Description of *Priapella chamulae* sp. n. – a new poeciliid fish from the upper río Grijalva system, Tabasco, Mexico (Teleostei: Cyprinodontiformes: Poeciliidae)

Manfred Schartl [1], Manfred K. Meyer [2] & Brigitta Wilde [1]

[1] Physiologische Chemie I, Universität Würzburg, Biozentrum, Am Hubland, D-97074 Würzburg, Germany

[2] Schwalheimer Hauptstr. 22, D-61231 Bad Nauheim, Germany

Zusammenfassung. *Priapella chamulae* sp. n., aus den Nebenflüssen des río Tacotalpa und río Pichucalco, río-Grijalva-System, Tabasco, Mexico, wird beschrieben. Sie unterscheidet sich deutlich durch ihre morphometrischen Merkmale, Besonderheiten des Gonopodiums und andere morphologische Charakteristika von den anderen Arten der Gattung. Eine, auf mitochondrialer DNA-Sequenz basierende phylogenetische Analyse führte zu ähnlichen Ergebnissen zum Status der neuen Art als separates Taxon und ihrer Verhältnisse zu den am nächsten verwandten Arten.

Resumen. Se describe *Priapella chamulae* sp. n. de los afluentes de los ríos Tacotalpa y Pichucalco, del sistema del río Grijalva, Tabasco, Méjico. Se diferencia claramente de las otras especies del género por rasgos morfométricos, características del gonopodio y otros caracteres morfológicos. Un análisis filogenético basado en secuencias del DNA mitocondrial condujo a resultados similares con respecto al estatus como taxón diferente y su relación respecto a las especies más cercanamente emparentadas.

Abstract. *Priapella chamulae*, new species, is described from the tributaries of río Tacotalpa and río Pichucalco, río Grijalva system, Tabasco, Mexico. It is clearly distinguished by metrics, gonopodial and other morphological characteristics from all other species of the genus. A mitochondrial DNA-sequence based molecular phylogenetic analysis revealed similar results on the status of the new species as a separate taxon and its relation to the other closest related species.

Introduction

Rosen & Bailey (1963) combined the genus *Priapella* together with the genera *Alfaro*, *Xiphophorus* and *Poecilia* to constitute the tribus Peociliinae. At that time the genus *Poecilia* included the genera *Lebistes*, *Limia*, *Micropoecilia*, *Mollienesia* and *Pamphorichthys*. According to Rosen (1979) *Xiphophorus* is the most closely related genus to *Priapella*. Later, Parenti (1981), Parenti & Rauchenberger (1989) established the supertribus Poeciliinae and included all remaining genera of Poeciliinae except *Tomeurus*. The tribe Poeciliinae sensu Rosen & Bailey (1963) was adopted by the authors. Meyer *et al*. (1994) generally confirmed by DNA-sequence based phylogenetic methods earlier studies that used morphological and metric analyses. On the contrary, Rodriguez (1997) strongly advocates for an exclusion of *Priapella* from Poeciliinae. Gheodotti (2000) finally establishes for the genus *Priapella* an own tribe, Priapellini, and points out the close relationship to Alfarini and Gambusiini.

The poeciliid genus *Priapella*, which includes *P. compressa* Alvarez, 1948, *P. intermedia* Alvarez, 1952, *P. olmecae* Meyer & Perez, 1990 and the type species *P. bonita* (Meek, 1904), has a wide range in southeastern Mexico and is mostly found in small numbers in constantly oxygen-rich habitats. Its known distribution extends along the Atlantic slopes from the southern río Papaloapan basin, Veracruz, Mexico, to the upper reaches of the río Grijalva system, Chiapas, Mexico. *Priapella* as far as known is not represented in the río Usumacinta system, although some authors (Alvarez, 1970; Lozano Vilano *et al*., 1987 and Miller, 1976) refer the río Michol to the upper watercourses of the río Usumacinta. Of all species of the genus, *Priapella intermedia* has the greatest range of nearly 2000 square kilometers in the upper río Coatzacoalcos basin north to the upper río Papaloapan system. All others have a more restricted range, of which *Priapella compressa* is only know from two tributaries of the

río Michol, río Grijalva system, Chiapas. *Priapella olmecae* has been found exclusively in some brooks of the Los Tuxtlas mountains, Veracruz and *Priapella bonita* is reported from the upper río Tonto, río Papaloapan system (MEYER & PEREZ, 1990). The present paper describes a new species of *Priapella* from the headwaters of the río Tacotalpa and río Pichucalco, Tabasco, Mexico.

Materials and methods

All material of *Priapella* used for the morphological comparison stemmed from the private fish collection of MANFRED MEYER, Bad Nauheim, and of The Natural History Museum, London: *Priapella compressa*, río Otolum, southern tributary of río Michol (Tulijá system), Palenque ruinas and río Paxilha, southern tributary of río Tulijá, Aqua Azul, Chiapas, Mexico; *Priapella intermedia*, río de la Lana, Papaloapan basin, Oaxaca, and northern tributary of río Junapan, 5 km north of Donaji, río Coatzacoalcos basin, Oaxaca, Mexico; *Priapella olmecae*, río de la Palma, Veracruz, Mexico; *Priapella bonita*, Refugio, Veracruz, Mexico.

Fish used for the molecular phylogenetic analyses were *Priapella compressa* from Palenque ruinas and Aqua Azul (Chiapas), *Priapella olmecae* from Laguna Escondida (Veracruz), *Priapella intermedia* from río de la Lana (Oaxaca), Jesus Caranza (Veracruz) and río Sarabia (Oaxaca), *Priapella chamulae* from Tapijulapa (Tabasco). *Xiphophorus maculatus* from río Jamapa (strain Jp163a) was used as outgroup.

Measurements were made by vernier calipers, reading to 0.1 mm. Measurements and counts follow standard practice (MILLER, 1948). The length of distal tip of gonopodium ray 4a and 3 is measured on a horizontal line from the distal tip of ray 4p to distal tip of gonopodium hook. The depth of gonopodium is measured on a vertical line from ray 3 to ray 5p exactly where the serrae 4p starts to nestle against ray 4a.The number of specimens for all counts is greater or equal to 5. The total gill-raker count of the first gill arch includes all gill rakers in the angle of the gill arch. The last two rays in the dorsal fin are counted as a single ray. Vertebral counts include the hypural plate as one vertebra. The nomenclature of the sensory canal system of the head follows the standard of GOSLINE (1949) and parts of the gonopodial system follow ROSEN & GORDON (1953), ROSEN & KALLMAN (1959) and ROSEN & BAILEY (1963). Genomic DNA was isolated from pooled organs of individual fish as described by SCHARTL *et al.* (1995) or from dorsal fin clips according to ALTSCHMIED *et al.* (1997). Sequences from the mitochondrial D-loop region and the *cytochrome b* gene were amplified by PCR. For the D-loop the primer pairs L15995 (5'AACTCTCACCCCTAGCTCCCAAAG3')/H16498 (5'CCTGAAGTAGGA ACCAGATG3') and L15513 (5'CTRGGAGACCCNGAAAACTT3')/ H16100 (5'ATGTAG GGTTACAYTACTTTTAAATGG3') and for *cytochrome b* the primer pair L14724 (5'CGA AGCTTGATATGAAAAACCATCGTTG3' and H15149 (5'AAACTGCAGCCCCTCAGAA TGATATTTGTCCTCA3') were used. The PCR was done under the following conditions: denaturation 95 °C for 30 sec, annealing 52 °C (for D-loop primers L15995/H16498), 54 °C (for D-loop primers L 15513/H16100) or 50 °C (for Cytochrome *b*) for 30 sec, extension 72 °C for 45 sec. 31 cycles were run from less than 100 ng genomic DNA. In each case a single PCR product was obtained and sequenced directly. Nucleotide sequences were analysed using programs of the GCG package, version 9.1 (Genetics Computer Group, Madison, Wisc.). Multiple sequence alignments were generated using PILEUP of GCG. Phylogenetic analyses were done with PAUP (SWOFFORD, 1989) as part of the GCG package. Heuristic and branch-and-bound tree searches were performed using both parsimony and distance (minimum evolution). Neighbour-joining (NJ) trees were also constructed. Robustness of the trees was tested by bootstrap analyses using 100 replicas or in the case of NJ trees 1000 replicas. Pair-wise distances were calculated by using the program DISTANCES as part of GCG using all distance correction methods implemented in the program. All DNA sequences generated in this study are deposited in GenBank.

Figs. 1–2. 1. *Priapella chamulae*; Mexico: arroyo 3 km NW Tapijulapa, holotype, MTD F 28717, male, 26.5 mm SL. **2**. *Priapella chamulae*; Mexico: arroyo 3 km NW Tapijulapa, paratype, MTD F 28718, female, 41.9 mm SL.

Abbreviations

APL = distance anus to pectoral fin; BD = depth of body; BMNH = fish collection of The Natural History Museum, London, England; CPL = length of caudal peduncle; CPD = depth of caudal peduncle; DDG = depth of gonopodium tip; ED = diameter of eye; F = female; GL = length of gonopodium; HL = length of head; HT = holotype; IOW = interorbital width; LDG = length of gonopodium tip; M = male; MTD F = fish collection of the Museum fuer Tierkunde, Dresden, Germany; PDL = predorsal length; PL = length of pectoral fin; PT = paratype; SMF = fish collection of the Forschungsinstitut und Museum Senckenberg, Frankfurt/Main, Germany; SNL = length of snout; SL = standard length; TL = total length; VL = length of ventral fin; ZFMK = fish collection of the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.

Priapella chamulae, new species (Figs. 1–5)

Holotype. Male (MTD F 28717), 26.5 mm SL; arroyo 3 km NW Tapijulapa, río Tacotalpa system, Tabasco, Mexico, M. Schartl & J. Parzefall *leg*., February 25th, 2000.

Paratypes. 3 males, 2 females (MTD F 28718–28722), 2 males, 2 juveniles (ZFMK 39938–39941), 3 males, 1 female, 2 juveniles (BMNH 2005.5.10.4–9), 2 males, 1 female (SMF 30086); arroyo 3 km NW Tapijulapa, río Tacotalpa system, Tabasco, Mexico, M. SCHARTL, M. SCHARTL & K. LAMPERT *leg*., March 20th, 2005. 2 females, 2 males, 2 juveniles (SMF 30087), río el Azufre approx. 6 km E Santa Ana on Hwy 195, río Pichucalco system, border Tabasco/ Chiapas, Mexico, E. HNILICKA, D. VOGEL, E. MÜLLER & M.K. MEYER *leg*., February 22 th, 1980.

Diagnosis

Priapella chamulae is a large sized species of *Priapella* (max. SL 48 mm), which is distinguished from all other species of the genus by the following characters: membranous hook of the gonopodium ray 3 well developed and semicircularly bent, vs. slightly bent *in P. bonita, P. compressa*, *P. intermedia* and *P. olmecae*; subdistal plate-like membranous process on gonopodium ray 3 well developed, vs. not prominent in *P. compressa* and *P. intermedia*; spines of gonopodium ray 3 long and not numerous, vs. numerous and densely crowded in *P. compressa* and *P. intermedia,* and short and not densely crowed in *P. olmecae;* distal part of gonopodium ray 4p slightly bent, vs. strongly bent in *P. bonita*, *P. compressa*, *P. intermedia* and *P. olmecae*.

P. chamulae is also distinguished by the following unique combination of characters: length of gonopodium short; frequency distribution of SL/GL radius 3.30–3.50, vs. 2.60–2.75 in *P. olmecae*, 3.00–3.20 in *P. compressa*, 2.60 in *P. bonita* and 3.50–3.60 in *P. intermedia*; 10 to 12 gill rakers, vs. 15–16 in *P. bonita*, 12 to 13 in *P. compressa*, 12 to 14 in *P. compressa*; 9 dorsal fin rays, vs. 8 in *P. bonita*, 10 in *P. compressa*.

Description

Body deep, head long and sharply pointed, 25.5–27.5 % of SL. Longitudinal scale series 27–(rarely) 29; predorsal scale series 13-14; scale series around caudal peduncle 16. Number of vertebrae 30 to 31. Gill rakers on first arch 10 to 12+1.

Teeth of upper and lower jaws unicuspid and recurved; those of outer row enlarged and spear-like shaped, not numerous and widely spaced; spear-like shaped inner teeth not numerous. Upper pharyngeal bones kidney-shaped. Teeth of the medial region somewhat enlarged, each side with a series of 5–6 rows, teeth small and conical. Lower pharyngeal bone (ceratobranchial 5) with a total of 60–70 large unicuspid teeth, 6–8 on posterior rows, 6–7 on middle rows. Teeth of medial region very large. Both halves of lower pharyngeal antler-shaped, closely together on a small part along midline. Arms of pharyngeal very long and split at the ends. Ceratobranchial 4 without teeth, hypobranchial 4 absent.

Supraorbital canal system well developed, sections 1+2a, 2b-4a, 4b-6a, 6b–7 usually represented as grooves and pits; preopercular canal with 7 pores (8–12, U, V); preorbital canal with 4 pores (sometimes represented as groove); mandibular canal with 4 pores (W-Z).

Gonopodium short and compact, 3.3 to 3.5 times in SL; ray 3 broadly expanded, terminating in a short and massive semicircularly bent membranous gonopodium hook, distal spine-like bony segment of ray 3 very long, angular and directed to subdistal spine-like series, 6 to 7 slightly angulate spine-like series long and slender, plate-like process of membranous tissue ventral to spine-like series well developed, base of ray 3 somewhat thickened and subdivided in 4 to 5 segments; ray 4a longest and partly bent over the gonopodium hook of ray 3, subdistal segments of ray 4a broader than long; ray 4p straight and slightly bent on tip, proximal serrae with 9 to 11 thorns; ray 5 shorter than rays 3 and 4. Rays 6 and 7 thickened distally, tips broadly expanded and curved dorsally.

Gonopodial suspensorium with three well developed gonapophyses, gonapophyses I, II and III long and slender, each with an uncinus (interpreted by ROSEN & BAILEY (1963) as parapophyses), parapophyses present on gonapophysis I, II and III, shaft tips of gonapophysis

Table 1. Measurements (in mm) of holotype and paratypes of *Priapella chamulae* sp. n.

	TL	SL	HL	SNL	BD	IOW	GL	ED	APL	CPL	CPD	PL	VL	PDL
01.HT(M)	34.00	26.50	6.60	1.80	8.90	2.20	8.70	2.50		7.30	5.40	5.10	2.70	15.40
02.PT(F)	50.50	38.40	10.20	2.90	14.50	4.80		3.70	12.60	10.40	8.20	7.20	5.30	25.00
03.PT(F)	59.10	46.80	11.30	3.40	15.20	5.80		4.10	14.80	11.40	8.80	8.90	6.00	29.70
04.PT(F)	57.30	45.60	10.90	3.30	14.90	5.70		4.20			8.40	8.70	5.90	27.90
05.PT(F)	53.40	41.90	10.40	3.20	14.70	5.10		3.60	13.80	10.30	7.60	8.20	5.50	26.90
06.PT(M)	32.00	25.40	6.50	1.80		2.10	8.30	2.60		7.20	5.10			14.80
07.PT(F)	56.10	45.20	10.80	2.90	14.20	5.40		3.60	15.40	10.80	9.70	8.80	5.90	28.80
08.PT(M)	41.60	32.30	8.00	2.10	12.30	3.60	9.70	3.10		9.00	7.90	6.40	3.60	19.70
09.PT(M)	37.10	28.80	7.50	1.90	9.40	2.80	8.90	2.80	6.70	8.20	7.30	5.50	3.20	16.80
10.PT(M)	39.20	30.70	7.80	2.00	10.60	3.20	9.20	2.90	7.30	8.60	7.60	5.90	3.40	18.60
11.PT(M)	41.40	32.00	8.00	2.30	12.10	3.70	9.60	3.20	8.10	8.80	8.00	6.30	3.70	19.60
12.PT(M)	31.60	24.90	6.30	1.70	8.30	2.00	8.10	2.30		6.60		4.90	2.70	14.90
13.PT(M)	39.30	30.60	7.90	2.10	10.40	3.30	9.20	2.90	7.80	8.60	7.70	6.00	3.30	18.80
14.PT(M)	30.60	23.40	6.00	1.60	8.10	1.90	8.00	2.20		6.40	5.20	4.80	2.60	14.40
15.PT(M)	39.10	30.40	7.80	2.00	10.30	3.20		2.80	7.70	8.50	7.80	5.80	3.40	18.70
16.PT(M)	39.30	30.90	7.90	2.10	10.50	3.20	9.10	3.00	7.90	8.60	7.80	5.90	3.50	18.10

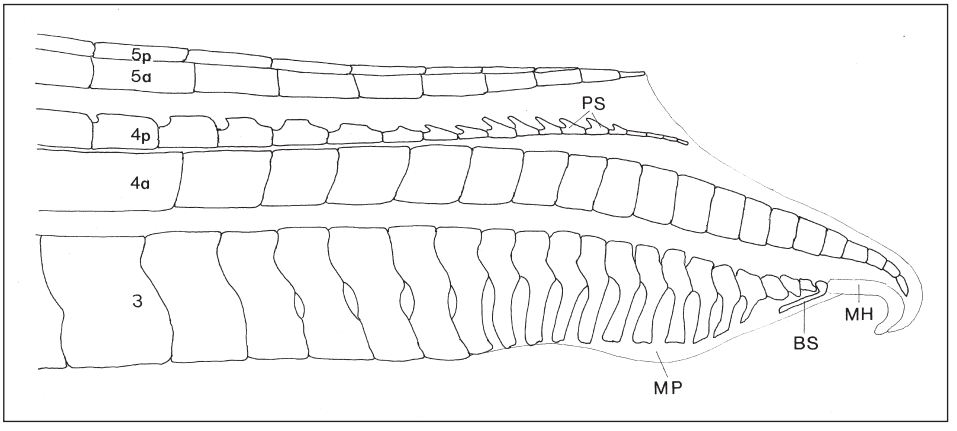

Fig. 3. Gonopodium tip of *Priapella chamulae*; Mexico: arroyo 3 km NW Tapijulapa. BS – distal bony segment of gonopodium ray 3, MH – membranous hook of gonopodium plate of gonopodium ray 3, MP – membranous plate of gonopodium ray 3, PS – proximal serrae of gonopodium ray 4p.

I and II angular and curved ventrally, gonapophysis III curved anteriorly. Ligastyle very long and slender. Gonactinost 1 without inferior wing-like appendage, gonactinostal complex 2 to 4 in front with a superior lateral wing, gonactinosts 5 to 9 without bony plates or outgrowths.
Dorsal fin with 9–10 rays (first 3 rays simple, all others branched), origin of dorsal fin posterior to the insertion of anal fin; caudal fin with 29 to 30 (14 branched) rays; anal fin 10 rays (first 2 to 3 rays simple, all others branched); pectoral fin with 13 to 14 rays (first 2 and

Figs. 4–5. 4. *Priapella chamulae*; Mexico: arroyo 3 km NW Tapijulapa, aquarium specimen, male.
5. *Priapella chamulae*; Mexico: arroyo 3 km NW Tapijulapa, aquarium specimen, female.

last 2 rays simple, all others branched); ventral fin with 6 rays (first and last ray simple, all others branched), in females not reaching to the anal fin base and in males reaching base of gonopodium, first ray thin and bent distally. Adult males with a prominent keel, starting on the edge of caudal peduncle and ending near base of gonopodium; keel with small scales.
Males and females without sex specific coloration (Figs. 4–5). Body color of adult females and males greyish yellow; lower posterior body sides intensely orange-yellow; iris intense iridescent blue. Border of dorsal fin and upper and lower ramus of caudal fin with light blueish-white color, all other fin hyaline.

Etymology

The new taxon is named in honour the native population of the Chamula, who live in central Chiapas and on the Tabasco border, Mexico.

Comparison and relationships

RODRIGUEZ (1997) gives the following derived characters for the genus *Priapella*: gonopodium ray 3 with the most distal segment modified into a forward-curved bony hook, a long membranous segment posterior to the ray joining with the last segments of ray 4a, the membranous segment becoming flat at the junction and gonopodium ray 4a with 10-13 distal segments extending far behind the tip of ray 4p. All these characters are present in *P. chamulae*. On the basis of these synapomorphies, *P. chamulae* is unequivocally attached to the genus *Priapella*.

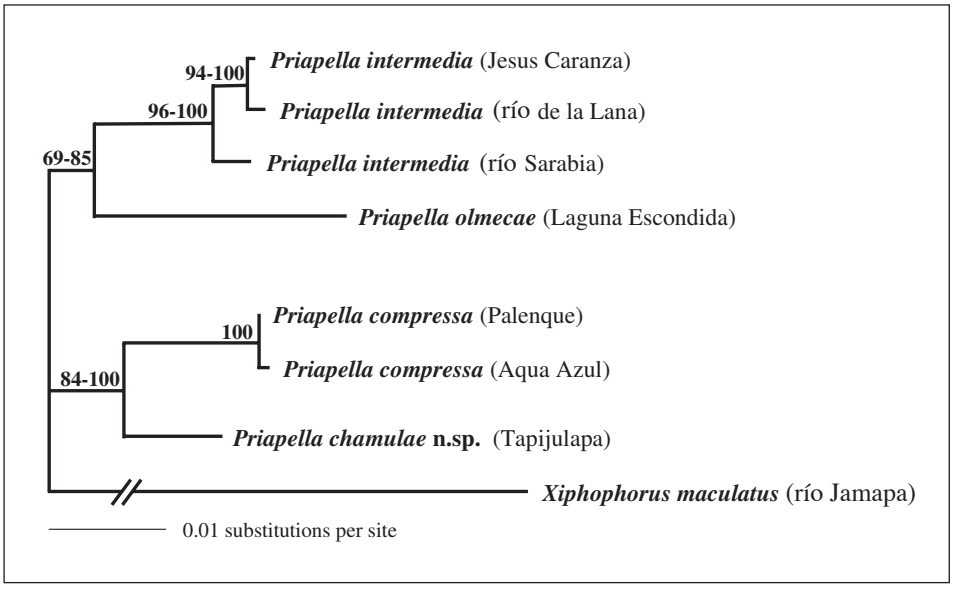

Fig. 6. Phylogram of *Priapella chamulae* and related *Priapella* species based on mitochondrial DNA sequences. 50 % majority rule consensus tree rooted on *Xiphophorus maculatus* as outgroup. Minimal and maximal bootstrap values obtained using different types of analysis (see Material and Methods) are indicated above the branches.

Table 2. Pairwise distance matrix using Jukes-Cantor as correction method.
int JC, *Priapella intermedia* from Jesus Cranza; int LL, *P. intermedia* from río de la Lana; int RS, *P. intermedia* from río Sarabia; compPal, *P. compressa* from Palenque; compAA, *P. compressa* from Aqua Azul; cham, *P. chamulae* from Tapijulapa; olme, *P. olmecae* from Laguna Escondida; Xmac, *Xiphophorus maculatus* from río Jamapa.

	int JC	**int LL**	**int RS**	**compPal**	**compAA**	**cham**	**olme**	**Xmac**
int JC	0.00	0.15	0.62	3.63	3.71	3.31	3.55	14.96
int LL		0.00	0.77	3.79	3.87	3.47	3.71	14.96
int RS			0.00	3.63	3.71	3.31	3.55	15.05
compPal				0.00	0.08	2.03	4.69	15.05
compAA					0.00	2.11	4.77	15.05
cham						0.00	4.28	14.58
olme							0.00	15.62
Xmac								0.00

By morphological criteria *P. chamulae* is most closely related to *P. intermedia* and *P. compressa*. There are several synapomorphies that unite *P. chamulae* with *P. compressa* and *P. intermedia,* namely: numerous, long and pointed subdistal spines of gonopodium ray 3; subdistal segments of gonopodium ray 4a opposite serrae shorter than high. However, *P. chamulae* is recognized as a separate species, because it does not share the following synapomorphies between *P. compressa* and *P. intermedia*: distal tip of gonopodium long (LDG/DDG radius 0,85–0,95); s-like form of the distal part of gonopodium ray 4p. On the other hand there is one autapomorphy of *P. chamulae*: terminal segment of gonopodium ray 3 formed by a semicircular hook. *Priapella chamulae* is further distinguished from *P. intermedia* and *P. compressa* by fewer

subdistal spines of gonopodium ray 3 (3–5 vs. 6–7, 5–7), from *P. intermedia* by much longer first isolated spine of gonopodium ray 3, and a much longer distal spine-like bony segment of ray 3, from *P. olmecae* by longer spines of gonopodium ray 3; and from *P. bonita* and *P. compressa* by fewer dorsal fin rays (9 vs. 8 and 10) and fewer gill rakers (10–12 vs. 15–16 and 12–13).

A molecular phylogenetic analysis was performed using mitochondrial D-loop and cytochrome *b* sequences. The resulting data set consists of approx. 1300 bases for each species. The genetic distances calculated with each of the distance correction methods revealed that the genetic distance between *P. chamaulae* and the closest related taxa, the two populations of *P. compressa*, is considerably higher than the values obtained for different populations of a species.

The molecular data were analyzed with maximum likelihood, parsimony and neighbour-joining methods which yielded almost identical phylogenetic results. The topology of the resulting trees was always the same. Two major branches were resolved, which unite *P. intermedia* and *P. olmecae* in one group and *P. compressa* and *P. chamulae* in the other. The new species is clearly separated from *P. compressa*; similar to the split between *P. intermedia* and *P. olmecae*. It should be noted that different, distantly located populations of *P. intermedia* and the two populations of *P. compressa* are each closely clustered in the tree, thus demonstrating the reliability of the molecular tree for resolving relationships on the population vs. species level.

Distribution

Priapella chamulae is known from the upper río Grijalva system in the Teapa area, Tabasco and Chiapas, Mexico.

Habitat notes

The collection site is a small brook, approx. 0.5 to 1 m wide, that flows into a tributary to the río Tacotalpa, close to a bridge, a few hundred meters on an unpaved road that branches of into northeasterly direction from the main road from Tapijulapa to Jamapa between the small settlements of Zunu y Patastal and Madrigal (Cuarta sección). At the type locality (N 17°29'30.9", W 92°48'53.9") on February, 25th, 2000 at late afternoon the water had a temperature of 26 °C, a conductivity of 360 mS, pH 8.0, and a total hardness of 10–15. The water was crystal clear and fast flowing with no aquatic vegetation. The substratum consisted mainly of gravel and sand. The brook flows in a deep indentation and is fully shadowed by the vegetation. Accompanying poeciliid fishes were *Pseudoxiphophorus bimaculatus*, *Gambusia* spec., *Heterophallus milleri*, *Poecilia mexicana* and a Characid, *Astyanax mexicanus*.

Acknowledgements

The authors gratefully acknowledge the collaboration and assistance of Prof. Dr. JAKOB PARZEFALL (Hamburg), MAXIMILIAN SCHARTL (Würzburg), Dr. KATHRIN LAMPERT (Würzburg), Dr. AXEL ZARSKE (Dresden), JAMES MACLAINE (London), ROSEMARIE RÖDER (Würzburg), KORNELIA MEYER (Bad Nauheim), KEES DE JONG (Hoorn), KLAUS SCHNEIDER (Münchsmünster), GÜNTER RICKLING (Bremen), DIETER VOGEL (Frankfurt), EWALD MÜLLER (Ober-Schmitten) and the late ERICH HNILICKA (Puebla).

Literature cited

ALTSCHMIED, J.; HORNUNG, U; SCHLUPP, I; GADAU, J.; KOLB, R. & SCHARTL, M. (1997): Isolation of DNA suitable for PCR for field and laboratory work. – BioTechniques, **23**: 228–229.

ALVAREZ, J. (1970): Peces Mexicanos (Claves). – Ser. Inv. Pesq., Inst.. Nat. Inv. Biol. Pesq. México: 166.

GHEDOTTI, M.J. (2000): Phylogenetic analysis and taxonomy of the poeciliid fishes (Teleostei: Cyprinodontiformes). – Zool. Jour. Linn. Society, **130**: 1–53.

GOSLINE, W.A. (1949): The sensory canals of the head in some cyprinodont fishes, with particular reference to the genus *Fundulus*. – Occ. Papers Mus. Zool. Univ. Michigan, **519**: 1–17.

LOZANO VILANO, M. DE & CONTRERAS BALDERAS, S. (1987): Lista Zoogeográfica y Ecológica de la Ictiofauna Continental de Chiapas, Mexico. – Southwestern Naturalist **32**: 223–236.

MEYER, A.; MORRISSEY, J.M. & SCHARTL, M. (1994): Recurrent origin of a sexually selected trait in *Xiphophorus* fishes inferred from molecular phylogeny. – Nature, **386**: 539–542.

MEYER, M. & PÉREZ, H.E. (1990): *Priapella olmecae* sp. n., a new species from Veracruz (México), (Teleostei: Poeciliidae). – Zool. Abh. (Dresden) **45**: 121–126.

MILLER, R.R. (1948): The cyprinodont fishes of the Death Valley system of eastern California and southwestern Nevada. – Misc. Publ. Mus. Zool. Univ. Michigan, **68**: 1–155.

MILLER, R.R. (1976): Geographical distribution of Central American freshwater fishes, with addendum: 125–156. In: T. B. THORSON (ed.), Investigations of the Ichthyofauna of Nicaraguan Lakes. – School Life Sci, Univ. Nebraska, Lincoln.

PARENTI, L.R. (1981): A phylogenetic and biographic analysis of cyprinodontiform fishes (Teleostei, Atherinomorpha). – Bull. Am. Mus. Nat. Hist., **168**: 335–557.

PARENTI, L.R. & RAUCHENBERGER, M. (1989): Systematic overview of the poeciliines. In: MEDDE G.K., SNELSON F.F. Jr., (eds.): Ecology and evolution of livebearing fishes (Poeciliidae). Englewood Cliffs, New Jersey: Printice Hall.

RODRIGUEZ, C.M. (1997): Phylogenetic analysis of the tribe Poeciliini (Cyprinodontiformes: Poeciliidae). – Copeia, (4): 663–679.

ROSEN, D.E. (1979): Fishes from the uplands and intermontane basins of Guatemala: revisionary studies and comparative geography. – Bull. Amer. Mus. Nat. Hist., **162**: 267–376.

ROSEN, D.E. & GORDON, M. (1953): Functional anatomy and evolution of male genitalia in poeciliid fishes. – Zoologica, **38**: 1–47.

ROSEN, D.E. & KALLMAN, D. (1959): Development and evolution of skeletal deletions in a family of viviparous fishes (Cyprinodontiformes, Poeciliidae). – Quart. Jour. Florida Acad. Sci., **22**: 169–190.

ROSEN, D.E. & BAILEY, R.M. (1963): The poeciliid fishes, their structure, zoogeography, and systematics. – Bull. Amer. Mus. Nat. Hist., **126**: 1–176.

SCHARTL, M.; WILDE, B.; SCHLUPP, I. & PARZEFALL, J. (1995): Evolutionary origin of a parthenoform, the Amazon Molly *P. formosa*, on the basis of a molecular genealogy. – Evolution, **49**: 827–835.

SWOFFORD, D.L. (1989): PAUP: phylogenetic analysis using parsimony. Version 9.1. – Smithonian Institution, Washington.

Received 27.06.05, accepted 21.07.05.