The remarkable diversity of subterranean Cirolanidae (Crustacea: Isopoda) in the peri-Caribbean and Mexican Realm

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We dedicate this paper to the memory of Jan H. Stock, indefatigable promoter of stygobiological research in the West Indies, almost ten years after his untimely death.

Abstract

With 42 endemic species (one of them with two subspecies) described to this day, most of them belonging to 11 endemic genera, the peri-Caribbean – Mexican zone has definitely the richest fauna of stygobitic (entirely subterranean-adapted) cirolanids of the world. After a succinct presentation of the various habitats for stygobitic cirolanids in the zone, the species are grouped together (Table 1) according to their affiliation to habitats of freshwater or of marine water – water salinity being considered the most reliable common denominator. A check-list in alphabetical order follows, including references, known distribution, information on habitats, etc. That this is a case of very high biodiversity of stygobitic Cirolanidae results from comparison with the situation in the rest of the world. Some aspects of morphology in relation to systematics are reviewed (i.a.: evolutive significance of some morphological adaptations; monophyly of stygobitic genera). Attempts are made to reply to questions like: what can we know about ancestors of stygobitic species? Can age of stygobitic taxa, or lineages, be appreciated with some degree of reliability? What can we guess about the roots of present-day diversity (two types of habitat requiring different explanation for time and mode of groundwater colonization being recognized)? How deep are these roots? What is the legacy of Tethys? This case of high biodiversity could be explained through the rich, turbulent history of this vast and fragmented area; through the abundance and extraordinary diversity of habitats propitious for stygoevolution; and through the (supposed) abundance and high diversity of potential marine ancestors. A final part of the paper is devoted to endangered or already destroyed habitats and fauna, with a plea for protection.

Key words: stygobitic Cirolanidae, Caribbean-Mexican area, subterranean aquatic habitats, biodiversity, stygoevolution

Résumé

Avec 42 espèces endémiques actuellement décrites (une de celles – ci avec deux sous-espèces), appartenant pour la plupart à 11 genres endémiques, la zone Caraïbe-Mexicaine possède sans doute la faune de cirolanides stygobies la plus riche du monde. Après une présentation succincte des divers habitats peuplés par des cirolanides stygobies dans la zone, les espèces sont groupées (Tableau 1) d'après ces habitats: eau douce ou eau marine – la salinité de l'eau étant considérée comme dénominateur commun le plus digne de confiance. Une liste des taxons en ordre alphabétique présente les références, la distribution connue, des informations sur les habitats, etc. Une comparaison avec la situation pour le reste du globe montre qu'il s'agit ici d'un cas de biodiversité remarquablement grande. Sont passés en revue plusieurs aspects concernant des relations entre morphologie et systématique (signification évolutive de certaines adaptations morphologiques; monophylie des genres stygobies). On essaie de fournir des réponses à des questions comme: qu'est-ce que peut être connu sur les ancêtres des espèces stygobies? Est-ce que l'âge des taxons (ou des lignées) stygobies peut être apprécié avec un certain degré de certitude? Qu'est-ce qu'on peut supposer concernant les racines de la diversité actuelle (deux types d'habitat demandant des explications différentes pour le temps et la modalité de la colonisation des eaux souterraines étant distingués)? Combien profondes sont ces racines? Quel est, dans ce cas concret, l'héritage de la Tethys? Ce cas de biodiversité pourrait être expliqué par l'histoire riche et mouvementée de cette zone vaste et fragmentée; par l'abondance et l'extraordinaire diversité des habitats propices à la stygoévolution; ainsi que par l'abondance et la diversité (supposées) des ancêtres marins potentiels. Une section finale du travail est consacrée aux habitats et à la faune menacés ou déjà détruits.

Mots-clés: Cirolanidae stygobies, zone Caraïbe-Mexicaine, habitats aquatiques souterrains, biodiversité, stygoévolution.

Introduction

Although the first subterranean cirolanid isopod of the Caribbean – Mexican zone was discovered more than one century ago, it was only during the last half of the previous century that research on this group of stygobitic crustaceans has assumed large proportions, thanks to increasing interest in speleology and stygobiology and to improving techniques for exploration and zoological sampling. This has led to discovery and description of a remarkable large number of species entirely bound to subterranean aquatic habitats of various kinds, making this zone the most extraordinary "hot spot" of the world for stygobitic Cirolanidae. The time seems to be ripe for attempting a synthetic presentation of known facts, focusing on diversity and its possible explanation, in a naturalistic spirit, and limiting to a minimum reasonable speculation not dictated by fashions. In order to avoid this paper taking exaggerated proportions, almost no reference to stygobionts other than Cirolanidae and to "generalized tracks" will be made. Also reference to publications not directly dealing with Cirolanidae has been limited to some of

those shedding more light on aspects directly concerning the present paper.

The stage

The zone dealt with in this paper is called "Caribbean-Mexican basin" by ARGANO (1972), "The (sub) tropical Atlantic" by STOCK (1994), "the Central American/Caribbean intermediary areas" by BANARESCU (1995), or "Western Atlantic" by BRIGGS (1995) – who distinguishes here a "West Indian Province" and a "Caribbean Province". The wording used in the title is from Stygofauna Mundi (BOTOSANEANU, 1986). Stygobitic cirolanids of the peri-Caribbean – Mexican zone inhabit wholly or partially submerged caves and groundwater of varying salinity, all situated in karstic limestone. Due to locally characteristic differences in habitat type, each area within the zone will be considered separately. Generalized descriptions of habitat, geological setting, hydrology, water quality, and cirolanid stygofauna will be presented. Distribution of cirolanid species within the zone is illustrated in Fig. 1.

Bermuda is a mid-Atlantic volcanic seamount, capped with Pleistocene aeolian and marine limestone. Karstic caves in Bermuda are concentrated in a small area of the island where the oldest limestone outcrops. Tidal, sea level pools occur at entrances and in the dark interior of the caves. Although the upper (dry and shallow submerged) portions of Bermuda caves are dominated by collapse features, extensive horizontal passage development typically occurs at 18 m depth. The presence of large speleothems (stalactites, stalagmites, etc.) in all parts of the underwater caves indicates that the entire known portions were completely dry and air-filled for long times during glacial periods of lowered sea level. While surface waters in Bermuda's cave pools range from slightly brackish to nearly fully marine, deeper waters below about 3-5 m depths approach fully marine salinities. One stygobitic cirolanid, *Arubolana aruboides*, is known from Bermuda.

The Bahamas archipelago consists of a series of shallow banks made up of a continuous, up to 5700 m thick, sequence of carbonates of shallow water origin which began depositing during the Jurassic. As the banks gradually subsided, carbonate deposition has kept pace, maintaining a shallow water environment. The banks are separated from one another by deep water channels reaching 2,000 m depths. Water-filled caves in the Bahamas are locally referred to as "blue holes". Inland blue holes occur in the interior of islands, while ocean blue holes are situated offshore, in shallow water. While many inland and ocean blue holes are karstic sinkholes with no passage development, others are parts of an extensive network formed either by limestone dissolution at the fresh/salt-water interface (flank margin caves) or by slump faulting occurring along the platform margins (fault line caves). Ocean holes typically have reversing, high velocity, tidal currents which flush the caves with seawater, while inland caves lack perceptible currents and have a fresh to brackish water lens overlying fully marine waters. Stygobitic fauna of the Bahamas includes seven species of cirolanids from three genera, *Bahalana*, *Cirolana* (subgenus *Cirolana*) and *Exumalana*. The northern coast of the Yucatan Peninsula is composed of

Pleistocene and Holocene limestone, while Miocene to Eocene age rocks are exposed in the interior. Northern Yucatan is generally low, with little relief, and surface rivers or streams are absent. Water-filled caves are locally referred to as cenotes, a Spanish corruption of the Mayan word "dzonot". The most extensive underwater cave systems in the world are located along the eastern Caribbean coastline, with Systema Ox Bel Ha at 130 km being the world's longest. In the interior of the Peninsula, a well defined semicircle of cenotes, mostly in the form of deep sinkholes, outlines the deeply buried rim of the 65 million year old Chicxulub impact crater. Groundwater throughout the Peninsula consists of a fresh water lens of varying thickness, floating on top of denser seawater. The depth of the halocline boundary between fresh and saltwater varies from 10 m depth along the coast to more than 60 m in the interior. The stygobitic fauna of Yucatan thus includes both freshwater and marine species. Seven species of stygobitic cirolanids from five genera, *Metacirolana*, *Cirolana* (subgenus *Anopsilana*), *Creaseriella*, *Haptolana* and *Yucatalana*, have been described from the Yucatan Peninsula (including Cozumel and Belize).

The Greater Antilles consist of the four large islands of Puerto Rico, Hispaniola (with Haiti and the Dominican Republic), Cuba, and Jamaica. They are part of a lower Cretaceous to Holocene island arc chain making up a submerged mountain range extending from Central America eastwards through the Caribbean. Each of the four islands is encircled by a coastal plain, backed on the north coast of Cuba, Jamaica, and Hispaniola by Pleistocene-raised shorelines that reach heights of 300 m. The extensive limestone outcrops on these islands have given rise to a tropical karst landscape, characterized by subterranean drainage, well developed cockpit and tower karst, and numerous caves including large river caves, deep sinkholes and long horizontal caves near the coast that formed under the influence of palaeo-sea levels. Two species each of stygobitic cirolanids are known from Cuba (*Haptolana* and *Cirolana*, subgenus *Anopsilana*), Jamaica (*Arubolana* and *Cirolana*, subgenus *Anopsilana*) and Hispaniola (both *Cirolana*, subgenus *Anopsilana*).

The Netherlands Antilles include the islands of Aruba, Bonaire and Curaçao in the southern Caribbean. The islands formed as a result of volcanic activity 90-95 million years ago, but half of the present day surface consists of Neogene or Quaternary limestone. Caves are generally small, but stygobitic fauna is also found in karstic springs, wells, anchialine pools and the marine interstitial. One stygobitic ciroland (*Arubolana*) is known from Aruba.

The Cayman Islands are composed of two distinct limestone formations; dense and highly karstified Oligocene-Miocene limestone forms the central core of each island, and is surrounded by a coastal limestone terrace of Pleistocene age called "ironshore". The island of Cayman Brac, due to its greater elevation, has more numerous and larger caves. One species of stygobitic cirolanid (*Cirolana*, subgenus *Anopsilana*) is known from Grand Cayman.

One stygobitic cirolanid, *Zulialana coalescens*, is described from the Sierra de Perijà in northwestern Venezuela. This region is a tropical rainforest with well developed karst in Cretaceous limestone.

The stygobitic cirolanid, *Antrolana lira*, is restricted to the Shenandoah Valley including caves in Augusta County, Virginia and Jefferson County, West Virginia. This isopod inhabits pools that intersect the groundwater table. Limestone in this area is Upper Cambrian in age.

Caves and groundwater habitats in Central and West Texas including the Balcones Escarpment and Edwards Plateau are inhabited by two stygobitic cirolanids, *Speocirolana hardeni* and *Cirolanides texensis texensis*. The Edwards Aquifer which underlies this area has the highest diversity of stygobites in the United States (LONGLEY, 1986). The Edwards limestone which outcrops over most of this area was deposited in a shallow sea starting in the early Cretaceous. The receding shoreline passed through this area in the early Tertiary.

The Sierra Madre Oriental of northeastern Mexico contains a wide variety of groundwater habitats (e.g., caves, thermal springs, wells, mines, and spring-fed pools) and an exceptionally diverse assortment of stygobitic cirolanids including 16 species from 4 genera (*Cirolanides*, *Mexilana*, *Speocirolana* and *Sphaerolana*). All of these systems contain freshwater, although water in thermal springs can be highly mineralized. During the Mesozoic, a thick layer of limestone was laid down in the shallow sea extending from south central Texas, across Mexico and Belize, and into Guatemala. In the late Cretaceous and early Tertiary, a series of mountain-building events known as the Laramide Orogeny uplifted, distorted and compressed these rocks creating the coastal ranges of the Sierra Madre Oriental.

Water salinity apparently being the best possible "common denominator", we make an attempt to group together the species considered in this paper according to their affiliation to either freshwater or marine habitats. Needless to say, in rather many cases, it is difficult to appreciate correctly the situation, owing to problems with obtaining reliable data during difficult exploration, or brought about by sampling quite near (just above or just below) haloclines. Moreover, some species are certainly more or less euryhaline. For a few species - included or not in Table 1 - the situation is at present rather problematic (*Arubolana imula* and *parvioculata*, *Bahalana cardiopus*, *Speocirolana thermydronis*, *Yucatalana robustispina*: see explanatory notes under "The actors").

The actors

Here follows a concise presentation of all 42 described stygobitic species (one of them with two subspecies) of the peri-Caribbean and Mexican realm, in alphabetical order. For each species: publications, other than that containing the original description, bringing some relevant additional information; male/female described; known distribution; habitats of freshwater/saline water; some additional information. To these 42 species, two more should be added: that, from Cuba, mentioned in the "Appendix to the check-list" and described as *Bahalana bowmani*; and a new species of *Bahalana* from Abaco, the Bahamas, described by BOTOSANEANU & ILIFFE in a separate paper in this same volume of the Bulletin (pp. 27-31).

Genus *Antrolana* BOWMAN, 1964

1. *Antrolana lira*
BOWMAN, 1964
Fig. 7

COLLINS & HOLSINGER, 1981; HOLSINGER *et al.*, 1994; HOLSINGER, 2005
♂,♀
Phreatic water in ten caves in the Shenandoah Valley karst region of northwestern Virginia and eastern West Virginia, USA
Freshwater

Genus *Arubolana* BOTOSANEANU & STOCK, 1979

2. *Arubolana aruboides*
(BOWMAN & ILIFFE, 1983)

Originally described in *Bermudalana* n.g.; transferred by NOTENBOOM, 1984, *Bermudalana* being synonymized with *Arubolana*.
NOTENBOOM, 1984; BOTOSANEANU & ILIFFE, 1997
♂,♀
Bermuda, Hamilton Parish: Church Cave (Paynter's Vale Cave), Wonderland Cave (Whitby Cave, Fantasy Cave), Bitumen Cave, Wilkinson Quarry Cave (this last cave: new record)
Salt water; salinity variable with depth but species found only in deeper, salt water

3. *Arubolana imula*
BOTOSANEANU & STOCK, 1979
Fig. 16

NOTENBOOM, 1984
♂,♀
Aruba by Lago Colony: Mangel Cora Tunnel
Fully marine water (?), although in original description ". . . brackish (chlorinity 3600 mg/l)"

4. *Arubolana parvioculata*
NOTENBOOM, 1984

♂,♀
Jamaica, Discovery Bay: interstitial in dry bed of Rio Secco near sea shore (possibly also in marine interstitial)
Water salinity very different in various holes dug in sediment
Microoculate

Genus *Bahalana* CARPENTER, 1981

5. *Bahalana caicosana*
BOTOSANEANU & ILIFFE, 2003a
Plate 1(a)

♂,♀
North Caicos Island, Sandy Point: Cottage Pond (anchialine cave). Middle Caicos Island, Conch Bar: Conch Bar Cave
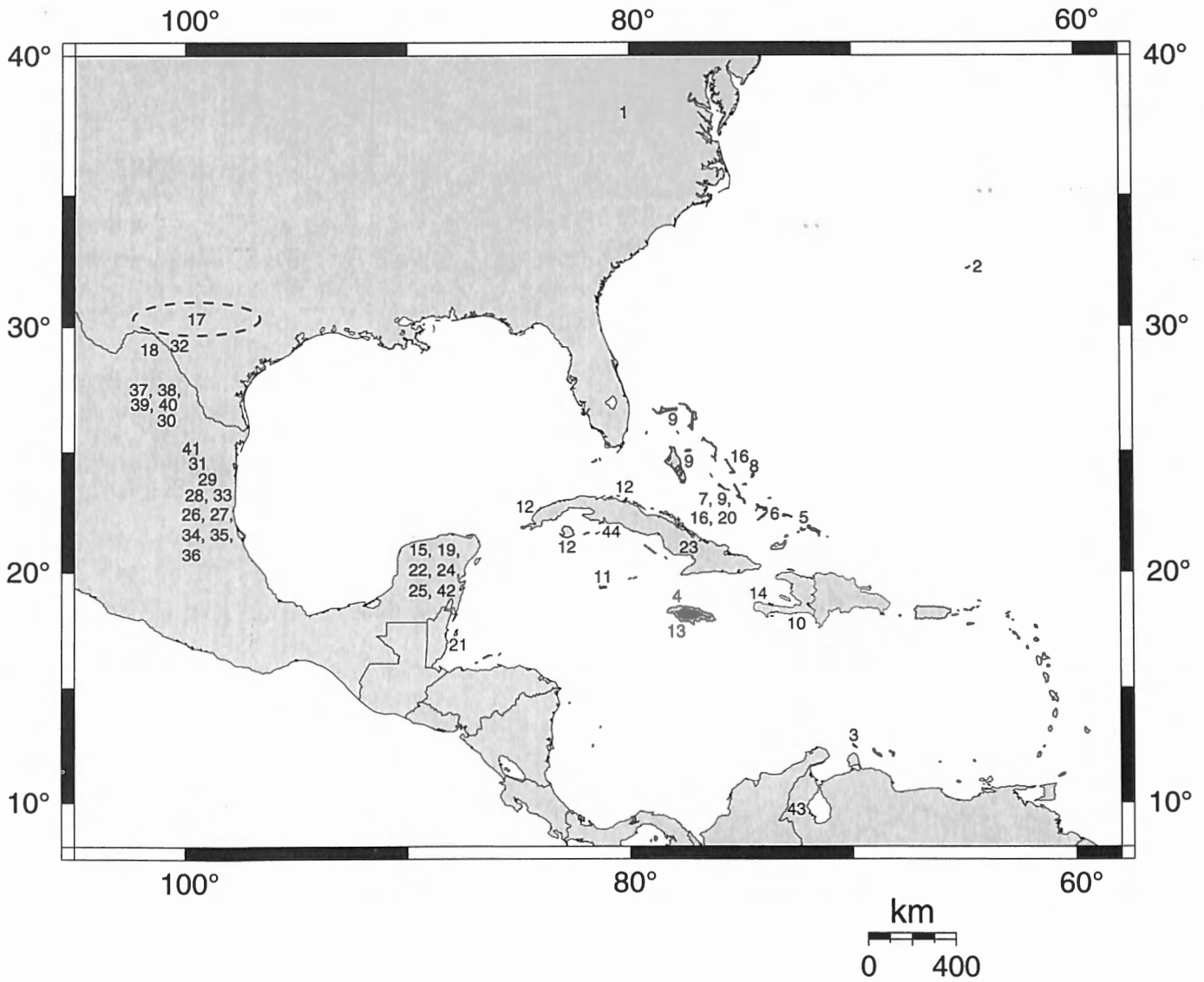Fully marine salinity

Figure 1: Map of the peri-Caribbean – Mexican zone illustrating the distribution of endemic stygobitic Cirolanidae. Numbers refer to the species presented in that order under the section entitled "The actors": 1. *Antrolana lira*, 2. *Arubolana aruboides*, 3. *Arubolana imula*, 4. *Arubolana parvioculata*, 5. *Bahalana caicosana*, 6. *Bahalana cardiopus*, 7. *Bahalana exumina*, 8. *Bahalana geracei*, 9. *Bahalana yagerae*, 10. *Cirolana (Anopsilana) acanthura*, 11. *Cirolana (Anopsilana) crenata*, 12. *Cirolana (Anopsilana) cubensis*, 13. *Cirolana (Anopsilana) pleoscissa*, 14. *Cirolana (Anopsilana) radicicola*, 15. *Cirolana (Anopsilana) yucatană*, 16. *Cirolana (Cirolana) troglexuma*, 17. *Cirolanides texensis texensis*, 18. *Cirolanides texensis mexicensis*, 19. *Creaseriella anops*, 20. *Exumalana reptans*, 21. *Haptolana belizana*, 22. *Haptolana bowmani*, 23. *Haptolana trichostoma*, 24. *Haptolana yunca*, 25. *Metacirolana mayana*, 26. *Mexilana saluposi*, 27. *Speocirolana bolivari*, 28. *Speocirolana disparicornis*, 29. *Speocirolana endeca*, 30. *Speocirolana fustiura*, 31. *Speocirolana guerrai*, 32. *Speocirolana hardeni*, 33. *Speocirolana lapenita*, 34. *Speocirolana pelaezi*, 35. *Speocirolana prima*, 36. *Speocirolana pubens*, 37. *Speocirolana thermydronis*, 38. *Speocirolana zumbadora*, 39. *Sphaerolana affinis*, 40. *Sphaerolana interstitialis*, 41. *Sphaerolana karenae*, 42. *Yucatalana robustispina*, 43. *Zulialana coalescens*

(a) *Bahalana caicosana*

(b) *Cirolana (C.) troglexuma*

(c) *Creaseriella anops*

(d) *Exumalana reptans*

(e) *Yucatalana robustispina*
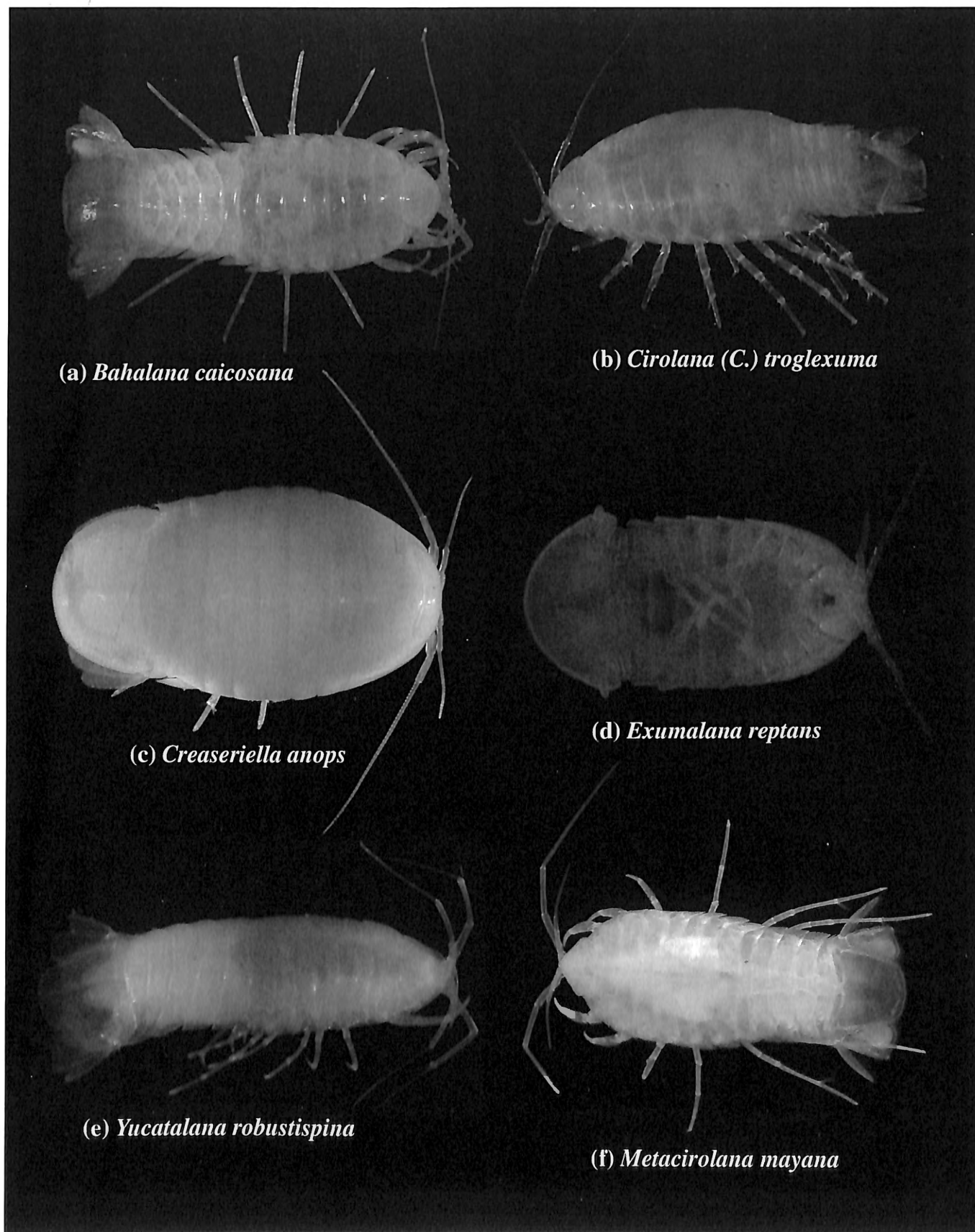
(f) *Metacirolana mayana*

Plate 1: Digital photographs of live stygobitic cirolanids: (a) *Bahalana caicosana*, (b) *Cirolana (C.) troglexuma*, (c) *Creaseriella anops*, (d) *Exumalana reptans*, (e) *Yucatalana robustispina* and (f) *Metacirolana mayana*.
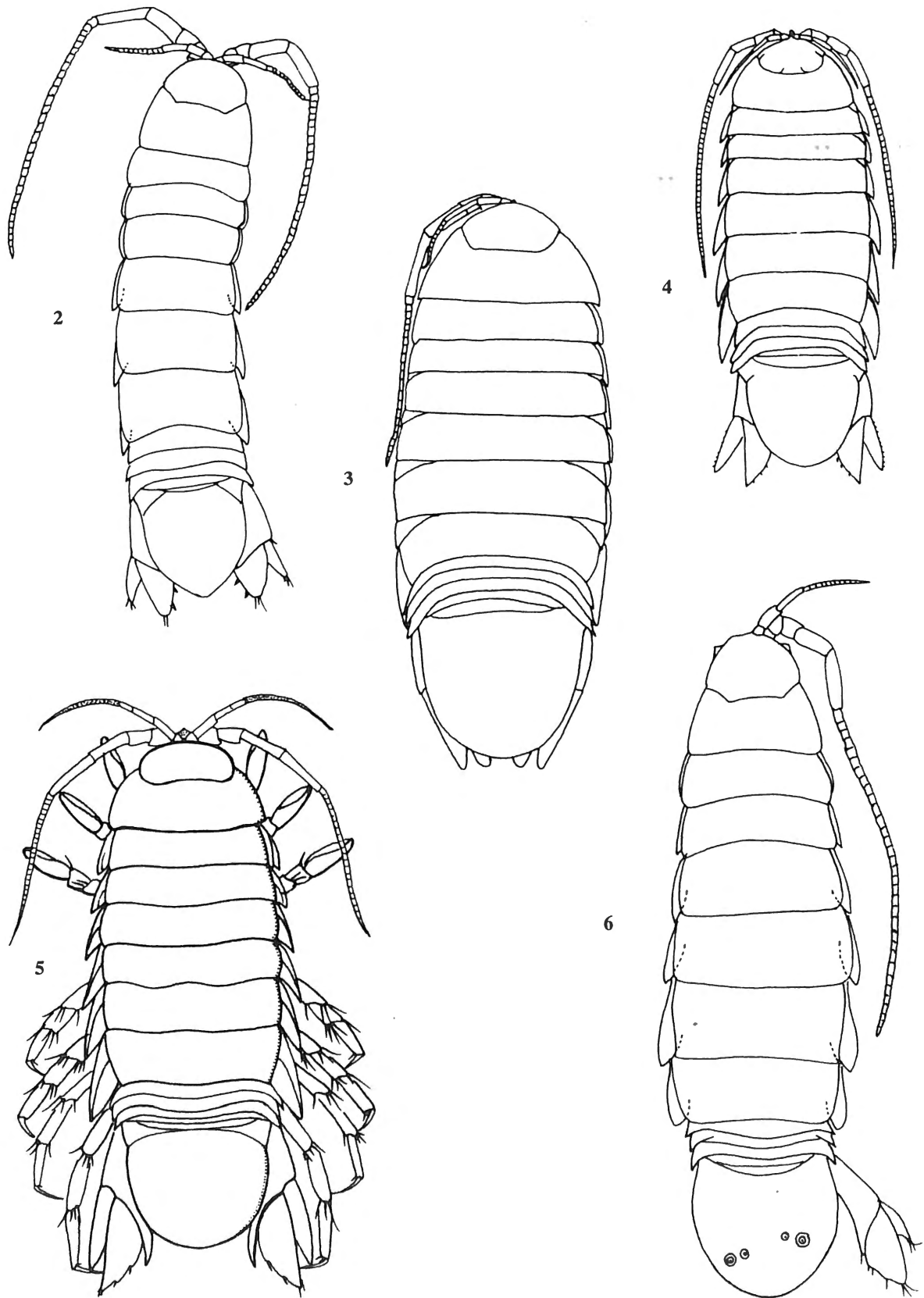
Figure 2: *Speocirolana thermydronis*, male (redrawn from BOTOSANEANU *et al*. 1998). **Figure 3:** *S. pubens* (redrawn from BOWMAN 1981). **Figure 4:** *S. prima*, male (redrawn from SCHOTTE 2002). **Figure 5:** *S. pelaezi*, female (redrawn from BOLIVAR Y PIELTAIN 1950). **Figure 6:** *S. zumbadora*, female (redrawn from BOTOSANEANU *et al*. 1998)
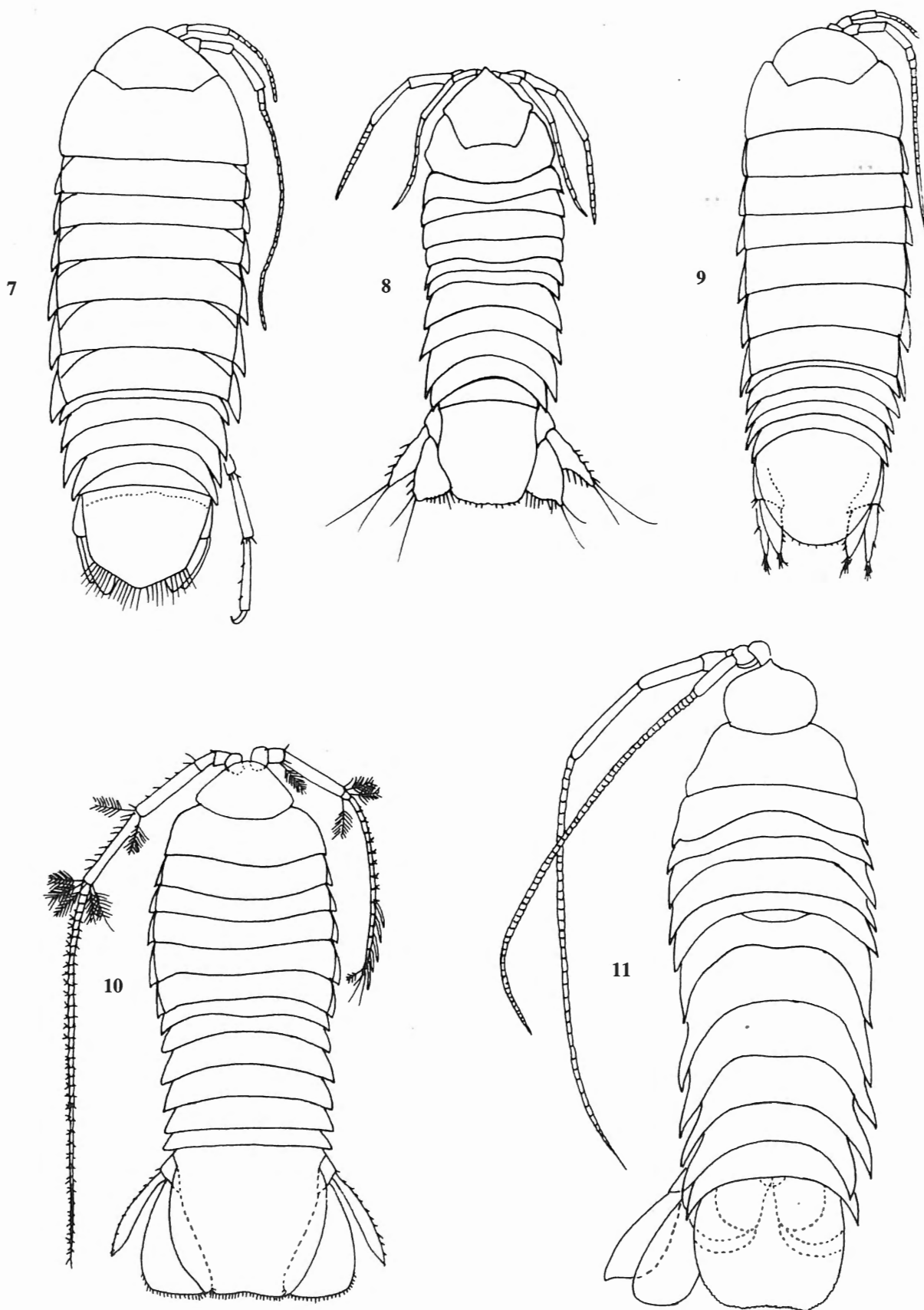
Figure 7: *Antrolana lira* (redrawn from BOWMAN 1964). **Figure 8:** *Yucatalana robustispina*, female (original drawing). **Figure 9:** *Cirolanides texensis texensis* (redrawn from BOWMAN 1964). **Figure 10:** *Bahalana yagerae*, male (redrawn from CARPENTER 1994). **Figure 11:** *B. exumina*, male (redrawn from BOTOSANEANU & ILIFFE 2002).
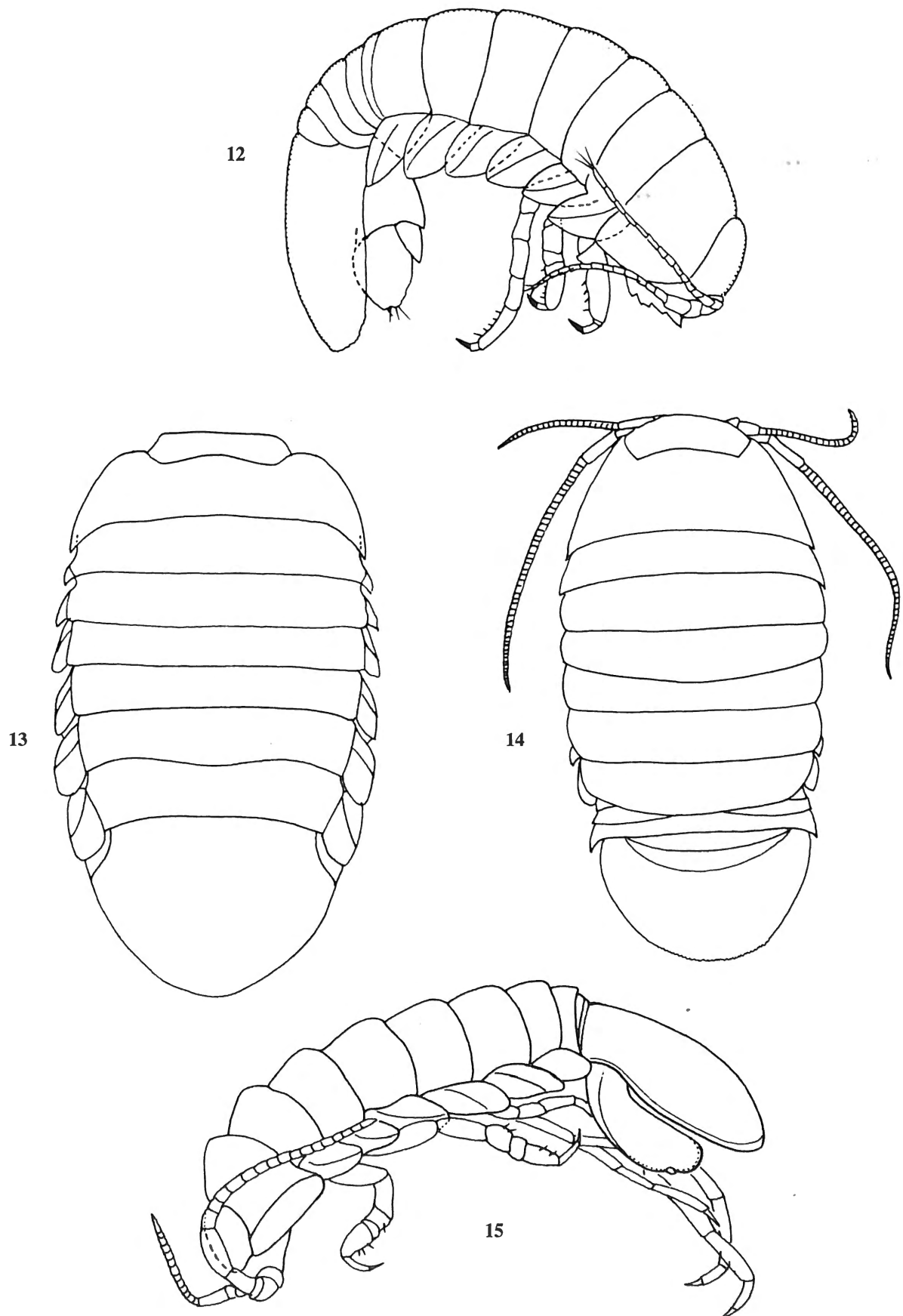
Figure 12: *Exumalana reptans*, female (redrawn from BOTOSANEANU & ILIFFE 2003). **Figure 13:** *Zulialana coalescens* (redrawn from BOTOSANEANU & VILORIA 1993). **Figure14:** *Creaseriella anops*, female (original drawing). **Figure 15:** *Sphaerolana interstitialis*, male (original drawing).
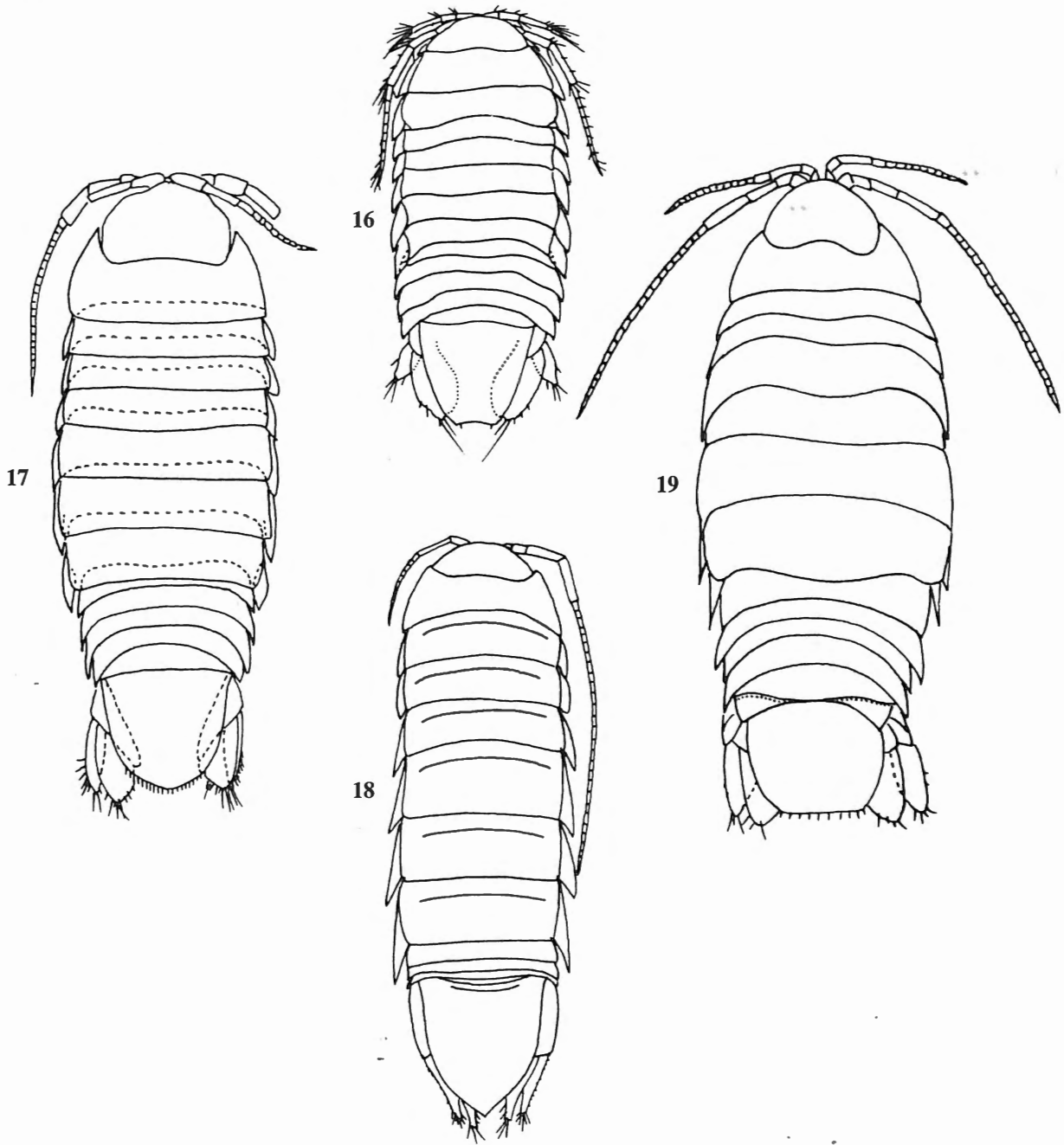
Figure 16: *Arubolana imula*, male (redrawn from BOTOSANEANU & STOCK 1979). **Figure 17:** *Cirolana (Anopsilana) radicicola*, male (redrawn from NOTENBOOM 1981). **Figure 18:** *Mexilana saluposi*, female (redrawn from BOWMAN 1975). **Figure 19:** *Cirolana (Cirolana) troglexuma*, female (original drawing).

Closely related to *B. geracei* and *B. cardiopus*, not to *B. yagerae* or *B. exumina*

6. *Bahalana cardiopus*
NOTENBOOM, 1981

BOTOSANEANU & ILIFFE, 1999
♂,♀

Bahamas. Mayaguana Island, Little Bay: Mount Misery Cave; Acklins Island: Duncan Pond Cave.
Water salinity, according to NOTENBOOM, 1981, only ca. 10 g/l (but this is highly improbable)
Only very slight differences from *B. geracei*.

7. *Bahalana exumina*
BOTOSANEANU & ILIFFE, 2002(a)
Fig. 11

♂
Bahamas, Exumas, Great Guana Cay: Oven Rock Cave
Fully marine salinity
Maybe not far from *B. geracei* and *B. cardiopus*

8. *Bahalana geracei*
CARPENTER, 1981

NOTENBOOM, 1981
♂,♀

Bahamas, San Salvador Island: Dixon Hill Lighthouse Cave
Fully marine salinity (but cave ca. 1 km distant from ocean)

9. *Bahalana yagerae*
(CARPENTER, 1994)
Fig. 10

Originally described in *Dodecalana* n.g.; transferred by BOTOSANEANU & ILIFFE, 1997, *Dodecalana* being synonymized with *Bahalana*.
BOTOSANEANU & Iliffe, 1997, 2002a, 2003a
♂,♀

Grand Bahama Island: Bahama Cement Cave, Old Freetown Cave, Lucayan Cavern; Sweetings Cay (adjacent to Grand Bahama Island): Janet Pyfrom's Blue Hole, Asgard Cave, Virgo Blue Hole, Sagittarius Blue Hole, Lucy's Cave; Great Exuma Island: Basil Minn's Blue Hole; Andros Island: Conch Sound Blue Hole.
Fully marine salinity
Species distinct from all others by absence of pereiopods VII in mature specimens.

Genus *Cirolana* LEACH, 1818
(sg. *Anopsilana* PAULIAN &
DELAMARE DEBOUTEVILLE, 1956)

Most species in this subgenus are marine/epigean, some of them stygophilic.

10. *Cirolana (Anopsilana) acanthura*
(NOTENBOOM, 1981)

Originally described in *Haitilana* n.g. Transferred to *Anopsilana* in BOTOSANEANU *et al.*, 1986, *Haitilana* being synonymized with *Anopsilana* in that publication.
♀
Haiti: well at Marigot, southern coast of Département de l'Ouest.
Freshwater

11. *Cirolana (Anopsilana) crenata*
(BOWMAN & FRANZ, 1982)

Originally described in g. *Anopsilana*
♂,♀
Grand Cayman Island, NW end: West Bay Cave.
Weakly brackish water

12. *Cirolana (Anopsilana) cubensis*
HAY, 1903

BOLÍVAR Y PIELTAIN, 1950; RIOJA, 1953, 1956 (in this last publication as n.g. *Troglocirolana*); SILVA TABOADA, 1974. Transferred to *Anopsilana* in BOTOSANEANU *et al.*, 1986, *Troglocirolana* being synonymized with *Anopsilana* in that publication.
♂,♀
Cuba. Pinar del Río: Caverna en San Isidro; Habana: Cueva between Madruga and Aguacate, Cueva del Quintanal, Cueva de la Yagruma. Matanzas: Cueva de Suárez. Isla de Pinos: Cueva de los Camarones, Cueva de los Murciélagos.
Freshwater

13. *Cirolana (Anopsilana) pleoscissa*
(BOTOSANEANU & ILIFFE, 1997)

Originally described in *Jamaicalana* n.g. Transferred by BOTOSANEANU & ILIFFE, 2000, *Jamaicalana* being synonymized with *Cirolana (Anopsilana)* in that publication.
♀
Jamaica, Westmoreland Parish: Revival Water Pump Cave
Freshwater

14. *Cirolana (Anopsilana) radicicola*
(NOTENBOOM, 1981)
Fig. 17

Originally described in *Haitilana* n.g. Transferred in BOTOSANEANU *et al.*, 1986, *Haitilana* being synonymized with *Anopsilana* in that publication.
♂,♀
Haiti, southern peninsula, near Jérémie: "Source Débarasse", large karstic spring flowing from cave.
Freshwater

15. *Cirolana (Anopsilana) yucatana*
BOTOSANEANU & ILIFFE, 2000

♀
Mexico, Yucatan, Mucuyché: Cenote Dzonotila.

Freshwater

Genus *Cirolana* LEACH, 1818
(sg. *Cirolana*)

Almost all described species are marine/epigean.

16. *Cirolana (Cirolana) troglexuma*
BOTOSANEANU & ILIFFE, 1997
Fig. 19, Plate 1(b)

BOTOSANEANU & ILIFFE, 1999, 2003b. The species has been rediscovered (2003, 2004) both in the type locality and in a new one (Basil Minn's Blue Hole); these records not published.
♀
Bahamas. Exuma Cays, Great Guana Cay: Oven Rock Cave; Great Exuma Island: Basil Minn's Blue Hole; Cat Island: Big Fountain Blue Hole (this last record not yet published).
Fully marine salinity

Additional note: in BOTOSANEANU & ILIFFE, 1997, two subgenera are recognized in g. *Cirolana*.

Genus *Cirolanides* BENEDICT, 1896

17. *Cirolanides texensis texensis*
BENEDICT, 1896
Fig. 9

BOWMAN, 1964, 1972, 1992; BOTOSANEANU & ILIFFE, 2002b (here, *inter alia*: updated distribution)
♂,♀
36 records (caves, phreatic waters, springs) all from Texas (counties Bexar, Burnet, Comal, Crockett, Edwards, Hays, Kendall, Kerr, Medina, Real, Schleicher, Terrell, Uvalde, Val Verde) all in the southern part of Edward's Plateau.
Freshwater

18. *Cirolanides texensis mexicensis*
BOTOSANEANU & ILIFFE, 2002b

BOTOSANEANU *et al.*, 1998; BOTOSANEANU & ILIFFE 1999.
♂,♀
N. Mexico. Nuevo León, Lampazos: Cueva de El Tule, Cueva de La Espantosa; Coahuila, west and north from Ciudad Acuña: Sótano de Amezcua.
Freshwater

Genus *Creaseriella* RIOJA, 1953

19. *Creaseriella anops*
(CREASER, 1936)
Fig. 14, Plate 1(c)

Originally described in *Cirolana*; transferred by RIOJA, 1953 to *Creaseriella* n.g.
Creaser, 1938; BOLÍVAR Y PIELTAIN, 1950; RIOJA, 1953; REDDELL, 1977; PÉREZ ARANDA, 1984; BOTOSANEANU & ILIFFE, 1997, 1999, 2002a; ESCOBAR *et al.*, 2002.
♂,♀

Mexico, Yucatan Peninsula: numerous caves (some of them true cenotes) in the states Quintana Roo or Yucatan. To those in the various publications above mentioned should be added the following new records: from Quintana Roo - Cenote Kaape Ha (Del Mar), Systema Ox Bel Ha, Tulum; from Yucatan - Cenote San Miguel and Cenote Chean Kab, both at Huhi, and Cenote San Antonio at Homun.
Freshwater

Genus *Exumalana* BOTOSANEANU & ILIFFE, 2003(b)

20. *Exumalana reptans*
BOTOSANEANU & ILIFFE, 2003(b)
Fig. 12, Plate 1(d)

♀
Bahamas, Exumas, Norman's Pond Cay: Norman's Pond Cave ("inland blue hole").
Water fully marine

Genus *Haptolana* BOWMAN, 1966

21. *Haptolana belizana*
BOTOSANEANU & ILIFFE, 1997

♂
Belize: Inland Blue Hole, Caves Branch.
Freshwater

22. *Haptolana bowmani*
BOTOSANEANU & ILIFFE, 1997

♂,♀
Mexico, Yucatan: Grutas de Tzab-Nah (Dzab Nah) 2 km S of Tecoh on road to Telchaquillo; immatures probably of the same species from three other Yucatan localities: Cenote Kambul (published as Noc Ac), Cenote Mucuyché, Cenote Yuncu.
Freshwater, at least in type locality

23. *Haptolana trichostoma*
BOWMAN, 1966

SILVA TABOADA, 1974
♂
Cuba, Province Camagüey, Sierra de Cubita: Cueva Bonita, Cueva de la Lechuza.
Freshwater
Considered by BOTOSANEANU & ILIFFE, 2000 as not being closely related to *H. belizana*, *H. bowmani* and *H. yunca* which could have a common marine ancestor.

24. *Haptolana yunca*
BOTOSANEANU & ILIFFE, 2000

♀
Mexico, Yucatan, Yuncu: (deep) Cenote Sabakha.
Caught in freshwater near halocline

Genus *Metacirolana* NIERSTRASZ, 1931

The bulk of species in this genus are marine/epigean.

25. *Metacirolana mayana*
(BOWMAN, 1987)
Plate 1(f)

Originally described as *Bahalana*; transferred by BOTOSANEANU & ILIFFE, 2002a.
BOTOSANEANU & ILIFFE, 1997, 1999, 2002a; CARPENTER, 1994.
♂,♀
Mexico, Yucatan, Quintana Roo. Isla Cozumel: Cueva Quebrada, Cenote Aerolito, Cenote Tres Potrillos. Other localities in Quintana Roo: Cenote Temple of Doom Cave (near Tulum), Cenote Crustacea, originally published as Aayin Aak (Puerto Morelos), Cenote 27 Steps (Akumal). One additional known locality in Quintana Roo has never been published: Cenote Chac Mool (Puerto Aventuras).
Fully marine water

Genus *Mexilana* BOWMAN, 1975

26. *Mexilana saluposi*
BOWMAN, 1975
Fig. 18

♂,♀
Mexico, San Luis Potosí, 4 km NW Micos: Cueva del Huisache
Probably freshwater

Genus *Speocirolana* BOLÍVAR Y PIELTAIN, 1950

Originally described as sg. of *Cirolana* LEACH. Elevated to generic rank by BOWMAN, 1964.

27. *Speocirolana bolivari*
(RIOJA, 1953)

Originally described in sg. *Speocirolana* of *Cirolana*.
REDDELL & MITCHELL 1971a,b; BOWMAN 1981; BOTOSANEANU & ILIFFE, 1999; BOTOSANEANU et al., 1998.
♂,♀
Mexico. Tamaulipas: Cueva (Grutas) de Quintero (Sierra de El Abra); "Bee Cave" (Sierra de Guatemala); Cueva del Nacimiento del Río Frío (Municipio Gómez Farias, Ejido El Nacimiento); Ojo Encantado (Jaumave, Cañón Trejo). San Luis Potosí: spring at La Laja. Nuevo León: Sima Chupacable (Potreritos).
Freshwater
Discussion of variability, characters enabling or not distinction from the closely related and sometimes coexisting *S. pelaezi*, possibility of hybridization, relative abundance of these two species: RIOJA, 1953; COLE & MINCKLEY, 1966; MINCKLEY & COLE, 1968; BOWMAN, 1981; BOTOSANEANU & ILIFFE, 1999; BOTOSANEANU et al., 1998.

28. *Speocirolana disparicornis*
BOTOSANEANU & ILIFFE, 1999

♂,♀
Mexico, Tamaulipas, Jaumave: Guayatejó spring
Freshwater

29. *Speocirolana endeca*
BOWMAN, 1981

♂,♀
Mexico, Tamaulipas, NW of Ciudad Victoria: Sótano de las Calenturas (Yerbabuena); Cueva del Tecolote (Los San Pedro).
Probably freshwater

30. *Speocirolana fustiura*
BOTOSANEANU & ILIFFE, 1999

♂
Mexico, Nuevo León, Potreritos: Sima Chupacable
Freshwater

31. *Speocirolana guerrai*
CONTRERAS-BALDERAS & PURATA-VELARDE, 1982

♂,♀
Mexico, Nuevo León, Linares: Cueva de la Chorrera
Freshwater
Considered as more closely related to *S. pubens*

32. *Speocirolana hardeni*
BOWMAN, 1992

♂,♀
S. Texas: several wells, artesian wells, or springs in the counties Bexar and Val Verde
Freshwater
Considered as most closely related to *S. thermydronis*

33. *Speocirolana lapenita*
BOTOSANEANU & ILIFFE, 1999

♂,♀
Mexico, Tamaulipas, Ciudad Victoria: Manantial La Penita
Freshwater
Apparently related to *S. guerrai* and *S. pubens*.

34. *Speocirolana pelaezi*
(BOLÍVAR Y PIELTAIN, 1950)
Fig. 5

Originally described in sg. *Speocirolana* of *Cirolana*.
RIOJA, 1953; REDDELL & MITCHELL, 1971 a, b; BOTOSANEANU et al., 1998; BOTOSANEANU & ILIFFE, 1999.
♂,♀
Mexico. San Luis Potosí: Cueva de los Sabinos, Sótano de Pichijumo, Sótano de las Piedras, Sótano del Tigre, Sótano de la Tinaja, Sótano del Arroyo, Cueva Chica, Cueva de la Curva, Sotanito de Montecillos. Tamaulipas, Sierra de El Abra: Cueva de la Florida, Cueva de El Pachón, Grutas

(Cueva) de Quintero; Tamaulipas, Sierra de Guatemala: Cueva de la Mina; also in Tamaulipas are: Cueva del Nacimiento del Río Frío (Municipio Gómez Farias, Ejido El Nacimiento) and Ojo Encantado (Jaumave, Cañón Trejo).
Freshwater
For various observations: see last paragraph of text for *S. bolivari*

35. *Speocirolana prima*
SCHOTTE, 2002
Fig. 4

♂,♀
Mexico, Tamaulipas: Nacimiento de Río Mante just south of Ciudad Mante
Freshwater
"...most like *S. pubens*..."

36. *Speocirolana pubens*
BOWMAN, 1981
Fig. 3

♂,♀
Mexico. San Luis Potosí, San Nicolás de los Montes: Cueva de la Bonita; Tamaulipas, 14 km of Ocampo: Cueva del Ojo de Agua de Manantiales
Freshwater
Considered as more closely related to *S. guerrai*

37. *Speocirolana thermydronis*
COLE & MINCKLEY, 1966
Fig. 2

MINCKLEY & COLE, 1968; COLE, 1984; BOWMAN 1992; BOTOSANEANU *et al.*, 1998.
♂,♀
Mexico, Coahuila: several "pozos" (thermal springs and associated habitats - marshes) SW of Cuatro Ciénegas, for instance Pozos de la Becerra and El Majarral; El Potrero 1 and El Potrero 2 (Municipio Melchor Múzquiz).
Thermal, possibly rather highly mineralized water
Considered as closely related to *S. hardeni*.

38. *Speocirolana zumbadora*
BOTOSANEANU *et al.*, 1998
Fig. 6

♀
Mexico, Coahuila, Municipio La Madrid: Cueva La Zumbadora
Freshwater

Genus *Sphaerolana* COLE & MINCKLEY, 1970

39. *Sphaerolana affinis*
COLE & MINCKLEY, 1970

COLE 1984; BOTOSANEANU *et al.*, 1998.
♂,♀
Mexico. Coahuila: various "pozos" ("springfed wells") near Cuatro Ciénegas; Cueva La Zumbadora (Municipio La Madrid). Nuevo León: flooded mine near Cueva de la Boca (Villa Santiago)
Freshwater

40. *Sphaerolana interstitialis*
COLE & MINCKLEY, 1970
Fig. 15

COLE, 1984; BOTOSANEANU *et al.*, 1998
♂,♀
Mexico. Coahuila: small springs and "pozos" near Cuatro Ciénegas. Tamaulipas: Manantial de San Rafael de los Castro (Municipio Ciudad Mante).
Freshwater

41. *Sphaerolana karenae*
RODRÍGUEZ-ALMARAZ & BOWMAN, 1995

♂
Mexico, Nuevo León: small spring adjacent to Pilón River, Montemorelos; mine near Cueva de la Boca, (Villa) Santiago
Freshwater

Genus *Yucatalana* BOTOSANEANU & ILIFFE, 1999

42. *Yucatalana robustispina*
BOTOSANEANU & ILIFFE, 1999
Fig. 8, Plate 1(e)

BOTOSANEANU & ILIFFE, 2000, 2002a
♂,♀
Mexico, Yucatan: Cenote Pabakal (Eknakan); Cenote Kankirixche, Cenote Kakuel, Cenote Chuih-Hol Dos (all three: Mucuyché); Cenote Xacha, Huhi, Cenote San Geronimo, Sotuta (these latter two records not yet published).
Probably caught both above or below the halocline

Genus *Zulialana* BOTOSANEANU & VILORIA, 1993

43. *Zulialana coalescens*
BOTOSANEANU & VILORIA, 1993
Fig. 13

♂,♀
NW Venezuela, Estado Zulia, Sierra de Perijá: Cueva de Toromo, near hacienda Medellín. A second population of this species has been recently discovered by Francesco F. Herrera (IVIC, Caracas) in a cave about 100 km distant from the type locality, but still in Sierra de Perijá: Mara 2 Cave, Guasare river basin.
Freshwater

Appendix to the check-list

In ORTIZ *et al.* (1997), the blind and depigmented cirolanid *Bahalana bowmani* is described from "Cueva del Humo, Playa Girón, Provincia de Matanzas, Cuba" (fully marine

water). This species is certainly not a *Bahalana*, lacking the distinctive characters of this genus. Moreover, information on some relevant morphological details is lacking from its description and illustration. Being unable to decide about the genus to which it belongs, we could not place it in the checklist. In the same publication, *Anopsilana magna* n. sp. is described from a cave with fully marine water near the locality of "*Bahalana bowmani*". Although depigmented, this species has very large facetted eyes; being quite probably not a stygobiont, it will not be taken into consideration in this paper.

The case of the extremely poorly described and unrecognizable *Conilera stygia* PACKARD, 1894 from Monterrey, Nuevo León, Mexico, has been discussed in several publications; it is considered as probably being a species of *Speocirolana*.

***

Several cases of coexistence of two species at one site are documented at present: *Bahalana exumina* and *Cirolana (C.) troglexuma* in Oven Rock Cave; *B. yagerae* and *C. (C.) troglexuma* in Basil Minn's Blue Hole; *Speocirolana bolivari* and *S. pelaezi* in Cueva de Quintero, Cueva del Nacimiento de Río Frío, and Ojo Encantado; *S. bolivari* and *S. fustiura* in Sima Chupacable; *S. zumbadora* and *Sphaerolana affinis* in Cueva La Zumbadora; *Sphaerolana affinis* and *S. interstitialis* in springs and "pozos" near Cuatro Ciénegas. Moreover, there is very probably coexistence of *Cirolanides texensis texensis* and of *Speocirolana hardeni* at some Texan sites. Likewise, coexistence will possibly be discovered also for *Speocirolana thermydronis* and *Sphaerolana (affinis? interstitialis?)* at some sites in the neighbourhood of Cuatro Ciénegas.

A uniquely high biodiversity of stygobitic Cirolanidae

The peri-Caribbean and Mexican Realm is the most extraordinary area of the world in this respect, with 42 endemic species (one of them with two subspecies) described to this day, most of them belonging to 11 genera endemic for the area - some of these morphologically very remarkable. Exceptional cases of specific diversification are offered by *Speocirolana*, *Bahalana*, or *Cirolana (Anopsilana)*, and those of *Sphaerolana*, *Haptolana*, or *Arubolana* are, too, highly interesting. The tropics of the Western Atlantic have been for stygobitic Cirolanidae a centre of strong evolutionary radiation (BRIGGS, 1995: 238-242 discusses the contrast with the comparatively poor faunal area represented by the tropics of the Eastern Atlantic). Undoubtedly, more discoveries can be expected, especially in Mexico, and maybe also in the practically unexplored smaller Central American countries, when their anchialine habitats are explored by diving. There is a clear contrast even with the zone of the globe second in biodiversity: the European Mediterranean *sensu lato*. It is not possible to offer really exact figures of stygobitic species for this zone, because there are still some *sub judice* taxonomic problems with the generic complex *Typhlociro-*

lana RACOVITZA - *Turcolana* ARGANO & PESCE - *Marocolana* BOULANOUAR *et al.* There are about 20 species described in this complex (possibly not all will prove to be valid, whereas additional species will be described); together with five species described in *Sphaeromides* DOLLFUS (one with one subspecies, one with two), one in *Faucheria* DOLLFUS & VIRÉ, one in *Kensleya* BRUCE & HERRANDO-PÉREZ, and one in *Metacirolana*, this would give a total of slightly more than 25 endemic species in seven genera. There is, too, an ecological difference between the stygobitic cirolanid fauna of the two zones: genuine anchialine species are very poorly represented in the Mediterranean - possibly as result of the hypersalinity/drying-up crisis during the late Miocene (Messinian) having forced ancestors of the stygobitic taxa directly into near-littoral subterranean freshwater habitats (STOCK, 1981).

The contrast becomes very impressive when we reach non-Mediterranean Africa (one species of *Cirolana (Anopsilana)* known from Madagascar; two of *Skotobaena* FERRARA & MONOD and one of *Haptolana* known from the Horn of Africa), to the enormous mass of Pacific islands (3 species of *Cirolana (Anopsilana)* described from Sulawesi, the Philippines, and Palau Islands), and to Australia (only one species of *Haptolana* described; but - information *in litt.* from N.L. BRUCE – two or possibly three more cirolanids recently discovered from the extraordinarily productive "calcretes" of Northwestern Australia).

Genera *Annina* BUDDE-LUND and *Saharolana* MONOD, whose species cannot be considered as clearly stygobitic, have been omitted from these considerations. In our opinion, the future will not bring drastic changes in the situation as here sketched.

Some aspects of morphology in relation to systematics

The vast array of morphological (and other) adaptations of Cirolanidae to hypogean life has been summarized by BOTOSANEANU (2001). Only two facts of paramount importance in the evolution of stygobiont Cirolanidae will be evoked here. First: the highly diversified pereiopodal morphology with more or less strongly raptorial structures affecting various groups of pereiopods, is, possibly, *grosso modo*, a result of partly abandoning feeding by scavenging (raptorial pereiopods are an exception in epigean-marine cirolanids) for an actively prey-grasping mode of life. Second: the occurrence in possibly phylogenetically widely distant taxa, of highly modified tailfans and especially uropods, having completely lost their natatory function (a result of abandoning active swimming for creeping in smaller bodies of water). It may be suspected that drastic remoulding of the tailfan has had a mechanical impact on the pleonal type of segmentation - considered by BOWMAN (1975) as being of prime importance for grouping cirolanid genera, as well as for realization of a morphology making more or less complete rolling into a ball possible. We believe that characters resulting from these major evolutionary events and shared by congeneric species can be considered as synapomorphies; whereas much caution is recommended when making use of them for deciding about

kinship between genera (BOTOSANEANU & VILORIA, 1993:169). As aptly worded by CAVALLI-SFORZA *et al.* (1994:372) "Natural selection causes convergence, or divergence in ways and directions that have nothing to do with coancestry".

Characters from almost all parts of the cirolanid body have been successfully used in systematics - a partial exception being the mouthparts. Different morphological characters may have quite different evolutive (phylogenetic) strength and significance- a field for future research in cirolanid systematics. For the time being, experience shows that, besides characters mentioned above, good tools for systematics are those offered by: rostrum-lamina frontalis-clypeolabrum; pleopodal morphology and setation; the penes.

About possible monophyly of some stygobitic genera

This is a study of biodiversity, and by no means one of cladistics. Nevertheless, here are succinct remarks on the possible monophylg of some genera represented in the area. There were difficulties with *Anopsilana* (discussion of various aspects: MONOD, 1976; BOWMAN & FRANZ, 1982; BRUCE, 1981, 1992; BRUSCA *et al.*, 1995; BOTOSANEANU & ILIFFE, 1997) considered as morphologically not sharply distinct from *Cirolana* (a problem having received a provisional solution by distinction of two subgenera: BOTOSANEANU & ILIFFE, 1997) or as a polyphyletic taxon - conclusion drawn, probably, from the geographical distribution, because we have not seen morphological arguments. In our opinion these difficulties have been exaggerated; we can very well imagine the origin of various members of *Anopsilana* across the globe either from various marine-epigean species of *Cirolana* (which, of course, would displace the question to: is *Cirolana* monophyletic, or not?); or, in some cases, even polytopically from various populations of one epigean *Cirolana* - which would be a case similar to those of *Astyanax fasciatus/Anoptichthys* in Central Mexico (i.a.: WILKENS, 1981) or of *Asellus aquaticus* with its various "cave forms".

Despite impressive diversity of habitus in various species, *Speocirolana* also is very probably monophyletic, monophyly being supported by a good number of shared morphological details (for instance: BOTOSANEANU *et al.*, 1998) and also by the remarkable compact distribution of most species in northeastern Mexico (SCHOTTE, 2002: fig. 4), a fine example of speciation by geographic isolation.

Shared characters for various species of *Haptolana* are summarized in BRUCE & HUMPHREYS, 1993 and in BOTOSANEANU & ILIFFE (1997, 2000), and at least some of them are probably synapomorphic.

Bahalana is an example of a monophyletic genus (BOTOSANEANU & ILIFFE, 2003a) not needing much discussion; and a fine example of speciation by insular isolation. As to *Arubolana*, despite the remarkable disjunct distribution of its species, there can be no doubt about monophyly (BOWMAN & ILIFFE, 1983; see also BRIGGS, 1995:238 for discussion of the role played by the Gulf Stream as "Bermuda's

lifeline carrying...genetic reinforcement for a thriving tropical community across some 1200 km of ocean").

All this does not mean that generic attribution of some species will not be questioned in the future, as it has been in the past for other species. We can only hope that authors attempting revisions in the future will take into account the elementary fact, often neglected by cladists, that subterranean life has generated characteristics strongly blurring the image of phylogenetic relationships.

The questions

What can we know about ancestors of stygobitic species?

There is a consensus between various authors that all stygobitic Cirolanidae in the area are of marine origin. There has been some discussion around *Antrolana lira*, not questioning its marine origin but considering it as an exceptional case: the only taxon found in an area unexposed to marine water since the Paleozoic (detailed discussion in BOWMAN, 1964; see also COLLINS & HOLSINGER, 1981). However, recently published evidence (KOENEMANN & HOLSINGER, 2001: fig. 26) shows that during middle to late Cretaceous, the localities of *A. lira* in Virginia were flooded by a continental marine embayment: which confirms the marine origin of this species. The alternative "shallow water ancestors" versus "deep sea ancestors" has been discussed in several publications not specifically devoted to Cirolanidae (i.e.: ILIFFE *et al.*, 1983; HART *et al.*, 1985; MANNING *et al.*, 1986; STOCK, 1986a; ANKER & ILIFFE, 2000). Origin from taxa of shallow marine water seems clearly more plausible if the anoxia crisis with its catastrophic consequences in the Atlantic waters deeper than 200 m at the Mesozoic/Tertiary boundary, as well as at the Oligocene/Miocene boundary, are taken into consideration. Nevertheless, the problem cannot be considered as definitely settled. That the immediate ancestors were animals well preadapted to hypogean life seems to be a strongly founded opinion (importance of preadaptation in the case of Cirolanidae has been stressed by BOTOSANEANU, 2001).

Very little concrete evidence can be gathered, without falling into wild speculation, about the actual ancestors. It should be kept in mind that "the subterranean often convergent evolution of characters might obscure the phylogenetic relationships between marine epigean and stygobiont taxa" (GALASSI, 1997); and the possibility of speciation, in some cases, from already stygobitic ancestors (HOLSINGER, 2004) should not be excluded. There is more solid evidence for the species of sg. *Anopsilana*, very probably derived from marine-epigean *Cirolana* spp., and for the subterranean *Metacirolana*, for which descent from congeneric marine/epigean species is quite plausible (according to KENSLEY & SCHOTTE, 1989, from epigean marine waters of the Caribbean, not including the Gulf of Mexico, two species of *Anopsilana*, five of *Cirolana*, and four of *Metacirolana* are known).

Can the age of stygobitic taxa and lineages be appreciated with some degree of reliability?

This is a ticklish question. To correlate age with the geological age of the rock in which the habitat of the stygobiont is developed, would be simply absurd (MONOD, 1975). It would be equally wrong to correlate it with the supposed time of emergence above sea level of its habitat, because it is quite possible (and in some cases quite probable) that a long period of stygoevolution below sea level has preceded this emergence. Several authors have published ideas in this context (HART *et al.*, 1985; STOCK, 1986a, 1994; ILIFFE, 1990; ANKER & ILIFFE, 2000; KORNICKER & ILIFFE, 2000; and interestingly, some additional evidence seems to come from palaeontology: LOZOUET, 2004). This idea is aptly worded, for instance, in STOCK (1994:109-110): "...stygobionts did not need subaerial edifices to evolve, their marine ancestors could have lived on shallow submerged banks or sea mounts and then adapted to subaerial conditions after such banks arose above sea-level".

Can the age of a taxon or lineage be correctly inferred from morphology? If unconditionally answering with "yes", this would imply that we believe that rates of stygoevolution are identical in all lineages - something which cannot be accepted. Nevertheless, a morphological diversification like that seen in *Speocirolana* could be evidence for long-lasting evolution. Genera in the fauna of the zone, with morphology most radically moulded by subterranean life, are *Sphaerolana, Zulialana, Exumalana,* and *Yucatalana*: are they all very old/ the oldest? In some cases possibly yes (*Sphaerolana, Zulialana*), in some others possibly not (*Exumalana, Yucatalana*); if such speculation can be made, it is because morphological evidence seems to be supported by evidence from habitat and distribution. At the opposite end of the spectrum we have the least radically transformed taxa: still macro-oculate like *Anopsilana magna*, or, for instance, micro-oculate like *Arubolana parvioculata*: in such cases and possibly also in that of *Cirolana (Cirolana) troglexuma* there is serious evidence for relatively recent stygobitization.

What can we guess about the roots of present day diversity?

Various authors have expressed opinions (sometimes contradictory - even in publications by the same author!) about time of groundwater colonization in various parts of the peri-Caribbean/Mexican Realm. Here follows an incomplete list of such publications.
- Concerning more than one geographic unit belonging to our zone: ALVAREZ *et al.*, 2005; HART *et al.*, 1985; HOLSINGER, 2000; HUMPHREYS, 2000; ILIFFE, 1992a, 2000, 2005; MONOD, 1975; NOTENBOOM, 1984; SKET, 1996, 2005; STOCK, 1986a, 1994.
- Bermuda: ANKER & ILIFFE, 2000; BOWMAN & ILIFFE, 1983; BRIGGS, 1995; ILIFFE, 1994, 2003, 2004; ILIFFE *et al.*, 1983; HART *et al.*, 1985; MANNING *et al.*, 1986; SKET & ILIFFE, 1980; STERRER, 1998.
- Texas: HENDRICKSON & KREJCA, 2000; HOLSINGER & LONGLEY, 1980; LONGLEY, 1986, 2004; MITCHELL &

REDDELL, 1971.
- Mainland of Mexico: ARGANO, 1972; BOTOSANEANU *et al.*, 1998; COLE, 1984; COLE & MINCKLEY, 1966, 1970; HENDRICKSON & KREJCA, 2000; VILLALOBOS *et al.*, 1999.
- Yucatan Peninsula: ILIFFE, 1992b, 1993; REDDELL, 1977; SCHMITTER-SOTO *et al.*, 2002; SUÁREZ-MORALES *et al.*, 2004; WILKENS, 1982.
- Bahamas, Turks and Caicos: ALVAREZ *et al.*, 2004; BOTOSANEANU & ILIFFE, 2003a,b; FOSSHAGEN & ILIFFE, 2004a,b; KOENEMANN *et al.*, 2003, 2004; KORNICKER *et al.*, 2002.
- Greater Antilles: BRIGGS, 1984; KORNICKER & ILIFFE, 1992; JAUME, 2001; JUARRERO & ORTIZ, 2000; STOCK, 1977, 1981, 1986b.
- Aruba: BOTOSANEANU & STOCK, 1979.
- Sierra de Perijà (Venezuela): BOTOSANEANU & VILORIA, 1993.

Two types of habitat requiring different explanations for time and mode of groundwater colonization

Despite differences in interpretation of known facts by various authors, most situations may be reduced to two main types of habitat and groundwater colonization history. The author having most consistently considered this problem, offering solid generalizations is STOCK (1986a, 1986b, 1994), and we shall mainly borrow ideas from these publications. STOCK (1986a:929-930) criticizes the idea that "all stygobionts, be they high-salinity or low-salinity ones, have supposedly evolved to an identical evolutionary scenario and time-scale". Zones of two distinct types can be distinguished in the peri-Caribbean and Mexican Realm:

a). Lower ("sinking", or "subsiding") zones more or less recently emerged form the sea, habitats with fully or nearly fully marine water and still in (indirect) contact with the sea: Bahamas and Turks and Caicos, Cayman Islands, Yucatan-Belize-Cozumel, near-shore localities of some greater Antilles. For such zones a "passive" ("regression") model of colonization of relatively recent date is proposed, with shorter periods available for stygoevolution.

b). Higher ("emerging", or "rising") zones, since long/very long time not flooded by the sea, habitats generally with freshwater (possibly sometimes slightly brackish), and without contact with the sea: mainland of Mexico, Virginia, Texas, more or less inland localities on some Greater Antilles, Sierra de Perijá. For such zones, an "active" model of colonization is proposed, having started long ago either by geotectonic positive movements or by eustatic regressive sea level movements. This has allowed deeper penetration of the colonized territories (with, in some cases, impressive "climbing" of stygobionts in the mountains: *Zulialana coalescens* to 400 m. a.s.l., *Speocirolana thermydronis* to about 600 m., *S. pubens* to about 800 m., *S. endeca* to 1460 m., *S. fustiura* to more than 1500 m. a.s.l.).

In other words: the most reliable element for inferring time and mode of stygoevolution seems to be the transition from marine to freshwater. Table 1 summarizes what we know about stygobitic species belonging to one of the two categories. The situation of *Cirolana (Anopsilana)* spp. is seem-

Table 1

SPECIES BOUND TO FRESHWATER OR NEARLY FRESHWATER	SPECIES BOUND TO FULLY OR NEARLY FULLY MARINE WATER
Antrolana lira	*Arubolana aruboides*
Cirolana (Anopsilana) acanthura	*Arubolana imula* (?)
Cirolana (Anopsilana) crenata	*Bahalana caicosana*
Cirolana (Anopsilana) cubensis	*Bahalana exumina*
Cirolana (Anopsilana) pleoscissa	*Bahalana geracei*
Cirolana (Anopsilana) radicicola	*Bahalana yagerae*
Cirolana (Anopsilana) yucatana	*Cirolana (Cirolana) troglexuma*
Cirolanides texensis texensis	*Exumalana reptans*
Cirolanides texensis mexicensis	*Metacirolana mayana*
Creaseriella anops	"*Bahalana bowmani*"
Haptolana belizana	(*species inquirenda*)
Haptolana bowmani	**SPECIES COLLECTED FROM**
Haptolana trichostoma	**WATERS OF VARIABLE OR**
Haptolana yunca	**QUESTIONABLE SALINITY**
Mexilana saluposi	*Arubolana parvioculata*
Speocirolana bolivari	*Bahalana cardiopus*
Speocirolana disparicornis	
Speocirolana endeca	
Speocirolana fustiura	
Speocirolana guerrai	
Speocirolana hardeni	
Speocirolana lapenita	
Speocirolana pelaezi	
Speocirolana prima	
Speocirolana pubens	
Speocirolana thermydronis	
Speocirolana zumbadora	
Sphaerolana affinis	
Sphaerolana interstitialis	
Sphaerolana karenae	
Zulialana coalescens	

ingly contradictory: origin probably not very old, but most species living in freshwater: a hint to importance of speed of stygoevolution in different lineages. And, from all points of view, the situation of Bermuda is a very special one.

How deep are the roots?

It is true that the idea has been expressed (HART *et al.,* 1985; MANNING *et al.,* 1986) that "marine caves of Bermuda and the Caribbean" could have been invaded as early as the Jurassic by ancestors of stygobitic species, thus before the opening of the Atlantic, on both sides of the forming ocean (and STOCK, 1986a, agrees with this idea.) But it is likely that the most propitious time for the starting of a flourishing period of stygoevolution in the area was the Cretaceous, a period coinciding with the opening of the Atlantic. As early as the Aptian time (ca 124 My ago) a Caribbean Province became distinct as result of the Atlantic Ocean spreading in such a manner that the Caribbean shallow waters became geographically isolated, gene flow from the East being interrupted. But it is especially during the Late Cretaceous, a period vividly characterized by BRIGGS (1995) as a momentous period in the Earth's history when - under a greenhouse climate - high sea level had resulted in the formation of extensive epicontinental seas, the epicontinental flooding allowing rivers to deposit sediments in the shallow sea waters. All this suggests ideal conditions for development of the deep roots

of cirolanid stygoevolution and for making from the Western Atlantic a centre of evolutionary radiation (in contrast with the faunistically much poorer Eastern Atlantic) and it seems plausible that the Palaeocene (a period of disappearance of the epicontinental seas, a period of shallow, tropical seas, as result of the fall of eustatic sea level at the end of the Cretaceous) was a period of (generic?) diversification and establishment of centres of endemism; and that the appearance of most present day species occurred from the Miocene through the Pleistocene.

What is the legacy of Tethys?

The Tethys Sea, restricted prior to the Cretaceous to Mediterranean Europe and the Indo-Pacific, spread westwards in the early Cretaceous across the developing North Atlantic to the New World tropics, to form a circumtropic marine belt (disrupted during the Miocene). A vast amount of evidence from practically all groups of stygofauna has accumulated, pointing to the importance of the Tethys in generating distributional patterns indubitably inherited from this circumglobal sea, and we cannot here refer to the vast bibliography on the subject.

Concerning Cirolanidae we can, first, distinguish a fine case of what could be called «a loud echo from Tethys»: that of *Haptolana.* From this genus, six species are described: *H. trichostoma* from Cuba; *H. bowmani, H. belizana,* and *H. yunca* from Yucatan; *H. somala* MESSANA & CHELAZZI, 1984, from northern Somalia; and *H. pholeta* BRUCE & HUMPHREYS, 1993, from W. Australia (Barrow Island). This is an exemplary case of a Tethysian pattern of distribution. Morphological evidence shows that there is close relationship between the three Yucatan species, all well distinct from the Cuban *H. trichostoma* (BOTOSANEANU & ILIFFE, 2000) and that there is more similarity between the Yucatan species and those from Somalia and from Australia (BOTOSANEANU & ILIFFE, 1997).

On the other hand, there are «muffled echoes» of Tethysian descent which can be traced from relationships between stygobitic genera a). in the Western Atlantic and b). in the Mediterranean *sensu lato.* Table 2 (data mainly from BOTOSANEANU *et al.,* 1986) summarizes what we can say at present about these relationships. It is certain that these data will be strongly refined in the future.

How could this high biodiversity be explained?

1). Through the rich, turbulent history of this vast and fragmented area, with many phases of marine transgressions/regressions affecting its various parts, and with alternatingly rising and subsiding zones either continental or never having been part of a continental block. Climatic changes, although not particularly severe, have certainly been very important; a factor of paramount importance in the passive colonization of subterranean habitats by marine ancestors of stygobionts (see BOTOSANEANU & HOLSINGER, 1991) has been represented by the strong tropical storms sweeping the area. With respect to all this, the contrast with, for instance, the eastern

Table 2: Genera of stygobitic Cirolanidae in two geographically disjunct groups with Tethysian ties.

West Atlantic		Mediterranean (sensu lato)
	"Cirolana-group"	
Creaseriella		
Haptolana		*Haptolana*
	"Sphaeromides-group"	
Antrolana		*Sphaeromides*
Bahalana		"Typhlocirolana-complex":
Cirolanides		*Typhlocirolana*
Mexilana		*Turcolana*
Speocirolana		*Marocolana*
Metacirolana		*Metacirolana*
	"Faucheria-group"	
Sphaerolana		*Faucheria*
		Kensleya
		Skotobaena

N.B. The position of *Arubolana*, *Yucatalana*, *Zulialana*, and *Exumalana* in such a table is at present uncertain.

Atlantic is considerable.

2). Through the abundance and extraordinary diversity of habitats propitious for stygoevolution (see "The stage" for details). This has too, certainly been of paramount importance in determining the present-day diversity of Cirolanidae and other stygobionts.

3). Through the supposed abundance and high diversity of potential marine ancestors. If we consider the present-day fauna of marine-epigean Cirolanidae in the area (KENSLEY & SCHOTTE, 1989 enumerate only 24 species in five (four) genera for the Caribbean not including the Gulf of Mexico; from an *in litteris* information from N.L. BRUCE, we learn that from the whole western North Atlantic, 35 species in 16 genera are recorded at present) this does not seem particularly rich (STOCK, 1994 observes that "the number of stygobiont taxa is always much higher than the number of marine taxa of the same genus"). Of course, our exact knowledge about the ancestors of stygobitic Cirolanidae is extremely limited; nevertheless, there is evidence from palaeontology about the marine fauna of the area having been particularly rich during the Cretaceous.

Endangered or already destroyed habitats and fauna: a plea for protection.

At least three stygobitic cirolanids are currently on endangered species lists. *Arubolana aruboides* and 24 other stygobitic taxa from Bermuda are considered as "critically endangered" on the IUCN Red List. *Creaseriella anops* from Yucatan is listed as threatened in the official Mexican endangered species list - la Norma Oficial Mexicana (NOM-059-ECOL-2001). *Antrolana lira* from Virginia is designated as threatened by the U.S. Fish and Wildlife Service.

Futhermore, a number of significant habitats are threatened. Cuatro Cienegas, or "Four Marshes", located in Mexico's Chihuahuan Desert has been set aside as a biological reserve, but is still threatened by mining of gypsum and increased rec-

reational use. Bermuda caves inhabited by *Arubolana aruboides* are threatened by groundwater pollution, quarrying of limestone and development (ILIFFE *et al.*, 1984; ILIFFE, 2003). Many cenotes along the Caribbean coastline of the Yucatan Peninsula have been set up for use by recreational scuba divers. An epigean fish, *Astyanax mexicanus*, which is normally restricted to surface pools of the cenotes has learned to follow divers into the caves, feeding off stygobitic crustaceans illuminated by the diver's lights. Considering that some caves are visited by hundreds of divers each week, the cave fauna of the entire area has been severely impacted and in places is locally extinct. So-called "deep well injection" (to 30 to 100 m depths) of partially treated sewage and other waste waters going on in Bermuda and the Yucatan Peninsula, among other areas, is particularly troubling. Cave and groundwater are naturally depleted in dissolved oxygen due to limited contact with the atmosphere, long residence times of the water and absence of photosynthetic oxygen production. Enrichment of subterranean waters with excess organic material in the waste water stimulates growth of bacteria, consumption of the limited oxygen and results in anoxia, anaerobic hydrogen sulfide production and extermination of all aerobic organisms.

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