FACULTY OF SCIENCE

UNIVERSITY OF COPENHAGEN

Evolution of anchialine, cave endemic spionids (Spionidae, Annelida): the first clade of cave annelids with full-Tethyan distribution.

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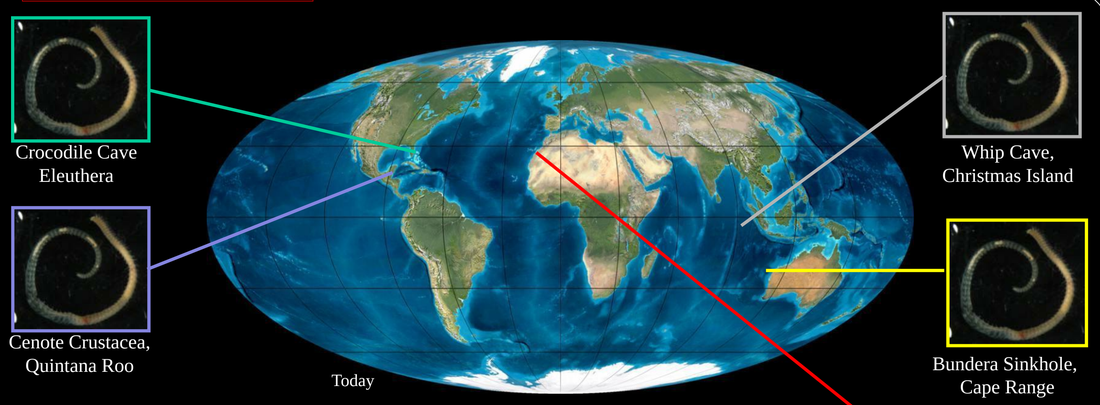
Spionidae is one of the most species-rich families of marine annelids with hundreds of described taxa all over the world. Although most species are infaunal, spionids have been recorded from a variety of marine habitats, including rocky substrates, hydrothermal vents, or as endosymbionts in sponges or parasites of bivalves. Until now, only Prionospio thalanjii from Bundera sinkhole (Western Australia) was considered a cave endemic species .

We here describe three new cave species of Prionospio collected from anchialine caves in Bahamas, Canary Islands and Christmas Island. Unlike their marine relatives, the four cave endemic spionids were found in the water column of these caves, far from the bottom. Phylogenetic analyses based on five molecular markers and 29 morphological characters yielded a well-supported clade grouping the four cave endemic species. This clade was nested within the family, but next to rather than among the marine *Prionospio* species included in the analyses. Character reconstruction based on light and scanning electron microscopy investigations showed that the clade is characterized by blunt prostomium, absence of eyes, small nuchal organs, presence of more than 30 pairs of branchiae, absence of notopodial hooks, neuropodial hooks from segment 60, and bilobed pygidium bearing one short, dorsal cirrus. This is the first lineage of cave endemic annelids with a full-Tethyan distribution. Similar distribution patterns have been described in several groups of crustaceans, including Remipedia or Atyidae.

DISTRIBUTION



Distribution of the continents in the Early Jurassic, showing the approximate position of the caves

Five species found in anchialine caves around Ancient Tethyan coast-lines, suggesting that they could represent an ancient, relictic clade of cave annelids

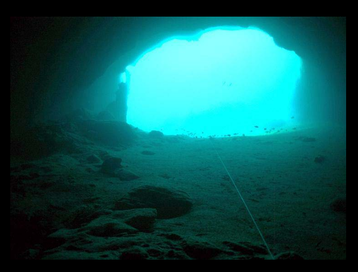
Disjunt full-Tethyan distribution, exclusively in caves

ECOLOGY

		Salinity	FSW layer	Geology	Landmass	Age	Currents	Light	O.M. Source
Túnel Atlántida	Lanzarote, CAN	Marine	No	Volcanic	Oceanic Isl	15 myr	Tidal	No	Marine P.O.M
Whip Cave	Christmas Isl, AU	Marine	Yes	Lim. on volcanic	Oceanic Isl	10 myr	No	No	Marine P.O. M.?
Bundera Sinkhole	Cape Range, AU	Marine	Yes	Limestone	Continent	>200 myr	No	No	Bacterial chemosynthesis
Crocodile Cave	Eleuthera, BH	Marine	Yes	Limestone	Island	>200 myr	Tidal	No	Marine P.O. M.
Cenote Crustacea	Quintana Roo, MX	Marine	Yes	Limestone	Continent	>200 myr	No	No	Bacterial chemosynthesis

Ecological traits of the sampled localities. *Abbreviations: AU, Australia; BH, Bahamas, CAN, Canarias Islands; FSW, freshwater; MEX, México; O.M., organic matter, P.O.M., particulate organic mater.*

Túnel de la Atlántida, lava tube (E. Dominguez)



Crocodile cave, Eleuthera (T. Iliffe)

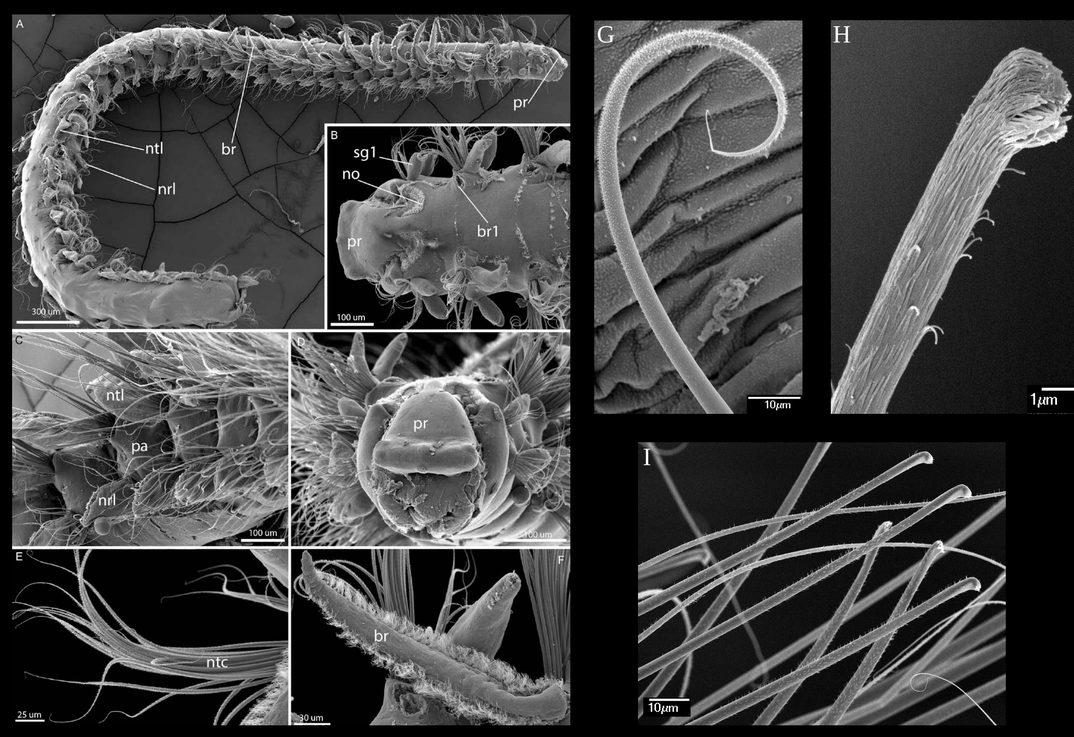
Whip Cave, Christmas Isl (T. Iliffe)

Ecology of the '*Spelaeospio*' species:

- Collected from the water column or artificial substrates.
- Never found in mud or sandy sediment samples.
- Free living, no tubes.

Hard substrates in anchialine caves

MORPHOLOGY AND BEHAVIOR



SEM micrographs, *Prionospio* n. sp. (Lanzarote). A. Overview anterior fragment. **B**. Prostomium, dorsal view. **C**. Parapodia from midbody. **D**. Prostomium frontal view. **E**. Capillary notochaeta. **F**. Branchiae. **G**. Blade chaeta. **H**. Detail of a neuropodial hook. **I**. Neuropodial hooks. *Abbreviations: br, branchiae, br1, scar of the first branchiae; nrl, neuropodial lobe; ntl, notopodial lobe; ntc, notochaeta; pa, parapodia; sg1, first segment.*

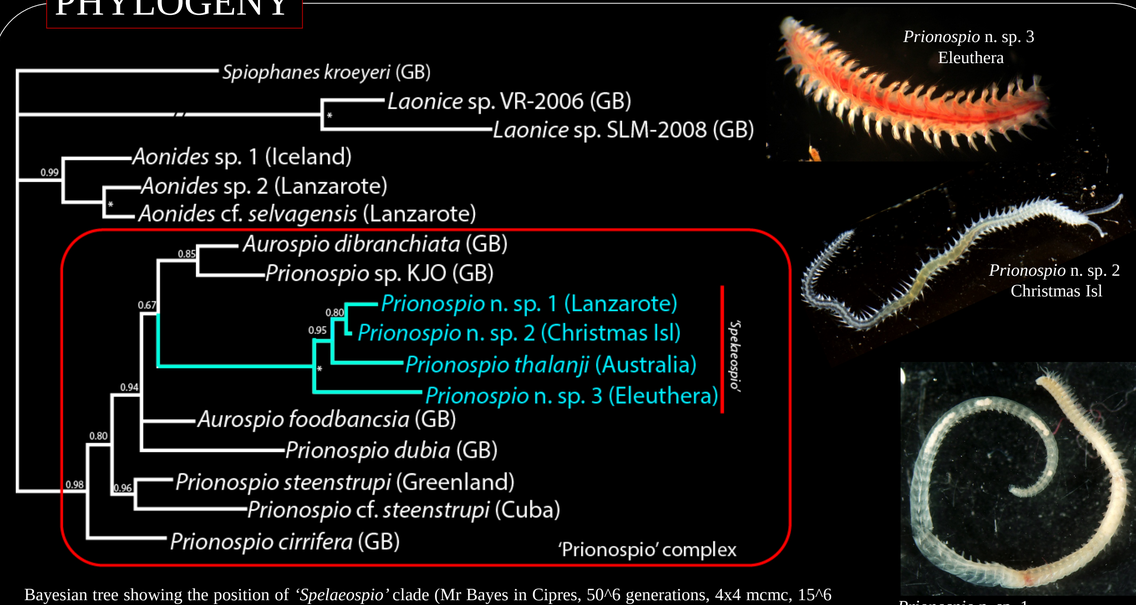
LM micrograph, *Prionospio* n. sp. (Lanzarote). Pygidium

Snapshots from video recording showing swimming behavior of *Prionospio* n. sp. (Lanzarote). Time interval between pictures, 0.3 s

DIAGNOSIS OF SUBGENUS *'SPELAEOSPIO'* (synapomorphies bold): body long, more than 60 segments. Prostomium rectangular. Eyes reduced or absent. Nuchal organs short. More than 25 of smooth branchial pairs from segment 2. **Notopodial hooks absent. Neuropodial hooks after segment 30. Pygidium with one ventral cirri and two lateral leaflike appendages.**

Four new species with distinct morphology, three synapomorphies and swimming behavior

PHYLOGENY



Prionospio n. sp. 3
Eleuthera

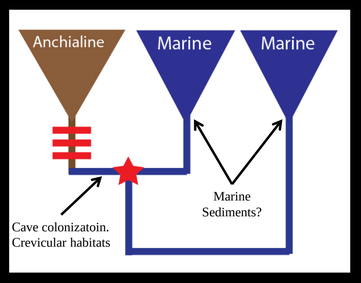
Prionospio n. sp. 2
Christmas Isl

Prionospio n. sp. 1
Lanzarote

Bayesian tree showing the position of '*Spelaeospio*' clade (Mr Bayes in Cipres, 50^6 generations, 4x4 mcmc, 15^6 burnin). Combined molecular (18S, 28S, H3, CO1, 16S) and morphological (28 binary and multistate characters, "c-coding" method) partitioned analyses. Taxon sampling based on "Spionidae clade 2" (Sigvaldadottir 1998). Bayesian posterior probabilities above branches. ML tree (RAxML) congruent in topology.

Subgenus *Spelaeospio* nested within the unsolved *Prionospio* complex

DISCUSSION AND PERSPECTIVES

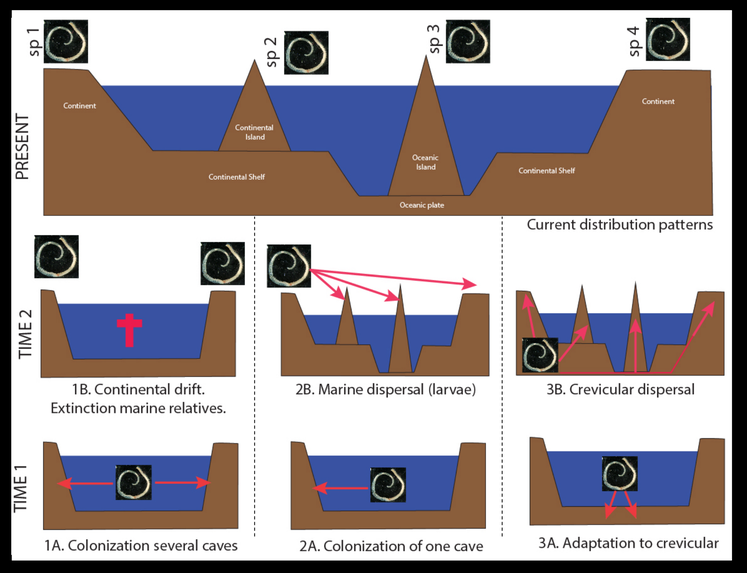


*Our trees show cave colonization in correlation with the origin of the subgenus '*Spelaeospio*' (Above).

*The internal topology of the clade is congruent with the age of the areas, but not with the extant geographical position, with the derived branching off species inhabiting young, oceanic islands.

*The presence of '*Spelaeospio* in oceanic islands rejects a purely vicariant model (Right, 1).

*The adaptations of the species to crevicular habitats somehow favours the third possible scenario (Right, 3), although more research is necessary.



Adaptation of the main biogeographical scenarios for the origin of cave faunas to the current study.

1. Relictic model (Humphreys, 2000).
2. Dispersal model (Kano & Kase 2000).
3. Zonal model and crevicular dispersal (Hart, 1985).

PROBLEMS:

- Relatively poor taxon sampling – Key representatives of the *Prionospio* clade are missing (*P. banyulensis, Minuspio*, deep sea).
- Lack of vouchers for many GenBank sequences, which prevents species re-identification.
- Missing data from GenBank sequences.

ON GOING WORK:

- More extensive phylogenetic and biogeographic analyses (parsimony, maximum likelihood).
- More concise morphological and ecological character reconstruction and correlation.