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An early winged crown group stick insect from the Early Eocene amber of France (Insecta, Phasmatodea)

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Abstract. The new stick insect family Gallophasmatidae, based on *Gallophasma longipalpis* **gen. et sp.n.**, from the Earliest Eocene French amber has a pattern of tegmina venation typical of Archaeorthoptera, also present in at least some Mesozoic 'Phasmatodea'. On the other hand, *Gallophasma* displays in its body anatomy some apomorphies of the extant Euphasmatodea, e.g. fusion of metatergum and abdominal tergum 1, correlated with the reduction of abdominal sternum 1 to lateral triangular sclerites. A unique autapomorphy of *Gallophasma* is the presence of annulated and apparently multi-segmented or pseudo-segmented cerci; all other Phasmatodea have one-segmented cerci. The venation of the tegmina of *Gallophasma* differs from that of extant winged Phasmatodea in the plesiomorphic absence of a knob-like dorsal eversion. This and other differences in the wing venation between extant and extinct Phasmatodea might have been caused by the loss of wings at some point in the evolutionary history of the order and their secondary gain in a subclade of the extant phasmids.

Introduction

The phylogenetic relationships of the Phasmatodea remain controversial, despite several recent morphological and/or molecular works, with possible relationships with Dermaptera, Embioptera, Grylloblattodea + Dictyoptera, Dictyoptera or Orthoptera [for a summary of the state of the art, see Delclòs *et al*. (2008: 370)].

Pre-Cenozoic taxa currently assigned to the 'Phasmatodea' sensu Gorochov (1994) are known from the Middle Triassic, Jurassic and Cretaceous (Nel *et al*., 2004). Tilgner (2001) doubted that these fossils could be related to the extant group Phasmatodea (his 'Phasmida'), as the apomorphic characters of the Euphasmatodea Bradler, 1999 (= Euphasmida sensu Tilgner, 2001), especially the fusion of the first abdominal tergite with the thorax, cannot be observed in these fossils. It is impossible to decide if this is because of the preservational state of these fossils or because they are truly absent.

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Delclòs *et al*. (2008) demonstrated that at least some of the pre-Cenozoic 'Phasmatodea' have a pattern of wing venation of the 'orthopteroid' type (*Orephasma* Ren, 1997; *Aeroplana* Tillyard, 1918; *Chresmoda* Germar, 1839), suggesting close affinities of these fossil insects with the clade Archaeorthoptera Béthoux & Nel, 2002. Nevertheless, no certain affinity of these pre-Cenozoic phasmid-like insects and the true Euphasmatodea has been demonstrated. It is very hard to determine if the wing venation of the extant winged representatives of Euphasmatodea also possesses these structures of 'orthopteroid' type, owing to the strong sclerotization of the wing bases and basal displacement of the stems of the median and cubital veins.

Here we describe a new Eocene phasmid taxon showing well-preserved tegmina displaying plesiomorphic traits observed in pre-Cenozoic 'Phasmatodea' as well as apomorphies of the extant Euphasmatodea in the body anatomy. The new fossil taxon hence occupies an intermediate position between Euphasmatodea and the Mesozoic putative stem-group phasmids.

The following abbreviations have been used throughout: CuA, cubital anterior; CuP, cubital posterior; M, media; MA, medial anterior; MP, medial posterior; R, radial; RA, radial anterior; RP, radial posterior; ScP, subcosta posterior.

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Taxonomy

Order Phasmatodea Jacobson & Bianchi, 1902
Clade Euphasmatodea Bradler, 1999
Family Gallophasmatidae **fam.n.**
Type genus. *Gallophasma* **gen.n**.

Diagnosis. Fully winged in both sexes; tegmina without 'knob-like dorsal eversion' (see below); absence of an area apicalis; ocelli present; third antennomere not especially elongate; a series of very short flagellomeres distal of third antennomere; maxillary palps very elongate, much longer than head; hind femora very elongate, much longer than mid femora; pronotum short, longer than wide, with expanded lateral sides; ovipositor very long, longer than head; cerci with four apparent 'segments', the most basal one annulated.

Gallophasma gen.n.

Type species. Gallophasma longipalpis **sp.n.**

Etymology. Named after Gallia, the Latin name for France and *Phasma*.

Diagnosis. As for family.

G*allophasma longipalpis* **sp.n.**
(Figs 1, 2)

Description. From holotype if not specified. Head transverse, 1.15 mm long, 1.2 mm wide, prognathous (MNHN A30856); gula hardly visible but present, of moderate length, between cervix and posterior tentorial pits; eyes well developed, diameter 0.6 mm; one lateral ocellus preserved near eye; maxillary palp 2.9 mm long, six-segmented (Fig. 1E); galea 0.63 mm long, 0.3 mm wide; antenna very elongate with more than 60 antennomeres, scape 0.35 mm long, pedicel 0.04 mm long, first flagellomere 0.17 mm long, flagellomeres 2–6 0.06 mm long, subsequent flagellomeres of nearly identical length and shape, 0.3 mm long; all antennomeres with elongate erected sensilla (MNHN A30856), nearly absent in MNHN A30855.

Pronotum covered with small setae, rather flat, longer than wide but with expanded lateral sides, 2 mm long, 1.3 mm wide (MNHN A30856); two weak transverse furrows on sides of anterior part of pronotum; thorax *c*. 6.1 mm long.

Tegmina 11.46 mm long (MNHN A30855) (Fig. 2B), in MNHN A30856 10 mm long, 1.85 mm wide, slightly shorter than hind wing, 11.3 mm long, without any knob-like dorsal eversion; area between costal margin and ScP 0.9 mm wide with at least four anterior branches of ScP; apex of ScP 5.5 mm from wing base; RP separating from RA 3.5 mm from wing base (MNHN A30856); RA straight and simple, reaching anterior wing margin 7 mm from wing base; RP with two long and straight branches, separating 1.25 mm distal of its base; convex MA separating from slightly less convex MP + CuA at same point where M + CuA separates from R; MA closely parallel to R for 1.75 mm and diverging from it near base of RP; a weak but distinct furrow between R and M + CuA (or MA) from wing base to point of divergence between MA and R; MA with three distal branches in MNHN A30855, but with only one very distal fork in MNHN A30856, 8 mm from its base; MA ending near wing apex; common stem of MP + CuA 1.9 mm long, distally divided into slightly concave MP (subdivided into three long and straight branches), and a more convex simple CuA; basal part of CuP partly overlapping R + M + CuA; concave CuPa (anterior branch of CuP) emerging 0.5 mm from wing base and reaching MP + CuA 0.4 mm distally; concave CuPb (posterior branch of CuP) straight and closely parallel to MP + CuA; four veins (CuPb plus anal veins?) making a kind of rather broad cubito-anal fan, 5.2 mm long and 1 mm wide; the second of these veins basal to CuP with three branches (in MNHN A30855 and MNHN A30857), simple in MNHN A30856; vannus visible (MNHN A30856); numerous crossveins mainly in posterior part of basal half of wing.

Hind wings overlapped by tegmina, only their apices being visible.

Fore femora with small setae, tibia 3.5 mm long, setose with two distinct apical spurs, tarsi 1.5 mm long; mid femora 2.9 mm long, setose with a distinct apical spur, tibia 3.4 mm long, setose with distinct subapical (one) and apical (two) spurs, tarsi 1.3 mm long; hind femora 6.8 mm long, with two distinct apical spurs; all tibiae without area apicalis; all tarsi five-segmented, with tarsomere 1 the longest, 0.5 mm long, second 0.2 mm, third 0.1 mm, fourth (partly concealed by fifth) 0.05 mm, fifth 0.26 mm; arolia broad, semicircular, 0.2 mm long, longer than tarsal claws (Fig. 1F).

Abdomen 3 mm long, 0.6 mm wide; nine complete abdominal segments observed (only tergites preserved); first segment visible laterally with sternite triangular in shape and with spiracle, ventrally covered by metathoracic sternite (Fig. 1B); tergite 1 partly preserved and with a weak suture with metatergum. Genital appendages of MNHN A30856 nearly completely missing, presence versus absence of vomer sensu Bradler (1999) not decidable; ovipositor well developed (MNHN A30857), *c*. 3.0 mm long, longer than cerci, cerci with four apparent 'segments', 1.9 mm long, with first segment apparently annulated (Fig. 2A).

Material. Holotype MNHN A30855 (PA 16000, head and pronotum fragmentary, one tegmina complete, fragments of other and one hind wing preserved, female?); paras MNHN A30856 (PA 1574, nearly complete specimen, with part of head and ventral part of thorax and abdomen missing, three legs preserved, wing overlapped over thorax and abdomen, male?), MNHN A30857 (PA 16095, specimen in poor condition, but with apex of abdomen preserved, female). Deposited at the Palaeontology Department, MNHN, Paris, France.

Etymology. Named after the very elongate maxillary palps.

Type strata. Lowermost Eocene, in amber, *c*. −53 Myr, Sparnacian, level MP7 of the mammal fauna of Dormaal (Nel *et al*., 1999).

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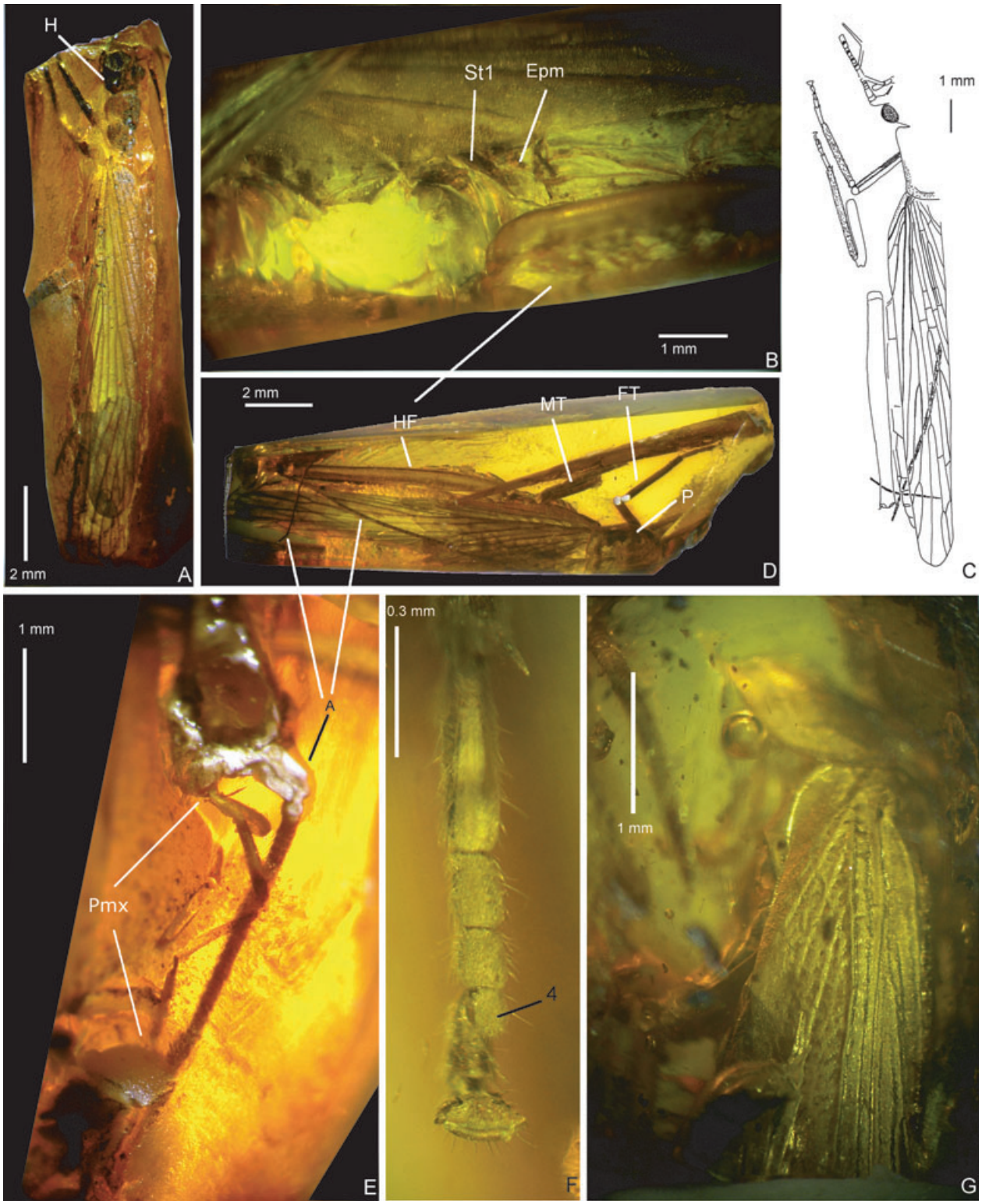

Fig. 1. *Gallophasma longipalpis* **gen. et sp.n.**, (A) holotype MNHN A30855. Habitus. (B) holotype MNHN A30855. Lateral view of thorax and base of abdomen. (C) paratype MNHN A30856. Habitus. (D) paratype MNHN A30856. Habitus. (E) paratype MNHN A30856. (F) paratype MNHN A30856. Tarsus. (G) paratype MNHN A30857. Tegmina base. Abbreviations: 4, fourth tarsomere; A, antenna; Epm, metathoracic epimere; FT, fore tibia; H, head; HF, hind femur; MT, middle tibia; P, pronotum; Pmx, maxillary palps; St1, sternite 1.

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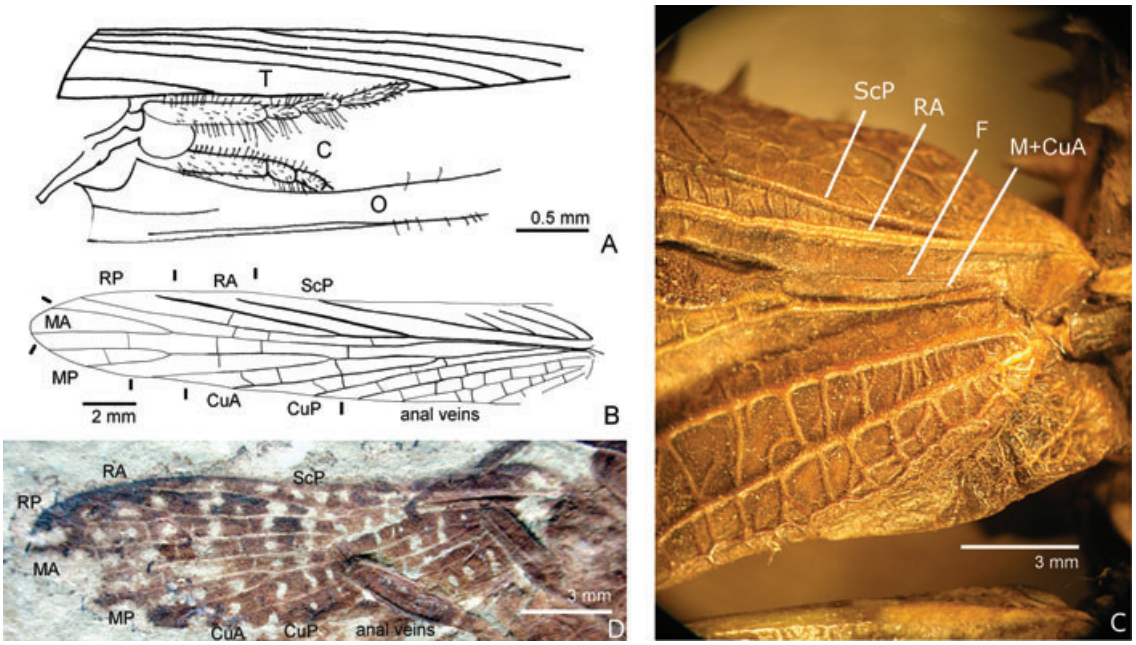

Fig. 2. (A, B) *Gallophasma longipalpis* **gen. et sp.n.** (A) paratype MNHN A30857. Tip of abdomen. (B) holotype MNHN A30855. Fore wing. (C) *Phasma gigas* (Linné, 1758), tegmina base of male. (D) Phasmatodean from the Lower Cretaceous of Santana Formation, Brazil. Abbreviations: C, cerci; CuA, cubital anterior; CuP, cubital posterior; F, furrow; M, media; MA, medial anterior; MP, medial posterior; O, ovipositor; RA, radial anterior; RP, radial posterior; ScP, subcosta posterior; T, tegmina.

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

Discussion

We attribute these three fossils to the genus *Gallophasma* **gen.n**. because they have similar wing venation and share the diagnostic characters listed above. The attribution to the same species is more elusive as there are some differences in their tegmina venation (branches of MA and of anal veins), and in the antennal setation. These differences could be attributed to either sexual dimorphism or intraspecific variation. Strongly erected sensilla as in MNHN A30856 are present in males of some extant Phasmatodea (Phyllidae; Zompro, 2004). Thus, MNHN A30856 could be a male and MNHN A30855 a female, but it cannot be excluded that the nearly complete absence of setae on the antennae of MNHN A30855 could be due to the state of preservation. Pending the discovery of additional material, we place the three fossils in the same species. *Gallophasma* has the general habitus of other phasmids. More precisely, its habitus resembles that of the representatives of the Baltic amber family Archipseudophasmatidae Zompro. They have similar shape of thorax, legs, head and wings (Zompro, 2001). *Gallophasma* has two transverse furrows on the sides on the anterior part of the pronotum that could correspond to the prothoracic defence glands present in all Phasmatodea, including *Timema* Scudder, sister to all extant euphasmatodean stick insects, and the Baltic amber Archipseudophasmatidae (Tilgner *et al*., 1999; Tilgner, 2001).

A putative synapomorphy between *Gallophasma* and Euphasmatodea is the fusion of the metatergum and abdominal tergum 1, correlated to the reduction of abdominal sternum 1 to lateral triangular sclerites, each with a spiracle (Bradler *et al*., 2003; Zompro, 2004, 2005). These traits do not occur in *Timema*, the potential sister group of Euphasmatodea (Tilgner *et al*., 1999; Bradler *et al*., 2003; Whiting *et al*., 2003; Zompro, 2004). Furthermore, *Gallophasma* does not have the main apomorphy of the Timematodea Kevan, 1982 (tarsi apparently three-segmented). *Gallophasma* also shares with extant Euphasmatodea having the tegmina shorter than the hind wing, which might be a potential synapomorphy (but see below). Two further possible synapomorphies of *Gallophasma* with the Euphasmatodea are the presence of a faint furrow between the median and radial veins and the basal part of CuP partly overlapping the stem R + M + CuA, present in recent winged phasmids (cf. Figs 1C, G, 2B, C).

Gallophasma has cerci with four apparent 'segments', unlike all extant Phasmatodea, including *Timema*, but also Mantophasmatodea. Multi-segmented cerci occur in Plecoptera, Zoraptera, Embioptera, Blattodea, Mantodea and Isoptera. Extant Dermaptera have one-segmented cerci, but some Jurassic earwigs and the first larval stages of some extant species have multi-segmented cerci. All the Mesozoic phasmatodean fossils (including *Chresmoda*) with well-preserved cerci have one-segmented cerci. Extant Orthoptera also have one-segmented cerci, but Grylloidea: Myrmecophilidae have cerci with apparent segmentation (Chopard, 1949; Baccetti, 1975). It is not possible to determine whether *Gallophasma*

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has truly or pseudo-segmented cerci. If we place *Gallophasma* among Euphasmatodea, it implies that the presence of four-'segmented' cerci is an autapomorphy of this taxon.

Zompro (2004) proposed a truncated tegmina as a putative synapomorphy of the extant Verophasmatodea Zompro, 2004 (= Euphasmatodea minus the apterous *Agathemera* Stål, 1875 in Agathemerodea sensu Zompro, 2004). Bradler *et al*. (2003) remarked that some extant phasmids [male *Heteropteryx dilatata* (Parkinson)] have the tegmina as long as the hind wing and reaching the apex of the abdomen. Zompro (2001: 231) stated that the 'wing venation of the two adult male Archipseudophasmatidae examined indicates a closer relationships to the (modern) Pseudophasmatidae, since the radial vein is branched'. However, this argument is rather weak, as the pattern of the distal branching of the main veins in extant stick insects is rather variable (A. Nel & E. Delfosse, personal observation). Furthermore, the extant Pseudophasmatidae have reduced tegmina, but with a pronounced 'knob-like dorsal eversion' (a pronounced hump in the area between the radius and media that could be correlated with the presence of a particular folding of the hind wing; Key, 1991), unlike the Archipseudophasmatidae and *Gallophasma*. All extant male winged Euphasmatodea have a more or less pronounced 'knob-like dorsal eversion' in their tegmina, which seems to constitute a synapomorphy of these taxa, not present in the Archipseudophasmatidae and *Gallophasma*. Thus, *Gallophasma* (and probably the Archipseudophasmatidae if they have similar tegmina venation) belong to the Euphasmatodea, but are in basal positions relative to the clade that would comprise the extant winged Euphasmatodea [if we follow Whiting *et al*. (2003)]. It is very difficult to determine the position of *Gallophasma* relative to the lineages of apterous phasmids that are not included in the clade of winged phasmids sensu Whiting *et al*. (2003). Unlike the Archipseudophasmatidae, *Gallophasma* has no area apicalis in both the fore and mid tibiae and a moderately developed gula, which could constitute synapomorphies with the 'taxon B' of 'Anareolatae' sensu Bradler (1999). At this stage, the cladogram in Fig. 3 summarizes the position of *Gallophasma* among the extant and Cenozoic Phasmatodea.

A further problem concerns the position of the 'apterous' Agathemerodea. The exact position of the Archipseudophasmatidae relative to the Agathemerodea is uncertain, as Zompro (2004) proposed the structure of muscles of the abdomen, a character obviously not observable in the fossil Archipseudophasmatidae, as a synapomorphy for his clade Verophasmatodea (including the Archipseudophasmatidae). The position of *Agathemera* is controversial as Whiting *et al*. (2003) placed it as a derived lineage, and absolutely not near the base of the phylogenetic tree of the Euphasmatodea, unlike Zompro (2004) or Klug & Bradler (2006).

Gallophasma differs from the Archipseudophasmatidae in the absence of an area apicalis; the presence of ocelli; the third antennomere not especially elongate; the presence of a series of very short flagellomeres distal of the third antennomere; maxillary palps very elongate, three times longer than the head; and hind femora very elongate, much longer than the mid femora; four-'segmented' cerci. These characters justify placing *Gallophasma* in a separate family.

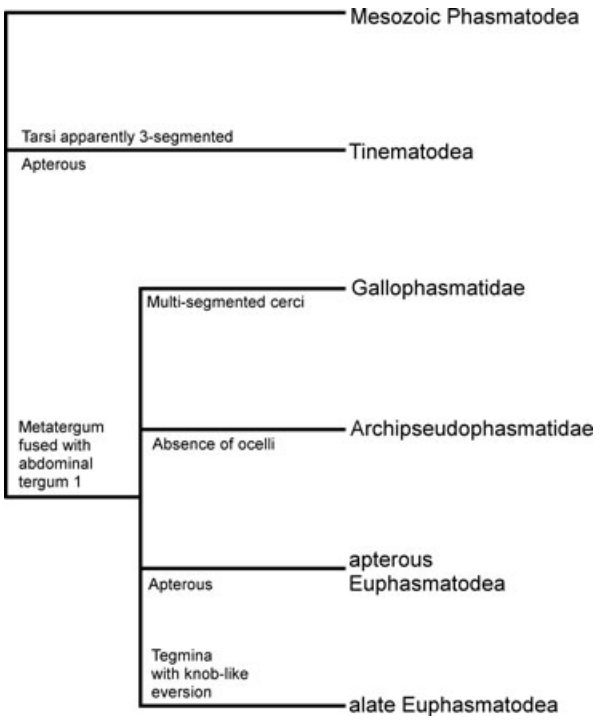

Fig. 3. Hypothetical cladogram summarizing the state of knowledge and position of *Gallophasma* in extant and Cenozoic Phasmatodea. The most important apomorphies of the clades are indicated.

The tegmina of *Gallophasma* is complete and its wing venation is well preserved, showing several important characters that remain unknown in the described Archipseudophasmatidae (Zompro, 2001, 2004, 2005), especially specialized structures of the cubito-median veins, namely basal fusion of convex CuA with R + M into a common stem; separation of M + CuA into a forked convex branch MA and a more neutral but convex posterior branch MP + CuA; concave CuP divided into branches, one of them (CuPa) reaching the posterior branch of M + CuA; convex CuA(+CuPa) separating from weakly concave MP some distance from wing base. Identical structures are found in Mesozoic taxa that were considered as stem group Phasmatodea, namely the marine insect *Chresmoda*, the Jurassic *Orephasma* and the Triassic *Aeroplana* (Delclòs *et al*., 2008: fig. 6).

An alternative interpretation could be that the anterior branch of M + CuA is M, and the posterior branch is CuA (+CuPa); but under this interpretation, the distal branch of CuA (+CuP) should not be weakly concave, but should have the same convexity as in its basal part. Thus, we prefer the first interpretation.

The basal fusion of CuA with R + M plus the presence of an anterior branch of CuP reaching CuA are putative synapomorphies of the 'orthopteroid' lineage (clade Archaeorthoptera Béthoux & Nel) (Béthoux & Nel, 2002).

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This pattern of basal parts of cubital and median veins is not clearly visible in the extant winged Phasmatodea because all these veins are obscured close to the wing base in a sclerotized zone. The euphasmatodean *Gallophasma*, *Chresmoda*, *Orephasma* and *Aeroplana* share a closely similar wing shape and these venation structures, which strongly suggest that these Mesozoic taxa are related to the Phasmatodea. They could well belong to the stem group of the extant Phasmatodea. The patterns of venation of the tegminae of the other Mesozoic Phasmatodea are very close to that of *Gallophasma* in the preserved structures (unfortunately, the structure of the bases of M, CuA and CuP is not clear in many of these fossils): all have RA simple, RP, MA, MP and CuA with few branches, all closely parallel, MP and CuA separating from a common stem (see, for example, *Aethephasma* Ren or *Palaeochresmoda* Nel *et al*.) (Ren, 1997; Nel *et al*., 2004). An undescribed specimen from the Lower Cretaceous of Liaoning Province (China), stored in the MNHN collection (specimen MNHN A31857) shows a convex RA, a forked concave RP, a forked convex MA, a common stem MP + CuA, with a forked slightly concave MP and a simple convex CuA, a common basal stem M + CuA emerging from R + M + CuA, a simple concave CuP, as in *Gallophasma* (Fig. 2D). This fossil supports our preferred interpretation of a common stem MP + CuA because of different convexity of these veins after their separation.

More precisely, the fusion of CuA with MP is a specialized character present in many representatives of the Palaeozoic archaeorthopteran order Caloneurodea, except in *Permostridulus* Béthoux *et al*. (2003). This fusion of MP with CuA is perhaps also present in the Titanoptera (Sharov, 1968). Thus, the fusion of MP with CuA could either be a synapomorphy of the Phasmatodea with the Caloneurodea and/or the Titanoptera, reversed in some Caloneurodea, or a convergence, but this is not within the scope of the present paper. It remains that the Phasmatodea are not 'descended' from Caloneurodea because the latter have a further synapomorphy, which is the closely parallel veins CuP and CuA, absent in all Phasmatodea.

The demonstration of affinities of Mesozoic fossils with extant stick insects indicates that the origins of Phasmatodea extend perhaps as far back as the Triassic (Nel *et al*., 2004). Sandoval *et al*. (1998) proposed an age of approximately 20 Myr for the split between *Timema* and all other extant Phasmatodea, based on molecular rates for base substitution. Tilgner (2001) stated that this hypothesis probably underestimated the age of the Timematodea. A representative of this group was described by Zompro (2005) from Baltic amber (*c*. −45 Myr, Eocene). Wedmann *et al*. (2007) described a true leaf insect from Messel (−47 Myr), suggesting a Cretaceous age for the Euphasmatodea. The Early Eocene age (−53 Myr) of *Gallophasma* and the Eocene age of the Baltic amber Archipseudophasmatidae also support a high diversity of the Phasmatodea during the Paleocene/Eocene and greater age for the basal node, for sister group Timematodea.

Whiting *et al*. (2003) suggested that the common ancestor of Phasmatodea (including the Timematodea) was apterous and that wings of the extant winged Euphasmatodea were derived secondarily. This hypothesis was disputed by Trueman *et al*. (2004) [but see Whiting & Whiting (2004); secondary wing gain is possible as demonstrated in Dermaptera, see Pantel (1917)]. *Timema* and probably the Baltic amber *Electrotimema* Zompro (known only from a late instar subimago) are apterous.

The Mesozoic Phasmatodea and *Gallophasma* (and probably also the Archipseudophasmatidae) were fully winged, but with a venation that strongly differs from those of the winged extant Euphasmatodea, in the absence of 'knob-like dorsal eversion', and basal parts of M + CuA and CuP not strongly concentrated at the wing base (both probably plesiomorphies). Consequently, the wings were probably lost convergently in Timematodea and at least some members of the Euphasmatodea. This need not contradict Whiting *et al*.'s (2003) hypothesis of a possible secondary gain of the wings in some extant Euphasmatodea. The important venation differences between the Cretaceous Phasmatodea and the Eocene *Gallophasma* on the one hand, and the extant Euphasmatodea on the other, suggest that significant changes (that could be correlated with secondary gain of the wings) occurred for this structure in the extant Euphasmatodea perhaps once, with some subsequent repeated loss of wings in various lineages.

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