

A NEW DAMSELFLY FAMILY FROM THE UPPER PALAEOCENE OF ARGENTINA

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ABSTRACT. A new family of damselflies, based on *Latibasalia elongata* gen. et sp. nov. and *L. quispeae* gen. et sp. nov., is erected from the Upper Palaeocene Maíz Gordo Formation, north-western Argentina. Latibasaliidae fam. nov. can be included in the Zygoptera: Caloptera: Eucalloptera: Amphipterygida: Amphipterygoidea. Its phylogenetic relationships within the clade Eucalloptera Bechly, 1996 are discussed. Within Amphipterygoidea, Latibasaliidae could be closely related to Pseudolestidae or to the 'thamatoneurid' genera *Petrolestes* and *Congqingia* because they share the absence of secondary antenodal crossveins of first and second rows and the absence of antesubnodal crossveins. These characters could be potential synapomorphies of these taxa but they are somewhat homoplastic within the Zygoptera.

KEY WORDS: Insecta, Odonata, Zygoptera, Latibasaliidae, Latibasalia, Late Palaeocene, Argentina.

THE oldest representatives of the clade Amphipterygoidea Selys, 1853 (*sensu* Bechly 1996) are *Euarchistigma* Carle and Wighton, 1990 (Lower Cretaceous of Brazil, included in Thamatoneuridae Tillyard and Fraser, 1938 by Bechly 1999), and *Congqingia* Zhang, 1992 (Upper Jurassic of China; Zhang 1992). Bechly (1996) synonymized the Congqingiidae Zhang, 1992 with the Thamatoneuridae: Dysagrionae Cockerell, 1908. The Lower Cretaceous *Cretarchistigma* Jarzembowski *et al.*, 1998 (with two species, *C. greenwoodi* Jarzembowski *et al.*, 1998 and *C. (?) essweini* Bechly, 1998) was originally considered to be related to *Euarchistigma*, but Bechly (1998a, 1999) transferred it to the Zygoptera '*Familia incertae sedis* (probably Hemiphlebiidae)'. The Dysagrionae is also represented in the Palaeogene of North America by the genera *Petrolestes* Cockerell, 1927, *Dysagrion* Scudder, 1878 and *Phenacolestes* Cockerell, 1908 (Cockerell 1908, 1927). The Eocene genus *Protamphipteryx* Cockerell, 1920 (Green River Formation, USA) may belong to the modern group Amphipterygidae but it is rather poorly described and needs revising (Cockerell 1920; Nel and Paicheler 1993). Thus, the present discovery of a fossil wing in deposits of late Palaeocene age in Argentina, representing new taxa clearly related to the Amphipterygoidea, is of great interest for better understanding the past diversity of this group.

The specimens were collected from green shales of the Maíz Gordo Formation in north-west Argentina at latitude 24°20'S, longitude 64°28'W (Petrulevičius 2001). This formation has been considered to be late Palaeocene in age by several authors (Volkheimer *et al.* 1984; Marshall *et al.* 1997; Quattrocchio *et al.* 1997).

The specimens are stored in the Departamento Científico Paleozoología Invertebrados, Museo de la Plata, La Plata (MLP). They were originally partly covered by sediment, and were prepared with a pneumatic hammer. Drawings and photographs were taken with the specimens under 96 per cent alcohol for better observation of the wing venation.

We follow the wing venation nomenclature of Riek (1976) and Riek and Kukalová-Peck (1984) as amended by Kukalová-Peck (1991), Nel *et al.* (1993) and Bechly (1996). The higher classification of fossil and extant Odonoptera and the familial and generic characters followed here are based on the phylogenetic system proposed by Bechly (1996). A new term 'nodal cell' (Text-fig. 4A-B) is introduced to describe the autapomorphic nodal structure present in the new family (see below for details).

SYSTEMATIC PALAEONTOLOGY

Order Odonata Fabricius, 1793

Euzygoptera Bechly, 1996

Family Latibasaliidae fam. nov.

Type genus. Latibasalia gen. nov.

Phylogenetic definition. Latibasaliidae fam. nov. includes all damselflies that are more closely related to *Latibasalia elongata* gen. et sp. nov. than to any of the type species of the other type genera of the Zygoptera family-group taxa *sensu* Bechly (1996) (stem-based definition).

Diagnosis. All known characters are from the wing: (1) terminal kink of the CP reduced; (2) nodal furrow reduced; (3) midfork symmetrical and recessed basally to a position between 12 and 26 per cent of wing length; (4) pterostigmal brace vein not present; (5) discoidal cell more or less rectangular; (6) coloured wings; (7) lestone oblique vein absent; (8) all secondary antenodal crossveins between ScP and RA distal of Ax₂ suppressed; (9) antesubnodal space without crossveins; (10) cubito-anal area broad, with at least three rows of cells between CuA and posterior wing margin; (11) MAb highly obliquely directed towards wing base; (12) presence of a 'nodal cell', distally limited by a strongly developed first postnodal crossvein and forming a triangle or quadrangle with ScP and nodal Cr (strict autapomorphy); (13) a smooth 'Z-like' kink of ScP at nodus; (14) postnodal and postsubnodal crossveins very numerous but not aligned; (15) at least CuA, MP and MA reaching posterior wing margin at right angle; (16) at least 2–3 long secondary longitudinal veins between all the main longitudinal veins; (17) nodal Cr and subnodal crossvein very oblique and strong; (18) nodal Cr branching from ScP distinctly basal of fusion of ScP with costal margin; (19) base of RP2 several cells distal of subnodus.

Remarks. Characters 1 and 2 are potential (but dubious) synapomorphies of the Zygoptera. Characters 3 and 4 are synapomorphies of the Caloptera Belyshev and Haritonov, 1983 (*sensu* Bechly 1996). Characters 5–7 are synapomorphies of the Eucaloptera Bechly, 1996. Characters 8 and 9 are synapomorphies of the Amphipterygida Bechly, 1996. Characters 10–13 are autapomorphies of Latibasaliidae fam. nov. Characters 10 and 11 are convergently present in the Epallagoidea Needham, 1903 (*sensu* Bechly 1999) (e.g. *Litheuphaea carpenteri* Fraser, 1955, *Parazacallites aquisextana* Nel, 1988 and *Zacallites balli* Cockerell, 1928) and in the amphipterygoid *Thaumatoneura* McLachlan, 1897 (Fraser 1940; Nel and Paicheler 1993; Bechly 1998b). However, no other Odonata, has a vein MAb directed so obliquely towards the wing base as *Latibasalia*. Character 13 is convergently present in Calopterygomorpha Bechly, 1996.

Genus LATIBASALIA gen. nov.

Derivation of name. Latin, *latus*, wide, *basis*, base, and *ala*, wing, after the wide basal part of the wings.

Type species. *Latibasalia elongata* sp. nov.

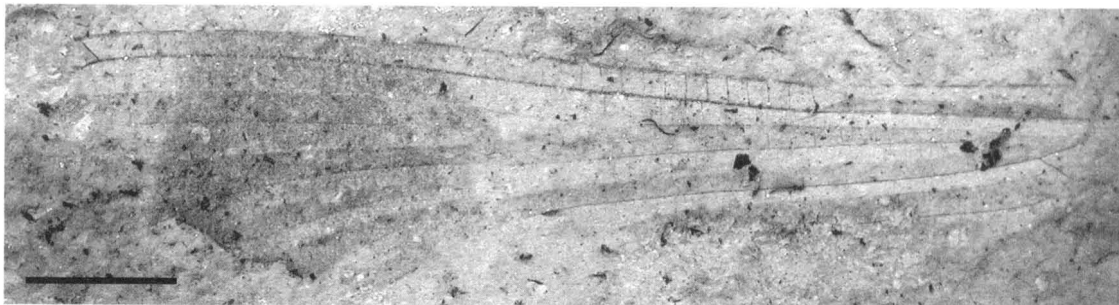
Diagnosis. As for the family.

Latibasalia elongata gen. et sp. nov.

Text-figures 1, 3A, 4A

Derivation of name. Latin, *elongata*, elongated, after the elongated shape of the wing compared to that of *L. quispeae* sp. nov.

Holotype. Specimen MLP 29422, Departamento Científico Paleozoología Invertebrados, Museo de La Plata, Argentina.



TEXT-FIG. 1. *Latibasalia elongata* gen. et sp. nov., holotype MLP 29422; scale bar represents 3 mm.

Type locality and horizon. Province of Jujuy, El Fuerte, latitude 24°20'S, longitude 64°28'W, green shales, Maíz Gordo Formation, late Palaeocene (Volkheimer *et al.* 1984; Marshall *et al.* 1997; Quattrocchio *et al.* 1997).

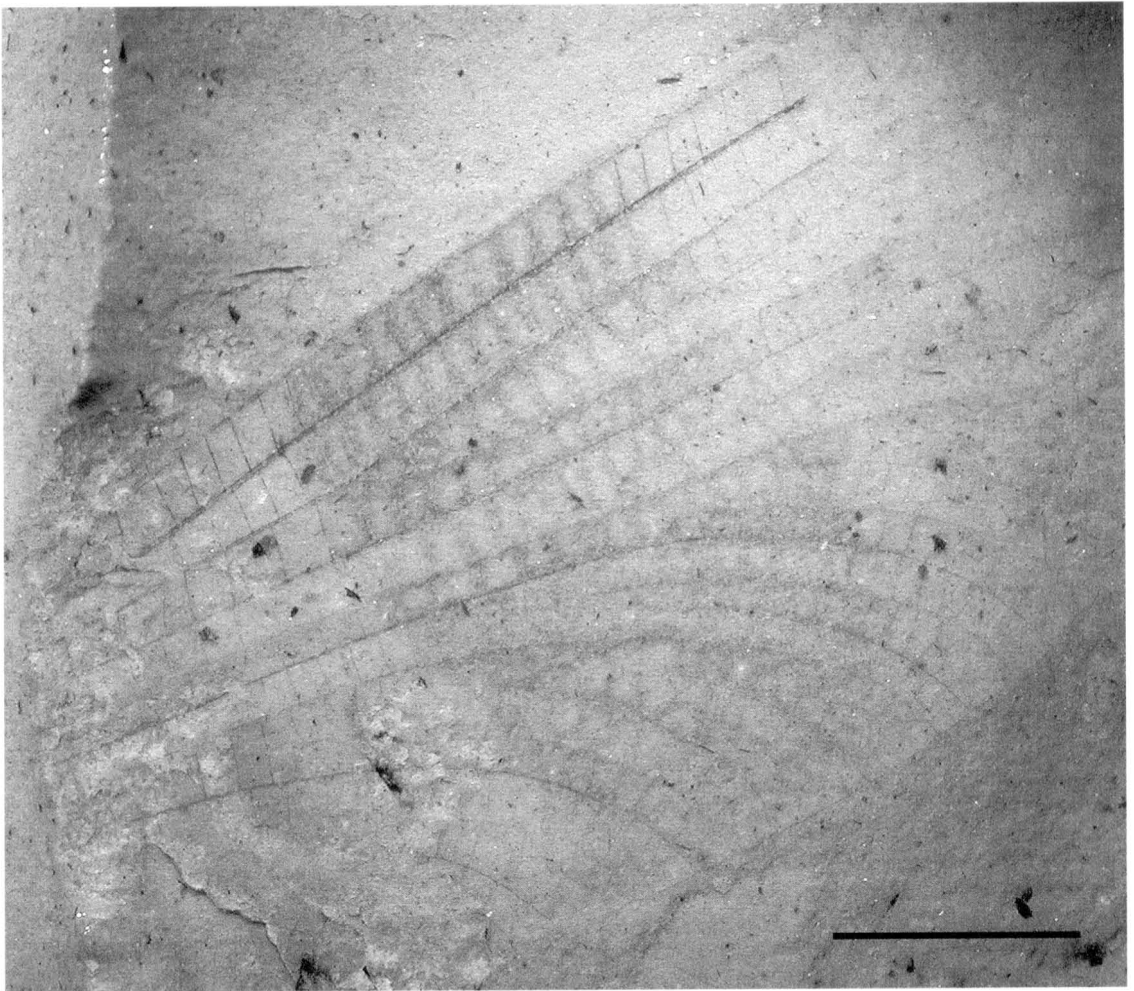
Diagnosis. The main venational characters of this species are as follows: (1) triangular 'nodal cell' formed by ScP, nodal Cr and first postnodal crossvein; (2) base of RP2 well distant from subnodus (eight cells); (3) base of IR1 only three cells distal of that of RI2; (4) wing more slender than that of *L. quispeae* sp. nov.; (5) dark area in a more distal position than in *L. quispeae*; (6) 'Z-kink' of ScP smoother than in *L. quispeae*.

Description. Counter-imprint of a wing with the extreme apex, base and posterior part missing; trace of colouration preserved; length of the preserved part, 19.68 mm; width of the preserved part, 4.86 mm; distance from the distal part of the discoidal cell to nodus, 3.9 mm; from nodus to pterostigma, 14.5 mm; pterostigma 0.4 mm wide at the base, probably covering several cells, anterior side of pterostigma very oblique; no secondary antenodal and antesubnodal crossveins between the level of discoidal cell and nodus, primary antenodal crossveins not preserved; midfork of RP into RP1/2 and RP3/4 symmetrical and at the same level as bifurcation of MA into MAa and MAb, five cells basal of nodus; distal part of discoidal cell rectangular and free of crossveins; posterior margin of discoidal cell (= MP + CuA) exactly aligned with MP; MAb directed towards wing base, with a rather strong obliquity; basal free part of CuA rather long (0.4 mm) and aligned with MAb; distal of its fusion with AA, CuA is simple, not forked; at least three rows of cells between CuA and posterior wing margin; at least two long and curved secondary longitudinal veins in cubito-anal area; presence of a smooth 'Z-like' kink of ScP at nodus; nodal Cr and subnodus vein very oblique and strong; nodal Cr branching from ScP 0.4 mm basal of the fusion of ScP with costal margin; first postnodal crossvein strongly developed, distinctly stronger than other postnodal crossveins, and forming a triangle with ScP and nodal Cr that we propose to name 'nodal cell' (Text-fig. 4A–B); subnodus vein strong; terminal kink of the CP reduced; nodal furrow reduced; 21 preserved postnodal crossveins located about 0.4 mm apart (probably about 40 postnodal crossveins in total); 22 preserved postsubnodal crossveins; postnodal and postsubnodal crossveins not aligned; presence of a dark strip covering one-third of the length of the area between nodus and pterostigma, situated four cells basal of pterostigma, with poor quality preservation of the fossil (crossveins are not visible in this area); base of RP2 at about 11 cells distal of subnodus; base of IR1 about three cells distal of that of RP2; basally one row of cells in the area between CuA and MP, probably distally greatly widened; also one row of cells in postdiscoidal area for a long distance; this area is probably distally widened, about 4.6 mm distal of nodus level; area between RP3/4 and MA with one row of cells for a long distance and with at least two or three long secondary longitudinal veins in its distal third; area between RP3/4 and IR2 with at least four long secondary longitudinal veins in its distal half; area between IR2 and RP2 with three long secondary longitudinal veins; area between RP2 and IR1 with two secondary longitudinal veins; area between IR1 and RP1 with one row of cells.

Latibasalia quispeae sp. nov.

Text-figures 2, 3B, 4B

Derivation of name. After Ms. Miriam Quispe, a friend from El Fuerte.



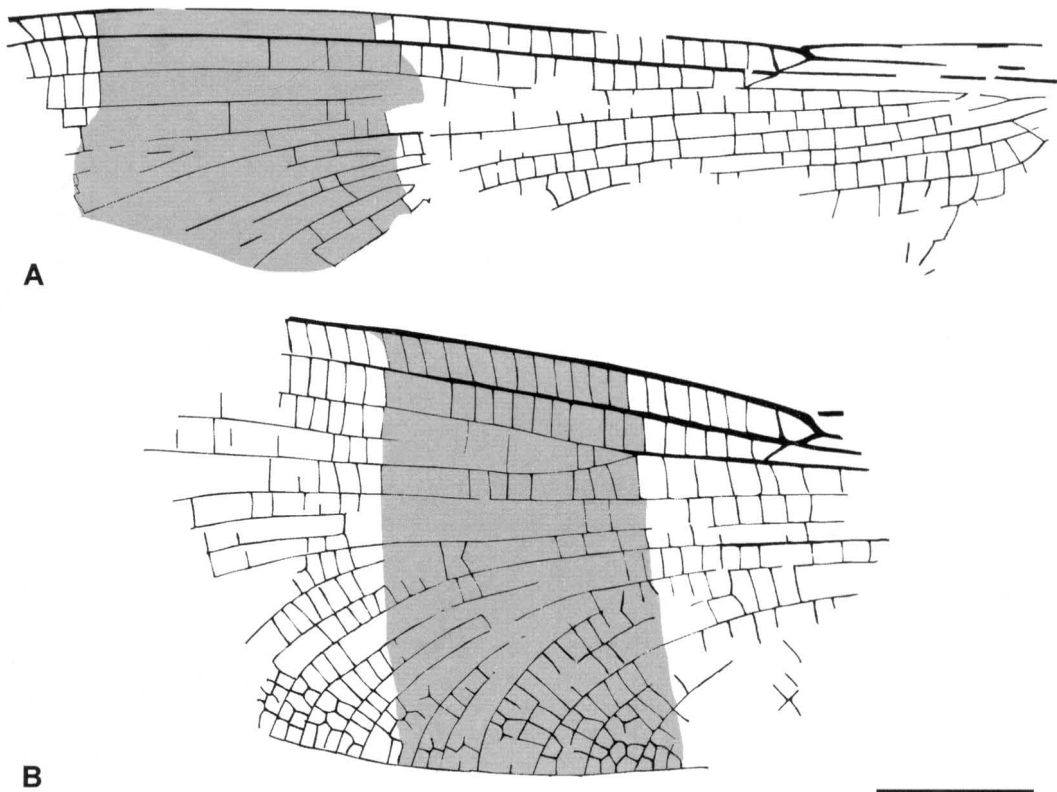
TEXT-FIG. 2. *Latibasalia quispeae* gen. et sp. nov., holotype MLP 29423; scale bar represents 3 mm.

Holotype. Specimen MLP 29423, Departamento Científico Paleozoología Invertebrados, Museo de La Plata, Argentina.

Type locality and horizon. As for *Latibasalia elongata*.

Diagnosis. The main venational characters of this species are: (1) quadrangular 'nodal cell' formed by ScP, nodal Cr, RA and first postnodal crossvein; (2) base of RP2 only four cells distal of subnodus; (3) base of IR1 eight cells distal of that of IR2; (4) wing broader than that of *L. elongata* sp. nov.; (5) dark area in a more basal position than in *L. elongata*; (6) 'Z-kink' of ScP stronger than in *L. elongata*.

Description. Counter-imprint of a wing with the apex and base missing; trace of colouration preserved; length of the preserved part, 14.07 mm; width of the wing 8 mm; at least five rows of cells between distal part of CuA and posterior wing margin; at least four long and curved secondary longitudinal veins in cubito-anal area; presence of a smooth 'Z-like' kink of ScP at nodus; nodal Cr and subnodus vein very oblique and strong; nodal Cr branching from ScP 0.4 mm basal of the fusion of ScP with costal margin; first postnodal crossvein strongly developed, distinctly stronger

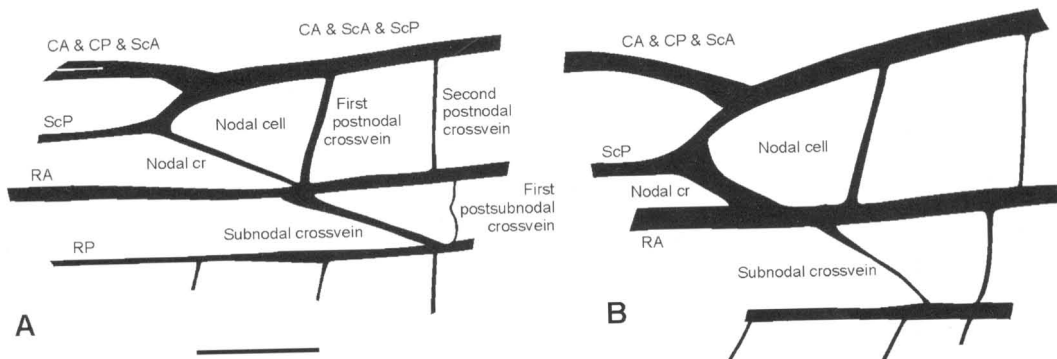


TEXT-FIG. 3. A, *Latibasalia elongata* gen. et sp. nov., holotype. B, *Latibasalia quispeae* gen. et sp. nov., holotype. Reconstruction of general habitus; scale bar represents 3 mm.

than other postnodal crossveins; quadrangular 'nodal cell' formed by first postnodal crossvein, ScP, RA and nodal Cr; short and basally positioned nodal Cr (Text-fig. 4); subnodus vein strong; 25 preserved postnodal crossveins located about 0.4 mm apart; 21 preserved postsubnodal crossveins; postnodal and postsubnodal crossveins not aligned; four cells distal of the subnodus there is a dark strip crossing the wing (wing membrane darkened around crossveins) in a more basal position than in *L. elongata*; base of RP2 at about six cells distal of subnodus; base of IR1 eight cells distal of IR2; CuA distally strongly curved; at least CuA, MP and MA reaching posterior wing margin at right angle; five long longitudinal secondary veins between CuA and MP, distally curved and parallel to MP; two long longitudinal secondary veins between MP and MA; at least three long longitudinal secondary veins between MA and RP3/4; two between RP3/4 and IR2.

Remarks. The type specimens of *L. quispeae* and *L. elongata* are certainly not the fore- and hindwings of the same species because of the great difference in the position of the bases of RP2 and of the form of the 'nodal cell'. In all Zygoptera species, the distal halves of the fore- and hind wing are nearly identical.

Phylogenetic systematics of Latibasaliidae. Following the phylogenetic system proposed by Bechly (1996, 1999), Latibasaliidae fam. nov. could be included in the Zygoptera because it has two of the putative synapomorphies of this clade, i.e. a reduction in the terminal kink of the CP and of the nodal furrow. The third nodal character proposed by Bechly (obliteration of the tubular sclerotized canal of ScP along the venter of the postnodal costal margin) cannot be observed in our fossils. Bechly (1996) established the polarity of these characters on the assumption that the Tarsophlebiidae is the sister group of the 'modern Odonata' (= Zygoptera + Epiproctophora), which remains controversial (Fleck *et al.* in manuscript). The more basal clades Protanisoptera, Triadophlebiomorpha



TEXT-FIG. 4. A, *Latibasalia elongata* gen. et sp. nov., holotype. B, *Latibasalia quispeae* gen. et sp. nov., holotype. Reconstruction of nodal structures, with 'nodal cell'; scale bar represents 0.5 mm.

and Protozogyoptera have the same character states as Zygoptera (Nel *et al.* 2001; Huguet *et al.* in press). Thus, the polarity of these two characters could be contrary to that proposed by Bechly (1996) and the proposed character states plesiomorphic in Zygoptera.

Nevertheless, the Latibasaliidae also shares with the Zygoptera some character states that are absent in the Epiproctophora, i.e. (1) discoidal cell quadrangular, not divided into a triangle and a hypertriangle (plesiomorphy); (2) CuA with no secondary branching into CuAa and CuAb (plesiomorphy); (3) absence of the oblique vein; (4) vein RP2 distally displaced far from subnodus; (5) very numerous and dense postnodal crossveins. The other synapomorphies of the Epiproctophora are unknown in the Latibasaliidae. Thus, even if it is with some uncertainty, their attribution to the Zygoptera is more probable than to Epiproctophora.

The Latibasaliidae shares with Caloptera Belyshev and Haritonov, 1983 (*sensu* Bechly 1996) the presence of a midfork recessed basally to a position between 12 and 26 per cent of wing length (convergent to Lestinoidea and Hypolestinae; Bechly 1996), and an obsolete pterostigmal brace vein. Within this clade, *Latibasalia* cannot be included in Sieblosiidae Handlirsch, 1907 because in this family the nodal and subnodal veinlets are less oblique and with a transverse or even with reversed obliquity. In addition there is a highly specialised nodus that seems to be traversed by the ScP because the terminal kink of CP is shifted basally together with the nodal and subnodal veinlets, and the nodal membrane sclerotisation is reduced (Bechly 1996).

The Latibasaliidae has nearly all the synapomorphies of Eucaloptera Bechly, 1996, i.e. (1) rectangular discoidal cell; (2) reduced lestine oblique vein; (3) strong tendency towards coloured wings (convergent to Eurypalpida). The very oblique basal margin of the pterostigma developed as an apparent secondary branching of RA, which Bechly (1996) considered to be a synapomorphy of the Eucaloptera, is highly homoplastic within this group. For example, in many Eucaloptera, the pterostigma is reduced or absent, and in *Dysphaea* Selys, 1853, the obliquity of its basal margin is reversed. Furthermore, the pterostigma of some other Zygoptera also have a very oblique basal margin (some Megapodagrionidae, *Paraphlebia* Hagen, 1861 and *Philogenia* Selys, 1862 among others). The pterostigma of Latibasaliidae has an oblique basal margin, but it is not developed as an apparent secondary branching of RA.

The Latibasaliidae does not fit into the sister group of Amphipterygida, the Calopterygomorpha Bechly, 1996, which has very numerous and dense antenodal crossveins (distance less than 1.0 mm). The presence of a 'Z-like' kink in ScP at the nodus in the Latibasaliidae is probably a convergence with the Calopterygomorpha and most Anisoptera.

Within the Eucaloptera, the Latibasaliidae shares with Amphipterygida Bechly, 1996 the following characters: (1) all secondary antenodal crossveins between ScP and RA distal of Ax2 suppressed, also convergently present in *Litheuphaea* (Bechly 1998b); (2) antesubnodal space at least without crossveins in its basal half. Bechly (1996) gave no wing venational autapomorphies of Diphlebiidae Heymer, 1975 (= Diphlebiinae + Philoganginae). The Philoganginae Kennedy, 1920 have very slender wings with parallel costal and hind margins, and antesubnodal crossveins and antenodal crossveins of the first and second rows are present. The Diphlebiinae have antenodal crossveins in the first row, unlike the Latibasaliidae.

The Amphipterygoidea Tillyard, 1917 shares with the Latibasaliidae the presence of a nodus in a very basal position (distinctly at less than 40 per cent of wing length), and a midfork that is further recessed basally (Bechly 1996). *Latibasalia* cannot be included in the Pseudolestidae Fraser, 1957 because it has the following characters: (1) wide cubito-anal area; (2) highly specialized nodus with a nodal cell; and (3) MAb obliquely directed towards wing base.

Latibasalia shares with the Thaumtoneuridae Tillyard and Fraser, 1938 the antesubnodal space without any

crossveins, but this character is also convergently present in the Diphlebiinae, Pseudolestidae, Rimanellidae and Euzygoptera. It cannot be included in the Thaumtoneuridae because: (1) it has no crossveins in the antenodal space; (2) in this family, the basal costal margin between wing base and nodus is distinctly curved. Character 2 is a synapomorphy of Thaumtoneuridae *sensu* Bechly (1996). This family includes the Thaumtoneurinae (fossil *Euarchistigma* Carle and Wighton, 1990 and Recent *Thaumtoneura* McLachlan, 1897) and the fossil Dysagrioninae (*Petrolestes* Cockerell, 1927; *Congqingia* Zhang, 1992; *Dysagrion* Scudder, 1878; and *Phenacolestes* Cockerell, 1908). *Latibasalia* does not have the synapomorphies of the Thaumtoneurinae: (1) nodus in an extremely basal position; (2) subnodus between the bases of IR2 and RP3/4 that are strongly shifted basally, these correlating with a large number of postnodal crossveins; and (3) a perfectly rectangular discoidal cell. It also does not have the synapomorphy of the Dysagrioninae, namely the unique shape of the discoidal cell. It cannot be considered a representative of the stem group of Thaumtoneuridae because of its several autapomorphies (see diagnosis), nor can it be included in the Amphipterygidae Tillyard, 1917 because in this family the discoidal vein MAb has a distal obliquity (apex of discoidal cell acute) (Bechly 1996). *Latibasaliidae* is, therefore, a new family of damselflies that fits into Amphipterygoidea. It could be more closely related to Pseudolestidae (or perhaps to the 'thaumtoneurid' genera *Petrolestes* and *Congqingia*) because these share the absence of secondary antenodal crossveins of the first and second rows and of the antesubnodal crossveins, characters that could be potential synapomorphies of these taxa, but they are homoplastic within the Zygoptera.

Taphonomic remarks. The dark zone on the wing of the specimens of *Latibasalia elongata* and *Latibasalia quispeae* are more poorly preserved than the hyaline areas. This zone is interpreted as a dark coloured pattern, and is also present in the wings of many Caloptera. Interestingly, the exact opposite pattern occurs in Messinian Anisoptera: Libellulidae from Italy and Mesozoic Anisoptera: Aeschnidiidae (Fleck and Nel in manuscript), in which dark zones are better preserved. Although the lithologies and taphonomy of the Italian Miocene, and the English Wealden and Chinese Liaoning successions (both Cretaceous) are obviously different, this phenomenon could be related to differing chemical composition of the wing pigments rather than to taphonomic processes.

On the other hand, specimens of *Latibasaliidae* differ in the arrangement of the dark zones, which could be a result of taphonomic processes. The dark zone of the holotype of *Latibasalia elongata* is evenly diffused and in the holotype of *Latibasalia quispeae* it is pronounced around the veins, becoming less dark towards the centre of cells. These differences between dark and hyaline zones could be related to directional alteration (*sensu* Fernández-López 2000) and different durations of biostratigraphic processes.

CONCLUSIONS

These new discoveries support the apparent high level of endemism of the odonatofauna of the Maíz Gordo Formation, previously noted by Petrulvičius *et al.* (1999) and Petrulvičius and Nel (2002), but increased knowledge of the Palaeogene insect fauna of South America is necessary to confirm this hypothesis. Discoveries of new exposures, especially in the northern part of the subcontinent are urgently needed.

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