A new, disjunct species of *Speleonectes* (Remipedia, Crustacea) from the Canary Islands

Stefan Koenemann · Armin Bloechl · Alejandro Martínez · Thomas M. Iliffe · Mario Hoenemann · Pedro Oromí

Abstract We describe *Speleonectes atlantida* n. sp. as the third species of Remipedia that was found outside the main distribution area of this group in the Caribbean region. *S. atlantida* was collected by cave divers equipped with closed circuit rebreathers from the far interior of the Túnel de la Atlántida, an anchialine volcanic lava tube, on the Canarian island of Lanzarote. The new species occurs in sympatry with *S. ondinae*, to which it is morphologically closely related. *S. atlantida* can be distinguished from *S. ondinae* by a more slender habitus and smaller pleurotergites in the posterior trunk. The valid status of *S. atlantida* as a new species of Remipedia could be corroborated by intra- and interspecific comparisons of 16S rDNA and CO1 sequence data.

Keywords Marine biogeography · Anchialine cave · Sub-seafloor cave · Lava tube

Introduction

One of the central objectives of the Atlántida 2008 Cave Diving Expedition on the Canarian island Lanzarote was the collection of a few specimens of the remipede crustacean *Speleonectes ondinae* (García-Valdecasas, 1984). The specimens were crucially important for an ongoing comprehensive phylogenetic and phylogeographic analysis of the Remipedia based on DNA sequence data. *S. ondinae* was, until now, one of the two known remipede species that are separated by long geographic distances from the main distribution area of this group. The second disjunct species, *Lasionectes exleyi* Yager and Humphreys, 1996, was collected from a cave on the Cape Range Peninsula in Western Australia, while all remaining remipedes inhabit insular or coastal anchialine cave systems in the Caribbean Sea.

The discovery of a second remipede species in the submerged part of the Túnel de la Atlántida came as a complete surprise. Since the mid-1980s (Iliffe et al. 1984), *S. ondinae* has been the sole representative of the Remipedia in the eastern Atlantic, and it is now protected as an endemic species of the Canary Islands. First indications of the presence of a second species emerged, when team members managed to collect three living adult individuals during a single dive. Two of the three specimens, each kept in a separate container, showed an almost identical swimming behavior, while the movements of the third individual appeared distinctly different (see description below).

We could corroborate these initial observations through detailed morphologic examinations and DNA sequence data, both of which unambiguously support the status of *S. atlantida* as a second valid species of Remipedia from Lanzarote.

Materials and methods

Specimen collection and preparation

Specimens were collected by cave divers using closed circuit rebreathers. After visual observation in the water

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column, animals were collected individually, along with ambient water, in clear glass or plastic tubes to minimize damage and stress. Three of the eight dives made during the expedition yielded successful collections of remipedes. In total, we collected six specimens of the new species *S. atlantida*, one specimen of *S. ondinae* (16 mm), and one juvenile specimen (6 mm) that could not be classified unambiguously. On 19 March 2008, three specimens were collected from a large dome-like room connecting upper and lower levels of the lava tube at about 250 m penetration into the underwater cave and 20 m water depth, while a fourth specimen was found in the upper tube at 10 m depth on the same dive. On 22 March, a single specimen was found in the main tube at about 500 m penetration and 25 m depth. Finally, on 23 March, three specimens were collected past the sand mountain at 700–1,000 m penetration and 30 m depth. Living specimens were video-recorded and photographed in a field laboratory within several hours after collection. All animals were fixed in 96% EtOH for subsequent morphologic examinations and DNA extractions. One specimen was transferred to glycerin, dissected and mounted on slides for the taxonomic description.

Genetic analysis

We used the Qiagen Mini Kit to extract DNA from four specimens of *S. atlantida* n. sp. (see "Material examined", below) and one specimen of *S. ondinae*. Fragments of cytochrome oxidase subunit 1 (CO1) and 16S rDNA (16S) were amplified through standard polymerase chain reaction (PCR). CO1 fragments ranged from 616 to 672 bp, those of 16S from 807 to 974 bp.

For amplification of CO1 fragments, our forward primer, T7MH51, included LCOI 1490 (Folmer et al. 1994) and a universal T7 primer. The reverse primer, SP6MH50, was a combination of HCOI 2198 (Folmer et al. 1994) and Sp6 (Table 1). The primers for the 16S rRNA region were mt16S-ar and mt16S-br (Palumbi et al. 1991) (see also Table 1).

The PCR products were purified using the NucleoSpin Extract II kit from Macherey-Nagel, and bidirectionally sequenced by Macrogen (Korea) using the primers Sp6 and T7 for CO1, and mt16S-ar and mt16S-br for 16S. The Genbank accession numbers are shown in Table 2.

The size and quality of both PCR and purified products were examined on a 1.4% agarose gel. The sequences were assembled with Seqman II from Lasergene and aligned with MUSCLE (Edgar 2004).

Pre-analyses based on 16S sequence data showed a close relationship between *S. tulumensis* and *S. ondinae*. Therefore, the 16S rDNA sequence of *S. tulumensis* (Accession number: NC_005938) was added to the 16S alignment presented herein. For comparison of CO1 data, the following sequences from Genbank were added: *S. benjamini* (FJ527841), *Pleomothra apletocheles* (FJ527840), *Godzilliognomus frondosus* (FJ527839), *Cryptocorynetes haptodiscus* (FJ527837), and *S. tulumensis* (NC_005938).

We used MEGA4 (Tamura et al. 2007) to conduct a neighbor-joining analysis for CO1, and to calculate pairwise distances for 16S sequences. The resulting CO1 sequences of LZ 1.1, DZUL 9999-GBIF, and LZ 2.1 were identified as numts (nuclear copies of mitochondrial derived genes) and therefore excluded from analysis.

Systematics

Speleonectes atlantida n. sp. (Figs. 1, 2, 3, 4)

Type locality Túnel de la Atlántida, Jameos del Agua, Corona lava tube, Lanzarote (Canary Islands).

Etymology The epithet of the new species refers to the type locality, the Túnel de la Atlántida.

Material examined Holotype (catalogue number TFMC CR-23): 24 trunk segments, 20 mm; collected by T. Iliffe, 23 Mar. 2008. Paratype 1 (LZ 2.1; Fig. 1): 23 trunk

Table 1 List of gene regions and primers used for DNA analyses

Gene region	Primer	Primer sequences (5′-3′)	Ann. temp.
PCR primers			
CO1	T7MH51	TAATACGACTCACTATAGGGTAAACTTCAGGGTGACCAAAAAATCA	50°C
CO1	SP6MH50	ATTTAGGTGACACTATAGAATGGTCAACAAATCATAAAGATATTG	50°C
16S	mt16S-ar	CGCCTGTTTATCAAAAACAT	46°C
16S	mt16S-br	CCGGTCTGAACTCAGATCACGT	46°C
Sequencing primers			
CO1	Sp6	ATTTAGGTGACACTATAGAAT	50°C
CO1	T7	TAATACGACTCACTATAGGG	50°C

Table 2 Genbank accession numbers of 16s rDNA and CO1 for *Speleonectes ondinae* and *S. atlantida*

	16S	CO1
S. atlantida DZUL 9999-GBIF	FJ905031	FJ905038
S. atlantida LZ1.1	FJ905032	FJ905036
S. atlantida LZ2.1	FJ905033	FJ905039
S. atlantida LZ 2.3	FJ905034	FJ905040
S. ondinae LZ1.2	FJ905035	FJ905037

segments, 16 mm; collected by T. Tysall, 19 Mar. 2008; completely dissected for description (Figs. 1,2,3,4); remaining body parts used for DNA analyses. Paratype 2 (DZUL 9998-GBIF; Fig. 1): 23 trunk segments, 17 mm; collected by T. Iliffe, 23 Mar. 2008. Paratype 3 (LZ 1.1): 22 trunk segments, 9 mm; collected by T. Iliffe, 19 Mar. 2008; three trunk segments used for DNA analysis. Paratype 4 (DZUL 9999-GBIF): 22 trunk segments, ca. 8 mm; collected by T. Iliffe, 19 Mar. 2008; partly dissected for morphological comparisons; some trunk limbs used for DNA analysis. Paratype 5 (LZ 2.3): 20 trunk segments, 5.7 mm, collected

by T. Iliffe, 22 Mar. 2008; partly used for DNA analyses. All specimens are preserved in ethanol; dissected body parts are stored in glycerine. The holotype will be deposited at the Museo de Ciencias Naturales de Tenerife (TFMC), Canary Islands; the dissected paratypes remain in the research collections of Institute for Animal Ecology and Cell Biology, University of Veterinary Medicine Hannover (paratypes 1 and 3), and the Department of Animal Biology, University of La Laguna (paratypes 2 and 4; catalogue numbers DZUL 9998-GBIF and DZUL 9999-GBIF, respectively).

Diagnosis Speleonectes atlantida is a comparatively long and slender species (Fig. 1). The trunk segments are equipped with isomorphic sternal bars, and angular pleural tergites that point posteriorad. The dorsal ramus of the antennule is composed of 12 articles, the ventral ramus has 8 articles. The claws of maxilla and maxilliped are arc-shaped, with approximately 12 denticles.

Description (based on three adult specimens) Body length up to 20 mm, with 23–24 trunk segments. Head shield subrectangular, slightly longer than trunk segments 1–4 (Fig. 1B–E).
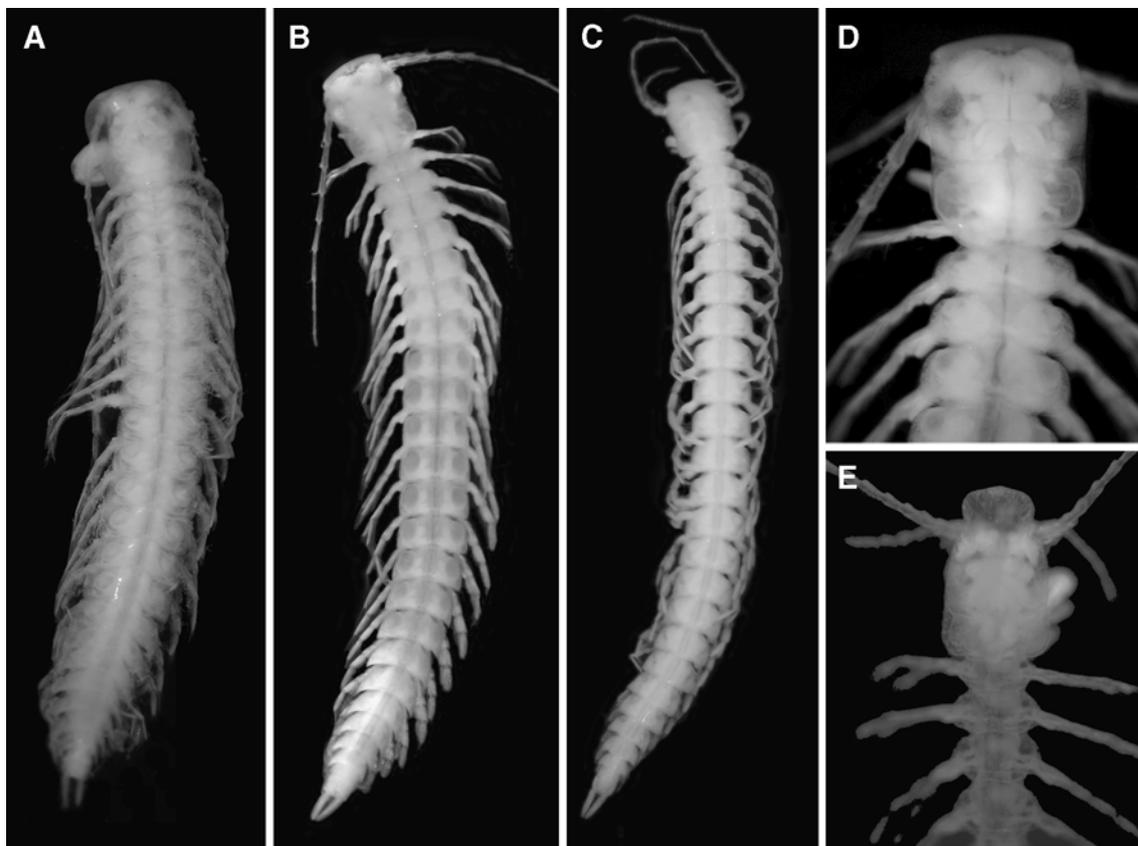

Fig. 1 Specimens of *Speleonectes ondinae* (**A**) and *S. atlantida* n. sp. (**B–E**); all dorsal views. **A** Specimen LZ 1.2 (16 mm); **B** paratype 2 (DZUL 9998-GBIF; 17 mm); **C** paratype 1 (LZ 2.1; 16 mm); **D** enlarged view of paratype 2; **E** head and anterior trunk of juvenile specimen (6 mm) that could not be assigned to either one of the two species (LZ 2.2). Specimens are not shown at the same scale

Fig. 2 *Speleonectes atlantida* n. sp.; paratype 1 (LZ 2.1). **A** Antennule. **B** Antenna; *black dots* indicate reconstructed (broken) setae. **C** Frontal filaments. **D** Labrum. **E** Left mandible. **F** Details of right mandible. **G** Details of left mandible. *Scale bars* (**A–E**) 0.1 mm
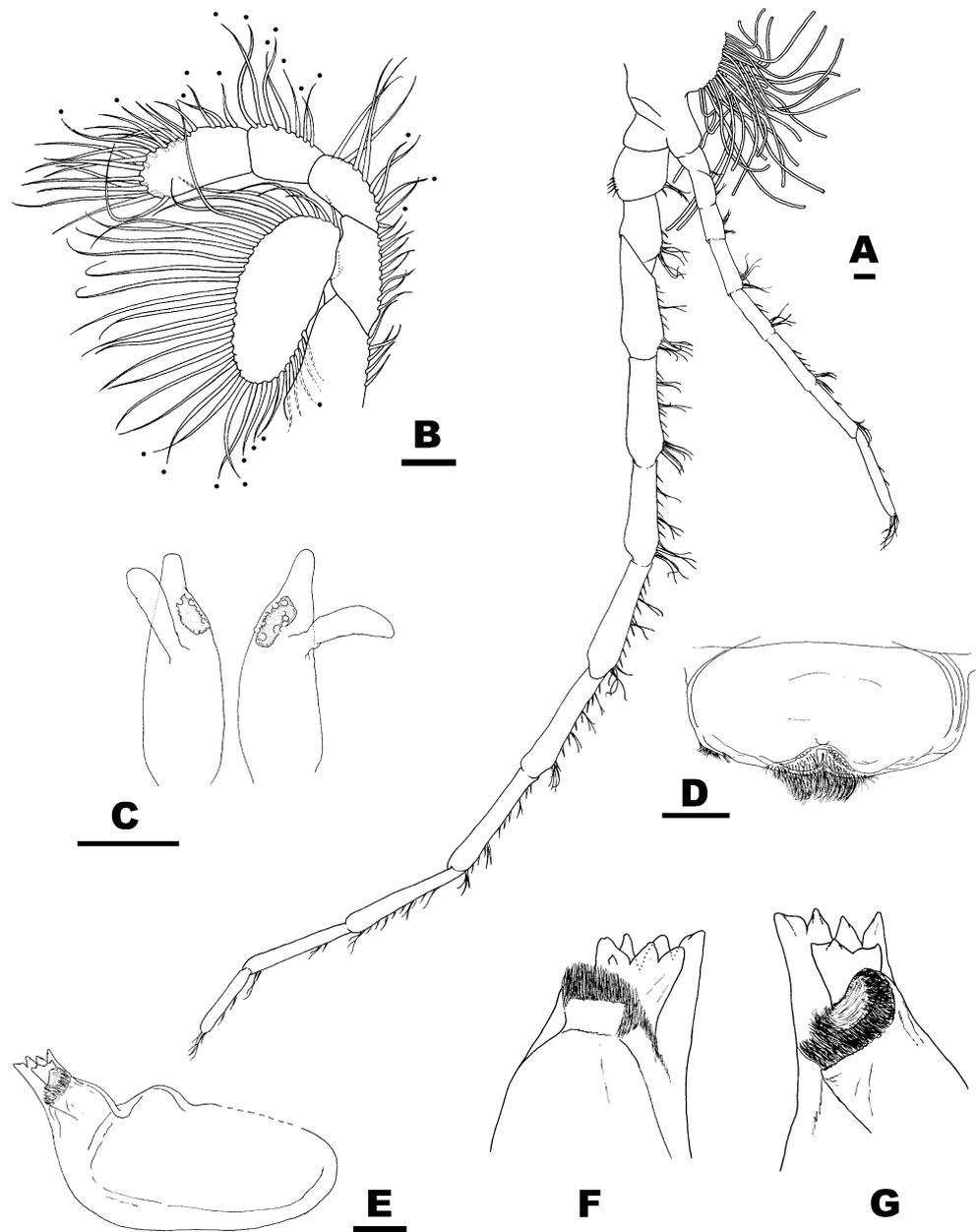
Frontal filaments relatively short and dilated, with slender tip; short medial processes as long as main filaments (Fig. 2C). First trunk segment reduced, partly covered by head shield (Fig. 1D); pleural tergites of anterior trunk segments with broadly rounded distolateral corners, becoming angular in mid and posterior trunk. Sternal bars isomorphic.

Antennule (Fig. 2A): Peduncular pad small, with a field of relatively few aesthetascs. Dorsal flagellum with 11 articles, reaching approximately 30% of body length. Ventral flagellum with 8 articles, slightly longer than head shield.

Antenna (Fig. 2B): Proximal segment of protopod with five setae; distal segment shorter and narrower, with 8–9 setae.

Exopod much longer and wider than adjacent segment of protopod, equipped with long marginal setae. First segment of endopod with 9 setae; second segment with approximately 7 setae; third segment slightly larger than previous segments, bearing 20–22 setae, arranged in 2 rows along apical margin. All setae plumose.

Labrum (Fig. 2D): Corners rounded with few fine setules; funnel-shaped cavity surrounded by dense field of fine setules, bilaterally with rows of denticles.

Mandible (Fig. 2E–G): Coxopodite oval, more than twice as long as wide. Incisor process and lacinia mobilis of right mandible each with 3 stout denticles (Fig. 2F). Incisor

Fig. 3 *Speleonectes atlantida* n. sp.; paratype 1 (LZ 2.1). **A** Maxillule. **B** Maxilla. **C** Maxilliped. **D** Stout setulose seta from maxillular segments 3 and 4. **E** Detail of first maxillular endite. **F** Terminal claw of maxilliped. *Scale bars* (**A–C**) 0.1 mm
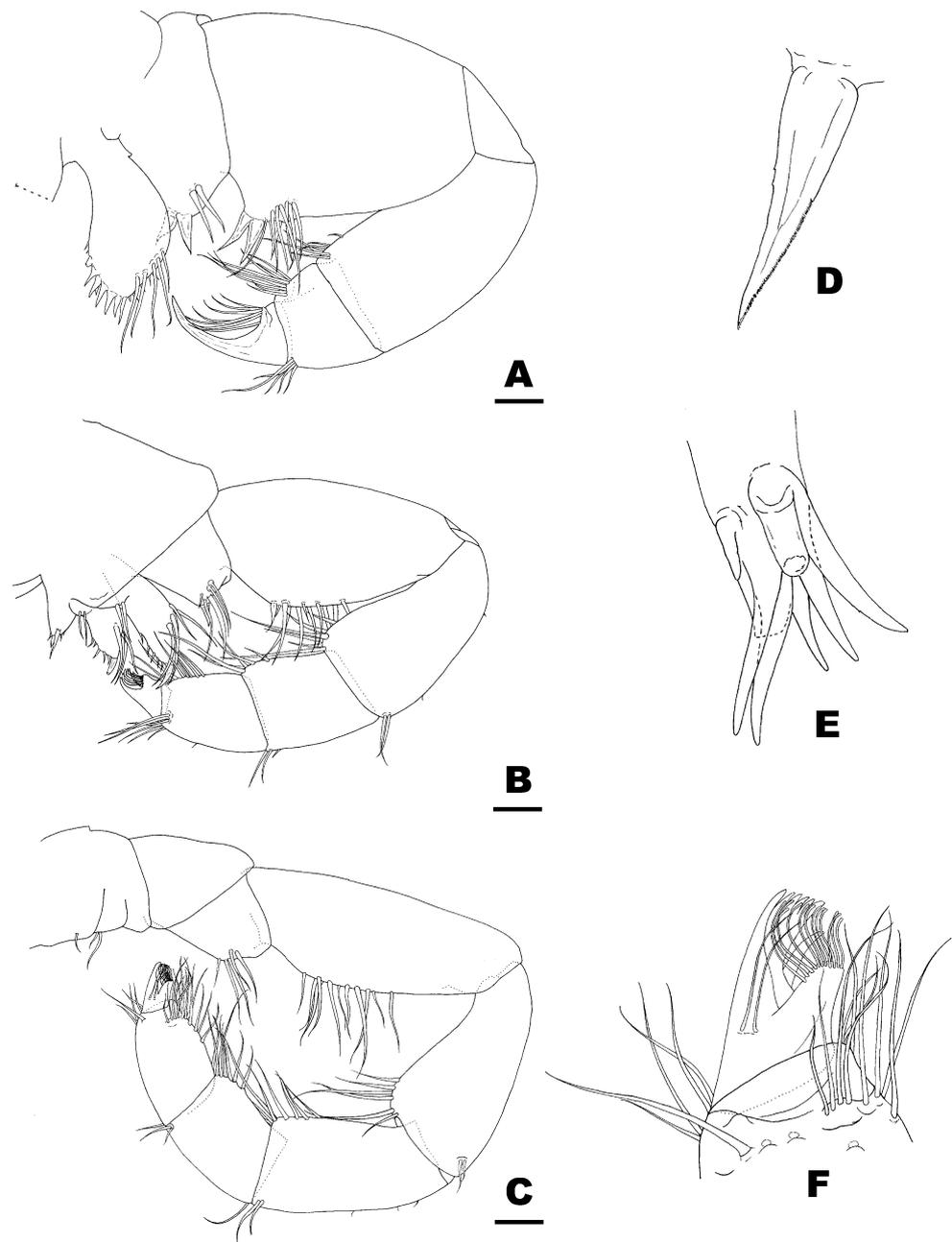
process of left mandible with 4 stout denticles, lacinia mobilis with irregular apical margin (Fig. 2G). Apical surface of molar process with numerous plumose setae.

Maxillule robust (Fig. 3A, D, E): Endite of segment 1 with 7–8 stout setae of variable length, one of which with serrated margin (Fig. 3E). Segment 2 with large spatulate endite, bearing 7 short stout setae on distolateral margin (all simple except 1 stout plumose seta on apex), 5 long slender setae on distomedial margin; and row of 9 simple, short fine setae along entire distal margin. Segment 3 with broadly rounded endite; apex with 2 stout setulose setae (Fig. 3D)

accompanied by 2 slender setae. Lacertus (segment 4) robust, with oblique, evenly expanded medial margin; proximal corner with 2–4 stout setulose setae and 2 groups of long slender setae. Segment 5 with distomedial field of few setae. Segment 6 short, with 2 disjunct distal fields of setae. Claw well-developed, long, with medioproximal field of setae.

Maxilla about as long as maxillule, but lacertus only weakly expanded (Fig. 3B): First (proximal-most) endite of segment 1 bearing apically 2 stout and 2 short fine setae; endites 2 and 3 each with 1 large stout apical seta; medial

Fig. 4 *Speleonectes atlantida* n. sp.; paratype 1 (LZ 2.1). **A** Anal somite, with caudal rami. **B** Short serrated seta of trunk limbs. **C** Trunk limb from 14th trunk segment; *black dots* indicate reconstructed (broken) setae. *Scale bars* **A** 0.1 mm, **B** 0.01 mm, **C** 0.1 mm
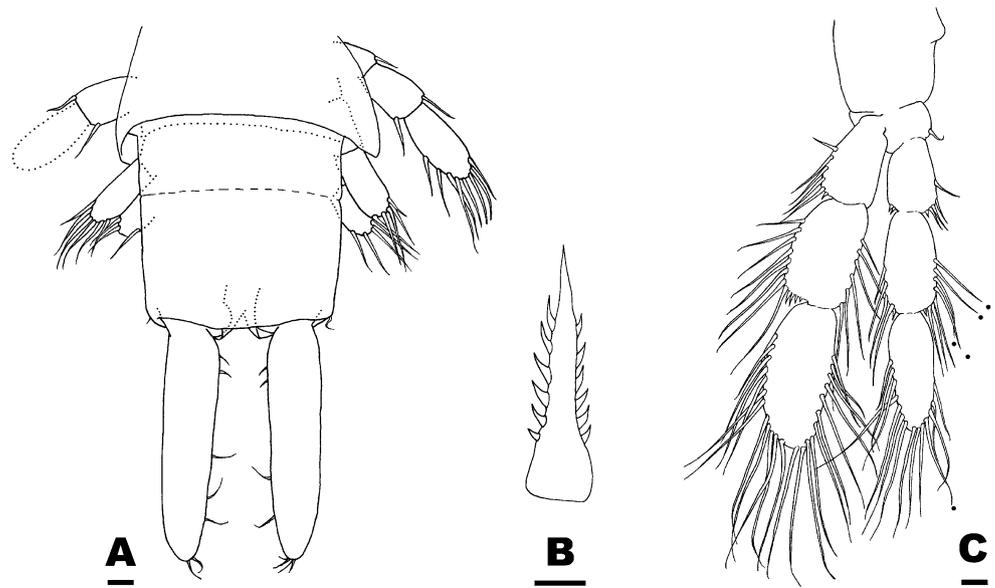
margins with 2–6 short fine setae, lateral margins with 4–5 very long slender setae of variable length. Segment 2 with subrectangular endite, bearing 1 stout seta and 4 long slender setae. Lacertus (segment 3) slightly expanded, inner margin bearing a double row of about 11 setae of variable length. Segment 4 expanded, but shorter than segment 3; segments 4, 5, and 6 gradually decreasing in width and length, bearing fields of few setae on distomedial and distolateral margins. Arc-shaped claw with approximately 12 fused (but comparatively deeply incised) denticles flanked by 2 stronger, free denticles (see Fig. 3F).

Maxilliped much longer than maxilla (Fig. 3C): Proximal segments 1–3 bearing only a few setae. Lacertus (segment 4) long and relatively slender (i.e., only weakly expanded), bearing about 11 setae of variable length arranged in a double row. Segment 5 expanded, shorter than segment 4, with field of few setae on mediodistal margin. Segments 6–8 gradually decreasing in length, equipped with rows of mediodistal setae. Claw similar to that of maxilla (Fig. 3F).

Trunk limbs (TL) largest in mid-trunk region (Fig. 4C): Exopod of TL 14 longer and more robust than endopod. Segment 1 of exopod with 5 long lateral setae, and 1 short, serrated distolateral seta (Fig. 4B). Segment 2 equipped with rows of long lateral and medial setae, and 4 short, serrated distolateral setae. Segment 3 longer than segment 2, bearing rows of long setae on inner and outer margins. Endopod slender. Segment 1 short. Segment 2 with several lateral setae. Segment 3 bearing rows of long distolateral and -medial setae, and 1–2 short serrated setae on distomedial and -lateral corners. Segment 4 narrow, tapering apically, with rows of long marginal setae. All long and slender setae plumose.

Anal segment wider than long (Fig. 4A): Wider than long. Caudal rami 1.9 times longer than anal somite, with short lateral and apical setules.

Morphological variability and comparison with *Speleonectes ondinae*

All extant species of Remipedia are assigned to the order Nectiopoda Schram, 1986 that is composed of three families, the Godzilliidae Schram et al. 1986, the Micropacteridae Koenemann et al. 2007, and the Speleonectidae Yager, 1981. The new species *S. atlantida* lacks all diagnostic characters that define the families Godzilliidae and Micropacteridae, in particular the absence of fused articles in maxilla and maxilliped. Consequently, *S. atlantida* can be unambiguously assigned to the family Speleonectidae. This family contains four genera, three of which are distinguished by well-defined apomorphies that *S. atlantida* does not share. These apomorphies are dense fields of setae or discoid organs on maxillae and maxillipeds in *Cryptocorynetes* Yager, 1987a, *Kaloketos* Koenemann et al. 2004, and *Lasionectes* Yager and Schram, 1986. Therefore, *S. atlantida* is assigned to the genus *Speleonectes*.

The new species is morphologically closely related to *S. ondinae*. We observed the first apparent differences between *S. atlantida* and *S. ondinae* immediately after collection of the animals, when we compared the swimming behavior of three individuals in separate 25-ml glass vials next to each other. While two individuals (that were later identified as *S. atlantida*) swam vigorously, making frequent abrupt turns, the swimming behavior of *S. ondinae* appeared tranquil and relaxed. These behavioral differences seemed consistent in all individuals collected.

The most apparent morphological differences between *S. atlantida* and *S. ondinae* are listed in Table 3. Morphological characters that distinguish the new species from *S. ondinae* could only be observed in adult specimens (16–20 mm), the juvenile specimens (6–9 mm) could not be identified unambiguously. The designation of the juvenile specimens LZ 1.1 and DZUL 9999-GBIF as paratypes of *S. atlantida* is based on DNA analysis.

The detailed description of *S. ondinae* by Schram et al. (1986) illustrates conspicuous morphologic variation concerning the stout setulose ("subsetulate") setae on the corners of the maxillular lacertus. Although Schram et al. found a constant number of five corner setae in their specimens ($n=6$), the form of these setae varied from stout and robust to long and slender among specimens. This occurrence of setal form variation within a species is unique in remipedes. All currently known speleonectids have one or two similarly shaped corner setae on the maxillular lacertus, and the number of these corner setae is constant within species (2 ± 1). In our specimen of *S. ondinae* (LZ 1.2), the maxillular endite of the left fourth segment is equipped with six setulose stout setae (concordant with Fig. 11 IVb in Schram et al.), while the right lacertus bears eight stout setae; the setulose setae on the endite of segment three are much shorter and more robust than those on the lacertus (and more robust than shown in the illustrations of *S. ondinae* by Schram et al.). In the course of this study, we examined another specimen of *S. ondinae* from the collection of the Zoological Museum in Hamburg (catalogue nr. K-41940; Biozentrum Grindel und Zoologisches Museum). This adult individual measured 13.5 mm and had 23 trunk segments; both endites of the fourth maxillular segments were equipped with three corner setae.

Asymmetrical variation of corner setae was also found on the fourth maxillular segment in two of the three adult specimens of *S. atlantida*, with left and right maxillules bearing three and four setae in paratype 1 (LZ 2.1), two and four setae in paratype 2 (DZUL 9998-GBIF), while both maxillules had three setae in the holotype.

Furthermore, we observed unusual structures in the frontal filaments of the new species *S. atlantida*. Both frontal filaments of the dissected specimen LZ 2.1 had unusual granular cavities in the distal parts of the main filaments. Due to the limited number of available (dissectible) specimens, we are not able to verify whether this structure is a (new) character, an artifact, or an aberration.

DNA analysis

The neighbour-joining analysis based on 16S sequences shows distinct branch lengths for two terminal taxa, *S. tulumensis* and *S. ondinae*, and a clade with the adult paratype of *S. atlantida* n. sp. (LZ 2.1) joined by three juveniles (LZ 1.1, LZ 2.1, LZ 2.3, and DZUL 9999-GBIF). Sequences in this clade differed by only 1–3 nucleotide substitutions on a total sequence length of more than 800 bp (Fig. 5).

We also obtained CO1 sequences from the new species *S. atlantida* (paratype LZ 2.3) and *S. ondinae*. The genetic distance of 0.133 between those two species indicates a relatively close relationship compared to other remipedes included in this analysis (Table 4). However, it is clearly larger than a mean intraspecific divergence of 0.005 that we found for 13 CO1 sequences from five species of Remipedia (not shown).

Therefore, both 16S and CO1 analyses corroborate the morphological data, confirming the valid status of *S. atlantida* as a new species of Remipedia.

The biogeography of Remipedia

Both the taxonomic diversity and the density of geographic distributions of remipedes are highest in the northern Caribbean region. At present, *S. atlantida* n. sp. is only the third species known to occur outside this main distribution area (Table 5). Regardless of possible sampling bias, one reason for the high diversity of Remipedia in the

Table 3 Morphological characters that distinguish *Speleonectes atlantida* n. sp. from *S. ondinae*

| Characters	*Speleonectes atlantida* n. sp.	*Speleonectes ondinae*
Habitus; arrangement of trunk somites	Slender; loose	Compact; narrow
Pleurotergites in posterior trunk, distolateral corners	Short, angular	Long, arcuated
Antennal exopod, inner margin	With long setae	With short setae
Brachium of maxilla	Comparatively long and slender	Short and robust
Maxillule, endite of segment 1	With 7–8 setae (1 serrate)	With 7 setae (1 setulose, 1 serrate)
Maxillule, endite of segment 2	Large and broad, with 7 short stout setae	Narrower, with 5 short stout setae
Maxillule, endite of segment 4	2–4 stout setulose corner setae	3–8 stout setulose corner setae
Claws of maxilla and maxilliped	Comparatively short	Long and slender
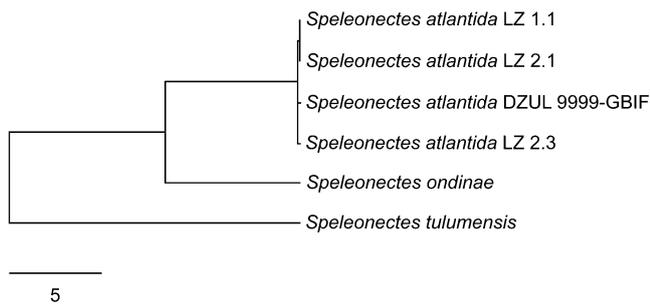
Fig. 5 Neighbor-joining tree based on 16S sequences from three species of Remipedia, including *Speleonectes ondinae* and four specimens of *S. atlantida* n. sp., both from Lanzarote, and *S. tulumensis* from the Yucatan Peninsula

Caribbean is certainly the presence of numerous, often extensive, anchialine limestone caves. Moreover, in the Bahamas archipelago, many caves are situated on shallow-water carbonate platforms. The heterogeneous hydrogeologic formation of this region appears ideal for allopatric speciation events.

By contrast, the submerged part of the Corona lava tube on Lanzarote is a single conduit without side passages. The total length of the flooded sections is about 1,700 m, including the Túnel de la Atlántida that extends horizontally below the sea floor for more than 1,400 m. Compared to Bahamian limestone caves, the lava tube, with an estimated age of 20,000 years, is relatively young (Carracedo et al. 2003; see also Wilkens et al. this issue). Therefore, the discovery of a second, sympatric species of *Speleonectes* in this comparatively young and homogeneous cave system was quite unexpected.

The occurrence of sympatric species of Remipedia is common in Caribbean cave systems, where up to six species (representing three genera) have been found in the same cave (Koenemann et al. 2004). Caribbean limestone caves usually have a complex topography, and the presence of large speleothems in some systems indicates a geological history with long dry periods, during which these formations must have been deposited. Therefore, shallow-water Caribbean caves were presum-

ably affected by multiple sea level changes during Pleistocene glacial and interglacial cycles. The combination of heterogeneous geomorphological settings with changing coastlines after marine regressions during the Pleistocene have most likely led to repeated temporal isolations of stygobiontic populations.

Most Caribbean anchialine caves are also more complex than lava tubes from an ecological point of view. In large extensive limestone caves, variation of salinity caused by inflow of terrestrial freshwater is buffered by anchialine lagoons and sections with different depths. These conditions may have favored sympatric speciation in different ecological niches within the same cave system.

The Corona lava tube, on the other hand, presents an entirely different scenario. The cave is a relatively linear and homogeneous system. The different sections along the flooded areas of the cave are not isolated from each other; there is a continuous flow of tidal currents, and the stygobiontic fauna is distributed evenly throughout the lava tube. Terrestrial input is limited to occasional rainfall; there is only a single, small and shallow anchialine lagoon, and homeostatic conditions prevail in the water column throughout the lava tube. Thus, considering these geological and ecological settings, the probability of radiation within the cave system appears rather unlikely, and the question is how speciation events can occur in this system. Based on the data collected during the Atlántida Expedition, we think that the Corona lava tube is a much more complex cave system than previously assumed.

The terrains of Lanzarote are mostly composed of porous rocks that facilitate the saltwater infiltration in coastal areas. The porosity of these materials in the coastal lowlands and the scarcity of rainfall are factors that constitute a continuous anchialine water mass around most of the island. A connection between anchialine coastal waters and the water column of the lava tube has been demonstrated by the distribution of several endemic species (Wilkens et al. 1986; 1993). For example, the ostracodes *Danielopolina wilkensi* and *D. phalanx* are both known to occur as sympatric species in the water column of the Túnel

Table 4 CO1 pairwise distances based on Kimura 2-parameter model

	1	2	3	4	5	6	7
1. *Speleonectes tulumensis*	-						
2. *Speleonectes benjamini*	0.238	-					
3. *Pleomothra apletocheles*	0.298	0.372	-				
4. *Godzilliognomus frondosus*	0.278	0.288	0.387	-			
5. *Cryptocorynetes haptodiscus*	0.219	0.201	0.335	0.270	-		
6. *Speleonectes ondinae*	0.223	0.251	0.315	0.298	0.217	-	
7. *Speleonectes atlantida* LZ 2.3	0.228	0.292	0.337	0.315	0.249	0.133	-

Table 5 Geographic distributions of Remipedia, including undescribed species (for which a description is planned or in preparation) and several unidentified new species (for which exact classifications depend on additional material)

	Gr. Bahama Bank				Little Bah. Bank		Caicos Bank								
	Andros	Exuma Cays	Eleuthera	Cat Island	Grand Bahamas	Abaco	North Caicos	Middle Caicos	Providenciales	San Salvador	Cuba	Hispaniola	Yucatán	Lanzarote	Western Australia
Micropacteridae															
Micropacter yagerae Koenemann et al., 2007									●						
Godzilliidae															
Godzilliognomus frondosus Yager, 1989					●	●									
Godzilliognomus cf. *frondosus* (unidentified species)	●														
Godzilliognomus n. sp. (in preparation)			●												
Godzillius robustus Schram et al., 1986	●						●								
Pleomothra apletocheles Yager, 1989					●	●									
Pleomothra fragilis Koenemann et al., 2008	●														
Pleomothra n. sp. (in preparation)			●												
Pleomothra cf. *apletocheles* (unidentified species)				●											
Speleonectidae															
Cryptocorynetes haptodiscus Yager, 1987a					●	●									
Cryptocorynetes longulus Wollermann et al., 2007				●											
Cryptocorynetes cf. *longulus* (unidentified species)	●														
Cryptocorynetes n. sp. (in preparation)			●												
Kaloketos pilosus Koenemann et al., 2004							●								
Lasionectes entrichoma Yager and Schram, 1986								●	●						
Lasionectes exleyi Yager and Humphreys, 1996															●
Speleonectes benjamini Yager, 1987a					●	●									
Speleonectes emersoni Lorentzen et al., 2007												●			
Speleonectes epilimnius Yager and Carpenter, 1999										●					
Speleonectes gironensis Yager, 1994											●				
Speleonectes kakuki Daenekas et al., 2009			●	●											
Speleonectes lucayensis Yager, 1981	●			●	●	●									
Speleonectes minnsi Koenemann et al., 2003		●													
Speleonectes ondinae (G. Valdecasas, 1984)														●	
Speleonectes atlantida n. sp.														●	
Speleonectes parabenjamini Koenemann et al., 2003		●													
Speleonectes tanumekes Koenemann et al., 2003		●													
Speleonectes tulumensis Yager, 1987b													●		
Speleonectes cf. *tulumensis* (undescribed species)													●		
Speleonectes spp. (unidentified species)	●	●	●	●	●	●									

de la Atlántida; however, *D. wilkensi* has also been found in wells outside the lava tube (Kornicker and Iliffe 1995; 1998). Other species that have been recorded both from the lava tube and anchialine waters outside the cave system include *Munidopsis polymorpha*, *Parhyale multispinosa*, *Heteromysoides cotti*, *Hadzia acutus*, and *Halosbaena fortunata* (Stock 1987; Wilkens et al. 1986; 1993). The anchialine waters connected with the ecologically homoge-neous lava tube provide extra habitat space, and this extensive network of interstitial clefts and crevices offers ideal opportunities for speciation by sympatric isolation. Although remipedes have never been found outside the lava tube system on Lanzarote, the distribution of species in Caribbean cave systems suggests that dispersal through subterranean flooded crevices must have occurred repeat-edly in the course of time (see Table 5).

On several diving expeditions during the last three decades, remipedes have been found in certain sections of the Túnel de la Atlántida. For example, the dome room at 250 m penetration depth was usually inhabited by several individuals (see map in Wilkens et al. this issue). This section of the cave appears to be out of the main flow path of tidal exchange (the tidal range within the cave is 2 m), and perhaps this explains an apparent preference of remipedes for this area. Although remipedes have not yet been observed closer to the entrance of the Jameos del Agua section, individuals have been found in the Los Lagos lakes further inland on previous expeditions.

During the Atlántida 2008 Expedition, we were able to collect for the first time specimens from sections of the main tube beyond the Montaña de Arena region at more than 700 m horizontal penetration (see map in Wilkens et al. this issue). This discovery implies that remipedes also inhabit the most remote sections of the Túnel de la Atlántida. However, owing to the great clarity of the cave water, the large average size of the cave passage, and the conspicuous appearance of remipedes (i.e., size and color), the fact that divers have always observed relatively few remipedes suggests that the Túnel de la Atlántida is inhabited by rather small populations.

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