

THE FIRST 'CICADA-LIKE HOMOPTERA' FROM THE TRIASSIC OF THE VOSGES, FRANCE

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ABSTRACT. The first Cicadomorpha, *Gallodunstania grauvogeli* gen. et sp. nov., is described from the Triassic of the Vosges (France) and is provisionally attributed to the Palaeontinoidea family Dunstaniidae.

FOSSIL Cicadomorpha (Palaeontinoidea) are known from the Upper Permian of Southern Africa, the Triassic to the middle Cretaceous of Russia, the Triassic of Australia, the Lower Cretaceous of Brazil (Ueda 1997) and the Upper Jurassic to the Lower Cretaceous of Europe. Until now the group was unknown in the Triassic of Western Europe. The discovery, in the Lower–Middle Triassic of the Vosges, of a new species of Dunstaniidae, clearly belonging to a new genus, increases our knowledge on the diversity of this group.

SYSTEMATIC PALAEOLOGY

We follow the wing venation nomenclature proposed by Kukalová-Peck and Dworakowska (1988).

Infra-order CICADOMORPHA Latreille, 1802
Superfamily PALAEOANTINOIDEA Handlirsch, 1906
Family DUNSTANIIDAE Tillyard, 1916
Genus GALLODUNSTANIA gen. nov.

Derivation of name. After *Gallia*, the ancient Latin name for France and after *Dunstania*, which is the type genus of the family Dunstaniidae.

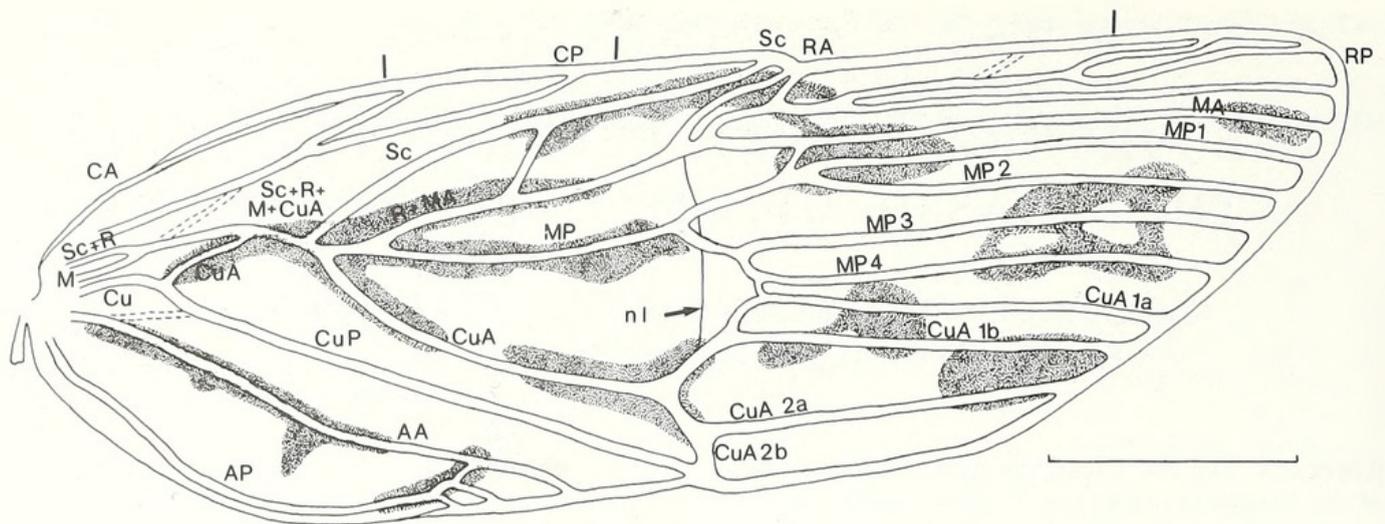
Type species. *Gallodunstania grauvogeli* sp. nov.

Diagnosis. Vein CP well developed and bifurcated distally. Sc + R, M and Cu strongly approximate and parallel basally. CuA fused with Sc + R + M for a short distance; CuA closes distally the basal cell. Sc separates from R + M + CuA near the wing base and it distally fused with a costal branch of R + MA. AP is more-or-less parallel with the anal margin of the wing. AA and AP distally fused into a 'Y' vein. Sc, RA and a short branch of RP reach the nodus. CuA divided into three distal branches, the anterior one may be fused with the posterior branch of MP. There are no crossveins in the apical part of the wing.

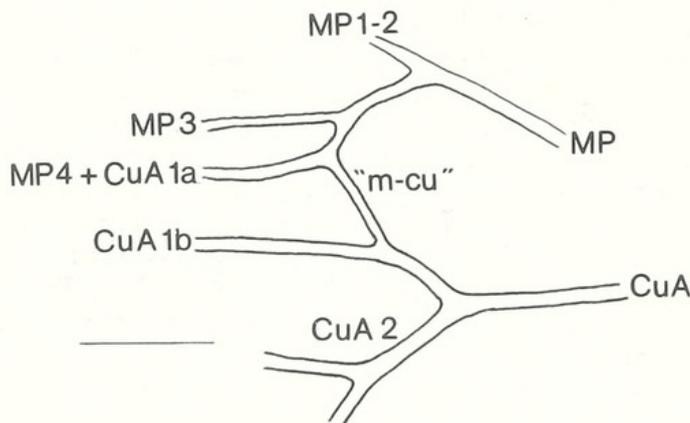
Gallodunstania grauvogeli gen. et sp. nov.

Text-figures 1–3

Derivation of the species name. After the late Louis Grauvogel who collected the type material.



TEXT-FIG. 1. *Gallodunstania grauvogeli* gen. et sp. nov.; holotype, specimen 9152 a; forewing, Scale bar represents 5 mm.



TEXT-FIG. 2. *Gallodunstania grauvogeli* gen. et sp. nov.; paratype, specimen 9151 a; area of the forewing crossvein 'm-cu'. Scale bar represents 2 mm.

Types. Holotype specimen 9152a (counterpart) and b (part) (Text-figs 1, 3); paratype specimen 9151a (part) and b (counterpart) (Text-fig. 2); Grauvogel and Gall coll., located at the Institut de Géologie, Université Louis Pasteur, Strasbourg.

Type locality and horizon. 'Grès à Voltzia', Upper Buntsandstein (Lower Anisian, Lower Triassic; Gall 1971), Vosges, Bust, Bas-Rhin, France.

Material. Two wings both represented by a part and counterpart 26 mm long: the holotype (9152) is entire, whereas the anal area is missing in the paratype (9151). The latter is surrounded by a lot of plant debris. The proposed reconstruction (Text-fig. 1) is based on both specimens. The three hypothetical 'veins', indicated by dotted lines in this reconstruction, may be due to artefacts. Thus, they are not taken into account in the description.

Diagnosis. As for genus (this is the only recognized species).

Description. Some traces of coloration are present on both wings and are indicated by stippled areas in the reconstruction. A nodal line (nl) is clearly visible but is not a vein. The nodus is located in the distal half of the wing, slightly after its middle. The nodal structures, which are poorly preserved, are indicated by a strong bend of the costal margin. Veins C and CA are joined basally and fused distally. The concave vein CP is well

TEXT-FIG. 3. Holotype; specimen 9152 a; $\times 5$.

separated basally from C and CA, divided into two branches 6.3 mm from the base of the wing and reaches the costal margin basal of nodus. Veins Sc + R, M and Cu are respectively convex, concave and concave at their base, are well separated basally and are closely parallel over 1.5 mm (maximum distance between Sc + R and M = 0.15 mm, between M and Cu = 0.11 mm). Veins Sc + R and M are fused into a strong convex vein, 2.2 mm distal of base of wing. The convex vein CuA is fused with Sc + R + M over 1.3 mm, 3.7 mm distal of base of wing. Sc is separated from R, 5.7 mm distal of base of wing and reaching nodus. At 6 mm from base of wing, basal of nodal line, CuA is directed towards the anal area. R + MA and MP separate 7 mm from base of wing. A strong oblique branch of R + MA is directed towards Sc, 9.6 mm from base of wing. A short branch (RA?) of R + MA is aligned with the nodal line and reaches the nodus. More distally, RP(?) and MA(?) diverge. A short branch of RP(?) ends in the nodus. The main branch of RP(?) divides into two branches, RPa and RPb. RPa bifurcates before reaching the costal margin near the apex. RPb is more-or-less parallel with the costal margin and ends at the apex. MA(?) is nearly straight and parallel with RPb. MP forks into two branches, MP1-2 and MP3-4 (*sensu* Shcherbakov 1984), opposite the nodal line. The common stem of MP1-2 is twice as long as that of MP3-4. MP1-2 is divided into MP1 and MP2, and MP3-4 is divided into MP3 and MP4 (Text-figs 1-2). Distal branches of MP nearly straight and parallel with those of R + MA. A crossvein is present between MP1 and MA opposite the nodus. CuA is divided into CuA1 and CuA2 opposite the nodal line. CuA1 is directed towards the costal margin for a short distance, with an apical bend, and is parallel with the distal branches of MP, R and MA before reaching the apical margin. In the holotype, a strong supplementary vein, looking like a supplementary branch of CuA1, lies between MP4 and CuA1 opposite the nodus. In the paratype, the oblique 'crossvein' between CuA1 and MP4 looks like the basal part of a branch of CuA1 that would be fused distally with MP4, although this branch of CuA1 seems to be absent. CuA2 has two branches: the posterior one, CuA2b, fused with CuP at the anal margin opposite nodal line; and the anterior one, CuA2a, more-or-less parallel with posterior margin and distal branches of CuA1, MP, R and MA and reaching the apical margin. Cu is basally parallel with Sc + R and M but has a distal posterior bend opposite the point of fusion of Sc + R and M, and is divided into CuA and CuP, 2.7 mm from the base of the wing. The convex vein CuA is fused for a short distance with Sc + R + M. The concave CuP is nearly straight, and is strong and fuses with the anal margin and CuA2 opposite the nodal line. AA and AP (respectively convex and concave veins) are clearly separated at the base of the wing. AA is nearly straight, reaching the posterior margin distinctly basal of the nodal line and more-or-less parallel with CuP. AP is more-or-less parallel with the anal margin, and is divided into two short branches ending in posterior margin basal of AA, AA and AP distally fused into a 'Y' vein.

Dimensions of the holotype: wing 26.7 mm long and 8.5 mm wide; distance between base and nodus 15.7 mm; distance between nodus and apex 11.2 mm; distance between CP and nodus 4.3 mm; AP reaching posterior margin 9.9 mm from base; AA reaching posterior margin 11.2 mm from base; CuP reaching anal margin 13.4 mm from base.

Remarks. The two specimens probably belong to the same species since all the preserved characters are identical, except for the presence of a supplementary branch of CuA1 in the holotype, this branch probably being fused with MP4 in the paratype.

The wing venation of *Gallodunstania grauvogeli* gen. et sp. nov. is similar to that of the Cicadomorpha *sensu* Shcherbakov (1984) and Carpenter (1992). Nevertheless, because of the lack of an available phylogenetic analysis of this group, it is impossible to use cladistics to define the relationships of *Gallodunstania*. Thus, we attempt to classify it provisionally using the method of global similarity.

We include *Gallodunstania* gen. nov. in the infra-order Cicadomorpha (*sensu* Shcherbakov 1984) on the basis of the following shared characters: (1) CuA and CuP basally fused; (2) basal cell and basal part of CuA long; (3) fusion (at least partly) of AA and AP in distal third of anal area before reaching anal margin; (4) macrosculpture well developed; (5) nodal line clearly defined; (6) nodus well pronounced; (7) CA strongly curved at base of wing; and (8) basal cell closed by an anastomosis between CuA and Sc + R + M.

Wootton (1968) divided Cicadomorpha (Cicadoidea) into two evolutionary lines, one leading to the Tettigarctidae and Cicadidae and the second comprising Dunstaniidae, Mesogereonidae and Palaeontinidae. Later, Shcherbakov (1984) considered Cicadomorpha in a wider sense and divided it into Prosboloidea, Pereborioidea, Scytinopteroidea, Palaeontinoidea, Cicadoidea, Cercopoidea and Cicadelloidea. Affinities of *Gallodunstania* gen. nov. with Cercopoidea and Cicadelloidea are provisionally excluded because these groups do not share with it any nodal structures or nodal line. The structure of the anal veins in *Gallodunstania* gen. nov. is similar to that of the Cicadoidea Latreille, 1802 (Recent and fossil). Nevertheless, it cannot be included in this superfamily because of the following non-shared characters: (1) presence of a long CP (possible plesiomorphy); (2) absence of apical cells in radial and median areas; and (3) presence of a long and strong vein between CuA and MP4, looking like a branch of CuA and named 'crossvein m-cu' by Shcherbakov (1984, p. 89) and Carpenter (1992, p. 215) (possible derived character). We provisionally exclude *Gallodunstania* gen. nov. from the superfamily Prosboloidea Handlirsch, 1906 because: (1) it has a long and strong 'crossvein m-cu'; (2) CuA is bifurcated in the nodal line. The superfamily Pereborioidea Zalesky, 1930 is excluded because: (1) RA has no postnodal branches; (2) the nodal line is well pronounced; and (3) the 'crossvein m-cu' is long and strong. *Gallodunstania* gen. nov. does not share the following characters with the superfamily Scytinopteroidea Handlirsch, 1906: (1) the nodus is well pronounced; (2) the distal free part of Sc begins distad of the basal cell; and (3) CuA is bifurcated in the nodal line.

Only the superfamily Palaeontinoidea Handlirsch, 1906 shares with *Gallodunstania* gen. nov. the following diagnostic characters: (1) R is not divided at the base of the wing; (2) Sc and R are separated distad of the basal cell; (3) the nodal line is well developed; (4) there is a long and strong convex vein between CuA1 and MP4 (= 'crossvein m-cu' *sensu* Shcherbakov 1984), which could be a supplementary branch of CuA1; (5) CuA is bifurcated in the nodal line; and (6) the anal area is distally bent backward.

The long and strong vein that Shcherbakov considered as a 'crossvein m-cu' could be a synapomorphy of *Gallodunstania* gen. nov. and Palaeontinoidea because this character is only present in this group. The vein MP in the Palaeontinoidea is basally divided into two branches MP1-2 and MP3-4 which are distally subdivided into MP1 and MP2, and MP3 and MP4, and not into MP1 and MP2-4. If we accept this assumption for *Gallodunstania* gen. nov., then the supplementary vein between MP4 and CuA1 reaching the apical margin in the holotype has to be considered as a further branch of CuA1. Furthermore, in the paratype this vein seems to be fused with MP4, showing only its basal portion looking like a very strong oblique vein between CuA1 and MP4. This interpretation implies that the very long and strong oblique vein 'm-cu' between CuA1 and MP4, present in all Palaeontinoidea, is not a simple crossvein but the basal portion of a supplementary branch of CuA1 distally fused with MP4. This is particularly clear in *Pseudocossus turgaiensis* Becker-Migdisova and Wootton, 1965 in which the two veins are only partly fused (Becker-Migdisova and Wootton 1965).

The alternative hypothesis in which the vein MP of the Palaeontinoidea is basally divided into 'MP1' and 'MP2-4' does not explain: (1) the very strong oblique vein 'm-cu' present in all Palaeontinoidea; (2) the fusion of 'MP4' with 'MP3' in all Palaeontinidae; (3) the division of

'MP1' into two secondary branches 'MP1a' (= MP1 *sensu* Shcherbakov) and 'MP1b' (= MP2 *sensu* Shcherbakov) in all Palaeontinoidea; and (4) the secondary branching of 'MP4' (= supplementary longitudinal vein between MP and CuA1) on 'MP3' in *Gallodunstania* gen. nov.

A specimen of *Fulgoridium* sp. (Fulgoroidea: Fulgoridiidae; Liassic of Germany) figured by Ansoerge (1996, text-fig. 36) also shows a division of CuA into three main longitudinal branches. Even if the anterior branch of CuA of *Fulgoridium* sp. is not similar (and was probably acquired convergently) with those of the Palaeontinoidea, it gives some evidence of the possible presence of a three-branched CuA in some Euhemiptera.

Nevertheless, the attribution of *Gallodunstania* gen. nov. to the Palaeontinoidea is provisional because vein AP of *Gallodunstania*, which is more-or-less parallel with the anal margin, looks different from those of the other known Palaeontinoidea.

Palaeontinoidea is divided into three fossil families (Shcherbakov 1984): Mesogereonidae Tillyard, 1921, Palaeontinidae Handlirsch, 1906 and Dunstaniidae Tillyard, 1916.

Gallodunstania galli gen. et sp. nov. differs from the Mesogereonidae since: (1) its nodus is well pronounced; (2) its veins MP1 and MP2 are not fused; (3) and the 'crossvein m-cu' is not close to the base of the wing. It differs from the Palaeontinidae since: (1) its CP (= Sc *sensu* Carpenter 1992) is well developed; and (2) its vein RP (= R *sensu* Carpenter 1992) is branched. The reduction of CP in the Palaeontinidae, as proposed by Carpenter (1992), is not very clearly established since *Asiocossus* Becker-Migdisova, 1962 (Triassic of Russia; included in the Palaeontinidae by Carpenter 1992), clearly shows a long and strong vein CP, with four or five costal branches. Thus character (1) listed above is not very convincing.

We provisionally include *Gallodunstania* gen. nov. in Dunstaniidae since it has the diagnostic characters proposed by Shcherbakov (1984) and Carpenter (1992): (1) a long CP reaching the costal margin close to the nodus; (2) long AA and AP; (3) postnodal and prenodal parts of forewing approximately equal in area; (4) RP branched (like in *Dunstaniodes* Becker-Migdisova and Wootton, 1965; Triassic of Russia); and (5) stem of MP1-2 more than twice as long as that of MP3-4.

As this attempt of classification is based on the method of global similarity, polarization of the characters is not possible and no phylogenetic conclusion can be inferred from this study. The superfamilies Prosboloidea, Palaeontinoidea and the families Dunstaniidae and Palaeontinidae are probably poly- or paraphyletic. Furthermore, Sorensen *et al.* (1995) considered that the various families included in Prosboloidea belong to the crown group of Cicadomorpha and that the latter is the polyphyletic.

CONCLUSIONS

The present classification of 'Cicadomorpha' probably does not reflect its phylogeny. A cladistic study should be undertaken in order to understand the phylogenetic history of this group. Therefore, any definite conclusion concerning the affinities of *Gallodunstania* gen. nov. has to wait.

Nevertheless, the present discovery strongly suggests that Palaeontinoidea were probably widespread during the Triassic, even if it is still impossible to make any palaeobiogeographical analysis, because of the lack of an accurate knowledge of their phylogeny.

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