A new hoverfly genus from the Oligocene of France with unusual morphology

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Here, we describe *Intricodon cryptodaemoniacus*, a new fossil genus and species of hoverfly (Diptera: Syrphidae), representing the second described hoverfly from the middle Oligocene of Céreste (Luberon, Southern France). It has unique, highly specialized characters like hind legs strongly thickened with processes on femur and tibia and the shape of the wing veins R_{4+5} and M_1. Based on the visible characters on the well preserved compression fossil specimen, the new genus resembles some taxa currently attributed to the Merodontini in the wing venation and/or leg morphology. The systematic affinities and potential palaeoecology of the new genus are discussed through the comparison to the more similar Recent genera.

Key words: Insecta, Diptera, Syrphidae, Merodontini, Oligocene, Cenozoic.

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Introduction

With more than 6,200 extant species, Syrphidae are a highly diversified group of Diptera. They exhibit a wide range of ecological strategies and provide important ecosystem services (Ssymank et al. 2021). Recent phylogenetic inferences have estimated their origin in the Cretaceous period, followed by a rapid radiation during the Paleogene (Mengual et al. 2023; Wong et al. 2023; Wu et al. 2024).

Although more than 100 fossil species of hoverflies have been described so far (Evenhuis 1994), the number of described fossil hoverflies is low compared to many other fly families (e.g., Tipuloidea or Sciaroidea). Several new Syrphidae have been documented in recent studies, and numerous others still remain to be described (Nidergas et al. 2018; Hadrava et al. 2020). Describing and classifying new fossil taxa is important for understanding the morphological evolution of the study group throughout the ages (e.g., Daňková et al. 2025), and for improving the molecular phylogeny dating, using them as calibrating points.

In the present study, we describe a new genus and species from the Oligocene lacustrine deposits near the village of Céreste, Luberon, southern France.

Institutional abbreviations.—PNRL, Réserve naturelle nationale géologique du Lubéron, France.

Other abbreviations.—C, costa; CuA, cubitus anterior; dm-m, crossvein between M_1 and M_4; M, median vein; M_1, first branch of M; M_4, second branch of M; m-cu, crossvein between M_4 and CuA; R, radial vein; R_1, anterior branch of R; r_1, cell between R_1 and R_{2+3}; R_{2+3}, second branch of R; r_{2+3}, cell between R_{2+3} and R_{4+5}; R_{4+5}, third branch of R; r_{4+5}, cell between R_{4+5} and M_1; r-m, crossvein between R_{4+5} and M_1; Rs, radial sector; Sc, subcosta; sprs, spurious vein.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in Zoobank LSID: urn:lsid:zoobank.org:pub:467F5171-4DCD-4F20-BB0E-93909B21D378.

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Material and methods

The fossiliferous outcrop is located west of La Bastide du Bois, south of the small village of Céreste, in Luberon (France); for details on the site and the fossil assemblage, see Nel et al. (2024 and references therein). These fossiliferous sites are protected by the Réserve naturelle nationale géologique du Lubéron (Coster and Legal 2021).

The fossil was found in the year 2000 by AN. Drawings were made with Inkscape v0.92 using a drawing tube mounted on a Nikon D800. Photographs were made with a reflex Nikon D800 mounted on a Nikon SMZ25 stereomicroscope, manipulated with DxO PhotoLab v1.1.2 and Gimp v2.8.6 and then focus-stacked with the "D-map" algorithm on Zerene Stacker v1.04. We follow Ssymank et al. (2021) for the morphological terminology.

Systematic palaeontology

Order Diptera Linnaeus, 1758

Family Syrphidae Latreille, 1802

Subfamily Eristalinae Newman, 1834

Tribe ?Merodontini Edwards, 1915

Genus *Intricodon* nov.

Zoobank LSID: urn:lsid:zoobank.org:act:24010AA2-4B4F-4172-9EA6-7511F12BAC32.

Type species: *Intricodon cryptodaemoniacus* gen. et sp. nov.; see below.

Etymology: Combination of Latin *intricatus*, complicated; in reference to the difficulty placing this fossil genus in an extant tribe due to its unusual morphology; and the suffix *odon*, which refers to the extant genus *Merodon* Meigen, 1803, due to the likely taxonomic affinity between *Intricodon* and the Merodontini tribe.

Diagnosis.—As for the type species, by monotypy.

Remarks.—The new fossil genus is assigned to the Syrphidae (Fig. 1) with no doubt due to the characteristic wing venation, with the presence of the vena spuria crossing the r-m vein between veins Rs-R_{4+5} and M, and the veins M_1 and dm-m running parallel to the wing margin (Fig. 2). It does not seem to be related to the subfamily Microdontinae nor the tribe Volucellini because its vein M_1 is not recessive (i.e., apically making an obtuse angle with the vein R_{4+5}, directed toward the wing base instead of the wing apex when joining the vein R_{4+5}), and its vein R_{2+3} is not basally curved as in Microdontinae (Reemer and Ståhls 2013). *Intricodon* gen. nov. is also not related to Syrphinae, because of its complex venation with strongly sinuate dm-m and distal part of M_1 (false margin), strongly thickened legs, while Syrphinae have generally thin legs and a straighter false margin of the wing. Our new genus seems to be not related to subfamily Pipizinae because of the ending point of costa after wing apex and the vein R_{4+5} is apically curved in *Intricodon* gen. nov. while the latter vein is straight apically in this group (Mengual et al. 2015). The remaining possible attribution is the paraphyletic Eristalinae sensu lato.

Young et al. (2016) divided the Eristalinae into the Brachyopini, Callicerini, Cerioidini, Eristalini, Merodontini, Milesiini, Rhingiini, Sericomyiini, and Volucellini. Moran et al. (2022: 129) indicated that the "tribes Cerioidini, Volucellini and parts of Merodontini (including Merodon)" would be placed "outside of an otherwise monophyletic Eristalinae". However, Wong et al. (2023) placed the Brachyopini, Callicerini, Cerioidini, Eristalini, Merodontini, Milesiini, Rhingiini, and Volucellini in Eristalinae, excluding the tribe Sericomyiini. Thus there seems that there is still no real consensus in the definition and limits of the Eristalinae.

The Sericomyiini have the apices of R_1 and R_{2+3} strongly approximate, unlike in the new fossil. The Volucellini, Cerioidini, Eristalini, and Milesiini have a shape of M_1 and R_{4+5} very different from that of *Intricodon* gen. nov. Also the Cerioidini *Monoceromyia* Shannon, 1925, *Polybiomyia* Shannon, 1925, and *Sphiximorpha* Rondani, 1850, have the abdomen constricted. *Ceriana* Rafinesque, 1815, *Monoceromyia* Shannon, 1925, *Primocerioides* Shannon, 1927, and *Sphiximorpha* Rondani, 1850, have a frontal proeminence, absent in *Intricodon* gen. nov. (Van Steenis et al. 2016). The Brachyopini and Rhingiini have M_1 making a right angle with R_{4+5}, vs. distinctly acute in *Intricodon* gen. nov.

Intricodon gen. nov. shares some morphological characteristics with Merodontini that can be potential synapomorphies: R_1 joining C beyond 0.6 of the distance from Sc to R_{2+3}, M_4 ending in posterior margin of wing ("dm-m stump vein present"), as proposed by Doczkal and Pape (2009) and Doczkal et al. (2016). But these characters are also present in some other groups. Also the distal end of M_1 is more or less recurrent, forming an acute outer angle with R_{4+5} in nearly all Merodontini (Vockeroth 1964; Vockeroth and Thompson 1981; Hurkmans 1993; Doczkal and Pape 2009; Morales et al. 2009; Doczkal et al. 2016; Liu et al. 2022), while it is ending directly into R_{4+5} without making a strong curve in *Intricodon* gen. nov.

In *Myolepta* Newman, 1838 (Brachyopini), *Notiocheilosia* Thompson, 1972, *Cyphipelta* Bigot, 1859, and other genera currently placed in the Merodontini, such as *Cepa* Thompson & Vockeroth in Thompson, 2007, *Nausigaster* Williston, 1883 (a genus placed as sister group of the Merodontini by Doczkal and Pape, 2009) and *Psilota* Meigen, 1822, the distal end of M_1 is not recurrent, but progressive (directed to the apex) and forming an acute angle with R_{4+5} as in *Intricodon* gen. nov. (Bezzi 1925; Hull 1949; Thompson 1972, 1999, 2007, 2008; Vockeroth and Thompson 1981; Barahona-Segovia and Barceló 2019; Young et al. 2020). Unlike in the other genera listed above, in the genera *Cepa*, *Nausigaster*, and *Psilota* the wing vein M_1 has a pronounced curve midway somewhat similar to that in *Intricodon cryptodaemoniacus* gen. et sp. nov. And here, the medial antero-posterior length of the tergite III is distinctly smaller than tergites II and IV, which is also the case in *Nausigaster*, while *Psilota* has the tergites III and IV of nearly the same lengths. In *Cepa* and *Psilota* the vein R_{4+5} is nearly straight in nearly all its course as in *Intricodon* gen. nov., while in some *Nausigaster* species (but not all) the vein R_{4+5} has a smooth curve midway (Hull 1949; Thompson 1972). Additionally, in *Cepa*, *Nausigaster*, and *Psilota* the vein R_{4+5} has not a pronounced posterior curve just basal of its fusion with M_1, like in *Intricodon* gen. nov. *Nausigaster* strongly differs from *Intricodon* gen. nov. in the shape of the abdomen with long tergite IV (Williston 1883: pl. 2: 15). *Psilota* also has a very different shape of abdomen with tergite III as long as tergite II (Young et al. 2020). *Cepa* also has a very different shape of abdomen, small oval, and compact (Thompson 1999, 2007).

Because of the similarities in venation with *Nausigaster* and the strong similarities in the hind leg morphology with *Merodon*, we propose to provisionally put *Intricodon* gen. nov. in the Merodontini. Nevertheless, Wong et al. (2023) did not include *Nausigaster* in their phylogenetic analysis. Wu et al. (2024: 8) indicated that "Due to the lack of data on *Psilota* Meigen, 1822, and *Nausigaster* Shannon, 1921, our study was unable to fully validate the monophyly of the Merodontini". Rotheray et al. (2000: 133) indicated that "*Nausigaster* larvae were completely different [from those of the Merodontini] and were closely related to *Criorhina* Meigen, 1822, in the Xylotini". *Cepa* was not included in the analyses of Wong et al. (2023) and Wu et al. (2024). In the analysis of Wong et al. (2023: fig. 2), *Psilota* does not fall at all with *Merodon*. Thus the positions of *Nausigaster, Psilota*, and *Cepa* need to be clarified to precise that of *Intricodon* gen. nov.

Some extant genera have their R_{4+5} pedicel greatly reduced and weakly marked, with the conjunction point between R_{4+5} and M_1 almost reaching the tip of the costa, as it is the case in the New World genus *Nausigaster.*

Stratigraphic and geographic range.—Oligocene, Céreste, France.

Intricodon cryptodaemoniacus sp. nov.

Figs. 1–5.

Zoobank LSID: urn:lsid:zoobank.org:act:5453A719-68A2-4717-94A0-9F5B161C1EB3.

Etymology: From Greek *crypto*, hidden and *daemon*, demon; in reference to the ornamentation of abdomen that looks like a demoniac angry face when watched upside-down.

Type material: Holotype PNRL 2071, a nearly complete male, part.

Type locality: Céreste, Alpes-de-Haute-Provence, France.

Type horizon: Campagne–Calavon Formation (European Mammal Reference Levels biozone MP23–24, 33.9–27.82 Ma) (Feist 1977; Cavelier et al. 1984; Apostolescu and Guernet 1992; Ménouret 2014), Rupelian, Oligocene.

Material.—Holotype only.

Diagnosis.—Small-sized species; head deformed but with face not pronounced (Fig. 1), compound eyes holoptic; basoflagellomeres oval-shaped. At least wing veins C, Sc, R, and M with microtrichia as long as the width of the veins; costa ending significantly after wing apex; subcostal vein basally straight, not running parallel to vein R, and making a pronounced angle at its apical 4/5; vein R_1 slightly thicker than

Fig. 1. Syrphid hoverfly *Intricodon cryptodaemoniacus* gen. et sp. nov., holotype PNRL 2071, from Oligocene of Céreste, France. Photograph of habitus.

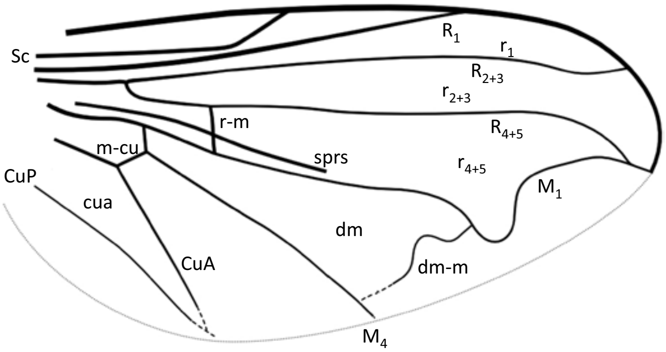

Fig. 2. Syrphid hoverfly *Intricodon cryptodaemoniacus* gen. et sp. nov., Reconstruction of wing. Abbreviations: CuA, cubitus anterior; cua, cubital cell; CuP, cubitus posterior; dm, cell between M_1 and M_4; dm-m, crossvein between M_1 and M_4; M, median vein; M_1, first branch of M; M_4, second branch of M; m-cu, crossvein between M_4 and CuA; R, first branch of radius; R_1, anterior branch of R; r_1, cell between R_1 and R_{2+3}; R_{2+3}, second branch of R; r_{2+3}, cell between R_{2+3} and R_{4+5}; R_{4+5}, third branch of R; r_{4+5}, cell between R_{4+5} and M_1; r-m, crossvein between R_{4+5} and M_1; Sc, subcosta; sprs, spurious vein. Not to scale.

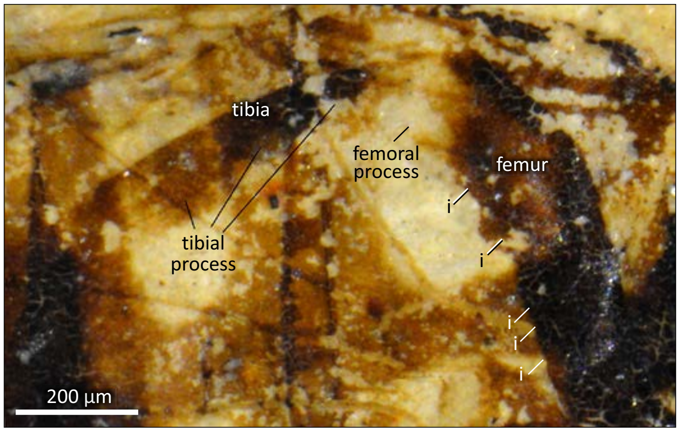

Fig. 3. Syrphid hoverfly *Intricodon cryptodaemoniacus* gen. et sp. nov., holotype PNRL 2071, from Oligocene of Céreste, France. Photograph of hind leg. Abbreviation: i, indentations of femur.

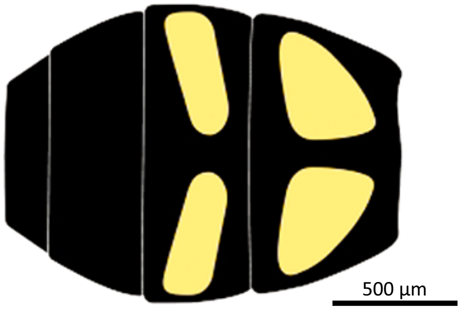

Fig. 4. Syrphid hoverfly *Intricodon cryptodaemoniacus* gen. et sp. nov. Reconstruction of abdomen.

costa (ratio 4:3); crossvein r-m very long, about 0.8 the length of part of R_{4+5} basal to its junction with r-m; vein R_{2+3} nearly straight before its apical 4/5, and apically curved; vein R_{4+5} strongly curved basally, straight till distal 2/3 of its course after vein r-m, and finally curved downward and obliquely ending into M_1; vein M_1 making a strong U-shaped curve in its apical third (Fig. 2), and strongly concave apically; veins R_{4+5} and M_1 joining together to form a pedicel half as long as r-m; vein dm-m strongly curved apically before its confluence point with M_1. Hind femur strongly thickened with processes on femur and tibia (Fig. 3). Abdomen oval shaped (Fig. 4); tergites more densely setose laterally than in their median parts; medial length of tergite III distinctly shorter than the lengths of the tergites II and IV; abdominal tergite II with two sub-triangular pale spots with rounded angles, and tergite III with two oblique elongate sub-rectangular spots, 3× as long as wide.

Description.—*Body*: 5.3 mm long. *Head*: 1.8 mm high, 1.1 mm long; face poorly preserved but apparently not produced; compound eyes poorly preserved, holoptic, diameter ca. 0.39 mm. Thorax ca. 0.84 mm long, 0.90 mm high; no visible setae on thorax. *Wing*: hyaline, ca. 4.1 mm long, 0.79 mm wide; basal part of pterostigma between Sc and R_1 hyaline. *Legs*: Hind femur bicolor, strongly thickened, with dorsal margin making a smooth obtuse angle, about 153°, and a large, clear-coloured anteroventral apical process and at least five indentations along its anteroventral margin, gradually larger towards apex; hind tibia strongly thickened and flattened toward its apex (maximum width about 1.3× basal width), with a short, strong ventral process basally, and a strongly flattened "plate" on apical half, five times as long as wide, with a dense line of small punctuations, which could be interpreted as the bases of setae. *Abdomen*: Ovoid, 1.27 mm long, 1.01 mm wide; tergite III apparently slightly shorter than tergite II and IV; tergites II and III with two pale elongate spots, separate by a brown median zone, those of tergite II being subtriangular with anterior margin rounded, postero-distal angle acute, and postero-proximal angle straight, those of tergite III sub-quadrangular, about 3× longer than wide; spots of tergites II and III with about same inclination with posterior margin of tergites II, viz. 11–16°; tergite IV uniformly dark, without apparent markings. *Genitalia*: Hypandrium large, as long as tergite IV, almost reaching middle of tergite III in dorsal view.

Remarks.—Nidergas et al. (2018) already described the pipizine syrphid genus and species *Oligopipiza quadriguttata* from the same layers. Syrphids are not infrequent in these layers and at least two other species need to be described.

The highly specialized hind leg of *Intricodon cryptodaemoniacus* gen. et sp. nov. strongly resembles those of some extant species of *Merodon* and *Eumerus* Fabricius, 1798, in

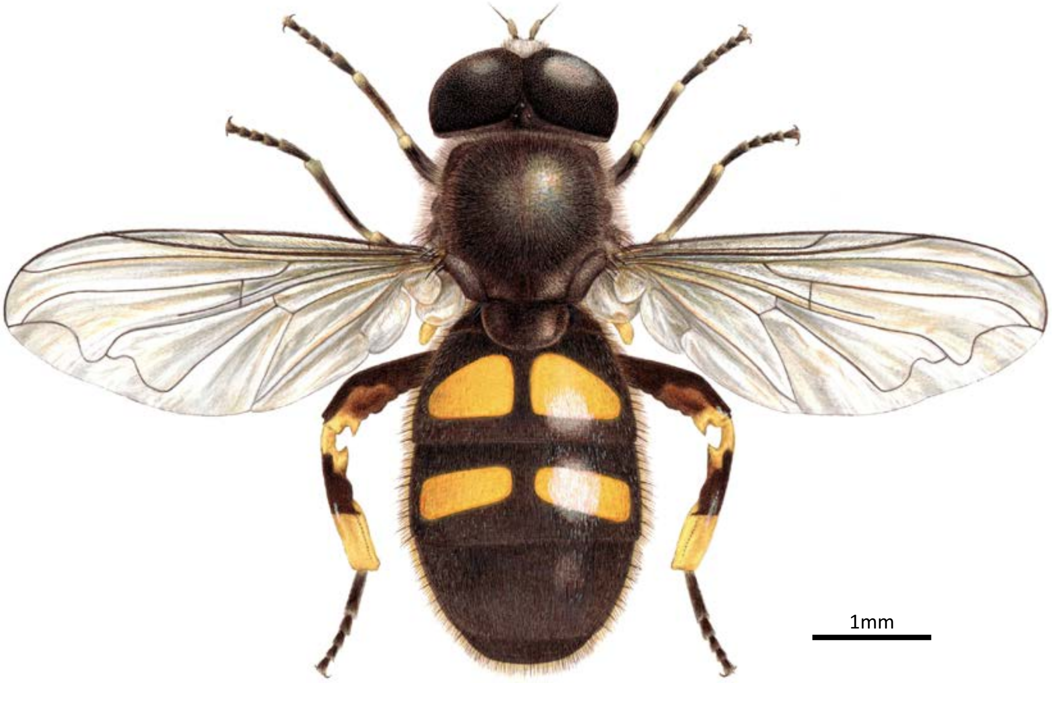

Fig. 5. Syrphid hoverfly *Intricodon cryptodaemoniacus* gen. et sp. nov.. Reconstruction of habitus (artwork by Carim Nahaboo).

the presence of an apical anteroventral process and indentations along the apicoventral margin of the metafemur and of a strong ventral tooth on the metatibia (Speight and Langlois 2020; Speight et al. 2021). Nevertheless, species of *Merodon* and *Eumerus* differs from the new fossil in the abdomen with tergite 3 as long as or longer than tergite 2 (Vujić et al. 2018; Speight et al. 2021).

No Eristalinae sensu lato (and even no extant Syrphidae) have a vein dm-m strongly curved close to M_1 similar to that of *Intricodon cryptodaemoniacus* gen. et sp. nov., even if in some species of *Myolepta* and *Nausigaster*, this vein is curved near M_4 and less than in *Intricodon cryptodaemoniacus* gen. et sp. nov. (Fluke and Weems 1956; Thompson, 1972). Also, no extant genus has such unusual venation similar to *Intricodon cryptodaemoniacus* gen. et sp. nov., with R_{4+5} fused with M_1 and curved downward apically.

Stratigraphic and geographic range.—Oligocene, Céreste, France.

Discussion

The chaetotaxy on the wing veins *Intricodon cryptodaemoniacus* gen. et sp. nov. is very unusual. The selective advantage that would have led to this character remains unknown, as well as for the specialized structures on the hind femur and tibia of *Intricodon cryptodaemoniacus* gen. et sp. nov. There is a sexual dimorphism in some extant species of *Merodon* in the shape and development of the hind femoral and tibial processes, less developed in females than in males (Vujić et al. 2022). Thus, these structures could be related to the mating behavior in these flies.

Larvae of *Merodon* and *Eumerus* are phytophagous in soils or saprophagous (Orengo-Green et al. 2024; Gisbert 2024). Larvae of *Nausigaster* have been recorded from decaying cacti and bromeliads. It seems that, to date, nothing is known on the biology of the genus *Cepa* (Barahona-Segovia and Barceló 2019). Larvae of few *Psilota* species have been found in sap runs under tree bark (Kassebeer et al. 1998), otherwise, the biology of many species in this genus is unknown (Young et al. 2020). It is possible but not demonstrated that the larvae of *Intricodon cryptodaemoniacus* gen. et sp. nov. were phytophagous or saprophagous too.

Conclusions

Intricodon cryptodaemoniacus gen. et sp. nov. is a very enigmatic taxon, with a wing venation strongly different from those of the other Syrphidae. It confirms the richness and diversity of the syrphids in the Oligocene insect assemblage of Céreste. It also shows that, despite its relatively young age compared to the antiquity of this family, the Oligocene Syrphidae comprised some very original forms, and not only representatives of extant genera.

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