

# A “stick insect-like” from the Triassic of the Vosges (France) (“pre-Tertiary Phasmatodea”)

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**Résumé – Un “phasme” du Trias des Vosges (Insecta: “Phasmatodea pré-Cénozoïque”).** – *Palaeochresmoda grauvogeli*, nouveau genre et espèce d'insecte semblable à un phasme, est décrit du Trias inférieur-moyen de France. C'est le plus ancien Prochresmodidae, et probablement ‘Phasmatodea’, connu. L'accent est mis sur l'importance des analyses phylogénétiques dans les estimations de la paléobiodiversité des insectes et de l'importance des crises qui ont pu l'affecter.

**Abstract –** *Palaeochresmoda grauvogeli*, new genus and species of “stick insect-like” is described from the Lower-Middle Triassic of France. It is the oldest known Prochresmodidae and probably “pre-Tertiary Phasmatodea”. The importance of phylogenetic analyses is emphasized for the estimations of the insect palaeobiodiversity and the crises that could have affected it.

Stick insects are not frequent in the fossil record. Furthermore, the affinities of many of the described taxa remain uncertain. This situation is due to the incomplete state of preservation of fossils (in particular the pre-Tertiary taxa), but also to the confusion occurring in the definition and affinities of the order Phasmida (other names Phasmatodea, Phasmoptera, Phasmoptera, Phasmatida, Phasmodea). Bradley & Galil (1977) proposed a classification of the recent representatives of this order, but without phylogenetic analysis. Tilgner *et al.* (1999) clarified the phylogeny of the recent stick insects. The autapomorphies they proposed concerned the body structures. Tilgner (2001) discussed the position of the “pre-Tertiary Phasmatodea” attributed to the “Phasmoptera” *sensu* Gorochov (1994) and concluded that they are probably not related to the recent taxa. Zompro (2001b) revised the Baltic amber Phasmida. The Cenozoic and recent representatives of this last group are separated into three suborders Timematodea, Anareolatae and Areolatae on the basis of the tarsi and

tibial structures, not available in nearly all the pre-Tertiary taxa (Zompro 2001a,b). The oldest accurate Phasmida are probably Cenozoic.

The phylogenetic relationship between the Tertiary and recent Phasmida and the pre-Tertiary taxa currently attributed to this order remain uncertain. Sharov (1968), followed by Gorochov (1995, 2000), considered that the recent stick insects are closely related to the Orthoptera on the basis of wing venation structures. More precisely, Sharov (1968) considered that stick insects have an anterior branch of “cubital vein” that reaches “median vein”, documented in the Triassic fossil *Aeroplana* Tillyard 1918 but also in the Upper Jurassic (or Lower Cretaceous?) *Orephasma* Ren, 1997. Béthoux & Nel (2002a,b) noted that this organization of the cubito-median veins is typical of the clade Panorthoptera. Thus, these presumed “fossil stick insects” should be considered as genuine “orthopteroid” insects. Nevertheless, Tilgner (2001) indicated that the recent Phasmida have not such anterior branch of cubital vein reaching median vein. He added that the possible sister group of Phasmida could be the Embidiina (= Embioptera). After a molecular analysis, Maekawa *et al.* (1999) indicated that the recent Phasmida could

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be the sister group of the recent (Grylloblattida + Dictyoptera). These authors did not consider the Embidiina in their analysis. More recently, Beutel & Gorb (2001) proposed a similar result as they considered the recent Phasmida *sensu* Tilgner (2001) as the sister group of [Mantodea + (Isoptera + Blattodea)]. Their result is based on two potential synapomorphies. Wheeler *et al.* (2001) contradicted this result, supporting a sister group relationship between recent Phasmida and Orthoptera, based on four potential synapomorphies. Gorochov (2001a) considered, in an “evolutionary taxonomy” approach based on “intuitive measuring of value of qualitative distinctions” (Gorochov 2001b), that “Phasmatoptera and Orthoptera are possible descendants of some unknown Carboniferous, more or less cockroach-like Titanoptera” (see also Gorochov & Rasnitsyn 2002: fig. 430). The problem is that the group Titanoptera is till now restricted to Triassic (plus one, undescribed, recently discovered specimen in the Upper Permian of France) and really not similar to cockroaches. Lastly, Grimaldi (2001) proposed to include the recent [“Phasmida” + Timemidae] in an unresolved trichotomy with the two fossil groups Caloneurodea and Titanoptera, on the basis of the reduction of the cerci, the resulting clade being in an unresolved polytomy that would concern all the polyneopteran orders. If both Caloneurodea and Titanoptera have a wing venation of “orthopteroid” type (Béthoux & Nel, 2002a,b), it is not so obvious for recent Phasmida, as noted above.

In conclusion, there is still no consensus on the phylogenetic relationships of recent Phasmida. Furthermore, the identity of the recent Phasmida with the “pre-Tertiary Phasmatoidea” is questionable. If at least some “pre-Tertiary Phasmatoidea” (*Aeroplana*, *Orephasma*) are probably related to the Panorthoptera on the basis of shared forewing venational structures, the monophyly of a group that would comprise both pre-Tertiary and recent Phasmida is also debatable.

We describe herein a new “stick insect”-like fossil wing from the Triassic of the “Grès à Voltzia” of the Vosges in France. This “stick insect” is in the Collection “Grauvogel & Gall” that comprises 5.300 specimens of insects, with about 200 species (Marchal-Papier 1998). Numerous recent orders were already present (Blattodea 41%, Diptera 5%, Orthoptera 3%, Ephemeroptera 15%, Coleoptera 12%, Homoptera 9%, Heteroptera 9%, Mecoptera, Odonata), with several already described taxa (see in Marchal-Papier 1998). Some other Triassic “stick insects” are already known from the Madygen Formation (Kirghizistan) (Martynov 1928; Sharov 1968; Vishniakova 1980; Gorochov 1994) and from the Ipswich Formation (Queensland, Australia) (Tillyard 1918).

We cannot follow the wing venation nomenclature proposed by Sharov (1968) even if it could facilitate the comparison with the fossil taxa previously described, because vein convexities do not correspond. As example, the vein that Sharov named CuA2 is clearly concave in our fossil, instead of being convex as it should be for all the anterior veins (Kukalová-Peck 1991). Even if we have no definite proof of the affinities of our fossil with the “orthopteroid” lineage, we prefer to use the nomenclature of Béthoux & Nel (2002a,b) proposed for the ground plan of the “orthopteroid” insects, modified from Kukalová-Peck (1991: fig. 6.18A) and Kukalová-Peck & Brauckmann (1992). Unlike that of Sharov, this last nomenclature is not contradicted by the available data concerning the present fossil.

### Stratigraphic distribution

The “Grès à Voltzia” corresponds to the upper part of the Bunter Sandstone, which represents the upper part of the Lower Triassic with a German facies. However the age of the “Grès à Voltzia” from the Vosges Mountains is early Anisian, which corresponds to the basal part of the Middle Triassic in the Alpine stratigraphy (Durand & Jurain 1969; Gall 1971).

## SYSTEMATIC PALAEONTOLOGY

Family **PROCHRESMODIDAE** Vishniakova, 1980

GENUS **Palaeochresmoda** n. gen.

**Type species** – *Palaeochresmoda grauvogeli* n. sp.

**Etymology** – After Palaeo (Greek for ancient) and fossil genus *Chresmoda* Germar, 1839.

**Diagnosis** – This taxon is closely related to the two genera *Prochresmoda* and *Triassophasma*. Forewing with area between ScP and anterior wing margin narrow, RP simple, no secondary longitudinal vein between RP and MA, the branches of MA, base of MA basally recessed, common stem of MP with CuA short.

*Palaeochresmoda grauvogeli* n. sp.  
(fig. 1A-B)

**Material** – Holotype specimen n° 9149 (233/10), Coll. Grauvogel – Gall, housed in EOST, Université Louis Pasteur, Strasbourg (France).

**Etymology** – After Dr. Léa Grauvogel-Stamm, palaeobotanist at the University of Strasbourg.

**Type horizon** – Upper Buntsandstein, “Grès à Voltzia des Vosges”, Anisian, Lower-Middle Triassic.

**Type locality** – Hangviller, Moselle, France.

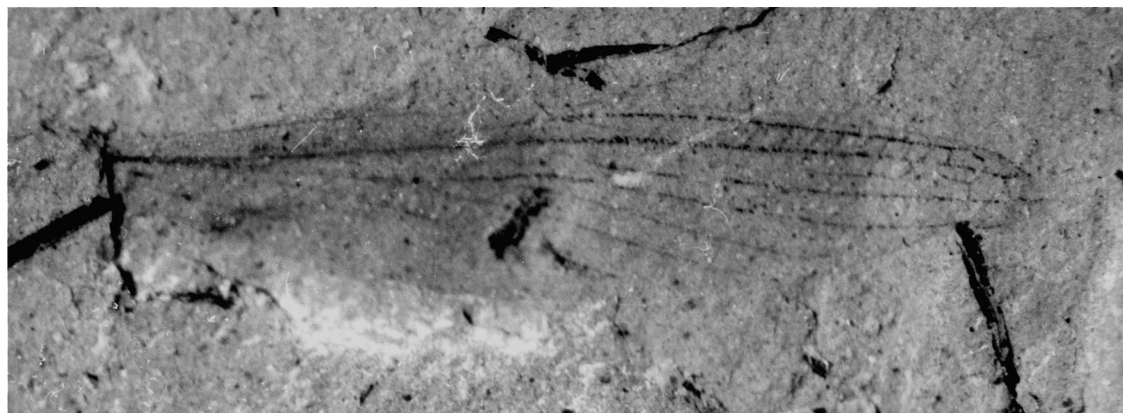
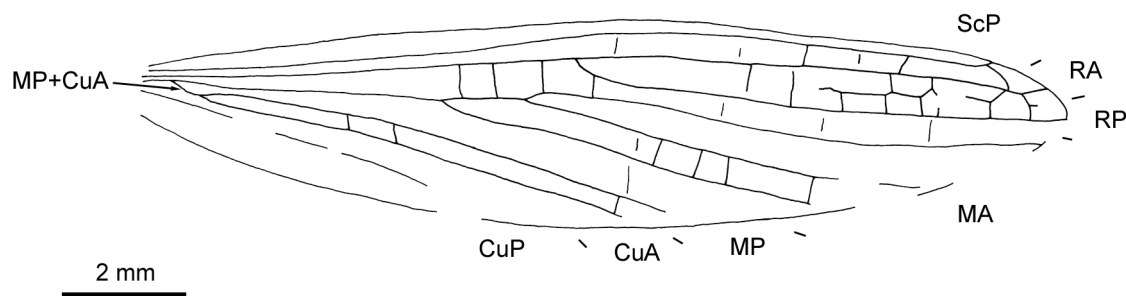
**Diagnosis** – That of the genus.

**Description** – A single forewing, nearly complete; basal half more poorly preserved than distal half; wing hyaline; 15.1 mm long, 3.3 mm wide; no “precostal” area; concave ScP long and straight, extending close to wing apex, 1.5 mm apart; convex RA parallel at length to ScP, with few cross-veins between them; base of RP 7.3 mm of wing base; RP simple, basally curved and distally straight, reaching wing apex; a weak secondary zigzagged longitudinal vein between RA and RP; RP and MA well separated, with few cross-veins preserved between them; concavity of RP and all branches of MA weakly pronounced; MA separated from MP + CuA very close, 0.6 mm, to wing base; first branch of MA 4.4 mm, well distal of base of MA but well basal of base of RP; MA divided into 3 posterior branches, weakly curved and more or less parallel; MP and CuA separated very close, about 0.5 mm, of their origin; MP clearly concave, simple and straight; CuA clearly convex, simple and straight; a distal CuP poorly preserved, simple and straight, reaching posterior wing margin; the anterior branch of CuP that should be present between CuP and MP + CuA (ground plan of the orthopteran lineage, Béthoux & Nel, 2002a,b) is not visible; anal area reduced.

**Discussion** – As already noted above, the monophyly of the “Phasmoptera” *sensu* Gorochov (2000) is ques-

tionable. But also the definition of this group is not very clear (see remarks on the separation between Phasmomimidae and Susumaniidae). No list of autapomorphies is available for this group. Nevertheless, the elongate wing, reduced anal area, unbranched RP, and straight veins suggest affinities of the present fossil with “Phasmoptera” *sensu* Gorochov (2000). This last author divided this group into Susumaniioidea Gorochov, 1988, Prochresmodoidea Vishniakova, 1980, Aeroplanoidea Tillyard, 1918 and Xiphopteroidea Sharov, 1968. We compare *Palaeochresmoda* to these three groups. As no phylogenetic analysis of “Phasmoptera” or “pre-Tertiary Phasmatodea” is available, the characters are not polarized. Thus, we can only make a preliminary study, based on the global similarity of our fossil with the other fossil taxa.

**1. Comparison with the Susumaniioidea Gorochov, 1988.** – Gorochov (1995) attributed several Mesozoic and Lower Cenozoic taxa to the Phasmomimidae Sharov, 1968 and this group to the Orthoptera: Ensifera *incertae sedis* on the basis of few body characters of rather uncertain polarity (4-segmented tarsus without arolium, carnivorous mandibles). Gorochov (2000) restricted the



**Figure 1**

A, *Palaeochresmoda grauvogeli* n. sp., holotype specimen 233/10, forewing reconstruction. – B, *Palaeochresmoda grauvogeli* n. sp., holotype specimen 233/10, forewing, photograph (scale bar = 2 mm).



Phasmomimidae Sharov, 1968 to the two genera *Phasmomima* Sharov, 1968 and *Jurophasomima* Gorochov, 1988. Within Phasmatoptera, Gorochov (2000) erected the superfamily Susumaniioidea and the family Susumaniidae for the Susumaniinae Gorochov, 1988, previously considered as Phasmomimidae (Gorochov 1988). He characterized this group relatively to the Permo-Triassic Prochresmodoidea Vishniakova, 1980 and the Triassic Xiphopteroidea Sharov, 1968 in “the reduction of secondary C in forewing” and in “proximal origin of RP in both wing pairs, in basal halves of wings”. Gorochov (2000) listed in this family the following genera: *Palaeopteron* Rice, 1969 (Upper Cretaceous, Labrador, Canada, Rice 1969), *Coniphasma* Birket-Smith, 1981 (Upper Cretaceous, Greenland, Birket-Smith 1981; Kevan & Wighton 1983), *Promastacoides* Kevan & Wighton, 1981 (Paleocene, south-central Alberta, Canada, Kevan & Wighton 1981, 1983), *Cretophasmomima* Kuzmina, 1985 (Lower Cretaceous, Baissa, Siberia), *Paraphasmomimella* Kuzmina, 1985 (Lower Cretaceous, Baissa, Siberia), *Eosusumania* Gorochov, 1988 (Lower Cretaceous, Siberia), *Prosusumania* Gorochov, 1988 (Lower Cretaceous, Siberia), *Cretophasmomimoides* Gorochov, 1988 (Lower Cretaceous, Siberia), *Susumania* Gorochov, 1988 (Upper Cretaceous, Siberia), *Kolymoptera* Gorochov, 1988 (Upper Cretaceous, Siberia), *Hagiphasma* Ren, 1997 (Upper Jurassic or more probably Lower Cretaceous?, Liaoning province, China, see Swisher *et al.*, 2001), *Aethephasma* Ren, 1997 (Upper Jurassic or Lower Cretaceous?, Hebei province, China), *Orephasma* Ren, 1997 (Upper Jurassic or Lower Cretaceous?, Hebei province, China, Ren 1997), *Phasmomimoides* Sharov, 1968 (Upper Jurassic, Karatau, Kazakhstan). Gorochov (2000) also “possibly” attributed *Phasmomimula* Kevan & Wighton, 1981 (Paleocene, south-central Alberta, Canada) to this family. It is based on a very poorly preserved hindwing. The vein RP of all these taxa is forked.

*Palaeochresmoda* n. gen. differs from the Susumaniidae in its vein RP simple, branching from R in the middle of the wing.

Note. Gorochov (1988) considered *Paraphasmomima* Zherikhin, 1985 as a Phasmomiminae but the same author (2000) excluded it from the Phasmomimidae and considered that its relationships “remain unknown”. The wing base of *P. sharovi* is not preserved, but the organization of its radial and median areas is similar to that of the Susumaniidae (Zherikhin 1985).

**2. Comparison with the Xiphopteroidea Sharov, 1968.** – Sharov (1968) divided this group into Xiphopteridae Sharov, 1968, Aeroplanidae Tillyard, 1918, Aerophasmatidae Martynov, 1928, Necro-

phasmatidae Martynov, 1925 and Cretophasmatidae Sharov, 1968. Gorochov (1994) only included the Xiphopteridae in this superfamily and transferred the Aeroplanidae, Aerophasmatidae, Cretophasmatidae into the superfamily Aeroplanoidea. He added nothing concerning the Necrophasmatidae in this paper.

Gorochov (1994) “characterized” the Xiphopteroidea on the basis of a well-developed precostal area and vein “MP + CuA1” (= MP) pectinate in forewing. In *Palaeochresmoda* n. gen., MP is simple and the precostal area is reduced, no visible.

**3. Comparison with the Necrophasmatidae (*Necrophasma shabarovi* Martynov, 1925, Upper Jurassic, Karatau, Kazakhstan).** – Sharov (1968) already stated that this family has possibly no relation with the “Phasmatoidea”. This taxon has a MA with a fork in a very basal position and a MP posteriorly pectinate, unlike *Palaeochresmoda* n. gen.

**4. Comparison with the Aeroplanoidea Tillyard, 1918.** – The Aeroplanoidea *sensu* Gorochov (1994) comprises the Aeroplanidae and Aerophasmatidae, with the three subfamilies Aerophasmatinae, Cretophasmatinae and Chresmodellinae Bode, 1953. The Aeroplanidae (*Aeroplana* Tillyard, 1918 and *Paraplana* Sharov, 1968) have a very basal separation of RP from RA, RP with several branches (only in *Paraplana*), MA with one fork; MP and CuA with several branches, unlike *Palaeochresmoda* n. gen. Among the Aerophasmatidae, *Aerophasma* Martynov, 1928 has also a very basal separation of RP from RA and RP and MP with several branches. Unlike *Palaeochresmoda* n. gen., *Schesslitzella* Kuhn, 1952 (= *Chresmodella* Bode, 1953, in Chresmodellinae) has a separation of RP and RA basal of the branches of MA, after the reconstructions of Gorochov (1993) and Ansorge (1996a) (note that this last author erroneously figured a common stem of MP + CuA + CuP). *Durnovaria* Whalley, 1985 (in Chresmodellinae), *Cretophasma* Sharov, 1968 (in Cretophasmatinae) and *Jurophasma* Gorochov, 1993 have the same relative positions of base of RP and branches of MA as in *Schesslitzella* (Sharov 1968; Whalley 1985; Martins-Neto 1989; Ansorge 1996b). *Baissophasma* Gorochov, 1993 has a MP forked, a broad area between ScP and anterior wing margin, and main veins very parallel (Gorochov 1993).

**5. Comparison with the Prochresmodoidea Vishniakova, 1980.** – This group comprises the two families Permophasmatidae Gorochov, 1992 and Prochresmodidae Vishniakova, 1980 (Gorochov 1994). *Permophasma* Gorochov, 1992 (unique representative of Permophasmatidae) is based on a poorly preserved

forewing from the Upper Permian of Mongolia (Gorochov 1992). All the structures of the distal half of wing and of wing base are unknown. Thus, its attribution to the “Phasmoptera” rather than to the Orthoptera is questionable. Gorochov (1994) characterized Permophasmatidae on the basis of: (1) presence of branches of RP (more precisely one fork of RP is preserved on the type specimen); (2) “MP + CuA1” very bulging. This vein is the most basal branch of MA. The organization of the branches of MA is very similar in *Prochresmoda media* (see Gorochov 1994: figs 2a and 2h); (3) rare cross-veins. This last character is surprising because Gorochov (1994) figured a zigzagged intercalary vein with several cross-veins between RP and RA. The presence of such a structure is rather related to a greater number of cross-veins than in other “pre-Tertiary Phasmatodea”. This last character alone is apparently unique within the “pre-Tertiary Phasmatodea” and would be sufficient to “characterize” the Permophasmatidae. Nevertheless, the discovery of new specimens of *Permophasma* would be welcome to clarify the identity and position of this enigmatic taxon.

*Palaeochresmoda* shares with the Prochresmodidae its simple RP. It would differ from this group in its fewer cross-veins but this character is uncertain in *Palaeochresmoda*. This family comprises the two genera *Prochresmoda* Sharov, 1968 and *Triassophasma* Gorochov, 1994. *Palaeochresmoda* is strikingly similar to both these genera. The only differences are: absence of intercalary longitudinal vein between RP and MA and between the branches of MA, together with the very short common stem of MP + CuA (= “CuA2 + CuP” *sensu* Gorochov 1994). They exclude an attribution to any of the *Prochresmoda* of *Triassophasma* spp. *Palaeochresmoda* shares with *Prochresmoda* its area between ScP and anterior wing margin narrower than in *Triassophasma* (one of the main differences between the two genera, after Gorochov 1994). We attribute *Palaeochresmoda* to the Prochresmodidae on the sole basis of the global greater similarity between them. As the characters are not polarized, this attribution is only provisional. A phylogenetic analysis of the “pre-Tertiary Phasmatodea” will be necessary before any definite conclusion about its relationships.

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Note. *Chresmoda* Germar, 1839 is an enigmatic taxon, known from the Upper Jurassic of Germany, Lower Cretaceous of Spain and England, and Mesozoic of China (Martínez-Delclós 1989). Sharov (1968) included it into the “Phasmatodea”. Vishniakova (1980) and Carpenter (1992) considered this genus as an Orthoptera: Caelifera of uncertain assignment. A complete revision of its wing venation should be welcome because its general body shape is strikingly similar to that of the *Prochresmoda* spp (Sharov 1968).

**6. Comparison with the Upper Eocene Archipseudophasmatidae Zompro, 2001 (Baltic amber).** – *Archipseudophasma phoenix* Zompro, 2001 is the oldest known accurate Phasmatodea. It differs from *Palaeochresmoda* in its branched RP (Zompro 2001b: 236).

Except for the relatively dubious *Permophasma kovalevi* Gorochov, 1992, based on an Upper Permian fragmentary wing, *Palaeochresmoda* is the oldest known “pre-Tertiary Phasmatodea”. The situation occurring in this “group” is typical of the problems related to the estimations of past insect diversity. If the “pre-Tertiary Phasmatodea” were included in the same clade with the Cenozoic and recent Phasmida, and if *Permophasma* was a genuine representative of this clade, then this group would be Upper Permian. If the “pre-Tertiary Phasmatodea” and the recent Phasmida are not in the same clade, then the oldest known Phasmida would be Cenozoic. Thus, it is still not possible to establish in which way these groups were affected by the “Cretaceous-Cenozoic crisis”. If *Permophasma* is not a Phasmatodea, then the oldest representative of this group would be Lower-Mid Triassic. Thus, it is not possible to determine if the “pre-Tertiary Phasmatodea” were affected or not by the “Permo-Triassic crisis”. Lastly, if the “pre-Tertiary Phasmatodea” is not a monophyletic group, counting it in the estimations of the past biodiversity would have no sense (contra Labandeira 1994; Labandeira & Sepkoski 1993). All these still unresolved problems show the importance of making phylogenetic analyses before any evaluation of the palaeobiodiversity and its crises.

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