Cladocera of the Lençóis Maranhenses (NE - Brazil): faunal composition and a reappraisal of Sars' Method

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(With 12 figures)

Abstract

We studied the Cladocera of a group of ephemeral interdunal pools in the Lençóis Maranhenses, Maranhão State (NE - Brazil) and recorded 34 species. The fauna was overwhelmingly neotropical, with no evidence of invasive species. Species composition differed in Lagoa da Colher, an acid system. We provide notes on behaviour, morphology and taxonomy of some lesser-known anomopods, with emphasis on the Chydoridae. We figure male *Oxyurella longicaudis, Chydorus eurynotus, Disparalona leptorhyncha, Alonella dadayi* and *A. clathratula*. We provide notes on the "Sars' Method", hatching of freshwater crustaceans from dry mud, a simple technique that complements the information of hit-and-run surveys. About half of the total species number (44%) was revived through this method; 18% of species were additional to field-collected samples. The Sars' method also yielded abundant specimens of rare species, useful for identification and studies on behaviour.

Keywords: Cladocera, Lençóis Maranhenses, Sars' method, hatching, ephemeral dune pools.

Cladocera dos Lençóis Maranhenses (NE-Brasil): composição faunística e uma reavaliação do método de Sars

Resumo

Os cladóceros de um grupo de lagoas temporárias dulcícolas interdunares nos Lençóis Maranhenses, Maranhão (NE - Brasil) foram estudados e registraram-se 34 espécies. A fauna foi tipicamente neotropical, sem evidências de espécies invasoras. A composição de espécies foi diferenciada na Lagoa da Colher, que constitui um sistema ácido. Informações sobre comportamento, morfologia e taxonomia de alguns anomópodes menos conhecidos são fornecidas, com ênfase nos membros da família Chydoridae. Os machos das espécies *Oxyurella longicaudis, Chydorus eurynotus, Disparalona leptorhyncha, Alonella dadayi* e *A. clathratula* foram registrados com desenhos. Foram dadas informações sobre o "método de Sars", o qual consiste na eclosão de microcrustáceos de água doce a partir de ovos de dormência presentes no sedimento seco, uma técnica simples, que complementa as informações de coletas realizadas em limitados intervalos de tempo e espaço. Aproximadamente metade das espécies encontradas (44%) também estava presente nas culturas; 18% das espécies foram registradas apenas nas culturas e complementaram as amostras obtidas no campo. Com o "método de Sars", também se registraram abundantes espécimes de espécies raras, o que se mostra útil para a identificação e estudos sobre comportamento.

Palavras-chave: Cladocera, Lençóis Maranhenses, método de Sars, eclosão de ovos, lagoas temporárias interdunares.

1. Introduction

During 1996 and 1997 (KVD), ephemeral pools were sampled in the NE of the Lençóis Maranhenses, Maranhão state, Brazil. Five lagoon systems and smaller pools were studied. Studies on limnology and phytoplankton communities of interdunal pools and a few permanent lakes in the area were carried out by Moschini-Carlos et al. (2008); Espíndola et al. (1998); ichtyofauna by Garavello et al. (1998). Little is known about the zooplankton of the Lençóis (Rocha et al., 1998). Branchiopod research in the Neotropics is becoming increasingly sophisticated, with Mexico, Brazil and Venezuela taking the lead (e.g., Hollwedel et al., 2003; Elmoor-Loureiro, 2007; Zoppi de Roa and Vasquez, 1991; Elías-Guttierez et al., 2008; Zoppi de Roa and López, 2008). Yet, more faunistic studies from Brazil are required (e.g., Hollwedel et al., 2003; Elmoor-Loureiro, 2007), as many species remain poorly known while new taxa keep being discovered (e.g. Sinev and Hollwedel, 2002) and checklists (e.g., Green, 1981) need updating.

Specimens from our surveys in the Lençóis previously used in studies of Neotropical Cladocera include *Leydigia parva* (Daday, 1905), allocated to the new genus *Parvalona* in Van Damme et al. (2005). Also, the redescriptions of the Cladocera *Leydigia* cf. *ciliata* Birabén, 1939, *Ilyocryptus sarsi* Stingelin, 1913 and *Macrothrix paulensis* (Sars, 1900) included animals from the Lençóis (Kotov et al., 2002, 2003; Kotov and Hollwedel, 2004). The current paper, based on the 'licentiate' (M. Sci.) thesis of Kay Van Damme (1998), with some new records and updates in taxonomy, discusses the full complement of Cladoceran taxa found. Limnological data gathered in the field by M.O.A. Ibañez Rojas and KVD in August 1996, was written up in an unpublished report (Ibañez, MSR. and Ibañez, MOA., 1996), integrated in the thesis.

1.1. Study area – the Lençóis Maranhenses

The Lençóis Maranhenses is a 155,000 ha coastal National Park in NE - Brazil, situated between 02° 19'-02° 45' S and 42° 45'-43° 29' W (Abakerli, 2001), with a perimeter of 270 km and extending 50 km inland (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, 1989; Secretaria de Estado do Meio Ambiente e Turismo, 1991). The name originates from its blanket of white sands. The Lençóis are a unique 'tropical desert', consisting of high transverse sand dunes, perpendicular to the dominant wind direction. In depressions between the dunes, thousands of intermittent freshwater pools form as a result of the rains and rise from the aquifer (Nov-May). The temporary pools cover 41% of the dune field (Levin et al., 2007) and are relatively large for dune pools (Moschini-Carlos et al., 2008). Mean annual temperature is about 26 °C (16-36 °C), annual precipitation is 1500-1750 mm and the area is subject to strong SE-winds (Secretaria de Estado do Meio Ambiente e Turismo, 1991). The eastern border of the "big Lençóis" is formed by the Rio Preguiças. The river and surrounding areas hold a valuable fauna (e.g., *Trichechus manatus* Linnaeus, 1758; *Trachemis adiutrix* Vanzolini, 1995) (Abakerli, 2001; Vanzolini, 1995), vegetation in Carvalho (1993). This Brazilian National Park is under pressure from tourism, off-track rallies and infrastructure works (Abakerli, 2001). At the time our collection was made (1996-1997), the aquatic environment of the Lençóis was still in pristine condition, relatively free of invasive species and human disturbance.

The Lençóis are an Ice Age Relict, of Pleistocene (or late Pliocene) age. During low sea levels, its area extended north and was much larger. The age of the dunes is between 12,000 and 5,000 years (Carvalho, 1993; Dominguez and Bittencourt, 1996; Pessenda et al., 2004). The thousands of large and small pools that form annually are an ideal study area for freshwater branchiopods capable of surviving drought by forming resting eggs.

1.2. Description of habitats and sampling sites (Figures 1-2)

All localities sampled were in the East, near the village of Atins (Figure 1) at the mouth of the Preguiças River. Dune pools are of two types: type I, clear waters (Figure 2a) with pH neutral to basic, and type II, dark acid waters. Type I waterbodies are electrolyte-poor, oligotrophic "white" waters, mostly poor in vegetation, low in conductivities (77-90 and 134-152 µS.cm^{-1}), high in oxygen (7.63-8.89 mgO$_2$L^{-1}). One Type II water, Lagoa da Colher, had lower pH (4.2-5.7), low conductivities (84-90 µS.cm^{-1}) and lower oxygen levels (7.56-7.87 mgO$_2$L^{-1}), very low in two fragmented pools (0.95-0.99 mgO$_2$L^{-1}), which were high in phosphate (376-486 µg.L^{-1}) and with humic acids, coloured dark brownish red. Low vegetation (Xyridacaea, Echinocaulaceae) in the dry pools fix the sand, helping to maintain a branchiopod eggbank (Figure 2).

S1. Dune Pool 1 west of Atins (2° 34' 42" S and 42° 46' 36" W). Main pool 120 × 40 m, 1 m deep, oriented SW-NE. Three samples, one from main water, sandy bottom devoid of vegetation and with little detritus (S1A), one from vegetation in main water (S1C) and from small pool split off by drying, shallow, with vegetation (S1B). Main water a typical dune pool with clear water and low conductivities (77-88 µS.cm^{-1}), temperatures 29-33 °C, pH 7.3-7.7, and oxygen near saturation (7.63-8 mgO$_2$L^{-1}). Vegetation: none in S1A; S1B-C with *Utricularia* sp. in water, *Xyris* sp., *Paepalanthus* sp. on sides, scarce submerged Cyperaceae and Juncaceae. Floating vegetation (S1C) *Nymphoides* sp. Invertebrate fauna rich (aquatic insects, cnidarians *Hydra* sp., oligochaete *Pristina evelinae* Marcus, 1943, etc). Branchiopods dominated by *Cyclestheria hislopi* (Baird, 1859), *Leydigiopsis curvirostris* Sars, 1901, *Alona ossiani* Sinev, 1998 in main water (S1A). Between vegetation (S1C), *Latonopsis australis* Sars, 1888 and *Ephemeroporus* sp. In smaller pool (S1B), mainly *Leydigiopsis* and *Alona ossiani*. Sampled 16.VIII.1996 by K. Van Damme and D. Van Damme. **S2. Dune Pool 2 west of Atins** (2° 34' 38" S and 42° 45' 59" W). Sampled in dry season, 23.XII.1997 by K. Van Damme. In the culture, *Chlamydotheca* (ostracod), rotifers, copepods, nematodes. Cladocera, see Table 1. **S3. Dune Pool 3 west of Atins** (2° 34' 31" S and 42° 43' 20" W). Sickle-shaped dune pool, 1 km × 100 m, 2 m deep, drying out and fragmenting in three smaller pools. Largest pool transparant, smaller ones reddish brown. Conductivity low (84 µS.cm^{-1}), oxygen near saturation (8.24-8.38 mgO$_2$L^{-1}), temperature 31-34 °C in the larger waterbody (S3A), up to 36 °C in the smaller (S3D). Water neutral to basic (pH 6.35-9.16). Flora and accompanying fauna largely as for S1, but with *Ampullaria* sp. (Mollusca), freshwater crabs (*Pseudotelphusa*), small fish and ostracods (*Stenocypris*). *Cyclestheria hislopi* in the main pool, *Alona ossiani, Alona verrucosa* Sars, 1901, *Ephemeroporus* and *Macrothrix* in the smaller (S3B-C). Samples taken 16.VIII.1996 by K. Van Damme and D. Van Damme. **S4. Lagoon W of Mandacaru, SE of Atins** (2° 35' 50" S and 42° 42' 46" W). Just outside of the mobile dunes between dunes fixed by cerrado-vegetation. Main water 100 × 80 m, up to 3 m deep (S4A). An additional ditch just adjacent to the waterbody (S4B). Conductivity highest in the waters sampled here (134-152 µS.cm^{-1}), oxygen near saturation (8.47-8.44 mgO$_2$L^{-1}), water temperatures 31 °C and pH 8.43-8.48. Dense macrophyte stands. Fauna

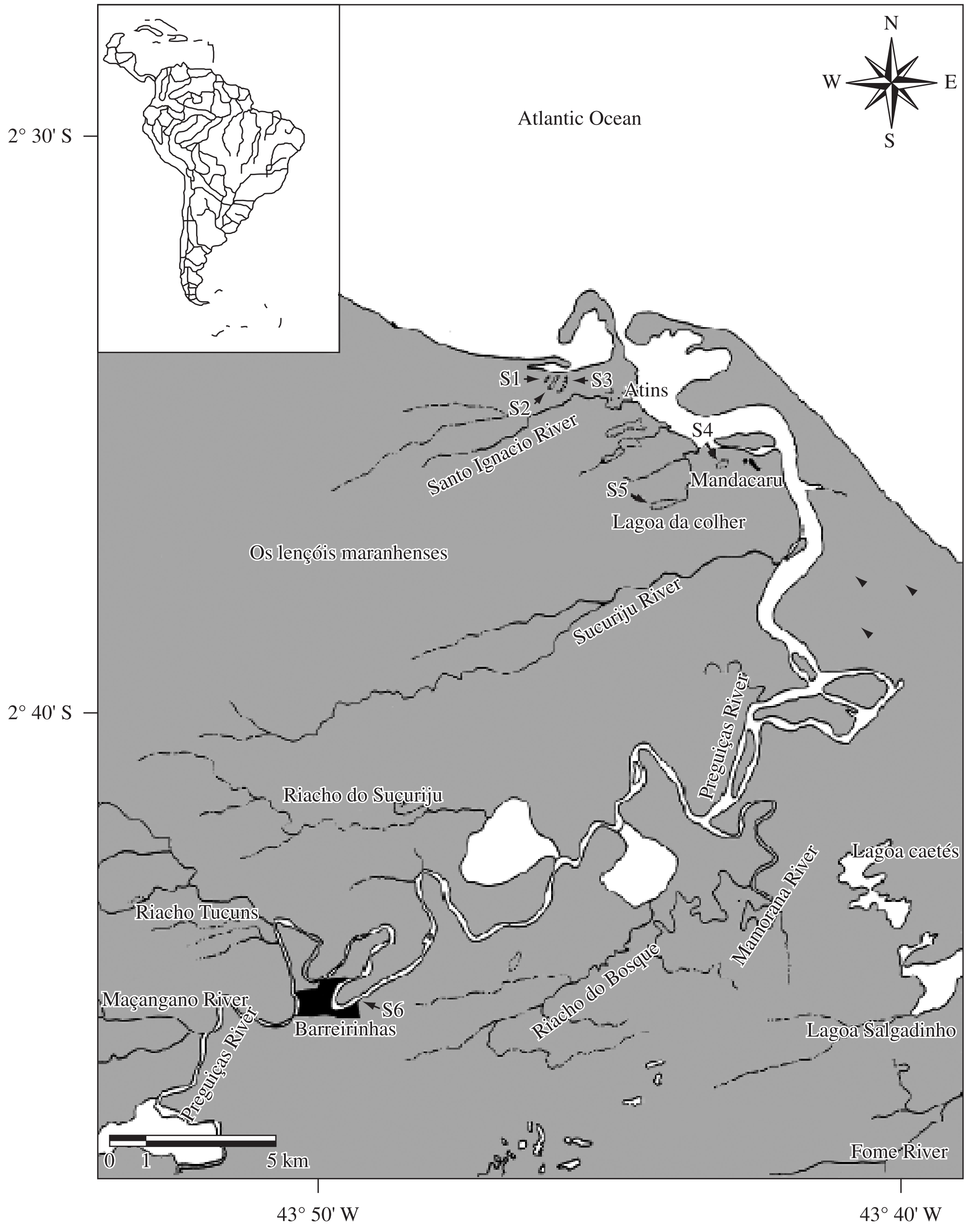

Figure 1. Map with localities in the Lençóis Maranhenses National Park (NE - Brazil) sampled for this study.

with amphibians, small fish (even though the water is temporary), *Ampullaria* (mollusca), copepods, aquatic insects as for previous, and ostracods (*Stenocypris* sp.); a drought-resistant larva of *Pantala flavescens* appeared in cultures from this locality (Van Damme and Dumont, 1999). Branchiopod fauna with *Cyclestheria*, *Eulimnadia* cf. *colombiensis* Roessler, 1989, *Chydorus eurynotus* Sars, 1901, *Alonella clathratula* Sars, 1896, *Leydigiopsis, Ephemeroporus hybridus* (Daday, 1905), *Alona verrucosa.* Sampled 16.VIII.1996 (wet samples) by K. Van Damme, this water dries out completely in summer, mud samples taken on 24.XII.1997 by K. Van Damme. **S5. Lagoa da Colher, acid lagoon in cerrado, SW of Mandacaru** (2° 36’ 45” S and 42° 43’ 30” W). Largest of all waters investigated (2.5 × 0.5 km), up to 2 m deep. Main waterbody (S5A-B) and two adjacent pools (S5C-D) sampled. Swamp-like at margins, fragmented into dystrophic pools, rich in detritus. Not transparent as previous pool, with abundant

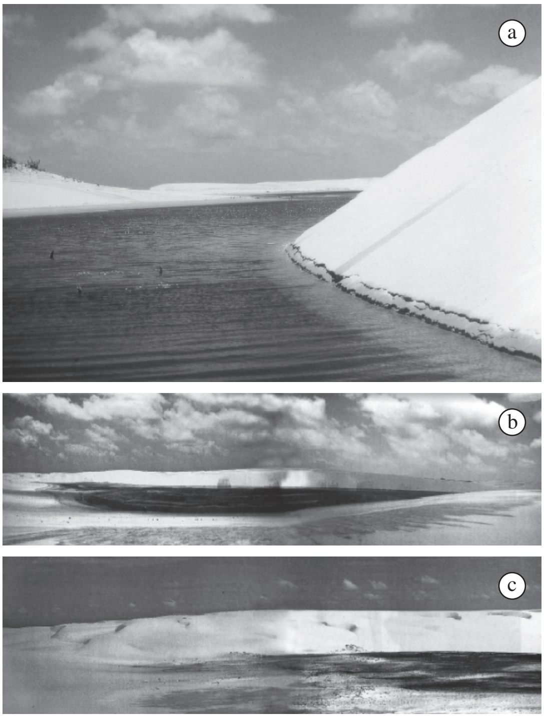

Figure 2. The Lençóis Maranhenses ephemeral dune pools W of Atins. a) - b) Waterfilled pools in rainy season, sampling sites 2 (a) and 3 (b), W of Atins. c) Same locality as b, in dry season. Small grassy herbs (dark areas; mainly *Xyris* sp., Xyridaceae and *Paepalanthus* sp., Eriocaulaceae) fix the sand and allow the persistence of local branchiopod eggbanks. Photos by KVD.

Juncaceae; marginal pools dark brown. Conductivity 84-88 μS.cm^{-1}, oxygen near saturation (7.56-7.87 mgO$_2$L^{-1}) in main pool (S5A-B) but nearly anoxic in smaller pools (0.95-0.99 mgO$_2$L^{-1}; S5C-D). Temperature ca 30-32 °C, pH between 4.25 and 5.7 in main waterbody (S5A-B), very low (4.2-4.24) in smaller waterbodies (S5C-D). Total PPO$_4^{3-}$ extremely high in latter two habitats, which were filled with leaf litter (376-486 μg.L^{-1}). Marginal vegetation *Drosera* sp., Poaceae, Cyperaceae and Juncaceae. Branchiopods: *Macrothrix, Streblocerus, Ilyocryptus* and *Disparalona*. Most acid waters with relatively larger abundances of *Alonella, Alona iheringula* Kotov and Sinev, 2004 and *Chydorus dentifer* Daday, 1905. Fish stomachs contained *Cyclestheria* and *Leydigiopsis*, rare in water samples. Samples taken on 17.VIII.1996 by K. Van Damme and D. Van Damme. **S6. Rio Preguiças at Barreirinhas boat port.** No vegetation at sampling point. Zooplankton dominated by *Bosminopsis deitersi* Richard, 1895. Sample 17.VIII.1996 by K. Van Damme.

2. Materials and Methods

2.1. Wet samples

Qualitative samples were taken using a plankton net of 35µm mesh. Fixation with 4% formaldehyde. Emphasis on the littoral (aimed at collecting Chydoridae). Temperature and conductivity measured with a Beckman field sensor; oxygen by Winkler titration. Animals were observed live using a Leica Wild M10 stereomicroscope under natural light and drawn with a Leica Orthoplan II microscope under dark field with *camera lucida*.

2.2. Mud samples and Sars' method

Samples were collected from the upper layer of soil, mostly curled up crusts, about 300 g per locality, from the middle and the sides of depressions. If still wet, mud samples were first dried, sealed in plastic bags, stored in darkness at room temperature. A fraction of sample was incubated by adding 1.8 L of cold (6-10 °C) distilled water to 30(-40)g of sediment in a 2 L plastic aquarium. Water added was cold, a cue for hatching. Culture next placed in a water bath at 25-28 °C, under constant light (1,500 Lux) in the first week and a photoperiod of 12/12 after; moderate aeration (no constant addition of oxygen and no water movement). If fungi developed, the culture was diluted. Not too much sediment was used, to ensure maximal hatching (fine layer of sediment on bottom instead of a thick layer that might cover ephippia). Crusts were fragmented gently with a forceps to disperse material; material sticking to the sides was rinsed down using a pipette. Distilled water was added from time to time. Filamentous algae were removed if developing abundantly, but virtually no other maintenance needed. Larger animals that may prey on cladocerans were removed but small ostracods that seemed to have a positive effect on Chydoridae were not. Incubations were maintained for more than two years and checked weekly, either by filtering over a 35 µm plankton net or by pipetting up the animals. Young stadia were attracted by a beam of flashlight. Animals picked out were transferred to fresh cultures with distilled water (same temperature as original) and fed algae (*Scenedesmus*). Not all animals thrived well outside the original culture, e.g., *Leydigiopsis* and *Leydigia* needed detritus of the original culture. No plants or food was added to the cultures, but plants that appeared from seed banks were kept. To test temperature tolerances, we lowered the temperatures (from 28 to 25 to 20 °C) and checked a few days later (in most cases, temperatures below 20 °C resulted in rapid loss of diversity and abundance).

3. Results –Taxonomical Accounts and Observations

An overview of species recorded is given in Table 1.

DAPHNIIDAE

Simocephalus cf. *brehmi* Gauthier, 1939 - Figure 3

(*Simocephalus acutirostratus* species group)

Zoppi de Roa and Vasquez (1991; *S. acutirostratus*); Brehm (1937, 1938; *S. acutirostratus*); Elmoor-Loureiro (1997; *S. acutirostratus*).

Table 1. Branchiopoda from the Lençóis Maranhenses (NE-Brazil). Distributions: CT (circumtropical), N (Neotropical), US-N (Southern US and Neotropics), N* (Neotropics, records outside this region are unclear). (x) indicates skeletal parts, no complete specimens, x indicates a single specimen, X several specimens.

	S1A	S1B	S2cult	S3A	S3B	S3C	S3D	S4	S4cult	S5A	S5B	S5C	S5D	S6	Distr
Cyclestherida															
Cyclestheria hislopi	X	X	X	X	X	X	X	X	X	X	-	-	-	-	CT
Spinicaudata															
Eulimnadia cf. *colombiensis*	(x)	(x)	X	(x)	-	-	-	-	X	-	-	-	-	-	N
Ctenopoda															
Latanopsis australis	X	X	X	X	X		-	X	X	X	-	X	-	-	CT
Anomopoda															
Daphniidae															
Ceriodaphnia cornuta	-	-	-	-	-	-	-	-	X	-	-	-	-	-	CT
Scapholeberis freyi	-	-	-	-	-	-	-	-	X	x	-	-	-	-	N
Simocephalus cf. *brehmi*	-	X	-	-	X	-	-	-	X	-	-	-	-	-	N
Bosminidae															
Bosminopsis deitersi	-	-	-	-	-	-	-	-	-	-	-	-	-	X	CT
Ilyocryptidae															
Ilyocryptus sarsi	-	X	-	X	X	-	-	X	-	X	X	X	X	-	N
Ilyocryptus spinifer	-	-	-	-	-	-	-	-	-	-	X	-	-	X	CT
Macrothricidae															
Macrothrix sioli	-	-	-	-	-	-	-	-	-	-	X	-	-	-	N
Macrothrix elegans	X	-	X	-	X	X	-	X	-	-	X	-	-	-	N
Macrothrix paulensis	-	-	-	-	-	-	-	-	-	-	-	-	X	-	N
Streblocerus pygmaeus	X	X	-	X	X	X	X	X	-	X	X	-	X	-	N*
Chydoridae – Aloninae															
Alona brandorffi	-	-	-	-	-	-	-	X	-	-	-	-	-	-	N
Alona iheringula	-	-	-	-	-	-	-	-	-	-	-	-	X	-	N
Alona monacantha	-	-	-	-	-	-	-	-	-	-	-	-	X	-	N
Alona n.sp. (verrocosa group)	-	-	-	X	-	-	-	-	-	-	-	-	X	-	N
Alona ossiani	X	X	-	X	X	-	-	-	-	-	-	-	X	-	N
Alona verrucosa	-	-	X	X	-	-	-	-	-	-	-	-	-	-	N
Camptocercus sp.	-	-	-	-	-	-	-	-	-	-	-	-	(x)	-	-
Graptoleberis occidentalis	-	-	-	-	-	-	-	X	-	-	-	-	-	-	N
Karualona muelleri	X	-	-	X	-	-	X	X	X	-	-	-	-	-	N
Leberis davidi	-	-	X	-	-	-	-	-	-	-	-	-	-	-	N
Leyidigia cf. *striata*	-	-	X	-	-	-	-	-	-	-	-	-	-	-	N
Leydigiopsis curvirostris	X	X	X	X	X	X	X	X	X	X	-	-	-	-	N
Leydigiopsis ornata	-	-	-	-	-	-	-	X	X	-	-	-	-	-	N
Oxyurella longicaudis	-	-	X	(x)	-	-	-	-	-	-	-	-	-	-	US-N
Parvalona parva	-	-	-	-	-	-	-	X	-	-	-	-	-	-	N
Chydoridae – Chydorinae															
Alonella dadayi	-	-	-	-	-	-	-	-	-	-	-	-	X	-	US-N
Alonella clathratula	-	-	-	-	-	-	-	X	-	-	-	-	-	-	CT
Chydorus dentifer	-	-	-	-	-	-	-	-	-	-	-	-	X	-	N
Chydorus eurynotus	-	-	-	-	-	-	-	X	X	-	-	-	-	-	CT
Disparalona leptorhyncha	-	-	-	-	-	-	-	-	-	X	-	-	-	-	N
Dunhevedia odontoplax	-	-	X	-	x	-	-	-	X	-	-	-	-	-	N
Ephemeroporus acanthodes	X	X	-	-	-	-	-	-	-	-	-	-	-	-	US-N
Ephemeroporus hybridus	X	X	X	X	X	-	X	X	X	-	-	-	-	X	US-N
# clad. spp. per sample	8	8	9	9	9	3	4	12	10	6	5	2	10	3	
# clad. spp. per locality	11		9	12				14		17				3	

The *S. acutirostratus*-group stands out by two supra-anal angles (Figure 3f) and a pecten on the basal claw of the postabdomen (Figure 3g, h), combined with a long rostrum (Figure 3a-c); Neotropical *S. acutirostratus* need re-examination (Orlova-Bienkowskaja, 2001). Specimens from the Lençóis do not fit *S. acutirostratus* (from N. America), nor *S. brehmi* (from Africa). Characters that distinguish them are: 1) an acute proximal angle on the postabdomen (Figure 3f; like *S. brehmi*) and distal marginal spine on the postabdomen less than half its length from the basal claw (Figure 3h; unlike *S. brehmi*), 2) shallow to no depression above and below posterior valve prominence (Figure 3a; like *S. acutirostratus*), which has long spines (Figure 3d); 3) An elongate, sharp rostrum and relatively large eye and ocellus (Figure 3b, c).

Our animals may represent a new Neotropical representative of the *S. acutirostratus* group. Pending assignment of a name, we here refer to it as

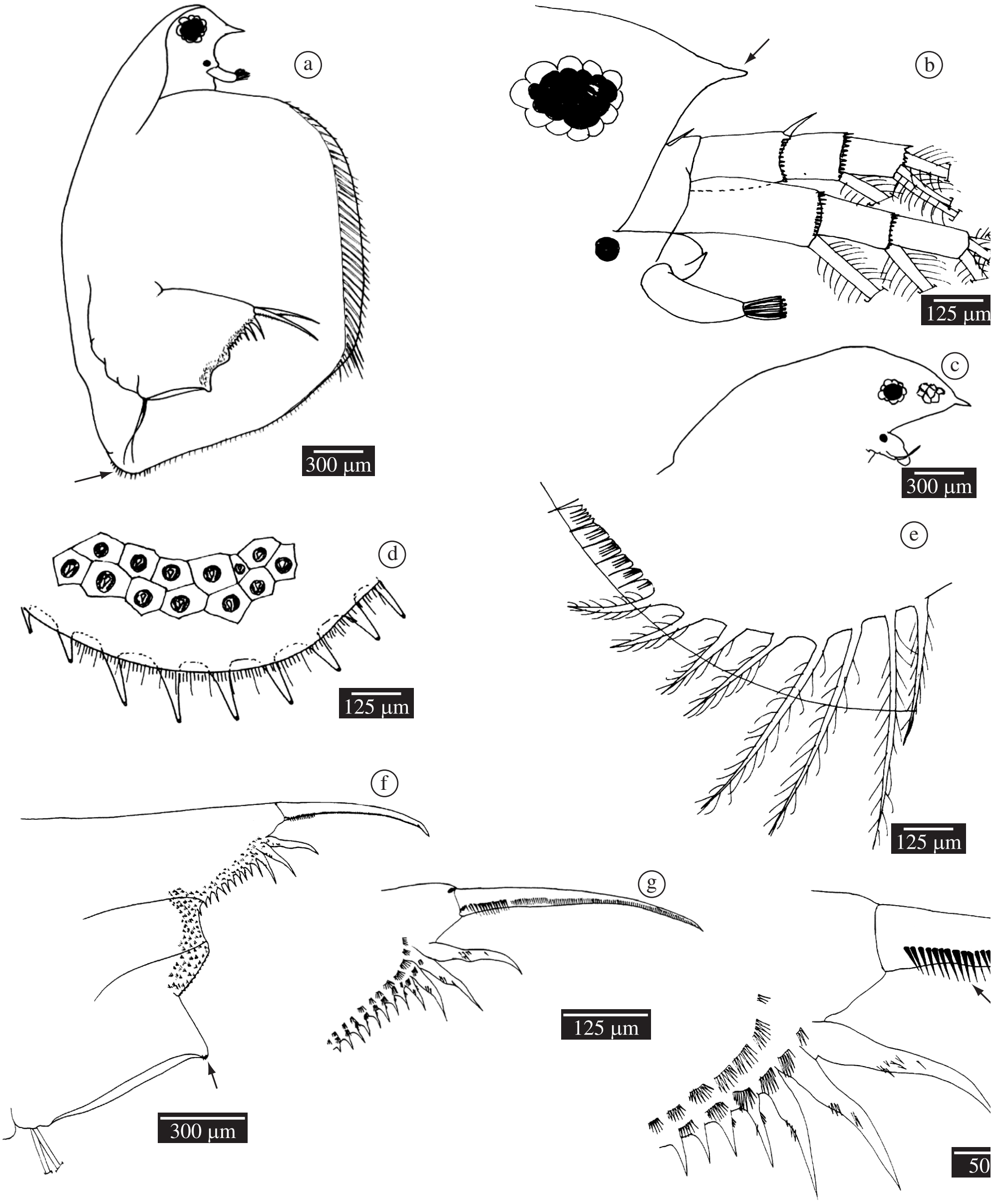

Figure 3. *Simocephalus* cf. *brehmi* Gauthier, 1939 of the *Simocephalus acutirostratus* species group, adult parthenogenetic females from dune pools W of Atins, Lençóis Maranhenses, NE-Brazil. a) Habitus; b) Head with pointed rostrum (arrow); c) Idem; d) Posterodorsal valve corner with ornamentation and armature; e) Posterior ventral valve setae; f) Postabdomen with acute supra-anal angle (arrow); g) Idem, distal portion, h) Idem, detail of distal portion showing well-developed proximal pecten (arrow).

Simocephalus cf. *brehmi.* Other regional records likely correspond to the same taxon (e.g., Brazil, Brehm, 1937, 1938; Venezuela, Zoppi de Roa and Vasquez, 1991; Elmoor-Loureiro, 1997).

Few specimens in samples from S1(C) and S3, between vegetation. The species hatched from the culture of S4.

Scapholeberis freyi Dumont and Pensaert, 1983

(= *Scapholeberis armata freyi* Dumont and Pensaert, 1983)

Only one specimen was found of this species in the Lençóis at a pH of 5.4 (in S5A), yet the animal developed in our cultures from S4. Dumont and Pensaert (1983) considered this a subspecies of the North American *S. armata,* but it likely represents a good species, restricted to the Neotropics, although a thorough revision of the genus, including limbs, is necessary. Elmoor-Loureiro (2000) confirmed this animal to have a wide distribution in Brazil.

ILYOCRYPTIDAE

Ilyocryptus sarsi Stingelin, 1913

A member of the *I. sordidus* group, redescribed on specimens from the Lençóis (Kotov et al., 2002; Kotov and Stifter, 2007). Present in most waters of the Lençóis, with more specimens in the acid waters of S5. For keys to the genus *Ilyocryptus,* see Kotov and Stifter (2007). A second species of *Ilyocryptus* occurred in Lagoa da Colher and Rio Preguiças (Table 1).

MACROTHRICHIDAE

Macrothrix elegans Sars, 1901

Abundant in the Lençóis, in nearly all samples. Larger populations in small pools at low pH and oxygen levels (S5). Appeared in the cultures; live observations correspond to those by Sars (1901). Could be cultured easily at 25 °C and fed algae. One of the most common *Macrothrix* species in the Neotropics (Kotov et al., 2004). Two other *Macrothrix* species were found, both of the *M. paulensis*-group, *Macrothrix paulensis* (Sars, 1900) and the large (0.7 mm) *M. sioli* (Smirnov, 1982), both restricted to the acid systems (Table 1). For notes on Neotropical *Macrothrix* and *M. paulensis*-group, see Kotov and Hollwedel (2004).

Streblocerus pygmaeus Sars, 1901

This small species occurred in nearly all pools sampled, including the acid Lagoa da Colher. Did not appear in our cultures.

CHYDORIDAE

Leydigiopsis curvirostris Sars, 1901 – Figure 4

Redescribed by Sinev (2004b). Females 0.8-1 mm, easily recognised by the curved elongate rostrum, the tip about two antennular lengths from the antennule itself (Figure 4a, b) and ocellus of similar size as eye. Head pores connected, with constricted margins (Figure 4c). Postabdomen rather wide, about 2.5 times as long as wide (Figure 4f), with minute basal spine on basal claw and straight marginal teeth (Figure 4e). Marginal teeth single, 20-25 in number of which 1-16 large postanal; preanal margin about as long as anal margin (Figure 4f); lateral fascicles in groups of three-four denticles (Figure 4e). Second limb with relatively larger teeth on seventh scraper (Figure 4g). Males 0.8 mm long, body oval with dimensions 1.8 times as long as wide, shorter rostrum than female, reaching just beyond antennular apex (Figure 4c). Male and female postabdomen similar, with low sexual dimorphism, typical for genus (Figure 4d).

Biology. Besides Sars (1901), no notes of live *Leydigiopsis* exist. We observed a similar feeding behaviour as in benthic *Leydigia,* studied by Fryer (1968), and active use of the exopodite pump. *Leydigiopsis* is a burying animal, reddish brown to red in colour, those ventures in water when disturbed or in the absence of detritus; it rarely leaves the bottom. Swimming is more efficient than in *Leydigia*. When stirred up in light, *Leydigiopsis* moves back towards the detritus. The species only hatched after two months, late in the succession of the pools. Temperatures for maintaining the population below 25 °C were suboptimal to 28 °C or higher. Could not be fed on algae (these clogged the feeding apparatus) or ciliates, only thrived in detritus from the original culture.

Neotropical species, mainly in the north: Venezuela (Rey and Vasquez, 1986b; Zoppi de Roa and Vasquez, 1991), Brazil (Sars, 1901) and Mexico (Elías-Gutiérrez et al., 2001). Common in the Lençóis and one of the main cladocerans in S1, but absent from acid waters; appeared in the cultures.

Leydigiopsis ornata Daday, 1905 – Figure 4

Redescribed by Rey and Vasquez (1986a), but rarely figured. Compared to the previous, *L. ornata* has a shorter rostrum, from antennular apex to rostral tip about once the length of the antennule (Figure 4h-k). Size about 0.9 mm, body 1.5 times as long as high, with highest point in the middle and round posterodorsal corner (Figure 4j). Ocellus similar to 1.5-1.8 times as large as the eye, but never larger (as in *L. megalops* Sars, 1901). Postabdomen elongate, three times as long as wide (Figure 4r). Postanal margin with 13-15 long marginal spines of which 10-11 distalmost longer (Figure 4q); distal spines strongly curved (Figure 4p). Preanal margin 1.5 to two times as long as anal margin, postanal margin relatively straight and parallel to ventral margin (Figure 4q). Small basal spine on terminal claw, but more a merged group of spinules (Figure 4h). Main head pores not constricted as in previous species, but straight lines and small pores minute and adjacent (Figure 4c). Second antenna with thick seta on first exopod segment (Figure 4m). Labral keel with elongate apex,

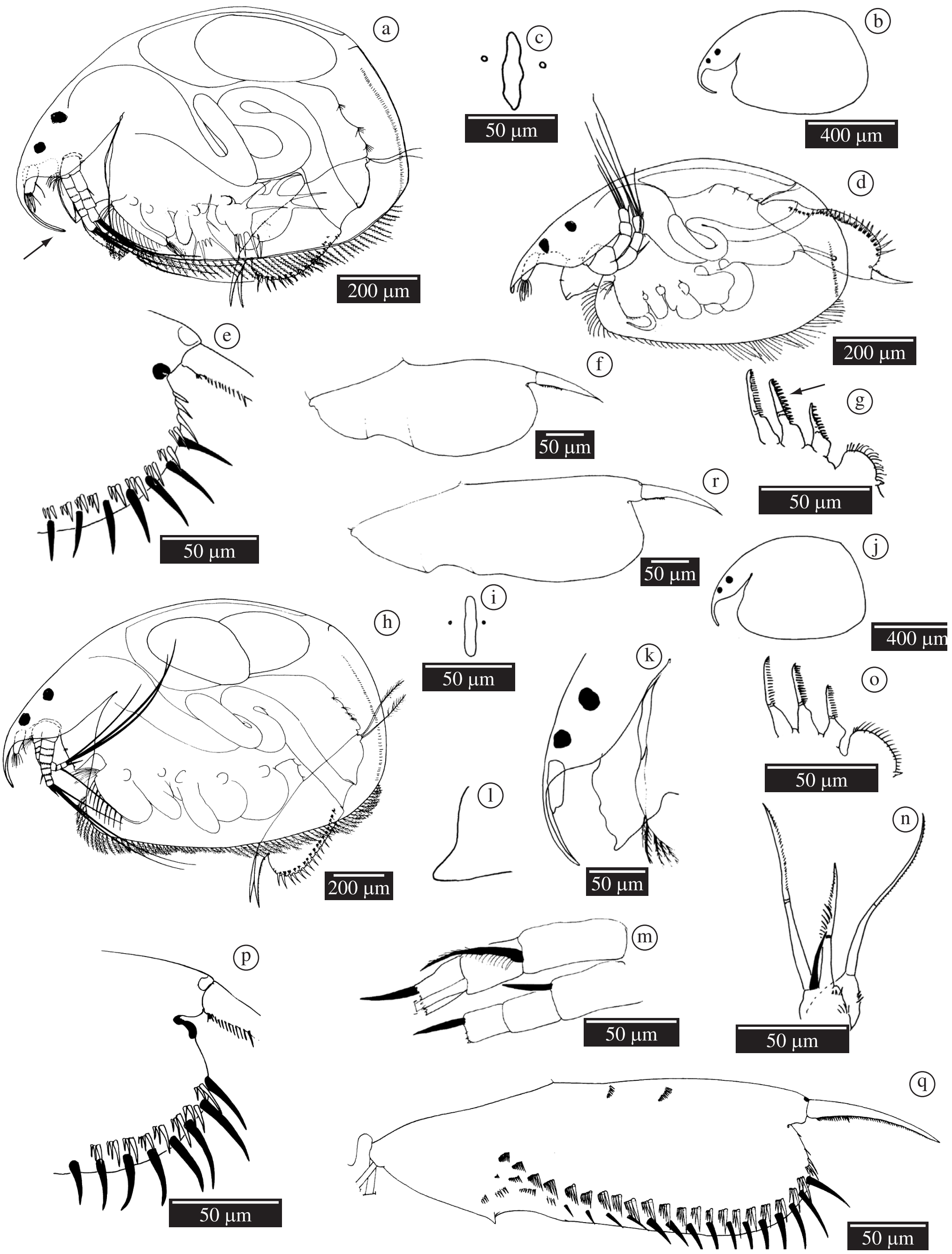

Figure 4. *Leydigiopsis* species, hatched from dried mud from the Lençóis Maranhenses. *Leydigiopsis curvirostris* Sars, 1901 adult parthenogenetic female (a-c,e-g) and male (d) and *Leydigiopsis ornata* Daday, 1905, adult parthenogenetic female (h-r). a) *L. curvirostris, a*dult parthenogenetic female, habitus; b) Idem, body outline; c) Head pores; d) Adult male; e) Postabdomen female, distal portion; f) Postabdomen, shape; g) Second limb, scrapers 6-8 and gnathobasic hillock; h) *L. ornata,* adult parthenogenetic female; i) Head pores; j) Body outline; k) Head and rostrum; l) Ventral tip labral keel; m) Antennal segments and spines; n) First limb, ODL and IDL; o) Second limb, scrapers 6-8 and gnathobasic hillock; p) Postabdomen, distal portion; q) Postabdomen, complete.

blunt, with a depression just above it (Figure 4l-k), sometimes with wavy margin (Figure 4k). First limb IDL with three setae of which longest three times the shortest seta (Figure 4n); second limb seventh scraper with fine armature (Figure 4o), not thick as in previous species.

Note. The species that seems closest to *L. ornata* is *L. megalops* (see Sinev, 2004b); length of rostrum and postabdomen are similar. In *L. ornata* the ocellus is smaller, mostly as small as the eye up to maximally two times as large, never three times as in *L. megalops* (according to Sars, 1901), seta on first exopod segment in *L. ornata* rather thick near the base. Postabdomen differs in general shape, that of *L. megalops* widens more towards the distal end (in Sinev, 2004b). In the populations in the Lençóis, *L. ornata* specimens had fewer marginal spines (13-15) in comparison to the redescription in Rey and Vasquez (1986a).

Biology (live observations) as for *Leydigiopsis curvirostris*, but swims faster and is more active under the same conditions (when both were seen together). Colour also differs, with *L. ornata* more yellow brown to brown, whereas *L. curvirostris* always had a reddish hue.

Only found in the Lençóis in samples and culture from Mandacaru (S4), sympatric with *L. curvirostris*. Neotropical species, found in Paraguay (Daday, 1905), Brazil (e.g. Brehm, 1937; Hollwedel et al., 2003), Venezuela (Orinoco, Rey and Vasquez, 1986a-b).

Parvalona parva (Daday, 1905) – Figure 5

Syn. *Leydigia parva* in Daday (1905); *Alona parva* in Smirnov (1971); Elmoor-Loureiro (1997); not *Birgeia travasossi* Bergamin, 1939; *Parvalona parva* in Van Damme et al. (2005); Elmoor-Loureiro et al. (2009).

Conspicuous chydorid, about 0.7 mm long, adapted to benthic life, similar to *Leydigia* (Figure 5a), but with a different postabdomen shorter lateral spines and longer basal spine on basal claw (Figure 5c). Originally *Leydigia parva*, transferred to *Alona* by Smirnov (1971), now considered as *Parvalona*. Redescription, including limbs, was based on type material and on specimens from the Lençóis, the first locality in Brazil (Van Damme et al., 2003).

Previously considered rare, Elmoor-Loureiro et al. (2009) showed it is actually widespread in Brazil and described the male. The latter has a peculiar,

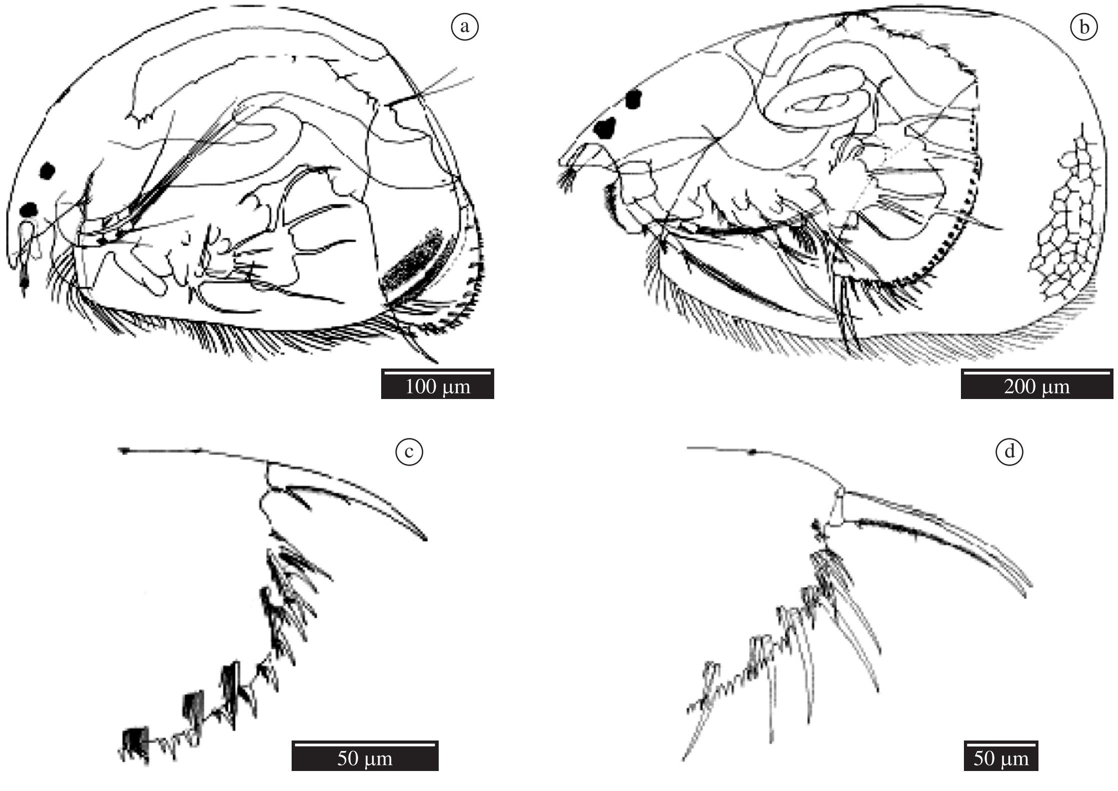

Figure 5. *Parvalona parva* (Daday, 1905) (a,c) and *Leydigia* cf. *striata* Birabén, 1939 (b,d), adult parthenogenetic females, from pool W of Mandacaru, Lençóis Maranhenses (*L.* cf. *striata* hatched from dried mud). a)-b) Habitus; c)-d) Postabdomen, distal portion.

elongate postabdomen, completely different from the female. Elmoor-Loureiro et al. (2009) found *Parvalona parva* under similar conditions as in S4, a small waterbody, between macrophytes and low conductivity (59 µS.cm^{-1}), pH just above neutral and oxygen levels 7.31 mg.L^{-1}. In the Lençóis, only two specimens were found in a sample at Mandacaru (S4A).

Neotropical species, only recorded in Brazil and Paraguay/Argentina (Daday, 1905; Van Damme et al., 2005; Elmoor-Loureiro et al., 2009).

Leydigia cf. *striata* Birabén, 1939 – Figure 5

Synonymy in Kotov et al. (2003); Kotov (2009)

A conspicuous *Leydigia* with short basal spine on postabdominal claw and setulated labral keel (Figure 5b), postabdomen with minute denticle in basal claw (Figure 5d). Specimens from the Lençóis served partly for redescription of this Neotropical species in Kotov et al. (2003). For a complete key to *Leydigia*, see Kotov (2009). Found through artificial hatching (S2), not in the samples. Bottom dweller, behaviour corresponded largely to observations in Fryer (1968). Hatched relatively late (like *Leydigiopsis*), after 1.5 months of culture, and thrived best in its original detritus at 25 °C.

Alona iheringula Kotov and Sinev, 2004 – Figure 6

Syn. *Alona iheringi* Sars, 1901 in Sars (1901); *Alona "iheringi"* in Hollwedel et al. (2003); *Alona rustica* Sars, 1862 in Elmoor-Loureiro (1998); Rey and Vasquez (1986b); Zoppi de Roa and Vasquez (1991).

Species of the *A. rustica*-group. Originally described as *Alona iheringi* Sars, 1901, redescribed by Sinev (2001). Kotov and Sinev (2004) argued that the latter name is invalid and proposed the name *Alona iheringula* for this taxon.

Similar to *A. guttata* Sars, 1862 and *A. costata* Sars, 1862, but postabdomen tapering distally, with relatively large teeth and a protruding dorsodistal margin with rounded corner (Figure. 6d, e). Body size about 0.5 mm, high, arched dorsum, body dimensions about 1.8 longer than high (Figure 6a). Labral keel with indentation and well developed labral setules (Figure 6c). Postabdomen with about seven well-developed merged postanal teeth, and up to three rows of lateral fascicles (Figure 6d, e). Second antenna with long spines, endopod spine on first segment reaching just beyond half of second segment, first exopod seta reaching half of third exopod segment (Figure 6f).

Valve ornamentation from smooth to tuberculate (Figure 6a) in a single population; half of the specimens showed valve retention (Figure 6b), known in few species with benthic lifestyle, like *Monospilus* and *Ilyocryptus*, but uncommon in Chydoridae.

In the Lençóis, found in one waterbody near Lagoa da Colher (S5D) between detritus and filamentous algae, at pH 4.2. Its closest relative, the Palaearctic *A. rustica,* is known from acid systems as well (Fryer, 1993); acid tolerance is perhaps a physiological adaptation typical for the *A. rustica*-group, to which this species belongs.

Alona monacantha Sars, 1901

Specimens in the Lençóis had three denticles on the posteroventral corner of the valves, known as var. *tridentata* Stingelin, 1905 (see Smirnov, 1971). We found no differences with real *A. monacantha* and the number of denticles varied. Actually a Neotropical species (Sinev, 2004a), but only two specimens retrieved from one locality in the Lençóis (S5D).

Alona ossiani Sinev, 1998

A. affinis (Leydig, 1860) in Sars (1901); Stingelin (1914); *Alona affinis* f. *ornata* Stingelin, 1895 in Zoppi de Roa and Vasquez (1991); *Biapertura affinis* in Elmoor-Loureiro (1997, 1998); *A. ossiani* in Sinev (1998); Hollwedel et al. (2003); Elmoor-Loureiro (2007).

Neotropical species of the *A. affinis* species complex (Sinev, 1998). Although abundant in the samples (S1, S3), females, males and ephippial females, this species did not appear in the cultures. Common in dune pools S1 and S3 and tolerant of acid (pH 4.2) conditions (S5D).

Alona verrucosa Sars, 1901

Alona verrucosa in Sars (1901); Brehm (1937, 1938); *Biapertura pseudoverrucosa verrucosa* in Smirnov (1971); Elmoor-Loureiro (1998);

Alona with S-shaped short postabdomen and short basal spine on the basal claw, redescribed in Sinev and Hollwedel (2002). In life, a slow and inefficient swimmer, comparable to *A. guttata*, bottom feeder, largely substrate-bound between detritus and filamentous algae. Scrapes off sand particles. Named "*verrucosa"* after the tubercles on the valves, but this is a plastic trait; specimens in cultures did not develop tubercles, whereas populations in the samples did. Twelve years after collecting mud from the Lençóis, *A. verrucosa* still hatched from unused material. Stenothermic, prefers temperatures around 25 °C; at 20 °C or lower, ephippial females and males occur, and postabdomen deformities result from defectuous moulting.

True *A. verrucosa* is Neotropical (Sinev and Hollwedel, 2002), and the species group is under revision. Abundant in cultures from S2. Also in acid (pH 4.2) pools, including with low oxygen in Lagoa da Colher, which shows that *A. verrucosa* Sars, 1901 may tolerate a wide range of pH, even dystrophic pools or swamps.

Two additional species from the *A. verrucosa*-group were found in the Lençóis: *Alona brandorffi* Sinev and Hollwedel, (2002). One specimen found of this strange *A. verrucosa*-like species, from S4. The record from the Lençóis is the second in Brazil (first in Sinev and Hollwedel, 2002). Third species is *Alona* sp.

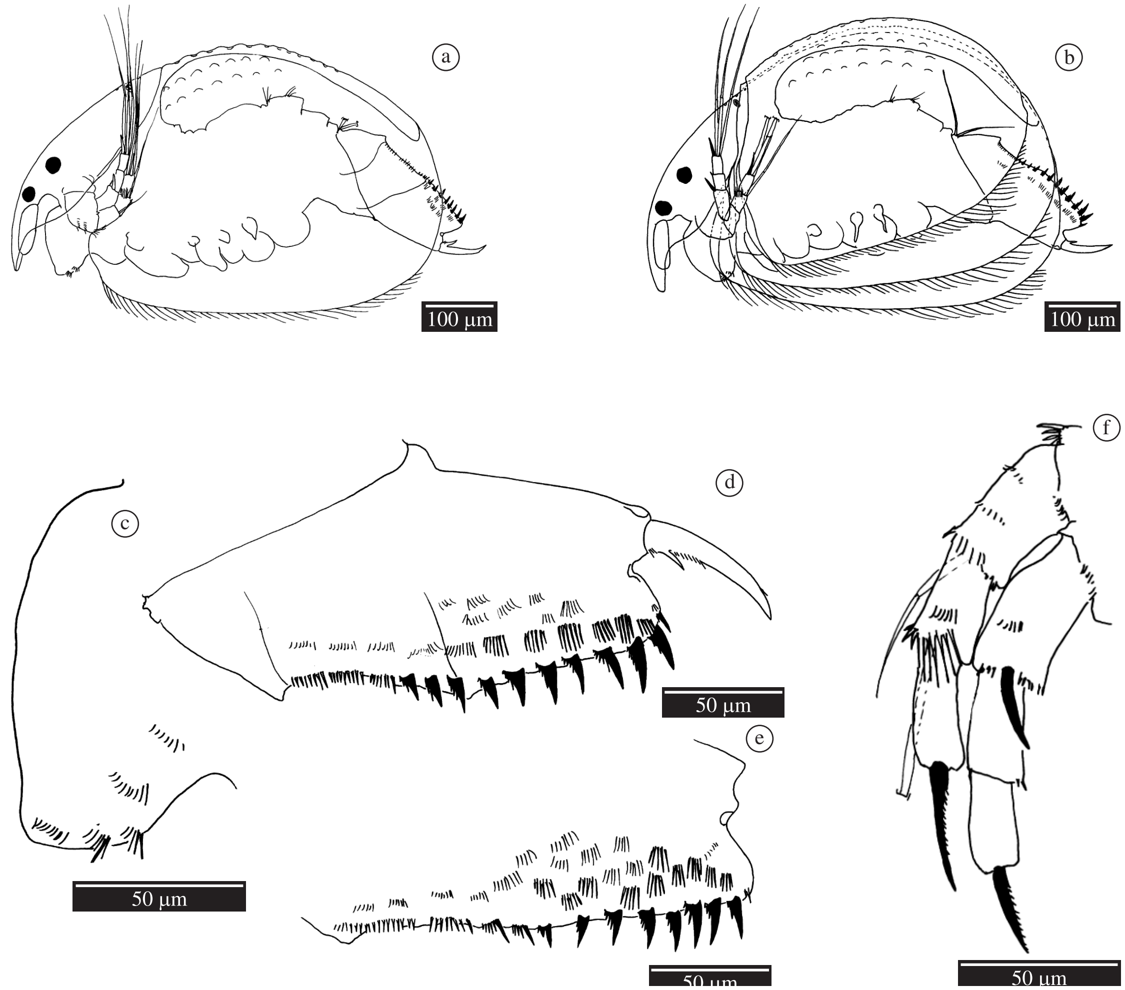

Figure 6. *Alona iheringula* Kotov and Sinev, 2004, adult parthenogenetic females from Lagoa da Colher, Lençóis Maranhenses with shedded (a) and non-shedded valves (b), from a single sample. a) Habitus 'normal' female; b) Habitus female with non-shedded valves; c) Labral keel; d) Postabdomen; e) Idem, armature of different specimen; f) Second antenna, terminal setae not shown.

(*verrucosa*-group). This is similar to *A. verrucosa,* found in S4B together with two previous species. This species is currently under investigation; will be described as new; it is not unique to Brazil.

Oxyurella longicaudis (Birge, 1910) – Figure 7

Euryalona tenuicaudis in Daday (1905); *Odontalona longicaudis* in Birge (1910); *Oxyurella longicaudis* in Bergamin (1941); Smirnov (1971); synonymy and good drawings in Hollwedel et al. (2003).

Easily distinguished from other *Oxyurella* by absence of setules on labral keel and strong distal teeth on postabdomen (Hollwedel et al., 2003). Females redescribed by Hollwedel et al. (2003). Males are undescribed, except for a sketch by Brehm (1938). We show postabdomen (Figure 7e) and habitus (Figure 7b).

Parthenogenetic females from the Lençóis were bright orange to red, 0.6 - 0.8 mm, oval-rectangular, about 1.6 times as long as high; eye larger than ocellus (Figure 7a), postabdomen elongate, about four times as long as wide and with two strongly developed distal teeth, at least twice as large as those adjacent (Figure 7c), claw with basal spine at some distance from base (about as long as basal spine; Figure 7c). Specimens from the Lençóis retained valves (Figure 7a-b). Valve ornamentation faint hexagonal. Main head pores three, separate (not four as commonly accepted for genus), antennule (Figure 7d) with sensory seta on strong projection. Male 0.6 mm, also retains valves. Rostrum shorter than in female, ocellus relatively smaller (Figure 7b). Postabdomen different from that of female, elongate, three to 3.5 times as long as wide, without strong marginal teeth; instead 16 - 18 marginal postanal

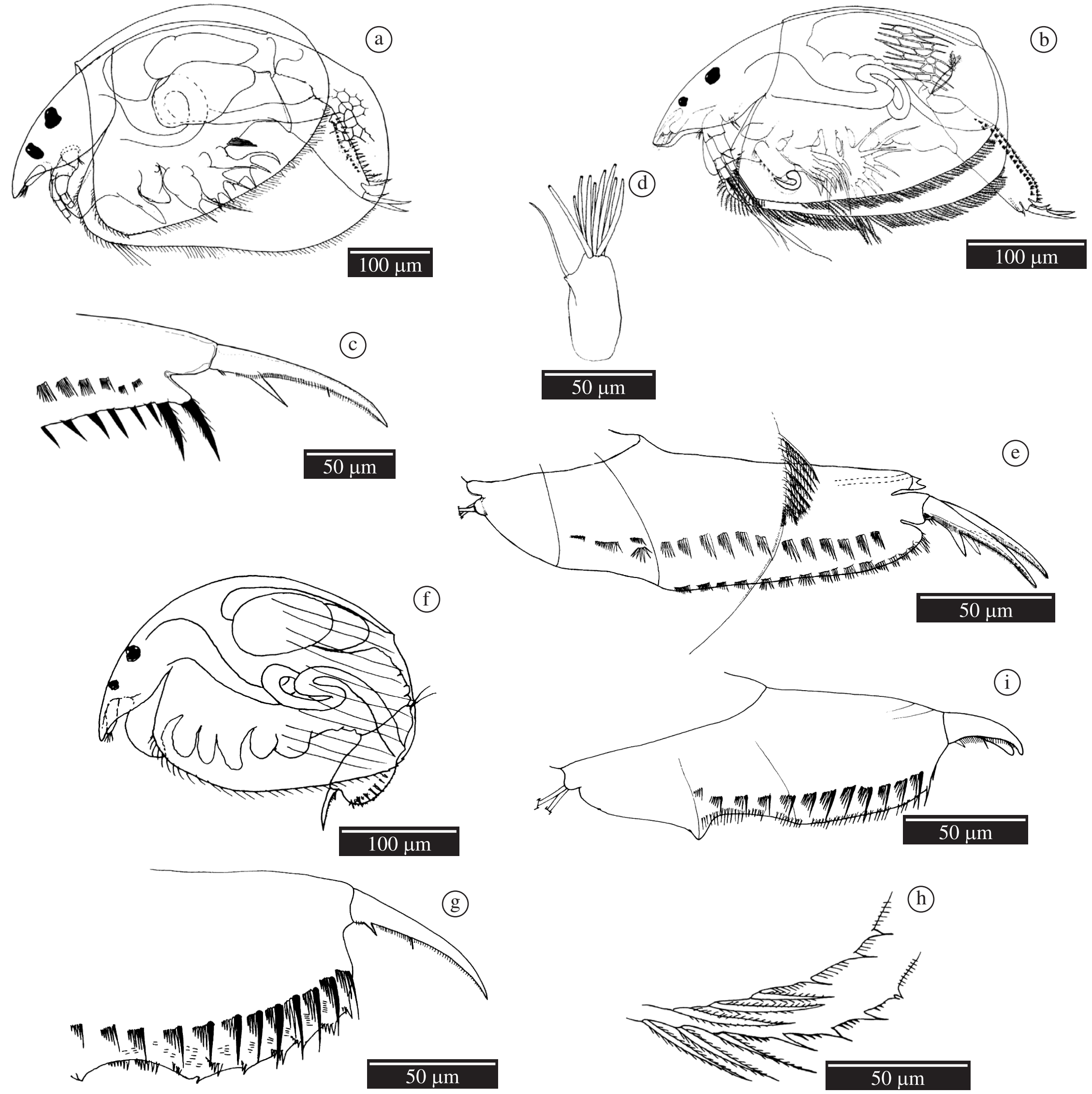

Figure 7. *Oxyurella longicaudis* (Birge, 1910) adult parthenogenetic female (a, c, d) and male (b-e) and *Karualona muelleri* (Richard, 1897), adult parthenogenetic female (f-h) and male (i), hatched from dried mud from the Lençóis Maranhenses. a) Habitus female *O. longicaudis* with non-shedded valve; b) Habitus adult male with non-shedded valve; c) Postabdomen female, distal part; d) First antenna female; e) Postabdomen adult male; f) Habitus female *K. muelleri;* g) Female postabomen, distal portion; h) Female, posteroventral corner of valves; i) Male postabdomen.

groups of three to eight spinules each which do not strongly increase in size distally (Figure 7e). Gonopores open ventrally from basal claws on projection and with stylet (Figure 7e). Basal claw with well developed basal spine, as in female (Figure 7e).

Note. *O. longicaudis* retained its valves (Figure 7a), as *A. iheringula* (Figure 6b). Both males and females of *O. longicaudis* displayed the same feature (Figure 7a, b). Such valve retention was noted earlier by Smirnov (1971) on a specimen from Argentina.

O. longicaudis was one of the first species to appear in the cultures, after two weeks. Adults were conspicuous by their bright orange to red colour. They occurred in all parts of the aquarium, on the bottom, between coarse sand (even 5 cm down in sand, visible from behind the glass), against the walls of the aquarium. Large populations formed quickly, persisted for a long time, and animals were easy to keep, tolerant to temperature changes and easy to culture separately on *Scenedesmus* at 25 °C. Active animals, both in swimming and in foraging; move abruptly, similar to European *O. tenuicaudis*.

Only one exuvium of this species was found in wet samples. Occurs in the South of the US and in the Neotropics (Birge, 1910; Smirnov, 1971). Recorded from Brazil (Elmoor-Loureiro, 1998, 2007; Brehm, 1937, 1938; Hollwedel et al., 2003), yet seems relatively rare.

Karualona muelleri (Richard, 1897) – Figure 7

Alonella karua in Sars (1901); Bergamin (1941); *Biapertura karua* in Smirnov (1971); Elmoor-Loureiro (1998); *Alona mülleri* in Brehm (1937); Vávra (1900); *Karualona muelleri* in Sinev and Hollwedel (2005). Not *Alona karua* King, 1853 sensu King (1853), see Sinev and Hollwedel (2005)

Formerly *Alonella karua* (e.g., in Sars, 1901) or *Alona karua* (e.g., in Smirnov, 1971), this species complex is now placed in *Karualona*. Two species in the Neotropics: *K. penuelasi* (Dumont and Silva-Briano, 2000) and *K. muelleri* (Sinev and Hollwedel, 2005). Our specimens (Figure 7f) are closest to *K. muelleri*, which has a short basal spine on the postabdomen and well-developed distal spines in the lateral fascicles (Figure 7g), and two to five relatively small denticles on the posteroventral corner (Figure 7h). Male (Figure 7i) with a postabdomen about three times as long as wide, slightly tapering distally; lateral fascicles with distal spinules reaching just over the dorsal margin, marginal denticles fine, not clearly grouped; small basal spine on basal claw, not longer than a third of the width of this claw at base (Figure 7i), which is shorter than anal margin; gonopores open subterminally and ventrally at some distance from basal claw, not on a projection, nor a strong embayment. Dorsodistal angle of male postabdomen not protruding, preanal corner strongly developed and conical (Figure 7i).

Biology. Sars (1901) observed that this species "*was easily recognizable even with the naked eye, by the dark brownish hue and jerky movements*". Our specimens were transparent, yet swimming was indeed conspicuous: *K. muelleri* never remains long in one place. It moves by fast, spiralling bursts to the surface, then sinks again; grazes on the walls of the aquarium and on substrate, but feeding not studied in detail since animals are hard to track. Not tolerant of strong temperature fluctuations and could not be kept in a *Scenedesmus* culture; sudden temperature drops (from 28 to 20 °C) killed most of the parthenogenetic females.

Leberis davidi (Richard, 1895)

Alona davidi in Richard (1897); Vávra (1900). *Alonella diaphana* in Sars (1901); Brehm (1937); *Alonella punctata* in Daday (1905); *Alonella davidi* in Birabén (1939); *Alona davidi davidi* in Smirnov (1971); *Leberis davidi* in Sinev et al. (2005).

Listed under different names for South America (*Alonella davidi, Alona davidi* or *Alona diaphana*), *Alona davidi* was moved into *Leberis* and redescribed by Sinev et al. (2005). Our specimens from the Lençóis were included in the study of Neotropical *L. davidi*, its redefinition and separation from *L. diaphanus* (Sinev et al., 2005).

Little is known about the ecology of *Leberis*, except that it is common in temporary pools. Sars (1888) provided notes on *L. diaphanus*. Observed alive, we found that the highly transparent *L. davidi* does not move like the majority of Aloninae but swims in short and fast bursts; yet seems to feed on the bottom, therefore almost combines a semi-planktonic with epi-benthic/littoral lifestyle. During feeding, *L. davidi* "grazes" detritus and was seen to actively roam shedded chydorid and ostracod valves. *L. davidi* is stenothermic and thrived best above 20 °C, males and (black) ephippial females appeared in abundance at 20 °C.

Neotropical, e.g., found in Haiti, Mexico, Argentina, Peru, Brazil (Sinev et al., 2005); *Leberis davidi* was not found in any of the samples of the Lençóis, but only from the culture from S2.

Graptoleberis occidentalis Sars, 1901 – Figure 8

Graptoleberis testudinaria var. *occidentalis* in Sars (1901); *G. testudinaria occidentalis* in Smirnov (1971); *Graptoleberis testudinaria* in Bergamin (1941); Birabén (1939); Elmoor-Loureiro (1997); *Graptoleberis occidentalis* in Elmoor-Loureiro (2007).

Habitus and general characters in *Graptoleberis* are similar worldwide, but the genus needs revision. Specimens from the Lençóis have the general *Graptoleberis* characters, typical head pore arrangement (Figure 8a-d), labral keel (Figure 8c) and denticles in the posteroventral valve corner (Figure 8g). In comparison with true *Graptoleberis testudinaria testudinaria* from the Palaearctic (specimens from Belgium), the Neotropical *Graptoleberis testudinaria occidentalis* has: 1) relatively smaller denticles in the posteroventral valve corner (Smirnov, 1971) (Figure 8b versus Figure 8g); 2) postabdomen with fewer marginal denticles per group and decreasing in number distally (Figure 8f versus Figure 8i); and 3) relatively broader postabdomen (Figure 8e). These subtle differences confirm at least subspecies status of *Graptoleberis testudinaria occidentalis* as suggested by Smirnov (1971); perhaps it is a valid species, *Graptoleberis occidentalis* Sars, 1901 as suggested here. The name was used earlier for Brazil (Elmoor-Loureiro, 2007); a final decision on the status depends on revision of the species, including limbs, described for Iberian populations in Alonso (1996). It is possible that more than one species of *Graptoleberis* may occur in the Neotropical region.

Disparalona leptorhyncha Smirnov, 1996 – Figure 9

Syn. *Leptorhynchus rostratus* Daday, 1905. *Disparalona leptorhyncha* in Smirnov (1996); *Disparalona acutirostris* in Elmoor-Loureiro (1997, 1998).

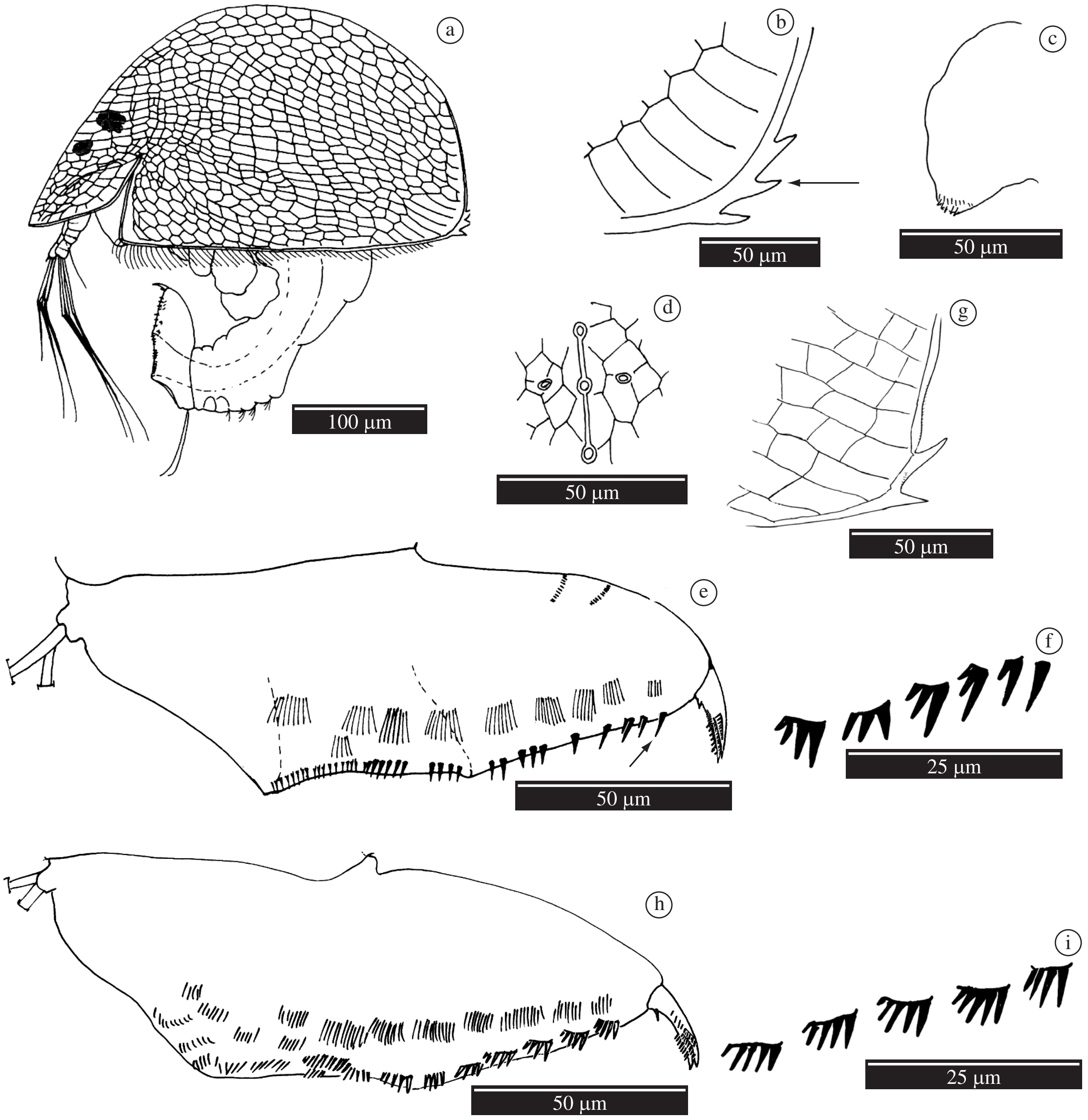

Figure 8. *Graptoleberis testudinaria occidentalis* Sars, 1901 or *Graptoleberis occidentalis* Sars, 1901 from pool W of Mandacaru, Lençóis Maranhenses (a-f) versus *Graptoleberis testudinaria testudinaria* Fischer, 1848 from Belgium (g-i), adult parthenogenetic females. a) Habitus; b) Posteroventral valve corner with denticles; c) Labral keel; d) Head Pores; e) Postabdomen; f) Marginal denticles; g-i) Posteroventral corner of valves, postabdomen and marginal denticles of Belgian population.

Described as *Leptorhynchus rostratus* by Daday (1905) from Paraguay, moved into *Disparalona* by Smirnov (1996), nomenclatural situation is confusing. Limbs of *D. leptoryncha* are unknown, but described for *D. leei* and *D. rostrata* (Alonso, 1996; Michael and Frey, 1984).

Parthenogenetic female ca. 0.5 mm long, dimensions length/height 1.75, with rostrum acute (Figure 9d), reaching three times the antennular length beyond its apex and curved posteriorly (Figure 9a). Dorsum evenly curved, not humpbacked, moderately arched and posterior margin straight; ocellus smaller than eye, ornamentation hexagonal, with fine striation, labral keel not developed (Figure 9a). Marginal setae on valves densely setulated (Figure 9b), decreasing in size in posteroventral corner (Figure 9c). Head pores as for genus, two main pores with smaller pores perpendicular on axis of main pores (Figure 9e;

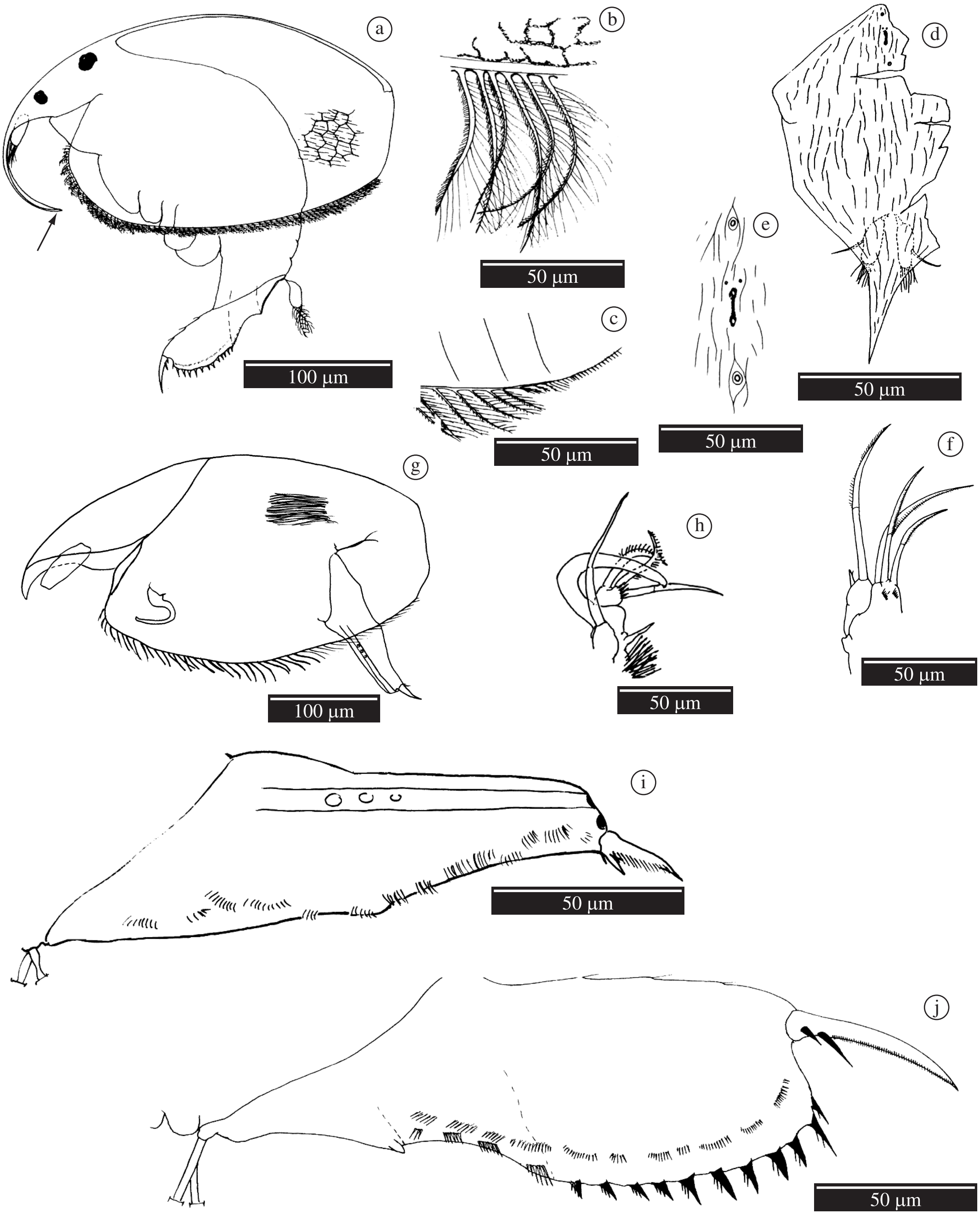

Figure 9. *Disparalona leptorhyncha* Smirnov, 1996, adult parthenogenetic female (a-f, j) and male (g-i) from Lagoa da Colher, Lençóis Maranhenses. a) Adult parthenogenetic female, habitus; b) Medial valve setae; c) Posteroventral valve corner and setae; d) Head Shield; e) Head pores; f) First limb, ODL and IDL; g) Adult male; h) Idem, First limb IDL and ODL with clasper; i) Male postabdomen; j) Female postabdomen.

posterior pore not shown). Headshield with fine striation; posterior margin of head shield not round and wavy but tapering and ending on a blunt corner (Figure 9d). Postabdomen about three times as long as wide with well developed, concave postanal margin which reaches beyond the preanal corner and is about twice as long as the anal margin (Figure 9j). Postanal marginal teeth 10-11 with small denticles on frontal margin, three to four separated groups in anal margin; basal claw with two basal spines, longest about twice thickness of claw at base. Marginal fascicles minute, no differentiation between the spinules and many per fascicle (up to 20) (Figure 9j). First limb with IDL with three setae, of which one curved and longer, twice as thick as others at the base but not strongly hooklike as in *D. hamata* (Smirnov, 1996) (Figure 9f); ODL with two setae of which one strongly reduced (Figure 9f). Male smaller than female, ca. 0.4 mm and more elongate (1.9 times as long as high), with sharp rostrum, latter not as long as in the female, instead just reaching beyond the antennules (Figure 9g). First limb with copulatory hook relatively fine and narrowing distally (Figure 9h). Male postabdomen (Figure 9i) slender, about four times longer than wide, with straight anal margin, postanal margin strongly tapering from there and slightly convex; marginal and lateral armature very fine, hard to distinguish; gonopores open terminally, ventrally from the basal claw, just below it; basal claw short, but with well developed basal spine, about as thick as basal claw at base (Figure 9i).

Note. *D. leptorhyncha* is easily recognised by: elongate rostrum (Figure 9a), reduced labral keel and broad postanal portion of postabdomen, reaching deeper than preanal corner (Figure 9j).

In the Lençóis, we only retrieved *D. leptorhyncha* from the acid main lagoon at Lagoa da Colher between vegetation. Little is known about this species; Daday (1905) found it in temporary swamps ('bañados') and marshes. Rare in the Neotropics, in Brazil and Paraguay (Smirnov, 1996).

Alonella clathratula Sars, 1896 – Figure 10

Alonella clathratula in Sars (1901); Daday (1905); Elmoor-Loureiro (1997); *Alonella excisa clathratula* in Stingelin (1914; var.); Uéno (1967).

Parthenogenetic females of *A. clathratula* from the Lençóis measured ca. 0.3 - 0.35 mm long, were 1.8 longer than high, had hexagonal ornamentation on the valves with faint striation and a blunt, moderately developed posteroventral denticle (Figure 10a). Rostrum reaching beyond the antennule by once its length, labral keel well developed with broad apex (no embayment seen), ventral valve margin with embayment just before middle, dorsal margin not strongly curved, with highest point near middle (Figure 10a). Postabdomen of the female about three times as long as wide, with well developed preanal corner, convex anal margin and straight postanal margin with five to six strong marginal teeth (Figure 10c). Basal claw with two basal spines, longest reaching just beyond a third of claw length (Figure 10c). Male (Figure 10b) slightly smaller than female (0.28 - 0.3 mm), with large eye and high head (highest point anterior), body tapering distally in lateral view, rostrum shorter than in female and small blunt denticle present (Figure 10b). Ornamentation similar, thicker lines in front (Figure 10b). Postabdomen strongly dimorph, with strongly developed, deep preanal portion (shape parallels that of male *C. sphaericus*), deeply convex anal margin and parallel, narrow ventral and dorsal margins (Figure 10d). Gonopores lateral, adjacent to basal claw; with well developed basal spine (Figure 10d).

In habitus, *A. clathratula* is relatively longer and not as high in the anterior part than the similar *A. excisa* or *A. exigua* (depicted in Alonso, 1996). Its postabdomen is rather straight, with parallel ventral and dorsal margins; specimens from the Neotropics have relatively large marginal teeth on the postabdomen.

A. clathratula was described from Australia by Sars (1896) but this form is widespread in the tropics, including the Neotropics (Sars, 1901). Several authors consider *A. clathratula* a variety of *A. excisa* (Stingelin, 1914; Uéno, 1967; Harding, 1955), but it is definitely a species and maybe even a small separate species complex. Occurred in the Lençóis only in S4 (relatively common here).

Alonella dadayi Birge, 1910 – Figure 10

Leptorhynchus dentifer Daday, 1905; *Disparalona dadayi* in Van de Velde et al. (1978); Elmoor-Loureiro (1998); *Alonella dadayi* in Hollwedel et al. (2003).

Good drawings of this species by A.A. Kotov, in Hollwedel et al. (2003) are based on specimens from the Pantanal (Brazil). We here provide a drawing of the habitus (Figure 10e) and male postabdomen (Figure 10k). Females are small, 0.28-0.33 mm, have a strongly elongate, curved rostrum (Figure 10e) and eye and ocellus of similar size to eye maximally twice as large as ocellus (Figure 10f); labral keel has a small indentation (Figure 10g) and posteroventral corner with acute denticle (Figure 10h). Striation is well expressed, longitudinal, continuing on head shield (Figure 10e, f). Female postabdomen compact, about 1.7 times as long as wide, has a deep and sharp preanal corner with long spinules (Figure 10i), postanal margin tapering distally, basal claw as long as anal margin, and basal spines small, longest not reaching a third of claw length. Postanal margin with nine to ten very long marginal spines, up to nine times as long as wide (Figure 10i). Male smaller, 0.26 mm, copulatory hook narrow, (Figure 10j), postabdomen similar to that of female but with less expressed preanal corner or portion and with finer armature and marginal spines (Figure 10k). Gonopores open laterally, close to the basal claw, latter with long basal spine, nearly reaching half the basal claw (Figure 10k).

Described from Southern US (Louisiana, Texas; Birge, 1910) and widespread in Neotropics (Hollwedel et al., 2003). In the Lençóis in the most acid (pH 4.2) and oxygen-poor system (locality S5D); its Palaearctic congener, *A. nana*, is also mostly found in acid systems (Fryer, 1993).

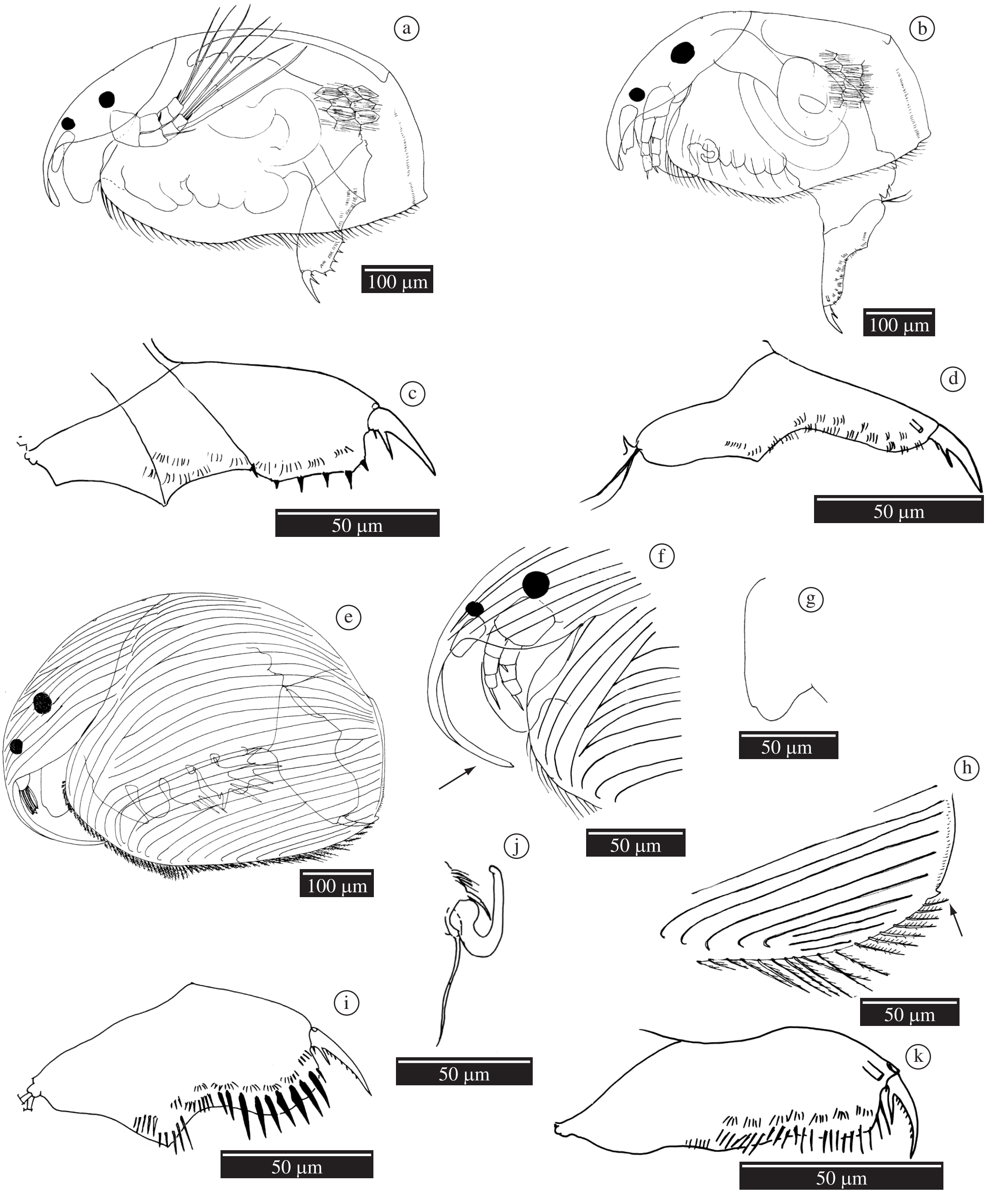

Figure 10. *Alonella* species from pool W of Mandacaru, Lençóis Maranhenses. *Alonella clathratula* Sars, 1896 female (a-c) and male (b-d) and *Alonella dadayi* Birge, 1910 female (e-i) and male (j, k). a) Adult parthenogenetic female, *A. clathratula*, habitus; b) Adult male, habitus; c) Female postabdomen; d) Male postabdomen; e) Adult parthenogenetic female *A. dadayi*, habitus; f) Head and rostrum; g) Labral keel; h) Posteroventral valve corner with denticle; i) Postabdomen; j) Male, clasper or copulatory hook on first limb of male; k) Male Postabdomen.

Note: In comparison to previous species, postabdomen morphology of *A. clathratula* and *A. dadayi* strongly differs in both males and females, sexual dimorphism stronger expressed in *A. clathratula*. Differences can also be seen when morphology of the related *A. nana* and *A. excisa* (Alonso, 1996), or their habits (Fryer, 1968) are compared. There may be two distinct lineages under *Alonella*. Further investigation should test if morphological divergences confirm two different lines. In other words, if the "dwarfs" of an *A. nana*-line (*A. nana, A. dadayi, A. pulchella*) show additional differences with the elongate more species of an *A. exigua*-line (*A. exigua, A. excisa, A. clathratula, A. breviceps*; = 'true' *Alonella*), suggested by postabdomen and habitus.

Chydorus eurynotus Sars, 1901 – Figure 11

Chydorus eurynotus in Sars (1901); Uéno (1967); Harding (1955); Smirnov (1996); *C. eurynotus eurynotus* in Smirnov (1971); synonymy (e.g. *C. flavescens*, *C. nomeralis*) in Smirnov (1971 and references therein); see also Elmoor-Loureiro (1997, 1998) for references from Brazil.

Parthenogenetic females globular, of typical *Chydorus* habitus (Figure 11a), 0.3 - 0.5 mm; moderately expressed ventral flange in anterior view (Figure 11b). Eye 1.6 times larger than ocellus (diameter). Ventral embayment in posterior portion of valves with ventral setae deep convex in median part (Figure 11f), setae decreasing in size distally, ending in thick, spiniform setae (Figure 11f). Head shield with broad posterior, acute and strongly narrowing frontal part and rostrum (Figure 11d). Labral keel relatively small, round (Figure 11e). Antennal setae 003/113, spines 001/001 (first exopod seta present; Figure 11c). Postabdomen elongate, 3 - 4 times as long as wide, and with dorsodistal angle protruding, angle rounded to square (Figure 11g, h). Marginal spines in postanal portion seven to nine, two distalmost spines markedly larger; lateral fascicles minute in long curved groups (Figure 11g). Basal claw as long as anal margin or longer (Figure 11g); Thick and broader denticles in proximal part of pecten on basal claw (Figure 11i); two basal spines, longest reaching up to one fourth of claw length (Figure 11i). First limb with IDL with one seta with a thick base, twice as thick as other IDL setae, curved but with slender distal part, not strongly hooklike; smallest seta on IDL scraper-like; ODL with two setae, one strongly reduced (Figure 11j). Male 0.4 mm, more elongate than female, and oval, about 1.5 times as long as high with ventral portion of valves deepest in middle, dorsum moderately curved and posterodorsal corner high (Figure 11k), eye just larger than ocellus. Postabdomen about three times as long as wide, straight and rectangular, with parallel anal and ventral margins (Figure 11k-l). Moderate preanal corner, but well expressed postanal corner, after which the postanal portion is short and straight, forming a dorsodistal angle (Figure 11l). Basal claw shorter than anal margin, with short basal spine, nearly as thick as claw width at base; gonopores open at some distance from basal claw in ventral margin, without embayment or projection (Figure 11l).

Note. The male, only reported by Sars (1901), is atypical in comparison to most *Chydorus* species. Shape of its postabdomen is remarkably similar to that of male *C. dentifer*, shown in Smirnov (1992), and also links with *C. ovalis* were suggested (Sars, 1901). Female *C. eurynotus* has an elongate postabdomen, also found in *C. ventricosus*, but the latter species lacks a dorsodistal angle here. A good character to recognise *C. eurynotus*, are conical denticles in the proximal pecten (on the basal claw of postabdomen), shown in Figure 11i; Figure 11h is from the paralectotype from Sars' collection, which we used to confirm our specimens as *C. eurynotus*.

Abundant in culture from Mandacaru (S4) and present in samples from same locality. Hatched within first weeks of wetting, but populations disappeared after a few months. Red to reddish brown in life and a slow swimmer (in comparison to *C. sphaericus*). Fed on filamentous algae, did not thrive on a *Scenedesmus* culture. *C. eurynotus* is circumtropical, but may comprise more than one species (Smirnov, 1996).

Chydorus dentifer Daday, 1905 – Figure 12

Chydorus ventricosus var. *dentifer* Daday, 1905; *Chydorus dentifer* in Smirnov (1996).

Cannot be mistaken for any other chydorine (Smirnov, 1996) by the blunt denticle in the posteroventral valve (Figure 12e, i). A large *Chydorus* (Figure 12a), 0.6 - 0.8 mm, in appearance similar to *Pleuroxus* because of a long rostrum and body tapering posteriorly, but with marginal valve setae strongly invaginated (Figure 12e). Body high in anterior part, tapering distally and with straight posterior margin (Figure 12a). Peculiar "club-like" structure in frontal valve margin (Figure 12f) (Smirnov, 1996). Antenna with setae 003/113, spines 001/001 (first exopod seta present; Figure 12b, c). Postabdomen elongate, four times as long as wide (Figure 12h) with long basal spine, reaching halfway basal claw (Figure 12g). Three distalmost marginal denticles stronger than others (Figure 12h), in all 9-10 postanal marginal teeth; preanal corner well developed, postanal corner sharp (Figure 12h). IDL on first limb with one hook-like seta, with strong denticles in distal half, smallest seta on IDL scraper-like with thick base (Figure 12d). ODL with two setae, one reduced, one well developed (Figure 12d).

Note. Male (Smirnov, 1996) with postabdomen similar to *C. eurynotus*, square and elongate. Both species may be related, as both have an extra seta on the exopod, which is absent in the *C. sphaericus*-line. Limb morphologies remain unpublished of most *Chydorus* species yet several lineages in the genus have been suggested (Smirnov, 1996).

Neotropical species (Smirnov, 1996; Daday, 1905), also reported from Brazil (Elmoor-Loureiro, 2007), rarely encountered and there is nothing known about its ecology; *C. dentifer* was found in the Lençóis only in one sample, with the highest acidity (pH 4.2) (S5D). *C. dentifer* also occurred in the Rio Nhamundá (Brazil) in acid conditions, pH 5.2 (Brandorff et al., 1982).

Dunhevedia odontoplax Sars, 1901

Dunhevedia odontoplax in Sars (1901); Daday (1905); Uéno (1967); Zoppi de Roa and Vasquez (1991); Valdivia Villar (1987).

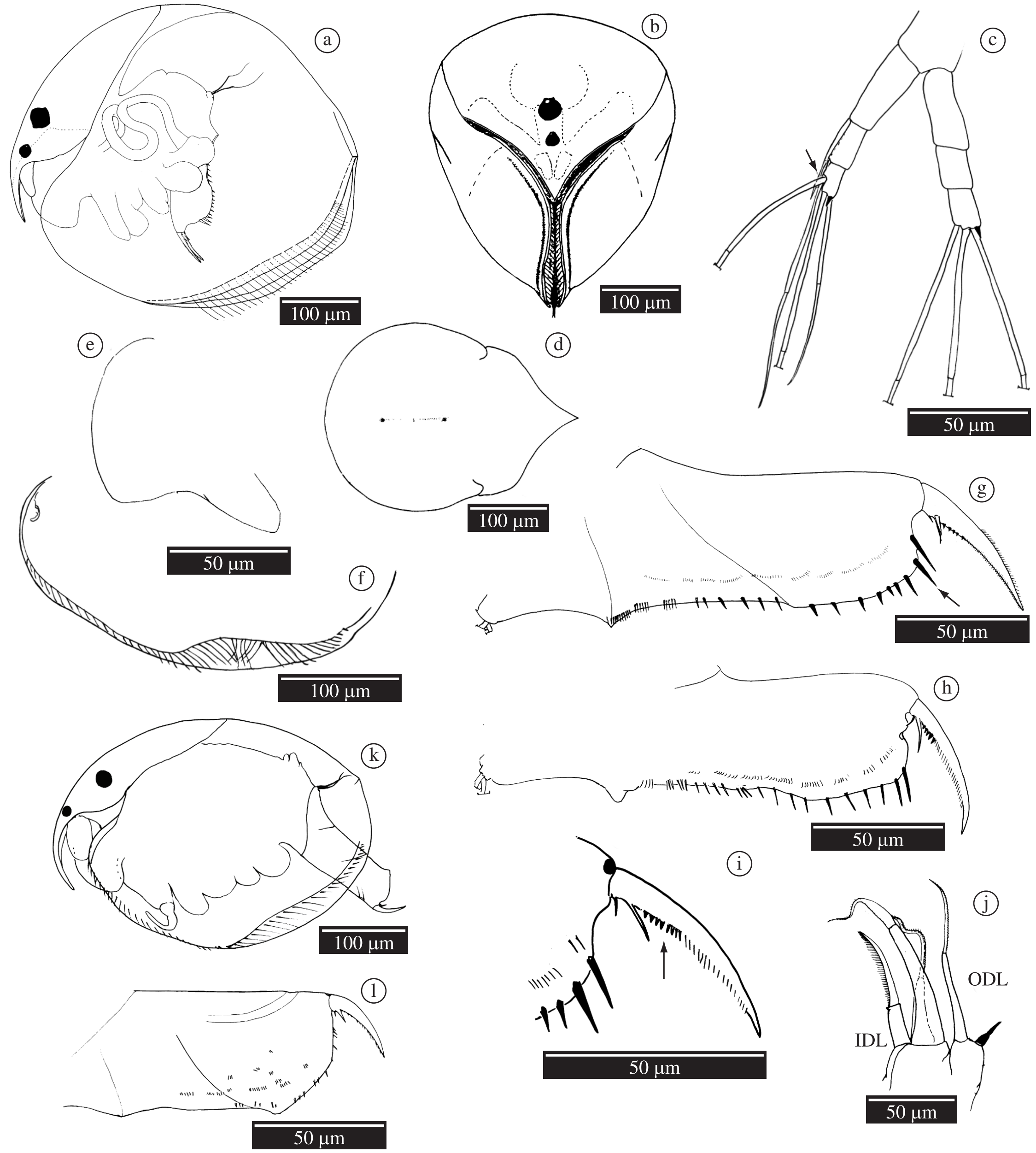

Figure 11. *Chydorus eurynotus* Sars, 1901, adult parthenogenetic female (a-j) and male (k, l). Specimens from pool W of Mandacaru, Lençóis Maranhenses, except for Figure 11h, a paralectotype of G.O. Sars' collection, labeled Zool. Mus. Oslo F. 12358d, Mp. 176, Col. G.O. Sars. a) Adult parthenogenetic female, habitus, lateral view; b) Idem, frontal view; c) Second antenna; d) Head Shield; e) Labral keel; f) Valve margin; g) Postabdomen; h) Idem, Lectotype; i) Postabdomen, basal claw; j) First limb, IDL and ODL; k) Adult male; l) Idem, postabdomen.

One specimen in wet sample S3, but abundant after one month in culture from S2 at 20-35 °C. *D. odontoplax* swims rapidly, by abrupt moves (Sars, 1901), after which it attaches to the walls of the aquarium. It avoids the bottom, prefers the upper water layers and is hyponeustonic. When a plastic plate was put in our culture, *Dunhevedia* specimens gathered on its underside and circled like a *Gyrinus* beetle. This suggests a preference of *Dunhevedia* for floating vegetation (e.g., *Nymphoides*) in nature.

Ephemeroporus hybridus (Daday, 1905)

Syn. See Hollwedel et al. (2003)

In all pools, but absent from acid Lagoa da Colher and Preguiças River. Abundant in vegetation (e.g., S1C) and major diet item in stomachs of small fish (in S3). Biology. First anomopod to appear in our cultures, after two weeks. Fast swimmer, like *C. sphaericus*, forms schools. In life, grazes on plants and walls of the aquarium. Transparent, ephippial females black

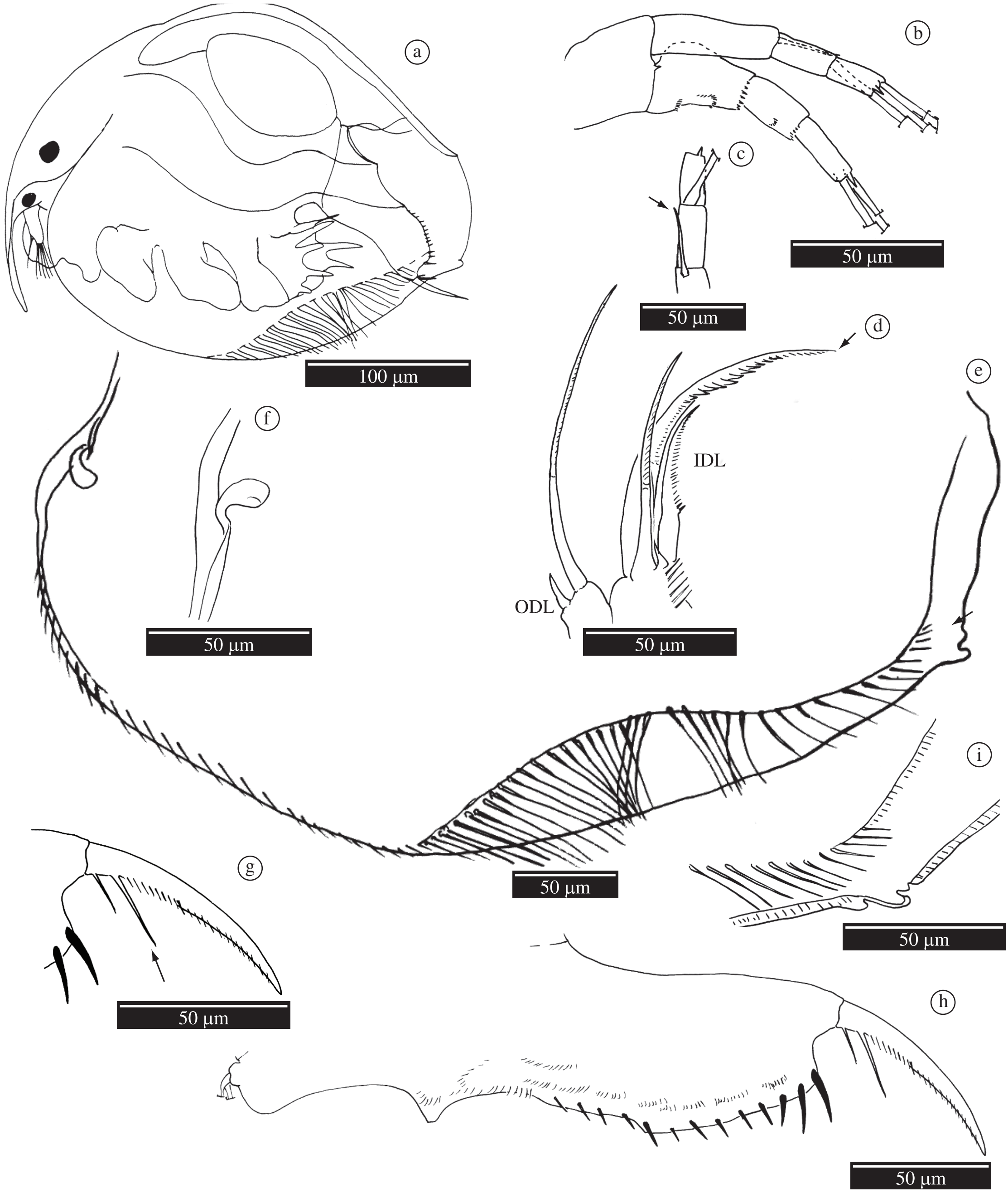

Figure 12. *Chydorus dentifer* Daday, 1905, adult parthenogenetic female from Lagoa da Colher, Lençóis Maranhenses. a) Habitus; b) Second Antenna; c) Idem, showing the seta on first segment; d) First limb, IDL and ODL; e) Valve setulation; f) Valve, anterior flange; g) Postabdomen, distal end; h)Postabdomen, complete; i) Posteroventral valve corner.

and opaque around the ephippium. Easy to separate and culture on algae, and tolerant to temperature shifts, still viable around 20 °C.

Ephemeroporus acanthodes Frey, 1982

Similar to *E. hybridus,* labral keel with single tooth, but no denticle on posteroventral valve corner (Smirnov, 1996). Rare in the Lençóis, in one locality (S1). A species from Southern US, Central Americas and Mexico (Smirnov, 1996; Elías-Gutierrez, 1999), sporadic in the Neotropics, including recently in Brazil (Serafim et al., 2003).

4. Discussion

4.1. Diversity, ecology and biogeography

Diversity - We recorded 34 Cladocera species, from only 12 wet and two mud samples. This compares well with species numbers from the Amazon (34 species; Brandorff et al., 1982), Paraná (39 species; Elmoor-Loureiro, 2007), Venezuela, Mantecal grasslands (33 species; Zoppi de Roa et al. 1985; 24 species; Zoppi de Roa and Vasquez, 1991). Extensive surveys yield more species, e.g., in Venezuela, Orinoco (59 species; Rey and Vasquez, 1986b) and Brazil, Pantanal (50 species, Hollwedel et al., 2003) or Paraná (63 species from 108 samples, Serafim et al., 2003). Undoubtedly, such sampling in the Lençóis will also reveal higher species numbers. Considering total number of species per sample, most samples have a similar richness (about seven species on average, up to 12 per sample), including the two cultures (9 - 10 species each; Table 1).

Ecology – A difference in species composition between acidic and basic pools was observed. In 'white' waters, the fauna consisted mainly of *Cyclestheria hislopi, Latonopsis australis, Ephemeroporus hybridus, Leydigiopsis curvirostris* and *Alona ossiani*; in S4, mostly *Leydigiopsis curvirostris* and *Chydorus eurynotus* occurred, with *Alonella clathratula*. In acid waters, *Latonopsis australis, Streblocerus pygmaeus, Ilyocryptus* and *Macrothrix* were abundant, and few were even restricted to pools with low pH (*Alona iheringula, Alonella dadayi, Disparalona leptorhyncha, Chydorus dentifer*). The abundance of *Latonopsis australis, Ephemeroporus hybridus* and *Chydorus eurynotus* in the first type of waters, corresponds with findings in Venezuela (Rey and Vasquez, 1986b). Several of the species from the temporary dune pools in the Lençóis are typical for temporary swamps or floodplains rich in vegetation, like the Orinoco, Pantanal or Paraná. *Oxyurella longicaudis, Ephemeroporus hybridus, Leydigiopsis curvirostris, Dunhevedia odontoplax* occur in such habitats (Brehm, 1937, 1938; Rey and Vasquez, 1986b; Zoppi de Roa and Vasquez, 1991; Hollwedel et al., 2003; Elmoor-Loureiro, 2007). Preference or occurrence of *Streblocerus pygmaeus* for acid waters corresponds with observations by Rey and Vasquez (1986b) in similar habitats from Venezuela. In littoral samples from floodplains of the Rio Nhamundá (Amazon Basin, Brazil; Brandorff et al., 1982), also *Streblocerus pygmaeus, Chydorus dentifer, Alonella dadayi, Macrothrix sioli, Alona ossiani, Ilyocryptus spinifer* and *Cyclestheria hislopi* occur, which largely corresponds with acid water communities in the Lençóis. In contrast to Rey and Vasquez (1986b), who found *Leydigiopsis curvirostris* mainly in waters with low pH, this species was very rare in our samples from the acid Lagoa da Colher, yet abundant in the samples with neutral to basic pH.

Although based on a limited set of samples, the former illustrates that "white" and "black" waters in the tropics may have characteristic, different, equally rich cladoceran communities. Similar ideas were suggested in a comparison between temporary systems from Venezuela (Rey and Vasquez, 1986b) or Brazil (Brandorff, 1978; Brandorff et al., 1982), but deserve more thorough attention. The cladoceran communities in the Lençóis clearly differ. As conductivities of all waters in the Lençóis were similar (low), this abiotic factor cannot lie at the basis of shaping our communities. In our opinion, pH strongly determines cladoceran communities in the Lençóis. Species need specific physiological adaptations (see Fryer, 1993) and clearly several preferred dystrophic pools with pH 4.2 and low oxygen (0.95 - 0.99 mgO_2L^{-1}) e.g. *Streblocerus pygmaeus, Macrothrix paulensis, Alona iheringula, Alona ossiani, Alonella dadayi* and *Chydorus dentifer*. For the phytoplankton, Moschini-Carlos and Pompêo (2001) found that acidity was a dominant factor in determining species composition in these dune pools; we can confirm this for the Cladocera (Van Damme, 1998; this study).

Biogeography – Most Cladocera found are South American: 70% are Neotropical, 12% Neotropical/Southern US and 18% Circumtropical (Table 1; distribution of *Camptocercus* sp. not included). Some species with circumtropical distribution may need further taxonomic study (*Simocephalus* cf. *brehmi, Latonopsis australis, Alonella clathratula*). Some seem relatively rare, such as *Ephemeroporus acanthodes* and *Oxyurella longicaudis*, which occur in North and Central America, or the true Neotropical *Chydorus dentifer*. We found no local endemics, not surprising, bearing in mind that the dunes of the Lençóis are young (Pleistocene).

4.2. Note on behaviour and ecology

Our observations of live behaviour show niche separation in the Chydoridae under study. Such differences were known for a number of species (Smirnov, 1971; Fryer, 1968), yet Chydoridae are still largely thought of as forming a single ecological entity. From our observations, some species are strongly associated with bottom detritus, which they rarely leave (*A. verrucosa, Leydigia, Leydigiopsis*), being slow swimmers, crawling on the bottom. *Dunhevedia*, in contrast, is hyponeustonic and forages on the underside of floating material. *Ephemeroporus* is a strong swimmer that avoids the bottom and prefers plants, or grazes on walls of aquaria. *Chydorus eurynotus* prefers bottoms with filamentous algae and moves more slowly than the active *C. sphaericus*. *Leberis* and *Karualona* swim fast, in short bursts, switching between substrate and water column, latter is a most active animal. Its behaviour differs from that of most *Alona* (e.g., in Fryer, 1968; *A. affinis*). *Oxyurella longicaudis* seems to be a generalist, found on the substrate, walls, in the water or even interstitially.

The timing of hatching also differed between species, the benthic *Leydigia* and *Leydigiopsis* appearing later than the planktonic-phytophilous *Ephemeroporus* or the generalist *Oxyurella*. It may be possible that benthic taxa "postpone" hatching in nature, to a time when detrital layers are well established.

4.3. Advantages of Sars' Method

Six species (*Ceriodaphnia cornuta, Scapholeberis freyi, Leydigia ciliata, Oxyurella longicaudis, Leberis davidi* and *Dunhevedia odontoplax*), were virtually absent from wet samples, yet developed in the cultures. Nearly half of the total (44%) was recovered through artificial hatching on just small parcels of sediment. In addition to classical hit-and-run sampling, dry mud offers an interesting way of obtaining more specimens and species. Due to temporal variability in abundance, several species may be overlooked in sampling campaigns.

The method is not new. Sars adopted it in the first part of the 1880's, for the first time in a paper entitled "On some Australian Cladocera, raised from dried mud" (Sars, 1885; Christiansen in Sars, 1993). He used the term "artificial hatching" in several of his later studies. He carefully prepared aquaria with dry sediments, adding plants that were washed for contaminants, watching the animals closely with a magnifying glass, describing their behaviour and making colour drawings in vivo. Sars kept his animals "domesticated" for years and wrote about the advantages of his method:

> [...] I have now convinced myself, that by far the best method of studying extraneous freshwater Entomostraca is that there practiced, viz, to raise the species from dried material taken in the respective regions from suitable localities. True, the arrangement of the aquaria for this purpose requires much care, and also much expenditure of time to examine the aquaria, and to await the development of the species; but, on the other hand, it is evident that the investigations made in such cases admit of a very superior completeness both morphologically and biologically, than those instituted on preserved specimens. Indeed, it is both very amusing and instructive to watch these little creatures in the living state, and to obtain information about their different habits and their development from generation to generation, each aquarium representing, as it were, an isolated part of their native dwelling places. As, moreover, the different species pertaining to a certain locality do not, as a rule, appear simultaneously, but rather in a definite succession, any sample of plankton taken occasionally will give a far less complete idea of the fauna than a continuous series of hatching experiments instituted on a parcel of mud from the same locality (Sars, 1901).
>
> The great advantage attained by this method for the study of exotic freshwater Entomostraca will be easily appreciated. For thereby not only will, as a rule, a sufficient number of specimens of each species be obtained for examination and comparison, but this method permits the study of the biological relations of the species, their growth, movements, propagation, and seasonal variation. Especially as regards the Cladocera, the said method has proved to be of invaluable service, as these very delicate organisms scarcely admit of being satisfactorily examined except in the fresh and living condition (Sars, 1916).

Sars therefore showed that waterbodies do not necessarily need to contain water to be faunistically studied. Actually, most of his descriptions of tropical freshwater cladocerans were derived from dry mud, sent by researchers worldwide (Sars, 1888, 1894, 1896, 1916), including from South America (Sars, 1901). The method has proven itself in the past yet is often reinvented by researchers, ignoring Sars' work.

Mud samples give a more realistic view of true species richness, as classic sampling reflects the community only one point in time. Harding (1955) noted that his sampling of Titicaca Lake could be considered reliable, as the same species appeared in his mud cultures. The fact that 44% of our species turned up in aquaria from sediment, carries a similar message. Also other groups appear (ostracods, copepods, rotifers, nematodes, gastrotriches and oligochaetes), even Odonata larvae (Van Damme and Dumont, 1999). As Sars understood a century ago, the technique provides several advantages. We list seven here: 1) rich, fresh material of a significant number of species; 2) improved identification due to abundant material and the possibility to obtain males and ephippial females; 3) assessment of phenotypical variation (e.g., valve ornamentation); 4) possibility of observing animals in vivo to study their behaviour and feeding, useful in interpreting their role in the ecosystem; 5) a better estimation of true diversity (eggbank) than classical sampling; retrieval of species that are rare in wet samples; 6) succession of species, as some species hatch later than others; 7) low cost.

In addition, the method allows one to see live animals. Setting up cultures is cheap and requires little maintenance. We baptise the technique of hatching dry mud for the study of micro-crustaceans here as "Sars' method", in honour of his work. As Sars did not leave specifics on how he prepared cultures, we hope our description may be useful to future students. To us, the technique provides a useful tool for cladoceran taxonomy and biology. Twelve years after collection, ephippia from the Lençóis mud samples still yield abundant specimens.

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