

# New Early Jurassic sawflies from Luxembourg: the oldest record of Tenthredinoidea (Hymenoptera: “Symphyta”)

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*Pseudoxylocerus bascharagensis* gen. et sp. nov., the oldest representative of the Tenthredinoidea and Xyelotomidae, based on a single forewing, and an enigmatic “Symphyta” family *incertae sedis*, based on a hindwing, are described from the Toarcian of Luxembourg. The relationships of the genera currently included in Xyelotomidae are briefly discussed. The genera *Undatoma*, *Liaotoma*, *Leridatoma*, and *Davidsmithia* have the unique apomorphy in the wing venation of the Tenthredinoidea minus Xyelotomidae. The Xyelotomidae is probably a paraphyletic family. Only a phylogenetic analysis will help to solve these problems. There is no evidence supporting the previous assignments of the fossil genera *Vitimilarya* and *Kuengilarva* to the family Xyelotomidae.

Key words: Hymenoptera, Tenthredinoidea, Xyelotomidae, *Pseudoxylocerus*, Toarcian, Luxembourg.

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## Introduction

Although the oldest known Hymenoptera are represented by few Triassic species (Schlüter 2000), this order has still a low diversity in the Liassic, with a record of about ten families (Ross and Jarzembowski 1993; Rasnitsyn 2002). The hymenopteran material is extremely rare in the Toarcian of Western Europe (Zessin 1981, 1985; Ansorge 1996; Rasnitsyn et al. 2003). There are only a fore- and a hindwing of Hymenoptera among two thousand fossil insects that one of us (MH) collected in the Toarcian of Bascharage (Luxembourg), which also supports the rarity of the Hymenoptera in the Liassic of Western Europe. Some taphonomic bias can be advocated for the marine localities of the Toarcian of Western Europe. But the hymenopteran percentage varies from 0.4 to 5% in the Asian Liassic localities of the former Soviet Union (Rasnitsyn et al. 2003), which is very low compared to the percentages for the lacustrine localities of the French Cenozoic, ranging between 8 and 35% of the insect specimens (Nel personal observation). This order had probably a low ecological importance in the Liassic ecosystems.

Although currently considered as one of the most basal lineages of the order, the family Xyelotomidae Rasnitsyn, 1968 was still unknown in the Liassic, its oldest representatives being Middle Jurassic. The present discovery fills a gap in the fossil record of the Xyelotomidae that was expected to be present in the Early Jurassic, basing on the current knowledge on the hymenopteran phylogeny. It is also important for the knowledge of wing structures in this “basal” group of the clade Tenthredinoidea, and one of the most basal lineages in Hymenoptera (Rasnitsyn 2001).

We follow the wing venation terminology of Huber and Sharkey (1993). The material described in this paper belongs to the collection of Michel Henrotay, deposited in the Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris, France, abbreviated MNHN-LP-R.

## Systematic palaeontology

Superfamily undetermined

Family “Symphyta” *incertae sedis*

Figs. 1, 2.

*Type locality*: Bascharage, Grand-Duché-du-Luxembourg (Henrotay et al. 1998).

*Type horizon*: Early Toarcian.

*Material*.—MNHN-LP-R. 11199 (BTDK 199a, b), print and counterimprint of a well-preserved hindwing, with the jugal and anal region partly destroyed.

*Description*.—Hindwing hyaline; 5.9 mm long, 2.4 mm wide at level of apex of Sc, width at wing base unknown; jugal lobe not preserved; vein C present, distally fused with R1; basal hamuli not preserved; bases of distal hamuli preserved as four very small circles in costal vein C, close to its point of fusion with R1 (Fig. 2B); vein Sc tubular, closely parallel to but distinct of R and R1; distance from wing base to apex of Sc 2.5 mm; distance between Sc and R 0.05 mm; veins R, R1 and Rs well defined, tubular; cell [R1] large, 3.3 mm long, 0.4 mm wide, distally closed; cross-vein 1r-m tubular, subvertical, 0.4 mm long; cross-vein 2r-m absent, i.e. cells [1Rs] and [2Rs] fused; cell [1+2Rs] large, 1.7 mm

long, 0.7 mm wide; cell [1M], 1.8 mm long, 0.7 mm wide; cross-veins 3r-m, m-cu, cu-a, and a present and tubular; cell [1A] very long and broad, with its petiole relatively short, 0.3 mm long; no rudiment of free base of Cu; M between M + Cu and 1r-m distinctly bent; veins M + Cu, M, Cu, 1A, and 2A tubular.

*Discussion.*—This fossil has plesiomorphic states for the hindwing hymenopteran characters proposed by Ronquist et al. (1999) (characters 98 to 106 and 108 to 110) or proposed by Vilhelmsen (2001) (characters 177 to 183). The characters 96, 97, and 107 of Ronquist et al., which concern the structure of the jugal lobe and the convexity of median vein, are unknown in this fossil. In Xyelidae, Tenthredinoidea, and Pamphilioidea, all these characters are in their plesiomorphic state, except for the character “Sc of hindwing present (plesiomorphy) versus absent (apomorphy)”. Sc of hindwing is present in Cimbicidae, Pamphiliidae, Xyelidae, and the Mesozoic family Gigasiricidae. This character is unknown in Xyelotomidae and Electrotomidae. In Cimbicidae, the hindwing Sc is a small vein at wing base. In Pamphiliidae and Gigasiricidae, it is long parallel with R, as in our fossil. But this character alone is not sufficient for a familial attribution of this fossil because it is a plesiomorphy. This fossil has absolutely no rudiment of basal free part of Cu, unlike in Xyelidae and Gigasiricidae (see Rasnitsyn 1990: 184–185, fig. 147 and personal communication). Schulmeister (2003) considered the presence of basal free part of Cu as a plesiomorphy uniquely present in Xyelidae among recent Hymenoptera. Thus, its absence in this fossil would exclude it from the Xyelidae and Gigasiricidae. Also after Schulmeister, the absence of 2r-m in this fossil is an apomorphy present in nearly all Hymenoptera, except some Xyelidae (*Macroxyela*). We prefer to consider it as a Hymenoptera “Symphyta” *incertae sedis*, not related to the Xyelidae and Gigasiricidae. The main interest of this fossil is to confirm the presence of an independent vein Sc in the hindwing of the early Jurassic Hymenoptera: “Symphyta”.

## Superfamily Tenthredinoidea Latreille, 1802

### Family Xyelotomidae Rasnitsyn, 1968

*Type genus:* *Xyelotoma* Rasnitsyn, 1968 (type species *X. nigricornis* Rasnitsyn, 1968, Upper Jurassic, Callovian–Kimmeridgian or Oxfordian–Kimmeridgian (Zherikhin and Gratshev 1993; Mostovski and Martínez-Delclòs 2000), Karatau, Chimkent region, Southern Kazakhstan).

*Included genera.*—*Xyelocerus* Rasnitsyn, 1968 (type species *Xyelocerus admirandus* Rasnitsyn, 1968, Upper Jurassic, Callovian–Kimmeridgian or Oxfordian–Kimmeridgian, Karatau, Chimkent region, Southern Kazakhstan).

*Pseudoxyela* Rasnitsyn, 1968 (type species *P. heteroclita* Rasnitsyn, 1968, Upper Jurassic, Callovian–Kimmeridgian or Oxfordian–Kimmeridgian, Karatau, Chimkent region, Southern Kazakhstan).

*Undatoma* Rasnitsyn, 1977 (type species *U. dahurica* Rasnitsyn, 1977, Upper Jurassic/Lower Cretaceous, Unda river, Chita Province, Transbaikalia (Far Eastern Russia);

other species: ?*U. undurgensis* Rasnitsyn, 1990, ?*U. taksha* Rasnitsyn, 1990, both from the Lower Cretaceous of Transbaikalia, *U. rudwickensis* Rasnitsyn and Jarzembowski, 1998, Lower Cretaceous, Lower Barremian, West Sussex, England, *U. stigmatica* Rasnitsyn and Jarzembowski, 1998, Lower Cretaceous, Upper Berriasian, Dorset, England, *U. bicolor* Rasnitsyn and Jarzembowski, 1998, Lower Cretaceous, Upper Hauterivian, Surrey, England).

*Liaotoma* Ren et al., 1995 (type species *L. linearis* Ren et al., 1995, Late Jurassic or Lower Cretaceous?, Liaoning Province, China). Ren et al. (1995: 194, text-fig. 3-69) only compared this taxon with *Dahurotoma* Rasnitsyn, 1990 and “*Protenthredo*” Hong, 1982. In fact, *L. linearis* shows no significant difference with *U. rudwickensis*, except, maybe, in the shape of the pterostigma, which is apparently narrower in *L. linearis* than in *Undatoma*. A revision of the type specimen of *L. linearis* is necessary in order to determine whether *Liadotoma* is a junior synonym of *Undatoma*.

*Dahurotoma* Rasnitsyn, 1990 (type species *D. robusta* Rasnitsyn, 1990, Lower Cretaceous, Transbaikalia).

*Leridatoma* Rasnitsyn and Ansoerge, 2000 (type species *L. pulcherrima* Rasnitsyn and Ansoerge, 2000, Lower Cretaceous, Spain).

*Davidsmithia* Pagliano and Scaramozzino, 1990, one species *D. suni* (Hong, 1982), Upper Jurassic/Lower Cretaceous, Guyong Basin, Neimenggol Region, China. *D. suni* was originally described in the genus *Protenthredo* Hong, 1982, as the type genus of the fossil family Protenthredinidae Hong, 1982. As the generic name *Protenthredo* was preoccupied by *Protenthredo* Pongracz, 1928 (in Tenthredinidae), Pagliano and Scaramozzino (1990: 5, line 10) proposed a generic name *Davidsmithia* for this taxon, but the same authors proposed the genus name *Thomasia* in the same page, line 45. Abe and Smith (1991) noted the problem but did not solve it. We propose as the valid name the first one: *Davidsmithia*. Rasnitsyn and Ansoerge (2000: 59) erroneously indicated that Pagliano and Scaramozzino proposed the new name *Xaxaxis* to replace *Protenthredo* Hong, 1982, but in fact these last authors (1990: 6) proposed *Xaxaxis* to replace *Euryxyela* Hong, 1984. Abe and Smith (1991) put *Protenthredo* Hong, 1982 in Xyelotomidae, without further explanation, and did not synonymize the Protenthredinidae with the Xyelotomidae. A revision of the type specimen is necessary before any definite conclusion about the position of this enigmatic genus.

*Vitimilarya* Rasnitsyn, 1969 (type species *V. paradoxa* Rasnitsyn, 1969, Early Cretaceous, Baissa, Vitim river, Transbaikalia). This species is based on a larva that Rasnitsyn (1969) put in “Tenthredinoidea *incertae sedis*” but that was transferred later in to the Xyelotomidae (Rasnitsyn 1990; Abe and Smith 1991).

*Kuengilarva* Rasnitsyn, 1990 (type species *K. inexpectata* Rasnitsyn, 1990, Lower Cretaceous, Transbaikalia). This taxon is also based on a larva that Rasnitsyn (1990) attributed to the Xyelidae or Xyelotomidae.

*Remarks on the family composition.*—Rasnitsyn (1988: 120,

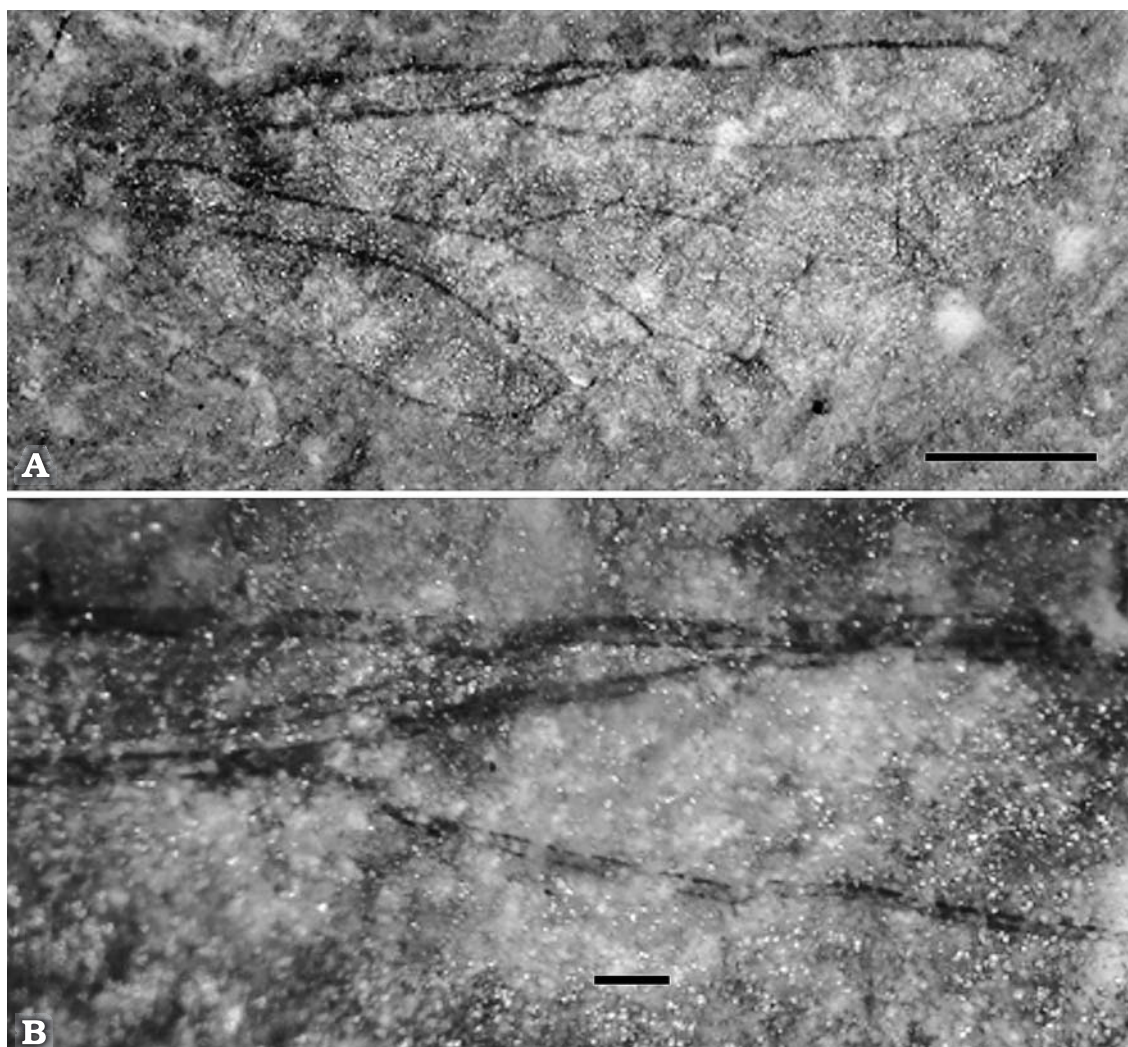


Fig. 1. Photograph of “Symphyta” family *incertae sedis*, MNHN-LP-R. 11199. **A.** General habitus; scale bar 1 mm. **B.** Apex of Sc; scale bar 0.1 mm.

fig. 1; 1996: 14; 2002: fig. 331) clearly considered the Xyelotomidae as a paraphyletic, “ancestral” group of the other Tenthredinoidea, with no recorded autapomorphies. At least, the three genera *Undatoma*, *Liaotoma*, *Leridatoma*, and *Davidsmithia* have their forewing vein Sc “not developed, at least not as a longitudinal trunk” (Rasnitsyn 1977—English translation in 1978, 1990; Hong 1982: 93, fig. 19; Ren et al. 1995: 194, text-fig. 3-69; Rasnitsyn et al. 1998). This character state is currently supposed to be the unique apomorphy in the wing venation of the Tenthredinoidea minus Xyelotomidae (Rasnitsyn 1988, 2001; Ronquist et al. 1999; Schulmeister, 2003). Thus, it would support the possible exclusions of *Undatoma*, *Liaotoma*, *Leridatoma*, and *Davidsmithia* from the Xyelotomidae. The longitudinal part of Sc is absent or very weak and Sc1 and Sc2 are absent in *Xyelocerus admirandus* (after Rasnitsyn 1968: 226, text-fig. 35, 1996: fig. 5). On the contrary, the genus *Pseudoxyela* has “retained” Sc and R separated and parallel, and the forewing Sc is basally free and distally fused with R in *Dahurotoma* and probably *Xyelotoma*.

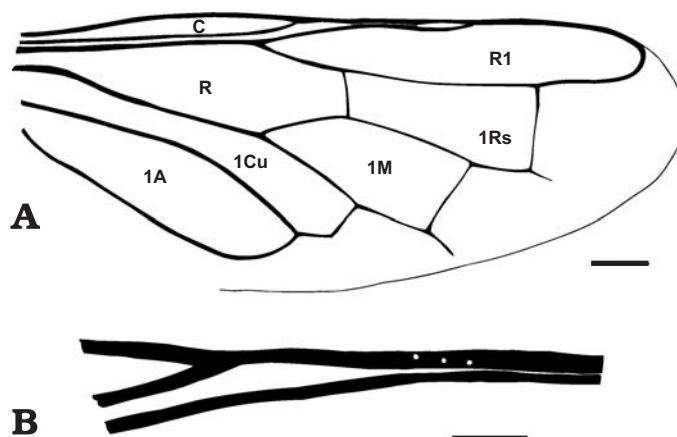


Fig. 2. Interpretation of “Symphyta” family *incertae sedis*, MNHN-LP-R. 11199, hind wing. **A.** General habitus; scale bar 2 mm. **B.** Apex of Sc; scale bar 0.5 mm.

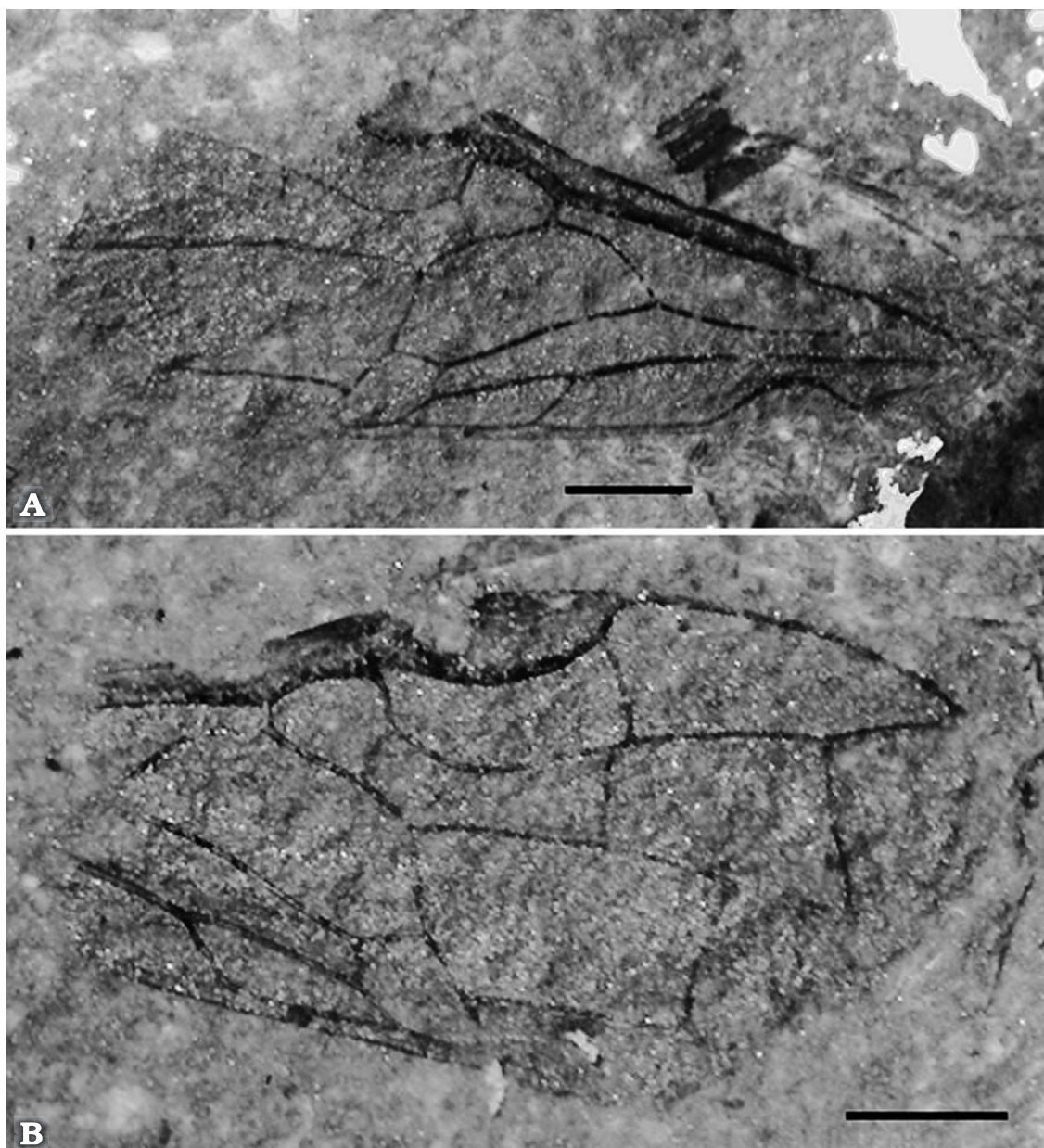


Fig. 3. Photograph of *Pseudoxylocerus bascharagensis* gen. et sp. nov., holotype MNHN-LP-R. 11198. A. Part. B. Counterpart. Scale bars 1 mm.

The structure of the prosternum (character 34, state 1 of Ronquist et al. 1999) is a potential apomorphy of the Xyelotomidae but it is present in several other hymenopteran groups (e.g., Megalyridae and Stephanidae). Furthermore, it is unknown in several species currently attributed to the Xyelotomidae. At least in *Undatoma* and *Thomasia*, the body characters are too badly known and cannot be used in a phylogenetic analysis. Ren et al. (1995) did not describe the body structures of *Liaotoma*. This suggests that the Xyelotomidae could be an artificial group of taxa with no direct common ancestor.

Only a detailed phylogenetic revision of the Xyelotomidae and the Tenthredinoidea will help to solve the problems in the definition of the Xyelotomidae and the positions of

the genera *Undatoma*, *Liaotoma*, *Leridatoma*, and *David-smithia*.

Lastly, it is not possible to have a correct proof of the attribution of *Vitimilarya* and *Kuengilarva* to the strictly fossil family Xyelotomidae, because the hymenopteran larvae are very different from the adults.

#### Genus *Pseudoxylocerus* nov.

*Type species: Pseudoxylocerus bascharagensis* sp. nov.

*Etymology:* After the similarity with the genus *Xylocerus*.

*Diagnosis.*—Similar to *Xylocerus*, from which it differs in having the vein Sc long, parallel, strongly approximate to, but distinctly separated from R; Sc2 present, but very short; Sc1 long, oblique (we follow Rasnitsyn 1996: fig. 5a, who

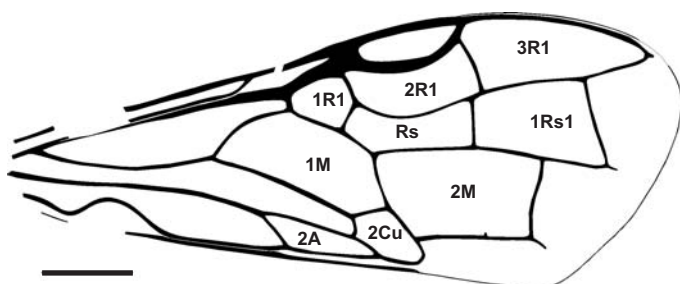


Fig. 4. Composite reconstruction of *Pseudoxyelocerus bascharagensis* gen. et sp. nov., holotype MNHN-LP-R. 11198; scale bar 2 mm.

figures no veins Sc, Sc1, and Sc2 in *Xyelocerus*). Further differences concern larger cell [M1] in *Pseudoxyelocerus* than in *Xyelocerus*, while cell [2Cu] is about the same size in two taxa. In *Xyelocerus* veins M and Cu not extended distal of the levels of 3r-m and 2m-cu respectively, instead of being shortly extended in *Pseudoxyelocerus*. The pterostigma is broader in *Pseudoxyelocerus* than in *Xyelocerus*.

#### *Pseudoxyelocerus bascharagensis* sp. nov.

Figs. 3, 4.

*Holotype and only known specimen*: MNHN-LP-R. 11198 (IB00976a-b), Part and counterpart of a well-preserved forewing.

*Type locality*: Bascharage, Grand-Duché-du-Luxembourg (Henrotay et al. 1998).

*Type horizon*: Early Toarcian.

*Etymology*: After the outcrop Bascharage.

*Diagnosis*.—Same as for the genus.

*Description*.—Forewing hyaline, 7.8 mm long, 3.1 mm wide; vein Sc long parallel, strongly approximate to but distinctly separated of R; Sc2 very short, 0.05 mm long, Sc1 oblique, 0.1 mm long, ending on C 0.4 mm basal of Rs; Rs very short but distinct, 0.2 mm long, not aligned with M; M + Cu basally curved but not angled; base of M 2.4 mm from wing base; M strongly curved, 1.1 mm long; Rs + M 0.6 mm long; pterostigma 1.4 mm long, 0.5 mm wide; cross-vein 2r-rs 0.6 mm long, from a position near apex of pterostigma to a position distinctly distal to 2r-m; no supplementary cross-vein in cell [3R1]; Rs not distally forked; vein “a” oblique, 1.0 mm basal of 1cu-a; cell [1M] very large, 2.0 mm long, 0.8 mm wide; cell [1R1] small, 0.7 mm long, 0.6 mm wide; cell [2Cu] small, 0.9 mm long, 0.4 mm wide; cell [Rs] elongate, close distally, 1.4 mm long, 0.5 mm wide; cell [2A] triangular, 1.3 mm long; vein 2A + 3A with a strong basal double curve; veins M and Cu shortly but distinctly extended distal of the levels of 3r-m and 2m-cu respectively.

*Discussion*.—After the phylogeny of the Hymenoptera of Rasnitsyn (2001), mainly inspired from Ronquist et al. (1999), and globally congruent with the analysis of Schulmeister et al. (2002), *Pseudoxyelocerus bascharagensis* gen. et sp. nov. has three of the main forewing synapomorphies of the clade Tenthredinoidea *sensu* Rasnitsyn (2001: fig. 331),

i.e., cell [1M] (= cell 1m<sub>cu</sub> *sensu* Rasnitsyn 2001) large (character 91, state 1 of Ronquist et al. 1999); cross-vein 2r-rs (= 2r *sensu* Ronquist et al. 1999) from a position near apex of pterostigma to a position distinctly distal to 2r-m (character 84, state 1 of Ronquist et al. 1999) (character unknown in Argidae and Pterygophoridae because 2r-rs is absent in these groups); vein Rs (= first abscissa of Rs *sensu* Ronquist et al. 1999; = RS *sensu* Rasnitsyn 2001) short before its fusion with vein M (character 77, state 1 of Ronquist et al. 1999) (but character convergently present in Pamphiliidae, also Schulmeister (2003) noted that some variation can affect this structure within a genus or even within a species). *Pseudoxyelocerus bascharagensis* gen. et sp. nov. can be included in the Tenthredinoidea. This taxon has not the character state “Sc appressed to or fused with R” (character 74, state 1 of Ronquist et al. 1999; see also Schulmeister, 2003: 214), which is an apomorphy of the Tenthredinoidea minus Xyelotomidae. This plesiomorphic state of character is not sufficient alone to include *Pseudoxyelocerus bascharagensis* gen. et sp. nov. in the fossil family Xyelotomidae, most basal lineage of this superfamily. Nevertheless, we provisionally attribute it to this family because of its great similarities with *Xyelocerus admirandus*.

## Comparison of *Pseudoxyelocerus* gen. nov. with the other described Xyelotomidae

*Xyelotoma* is based on a poorly preserved specimen, with the apical half of forewing missing (Rasnitsyn 1968: text-fig. 34; 1969: fig. 81). It differs from *Pseudoxyelocerus* gen. nov. and *Xyelocerus* in its basal part of vein Rs shorter before its fusion with vein M, its cell [1R1] larger, and its cell [1M] shorter.

*Pseudoxyela* differs from *Pseudoxyelocerus* gen. nov. and *Xyelocerus* in the presence of a supplementary vein in cell [3R1], distal of 2r-rs (Rasnitsyn 1968, 1969).

*Undatoma* and *Liaotoma* differ from *Pseudoxyelocerus* gen. nov. in the vein Sc “not developed, at least not as a longitudinal trunk” (Rasnitsyn 1977, 1990; Rasnitsyn et al. 1998; Ren et al. 1995: 194, text-fig. 3-69).

*Dahurotoma* has a vein Sc basally separated from R, distally fused with it, and with a distal Sc1 distinct and perpendicular to R and C, unlike *Pseudoxyelocerus* gen. nov. (Rasnitsyn 1990: text-fig. 139). Furthermore, its cell [1M] is smaller and its cell [2Cu] larger than those of *Pseudoxyelocerus* gen. nov.

*Davidsmithia* and *Leridatoma* can be separated from *Pseudoxyelocerus* gen. nov., basing on absence of a forewing vein Sc and their distinctly longer cell [2Cu].

As they are described after larvae, *Vitimilarva* and *Kuengilarva* cannot be compared with *Pseudoxyelocerus* gen. nov.

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