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The Larva and Pupa of the Caddisfly Genus *Setodes* in North America (Trichoptera: Leptoceridae)

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Among the leptocerid caddisflies of North America there are many species which are not known in the larval stage. All but one of the genera, however, contain a sufficient number of species for which larva-pupa-adult associations have been established to permit the construction of fairly reliable generic keys to the immature stages, such as those by Ross (1944, 1959). The genus *Setodes* is the exception. For none of the Nearctic species have immature and mature forms been associated. In Ross' keys to the genera of leptocerid larvae, specimens characterized chiefly by strongly developed sclerotized plates on the caudal face of the anal prolegs were tentatively assigned to *Setodes*, because these unusual larvae clearly do not fit readily into any of the other North American genera.

Descriptions of *Setodes* larvae in Europe in recent years have left little doubt that Ross' tentative assignment was correct: *Setodes hungarica* Ulmer (Botosaneanu, 1959); *Setodes punctata* Fabricius (Botosaneanu and Sykora, 1963). Larvae of both species were associated with mature pupae, and both have the sclerotized plates on the caudal face of the anal prolegs as illustrated by Ross (*op. cit.*). The larva of a third European species was described by Murgoci (1959); the identity is not clear, but Boto-

saneanu and Sykora (1963) suggested that this is the larva of *S. argentipunctella* McLachlan. Hickin (1967) provided a description of the larva of *S. argentipunctella*, but details of the plates of the anal prolegs were not given. Illustrations of the larva of a Japanese species assigned to *Setodes* by Akagi (1957) show that similar larval characteristics occur in the Asian fauna.

Knowledge concerning the comparative morphology of larval and pupal stages of *Setodes* from various parts of the world has, then, been steadily accumulating, although few observations have been offered on the biology of the group. For the North American fauna nothing has been added since the original tentative allocation of these larvae to *Setodes* by Ross in 1944. In North America, six species are known, and only from the adult stage. These are confined to the eastern half of the continent, extending as far west as Oklahoma: *Setodes incerta* (Walker), *S. stehri* (Ross), *S. oxapia* (Ross), *S. guttata* (Banks), *S. oligia* (Ross), and *S. epicampes* Edwards.

In the summer of 1969, larvae possessing the sclerotized anal plates were collected in Michigan (by D.M.). Rearing them to the adult stage established that the species was *Setodes incerta* (Walker). Additional observations were made in the summer of 1970.

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Based upon that association, this paper offers the first detailed information on the morphology of the larva and pupa of this genus in North America (by G.B.W.), and on the behaviour of the larva as well (by D.M.). Diagnostic genitalic characters for the female of *S. incerta* were not previously known and are illustrated. The larva of another species of *Setodes* from South Carolina is briefly characterized, although no specific association has yet been established for it.

The larvae of *S. incerta* were collected in the Ocqueoc River, near the northern tip of Michigan's lower peninsula, in a region of strong current, upstream from Ocqueoc Falls. The initial collection was made by examining rocks taken from a depth of less than 2 feet. Laboratory observations indicated that the larvae were burrowers, and in subsequent collecting, screening of sand from the lec of rocks provided a larger number of larvae in a given time.

After transportation to a laboratory at the University of Michigan Biological Station, the animals were maintained in individual stender dishes, mostly without aeration, at room temperature (20–25°C). Plant material was present in all containers and the water was changed every 2 or 3 days.

Enchytraeid worms were provided daily as food until the animals closed their cases for pupation. At that time the cases were transferred to clean stender dishes until the larval sclerites were extruded by the pupa. The sclerites were then placed in labelled vials and the pupal cases transferred to rearing cages for capture of adults upon emergence. Some of the insects were preserved in the larval and pupal stages to provide adequate material for morphological study.

Larval behaviour was observed daily, and some aspects were recorded on motion picture film, using Kodak Double-X negative film in a Bolex H-16 Rex 3 camera. With the aid of extension tubes on a Switar 25 mm lens, magnifications of 1 to 2.4 were obtained. The illustrations of larval behaviour (Fig. 15) were printed from this film.

Specimens are deposited in the collections of the Department of Entomology and Invertebrate Zoology, Royal Ontario Museum.

Setodes incerta (Walker)

Leptocerus incertus Walker 1852, p. 71.

Setodes incerta McLachlan 1863, p. 158, 163.

Setodes vernalis Betten 1934, p. 277, pl. 36, figs. 7–9.

Setodes incerta Betten and Mosely 1940, p. 69, fig. 33.

Setodes incerta Ross 1944, p. 302, figs. 737 (*S. vernalis*), 872.

LARVA—(Figs. 1, 2, 8–11). Full-grown larva 5–6 mm in length, uniformly whitish in overall colour, sclerotized portions pale yellow, affording little contrast in colour with the unsclerotized portions. Head without contrasting colour pattern, and with several structures typical for the Mystacidini: gular sclerite rectangular, extending posterad to occipital foramen; antennae long and stout; labrum with only primary setae; mandibles with teeth arranged around edge of a central cavity, but with a patch of stout spines in this central area on left mandible; maxillary palpi not projecting conspicuously beyond anterior edge of labrum. Thorax as illustrated; trochantin of fore legs rather truncate anteriorly, as in *Mystacides*; hind legs without dense row of swimming hairs, tibia of hind legs with constriction and secondary suture, apparently dividing it into two equal parts as in *Mystacides* and *Trianenodes*; metasternum with transverse row of about 17 dark setae, terminating on each side in a patch of about a dozen setae. Abdomen with pair of single posteroventral gills on segments II to VII inclusive; first abdominal segment with lateral humps roughened with tiny spines, and bearing a short sclerotized bar, line of 6–8 dark setae between lateral and dorsal humps, sternum with curved line of about a dozen dark setae; segment VIII with row of about 30 small sclerotized points along each side; lateral line of very short setae on segments III to VII inclusive; segment IX with sclerotized, but lightly pigmented, plate bearing 4–5 pairs of moderate to stout setae along posterior margin; caudal face of anal prolegs with sclerotized concave plate on each side of anal opening, each plate extending into a median ventral lobe and an ovoid lobe arising near base of anal claw, all plates armed around margins with

Figures 1–3, *Setodes incerta*, larva
 1. Head and thorax, dorsal view. 2a. Larva, lateral view. 2b. Right metathoracic leg, lateral view. 2c. Trochantin and base of prothoracic leg, lateral view. 2d. Lateral hump of first abdominal segment, lateral view. 2e. Sclerotized plates on base of anal prolegs, caudal view. 2f. Claw of anal proleg. 3a. Larval case. 3b. Posterior opening of larval case.

short spines; anal claws each with two small dorsal accessory hooks.

Case (Fig. 3) of rock fragments, slightly curved, but with little taper; posterior end open, diameter of opening not reduced with silk or rocks; length, for full-grown larvae, 6–7 mm, scarcely longer than larva itself.

PUPA—(Figs. 4, 5, 6). Length 6 mm. Head unlike that in *Mystacides* and *Triaenodes* in having prominent tubercle arising between bases of antennae, and with two additional tubercles on each side between base of antenna and mandible; labrum with patches of stout setae and pair of thorny protuberances; mandibles well sclerotized, much as in *Mystacides* (Yamamoto and Wiggins, 1964, fig. 10), blade fairly straight, with single row of minute teeth extending full length, blade not curved as in *Triaenodes*. Abdominal sclerites different from *Mystacides* and *Triaenodes* in that one additional segment, VII, bears a pair of hooked plates, and plate 5P is narrower and bears only three hooks, in contrast to 6–10 in the other genera; anal appendages with prominent dorsal and ventral spiny lobes, roughly midway between origin and apex, seen to best advantage in lateral view; proximal portion before these lobes longer in male than in female.

Case closed at both ends with rock fragments and silk, leaving a round central hole, lip of the hole somewhat raised (Fig. 7); length 5–7 mm.

ADULTS—The diagnostic features of the female genitalia of *S. incerta* are illustrated here for the first time (Fig. 14). They show a clear generic affinity in structure to those of the other three North American species for which the female is known: *S. stehri* (Ross) (Ross, 1941, fig. 80); *S. oligia* (Ross) (Ross, 1944, fig. 871); *S. epicampes* Edwards (Edwards, 1956, figs. 4, 5). Comparison of the diagnostic details in these figures indicates that the female of *S. incerta* is distinguished by having segment x truncate posteriorly in lateral view. Segment x of *S. incerta* also bears a deep median notch, and is subtended at the base on segment ix by a pair of raised ridges. These characters are not, however, illustrated for the other species. A noteworthy structural detail of

S. incerta is the pair of sclerotized, invaginated pockets in the sternum of segment VIII, presumably to receive the ends of the long claspers of the male during copulation. Similar sclerotized pockets are shown for *S. stehri* (Ross, 1941, fig. 80) but it is not clear whether or not these structures occur in the other two species.

The diagnostic characteristics of the male genitalia in *S. incerta* were described and illustrated previously (Betten and Mosely, 1940, p. 69, fig. 33; Ross, 1944, fig. 872), but are included here (Fig. 13) to make the present paper a more useful reference for identification of *S. incerta* in its larval, pupal, and adult stages.

MATERIAL EXAMINED—MICHIGAN, Ocqueoc River, Presque Isle Co., 20 June 1969, 12 larvae; 1 July 1969, many larvae, reared and preserved as pupae and adults; all collected by D. Merrill.

Setodes sp.

LARVA—Larvae of this genus were also collected from the Chattooga River in South Carolina. These larvae were burrowing in accumulations of sand lying in the lee of large rocks in the riffle areas of the river. Depth of water was about 1 foot. The collection comprises two types of larvae: one having a light yellowish head with no distinguishing colour pattern, as in *S. incerta*; the other having a dark brown head, with some indistinct lighter patches and some darker patches on the pronotum (Fig. 12). No other distinctions among these two larval types and the larva of *S. incerta* from Michigan were found. All have similar sclerotized plates on the anal prolegs, and a subdivided hind tibia. The light-coloured larvae may be conspecific with those of *S. incerta*, but the dark-headed larvae very likely belong to a different species.

The larval cases of both types of South Carolina specimens are also of sand grains, but many of these are black and have a flattened flaky texture. The posterior opening is the full diameter of the case as in *S. incerta*.

MATERIAL EXAMINED—SOUTH CAROLINA, Chattooga River at Burrell's Ford Campground, near Route 107, Oconee Co., 18–19

Figures 4–11, *Setodes incerta*
 4a. Head of pupa, dorsal view. 4b. Head of pupa, lateral view. 5a. Mandibles of pupa, dorsal view. 5b. Labrum of pupa, dorsal view. 6a. Abdomen of pupa with sclerites enlarged, dorsal view. 6b. Anal appendage of pupa, dorsal view. 6c. Anal appendage of pupa, mesal view. 7. Pupal case, anterior opening. 8. Labrum of larva, dorsal view. 9. Head of larva, ventral view. 10. Labium and maxillae of larva, ventral view. 11. Mandibles of larva, dorsal view.

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Figure 12, *Setodes* sp.
Head and thorax of larva, dorsal view.

May 1970, many larvae, G. B. Wiggins and T. Yamamoto.

Cases and Case-building—The slightly curved cylindrical cases of the larvae were constructed of fine, flattened sand grains closely fitted together. The size of the grains was variable, but rarely exceeded 0.5 mm in their largest dimension. The majority of the grains measured 0.3 mm or less. The outside diameters of the larval cases averaged 1 mm, and the lengths, at the time of collection, ranged from 3 to 7 mm. Pupal cases ranged in length from 5 to 7 mm, and were just sufficient to enclose the insect.

Five larvae were evicted from their cases and were placed in stender dishes with sand, filamentous algae, and *Utricularia*. As the naked larvae crawled on the sand, they applied silk to the grains, and thus formed masses of sand grains loosely bound to-

gether. Within a short time, each larva burrowed into the sand, making further observations impossible. By the following day each larva had a new case, the definitive portion of which was 3 to 5 mm in length. Two of the cases had a few millimeters of loosely organized sand at the posterior end.

One can infer that as the larvae burrowed they continued to apply silk to the grains around them, forming a rough provisional case in this manner. As this tube was lengthened to encompass more of the body, the building pattern progressed to greater selectivity of grains and more careful attachment, ultimately giving rise to the definitive case, which was essentially identical to the larva's original case. The progression from provisional to definitive building has been described elsewhere for several species of caddis larvae (Bierens de Haan, 1922; Gorter, 1929; Fankhauser and Reik, 1935; Copeland and Crowell, 1937; Neilsen, 1942, 1948).

On only one occasion was a larva observed in the process of adding a sand grain to the rim of its case. A high degree of selectivity on the part of the larva was indicated by the large number of sand grains that were picked up, tested in several positions against the rim, and finally rejected before a suitable grain was found.

Burrowing—The five larvae that had built new cases continued to burrow in the sand even after their case-building activity had apparently ceased. When five additional larvae were provided with sand in their containers, they too proceeded to burrow with their cases. Daily observations on the 10 larvae indicated a strong tendency to position themselves with one end of the case buried in the sand and the other end nearly flush with the surface (Fig. 15a). This position was seen in 88 out of 112 observations. In a majority of the observations, the case position differed from one day to the next, indicating some degree of mobility even under these unnatural conditions.

Occasionally at the time of an observation, a larva had apparently reversed its position in the case and was beginning to burrow, its posterior end clearly visible

through the opening of the case at the surface of the sand substrate. During some of these observations it was possible to insert a worm or another small object through the opening. Invariably the larva moved backward rapidly and ejected the intruding object.

It is possible that the open posterior end of the case is associated with the animal's burrowing habits, permitting reversal of larval direction without the necessity of reversing the case. The unusual sclerotization at the larva's posterior end appears to compensate for the vulnerability resulting from the open-ended case.

Adaptations to Current—Because of its obvious protective advantage, burrowing may also be an adaptation for survival in rapid currents. Another behaviour pattern observed in larvae of *S. incerta* that may be an adaptation to the habitat was a tendency to fasten both ends of the case to the substrate when they were not actively moving about. This was particularly noted among larvae in containers without sand. Larvae of many species fasten the anterior ends of their cases to the substrate when at rest (Lestage, 1921), but attachment of both ends generally indicates the approach of pupation. In *S. incerta*, attachment at both ends appears

Figures 13-14, *Setodes incerta*
 13a. Male genitalia, lateral view. 13b. Male genitalia, dorsal view. 13c. Male genitalia, ventral view. 14a. Female genitalia (abdominal segments in Roman numerals) lateral view. 14b. Female genitalia, dorsal view. 14c. Female genitalia, ventral view.

to provide additional protection against being swept away by the current. This behaviour by the larvae of *Setodes* probably is unusual because most other caddis larvae inhabiting streams and building portable cases cannot extend the head from either end of the case.

Camouflage Behaviour—Frequently a larva was observed holding a large grain of sand (hereafter called a rock) over the mouth of the case. Sometimes the rock was loosely attached to the rim of the case and was seized by the larva when there was a change in the light pattern or a disturbance in the water. This practice appeared to provide excellent camouflage as long as the animal remained motionless. If a worm was placed near the larva under these circumstances, the larva continued to hold the rock, sometimes manipulating it, until the worm was within reach. Then it released the rock and seized the worm (Fig. 15 c, d, e).

This behaviour was seen in 10 out of 12 larvae observed daily during July 1970. In 80 observations, 42 were made under conditions where camouflage behaviour might occur, i.e. one end of the case flush with the surface and the animal facing upward. Camouflage behaviour actually occurred during 24 of these observations. In eight others, the larva was manipulating a rock but did not hold it still.

It is possible that this behaviour is derived from the manipulation of sand grains for purposes of case-building, but the large size of the grain and its loose attachment to the rim of the case suggest that it is a special adaptation of the more primitive behaviour pattern.

Feeding—Filamentous algae (*Spirogyra*) from the collecting site were provided initially until the supply was depleted. The principal food provided for the larvae was encytraeid worms. The larvae seized and ate the worms without hesitation, even when the worm was nearly as large as the larva and writhed violently in the larva's grasp.

Usually while the animal was feeding, its respiratory current was reversed, propelled anteriorly instead of posteriorly. This phenomenon has been observed in several spe-

cies of caddis larvae, and is currently under investigation by one of us (D.M.).

No attempt was made to examine stomach contents of freshly caught larvae, although fecal pellets in the containers were collected and examined the first morning after the capture of the larvae. Most of the contents were filamentous algae and other plant material, but several minute head capsules of insects were also found. Thus, it seems that these larvae are omnivorous. The avidity with which they seized and ate the worms leaves little doubt that animal food is an important component of their diet.

Cannibalism sometimes occurred when larvae were kept in the same container. Experiments on a small number of larvae indicated that this tendency can be suppressed by provision of an adequate food supply.

General Conclusions—1. There seems to be general agreement in the morphological details of larvae and pupae among the North American, European, and Asian species of *Setodes* for which these stages are known. In the larvae differences exist at the specific level in the colour pattern of the head and thorax, the shape of the sclerotized plates of the anal prolegs, and the presence or absence of abdominal gills.

2. Ulmer (1955), in discussing the interrelationships of the genera comprising the Mystacinini, assigned *Setodes* to a group in which the posterior tibia of the larva is not secondarily divided, and in which the dark, sclerotized ridge on the lateral hump of the first abdominal segment is absent. No information on North American larvae of *Setodes* was available to Ulmer. It is noteworthy, then, that with this information now available, *Setodes* emerges as a genus comprising species with a clearly divided hind tibia (Fig. 2b), and a lateral sclerite on the first abdominal segment (Fig. 2d), along with species evidently lacking these features. There appears to be no mention in the recent literature of a subdivided hind tibia in the European larvae of *Setodes*, although a clear constriction in the tibia is shown in an illustration of *Setodes* sp. by Murgoci (1959, fig. 5c). Whatever may be the functional significance of this character, it seems that the subdivided hind tibia of the larva can no longer

be regarded as a consistent generic character in the way that Ulmer did. Another possibility is that further study of all stages of the species now assigned to *Setodes* will show consistent groupings, and may ultimately require recognition of an additional genus. This discordance may, however, be another example of the residue of characters in the Leptoceridae which apparently cannot be completely aligned with a generic classification. The diverse shapes taken by the gular sclerite in species of *Athripsodes* appears to be one such set of characters.

3. Most of the information now available indicates that *Setodes* larvae inhabit cool running waters, although *S. argentipunctella*

is reported to inhabit lakes as well (Hickin, 1967). Our observations indicate that these larvae are strongly inclined to burrow in the sand of river bottoms, but thus far there is little to support this view from the European observations. Murgoci (1959) assigned larvae of *Setodes* sp. collected in rivers in Romania to "la biocénose pétricole du biotype lotique," where they were evidently taken in company with larvae of *Psychomyia*, *Hydropsyche*, *Lepidostoma*, *Brachycentrus*, and *Sericostoma*. This same author regarded the concave sclerotized plates of the anal prolegs as an adhesive organ by which the larva maintains its case on rocks in the current, aided by secretion from a pair of glands

Figure 15, *Setodes incerta* larva and case; case diameter is 1 mm. 15a. Partially buried in sand, anterior end uppermost. 15b. Posterior end of case showing wide opening and plates on bases of anal prolegs. 15c, d, e. Camouflage behaviour of larva in case; c = case; r = rock; arrow indicates head of larva protruding from case. 15c. Rock held over mouth of case. 15d. Rock manipulated to a different position. 15e. Rock cast aside, larva feeding on worm.

situated near the ventral edge of the sclerotized plates. Evidence supporting this interpretation is, however, lacking.

Our observations prompt us to offer a different interpretation of the function of these sclerotized plates of the anal prolegs, which are so remarkable among case-building caddis larvae. Larvae of *Setodes* have a second unusual feature—a behavioural pattern of case-making that produces a case with little taper from end to end, with the openings at both ends unrestricted with silk or sand grains, and equal to the full inside diameter of the case (Figs. 3, 15b; Murgoci, 1959, fig. 3c). Although there appears to be some diversity in the extent to which the cases of different species of *Setodes* taper posteriorly, the larval case in species such as *S. incerta* contrasts strikingly with the larval cases of most Trichoptera that build portable cases. In other genera the case has a definite taper from front to rear, and the posterior opening is usually further reduced with silken secretion and other materials.

The interpretation offered here is that the sclerotized plates and the case with two open ends are components of an integrated morphological-behavioural-character complex enabling the larva to extend its head, thorax and legs from either end. The sclerotized plates on the caudal face of the anal prolegs protect the larva against intrusions through whichever opening harbours its posterior end. Our observations demonstrate that the larva does actively repel, with these plates, intrusions through the distal end of its case. Evidence indicates that *Setodes* larvae do not always burrow in the beds of the rivers they inhabit, but that they also do occur on the rocks of the river bed. This character complex seems to serve the larvae well in both habitats by permitting them: to

burrow in the bottom, advancing from either end; to burrow to the depth of the case, and take up a feeding position with the head level with the river bed; or to fasten both ends of the case to a rock for added stability while feeding in strong currents. This interpretation is consistent with the evidence now available, and is offered as a conceptual basis for further observations on the biology of these remarkable insects.

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Summary—This paper provides morphological details for the larva and pupa of *Setodes incerta* (Walker) from Michigan, the first North American species in this genus for which this information is available. The male and female genitalia of this species are also illustrated, the latter for the first time. The larva of another species of *Setodes* from South Carolina, unidentifiable to species, is also briefly described and illustrated. Larvae of these two North American species are shown to be discordant with European larvae of *Setodes* in having a secondary division in the hind tibia, a character previously considered to be generic.

Observations on aspects of the behaviour of the larva of *S. incerta* are presented: case-building, burrowing, adaptations to current, camouflage behaviour, and feeding. Arising from these is an overall interpretation of the function of the unusual morphological and behavioural characteristics of larvae of the genus *Setodes*.

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