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Revision of monogeneans parasitising *Lythrurus* (Cypriniformes: Leuciscidae) in eastern U.S.A., with description of *Dactylogyrus lythruri* sp. n. and new records of *Dactylogyrus crucis* Rogers, 1967 (Monogenoidea: Dactylogyridae)

Donald G. Cloutman[1], **Andrew B. Adrian**[2], **Chris T. McAllister**[3], **Bruce W. Stallsmith**[4], **Thomas J. Fayton**[5] and **Henry W. Robison**[6]

[1] P.O. Box 197, Burdett, Kansas, U.S.A.;

[2] Office of the Chief Information Officer, NASA Headquarters, Washington, D.C., U.S.A.;

[3] Division of Science and Mathematics, Eastern Oklahoma State College, Idabel, Oklahoma, U.S.A.;

[4] Department of Biological Sciences, University of Alabama in Huntsville, Huntsville, Alabama, U.S.A.;

[5] Department of Microbiology and Immunology, Cornell University, Ithaca, New York, U.S.A.;

[6] 9717 Wild Mountain Drive, Sherwood, Arkansas, U.S.A.

Abstract: A revisionary study revealed two species of monogeneans, *Dactylogyrus crucis* Rogers, 1967 and *Dactylogyrus lythruri* sp. n., parasitising *Lythrurus* Jordan (formerly a subgenus of *Notropis* Rafinesque, 1818). New records and updated taxonomy of seven of 12 known minnows of the genus of *Lythrurus* are provided for *D. crucis*. A record of *Dactylogyrus attenuatus* Mizelle et Klucka, 1953 (syn. *Dactylogyrus umbratilus* [Kimpel, 1939], nomen nudum) on *Lythrurus umbratilis* (Girard) is referrable to *D. crucis*. *Dactylogyrus lythruri* is described from eight species of *Lythrurus*. It most closely resembles *Dactylogyrus beckeri* Cloutman, 1987, but is distinguished by having a smaller base of the male copulatory organ (MCO) and lacking a ventral enlargement of the distal end of the basal process. Previous reports of *Dactylogyrus banghami* Mizelle et Donahue, 1944 and *Dactylogyrus* cf. *beckeri* Cloutman, 1987 from *Lythrurus atrapiculus* (Snelson) and *Lythrurus bellus* (Hay) from Alabama, and *Dactylogyrus confusus* Mueller, 1938 from *L. umbratilis* in Illinois are herein relegated to *D. lythruri*. Four species of *Lythrurus* appeared not to be infected with *Dactylogyrus*.

Keywords: Monogenoidea, Dactylogyridae, *Dactylogyrus crucis*, *Dactylogyrus lythruri* sp.n., *Lythrurus umbratilis*, redfin shiner.

Lythrurus Jordan, as presently hypothesised, comprises a monophyletic clade of 11 described and one undescribed novel species of minnows (Teleostei: Leuciscidae) in eastern North America (Pramuk et al. 2006, Page and Burr 2011, Page et al. 2013, Robison and Buchanan 2020).

Our knowledge of monogeneans parasitising *Lythrurus* is limited to the following reports of *Dactylogyrus* Diesing, 1850 (Monogenoidea: Dactylogyridae): *Dactylogyrus umbratilus* (Kimpel, 1939) from *Lythrurus umbratilis* (Girard) in Illinois (Kimpel 1939); *D. umbratilus* considered a *nomen nudum* by Yamaguti (1963); Kimpel's *nomen nudum* identified as *Dactylogyrus attenuatus* Mizelle et Klucka, 1953 by Kritsky et al. (1977); *Dactylogyrus confusus* Mueller, 1938 from *L. umbratilis* in Illinois (Kimpel 1939); *Dactylogyrus banghami* Mizelle et Donahue, 1944 from *Lythrurus atrapiculus* (Snelson) and *Lythrurus bellus* (Hay) in Alabama (Rogers 1967); Rogers' (1967) material from *Lythrurus* identified as an undescribed species, *Dactylogyrus* cf. *beckeri* Cloutman, 1987 (Cloutman and Rogers 2005); and *Dactylogyrus crucis* Rogers, 1967 from *L. atrapiculus* and *L. bellus* in Alabama (Rogers 1967).

Results of a comprehensive survey reported herein indicate that some of these records are in need of further revision. Furthermore, taxonomic revisions of the genus *Lythrurus* in recent years (Snelson and Pflieger 1975, Schmidt et al. 1998, Pramuk et al. 2006, Hopkins and Eisenhour 2008) necessitate revision of outdated host-parasite lists.

In this report, we reduce the number of species of *Dactylogyrus* known to parasitise species of *Lythrurus* to two. We describe *Dactylogyrus lythruri* sp. n. (previously reported as *D. confusus* [see Kimpel 1939], *D. banghami* (see Rogers 1967), and *D.* cf. *beckeri* [see Cloutman and

Address for correspondence: Chris T. McAllister, Science and Mathematics Division, Eastern Oklahoma State College, Idabel, Oklahoma 74745, U.S.A. Phone 580-376-5239; E-mail: cmcallister@se.edu

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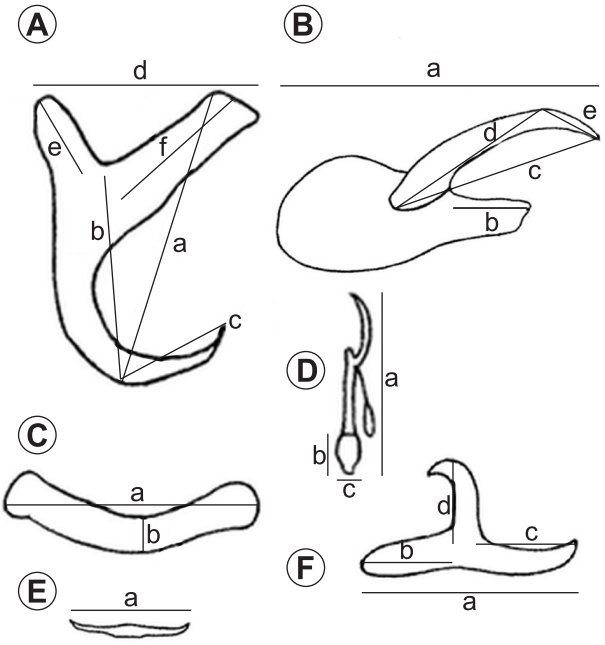

Fig 1. Measurements of sclerites of the *Dactylogyrus perlus* Mueller, 1938 complex. **A** – dorsal anchor. *Abbreviation*: a – total length; b – main part length; c – point; d – base length; e – deep root length; f – superficial root length. **B** – male copulatory organ (MCO). *Abbreviation*: a – total length; b – basal process length; c – shaft total length; d – shaft proximal length; e – point length. **C** – dorsal bar. *Abbreviation*: a – length; b – width. **D** – hook. *Abbreviation*: a – total length; b – base length. c – base width. **E** – ventral bar. *Abbreviaton*: a – length. **F** – accessory piece. *Abbreviation*: a – total length; b – basal ramus length; c – distal ramus length; d – medial ramus length.

Rogers 2005]) and provide new host and geographic records for *D. crucis*. Where necessary, we also update the taxonomy and host lists of the two species of parasites.

MATERIALS AND METHODS

Taxonomy of fish hosts follows Pramuk et al. (2006), Page and Burr (2011) and Page et al. (2013). Gills of museum specimens of shiners from the University of Kansas (KU) and North Carolina Museum of Natural Sciences (NCSM), and uncataloged specimens collected by the authors and destroyed during necropsy were examined. Hosts were collected by seining or backpack electrofishing; localities, dates of collection and number of hosts examined are provided in Table 1. Immediately after capture, museum voucher specimens of hosts were fixed in 10% formalin and later preserved in 70% ethanol. Specimens collected by the authors were placed in jars containing a 1 : 4,000 formalin solution or were placed on ice immediately after capture; after approximately 1 hr, enough formalin was added to make a 10% solution (Putz and Hoffman 1963).

The parasites were collected directly from the gills of their hosts with small needles under a dissecting scope at ×20–30, and mounted in glycerin jelly or Grey and Wess medium, some unstained and others stained with Gomori's trichrome (Kritsky et al. 1978). Only the right gills of museum specimens of hosts were examined to minimise damage. Both right and left gills were examined from the other hosts.

Observations were made with an Olympus BX41 phase-contrast microscope. Drawings were traced from digital images taken with an Olympus OLY-200 video camera mounted on the microscope. Measurements, in micrometres (µm) unless otherwise indicated, were made with a calibrated ocular micrometre as presented by Mizelle and Klucka (1953) and Hoffman (1999) (see Fig. 1); ranges are followed by means and number of specimens measured in parentheses. Numbering of haptoral hooks follows Mizelle (1936); 4As (Mizelle and Price 1963) are considered to be ventral anchors (Kritsky and Kulo 1992). Prevalence, mean intensity and range of infection were calculated according to Bush et al. (1997). Type and voucher specimens were deposited in the Harold W. Manter Laboratory (HWML), University of Nebraska State Museum, University of Nebraska, Lincoln, Nebraska, U.S.A., and the United States National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C., U.S.A.

Type specimens of *Dactylogyrus banghami* (HWML 21545, 2 syntypes; USNM 1369119, 1 syntype); *Dactylogyrus beckeri* Cloutman, 1987 (USNM 1374680, holotype; USNM 1374681, 6 paratypes; USNM 1374682, 1 paratype), *D. boopsi* Cloutman, 1994 (HWML 36962, 3 paratypes; USNM 1378552, holotype; USNM 1378553, 6 paratypes), *Dactylogyrus confusus* (USNM 1367024, 5 syntypes), *Dactylogyrus crucis* (HWML 49266, 3 paratypes; HWML 49267, 3 paratypes; HWML 49268, 1 paratype), *Dactylogyrus hydrophloxi* Cloutman et Rogers, 2005 (HWML 45337, 3 paratypes; HWML 45338, 2 paratypes; USNM 1388642, holotype; USNM 1388643, 1 paratype), *Dactylogyrus magnibulbus* Cloutman et Rogers, 2005 (HWML 45339, 8 paratypes; HWML 45340, 3 paratypes; USNM 1388644, holotype; USNM 1388645, 5 paratypes; USNM 1388646, 1 paratype), *Dactylogyrus parvibulbus* Cloutman et Rogers, 2005 (HWML 45341, 3 paratypes; HWML 45342, 1 paratype; USNM 1388647, holotype; USNM 1388648, 3 paratypes; USNM 1388649, 2 paratypes; USNM 1388650, 1 paratype; USNM 1388651, 1 paratype), and *Dactylogyrus perlus* Mueller, 1938 (USNM 1367031, 1 syntype; USNM 1367034, 2 slides with 3 and 5 syntypes, respectively) were examined.

RESULTS

Seven species of *Lythrurus* (58%) were found to be parasitised by *Dactylogyrus crucis* and 8 (67%) by the new species (Table 1). No species of *Dactylogyrus* were found on 4 of the 12 (33%) species of *Lythrurus*. All seven species parasitised by *D. crucis* were also infected by the new species.

Dactylogyrus crucis Rogers, 1967

Synonyms: *Dactylogyrus umbratilus* (Kimpel, 1939) Monaco et Mizelle, 1955, *nomen nudum* according to Yamaguti (1963); *Dactylogyrus attenuatus* Mizelle et Klucka, 1953 of Kritsky et al. (1977) (*partim*; individuals from *Lythrurus umbratilis* in Illinois).

Type host and locality: *Lythrurus bellus* (Hay) – U.S.A.: Alabama: Lee County, unnamed creek on Wire Road, Auburn, Tallapoosa River System (32°33'96"N; 85°34'19"W) (Rogers 1967).

Site: Gills.

Type material: Holotype, USNM 1357103; 2 paratypes, USNM 1357104; 3 paratypes, HWML 49266; 3 paratypes, HWML 49267.

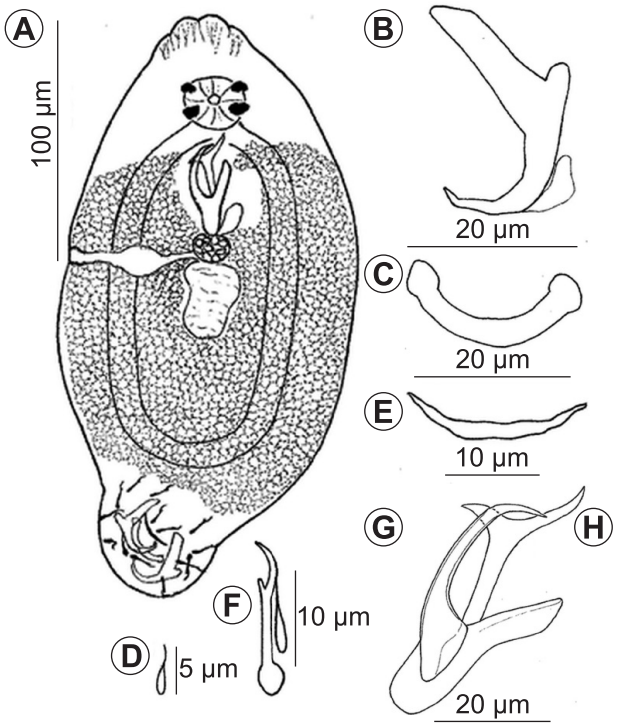

Fig 2. *Dactylogyrus lythruri* sp. n. (holotype, HWML 216191). **A** – whole mount (ventral view); **B** – anchor; **C** – dorsal bar; **D** – 4A; **E** – ventral bar; **F** – hook; **G** – male copulatory organ; **H** – accessory piece.

Other hosts, localities, prevalence, intensity ± standard deviation, and range of infection: Table 1.

Remarks. In an unpublished dissertation, Kimpel (1939) described *Neodactylogyrus* (= *Dactylogyrus*) *umbratilus*, but *D. umbratilus* was considered a *nomen nudum* by Yamaguti (1963) because it did not meet the criteria of publication required by the International Code of Zoological Nomenclature. Kritsky et al. (1977) examined the single available specimen of Kimpel's *nomen nudum* and considered it (erroneously, as shown below) to be a synonym of *D. attenuatus*, a species otherwise known only from the creek chub, *Semotilus atromaculatus* (Mitchill) (Hoffman 1999).

Attempts during this study to locate the type specimens of *D. attenuatus* at the University of Notre Dame, HWML and USNM for comparison failed, but based on drawings in the original descriptions of *D. umbratilus* (Kimpel 1939), *D. attenuatus* (Mizelle and Klucka 1953) and *D. crucis* (Rogers 1967), the dorsal anchor of *D. attenuatus* is considerably shorter in relation to base length than that of *D. umbratilus* and *D. crucis*. The shape of the dorsal anchors of *D. umbratilus* and *D. crucis* are indistinguishable. Kimpel (1939) did not report the length of the base of the dorsal anchor of *D. umbratilus*, and Rogers (1967) erroneously reported that of *D. crucis* as 4–6 (5), n = 20.

However, the length of the base of the dorsal anchor of *D. umbratilus* (13, n = 1, USNM 1368632) and *D. crucis* (10–13 [12], n = 3, HWML 49266) measured in this study was indistinguishable, but distinctly shorter than that of *D. attenuatus* (20–26 [22], n = 3) reported by Mizelle and Klucka (1953). The total lengths of the MCO reported for *D. umbratilus* (18–24 [20], n not given) by Kimpel (1939) and *D. crucis* (20–25 [22], n = 20) by Rogers (1967) were similar to each other, but were generally smaller than those for *D. attenuatus* (25–29 [27], n = 3) (Mizelle and Klucka 1953).

The accessory piece of *D. umbratilus* (see Kimpel 1939; USNM 73065) appears V-shaped as in *D. attenuatus* (Mizelle and Klucka 1953), whereas that of *D. crucis* is X-shaped (Rogers 1967). However, the small process forming the X-shaped accessory piece of *D. crucis* is sometimes obscured due to the angle of view, resulting in a V-shaped appearance of the accessory piece. The total length of the accessory piece was not reported for *D. umbratilus* by Kimpel (1939), but was 13 µm based on our measurement on the single specimen of USNM 1368632. This was very similar to total lengths of the accessory piece of *D. crucis* (9–13 [11], n = 20) reported by Rogers (1967), but generally smaller than those for *D. attenuatus* (16–18 [17], n = 3) reported by Mizelle and Klucka (1953). From these data, we consider *D. umbratilus* to be a synonym of *D. crucis* rather than *D. attenuatus*.

Dactylogyrus crucis is known only from species of *Lythrurus sensu* (Mayden 1989, Pramuk et al. 2006) (Rogers 1967, Hoffman 1999). Due to taxonomic changes in species of *Lythrurus* in recent years, a revised list of host species for *D. crucis* is in order. *L. umbratilis* was reported as *Notropis umbratilis atripes* by Kimpel (1939) and Kritsky et al. (1977), but the subspecies *atripes* is now considered a junior synonym of the eastern subspecies, *Lythrurus umbratilis cyanocephalus* (Copeland) (Snelson and Pflieger 1975, Gilbert 1978, 1998). Roger's (1967) host names for *D. crucis* are revised as follows: *Notropis roseipinnis* Hay is relegated to *Lythrurus atrapiculus* (Snelson) as a result of Snelson (1972) describing *Notropis atrapiculus* Snelson as a new species in a split from *N. roseipinnis* and Mayden (1989) raising *Lythrurus*, formerly a subgenus of *Notropis*, to genus rank; *Notropis bellus* (Hay) is considered to be *L. bellus* as a result of Mayden's (1989) elevation of *Lythrurus* to genus rank; and *Notropis ardens* (Cope) is changed to *Lythrurus fasciolaris* Gilbert due to Dimmick et al. (1996) elevating *Notropis umbratilis fasciolaris* (Gilbert) to species status, and applying it to Tennessee River populations formerly considered as *Lythrurus ardens* (Cope).

Dactylogyrus lythruri Cloutman, Adrian et McAllister sp. n. Fig. 2

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Synonyms: *Dactylogyrus confusus* Mueller, 1938 of Kimpel (1939) on *L. umbratilis* from Illinois; *Dactylogyrus banghami* of Rogers (1967) (*partim*; individuals from on *L. atrapiculus* and *L. bellus* in Alabama; *Dactylogyrus* cf. *beckeri* (Cloutman and Rogers 2005).

Description (based on 21 specimens): With characters of the genus as emended by Mizelle and McDougal (1970).

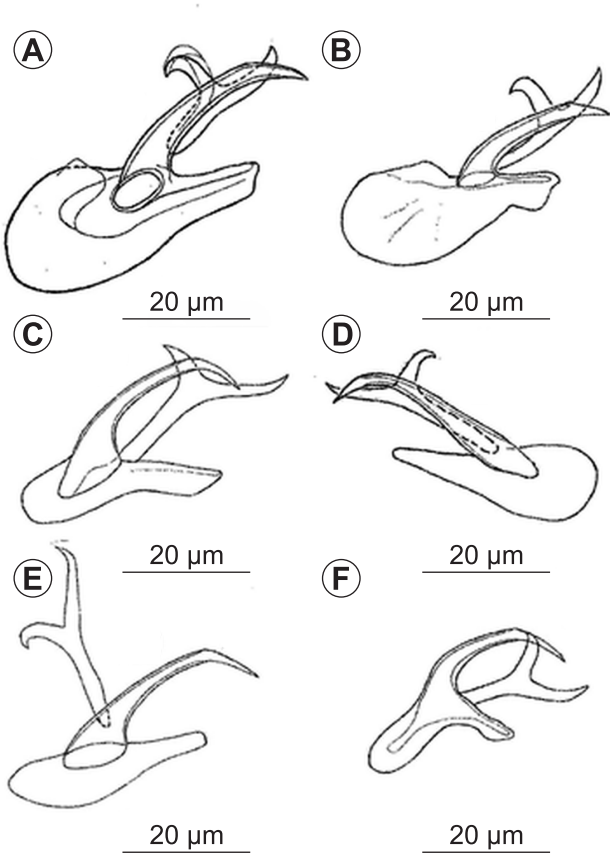

Fig 3. Male copulatory organ of selected species of the *Dactylogyrus perlus* complex. **A** – *Dactylogyrus beckeri* Cloutman, 1987, paratype from *Cyprinella galactura* (Cope) (USNM 1374680); **B** – *Dactylogyrus confusus* Mueller, 1938, syntype from *Clinostomus elongatus* (Kirtland) (USNM 1367024); **C** – *Dactylogyrus lythruri* sp. n., holotype from *Lythrurus umbratilis umbratilus* (Girard) (HWML 216191); **D** – *Dactylogyrus lythruri* sp. n., voucher from *Lythrurus umbratilis cyanocephalus* (Copeland) (USNM 1368632); **E** – *Dactylogyrus lythruri* sp. n., voucher from *Lythrurus bellus* (Hay) (HWML 45335); **F** – *Dactylogyrus perlus* Mueller, 1938, syntype from *Luxilus cornutus* (Mitchill) (USNM 1367034).

Body with thin tegument; 209–304 (244; n = 21) long, greatest width 91–129 (104; n = 21). Two pairs of anterior cephalic lobes, lateral pair smaller than medial pair. Head organs not observed. Two pairs of eyes approximately equal in size, anterior pair usually farther apart than posterior pair. Pharynx circular to oval (dorsal view), transverse diameter 19–27 (23; n = 17). Peduncle 0–8 (1; n = 20) long, 38–56 (45; n = 15) wide. Haptor 29–45 (36; n = 20) long, 44–64 (53; n = 20) wide.

Dorsal anchor comprising solid base, short deep root, elongate superficial root with flattened termination, short shaft with medial constriction, recurved point. Dorsal anchor 21–28 (24; n = 21) long; base length 15–22 (18; n = 21); deep root 2–5 (3; n = 21) long; superficial root 12–19 (15; n = 21) long. 4A 5–6 (6; n = 11) long. Dorsal bar broadly U-shaped, with terminal knobs, 19–30 (25; n = 21) long, 3–5 (4; n = 21) wide. Vestigial ventral bar without pointed knob in centre, 15–20 (16; n = 18) long. Fourteen hooks (7 pairs), similar in shape, normal in arrangement (Mizelle 1936). Each hook composed of bulbous base, slender shaft, erect thumb and delicate, sickle-shaped point provided with FH loop. Hook total lengths: nos. I, 13–16 (14; n = 21); II, 14–17 (15; n = 21); III, 14–18 (16; n = 20); IV, 15–20 (17; n = 21); V, 13–16 (15; n = 19); VI, 14–17 (15; n = 20); VII, 14–16 (15; n = 19).

Copulatory complex composed of male copulatory organ (MCO), articulated accessory piece. MCO with enlarged base bearing an elongate process and tubular shaft; shaft sharply bent near base, gently curving and tapering distally to a point. MCO 42–53 (46; n = 21) long; basal process slightly tapered distally, 12–18 (15; n = 21) long; shaft 32–39 (35; n = 21) long. Accessory piece with basal ramus bifurcated into medial ramus curving or hooking to a point at terminus and a distal ramus gently curving or recurving to a sharp point. Accessory piece 27–32 (29; n = 21) long; basal ramus 11–17 (14; n = 21) long, medial ramus 7–9 (8; n = 21) long; distal ramus 12–15 (14; n = 21) long. Vagina sclerotised. Vitellarium distributed from pharynx to haptor.

Type host: *Lythrurus umbratilis umbratilis* (Girard), western redfin shiner.

Type locality: U.S.A.: Kansas: Douglas County, Rock Creek, Kansas River Drainage of the Missouri River System (38°50'56"N; 95°26'39"W), 8 July 2002.

Site: Gills.

Type material: Holotype, HWML 216191; 20 paratypes, HWML 216192 (15 specimens from type locality), HWML 216193 (5 specimens from Butler County, Kansas) (Table 1).

Prevalence, intensity ± standard deviation, and range of infection at type locality: 10 of 10 (KU 34562) (100%, 3.6 ± 2.3, 1–7, right gills only).

Other hosts, localities, prevalence, intensity ± standard deviation, and range of infection: Table 1.

Etymology: *Dactylogyrus lythruri* is named after the genus of its hosts.

Remarks. *Dactylogyrus lythruri* most closely resembles *D. beckeri* in the *D. perlus* (= *banghami*) complex (Cloutman 1987, Cloutman and Rogers 2005) by possessing anchors with a short shaft and point with recurved tip, an MCO possessing a relatively large base with a distinct anterior process and a curved tubular shaft that attenuates to a point, and a bifurcate accessory piece (Figs. 2, 3). The MCO of *D. lythruri* (42–53 [46] long) is generally smaller than that of *D. beckeri* (46–65 [58] long) (Cloutman and Rogers 2005). The base and basal process of the MCO of *D. lythruri* (Fig. 3C–E) is less robust than that of *D. beckeri* (Fig. 3A) (see Cloutman 1987). The shaft of the MCO of *D. lythruri* bends fairly sharply near the base, whereas that of *D. beckeri* is more uniformly curved (Cloutman 1987; Fig. 3A, C–E).

Dactylogyrus confusus was reported by Kimpel (1939) (USNM 1368632) from *L. umbratilis* in Illinois, but examination of the original description (Mueller 1938) and 5 syntypes (USNM 1367024) from the redfin dace, *Clinostomus elongatus* (Kirtland) in New York, reveals trenchant differences in the MCO. *Dactylogyrus confusus* possesses

Table 1. Hosts, localities, dates of collection (reference or host museum number), prevalence (%), mean intensity ± 1 SD, and range of *Dactylogyrus* spp. parasitising *Lythrurus* spp. n = number of fish examined at that locality, - = not found at that locality.

Host species, common name Locality, date, reference or museum number	Geographic coordinant	n	*Dactylogyrus crucis* Prevalence (%), mean intensity ± 1 SD, range Museum accession number	*Dactylogyrus lythruri sp. n.* Prevalence (%), mean intensity ± 1 SD, range Museum accession number
Lythrurus alegnotus (Snelson), warrior shiner				
AL: Tuscaloosa Co., Cribbs Mill Creek R., 11 Oct 1909 (KU 14488)	33°11'00"N;87°31'10"W	5	–	–
Lythrurus ardens (Cope), rosefin shiner				
NC: Rockingham Co., Dan R., 5 May 1987	36°29'07"N;79°43'11"W	6	–	–
VA: Montgomery Co., South Fork Roanoke R., Aug 1987 (KU 22228)	37°13'39"N;80°12'32"W	10	–	–
VA: Roanoke Co., Back Cr., 3 Apr 1952 (KU 3282)	37°10'57"N;79°56'08"W	10	–	–
Lythrurus atrapiculus (Snelson), blacktip shiner				
AL: Geneva Co., Flat Cr., summer 1965 (Rogers 1967)	31°02'36"N;86°06'05"W		HWML 49268, 1 paratype	–
AL: Russell Co., Uchee R., summer 1965 (Cloutman and Rogers 2005)	32°22'39"N;85°04'51"W		–	HWML 45336, 4 vouchers
Lythrurus bellus (Hay), pretty shiner				
AL: Lee Co., unnamed cr., summer 1965 (Rogers 1967)	32°33'96"N;85°34'19"W		USNM 1357103, holotype USNM 1357104, 2 paratypes HWML 49266, 3 paratypes HWML 49267, 3 paratypes	HWML 45335, 3 vouchers
MS: Lowndes Co., Catalpa Cr., 7 Apr 1982 (KU 20302)	33°25'34"N;88°39'37"W	5	60%, 6.0 ± 4.0, 2–10 HWML 216178, 3 vouchers	80%, 5.5 ± 1.6, 1–8 HWML 216194, 5 vouchers
Lythrurus fasciolaris (Gilbert), scarlet shiner				
AL: Lauderdale Co., Colbert Cr., date unkown (Rogers 1976)	34°52'31"N;87°52'38"W		No data	–
AL: Lauderdale Co., Little Cypress Cr., 14 Jul 2009	34°56'58"N;87°41'42"W	3	100%, 13.0 ± 6.6, 7–20 HWML 216179,6 vouchers	100%, 9.3 ± 8.1, 2–18 HWML 216195, 5 vouchers
KY: Jefferson Co., Long Run Cr., 2 Jun 1958 (KU 4068)	38°14'15"N;85°26'09"W	3	100%, 4.3 ± 3.1, 1–7, right gills only HWML 216180, 5 vouchers	100%, 8.7 ± 0.6, 8–9, right gills only HWML 216196, 5 vouchers
TN: Cheatham Co., South Harpeth R., 27 Aug 1972 (KU 14963)	36°03'02"N;87°10'41"W	5	60%, 1.0 ± 0.0, 1, right gills only HWML 216181, 3 vouchers	20%, 2.0 ± 0.0, 2 right gills only HWML 216197, 2 vouchers
Lythrurus fumeus (Evermann), ribbon shiner				
OK: LeFlore Co., Little R., 18 Apr 1959 (KU 4528)	34°31'55"N;94°55'58"W	7	–	43%, 2.0 ± 1.0, 1–3, right gills only HWML 216198, 4 vouchers
OK: McCurtain Co., Yanubbee Cr., 18 Apr 1948 (KU 27792)	34°04'07"N;94°44'19"W	10	80%, 5.8 ± 5.9, 1–17, right gills only HWML 216182, 2 vouchers	70%, 1.7 ± 0.8, 1–3, right gills only HWML 216199, 5 vouchers
TX: Upshur Co., Little Cypress Bayou, 19 Mar 1976 (KU 17110)	32°46'35"N;94°56'48"W	5	20%, 1.0 ± 0.0, 1, right gills only HWML 216183, 1 voucher	100%, 4.6 ± 2.3, 1–7, right gills only HWML 216200, 5 vouchers
Lythrurus lirus (Jordan), mountain shiner				
GA: Floyd Co., Kykes Cr., 31 Mar 1950 (KU 18986)	34°15'15"N;85°04'47"W	10	–	–
TN: Bradley Co., Little Chatata Cr., 8 Nov 1970 (KU 18933)	35°12'38"N;84°47'45"W	5	–	–
Lythrurus matutinus (Cope), pinewoods shiner				
NC: Franklin Co., Tar R., 1 July 1966 (NCSM 3093)	36°08'32"N;78°22'20"W	10	–	–
NC: Granville Co., Tar R., 17 Jun 1980 (NCSM 9632)	36°18'43"N;78°45'01"W	10	–	–
NC: Orange Co., Eno R., 14 Apr 2005 (NCSM 43469)	36°05'06"N;79°03'42"W	10	–	–
NC: Wake Co., Upper Barton Cr., 1 June 1968 (NCSM 4882)	35°57'35"N;78°40'45"W	10	–	–
Lythrurus roseipinnis (Hay), cherryfin shiner				
MS: Clarke Co., Allen Branch, 21 Apr 1976 (NCSM 42987)	32°10'56"N;88°49'42"W	10	20%, 1.0 ± 0.0, 1, right gills only HWML 216184, 2 vouchers	10%, 3.0 ± 0.0, 3, right gills only HWML 216201, 2 vouchers
Lythrurus snelsoni (Robison), Ouachita shiner				
AR: Polk Co., Mountain Fork R., 27 Jul 1990	34°30'19"N;94°25'51"W	10	–	70%, 3.7 ± 2.4, 1–8 HWML 216202, 5 vouchers
AR: Polk Co., Mountain Fork R., 9 June 1994	34°30'19"N;94°25'51"W	11	–	1.3 ± 4.9, 1–2
Lythrurus umbratilis cyanocephalus (Copeland), eastern redfin shiner				
AR: Saline Co., North Fork Saline R., 29 Sep 1988	34°46'45"N;92°45'28"W	1	100%, 1.0 ± 0.0, 1 HWML 216185, 1 voucher	100%, 2.0 ± 0.0, 2 HWML 216203, 1 voucher
IL: Champaign Co., 16 Jul 1938 (Kimpel 1939, Kritsky et al. 1977)	40°06'N;88°15'W		USNM 1368632, 1 voucher	USNM 1368632, 1 voucher
OK: McCurtain Co., Yashau Cr., July 2014	34°46'45"N;92°45'28"W	3	33%, 4.0 ± 0.0, 4	100%, 5.3 ± 4.2, 2–10 HWML 216204, 3 vouchers
OK: McCurtain Co., Yashau Cr., 18 Sep 2015	34°46'45"N;92°45'28"W	4	25%, 2.0 ± 0.0, 2 HWML 216186, 2 vouchers	25%, 4.0 ± 0.0, 4 HWML 216205, 2 vouchers
Lythrurus umbratilis umbratilis (Girard), western redfin shiner				
KS: Butler Co., Thurman Cr., 29 Jun 1995 (KU 24272)	38°02'47"N;96°32'06"W	5	100%, 5.8 ± 2.4, 3–9, right gills only HWML 216187, 5 vouchers	100%, 6.6 ± 3.5, 3–10, right gills only HWML 216193, 5 paratypes
KS: Douglas Co., Rock Cr., 8 Jul 2002 (KU 34562)	38°50'56"N;95°26'39"W	10	90%, 7.8 ± 3.8, 3–14, right gills only HWML 216188, 5 vouchers	100%, 3.6 ± 2.3, 1–7, right gills only HWML 216191, holotype HWML 216192, 15 paratypes
Lythrurus cf. *umbratilis*, flamefin shiner				
AR: Garland Co., Bear Cr., 1 Jul 2014	34°32'08"N;93°16'58"W	7	14%, 1.0 ± 0.0, 1 HWML 216189, 1 voucher	–
AR: Garland Co., Bear Cr., 16 Oct 2014	34°32'08"N;93°16'58"W	5	–	–
AR: Garland Co., Bear Cr., 20 Nov 2017	34°32'08"N;93°16'58"W	5	–	–
AR: Garland Co., Bear Cr., 13 Jun 2019	34°32'08"N;93°16'58"W	1	–	–
AR: Polk Co., Ouachita R., 15 Aug 1994	34°38'36"N;94°11'56"W	10	40%, 3.0 ± 2.7, 1–7 HWML 216190, 2 vouchers	30%, 5.7 ± 4.0, 3–10 HWML 216206, 5 vouchers
AR: Polk Co., Ouachita R., 12 Mar 2017	34°38'36"N;94°11'56"W	1	–	-

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Table 2. Measurements of *Dactylogyrus lythruri* sp. n. from species of *Lythrurus* from various localities. Ranges for each morphometric parameter for each host and locality are followed by means and number of specimens measured in parentheses.

Host species	*L. atrapiculus*	*L. bellus*	*L. bellus*	*L. fasciolaris*	*L. fasciolaris*	*L. fasciolaris*	*L. fumeus*	*L. fumeus*	*L. fumeus*	*L. roseipinnis*	*L. snelsoni*	*L. umbratilis cyanocephalus*	*L. umbratilis cyanocephalus*	*L. umbratilis umbratilis*	*L. umbratilis umbratilis*	*L.* cf. *umbratilis*
Locality	Uchee Cr., AL	Catalpa Creek, MS	Unnamed Cr., AL	Little Cypress Cr., AL	Long Run Cr., KY	South Harpeth R., TN	Little R., OK	Yanubbee Cr., OK	Little Cypress Bayou, TX	Allen Br., MS	Mountain Fk., AR	N. Fork Saline R., AR	Champaign Co., IL	Rock Creek, KS	Thurman Cr., KS	Ouachita R., AR
Reference	Cloutman and Rogers (2005)	Present study	Rogers (1967)	Present study	Present study	Present study	Present study	Present study	Present study	Present study	Present study	Present study	Kimpel (1939)	Present study	Present study	Present study
Specimens examined	Vouchers	Vouchers	Vouchers	Vouchers	Vouchers	Vouchers	Vouchers	Vouchers	Vouchers	Vouchers	Vouchers	Voucher	Voucher	Types	Vouchers	Vouchers
	HWML 45336	HWML 216194	HWML 45335	HWML 216195	HWML 216196	HWML 216197	HWML 216198	HWML216199	HWML 216200	HWML 216201	HWML 216202	HWML 216203	USNM 1368632	HWML 216191, 216192	HWML 216193	HWML 216206
Body length		230–277 (255, 8)		228–400 (343, 10)	209–247 (238, 8)	171–220 (196, 2)	152–217 (188, 6)	160–228 (195, 5)	220–245 (235, 10)	209–239 (227, 3)		201		209–304 (248, 16)	198–247 (231, 5)	171–209 (191, 4)
Body width		87–141 (111, 8)		76–144 (112, 10)	95–122 (107, 8)	68–76 (72, 2)	53–114 (89, 6)	91–99 (96, 5)	99–129 (115, 10)	99–125 (115, 3)		65		91–129 (105, 16)	95–122 (103, 5)	50–65 (60, 4)
Peduncle length		0–4 (2, 7)		0–38 (6, 8)	0 (0, 4)	0–4 (2, 2)	0 (0, 4)	0 (0, 3)	0 (0, 7)	0–5 (2, 3)		0		0–8 (1, 15)	0 (0, 5)	0–23 (10, 4)
Peduncle width		38–49 (42, 7)		30–52 (44, 8)	39–54 (48, 4)	26–32 (29, 2)	34–39 (37, 4)	40–49 (43, 3)	38–49 (42, 7)	36–49 (43, 3)		24		38–56 (45, 10)	38–52 (44, 5)	22–27 (24, 4)
Haptor length		30–39 (35, 7)		37–50 (42, 8)	29–40 (33, 6)	31–32 (32, 2)	30–41 (36, 4)	23–35 (30, 3)	29–40 (34, 7)	30–38 (34, 3)		30		29–45 (35, 15)	30–38 (33, 5)	29–37 (32, 4)
Haptor width		38–54 (48, 7)		53–69 (61, 8)	53–57 (55, 6)	38–39 (39, 2)	30–48 (41, 4)	45–53 (49, 3)	45–53 (49, 7)	51–57 (54, 3)		42		44–64 (52, 15)	53–63 (56, 5)	39–41 (40, 4)
Dorsal anchor																
Total length	21–24 (22, 4)	22–26 (24, 8)	23–25 (24, 2)	23–26 (25, 10)	23–26 (24, 8)	21–24 (23, 2)	20–23 (22, 5)	23–25 (23, 5)	23–27 (24, 10)	20–25 (22, 3)	21–25 (23, 10)	24		21–27 (24, 16)	21–28 (25, 5)	23–25 (24, 4)
Base width	18–19 (18, 4)	16–18 (17, 8)	18–20 (19, 2)	15–20 (18, 10)	16–19 (18, 8)	17–18 (18, 2)	16–19 (17, 5)	15–18 (17, 5)	16–20 (18, 9)	17–21 (29, 3)	15–17 (16, 5)	16		16–22 (18, 16)	15–20 (17, 5)	17–20 (19, 2)
Deep root length	3–4 (3, 4)	2–5 (3, 8)	3 (3, 2)	3–5 (4, 10)	3–5 (4, 8)	3–4 (4, 2)	3–5 (4, 5)	3–4 (4, 5)	3–4 (3, 9)	4–5 (4, 3)	3–4 (4, 6)	5		2–5 (3, 16)	3–4 (4, 5)	3–4 (4, 2)
Superficial root length	13–15 (14, 4)	13–16 (15, 8)	13–14 (14, 2)	12–17 (15, 10)	15–17 (16, 8)	14 (14, 2)	12–15 (14, 5)	12–15 (14, 5)	13–17 (15, 10)	14–17 (16, 3)	11–16 (13, 6)	15		12–19 (15, 16)	14–17 (15, 5)	14–15 (15, 2)
Point length	2 (2, 4)	2–3 (2, 8)	2 (2, 2)	2–3 (2, 10)	2 (2, 8)	2 (2, 2)	2 (2, 5)	2 (2, 5)	2 (2, 10)	2 (2, 3)	2–3 (2, 10)	2		2–3 (2, 16)	2 (2, 5)	2 (2, 4)
4A length	5 (5, 1)		6 (6, 1)	5–7 (6, 7)	5 (5, 1)		5 (5, 2)	5 (5, 1)	5–6 (6, 2)					5–6 (6, 7)	5–6 (6, 4)	
Dorsal bar length	20–22 (21, 2)	19–24 (22, 7)	21–22 (22, 2)	18–26 (22, 10)	20–25 (23, 8)	23 (23, 2)	19–24 (21, 5)	24–26 (25, 4)	20–26 (22, 10)	20–28 (24, 3)	19–21 (20, 10)	17		19–30 (25, 16)	21–25 (23, 5)	19–23 (22, 3)
Dorsal bar width	3 (3, 2)	4–5 (4, 7)	3 (3, 2)	3–5 (4, 10)	3–5 (4, 8)	3–5 (4, 2)	3–4 (3, 5)	4–5 (4, 4)	3–4 (4, 10)		3 (3, 10)	4		3–5 (4, 16)	3–5 (4, 5)	3–5 (4, 4)
Ventral bar length	15 (15, 1)	16–17 (17, 4)	15 (15, 1)	16–18 (17, 5)	16–17 (17, 3)	16 (16, 1)		15–16 (16, 2)	15–18 (16, 8)	17–21 (19, 2)	15–17 (16, 8)	16		15–20 (17, 13)	15–17 (16, 5)	16 (16, 1)
Hook 1 total length	14–15 (14, 3)	14–15 (15, 7)	13–14 (14, 2)	12–15 (14, 10)	13–15 (14, 8)	12–13 (13, 2)	12–13 (13, 6)	13–14 (13, 3)	11–15 (13, 9)	13–15 (14, 3)	12–14 (13, 10)	12		13–16 (15, 16)	14–15 (15, 5)	13–14 (14, 2)
Hook 2 total length	14–15 (14, 3)	14–15 (15, 6)	13–14 (14, 2)	12–15 (14, 9)	13–15 (13, 8)	12–13 (13, 2)	12–13 (13, 4)	14 (14, 2)	13–15 (14, 9)	15 (15, 3)	12–14 (13, 7)	12		14–16 (15, 16)	12–15 (14, 5)	14–15 (15, 2)
Hook 3 total length	15 (15, 3)	15–16 (16, 6)	14–15 (15, 2)	13–15 (14, 9)	13–16 (14, 8)	13 (13, 2)	13–15 (14, 4)	15 (15, 2)	13–15 (15, 10)	15–18 (16, 3)	13–14 (14, 7)	14		14–17 (15, 16)	13–16 (15, 4)	14–16 (15, 2)
Hook 4 total length	15–17 (16, 3)	16–18 (17, 8)	15 (15, 2)	14–16 (15, 10)	14–17 (15, 8)	14–15 (15, 2)	14–17 (15, 4)	15–16 (15, 4)	14–16 (15, 9)	15–18 (17, 2)	13–15 (14, 10)	14		15–20 (17, 16)	15–17 (16, 5)	15 (15, 2)
Base length		3–5 (4, 8)		3–5 (4, 10)	2–3 (3, 8)	2–3 (3, 2)	2–3 (3, 3)	3–5 (4, 4)	3–5 (3, 9)	5–6 (6, 2)	2–3 (2, 8)	3		2–5 (3, 16)	3–5 (4, 5)	
Base width		2 (2, 8)		2–4 (3, 10)	2–3 (2, 8)	2 (2, 2)	2 (2, 3)	2–3 (2, 4)	2–3 (2, 9)	2–3 (3, 2)	2 (2, 8)	2		2–4 (3, 16)	2–3 (2, 5)	
Hook 5 total length	15 (15, 3)	15–16 (16, 6)	14–15 (15, 2)	14–16 (15, 10)	13–16 (14, 8)	12–13 (13, 2)	12–14 (13, 6)	12–15 (13, 3)	13–15 (14, 6)	15 (15, 2)	13–14 (14, 7)	13		14–18 (16, 15)	15–16 (16, 4)	15 (15, 1)
Hook 6 total length	14–15 (15, 3)	14–15 (15, 5)	14 (14, 2)	13–15 (14, 10)	13–15 (14, 8)	12 (12, 2)	13 (13, 1)	11–13 (12, 2)	12–14 (13, 5)	13 (13, 1)	12–14 (13, 9)	12		14–17 (15, 15)	15–16 (16, 5)	14 (14, 1)
Hook 7 total length	14–15 (14, 3)	14–15 (15, 6)	14–15 (15, 2)	12–15 (13, 10)	13–15 (14, 8)	12 (12, 2)	12–13 (13, 4)	12–13 (12, 3)	12–15 (14, 7)	12 (12, 2)	12–14 (13, 10)	12		13–16 (14, 14)	14–15 (15, 5)	13 (13, 1)
Male reproductive organ (MCO)																
Total length	42–47 (45, 4)	35–44 (41, 8)	43–46 (44, 3)	45–55 (49, 10)	38–51 (45, 8)	44–45 (45, 2)	40–46 (43, 6)	42–48 (44, 5)	38–50 (44, 10)	44–45 (45, 3)	38–44 (41, 10)	43	44	42–53 (46, 16)	44–47 (45, 5)	38–41 (40, 4)
Basal process length	12–15 (14, 2)	11–17 (14, 7)	14 (14, 2)	14–16 (15, 10)	14–16 (15, 6)	12–18 (15, 2)	11–16 (14, 6)	15–20 (17, 5)	13–16 (15, 10)	13–15 (14, 3)	11–13 (12, 10)	13	14	12–18 (15, 16)	13–17 (15, 5)	14–15 (14, 4)
Shaft total length	31–37 (34, 4)	27–32 (31, 8)	33–36 (35, 3)	33–41 (37, 10)	28–38 (35, 8)	35–38 (37, 2)	33–39 (36, 6)	35–38 (36, 5)	30–40 (35, 10)	33–35 (34, 3)	30–33 (32, 10)	32	33	32–39 (35, 16)	34–37 (35, 5)	30–33 (32, 4)
Shaft proximal length (SPL)	29–32 (30, 4)	25–30 (27, 8)	26–32 (30, 3)	27–34 (31, 10)	26–32 (30, 8)	27–29 (28, 2)	26–30 (28, 6)	28–30 (29, 5)	27–36 (29, 10)	28–29 (28, 3)	24–31 (27, 10)	28	28	27–32 (30, 16)	29–32 (31, 5)	25–26 (26, 4)
Point length (PL)	8–10 (9, 4)	8–10 (9, 8)	8–10 (9, 3)	8–11 (10, 10)	7–10 (9, 8)	9 (9, 2)	8–11 (9, 6)	8–10 (9, 5)	8–10 (9, 10)	8 (8, 3)	9–10 (10, 10)	8	8	9–11 (10, 16)	8–9 (9, 5)	8–9 (8, 4)
SPL/PL ratio	3.11–3.22 (3.19, 4)	2.78–3.50 (3.08, 8)	3.1–3.25 (3.16, 3)	2.90–3.60 (3.22, 10)	3.00–3.88 (3.36, 8)	3.00–3.22 (3.11, 2)	2.73–3.50 (3.20, 6)	2.90–3.63 (3.24, 5)	2.70–4.00 (3.31, 10)	3.50–3.63 (3.54, 3)	2.60–3.10 (2.78, 10)	3,5	3,5	2.45–3.22 (2.98, 16)	3.00–3.33 (3.18, 5)	2.89–3.25 (3.13, 4)
Accessory piece																
Total length	28–32 (30, 4)	28–32 (30, 8)	29–30 (30, 3)	29–34 (32, 10)	25–32 (30, 8)	32–35 (34, 2)	23–31 (28, 6)	29–32 (30, 5)	26–31 (29, 10)	29 (29, 3)	25–29 (27, 10)	26	27	27–32 (29, 16)	29–30 (30, 5)	24–29 (26, 4)
Basal ramus length	(11–15 (13, 4)	11–16 (14, 8)	14–16 (15, 3)	13–19 (15, 10)	13–15 (14, 8)	16–17 (17, 2)	12–18 (14, 6)	13–15 (15, 5)	13–16 (14, 10)	14–15 (14, 3)	10–15 (12, 10)	12	15	11–17 (14, 16)	14–15 (15, 5)	10–15 (12, 4)
Distal ramus length	(12–14 (13, 4)	14–16 (15, 8)	12–13 (13, 3)	13–15 (14, 10)	13–14 (14, 8)	14–15 (15, 2)	12–15 (13, 6)	13–14 (13, 5)	13–15 (14, 10)	11–12 (12, 3)	11–13 (12, 10)	12	12	12–15 (14, 16)	14 (14, 5)	11–13 (13, 4)
Medial ramus length	8 (8, 4)	7–8 (8, 8)	8 (8, 3)	7–8 (8, 10)	7–9 (8, 8)	8 (8, 2)	7–8 (8, 6)	7–8 (8, 5)	7–9 (8, 10)	7–8 (7, 3)	8 (8, 10)	8	7	7–9 (8, 16)	7–9 (8, 5)	7–8 (8, 4)

an MCO with a large expanded base and a basal process that is enlarged ventrally near the distal end (Fig. 3B). The enlargement of the distal end of the MCO is not obvious, probably due to angle of view, in Mueller's (1938) drawing. The base of the MCO of the type specimens of *D. lythruri* and Kimpel's specimen is less robust, and the basal process is not enlarged distally (Fig. 3C,D). The report of *D. confusus* from *L. umbratilis* (see Kimpel 1939, Hoffman 1999) is herein relegated to *D. lythruri*.

Dactylogyrus banghami was reported by Rogers (1967) from *L. atrapiculus* (HWML 45336) and *L. bellus* (HWML 45335) in Alabama, but Cloutman and Rogers (2005) reported Rogers' (1967) material as an undescribed species, *D.* cf. *beckeri*. *Dactylogyrus banghami* has been reported from a variety of leuciscid hosts (Hoffman 1999), but has been synonymised with *D. perlus* and considered to be found only on species of *Luxilus* Rafinesque (Cloutman 1988, Cloutman and Rogers 2005). *Dactylogyrus perlus* and *D. lythruri* differ most notably in the size and shape of the MCO. The MCO length of *D. perlus* is 35–42 (38) (Mueller 1938; USNM 1367031, USNM 1367034), that of *D. lythruri* is 42–53 (46). The basal process of the MCO of *D. perlus* (Fig. 3F) is inflated or enlarged ventrally near the distal end, whereas that of *D. lythruri* (Fig. 3C–D) is not. Reports of *D. banghami* (Rogers 1967) and *D.* cf. *beckeri* (see Cloutman and Rogers 2005) from *L. atrapiculus* and *L. bellus* from Alabama are herein relegated to *D. lythruri.*

Some sclerites of *D. lythruri* displayed minor variation in size among host species and localities (Table 2), but the basic shape of sclerites persists among different hosts and localities. Thus, *D. lythruri* is considered here to represent a single wide-ranging species limited to parasitising species of *Lythrurus*. Variation in size of sclerites with season and among localities has been observed within species of monogeneans (e.g., Ferdig et al. 1993, Mo 1993).

Taxonomic revisions of the hosts are provided in the Remarks section for *D. crucis*.

DISCUSSION

Dactylogyrus crucis and *Dactylogyrus lythruri* are known to parasitise only species of *Lythrurus*, thus displaying congeneric rather than strict host specificity. This host specificity is consistent with the trend that species of *Dactylogyrus* are typically found on one host species or a closely related group of hosts (Cloutman 1987, 1988, 2006, 2009, Gibson et al. 1996, Bakke et al. 2002, Cloutman and Rogers 2005, Šimková et al. 2006, 2017). Because of their high host specificity, species of *Dactylogyrus* are often good indicators of host relationships (Cloutman 1987, 1988, 2006). They are hypothesised to normally evolve from common ancestors as their respective hosts evolve from their respective common ancestors (Cloutman 1987, 1988, 2006), although host switching among closely related hosts may also occur (Cloutman 2006, Šimková et al. 2004, 2017).

Lythrurus is widely supported by morphological and molecular data to be a monophyletic genus (Schmidt et al. 1998, Pramuk et al. 2006, Hopkins and Eisenhour 2008). The presence of *D. crucis* on seven and *D. lythruri* on eight of the 12 species of *Lythrurus*, and only on *Lythrurus*, corroborates the close relatedness of these hosts.

The congeneric host specificity rather than strict host specificity, large distribution area in numerous drainages, and minor variation in size of sclerotised structures of *D. lythruri* among host species and localities could encourage the idea that *D. lythruri* may represent a complex of cryptic species not detected by morphometric data. The same could be said for *D. crucis*. Genetic studies will be necessary to resolve whether these two species represent widely distributed parasites with congeneric host specificity or more host-specific cryptic species.

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