Comp. Parasitol.
68(2), 2001, pp. 149–155

Development and Specificity of *Oochoristica javaensis* (Eucestoda: Cyclophyllidea: Anoplocephalidae: Linstowiinae)

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ABSTRACT: Because assumptions of strict host specificity and geographic isolation apparently have been used as criteria in determining species of *Oochoristica,* studies were conducted to address the effects that these assumptions could have on resolving the taxonomy of *Oochoristica.* Experimental infections of native fence lizards, *Sceloporus undulatus undulatus,* and Indo-Pacific geckos, *Hemidactylus garnotii,* demonstrated that the exotic tapeworm *Oochoristica javaensis* lacked host specificity. In addition, tapeworms with gravid proglottids, a stage of development that has not been previously reported for any species of *Oochoristica,* were obtained from both hosts. Evidence against the assumption of geographic isolation stems from the fact that lizard species known to harbor *Oochoristica* spp. have been introduced beyond their native ranges, and in some cases, these introductions predate the species descriptions. Lack of support for either assumption indicates a need for more rigorous analyses and experimentation to determine species of *Oochoristica.*

KEY WORDS: *Oochoristica javaensis,* Cestoda, *Hemidactylus turcicus, Hemidactylus garnotii, Sceloporus undulatus undulatus,* Mediterranean geckos, Indo-Pacific geckos, fence lizards, development, host specificity, biogeography, taxonomy.

Approximately 80 species have been described in the cosmopolitan genus *Oochoristica* Lühe, 1898 (Bursey and Goldberg, 1996a, b; Bursey et al., 1996, 1997; Brooks et al., 1999). These anoplocephalid cestodes predominantly parasitize lizards, but also snakes, turtles, and a few marsupials (Schmidt, 1986; Beveridge, 1994). Development has been examined for *Oochoristica vacuolata* Hickman, 1954, *Oochoristica osheroffi* Meggitt, 1934, and *Oochoristica anolis* Hardwood, 1932 (Hickman, 1963; Widmer and Olsen, 1967; Conn, 1985). Although larval and adult development has been examined for 3 species of *Oochoristica,* only Conn (1985) tried to determine host specificity experimentally. In his experiments, however, he was unable to infect wall lizards, *Podarcis muralis* (Laurenti, 1768) and mice, *Mus musculus* Linnaeus, 1758. Curiously, no other attempts have been made to determine the specificity of a species of *Oochoristica.* This is unfortunate in that, as Brooks et al. (1999) pointed out, one of the major criteria used in resolving the taxonomy of *Oochoristica* has been the assumption of a high degree of host specificity exhibited by species in this genus. They also mentioned restriction to particular geographic regions as a criterion that has ostensibly been used in the past to identify species of *Oochoristica.*

In a survey of helminths of the Mediterranean gecko, *Hemidactylus turcicus* (Linnaeus, 1758), from Louisiana, U.S.A., a species of *Oochoristica* was recovered (C. D. Criscione, unpublished data); however, there were difficulties in identifying this species. These problems were associated in part with the assumptions of strict host specificity and geographic isolation. It became apparent that in addition to the lack of specificity experiments, introduced and native host distributions were often ignored when identifying species of *Oochoristica.* Neither assumption has been properly addressed, and in order to validate the identification of any species of *Oochoristica,* these assumptions should be tested. In light of these problems with the taxonomy of *Oochoristica.* the primary objective of this study was to examine the development of *Oochoristica javaensis* Kennedy, Killick, and Beverley-Burton, 1982, and to test the assumption of specificity via experimental infections. In addition, we comment on the assumption of geographic isolation.

Materials and Methods

To minimize variation among hosts, gravid proglottids of *O. javaensis* were obtained from 15 worms recovered from the small intestine of a single female

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Table 1. Measurements of *Oochoristica javaensis* from experimentally infected *Hemidactylus turcicus* (HETU), *H. garnotii* (HEGA), and *Sceloporus u. undulatus* (SCUN) for days 1–30 postexposure; measurements in μm unless noted otherwise.

	HETU	HEGA		SCUN	
	Day 1 $n = 4$*	Day 7 $n = 1$	Day 28 $n = 4$	Day 10 $n = 2$	Day 30 $n = 2$
Total L† (mm)	0.26–0.37 (0.3 ± 0.03)‡	0.52	5.97–10.5 (8.32 ± 0.95)	0.36–0.37 (0.37 ± 0.01)	5.16–5.2 (5.18 ± 0.02)
Proglottid No.	0	0	30–47 (38.5 ± 3.6)	0	25–34 (29.5 ± 4.5)
Scolex W	109–129 (120 ± 4.4)	125	98–137 (117 ± 8.6)	117–133 (125 ± 8)	113–164 (139 ± 25.5)
L	44–101 (81.2 ± 13.1)	78	66–105 (84.8 ± 8.0)	82–86 (84 ± 2)	70–113 (91.5 ± 21.5)
Sucker W	43–51 (46 ± 1.9)	51	39–51 (45 ± 2.6)	51 (51 ± 0.0)	39–66 (52.5 ± 13.5)
L	51–74 (58.7 ± 5.2)	59	47–59 (53 ± 2.6)	55–62 (59 ± 3.5)	51–78 (64.5 ± 13.5)
Neck W	N/A§	N/A	125–179 (146 ± 13.1)	N/A	48–176 (162 ± 14)
L (mm)	N/A	N/A	0.65–1.32 (0.91 ± 0.14)	N/A	0.39–1.12 (1.01 ± 0.12)

* Number of worms used for measurements, which in this table, also refers to the sample size of each character measured.

† L = length, W = width.

‡ Range followed by mean ± 1 SE in parentheses.

§ N/A = not applicable.

Mediterranean gecko that was collected from Louisiana State University (LSU) in Baton Rouge, Louisiana, U.S.A. (30°24.92′N; 91°10.81′W). Laboratory-raised flour beetles, *Tribolium castaneum* Herbst, 1797, were used as potential intermediate hosts in the experiments. Groups of 10 flour beetles were placed in 100- × 15-mm plastic petri dishes lined with filter paper; the beetles were starved for 48 hr. Eight gravid proglottids were removed from each of the 15 worms, lightly dusted with flour beetle medium from Carolina Biological Supply Company, and placed in a single dish. Each petri dish contained gravid proglottids from a different parental worm. After 24 hr of exposure, the filter paper was replaced and beetles were fed ad libitum with flour beetle medium and slices of potatoes. Flour beetles were maintained at 25 ± 1°C until necropsy. Metacestodes recovered from *T. castaneum* on day 60 postexposure (PE) were used to infect experimental definitive hosts that included *H. turcicus* ($n = 16$), *Anolis carolinensis* Voigt, 1832 (green anole, $n = 10$), *Hemidactylus garnotii* Duméril and Bibron, 1836 (Indo-Pacific gecko, $n = 10$), *Sceloporus undulatus undulatus* (Bosc and Daudin, 1801) (southern fence lizard, $n = 5$), and *Rana sphenocephala* Cope, 1886 (southern leopard frog, $n = 5$). Indo-Pacific geckos were ordered from Glades Herp Inc. in Florida, U.S.A.; the fence lizards and tadpoles of the leopard frogs that had undergone metamorphosis in the laboratory were obtained from Glenn's Pond in Harrison County, Mississippi, U.S.A. Green anoles were caught on the campus of Southeastern Louisiana University in Hammond, Louisiana (30°30.67′N; 90°27.98′W), and Mediterranean geckos were collected in Fairview Riverside State Park, Madisonville, Louisiana (30°24.55′N; 90°08.41′W). To determine if the experimental hosts were naturally infected with tapeworms, feces were examined for proglottids 2 wk prior to infection. Only specimens not shedding proglottids were used in experimental infections.

Each potential definitive host was inoculated via stomach tube with 10 metacestodes obtained from the day 60 PE flour beetles. Experimental definitive hosts were maintained at 25 ± 4°C in 11.36-liter containers (40.64 × 27.94 × 15.24 cm) and provided refuge. Hosts were fed ad libitum with laboratory-reared crickets and mealworms and given a constant supply of water. Experimental vertebrate hosts were killed using an overdose of ether, and the body cavity, musculature, and all internal organs were examined for helminth parasites under a dissecting microscope. Tapeworms were killed with hot water (90°C), fixed and stored in alcohol–formalin–acetic acid (AFA), stained in Semichon's acetocarmine, dehydrated in ethanol, cleared in xylene, and mounted in Canada balsam. All measurements are in μm unless specified otherwise. We deposited voucher specimens of *O. javaensis* from *H. turcicus* in the United States National Parasite Collection (USNPC) (nos. 90344–90348). Specimens from experimental infections are available upon request from the senior author.

Results

Tribolium castaneum was readily infected with *O. javaensis* and represents a new inter-

Table 2. Measurements of *Oochoristica javaensis* obtained from experimentally infected *Hemidactylus garnotii* (HEGA), and *Sceloporus u. undulatus* (SCUN) for day 105 postexposure; measurements in μm unless noted otherwise.

Variable		HEGA		SCUN	
		Sample size*	$n = 5$†	Sample size	$n = 1$
Total	L‡ (mm)	5	61.6–86.9 (67.7 ± 48.3)§	1	54.5
Proglottid number		5	109–144 (128 ± 5.7)	1	140
Neck	W	5	166–229 (191 ± 10.7)	1	221
	L (mm)	5	1.16–1.79 (1.52 ± 0.12)	1	1.12
Scolex	W	5	90–191 (152 ± 17.7)	1	218
	L	5	78–277 (140 ± 36.3)	1	164
Sucker	W	5	35–90 (61.8 ± 9.5)	1	82
	L	5	47–82 (66.4 ± 6.4)	1	105
Immature proglottid	W	15	482–561 (520 ± 6.6)	3	379–403 (390 ± 7.1)
	L	15	300–387 (348 ± 7)	3	427–466 (443 ± 11.9)
Genital pore position‖		15	0.24–0.28 (0.27 ± 0.004)	3	0.24–0.28 (0.26 ± 0.01)
Mature proglottid	W	15	593–695 (643 ± 9.1)	3	403–411 (406 ± 2.7)
	L	15	616–790 (712 ± 12.4)	3	648–695 (679 ± 15.7)
Cirrus sac	W	15	43–51 (46.7 ± 0.47)	3	47–51 (49.7 ± 1.3)
	L	15	137–164 (146 ± 1.99)	3	109–121 (117 ± 4.0)
Ovary	W	15	265–351 (314 ± 6.0)	3	168–211 (91 ± 12.6)
	L	15	195–265 (230 ± 5.1)	3	133–187 (159 ± 15.7)
Vitellaria	W	15	137–191 (169 ± 4.5)	3	86–105 (96.3 ± 5.6)
	L	15	82–144 (118 ± 4.3)	3	82–101 (89.7 ± 5.8)
Testis	W	15	39–47 (43.5 ± 0.77)	3	35–39 (36.3 ± 1.3)
	L	15	35–55 (46.2 ± 1.3)	3	39–43 (41.7 ± 1.3)
Testes number		15	23–35 (30.8 ± 0.78)	3	21–30 (26.3 ± 2.7)
Gravid proglottid	W	15	571–749 (629 ± 12.6)	3	433–473 (453 ± 11.6)
	L (mm)	15	1.50–2.28 (1.92 ± 0.05)	3	1.48–1.52 (1.49 ± 0.01)
Oncosphere	W	15	20–34 (25.9 ± 1.04)	3	22 (22 ± 0.0)
	L	15	16–28 (21.5 ± 0.79)	3	18–20 (19.3 ± 0.67)
Hook	L	15	10–12 (11.6 ± 0.21)	3	12 (12 ± 0.0)

* Sample size refers to the total number of each character that was measured.

† Number of tapeworms measured.

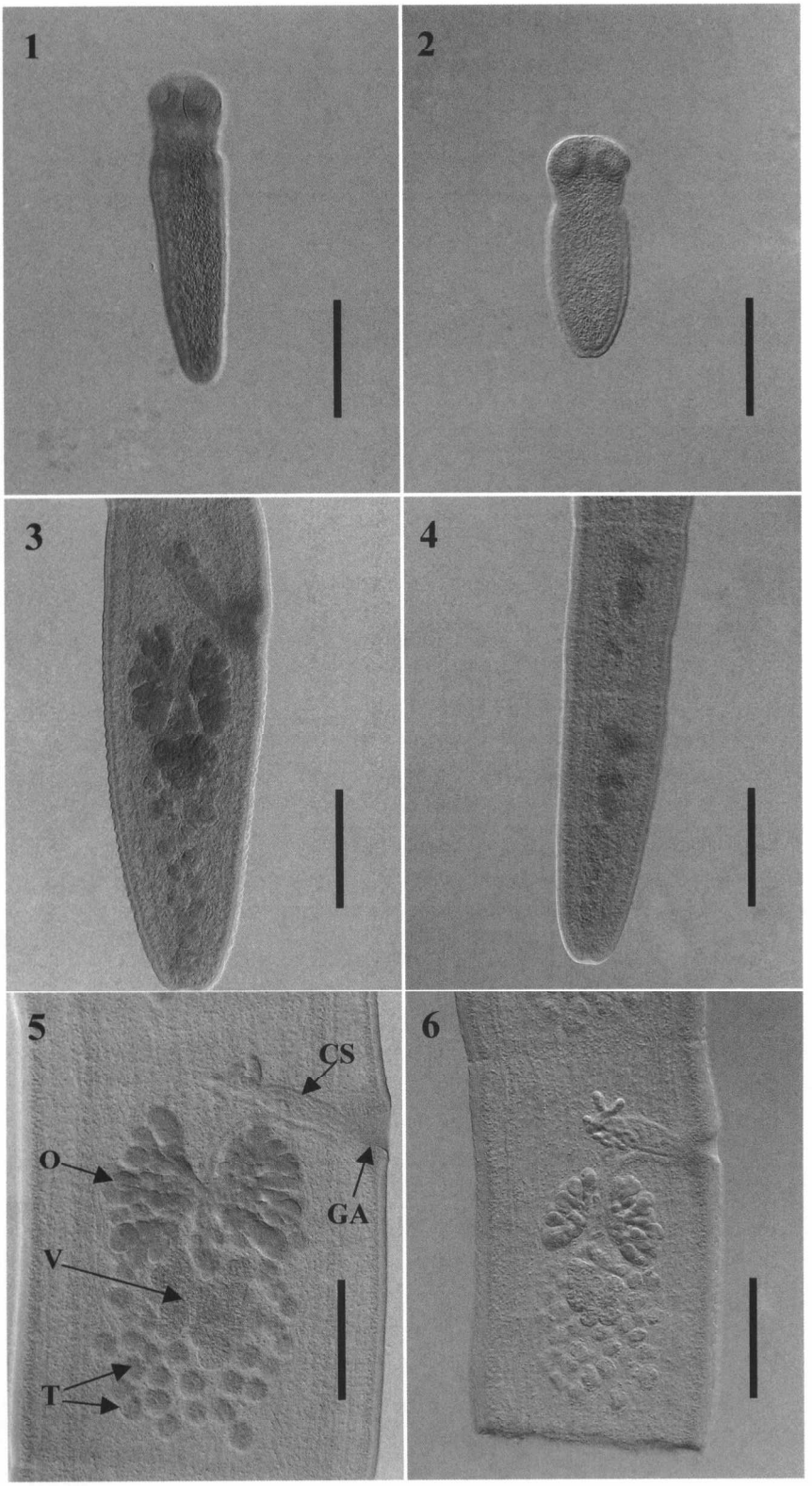
‡ L = length, W = width.

§ Range followed by mean ± 1 SE in parentheses.

‖ Genital pore position was calculated as a ratio of the position along the length of the mature proglottid from the anterior end (length to the center of the genital pore ÷ length of proglottid).

mediate host for the genus *Oochoristica*. *Oochoristica javaensis* became established in 7 individuals of the experimental definitive hosts. Successful infection occurred in only 1 of 16 *H. turcicus*; this Mediterranean gecko was examined on day 1 PE and had an intensity of 4. *Oochoristica javaensis* was recovered from 3 of 10 *H. garnotii* on days 7, 28, and 105 PE and had intensities of 1, 7, and 6, respectively. Three of 5 *S. u. undulatus* were infected with 2, 3, and 1 tapeworms on days 10, 30, and 105 PE, respectively. The 10 *A. carolinensis* and 5 *R. sphenocephala* were negative for infections. Measurements for specimens from experimental infections are in Tables 1 and 2.

Proglottid formation did not occur prior to day 28 PE (Figs. 1 and 2). Terminal proglottids of tapeworms recovered on day 28 PE from *H. garnotii* had developing ovaries, testes, vitellaria, and cirrus sacs (Fig. 3). A median terminal excretory pore was present in each terminal proglottid, and in 1 worm there was a developed genital atrium. Terminal proglottid length ranged from 514 to 822 (mean = 659, SE = 38.7, n = 7) and width from 174 to 277 (mean = 216, SE = 12.4, n = 7). Two of the worms from *S. u. undulatus* examined on day 30 PE also had developing reproductive organs (Fig. 4). One measured 442 × 158 (L × W); the other had been torn. The third tapeworm recovered from day 30 PE had been damaged in the mounting process; however, prior examination had shown that no more than 15 proglottids had formed, sexual primoridia had just begun to develop, and total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length did not exceed 1.2 mm. By day 105 PE, development of *O. javaensis* progressed to strobilas with gravid proglottids in both *H. garnotii* (Fig. 5) and *S. u. undulatus* (Fig. 6). Although it was possible that tapeworms from day 105 PE were natural infections because experimental definitive hosts were not laboratory-raised, prior fecal examinations were negative for all hosts used in experiments.

Discussion

Development of *Oochoristica javaensis*

Prior to the present study, the most developed stage experimentally obtained for a species of *Oochoristica* was a terminal mature proglottid (Conn, 1985). Our experimental infections with *O. javaensis* were successful in obtaining gravid specimens. Susceptible definitive hosts for *O. javaensis* included *H. turcicus, H. garnotii,* and *S. u. undulatus*; however, the fact that only 1 of 16 control hosts, *H. turcicus,* became infected suggests that exposure techniques may have been flawed. Possible problems may have been the temperature at which experimental hosts were housed or the inoculation method. When dealing with small hosts, the stomach tube may not be the best method, and another, such as placing metacestodes in gel capsules, may prove to be more efficient. Despite the scarcity of infections, however, the developing worms obtained from *H. garnotii* and *S. u. undulatus* indicated a lack of specificity for *O. javaensis.*

On day 105 PE, Conn (1985) recovered a single specimen of *O. anolis* from *A. carolinensis* that had mature proglottids with fully formed male and female reproductive systems. The terminal proglottid, however, still had a median excretory pore, suggesting that this specimen had not yet shed any proglottids. Specimens of *O. javaensis* from *H. garnotii* on day 28 PE also had median excretory pores in the terminal proglottids. Although most of the specimens that we recovered from day 28 PE did not have fully developed reproductive organs, their stage of development had greatly surpassed the developmental stage of *O. anolis* from day 28 PE (Conn, 1985). *Oochoristica anolis* from green anoles on day 28 PE had just begun to form proglottids with genital anlages and had a maximum total length of 3.25 mm (Conn, 1985). Widmer and Olsen (1967) reported immature *O. osheroffi* with a maximum total length of 4.14 mm on day 28 PE in the prairie rattlesnake, *Crotalus viridis* Rafinesque, 1818, but the mean total worm length from our study for day 28 PE was 8.32 mm (Table 1). These comparisons suggest a more rapid development in the definitive host for *O. javaensis* than for *O. anolis* or *O. osheroffi.* However, small sample sizes in our study and infection techniques differing from previous life cycle studies of *Oochoristica* spp. prevented definitive comparison of developmental patterns among species. Likewise, the low number of infections precluded examination of host-induced variation for *O. javaensis.* Although development in *S. u. undulatus* appeared slightly slower than in *H. garnotii* up to day 30 PE (Table 1), measurements of gravid specimens from *H. garnotii* and *S. u. undulatus* on day 105 PE (Table 2) may suggest plasticity for some characters.

Host specificity and geographic isolation

Results from our study experimentally demonstrated for the first time that a single species of *Oochoristica* can infect more than 1 species of host. *Oochoristica javaensis* infected hosts representing 2 unrelated lizard families, Phrynosomatidae for *S. u. undulatus* and Gekkonidae for *H. garnotii* (Estes et al., 1988; Pough et al., 1998). It is not known if the ecology of either *S. u. undulatus* or *H. garnotii* would predispose natural populations of these hosts to the establishment of *O. javaensis.* Development in different hosts demonstrated via our laboratory experiments, however, raises questions with regard to the use of host specificity as a taxonomic criterion for species of *Oochoristica.* Specificity in the laboratory and in the field should be examined for other species of *Oochoristica* in light of these results for 2 reasons. First, lack of speci-

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Figures 1–6. Development of *Oochoristica javaensis* from *Hemidactylus garnotii* (HEGA) and *Sceloporus u. undulatus* (SCUN) at different days postexposure. Photomicrographs were taken with differential interference contrast. Bars = 200 μm. 1. Day 7 in HEGA. 2. Day 10 in SCUN. 3, 4. Terminal proglottids from day 28 in HEGA and day 30 in SCUN, respectively. 5, 6. Mature proglottids from day 105 in HEGA and SCUN, respectively. CS = cirrus sac, GA = genital atrium, O = ovary, T = testis, and V = vitellaria.

ficity means that tapeworms of the same species will be exposed to different environments in different species of hosts, thus presenting opportunities for host-induced variation. If variation is induced, then this may affect the current morphometrically based taxonomy of species of *Oochoristica*. Second, a better understanding of the degree to which species of *Oochoristica* can switch hosts is imperative in light of the conservation implications associated with introduced organisms and their parasites (see Barton, 1997).

Introduced lizards will have consequences not only for conservation, but also for parasite taxonomy. If in the past, species of *Oochoristica* have been transmitted with their exotic lizard hosts, then current assumptions of biogeographic isolation may be incorrect. This is not to say that there was never a biogeographic pattern that paralleled *Oochoristica* speciation, but especially because of anthropogenic effects, species of *Oochoristica* may have colonized new areas before many of them were ever described (see Bursey et al. [1996] for a list of authority dates). This possibility exists because records of some introduced geckos, i.e., *H. turcicus* in Florida (Stejneger, 1922) and *Hemidactylus mabouia* (Moreau de Jonnès, 1818) in South America and the Caribbean (Kluge, 1969), predate many *Oochoristica* species descriptions.

It is interesting to note that several authors (Bursey and Goldberg, 1996b; Bursey et al., 1996; Brooks et al., 1999) listed *O. vanzolinii* as a Neotropical species of *Oochoristica* from Brazil without regard to the fact that it was described from the introduced house gecko, *H. mabouia* (Rêgo and Oliveira Rodrigues, 1965). It has been hypothesized that *H. mabouia* naturally colonized the New World via rafting or was transported during the slave trades over 400 yr ago (Kluge, 1969). In either case, *H. mabouia* colonized the New World from Africa, thus presenting the opportunity for parasite transport. It is also interesting to note that in describing *O. javaensis*, Kennedy et al. (1982) listed *O. vanzolinii* as the species that most resembled their specimens.

Brooks et al. (1999) stated that both assumptions, specificity and geographic isolation, were not evidence for new species, and suggested that in describing new species many morphological characters should be provided. We strongly support their contention; however, the full extent to which certain features are plastic is still unknown for this genus. As indicated by Criscione and Font (2001), proglottid morphology of *O. javaensis* exhibited a high degree of plasticity that may have resulted from a crowding effect (Read, 1951). Providing more characters may alleviate some problems, but it will not solve the underlying difficulties associated with the taxonomy of *Oochoristica*. The morphologically based taxonomy of *Oochoristica* will only be validated upon experimentation establishing the variation of characters within the genus and/or the use of molecular data.

Acknowledgments

We express our gratitude to Dr. Richard Seigel, Caroline Kennedy, and Tom Lorenz for collecting the fence lizards and leopard frogs, and to Amanda Vincent and Jonathan Willis for their help with experiments and care of lizards. Thanks are also extended to Dr. Murray Kennedy and Dr. Bruce Conn for loaning us specimens of *Oochoristica* from their private collections, and to Judith Price at the Canadian Museum of Nature (CMNPA) and Pat Pilitt, Dr. Eric Hoberg, and Dr. J. Ralph Lichtenfels at the USNPC for their assistance and loan of specimens.

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