

## A NEW BITING MIDGE FROM UPPER CRETACEOUS (CENOMANIAN) AMBER OF NEW JERSEY (DIPTERA: CERATOPOGONIDAE)

WILLIAM L. GROGAN, JR., AND RYSZARD SZADZIEWSKI

Department of Biological Sciences, Salisbury University, Salisbury, Maryland 21801 and  
Department of Invertebrate Zoology, University of Gdansk, Czołgostow 46, 81-378 Gdynia, Poland

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ABSTRACT—*Culicoides? casei* n. sp., a new fossil biting midge from Upper Cretaceous (Cenomanian) amber of the Raritan Formation of New Jersey, is described and illustrated. It is the oldest (about 94 Ma) described ceratopogonid from North America, and is tentatively placed in *Culicoides* because its genitalia most closely ally it with that genus. Other characters that indicate its affinity with *Culicoides* include cylindrical fourth tarsomeres, wing with prominent microtrichia, and a swollen third palpal segment with a very large sensory pit. Characters it possesses that are found in *Ceratopogon* include long prominent cerci, palisade setae on hind tarsomere one, radial cells of wing separated by a small intermediate vein, and macrotrichia near the wing tip.

*Simulidium priscum* Westwood from the Purbeck Formation of the Upper Jurassic (about 140 Ma) of England appears to be a species of *Leptoconops*, a primitive bloodsucking ceratopogonid. *Pseudosimulium humidum* (Westwood), also from the Purbeck Formation, which was formerly considered to be the oldest fossil ceratopogonid, is not considered to belong to the Ceratopogonidae.

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### INTRODUCTION

TWO SMALL, poorly preserved Diptera were illustrated and described by Westwood (*in* Brodie, 1845) as *Simulium humidum* (Simuliidae) from the Purbeck Formation of the Upper Jurassic (about 140 Ma) in England. Handlirsch (1908) assigned this species to the new genus *Pseudosimulium*, in the family Psychodidae. Subsequently, several authors (Smart, 1945; Stone, 1963; Rubtsov, 1974; Rohdendorf, 1964) assigned *Pseudosimulium humidum* to the family Simuliidae. Recently, Craig (1977) correctly concluded that *P. humidum* does not belong to the Simuliidae and suggested that this species was a member

of, or is closely related to, the family Ceratopogonidae. However, the authors agree with W. W. Wirth and A. Borkent (personal commun.) that *P. humidum* does not belong to the Ceratopogonidae based upon characters of its head, wing, body, and legs. No further suggestions as to the familial status of this enigmatic species are offered.

However, Westwood (1854) subsequently published an illustration of a fossilized wing from the same Jurassic Purbeck Formation labeled *Simulidium priscum* W., which qualifies them as valid new genus and species names. This specimen is not in the British Museum (Natural History) where Westwood's other

fossil specimens are located and is presumably lost according to its present curator, P. E. S. Whalley (A. Borkent, personal commun.), but Westwood (1854, p. 384) referred to it as "the wing of a small Dipterous insect, apparently allied to *Simulium*." The authors, along with A. Borkent and W. Wirth (personal commun.), conclude that if the illustration of *Simulidium priscum* Westwood (1854) is accurate, it probably represents a species of *Leptoconops*, a primitive vertebrate bloodsucking genus of ceratopogonids (Borkent et al., 1987). If indeed it is a ceratopogonid and a species of *Leptoconops*, as it appears to be, it would represent the oldest fossil biting midge.

Fossils that are unquestionably ceratopogonids have been recorded from Lower Cretaceous (Neocomian) Lebanese amber (about 125 Ma) by Schlee and Dietrich (1970). These specimens still await a formal description but other ceratopogonids have been described from Upper Cretaceous amber. Boesel (1937) described six species from Canadian amber (Campanian; 74 Ma), and Remm (1976) described nine species from Siberian amber (Coniacian-Santonian; about 80 Ma).

Ceratopogonidae are also known from Tertiary and Quaternary deposits from many parts of the world. The Baltic ambers of Eocene age (about 40 Ma) are especially rich in fossil ceratopogonids (Meunier, 1904). Szadziewski (1988) recently completed a study of some 1,100 fossil specimens from Baltic amber containing over 100 species in some 20 genera, representing all modern subfamilies and most tribes of the Ceratopogonidae.

The genus *Culicoides* with over 1,000 Recent species is a cosmopolitan group of vertebrate blood-feeding biting midges and the largest genus of ceratopogonids. Twenty-eight species of fossil *Culicoides* have been described as follows: four species from Late Cretaceous Siberian amber (Remm, 1976); seven species from Eocene amber (Szadziewski, 1988); 12 species from early Miocene strata in Rott, West Germany (Statz, 1944); and five species from Miocene silicified nodules in California (Palmer, 1957; Pierce, 1966). The California Miocene species are described from pupae, which are poorly known among Recent species and therefore have little taxonomic value.

Through the courtesy of D. Baird (Princeton University), we have studied a piece of amber collected by G. R. Case in 1966 from the Raritan Formation of New Jersey. Enclosed in this amber were three Diptera, two nonbiting midges of the family Chironomidae (subfamily Orthocladiinae) and one biting midge of the family Ceratopogonidae. Photographs of these insect inclusions and a brief report of this discovery appear in Case (1982). The ceratopogonid specimen described herein is presented in Case (1982, fig. 16-12), but that photograph elucidates few of the structural details of the specimen due to its position in the amber and its small size.

The amber containing these three insects is very brittle (more so than Baltic amber), is the color of dark honey, and is quite transparent. The amber was prepared for study as follows: the amber was cut with a jewelry saw into three pieces each containing an insect, and the piece containing the ceratopogonid (herein designated PU 88892A) was ground and polished with fine sandpaper and powdered chalk into a cubic shape roughly  $5 \times 5 \times 4$  mm. The junior author has successfully introduced Canada balsam into Baltic amber containing ceratopogonids in order to fill empty cavities of the body and other structures. This has enabled detailed study of structures not otherwise readily visible, such as the male genitalia. Because of the fragile nature of the amber containing PU 88892A, small holes were not drilled into the amber for this purpose. The polished amber containing PU 88892A was glued to a glass cover slip with Canada balsam, covered with a smaller cover slip in the the same manner, and then imbedded in plasticine on a microscope slide. Examinations were made with dissecting and compound microscopes at

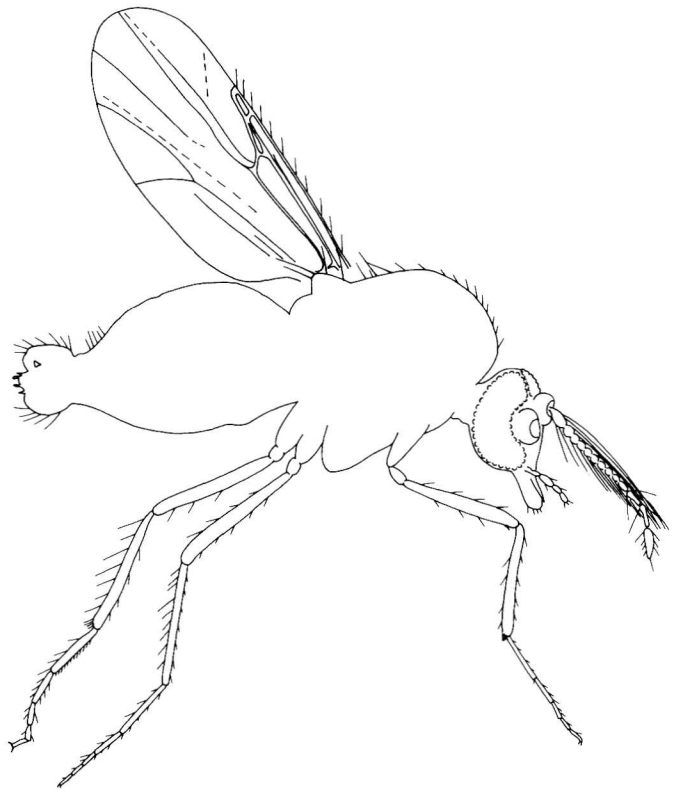


FIGURE 1—Habitus of *Culicoides? casei* n. sp., holotype (PU 88892A),  $\times 50$ .

magnifications ranging from  $40\times$  to  $240\times$ . Measurements were made with an ocular micrometer and drawings with a camera lucida. For an explanation of general terms dealing with the Ceratopogonidae, see Downes and Wirth (1981).

#### SYSTEMATIC PALEONTOLOGY

Class INSECTA Linnaeus, 1758

Order DIPTERA Linnaeus, 1758

Family CERATOPOGONIDAE Newman, 1834

Genus *CULICOIDES* Latreille, 1809

*CULICOIDES? CASEI* n. sp.

Figures 1, 2

*Diagnosis.*—Unique among *Culicoides* in having male genitalia with long slender cerci that extend well beyond the distal margin of tergite IX.

*Holotype description.*—Male. Head: brown, eyes narrowly separated (Figure 1); pubescence not visible (this character not usually visible in amber specimens); antenna (Figures 1, 2.1) with 13 flagellomeres; flagellomeres 2–9 globular, 10 slightly elongated, 11–13 elongated; sensilla coeloconica not visible on flagellomere 1 or others; proximal 10 flagellomeres with whorl of sensilla chaetica forming the dense plume that extends beyond flagellomere 12; flagellomeres with lengths in proportion of 15-7-5-5-5-5-5-5-7-16-19-20; antennal ratio, derived by dividing the combined lengths of proximal 10 flagellomeres into combined lengths of distal 3, is 0.86; total flagellum length  $525 \mu\text{m}$ ; proboscis moderately long (Figure 1); palpus (Figures 1, 2.2) 5-segmented; 3rd palpal segment (Figure 2.2) slightly swollen,  $40 \mu\text{m}$  long, distal portion of mesoventral surface with very large sensory pit bearing numerous sensilla capitata; 4th and 5th palpal segments  $24 \mu\text{m}$  long. Thorax: shining brown; scutum with short sparse setae, dense pubescence and long supraalar

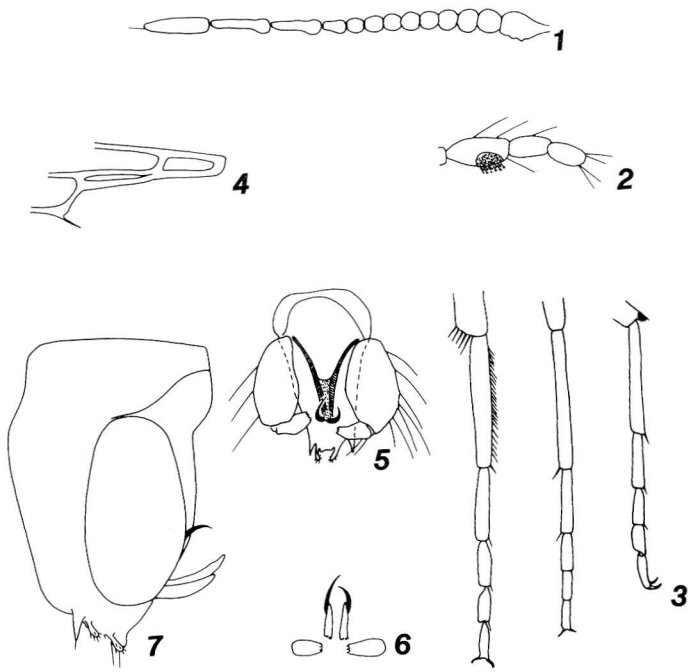


FIGURE 2—*Culicoides? casei* n. sp., holotype (PU 88892A). 1, antennal flagellum,  $\times 100$ ; 2, palpus,  $\times 200$ ; 3, tarsi, from right to left of fore, mid, and hind legs,  $\times 100$ ; 4, radial cells of wing,  $\times 100$ ; 5, male genitalia, ventral view,  $\times 100$ ; 6, tips of gonocoxites and parameres,  $\times 100$ ; 7, male genitalia, lateral view,  $\times 200$ .

setae; humeral pits present; scutellum with two lateral and four medial long setae; legs slender, unarmed (Figure 1); hind tibial comb with five setae; tarsi (Figure 2.3) with apical spines on tarsomeres 1–3 of fore leg, 1–2 of mid leg, and 1–4 of hind leg; hind tarsomere 1 with weak row of palisade setae; tarsal ratios 2.0, 2.3, 2.0 of fore, mid, and hind legs, respectively; 4th tarsomeres cylindrical; 5th tarsomeres elongate with small, equal-sized simple claws and vestigial empodia; wing length 0.83 mm, breadth 0.33 mm, venation as in Figure 1; membrane transparent without distinct pattern, covered with distinct microtrichia and macrotrichia near tip; two radial cells present, the first slit-like and about 1.25 times longer than the rhomboidal second (Figure 2.4); costal ratio 0.62; media petiolate, forking well beyond r–m crossvein, vein M2 obsolete basally; cubitus forking at level midway between r–m crossvein and medial fork; cell R5 with forking intercalary vein; halter brown. Abdomen: grayish brown; short, as typical of male *Culicoides*; genitalia as in Figure 2.5–2.7, rotated 90°; sternite IX moderately long with broad, deep caudomedian excavation; tergite IX tapering slightly distally and extending well beyond gonocoxite, apicolateral processes long, slender with apical setae, cerci long, slender extending beyond distal margin of tergite IX, remnants of segment X readily visible; gonocoxite straight, about twice as long as broad with long lateral setae; gonostylus broad basally, slightly curved and tapering distally, tips apparently broken off; aedeagus v- or y-shaped, slightly longer than broad, basal arch 0.55 of total length; basal arm and lateral margin heavily sclerotized; distal portion tapering to an apparently truncate tip; parameres apparently separated; distal portions with long, slender tips that curve ventrally.

**Remarks.**—This new species is provisionally assigned to *Culicoides* because its aedeagus and parameres most closely resemble other species of this genus, and the general features of its body conform with *Culicoides*. However, the assignment of this

species to *Culicoides* is tentative for several reasons. Although most species of Recent *Culicoides* have patterned wings, the wing of *Culicoides? casei* is apparently unpatterned. This may or may not be indicative of a patterned wing in this species in a living state. The wings of four species of *Culicoides* from Upper Cretaceous Siberian amber studied by Remm (1976) and those of 7 species from Baltic amber studied by Szadziewski (1988) are also devoid of a pattern. It is highly probable that some of these fossil *Culicoides* originally had patterned wings but the pattern may have faded or was chemically altered during the fossilization process. Furthermore, the small intermediate vein separating the radial cells of *C.? casei* is not typical of *Culicoides* but more reminiscent of *Ceratopogon*.

The male genitalia of *C.? casei* are apparently unique for *Culicoides* because of their long cerci that extend beyond tergite IX. The male genitalia of *C. succineus* Remm (1976) are somewhat similar to those of *C.? casei*, but its cerci are not prominent, the gonocoxites are more slender, and sternite IX has a shallow caudomedian excavation. The cerci of all Recent *Culicoides* are generally small and are located on the ventral surface of tergite IX. However, several genera of Ceratopogonini and Stilobezziini have prominent, elongate cerci, such as in some species of *Ceratopogon* and *Stilobezzia*. The weak palisade setae on hind tarsomere 1 of *C.? casei* is also not typical of *Culicoides* but more closely resembles the condition in some species of *Ceratopogon*.

The dark brown color of the thorax of *C.? casei* is also not typical of most species of *Culicoides*, which are usually grayish to grayish brown in color. This darker color of *C.? casei* may be the result of alteration of the original color from the resin or from carbonization during fossilization.

Finally, the authors again emphasize that the assignment of *C.? casei* as a species of *Culicoides* is tentative, as it does not fit all of the criteria of that genus. In fact, it also exhibits characters which seem to ally it with *Ceratopogon* as well. It may belong to an undescribed genus, but we hesitate to distinguish it as such due to the fact that it is a male, and its characters do not seem to warrant such action now. It may in fact belong to a genus that is the sister group of the Culicoidini and Ceratopogonini, but only the discovery of related fossil forms will determine this.

**Etymology.**—We are pleased to name this new species in honor of its collector, Gerard R. Case.

**Material.**—*Holotype male.*—Princeton University Museum of Natural History (PU 88892A). New Jersey, Middlesex County, Sayreville, clay pits east of corner of Main St. and Truman Ave., 27 March 1966, Gerard R. Case, imbedded in amber from the Woodbridge Clay Member of the Raritan Formation, Upper Cretaceous (late Cenomanian).

**Stratigraphic occurrence.**—Christopher (1982) has recently reviewed earlier stratigraphic studies of the Raritan Formation and assigned the Woodbridge Clay Member to his palynological zone IV, the *Complexiopollis-Atlantopollis* Assemblage Zone. He dates this zone (IV) as mainly late Cenomanian but also extending into the early Turonian. Using this interpretation, the position of the Woodbridge Clay would be late Cenomanian, or about 94 Ma.

#### DISCUSSION

The six species of ceratopogonids described from Canadian amber by Boesel (1937) were previously the oldest described members of the family from North America. McAlpine and Martin (1969) placed the Canadian ambers from the Cedar Lake, Manitoba region, from which Boesel's (1937) specimens originate, from the Foremost Formation (Belly River Series), Upper Cretaceous (Campanian). McAlpine and Martin dated the spec-

imens described by Boesel (1937) and 132 undescribed fossil ceratopogonids in the Canadian National Collection from Cedar Lake and southern Alberta at 74 Ma. The nine species of ceratopogonids described by Remm (1976) from the eastern Taimyr, Siberia, were listed by him as Upper Cretaceous, Kheta Series?, Coniacian–Santonian?, giving them an approximate age of 80 Ma. For the present, *C. casei* is the oldest described ceratopogonid from the Cretaceous, and undoubtedly the oldest known ceratopogonid from North America.

Remm (1975) proposed a radical new classification of the Ceratopogonidae based on 21 characters that essentially reversed the systematic order proposed by Wirth (1952, 1965), Downes and Wirth (1981), and others. Although many of his characters are valid, the present authors believe he erred when he determined the polarity of some character states. As a result, Remm (1975) concluded that the predaceous ceratopogonids of the subfamily Ceratopogoninae, in which the female devours the male during the mating process (Downes, 1977), are the most primitive in the family. This would mean that the tribes Heteromyiini, Sphaeromyiini, Palpomyiini, and Stenoxenini (the subfamily Palpomyiinae of Remm, 1975) would be ancestral to the other Ceratopogoninae, which includes the tribes Culicoidini, Ceratopogonini, and Stilobezziini. Borkent et al. (1987), in a recently published cladistic analysis of the subfamilies of the Ceratopogonidae, indicated that this is highly unlikely. It is interesting to note that none of the genera of Remm's Palpomyiinae have been found in Cretaceous amber and these tribes are rare or absent in Baltic amber. All of the Cretaceous amber ceratopogonids described thus far are apparently members of the Culicoidini or Ceratopogonini (Remm, 1976). Some of the undescribed species in the Canadian National Collection from Cretaceous Canadian amber apparently belong to *Leptoconops* and the Ceratopogoninae but not the Palpomyiinae sensu Remm (1975) (Borkent, personal commun.).

The absence of higher predaceous ceratopogonids and the presence of vertebrate bloodsucking forms in Cretaceous ambers does not prove that the latter represents the plesiomorphic condition among the Ceratopogonidae. However, outgroup comparisons with other families of the Culicomorpha do indicate that bloodsucking is plesiomorphic for these families of Diptera as it is characteristic of Culicidae, Simuliidae, and Chaoboridae (Borkent et al., 1987). Furthermore, bloodsucking mouthparts are exhibited in the sister group of the Ceratopogonidae, the Chironomidae, in the primitive austral genus *Archaeochlus* (Downes and Colless, 1967). In addition, bloodsucking is also typical of the early lineages of ceratopogonids in *Leptoconops* and *Austroconops* (Borkent et al., 1987). Finally, since bloodsucking obviously represents the plesiomorphic condition in the Chironomidae (*Archaeochlus*), and this sister group of the Ceratopogonidae has recently been discovered in Jurassic strata (Kalugina and Kovalev, 1985), it would therefore follow that the Ceratopogonidae also date from at least this period. The Jurassic *Simulidium priscum* Westwood (1854), which in fact seems to be a *Leptoconops*, is evidence that ceratopogonids existed during the Jurassic.

These facts further support the views of Downes (1958, 1977), Glukhova (1977), and Borkent et al. (1987) that the Culicoidini, as vertebrate blood feeders, are the most plesiomorphic among the Ceratopogoninae. The authors also concur with Downes (1977), Glukhova (1977), and Borkent et al. (1987) that the predaceous Ceratopogoninae are younger lineages than the Culicoidini and that the four tribes (Palpomyiinae, sensu Remm, 1975) in which the female devours the male during mating represent the most apotypic condition within this subfamily.

The presence of vertebrate blood-feeding ceratopogonids such as *Leptoconops* from Jurassic strata (Westwood, 1854) and *Cu-*

*licoides* in Upper Cretaceous amber from Siberia (Remm, 1976) and possibly New Jersey also permits inferences on this type of feeding behavior in early biting midges. Remm (1976, p. 108) apparently recognized the significance of this fact thusly, "It is interesting to note that most of the present-day species of *Culicoides* are blood-sucking insects that attack warm-blooded animals, which prompts us to ponder the presence of warm-blooded vertebrates in the Upper Cretaceous fauna of the Taimyr Peninsula." It has long been assumed that vertebrate blood-feeding Diptera such as *Culicoides* and mosquitoes (Culicidae) fed early in their evolutionary development upon warm-blooded birds and mammals. This widely held view was thought to be correct since today few of these biting flies feed on cold-blooded vertebrates (Downes, 1958). There is no doubt that birds and mammals were present in the early to mid Cretaceous but they were not the dominant vertebrates then. The recent evidence that some dinosaurs were probably warm-blooded (Bakker, 1972; Ostrom, 1974; Ricqlès, 1974) also suggests that biting Diptera such as *Leptoconops* and *Culicoides* could have just as easily obtained blood meals from these large and numerous endotherms.

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