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Speleonectes kakuki, a new species of Remipedia (Crustacea) from anchialine and sub-seafloor caves on Andros and Cat Island, Bahamas

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Abstract

A new species of the crustacean class Remipedia is described, illustrated and compared to closely related taxa. *Speleonectes kakuki* n. sp. inhabits at least four widely separated anchialine cave systems on the Great Bahama Bank. A total of ten specimens were collected from caves on Andros and Cat Island. *Speleonectes kakuki* can be distinguished from other species of remipedes by the presence of heteromorphic sternal bars and comparatively robust and pilose prehensile cephalic limbs. It is the first remipede to be collected from an offshore cave, whereas as all previously known remipede habitats are inland sites. The presence of remipedes in sub-seafloor caves is highly significant in that it suggests the anchialine habitat is much more extensive than previously thought and may extend for hundreds of kilometers beneath the shallow waters of limestone banks to link widely separated inland caves.

Key words: Remipedia, Speleonectidae, sub-seefloor cave, anchialine caves, Bahamas

Introduction

The identification and recognition of a new species of *Speleonectes* is based on several specimens from Cat Island, Bahamas, collected in 2004. When we compared these specimens with older collection material, we found samples from 1985 and 2001 that comprised as yet unidentified remipedes belonging to the new species. The older samples were collected from three caves on Andros.

Its occurrence in several cave systems on two islands on the Great Bahama Bank makes *Speleonectes kakuki* n. sp. one of the most widely dispersed species in the family Speleonectidae Yager, 1981. At present, the remipede order Nectiopoda Schram, 1986 is composed of three families, eight genera and 20 species (Table 1). While the majority of species is known only from single localities, a number of godzilliid and speleonectid taxa have been reported from both Grand Bahama and Abaco Island, two islands on the Little Bahama Bank. These include *Pleomothra apletocheles* Yager, 1989, *Godzilliognomus frondosus* Yager, 1989, *Cryptocorynetes haptodiscus* Yager, 1987a, *S. benjamini* Yager, 1987a, and *S. lucayensis* Yager, 1981 (one specimen from Abaco Island collected by TMI in 2006). *Lasionectes entrichoma* Yager & Schram, 1986 is known from North Caicos and Providenciales, both on the Caicos Bank. On the Yucatan Peninsula, *S. tulumensis* Yager, 1987b occurs in a number of caves that are probably part of a hydrologically interconnected system of anchialine tunnels.

The Bahamas archipelago consists of two major shallow-water banks, each containing multiple islands. The Great Bahama Bank is a large, shallow-water carbonate platform that includes the islands of New Providence, Bimini, Andros, Cat, Eleuthera, Great Exuma and Long Island. The Great Bahama Bank is separated from the Little Bahama Bank (containing the islands of Grand Bahama and Abaco) by the Northeast

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(3800 to 4700 m deep) and Northwest (700 to 2800 m deep) Providence Channels. Additional smaller banks within the archipelago include the Cay Sal, Acklins-Crooked, San Salvador, Rum, Mayaguana, Inagua, Caicos and Silver Banks. The banks are made up of limestone of shallow-water origin that has been deposited to a depth of at least 4500 m since the Cretaceous (Mullins & Lynts 1977).

TABLE 1. The three families of the remipede order Nectiopoda, including all currently described genera and species.

Family Micropacteridae
Micropacter yagerae Koenemann *et al.*, 2007a
Family Godzilliidae
Godzilliognomus frondosus Yager, 1989
Godzillius robustus Schram *et al.*, 1986
Pleomothra apletocheles Yager, 1989
Pleomothra fragilis Koenemann *et al.*, 2008
Family Speleonectidae
Cryptocorynetes haptodiscus Yager, 1987a
Cryptocorynetes longulus Wollermann *et al.*, 2007
Kaloketos pilosus Koenemann *et al.*, 2004
Lasionectes entrichoma Yager & Schram, 1986
Lasionectes exleyi Yager & Humphreys, 1996
Speleonectes benjamini Yager, 1987a
Speleonectes emersoni Lorentzen *et al.*, 2007
Speleonectes epilimnius Yager & Carpenter, 1999
Speleonectes gironensis Yager, 1994
Speleonectes kakuki Daenekas *et al.*, new species
Speleonectes lucayensis Yager, 1981
Speleonectes minnsi Koenemann *et al.*, 2003
Speleonectes ondinae (Garcia-Valdecasas, 1984)
Speleonectes parabenjamini Koenemann *et al.*, 2003
Speleonectes tanumekes Koenemann *et al.*, 2003
Speleonectes tulumensis Yager, 1987b

Within the Bahamas, a number of strictly anchialine species are widely distributed on a single bank. Species inhabiting caves on both the Exuma Cays and Andros Island on the Great Bahama Bank include the epacteriscid copepods *Bomburiella gigas*, *Azygonectes intermedius*, *Oinella longiseta*, and *Bofuriella vorata* (Fosshagen & Iliffe 2004); and the halocyprid ostracode *Spelaeoecia styx* (Kornicker *et al.* 2007). The halocyprid ostracode *S. capax* inhabits caves on Long Island and the Exumas on the Great Bahama Bank, while *Deeveya styrax* occurs on Abaco and Sweeting's Cay on the Little Bahama Bank (Kornicker *et al.* 2007). The cirolanid isopod *Cirolana* (*Cirolana*) *troglexuma* is found on the Exumas, Eleuthera and Cat Island (Botosaneanu & Iliffe 2007). The hadziid amphipod *Bahadzia williamsi* inhabits caves on Grand Bahama and Abaco (Holsinger & Yager 1985). The mysid *Stygiomysis clarkei* occurs on the Caicos Bank islands of Providenciales and North Caicos (Bowman *et al.* 1984). *Lucifuga spelaeotes*, a bythitid cave-fish, is known from Berry, New Providence, Eleuthera, Great Exuma and Long Islands (all on the Great Bahama Bank), while *L. lucayana* occurs on Grand Bahama and Abaco on the Little Bahama Bank (Møller *et al.* 2006).

Other anchialine species have been found to occur in caves on more than one bank. The cirolanid isopod

Bahalana yagerae is known from Andros, the Exumas and Grand Bahama Island on two banks (Botosaneanu & Iliffe 2002), while *B. cardiopus* inhabits Mayaguana and Acklins Island on two of the smaller banks (Iliffe & Botosaneanu 2006). The epacteriscid copepod *Cryptonectes brachyceratus* occurs on three banks, and is known from Acklins, the Exumas and Sweeting's Cay (Fosshagen & Iliffe, 2004). The bresilioid shrimp *Agostocaris williamsi* is present on Grand Bahama and the Caicos Islands, at nearly opposite ends of the Bahamas archipelago (Hart & Manning, 1986). The pardaliscid amphipod *Spelaeonicippe provo* occurs on the Exumas and the Caicos Islands (van der Ham, 2002). Two thermosbaenaceans *Tulumella bahamensis* and *T. grandis* both inhabit caves on Abaco, Grand Bahama and Andros (Yager, 1987c).

Additional anchialine species occur both in the Bahamas and in other locations as well. The ridgewayiid calanoid copepod *Brattstromia longicaudata* inhabits caves on both Grand Bahama and in Belize (Fosshagen & Iliffe 2004). The laophontid harpacticoid copepod *Paralaophonte echinata* has been collected from a cave on San Salvador, Bahamas, and from interstitial sandy sediments on Isla la Tortuga, Venezuela (Fiers 1986). The atyid shrimp *Typhlatya garciai* is known from caves on Providenciales in the Caicos Islands and Holguín and Pinar del Río Provinces in Cuba (Buden & Felder 1977). The hippolytid shrimp *Barbouria cubensis* occurs in caves on Abaco, the Caicos Islands, the Exumas, Mayaguana, and San Salvador, in addition to Bermuda, Cuba, Cayman Islands, and Jamaica (Hart & Manning 1981). Another hippolytid shrimp, *Janicea antiguensis*, has been reported from caves on Grand Bahama and Andros, as well as from cryptic habitats (reef caves, interior of ship wrecks, sea wall) on Antigua, Bermuda, Isla Cozumel (Mexico), the Cape Verde Islands, the Canary Islands, São Tomé and in Brazil (Wirtz 2004). A third hippolytid species, *Parhippolyte sterreri*, inhabits caves on Grand Bahama, Andros and the Exumas, in addition to Bermuda and Isla Cozumel (Kensley 1988). The lysianassoid amphipod *Socarnopsis catacumba* is known from Andros, the Exumas and Grand Bahama, as well as Cuba and Isla Cozumel (Clark & Barnard 1985). The mysid *Stygiomysis holthuisi* occurs on Grand Bahama, Anguilla, the Yucatan Peninsula and Isla Cozumel (Mexico), Puerto Rico and St. Martin (Pesce & Iliffe 2002).

Systematics

***Speleonectes kakuki*, new species**
(Figs. 1–5)

Type locality: Guardian Cave, North Andros, Bahamas.

Material examined (see also appendix): BAHAMAS - **North Andros, Guardian Blue Hole**: **Holotype** (USNM 1120738; our ID = BH-321; Figs. 1, 2), 32 trunk segments, 26 mm; collected by B. Kakuk, 24 Jul. 2000; limbs of trunk segment 10 used for DNA analyses. Paratype 1 (our ID = BH-330), 33 trunk segments, 23.4 mm; collected by B. Kakuk, 3 Jan. 2001; completely dissected for description (Figs. 2–5); remaining body parts used for DNA analyses. **North Andros, Conch Sound Blue Hole**: Paratype 2 (USNM 1120739; our ID = BH-335), 33 trunk segments, 18 mm; collected by B. Kakuk, 27 Jan. 2001; one maxillule dissected. Paratype 3 (our ID = BH-334), 35 trunk segments, 26.5 mm; collected by B. Kakuk, 21 Jan. 2001. **South Andros, Stargate Blue Hole**: Paratype 4 (our ID = BH-82), 31 trunk segments, 19 mm; collected by R. Palmer, Feb. 1985. **Cat Island, Gaiter's Blue Hole:** Paratype 5 (our ID = 04-021.1), 32 trunk segments, 24 mm; used for DNA analyses; collected by T. Iliffe, 14. Aug. 2004. Paratype 6 (USNM 1120740; our ID = 04-021.2), 33 trunk segments, 24 mm; used for DNA analyses; collected by T. Iliffe, 14. Aug. 2004. Paratype 7 (our ID = 04-021.3), 32 trunk segments, 19 mm; used for DNA analyses; collected by T. Iliffe, 14. Aug. 2004. Paratype 8 (our ID = 04-021.4), 32 trunk segments, 22 mm; collected by T. Iliffe, 14. Aug. 2004; completely dissected for description (Fig. 5). Paratype 9 (our ID = 04-021.5), 34 trunk segments, 19 mm; collected by T. Iliffe, 14. Aug. 2004.

All specimens are preserved in alcohol; dissected body parts and/or specimens are stored in glycerine. The holotype, paratype 2 and paratype 6 have been deposited in the National Museum of National History, Smithsonian Institution; all remaining types remain in the research collections of JY and SK.

Etymology: The new species is named to honor the cave diver Brian Kakuk, who collected numerous fish and invertebrates from Bahamian caves, including the new species described herein, which he generously provided for scientific research.

Diagnosis: *Speleonectes kakuki* is a large and robust species (Fig. 1). Trunk segments equipped with well-developed, angular pleural tergites and heteromorphic sternal bars. Dorsal ramus of antennule composed of 12 articles, ventral ramus with 9–10 articles. Maxillule, maxilla and maxilliped stout; lacertus and brachium of maxilla and maxilliped pilose, with arc-shaped terminal claws composed of 12–14 denticles. The anal somite is longer than wide, with caudal rami approximately as long as the anal somite.

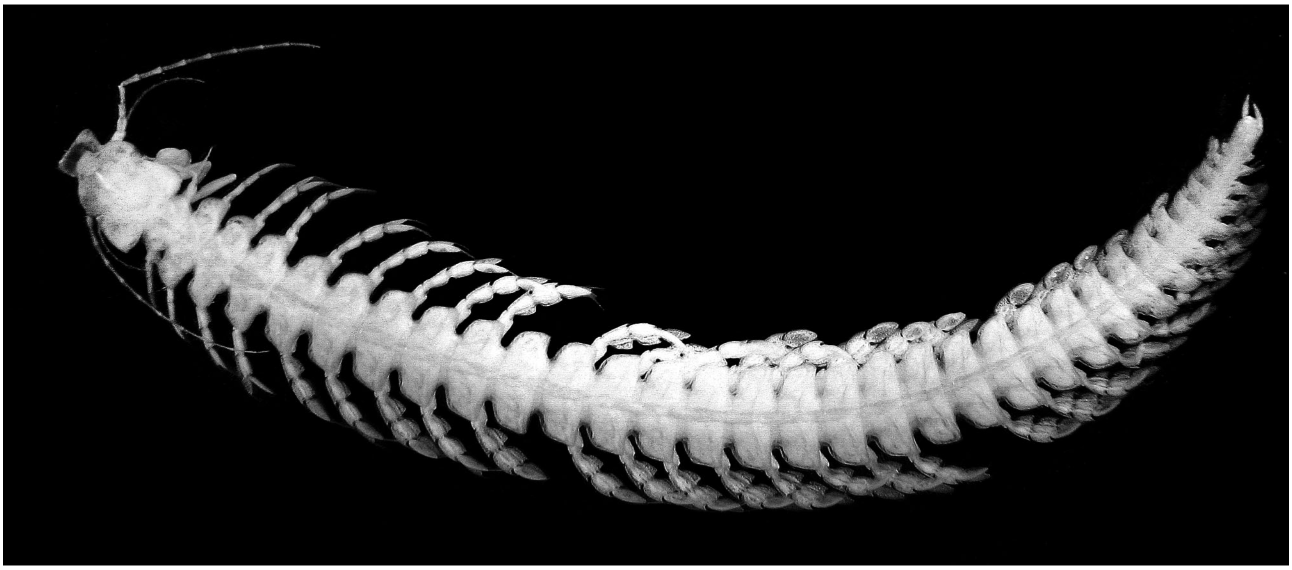

FIGURE 1. *Speleonectes kakuki* n. sp. Dorsal view of holotype BH-321 (North Andros); limbs of trunk segment 10 used for DNA analyses; right limb of trunk segment 19 lost. Photo by A. Bloechl.

Description: Body length up to 26.5 mm, with 32–35 trunk segments. Head shield subrectangular to trapezoidal, tapering anteriorly, as long as trunk segments 1–3 (Fig. 2A–C). Frontal filaments with relatively short medial processes (Fig. 3F). First trunk segment small, pleural tergite reduced; pleural tergites of remaining trunk segments well-developed, with angular distolateral corners pointing posteriorly. Sternal bars heteromorphic; with parallel margins on segments 1–13; large, with concave distal margin on segment 14; narrow, with parallel margins approximately up to segment 20, becoming triangular flaps towards trunk terminus (Fig. 2D). Posterior-most trunk segment (adjacent to anal somite) sometimes naked (without tergites and limb buds).

Antennule (Fig. 3A): Peduncular pad small, with a field of closely packed aesthetascs. Dorsal flagellum with 12 articles, reaching approximately 25% of body length. Ventral flagellum with 9–10 articles (sutures of proximal articles indistinguishable), as long as head shield.

Antenna (Fig. 3B): Proximal segment of protopod with four fine setae; distal segment shorter, with 9–10 setae. Exopod oval, slightly wider and shorter than protopod, equipped with 28–32 setae. First segment of endopod with 7–9 setae; second segment with 8–10 setae; third segment slightly larger than previous segments, bearing 20–22 setae arranged in 2 rows along distal margin. All setae plumose.

Labrum (Fig. 3G): Corners rounded with few fine setules; funnel-formed cavity surrounded by numerous fine setae, unilaterally with rows of denticles.

Mandible (Fig. 3C–E) broadly rounded, more than twice as long as wide. Incisor process and lacina mobilis of right mandible each with 3 stout denticles (Fig. 3E). Incisor process of left mandible with 4 stout denticles, lacina mobilis crescent-shaped, concave apical margin serrated (Fig. 3D). Apical surface of molar process with fine setae of variable length.

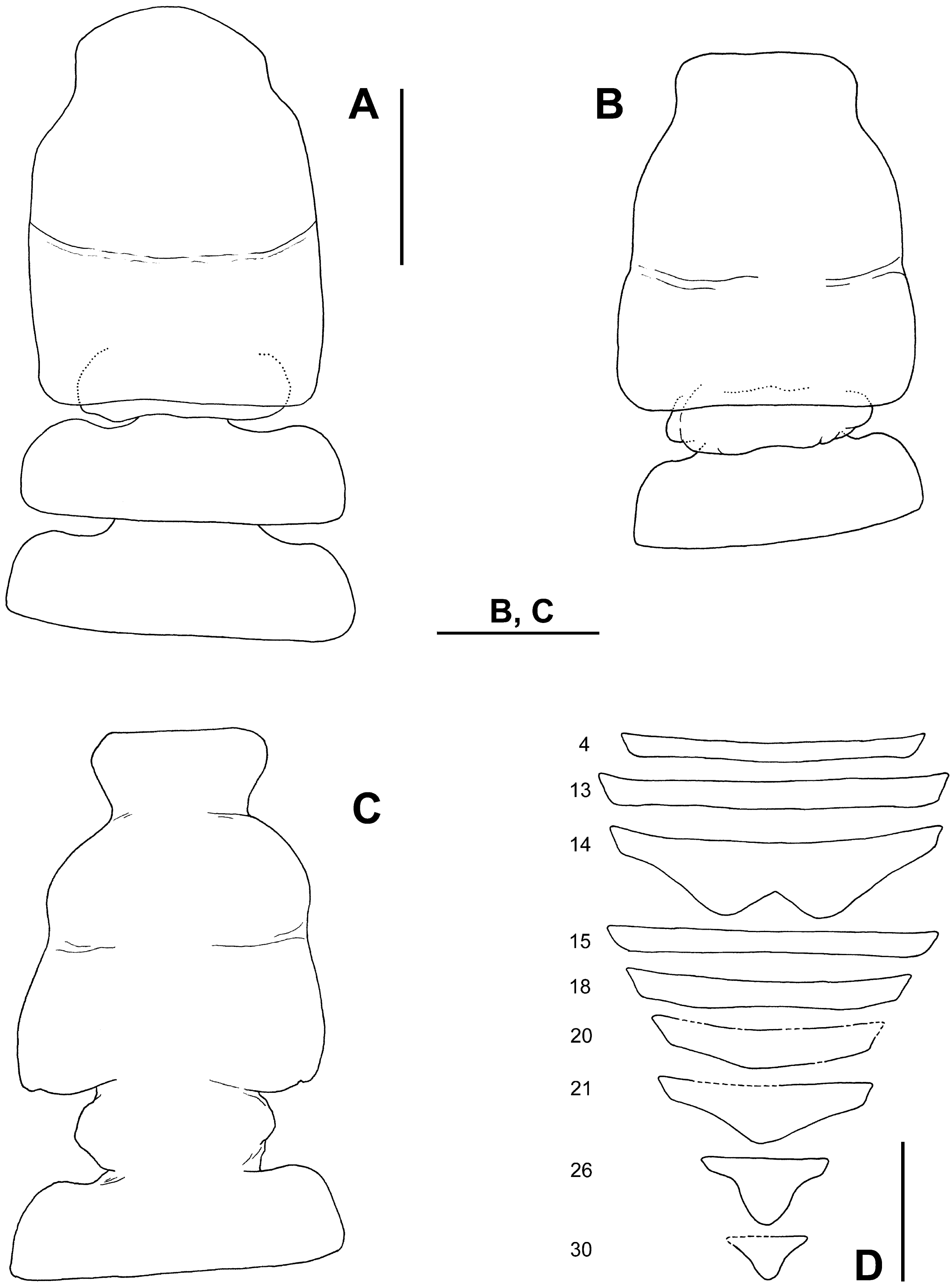

FIGURE 2. *Speleonectes kakuki* n. sp. Morphological variation of head shields (A–C), and sternal bars (D). A, paratype 1 (BH-330, North Andros), scale bar = 1 mm. B, paratype 8 (04-021.4, Cat Island). C, holotype (BH-321, North Andros). D, sternal bars of paratype 8 (04-021.4), scale bar = 0.3 mm. Numbers indicate individual trunk segments, from anterior to posterior; scale bar B, C = 1 mm.

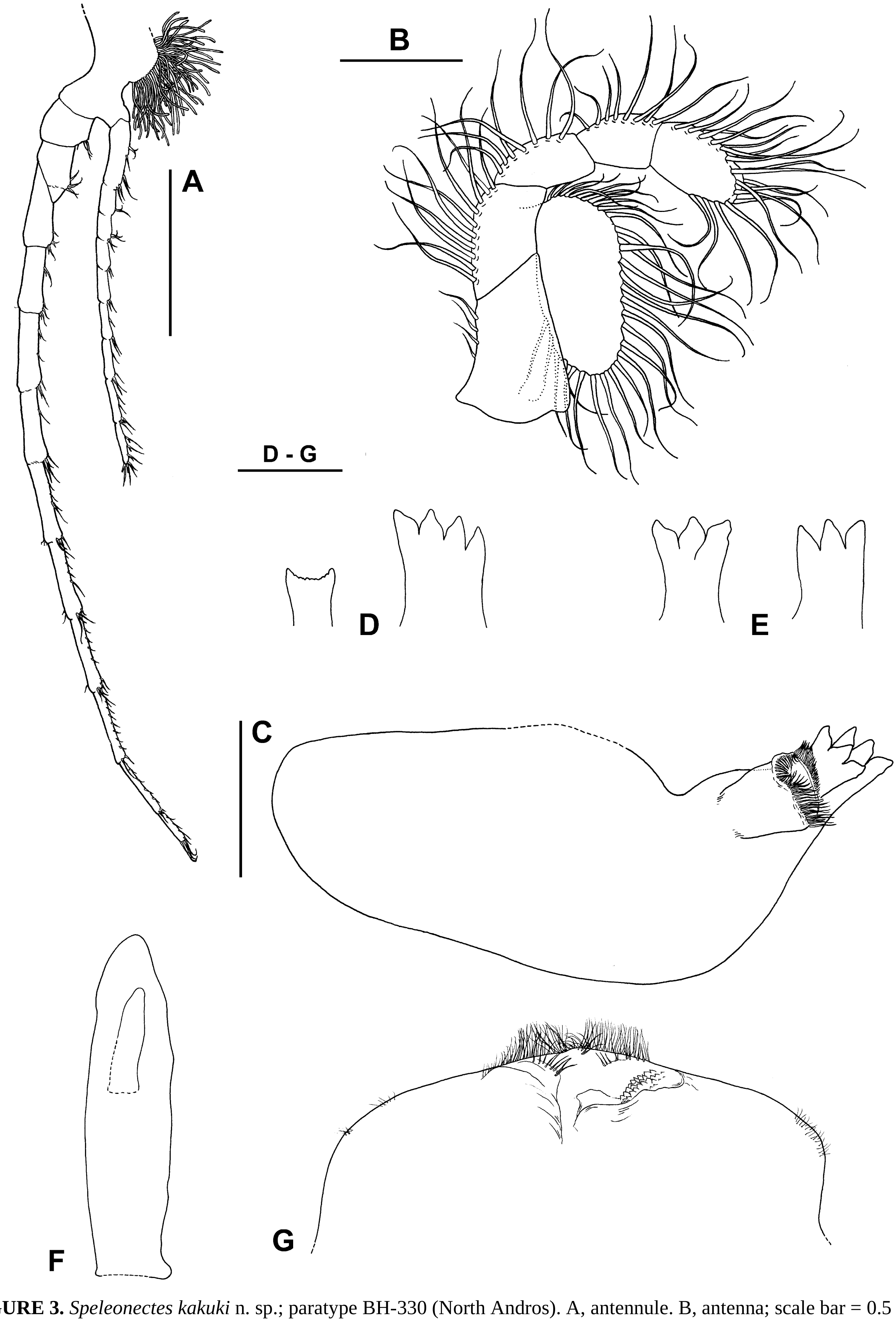

FIGURE 3. *Speleonectes kakuki* n. sp.; paratype BH-330 (North Andros). A, antennule. B, antenna; scale bar = 0.5 mm. C, right mandible; scale bar = 0.2 mm. D, lacinia mobilis (left) and incisor process (right) of left mandible. E, lacinia mobilis (left) and incisor process (right) of right mandible. F, frontal filament. G, labrum. Scale bar D–G = 0.1 mm.

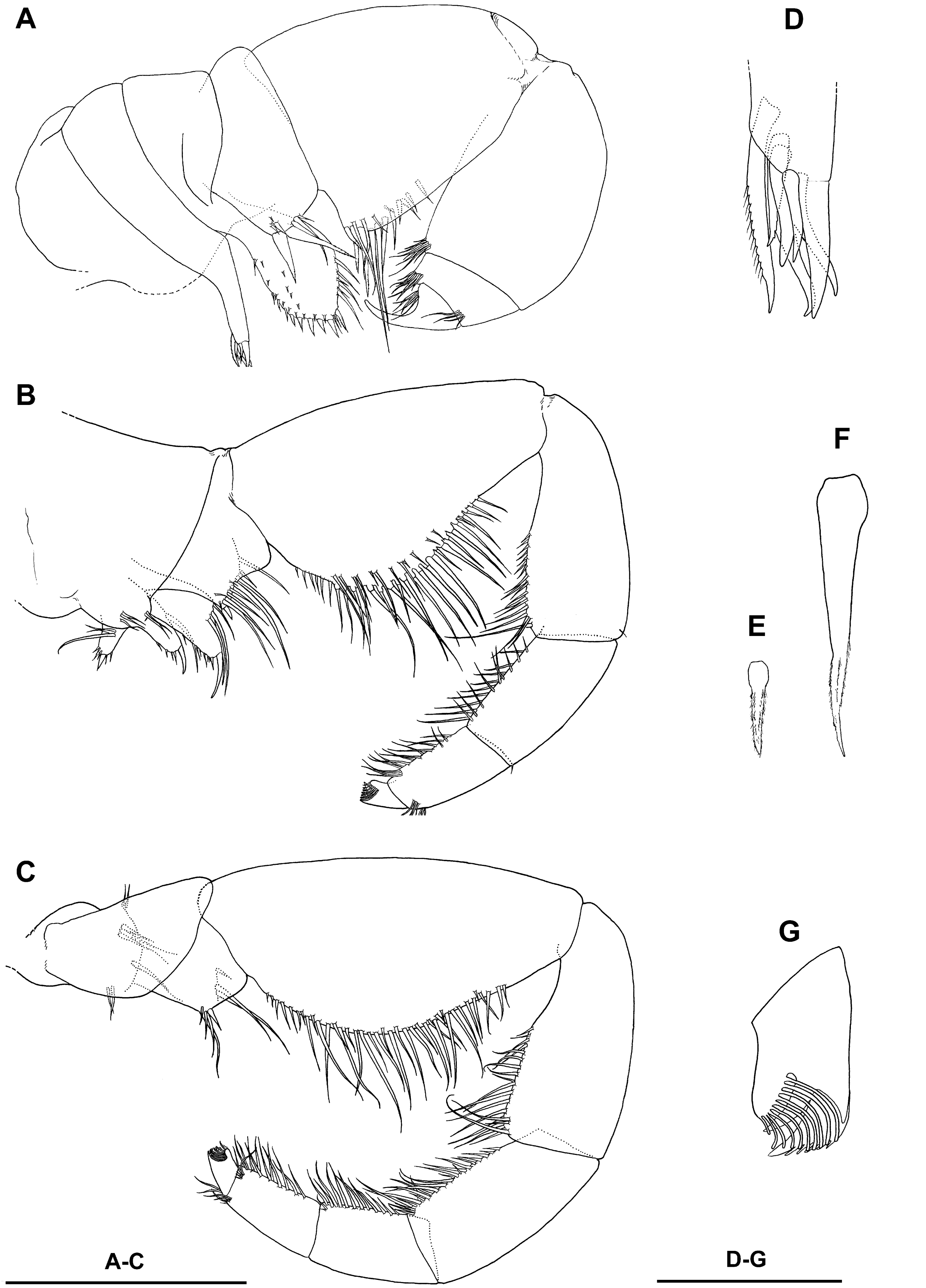

FIGURE 4. *Speleonectes kakuki* n. sp.; paratype BH-330 (North Andros). A, maxillule. B, maxilla. C, maxilliped. D, endite, segment 1 of maxillule. E, short serrated seta, segment 2 of maxillule. F, stout serrated seta, segment 4 of maxillule. G, claw of maxilla. Scale bars: A–C = 0.5 mm; D–G = 0.1 mm.

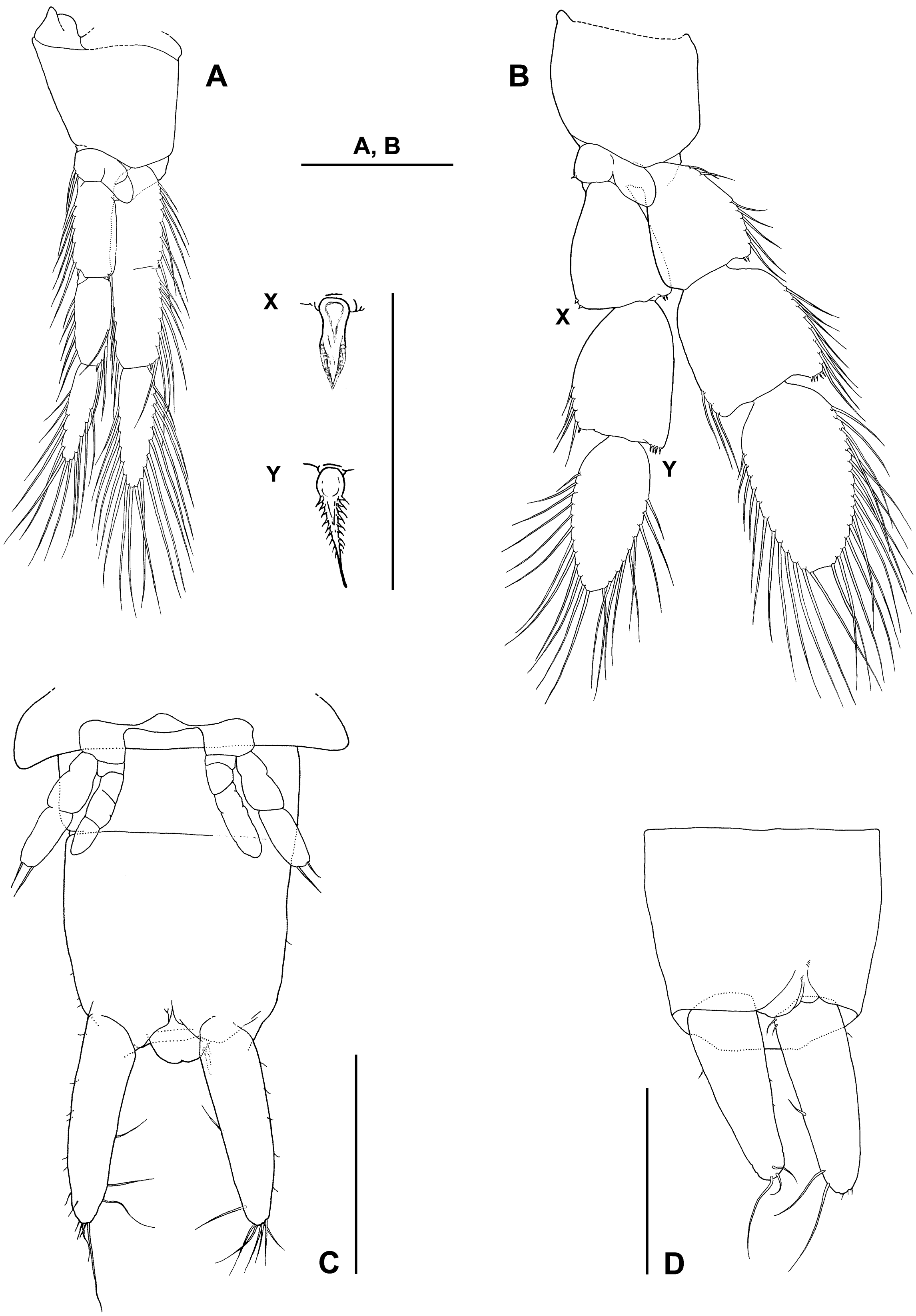

FIGURE 5. *Speleonectes kakuk*i n. sp.; A, B, D, x, y = paratype BH-330; C = paratype 04-021.4. A, trunk appendages of segment 1. B, trunk appendages of segment 14, with enlarged short seta of segment 2 (x) and segment 3 (y) of endopod. C, ventral view of anal segment and adjacent trunk segment; scale bar = 0.5 mm. D, ventral view of anal segment; scale bar = 0.5 mm. Scale bars: A, B = 0.5 mm; x, y = 0.1 mm.

Maxillule robust (Fig. 4A, D–F): Segment 1 with relatively long endite, apical margin equipped with 6–7 stout setae of variable length, 2 of which setulose and finely serrated (Fig. 4D). Segment 2 with large, broadly rounded spatulate endite; distolateral margin with 4 long and 2 short setae; distomedial margin with 10 setae (becoming increasingly longer and stouter towards apex), accompanied by irregular rows of very short, stout setae; all setae on endite of segment 2 simple, except 1 plumose, rasp-like seta on apex (Fig. 4A, E). Segment 3 with slightly rounded medial endite; apex with 2 very stout, long and rasp-like setae accompanied by several slender setae of variable length (Fig. 4A, F). Segment 4 (lacertus) robust, with oblique, evenly expanded medial margin, bearing 12–13 setae of unequal length arranged in a double row; proximal corner with 2–3 stout, rasp-like setae. Segment 5 comparatively robust, with distomedial field of setae. Segment 6 short, with 2 disjunct distal fields of setae. Claw well-developed, with medioproximal field of setae.

Maxilla longer than maxillule (Fig. 4B, G): Endites of segment 1 each with 1 large apical seta accompanied by 4–6 apical and subapical setae of variable length; largest endite with distinct subapical angle bearing 3–4 long setae. Segment 2 relatively well-developed, saddle-shaped, with row of about 12 setae of variable length. Segment 3 large, bulging inner margin with a double row of 41–48 setae of variable length. Segment 4 expanded, but shorter than segment 3; segments 4, 5 and 6 gradually decreasing in width and length, bearing double rows of setae along medial margins. Arc-shaped claw with 12–14 fused denticles flanked by 2 stronger free denticles (Fig. 4G).

Maxilliped relatively robust, longer than maxilla (Fig. 4C). Proximal segments 1–3 bearing only a few setae. Segment 4 very long, medial margin evenly expanded, equipped with 37–48 long and short setae arranged in a double row. Segment 5 expanded, but distinctly shorter than segment 4, with row of setae on mediodistal margin. Segments 6–8 with similarly appearance, gradually decreasing in length and width, with double rows of mediodistal setae. Claw similar to that of maxilla.

Biramous, paddle-shaped trunk limbs (TL) largest in mid-trunk region, becoming gradually smaller and less developed towards posterior end of trunk (Fig. 5A–C). Reduced first trunk segment (TS) bearing a pair of relatively slender limbs (Fig. 5A), appendages of mid-trunk region (TS 4-20) broad and expanded (Fig. 5B). Most trunk appendages equipped with 3 types of setae: relatively long, finely plumose setae on lateral and/or medial margins of individual limb segments, and very short, but robust setae with either plumose (Fig. 5x) or serrated (Fig. 5y) margins on distal corners of limb segments.

TL 1 (Fig. 5A): Endopod shorter than exopod. All segments of both exopod and endopod with long plumose setae on lateral margins, distal segments also with long setae on medial margins; all short setae on distal corners with serrated margins.

Larger trunk limbs (represented by TL 14) less setose than TL 1 (Fig. 5B, x, y). Segment 1 of exopod with 4–7 lateral setae and 2 short serrated distolateral setae; segment 2 expanded, with 6–8 long lateral, 3 long medial setae, and 4–5 serrated distolateral setae; segment 3 broad, oval, with rows of long setae on inner and outer margins. Endopod approximately as long as exopod, but slenderer; segment 1 short, with 1 short, plumose lateral seta; segment 2 with 1–2 short plumose setae on distolateral corner and 1–2 short serrated setae on distomedial corner; lateral margin of segment 3 with 2–4 long setae and 1–2 short serrated setae on corner, medial corner with 3–4 short plumose setae; segment 4 narrow, lanceolate, with rows of long setae on margins.

Anal segment (Fig. 5C, D): Slightly longer than wide. Caudal rami approximately as long as anal somite, with short lateral setules and several longer apical and subapical setae.

Discussion

Morphological variability

The examined specimens of *Speleonectes kakuki* n. sp. exhibited apparently unusual morphological variability in the shape of the head shield. While some head shields had a subrectangular shape (Fig. 2A), others appeared more trapezoidal (Fig. 2B), with the anterior part more or less distinguished as a flap-like extension (Fig. 2C). We observed this variability in specimens from different cave systems, i.e., in specimens from Gaiter's Blue Hole (Cat Island) as well as from Guardian Blue Hole (North Andros). Therefore, we can exclude morphological variation as a result of geographically isolated subpopulations on separated islands. It seems likely that the differently shaped head shields are rather an artifact caused by dissimilar preservation techniques of live animals. The head shields of all known Remipedia have a 3-dimensional shape, with recurved lateral and anterior margins. It seems that the recurved margins have straightened in some specimens after preservation, resulting in more trapezoidal, extended shapes.

Another case of apparent morphological variability concerns the anal somite. Most specimens had an anal somite that was slightly longer than wide (Fig. 5D). However, in two specimens (the holotype and paratype 04-021.4), the anal segments appeared almost twice as long as wide (Fig. 5C). In these specimens, the posterior-most trunk segment, adjacent to the anal somite, was completely naked, lacking pleurotergites and limb buds. These naked trunk segments were separated from the anal somite by a faint suture. This morphological peculiarity has also been observed in *Speleonectes epilimnius* (Yager & Carpenter 1999).

Morphological comparisons with other remipedes

In remipede crustaceans, the morphological particularities of three pairs of prehensile cephalic limbs serve as a valuable set of diagnostic characters. Based on prehensile limb morphology, the new species *Speleonectes kakuki* is a typical representative of the family Speleonectidae. It lacks the distinct characteristics of the families Godzilliidae Schram *et al.*, 1986 and Micropacteridae Koenemann *et al.*, 2007a, both of which are defined, *inter alia*, by advanced degrees of subdivision of maxillule and maxilla into lacertus and fused brachium, and a reduction of the ventral ramus of the antennule.

Within the Speleonectidae, the new species can unambiguously be assigned to the genus *Speleonectes*. It can be clearly distinguished from the genera *Cryptocorynetes* Yager, 1987a and *Kaloketos* Koenemann *et al.*, 2004, both of which are characterized by dense fields of modified setae, e.g., as discoid organs (*Cryptocorynetes*) or feathered setae (*Kaloketos*), on their prehensile limbs; these apomorphies are lacking in *S. kakuki*. Similarly, both species in the genus *Lasionectes* Yager & Schram, 1986 feature relatively small first maxillules, and both maxillae and maxillipeds with "longfinger-type" of terminal claws. In *Speleonectes kakuki*, the maxillule is relatively large and robust, while maxilla and maxilliped bear arc-shaped ("horseshoe-type") terminal claws (see Koenemann *et al.* 2007b for definition of terms).

All three pairs of prehensile limbs are relatively large and robust in *S. kakuki*; all three limbs have long lacerti with expanded medial margins; maxilla and maxilliped bear comparatively dense rows of setae along their medial margins. This combination of characters is found only in two other species of *Speleonectes, S. gironensis* Yager, 1994 and *S. lucayensis* Yager, 1981. However, the trunk segments in *S. gironensis* are equipped with isomorphic sternal bars (distinctly heteromorphic in *S. kakuki*), both rami of the antennule have fewer articles, and the biramous trunk appendages are much slenderer than in *S. kakuki*.

The closest morphological affinities can be found between *S. kakuki* and *S. lucayensis*. According to the detailed redescription by Schram *et al*. (1986), *S. lucayensis* can be differentiated from *S. kakuki* by the following features:

- the ventral ramus of the antennules has 8 articles (9–10 in *S. kakuki*);
- the sternal bar on TS 14 has a very wide concave distal margin (narrow, v-shaped in *S. kakuki*);
- the first maxillular endite bears 7 simple terminal setae (6–7 setae in *S. kakuki*, 2 of which setulose and serrated);
- the second maxillular endite has a subrectangular shape (broadly rounded in *S. kakuki*);
- the third maxillular endite has a cone-shaped apex, with 2 relatively short, very robust simple setae (reduced endite with 2 long, rasp-like setae in *S. kakuki*);
- the fourth maxillular endite bears 1 short, robust simple seta (2 long, rasp-like setae in *S. kakuki*);
- the segments of the larger trunk limbs are equipped with short "comb setae" (finely serrated in *S. kakuki*; see Fig. 5y).

Ecological profiles of the collection sites

Guardian Blue Hole is located on the eastern (Tongue of the Ocean) side of North Andros Island, about 1.5 km north of Cargill Creek. The primary entrance of this fracture cave (sensu Mylroie & Carew 1995) consists of a 60 m long by 25 m wide pond situated 230 m inland from the coastline. It is one of the largest (700+ m) and deepest (133 m) fracture caves in the Bahamas. A second entrance is a very small gap between boulders on the floor of the jungle 425 m south of the main entrance pond. The cave was named for a solitary barracuda that at one time inhabited the main entrance pond. This pond is fresh, with a halocline occurring at about 10 m depth. The vertical walls of this fracture cave have been enlarged by dissolution (Fig. 7). In shallower depths, the walls of the cave are highly decorated with stalactites and stalagmites. Several deep pits within the cave drop from 45 m depths to more than 130 m. A layer of hydrogen sulfide is typically present at the halocline. This cave is biologically depauperate, with only small shrimp, possibly *Agostocaris* sp., and a few remipedes observed on multiple dives. The specimens of *Speleonectes kakuki* described herein were collected at 33 m depth, about 90 m inside the cave from the main entrance.

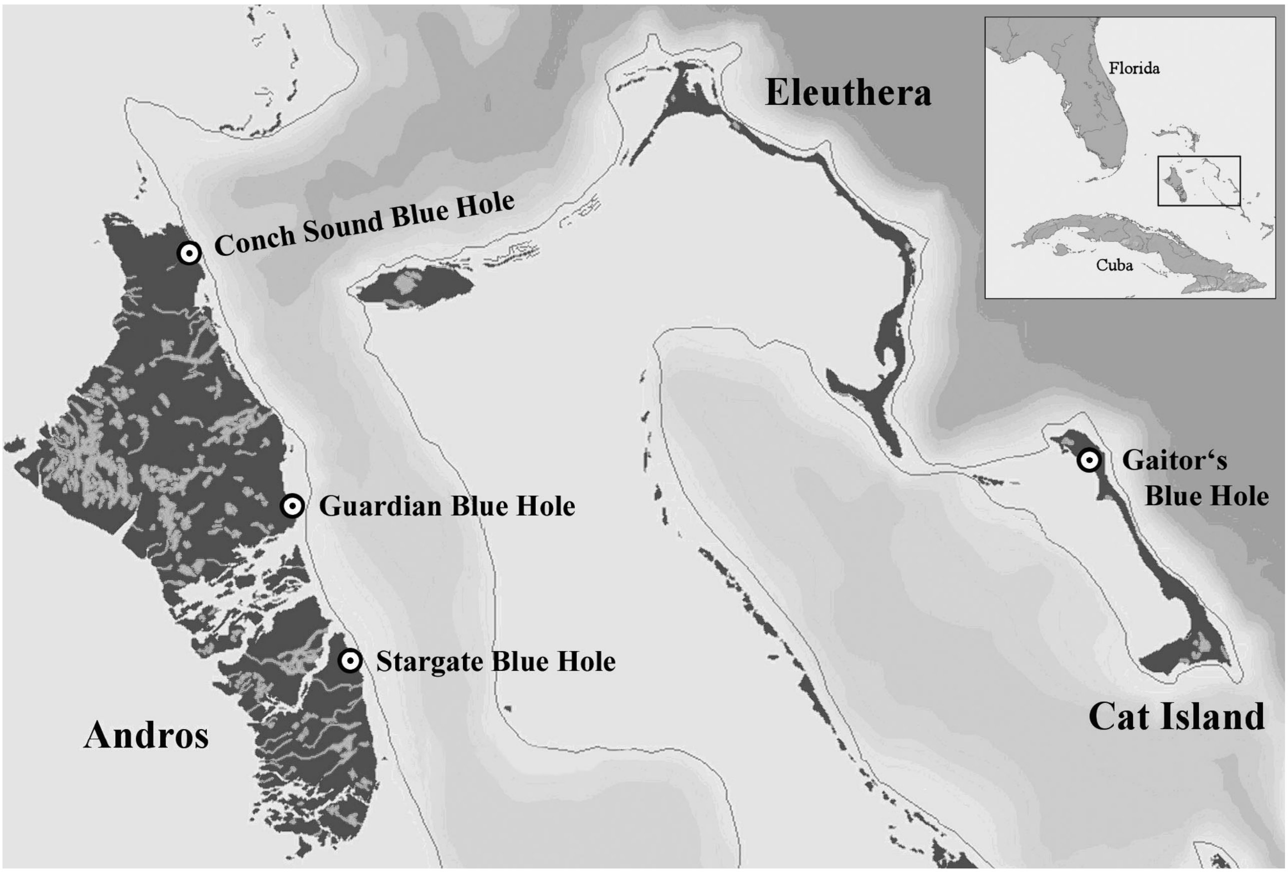

FIGURE 6. Collection localities of *S. kakuki* n. sp. The thin gray line demarcates the area of the Great Bahama Bank. Map (modified) with kind permission of Demis (www.demis.nl).

Conch Sound Blue Hole is an ocean blue hole located at the northeast corner of North Andros Island, about 3 km south of Nicholls Town. The entrance consists of a submerged depression about 20 m from the coastline in a shallow bay. Strong tidal currents flow through the cave so it can only be explored at the change of the tide when currents slow, go slack and then reverse direction. The main passage extends to the south, out under the bay and away from land (see map in Palmer 1997: 48–51). It has been explored by Brian Kakuk for more than 1,600 m at a maximum depth of 36 m. At his limits of penetration into the cave, Kakuk discovered a dome room with a depth of 20 m at the ceiling. There, he has collected remipedes, thermosbaenaceans, the blind cave fish *Lucifuga spelaeotes*, the halocyprid ostracode *Deeveyia bransoni* and myodocopid ostracodes

Harbansus paucichelatus, *Eusarsiella paniculada*, *E. fax*, and *Rutiderma flex* (Kornicker *et al*. 2007). The Conch Sound specimen of *Speleonectes kakuki* was collected at a depth of 23 m and a distance of 1,625 m from the entrance in a large room filled with hydrogen sulfide nearly to the ceiling. A layer of warm clear water at the top of the room was contained with large numbers of stygobitic animals.

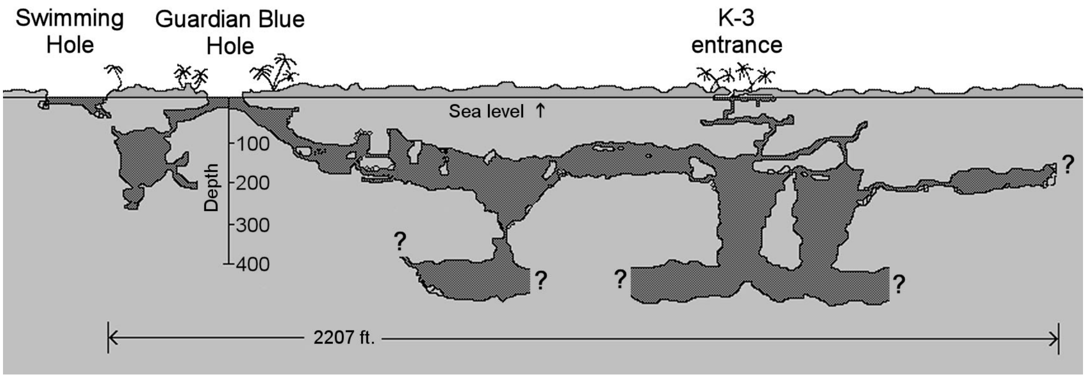

FIGURE 7. The Guardian Blue Hole cave system, North Andros Island, Bahamas. Question marks indicate unknown cave sections; all distances in feet. Modified from unpublished original map by Brian Kakuk, adopted by Kornicker *et al.* (2007).

Stargate Blue Hole is located about 500 m inland from the east coast of South Andros Island on the west side of The Bluff village. It is part of a major north-south bank margin fracture zone paralleling the underwater escarpment that separates the Great Bahama Bank from the Tongue of the Ocean. This fracture extends for tens of kilometers and was formed as a result of glacio-eustatic sea level changes and gravitational stresses along the edge of the limestone bank (Palmer 1986a, b).

The entrance to this cave is a partially roofed-over cavern with a vertical drop of 6 m to water level. The restricted nature of the entrance limits organic input and as such, the surface water is relatively clear. Underwater, a shaft drops vertically to depths in excess of 80 m, while rift-like passages extend north and south. To the north, a 10 m wide passage with the roof at -20 m depth extends for 107 m to a breakdown choke. To the south, a similar passage runs for 100 m to another choke, passable on the right hand side at -37 m to reach an extremely loose boulder chamber that chokes again after a further 30 m.

Water column profiles in Stargate were obtained in August 1997 by lowering a Hydrolab Water Quality Multiprobe Logger from the surface to 80 m depth (Fig. 8). Surface waters in the entrance pool were found to have a salinity of 3.4 ppt. A halocline between 22–27 m depth marked the transition to 37 ppt salinity. The general temperature trend in the water column involved a decrease from 27.4 ºC at the surface to 25.0 ºC at 80 m. However, secondary temperature maxima occurred above and below the haloclines at 10.2 m (25.82 ºC) and 30.2 m (26.12 ºC). The pH decreased from 8.7 at the surface to 8.18 at 80 m. A secondary pH minimum of 8.21 occurred at 22–24 m, while a secondary maximum of 8.55 was found at 30 m. Dissolved oxygen decreased from 5.67 mg/l at the surface to 0 at 80 m depth. A secondary oxygen maximum of 2.96 mg/l occurred at 31 m depth.

In addition to the remipede *Speleonectes kakuki*, other stygobitic species found in Stargate include the ridgewayiid calanoid copepods *Stargatia palmeri* and *Robpalmeria asymmetrica* (Fosshagen & Iliffe, 2003), the epacteriscid calanoid copepod *Bomburiella gigas* (Fosshagen and Iliffe 2004), and the hadziid amphipod *Bahadzia setimana* (Stock 1986).

Gaiter's Blue Hole consists of a 50 m diameter circular pond located 900 m inland from the west coast of Cat Island near Dumfries settlement (Palmer 1986c). This blue hole has a 1–2 m thick, deep purple colored H_2S layer at 6 m depth that blocks out all light. Below this layer, the water clears up and another, less dense H_2S zone and a thermocline occur at -12 m. The floor of the hole slopes gently down to a deep shaft on the northern side that descends in vertical steps past sheer rock faces. The cave appears to end in a larger room with depths reaching 37 m. Remipedes, the amphipod *Bahadzia* cf. *williamsi*, and the shrimp *Agostocaris* sp. were collected in clear saltwater at 24–37 m depths.

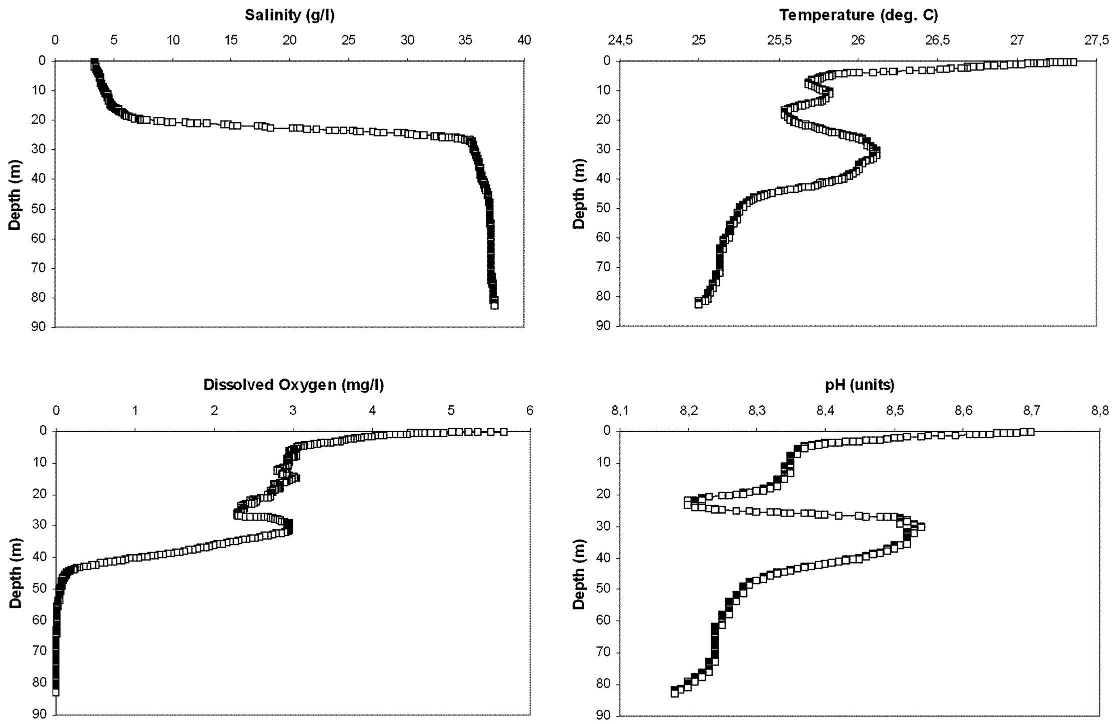

FIGURE 8. Salinity, temperature, dissolved oxygen, and pH water column profiles from Stargate Blue Hole, South Andros, Bahamas, taken on 20 August 1997 with an YSI Model 600XLM multi-parameter water quality monitor. Squares represent individual data points.

Stargate on South Andros and Conch Sound on North Andros are separated by a straight line distance of 117 km, while Stargate is located 204 km away from Gaiter's Blue Hole on Cat Island. However, due to the highly irregular shape of the Grand Bahama Bank and intervening deep waters of the Exuma Sound and Tongue of the Ocean, the minimum linear distance across shallow-water sections of the Bank between Gaiter's and Conch Sound is more than 550 km.

Speleonectes kakuki is the first remipede to be collected from a cave that does not fit the currently accepted definition of an anchialine environment – "bodies of haline water, usually with a restricted exposure to open air, always with more or less extensive subterranean connections to the sea, and showing noticeable marine as well as terrestrial influences" (Stock *et al.* 1986). Cave or crevices opening under sea level have been termed "submarine caves", and due to their lack of a terrestrial influence, were not considered to be anchialine. Conch Sound Blue Hole lacks any terrestrial input as its entrance is on the sea bed and it extends entirely beneath the floor of the ocean. Although strong tidal currents flush into and out of the entrance region of Conch Sound, at a horizontal distance of more 1,600 m from the entrance, stratified water masses contain typical anchialine fauna including *Speleonectes kakuki*, as well as the halocyprid ostracode *Deeveyia bransoni*, thermosbaenaceans and the cave fish *Lucifuga spelaeoetes* (Kornicker *et al.* 2007). *Deeveyia bransoni* has also been collected from stratified marine waters below 60 m depth in Double Drop Blue Hole, another submarine cave located offshore from South Andros Island. The presence of otherwise anchialine taxa in submarine caves indicates that the anchialine habitats do not require terrestrial influences. Instead, the defining characteristic of the anchialine habitat appears to be the relatively long (months to multiple years) residence times of marine waters in the subterranean environment.

In this new sense, anchialine habitats are not restricted to being located beneath islands or other land masses, but also occur beneath the sea floor of shallow-water platforms such as limestone banks and continental margins. Thus, they cover a much larger area than had previously been thought and may explain the occurrence of anchialine stygobionts such as *Speleonectes kakuki* in caves on widely separated islands.

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Appendix. Collection data of *Speleonectes kakuki* n. sp.

Collection date	Label	Number of specimens	Island	Locality
Jul. 2000	BH-321	holotype	North Andros	Guardian Blue Hole
Feb. 1985	BH-82	1 paratype	South Andros	Stargate Blue Hole
Jan. 2001	BH-330	1 paratype	North Andros	Guardian Blue Hole
Jan. 2001	BH-334	1 paratype	North Andros	Conch Sound Blue Hole
Jan. 2001	BH-335	1 paratype	North Andros	Conch Sound Blue Hole
Aug. 2004	04-021.1-5	5 paratypes	Cat Island	Gaiter´s Blue Hole