

First record of the enigmatic genus *Redudasys* Kisiielewski, 1987 (Gastrotricha: Macrodasysida) from the Northern hemisphere

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ABSTRACT

Gastrotricha Metschnikoff, 1865 is a small phylum of acoelomatic animals common in both marine and freshwater environments. To date, close to 800 species are known from all over the world. The order Macrodasysida Remane, 1925 [Rao & Clausen, 1970] is almost exclusively marine except for the rare genera *Marinellina* Ruttner-Kolisko, 1955 and *Redudasys* Kisiielewski, 1987. In this study, we present morphological and molecular data for a potentially new species of *Redudasys* from the Edwards Aquifer, Texas, USA. It is the first record of the genus from the Northern hemisphere. It has only previously been reported from Brazil. The Texan specimen, designated as *Redudasys* sp., has a single pair of anterior adhesive tubes and is considerably shorter than the specimens reported from Brazil. Molecular data from the 18S rRNA and COI mtDNA genes support a close relationship of *Redudasys* sp. to *Redudasys fornerise* Kisiielewski, 1987. Barcodes are provided for both *Redudasys* sp. and *R. fornerise*. The limited material obtained does not justify the description of a new species, but the record is certainly important from a biogeographical standpoint. The colonization and invasion of marine species into freshwater habitats, in particular those of the Edwards Aquifer, is discussed. Although certain marine gastrotrichs appear to have an astonishing ability to adapt to changes in salinity *Redudasys* is likely to be a marine relic.

KEY WORDS

Redudasysidae,
biogeography,
artesian outflow,
Edwards Aquifer,
Texas,
new record.

RÉSUMÉ

Première signalisation du genre énigmatique Redudasys Kisielewski, 1987 (Gastrotricha: Macrodasysida) dans l'hémisphère nord.

Les Gastrotriches Metschnikoff, 1865 forment un petit phylum d'animaux acoelomates, communs à la fois dans l'environnement marin et en eau douce. À ce jour, près de 800 espèces sont connues à travers le monde. L'ordre Macrodasysida Remane, 1925 [Rao & Clausen, 1970] est presque exclusivement marin, sauf les genres *Marinellina* Ruttner-Kolisko, 1955 et *Redudasys* Kisielewski, 1987 qui sont rares. Dans cette étude, nous présentons des données morphologiques et moléculaires pour une espèce potentiellement nouvelle de *Redudasys* originaire de l'aquifère d'Edwards, Texas, USA. Il s'agit de la première signalisation dans l'hémisphère nord pour ce genre, précédemment mentionné uniquement du Brésil. Le spécimen du Texas, désigné ici comme *Redudasys* sp. possède une seule paire de tubes adhésifs antérieurs et est considérablement plus petit que les spécimens rapportés du Brésil. Les données moléculaires des gènes 18S rRNA et COI mtDNA supportent l'hypothèse d'une parenté étroite de *Redudasys* sp. avec *Redudasys formerise* Kisielewski, 1987. Les données barcode sont fournies pour les *Redudasys* sp. et *R. formerise*. La faible quantité de matériel obtenu ne justifie pas la description d'une nouvelle espèce, mais la signalisation est certainement importante du point de vue biogéographique. La colonisation et l'invasion d'espèces marines dans les habitats d'eau douce, en particulier ceux de l'aquifère d'Edwards, sont discutées. Bien que certains gastrotriches marins semblent avoir une capacité étonnante à s'adapter aux changements de salinité, *Redudasys* est probablement une relict marine.

MOTS CLÉS

Redudasysidae,
biogéographie,
écoulement artésien,
aquifère d'Edwards,
Texas,
signalisation nouvelle.

INTRODUCTION

Gastrotricha Metschnikoff, 1865 are microscopic aquatic organisms and a common component of the interstitial, epibenthic and periphytic fauna. The group is cosmopolitan with close to 800 species (see Balsamo *et al.* 2009, 2013; Hummon & Todaro 2010; Kolicka 2014 and references therein). The group is classified into the two orders Chaetonotida Remane, 1925 [Rao & Clausen, 1970] and Macrodasysida Remane, 1925 [Rao & Clausen, 1970]. Chaetonotida contains tenpin-shaped species with representatives in both freshwater and marine habitats, while the strap-shaped species of Macrodasysida are almost exclusively marine. Only two nominal species of Macrodasysida, *Marinellina flagellata* Ruttner-Kolisko, 1955 and *Redudasys formerise* Kisielewski, 1987, have been recorded from freshwater habitats.

Marinellina flagellata was described from the river Ybbs at Lunz in Austria from two, apparently immature, specimens. Attempts at rediscovering the species at the type locality have failed. However, a freshwater macrodasysidan has been found in another Austrian stream but it is not clear if this specimen belong to *M. flagellata* (see Todaro *et al.* 2012). Recently Araújo *et al.* (2013) reported an apparently different species of *Marinellina* Ruttner-Kolisko, 1955 from the state of Minas Gerais, Brazil.

Redudasys formerise has so far only been reported from the type locality, Represa do Broa, state of Sao Paulo, Brazil (Kisielewski 1987a; Todaro *et al.* 2012). In addition, Garraffoni *et al.* (2010) reported a representative of *Redudasys*, *Redudasys* sp., in high numbers from the Cabral Mountains, state of Minas Gerais, Brazil. It is apparently different from *R. formerise* but its taxonomic status has yet

to be assessed (Todaro *et al.* 2012). Hence, the scarcity of data available to date may give the false impression of a purely tropical distribution of *Redudasy*.

In this study we present morphological and molecular data of a potentially new subtropical species of *Redudasy* from San Marcos, Texas, USA. It is the first record of the genus from the Northern hemisphere.

MATERIAL AND METHODS

STUDY AREA

The San Marcos springs are an artesian outflow from the Edwards Aquifer located on the eastern edge of Edwards Plateau, Texas, USA. Springs of the Edwards Aquifer provide most of the water for the San Marcos River that runs for 121 kilometers before it joins the Guadalupe River to the southeast. In 1849, a dam was built just downstream from the springs resulting in Spring Lake, which served as a recreational center and amusement park known as Aquarena Springs during the greater part of the 1900s. During the 1990s, Texas State University purchased the park and the surrounding area, now known as Meadows Center for Water and the Environment.

COLLECTION AND DOCUMENTATION

Collection was done by SCUBA on June 16, 2012 at a water temperature of 23–25°C. Samples were collected in 0.5L plastic jars at 3–9 meters by scooping up the top layer of the sediment. Samples contained clean sand, pebbles, algae and organic material. All samples were processed within 24 hours. Subsamples were treated with a 1% solution of MgCl₂ to anaesthetize the animals and subsequently transferred to a small petri dish. Individual specimens were picked out with a micropipette under an Olympus LMS225R dissecting microscope. Specimens were mounted alive on a glass slide and subsequently studied and documented under an Olympus BH-2 microscope equipped with DIC optics and a Canon EOS Rebel T1i digital camera. After documentation specimens were transferred to 95% EtOH for further treatment.

The position of certain morphological characters along the body are given in percentage units (U) of the total body length following the convention of Hummon *et al.* (1992).

SEQUENCING AND MOLECULAR ANALYSIS

Extraction, amplification and sequencing follow Kånneby *et al.* (2012). A complete list of taxa included in the analysis can be found in Table 1. The 18S rDNA and COI mtDNA genes were aligned with MAFFT v.7 (online version). The 18S rRNA gene was aligned using the Q-INS-i algorithm, taking the secondary structure of RNA into account, while COI was aligned using the G-INS-i algorithm (Katoh & Standley 2013). The concatenated dataset (18S rDNA + COI mtDNA) was analyzed with MrBayes v.3.2 (Ronquist *et al.* 2012) under the mixed model setting with estimated proportion of invariable sites and gamma distributed rate variation across sites. To ensure sufficient mixing and a reliable sample from the posterior distribution the dataset was analyzed with 8 MCMC chains for each run and a heating parameter of 0.1. The analysis was run for 20 million generations with default setting of priors. Convergence of the two runs was ascertained by checking the log likelihood graphs, the average standard deviation of split frequencies and the potential scale reduction factor (PSRF). After a burnin of 5 million generations, chains were sampled every 1000th generation. Members of Muselliferidae Leasi & Todaro, 2008 and Xenotrichulidae Remane, 1927 were used as outgroups (Table 1).

Uncorrected pairwise distances were computed with MEGA6 (Tamura *et al.* 2013).

ABBREVIATIONS

DLS	dorsolateral sensory hairs;
E	egg;
NA	not available;
PhiJ	pharyngeal intestinal junction;
PhL	length of pharynx;
PP	pharyngeal pores;
TbA	anterior adhesive tubes;
TL	total body length;
TbP	posterior adhesive tubes.

TABLE 1. — Gastrotrich taxa used in the phylogenetic analysis and their respective Genbank accession numbers. Abbreviations: see Material and methods.

Taxon	Origin	Reference	18S/COI Accession number
Macrodasysida Remane, 1925 [Rao & Clausen, 1970]			
Cephalodasyidae			
Hummon & Todaro, 2010			
<i>Cephalodasys</i> sp.	White Sea, Russia	Petrov <i>et al.</i> 2007	AY963691
<i>Dolichodasys</i> sp.	San Isidoro, Italy	Todaro <i>et al.</i> 2003	AM231778
<i>Mesodasys laticaudatus</i> Remane, 1951	Albinia, Italy	Todaro <i>et al.</i> 2011	JF357657/JF432043
<i>Mesodasys laticaudatus</i> Remane, 1951	Bohuslän, Sweden	Todaro <i>et al.</i> 2011	JF357668/JF432050
<i>Mesodasys littoralis</i> Remane, 1951	Bou Fichta, Tunisia	Todaro <i>et al.</i> 2011	JF357658/JF432044
<i>Paradasys</i> sp.	Ionian Sea, Italy	Todaro <i>et al.</i> 2003	AM231781
<i>Pleurodasys helgolandicus</i> (Remane, 1927)	NA	Paps & Riutort 2012	JF970236
<i>Pleurodasys helgolandicus</i>	Ibiza, Spain	Todaro <i>et al.</i> 2012	JN203486
Dactylopodolidae Strand, 1929			
<i>Dactylopodola</i> cf. <i>baltica</i> (Remane, 1926)	Ras Alard, Kuwait	Todaro <i>et al.</i> 2011	JF357650
<i>Dactylopodola mesotyphle</i> Hummon, Todaro, Tongiorgi & Balsamo, 1998	Punta Ala, Italy	Todaro <i>et al.</i> 2011	JF357651/JF432036
<i>Dactylopodola typhle</i> Remane, 1927	Bou Fichta, Tunisia	Todaro <i>et al.</i> 2011	JF357652/JF432037
<i>Dactylopodola typhle</i> Remane, 1927	Torre Civette, Italy	Todaro <i>et al.</i> 2011	JF357653/JF432038
Macrodasysidae Remane, 1926			
<i>Macrodasys</i> sp. 1	Torre Civette, Italy	Todaro <i>et al.</i> 2011	JF357654/JF432040
<i>Macrodasys</i> sp. 2	Bohuslän, Sweden	Todaro <i>et al.</i> 2011	JF357670/JF432052
<i>Urodasys</i> sp.	NA	Giribet <i>et al.</i> 2004	AY218102
<i>Urodasys</i> sp.	Florida, USA	Sørensen <i>et al.</i> 2006	DQ079912
Planodasyidae Rao & Clausen, 1970			
<i>Crasiella</i> sp.	Ilha Bela, Brazil	Todaro <i>et al.</i> 2012	JN203488
<i>Megadasys</i> sp.	Grotto del Ciolo, Italy	Todaro <i>et al.</i> 2011	JF357655/JF432042
<i>Megadasys</i> sp. 1	Porto Cesareo, Italy	Todaro <i>et al.</i> 2011	JF357656/JF432041
Redudasyidae Todaro, Dal Zotto, Jondelius, Hochberg, Hummon, Kånneby & Rocha, 2012			
<i>Anandrodasys agadasys</i> (Hochberg, 2003)	St. John Island, USA	Todaro <i>et al.</i> 2012	JN203487
<i>Redudasy</i> sp.	San Marcos, Texas, USA	This study	KJ950121/KJ950123
<i>Redudasy fornerise</i> Kisielewski, 1987	Represa do Broa, Brazil	Todaro <i>et al.</i> 2012; This study	JN203489/KJ950122
Thaumastodermatidae Remane, 1927			
<i>Acanthodasys</i> sp. A	Capraia, Italy	Todaro <i>et al.</i> 2011	JF357638
<i>Acanthodasys aculeatus</i> Remane, 1927	Capraia, Italy	Todaro <i>et al.</i> 2011	JF357639
<i>Diplodasys ankei</i> Wilke, 1954	Meloria, Italy	Todaro <i>et al.</i> 2011	JF357624
<i>Diplodasys ankei</i> Wilke, 1954	Bohuslän, Sweden	Todaro <i>et al.</i> 2011	JF357667/JF432049
<i>Diplodasys meloriae</i> Todaro, Balsamo & Tongiorgi, 1992	Meloria, Italy	Todaro <i>et al.</i> 2011	JF357640/JF432031
<i>Diplodasys</i> sp.	Kuwait	Todaro <i>et al.</i> 2011	JF357641/JF432032
<i>Oregodasys ocellatus</i> (Clausen, 1965)	Meloria, Italy	Todaro <i>et al.</i> 2011	JF357642
<i>Oregodasys ruber</i> (Swedmark, 1956)	Meloria, Italy	Todaro <i>et al.</i> 2011	JF357625/JF432020
<i>Oregodasys tentaculatus</i> (Swedmark, 1956)	Meloria, Italy	Todaro <i>et al.</i> 2011	JF357628/JF432021
<i>Pseudostomella etrusca</i> Hummon, Todaro & Tongiorgi, 1993	Albinia, Italy	Todaro <i>et al.</i> 2011	JF357633/JF432026
<i>Ptychostomella</i> sp. 1	Ilha Bela, Brazil	Todaro <i>et al.</i> 2011	JF357643/JF432033
<i>Ptychostomella tyrrhenica</i> Hummon, Todaro & Tongiorgi, 1993	Albinia, Italy	Todaro <i>et al.</i> 2011	JF357634/JF432027

TABLE 1. — Continuation.

Taxon	Origin	Reference	18S/COI Accession number
<i>Tetranchyroderma</i> cf. <i>antenniphorum</i> Hummon & Todaro, 2010	Kuwait	Todaro <i>et al.</i> 2011	JF357645
<i>Tetranchyroderma cirrophorum</i> Lévi, 1950	Capraia, Italy	Todaro <i>et al.</i> 2011	JF357635/JF432028
<i>Tetranchyroderma esarabdophorum</i> Tongiorgi & Balsamo, 1984	Mahdia, Tunisia	Todaro <i>et al.</i> 2011	JF357627
<i>Tetranchyroderma hirtum</i> Luporini, Magagnini & Tongiorgi, 1973	Capraia, Italy	Todaro <i>et al.</i> 2011	JF357628/JF432023
<i>Tetranchyroderma pachysomum</i> Hummon, Todaro & Tongiorgi, 1993	Meloria, Italy	Todaro <i>et al.</i> 2011	JF357636/JF432029
<i>Tetranchyroderma papii</i> Gerlach, 1953	Sardegna, Italy	Todaro <i>et al.</i> 2011	JF357637/JF432030
<i>Tetranchyroderma quadritentaculatum</i> Todaro, Balsamo & Tongiorgi, 1992	Albinia, Italy	Todaro <i>et al.</i> 2011	JF357629
<i>Tetranchyroderma quadritentaculatum</i> Todaro, Balsamo & Tongiorgi, 1992	Punta Ala, Italy	Todaro <i>et al.</i> 2011	JF357647/JF432024
<i>Tetranchyroderma thysanophorum</i> Hummon, Todaro & Tongiorgi, 1993	Fautea, Corsica, France	Todaro <i>et al.</i> 2011	JF357646/JF432025
<i>Tetranchyroderma</i> sp. 1	Bohuslän, Sweden	Todaro <i>et al.</i> 2011	JF357672
<i>Tetranchyroderma</i> sp. 3	Ilha Bela, Brazil	Todaro <i>et al.</i> 2011	JF357648/JF432035
<i>Tetranchyroderma</i> sp. 4	Ilha Bela, Brazil	Todaro <i>et al.</i> 2011	JF357644
<i>Thaumastoderma moebjergi</i> Clausen, 2004	Bohuslän, Sweden	Todaro <i>et al.</i> 2011	JF357671
<i>Thaumastoderma ramuliferum</i> Clausen, 1965	Punta Ala, Italy	Todaro <i>et al.</i> 2011	JF357649
<hr/>			
Turbanellidae Remane, 1927			
<i>Paraturbanella dohrni</i> Remane, 1927	Punta Ala, Italy	Todaro <i>et al.</i> 2011	JF357659
<i>Paraturbanella pallida</i> Luporini, Magagnini & Tongiorgi, 1973	Capraia, Italy	Todaro <i>et al.</i> 2011	JF357660/JF432045
<i>Paraturbanella teissieri</i> Swedmark, 1954	Punta Ala, Italy	Todaro <i>et al.</i> 2011	JF357661
<i>Turbanella bocqueti</i> Kaplan, 1958	Tramore, Ireland	Todaro <i>et al.</i> 2011	JF357662/JF432046
<i>Turbanella cornuta</i> Remane, 1925	Chioggia, Italy	Todaro <i>et al.</i> 2011	JF357663/JF432047
<i>Turbanella lutheri</i> Remane, 1952	Torö, Sweden	Todaro <i>et al.</i> 2011	JF357669/JF432051
<hr/>			
Xenodasyidae Todaro, Guidi, Leasi & Tongiorgi, 2006			
<i>Xenodasy riedli</i> (Schoepfer-Sterrer, 1969)	St. John Island, USA	Todaro <i>et al.</i> 2012	JN203490
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Chaetonotida Remane, 1925 [Rao & Clausen, 1970]			
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Muselliferidae Leasi & Todaro, 2008			
<i>Musellifer delamarei</i> (Renaud-Mornant, 1968)	NA	Todaro <i>et al.</i> 2006	AM231775
<i>Musellifer reichardtii</i> Kånneby, Atherton & Hochberg, 2014	Capron Shoal, Florida, USA	Kånneby <i>et al.</i> 2014	KF578503
<hr/>			
Xenotrichulidae Remane, 1927			
<i>Draculiciteria tessellata</i> (Renaud Mornant, 1968)	Punta Ala, Italy	Kånneby <i>et al.</i> 2012	JN185457/JN185541
<i>Draculiciteria tessellata</i> <i>Heteroxenotrichula squamosa</i> Wilke, 1954	St. John Island, USA Punta Ala, Italy	Kånneby <i>et al.</i> 2012 Kånneby <i>et al.</i> 2013	JN185470/JN185549 JQ798542
<i>Xenotrichula intermedia</i> Remane, 1934	Mahdia, Tunisia	Todaro <i>et al.</i> 2011	JF357664/JF432047
<i>Xenotrichula punctata</i> Wilke, 1954	Östersidan, Sweden	Kånneby <i>et al.</i> 2012	JN185464
<i>Xenotrichula velox</i> Remane, 1927	Åhus, Sweden	Kånneby <i>et al.</i> 2012	JN185499
<i>Xenotrichula</i> sp.	NA	Paps & Riutort 2012	JF970234
<i>Xenotrichula</i> sp. 1	St. John Island, USA	Kånneby <i>et al.</i> 2012	JN185466/JN185545

TABLE 2. — Selected characters for species within *Redudasys* Kisielewski, 1987 and *Marinellina* Ruttner-Kolisko, 1955. Abbreviations: See Material and methods. All measurements in micrometers.

	<i>Redudasys</i> sp. (Texas)	<i>Redudasys</i> <i>fornerise</i> Kisielewski, 1987	<i>Redudasys</i> sp. (Brazil)	<i>Marinellina</i> <i>flagellata</i> Ruttner-Kolisko, 1955	<i>Marinellina</i> sp.
TL	242	300 – 414	280 – 462	220	405
Length TbA shorter	Absent	3 – 9	Absent	Absent	Absent
Length TbA longer	9 – 10	9 – 14	Present	10	Present
Length TbP inner	10 – 12	8 – 12.5	7 – 13	20	Present
Length TbP outer	15 – 17	11 – 17	12 – 17.5	20	Present
PhL	92	101 – 154	87.5 – 154	NA	156
PhJ	U38	U35 – 36	NA	NA	NA
PP	U33	U31	NA	Absent?	NA

SYSTEMATICS

Phylum GASTROTRICHA Metschnikoff, 1865

Order MACRODASYIDA Remane, 1925

[Rao & Clausen, 1970]

Family REDUDASYIDAE Todaro, Dal

Zotto, Jondelius, Hochberg, Hummon,

Kånneby & Rocha, 2012

Genus *Redudasys* Kisielewski, 1987

Redudasys sp.

(Figs 1-3; Tables 2, 3)

MATERIAL EXAMINED. — One specimen that is no longer extant. Specimen prepared for sequencing of 18S rRNA and COI mtDNA. GenBank Accession numbers: KJ950121 and KJ950123.

DISTRIBUTION. — In fine to medium grained sand with some organic content at 3-9 meters. Spring Lake, San Marcos, Texas, USA (29°53'36"N; 97°55'53"W), June 17, 2012.

DESCRIPTION

Redudasys with total body length of 242 µm. Body width at head (U12), neck (U24), trunk (U76) and base of caudal lobes (U94) is, 47 µm, 34 µm, 47 µm and 21 µm, respectively. Head with clearly distinguishable sensory cilia. Slight neck constriction present. Trunk of approximate equal width and not wider than widest part of head, narrowing toward the caudal end which indents at U95. Body surface transparent, without cuticular structures.

Apparently only a single pair of TbA present, 9-10 µm in length, and located at U13. Two pairs of TbP: inner pair 10-12 µm in length and outer pair 15-17 µm in length.

Sensory cilia abundant in anterior head region and reach lengths up to 25 µm. Antermost cilia surrounding mouth appear stiffer and are shorter, approximately 10 µm in length. At least seven pairs of dorsolateral to lateral sensorial hairs observed, posteriormost pair inserted just anterior to caudal indent. Ventral ciliation apparently in somewhat regularly spaced tufts from U8 to U50. Posterior to U50, tufts are medial in distribution.

Mouth terminal. Pharynx 92 µm long with pharyngeal intestinal junction located at U38. Pharyngeal pores could not be detected in the live specimen but they were subsequently detected in photos, they are located in the posterior part of the pharynx at approximately U33. Intestine straight, narrowing towards its posterior end, with anus at approximately U90.

One egg, approximately 50 µm in diameter, present dorsally in mid-posterior trunk region. Sperm or accessory reproductive organs not detected.

REMARKS

Compared to other specimens of *Redudasys*, the most notable difference of the Texan specimen is its smaller size. The shortest total body lengths reported for *R. fornerise* and *Redudasys* sp. from Brazil are 300 µm and 280 µm, respectively (Kisielewski 1987a;

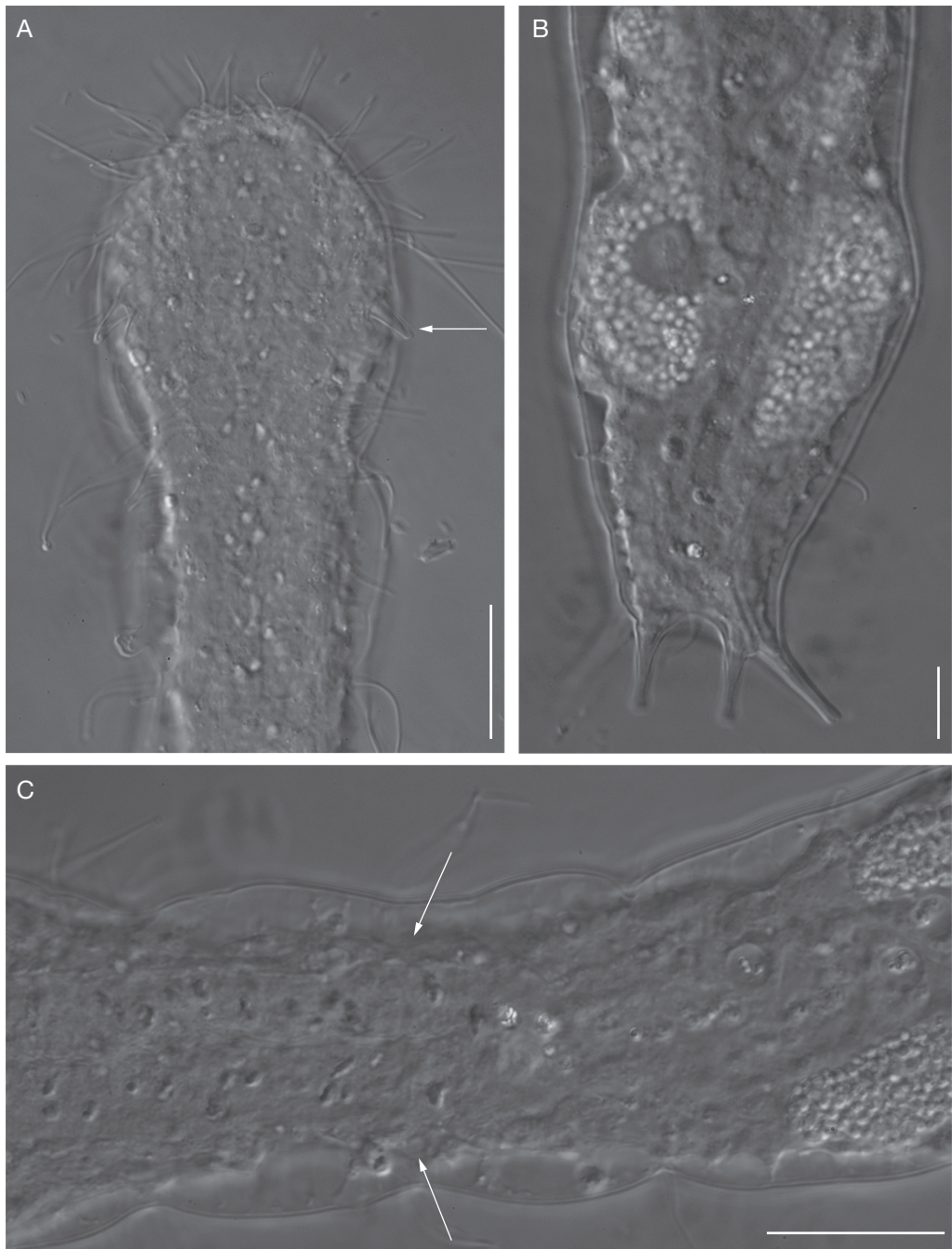


FIG. 1. — *Redudasys* sp. found in San Marcos, Texas: **A**, ventral view of anterior portion of body showing the anterior adhesive tubes (arrow) and the sensorial hairs of the head; **B**, posterior portion of body showing the caudal lobes with posterior adhesive tubes; **C**, posterior part of pharynx showing the position of pharyngeal pores (arrows). Scale bars: A, C, 20 μ m; B, 10 μ m.

TABLE 3. — Single pure characters for each species based on an alignment of only the taxa within Redudasyidae. For each gene the unique nucleotide and its position in the alignment are given. The number within parenthesis corresponds to the same position in the original unaligned sequence. Only the ten first unique positions are presented for each species where applicable. Abbreviations: see Material and methods.

Species	Gene	Unique nucleotide with position in alignment and in original sequence
<i>Redudasys</i> sp.	18S	C, 127 (123); T, 134 (130); A, 150 (145); G, 194 (175); T, 208 (189); G, 687 (658); A, 1352 (1316); T, 1449 (1318); A, 1647 (1516); T, 1804 (1673)
	COI	T, 1 (1); T, 10 (10); C, 14 (14); T, 22 (22); G, 34 (34); C, 44 (44); T, 46 (46); C, 48 (48); T, 49 (49); T, 67 (67)
<i>Redudasys formerise</i> Kisielewski, 1987	18S	A, 124 (122); A, 125 (123); A, 126 (124); T, 129 (127); A, 131 (129); A, 134 (132); T, 150 (147); T, 153 (150); C, 208 (191)
	COI	A, 1 (1); C, 10 (10); T, 14 (14); G, 22 (22); A, 34 (34); T, 44 (44); A, 46 (46); T, 48 (48); C, 49 (49); C, 67 (67)
<i>Anandrodasys</i> <i>agadasys</i> (Hochberg, 2003)	18S	C, 20 (20); T, 21 (21); C, 23 (23); A, 24 (24); C, 28 (28); A, 29 (29); C, 43 (43); A, 56 (56); G, 61 (61); T, 80 (80)
	COI	NA

Garraffoni *et al.* 2010), compared to 242 μm for the Texan specimen (Table 2). However, our specimen could be a young adult, judging from the presence of only a single egg, and it may attain a larger body size as it matures. The Texan specimen can be separated from *R. formerise* based on the following combination of morphological characters: (i) a single pair of anterior adhesive tubes, and (ii) a shorter body length. Although the second pair of anterior adhesive tubes can be hard to detect, they appear absent in our specimen. The only apparent difference from the Brazilian *Redudasys* sp. reported by Garraffoni *et al.* (2010) is the shorter body length (Table 2). The exact distribution of lateral and/or dorsolateral sensorial hairs cannot be justified from the single specimen obtained in this study. However, since the specimen from Texas is geographically far separated from the Brazilian taxa, it is plausible that it is new to science.

The classification of our specimen within the family Redudasyidae and the genus *Redudasys* is based on the presence of pharyngeal pores in the posterior part of the pharynx and the unequal length of the inner and outer pair of TbP. The Bayesian analysis of the concatenated data set of 18S rDNA and COI mtDNA give maximum support for the inclusion of our specimen within Redudasyidae. The uncorrected pairwise distance based on COI mtDNA, between the Texan specimen and *R. formerise* is 0.175. In order to diagnose the Texan specimen, we

have provided the position of the ten first unique nucleotides for each taxa for which sequence data is available within Redudasyidae (Table 3). However, it should be noted that *R. formerise* is the only other freshwater macrodasyidan for which sequences are available on GenBank.

DISCUSSION

All in all there are now five taxa of the predominantly marine Macrodasyida that have been reported from freshwater (Table 2). They are all characterized by a reduction of the number of adhesive tubes, only anterior and posterior adhesive tubes are typically present (Kisielewski 1987; Todaro *et al.* 2012). The poor description of *M. flagellata* and the fact that it is based on apparently immature specimens further complicates the morphological separation of *Marinellina* and *Redudasys* (see Kisielewski 1987). However, there are some characters that can be used to distinguish *Marinellina* from *Redudasys*: i) the TbP of *M. flagellata* are of equal length, while in *Redudasys* the inner pair of TbP are shorter than the outer pair; ii) the absence of pharyngeal pores in *M. flagellata*. Ruttner-Kolisko (1955) was well aware of the presence of pharyngeal pores in Macrodasyida and hypothesized that the reduction of these pores were an adaptation to a life in a freshwater environment. However, it should be noted that pharyngeal

pores are sometimes difficult to observe and this may be especially true for such a small species as *M. flagellata*. It is also possible that *M. flagellata* is in fact a juvenile form of *Redudasys*. To disentangle such a relationship it would be appropriate to collect and sequence several specimens of *Marinellina* from the type locality in Austria. This however appears a daunting task since all attempts at rediscovering *M. flagellata* at the type locality have failed. The new findings of a hypothesized member of *Marinellina*, designated as *Marinellina* sp., from Brazil by Araujo *et al.* (2013) may shed some light on this issue if it is formally described. This taxon has a much greater body length than *M. flagellata*. Whether pharyngeal pores are absent and the TbP are of unequal length or not is not mentioned in the short description.

Turbanella cornuta Remane, 1925, *Turbanella hyalina* Schultz, 1853 and *Turbanella lutheri* Remane, 1952 have been reported from the Baltic Sea at salinities of 0.2–0.6‰ (Jansson 1968), although these species are well known from localities with proper marine salinity (Kieneke *et al.* 2012). Kisielewski (1987b) reported *T. lutheri* from freshwater beach seeps in Roscoff, France. Moreover, several marine chaetonotidans have been recorded from brackish environments in the Baltic Sea (e.g., Hummon 2008; Kanneby *et al.* 2013). This suggests that certain taxa of both Macrodasysida and Chaetonotida have a remarkable tolerance to adapt to changes in salinity. It has to be stressed that future genetic studies could demonstrate that these taxa are indeed complexes of cryptic species where each species is adapted to a narrower range in salinity. *Redudasys* on the other hand is likely to be a marine relic. It has strong morphological affinities with marine Macrodasysida, e.g., a strap-shaped body, the inverted Y-shaped pharynx lumen and the presence of pharyngeal pores (Kisielewski 1987a) and presumably was derived from marine ancestors by stranding following the regression of marine embayments. All localities where the taxon hitherto has been found are far away from marine waters (the closest is Spring Lake in this study, approximately 221 km from the Gulf of Mexico).

Holsinger & Longley (1980) noted that there was a “strong possibility” that species of amphipod crustaceans in artesian wells of the Edwards Aquifer

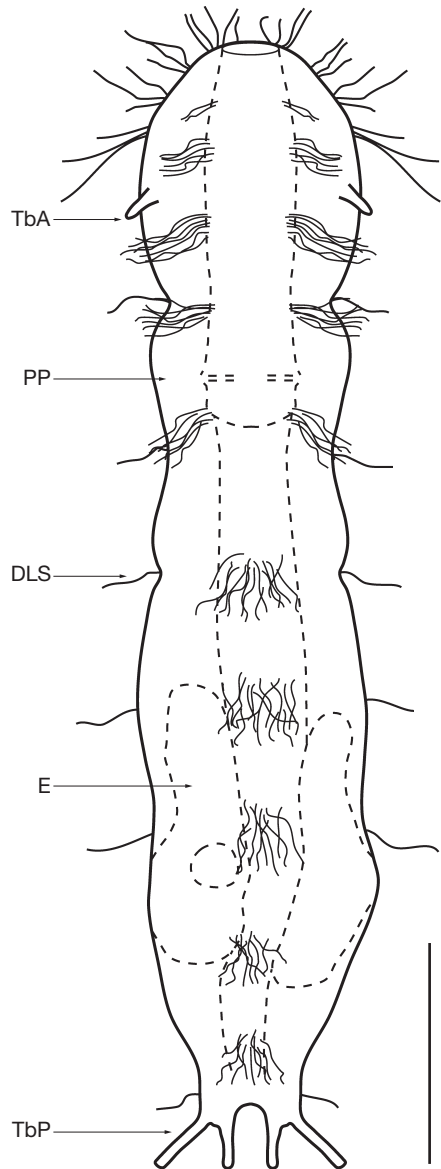


FIG. 2. — Schematic drawing of the ventral side of *Redudasys* sp. found in San Marcos, Texas. Abbreviations: see Material and methods. Scale bar: 50 μ m.

were derived from marine ancestors. These ancestors invaded newly opened freshwater habitats during the late Cretaceous, when a large embayment covered central Texas. These authors postulated the existence of marine relic species in groundwater and

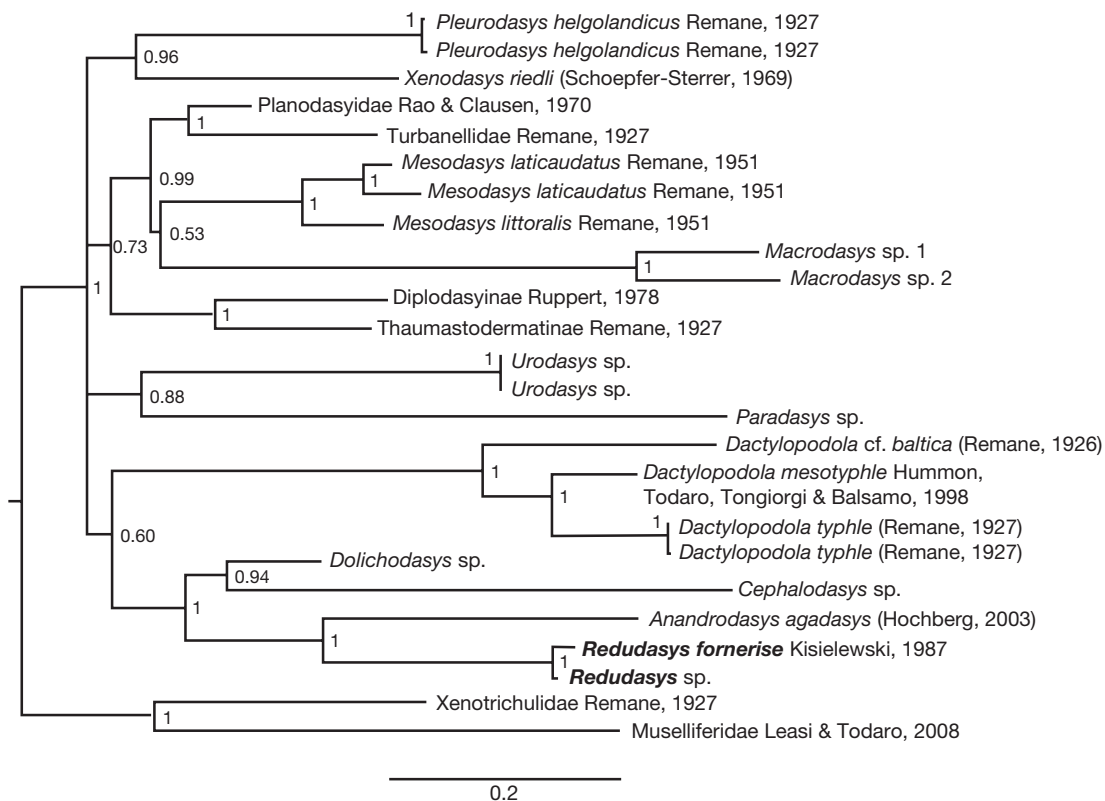


Fig. 3. — Majority rule consensus tree of the phylogenetic relationships of Macrodasysida inferred from Bayesian analysis of the 18S rRNA and COI mtDNA genes. Numbers at nodes represent posterior probability. *Redudasys* sp. from Texas and *Redudasys formerise* are highlighted in bold font. The outgroup is represented by members of Muselliferidae Leasi & Todaro, 2008 and Xenotrichulidae Remane, 1927 (Chaetonotida). The clades Planodasyidae, Muselliferidae Thaumastodermatinae, Turbanellidae and Xenotrichulidae have been collapsed for clarity. Dactylopodolidae was not collapsed, since it appears close to Redudasysidae.

cavernous limestone buried under late Cretaceous sediments and later exposed by uplift and faulting of the Balcones fault line during the Miocene. Gibson *et al.* (2008) expanded on these ideas, commenting that the rare crustaceans *Ingolfiella* sp., *Tethysbaena texana* (Maguire, 1965), and certain stygiobiontic amphipods, also found in the Edwards Aquifer, appear to have a Tethys Sea origin and colonized the area during regression of a Cretaceous sea.

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