

The first pipizine hoverfly from the Oligocene of Céreste, France

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The Oligocene *Oligopipiza quadriguttata* Nidergas, Hadrava, and Nel gen. et sp. nov. is the first fossil Pipizinae found in the lacustrine outcrop of Céreste (South-East of France). It differs from the other Pipizinae in the male genitalia, with a surstylus without tooth and shorter than epandrium, and a long epandrium with a very deep and narrow median theca. It is compared to other extant and fossil Pipizinae. Its position in this clade is supported by its inclusion in previous morphological phylogenetic analysis of the Syrphidae. Palaeoecological inferences for the paleobiota of Céreste are made based on this taxon and point to the presence of a mixed forest. The taphonomy of these flies is discussed. They were probably embedded in surface microbial mats. The pollinator role of *Oligopipiza quadriguttata* is also discussed on the basis of the presence of pollen surrounding the fossil flies.

Key words: Insecta, Syrphidae, Pipizinae, palaeoecology, Paleogene, France.

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Introduction

With more than 6000 described extant species living in all climatic regions (except Antarctica, Spitsbergen, and some remote oceanic islands), the Syrphidae are one of largest families of Diptera in number of species. They have important roles in ecosystems as pollinators (Szymank et al. 2008; Glaum 2017; Lefèbvre et al. 2018) and as aphid predators (Rojo et al. 2003; Bičík and Láska 2011). Grimaldi (1999) considered that the Syrphidae radiated during the Cretaceous. Wiegmann et al. (2003) dated the clade Schizophora between 107 and 84 Myrs and considered the Syrphidae as their sister group, suggesting the same minimum age for this family. Wiegmann et al. (2011) dated the Syrphidae from ca. 100 Myrs. The “mid” Cretaceous corresponds to the period of radiation and diversification of the angiosperms (Barba-Montoya et al. 2018). Young et al. (2016) and Pauli et al. (2018) recently proposed the Syrphidae as sister group of the Pipunculidae + Schizophora. Nevertheless, the oldest

accurate fossil members of the Syrphidae and Pipunculidae are dated from the Eocene (Dirickxs 2009; Archibald et al. 2014). Kovalev (1979) recorded what may be the oldest example of Syrphidae from the Late Cretaceous resins of the Taimyr in Siberia, but this fossil has never been described or re-examined (Evenhuis 1994). Fossil Syrphidae are poorly known compared to extant hoverflies, with ca. 106 described species all over the world (Hull 1945; Evenhuis 1994; Kotthoff and Schmid 2005; Dirickx 2009). The last description of a fossil syrphid dates back thirteen years ago (Kotthoff and Schmid 2005).

The extant Pipizinae are widely spread in all world ecozones except in the Polar ecozones and the Afrotropical region (Thompson 1972; Vujić et al. 2013; Mengual et al. 2015). It contains approximately 180 species distributed in eight genera: *Claussenia* Vujić and Ståhls, 2013, *Cryptopipiza* Mutin, 1998, *Heringia* Rondani, 1856, *Neocnemodon* Goffé, 1944, *Pipiza* Fallén, 1856, *Pipizella* Rondani, 1856, *Trichopsomyia* Williston, 1888, and *Triglyphus* Loew, 1840.

Pipizines have long been considered as a tribe of the subfamilies Syrphinae or Eristalinae (Ståhls et al. 2003; Hipa and Ståhls 2005). They have strong morphological similarity with the Eristalinae (e.g., pilose postpronotum), but they share ecological and biological characteristics with the Syrphinae (Mengual et al. 2015). Larvae are aphid predators on several species of plants, like *Rumex* Linnaeus, 1753, *Prunus* Linnaeus, 1753 or *Ulmus* Linnaeus, 1753 according to the “Syrph The Net” database (Speight and Castella 2016).

Only few fossils are currently attributed to the Pipizinae, viz., *Pipiza melanderi* Hull, 1945 (lowermost Oligocene of Florissant, USA), *Pipiza venilia* Heyden, 1870 (Oligocene of Rott, Germany), *Pseudopipiza antiqua* Hull, 1945, *Pseudopipiza europa* Hull, 1945, and *Palaeopipiza xenos* Meunier, 1902, (Eocene, Baltic amber) (Heyden 1870; Meunier 1902; Hull 1945; Evenhuis 1994). Théobald (1937) described and listed all the known fossil Syrphidae from France, but none was described from the middle Oligocene of Lubéron. In this paper, we describe one new genus and species of the Pipizinae from the middle Oligocene of Céreste, Lubéron, in Southern France. We also discuss the systematic position of the newly described pipizine fossil based on a morphological phylogenetic analysis.

Institutional abbreviations.—RNGL, Public Museum of the Réserve Naturelle Géologique du Lubéron, Apt, France.

Other abbreviations.—BSE, back-scattered electrons; dm-cu, distal median cubital crossvein; EDS, energy-dispersive X-ray spectroscopy; M1, first branch of median vein; R1, R2+3, R4+5, branches of radius; r-m, radial median crossvein; Sc, subcostal vein; sv, supplementary pseudovein.

Material and methods

In total, 15 fossil specimens of the new genus and new species were collected, by digging and splitting the laminites with a hammer and a spatula, during the last 25 years in the National Geological Reserve of Lubéron, Céreste, France, from middle Oligocene clay-limestone laminite (base of late Rupelian) (Cautru and Gigot 1982; Ducreux et al. 1985). The 15 specimens of the type series, described herein, are deposited at the public collection of the Réserve Naturelle Géologique du Lubéron at Apt, France. All the specimens were chosen to form the type material.

The Oligocene paleolatitude of the outcrop of Céreste was very close to the modern one. The paleoclimate in the area was cooler than during the Eocene but still relatively warm (Pound and Salzmann 2017). The layers that contain insects at Céreste are very thin clay-limestone laminite rich in Silica and calcium carbonates. The fossil insects contain a great quantity of carbon and sulfur, unlike the sediment (SOM: fig. 1 in Supplementary Online Material available at http://app.pan.pl/SOM/app63-Nidergas_etal_SOM.pdf). The good 3D preservation of very tiny morphological structures (setae on eyes, body and wings) suggests that the insects are

compressed “mummies”. These animals were probably embedded in microbial mats that were originally floating at the water surface (Nel 1991).

Drawings were made with a drawing tube attached to a Nikon SMZ1500 stereomicroscope and digitized using Adobe® Photoshop-Elements 12. Then, drawings were vectorized and reworked with Inkscape v0.92. Photographs were made with a reflex camera Nikon D800 mounted on a Nikon SMZ25 stereomicroscope, edited with DxO PhotoLab v1.1.2 and then focus-stacked with the “D-map” algorithm on Zerene Stacker v1.04. We used environmental scanning electron microscopy (ESEM) to obtain microstructural details of these fossils, with the back-scattered electrons (BSE) mode. We used Energy-dispersive X-ray spectroscopy (EDS) in order to analyze the element composition of the fossils and its matrix. Then the spectra were plotted in R and reworked on Inkscape v0.92. Electron microscopy in BSE mode (SEM BSE) makes it possible to highlight differences in chemical composition (atomic number contrast) between the mineral matrix and the fossilized residues, in addition to the microtopographic differences revealed by the conventional mode. EDS spectrometry makes it possible to know the chemical nature of these differences and to identify the elements involved in the fossilization process, which can provide information on the sedimentary conditions, the taphonomic process and the initial nature of the fossilized organic elements. These two methods are mainly allowed by the use of the environmental mode to overcome the need to metallize the samples.

We followed Thompson (1999) for morphology nomenclature. The systematics of hoverflies follows Mengual et al. (2015). A new phylogenetic analysis to assess the systematic position of this new fossil was performed using 111 characters and 96 species, including the new fossil taxon, based on the morphological matrix used by Mengual et al. (2015), based on 111 characters and 96 species including the new fossil taxon (see SOM; Mengual et al. 2015; Hipa and Ståhls 2005). The tree research was performed using Wagner’s parsimony in PAUP* 4.0 b10 (Swofford 2002), with the following parameters: heuristic search 100 replicates, non-ordered characters, and TBR recombination.

Systematic palaeontology

Order Diptera Linnaeus, 1758

Family Syrphidae Latreille, 1802

Subfamily Pipizinae Williston, 1885

Genus *Oligopipiza* Nidergas, Hadrava, and Nel nov.

Etymology: Combination of Oligo in reference to Oligocene and *Pipiza*, the type genus of the subfamily.

Type species: *Oligopipiza quadriguttata* sp. nov., by monotypy, see below.

Diagnosis.—Same as for the type species.

Oligopipiza quadriguttata Nidergas, Hadrava, and Nel sp. nov.

Figs. 1–7.

Etymology: Combination of Latin *quadric*, four and *guttata*, drop; in reference to the shape of the yellow maculae on tergites II and III.

Type material: Holotype: RNGL-S01 (male). Paratypes: RNGL-S10 (female allotype), RNGL-S03, RNGL-S07, RNGL-S08 (males), RNGL-S02, RNGL-S04–06, RNGL-S09–15 (females). Nearly complete specimens with wings and legs preserved as imprint and counter-imprint; all from the type locality; coll. AN.

Type locality: Céreste, Lubéron, South-East France.

Type horizon: Middle Oligocene.

Material.—Type material only.

Diagnosis.—Medium-sized species, ca. 6–8 mm long; face simple, flat; basoflagellomere rounded; hind femora 4× longer than wide; abdomen ovoid, 1.5× longer than wide, dark; tergites II and III with two yellow maculae on each.

Head without frontal prominence; face simple, not protruding, and apparently concave below antennal fossa; antenna shorter than head, arista bare; no pronounced gibbosity above antennal bases; eyes pilose (Fig. 3B), holoptic in male, dichoptic in female; anterior mesopleuron possibly pilose; posterior anepisternum and anterior anepimeron hairy; metanotum (subscutellum) bare; no bristles on posterior margin of scutellum; no spurs on mid and hind coxae and hind trochanters; crossvein r-m slightly curved and ending before middle of cell dm; R_{2+3} perpendicular to costa; R_{4+5} making a strong curve basal of r-m, straight distal of r-m, and slightly curved just before crossvein M_1 insertion; cell R_{4+5} acute apically because M_1 is making an acute angle with the vein R_{4+5} ; R_{4+5} pedicel straight and short; abdomen emarginated, not petiolate, oval; four visible abdominal tergites in male, five in female; tergites II to IV entirely pilose; male genitalia very large, about 0.4× abdomen length; surstylus without tooth, shorter than epandrium, epandrium long, with a very deep and narrow median theca, from cerci to basal 3/10 of theca.

Description.—The abdominal ornamentation pattern on tergites II and III is subject to variations in size and shape (Fig. 7), but the general pattern is the same, viz. two ovoid to sub-rectangular yellow maculae on tergite II and two “water drop-shaped” to sub-triangular maculae on tergite III. The asymmetry of these spots is probably due to taphonomical artefacts.

Holotype (male RNGL-S01): Head: face simple, not protruding, apparently concave below antennal fossa; frons rounded; eyes holoptic, suture 0.15× tergite III length, anterior angle about 100–110°, size of ommatidia uniform all over eyes, size 22.5 μm , about 0.45× maximum width of epandrium theca indentation; antenna very short, less than 1/5 as long as head length, scape and basoflagellomere rounded, arista at basal third of basoflagellomere, apparently bare.

Thorax: mesoscutum and scutellum apparently completely dark; at least posterior anepisternum and anterior anepimeron hairy.

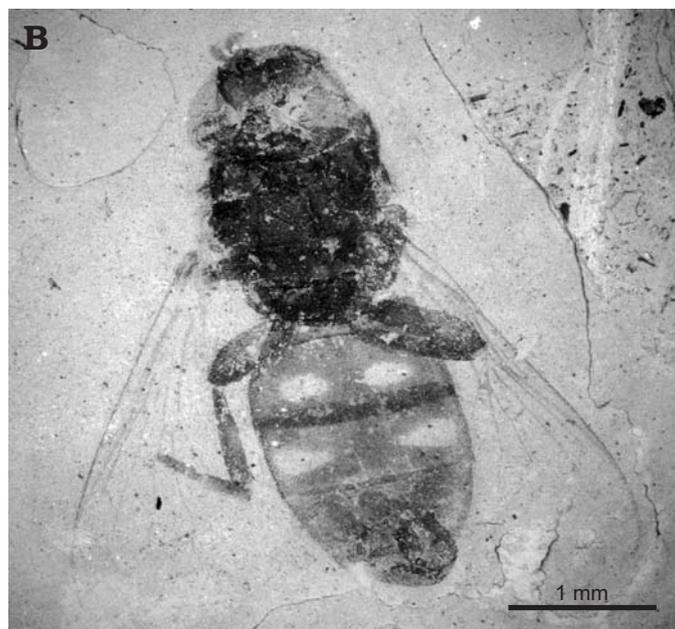
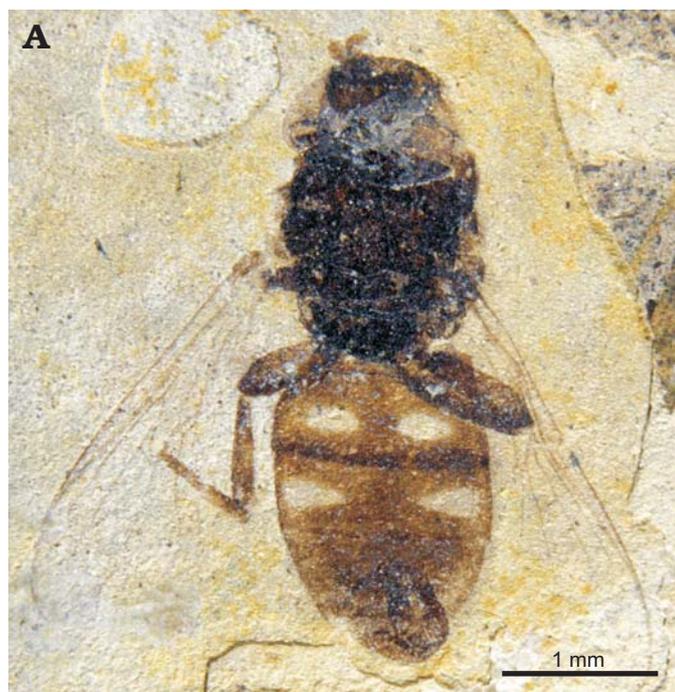


Fig. 1. Pipizine hoverfly *Oligopipiza quadriguttata* Nidergas, Hadrava, and Nel gen. et sp. nov., holotype RNGL-S01; Rupelian, Céreste, France. Imprint of male habitus. Normal light photograph (A), ESEM photograph (B).

Legs: covered with pale short bristles; hind femora 4× as long as wide, locally covered with long hairs between apical 1/5 and apical 3/5, about 2× longer than hind tibia basal width; apex of hind tibia 1.8× as large as base; length of hind metatarsus about 0.56× hind tibia length; hind tarsomeres II, III, IV, and V of equal lengths; claws basally pale and black in its apical third.

Wing: hyaline, with pale veins; R_{4+5} and R_{2+3} straight, crossvein r-m before middle of cell dm, spurious vein sv distinct.

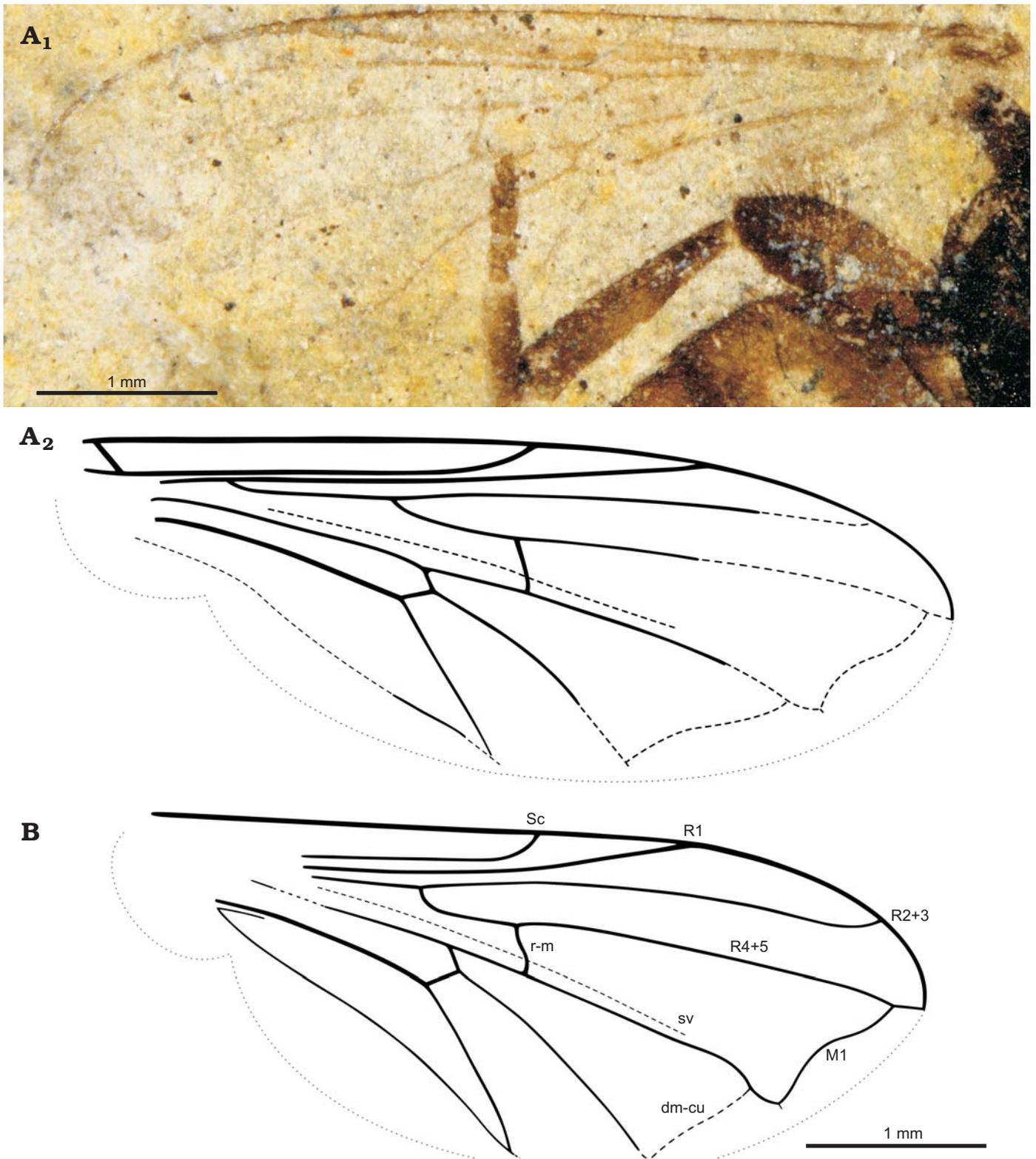


Fig. 2. Pipizine hoverfly *Oligopipiza quadriguttata* Nidergras, Hadrava, and Nel gen. et sp. nov., Rupelian, Céreste, France. Wing venations. **A.** Holotype RNGL-S01, normal light photograph (A₁), reconstruction (A₂). **B.** Allotype RNGL-S10, reconstruction. Abbreviations: dm-cu, distal median-cubital crossvein; M1, first branch of median vein; R1, R2+3, R4+5, branches of radius; r-m, radial median crossvein; Sc, subcostal vein; sv, supplementary pseudovein.

Abdomen entirely covered with hairs, as long as basal width of hind tibia, apparently erected as it is visible for those situated on the sides of tergites; tergite I dark; tergites

II and III dark, each with two pale maculae, probably originally yellow; tergite IV completely dark.

Genitalia: theca of epandrium about 0.5× as long as terg-

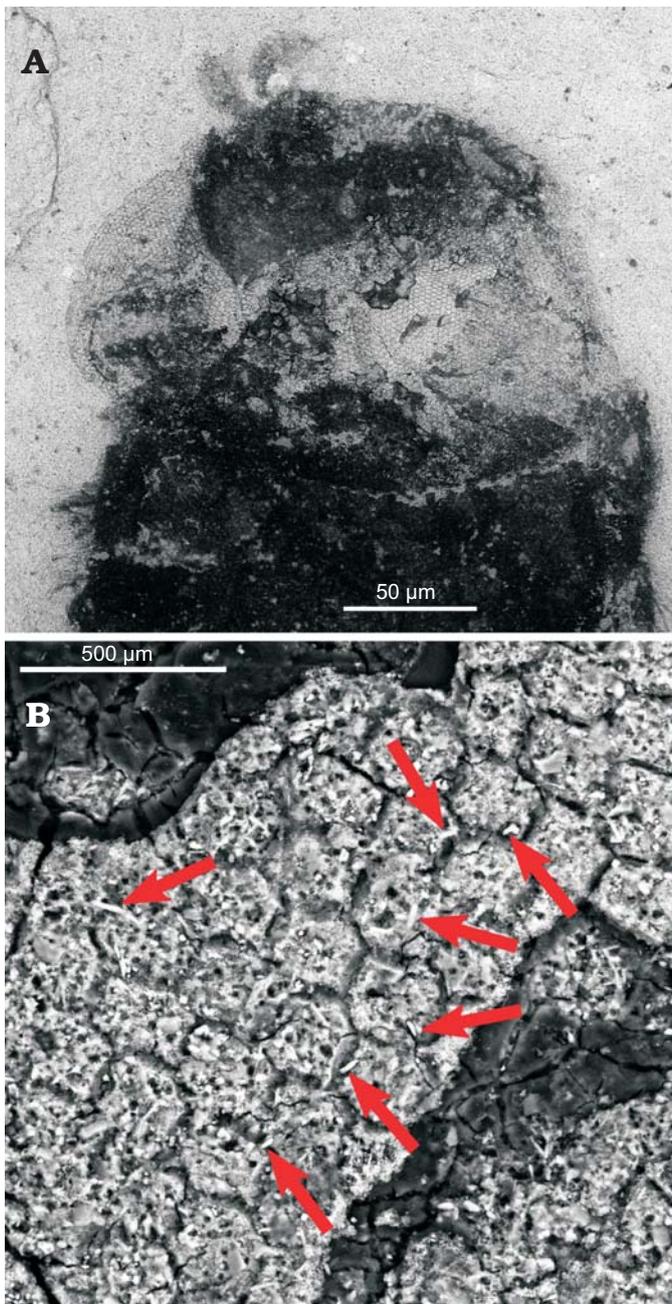


Fig. 3. Pipizine hoverfly *Oligopipiza quadriguttata* Nidergras, Hadrava, and Nel gen. et sp. nov., holotype RNGL-S01, Rupelian, Céreste, France. **A.** Head, ESEM photograph. **B.** Eye's ommatidia, arrows point to microtrichia.

ite III, about $1.1\times$ as long as wide, with a deep and narrow indentation opened from cerci to basal $3/10$, $7.1\times$ as long as wide; cerci about $3\times$ times as long as maximum width of epandrium indentation; surstyli short without tooth; hypandrium not visible.

Allotype (female RNGL-S10): It completes the description as follows: frons pilose; wing 4.5 mm long; crossvein r-m ending at basal fourth of cell dm, cell R_{4+5} acute apically, upper crossvein M_1 curved at its center; tergite I with posterior margin wave-shaped. Terminalia not visible. Sexual dimorphism: eyes dichoptic; tergite V visible; ab-

sence of hairs on hind femur (but this character could be a fossilization artefact).

Dimensions (taken on all specimens): body lengths vary between 6.8–8.1 mm (average value 7.4 mm); abdomen lengths vary between 2.7–4.5 mm (average value 3.6 mm); widths vary between 2.1–3.1 mm (average value 2.5 mm).

Stratigraphic and geographic range.—Rupelian (33.9–28.4 MYR BP), middle Oligocene; Céreste, at the boundary between the Vaucluse and the Alpes-de-Haute-Provence (43.9°N, 5.6°E), France.

Discussion

Oligopipiza gen. nov. is indisputably attributed to the Syrphidae due to the characteristic wing venation, and can be

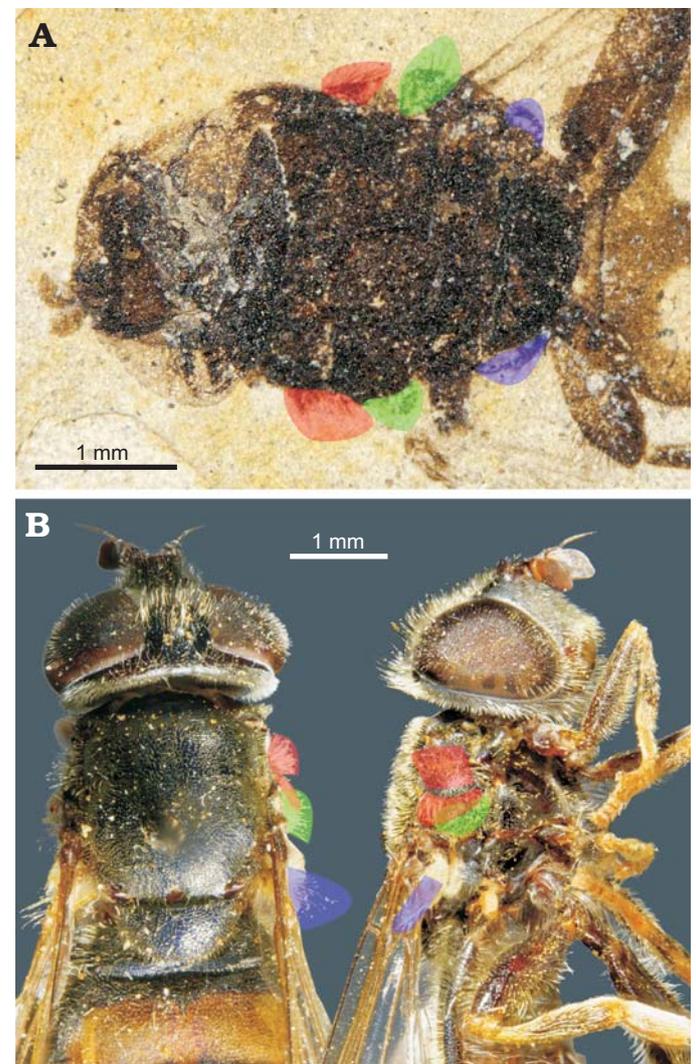


Fig. 4. Dorso-lateral pilosity of thoracic pleura of pipizine hoverflies. **A.** *Oligopipiza quadriguttata* Nidergras, Hadrava, and Nel gen. et sp. nov., holotype RNGL-S01, Rupelian, Céreste, France. **B.** Extant *Pipiza festiva* Meigen, 1822. Red, posterior anepisternal setae; green, anepimeral setae; blue, calypter setae.

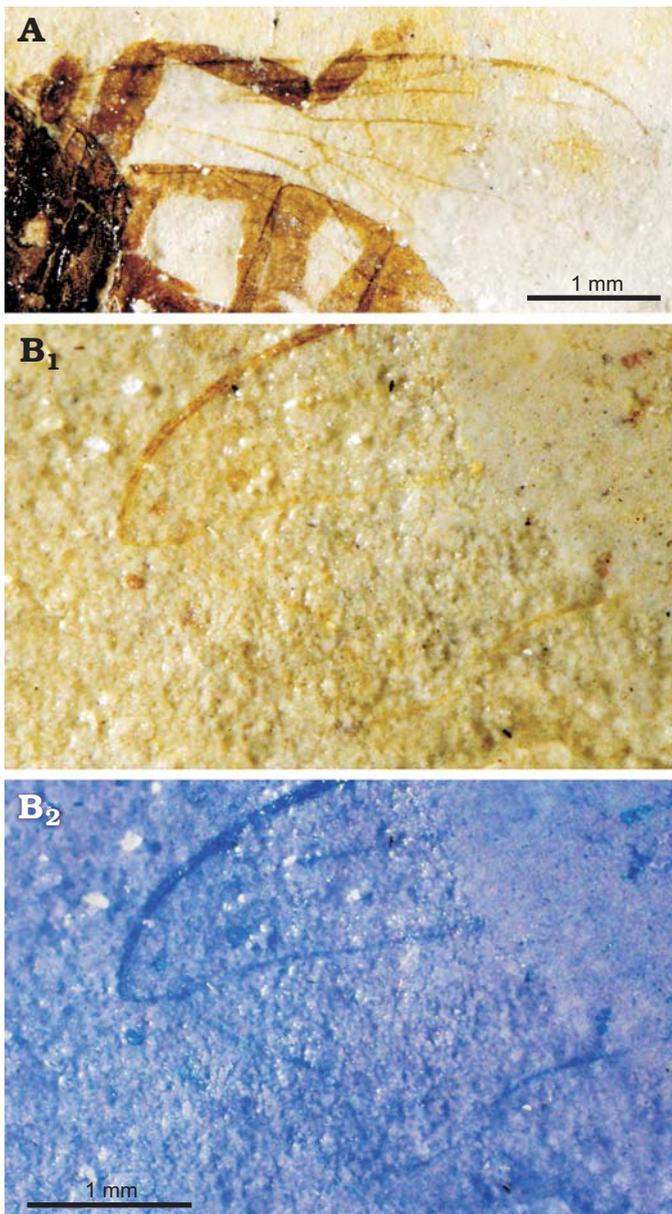


Fig. 5. Pipizine hoverfly *Oligopipiza quadriguttata* Nidergras, Hadrava, and Nel gen. et sp. nov., allotype RNGL-S10, Rupelian, Céreste, France. A. Wing. B. Wing apex, normal light photograph (B₁), treated to better show veins (B₂).

attributed to the Pipizinae because of the following characters (after Hippa and Ståhls 2005; Vujić et al. 2013; and Mengual et al. 2015): shape of face simple (reversal, present in Pipizinae, but also in *Microdon* [Microdontinae] and *Eumerus* [Merodontini]); arista bare; metanotum (subscutellum) bare (present in Pipizinae, but also *Microdon* and *Ubristes* [Microdontinae]); microtrichia retrolaterally on apical part of metatibia absent (character of Pipizinae but also in some genera of other tribes); wing vein R₄₊₅ straight, not sinuate; crossvein r-m sub-perpendicular to R₄₊₅ and ending before middle of discal cell; vein M₁ making an acute angle with R₄₊₅; antetergite fused to tergite I (general shape of tergite I identical to that of *Pipizella*) (character of the

Pipizinae but also is? present in other tribes); 1st abdominal spiracle and metasternum of pipizine type (character of the Pipizini but also in some genera of other tribes; Thompson 1972: fig. 2.3); abdominal terga laterally bordered (presence of a thicker sclerotized line at margins of tergites). These characters are putative synapomorphies of the Pipizinae but they are subject to convergencies in some other tribes. Nevertheless their combination is found only in Pipizinae.

Oligopipiza differs from the extant genera of Pipizinae as follows: *Cryptopipiza* Mutin, 1998 (replacement name for

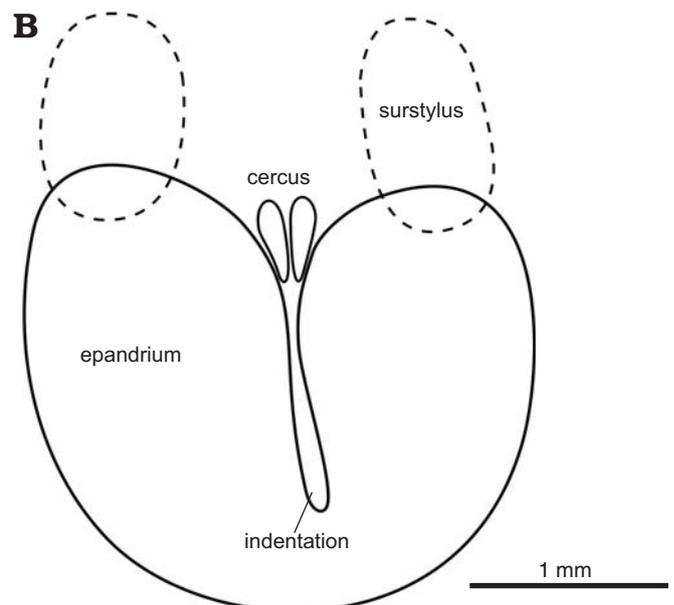
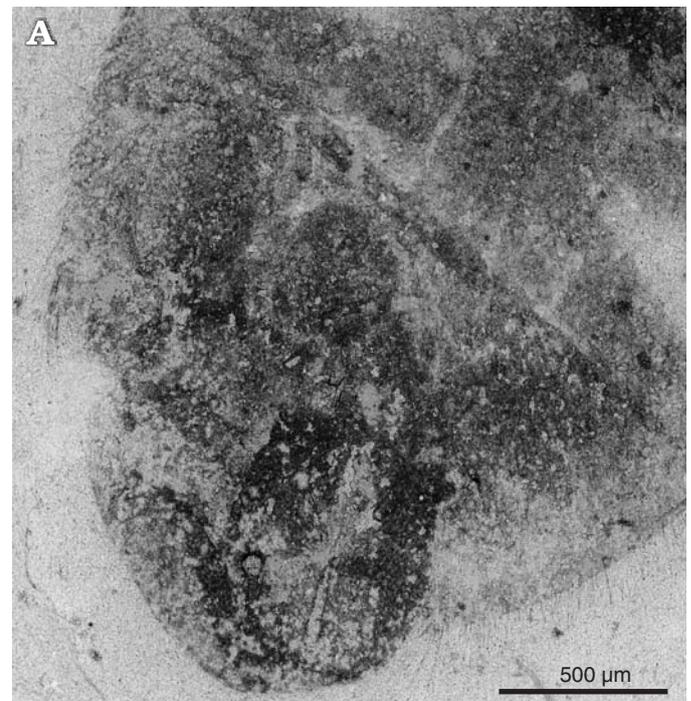


Fig. 6. Pipizine hoverfly *Oligopipiza quadriguttata* Nidergras, Hadrava, and Nel gen. et sp. nov., holotype RNGL-S01, Rupelian, Céreste. Male epandrium. ESEM photograph (A), reconstruction (B).

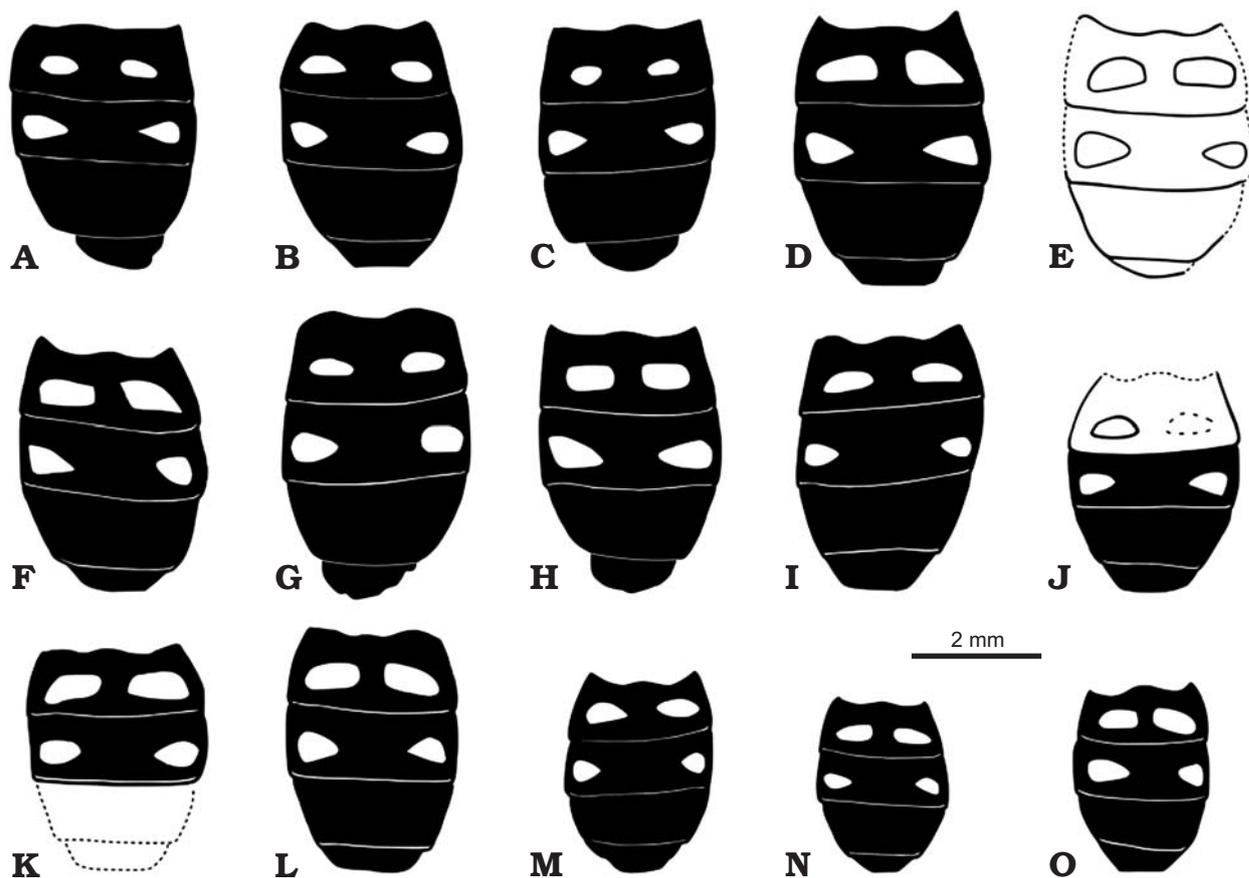


Fig. 7. Pipizine hoverfly *Oligopipiza quadriguttata* Nidergras, Hadrava, and Nel gen. et sp. nov., Rupélian, Céreste, France. Reconstructions of abdomens of all type specimens. **A.** RNGL-S1 (holotype, male). **B.** RNGL-S2 (female). **C.** RNGL-S3 (male). **D.** RNGL-S4 (female). **E.** RNGL-S5 (female). **F.** RNGL-S6 (female). **G.** RNGL-S7 (male). **H.** RNGL-S8 (male). **I.** RNGL-S9 (female). **J.** RNGL-S10 (female). **K.** RNGL-S11 (female). **L.** RNGL-S12 (female). **M.** RNGL-S13 (female). **N.** RNGL-S14 (female). **O.** RNGL-S15 (female).

Pseudopipiza Violovitsh, 1985), has a surstylus longer than the epandrium, itself very broad and short, while the surstylus is shorter than epandrium in *Oligopipiza* (Violovitsh 1985). *Triglyphus* Loew, 1840 is excluded because *Oligopipiza* has more than three visible abdominal tergites (three in *Triglyphus*). The median indentation between the two lobes of male epandrium is very deep and narrow, so that the basal part of epandrium is very narrow, which is not the case for *Heringia* Rondani, 1856 and *Pipiza* Fallén, 1810 (Vujić et al. 2008, 2013). The head of *Pipiza* is also angular between the frons and the face, at the lunule, unlike *Oligopipiza*, which does not have this angle. *Oligopipiza* could share with *Trichopsomyia* Williston, 1888 the possibly pilose anterior mesopleuron, but its median indentation between the two lobes of male epandrium is very deep and narrow, unlike in this extant genus (Thompson 1981). *Neocnemodon* Goffe, 1944 is excluded because of the absence of spurs on mid and hind coxae and hind trochanters in *Oligopipiza* (Thompson 1972; Speight and Smith 1975). Affinities with *Claussenia* Vujić and Ståhls, 2013 are excluded because the female of *Oligopipiza* has no bristles on posterior margin of scutellum while *Claussenia* has 4–6 such long back bristles (Claussen et al. 1994; Vujić et al. 2013). Additionally *Claussenia* has a

tooth on the surstylus unlike *Oligopipiza*. *Pipizella* Rondani, 1856 is excluded because the cell R_{4+5} of *Oligopipiza* is acute apically as upper crossvein M_1 is not perpendicular to R_{4+5} and the basoflagellomere is rounded (not elongated as in *Pipizella* or *Heringia*).

Among the fossil syrphids attributed to the Pipizinae, *Oligopipiza* has the eyes not densely pilose unlike *Palaeopipiza xenos* Meunier, 1902, and their ornamentations of the abdomen are different. Hull (1945) suggested placing *Palaeopipiza* in the Eumerini. After Meunier (1902) and Hull (1945), the type of *Pipiza venilia* should be restudied; its generic attribution is uncertain. *Pipiza melanderi* has pale spots on all abdominal segments unlike *Oligopipiza*. The genus *Pseudopipiza* Hull, 1945 is supposed to differ from *Pipiza* “in the face and in the confluence point of the apical cross vein M_1 being practically at wing tip” (Hull 1945: 294), which is clearly the case in the type species *Pseudopipiza antiqua* but not in *Pseudopipiza europa* (see Hull 1945: pl. 13: 113 and 121). The later has its confluence point between R_{4+5} and M_1 very far from wing margin. *Pseudopipiza europa* should be revised. *Pseudopipiza* differs from *Oligopipiza* as follows: a very short crossvein $r-m$ (long in *Oligopipiza*), part of M basal of $bm-cu$ making a strong angle with part of M

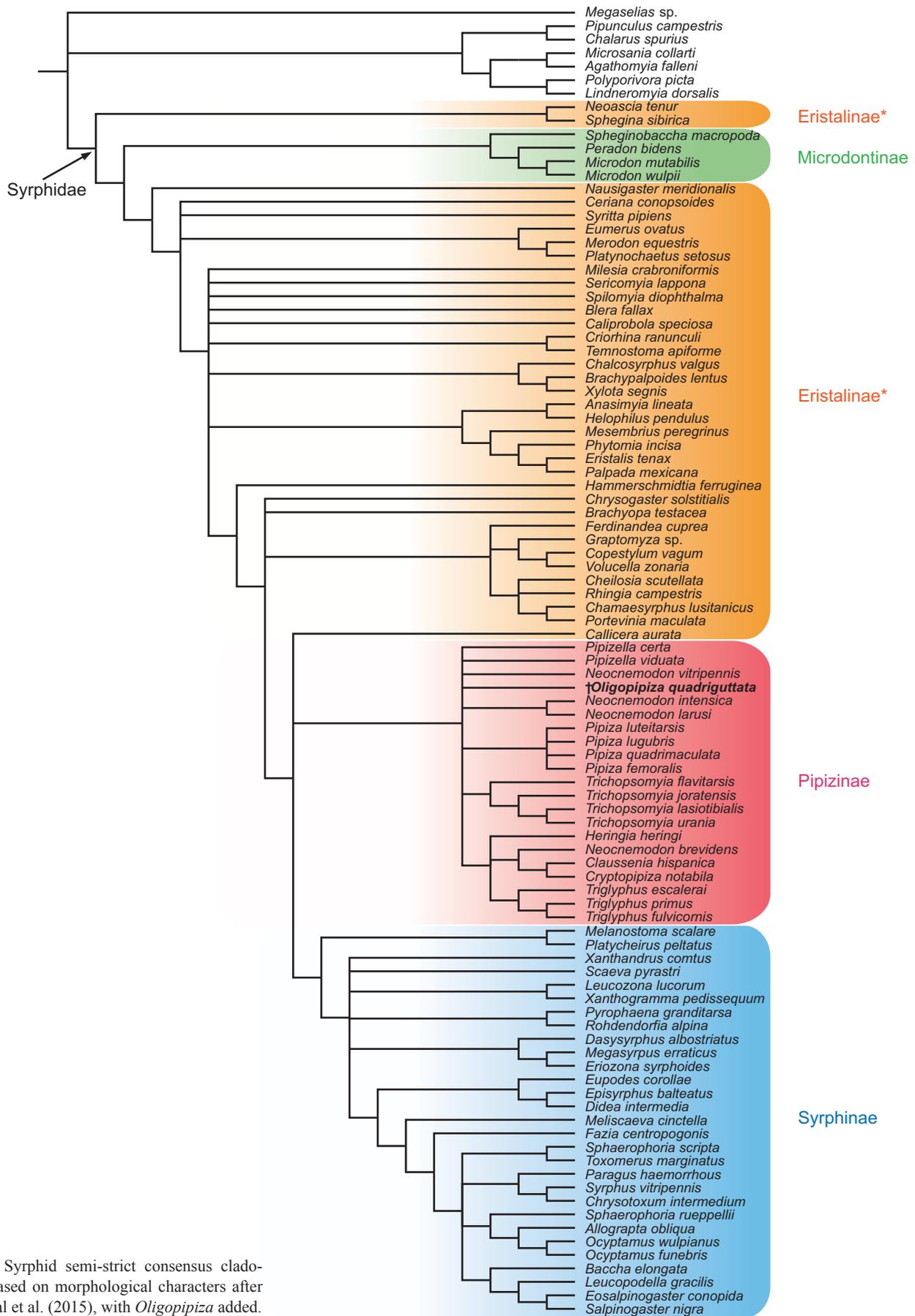


Fig. 8. Syrphid semi-strict consensus cladogram based on morphological characters after Mengual et al. (2015), with *Oligopipiza* added.

distal of it, part of R_{4+5} basal of r-m straight (making a strong curve in *Oligopipiza*), and crossvein dm-cu far from the posterior wing margin (close to it in *Oligopipiza*).

Phylogenetic placement of *Oligopipiza* and its implications.—The phylogenetic analysis gave 650 equally most parsimonious cladograms, of length = 945 steps. The strict consensus and the semi-strict consensus cladograms (Fig. 8) differ only in the hierarchy between the three species of *Triglyphus*. The obtained phylogeny is similar to the combined morphological and molecular one of Mengual et al. (2015: fig. 2). The Eristalinae appear non monophyletic with the Microdontinae between “inner” and “outer” Eristalinae. The Pipizinae and the Syrphinae are sister groups. The Pipizinae are monophyletic, but their phylogeny is clearly less solved than in Mengual et al. (2015). *Oligopipiza* falls in this clade, supporting the attribution of this taxon.

Palaeoecological inferences for *Oligopipiza quadriguttata*.—About 23% of extant European species of pipizine hoverflies are associated with coniferous/mixed forests, with 57% for *Neocnemodon* species, 66% for *Trichopsomyia*, and 16% for *Pipizella* (Speight and Castella 2016). The paleoflora from Céreste corresponds to a mixed mesophytic forest with *Pinus* spp., under a tropical warm climate (Thiébaud 1999; Gregor 2002). We found numerous pollen grains around the majority of the specimens of *Oligopipiza quadriguttata*, which have two aerial bags, about 60 μm in size (SOM: fig. 2), so they probably are pollens of Pinaceae. Even if only macrofossil of *Pinus* sp. are recorded at Céreste (Gregor 2002), some palynological analyses by extraction in these sediments need to be done. This observation suggests that *O. quadriguttata* was living in a mixed forest, confirming the results of Gregor (2002), but we cannot confirm it was a pollinator of conifer because there is no extant species of European pipizine pollinators of conifers. Fossil Aphididae and Psylloidea are known from the same outcrop (Heie and Lutz 2002), *Oligopipiza* was probably a predator of these insects, as for the extant taxa (Mengual et al. 2015).

Conclusions

We described *Oligopipiza quadriguttata* Nidergras, Hadrava, and Nel gen. et sp. nov. representing the first known Syrphidae from the Oligocene of the lacustrine outcrop of Céreste (Lubéron, France). It belongs to the subfamily Pipizinae, confirming that this clade was already rather diverse during the Eocene–Oligocene. It also supports the presence of a mixed forest in the corresponding palaeoenvironment.

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