

A NEW GENUS AND SPECIES OF THE DEEP-SEA FAMILY CORONARCTIDAE (TARDIGRADA) FROM A SUBMARINE CAVE WITH A DEEP-SEA LIKE CONDITION.

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A new genus and species of the deep-sea family Coronarctidae (Tardigrada, Arthrotardigrada), collected from a sublittoral submarine cave in the French Mediterranean Sea, is described and illustrated. Tardigrades were only present in the first centimetres of the cave sediment (1.5-2 cm), where the 80 % of meiofauna, largely dominated by nematodes, is also concentrated. *Trogloarctus trionyches* gen. et sp. n. was only identified at the stations with complete darkness, mainly at the far end station. The new genus *Trogloarctus* shows several characters, distinguishing it from all known Coronarctidae: presence of only one somatic cirrus (cirrus E), three claws on each leg (reduction), and an absence of large accessory spine on the fourth pair of legs. The presence of bar shaped placoids in the pharyngeal bulb may be regarded as a plesiomorphic character. These differences involve the modification of the previous diagnosis of the family Coronarctidae in order to accommodate the new genus *Trogloarctus*. Ecology and geographical distribution of Coronarctidae is reviewed.

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INTRODUCTION

Deep-sea tardigrades have only been recorded since the mid-1960's, at the same time as the first deep-sea meiofauna studies. THIEL (1966) provides the first record of deep-sea tardigrades collected from the abyssal zone (-2600 to -4690 m depth) during the 1964/65 R/V *Meteor* cruise in the north-western Indian Ocean. However, the taxonomic history of the deep-sea Tardigrada started only 20 years ago when RENAUD-MORNANT (1974, 1975) discovered a new family of Arthrotardigrada: the Coronarctidae. This family was described from the Tardigrada collected by THIEL (1966) and the specimens collected during the *Wald*-cruise of the R/V *Jean Charcot* near the Walvis Ridge (SW Africa). Additional records from the NE Atlantic Ocean (*Eastward* and *Cape Hatteras* expeditions), NW Atlantic Ocean (*Biogas* cruises) and the Indian Ocean (Mozambique Channel, *Benthesi* expedition), widen the geographical range of Coronarctidae distribution (RENAUD-MORNANT 1987). More recent studies are discovering the presence of deep-sea tardigrades from surprising habitats such as the manganese nodule area of the eastern South Pacific (BUSSAU 1992). Mediterranean deep-sea Tardigrada do exist, but until now descriptions are lacking.

Investigations on marine cave fauna have revealed the existence of a unique community including an outstanding variety of endemic fauna, exhibiting unusual characteristics (LILFFE 1992). Many new high taxa of the Crustacea such as the class Remipedia (YAGER 1981), are primitive forms representing Mesozoic relicts (LILFFE & al. 1983; YAGER 1986; YAGER & HUMPHREYS 1996) that have survived sea level regressions. Marine caves and crevicular habitats may have served as refuges during these periods of time (HART & al. 1985). Finally, 'evidence of dispersal by sea floor spreading while maintaining ties to deep water' (HART & al. 1985) is supported through many examples of cave animals also found in deep-sea. Namely, Crustacea such as Peracarida (BOWMAN & LILFFE 1985), Copepoda (BOXSHALL 1989; HUYS 1993), and Decapoda (LILFFE & al. 1984), as well as Annelida Oligochaeta (ERSÉUS 1986), and Polychaeta (PETTIBONE 1989).

Environmental features of submarine caves are considered very similar to those of deep-sea habitat (RIEDL 1966). Both habitats may be considered climatically stable and non-rigorous environments (POULSON 1971), sharing features such as lack of light, limited food resources and in some cases lack of hydrodynamism. Despite these similarities one of the most important deep-sea factors,

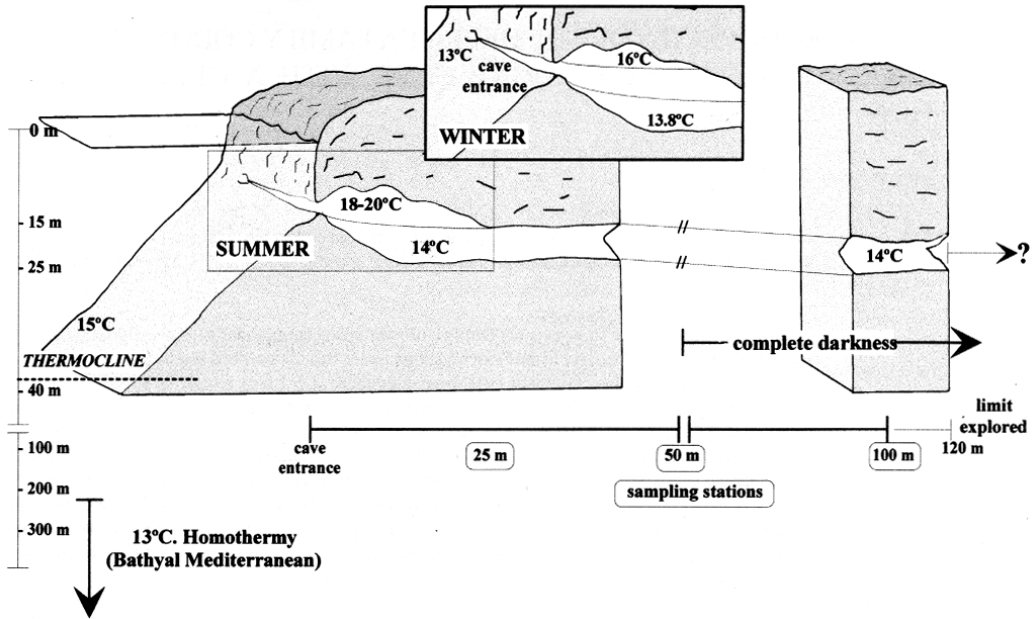


Fig. 1. Diagrammatic representation of the submarine cave, showing temperature conditions in summer and winter, and sampling stations at 25, 50, and 100 m from the cave entrance (near the explored limit) (Modified after BOURY-ESNAULT & al. 1993). The entrapment of water with stable temperature conditions resembles the warm homothermy of bathyo-abyssal Mediterranean water.

homothermy, is normally absent in littoral caves. This is not the case for the recently discovered Mediterranean cave called 'Trois Pépés', near Marseille. This cave consists of a 120 m long blind tunnel, with complete darkness after 50 m from the entrance. The floor of the cave is covered by muddy sediments, and slopes downwards (from -15 to -25 m depth) trapping homotherm water. This entrapment of water results in stable temperature conditions (13-14.5°C) resembling the 'warm' homothermy of bathyo-abyssal Mediterranean water. The cave is considered by VACELET & al. (1994) as 'a unique deep-sea habitat in the SCUBA zone'. Faunal similarities between the cave and the sessile benthic biota of the deep Mediterranean have been recently reported for brachiopods (LOGAN & ZIBROWIUS 1993) and hexactinellid sponges (VACELET & al. 1994). Previous works on marine cave tardigrades are practically unknown. The only study about cave tardigrades was carried out on the Italian coasts, where GRIMALDI DE ZIO & al. (1982) described four new species of the family Halechiniscidae.

As part of the French Program 'Dynamique de la Biodiversité et environnement' the floor sediments of the cave were sampled to study the biodiversity of meiofauna in aphotic Mediterranean environments. In this easily accessible 'bathyal sampling site' invertebrates representative of Mediterranean deep-sea meiofauna were expected

to be found. The study of tardigrades has revealed an interesting new genus and species belonging to the deep-sea family Coronarctidae previously unknown in the Mediterranean Sea. The new taxa *Trogloarctus trionyches* gen. et sp.n. has been identified from the more remote cave sample. This paper gives an amended diagnosis of the family Coronarctidae to accommodate the new genus and presents a full description of the new genus and species *Trogloarctus trionyches*.

MATERIAL AND METHODS

The cave called 'Trois Pépés' (Fig. 1), is located near La Ciotat (East of Marseille, French Mediterranean). It is a 120 m-long inwardly-descending gallery running within an oblique stratum in an Upper Cretaceous conglomerate (VACELET & al. 1994). The floor slopes from -15 m at the entrance to -25 m at the far end (the terminus has not yet been reached). The gallery slopes downwards trapping cold water (13.0°C winter to 14.5°C summer). Salinity of the cave is similar to open water near the entrance (38.2‰). Darkness is complete after 50 m from the entrance. Covering the floor there are several meters of muddy sediment with traces of biogenic activity, such as echiurid burrows resembling those photographed in the Ionian Sea at 2200-2400 m (BOURY-ESNAULT & al. 1993).

Sediment samples were collected by SCUBA divers with hand-driven Plexiglas corers (10 cm² area), at 25, 50, and 100 m from the cave entrance. The corers were sectioned into 5 portions (0-2, 2-5, 5-8, 8-11 and 11-14 cm). Ludox-TM centrifugation technique was used for meiofauna extraction. Only the first portion (0-1.5, or 0-2 cm) of samples at 50 and 100 m from the entrance contained tardigrades.

Observations of tardigrades were made on specimens mounted in glycerol, using a coverslip with supports to prevent body deformations. Interference-contrast (Olympus, Nomarski) was used for observations and photo micrographs of the specimens. All drawings have been prepared using a camera lucida on a Wild microscope (x 1 250).

The type series of *Trogloarctus trionyches* gen. et sp. n. is deposited in the collections of the Muséum National d'Histoire Naturelle de Paris (MNHN).

SYSTEMATICS

Family Coronarctidae RENAUD-MORNANT, 1974

Emended diagnosis. Marine Arthrotardigrada with cylindrical worm-like body. Trunk cuticle smooth, with folds, bearing three somatic cirri (B, C, and E) or only one (E). Eleven cephalic sense organs present, including large flattened secondary clavae (occasionally occurring as indistinct areas). Three or four claws on each foot displaying more or less important heterometry, and connected to foot by membranes.

Trogloarctus gen. nov.

Diagnosis. Coronarctidae. Elongated body with cuticular folds. Only one pair of somatic cirri (cirrus E) with accordion-like scapus. Eleven cephalic sense organs. Primary clava small and globular, inserted separately from cirrus A. Secondary clava flattened and not pronounced. Small cephalic cirri consisting of two parts: scapus and flagellum. External cirri equally distant from the internal cirri and the primary clavae. Spines on all legs. Three claws on each foot, very long on fourth leg. Buccal apparatus with bar shaped placoids, but without stylet supports.

Type and only species. *Trogloarctus trionyches* gen. et sp.n.

Etymology. A combination of the Greek words *trogodytes* (cave dweller) and *arktos* (bear), meaning 'the bear living in the cave'. Gender: masculine.

Trogloarctus trionyches gen. et sp. n. (Figs 2-3)

Material examined. Holotype female, 102 µm length, from 'Trois Pêpés' cave (sta. 100m A1, type locality) (slide 1 - 3PP271094). Three paratypes, 1 female and 2 moulting specimens, from type locality (slides 2-4, 3PP271094).

Description

Holotypic female 102 µm length and 22 µm wide (pharyngeal bulb level, between first and second pair of legs) (see measurements in Table 1). Body elongated and weakly segmented. Cuticle smooth and transparent, showing several folds between the legs, 6-8 noticeable folds between the first and second pair of legs, giving a nearly annulated look. Cirrus E dorso-laterally inserted and upward directed, with accordion-like scapus (5 µm), bent flagellum (8 µm) and frayed-like tip including a distinctly refractile structure (may be 'van der Land body').

Head subconical, slightly rounded, and narrower than body. The mouth opening is terminal, and may be protrusile. Internal cirri (3 µm) inserted laterally and close to the mouth opening. Medial cirrus very small (2.4 µm), inserted middorsally at the same level of the external cirri. Ventro-lateral external cirri (6 µm) are equally distant from the internal cirri and the primary clavae. Lateroventral flattened secondary clavae (difficult to see) without dorsal or ventral lobes. Primary clava and cirrus A are inserted separately (2-3 µm apart) on a small cephalic lobe, in a midlateral position. Cirrus A small (6 µm), primary clava ovoid (4 x 3 µm diameter).

Legs bearing small spines 3-3.7 µm length on the medial portion of P1, P2 and P3. Spine of P4 is 4 µm length, with large cylindrical papillar base including a refractile van der Land body, and thin flagellum. There are three nearly equally-sized claws on each leg, curved and medium sized on P1-P3 (11 µm) with a very fine accessory spine; and longer claws (15 µm), slowly curved, on P4. Proximal part of claws are connected to foot by membrane.

Internal structures. Cephalic region with a pair of 3 brown spherical spots, may be lipidic drop, at each side (2-3 µm diameter). Cephalic spherical spots are present in all specimens (> 10), always the same number, location and size. In several specimens, the cephalic region is filled with globular bodies, and cerebral lobes are difficult to see.

Circular mouth opening, surrounded by a cuticular membrane that may be protrusile. Buccal tube is 30 µm length and very refringent, may be with calcium carbonate incrustations. Stylets are fine, 25 µm length. The furca is supported directly by the bulb. Stylet supports are absence.

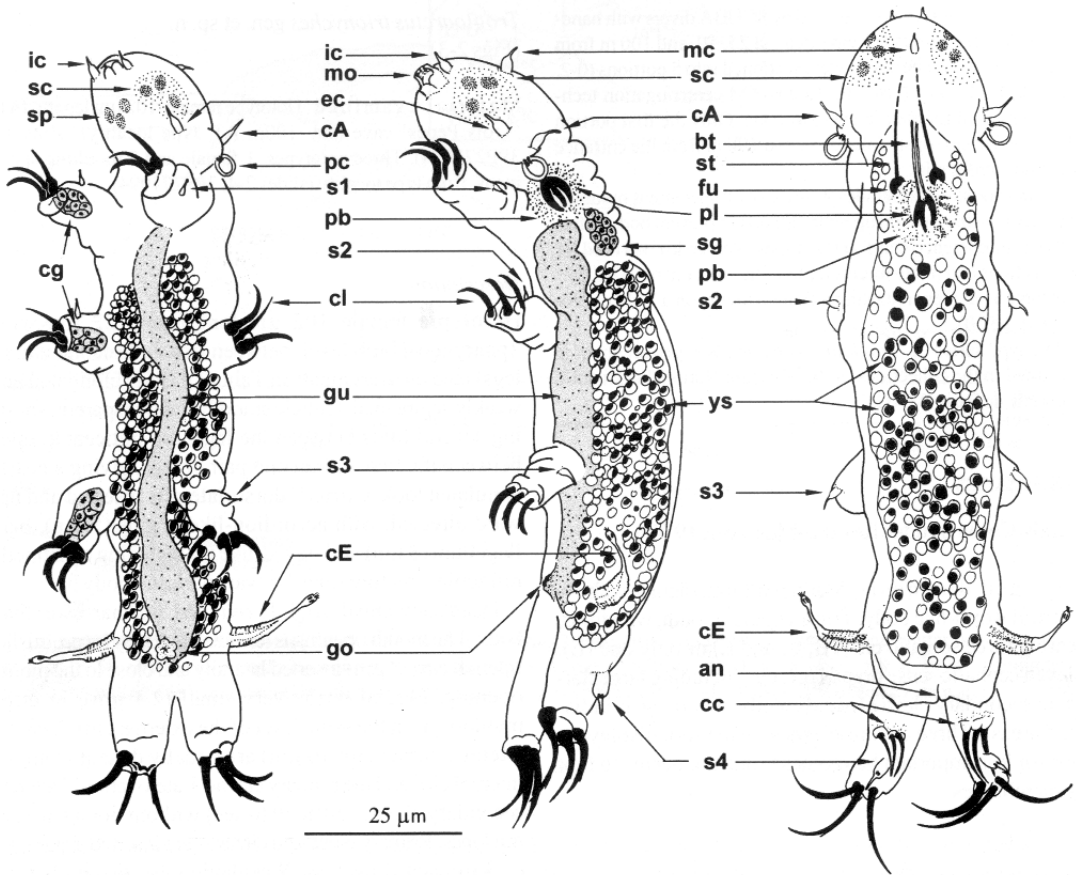


Fig. 2. *Troglorctus trionyches* gen. et sp.n. Ventral and lateral views of a paratyptic female, and dorsal view of a moulting female. an, anus; bt, buccal tube; cA, lateral cirrus (cirrus A); cc, claws in a moulting animal; cE, cirrus E; cg, claw gland; cl, claw; ec, external cirrus; fu, furca; go, gonopore; gu, gut; ic, internal cirrus; mc, median cirrus; mo, mouth; pb, pharyngeal bulb; pc, primary clava; pl, placoids; s1-s4, legs I-IV sense organs; sc, secondary clava; sg, salivary gland; sp, spots; st, stylet; ys, yellowish spheroids.

Pharyngeal bulb is spherical, 7-9 µm diameter. There are 3 strong placoids in the bulb, close to the buccal tube, having all the same refringence. Two salivary glands are located posteriorly to the pharyngeal bulb. All legs with well developed digit glands (claw glands).

Gut finely dotted, linear, and without diverticula. Coelomocytes and other globular structures (brown-yellow refringent cells, may be vacuolar reserve cells) are present in the body cavity, showing different degree of development.

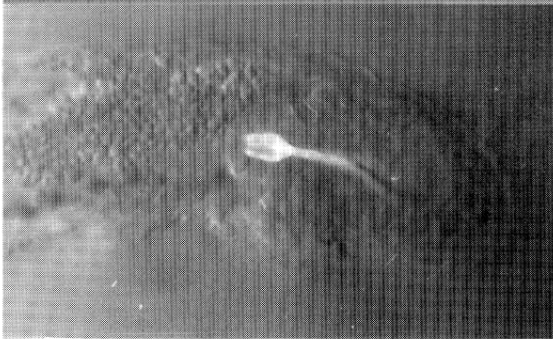
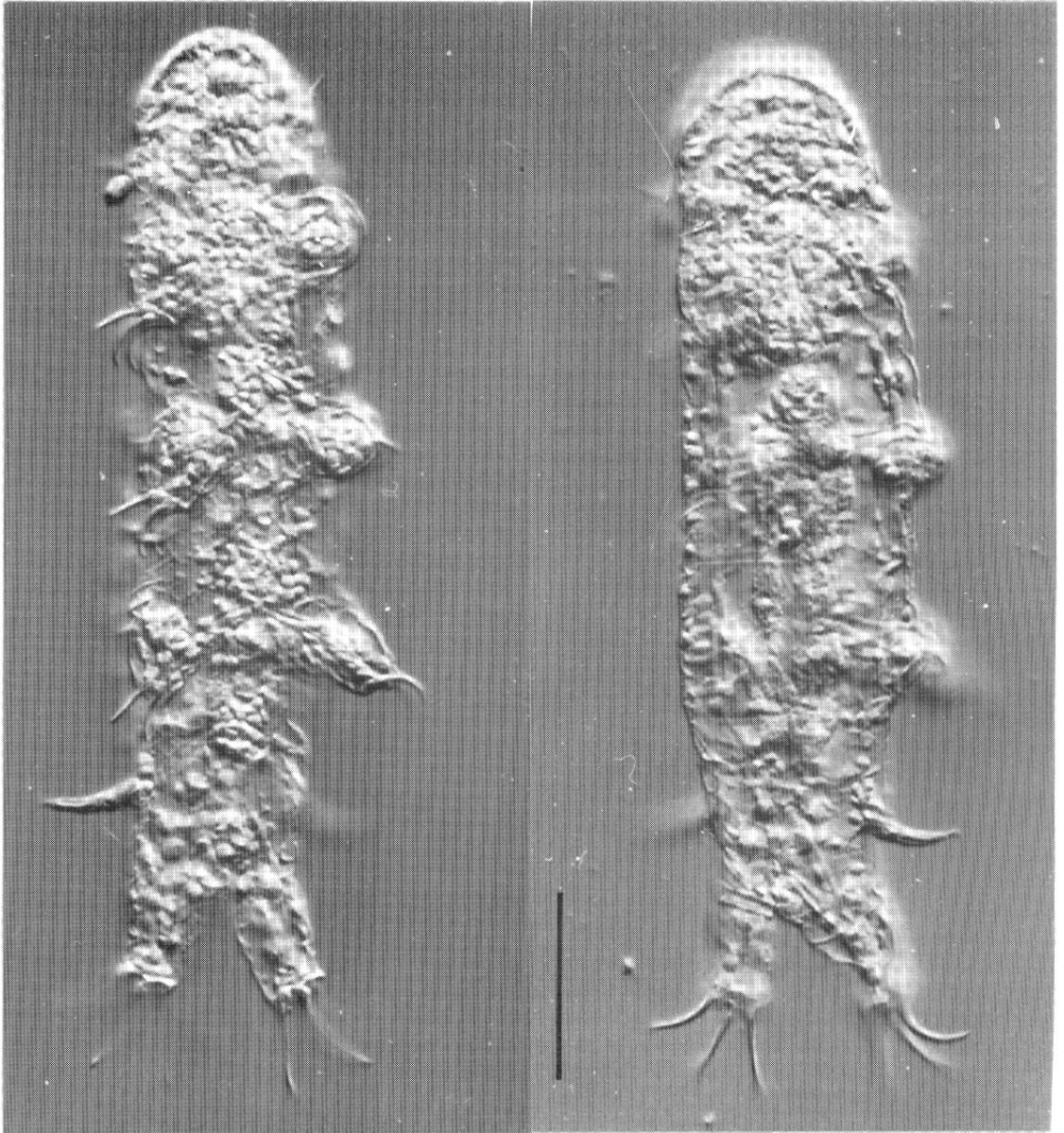
No sexual dimorphism was observed on external somatic formations. It seem that we have found only females, with the six platted rosette gonopore.

Etymology. A combination of the Greek words *tria* (three) and *onych-* (stem of *onyx*: claw), meaning 'three claws'.

Fig. 3. *Troglorctus trionyches* gen. et sp.n. Interference-contrast micrographs. A, B. Ventral and dorsal microscopical sections of the same specimen. C. Lateral view showing buccal tube and the 3 strong placoids in the bulb. D. Female gonopore. E. Cephalic region, anteroventral view, showing buccal opening, internal cirri, and the limits of secondary clavae (difficult to see). Scale bar: 20 µm. →

A

B



C

D

E

DISCUSSION

Relationships between Trogloarctus gen. n. and the family Coronarctidae.

Trogloarctus gen. n. shares some morphological features with the family Coronarctidae that readily distinguishes these taxa from any other known marine arthrotardigrades. Namely, the worm-like appearance with cylindrical elongated body, narrow head, and short legs with outstanding claws morphology (both shape and size) (RENAUD-MORNANT 1975). However, comparing *Trogloarctus* gen. n. with the recent emended diagnosis of the family Coronarctidae by RENAUD-MORNANT (1987), the new genus displays distinct plesiomorphic and apomorphic characters. These apomorphic characters are: The presence of only one somatic cirrus: E, three claws in each leg (reduction), absence of large accessory spine on the fourth pair of legs. The location of the external cirri is unique, they are moved backwards closer to the cirri A and primary clavae. On the other hand the presence of bar shaped placoids in the pharyngeal bulb, may be regarded as a plesiomorphic character. These differences involve the modification of the previous diagnosis of the family Coronarctidae in order to accommodate the new genus *Trogloarctus*.

Morphological differences between Coronarctus and Trogloarctus gen. n.

Size, number of claws, and absence of somatic cirri, other than cirrus E, are considered as the more evident differences between the genera *Coronarctus* and *Trogloarctus*. Length of the smaller species of *Coronarctus*, *C. disparilis*, is more than 2 times of *Trogloarctus trionyches* gen. et sp. n. (220 μm vs. 105 μm), and the larger species, *C. laubieri*, may reach 560 μm .

There are two trends on claw morphology in the genus *Coronarctus*, species showing claw homometry, and species with strong heterogeneity both in size and morphology (RENAUD-MORNANT 1987). As the *Coronarctus* species *C. stylisetus* and *C. fastigatus*, *Trogloarctus* shows homometric claws in all legs, but the number of claws in the legs is quite different (three vs. four).

Cephalic cirri are also different between the two genera. *Coronarctus* species have thread or leaf-like cephalic cirri, while *Trogloarctus* cirri are cylindrical. Although both genera show very reduced cephalic cirri, there are two species of *Coronarctus* (*C. stylisetus* and *C. fastigatus*) with more developed cirri. It seems that long-cirred species live in shallower water than short-cirred ones (RENAUD-MORNANT 1987). Following this hypothesis *Trogloarctus trionyches* belongs to the short-cirred and deep-sea species.

Table 1. Measurements (in μm) of 4 females of *Trogloarctus trionyches* gen. et sp. n. Holotype (Holot.) and three paratypes (p1-p3).

Character	Holot.	p1	p2	p3	Mean	SD
Body length	102.5	109.8	108.6	97.6	104.6	5.67
Body width	22.0	26.8	24.4	24.4	24.4	1.99
Pharynx bulb	7.3	9.8	9.8	8.5	8.8	1.17
Median cirrus	2.4	2.4	3.1	2.4	2.6	.30
Internal cirri	3.1	3.7	3.7	3.7	3.5	.31
External cirri	6.1	6.1	6.1	6.1	6.1	.00
Lateral cirri (A)	6.1	7.3	6.1	6.1	6.4	.61
Primary clavae	4.3	3.7	4.3	3.7	4.0	.35
Cirri E	13.4	14.6	14.6	13.4	14.0	.70
1st leg spine	3.7	3.7	3.7	3.8	3.7	.06
2nd leg spine	3.7	3.7	3.7	3.9	3.7	.12
3rd leg spine	3.1	4.9	3.7	4.3	4.0	.79
4th leg spine	4.3	4.9	4.9	4.9	4.7	.31
1st leg claws	11.0	9.8	9.8	9.8	10.1	.61
2nd leg claws	11.0	9.8	9.8	9.8	10.1	.61
3rd leg claws	11.0	11.0	9.8	9.8	10.4	.70
4th leg claws	15.9	14.0	13.4	14.6	14.5	1.04

Primary clava of *Coronarctus* species displays evident variability, from medium sized globular and well individualised (pedunculate) clavae, to a cuticular embedding clavae with vestigial or absent peduncle. *Trogloarctus* shows a simple *Styraconyx* primary clavae, with very distinct van der Land's body at the base. Secondary clavae in *Trogloarctus* is very difficult to see, lacking dorsal or ventral lobes. These features are different from those found in all *Coronarctus* species.

Pharyngeal placoids were not originally described in the family Coronarctidae, however all *Coronarctus* species have drop-shaped placoids in front of the pharyngeal bulb (R.M. Kristensen, pers. commn). *Trogloarctus* displays strong bar-shaped placoids in the pharyngeal bulb, which must be considered as a plesiomorphic condition.

Somatic cirri B and C are present in all species of *Coronarctus*, while they are lacking (apomorphic condition) in *Trogloarctus*. Cirri E are very aberrant in *Trogloarctus*, mainly because the frayed tip structure. *Coronarctus* species display more or less strong spikes dorsally over P4. These spikes are not evident in *Trogloarctus*, but there are two spike-like and very small cuticular projections in the caudal region, near the anus.

Developmental stages in Trogloarctus nov. gen.

Postembryonic developmental stages of *Coronarctus laubieri*, have been well documented by RENAUD-MORNANT (1988). She considers two larval stages (the second one with sexual differentiation), and three adult stages according to the maturation of gonads and gametes, or the beginning of a new gonadal cycle (preadult, mature adults and senior stage).

Only female specimens of *Trogloarctus trionyches* were collected in the submarine cave, 7 specimens in July and 4 specimens in October 1994. All animals show the six platted rosette gonopore, and different stages of accumulation of digestive material. The absence of males contrasts with the high proportion of males and strongly pronounced protandry showed for *Coronarctus laubieri* by RENAUD-MORNANT (1988).

Attending to gut development, abundance and location of yellowish spheroids (reserve globular cells), moult and reproductive system, it is possible to differentiate 4 physiological stages (no specimen has been identified in the larval stage). 1) Preadult animals with large gut (finely dotted), and a well delimited dorsal sac full of yellowish spheroids. These spheroids remain stained with Rose of Bengal longer than other body cells. Evident salivary glands. Claw glands, difficult to see. 2) Preadult animals ready to maturity moult. Thin gut, finely dotted. Medium, equally sized, yellowish spheroids ($\varnothing = 2-3 \mu\text{m}$) invading the

entire body cavity. Well developed claw glands in all legs. 3) Moulting animals (may be maturity moult). Old cuticle slowly detached from the new cuticle. Retracted new claw in the inner of each leg. Very thin and finely dotted gut. Yellowish spheroids invading the entire body cavity, including one of fourth legs. These spheroids are not equally sized, some of them having 4-6 μm diameter. Claw glands well developed, in all legs. Tip of cirri E may be enlarged and conspicuous frayed. Small yellow drops (air drop?) may be noted at the tip of all cephalic cirri and leg spikes, showing that tips of cirri and spikes are open. 4) Mature animal. Presence of ovocytes ($\varnothing = 8-10 \mu\text{m}$). Weak seminal receptacles and genital ducts (difficult to see, only identified in one specimen). Yellowish spheroids nearly absent. Medium sized and transparent gut.

Ecology and geographical distribution of Coronarctidae

Ecological data for deep-sea tardigrades are normally restricted to depth and some sediment characteristics, when sediment is not pure mud. *Coronarctus disparilis* was identified by RENAUD-MORNANT (1987) in black volcanic sand with pumice, at -3400 m depth in the Mozambique Channel (Indian Ocean), and *C. stylisetus* from medium coarse quartz sand off the coast of North Carolina, while all other *Coronarctus* species have been identified from muddy sediments. *Coronarctus* species are known from sediments deeper than 1600m, except *C. stylisetus* and *C. fastigatus*, identified at 104 and 675 m depth, respectively.

The floor of the cave 'Trois Pépés' is mainly composed of mud. Mud fraction increases strongly from the first sampling station (at 25 m from the cave entrance, 40-50 % of mud) to the far end station (100 m from the entrance, 80-90 % of mud). The rest of the sediment was not mineral but biotrititic, mainly consisting of sponge spicules, foramimifers, bryozoan skeletons, polychaete tubes, and marine vegetal detritus (bits of *Posidonia* leaves, only found at the 25 m station). All these biotrititic rest may change pure mud structure, increasing habitat heterogeneity. Sponge spicules and other biotrititic particles may act as anchorage for semi-sessile meiofauna groups, such as tunicates or stolonial hydroids, already found in the cave sediment. *Trogloarctus trionyches* has only been identified at the stations with complete darkness, mainly at the far end station. Tardigrades were only present in the first centimetres of the cave sediment (between 0 and 1.5-2 cm), where the 80 % of meiofauna, largely dominated by nematodes, is also concentrated (GOURBAULT & VILLORA-MORENO, own obs.).

There is no doubt that *Coronarctus* is a bathyal-abyssal genus. General features of the family Coronarctidae may be considered as adaptations to deep-sea habitat.

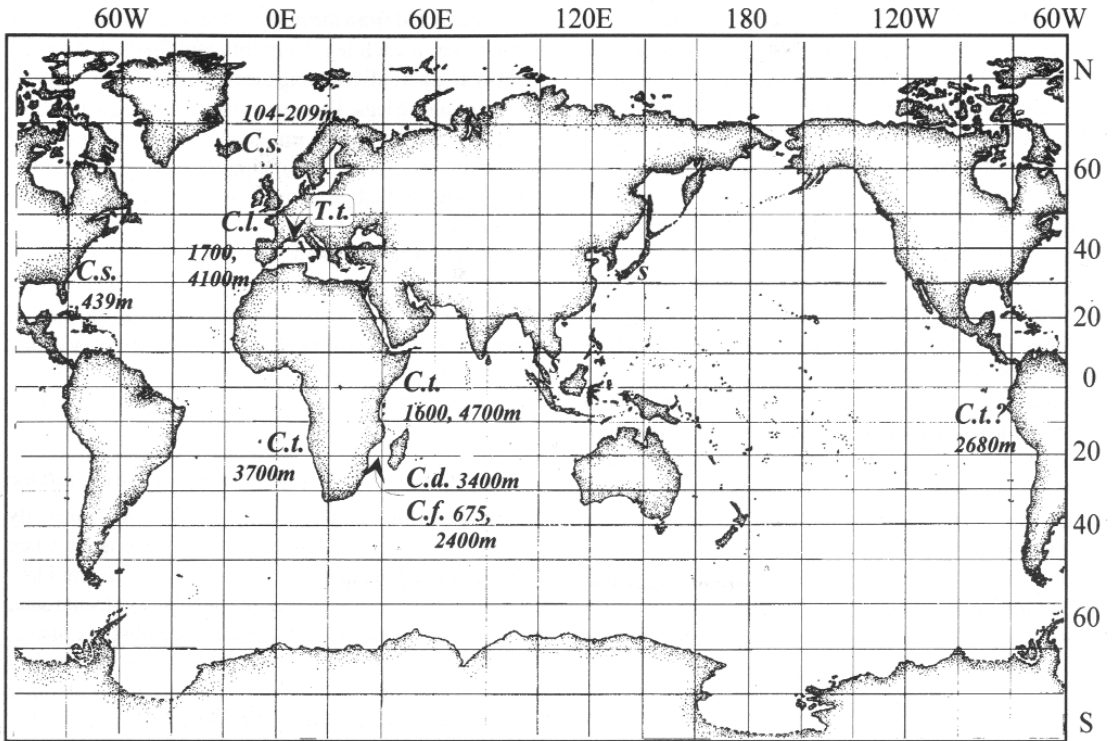


Fig. 4. World distribution of Coronarctidae. *Coronarctus tenellus* (C.t.), *C. stylisetus* (C.s.), *C. laubieri* (C.l.), *C. disparilis* (C.d.), *C. fastigatus* (C.f.), and *Troglorctus trionyches* gen. et sp.n. (T.t.).

Coronarctidae seems to be mainly restricted to deep muddy sediments. The genus *Coronarctus* displays a circumglobal distribution, but references are more abundant from the North Atlantic and Indian Oceans. *Coronarctus tenellus* has always been recorded deeper than 1600 m, from the Indian Ocean, South Atlantic and South Pacific Oceans. The remaining species of *Coronarctus* are known only from their type locality (see map Fig. 4). Shallowness records are for *C. stylisetus* from the North Atlantic (Cape Hatteras, 439 m; Faroe Bank, 104-209 m), and for *C. fastigatus* from the Indian Ocean (Mozambique Channel, 675 m) (RENAUD-MORNANT, 1987). This work constitutes another example of cave animals also found in deep-sea, supporting the hypothesis of HART & al. (1985) about the dispersal by sea floor spreading, while maintaining ties to deep water. The presence of the family Coronarctidae in a marine cave of the Mediterranean Sea contributes to the discussion about the origin and existence of the Mediterranean deep-sea fauna.

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