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## Research article

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# The first sawfly from the Oligocene of Céreste (Southern France) (Hymenoptera: Tenthredinidae)

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**Abstract.** *Luberotenthredo cerestensis* gen. et sp. nov. is the first record of the sawfly family Tenthredinidae from the Oligocene of Céreste (Southern France). This taxon is described and illustrated based on a well-preserved specimen. This genus resembles the extant genus *Perineura* (subfamily Tenthredininae, tribe Perineurini) with which it shares forewing venation similarities and numerous morphological characters. This new taxon is the first fossil representative of the tribe Perineurini and can be used as a calibration point for future investigation of the diversification of the family Tenthredinidae.

**Keywords.** Fossil record, Insecta, Perineurini, ‘Symphyta’, Tenthredininae.

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## Introduction

The family Tenthredinidae Latreille, 1818 is relatively well-known in the fossil record, with numerous representatives of the subfamilies Nematinae Thomson, 1871 (see list in Nel 2022), Blennocampinae Jakovlev, 1892 (Nel *et al.* 2022a), and Allantinae Rohwer, 1911 (see list in Nel *et al.* 2022b) already described. This well-documented fossil record is not surprising given the relatively old age of the clade, arising during the Cretaceous, and their abundance and diversity in modern ecosystems (i.e., the Tenthredinidae are the most diversified symphytan lineage) (e.g., Nyman *et al.* 2019; Niu *et al.* 2022).

The subfamily Tenthredininae Latreille, 1818 is no exception to this observation and is also well-represented in the fossil record. Taeger *et al.* (2010) and Vilhelmsen & Engel (2012) reviewed and summarized the list of the fossil species currently placed in this subfamily, viz. *Macrophya adventitia* Lewis, 1969, *Macrophya pervetusta* Brues, 1908, *Nortonella typica* Rohwer, 1908, *Sambia succinica* Vilhelmsen & Engel, 2012, *Taeniurites fortis* Cockerell, 1917, *Tenthredinites bifasciata* Meunier, 1915, *Tenthredo fenestralis* (Cockerell, 1927), *Tenthredo oblita* (Cockerell, 1917), *Tenthredo toddi* (Cockerell, 1914), *Tenthredo avia* (Brues, 1908), *Tenthredo gervaisi* Heer, 1861 (a nomen nudum as Heer 1861: 153) only listed this species name in a catalogue of fossil insects from the Oligocene of Aix-En-Provence), *Tenthredo infossa* Brues, 1908, *Tenthredo meunieri* Taeger, Blank & Liston, 2009 (new name for *Tenthredo fasciata* Meunier, 1922), *Tenthredo miocenica* Zhang & Zhang, 1990, *Tenthredo petrae* Zhang & Zhang, 1990, *Tenthredo primordialis* Piton, 1940, *Tenthredo rhyisia* Zhang, 1989, *Tenthredo saxorum* Rohwer, 1908, *Tenthredo submersa* Cockerell, 1907, *Tenthredo toddi* Cockerell, 1914, and *Tenthredoides plurilocellata* Zhang, 1989. All these fossils span the Cenozoic, more precisely a period between the Paleocene and the Miocene. Interestingly, the age of the known Tenthredinidae fossils is in agreement with the time divergence estimate proposed for the family (e.g., Nyman *et al.* 2019; Niu *et al.* 2022). The diversification of the family has been shown to be linked to the diversification of flowering plants (angiosperms) (Nyman *et al.* 2019). This ‘co-diversification’ probably took place during the Angiosperm Terrestrial Revolution (ATR, 100–50 Ma, Benton *et al.* 2022). A transitional period in flora assemblages resulted from the transition between ecosystems dominated by the gymnosperms to ecosystems dominated by the angiosperms, resulting in drastic diversification of many insect families (e.g., discussed in Benton *et al.* 2022) and the decline of others (e.g., Jouault *et al.* 2022). Improving documentation of the paleoentomofauna before and around this critical period is crucial for a better understanding of its impact on the evolutionary history of the Insecta Linnaeus, 1758.

Here we embrace this vision and describe the first Tenthredinidae from the Oligocene lacustrine Campagne-Calavon Formation (Céreste, Luberon, Southern France). This specimen is placed in the subfamily Tenthredininae, within Perineurini Rohwer, 1911 (*sensu* Wei & Nie 1998), and resembles the extant genus *Perineura* Hartig, 1837 (see Discussion).

## Material and methods

The fossiliferous outcrop is located west of La Bastide du Bois, south of the small village of Céreste, in Luberon (France). This site and the other fossiliferous localities located south of Céreste have yielded a rich insect fauna, an impressive flora (Saporta 1891) as well as vertebrates (Sauvage 1880; Sigé 1971; Schmidt-Kittler & Storch 1985; Gaudant 1997; Brinkmann & Rauhe 1998; Mayr 1999, 2000; Roux 2002; Duhamel & Louchart 2020; Duhamel *et al.* 2020). These fossiliferous sites are protected by the Luberon National Geologic Nature Reserve (Coster & Legal 2021).

The laminated limestones that yielded the fossils belong to the lacustrine Campagne-Calavon Formation dated as Rupelian (biozone MP23–24, 33.9–27.82 Ma) based on biostratigraphic data from gastropods (Cavelier *et al.* 1984), charophytes (Feist 1977), ostracods (Apostolescu & Guernet 1992), and mammals (Helmer & Vianey-Liaud 1970; Ducreux *et al.* 1985). The Campagne-Calavon Formation documents a quiet, calm, and shallow lacustrine environment, characterized by periodic variations of salinity (Ducreux 1982; Lutz 1984). The fossil ichthyofauna consists of a mixture of freshwater and euryhaline taxa (Gaudant 1997, 2013, 2015). Insect fossils from Céreste have probably been deposited onto sticky biofilms. They are mostly complete, and reasonably well preserved.

The holotype was collected during fieldwork in April 2023. The new fossil was carefully prepared using an air scribe under a stereo microscope. The specimen was photographed using a Canon 50D camera with an attached Canon 65 MPE camera lens and mounted on an automated stacking rail (StackShot). All images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus ver. 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019 software.

The specimen is stored in the Musée de Géologie, Réserve géologique du Luberon, Parc naturel régional du Luberon, Apt, France.

We follow the list of tribes and genera of Tenthredininae of Wei & Nie (1998) and (in part) Taeger *et al.* (2010). We follow the wing venation nomenclature adapted from Goulet & Huber (1993).

## Results

Class Insecta Linnaeus, 1758  
Order Hymenoptera Linnaeus, 1758  
Family Tenthredinidae Latreille, 1818  
Subfamily Tenthredininae Latreille, 1818  
Tribe Perineurini Rohwer, 1911 (sensu Wei & Nie 1998)

## Remark

Most fossil species currently placed in the genus *Tenthredo* Linnaeus, 1758 should be revised because, in many cases, these attributions were only a way to indicate affinities with the family Tenthredinidae.

Genus *Luberotenthredo* gen. nov.  
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## Type species

*Luberotenthredo cerestensis* sp. nov.

### Diagnosis

Antennae very long; antennomeres very long (more than twice as long as wide); all flagellomeres elongate and slightly truncate obliquely distally; 3<sup>rd</sup> antennomere as long as 4<sup>th</sup>; tergum 1 with median furrow. Forewing with crossvein 1cu-a distad middle of cell 1M; 2+3-A strongly sinuous, short fusion of 2+3-A with 1-A; ratio of lengths of basal/distal parts of forewing anal cells 0.8. Hind wing with two central cells (i.e., Rs and 1M); anal cell not sessile.

### Etymology

Named after the Luberon mountain and the genus *Tenthredo*. Gender neutral.

*Luberotenthredo cerestensi* sp. nov.

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Figs 1–4

### Diagnosis

As for the genus, by monotypy (vide supra).

### Etymology

Named after the small village of Céreste (Luberon, Southern France).

### Type material

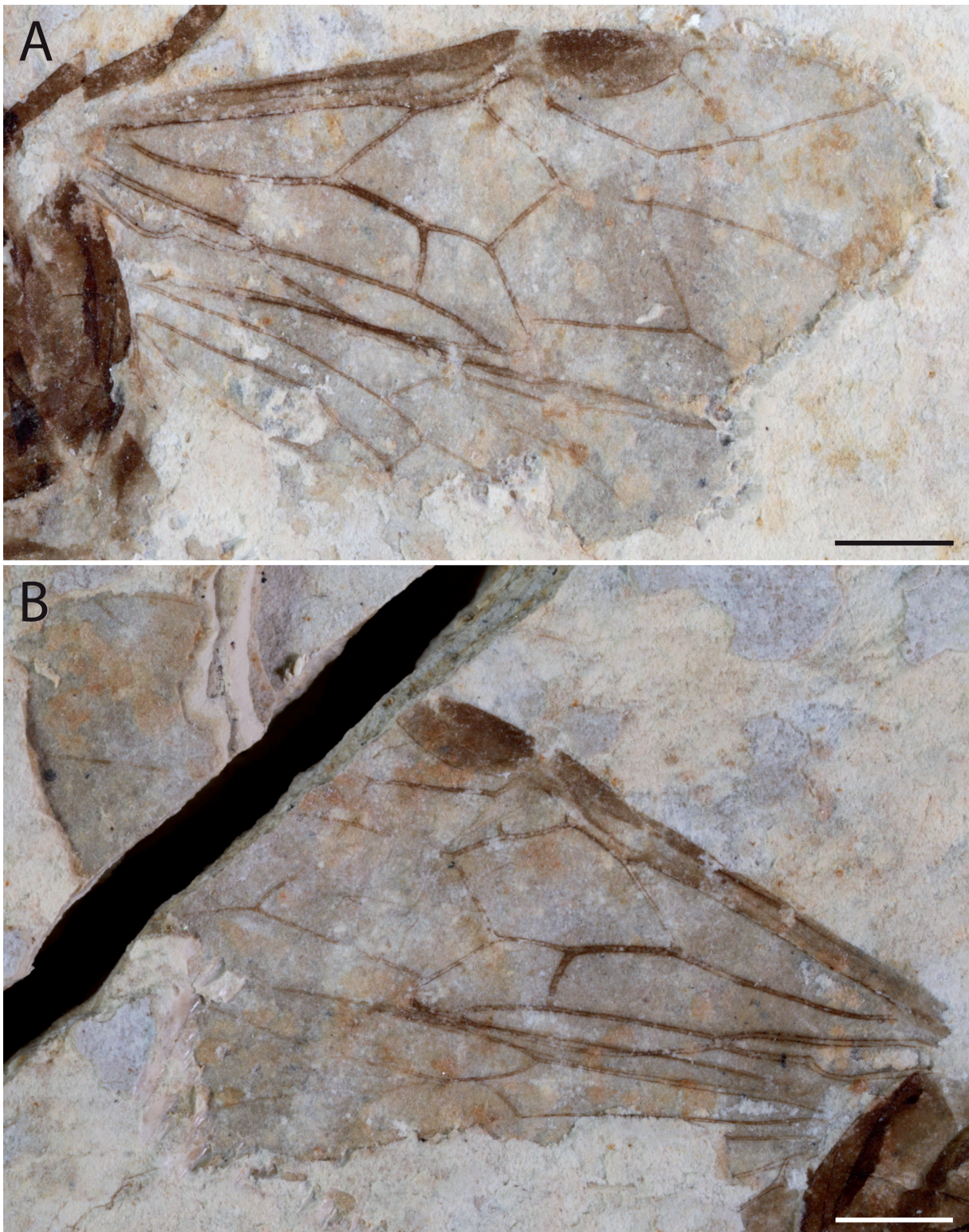
#### Holotype

FRANCE • ♀ (imprint of a complete specimen fossilized in dorsal view); Alpes-de-Haute-Provence, South of the village of Céreste; Early Oligocene, ‘Calcaire de Campagne-Calavon’ Formation; PNRL 2716, stored in the Musée de Géologie, Réserve géologique du Luberon, Parc naturel régional du Luberon, Apt, France.



**Fig. 1.** *Luberotenthredo cerestensi* gen. et sp. nov., holotype (PNRL 2716). Photograph of habitus. Scale bar = 2 mm.





**Fig. 2.** *Luberotenthredo cerestensis* gen. et sp. nov., holotype (PNRL 2716). Photographs. **A.** Right wings. **B.** Left wings. Scale bars = 2 mm.



**Type locality and horizon**

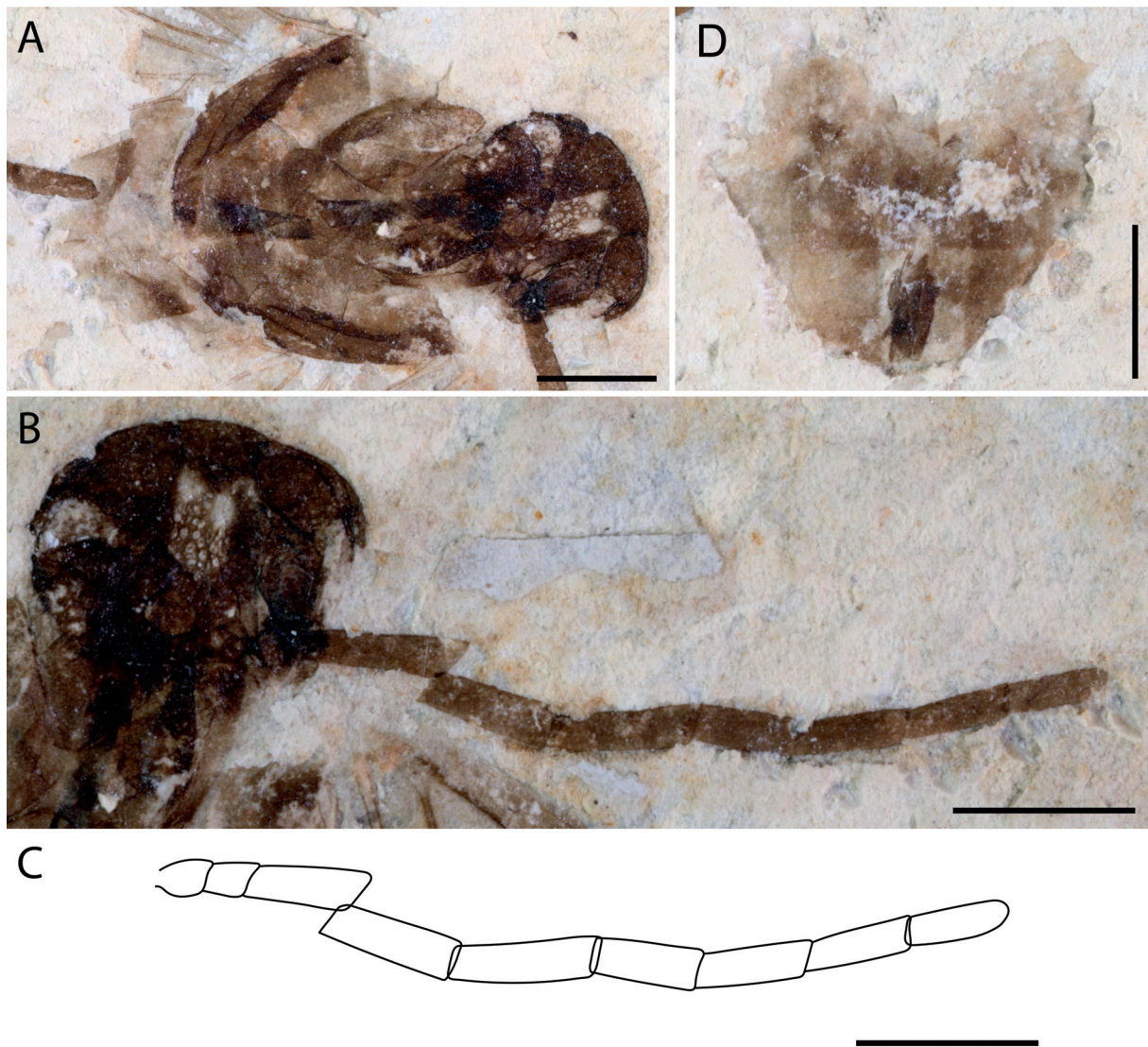
France, Alpes-de-Haute-Provence, South of the village of Céreste, Early Oligocene, ‘Calcaire de Campagne-Calavon’ Formation.

**Description**

MEASUREMENTS. Body length 8.7 mm.

COLOR. Body brown with darker head; compound eyes dark brown; wings hyaline, pterostigma dark brown anteriorly and lighter posteriorly.

HEAD. Deformed and poorly preserved, 1.4 mm long, 2.0 mm wide; compound eyes large, occupying most of head lateral surface, deformed; mouthparts not preserved except left mandible with at least one apical and two preapical teeth; antennae very long, slightly longer than abdomen; scape and pedicel

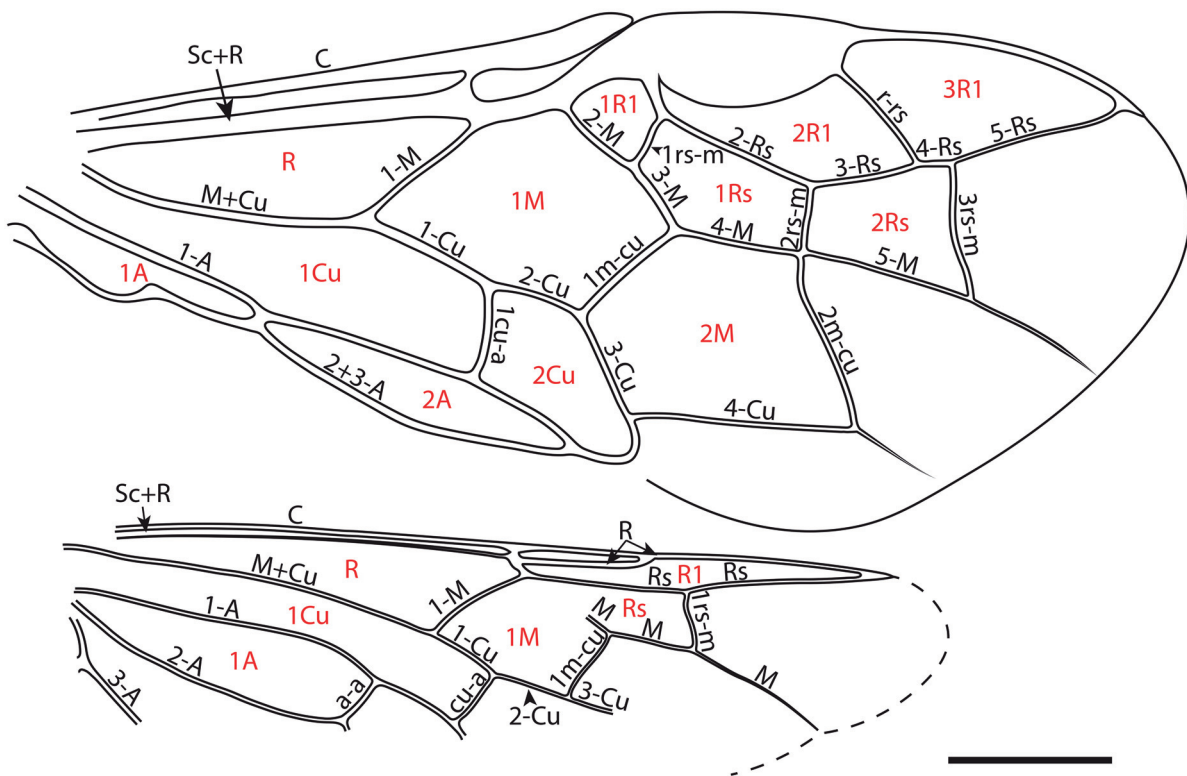


**Fig. 3.** *Luberotenthredo cerestensis* gen. et sp. nov., holotype (PNRL 2716). Photographs. **A.** Head and thorax. **B.** Head and antenna. **C.** Reconstruction of antenna. **D.** Apex of abdomen. Scale bars = 1 mm.

very short; seven flagellomeres; third antennomere as long as fourth; preapical flagellomeres cylindrical, elongate, slightly truncate obliquely.

THORAX. ca 3.0 mm long, 2.8 mm wide, apparently smooth (deformed by compression); pronotum markedly constricted medially; propleuron short and head close to thorax; legs not preserved.

FOREWING. Complete, 7.5 mm long, 2.9 mm wide; short anterior Sc branch located slightly anterior Sc+R and 1-M meeting point; pterostigma 1.3 mm long, 0.5 mm wide, strongly arched along cell 2R1, slightly arched along anterior wing margin; M+Cu slightly curved; 1-M slightly longer than 1-Cu, nearly straight; vein R clearly deviated between junctions of 1-M and Sc; fusion of M with R very long, longer than half length of vein 1-M; vein 2-M meeting R more than halfway between short anterior Sc branch and pterostigma; vein 2-M slightly longer than 1rs-m; Rs emerging at pterostigmal base; 2-Rs nearly straight, longer than 3-Rs; r-rs crossvein located in pterostigma distalmost part, meeting Rs anterior 3rs-m, enclosing cell 2R1; 4-Rs and 5-Rs nearly aligned with 4-Rs extremely short (more than twice shorter than 3-Rs); cell 1R1 trapezoidal, 0.5 mm long; cell 1Rs 1.2 mm long, enclosed distally by subvertical 2rs-m (the latter lightly longer than 1rs-m); 3-M shorter than 4-M; cell 2Rs 0.9 mm long, distinctly wider along sinusoidal 3rs-m; 1-Cu and 2-Cu nearly straight, 1-Cu longer than 2-Cu; 1m-cu meeting Cu at an angle of ca 110°, 1-M and 1m-cu subparallel and of similar lengths; cell 1Cu elongate, longer than cell R; 1cu-a (nervulus) located slightly distad middle of cell 1M; cell 2Cu short trapezoidal; cell 2M fully enclosed distally by long slightly sinusoidal crossvein 2m-cu; vein 1-A long, nearly straight; vein 2A+3-A complete, strongly sinuate in first half, fused with to 1-A on a short distance; cell 1A shorter than cell 2A, ca 0.8 × length of cell 2A.



**Fig. 4.** *Luberotenthredo cerestenssis* gen. et sp. nov., holotype (PNRL 2716). Reconstructions of the wing venations with names of cells and veins labeled. Scale bar = 1 mm.

HIND WING. ca 6.3 mm long; thin costal cell present; thin space between C and R along anterior wing margin; M+Cu long, nearly straight, fork located anterior to Rs origin: 1M long, slightly arched, apparently meeting Rs (i.e., no rs-m crossvein present); abscissae of Rs distad meeting point with 1-M long and nearly straight; cell R1 elongate and thin; cell Rs virtually fully enclosed (second abscissa of M difficult to interpret); crossvein 1rs-m located near middle of cell R1; cell 1M trapezoidal, rather broad, 1.4 times as long as wide; 1-Cu and 2-Cu of similar lengths, closed distally by 1m-cu; cell 1Cu elongate, rectangular, closed distally by cu-a; 1-A long slightly sinusoidal; crossvein a-a located at level of 1-M origin; 2-A long, slightly arched; cell 1A wider than 1Cu but shorter; vein 3-A present, short.

ABDOMEN (partly preserved). Without visible surface sculpture, virtually 4.5 mm long, 2.4 mm wide; ovipositor sheath short and broad, 0.8 mm long.

### Remarks

The new fossil differs from the genus *Sambia* Vilhelmsen & Engel, 2012 (Eocene Baltic amber) in the forewing veins 2+3-A, which are fused with 1-A on a short distance (vs a long crossvein in-between) and its elongate flagellomeres (Vilhelmsen & Engel 2012). With the lower Oligocene genus *Nortonella* Rohwer, 1908 it shares the vein 2+3-A shortly fused with 1-A (Rohwer 1908: fig. 1). But *Nortonella* has the crossvein 1cu-a very close to the base of 1-M, versus about midway between the base of 1-M and 3-Cu in the new fossil and in several extant species of the genus *Perineura* Hartig, 1837 (see photographs of the holotype UCM 4517: <https://invertpaleosearch.colorado.edu/>). The new fossil can be separated from the lower Oligocene genus *Taeniurites* Cockerell, 1917 by the vein 2+3-A, which is shortly fused with 1-A (vs separated) and vein 1cu-a about midway between the base of 1-M and 3-Cu, vs very close to the base of 1-M (Cockerell 1917). The Uppermost Oligocene genus *Tenthredinites* Meunier, 1915 is based on a poorly preserved specimen (Meunier 1915), which is probably lost. Rodriguez *et al.* (2017) suggested it could be a Pompilidae Latreille, 1805. The Miocene genus *Tenthredoides* Zhang, 1989 differs from the new fossil in the vein 1cu-a, which is very close to the base of 1-M (Zhang 1989: text-fig. 224).

### Discussion

#### Attribution to Tenthredinidae Latreille, 1818

The new fossil is placed in Tenthredinidae because of the following characters, after Goulet (1992): pronotum markedly constricted medially; propleuron short and head close to thorax; length of flagellomere 1 less than one-third that of antenna; flagellum thread-like; flagellum with five or more flagellomeres (seven in the new fossil); flagellomeres cylindrical; ocelli in dorsal view forming an angle.

After the key to the tenthredinid subfamilies of Goulet (1992), it would fall either in the Tenthredininae or the Allantinae because of the following characters (wing venation nomenclature not adapted): fore- and hind wings longer than length of abdomen; veins 1m-cu and Cu of forewing meeting at an angle of ca 110°; in forewing, length of vein 1-M (= distance between junctions of veins M with M+Cu and those of Rs+M (= 2-M) with R) 1.8 times length of vein 1m-cu; forewing with main axis of vein M and that of 1m-cu subparallel; vein R of forewing clearly deviated between junctions of M and Sc; R between junctions with M and Rs+M (= 2-M) long (a Tenthredininae character); basal anal cell clearly constricted along vein 2A and 3A (an Allantinae character); crossvein of anal cell of forewing very short (a Tenthredininae character).

Smith (2003a: 148) characterized the Allantinae, among other characters, as follows: “veins M (= 1-M) and Rs+M (2-M) meet Sc+R at the same point”, and “vein 2A+3A (= 2A+3-A) connected to 1A (= 1-A) by an anal crossvein”. Both characters are absent in the new fossil.



Nevertheless, some allantine taxa have a ‘R between junctions with M and Rs+M long’ (corresponding to the fusion of M with R very long, longer than half length of vein 1-M). It is the case for the genera *Athlophorus* Burmeister, 1847 and *Hemathlophorus* Malaise, 1945 (see Malaise 1947; Saini *et al.* 1986; Saini & Vasu 1997). The new fossil strongly differs from these genera in the presence of the vein Irs-m in the forewing and the connection between 1-A and 2+3-A. Notice that Lacourt (1996) placed these genera in Athlophorini Lacourt, 1996, and together with Sioblini Takeuchi, 1952, they form the subfamily Sioblinae (defined in the above-mentioned publication). The other taxa of these Sioblinae were placed in Tenthredininae, while the Athlophorini were maintained in Allantinae by Wei & Nie (1998). As defined by Lacourt (1996), the Sioblinae are characterized by the anal cell having either no or a long crossvein, unlike in the new fossil. Thus, the limits and delineations of the subfamilies Tenthredininae and Allantinae are still unclear.

After the key to the Central America and Neotropical tenthredinid subfamilies of Smith (2003b), the new fossil falls into the Tenthredininae due to the characters (wing venation nomenclature not adapted): forewing with vein 2+3-A complete; anal cell of forewing with 2+3-A either or not separated from 1-A by an anal crossvein; vein R of forewing clearly deviated between junctions of 1-M and Sc; vein 2rs-m present in forewing; forewing with 2+3-A fused with 1-A at center (crossvein between them extremely short); forewing with fusion of M with R very long. Also, the new fossil has the diagnostic characters of the Tenthredininae as proposed by Smith (2003b: 34): “veins 1-M and 1m-cu parallel or subparallel, vein 1-M meeting Sc+R far anterior to the point where 2-M (Rs+M sensu Smith 2003b) re-emerges from R+M, and vein 2+3-A complete, connected to 1-A by a crossvein or fused to 1-A near its center”. On the new fossil, the presence versus absence of the epicnemium cannot be clearly observed while this character is used to diagnose the subfamily.

Zombori (1982: 455) characterized the European Tenthredininae by the following states of characters, all present in the new fossil: “The most conspicuous feature of the subfamily is its subcosta (in fact vein R), since it is twice angled, first at the point of issue of intercostal vein (i.e., at the base of the short anterior Sc vein) and second time at the point of junction of vein 1-M with subcosta (in fact R). The radial cell of forewing is always divided by a crossvein. Points of origin of vein M (= 1-M) and that of Rs+M (= 2-M) on subcosta (R+M) are far from each other, this distance at least as long as same between the point of origin of latter from pterostigma. Vein M (= 1-M) and first recurrent vein (= 1m-cu) are parallel, occasionally diverging towards pterostigma. Lanceolate cell of forewing rather variable: constricted or with a crossvein. The number of antennal joints is 8-9”; apex of vein R short and bent down to meet the apex of the vein 1-M (sensu Zombori, 1982) and vein R+M very long, longer than half the length of the vein 1-M (sensu Zombori, 1982). Following the above-mentioned characters, the new fossil can be attributed to the Tenthredininae.

#### **Attribution to Perineurini Rohwer, 1911**

Goulet (1996: 7) indicated that “within the Tenthredininae, the genera *Aglaostigma* Kirby, 1882, *Beldonea* Cameron, 1899 and *Flagellaria* Saini *et al.*, 1985 and the tribes Macrophyini, Scipterygini Benson, 1946, and Tenthredinini Latreille, 1818 form a monophyletic lineage” on the basis of the shape of the teeth of the tarsal claws (not visible on the fossil) and the “veins 2-A and 3-A” of the forewing “hardly sinuated”, which is not the case in the new fossil (compare with Goulet 1992: figs 112–113; see also Taeger 1991; Wei 1997, 2006). Goulet (1996: 9) separated the Tenthredinini from the Macrophyini on the basis of body characters that are not preserved or visible on the new fossil, and on the presence of a long crossvein in the anal cell of the forewing (except in some *Rhogogaster* Konow, 1884 and *Tenthredo* (*Adungia*) *kingdonwardi* Malaise, 1945), vs very short to absent in the Macrophyini and the new fossil. Nevertheless, following the key of Smith (2003b) to Central America and Neotropical genera of the Tenthredininae, the new fossil would fall near the Macrophyini genus *Pachyprotasis* Hartig, 1837, excluding the two genera *Tenthredo* Linnaeus, 1758 and *Filacus* Smith & Gibson, 1984, because of the following characters: “antenna

slender, longer than twice head width” and “3<sup>rd</sup> and 4<sup>th</sup> antennomeres subequal in length” vs “antenna ½ times or less head width” and “3<sup>rd</sup> antennomere longer than 4<sup>th</sup>”. Furthermore, the new fossil shares with *Pachyprotasis* the character “forewing with anal cell broadly constricted medially”. But the forewing 2+3-A of the new fossil is fused with 1-A at one point close to the center, as in *Filacus* (see Smith 2003b: fig. 3), while the fusion between 1-A and 2+3-A is much longer in *Pachyprotasis* (Smith & Gibson 1984; Zhong *et al.* 2010a, 2010b, 2017, 2018, 2020, 2021, 2022). Among the other genera of the Macrophyini, affinities with the genera *Macrophya* Dahlbom, 1835, *Pseudomacrophya* Enslin, 1913, and *Deda* Gibson, 1980, are also excluded because of their shorter antenna with flattened antennomeres (Gibson 1980a, 1980b; Zombori 1982; Liu *et al.* 2023). In the Sciapterygini genus *Zaschizonyx* Ashmead, 1898, the fusion between 1-A and 2+3-A is also much longer than in the new fossil (Goulet 1992: figs 339–340). *Tianmuthredo* Wei, 1997 and *Renothredo* Wei, 1998 (in Wei & Nie 1998) (replacement name for *Rena* Wei, 1997) (both in Sciapterygini) share with the new fossil a short and constricted stalk present at about one third of the anal cell of the forewing, but *Tianmuthredo* has very short antennae, unlike the new fossil (Wei 1997; Taeger & Kramp 2017). *Renothredo* has the antennae shorter than the abdomen (vs as long or slightly longer than the abdomen in the new fossil), the forewing with 1cu-a located anteriorly the middle of the cell 1M (vs distad middle in the new fossil), a cell 2M elongate with 2m-cu located distad 2rs-m (vs cell 2M quadrate with 2m-cu aligned with 2rs-m), and the anal cells constricted close to the middle, while the constriction is more basal in the new fossil (Wei 1997). *Elinora* Benson, 1946 and *Elinopsis* Lacourt, 1986 (Elinorini) have short antennae with short flagellomeres, which strongly differs from the long antennae and long flagellomeres of the new fossil (Lacourt 1986).

Affinities with the Sioblinae (genera *Siobla* Cameron, 1877 and *Conaspidia* Konow, 1898) are excluded because they have a long oblique crossvein between 1-A and 2+3-A (Wei & Nie 1997; Niu & Wei 2010, 2021; Shinohara *et al.* 2013).

Wei & Nie (1998) listed the Eriocampini in the subfamily Tenthredininae. They have the veins 2-A and 3-A of the forewing strongly sinuate (Smith 1979: fig. 32). But Smith (1979) indicated that in the Eriocampini, the forewing vein 1-M meets the vein Sc+R slightly basad the point where vein 2-M meets Sc+R, unlike in the other Tenthredininae, and in the new fossil. *Eriocampa* Hartig, 1837, *Eriocampopsis* Takeuchi, 1952, *Armitarsus* Malaise, 1931, and *Pseudosiobla* Ashmead, 1898 also have a long crossvein in the anal area (Shinohara 2002; Wei & Niu 2010).

*Beldonea* Cameron, 1899 also shares with the new fossil a short and constricted stalk present at about the basal third of the anal cells of the forewings (Wei, 1996). But the Beldoneini Wei, 1997 (only *Beldonea* sensu Lacourt 1996, but also several other genera sensu Wei 1997) have distinctly serrate or beads-like flagellomeres, unlike the new fossil (see also Saini *et al.* 1985; Smith 2012). In the new fossil, the flagellomeres are distally slightly truncated obliquely. The genus *Cornoculosuna* Wei, 1998 (replacement name for *Oculocornia* Wei, 1997) shares with the new fossil elongate flagellomeres but these are distinctly serrate in the former (Wei 1997: fig. 15). *Cromaphya* Rohwer, 1921 has serrate antennae, with the 3<sup>rd</sup> antennomere much longer than the 4<sup>th</sup> (Rohwer 1921). Taeger *et al.* (2010) synonymized the genus *Enisciocera* Malaise, 1935 with *Cromaphya*, but Niu & Wei (2016a: 384) separated the two genera, indicating that the former has simple flagellomeres. After Malaise (1935: 177, fig. 6), *Enisciocera* has a venation rather similar to that of the new fossil, especially with the vein 2A+3-A of the forewing distinctly sinuate and touching 1-A in one point only. Nevertheless, it has the 3<sup>rd</sup> antennomere much longer than the 4<sup>th</sup>, and the flagellomeres “protruding below at apex”, which is apparently not the case for the new fossil. *Enisciocera* also has shorter flagellomeres and a much longer cell 1M in the forewings than in the new fossil.

Nearly all Neocolochelynini Wei & Nie, 1998 (*Neocolochelyna* Malaise, 1937, *Colochela* Malaise, 1937, *Corymba* Konow, 1903, *Neocorymba* Saini *et al.*, 1985), except *Colochelyna* Konow, 1898, share

with the new fossil the presence at most of a very short crossvein between 2A+3-A and 1-A; in many cases, there is even no junction between these veins (Saini *et al.* 1985; Niu & Wei 2016b; Niu *et al.* 2016). The genus *Colochelyna* has a long and subvertical crossvein at about the middle of the forewing anal cell (Lacourt 1996; Niu & Wei 2016b). Nevertheless, all these genera have the 3<sup>rd</sup> antennomere longer than the 4<sup>th</sup>, unlike in the new fossil.

The new fossil shares a series of characters with the Perineurini, viz. very long antenna with very long flagellomeres, obliquely truncate, 3<sup>rd</sup> antennomere as long as 4<sup>th</sup>, very similar wing venation, especially with forewing with 2+3-A strongly sinuated, with a very short crossvein or touching 1-A. Within this tribe, *Tenthredopsis* Costa, 1859 (Palaeartic, Oriental, including *Thomsonia* Konow, 1884) has the tergum 1 without median furrow, unlike in the new fossil, *Perineura* (Palaeartic, Oriental), *Aglaostigma* Kirby, 1882 (Nearctic, Palaeartic, and Oriental), and *Ussurinus* Malaise, 1931 (Palaeartic) (Malaise 1931; Zhelokhovtsev 1988; Blank & Ritzau 1998; Haris & Gyurkovics 2014).

The new fossil can be separated from the Nearctic, East Palaeartic, and Oriental genus *Lagium* Konow, 1904 because of the proportion of the basal/distal parts of the anal cell (0.8 in the new fossil vs 0.5 in *Lagium*) (Smith 1986; Goulet 1992). The East Palaeartic and Oriental genus *Adungia* Malaise, 1945 (considered as a subgenus of *Tenthredo* Linnaeus, 1758 by Taeger *et al.* 2010) also has a very short crossvein or fusion of 2+3-A with 1-A, quite similar to the situation in the new fossil and *Perineura* (Wei & Niu 2009: fig. 1). The proportion of the basal/distal parts of the anal cell is ca 0.6 in *Adungia*, a situation intermediate between *Lagium* and the new fossil. *Adungia* differs from the new fossil in the basal position of the vein 1cu-a, vs distal from the middle of the cell 1M in the latter (Wei & Niu 2009). The Nearctic genus *Leucopelmonus* MacGillivray, 1916 has the length of cell 1A between 0.5–0.6 times that of cell 2A (Goulet 1992). Important differences between *Leucopelmonus* and *Lagium* are the proportion between the distance between the cenchri and the median length of the mesopostnotum (Goulet, 1992), but the cenchri are not visible on the fossil.

The new fossil shares with *Perineura* a short fusion of 2+3-A with 1-A in the forewings, while *Aglaostigma* has these veins distinctly separated with or without a short crossvein between them (see <https://tinyurl.com/bdcwrjv2>) (Togashi 1993; Blank & Ritzau 1998). Also, *Aglaostigma* has the cell 1A of the forewing subequal in length to the cell 2A (Smith 1986), while it is shorter in the new fossil, with a proportion of 0.8 between the lengths of the two cells, similar to the situation in *Perineura* (Togashi 1993). *Ussurinus* also has a short crossvein in the anal cells and only one central cell in the hind wing of female (vs two in the new fossil and *Perineura*) (Zhelokhovtsev 1988: 93). Nevertheless, the new fossil cannot be placed in the genus *Perineura* because of its forewing with the vein 1cu-a distad the middle of cell 1M (vs 1cu-a located in the basal third or more basally in all the species in *Perineura*) (Togashi 1993, 2007; Yan *et al.* 2009). The new fossil also differs from *Perineura* by not having a sessile anal cell in the hind wing.

The new fossil is attributed to the Perineurini mainly on the basis of its wing venation and the shape of its antennae. However, it can be separated from all the genera of this tribe because of the above-listed characters, although it seems to be more similar to *Perineura* than to other genera. Benson (1952) indicated that the biology of *Perineura rubi* (Panzer, 1808) is unknown but that it is associated with *Rubus* L. and lives in forests with *Fagus* L. and *Quercus* L. Magis (2015) added that this species is very frequently found around *Rubus* spp., and suggested that some *Rubus* spp. could be the host plant(s). Neither *Rubus* nor *Fagus* or *Quercus* are recorded in the macroflora of Céreste (Gregor 2002), but these genera are known in other Oligocene European deposits. Therefore, *Luberotentredo* gen. nov. could have a diet similar to that of the *Perineura* genus or else feed on other Rosaceae Juss. or Fagaceae Dumort. present in the Céreste deposit.



## Conclusion

The extant genus *Perineura* is distributed in the Palaearctic and Oriental regions. All the genera currently placed in the Perineurini are unknown in the fossil record, thus *Luberotentredo cerestensis* gen. et sp. nov. is the first fossil of this tribe. This new taxon confirms that the Tenthredininae were already diversified in the Oligocene. This fossil will help to improve the time divergence estimate of the Tenthredinidae in future works on the phylogeny of this group.

## Competing interests

The authors have declared that no competing interests exist.

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