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Exceptionally well-preserved dragonflies (Insecta: Odonata) in Mexican amber

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Dragonflies (odonatans) are comparatively rare as amber inclusions, and most are not well preserved on account of their size. Here, we report a single piece of Mexican amber with one complete dragonfly and two damselflies. The dragonfly is attributed to the extant gomphid *Erpetogomphus* Selys Longchamps, and the damselflies belong to the extant coenagrionid *Argia* Rambur. Both genera are nowadays distributed widely in Mexico. The new discovery dates the origins of these two genera to the Miocene at least.

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Key words: Gomphides, Coenagrionidae, Odonata, Miocene, Mexican amber.

DRAGONFLIES (odonatans) have been widely reported from Baltic, Dominican, Mexican, Burmese, French, Jordanian, South Dakotan and Lebanese amber (Bechly 1996a, Fleck *et al*. 2000, Bechly & Wichard 2008, Lak *et al*. 2009, Poinar 1996, Nel *et al*. 2010, Azar *et al*. 2010, Ross *et al*. 2016, Zheng *et al*. 2016, 2017, Pinkert *et al*. 2017). They are rare compared with most other insects, but have an extraordinarily high diversity in mid-Cretaceous Burmese amber (Zheng *et al*. 2017), followed by Eocene Baltic and Miocene Dominican amber; other records are scarce. Most previously reported odonatans are damselflies (small, slender dragonflies), whereas true dragonflies are extremely rare (Bechly & Wichard 2008, Pinkert *et al*. 2017, Zheng *et al*. 2017).

The Miocene Mexican amber yields diverse plants, arthropods and a few lizards (Solórzano-Kraemer 2007, Calvillo-Canadell *et al*. 2010), but only two coenagrionid damselflies, *Neoerythromma* sp. and *Nehalennia* sp., have been described previously (Ross *et al*. 2016). Here, we report an amber inclusion with one complete true dragonfly and two damselflies from Mexican amber. The true dragonfly is attributed to the extant gomphid *Erpetogomphus* Selys Longchamps, 1858, and the damselflies belong to the extant coenagrionid *Argia* Rambur, 1842, both currently distributed widely in Mexico.

Geological background

The amber was collected from Simojovel de Allende, Chiapas State, southeast Mexico (the site of a mine; Fig. 1). Mexican (or Chiapas) amber has been found in the La Quinta Formation, Mazantic Shale and Balumtum Sandstone in ascending stratigraphic order, all Miocene strata (Serrano-Sánchez *et al*. 2015). The Chiapas amber is considered to have originated from the leguminosan trees *Hymenaea mexicana* Poinar & Brown, 2002 and *Hymenaea allendis* Calvillo-Canadell *et al.* 2010, which grew along the ancient coast in estuarine habitats resembling modern mangrove forests (Calvillo-Canadell *et al*. 2010). The age of the Chiapas amber is considered to be early Miocene (22.8 Ma) based on the fossil inclusions, isotopic evidence ($^{87}Sr/^{86}Sr$) from gastropod shells and other palaeontological evidence (corals, molluscs and microfossils) from the Finca Carmitto Member (Solórzano-Kraemer 2010, Perrilliat *et al*. 2010, Serrano-Sánchez *et al*. 2015). The resin is interpreted to have been deposited in an estuarine tidal environment (Solórzano-Kraemer 2010, Huys *et al*. 2016).

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Fig. 1. Photograph of an amber mine in Simojovel de Allende, Chiapas State, southeast Mexico.

Material and methods

The amber piece is yellow and translucent, 94 mm long, 64 mm wide and 21 mm thick, weighing 56.4 g (Fig. 2). Photographs were taken using an OLYMPUS Stylus TG-4 camera and the line drawings were prepared from photographs using image-editing software (CorelDraw X7 and Adobe Photoshop CS6). The specimen is currently housed in the Stephen Hui Geiligical Museum of the University of Hong Kong, but will later be moved to Rongxin Amber Museum of Hong Kong. All taxonomic acts established in the present work have been registered in ZooBank (see below), together with the electronic publication LSID: urn:lsid:zoobank.org:pub:B1C0BDCD-017C-49ED-9C0E-8582691D9726.

The nomenclature of the dragonfly wing venation used in this paper is based on the interpretations of Riek (1976) and Riek & Kukalová-Peck (1984), as modified by Nel *et al*. (1993) and Bechly (1996b). The higher classification of the Central American Anisoptera follows Garrison *et al*. (2006). The family characters followed in the present work are based on the phylogenetic system proposed by Bechly (1996b, 2007). Venational abbreviations are as follows: AA, anterior anal; AL, anal loop; AP, anal posterior; Arc, arculus; Ax, primary antenodal crossvein; Bqs, bridge-crossveins; Cr, nodal crossvein; CuA, cubitus anterior; CuP, cubitus posterior; DC, discoidal cell; DT, discoidal triangle; HT, hypertriangle; IR, intercalary radial vein; MA, anterior median; MP, posterior median; Msp1, median supplement; N, nodus; 'O', oblique vein; PC, paranal cell; PsA, pseudo-anal vein; P-IR1, pseudo-IR1; Pt, pterostigma; RA, anterior radius; RP, posterior radius; Rsp1, radial supplement; ScP, posterior subcosta; SdC, subdiscoidal cell; SdT, subdiscoidal triangle; Sn, subnodal crossvein. All measurements are given in millimetres.

Fig. 2. Photograph of the amber block hosting the specimens of *Erpetogomphus shii* sp. nov. and *Argia* sp. (RX001).

Systematic palaeontology

Order ODONATA Fabricius, 1793
Suborder ANISOPTERA Selys Longchamps, 1854
Family GOMPHIDAE Rambur, 1842

Erpetogomphus Hagen in Selys Longchamps, 1858

Type species. *Ophiogomphus crotalinus* (Hagen in Selys Longchamps, 1854) by original designation.

Erpetogomphus shii sp. nov. (Figs 2–4)
(urn:lsid:zoobank.org:act:BB70CE83-F187–4576-9F77–443B1CD53036)

Etymology. The specific name is after Mr. Shi Yuxin who allowed us to study the unique type specimen.

Holotype. Specimen number RX001, a complete dragonfly (female), deposited in Rongxin Amber Museum of Hong Kong.

Locality, unit and age. Simojovel de Allende, Chiapas State, southeast Mexico; La Quinta Formation; early Miocene.

Diagnosis. Wing smaller than extant representatives of the genus, *ca* 20 mm long.

Description. A complete dragonfly with right forewing and hindwing well exposed (Fig. 3A–H). Head with eyes well separated (Fig. 3A); ocelli large, vertex with apparently complete postocellar ridge and median trough; occiput with transverse ridge covered with fringe hairs (Fig. 3B). Female vulvar lamina bifid; cerci with acute apex longer than epiproct. No expansion on segments 8 and 9 (Fig. 3C, D). Right forewing well preserved (Figs 3E, 4A). Wing hyaline, 19.81 mm long; width at level of N 5.83 mm; distance from Arc to N 8.62 mm, from N to Pt 6.06 mm, from Pt to wing apex 3.63 mm. Pt 2.34 mm long and 0.69 mm wide, narrowly elongate with basal side more oblique than distal side, covering four cells. Pt-brace weakly oblique, aligned with basal side of Pt. Primary antenodal crossvein Ax2 at level of distal end of DT. Three secondary antenodal crossveins present between Ax1 and Ax2; ten secondary antenodal crossveins in first row distal of Ax2. Ten postnodal crossveins present before Pt, non-aligned with 12 postsubnodal crossveins; seven postn-

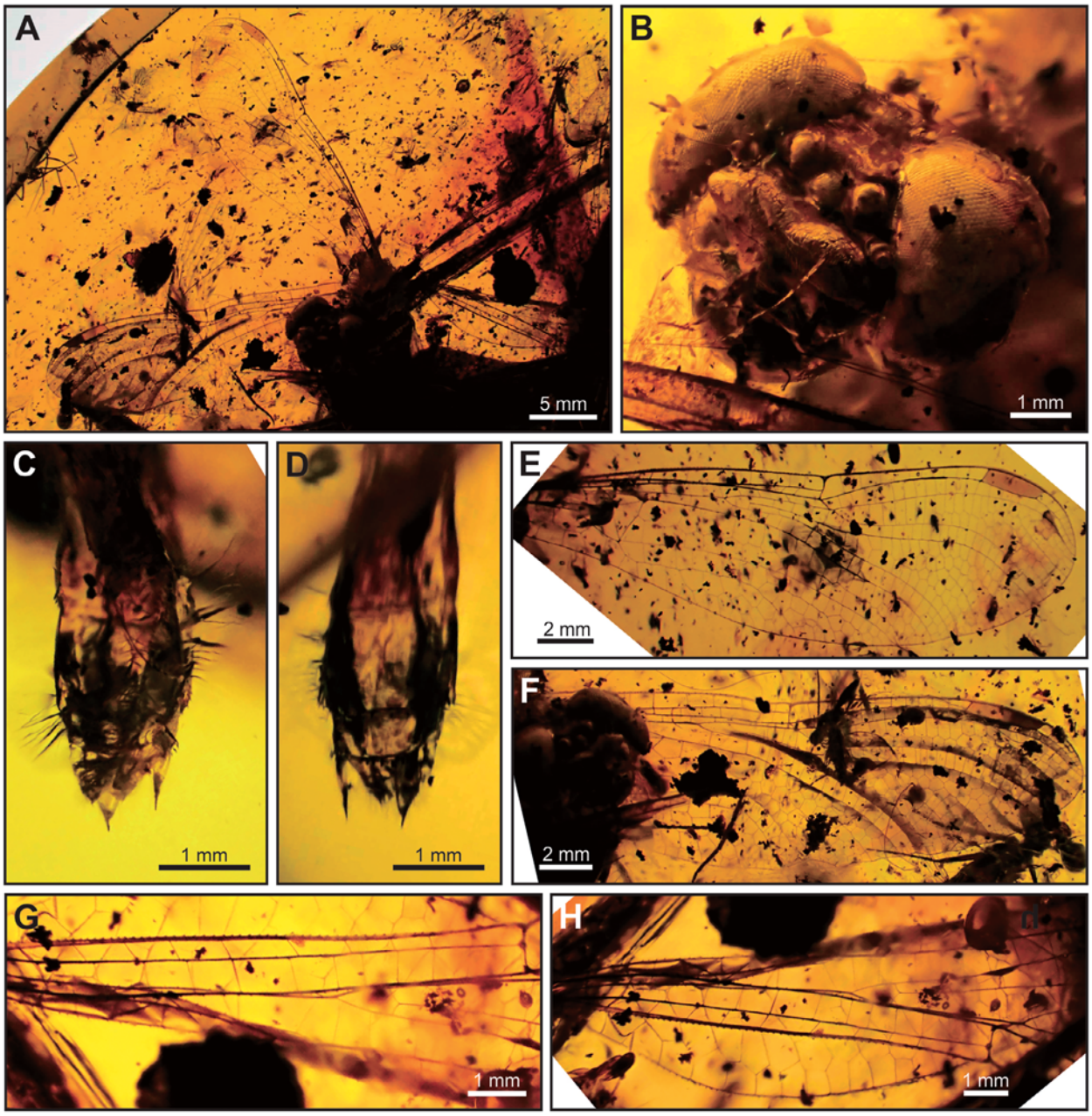

Fig. 3. Photographs of dragonfly *Erpetogomphus shii* sp. nov., holotype (RX001). **A**, Anterior body (dorsal view); **B**, Head; **C**–**D**, Anal terminal; **E**, Right forewing; **F**, Right hindwing; **G**–**H**, Left hindwing base.

odal crossveins and six postsubnodal crossveins present distal of Pt. One oblique crossvein 'O' probably present between RP2 and IR2, two cells distal of Sn. RP and MA separated in Arc. Median and submedian spaces free of crossveins. HT free, 2.04 mm long and maximum 0.43 mm wide. DT 0.86 mm distal of Arc, wide and free, with anterior side 1.24 mm long, basal side 1.24 mm long, and distal side (MAb) 1.71 mm long. SdT wide and free, limited by strong and oblique PsA, with length of PsA 1.13 mm long, basal side 1.76 mm long, and distal side 1.24 mm long. Postdiscoidal area with two rows of cells to level of 'O' and five cells along posterior wing margin. No Rsp1 or Msp1. Basal part of area between RA and RP with five crossveins basal of RP3/4 and three crossveins distal to base of RP3/4 and basal to Sn. Three antefurcal crossveins between RP and MA basal of midfork. RP2 base slightly distal of Sn. Area between RP2 and IR2 with one row of cells in-between. Base of IR1 short, zigzagged, originating four cells and 1.4 mm basal of Pt-brace, but disappearing distally. P-IR1 well defined, branching just below distal part of Pt. RP1 and RP2 basally parallel with Pt; area between RP1 and RP2 narrow with one row of cells basally and becoming divergent distally, with two rows below Pt-brace, and at least eight cells along wing margin. RP3/4 and MA running almost parallel basally, divergent distally, with one row of cells before 'O' and two rows in-between along wing

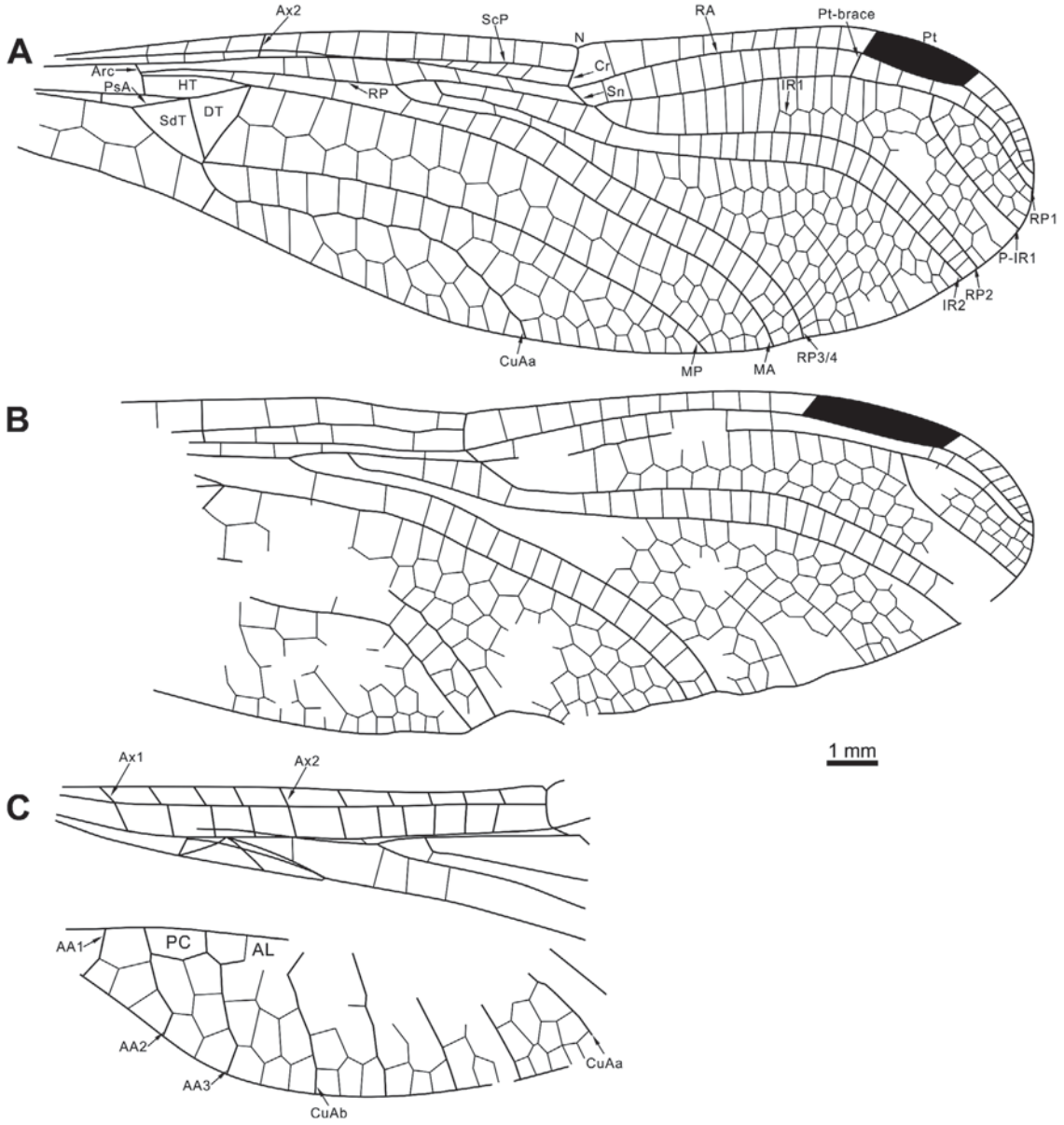

Fig. 4. Line drawing of the dragonfly *Erpetogomphus shii* sp. nov., holotype (RX001), showing wing venation. **A**, Right forewing; **B**, Right hindwing; **C**, Left hindwing base.

margin. Area between CuA and MP with one row of cells basally and 10 cells along wing margin. Anal and cubito-anal areas with 1–3 rows of cells. CuAa strongly curved towards secondary anal vein AA1b.

Right hindwing (Figs 3F, 4B) with base half overlapped by head. Visible wing length 17.86 mm; width at level of N 6.23 mm; distance from N to Pt 6.58 mm, from Pt to wing apex 4.51 mm. Pt 2.89 mm long and 0.55 mm wide, narrowly elongate, with basal side somewhat more oblique than distal side, covering three cells. Pt-brace weakly oblique, aligned with basal side of Pt. Ax2 at level of distal end of DT. Four secondary antenodal crossveins of first row and four of second row distal of Ax2, non-aligned. Ten postnodal crossveins and eight postsubnodal crossveins present before Pt, non-aligned; seven postnodal crossveins and three postsubnodal crossveins present distal of Pt. Postdiscoidal area with two rows of cells basally, expanded distally with ca. 10 cells along posterior wing margin. No Rsp1 and Msp1. Basal part of area between RA and RP with two crossveins present basal of RP3/4, and two crossveins distal of base of RP3/4 and basal of Sn. Area between RP2 and IR2 with one row of cells. IR1 zigzagged and long, originating seven cells basal of Pt-brace, but disappearing distally. Pseudo-IR1 well defined, branching just below distal part of Pt. RP1 and RP2 basally parallel with Pt; area between RP1 and RP2 narrow with one row of cells basally and widening distally, with two rows before Pt-brace, and ca six cells along wing margin. RP3/4 and MA running almost parallel basally, with one row of cells near wing margin and two cells along wing margin. Area between CuA

and MP with one row of cells basally, and two cells along wing margin. Cubito-anal area broad, with maximum of four rows of cells between CuA and posterior wing margin.

Left hindwing (Figs 3G–H, 4C) with wing base overlapped, but some characters available. Three antenodal and three subantenodal crossveins present between Ax1 and Ax2, non-aligned. Five antenodal and six antesubnodal crossveins present distal of Ax2. HT, DT and SdT free. AL two-celled but very badly defined, posteriorly opened. PC one cell long and elongate. CuAa ending on posterior wing margin just below N, with five well-defined posterior branches. Anal margin curved without any angle or anal triangle (female specimen).

Remarks. The new dragonfly can be attributed to Gomphidae Rambur, 1842 based on the following combination of characters (Bechly 2007): well-defined discoidal and subdiscoidal triangles, secondarily unicellular; trigonal planate present; hypertriangle with distinctly curved anterior margin; anal loop reduced to only one or two cells or even completely suppressed; only 1–4 antefurcal crossveins in forewings, and one or two in hindwings between arculus and midfork; branching of RP at midfork symmetrical; oblique vein 'O' less than three cells distal of subnodus; CuAa distinctly shortened and with distinct course (distally convergent with wing margin, instead of running parallel to it) with reduced pectinate branching; and costal margin and RA thickened along pterostigmata.

Because the age of Mexican amber is relatively young and the fauna has high endemicity, we have compared the dragonfly in detail with the New World extant Gomphidae. Following Garrison *et al*. (2006), the head, female genital structures and wing venation of this fossil occur only in extant *Erpetogomphus* Hagen in Selys Longchamps 1858 based on the following combination of characters: oblique vein 'O' only two cells distal of subnodus; no 'basal subscostal crossvein' basal of Ax1 between ScP and RA; no basal antesubcostal crossvein between RA and RP above hypertriangle; well-defined pseudo-IR1; IR1 weak and zigzagged; Pt covering only four cells; only four double cells between MAa and RP3/4 near posterior wing margin; only 3–4 secondary antenodal crossveins between Ax1 and Ax2; and anal loop posteriorly open and divided into two relatively large cells. Following Garrison (1994a) and Bailowitz *et al*. (2013), the extant species are differentiated mainly by the male terminalia, not available in the new dragonfly. Thus, it is not possible to compare the fossil with these species. However, the extant *Erpetogomphus* species have wing lengths generally between 21 and 36 mm, larger than in the present fossil (Garrison 1994a). Here we propose to give it a formal species name based on this difference, and also because it is the first fossil record of this genus widely distributed in the USA, Mexico and Central America.

Suborder ZYGOPTERA Selys Longchamps, 1854
Family COENAGRIONIDAE Kirby, 1890

Argia Rambur, 1842

Type species. *Agrion fumipennis* Burmeister, 1839 (by subsequent designation of Kirkby 1890).

Argia sp. (Figs 5–6)

Material. Specimen number RX001, damselfly A (male), complete; specimen number RX001, damselfly B (male), complete.

Locality, unit and age. Simojovel de Allende, Chiapas State, southeast Mexico; La Quinta Formation; early Miocene.

Description. Damselfly specimen A complete individual (Fig. 5A) preserving anal terminal (Fig. 5C). Head with eyes well separated (Fig. 5B). Tibial spines longer than interval separating them (Fig. 5B). Right forewing complete (Figs 5D, 6). Wing length 19.65 mm, width at level of N 2.87 mm; distance from wing base to Arc 3.37 mm, from Arc to N 3.29 mm, from N to Pt 10.77 mm, from Pt to wing apex 2.22 mm. Primary antenodal crossveins preserved, Ax0 close to wing base, Ax1 2.14 mm distal of Ax0, Ax2 1.04 mm distal of Ax1; no secondary antenodal and antesubnodal crossveins present. Sixteen postnodal crossveins and 15 postsubnodal crossveins present before Pt, well-aligned (except for last one). Six postnodal crossveins and five postsubnodal crossveins present distal of Pt, partly aligned. Arc angular and slightly basal of Ax2. DC basally closed, free, with acute distal angle; length of basal side 0.3 mm, anterior side 0.27 mm, distal side 0.79 mm, and posterior side 0.93 mm. Subdiscoidal cell free and elongate, 1.51 mm long and 0.35 mm wide. CuP just below Ax1. Nodal structures well preserved (Fig. 5D), Sn aligned with Cr. Midfork (base of RP3/4) just below N. IR2 aligned with Sn, one cell and 0.32 mm distal of midfork. RP2 originating eight cells distal of Sn, lying 6.25 mm distally, nearer to N than to Pt. IR1 originating three cells distal of base of RP2 and five cells basal of Pt-brace. RP1 with weak angle below pterostigmal brace. MA distally zigzagged and long, reaching posterior wing margin just below Pt. MP curved and long, ending on posterior wing margin slightly basal of IR1 base. CuA distally zigzagged and long, ending on posterior wing margin just below RP2 base. Pt covering one cell, 0.74 mm long and 0.44 mm wide. Damselfly specimen B preserving complementary features of the head, thorax (Fig. 5E), abdomen (Fig. 5F) and left hindwing (Fig. 5G–H)

Remarks. The new damselflies can be attributed to Coenagrionidae Kirby, 1890 based on the following combination of characters: only Ax1 and Ax2 retained in antenodal space; no antesubnodal and antefurcal crossveins; Sn aligned with IR2; postnodal crossveins aligned with rows of crossveins below, forming pseudo-transverse-veins; oblique vein 'O' absent; RP1 kinked

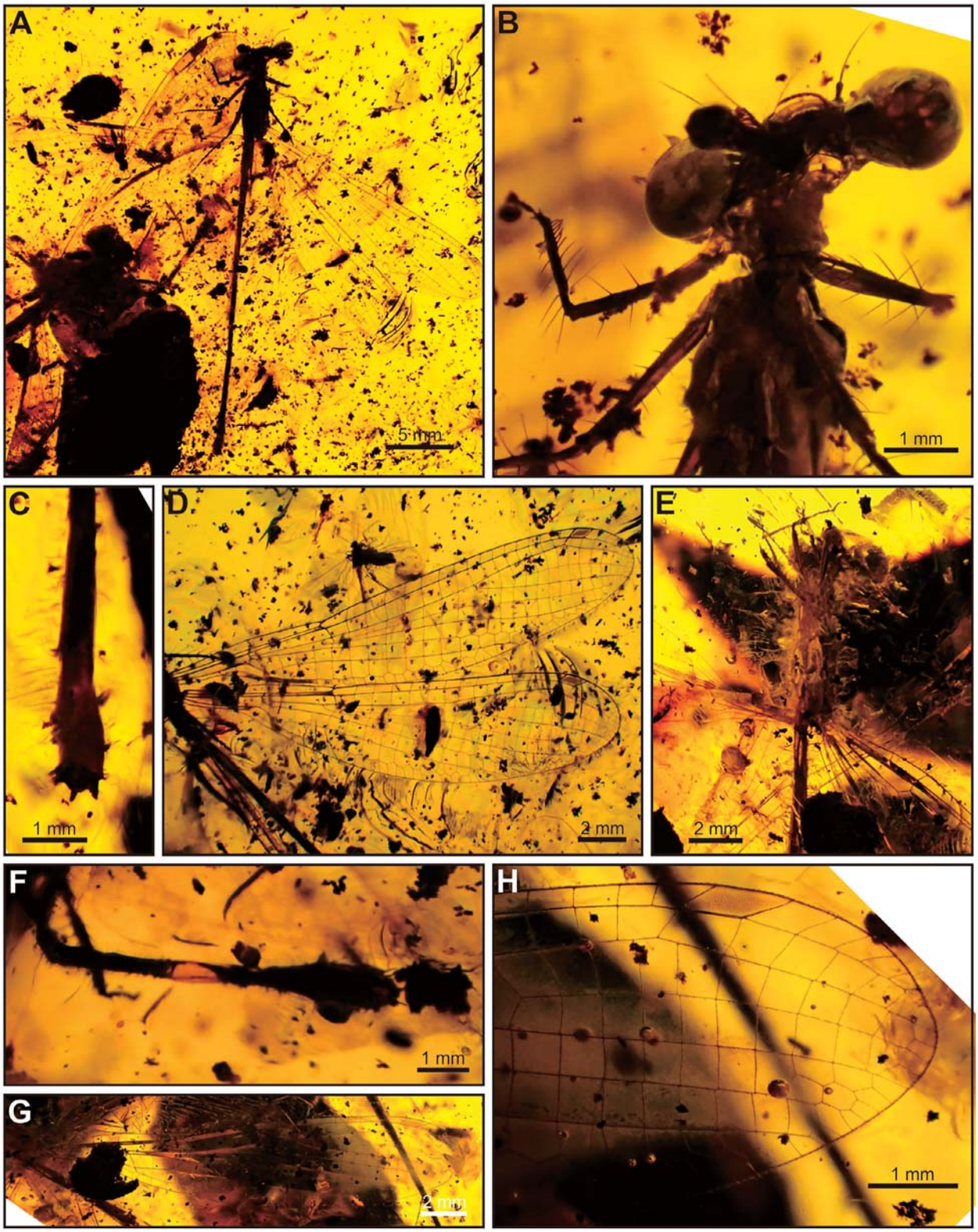

Fig. 5. Photographs of the damselfly *Argia* sp., specimens A and B (both in RX001). **A**–**D**, Damselfly specimen A; **A**, Complete damselfly; **B**, Head; **C**, Anal terminal; **D**, Right forewing and hindwing; **E**–**H**, Damselfly specimen B; **E**, Head and thorax; **F**, Abdomen; **G**, Left hindwing; **H**, Left hindwing apex.

at Pt-brace; Pt one cell long; longitudinal veins rather straight and long; only one row of cells between CuA and wing margin; all intercalary veins (except IR1 and IR2) suppressed; and discoidal cell closed with distal vein MAb very oblique.

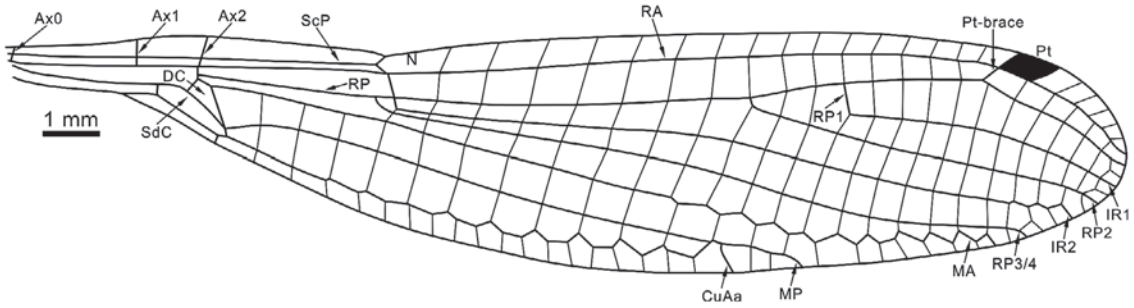

Fig. 6. Line drawing of the damselfly *Argia* sp., specimen A (RX001), showing wing venation (right forewing).

Within Coenagrionidae, they can be attributed to *Argia* based on the following unique combination of characters [according to Garrison (1994b) and Garrison *et al*. (2010)]: basal part of CuA not aligned with cross-veins between AA and posterior wing margin; venation at wing apex not especially dense; wings narrow; wings stalked well before level of AA so that distance between end of petiole and origination of CuP longer than CuP (few other New World genera show this structure, viz., *Acanthallagma*, *Apanisagrion* and some *Enallagma*); tibial spines longer than interval separating them (other genera, except for *Nehalennia*, have tibial spines shorter than interval separating them); males with specialized pair of pad-like structures (tori) on declivous posterodorsal surface of abdominal segment 10 (no such structures present in other genera).

Argia is distributed widely in North, Central and South America, with *ca* 150 species described. The extant species of *Argia* are differentiated on the basis of the body colorations and male genitalia not available here (Garrison 1994b, 1996, Garrison & von Ellenrieder 2015, 2017). Although the damselflies are probably the first definite fossil *Argia*, their lack of characters useful for specific differentiation has led us to describe them under open nomenclature. Ris (1910) considered that the latest Eocene *Trichocnemis aliena* Scudder, 1892 (an isolated wing, placed in Platycnemididae; Florissant, Colorado, USA; Scudder 1892) is 'most probably a hindwing of *Argia*'; however, it is barely attributable to an established genus (Nel & Papazian 1990). Another two Argiinae of undetermined genera are recorded from the Oligocene of France (Nel & Papazian 1990).

Conclusions

One complete dragonfly and two damselflies are described herein from a single piece of Mexican amber. The new gomphid dragonfly is attributed to *Erpetogomphus shii*, and the two coenagrionid damselflies are assigned to *Argia* sp. *Erpetogomphus shii* is the first-known complete amber-hosted Anisoptera. The new discovery extends the origins of *Erpetogomphus* and *Argia* back to at least the early Miocene.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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