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NEW BITING MIDGES (DIPTERA: CERATOPOGONIDAE) IN LATE CRETACEOUS VENDEAN AMBER

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ABSTRACT

The ceratopogonids from Late Cretaceous (Cenomanian to Santonian) amber of Vendée, in northwestern France, are studied. The new species *Leptoconops* (*Leptoconops*) *gravesi* n. sp., *Leptoconops* species undetermined, and *Culicoides doyeni* n. sp., are described, illustrated, and compared with other fossil species known for these two genera.

Keywords. Insecta, Leptoconopinae, Ceratopogoninae, France, Cretaceous

RÉSUMÉ

Les Cératopogonides fossilisés dans l'ambre crétacé supérieur (Cénomanien à Santonien) de Vendée, dans le nord-ouest de la France, sont étudiés. Les nouvelles espèces *Leptoconops* (*Leptoconops*) *gravesi* n. sp., *Leptoconops* espèce indéterminée, et *Culicoides doyeni* n. sp., sont décrites, illustrées, et comparées aux autres espèces fossiles connues pour ces deux genres.

Mots-clés: Insectes, Leptoconopinae, Ceratopogoninae, France, Crétacé

INTRODUCTION

The first fossil Ceratopogonidae from Cretaceous French amber were illustrated by Schlüter (1978) based upon four individuals that he found in Cenomanian amber of Anjou, in northwestern France. These were formally described by Szadziewski and Schlüter (1992) as *Atriculicoides cenomanensis*, *A. incompletus*, *Austroconops borkenti*, and *Leptoconops* sp. New studies were recently initiated after the discovery of several Cretaceous amber deposits in other regions of France, that revealed an abundant new material of biting midges. The Albian-Cenomanian amber of Charentes, in southwestern France, contains about 4% of ceratopogonids (62 specimens out of 1500 arthropod inclusions), with *Leptoconops daugeroni* Choufani, Azar & Nel, as the first and only described species (Choufani & others, 2011). The Santonian amber of Provence, in southeastern France, is poorly fossiliferous but remarkably contains up to 15% of ceratopogonids (2 specimens out of 13 arthropods) representing two species: *Devalquia brisaci* Choufani & Nel, and *Metahelea roggeroi* Choufani & Nel (in Choufani & others, 2013). The present study aims to describe and illustrate the diversity of biting midges most recently discovered from Late Cretaceous (Cenomanian to Santonian) amber of Vendée, in northwestern France. Ten out of the 171 arthropod inclusions found in this amber deposit are assignable to Ceratopogonidae, but only three of them are complete or visible enough for the present study, which represent three different species.

MATERIAL AND METHODS

The three specimens are preserved in separate pieces of amber that were respectively collected in 2002 by Fanny Dupé, Dominique Doyen, and Didier Graves from a deposit exposed briefly during construction along the D32 road between La Garnache and Challans, in the department of Vendée, northwestern France. The exact age of the amber-bearing stratum remains uncertain within the Middle

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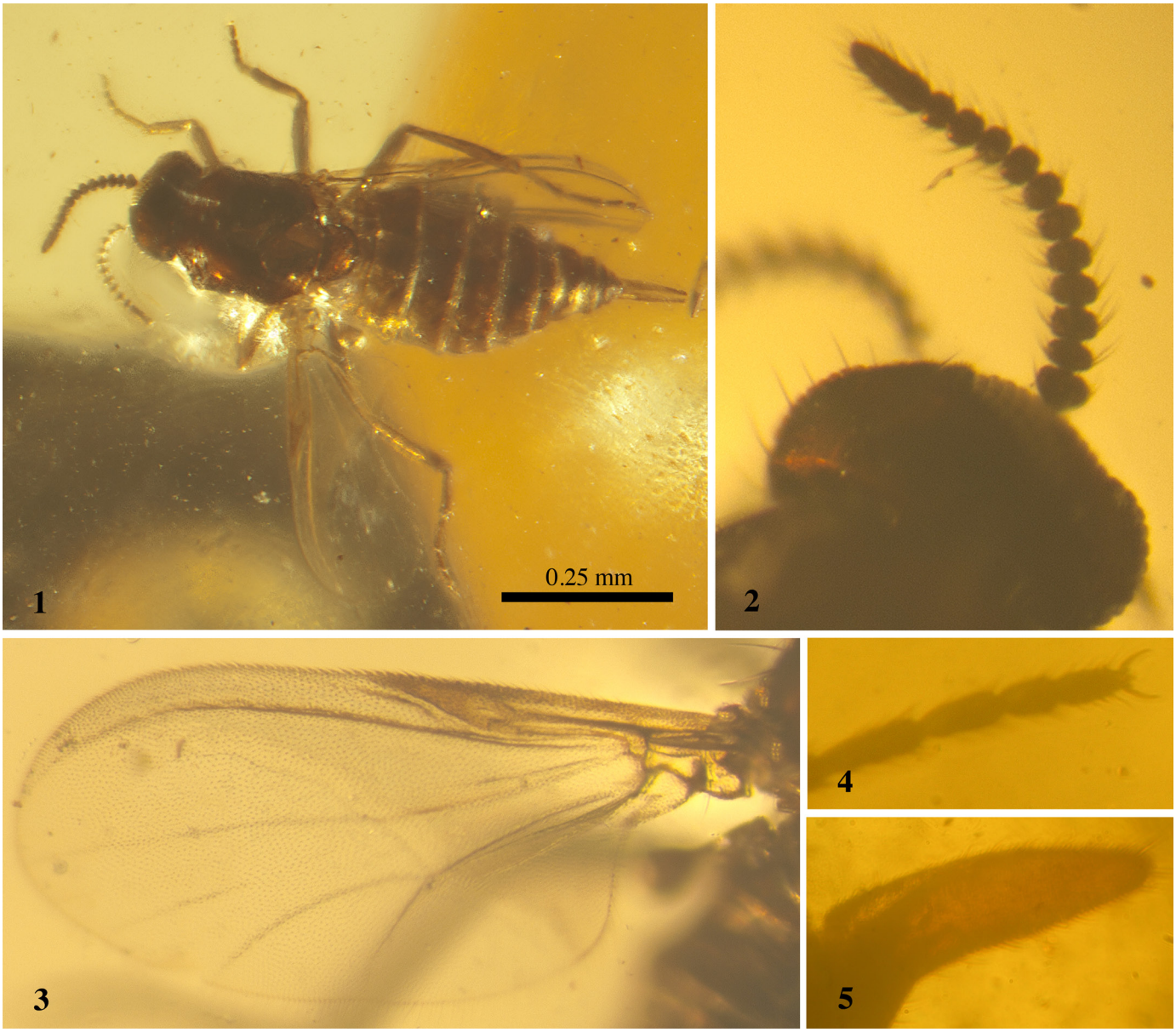

Figure H1. *Leptoconops gravesi* n. sp., holotype female IGR.GAR-72.1. *1*, habitus in dorsal view; *2*, detail of head and antenna; *3*, wing; *4*, tarsal claws; *5*, cerci.

Cenomanian to Early Santonian interval (Late Cretaceous, 97–85 Ma), as discussed by Perrichot and Néraudeau (2014: 10A in this volume). The specimens were each contained in a piece of clear yellow to orange amber, and two of the three pieces contained other syninclusions rendering their observation difficult (see detailed list in the material sections of the descriptions below). These pieces were divided and the resulting fragments polished to optimize the dorsal, profile, and frontal views whenever possible. The study was done under incident and transmitted light using an Olympus SZ9 stereomicroscope and an Olympus inverted microscope, both equipped with a digital camera for photographs and an ocular micrometer for measurements. Each amber piece was ultimately embedded in a block of epoxy resin for preservation and easier manipulation. The material is now housed in the amber collection of the Geological Department and Museum of the University Rennes 1, France.

SYSTEMATIC PALEONTOLOGY

Family CERATOPOGONIDAE Newman, 1834
Subfamily LEPTOCONOPINAE Noè, 1907
Genus LEPTOCONOPS Skuse, 1889

Subgenus LEPTOCONOPS Skuse, 1889
LEPTOCONOPS (LEPTOCONOPS) GRAVESI, new species
Figure H1

Type material.—Holotype female IGR.GAR-72.1 (ex coll. Graves), originally preserved with a scelionine wasp and an earwig nymph (the latter described by Engel & Perrichot, 2014: 10J in this volume) in Late Cretaceous (Middle Cenomanian to Early Santonian, 97–85 Ma) Vendean amber, France; deposited in the Geological Department and Museum of the University Rennes 1, France.

Type locality.—La Robinière, departmental road D32, about 2.5 km south-west of La Garnache, Vendée, France.

Etymology.—The specific epithet is a patronym for Didier Graves, the specimen's collector.

Diagnosis.—Female. Antenna with 12 flagellomeres, flagellomeres 2-5 transverse, flagellomeres 6-11 spherical, terminal flagellomere as long as the three preceding ones combined; wing with costa prolonged beyond R3; tarsal claw with small denticle at its base and no setae; cerci much elongate, not triangular, with two long apical setae; ratio body length /wing length = 1.38.

Description.—Body stout, total length (without cerci) 0.68 mm. Head with seven setae on vertex but no pair of setae on frons; eyes bare, separated dorsomedially and large, largest diameter (D) 110 µm, small diameter (d) 55 µm; antenna with flagellum 223 µm long; flagellomeres 2-5 transverse, 6-11 spherical, each 16.7 µm in diameter; terminal flagellomere 36.2 µm long, 2.2× as long as flagellomeres 11 or 10 alone, and as long as preceding three flagellomeres combined; palpus four-segmented; third palpal segment 30.6 µm long, 12.5 µm wide; fourth palpal segment slender, 27.8 µm long.

Thorax: 0.21 mm µm long, 0.17 mm µm wide; scutum not prolonged beyond head with around 10 setae; scutellum with rounded margin and two median setae.

Wing 0.49 mm long, 0.17 mm wide; radial cells short, R1 and R3 joining costa in a thickened pterostigma; costa prolonged beyond R3; crossvein r-m absent; vein R4+5 reaching wing apex; median branches reaching wing margin; intercal vein not running close to M.

Legs slender, hairy; length of profemur 0.12 mm, protibia 0.097 mm, protarsi 0.21 mm; mesofemur 0.13 mm, mesotibia 0.097 mm, mesotarsi 0.167 mm; metafemur 0.14 mm, metatibia 0.167 mm, metatarsi 0.194 mm; protibial spur thickened; apex of metatibia with comb of four major spines and a row of smaller spines; metatibial spur not very thick; all basitarsomeres with row of dense setae; fourth tarsomere cylindrical; fifth tarsomere more elongate than fourth; claws sharp, of medium size, equal on all legs, with a small basal tooth and a bristle on each claw; empodia present, small.

Abdomen 0.39 mm long (without cerci), 0.22 mm wide; cerci lamellar, elongate, 0.10 mm long, 41.75 µm wide, with dorsal and ventral margins parallel within anterior half of length, tapering to rounded apex for posterior half of length, dorsally and ventrally with a series of small setae, and apically with two longer setae.

Comments.—According to the phylogenetic analysis proposed by Borkent and Craig (2004), *Leptoconops gravesi* n. sp. has two synapomorphies supporting its placement within the clade (*Leptoconops* + *Minyohelea*), i.e. 'radial cells very short' and 'female wing with R1 and R3 joining costa in a thickened pterostigma'. It also has the following synapomorphies of *Leptoconops*: 1) 'wing without r-m', a character that Borkent and Craig (2004) indicated as 'unique within at least the Culicomorpha'; 2) 'female cerci elongate and laterally compressed'.

Within the genus *Leptoconops*, the female cerci elongate and laterally compressed is the synapomorphy of the group of subgenera (*Holoconops* Kieffer + (*Megaconops* Wirth & Ashley + *Leptoconops* s. str. + *Proleptoconops* Clastrier)) as defined by Borkent (1995), thus excluding affinities of *L. gravesi* n. sp. with the other subgenera *Styloconops* Kieffer and *Brachyconops* Wirth & Ashley, which have short female cerci, a reversal to the plesiomorphic condition according to Borkent and Craig (2004). Following the key of Sontag and Szadziewski (2011), *L. gravesi* would fall in the extinct subgenus *Palaeoconops* Borkent (type species *L. amplificatus* Borkent), because of its costa prolonged beyond R3. Species of this last subgenus have also elongate cerci, as our fossil. Nevertheless, *Palaeoconops* differs from our fossil by having 13 flagellomeres instead of 12 and thick spines on first tarsomere of all legs. Affinities with *Holoconops* can be also excluded by the presence of 12 flagellomeres in our fossil, as opposed to 10–11 flagellomeres in *Holoconops* (Wirth & Atchley, 1973; Szadziewski & Arillo, 2003). Following the key of Downes and Wirth (1981), *L. gravesi* falls in the subgenus *Leptoconops* rather than *Megaconops* Wirth & Atchley on the basis of the absence of a pair of setae on frons and the presence of a basal tooth and bristle on the female claw.

We compare *L. gravesi* with other fossil *Leptoconops* described by Szadziewski (1988, 1996, 2004), Kalugina (1991), Borkent (1995, 1996, 1997), Szadziewski and Arillo (2003), Szadziewski and Poinar (2005), Poinar (2008), and Choufani and others (2011). Unfortunately, the *Leptoconops* species described by Szadziewski & Schluter (1992) from the Cenomanian French amber is too incompletely described for an accurate comparison. The presence of the inner tooth on claws of *L. gravesi* n. sp. excludes affinities with *L. succineus* Szadziewski, *L. burmiticus* Szadziewski, *L. rossi* Szadziewski, *L. zherikhini* Szadziewski & Arillo, *L. nosopheris* Poinar, *L. subrossicus* Szadziewski & Poinar and *L. boreus* Kalugina. *Leptoconops gravesi* has flagellomeres 2-5 transverse and 6-11 spherical, which excludes affinities with *L. daugeroni* Choufani & others (flagellomeres 2-11 spherical), *L. myanmaricus* Szadziewski (2-11 cylindrical) and *L. rovnensis* Sontag & Szadziewski (2-3 transverse, 4-11 spherical). *Leptoconops sibiricus* Szadwiewski has the costal vein very short, not extending beyond R3, the terminal flagellomere 4× as long as the preceding one (as opposed to 2.2× in *L. gravesi*), and the upper surface of claws with setae, unlike *L. gravesi*. *Leptoconops primaevus* Borkent and *L. copiosus* Borkent, do not have any long setae at apex of cerci, unlike *L. gravesi*. The small inner tooth at the base of claw of *L. gravesi* excludes affinities with *L. curvachelus* Borkent that has a large thick inner tooth. Finally, *L. gravesi* differs from *L. clava* Borkent by the absence of small empodia and absence of tibial spur on midleg.

LEPTOCONOPS species undetermined

Figure H2

Material examined.—Female IGR.GAR-31 (ex coll. Dupé), in Late Cretaceous (Middle Cenomanian to Early Santonian, 97–85 Ma) Vendean amber, France; deposited in the Geological Department and Museum of the University Rennes 1, France.

Type locality.—La Robinière, departmental road D32, about 2.5 km south-west of La Garnache, Vendée, France.

Description.—Female. As this specimen is much damaged from head to thorax, several structures could not be examined. Total body length unknown. Head only partly visible, one eye partly visible, 117 µm in diameter, bare; at least three setae on vertex behind compound eye; antenna with 12 flagellomeres, flagellomeres 2-11 more or less spherical, all 23 µm in diameter; terminal flagellomere 53 µm long, 2.3× as long as preceding one; proboscis elongate; lacinia with at least

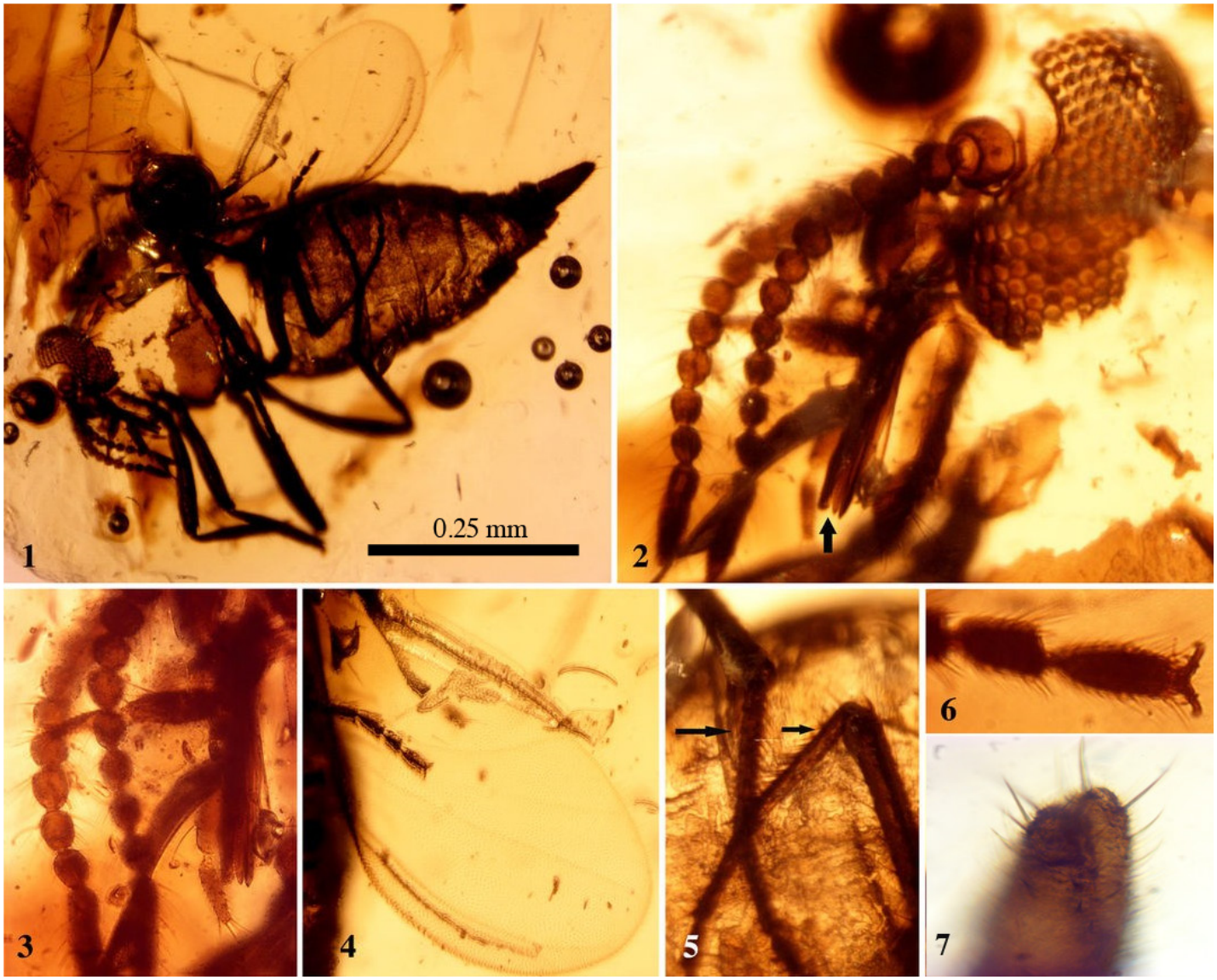

Figure H2. *Leptoconops* sp., specimen female IGR.GAR-31. *1*, Habitus in left profile view; *2*, detail of head with indication of lacinia (arrow); *3*, detail of flagellomeres 5-12 and mouthparts showing palps and lacinia with denticles; *4*, wing; *5*, metabasitarsomeres (arrows); *6*, tarsal claws; *7*, cerci.

10 denticles; palpus four-segmented, third segment ovoid, fourth segment slender with three apical setae.

Thorax damaged. Wing 0.35 mm long, 0.16 mm wide; surface covered by microtrichia, venation identical to that of *Leptoconops gravesi* (nº IGR.GAR-72.1).

Legs: length of profemur 0.26 mm, protibia 0.22 mm, protarsomeres 0.27 mm; mesofemur and metafemur 0.36 mm, slender; fourth tarsomere cylindrical, fifth tarsomere longer than fourth; foreleg tibial spur thickened; hind leg tibial comb composed of a row of five long and thick setae intermixed with smaller ones and a row of short, strong and straight setae; hind leg basitarsus with thick spines on one side and with long setae on other side; tarsal claws with a strong inner tooth in basal third; empodia absent.

Abdomen broad, 0.73 mm long, 0.4 mm wide; two visible spermathecae visible in segment 8, maybe moved from their original place by damages caused to the specimen; cerci elongate, 0.083 mm long, 33.4 µm wide, with dorsal and ventral margins converging for entire length to broadly acute apex, dorsally and ventrally with a series of small setae, and apically with two longer setae.

Comments.—The wing venation and long cerci are typical of *Leptoconops*. Similarly to *L. gravesi* n. sp. described above, the presence of inner tooth on claws of *L. gravesi* n. sp. excludes affinities with *L. succineus*, *L. burmiticus*, *L. rossi*, *L. zherikhini*, *L. nosopheris*, *L. subrossicus*, and *L. boreus*. Our fossil has flagellomeres 2-11 spherical, which excludes affinities with *L. myanmaricus* (2-11 cylindrical) and *L. rovnensis* (2-3 transverse, 4-11 spherical). The extend of costal vein beyond R3 and terminal flagellomere only 2.3× as long as preceding one, instead of 4×, exclude affinities with *L. sibiricus*. *Leptoconops primaevus* and *L. copiosus* differ from IGR.GAR-31 in the absence of the two long setae at apex of cerci. Also affinities with *L. clava* can be excluded because IGR.GAR-31 lacks the midleg tibial spur. Affinities with *L. daugeroni* can be excluded because IGR.GAR-31

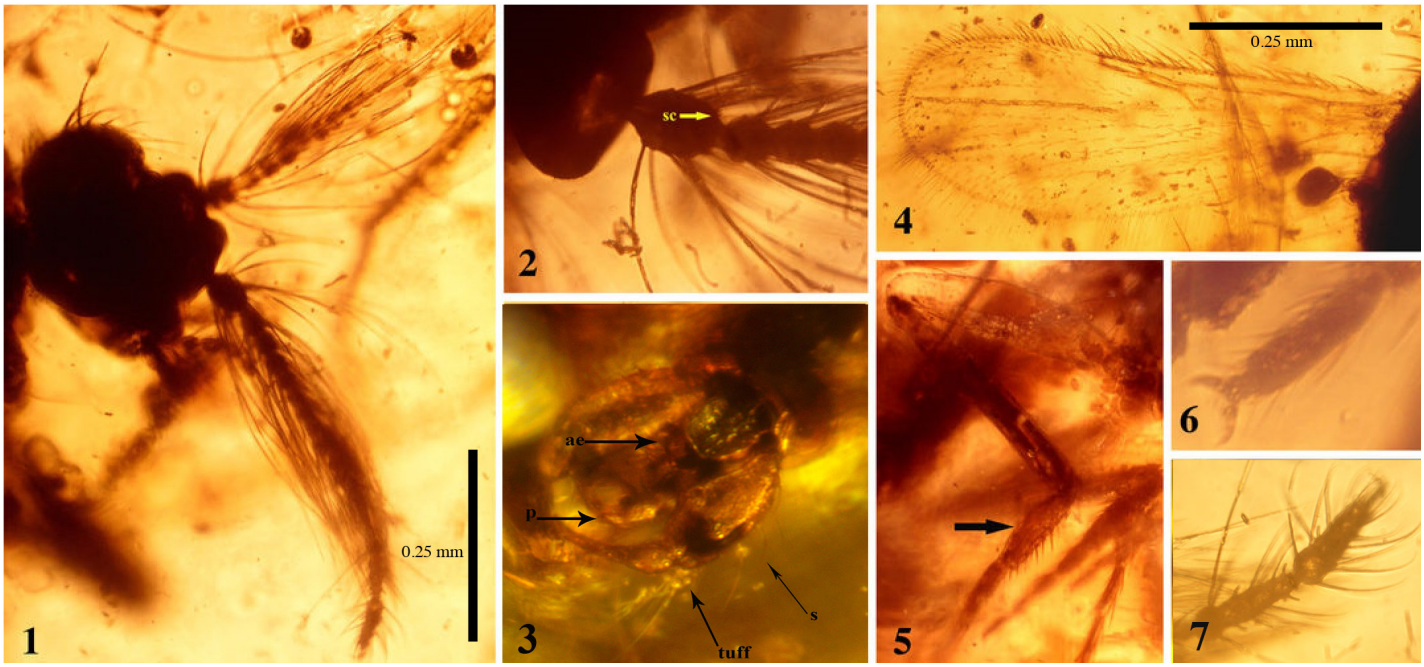

Figure H3. *Culicoides doyeni* n. sp., holotype male IGR-GAR-127.2. *1*, Head showing plumose antennae and palp; *2*, base of antenna with indication of sensilla coeloconica (sc); *3*, genitalia in ventral view (ae: aedeagus; p: parameres; s: setae; tuff: tuff of setae); *4*, wing; *5*, metabasitarsus with palisade (arrow); *6*, tarsal claws; *7*, apical two flagellomeres.

has only three apical setae on fourth palpomere, instead of six. *L. curvachelus* has thick setae on first and fifth tarsomeres of its legs and has not a pair of apical setae on cerci, unlike IGR.GAR-31, which has thick setae only on first tarsomere of hind leg and two elongated setae on apex of cerci.

Affinities with *L. gravesi* can be excluded on the basis of the shorter cerci, different proportions in leg structures, all flagellomeres rounded, not transverse, and presence of a stronger basal tooth on claws in specimen IGR.GAR-31. Therefore, it corresponds to a different, probably new species. Nevertheless we prefer not to give it a formal name because of its incomplete state of preservation, and maintain it as a *Leptoconops* species of uncertain subgenus attribution.

Subfamily CERATOPOGONINAE Newman, 1834
Tribe CULICOIDINI Kieffer, 1911
Genus CULICOIDES Latreille, 1809
CULICOIDES DOYENI new species
Figure H3

Type material.—Holotype male IGR.GAR-127.2 (ex coll. Doyen), originally preserved with a Berothidae (Neuroptera), a Thysanoptera, and a Coleoptera indeterminate; in Late Cretaceous (Middle Cenomanian to Early Santonian, 97–85 Ma) Vendean amber, France; deposited in the Geological Department and Museum of the University Rennes 1, France.

Type locality.—La Robinière, departmental road D32, about 2.5 km south-west of La Garnache, Vendée, France.

Etymology.—The specific epithet is a patronym for Dominique Doyen, the specimen's collector.

Diagnosis.—Wing covered with macrotrichia; costa ending at R3; vein R4+5 absent; cells r1 and r2 small to moderately large, distinctly longer than broad, touching but separated; second radial cell square ended; a single row of hairs on wing fringe; eyes narrowly separate above antennae; palpus five-segmented; antenna with 13 flagellomeres, first one with sensilla coeloconica; flagellomeres 11-13 elongate; terminal flagellomere without apical stylet-like prolongation but rounded apex; all legs having nearly similar tarsal ratios; mesobasitarsus with only slender setae, without small spines; metabasitarsus with palisade-like setae, without subbasal spine; gonostylus with a thick base tapering to pointed apex, not divided apically nor with subapical lobe.

Description.—Head: eyes bare, separated dorsomedially by two ommatidial distance; vertex with more than 12 setae; antenna with plumes directed towards apex of flagellum; pedicel 100 µm long, 140 µm large; flagellum 416 µm long; only last three flagellomeres elongate, nearly equal in length, 62 µm long, the last two flagellomeres with sensilla basiconica; first flagellomere with sensilla coeloconica, with two whorls of long setae; palpus five-segmented, third palpal segment ovoid, 24 µm long, 14 µm wide, with three long sensillae medially; fourth and fifth palpal segments slender, each 18 µm long, 12 µm wide.

Thorax: 0.4 mm long, 0.388 mm wide; scutellum rounded, with four setae; scutum very hairy; katepisternum lacking setae.

Wing 0.608 mm long, 0.24 mm wide; membrane and veins covered with short macrotrichia; radial cells small and nearly equal, almost touching, both distinctly longer than broad; second radial cell square-ended; costal vein not extending beyond R3; CR 0.65; r-m oblique; medial bifurcation not visible but most likely distal to r-m; M2 partially reduced; no patterns of dark and light spots.

Legs slender, very hairy; protibial spur with a small comb; mesotibia apparently with a spur; metatibial comb barely visible;

metabasitarsus with stout setae; fourth tarsomere cylindrical; tarsal claws simple, empodia absent.

Abdomen: tergite IX shorter than gonocoxite with small cerci; apicolateral processes not visible; gonocoxites long, with bases not contiguous, and with elongated lateral setae and a tuff of setae near the outer apical angle; gonostylus not forked, single, with thick base, gradually tapering to apex, apex not divided, with no apical tooth nor setae; aedeagus short, with short basal arms, lateral arms longer, arched, bound into slightly longer caudal arm; parameres symmetric, a little extended beyond apex of gonocoxite, with simple rounded apex directed inward.

Comments.—Following the keys of Szadziewski (1996), our fossil is distinguishable from *Lebanoculicoides* Szadziewski, by the absence of vein R4+5; from *Archiculicoides* Szadziewski, by the absence of apical stylet-like prolongation of terminal flagellomere but the presence of a rounded apex; from Leptoconopinae on the basis of the eyes narrowly separated above antennae, and the palpus five-segmented; from *Austroconops* Wirth & Lee, *Archiaustroconops* Szadziewski, and *Minyohelea* Borkent (incl. *Lebanoconops* Szadziewski), on the basis of tarsal ratios of all legs nearly similar; from *Brachycretacea* Szadziewski, by the presence of five palpal segments instead of four; from *Heleageron* Borkent, by the wing with cells r1 and r2 feebly separated; from *Protoculicoides* Boesel, by the costa ending at R3 and radial cells small to moderately large (as opposed to a costa prolonged to wing apex and very large radial cells in *Protoculicoides*); from *Washingtonhelea* Wirth & Grogan, *Ceratopogon* Meigen, *Palaeobrachypogon* Borkent, and *Peronehelea* Borkent, by the absence of sub-basal spine on metabasitarsus; and from *Atriculicoides* Remm, by its flagellomeres 11-13 elongate (as opposed to flagellomeres 10-13 in *Atriculicoides*), a situation similar to what is seen in *Culicoides*. Our fossil is also distinguishable from *Devalquia* Choufani & Nel, by the presence of a sensilla coeloconica on the first flagellomere, the presence of a single row of hairs on the wing fringe, and the second radial cell square-ended (as opposed to narrowed in *Devalquia*; see Choufani & others, 2013).

It is not possible to compare this fossil to the numerous recent species of *Culicoides*; we only compare it to other Cretaceous species. Following the keys of males proposed by Borkent (1996), *C. doyeni* n. sp. is distinguishable from *C. filipalpis* Remm, *C. tyrrelli* Boesel, and *C. bifidus* Borkent, by its gonostylus tapering to pointed apex, not divided apically nor with subbapical lobe; from *C. bullus* Borkent, and *C. succineus* Remm, by its gonostylus with a thick base, gradually tapering to apex; from *C. sphenostylus* Remm, *C. obuncus* Borkent, *C. annosus* Borkent, and *C. casei* Grogan & Szadziewski, by its wing with macrotrichia present all over the wing, and especially basal to fork of M and Cu (as opposed to a wing with macrotrichia restricted to an area distant from M and Cu in these species). It differs from *C. canadensis* (Boesel, 1937) in the radial cells weakly separated and square-ended (well separated and nearly as long as broad in *C. canadensis*); from *C. agamus* Borkent, by the second radial cell relatively thinner compared to its length, and presence of palisade-like setae on metabasitarsomere. According to the keys of Borkent (1995), *C. doyeni* n. sp. is also distinguishable from *C. kaluginae* Remm, by the mesobasitarsomere with only slender setae, without small spines.

The comparison with species of *Culicoides* known only by females is more tentative and limited to characters that are supposedly not dimorphic. *Culicoides doyeni* n. sp. is distinguishable from *C. grandibocus* Borkent, by its wing with macrotrichia not restricted to the distal half; from *C. yoosti* Borkent, by its metabasitarsomere with stout, palisade-like setae (no such setae visible in *C. yoosti)*; and from the very distinctive *C. truncatus* Borkent, by its antenna with 13 flagellomeres (as opposed to only five flagellomeres in *C. truncatus*).

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