STYGOFAUNA IN SEMI-ARID TROPICAL WESTERN AUSTRALIA: A TETHYAN CONNECTION?

by

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INTRODUCTION

The recent finding, in semi-arid Western Australia, of a rich troglobite fauna derived from wet tropical forest communities (HUMPHREYS *et al.*, 1989), has confirmed the richness of the cave fauna of tropical Australia (HOWARTH, 1988). However, the aquatic fauna of these areas is poorly known, both as to is occurrence and affinities. Australia is the flattest and driest continent and there are large areas of hypersaline groundwaters. Salination problems, resulting both from the clearing of vegetation and from the utilisation of potable groundwaters, are likely already to have changed substantially the stygofauna in some areas.

I provide here a synopsis of recent findings of a rich stygofauna occupying diverse subterranean waters of

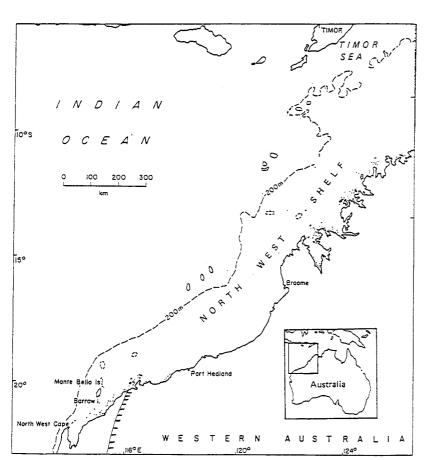


Fig. 1 - Locality map showing the location of features mentioned in the text. The hatched line west of the $116^{\circ}E$ mark represents the border between the middle Mesozoic (100 Ma) or Tertiary (c. 19 Ma; Cape Range and Barrow I.) formations to the west and the Pre-Cambrian Pilbara Craton to the east. The latter has not undergone major regional deformation since 2400 Ma (TRENDALL, 1990) and has been emergent continuously for > 600 Ma.

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north western Australia. The North West Cape peninsula is relatively pristine, while Barrow Island contains an oilfield that has been in production for >30 years.

I - THE AREA

The north-west of Western Australia is currently arid to semiarid and experiences highly unpredictable rainfall (HUMPHREYS et al, 1989). In this area a rich stygofauna has recently been found which inhabits the low-lying areas of the North West Cape peninsula (Fig. 1) and Barrow Island, 160 km to the north east, part of the same geological formation. This Cape Range Formation is an anticline capped with Lower Miocene marine limestones some of which are highly cavernous (HUM-PHREYS et al., 1989).

II - THE FAUNA

The North West Cape peninsula has a stygofauna known for c. 30 years which comprises the only vertebrate troglobites in Australasia, the Blind Gudgeon, *Milyeringa veritas* and the Cave Eel, *Ophisternon candidum*, and two congeneric shrimps, supposedly sympatric, *Stygiocaris lancifera* and *S. stylifera* (HOLTHUIS 1960; *cf.* HUMPHREYS and ADAMS, 1991).

| Major taxon | Genus and species | Locality | |
|---------------------------------|--------------------------------------|----------|--|
| Pisces: Perciformes: Eleotridae | Milyeringa veritas Whitley | NWCP | |
| Pisces: Synbranchiformes | Ophisternon candidum (Mees) | NWCP | |
| Decapoda: Atyidae | Stygiocaris lancifera Holthuis | NWCP | |
| Decapoda: Atvidae | Stygiocaris stylifera Holthuis | NWCP, BI | |
| Isopoda: Cirolanidae | Haptolana sp. nov. | BI | |
| Thermosbaenacea | Halosbaena tulki Poore and Humphreys | NWCP | |
| Amphipoda: Melitidae* | New genus, 3 species | NWCP, BI | |
| Amphipoda | ? | BI | |
| Copepoda: Harpacticoida | ? | NWCP | |
| Copepoda: Cyclopoida | ? | NWCP, BI | |
| Turbellaria | ? | NWCP | |

Tabl. 1 - The composition of the stygofauna of the north west of Western Australia. About half of this fauna has been found since 1991. NWCP = North West Cape Peninsula; BI = Barrow Island.

*sensu BOUSFIELD, 1973.

Recent work has yielded further taxa on the peninsula (Tabl. 1) including three species of Amphipoda two of which are congeneric melitids separated by altitude, possibly during the uplift of Cape Range which forms the spine of the North West Cape peninsula; one of these is the only known aquatic species in Cape Range (HUMPHREYS and ADAMS, 1991). Harpacticoid and cyclopoid Copepoda are widely found in the coastal plain locations as are turbellarians. The anchialine system occupied by *Stygiocaris lancifera* and *M. veritas* on the North West Cape peninsula contains the only known southern hemisphere representative of the crustacean order Thermosbaenacea, a new species of *Halosbaena* (Tabl. 1; POORE and HUMPHREYS, 1992).

This fauna is represented on Barrow Island by Stygiocaris stylifera. In addition there are cyclopoid copepods, two amphipoda including a melitid, and a cirolanid isopod, a new species of Haptolana (N. BRUCE, pers. comm., 1992).

As so little work has been conducted in the region, a much richer fauna is to be expected.

III - THE AFFINITIES OF THE FAUNA (Tabl. 2).

Stygiocaris lancifera and S. stylifera were described from the same location (HOLTHUIS, 1960) and subsequent work has confirmed their sympatry on the North West Cape peninsula using protein electrophoresis (HUMPHREYS and ADAMS, 1991 and unpublished). S. stylifera was found in 1992 in anchialine systems on Barrow Island and the identity confirmed by L.B. HOLTHUIS and by protein electrophoresis (HUMPHREYS and ADAMS, unpublished).

Tabl. 2 - The affinities of genera from the stygofauna of north west of Western Australia. NWCP = North West Cape peninsula; BI = Barrow Island. T = Tethyan distribution.

| Taxon | Genus | Tethyan? | Affinities |
|------------------------------|---------------------|----------|--|
| Crustacea Thermosbaenacea | Halosbaena | Т | West Indies, Columbia, Canary Is (Poore & Humphreys 1992) |
| Amphipoda: Melitidae* | New genus, 3 spp. | - | - |
| Amphipoda | ? | - | - |
| Isopoda: Cirolanidae | Haptolana | T | Cuba, Somalia (Messana 1988) |
| Copepoda | ? | - 1 | - |
| Decapoda: Atyidae Pisces | Stygiocaris, 2 spp. | Т | Madagascar (Banarescu 1990) |
| Perciformes: Eleotridae | Milyeringa | - | - |
| Synbranchiformes | Ophisternon | - | Circum tropical (Mexican caves) |

Stygiocaris belongs to the Typhlatya series of species which have a Tethyan disjunct range encompassing the Caribbean, the western Balkans, Madagascar, Western Australia and parts of the Indo-west Pacific. The closest relative of *Stygiocaris* is *Typhlopatsa* of Madagascar and BANARESCU (1990) considers their disjunct range a consequence of their ancestors being in a southern arm of the Tethys which separated the two mainlands then much closer.

The cirolanid isopod is a new species of *Haptolana* (N.L. BRUCE; pers. comm., 1992), which occurs in the anchialine system occupied by *Stygiocaris stylifera* on Barrow Island; *Haptolana* is known elsewhere only from Somalia and Cuba (MESSANA and CHELAZZI, 1984; MESSANA, 1988). Cirolanids are present in subterranean waters of the Caribbean area, circum-Mediterranean and the Horn of Africa, a distribution suggesting a Tethyan marine origin with dispersal and isolation due to marine regressions (KENSLEY and SCHOTTE 1989). Hence, they have a similar pattern of distribution to the Thermosbaenacea although the more heroic hypotheses about their origin (tectonic plate riders) have not been invoked, perhaps due to the uncertainty about their generic status (MESSANA and CHELAZZI, 1984; MESSANA, 1988).

The thermosbaenacean is a new species of *Halosbaena* (POORE and HUMPHREYS, 1992) which occurs in the anchialine system occupied by *Stygiocaris lancifera* on the North West Cape peninsula. *Halosbaena* is known elsewhere only from Caribbean islands, the Atlantic coast of Columbia and the Canary Islands (POORE and HUMPHREYS, 1992). Thermosbaenaceans are present in subterranean waters of the circum-Caribbean and Mediterranean areas and their associated islands, from Somalia and Cambodia (Tabl. 3). Hence, they have a disjunct tethyan distribution pattern similar to the circlanids. However, owing to the distribution of species within genera, more varied and heroic hypotheses (e.g. tectonic plate riders) about their origin have not been invoked.

Tabl. 3 - Distribution of the families (after MONOD and CALS, 1988) and genera of Thermosbaenacea.

| Family Genus | Distribution |
|-----------------|---|
| Thermosbaenidae | |
| Thermosbaena | Tunisia |
| Monodellidae | |
| Monodella | Land to north and east Mediterranean, Morocco, Somalia, West Indies, Texas. |
| Halosbaenidae | |
| Limnosbaena | Bosnia |
| Theosbaena | Cambodia |
| Halosbaena | Caribbean islands, Canary Islands, Columbia, Western Australia |
| Tulumella | Bahamas, Mexico |

The Blind Eel, Ophisternon candidum, belongs to a circum-tropical genus mainly of fresh water and comprises six species. Their distribution is vicariant with species in northern Australia (candidum and gutturale), India to the Philippines (bengalense), West Africa - Guinea to the Niger delta (afrum), the Caribbean fringe (aenigmaticum), and in Mexican caves (infernale).

The new genus of Melitidae (Amphipoda) has one species on the coastal plain in anchialine waters and another one (W. D. WILLIAMS, pers comm., 1992) in Cape Range caves well above sea level and with genetic discontinuities between the major cave areas (HUMPHREYS and ADAMS, 1991). The melitids are a primarily marine group mainly in tropical and south-temperate regions.

IV - ORIGINS

I want to address the questions arising from the discovery of the Order Thermosbaenacea in Australia and by its occurrence there in Tertiary formations. The literature on thermosbaenaceans is examined as that Order seems to have inspired the greatest diversity of hypotheses. Many hypotheses place the colonisation period of "tethyan relicts" much earlier in time than the deposition of the sediments that gave rise to the Cape Range Formation (early Miocene). Does this information help to substantiate or refute any of the proposed hypotheses?

V - THE SPECIFIC FORMATION

The current land fringes the extensive and shallow North West Shelf which, around the north of Australia, is broadly contiguous with the Sahul Shelf, itself broadly contiguous with the Arafura Shelf (VEEVERS, 1991). On a number of occasions during periods of lowered sea level, as recently as the Holocene, these shelves would have been emergent (CHAPPELL and THOM, 1977) and formed an extensive, low coastal plain similar to those found bordering the North West Cape peninsula today. This plain would have provided a continuous suitable habitat for the current stygofauna thus linking the Miocene formations with the Pre-Cambrian Pilbara Craton to the north-east.

The Pilbara Craton has been continuously emergent for > 600 Ma; Mesozoic deposits abut the western border and these are themselves fringed with the Tertiary deposits in which the current fauna is found. The area has mainly been fringed with shallow marine environments since the Triassic (c. 200 Ma) with occasional low emergence (HOCKING, 1990). In the Mesozoic and the Miocene the Pilbara Craton was isolated by shallow inland seas. Hence, the presence of thermosbaenaceans in Tertiary Cape Range Formation need not be indicative of the time of colonisation by thermosbaenaceans of the Australian plate - they could have migrated from the Pilbara Craton or the Mesozoic deposits on many occasions. The occurrence of *Stygiocaris stylifera* on both Barrow Island and the North West Cape peninsula is evidence for the suitability of the substrate for such migration.

VI - PLATE TECTONICS

Most thermosbaenaceans are known from anchialine systems or near coastal caves but some are isolated well inland. The origin of anchialine cave fauna is most likely to be from the continental margins (STOCK, 1986a, 1986b; DANIELOPOL, 1990) rather than, as proposed by lliffe *et al.*, (1984), from the deep sea. Inland populations of this tethyian relict stygofauna have been explained using models involving isolation of fauna due to marine regression (STOCK, 1977, 1980). However, the wider distribution is explained by the Two-step Model (BOUTIN and COINEAU, 1990) which incorporates active marine dispersal of the genera followed by vicariance resulting from the movement of tectonic plates.

For example, the thermosbaenacean genera Monodella and Halosbaena occur on both sides of the Atlantic and on the shores of the Indian Ocean. This distribution has been explained by cave colonisation and subsequent dispersal through sea floor spreading and continental drift as the Atlantic opened up (STOCK and LONGLEY, 1981; ILIFFE et al., 1984; HART et al., 1985; WÄGELE, 1985; WILKENS et al., 1986). Under this model the thermosbaenacean genera of the Greater Tethys invaded the proto-Mediterranean and proto-Caribbean during the Triassic and Jurassic (225-160 million years ago; CALS and BOUTIN, 1985) and became separated by the breakup of Pangea in the Mesozoic (WILKENS et al., 1986). At that time (Early Cretaceous) the plate that is now Western Australia formed the eastern shore of Greater Tethys (HOWARTH, 1981). The finding of Halosbaena in Australia is consistent with this hypothesis but presupposes a remarkable degree of morphological conservatism over 200 million years; Halosbaena sp. nov. is very close morphologically to both its Caribbean and Canary Islands congenors (POORE and HUMPHREYS, 1992).

VII - PROSPECTS

On both sides of the Atlantic Ocean thermosbaenaceans co-occur with many other relictual crustacea, both orders and families (SHRAM, 1986; NEWMAN, 1991). The finding of Mystacocarida (NEWMAN, 1991), as well as Thermosbaenacea in Western Australia is indicative of poor sampling of stygofauna in Australia and suggests that further work may reveal some of these other relictual taxa (POORE and HUMPHREYS, 1992); the discovery of cirolanid isopods on Barrow Island is the first such find.

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ABSTRACT

The coastal plain fringing the North West Cape peninsula of semi-arid tropical Western Australia contains a poorly known stygofauna; a root-feeding fauna (Heteroptera: Meenoplidae) inhabits the aerial spaces. The fauna includes the only known vertebrate troglobites in Australasia (fishes) and several species of crustacea including the only known member of the Order Thermosbaenacea in the southern hemisphere, considered a Tethyan relic. Barrow Island, 160 km to the north-east across the North West Shelf, also contains a relict stygofauna with some affinities to the fauna of the North West Cape peninsula as well as having unique characteristics.

Lower sea levels, as recently as the Holocene, would have broadly exposed the North West Shelf, itself contiguous with similar shelves around the north of Australia. This vast coastal plain would have provided a continuous ecosystem linking the Tertiary deposits of the North West Cape and Barrow Island, with formations of sufficient age to provide the linkage required if tectonic plate rafting is to be a tenable zoogeographic hypothesis for Tethyan relicts.

RESUME

La plaine côtière bordant la péninsule du "North West Cape", située dans la partie tropicale semi-aride de l'Australie occidentale, présente une faune stygobie faiblement connue ; une faune s'alimentant à partir des racines (Heteroptera : Meenoplidae) peuple les espaces aériens. La faune souterraine de cette région comprend les seuls vertébrés troglobies connus d'Australasie (Poissons) et plusieurs espèces de Crustacés incluant la seule espèce connue dans l'hémisphère sud, de l'ordre des Thermosbaenacés, qui est considérée comme une relicte de la Téthys. Barrow Island, située à 160 km au nord Est de la "North West Shelf", renferme également une stygofaune relicte qui présente quelques affinités avec la faune de la péninsule du North West Cape" et qui a des caractéristiques tout à fait particulières.

REFERENCES

- BANARESCU, P. 1990 Zoogeography of fresh waters, Vol. 1. General Distribution and dispersal
- BOUSFIELD, E. L. 1973 Shallow-water gammaridean Amphipoda of New England. Cornell University Press, Ithaca, 312 pp.
- BOUTIN, C. and N. COINEAU 1990 "Regression Model", "Modèle Biphase" d'évolution et ori- ILIFFE, T. M., WILKENS, H., PARZEFALL, J. and gine des micro-organismes stygobies interstitiels continentaux. Rev. Micropaléontol., 33, p. 303-322.
- CALS, P. and C. BOUTIN 1985 Découverte au KENSLEY, B. and M. SCHOTTE 1989 Guide to Cambodge, domaine ancien de la Tethys orientale, d'un nouveau 'fossile vivant' Thermosbaena cambodjiana n. g., n. sp. (Crustacea, Thermosbaenacea). C. R. Acad. Sci., Paris, série D, 300, 8, p. 337-340.
- CHAPPELL, J. and B. G. THOM 1977 Sea levels and coasts, p. 275-291. In: Sunda and Sakul: Prehistoric studies in southeast Asia, Melanesia and Australia, Allen, J., Golson, J. & Jones, R. (Eds). Academic Press, London.
- DANIELOPOL, D. L. 1990 The origin of the anchialine cave fauna - the "deep sea" versus the "shallow water" hypothesis tested against the empirical evidence of the Thaumatocyprididae NEWMAN, W. A. - 1991 - Origins of southern hemi-(Ostracoda). Bijd. Dierk., 60, p. 137-143.
- HART, C. W., MANNING, R. B. and T. M. ILIFFE -1985 - The fauna of Atlantic marine caves: while maintaining ties to deep waters. Proc. Biol. Soc., Washington, 98, p. 288-292.
- HOCKING, R. M. 1990 Carnarvon Basin. In: Geology and mineral resources of Western Australia, Western Aust. Geol. Survey, Memoir 3, p. 457-495.
- HOLTHUIS, L. B. 1960 Two new species of Atyid shrimps from subterranean waters in N.W. Australia (Decapoda: Natantia). Crustaceana, 1, p. 47-57.
- HOWARTH, F. G. 1988 Environmental ecology of North Queensland caves: or Why there are so many troglobites in Australia, p. 76-84. In: Tropicon Conference, Lake Tinaroo, Far North Queensland, 27-31 Dec. 1988, Pearson, L. (Ed.). Australian Speleological Federation, Cairns.
- HOWARTH, M. K. 1981 Palaeogeography of the Mesozoic, p. 197-220. In: The evolving Earth, Cooks, L. M. R. (Ed.). Oxford University Press, Oxford.
- HUMPHREYS, W. F. 1990 The biology of a troglobitic schizomid (Chelicerata: Arachnida) from caves in the semi-arid Cape Range, Western Australia. Act. zool. Fennica, 190, p. 181-186.
- HUMPHREYS, W. F. and M. ADAMS 1991 The subterranean aquatic fauna of the North West

Cape peninsula, Western Australia. Records Western Aust. Mus., 15, p. 383-411.

- of freshwater animals. AULA-Verlag Wiesbaden. HUMPHREYS, W. F., ADAMS, M. and B. VINE -1989 - The biology of Schizomus vinei (Chelicerata: Schizomida) in the caves of Cape Range, Western Australia. J. Zool., London, 217, p.177-201.
 - D. WILLIAMS 1984 Marine lava cave fauna: composition, biogeography and origins. Science, 225, p. 309-311.
 - the marine isopod crustaceans of the Caribbean. Smithsonian Institution Press, Washington.
 - MESSANA, G. 1988 Stygobitic isopods of East Africa. Biogeographica, 14, p. 113-124.
 - MESSANA, G. and L. CHELAZZI 1984 The fauna of subterranean waters of East Africa, and particularly of Somalia. Stygologia, 2 p. 339-351.
 - MONOD, T. and P. CALS 1988 Systématique et évolution des Thermosbénacés (Arthropodes, Crustacés), d'après l'ordonnance des structures épidermiques superficielles. C. R. Acad. Sci., Paris, 306, (Série III), p. 99-108.
 - sphere endemism, especially among marine crustacea. Mem. Queensland Mus., 31, p. 51-76
- evidence of dispersal by sea floor spreading POORE, G. and W. F. HUMPHREYS 1992 First record of Thermosbaenacea (Crustacea) from the Southern Hemisphere: a new species from a cave in tropical Western Australia. Invertebrate Taxonomy, 6, p. 719-725.
 - SCHRAM, F. R. 1986 Crustacea. Oxford University Press, Oxford.
 - STOCK, J. H. 1977 The taxonomy and zoogeography of the Hadziid Amphipoda, with emphasis on the West Indian taxa. Stud. Fauna Curaçao, Amsterdam, 55, p. 1-130.
 - STOCK, J. H. 1980 Regression model evolution as exemplified by the genus Pseudoniphargus (Amphipoda). Bijdr. Dierk., 50, p. 105-144.
 - STOCK, J. H. 1986a Deep sea origin of cave fauna, an unlikely supposition. Stygologia, 2, p. 105-111.
 - STOCK, J. H. 1986b Two new amphipod crustaceans from the genus Bahadzia from the "blue holes" in the Bahamas and some remarks on the origin of insular stygofaunas of the Atlantic. J. nat. hist., 20, p. 921-933.
 - STOCK, J. H. and G. LONGLEY 1981 The generic status and distribution of Monodella texana Maguire, the only known north American Thermosbaenacean. Proc. Biol. Soc., Washington, 94, p. 569-578.
 - TRENDALL, A. F. 1990 Pilbara Craton, Introduction. In: Geology and mineral resources of

Western Australia. Western Aust. Survey, Memoir 3, p. 128-194.

- VEEVERS, J. J. 1991 Mid-Cretaceous tectonic climax, Late Cretaceous recovery, and Cainozoic relaxation in the Australian Region, p. 1-14. In: The Cainozoic in Australia: a re-appraisal of the evidence, M. A. J. Williams, P. De WILKENS, H., PARZEFALL, J. and T. M. ILIFFE -Deckker and A. P. Kershaw (Eds). Geological Society of Australia Special Publication No. 18, Sydney.
- Geol. WÄGELE, J.-W. 1985 On the Tethyan origin of the stygobiont Anthuridea Curassanthura and Cyathura (Stygocyathura), with description of Curassanthura canariensis n. sp. from Lanzarote (Crustacea, Isopoda). Stygologia, 1, p. 258-269.
 - 1986 Origin and age of the marine stygofauna of Lanzarote, Canary Islands. Mitt. hamb. zool. Mus. Inst., 83, p. 223-230.