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)

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**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 *Lythrurus* are provided for *D. crucis*. A record of *Dactylogyrus attenuatus* Mizelle et Klucka, 1953 (syn. *Dactylogyrus umbratilis* [Kimpel, 1939], nomen nudum) on *Lythrurus umbratilis* (Girard) is referable 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 umbratilis* (Kimpel, 1939) from *Lythrurus umbratilis* (Girard) in Illinois (Kimpel 1939); *D. umbratilis* 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 Pfieger 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...
**Fig 1.** Measurements of sclerites of the *Dactylogyrus perulus* 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. Abbreviation: a – length. F – accessory piece. Abbreviation: a – total length; b – basal ramus length; c – distal ramus length; d – medial ramus length.

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, USA, 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 136919, 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 hydrophloxii* 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 perulus* 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 umbratilis* (Kimpel, 1939) Mannon et Mizelle, 1955, *nomen nudum* according to Yamaguti (1963); *Dactylogyrus attenuatus* Mizzelle 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°33’36"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.
**Remarks.** In an unpublished dissertation, Kimpel (1939) described *Neodactylogyrus (= Dactylogyrus) umbratilis*, but *D. umbratilis* 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. umbratilis* (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. umbratilis* and *D. crucis*. The shape of the dorsal anchors of *D. umbratilis* and *D. crucis* are indistinguishable. Kimpel (1939) did not report the length of the base of the dorsal anchor of *D. umbratilis*, 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. umbratilis* (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. umbratilis* (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. umbratilis* (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. umbratilis* 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. umbratilis* 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 Pfieger 1975, Gilbert 1978, 1998). Roger’s (1967) host names for *D. crucis* are revised as follows: *Notropis roseipinnis* Hay is relegated to *Lythrurus atrapusculus* (Snelson) as a result of Snelson (1972) describing *Notropis atrapusculus* 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 Dimmock 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

ZooBank number for species:
urn:lsid:zoobank.org:act:EFC6B469-1039-424D-8232-DA972E7D9A22

**Synonyms:** *Dactylogyrus confusus* Mueller, 1938 of Kimpel (1939) on *L. umbratilis* from Illinois; *Dactylogyrus banghami* of Rogers (1967) (partim; individuals from on *L. atrapusculus* 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),

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**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.
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 *Lythrurus* 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...
| Host species, common name | Geographic coordiant | n | Dactylogyrus crucis | Dactylogyrus lythri sp. n. |
|---------------------------|---------------------|---|-------------------|-----------------------------|
| Lythurus aegliostus (Snelson), warrior shiner | AL: Tuscaloosa Co., Criggs Mill Creek R., 11 Oct 1909 (KU 14488) | 33°11'00"N;87°31'10"W | 5 | 100%, 3.6 ± 2.3, 1–7, right gills only | HWML 126184, 2 vouchers |
| Lythurus ardens (Oken), rosefin shiner | NC: Rockingham Co., Dan R., 5 May 1987 | 34°29'07"N;79°43'11"W | 6 | 100%, 13 ± 6.6, 7–20 | HWML 126197, 6 vouchers |
| | VA: Montgomery Co., South Fork Roanoke R., Aug 1987 (KU 22228) | 37°13'59"N;80°12'32"W | 10 | 100%, 9 ± 8.1, 2–18 | HWML 126195, 5 vouchers |
| | VA: Roanoke Co., Back Cr, 3 Apr 1952 (KU 3282) | 37°10'57"N;79°56'08"W | 10 | 100%, 9 ± 8.1, 2–18 | HWML 126195, 5 vouchers |
| Lythurus atrapruli (Snelson), blacktip shiner | AL: Geneva Co., Flat Cr., summer 1965 (Rogers 1967) | 31°02'36"N;86°00'05"W | HWML 49268, 1 paratype | HWML 45336, 4 vouchers |
| | AL: Russell Co., Uchee R., summer 1965 (Cloutman and Rogers 2005) | 32°22'39"N;85°04'51"W | – | – | – |
| Lythurus bellus (Hay), pretty shiner | MS: Lowndes Co., Cataula Cr., 7 Apr 1982 (KU 20302) | 33°25'34"N;88°39'37"W | 5 | 60%, 6 ± 0.4, 2–10 | HWML 126178, 3 vouchers |
| | HWML 49268, 3 paratypes | | | HWML 45336, 4 vouchers | |
| Lythurus fasciolaris (Evermann), ribbon shiner | OK: LeFlore Co., Little R., 18 Apr 1959 (KU 4528) | 34°31'55"N;94°55'58"W | 7 | 43%, 2 ± 1.0, 1–3, right gills only | HWML 126198, 5 vouchers |
| | OK: McCurtain Co., Yanubbee Cr., 18 Apr 1948 (KU 27792) | 34°06'07"N;94°44'19"W | 10 | 80%, 5 ± 5.9, 1–17, right gills only | HWML 126182, 2 vouchers |
| | TX: Uphur Co., Little Cypress Bayou, 19 Mar 1976 (KU 17110) | 32°46'35"N;94°56'48"W | 5 | 20%, 1 ± 0.0, 1, right gills only | HWML 126183, 1 voucher |
| Lythurus litorius (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 | – | – |
| Lythurus matutinus (Cope), pinewoods shiner | NC: Franklin Co., Tar R., 1 July 1966 (NCSM 3983) | 36°08'32"N;78°22'20"W | 10 | – | – |
| | NC: Granville Co., Tar R., 17 Jun 1980 (NCSM 9632) | 36°14'43"N;87°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 | – | – |
| Lythurus 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, 1, right gills only | HWML 126184, 2 vouchers |
| | HWML 45336, 4 vouchers | | HWML 126198, 5 vouchers | | |
| Lythurus scincus (Robinson), Osceola shiner | AR: Polk Co., Mountain Fork R., 27 Jul 1990 | 34°30'19"N;84°25'51"W | 10 | – | 70%, 3 ± 2.4, 1–8 |
| | AR: Polk Co., Mountain Fork R., 9 June 1994 | 34°30'19"N;84°25'51"W | 11 | – | HWML 126202, 5 vouchers |
| | 1.3 ± 4.9, 1–2 | | | | |
| Lythurus umbritatis cyanopechatus (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, 1 | HWML 126185, 1 voucher |
| | IL: Champaign Co., 16 Jul 1938 (Kimpel 1939, Kritsky et al. 1977) | 40°06'N;88°15'W | 10 | – | USNM 1368632, 1 voucher |
| | OK: McCurtain Co., Yashau Cr., 18 Apr 1948 (KU 27792) | 34°46'45"N;92°45'28"W | 3 | 33%, 4 ± 0.0, 4 | USNM 1368632, 1 voucher |
| | OK: McCurtain Co., Yashau Cr., 18 Sep 2015 | 34°46'45"N;92°45'28"W | 4 | 25%, 2 ± 0.0, 2 | HWML 226186, 2 vouchers |
| Lythurus umbritatis 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 ± 2.4, 3–9, right gills only | HWML 126187, 5 vouchers |
| | KS: Douglas Co., Rock Cr., 8 Jul 2002 (KU 34562) | 38°50'56"N;95°26'39"W | 10 | 90%, 7 ± 3.8, 3–14, right gills only | HWML 126188, 5 vouchers |
| | HWML 126191, holotype | | HWML 126192, 15 paratypes | | |
| Lythurus cf. umbritatis, flamelnin shiner | AR: Garland Co., Bear Cr., 1 Jul 2014 | 34°32'08"N;93°16'58"W | 7 | 14%, 1 ± 0.0, 1 | HWML 126189, 1 voucher |
| | AR: Garland Co., Bear Cr., 16 Oct 2014 | 34°32'08"N;93°16'58"W | 5 | – | HWML 126189, 1 voucher |
| | AR: Garland Co., Bear Cr., 20 Nov 2017 | 34°32'08"N;93°16'58"W | 5 | – | HWML 126189, 1 voucher |
| | AR: Garland Co., Bear Cr., 13 Jun 2019 | 34°32'08"N;93°16'58"W | 1 | – | HWML 126189, 1 voucher |
| | AR: Polk Co., Ouachita R., 15 Aug 1994 | 34°38'36"N;84°11'56"W | 10 | 40%, 3 ± 2.7, 1–7 | HWML 126190, 2 vouchers |
| | AR: Polk Co., Ouachita R., 12 Mar 2017 | 34°38'36"N;94°11'56"W | 1 | – | HWML 126206, 5 vouchers |
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. atranchus | L. bellus | L. bellus | L. fascioloides | L. fascioloides | L. fascioloides | L. fumosus | L. fumosus | L. roseipenis | L. umbratilis cya-bratilis | L. umbratilis cya-bratilis | L. umbratilis umbratilis | L. cf. umbatilis |
|--------------|-------------|----------|----------|----------------|----------------|----------------|-----------|-----------|-------------|----------------|----------------|----------------|-------------|
| Locality     | Uchee Cr., AL | Catalpa Creek, MS | Unnamed Cr., AL | Little Cypress Cr., AL | Long Run Creek, KY | Little R. peth R., Tkon | Yancobee Cr., OK | Little Cypress Bayou, TX | Allen Br., MS | Mountain Fk., AR | N. Fork Salmon R., AR Co., ID | Champaign Rock Creek, KS | Thurman Cr., AR | Ouachita Cr., AR |
| Reference    | Cloutman and Rogers (2005) | Rogers (1967) | Rogers (1967) | Cloutman and Rogers (2005) | Rogers (1967) | Rogers (1967) | Rogers (1967) | Rogers (1967) | Rogers (1967) | Rogers (1967) | Rogers (1967) | Rogers (1967) | Rogers (1967) |
| Specimens examined | HWML 4536 | Vouchers | Vouchers | HWML 21601 | Vouchers | Vouchers | HWML 25181 | Vouchers | HWML 216019 | Vouchers | Vouchers | Vouchers | Vouchers |
| Body length  | 230–277 (255.8) | 228–460 (244.10) | 209–247 (228.81) | 171–230 (196.62) | 152–217 (188.6) | 160–228 (195.5) | 220–245 (235.10) | 209–239 (227.3) | 199–225 (195.5) | 155 (155) | 155 (155) | 155 (155) | 155 (155) |
| Body width   | 87–141 (111.8) | 76–144 (102.8) | 95–122 (107.0) | 68–76 (72.2) | 53–114 (89.66) | 99–99 (86.54) | 99–99 (86.54) | 99–99 (86.54) | 99–99 (86.54) | 99–99 (86.54) | 99–99 (86.54) | 99–99 (86.54) | 99–99 (86.54) |
| Peduncle length | 2–4 (2.7) | 0.6 (0.6) | 0.6 (0.6) | 0.6 (0.6) | 0.6 (0.6) | 0.6 (0.6) | 0.6 (0.6) | 0.6 (0.6) | 0.6 (0.6) | 0.6 (0.6) | 0.6 (0.6) | 0.6 (0.6) | 0.6 (0.6) |
| Peduncle width | 38–40 (4.7) | 30–52 (44.8) | 39–54 (44.8) | 26–32 (29.2) | 34–39 (37.9) | 40–49 (43.3) | 38–40 (42.7) | 36–49 (43.3) | 38–40 (42.7) | 36–49 (43.3) | 38–40 (42.7) | 36–49 (43.3) | 38–40 (42.7) |
| Haptor length | 30–39 (35.7) | 37–50 (42.8) | 29–30 (40.3) | 31–32 (32.6) | 30–41 (36.4) | 33–35 (35.0) | 29–30 (34.7) | 30–38 (34.8) | 30–38 (34.8) | 30–38 (34.8) | 30–38 (34.8) | 30–38 (34.8) | 30–38 (34.8) |
| Haptor width  | 38–54 (48.7) | 31–69 (61.6) | 53–57 (53.5) | 38–39 (39.2) | 30–48 (41.3) | 45–53 (49.1) | 51–57 (57.4) | 38–53 (53.7) | 38–53 (53.7) | 38–53 (53.7) | 38–53 (53.7) | 38–53 (53.7) | 38–53 (53.7) |

**Locality**

**Specimens examined**

**Referene**

**Host species**

**Locality**

**Reference**

**Specimens examined**

**Locality**

**Reference**

**Specimens examined**

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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.

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.

Acknowledgements. We thank J. Ralph Lichtenfels and Eric Hoberg (USNPC) and Scott L. Gardner (HWML) for loaning specimens of Dactylogyrus. Andy Bentley, University of Kansas, Bernard Kuhajda, University of Alabama, and Wayne C. Starnes, North Carolina Museum of Natural Sciences, loaned some host specimens. Scientific Collecting Permits were issued to CTM by the Arkansas Game and Fish Commission and Oklahoma Department of Wildlife Conservation. Part of this work was done under Alabama Space Grant Consortium NASA Training Grant NNG-05GE80H awarded to Bruce W. Stallsmith.

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