

Perforissidae (Hemiptera: Fulgoroidea) from the Lower Cretaceous San Just amber (Eastern Spain)

Enrique PEÑALVER^{1,*} & Jacek SZWEDO²

¹Instituto Geológico y Minero de España, Ríos Rosas 23, 28003 Madrid, Spain.

E-mail: e.penalver@igme.es

² Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, PL 00-679 Warszawa, Poland.

E-mail: szwedo@miiz.waw.pl

*Corresponding author

ABSTRACT

A new genus, *Iberofoveopsis* gen. nov., and its type species *Iberofoveopsis miguelesi* sp. nov., belonging to the extinct family Perforissidae Shcherbakov, 2007 (Hemiptera: Fulgoroidea), are described on the basis of a female specimen. This new perforissid is preserved in Lower Cretaceous (Albian) amber from the San Just outcrop of Teruel Province, Eastern Spain. The Perforissidae, a recently described family, contains six genera recorded from the New Jersey, Taimyr, Burmese, and Spanish ambers, and laminated sedimentary rocks of Mongolia. The new genus mainly differs from the five previously described taxa in tegmine venation, features of the ovipositor, and the abundance and distribution of sensory pits on head and pronotum.

KEY WORDS: Hemiptera. Fulgoroidea. Perforissidae. New genus and species. Amber. Cretaceous. Spain.

RESUMEN

Iberofoveopsis gen. nov. perteneciente a la extinta familia Perforissidae Shcherbakov, 2007 (Hemiptera: Fulgoroidea) y su especie tipo *Iberofoveopsis miguelesi* sp. nov. son descritos a partir de un ejemplar hembra. El nuevo perforísido está conservado en ámbar del Cretácico temprano (Albiense) del yacimiento de San Just en la provincia de Teruel (Este de España). La familia Perforissidae, recientemente descrita, cuenta actualmente con seis géneros hallados en ámbar de New Jersey, Taimyr, Birmania (Myanmar) y España, y en rocas laminadas de Mongolia. El nuevo género principalmente difiere de los cinco anteriormente conocidos en la venación del tegmen, el ovipositor y en la abundancia y distribución de depresiones sensoriales en la cabeza y el pronoto.

PALABRAS CLAVE: Hemiptera. Fulgoroidea. Perforissidae. Nuevo género y especie. Ámbar. Cretácico. España.

INTRODUCTION

In 2007, Shcherbakov described a new family of Cretaceous planthoppers, the Perforissidae, which previously comprised two subfamilies and five monospecific genera, based on fossils from the Taimyr, New Jersey and Burmese ambers, and laminated sedimentary rocks of Mongolia (Shcherbakov 2007).

A new specimen belonging to this family was found in 2007 during a palaeontological excavation in the amber-bearing locality named San Just, located in the Utrillas-Escucha area of Eastern Spain (see Peñalver et al. 2007, Delclòs et al. 2007).

The main outcrops of amber in the Utrillas-Escucha area are located along the northern margin of the Aliaga sub-basin, one of the Mesozoic sub-basins described by Salas & Guimerà (1997) as forming part of the Maestrat Basin (northeast of Spain). The Maestrat Basin was originated by listric faults during the Late Oxfordian-Albian interval (Salas et al. 2001). Amber with insect inclusions has been

found in a one-metre thick bed of grey-black claystones, which underlies a sandstone stratum and also contains abundant plant remains. Stratigraphically, the site occurs within the La Orden Member of the Albian Escucha Formation, deposited in a fluvial delta plain environment (Querol et al. 1992). Based on palynology, Peyrot et al. (2007) indicated a late Aptian-early Albian age for the basal part of the Escucha Formation in the Maestrat Basin. More recently, Moreno-Bedmar et al. (2008) used ammonoids to limit this age, indicating that Maestrat Basin depocentre is Lower Albian in age.

As the fossil shows unique characteristics, we describe it herein as a new genus and species. The small amber fragment containing the planthopper was embedded in epoxy resin using the procedure described in Corral et al. (1999). Drawings and photos presented in this paper were made using an Olympus BX51 microscope and an Olympus V-DA camera lucida.

Wing nomenclature follows the modified interpretations of Emeljanov (1977), Dworakowska (1988), and Anufriev & Emeljanov (1988).

SYSTEMATIC PALAEOLOGY

Order: Hemiptera Linnaeus 1758

Suborder: Fulgoromorpha Evans 1946

Superfamily: Fulgoroidea Latreille 1807

Family: Perforissidae Shcherbakov 2007

Subfamily: Cixitettiginae Shcherbakov 2007

GENUS *Iberofoveopsis* gen. nov.

Type species: *Iberofoveopsis miguelesi* sp. nov.

Diagnosis: Costal margin of tegmen widened at base, gibbous in basal portion (costal margin gibbous about midlength in *Foveopsis*); costal cell wide distally (costal cell very narrow distally in *Foveopsis*); stem Sc+R leaves basal cell with a very short stalk. Stems M and CuA leave basal cell with a short common stalk, distinctly shorter than arculus (stalk of Sc+R about as long as arculus in *Foveopsis*); branch CuA₂ forked slightly apicad of claval apex, branch CuA_{2a} forked apicad of apical line of veinlets (CuA_{2a} simple in *Foveopsis*); clavus closed and claval apex angulate (clavus open in other Perforissidae); ovipositor very long, slightly longer than half hind tibia length (ovipositor in *Foveopsis* is shorter compared to new genus, and it is clearly shorter than half hind tibia length).

Etymology: Combination of prefix “ibero” in reference to the Bronze Age inhabitants of southern and eastern Spain (where the type locality is located), who later gave their name to the whole Iberian Peninsula with *Foveopsis*, the most similar genus within the Cixitettiginae. Gender: feminine.

Discussion: This new genus belongs to the subfamily Cixitettiginae Shcherbakov, 2007 based on the presence of hind tibia, first and second tarsomeres with uniserial apical pectens, and the tegmen costal margin gibbous basally, as opposed to at midlength. A gibbous costal margin is typical of representatives of the subfamily Perforissinae Shcherbakov, 2007, but is also present in the genus *Foveopsis* Shcherbakov, 2007. Cixitettiginae now contains four genera from the Taimyr, Burmese, and Spanish ambers, and from sedimentary rocks of Mongolia. The most similar genus to *Iberofoveopsis* gen. nov. within the Cixitettiginae is *Foveopsis* (from Burmese amber).

Iberofoveopsis miguelesi sp. nov.

Figure 1; Plate 1

2007 Homoptera Cicadomorpha, Delclòs et al.: p. 144, fig. 4B

Holotype: Alate specimen CPT-4132, female, deposited in the Fundación Conjunto Paleontológico de Teruel-Dinópolis (Teruel, Spain). Specimen complete (Fig. 1)

associated with the following syninclusions: four dipterans (CPT-4151–4154), five hymenopterans (CPT-4076, CPT-4077, CPT-4088, CPT-4089 and CPT-4126), and a fragment of spider web in contact with the holotype. The holotype was isolated within a small piece of transparent amber (5 x 3 x 3 mm) and embedded in a regular prism (piece 13 x 3 x 3 mm) of epoxy resin for optimal viewing. It was possible to study the specimen in dorsal, ventral, lateral and frontal views.

Etymology: Named in memoriam of Mr. Miguel Ángel González Míguez “Migueles”.

Type locality: San Just outcrop, in the municipality of Utrillas, near the village of Escucha (Teruel Province, Spain) (Peñalver et al. 2007).

Stratum typicum: The amber-bearing strata are included within the Escucha Formation of the Maestrat Basin. These strata consist of carbonaceous lutites deposited in deltaic and estuarine environments, and are Lower Cretaceous (Lower Albian) in age (Peñalver et al. 2007, Delclòs et al. 2007).

Diagnosis: As for the genus. Additional character: tibio-metatarsal formula 9 : 7 : 7.

Description: Adult female (Pl. 1, fig. A). Total length about 3.93 mm. Head (including compound eyes) about as wide as pronotum, c. 0.91 mm; vertex short, about 4.5 times as wide as long in mid line, partly covered by the anterior margin of pronotum; compound eyes bulging laterally. Frons slightly wider (c. 0.52 mm) than long along mid line (c. 0.48 mm), with distinct median carina, median carina protruded, slightly arched in lateral view; lateral margins carinate, slightly sinuous in lower portion; each half of frons with 16 large sensory pits (upper-median group contains 12 pits, smaller the external-lateral ones, and lower group contains 4 pits; Fig. 1A – median). Postclypeus slightly longer than frons in mid line (c. 0.56 mm), with median carina and lateral carinae, slightly produced in lower portion (Fig. 1A – right), median carina and lateral carinae of postclypeus exceeding to anteclypeus. Antennal scapus short, pedicel subcylindrical, covered with short setae, flagellum 0.37 mm long. Rostrum c. 0.35 mm long, reaching hind coxae, apical segment slightly shorter (c. 0.15 mm) than subapical one.

Pronotum about as wide as head (including compound eyes), c. 0.91 mm, c. 0.39 mm long along mid line (c. 0.52 mm long in total), with anterior margin distinctly arcuate, distinctly produced over head, posterior margin shallowly incised; median carina of pronotum distinct; 29 sensory pits on each half of disc (Fig. 1A – left); lateral lobes of pronotum rounded, declivous, with group of 6 sensory pits.

Mesonotum in mid line distinctly longer (c. 0.61 mm) than pronotum in mid line, with obscure lateral carinae and 3 sensory pits laterad of lateral carinae (Fig. 1A – left).

Tegula small.

Wings overlapping: hind wings folded and obscured (Pl. 1, fig. C). Tegmen 3.3 times as long as wide (3.3 mm long, 1 mm wide), with narrow appendix; unicolorous, veins delicately granulate (Pl. 1, fig. D), and polygonal reticulated

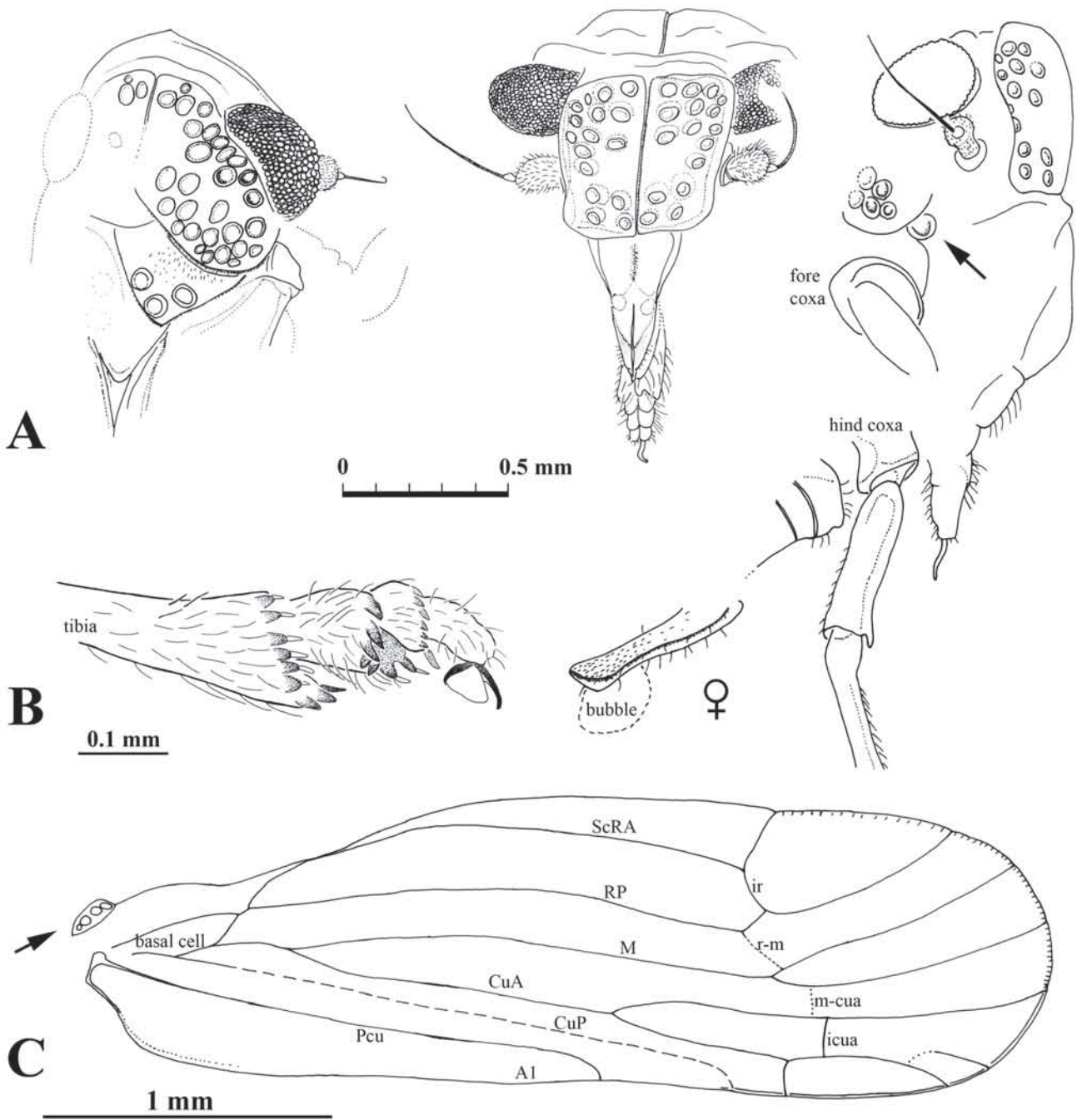


Figure 1. Camera lucida drawings of *Iberofoveopsis miguellesi* gen. et sp. nov. (Perforissidae: Cixitettiginae) from the Lower Cretaceous amber of San Just, Eastern Spain (Holotype: CPT-4132). A) From left to right, head in dorsal, frontal (rostrum in oblique view) and lateral views, also showing the visible portion of the abdomen and the ovipositor; arrow indicates the location of a large sensory pit close to the fore coxa and pronotum. B) Distal hind tibia and tarsomeres (oblique view). C) Tegmen (dotted line indicates poorly preserved veins); arrow near base indicates the position of a small plate with four pits, apparently of sensorial function.

sculpture on dorsal portion of the wing membrane (Pl. 1, fig. E). Costal margin widened at base, sinuate sub-basally; basal cell elongate, about 4 times as long as wide; stem Sc+R leaving basal cell with a short stalk; branch ScRA not forked before apex, curved and subparallel to costal margin; branch RP not forked before apex; stems M and CuA leaving basal cell with a short common stalk (slightly shorter than basal cell); stem M not forked up to level of nodal line, stem CuA forked slightly apicad of claval veins junction,

branch CuA₁ simple, branch CuA₂ forked slightly apicad of claval apex, branch CuA_{2a} forked in apical portion, apicad of *icua* veinlet. Clavus long, apex of clavus reaching $\frac{2}{3}$ of tegmen length, claval apex angulate, clavus closed; claval veins Pcu and A₁ fused at $\frac{4}{5}$ of clavus length. Veinlet *ir* at level of nodal line, veinlet *r-m* oblique, at level of nodal line, apparently reaching M₁₊₂ branch (portion obscured), veinlet *m-cua* at level of nodal line, connecting branches M₃₊₄ and CuA₁, one veinlet *icua* almost at the same level.

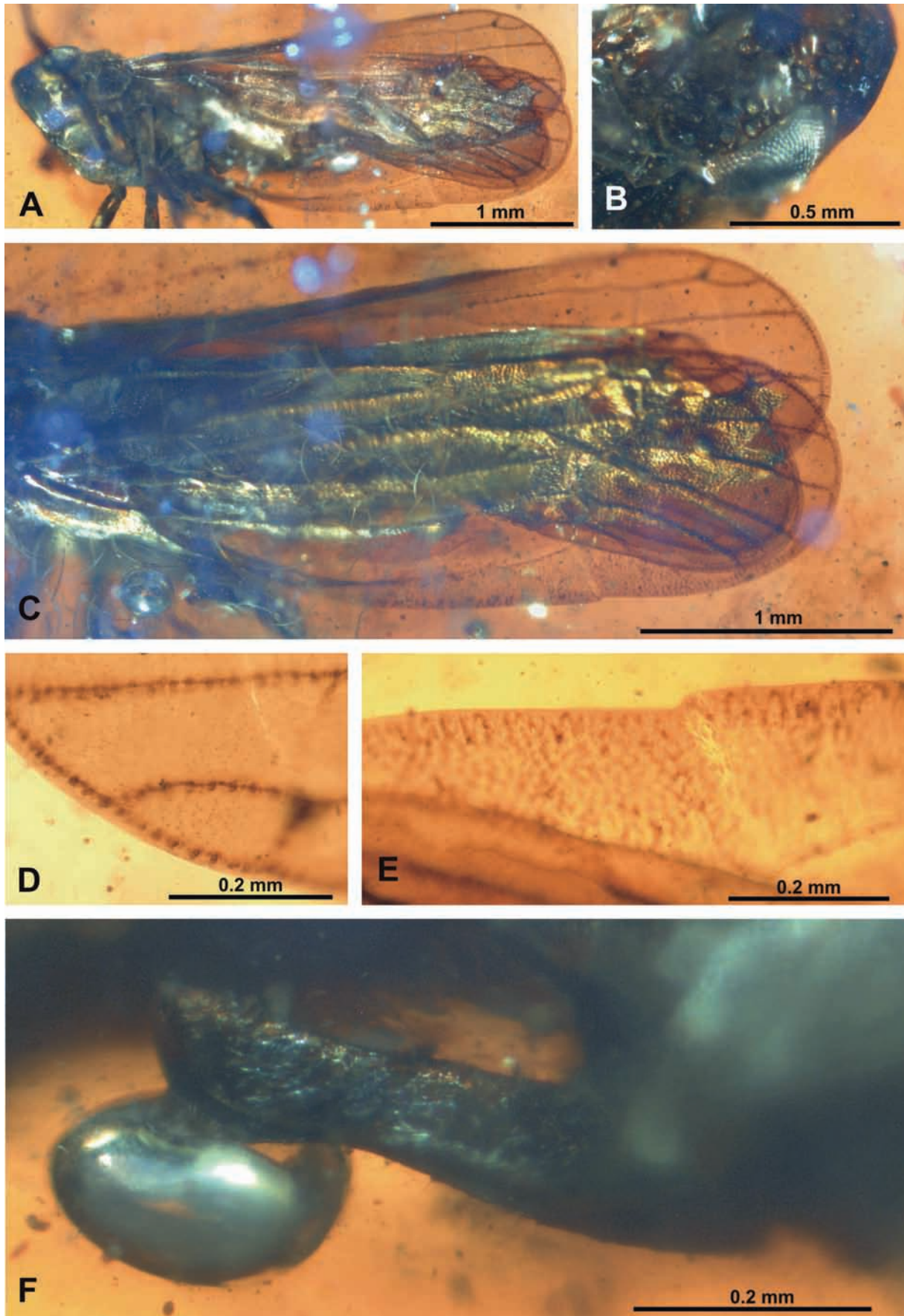


Plate 1. Photomicrographs of *Iberofoveopsis miguelesi* gen. et sp. nov. (Perforissidae: Cixitettiginae) from the Lower Cretaceous amber of San Just, Eastern Spain (Holotype: CPT-4132). A) Habitus in lateral view. B) Dorsal view of the head showing sensory pits. C) Tegmen. D) Detail of the granulate veins at the ventral apex of the tegmen. E) Detail of the polygonal reticulated sculpture at the tegmen's dorsal margin. F) Genitalia.

Legs – Fore leg 1.5 mm long, fore femur about as long as fore tibia, fore tibia subquadrate in cross section, merely widened apicad, length of fore tarsomeres: I 0.14 mm, II 0.09 mm, III 0.09 mm, tarsal claws and arolium distinct. Mid femur 0.6 mm long, mid tibia subquadrate in cross section, merely widened apicad: tarsal claws and arolium as in fore leg. Hind legs slender, 1.8 mm long with uniserial tibial and tarsal apical pectens; hind tibia 0.96 mm long, widened apicad, apical row of at least 9 teeth with subapical setae (Fig. 1B). Basitarsomere 0.16 mm long with at least 7 apical setigerous teeth, about as long as combined length of mid and apical tarsomeres; midtarsomere 0.09 mm long, with at least 7 apical setigerous teeth; apical tarsomere longer than mid tarsomere (0.14 mm) with distinct claws and wide arolium (Fig. 1B). Tibio-metatarsal formula 9 : 7 : 7.

Abdomen not visible, approximately as long as ovipositor.

Ovipositor ensiform, straight and very long (Fig. 1A –right- & Pl. 1, fig. F), not addressed to pygofer, slightly longer than half of hind tibia, 0.58 mm long, 0.11 mm wide. Gonoplasts fused in dorsal portion forming a tube or sheath opened in ventral margin.

DISCUSSION

This new genus, *Iberofoveopsis*, differs from other Perforissidae in having a closed clavus, i.e. joined veins $Pcu+A_1$, which reach the margin of the tegmen basad of claval apex. Apart of the diagnostic characters, the new genus differs from *Foveopsis*, the most similar genus of Cixitettiginae, in having 29 (as opposed to 17) sensory pits on each half of the pronotum disc, and in having a mesonotum with three sensory pits at different positions. *Iberofoveopsis* gen. nov. differs from the genera *Cixitettix* and *Tsaganema* in the shape of tegmen, which is gibbous with a sub-basal concavity (unicolorous and not gibbous in *Cixitettix* and *Tsaganema*), and in the abundance and distribution of sensory pits in the head and pronotum. In respect to other characters: in *Cixitettix* the stems Sc+R, M and CuA leave the basal cell separately and the posterior margin of the pronotum is deeply incised: in *Tsaganema*, the costal area is very narrow distally, and the ovipositor is longer than hind tibia and addressed to the pygofer.

Two structures figured and marked with arrows (Fig. 1) call for further discussion. The huge sensory pit at base of *Iberofoveopsis*' fore coxa, near the lower margin of pronotum (Fig. 1A – right) could be related to the pits present on head, pronotum and mesonotum; that is, it could be a proprioceptor or have a hygroreceptive function. However, there are no setae visible. Another similar structure is figured on Figure 1C and appears as a plate with a few sensory pits. It is unclear if this structure is part of the tegmen base or part of the thorax. These pits differ in shape from sensory pits on the body. Sensory pits with seta at the tegmen costal margin are present in the recent genus *Borysthenes* Emeljanov, 1989 (Cixiidae: Borystheninae). However, no setae are visible on these pits of the fossil specimen. On the other hand, some Fulgoroidea have this basal portion of

the tegmen thickened, with the base of costal complex of veins, i.e. CA and composed Pc+CP, shifted to form a distinct area. When discussing this portion of tegmen, Dworakowska (1988) defined the lateral surface of these composite veins as an “epipleuron” by analogy with the corresponding structure on beetle elytra. In most of the Fulgoroidea, the precosta (Pc) is quite low and forms the lowest part of this epipleuron. Of the three costal complex veins, the costa posterior (CP) is the only vein which contains costal nerve and costal trachea as well as a haemolymph channel. All sensillae associated with Pc and CA are innervated by the costal nerve and costal trachea applies to the tracheation (Dworakowska 1988). As such, the structure present on the base of tegmen of *Iberofoveopsis* gen. nov. may be related to this complex of veins, or “epipleuron”.

The other possibility is that this sensory structure is a part of the thorax sternite, but the function of these pits remains unclear (hygroreceptors or proprioceptors?).

As previous specimens of Perforissidae have been found in the Cretaceous deposits of Asia and North America, this discovery extends the distribution of the family to Europe. As originally defined, the Perforissidae contained two subfamilies: Perforissinae Shcherbakov, 2007 with *Perforissus muiri* Shcherbakov, 2007 from the Upper Cretaceous New Jersey amber and *Cretargus emeljanovi* Shcherbakov, 2007 from the Upper Cretaceous Taimyr amber; and Cixitettiginae Shcherbakov, 2007, comprising *Cixitettix yangi* Shcherbakov, 2007 from the Upper Cretaceous Taimyr amber, *Foveopsis fennahi* Shcherbakov, 2007 from the Lower Cretaceous Burmese amber and *Tsaganema oshanini* Shcherbakov, 2007 from the Lower Cretaceous of Mongolia (Shcherbakov 2007). Forms belonging to this family are also recorded in the Lower Cretaceous Lebanese and Jordanian ambers (Kaddumi 2007).

Shcherbakov (2007) interpreted Perforissidae as a neotenuous offshot of the common ancestors of all recent Fulgoroidea, i.e. the Jurassic paraphyletic family Fulgoridiidae. Placement of the Perforissidae is not fully clear, as both nymphs and adults are highly derivative; however, preliminary analysis of the nymphal and imaginal characters of the Cretaceous families Perforissidae, Mimarachnidae and Neazoniidae allowed the Perforissidae to be placed close to the Cixiidae and Delphacidae, with this lineage related to the Neazoniidae and Kinnaridae + Meenoplidae lineage. On the other hand, the Perforissidae shares some features with Mimarachnidae, e.g. type of tegmen venation, and presence of sensory pits in imagines (Szwedo 2009). Features shared by Perforissidae, Cixiidae and Delphacidae, and Kinnaridae + Meenoplidae e.g., sensory pits on the face arranged in rows, nymphal metatarsal segments with more than three apical teeth seem to be the plesiomorphic condition, according to Emeljanov (2001). On the other hand, the presence of sensory pits on the meso- and metanotum could be treated as a synapomorphy for the group of families (Szwedo 2009). Sensory pits are specific organs in fulgoroid larvae and are very rare in adults (Emeljanov 2001), usually placed on head and thorax. Gnezdilov & Wilson (2007) also described sensory pits on abdominal sternites in some genera of the

Nogodinidae tribe Mithymini. Similar analogous sensory organs are also known for the Cixiidae (Bennini Metcalf, 1938 and Bennarellini Emeljanov, 1989), Achilixidae (Achilixinae Muir, 1923 and Bebaiotinae Emeljanov, 1991), and Tropiduchidae (*Alleloplasis* Waterhouse, 1839). Emeljanov (2001) suggested that sensory pits arranged in rows, with setiform sensilla directed to adjoining carina, is the plesiomorphic condition of Fulgoroidea as a whole. Contrary to this, Gnezdilov & Wilson (2006) suggested that the lack of sensillae on the sensory pit border may be treated as a plesiomorphic character. As such, more data must be collected and more detailed morphological and ultrastructural studies are necessary to resolve these contradictory interpretations.

Shcherbakov (2007) also stated that the Perforissidae were an early attempt to construct leafhopper-like forms from planthoppers essentially quasi-leafhoppers as a response to the colonization of the earliest angiosperms (or proangiosperms) in coastal-littoral environments. Multiple sensory pits in adults and nymphs indicate that the Perforissidae inhabited biotopes with highly variable and/or extreme humidity. The Perforissidae (both adults and nymphs) look more “leafhopper-like” than any other planthopper group with exception of the Tettigometridae. It could therefore be speculated that they lived on low herbaceous and/or cheirolepidiaceae plants (Shcherbakov 2007). Evolution of the proangiosperms into angiosperms (angiospermization) is considered to have been ruled by neoteny (Ponomarenko 1998), like that of their presumed trophic associates, the Perforissidae. Perforissidae presumably became extinct by being outcompeted by the Cicadellidae, which are known since the Early Cretaceous (Shcherbakov & Popov 2002). Another possible cause for their extinction is that they were trophically associated with groups of early angiosperms or proangiosperms which did not survive into the Cenozoic (Szwedo 2009).

ACKNOWLEDGMENTS

We thank Rafael López del Valle (Museo de Ciencias Naturales de Álava) for his help. We are grateful to Dr. Sarah K. Martin (Monash University, Clayton) for improving the English of the manuscript, and Dr. Antonio Arillo (Complutense University of Madrid) and Dr. André Nel (MNHN, Paris) for careful reviews of the manuscript. We also wish to express our gratitude to the “Dirección General de Patrimonio Cultural del Gobierno de Aragón” and the “Fundación Conjunto Paleontológico de Teruel-Dinópolis” for their efforts and promotion of the study of the San Just amber. “Caja Rural de Teruel” partially sponsored a paleontological excavation. The first author receives support from a “Ramón y Cajal” contract of the Spanish Ministry of Science and Innovation. The second author benefitted from a visit to the MNHN, supported by the SYNTHESYS FR-TAF-1266 Project, financed by European Community Research Infrastructure Action under Program FP6 “Structuring the European Research Area”. This study is a contribution to project CGL2008-00550/BTE: “The Cretaceous amber of Spain: a multidisciplinary study”, of the Spanish Ministry of Science and Innovation.

REFERENCES

- ANUFRIEV, G.A. & EMELJANOV, A.F. 1988. Podotryad Cicadinea (Auchenorrhyncha) – tsikadovye. *In*: Ler, P.A. (Ed.), *Opredelitel' nasekomykh Dalnego Vostoka SSSR*. Vol. 2. Nauka, Leningrad, 12–495. [Suborder Cicadinea (Auchenorrhyncha). *In*: Ler, P.A. (Ed.), *Keys to insects of the USSR Far East*. Vol. 2. Nauka, Leningrad: 12–495.] [In Russian].
- CORRAL, J.C., LÓPEZ DEL VALLE, R. & ALONSO, J. 1999. El ámbar cretácico de Álava (Cuenca Vasco-Cantábrica, norte de España). Su colecta y preparación. *Estudios del Museo de Ciencias Naturales de Álava*, 14 (Publicación especial, número 2): 7–21.
- DELCLÒS, X., ARILLO, A., PEÑALVER, E., BARRÓN, E., SORIANO, C., LÓPEZ DEL VALLE, R., BERNÁRDEZ, E., CORRAL, C. & ORTUÑO, V.M. 2007. Fossiliferous amber deposits from the Cretaceous (Albian) of Spain. *Comptes Rendus Paleovol*, 6: 135–149.
- DWORAKOWSKA, I. 1988. Main veins of the wings of Auchenorrhyncha. *Entomologische Abhandlungen Staatliches Museum für Tierkunde Desden*, 52: 63–108.
- EMELJANOV, A.F. 1977. Gomologia krylovykh struktur u tsikadovykh i primitivnykh Polyneoptera. Nomenklatura i gomologia zhilok u nasekomykh. [Homology of wing structures in Cicadina and primitive Polyneoptera. Terminology and homology of venation in insects.] *Trudy Vsesoyuznogo Entomologicheskogo Obshchestva*, 58: 3–48. [In Russian].
- EMELJANOV, A.F. 2001. Larval characters and their ontogenic development in Fulgoroidea (Cicadina). *Zoosystematica Rossica*, 9 (1): 101–121.
- GNEZDILOV, V.M. & WILSON, M.R. 2006. Systematic notes on tribes in the family Caliscelidae (Hemiptera: Fulgoroidea) with the description of new taxa from Palaearctic and Oriental Regions. *Zootaxa*, 1359: 1–30.
- GNEZDILOV, V.M. & WILSON, M.R. 2007. A new genus and a new species of the tribe Mithymnini (Hemiptera: Fulgoromorpha: Nogodinidae) from Namibia, with sternal sensory pits in the adult. *Zootaxa*, 1453: 55–62.
- KADDUMI, H.F. 2007. Amber of Jordan: the oldest prehistoric insects in fossilized resin. 3rd edition. Eternal River Museum of Natural History: 168 pp.
- MORENO-BEDMAR, J.A., BULOT, L., LATIL, J.L., MARTÍNEZ, R., FERRER, O., BOVER-ARNAL, T. & SALAS, R. 2008. Precisiones sobre la edad de la base de la Fm. Escucha, mediante ammonioideos, en la subcuenca de la Salzedella, Cuenca del Maestrat (E Cordillera Ibérica). *Geo-Temas*, 10: 1269–1272.
- PEÑALVER, E., DELCLÒS, X. & SORIANO, C. 2007. A new rich amber outcrop with palaeobiological inclusions in the Lower Cretaceous of Spain. *Cretaceous Research*, 28: 791–802.
- PEYROT, P., RODRÍGUEZ-LÓPEZ, J. P., LASSALETTA, L., MELÉNDEZ, N. & BARRÓN, E. 2007. Contribution to the palaeoenvironmental knowledge of the Escucha

- Formation in the Lower Cretaceous Oliete Subbasin, Teruel, Spain. *Comptes Rendus Palevol*, 6: 649–481.
- PONOMARENKO, A.G. 1998. Paleobiology of angiospermization. *Paleontological Journal*, 32: 325–331.
- QUEROL, X., SALAS, R., PARDO, G. & ARDEVOL, L. 1992. Albian coal-bearing deposits of the Iberian Range in northeastern Spain. pp 193–208. In P.J. McCabe & J.T. Parrisch (eds.), *Controls on the Distribution and Quality of Cretaceous Coals*. Geological Society of America. Special Paper 267; Boulder, Colorado.
- SALAS, R. & GUIMERA, J. 1997. Estructura y estratigrafía secuencial de la cuenca del Maestrazgo durante la etapa de rift Jurásica superior-Cretácica inferior (Cordillera Ibérica Oriental). *Boletín Geológico y Minero*, 108: 393–402.
- SALAS, R., GUIMERA, J., MAS, R., MARTÍN-CLOSAS, C., MELÉNDEZ, A. & ALONSO, A. 2001. Evolution of the Mesozoic Central Iberian Rift System and its Cainozoic inversion (Iberian chain). pp. 145–185. In P.A. Ziegler, W. Cavazza, A.H.F. Robertson & S. Crasquin-Soleau (eds.), *Peri-Tethys Memoir 6: Peri-Tethyan Rift/Wrench Basins and Passive Margins*. Mémoires du Muséum National d'Histoire Naturelle, Paris.
- SHCHERBAKOV, D.E. 2007. An extraordinary new family of Cretaceous planthoppers (Homoptera: Fulgoroidea). *Russian Entomological Journal*, 16 (2): 139–154.
- SHCHERBAKOV, D.E. & POPOV, YU.A. 2002. 2.2.1.2.5. Superorder Cimicidea Laicharting, 1781 Order Hemiptera Linné, 1758. The bugs, cicadas, plantlice, scale insects, etc. (= Cimicida Laicharting, 1781, = Homoptera Leach, 1815 + Heteroptera Latreille, 1810), in RASNITSYN A.P. & QUICKE D.L.J. (eds), *History of Insects*. Kluwer Academic Publishers, Dordrecht: 143–157.
- SZWEDO, J. 2009. First discovery of Neazoniidae (Insecta, Hemiptera, Fulgoromorpha) in the Early Cretaceous amber of Archingeay, SW France. *Geodiversitas*, 31 (1): 105–116.

Received: 27th August 2009

Accepted: 30th September 2009