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Adaptations in morphology and life cycle of subterranean populations of *Caecidotea racovitzai australis* from South Florida (Isopoda: Asellidae)

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ABSTRACT

Five species of Asellidae are reported from central and northern Florida: three are epigean (*Caecidotea racovitzai australis, C. obtusa, Lirceus lineatus*), and two are hypogean (*C. hobbsi, Remasellus parvus*). During a 3-year sampling project in the surficial aquifer of the karstic limestone in Everglades National Park, South Florida, we collected several specimens of an Asellidae not belonging to any of the hypogean species known for Florida. They were identified as *C. racovitzai australis* by their diagnostic characters, and by comparison with specimens we collected in central Florida, but their habitus was different due to the lack of pigmentation and microphtalmy. The first morph (morph A) was of small size, less abundant, represented mostly by juveniles collected in wells up to 7.5 m depth. The second morph (morph B) was of normal size, most abundant, most of the specimens were adults and collected in crayfish holes. The peculiar features, and the distribution of the two morphs, suggest that the Everglades populations are undergoing a stygobization process. Populations of *C. racovitzai australis* probably reached the Everglades through dispersal in surface waters, but the recent geological age of the area (5,000 ys) may not have allowed sufficient time for them to completely adapt to life in groundwater.

Key words: Asellidae, *Caecidotea*, karst, Everglades, stygobite

INTRODUCTION

Florida limestone is very new, being 50-60 million years old. Karst features in Florida include sinkholes, springs, caves, sinking streams, internally-drained basins, subsurface rather than surface drainage networks, and highly transmissive but heterogeneous aquifers. The high productivity of the Floridian aquifer is due to the development of secondary porosity caused by dissolution or karst processes. Karst features, including caves and springs, are more common in the northern two-thirds of the peninsula and in the central panhandle, where carbonate rocks are at or near the land surface (Randazzo and Jones 1997). In Southern Florida, karst limestone of Pleistocene origin underlies peat and marl deposits; the Miami Limestone and Fort Thompson Formation form the Biscayne aquifer in the upper part of the surficial aquifer. The marine limestone of the Fort Thompson Formation is 3-17 m deep, and it thickens slightly to the east, where it underlies the Miami Limestone (Fish and Stewart 1991). The Fort Thompson Formation is generally riddled with numerous, small solution cavities (6 cm or less Ø) so that this formation is highly permeable (Fish and Stewart 1991, Cunningham et al 2004, 2006). The Miami Limestone does not have such a well-developed network of cavities, which in many areas are partly clogged with lime, mud and sand, reducing the average hydraulic conductivity to much less than the underlying limestone of the Fort Thompson Formation (Fish and Stewart 1991).

Karst systems in South Florida are hydrologically very open, and numerous epigean invertebrates often penetrate the aquifer by means of solution holes, some of them establishing permanent populations in the aquifer (Bruno et al 2003; Bruno and Perry 2004; 2005).

Southern Florida is mostly occupied by the Everglades, an extensive subtropical wetland ecosystem that formed during the past 5,000 years when peat and marl were deposited within a pre-existing limestone depression in the southern peninsula (Gleason and Stone 1994). Freshwater marshes in the southern Everglades include a variety of vegetation communities along a hydroperiod gradient that ranges from deep sloughs and ponds that are flooded most of the year in wet years, to higher-elevation marl prairies that are inundated for 3-7 mo/yr on average, to a mean depth of 10 cm (Olmstead et al 1980). The Rocky Glades consist of marl-prairie habitats in the higher elevation areas eastern part of Everglades National Park (ENP) between Shark River and Taylor sloughs. In the Rocky Glades, a high degree of dissolution of the oolitic limestone bedrock has occurred with time, producing a typical karstic landscape with thousands of solution holes (Hoffmeister 1974), which provide a vertical dimension of habitat for aquatic organisms. During the wet season (June-October), rainfall and ground-water-recharge fill the solution holes, and lower-elevation areas of the Rocky Glades can be flooded in years of high rainfall. In the dry season (November-May), surface water disappears as a result of evaporation, percolation, and evapotranspiration. In the Rocky Glades, the presence of solution holes and below-ground, near-surface habitat allows for survival of a great variety of organisms. This is related to small differences among the different solution holes and because surface-dwelling aquatic organisms find refuge from the drought and from predators in solution holes during the dry season (Loftus et al 1992; Bruno and Perry 2004).

In this study we present the first faunistic data on the Asellidae of Everglades National Park. The family Asellidae comprises species of freshwater isopods from Eurasia, North Africa and North America; the family has numerous subterranean representatives, living in karst and unconsolidated sediments. Subterranean Asellidae show the typical stygobitic morphological adaptation, such as lack of eye and pigmentation; they are limnicoid stygobites *sensu* Coineau and Boutin (1992), i.e. their ancestors lived in surface freshwaters before groundwater colonization.

Seven genera of Asellidae are exclusive of North America (Hubricht and Mackin 1949; Bowman 1975; Lewis 2001; Lewis et al 2003) in phreatic and karstic systems, with one exception (see below): 1) *Lirceus* Rafinesque-Schmaltz, 1820, with 16 species widely distributed in the United States, only two species living in caves, the remaining ones in surface habitats; 2) *Caecidotea* Packard, 1871, the most diverse genus, with more than 50 species and subspecies, widely distributed in the United States, including surficial and subterranean species; 3) *Salmasellus* Bowman, 1975, monotypic, one stygobitic species recorded from Alberta, Canada; 4) *Lirceolus* Bowman and Longley, 1976, six stygobitic species distributed in Mexico and Texas; 5) *Calasellus* Bowman, 1981, two stygobitic species from California; 6) *Remasellus* Bowman and Sket,1985, monotypic, one subterranean species recorded from Florida; 7) *Columbasellus* Lewis, Martin and Wetzer, 2003, monotypic, one hyporheic species from Washington State.

In Florida five species of Asellidae are reported (Fig. 1): 1) *Caecidotea racovitzai australis* (Williams, 1970): an epigean species living in creeks and rivers of Taylor, Lafayette, Jackson, Madison, Seminole, Liberty, Orange Counties in Florida, and in Georgia (the nominal subspecies, *C. racovitzai racovitzai*, is distributed in epigean habitats of southeastern Canada and northeastern U.S.) (Williams 1970); 2) *Lirceus lineatus* (Say, 1818), epigean species living in creeks, lakes and swamps of Columbia, Alachua, Washington and Jackson Counties in Florida, and widespread throughout the eastern United States and in all the Great Lakes (Hubricht and Mackin 1949); 3) *Caecidotea obtusa* (Williams, 1970): an epigean species living in swamps, roadside ditches, ponds, rivers, streams of Liberty, Jefferson, Jackson, Escambia Counties in Florida, and in Georgia and Louisiana (Williams 1970); 4) *Caecidotea hobbsi* (Maloney, 1939): the endemic "Florida cave isopod" an hypogean species collected in Dudley Cave (Alachua County), Gerard's cave (Jackson County), Roosevelt Cave (Marion County), in a well near Micanopy (Alachua County) and in crayfish burrows (Calhoun County) (Maloney 1939; Van Name 1942; Steeves 1974); 5) *Remasellus parvus* (Steeve, 1964), the endemic "swimming little Florida cave isopod", an hypogean species collected in Ten Inch Cave (Alachua County), Splint Sink (Wakulla County) and Peacock Spring (Suwannee County) cave systems (Steeves 1964; Bowman and Sket 1985).

Before our research, there were no records of Asellidae from South Florida. The objectives of this work were: 1) to assess the presence and distribution of Asellidae in Everglades National Park, South Florida; 2) to assess the adaptations of the collected taxa to the hydrological cycle in the Everglades, in particular to survive the dry season.

METHODS

Fauna from groundwater of ENP and adjacent areas was investigated in an intensive three-year sampling project in the Rocky Glades (Fig. 1) from June 2000 to May 2004. A total of 1,548 groundwater samples were collected with an electric pump, from three sets of wells in the Rocky Glades area (for more details on the wells features and location, see Bruno and Perry 2004, 2005; Bruno et al 2003). In the same period, samples were collected from flooded solution holes in the Rocky Glades with a hand pump. A second, more exhaustive, sampling strategy was developed in January-March 2002, the resulting specimens are listed in Table 1 as collected by Campanaro. We sampled twice at 3, 4.5, 6, 7.5, 9, 10.5, 12 m depth from a set of 10 previously investigated wells, using an electric pump. At the same stations, we set traps and artificial substrates. Traps were built with modified PVC test-tubes (length 10 cm; inner diameter 2.8 cm) and baited with ham, set in place and retrieved after 24 hours. Two kinds of artificial substrates were built with PVC pipes (length 30 cm, inner diameter 4 cm and eight large holes on the lateral surface; length 25 cm, inner diameter 8 cm without holes on the side) and filled with air conditioning filtering plastic material, set in place and retrieved after periods of time varying from 8 to 35 days. We collected from crayfish holes (*Procambarus alleni* Faxon, 1884) with a hand pump inserted at the bottom of the crayfish hole, at a maximum depth of 20 cm. In permanent water bodies in the Rocky Glades (Chekika air boat ramp and Pine Glades Lake) and in the southern part of ENP (Nine Miles Pond and Paurotis

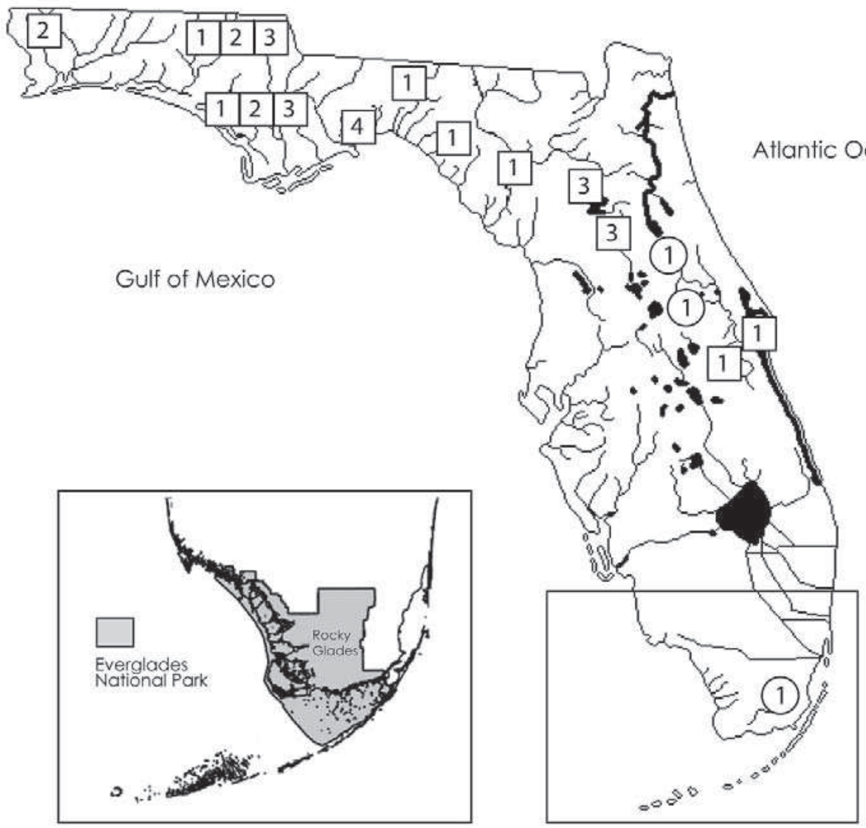

Fig. 1 - Map of Florida, and locations where Asellidae have been collected. 1) *Caecidotea racovitzai australis*; 2) *Caecidotea obtusa*; 3) *Caecidotea hobbsi*; 4) *Remasellus parvus*. Squares: data from literature; circles: our collections. The inset map of extreme southern Florida, showing the boundaries of Everglades National Park and the general location of the Rocky Glades.

Pond) we sampled with a D-frame benthos net and we set baited traps. A small artesian seepage, in the Hole in the Donut area adjacent to Daniel Beard Research Center, was sampled when water seeped from several solution holes with a plankton net placed on top of the largest hole and retrieved after 24 hours.

Isopods were sampled also in selected sites in central Florida (Fig. 1): Alexander Spring and Alexander Spring Run (St. John's River watershed, Lake County), Wekiwa Spring and Wekiwa Spring Run (St. John's River watershed, Seminole County), Econlockhatche River (St. John's River watershed, Seminole County), to collect reference specimens from surface habitats: isopods were visually sampled from rotting vegetation and benthic detritus.

RESULTS

The dominant subterranean group in ENP are copepods (Bruno et al 2005), mostly surface taxa, distributed to a depth of 12 m during the dry season (Bruno and Perry 2004, 2005). Few specimens of the amphipod *Crangonyx* sp. were also collected (Bruno, unpubl.). In ENP, a total of 326 Asellidae were collected, mostly during the 2002 intensive campaign and exclusively from groundwater with hand or electric pumps, and by filtering artesian seeps (Table 1). The most successful method was hand-pumping from crayfish holes during the dry season (158 specimens collected from 8 samples). Traps and artificial substrates were not effective in collecting specimens from groundwater, nor was kick sampling in surface waters. Overall, it appears that in ENP isopods populations live mostly in groundwater habitats (Table 1). One adult male and one female were identified in the stomach content of one specimen of *Monopterus albus* (Zuiew, 1793) (Asian swamp eel), captured in a canal along the eastern border of ENP (Loftus, unpubl.).

All the Asellidae that we collected in central and in southern Florida, included all the specimens from ENP, were identified as *Caecidotea racovitza australis* by morphological analysis. In particular, the male pleopods (Fig. 2) correspond to those reported for the nominal species (Williams 1970) for the following diagnostic characters: 1) protopod of the pleopod I subrectangular, with 2 or 3 retinacula; endopod with rounded margins; 2) protopod of pleopod II subsquare; distal segment of the exopod ovate, with plumose spines at margin; endopod tip with wide cannula and wide caudal process inwardly-bent and pointed, mesial process well-developed, curved and acutely pointed, almost as long as the cannula.

However, the specimens collected in ENP do not

Table 1 -Number of individuals collected at each date, each sampling site, and morph of the specimens collected. Abbreviations as follows: collecting habitat: W = well, SH = solution hole, AS = artesian seep, CH = crayfish hole, FS = fish stomach; method and collector: EP = electric pump, HP = hand pump, PN = plankton net, Br = M. C. Bruno, Cam = A. Campanaro; morph: A = small size, depigmented, microphtalmous, B = normal size, depigmented, microphtalmus.

Date	Collecting Habitat	Method and collector	Number of individuals	Morph
Feb-98	W 3 m	EP-Br	1 juv	A
Oct-98	W 3 m	EP-Br	1 juv	A
Oct-98	W 3 m	EP-Br	1 juv	A
Jan-99	SH	HP-Br	6♂	B
Feb-99	W 3 m	EP-Br	1 juv	A
May-00	SH	HP-Br	1♂	B
Jan-01	W 3 m	EP-Br	1 juv	A
Jan-01	W 3 m	EP-Br	2 juv	A
Jan-01	W 3 m	EP-Br	1 juv	A
Feb-01	SH	HP-Br	1♂	B
Feb-01	W 3 m	EP-Br	3 juv	A
Mar-01	W 3 m	EP-Br	1♂ 2♀	B
Mar-01	W 7.5 m	EP-Br	1 juv	B
Mar-01	W 4.5 m	EP-Br	1 juv	A
Apr-01	W 3 m	EP-Br	1♀ 2♂	B
Jul-01	W 4.5 m	EP-Br	3 juv	A
Jul-01	W 4.5 m	EP-Br	2 juv	A
Jul-01	W 7.5 m	EP-Br	2 juv	A
Aug-01	W 3 m	EP-Br	2 juv	B
Aug-01	W 3 m	EP-Br	1 juv	A
Sep-01	W 3 m	EP-Br	1 juv	A
Oct-01	W 3 m	EP-Br	1 juv	A
Oct-01	W 4.5 m	EP-Br	1♂	A
Oct-01	W 3 m	EP-Br	1 juv	A
Nov-01	W 4.5 m	EP-Br	1 juv	A
Dec-01	W 3 m	EP-Br	1 juv	A
Dec-01	W 4.5 m	EP-Br	1 juv	A
Jan-02	W 3 m	EP-Cam	1 juv	A
Jan-02	W 6 m	EP-Cam	1 juv	A
Jan-02	AS	PN-Cam	2♀ 1♂	B
Feb-02	W 3 m	EP-Cam	1 juv	B
Feb-02	W 3 m	EP-Cam	1 juv	A
Feb-02	W 4.5 m	EP-Cam	2 juv	A
Feb-02	W 6 m	EP-Cam	5 juv	A
Feb-02	W 6.5 m	EP-Cam	1 juv	A
Feb-02	W 3 m	EP-Cam	3 juv	B
Feb-02	W 3 m	EP-Cam	3 juv	A
Feb-02	W 4.5 m	EP-Cam	4 juv	A
Feb-02	W 7.5 m	EP-Cam	1 juv	A
Feb-02	CH	HP-Cam	1♀	B
Feb-02	CH	HP-Cam	9♂, 19♀	B
Feb-02	CH	HP-Cam	25♂, 53♀	B
Feb-02	CH	HP-Cam	11♂, 16♀	B
Feb-02	FS	Cam	1♂, 1♀	B
Mar-02	CH	HP-Cam	20♂, 26♀	B
Mar-02	W 7.5 m	EP-Cam	1 juv	A
Mar-02	W 3 m	EP-Cam	1 juv	A
Mar-02	CH	HP-Cam	6♂, 20♀	B

Apr-02	W 4.5 m	EP-Br	1 juv	A
Apr-02	W 6 m	EP-Br	1 juv	A
Apr-02	W 3 m	EP-Br	6 juv	A
Apr-02	W 3 m	EP-Br	1♀	B
Apr-02	W 7.5 m	EP-Br	3 juv	A
May-02	CH	HP-Br	1♀, 1♂	B
May-02	CH	HP-Br	4♀ 3♂	B
Jun-02	W 3 m	EP-Br	1♀	B
Jul-02	AS	PN-Br	2♂	B
Jul-02	AS	PN-Br	24 juv	B

correspond to the typical epigean morphology and to the known descriptions of *C. racovitzai australis* (species with pigmentation, eyes well-developed, large size, Figs 3a-4a). In fact, ENP specimens could be assigned to two morphs, both characterized by lack of pigmentation and microphtalmy (Fig. 4b): morph A (59 specimens, Table 1), of small size (1.3-1.5 mm) (Fig. 3b); morph B (267 specimens, Table 1), of normal size (3.5-7 mm) (Fig. 3c). Morph B was the most abundant, most of the specimens were adults (6 juveniles of this morph collected over a total of 23 specimens) and they were collected almost exclusively in crayfish holes (Table 1). Specimens belonging to morph A were collected exclusively in wells at 3-7.5 m depth, with low abundances and they were mostly juveniles (only 1 adult of this morph collected over a total of 35 specimens) (Table 1).

Specimens from Central Florida exhibit normal pigmentation, eyes-development (Fig. 4a) and size (Fig. 3a).

DISCUSSION

We report the first record of *C. racovitzai australis* in Southern Florida: Everglades National Park represents the southern limit of the known distribution of this species. The other four species of Asellidae, the epigean *C. obtusa, Lirceus lineatus* and the hypogean *C. hobbsi* and *Remasellus parvus*, appear to have a distribution restricted to Northern and Central Florida. The approximately 5,000 years of age of the Everglades may not be enough time for *C. hobbsi* and *R. parvus* to disperse there from the north, following the subterranean colonization way.

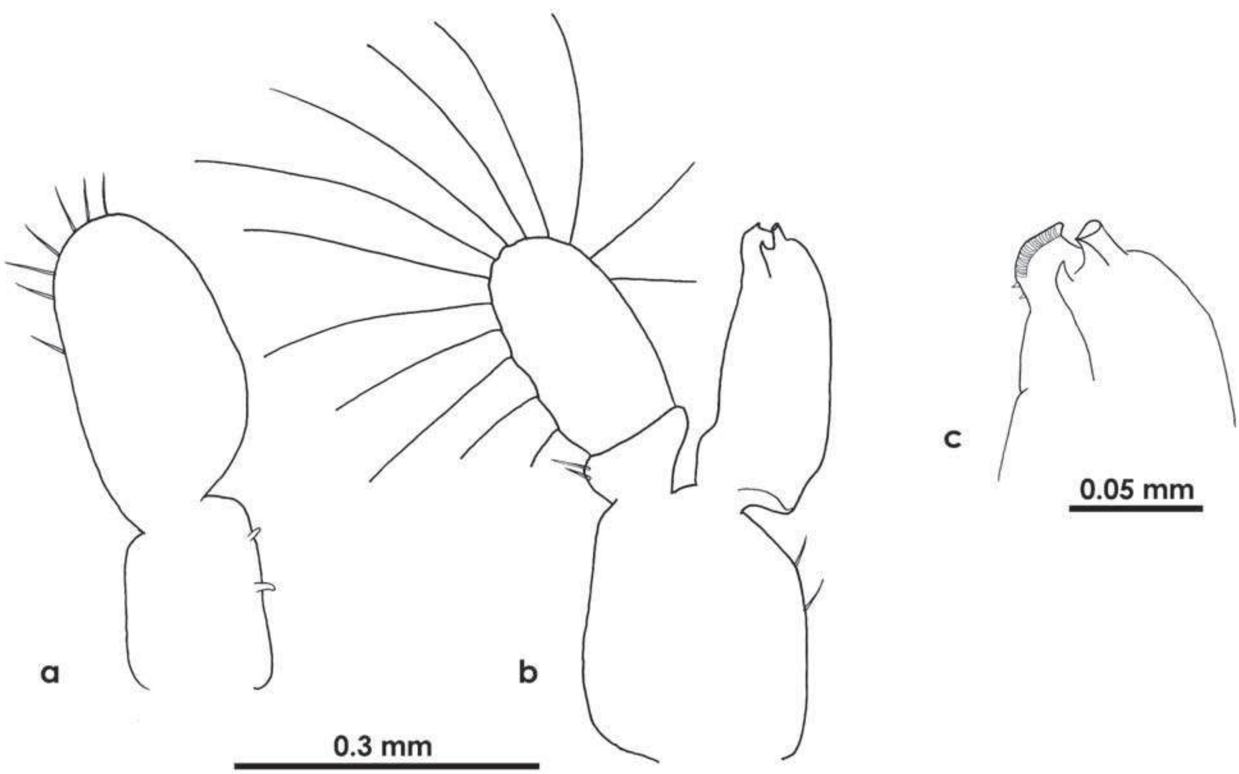

Fig. 2 - Diagnostic characters of *Caecidotea racovitzai australis:* male, collected from a crayfish hole, morph B a) I pleopod; b) II pleopod; c) endopod tip of the II pleopod.

Morphological variability and pre-adaptation of *C. r. australis* to subterranean life were shown by our studies. Morphological variability was already recorded by Williams (1970) who described two subspecies: *C. r. racovitzai* and *C. r. australis*, which can be distinguished by antenna/body length; shape of distal segment of first pleopod; length of distal segment of exopod of pleopod II; width of cannula. Such variability was not present in ENP specimens, which all showed the typical diagnostic characters of *C. r. australis*. However ENP populations differ from central and northern Florida ones: they have reduced eyes and pigmentation and different degrees in body size (Figs 3-4). Specimens of ENP can be classified as stygophile, i.e. organisms that actively exploit resources in the groundwater system, and actively seek protection from unfavorable situations in the surface environment resulting from biotic or abiotic processes (Gibert et al 1994). Other examples of stygophilic forms (with reduced eyes and pigmentation) can be found in *Proasellus* Dudich, 1925 (Argano and Pesce 1980, Baratti and Messana 1990), supporting the idea that stygobization (i.e. increasing degree of adaptation to groundwater life, from stygoxene organisms, to stygophiles, and finally to stygobites) is in progress in different lineages of Asellidae.

The body size, eyes development and tegument pigmentation differentiate the epigean-populations of Central Florida from the hypogean population of ENP. Thus, populations in Everglades National Park appear to be undergoing a stygobization process, possibly due to the ecological pressures of the wide seasonal changes in water levels and surface water temperature, and the strong predatory pressure by fishes and other invertebrates. In fact, specimens were never collected, during the dry season, in solution holes or small ponds, where predators tended to concentrate (Rader 1999). The record of two adults in the stomach of a fish, suggests how isopods could occasionally enter the surficial waters.

In an evolutionary-biogeographical scenario it is likely that *C. racovitzai australis* reached the Everglades through dispersion in surface waters that are generally well interconnected, particularly in Florida where lakes

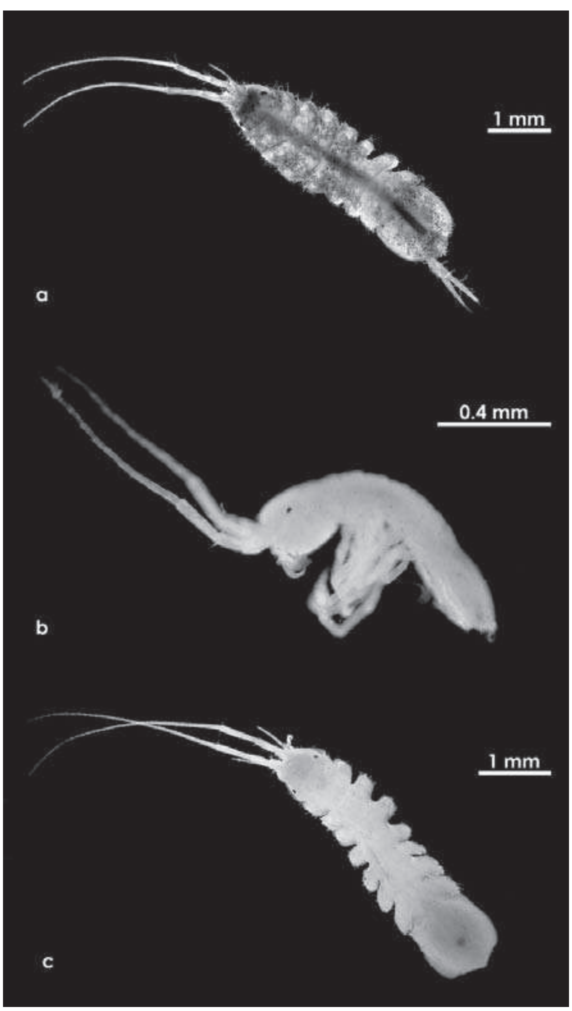

Fig. 3 - Pictures of the different morphs of *Caecidotea racovitzai australis* present in Florida: a) specimen from Wekiwa Spring (Seminole County); b) Morph A collected in a well in Rocky Glades (ENP); c) Morph B collected in a crayfish hole in Pineland (ENP).

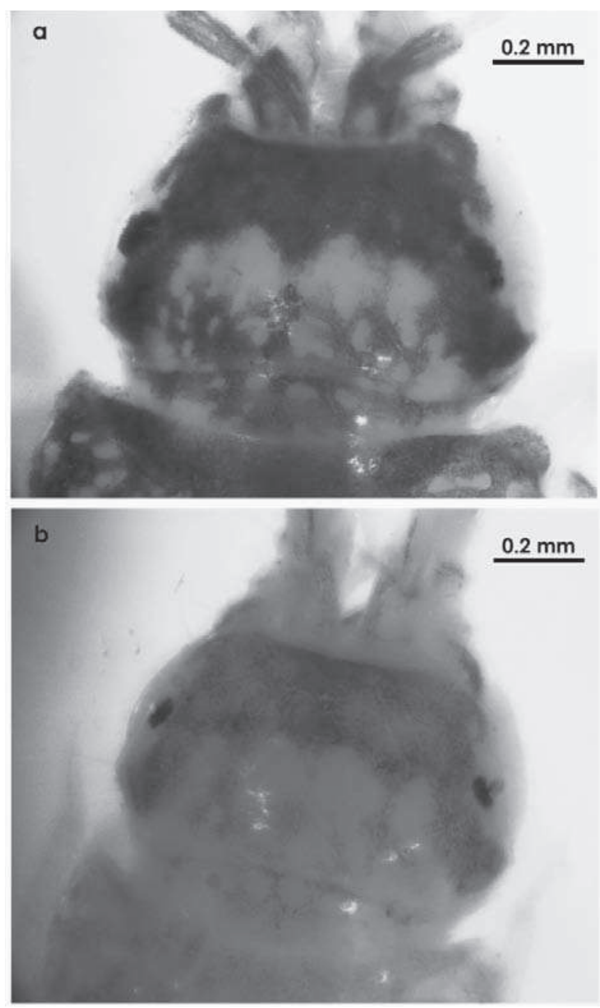

Fig. 4 - Pictures of the cephalothorax of *Caecidotea racovitzai australis*: a) specimen collected in Econlockhatchee River (Central Florida), epigean morph; b) specimen collected in a crayfish hole in Pineland (ENP), stygophile morph.

and wetlands cover a substantial part of the territory. The recent geological age of the Everglades may not have allowed sufficient time for populations of *C. racovitzai australis* to completely adapt to life in subterranean habitats.

The two morphs collected in ENP could correspond to two stages in the life cycle of *C. racovitzai australis*; in fact most of the juveniles collected belonged to the morph A and adults to morph B. Adults (morph B) were concentrated in the crayfish holes which, for their small size, might represent the most appropriate refuge for small invertebrates (Rader 1999). The same habit was reported for *C. hobbsi* (Steeves 1964). Juveniles (morph A) were collected in groundwater habitats and it is possible that their smaller size increases the ability to move through the porous matrix of the surface limestone. In fact, karst aquifers are traditionally characterized by three types of porosity: interparticle matrix porosity, fracture porosity, and large cavernous porosity (Martin and Screaton 2001). In the young eogenetic karst that defines the Pleistocene limestone of the Biscayne aquifer, however, a fourth porosity type, touching-vug porosity, is especially important in terms of conveyance of ground water (Vacher and Mylroie 2002; Cunningham et al 2006), and thus the porosity could represents a preferential pathway for the movement of organisms. In particular, it is possible that different developmental stages of *C. racovitzai australis* in the Everglades follow the yearly hydrological cycle moving from surface waters, where the adults reproduce, to groundwater, where the juveniles complete the larval development.

The colonization of the subterranean environment is a debatable matter, and follows two main models. The subterranean environment has been viewed as a "special" one, where animals actively find a refuge against climatic vicissitudes (the "refugium model", Vandel 1964; Barr 1968). On the other hand, according to the "active colonization model" (Rouch and Danielopol 1987), the subterranean environment is viewed as a "normal" one, i.e. it does not represent a refuge. Following this model, there are no compelling forces to colonize the subterranean environment, but preadaptations to life in the sediment such as the appearance of progenetic forms in an epibenthic population may be positively selected (Coineau and Boutin 1992). According to Stoch (1995), surface populations invade subterranean habitats to exploit a new set of resources; and only stochastic colonization by a founder with preadaptation to the new site is an event conducive to speciation. In this perspective, the morphs of *C. r. australis* of ENP could represent a phase in the colonization process of surficial karstic groundwater. Populations such as those collected in central Florida are epigean benthic forms with little or no apparent stygomorphy and could represent potential epigean ancestors of stygobionts. Populations in ENP are semi-hypogean, eyes and pigment have become rudimentary, preadaptation to life in subterranean waters are represented by paedomorphic individuals. A last step would be represented by stygobitic populations, restricted to life in subterranean waters. This colonization may be followed by the interruption of gene flow and speciation, following the "adaptive zone model" (Stoch 1995).

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