Amphipoda (Crustacea) from the Indo-Pacific Tropics: A Review[1]

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Introduction

The gammaridean Amphipoda are the dominant peracaridan group of crustaceans in most shallow seas, including the tropics. This discussion reviews the status of our knowledge of this group in Indo-Pacific tropical zones, especially on coral reefs.

Gammaridean Amphipoda are laterally compressed malacostracans lacking a carapace, bearing 7 pairs of thoracic legs and an abdomen carrying 3 pairs of pleopods, 3 pairs of uropods and a telson. The head bears 2 pairs of antennae, the first pair weakly biramous, or not, and a pair of maxillipeds. The first 2 pairs of thoracic legs, called gnathopods, have functional and morphological distinctions from the remaining 5 pairs of walking legs. Body length ranges between 1 and 300 mm but most tropical amphipods fall in the range of 1 to 8 mm, rarely as large as 12 mm.

Gammaridean Amphipoda are primarily freely motile, minute, shrimp-like crustaceans found nestling in anastomoses, hovering or swimming slightly above substrates, and inhabiting fixed or mobile abodes either self-constructed or borrowed from the environment. Many are commensals or inquilines found on invertebrate hosts. Their populations are especially dense in fleshy algae, less so in coral rubble or sedimentary substrates.

The taxonomy of Amphipoda has never been a subject of intensive study in the tropics. Because few specialists have resided in the tropics, most studies have been based on museum collections, on materials often poorly preserved, broken or sparsely represented. The short bibliography presented herein contains mainly recent papers within which are cited most of the early literature.

Collection of Material

Tropical amphipods are so small-bodied that their collection by means of ocular techniques is difficult or impossible. The most rewarding method of collec-

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[1] Paper presented at a Colloquium on "The need for faunistic information on Pacific coral reefs", International Symposium on Indo-Pacific Tropical Reef Biology, Guam and Palau, June 23–July 5, 1974.

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tion is the "formalin-wash" method: a bucket of seawater is laced with pure formaldehyde; substrate, composed of corals heads and algae, is added to the mixture. The dilute formaldehyde poisons the amphipods and forces most of them to leave their hiding places, swim a few seconds, die, and fall to the bottom of the bucket. The mass of substrate is shaken vigorously in the water and then discarded (preferably in deep water so as not to poison the environment). The debris and dead animals in the bottom of the bucket plus the water are strained through a very fine mesh (50–100 per inch), then preserved and labeled in a container of seawater mixed with 1 part of pure formaldehyde to 10 parts of seawater. After a few days of hardening in the solution, the amphipods can be sorted from the sample in freshwater and represerved in 70 percent alcohol. Cleaning of debris from the specimens with a fine brush is advisable. Rewashing of the amphipods in fresh alcohol in a few days helps in removing coagulated proteins which foul the surfaces of the specimens.

The massive wash technique can be concentrated intensively on a particular substrate, such as sea-urchin spines, surfaces of anemones, species of hydroids or coral heads so as to determine precisely the abode of various amphipods.

Sublittoral collections by scuba divers require careful and rapid removal of substrate to plastic bags securely tied to prevent escape of highly motile small crustaceans. This tedious and skilled procedure has rarely been perfected for any collections as yet reported in the literature and therefore sublittoral amphipods of the tropics are known only sketchily from chance collections obtained by diving or dredge.

Preservation of material should be completed in the field rapidly as deterioration of dead specimens in warm climates is swift.

Collectors of specimens requesting identification from a taxonomist should undertake preliminary identifications, sort the material into lots of individual species, submit the material in clean alcohol, place the specimens in small vials apart from paper labels (the labels erode and break the specimens), and should ensure that the purpose of their request for identification is germane. Submission of poorly preserved, broken and sparse materials from which little ecological information is obtainable, is a spurious procedure.

The identification of amphipods is fraught with difficulties owing to the widely scattered, often old and unavailable literature and the small size, and fragility of the specimens. A handbook for identification of genera (Barnard, 1969) requires high precision in analyses through careful and particulate dissection. Further identification to specific level is immensely difficult in tropical species because many species remain undescribed and many others have poor descriptions and a paucity of illustrations. Careful attention to the most minute of details is necessary to confirm an identification even to generic level. The paucity of specialists studying tropical amphipods is paramount.

Ecology

Most of our ecological knowledge about tropical amphipods rests on information concerning their sites of collection and inferences as to their activities and phylogeny based on analyses of their morphology. Tropical amphipods can be divided into 8 categories of habitat, the first 6 of which have a direct relation to gross activities connected with abode and feeding, and the last 3 (item 6 forming an overlap) of which have a stronger relationship to ionic balance than to feeding-abode positions. In a sense, the last 3 also have a positive relationship to low levels of biocompetition (the *Capitella capitata* syndrome).

1. Nestling. A slight majority of Indo-Pacific amphipods nestle in anastomoses, and crevices formed by algal interstices (e.g. *Sargassum* and *Caulerpa*) and pores of coral rubble or dead bases of fixed reef elements. These are the "ordinary" amphipods. Diverse genera include herbivorous and particulate-feeding *Hyale, Elasmopus, Maera*; genera with fewer species but numerous individuals include *Mallacoota* and *Parelasmopus.* Nestlers occupy so many habitats that occasional species are mistakenly labeled as commensals when they are simply coincidental associates.

2. Domicoly. About one third of Indo-Pacific tropical amphipods belongs to the tube-forming families, Corophiidae, Ampithoidae and Ischyroderidae. Domiciliary cylinders are spun from a web secreted by 2 pairs of thoracic legs (pairs 3–4) and attached to wave-protected substrates, either hard or soft. Soft substrates include algae, especially rhizomes, sea-grass and external surfaces of sessile invertebrates such as sponges and ascidians. The enhoused amphipods probably move freely outside their homes in search of detritus or reach outward for food with their antennae and anterior thoracic appendages. Many of these species have minor posterior morphological adaptations for grasping and withdrawing rapidly into their tubes. Dominant genera include *Lembos, Gammaropsis* (=*Eurystheus*), *Ampithoe, Cymadusa, Corophium* and *Grandidierella,* the former four genera occurring on coral reefs, the latter two in river mouths or muddy environments. Tube-building amphipods are known to form their tubes as linings in existing pores such as barnacle and mollusk burrows and are suspected of stealing empty tubes formed by domicolous polychaetes such as *Polydora.* Such bizarre genera as *Cerapus* cement sand grains together into a mosaic forming a truncate cone and live in this mobile tube in the fashion of hermit crabs. *Concholestes* occupies tiny scaphopod shells in the same manner. The diverse family Ampeliscidae, builder of tubes occurring on soft bottom sediments, is well known on the Asiatic coastal shelf but is almost uncollected in oceanic islands.

3. Inquilines. Parasitic and commensal amphipods are known or suspected in the families Acanthonotozomatidae, Amphilochidae, Anamixidae, Colomastigidae, Dexaminidae, Leucothoidae, Liljeborgiidae, Lysianassidae and Stenothoidae. Perhaps certain members of Podoceridae represent the first stage in this trophic sequence as they are often found in hydroid clumps and may crop the polyps carnivorously. Few true carnivores are found in the Amphipoda except in bathy-

pelagic zones. Inquilinous positions range from simple protective associations to associations in which the amphipod utilizes its piercingsucking or slime-lapping mouthparts to the disadvantage of the host. All of our tropical knowledge concerning these relationships is circumstantial, based on records of obligatory amphipod-host coupling and study of mouthparts. No information on precise food content of the amphipod or damage to the hosts is known in tropical seas. Most amphipod collections have come from massive environmental samples but we know for certain that: (a) *Leucothoe* inhabits ascidian branchial baskets and probably also lives in sponges, (b) *Anamixis* has a morphology similar to *Leucothoe* and bears a special piercing stylet near the mouth, (c) certain dexaminids such as *Polycheria* inhabit tests of tunicates but probably filter out detritus-diatoms after being safely ensconced in their burrows, (d) Amphilochidae (*Amphilochus, Gitanopsis*) occur mainly on coralline algae and on scleractinian corals of similar brown and red colors seen in the amphipod and may be slime-lappers; one species has recently been found commensal with hermit-crabs in east Africa, (e) Acanthonotozomatidae have strong piercing-sucking mouthparts and have occasionally been collected on large decapods, and, (f) many Liljeborgiidae (*Listriella*) are probably members of commensal teams composed of a burrowing polychaete (maldanid) and a crab (or other crustacean). An especially important unstudied but potential association might be a coupling to sipunculids, the vastly important group of reef-boring worms. Cyproidins (Amphilochidae) have their coxae modified as a shield to resemble the form of a compressed ostracod and these may occupy positions where they are tightly squeezed into spaces such as mantle cavities of mollusks.

4. Burrowers. Records of infaunal sediment burrowers from oceanic islands are almost non-existent, owing largely to the lack of dredge hauls on finer sands of lagoons and river mouths but also to the sparsity of sufficiently fine and compact sediments on reef-bound islands. Shelf-sediments of the Asiatic continent and large islands contain the ordinary complement of Phoxocephalidae, Haustoriidae and Oedicerotidae found in cool climates. One species of tropical *Chelura* burrows into wood, primarily as a successor to the isopod *Limnoria* which forms the main burrow and is followed by *Chelura* which slowly enlarges the galleries, perhaps simply as a rasping microbial feeder. Species of Eophliantidae form burrows in rhizomes of algae but appear to be rare or absent in tropical waters.

5. Neritics. The nekton of waters overlying coral reefs, lagoons and shelf sediments contains neritic amphipods, most of which are primarily benthonic but which enter the nekton at night or possibly during reproductive phases. These amphipods come mainly from non-phycophilic bottom habitats. Male amphipods, bearing enlarged eyes and powerful swimming adaptations, can often be attracted in dense swarms to night lights. One genus, *Synopia*, has ultramarine colored species but has rarely been collected in this century.

6. Strand. Beach wrack contains semi-terrestrial amphipods of the superfamily Talitroidea. Individuals congregate at the moist interface between sand and decaying vegetation and usually form galleries in the substrate. The great ability

to jump makes these amphipods difficult to collect. One good method of collection is to place a shallow pan of water laced with formaldehyde on the beach, then stir and disturb the habitat so as to set the hoppers into motion. Many animals will fall into the lethal trap of liquid, swim a few minutes and die. Talitroideans extend inland on atolls and high islands to altitudes of 3000 m, living in leafmold, mosses and aquatic environments. Inland species are usually distinct from those occupying the beaches, except on the smallest of insular fragments.

7. Estuarine. The smallest stream, if egressing into a muddy microestuary, may provide adequate dilution to support the *Melita*-habitat on tropical shores. Large to small estuaries are characterized by the nestler *Melita* and often may contain tube-builders such as *Corophium* and *Grandidierella*. Occasional species of *Corophium* dig their burrow-tube into the substrate whereas others attach the tube to hard substrates such as submerged logs or twigs. The numerous species of *Melita* may be found in drowned shore grasses, submerged coconuts and oyster beds.

8. Anchialine ("near-the-sea"). This environment, composed of pools near the sea, is recently named and is now being explored widely. In the Hawaiian Islands and Bonin Islands, unusual species of amphipods have been found in ponds containing brackish water, part of which percolates from the sea and which may be under tidal influences. One taxon in Hawaiian "lava-ponds", *Paramoera*, is a marine genus of cold-temperate provenance now apparently extinct on shores of subtropical islands but which is persistent and speciating in tidal pools within 100 m of shore. Inland pools are usually brackish or hypersaline and often interconnected through pores in the lava. Recent (post-Pleistocene) lava flows are most favorable to this development. The presence of blind and pigmentless amphipods suggests that part of the anchialine environment is hypogean. Certain pools actually are cave-like open ends of lava tubes. The phyletic structure of anchialine amphipods suggests that a wide spectrum of intergradation between anchialine, lacustrine, riparian and subterranean environments will be discovered. The anchialine environment is one of the first aquatic environments offered to marine amphipods invading non-marine habitats. On oceanic islands, inland amphipods have direct marine antecedents whereas on continents and large islands, like Madagascar, some of the subterranean amphipods have indirect marine origins, having left the seas so long ago that their direct origins lie in the endemic, highly speciated and massively distributed subterranean fauna of the world. Large tropical sea-lakes such as Chilka Laka support a diverse amphipodan fauna of marine origin containing non-marine or quasi-marine genera shared with Australia and New Zealand. A flavor of Gondwanaland is suggested in some of the known amphipod distributions.

Life History

Female amphipods lay eggs in a thoracic sternal brood pouch composed of setose lamellae. Males have tiny penial spouts on the sternal thorax which apparently are too small for copulation but simply exude sperm or spermatophores for fertilization of the eggs during natatory amplexus between the sexes. Eggs hatch as miniature adults and the first rapid ecdysis may often occur while the young are retained in the brood pouch for a few days.

Length of life in tropical amphipods is unknown. Several known cold-water amphipods live as long as a year or more, reproduce one to several times but usually have a long-term overwinter resting stage. Tropical amphipods presumably have a much shorter life span, reproduce year round but perhaps in modal peaks and presumably most species would reproduce several times before the onset of senility, as indicated by low numbers of eggs seen in ovigerous females. High mortality often occurs in the ecdysial process. Amphipods are prey to predators in most phyla.

Dispersal

Amphipods, lacking larvae, hatch their young as miniature adults in a brood pouch. Dispersal therefore is confined to adult (-like) stages. Amphipods inhabiting algae as their primary nestling site easily can be envisioned to journey long distances aboard viable algae entrained in trans-Pacific currents. The *Galathea Expedition* found such algae and ovigerous amphipods on the high seas 1500 miles from land east of the Philippine Islands. Long journeys would require reproduction of the amphipods en route. There appear to be one or more species or morphs of *Hyale* commonly occurring on such flotsam possibly as a more or less permanent and indiginous faunule maintaining gene flow from place to place through the tropical Pacific. Tube-builders can be envisioned as migratory inhabitants of large floating platforms such as tree trunks. Inquilinous associates of ascidians and sponges could also be transported in their hosts attached to rafting materials.

How benthic species inhabiting sediments and coral rubble are transported is a far more difficult situation to explain, and should be of primary interest as a research project.

Biogeographic Patterns

Gammaridean Amphipoda are apparently cold-adapted phyletically. They flourish more in cool and cold waters than in warm. The enlarged body size of cold-water amphipods, of course, makes them conspicuous but one must also evaluate the large number of species and genera in cold-waters. North boreal waters contain a known 240 genera[2] and 1400 species in contrast to a known 180 genera and 700 species in the Indo-Pacific tropical zone, 0–100 m. Tropical seas are admittedly much underexplored. Nevertheless, the broad outlines of generic diversity appear to have been delineated in the tropics and the picture suggests that

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[2] Based on counts of genera and northern species from personal list current to 1973; species from Indo-Pacific tropics based on count from Barnard (1965) plus recent papers by Barnard, Bousfield, Imbach, Ledoyer, Myers, Rabindranath, Rao and Sivaprakasam. Genera rounded off to nearest 10, species rounded off to nearest 100.

cold northern waters will prove to have a reasonably high number of genera compared with tropical waters. This situation contrasts sharply with the ordinary system in most marine animal groups in which the tropics harbor high densities of genera and species and usually contain the most primitive members. Evolutionary pathways in the ordinary group then spin outward from the tropics towards the poles in centripetal manner. In amphipods the situation appears reversed, with high densities of genera and species and many primitive members in north boreal waters, with evolutionary pathways directed centrifugally into the tropics and across the tropical frontier into southern coldwaters. In the south are found highly advanced taxa which have also contributed a centrifugal input to tropical faunas.

The heaviest concentration of genera and species in the primitive family Gammaridae is found in cold arctic, subarctic and boreal waters of the northern hemisphere. This group has widely invaded Palearctic and Nearctic freshwaters (500+ species). A limited number of genera of Gammaridae occurs in the tropics and a very small number occurs in antiboreal waters, suggesting that the north boreal region is the source of the major evolutionary events leading outward from the Gammaridae to the other 50 families in the suborder. There is no evidence that the north boreal evolutionary center is a functional relict of a vastly contracted distributional pattern.

The present distribution of freshwater amphipods suggests that a degree of control was exerted by events in the ultimate breakup of Panagea in middle to late Cretaceous and by glaciation in late Cenozoic.[3] A major barrier to outward dispersal or survival of Palearctic Gammaridae prevented their colonization south of the present-day Sonora-Sahara climatic frontier. A minor barrier prevented more than token survival of freshwater genera in the Nearctic. This may have been related to dispersal of the continents involved during the last days of Laurasia or may be related to extirpation of the fauna by glaciation in North America. Glaciation did not ultimately impede west European diversity perhaps because of repopulation of that area from a rich reservoir of species unaffected by glaciation in Asia. The presence of a congruent, modern, warm Tethyan faunule in both America and southern Europe suggests a persistence from Laurasian times although our understanding of dispersal mechanisms is poor in amphipods and there may be ways for freshwater amphipods to migrate across great sea barriers. If the Tethyan congruence proves to be a relict of late Laurasian times then the impoverishment of Nearctic boreal faunas is difficult to explain except in terms of glaciation. Western Nearctica is today populated with sparse immigrants directly from the sea (*Anisogammarus*) and much of the epigean eastern Nearctica is today populated with one dominant genus with marine affinities (*Gammarus*). The earliest fossil amphipod

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[3] The comments in this paragraph are entirely hypothetical and written so as to stimulate dialogue; there is no evidence that amphipods existed during panagenic times; the main evolutionary features of amphipods can be interwoven entirely within Cenozoic times, although the modern, warm, trans-Tethyan distribution of certain freshwater genera is difficult to explain except on a basis that they existed in Laurasian times. We know nothing about possible distinctions in suitability of biotopes between Eurasia and North America.

comes from the upper Eocene and is reasonably modern in appearance, suggesting that amphipods arose no later than the late Mesozoic.

That the Nearctic freshwater Gammaridae radiated primarily in the early Cenozoic after breakup of Panagea is suggested by their presence in regions formerly a part of Gondwanaland. Freshwater Gammaridae of Australia and southern Africa cannot be derived from direct marine ancestors on adjacent shores, though our knowledge on this point is very sketchy. South America lacks freshwater Gammaridae entirely except for sporadic anchialine invasions in the far south and, instead, its freshwaters, such as the Amazon and Lake Titicaca, contain many species of the highly advanced tropical Hyalellidae. East African rift lakes are apparently devoid of amphipods, a strange and unexplained situation perhaps related to great pliocene droughts. In Australia and New Zealand some of the niches apparently open to lacustrine-fluvial amphipods have been filled with members from other advanced families, directly immigrant from the sea.

Marine waters of the southern hemisphere appear to be dominated by families immediately descendent from Gammaridae. Although modern freshwater faunas adjacent to the ancient Tethyan Seaway show congruency, modern marine faunas do not, probably owing to faunal displacements from divergencies in marine climate. Few common denominators occur between the Mediterranean Sea and the Gulf of Mexico, though a stronger connection occurs between tropical west Africa and the Caribbean Sea. The warm-temperate of the northwestern Atlantic appears to be a recently developed and impoverished fauna containing east Pacific elements. Warm-temperate Australia and the Mediterranean have several common elements, with the direction of evolutionary flow moving from Australia outward.

Despite these assertions on the general biogeographic pattern in amphipods, there is no evidence to contradict the probability that the most primitive living members of 17 families today live in the marine tropics.[4] Very few of these families (3) are endemic to tropical waters but most of them are each typified by a primitive genus which today has its greatest diversity of species residing in tropical waters. Advanced genera occur in cooler waters towards either pole, suggesting a normal centripetal evolutionary pattern. Many of the remaining 33 families are poorly represented in tropical waters, though most of them occur in both northern and southern hemispheres suggesting that evolutionarily they pass easily through the tropical frontier but are basically cold-adapted and survive poorly in warm waters. Passage through the tropical frontier is difficult to explain, though it is presumed that periods of heavy cool-water upwelling along the eastern margins of oceans

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[4] List of families with their hypothetically most primitive living genera dominant in the tropics, asterisks denoting families endemic to tropics: Amphilochidae, Ampithoidae, *Anamixidae, *Bateidae, Colomastigidae, Corophiidae (*Gammaropsis* most primitive?), Hyalellidae, Hyalidae, Ischyroceridae, *Kuriidae, Leucothoidae, Liljeborgiidae, Ochlesidae, Phliantidae, Podoceridae, Stenothoidae, Talitridae. Unknown families: Ampeliscidae, Cheluridae, Lafystiidae, Laphystiopsidae, Lysianassidae, Phoxocephalidae, Sebidae. All other families dominantly cool-water. The most primitive phyletic line in Gammaridae is debatable, but possibly is found in the tropically dominant *Melita*-group.

might provide the environmental pathway. Tropical submergence is a poor explanation for transgression through the tropics, because most shallow-water amphipods are heavily dependent on their vision. Descent to cool deep waters of the tropics during a long term evolutionary migration across the tropics appears impossible because amphipods generally lose their eyes as an adaptation to lightless depths and presumably could not regain such eyes once across the barrier and again emergent in shallow water. Almost all benthic amphipods endemic to bathyal and abyssal depths are blind. None of these taxa can be shown to be ancestral to any shallow water gammarideans, thus suggesting that once blind, these taxa forever produce blind descendents. Very few blind species of amphipods occur in shallow seas and most of these appear either to occur in peripheral environments where they are invading hypogean environments or to be emergent from hypogean environments into very specialized peripheral marine habitats.

Many amphipods have a wide range in the Indo-Pacific, from Hawaii to Madagascar. Many others, however, appear to have limited distributions generally divisible into continental and oceanic. The highly isolated Hawaiian chain contains numerous endemic species, sufficient to qualify the archipelago as a biogeographic province. Hawaiian amphipods are a very unusual marine order in that almost 20 percent of the species have origins in cold-temperate waters. No sibling flocks of species have evolved within that archipelago (eastern section only), apparently owing to the contiguity of the islands, but false sibling flocks have evolved from recurrent invasion by a common ancestor. No more than 3 species occur in each of the false sibling flocks apparently owing to the relative youth of the archipelago.

Micronesia and Polynesia contain several unusual endemic genera and species (Schellenberg 1938, Barnard 1965, Croker 1971) but extended explorations in the heart of the Indo-Pacific are necessary to verify these as endemic to the oceanic fauna.

Evidence of generally recent or progressively active evolution is suggested by the presence in high densities of sympatric sibling flocks of species, and cognate genera of very close affinity. The best marine example of this in amphipods occurs in southern Australia where at least 4 families, Dexaminidae, Phoxocephalidae, Amphilochidae, and Leucothoidae and part of a fifth family, Gammaridae have extremely high densities of species in various genera or sections of genera. Many factors may permit survival of these dense species-flocks but obviously their production occurred from a balance of genetic change and natural selection within a series of events in the environment that provided disruption, temporary isolation and rejoining of congruous habitats. We know little about generalities of evolutionary life in amphipods. We are unable to determine whether in southern Australia we are now observing the results of several recent environmental revolutions, and a highly packed series of habitats in which natural selection through competetion will rapidly deplete species recently thrust together, or whether the environment is so especially rich in niches that a series of closely similar species, evolved long ago, can survive indefinitely in close proximity. A similar high density of a few generic flocks is also seen in the Sea of Okhotsk and one generic flock occurs in New England in a region impoverished of other fully marine amphipods. These flocks are notable because they stand out so strongly from the general faunistic background in their respective provinces.

In the tropics of the Indo-Pacific species-flocks may occur in dominant genera such as *Hyale, Maera, Melita, Gammaropsis, Lembos,* and *Grandidierella* but no special studies have been undertaken on this subject and few localities have been explored intensively. The largest known number of species in one system is the 14 species of *Maera* known on the coasts of India; most of these are widespread throughout the Indo-Pacific; several appear to be closely related to each other but a recent study on Mexican sibling species of *Elasmopus*, a genus similar to *Maera*, suggests that the morphological distinctions between species in a flock of *Maera* species would be much less than now known among the species of India. Flocks of species in the widely distributed river-mouth genus *Melita* are primarily allopatric. Many species of *Gammaropsis* appear to be closely related to one another but our knowledge of their sympatry is poor. There is an apparent flock of morphs in the genus *Mallacoota* centered in the Philippine-Indonesia sector but it has not been clarified. Hence, the tropics, so far, present a picture of diffusion.

At species level the centripetal dispersal of tropical amphipods is best seen within the fragments of warm-temperate environment found on most continental coasts. These regions usually contain one or two species each of several genera such as *Maera* and *Elasmopus* which have apparent tropical ancestors, but the boreal boundary is much more stringent, suggesting that once adapted to warm waters, reentry and readaptation to cold waters is sufficiently difficult and of such long-term basis that linkage species have long ago become extinct.

The general sparseness of amphipods in tropical regions may also have an explanation in biotic factors: that amphipods are constrained in their evolutionary success because of their low competitive level against other orders of marine organisms, either predators or organisms sharing similar resources.

Future Studies

A vast taxonomic effort is required to delineate tropical Indo-Pacific amphipods, now numbering 700 species but which may exceed twice that number. Much revisionary work is needed to clarify known species by improving descriptions and illustrations and by making careful interregional comparisons of material. Hopefully much of this work can be accomplished by taxonomists resident in the tropics. The advantages of this residence lie in the opportunity to study fresh materials day by day, to sort out color-pattern phenotypes, to catch and identify juveniles, to make careful ecological observations so as to suggest important avenues of research in functional morphology and to stimulate the interest of colleagues who often bring the taxonomist crucial materials overlooked in the press of analyzing massive samples.

Careful study of phenotypy in individual species collected from diverse and disjunct localities is required to understand the expression of clines, routes of immigration, founder effects, presence of cryptosibling species, possible occurrence of ecotypes within inquilinous species and the roles of diversity and competition affecting morphology of a species.

Keys and handbooks for the identification of tropical species, both phyletic and faunistic, should stimulate functional studies by facilitating the tedious identification procedures and ensuring accurate identification, crucial to the successful replication of experimental models.

The study of inquilinous species should be fully as rewarding as have been those famous studies on commensal shrimp but an order of magnitude of smaller amplitude will increase the difficulties of observation.

High numbers of sympatric species within several genera offer superb material for study of niche-functions and evolutionary elaboration. Many amphipods should be readily culturable in the laboratory for discovery of information on life histories, food preferences and behavior. Turnover of populations is probably of short-term in many species, thus affording valuable material for genetical studies.

The ultimate topic of interest is the general theory of evolution in the Amphipoda so as to determine whether the tropics are primarily an ultimate repository of the most highly advanced and specialized taxa or whether the north boreal region might contain the principal evolutionary center of the group. The evolutionary filter effect that may have occurred during transgressions of the tropical frontier from one hemisphere to another may also be explorable in tropical faunas. Students of this persuasion will be highly interested in tracing ancestral lines and determining patterns of dispersal while attempting to establish alternatives of primitive and specialized morphology and function.

Intensive Taxonomic Effort

To complete an intensive taxonomic elaboration of tropical Amphipoda in this century will require no less than the organization of at least one team of several experts and their assistants who can migrate during 3 decades through 10–20 biotic provinces. The team would collect, process, describe and compare materials from important faunistic subdivisions. The team should be so organized as to: permit revolving membership of experts in subspecialties, to avoid ennui, to prevent monopoly of viewpoint, and to present a reasonably uniform series of published results (format).

Support for such a team should come from an International Taxonomic Center, an institutional idea long overdue. The plethora of information in taxonomy has reached such confounding proportions in many biotic groups that chaos is imminent. Nomenclatural citations and biogeographic data are so numerous and bulky that mechanical memory devices and computational systems are necessities to specialists embracing biotic groups containing 1000 or more species. Without such aids specialists will be forced to confine themselves to increasingly narrower disciplines that may hinder the wide perspective needed by the evolutionist. A taxonomic center could provide daily updated information from its memory bank so that any scientist could be appraised of the current status on the information pool for any taxonomic group.

Without such tools, without such organized effort among taxonomists, and without funds, the elucidation of alpha-taxonomy in amphipods is going to be a slow and tedious process, grinding forward in fits and starts, fraught with numerous nomenclatural and systematic errors and inconsistent efforts for many decades if not centuries. Until alpha-taxonomists have completed the major share of their duties, other biologists who follow in their footsteps will also be approaching their studies with inadequate and inconsistent background information as to phyletic and faunistic conditions in various biotopes.

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