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Vincent H. Resh

John C. Morse

Ian D. Wallace

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The Evolution of the Sponge Feeding Habit in the Caddisfly Genus *Ceraclea* (Trichoptera: Leptoceridae)[1]

VINCENT H. RESH[2]
Water Resources Laboratory, University of Louisville, Louisville, KY
JOHN C. MORSE[3]
Department of Entomology, University of Georgia, Athens, GA
IAN D. WALLACE[4]
Department of Zoology, University of Newcastle Upon Tyne, Newcastle, Great Britain

ABSTRACT

A phylogeny is proposed for 11 species of *Ceraclea* caddisflies which feed on freshwater sponge during the larval stage of their life cycle. Based on this evolutionary scheme, further probable sponge feeders are postulated. Some morphological differences of the sponge feeders are described. The obligate sponge feeders are morphologically and ecologically different from other species of the genus which may feed on sponge when it is available or when other food sources are scarce, and from the other species of *Ceraclea* which appear never to eat sponge.

Systematic studies of caddisflies have been based primarily on adult morphological characteristics. Potential evolutionary evidence that could be obtained from interspecific comparisons of larval morphology and ecology has been neglected because the immature and adult stages of most species have not been associated. This study attempts to draw together taxonomic, ecological, and morphological information obtained from detailed studies of the immature and adult stages of sponge feeding caddisflies in order to develop a phylogenetic history of this unusual feeding habit.

Studies of caddisfly feeding habits have indicated a wide range of potential food sources (Slack 1930, Cummins 1973). Of particular interest have been several European and North American references to aquatic insects ingesting particles of freshwater sponges (Porifera: Spongillidae). Most observations of sponge feeding by aquatic insects have been made on caddisflies of the family Leptoceridae; but larvae of spongilla flies (Neuroptera: Sisyridae) (Brown 1952, Parfin and Gurney 1956), and larval chironomids *Xenochironomus xenolabris* (Keiffer) (Roback 1963, 1968, Wundsch 1943, 1952), and *Demeijerea rufipes* (L.) (Maitland 1967, Wundsch 1943, 1952), also utilize this food source.

The presence of sharp, indigestible spicules may be a deterrent to most potential predators of freshwater sponge. Spongilla fly larvae avoid these obstacles by piercing the sponge and sucking its fluids. The gut contents of the caddisflies and midges include spicules, which indicates that these larvae do ingest the sponge; but how these sharp particles are kept from damaging the digestive tract, is unknown. The evolution of the morphological structures of *Ceraclea* larvae, upon which this paper is based, seems to have occurred independently of their food habits and makes no apparent contribution to the ability of these species to ingest the spicules.

Leptoceridae systematics have been recently revised by the separation of the large genus *Athripsodes* into 2 genera, *Athripsodes* Billberg and *Ceraclea* Stephens (Morse and Wallace 1976). Although most references to leptocerid sponge feeding mention the genus *Athripsodes*, the sponge feeding caddisflies actually belong to the genus *Ceraclea*. European and Japanese workers have been able to identify and discuss sponge feeding at the specific level, e.g., *Ceraclea fulva* (Rambur) by Siltala (1907) (as *Leptocerus fulvus*) and Lepneva (1966) (as *Athripsodes fulvus*); *C. senilis* (Burmeister) by Lepneva (1966) (as *A. senilis*) and Siltala (1907) and Nielsen (1948) (as *L. senilis*); *C. nigronervosa* (Retzius) by Nielsen (1948) (as *L. nigronervosus*) and Maitland (1966, 1967) (as *A. nigronervosus*); *C. albimacula* (Rambur) by Satija (1964) (as *A. alboguttatus*); and *C. biwaensis* by Tsuda and Kuwayama (1954) (as *L. biwaensis*). However, most references to sponge feeding by North American caddisflies have been at the generic or family level.

The earliest description of sponge feeding by a North American species was by Krecker (1920), who described a caddisfly larva he assigned to the family Rhyacophilidae feeding on *Spongilla fragilis* Leidy in Lake Erie. From the description of the larval case, this species is in the leptocerid genus *Ceraclea*, and is probably *C. resurgens* (Walker). In addition, Ross (1944) and Roback (1968) reported that larvae described as *Athripsodes* sp. *a* were found in association with freshwater sponge. Through rearing, sp. *a* has been associated with the adult of *C. transversa* (Hagen) (=*A. angusta* (Banks)). Other references to *Ceraclea* sponge feeding in North America incude Lehmkuhl's (1970) reference to an *Athripsodes* sp. (which has been identified as *C. resurgens*), and Roback's (1968) report on *Athripsodes* nr *transversa*, which is probably *C. spongillovorax* (Resh).

In addition to feeding on freshwater sponge as evidenced by the presence of sponge spicules in the

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[2] Present Address: Div. of Entomol. and Parasitol., Univ. of Calif., Berkeley, CA 94720.

[3] Present Address: Dept. of Entomol. and Eco. Zool., Clemson Univ., Clemson, SC 29631.

[4] Present Address: Merseyside Co., Museum, William Brown St., Liverpool 1, Great Britain.

gut (Roback 1968, Lehmkuhl 1970), *Ceraclea* caddisflies also incorporate sponge spicules into their cases; often living pieces of sponge are attached to the outside of the case and appear to become established there. Clady (1969) reported *Limnephilus* larvae (Limnephilidae) incorporating pieces of living sponge into their cases, but this is probably an exception to normal limnephilid case-making behavior.

Also, Hickin (1967) included early accounts of the polycentropodid caddisfly, *Ecnomus tenellus* Rambur, occurring in freshwater sponge. However, these records probably represent a coincidental association, and this is not the usual larval habitat of this species. Most likely, the association of caddisflies with freshwater sponge is limited to the monophyletic genus *Ceraclea*.

The broad outlines of the evolution within the leptocerid tribe Athripsodini (which includes *Ceraclea*) have been discussed by Morse and Wallace (1976), while details of evolutionary development of adults within *Ceraclea* have been elaborated by Morse (1975). The following discussion further substantiates those hypotheses and the proposed phylogeny of the sponge feeding habit in the genus *Ceraclea* presented in Fig. 1.

As inferred by ex-group comparisons (Ross 1974) with closely related leptocerids, the larva of the ancestral species of Athripsodini probably had a long head with simple frontal lines, a triangular gular sclerite (submental apotome), and long antennae in the last instar. Its mesonotum bore a pair of sclerotized bars of essentially one dark color. The abdomen had no pleural gills on the 2nd segment and had 2 pairs of long setae on the ninth tergum. The larva built a slightly curved, rather cylindrical case of sand or plant material, and probably did not feed on sponges.

Morse and Wallace (1976) discussed 6 apomorphic morphological character states of the adults and larvae of the ancestor of *Ceraclea* to suggest the monophyly of the genus. This ancestor of the genus *Ceraclea* may have been the 1st species able to ingest whole particles of freshwater sponges. This is indicated not only by numerous observations and published reports for living species of the subgenus *Ceraclea* but by observations of a sponge feeding species in each of the other 2 subgenera, *Arthripsodina Kimmins and Pseudoleptocerus* Ulmer (K.M.F. Scott, pers. com.). Since no other caddisflies employ this habit, and since at least some members of each of the major lines in these genera eat sponge particles, the hypothesis with the least number of assumptions is that the generic ancestor was the original species to acquire this peculiar ability. Certain of its descendants retain the habit while numerous others rarely, if ever, use it.

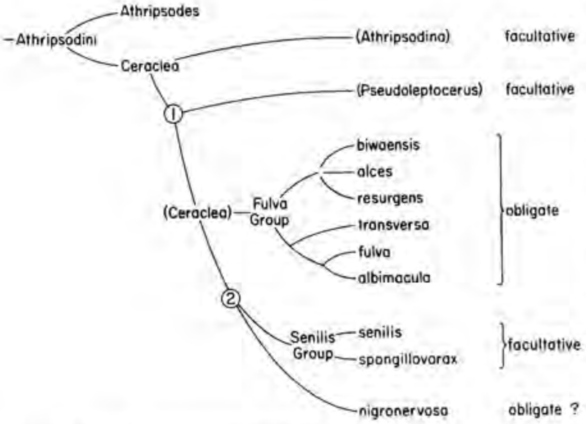


FIG. 1.—A proposed phylogeny of the sponge feeding habit in the genus *Ceraclea*.

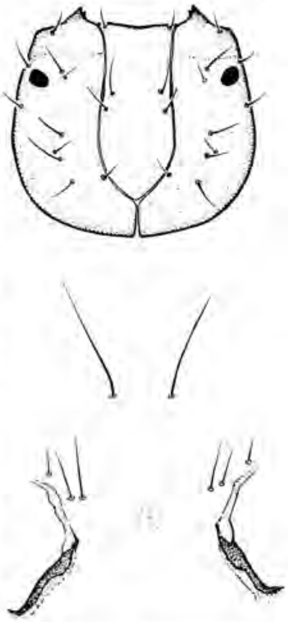


FIG. 2.—*Ceraclea transversa* (Hagen), head and mesonotum.

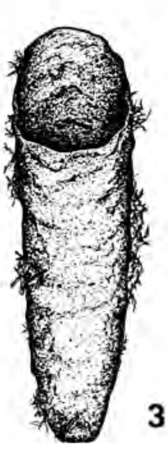


FIG. 3.—*Ceraclea transversa* (Hagen), larval case.

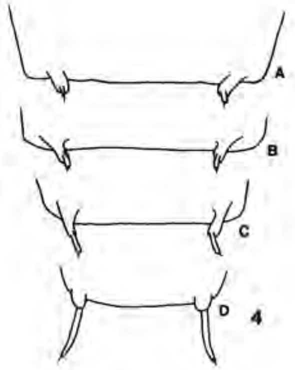
All members of the Fulva Group of Morse (1975) (subgenus *Ceraclea*), for which larval habits are known, feed on freshwater sponge and appear to require it to complete their life cycles. These include *C. biwaensis* (Tsuda and Kuwayama), *C. alces* (Ross), *C. resurgens* (Walker), *C. transversa* (Hagen), *C. fulva* (Rambur), and *C. albimacula* (Rambur). Probably an early ancestor of this group restricted its feeding habits exclusively to freshwater sponge. Several other modifications apparently took place in the larval stage of this ancestor, including (1) a loss of the lines demarcating the parafrontal regions on the head (Fig. 2, cf. Ross 1944, Fig. 763–8), (2) the development of a dichromatic condition of the mesonotal bars, which suggests differences in the underlying musculature (Fig. 2), (3) the loss of one pair of long setae on the 9th abdominal tergum, (4) the evolution of a case-making behavior in which the larva attached almost no sand grains to the secreted silk matrix (Fig. 3), and (5) a reduction in the length of the last instar antennae (Fig. 4). Further evidence supporting an inference for monophyly of the Fulva Group of *Ceraclea* is shown in Table 1.

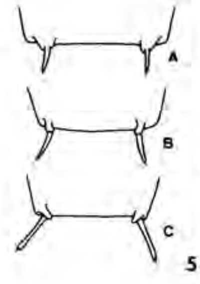
The antennae of larval *Ceraclea* arise from anteriorly directed conical projections of the head capsule. Those of non-sponge feeders, such as *C. dissimilis* (Fig. 5), reach clearly beyond the projection in all

Table 1.—Evidence supporting inferences for monophyly of *Ceraclea* ancestors (Figure 1).

Ancestor	Sister Group	Ontogenetic Stage or Sex	Character	Ancestral State	References* & Figure #	Derived State	References* & Figure #
Ceraclea	*Athripsodes*	adult	midcranial sulcus	present	M 21	absent	M 22
			4th maxillary palp segment	completely sclerotized	M 23	flexible	M 24
		male	10th tergum	divided	M 30	fused	M 29B 33B-108B
		larva	parafrontal lines	absent	MW 4 L 702A,711A 715A	present	MW 24 L 718A,727A 741A
			head capsule (length/width)	long (c. 1.25)	MW 4 L 702A,711A 715A	broad (c. 1.00)	MW 24 L 718A,727A 732A,741A
			gular sclerite (submental apotome)	triangular	MW 5 L 702B,711B 715B	trapezoidal	MW 25 L 718C,727B 732B,741B
1	(*Athripsodina*)	male	ventral apex of phallobase	short	M 31A, 63D-108D	long	M 33D 44D-62D
			subanal plate	absent	M 63A-108A	present	M 29,47A 62A,*et al*
(*Ceraclea*)	(*Pseudoleptocerus*)	male	dorsal phallic parameres	present	M 31A,B 60D-62D	absent	M 33D-57D
Fulva Group	2	male	apex of 10th tergite	undivided	M 43B-57B	3-pronged	M 33B-42B 33E-42E
			mesal ridge of coxopodite	narrow	M 43C-57C	broad	M 33C-42C R 784B,785B
			harpago	simple	M 43C-57C	with mesal triangular projection	M 33C-42C R 784B,785B
			apical lobe of coxopodite	nearly straight	R 774A-783A 786A-791A M 43A-57A	bent caudad near base	M 33A-42A R 784A,785A
		female	internal vaginal structure	narrow	R 792B-796B 802B-807B	with broad lateral expansions	R 800B,801B
		larva	parafrontal lines	present	L 741A MW 24 R 763-768	absent	L 732A RMW 2
			mesonotal bars	monochromatic	MW 26 R 763-765	dichromatic	RMW 2
			long 9th tergal setae	4	R 770	2	MW 28
			case construction	with sand	MW 31, 32 R 809	almost no sand	L 736 RMW 3
			antennae of last instar	long	MW 24 RMW 5A	short	L 732A
2	Fulva Group	female	median 9th sternal plate	absent	R 800A	present	R 802A,807A
Senilis Group	Nigronervosa Group	male	ventral lobe of coxopodite	short and broad	M 49A-57A R 776A-778A 786A-787A	long and narrow	M 44A-47A R 788A,790A

* L = Lepneva (1966), M = Morse (1975), MW = Morse and Wallace (1976), R = Ross (1944), RMW = this paper.





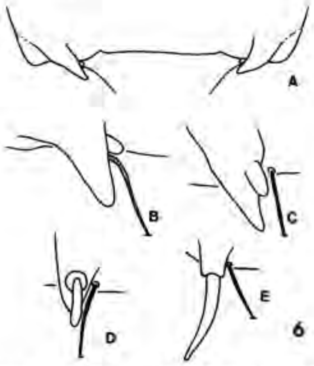


FIG. 4.—*Ceraclea senilis* (Burmeister), anterior dorsal part of the head capsule with antennae; A. final instar; B. penultimate instar; C. antepenultimate instar; D. pre-antepenultimate instar.

FIG. 5.—*Ceraclea dissimilis* (Stephens), anterior dorsal part of head capsule with antennae. A. final instar; B. antepenultimate instar; C. pre-antepenultimate instar.

FIG. 6.—*Ceraclea nigronervosa* (Retzius). A. anterior dorsal part of the head capsule with antennae, final instar; B. detail of right antennae, final instar; C. detail of right antennae, penultimate instar; D. detail of right antennae, antepenultimate instar; E. detail of right antennae, pre-antepenultimate instar.

larval instars. The second instars of sponge feeders similarly have a strongly projecting sensillum, but its growth does not keep pace with that of the rest of the head capsule, and by the final instar the small antenna only reaches slightly beyond the tip of the projection. *C. senilis* is a typical example of this (Fig. 4). In the extreme case of *C. nigronervosa*, the actual size of the sensillum (which lacks the distal seta found in other species), is reduced at each moult. By the final instar it is very small, protruding out of a depression on the inner face of the conical projection which completely overshadows it (Fig. 6).

The phylogenetic study by Morse (1975) suggests that other species whose larval habits are not yet known, including *C. cama* (Flint), *C. vertreesi* (Denning), *C. alboguttata* (Hagen), and *C. latahensis* (Smith), are also members of the Fulva Group. It is probable that the last three species and *cama*, which represents the oldest extant line in the group, are also sponge feeders.

In the Senilis Group of Morse, the larva of *C. senilis* (Burmeister) attaches almost no sand grains to the case silk matrix. The entire strength of the case is derived from this matrix without any need for extraneous support material. The final instar antennae of *C. senilis* larvae are very short as well. The larva of *C. spongillovorax* also has relatively short antennae but still incorporates a few sand grains and sponge spicules in its case. In most respects, however, the larvae and adults of these 2 species have not diverged markedly in appearance from those of other non-Fulva Group species. Lepneva (1966) mentioned 2 races of *C. senilis*, one which feeds on sponge and another which feeds on algae. This reference to alga feeding may be incorrect and refer to another species since populations of *C. senilis* examined in Britain have only been found feeding on freshwater sponge.

The ecology and particular case-making habits of the larva of *C. nigronervosa* (Retzius) of the Nigronervosa Group, have been discussed by Nielsen (1948) and Maitland (1966, 1967). The sulci outlining the parafrontal areas of this species are replaced by a wide white space that divides the dark median part from the lateral head area and extends from the periocular region to the occipital foramen. The larval features are not markedly different from other non-sponge feeding species of *Ceraclea*, with the exception of the antennae which are very short in the final instar (Fig. 6). The case is made of particularly thick secretion and has bands of sand grains incorporated into the exterior of the matrix, running from the posterior to anterior ends of the case. The larvae of British populations of this species have not been found away from sponge, indicating that it may be an obligate sponge feeder.

The genus *Ceraclea* includes non-sponge feeding species whose larvae differ markedly in morphology and ecological habits from those characteristic of the sponge feeders (Resh 1976). Future studies of the sponge feeding species should concentrate on morphological developments that have enabled certain species of *Ceraclea* to utilize this peculiar food source and the structural and physiological changes in the silk glands that have enabled the case to be constructed entirely of silk secretion. The genus *Ceraclea* is worldwide in distribution, and species of both feeding types are commonly encountered by hydrobiologists and aquatic entomologists. Natural history observations, coupled with detailed morphological studies, will elucidate further the phylogenetic relationships and implications of this unusual feeding behavior.

The goal of this study has been to combine taxonomic, morphological, and ecological information into a composite phylogenetic study of the sponge feeding habit in the caddisfly genus *Ceraclea*. The result of this effort has been the extension of a descriptive systematic approach into one emphasizing predictive ecology. Our hypothesis is that the 4 species of the Fulva Group, whose feeding habits have not been observed, will eventually be recognized as obligate "predators" of sponge and that other species of the genus may be found to use this food source as obligate or facultative feeders.

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