CAVE-DWELLING DECAPOD CRUSTACEANS OF AUSTRALIA AND PAPUA NEW GUINEA

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Abstract

Three families of decapod crustaceans are represented in the cave faunas of Australia and Papua New Guinea. One family, the Sundathelphusidae, occurs in caves in both countries while the remaining two families are recorded from the Australian cave fauna. The distribution of the families in the region is compared with the distribution of karst areas. The Australian cave decapod fauna is compared with the much better documented American cave fauna. Some hypotheses are advanced to explain the evolution of this element of the Australian cave fauna.

INTRODUCTION

The Order Decapoda includes the large commonly known crustaceans such as prawns, lobsters, crayfish and crabs. It is the largest order of crustaceans with well over eight thousand species (Chace, 1951). The group is mainly marine in habitat but several families are restricted to freshwater and a few others have some species which pass through their entire life cycle in freshwater. It is these freshwater groups which are of the greatest interest from the biospeleological point of view as they include by far the greatest proportion of decapods found in caves. Marine decapods are rarely found in caves (Holthuis, 1956; Vandel, 1965). Land crabs of the Family Gecarcinidae have been found in some caves in the West Indies (Peck, 1975; Hobbs, Hobbs & Daniel, 1977). Freshwater decapods found in caves include shrimps, prawns, crayfish and crabs.

Representatives of fifteen families of decapods have been found in caves containing freshwater (Table 1). They have been found on all continents (except Antarctica) and a number of islands including Cuba and New Guinea. They cover the entire spectrum of adaptation to the spelean environment from accidental occurrences to troglobites. Of the fifteen families, four have representatives which pass their entire life cycle in the freshwaters of Australia and Papua New Guinea. They are the Palaemonidae, Atyidae, Parastacidae, and Sundathelphusidae. Of these families, the last three have been found in Australian caves while the Sundathelphusidae is the only family so far known to occur in caves in Papua New Guinea.

CAVERNICOLOUS DECAPODS OF AUSTRALIA AND PAPUA NEW GUINEA

Order Decapoda

Suborder Pleocyemata

Infraorder Caridea

Family Atyidae

This family has over one hundred species and is very widely distributed (Kaestner, 1970). It includes at least twenty-six troglobites (Williams, 1964;

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Table l

Decapod families with	freshwater*	cave-dwelling members
FAMILY		DISTRIBUTION
Atyidae 7	shrimps	FW only
Alpheidae	and	FW + marine
Palaemonidae	prawns	FW + marine
Cambaridae]		FW only
Astacidae	crayfish	FW only
Parastacidae		FW only
Aeglidae	"crabs"	FW only
Pseudothelphusidae		FW only
Potamocarcinidae		FW only
Potamonautidae		FW only
Gecarcinucidae		FW only
Potamidae	crabs	FW only
Parathelphusidae		FW only
Sundathelphusidae		FW only
Grapsidae		FW + marine
<pre>*"freshwater" as used here includes slightly brackish and semiterrestrial habitats.</pre>		

Monod, 1975). This high proportion of troglobitic species is regarded as a sign of the great age of the family (Carpenter, 1977). In Australia, the family is represented by six genera and about fifteen species (Riek, 1953; Bishop, 1967; Williams, 1977). These species range in distribution from North West Cape in Western Australia to Tasmania. Most species are found in the eastern states. Species from four genera have been collected from Australian caves while a fifth genus may have one subterranean species. Atyids are commonly referred to as shrimps.

Atya. This genus is very widely distributed and has one species in Australia. Atya striolata occurs in coastal streams from southern Queensland to southern New South Wales. It has been recorded as a "facultative troglobe" from Gloucester Caves in New South Wales (Bishop, 1967). This classification implies that this species is a first level troglophile in the system of Hamilton-Smith (1967). Other species of Atya have been found in caves overseas (Peck, 1975).

Caridina. This is another widely distributed genus, with several species reported from caves in other countries (Holthuis, 1956). There are seven Australian species ranging from the vicinity of Darwin down to south-eastern New South Wales (Bishop, 1967). Caridina thermophila is known only from the waters of a bore drain near Muttaburra in central Queensland (Riek, 1953). Although the species exhibits no morphological adaptations to the subterranean environment, it is possible that it occurs in artesian waters (Williams, 1964).

Paratya. The genus is found in the eastern Pacific area from Siberia to New Zealand (Carpenter, 1977). There appears to be only one Australian species but it exhibits some morphological variability (Williams, 1977). Paratya australiensis occurs in the eastern coastal regions of Queensland, southeastern Australia and Tasmania. Its occurrence in caves is restricted to a small area in Victoria. It is recorded from Moon Cave, Buchan and Cave M-35, Murrindal (Hamilton-Smith, 1967). The New Zealand species P. curvirostris has also been found in caves (Williams, 1964). It seems probable that both species are first level troglophiles.

Parisia. This genus demonstrates a remarkable disjunct distribution with one species in Zanzibar, three in Madagascar and two in Australia (Holthuis, 1956; Williams, 1964; Gordon & Monod, 1968). All six species are troglobites, and all are known from a single type locality. The two Australian species are Parisia unguis and P. gracilis. The only recorded locality for both species is Brennon's Brook in Sixteen Mile Cave near Katherine in the Northern Territory (Williams. 1964). Erennon's Brook is about ninety metres below the surface and only eight metres of the brook is accessible. In both species, the eyes are reduced and lacking in pigment (Williams, 1964).

Stygiocaris. This is the only atyid genus known to occur in Western Australia, and it is endemic to that state (Bishop, 1967). There are two species -Stygiocaris lancifera and S. stylifera. They are known only from the slightly brackish waters found below the coastal limestone platform of North West Cape (Holthuis, 1960). Both species are recorded from the western side of the peninsula in various wells and waterholes on Yardie Creek station (Holthuis, 1960; Mees, 1962). In addition, Stygiocaris stylifera has been found in Kubura Well on the eastern coastal platform (Cawthorn, 1963). Neither of the two species has been found in the caves of the intervening Cape Range which is generally lacking in water (Cawthorn, 1963). Both species are classified as troglobites. They possess strongly reduced, unpigmented eyes. These species are closely related to Typhlopatsa pauliani which is known only from Mitoho Cave in Madagascar (Holthuis, 1956, 1960).

Infraorder Astacidae

Family Parastacidae

The Parastacidae are the southern hemisphere crayfish. There are some one hundred and twenty species (Hobbs, 1974a). They are found in South America, Madagascar, New Guinea, New Zealand and Australia (Riek, 1969). Of the fourteen genera, only *Cherax* is shared between two of these areas. It is found in Australia and New Guinea. This high degree of endemicity is regarded as a sign of the antiquity of the family despite the lack of pre-Pleistocene fossil material (Hobbs, 1974a; Carpenter, 1977). The family reaches its greatest diversity in Australia which contains about eighty percent of the currently recognised species (Hobbs, 1974a). Species are found in all Australian states although the majority occur in the eastern states. The family is poorly represented in the western half of the continent with the exception of the south-western corner where there are eleven species, all of which are endemic to that area (Riek, 1967).

The only recorded cave localities for this family are in Australia. They have been recorded from caves in both eastern Australia and the south-western corner (Hamilton-Smith, 1967). There is, at present, no published information on the biology of the species inhabiting the eastern caves. They are regarded as accidental occurrences only (Hamilton-Smith, 1967). *Euastacus spinosus* has been observed on several occasions in River Cave in the Windy Gap area near Kempsey during

field work by G.D. Campbell. This species shows no obvious adaptation to the cave habitat. The crayfish found in Western Australian caves have received more attention but again, there is very little in the way of published work. The crayfish found in these caves are of the genus *Cherax* (Hamilton-Smith, 1967). Research by Muir has indicated that the cave populations are isolated and they have achieved some degree of physiological adaptation to the subterranean environment (Hamilton-Smith, 1967). These animals are regarded as first level troglophiles and are presumably conspecific with the surface forms in the area. Certainly, there is a large amount of work yet to be done on the crayfish in Australian caves.

Infraorder Brachyura

Family Sundathelphusidae

As defined by Bott (1969), this family consists of some thirty-seven species which range from Sri Lanka to Fiji (Bott, 1970, 1974). The family does not occur on the Asian mainland. The fifteen species recognised by Bott from Australia and New Guinea are placed in three genera - *Rouxana*, *Geelvinkia* and *Holthuişana*. The first two genera are endemic to New Guinea while *Holthuişana* is found in Australia and Fiji as well. Although these crabs are commonly referred to as freshwater animals, many of the species are semiterrestrial in their habits (Bott, 1972; Greenaway & MacMillen, 1978). The records listed below are the first for crabs of this family from caves. The only other crab known to pass its life cycle in freshwater in either of the two countries is the crab *Halicarcinus lacustris* from the largely marine family Hymenosomatidae. It occurs in south-eastern Australia, Lord Howe Island, Norfolk Island and New Zealand but has not been recorded from caves (Walker, 1969).

Holthuisana. This genus has been divided into two subgenera by Bott (1969). The subgenus Holthuisana is restricted to New Guinea while Austrothelphusa is said to occur in Australia and Fiji (Bott, 1970). An analysis of specimens, both in the field and in museums, has indicated that Bishop (1963) has more accurately analysed the taxonomy of the Australian species than has Bott. Thus, it appears that there are six or seven species. Further specimens are required from Cape York to clarify the situation. In Australia, most of the species are restricted to Cape York but one species does not occur there. Holthuisana transversa is widely distributed on the continent being found in all mainland states with the exception of Victoria. There is no overlap with Halicarcinus lacustris. Four specimens of H. transversa have been collected from Niggle Cave near Camooweal in north-west Queensland. These specimens are held in the Queensland Museum - specimen no. 3179. The animals were collected from burrows near the permanent lakes within the cave. The burrows were in mud with the entrances built up above the surface of the mud. This is the characteristic burrow entrance found in the surface-dwelling specimens of H. transversa. In this species, the young hatch from eggs as small crabs which are retained by the female for some time in the pouch formed by the abdomen and pleopods beneath the thoracic sternites. The female collected from Niggle Cave was found to have young in this pouch. There is no information available on the distribution of this species within the cave. The specimens exhibit no morphological differences from epigean examples of this species. H. transversa can therefore be considered to be a first level troglophile.

Genus unknown. The biologists on the 1978 expedition to the Atea Kananda region of the Muller Ranges in Papua New Guinea collected several crabs of a species which is referable to the family Sundathelphusidae. However, the

species cannot be placed in any of the currently recognised genera of the family. Work is currently being carried out to describe this species in relation to those already described by Bott (1974) from New Guinea. The crabs were observed in several areas within the extensive Atea Kananda system including regions at some considerable distance from the surface. They were found both in and out of water. Some specimens were found on the surface near the entrance to the cave suggesting that the animal may be distributed in surface waters also. The crabs were also collected from a cave in the nearby Mamo area. The specimens display considerable morphological adaptation to the subterranean environment in comparison to the Australian species, H. transversa. There is a considerable elongation of the walking legs relative to the carapace width. There is also a reduction of the pigmented area of the eyes. In some specimens, there also seems to be a shortening of the eyestalks. On the basis of these observations, it seems that the species should be classified as a first level troglophile although it seems likely that those specimens at some distance from the entrance may constitute physiologically distinct populations.

OTHER RECORDS

The above records for cave dwelling decapods include those reports and specimens which could be placed in a particular family. Quite often, lists of cave fauna are published giving only the common names of the animals concerned. This creates difficulties when it comes to a consideration of cave biogeography as it is impossible to distinguish most species of decapods on the basis of their common names. Indeed, in some cases, it is impossible to determine whether or not they are decapods. So, records of this type have been listed separately.

<u>Freshwater crabs</u>. The British New Guinea Speleological Expedition of 1975 collected or observed freshwater crabs in a number of caves in the vicinity of Telefomin in New Guinea (Chapman, 1976). Beck & Goulbourne (1976) were astonished to find that the only usable ledge in the shaft of Tina Bu Tem cave 'was infested with crabs'. The crab was also found at one locality on the surface (Chapman, 1976). These crabs have not as yet been examined at any taxonomic level. Attempts are being made at present to borrow the specimens. It seems likely that the crabs are first level troglophiles.

<u>Cave "shrimps</u>". The term shrimp is used for a great variety of crustaceans including amphipods, isopods, some decapods and a number of smaller groups as, for example, the mountain shrimps or syncarids which are found in some Tasmanian caves (Lake & Coleman, 1977). As a result, reports of cave shrimps from the Chillagoe area are recorded here as decapods with a considerable degree of reservation. Colourless cave shrimps have been reported from caves in the Chillagoe region on several occasions (Wilson, 1974; Parr, 1975; Robinson, 1975). They have been found in Christmas Pot (CH-144) in Suicide Bluff and Narahdarn Cave (CH-34) in Carpentaria Bluff (Robinson, 1975). It is of some interest to note that these are two of the three caves known to descend into the phreatic zone in this area (Wilson, 1975). The other cave is Ti-tree Cave (CH-43, CH-101).

<u>Colourless prawns</u>. Williams (1964) recorded an unconfirmed report of colourless prawns from deep gold mines in the Maryborough area of Victoria which are no longer being worked. No further information has been published on these animals. Other decapods have been recorded from abandoned mines overseas (Horst, 1972).

DISCUSSION

Any consideration of the freshwater decapod fauna found in caves in Australia and Papua New Guinea is plagued with difficulties. It is not simply that the cave fauna has not been examined in any great depth, but the surface fauna, particularly in Papua New Guinea, is so poorly known that is is difficult to make generalisations or comparisons. However, some points can be made, at least with regard to the Australian forms.

With the exceptions of *Stygiocaris* and *Parisia*, all of the forms currently found in caves occur on the surface in the same region. As a result, those karst areas where surface decapods are absent rarely contain subterranean decapods. The most obvious example of this situation is found in the Nullarbor which, despite the large amounts of water present in the caves, has not yielded any subterranean decapods. This does not imply that there will be subterranean decapods in all those karst areas where decapods are found on the surface. This is patently not true. Species which are found only in one or two caves in a single karst area are often found on the surface in several. The vast majority of surface forms do not occur in caves at all. This is most obvious in the crayfish. This is quite different from the situation in North America.

The surface freshwater decapod faunas of Australia and North America are remarkably similar. They are both dominated, in terms of species numbers, by crayfish with relatively small proportions of atyids and palaemonids. Australia has the added bonus of several species of freshwater crabs. In the other three continents with well developed freshwater faunas, the decapod fauna tends to be dominated by the freshwater crabs. Despite the similarities in the general composition of the two faunas, there is a considerable difference in the proportion of troglobitic decapods found in the two countries. As well as two atyids, there are three palaemonids and at least twenty-one crayfish occurring as troglobites in North America (Strenth, 1976; Hobbs et al., 1977). This represents slightly more than ten percent of the total freshwater decapod fauna. The number of other decapods associated with caves is not known (Hobbs et al., 1977). The palaemonid genus Palaemonetes has six species in North America and a further three in Mexico (Strenth, 1976). Three of the North American species are troglobitic. The only Australian species of Palaemonetes occurs in the south-west of Western Australia. As there is only one Australian species, a comparison of the two areas is difficult. Some comparison can, however, be made for the crayfish.

The North American crayfish are placed in the families Cambaridae and Astacidae (Hobbs, 1974b). The American cambarids are further divided into two subfamilies - Cambarinae and Cambarellinae. All of the cavernicolous crayfish in North America belong to the Cambarinae (Hobbs et al., 1977). As well as the twenty-one troglobites, there are twenty-three other species known from caves. This represents some twenty percent of the total number of crayfish species in North America. With the exception of Troglocambarus maclanei, the cavernicolous forms belong to the three largest genera in this subfamily (Hobbs, 1974b). It is interesting to note that Cherax and Euastacus are the two largest genera of Australian crayfish (Riek, 1969). The evolution of the North American cavernicolous crayfish has been complex (Hobbs et al., 1977). In each of the three large genera, there have been several invasions of the cave habitat with the possibility of some adaptive radiation once These incursions have been separated both temporally and spatially. there. Herein lies the major difference between the American and the Australian

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crayfish. The Australian crayfish have not had, or have not taken, the opportunity to enter the spelean environment until relatively recently. On the basis of the available data, it is impossible to determine which of these options is more likely.

The atyids of mainland North America show a distribution pattern which is similar to that of the Australian atyids. Of the five species known from North America, the two species of *Palaemonias* are troglobites while the three species of *Syncaris* are epigean forms (Pennak, 1953; Hobbs et al., 1977). *P. ganteri* is known only from within the Mammoth-Flint Ridge cave system in Kentucky while *P. alabamae* has been found in two caves in Madison County, Alabama (Hobbs et al., 1977). The species of *Syncaris* were described from the San Francisco-Los Angeles area but it seens that only one of these Californian species is currently extant (Pennak, 1953). The subterranean forms are thought to have evolved from a common epigean ancestor which was not necessarily closely related to *Syncaris*. They now represent relict populations as do *Stygiocaris* and *Parisia*.

The relict nature of Stygiocaris and Parisia has been questioned by Mees (1962) and Bishop (1967). Mees suggests that the relationship between Stygiocaris and Typhlopatsa is a morphological similarity rather than a true evolutionary kinship. He further suggests that the two species have arisen from distinct marine ancestors. These suggestions are made without 'even the slightest knowledge of shrimps' (Mees, 1962). More recently, the family has been divided into a number of "series" including one composed entirely of troglobitic forms, although not including all troglobitic atyids (Monod, 1975). This group - "la serie typhlatyienne" - includes both Stygiocaris and Typhlopatsa (but not Parisia) and is considered to be a monophyletic group derived from a marine ancestor possibly during the Cretaceous (Monod, This would seem to be a much more economical hypothesis than one 1975). which would require a number of fairly recent marine ancestors which have subsequently disappeared without trace, leaving a group of freshwater forms showing a great deal of convergence. Bishop (1967) states that the Stygiocaris-Typhlopatsa relationship and the disjunct distribution of Parisia 'may not have great zoogeographical significance in view of the close relationship of Parisia and Caridina'. As neither Parisia nor Caridina is closely related to Stygiocaris or Typhlopatsa, the connection here is somewhat obscure. In addition, Holthuis (1956) considers that Parisia is more closely related to Caridella although it strongly resembles Caridina while Williams (1964) states that 'the generic similarities between the species described here and the previously described species of Parisia appear strong'. Thus, the available evidence supports the idea that both genera are relicts which are not associated with the remainder of the Australian atyid fauna or with each other. The relict nature of the two genera is a partial explanation of their origins as troglobites.

If it is accepted that both genera are relicts, it seems likely that the ancestors of both previously occupied larger areas of Australia as epigean forms. With the progressive increase in the aridity of the continent during the Pleistocene, the available habitat decreased and the animals retreated to cave systems. In the case of the Australian species of *Parisia*, there is no available evidence of the selection pressures which may have lead to the development of the two species. It is probable that Brennon's Brook forms part of a much larger freshwater system and the explanation may lie there. The ancestral form of *Stygiocaris* was presumably restricted to the North West Cape region. With changes in sea level during alternating periods of

glaciation and thawing, it is likely that the range of the species varied in this area. It may have been that, during a period of low sea level, two populations were formed, one on either side of the Cape Range. These populations changed gradually in isolation resulting in the development of specific differences. A later rise in sea level resulted in the reunion of the two habitats but the movement of only one species. The next decrease in sea level gave the present situation with one species separated into two populations, one on either side of the peninsula and the other species found only on one side. The two populations of *S. stylifera* have been separated for some time and are now showing some morphological differences although these are not sufficient to require the construction of separate taxa (Cawthorn, 1963).

The study of the Australian cave decapod fauna is still in its formative stages. There is still a great deal to be learnt. At this stage, it is important to gather basic information such as the distribution of decapods in caves and their relation to the surface.

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