

Stygofauna from Cape Range peninsula, Western Australia: Tethyan relicts

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Abstract

The biology and distributions of the stygofauna from Cape Range peninsula are reviewed. This stygofauna comprises seven elements: two species of teleost fish, the blind gudgeon *Milyeringa veritas* Whitley, 1945 (Perciformes: Eleotrididae), and the blind cave eel *Ophisternon candidum* (Mees, 1962) (Synbranchiformes: Synbranchidae); and five species of malacostracan crustacean, *Stygiocaris lancifera* Holthuis, 1960 and *Stygiocaris stylifera* Holthuis, 1960 (Decapoda: Atyidae), *Halosbaena tulki* Poore and Humphreys, 1992 (Thermosbaenacea), and two undescribed species of Amphipoda. All seven elements are macrofaunal and exhibit troglobitic morphology. Meiofaunal elements (protists, turbellarians, nematodes, oligochaetes, copepods, and acarines) are cited. The gastropod *Iravadia* sp. is recognized as possibly a marine stygophile.

The seven species are known only from the limited fresh groundwaters of the area. The atyids, thermosbaenacean, one amphipod and both species of fish are widespread in subterranean fans of freshwater about stream courses of the coastal plains; in marked discontinuity, the eriopisid amphipod from pools in four caves on Cape Range occurs at elevations of 110 m or higher above sea level. These cave pools are probably perched. Possible evolutionary, ecological and physical causes for the discontinuity in distribution between the coastal and Range species are discussed.

Antecedents of all elements of the Cape Range stygofauna are regarded to have evolved in the Tethys Sea, and invasion into groundwaters of the peninsula is considered to have occurred *in situ* throughout the whole sedimentary basin wherein the peninsula developed. Two phases of invasion are proposed: the first concomitant with initiation in uplift of the Cape Range anticline involved the thermosbaenacean and eriopisid Range dwelling amphipod from marine ancestors; the second phase at a much later time involving the two species of fish and atyids from fresh waters of the Ashburton River, then much closer to Cape Range than it is now.

Introduction

In Western Australia, there are 21 cave areas in four regions (Matthews 1985): Kimberley; Nullarbor Plain; between Eneabba and Augusta; and on Cape Range peninsula. The present contribution to the Symposium reviews information on the stygofauna from Cape Range peninsula (Figure 1). The stygofauna from this peninsula inhabits a freshwater oasis beneath an arid land surface, part of the Ashburton district of the Eremaean floristic province of desert adapted plants (Burbidge 1960), and is bounded by marine waters on all sides except to the south where it is confluent with hypersaline ground waters. The present contribution also speculates on the zoogeographic origins of the fauna.

The world stygofauna is of considerable zoological interest (Botosaneanu 1986), yielding important information bearing on wider issues concerning the evolution of life on earth. Indeed, the stygofauna of a particular region may comprise phylogenetic and zoogeographic relicts (thereby giving valuable insights into systematics of the relevant taxa) possibly co-occurring with surface forms undergoing incipient speciation whilst in the process of adapting to the stygal biotopes. Furthermore, the stygofauna within a particular region may also

comprise elements from more than one phase of invasion. Noted biospeleologist A. Vandel (1965) considered that stygobionts evolve predominantly from species originally inhabiting nearby surface habitats. Consequently, subterranean faunas in widely separated cave areas rarely share common ancestors.

The characteristic conditions of stygal biotopes have been documented in the reviews of, for example, Vandel (1965), Barr (1968), Culver (1982), Howarth (1983), and Holsinger (1988). The lack of light precludes photosynthesis so that much of the food supporting groundwater ecosystems is allochthonous in origin and typically limited or unpredictable in supply (Culver

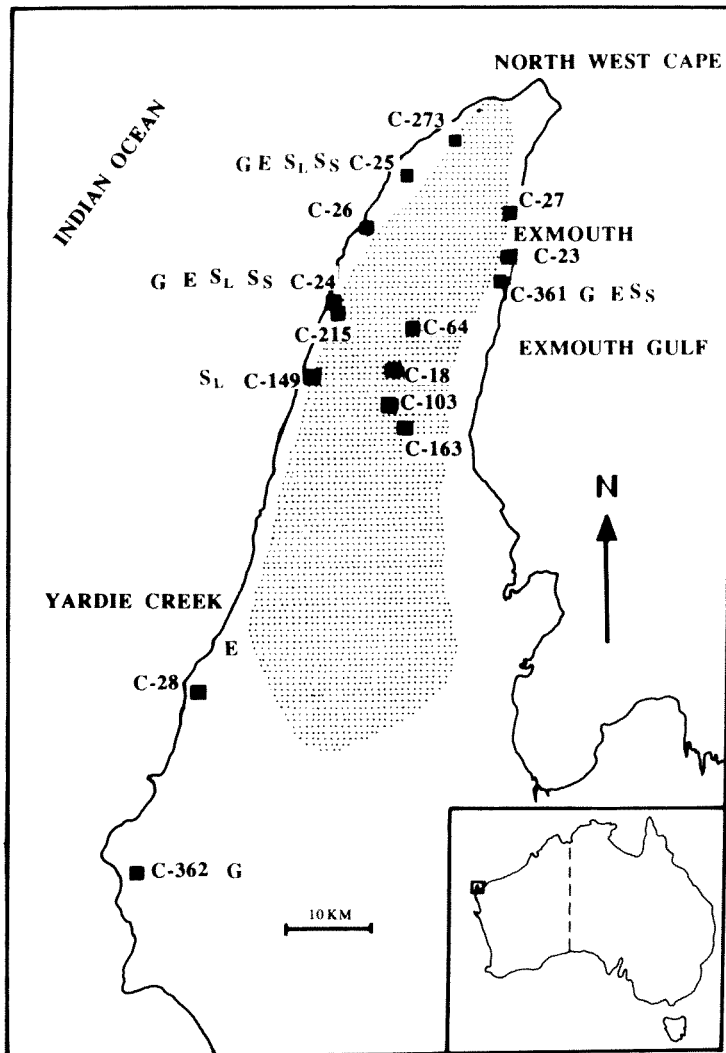


Figure 1. Map showing Cape Range peninsula, Western Australia, and the locations of wells and caves mentioned in the text. The stippled area indicates the position of Cape Range. The letter symbols denote sites where species have been found as follows:- E: swamp eel, *O. candidum*; G: blind gudgeon, *M. veritas*; S_L : *S. lancifera*; S_S : *S. stylifera*.

1982). Moreover, no light is available to provide diurnal or seasonal cues controlling biological processes such as activity patterns and reproduction. In subterranean environments, diurnal and annual variations in temperature are markedly damped in comparison with temperature variations in terrestrial environments, but considerable variation can occur in both water salinity and in granulometry of underlying sediments (Botosaneanu 1986). Other features of many subterranean waters in limestone include high carbon dioxide concentration (Jennings 1985) and moderate levels of oxygen (Freeze and Cherry 1979); for example, Jasinska (1990) recorded 64 - 89% oxygen saturation in epiphreatic streams in caves at Yanchep, Western Australia.

Cavernicoles with an obligatory dependence upon cave environments are 'trogllobites'; they are usually recognised by a common, convergent morphotype: eyeless, non-pigmented, and with long antennae and limbs. 'Troglophiles', on the other hand, use caves facultatively. 'Trogloxenes' frequently occur in caves but do not complete their life cycle there and usually feed outside the cave. 'Accidentals' are species which wander, fall or are accidentally swept into caves. The term stygofauna refers to obligate aquatic cavernicoles, also known as stygobionts, inhabiting a wide range of interstitial to open habitats or biotopes (particularly of fresh water) in subterranean streams and pools (Botosaneanu 1986). Facultative aquatic cavernicoles are called stygophiles.

Connections between epigeal and the stygal aquatic habitats are frequently established through channels formed by water in limestone and they are important conduits through which epigeal species may colonize stygal biotopes. Caves facilitate access into subterranean waters and historically have provided windows to study the composition and ecology of the groundwater fauna of a region. The subterranean fresh waters of Cape Range peninsula overlie water of marine origin (Allen 1993) and access is gained through caves and through man-made wells such as those described by Mees (1962).

The stygofauna

This paper concentrates on the macroscopic stygobionts from Cape Range peninsula exceeding 1 mm in length. All are freshwater inhabitants; no marine stygobionts have yet been recorded from the area, but given the experience elsewhere of finding a rich fauna of zoogeographical and phylogenetic relicts in anchialine biotopes [i.e. marine or brackish water in limestone caves in direct contact with the sea (Botosaneanu 1986; Holsinger 1988)], it is clear that intensive studies should be undertaken of this habitat on the peninsula. Meiofaunal elements [i.e. animals retained on sieves of mesh sizes ranging between 42 μm and 1 mm (Higgins and Thiel 1988)] are known from cave aquatic ecosystems elsewhere (see relevant chapters in Botosaneanu 1986) and indeed protists (two species: *Euplotes* sp. and *Paramecium* sp.), turbellarians, nematodes, oligochaetes, acarines, ostracods and copepods have been collected from ground waters of the coastal plains flanking the peninsula. No freshwater stygophiles have been recorded from the peninsula, but given the absence of persistent epigeal water-bodies in the area, the dearth of such stygophiles is not surprising. However, some insects do utilize groundwaters either as adults (e.g. water beetles from the Gnamma Hole C-105) or during larval stages [e.g. *Chironomus (Kiefferulus) intertinctus* from Mowbowra Well C-361]. Marine stygophiles could utilize anchialine habitats; indeed, the gastropod *Iravadia (Iravadia)* sp. (Family Iravadiidae) from brackish water in Bundera sinkhole (C-28; Slack-Smith 1993) may represent the first marine/estuarine stygophile recorded from the region.

Table 1. Numbers of species from caves of four karst systems, Tasmania. From Table 1 of Eberhard (1992:87) with the number of stygobionts calculated here from species lists in Appendices 4, 5 and 7 of Eberhard (*ibid.*).

Taxon	Precipitous Bluff	Exit Cave	Vanishing Falls	Kubla Khan
Platyhelminthes	1	2	1	3
Nematomorpha	1	1	0	0
Nemertea	0	1	0	0
Annelida	2	2	1	5
Myriapoda	3	3	3	5
Crustacea	4	13	7	6
Arachnida	14	20	9	21
Insecta	9	25	7	23
Mollusca	12	6	2	5
No. of troglobites	15	15	14	11
Possible troglobites	4	1	3	2
No. of accidentals	7	20	1	19
Total no. of taxa	46	73	30	71
No. of stygobionts	3	7	5	0

Animals in the accidental category, e.g. terrestrial forms falling down wells, have been recorded (Mees 1962), but it is not known how important this food source is for the stygofauna of Cape Range peninsula.

General accounts of the stygobionts from Cape Range peninsula may be found in Mees (1962), Cawthorn (1963), and Richards (1963). The comprehensive paper by Humphreys and Adams (1991) includes detailed distributional, abundance and genetic data of the fauna, and discusses the possible age of the fauna and its distribution in relation to the distribution and quality of ground water. Humphreys (1993a) reviewed the affinities and origins of the stygofauna from Cape Range peninsula and nearby Barrow Island. The seven species of stygobiont comprise two species of bony (teleost) fish (Osteichthyes : Chordata), and five species of 'shrimps' (Malacostraca : Crustacea). This fauna is not rich in comparison with the species richness of some other ground waters (21 species of stygobionts, 17 of them crustacean, occur in a deep well in Texas; Holsinger and Longley 1980), but is comparable with the numbers and phyletic diversity from Tasmanian caves (Table 1)(Eberhard 1992). At least four phyla, Platyhelminthes [turbellarians (Humphreys 1993a)], Annelida (oligochaetes), Nematoda and Ciliophora are represented but as yet undescribed, and representatives from only two phyla, Chordata (Class Osteichthyes) and Arthropoda (Crustacea), have been described formally to date.

The significance of the Cape Range peninsula stygofauna rests not only with the species number but also with the kinds of animals represented, their endemicity and zoogeographic origins. For example, the two species of subterranean fish from Cape Range peninsula are the only troglobitic vertebrates in Australia (Humphreys and Adams 1991): *Hypseleotris compressa* from a well east of Carnarvon [recorded by Whitely (1947) - as *Carassiops compressus*], is most probably an accidental (Dr G R Allen, pers. comm. 19 February 1993). Unfortunately, little information is available directly concerning the biology and phylogenetic

relationships of each species, and consequently origins of this stygofauna are here sought indirectly - firstly by reviewing the knowledge for each species, then searching for trends within the relevant family which can be used as a basis for speculating on the origins of the stygofauna from the peninsula.

Worldwide, fish from 19 families, totalling 92 species, have typical stygobiontic morphology [reduced or absent eyes, scales, pelvic fins and pigment (Vandel 1965)] but only 56 of these species (representing 14 families) are known to be authentic troglobitic cavernicoles: the habitats occupied by the remaining 36 species have to be verified (Thinès and Proudlove 1986). The two species of cavernicolous fish from Cape Range peninsula, *Milyeringa veritas* and *Ophisternon candidum*, represent the two families Eleotrididae and Synbranchidae respectively. In most subterranean ecosystems, just one species of stygobiontic fish occurs, but Thinès and Proudlove (1986) listed eight instances where two strictly hypogean species co-occur under sympatry.

***Milyeringa veritas* Whitely, 1945. Family Eleotrididae, Order Perciformes.**

The genus *Milyeringa*, described for subterranean eleotridids from Cape Range peninsula, is monospecific and endemic to the area. *M. veritas* is eyeless, and the brain is visible through the braincase. They have a well-developed system of sensory papillae on the head, which lacks thin scales. Coloration in life has been variously described as generally pale grey, with purple, pink and yellow tints about the head (Whitely 1945) to 'generally white, sometimes slightly pink' (Allen 1989: 194). Blind gudgeons grow to a standard length (snout tip to base of tail) of about 45 mm. They swim very sluggishly. Allen (1989) considered them to feed opportunistically upon detritus, algae and whatever animals, including insects, accidentally fell into the waters of the wells and sink-holes. Little else is known of their biology.

Initially recorded from Milyering Well (C-24), the distribution of *M. veritas* is now known to be widespread throughout the groundwaters of the coastal plains of the peninsula (Figure 1), extending from Mowbowra Well (C-361) on the east to Jarvis Well (C-362) south of Yardie Creek on the west (Humphreys and Adams 1991). *M. veritas* is abundant compared to *O. candidum*, but taking into account the small area occupied by this species, the recommendation of Michaelis (1985) that the blind gudgeon be classified as rare and given total protection is quite sound.

Whitely (1945) erected the new family Milyeringidae within the order Gobioidae to accommodate the new genus and species. The eleotridid affinities were recognized by Mees (1962: 29) who wrote with delightful acerbity that 'it should be remarked that the creation of a new family or other high systematic unit for a new species is about the cheapest way to escape from the trouble of finding its true affinities'. The ancestry and close relatives of the genus *Milyeringa* remain to be elucidated. Whitely thought the species may have evolved from a gudgeon similar to *Carassiops* (now itself a junior synonym of *Hypseleotris*) of the Eleotrididae. Mees (1962) quoted the opinion of Dr Boeseman that *M. veritas* is closest to *Prionobutis microps*, a species of mainly estuarine and adjacent freshwaters of New Guinea and northern Australia. Dr Allen (quoted in Humphreys and Adams 1991) regards the closest affinity of *M. veritas* possibly to lie with another eleotridid, *Butis*. *Butis butis* is commonly found in estuaries of the Indo-Australian Archipelago (Allen 1982). When phylogenetic relationships between members of the family Eleotrididae are established, the occurrence of two species of the genus *Typheleotris* from subterranean biotopes on Madagascar (Thinès and Proudlove 1986 - these authors list both *Milyeringa* and *Typheleotris* within the family

Gobiidae) is likely to exemplify the tenet that cave fish originate from nearby epigeal forms (Vandel 1965) - rather than indicating propinquity of descent between species from Western Australia and Madagascar.

The family Eleotrididae comprises about 40 genera (Nelson 1984). Eleotridids, commonly known as sleepers [because of their habit of resting motionless near the bottom of water bodies (Dr G R Allen, pers. comm. 14 July 1993)], are widespread in shallow marine through brackish to fresh waters of tropical and subtropical zones, particularly of the Indo-Pacific region (Nelson 1984). The greatest proliferation of freshwater species has occurred in the Australia-New Guinea region (Dr G R Allen, pers. comm. 19 February 1993).

***Ophisternon candidum* (Mees, 1962). Family Synbranchidae, Order Synbranchiformes**

Synbranchids, also known as swamp eels, have a distinct lack of external features rendering identification to species difficult (Moyle and Cech 1982). Adults lack the paired pectoral and pelvic fins, and the long dorsal caudal and anal fins are reduced to a rayless ridge or the caudal fin may be absent. Body scales are restricted to the caudal region or are absent (Rosen and Greenwood 1976). The small eyes are covered by a fold of skin; in burrowing and subterranean forms, there is an even greater trend towards eye reduction (Rosen and Greenwood 1976). The blind cave eel *O. candidum* is eyeless, and the only fin, the caudal, is reduced to a rayless membrane (Allen 1989). Coloration in life was described by Mees (1962: 28) as 'a very striking pure white'. The maximum length attained is about 40 cm (snout tip to furthest projection on the tail, Allen 1989). The diet of *O. candidum* is unrecorded, but synbranchids are generally recognized as nocturnal predators (Moyle and Cech 1982).

Originally described from Tatabiddi Well (C-26), specimens have been seen at locations on the coastal plains from Mowbowra Well (C-361) around the peninsula to an un-named well south of Yardie Creek (Humphreys and Adams 1991). The cave eels from Cape Range peninsula are seen very infrequently (Humphreys and Adams 1991) and the species has been classified as vulnerable by Michaelis (1985).

Following their revision, Rosen and Greenwood (1976) recognized fifteen species within five genera in the Synbranchidae, distributed in tropical and subtropical areas - particularly of Asia and Australasia. They exhibit marked habitat plasticity, being predominantly freshwater inhabitants but extending into brackish and estuarine waters; the same species may occupy a range of epigeal habitats from streams and lakes to swamps and marshes. Swamp and marsh dwellers often show amphibious or burrowing habits (Rosen and Greenwood 1976). According to Rosen and Greenwood (1976: 5), 'many, and probably most, synbranchids are capable of some form of aerial respiration'. In addition to *O. candidum*, two other synbranchids from caves are troglobitic: *Ophisternon infernale* from Yucatan and Mexico, and *Monopterus indicus* from Kerala State, India (Rosen and Greenwood 1976).

The sister relationships of *O. candidum* have still to be elucidated. Mees (1962) described the species as *Anommatophasma candidum* recognizing superficial similarities between the local species and *Synbranchus infernalis* from Hoctun Cave, Yucatan, but erected the new genus because of the position of the anus within the anterior half of the body in the specimens from Cape Range peninsula. Rosen (1976), in describing the distribution of the six extant species of *Ophisternon* (Figure 2), observed that the distribution is Gondwanian and concluded that the disjunctions result from the fragmentation of the southern continent. Banareescu (1990: 203) drew a slightly different interpretation, concluding that the 'general range of the

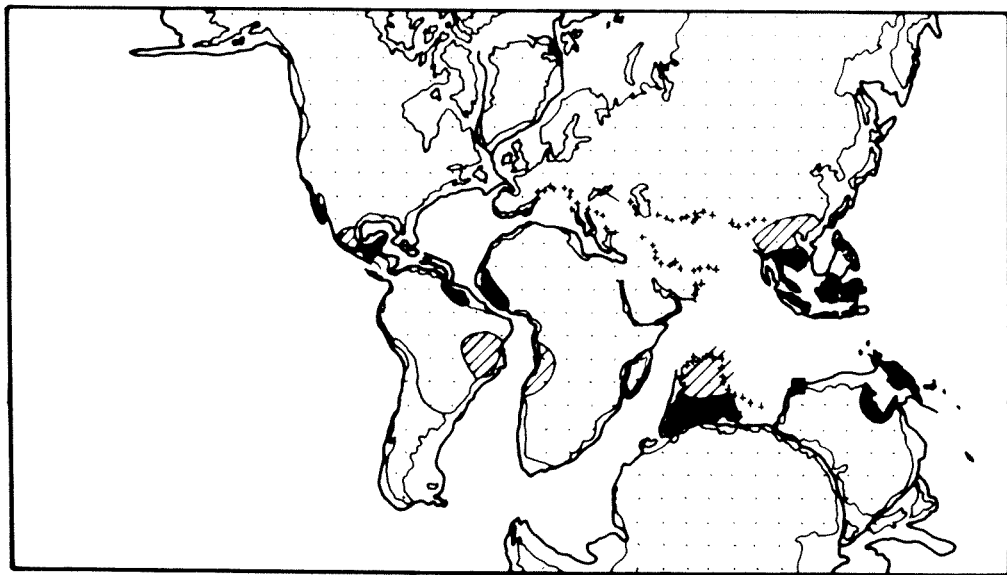


Figure 2. Map showing the present world distribution of *Ophisternon*. Distributional data from Rosen (1976), and plotted on a map of the Hauterivian (early Cretaceous) world (120 Ma) from Smith and Briden (1977: 19 Map 8, Mercator projection). [In presenting the distribution of *Ophisternon* and the crustaceans in Figures 3 a-c this way, it is only intended to draw attention to the Tethyan affinities of these taxa, and no imputation is intended whatsoever on their movements through time or timing of their invasions into the stygal realms].

family' (i.e. Synbranchidae) 'and of the genus *Ophisternon* is Tethyan rather than Gondwanian'.

Fishes represent a particularly diverse group of vertebrates, and there is considerable debate concerning the evolutionary history and relationships between the various groups. Seemingly, there is consensus that teleosts had evolved by the Mid Triassic (Greenwood *et al.* 1966), and that all four extant clades had done so by the Upper Cretaceous (Pough *et al.* 1990), with the greatest radiation in the Tertiary (Romer 1955). The true spiny-rayed fishes, Superorder Acanthopterygii (Nelson 1984), are monophyletic (Pough *et al.* 1990). Greenwood *et al.* (1966) suggested that the paucity of the Early Mesozoic teleost fossil record (other than from Triassic and Jurassic strata in the area of the Tethys Sea) is due to an origin in fresh waters for these fishes. However, the relationships of the synbranchids and eleotridids to the rest of the acanthopterygian evolutionary stream remains obscure, and will undoubtedly remain so for a long while pending a change to the view [for example as expressed by Romer (1955: 113)] that swamp-eels and gudgeons belong to taxa which are 'relatively unimportant, aberrant, "odds and ends" of the spiny teleost stock'. In view of the disparate number of extant taxa, Synbranchidae with five genera and 15 species, Eleotrididae with 40 genera and very speciose (Nelson 1984), it is tempting to suggest that synbranchids represent an early radiation, and eleotridids a comparatively recent radiation, in the stream, of teleost evolution.

The crustacean stygobionts from Cape Range peninsula, *Stygiocaris* (two species), two undescribed species of amphipod, and *Halosbaena tulki*, all within the class Malacostraca, are introduced in their chronological order of discovery, not in any phylogenetic sequence.

***Stygiocaris lancifera* Holthuis, 1960 and *Stygiocaris stylifera* Holthuis, 1960. Family Atyidae, Order Decapoda.**

Shrimps (or prawns) of the genus *Stygiocaris* are caridean decapods with chelate pereopoda 1 and 2. Morphological differences between the two species *S. lancifera* and *S. stylifera* are small. As Williams (1964: 104) noted, each of the features identified by Holthuis (1960) by which the species can be distinguished, namely, the shape of the posterior angle of the pleuron of abdominal somite five, the relative length abdominal somite six, the relative length of the telson, and with *S. stylifera*, the constant absence of the pterygostomial spine on the carapace, and the occasional presence of a tooth on the posterolateral angle of abdominal somite six, is 'open to ambiguity'. Difficulty in distinguishing between the species on the basis of morphological criteria was encountered by Humphreys' field colleagues (Humphreys and Adams 1991), and the present author once doubted the validity of two species. However, the allozyme genetic data provided by Humphreys and Adams (1991) gives strong support for the validity of both species. These shrimps are transparent and colourless in life, the condition characteristic of true stygobiontic decapod crustaceans (Holthuis 1986a), with the thoracic organs visible as a yellowish mass (Holthuis 1960). In addition to this lack of pigmentation, the troglobitic facies include strong reduction in eyes and these lack ommatidia. The maximum length of *S. lancifera* in the type series was 14 mm (total of 147 specimens) and of *S. stylifera* 18 mm (15 specimens) (Holthuis 1960). There is no knowledge of the diet of these shrimps, but atyids are generally considered to be detrital feeders, using long brush setae on the tips of their dactyls, especially on pereopod 1, for this purpose (Fryer 1960). Nor is there any published information on development in *Stygiocaris* spp. Atyids show a range of developmental patterns. Eggs are cemented to the pleopods of females and carried until they hatch either as zoeal larvae or as young adults. There is no obvious advantage for larval stages of atyids inhabiting restricted subterranean waters, and indeed Bruce (1992) recorded large ova from *Pycneus raptor*, a recently described troglobitic atyid from the Northern Territory, suggestive of direct development.

The atyids from Cape Range peninsula are reasonably abundant in ground waters from the coastal plain between Tulki (C-149) and Mowbowra (C-361) Wells (Humphreys and Adams 1991)(Figure 1). Humphreys and Adams (1991) detected geographic separation between the two species, identifying their samples from Milyering Well (C-24), Kudamurra Well (C-25), Tulki Well (C-149) and 5 Mile Well (C-273) as *S. lancifera*, and the two samples from Kubura Well (C-27) and Mowbowra Well (C-361) as *S. stylifera*. Thus, *S. lancifera* is distributed along the north-western flanks, and *S. stylifera* along the north-eastern flanks of the peninsula (Humphreys and Adams 1991). These authors were unable to determine whether the two species are still sympatric about the area of Milyering (C-24) and Kudamurra Wells (C-25) as was clearly the case in the collections made available to Holthuis (1960).

The majority of atyids are freshwater inhabitants, but tolerance of sea water salinities is evident in some species (Banareescu 1990). The family Atyidae [comprising four subfamilies (Holthuis 1986b)] has a circumtropical distribution, with all genera having restricted ranges (Banareescu 1990). The epigeal genera of the subfamily Atyinae have a circum-tropical distribution and the one hypogean species is widely and disjunctly distributed from pools in coral limestone; the Caridellinae is disjunctly distributed in Africa, Madagascar, north-western Australia, the Philippines and Hawaii with five genera having hypogean representatives; and the Paratyinae (with two genera of hypogean representatives) and Typhlatyinae (with five genera of hypogean representatives) have Tethyan distributions (Holthuis 1986a, Banareescu

1990). In Australia, all four subfamilies are represented, with epigeal atyids widespread in northern and eastern Australia (Williams 1980). Holthuis (1986a) listed 40 species (in 12 genera) of troglobitic atyid, including the genera *Stygiocaris* (two species) and *Parisia* (two species) from Australia. Subsequently, two new genera and species, *Pycneus morsitans* (Holthuis 1986a) and *Pycnisia raptor* (Bruce 1992) have been described from limestone caves in the Gibson Desert and near Katherine, Northern Territory, respectively. Thus, the Australian subterranean troglobitic atyids, for which there are four genera - three endemic (*Stygiocaris*, *Pycneus*, *Pycnisia*) and two monotypic (*Pycneus*, *Pycnisia*) have very restricted distributions within the north-western quadrant of the continent. However, Williams (1964) cited the occurrence of a stygophilic atyid, *Paratya australiensis australiensis*, from the Buchan caves in eastern Victoria. Indeed, since atyids are typically nocturnal, it will not be surprising to find more stygophylic forms where epigeal and hypogean waters are connected.

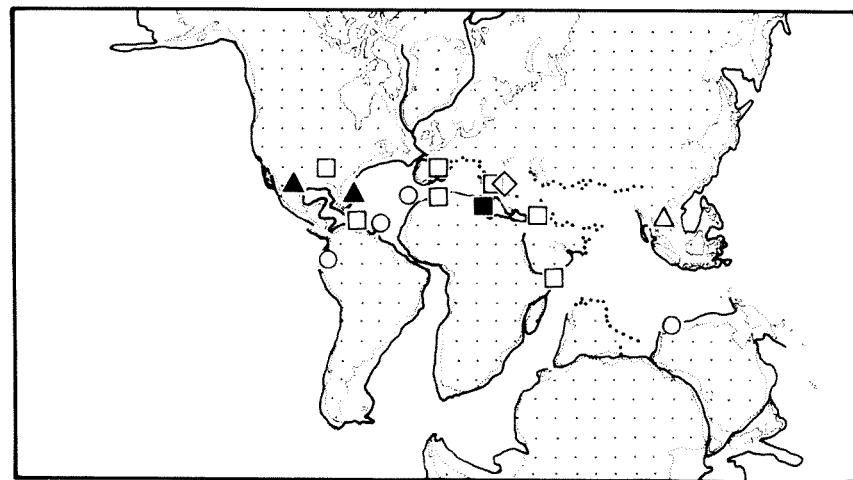
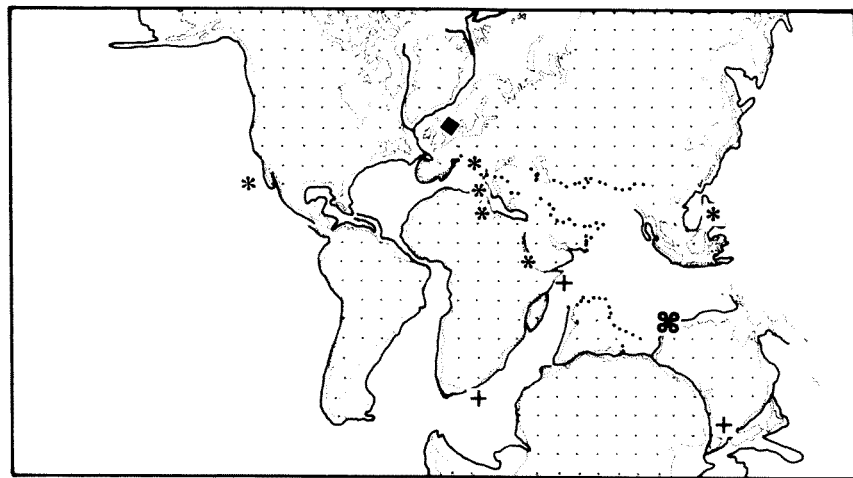
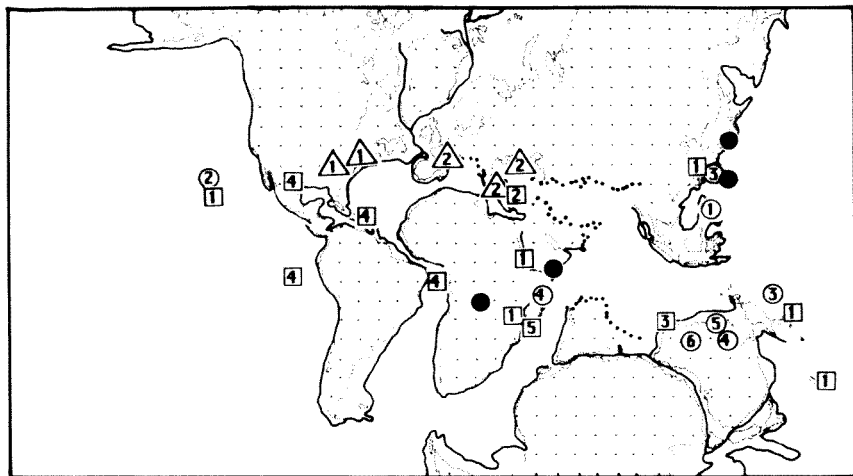
No attempt has been made recently to assess the sister relationships of the world atyids. The Atyidae, with most members adapted to fresh waters, comprises an older group of caridean prawns than do members of the family Palaemonidae which have closer affinities with marine environments (Vandel 1963, Banarescu 1990). *Parisia*, *Pycneus* and *Pycnisia* all belong to the subfamily Caridellinae and cannot, therefore, be closely related to *Stygiocaris* (of the subfamily Typhlatyinae). Distribution of the hypogean Atyidae (from Holthuis 1986a) is illustrated in Figure 3a. In describing *Stygiocaris*, Holthuis (1960) drew attention to the close morphological similarity between the genus and *Typhlopatsa* (one species) from Madagascar. Indeed, he suggested that *Stygiocaris* might even be considered as a subgenus of *Typhlopatsa*. However, as noted by Mees (1962), this morphological similarity is more likely to be an example of convergent evolution under similar environmental conditions than due to close genetic relatedness. As with the eleotridids discussed above, it is more likely that both the Australian and Madagascan atyid troglobites evolved separately from nearby epigeal relatives rather than from common subterranean ancestors. Banarescu (1990: 250) observed that 'most or all subterranean genera of atyid prawns are Tethys marine relicts in fresh water.'

Given their exoskeleton only slightly chitinised, atyids would not be expected to have an extensive fossil record. Even so, fossils have been recovered from Cretaceous beds in Brazil and from Oligocene beds in France (Glaessner 1969). In view of their present circum-tropical distribution, numerous stygal species and appearance from at least the Cretaceous, we might surmise, therefore, that ancestral atyids were widespread across near-shore environments of the Tethys Sea in Cretaceous times, and given appropriate conditions and stimuli, many populations had the genetic capacity to colonise fresh waters and even the stygal realm.

Amphipoda. Superfamily Melitoidea.

Amphipods comprise a diverse group of somewhat cryptic crustaceans of predominantly nocturnal habits which are not widely known in Australia. They have been described (Barnard and Barnard 1983) as unusual animals because they have an affinity for cold water, and as unusual amongst crustaceans because, along with the isopods, mysids and tanaidaceans, females brood their young in a pouch situated between the pereopods. Most are markedly laterally flattened, and few exceed 2 cm in length. Many are detritivores, others feed on periphyton. They are known from practically every marine and freshwater biotope.

Amphipods have been collected from ground waters in two areas on Cape Range peninsula, the coastal plain (Humphreys 1993b), and from four caves (C-18, C-64, C-103, and C-163) on Cape Range (Figure 1). I have no information concerning the coastal amphipods and they will



not be mentioned further in this text. The amphipods from the Range belong to a new genus of eriopisid currently being described within the *Eriopisa*-*Psammogammarus*-*Victoriopisa* complex. I will not pre-empt here that paper with a detailed discussion of the affinities of the Cape Range specimens. I can find morphological evidence of only one species, but with variation in details of the urosome, gnathopods and mouthparts. Humphreys and Adams (1991) detected some allozyme variation, but insufficient to indicate the populations had undergone enough genetic separation to delineate more than one species. However, Adams and Humphreys (1993) present evidence indicating that there is no gene flow between these populations of cave eriopisids.

Eriopisids are primitive melitids, and their present disjunct distribution (Figure 3b) is suggestive of an ancestry based in the Tethys. Clearly embedded in the melitid genome is a tendency to burrow into subterranean biotopes: melitids, for example, are also possibly ancestral to the hadziids (Barnard and Barnard 1983), almost all of which are blind stygobionts with a Tethyan distribution.

Amphipods have left a small fossil record (the oldest dating from the Upper Eocene), but the Barnard's considered that the first great diversifications of freshwater forms occurred across Pangaea, and if so, it is unlikely that a diverse amphipod fauna had not developed throughout the Tethys Sea.

Halosbaena tulki Poore and Humphreys 1992. Order Thermosbaenacea.

The latest crustacean taxon to be recognized so far from Cape Range peninsula is the Thermosbaenacea. Thermosbaenaceans are small, blind malacostracans <4 mm in length with a short carapace, which in females usually forms a dorsal brood pouch. They have been recorded from a number of stygal biotopes, including hot springs, fresh ground water, marine interstitial and anchialine pools (Kaestner 1970; Stock 1986). Their ancestral habitat probably was brackish coastal ground water (Kaestner 1970; Stock 1986).

Poore and Humphreys (1992) recently described *Halosbaena tulki* from un-named cave C-215 on the western flanks of the Range (Figure 1). Family placement of this genus is uncertain (Poore and Humphreys 1992). The water in C-215 was estimated from conductivity to vary between 1.4 and 1.7 g L⁻¹ (Poore and Humphreys 1992). The relation of this cave to the geological strata is described in Poore and Humphreys (1992). *H. tulki* is now known to be widespread in ground waters of the peninsula (Humphreys 1993a) and has been collected at times in large numbers (Dr W.F. Humphreys, pers. comm. 8 July 1993).

◀ **Figure 3.** Maps showing world distribution of hypogean crustacean taxa relevant to the text.

3a: present distribution of hypogean shrimps of the Atyidae, after Holthuis (1986a and b), and Bruce (1992). Atyinae: ● =*Caridina*; Caridellinae = ○: 1=*Edoneus*, 2=*Halocaridina*, 3=*Halocaridinida*, 4=*Parisia*, 5=*Pycneus*, 6=*Pycnisia*; Paratyinae = △: 1=*Palaemonias*, 2=*Troglocaris*; Typhlatyinae □: 1=*Antecaridina*, 2=*Spelaecaris*, 3=*Stygiocaris*, 4=*Typhlata*, 5=*Typhlopatsa*.

3b: present distribution of amphipods of the *Eriopisa*-*Psammogammarus*-*Victoriopisa* complex, after Barnard and Barnard (1983). ◆ =*Eriopisa*, ⌘ =eriopisid, * =*Psammogammarus*, + =*Victoriopisa*.

3c: present distribution of thermosbaenaceans, after Stock (1986) and Humphreys (1993a). ○ =*Halosbaena*, ◇ =*Limnosbaena*, □ =*Monodella*, ■ =*Thermosbaena*, △ =*Theosbaena*, ▲ =*Tulumella*.

Thermosbaenaceans comprise a small group of 16 species with strongly conservative morphological. They have now a disjunct distribution throughout the area covered by the former Tethys Sea (Figure 3c).

Distribution

There are two zoogeographic components to the stygofauna of Cape Range peninsula: the coastal component comprises *M. veritas*, *O. candidum*, *S. lancifera*, *S. stylifera*, *H. tulki* and one species of amphipod; the Range fauna comprises the one species of eriopisid amphipod. Distribution of this stygofauna is controlled by the interaction between geology, climate and hydrology of the area. The geology of the peninsula has been described in detail by Condon *et al.* (1955), Condon (1968), Hocking *et al.* (1987). The Cape Range anticline is structured from three Miocene limestone sequences: the basal Mandu Limestone an impermeable fine-grained massive calcarenite and marl at its lowest exposures grading upwards to chalky and friable calcarenite, is overlain by Tulki Limestone (Late Oligocene - Early Miocene) capped by Trealla Limestone. Both the Tulki and Trealla limestones are hard, crystalline and cavernous. Structure of the coastal plains which form lowland corridors along both eastern and western flanks of Cape Range is discussed in detail by Wyrwoll *et al.* (1993).

Vine *et al.* (1988) and Wyrwoll (1993) described the climate of Cape Range peninsula. Rainfall, 254 mm *per annum* on average, is highly variable (variability index 1.5 - 1.75). Substantial falls >100 mm per rainfall event, recorded on 11 occasions in the years 1957 - 1969 and 1976 - 1986 inclusive, result from cyclonic storms (summer) and jet stream activities (late summer to autumn).

Surface waters are temporary features of the peninsula's landscape now, but the deep gorges, together with the dendritic drainage patterns attest to significant overland water flow at times now and in the past. Rainwater infiltrates directly into the groundwater by direct percolation through the limestones (Forth 1973), but at times of heavy storm activity, much of the rain falling directly onto Cape Range discharges via overland flow through the gorges onto the coastal plains (Hocking *et al.* 1987). This surface run-off from the range, combined with surface overland flow of the coastal plains, discharges seawards along the coastal streams, from which significant amounts of fresh water infiltrate through the gravelly stream beds, thereby recharging the groundwater aquifer (Forth 1973). On the broad summit of the anticline where centripital drainage systems lead into caves (Condon *et al.* 1955), significant volumes of water probably also discharge into those caves which open vertically downwards and from there infiltrate into the Cape Range. Dry Swallett (C-18), for example, flooded to a depth of 27 m following 230 mm of rainfall on 19 - 20 May, 1984, and this water had drained away (into Tulki Limestone) by 22 May (Vine *et al.* 1988).

Forth (1973), Humphreys and Adams (1991) and Allen (1993) all give valuable accounts of the groundwater resources of Cape Range peninsula. About the coastal plains, a subterranean freshwater aquifer of low relief [variously estimated to reach an elevation of 0.7 m (Bestow 1966) or <5 m (Hocking *et al.* 1987)] overlies impermeable sequences of the lower Mandu Calcarenite, or, coastwards, saline water. How far this aquifer penetrates beneath Cape Range has yet to be ascertained, but allozyme data for *M. veritas* (providing evidence of inter-population connectedness through genetic relatedness) indicating that blind gudgeon populations are connected along the coastal corridors and around the northern limit of, rather than directly across, Cape Range (Humphreys and Adams 1991) might be indirect evidence

for the presence of an impermeable barrier separating the coastal aquifers of the eastern and western sides of the peninsula. Indeed, the coastal stygobionts seem to be absent from ground waters beneath all but the margins of Cape Range (Dr W.F. Humphreys, pers. comm., 8 July 1993). Alternatively, the absence of coastal stygobionts beneath Cape Range might be an artefact of sampling, or else due to a lack of suitable fissures for habitation and/or total lack of food supplies in the aquifer continuous from east to west coastal corridors beneath Cape Range.

Within Cape Range itself, standing water occurs at altitudes ranging from 110 m (C-64) to, in (C-18, C-103 and C-163), above 200 m above sea level (Humphreys and Adams 1991); C-64 is described 'to always contain water' (Humphreys and Adams 1991: 396), and following heavy rains water outflows temporarily (Mr B. Vine, pers. comm. 7 July 1993). These elevated fresh waters in Cape Range have been interpreted by Poore and Humphreys (1992) as perched. Permanent perched water tables, resulting from heterogeneity in the permeability of the substrate (Freeze and Cherry 1979), are not unknown in limestone areas (Freeze and Cherry 1979, Esteban and Klappa 1983) and give rise to an important stygal biotope (the *nappes éluviales ou colluviales de déversement*; see, for example, the endpaper in Botosaneanu 1986). No hydrological/geological data are yet available to confirm whether the elevated waters in caves C-18, C-64, C-103 and C-163 are perched waters or the upper levels of conduits connecting with the coastal aquifer, but as observed by Humphreys and Adams (1991), their permanence is indicated by the presence of amphipods in these cave pools.

The waters in caves on Cape Range have salinity = 0 g L⁻¹ (Humphreys and Adams 1991). Humphreys and Adams (1991: Figure 8) proposed a model for the conformation of salinities of the coastal aquifer in relation to propinquity to the coastal stream channels and to the sea: water of low salinity discharging along coastal stream courses infiltrates into ground water of higher salinities. Consequently, the salinity in the upper layers of the groundwater increases along a transect from the foot of the Range to the sea, with total dissolved solids increasing from 430 mg L⁻¹ near the base of Cape Range to more than 2850 mg L⁻¹ near the coast (Humphreys and Adams 1991); the maximum salinity they recorded was 16 g L⁻¹ (from Bundera Sinkhole C-28). Furthermore, Humphreys and Adams (1991) suggested that there could be a narrow corridor of fresh water adjacent to or in the foothills of the Range which would provide freshwater connections between the fans of lower salinity ground water about the coastal stream courses. These authors calculated significant regressions of increasing salinity and ionic concentrations (of Na⁺, K⁺, Ca²⁺, Mg²⁺ and Cl⁻) on distance around the coast proceeding from the most southerly cave on the east side of the peninsula anti-clockwise around the peninsula. No data are available concerning the depth of ground water of low salinity about the peninsula, but depths are not considerable: Humphreys and Adams (1991) present evidence of bores and springs which have either dried up or else gone saline since the 1970's, and Forth (1973) calculated that a 75 mm lowering of the watertable at the Exmouth township borefield would reduce freshwater storage there by 20%. Between the freshwater fans, ground waters are absent or saline (Sofoulis 1951). Mixing between the fresh and marine ground waters is controlled in part by the presence of caverns and variations in limestone permeability (Forth 1973), and tidal forcing. Tidal fluctuations of 15 cm in groundwater levels have been observed in Kudamurra (C-25), Tantabiddi (C-26) and Milyering (C-24) Wells to the west of Cape Range (Mees 1962); on the eastern side of the peninsula, tidal fluctuations of 15 cm have been recorded within the Exmouth water supply borefield and tidal influences have been detected 3.5 km inland (Forth 1973).

Humphreys and Adams (1991, Table 8) provide data on nine water chemistry parameters (pH, salinity, Na⁺, K⁺, Ca⁺⁺, Mg⁺⁺, Cl⁻, total P and total N) for waters in which the coastal shrimps, cave eel, blind gudgeon, and Range amphipod, have been found. The maximum salinity recorded for waters from which shrimps and swamp eels have been collected was 5 g L⁻¹, and the blind gudgeon has been observed in water where a salinity of 16.1 g L⁻¹ has been recorded. Presumably the thermosbaenaceans and coastal amphipods have similar salinity tolerances as do the other coastal stygobionts. The stygobionts, evidently, are restricted to groundwaters of low salinity: none have been recorded on the coastal plains from those ground waters of higher salinities between the freshwater fans, but this may be due in part to these waters being inaccessible for faunal sampling, and no physiological studies have yet been undertaken to ascertain the upper salinity tolerance limits for these species.

There is a marked geographic discontinuity between the eriopisid amphipods from caves on Cape Range at elevations above 100 m and the remainder of the coastal plains stygofauna (Figure 1). This discontinuity in faunal distributions may be due entirely to the perched waters within Cape Range and the coastal aquifers never having been in contact; it is unlikely to be based on the slight differences in water quality or chemistry recorded by Humphreys and Adams (1991: Table 6). If the two groundwater resources on the peninsula have never been in contact, then the most parsimonious explanation of the maintenance of two discrete groundwater faunas in the area requires two phases of invasion; the first by ancestors to the Range eriopisids into the early anticline and being carried upwards with increasing elevation above sea level of the anticline (Humphreys 1993). Consequently, the coastal elements must have evolved following a much later phase of invasions into the ground waters of the peninsula. However, it may be pertinent to explore other models for the evolution of this stygofauna, particularly as indicated by Humphreys and Adams (1991), the youthful geological age of the coastal formations does not seem to be sufficient for the stygofaunal species there to have developed, *in situ*, the troglobitic morphological expressions they show. We should also consider the possibility that more than one species colonised the stygal biotopes of Cape Range peninsula during each phase of invasion, for which there is evidence of two.

Origins

Finally, two issues are raised, the zoogeographical relationships of the stygofauna, and the entry route into the stygal realms of Cape Range peninsula.

To assess zoogeographical relationships, it is necessary to consider the stygobionts in terms of their higher classification: there is no knowledge on their closest relatives or ancestors. Consideration of the distributions of related (congeners in the case of *O. candidum* and *H. tulki*, more distantly related in the other) forms all indicate strongly that the ancestry of the known stygofauna from Cape Range peninsula is rooted in the Tethys Sea. Humphreys (1993a) recognized the thermosbaenaceans, and atyid shrimps from Cape Range peninsula to have, possibly, Tethyan affinities. This large sea [which persisted from the Triassic (200 Ma) until the late Eocene (40 Ma) (Smith and Briden 1977)] separating the continents of Gondwana and Laurasia and with an extensive side arm between South Africa and India, must have been a major theatre for evolutionary events and radiations. It would be surprising, indeed, if some of the marine life of the Tethys did not colonise the inland waters of continents once bordering the Sea: throughout this long period, the northern coastline of Australia opened onto the Tethys Sea (Smith and Briden 1977). Tethyan relicts would be expected to

show disjunct distributions on landmasses which originally bordered the Tethys Sea but which are now widely separated through continental drift: the Caribbean, about the Mediterranean - Georgia axis, on India and south east Asia, and Madagascar. Such zoogeographic relationships have been demonstrated in the present account for all stygobionts from the Cape Range peninsula discussed here, although we probably have to seek out their early antecedents to detect the Tethyan affinities of the eleotridids. Diversification of this clade may have been predominantly a post-Tethyan event.

Identification of a Tethyan fauna at Cape Range peninsula is significant from zoological and conservation perspectives. The zoogeographical relationships of the Australian crustacean fauna is a composite of cosmopolitan, predominantly Palaeartic, Gondwanian and endemic elements (Williams 1981). Williams does not identify specifically a Tethyan element, although it may be subsumed in his categorisation of a circumtropical component. Some groups with northern affinities are thought to have island hopped into Australia in comparatively recent times. Similarly, McDowall (1981) does not recognize Tethyan elements in the Australian freshwater fish fauna, but he does comment (p. 1258) that distribution of the genus *Ophisternum* 'looks strongly Gondwanian'. The Tethyan elements I am identifying here belong to lineages which clearly could have been extant during the Early Cretaceous. The significance of this stygofauna for conservation is implicit in the antiquity of the fauna, and its present day relictual distribution. *M. veritas*, *O. candidum*, *S. lancifera*, *H. tulki* and two species of amphipod are endemic to the peninsula; *S. styliifera* is restricted to Cape Range peninsula and Barrow Island (Humphreys 1993a). Is there relevance in the similarity of how both landmarks have been viewed - between the sense of remoteness and awe with which we regard Cape Range peninsula at the edge of Australia, and for the ancient Greeks, the mythological Tethys at the edge of the world?

Attention is drawn here to the Tethyan affinities even though it must be recognized that some of the ancestors may have inhabited coastal fresh waters along the northern coasts of Gondwana instead of the Tethys Sea *sensu stricto*. That is, I am drawing here a real distinction between the zoogeographical affinities of this warm water fauna and affinities of the southern, cool water fauna including crangonyctoid amphipods and phreatoicid isopods which are widely recognized as Gondwanian.

What routes were available for epigeal forms to colonise stygal biotopes of Cape Range peninsula? Three scenarios have been discussed.

- 1) *In situ* evolution of the coastal stygofauna: discounted by Humphreys and Adams (1991) because the high degree of troglomorphy, which would take a long time to achieve, is not consistent with the geological youthfulness of the platforms, a youthfulness challenged by Wyrwoll *et al.* 1993).
- 2) Fauna originating in Greater Tethys, undergoing vicariance by seafloor spreading and colonising geological areas in Australia older than Cape Range (e.g. Pilbara Craton) and later migrating to Cape Range through coastal limestones at times of lower sea level. This possibility is variously presented by Humphreys and Adams (1991) and Poore and Humphreys (1992), and explicitly by Humphreys (1993a,b). The occurrence of common taxa on Barrow Island is consistent with this view (Humphreys 1993a).
- 3) *In situ* evolution on the Range and the coastal plain: discounted by Humphreys and Adams (1991) because of a lack of taxa common to the two areas. However, Humphreys (1993a, b), used the palaeogeographical evidence of the Pilbara Craton north east of Cape Range peninsula (emergent for >600 Ma), fringed by shallow marine environments since

the Triassic (c. 200 Ma) peninsula and occasionally emergent low, coastal plains along the northern coastline of Australia to indicate that environments suitable for colonisation by the ancestors of the present stygofauna from Cape Range peninsula have been comparatively widespread about the northwestern corner of Australia, ever since the Mesozoic.

The process of colonisation of the stygal realm at Cape Range peninsula could have begun concomitantly with the formation of limestone throughout the area by adaptive shift in some species as envisaged by Howarth (1973, 1981). There must have been an extensive area of shallow water, perhaps with significant input of fresh water. Activities of the benthic biota would have helped generate fissures and crevices in limestone reefs (James 1983). Marine animals which naturally utilise sediments and with a capacity to tolerate brackish water would have been able to exploit developing stygal biotopes even as the anticline was uplifting. As the uplift continued, fresher, aggressive, water would have facilitated development of subterranean fissures and caves. That is, some of the stygobionts could have developed *in situ* throughout the general area of deposition of limestones of which part form the present Cape Range peninsula. There could have been another invasion at a later geological time from freshwater bodies in the nearby early Ashburton catchment: indeed, there could have been direct connections at the time between epigeal and hypogean waters in the area Wyrwoll *et al.* (1993). In view of their present day, highly disjunct, world distributions and environmental responses, the eriopisid amphipods (at least those from the Range) and thermosbaenaceans are candidates to be regarded as amongst the first invaders, initially under marine conditions, of stygal habitats at Cape Range peninsula. The two species of fish and atyid shrimps probably invaded the stygal realms at Cape Range peninsula during some later invasion events from fresh waters of the early Ashburton river system adjacent to the Cape.

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