

First Cenomanian record of insects in the Southern Hemisphere, with Perforissidae (Fulgoroidea) and Cupedidae (Coleoptera) from Southern Patagonia, Argentina



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ABSTRACT

The discovery of the southernmost world record (49.5°S) of a Late Cretaceous insect fauna and plant-insect interactions is reported herein. The new locality is from the middle Cenomanian lacustrine deposits of the Mata Amarilla Formation belonging to the Austral foreland Basin, southwest Patagonia, Argentina. A first trip to the locality yielded few specimens of Coleoptera, among them an Archostemata: Cupedidae, and also a tiny specimen of Fulgoroidea: Perforissidae represented by *Aonikenkissus zamunerae* gen. et sp. nov. The Perforissidae were previously recorded from the Berriasian (?)–Barremian, Aptian, Albian, Turonian and Santonian in the Northern Hemisphere. The new species represents the first record of Perforissidae for South America and for the whole Southern Hemisphere. The new record suggests that the Perforissidae had a broader biogeographical distribution, and seem to have been cosmopolitan in the mid-Cretaceous. The Cupedidae reported herein is the first record for the Cenomanian and the first record of the genus *Zygadenia* in South America. Insect traces found in the same strata are made in an angiosperm palmatilobed leaf and correspond to a piercing and sucking type of damage. This type of damage is compared to recent stippling and to isolated piercings.

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1. Introduction

The discovery of the southernmost world record (49.5°S; palaeolatitude $\approx 54^\circ$) of a Late Cretaceous insect fauna and plant-insect interactions is reported herein. The insects and traces were found in lacustrine deposits of the Mata Amarilla Formation that belongs to the Austral foreland Basin (=Magallanes Basin) in southwest Patagonia (Feruglio in Fossa Mancini et al., 1938; Leanza, 1972) (Fig. 1). This formation has a rich fauna of both marine invertebrates (Ihering, 1907; Wilckens, 1907; Feruglio, 1936; Riccardi,

1984a; 1984b; 2002; Riccardi and Rolleri, 1980; Riccardi et al., 1987; Griffin and Varela, 2012) and marine and continental vertebrates as crocodiles, turtles, theropods, plesiosaurs and sauropod dinosaurs (Goin et al., 2002; Lacovara et al., 2004; Novas et al., 2004a, 2004b, 2005, 2008; Cione et al., 2007; O’Gorman and Varela, 2010). It is also known for the richness in plants, especially unusual early angiosperm dominant floras (Berry, 1928, 1937; Frenguelli, 1953; Iglesias et al., 2007, 2009; Zamuner et al., 2004).

The Mata Amarilla Formation is considered as Cenomanian-Coniacian by Riccardi and Rolleri (1980) based on ammonites found in associated marine facies. Recently, precise U-Pb dating using laser ablation in zircons from continental facies from the middle section of the formation, gave 96.23 \pm 0.71 Ma in a tuff horizon about 28 meters above of the corresponding horizon where the insect and interactions were found (Varela, 2011; Varela et al., 2012a). On that basis, the new fossil record could be well

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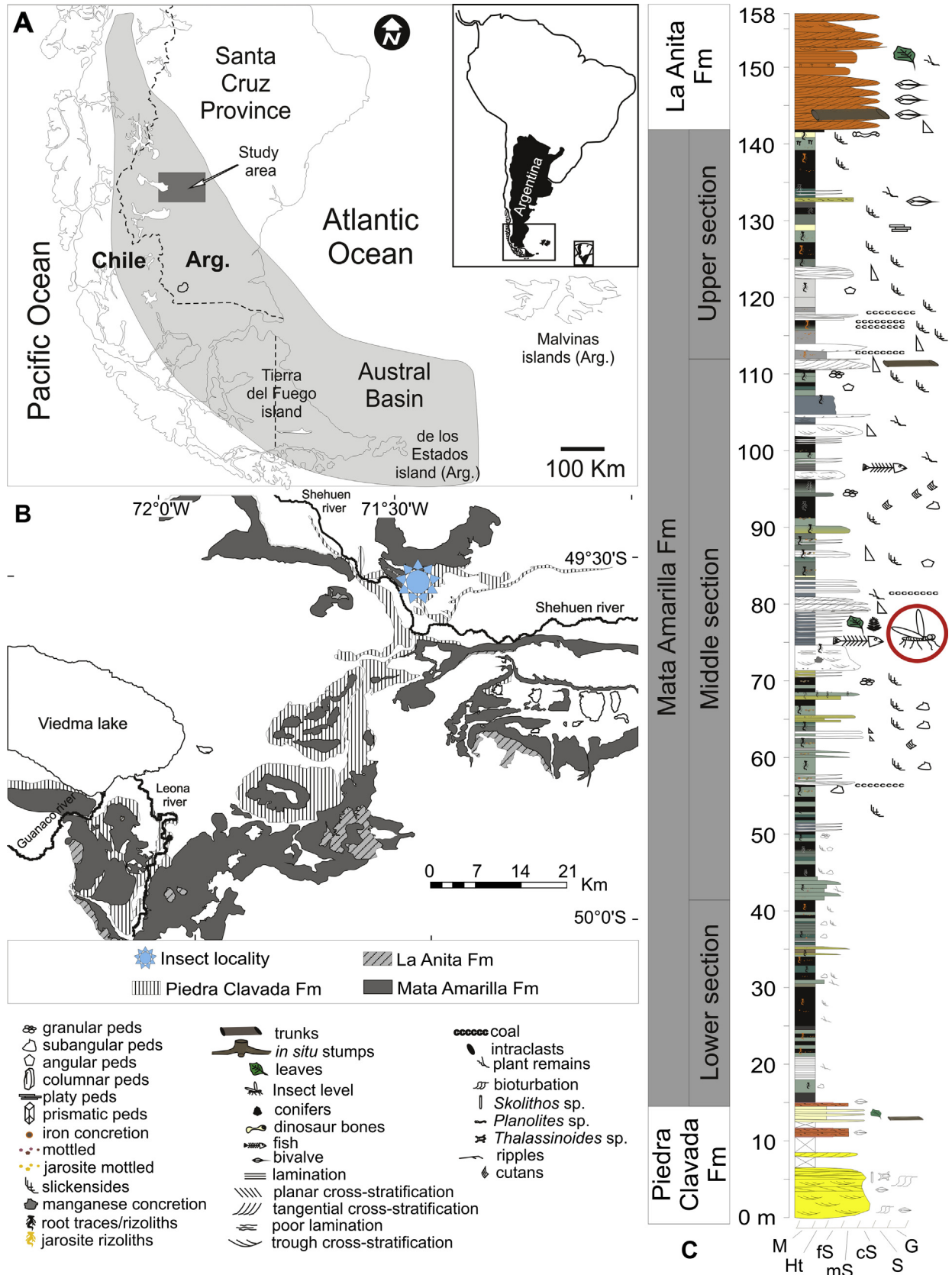


Fig. 1. A, regional location map showing study area in dark gray. B, detailed map of study area. C, geological section of Mata Amarilla Formation (middle Cenomanian) at the studied locality. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

restricted to the middle Cenomanian. The underlying Piedra Clavada Formation is well limited to the early/middle Albian by ammonoids (Piatnitzky, 1938; Riccardi et al., 1987) and palynomorphs (Archangelsky et al., 2008) with a transitional conformity between both units.

The entomofauna is composed by Fulgoroidea and Coleoptera. The specimen described herein belongs to Perforissidae Shcherbakov, 2007, a small and recently recognized extinct fulgroid family. The Perforissidae have 7 genera and were only known in the Cretaceous of the Northern Hemisphere (Shcherbakov, 2007; Peñalver and Szwed, 2010; Nel et al., 2012; Szwed et al., 2013). They are present in the Lower Cretaceous of Lebanese (Berriasian-Barremian; Szwed et al., 2013) and Burmese (Albian; Shcherbakov, 2007) ambers and Tsagan-Nur deposits (?Aptian; Shcherbakov, 2007), the Upper Cretaceous of New Jersey (Turonian; Shcherbakov, 2007), Taimyr (Santonian; Shcherbakov, 2007) and San Just (Albian; Peñalver and Szwed, 2010) ambers (see distribution in Fig. 1). Perforissidae is an enigmatic group concerning its evolutionary relationships within Fulgoroidea (Shcherbakov, 2007; Peñalver and Szwed, 2010). The Coleoptera are represented by fragmentary specimens. Among them it is remarkable one Cupedidae, that extends the distribution of this family in the Upper Cretaceous.

Insect traces were found in an angiosperm palmated leaf, corresponding to a piercing and sucking type of damage *sensu* Labandeira et al. (2007). Piercing and sucking fossil damage is discussed and compared to recent stippling. Stippling injuries are described from a recent species of Cicadellidae (Auchenorrhyncha) hosting Bignoniaceae leaves.

Mesozoic localities with insects become more and more recorded in last years in Argentina where several outcrops from Patagonia and Cuyo (west-central) geographic regions preserve some prospective insect faunas from the Middle–Upper Jurassic (Andrade de Moray and Genise 2005; Petrulevičius 2007) and the Cretaceous (Petrulevičius and Nel, 2003; Petrulevičius et al., 2005, 2010).

Upper Cretaceous insect localities are less common than those from the Lower Cretaceous in the world. In the same way the number of collected insects in the Upper Cretaceous is scarce in relation to the abundant material known from the Lower Cretaceous (Zherikhin, 2002). Even more, the Cenomanian localities with compressions of insects are few and only two were known outside Eurasia: the Canadian Knob Lake (Carrano, 2011) and the Lebanese Nammoura (Nel et al., 2004). In this sense, the discovery of a new locality in the middle Cenomanian of the South Hemisphere increases the interest for the understanding of the insect diversity and biogeography in the Upper Cretaceous.

2. Study area, material and methods

The insects and plant-insect interactions were recovered from the Cerro Waring Locality (Fig. 1, S 49° 31' and W 71° 30'00B4), from the Mata Amarilla Formation, in a fossiliferous level situated stratigraphically above the MAL and MEL plantiferous levels from Iglesias et al. (2007) and 28 m below the dated tuff level (Fig. 1). The specimens were found along with freshwater fish scales, fern, conifer and angiosperm remains, interpreted as a lacustrine palaeoenvironment along diverse vegetation in a continental lowland area (Varela, 2011). The insects and leaves with traces are kept in the collection of the Museo Provincial Padre Manuel Jesús Molina, Río Gallegos, Santa Cruz Province, Argentina with acronym MPM.

For wing venation nomenclature the system proposed by Kukalová-Peck (1983, 1991) and Dworakowska (1988) is followed, also used in previous works of the first author (JFP) dealing with Fulgoroidea (Petrulevičius, 2005; Solórzano Kraemer and

Petrulevičius, 2007). The forewing venation of Perforissidae is reduced. There are four main visible veins in the remigium interpreted as subcosta posterior plus radius anterior (ScP+RA), radius posterior (RP) media posterior (MP) and cubitus anterior (CuA). In some genera, and this is the case for the described species, the MP is fused with the CuA in the proximal part of the wing. More recent interpretations of wing venation of Fulgoroidea, like that of Nel et al. (2012), coincide in general with the Kukalová-Peck's system and with the present contribution specifically in the fusion of MP with CuA. They differ with Kukalová-Peck's system in the path of some veins like in the cubital system but the explicitly of this details exceeds the aims of this paper.

The Perforissidae and fossil leaf (Fig. 2A) were photographed with a Nikon D5000 camera and detail of the traces with an Olympus microscope BX51 with an Olympus epifluorescent unit and a Endow GFP BP filter (440–640 nm), connected to an Olympus Evolt E-330 camera, from the Instituto de Fisiología Vegetal (INFIVE) from La Plata National University (UNLP). The Perforissidae was drawn with a camera lucida attached to a Wild M5 stereomicroscope. The damaged recent leaves of *Tecoma stans* (Linnaeus) Juss. ex Kunth (Bignoniaceae) and the leafhoppers of the genus *Rhabdotalebra* Young (Cicadellidae: Typhlocybinae: Alebrini), producers of the stippling, were collected on May 15, 2012 at La Plata (Buenos Aires, Argentina; S 34°55' and W 57°57'). The insects correspond to an undescribed species (Catalano et al., in prep.) found to damage a new host plant for the genus *Rhabdotalebra* (Catalano et al., 2010). Photograph of the whole leaf was taken just after collection (Fig. 2B) with a camera Nikon D5000. In an attempt to better photograph the insect on the leaf the latter was frozen at –18 °C for about 5 minutes. See the freezing of the areolas that became black at the apex of the leaf (Fig. 2B detail). The damages became brown forming a ring sometimes open like a horseshoe (Fig. 2C details). After freezing, the leaf together with the insect were exposed to 4 °C to take the detailed photo of the Fig. 2B. Another leaf was dehydrated after putting it between card papers for a week (Fig. 2C) and photographed in details under a Leica microscope DM2500. The leaves and insects were collected on May, 14th (autumn) from La Plata, Buenos Aires, Argentina. Specimens are housed in the Entomological collection (Box No. 2012) of the Museo de La Plata (MLP), La Plata, Argentina.

3. Systematic palaeontology

Fulgoromorpha Evans 1946

Fulgoroidea Latreille 1807

Family Perforissidae Shcherbakov, 2007

Genus *Aonikenkissus* gen. nov. Petrulevičius, Varela, Iglesias and Poiré

Derivation of name. From the Aonikenk, ancient inhabitants of south Patagonia; and *Issus*, recent genus of the Issidae.

Type species. *Aonikenkissus zamunerae* gen. nov. et sp. nov., by monotypy and present designation.

Diagnosis. Tegmina gibbous with four main stems and distal branching (5–7 (?) apical cells); tegmen dark with pale-margined veins; costal area distally narrow; ScP+R, MP and CuA1+2 sinuous and subparallel in all their trajectory; crossveins r–m, m–cua and icua aligned; MP not stalked with ScP+R; CuA+MP stem as long as basal cell; CuA forked; basal part of MP near to CuA.

Aonikenkissus zamunerae sp. nov. Petrulevičius, Varela, Iglesias and Poiré

Figs. 3–4

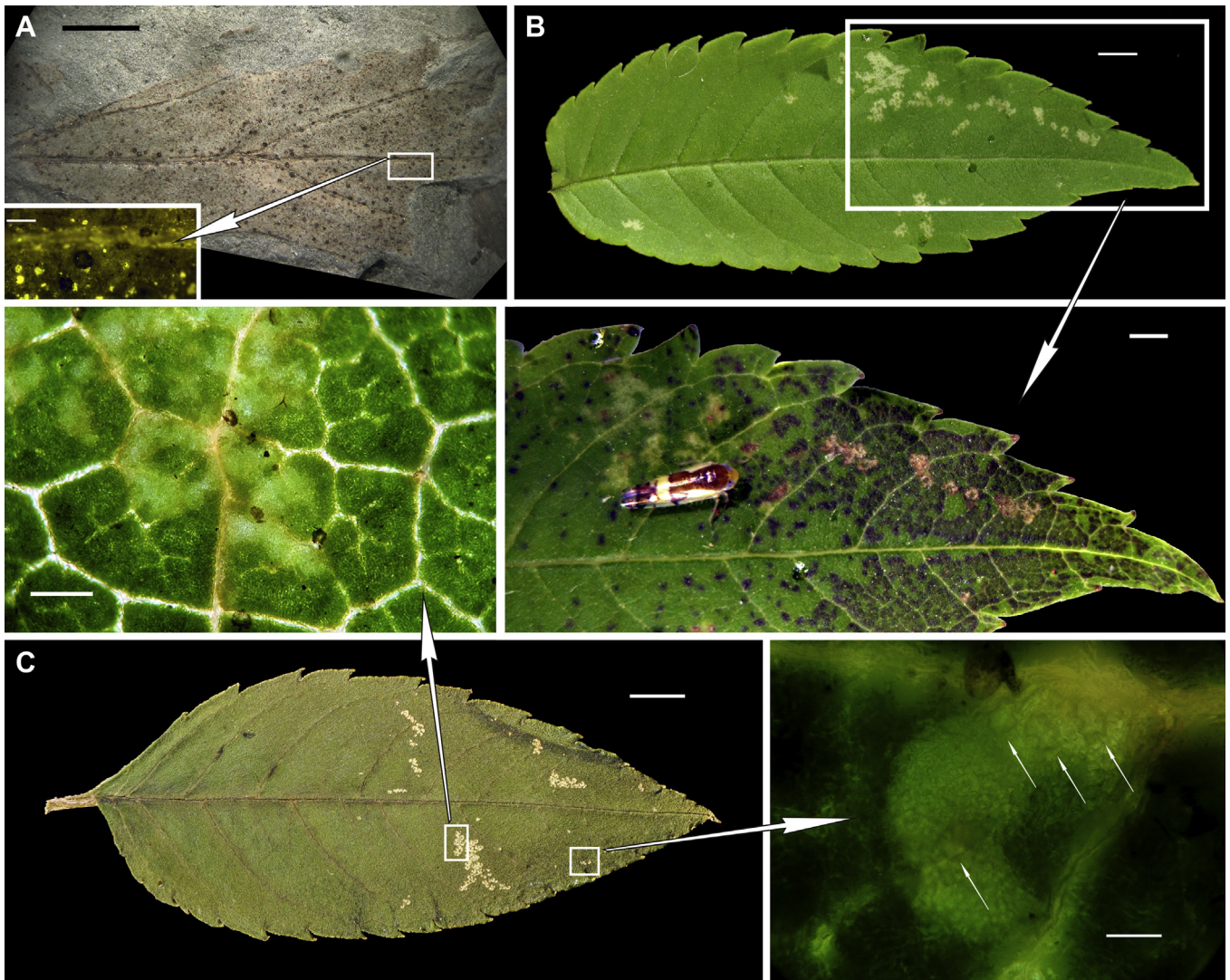


Fig. 2. Insect damages in fossil and recent leaves. A, pentalobate leaf from Mata Amarilla Flora (MA106 angiosperm leaf morphotype; Iglesias et al., 2007), MPM-PB-1462. Note in the detail, the damages with a central undamaged area and surrounding the damaged ring, image with epifluorescence technique. B and C, recent leaves of *Tecoma stans* with stippling made by an undescribed species of *Rhabdotalebra* (Cicadellidae: Thyphlocybinae: Alebrini). B, fresh leaf, note in the detail the changes made to the damage after freezing the leaf, the producer was photographed in cold conditions (4 °C). After freezing, the habitus of the damage became similar to that of the fossil. C, dehydrated leaf, above, detail of a group of circular and horseshoe damages, right, detail of the individual injuries (marked by arrows) of a damage. Scale bars represent 3 mm in A, 0.2 mm in detail, 2 mm in B, 1 mm in detail, 4 mm in C, 0.2 mm in detail above, 0.5 mm in right detail.

Derivation of name. Named after Alba B. Zamuner, one of our co-authors, great colleague and outstanding paleobotanist from the Paleobotany Division at La Plata Museum. She passed away in August 10, 2012.

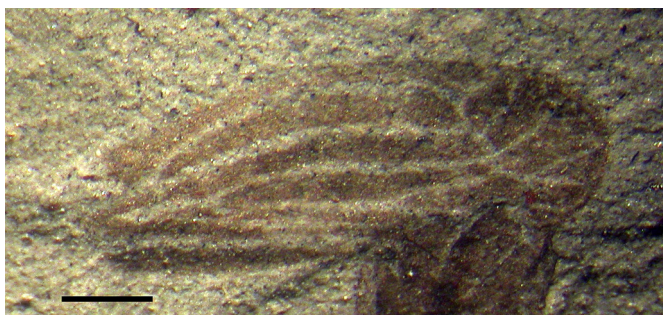


Fig. 3. *Aonikenkissus zamunerae* gen. et sp. nov., holotype MPM-PI-14932. Photograph of the tegmina. Scale bar represents 0.5 mm.

Material. Fragment of body and fore wing, MPM-PI-14932.

Diagnosis. As for the genus.

Age and Outcrop. Middle Cenomanian (96.23 ± 0.71 Ma), Mata Amarilla Formation, Cerro Waring, South Patagonia, Argentina.

Description. From fore wing; tegmina 3 mm long 1.2 mm wide; anterior areas not broadened; cells darkened with veins pale-margined (Fig. 3–4A); costal margin convex but slightly concave at the basal half (slightly sinuate), gibbous about mid-length; four main branches, i.e., ScP+RA, RP, MP, and CuA; MP+CuA stem about as long as basal cell, 0.23 mm long; arculus short; ScP+RA, RP and MP sinuous and running almost parallel; vein CuA not curved as three previous veins and running parallel to the claval fold; CuA bifurcating 0.57 mm basal to the crossveins, CuA1+2 slightly sinuous and fusing (?) with MP for a distance; CuA3+4 not changing direction from CuA; AA long running parallel to the claval fold; AP just preserved; posterior wing margin preserved only basal to the joining of AA with AP; RA with one branch;

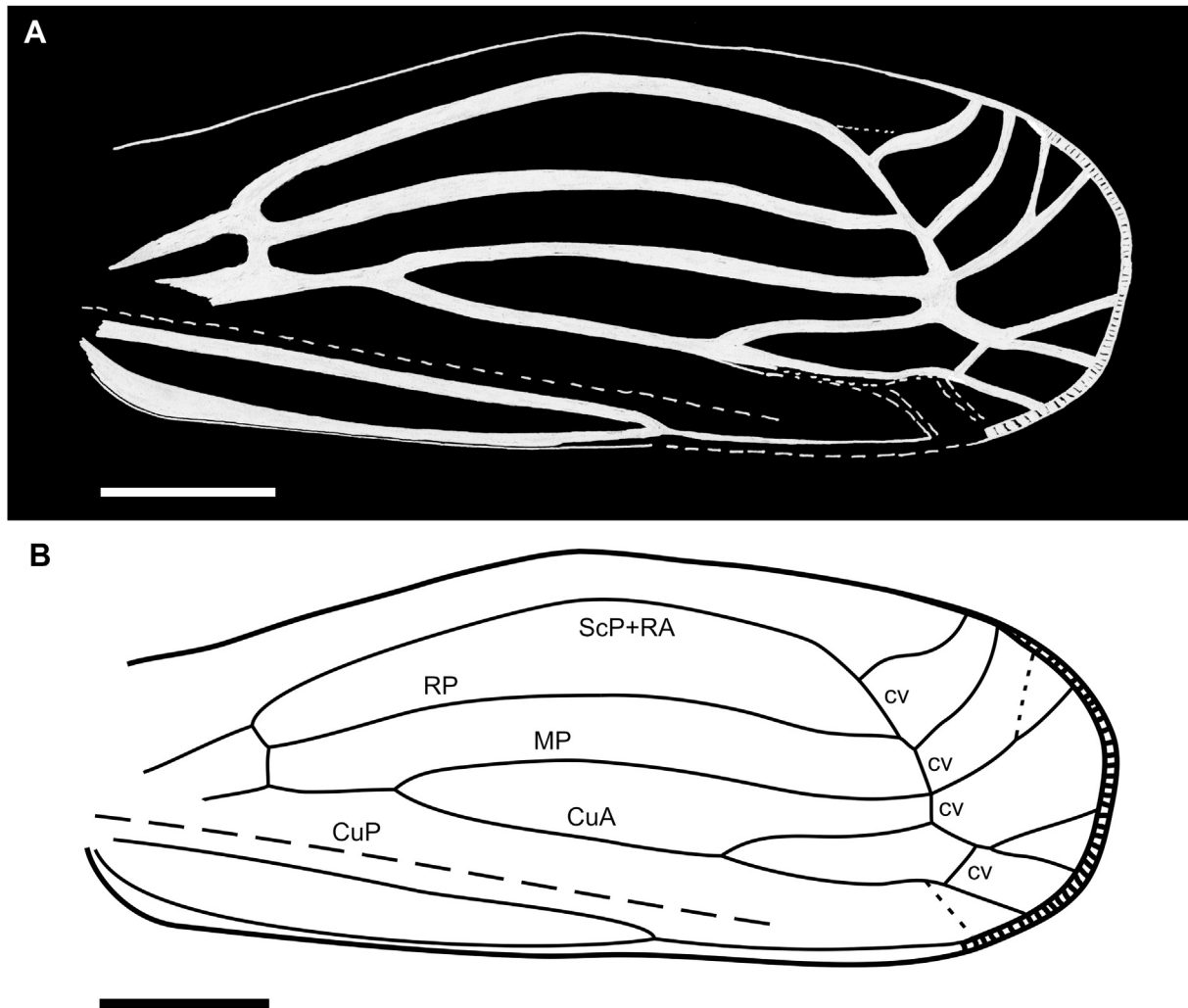


Fig. 4. *Aonikenkissus zamunerae* gen. et sp. nov., holotype MPM-PI-14932. A, drawing of the tegmina. B, interpretation of wing venation. Scale bars represent 0.5 mm.

RP with one branch; MP with two (?) apical branches; CuA with three (or four ?) branches; 5–7 (?) apical cells; crossveins ra-rp, rp-m and mp-cua aligned; consequently to the alignment of these crossveins, the ScP+RA, the crossveins and the CuA1+2 result in a particular z-like drawing; crossvein cua1+2-cua3+4 (icua) distal to fusion of MP with CuA (? mp-cua); AP and AA+AP seems to be in straight line; crimped marginal membrane visible between RP to CuA.

Discussion. Main veins of the specimen are interpreted as ScP+RA, RP, and MP+CuA that separates into MP and CuA (Fig. 4B). Presence of a distal bifurcation of the fourth vein makes us to interpret it as the CuA basally fused to the MP. There is no stalk between the ScP+RA and RP; they are separated at the basal cell.

The specimen is included in Perforissidae because it shares all characters present in the fore wing of the family, i.e., wings small to minute (3–5 mm), tegmina narrow with four main stems (ScP+RA, RP, MP and CuA) and little distal branching (6–10), and a basal fusion of MP with CuA. The new genus shares some characters with *Perforissus* from the Late Cretaceous of New Jersey (Shcherbakov, 2007), i.e., tegmina gibbonous about midlength; dark tegmen with pale-margined veins, a distally narrow costal area; MP+CuA stem equal than basal cell; ScP+RA, RP and MP sinuous and subparallel basal to crossveins; but differs with *Perforissus* in RP not stalked with ScP+RA; CuA forked and the crossveins ra-rp, rp-m, m-cua

aligned. In *Aonikenkissus* nov. gen. the veins themselves are not visible, but only the pale marginal area surrounding them. In *Perforissus*, as it is included in amber, it is possible to see the pale marginal area and the veins running, predominantly, at equal distance from both margins of it (see figs. 1, 3–5, 7 in Shcherbakov, 2007). Veins are interpreted in *Aonikenkissus* nov. gen. based on *Perforissus* model (Fig. 4B). The unique other genus with RP not stalked with the ScP+RA is *Cixitettix*. It differs from the new genus in having a single CuA, MP+CuA stem longer than basal cell and the tegmina widened to 2/3. Shcherbakov (2007) proposed two subfamilies within the Perforissidae. The definition of the taxa includes characters from the wing and hind leg tibia and tarsomere morphology (Shcherbakov, 2007). The wing character defining the Perforissinae, which is the costal margin gibbonous at midlength (Shcherbakov, 2007; Peñalver and Szwed, 2010; Szwed et al. 2013) is also present in three genera of the other subfamily, the Cixitettiginae: *Foveopsis* (Shcherbakov, 2007), *Iberofoveopsis* (Peñalver and Szwed, 2010), and *Aafrita Szwed and Azar* (2013). In accord to this, the subfamilial categories have to be confirmed or redefined in the future for the Perforissidae. Within the family, the new specimen can be well placed in a new genus because a unique set of characters respect to the other genera, i.e., tegmina gibbonous about midlength; tegmen dark with veins pale-margined; costal area distally narrow; ScP+RA not stalked with RP; CuA stem equal

Table 1
Comparison of *Aonikenkissus* gen. nov. with the other genera of the family. Selected characters.

| Characters \ genera | <i>Tsaganema</i> | <i>Cixitettix</i> | <i>Foveopsis</i> | <i>Iberofoveopsis</i> | <i>Aafrita</i> | <i>Aonikenkissus</i> gen. nov. | <i>Perforissus</i> | <i>Cretargus</i> |
|--|---------------------------------------|-----------------------------------|------------------|-----------------------|----------------|--|-----------------------------|----------------------------|
| Teeth in hind leg pectens | Metatibia 1st tarsus 2nd tarsus | Uniserial | | | | ¿? | Triserial Biserial no | Biserial Uniserial |
| Tegmen color pattern | | Contrasting pale and dark pattern | Unicolor dark | | | Cells darkened, veins pale margined | | Pale with dark markings |
| Tegmen shape | | Parallel sided | Widened to 2/3 | Gibbous at 1/2 | | | | |
| Length MP+CuA stem versus basal cell | | Equal | Longuer | Equal | Shorter | | Shorter | Shorter |
| ScP+RA +RP stalk | | Short | No | Long | Short | | Long | |
| CuA | | Normally unforked | Unforked | Forked | | No | Unforked | |
| Wing length versus crossveins to apex length | | ~1/3 | | ~1/4 | | ~1/5 | | ¿? |

than basal cell; CuA forked; basal part of MP near to CuA. *Aonikenkissus* nov. gen. has an unique character within the family: the forewing has the crossveins ra-rp, rp-m, and the m-cua aligned. Differences and similarities with the other genera of Perforissidae are detailed in Table 1.

Coleoptera Linné, 1758
Archostemata Kolbe, 1968
Cupedidae Laporte, 1836
Notocupedini Ponomarenko, 1968
Genus *Zygadenia* Handlirsch, 1906

Zygadenia sp. 1
Fig. 5A

Material. MPM-PI-14716.

Age and Outcrop. Middle Cenomanian, Cerro Waring, South Patagonia, Argentina.

Remarks. The elytrum is fragmentarily preserved but shows the typical venation and ornamentation of the family Cupedidae (see Ponomarenko, 1966, 2000, 2006). The specimen MPM-PI-14716 (Fig. 5A) could be attributed to the genus *Zygadenia* Handlirsch, 1906 (see Ponomarenko, 1966, 2000) because it has a distinct venation with two rows of cells between main veins, the main veins of the elytrum sharply distinct from the intercalaries forming large quadrangular cells, and the main veins seem to coalesce before the apex. Handlirsch (1906) proposed the generic name *Zygadenia* for the isolated elytra of Cupedidae with certain characters. Ponomarenko (2000) synonymised *Notocupes* Ponomarenko, 1968 (Ponomarenko, 1968) with *Zygadenia*, but it could be a better practice to use the name *Zygadenia* for isolated elytra (Ponomarenko and Ren, 2010). The specimen seems to be a new species but it is not described for the moment because of its fragmentary condition and the possibility of finding new material in the future.

Coleoptera indet.
Fig. 5B–J.

Material. MPM-PI-14717, MPM-PI-14718, MPM-PI-14719, MPM-PI-14720, MPM-PI-14721, MPM-PI-14722, MPM-PI-14723, MPM-PI-14724, MPM-PI-14725.

Remarks. From the same strata were recorded several disarticulated insects attributed to Coleoptera, most of them correspond to elytra but also other parts as abdominal ventrites. Isolated elytra from the Cretaceous usually could not be assigned to familial level (Ponomarenko, 2006). Only the Archostemata Cupedidae Laporte, 1836 could be attributed without doubts and sometimes to generic level (Ponomarenko, 2006). There are 8 different morphotypes of elytra that could not be assigned certainly to any family of Coleoptera. One specimen has longitudinal punctate rows

(Fig. 5B), others have uniformly punctate grooves (Fig. 5C–D) and the dominant morphology has neither veins nor cells (Fig. 5E–I). There is also an isolated abdomen of Coleoptera MPM-PI-14725 (Fig. 5J) that has five ventrites with the metacoxae cavities not dividing the ventrite 1 and an apparently rugose texture; characters that coincide with archostematan morphology, but the specimen is too incomplete to be assigned to any family.

4. Palaeobiogeography

Aonikenkissus zamunerae gen. nov. sp. nov. significantly enlarges the geographic distribution of Perforissidae (Fig. 6) being the southernmost species and the first record in the Southern Hemisphere. The Perforissidae are not represented in the Northern Hemisphere during the Cenomanian; but there are Upper Cretaceous records in the Santonian of Taimyr and the Turonian of North America (Fig. 6). In this context the family distribution could be inferred as widespread at least in the mid-Cretaceous; also considering that the taxon is under-sampled because of its small size and the few paleoentomologists in the Southern Hemisphere. The latest hypothesis could explain also the first record of the archostematan genus *Zygaenia*, very well represented in the Jurassic-Lower Cretaceous of Eurasia and incipiently recorded in the South Hemisphere as in the Jurassic of Australia (Martin, 2010) and the present record. The gap in the record of Cupedidae in the Cenomanian (Ponomarenko, 2002; Soriano and Delclòs, 2006), is filled by the present record and possibly due to the scarcity of Upper Cretaceous localities with beetles, mainly three in the world (Ponomarenko, 2002).

In the Figure 6 are plotted all the records of Perforissidae in the Cretaceous and the Upper Cretaceous record of Cupedidae. In the same Figure it is seen that the record of Perforissidae is clearly related to amber localities, whereas the record of Cupedidae is related to compression localities. Among all the localities only two, the New Jersey amber and Mata Amarilla have both taxa, Perforissidae and Cupedidae (circles and squares in Fig. 6). The surprising first insects recorded in Mata Amarilla and the fact that the locality bears one of the southernmost entomofauna in the world for the Late Cretaceous, show that the sequences at the Austral Basin in Argentinean Patagonia are very interesting and promising.

5. Perforissidae paleoecology and plant-insect interactions

In the case of Perforissidae it is difficult to make actualistic ecological inferences, not only because it is an extinct family, but also because it has obscure phylogenetic relationships within the Auchenorrhyncha and more precisely the Fulgoroidea. But due to the biogeographic pattern, rarity of the taxon and age, it results very interesting to discuss about the possible host plants and climatic conditions inhabited by this family. It is possible to

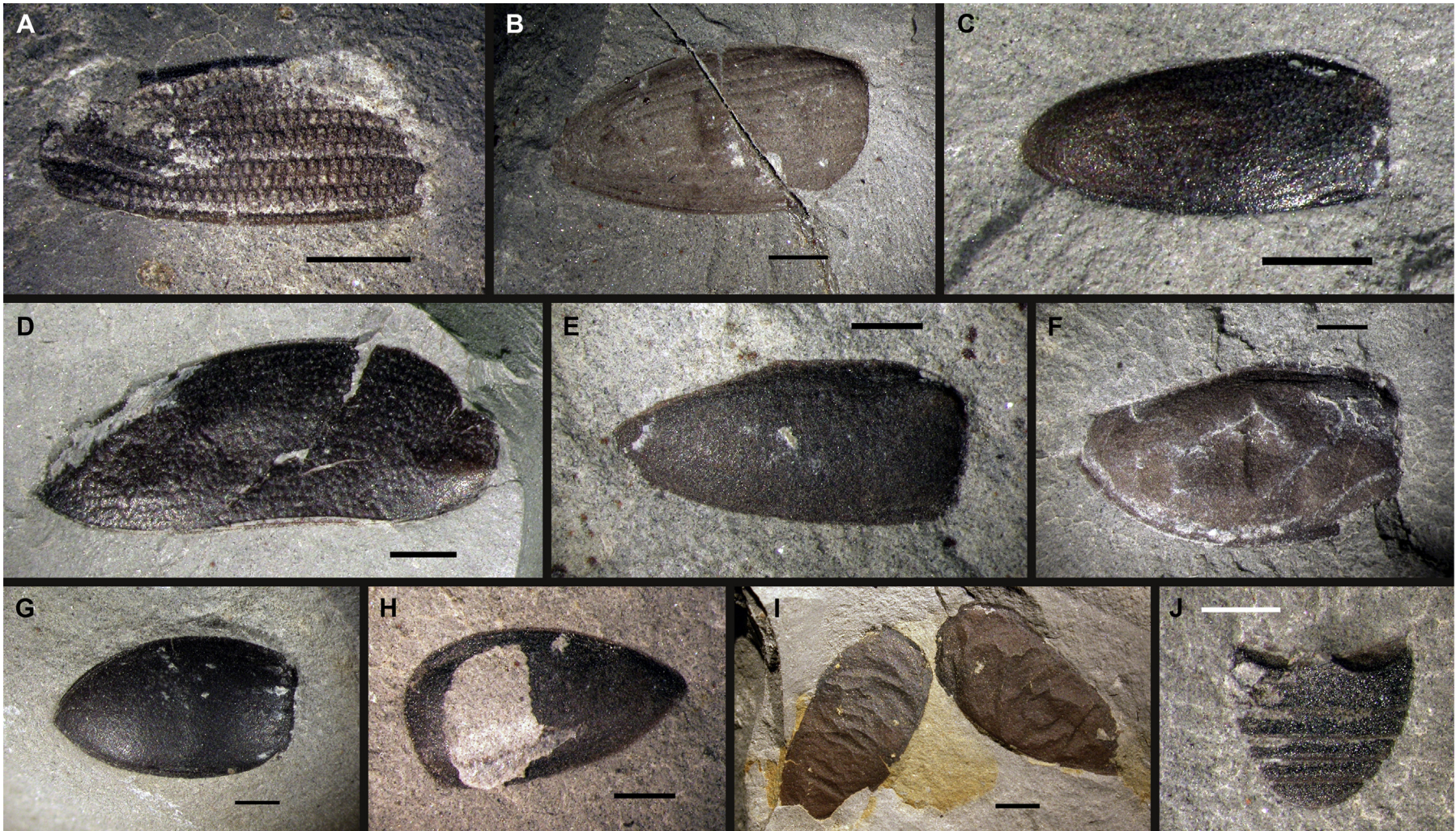


Fig. 5. A, *Zygadenia* sp. 1, MPM-PI-14716. B– I, Coleoptera indet., elytra. B, MPM-PI-14717. C, MPM-PI-14718. D, MPM-PI-14719. E, MPM-PI-14720. F, MPM-PI-14721. G, MPM-PI-14722. H, MPM-PI-14723. I, MPM-PI-14724. J, Coleoptera indet., ventral view of abdomen, MPM-PI-14725. Scale bars represent 2 mm in A and I, 1 mm in B–H and J.

| | | | | |
|------------|-------|---------------|-------|---|
| CRETACEOUS | Upper | Maastrichtian | 70.6 | |
| | | Campanian | 83.5 | |
| | | Santonian | 85.8 | <i>Cretargus</i> <i>Cixitettix</i> |
| | | Coniacian | 88.6 | |
| | | Turonian | 93.6 | <i>Perforissus</i> Cupedidae |
| | | Cenomanian | 99.6 | <i>Aonikenkissus</i> gen. nov. Cupedidae |
| | | Albian | 112 | <i>Foveopsis</i> <i>Iberofoveopsis</i> |
| | | Aptian | 125 | <i>Tsaganema</i> |
| | Lower | Barremian | 130 | |
| | | Hauterivian | 133.9 | <i>Aafrita</i> |
| | | Valangian | 140.2 | ? |
| | | Berriasian | 145.5 | |



Fig. 6. World map with the localities and geological periods recording the Perforissidae (circles) and the Upper Cretaceous Cupedidae (squares). Geological periods with Perforissidae record in gray. Amber localities in color, Compressional ones in white. 1, Taimyr amber; 2, New Jersey amber; 3, Kyzyl-Syr; 4, Cerro Waring (Mata Amarilla Formation); 5, Burmese amber; 6, San Just amber; 7, Tsagan-Nur; 8, Lebanese amber. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

indirectly restrict and hypothesize the life style and interactions of the group in relation to the physical environment and floral aspects of the taphocenosis of the concerned strata, and from some morphological features of the insect that permit some discussions.

Mata Amarilla Formation is known for their well preserved compression floras and petrified forests. These Cretaceous forests were dominated by Podocarpaceae (Zamuner et al., 2004; Iglesias et al., 2007), associated to both coastal–littoral marine and lowland environments (Varela, 2011). Understory and remaining flora, as the flora associated to the Perforissidae fossiliferous strata (Fig. 1), were mostly herbaceous or low shrubs dominated by ferns and primitive angiosperms (Iglesias et al., 2007, 2011). The angiosperm leaves associated to the perforissid have a relative high morphological diversity with broad and entire margins related to warm and wet environments; although brachyphyllous conifers are also present (Iglesias et al., 2007). The record of broad leaves with damages adds the possibility to maintain leafhopper-like animals related to them.

The sensory pits retained in the adults of some Fulgoroidea are presumed hygroreceptors (Shcherbakov, 2007). Although there is no empirical demonstration about the function of these organs (Bräunig et al., 2012), they are usually related to extreme xerophiles or hygrophiles, and they are also found in presence of strong seasonal variation (Shcherbakov, 2007). In the same way, Gnezdilov (2012) pointed that species with sternal sensory pits in the imago inhabit arid biotopes. So, the multiple presence of pits in Perforissidae could indicate that they inhabited biotopes with highly variable or extreme humidity, possibly coastal–littoral environments (Shcherbakov, 2007). After the geological reconstruction (Varela et al., 2011), the inhabited environment of *Aonikenkissus zamunerae* in Mata Amarilla Formation corresponds to a lowland area, probably a coastal lake; and in agreement to the regional reconstruction is relatively far (more than 200 km) from the sea (Varela, 2011; Varela et al., 2013).

These animals depend on plants to feed, but up to date, there are not evidence about their diet preferences. Perforissids have in general a morphology of the rostrum comparable to that of recent plant/leafhoppers and suitable to produce similar plant damages like piercing and sucking (Fig. 2). Based on the whole body and 3D preservation in amber, Shcherbakov (2007) interpreted the Perforissidae as an early attempt to construct leafhopper-like forms from a planthopper group. This “cicadelization” (attempt to construct cicadellid forms; Shcherbakov, 2007) could imply a leafy diet for these insects as for the recent Cicadellidae. Damages by recent leafhoppers can be recognized because they introduce their stylets in the mesophyllous of the leaves and suck their fluids producing different foliage injuries, like stipples, burning (Backus et al., 2005) and isolated piercings (Backus et al., 1988). All Auchenorrhyncha have intracellular penetration style contrary to the Sternorrhyncha that have intercellular penetration (Backus et al., 2005; Tjallingii, 2006). Different species use different feeding strategies as cell rupturing and salivary sheaths, the latter one used by most of auchenorrhynchans (Backus et al., 2005). These two strategies could be differentiated from the surface of Recent leaves. Cell rupturing in the case of stippling produces different white “drawings” as stars, horseshoes or rings (See Fig. 2B–C; also Cranshaw, 2010; Brentassi et al., 2010). Salivary flanges (and underlying sheaths) could be visible but using a previous staining method (Backus et al., 1988).

Angiosperm leaves recorded at Mata Amarilla Formation show leaf damages that can be unequivocally assigned to diverse arthropod actions. The Fig. 2A shows possible piercing and sucking damages in a palmatilobed angiosperm leaf, similar to DT46 leaf damage type from Labandeira et al. (2007).

Several recent species of Thyphlocybae produce stipples resulting in different white “drawings” in angiosperm leaves. In Fig. 2B and 2C are shown the damages produced by an undescribed species of the genus *Rhabdotalebra* (Cicadellidae: Thyphlocybae: Alebrini; Catalano et al., in prep.) formed by rings or horseshoes. These damages are grouped around the principal veins, producing stippling sometimes in high concentration in *Tecoma stans* (Bignoniaceae) leaves. Each ring is the result of several injuries (Fig. 2C details). Individual injuries forming horseshoe to ring forms are in turn aggregated in patches, or linear or zigzag patterns (Petrulevičius, pers. obs.). So, the damages by this species have inclusive spatial levels of complexity.

When freezing the leaf of Fig. 2B, the white stipples turned to brown. The central part surrounded by the ring remained green, as well as the surrounding surface (not injured) of the leaf (Fig. 2C details). The result unexpectedly and interestingly is quite similar to the fossil damages found in the Cretaceous leaf (Fig. 2A). Considering this result it was interpreted that in some damages like the DT46 of Labandeira et al. (2007) and that on the leaf here described stipples have not to be discarded as a possible explanation. Then it is considered the possibility of production of fossil piercing and sucking damages (sensu Labandeira et al., 2007) since the middle Cretaceous in angiosperm leaves, either by one central piercing (and sucking by a salivary sheath) or by several injuries ring like performed. Coincidentally, stipples are known to be produced in recent times by the thyphlocybines which have a pantropical distribution and seem to have arisen during the Cretaceous (Dietrich, 1999). Obviously, it is not possible to know what kind of damage produces our insect, the plant organ or even the kind of plant on which it feeds, brachyphyllous or low herbaceous, as interpreted by Shcherbakov (2007) or angiosperm understory forest and low shrubs with broad leaves which are the dominant plants in Mata Amarilla (Iglesias et al., 2007). The record of damages is restricted for the moment in Mata Amarilla to an angiosperm broad leaf possibly belonging to a forest understory plant (Fig. 2A).

Shcherbakov (2007) referred as possible causes of Perforissidae extinction the competition with the Cicadellidae or the fact that they were trophically associated with earliest angiosperms or “proangiosperms” (Shcherbakov, 2007; term referring in part ? to gymnosperm Hirmerellaceae), lineages not surviving (for the authors) into the Cenozoic (Shcherbakov, 2007; Peñalver and Szewdo, 2010). Although almost all angiosperms known in the Mata Amarilla Fm. are extinct by the latest Cretaceous, it has to be taken into account that Perforissidae seem to be strongly underrepresented in the fossil record as compressions by taphonomical and collection biases (due to its small size), so its extinction still could be somewhere before or after the Cretaceous/Paleogene (K/Pg). Besides, one of the groups considered extinct in the Cretaceous, the Hirmerellaceae producing *Classopollis* pollen surpassed the Upper Cretaceous, and are found in the Paleocene of Patagonia (Archangelsky and Romero, 1974; Pöthe de Baldi, 1984; Quattrocchio and Ruiz, 1999) and Northwest Argentina (Petrulevičius, 1996; Quattrocchio and Del Papa, 2000). In this sense the K/Pg boundary seems not to be critical for these plants nor for other insect groups as the Odonata that recognize a crisis through changes of the morphology/taxonomy between the Early and Late Cretaceous and not between the K/Pg boundary (Nel et al., 2010). Studies on insects and plant–insect interactions are needed for the Southern Hemisphere to better compare how stronger were environmental changes between the Early and the Late Cretaceous and K/Pg boundary transition.

6. Discussion about climate

The Mata Amarilla Formation represents a continental low-land area eventually flooded by epeiric seas, although only the lower and the upper sections of Mata Amarilla Formation were developed in a mixed littoral environment (Varela et al., 2011). Multiple stacked paleosoils are recognized throughout the Mata Amarilla Formation. Although the middle section preserves the most characteristic paleosoils, where the insect remains were found, associated to margins of shallow lakes (Fig. 1). The histosols, vertisols, alfisols and inceptisols recognized at the Middle Section of the unit indicate temperate warm climate, i.e., mean annual precipitations ~1000 mm, and mean annual temperatures close to 20 °C (Varela et al., 2012b). Geological indicators in the soils, detected marked seasonal dry periods, explained by not evenly distributed rains through the seasons (Varela et al., 2012b).

The angiosperm leaf characters as margin type and size described for the Mata Amarilla Formation flora, also are related to warm and humid climates (Iglesias et al., 2007). On the other hand, the presence of defined wood rings in most of the conifer trunks preserved in the Lower Section of the unit, allows inferring growth rate seasonality linked to some kind of seasonality in the water supply (Zamuner et al., 2004).

Cretaceous Cupedidae could be correlated mainly with warm climates (Soriano and Delclòs, 2006) but some records are outside to the subtropical climate area proposed by Spicer et al. (1994). This is the case of the Siberian Kyzyl-Syr locality, unique previous record of the genus *Zygadenia* (Ponomarenko, 1969) in the Late Cretaceous (Soriano and Delclòs, 2006). The other record of the family in the Late Cretaceous is from the Turonian New Jersey amber (Fig. 6). The record of Cupedidae in the Late Cretaceous is rare, in contrast to the Early Cretaceous (4 vs. 57 species, Soriano and Delclòs, 2006 and this work).

The climate inferred by geological indicators is indicative of biotopes with highly or extremely variable humidity, the same seems to be marked by grow rings in the fossil woods. This climate is probably related with the presence of the multiple sensory pits of the Perforissidae.

7. Concluding remarks

Perforissids are rare in the fossil record and mainly recorded in amber, excepting only two occurrences in compressional lacustrine deposits: the Mongolian record (Ponomarenko and Ren, 2010) and the specimen described here. This fact could be related to the tiny size of the specimens that are more suitable to be trapped in resins and not normally preserved nor recognized in compressions. The Argentinean specimen represents the first Perforissidae recorded for the whole Southern Hemisphere. This discovery confirms that the family was widely distributed in both hemispheres during the mid-Cretaceous.

Coleoptera is the most abundant group of the new insect fauna. The discovery of a Cupedidae fills the Upper Cretaceous world gap for this family in the Cenomanian and gives the first record of the genus *Zygadenia* in South America.

Insect traces found in Mata Amarilla are recorded in an angiosperm broad leaf and correspond to a piercing and sucking type of damage. This type of damage was compared, via experimentation, with recent stipples, arriving to the possibility of production either by one central piercing (and sucking by a salivary sheath) or by several ring-like injuries.

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