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LARVAE OF THE CADDIS FLY GENUS RHYACOPHILA IN EASTERN NORTH AMERICA (TRICHOPTERA: RHYACOPHILIDAE)

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Introduction

The caddis fly genus Rhyacophila, one of the largest genera in the Trichoptera, has at least 250 species. Of the more than 90 species known from North America, 26 have been recorded from east of the Great Plains. Although nearly a third of the world fauna is found in North America, the larvae of only 7 species, 1 from the west and 6 from the east, have been described. Larvae of 69 species that occur in other parts of the world have been described; Ulmer (1957, pp. 123-128) gave a complete bibliography to these descriptions.

The larvae of 17 of the 26 eastern species have been correlated with their adults, 11 of these being described here for the first time, and 5 additional larval forms recognizable in the material at my disposal are being described herewith also. Because of lack of material, the larvae of fenestra and ledra could not be separated. I am thus able to recognize 21 distinct larval forms. I believe I do not have larval material for the following four species known from the east: montana Carpenter, vuphipes Milne, parantra Ross, and teddyi Ross.

It was hoped that this larval study would substantiate Ross' theory (1956) of the phylogeny of the genus based on male genitalia. Such proof was not found, although species obviously very closely related as adults are very similar as larvae. No characters were found that tended to substantiate the branches or large groups proposed by Ross. The situation becomes even more chaotic when one considers the larvae from other parts of the world. The lack of order may be partially due to convergence of larvae with similar habits—perhaps the larvae with edentate mandibles are more predaceous than those with toothed mandibles; or perhaps the correct phylogenetic scheme for the genus has not yet been discovered.

The length given is that of the longest larva seen. Where not given, the length of the prepupa is generally one-fourth to one-third less than the length of the mature larva. The term "prepupa" refers to a larva that has spun the pupal cocoon, but has not yet transformed to the pupa.

I have made no attempt to give a complete bibliography for each species. Rather, the original description is cited, and one or two recent redescriptions, if necessary for recognition of the species, plus all references adding to the knowledge of the immature stages.

All the material is in the author's collection unless otherwise indicated: Illinois Natural History Survey (INHS), Cornell University (CU), and the United States National Museum (USNM).

I am indebted to Dr. H. H. Ross of the Illinois Natural History Survey and to Dr. H. Dietrich of Cornell University for the use of material in their collections.

Because of the tight cocoon that the rhyacophiline larva spins around itself before pupating, the metamorphotypic method is very effective for associating all stages. Within the cocoon are found the larval sclerites, the pupa, and, for a short while before emergence, the fully developed genitalia which are visible within the pupal skin. A specimen exhibiting all these conditions was named a metamorphotype by Milne (1938).

Genus Rhyacophila Pictet

Rhyacophila Pictet, 1834, p. 181.—Ross, 1956, pp. 75-109 (descriptions of most species and phylogeny within the genus).

The larvae of this genus have been accurately characterized by Nielsen (1942, pp. 337–358) and Ulmer (1957, pp. 128–131). For this reason, I will give only the key larval characters of the genus: Shape campodeiform. Pronotum sclerotized, mesonota and metanota membranous; no prosternal sclerite. Foreleg generally broader than other legs but not chelate. Gills present or absent, but neither borne on long conical projections nor occurring as areas of 50 or more individual

filaments. Abdomen tapering gradually from the second or third segment; segmentation distinct. Anal prolegs well developed and extending beyond the tenth segment of the abdomen.

Key to larval forms

1.	Anal proleg with an apicolateral spur (fig. $1,b$)
	Anal proleg without such a spur (fig. $2,b$) 6
2(1).	Apicolateral spur of proleg short and sharply decurved (fig. $6,b$) 3
	Spur long and evenly curved (fig. $1,b$)
3(2).	Body segments with alternating dark and light bands melita
	Body segments not contrastingly banded amicis
4(2).	Frontoclypeus with dark transverse bands anteriorly and posteriorly
	(fig. 1,c)
	Frontoclypeus without bands
5(4).	Head uniformly colored (fig. 4,c) atrata
	Head with a dark transverse band posteriorly (fig. 6,c).
	(angelita?) species 1
6(1).	Abdomen bearing gills acropedes
	Abdomen without gills
7(6).	Anal prolegs with a basoventral hook (fig. 2,b)
	Anal prolegs without a free basoventral hook
8(7).	Anal claw without ventral teeth (fig. $5,d$)
. ,	Anal claw with ventral teeth (fig. $2,b$)
9(8).	Head equal in length and width; pronotum with 6-8 dark anterolateral
	setae in addition to corner setae (fig. 5,a) minora
	Head slightly longer than wide; pronotum with 1-2 dark anterolateral
	setae in addition to corner setae (fig. 5,c) manistee
10(8).	Frontoclypeus with a distinct dark V posteriorly (fig. 2,c); mandibles
(-)	edentate (fig. 2,a) torva
	Frontoclypeus without distinct V (fig. 3,a); mandibles toothed apically
	(fig. $11,b$)lobifera
11(7).	Second segment of maxillary palpus subequal to first glaberrima
(.,.	Second segment of maxillary palpus longer than first
12(11).	Anal claw without ventral teeth (fig. 11,d), carolina group 13
	Anal claw with ventral teeth (fig. 8,b), invaria group
13(12).	Head with a distinct pattern of infuscations and muscle scars (fig. 10,b).
	fenestra and ledra
	Head nearly concolorous
	Head slightly darker posteriorly (fig. 11,a) (Arkansas and Oklahoma).
	kiamichi
	Head uniformly golden brown (fig. 11,c) (Appalachian region).
	(carolina?) species 5
15(12).	Head and pronotum nearly black with a conspicuous pattern of pale
, ,	muscle scars and spots (fig. 9,b) (carpenteri?) species 2
	Head not marked as above
16(15).	Head narrowed on posterior half, yellowish (fig. 10,a).
, ,	(banksi?) species 3
	Head either widening posteriorly or parallel sided
17(16).	Head nearly parallel sided, either uniformly blackish or golden brown;
	pronotum slightly darker on anterior fourth (fig. 9,a) nigrita
	Head distinctly widening posteriorly, often with an indistinct pattern;
	pronotum often with a central dark spot (fig. 8,a)

18(17). Head darkest anteriorly, paling gradually posteriorly.

(mycta?) species 4 Head not as above, generally with an indistinct pattern (fig. 8,a,c). 19(19). Frontoclypeus narrowing rapidly to posterior point (fig. 8,c); head nearly black dorsally. shenandoahensis Frontoclypeus narrowing more gradually (fig. 8,a); head only slightly 20(19). Anal claw with a second ventral tooth (fig. 8,b) invaria Anal claw generally lacking second ventral tooth (fig. 8,d) vibox

Rhyacophila fuscula (Walker)

FIGURE 1

Neuronia fuscula Walker, 1852, p. 10.

Rhyacophila fuscula (Walker) Lloyd, 1921, p. 112 (larva).—Betten, 1934, p. 130 (male and female genitalia, larva).—Ross, 1944, p. 36 (male and female genitalia, larva).

This is the commonest species of Rhyacophila found in eastern North America. It is known from almost all the states and provinces west to Michigan and south along the mountains into Georgia.

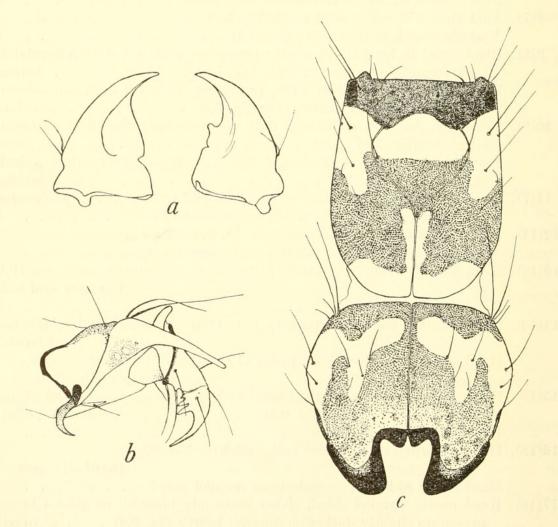


FIGURE 1.—Rhyacophila fuscula: a, mandibles, dorsal aspect; b, anal proleg, lateral; c, head and pronotum, dorsal.

An adequate description of the larva of this species was published as early as 1921. The larvae may be recognized from existing descriptions; male metamorphotypes collected in many locations supplied additional proof of the correctness of the association of stages. The larvae of this ubiquitous form may be easily recognized by the striking pattern of the head and pronotum and the apicolateral spur on the anal prolegs.

Description: Length, 25 mm. Head, brownish yellow, with a black band along the anterior margin, and an irregular W-shaped dark brown band posteriorly (fig. 1,c); second segment of maxillary palpus about twice as long as first; mandibles edentate (fig. 1,a). Thorax, pronotum brownish yellow, with a brown band along anterior margin and on posterior half; fore femora considerably broadened. Abdomen, anal proleg with basoventral hook and apicolateral spur; claw with 1 small and 2 large ventral teeth (fig. 1,b).

Material examined: Many larvae and pupae from various localities in Georgia, Maine, Massachusetts, New Hampshire, New York,

North Carolina, Ontario, South Carolina, and Virginia.

Remarks: The larvae of fuscula may be found in almost any running water that is cool and unpolluted. They have not been found in the smallest spring runs, but otherwise are found under rocks in riffles of streams as much as 10 yards or more in width.

The adults have a long flight period—from June into September—with the peak of abundance in late June or July. Correlated with the long emergence period of the adults is the variation in size of the larvae that are collected at any one time, especially in the fall and early spring. The species overwinters as developing larvae.

Rhyacophila torva Hagen

FIGURE 2

Rhyacophila torva Hagen, 1861, p. 296.—Ross, 1956, p. 77 (male genitalia).

The species torva is quite widespread, in the eastern region, but rarely abundant; it is known from the District of Columbia, Maine, Massachusetts, New Hampshire, New Jersey, New York, North Carolina, Tennessee, and Virginia.

Male metamorphotypes from North Carolina and Massachusetts established the identity of the larvae of this species. Both Vorhies (1909) and Lloyd (1921) described larvae that they assigned to this species; however, the larvae they described were not of torva, but of a species close to vibox Milne. The coloration of the head, especially of the dark V posteriorly on the frontoclypeus, the edentate mandibles, and the structure of the anal proleg combine to make this larva easily recognized.

Description: Length, 13 mm. Head, brownish yellow, irregularly infuscate posteriorly, with a conspicuous dark V-shaped mark posteriorly on the frontoclypeus; muscle scars dark, conspicuous (fig. 2,c); second segment of maxillary palpus twice as long as first; mandibles edentate (fig. 2,a). Thorax, pronotum brownish yellow, slightly infuscate

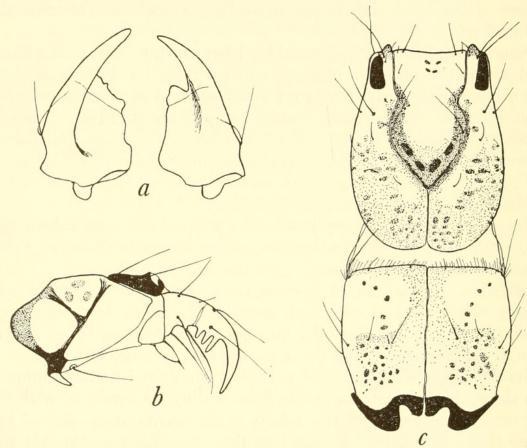


FIGURE 2.—Rhyacophila torva: a, mandibles, dorsal aspect; b, anal proleg, lateral; c, head and pronotum, dorsal.

mesally; muscle scars dark, conspicuous; fore femora slightly broadened. Abdomen, anal proleg with a basoventral hook; claw with 3 ventral teeth (fig. 2,c).

Material examined: Massachusetts, Montague, Feb. 7, 1959, 1 larva, 1 ♂ and 1 ♀ pupa. New York, Ithaca, Buttermilk Falls, May 3, 1956, 1 larva. North Carolina, Mount Mitchell, Camp Alice, Sept. 16, 1958, 1 prepupa; Great Smoky Mountains National Park, Couches Creek, July 2, 1958, 1 ♂ pupa.

Remarks: The larvae seem to be inhabitants primarily of tumbling brooks about 2–3 yards in width.

The adults are often the first species of the genus on the wing. I have taken them as early as the first of April in Massachusetts; however, emergence evidently occurs over a considerable period of time for adults are taken well into July. The discovery of a prepupa in North Carolina in the fall indicates that a certain percentage of the population, which undoubtedly produces the early spring adults,

overwinters in this stage. Other overwintered larvae have been taken in the spring; these would produce the late-season adults.

Rhyacophila lobifera Betten

FIGURE 3,a,b

Rhyacophila lobifera Betten, 1934, p. 131 (male and female genitalia, larva and pupa).—Ross, 1944, p. 35 (male and female genitalia, larva and pupa).

This species is apparently restricted to the central states: Illinois, Indiana, Ohio, and Oklahoma.

The description is based on determined material from the Betten and the Illinois Natural History Survey collections. The larvae are

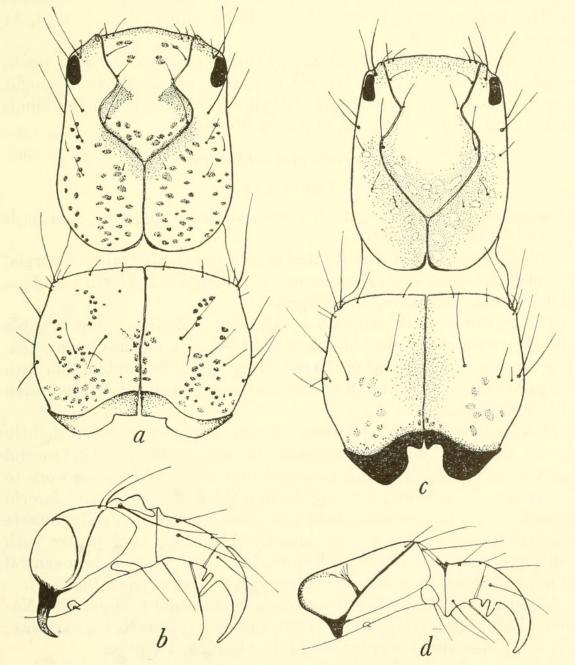


FIGURE 3.—Rhyacophila lobifera: a, head and pronotum, dorsal aspect; b, anal proleg, lateral. R. glaberrima: c, head and pronotum, dorsal; d, anal proleg, lateral.

easily recognized by the dark spots on the head and pronotum, the basal hook on the anal prolegs, and the apical teeth on the mandibles.

Description: Length, 24 mm. Head, yellowish, darker around posterior half of frontal sutures; muscle scars dark, conspicuous (fig. 3,a); second segment of maxillary palpus about twice length of first; left mandible with 2 apical teeth, right with 1 mesal and 3 apical teeth, of which the middle is longest (like fig. 11,b). Thorax, pronotum yellowish, with dark muscle scars; posterior margin mostly pale, only shallowly indented near middle; fore femora but slightly wider than other femora. Abdomen, anal proleg with a basoventral hook; claw with 1 large and 1 small ventral tooth (fig. 3,b).

Material examined: Illinois, Lake Bluff, Pettibones Creek, 4 larvae (CU). Indiana, near Cicero, Upper Hinkle Creek, Apr. 4, 1954, 11

larvae (INHS).

Remarks: Ross (1944, p. 35) stated that the larvae "frequent small, rapid, clear streams that are of temporary nature during drought years. The adults appear during April and May in southern Illinois and during May and June in northern Illinois."

Rhyacophila glaberrima Ulmer

FIGURE 3,c,d

Rhyacophila glaberrima Ulmer, 1907, p. 85 (male genitalia).—Ross, 1944 (male and female genitalia, larva).

This species is widely distributed east of the Great Plains: Georgia, Illinois, Massachusetts, New Hampshire, New York, North Carolina, Nova Scotia, Tennessee, and Virginia.

The larvae were determined by the key and description of Ross (1944), whose association of stages is based on a mature male pupa. The short second segment of the maxillary palpus in combination with the presence of ventral teeth on the anal claw permits easy recognition

of this species.

Description: Length, 12 mm. Head, brownish yellow, slightly darker centrally; muscle scars paler, inconspicuous (fig. 3,c); second segment of maxillary palpus subequal to first; mandibles too worn to be certain of dentation, but may be like those of carolina and invaria groups. Thorax, pronotum brownish yellow, darker centrally; muscle scars dark; fore femora very broad. Abdomen, anal proleg with neither basal hook nor apical spur, but with a short basoventral process attached to membrane; claw with 2 ventral teeth (fig. 3,d).

Material examined: North Carolina, Great Smoky Mountains National Park, Indian Gap, July 1, 1958, 1 prepupa; Blue Ridge Parkway,

Crabtree Meadows Campground, July 31, 1959, 1 ♀ pupa.

Remarks: The few larval collections and the many adult collections of this species suggest that there is a preference for small brooks that

cascade over rocks and boulders. The Illinois collection was made in a small dry streambed under a damp stone.

The adults of this species have been collected from June through August, even in the same locality. The mature male pupa was found in Illinois in early October.

Rhyacophila atrata Banks

FIGURE 4

Rhyacophila atrata Banks, 1911, p. 351.—Ross, 1938b, p. 4 (male genitalia).

This small species is known from Massachusetts, New Hampshire, New York, and North Carolina.

A male metamorphotype from North Carolina assures the association of larvae and adults. The larvae may be recognized by their small size, immaculate head, and apicolateral spur on the anal proleg.

Description: Length, 8 mm. Head, brownish yellow, immaculate (fig. 4,c); second segment of maxillary palpus about $1\frac{1}{2}$ times as long as first; left mandible with 2 apical teeth, right with 3 apical teeth all about the same length (fig. 4,b). Thorax, pronotum brownish yellow, becoming pale brown posteriorly; fore femora greatly broad-

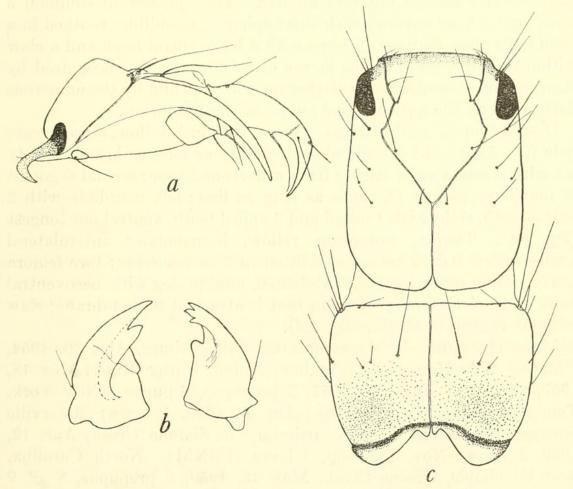


Figure 4.—Rhyacophila atrata: a, anal proleg, lateral aspect; b, mandibles, dorsal; c, head and pronotum, dorsal.

ened. Abdomen, anal proleg with both basoventral hook and apicolateral spur; claw without ventral teeth (fig. 4,a).

Material examined: New Hampshire, Pinkham Notch, Cutler River, May 18, 1957, 2 larvae. New York, near DeBruce, Willewemoc River, 1 prepupa. North Carolina, near Highlands, Greens Creek, May 19, 1959, 1 prepupa, 1 of pupa.

Remarks: The larvae were found in streams 2-5 yards wide; they are found in the riffles of the clear cold streams.

The adults are collected from early spring into summer. Emergence by late May indicates that some overwinter as mature larvae or prepupae.

Rhyacophila minora Banks

FIGURE 5,a,b

Rhyacophila minora Banks, 1924, p. 444.—Ross, 1956, p. 96 (male genitalia).

This species has a wide range in the Appalachian Mountains: Maine, Massachusetts, New Hampshire, New York, North Carolina, Nova Scotia, and South Carolina.

The larvae were associated with the adults through male metamorphotypes collected in North and South Carolina. The larvae of manistee and minora are very similar. They possess in common a short broad head covered with short spicules, mandibles toothed in a similar manner, and anal prolegs with a basoventral hook and a claw without ventral teeth. The larvae of minora may be recognized by their quadrate head without darker muscle scars and by the numerous dark setae on the anterolateral angles of the pronotum.

Description: Length, 12 mm. Head, brownish yellow, muscle scars pale (fig. 5,a); head capsule almost exactly as long as broad; closely set with spicules each arising from a darkened base; second segment of maxillary palpus $1\frac{1}{2}$ times as long as first; left mandible with 2 apical teeth, right with 1 mesal and 3 apical teeth, ventral one longest (fig. 5,b). Thorax, pronotum yellow, immaculate; anterolateral angles with 6–8 dark setae in addition to 3 corner setae; fore femora broader than other femora. Abdomen, anal proleg with basoventral hook and apicolateral projection that is attached to membrane; claw without ventral teeth (like fig. 5,d).

Material examined: Massachusetts, Williamsburg, Apr. 30, 1954, 1 larva. New Hampshire, Pinkham Notch, Cutler River, May 18, 1957, 14 larvae—June 12, 1957, 2 prepupae, 3 pupae. New York, Tennanah Lake, Trout Brook, Apr. 4, 1959, 1 larva; Slaterville Springs, Wildflower Preserve, tributary of Sixmile Creek, Apr. 12, 1959, 1 larva—Nov. 13, 1960, 1 larva (USNM). North Carolina, near Highlands, Greens Creek, May 18, 1959, 5 prepupae, 8 ♂♀ pupae. South Carolina, Walhalla Fish Hatchery, East Branch Chatooga River, May 18, 1959, 5 ♂♀ pupae.

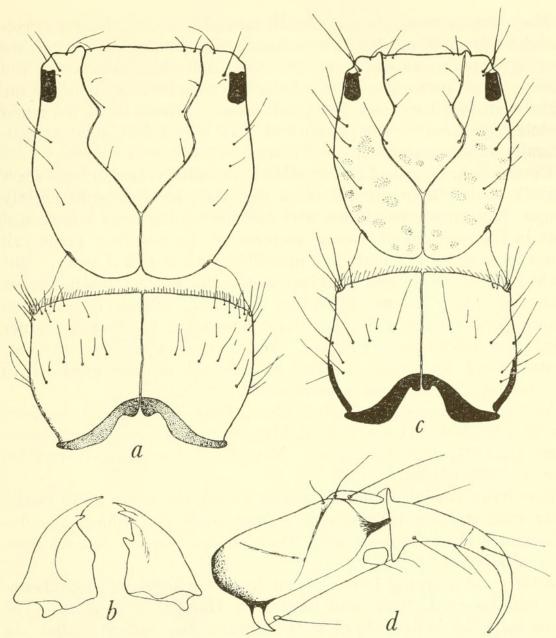


FIGURE 5.—Rhyacophila minora: a, head and pronotum, dorsal aspect; b, mandibles, dorsal.

R. manistee: c, head and pronotum, dorsal; d, anal proleg, lateral.

Remarks: The immature stages of *minora* were found in the riffles of small brooks, generally less than 3 yards wide. The larvae of *manistee* are found in considerably larger streams.

The adults of *minora* apparently emerge in late May in the southern Appalachians and about a month later in the Northeast. A single, nearly full grown larva found in November shows that the species probably overwinters in this stage.

Rhyacophila manistee Ross

FIGURE 5,c,d

Rhyacophila manistee Ross, 1938a, p. 104 (male genitalia).

This species has previously been recorded from Michigan; it is now recorded from New Hampshire and New York.

The association of stages is based on male metamorphotypes collected in New Hampshire. The larvae of this species and minora are very similar, as would be expected from the similarity of the adults. The larvae of manistee however, may be recognized by the slightly greater length of the head capsule, which bears darkened muscle scars, and by the presence of only 1 or 2 dark setae anterolaterally on the pronotum.

Description: Length, 12 mm. Head, brownish yellow, muscle scars slightly darker than ground color (fig. 5,c); head capsule slightly longer than broad, closely set with spicules arising from a darkened spot in the integument; second segment of the maxillary palpus $1\frac{1}{2}$ times as long as the first; left mandible with 2 apical teeth, right with 1 mesal tooth and 3 apical teeth, the ventral tooth longest (like fig. 5,b). Thorax, pronotum brownish yellow, immaculate; anterolateral angles with 1 or 2 dark setae in addition to corner setae; fore femora much widened. Abdomen, anal prolegs with basoventral hook and with a short apicolateral process attached to membrane; claw without ventral teeth (fig. 5,d).

Material examined: New Hampshire, Twin Mountain, Ammonoosuc River at Zealand Campground, May 18, 1957, 1 larva, 3 prepupae—June 11, 1957, 2 ♂ 1 ♀ pupae. New York, Rockland, Beaverkill, Apr. 4, 1959, 1 larva.

Remarks: The larvae of this species inhabit the wider (5–10 yards) clear cold streams with alternate long pools and riffles: the fly-fisherman's ideal trout stream. This habitat is quite distinct from that of minora.

Adults are a spring form, known from Michigan in May (Leonard and Leonard, 1949) and from New Hampshire in June. The larva collected in late April is fully grown and indicates that the species must overwinter as grown larvae.

Rhyacophila melita Ross

FIGURE 6,a,b

Rhyacophila melita Ross, 1938a, p. 104 (male genitalia).

This species, previously recorded only from Michigan, also occurs in New Hampshire and New York.

A single male metamorphotype collected in New York establishes the identity of the larva. The larvae of *melita* are the most striking of any species in the genus yet encountered in the east. The combination of black bands on the body segments and the striking color pattern on the head and pronotum are distinctive. Description: Length, 15 mm. Head, yellow, becoming golden anteriorly; a dark median longitudinal bar dorsally (fig. 6,a), a pair of dark bars sublaterally on venter, second segment of maxillary palpus slightly longer than first; mandibles edentate (like fig. 2,a). Thorax, pronotum yellow on anterior third, deep brown on posterior two-thirds; mesonota and metanota with dark bars on posterior halves; fore femora broader than other femora. Abdomen, segments 1–8 dorsally blackish brown on posterior half; anal prolegs with a basoventral hook, and an apicolateral spur that is short, decurved, and with apex turned laterally; claw with 2 large ventral teeth (fig. 6,b).

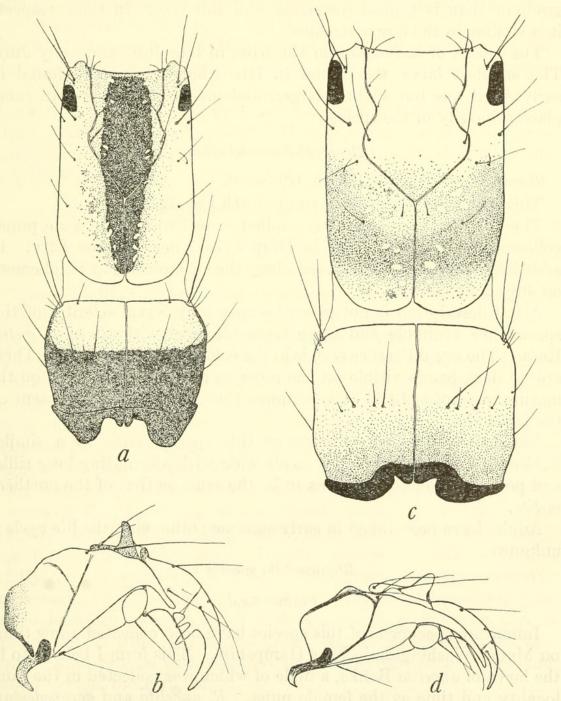


FIGURE 6.—Rhyacophila melita: a, head and pronotum, dorsal aspect; b, anal proleg, lateral. R. species 1: c, head and pronotum, dorsal; d, anal proleg, lateral.

Material examined: New Hampshire, Twin Mountain, Ammonoosuc River at Zealand Campground, May 18, 1957, 1 larva—June 11, 1957, 1 larva, 1 pupa—Aug. 25, 1957, 1 larva. New York, Rockland, Beaverkill, Apr. 4, 1959, 1 larva; near DeBruce, Willewemoc River, 12 larvae, 7 prepupae; East Meredith, Kortright Creek, June 6, 1959, 1 ♂ 4 ♀ pupae.

Remarks: The larvae of this species were found primarily in the large streams that alternate in long pools and riffles, similar to the habitat of the larvae of manistee. Although Kortright Creek is only about 2–3 yards wide, it flows in open pastures and has a much lower gradient than is typical for streams of this size. In these respects it is similar to the larger streams.

The adults of *melita* are on the wing in late June and early July. The smallest larva was found in late August. Another found in early April was but slightly larger, and indicated that growth takes place primarily in the spring.

Rhyacophila amicis Ross

Rhyacophila amicis Ross, 1956, p. 120 (male).

This species is known only from North Carolina.

The only material of *amicis* studied were two mature male pupae collected on May 19, 1959, in Deep Creek, near Bryson City. In addition, one male was collected along the Oconoluftee at Smokemont on July 2, 1958.

A full description is not given because only larval sclerites of this species are available and these seem identical with those of *melita* Ross. The one difference seen is in the coloration of the pupa. There are no dark bands visible on the pupa as are to be seen even on the mature pupa of *melita*. It is assumed that these bands are absent on the larva also.

The two collections I made of this species were in a similar habitat. The stream is 5-10 yards wide with alternating long riffles and pools. The habitat seems to be the same as that of the northern melita.

Adults have been taken in early summer; otherwise, the life cycle is unknown.

Rhyacophila species 1

FIGURE 6,c,d

Immature specimens of this species have been collected a few times on Mount Washington in New Hampshire. This form I believe to be the larva of angelita Banks, a male of which was collected in the same locality and time as the female pupa. R. angelita and acropedes are the only species known to occur in both eastern and western North

America. In eastern North America angelita is known to occur only in New Hampshire.

The larvae are easily recognized by the combination of an apicolateral spur on the anal prolegs and a dark transverse band on the genae.

Description: Length of prepupa, 13 mm. Head, yellow with a brown transverse band posteriorily on the genae; few pale inconspicuous muscle scars in this band (fig. 6,c); second segment of maxillary palpus twice as long as first; mandibles worn, but probably like those of torva. Thorax, pronotum yellow on anterior half, pale brown on posterior; femora of forelegs slightly broader than those of other legs. Abdomen, anal proleg with basoventral hook and apicolateral spur; claw with 1 small ventral tooth (fig. 6,d).

Material examined: New Hampshire, Mount Washington, Cutler River in Tuckermans Ravine, Aug. 4, 1958, 1 prepupa, 1 pupa—

Aug. 24, 1957, 2 ♀ pupae.

Remarks: The specimens were collected from a tumbling mountain torrent of about 3-5 yards width. They were associated with larvae of *acropedes*. The emergence period is in late August; the rest of the life cycle is unknown.

Rhyacophila acropedes Banks

FIGURE 7

Rhyacophila acropedes Banks, 1914, p. 201.—Ross, 1938b, p. 4 (male genitalia).

This species like angelita, has a wide range in western North America and is also found in northeastern area; it has been found in Labrador, Maine, Michigan, New Hampshire, and New York.

The association of stages is based on mature male metamorphotypes taken in New Hampshire, as well as on determined larvae lent by Ross. The larvae are immediately recognizable by the clusters of bushy

gills on the abdomen; no other eastern species possess gills.

Description: Length, 21 mm. Head, yellow brown, with darker muscle scars; paler on posterior quarter, this area sharply set off from darker anterior portion; posterior half of frontoclypeus darker along sutures (fig. 7,c); second segment of maxillary palpus twice as long as first; left mandible with 2 apical teeth, right with 2 apical teeth and a large mesal tooth (fig. 7,a). Thorax, pronotum yellow brown, slightly darker anteriorly; muscle scars slightly darker posteriorly; fore femora much broadened. Abdomen, clusters of branching gills present laterally on segments 1–8; first segment with 1 pair, eighth segment with 2 pairs, 2–7 with 3 pairs; each cluster with 12–15 filaments. Anal prolegs with a basoventral hook; claw with 1 large and 1 small ventral tooth (fig. 7,b).

Material examined: Michigan, Curran, Yoder Creek at Route 72, May 21, 1936, 3 larvae (INHS). New Hampshire, Pinkham Notch, Cutler River, May 18, 1957, 5 larvae—Aug. 4, 1958, 1 larva—Aug. 24, 1957, 1 larva; Mount Washington, Cutler River in Tuckermans Ravine, Aug. 4, 1958, 12 ♂♀ pupae—Aug. 24, 1957, 20 larvae.

Remarks: The larvae were taken in a rushing mountain torrent about 3-5 yards wide. Adults were also collected on Mount Katahdin,

Maine, beside a similar torrent.

The larvae collected on Mount Washington show a steady increase in size from those collected in late August through the spring months to the few collected in early August. The adults emerge primarily in August.

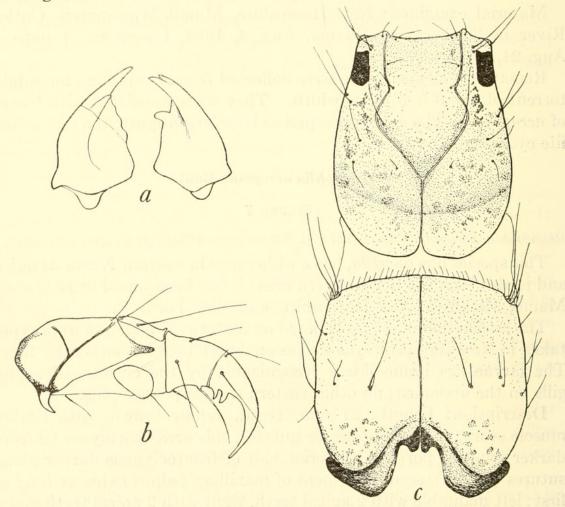


FIGURE 7.—Rhyacophila acropedes: a, mandibles, dorsal aspect: b, anal proleg, lateral; c, head and pronotum, dorsal.

Rhyacophila invaria group

This is the largest group of species in the genus in eastern North America, containing 8 species. To date, larvae of *invaria* (Walker), nigrita Banks, vibox Milne, and shenandoahensis Flint have been reared. In addition, I can recognize three more larval forms in the material at my disposal. The known ranges indicate that these three are probably larvae of banksi Ross, carpenteri Milne, and mycta Ross.

The separation of the larvae of certain species in this group, especially of *vibox* and *invaria*, is not at all satisfactory.

The larvae agree on the following characteristics: head long and narrow, generally about 1½ to 2 times as long as broad, and at most only slightly widened posteriorly. Second segment of maxillary palpus about twice as long as first; left mandible with 2 apical teeth, right with 3, of which mesal one is longest. Anal proleg without basoventral hook and apicolateral spur, although short processes which are not free of the membrane are present at both places; claws with ventral teeth.

Rhyacophila vibox Milne

FIGURE 8,d

Rhyacophila vibox Milne, 1936, p. 101 (male and female genitalia).—Ross, 1944, p. 36 (male and female genitalia, larva).

Rhyacophila torva (nec Hagen) Vorhies, 1909, p. 713 (larva, unquestionable vibox).—Lloyd, 1921, p. 114 (larva, probably vibox).

Adults of *vibox* are known to occur in many of the Northeastern and North Central states: Illinois, Michigan, Massachusetts, New Hampshire, New York, Ontario, Quebec, Vermont, and Wisconsin.

The larvae of this species were reared and described by Ross, who furnished a determined series of larvae for study. The larval description of Vorhies closely matches the larvae here described; furthermore, no other species in this group is known to occur in the North Central states. The description of Lloyd, who worked around Ithaca, N.Y., is of the larvae of either *invaria* or *vibox*, and inasmuch as *vibox* was collected near Ithaca, the description is assigned here. In any case, neither description is of the larva of *torva*, but of a species near *vibox*.

The larvae of *vibox* are extremely similar to those of *invaria*. The characters here used for their separation may not hold when more material becomes available. It seems that the larvae of *vibox* have the dark shading continuous to the oral margin of the frontoclypeus, and the anal claws rarely have a second small ventral tooth.

Description: Length, 16 mm. Head, brownish yellow, darker centrally and anteriorly; muscle scars faintly indicated by pale spots posteriorly; head capsule slightly broadened posteriorly; frontoclypeus with posterior portion slightly elongated so that arms of frontal suture meet at slightly less than 90° (like fig. 8,a); second segment of maxillary palpus twice as long as first; left mandible with 2 apical teeth, right with 3 apical teeth, mesal one longest (like fig. 11,b). Thorax, pronotum brownish yellow, a slightly darker oval spot posteromesally; fore femora considerably broadened. Abdomen, anal proleg with short basoventral and apicomateral processes, neither free of membrane; claw only rarely with a small second ventral tooth (fig. 8,d).

Material examined: Illinois, Elgin, Trout Spring, Mar. 7, 1936, 4 larvae (INHS). New Hampshire, Twin Mountain, Zealand Campground, small stream, May 18, 1957, 7 larvae. New York, Dryden, Ellis Hollow, Jan. 31, 1957, 2 larvae—May 4, 1957, 4 larvae—May 29, 1959, 3 larvae, 2 prepupae, 1 pupa—July 14, 1956, 1 prepupa; Cortland, Fish Hatchery, July 8, 1959, 1 larva.

Remarks: The larvae of this species were collected only in springs and the small brooks below them. I have not taken the larvae from streams more than 2 feet wide.

Adults of *vibox* have been collected in June and early July, but probably could be taken in August. Larvae have been collected from January until early July, with prepupae found from late May and into July.

Rhyacophila invaria (Walker)

FIGURE 8, a, b

Polycentropus invarius Walker, 1852, p. 101.

Rhyacophila invaria (Walker) Ross, 1938b, p. 6 (male genitalia).

This species has only been recorded a few times from the North-eastern states: Maine, Massachusetts, New York, Nova Scotia, Pennsylvania.

Several male metamorphotypes were collected in Massachusetts, and thus the larval and adult stages were linked. The larvae are very similar to those of *vibox*. The *invaria* larvae studied have the antetior half of the frontoclypeus pale and have a small second ventral tooth on the anal claw.

Description: Length, 15 mm. Head, brownish yellow, darker along anterior margin and mesally; muscle scars pale, inconspicuous; head capsule distinctly widening toward posterior (fig. 8,a); second segment of maxillary palpus twice as long as first; left mandible with 2 apical teeth, right with 3 apical teeth, middle one being longest (like fig. 11,b). Thorax, pronotum brownish yellow, with oval dark mark posteromesally; fore femora much broadened. Abdomen, anal proleg with both basoventral and apicolateral processes, neither free of membrane; claw with 2 ventral teeth (fig. 8,b).

Material examined: Massachusetts, Sunderland, Fish Hatchery, Aug. 6, 1954, 2 prepupae, 3 & pupae—Aug. 9, 1954, 7 & pupae—Oct. 20, 1954, 2 larvae—Nov. 9, 1953, 1 larva; Montague, Feb. 7, 1959, 1 larva.

Remarks: The two streams where the larvae of this species were collected are small, about 2 feet wide, clear, and cold.

Adults were collected at the Sunderland locality from early July to early August. The larvae collected in October were nearly half grown; those collected in November and February appear to be fully grown.

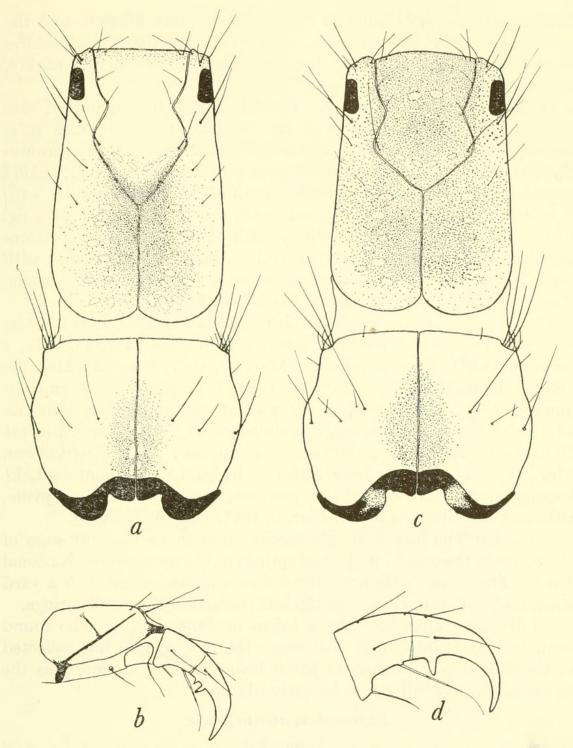


FIGURE 8.—Rhyacophila invaria: a, head and pronotum, dorsal aspect; b, anal proleg lateral. R. shenandoahensis: c, head and pronotum, dorsal. R. vibox: d, anal claw, lateral.

Rhyacophila shenandoahensis Flint

FIGURE 8,c

Rhyacophila shenandoahensis Flint, 1958, p. 21 (male and female genitalia).

This species has been collected only in the mountains of Shenandoah National Park and those nearby.

Male metamorphotypes establishing the identity of the larva of this species, have been collected on several occasions. The larval head capsule is very similar to that of *invaria*, but differs in that the apex of the frontoclypeus is rather blunt so that the frontal sutures meet at 90° or more, and the head is generally marked very darkly, appearing almost black to the naked eye.

Description: Length, 16 mm. Head, brownish yellow, marked with deep brown, both mesodorsally and ventrally; muscle scars pale, inconspicuous, head capsule slightly wider posteriorly; apex of frontoclypeus blunt, frontal arms meeting at 90° or more (fig. 8,c); second segment of maxillary palpus twice length of first; left mandible with 2 apical teeth, right with 3 apical teeth, mesal one longest (like fig. 11,b). Thorax, pronotum yellow, with dark oval mark posteromesally; fore femora much broadened. Abdomen, anal proleg with short basoventral and apicolateral processes, not free of membrane; claw with a second small ventral tooth (like fig. 8,b).

Material examined: Virginia (Shenandoah National Park), White Oak Canyon, Mar. 29, 1957, 1 larva, 2 prepupae—Mar. 26, 1961, 1 larva (USNM); Hogcamp Brook, Mar. 28, 1957, 6 larvae—Mar. 26, 1961, 1 larva (USNM)—May 23, 1959, 1 prepupa, 27? pupae—June 4, 1957, 5 prepupae, 3 7? pupae; Skyline Drive, Milepost 71.5, Mar. 29, 1957, 2 larvae, 3 prepupae; Skyline Drive, Milepost 79.5, May 23, 1959, 2 larvae, 2 7 pupae; near Waynesboro, Mar. 29, 1957, 1 larva; near Natural Bridge, Cave Mountain Lake Campground, Mar. 29, 1957, 1 prepupa, 1 pupa; near Sperryville, tributary of Thornton River, Mar. 9, 1961, 1 larva (USNM).

Remarks: The larvae of this species seem to be the only ones of the genus in the small brooks and springs of the Shenandoah National Park. The larvae were not collected in brooklets more than a yard wide, and were often found in the leaf packets in the small springs.

Adults were most commonly taken in June, but may be found from late May into July. Although the larvae were not collected in the fall, they probably do hatch before winter, inasmuch as the larvae are nearly full grown by early March.

Rhyacophila nigrita Banks

FIGURE 9,a

Rhyacophila nigrita Banks, 1907, p. 132.—Betten, 1934, p. 132 (male genitalia).

This species is known from New York, North Carolina, Tennessee, and Georgia and may be expected in the remainder of the Appalachian region. The male genitalia and the coloration of the larvae of the specimens from New York are slightly different from those of the southern mountains. It may well be that two closely related species are involved.

Mature male metamorphotypes collected in Georgia, New York, and North Carolina form the basis for the association of the stages.

The long parallel-sided head of the larva separates this species from others in the *invaria* group, except for species 2 which has a distinctive color pattern on the head and pronotum. The larva is similar in many respects to that of species 4, but seems to have a longer, more nearly parallel-sided head capsule.

Description: Length, 14 mm. Head, nearly uniform black (southern) or golden brown (northern), slightly paler around eyes and posteriorly on frontoclypeus; head capsule long and parallel sided (fig. 9,a), second segment of maxillary palpus twice length of first,

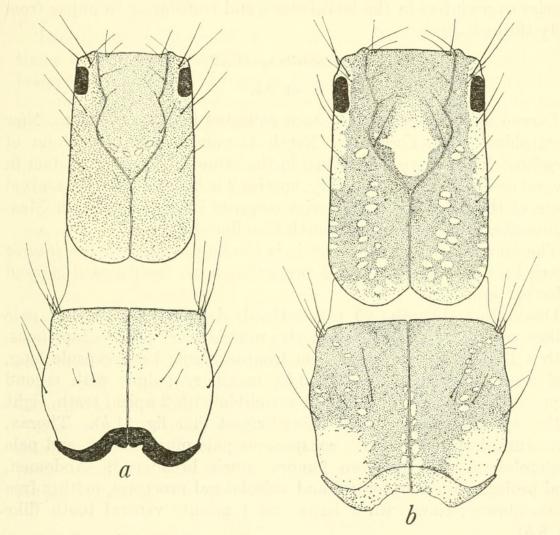


FIGURE 9.—Rhyacophila nigrita: a, head and pronotum, dorsal aspect. R. species 2: b, head and pronotum, dorsal.

left mandible with 2 apical teeth, right with 3 apical teeth, mesal one longest (like fig. 11,b). Thorax, pronotum brownish yellow, darker on anterior fourth; fore femora much broadened. Abdomen, anal proleg with short basoventral and apicolateral processes, neither free of membrane; claw with second small ventral tooth (like fig. 8,b).

Material examined: Georgia, Rabun County, Black Rock Mountain State Park, July 3, 1958, 3 prepupae, 8 ♂♀ pupae. North Carolina, Highlands, Biological Station, July 1, 1958, 1 ♂ pupa—July 4, 1958, 1

larva, 1 prepupa; near Highlands, Greens Creek, May 19, 1959, 2 larvae, 3 prepupae, 9 ♂♀ pupae; Blue Ridge Parkway, milepost 251, May 22, 1959, 1 prepupa, 3 pupae. New York, Slaterville Springs, Wildflower Preserve, tributary to Sixmile Creek, Apr. 12, 1959, 1 larva—June 7, 1958, 2 ♂ pupae—Nov. 13, 1960, 3 larvae. Remarks: All the larval collections of this species were made in

Remarks: All the larval collections of this species were made in small brooks, less than a yard wide, that have a rather low gradient.

The adults were collected from late May into July. The collecting of well-grown larvae in late fall and early spring indicates that the species overwinters in the larval stage and transforms to pupae from May through June.

Rhyacophila species 2

FIGURE 9,b.

Larvae of this species have been collected in Massachusetts, New Hampshire, New York, and North Carolina. Because adults of carpenteri Milne have been taken in the same general area, in fact in several cases in the same locality, species 2 is believed to be the larval stage of this species. The species carpenteri is recorded from Massachusetts, New Hampshire, North Carolina, Quebec.

The larva is very distinctive; it is the only species in the *invaria* group in which the head and pronotum have such a well-marked color pattern.

Description: Length, 20 mm. Head, deep reddish brown, pale yellow around eyes, and posteriorly; muscle scars pale, conspicuous, with a large pale central spot on frontoclypeus; head capsule long, and nearly parallel sided (fig. 9,b), maxillary palpus with second segment twice length of first; left mandible with 2 apical teeth, right with 3 apical teeth, mesal one being longest (like fig. 11,b). Thorax, pronotum deep brown, with conspicuous pale muscle scars, and pale posterolateral quarter; fore femora much broadened. Abdomen, anal prolegs with basoventral and apicolateral processes, neither free of membrane; claw with 1 large and 1 minute ventral tooth (like fig. 8,b).

Material examined: Massachusetts, Amherst, Fort River, April 1951, 1 prepupa—Jan. 26, 1954, 1 larva; North Amherst, Cushman Brook, May 3, 1954, 3 prepupae. New Hampshire, Twin Mountain, Ammonoosuc River at Zealand Campground, June 11, 1957, 1 prepupa, 1 pupa. New York, near DeBruce, Willewemoc River, 2 larvae, 2 prepupae, 4 pupae; Rockland, Beaverkill, Apr. 4, 1959, 14 larvae—Dec. 6, 1959, 6 larvae; Slaterville Springs, Wildflower Preserve, tributary of Sixmile Creek, Apr. 12, 1959, 1 larva—Nov. 13, 1960, 1 larva (USNM). North Carolina, Bryson City, Deep Creek at campground, Sept. 13, 1958, 1 larva.

Remarks: Almost all the collections of this species were made in streams 5–10 yards wide, although a few larvae were collected in much smaller brooks.

Larval data indicates that emergence takes place primarily in June. Adults of *carpenteri* are generally taken in June, although in the mountains they linger well into August. Nearly fullgrown larvae have been taken in the late fall, winter, and early spring months.

Rhyacophila species 3

FIGURE 10,a

The distinctive larva of this form was collected only twice, both times in the same locality, Pinkham Notch, N.H. Species 3 is believed to be the larval stage of *R. banksi* Ross, which is an unreared member of the *invaria* group, and is known to occur rather commonly in Vermont and the White Mountains of New Hampshire.

This larval form is easily recognized by the shape of the head, for no other species yet found in the east has a head capsule that gradu-

ally narrows toward the rear.

Description: Length, 16 mm. Head, uniformly yellow; head capsule widest at eyes, becoming distinctly narrowed on posterior third (fig. 10,a); second segment of maxillary palpus twice as long as first; left mandible with 2 apical teeth, right with 3 apical teeth, of which the mesal is longest (like fig. 11,b). Thorax, pronotum uniformly yellow; fore femora much broadened. Abdomen, anal prolegs with basoventral and apicolateral processes, neither free of membrane; claw with 1 minute ventral tooth.

Material examined: New Hampshire, Pinkham Notch, Cutler River, May 18, 1957, 2 larvae—June 12, 1957, 3 prepupae.

Remarks: The immature stages of this species were collected in a small (about 2–3 yards wide) cold mountain brook. The prepupae present indicate that emergence takes place in late June or July. Adults of banksi have been taken from late June to late July.

Rhyacophila species 4

Larvae of this form were taken at high altitudes in North Carolina. It would not be surprising if these are larvae of mycta Ross which occurs at the higher elevations in this area. The larvae may be recognized by the coloration and the slight widening of the head capsule posteriorly. It is very similar in coloration to the northern larvae of nigrita, but seems to have a proportionately broader head. Only one of the larvae was over 20 mm; the rest were 12–15 mm.

Description: Length, 23 mm. Head, golden brown, becoming slightly darker anteriorly; head capsule slightly wider posteriorly;

second segment of maxillary palpus twice as long as first; left mandible with 2 apical teeth, right with 3 apical teeth, mesal one longest. Thorax, pronotum golden brown, immaculate; fore femora much broadened. Abdomen, anal prolegs with basoventral and apicallateral processes, but not free of membrane; claw with 2 ventral teeth.

Material examined: North Carolina, Mount Mitchell, Camp Alice, Sept. 1, 3, 1959, 3 larvae—Sept. 16, 1958, 2 larvae; Mount Mitchell, Sept. 1, 1959, 1 larva; Blue Ridge Parkway, Crabtree Meadows Campground, Sept. 2, 1959, 1 larva; Great Smoky Mountains National Park, Indian Gap, July 4, 1958, 1 larva.

Remarks: The larvae were collected in tumbling mountain brooks, generally less than 2 yards in width.

Because pupae or prepupae of this species were not collected, the flight period cannot be given. The adults of *mycta* have been recorded from late May through June.

Rhyacophila carolina group

This group of five species, all closely related on the basis of male genitalia, shows a very uniform structure in the larval stage. To date, larvae of kiamichi Ross, fenestra Ross, and ledra Ross have been reared. In addition, another larval form, almost certainly the larva of carolina Banks, is present in material I have collected along the length of the eastern mountains. I have not had any larvae of ledra to study, but Ross (1944) was unable to separate larvae of this species from those of fenestra.

The larvae of this group have the following characters in common: Head short, only slightly longer than broad, much widened posteriorly; second segment of maxillary palpus about twice as long as first; left mandible with 2 apical teeth, right with 3 apical teeth, of which the middle is the longest; anal prolegs with neither basoventral hook nor apicolateral spur, claw without ventral teeth.

Rhyacophila ledra Ross

Rhyacophila ledra Ross, 1939, p. 65 (male genitalia). Ross, 1944, p. 37 (male genitalia, larva).

R. ledra has been recorded from Georgia, Illinois, Ohio, and Tennessee. In 1944 Ross indicated that in the basis of the material available he could not separate the larvae of ledra and fenestra. I have seen no larvae definitely of this species, but there is a series of larvae (USNM) from Vienna, Va., with the fenestra-type coloration that may well be ledra. The head pattern in these is much fainter; because this faintness could easily be due to age and fading, no attempt is made to separate the species at this time.

Rhyacophila fenestra Ross

FIGURE 10,b

Rhyacophila fenestra Ross, 1938a, p. 102 (male and female genitalia, larva).—Ross, 1944, p. 36 (male and female genitalia, larva).—Ross, 1956, p. 7, 90 (larva, male genitalia).

This species still is known to occur only in Illinois; it is common in the southern part of the state.

The following description is based on a series of determined larvae from Ross. The larvae of this species and of *ledra* correspond in

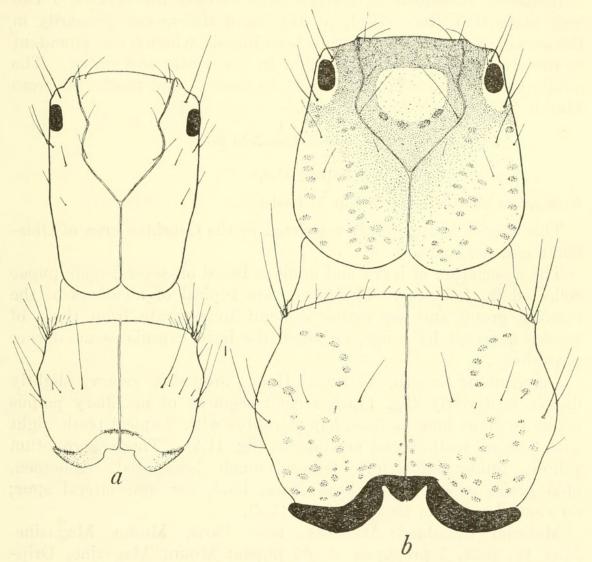


FIGURE 10.—Rhyacophila species 3: a, head and pronotum, dorsal aspect. R. fenestra: b, head and pronotum, dorsal.

structure with the other members of the group, yet possess a color pattern on the head and pronotum strikingly different from the rest of the species.

Description: Length, 16 mm. Head, brownish yellow, becoming infuscate mesally and anteriorly, but leaving a large pale central spot on frontoclypeus; muscle scars dark and conspicuous laterally

and posteriorly (fig. 10,b). Second segment of maxillary palpus about twice as long as first. Left mandible with 2 apical teeth, right with 3 apical teeth, mesal one longest (like fig. 11,b). Thorax, pronotum yellow, muscle scars dark and conspicuous; fore femora much broadened. Abdomen, anal proleg with neither basoventral hook nor apicolateral spur; ventral teeth lacking on claw (like fig. 11,d).

Material examined: Illinois, Hardin County, Karbers Ridge, May 1, 1936, 5 larvae (INHS).

Remarks: Inasmuch as I have not collected the species, I can only state that Ross (1944, p. 37) found the species primarily in the area of Ozarkian Uplift in Southern Illinois, where it was abundant in the clear rapid streams that flow in the winter and spring. The adults were recorded from April 21 to June 6, and the larvae from March 23 to May 26.

Rhyacophila kiamichi Ross

FIGURE 11,a,b

Rhyacophila kiamichi Ross, 1944, p. 37 (male).

This species is apparently restricted to the Ozarkian area of Oklahoma and Arkansas.

The association of larva and adult is based on several male pupae collected in Arkansas. The larvae are typical of members of the carolina group and are rather difficult to separate from those of species 5 except by range, although the head capsule seems darker posteriorly.

Description: Length, 14 mm. Head, brownish yellow, slightly darker posteriorly (fig. 11,a); second segment of maxillary palpus about twice as long as first; left mandible with 2 apical teeth, right with 3 apical teeth, mesal one longest (fig. 11,b). Thorax, pronotum yellow, immaculate; fore femora much broadened. Abdomen, anal proleg with neither basoventral hook nor apicolateral spur; no ventral teeth on claw (like fig. 11,d).

Material examined: Arkansas, near Paris, Mount Magazine, May 16, 1958, 3 prepupae, 8 ♂♀ pupae; Mount Magazine, Dripping Springs, May 16, 1958, 1 prepupa, 7 ♂♀ pupae; Mena, May 15, 1958, 1 larva, 3 prepupae, 6 ♂♀ pupae; Dover, May 17, 1958, 5 pupae.

Remarks: All the collections were made in small brooks ranging in width from a foot to several yards. Most of the streams were comparatively warm and slightly turbid.

The type series of adults was collected in early May. In Arkansas many were on the wing in late May; as many more were ready to

emerge, and a few still to pupate. Emergence evidently continues into June at least.

Rhyacophila species 5

FIGURE 11,c,d

The larva of this form has been taken in Massachusetts, New Hampshire, New York, North Carolina, and Tennessee. The only species in the *carolina* group with a known similar distribution is *carolina* Banks.

The larvae are very much like those of *kiamichi*, from which they are widely separated geographically. They seem also to have the

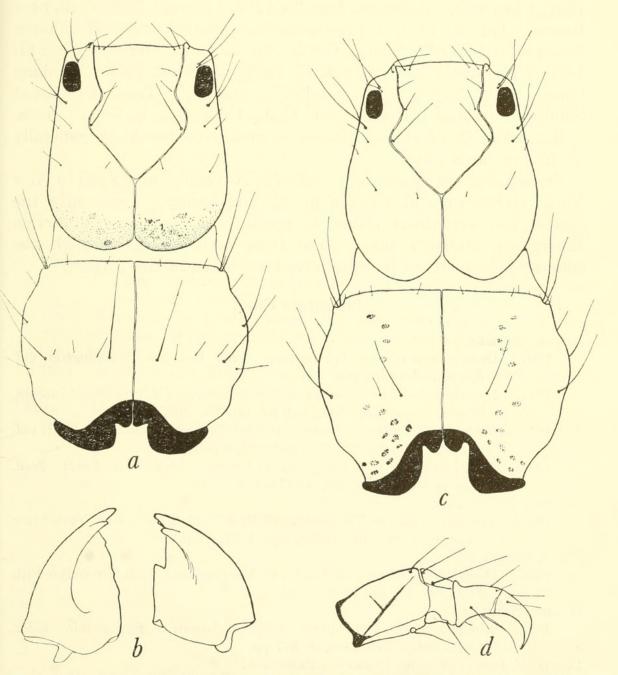


FIGURE 11.—Rhyacophila kiamichi: a, head and pronotum, dorsal aspect; b, mandibles, dorsal. R. species 5: c, head and pronotum, dorsal; d, anal proleg, lateral.

head uniformly colored, with a few inconspicuous muscle scars on the pronotum.

Description: Length, 14 mm. Head, golden, immaculate (fig. 11,c); second segment of maxillary palpus about $1\frac{1}{2}$ times length of first; left mandible with 2 apical teeth, right with 3 apical teeth, mesal one longest (like fig. 11,b). Thorax, pronotum golden, with faint indications of muscle scars; fore femora much broadened. Abdomen, anal proleg with neither basoventral hook nor apicolateral spur; claw without ventral teeth (fig. 11,d).

Material examined: Massachusetts, Chesterfield, July 6, 1958, 1 prepupa. New Hampshire, Pinkham Notch, Cutler River, Aug. 24, 1957, 1 prepupa; Fabayan, Aug. 25, 1957, 1 larva. New York, near Roscoe, Apr. 4, 1959, 1 prepupa; Slaterville Springs, Wildflower Preserve, tributary to Sixmile Creek, Nov. 13, 1960, 2 larvae—Nov. 14, 1957, 1 prepupa. North Carolina, Pisgah National Forest, Looking Glass Creek, July 5, 1958, 1 larva, 1 prepupa. Tennessee, Great Smoky Mountains National Park, Cades Cove, Apr. 6, 1941, 1 larva.

Remarks: This form was found in small cold brooklets, generally about 1-3 yards wide.

Prepupae of the species were taken in November and April in New York; larvae were also taken in fall and spring. Apparently the species can overwinter either as prepupae or fully grown larvae. Emergence probably takes place from early spring through the summer inasmuch as prepupae have been taken in late August.

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