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Life History of *Ceratocombus Vagans* (Hemiptera: Heteroptera: Ceratocombidae), With Notes on the Immature Stages

John D. Lattin
Oregon State University

LIFE HISTORY OF *CERATOCOMBUS VAGANS* (HEMIPTERA: HETEROPTERA: CERATOCOMBIDAE), WITH NOTES ON THE IMMATURE STAGES

John D. Lattin[1]

ABSTRACT

The biology and life stages of *Ceratocombus vagans* are given together with distributional notes. The current systematic position of Ceratocombidae is reviewed. This species is one of the most generalized Hemiptera: Heteroptera known. Its predatory habits lend credance to the idea that primitive Hemiptera: Heteroptera were predaceous as suggested by Stys and others. *Ceratocombus vagans* occurs in moss, leaf litter, and under loose bark. It has wide distribution in much of North America.

The family Ceratocombidae as presently known contains eight genera and about 50 species world-wide (Štys 1995). This author suggested that a great many more species remain to be discovered and described, particularly in the tropical regions of the world. Species of Ceratocombidae are very small in size—usually under 2 mm in length—a factor contributing to their obscurity, especially when combined with their cryptic habits in leaf-litter, rotting bark and mosses. Collecting is best accomplished by sifting or by the use of a Tullgren separator. These tiny predators are among the most generalized true bugs known to us (Štys 1995); being placed in the Diposcomorpha near the base of the Hemiptera: Heteroptera immediately above the Enicocephalomorpha (Schuh and Štys 1991, Wheeler et al. 1993). *Ceratocombus vagans* McAtee and Malloch, originally described from Maryland and subsequently found throughout the eastern United States and now in Oregon and Washington.

According to Štys (1995), there are three subgenera and about 25 described species of *Ceratocombus* (Signoret) known today. Only three species are known from Canada and the United States and Puerto Rico. Just a handful of publications have appeared on *Ceratocombus vagans* since its description; usually short notes recording its presence and perhaps the habitat in which the specimens were found (e.g. Usinger 1946).

Aside from a few scattered notes, the only biological work that has been done on this family was that of Butler (1923) who dealt with several species found in England, including *Ceratocombus coleoptratus* (Zetterstedt). Butler provided an illustration and brief description of *C. coleoptratus*. The immature stages received little attention from entomologists after Butler's work until Štys (1959) published a paper describing and discussing the final nymphal instar of *Ceratocombus (Ceratocombus) coleoptratus* taken from *Sphagnum* moss in South Bohemia, Czechoslovakia (also by use of a Tullgren

[1]Department of Entomology, Oregon State University, Corvallis, OR 97331-2907.

sampler). Additional information was given on the biology of this species. His careful examination and descriptions provided the first review of the nymph of any species. The works by Štys have provided us with a much better understanding of the important systematic position this small group of bugs occupies in the phylogenetic considerations of the Hemiptera: Heteroptera. The reader is referred to Štys (1995) for greater details and to Wheeler et al. (1993) for additional information on the phylogeny of the Hemiptera, including the position of the Dipsocomorpha.

I was fortunate enough to find this tiny species in the sphagnum bogs of northern Michigan in the vicinity of the University of Michigan Biological Station at Douglas Lake (known affectionately as the "Bug Camp" for many decades). Most of the morphological and biological notes came from studies made there in summer of 1950 while a student at the Biological Station. Subsequently, I found it in Oregon and in samples from North Cascades National park at the extreme northern edge of Washington (Lattin 1997) where it was remarkably common in pitfall traps placed in the riparian zone of Big Beaver Creek. It appears therefore, that *C. vagans* has a boreal distribution whose range extends westward to the Pacific Coast.

Systematics. Much has happened since *Ceratocombus vagans* was described by McAtee and Malloch (1925) with the holotype from Glen Echo, Md. Originally placed in the family Cryptostemmatidae by these authors, it was moved to the family Ceratocombidae Fieber and more recently (Henry 1988) to the nominate subgenus *Ceratocombus* (*Ceratocombus*) Signoret. The reader is referred to Štys (1995) and the section on the Euheteroptera: Dipsocoromorpha he authored for a thorough discussion of current taxa and their placement. Štys recognized five families and three of these are known from North America (and elsewhere): Ceratocombidae, Dipsocoridae, and Schizopteridae. All are poorly known and although rarely collected are of great interest because of their phylogenetic position within the Hemiptera: Heteroptera. Henry (1988) cites Florida, Maryland, New York, Ontario and Virginia in his coverage of distribution with the added note of Panama. The Ontario record is from Walley (1935), the locality was Biscotasing, Ontario. Somewhat later, Usinger (1946) reported *C. vagans* from the summit of Brasstown Bald, Georgia (ca. 1370 m elev.) and Puerto Rico (Barber 1939, Usinger 1946). I have seen specimens from Arkansas (Illinois Natural History Survey, INHS); Illinois (INHS); Indiana (INHS); Iowa (H.M. Harris Coll.); Kansas (University of Kansas, UK); Kentucky (INHS); Louisiana (INHS); Michigan (this study); Oregon (Oregon State University Collection, OSUC); Washington (North Cascades National Park Collection, NCNPC). Once appropriate collecting techniques are used, additional localities are certain to be reported.

Several workers have mentioned the type of habitat in which *Ceratocombus vagans* was collected. Blatchley (1926) collected *C. vagans* ". . . beneath vegetable debris and between roots of tufts of grass along the bay front; in spring taken by sweeping in low moist grounds. At the Park [Blatchley refers to Royal Palm Park, Fla.], it was very common in the dense hammock on decaying leaves of royal palm and on the herbage in the everglades." Usinger (1946) reported taking *C. vagans* ". . . amidst loose frass beneath the bark of a decaying tree near the summit of Brasstown Bald, Georgia...Both macropterous and brachypterous specimens were very abundant on the ground beneath leaf mold and numerous small fruits of a fallen Sierra palm near the summer of El Yunque, Puerto Rico . . ." Specimens have been taken at Lawrence, Kansas from the grass overhanging the edge of a small pond. In Illinois, it was taken from material gathered from under logs and from gen-

eral leaf debris on the forest floor (data from specimens from the Illinois Natural History Survey).

The Oregon specimens were collected by me from a locality near Corvallis from leaf litter at the edge of a tiny stream in MacDonald Forest and from the H.J. Andrews Experimental Forest, a Long-Term Ecological Research site east of Eugene, Oregon in an old-growth Douglas-fir site of 6400 ha. These latter specimens came from litter taken at the edge of a small seep in an opening in the forest via a Tullgren funnel. The specimens from Washington were taken in the riparian zone of Big Beaver Creek in the North Cascades National Park via pitfall traps.

In Michigan, this species was collected from sphagnum moss found in bogs, where it was restricted to the hummocks of the moss. It was also collected in clumps of grass and sedge around a small beach pool. In every case where the habitat was noted, moisture was present, a factor that seems to determine the habitat for C. *vagans*.

METHODS

The University of Michigan Biological Station is located on the southeast shore of Douglas Lake in Cheboygan County, Michigan. Several bogs are this area and these were visited to collect *C. vagans*. Mud Lake, located about 6.4 km northeast of the Biological Station in Sec 7, Inverness Township, Cheboygan County, Michigan, was also included in this study. Specimens had previously been taken there by H. B. Hungerford, R. I. Sailer and others. The collecting was confined to the sphagnum moss mat that was located on the southeast shore where the mat was about 30 m from the edge of the water. The sphagnum forms hummocks around each shrub and tree and these hummocks were the best collecting sites for *C. vagans*. Malone Lake, located about 15 km north of the Biological Station in Sec 11, Hebron Township, Cheboygan County, Michigan was another site. Here the sphagnum mat supported a heavy growth of leatherleaf (*Chamaedaphne calyculata* (L.) Moench). The third locality was a small bog .8 km southeast of Stutsmanville, Emmet County, Michigan (R6W, T36N, Sec 23 NE ¼). Here the sphagnum was confined to a narrow zone about 6 m from the edge of the water. The fourth locality was a small pond located about 9 m from the edge of the northwest shore of Burt Lake, Cheboygan County, Michigan (R3W, T36N, Sec 5, SE ¼). Specimens were collected in the small clumps of grass and sedge that grew at the waters edge. The precise habitat is somewhat different from those found in bogs, although both habitats had moisture and some cover. The fifth locality was Bryant's Bog, located on the southwest shore of Douglas Lake, Cheboygan County, Michigan (R3W, T37N, Sec 30), where specimens were collected from the sphagnum moss that was found around the western edge of this bog lake remnant. As at Mud Lake, the hummocks around the trees and shrubs provided habitats for *C. vagans*. The final locality was Devil's Pond, located 305 m northwest of Bass Lake in Sec 31, Summit Township, Mason County, Michigan. Here the sphagnum occurred in and around a mixed growth of trees and shrubs with some open areas.

Live material. Specimens of *C. vagans* were collected by bringing in sacks of sphagnum moss from the bogs for examination in the laboratory. Field inspection of the moss was found to be unproductive. The moss was removed and shaken in small quantities over a piece of white paper. Specimens were picked up with a fine brush and placed individually in small glass dishes, with the specimen on a small disk of blotting paper. A small piece of sphagnum was placed in the dish and changed as necessary. The paper was

kept moist by daily application of water. Too much water killed the specimens if caught in the water film, or they would die if the paper dried out. The paper was changed every few weeks, because of the growth of fungi. The fungus had no apparent affect on the nymphs or adults.

The cast skins of the nymph were removed and placed in numbered bottles of alcohol, keeping the exuviae of each specimen together. As adults appeared, they were placed with others of the opposite sex to obtain eggs. Later, better results were obtained if a number of males and females were placed in the same dish, increasing chances of mating. Pieces of sphagnum were present in each of the dishes to provide the necessary material for the deposition of the egg. When a specimen would die, it was placed in alcohol with any cast skin of the same individual. Various parts of *C. vagans* were mounted on slides for further study.

RESULTS

General behavior. All five instars of *C. vagans* were collected and observed. *Ceratocombus vagans* is constantly moving, running in short, rapid bursts. Neither flight or jumping was observed. When stopped, it would clean its rostrum and antennae, using the setal combs located on the front tibiae (Fig. 7), sitting back on the middle and hind legs. Besides being caught in slightly shady habitats, it has been taken at lights in other parts of its range. Obviously, those adults attracted to light were macropterous rather than micropterous, the usual condition.

Feeding habits. *Ceratocombus vagans* is predacious in its feeding habit, lending credance to the fact that primitive Hemiptera: Heteroptera were predaceous. This was suspected from the manner in which the beak is held. Moreover, a 3-segmented beak, such as that of *Ceratocombus*, usually indicates predacious habits in the Hemiptera: Heteroptera. Nymphs and adults were supplied with a variety of organisms that were found in sphagnum, but it was not until late summer that any were actually seen to feed. The first such observation was made when a female adult was seen feeding on an adult male. Later, other specimens were observed feeding on small mites and Collembola that were common in the moss. When feeding on Collembola, *C. vagans* inserted its beak between the abdominal segments, where the body wall was lightly sclerotized. The bug would stalk the victim, then make a single jab with its beak and immediately withdraw it. Shortly, the springtail would stop moving and *C. vagans* would again approach the victim and proceed to feed. After sucking out the body juices, the victim would be abandoned. If the predator was disturbed while feeding, it would leave but often would return after a short time and resume feeding, using its front legs to hold the victim while feeding. Afterwards, it cleaned its beak and antennae as described. Occasionally, this species was observed to insert the stylets into the sphagnum, apparently to obtain water.

Seasonal occurrence. In Michigan, first instar nymphs were collected in the middle of June along with a few second instar nymphs. The first adults appeared towards the end of July and both late instar nymphs and adults were taken until the middle of August, at which time the study was terminated. Material studied from Illinois contained nymphs taken every month of the year except May, June and July, while adults were taken from May through October. Judging from the material from Illinois, it seems that there the winter is spent as a partially grown nymph. In Michigan it appeared that they wintered in the egg stage, since the first instar nymphs were taken in June and the eggs were taken during the latter part of August.

The sphagnum mat is flooded during the spring months, producing excessive moisture that would be detrimental to both nymphs and adults. If the winter is passed in the egg stage in northern Michigan it is quite likely that the eggs were able to withstand this inundation without being seriously affected. In Illinois, where this species was collected largely in leaf mold, it is possible that the amount of moisture during the winter and spring months would not be fatal to the nymphs. Two explanations are possible—that the habitat is somewhat different from that found in the bogs or that hibernation occurs in slightly higher habitats.

Description of life stages. Egg. Length, 0.45mm; diameter, 0.14mm. Form subcylindrical, elongate, ends rounded, operculum rimmed, projecting beyond end of egg, suture not discernable before hatching (Figs. 8a,10). Chorionic spines minute, solid with blunt end, peg-like, longest at opposite end from operculum (Fig. 8b). Sculpturing minutely hexagonal over entire surface (Fig. 8c). (Cobben 1968) provided a detailed description of *Ceratocombus coleoptratus* from Europe. According to him, there were no clearly defined aeropylar canals but there were three micropylar openings.

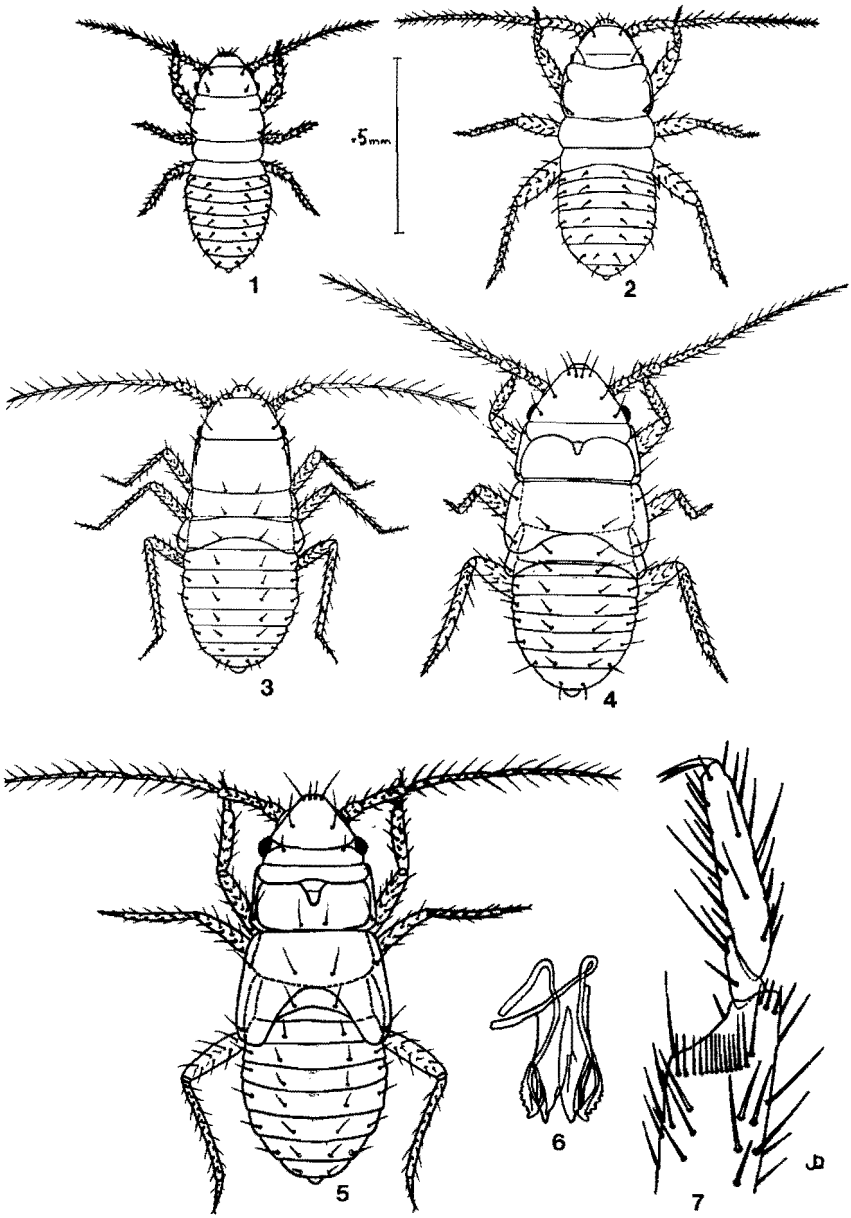
The first eggs were obtained by dissecting gravid females to observe their size and shape. Only a single egg was found in the mature state in each of the egg-bearing females examined. The first deposited eggs were in the blotting paper on the bottom of a Stender dish with only a small circular hole to be seen. All that showed from above was a small circular hole. When the eggs were dissected out of the paper, they agreed perfectly with those dissected from the females. Eggs were found deposited in sphagnum at a later date (Fig. 9) where the deposition was confined to the terminal compact leaf clusters. They were inserted by means of the toothed ovipositor (Fig. 6). Wygodzinsky (1947, 1948, 1950) reported on the eggs found in the Schizopterinae (Cryptostemmatidae) closely related to the Ceratocombidae. He concluded that at most, only two mature eggs could be found in an adult (only one such individual found) whereas most specimens contained only a single egg. These excellent papers have many fine drawings including some of the nymphal instars of other species. Although the paper deals with another subfamily, it contains valuable information that may be applicable to other related taxa.

First instar. (Fig. 1) Reddish, elongate, legs darker than body. Head triangular; pronotum trapezoidal, apical constriction broadly interrupted in middle. Abdominal segments with long setae on lateral margins and in submedial position. Legs and antennae setose. Rostrum 3-segmented; tarsal formula 1,1,1. Width of head across eyes 0.16–0.18 mm (7 individuals); length about 0.6 mm. Duration of instar 8 days.

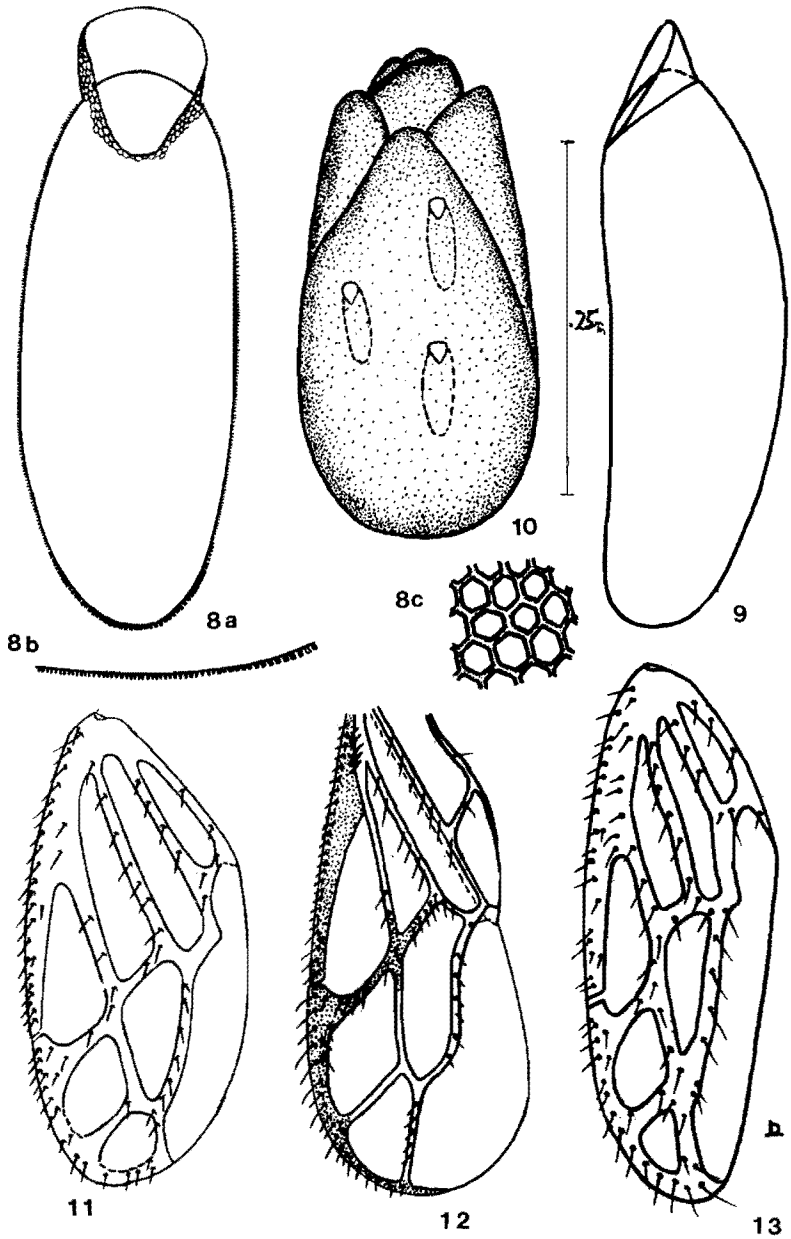
Second instar. (Fig. 2) Color as in first instar. Lateral edge of pronotum marginate, slight transverse impression apically. Width of head through eyes 0.19–0.22 mm (12 individuals); length about 0.75 mm. Duration of instar 8 days.

Third instar. (Fig. 3) Color same as previous instars. Wing pads appear for first time, anterior pair slightly exceeding anterior margin of metathorax, posterior pair slightly exceeding anterior margin of second abdominal segment. Width of head through eyes 0.23–0.28 mm (33 individuals); length about 0.85 mm. Duration of instar 10–14 days.

Fourth instar. (Fig. 4) Color same as previous instars. Apical transverse impression of pronotum ending medially in a fovea. Anterior wing pads almost attaining posterior margin of metathorax, posterior pair reaching anterior margin of third abdominal segment. Width of head through eyes 0.29–0.30 mm (35 individuals). Length about 0.95 mm. Duration of instar 10–14 days.



Figures 1–7. *Ceratocombus vagans* nymphal stages, first instar (1), second instar (2), third instar (3), fourth instar (4), fifth instar (5). Figure 6. Adult female *C. vagans*, ovipositor. Figure 7. *C. vagans*, portion of front tibia and tarsus showing tibial comb and number of tarsal segments.



Figures 8–13. Egg of *Ceratocombus vagans*, top view (8a), detail of the chorionic processes (8b), detail of egg sculpturing (8c), side view (9). Figure 10. Eggs *in situ* in leaf bud of sphagnum. Figure 11–13. Hemelytra of *C. vagans*, micropterous female (11), macropterous female (12), micropterous male (13).

Fifth instar. (Fig. 5) Dorsal aspect of head with sub-basal, transverse impression. Anterior wing pads reaching third abdominal segment, covering posterior pair. Width of head through eyes 0.312–0.336 mm (37 individuals); length ca. 1.2 mm. Duration of instar 10–14 days. Total duration of nymphal stadia ranged from 8–14 days in the laboratory.

Adult. Elongate oval, female broader posteriorly. Pale to dark brown, antennae and legs straw-colored. Antennae 4-segmented with apical two segments slender and whip-like. Beak 3-segmented and tapered. Head subtriangular. Pronotum with apical transverse impression broadly interrupted at middle; posterior margin with impressed line; a medial longitudinal impressed line. Macropterous form: hemelytra semi-transparent, venation distinct, membrane normal in size (Fig. 12); hind wings membranous with subapical notch, two veins apparent. Micropterous form; hemelytra opaque, veins thick and indistinct, membrane reduced (Figs. 11, 13), hemelytra meet in straight line down the back in male; hind wings small, pad-like, ovipositor with teeth (Fig. 6). Tarsal formula 2,2,2. Length 0.75 mm–1.75 mm, width of head through eyes 0.31–0.36 mm, females larger than males.

DISCUSSION

Ceratocombus vagans McAttee and Malloch is widely distributed, ranging from Canada to Panama, and New York to Kansas and in Washington and Oregon. In Michigan, this species was collected in hummocks of sphagnum moss under small trees and shrubs in which the moss was moist but not saturated or heavily shaded and in clumps of grass and sedge along the margin of an old beach pool. Elsewhere, the bug has been taken from leaf litter on the ground and in frass under the bark of a dead tree. Moisture is one of the main factors that determines the habitat of this species. The males and females occur in macropterous and micropterous forms.

In the laboratory, the total life cycle from egg to adult was about 2 months. It is suggested that in northern Michigan, the insect overwinters in the egg stage but as a late instar nymph in Illinois and points south.

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