

Systematic Palaeontology (Invertebrate Palaeontology)

# New genus of leaf-mimicking katydids (Orthoptera: Tettigoniidae) from the Late Eocene–Early Oligocene of France and England

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## Abstract

A new leaf-mimicking katydid (Orthoptera: Tettigoniidae: Pseudophyllinae), *Archepseudophylla fossilis* gen. et sp. nov. is described based on tegmina from the Early Oligocene of France. *Lithymnetes laurenti* Théobald, 1937 from the Late Eocene of France is transferred to *Archepseudophylla* comb. nov. The enigmatic '*Poekilloptera*' *melanospila* Cockerell, 1921 from the Early Oligocene of the Isle of Wight (UK) is transferred to *Archepseudophylla* comb. nov. The present discoveries in the Palaeogene of the Isle of Wight, Céreste, and Marseilles Basins represent the first fossil records of Pseudophyllinae. In addition, these records support warm and humid forest conditions near the palaeolakes of the Isle of Wight, Camoins-les-Bains, and Céreste. **To cite this article:** A. Nel et al., C. R. Palevol 7 (2008).

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## Résumé

**Une nouvelle sauterelle-feuille (Orthoptera: Tettigoniidae: Pseudophyllinae), *Archepseudophylla fossilis* gen. et sp. n., est décrite sur la base de tegmens de l'Oligocène inférieur de France.** *Lithymnetes laurenti* Théobald, 1937, de l'Éocène terminal de France, est transféré dans le genre *Archepseudophylla* comb. n. L'énigmatique « *Poekilloptera* » *melanospila* Cockerell, 1921 de l'Oligocène inférieur de l'île de Wight (Angleterre) est transféré dans *Archepseudophylla* comb. n. Ces nouvelles découvertes dans le Paléogène des bassins de l'île de Wight, de Céreste et de Marseille représentent les premiers Pseudophyllinae fossiles connus. De plus, ces fossiles soutiennent l'existence d'anciennes forêts humides et chaudes près de ces paléolacs. **Pour citer cet article :** A. Nel et al., C. R. Palevol 7 (2008).

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**Keywords:** Insecta; Tettigoniidae; Pseudophyllinae; Paleogene; France; UK; Leaf-mimicry

**Mots clés :** Insecta ; Tettigoniidae ; Pseudophyllinae ; Paléogène ; France ; Angleterre ; Mimétisme

## 1. Introduction

Mimicry enables an individual to gain an advantage by looking like the individuals of a different species, or for camouflage. The most common occurrence of crypsis is insects copying leaves and stems,

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such as phasmids (Phasmatodea), mantids (Mantodea), larvae of geometrid moths (Lepidoptera) and katydids (Orthoptera: Tettigoniidae). However, the fossil evidence of insect mimicry is rare or delicate to interpret [4,5,11,17]. As an example, wings that Papier et al. [11] described from the Triassic of France are really looking like angiosperm leaves, but no such leaves are known in these strata.

Fossil tettigoniids are not infrequent in the Cenozoic deposits, even if the pre-Tertiary record of this family is relatively scarce [3]. But nearly all the previously known Cenozoic representatives of this group had not developed leaf-mimicry, except for the rather enigmatic species *Lithymnetes laurenti* Théobald, 1937.

This genus *Lithymnetes* Scudder, 1878 is known through *L. guttatus* Scudder, 1878 from the Oligocene of the USA, and *L. laurenti* from the Late Eocene of France. *L. guttatus* has not developed clear leaf-mimicry, unlike *L. laurenti*, but Sharov [14] indicated that the latter could not be related to *Lithymnetes* or to the Tettigoniidae, but could belong to Hagloidea: ‘Prophalangopseinae’. Unfortunately, the type specimen of *L. laurenti* from the Late Eocene of Célas (Gard, France) is lost. Nel [6] noted the presence of fossils that he attributed to this species in the Oligocene palaeolake of Céreste (Lubéron, France). Until now, none of the numerous specimens collected from Céreste was preserved well enough for an accurate attribution to the Tettigoniidae versus Hagloidea. Fortunately, thanks to the recent field researches that we have undertaken at Céreste with the help of a group of amateur palaeontologists of the SAGA (‘Société amicale des géologues amateurs’, Paris), we found two tegmina with the venation exquisitely preserved. Also we discovered two other tegmina in the Oligocene of Camoins-les-Bains, near Marseilles (France). ‘*Poekilloptera*’ *melanospila* Cockerell, 1921, from the Isle of Wight, UK, was originally described as belonging to the bug family Fulgoridae (Hemiptera: Homoptera) [2]. Szwedlo, Bourgoïn and Lefebvre [15] considered that it was not a homopteran and thus it was regarded as *incertae sedis*.

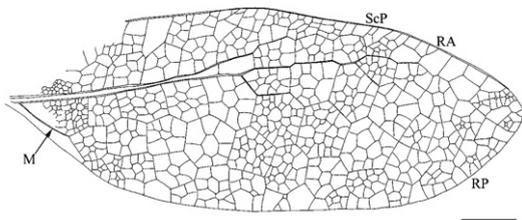


Fig. 1. *Arcepseudophylla fossilis* gen. et sp. nov., holotype R.63854, drawing of tegmina (scale bar = 5 mm).

Fig. 1. *Arcepseudophylla fossilis* gen. et sp. nov., holotype R.63854, dessin de la tegmina (échelle = 5 mm).

The new specimens from France have enabled the accurate identification of this material as leaf-mimicking katydids (Orthoptera: Tettigoniidae: Pseudophyllinae).

## 2. Systematic palaeontology

Family Tettigoniidae Krauss, 1902

Subfamily Pseudophyllinae Burmeister, 1840

Genus *Arcepseudophylla* gen. n.

### 2.1. Type species

*Arcepseudophylla fossilis* sp. nov. Other included species: *Arcepseudophylla laurenti* (Théobald, 1937) comb. nov., and *Arcepseudophylla melanospila* (Cockerell, 1921) comb. nov.

### 2.2. Etymology

Named after Arche (in Latin) and *Pseudophylla* in reference to its leaf-like tegmina and antiquity.

### 2.3. Diagnosis

Tegmina covered by a net of large polygonal cells, subdivided into smaller cells; subcostal area broad, but covering only 36% of wing width; ScP and radius strongly diverging at about 40% of wing length; RA, RP and median vein strongly zigzagged; RP and median vein distally vanishing in the net of large cells; apex of tegmina rounded.

*Arcepseudophylla fossilis* sp. n. (Figs. 1–5)

### 2.4. Description

Holotype (Figs. 1–3): tegmina elongate, with oval apex, 35.0 mm long, 13.8 mm wide; area between ScP and Costa very broad, 4.5 mm wide, but covering only 36% of whole wing width in its broadest part, divided



Fig. 2. *Arcepseudophylla fossilis* gen. et sp. nov., holotype R.63854, photograph of imprint (scale bar = 5 mm).

Fig. 2. *Arcepseudophylla fossilis* gen. et sp. nov., holotype R.63854, photographie de l’empreinte (échelle = 5 mm).

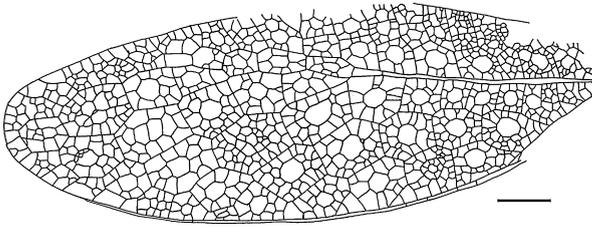


Fig. 3. *Arcepseudophylla fossilis* gen. et sp. nov., paratype R.63885, drawing of tegmina (scale bar = 3 mm).

Fig. 3. *Arcepseudophylla fossilis* gen. et sp. nov., paratype R.63885, dessin de la tegmina (échelle = 3 mm).

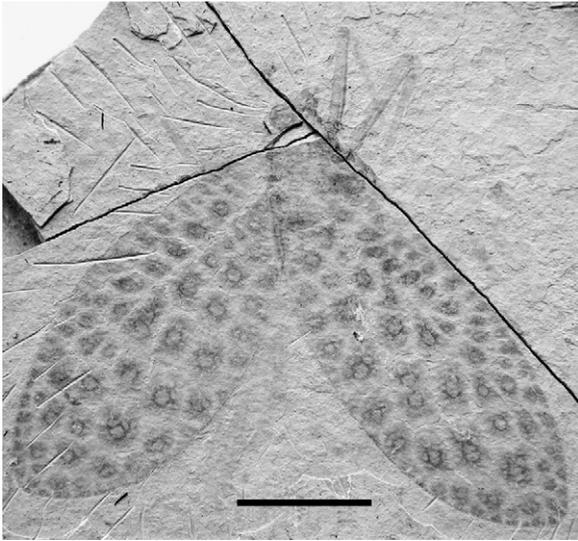


Fig. 4. *Arcepseudophylla fossilis* gen. et sp. nov., paratype R.63886, photograph (scale bar = 10 mm).

Fig. 4. *Arcepseudophylla fossilis* gen. et sp. nov., paratype R.63886, photographie (échelle = 10 mm).

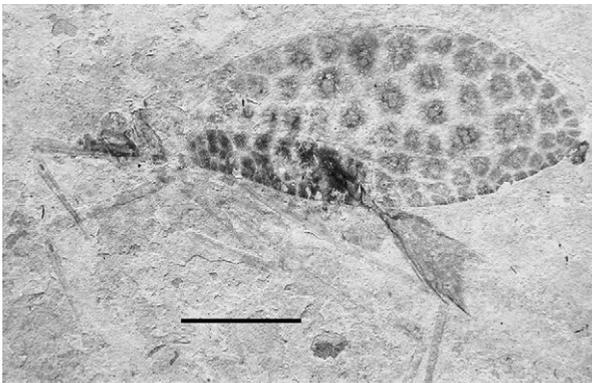


Fig. 5. *Arcepseudophylla fossilis* gen. et sp. nov., paratype R.63887, photograph (scale bar = 10 mm).

Fig. 5. *Arcepseudophylla fossilis* gen. et sp. nov., paratype R.63887, photographie (échelle = 10 mm).

into two rows of large quadrangular or pentagonal cells by secondary branches of ScP, these branches being zigzagged and these large cells subdivided into a net of smaller cells by veinlets; ScP and radius R closely parallel in basal 40% of wing length, but strongly diverging distally, with a row of five large pentagonal to heptagonal cells between them; ScP strongly zigzagged in its distal part, ending on costa 26.0 mm from the wing base and 10.7 mm from the wing apex; basal part of the radius straight; RP separating from RA 16.9 mm from the wing base; RA distally zigzagged, distally parallel to costa and ending on the posterior wing margin, 1.5 mm close to wing apex, area between RA and costa 1.7 mm wide near the wing apex; RP strongly zigzagged and rather indistinct in its distal part; area between RA and RP with two rows of very large quadrangular to octagonal cells, all of them being secondarily divided into smaller irregular cells by veinlets, but frequently with a central cell or group of very small cells; median vein straight at its very base and strongly zigzagged distally, more or less vanishing in a net of very large cells identical to those of the area between RA and RP; 3–4 rows of large cells in the area between the radius/RP and the posterior wing margin; a large cell at the wing base below the median vein; cubito-anal area not visible, probably fossilized inside the matrix, this structure being currently perpendicular to the main part of the wing in the Tettigoniidae.

The paratype specimens from Céreste (Figs. 4 and 5) have nearly the same tegmina venation. Their tegmina are covered by a net of dark spots located in the central part of the polygonal cells.

## 2.5. Material

Holotype specimen MNHN-LP-R.63854 (Camoins-les-Bains), imprint and counterprint of a nearly complete tegmina, with only antero-basal angle missing; no trace of coloration preserved, paratypes from Céreste: specimens MNHN-LP-R.63885, R.63886, R.63887, other material: 11 other specimens, Laboratory of Palaeontology, National Museum of Natural History, Paris, France.

## 2.6. Etymology

After the fossil state of this species.

## 2.7. Type strata and locality

Early Oligocene [9,12], Camoins-les-Bains, Marseilles Basin, Bouches-du-Rhône, France.

## 2.8. Locality of other material

Early Oligocene, Céreste, Alpes-de-Haute-Provence, France.

## 2.9. Discussion

The type specimen of *L. laurenti* from Célas (Gard, France) is lost, but it is clearly visible on the photograph in Théobald [16 (pl. 1, Fig. 1)] that it had a colour pattern nearly identical to that of the specimens from the Oligocene of Céreste. The reconstruction of the tegmina venation of Théobald [16 (p. 114, text-fig. 8)] is certainly erroneous, as at least its distal branches of RA and RP were zigzagged as in the material from Céreste (visible on the photograph). The tegmina veins of *Lithymnetes guttatus* are not zigzagged [13 (pl. 17, fig. 14)]. Therefore, *L. laurenti* has to be removed from the genus *Lithymnetes* and transferred to the genus *Archepseudophylla* gen. nov. as *Archepseudophylla laurenti* comb. nov. It belongs to the Tettigoniidae, and not to the Hagloidea: ‘Prophalangopseinae’ (contra [14]). *A. laurenti* differs from the material from Céreste by its smaller dimensions (tegmina length 25 mm, instead of 32 to 35.5 mm in the material from Céreste). Nel [6] already noted this difference, but considered that it was not sufficient for a species separation. At that time, he had only three specimens available from Céreste, but the same range of wing lengths is now observable on 15 specimens. This strongly supports a specific separation between the fossils from Célas and Céreste. There is no clear difference between the tegmina venation and dimensions of the specimens from Camoins and Céreste. The unique difference is the absence of spot pattern on the tegmina of the specimen from Camoins, but this is probably related to its preservation as an imprint without any trace of coloration preserved, and not a mummy of the animal itself as for the Céreste’s material. Therefore we consider that they belong to the same species.

‘*Poekilloptera melanospila* Cockerell, 1921 from the Bembridge Marls, Isle of Wight, of Early Oligocene age, was originally placed in Hemiptera: Fulgoridae; however, Szwedo et al. [15] considered that it was not a homopteran (the recent genus *Poekilloptera* Latreille 1796 belongs to the Hemiptera: Flatidae). Szwedo (pers. comm.) suggested that it might be a plant fossil; however, Margaret Collinson (pers. comm.) examined it and confirmed it is not a plant. Specimen In.24356 at the Natural History Museum, London, is the holotype (Fig. 6). It consists of a fragment of wing, clearly showing the subdivided large polygonal cells with a central

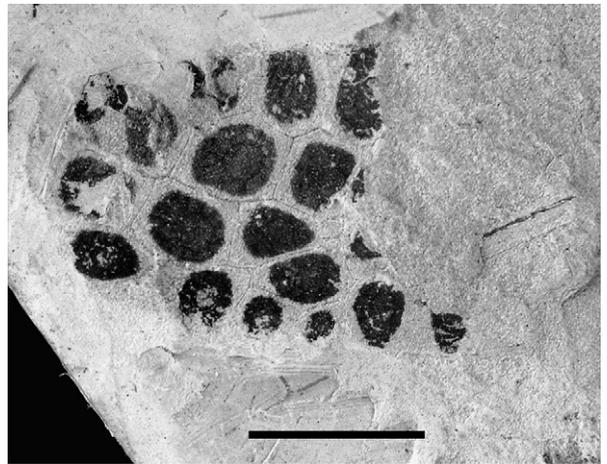


Fig. 6. *Archepseudophylla melanospila* (Cockerell, 1921) comb. nov., holotype In.24356, photograph (scale bar = 5 mm).

Fig. 6. *Archepseudophylla melanospila* (Cockerell, 1921) comb. nov., holotype In.24356, photographie (échelle = 5 mm).

colour spot, characteristic of *Archepseudophylla*. Unfortunately, it is too fragmentary to work out the full length of the tegmen, so it is uncertain whether it is conspecific with *A. fossilis* or *A. laurenti* or constitutes a separate species. For the moment, it should be regarded as a separate species, *Archepseudophylla melanospila* (Cockerell, 1921) comb. nov. One of us (A.R.) has found an additional specimen in the collections of the Natural History Museum, London, In.25803/In.17326 (the counterpart is only a fragment) (Fig. 7). The specimen consists of wings, thoracic segments, pronotum and antennal bases. The wings are crumpled and fragmentary, with the characteristic subdivided polygonal cell and central colour spot, though unfortunately the length of the tegmina cannot be ascertained. The polygonal cells are similar in size to those of the holotype of *Archepseudophylla melanospila*, so this specimen should be regarded as conspecific. The thoracic segments

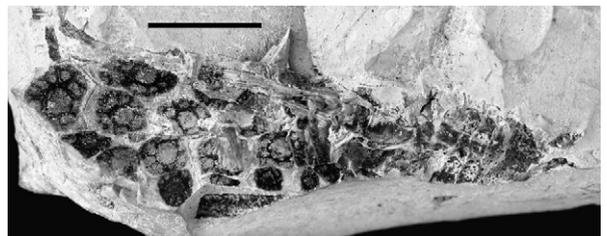


Fig. 7. *Archepseudophylla melanospila* (Cockerell, 1921) comb. nov., In.25803, photograph (scale bar = 5 mm).

Fig. 7. *Archepseudophylla melanospila* (Cockerell, 1921) comb. nov., In.25803, photographie (échelle = 5 mm).

and pronotum have a distinctive punctate ornament, the pronotum is 3.7 mm wide and the basal antennal segment is 0.7 mm wide. It is hoped that more complete material of *A. melanospila* will be found in due course.

The tegmina of *Archepseudophylla* are clearly leaf-like, with a broad subcostal area, veins ScP and radius closely parallel and displaced close to the middle part of the wing, and a net of large polygonal cells, subdivided into smaller cells, looking like the cells of a large leaf. Such wings can be found in some recent Tettigoniidae of the subfamilies Phaneropterinae Burmeister, 1838 and Pseudophyllinae Burmeister, 1840 [10]. The current classification of the tettigoniid subfamilies is not based on tegmina venation, but on other body characters, not available in *Archepseudophylla fossilis* [1]. Nevertheless, affinities with Phaneropterinae are unlikely because of the strong divergence between ScP and RA in the distal part of wing, not shared by leaf-like Phaneropterinae (see [10]). Within the Pseudophyllinae, *A. fossilis* looks like some recent Neotropical Pterochrozini Brunner von Wattenwyl, 1895 (*Pterochroza* Serville, 1831), Pterophyllini (*Scopioricus*), and Australian and Madagascarian Simoderini Brunner von Wattenwyl, 1895 (*Lonchitophyllum* Brunner von Wattenwyl, 1895 or *Phyrama* Karsch, 1889). But we could not find a recent taxon with such a strongly zigzagged RP and with a relatively reduced subcostal area, covering only 36% of wing width.

The specimens of *Archepseudophylla* constitute the first fossil records of the tettigoniid subfamily Pseudophyllinae. Because of the presence of strong convergence of mimicry in the tegmina among the tettigoniid tribes and genera, it is not possible to ascertain its affinities within the Pseudophyllinae.

### 3. Conclusions

The tegmen of *Archepseudophylla* is mimicking a large leaf attacked by microscopic fungi (large dark round spots). Such large rounded leaves are very rare at Céreste and have not been recorded at Camoins-les-Bains, probably due to taphonomic biases. The presence of an insect mimicking them supports their presence in the ancient environment. The recent leaf-mimicking katydids live in warm forest environments in the intertropical areas. The present discoveries in the Early Oligocene suggest warm and humid forests around the palaeolake of Céreste, Camoins-les-Bains, and the Isle of Wight. Similar inferences can be made after the presence of numerous Isoptera: Mastotermitidae in the same layers of Camoins and the Isle of Wight (not yet found at Céreste), as the only living representa-

tive of the latter family occurs in the warm savannahs and forests of northern Australia [7]. Nevertheless, the Late Eocene and the Earliest Oligocene of western Europe were periods of cooling, while the Oligocene palaeolakes of Céreste and Camoins-les-Bains correspond to a period of warming (Collomb et al., in prep.). Thus *Archepseudophylla* and *Mastotermites* cannot be considered as good temperature indicators. Maybe they are only indicators of humid forests under more or less warm climates. The reconstruction of the palaeoenvironmental conditions of the formation of the palaeolake of Camoins infers to an Oligocene basin similar to the ‘actual tropical lagoon’ [12], supporting the present inferences. *Archepseudophylla fossilis* is the second insect present at both Céreste and Camoins-les-Bains, with *Lestes ceresti* Nel & Papazian, 1985 [8], supporting a close age for the two palaeolakes.

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