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BITING MIDGES *(DIPTERA : CERATOPOGONIDAE)* FROM UPPER CRETACEOUS (CENOMIAN) AMBER OF FRANCE

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Mots-clés : *Atriculiciodes, Austroconops, Leptoconops,* espèces nouvelles, France, fossile, crétacé supérieur.

Résumé. — Cératopogonidés *(Diptera : Ceratopogonidae)* de l'ambre français du Crétacé supérieur. — Trois espèces nouvelles de *Ceratopogonidae* de l'ambre du Crétacé supérieur (Cenomanium — 95 millions d'années), originaires du nord-ouest de la France, sont décrites : *Atriculicoides cenomanensis, A. incompletus* et *Austroconops borkenti.* Une quatrième espèce découverte dans cette résine fossile est provisoirement placée dans le genre *Leptoconops.* Le genre fossile *Atriculicoides,* décrit de l'ambre sibérien du Crétacé supérieur, est signalé pour la première fois en Europe. Une espèce fossile de la sous-famille *Austroconopinae* est rapportée pour la première fois à un genre *(Austroconops)* décrit d'après une espèce contemporaine *(A. mcmillani).*

Summary. — Three new species of fossil biting midges from Upper Cretaceous (Cenomian — 95 Ma) amber of NW France are described and illustrated. They are : *Atriculicoides cenomanensis, A. incompletus* and *Austroconops borkenti.* A fourth species discovered in this fossiliferous resin is tentatively assigned to *Leptoconops.* The extinct genus *Atriculicoides,* originally described from Upper Cretaceous Siberian amber, is reported for the first time from Europe. A fossil species is recorded for the first time in the extant genus *Austroconops* and the subfamily *Austroconopinae.*

The Ceratopogonidae are typical small flies of the suborder Nematocera. There are presently nearly 5.000 known species grouped in over 80 genera. Fossil biting midges are known from sedimentary rocks and fossil resins or ambers from many sites in the Northern Hemisphere sensu Laurasia (Szadziewski, 1988; Grogan & Szadziewski, 1988; Kohring & Schlüter, 1989). More than 150 fossil species have been described thus far in the family and at least further 50 are under study.

The oldest fossil ceratopogonid appears to be *Simulidium priscum* Westwood, 1854 from the Purbeck Formation of the Upper Jurassic (ca. 140 Ma) of England, which is apparently a species of *Leptoconops* (Grogan & Szadziewski, 1988). Fossils that are unquestionably biting midges have been recorded from Lower Cretaceous Lebanese amber (ca. 125-130 Ma) by Schlee & Dietrich (1970). The oldest (94 Ma) described biting midge is *Culicoides casei* Grogan & Szadziewski, 1988 from Cenomanian amber of New Jersey. Other Mesozoic biting midges have been recorded from French amber

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(Cenomanian — 95 Ma) by Schlüter (1978), from Siberian amber (Coniacian, Santonian ?, ca. 85 Ma) by Remm (1976) and Kalugina (1977), and from Canadian amber (Campanian — ca. 80 Ma) by Boesel (1937), McAlpine & Martin (1969), Downes & Wirth (1981).

Schlüter (1978) discovered in a sample of Cenomanian fossiliferous resin from the Paris Basin at least 73 arthropod inclusions, among them 9 specimens of Diptera, i.e. 4 Ceratopogonidae, 1 Limoniidae, 1 Cecidomyiidae, 1 Mycetophilidae, 1 undetermined Nematocera, and 1 Empididae. The specimens described herein are presented in Schlüter *(loc. cit.)* as Ceratopogonidae species A-D. Three of the four biting midges described by Schlüter have been re-examined, since the fourth one (species D) now placed in *Leptoconops* is presently not available. The specimens of fossil biting midges have been recorded in isolated amber pieces which were separated by W. G. Kühne, L. Kubig and T. Schlüter of Freien Universität Berlin in 1971 from Lower Cenomanian dark clayey layers of clay pits at Bezonnais near Ecommoy, (Dept. Sarthe), and Durtal (Dept. Maine-et-Loire) in NW France. The exact stratigraphic age is indicated by the associated pollen assemblage with the species *Retitricolpites sarthensis,* an index fossil to be correlated with *Acanthoceras rhotomagense* (Laing, 1975; Schlüter, 1989). The absolute age of these fossils is about 95 Ma.

Inclusions were prepared for present examination in the manner described by Szadziewski (1988). An epoxy resin in which the amber pieces were enclosed was ground to the amber surface and Canada balsam was used to fill empty cavities of the insect body. This allowed detailed study of structures not otherwise visible.

SYSTEMATIC PALEONTOLOGY

Class **Insecta** Linnaeus, 1758

Order **Diptera** Linnaeus, 1758

Family ***Ceratopogonidae*** Newman, 1834

Genus ***Atriculicoides*** Remm, 1976

Atriculicoides cenomanensis, sp. n., (fig. 1 to 13)

Ceratopogonidae species A : Schlüter, 1978 : 96 (brief description, sex not indicated, fig. 76-78, table 6 : 6; table 12: 5-7).

Diagnosis : Males of this species can be readily distinguished from other *Atriculicoides* by their 5-segmented palpi with a well developed sensory pit, and wing membrane covered with macrotrichia only on the distal half.

Description. — *Male :* poorly preserved, distorted, and embedded in amber with an air bubble. The body and the air bubble have been filled with Canada balsam. Total length about 1.1 mm. Body dark brown, flagellum pale brown.

Eyes probably pubescent and contiguous above antennae. Antennal flagellum composed of 13 flagellomeres, plume well developed (fig. 1). Flagellomeres II-IX short while distal 4 elongate (fig. 2). All flagellomeres separate and devoid of sensilla coeloconica. Total length of proximal 9 flagellomeres 292 µm. Distal 4 flagellomeres with lengths as follows (in µm) : X — 56, XI — 64, XII — 64, XIII — incomplete. Proboscis short and relatively slender (fig. 3). Palpus 5-segmented (fig. 4). Third palpal segment swollen on basal half, measuring 52 µm in total length, with a sensory pit open at midlength.

Scutum covered with numerous, strong setae (fig. 5). Scutellum with rounded apex bearing about 10 strong setae (fig. 6). Legs moderately slender, unmodified. Tibial comb not visible. All tarsomeres probably armed with apical indistinct spines (fig. 7, 8). Hind basitarsus with palisade setae (fig. 8). Claws on all legs short, simple and equal, with bifid apices (fig. 9). Empodia rudimentary (fig. 9). Tarsal ratio of fore leg 2.0, of hind leg 2.2.

Wing length 0.77 mm, costal ratio 0.58. Both radial cells well developed (fig. 10). Media petiolate. Radial veins, media and cubitus bearing distinct setae. Wing membrane covered with well developed microtrichia. Macrotrichia present only in cell r5, and in cells m1 and m2 at wing tip.

Genitalia rotated 90°. Sternite IX barely visible, apparently as in fig. 11. Tergite IX well developed but not reaching tip of gonocoxite (fig. 12); apicolateral processes (only one visible) distinctly triangular and pointed (fig. 13). Gonocoxites straight, without special armature. Gonostyli long and slender, slightly swollen on basal third and at apex. Parameres and aedeagus barely discernible. In antero-ventral view is a forked structure which resembles a laterally shifted tip of the aedeagus (fig. 12).

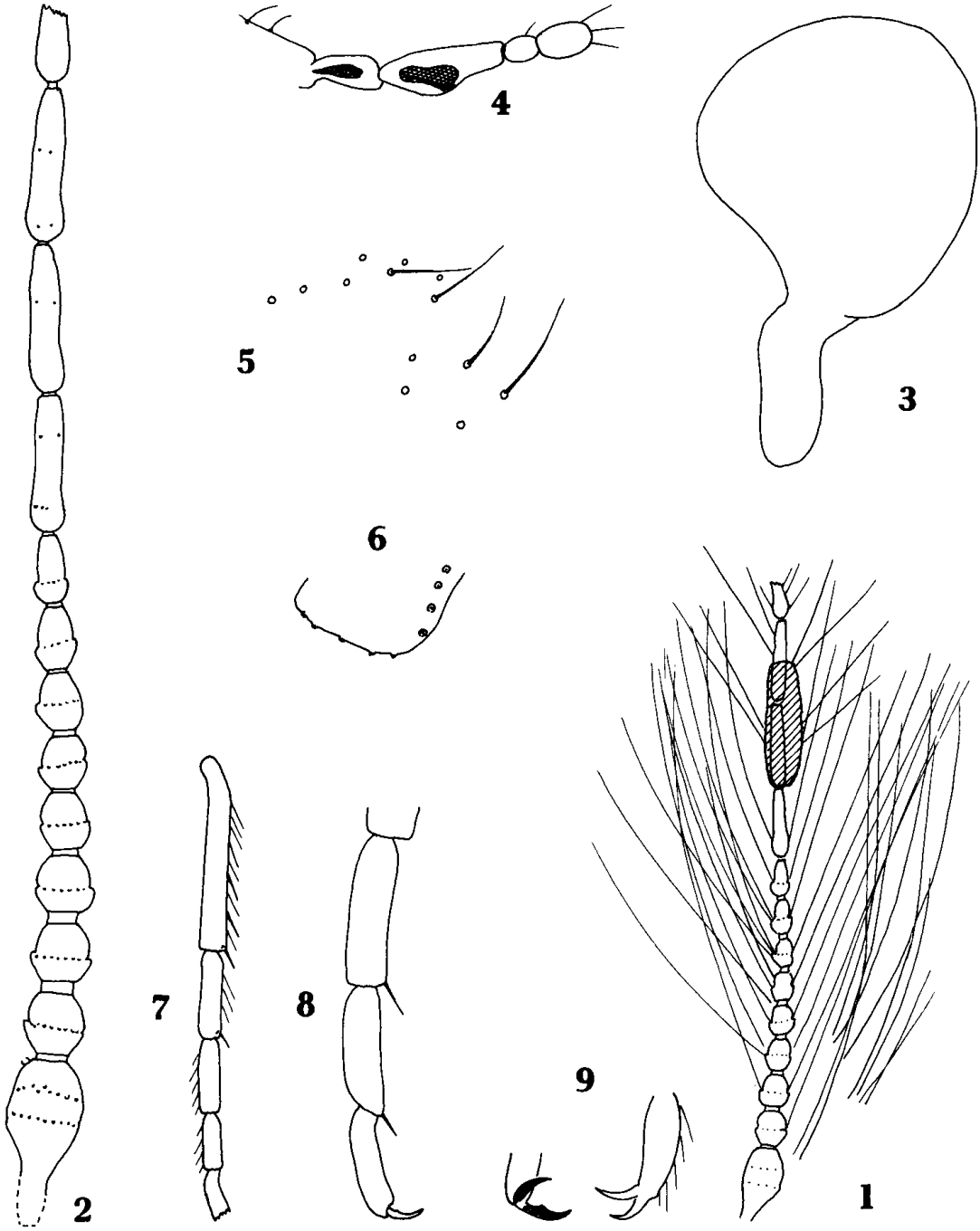


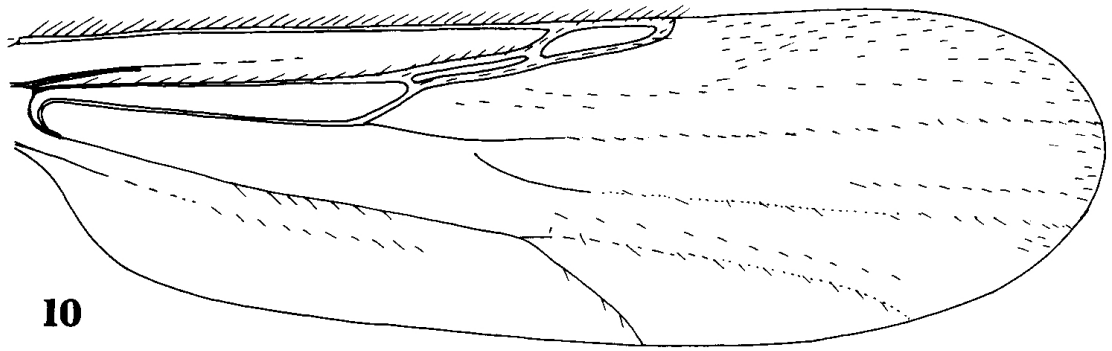
Fig. 1 to 9, *Atriculicoides cenomanensis*, sp. n., male, — 1, 2, flagellum. — 3, lateroventral view of head. — 4, palpus. — 5, some setae of scutum. — 6, laterodorsal view of somewhat distorted scutellum. — 7, tarsomeres 1-4 of hind leg. — 8, tarsomeres 3-5 of hind leg. — 9, claws of hind leg.

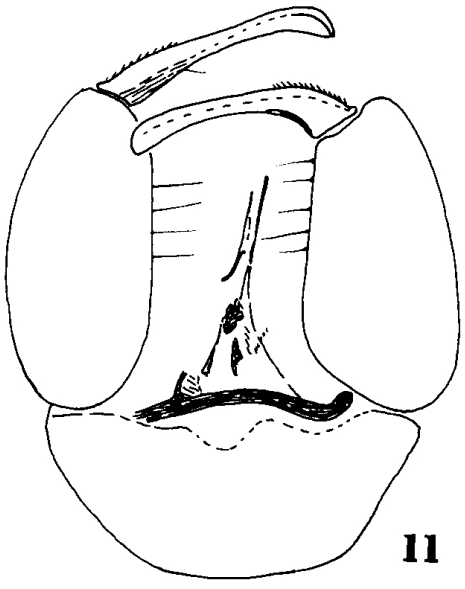
Female. — Unknown.

Material examined. — Holotype male labelled: Cer Ce Du 1, stratum typicum — C4; Durtal, Dept. Maine-et-Loire, collected by *W. G. Kühne*, 1971. The holotype is deposited in the collection of Museum of the Earth, Warsaw.

Discussion. — *Atriculicoides* is a fossil genus described from Upper Cretaceous Siberian amber by Remm (1976). It presently includes two very similar species, *A. macrophthalmus* Remm and *A. squamiciliatus* Remm. They both have a short proboscis with 5-segmented palpi, hairy wings with a long costa (CR 0.70-0.75), well developed first radial cells, and the third palpal segment with numerous sensilla capitata scattered over the entire inner surface. Females have unmodified legs with rudimentary empodia, and males have the distal 4 flagellomeres elongated and slender gonostyli as in *A. cenomanensis*, sp. n. Examination of specimens of *A. macrophthalmus* from the type series indicates that both sexes lack sensilla coeloconica on their flagella.

Atriculicoides cenomanensis seems to be typical member of the genus. It has somewhat lower costal ratio (0.58), less developed macrotrichia on its wing membrane, and the sensilla capitata of third palpal segment are grouped in a sensory pit. This is the first record of the genus in Europe.





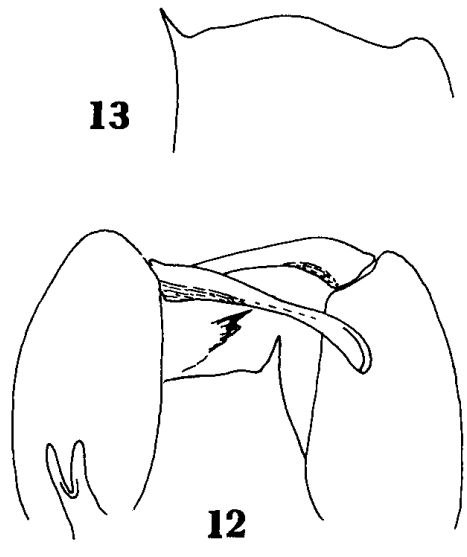


Fig. 10 to 13, *Atriculicoides cenomanensis*, sp. n., male.— 10, wing. — 11, 12, genitalia. — 13, dorsal view of tergite IX (right apicolateral process indiscernible).

Atriculicoides incompletus, sp. n., (fig. 14 to 17)

Ceratopogonidae species B *(Forcipomyia?)* : Schlüter, 1978 : 97 (brief description, sex not indicated, fig. 79, 80, table 6 : 7, table 12 : 1 — 3).

Diagnosis : A female of the species differs from all others in the genus in having a 4-segmented palpus with the third palpal segment greatly enlarged and bearing numerous sensilla capitata on its inner surface.

Description. — *Female :* described from an incomplete highly distorted specimen which is missing the abdomen and the dorsal portion of the thorax. The head and thorax are brown.

Eyes barely visible. Flagellum composed of 13 units. Flagellomeres II-VIII short, transverse to ovoid (fig. 14). Distal five flagellomeres elongated. Sensilla coeloconica absent on first flagellomere, not visible on others. Last flagellomere is probably longer than preceding one (as shown in fig. 14). However, this is not certain because the flagella are obliquely situated in amber. Proboscis short and slender. Palpus 4-segmented. Third palpal segment (fig. 15) greatly enlarged, with numerous sensilla capitata scattered in a shallow depresion on its inner surface. Last palpal segment slender and relatively long.

Legs slender, barely visible. Fourth tarsomeres cylindrical. Claws short and equal (fig. 16). Only one wing complete; length ca. 0.65 mm, costal ratio ca. 0.71 (fig. 17). Length of costa 465 µm. Both radial cells well developed. Media petiolate. Wing membrane covered with distinct microtrichia. Macrotrichia well visible on distal half of wing and probably covering the entire wing membrane.

Male. — Unknown.

Material examined. — Holotype female labelled as follows : Cer Ce Du 2, stratum typicum — C4; Durtal, Dept. Maine-et-Loire, collected by *W. G. Kühne,* 1971. The holotype is deposited in the collection of Museum of the Earth, Warsaw.

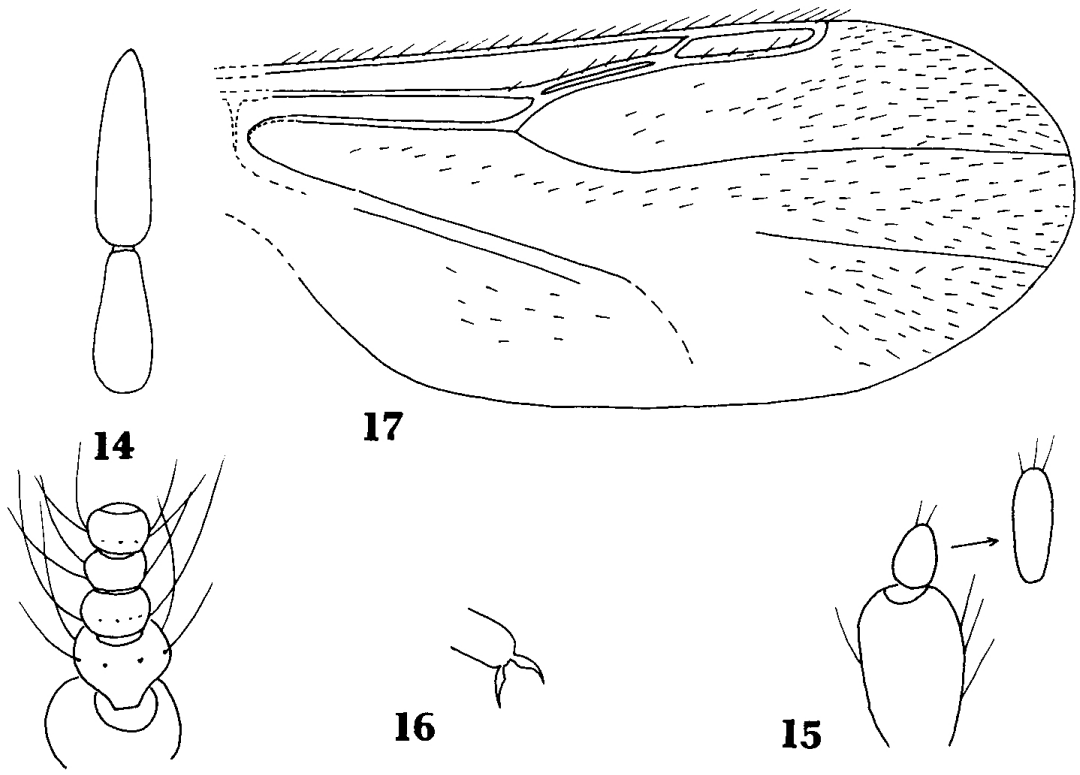


Fig. 14 to 17, *Atriculicoides incompletus,* sp. n., female. — 14, four proximal and two distal flagellomeres. — 15, two distal palp segments. — 16, claws. — 17, wing.

Discussion. — The female of *A. incompletus* has fused 4th and 5th palpal segments, which in other species of *Atriculicoides* are separated. It appears that the generic assignment of the species is correct despite the low number of palpal segments, as there are species of *Nannohelea* and *Forcipomyia* which exhibit a similar condition.

Subfamily ***Austroconopinae*** Borkent, Wirth & Dyce, 1987

Genus ***Austroconops*** Wirth & Lee, 1958

Austroconops borkenti, sp. n., (fig. 18 to 24)

Ceratopogonidae species C : Schlüter, 1978 : 98 (brief description, sex not indicated, fig. 81, 82, table 12 : 8).

Diagnosis : A female of this species can be distinguished from females of *Austroconops mcmillani* by its slender third palpal segment.

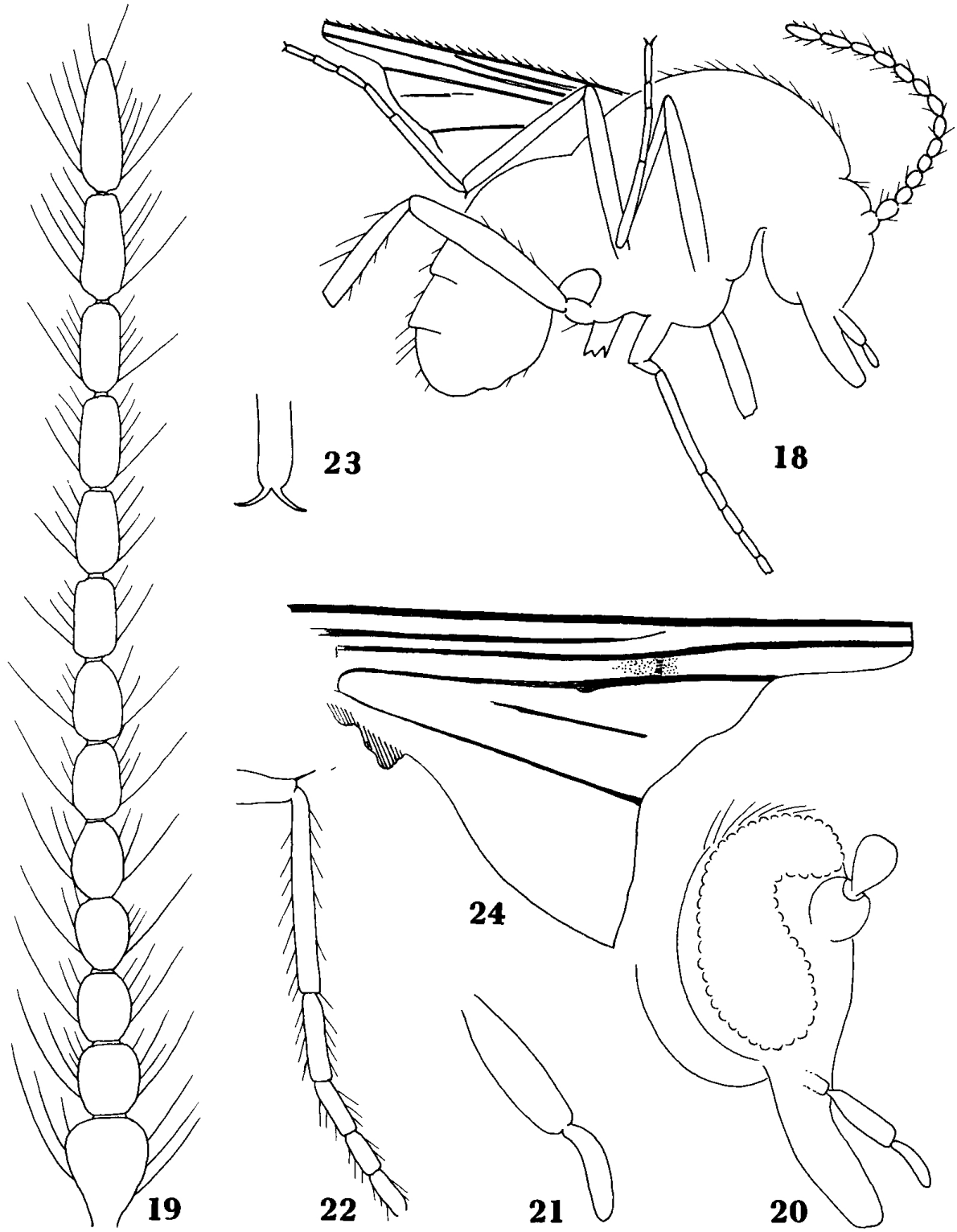


Fig. 18 to 24, *Austroconops borkenti,* sp. n., female. — 18, total habitus. — 19, flagellum. — 20, lateral view of head. — 21, palpus. — 22, tarsus of middle leg. — 23, claws of fore leg. — 24, preserved portion of wing.

Description. — *Female :* incomplete specimen embedded in a small non transparent amber piece containing much debris. Body dark, total length 0.9 mm (fig. 18).

Eyes probably separated, pubescence not visible. Flagellum composed of 13 flagellomeres, total length 540 µm, antennal ratio 0.80. Lengths of flagellomeres increase gradually from the second to thirteenth one (fig. 19). Proboscis long and slender, distinctly bent forward (fig. 20). Palpus 4-segmented. Sensilla not visible. Third palpal segment slender and slightly bent, length 44 µm.

Scutum convex and covered with short setae. Scutellum barely visible. Legs slender. Length of hind femur about 345 µm. Fourth tarsomeres cylindrical (fig. 22). Claws short, equal and simple (fig. 23). Empodia not visible. Only basal portion of one wing preserved (fig. 24). Costal vein probably very long, preserved part measuring 533 µm. Subcosta clearly visible and long. Two long radial veins present. A barely discernible transverse vein (r-m?) present at the level of subcostal tip. Wing membrane covered with distinct and sparse microtrichia. Macrotrichia not visible.

Abdomen short and blunt. Cerci not discernible.

Male. — Unknown.

Material examined. — Holotype female labelled as follows : Cer Ce Bez 1, stratum typicum — C4; Bezonnais Dept. Sarthe, collected by *W. G. Kühne, L. Kubig* and *T. Schlüter,* 1971. The holotype is deposited in the collection of Museum of the Earth, Warsaw.

Etymology. — This species is named for Dr. Art Borkent of Salmon Arm, British Columbia, Canada, in recognition of his contributions to the study of Ceratopogonidae.

Discussion. — The generic placement of *Austroconops borkenti* seems to reasonable as the characters found fit this genus the best. The only living representative of that genus and the subfamily Austroconopinae, *A. mcmillani* Wirth & Lee from Australia (Borkent *et al.,* 1987), has relatively well developed empodia which are not discernable in the new species. However, according to Borkent *(pers. comm.)* the empodia of *A. mcmillani,* even in specimens mounted in Canada balsam, are difficult to discern like those of many members of the Ceratopogonini.

A female of the new species can be distingushed from females of *A. mcmillani* by its slender third palpal segment. The female of the latter species has a swollen third palpal segment, about 2.2 times as long as its greatest width, which in the new species is cylindrical and about 3.0 times as long as the greatest width.

This is the first record of a fossil in Austroconopinae which indicates that this subfamily was more widely distributed during the Upper Cretaceous period than now.

Subfamily ***Leptoconopinae*** Noé, 1907

Genus ***Leptoconops*** Skuse, 1889

Leptoconops species indet.

Ceratopogonidae species D : Schlüter, 1978 : 100 (brief description, sex not indicated, fig. 83, table 12 : 4).

Discussion. — We have not been able to examine the specimen briefly described by Schlüter as *species D.* However certain characters illustrated by Schlüter such as long cerci, wing venation and short flagellum suggest that it is a female of *Leptoconops.* The genus *Leptoconops* has apparently existed as early as the Upper Jurassic (Grogan & Szadziewski, 1988). All fossil biting midges studied in that genus from the Upper Cretaceous Siberian amber (Kalugina, *pers. comm.*), Eocene Baltic amber (Szadziewski, 1988), and Tertiary amber of Sakhalin (Szadziewski, 1990) belong to the subgenus *Leptoconops.*

CONCLUSION

The biting midges described in this paper are the oldest described species in the family (see Grogan & Szadziewski, 1988; Szadziewski, 1988). Both the *Leptoconops* and *Austroconops* from this amber appear to be vertebrate bloodsuckers. The short proboscis of members of *Atriculicoides* draws into question the feeding habits of females of this genus. Such characters as unmodified legs with short and equal claws on all legs, rudimentary empodia and numerous sensilla on the third palpal segment may suggest that they were ectoparasites on vertebrates. The short proboscis does not prove that females of *Atriculicoides* were predatory or parasitic on insects because many species of *Leptoconops*, which are typical vertebrate bloodsuckers have short or even very short mouthparts.

The systematic position of *Atriculicoides* in the family Ceratopogonidae is not clear. It can not be placed in the tribe Culicoidini as proposed by Szadziewski (1988) as the antennae lack sensilla coeloconica surrounded with a ring of short setae that are typical of this tribe. In addition, in males the distal 4 flagellomeres are elongated while in the Culicoidini only the distal 3 are. A similar situation occurs in another fossil genus *Protoculicoides* Boesel (only female known) from Canadian amber, which lacks sensilla coeloconica, and has unspecialized legs and a long proboscis (Szadziewski, 1988). Both of these fossil genera have long radial veins and well developed radial cells as in *Austroconops* (Borkent *et al.*, 1987).

Acknowledgments

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Kenneth A. SPENCER. — **Host Specialization in the World Agromyzidae (Diptera).** Dordrecht : Kluwer Academic Publishers, 1990, XII + 444 pp.

Cet excellent ouvrage vient après une série d'autres, publiés par le même auteur, qui traitaient principalement des Agromyzidae des faunes régionales : U.S.A. (1986), Australie (1977), Fennoscandia (1976) Venezuela (1973), Canada et Alaska (1969) etc. sans oublier les travaux relatifs aux Agromyzidae d'intérêt économique. Kenneth Spencer est un auteur dont l'immense oeuvre fait autorité en systématique de ces Diptères. Le présent livre donne une nouvelle dimension à son oeuvre : il traite, sur un plan mondial, les espèces de ce groupe en relation avec leurs plantes-hôtes connues. Il donne toute l'information de base nécessaire à ceux dont la première préoccupation est la relation insectes/plantes. Il alimente ainsi la discussion actuelle sur la relation plante/insecte, la spécialisation et la coévolution.

Les Agromyzidae sont traités dans l'ordre systématique des plantes-hôtes. L'auteur suit la classification de Cronquist mais il discute chaque fois qu'il est nécessaire le point de vue d'autres auteurs. Cependant, malgré cette énorme somme de documents, la phylogénie du groupe n'a pas été suffisamment approfondie.

Dans une première partie (Chapitres 1-4) sont catalogués tous les genres de plantes connus comme plantes-hôtes d'Agromyzidae. Des tableaux synoptiques aident le lecteur à se retrouver et des commentaires sur pratiquement toutes les espèces éclairent chaque cas.

Les dessins qui accompagnent la partie systématique sont très abondants (1439) et d'une grande utilité. Ils concernent principalement les genitalia mâles dont la connaissance est indispensable pour la détermination des espèces surtout dans les cas délicats où la morphologie externe n'offre pas de caractères discriminants. Les dessins des larves et des parties des plantes attaquées par ces dernières sont également très utiles. Ils faciliteront la reconnaissance des Agromyzidae par tous ceux, non spécialistes, qui aimeraient les déterminer pour des raisons professionnelles ou autres. Ce travail de détermination est de plus facilité par l'utilisation parallèle des tableaux des espèces des Agromyzidae connues de chacune des familles, tribus, genres ou espèces des plantes attaquées.

Dans ces 4 chapitres est traitée approximativement la moitié des espèces de la famille (1300 espèces sur un total de 2500) qui correspond à la totalité des espèces dont les plantes-hôtes sont connues.

Les Agromyzidae montrent un très haut degré de spécialisation vis-à-vis de leurs plantes-hôtes (chapitre 5). En effet, le nombre des espèces polyphages n'excède pas 16 (soit 0,6%). Elles sont traitées dans le chapitre 4 où l'auteur discute un par un tous les cas de polyphagie de ce groupe. Il considère l'aptitude à la polyphagie non comme un phénomène statique mais comme un processus dynamique. Il entreprend également la comparaison de la polyphagie des Agromyzidae avec celle d'autres groupes d'insectes.

Dans le chapitre suivant (chapitre 6), l'auteur révéle d'une façon succinte ses opinions sur la phylogénie, la coévolution (Agromyzidae/plantes) et la colonisation. Il considère, que mettre en parallèle la phylogénie des Agromyzidae et celle des plantes-hôtes est une «.. oversimplification of the problem ». Il ne tranche pas non plus le débat : coévolution ou colonisation. Il porte des exemples qui plaident pour la coévolution et d'autres pour la colonisation. Cependant sa préférence va à une «.. sequential colonisation ».

Dans un appendice taxinomique sont rassemblés les descriptions des nouvelles espèces, les nouvelles synonymies et combinaisons et les nouveaux statuts. Ceci a l'avantage d'alléger le texte mais ne préserve pas de certains oublis comme, entre autres, la synonymie d'*Agromyza frontella* avec *A. drepanum* annoncée dans la page 133 et non établie dans l'appendice.

L'index, bien conçu et complet, permet de retrouver rapidement le taxon recherché, quelques omissions ou erreurs de pagination n'enlèvent rien à son utilité.

On ne peut pas terminer sans mentionner le travail qu'a fourni Ann Spencer pour l'illustration de l'ouvrage. La précision et la qualité des dessins sont remarquables. Kenneth Spencer nous offre avec ce nouveau livre un instrument de travail très précieux, utile pour le spécialiste aussi bien que pour le simple naturaliste. Un livre qui ne doit manquer à aucune bibliothèque entomologique.

L. TSACAS