Eur. J. Entomol. **99**: 111–116, 2002
ISSN 1210-5759

Raphogla rubra gen. n., sp. n., the oldest representative of the clade of modern Ensifera (Orthoptera: Tettigoniidea, Gryllidea)

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Key words. Insecta, Orthoptera, Ensifera, Tettigoniidea, Gryllidea, Hagloidea, Raphoglidae fam. nov., Upper Permian, France, phylogenetic significance

Abstract. *Raphogla rubra* gen. n., sp. n., oldest representative of the (Tettigoniidea & Gryllidea) is described from the Upper Permian of the Lodève basin (France). Its phylogenetic relationships within the Ensifera are discussed. The new taxon occupies a very basal position, probably as sister group of the whole group (Tettigoniidea & Gryllidea).

INTRODUCTION

The infraorder Tettigoniidea *sensu* Gorokhov (1996) comprises three superfamilies, the Hagloidea, the Stenopelmatoidea and the Tettigonioidea. The approach of this author was done in a non-cladistic perspective: by way of an example, the Hagloidea, *sensu* Gorokhov (1996), is clearly a paraphyletic group and the Tettigonioidea and Stenopelmatoidea are considered as "descents" of the Hagloidea. In a more recent work, based on a phenetic analysis of molecular characters, Flook et al. (1999) proposed an unresolved trichotomy across these three superfamilies. The phylogenetic relationships between these three groups remains unresolved.

Gorokhov (1986) considered the Hagloedischiidae (*Hagloedischia primitiva* Gorokhov, 1986, Middle or Upper Trias, Madygen, Russia) as the "ancestor" group of the whole superfamily Hagloidea and, consequently, of the whole infraorder Ensifera. Furthermore, the same author considered the "primitive" Hagloidea as the "ancestors" of another infraorder, Gryllidea (= modern and fossil Grylloidea + fossil Gryllavoidea) (Gorokhov, 1995, 1996), in which the most "primitive" taxon would be the Triassic superfamily Gryllavoidea, comprising one family (Gryllavidae) with four genera (*Gryllavus* Sharov, 1971, *Paragryllavus* Gorokhov, 1986, *Zagryllavus* Gorokhov, 1986, *Galliagryllavus* Papier et al., 2000). Flook et al. (1999) proposed a different schema in which the modern Grylloidea fall as sister group of the whole Tettigoniidea (= Hagloidea & Stenopelmatoidea & Tettigonioidea). Lastly, Gorokhov (1996) considered the (Gryllidea + Tettigoniidea) as descendents of the paraphyletic fossil superfamily Oedischioidea.

A complete phylogenetic analysis of the relationships of fossil and modern (Grylloidea + Tettigoniidea) is necessary and will be presented in a forthcoming paper.

We describe herein a new genus and species, based on a fossil wing from the Upper Permian of the Lodève basin (Hérault, France), which occupies a very basal position relative to the group (Tettigoniidea & Gryllidea). It is the most ancient known representative of this group. Its set of character states shows us the primitive condition of this taxon, and are helpful for a future cladistic analysis.

The present insect was found close to village Octon in site F21 named "le Moural" of the Salagou Formation (Odin, 1986) from the Saxonian Group (Gand et al., 1997) (Fig. 1). It is the sixth insect taxon described from the Lodève Permian basin (Nel et al., 1999a, b, c). The channel siltstone body (Garric, 2000) containing *Raphogla rubra* gen. nov., sp. nov. has supplied also *Lodevia longialata* Nel et al., 1999 which is close to *Permepallage augustissima* Martynov, 1938 from the lowermost Kazanian of Russia (Nel et al., 1999c). It is possible that "le Moural" insect-beds are of same age.

TAXONOMIC PART

In the following study, we follow the nomenclature for wing venation proposed by Sharov (1968) and Gorokhov (1986), except for the replacement of vein names $1MA_1$ by MA1a and $2MA_1$ by MA1b, in order to abbreviate the names of veins in increasing order of specialisation. The nomenclature of the veins of the cubital area is emended as follows: we consider that the most basal posterior branch of MP + CuA1 is not a branch of CuA2 (for explanation see below).

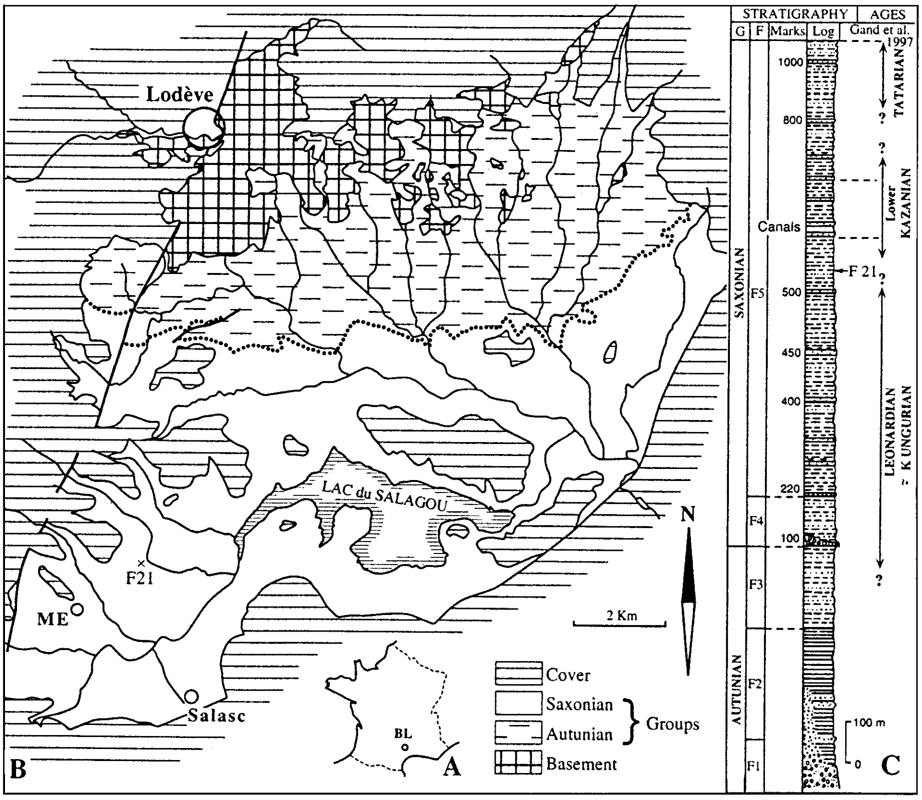

Fig. 1. A – the Lodève basin in France; B – location of the F21 site 'le Moural' in the Lodève Permian basin with *Raphogla rubra* gen. n., sp. n.; C – stratigraphical location of the *Raphogla rubra* n.g., n. sp. level (F21) in the Salagou Formation (Saxonian Group).

Order Orthoptera Olivier, 1789

Suborder Ensifera Chopard, 1920

Family Raphoglidae fam. n.

Included taxa. The type genus *Raphogla* gen. n.

Diagnosis. This family is characterized as follows: (1) vein "C" (*sensu* Gorokhov, 1986) very short; (2) very broad area between anterior margin and Sc; (3) Sc ending on anterior margin well basal of wing apex; (4) RS separates from R far distally; (5) RS moderately long basal of a short fusion with the anterior branch MA1a of MA; (6) a fusion of MP with CuA1; (7) MA2 basally curved towards the anterior branch of MP + CuA1; (8) MP + CuA1 with only one simple anterior branch; (9) MA1 straight; (10) distal origin of MA2. The Raphoglidae are mainly characterised by the unique combination of characters (2), (8), and (5) (a probable plesiomorphy within the clade [Tettigoniidea & Gryllidea]).

Genus *Raphogla* gen. n.

Type species. *Raphogla rubra* sp. n.

Etymology. Recombination of the letters of *Prohagla*.

Diagnosis. That of the family.

Raphogla rubra sp. n.

(Figs 2–3)

Diagnosis. That of the family.

Description (Figs 2, 3). Part and counterpart of an almost complete forewing, probably coriaceous (the postero-proximal part missing). Total length, 36.9 mm, maximum width, 12.5 mm. The fossil is deformed, curved, its apical part being vertical and proximal part horizontal. "C" reaching anterior wing margin at the base of the wing. Branches between "C" and anterior margin numerous and dense. Sc reaching the anterior margin, 9.0 mm before apex. Area between anterior margin and Sc broad, covering about 56% of the length of anterior margin (max. width, 3.5 mm). Sc concave, with numerous anterior concave branches, with convex intercalary veins between them. Branches of Sc irregularly ramified. Cross-veins regularly arranged. Area between Sc and R narrow (almost constant width, 1.0 mm), with cross-veins regularly arranged, more densely in their distal parts. R dividing into RA and RS soon after midwing. RA convex, with two anterior branches, very similar to those of Sc. One posterior branch of RA reaching RS near wing apex. RS long, 2.6 mm long before its fusion with MA1a. Fusion of RS with MA1a short (5.5 mm). RS ramified, with seven branches reaching apical region. Cross-veins regularly arranged in radial area. MP separating from MA at basal third of wing. Base of MA2 4.9 mm distal of base of MP and 4.4 mm basal of division of MA1 into MA1a / MA1b. Common stem of MA1 straight. MA1a very short before its fusion with RS. MA1a and MA1b parallel with the posterior branches of RS. MP + CuA1 with one anterior branch. MA2 directed towards the anterior branch of MP + CuA1, distally abruptly diverging and parallel to MA1b (Fig. 2). Cross-veins in the areas between RS and

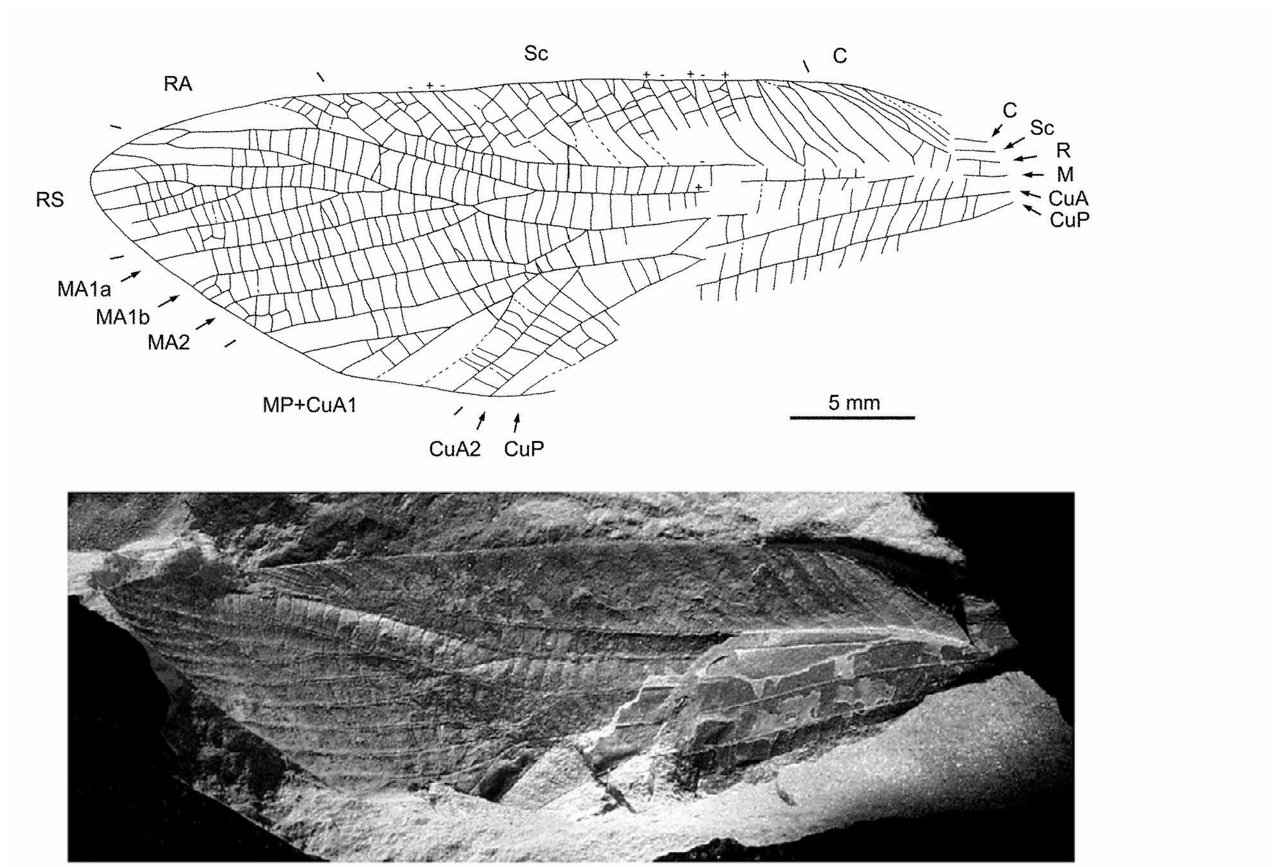

Fig. 2. Forewing, *Raphogla rubra* gen. n., sp. n., holotype specimen Ld LAP 415 B (counterprint). A – reconstruction; B – photograph.

MP / MP + CuA1 regularly arranged, with few reticulations close to posterior wing margin. MA1a, MA1b and MA2 parallel and not ramified. Areas between these veins equally wide in their postero-distal part. MP long basal to its fusion with CuA1. CuA dividing into CuA1 and CuA2 opposite base of MP. MP + CuA1 with five posterior branches and one anterior branch arising distal of first posterior branch of MP + CuA1 (which is not the distal branch of CuA2 *sensu* Sharov, 1968, called 1CuA2 by Gorokhov, 1986, see below). Cross-veins between posterior branches of MP + CuA1 and between CuA2 numerous and denser than in others parts of the wing. CuA2 and CuP apparently not ramified and straight. Anal area not preserved.

Holotype. Specimen Ld LAP 415ab, coll. Lapeyrie, Musée Fleury, Lodève, France.

Geological settings. The fossil was found at the fossiliferous site F21 D located at “Le Moural D”, Salagou Formation, level n° 500, Lodève Basin, Hérault, France (Fig. 1); Lower Kazanian (?), Upper Permian.

Etymology. Term *rubra* after the red colour of the sediment embedding the fossil.

PHYLOGENETIC SIGNIFICANCE

No cladistic analysis of the Ensifera is available that includes both modern and fossil taxa. The works of Sharov and Gorokhov are not based on the principles of consequent Phylogenetic Systematics (*sensu* Hennig, 1966, 1969), as these authors admit paraphyletic taxa and do not base their character polarization on outgroup comparison. We compare *Raphogla* with the groups defined by Sharov and Gorokhov, without any assumption on their monophyly.

The Xenopteroidea *sensu* Gorokhov (1995) are supposed to be the “sister group” of (Oedischioidea & Tettigoniidea & Gryllidea). It must be noted that Gorokhov (1996) grouped Oedischioidea and Xenopteroidea together within an artificial group “Oedischiidea”, and considered them as the “ancestral” group of the Caelifera. Thus, the phylogenetic relationships of the Xenopteroidea, Oedischioidea, and (Tettigoniidea & Gryllidea) are chaotic. The Xenopteroidea differ from *Raphogla* and (Tettigonoidea & Gryllidea) in their MA2 being not bowed, absence of ramifications of the branches of Sc, absence of cross-veins and absence of intercalary convex veins in the area between Sc and anterior margin.

Two characters would exclude *Raphogla* from the families of “Oedischioidea” (without any assumption on the monophyly of this group) that have a fusion of RS with MA1 (several families have not): (1) a broader area between the anterior margin and Sc, with numerous concave branches of Sc and intercalary convex veins; (2) MA2 bowed towards MP + CuA1, instead of being parallel to it in Oedischioidea. curved in Hagloidea). Among

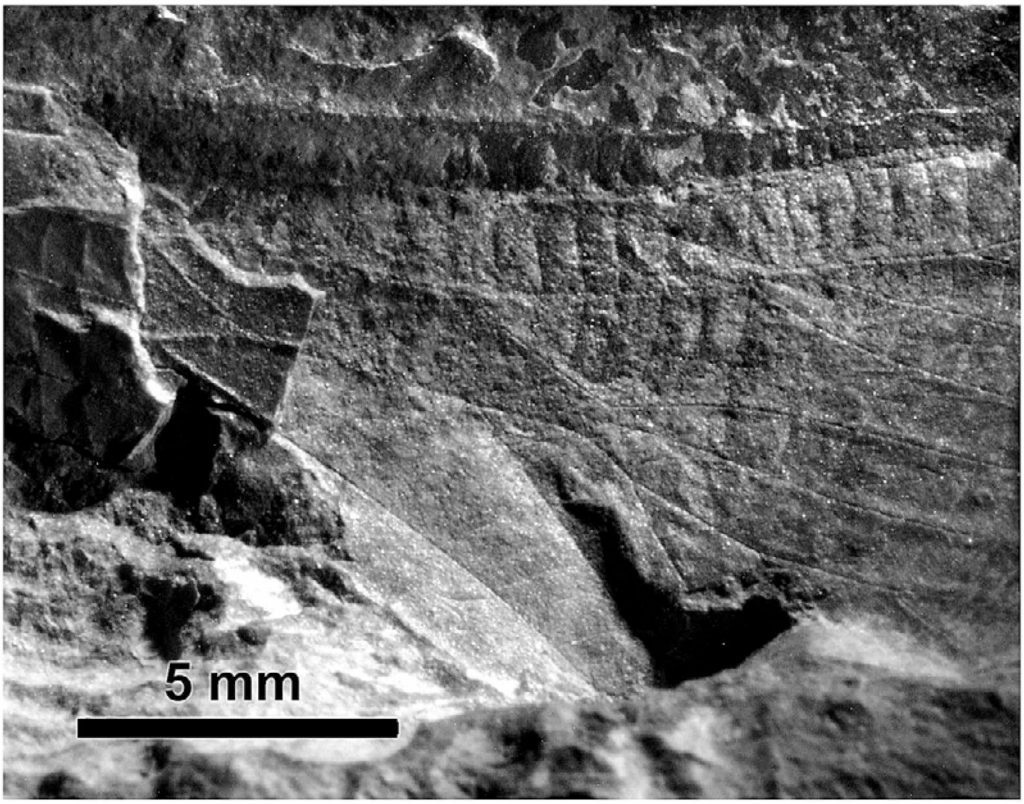

Fig. 3. Photograph of the central region of the forewing. *Raphogla rubra* gen. n., sp. n., holotype specimen Ld LAP 415 A (print).

others, the Pruvostitidae Zalessky, 1929 have a broad costal area with numerous branches and cross-veins but no bowed MA2. The Mesoedischiidae (*Mesoedischia* Sharov, 1968) have a broad costal area but without cross-veins, but no MA2 bowed towards MP + CuA1. Furthermore, in Mesoedischiidae, the CuA1 is fused with MP in a very basal position.

Raphogla shares with all Hagloidea (clearly visible in *Hagla contorta* Riek, 1974, *Archihagla* Sharov, 1968 (see Gorokhov, 1986), *Proisfaroptera martynovi* Sharov, 1968, *Archaboilus shurabicus* Sharov, 1968, *Paracyrtophyllites* Sharov, 1968, *Modihagla* Gorokhov, 1986, *Cantohagla* Gorokhov, 1986, almost all Voliopinae Gorokhov, 1986, etc.), but also with the Gryllidea: Gryllavidae and Protogryllidae (Sharov, 1971; Gorokhov, 1985), the character state "a unique and simple anterior branch of MP + CuA1 (of still undeterminable nature), arising just distal of the first posterior branch of the same vein MP + CuA1". The polarity of this character remains uncertain because of the absence of cladistic analysis of the wing venational characters of the Orthoptera. Nevertheless, this character is absent in "Oedischiidea" *sensu* Gorokhov (1995) and even in Pruvostitidae that would show some resemblance with the Hagloidea, particularly in the area between anterior margin and Sc. This character seems to be present only in *Raphogla*, Hagloidea, Gryllavidae, and Protogryllidae. This vein is difficult to recognize in modern Grylloidea, Stenopelmatoidea and Tettigonioidea because of their highly derived wing venation. Nevertheless, it is present in the fossil Tettigonioidea: Haglotettigoniidae Gorokhov, 1988 (*Haglotettigonia egregia* Gorokhov, 1988, supposed sister group of the Tettigoniidae, after Gorokhov, 1988a, b, 1995) and at least some modern Saginae. Thus, if the attribution of the Haglotettigoniidae to the Tettigonioidea proposed by Gorokhov is correct, this character could be a potential synapomorphy of the (Tettigoniidea + Gryllidea), also present in *Raphogla*, but this assumption can only be tested after a cladistic analysis based on outgroup comparison (and not on ground plan assumptions) (Bethoux & Nel, 2001).

Raphogla can be excluded from the clade Gryllidea (= [Gryllavidae & Gryllidae]) because it has not their synapomorphic character "a very long area of MP + CuA1 nearly reaching the apical region of the wing" (Carpenter, 1992; Gorokhov, 1995). Gorokhov (1995) divided the Hagloidea into Hagloedischiidae Gorokhov, 1986, Tuphellidae Gorokhov, 1988, Haglidae Handlirsch, 1906 & Prophalangopsidae Kirby, 1906.

Raphogla differs from all Hagloidea by a relatively long true fusion of RS with MA1a, which is also present in some Oedischioidea (*Metoedischia* Martynov, 1928, *Elcanoedischia* Gorokhov, 1987 among others). This character is currently considered as "primitive" (Sharov, 1968; Carpenter, 1992; Gorokhov, 1996). This fusion is considered to be lost secondarily, or nearly so, in Hagloidea [≈ Haglidae *sensu* Sharov (1968) or Carpenter (1992)]. In a few taxa, i.e. *Hagloedischia primitiva* Gorokhov, 1986 (Hagloedischiidae), *Hagloptera intermedia* Gorokhov, 1986 and *Proisfaroptera martynovi* Sharov, 1968 (both Haglidae), only a single point of contact is still visible between MA1 and RS. Nevertheless, Sharov (1968) considered that the male "Haglidae" "retain the rudiment of the fusion between the anterior branch MA1 with RS in the form of an oblique vein crossing the cross-veins", as in *Paracyrtophyllites* Sharov, 1968, *Tuphella* Gorokhov, 1986, etc.

Contrary to Gorokhov (1986: 99)'s opinion, it is not obvious that this "oblique vein crossing the cross-veins" is really the rudiment of the branch MA1. It is rather a composite vein obtained by the fusion into a "pseudo-vein" of a set of modified strongly curved cross-veins, similarly to that which occurs for the "pseudo-veins" psm and pscu of the Neuroptera: Chrysopidae (Adams, 1996). The gradation between the two states "separate close cross-veins between MA1 and RS" to "nearly complete fusion between these cross-veins into a pseudo-vein" is illustrated in the hagloid series of taxa: *Phonovoliopus musicus* Gorokhov, 1986 → *Voliopus ancestralis* Gorokhov, 1986 → *Platyvoliopus maximus* Gorokhov, 1986 → *Zeunerophlebia gigas* Sharov, 1968. Note that we do not pretend that this series of taxa has any phylogenetic significance. Furthermore, the alleged female of *Zeunerophlebia gigas* has not this structure (Sharov, 1968). This structure of a "pseudo-vein" between MA and RS is probably a specialization related to a stridulatory apparatus, not homologous to a fusion of MA1 with RS. The presence of a true fusion between RS and MA1 in *Raphogla* suggests that it could hold in a very basal position in the crown group of the Hagloidea.

Furthermore, *Raphogla* differs from all fossil and modern Hagloidea by: (1) its greater distance between the base of MP and the point of division of MA into MA1 and MA2; (2) its straight MA1 (that is: the absence of a lanceolate area); and (3) its non S-shaped CuP.

Raphogla cannot be considered as a Tettigoniidea because it has a fusion of RP with a branch of MA, probably secondarily lost in this group, and its vein 'C' is distinctly shorter than in the Tettigoniidea.

Furthermore, its "RS dichotomous, not pectinated and with numerous (seven) branches" is probably a character state plesiomorphic relative to the situation in both Gryllidea (branches reduced and short) and Tettigoniidea (some have 5 branches). In these groups, either RS has distinctly fewer branches or, when they have many, they are pectinated. In Oedischioidea, RS also has numerous branches, frequently subdivided, as in *Raphogla*. Thus, *Raphogla* does not probably belong to the stem group of the Gryllidea or to that of the Tettigoniidea. Nevertheless, it belongs to the stem group of the (Gryllidea & Tettigoniidea). It could correspond to the sister group of (Gryllidea & Tettigoniidea).

Hagloedischia has also the character "RS dichotomous, not pectinated" but with only four branches: it has a "lanceolate area" (*sensu* Gorokhov, 1995) but not the vein 2CuA2 (*sensu* Gorokhov, 1995; "handle" *sensu* Bethoux & Nel, 2001) (specialized cross-vein between MP + CuA1 and CuA2, see remark below). Thus, it could be in a basal position in the (Gryllidea & Tettigoniidea), even if in a less basal position than *Raphogla*. Gorokhov (1986) made a remark in this connection indicating that the Hagloedischiidae are "primitive" relative to the Hagloidea, which he considered as the "ancestral" group of the Gryllidea and Tettigoniidea.

A future cladistic analysis of the (Tettigoniidea & Gryllidea) is obviously necessary to clarify the phylogenetic relationships within this group. It will have to include *Raphogla* as the first outgroup.

Remark. Problem of the vein 1CuA2 sensu Gorokhov (1986)

Gorokhov (1986) after Sharov (1968), considered that CuA2 has two branches. One he named 1CuA2, directly directed towards the posterior wing margin and the second, named 2CuA2, directed towards MP + CuA1, fused with this vein and separated again to constitute the most basal posterior branch of MP + CuA1. In *Raphogla* (see description below and Fig. 1–2) and *Hagloedischia*, there is no division of CuA2 into a posterior branch and an anterior branch that would be directed towards MP + CuA1. The same situation occurs in all the "Oedischioidea", considered as "primitive" by Gorokhov (1996). Therefore, the putative division of CuA2 into two branches is not in the "ground-plan" of the (Tettigoniidea & Gryllidea). It is more likely that the vein between CuA2 and MP + CuA1 interpreted by Gorokhov and Sharov as a branch of CuA2 is a modified cross-vein related to the male sound apparatus, as it is absent in all known female Hagloidea. Note that the closure of the lanceolate area is obtained due to a similar phenomenon, clearly visible in Voliopinae (see discussion above).

CONCLUSION

This new fossil yields us information about the "primitive" states of the whole infraorder Tettigoniidea, and its deep antiquity. The study also allows the emendation of the wing venational terminology. Unfortunately, the phylogenetic relationships within and between the different groups remain unclear, especially with respect to the origin of the (Tettigoniidea & Gryllidea).

The discovery of a taxon belonging to the stem group of the (Tettigoniidea & Gryllidea) supports the presence of derived Tettigoniidea and Gryllavidae in the Lower/Middle Triassic (Sharov, 1968; Papier et al., 1997, 2000).

Hagloedischia (Madygen, Middle / Upper Triassic; Gorokhov, 1986) may also lie in a very basal position within the (Tettigoniidea & Gryllidea), although less so than *Raphogla*. *Hagloedischia* appears to be a "relic" taxon for the Middle / Upper Triassic.

The evolution of the biodiversity of this group, throughout the PT transition, remains mainly unresolved. The only sure conclusion is that the (Tettigoniidea & Gryllidea) were already present before the transition. A rapid diversification of this group may have occurred during the Lower Triassic.

ACKNOWLEDGEMENTS. This paper is a contribution to the project "Paléontologie et Biostratigraphie du Permien" of the UMR 5554 of CNRS: "Biogéosciences" and the "UPRES" project "Systématique et crises de la biodiversité chez les insectes" in the Laboratoire d'Entomologie du Muséum National d'Histoire Naturelle, Paris. This work was supported by the UMR 5120 and 5554 of CNRS and by a grant "Germaine Cousin" of the Société Entomologique de France.

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Received January 12, 2001; revised June 30, 2001; accepted August 31, 2001