

A PLANT HOPPER (NOGODINIDAE) FROM THE UPPER PALAEOCENE OF ARGENTINA: SYSTEMATICS AND TAPHONOMY

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Abstract: A new taxon of plant hopper, *Celinapterixini*, is erected based on *Celinapterix bellissima* gen. et sp. nov. from the Upper Palaeocene Maíz Gordo Formation, north-west Argentina. Its phylogenetic relationships within the Fulgoroidea and Nogodinidae are discussed. The Danish Eocene species *Hammapterix paucistrata* (Henriksen) is transferred to the Nogodinidae and placed in a new genus, *Henriksenopterix*, based on wing-venation characters. The new plant hopper is an unusual case of articulated preservation from the Maíz Gordo Formation. The palaeoenvironment is interpreted as a carbonate mudflat subenvironment with a low flow of energy, created during a period of contraction of

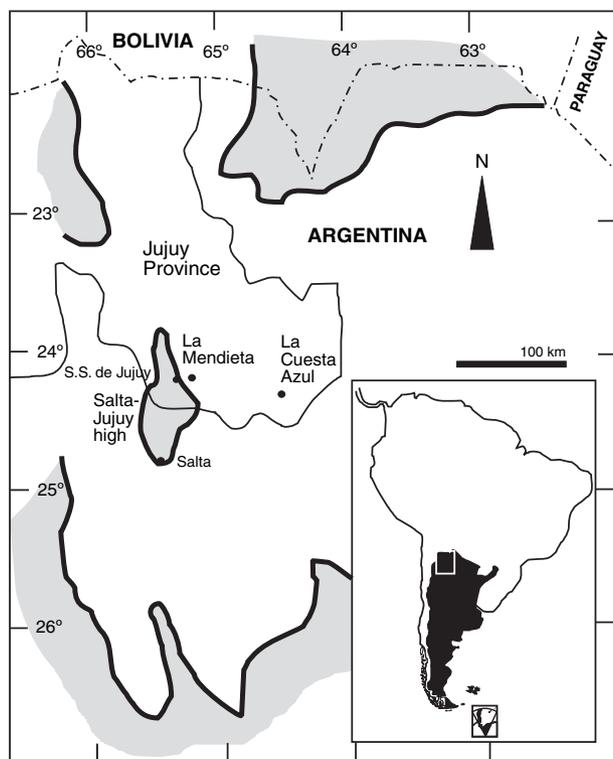
the lacustrine system. The plant hopper is considered to have sunk and been buried in a soupy substrate. Early fossil-diagenesis seems to have occurred over an extended period of time, because although the specimen preserves all original soft-body parts, these occur as an amorphous mass owing to tissue decomposition. The occurrence of three-dimensional preservation suggests the absence of fossil-diagenetic compression; the sediments seem to preserve more-or-less their original thickness.

Key words: Insecta, Fulgoroidea, Denmark, *Celinapterixini*, Argentina, taphonomy, lacustrine environment.

RECENT Nogodinidae are represented mostly in the tropical and subtropical areas of the world (Carver *et al.* 1991). The absence of recent nogodinids in Europe is due to its local extinction after the Palaeogene. The Nogodinidae have an extremely poor fossil record. Two species have been recorded from the Eocene: *Tritophania patruelis* Jacobi, 1937 and *Eobladina antiqua* Haupt, 1956, from Baltic amber and Germany, respectively, and one species has been reported from the upper Palaeocene from Denmark: *Hammapterix paucistrata* Henriksen, 1922. *T. patruelis* was placed in the Nogodinidae by Carpenter (1992) and redescribed by Szwedo and Stroiński (1999). *H. paucistrata* is placed in a new genus and transferred to the Nogodinidae herein. The remaining fossil species, *Tonacatecutlius gibsoni* Stroiński and Szwedo, 2000 and *Tainosia quisqueyae* Szwedo and Stroiński, 2001, are of Miocene age and from Mexican and Dominican amber. They belong to extinct genera from recent tribes of Nogodinidae (Stroiński and Szwedo 2000; Szwedo and Stroiński 2001).

The specimen described herein represents the first record of fossil Nogodinidae from South America and is one of the oldest records of the family. It is from the Maíz Gordo Formation of north-west Argentina, which is considered to

be late Palaeocene in age (Volkheimer *et al.* 1984; Marshall *et al.* 1997; Quattrocchio *et al.* 1997) and has yielded many other fossil insects [mainly Odonata and Bittacidae (Mecoptera)] (Petrulevičius 1999, 2001, 2003; Petrulevičius and Nel 1998, 2002a, b, 2003, 2004; Petrulevičius *et al.* 1999). More specifically it is from green shale facies in the middle part of the formation at the La Cuesta Azul locality (latitude 24°19' S, longitude 64°28' W) (Petrulevičius 2001) (Text-fig. 1). The strata exposed at this locality were deposited on the south-west margin of the Lomas de Olmedo depocentre (Salfity and Marquillas 1994). The green shale facies is succeeded by a stromatolitic boundstone facies representing progressive shallowing of the lacustrine system in the carbonate mudflat facies association (Del Papa 1994, 1999; Del Papa and Marquillas 1990). The geographical position of the locality, with respect to the location of the basin and the development of the carbonate mudflat facies, suggests a period of contraction of the lacustrine system. This period could be laterally associated with the uppermost part of the section of the La Mendieta locality (Text-fig. 1) (Petrulevičius *et al.* 1999; Petrulevičius 2001; Petrulevičius and Nel 2002a). This suggested association is based on the structure and stratigraphy of the basin, but the contemporaneity of the sediments is unproven.



TEXT-FIG. 1. Location of the La Cuesta Azul locality. Palaeogeographical map of the Santa Bárbara Subgroup, redrawn from Salfity and Marquillas (1994) and del Papa (1999). Structural highs are indicated by shading.

Extant Nogodinidae occur mostly in tropical and subtropical areas of the world (Carver *et al.* 1991). The present distribution of the family in the Neotropical region ranges from subtropical northern Argentina and Chile to Mexico (Penny and O'Brien 2000). Thus the occurrence of the new fossil coincides with the current distribution of the Nogodinidae in Argentina. Neotropical nogodinids are restricted to the Nogodininae: Nogodinini and Bladinini (Penny and O'Brien 2000).

MATERIAL AND METHODS

The specimen is housed in the Departamento Científico Paleozoología Invertebrados, Museo de la Plata, La Plata, Argentina (MLP 29016). It was originally partly covered, and was prepared with a pneumatic hammer.

The wing venation nomenclature of Kukulová-Peck (1983, 1991) and Dworakowska (1988) is used. I follow the phylogenetic system of Cimicida (= Homoptera + Heteroptera) proposed by Shcherbakov and Popov (2002) and the phylogenetic classification of Auchenorrhyncha proposed by Emeljanov (1990). Some familial characters used here are based on Shcherbakov (1981).

The taphonomy of the specimen is analysed following the methodology and theoretical framework of Fernández-López (1984, 1988, 1999, 2000) and Fernández-López and Fernández-Jalvo (2002). The terms and concepts used are as follows: (1) biostratinomy, modifications of taphonomic entities from death or production to burial; (2) production, processes from which taphonomic entities originated (i.e. death of an entire organism or disarticulation); (3) ademic, a palaeobiological entity inferred from a taphonomic element registered outside its living place; (4) allochthonous, a taphonomic element buried outside its place of production; (5) fossil-diagenesis, events that occurred between burial and collection of taphonomic elements.

SYSTEMATIC PALAEOLOGY

HEMIPTERA Linné, 1758

FULGOROIDEA Kirkaldy, 1907

NOGODINIDAE Muir, 1930 *sensu* Fennah, 1978, 1984, 1987

NOGODININAE *sensu* Fennah, 1987

Genus HENRIKSENOPTERIX gen. nov.

Derivation of name. Greek *pteryx*, wing, and dedicated to K. L. Henriksen who discovered and described the type species.

Type species. *Hammapterix paucistriata* Henriksen, 1922, p. 23, fig. 12.

Diagnosis. The main characters of this taxon are: (1) forewing with short basal cell; (2) absence of the basical plate in forewings; (3) CP running at some distance from wing margin, and several crossveins between them; (4) simple costal margin; (5) membranous wings without granules; (6) broad basal cell; (7) row of aligned transverse veinlets distal of rp-mp and mp-cua crossveins; (8) developed ScP; (9) RA passing into the anterior margin (basal to the antero-apical angle) of wing; (10) postero-apical angle more or less distant from apex of clavus; (11) RA1+2 sigmoid; (12) MP vein supernumerary; (13) venation smooth; (14) middle part of CA and CP1+2 slightly concave (posteriorly curved).

Remarks. Of these characters, 1 is a synapomorphy of Fulgoroidea (Shcherbakov and Popov 2002); 2 is a synapomorphy of Fulgoroidea except the Tettigometridae; 3 is a synapomorphy of Issidae, Nogodinidae, Ricaniidae, Flatidae, Tropiduchidae, Lophopidae and Erybrachyidae; 4–5 are plesiomorphies of *Henriksenopteryx*; 6 is a synapomorphy of Nogodininae; 7 is convergently (?) present in Nogodinini and Sassulina; 8 seems to be a plesiomorphy (?) shared with *Celinapterix*; 9–10 are present in

Nogodinidae, Tropicuchidae and Lophopidae and absent in Ricaniidae (Shcherbakov 1981); 11–14 are autapomorphies of *Henriksenopterix*. Two of the last characters are convergently (?) present in *Celinapterix*.

Henriksenopterix paucistriata (Henriksen, 1922) was originally described as a species of *Hammapterix* (Henriksen 1922). This genus was considered to belong to the Ricaniidae and was only known from incomplete forewings from the Eocene of North America and Europe (Carpenter 1992). In this work the European species described by Henriksen (1922) and Piton (1940) are considered to belong to other genera because of several differences observed in wing venation. The species of Piton (1940) is not well preserved but seems to be a Ricaniidae, as the RA seems to end at the antero-apical angle of the wing; regrettably the clavus is not visible in the drawing of Piton (1940) to confirm the attribution to the Ricaniidae. *Henriksenopterix* could not be included in the Ricaniidae because the RA passes into the anterior margin of the wing (basal to the antero-apical angle), and the postero-apical angle is more or less distant from the apex of the clavus. In the Ricaniidae the RA passes into the antero-apical angle of the wing, and the postero-apical angle is immediately beyond the apex of the clavus.

As Henriksen (1922) noted, the specimen lacks many important characters. However, it may be assigned to the Nogodininae based on: (1) the presence of a broad basal cell, a synapomorphy of the Nogodininae; and (2) the presence of transverse veinlets distal of rp-mp and mp-cua crossveins, a character present in the Nogodinini and Sassulina.

Henriksenopterix also has the vein ScP+RA+RP with a long stalk, which is a feature of Nogodinina. The genus shares some derived characters with *Celinapterix*, i.e. sigmoid RA1+2; smooth venation; middle part of CA, CP1+2 slightly concave (posteriorly curved). However, the new genus has a supernumerary MP vein, an autapomorphic character absent from *Celinapterix*.

Differences from *Hammapterix* (Scudder 1890) are sufficient to attribute the new species to a new genus. Furthermore, some characters found in *Henriksenopterix* are sufficient to create a suprageneric taxon. However, because of its fragmentary condition (principally lack of clavus and hind leg), this is currently considered unwise until more complete material is available.

CELINAPTERIXINI taxon nov.

Type genus. *Celinapterix* gen. nov.

Diagnosis. The main characters of this taxon are: (1) forewing with short basal cell; (2) long AA3+4 + AP1+2

(1A + 2A of Shcherbakov and Popov 2002) entering the commissural margin before claval apex; (3) absence of the basicubital plate in forewings; (4) AA3+4 + AP1+2 (claval vein of Emeljanov 1990) passing into Ap3+4 near the apex of the clavus; (5) CP running at some distance from wing margin, and several crossveins between them; (6) simple costal margin; (7) membranous wings without granules; (8) second tarsus with two long spines; (9) row of spines on the apical margin of the hind basitarsus; (10) broad basal cell; (11) slightly curved row of four preserved teeth in the distal part of the first tarsus; (12) developed ScP; (13) RA passing into the anterior margin (basal to the antero-apical angle) of wing; (14) postero-apical angle more or less distant from apex of clavus; (15) hind basitarsus about 1.5 times the length of the second; (16) unaligned row of transverse veinlets distal of rp-mp and mp-cua crossveins; (17) RA and first vein of RP sigmoid; (18) third tarsus about one-half of the length of the basitarsus; (19) CuA with a divergent CuA1+2 (diverging at an acute angle from CuA3+4) resulting in a large cell (closed by a crossvein); (20) MP and CuA partially fused so the distal mp-cua crossvein is lost; (21) broad subcostal area; (22) middle part of CA and CP1+2 slightly concave (posteriorly curved); (23) smooth venation.

Remarks. Of these characters, 1–2 are synapomorphies of Fulgoroidea (Shcherbakov and Popov 2002); 3 is a synapomorphy of Fulgoroidea (except Tettigometridae); 4–5 are synapomorphies of Issidae, Nogodinidae, Ricaniidae, Flatidae, Tropicuchidae, Lophopidae and Erybrachyidae; 6–7 are plesiomorphies of *Celinapterixini*; 8 is convergently present in Tettigometridae, Tropicuchidae, Issidae, Nogodinidae and Flatidae; 9 is present in Nogodinidae (except Lipocallini); 10 is a synapomorphy of Nogodininae; 11 is convergently (?) present in Nogodinini and Sassulina, and a plesiomorphy (?) of *Celinapterixini*; 12 seems to be a plesiomorphy shared with *Henriksenopterix*; 13–14 are present in Nogodinidae, Tropicuchidae and Lophopidae but absent in Ricaniidae (Shcherbakov 1981); 15 seems to be a symplesiomorphy of *Celinapterixini* and Gastriniinae; 16–23 are autapomorphies of *Celinapterixini*, with character 23 convergently (?) present in *Henriksenopterix*.

Genus CELINAPTERIX gen. nov.

Derivation of name. Greek *ptērix*, wing, and dedicated to Maria 'Celina' Digiani.

Type species. *Celinapterix bellissima* sp. nov.

Diagnosis. As for *Celinapterixini*.

Celinapterix bellissima gen. et sp. nov.

Text-figures 2–3

Derivation of name. Latin *bellissimus* (superlative of *bellus*), meaning the most beautiful; referring to the beauty of the specimen.

Holotype. Specimen MLP 29016, in the Departamento Científico Paleozoología Invertebrados, Museo de La Plata, Argentina.

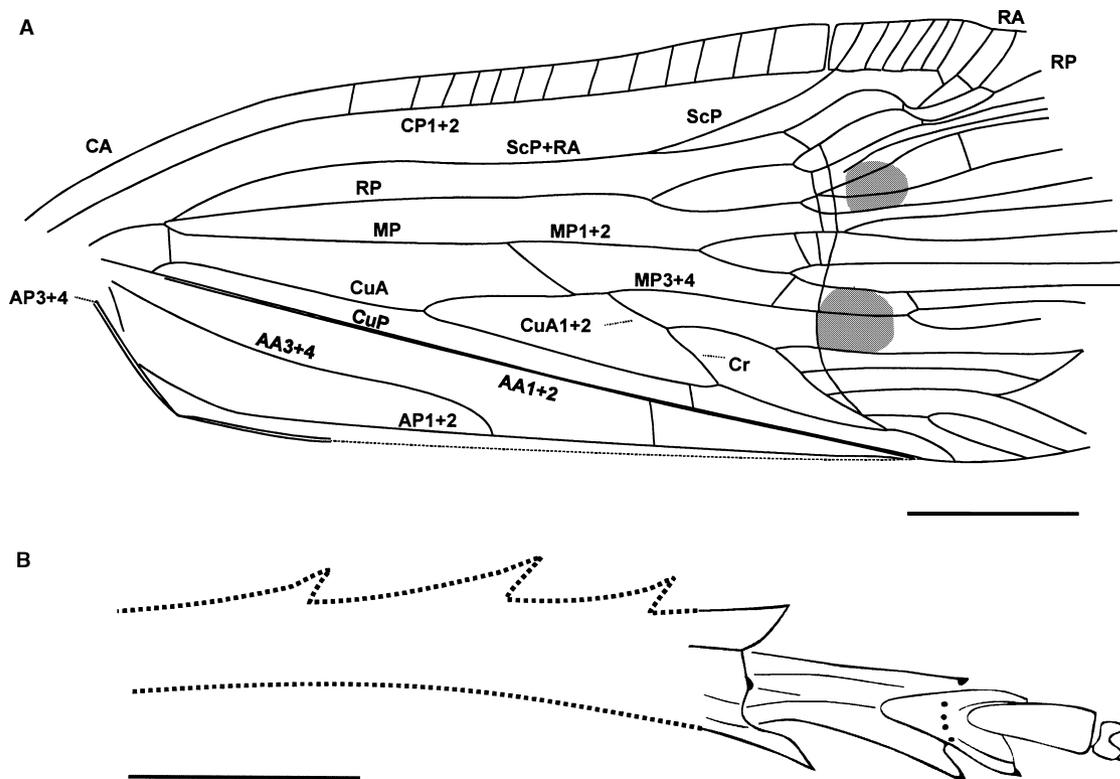
Type locality and horizon. La Cuesta Azul, province of Jujuy, north-west Argentina, at latitude 24°19' S, longitude 64°28' W (Petrulevičius 2001). Maíz Gordo Formation, late Palaeocene (Volkheimer *et al.* 1984; Marshall *et al.* 1997; Quattrocchio *et al.* 1997).

Diagnosis. As for *Celinapterixini*.

Description. Part and counter-part of a forewing (with the extreme apex missing) and hind leg tarsi; hindwing fragments poorly preserved; trace of coloration preserved.

Forewing: length of the preserved part, 6.5 mm; width of the preserved part, 2.56 mm; tenuous crossveins in all membrane; middle part of CA, CP1+2 and ScP+RA slightly concave (posteriorly curved); area between CP1+2 and CA developed and with numerous (distally preserved) veins; ScP+RA and RP free from

the base of the wing, just after separation of MP; basal stem from which veins ScP+R and M arise; RA1+2 and RA3+4 sinuous; RP sinuous, follows RA; RA passing into the anterior margin (basal to the antero-apical angle) of wing; ScP ending at the vein CP1+2 and diverging from RA at the same level of the bifurcation of RP1+2 and RP3+4; MP bifurcating at one-half of the second third of the wing; crossvein between bases of MP and CuA (= arculus of Shcherbakov 1981); basal cell (of Shcherbakov 1981) short, broad and subtriangular in shape; MP3+4 fused shortly with CuA1+2 (without a crossvein between them); row of unaligned transverse veinlets distal of rp-mp and mp-cua crossveins; CuA and CuP bifurcating at the base; CuA running parallel to CuP; CuA1+2 bifurcating at 45 degrees at the end of first third of the wing and fusing with MP3+4; CuA1+2 with five main branches, the anterior and the posterior divided into two main veins; crossvein between CuA1+2 and CuA3+4 closing a cell cua; CuA ending somewhat sigmoid at wing margin distal to CuP; postero-basal to antero-distal line of crossveins (two preserved) after distal end of CuA veins; straight CuP ending at the beginning of the distal fourth of the wing, forming a long clavus; closed clavus ending somewhat before the postero-distal apex of the wing; short and distinctive distal crossvein between CuA3+4 and CuP; AA1+2 runs parallel to CuP; claval suture pronounced; AA3+4 ending at median part of posterior portion of AP1+2 (nearly at a right angle); AP1+2 diverging at distal third of the basal margin of the clavus, running distally, and ending in AP3+4 just before the end of the clavus; AP3+4 running parallel



TEXT-FIG. 2. *Celinapterix bellissima* gen. et sp. nov., holotype MLP 29016. A, left wing from counterpart; scale bar represents 1 mm. B, hind tarsus from part; scale bar represents 0.2 mm.

(nearly touching) the basal margin of the clavus, touching the margin at the postero-basal corner and then running parallel to (nearly touching) the posterior margin of the clavus; tenuous crossveins between AA1+2 and AA3+4; numerous veinlets between CP1+2 and ScP, CuA and CuP, and AA1+2 and AP1+2.

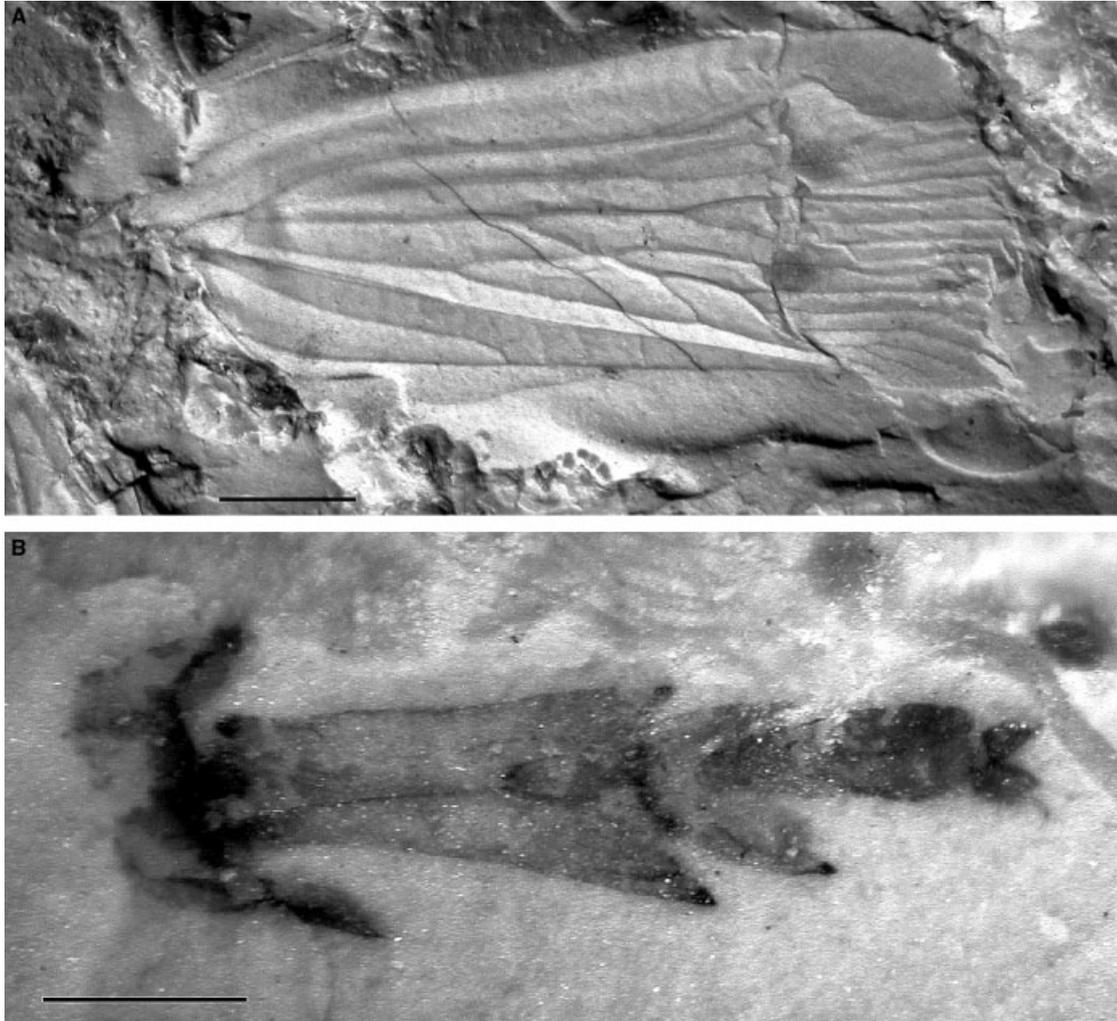
Tibia and tarsus of hind leg: distal part of the tibia with three lateral spines and two well-developed apical spines; first tarsus with two well-developed spines and an apical, slightly curved, row of four preserved teeth (originally six?); second tarsus small with two well-developed spines (one is covered by the hind tarsus); length ratio of the basitarsus/third tarsus is 1:0.5; length ratio of the basitarsus/second tarsus is 1.5:1; length ratio from each point of insertion (dorsal view) (excluding spines length) of the basitarsus/second tarsus is 1.4/5; arolium developed with two lobules; one curved claw preserved.

Discussion. Following the phylogenetic system of Cimicida (= Homoptera + Heteroptera) proposed by Shcherbakov and Popov (2002), *Celinapterix* gen. nov. possess two synapo-

morphies of the Fulgoroidea: (1) forewing with short basal cell; (2) long AA3+4 + AP1+2 (1A + 2A of Shcherbakov and Popov, 2002) entering the commissural margin before the claval apex.

Emeljanov (1990) proposed a phylogenetic system for the Fulgoroidea. He included the families Achilixiidae, Hypochthonelidae and Gengidae in the Achilidae, Flatidae and Eurybranchyidae, respectively. The Acanalonidae was included in the Issidae, and the Bladininae was removed from the Nogodinidae and placed in the Issidae. Following the system proposed by Emeljanov (1990), *Celinapterix* possesses one of the synapomorphies of all Fulgoroidea except the Tettigometridae, i.e. loss of the basibital plate in forewings. *Celinapterix* cannot be included in the Tettigometridae because the AA3+4 + AP1+2 passes into Ap3+4 at a considerable distance from the apex of the clavus and the CP is at or near the anterior margin without crossveins between them (Shcherbakov 1981).

Emeljanov (1990) proposed a synapomorphy of the group formed by the Achilidae, Dictyopharidae, Fulgoroidea, Issidae, Nogodinidae, Ricaniidae, Flatidae, Tropiduchidae, Lophopidae



TEXT-FIG. 3. Reconstruction of *Celinapterix bellissima* gen. et sp. nov. from part and counterpart, holotype. A, wing; scale bar represents 1 mm. B, hind tibia and tarsus; scale bar represents 0.5 mm.

and Eurybranchyidae, i.e. V-shaped amplification of the veins R (?) (ScR of Emeljanov 1990) and AA3+4 + Ap1+2 in the forewings. This character is not obvious in *Celinapterix* and presents homoplasy in different genera of different families, i.e. *Ommatidiotus* (Issidae) and *Bladina*. Even genera belonging to basal families, such as Cixiidae (*Pintalia*), have some V-shaped amplification of these two veins.

Celinapterix shares with the group formed by the Issidae, Nogodinidae, Ricaniidae, Flatidae, Tropiciduchidae, Lophopidae and Eurybrachyidae two synapomorphies of the forewing, i.e. AA3+4 + Ap1+2 (claval vein of Emeljanov 1990) ending at the apex of the clavus and CP with crossveins to the costal margin. The families Tropiciduchidae, Lophopidae and Eurybrachyidae share one synapomorphy that is absent in *Celinapterix*, i.e. in frontal view, an approximately lanceolate marginal cell behind the apex of the clavus (Emeljanov 1990). Other differences are listed as features of these families: in the Eurybrachyidae the CP is developed just to the mid length of the wing; in Lophopidae and Tropiciduchidae the trunk of ScP+RA + is RP longer than the basal trunk (CP3+4 + ScP + R + M). The other difference that excludes the Eurybrachyidae, Lophopidae and Tropiciduchidae is the presence in *Celinapterix* of a large, broad, basal cell, a character absent from these families. *Celinapterix* could not be included in the Ricaniidae, Eurybrachyidae or Lophopidae because the second tarsus of the hind leg has two spines. It also could not be included in the Ricaniidae for the same reasons that *Henriksenopterix* is excluded, i.e. RA passes into the anterior margin (basal to the antero-apical angle) of the wing, and the postero-apical angle is more or less distant from the apex of the clavus. The Ricaniidae have the apomorphic states of these characters, i.e. RA passes into the antero-apical angle of the wing, and the postero-apical angle immediately beyond apex of clavus. *Celinapterix* cannot be included in the Issidae because of its broad basal cell; in the Issidae the basal cell is obsolete or narrow (Fennah 1954; O'Brien and Wilson 1985). The Issidae *sensu* Emeljanov (1999) have (among other characters) monomorphic, coriaceous and convex forewings. Regrettably, *Celinapterix* lacks ovipositor characters. These possess the main characters postulated by Emeljanov (1990, 1999) to separate the Nogodinidae from the Issidae. Other differences with the Issidae are features of the different subfamilies: in the Caliscelinae the RP diverges from the ScP+RA at about the level of the apex; in the Tonginae and Trienopinae the postero-apical wing angle is coincident with the apex of the clavus, and the RA has many long branches in the basal half of the wing; in the Issinae the CP is not developed and there are no crossveins to the costal margin. *Celinapterix* cannot be included in the Flatidae because the clavus is tuberculate and the basal cell is narrow.

Celinapterix can be included in the Nogodinidae: Nogodininae because it has the unique synapomorphy of the taxon (i.e. a broad basal cell). It also has a second tarsus with two long spines, a character convergently (?) present in the Tettigometridae, Tropiciduchidae, Issidae, Nogodinidae and Flatidae. The Nogodinidae *sensu* Fennah (1978, 1984, 1987) contains two subfamilies and six tribes based on characters of the ovipositor, tarsi and wing venation. All the remaining genera of the family not included in the Gastriniinae Fennah, 1987 are here considered to be Nogodininae. Thus, the Nogodininae including the

Nogodinidae *sensu* Fennah (1978, 1984) have a broad basal cell, and the second tarsus with two long spines. In the Gastriniinae the ScP+R is fused for a long distance to the CP, the MP diverges distally, the basal cell is absent and CuA is without branches. Fennah (1987) noted that the first tarsus in the Gastriniinae is much longer (about double the length) than in the other Nogodinidae (see Fennah 1987, p. 365, Text-fig. 6). In the Nogodininae the basitarsus and second tarsus are subequal. The presence of a basitarsus that is longer than the second tarsus is also observed in *Celinapterix*, which probably implies that these taxa are symplesiomorphic.

Among the Nogodininae, the presence of a row of spines on the apical margin of the hind basitarsus excludes its attribution to the tribe Lipocallini (Fennah 1984). The tribes Epacriini and Bladinini are excluded because *Celinapterix* has a row of unaligned transverse veinlets distal of rp-mp and mp-cua crossveins. An aligned row of transverse veinlets distal of these crossveins is present in the Varsiini: Sassulina and the Nogodinini, but this character could be due to convergence in these two tribes because the Nogodinini have a strong row of crossveins, and in the Sassulina the row is weak. On other hand, this character is in conflict with the character 'presence/absence of setose eminence distal to the spines', present in all Varsiini (Sassulina+Varciina) and absent in Nogodinini (Fennah 1978). The presence of a row of unaligned transverse veinlets distad of rp-mp and mp-cua crossveins seems to be an autapomorphy of *Celinapterix*.

Celinapterix has a slightly curved row of four preserved teeth in the distal part of the hind basitarsus. The disposition of the teeth seems to be different from the curved arrangement present in the Pisachini and Varciini. Thus, it is possible that there is no setose eminence distal to the spines, and that *Celinapterix* cannot be included in these tribes. The tribes without the setose eminence (which seems to be a plesiomorphy) are the Nogodinini, Epacriini, Bladinini and Mithymnini (*sensu* Fennah 1984). The Mithymnini could be excluded because of their submarginal CP and specialized wings, and the Nogodinini could be excluded because (as in other Nogodininae) the hind basitarsus and second tarsus are about the same length.

Celinapterix has a sigmoid RA, a character also present in other Nogodinidae such as *Henriksenopterix* (see above), Varsiini: Sassulina as *Sassula* and *Mindura*, and *Bladinini*: Gaetuliina as *Gaetulia* and *Salona*. This character could be regarded as present in the stem group of the Nogodinidae and either lost or acquired many times during the evolution of the group. Regardless, *Celinapterix* has a sigmoid RA and first vein of RP, as any other Nogodinidae.

Celinapterix has a developed ScP and a hind basitarsus about 1.5 times the length of the second, which seems to be plesiomorphic at familial level. Other characters seem to be apomorphic, i.e. (1) unaligned row of transverse veinlets distal of rp-mp and mp-cua crossveins; (2) RA and first vein of RP sigmoid; (3) third tarsus about half the length of the basitarsus; (4) CuA with a divergent CuA1+2 (diverging at an acute angle from CuA3+4) resulting in a large cell (closed by a crossvein); (5) MP and CuA partially fused so the distal mp-cua crossvein is lost; (6) broad subcostal area; (7) middle part of CA and CP1+2 slightly concave (posteriorly curved); (8) smooth venation. These characters allow the erection of a new taxon at suprageneric level (*Celinapterixini*) among the Nogodininae.

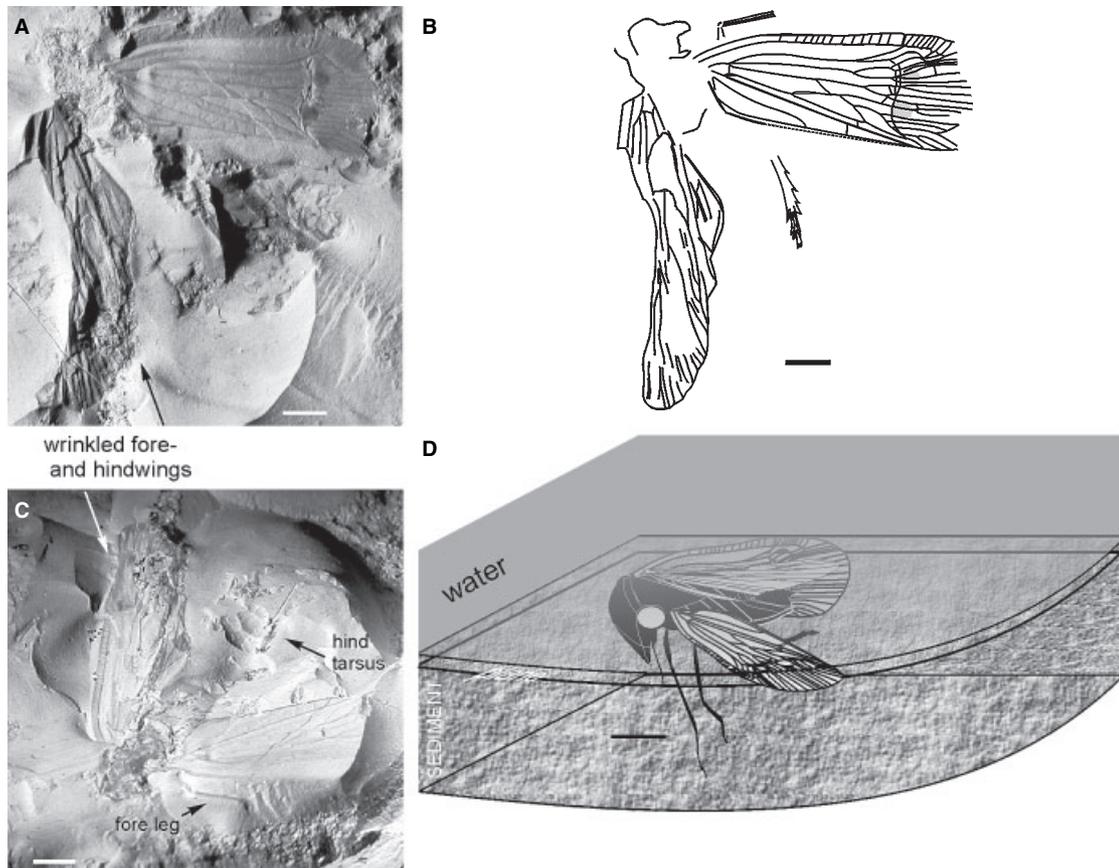
All other fossil representatives of the Nogodinidae are unrelated to *Celinapterix*, and some of them are included in recent tribes. The American fossils included in the Nogodininae are *Tonacatecutlius gibsoni* from Mexican amber (Stroiński and Szwedo 2000) and *Tainosia quisqueyae* from Dominican amber (Szwedo and Stroiński 2001). These species possess all of the characters of Nogodinini: Nogodinina (Szwedo and Stroiński 2001). *Tritophania patruelis* (Jacobi (1937) and *Eobladina antiqua* (Haupt 1956) recorded from Europe belong to the Bladinini (Szwedo and Stroiński 2001). The latter is a Nogodinidae as Haupt (1956) noted (contrary to Carpenter 1992; who placed it in the Ricaniidae), but the internal relationships within the Bladinini are not clear because of its fragmentary condition. The presence of a long stalk between ScP + R in *T. patruelis* and *E. antiqua* excludes any relationships with *Celinapterix*.

TAPHONOMY

The taphonomy of the insect assemblages of the Maíz Gordo Formation has been discussed by Petrulėvičius (2001, 2002). Taphonomic cycles were identified and

interpreted as palaeoenvironmental cycles probably related to Milankovitch orbital cyclicity (Petrulėvičius 2002). Of 7758 taphonomic elements (insects) recovered from the formation at five localities, only 0.09 per cent are considered to be complete articulated specimens. The remaining 99.91 per cent of specimens are disarticulated and fragmented, and are mainly represented by Coleoptera elytra.

Thus the insect described herein is a rare example of an articulated specimen. It is embedded in a matrix of green pelitic mudstone (Text-fig. 4). The visible elements are three wings and one fore leg, articulated to the body, and the tibia and tarsus of the hind leg. The left forewing is parallel to the bedding plane; the right wings and the legs are oblique to it (Text-fig. 4C–D). The tarsus and tibia of the hind leg are articulated, with the tarsus parallel to the bedding plane, but the tibia is oblique. The tarsus is 0.4 mm beneath the wings. The wings are three-dimensionally preserved, retaining all convex–concave details in the venation. The forewing parallel to the bedding plane is not deformed; the oblique wings are



TEXT-FIG. 4. *Celinapterix bellissima* gen. et sp. nov. A, photograph from above (general habitus of the counterpart). B, composite reconstruction from above (general habitus of the counterpart). C, photograph in perspective of the stratification plane (general habitus of the part). D, interpretation of early fossil-diagenesis. The left forewing is parallel to the bedding plane; right wings and legs are oblique. The tarsus is parallel to the bedding plane, whereas the tibia is oblique. Scale bars represent 1 mm.

deformed and wrinkled (Text-fig. 4A-C). The forewing has two circular brown spots in the distal part of the remigium. The visible legs are brown in colour. The other legs are apparently preserved but are deeply embedded in the matrix. The body is preserved as an amorphous mass readily distinguishable from the surrounding sediment.

Interpretation. The nogodinid is an ademic (terrestrial) organism from the lake. It seems that the production of the taphonomic element was simultaneous with the death of the plant hopper. This could have occurred either on the water surface or on the lake bottom; the allo-/autochthony cannot be precisely established. Insects with a low surface/volume ratio sink faster than those with a higher ratio (Martínez-Delclòs and Martinell 1990). The plant hopper presumably had a large surface area as at least three wings were spread. It could have died on the water surface if the surface tension of the water was not surpassed.

The usual configuration of a buoyant winged insect (Petrulevičius pers. obs.; see Martínez-Delclòs and Martinell 1993, pl. 1, fig. G) is with wings, thorax and head touching the surface of the water, the abdomen slightly bent down, and legs pointing downwards. Insects that sink in a calm environment fall slowly without modification of this configuration (Martínez-Delclòs and Martinell 1993). Thus, the described fossil appears to have remained in the original buoyant position when it sank in a low-energy environment.

The situation in which articulated specimens have a long biostratinomy is possible with the concurrence of anoxic and calm conditions. Experiments have shown that insects (Vespidae and Muscidae) may remain articulated and intact for up to one year after sinking in anoxic, calm (and dark) conditions set up in the laboratory (Peñalver Molla 2002). In the case of the fossil considered herein, the biostratinomic process seems to have been short, as the body is preserved as an amorphous mass, and the wings and legs with tarsus and claws are still articulated.

Full articulation of specimens is uncommon at the La Mendieta locality and in general in the Maíz Gordo Formation (based on examination of 18,600 insects recovered from five localities; Petrulevičius 2001, 2002). However, the vast majority of specimens (disarticulated or articulated) are preserved three-dimensionally, with their original thickness retained, and undeformed. Three-dimensional preservation of specimens is interpreted as a result of the absence of compressional deformation during fossil-diagenesis.

The insect is considered to have sunk through quiet water. On reaching the bottom it sank into a soupy substrate (Text-fig. 4D). Fossil-diagenesis seems to have occurred over an extended period of time but in a highly stable system because the soft parts of the body occur as

a decomposed amorphous mass. Although it is not possible to demonstrate a lack of micro-organism activity during biostratinomy, it is certain that micro-organism decomposition took place as the body has completely disintegrated but the appendages and wings remain attached.

CONCLUSIONS

The specimen described herein is of interest because the Nogodinidae have a very poor fossil record. It is one of the oldest representatives of the Nogodinidae and the first fossil from South America. Its latest Palaeocene age post-dates the Cretaceous isolation of South America; it probably represents an extinct lineage present on this continent during the Paleogene. However, the antiquity of the family is demonstrated by its subtropical cosmopolitan distribution (i.e. it is older than the Cretaceous isolation of South America). The specimen provides another example of the exceptional diversity of fossil insects preserved in the Maíz Gordo Formation. The insect is presumed to have fallen into a low-energy lacustrine environment where it sank through the water column and was embedded by its own weight in soupy sediment. Decomposition of soft-body parts occurred, but there was no compressional deformation.

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