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Research article

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The oldest fossil of the family Issidae (Hemiptera, Fulgoromorpha) from the Paleocene of Menat (France)

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Abstract. The taxa *Cubicostissus palaeocaeni* gen. et sp. nov. are described from the Paleocene of Menat (Central France) as the oldest representative of the family Issidae for which all currently known fossils are reviewed. With a unique combination of characters, the specimen represents the first fossil described for the tribe Hysteropterini. Its occurrence in the European Paleocene shows that its lineage, and therefore the Issidae, were already present at least some 60 Ma. It allows to discard the hypothesis of an Eocene origin for the family, which is in accordance with a recent molecular calibration of the family, reporting the tribe as old as the Upper Cretaceous.

Keywords. Issidae, Hysteropterini, fossil, Paleocene, Menat.

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Introduction

Records of fossil Issidae Spinola, 1839 are rare, making their recognition and knowledge important landmarks in the understanding of the evolution of the family and essential for the calibration of a molecular phylogeny of the family. The oldest issid fossil is reported from Canadian amber 78–79 Ma (Skidmore 1999 in McKellar *et al.* 2008). It was collected in southern Alberta, Canada and K.G.A. Hamilton determined it as a possible issid nymph (C.A.S. # 1121, Canadian amber inclusions in the Canadian National Collection of Insects). However, this identification remains doubtful, needs to be confirmed and will not be considered in this paper.

Only eight other issid fossils have been described to date (Bourgoin 2020). They have recently been reviewed as belonging to different tribes (*sensu* Wang *et al.* 2016):

- Issini Spinola, 1839: *Issites glaber* Haupt, 1956 from the Lutetian (47.8–41.2 Ma), reviewed by Gnezdilov & Bourgoin (2016). According to Steinheimer & Hastings (2018), fossils from the Geiseltal, from where this specimen originates, are now more precisely dated from the middle Eocene late Geiseltalian (47.5–42.5 Ma). At that time, Geiseltal was located in a network of large subtropical islands distributed in northern Germany and France (Hellmund 2018: fig. 2).
- Parahiraciini Cheng & Yang, 1991: *Bolbossus bervoetsi* (Gnezdilov & Bourgoin, 2016) from Baltic amber dated upper Eocene (Priabonian, 37.8–33.9 Ma) (Gnezdilov & Bourgoin 2016). Baltic amber flora was recently redefined as characteristic of warm-temperate and humid forests (Sadowski *et al.* 2017), confirming a late Eocene age of the Baltic amber versus the traditional perception of a dense tropical rainforest of an early to middle Eocene age (Weitschat & Wichard 2010).
- Thioniini Melichar, 1906: *Thionia douglundbergi* Stroiński & Szwedo, 2008, described from the Miocene Burdigalian (20.44–15.97 Ma) Dominican amber (Stroiński & Szwedo 2008; PaleoBioDB 2019). Another, as yet undescribed specimen, probably belonging to the same species taxon, but from the Mexican Chiapas amber, is known by the authors. The Chiapas amber is also dated from the same period (Huys *et al.* 2016; PaleoBioDB 2019).

The last four other species are all collected from the Isle of Wight and dated Priabonian (37.8–33.9 Ma). They have recently been described and are tentatively placed within Issidae (Szwedo *et al.* 2019): *Krundia korba* Szwedo, 2019, *Breukoscelis phrikkosus* Szwedo, 2019, *Breukoscelis vadingratshevi* Szwedo, 2019 and *Uphodato garwoterus* Szwedo, 2019. However, none of these four imprints exhibits a typical issid conformation and their place within Issidae is problematic. In the absence of a revision of these fossils, which is out of scope for this paper, we regard them as being in an *incertae sedis* position within Issidae, although they should be excluded from this family.

We, therefore, report here only the fifth other fossil issid specimen. It originates from the well-known Paleocene deposit of Menat in France and represents the oldest Issidae fossil taxon known, additionally belonging to the Hysteropterini tribe for which no fossil data was available until now.

Material and methods

The type material (a single forewing imprint of 1 cm, close to another beetle imprint) is deposited in the Musée de la Paléontologie, Menat, France, with the registration number NEL 3485. Observations were made using a light stereo microscope Nikon SMZ 1500 with normal and polarized light. Photographs were made using a digital camera Nikon D800 with Auto-Montage™ system and cleaned using Adobe®Photoshop software. Drawings were made using camera lucida. Numerical ages of stages and epoch follows the latest International Chronostratigraphic chart (ver. 2019/05). Venation terminology follows Bourgoin *et al.* (2015) and Issidae classification Wang *et al.* (2016), updated in Zhao *et al.* (2019).

Results

Class Insecta Linnaeus, 1758
Order Hemiptera Linnaeus, 1758
Suborder Auchenorrhyncha Duméril, 1806
Infraorder Fulgoromorpha Evans, 1946
Superfamily Fulgoroidea Latreille, 1807
Family Issidae Spinola, 1839
Subfamily Hysteropterinae Melichar, 1906 (sec. Zhao *et al.* 2019)
Tribe Hysteropterini Melichar, 1906

Genus *Cubicostissus* Bourgoin & Nel gen. nov.

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Type species

Cubicostissus palaeocaeni sp. nov., designated here by monotypy.

Diagnosis

Cubicostissus gen. nov. separates from other Hysteropterini genera by their forewing more than 2.5 as long as wide, wider before mid-length, with anterior margin slightly and regularly convex and posterior margin slightly concave at the end of the clavus. The postcostal cell forms a narrow band, slightly narrower than the radial cell band, and as wide as C1 cell. ScP+RA and RP fork late with ScP+R more than 2.5 times as long as basal cell. MP forks in C3 at the same level of Pcu and A1 fusion and CuA remains single up to the apical level of the clavus, then forks in an open C5. CuP is almost straight, connected by transverse veins to CuA. Pcu and A1 are connected in the last quarter of the clavus.

Etymology

Arbitrary combination referring to the forewing CuA vein (*cupito costa*) single and the generic name *Issus*.

Note

Previously placed in Issinae sec. Wang *et al.* (2016), Hysteropterini were recently regarded deserving a subfamily rank (Zhao *et al.* 2019). They differ from Issinae Issini by their late forking of CuA after the end of the clavus while CuA forks well before in Issini genera. By its venation schema, *Cubicostissus* gen. nov. tegmen approaches species of *Tshurtshurnella* Kusnezov, 1927, but it appears more elongated: 2.6 times as long as wide ($\times 2$ or less in *Tshurtshurnella*) and with a late fusion of Pcu and A1 in the last quarter of the clavus (earlier in *Tshurtshurnella*). From *Hysteropterum* Amyot & Audinet-Serville, 1843, it differs by the elongated tegmen, the absence of identified apical cells, the presence of some transverse veins between CuA and CuP and, at mid-length, the costal area almost as wide as C1 and the open radial cell. Its simpler venation also easily separates this new taxon from all the other issid fossils currently known.

Cubicostissus palaeocaeni Bourgoin & Wang sp. nov.
[urn:lsid:zoobank.org:act:3E61A3B6-E035-41B1-96CD-B450B0F71F93](https://doi.org/10.3897/ejt.596.3E61A3B6-E035-41B1-96CD-B450B0F71F93)

Figs 1–2

Diagnosis

Described from a single imprint from Menat (Fig. 1). Separated from all Hysteropterini species by its elongated forewing, the narrow postcostal band and the conformation of the venation.

Etymology

The specific epithet means ‘from the Palaeocaenum (Paleocene)’ and refers to the age of the deposit where the fossil was discovered.

Material examined

Holotype

FRANCE • 1 specimen; Puy-de-Dôme, volcano-sedimentary maar of Menat; Paleocene, Selandian; Musée de la Paléontologie, Menat; NEL 3485.

Description

Forewing (Figs 1–2) 2.6 times as long as wide, wider before mid-length: 4.04 mm long, 1.63 mm wide before mid-length at MP forking level. Basal cell (bc) short, 0.29 mm long. No hypocostal plate. Anterior margin slightly and regularly convex, maximum convexity at level of MP fork. Posterior margin slightly concave at the end of the clavus. Common stem ScP+R more than twice as long as basal cell (0.67 mm long). Postcostal cell forming a narrow band, slightly narrower than radial cell, itself narrower than basal cell. ScP+R forking late: ScP+R 2.7 times as long as basal cell. Radial cell open, as wide as C1 cell before mid-length of tegmen, with ScP+RA and RP running parallel. Vein MP 1.33 mm long, forking late in cell C3 at same level of fusion of Pcu and A1; MP1+2 in straight line with vein MP; MP3+4 diverging posteriorly. CuA almost straight, single up to apical level of clavus, separated from MP and MP3+4 by

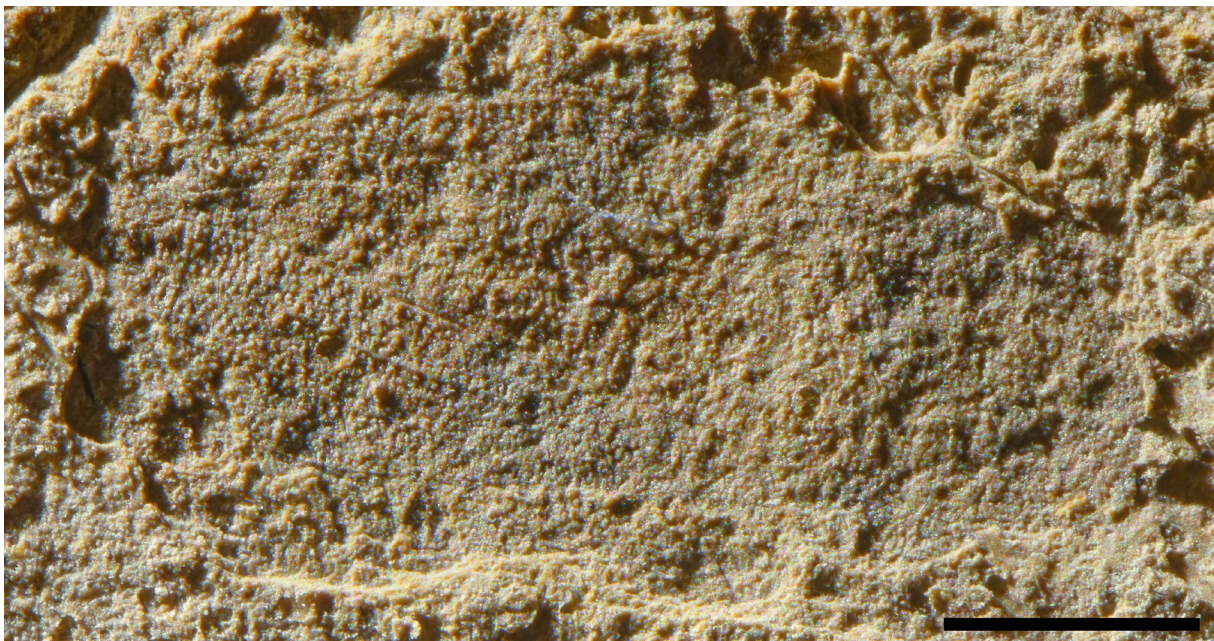


Fig. 1. Forewing of *Cubicostissus palaeocaeni* gen. et sp. nov. (NEL3485). Scale bar = 1 mm. Photograph© T. Schubnel.

a wide area (open median cell) almost as wide as area width between MP+MP₃₊₄ and costal margin. C5 cell open. CuA connected with parallel CuP before mid-length of tegmen by four transverse veins. Just before reaching clavus, apically forked with CuA1 starts running parallel to the tegmen margin and CuA2 joining tegmen margin. Pcu and A1 connecting late in the last quarter of a long closed clavus. A1 closely parallel to posterior margin. Traces of brownish coloration and small micro-granulations are visible in cubito-anal and subcostal areas (Fig. 1).

Discussion

The short basal cell and the Y-shaped Pcu-A1 veins place the fossil within the Fulgoromorpha (Shcherbakov 1996). The issidized tegmen (Gnezdilov 2013a) and the tegmen venation are specific for genera of Issidae: Hysteropterinae: Hysteropterini, particularly characterized by a CuA single, forking only at the extremity of the clavus, with CuA1 running parallel to the wing margin. Unfortunately, the distal part of the tegmen is not sufficiently preserved to further refine the comparison with other genera of Hysteropterini. However, the combination of the following characters separates the specimen from all other Hysteropterini as a new species in a new genus: the late forking of ScP+R, the late fusion of Pcu and A1, and the particularly elongated tegmen with a narrow postcostal cell.

Although the entomofauna of the Paleocene volcano-sedimentary maar of Menat (Puy-de-Dôme, France) is very diverse and rich in insect fossils (Wedmann *et al.* 2018), only a few planthoppers have been described in Cixiidae (Szwedo *et al.* 2006) and in Lophopidae (Stroiński & Szwedo 2012), but no Issidae have yet been documented. Moreover, issid fossils remain rare, as only four of them have been described to date and with an unequivocal placement among the Issidae. The discovery of the oldest fossil of Issidae and the first one of the tribe Hysteropterini is therefore notable. Particularly, it allows dating for both the Issidae and the Hysteropterini from at least the Paleocene, discarding the hypothesis of Issidae as an Eocene lineage (Gnezdilov 2013b).

The age of the Menat beds was previously reported as Thanetian (58.7–55.8 Ma) (Kedves & Russel 1982; PaleoBioDB 2019) based on basalts associated with the Menat maar. Since then, it has been re-evaluated as being Selandian (61–60 Ma) based on magnetostratigraphy (Wappler *et al.* 2009; Mayr *et al.* 2019). This age is in agreement with the results of a molecular calibration analysis (Bourgoin *et al.* 2018) that

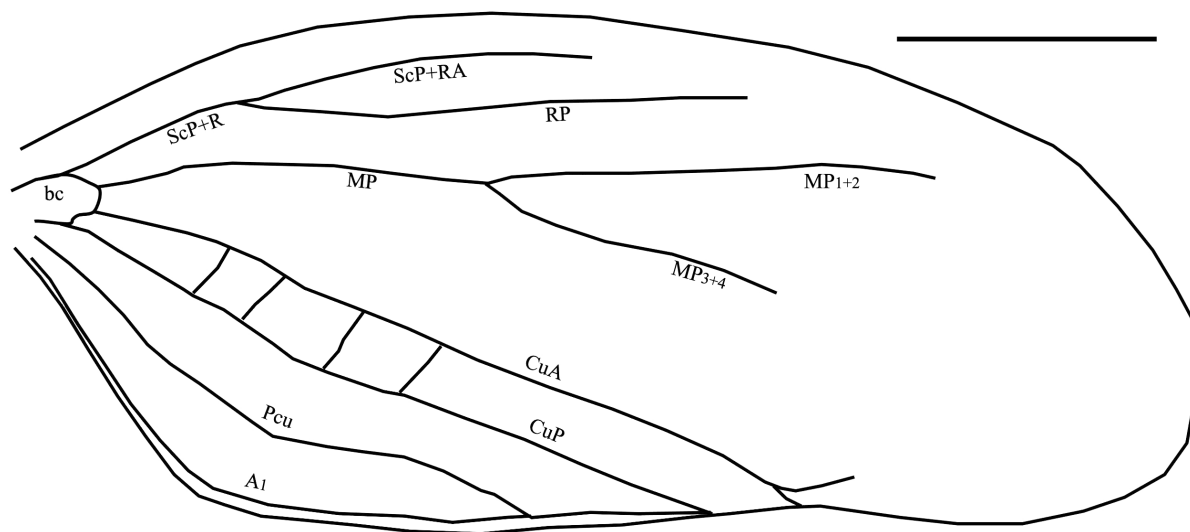


Fig. 2. Forewing of *Cubicostissus palaeocaeni* gen. et sp. nov. Scale bar = 1 mm

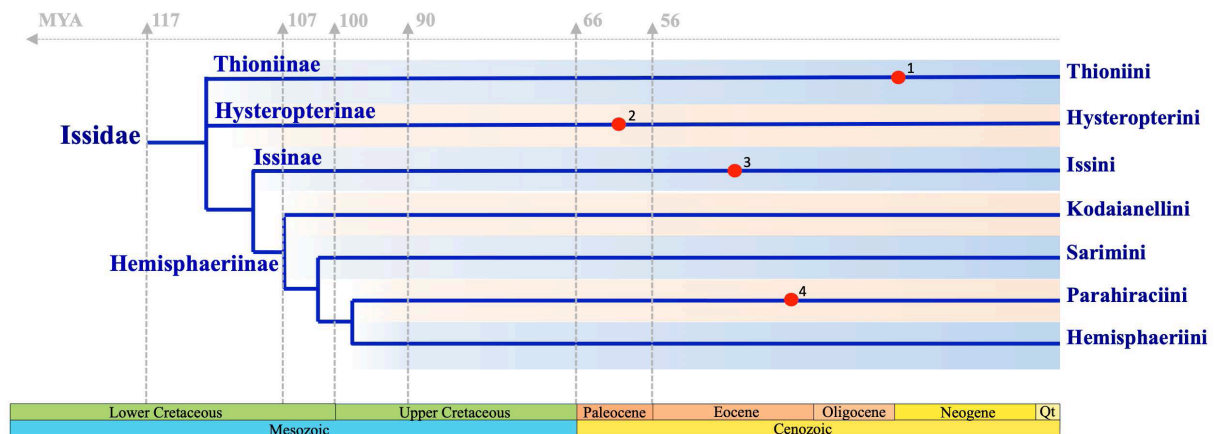


Fig. 3. Current phylogeny of Issidae, modified from Wang *et al.* (2016) according to Zhao *et al.* (2019) and labelled with molecular calibration data from Bourgoin *et al.* (2018). Red dots refer to the fossils known with their minimal age according to their deposit. **1.** *Thionia douglundbergi* Stroinski & Szwedo, 2008 (15.97 Ma). **2.** *Cubicostissus palaeocaeni* gen. et sp. nov. (60 Ma). **3.** *Issites glaber* Haupt, 1956 (42.5 Ma). **4.** *Bolbossus bervoetsi* (Gnezdilov & Bourgoin, 2016) (33.9 Ma). Priabonian fossils from the Isle of Wight (Szwedo *et al.* 2019) remain *incertae sedis* and are not figured.

dated Hysteropterini and Issidae even before the Paleocene, from the upper Cretaceous around 78 Ma and from the Lower Cretaceous around 115 Ma, respectively (Fig. 3).

Charcoal occurs in almost all horizons in the Menat beds, which testifies to the frequent occurrence of wildfires during the Paleocene in the vicinity of the Menat paleolake (Wedmann *et al.* 2018), supporting a subtropical climate with dry and wet seasons. Such a palaeoenvironment is in accordance with current environmental characteristics of Issidae: Hysteropterini being particularly well distributed in circum-Mediterranean dry habitats.

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References

- Bourgoin T. 2020. FLOW (Fulgoromorpha Lists On the Web): a World Knowledge Base dedicated to Fulgoromorpha. Version 8, updated 3 June 2019. Available from <http://hemiptera-databases.org/flow/> [accessed 15 Jan. 2020].
- Bourgoin T., Wang R.R., Asche M., Hoch H., Soulier-Perkins A., Stroński A., Yap S. & Szwedo J. 2015. From micropterism to hyperpterism: recognition strategy and standardized homology-driven terminology of the forewing venation patterns in planthoppers (Hemiptera: Fulgoromorpha). *Zoomorphology* 134 (1): 63–77. <https://doi.org/10.1007/s00435-014-0243-6>
- Bourgoin T., Guilbert E. & Wang M. 2018. Issidae molecular K-libration. *In*: 8th European Hemiptera Congress and 11th International Workshop on Leafhoppers and Planthoppers of Economic Importance, 24–29 June 2018: 36. University of Silesia, Zawiercie, Poland.

- Gnezdilov V.M. 2013a. “Issidisation” of fulgoroid planthoppers (Homoptera, Fulgoroidea) as a case of parallel adaptive radiation. *Entomological Review* 93: 825–830. <https://doi.org/10.1134/S001387381307004X>
- Gnezdilov V.M. 2013b. A modern classification of the family Caliscelidae Amyot et Serville (Homoptera, Fulgoroidea). *Zoologicheskii Zhurnal* 92: 1309–1311. [English translation in *Entomological Review* 2014 94: 211–214.] <https://doi.org/10.1134/S0013873814020092>
- Gnezdilov V.M. & Bourgoïn T. 2016. On the taxonomic position of *Issus reticulatus* Bervoets, 1910 (Hemiptera: Fulgoroidea: Issidae) from Baltic amber. *Entomological Review* 96 (5): 631–633. <https://doi.org/10.1134/S0013873816050092>
- Hellmund M. 2018. The former Geiseltal Museum (1934–2011), the Eocene Geiseltal Fossilagerstätte (Germany) and the scientific meaning of Ben Barnes as a pioneer of systematic quantitative vertebrate excavations in the Geiseltal Lignites. *Anuário do Instituto de Geociências – UFRJ* 41 (1): 108–119. https://doi.org/10.11137/2018_1_108_119
- Huys R., Suárez-Morales E., Serrano-Sánchez M. de Lourdes, Centeno-García E. & Vega F.J. 2016. Early Miocene amber inclusions from Mexico reveal antiquity of mangrove-associated copepods. *Scientific Reports* 6: 34872. <https://doi.org/10.1038/srep34872>
- Kedves M. & Russell D.E. 1982. Palynology of the Thanetian layers of Menat. The geology of the Menat Basin, France. *Palaeontographica, Abteilung B* 182: 87–150.
- Mayr G., Hervet S. & Buffetaut E. 2019. On the diverse and widely ignored Paleocene avifauna of Menat (Puy-de-Dôme, France): new taxonomic records and unusual soft tissue preservation. *Geological Magazine* 156 (3): 572–584. <https://doi.org/10.1017/S0016756818000080>
- McKellar R.C., Wolfe A.P., Tappert R. & Muehlenbachs K. 2008. Correlation of Grassy Lake and Cedar Lake ambers using infrared spectroscopy, stable isotopes, and palaeoentomology. *Canadian Journal of Earth Sciences* 45: 1061–1082. <https://doi.org/10.1139/E08-049>
- PaleoBioDB 2019. Paleodatabase. Available from https://paleobiodb.org/classic/displayStrata?geological_group=&formation=Menat&group_formation_member=Menat [accessed 21 Aug. 2019].
- Sadowski E.M., Schmidt A.R., Seyfullah L.J. & Kunzmann L. 2017. Conifers of the ‘Baltic amber forest’ and their palaeoecological significance. *Stapfia* 106: 1–73.
- Shcherbakov D.E. 1996. Origin and evolution of the Auchenorrhyncha as shown by the fossil record. In: Schaefer C.W. (ed.) *Studies on Hemipteran Phylogeny*: 31–45. Thomas Say Publications in Entomology, Lanham, Maryland.
- Skidmore R.E. 1999. *Checklist of Canadian Amber Inclusions in the Canadian National Collection of Insects*. Research Branch Agriculture and Agri-Food Canada, electronic publication, but no longer available.
- Steinheimer F.D. & Hastings K.A. 2018. Halle: the Geiseltal collection of Martin Luther University, Halle-Wittenberg. In: Beck L.A. & Joger U. (eds) *Paleontological Collections of Germany, Austria and Switzerland: the History of Life of Fossil Organisms at Museums and Universities*: 271–280. Natural History Collections, Springer, Cham. https://doi.org/10.1007/978-3-319-77401-5_25
- Stroiński A. & Szwed J. 2008. *Thionia douglundbergi* sp. nov. from the Miocene Dominican amber (Hemiptera: Fulgoromorpha: Issidae) with notes on extinct higher planthoppers. *Annales Zoologici* 58 (3): 529–536. <https://doi.org/10.3161/000345408X364355>
- Stroiński A. & Szwed J. 2012. The oldest known Lophopidae planthopper (Hemiptera: Fulgoromorpha) from the European Palaeocene. *Geobios* 45: 413–420. <https://doi.org/10.1016/j.geobios.2011.10.007>

Szwedo J., Bourgoïn T. & Lefebvre F. 2006. New Mnemosynini taxa (Hemiptera, Fulgoromorpha: Cixiidae) from the Palaeogene of France with notes on their early association with host plants. *Zootaxa* 1122: 25–45.

Szwedo J., Drohojowska J., Popov Y.A., Simon E. & Węgierek P. 2019. Aphids, true hoppers, jumping plant-lice, scale insects, true bugs and whiteflies (Insecta: Hemiptera) from the Insect Limestone (latest Eocene) of the Isle of Wight, UK. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*. <https://doi.org/10.1017/S175569101900001X> [published online 9 Aug. 2019].

Wang M., Zhang Y.L. & Bourgoïn T. 2016. Planthopper family Issidae (Insecta: Hemiptera: Fulgoromorpha): linking molecular phylogeny with classification. *Molecular Phylogenetics and Evolution* 105: 224–234. <https://doi.org/10.1016/j.ympev.2016.08.012>

Wappler T., Currano E.D., Wilf P., Rust J. & Labandeira C.C. 2009. No post-Cretaceous ecosystem depression in European forests? Rich insect feeding damage on diverse middle Palaeocene plants, Menat, France. *Proceedings of the Royal Society of London B: Biological Sciences* 276: 4271–4277. <https://doi.org/10.1098/rspb.2009.1255>

Wedmann S., Uhl D., Lehmann T., Garrouste R., Nel A., Gomez B., Smith K. & Schaal S.F.K. 2018. The Konservat-Lagerstätte Menat (Paleocene; France) – an overview and new insights. *Geologica Acta* 16 (2): 189–213. <https://doi.org/10.1344/GeologicaActa2018.16.2.5>

Weitschat W. & Wichard W. 2010. Baltic Amber. In: Penney D. (ed.) *Biodiversity of Fossils in Amber from the Major World Deposits*: 80–115. Siri Scientific Press, Manchester.

Zhao S., Bourgoïn T. & Wang M. 2019. The impact of a new genus on the molecular phylogeny of Hemisphaeriini (Hemiptera, Fulgoromorpha, Issidae). *ZooKeys* 880: 61–74. <https://doi.org/10.3897/zookeys.880.36828>

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