: The male GN1 propod is subchelate in all outgroup taxa. This condition is scored as plesiomorphic.
- 8: A pellucid lobe is present on the male GN1 merus in *Protorchestia*, but not in *Hyale* or *Orchestia*, and thus is not resolvable by outgroup. Using functional groups, the pellucid lobe is present in two taxa of the FOG, and is considered plesiomorphic.
- 9: Female GN1 carpus wider than merus occurs in all outgroup taxa, and is considered plesiomorphic. *Hyale*, *Protorchestia*, and *Hyalella* have non-simple female GN1, which may affect the validity of this judgement. It may be argued that a wide carpus in a pellucid-lobe-bearing GN1 may not be homologous with a wide carpus in a simple GN1.
- 10: The female GN1 propod is subchelate in *Protorchestia*, *Hyale*, and *Hyalella*, and weakly subchelate in *Orchestia*. Weak subchelation is considered plesiomorphic for the FIG.
- 11 and 12: The shape of the female GN2 basis is unresolvable with outgroups. *Protorchestia*, *Hyale*, and *Hyalella* have a linear GN2 basis anterior margin, but *Orchestia* has the broadly convex condition. Within the FOG, *Cerrorchestia* has a semi-linear GN2 basis, while *Floresorchestia*, *Tethorchestia*, and *Platorchestia* have the typical beachflea broadly expanded basis. Within the FIG, a sinuous basis occurs in some taxa. Arbitrary scoring was established as follows: a linear or semi-linear basis is scored as 00, sinuous as 01, and the broadly expanded state as 11. It is acknowledged that the sinuous condition may be a reversion from the broadly expanded state.
- 13: The dactyls of P3 and P4 are similar in *Protorchestia*, *Hyale*, and *Hyalella*, but not in *Orchestia*. The similar state occurs only in the FOG, and is scored as plesiomorphic.
- 14: Short ungues are evident in all the TOG taxa. This state is considered plesiomorphic.
- 15: The pleopod rami length character states are unresolvable by outgroup or functional group comparison, as both character states occur in each subgroup of both. The

condition of rami longer than or equal to peduncle is set as plesiomorphic, following the state shown by *Protorchestia* and *Hyale*.

- 16: The pleopod inner and outer rami are of approximately equal length in the TOG, and this state is considered plesiomorphic.
- 17: The relative lengths of the rami of PL2 and PL3 are about the same in all outgroup taxa (although *Orchestia* shows a tendency toward reduction). This state is considered plesiomorphic. The shortened rami of PL3 is scored as apomorphic.
- 18: The state of the inter-ramal spine is unresolvable by outgroup or functional group. Scoring the large spine as plesiomorphic follows the character states occurring in *Protorchestia* and *Hyale plumulosa*.
- 19: The outer ramus of U1 is unarmed in *Protorchestia*, and spinose in *Hyale*, *Orchestia*, and *Hyalella*. The spinose state occurs in only two taxa of the FIG, and is scored as apomorphic, on the assumption that it is a reacquisition. The possibility of incorrect scoring is acknowledged. This character is particularly subject to homoplasy, as smooth and spinose states can occur within the same genus (eg., *Pseudorchestoidea*).
- 20: *Protorchestia*, *Hyale*, and *Hyalella* have 1 row of dorsal spines on the inner ramus of U1, whereas *Orchestia* has two rows. Both states also occur in the FOG. The single spine row is scored as plesiomorphic, after *Hyale*, and *Protorchestia*.
- 21: The inner ramus of U2 has one spine row in *Protorchestia*, *Hyale*, *Hyalella*, and *O. gammarcella*, but not in *O. grillus*. Both states occur within the FOG. The single spine row is scored as plesiomorphic.
- 22: The peduncle of U3 bears several lateral spines in *Hyalella* and *Orchestia*, but only one or two in *Protorchestia* and *Hyale*. Outgroup analysis therefore cannot resolve these states. The functional group comparison sets the plesiomorphic state as several lateral spines. Within many of the urosome characters, extra spines and spine rows seem to be a trend within the beachfleas, and may represent apomorphies rather than plesiomorphies. Functional group decisions are retained to follow the rules of Watrous and Wheeler (1981).
- 23: Apical and marginal spines occur on the ramus of U3 in *Protorchestia*, *Hyale*, and *Orchestia*. *Hyalella* shows no marginal spines, but is omitted from consideration for

this character. Functional group comparison supports the scoring of marginal spine occurrence as plesiomorphic.

- 24: Very setose oöstegites occur in all outgroup taxa, and the setose state is accepted as plesiomorphic.
- 25: Small gills with little size difference occur in *Protorchestia*, *Hyale*, and *Hyalilla* (although the latter taxon has subsidiary ventral gills, which may disqualify it from consideration). *Orchestia* tends toward an intermediate state, but still does not display the enormous differences in size between G1 and G2, shown by the FIG. Small gills are accepted as plesiomorphic.
- 26 and 27: Detailed gill information is not available for the outgroup taxa. Functional group comparison establishes that lack of secondary lobes is the plesiomorphic condition.
- 28: The dactyls of *Protorchestia* and *Hyale* have no cusps, whereas those of *Orchestia* do. Since the character is unresolvable by the criteria and groupings used here, the non-cusped condition is scored as plesiomorphic, to follow *Hyale*.

In the following analyses of the New World taxa, *Chelorchestia* refers to the species *Chelorchestia costaricana*, and *Cerrorchestia* refers to the species *Cerrorchestia hyloruma*. The species used in the New World landhopper analysis (and their character states) are listed in Table 13. The characters and polarities discussed above are listed in Table 12.

Table 12: Characters and phyletic character polarity of Central American landhoppers and selected beachfleas.

Char. No.	CHARACTER	PLESIOTYPIC STATE	APOTYPIC STATE
1	m. Antenna 2 peduncle	not incrassate	incrassate
2	Antenna 1 segments 2,3	segment 2 equal to segment 3	segment 3 longer than segment 2
3	Maxilliped palp segment 2	with large inner lobe	inner lobe narrow or lacking
4	MXPd palp segment 4	present and distinct	tiny, button-like or lacking
5	MXPd outer plate pellucid lobe	large, encompassing entire tip	small, inner-distal or lacking
6	MXPd inner plate apical spine teeth	robust	small or lacking
7	m. gnathopod 1 propod (segment 6)	subchelate	simple
8	m. GN1 merus (segment 4)	pellucid lobe present	pellucid lobe absent
9	f. GN1 carpus (segment 5)	wider than merus	equal to merus
10	f. GN1 propod (segment 6)	weakly subchelate	simple
11, 12	f. GN2 basis anterior margin	almost linear or anteriorly expanded	broadly convex Intermediate state: sinuous
13	Pereopods 3-4, dactyls	P3 and P4 dactyls similar	P4 dactyl stout and pinched
14	Pereopods 6-7, unguis	short; ratio of unguis to dactyl base less than 0.5	long; ratio greater than or equal to 0.5
15	Pleopod 2 rami	rami greater than or equal to peduncle	rami much shorter than peduncle
16	Pleopod rami	inner ramus equal to outer ramus	rami distinctly unequal
17	Pleopod 3 rami	length similar to PL2	very short
18	Uropod 1 interramal spine	large	small or lacking
19	U1 outer ramus	unarmed	spinose
20	U1 inner ramus	1 row marginal spines	2 rows marginal spines
21	U2 inner ramus	1 row marginal spines	2 rows marginal spines
22	U3 peduncle	several lateral spines	1 or 2 lateral spines
23	U3 ramus	apical and marginal spines	apical spines only
24	Oöstegite 1 (on (ovigerous f. GN2)	setose (more than 15 setae)	sparsely setose (less than 14)
25	Gills	small; little size difference	large; G1 and G5 much larger than G2, G3, G4
26	Gill 1 (on GN2)	1 or no secondary lobes	2 or more secondary lobes
27	Gill 5 (on P6)	no secondary lobes	1 or more secondary lobes
28	Dactyls	lacking cusps	with cusps

Table 13: Binary character data for New World landhoppers and selected other species, using characters and polarity established in this work.

CODE	TAXON	CHARACTER		
*		1 1234567890	111111112 1234567890	22222222 12345678
A	<i>Caribitroides jamaicensis</i>	0000101101	0111101000	01011011
B	<i>Caribitroides</i> sp. A	0001101101	0111101000	01111011
C	<i>Caribitroides</i> sp. B	0010101101	0111100000	01111011
D	<i>Caribitroides newtoni</i>	0011101111	0111000000	01111011
E	<i>Caribitroides tuxtlenensis</i>	0001111111	0111011000	01111001
F	<i>Mezitroides pexei</i>	0010101111	0111000010	01111111
G	<i>Mezitroides chiapensis</i>	0001101111	0111000010	01111111
H	<i>Tethorchestia antillensis</i>	0001000100	1110100000	10000001
I	<i>Platorchestia platensis</i>	1001100110	1100000101	10000001
J	<i>Cerrorchestia hyloraina</i>	0001110001	0010111000	01101001
K	<i>Floresorchestia venezuelae</i>	0101010010	1100000101	10010001
L	<i>Chelorchestia costaricana</i>	0001010010	0000000000	01101010
M	<i>Talitriator eastwoodae</i>	0110101101	0001011001	11111010
N	<i>Talitroides topitotum</i>	0111111111	0011011000	00111011

7.2 Old World Landhoppers

Principal component analysis of 14 taxa including *Talitriator* and *Talitroides* showed that these two taxa are relatively remote from the Central American landhoppers. (Figure 34). The cumulative eigenvalue for the first three axes was only 63 % . Since the generic Wagner cladogram showed separation between Old and New World landhoppers, and principal components analysis on the species data showed the two groups to be more remote from the New World landhoppers than *Chelorchestia*, the Old World landhoppers were deleted from the species analysis.

7.3 Phenetics

The twelve taxon principal components analysis (Figure 35) showed a strong cluster of *Caribitroides* and *Mexitroides* species. *Cerrorchestia* and *Chelorchestia* were well separated from both the landhopper and beachflea groups. *Tethorchestia* was more closely associated with the beachfleas *Floricorchestia* and *Platorchestia* than with any landhopper. The first three axes of the analysis had a cumulative eigenvalue of 70 %.

Average linkage phenograms for the species data gave almost identical results with both simple matching and Jaccard coefficients (Figure 36 and Figure 37). In both cases, the Jamaican species form one subgroup, *Mexitroides* and *C. newtoni* another subgroup, and *C. turtlensis* the final subgroup of the non-sexually dimorphic species. *Cerrorchestia* and *Chelorchestia* cluster with the landhoppers rather than the beachfleas.

7.4 Cladistics

The three cladograms agree with phenetic methods (particularly the Jaccard coefficient UPGMA result). In each case, the landhoppers, including *Cerrorchestia*, are shown as more closely related to *Chelorchestia* than the beachfleas (see Figure 38, Figure 40, and Figure 39). In all cladograms, the highest step numbers occurred in characters 3, 4, 6, 8, 9, 15, 17 and 27 (see Table 12), which include reductions or losses of small structures. These characters are particularly subject to homoplasy and, in some cases, the phyletic polarity of the character is doubtful.

Camin-Sokal parsimony, which does not allow reversions, produced a tree of 59 steps (Figure 38). This is the highest step number of the three algorithms. A tree of 51 steps

Table 14: Species principal components analysis eigenvalues for each taxon. PRIN: principal axis

EIGENVALUES				
CODE	TAXON	PRIN 1	PRIN 2	PRIN 3
A	<i>Caribitroides jamaicensis</i>	2.21	0.47	2.20
B	<i>C. sp. B</i>	2.78	0.93	0.89
C	<i>C. sp. A</i>	2.35	-0.18	1.68
D	<i>Meritroides pocki</i>	3.13	2.22	-2.22
E	<i>C. newtoni</i>	2.22	0.98	-0.89
F	<i>M. chiapensis</i>	2.50	1.52	-2.05
G	<i>C. tuxtensis</i>	1.58	-1.32	0.46
H	<i>Tethorchestia</i>	-3.41	0.53	2.39
I	<i>Platorchestia</i>	-5.50	2.42	0.37
J	<i>Cerrorchestia</i>	0.06	-4.47	1.56
K	<i>Floresorchestia</i>	-6.18	0.93	-0.99
L	<i>Chelorchestia</i>	-1.77	-4.03	-3.39
eigenvalue		11.36	4.94	3.57
cumulative proportion		0.40	0.58	0.71

Table 15: Character coefficients for each character in the eigenvectors of the first 3 principal axes of the species principal components analysis. Asterisks indicate particularly high loading for that axis.

Character	Eigenvectors		
	principal axis 1	principal axis 2	principal axis 3
01	-0.15	0.15	0.03
02	-0.17	0.06	-0.09
03	0.14	0.17	-0.12
04	-0.14	-0.15	-0.05
05	0.20	0.10	0.11
06	-0.10	-0.33 *	-0.12
07	-0.26 *	0.16	0.00
08	0.14	0.31 *	0.16
09	-0.06	0.10	-0.43 *
10	0.27 *	0.01	0.08
11	-0.27 *	0.16	0.10
12	0.04	0.40 *	0.12
13	0.24 *	0.03	0.22 *
14	0.26 *	0.16	0.00
15	0.06	-0.10	0.43 *
16	0.03	-0.27 *	0.13
17	0.10	-0.21 *	0.30 *
18	-0.24 *	0.16	-0.04
19	0.12	0.18	-0.28 *
20	-0.24 *	0.16	-0.04
21	-0.27 *	0.16	0.10
22	0.27 *	-0.16	0.10
23	0.21	-0.16	-0.21
24	0.17	0.21 *	-0.05
25	0.27 *	-0.16	-0.10
26	0.12	0.18	-0.28 *
27	0.21	0.07	-0.19
28	0.05	0.26 *	0.30 *

(Figure 39) was obtained using Wagner parsimony. The third method, using a mix of Camin-Sokal and Wagner parsimony, produced a 54 step tree (Figure 40). Camin-Sokal parsimony was used for characters 2, 4, 7, 13, 16, 17, 18 and 25 (see Table 12). The other characters were treated as freely reversible (Wagner parsimony).

7.5 Discussion

The plots of principal axes are a useful visual representation of the positions of the taxa in the "hyperdimensional cloud" of OTU's (Sneath and Sokal, 1973). Since the relative positions of the taxa do not actually change, the technique provides a representation of the data in which groups can be distinguished without manipulating their positions. This is useful for comparison with clustering methods, which do modify the positions of the OTU's relative to each other (McNeil, pers. comm.).

The first three axes of the principal component analysis (Figure 35) had a cumulative eigenvalue of 70 %, indicating that 70 % of the variation in the data can be explained by these axes. This provides a satisfactory model of similarities, based on the criterion of Sneath and Sokal (1973).

The first axis of a principal component analysis often represents size factors, indicated by eigenvectors with the same sign, and nearly equal values (Wiley, 1981). This is not the case in Table 14, where the first axis eigenvectors have variable values and signs. High positive character loading is shown in characters 7, 10, 13, 14, 22 and 25, and high negative loading in characters 11, 18, 20 and 21. These characters, with the exception of character 13, include all the most distinctive differences between beachfleas and landhoppers. Axis 1 can be interpreted as the axis of terrestrial morphology. Positively loaded characters reflect major morphological trends in landhoppers. Negative loading reflects, for the most part, apomorphic characters of beachfleas (see Table 12).

The second axis shows high loading on a mixture of beachflea and landhopper characters, and may be interpreted as showing finer distinction between the two groups, and initial divisions within the groups. Characters with high loading in the third axis tend to be those that distinguish landhoppers from *Chelorchestia*. The third axis is apparently not dominated by the morphological consequences of sexual dimorphism or lack thereof, and might thus be interpreted as an indicator of differences between species rather than species groups.

The phenetic methods do not support the derivation of New World landhoppers from

beachfleas. The remoteness of the beachfleas in both PCA and UPGMA analyses may be partially an artifact of the data set (designed to distinguish landhopper species from one another), but the agreement of generic and specific analyses in not supporting the above hypothesis constitutes a compelling reason to reject it.

An evolutionary history which allows no character reversions is unrealistic for talitrid amphipods, a group commonly thought to exhibit extensive neoteny. There is also no need to postulate separate derivations of the dactyl cusps on the beachflea and landhopper lineages, since the trace of cusps that *Chelorchestia* shows (as opposed to the completely smooth dactyls of cuspless taxa such as *Protorchestia*) suggests a loss of cusp (reversion) rather than the acquisition of a trace of cusp in recent evolutionary time. Therefore, the Camin-Sokal tree (Figure 38) is not thought to represent the most plausible estimate of relationships.

In the Wagner tree (Figure 39), the landhoppers show some character reversions which seem unlikely (for example, character 4: maxilliped palp segment 4; character 17: pleopod 3 rami). The loss of maxilliped apical spine teeth in the ancestral form to the entire *Chelorchestia*/ landhopper line and subsequent reacquisition after the divergence of *C. turtlensis*, and the removal of this taxon from the other Mexican species thereby, seems particularly unlikely. Although this is the lowest step number of the three methods, and there is a minimum number of steps to the branch tips, this is probably not the most plausible model of relationships.

In the mixed Camin-Sokal/ Wagner tree (Figure 40), reversions occurred in characters 8, 9, 23 and 28. Character 8 (male GN1 merus pellucid lobe) is a relatively minor loss, the reacquisition of which could be accomplished by a neotenic event. Character 9 (female GN1 carpus width) is relatively uninformative in phyletic terms, and may also be reversible by minor changes. The reversion in character 28 is the reduction of dactyl cusps to traces in *Chelorchestia*, discussed above. Character 23 is a relatively minor matter of extra spines which only showed in a few *C. jamaicensis* specimens.

Despite the questionable reversions in characters 8 and 9, Figure 40 is thought to represent the best estimate of relationship, due to the relatively low step number and lack of implausible reversions. In this scenario, the landhoppers and palustral *Chelorchestia* shared a common ancestor, and *Cerrorchestia* is derived directly from the palustral lineage.

The lack of concordance between algorithms (although relatively minor in comparison with the generic analysis) suggests that there are still inconsistencies and/or homoplasies in

the data. By strict Hennigian rules, it is not valid to consider losses as apomorphies, since it is easier to lose a feature than to acquire a new feature (Wiley 1981). The strong tendency to loss rather than acquisition among talitrids is, of course, the greatest impediment to phylogenetic analyses based on the morphology of these organisms.

Characters which are losses can be useful in phylogenetics if the principle of evolutionary reduction (Dollo's law) is accepted. This principle states that the full range of phenotypes of an organism never reverts exactly to the ancestral condition or, more simply, lost morphological structures are usually not regained (Bull and Charnov, 1985). By this criterion, trees with many reversions are not plausible hypotheses. The possibility of character reversions cannot be rejected completely, however. Blackburn (1984) pointed out that relatively minor genotypic changes (for example, the inhibition of a suppressor regulatory gene) may have large phenotypic consequences.

A pertinent example is the occurrence in newly hatched *Keratroides vulgaris* and *K. kershawi* of long plumose setae on the pleopods. Adults of these taxa lack any setae on the pleopods (Friend, 1979). A relatively minor neotenic event could allow the retention of these setae in adult instars, producing the apparent reacquisition of a lost structure. A compromise between the above views is the mixed Camin-Sokal/ Wagner result (Figure 40). In this method, reversions from the apotypic to the plesiotypic state are not allowed in those characters in which such a reversion is deemed very unlikely (by the author), but are allowed in the other characters.

An alternative to morphology-based phylogenies would be a molecular phylogeny, based on gel electrophoresis and allozyme or other molecular data. Mickevich and Johnson (1976) argued that morphological data are more labile than molecular data; that mosaic evolution, convergence, and parallelism (all of which probably occur in talitrid amphipods) cannot be detected in phenetic methods; and that, given consistency within the data sets, cladistic phylogenies based on morphology agree with those based on allozyme data. If molecular data could be obtained for the New World landhoppers, it would serve as an informative comparison with morphology-based analyses.

7.6 Phylogeny

Based on the preceding analyses, two phylogenies (Figure 41 and Figure 42) were constructed. These two hypotheses differ mainly in the closeness of the Jamaican species of *Caribitroides* to *Mezitroides*, and the derivation of *Cerrorchestia*. Although phylogeny A

(Figure 41) appears at first to be the more logical (in the separation of the Jamaican and Mexican clades) there are several factors that argue against it. A large phyletic (and chronological) separation between the Jamaican and Mexican clades of *Caribitroides* might be expected to produce relatively large morphological changes between the two, which are not evident. The distinct differences between *Caribitroides* and *Meritroides*, much greater than the differences between the congeneric Mexican and Jamaican *Caribitroides*, argues that these two genera have diverged to a much greater extent than have species of *Caribitroides*, despite the geographic distance involved.

The other implausibility in phylogeny A is the early derivation of *Cerrorchestia*. It is possible that this taxon may have persisted unchanged through the geological time during which *Caribitroides* and *Meritroides* evolved into their present form, but if so, it might be expected to have a more widespread range, and/or to have at least lost its sexual dimorphism. Since loss of sexual dimorphism is so common among landhoppers, and since *Cerrorchestia* does indeed seem to share a common ancestor with *Caribitroides* and *Meritroides*, it would seem most likely that *Cerrorchestia* is a much younger taxon than the other New World landhoppers, otherwise it too might be expected to have lost the morphological differences between the sexes. Other evidence, such as its tolerance for immersion in freshwater, and relatively restricted range, also point to relative youth. Therefore, the concept of long persistence indicated in phylogeny A seems far less likely than the derivation of *Cerrorchestia* as a younger taxon, as proposed by phylogeny B (Figure 42).

Chelorchestia may have given rise to a sexually dimorphic, cloud forest dwelling landhopper in the recent geological past. *Chelorchestia vaggala* may have evolved on San Cristóbal Island (Bowman, 1977), which is no more than 3.5 million years old (Hall, 1983; Hickman and Lipps, 1985). The relatively recent evolution of *Cerrorchestia* directly from *Chelorchestia* seems to be the most plausible explanation of its origin. For this reason, phylogeny B is chosen as the most likely evolutionary scenario for this taxon.

The relationships among species of *Caribitroides* and *Meritroides* are less obvious than for *Cerrorchestia*, and the difference in likelihood between the scenarios offered in phylogeny A and phylogeny B is less clear. Given the differences between *Caribitroides* and *Meritroides*, however, it is thought that phylogeny B may be a marginally more likely scenario for these taxa. Since phylogeny B offers the most plausible hypothesis of evolution for American landhoppers, it is chosen as the best representation, pending improved

understanding of the relationships among landhopper species, further exploration of Central American forests for amphipod presence, ranges, and new species, and an adequate taxonomy of New World palustral taxa.

Wiley (1981) discussed the concepts of monophyly, paraphyly and polyphyly, and supported the definitions of these terms proposed by Farris (1974). A monophyletic group includes a common ancestor and all of its descendants. A paraphyletic group includes a common ancestor and some but not all of its descendants. A polyphyletic group is a group in which the most recent common ancestor is assigned to some other group, and not to the group itself. In taxonomic terms, all members of a monophyletic group are expected to be members of the same taxon (Wiley, 1981).

It can be argued that the phylogeny proposed above is paraphyletic. First, *Mezitroides* is segregated as a separate taxon from *Caribitroides*, whereas by the above view it should be congeneric. Second, the *Cerrorchestia*/*Chelorchestia* clade does not include all descendants of their common ancestor.

Mezitroides as a taxonomic concept is based on one unique apomorphy (character 26: two secondary lobes on gill 1). The spinose outer ramus of uropod 1 may be a reacquisition of a character suppressed in its ancestors. Other characters that distinguish *Mezitroides* from *Caribitroides* are plesiotypic retentions. With the extreme tendency to parallel losses and mosaic evolution within the Talitridae, retention of plesiomorphies may be as evolutionarily informative as apotypic losses, in morphology-based analyses. This is, of course, in direct contrast to the Hennigian view the symplesiomorphies provide no information on how taxa are related (Wiley, 1981).

The segregation of *Mezitroides* as a distinct genus is plausible, based on the extreme tendency among talitrids for mosaic evolution of characters, and the recent trends in generic definitions (Bousfield, 1971, 1973, 1982, 1984; Bousfield and Heard, 1986; Bousfield and Howarth, 1976; Friend, 1980, 1982, 1987). The extremely uncertain taxonomy of the palustral talitrids would require an extensive study and world revision of talitrid taxa (which is beyond the scope of this work), before a complete (monophyletic) phylogenetic analysis of these amphipods would be possible. In addition, formal recognition of the Jamaican taxa awaits the completion of their taxonomy (Bousfield, in prep). Further landhopper taxa may yet be discovered in the Greater Antilles. Within the limitations of the present taxonomy, phylogeny B constitutes an adequate working hypothesis of the relationships among New World landhoppers. This hypothesis can be refined as further information is developed.

Figure 34: Relative positions of New World landhoppers and selected talitrid species in a three dimensional space representing the first three axes of a principal components analysis. The scale on the right represents the first principal axis, the vertical scale the second and the scale on the left the third. The largest and darkest objects are closest to the viewer, and the smallest and faintest are farthest away. The key on the right lists the taxa in order of their distance from the viewer. *C.*—*Caribitroides*, *M.*—*Meritroides*

A: M. chiapensis
 B: C. newtoni
 C: C. sp. B
 D: Talitriator
 E: C. jamaicensis
 F: C. sp. A
 G: Talitroides
 H: Tethorchestia
 I: C. tuxtlensis
 J: Platorchestia
 K: Floresorchestia
 L: Chelorchestia
 M: Cerrorchestia
 N: M. pecki

Figure 35: Relative positions of New World landhoppers and selected New World talitrid species in a three dimensional space representing the first three axes of a principal components analysis. The scale on the right represents the first principal axis, the vertical scale the second and the scale on the left the third. The largest and darkest objects are closest to the viewer, and the smallest and faintest are farthest away. The key on the right lists the taxa in order of their distance from the viewer. *C.*-*Caribitroides*, *M.*-*Mexitroides*

A: C. jamaicensis
 B: C. sp. B
 C: C. sp. A
 D: M. pecki
 E: C. newtoni
 F: M. chiapensis
 G: C. tuxtlenensis
 H: Tethorchestia
 I: Platorchestia
 J: Cerrorochestia
 K: Floresorchestia
 L: Chelorchestia

Figure 36: Cluster analysis of New World landhoppers and selected talitrids using the simple matching coefficient. *C.*–*Caribitroides*, *M.*–*Mexitroides*

Figure 37: Cluster analysis of New World landhoppers and selected talitrids using the Jaccard coefficient. *C.*-*Caribitroides*, *M.*-*Mexitroides*

Figure 38: Cladogram of New World landhoppers and selected talitrids using Camin-Sokal parsimony. Numbers are characters, and their placement on the tree indicates a change from plesiotypic to apotypic state. *C.*—*Caribitroides*, *M.*—*Mezitroides*

Figure 39: Cladogram of New World landhoppers and selected talitrids using Wagner parsimony, rooted by defining the ancestral character states. Numbers indicate the change of that character from plesiotypic to apotypic state. Bracketed numbers indicate a reversion of that character. *C.*–*Caribitroides*, *M.*–*Mezitroides*

Figure 40: Cladogram of New World landhoppers and selected talitrids using mixed Camin-Sokal and Wagner parsimony. Numbers indicate the change of that character from plesiotypic to apotypic state. Bracketed numbers indicate a reversion of that character. *C.* - *Caribitroides*, *M.* - *Mezitroides*

of females. The recurring evolution of freshwater tolerant species from estuarine /marine ancestors in supralittoral *Orchestia* was considered to be significant in the colonization of land (Wildish, 1979).

Values for the osmotic pressure of talitrid haemolymph were summarized by Spicer, *et al* (1987) as follows:

<i>Orchestia gammarellus</i>	828
<i>Platorchestia platensis</i>	806
<i>Talorchestia capensis</i>	836
<i>Orchestia carimana</i>	360
unidentified euterrestrial	400

It is noteworthy that *O. carimana*, a talitrid that has been found in fresh water far inland, and at 1500 m on Mount Olympus, Greece (Spicer, *et al*, 1987), and the unidentified euterrestrial species, have osmotic pressures half the values of supralittoral species. This is an argument in support of physiological differences in osmoregulation between supralittoral and landhopper species hypothesized by Duncan (1985). Further studies are of course necessary, but it may be speculated that this pattern will continue. *O. carimana* occurs in fresh water and in estuaries. It might be considered palustral. Studies of other palustral species are badly needed to provide comparative information.

Preliminary studies of talitrid cuticle composition suggest that landhoppers may have considerably more calcium compounds in the cuticle than do supralittoral species (Spicer, *et al*, 1987). Although only *Arcitalitrus* has been studied in this detail, these authors felt that an important physiological difference may exist between supralittoral species and landhoppers as regards the mechanism of calcification. Another aspect of ionic regulation, the concentration of copper, was found to show a gradient of terrestriality, with euterrestrial talitroideans having the highest copper concentrations (Spicer, *et al*, 1987).

Most amphipods are considered to have ammoniotelic metabolisms, and the excretion of gaseous ammonia was recently demonstrated for *Orchestia gammarellus* in air (Spicer, *et al*, 1987). Terrestrial woodlice also retain an ammoniotelic nitrogenous excretion, and give off ammonia gas in periodic bursts during a 24 hour cycle, usually with the maximum release of both ammonia and water occurring while the animals are resting in high humidity (Sutton, 1972). It seems likely that landhoppers, which inhabit relatively moist environments, will also retain similar patterns of nitrogen excretion.

Figure 41: Phylogeny A: An hypothesis of the phylogeny of the New World landhoppers, based on Camin-Sokal parsimony, showing the derivation of *Cerrorchestia* from the ancestral landhopper line. All members of *Caribitroides* are derived from this clade. *C.*–*Caribitroides*, *M.*– *Mezitroides*

Figure 42: Phylogeny B: A second hypothesis of the phylogeny of the New World landhoppers, based on mixed Camin-Sokal/ Wagner parsimony, with the *Caribitroides* clade and *Cerrorchestia* as separate derivations from a palustral ancestor. *C.*–*Caribitroides*, *M.*–*Mezitroides*

Chapter 8 ZOOGEOGRAPHY

8.1 Hypotheses

There are three biogeographic hypotheses which could be used, in whole or in part, to explain the phylogeny and distribution of Central American/Caribbean landhoppers. These are:

- 1. world continental drift (vicariance);
- 2. Caribbean dispersal by water without tectonic factors;
- 3. local Caribbean tectonic movement (vicariance).

The first hypothesis assumes that all landhoppers are monophyletic, and probably derived from the early landhoppers of Gondwanaland (see Bousfield, 1984). The second and third hypotheses could be applied to either a monophyletic or paraphyletic derivation of landhoppers. There is no fossil record available. Data such as fully comparative life histories, accurate geographic ranges, and even the taxonomy of the Jamaican landhoppers and many palustral and beachflea taxa are still very inadequate. Each hypothesis can only be examined on the basis of what little evidence is available.

A long-distance dispersal scenario for Caribbean biogeography is possible. Pregill (1981) cites late Miocene records of megalonychid sloths in North America as proof that since these arrivals must have crossed the water barriers to get there, they could also have crossed water barriers to reach the West Indies without the necessity of any tectonic movement of West Indian islands. The uneven distribution of vertebrate taxa is therefore said to support slow and random dispersal to the West Indies, with "founder effect" radiations from one or a few colonizations.

There is little hard evidence to support static positions of the West Indies. However, the geological evidence for tectonic origin and movement of the Antilles with relation to each other and the continental mainlands is very convincing. This has been reviewed and synthesized by Burke, Cooper, Dewey, Mann and Pindell (1984). Biogeographers note that there need not have been direct land connections between the plate fragments, but that in the course of tectonic movements, the landmasses were close enough to allow effective short-distance dispersal (Buskirk, 1985; Hedges, 1982; MacFadden, 1980; Rosen, 1985).

Of pertinence to Caribbean dispersal is the relative usefulness of small islands as "way posts" in island hopping. Linhart (1980) found that the dynamics of colonization by plants are erratic, and are in marked contrast to consistent patterns found in avifauna. Cay flora is composed primarily of species found on beaches, mangrove swamps, seaside thickets and other coastal formations. Small islands are unlikely to support landhoppers, and only hardy beachflea taxa would be likely to be able to use island chains as stepping stones. "Sweepstakes dispersal" is a particularly good description for island hopping, as the chances of winning through are very small.

8.2 Tectonics

The most recent synthesis of Caribbean tectonics (Burke, *et al*, 1984) indicates eastward movement of land arcs and sea floor from the Pacific. An arc composed of Cuba, northern Hispaniola above the Enriquillo Basin, and Puerto Rico passed through the present location (relative to North and South America) of Central America during the early Tertiary, to collide with the Bahamas Platform. Subsequent movement of the new Caribbean plate shifted Jamaica/ Southern Hispaniola and the Chortis Block (Guatemala/ Honduras/ Nicaragua) eastward. The mechanism of movement was subduction of the eastern seafloor beneath the Lesser Antilles arc, from the Miocene to the present (Burke, *et al*, 1984). The collision of southern Hispaniola with northern Hispaniola, and a series of major orogenies in Central America occurred during the Pliocene (Burke, *et al*, 1984; Bartlett and Barghoorn, 1973; Maldonado-Koerdell, 1964).

Buskirk (1985) has correlated patterns of Caribbean biogeography with tectonic movements, proposing three major invasions of the Greater Antilles, as follows:

- 1. Early dispersal into the Cuban Plateau from North America and México during the Eocene/Paleocene.
- 2. Introduction from South America northward through the Lesser Antilles, approximately in the Miocene.
- 3. Colonization of Jamaica during the Miocene and Pliocene from Central America.

8.3 Ancestral Forms

The superfamily Talitroidea may have originated in Gondwanaland (Bulycheva, 1957; Friend, 1980; Friend and Richardson, 1986). The ancestors of the New World palustral amphipods may have also originated in Gondwanaland. The ancestral form might have been similar to *Microrchestia* Bousfield 1984, a plesiomorphic palustral genus with representatives in the Old World (Gondwanaland regions) and South America (Bousfield, 1984). From southern South America, this ancestor may have spread north in estuaries and salt marshes, until the proximity of the northern tip of South America and the Cuban arc allowed it to cross into North America. The ancestral form may then have given rise to *Chelorchestia* (and possibly *Uhlorchestia*) in isolation from more primitive groups, when movement of the Cuban arc eastward isolated it by opening a large water barrier between North and South America. *Uhlorchestia* Bousfield 1984, is similar to *Chelorchestia*, but it possesses a greater number of plesiomorphic characters. Both genera are considered to be slightly more advanced in many characters than the Old World palustral genera (Bousfield and Heard, 1986).

Around the edges of the Gulf of México, a number of geologically old uplands experienced uplift and/or folding during the Laramide orogeny of the late Cretaceous and Paleocene (King, 1977). These include the highlands of Oaxaca, Chiapas, the Cordilleras Central of Guatemala and Honduras, and the Maya Mountains of Belize (Maldonado-Koerdell, 1964; Weyl, 1980). The Sierra Madre Oriental and Marathon systems also underwent uplift during this orogeny (King, 1977; Maldonado-Koerdell, 1964; West, 1964). Since most of the coastal lowlands of the Caribbean were not emergent until the mid-Tertiary, these highland areas may have provided moist forest regions in close contact with ocean shore, offering appropriate habitat for the proliferation of palustral amphipods into inland locations.

Invasion of land by a palustral ancestral form in the mid-Tertiary could have been aided by cool climate. Depressed temperatures occurred throughout the Oligocene period, with equatorial temperatures lower than the present (Graham and Jarzen, 1969; White, 1986; Wolfe, 1978). Cooler temperatures cause the lowering of altitudinal climate and vegetation zones (Brown, 1982; Graham, 1982; Haffer, 1981; Toledo, 1982). During the Oligocene, moist forest conditions would have occurred at lower altitudes than normal, and in lowland areas than would normally be too dry to support amphipod populations. This would allow expansion of range of newly terrestrial forms, and rapid divergence from their palustral ancestors (Figure 42, event A).

8.4 *Caribitroides*

By the early Miocene, the ancestral *Caribitroides* may have been well adapted to the leaf litter niche, in wet forests of México, and may have lost sexual dimorphism. The northern and southern populations of ancestral *Caribitroides* may have been genetically isolated by a seawater barrier at the Isthmus of Tehuantepec (West, 1964; Weyl, 1980), either as a vicariant event of marine transgression or as a dispersal event from the Chiapas highlands to the Oaxaca highlands (or vice versa) (Figure 42, event B).

The prevailing winds and currents in the Caribbean south of Cuba are at present mainly from east to west (Collier, 1964; Valentine, 1973). In the early Miocene, these currents may have been different. The Chortis block, and Panamá/Costa Rica arc were well west of their present position, and the Caribbean open to the Pacific. Also, the present day pattern of circulation in the oceans is mainly dependent upon the cold deepwater currents generated by the Antarctic ice cap (Sverdrup, Johnson and Fleming, 1942; Valentine, 1973). The glaciation of Antarctica occurred mid to late Miocene (Raven and Axelrod, 1975; White, 1986). Thus early to mid-Miocene currents in the proto-Caribbean may not have opposed movement of water masses from west to east. Rafts of rain forest vegetation could have drifted from the Chiapas massif to Jamaica, which became emergent during this time (Buskirk, 1985, and references therein), and was much closer to mainland México than it is today.

Once Jamaica had developed sufficient elevation to form wet forests (late Miocene/Pliocene), the *Caribitroides* ancestor may have arrived by rafting dispersal (Figure 42, event D). Large vegetation mats are common in modern tropical rivers, and, during floods, freshwater surface layers can form over the denser ocean water for many miles from the mouths of rivers (Darlington, 1957). The Motagua River presently occupies the Motagua Fault in Guatemala (Weyl, 1980), and during the Miocene, an even larger river may have occupied this fracture line between the Chortis Block and México (the Motagua/Chixoy Polochic fault system), along which Chortis was slipping eastward (Burke, *et al.*, 1984; Weyl, 1980). Vegetation mats floating on fresh or brackish water packages may have carried even a *Caribitroides* ancestor of poor vagility successfully to Jamaica.

Jamaica may not have had a direct (dry) land connection to México, as shown by the evidence of primary freshwater fish (Briggs, 1984). However, the biogeographic origins of Jamaica's flora and fauna shows a distinct affinity to Central America; much more so than

the other Greater Antilles (Buskirk, 1985; Pregill and Olson, 1981). This suggests that while Jamaica was close to the Chortis Block, over-water dispersal may have been effective over the short distance between them. Much of the Jamaican biota shows clear affinities with the mainland, and the source populations were probably on the Chortis Block (Buskirk, 1985; Howard, 1973; MacFadden, 1980).

It is noted that in the Antilles, vertical changes may be more significant than horizontal ones, and that elevation is an important factor in accounting for diversity (Buskirk, 1985; Pregill and Olson, 1981). Representatives of *Caribitroides* occur in Jamaica, Hispaniola and Central America, but not in Cuba or Puerto Rico (Bousfield, 1984). Altitude is an important factor, and landhoppers seem to occur only in highland areas with at least 1000 meters elevation or in undisturbed forests contiguous with and windward to such highlands. No landhoppers have been found in lowland Jamaica (Lindeman, unpublished; Peck, pers. comm.). On Jamaica, *Caribitroides* may have proliferated as the island was uplifted, and the present day highlands established. Isolation of the island proceeded by tectonic displacement eastward, and subsidence of the Nicaragua Rise. (Buskirk, 1985), removing the possibility of island hopping.

Bousfield (1984) mentioned the existence of a landhopper in Hispaniola, attributing it to *Caribitroides*. The association of Jamaica and Hispaniola might have allowed for ocean dispersal between them at an early stage, establishing a *Caribitroides* population in the Southern Highlands of Hispaniola. The extremely arid Central Depression, with its salt/gypsum soil (Howard, 1973) may have proved an impassable barrier for landhoppers, and prevented establishment of a landhopper population in the Northern Highlands.

Cuba apparently has no landhoppers at present (Bousfield, 1984). This is unsurprising, because the only portion of the island with elevations over 1000 meters is the Sierra Maestra range in Oriente province. This does not seem to support forest types suitable for landhoppers, (Howard, 1973). During the climatic cycles of the Pleistocene, when the West Indies were drier than they are now (Pregill and Olson, 1981), any landhoppers which may have been present probably became extinct. The absence of landhoppers from Puerto Rico is subject to the same arguments, although the cloud forests of the Luquillo Mountains (Howard, 1973) would seem to be perfect landhopper habitat. There is general agreement that the distribution of species in the Antilles is affected as much by extinction as speciation (Buskirk, 1985; MacFadden, 1980; Pregill and Olson, 1981; Rosen, 1975).

At about the mid-Miocene, climatic patterns similar to those of the present were established. Low latitude temperatures increased as polar temperatures fell (White, 1986; Wolfe, 1978; Valentine, 1984). Vegetation zones would have been elevated, and grassland, dry forests, and other xeric areas would have expanded. These changes were probably not as severe as those of the Pleistocene (see Brown, 1982; Haffer, 1981; Toledo, 1982), but may have been a factor in restricting the ranges of landhoppers, and reducing gene flow between major populations of *Caribitroides*. The Tehuantepec lowland may have provided a long term barrier, first as a water barrier (Weyl, 1980), then as unfavourably dry land (Gómez-Pompa, 1973), separating the northern population of *Caribitroides* from its southern offshoot, which became *Meritroides*.

The Pliocene was an epoch of particularly active vulcanism and uplift throughout Central America (King, 1977; Maldonado-Koerdell, 1964; West, 1964; Weyl, 1980). Many of the old highlands were rejuvenated at this time (Weyl, 1980), and the present day volcanic axis of Central America began to form. These physical factors, combined with the warmer climate, may have brought about the distribution of landhopper species in wet forest habitats associated with highlands, much as they occur today. The Sierra de Tuxtla was uplifted during the Pliocene (Andrle, 1964), and was probably colonized soon after the establishment of appropriate forest and climate by *Caribitroides* from Oaxaca or the Sierra Madre Oriental (Figure 42, event C).

Volcanic eruptions have, even in historical times, destroyed large areas of forest in the Los Tuxtlas upland (Andrle, 1964). This may have had important effects on the evolution of *Caribitroides tuxtlaensis*, in that destruction of large areas of habitat would have greatly reduced population numbers, causing reduced genetic variability, and hence a greater potential for genetic drift (see Brown, 1982; Bush, 1975; Haffer, 1981; Mayr and O'Hara, 1986). Catastrophic events in the Caribbean region, as well as tectonics, may thus have affected landhopper evolution.

The *Caribitroides* ancestral form may have been widespread in the Maya Mountains of Belize, the northern and eastern (Lacandona) highlands and Sierra Madre of Chiapas, the Sierras de Cuchumatanes and Chuacus of Guatemala, and the Cordillera Central of Honduras, during the Pliocene. As the Pliocene uplift continued, these areas may have become effectively more isolated from each other by drier conditions in the lowlands between them. To the south, the Nicaragua Depression, which underwent downwarping throughout the Pliocene and Pleistocene (Weyl, 1980), would have been a barrier for landhoppers.

Pleistocene glacial cycles may be responsible for the present pattern of landhopper distribution as they are for other taxa (Brown, 1982; Haffer, 1981; Mayr and O'Hara, 1986). Expansion of moist forest would allow expansion of ranges and communication with other highland habitats, but the subsequent contraction of ranges in the dry parts of the cycles might cause extinction of populations in precariously small habitats. Colder conditions may have eliminated *Caribitroides* from the Sierra Madre Oriental. Dry climate may have eliminated landhoppers from the Sierra Madre del Sur, and the Mesa Central, leaving *Caribitroides newtoni* surviving in the moistest eastern part of the Sierra Madre de Oaxaca, and *C. tuxtlensis* in the Los Tuxtlas refuge.

In Jamaica, such climatic cycles, with the concomitant isolation of each highland population through elevation of vegetational/climatic zones, could easily have produced the present species distribution pattern. An early speciation event (possibly isolation of the eastern and western portions of the island) would have produced *C. sp. B* (Figure 42, event F). Climatic isolation of Mount Diablo from the Blue Mountains may have been of sufficient duration to allow the Mount Diablo endemic population (*C. sp. A*) to diverge from *Caribitroides jamaicensis* (Figure 42, event G). A complete phylogeny of all species of *Caribitroides* must await the full taxonomic description of all Jamaican species (Bousfield, in prep.).

In Chiapas, the present collection sites of *Mexitroides chiapensis* border the Lacandona refuge (Toledo, 1982), and this species may be endemic to this region. It may have had a range extending into the Sierra de Cuchumatanes, but been eliminated there by glaciation of these mountains (Weyl, 1980). Potential populations or species of *Mexitroides* in Guatemala and Honduras may be discovered in the future if their habitat has not already been destroyed by man.

Before deforestation by humans, the Sierra Madre de Chiapas had a tropical deciduous habitat (Breedlove, 1973), which may have been suitable for landhoppers. It is separated from the present collection sites of *M. chiapensis* by the Central Depression of Chiapas, currently a very xeric area. An invasion of *Mexitroides* into Oaxaca during a period of lowered vegetational zones may have occurred from either the Sierra Madre or the northern highlands, resulting in the establishment of *M. pecki* in the same range as *C. newtoni* (Figure 42, event E). Until the Sierra Madre de Chiapas is carefully examined for landhoppers, it cannot be established whether *M. pecki* also occurs in Chiapas, or evolved on the Oaxaca massif as a result of founder effect after a dispersal event from the *M. chiapensis* population.

8.5 *Cerrorchestia*

Cerrorchestia, the plesiomorphic landhopper of Costa Rica/Panamá, was probably derived from a *Chelorchestia*-like ancestral form, but whether this ancestor is common to *Caribbitoides*, as in Figure 41, or a separate derivation, as in Figure 42, is uncertain. A form of *Chelorchestia* may have moved down into the Costa Rica/Panamá arc from the Chortis block, and remained in a more or less semiterrestrial state on the islands (the Nicoya peninsula/ Tilaran, the Talamanca batholith, and an old area of eastern Panamá) emergent in the Miocene (Weyl, 1980). *Cerrorchestia* may have been derived from this ancestor during the late Miocene and Pliocene uplift (Weyl, 1980) of most of Costa Rica and Panamá.

The likelier alternative is that *Cerrorchestia* is directly derived from *Chelorchestia* (Figure 42) in a relatively recent evolutionary event, comparable to the generation of *Chelorchestia vaggala* (Bowman, 1977) on the Galápagos. A population of ancestral *Chelorchestia* may have become isolated during the Pliocene uplift of the Costa Rica/Panamá arc, and given rise to a forest dwelling terrestrial species, which proliferated with the development of modern relief and wet forests.

At present, an effectively continuous strip of montane forest runs from the northernmost volcano of the Cordillera de Guanacaste in Costa Rica to the eastern terminus of the Cordillera Central of western Panamá (Holdridge, 1967; Porter, 1973). Although this may have been fragmented during the Pleistocene climatic cycles, it has re-formed, allowing gene flow between populations of *Cerrorchestia*. This lack of isolation or major barriers may be the reason for lack of distinct speciation, although Panamanian populations show some differences from those in Costa Rica. Investigation of the Darién of Panamá, and the highlands of Colombia and Venezuela is needed, to determine whether or not landhoppers may be present (none were found there in four months of work by S. Peck)

A notable example of the geographic requirements of landhoppers derived from a palustral ancestor is that of *Chelorchestia vaggala*, found only on San Cristóbal Island in the Galápagos. This island has a permanent freshwater lake at 700 m., and the only permanent freshwater stream in the archipelago. Even during the dry season, the higher parts of the island are bathed in a fine mist. Landhoppers were collected in moist areas with growths of mosses, liverworts, ferns, epiphytes on the trees (where present), and tree ferns (Bowman, 1977). This site is clearly a type of cloud forest, and is probably maintained as much by condensation and groundwater as by precipitation (which is rather low). Bowman (1977)

stated that, "It is evident, therefore, that the southern slope of El Junco provides enough soil moisture for the needs of land-hoppers. It is probably not just by chance that although Dr. Vagvolgyi collected land snails at many localities throughout the Galápagos Islands, he encountered land-hoppers only on San Cristóbal."

Of great interest is the ancestry of the terrestrial talitrid which has been reported from Cocos Island (Bousfield, 1982). If it is congeneric with *Cerrorchestia*, the geology and age of the island could be compared with that of the Costa Rica/Panamá arc, to provide more information on the possible age of the genus. A comparison with *Chelorchestia vaggala* would also be pertinent. Since the Galápagos are only about 3 million years old (Hall, 1983; Hickman and Lipps, 1985), the evolution of *Chelorchestia vaggala* is necessarily a very recent event. It provides an example both of the development of terrestrial species from *Chelorchestia* and of the dispersal ability of the ancestral form.

The main argument that *Cerrorchestia* is a younger taxon than *Caribitroides* rests upon the retention of plesiomorphic sexual dimorphism. Most terrestrial lineages seem to tend toward loss of sexual dimorphism (Friend and Richardson, 1986). *Cerrorchestia* may be in the process of changing to a non-sexually dimorphic form, indicated by the presence of males with feminized gnathopods. These specimens of *Cerrorchestia* may represent an intermediate stage in the development of a new non-sexually dimorphic taxon.

The requirements for New World landhopper populations seem to be areas where highlands intercept onshore trade winds or moist air masses, such that a very wet forest (maintained by high rainfall and/or condensation from clouds) is developed. Analysis of world landhopper zoogeography may show the same pattern, although some apomorphic Old World species have penetrated drier areas. Except for one species, the distribution of landhoppers in Australia fits well with the 760 mm isohyet (Friend and Richardson, 1986). Under this hypothesis, the lack of landhoppers in the Yucatán Peninsula is explicable as a function of inconsistent moisture levels, and lack of a nearby highland refugium during Pleistocene climatic cycles.

8.6 Predictions

The biogeography model presented above can offer several predictions. In México and Central America, the ecological refuge areas described by Brown (1982) often coincide with landhopper collection sites. Refuge areas of México (see Toledo, 1982) may harbour undiscovered species of landhopper. The Cordoba area may house a relict species, if any

uncut forest remains at elevations which do not experience much frost. The Sierra Madre del Sur and Mesa del Sur are probably too dry for landhoppers, but should be examined, as should the Maya Mountains of Belize. *Meritroides* is likely to occur in uncut forests of the Sierra Madre de Chiapas, Sierras de Cuchumatanes and Chuacus of Guatemala, and the Cordillera Central of Honduras. Populations may occur in the highest regions of the Matagalpa formation of Nicaragua, although these small uplands may not provide sufficient moisture. South and east in Nicaragua are only lowlands, lacking in any refuge areas (Brown, 1982), which are probably a major barrier to landhoppers. These lowlands form a geographic break between the southern possible range of *Meritroides* and the most northern occurrence of *Cerrorchestia* in Costa Rica. In the Caribbean, each highland area of Jamaica has one or more species of *Caribitroides* (Bousfield, 1984, pers. comm.; and Lindeman, unpublished). There may be one or more species in the southern peninsula of Hispaniola, and possibly in the Cordillera Central and/or Cordillera Septentrional, although this is less likely.

Cerrorchestia probably occurs throughout the Tilarán and Talamanca ranges of Costa Rica, reaching relatively far into the lowlands where uncut forest exists on the Caribbean side, but is limited on the Pacific side by the leeward edge of cloud forest. This pattern probably continues into Panamá. Near the Panamá Canal, populations of *Cerrorchestia* most likely exist in a mosaic which changes with rainfall fluctuations. The source populations for central and eastern Panamá are most likely centered on higher localities with patches of cloud forest, as documented by Myers (1969). Exploration east of the Río Chepo Bayano may disclose *Cerrorchestia* populations in the Serranía de Cañazas, the eastern part of the Serranía de Darién including Cerro Tacarcuna, the Serranía de Pirre and the Serranía del Sapo, all of which have cloud forest at their highest elevations (Myers, 1969). The valley of the Río Atrato, a lowland area probably subject to marine incursions (Weyl, 1980), may be unfavourable habitat for landhoppers, and may be the eastern limit of *Cerrorchestia*. Collecting in the Serranía de Abibe in Colombia would be needed to establish the range boundary of *Cerrorchestia* with confidence.

The northern Andes would seem to have the climatic/geographic conditions required for the presence of landhoppers (onshore winds rising up the slope of the mountains, producing very heavy rainfall and a very wet forest type). No landhoppers have been collected from these wet forests, despite their exploration in recent years by entomologists familiar with landhoppers. The absence of terrestrial amphipods in these localities is puzzling, given

the presence of palustral talitrids in seashore habitats, and the evolution of *Chelorchestia vaggala* in the Galápagos. It may be that landhoppers have been excluded from Andean forests by a superior competition among the leaf litter macrofauna, that conditions for the development of a landhopper (isolation of a palustral population and subsequent selection toward full terrestriality) somehow did not arise on the South American mainland, or some combination of these and other factors. The final possibility is that landhoppers do exist in the Andes, but in some sort of particularly restricted habitat which has simply not been completely explored by biologists familiar with the existence of these organisms. Further study of Andean cloud forest leaf litter may provide further information.

8.7 Summary

The distribution and phylogeny of New World landhoppers can be explained by local Caribbean tectonic movements. The entry of the ancestral palustral forms into North America can be explained by the early passage of the Cuban Arc between North and South America, providing a sufficient reduction of water barriers for palustral amphipods to enter North America by island hopping. The movement of the Cuban Arc away from South America allowed the development of North American palustral taxa in isolation from their South American relatives. Subsequent tectonic events in the Caribbean allowed the divergence of the *Caribitroides* ancestor from other palustral populations, and provided for the spin-off of populations into Jamaica, Hispaniola and México (often requiring short dispersal events over water). The final development of the Costa Rica/Panamá Arc saw the evolution of *Cerrorchestia* from a *Chelorchestia*-like ancestor, in the islands of the young arc, and its subsequent proliferation in the high forests of the uplifted isthmus. The present species distributions of *Caribitroides* are due in part to Pleistocene climatic cycles and their effects on the specific forest habitat required by landhoppers. *Cerrorchestia* was less affected by these climatic cycles partly because the effects were less severe on the isthmus, and partly due to the fortuitous combination of topography and climate, which maintains an almost continuous band of appropriate forest down the entire spine of the Costa Rica/ Panamá Arc.

Chapter 9 EVOLUTIONARY ASPECTS OF TERRESTRIALITY IN LANDHOPPERS

9.1 The Leaf Litter Habitat

Plant litter produced by macrophytes plays an important role in nutrient circulation and energy flow between plants and the soil reservoir. The activity of soil and/or litter dwelling organisms (breaking down organic particles into smaller pieces to facilitate fungal, microbial and chemical decomposition) sometimes constitutes a rate-determining step in nutrient cycling, and can regulate nutrient availability and turnover rates in the entire community (Pianka, 1978).

Decomposition of litter originates with infection by microorganisms, even before the vegetation is shed from the parent plant. The initial infection may vary with pH (fungi are associated with acid conditions and bacteria with alkaline). These parasites of living tissue may persist after the fall of the litter, but more usually are replaced by litter and soil species. Decomposition of litter varies with species and site characteristics. Herbaceous vegetation breaks down more rapidly than woody materials and leaves with higher contents of polyphenols and other secondary compounds break down more slowly than leaves with lower contents of such substances.

The rate of leaf decomposition may be influenced by the position of the leaves on the tree. Leaves in exposed positions ("hard leaves") tend to have a higher polyphenol content than leaves occupying shaded positions ("soft leaves"). "Soft" leaves disappear from the litter more quickly than "hard" ones. Large amounts of lignin retard decomposition, and the rate is slower in older than in younger vegetation. Decomposition proceeds more rapidly in well-aerated, neutral or slightly alkaline conditions, and in situations where there is neither an excess nor a deficiency of moisture (Wallwork, 1970).

Decomposition by microorganisms brings about changes in the composition of the leaf litter, and renders it more acceptable to the litter-feeding detritivores such as earthworms, insects, millipedes, woodlice, collembolans, mites, protozoans and amphipods. Feeding activity by these animals accelerates the physical disintegration of the litter and also is necessary for the continued activity of microorganisms. The feces of detritivores support a

rich microbial growth, and these microorganisms are the principal agents of conversion of organic material into humus complexes (Wallwork, 1970).

In tropical forests, litter fall can vary according to: (1) the species composition of the forest, (2) seasonality of each species, (3) canopy characteristics such as number and height of canopy layers and amount and (4) type of understory, and the geography and climate of the site, which affects the amount and seasonality of rainfall (Friend, 1980; Lawrence, 1953; Medwecka-Kornas, 1971; Wallwork, 1976). The leaf litter builds up during the dry season and decreases during the wet season, due to higher rates of decomposition in the wet season (Levings and Windsor, 1982; Wallwork, 1976).

The physical characteristics of the litter are dependant to a great extent on the forest it is derived from, which is dependant in turn upon temperature and moisture (climate) of the geographic area (Holdridge, 1967). The timing and amount of rainfall affects litter organisms directly by changing the amount of moisture available and the relative humidity and saturation deficit of the litter atmosphere, and indirectly by affecting the timing, duration and possibly the amount of litterfall, and the rate of attack by microorganisms. Leaching by rainfall also affects the suitability of litter as food.

The length of the rainy season and the distribution of rainy periods during the dry season strongly affects litter arthropod populations. Dry conditions always reduce arthropod activity. Regular showers or water input through condensation maintain litter moisture at a higher level than heavy, infrequent storms. Groundwater may affect the relative humidity of soil and leaf litter atmospheres, and may, in concert with local topography, create and maintain moister patches of litter, which may provide microclimate refugia for litter arthropods during the dry season, or be a site of enhanced survivorship or activity when litter conditions are poor (Levings and Windsor, 1982; Wallwork, 1970). Inland from the ocean shore, rainfall, streams, and groundwater affect litter moisture. In very wet forests such as the elfin forest, the litter is highly saturated, and might be considered almost a freshwater habitat.

Temperature within the leaf litter is controlled to a great extent by the forest canopy, which affects the amount of solar radiation reaching the ground. Changes in leaf litter temperature have a lower amplitude than changes in air temperature. The amount of water affects temperature fluctuations, since higher moisture contents reduces the amplitude of temperature change (Lawrence, 1953; Wallwork, 1970). Penetration of light into the leaf litter depends on the canopy, the topographical situation, the amount of understory growth,

and the nature of the leaf litter itself. Light may be an important factor in triggering the activity patterns of leaf litter animals, but the interdependence of light, humidity and temperature factors make it difficult to separate their effects.

Terrestrial amphipods thus occupy a habitat defined to a great extent by climate, which affects the type and ecology of forest and, therefore, of forest leaf litter. A characteristic of the geographic sites inhabited by landhoppers is the relatively even rainfall and high moisture of the leaf litter throughout the year. At the higher elevations, which seem to be the preferred habitats of New World species, variability in cloud forest leaf litter moisture and air humidity is minimal, and the likelihood of seasonality in food sources (litterfall) and palatability (microorganism pre-processing of fresh litter) is even less than in lowland rain forests.

Diurnal variability in humidity is a noteworthy factor during the dry season, but much less so in the rainy season. Landhoppers, with the exception of a few burrowing species (see Friend and Richardson, 1986), move through the pore spaces, cavities and channels of the leaf litter, and venture up the trunks of trees into the epiphyte layers. They live within their food supply, and the availability of appropriately aged leaves, while possibly subject to some seasonal variation, is probably not limiting to macrofauna capable of travelling to sites of optimal food, shelter and moisture. Moisture may be the single most important factor in the distribution of landhoppers, as indicated by their general absence (with a few exceptions) in dry forest types and areas where human activities have cleared the forests.

The tolerance of landhoppers for the highly saturated and acidic conditions of cloud forest leaf litter may be coupled with an ability to consume poorly decomposed leaves. Since decomposition is retarded by high moisture levels and acidic pH (Wallwork, 1970), it would follow that the ability to utilize poorly decomposed leaves would provide a competitive advantage over other detritivores which might normally utilize leaves in which decomposition has proceeded to a greater extent than is normal in the cloud forest. The remarkably low densities of litter arthropods other than amphipods in the highly saturated elfin forest suggests that some factor(s) favour amphipods in these conditions. Many arthropods such as ants may possibly experience waterlogging of the tracheae, or a strong tendency to fungal infections in the elfin forest, whereas amphipods can tolerate very wet conditions, and long periods of immersion. Landhoppers may also have a gut flora which has coevolved with them to specialize in feeding on soaked leaf litter. The limitation of landhoppers to litter of a certain minimum moisture level may be partially due to moisture and osmotic

requirements, and partially due to their exclusion from drier habitats by competition by other litter arthropods.

9.2 The Fossil Record

The fossil record of the entire order Amphipoda consists of eighteen taxa in seven genera, all of them European, and no fossil dated earlier than the Eocene (Hessler, 1969). The fossil *Paleogammarus* (Just, 1974), from Baltic amber, is very similar to the extant Crangonyctidae, suggesting that this freshwater family was well established by the Eocene. Landhoppers occupy a habitat that does not lend itself to fossilization, because scavengers, detritivores and fungi of the tropical forest leaf litter process dead material quickly (Friend, 1980; Forsyth and Miyata, 1984). Their delicate exoskeletons are particularly prone to decay, aside from the observed tendency (Lindeman, unpublished) toward cannibalization of injured or dead amphipods by others. Only a rare chance event such as preservation in amber would be likely to provide fossils.

In contrast, isopods are a relatively old group (Kukalova-Peck, 1973), with fossils of marine representatives dating back to the Carboniferous and Permian. The fossil record for terrestrial isopods is restricted to the Tertiary (Schram, 1986), although the evolution of terrestriality in isopods may be much older.

9.3 Morphology

The most striking feature of landhopper morphology is the tendency to reductions and losses of setation and appendages. Landhoppers tend to be extremely smooth bodied in comparison to beach forms, especially those which burrow. Sand burrowers tend to be highly setose (see Bousfield, 1973), while non-burrowing species such as *Tethorchestia* and *Orchestia grillus* are much smoother. The tendency to reduction extends to cuticular microstructures (Halcrow and Bousfield, 1987; Holmquist, 1982). Reducing surface area and breaks in the integument might help to reduce water loss, since talitrids lose water from the entire body surface (Spicer *et al*, 1987). Fewer setae would reduce the tendency for bits of dirt and detritus to cling to the body surfaces, and allow more efficient movement within the crevices of the leaf litter.

Loss of pleopods may also be related to water conservation. Pleopods have been shown in several studies (Spicer, *et al*, 1987) to be highly permeable sites of water loss. Some highly

derived species (see Friend, 1982) have lost the rami completely and the peduncles are very reduced as well. Friend and Richardson (1986) proposed that, in landhopper species that retain elongate pleopods, these structures may be used to move air in the ventral groove or agitate the exosomatic water film that covers the gills and ventral groove surfaces. This may be so, but the pleopods of *Cerrorchestia hyloraina* and *Caribitroides tuztlensis* do not beat constantly in air.

Distinctive differences in gills occur between beach taxa and terrestrial taxa. Beach species tend to have relatively small gills (Bousfield, 1982). This may be related to the physiological demands of a hypertonic environment. The delicate membrane and high blood flow required for gas exchange may make these structures susceptible to cell crenelation and water loss when exposed to salt. Landhoppers, on the other hand, may live in a basically freshwater environment (although chemical analysis of leaf litter water has not been done, and could conceivably show unexpected levels of total dissolved solids), which is hypotonic with regard to their fluids. Acquisition of water through the gill membranes may be less dangerous to water balance than loss. Beach amphipods may be constrained in gill size by their environment, whereas estuarine and terrestrial forms may encounter more difficulty conserving ions than conserving water.

It is notable that *Chelorchestia costaricana* has large lobate gills which are more comparable to those of most landhoppers than the gills of any beachflea. If estuarine species spend some of their time submerged, selection toward large gills to cope with lower oxygen levels in water would be possible. This may be carried over into landhoppers because heavy rains and flooding streams can soak the leaf layer thoroughly. Behavioural responses (such as climbing or migration) may be coupled with high tolerance for freshwater immersion (see Chapter 5) as adaptations to their leaf litter niche. Unfortunately, amphipod systematists, with the notable exception of Friend (1979, 1980, 1982, 1987), tend to, at best, only comment briefly on gills, so comparison of gill morphology is very difficult, unless specimens are readily available.

Long, slender limbs are a characteristic of most landhoppers, as compared to the more robust build of most beachfleas. An exception is one Tasmanian landhopper, which has a distinctive "burrowing" facies, with short, strong pereopods, a broad shallow body and a rounded cephalon reminiscent of the collum of burrowing millipedes (Friend, 1980). A beach taxon which moves about actively at night at the edge of the wave zone (Lindeman, unpublished observations) is *Pseudorchestoidea*, which has long limbs and a slender

body (although it tends to be spinier than most landhoppers). The blind cave talitrid *Spelaeorchestia koloana* is slim and long legged (Bousfield and Howarth, 1976), as well. Generalizations about any morphological tendency should probably be approached with caution, since convergence is so widespread among the Talitridae.

Enlargement of the eye is thought to be a "tendency" in terrestrial amphipods (Bousfield, 1981, 1982, 1984; Hurley, 1968). The largest eyes relative to head sizes occur in the sandhoppers (see Bousfield, 1982), rather than landhoppers. The studies available on talitrid vision document lunar and solar directional orientation, and form vision for several species of beach talitrids (Williamson, 1951; Papi and Pardi, 1963). It can be speculated that males might use their large GN2 propods for visual signalling and agonistic display, as male fiddler crabs do with their large claws (Kaestner, 1970). Such visual cues would be particularly effective on a beach, where many amphipods move about in clear view of one another, but probably less effective in leaf litter.

Landhoppers may navigate visually to some extent, and may move toward shadows. Large eyes are not necessary for phototaxis, as demonstrated by the ability of the eyeless *Spelaeorchestia* to avoid light (Bousfield and Howarth, 1976). Landhoppers may use their large eyes mainly to enhance their ability to move about rapidly, and in concert with chemical clues to identify other landhoppers and/or potential predators.

The most notable tendency among landhoppers is the loss of sexual dimorphism and convergence of both sexes to the female form. Loss of sexual dimorphism is usually attributed to neoteny (Bousfield, 1984; Hurley, 1968). The fundamental mechanism of selection has been to successfully utilize rotting angiosperm driftwood and leaves as a diet (Wildish, 1972; 1982b). Several important questions remain unanswered:

- 1. why do so many landhoppers lose their sexual dimorphism and what is the selection against dimorphism in the leaf litter niche;
- 2. why of all the sandhoppers, some of which are highly derived, has only *Talitrus saltator* lost sexual dimorphism of the gnathopods (it retains dimorphism of the antennae).

Selection against the large GN2 propod may include reduced agonistic display in a leaf litter habitat, reduction of precopulatory grasping behaviour, increased need for grooming in terrestrial habitats, and the inefficiency of energy investment in a large structure of diminishing function. Reduction of sexual dimorphism may also be tied to the K-selective

(see Pianka, 1978) tendency to slow growth and sexual maturity at an earlier growth stage (Wildish, 1979), and to the sex determining mechanisms discussed below.

9.4 Reproduction

In comparison with aquatic amphipods, most landhoppers are strongly K-selected, with smaller broods, larger individual eggs in relation to their smaller body size, and with slower growth rates (Wildish, 1982a). In a terrestrial existence, broadcasting large numbers of small, poorly developed young would be inefficient. Finding a suitable mate also may be difficult. This may explain the apparent difference in activity levels between males and females. It may be that males are more active and move about in search of receptive females, while the females (particularly those with eggs or young) are somewhat less active.

Juveniles and adults may be subject to different selective factors, and reproductive effort should reflect environmental factors operating upon adults, whereas expenditure per progeny will be strongly influenced by juvenile environments (Pianka, 1978). One selective mechanism for larger young is inherent in the physiology of water loss. Small animals lose water faster than larger ones (Lazo-Wasem, 1984; Spicer, *et al*, 1987). It follows that in a terrestrial forest (particularly forest types drier than cloud forest), any mechanisms that give an advantage in water conservation will be selected for. Other advantages of larger young may be enhanced ability to find food or shelter and to escape predators and entrapment by water.

Morino (1978) and Wildish (1982a) classified amphipod life histories as follows:

- Type 1a. Breeding throughout the year (can be either iteroparous, with several broods produced during an individual's lifespan, or semelparous, with a single brood produced during the lifespan)
- Type 1b. Breeding restricted seasonally (iteroparous or semelparous)
- Type 2. Two or more generations completing a yearly life cycle (semiannual)
- Type 3. One generation completing a yearly life cycle (annual)
- Type 4. Two years or more necessary for breeding (biannual, or perennial, for over two years)

This classification can be used to describe the life histories of populations, but cannot be safely applied to an entire species with large geographic or ecological ranges, due to the effects of temperature and photoperiod on growth rates, moult rates, rate of attainment of reproductive maturity, and breeding periodicity. For example, a hot spring population of *Hyaletta azteca* had a Type 1 life cycle of continuous reproduction, while a population in a nearby stream, with a much cooler temperature regime, had a more restricted breeding season (Strong, 1972). In a cold lake in British Columbia, a population of *H. azteca* had a Type 3 life cycle (Mathias, 1971), while in a warmer Michigan lake, a Type 2 life cycle was reported (Cooper, 1965).

Similar life history variations were reviewed by Morino (1978) and Wildish (1982a). They noted that life history conversions from one type to another are apparently easily accomplished in amphipods, and may contribute to successful penetration of new habitats. Friend and Richardson (1986) proposed that the comparison of the life histories of several species in the same geographic location (and temperature/ daylength regime) may be valid, and in that case, that the life history types reflect a continuum of increasing K-selection.

9.5 Movement and Behaviour

Many aspects of the behaviour of landhoppers have been documented for beachfleas and sandhoppers as well, and constitute preadaptations for terrestrial life (Friend and Richardson, 1986). These include movement along a moisture gradient, nocturnal activity patterns, avoidance of bright light, eating of moulted exoskeletons and cast feces (the former probably for conservation of calcium and other trace substances, and the latter probably for re-inoculation of gut flora after moulting), and the hopping escape response.

Loss of swimming and the development of tree climbing seem to be behaviours unique to landhoppers among amphipods. Loss of swimming may be explicable as a functional effect in those landhoppers with extreme reduction of pleopods, but is less clear in those landhoppers which still beat their pleopods when immersed. Tree climbing may serve a specific purpose, such as avoiding immersion during heavy rains or flooding, or may be simply an aspect of the high levels of activity of these animals, and may reflect the relative continuity of the leaf litter and tree epiphyte layers.

9.6 Physiology

Friend and Richardson (1986) suggested that landhoppers and beach talitrids must have different physiological adaptations, since few supralittoral forms have dispersed into terrestrial habitats, and landhoppers have relatively few morphological differences (barring the notable differences in gill morphology) from supralittoral species. Duncan (1984) also proposed a definite difference in physiology between truly terrestrial species and supralittoral forms: specifically, that landhoppers were basically adapted to a freshwater environment, while supralittoral species were adapted to a saltwater environment.

Studies on desiccation are relatively scarce, and comparative studies including landhopper species are not available. Since the size of the animal affects the rate of water loss, comparisons between large beachfleas and smaller landhoppers may not provide useful information (Spicer, *et al.* 1987). Some indication that there are degrees of desiccation resistances among landhopper species was documented by Richardson and Devitt (1984). The ability to produce drier feces is greater in the more terrestrial species of woodlice (Sutton, 1972). No data are available on water extraction in amphipods, but a similar ability may exist in the most highly derived landhoppers.

In the most apomorphic terrestrial isopods there is a progressive tendency for respiration (and hence transpiration) to be concentrated in the gill region. This is attributed to the pseudotracheae. In primitive woodlice, 80 % of water loss occurs over the body surface, and only 20 % across the pleopod gills (Sutton, 1972). Both beachfleas and landhoppers seem to lose water from the whole body surface, but the relative importance of different potential sites of water loss has not been quantified for any talitrid (Spicer, *et al.*, 1987). It is possible that water loss is reduced over the general body surface in the most apomorphic landhoppers, and water loss through the gills may be minimized by controlling the exosomatic water film in the ventral grooves.

It has been suggested that physiological adaptations to retain ions in the body have been more important in the evolution of landhoppers than adaptations to resist desiccation (Friend and Richardson, 1986; Spicer, *et al.*, 1987). Since talitrids have colonized freshwater and terrestrial habitats, well developed powers of osmotic regulation may be inherent in the talitroideans, and constitute a preadaptation to terrestriality. Wildish (1970) has shown that salinity can affect the distribution of species of *Orchestia* in estuaries, and noted (Wildish, 1982a) that low salinities affected the intermoult period, breeding season and mortality

of females. The recurring evolution of freshwater tolerant species from estuarine /marine ancestors in supralittoral *Orchestia* was considered to be significant in the colonization of land (Wildish, 1979).

Values for the osmotic pressure of talitrid haemolymph were summarized by Spicer, *et al* (1987) as follows:

<i>Orchestia gammarellus</i>	828
<i>Platorchestia platensis</i>	806
<i>Talorchestia capensis</i>	836
<i>Orchestia carimana</i>	360
unidentified euterrestrial	400

It is noteworthy that *O. carimana*, a talitrid that has been found in fresh water far inland, and at 1500 m on Mount Olympus, Greece (Spicer, *et al*, 1987), and the unidentified euterrestrial species, have osmotic pressures half the values of supralittoral species. This is an argument in support of physiological differences in osmoregulation between supralittoral and landhopper species hypothesized by Duncan (1985). Further studies are of course necessary, but it may be speculated that this pattern will continue. *O. carimana* occurs in fresh water and in estuaries. It might be considered palustral. Studies of other palustral species are badly needed to provide comparative information.

Preliminary studies of talitrid cuticle composition suggest that landhoppers may have considerably more calcium compounds in the cuticle than do supralittoral species (Spicer, *et al*, 1987). Although only *Arcitalitrus* has been studied in this detail, these authors felt that an important physiological difference may exist between supralittoral species and landhoppers as regards the mechanism of calcification. Another aspect of ionic regulation, the concentration of copper, was found to show a gradient of terrestriality, with euterrestrial talitroideans having the highest copper concentrations (Spicer, *et al*, 1987).

Most amphipods are considered to have ammoniotelic metabolisms, and the excretion of gaseous ammonia was recently demonstrated for *Orchestia gammarellus* in air (Spicer, *et al*, 1987). Terrestrial woodlice also retain an ammoniotelic nitrogenous excretion, and give off ammonia gas in periodic bursts during a 24 hour cycle, usually with the maximum release of both ammonia and water occurring while the animals are resting in high humidity (Sutton, 1972). It seems likely that landhoppers, which inhabit relatively moist environments, will also retain similar patterns of nitrogen excretion.

Few data are available on temperature tolerances and acclimation in talitrids. Temperature preferences and tolerances may be shown to be important in geographic and microclimatic distributions of species. Acclimation may play an important role in allowing gene flow between populations of landhoppers which are otherwise isolated by different temperature regimes (for example cloud forest and lowland demes). It is possible that supralittoral species may have higher temperature tolerances than landhoppers, since it is invariably cooler under a forest canopy than on an open beach. Burrowing supralittoral species may be able to avoid high temperatures to some extent. Those beachfleas which do not burrow may have the highest thermal tolerances, but their acclimation abilities may be less well developed than those of landhoppers.

9.7 Sex Determination

Sex determining mechanisms may have had important effects on the evolution of landhoppers, through regulation and expression of secondary sexual characteristics. Among talitroidean amphipods, the young resemble females, and expression of male secondary sex characteristics occurs over several subadult moults (Bousfield, 1973; Geisler, 1944; Wildish, 1972). Experimentally induced sex inversions among amphipods and isopods (Ginsberger-Vogel and Charniaux-Cotton, 1982) have shown that:

- 1. each individual possesses genes for male and female morphogenesis
- 2. the development and activity of the androgenic gland is responsible for male morphogenesis
- 3. in the absence of an androgenic gland, female morphogenesis is realized.

Polygenic sex determination, in which genes occurring on other chromosomes affect the expression of sex, has been suggested as an explanation for the disturbance of normal sex ratios by environmental influences. Photoperiod and infection by microorganisms have been demonstrated to impose a sexual phenotype in animals of the opposite genetic sex. Long daylengths induce higher ratios of males in offspring of *Gammarus duebeni* and *Gammarus zaddachi*. The mechanism of this effect is thought to be the action of light on the differentiation of the androgenic glands via the neurosecretory cells (an epigenetic mechanism). The sensitive phase is the period in the juvenile corresponding to the differentiation of the androgenic gland (Ginsburger-Vogel and Charniaux-Cotton, 1982).

Female-biased sex ratios in some populations of *Gammarus duebeni* and *Orchestia gammarellae* were traced to infection by microsporidians transmitted in the egg cytoplasm (but see Wildsih, 1977; 1987 for a fuller discussion of biased sex ratios), which caused juveniles to develop as females regardless of genetic sex. For *Gammarus*, high salinity and low temperature inhibited microsporidian infections of the egg. In *Orchestia* high salinity and high temperature seemed to inhibit infection, or the feminizing effects thereof. Males often hatched from uninfected eggs, and infected males were intersexes. These results were not invariable, and events such as genetic males that were phenotypically female and produced all-male broods at high temperatures showed that the sex determination system is not fully understood (Bull, 1983). The effects of this microsporidian may explain the "feminized" males in samples of *Cerriorchestia*. If this species is subject to a similar suppression of male sexual characteristics as in the above example, then the males which lacked those characteristics may have come from eggs infected by just such a microsporidian.

Among amphipods, then, sex is determined by a complex of polygenic systems and environmental factors. Monosex progeny are common, individual sex conversion is possible and sex ratios are labile (often deviating from 1:1) (Ginsburger-Vogel and Charniaux-Cotton, 1982). The complexity of sex determination may have enhanced the tendency of landhoppers to lose sexual dimorphism, by providing numerous pathways through which this change may have become fixed in the genome of landhopper populations.

9.8 Evolutionary Mechanisms

The Britten-Davidson model of eukaryote gene regulation (Britten and Davidson, 1971) postulates a hierarchical regulatory system that controls the operation of batteries of genes. In this hypothesis, a sensor gene, upon receiving a stimulus (possibly hormonal), causes an integrator gene to produce a specific "activator RNA". The activator RNA is detected by receptor genes, which cause the structured gene(s) to transcribe and build the final protein product. This activity could be linear as described above, or there could be nested hierarchies of regulatory genes. A single integrator could cause an entire battery of structural genes to build proteins, or there could be a hierarchy of integrated gene battery sets controlled by a series of master sensors.

One of the major evolutionary consequences of the existence of a regulatory system in the genome is that changes may occur among both structural and regulatory genes. Mutations within genes, or chromosome structural aberrations could extensively repattern

genetic activity. Mutation at a sensor site could cause deactivation of an entire gene battery, or a switch to a new activator substance; in which case the sensor and its hierarchy would function in new biochemical circumstances. Mutation at an integrator site could cause deactivation or change in the composition of a battery. Mutation at a receptor site could change which structural genes are controlled by that site, and could cause it to become part of one or more new gene batteries. If mutations occurred to more than one type of regulatory gene, the resulting changes could involve large numbers of structural genes. The end result could be changes involving the groundplan of the organism (through developmental fields and changes in physiological and developmental responses to environmental stimuli), and hence large morphological distance between the ancestor and descendant (Valentine and Campbell, 1975).

An example of a gene battery effect in amphipods which could produce a major morphological change is the expression of male secondary sex characteristics. As noted in the previous section, sex determination in amphipods is apparently polygenic, and the expression of male morphogenesis is controlled by the androgenic gland. In a mutation of the proper sensor, integrator and/or receptor genes, the development of the androgenic gland could be affected such that the physiological/ hormonal output would not produce secondary sex characteristics in otherwise fully functional males. Since such an effect is easily imposed upon the genome by external factors (microsporidian infection, temperature, or light regime), a minor change within the hierarchical regulatory system could fix the effect genetically, and the population could lose sexual dimorphism.

The hypothesis of regulatory gene batteries opens great potential for the influence of environment on morphogenesis. Matsuda (1982) discussed the evolutionary process of talitrid amphipods (involving neoteny in changing environments), proposing that it consists of (1) environmental induction of structural changes as a result of altered activity of the preexisting endocrine mechanisms; and (2) natural selection, resulting in canalization of development and genetic assimilation of the modified (neotenuous) phenotype.

Balon (1983) discussed epigenetic mechanisms as an evolutionary process. He proposed that there are two sources of significant variation upon which selection acts: genetic variation and epigenesis. Epigenetic processes (the interactions among gene products, cells, tissues, organs and the environment in the formation of an organism) operate mainly in early ontogeny, and trigger a chain reaction of changes in induction, regulation and control of the formation of vital structures and functions. Ontogeny proceeds in a saltatory fashion;

changes in form and function are prepared at varying rates during longer intervals, but become operational at accelerated rates during brief intervals called thresholds. The earlier or later appearance of thresholds in early ontogeny causes changes in morphology, physiology, life history traits, reproductive styles, and ethology. These shifts will have developmental, adaptive or evolutionary consequences, depending on the selection forces in operation upon the population, and the environmental cues acting upon the development of the individual.

Balon (1983) categorized populations (or species) into generalists and specialists (not synonymous with *r* and *k* strategists, as in Pianka, 1978). Generalists often have a highly heterogeneous genome, the broadest epigenetic variation, an enhanced ability to survive in perturbed environments, early maturation and/or long reproductive interval, and delayed somatic differentiation. Specialization involves a process of "adulthood", in which age and size at maturation are delayed, brood size decreases, and life span is prolonged. The specialization results in a reduction in variation and epigenetic plasticity, such that environmental perturbations act more strongly upon the population. Under conditions of high environmental perturbation, the developmental thresholds can be canalized into paedomorphosis, which prevents extinction and creates a new evolutionary sequence along the paedomorphic trajectory, or affects a new morphological steady state of a higher taxonomic magnitude (Balon, 1983).

If stable conditions favour specialized traits, and perturbed conditions favour generalized traits, then perturbations could canalize epigenesis into repeated paedomorphosis. Such a cycle of minor changes in the amount of epigenetic and genetic variation could explain the strong tendency of talitrid amphipods toward loss of structures and juvenilization. The numerous instances of apparent neoteny in talitrid morphology have often been noted (Bousfield, 1982, 1983, 1984; Hurley, 1959, 1968; Matsuda, 1982).

If climatic variation produces drying of landhopper habitat, this might be sufficient environmental perturbation to force the genome into paedomorphosis. A specialized population adapted to stable conditions might then regain sufficient variation to persist in the changed environment. Natural selection would favour the slightly more generalized genome. In this way, the synanthropic landhopper taxa *Talitroides* and *Arcitalitrus* could have maintained the abilities of the generalist to thrive in habitats most other landhoppers could not tolerate, and colonize new areas readily. Many landhoppers show a blend of the characteristics of specialist and generalist. In talitrid amphipods, viable levels of variation may be maintained by such a cycle of paedomorphosis as described by Balon (1983), resulting in a strong

tendency to losses and reductions; specifically the loss of sexual dimorphism common to the taxa that colonize the fully terrestrial habitat.

9.9 Speciation

Three main modes of speciation in animals were reviewed by Bush (1975). He listed allopatric speciation as the most common mode, and listed two subdivisions, the vicariance type and the founder type. The vicariance type of allopatric speciation occurs when two relatively large populations are separated by a geographic barrier. Speciation results from cumulative adaptive changes at structural and regulatory genes. The founder type, or peripheral isolates (Wiley, 1981), occurs when a small population is isolated from the larger parent population by a geographic barrier. Speciation may include radical alterations in structural and regulatory genes, through genetic drift due to the small population size (although this is not necessarily the rule).

Parapatric speciation occurs when two populations of an ancestral species differentiate without a complete disjunction. This mode usually cannot be distinguished from allopatric speciation (Wiley, 1981). Sympatric speciation, in which new species are produced from ancestral species with no geographic segregation of populations, may result from minor changes in regulatory and structural genes.

Both types of allopatric speciation have probably occurred in terrestrial amphipods. In the New World, landhoppers flourish in wet forests caused by a combination of climatic and geographic factors. Climatic changes which cause the elevation of wet vegetation zones could produce "islands" of optimum habitat on higher elevations in a "sea" too arid for landhoppers to maintain viable populations. This would effectively isolate the major populations from one another. If this isolation persisted for a sufficiently long time, cumulative adaptive changes would cause divergence of the populations, and interbreeding could not be possible when climatic changes allowed expansion of territories. Peripheral demes may have been isolated in a similar way, allowing a small population (persisting in a refugium) to diverge genetically. Both types of allopatric speciation probably occurred among New World landhoppers, and is thought to have taken place in Tasmania, although the extremely restricted distributions of the Tasmanian species are thought to indicate that rafting was not an important process in their zoogeography (Friend, 1987). Some short-distance over-water dispersal may have taken place in the Caribbean (see Chapter 8).

Sympatric speciation may also have played a part in the zoogeography of landhoppers. Tamura and Koseki (1974) documented the apparent sympatric development of reproductively isolated populations of *Orchestia* [*Platorchestia*] *platensis japonica* through allochronic speciation. The breeding phases of the sub-populations occur at different times of year, with little overlap, and may be experiencing temporal reproductive isolation. If this temporal separation has reduced gene flow to a minimum, and sufficient time passes, the sub-populations may diverge until they are true species. It is possible that some mechanism may have produced a similar effect within populations of landhoppers. The likeliest mechanism to produce different growth and maturation rates is temperature, which would vary most between the dry season and the rainy season in lowland forests. If temperature effects caused divergence between, for example, the size and maturation rate of the earliest hatch and the latest hatch of the breeding season, sub-populations might develop which were out of phase with one another, as in the above example.

Chapter 10 LITERATURE CITED

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END

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FIN

8.3 Ancestral Forms

The superfamily Talitroidea may have originated in Gondwanaland (Bulycheva, 1957; Friend, 1980; Friend and Richardson, 1986). The ancestors of the New World palustral amphipods may have also originated in Gondwanaland. The ancestral form might have been similar to *Microrchestia* Bousfield 1984, a plesiomorphic palustral genus with representatives in the Old World (Gondwanaland regions) and South America (Bousfield, 1984). From southern South America, this ancestor may have spread north in estuaries and salt marshes, until the proximity of the northern tip of South America and the Cuban arc allowed it to cross into North America. The ancestral form may then have given rise to *Chelorchestia* (and possibly *Uhlorchestia*) in isolation from more primitive groups, when movement of the Cuban arc eastward isolated it by opening a large water barrier between North and South America. *Uhlorchestia* Bousfield 1984, is similar to *Chelorchestia*, but it possesses a greater number of plesiomorphic characters. Both genera are considered to be slightly more advanced in many characters than the Old World palustral genera (Bousfield and Heard, 1986).

Around the edges of the Gulf of México, a number of geologically old uplands experienced uplift and/or folding during the Laramide orogeny of the late Cretaceous and Paleocene (King, 1977). These include the highlands of Oaxaca, Chiapas, the Cordilleras Central of Guatemala and Honduras, and the Maya Mountains of Belize (Maldonado-Koerdell, 1964; Weyl, 1980). The Sierra Madre Oriental and Marathon systems also underwent uplift during this orogeny (King, 1977; Maldonado-Koerdell, 1964; West, 1964). Since most of the coastal lowlands of the Caribbean were not emergent until the mid-Tertiary, these highland areas may have provided moist forest regions in close contact with ocean shore, offering appropriate habitat for the proliferation of palustral amphipods into inland locations.

Invasion of land by a palustral ancestral form in the mid-Tertiary could have been aided by cool climate. Depressed temperatures occurred throughout the Oligocene period, with equatorial temperatures lower than the present (Graham and Jarzen, 1969; White, 1986; Wolfe, 1978). Cooler temperatures cause the lowering of altitudinal climate and vegetation zones (Brown, 1982; Graham, 1982; Haffer, 1981; Toledo, 1982). During the Oligocene, moist forest conditions would have occurred at lower altitudes than normal, and in lowland areas than would normally be too dry to support amphipod populations. This would allow expansion of range of newly terrestrial forms, and rapid divergence from their palustral ancestors (Figure 42, event A).