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UROTREMA SHIRLEYAE N. SP. (TREMATODA: DIGENEA: UROTREMATIDAE) IN NOROPS OXYLOPHUS AND N. CUPREUS (SQUAMATA: IGUANIA: POLYCHROTIDAE) FROM THE AREA DE CONSERVACIÓN GUANACASTE, COSTA RICA

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ABSTRACT: A new species of *Urotrema* inhabits *Norops oxylophus* and *Norops cupreus* from the Area de Conservación Guanacaste, Costa Rica. The new species is most similar to *Urotrema scabridum* but differs by having a relatively longer esophagus, at least 10% of the total body length versus 4–8% in *U. scabridum*; an oral sucker width:ventral sucker width ratio less than 1:1 (averaging 1:0.76) versus 1:1 or greater; an oral sucker width:pharyngeal width ratio less than 1:0.5 (averaging 1:0.42) versus greater than 1:0.5; and by having many transversely oriented posttesticular uterine loops versus a few vertically oriented posttesticular uterine loops.

The plagiorchoid Urotrematidae Poche, 1926, comprises *Urotrema* Braun, 1900, with 7 nominal species, and the monotypic *Urotrematulum* Macy, 1933, all of which inhabit mammals and lizards in the Nearctic and Neotropics. Bray et al. (1999) placed 2 additional genera, *Sinineobucephalopsis* Zhang, Pan & Li, 1987, and *Sinogastromyzontrema* Li, Zhang & Li, 1988, within the family. In a recent phylogenetic systematic analysis of the Bucephalidae, however, Overstreet and Curran (2002) supported the original authors' hypothesis that *Sinineobucephalopsis* and *Sinogastromyzontrema* are more closely related to members of the Bucephalidae than to Urotrematidae.

The taxonomic status of members of *Urotrema* is uncertain. Caballero (1942) recognized only 2 of the 5 nominal species of *Urotrema* known at that time, *Urotrema scabridum* Braun, 1900, inhabiting mammals, and *Urotrema wardi*, Perez-Viguera, 1940, inhabiting lizards. In doing so, he synonymized *Urotrema shillingeri* Price, 1931, in a muskrat, *Odatra zibthica*, from Maryland, *Urotrema lasiurensis*, Alicata, 1932, in the bats *Nycteris borealis* and *Nycteris humeralis* from Texas and Maryland, respectively, and *Urotrema minuta*, Macy, 1933, in the bat *Lasionycteris noctivagans* from Minnesota. Penner (1941) had previously considered the latter 2 species synonyms of *Urotrema schillingeri*. Caballero and Grocott (1960) synonymized *Urotrema aelleni* Baer, 1957, in *Myotis b. bocagei* from the Ivory Coast, with *Urotrema scabridum*. Finally, Bray et al. (1999) treated *Urotrema macrotestis* Mane-Garzon & Telias, 1965, in the water rat, *Holochilus brasiliensis vulpinus*, from Uruguay as part of what they termed the “*U. scabridum* complex.”

Urotrema scabridum recently has been reported in a number of polychrotid lizards (anoles) from various localities in the Caribbean and Central America: *Anolis olssoni* from Hispaniola, West Indies (Goldberg et al., 1998); *Anolis brevirostris* from the Dominican Republic (Goldberg et al., 1996); *Anolis sagrei* from Andros Island, Bahamas, and San Salvador (Goldberg et al., 1994); and *Anolis biporcatus* (= *Norops biporcatus*) from Aquacate, Panama Province, Panama (Bursey et al., 2003). As part of the ongoing inventory of eukaryotic parasites of vertebrates of the Area de Conservación Guanacaste, Costa Rica, we have discovered numerous specimens of a species of *Urotrema* inhabiting 2 species of polychrotid lizards. We de-

scribe this species as new herein and briefly discuss the status of members of the *U. scabridum* complex.

MATERIALS AND METHODS

Worms were collected alive from recently killed hosts, killed, and fixed by shaking in hot formalin, then stored in 70% ethanol. Specimens were stained with Mayer's hematoxylin, dehydrated, and mounted in Canada balsam. The first series of values given are the range, with the mean value in parentheses. All measurements are in micrometers unless otherwise stated. All figures were made with the aid of a drawing tube. The following abbreviations for collections are used: CNHE, Colección Nacional de Helmintos, Instituto de Biología, Universidad Nacional Autónoma de México; USNPC, United States National Parasite Collection, Beltsville, Maryland. Information concerning host identifications by specialists, digital images of hosts, and the disposition of host specimens and tissues is available via accessing <http://brookswb.zoo.utoronto.ca/index.html>.

DESCRIPTION

***Urotrema shirleyae* n. sp. (Figs. 1–3)**

Description (based on 94 specimens, 85 measured): Body elongate (Fig. 1), total body length (TBL) 0.93–4.8 mm (2.97 mm) by 160–550 (411) wide; maximum width at level of the ventral sucker. Tegument spined, very densely from the anterior end to level of the ovary; spines up to 10 long and 5 wide at base. Oral sucker subterminal 100–200 (153) long by 115–215 wide (170). Pharynx 40–90 (66) long by 38–95 (70) wide. Small glands free in the parenchyma surrounding the pharynx. Ratio of oral sucker width to pharyngeal width 1:0.30–0.46 (1:0.42). Prepharynx very short. Esophagus 190–500 (343) long, 10–20% (12%) of TBL. Intestine bifurcating 16–35% (19%) TBL from the anterior end. Posterior extent of ceca 15–24% (19%) of TBL from the posterior end. Forebody 18–32% (22%) of TBL from the anterior end. Ventral sucker 80–200 (130) long by 90–190 (130) wide. Ratio of oral sucker width:ventral sucker width 1:0.65–0.91 (1:0.76). Testes tandem; posterior testis 23–45% (29%) TBL from posterior end of body; anterior testis 95–310 (214) long by 110–335 (209) wide, posterior testis 112–300 (234) long by 93–305 (220) wide. Vasa efferentia may be inflated giving appearance of lobed testes. Vas deferens extending posteriorly from testes, ventromedially between ceca, entering cirrus sac proximally. Cirrus sac 100–325 (214) long by 30–100 (70) wide, width as percentage of length 33% (26–44%), containing coiled seminal vesicle filling most of the cirrus sac, terminal portion of the seminal vesicle extending anteriorly on dextral side, looping dorsally immediately anterior cirrus; cirrus poorly developed; pars prostatica weakly developed, with few prostatic cells present surrounding junction of ejaculatory duct and cirrus (Fig. 2). Genital pore subterminal, opening ventrally. Ovary spherical to subspherical, anterior to testes, 30% (26–38%) TBL from anterior end. Ovary 65–195 (134) long by 60–185 (129) wide. Ootype immediately posterior to ovary. Mehli's gland present, Laurer's canal not observed. Seminal receptacle present, dorsal to Mehli's gland (Fig. 3). Uterus intercecal, extending posteriad from ootype

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FIGURES 1–3. *Urotrema shirleyae* n. sp. 1. Ventral view of holotype. Scale bar = 500 μ m. 2. Terminal genitalia. C = cirrus; CS = cirrus sac; GP = genital pore; ISV = internal seminal vesicle; M = metraterm; P = prostatic cells. Scale bar = 100 μ m. 3. Ootype region. MG = Mehlis' gland; SR = seminal receptacle; UT = uterus; VR = vitelline reservoir. Scale bar = 100 μ m.

in tight transverse coils, descending to genital pore. Metraterm weakly developed, similar in length to cirrus sac. Eggs 21–25 (22) long by 10–11 (10) wide. Vitelline follicles in 2 lateral fields wrapped around ceca, both inter- and extracecal, several clusters of vitelline glands dorsally situated between ventral sucker and ovary (present in 84% of specimens); vitelline follicles extending anteriorly to ventral sucker, 19–28% (24%) TBL from the anterior end of the worm; posteriorly to anterior margin of anterior testis; total extent of vitelline fields 23–37 (30%) of TBL; follicles 37.5–47.5 long by 22.5–32.5 wide. Excretory pore, sub-terminal, opening dorsally. Excretory vesicle V-shaped.

Taxonomic summary

Type host: *Norops oxylophus* Cope, 1875 (Squamata: Iguania: Polychrotidae).

Other hosts: *Norops cupreus* Hallowell, 1860 (Squamata: Iguania: Polychrotidae).

Prevalence; intensity; site of infection: Thirty-eight percent (9/24); 21(4–39); small intestine.

Type locality: Rio Negro, near Buenos Aires, Sector Caribe, Area de Conservación Guanacaste, Guanacaste Province, Costa Rica (32°05.72'N, 39°37.70'W).

Type material: Holotype: USNPC 94426. Paratypes: USNPC 94427–94430.

Etymology: The species is named after Shirley Johansen.

Remarks

Specimens of the new species belong in *Urotrema* by having the terminal genitalia at the posterior end of the body, tandem testes near the posterior end of the hindbody, an ovary in the anterior hindbody separated from the testes by an extensive uterus, unlobed gonads, and vitelline follicles extending anteriorly to, or anterior to, the level of the ventral sucker. By having ceca that extend posterior to the posterior testis and vitelline follicles that do not extend anterior to the level of the posterior margin of the pharynx, the new species is more similar to members of the *U. scabridum* complex than to *U. wardi*, which also inhabits anoles. *Urotrema shirleyae* differs from all nominal species assigned to the *U. scabridum* complex by having a relatively longer esophagus, at least 10% TBL versus 4–8% TBL, and a relatively greater oral sucker width, with subsequently smaller oral sucker:pharynx width ratio (1:0.3–0.47, 1:0.42 vs. $\geq 1:0.5$) and oral sucker:ventral sucker width ratio (1:0.6–0.8, 1:0.76 vs. $\geq 1:1$). Finally, specimens attributed to *U. scabridum* from both chiropterans and lizards, including Braun's (1900) original description, have a few vertically oriented uterine loops extending from the sinistral side to the dextral side before crossing the body once again to the metraterm. *Urotrema shirleyae*, by contrast, exhibits many transversely oriented uterine loops between the posterior testis and the cirrus sac.

Most previous reports of *Urotrema* (Braun, 1900; Meyer and Reilly, 1950; Caballero et al., 1957; Mane-Garzon and Telias, 1965; Ubelaker, 1966; Nickel and Hansen, 1967; Webster, 1971; Martin, 1976; Coggins et al., 1981, 1982; Sellers, 1971; Sellers and Graham, 1987; Goldberg et al., 1994; Foster and Mertins, 1996; Goldberg et al., 1998; Guzman-Carnejo et al., 2003) have been from few, or individual, specimens, which seems to have led many to believe that there is a great deal of intraspecific variation in a few key characters examined. To test this hypothesis, we regressed all meristic characters listed in the description for 85 specimens of *U. shirleyae* against total body length (Fig. 4). All traits scaled positively and linearly with total body length, reducing variability in the measures. Figure 4 also includes regressed measures for specimens representing other members of the *U. scabridum* complex: *U. aelleni* (holotype from the University of Neuchâtel), *U. schillingeri* (USNPC 29725); *U. lasiurensis* (USNPC 30118); *U. minuta* (USNPC 29953) and various specimens of *U. scabridum* (CNHE 215–214; USNPC 51862; 78833; 79345; 80119; 80120; 80121; 83851; 92189).

Specimens currently assigned to *U. scabridum* show great variation in a number of characters. This result is not surprising if *U. scabridum* is a composite of a number of different species, as suggested by Bray et al. (1999). Nonetheless, small sample sizes preclude any further evaluation of the complex. We are able, however, to demonstrate that, based on 94 specimens collected from 2 host species in the same locality, all fixed and prepared in the same way, *U. shirleyae* represents a highly

consistent morphotype that does not vary to the same degree as does the collection of specimens currently assigned to *U. scabridum*. Examination of a voucher specimen (USNPC 92189) reported as *U. scabridum* in *Anolis biporcatus* (= *Norops biporcatus*) from Aquacate, Panama Province, Panama, by Bursey et al. (2003) revealed many post-testicular transverse uterine loops, similar to *U. shirleyae* and differing from the other members of the *U. scabridum* complex. That specimen also resembles *U. shirleyae* in ratios of oral sucker width:pharynx width (1:0.5) and oral sucker width:ventral sucker width (1:0.93). It differs from *U. shirleyae* in having a wider body, 22% TBL compared with 15–16% for comparable sized *U. shirleyae*, an ovary 220 long by 235 wide versus less than 195 in diameter, and an esophagus measuring 9% TBL. The specimen, which was collected from previously preserved hosts, is contracted, and we believe this accounts for the differences between that specimen and ours. Based on the structure of the uterine loops and the oral sucker width:ventral sucker width and oral sucker width:pharyngeal width ratios, we conclude that *U. scabridum* of Bursey et al. (2003) is *U. shirleyae*. *Norops biporcatus* is thus a new host and Aquacate, Panama Province, Panama, is a new locality for *U. shirleyae*.

DISCUSSION

During the course of the inventory in the Area de Conservación Guanacaste (ACG) to date, we have examined 62 specimens of 9 species of nonpolychrotid lizards, namely *Ameiva festiva*, *Basiliscus basiliscus*, *Cnemidophorus* sp., *Phyllodactylus* sp., *Sceloporus* sp., *Ctenosaura quinquecarinata*, *C. similis*, and *Iguana iguana*. As well, we have examined 124 specimens of 9 species of *Norops* (= *Anolis* in older literature), namely *Norops biporcatus*, *Norops capito*, *Norops carpenteri*, *Norops cupreus*, *Norops humilis*, *Norops limifrons*, *Norops oxylophus*, *Norops pachypus*, and *Norops tropidolepis*, and have found *U. shirleyae* only in *N. oxylophus* and *N. cupreus*. We have collected specimens of *Urotrema shirleyae* in several snakes from the ACG. This may indicate that *U. shirleyae* occasionally occurs in snakes as a result of predation on polychrotid lizards. At present, we do not have enough information about the biology of the snake hosts or a large enough sample size to determine if that suspicion is warranted. Consequently, we do not list those snakes as hosts for *U. shirleyae*.

Etheridge (1960) divided *Anolis* into alpha and beta groups based on osteological data. Combined osteological, karyological, and electrophoretic data suggest that members of the alpha group are paraphyletic, with a monophyletic beta (*Norops*) group arising from within that group (Guyer and Savage, 1986, 1992). Recently, Nicholson (2002) used ITS-1 nuclear DNA sequence data to produce 382 parsimony informative characters for the members of *Norops*. Phylogenetic analysis yielded 9 equally parsimonious trees with bootstrap values and decay indices indicating that many groupings are weakly supported. As a result, she did not propose formal recognition of the resultant clades. The consensus tree indicates that *N. auratus* is the basal-most member of the clade, followed by a split into 2 subgroups. *Norops tropidolepis* and *N. pachypus*, which we have sampled in Guanacaste, but which do not host *U. shirleyae*, are sister species in one of those subgroups. All other species of *Norops* we have examined belong to the other subgroup. *Norops oxylophus* and *N. cupreus*, which host *U. shirleyae*, belong to the most derived portion of this second subgroup, which is largely unresolved. *Norops cupreus* is a basal member of a derived clade within that largely unresolved group that also includes *N. limifrons* and *N. humilis*, which we have been examined and which have not been found to host *U. shirleyae*. It appears that

FIGURE 4. Regression analyses of *Urotrema shirleyae* n. sp. and members of the *U. scabridum* complex. **A.** Esophagus length plotted by total body length (TBL). **B.** Oral sucker width plotted by TBL. **C.** Oral sucker width pharynx width ratio plotted by TBL. **D.** Oral sucker width ventral sucker width ratio plotted by TBL. Units are in microns. Closed diamonds = *Urotrema shirleyae*; open diamond = USNPC-92189; closed square = *U. aelleni* (type); open square = CNHE 214–215; closed circle = USNPC-29953; open circle = USNPC 83851; closed triangle = USNPC 79345; short horizontal line = USNPC 80120; long horizontal line = USNPC 80121; X = USNPC 29725; + = USNPC 51862; * = USNPC 30118.

U. shirleyae parasitizes only basal members from this derived group of anoles.

In contrast, *Urotrema scabridum* has only been reported from 1 species within the first subgroup of *Norops*, *N. sagrei*, from Florida and Louisiana (Sellers and Graham, 1987; Goldberg et al., 1994). All other reports of *U. scabridum* inhabiting anoles, *Anolis armouri*, *Anolis barahonae*, *Anolis bahucoensis*, *Anolis brevirostris*, *Anolis chlorocyanus*, *Anolis coelestinus*, *Anolis distichus*, *Anolis olsoni* (Goldberg et al., 1994, 1996, 1998) and *Anolis carolinensis* (Sellers, 1971) have been from the paraphyletic alpha *Anolis* group.

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