

ON THE TETHYAN ORIGIN OF THE STYGOBIONT  
ANTHURIDEA *CURASSANTHURA* AND *CYATHURA*  
(*STYGOCYATHURA*), WITH DESCRIPTION OF *CURASSANTHURA*  
*CANARIENSIS* N. SP. FROM LANZAROTE  
(CRUSTACEA, ISOPODA)

BY

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SUMMARY

A second species of the hypogean genus *Curassanthura* Kensley, 1981 (Isopoda, Anthuridea, Paranthuridae) is described from the lava tunnel Jameos del Agua (Lanzarote, Canary Islands). Supposingly *Curassanthura* is a relict of a subterranean Tethyan fauna, which colonized macroporous sediments of coastal areas. The amphiatlantic distribution has probably been caused by continental drift. According to zoogeographical and morphological evidence it appears that the evolutionary scenario of the inland water subgenus *Stygocyathura* (Anthuridae) is of comparable nature. The combined influences of continental drift, active dispersion, and marine regressions are discussed for these anthurid taxa, whereas the importance of accidental transport and of competition is stressed.

ZUSAMMENFASSUNG

Eine zweite Art der hypogäischen Gattung *Curassanthura* Kensley, 1981 (Isopoda, Anthuridea, Paranthuridae) wird aus dem Lavatunnel Jameos del Agua (Lanzarote, Kanarische Inseln) beschrieben. Es wird vermutet, daß *Curassanthura* ein Relikt einer unterirdisch lebenden Tethys-Fauna ist, die küstennahe, grobporige Sedimente besiedelte. Die amphiatlantische Verbreitung ist auf Kontinentaldrift zurückzuführen. Zoogeographische und morphologische Hinweise deuten für die limnische Untergattung *Stygocyathura* eine ähnliche Verbreitungsgeschichte an. Das Zusammenwirken von Kontinentaldrift, aktiver Dispersion und mariner Regression wird für diese Anthuriden-Taxa diskutiert, auf die Bedeutung von zufälligem Transport und von Konkurrenzphänomenen wird hingewiesen.

INTRODUCTION

Prof. H. Wilkens (Hamburg, F.R.G.) recently discovered on Lanzarote (Canary Islands) in the cave Jameos del Agua (see Fage & Monod, 1936; Wilkens & Parzefall, 1974) a new anthurid isopod, which surprisingly turned out to be a new member of the monotypic genus *Curassanthura* (described from Curaçao by Kensley, 1981). The amphiatlantic distribution of this genus reminds us of the studies on the origin of the Caribbean stygobiont crustaceans (Stock 1976-1981) and incites considerations of the possible origin of other important, more frequent stygobiont anthurids, the members of the subgenus *Stygocyathura* Botosaneanu & Stock, 1982.

LE DOMAINE AQUATIQUE SOUTERRAIN DE LA PLAINE  
ALLUVIALE DU RHÔNE À L'EST DE LYON, 2.  
STRUCTURE VERTICALE DES PEUPELEMENTS DES  
NIVEAUX SUPÉRIEURS DE LA NAPPE <sup>1)</sup>

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SUMMARY

Sampling of three interstitial stations belonging to as many distinct hydrographic units of the same river system (the Rhône east from Lyon) proves the existence of three corresponding biocenoses. These are correlated with the hydrology and origin of the waters at each station.

Examination of the vertical distribution of the organisms in the upper layers of the substrate (form -0.5 to -3 m, the so-called "biological film"), reveals that the taxonomic diversity corresponds with the presence of different biocenoses in the biological film, and that the difference of the depth within the substrate is not expressed in the same way in each of the three stations.

These conclusions are based on factorial analysis by correspondences of the data obtained during a 3-years survey.

RÉSUMÉ

L'échantillonnage de trois milieux interstitiels appartenant à trois unités hydrographiques différentes d'un même système fluvial (le Rhône à l'est de Lyon), conduit, dans un premier temps, à la constatation de l'existence de trois entités faunistiques correspondantes. Ce résultat peut être mis en relation avec l'hydrologie et l'origine de l'eau de chaque station.

L'étude de la répartition verticale des organismes au sein des couches supérieures du sédiment ("pellicule biologique") permet, dans un deuxième temps, de constater qu'à cette différenciation taxonomique correspond l'existence de structures biocénétiques distinctes dans la pellicule biologique. L'effet de la profondeur ne se fait donc pas sentir de manière identique dans les trois stations. Ces conclusions sont basées sur une analyse factorielle des correspondances à partir des données obtenues pendant 3 ans.

I. INTRODUCTION

La distribution verticale des organismes au sein d'un sédiment immergé a été abordée à la fois par les benthologues et les phréatobiologistes. En effet, suite à la formulation du paradoxe d'Allen<sup>2)</sup>, les chercheurs ont souligné le rôle

<sup>1)</sup> Ce travail est extrait d'une thèse de doctorat de troisième cycle soutenue le 13 octobre 1983 à l'université Claude Bernard de Lyon.

<sup>2)</sup> "Les hydrobiologistes ont l'habitude de comparer les besoins alimentaires d'un poisson (truite par exemple) et la biomasse disponible au niveau du benthos. Or, la voracité du poisson est satisfaite bien que les possibilités soient 6 fois inférieures aux besoins selon les évaluations. Ce déficit est connu sous le nom de "paradoxe d'Allen" (Bou, 1977).

## SYSTEMATICS

**Curassanthura canariensis** n. sp.

Material — 10 specimens from the type locality, collected 1976-1983, Postmanca 3.5 mm, immature adult specimens 5-7.5 mm. All specimens deposited in the ZMH (Zoologisches Museum Hamburg).

Holotype — Immature adult, 7.5 mm, ZMH.

Locus typicus — Wilkens collected the species between lava gravel (diameter 2-5 mm) of the upper sublittoral of the Jameos del Agua, close to the entrance Jameo Grande. A connection with the sea exists at a distance greater than 1,400 m (the presently explored length of the submarine tunnel), the water in the tunnel has nearly the same salinity as the sea.

*C. canariensis* n. sp. lives between the gravel and disappears very quickly when exposed to light. Associated fauna: *Liagoceradocus* (or *Hadzia*) *acutus* (Amphipoda), *Typosyllis cornuta* (Polychaeta), Copepoda spp. (personal communication of Prof. Wilkens; see Iliffe et al, in preparation).

*Abbreviations used in text and figures:* A 1,2: antenna 1, 2; Md: mandible; Mx 1: maxilla 1; Mxp: maxilliped; P 1-7: pereopods 1-7; Plp 1-5: pleopods 1-5; Tel: telson; Urp: uropod; (M): postmanca stage.

Description of the holotype. — Blind, unpigmented paranthurid, about 11 times longer than wide. Cephalon slightly longer than wide, with small rostral point. Relative length of pereonites: cephalon  $<1 < 2 > 3 = 4 = 5 < 6 < 7$ , pleonites 1-5 together somewhat longer than pereonite 7, not fused (fig. 1). Pleonite 6 fused with telson.

A 1 (fig. 1) with 7 flagellar articles; first article with feather-like bristle, articles 4, 5 and 6 each with one aestetasc, last article short, with 4 setae; peduncle 3-segmented. First article of A 2 short, following 4 peduncular articles long and slender, flagellum 8-segmented; each flagellar article with 3-4 short setae, last article with 4 longer setae.

Mouthparts of stinging/sucking type, covered dorsally by labrum. Palp of Md 3-segmented, second article longest, with 1 seta, third article with 3 setae, the longest bearing short setules. Mx 1 lanceolate, apex laterally serrated with 17 indentations. Basipodite of Mxp with long, strong endite reaching beyond second palp article; palp 5-segmented, fourth article bearing 2 setae, last article with 4 setae (fig. 1).

P 1 subchelate, articles relatively slender with exception of the proximally broadening stout propodus; palm of propodus with basal tooth and row of 20 short pectinate spines (fig. 2) and a few scattered simple setae, palm with 2 small distal plumose setae. P 2-7 slender, not subchelate, articles elongate-cylindrical. Palm of P 2 with 6, palm of P 3 with 7 sensory spines, carpi each with 1 sensory spine. Propodus of P 4-7 with 3, carpus with 2 sensory spines. Basipodite of P 2-7 with 2-3 very long scolopidial feather-like setae.

Plp 1 operculiform, exopod with 10, endopod with 3 swimming setae, exopod about 5 times wider than endopod. Exopod of Plp 2 with 3, endopod with 2 swimming setae. Exopod of Urp very small (fig. 3) with 2 in situ medially directed plumose setae, apex with 1 long and 1 very short seta. Endopod of Urp considerably shorter than sympod and only half as wide. Telson proximal-

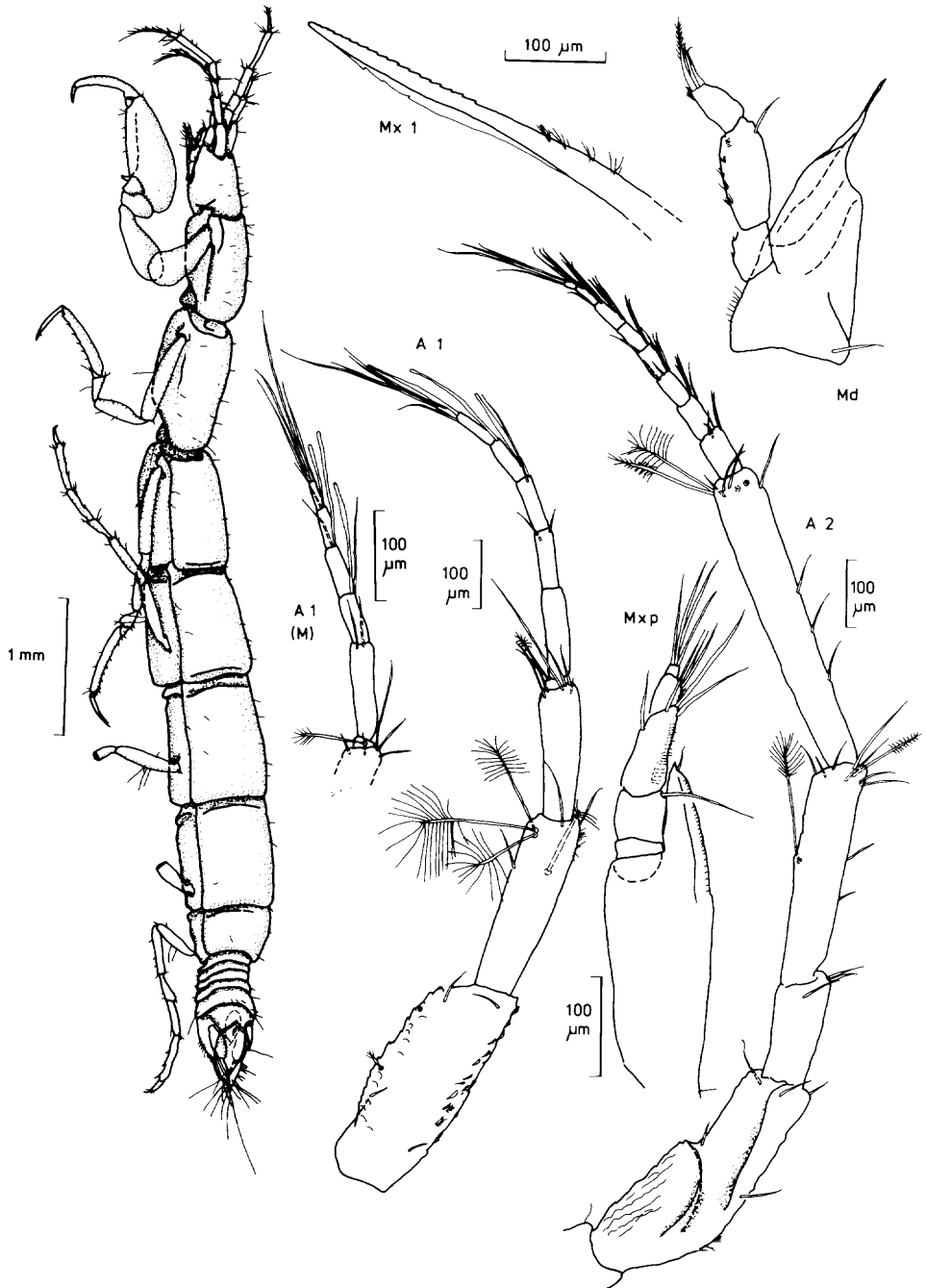


Fig. 1. *Curassanthura canariensis* n. sp. All figures except (M) (= postmanca) from holotype. Whole animal shown in dorsal view.

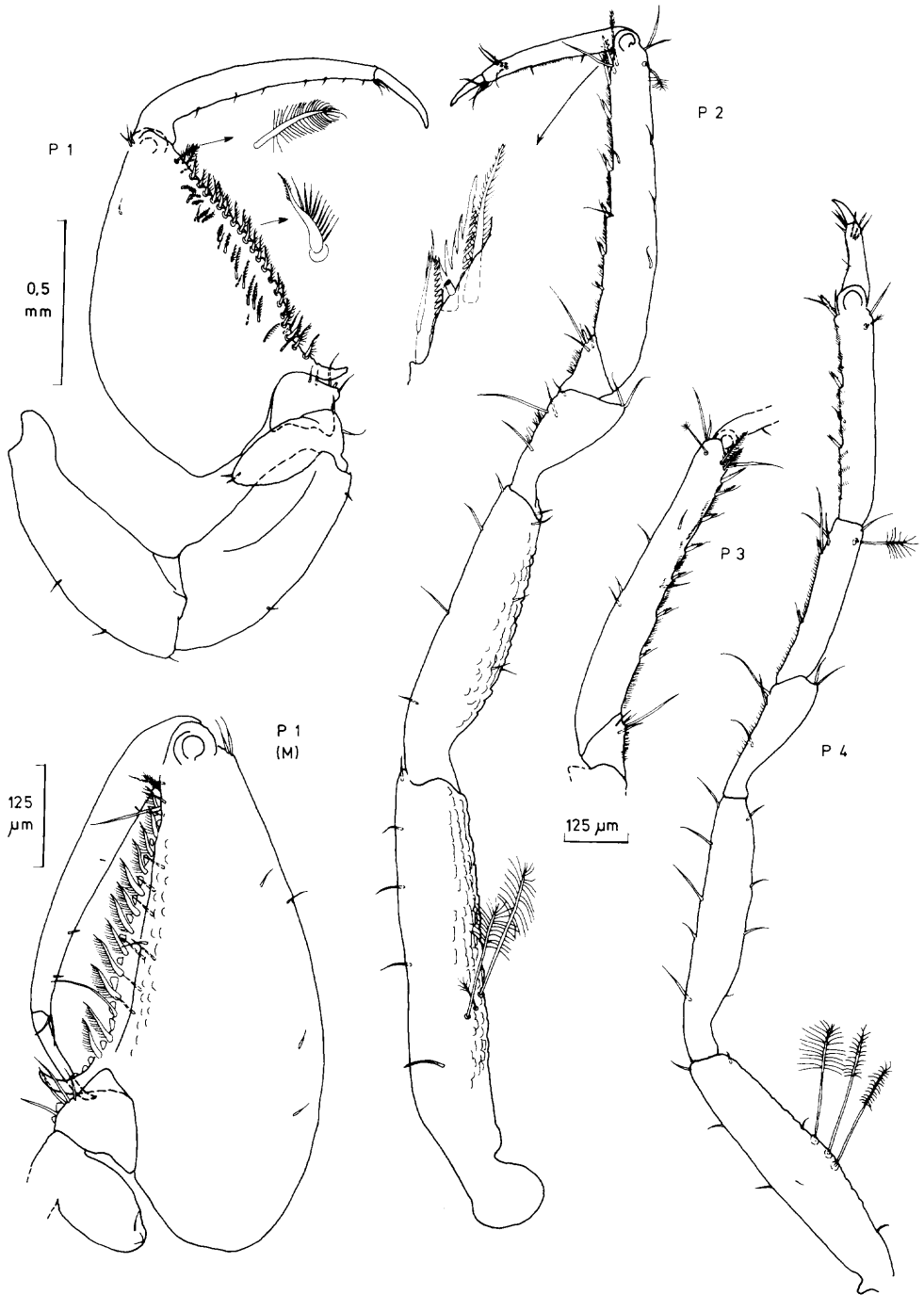


Fig. 2. *Curassanthura canariensis* n. sp. (M): postmanca stage. Arrows point to some enlarged drawings of characteristic spines of the pereopods.

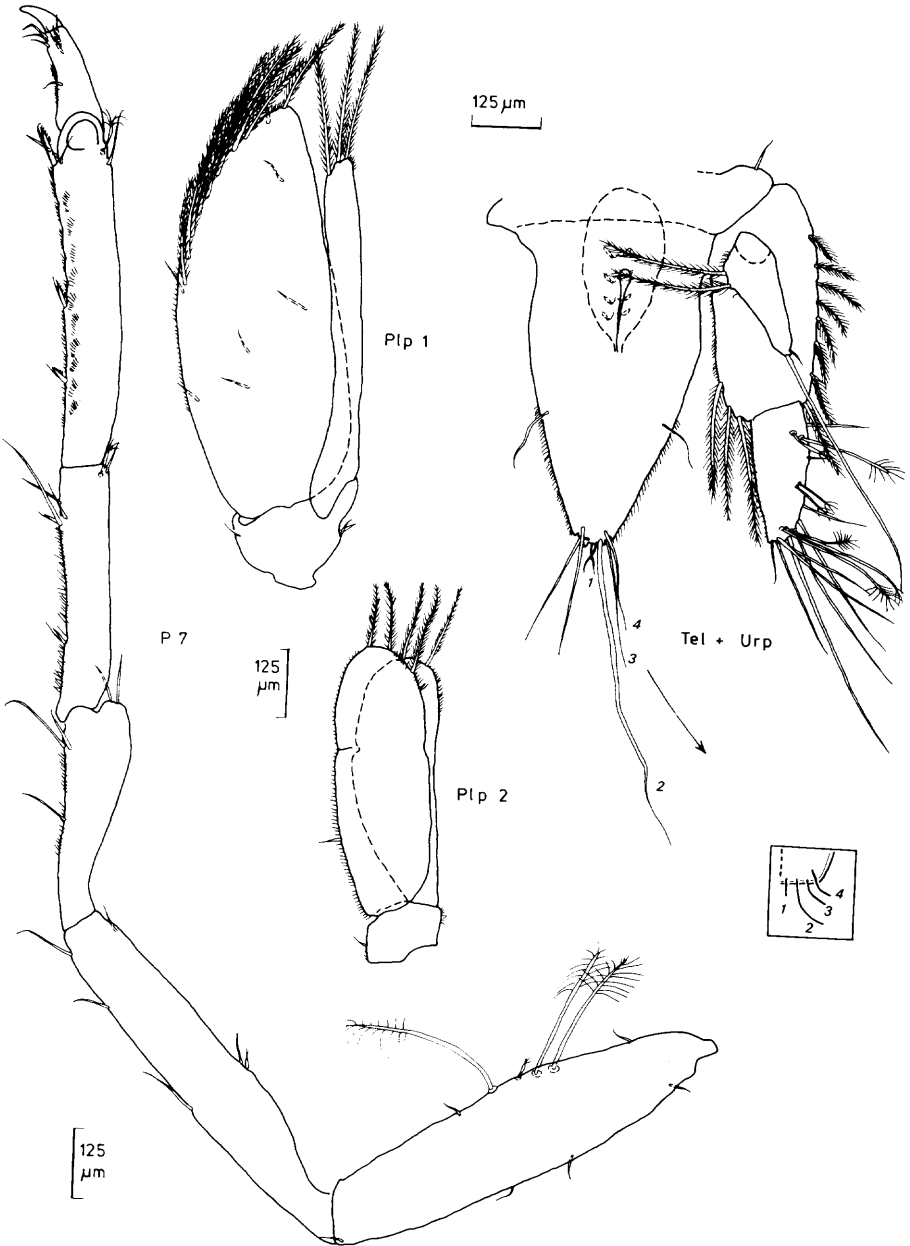


Fig. 3. *Curassanthura canariensis* n. sp., holotype. Diagram of half telsonic apex shows arrangement of setae.

ly wide, tapering to narrowly rounded apex. Single proximally staocyst with 4 pairs of sensory hairs visible through cuticle. Telsonic apex with 4 pairs of setae (fig. 3).

Variability. — The number of pectinate spines on the palm of the propodus of P 1 is only 12 in the postmanca stage and increases to 20 in the adult. The postmanca has only 6 flagellar articles on A 1 (instead of 7), but the setation of the distal articles is constant. The number of swimming setae on the pleopods is not constant in adult specimens, the exopod of Plp 1 can bear 6 to 10, the endopod 3 to 4 setae, the exopod of Plp 2 has 3 to 4 setae.

Comparison with *Curassanthura halma* Kensley, 1981. — Both species of *Curassanthura* have a similar morphology and differ only in minor details, the Caribbean species being much smaller and having less setae. In *C. canariensis* n. sp. the flagellum of A 1 has one article more than *C. halma* (7 instead of 6), the second palp article of the Mxp has 4 instead of 3 setae; there are much more pectinate spines on the propodal palm (20 instead of 8). The articles of P 2-7 are more slender and have a richer setation compared with *C. halma*, but the exopod of the Urop bears fewer setae (4 instead of 6), the setation of the uropodal endopod and of the telsonic apex is identical (see Kensley, 1981; Wägele, 1982a). *C. halma* is much smaller (2.0 to 2.3 mm) than *C. canariense* (3.5 to 7.5 mm).

#### THE EVOLUTIONARY SCENARIO OF CURASSANTHURA

There can be no doubt about the close relationship between the two species from Lanzarote and Curaçao. No species of the genus are known from the open sea, and as point of fact are not to be expected.

The marine benthos contains many species of highly evolved and successful Paranthuridae, which live on the sediment or on algae (i.e. *Leptanthura*). *Curassanthura* has typical morphological adaptations to a hypogean/interstitial way of life (Wägele, 1982a) and is at the same time phylogenetically an old form. The genus is the most primitive known of the stinging/sucking, predatory 'higher paranthurids' (Wägele, 1981). At the time of the origin of the genus *Curassanthura* species of the families Hyssuridae and Anthuridae, both normally belonging to the endofauna, and also the less specialized primitive Paranthuridae must already have existed in other marine biotopes. A species with the morphology of *Curassanthura* could only survive in a special niche, and this probably was the interstitial system of coarse sediments, as they occur close to or on the shore, in anchihaline habitats. Presently, the species seem to survive in ecological refuges, in which competitive pressure of other taxa is reduced.

As the Anthuridea neither have efficacious swimming stages nor planktonic larvae, their present distribution can only be explained by passive or slow ac-

tive dispersion. In the case of the hypogean genus *Curassanthura*, a population with a gene exchange that included both areas (West Indies-Canary Islands), nowadays separated by the Atlantic Ocean must once have existed. The same must be true for the other amphiatlantic genera, which occur in Jameos de Agua [*Speleonectes* (!) (Remipedia), *Spelaeonicippe* (Amphipoda), *Heteromysoides* (Mysidacea), *Gesiella* (Polychaeta); personal communication of Prof. Wilkens; see Iliffe et al., in preparation]. However, this distribution cannot be explained by continental drift alone. Dispersion phenomena are also important, as revealed by the geology of the places where the animals were discovered.

Lanzarote belongs together with Fuerteventura to the old part of the Canary Islands, with probably Palaeozoic sediments (Rothe & Schmincke, 1968). It seems that once a contact with the African continent existed, as indicated by fossils of terrestrial fauna (12 My old eggs of ostriches, eggs of terrestrial turtles). Volcanism began during the Upper Cretaceous (Rothe, 1968, Evers et al., 1970), although the lava tunnel of Jameos del Agua is only 3,000 to 5,000 years old (Wilkins & Parzefall, 1974). The relict taxa now found in this cave must have been living on Lanzarote before the formation of the Jameos, and somehow (?) managed to colonize it after it had been formed. It is not known, whether connections exist with other subterranean waters (older lava tunnels) or whether these hypogean genera live in other Canarian anchihaline caves; nevertheless, a local dispersal of these animals must have taken place.

Curaçao is of Miocene origin and separated by deep water from the neighbouring islands (Aruba, Bonaire). In spite of its geological youth it houses a rich stygofauna, descendents partly from continental, partly from marine ancestors (i.e. Stock, 1977a; Stock, 1982a). Considering its phylogenetic age *Curassanthura* must have had ancestors in other Caribbean areas. In this context it is interesting to bear in mind that *Curassanthura* probably also occurs in Cuba (Wägele, 1982a). Likewise it must be emphasized that the geological history of the Caribbean is rather complex, it is possible that a "proto-Antillean archipelago" linked North and South America in Cretaceous times (discussion in Hedges, 1982).

The most probable explanation for the amphiatlantic distribution is, as already mentioned, that of plate tectonics. *Curassanthura* seems not to belong to those stygobiont crustaceans, whose biogeography can be explained by Miocene/Pliocene marine regressions (Stock, 1977-1981), the genus already could have existed in the Upper Cretaceous.

This opinion is supported by the simultaneous occurrence of several amphiatlantic genera in the Jameos del Agua (see above). It is not very probable, that just here several marine immigrants of considerable phylogenetic age (*Speleonectes*!) and morphological specialization met. It rather appears as if here remains of an ancient hypogean Tethys-fauna are surviving. Discussing the discovery of *Spelaeonicippe* on Providenciales (Turks & Caicos Islands) Stock & Vermeulen (1982) indicate a different possible history: the genus is supposed to

be of Pleistocene/Holocene origin, a marine *Spelaeonicippe* being the ancestor. In this case the invasion of the subterranean habitats must have occurred twice, in analogous way, at two distant places. A marine ancestor still has to be found.

For a comprehensive analysis of the biogeography of single taxa we do not only require the data on the local geology and history, and on the biology and ecology of the species in question, but also on its phylogenetic relationships. Very often a satisfactory analysis is not possible and the considerations remain partially speculative. Nevertheless, they may lead to new discoveries and ideas.

Another group of hypogean anthurids seems to be much more successful than the few stygobiont paranthurids, namely the species of *Cyathura* (*Stygocyathura*).

#### THE PROBLEM OF THE ORIGIN AND BIOGEOGRAPHY OF *STYGOCYATHURA*

For many groups of hypogean crustaceans on continents and islands a polyphyletic origin has been proposed, assuming parallel invasions from marine ancestral biotopes (i.e. Bowman, 1981; Fryer, 1965; Monod, 1975; Stock, 1976 etc.). This seems to be evident as long as closely related marine relatives are known or are to be expected as possible ancestors (Ingolfiellidae: Stock, 1977b; Microparasellidae: Stock, 1977c; *Pseudoniphargus*: Stock, 1980; Bogidiellidae: Stock, 1981b). But a marine origin is not the only possibility. That a colonization of hypogean euryhaline biotopes is also possible by animals of limnetic origin is shown by the example of the genus *Hexabathynella* (see Schminkè, 1972) or of the Atlantasellidae and Microcerberidae (Wägele, 1983). A similar discussion has been summarized by Sterrer (1973) for the interstitial sand fauna. These species possibly colonized the sandy beaches of Pangaea, their ancestors being either of marine or limnic origin, plate tectonics and local dispersion being responsible for their actual distribution.

In the case of *Curassanthura* a general 'marine origin' seems most probable, but we must imagine that the genus itself always was restricted to macroporous interstices, close to the coast of the western Tethys Sea (present paper). A different situation is found in the genus *Cyathura* with its marine, euryhaline and limnic species, but in the following a mechanism of distribution similar to that of *Curassanthura* is proposed for the latter group of cyathurans (continental drift + local dispersion).

Wägele (1982b) asked, if the stygobiont cyathurans might have a common ancestor, as the species from Mexico, Sarawak, Réunion and New Caledonia have similar appendices masculinae. Botosaneanu & Stock (1982) in a study of several new species from the West Indies answer indirectly in the affirmative by the erection of the subgenus *Stygocyathura* for the mostly inland water stygobiont species. These have several corresponding apomorphies, belong to the same

taxon, thus with high probability are a monophyletic group. To the features listed by Botosaneanu & Stock (1982) we can add, that the telson is clearly broader than in the non-stygobiont species, the relation of width to length ranging from 1:1.5 to 1.8 instead of from 1:2.0 to 1:2.3.

As our knowledge of the morphology is rather incomplete in many cyathurans cladistic relationships are difficult to reconstruct. Nevertheless, the structure of the male copulatory organ (fig. 4) indicates some interesting evolutionary lines.

As far as is known, most of the marine species of *Cyatura* have a simple rod-like appendix masculina, similar to that of most other Isopoda. It must be considered plesiomorphic within the genus. Those species living in estuaries or on the sea-floor close to the mouth of rivers have a male stylet of the *carinata*-type; to this group we must also count the marine species *C. burbancki* (Northwestern Atlantic Ocean).

Compared with these benthic species the appendix is very variable in the interstitial/stygobiont group. It is indeed well-known that species of similar ecology and morphology evolve progamic isolating mechanisms. This explains the variability of copulatory organs in Microcerberidae (Isopoda) or in Bathynellacea (Syncarida).

Comparing the appendices masculinae it appears probable, that Botosaneanu & Stock (1982) are correct in assuming that *Cyathura numeae* could be an intermediat stage in the colonization of the subterranean biotopes, half-way between the sea and in less salty groundwaters. The morphology of the pereopods, the reduction of the endopod of Plp 1 point to the same conclusion. *C. sbordonii* (Mexico), *C. chapmani* (Sarawak) and *C. milloti* (Réunion) can be derived from the *numeae*-type. These 3 species have similar (homologous?) apical structures on the appendix, while the insular Caribbean species have a more derived morphology (fig. 4).

From this comparison the idea arises, that the brackish-water species (*carinata*-type) evolved from marine ancestors and spread over the Tethys-area (see also Burbank, 1967). The line culminating in *Stygocyathura* could have been derived from the *carinata*-type. *Stygocyathura* subsequently conquered the freshwater interstitial systems of the Tethys-area, the older successful species belonging to the *milloti-sbordonii-chapmani*-type, which survive in isolated localities to the present. They probably were not able to dominate in the marine biotopes, since we must assume that the *carinata*- and *numeae*-type still existed there (up to nowadays).

The occurrence on young islands or coastal areas can be explained not necessarily by the regression-model alone. It is well known that accidental colonization of islands can lead to successful dispersion and adaptive radiation of taxa that are rare on the adjacent ancestral areas.

In some other (Mesozoic?) crustacean taxa (i.e. Thermosbaenacea, some Cirolanidae) a similar mode of evolution is conceivable, a combination of con-

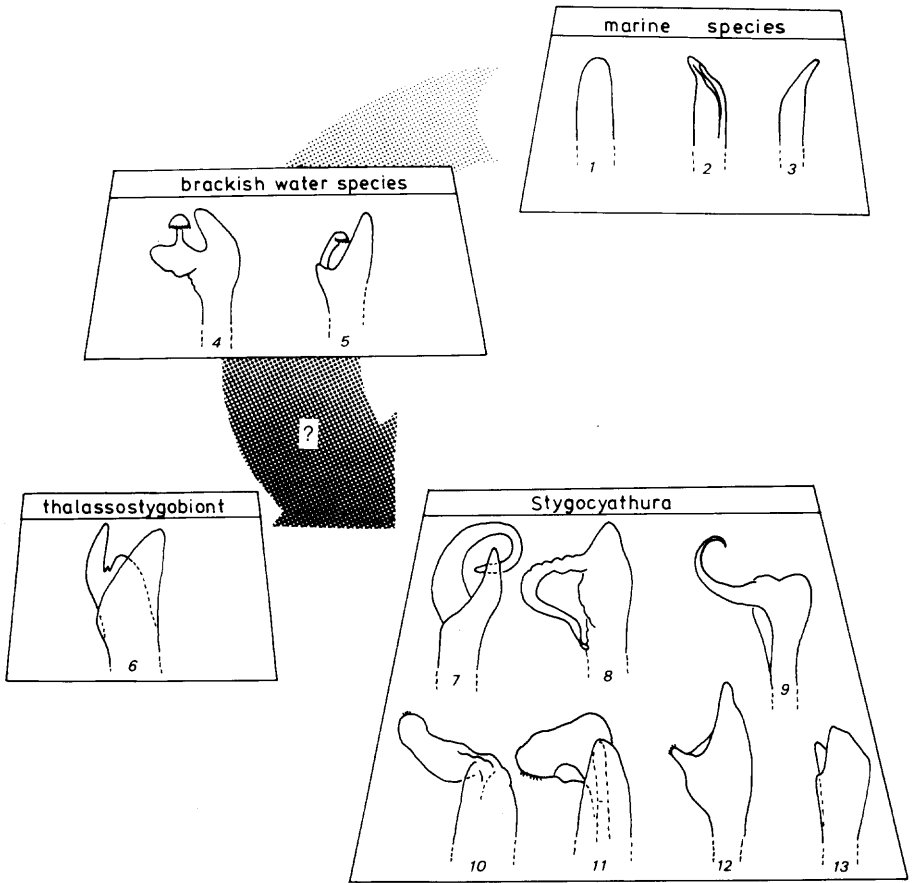


Fig. 4. Apical part of appendix masculina in species of *Cyathura*. Arrow indicates possible way of evolution (see text). 1: *C. profunda* (Southwest Atlantic), *C. munda* (California). 2: *C. cubana* (Cuba). 3: *C. rudloei* (Mozambique), possibly also *C. crucis* (St. Croix). 4: *C. carinata* (Europe), *C. burbancki* (off Georgia), *C. kikuchii* (Japan), *C. polita* (Atlantic coast of North America). 5: *C. muro-miensis* (Japan). 6: *C. numeae* (New Caledonia). 7: *C. milloti* (Réunion). 8: *C. chapmani* (Sarawak). 9: *C. sbordonii* (Mexico). 10: *C. hummelincki* (Aruba). 11: *C. curassavica* (Curaçao). 12: *C. salpiscinalis* and *C. motasi* (Haiti). 13: *C. specus* (Cuba).

tinental drift, local competition (as discussed by Stock (1981b, 1982b) for Hadziidae or Bogidiellidae and Thermosbaenacea), also of marine regression and active dispersion of single taxa being responsible for the present day distribution.

Studying the distribution of *Stygocyathura* in detail many problems turn up which remain unanswered. But the purpose of this discussion is to show that cladistic studies based on comparative morphology are as important as any other method used to gain biogeographic evidence.

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