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THE REMIPEDIA (CRUSTACEA):
A STUDY OF THEIR REPRODUCTION
AND ECOLOGY

by

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John R. Holsinger (Director)

ABSTRACT

THE REMIPEDIA (CRUSTACEA): A STUDY OF THEIR REPRODUCTION AND ECOLOGY

Jill Yager
Old Dominion University, 1989
Director: Dr. John R. Holsinger

Remipedes are an unusual group of troglobitic crustaceans that live exclusively in anchialine caves. Since their discovery in 1979, nine species have been described, seven of which are found in caves in the West Indies, one from the Yucatan Peninsula of Mexico and one from the Canary Islands. Most of what is known about these animals has come mainly from taxonomic descriptions. Little has been published about their reproductive biology or ecology. The objectives of this dissertation were to investigate the reproductive biology and ecology of the remipedes inhabiting Sagittarius Cave on Grand Bahama Island, Bahamas.

Sagittarius Cave was chosen as a study site because it was inhabited by several species of remipedes and because of its remote location and lack of disturbance by divers. The cave was sampled every three months for a year. The remipedes and associated fauna in the aphotic zone were collected, and physical factors such as salinity, dissolved oxygen, and temperature were measured. Sagittarius Cave is euhaline throughout but has two or more distinct density interfaces beneath which the water is very low in dissolved oxygen, usually less than 1 ppm. Remipedes are confined to this nearly anoxic habitat. Six species of remipedes were found in the cave along with a community of troglobitic organisms composed primarily of crustaceans. The six species of remipedes collected included two new monotypic genera.

The study of the reproductive biology was restricted to two species of remipedes, *Speleonectes benjamini* and *Godzilliognomus frondosus*, because of their abundance in the cave. These species were found to be simultaneous hermaphrodites. The occurence of mature oocytes was associated with mature spermatophores. Various degrees of oogenesis and spermatogenesis were documented in each individual. Emphasis was placed on the male reproductive system, and ultrastructural details of the sperm are given. The sperm is flagellated and packed into distinctly shaped spermatophores.

General information about remipede internal anatomy and a comparison of external morphology are included, as well as a key to all remipede species and an annotated check list.

Dedicated to the memories of

Boppy and Dad

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TABLE OF CONTENTS

CHAPTER 1. REMIPEDES AND THEIR ENVIRONMENT

CHAPTER 2. AN ECOLOGICAL STUDY OF REMIPEDES IN SAGITTARIUS CAVE

RESULTS AND DISCUSSION

CHAPTER 3. THE REPRODUCTIVE BIOLOGY OF REMIPEDES

OBSERVATIONS AND DISCUSSION

CHAPTER 4. GENERAL ASPECTS OF INTERNAL ANATOMY

LIST OF TABLES

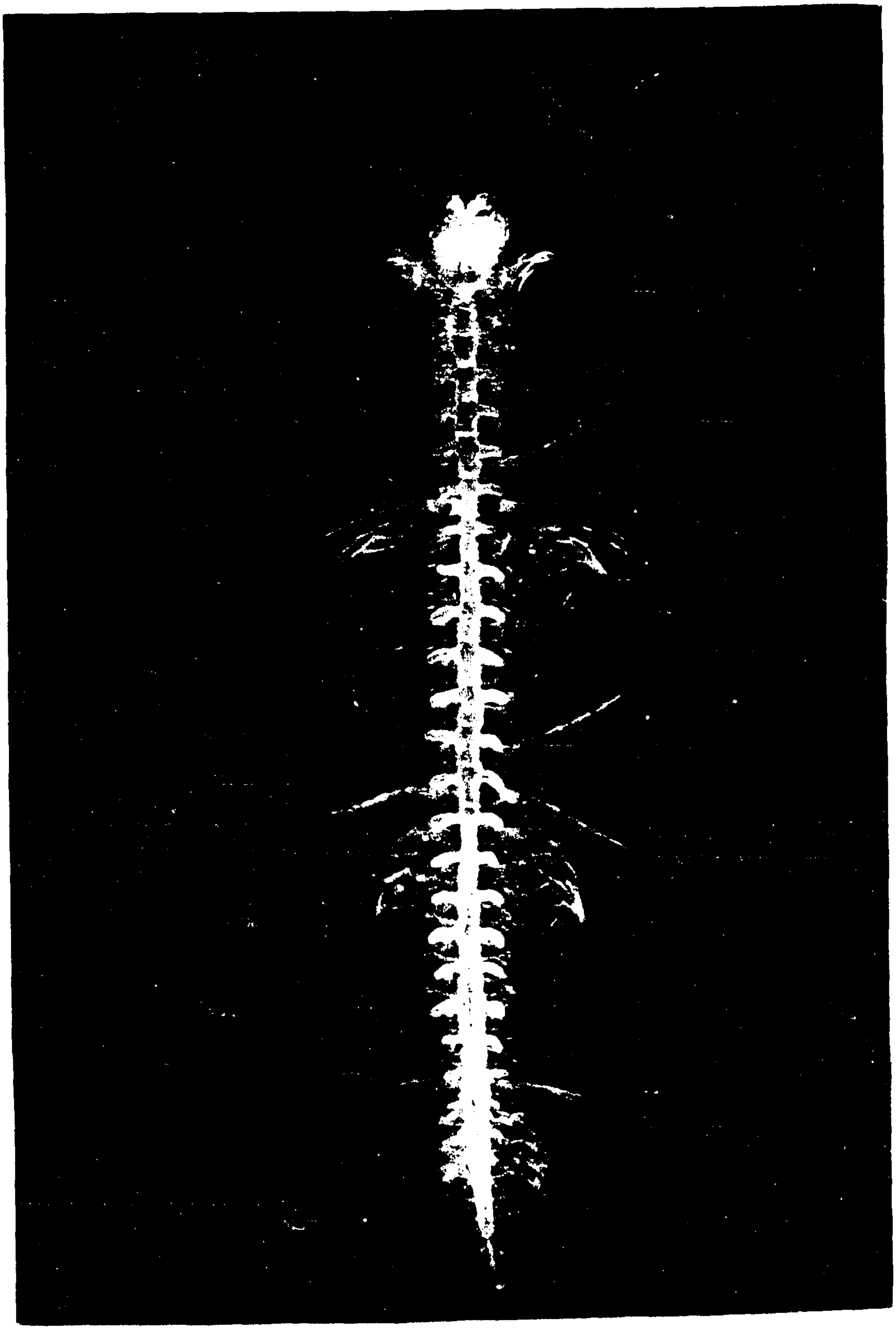
LIST OF FIGURES

GENERAL INTRODUCTION

In 1979 an unusual crustacean was discovered in a submerged cave on Grand Bahama Island. Although this animal clearly fit into the subphylum Crustacea, it possessed none of the definitive characters of the existing eight classes. Because of its wide array of unusual and possibly primitive characteristics, a new class of Crustacea was described. The class was given the name Remipedia because of the many paddlelike swimming appendages, and the first remipede crustacean was called Speleonectes lucayensis (Yager, 1981). This "cave swimmer" (Fig. 1) was discovered in Lucayan Cavern, an anchialine cave system on Grand Bahama Island. Remipedes are troglobitic (obligate cave-dwelling) crustaceans. They are found exclusively in anchialine caves systems (caves which have inland surface openings but subsurface connections to the sea).

Prior to the late 1970's anchialine pools and caves were primarily surveyed from the surface by biologists using dip nets or traps. The exciting discovery of the first remipede led to further exploration of the many anchialine caves of the Bahamas. The complexity of the

Figure 1. Speleonectes lucayensis, pictured live.
Approximate size = 22 mm.
(Photograph by Dennis W. Williams)



submerged cave environment was never conjectured to exist until a few trained cave divers began to notice more than just the beauty of the cave passages. The ability to access the submerged cave environment far from the cave entrance has resulted in the discovery of remarkable ecosystems inhabited by scores of new invertebrate species.

Although new remipede species have been discovered since 1979, most of what has been published consists of taxonomic descriptions. Until this study, few details were known about their reproductive biology. Additionally, their cryptic environment had not been studied in detail. The primary objectives of this research were to conduct a one year ecological study of the remipedes which inhabit one selected cave system, and to study their reproductive biology. Chapter 1 is an introduction to remipedes and their environment. It includes their distribution, biogeography, comparative morphology, and a key to the species. Characteristics of anchialine caves are described and several remipede habitats are compared. Environmental information is provided which represents over a decade of observations, collections, and exploration in various caves mainly throughout the Bahamas and Mexico. Personal communication with other cave divers, especially Dennis Williams, has allowed comparisons of different anchialine cave systems to be included.

The results of a one year ecological study of Sagittarius Cave on Grand Bahama Island is given in Chapter

2. The reproductive biology of two species from this cave is presented in Chapter 3. Special emphasis is placed on the male reproductive system, and ultrastructural details of sperm are included. During the reproductive study more was learned about the internal anatomy of remipedes. This information is found in Chapter 4.

One of the difficulties in studying remipedes is the logistics involved in finding them. Anchialine caves are often in remote areas, and locating cave entrances involves a combination of local knowledge, field vehicles, aerial surveys where possible, hours of walking, and the transportation of cave diving equipment. After arriving at a potential site there is no guarantee that the cave is inhabited by remipedes.

Chapter 1. **REMIPEDES AND THEIR ENVIRONMENT**

INTRODUCTION

Remipedes are free-swimming, troglobitic crustaceans characterized by a short head followed by an elongate, segmented trunk. Remipedes lack eyes and body pigmentation and have well-developed chemo and mechanosensory mechanisms for living in an environment devoid of light. One of the most distinguishing characteristics of the Remipedia is the trunk, which lacks tagmosis and is composed of numerous segments each bearing a pair of biramous swimming appendages. These characteristics are hypothesized for the primitive crustacean body plan. After analysis of many of its primitive features, the class Remipedia was placed at the base of the crustacean family tree (Schram, 1986).

DISTRIBUTION OF REMIPEDES

The Class Remipedia currently has nine species divided among six genera and two families (Table 1). Remipedes are recorded exclusively from anchialine caves in the North Atlantic Ocean and Caribbean region from about 30°-15° N latitude (Fig. 2). By far the largest number of species

Table 1. A list of known remipede taxa.

PHYLUM ARTHROPODA

SUBPHYLUM CRUSTACEA

CLASS REMIPEDIA

Order Nectiopoda

Family Speleonectidae:

Speleonectes lucayensis Yager, 1981

Speleonectes benjamini Yager, 1987a

Speleonectes ondinae (Valdecasas), 1985

Speleonectes tulumensis Yager, 1987b

Lasionectes entrichoma Yager and Schram, 1986

Cryptocorynetes haptodiscus Yager, 1987a

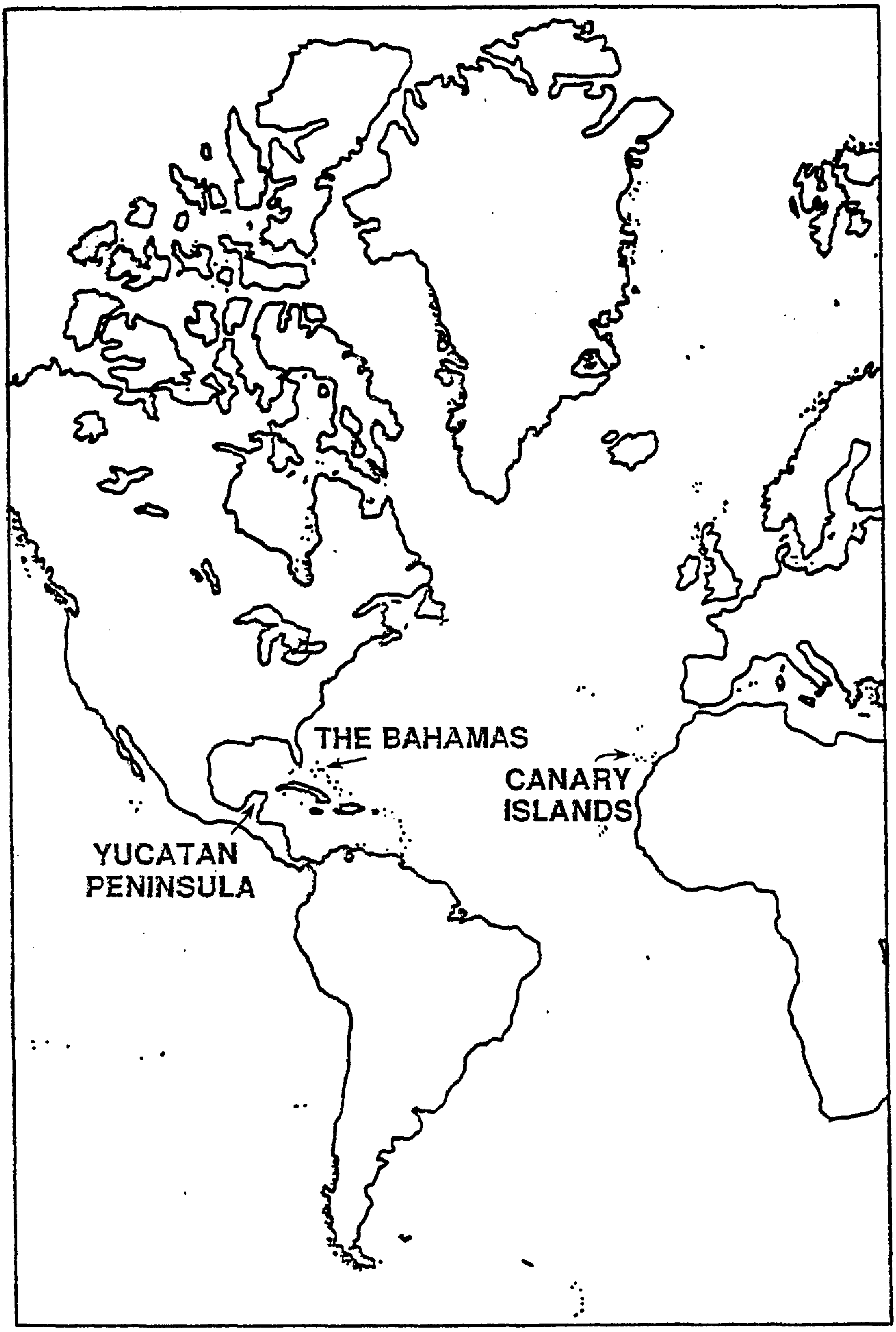
Family Godzilliidae

Godzillius robustus Schram, Yager, and Emerson, 1986

Godzilliognomus frondosus Yager, 1989b

Pleomothra apletocheles Yager, 1989b

Figure 2. Map showing the three major locations of remipedes in the North Atlantic and Caribbean.


THE BAHAMAS
CANARY ISLANDS
YUCATAN PENINSULA

are recorded from limestone caves along the Bahamian archipelago -- seven species have been collected in the Bahamas and in The Turks and Caicos. One species, Speleonectes tulumensis, is known from limestone anchialine caves along the eastern coast of the Yucatan Peninsula of Mexico. Speleonectes ondinae is recorded from a single lava tube in the Canary Islands, the only non-limestone cave site recorded for remipedes to date.

The anchialine caves investigated show differences in remipede composition. Although the distribution of remipedes species within the Bahamas remains to be determined because many islands are unsurveyed, two caves (Dan's and Sagittarius) are known to be inhabited by six species. In contrast, only one species, Speleonectes lucayensis, has been recorded from Lucayan Cavern, and its numbers are seemingly very low. In over 10 years of diving Lucayan Cavern, the most extensive submerged cave in the West Indies recorded to date, less than 20 individuals have been observed. Further south in The Turks and Caicos, Old Blue Hill Cave is inhabited by a relatively large population of one species, Lasionectes entrichoma. Caves of the Tulum region of Quintana Roo, Mexico, are also monospecific with respect to remipedes. No freshwater or open-ocean remipede species are known.

Remipedes have been found to date only in caves in the North Atlantic Ocean region. They were not found in caves investigated by cave divers on several Pacific Ocean islands (Guam, Palau, Philippines, Cook Islands, the Galapagos). An area worthy of future investigation is the Bahamas, as a detailed survey of Bahamian caves is virtually guaranteed to yield more remipedes. In addition many Caribbean islands have the potential for remipede habitat. Limestone anchialine caves have been reported in Cuba and the Dominican Republic. Remipedes have not yet been found on the island of Cozumel, yet they are present on the nearby mainland of the Yucatan Peninsula.

In addition to the nine extant species, the Class Remipedia contains an extinct species. A more detailed examination of the Lower Pennsylvanian fossil Tesnusocaris goldichi led Schram (1986) to place it into the class Remipedia. The fossil appears to have a biramous first antenna as well as trunk segments with pairs of homonomous paddlelike appendages. It was found in the Tesnus Formation of Texas, a sandstone formation approximately 350 million year old.

KEY TO THE SPECIES OF REMIPEDES

The following key to the nine known species of remipedes is modified from Yager (1989b).

1. Trunk pleura rounded posterolaterally; head shield
   subrectangular .... family Speleonectidae .. 2
   Trunk pleura pointed posterolaterally; head shield
   subtrapezoidal or convex laterally ....

.... family Godzilliidae 7

2. Segments distal to elbow of maxilla 2 and maxilliped enlarged distally and bearing discoid sensilla ....*Cryptocorynetes haptodiscus*

Segments distal to elbow of maxilla 2 and maxilliped not enlarged distally, lacking discoid sensilla 3

3. Maxilla 2 and maxilliped segment 3 rounded medially, biceps-like with moderate to long setae along rounded margin; distal claw complex with 1-2 anterior spines and posterior horseshoe-shaped arrangement of smaller spines .... genus *Speleonectes* 4

Maxilla 2 and maxilliped segment 3 subtriangular, with rows of setae of nearly equal length along entire margin of segment; distal claw complex tridentate, with long central spine flanked by 2 shorter subterminal spines ....*Lasionectes entrichoma*

4. Caudal rami elongate, over 3x length of anal segment ....*Speleonectes tulumensis*

Caudal rami less than 3x length of anal segment 5

5. Antenna 1 long, 1/2 - 2/3 body length. Maxilla 1 terminal fang long, slender, about 3x length of sixth segment. Sternal plates with pointed posterolateral processes ....*Speleonectes benjamini*

Antenna 1 short, less than 1/3 body length. Maxilla 1 terminal fang less than 3x length of segment 6.

Sternal plates absent or without posterolateral processes 6

6. Maxilla 1 segment 4 endite with 1-2 robust, broad-based setae. Caudal rami about equal to length of anal segment ....*Speleonectes lucayensis*

Maxilla 1 segment 4 endite with 5 moderately stout to robust setae. Caudal rami about 1.4-2x length of anal segment ....*Speleonectes ondinae*

7. Head shield subtrapezoidal. Maxilla 1 large in comparison to maxilla 2 and maxilliped; segment 4 with endite 8

Head shield convex midlaterally; Maxilla 1 segment 4 lacking endite. Maxilla 2 and maxilliped with leaflike setae on medial margin of segment distal to point of flexure. Body size small, less than 10 mm. Maximum number of trunk segments 16 ....*Godzilliognomus frondosus*

8. Maxilla 1 large, cheliform. Maxilla 2 and maxilliped with medial rows of candeliform setae; claw complex with 1 long medial spine and several shorter subterminal spines. Body length less than 20 mm ....*Pleomothra apletocheles*

Maxilla 1 segment 4 endite clublike and perpendicular to margin of segment. Maxilla 2 and maxilliped with grappling hook shaped claw complex of subequal spines.

Body length up to 40 mm or more ....

...................................*Godzillius robustus*

ANNOTATED CHECKLIST OF THE REMIPEDES

The information in this section includes original studies and major references to remipedes as well as information about the habitat.

ORDER NECTIOPODA

FAMILY SPELEONECTIDAE

Speleonectes lucayensis Yager

Speleonectes lucayensis.-- Yager, 1981:328.-- Abele, 1982:262.--Hessler, 1982:165.-- Schram, 1983:23-28, 334.-- Schram, Yager, and Emerson, 1986:6.--Schram, 1986:28, 36.-- Itô and Schram, 1988:250.--Itô, 1989:85.

Speleonectes sp.-- Boxshall, 1983:131, 137.-- Kunze, 1983:177.

Remipedia sp.-- Boxshall, 1983: 124-126, 128, 135, 139; Grygier, 1983: 79; Newman, 1983:107, 108, 113;

Type locality.-- BAHAMAS. Grand Bahama Island, Lucayan National Park, Lucayan Cavern.

Range.-- BAHAMAS. Known from the type locality and other anchialine caves. Abaco: Dan's Cave; So. Andros: Stargate Bluehole; Cat Island: Ishmael Gaitor's Bluehole; Grand Bahama Island: Bahama Cement Cave, Mermaid's Lair

(Old Freetown Cave System), Sagittarius Cave.

Comments.-- The type locality is one of the longest submerged caves in the world, with approximately 10 kilometers of surveyed passages. Of the 70 specimens of S. lucayensis collected from seven caves over a ten year period, only nine adults have been recorded. Five of the nine were collected from the type locality. The entrance to Lucayan Cavern includes a portion of dry cave which must be entered before gaining access to the surface pool. In the summer months the cave is a maternity colony for the buffy flower bat Erophylla sezekorni, which roost over the surface pool. Lucayan Cavern is now part of Lucayan National Park.

Speleonectes benjamini Yager

Speleonectes benjamini Yager, 1987a:302.-- Yager, 1989a:77.

Type locality.-- BAHAMAS. Grand Bahama Island, Sweeting's Cay, Asgard Cave.

Range.-- BAHAMAS. Grand Bahama Island: the type locality and Sagittarius Cave; Abaco: Dan's Cave.

Speleonectes ondinae (Valdecasas)

Morlockia ondinae Valdecasas, 1985:329.

Speleonectes ondinae.-- Schram, Yager, and Emerson, 1986:16.-- Schram, 1986:37.

Remipedia sp.-- Iliffe, et al., 1984:309.

Type locality.-- CANARY ISLANDS (Spain). Lanzarote, Jameos del Agua.

Range.-- CANARY ISLANDS. Known only from the type locality, a submerged lava tube.

Comments.-- This species was first described as *Morlockia ondinae* by Valdecasas (1985) but later placed in the genus *Speleonectes* by Schram, Yager, and Emerson (1986). The type locality, Jameos del Agua, is the only known non-limestone habitat for remipedes, as well as the only known location in the eastern North Atlantic Ocean. The waterfilled portion of the lava tube is entered through an underground restaurant and bar where the surface pool is lit with colored lights.

Speleonectes tulumensis Yager

Speleonectes tulumensis Yager, 1987b:160.

Type locality.-- MEXICO. Quintana Roo, near Pueblo of Tulum, Carwash Cenote.

Range.-- MEXICO. Known from the type locality and other anchialine caves in the Tulum region of Quintana Roo: Mayan Blue, Temple of Doom, and Najaron (Naharon) Cenotes; BELIZE. One specimen was collected from a cave on Caye Chapel, a small island off the coast of Belize City.

Comments.-- The specimens were found in aphotic euhaline water of anchialine caves (cenotes). This species is the only one known from the area to date.

Lasionectes entrichoma Yager and Schram

Lasionectes entrichoma Yager and Schram, 1986:65.-- Schram, Yager, and Emerson, 1986:23.-- Itô and Schram, 1988:250.-- Itô, 1989:86.

Lasionectes entrichomus.-- Schram, 1986:38.

Type locality.-- THE TURKS AND CAICOS. Providenciales, Old Blue Hill Cave.

Range.-- THE TURKS AND CAICOS. Known from Providenciales: the type locality and Airport Cave; North Caicos Island: Cottage Pond.

Comments.-- There is only one species currently recognized. Old Blue Hill Cave has two entrance pools along the collapsed margin of a large sinkhole. The western entrance pool is large and open to sunlight. It is teeming with copepods and the shrimp *Typhlatya garciai*. The water is very turbid due possibly to the presence of phyto and zooplankton as well as organic matter. The eastern entrance is dimly lit and accessed through a crack along the sinkhole margin. The water in this pool is very clear and lacks the great abundance of shrimp and copepods. The salinity of the surface pools measured about 20 ppt. *Lasionectes* is the shallowest occuring remipede species, found at about five meters, in the twilight zone of the cave. In the initial description of *L. entrichoma* Cottage Pond was incorrectly said to be located on Middle Caicos Island.

Cryptocorynetes haptodiscus Yager

Cryptocorynetes haptodiscus Yager, 1987a:302.

Type locality.-- BAHAMAS. Abaco, Dan's Cave.

Range.-- WEST INDIES. BAHAMAS. Abaco: the type locality; Grand Bahama Island: Mermaid's Lair (Old Freetown Cave System), Sagittarius Cave.

Comments.-- A single specimen of an undescribed species of Cryptocorynetes is recorded from Cottage Pond on North Caicos Island, The Turks and Caicos.

FAMILY GODZILLIIDAE

Godzillius robustus Schram, Yager, and Emerson

Godzillius robustus Schram, Yager, and Emerson, 1986:41.-- Itô and Schram, 1988:250.-- Itô, 1989:86.

Type locality.-- THE TURKS AND CAICOS. North Caicos Island, Cottage Pond.

Range.-- WEST INDIES. THE TURKS AND CAICOS. Known from the type locality; BAHAMAS. Abaco: Dan's Cave; Cat Island: Big Fountain Cave; Grand Bahama Island: Sagittarius Cave.

Comments.-- Cottage Pond is a large, beautiful lake surrounded by a luxurious growth of ferns. Beneath it lies a huge sinkhole approximately 56 m deep. At about 12 m a layer of hydrogen sulfide is encountered. The only two adult specimens of G. robustus (over 35 mm in length) were collected in this cave. To date, this species is the largest remipede.

Godzilliognomus frondosus Yager

Godzilliognomus frondosus Yager, 1989b.

Type locality.-- BAHAMAS. Grand Bahama Island, Sagittarius Cave.

Range.-- BAHAMAS. Known from the type locality and anchialine caves on Sweeting's Cay, Grand Bahama Island: Virgo Cave, Lucy's Cave, Asgard Cave; Abaco: Dan's Cave.

Comments.-- This is the smallest species of remipede found to date, averaging about 7 mm in length.

Pleomothra apletocheles Yager

Pleomothra apleotcheles Yager, 1989b.

Type locality.-- BAHAMAS. Abaco, Dan's Cave

Range.-- BAHAMAS. Known from the type locality and Sagittarius Cave on Grand Bahama Island.

Comments.-- P. apletocheles is the only species with a cheliform first maxilla.

REMIPEDE MORPHOLOGY

Remipedes (see Fig. 1) are blind, unpigmented, free-swimming crustaceans. Adults range in size from about 9 mm in the smallest species, Godzilliognomus frondosus, to 45 mm in the largest, Godzillius robustus. The body is composed of a short head with a cephalic shield. The elongate trunk lacks tagmosis and is divided into numerous platelike segments. The maximum number of adult trunk segments varies in species, from 16 in *Godzilliognomus frondosus* to 38 in *Speleonectes tulumensis*. Each trunk segment bears a pair of biramous swimming appendages. With their metachronal swimming pattern, remipedes look like "aquatic centipedes."

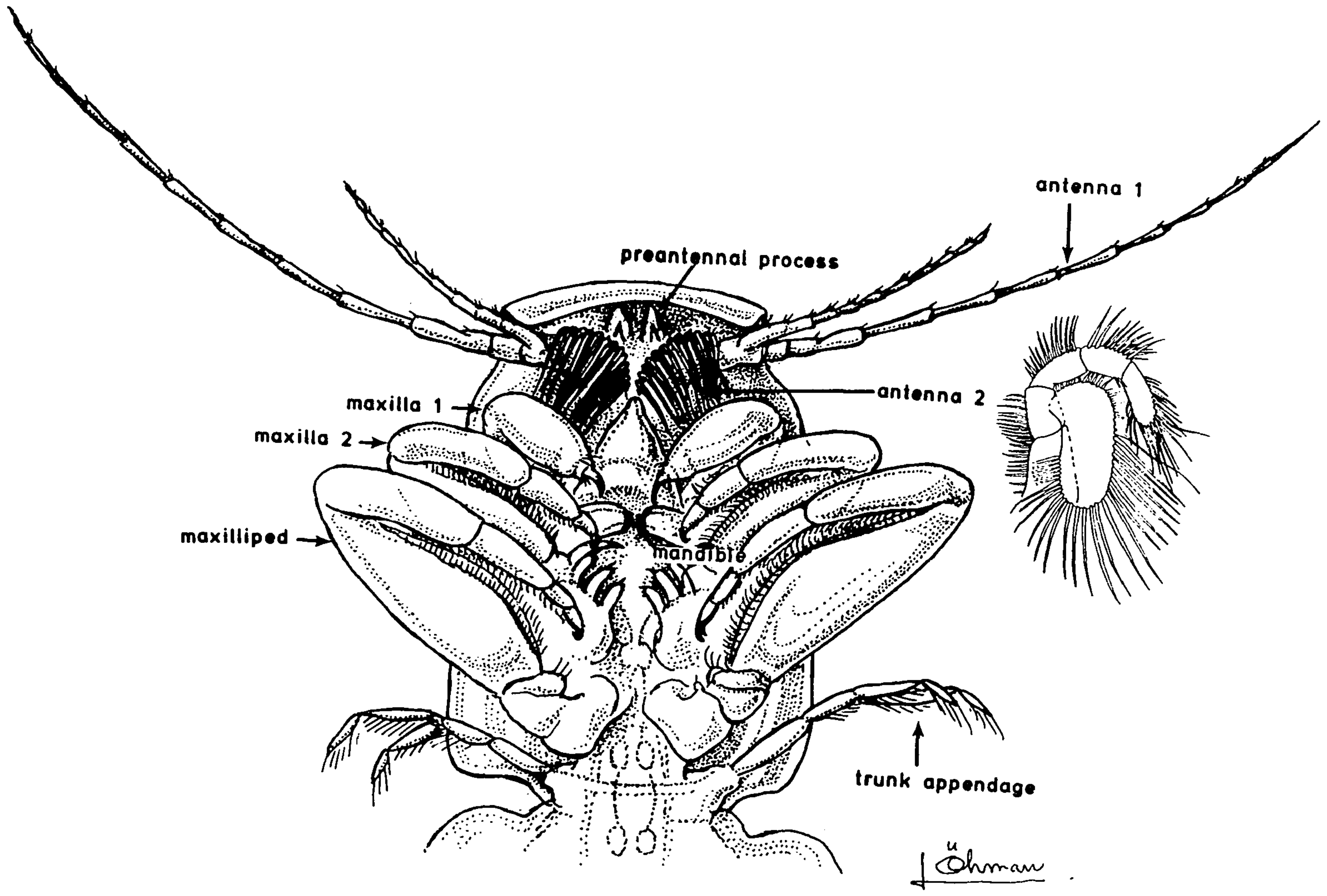
Cephalic shield

Cephalic shields vary in the two families. Speleonectids have a subrectangular shield with rounded posterior margins. Members of the Godzilliidae family bear either subtrapezoidal shields or shields which are convex laterally. In addition, *Pleomothra apletocheles* has spine-like projections extending from the posterolateral margins. At the anteroventral part of the head (Fig. 3) all species have a pair of slender, cylindrical pre-antennal processes (or frontal filaments) which are tapered distally and bear a small posterior projection. According to Ito and Takenaka (1988) these are an external portion of the organ of Bellonci.

First and second antenna

In their aphotic environment, remipedes depend on remote, non-visual sensing. Remipedes have a biramous first antenna (see Fig. 3). As in other crustaceans, this antenna functions for tactile sensing and is also modified

Figure 3. Diagrammatic representation of a typical remipede head. Antenna 2 (insert) is located posterior to the first antenna, and is not to scale.


antenna 1
preantennal process
antenna 2
maxilla 1
maxilla 2
maxilliped
mandible
trunk appendage
J Öhman

for apparent olfaction. The proximal segment of the first antenna is greatly enlarged and bears several rows of esthetascs. These long, thin sensilla function in crustacean chemoreception enabling the animals to detect relevant chemical cues for locating food, predators, and potential mates. Odors have to be detected and deciphered as to quality, quantity, as well as space and time parameters (Ache and Derby, 1985). Crustacean antennal receptors not only respond to a diverse array of chemical substances, but also to temperature and pH (Ache, 1982). In addition to the long esthetascs at the antenna base, the medial surface of each ramus bears clusters of several kinds of short, esthetasc-like setae (see Fig. 3B in Yager, 1987a). These are very similar to antennular mechano and chemoreceptor sensilla described for the brineshrimp *Artemia* (Tyson and Sullivan, 1979). Mechanoreceptor sensilla function as receptors for a variety of purposes including detection of vibrations generated in the water column (for a review of crustacean mechanoreception see Bush and Laverack, 1982).

The second antenna, posterior to the base of antenna 1, is a small, paddle-like structure bearing long, plumose setae (see Fig. 3). These smaller antennae are continually moved back and forth as the animal swims, possibly to provide a constant flow of water over the esthetascs at the base of the first antenna.

Mouth

The labrum is large and has a dense array of small setae posteromedially. The mandibles of remipedes originate at the side of the head and extend ventromedially under the labrum into the atrium oris or mouth cavity. The mandibles are palpless, bear cusped incisor processes and lacinia mobili, and broad molar processes. The paragnaths are round, platelike lobes with setose margins. The entire mouth area (see Fig. 3) is setose.

Prehensile feeding appendages

Posterior to the mandibles, three uniramous, prehensile feeding appendages are present: the first maxilla, second maxilla, and the maxilliped. The three prehensile appendages of all remipedes are subdivided into various distinct segments which vary in number according to appendage and/or species (Fig. 4). The appendages are distinguishing taxonomic features. The relative size ratio as well as morphology varies in species (Figs. 5, 6, 7). For example, maxilla 1 of <u>Pleomothra</u> <u>apletocheles</u> (Fig. 6B) is enormous in comparison to its maxilla 2 and maxilliped, while the first maxilla of <u>Godzilliognomus</u> <u>frondosus</u> (Fig. 7B) is small in comparison to its other two appendages.

First maxilla

The first maxilla (see Fig. 4) of all remipede species consists of seven segments except for that of <u>Pleomothra</u> <u>apletocheles</u> which has six. The proximal segment bears a

Figure 4. Diagrammatic representation of remipede prehensile feeding appendages. The various segments are numbered.

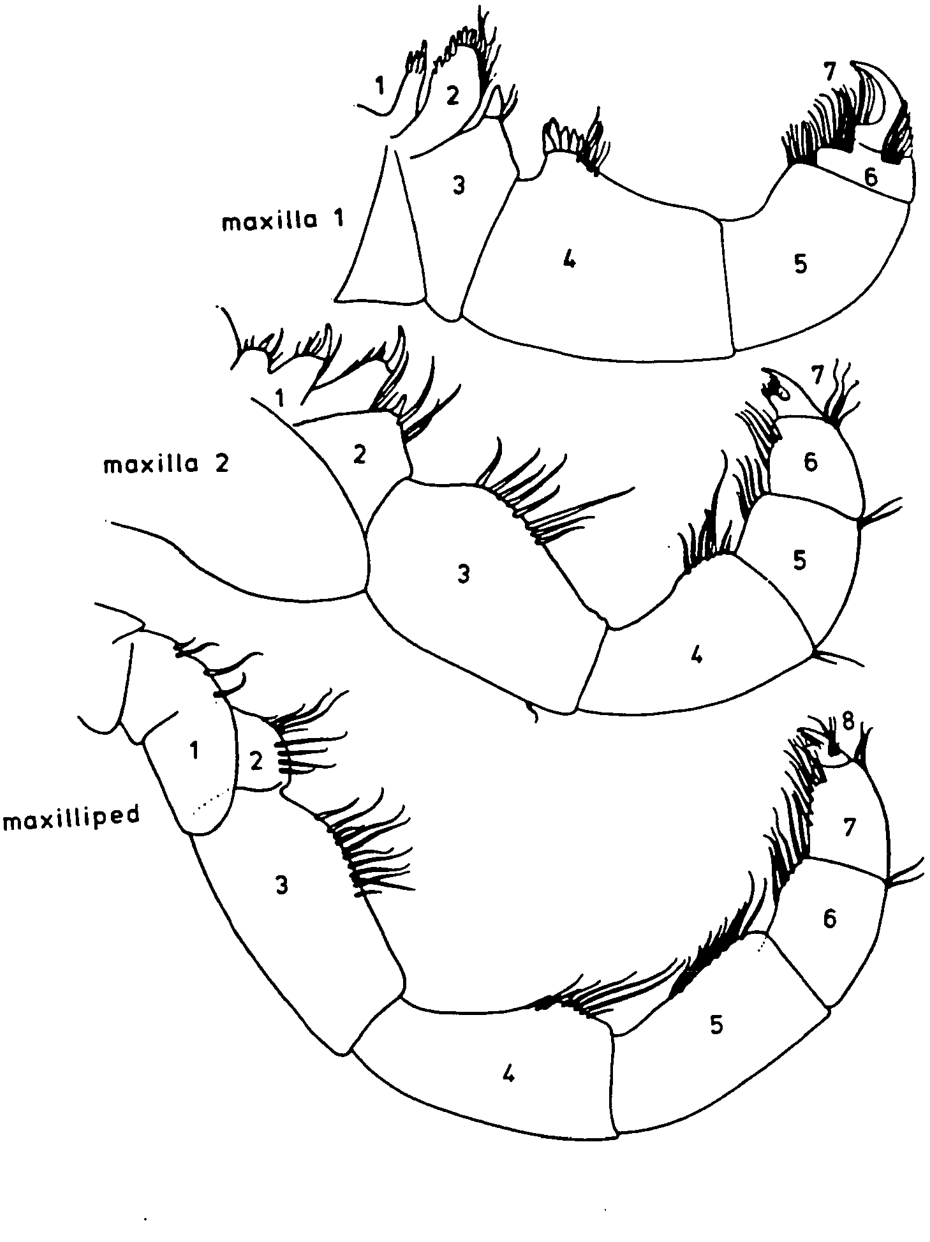

1
2
3
4
5
6
7
maxilla 1
1
2
3
4
5
6
7
maxilla 2
1
2
3
4
5
6
7
8
maxilliped

Figure 5. Ventral view of head.

A. *Speleonectes lucayensis*, 52x

B. *Speleonectes benjamini*, 28x

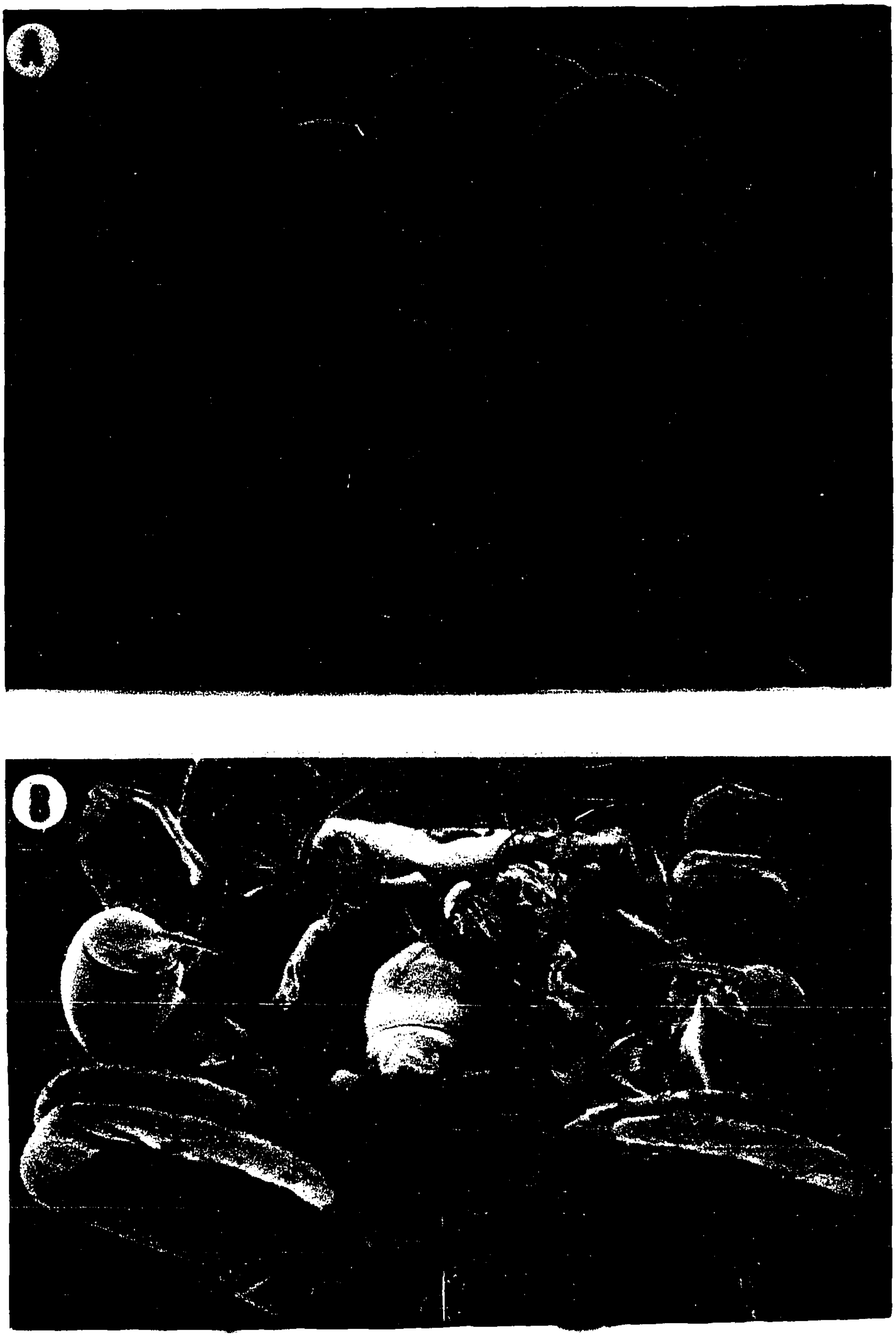

A
B

Figure 6. Ventral view of head.

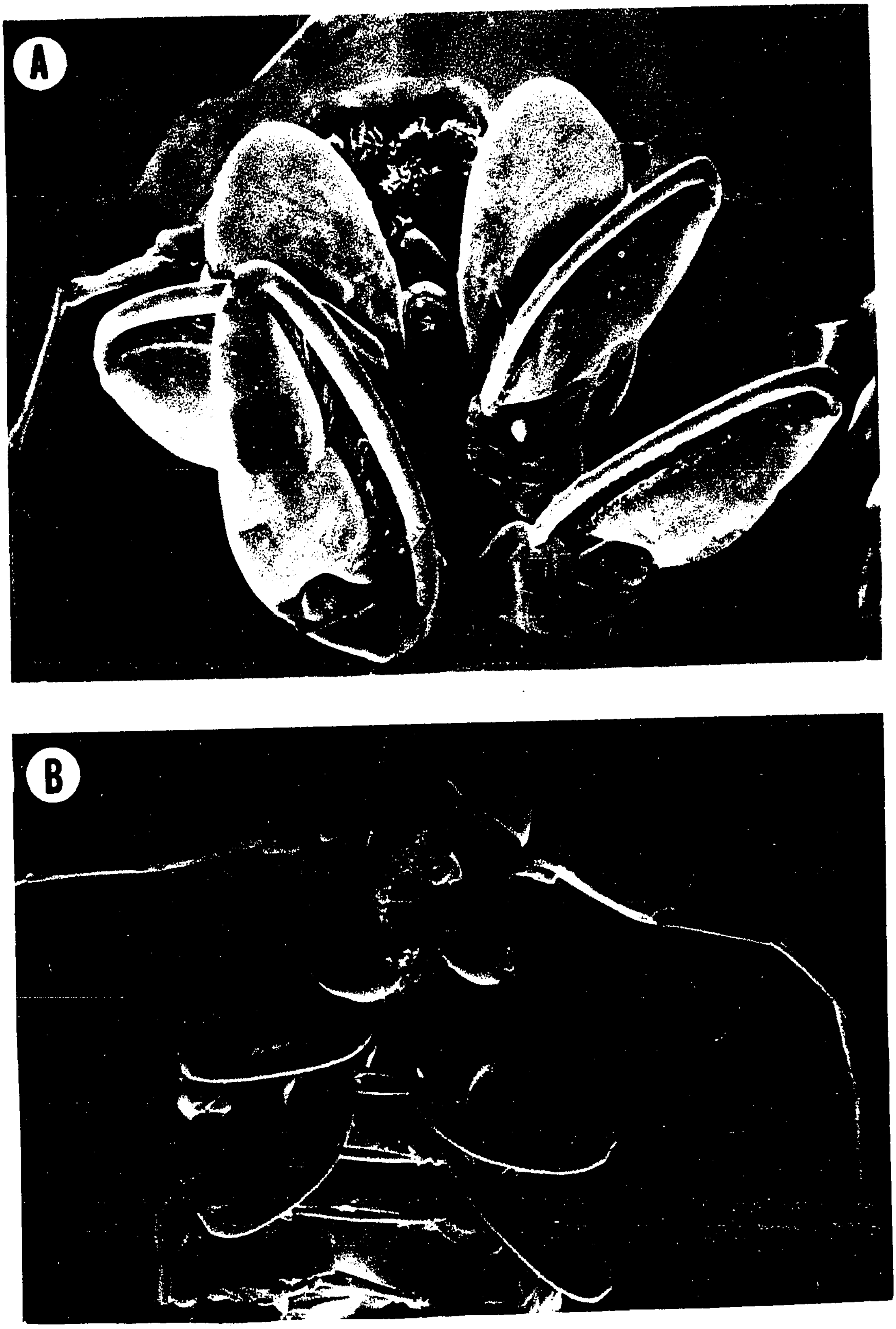
A. *Cryptocorynetes haptodiscus*, 54x

B. *Pleomothra apletocheles*, 16x

Figure 7. Ventral view of head.

A. *Godzillius robustus*, 10x

B. *Godzilliognomus frondosus*, 22x


A
B

long endite with terminal sclerotized spines. These spines lie over the mouth area and probably aid in breaking up or holding food particles. Segment 2 (see Fig. 4) has a platelike endite with short spines along the margin. Segment 3 varies. Members of the genus *Speleonectes* and *Lasionectes entrichoma* bear a conical medial endite with two robust, spinelike setae. The same segment on *Cryptocorynetes* bears at least three robust setae. In the godzilliids segment 3 differs: in *Pleomothra* it is a narrow, naked, elongate pedestal; in *Godzillius robustus* and *Godzilliognomus frondosus* the segment lacks a medial endite and bears one small seta. Segment 4 is also variable. In members of the genus *Speleonectes* the segment bears a medial endite with from 1-5 stout spinelike setae on the proximal margin. *Lasionectes* has a single small seta at the proximal margin of the endite. In *Pleomothra* the medial surface is extended distally to form the lower portion of a chela (see Fig. 6B). The same segment on *G. robustus* has a long clublike medial endite. *Godzilliognomus frondosus* lacks endites and has two rows of moderately long setae along the medial margin of the segment. With the exception of *P. apletocheles* segment 5 is distal to the point of flexure. In *P. apletocheles* the appendage flexes between segments 3 and 4 but not to form a prehensile position as in the other species. Instead, the grasping is achieved with the cheliform surface formed by segments 5 and 6 against the distal portion of segment 4. Also this species appears to lack the short sixth segment proximal to the fang. In other species segment 6 is short, at least less than half the length of segment 5. The distal segment (see Fig. 4A) of all remipedes bears a sclerotized fang with a subterminal pore. In two species, *Speleonectes lucayensis* and *S. benjamini*, the pore appears to be connected by a duct to a large secretory gland at the base of the appendage. The fang length varies in species. For example, in *S. benjamini* the fang is at least three times the length of the preceeding segment, while in *S. lucayensis* the fang is about twice the length of the preceeding segment.

Second maxilla and maxilliped

The maxilla 2 and maxilliped of each species are similar in form. The second maxilla (Fig. 4B) bears six or seven segments and the maxilliped (Fig. 4C) bears an additional segment. In all remipede species the first segment of the second maxilla bears three digitiform endites with terminal spines. These endites are absent on the maxilliped. The maxillary gland excretory ducts are large pores found at the base of the second maxilla. A distinctive feature in both the maxilla 2 and maxilliped is the size of the segment proximal to the point of flexure when compared to the size of the distal segments. In members of the genus *Speleonectes* the segment is rounded medially (biceps-like) and the distal segments become proportionately smaller. Also the apex of the biceps-like portion bears two rows of setae of various sizes. In the godzilliids, the segment proximal to the point of flexure is subtriangular in shape and massive in comparison to its long thin distal segments. The setae (see Figs. 6B, 7) of the massive segment are all of the approximate same length and are distributed in rows along the entire ventral margin of the segment. Lasionectes has the same large subtriangular shaped segment as well as rows of nearly equal setae along the margins, however the distal segments are not as narrow as those the Godzilliidae family. The second maxilla and maxilliped of Cryptocorynetes haptodiscus differ from all other species in that the segments distal to the point of flexure increase in size and become bulbous (see Fig. 6A). The medial surface of the segments are covered with highly modified discoid sensilla. Both the second maxilla and maxilliped of all species bear a distinctive claw complex on the distal segment (Fig. 8). It consists of sclerotized claws arranged in a semicircular pattern with an opposable thumblike pad which bears many long setae. In speleonectids the claw is horseshoe shaped; Godzillius and Godzilliognomus have a grappling hook arrangement. The claw of speleonectids has several cavities or pits on it (see Fig. 8A) which resemble pit sensilla found in the cheliceral digits of ticks. In the tick, these sensilla are thought to serve as both

Figure 8. Claw complex at terminus of second maxilla and maxilliped.

A. *Cryptocorynetes haptodiscus*, 2450x. Note pit in main part of claw.

B. *Godzillius robustus*, 239x


A


B

mechano and chemoreceptors. Sonenshine, et al. (1984) hypothesize that the sensilla also contribute to the perception of the female genital pheromone during copulation. This might also be the function of the pits found remipede claws, adding support for my hypothesis that one role of the claw complex may be for spermatophore transfer (see Chapter 3 on Reproduction).

Trunk

Remipede trunk appendages are all biramous, setose paddles which extend laterally from the body. The trunk limbs are basically similar, with a large protopod, a 3-segmented exopod, and a 4-segmented endopod. The terminal anal segment bears cylindrical caudal rami which range in size from over three times the length of the anal segment in *Speleonectes tulumensis* to shorter than the anal segment in *Godzillius robustus*. The anal opening is at the end of the anal segment and covered with a cuticular flap. However, in *Godzilliognomus* a much folded cuticular structure (Fig. 9) extends beyond the terminus of the anal segment. This small structure is composed of many thin folds of chitin with small fringed margins. The function of this structure is uncertain.

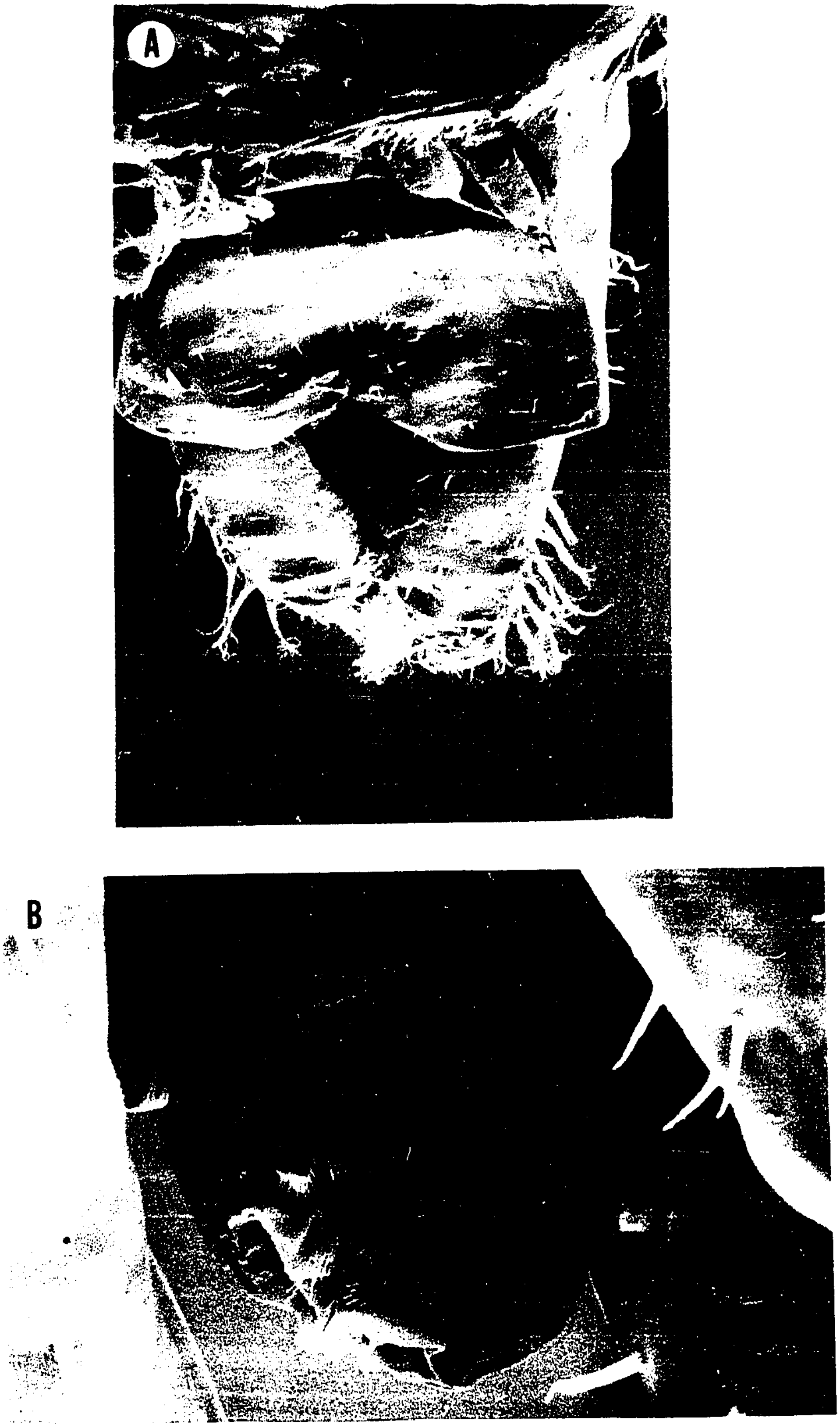
Pores and sensilla

The dorsal surface of remipedes is covered with pores which appear secretory in nature. In addition, remipedes have a vast array of very diverse setae and sensilla. The

Figure 9. Anal segment of <u>Godzilliognomus</u> <u>frondosus</u>.

A. Anal segment with convoluted terminus, 122x. Note tiny setae or microtrich sensilla on anal segment and caudal rami.

B. Convoluted terminus, 780x


A
B

body surface has integumental microtrich sensilla similar to that reported for the amphipod _Gammarus_ (Steele and Oshel, 1987). Microtrich sensilla are not an epicuticular decoration but a type of setae secreted by specialized auxiliary cells which contain dendrites. Examination with transmission electron microscopy (TEM) of such setae on _Cryptocorynetes haptodiscus_ indicates innervation. Highly modified sensilla (Figs. 6A, 10A) occur on the maxilla 2 and maxilliped of _C. haptodiscus_. These sensilla are round, on a pedestal, and covered with tiny projections. TEM has revealed one or two dendrites leading out into the stem of the pads, indicating that these pads have a sensory function. Maxilla 1 of _Pleomothra apletocheles_ bears unusual sensilla that can only be described as looking like shaving brushes (Fig. 10B). These sensilla are circular pads with small, fibrouslike projections on the distal surface. The sensilla are found on the cheliform extension opposed by the fang. The function of these sensilla in conjunction with the entire massive appendage is unknown. Unusual setae are also found on the inner surface of the second maxilla and maxilliped of several species. For example, _Godzilliognomus frondosus_ bears flattened, ribbed, leaflike setae (Fig. 11A) and _Pleomothra_ has rows of stout, tapered setae with a shape reminiscent of candlesticks (Fig. 11B).

Figure 10. Two types of sensilla.

A. Discoid sensilla of Cryptocorynetes haptodiscus, 3220x

B. Tomentose or shaving brushlike sensilla of Pleomothra apletocheles, 744x

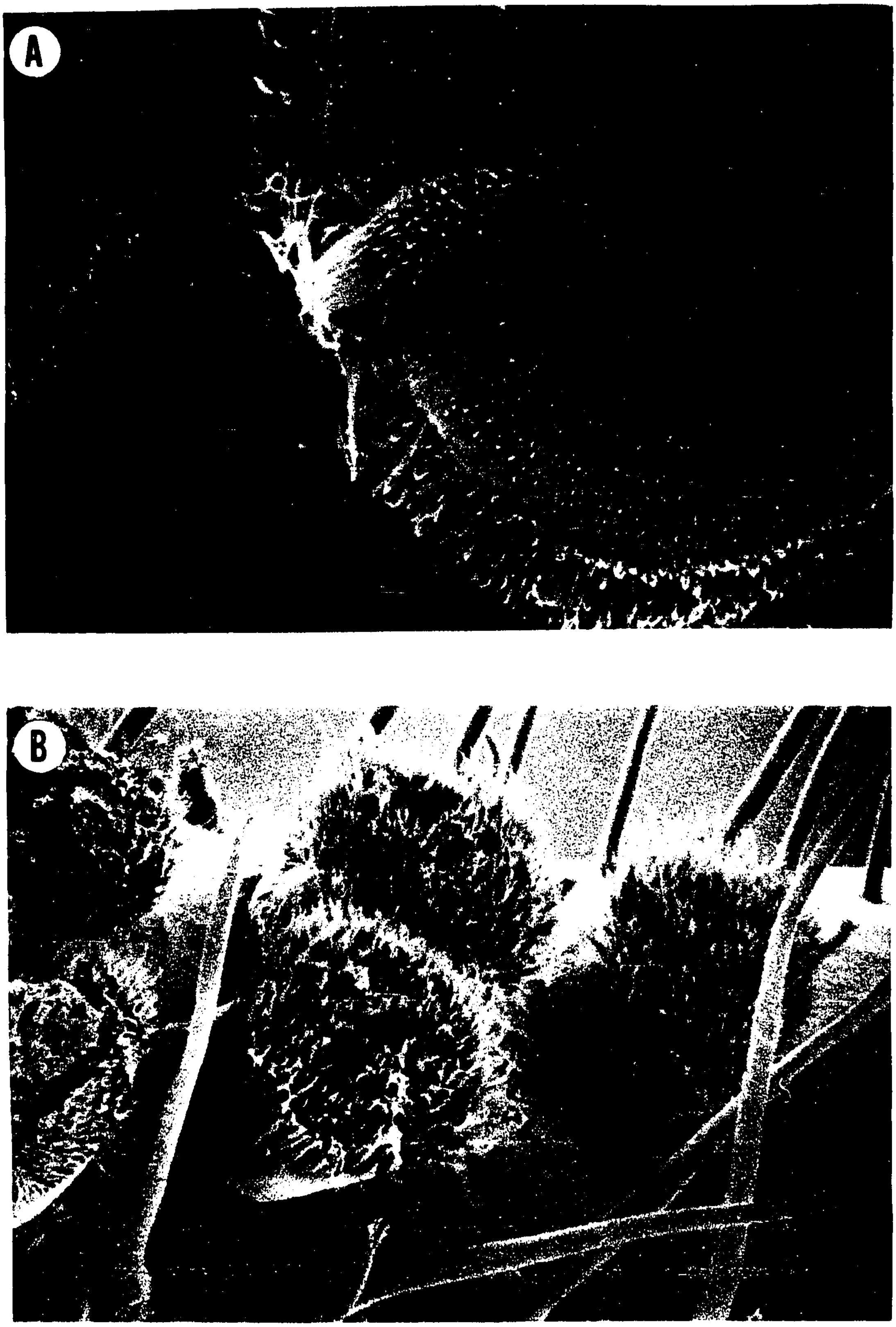
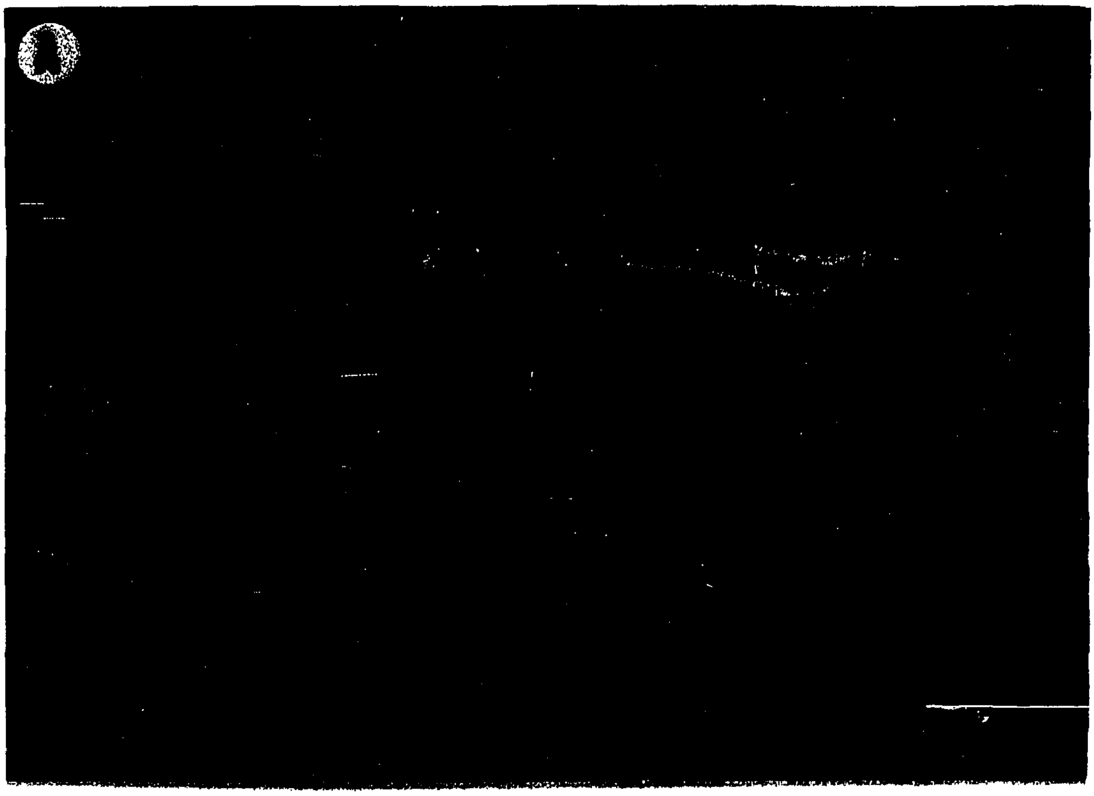

A
B

Figure 11. Two types of modified setae on second maxilla and maxilliped.

A. Leaflike setae of *Godzilliognomus frondosus*, 961x

B. Candlestick setae of *Pleomothra apletocheles*, 398x



Epibionts

Epibionts have been observed on the surface of some remipedes, especially those from Mexico. They include suctorians (Fig. 12A) and undetermined egg-shaped spheres (Fig. 12B) found in clusters. Also occasionally seen are chains of up to 13 spheres attached to the chitin. These spheres emanate from a raised area of the cuticle in ascending sizes. Patches of small volcano-shaped structures are present as well. Rod-shaped bacteria are commonly seen on the surface of remipedes when using scanning electron microscopy (SEM).

CHARACTERISTICS OF ANCHIALINE CAVES

The word "anchialine" was proposed by Prof. Lipke B. Holthuis (1973) as a term for land-locked coastal saltwater pools with subterranean connections to the sea. The term has been broadened and is now commonly used to describe caves having an inland surface opening with subsurface marine connections or influence (Fig. 13).

Anchialine caves usually contain a fresh or brackish water lens over sea water. This lens is a well-documented property of coastal aquifers. The relationship and position of the freshwater-saltwater interface is demonstrated by the Ghyben-Herzberg principle which shows that each foot of freshwater head above sea level depresses the interface 40 feet below sealevel (Back, et al., 1984;

Figure 12. Epibionts found on surface of Speleonectes tulumensis.

A. Suctorians, 25-38 um

B. Unidentified egglike spheres, 12-20 um

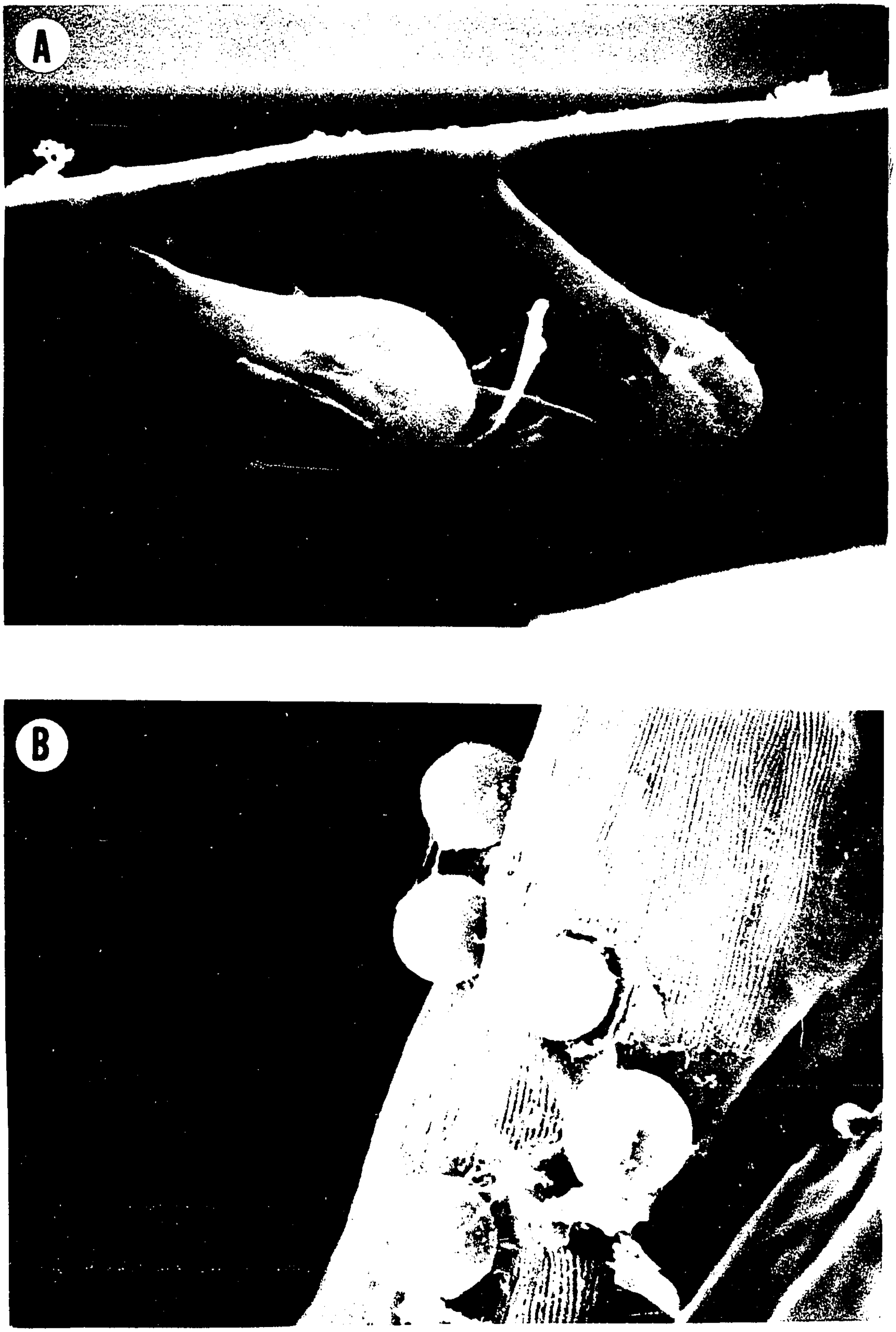
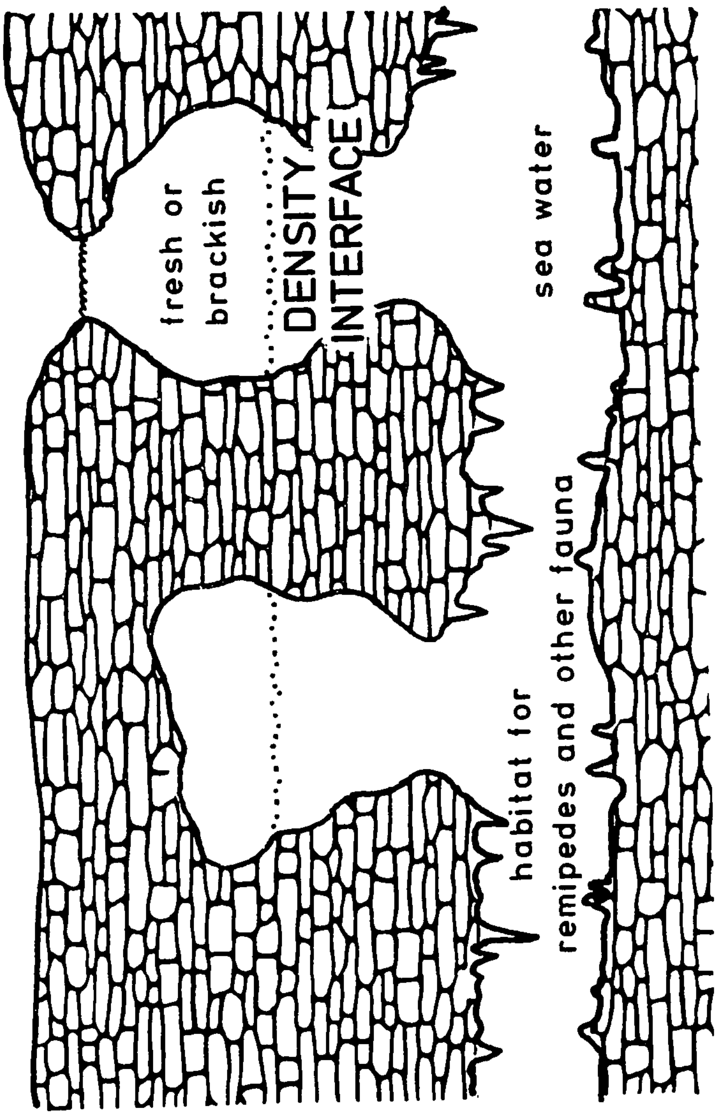

A
B

Figure 13. Diagrammatic representation of typical anchialine cave (from Yager, 1987a).


fresh or brackish
DENSITY INTERFACE
sea water
habitat for remipedes and other fauna

Palmer and Williams, 1984). Physical characteristics of the water column such as salinity, temperature, dissolved oxygen, and light intensity, vary horizontally and vertically. As with all caves, the ambient light diminishes with distance from the entrance through a twilight zone into a completely aphotic zone. Depending on the type of entrance, the light penetrates vertically or horizontally into the cave. Anchialine caves of the Bahamas typically have a fresh or oligohaline (0.5-5 ppt) lens floating on top of more dense mesohaline (5-18 ppt) to euhaline (30-40 ppt) water (Yager, 1987a). This forms a distinct density interface. In some caves several interfaces exist above euhaline water. The density interface can be easily detected by the diver because the visibility momentarily blurs due to the refractive differences. Associated with the interface is a thermocline which frequently differs several degrees above and below. The temperature and/or salinity gradients appear to maintain a distinct, integral density interface. This interface serves as a barrier for gas exchange. Water at the cave surface and down to the interface typically has a dissolved oxygen content of 4-6 ppm, while the more saline water directly below the density interface has been measured as low as 0.1 ppm (Holsinger and Yager, 1985; Yager, 1987a). Some cave systems have a layer of hydrogen sulfide beneath the density interface. The diver descends through the fresh or brackish layer, passes through the density interface, and enters an opaque layer containing hydrogen sulfide. Descending further one encounters clear water completely devoid of the compound. Cottage Pond, a large sinkhole in The Turks and Caicos, contains a layer of hydrogen sulfide beneath the interface. The gas is apparently supersaturated but prevented from reaching the surface by the density interface. When divers descended into the hydrogen sulfide and deeper, they disturbed the interface and the hydrogen sulfide was released. On the surface tiny bubbles of the gas could be heard and smelled as they effervesced.

In addition to spatial patterns, there are also temporal patterns within an anchialine cave. Daily tidal cycles cause the density interface to rise and fall. Full and new moon tides also cause a discernable change in the level. There are marked seasonal temperature changes within the cave environment. In Lucayan Cavern on Grand Bahama Island, the fresh water is relatively constant year-round with a temperature of about 22°C. The deeper salt water layer is influenced by the temperature of the nearby ocean. In summer the deeper water is warmer than the fresh water, while in winter it is colder.

Anchialine caves of Mexico have been discovered and explored on the island of Cozumel and along the east coast of the Yucatan Peninsula, in particular near Tulum in the state of Quintana Roo. These submerged caves are called cenotes, from the Mayan word "tznot" which means a deep, natural well. The Mexican anchialine caves are very similar to those in the Bahamas. The passages in most of the caves consist of huge tunnels with a deep fresh to oligohaline lens. In most of the caves explored near Tulum (Carwash, Najaron, and Mayan Blue) the freshwater lens extends to a depth of about 20-24 meters. In Temple of Doom Cenote the water measured 14 ppt at 18 m depth (Bowman, 1987). In Carwash Cenote at a depth of 18 m the salinity was 3 ppt and dissolved oxygen 4 ppm. At a depth of 24 m salinity was 36 ppt and dissolved oxygen 0.8 ppm. The more saline water is restricted to only 2-3 meters above the cave floor in some of these Mexican caves, and it is in this narrow saltwater zone that remipedes are found. Remipedes from West Indian and Mexican caves have always been found below the density interface in the deeper, low-oxygen water. Although some species live in polyhaline water (18-25 ppt), none have been found in fresh water. Remipedes collected in Mexican caves died immediately when small amounts of fresh water entered the collecting bottles. Many remipede species are rare in abundance. After extensive field work, fewer than 20 specimens have been collected for five of the nine species.

In contrast to limestone caves, the Jameos del Agua is an anchialine lava tube on the island of Lanzarote in the Canary Islands. The lava tube is euhaline throughout. According to cave diver Dennis Williams, the remipedes found in the lava tube were in water with a dissolved oxygen content of about 3 ppm. This is a higher oxygen content than is typically found in other remipede habitats. A freshwater lens occurs on the island and Williams (pers. comm.) feels that the remipedes may actually occur more commonly in crevicular habitat beneath the freshwater lens of the island where the seawater is possibly lower in dissolved oxygen.

Although anchialine caves similar to those in the Bahamas are found on the island of Bermuda, no remipedes have been discovered there to date, and it is not likely that remipedes inhabit the island. The island is oceanic in origin, formed by volcanic activity on the Mid-Atlantic Ridge in Late Cretaceous. Additionally, the environmental aspects differ. Bermuda caves apparently lack the low oxygen water and they are colder at depth than Bahamian caves. For example, in March, Cliff Pool Cave measured from 20°C at the surface to about 19° C at 18 m (Bowman and Iliffe, 1985). In contrast, March measurements for Sagittarius Cave, Bahamas, were 24° C at the surface and 25° C at 18 m.

COMMUNITY COMPOSITION OF ANCHIALINE CAVES

The animals of anchialine communities consist almost entirely of stygobiont crustaceans, that is, species that are confined to groundwater. This crustacean assemblage appears to be consistently and predictably present in anchialine caves of the West Indies and Mexico, and includes remipedes, thermosbaenaceans, ostracodes, hadziid amphipods, cirolanid isopods, mysids, and caridean shrimp. In addition to crustaceans, several species of troglobitic cave fish are common.

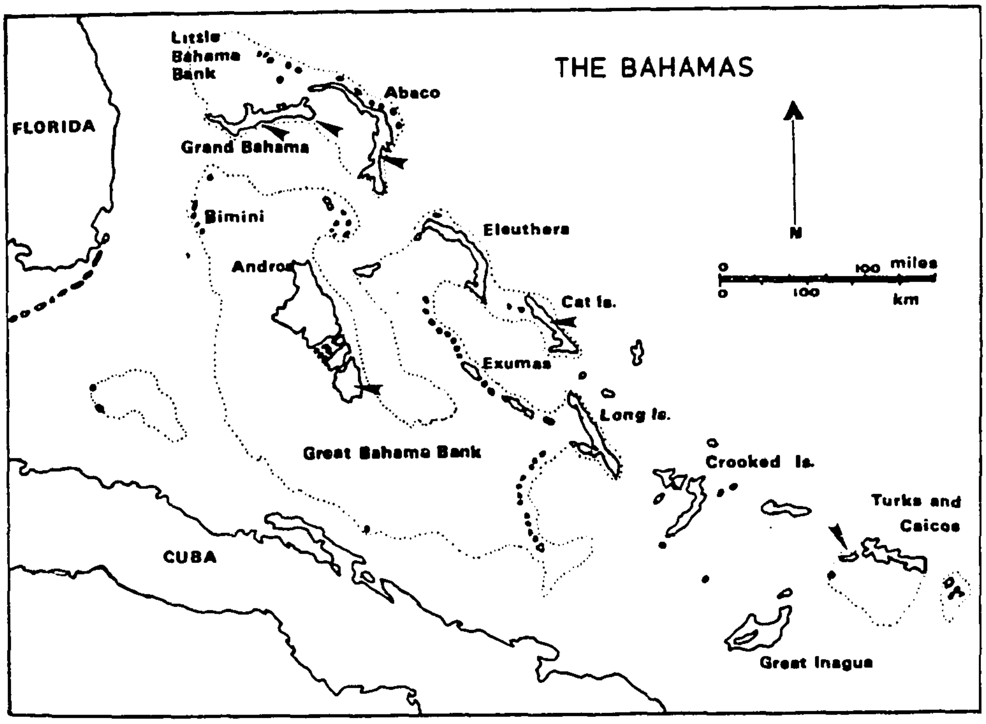
The diverse crustacean fauna apparently common in many anchialine cave systems is also found in some inland freshwater cave systems. The Edwards Aquifer, for example, is a huge groundwater system developed in Cretaceous limestone paralleling the Bacones Escarpment and Fault Zone in south central Texas. A single artesian well opening into the aquifer has yielded 22 troglobitic species to date, nearly half of which are amphipod crustaceans (Holsinger and Longley, 1980). According to Holsinger and Longley the overall taxonomic diversity of this amphipod fauna is probably one of the greatest in the world. In addition to ten species of amphipods, two species of isopods, two copepods, one thermosbaenacean, one shrimp, and one ostracod, two snails, one planarian, one beetle, and one salamander species have been collected from the well. All species are thought to be troglobitic. Holsinger and Longley (1980) attribute the concentration of such large numbers of species from the Edwards Aquifer to the physical extent of the system. In addition they also cite heterogeneity, relative old age and stability of the system as factors. The diversity found in anchialine caves is beginning to approach that of the Edwards Aquifer freshwater system. In addition, the community composition shows striking parallels. For example, Sagittarius Cave contains 18 known troglobitic species, the majority of which are crustaceans. There are six remipedes, four ostracodes, two amphipods, two thermosbaenaceans, one isopod, one mysid, one chaetognath, and one cave fish.

Some caves have a distinct bacterial community. Sulfide bacteria are visible as dense mats on the floor of the cave or floating in loose, filamentous colonies. In caves with a relatively large surface opening and detritus on the floor, a distinct layer of hydrogen sulfide is encountered beneath the density interface. This layer is usually opaque. The stratification in these caves is reminiscent of certain freshwater lake bacterial communities where the stratification is due to abiotic parameters such as light penetration, temperature, and oxygen concentration (Rheinheimer, 1985). In certain anchialine caves anaerobic bacteria in the sediments produce the hydrogen sulfide, the bulk of which apparently remains trapped at the density interface. There it is no doubt utilized by sulfide oxidizing bacteria. Whether the opacity of this layer is caused by bacteria or their by-products (such as elemental sulfur or sulfur-containing minerals) remains to be determined.

BAHAMIAN GEOLOGY AND KARST FORMATION

The Bahama Islands extend in a chain or archipelago for over 1400 km from Florida to Hispaniola (Fig. 14). Today these islands are the very subaerial tops of several large carbonate banks. The banks were once part of the Bahamas Platform, a huge limestone megabank estimated to have a depth of 5.4 km (Meyerhoff and Hatten, 1974) to 10 km (Uchupi, et al., 1971). Although the exact origin of the Bahamas Platform basement is subject to considerable geological debate, it is generally accepted that the carbonate sedimentation which formed the platform began in the Jurassic at the time of the opening of the Atlantic Ocean (Mullins and Lynts, 1977). The shallow-water carbonates represent approximately 150 million years of deposition on the slowly subsiding platform. According to Schlager and Ginsburg (1981), the tops of the Bahama banks have remained near sea level throughout their history. The original platform is now divided by deep water channels into two large broad banks, the Little Bahama Bank and the Great Bahama Bank (see area outlined in Fig. 14). Since before the Late Cretaceous these two banks have been separated by channels which today are from 1100 to 4500 m deep. The Northeast Providence Channel and the Tongue of the Ocean constitute the world's largest canyon system either submarine or subaerial (Andrews, et al., 1970). The southeastern part of the archipelago consists of smaller,

Figure 14. Map of the Bahamas. Arrows indicate locations of caves with remipedes (from Yager, 1987a).

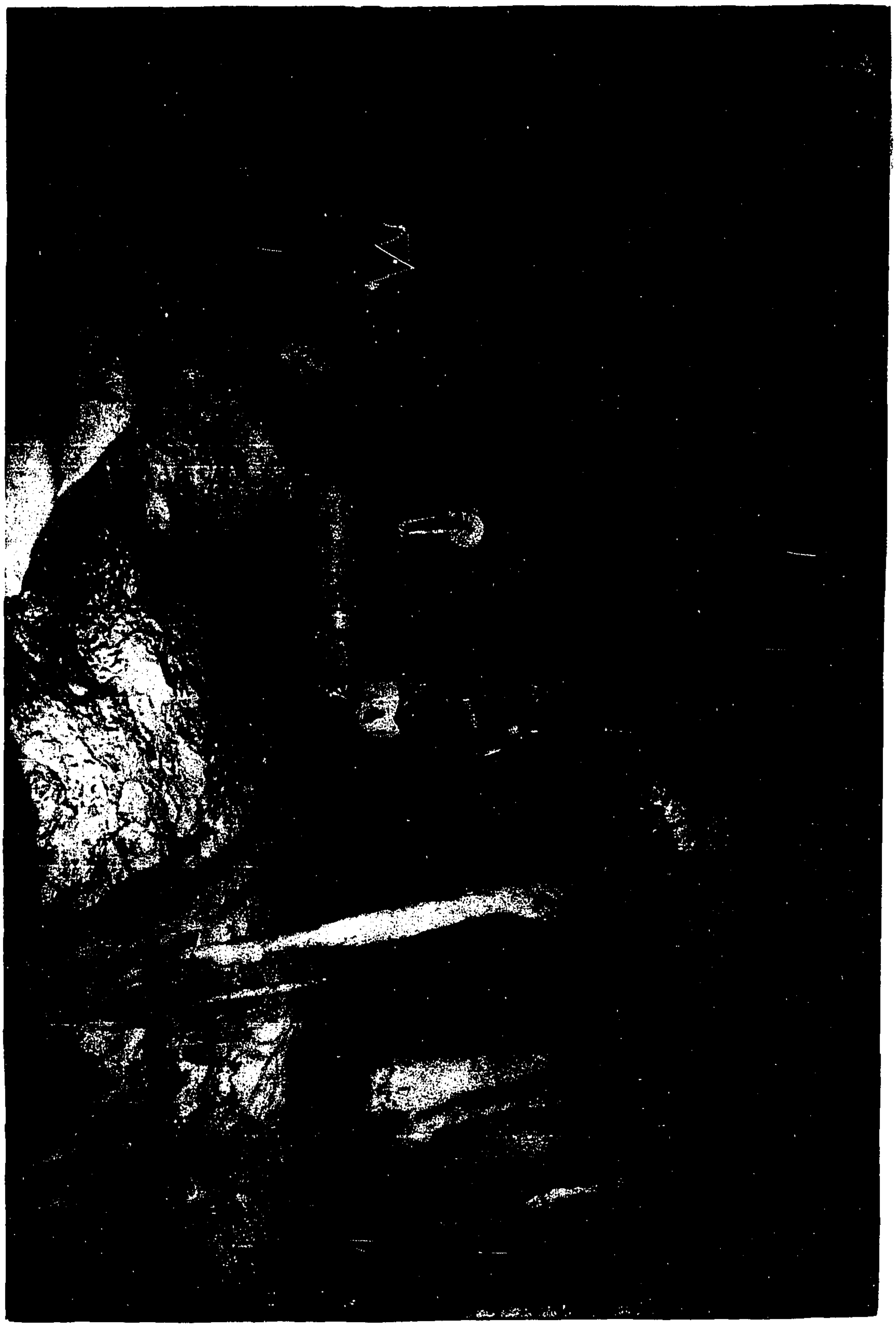

THE BAHAMAS
FLORIDA
Little Bahama Bank
Abaco
Grand Bahama
Bimini
Andros
Eleuthera
Cat Is.
Exumas
Long Is.
Crooked Is.
Turks and Caicos
Great Bahama Bank
CUBA
Great Inagua
N
0 100 miles
0 100 km

more segmented banks.

During the times when the banks were exposed, meteoric water formed a freshwater lens that floated on the more dense sea water that permeated the porous islands. Recent investigations have determined that diagenetic reactions in the fresh groundwater-seawater mixing zone have been responsible for massive dissolution (Back, et al., 1984). The corrosive action of this mixing zone is believed responsible for much horizontal cave development in the Bahamas (Palmer and Williams, 1984; Mylroie, 1988). The well-developed karst topography of the Bahamas has therefore been controlled in part by eustatic sea level fluctuations during glacial periods. Although the surface and subsurface Bahamian limestone is young, consisting almost entirely of upper Pleistocene and Holocene carbonate rocks, there are older, deeper caves present. Through the millenia, the dissolution process has resulted in cave systems occuring at almost all depths within the Bahama platform. Deeper caves represent the fossil remains of previous freshwater lenses (Choquette and Pray, 1970). Caverns as deep as 4000 m have been recorded from deep test wells drilled on the island of Andros (Spencer, 1967). During an oil test core project, caverns were encountered which forced "abandonment of the test when approximately 8000′ of drill pipe was lost in one of the caverns through a break in the 7" casing" (Spencer, 1967). The numerous cave systems of the Bahamas make up probably the greatest accumulation of submerged caves in the world. The banks are riddled with cave openings, both on the ocean floor and inland.

Bahamian caves are highly decorated with stalactites and stalagmites, and other more delicate speleothems (Fig. 15). The presence of these now submerged speleothems indicates that sea level was once lower and the caves were air-filled. (Speleothems form by an evaporative process when mineral-bearing rain water drips from the ceiling.) During maximum sea level depression, the entire Bahama Banks were exposed as dry land and the potential for greatly enlarged freshwater lenses would have existed. The highly decorated submerged caves found today indicate the influence of much rain water, further evidence that the freshwater lens was formerly more widespread than at present. Because of the numerous caves and crevices present, habitats suitable for colonization by anchialine fauna would have been prevalent (see Holsinger, et al., 1986; Yager, 1987a). Eustatic sea level changes may have had little effect upon most Bahamian anchialine cave fauna. The animals could have literally ridden up and down the water column in available crevicular habitat as sea level slowly rose and fell.

Figure 15. Author swimming above the permanent guideline in Sagittarius Cave. (Photograph by Dennis W. Williams).



BIOGEOGRAPHY

The Class Remipedia is divided into two families, five genera, and nine species (see Table 1). Remipedes have an apparent relict marine distribution. There are no known freshwater or epigean marine forms. Although the dispersal ability of remipedes is uncertain, their present distribution indicates that they are restricted to anchialine caves of the southern North Atlantic and the Caribbean. In addition to being distributional relicts, the remipedes are also phylogenetic relicts. The primitive remipedes no doubt belong to a very old lineage; they lack taxonomic affinity with other crustaceans. Remipedes or their predecessors have possibly occupied anchialine environments since the Jurassic (Holsinger, 1988). The distribution of remipedes on both sides of the Atlantic may be attributed to the breakup of a once continuous ancestral remipede stock by continental drift (Schram, et al., 1986; Holsinger, 1988). The putative remipede ancestor might have lived on both sides of the proto-Atlantic before the separation of Africa and what is now North and South America (Holsinger, 1988).

Five of the six remipede genera are monotypic. All but members of the genus *Speleonectes* are confined to the Bahamas. Two species (*S. lucayensis* and *S. benjamini*) are endemic to the Bahamas, *S. tulumensis* is found in anchialine cenotes of the Yucatan Peninsula of Mexico, and

S. ondinae is known from a single lava tube (Jameos del Agua, Lanzarote Island) in the Canary Islands. This general eastern Atlantic-West Indian distribution pattern is also shared by several other stygobiont species. For example, the amphipod genus *Spelaeonicippe* and the thermosbaenacean genus *Halosbaena* each have one member known from the Lanzarote lava tube and one from anchialine caves of the West Indies (Iliffe, et al., 1984). In addition to the remipede genus *Speleonectes*, four crustacean genera share nearly congruent ranges that extend from the Bahamas to the Yucatan Peninsula (Holsinger, 1989). They include five species of amphipod (*Bahadzia*), two thermosbaenaceans (*Tulumella*), three isopods (*Bahalana*), and two shrimp (*Agostocaris*). All of these species are found exclusively in anchialine caves or in groundwater. Their distributional pattern suggests that they may share a similar distributional history. According to Holsinger (1989) it is a result of fragmentation of earlier, continuous ranges of putative ancestors plus similar isolating events in the common areas of endemism.

Chapter 2. AN ECOLOGICAL STUDY OF REMIPEDES IN SAGITTARIUS CAVE

GENERAL DESCRIPTION OF SAGITTARIUS CAVE

Sagittarius Cave was first discovered by team members of an international cave diving expedition to the eastern end of Grand Bahama Island in 1983 (Palmer, 1985). The cave is one of six caves that make up the Zodiac Caverns which lie beneath the small island of Sweeting's Cay (Fig. 16). The cave entrances are either in Zodiac Creek, a small mangrove creek, or in saline lakes which occur inland.

The entrance to Sagittarius Cave is in the tidally-influenced lake located directly behind the government school house (Fig. 17). Along the eastern edge of the lake is a rock outcrop beneath which begins the cave entrance. With its lack of a large fresh or brackish water lens, Sagittarius Cave exhibits more of a marine influence than other anchialine caves having such a lens. The lake contains many marine forms such as needle-fish, sargent majors, angel fish, and juvenile groupers. Other marine mangrove swamp inhabitants, such as the jellyfish

Figure 16. Map of Grand Bahama Island. Note Sweeting's Cay at the east end of the island.

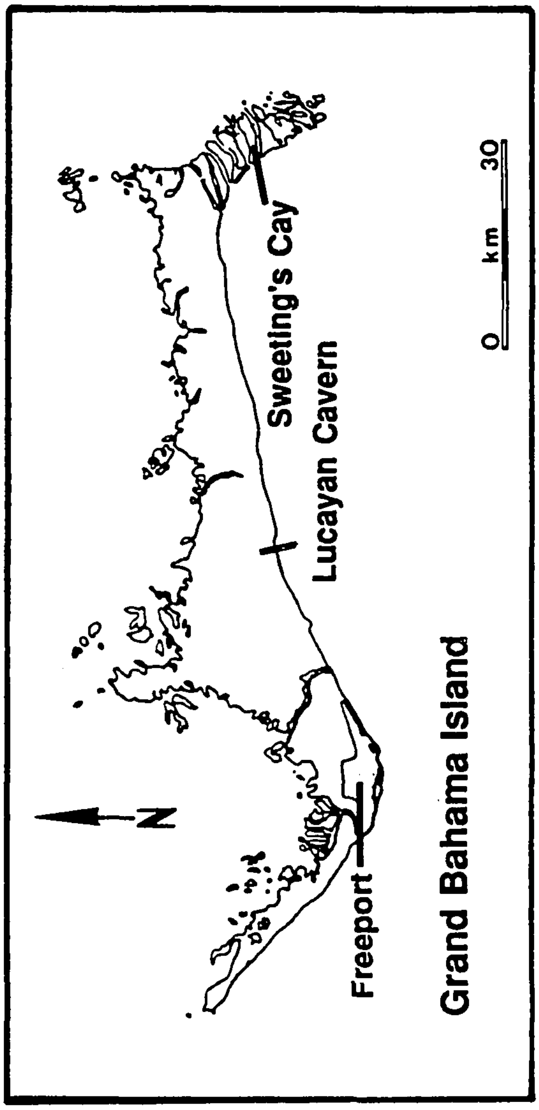
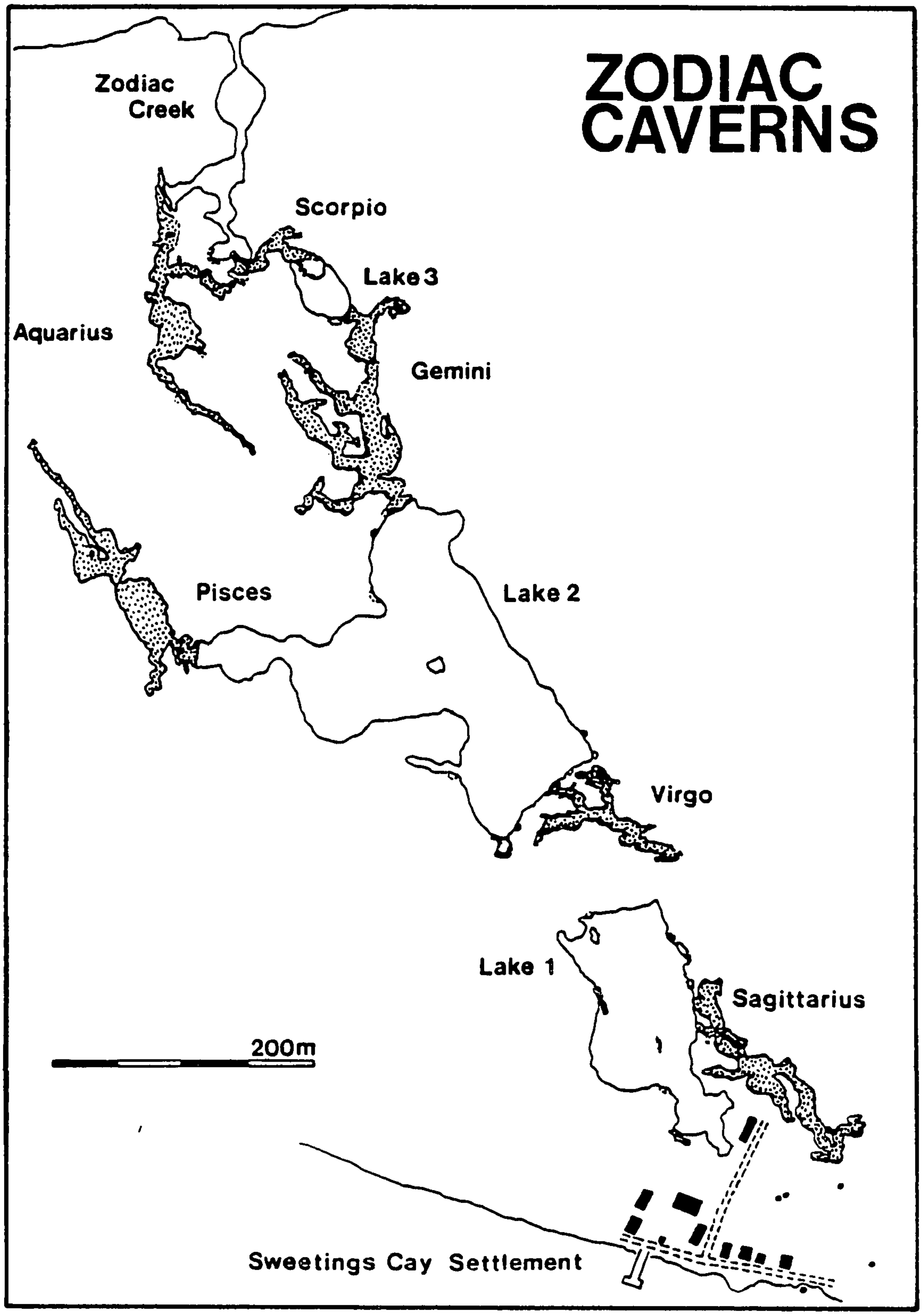

N
Grand Bahama Island
Freeport
Lucayan Cavern
Sweeting's Cay
0 km 30

Figure 17. Map showing the location of Sagittarius Cave on Sweeting's Cay. Stippled areas indicate the six submerged cave systems making up the Zodiac Caverns (from Palmer, 1985).


ZODIAC CAVERNS
Zodiac Creek
Scorpio
Lake 3
Aquarius
Gemini
Pisces
Lake 2
Virgo
Lake 1
Sagittarius
200m
Sweetings Cay Settlement

Cassiopeia, are common. These animals probably arrive from the nearby tidal creeks during spring tides or storms. For a detailed list of lake flora and fauna see Cunliffe (1985).

The cave is entered by descending along a vertical crack to a depth of about 12 m where the main horizontal passage is encountered. This passage continues deeper with additional branching passages. A total length of approximately 380 m has been surveyed (Palmer, 1985). The maximum depth measurable in the cave system was approximately 30 m, although small, deeper passages could be seen. The system has one inland surface opening at the end of the main passage, a small breakdown hole leading up into the mangroves. The hole is too small to permit human passage, and the ambient light which enters is quite dim. At the opening is a thin layer of brackish water. On the floor below is a steep slope of organic debris. Except for this layer of brackish water at shallow depths inland, Sagittarius Cave is euhaline throughout. The cave is very well decorated, with stalactites and stalagmites everywhere along the passages (see Fig. 15).

The walls and crevices of the cave entrance are covered with marine sponges and anemones. Hiding among the darker crevices are the fishes Opsanus beta and Eleotris pisonis. Descending along the entrance shaft a small room is encountered. Here the small hippolytid shrimp Janicea antiguensis is found in great numbers in the twilight zone, living on top of the thick organic material which has accumulated from the surface. The shrimp is also found beneath the inland surface opening on the pile of detritus. It has never been observed in the aphotic zone, and is not a troglobitic (obligate cave dwelling) species. Serpulid worms can be seen encrusting the walls with their thin, delicate tubes. In the cave passages the worms have heavily encrusted the walls, roof, stalactites and stalagmites. These filter feeders are mainly confined to the more oxygenated waters of the cave, above about 12-14 m in depth. In many cases very long tubes hang into the water column rather than encrusting close to the walls. Evidence of their past growth in deeper parts of the cave is indicated by abandoned tubes encrusted on speleothems and walls.

MATERIALS AND METHODS

Using a permanent guideline installed in the cave, reference points were marked on the line at four selected intervals. All points were set in the aphotic zone beneath the density interface in known remipede habitat. The cave was sampled in March, June, September and December 1987 and in March 1988. On each visit remipedes and associated fauna were sampled, remipede behavior observed, and data on water chemistry collected. Using plastic squeeze bottles with one-way valves, remipedes were randomly collected by two persons for approximately 20 minutes on each dive. Collections were primarily made in a large room (reference points 2 and 3) in water ranging in depth from 15-26 m. Prior to collection, casual observations of remipede behavior were made. To document the fauna associated with remipedes, collections were made using squeeze bottles, plastic bags, and a plankton net; sediment samples were taken. Remipedes and associated fauna were fixed either in 4% formalin in seawater or in 3% glutaraldehyde with 0.1 M sodium cacodylate or cave water as buffer.

Temperature was measured at various depths using a thermometer in a PVC housing. Dissolved oxygen was measured using CHEMetrics brand test kits (K7512 for levels of 1-

12mg/l and K7501 for levels of 1-2 mg/l). Additional water samples were collected at various depths and brought to the surface for measurements of salinity, hydrogen sulfide, hardness, ammonia, and nitrates. A refractometer was used to determine salinity. Hardness, hydrogen sulfide, ammonia, and nitrate were measured using CHEMetrics test kits (K4540, K9510B, K1510, and K6902D respectively).

All cave diving techniques and equipment used to conduct this study met the standards set by the National Speleological Society Cave Diving Section and the National Association of Cave Divers.

Total mean biomass of each of the six remipede species was computed by determining the wet weight of each individual. A 1-way analysis of variance (ANOVA) was used to determine whether there was a significant difference in biomass among the three most numerous species. It was calculated using mean biomass of each species per sampling date as dependent variables; sample dates were considered replicates.

RESULTS AND DISCUSSION

Remipede frequency distribution and biomass

At the beginning of this study three remipede species were known to inhabit Sagittarius Cave (Speleonectes lucayensis, S. benjamini, and Cryptocorynetes haptodiscus). The one year sampling period revealed the presence of three additional species of remipedes, bringing the total in the cave to six. The presence of Godzillius robustus is a range extension, as it was previously unrecorded from Grand Bahama Island. The two new monotypic genera were recently described by Yager (1989b).

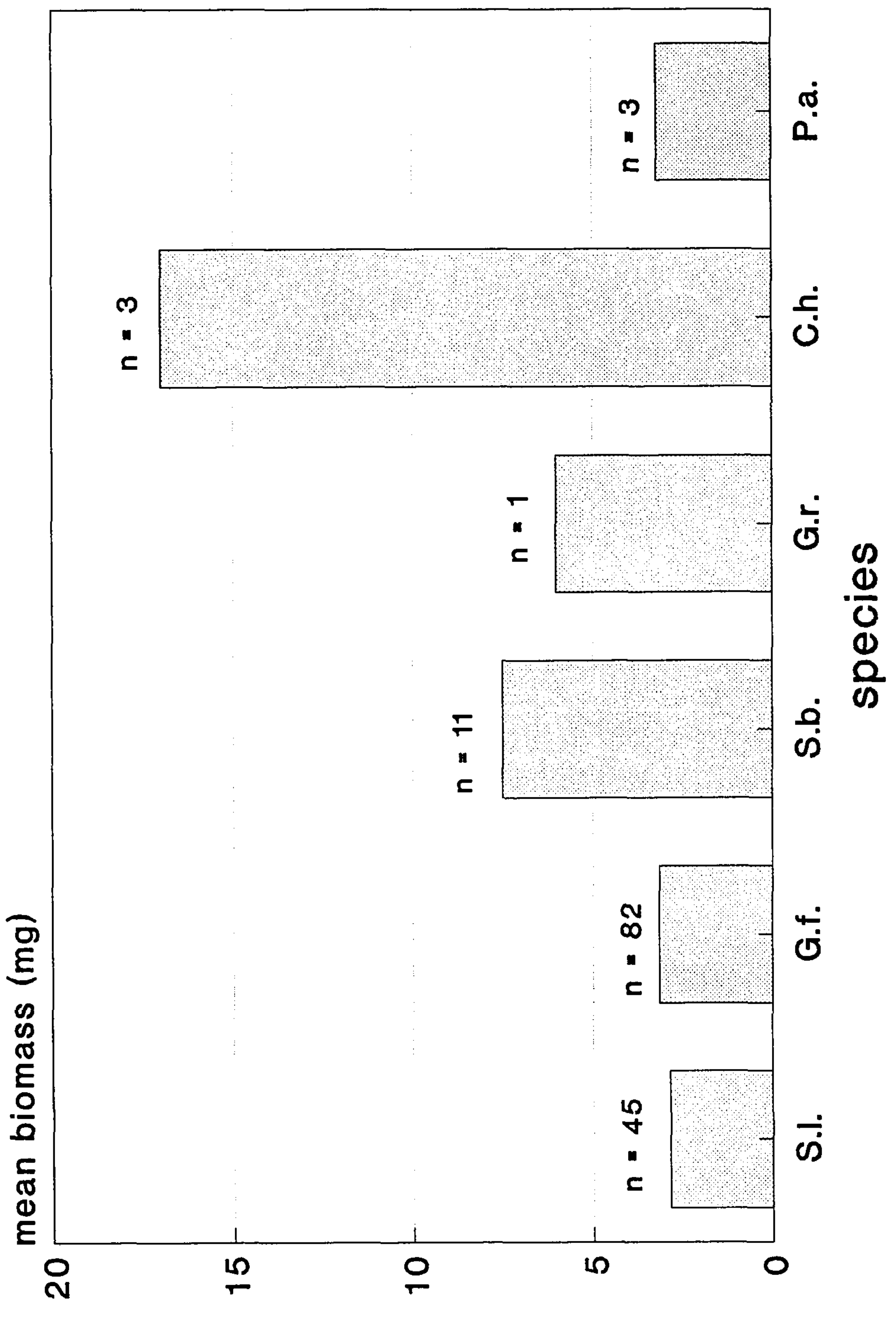
All six remipede species appear to occupy the same general habitat in Sagittarius Cave. They are never on walls or floors, but always in the water column beneath the density interface. Table 2 gives the frequency distribution of the remipedes captured during the sampling periods. Of the six remipede species, the most common one was the smallest species, Godzilliognomus frondosus. The next most common was Speleonectes lucayensis, followed by S. benjamini. The other three species were uncommon. Total mean biomass for each species is shown in Fig. 18. The 1-way ANOVA which was calculated for biomass indicates that there is not a significant difference among the total

Table 2. Frequency distribution of remipede species from Sagittarius Cave, Bahamas, based on random sampling for 20 minutes during five visits from March 1987 through March 1988.

Species	Mar	Jun	Sep	Dec	Mar	Total	Percent of total
Godzilliognomus frondosus	6	10	24	17	25	82	57%
Speleonectes lucayensis	1	6	21	11	6	45	31%
Speleonectes benjamini	1	2	4	3	1	11	8%
Cryptocorynetes haptodiscus	0	2	0	0	1	3	2%
Pleomothra apletocheles	0	2	0	0	1	3	2%
Godzillius robustus	0	0	1	0	0	1	0.7%

Figure 18. Total mean biomass of all remipedes collected in Sagittarius Cave from March 1987-March 1988. N = number sampled. Standard deviations = 1.86 for S.l., 1.26 for G.f., 4.95 for S.b.

Abbreviations: S.l. = *Speleonectes lucayensis*
G.f. = *Godzilliognomus frondosus*
S.b. = *Speleonectes benjamini*
G.r. = *Godzillius robustus*
C.h. = *Cryptocorynetes haptodiscus*
P.a. = *Pleomothra apletocheles*


mean biomass (mg)
20
15
10
5
0
n = 45
n = 82
n = 11
n = 1
n = 3
n = 3
S.l.
G.f.
S.b.
G.r.
C.h.
P.a.
species

biomass for the three most abundant species (F = 2.67; df = 2, 9; P > 0.05). Despite disparities in their abundance, the three most abundant species appear to represent nearly equivalent population biomass.

Potential resource partitioning

A basic ecological tenet of competition (niche) theory is that similar species occupying the same habitat will evolve differences (e.g. behavioral, physiological, or morphological) that minimize the impact of competition for resources (Krebs, 1985). Species interactions in aquatic cave communities have been studied mainly in Appalachian caves. The majority of amphipods and isopods are found in cave stream riffles rather than in pools because there is more dissolved oxygen as well as more food and fewer predators (Culver, 1982). Studies of amphipods and isopods sharing shallow stream riffles indicate that niche separation is occurring as a result of competition (Culver, 1970; Estes, 1978). Culver (1970) found two species, Stygobromus emarginatus (amphipod) and Caecidotea holsingeri (isopod) were excluded from riffles when the amphipod Gammarus minus was present. Estes (1978) detailed the microhabitat of the isopod Lirceus usdagalun in six stream locations with two velocity:depth profiles. He found the isopod shifted toward faster currents in the presence of competitors.

My direct observations suggest that the three most abundant remipede species occupy similar depths in the cave. The other three species were too infrequently seen to determine any kind of a distributional pattern. All of the remipedes appeared to be randomly distributed in the water column beneath the density interface. However, the cave is complex and has far more crevicular space than a human can enter. Deeper passages are present which are unexplored and/or unexplorable, thus there may be spatial partitioning occurring that is not evident. The presence of six species would appear to indicate that some sort of resource partitioning is taking place.

One method of minimizing competition may be through diet and/or foraging techniques. The diet of remipedes is unknown. They have not been observed taking prey, evidence for feeding is circumstantial, and gut content analysis inconclusive. However, based on their feeding appendage morphology and other differences, the remipedes in Sagittarius Cave are likely utilizing different food items. Their varied feeding appendages (see discussion in Chapter 1) may allow selective feeding or some fixed food preferences. Godzilliognomus frondosus differs from the two Speleonectes species in size, behavior, gut and feeding appendage morphology. These differences may account for divergent diets. G. frondosus is the smallest species, averaging 7 mm in length. The midgut epithelial cells contain huge lipidlike droplets whereas the lipidlike droplets in the midgut of S. benjamini are small. G.

frondosus is able to hang nearly motionless in the water column with slight movement of the trunk appendages. This small species may have a different foraging pattern, as it does not appear to roam like the other two. Speleonectes benjamini and S. lucayensis differ from each other in body size and in feeding appendage morphology. S. benjamini is larger (up to 14 mm), the first antenna is very long (over half the length of the body) and the first maxilla has a long slender fang at the tip. In contrast, S. lucayensis specimens were all apparent sub-adults, smaller (9 mm average), with a shorter antenna 1 and with a shorter, stouter fang on maxilla 1.

There may be an avoidance of competition via temporal partitioning of remipede life cycles. In the five sample periods from March 1987 to March 1988, no adult Speleonectes lucayensis was recorded. All of the specimens were apparent sub-adults, while those of S. benjamini were adults. Adults specimens of S. lucayensis have been collected on Grand Bahama Island from Lucayan Cavern, approximately 60 km east of Sagittarius Cave, as well as on other Bahamian islands. The sub-adults specimens of S. lucayensis from Sagittarius Cave have been examined and do not appear to be a new species. The basic morphology is the same as that of the adult, but sub-adults are smaller, slightly less setose, and have rounded tergites. Paraffin sections reveal the presence of ovaries and testes, but no mature oocytes or sperm were present. The apparent absence of adult individuals of S. lucayensis can be explained in several ways. Because of infrequent sampling we could have simply not been in the cave at the right time and adults may have been missed. It is also possible that the adults occupy deeper, inaccessible reaches of the cave or even another adjunct system. Finally, their population structure could be skewed toward the sub-adults at the times we were sampling.

Behavioral observations

An escape mode of swimming pattern was observed when remipedes were approached with the collection bottle. This was especially evident with the smallest remipede species, Godzilliognomus frondosus. This animal normally floats in the water column with little forward motion, maintaining its position by a slow metachronal beat of its trunk appendages. This is in sharp contrast to other larger species which seem continuously swimming over a broader range. When approached, G. frondosus "jumps" through the water column for a distance of approximately 10-15 cm by switching from metachronal to simultaneous beating of the trunk appendages. Although larger remipede species switch to this pattern of swimming when they detect our approach, they do not propel themselves as far and so do not appear to jump or dart through the water.

No feeding, courtship or mating behavior was observed.

At no time were any remipedes observed crawling on the bottom or resting. They were continually swimming in the water column. Remipedes showed no response to bright diving lights.

Associated fauna

In addition to the six remipede species, 13 invertebrate and 1 vertebrate species were recorded (Table 3). The shrimp are troglophilic or facultative cave dwelling species. They are known only from caves or cryptic habitats and show a small amount of eye and pigmentation reduction. With the exception of the shrimp and the tube worms (which also appear to be troglophilic), the remaining 12 species are troglobitic or cave-limited species. The abundance of most of the associated troglobitic species appears to be low when compared to the number of remipedes. The most frequently encountered species were ostracodes, thermosbaenaceans, and amphipods. In addition to the two new remipede genera and species, two new species of thermosbaenacean found in Sagittarius Cave have been described (Yager, 1987c). The chaetognath is the first eyeless species recorded (Thomas E. Bowman, pers. comm.) and is known only from this cave.

Table 3. List of fauna associated with remipedes in Sagittarius Cave between March 1987 and March 1988.

PHYLUM ANNELIDA

Class Polychaeta
Family Serpulidae -- tube worm in *Vermiliopsis* group

PHYLUM ARTHROPODA

SUBPHYLUM CRUSTACEA

Class Ostracoda
Family Halocyprididae -- *Deeveya styrax* Kornicker
Deeveya medix Kornicker
Deeveya spiralis Kornicker and Iliffe
Spelaeocia sagax Kornicker

Class Malacostraca
Order Amphipoda
Family Hadziidae -- *Bahadzia williamsi* Holsinger
Family Pardaliscidae -- *Spelaeonicippe* cf, *stocki*

Order Isopoda
Family Cirolanidae -- *Bahalana geracei* Carpenter

Order Mysidacea
Family Stygiomysidae -- *Stygiomysis holthuisi* (Gordon)

Order Thermosbaenacea
Family Halosbaenidae -- *Tulumella grandis* Yager
Tulumella bahamensis Yager
Order Decapoda
Family Hippolytidae -- *Janicea antiguensis* (Chace)

PHYLUM CHAETOGNATHA

Paraspadella, new species

PHYLUM VERTEBRATA

Order Pisces
Family Ophidiidae -- *Lucifuga spelaeotes* Cohen and Robins

In Sagittarius Cave the associated troglobitic fauna are seen throughout the water column above and below the density interface. However, the crustacean community appears to be most abundant beneath the density interface. In other anchialine caves where the density interface has a large salinity gradient (e.g. from polyhaline to euhaline) these same animals apparently have some degree of euryhalinity. In Sagittarius Cave, which lacks a large salinity gradient, the only crustaceans apparently confined to the water column beneath the density interface are the remipedes. These animals were never observed in the water column above the interface. The density interface is a distinct component of anchialine caves and apparently a key factor in the distribution of remipedes.

Water analysis

The entire cave system is euhaline throughout, averaging about 35 ppt. On each dive at least two distinct density interfaces were detected in the cave system. These interfaces were physically detected as distinct temperature differences and were seen as visible changes in the refractive property of the water. The two interfaces fluctuated seasonally and tidally. In March, 1987 the two density interfaces were evident at 17 m and 20 m; in June at 15 m and 18 m; in September at 20 m and 23 m; in December at 14 m and 18 m; and in March of 1988 at 14 m and 21 m. These interfaces usually corresponded to differences recorded in either the dissolved oxygen or temperature. No salinity gradients were detected with the refractometer that was used.

The most obvious temperature differentiation occurred as a result of seasonal changes between summer and winter (Fig. 19). The greatest amount of temperature fluctuation occurred from the surface to about 18 m. From about 18-20 m to the deepest reading, the year-round temperature remained relatively constant, varying only between 25° and 27° C.

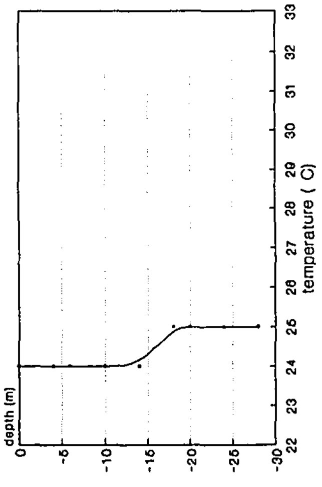
The average oxygen profile of the cave is shown in Figure 20. Water from the surface of the cave down to approximately 12-15 m was well oxygenated and consistently measured 5-6 ppm throughout the year, except in March 1988 when 8 ppm was measured at the surface. At about 15 m the oxygen level dropped abruptly from 5-6 ppm to 1-2 ppm. Below about 21 m the dissolved oxygen was recorded at less than 1 ppm, in some instances as low as 0.1-0.2 ppm. In the winter (December 1987 and March 1988) the low-oxygen layer was shallower than usual, occurring at about 9-10 m.

Results of the tests for ammonia, hydrogen sulfide and nitrates were below the level of detection for the test kits used. The hardness (calcium) for surface water averaged 5000 ppm, at 15 m it was 5500 ppm; at 18 m it was 6500 ppm; at 21 m it measured 4500 ppm.

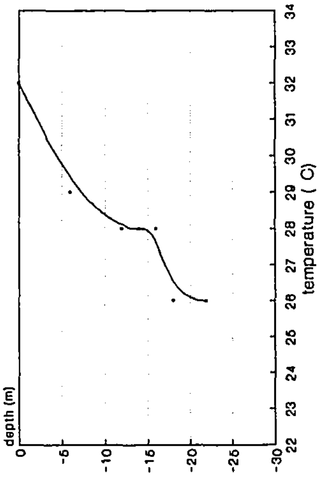
Feeding behavior hypotheses

The feeding behavior of remipedes has not been

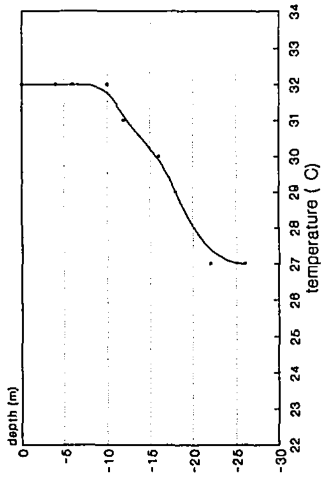
Figure 19. Temperatures recorded in Sagittarius Cave from March 1987-March 1988.



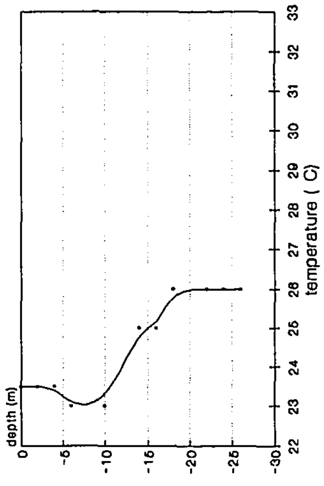
MARCH 1987



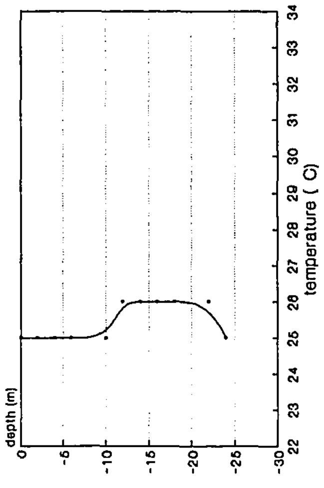
JUNE 1987



SEPTEMBER 1987

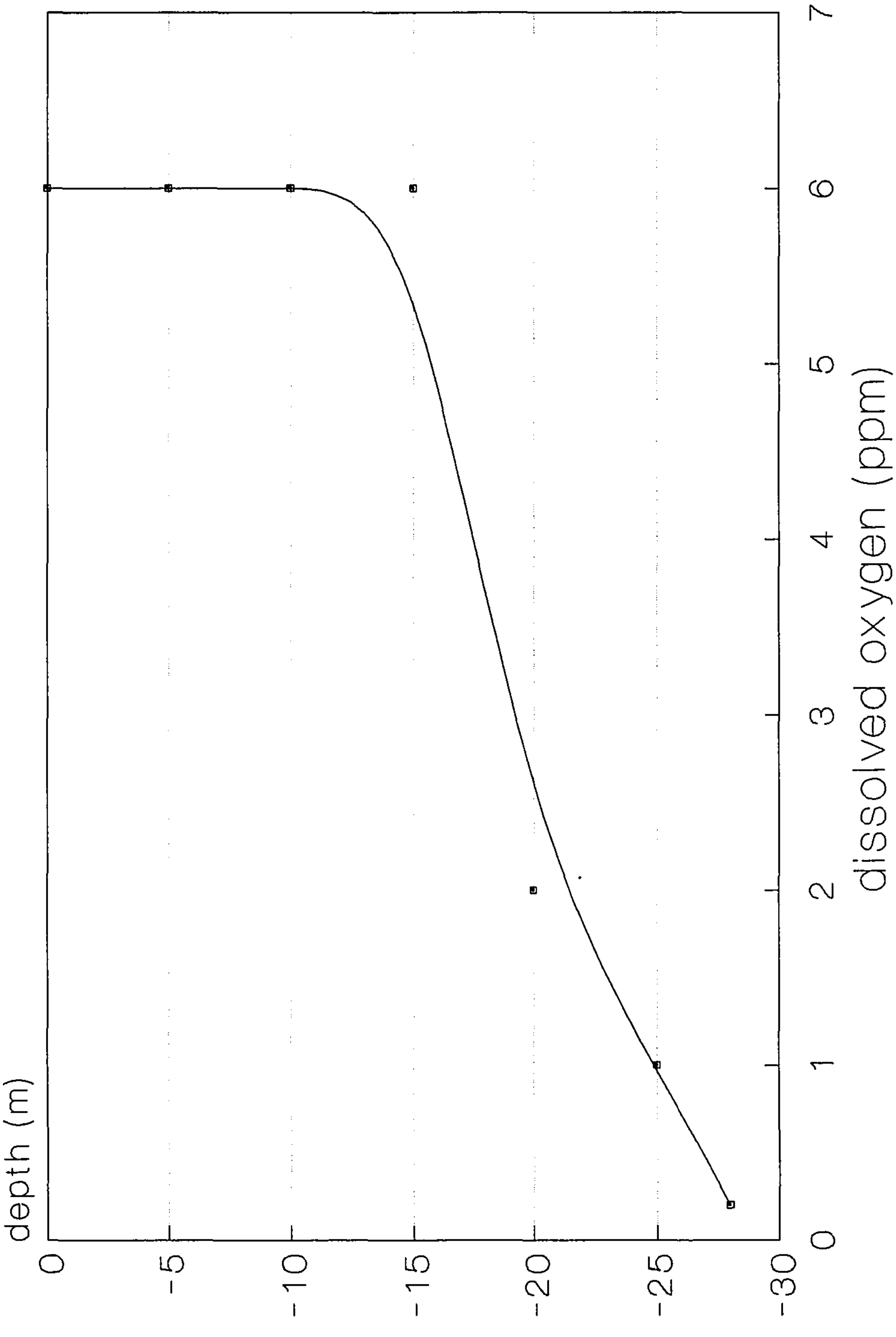


DECEMBER 1987



MARCH 1988

Figure 20. Average dissolved oxygen profile for Sagittarius Cave.


depth (m)
0
-5
-10
-15
-20
-25
-30
0
1
2
3
4
5
6
7
dissolved oxygen (ppm)

described. They have not been observed capturing prey. No food items have been found in the feeding appendages, mouth area, or gut, and fecal pellets have not been recovered. Based on feeding appendage morphology, remipedes appear to be predators. The first and second maxilla and maxilliped are large, grasping appendages. The cusped incisor process of the mandible is similar to that of other crustaceans where it is used for cutting and/or biting. Based on the examination of feeding appendages of each species, several possible feeding modes are presented.

Two species examined (*Speleonectes benjamini* and *S. lucayensis*) have a duct associated with the fang on the first maxilla. This duct has been traced to a gland at the base of the appendage. Differential staining suggests the gland contains at least two kinds of apparent secretory globules. It is possible that these secretions may be some sort of an enzyme which is injected into the prey to immobilize and pre-digest much like an arachnid. *Lasionectes entrichoma* from The Turks and Caicos inhabits a cave with a very large population of typhlatyid shrimp. One remipede was observed grasping a shrimp exoskeleton, apparently feeding (Schram, et al., 1986). For the remipede to successfully capture the shrimp would probably require rapid immobilization. The shrimp are about 15 mm in length and are capable of vigorous escape attempts when caught. After piercing the shrimp with the first maxilla, the other prehensile feeding appendages could be used to manipulate the shrimp next to the remipede mouth area where a hole could be cut in its carapace with the cusped incisor process and lacinia mobilis of the mandible. With the immobilizing enzyme also serving to break down the body tissue, the remipede could then suck the pre-digested shrimp fluid into the mouth area. Unfortunately, actual feeding has not been observed on a microscopic level, so details are unknown.

Although every remipede has a fang on the first maxilla, I have only confirmed the presence of a duct leading to an apparent secretory gland in the two species mentioned above. Another possible feeding method may involve crushing or nipping. Pleomothra apletocheles has a massive, cheliform first maxilla (see Fig. 6B). The appendage is very muscular and could be used to nip or crush food items. The second maxilla and maxilliped of Cryptocorynetes haptodiscus differ from other remipedes in that the distal segments are enlarged and covered medially with highly modified discoid sensilla (see Figs. 6A, 10A). This species must utilize the appendages for feeding or food capture in a different manner than the other species.

Despite their wide array of elegant feeding appendages, it is likely that remipedes are also opportunistic scavengers. The distal claw arrangements of the second maxilla and maxilliped could serve as scrapers and transfer small food fragments to the mouth. In Mexico, cave diver Mike Madden (pers. comm.) reported seeing many remipedes gathered around and on a dead cave fish. Although he could not get close enough to confirm what the remipedes were actually doing, he said it appeared that they were feeding on the fish.

Food web hypotheses

Little is known about the food web in anchialine caves. In the absence of primary production, the food web in air-filled caves depends on organic input from the surface. Organic matter such as plant material enters directly by streams and vertical shafts. Other sources of food include fecal material and dissolved organic matter which percolates through the rock. Organic input in anchialine caves appears restricted to surface entrances because in most caves there is little or no current to carry material in. With tidal fluctuations, it is possible that some dissolved and particulate material is flushed into the cave, especially after heavy rains. Particulate matter has been observed in the water column after storms. Interestingly, it appears confined to the water column above the density interface. This material has not been analyzed for carbon content. Any nutrients which would come through from the surface would be in the form of particulate organic matter or dissolved organic matter derived from water seeping through the porous limestone. In the aphotic zones of submerged caves, hundreds of meters from the surface opening, available food is probably not entirely from allochthonous sources.

Huge filamentous colonial sulfur bacteria of the Beggiatoa-Thiothrix group have been observed floating in the water column of almost every anchialine cave which I have dived. In addition to the floating bacteria, large filamentous mats have been observed on cave floors. These microbial mats are ubiquitous on surface sediment of coastal, oceanic and deep sea environments (Grant and Bathmann, 1987). The Beggiatoa biomass and extractable material may be used by invertebrate grazers and thus be the basis for the food chain in caves. It is possible that sufficient organic material washes underground through the porous rock and serves as the primary source of food for microbial decomposers and/or detritivores. However, organic sediment appears to accumulate only at the entrances of anchialine caves. Far from the surface openings of Lucayan Cavern what appeared to be organic detritus on the floors was analyzed by x-ray diffraction as nearly pure iron oxide (D. Gerhardt, pers. comm.). It may be possible that bacterial chemosynthesis plays a significant role in the primary productivity of some anchialine caves. The source of energy for bacteria may not be from organic input from the surface. This type of non-solar food chain has been hypothesized for deep sea thermal vent animals (Jannasch and Mottl, 1985). Bacteria probably play a major role in anchialine cave energetics, and it is a fascinating area for future investigations.

Trophic levels and energy flow in anchialine caves are no doubt complex. However, a simplified food web for Sagittarius Cave can be constructed. If bacterial biomass and suspended organic matter are used as the basis of the chain, this material may be fed upon by animals such as protozoans and other undetected microscopic organisms, as well as macroscopic detritivores (amphipods, isopods, thermosbaenaceans, etc.). Remipedes, probable carnivores, would feed on the other smaller crustaceans. They probably also utilize animal remains by scavenging. Because of their larger size and raptorial feeding appendages remipedes are possibly the top invertebrate carnivore in anchialine cave systems. No other crustacean living in the cave appears equipped with raptorial appendages or the body size to be able to catch and eat remipedes. It is probable that the only predator on remipedes is the blind cave fish. However, given the abundance of remipedes in contrast to the apparent scarcity of other crustacean prey, the possibility of remipede cannibalism cannot be excluded.

Chapter 3. REPRODUCTIVE BIOLOGY OF REMIPEDES

INTRODUCTION

This chapter will present a detailed histological description of the reproductive system of two remipedes, Speleonectes benjamini and Godzilliognomus frondosus. These two species were examined because they were the most abundant remipedes in Sagittarius Cave and because sperm were found in several specimens. This study focused mainly on the male reproductive system. Specimens of S. tulumensis from almost every month of the year were examined and although ovaries and testes were found, no mature sperm were observed. Several S. lucayensis sub-adults were examined and only small ovaries were present. Examination of serial cross sections also yielded more details about the general internal anatomy of various species. This information is included in Chapter 4.

Prior to this study no ultrastructural details were available for the reproductive anatomy of remipedes. Preliminary results of this study were published in Yager (1989a), giving ultrastructural details of the sperm and spermatophores of Speleonectes benjamini.

Certain general aspects of remipede reproductive anatomy have been mentioned in various papers, in some cases erroneously. The following is a review of what has been published.

Schram (1986) described the male reproductive system as extending from the head posteriorly and lying ventral to the gut. This was corrected by Itô and Schram (1988) when they stated that the testes of Lasionectes entrichoma originate in the posterior portion of the 7th trunk segment. They also stated that the testes originate ventral to the gut. After examination of many specimens of several species, I was unable to confirm this. In my investigations the testes were always found dorsal or dorsolateral to the gut.

Gonadal material seen as a strand leading from the second maxilla to approximately the 14th trunk segment was noted in the initial description of Speleonectes lucayensis (Yager, 1981). The presence of sperm was mentioned but not detailed in the species description of S. benjamini (Yager, 1987a). Originally it was thought the gonopores on the 14th trunk appendages served both male and female reproductive systems. Itô and Schram (1988) described a second pair of gonopores located on the 7th trunk appendages associated with the female reproductive system. They described the female gonopore and offered a general description of the reproductive system of L. entrichoma. Ovaries with immature oocytes and paired oviducts were noted for *S. benjamini* (Yager, 1987a). Ito and Schram (1988) confirmed that remipedes are hermaphroditic but were uncertain whether they were simultaneous or sequential hermaphrodites. Yager (1989a) confirmed that *S. benjamini* is a simultaneous hermaphrodite, finding both mature oocytes and spermatophores in the same individual.

The male gonopore has been illustrated with scanning electron micrographs for *Lasionectes entrichoma* (Schram, et al., 1986; Ito and Schram, 1988), *Speleonectes benjamini* (Yager 1987a, 1989a), *Cryptocorynetes haptodiscus* (Yager, 1987a), and *Pleomothra apletocheles* (Yager, 1989b).

MATERIALS AND METHODS

Remipede specimens used for transmission electron microscopy (TEM) were fixed in 3% glutaraldehyde with 0.1 M sodium cacodylate or cave water buffer, rinsed in the buffer and postfixed in 2% buffered osmium tetroxide. All specimens were dehydrated through a graded series of ethanol solutions up to 70% and stored until further preparation. Three methods of embedding were used for obtaining sections: paraffin, methacrylate, and epoxy resin.

For light microscopy, specimens were dehydrated from 70% ethanol through 100% to xylene and embedded in Paraplast or JB-4 methacrylate medium (Polyscience JB-4 embedding kit). Sections from 2-6 um were cut on a JB-4 or AO microtome and mounted on glass slides. Tissue was stained with Mallory's triple stain, hematoxylin-eosin (H & E), or a modified azan (Hubschman, 1962). In addition, the periodic acid-Schiff (PAS) and the Feulgen reactions were used.

For TEM examination post-fixed specimens were dehydrated through 100% ethanol into acetone and embedded in Polybed 12. Sections were cut with a diamond knife on an LKB Ultratome III, mounted on copper grids, stained with uranyl acetate and lead citrate, and viewed with a Hitachi

HU-11B electron microscope. Thick sections (1 um) were cut with glass knives, stained with methylene blue-azure II, examined and photographed with an Olympus Vanox AH-2 research microscope.

OBSERVATIONS AND DISCUSSION

A diagrammatic sketch of a remipede indicating approximate positions of the female and male reproductive systems is seen in Figure 21.

Ovary

The ovary of *Speleonectes benjamini* originates in the head at about the level of the maxilliped or the 1st trunk segment. The broad organ lies dorsal to the midgut and ventral to the simple circulatory vessel (Fig. 22). For a short distance of less than about one trunk segment the ovary may be a single organ with two symmetrical lateral components. In some sections it appears that what was initially described as a single ovary has an epithelial barrier separating it into two distinct parts. Further study is needed to clarify the issue. By about the posterior portion of trunk segment one the organ is separated into distinct paired ovaries. The medial margins of the ovaries lie closely together. The paired ovaries extend dorsally until about the 5th or 6th trunk segment. At that position I have found no histological evidence of a duct continuing to the gonopore. However, the oviducts should emerge and continue ventrally to the gonopore on the

Figure 21. Diagrammatic representation of remipede showing gonopores and the approximate location of female and male reproductive systems. Ventral view.

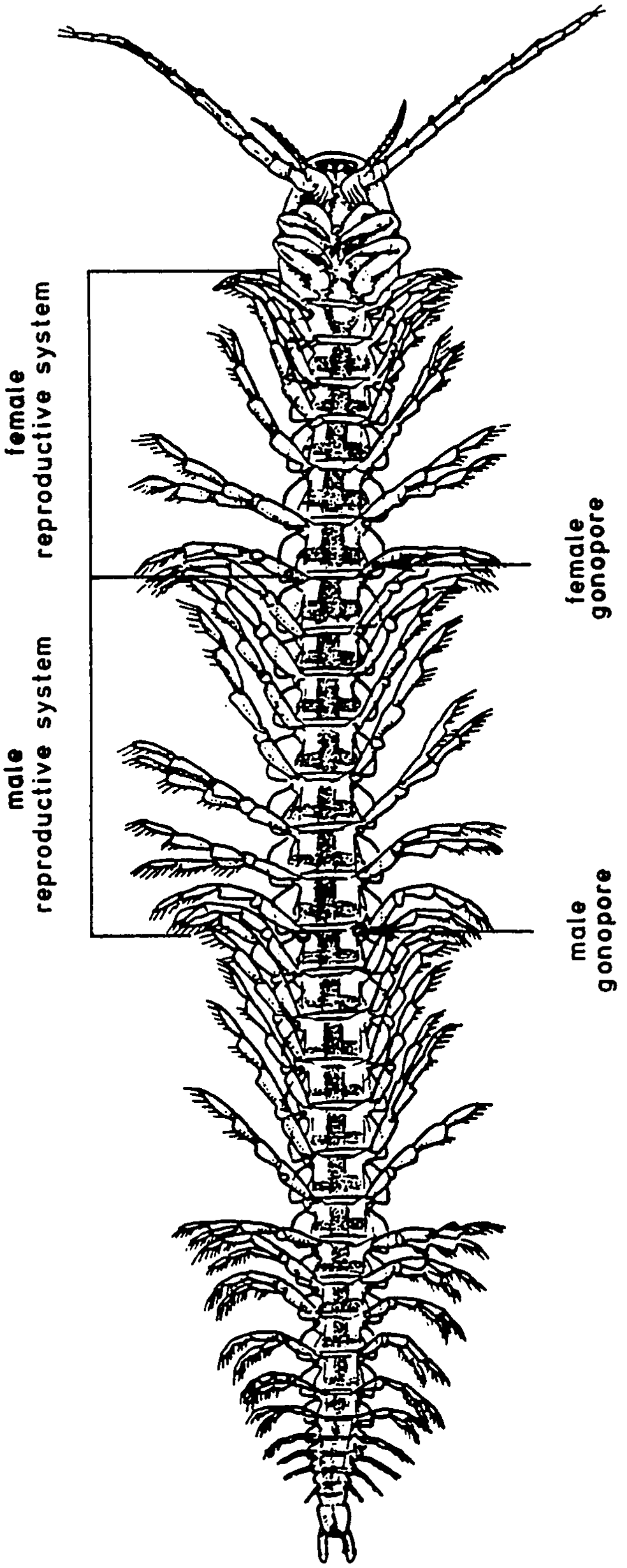
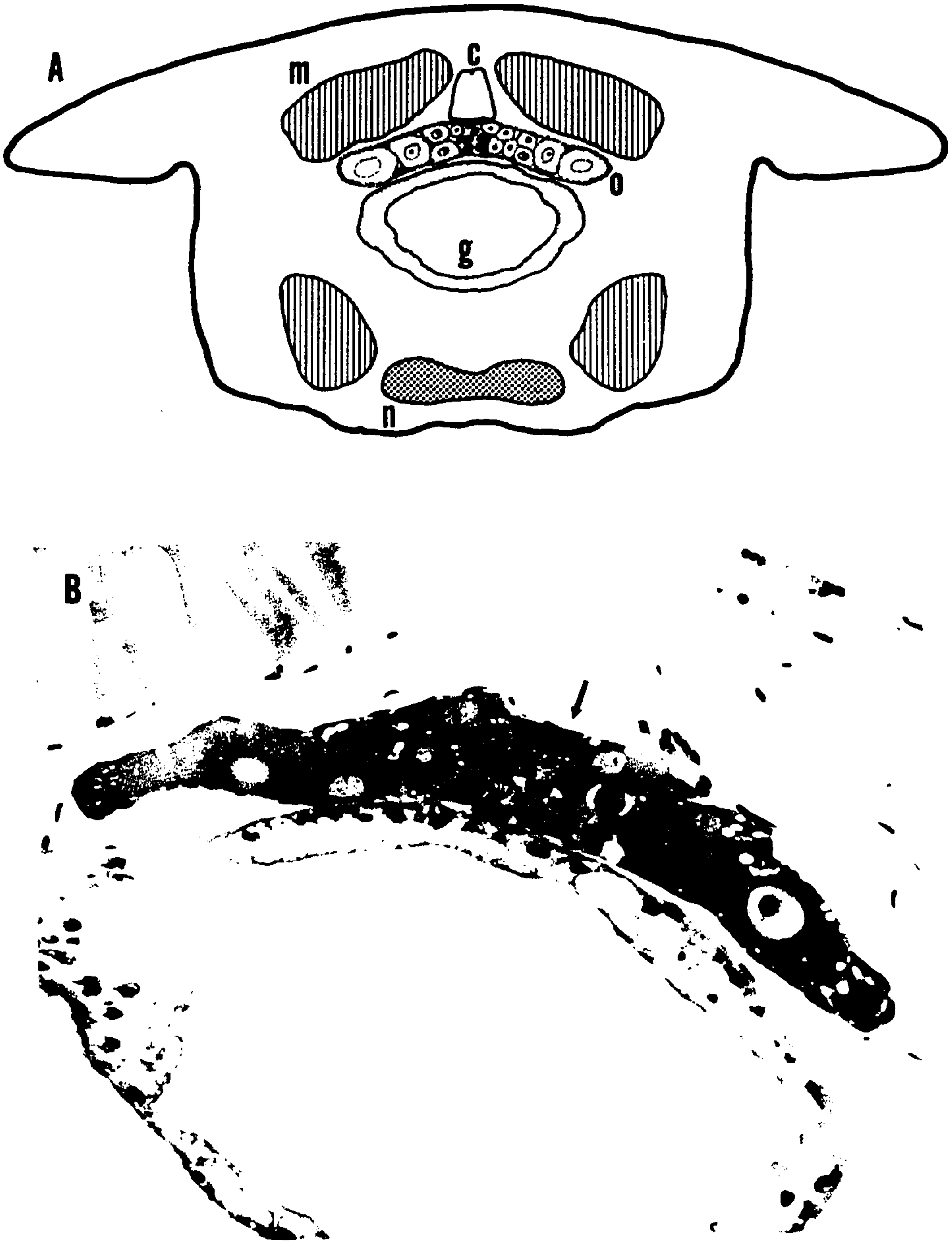

female reproductive system
male reproductive system
female gonopore
male gonopore

Figure 22. Ovary

A. Diagrammatic representation of a cross section of the female reproductive system of a remipede.

B. Ovary of Speleonectes benjamini. Arrow indicates zone of differentiation. Hematoxalin and eosin stain (H & E).

Abbreviations: c = dorsal circulatory vessel
g = midgut
m = muscle
n = ventral nerve cord
o = ovary


A
m
c
o
g
n
B

7th trunk appendage.

In Speleonectes benjamini the germinal zone appears at the anteromedial portion of the single ovary. Oogonia and immature oocytes can be observed (Fig. 22B). The elliptical nuclei of S. benjamini oogonia measure approximately 6 x 11 um. Oogonia of Godzilliognomus frondosus are about 9 um in diameter. Non-germinal squamous epithelial cells with flattened nuclei surround the ovaries. Because of insufficient ultrastructural details to confirm various degrees of development, the oocytes will be termed primary, intermediate and mature based on nuclear or cytoplasmic size.

Primary oocytes of Speleonectes benjamini are small and have a finely granular ooplasm. The entire elliptical cell is about 31 x 38 um and the large nucleus measures about 15 um in diameter. A large nucleolus with a diameter of about 4 um was present, as well as several smaller nucleoli. Primary oocytes were found in the ovary at about trunk segment 2. Young oocytes of Godzilliognomus frondosus were present in trunk segment 1. They were round and about 65 um in diameter with a nuclear diameter of 30 um. Primary oocytes have been found in individuals collected throughout the year.

Intermediate oocytes were distinguished from primary or immature oocytes by the presence of small granules in the cytoplasm. These opaque spheres are all the same approximate size. In both species, the intermediate oocytes were found in trunk segment 2. Oocytes of S. benjamini are elliptical, about 56 x 88 um, with nucleus of about 16 um and a nucleolar diameter of 6 um. Intermediate oocytes of G. frondosus were elliptical and measured about 100 x 180 um. The nucleus was about 41 um, and the nucleolus about 10 um.

The largest cross-sectioned diameter of mature oocytes of S. benjamini ranged from about 75 x 88 um to 100 x 160 um. They were found in trunk segments 3 and 4. The nuclear diameter ranged in size from about 35-50 um. The large nucleolus was about 13 um in diameter. The largest vitellogenic oocytes for G. frondosus ranged from approximately 150 x 225 um to 280 x 350 um. The nuclear diameter was about 66 um. The granular cytoplasmic inclusions in the intermediate oocytes of G. frondosus were large globules or droplets of varying sizes, from 6-10 um in diameter. Composition of these droplets was not determined.

In sagittal sections the ovary can be seen enlarging distally as the eggs develop. Oocytes are positioned along the ovary with the smallest (youngest) oocytes anteriorly and the largest (mature) oocytes proceeding posteriorly. The smallest oocytes are observed at the beginning of the ovary between about the level of the maxilliped and the first trunk segment. Mature oocytes have been found in the ovaries beginning at about trunk segment three and extending no further posteriorly than about the fourth trunk segment. These mature oocytes have been observed only in the ovaries dorsal to the midgut. The large eggs appear to be few in number, with no more than five observed in serial sagittal sections.

Histological differentiation between ovaries and oviduct was not apparent. In the two species examined there is evidence of differentiation or maturation of the oocytes after the ovary splits into the two lateral components. At this point, I refer to the paired "oviducts" of Ito and Schram (1988) as paired ovaries. Oocytes with a double layer of epithelial cells appear posteriorly in what may be the oviducts or the transitional tissue leading to them. However, the tubes containing the two above mentioned oocytes appear to lack the secretory and muscle cells commonly found in oviducts. The oviducts may be vestigial until the time of oviposition, or the oocytes may be conducted by body movement.

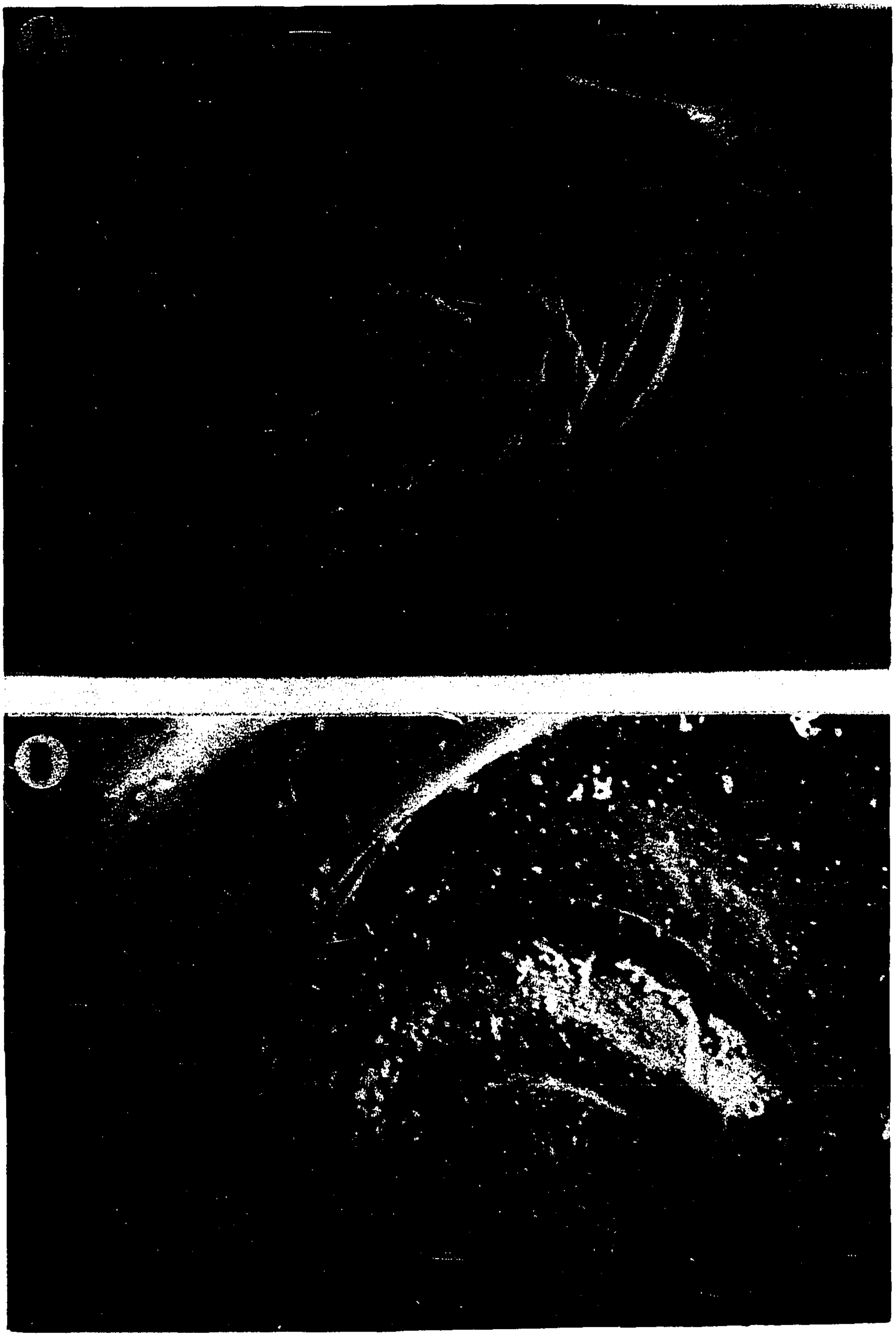
Female gonopore

The female gonopore (Figs. 21, 23) is located on the posterior side of the protopod of the 7th trunk appendage. The gonopore is similar in all species and consists of a narrow semicircular opening that leads into the protopod. The opening is beneath a chitinous rim and is covered by a semicircular pad. The entire complex is slightly raised or papillalike. The width of the gonopore of *S. benjamini*

Figure 23. Female gonopores

A. Female gonopore of *Speleonectes benjamini*, 579x

B. Female gonopore of *Godzillius robustus*, 311x



(Fig. 23A) is about 72 um, that of Godzilliognomus frondosus is about 67 um, and the largest species, Godzillius robustus (Fig. 23B) measures approximately 166 um. Examination of sectioned material from several species has revealed little microscopic detail of this area. Columnar epithelium lines the duct near the pore but no distinct seminal receptacle has been observed. No mature oocytes or sperm have been seen at or near the female gonopore.

Testes

The testes originate in the posterior portion of the 7th trunk appendage and extend to about the 10th. They are paired organs which lie dorsolateral to the midgut (Fig. 24). The outer surface is covered with thin, squamous epithelium. Clusters (cohorts) of cells at various stages of spermatogenesis can be observed in the testis of G. frondosus (Fig. 25A). The cells within each group appear to be in the same stage of differentiation. At least four cell types are apparent: 1) the nucleus is about 10-11 um in diameter with several nucleoli and a few scattered clumps of condensed chromatin throughout as well as along the edge of the nuclear envelope; 2) the nucleus is about 9-10 um in diameter, more dense, with several clumps of condensed chromatin equally throughout; 3) the nucleus is about 11-12 um, with a homogeneous distribution of dense chromatin. 4) the nuclear diameter is smaller, about 5-6

Figure 24. Diagrammatic representation of a cross section of the male reproductive system.

Abbreviations:
c = circulatory vessel
g = midgut
m = muscle
n = ventral nerve cord
t = testes

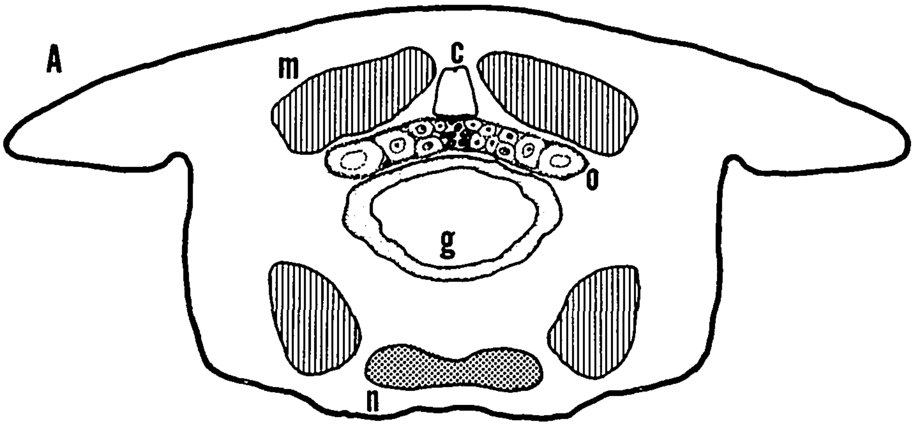

A
m
c
o
g
n

Figure 25. Testes

A. Testis of *Godzilliognomus frondosus*, with groups of cells at various stages of spermatogenesis.

B. Testis of *Speleonectes benjamini*


a


B

um in diameter, and is mostly condensed, darkly staining chromatin throughout. Mitochondria are present in the granular cytoplasm of all cell types observed.

The testes of Speleonectes benjamini (Fig. 25B) produce young spermatids with a round nucleus about 4-5 um in diameter (Yager, 1989a). Young round spermatids of Godzilliognomus frondosus also have a diameter of about 4-5 um. A flagellum with a distinct 9 + 2 microtubule arrangement and a diameter of 0.15 um was present in young spermatids of G. frondosus. Associated with the developing gametes are accessory cells located between the clusters of differentiating cells. These cells are known as Sertoli cells in vertebrates, and are called accessory, nutritive, nurse, follicle, or support cells in invertebrates. They are thought to play a role in the nutrition and mechanical support of the germ cells (Blades-Eckelbarger and Youngbluth, 1982). The accessory cells have irregularly shaped nuclei with small scattered clumps of heterochromatin, and the cytoplasm is less dense than that of the gametes.

At about trunk segment 10 there is a transition between testes and vas deferens. The squamous epithelial cells become cuboidal. In this area the young spermatids of S. benjamini and G. frondosus change from a round shape to an elongate one.

Vas deferens

The paired vas deferens (Fig. 26) are continuous with the testes and extend lateral to the midgut from about trunk segment 10 to 14. At the 14th trunk segment they pass ventrolaterally to the gonopore. Cuboidal epithelial cells (see Fig. 26A) surround the lumen of the vas deferens. They have a large, round to ovoid nucleus with a diameter of about 6 um, and they secrete a homogeneous, PAS-positive material into the lumen. From about trunk segment 10-12 the lumen is filled with elongate spermatids (Fig. 26A) measuring about 8-10 um in length and 3-5 um wide at the head end. The tail end is tapered and flagella are visible. The nucleus is Feulgen-positive and the acrosome is eosinophilic. As the spermatids mature and move toward the posterior portion of the vas deferens, they are bound into spermatophores. Spermatophores were found in specimens of *S. benjamini* in June and September 1987, and March 1988. Spermatophores were recorded from *G. frondosus* in specimens collected in March, 1987.

Spermatophore ultrastructure

Spermatophores (Figs. 26B, 27) form in the posterior portion of the vasa deferentia at about trunk segment 12 (Yager, 1989a). The lumen of the vas deferens increases in size to hold the spermatophores as well as a large volume of homogeneous PAS-positive flocculent material, probable mucopolysaccharides, as indicated by the PAS reaction. The

Figure 26. Vas deferens of _Speleonectes benjamini_

A. Vas deferens with elongate spermatids in lumen. (H & E stain)

B. Vas deferens with spermatophores. (PAS reaction)

A

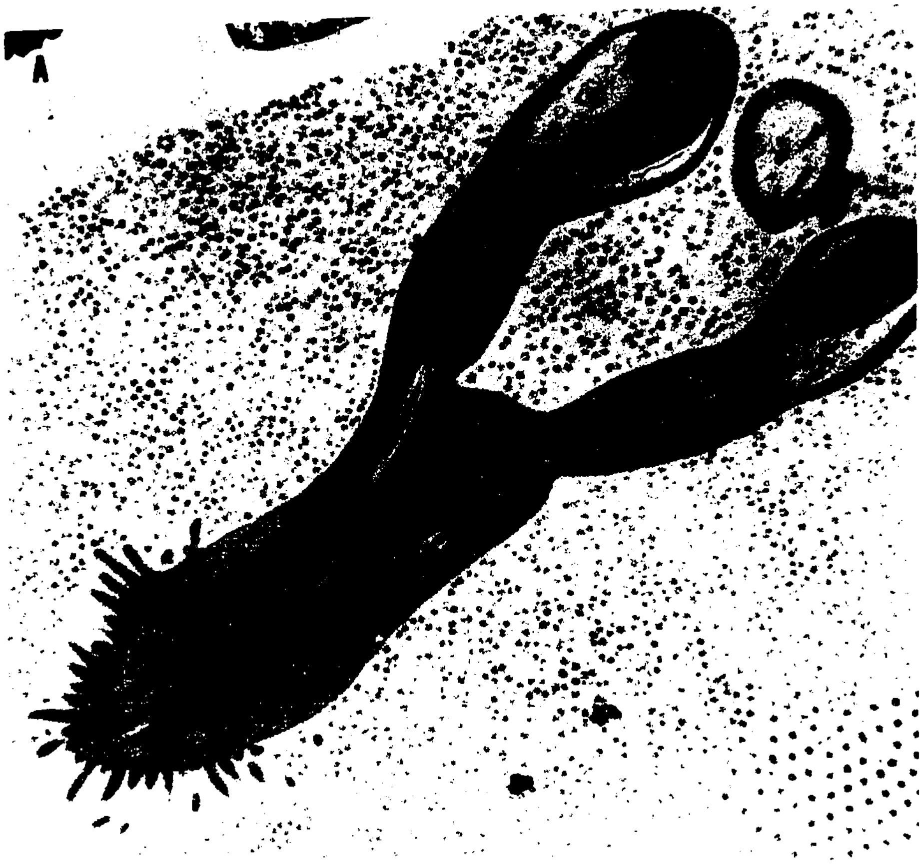
B

Figure 27. Spermatophore of _Speleonectes_ _benjamini_.

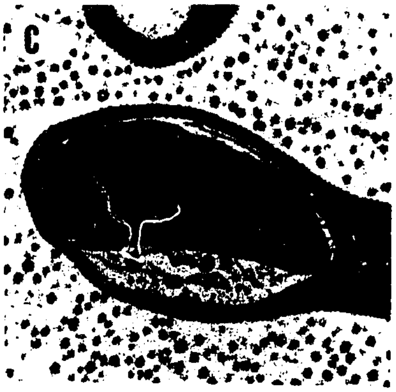
A. Entire spermatophore, about 38 um

B. Nucleus with cup-shaped acrosome

C. Nucleus with acrosome and possible acrosomal filament or rod


A


B


C

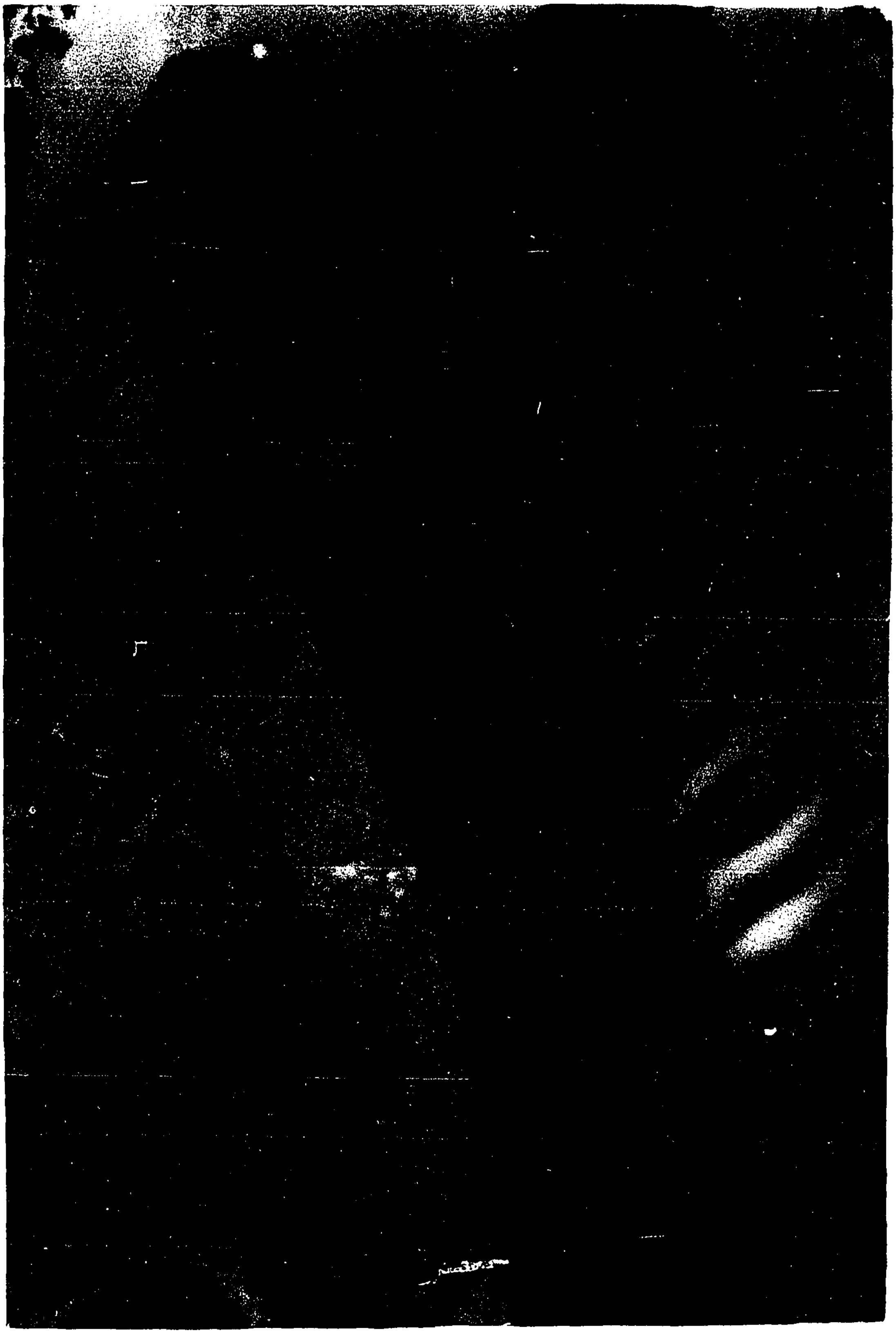
exact number of sperm per spermatophore has not yet been determined. Based on the number of visible flagella, the spermatophores of <u>Speleonectes benjamini</u> appear to hold from three to six sperm cells (Figs. 26B, 27A). The sperm nuclei are in separate extensions at one end of the spermatophore and their flagella extend into the single distal end. The distal portion is covered with small, cylindrical villi-like projections (see Fig. 27A). The small projections may serve as some sort of a coupling device to attach the spermatophores in or near the female gonopore. The spermatophore is about 38 um in length, PAS-positive and lacks a discernable membrane. Around the small distal projections the spermatophore is more PAS-positive. Differential staining adjacent to the projections is also evident at the TEM level (see Fig. 27A). The spermatophores of <u>G. frondosus</u> are similar in appearance to those of <u>S. benjamini</u>. However, they are shorter, approximately 22 um in length and appear to have only one or two sperm packaged into the proximal end. Flagella can be seen extending into the distal end of the spermatophore of <u>G. frondosus</u>, and the similar villi-like extensions are present.

The mature sperm of <u>S. benjamini</u> have an ovoid nucleus, cup-shaped acrosome, and flagellum with a 9 + 2 microtubular arrangement. The large, ovoid nucleus measures about 8-9 um by 5 um. The cup-shaped acrosome (see Fig. 27B) has granular bands of what may be actin in the subacrosomal space. What looks like an acrosomal filament or rod (see Fig. 27C) extends through the length of the nucleus. Centriole-like structures have been found in the distal portion of the sperm head. In the spermatophore, the flagellum (Fig. 28) appears to loop around the nucleus before extending into the distal end of the spermatophore. Several mitochondria are present in the cell, but because they did not fix well, no details are available. Although motility has not been confirmed, the arrangement of cellular ultrastructure suggests that the sperm are capable of movement.

Comparison of crustacean sperm morphology

Studies of crustacean sperm reveal a great diversity of sperm structure. In many cases sperm morphology can solve doubtful points of systematics and phylogeny (Brown, 1970; Wingstrand, 1978). The basic or generalized sperm model includes four features: an ovoid nucleus, acrosome, mitochondria, and flagella with a 9 + 2 microtubular arrangement. This basic sperm is well represented in the phylum Arthropoda and is considered conservative (Baccetti, 1970, 1979; Franzen, 1970, 1979). Any loss of the four structures probably constitute an irreversible evolutionary step (Brown, 1970). The Branchiopoda, Cephalocarida, Ostracoda, Copepoda and Malacostraca possess varied and/or aberrant sperm which lack flagella. Until this study only four crustacean groups were known to possess flagellate

Figure 28. Spermatophore of *Speleonectes benjamini*. Note flagellum extending from nuclear area into distal end of spermatophore.



sperm: the Branchiura, Cirripedia, Mystacocarida, and Ascothoracida (Grygier, 1981). The first three groups have flagellated sperm which deviate in some way from the conventional sperm model (see reviews by Adiyodi, 1985; Grygier, 1981; Pochon-Masson, 1983). Grygier (1981, 1982) described the sperm of Ascothoracida as having the most generalized sperm morphology known in Crustacea. Although generalized in other aspects, ascothoracid sperm is characterized by a cylindrical nucleus. The mature sperm of Speleonectes benjamini seem to resemble the basic sperm model with ovoid nucleus, acrosome, and simple flagellum. The remipede sperm contain several mitochondria, but a distinct arrangement of them is not evident. Two centrioles are found in the mid-piece of most invertebrate sperm. In this study only one centriole-like structure was observed. The ultrastructure of the flagella of S. benjamini shows a 9 + 2 microtubular arrangement. Although motility of remipede sperm has not been confirmed, the morphology observed is consistent with that of other motile sperm.

The horse-shoe crab Limulus (Subphylum Chelicerata, Class Merostomata) is the only arthropod considered to have the more generalized sperm morphology representing the basic sperm model (Fahrenbach, 1973; Baccetti, 1979). The sperm of S. benjamini appears to more closely resemble that of Limulus than the sperm of any other crustacean.

At present, the very limited amount of material of most species precludes a detailed and comprehensive study of Remipedia reproductive systems. Evolutionary inferences based on comparative sperm morphology therefore cannot be made. However, ultrastructural studies of the sperm and spermatophores from the recently described remipede *Godzilliognomus frondosus* is in progress. The results should give information that will provide a better understanding of the relationships within the Remipedia, among the Crustacea, and perhaps the arthropods in general.

With its wide array of primitive characters and no close alignment with any other crustacean class, the Remipedia have been placed at the base of the crustacean phylogenetic tree (Schram, 1986). The structure of the sperm of *Speleonectes benjamini* and *Godzilliognomus frondosus* indicates that at least two members of the group have retained primitive features in their reproductive biology.

Male gonopore

The male gonopore (Fig. 29) is a protuberance appearing at the posterior base of the protopod on the 14th trunk appendage. The anatomy differs slightly among species. For example, in *S. benjamini* the male gonopore lies beneath an extension of the protopod (Fig. 29B). The gonopore of *Pleomothra apletocheles* is a simple bulbous structure (Fig. 29C). The gonopore of *Godzilliognomus frondosus* is located on the underside of a huge lateral

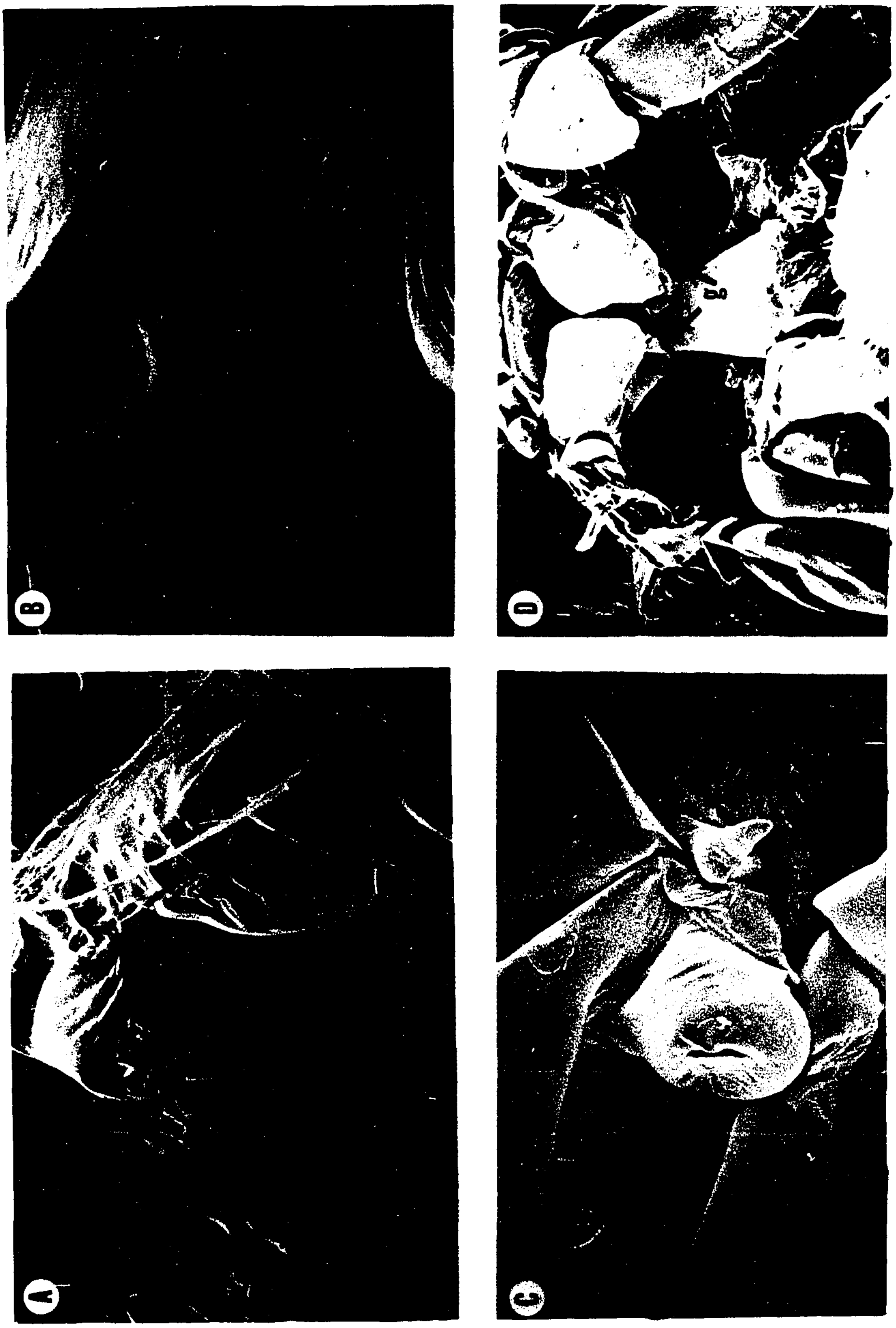
Figure 29. Male gonopores.

A. *Speleonectes lucayensis*, 311x. Note genital plate beneath each gonopore.

B. *Cryptocorynetes haptodiscus*, 276x

C. *Pleomothra apletocheles*, 142x

D. *Godzilliognomus frondosus*, 217x. Note porous genital plates beneath gonopores. g = gonopore


A
B
C
D

extension of the protopod (Fig. 29D).

Genital plate

Associated with the male gonopore is a genital plate. It has been detected using SEM for *Speleonectes lucayensis*, *S. tulumensis*, *S. benjamini*, and *G. frondosus* (see Figs. 29A, D). This plate is located posterior to the gonopore between the 14th and 15th trunk segments. The plate is oblong in shape, approximately 160 x 200 um in *S. tulumensis* and 150 x 200 um in *G. frondosus*. The surface is covered with many small pores. In *S. tulumensis* and *S. lucayensis* small, hollow-tipped sensilla-like structures emerge from the pores. In *G. frondosus* and *S. benjamini* the pores lack sensilla-like structures and appear secretory in nature. It is possible that the structures are present but retracted into the pores. Internally the plate is associated with columnar epithelial cells. The function of this plate is unknown. Perhaps the secretions form a kind of glue for egg or spermatophore attachment. However, every remipede specimen collected to date has been examined and no eggs or spermatophores have been found attached outside the body.

Development

To date, nothing is known about remipede development. Neither fertilized eggs nor embryos have yet been seen. In general, cave animals produce fewer, larger offspring. Although there is no direct evidence, it is hypothesized that remipedes have direct development. Support for this hypothesis is the fact that even the smallest juvenile collected to date has more than 14 trunk segments, and hence both male and female gonopores. In addition, remipedes appear to produce only a few large oocytes, another indication of direct development.

Three age classes have been determined in remipedes based on the number and shape of trunk segments, total body length, and biomass. Juveniles and sub-adults of several species have been collected. The juvenile and sub-adults can be recognized by their rounded tergites, while adult tergites are shorter and wider, giving a subrectangular appearance (Fig. 30). Juveniles are basically miniature copies of the adults but about one-third or less as long. Sub-adults have increased in length and are more than half the length of adults. However, they still retain the rounded tergites. Table 4 gives size and segment number comparisons for all apparent adults and for the smallest individuals collected to date.

Figure 30. Diagrammatic representation of three probable age classes of remipedes: adult, sub-adult and juvenile.

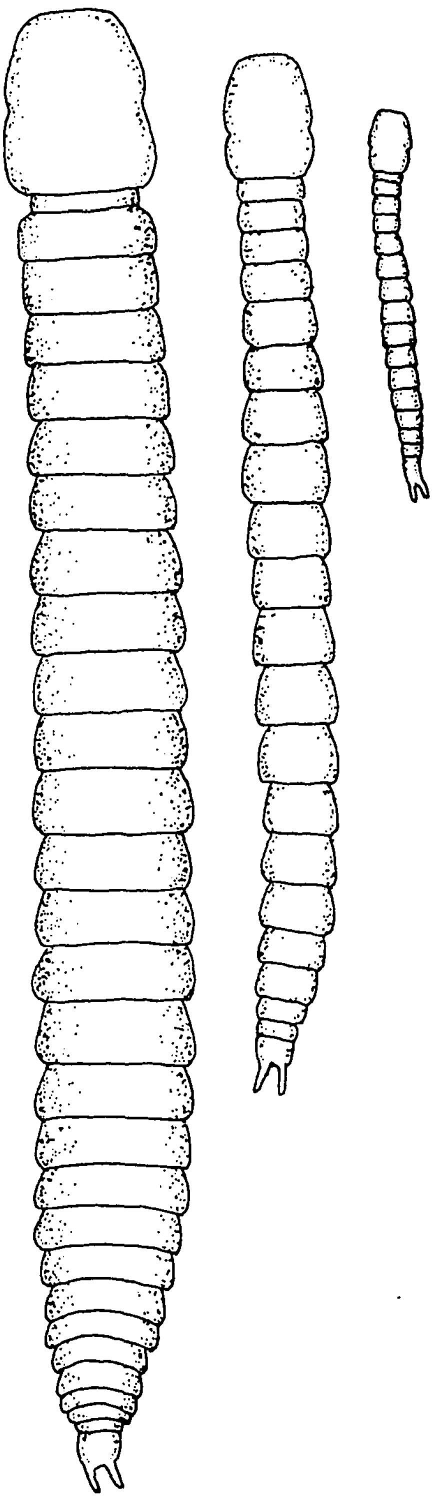


Table 4. Comparisons of trunk segment number and length of largest adult with smallest juvenile or subadult found for all species to date.

Species	Trunk segment number adult/juvenile	Total body length adult/juvenile
Speleonectes benjamini	27/20	18.0 mm/ 4.9 mm
Speleonectes lucayensis	32/16	24.0 mm/ 4.0 mm
Speleonectes ondinae	25/20	16.7 mm/10.1 mm (sub)
Speleonectes tulumensis	38/17	30.2 mm/ 7.2 mm
Cryptocorynetes haptodiscus	31/28	17.6 mm/ 9.7 mm (sub)
Lasionectes entrichoma	32/16	32.8 mm/ 9.0 mm
Godzillius robustus	29/26	45.1 mm/25.7 mm (sub)
Godzilliognomus frondosus	16/15	9.3 mm/ 3.7 mm
Pleomothra apletocheles	25/16	17.1 mm/ 5.2 mm

Reproductive behavior, a hypothesis

Remipedes have not been observed mating. They lack copulatory processes found in other crustaceans such as appendix masculina or penes. The animals have a very flexible body capable of assuming positions needed to facilitate copulation or spermatophore transfer. Ito and Schram (1988) hypothesized that the female gonopore pad is depressed inward by the male gonopore complex during copulation allowing eggs to be released while being fertilized.

Details of spermatophore morphology and further study of reproductive anatomy allow an additional hypothesis to be made. I propose that copulation may not take place. Instead, fertilization may be indirect by spermatophore transfer. The female gonopore of Speleonectes benjamini (see Fig. 23A) is about 72 um wide and 75 um in depth. The male gonopore complex (see Fig. 29A) is approximately 130 um wide. Measurements of the gonopores of several species indicate that for the most part, the male gonopore complex is wider than the female gonopore opening by almost half. Thus the ability to push the cuticular pad inside by insertion of the male gonopore complex may not be anatomically possible. The gonopore complex of Godzilliognomus frondosus is on the underside of a large triangular extension of the protopod which would have to be lifted up during copulation to expose the actual gonopore (see Fig. 29D). Also, because chitin lacks elastic properties, direct copulation may not be possible unless it occurs during a molt. I suggest that spermatophores are transfered from the male gonopore to the female gonopore by use of the prehensile second maxilla and/or maxilliped. In all species these appendages have a distal semicircular claw complex with a fleshy, subterminal thumblike pad (see Fig. 8). The pad bears long setae with finely serrate tips. The entire arrangement may be a modification that aids in sperm transfer. As spermatophores are released from the male gonopore they might be gathered by the second maxilla and/or maxilliped and adhere to the setae of the thumblike pad. The claw complex of S. benjamini is about 72 um wide, nearly matching the width of the female gonopore. The claws could hook into the top of the female gonopore while the thumblike pad pushes inside and spermatophores would then be deposited in the opening. The area of villi-like extensions of the spermatophore (see Fig. 27A) may serve as an adhesive or coupling device to keep the spermatophores in the oviducts. The spermatophore layer could then dissolve and the sperm swim to the oocytes where fertilization would occur. The claw complex might also be used to transfer eggs to the genital plate after fertilization. Another possibility is that the eggs are transferred from the female gonopore to the genital plate where they are held in place by secretions from the plate and externally fertilized. Internal fertilization would seem more likely, however, since each spermatophore bears only a few spermatozoa.

Chapter 4. GENERAL ASPECTS OF INTERNAL ANATOMY

Because sectioned material was examined while studying the reproductive system, additional information was learned about the internal anatomy of remipedes in general. It is included below.

Nervous system

The nervous system of remipedes consists of a well-developed supraesophageal ganglion (or brain) and a simple, ventral, ladderlike nerve cord. The ventral nerve cord extends the length of the trunk and bears a pair of ganglia on each trunk segment. The pre-antennal processes have dendrites leading to them from the brain indicating a probable sensory role (see Itô and Takenaka, 1988). Nerve fibers have also been observed leading out into the esthetascs of the first antenna. Studies of the innervation are incomplete.

Digestive system

The foregut extends from the mouth to about the level of the maxilliped. It can be distinguished from the midgut by the chitinous lining. Surrounding the mouth area or foregut are a series of large muscle bands which extend in several directions. The midgut is a simple tube extending the length of the trunk. The midgut has paired lateral diverticula in each trunk segment. Gut material appears to be an amorphous "soup". On occasion the midgut of individuals is filled throughout with a yellowish material but no distinct food items have ever been distinguished. Gregarines have been observed throughout the midgut of *S. tulumensis*, *S. benjamini*, and *G. frondosus*. These sporozoans are common crustacean parasites and have been described in considerable numbers, especially from decapods (Sprague, 1970). Evidently they are not especially harmful to their hosts.

The midgut cells of *Godzilliognomus frondosus* are large in comparison to *S. benjamini* due to the presence of vacuoles full of huge drops of apparent lipids. Lipidlike droplets in the midgut at trunk segment 12 measured up to 275 um in diameter for *G. frondosus*, while at the 12th trunk segment of *S. benjamini* most droplets were about 3-14 um. Exocytosis of the vacuoles apparently occurs, as the same lipidlike drops are present in the lumen of the midgut of *G. frondosus*. These lipidlike droplets are very evident when the animal is dissected because they leave the body and float around in the dissecting fluid. At the anal segment a short hindgut terminates in the anus.

Excretory system

A well-developed pair of maxillary glands lies in the posterolateral part of the head and terminates in excretory papilla on the second maxilla.

Circulatory system

The circulatory system of crustaceans is generally an open system with hemolymph flowing freely in the body cavity (McLaughlin, 1983). The presence of a heart in remipedes has not yet been confirmed by microscopy. Remipedes have a single, thin-walled dorsal vessel which extends the length of the body and appears to be circulatory in structure. Amebocytes have been found scattered throughout the hemolymph. Circulation of the blood is no doubt aided by metachronal swimming movements.

Respiratory system

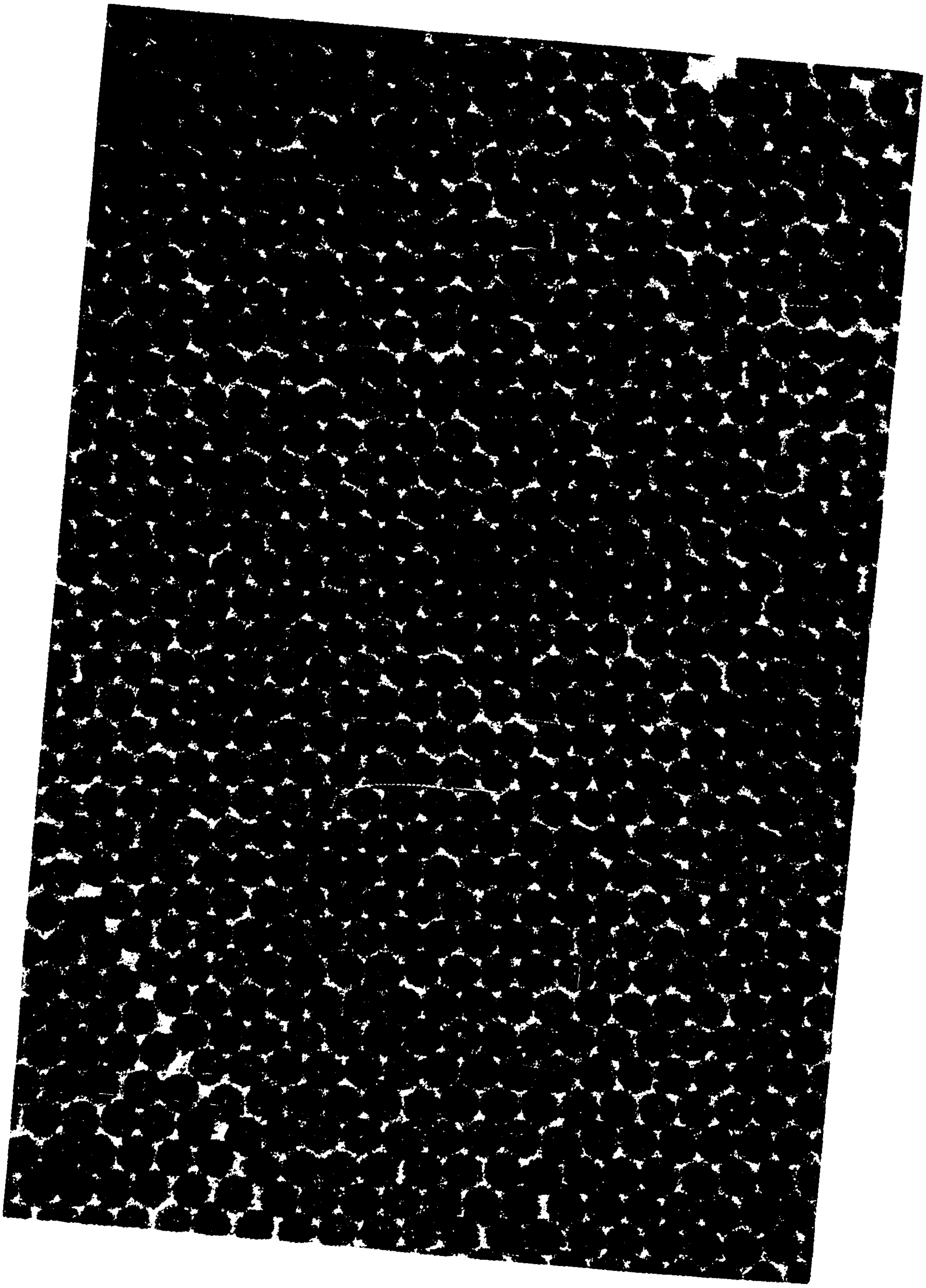
In most non-malacostracan crustaceans respiration takes place across the integumental surfaces (McLaughlin, 1983). Remipedes do not have specialized respiratory structures such as gills. Their broad paddle-like trunk appendages probably serve as the primary respiratory surfaces. *Godzilliognomus frondosus* has been observed to pump water anally during microscopic observations. Anal intake of water has been reported for a number of small crustaceans and has been considered a respiratory function, especially in water deficient in dissolved oxygen. However, Fox (1952) disputed the respiratory function and hypothesized that anal pumping serves as a type of natural enema for small crustaceans. Dall (1967) considered anal intake of water to be a type of gut osmoregulation, especially for gill-less microcrustaceans (for a review of crustacean osmotic and ionic regulation see Mantel and Farmer, 1983). To date, G. frondosus is the only remipede species observed to take in water through the anus, and it is the only species with the chitinous extension of the anal opening (see Fig. 9). Perhaps this highly folded structure serves to filter water being anally pumped into the gut.

Two remipede species examined (S. benjamini and G. frondosus) have large hemocyanin crystals (Figs. 31, 32) scattered throughout the tissue of head and swimming appendages. Hemocyanin, an oxygen-binding respiratory pigment, has been recorded in some but not all crustacean classes (for a review see Mangum, 1985). Crustacean hemocyanins occur extracellularly and have a high molecular weight (Snyder and Mangum, 1982).

The remipede hemocyanin crystals are nearly identical in appearance to hemocyanin crystals present in the horseshoe crab Limulus (Fahrenbach, 1970; Bijlholt, et al., 1982). In Limulus hemocyanin accumulates in numerous crystalline arrays which are produced in a special cell called a cyanoblast. When the cyanoblast is full it ruptures and releases hemocyanin crystals into the hemocoel (Fahrenbach, 1970). Limulus crystals are made up of hexagonally packed hollow-appearing cylinders which have a diameter of about 190 Å and a center-to-center spacing of

Figure 31. Large hemocyanin crystal in maxilla 2 of *Cryptocorynetes haptodiscus*, 33,000x. Arrow indicates rod-shaped bacteria.

Figure 32. High magnification of hemocyanin crystal of *Cryptocorynetes haptodiscus*, 116,000x.



260 Å. Remipede crystals are also composed of hexagonally packed hollow-appearing cylinders. The cylinders in both *C. haptodiscus* and *S. benjamini* have a diameter of about 600 Å. The center-to center spacing of *S. benjamini* is about 700 Å and about 750-800 Å for *C. haptodiscus*. This is three times the diameter of the crystals in *Limulus*! Some of the crystalline structures appear to be within a membrane-bound cell similar to what Fahrenbach (1970) calls a cyanocyte while other remipede crystals appear to be free in the tissue. The cylinders are stacked longitudinally.

Finding these hemocyanin-like crystals in the appendage tissue of remipedes may solve the intriguing question of their respiratory exchange in a nearly anoxic environment. Oxygen diffusion capacity is reduced by salinity, and it has reduced diffusibility across chitin (McMahon and Wilkens, 1983). Remipedes continually swim in the water column. Special mechanisms must exist which facilitate their oxygen uptake and transport. One mechanism may be the increased surface area on the broad segments of their paddlelike swimming appendages. The other mechanism is the presence of hemocyanin which removes oxygen from solution in the hemolymph and transports it. The constant body movement of the animals would maintain sufficient hydrostatic pressure to aid in hemolymph convection.

The ostracodes collected in Sagittarius Cave from low O_2 water were bright pink, but they faded when brought to the surface. A similar phenomenon was discovered accidentally by Fox (1945) when he looked at a Daphnia culture that had been kept in a closet. He found that a decrease in oxygen increased the hemoglobin. Therefore he hypothesized that the color change was brought about by a higher oxygen content of cultures kept in the light due to algal photosynthesis and an oxygen deficit in the dark. This is an excellent example of the production of a respiratory pigment in response to lowered oxygen that has since been confirmed in crayfish and lobster (Butler, et al., 1978; McMahon, et al., 1974) as well as other crustaceans.

Miscellaneous observations

While studying TEM micrographs of various body parts, rod-shaped bacteria (see Fig. 31) were observed in the tissue. They are loosely scattered throughout the tissue and do not appear to be associated with any particular cell type. The bacteria are approximately 0.3 um wide and 1.4 um long. It is interesting to speculate that this may be a situation analogous to thermal vent animals which have chemoautotrophic symbiotic bacteria living in their tissues (see Cavanaugh, 1985). The implications certainly warrant further study.

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EPILOGUE

Anchialine caves with their unique inhabitants and characteristics are threatened world-wide. In fact, almost all cave habitats are in danger. The land above these caves is being developed. Deforestation, bulldozing, and massive construction are destroying the recharge zone for freshwater aquifers. Pollution of groundwater from pesticides, waste disposal, chemical spills, and faulty septic systems is occurring. Many caves in the Bahamas have already been altered by saltwater intrusion caused by over-withdrawal of fresh water for drinking purposes. In addition to the above threats to submerged caves, there is also increased pressure from overuse by cave divers. The challenge of cave diving as well as the beauty of submerged caves is attracting more divers. The demand for more dive sites, especially ones that are highly decorated, is increasing. Those divers not properly trained in buoyancy control can break delicate speleothems and stir up sediment. There has been no study on the longterm effects of continual disturbance of the density interface. It is possible that more oxygen is released by a diver on one dive than has been present in the cave for thousands of years! Constant mixing of the two waters by divers could destroy the density interface and its diffusion barrier properties, thus affecting the community of organisms.

There are no laws that specifically protect submerged caves in the Bahamas or in Mexico. Fortunately the government of The Turks and Caicos is taking steps to protect anchialine and other caves in this tiny country. At the time of this writing, only one cave system out of thousands in the Bahamas has any kind of protection -- Lucayan Cavern is part of a national park. Public education and conservation ethics must go hand in hand with scientific endeavors. Habitats must be properly protected and managed. Hopefully, remipedes and their remarkable environment will provide fascinating areas of investigation for decades to come.

This dissertation cannot end without a few words on cave diving. Although I would like to encourage research in the exciting field of aquatic speleology, I don't want the excitement of biological discoveries and potential research to lure untrained divers into submerged caves. Submerged cave are deceptively alluring. They are extraordinarily beautiful. The water is usually crystal clear, it looks easy, and the challenge to enter becomes enticing. Every year due to a lack of judgment trained scuba divers and even scuba instructors die unnecessary and horrible deaths in caves. There are fewer than a thousand trained cave divers on the entire planet and we take our sport very seriously. To err in judgment will result in death. Cave diving requires not only extra and special equipment, but a certain non-ego threatening mind set. It is not a sport for machismo.

In the United States there are two excellent cave diving training organizations: the Cave Diving Section of the National Speleological Society (NSS) and the National Association for Cave Diving (NACD). For further information please contact:

NSS Cave Diving Section
P.O. Box 950
Branford, FL 32008

or

NACD
P.O. Box 14492
Gainesville, FL 32604

AUTOBIOGRAPHICAL STATEMENT

Jill Yager was born on November 20, 1945, in Louisville, Kentucky. She received her B.S. in Biological Sciences from Colorado State University in June, 1967 and earned her M.S. in Science Education -- Biology in 1982 from Florida Institute of Technology. She has authored or co-authored the following papers:

BOWMAN, T. E., ILIFFE, T.M., and J. YAGER. 1984. New records of the troglobitic mysid genus Stygiomysis: S. clarkei, new species, from the Caicos Islands, and S. holthuisi (Gordon) from Grand Bahama Island (Crustacea: Mysidacea). Proc. Biol. Soc. Wash. 97(3): 637-644.

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KORNICKER, L.S., YAGER, J., and D. WILLIAMS. Ostracoda (Halocyprididae) from anchialine caves in the Bahamas. Smithsonian Contrib. Zool., in press.

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YAGER, J. and D. WILLIAMS. 1988. Predation by gray snapper on cave bats in the Bahamas. Bull. Mar. Sci. 43(1): 102-103.

PROFESSIONAL AFFILIATIONS:

Biological Society of Washington
National Association of Cave Divers (NACD)
National Speleological Society (NSS)
Phi Kappa Phi Honor Society
Sigma Xi, The Scientific Research Society
The Crustacean Society

Director of Research, Island Caves Research Center, P.O. Box 490462, Key Biscayne, FL, 1987 to present.

Member of the Cave Species Specialist Group, International Union for the Conservation of Nature and Natural Resources (IUCN), 1985 to present.

Treasurer of the Latin American and Caribbean Federation of Speleology, (FEALC), 1983-1988.

Scientific advisor, Bahamas National Trust, Freeport Committee, 1985-1988.

Biology advisor, NSS Cave Diving Section, 1986 to present.

Collaborator in the Department of Invertebrate Zoology, National Museum of Natural History, 1987 to present.

GRANTS AWARDED:

Cave Research Foundation, Karst Research Fellowship, 1985.

American Museum of Natural History, Lerner-Gray Fund for Marine Research, 1986.

National Speleological Society, Ralph W. Stone Award, 1986.

National Speleological Society Cave Diving Section, 1987.

Old Dominion University, Department of Biological Sciences, 1984-1988, doctoral research fellowship.

Big blue hole out in the ocean
Where I dive straight down until I cannot see
Feel my way through a bevy of solutions
There I realize the answer is in me.

Jimmy Buffett, 1989