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C. R. Palevol 4 (2005) 17–24



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Systematic Palaeontology (Invertebrate Palaeontology)

Oldest representatives of the Sphecidae: Trypoxylini in the Early Eocene French amber (Insecta: Hymenoptera)

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Received 4 October 2004; accepted 9 November 2004

Available online 22 December 2004

Written on invitation of the Editorial Board

Abstract

The oldest representatives of the sphecid tribe Trypoxylini are described from the Early Eocene amber of France, i.e. *Eopison menieri* gen. n., sp. n. and *Pison eocenicus* sp. n. The fore wing venation of *Eopison* is more complete than those of any Recent Trypoxylini, suggesting that the reduction of the submarginal cells in Sphecidae has a complex history. Recent Trypoxylini are parasites on spiders. The present discoveries suggest that this type of trophic relations were already established during the Early Palaeogene and maybe the Late Cretaceous. **To cite this article:** A. Nel, C. R. Palevol 4 (2005).

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Résumé

Les plus anciens représentants de Sphecidae : les Trypoxylini de l'ambre de l'Éocène basal de France. *Eopison menieri* gen. n., sp. n. and *Pison eocenicus* sp. n., plus anciens représentants connus de la tribu Trypoxylini de sphécides, sont décrits de l'ambre de l'Éocène basal de France. La nervation de l'aile antérieure d'*Eopison* est plus complète que celles de tous les Trypoxylini actuels, suggérant que la réduction des cellules submarginales des Sphecidae a une histoire complexe. La présence de guêpes très proches des Trypoxylini actuels dans l'Éocène basal, groupe de parasitoïdes d'araignées, suggère que les mêmes relations de parasitisme étaient déjà établies au début du Cénozoïque, voire au Crétacé supérieur. **Pour citer cet article :** A. Nel, C. R. Palevol 4 (2005).

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Keywords: Insecta; Hymenoptera; Sphecidae; Craboninae; Trypoxylinigen, gen. n., sp. n.; Lowermost Eocene; French amber

Mots clés : Insecta ; Hymenoptera ; Sphecidae ; Craboninae ; Trypoxylini gen, n., sp. n. ; Ambre Éocène basal ; France

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1. Introduction

The Sphecidae are recorded since the Early Cretaceous [5,20]. Nevertheless, the fossil record of the Recent subgroups remains scarce and incomplete. Therefore, the present new taxa attributable to the Craboninae: Trypoxylini are of great interest for an estimation of the age of this Recent subfamily and tribe. It is reasonable to estimate that these Recent clades were already present during the Late Cretaceous and the Early Cainozoic. Recent Trypoxylini parasitise on spiders, which are very frequent and diverse in the Oise amber, represent about 10% of the arthropod inclusions. Sphecid wasps are also diverse and not infrequent, with at least the two species we describe herein, but also two other undescribed species, both represented by one specimen. This Early Eocene amber was deposited under a warm climate in a forestry and fluvial palaeoenvironment. The amber was produced by an angiosperm, unlike the Baltic amber of gymnosperm affinities [12,17].

We follow the body and wing venation terminology of Bohart and Menke [8].

Family Sphecidae Latreille 1802

Subfamily Craboninae Latreille, 1802

Tribe Trypoxylini Lepeletier, 1845

Genus *Eopison* gen. n.

Type species. *Eopison menieri* sp. n.

Eymology. After the Eocene age of the fossil and the Recent genus *Pison*.

Diagnosis. Antennal socket contiguous with frontoclypeal suture; mandible with a notch on its externo-ventral margin; forewing vein 1m-cu not ending in the second submarginal cell, but in its postero-basal angle; three submarginal cells present, with second large, complete, not petiolated (main visible difference with Recent and fossil *Pison*); marginal cell of forewing acute distally, with apex extending well beyond outer veinlet of submarginal cell 3; mesopleuron without coarse horizontal ridges; hindcoxa with an inner and an outer dorsal carinae; midtibia with one spur; no oblique groove on sterna 3 and 4; female pygidial plate very reduced or absent; metasoma compact and sessile.

2. *Eopison menieri* sp. n. (Fig. 1)

Material. Holotype PA 340 (female), allotype PA 2388 (male), other specimens attributable to this spe-

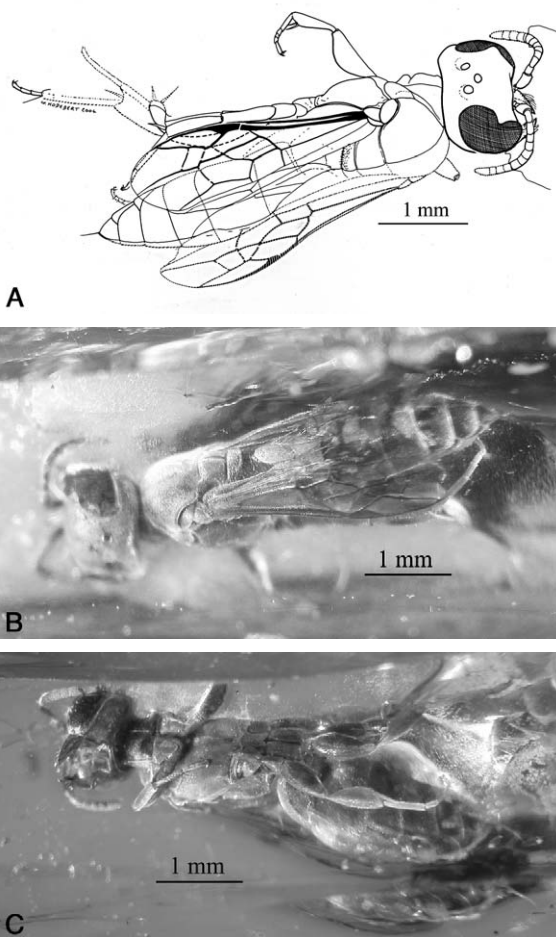


Fig. 1. *Eopison menieri* gen. n., sp. n., holotype PA 340. (A) Reconstruction of the general habitus. (B) Dorsal view. (C) Ventral view.
Fig. 1. *Eopison menieri* gen. n., sp. n., holotype PA 340. (A) Reconstitution de l'aspect général. (B) Vue dorsale. (C) Vue ventrale.

cies: PA 1931, PA 2384 6/7, and PA 2502 (sex unknown), all mounted in Canada Balsam, deposited in the 'Laboratoire de paléontologie', 'Muséum national d'histoire naturelle', Paris.

Eymology. After our colleague Prof. Jean-Jacques Menier, Entomology Department, MNHN, Paris.

Type strata. Lowermost Eocene, in amber, circa –53 Myr, Sparnacian, level MP7 of the mammal fauna of Dormaal [17].

Type locality. Farm Le Quesnoy, Chevière, region of Creil, Oise department (northern France).

Diagnosis. That of the genus.

Description. Body with hairs short and relatively sparse, all simple and unbranched. Head 0.80 mm long, 0.80 mm wide, 1.0 mm high, without mandibles; 12 antennal segments in both male and female; no visible papillae or setae on antennal segments; antennal socket contiguous with frontoclypeal suture; no subantennal sclerite; apical margin of last antennal segment rounded apically, not truncate; clypeus rounded rather than truncate, not divided into three parts by longitudinal lines, clypeus of male without brush; mandible entire exteroventrally but with a notch on its exteroventral margin; hypostoma not closing the mandibular socket; lateral ocellus normal, rounded; eye with inner orbit strongly emarginate.

Mesosoma 1.80 mm long, 0.9 mm wide; pronotal collar rounded in lateral view; mesopleuron without epicnemial carina; episternal sulcus reaching the ventral area of mesopleuron, not curving forward and then downward parallel to the front margin of mesopleuron; mesopleuron without coarse horizontal ridges; notauli present but short, not extending over three fourths of the scutal length; mesoscutum without oblique scutal carina; propodeum not distinctly toothed; propodeal dorsum finely chagrinate; apophyseal pit in posterior third of metasternum; metasternum with a median longitudinal carina; metasternum anteriorly as wide as posteriorly.

Profemur 0.64 mm long, 0.28 mm wide; tibia 0.4 mm long, 0.14 mm wide; tarsus 0.74 mm long; fore tarsal rake rudimentary, formed of very short dorsal setae, organised in four groups of a single and a pair of setae on tarsomere 1, and one pair of setae on other tarsomeres; mesofemur 0.70 mm long, 0.30 mm wide; tibia triangular, 0.74 mm long, 0.30 mm wide; tarsus 1.14 mm long; midcoxae not contiguous; metafemur 0.80 mm long, 0.36 mm wide; tibia 0.76 mm long, 0.26 mm wide; tarsus 1.20 mm long; meso- and metatibial spurs flattened with margins serrate; hindcoxa with an inner and an outer dorsal carinae; tibial spur formula 1-1-2; hind femur simple apically, only bearing a very small process on its inner and outer faces; hind leg with tarsomere 1 as wide as following tarsomeres, 0.60 mm long, length of following tarsomeres 0.60 mm; tarsal claws simple.

Forewing 2.80 mm long, 0.72 mm wide; stigma much smaller than first submarginal cell; prestigmal length of first submarginal cell distinctly shorter than half cell length; forewing with three submarginal cells;

second submarginal cell not petiolated, 0.26 mm long, third submarginal cell 0.24 mm long; vein 1m-cu not ending in second submarginal cell but in its postero-basal angle; marginal cell of forewing 0.78 mm long, 0.20 mm wide, acute distally, with apex extending well beyond outer veinlet of submarginal cell 3.

Hind wing poorly visible, circa 1.80 mm long; vein M diverging from M + Cu before vein cu-a; hamuli divided into two groups; jugal lobe small, at least in PA 1931.

Metasoma 2.50 mm long, 0.90 mm wide, sessile; first metasomal segment broader than long; no oblique groove on sterna 3 and 4; female pygidial plate very reduced or absent; male genitalia not visible, but sternum VIII elongate, narrow, and simple.

Discussion. After Brothers and Carpenter [9], *Eopison* gen. n. falls in the clade ‘sphecids + apids’ (= Sphecidae *sensu stricto* + Apoidea) and is excluded from the Heterogynaidae because of its meso- and metatibial spurs flattened with margins serrate, and mesotibia with only one spur (two in Heterogynaidae), among other characters.

Following the key to ‘Apiformes’ and Spheciformes’ of Finnamore and Michener [13], *Eopison* gen. n. falls into the Spheciformes (sphecid wasps) because of its body setae all simple, unbranched, and hind leg with tarsomere 1 as wide as following tarsomeres. Within this group, it would fall in the ‘Philanthidae’: ‘Philanthinae’ (= Philanthinae: Philanthini *sensu* Bohart and Menke [8]) because of the following characters: female fully winged; forewing with closed cells; mesotibia with one apical spur; tarsal claws simple; metasoma sessile; forewing with stigma much smaller than first submarginal cell; prestigmal length of first submarginal cell distinctly shorter than half cell length; mesoscutum without oblique scutal carina; pronotal collar rounded in lateral view; clypeus not divided into three parts by longitudinal lines; lateral ocellus normal, rounded; mesopleuron without epicnemial carina; mesopleuron with an episternal groove extending to ventral region; hind wing with vein M diverging from M + Cu before vein cu-a; mandible entire exteroventrally; metafemur simple, not modified apically; eye with inner orbit emarginate.

Following the key to sphecid subfamilies of Bohart and Menke [8], *Eopison* gen. n. would also fall in the Philanthinae or ‘Larrinae’ *sensu* Bohart and Menke [8] (= Craboninae *sensu* Ohl [18]) because of the follow-

ing characters: metasoma sessile; mid tibia with only one apical spur; episternal sulcus not curving forward and then downward parallel to front margin of mesopleuron; notauli present but short, not extending over three-fourths of scutal length; midcoxae not contiguous; clypeus not divided into three parts; hind femur not truncate at apex; hind ocellus normal; no oblique scutal carina; propodeum not distinctly toothed; fore wing with three submarginal cells.

Following Bohart and Menke [8] and Alexander [2], within the Recent sphecid wasps, only the Philanthini and the crabonine tribe Trypoxylini have the inner margin of compound eyes notched or emarginated. The fossil Burmastatinae Antropov, 2000 differ from *Eopison* gen. n. in its inner-eye orbit straight and their midtibia with two apical spurs, and the fossil Cirrosphecinae Antropov, 2000 differ from *Eopison* gen. n. in the forewing venation and dentate tarsal claw [5].

Alexander [2] indicated that there are few unambiguous synapomorphies of the Philanthinae. Those of the larva are unavailable in our specimens. The other putative synapomorphy of the Philanthinae is the presence of a male clypeal brush. The male specimen PA 2388 of *Eopison* lacks any clypeal brush. Furthermore, *Eopison* gen. n. differs from the Philanthinae in its antennal socket contiguous with frontoclypeal suture and in its hypostoma not closing the mandibular socket. The closed mandibular socket and the antennal sockets remote from the clypeus are synapomorphies of the Philanthinae but are also present in some other Sphecidae, after Alexander [2,3]. Alexander [1,3] also considered the closed mandibular socket, and the presence of a delimited subantennal sclerite, both absent in *Eopison* gen. n., as synapomorphies of the (Philanthini + (Cercerini + Aphilanthopini)). Therefore, *Eopison* gen. n. cannot be attributed to the Philanthinae.

Eopison gen. n. also differs from *Philanthus* Fabricius, 1790 and *Trachypus* Klug, 1810 in its forewing vein 1m-cu not ending in the second submarginal, cell but in its postero-basal angle. Thus, its discoidal cell is shorter than those of these genera. The apophyseal pit of *Eopison* gen. n. is in posterior third of its metasternum, and its metasternum has a median longitudinal carina as in the group ((*Trachypus* + *Philanthus*) + *Philanthinus*). But the metasternum of *Eopison* gen. n. is anteriorly as wide as posteriorly, unlike in this group.

The hind wing jugal lobe is small in Trypoxylini. This structure is not visible in the holotype and allo-

type of *Eopison*, but the third specimen PA 1931, attributable to this taxon, has a small jugal lobe. The Craboninae have their hindcoxa dorsally carinate as in *Eopison* gen. n. This last character is considered as a synapomorphy by Lomholdt [14 (p. 21)]. This would support the attribution of *Eopison* gen. n. to the Craboninae: Trypoxylini, but Menke [15 (p. 17)] indicated that a hindcoxal carina is not unique to the Craboninae and not universally present in this subfamily. Also, Alexander [3 (p. 36)] proposed to characterize the Philanthinae by the synapomorphic absence of this carina, thus the polarisation of this character remains somewhat uncertain.

Lomholdt [14] proposed a phylogenetic analysis of the 'Larrinae'. *Eopison* gen. n. falls into the Trypoxylini because of the following synapomorphies: pygidial plate lost or reduced; intercoxal carina present; eyes emarginate; hind wing hamuli divided into two groups. The same author considered the second submarginal cell petiolated as the synapomorphy that supports a very large clade that comprises the 'Craboniformia', the Mischophini *sensu stricto*, the Trypoxylini and two other genera. This would contradict the attribution of *Eopison* gen. n. to this clade, but the structures and sizes of the submarginal cells are very diverse in the Sphecidae, suggesting that this character is homoplastic. Therefore, we attribute *Eopison* gen. n. to the Trypoxylini.

After Bohart and Menke [8], *Eopison* gen. n. is more similar to *Pison* Jurine, 1808 than to other Recent trypoxylinae genera because of the following characters: three submarginal cells in fore wing; antennal socket contiguous with frontoclypeal suture; metasoma compact and sessile; mesopleuron without coarse horizontal ridges; marginal cell of forewing acute distally, with apex extending well beyond outer veinlet of submarginal cell 3; no oblique groove on sterna 3 and 4; no defined pygidial plate in female.

After Bohart and Menke [8 (p. 334)] and Menke [15], *Eopison* gen. n. shares with the Neotropical subgenus *Entomopison* Menke, 1968 (synonymised with *Pison* by Menke [15]), and with some *Pison* species from New Guinea and Australasia the presence of a notched exteroventral margin of mandible.

In Recent Trypoxylini and especially in Recent *Pison* species, when three submarginal cells are present, the second is petiolated, unlike in *Eopison* gen. n. [8 (pp. 327–328)]. The reduction in the number of sub-

marginal cells in Sphecidae occurs several ways, i.e. loss of the outer veinlet (1r-m) of second submarginal cell, loss of the inner veinlet (1r), loss of third submarginal cell. Therefore, it is admissible that a fossil genus of the lineage of Trypoxylini and maybe of *Pison* could have three well-developed submarginal cells.

Eight fossil Sphecidae are currently attributed to the Trypoxylini: four *Trypoxylon*, viz. *T. dominicanum* Prentice and Poinar, 1993, *T. eucharis* Prentice and Poinar, 1993, *T. pallidiventre* Prentice and Poinar, 1993, and *T. electrum* Antropov, 1995 (Oligocene/Miocene Dominican amber) that have long petiolated metasoma and one or two submarginal cells, and four *Pison*, viz. *P. antiquum* Antropov and Pulawski, 1996 (Oligocene/Miocene Dominican amber), *P. electrum* Antropov and Pulawski, 1989 (Late Eocene Baltic amber), *P. cockerellae* Rohwer, 1908 (Early Oligocene

of Florissant, Colorado, USA), and *P. oligocenium* Cockerell, 1908 (Late Eocene Baltic amber). They all differ from *Eopison* gen. n. in their very small second submarginal cell of forewing [4,6,10,11,19,21]. *P. antiquum* has no notch on posterior margin of mandible, unlike *Eopison* gen. n. and *P. electrum* [6,7,15].

3. Genus *Pison* Jurine, 1808

Pison eocenicum sp. n. (Fig. 2)

Material. Holotype PA 12238 1/4 (female). Paratypes PA 1129 (sex unknown, with two Coleoptera and a Diptera), PA 2360 1/4 (female, with three Mantodea), PA 2370 (female), PA 2527 (female?), PA 2363 (female), PA 2470 (female), mounted in Canada Balsam, deposited in the 'Laboratoire de paléontologie', 'Muséum national d'histoire naturelle, Paris, France.

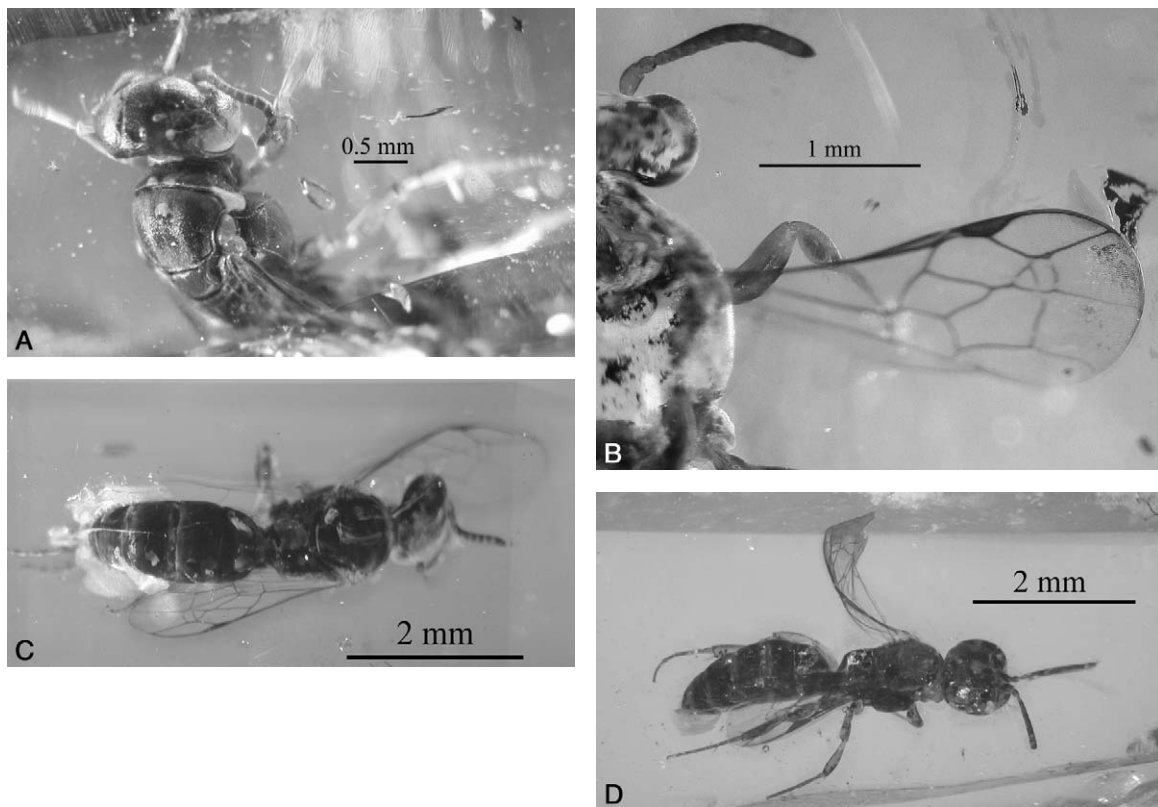


Fig. 2. *Pison eocenicum* sp. n. (A) Holotype PA 12238, dorsal view of head and mesosoma. (B) PA 2527, forewing. (C) PA 2363, dorsal view. (D) PA 2470, dorsal view.

Fig. 2. *Pison eocenicum* sp. n. (A) Holotype PA 12238, Vue dorsale de la tête et du mésosome. (B) PA 2527, aile antérieure. (C) PA 2363, vue dorsale. (D) PA 2470, vue dorsale.

Etymology. After the Eocene age of the fossils.

Type strata. Lowermost Eocene, in amber, *circa* - 53 Myr, Sparnacian, level MP7 of the mammal fauna of Dormaal.

Type locality. Farm Le Quesnoy, Chevrière, region of Creil, Oise department (northern France).

Diagnosis. Forewing second submarginal cell clearly smaller than others and petiolated; vein 1m-cu ending in first submarginal cell, well basal of second submarginal cell; an imaginary line between the apex of marginal cell and the distal hindcorner of the second discoidal cell not crossing third submarginal cell; second submarginal cell distinctly higher than its petiole; petiole distinctly shorter than anterior margin of third submarginal cell; forewing M diverging distal of crossvein cu-a; mandibles not notched; mesopleuron with fine horizontal ridges; propodeal dorsum with strong reticulation; scutum finely chagrinate.

Description. Body with hairs short and relatively sparse, all simple and unbranched.

Head *circa* 1 mm long, 1.28 mm wide; 12 antennal segments; no visible papillae or setae on antennal segments; antennal socket contiguous with frontoclypeal suture; no subantennal sclerite; apical margin of female last antennal segment rounded apically, not truncate; clypeus rounded, not divided into three parts by longitudinal lines; mandible entire externoventrally, and without a notch on its externoventral margin; hypostoma not closing the mandibular socket; lateral ocellus normal, rounded; eye with inner orbit emarginate.

Mesosoma 1.80 mm long, 1.0 mm wide; pronotal collar rounded in lateral view; mesopleuron without epicnemial carina; episternal sulcus reaching ventral area of mesopleuron, not curving forward and then downward parallel to front margin of mesopleuron; mesopleuron without coarse horizontal ridges but with fine horizontal ridges; notauli present but short, not extending over three-fourths of scutal length; scutum finely chagrinate; mesoscutum without oblique scutal carina; propodeum not distinctly toothed; propodeal dorsum with very strong reticulation; apophyseal pit in posterior third of metasternum; metasternum with a median longitudinal carina; metasternum anteriorly as wide as posteriorly.

Profemur 0.56 mm long, 0.24 mm wide; tibia 0.66 mm long, 0.24 mm wide; tarsus 0.66 mm long; fore tarsal rake rudimentary; mesofemur 0.66 mm long, 0.28 mm wide; tibia 0.64 mm long, 0.24 mm wide; tar-

sus 0.86 mm long; midcoxae not contiguous; metafemur 0.76 mm long, 0.20 mm wide; tibia 0.82 mm long, 0.20 mm wide; tarsus 1.10 mm long; meso- and metatarsal spurs flattened with margins serrate; hindcoxa with an inner and an outer dorsal carinae; tibial spur formula 1–1–2; hind femur simple apically, only bearing a very small process on its inner and outer faces; hind leg with tarsomere 1 as wide as following tarsomeres, 0.60 mm long, length of following tarsomeres 0.50 mm; tarsal claws simple.

Forewing 2.60 mm long, 0.80 mm wide; stigma much smaller than first submarginal cell; prestigmal length of first submarginal cell distinctly shorter than half cell length; forewing with three submarginal cells; second submarginal cell petiolated, 0.15 mm long, 0.10 mm wide, with petiole 0.02 mm long; third submarginal cell 0.12 mm long, with anterior side 0.10 mm long; vein 1m-cu ending in first submarginal cell, 0.16 mm basal of its postero-basal angle of second submarginal cell; marginal cell of forewing 0.68 mm long, 0.20 mm wide, acute distally, with apex extending well beyond outer veinlet of submarginal cell 3; an imaginary line between apex of marginal cell and distal hindcorner of second discoidal cell not crossing third submarginal cell; M-diverging 0.04 mm distal of crossvein cu-a.

Hind wing 1.72 mm long, 0.44 mm wide; vein M diverging from M + Cu 0.04 mm before vein cu-a; hind wing hamuli divided into two groups.

Metasoma *circa* 2.0 mm long, 0.96 mm wide, sessile; first metasomal segment broader than long; no oblique groove on sterna 3 and 4; female pygidial plate very reduced or absent.

Discussion. *Pison eocenicum* sp. n. can be attributed to the Sphecidae: Philanthinae or 'Larrinae' for the same reasons as above. Its inner margin of compound eyes is clearly notched. Thus, it could fall in Philanthini or Trypoxylini. The Philanthini are excluded because its antennal socket are contiguous with frontoclypeal suture and in its hypostoma is not closing the mandibular socket. It falls in the Trypoxylini because of the following synapomorphies: pygidial plate lost or reduced; intercoxal carina present; eyes emarginate; hind wing hamuli divided into two groups (clearly visible in PA 2340). *P. eocenicum* sp. n. is more similar to *Pison* than to other Recent trypoxylinae genera because of the following characters: three submarginal cells in forewing; antennal socket contiguous with frontocly-

peal suture; metasoma compact and sessile; mesopleuron without coarse horizontal ridges; marginal cell of forewing acute distally, with apex extending well beyond outer veinlet of submarginal cell 3; no oblique groove on sterna 3 and 4; no defined pygidial plate in female.

P. eocenicum sp. n. differs from *Eopison* gen. n. as follows: in forewing, second submarginal cell clearly smaller than others and petiolated; vein 1m-cu ending in the first submarginal cell, far from the second one; mandibles not notched; mesopleuron with fine horizontal ridges; propodeal dorsum with strong reticulation, instead of being finely chagrinated.

P. eocenicum sp. n. differs from *P. electrum* in its mandibles not notched and its vein 1m-cu ending well basal of second submarginal cell; an imaginary line between apex of marginal cell and distal hindcorner of the second discoidal cell not crossing the third submarginal cell; propodeal dorsum with very strong reticulation, instead of having sparse ridges. *P. eocenicum* sp. n. differs from *P. antiquum* in its second submarginal cell distinctly higher than its petiole; petiole distinctly shorter than the anterior margin of the third submarginal cell; vein 1m-cu ending more basal of second submarginal cell than in *P. antiquum*. *P. eocenicum* sp. n. differs from *P. cockerellae* in its scutum finely chagrinated instead of having coarse, dense punctures; propodeal dorsum with very strong reticulation, instead of having oblique ridges extending from the median carina; an imaginary line between apex of marginal cell and distal hindcorner of second discoidal cell not crossing the third submarginal cell. *P. eocenicum* sp. n. differs from *P. oligocenum* in its forewing M diverging distal of cross-vein cu-a, instead of slightly proximal; and its vein 1m-cu ending well basal of second submarginal cell.

4. Conclusion

These two Early Eocene Trypoxylini are morphologically very similar and closely related to the Recent representatives of this group of spider-hunting wasps. Together with the great abundance and diversity of spiders in the same amber, they support the great antiquity of this parasitism relation that probably originates during the Late Mesozoic. It is a further evidence of the antiquity and stability of the Recent families and

subgroups of insects [16]. It also questions the exact impact on the insects and other terrestrial arthropods of the alleged mass extinction at the Cretaceous–Cainozoic boundary.

Acknowledgements

We thank the company Lafarge-Granulat for the help with the sampling of the fossil and the family Langlois-Meurinne for the authorization of working in their property. We also thank G. Hodebert (MNHN) for the realization of the habitus drawing, G. De Ploeg for the delicate preparation of the material, and D. Neraudeau and V. Perrichot for their useful analyses of the first version of the paper.

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