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Ceraclea enodis, A New Species of Sponge-Feeding Caddisfly (Trichoptera:Leptoceridae) Previously Misidentified

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Ceraclea enodis, a new species of sponge-feeding caddisfly (Trichoptera:Leptoceridae) previously misidentified

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Abstract. A new species of Trichoptera, *Ceraclea* (C.) *enodis*, of the *Ceraclea* (C.) *senilis* Group, was discovered in freshwater sponge in the Little River in Montgomery County, North Carolina. Illustrations and descriptions of the male, female, larva, pupa, and larval case are given. Adults resemble those of *C. cancellata* (Betten), the mature larva looks like that of *C. maculata* (Banks), the younger larva may be confused with *C. transversa* (Hagen), and the pupa has anal rods rather like those of *C. spongillovorax* (Resh); but all life history forms can be distinguished reliably from these species by consistent morphological characters and the sponge habitat of late instar larvae. Although few or no larvae and pupae were found in streams near the type locality, adults are reported from Ontario to Georgia to Illinois and Michigan, suggesting that the species may be widespread but local in abundance. *Ceraclea enodis* was found in fairly clean, 1st- to 4th-order streams containing the freshwater sponge *Anheteromeyenia ryderi* Potts (Porifera:Spongillidae) and loose, flat rocks.

Key words: *Ceraclea enodis*, *Anheteromeyenia ryderi*, Leptoceridae, freshwater sponge, Trichoptera, larvae, pupae, adults.

Corbet et al. (1966) noted for *Athripsodes cancellatus* (now *Ceraclea cancellata* [Betten]) in Montreal that "among specimens possessing genitalia typical of this species, we encountered two size-groups". Other workers (e.g., C. R. Parker, US National Park Service, personal communication 1982 and 1994) have noticed the same phenomenon and Ross (1944) mentioned and illustrated considerable variation in the male genitalia of the species.

While conducting studies on the water quality of Little River in Montgomery County, North Carolina, D. R. Lenat and staff of the North Carolina Division of Environmental Management (DEM) discovered larvae of a species of *Ceraclea* that keyed to *C.* (C.) *transversa* (Hagen), but whose head color pattern, setation, and other features did not correspond well with illustrations and descriptions published by Resh (1976a) and Unzicker et al. (1982), suggesting that the species may be new to science. Furthermore, the larvae were found in only two locations, so there was concern that the species also was potentially endangered. To obtain additional information on this species, we were asked by the North Carolina Wildlife Resources Commission and the United States Fish and Wildlife Service to provide a status survey of known and suspected habitats for the species.

The purposes of this contribution are to describe a new species of *Ceraclea* that previously has been misidentified, to distinguish its larva and pupa and male and female from those of similar species, and to comment on its trophic habits and microhabitat.

Methods

Qualitative benthic collections were made in 1993 on 20 February, 13 April, 8 May, 15 May, 21 May, and 8–9 June, from the Little River, Montgomery County, North Carolina, at County Route 1349 using kick screens, dip nets, and visual inspection of substrate. An ultraviolet light (UVL) trap with a 15-watt BL bulb was operated on 13 April, 8 May, 15 May, and 8 June 1993 at the same location. On 8 June, a floating emergence trap and a Malaise trap were operated at this site. In addition to the original site, 22 other sites along Little River and adjacent

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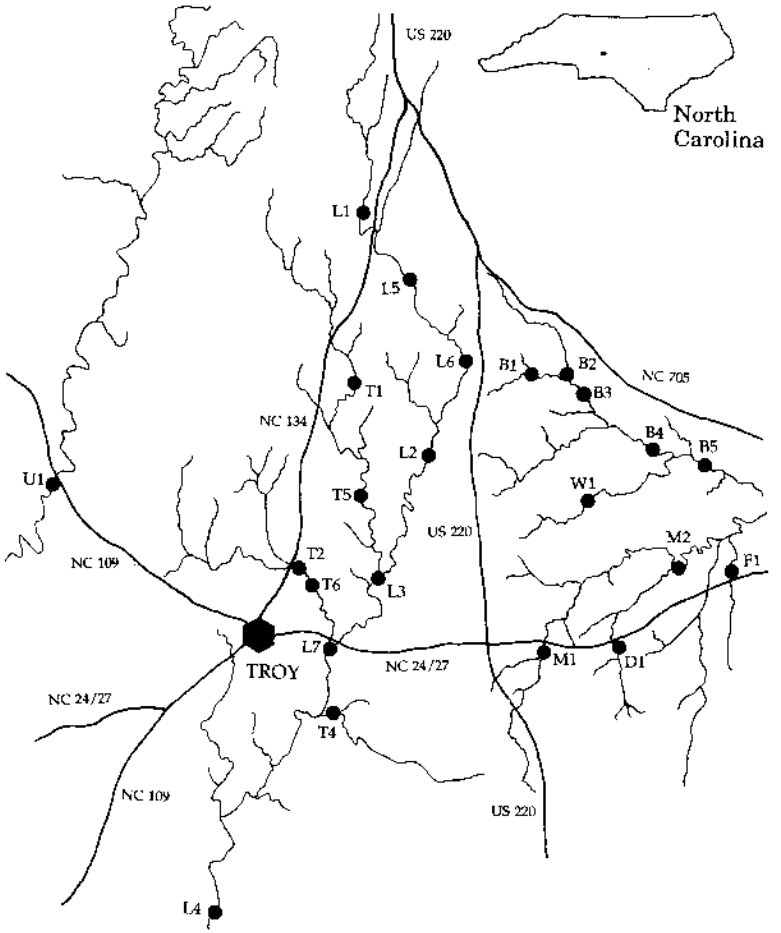


MAP 1. Locations near Troy, North Carolina, explored for *Ceraclea* (C.) *enodis* n. sp. (Trichoptera:Leptoceridae) and *Anheteromeyenia ryderi* (Potts) (Porifera:Spongillidae). Site numbers correspond with those in Table 1. B = Bear Creek, D = Dry Creek, F = Buffalo Creek, L = Little River, M = Mill Creek, T1 and T5 = West Fork of Little River, T2 and T6 = Densons Creek, T4 = Bridgers Creek, U = Uwharrie River, W = Wolf Creek.

streams and tributaries in Montgomery, Moore, and Randolph counties were scouted for specimens of the new species on 8–9 June and 15 June 1993 (Map 1, Table 1).

Adult specimens were compared with specimens named as "*Ceraclea* (*C.*) *cancellata* (Betten)" now in the collections of the Illinois Natural History Survey (INHS), the Clemson University Arthropod Collection (CUAC), the Royal Ontario Museum (ROM), and the University of Michigan (MU), and also with the type specimens of *C. cancellata* in the New York State Museum. Immature stages were compared with specimens in the CUAC. Type specimens of the new species are deposited in the United States National Museum of Natural History (USNM) and the institutions cited above. The voucher sample of sponge is in the collection of Dr. Michael Poirrier at the University of New Orleans.

Abdomens of several male and female specimens were cleared of muscle in an aqueous KOH solution over heat, followed by manual removal of tracheae and digestive tract, leaving an unobstructed view of the genitalia. Cleared abdomens were examined and illustrated under a Wild M5A dissecting microscope with a 10 × 10 ocular grid at magnifications of 12–200×.

TABLE 1. Ambient chemical data from the Little River at Route 1340, Montgomery County, North Carolina (DEM site L3), 1988–1992 (North Carolina DEM, 1992).

Variable	Observations	Median	Maximum	Minimum
DO (mg/L)	56	9.5	12.7	7.6
pH (SU)	56	7.2	8.0	6.1
Conductivity (μMho)	56	57.5	83.0	43.0
Total P (mg/L)	3	0.11	0.13	0.04
NH_4 (mg/L)	3	0.03	0.07	0.01
NH_2/NH_3 (mg/L)	3	0.38	0.39	0.04
Turbidity (NTU)	18	7	38	2.5
Hardness (mg/L)	18	18.5	35	13
Total residue (mg/L)	18	70.5	110	3
Total suspended residue (mg/L)[a]	18	5	13	1
Cu (μg/L)[a]	18	6	6	2

[a] Detectable levels were measured for only 15 of the 18 total suspended residue (mg/L) observations and for only 3 of the 18 Cu (μg/L) observations.

Several larval and pupal specimens of the new species were collected on 21 May 1993 and reared to adults in aerated containers of stream water with screened cups similar to those described by Edmunds et al. (1976, fig. 13).

Ceraclea (*C.*) *enodis*, new species

Description

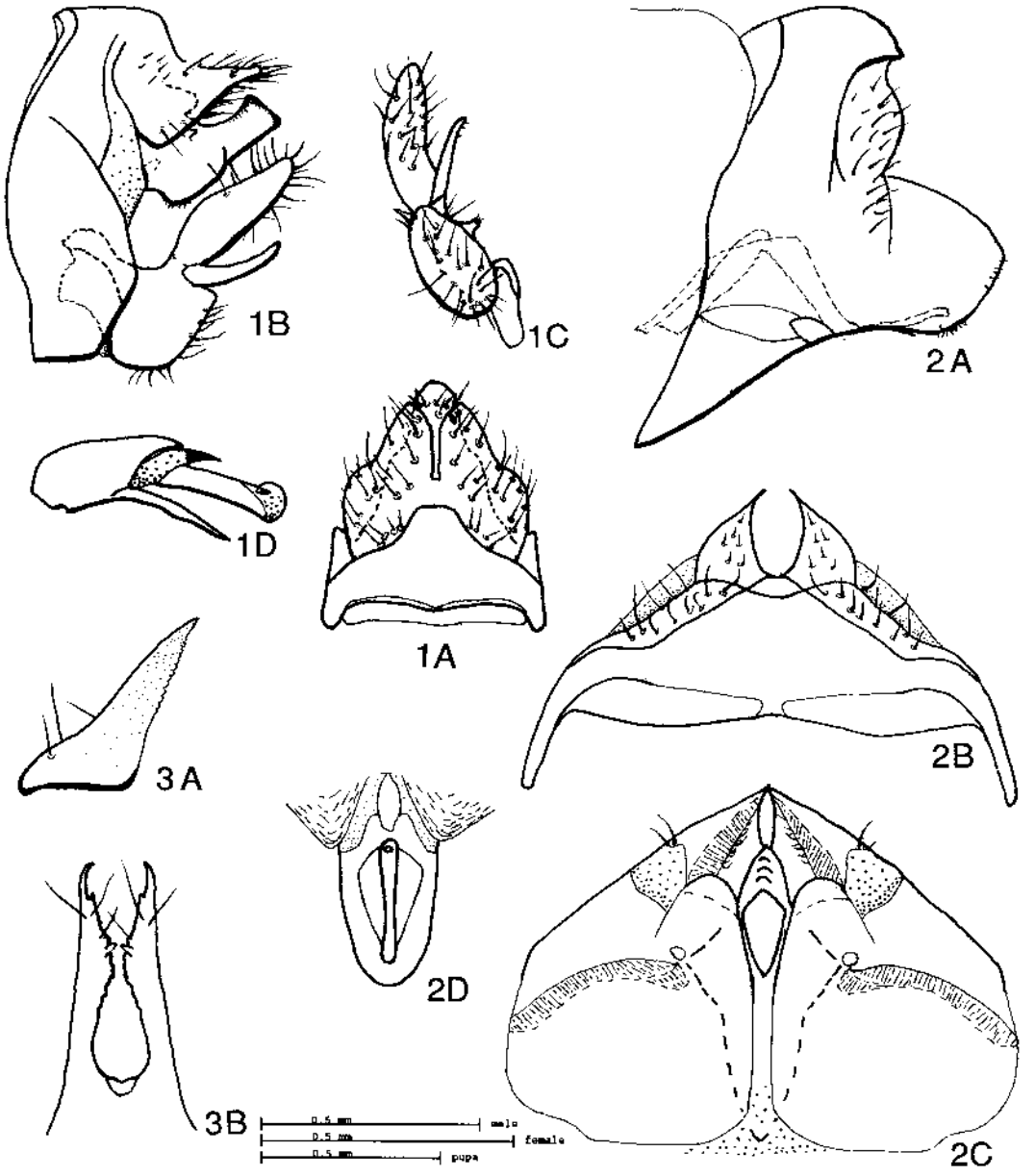
The species is new to science. Young larvae key to *Ceraclea transversa*, because of a lack of parafrontal lines, and mature larvae key to *C.* (*C.*) *maculata* (Banks) after parafrontal lines become fully expressed (Resh 1976a, Unzicker et al. 1982). Adults are identified as *C. cancellata* using the keys of Ross (1944) and Morse (1975). The pupa also varies from those illustrated by Resh (1976a). These various ontogenetic stages are recognizable by the following characteristics.

Adult color and size.—General structure conforming with that of genus *Ceraclea* (Morse 1975, Morse and Wallace 1976). Head and thorax rust orange; abdominal sclerites light brown. Palps, prothoracic, and mesothoracic legs dark brown, and metathoracic legs light brown. Apical half of each of basal segments of antennal flagellum dark brown; each tarsal segment darker brown apically. Forewings in alcohol uniformly brown except stigmata darker and arculus and stem of MP vein pale. Male 9.2–12.7 mm long (from front of head to tip of folded wings, mean = 10.9, $n = 16$) and female 8.4–12.0 mm (mean = 10.1, $n = 19$).

Male genitalia.—Tergum IX rounded apically (Fig. 1A), each pleuron IX with diagonal internal ridge, sternum short (Fig. 1B). Preanal appendages subtriangular in dorsal and lateral views (Figs. 1A, B), narrowly separated on midline for two-thirds their length. Tergum X somewhat rectangular and apically truncate in lateral view with numerous, tiny setae dorsally and on rounded, slightly differentiated and projecting, ventrolateral edges; rounded basomesal protuberance; and pair of subdorsal spines near base (Fig. 1B). Subanal plate small, hidden beneath tergum X. Inferior appendages each with base relatively short, smoothly rounded ventrally without hint of ventrobasal lobe; subapicodorsal lobe 1.3 times length of base; mesal ridge short and projecting mesad in caudal view (Fig. 1C), about two-thirds distance from ventral margin of base; harpago slender, with tiny subapicomesal setae. Phallus with pair of stout dorsal paramere spines one-third length of phallus and with ventral projection of phallobase three-fourths length of phallus (Fig. 1D).

Female genitalia.—Segment IX short, with tergum convex in lateral view (Fig. 2A). Preanal appendages short (Fig. 2B), tall, setateous, fused with terga IX and X. Gonopod plates separated in apical one-third by small sclerite; apicolateral grooves not angled, scarcely curved, each ending submesally near relatively deep pit (Fig. 2C). Spermathecal sclerite relatively narrow, slightly tapering to evenly rounded anterior end (Fig. 2D).

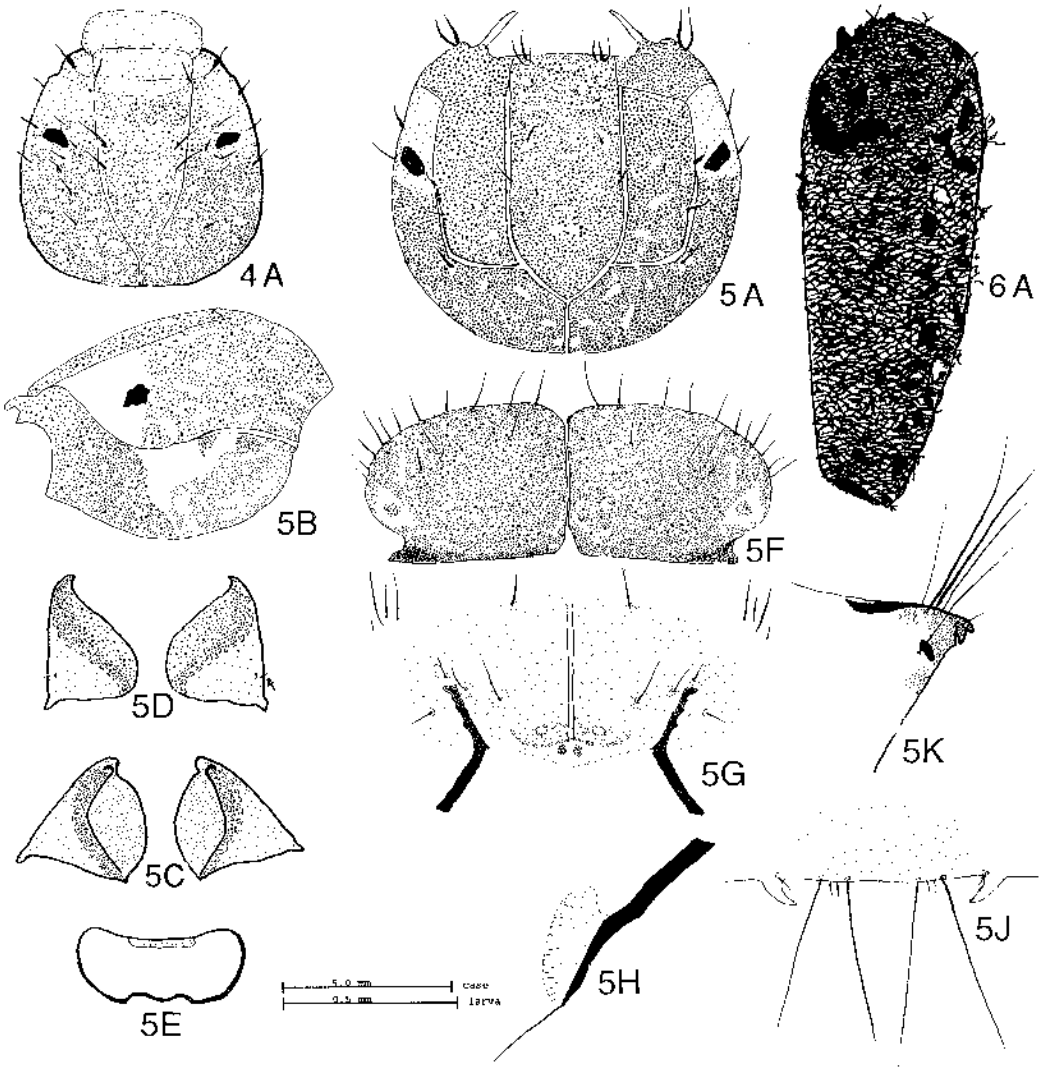
Pupa.—Mandibles each with 13 visible teeth on mesal margin (Fig. 3A); three basolateral se-



FIGS. 1–3. Adult genitalia and pupa of *Ceraclea* (C.) *enodis* n. sp. Figure 1. Male genitalia: A.—dorsal view; B.—left lateral view; C.—inferior appendage, caudal view; D.—phallus, left lateral view. Figure 2. Female genitalia: A.—left lateral view; B.—dorsal view; C.—ventral view; D.—spermathecal sclerite, ventral view. Figure 3. Pupa: A.—left mandible, dorsal view; B.—anal processes, dorsal view.

tae. Anal rods straight, mesal edge broadened near middle (Fig. 3B), each rod with three subapical setae and one "tooth" about two-thirds distance from base.

Larva.—Head brown with distinct pattern of light spots (Figs. 4A, 5A); parafrontal lines absent in early instars through antepenultimate larval instar (Fig. 4A, number of instars unknown), present in last two larval instars (Fig. 5A); antennae of last instar each nearly as long



FIGS. 4–6. Larvae and case of *Ceraclea* (*C.*) *enodis* n. sp. Figure 4. Antepenultimate instar larva: A.—head, dorsal view. Figure 5. Ultimate instar larva: A.—head dorsal view; B.—head, left lateral view; C.—mandibles, ventral view; D.—mandibles, dorsal view; E.—ventral apotome of head, ventral view; F.—pronotum, dorsal view; G.—mesonotum, dorsal view; H.—sclerite of left abdominal pleuron 1, left lateral view; J.—abdominal tergum IX, dorsal view; K.—left anal proleg, left lateral view. Figure 6. Case of ultimate instar larva: A.—ventral view.

as anterior edge of frons; 12 pairs of dorsal primary setae; width of frontoclypeus along anterior margin equal to width at posterior origin of parafrontal sutures; each gena with two dark spots in white region, several white spots in dark area posterolaterally (Fig. 5B); mandibles each with small tooth visible in ventral view (Fig. 5C), no basolateral setae in ventral view, tiny basolateral seta scarcely visible at 200× magnification in dorsal view with small pit beside it (Fig. 5D); ventral apotome with pair of fairly shallow posterior excisions (Fig. 5E). Pronotum with one large dark spot or small dark figure "8" in white region on each side of pronotum (Fig. 5F); fore trochantin with one dorsal seta. Mesonotum with relatively large sclero-

tized region (Fig. 5G); no setae along mid-dorsal groove; two distinct pits posteriorly near midline; sa1 each with one seta; sa2 each with four setae; sharply angled mesonotal bars dark posteriorly, slightly lighter anteriorly. Abdomen with sclerotized bar on each side of abdominal segment I (Fig. 5H) typical of genus (Morse and Wallace 1976); tergite IX with three small pairs and two long pairs of setae (Fig. 5J); each anal claw small and with single dorsal accessory spine; dark sclerotized bar rod-like on dorsal edge of each anal proleg (Fig. 5K); four dorsal setae on anal proleg, one seta anterior of dark ventrolateral sclerite of anal proleg, one small seta on light colored ventral sclerite of anal proleg, and one small seta on anal claw.

Case.—Entirely of silk and debris; sponge spicules incorporated mostly in anterior half (Fig. 6A).

Diagnosis

The male of *Ceraclea enodis* keys to *C. cancellata* in the work by Ross (1944), but can be distinguished from it by its generally smaller size (9.2–12.7 mm; *C. cancellata* males are 9.7–14.9 mm [mean = 12.6, $n = 16$]) and by the shorter and more rounded base of each inferior appendage of *C. enodis* (Fig. 1A), which contrasts with the sinuous caudal margin in lateral view in *C. cancellata* (Ross 1944, fig. 791A on right; Morse 1975, fig. 48A). The two paramere spines, visible in left lateral view, are also slightly longer and more pronounced in *C. enodis* (Fig. 1D) than in *C. cancellata* (Morse 1975, fig. 48D).

The females of *C. enodis* are very similar to those of *C. cancellata* and *C. maculata*. These three species have similarly curved apicolateral grooves of the gonopod plate (Fig. 2C; Ross 1944, figs. 797A, 798A). However, females of *C. enodis* are generally larger than *C. maculata* females (*C. maculata* are 5.7–11.2 mm long [mean = 7.9, $n = 17$]). (The *C. cancellata* females are 9.2–11.8 mm long [mean = 10.4, $n = 11$], about the same size as *C. enodis*.) The spermathecal sclerite in *C. enodis* is relatively narrow and tapers slightly to a rounded anterior end (Fig. 2D), whereas in *C. cancellata* the anterior end comes more to a point (Ross 1944, fig. 798A) and in *C. maculata* it is broader at the posterior end and slightly incised before coming to a point at the anterior end (Ross 1944, fig. 797A, as "*Athripsodes transversus*"). There is also a relatively deep pit near the submesal end of each apicolateral groove on the gonopod plate of *C. enodis* that is much shallower in *C. cancellata* and non-existent in *C. transversa*.

The pupal mandibles look similar to those of *C. cancellata* (Resh 1976a, fig. 47), but the teeth are more clearly defined, the curves are much smoother, and there are three setae present on the mandibles of *C. enodis* (Fig. 3A) that are not shown by Resh for mandibles of *C. cancellata*. The anal rods of the pupa are like those of *C. spongillovorax* (Resh), differing in that *C. enodis* only has one "tooth" (Fig. 3B) and *C. spongillovorax* has two (Resh 1976a, fig. 49).

The larva of *Ceraclea enodis* will key to *Ceraclea maculata* when parafrontal lines are present on the head and to *Ceraclea transversa* when they are absent (Resh 1976a, Unzicker et al. 1982). However, it can be distinguished from these species by the following diagnostic characteristics. In the last two instars, after parafrontal lines have developed, the longer antennae of *Ceraclea enodis* (Fig. 5A) distinguish it from *C. maculata* (Resh 1976a, fig. 6A). *Ceraclea enodis* has a white region on each side of the head containing two dark spots (Fig. 5H); *C. maculata* has a similar white region, but with three dark spots (Resh 1976a, fig. 6B). The white head region of *C. spongillovorax* head has only one dark spot (Resh 1976a, fig. 7B). There are about 11 setae along the anterior edge of each half of the pronotum of *C. enodis* (Fig. 5B) and about 14 on *C. maculata* (Resh 1976a, fig. 6A). Also, the white region with one dark spot or figure "8" on each side of the pronotum of *C. enodis* (Fig. 5B) is absent in *C. maculata* (Resh 1976a, fig. 6A). Importantly, larvae of no other *Ceraclea* species are known to have the two distinct transverse, submesal grooves present on the mesonotum, visible in at least the last three instars of *C. enodis* (Fig. 5C). Also, larvae of no other *Ceraclea* species are known with such an extensively sclerotized submesal region on the mesonotum (Fig. 5C; cf. *C. transversa* [Resh 1976a, fig. 3] and *C. maculata* [Resh 1976a, fig. 6A]). The larval mandibles of *C. enodis* (Figs. 5E, F) have fewer teeth than those of *C. transversa* and *C. maculata* (Resh 1976a, figs. 29, 37 respectively). The mandibles of *C. spongillovorax* (Resh 1976a, fig. 36) closely resemble those of *C. enodis* (Figs. 5E, F), each having only one ventral tooth; but the tooth is larger on each *C. spongillovorax* mandible. In all three of these previously described species, a

long seta is visible both in ventral and dorsal views, but in *C. enodis* there is only a tiny seta slightly posterior to a small pit that is visible only in dorsal view under 100–200× magnification (Fig. 5E). The ventral apotome of the head of *C. transversa* is much more nearly rectangular and has a single, broad, posterior emargination (Resh 1976a, fig. 60); the ventral apotome of *C. maculata* has the same oval shape as that of *C. enodis* (Fig. 5G), but the two emarginations of *C. maculata* are not as well defined (Resh 1976a, fig. 63).

This new species may be the same species as the smaller form of *C. cancellata* seen by other workers. The *C. enodis* male closely resembles the left illustration of Ross's (1944) figure 791A for "*Athripsodes cancellatus*", (the right illustration for figure 791A more closely resembles the holotype of *C. cancellata*, but not completely [Morse 1975]). Ross's discussion for this species indicated that "considerable variation occurs in both tenth tergite and claspers". All material of *Ceraclea cancellata* now at the Illinois Natural History Survey, where Ross worked in 1944, was examined in our study. Three females were *C. enodis*, but there were no males matching either Ross's left illustration (1944, fig. 791A) or *C. enodis* (Fig. 1) in this material. Whether Ross actually had specimens of *C. enodis* before him in 1944 cannot be confirmed from his illustration; indeed, his drawing of tergum X appears very different from that of *C. enodis* specimens we studied. Further variation is seen in the illustrations by Marshall and Larson (1982) for *Ceraclea cancellata* from Newfoundland. This suggests that (1) there may be additional cryptic species in a *Ceraclea cancellata* Complex, and (2) at least some of the published locality records for widespread *C. cancellata*, *C. maculata*, and *C. transversa* may be in error. A thorough re-examination of this species complex, perhaps through the use of modern techniques to compare allozyme or molecular characteristics, seems to be particularly warranted. Similar suggestions have been made recently for other complexes among Trichoptera now identified as *Diplectrona modesta* (Banks) (Morse and Barr 1990) and *Oecetis inconspicua* (Walker) (Floyd 1993, 1994).

Type material

Holotype.—♂, NORTH CAROLINA: Montgomery County, Little River at Rt. 1349, 15 km (9.3 mi) northeast of Troy [North Carolina DEM site L2], 8 June 1993, UVL, Morse and Whitlock (USNM).

Paratypes.—Same collection data as holotype, 7♂, 10♀, 1 larva, 1 pupa (USNM); 7♂, 8♀, 1 larva, 1 pupa (CUAC); 7♂, 7♀, 1 larva, 1 pupa (ROM).

Other material examined

CONNECTICUT: Windham County, Putnam, UVL, 1–15 July 1961, Klots, 3♂ (ROM). GEORGIA: Baker County, Ichuway River, 10 May 1955, Mohr, 2♂, (INHS). GEORGIA/SOUTH CAROLINA: Rabun/Oconee counties, Chattooga River at Rt. 28, 28 June 1991, Floyd and Nichols, 1♂ and 2♀ (CUAC). ILLINOIS: Elgin, Botanical Garden, 6 June 1939, Burks and Riegel, 5♀ (INHS). MICHIGAN: Houghton County, N. Br. Otter River, 11–27 July 1949, F.A. Leonard, 7♂ and 17♀ (MU). NORTH CAROLINA: Transylvania and Jackson counties, Whitewater River, 22 July 1993, Morse, 1♂ (CUAC). Wake County, Little River at NC 96, April 1982, Lenat, 2 larvae and 1 case (CUAC). ONTARIO: Nipissing District, Samuel de Champlain Prov. Pk., Rt. 17 west of Mattawa, 17 June 1971, 2♀ (ROM). Muskoka District, Fraserburg, 23 July 1967, Kohalmi, 1♂ (ROM). Durham County, Kendal, 19 July 1957, Wiggins, 1♀ (ROM). Peel County, Churchville, Credit River, 14 July 1952, Wiggins, 1♂ (ROM). SOUTH CAROLINA: Aiken County, Savannah River Plant, Upper Three Runs Creek, 1 July 1984, Morse, 7♀ (CUAC).

Etymology

The name "enodis" is derived from a Latin word meaning "smooth", referring to the bases of the male inferior appendages which are smooth, without bumps and curves.

Habitat

We found *Ceraclea enodis* only in fairly clean, 1st- to 4th-order streams containing the freshwater sponge *Anheteromeyenia ryderi* Potts (Porifera:Spongillidae) and plenty of loose, flat rock in either shallow pools or riffles, where it occurs more commonly in areas of rapid flow than in placid water. The region of the Little River where *A. ryderi* and *C. enodis* were common (Map 1, Table 1, stations L2 and L3) was the only region of the river consistently classified as "Ex-

cellent" by the North Carolina DEM (1989a). The lower station in this stream segment (L3) is the only location studied that is part of the North Carolina Benthic Macroinvertebrate Ambient Network (BMAN); it has the highest taxa richness of any Piedmont site sampled in North Carolina (North Carolina DEM 1989a and unpublished data). The L3 site drains an area of 276 km^2 (106 mi^2) and has an average flow of 3.1 m^3/s (110 cfs).

In 1989, the DEM described the L2 and L3 sites as follows: width (m) 15 and 20, respectively; average and maximum depths (m) 0.3 and 0.7 (L2) and 0.6 and 1.5+ (L3); canopy 60% and 30%, respectively; aufwuchs abundant, bank erosion slight, substrate 35% boulders, 25% rubble, 20% gravel, 20% sand, only a trace of silt (North Carolina DEM 1989b). Ambient chemical data for the L3 site for 1981–1988 did not indicate any water quality problems nor any appreciable between-year changes in water quality (Table 1).

The sponge colonies and their late-instar caddisflies invariably were found on the under sides of stones. The sponge seemed capable of withstanding a modest amount of fine sediment, but no specimens were found in areas experiencing heavy sedimentation. The habitat of early instar larvae of *C. enodis* is unknown.

Biology

Ceraclea enodis probably has a univoltine, synchronous life history as reported for other *Ceraclea* species by Resh (1976a, 1976b) since most larvae were in the same instar on each given collection date. According to Resh (1976a, 1976b), *Ceraclea* females deposit their egg masses directly on the surface of the water and the larvae hatch approximately 1–3 wk later; five instars and a pupal stage are completed, with the adult emerging the following spring; larvae make cases throughout their development, beginning in the first instar.

In previously identified sponge-feeding species, the digestive tracts were filled with sponge spicules (Roback 1968). The gut of a *C. enodis* specimen collected at the type locality contained many spicules, verifying that at least some larvae of *C. enodis* feed on whole pieces of freshwater sponge and also incorporate pieces in the anterior part of their cases. This behavior is unlike that of the sister species, *C. cancellata*, which is not found in patches of freshwater sponge (Resh 1974b, 1976a). This trophic differentiation between the two species, with the larva of *C. enodis* being a spongefeeder and the larva of *C. cancellata* a detritus feeder, is additional justification for recognizing *C. enodis* as a distinct species.

Freshwater sponge can be ingested in pieces by only a few engulfing predator arthropods such as crayfish, especially *Orconectes* (Pennak 1989), larvae of the chironomids *Demeijerea* species and *Xenochironomus xenolabis* (Keiffer) (Roback 1963, Hudson et al. 1990), and larvae of the caddisfly genus *Ceraclea* (Roback 1968, Lehmkuhl 1970, Resh 1976a, 1976b, Resh et al. 1976). The discovery of another species of the *Ceraclea senilis* Group associated with freshwater sponge is particularly noteworthy. Resh (1974b, 1976a, 1976b) and Resh et al. (1976) reported that larvae of two other species of the Group, *C. senilis* and *C. spongillovorax*, are facultative feeders on freshwater sponge. Also within the genus, each member of the *C. fulva* Group (Morse 1975) whose biology is known is an obligate spongefeeder; *C. nigronervosa* (Retzius, *C. nigronervosa* Group) may be an obligate spongefeeder (Solem and Resh 1981); and at least one species in each of the subgenera *Athripsodina* and *Pseudoleptocerus* are at least facultative spongefeeders (Resh et al. 1976). Because late instar larvae of *Ceraclea* (*C.*) *enodis* were found only in patches of freshwater sponge, either in furrows created by their feeding activities or beneath a surface layer which they had undercut, it is possible that sponge is a requirement for complete development of the species. If so, it is the only species of the *C. senilis* Group with an obligate sponge-feeding requirement.

Distribution

From the material examined, it appears that *Ceraclea enodis* has been misidentified as *C. cancellata*, *C. maculata*, or *C. transversa* and actually has a much wider range than originally believed by the North Carolina DEM staff. Specimens of *Ceraclea enodis* identified in our study come from numerous sites along the eastern coast, as far north and south as Ontario and Georgia, and as far west as Michigan and Illinois. The sponge host, *Anheteromeyenia ryderi*, is distributed in central and eastern North America, Belize, Ireland, and Scotland (Poirrier

TABLE 2. Locations in Montgomery, Moore, and Randolph counties, North Carolina, explored for sponges (*Anheteromeyenia ryderi* [Potts]) and larvae and pupae of *Ceraclea* (C.) *enodis*, n. sp. Sites correspond with those shown in Map 1. Abundance definitions: common = ≥10 specimens, scarce = 4–9 specimens, rare = 1–3 specimens, and none = no specimens.

Site	Road crossing	Stream	*A. ryderi* abundance	*C. enodis* abundance
L1	Rt. 1127	Little River	scarce	none
L2	Rt. 1349	Little River	common	common
L3	Rt. 1340	Little River	common	scarce
L4	Rt. 1565	Little River	none	none
L5	Rt. 1119	Little River	rare	none
L6	Rt. 1354	Little River	scarce	scarce
L7	Rts. 24, 27	Little River	rare	none
T1	Rt. 1311	W. Fk. Little R.	scarce	none
T2	Rt. 134	Densons Creek	scarce	none
T4	Rt. 1519	Bridgers Creek	rare	none
T5	Rt. 1340	W. Fk. Little R.	common	common
T6	Rt. 1323	Densons Creek	scarce	rare
B1	Rt. 1412	Bear Creek	none	none
B2	Rt. 1411	Bear Creek	none	none
B3	Rt. 1409	Bear Creek	common	common
B4	Rt. 1428	Bear Creek	common	common
B5	Rt. 1425	Bear Creek	rare	none
W1	Rt. 1403	Wolf Creek	scarce	rare
M1	Rts. 24, 27	Mill Creek	none	none
M2	Rt. 1275	Mill Creek	scarce	rare
D1	Rts. 24, 27	Dry Creek	common	rare
F1	Rts. 24, 27	Buffalo Creek	none	none
U1	Rt. 1153	Uwharrie River	scarce	none

1977). Therefore, voucher specimens of *Ceraclea* (C.) *senilis* Group species and *C. transversa* from previous ecological studies in eastern North America should be reviewed to verify original identifications.

Although the range of the species is broad, individual populations appear to be scattered and localized. Efforts to collect additional sponge and larvae from 22 other locations within 30 km of the type locality were generally less successful with increasing distance from that site (Map 1, Table 2). In some instances, sponge was present (scarce or rare) where no specimens of *C. enodis* were found (Table 2).

Status

Currently, the new species is listed in Category 2 of the United States federal endangered species list (Department of the Interior, Fish and Wildlife Service 1991). Category 2 designates "taxa for which information now in the possession of the [US Fish and Wildlife] Service indicates that proposing to list as endangered or threatened is possibly appropriate, but for which conclusive data on biological vulnerability and threat are not currently available to support proposed rules". Based on our status survey, we think that this particular caddisfly species is not threatened or endangered. Rather, it is considerably more widespread than originally suspected, and has simply been misidentified in previous studies. Sedimentation or other ecological changes that affect the vigor and production of the sponge host may have a directly correlated effect on its caddisfly predator, however, wherever they occur. Thus, management of water courses to maintain viable sponge colonies should provide effective measures for protecting populations of the caddisfly.

Phylogeny

Morse (1974, 1975) considered the presence of an elongate basoventral lobe of the male inferior appendage a homologue of the *Ceraclea*

(C.) *senilis* Group. Despite lacking this lobe, *Ceraclea enodis* is probably a member of the *C.* (C.) *senilis* Group as indicated by possession of other homologues internested hierarchically within the Group. The following homologues of the male genitalia (unless otherwise indicated) were presented by Morse (1974) as evidence for the monophyletic groups shown:

1. Tergum X with pair of ear-like basolateral lobes (Morse 1975, figs. 49A, 50A, 52A, 53A, 54A, 55A, 56A)—*C. nigronervosa* Group.
2. Inferior appendages each with elongate basoventral lobe (Morse 1975, figs. 44A, 45A, 46A, 47A)—*C. senilis* Group.
3. Tergum X apicolateral margins deeply excavated (Morse 1975, figs. 44A, 45A)—*C. punctata* and *C. uvalo*.
4. Harpago narrow (Figs. 1A, C; Resh 1974a, figs. 1, 4; Morse 1975, figs. 46A, 46C, 47A, 47C, 48A, 48C)—*C. spongillovorax, C. maculata, C. senilis, C. cancellata, C. enodis.*
5. Body and wings light color—*C. spongillovorax, C. maculata, C. senilis, C. cancellata, C. enodis.*
6. Larval frontoclypeus parallel-sided (New homologue; Resh 1976a, figs. 6A, 7A, 8; Wallace 1981, fig. 20)—*C. spongillovorax, C. maculata, C. senilis, C. cancellata, C. enodis.*
7. Phallic paramere spines absent (Morse 1975, fig. 46D)—*C. spongillovorax, C. maculata.*
8. Tergum X with differentiated, parallel, rounded, ventrolateral ridge on each side (Fig. 1A; Morse 1975, figs. 47A, 48A)—*C. senilis, C. cancellata, C. enodis.*
9. Inferior appendage mesal ridge setose, knoblike (Fig. 1C; Morse 1975, figs. 47C, 48C)—*C. senilis, C. cancellata, C. enodis.*

To these we add the following homologues supporting the monophyly of *C. cancellata* and *C. enodis*:

10. Tergum X truncate in lateral view (Fig. 1A; Morse 1975, fig. 48A).
11. Tergum X with pair of basal subdorsal spines (Fig. 1A; Morse 1975, fig. 48A).
12. Phallic paramere spines short, broad, with little basal sclerotization (Fig. 1D; Morse 1975, fig. 48D).
13. Inferior appendage basoventral lobe inconspicuous (Figs. 1A, C; Morse 1975, figs. 48A, 48C).

Notice that this last homologue (13) is a reversal from the Group homologue, a character presumably lost in the evolution of the ancestor of these latter two species. These characters were analyzed by MacClade version 3.01 (Maddison and Maddison 1992), with the resulting phylogeny provided in Figure 7. In this analysis, the tree length (S) was 12, the Consistency Index (CI) was 0.92, the Retention Index (RI) was 0.94, and the Rescaled Consistency Index (RC) was 0.86.

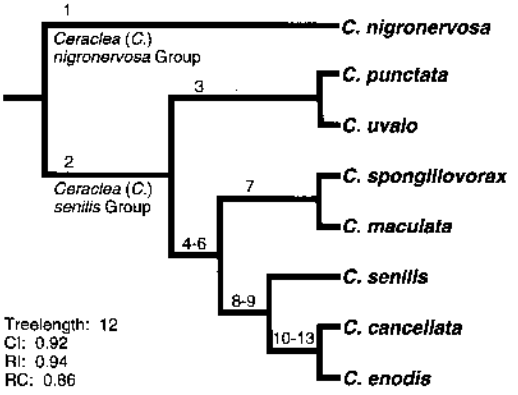


FIG. 7. Phylogeny of the species of the *Ceraclea* (C.) *senilis* Group (Morse 1975) (Trichoptera:Leptoceridae). The outgroup is *C. nigronervosa* of the *C. nigronervosa* Group (Morse 1975). Homologue (=synapomorphy) numbers correspond with those in the text.

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