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A new species of *Ceraclea* (Trichoptera:Leptoceridae) preying on snails

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Abstract. Ceraclea joannae, new species, feeds on the freshwater snail Somatogyrus virginicus Walker (Hydrobiidae). Our study is the first report of prey other than sponges for a Ceraclea species and the first report of snail predation by Trichoptera larvae in North America. Ceraclea joannae larvae and adults resemble those of *C. diluta* (Hagen); however, the larva of the new species has a dark head, sickle-shaped mandibles, and a dark pronotum except for a pair of unique, conspicuous, oblique, white bands; the male differs in the slightly longer superior appendages, more nearly straight ventral margins of tergum X, slightly stouter inferior appendages, and the more-tapered apex and less-pronounced ventral notch of the phallus. This new species of *Ceraclea* is known from only 3.2 km of the Little River (Montgomery County, North Carolina, USA), downstream of the developing town of Asheboro. Because of its rarity and limited distribution, *Ceraclea joannae* may be highly vulnerable to changes in water or habitat quality.

Key words: Ceraclea joannae, Somatogyrus virginicus, Leptoceridae, Athripsodina, Hydrobiidae, endangered species, North Carolina.

Larvae of the caddisfly genus Ceraclea (Trichoptera:Leptoceridae) occur in a wide range of lotic and lentic habitats, constructing cases of sand or of silk with occasional sponge spicules, sprawling on bottom sediments or climbing in vegetation, and feeding on collected bits of organic matter or shredded living tissue of plants or sponges (Merritt and Cummins 1996). Wiggins (1996) provided a summary of biological and diagnostic features of larvae of the genus. Life histories, food, and habitat characteristics have been studied in detail for C. resurgens (Walker) (Resh 1976a, Herrmann 1988), C. transversa (Hagen) (Resh 1976a, c), and C. ancylus (Vorhies) (Shapas and Hilsenhoff 1976, Resh 1976c, 1977). The biology and diagnosis of larvae of 19 North American Ceraclea species were summarized by Resh (1976b).

The Little River, near Star (Montgomery County), North Carolina, USA, is habitat for a highly diverse benthic fauna (North Carolina Division of Water Quality [NC DWQ] 2002). The larvae of 2 unidentified species of *Ceraclea* were encountered in the course of routine biomonitoring efforts in this stream. The 1st species, *Cer*-

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aclea (C.) enodis Whitlock and Morse, was described over 10 y ago (Whitlock and Morse 1994). Since 1991, the authors, JCM's daughter, and students from Clemson University and the South Carolina Governor's School for Science and Mathematics have made several trips to the stream to collect larvae and pupae and to attempt to capture or rear adults of the 2nd species. To the surprise of this research team, mature larvae of this 2nd species captured in winter months frequently were found with their heads inserted in the anterior opening of the Panhandle Pebblesnail, Somatogyrus virginicus Walker (Gastropoda:Hydrobiidae). Only one other species of caddisfly has been reported to feed on snails. Hudsonema amabile (McLachlan) (another species of Leptoceridae) feeds facultatively on the New Zealand Mudsnail, Potamopyrgus antipodarum (Gray), also a hydrobiid (Winterbourn and Mason 1983). During or before 1987, the New Zealand Mudsnail (but not its caddisfly predator) was introduced into the western USA, where it now occurs in several states (Cada et al. 2005). The possibility that the larva of this new species of Ceraclea also may prey on snails provided additional incentive to pursue its adults.

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Methods

Study area

The Little River and its tributaries make up NC DWQ subbasin 15 in the Yadkin River basin. The NC DWQ has summarized land use, water chemistry, and stream biology for this area in the latest basinwide assessment report (NC DWQ 2002). The Little River subbasin has the highest % forest (85%) of the 17 subbasins in the Cape Fear River Basin of North Carolina. This region lies within the Carolina Slate Belt, which generally has rocky streams. The headwater drains portions of the city of Asheboro, whereas the lower ½ of the river is downstream of the town of Troy.

Specimen collection, rearing, and storage

Larval specimens of the new species were collected from rocks in relatively infrequent shallow riffles in the Little River from 1991 through 2004, mostly by visual inspection. The rocks with highest densities of larvae were fist-sized, with upper surfaces covered by lush growths of riverweed, *Podostemum ceratophyllum* Micheaux. Larvae and pupae usually were seen around the edges of the riverweed on the sides of the rocks. Selected mature larvae and pupae were reared in aerated stream water (15.0–16.5°C). Diagnostic characteristics were illustrated from cleared and whole specimens using a Wild M5 dissecting microscope with a 10 \times 10 mm grid eyepiece.

Type specimens are deposited in the United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (NMNH); the Illinois Natural History Survey, Urbana, Illinois (INHS); or the Clemson University Arthropod Collection, Clemson, South Carolina (CUAC), as indicated.

Ceraclea (Athripsodina) joannae Morse and Lenat, new species (Figs 1-14)

Diagnosis

The male of this new species closely resembles that of *Ceraclea (Athripsodina) diluta* (Hagen) in the shape of tergum X and the inferior appendages (Morse 1975), but differs in the slightly longer superior appendages, more nearly

straight ventral margins of tergum X, slightly stouter inferior appendages, and the more-tapered apex and less-pronounced ventral notch of the phallus. The female of this new species also closely resembles that of C. diluta, with the gonopod plates and lamellae nearly identical in shape (Ross 1944); however, the apex of tergum IX is much more pronounced in this species, tergum X is shorter, and the spermathecal sclerite is relatively narrower. The larva keys to C. diluta in the work of Resh (1976b), but is remarkably different from that of C. diluta, with sickleshaped mandibles, a dark head, a dark pronotum except for a pair of conspicuous oblique white bands, faint mesonotal sa1 sclerites, and large and dark mesonotal bars. The oblique white bands on the pronotum of C. joannae are especially conspicuous and are unique among known North American Ceraclea species.

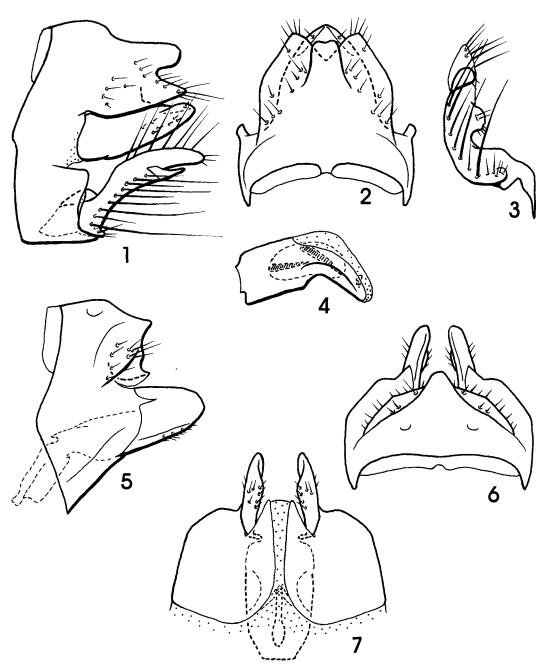
General description

Forewing length male = 10.0 mm (n = 7, range 9.4–10.4), female = 8.0 mm (n = 5, range 7.8–8.3).

Adult male.-Head near black dorsally, fuscous frontally, fulvous ventrally. Thoracic nota, palps, flagellae, forelegs, and abdominal sclerites dark fuscous. Antennal scapes and pedicels, middle and hind legs fulvous. Head and nota with mixture of fuscous and white hairs. White scale-like hairs covering legs and on bases of flagellar segments on basal ½ of each flagellum. Forewings fuscous, covered with mixture of fuscous and white hairs, appearing hoary, except white hairs more dense and conspicuous at arculus, apex of anal Y-commissure, basal fork of thyridial cell, behind basal fork of Rs + M, and on crossveins rs, (apparent) r-m, and m-cu. Hind wings broad, testaceous, with testaceous hairs, these hairs especially long on jugal margin.

Adult female.—Similar to male except abdomen bright green and hindwings narrower.

Male genitalia (Figs 1–4).—Segment IX tall and subrectangular in lateral view (Fig. 1), its tergum projecting conspicuously, but variably, over fused bases of superior appendages (Fig. 2). Superior appendages long and broad, extending caudad nearly to apex of tergum X, fused for more than ½ their length (Figs 1, 2). Sclerotization of tergum X ½ as long dorsally as ventrally, ventral margins nearly straight to rounded



FIGS 1–7. *Ceraclea joannae*, n. sp., male and female genitalia. Figs 1–4.—Male genitalia: 1, left lateral; 2, dorsal; 3, left inferior appendage, caudal; 4, phallus, left lateral. Figs 5–7.—Female genitalia: 5, left lateral; 6, dorsal; 7, ventral.

apex, with pair of apicodorsal flanges bearing few short sensilla laterally (Fig. 1). Inferior appendages slightly longer than tergum X, curved gradually caudad; coxopodite with small basoventral lobe, tapered and semimembranous subapicodorsal lobe with long dorsomesal setae, and semicircular mesal ridge; harpago flattened on caudal face and relatively broad in caudal view (Figs 1, 3). Phallus tubular basally, pair of paramere spines about equal in size and retracted to midlength with left paramere spine retracted nearly its own length further anteriorly than right spine; apical ½ of phallus separated from basal ½ in lateral view with shallow and broad ventral excision, with apicoventral sclerotization tapered to apex and divided on ventral midline and bearing longitudinal curved carina on each side (Fig. 4).

Female genitalia (Figs 5-7).-Segment IX subpentagonal in lateral view (Fig. 5), its sides each with rounded angle anteriorly, its dorsum convex and projecting posterad beyond superior appendages to apex of segment X, and its venter angled from anterior margin to bases of lamellae in straight line in lateral view (Figs 5, 6). Gonopod plates fused imperceptibly with sides of segment IX, separated on ventral midline, and extending posterad in pair of triangular points nearly ½ as long as lamellae (Fig. 7). Superior appendages very short, broadly rounded apically in dorsal view, with several moderately long setae (Figs 5, 6). Segment X relatively short, extending just beyond bases of lamellae (Figs 5, 6). Lamellae about as long as tall in lateral view, rounded apically, slightly concave mesally, each with longitudinal pad of setae ventrally (Figs 5, 7). Internal spermathecal sclerite parallel-sided most of its length in ventral view, slightly tapered near anterior end to truncate end (Fig. 7).

Last-instar larva (Figs 8–12).—Length ~7.0 mm. Head dark reddish brown, with few inconspicuous light muscle scars posteriorly, parafrontal lines and subocular lines present, antennae each about ½ as long as anterior edge of frontoclypeus (Fig. 8). Mandibles depressed and sickle-shaped, apical tooth long and sharp, dorsal and ventral edges of each mandible close together and with inconspicuous rounded subapical teeth (Fig. 9). Ventral apotome slightly concave anteriorly, with straight sides converging to rounded and bidentate posterior edge (Fig. 10). Pronotum divided medially into pair of dark reddish brown plates with dark posterior edges, each plate with conspicuous pale stripe from near middle of lateral margin to posteromedial corner, few vague dark spots in each stripe; anteromedial corners of plates each with small pale spot (Fig. 11). Mesonotal sa1 sclerites scarcely evident, darkest submedially, with few setae anteriorly; mesonotal bars dark on their mesal edges, slightly angled medially

near middle, rounded and divergent posteriorly (Fig. 12). Metanotum unsclerotized. Tergum IX with 1 pair of long setae and 1 pair of short setae. Dorsolateral sclerite on each anal leg rodlike.

Pupa (Fig. 13).—Length \sim 8.0 mm. Structure typical for genus. Posterior rods slightly sinuous, each nearly parallel-sided to 2 small mesal protrusions at $\frac{3}{3}$ length, apical $\frac{1}{3}$ with 3 setae and apex hooked moderately mesad (Fig. 13).

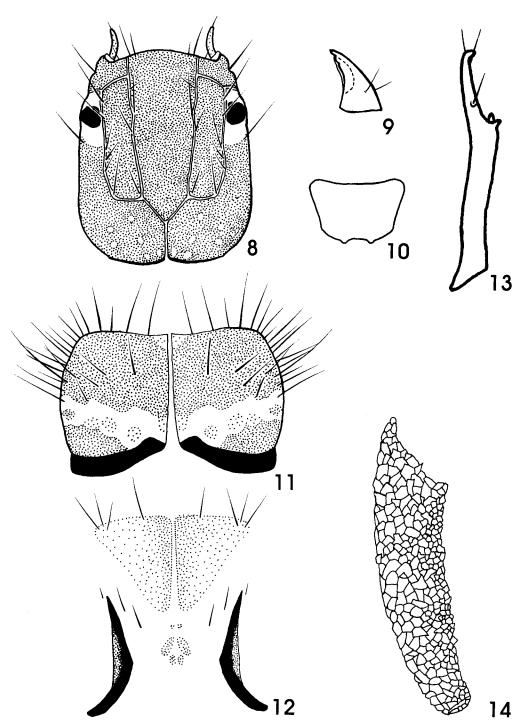
Larval case (Fig. 14).—Length \sim 8.0 mm. Made of sand grains. Tapered and slightly curved (Fig. 14), but not so strongly tapered and curved as for *C. diluta* (Resh 1976, fig. 93). With dorsal cowl anteriorly.

Pupal case.—Similar to larval case, but with anterodorsal cowl extended to allow sealed case to lie parallel to rock surface. Provided with horizontal slit anteriorly and oval opening posteriorly for water movement. Attached to rock substrate with silk anteriorly and posteriorly.

Type material

Holotype.—♂, USA. North Carolina: Montgomery County; Little River, 3 km (air) W Star; private rd upstream of White Oak Cr; nr Reynolds/Mabe Rd; 35.4095°N, 79.8171°W, el. 135 m; larva collected 5.iii.2004; adult reared at 15.0– 16.5°C, emerged 3.iv.2004; Coll. JC Morse, DR Lenat. Pinned. Deposited in the NMNH.

Paratypes.---USA. North Carolina: Same data as holotype except adults emerged 5-7.iv.2004, pinned, 63, 59 (43, 39 NMNH, 23, 29 INHS); same data as holotype, except larvae collected 2.iv.2004 and adults reared 10-15.iv.2004, in 80% ethanol, 6♂, 7♀(2♂, 3♀ NMNH, 2♂, 2♀ INHS, 2♂, 2♀ CUAC); same data as holotype, except preserved 27.iv.2004, in 80% ethanol, 1ð pupa, 2º pupae (NMNH); Little R., x.1989 [North Carolina: Montgomery County, State Route 1340, 5 km (air) W Star, 35.3874°N, 79.8316°W, el. 130 m, Lenat], in 80% ethanol, 5 larvae (CUAC); same, except 22.x.1994, JC Morse, JE Morse, in 80% ethanol, 5 larvae (CUAC); same, except 3.ii.1995, JC Morse, JE Morse, in 80% ethanol, 23 pupae, 19 pupa, 5 larvae (CUAC); same, except 1 larva preserved with head in S. virginicus shell (CUAC); same, except 13.i.1995, JC Morse, Prather, Li, Napolitano, Womble, in 80% ethanol, 8 larvae (4 larvae NMNH, 2 larvae INHS, 2 larvae CUAC).



FIGS 8–14. *Ceraclea joannae*, n. sp., last instar larva, pupa, and larval case. Figs 8–12.—Larva: 8, head, dorsal; 9, right mandible, dorsal; 10, ventral apotome, ventral; 11, pronotum, dorsal; 12, mesonotum, dorsal. Fig. 13.— Pupa, right anal rod, dorsal. Fig. 14.—Larval case, right lateral.

Etymology

Named for JCM's daughter, Joanna, who took an early interest in the species and assisted with its collection several times in the mid 1990s.

Biology

NC DWQ records for the downstream site (at State Route 1340) include 25 October 1989, 28 November 1995, and 8 August 2001. Data suggest a univoltine life cycle: hatching in late summer, growing through autumn and winter, pupating and emerging in early spring. Similarly, "C. diluta populations appear to have only a single larval cohort" (Resh 1976b). However, in contrast to the apparently restricted habitat of C. joannae, "C. diluta is distributed throughout the northeastern and central United States. This species is commonly found in a variety of stream and lake habitats" (Resh 1976b). Furthermore, C. diluta "appears to be able to withstand a wide range of current and oxygen requirements" (Resh 1976b).

Mature larvae captured in December, January, and February often were found with their heads buried deeply into the anterior opening of shells of Somatogyrus virginicus Walker (Gastropoda: Hydrobiidae). It is possible that the caddisflies were merely scavengers on the contents of shells in which snails had died. However, the following circumstantial evidence suggests that the larvae actually were subduing and preying on living snails: 1) Guts of C. joannae larvae contained only unrecognizable organic material, none of which appeared to be plant tissue. 2) The larval mandibles are much more nearly knife-like than the usually palmate form of mandibles in other species of Ceraclea (Resh 1976b), sickle-like, slender, depressed, and sharp apically, with dorsal and ventral edges close together and bearing only vestigial teeth (Fig. 11). 3) Under laboratory stress (recovering in warm water under a microscope after several hours on ice), 2 larvae were observed to cannibalize other, similarly stressed C. joannae larvae; i.e., at least under some conditions, they appear to be predatory. 4) In an aquarium, C. joannae larvae were observed to subdue S. virginicus snails, break through their opercula, and consume them (K. Kennedy, Star, North Carolina, personal communication). Research is needed to confirm the

hypothesis that *C. joannae* attack and consume living *S. virginicus* in nature.

The adults of this new caddisfly species emerge earlier in the spring than most other caddisflies. Despite repeated attempts, no adults were captured in the wild with light traps, Malaise traps, or sweep nets. All adult specimens were obtained by rearing. Because the water temperature of the rearing chamber (15.0–16.5°C) was warmer than in the Little River (~10°C) at the time of rearing, it is likely that adult emergence occurred at the River later than 4 to 7 April.

Discussion

Predatory behavior

Shell-invading predators of freshwater snails are well-known in Coleoptera, Diptera, and Heteroptera (Thorp and Covich 1991). Some species of Ceraclea feed obligatorily or facultatively on freshwater sponges (Resh et al. 1976), but otherwise are not known to feed as predators, preferring instead to function as collectors-gatherers and shredders-herbivores (Merritt and Cummins 1996). If it is demonstrated conclusively that C. joannae larvae attack living snails in nature, it will be the 1st report of such behavior for any caddisfly in North America and only the 2nd report for this behavior in any caddisflies. A common characteristic of these reported hosts of predatory Ceraclea species is their sedentary (sponges) or slow-moving (snails) behavior. Consumption of relatively immobile prey is consistent with creeping habits and the lack of preadaptations among Ceraclea larvae, either for rapid pursue-and-attack behavior or for lie-inwait behavior (JCM, unpublished observations). Future research is needed to understand both the physiological mechanisms that allow some Ceraclea species to ingest sponge spicules and the behavioral or physiological traits that enable others to overcome a hydrobiid operculum. It is also important to discover whether C. joannae requires snail prey to complete its development.

The snail "is widely distributed in piedmont streams from Virginia to Georgia" (R. Dillon, College of Charleston, personal communication). It is ranked in the NatureServe Explorer database (http://www.natureserve.org/explorer/) as G1G2 (imperiled), but Dillon is now convinced that the species "is not as endangered as some have feared" (R. Dillon, personal communication).

Distribution and site quality

Most work in the Little River subbasin has been conducted in July and August, but a more extensive survey of this subbasin (including all major tributaries) was conducted in October and November of 1989. Adjacent subbasins also have been extensively sampled by NC DWQ. Earlier work by the senior author on C. enodis also included widespread collections of caddisflies in this area. In spite of this rather detailed coverage, C. joannae has not been found outside of the small section of the Little River. Ceraclea joannae has been collected from only 2 sites on the Little River (~3 km apart), located upstream and downstream of the confluence with the West Fork of the Little River, in Montgomery County. This segment of the river, just outside Uwharrie National Forest, is designated as "High Quality Water" from the confluence of Suggs Creek to the confluence of Densons Creek. Details can found in the NC DWQ Redbook (http://h2o.enr.state.nc.us/admin/rules/).

This middle portion of the Little River is characterized by long runs, separated by short riffles. High-current riffle areas have growths of riverweed (Podostemum ceratophyllum Micheaux) on the larger rocks. The upstream site is ~12 m wide, whereas the downstream site is ~20 m wide. The most downstream of these sites (SR 1340) is a NC DWQ ambient-monitoring location with daily flow measurements, monthly water chemistry, and summer benthic macroinverterbrate collections every 5 y. These collections have produced an "Excellent" bioclassification since 1985, with apparently stable water quality. More detailed information can be found in the Biological Assessment Unit's Standard Operating Procedure (http://www.esb.enr.state.nc. us/BAUwww/benthossop.pdf). SR 1340 has the highest summer number of taxa of Ephemeroptera, Plecoptera, and Trichoptera (EPT taxa richness; 39-40 taxa) of any site in the North Carolina Piedmont, based on samples in 1985, 1988, and 1996. EPT taxa of interest (uncommon or intolerant, http://www.esb.enr.state.nc.us/BAUwww/ benthossop.pdf) at SR 1340 include Eurylophella enoensis Funk, Leptohyphes sp., Potamanthus sp., Agnetina sp., 3 species of Ceraclea, Lepidostoma sp., Goera sp., Micrasema benneti Ross, and Mystacides sp. Through the years, almost 200 macroinvertebrate taxa (76 EPT taxa) have been collected at SR 1340. This number would be greatly increased with the addition of spring and winter samples. Both the Little River and the nearby Uwharrie River support a diverse mussel community.

Status

Ceraclea joannae was cited by the US Fish and Wildlife Service (1994, p. 59022, as "Ceraclea sp., Lenat's ceraclea") in Category 2, for which further information is needed to justify listing it as endangered or threatened. Our paper provides some of this information, although further work is needed to verify the limited geographic range of this species. The NC DWQ Yadkin River Basin report (NC DWQ 2002) suggested that C. joannae might be a candidate for federal listing as an endangered species. All existing information implies that C. joannae has a very limited distribution and is found in only a few kilometers of the Little River in Montgomery County, North Carolina. Extensive collections by the NC DWQ in October and November 1989 (when larvae were found) did not find this species in other areas of the Little River, in any tributaries of the Little River, or in nearby rivers. Therefore, a single pollution event has the potential to eliminate the entire population. Even within the known range of this species, C. joannae is rare; intensive benthic macroinvertebrate collections by NC DWQ biologists seldom encountered >10 specimens. In addition to its rarity and limited geographic distribution, C. joannae is of interest because of its unusual ecology as a predator on freshwater snails, a feeding strategy previously unknown for caddisflies in North America.

Acknowledgements

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Literature Cited

- CADA, C. A., D. L. GUSTAFSON, B. L. KERANS, AND D. C. RICHARDS. 2005. New Zealand mudsnail in the western U.S.A. Department of Ecology, Montana State University-Bozeman, Bozeman, Montana. (Available from: http://www.esg.montana.edu/ aim/mollusca/nzms/)
- HERRMANN, S. J. 1988. New record and range extension for *Ceraclea resurgens* (Trichoptera: Leptoceridae) from Colorado, with notes on ecological conditions. Entomological News 99:253–259.
- MERRITT, R. W., AND K. W. CUMMINS (editors). 1996. An introduction to the aquatic insects of North America. 3rd edition. Kendall/Hunt Publishing, Dubuque, Iowa.
- MORSE, J. C. 1975. A phylogeny and revision of the caddisfly genus *Ceraclea* (Trichoptera: Leptoceridae). Contributions of the American Entomological Institute 11(2):1–97.
- NC DWQ (NORTH CAROLINA DIVISION OF WATER QUALITY). 2002. Basinwide assessment report, Yadkin River Basin. Environmental Sciences Section, North Carolina Division of Water Quality, Raleigh, North Carolina. (Available from: http:// www.esb.enr.state.nc.us/bar.html)
- RESH, V. H. 1976a. Life cycles of invertebrate predators of freshwater sponge. Pages 299–314 in F. W. Harrison and R. R. Cowden (editors). Aspects of sponge biology. Academic Press, New York.
- RESH, V. H. 1976b. The biology and immature stages of the caddisfly genus *Ceraclea* in eastern North America (Trichoptera: Leptoceridae). Annals of

the Entomological Society of America 69:1039-1061.

- RESH, V. H. 1976c. Life histories of coexisting species of *Ceraclea* caddisflies (Trichoptera: Leptoceridae): the operation of independent functional units in a stream ecosystem. Canadian Entomologist 108: 1303–1318.
- RESH, V. H. 1977. Habitat and substrate influences on population and production dynamics of a stream caddisfly, *Ceraclea ancylus* (Leptoceridae). Freshwater Biology 7:261–277.
- RESH, V. H., J. C. MORSE, AND I. D. WALLACE. 1976. The evolution of the sponge feeding habit in the caddisfly genus *Ceraclea* (Trichoptera: Leptoceridae). Annals of the Entomological Society of America 69:937–941.
- Ross, H. H. 1944. The caddis flies, or Trichoptera, of Illinois. Bulletin of the Illinois Natural History Survey 23:1–326.
- SHAPAS, T. J., AND W. L. HILSENHOFF. 1976. Feeding habits of Wisconsin's predominant lotic Plecoptera, Ephemeroptera, and Trichoptera. Great Lakes Entomologist 9:175–188.
- THORP, J. H., AND A. P. COVICH. 1991. Ecology and classification of North American freshwater invertebrates. Academic Press, San Diego, California.
- US FISH AND WILDLIFE SERVICE. 1994. Endangered and threatened wildlife and plants; animal candidate review for listing as endangered or threatened species: proposed rule. Federal register, part IV. US Department of the Interior 50 CFR part 17 59(219):58982–59028.
- WHITLOCK, H. N., AND J. C. MORSE. 1994. Ceraclea enodis, a new species of sponge-feeding caddisfly (Trichoptera:Leptoceridae) previously misidentified. Journal of the North American Benthological Society 13:580–591.
- WIGGINS, G. B. 1996. Larvae of the North American caddisfly genera (Trichoptera). 2nd edition. University of Toronto Press, Toronto, Ontario.
- WINTERBOURN, M., AND K. MASON. 1983. Freshwater life: streams, ponds, swamps, lakes and rivers. Mobile New Zealand Nature Series. A. H. and A. W. Reed, Wellington, New Zealand.

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