

King Crickets, Raspy Crickets and Weta, Their Wings, Their Fossil Relatives

Author: Béthoux, O.

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King crickets, raspy crickets and weta, their wings, their fossil relatives

O. BÉTHOUX

40 rue d'Aveillans, 38770 La Motte d'Aveillans, France. Email: obethoux@yahoo.fr

Abstract

Topographic homology conjectures (= THC's) in fore- and hind wing venation of extant king crickets, raspy crickets and weta are re-evaluated. Based on the premises that topological homology is established so that the amount of transformation that has to be assumed to explain differences between patterns is minimized, a new set of THC's (= STHC), based on morphological data on the species cf. *mexicanus* de Saussure, 1859: 209, *laudatum* Johns, 1997, *ornata* Willemse, 1963, cf. *bicornis* Karny, 1929a, *pinguipes*? Rentz in Morton & Rentz, 1983, *pinguipes* Rentz in Morton & Rentz, 1983, an undetermined species, *punctipennis* Walker, 1869, and *rufovaria* Kirby, 1888, is elaborated. Among other transformations, the occurrence of a re-routing of MP along CuA (i.e., the basal M + CuA stem splits into MA and MP + CuA, instead of into MA + MP and CuA) is demonstrated for *pinguipes*, *punctipennis*, and *rufovaria*. Concurrently, intra-specific variability in forewing venation is appreciated for *laudatum*, *ornata*, cf. *bicornis*, *pinguipes*, *punctipennis*, and *rufovaria*. A cladotypic-compliant nomenclatural scheme is elaborated based on the proposed THC's. The taxon *Agryllacris* nom.-dis.-typ. nov. is defined based on the character state 'in forewing, CuA + CuPaa with two distal branches only'; the taxon *Tagryllacris* nom.-dis.-typ. nov. is defined based on the character state 'in forewing, M + CuA splits into MA and MP + CuA'; the taxon *Etagryllacris* nom.-dis.-typ. nov. is defined based on the character state 'in forewing, CuA + CuPaa keep fused'; the taxon *Metagryllacris* nom. nov., dis. Zeuner, 1939, typ. nov. is defined based on the character state 'in forewing, MA fused with R at wing base'. Based on new data, the species †*perfecta* Sharov, 1968 is identified as a member of the taxon *Agryllacris*, and the fossil species †*megaptera* Gorochov, 1987a, †*simplicis* Gorochov, 1987a, †*elongata* Gorochov, 1987a, †*madygenioides* Gorochov, 1987a, †*perlonga* Gorochov, 1987a, and †*devexa* Gorochov, 1987a are considered as junior synonyms of †*perfecta*. The nomenclatural treatment is extended to the unrelated taxon †*Bintoniellidae* nom. Handlirsch, 1938, dis. Sharov, 1968, typ. nov., defined based on the character state 'in forewing, no distinct base of CuPaa diverging from CuPa (and fusing with CuA or M + CuA)'. Belonging to this taxon, the species †*primaria* Sharov, 1968 is considered as a junior synonym of †*triassica* Sharov, 1968: 168. A consequence of the assignment of †*perfecta* to *Agryllacris* is that this group stems in the Triassic, at least, i.e., ca 170 million years earlier than previously assumed. As a result, the loss of the complex 'tettigoniid-gryllid-like' (i.e., *Grylloptera*) stridulatory apparatus is no longer needed to account for the morphology of king crickets, raspy crickets and weta forewing. Finally, a refinement of the concept of parallelism is proposed based on transformations observed in the taxa *Agryllacris* and *Bintoniellidae*, and on their polarity and frequency of occurrence. The concept of parallelism is narrowed down, those of atavism and reversal discussed, and the concepts of iteronatism, cryptoparallelism, and pronatism proposed.

Key words

Archaeorthoptera, topological homology, wing venation pattern, iterative evolution

Introduction

Despite lack of consistent reconstruction of phylogenetic relationships among major ensiferan lineages (Legendre *et al.* 2010), it is generally admitted that king crickets, raspy crickets and weta diverged from a Mesozoic paraphyletic assemblage, namely the hagloideans (Gorochov 2001; Heads & Leuzinger 2011; Sharov 1968, 1971). Because hagloidean males possess the 'tettigoniid-gryllid-like' stridulatory apparatus in forewings (including a file, that defines the taxon *Grylloptera* nom. Haeckel, 1896, dis.-typ. Béthoux, 2012), some assumed that king crickets, raspy crickets and weta experienced a loss of the corresponding complex structures (Gorochov 2001; Sharov 1968, 1971; among others). However several authors recognized the wing venation of these insects as plesiotypic, compared to that of other ensiferans (Karny 1929b), and assumed a primary lack of the *Grylloptera* stridulatory apparatus (Zeuner 1939). The assumption that king crickets, raspy crickets and weta diverged from a group that already possessed the *Grylloptera* stridulatory apparatus, is primarily supported by the lack of evident Mesozoic remains.

The wing venation of extant king crickets, raspy crickets and weta is sparsely documented. Apart from Karny (1930), most papers by this author include incomplete drawings of wing venation (e.g., Karny 1928b). Several other contributions focus on species that most likely represent the most derived members of the group (e.g., Karny 1928a, Ragge 1955). Illustrations and observations by Zeuner (1939) are minimal and will prove partly inaccurate. This lack of data jeopardizes the identification of fossil stem-relatives of king crickets, raspy crickets and weta.

In order to obtain reference data for a discussion on the origin of these insects, a survey of the holdings of the Australian National Insect Collection and CSIRO Ecosystem Sciences (Canberra, Australia) was carried out, complemented by a survey of material housed at the Queensland Museum (Brisbane, Australia), and of a few other institutions. Preliminary results suggested that relatives of king crickets, raspy crickets and weta could be identified among Early Mesozoic orthopterans. This finding prompted a broadening of the scope of this contribution to include data on intra-specific wing venation variability in extant species, in order to assist delimitation of related fossil species.

The paper is organized as follows: a comparative analysis is carried out, aiming to develop wing venation topological homologies in selected species (and including data on intra-specific variability). Based on the resulting conjectures, a character-state-based nomenclatural treatment (i.e., cladotypic) is proposed, including the revision of several fossil taxa relevant for the following section; finally, conjectures and nomenclature are used to elaborate on evolutionary aspects.

Material and methods

I use the cladotypic nomenclatural procedure I elaborated (2007b, c; 2010) and Lanham's species names (Dayrat *et al.* 2004, Lanham 1965) [see introduction and application of this approach in JOR by Béthoux & Herd (2009)]. In order to avoid a mixing of names erected under distinct procedures, vernacular versions of taxon names erected under the Linnaean procedure will be used (e.g., gryllacrididaeans instead of Gryllacrididae). The position of the species surveyed in this contribution under the traditional nomenclatural procedure is provided in Appendix 1. In addition, traditional genera are indicated in this section, between inverted commas (except in Appendix 2). Appendix 2 provides a nomenclatural treatment at the specific and generic levels compliant with the ICZN. Appendix 3 provides provisional compositions for the newly defined taxa.

Specimens referred to as ANIC IWC OB, QM, PIN, NHM, and MHNG are housed at the Australian National Insect Collection and CSIRO Ecosystem Sciences (Canberra, Australia), the Queensland Museum (Brisbane, Australia), the Palaeontological Institute of the Russian Academy of Sciences (Moscow, Russia), the Natural History Museum (London, UK), and the Museum d'histoire Naturelle (Geneva, Switzerland), respectively. Other institutions are mentioned in the text.

Extant species and specimens used for this contribution are as follows [following Bengston (1988) for open nomenclature]:

Species cf. *mexicanus* de Saussure, 1859: 209 (currently assigned to the genus '*Anabropsis*' Rehn, 1901 under the Linnaean nomenclatural procedure).

–The studied specimen was determined at the genus level. Since the type-species of the corresponding genus is *mexicanus* de Saussure, 1859: 209, I refer to the species as cf. *mexicanus* in the following.

–Specimen illustrated (ANIC pinned collection): ANIC IWC OB 26, ♀, Monte Verde, Powell Prop., ca 1580 m., Costa Rica, 23.iii.1974, determined by D.C.F. Rentz.

Species *laudatum* Johns, 1997 (genus '*Transaevum*' Johns, 1997).

–Determination of specimens of this species was complicated by the claim of the existence of two distinct and undescribed species in the genus by Johns (1997; balanced in Monteith & Field 2001). However, only one species has been formally described. Observation of the 'type-series' of the presumed second species housed at the Queensland Museum (material labeled '*longihamatum*') revealed no distinctive features except a size comparatively smaller than material of *laudatum*, but nevertheless compatible with identity with this species. In addition, specimens of '*longihamatum*' were collected from a locality where *laudatum* occurs, rendering the distinctiveness of '*longihamatum*' unlikely according to G.B. Monteith (pers. com. 2010). I presume that specimens housed at the ANIC and at the QM indicated as belonging to *laudatum* were determined by P.M. Johns; determination of two unassigned ANIC specimens by O. Béthoux was based on the fact that the set of '*longihamatum*' specimens was composed of comparatively smaller specimens. All specimens were collected from Australia. Because of the large sample available, specimens belonging to the ANIC pinned collection with wings in resting position were excluded from the survey. The specimen of the paratype series of '*longihamatum*' illustrated on Fig. 3H,Q was excluded from the measurement survey.

–Specimens prepared and illustrated (ANIC IWC OB 1-9

from ANIC ethanol collection; ANIC IWC OB 10 from ANIC pinned collection): ANIC IWC OB 5, ♀, 17.37S 145.34E, BS3 Massey Crk., 27.ii-26.iii.1996; ANIC IWC OB 6, ♀, 17.07S 145.38E, Mt. Haig Road, 10 kms. ENE of Tinaroo Dam Wall, Atherton Tableland, QLD, 03.ii.1988; ANIC IWC OB 7, ♂, 17.02S 145.37E, Davies Crk., 15 km. from Kennedy Hwy., 21 km E. by S. of Mareeba, QLD, 01.iii.1988; ANIC IWC OB 8, ♀, 17.37S 145.34E, BS3 Massey Crk., QLD, 31.i-27.ii.1996; ANIC IWC OB 9, ♂, 17.37S 145.34E, BS3 Massey Crk., QLD, 04.ii-06.iii.1995, determined by O. Béthoux; ANIC IWC OB 10, ♂, Kuranda, QLD, 27.ii.1981, determined by O. Béthoux; QM (unnumbered, 'paratype series' of '*longihamatum*'), ♂, Charmillin Ck. Xing, 950 m., Tully Falls Rd., QLD, 8.xii.1989-5.i.1990 (only left forewing prepared).

–Specimens used for measurements survey (in addition to the illustrated ones):

Females: ANIC pinned collection, 15.47S 145.17E, Moses Ck., 4 km NE of Mt. Finnigan, nr. Cooktown, QLD, 14.x.1980 (paratype); ANIC pinned collection, Paluma, QLD, 17.x.1979 (paratype); ANIC pinned collection; Davies Ck. Rd., nr. Kuranda, QLD, 9.i.1979 (paratype); ANIC pinned collection; 16.50S 145.37E, 1.5 km S of Kuranda on Kennedy Hwy. 'Arona', QLD, 10.xii.2003 (2 specimens); ANIC pinned collection; 17.25.43S 145.19.13E, Atherton Tableland, Mt. Hypipamee Nat. Pk., QLD, 1-12.ii.1998; ANIC ethanol collection, 17.05S 145.35E, Mt. Haig, 22 km NE by N of Atherton, QLD, 16.iii.1988 (2 specimens); 16.16S 145.02E, Forestry Camp Mt. Windsor Tableland, NNW of Mt. Carbine, QLD, 23.i.1988; ANIC ethanol collection, 17.05S 145.35E, Mt. Haig, 22 km NE by N of Atherton, QLD, 16.iii.1988; ANIC ethanol collection, 17.06S 145.36E, Mt. Haig, QLD, 4.ii-17.iii.1995; ANIC ethanol collection, 17.28S 145.29E, Longlands Gap, QLD, 5-27.ii.1996; ANIC ethanol collection, 17.02S 145.37E, Davies Ck. (15 km from Kennedy Hwy.), 21 km E by S of Mareeba, QLD, 1.iii.1988 (2 specimens); QM ethanol collection, 16.26S 145.42E, Hughes Rd., Topaz, 4.xii.1993, QLD (2 specimens, paratypes); QM ethanol collection, 16.05S 145.25E, upper roaring meg, 680m, 6 km W. of Capte tribulation, QLD, 10-22.xi.1993, (3 specimens, paratypes); QM pinned collection, Cardwell Range, Upper Broadwater Ck Valley, QLD, 17-21.xii.1986, 700-800m (only left forewing observed; paratype); QM pinned collection, Douglas Ck. Rd., Kirrama Range, QLD (only left forewing observed; paratype); QM pinned collection, Upper Broadwater Ck. Valley, Cardwell Range, QLD, 17-21.xii.1986 (only right forewing observed; paratype); QM pinned collection, Head of Roots Ck, 12 km WNW Mossman, QLD, 28-29.xii.1990; QM pinned collection, Mt. Lewis Rd., QLD.

Males: ANIC pinned collection, 32 km NW of Kennedy Hwy., QLD, 24.xii.1979 (paratype); ANIC pinned collection, 15.47S 145.17E, Moses Ck., 4 km NE of Mt. Finnigan, nr. Cooktown, QLD, 16.x.1980 (only left forewing observed; paratype); ANIC pinned collection; 18.59S 146.10E, Birthday Ck., 6 km. NW by W of Paluma, QLD, 25.ix.1980 (paratype); ANIC pinned collection, Kuranda, QLD, 27.ii.1981 (2 specimens; in one, only left forewing observed); ANIC pinned collection; 16.50S 145.37E, 1.5 km S of Kuranda on Kennedy Hwy. 'Arona', QLD, 10.xii.2003; ANIC ethanol collection, Mt. Lewis Rd., Julatten, QLD, 12.xi.1975 (paratype); ANIC ethanol collection, 17.02S 145.37E, Davies Ck. (15 km from Kennedy Hwy.), 22 km E by S of Mareeba, QLD, 24.iii.1988; ANIC ethanol collection, 17.05S 145.35E, Mt. Haig, 22 km

NE by N of Atherton, QLD, 16.iii.1988; QM ethanol collection, 16.26S 145.42E, Hughes Rd., Topaz, QLD, 4.xii.1993 (paratype); QM ethanol collection, 1km S Cable Tower No7, Bellenden-Ker Range, QLD, 17-24.x.1981 (paratype); QM ethanol collection, upper roaring meg, 6 km W. Cape Tribulation, QLD, 8-9.xii.1993 (paratype); QM ethanol collection, upper Isley Ck., 9 km WSN of Edmonton, QLD, 29-30.xi.1993 (paratype); QM pinned collection, 17.16S 145.49E, Massey Range, 4 km W of Centre Bellenden Ker, 9-11.x.1991 (holotype); QM pinned collection, 32 km NW of Kennedy, QLD, 24.ii.1979 (paratype); QM pinned collection, 17.14S 145.48E, Massey Range, 6 km NW of Centre Bellenden Ker, 11-12.xi.1991 (only right forewing observed; paratype); QM pinned collection, Charmillin Ck. Xing, Tully Falls Rd., QLD, 8.xii.1989-5.i.1990 (2 specimens, both paratypes; only right forewings observed); QM pinned collection, head of Francis Ck, 12 km WNW Mossman, QLD, 30.xii.1989 (only right forewing observed); QM pinned collection, Mt Lewis Rd., 16km from Highway, QLD, 18.xii.1989-13.i.1990 (only left forewing observed).

Species *ornata* Willemse, 1963 (genus '*Exogryllacris*' Willemse, 1963).

–Determination of material of this species is straightforward as the species is very distinctive. All specimens were collected from Australia.

–Specimens prepared and illustrated (ANIC ethanol collection): ANIC IWC OB 15, ♂, 17.28S 145.29E, Longlands Gap, QLD, 1-30.xi.1995, determined by D.C.F. Rentz; ANIC IWC OB 16, ♂, 17.35S 145.34E, BS3 Massey Crk., QLD, 3.x-2.xi.1995, determined by D.C.F. Rentz.

–Specimens used for measurements survey (in addition to illustrated specimens):

Females: ANIC, pinned collection, Atherton tableland, QLD (only right forewing observed); ANIC, pinned collection, no data, collected by JT Doyer (only right forewing observed); ANIC ethanol collection, 17.33S 145.32E, Mt Fisher, QLD, 4.ii-21.iii.1995; ANIC ethanol collection; 17.27S 145.29E, Hugh Nelson Rd. QLD, 1-30.xi.1995; ANIC ethanol collection, 17.15S 145.38E, Lake Barrine, Atherton Tableland, QLD, 6.xii.1985; QM ethanol collection, 17.30S 145.36E Millaa Millaa Falls, 13-24.xi.1994 (three specimens); QM ethanol collection, 16.26S 145.42E, Hughes Rd., Topaz, QLD, 4.xii.1993; QM ethanol collection, 17.23S 145.28E, Upper Plath Rd., 9.xii.1995; QM ethanol collection, 17.17S 145.58E, Graham Range, 8-9.xii.1995; QM pinned collection, 17.26S 145.42E, Hughes Rd, Topaz, 6.xii.1993-25.ii.1994.

Males: ANIC pinned collection, Mt Haig, nr. Danbulla, QLD, 28.ix.1966; ANIC dry collection, Douglas Ck., lamb range, NE QLD, 12.x.1992 (only right forewing observed); ANIC ethanol collection, 17.37S 145.34E, Massey Ck., QLD, 2-20.xi.1995; QM ethanol collection, 17.28S 145.32E, Kenny Road, 25.xi.1994-10.i.1995; QM ethanol collection, 17.37S 145.46E, Palmerston NPE Margin, 10.xii.1995-7.ii.1996; QM ethanol collection, 17.27S 145.29E, Tower nr. the Crater NP, 25.xi.1994, 1230m; QM pinned collection, Bulurru, Topaz, 23.ix.1997 (only right forewing observed); QM pinned collection, 17.14S, 145.48E, Massey Range, 6 km NW of Centre Bellenden Ker, 11-12.x.1991 (only right forewing observed); QM pinned collection, 17.14S, 145.48E, Massey Range, 6 km NW of Centre Bellenden Ker, 11-12.x.1991.

Species cf. *bicornis* Karny, 1929a (genus '*Gryllotaurus*' Karny, 1929a).

–An issue similar to that faced with *laudatum* was raised by the claim that two species, similar but distinct from *bicornis* exist, but are undescribed yet (Johns 1997; balanced in Monteith & Field 2001). The selected material (illustrated and measured) was labeled '*biconulata*', presumably by P.M. Johns. Apart from a comparatively smaller size, material of '*biconulata*' does not significantly differ from that of *bicornis*, therefore I consider the existence of a '*biconulata*' dubious (specimens of intermediate size exist). In any case, the survey is based on material from a single species, either *bicornis*, or '*biconulata*'. At worst the intra-specific variability will have been underestimated. All specimens were collected from Australia.

–Specimens prepared and illustrated (all ANIC ethanol collection): ANIC IWC OB 11 and ANIC IWC OB 12, ♀, 17.06.S 145.37E, GS2 Mt. Edith, QLD, 4.ii-17.iii.1995; ANIC IWC OB 13, ♀, 17.33S 145.32E, BS2 Mt. Fisher, QLD, 21.iii-5.iv.1995; ANIC IWC OB 14, ♀, 17.25S 145.29E, GS3 Hugh Nelson Rd., QLD, 5.iii-4.iv.1995.

–Specimens used for measurements survey (in addition to the illustrated ones):

Females: ANIC ethanol collection, Mt Belleden-Ker, Summit, 11.iv.1979, QLD (indicated as 'paratype'); ANIC ethanol collection, 17.33S 145.32E, Mt. Fisher, QLD, 3.x-2.xi.1995 (four specimens); ANIC ethanol collection, 17.37S 145.34E, Massey Crk., QLD, 2-30.v.1996 (four specimens); QM ethanol collection, Belleden Ker Range, Summit TV Stn., QLD, 25-31.x.1981 (indicated as 'paratype'); QM ethanol collection, paratype; Belleden Ker Range, NQ, Cable Tower 3, 1054m, 1-7.xi.1981 (only right forewing observed);

Males: ANIC ethanol collection, 17.33S 145.32E, Mt. Fisher, QLD, 3.x-2.xi.1995; QM ethanol collection Belleden Ker Range, Summit TV Stn., 25-31.x.1981 (indicated as 'holotype').

Species *pinguipes*? Rentz in Morton & Rentz, 1983 (genus '*Bothriogryllacris*' Rentz in Morton & Rentz, 1983).

–The studied specimen was collected prior to investigations by Morton & Rentz (1983). It is housed in the ANIC pinned collection, together with *pinguipes* specimens. However based on its forewing venation, the specimen differs from representatives of species by its higher number of RP branches. Therefore I assume it could belong to a distinct species.

–Specimen prepared and illustrated: ANIC IWC OB 24, ANIC pinned collection, ♂, Stuart Hwy., 296 km S. of Tennant Crk., NT, Australia, 29.xi.1972.

Species *pinguipes* Rentz in Morton & Rentz, 1983 (genus '*Bothriogryllacris*' Rentz in Morton & Rentz, 1983).

–All specimens were collected from Australia and determined by D.C.F. Rentz. Only specimens from the ANIC ethanol collection were surveyed (*i.e.*, pinned specimens were excluded), because this sample appeared sufficient. Two specimens were excluded from survey because of dubious determination. Collecting data of these specimens are as follows: 32.29S 124.13E, 59 km ESE of Balladonia Motel, WA, 29.i.1991.

–Specimens prepared and illustrated: ANIC IWC 17, ♂, ca 30.39S 121.27E, 7-11 km N of Kalgoorlie, WA, 17.xi.1978; ANIC IWC OB 18, ♀, ca 30.39S 121.27E, 7-11 km N of Kalgoorlie, WA, 17.xi.1978; ANIC IWC OB 19, ♀, 24.51S 133.11E, Stuart Hwy., 41 km N of Erlunda, NT, 4.xi.1988; ANIC IWC OB 20, ♀, 20.52S 130.16E, Tanami Desert, NT, 21.iii.1988; ANIC IWC OB 21, ♀, 23.17S 133.39E, 50 km. NNW of Alice Springs, NT, 15.xii.1989; ANIC IWC OB 22, ♂, ca 20 km E of Norseman, WA, 12-13.i.1986; ANIC IWC OB 23, ♂, 32.13S, 123.15E, 38 km. WNW of Balladonia Motel, WA, 22.xi.1980.

–Specimens used for measurements survey (in addition to the illustrated ones):

Females: 26.00S 131.25E, 26 km WSW of Milga Pk., NT, 18.i.1982 (paratype); 26.09S 130.35E, 56 km W of Amata, Musgrave Ranges, SA, 20-21.i.1982 (paratype); 25.12S 132.05E, Lasseter Hwy., 35 km ENE. of Curtin Springs, NT, 8.xi.1988; 25.11S 133.11E, Stuart Hwy., 4 km N of Erlunda, NT, 4.xi.1988; 20.52S 130.16E, Tanami Desert, NT, 28.iii.1988; 30.42S 121.28E, 4 km N by E of Kalgoorlie, WA, 17.ii.1978 (6 specimens); 25.11S 133.1E, Stuart Hwy., 4 km N. of Erlunda, NT, 4.xi.1988; 25.21S 131.53E, Lasseter Hwy., 13 km E by S of Curtin Springs, NT, 8.xi.1988 (2 specimens); ca. 30.39S 121.27E, 7-11 km N of Kalgoorlie, WA, 17.xi.1978 (4 specimens); 30.47S 121.27E, Kalgoorlie (airport), WA, 16.ii.1978 (4 specimens); 24.51S 133.11E, Stuart Hwy., 1 km N of Erlunda, NT, 4.xi.1988; 28.47S 121.31E, 1 km S of Malcolm, WA, 19.ii.1978 (2 specimens).

Males: 26.00S 131.25E, 26 km WSW of Milga Pk., NT, 18.i.1982 (paratype); 26.00S 131.25E, 26 km WSW of Milga Pk., NT, 18.i.1982 (2 specimens; both paratypes); ca. 20 km E of Norseman, WA, 12-13.i.1986 (2 specimens); 1 km W of Sangsters Bore, Tanami Desert, NT, 20.iii.1985; 25.11S 133.11E, Stuart Hwy., 4 km N of Erlunda, NT, 27.x.1988; 20.52S 130.16E, Tanami Desert, NT, 18.iii.1988 (2 specimens); ca. 30.39S 121.27E, 7-11 km N of Kalgoorlie, WA, 17.ii.1978; 30.47S 121.27E, Kalgoorlie (airport), WA, 16.ii.1978 (4 specimens); 28.47S 121.31E, 1 km S. of Malcolm, WA, 19.ii.1978; ca. 30.39S 121.27E, 4 km N by E of Kalgoorlie, WA, 17.ii.1978.

Species 'sp. undet.'

–The corresponding specimen belongs to a set labeled as 'Gryllacrididae Genus 3 Sp. 1' in the ANIC pinned collection.
–Specimen illustrated: ANIC IWC OB 25, ♂, Yass, NSW., Australia, 13.xii.1932.

Species *punctipennis* Walker, 1869 (genus '*Xanthogryllacris*' Karny, 1937).

–All surveyed specimens belong to the ANIC ethanol collection, were determined by D.C.F. Rentz, and were collected from Australia.

–Specimens prepared and illustrated: ANIC IWC OB 36, ♀, 11.45S, 142.35E, Heathland, QLD, 1-21.iii.1992; ANIW IWC OB 37, ♂, 15.50S, 145.20E, Gap Ck., 5 km. ESE of Mt. Finnigan, nr. Cooktown, QLD, 13-16.v.1981; ANIC IWC OB 38, ♂, 15.28S, 145.15E, 1 km. w. of Cooktown, QLD, 12-13.v.1981.
–Specimens used for measurements survey (in addition to the illustrated ones):

Females: 12.45S 143.17E, 8 km E of Mt. Tozer, nr. Iron Range Nat. Pk., QLD, 8.vii.1986; 12.44S 143.16E, 6 km ENE of Mt. Tozer, nr. Iron Range Nat. Pk., QLD 1.vii.1986; Shiptons Flat, nr. Cooktown, QLD, 16-18.v.1981; 15.50S 145.20E, Gap Ck., 5 km ESE of Mt. Finnigan, nr. Cooktown, QLD, 13-16.v.1981; 11.45S 142.35E, Heatlands, QLD, 18.ix.1992-21.x.1992.

Males: 12.43S 143.17E, 9 km ENE of Mt. Tozer, Iron Range Nat. Pk., QLD, 10.vii.1986; 12.44S 143.14E, 9 km ENE of Mt. Tozer, nr. Iron Range Nat. Pk., QLD, 28.vi.1986-4.vii.1986; 12.43S 143.17E, 9 km ENE of Mt. Tozer, Iron Range Nat. Pk., QLD, 10.vii.1986; 15.50S 145.20E, Gap Ck., 5 km ESE of Mt. Finnigan, nr. Cooktown, QLD., 13-16.v.1981; 15.04S 145.07E, Mt. Webb Nat. Pk., nr. Cooktown, QLD, 27-30.iv.1981; 17.00S 145.50E, Pine Ck. (nr. CSIRO Tower), 11 km SE by S of Cairns, QLD, 18.ii.1988; 17.53S 146.09E, Dunk Island (airstrip), QLD, 17.iv.1990.

Species *rufovaria* Kirby, 1888 (genus '*Gryllacris*' Audinet-Serville, 1831).

–All specimens were collected from Australia, and all are housed at the ANIC (ethanol collection).

–Specimen prepared and illustrated: ANIC IWC OB 27, ♂, 10.27S, 105.40E, Christmas Island, Grants Well to Irvine, Hill Rd. track, 27.iv.1989, presumably determined by D.C.F. Rentz.

–Specimens used for measurements survey (in addition to the illustrated one; ♂ and ♀ treated together because of limited sample size):

Males: 10.27S 105.40E, Grants Well to Irvine, Hill Rd. track, Christmas Island, 27.iv.1989; 10.29S 105.38E, near Central Area, Workshop, Christmas Island, 17.iv.1989; 10.30S 105.55E, EW Parl track, Christmas Island, 28.iv.1989.

Female: 10.27S 105.40E, Grants Well to Irvine, Hill Rd. track, Christmas Island, 27.iv.1989.

Wings of illustrated extant specimens were cut off specimens preserved dry or under ethanol, softened as necessary, and mounted in white Euparal (Asco Laboratories, Manchester, UK). Left wings were mounted on their dorsal side, right wings on ventral side. As far as possible, wings were mounted unfolded.

Photographs reproduced on Figs 2-9, 11-19, 22, 23, 27, 28 were taken with a Canon EOS 450D digital camera coupled to a Canon 50 mm macro lens (and an extension tube as appropriate), and to a Canon MP-E 65 mm macro lens. Photographs reproduced on Figs 1, 21 were taken with a Nikon Coolpix C2500L. Other photographs were provided by various colleagues. For wings of extant material, transmitted light was obtained from a VisiLED ACT Basis for small wings, and from a regular light table for larger ones. Photographs were dust off manually using a stamp tool, and processed with Adobe Photoshop. Unless specified, photographs of fossil specimens were taken under dry conditions.

Except for drawings reproduced in Figs 1 and 24, drawings were prepared with the aid of a Zeiss SteREO Discovery V8 stereomicroscope equipped with a pair of W-PL 10×/23 eye pieces, a Plan Apo S 1.0x FWD objective, and a camera lucida. Due to the occurrence of structural folds in fore- and hind wings, and as a result of the compression of the three-dimensional structure that an insect wing is, creases occurred in many preparations of extant material, in particular in hind wings. For example, ScP seems to be located posteriorly with respect to RA on Fig. 18, but is actually 'creased' below RA. In forewings, the membranous area posterior to AA veins was also problematic to mount unfolded, because it tends to fold even once cover glass has been put on. Drawings were corrected manually, and with the aid of Adobe Photoshop for hind wings vannus (distortion transformation).

I use the conjecture of topological homology proposed by Béthoux & Nel (2001) for orthopterans, itself based on the serial insect wing venation pattern (Lameere 1922, 1923). Corresponding abbreviations and color-coding are as follows: CP, posterior Costa; ScA, anterior Subcosta; ScP, posterior Subcosta; R, Radius; RA, anterior Radius; RP, posterior Radius; M, Media (green); MA, anterior Media; MP, posterior Media; CuA, anterior Cubitus (orange); CuP, posterior Cubitus; CuPa, anterior branch of CuP (purple); CuPb, posterior branch of CuP; CuPaα, anterior branch CuPa (blue); CuPaβ, posterior branch of CuPa (red); AA1, first anterior Analis. Correspondence with some other conjectures for orthopterans can be obtained from Béthoux & Nel (2002a: table 2) and on Fig. 10. The criticism expressed by Gorochoff (2005) regarding Béthoux & Nel's (2001, 2002a) conjecture are addressed in Béthoux (2007a). Subsequent comments by Rasnitsyn (2007) are addressed in Béthoux (2008).

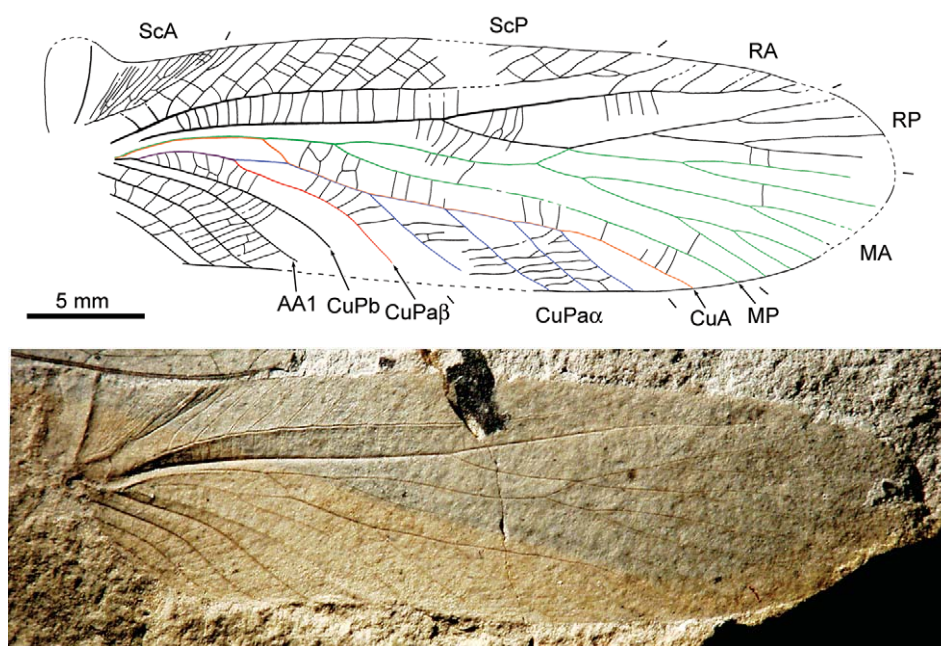


Fig. 1. Species †uralica Sharov, 1968, holotype (PIN 1700/4153), drawing and photograph (right forewing, negative imprint) (see text for abbreviations and color-coding). For color version, see Plate III.

Other abbreviations are as follows: LFW, left forewing; LHW, left hind wing; RFW, right forewing; RHW, right hind wing. A vein (or vein sector) is said to be convex if located on an elevation, and concave if located in a depression. I refer to cross-veins aligned longitudinally to main veins, which are secondary structures, as 'intercalary veins'.

Several transformation types are mentioned in the following and are better defined here. A translocation is the complete fusion of a vein (or one of its branches) with a surrounding vein (or branch), from the origin of the former, or from the wing base even. This transformation was documented in *Pantcholanvisiida* nom. Béthoux 2007d, dis. Béthoux & Nel 2002b, typ. Béthoux 2007d (Béthoux 2007d) and in mantodeans (Béthoux & Wieland 2009). The term 'abbreviation' refers to the complete lack of forewing apex, without alteration of the basal area morphology, common among orthopterans. The term 'pectinate fusion' refers to a case involving the successive pectinate emergence of branches of a vein fused with another, the former lacking a distinct main stem (documented in neuropterans, see Shi *et al.* 2012).

Measurements of forewing length of unprepared material were made using a caliper. Although measures were made once only, a confidence interval can be estimated based on the largest difference observed between left and right forewings of a single individual. This difference amounts to 1.1 mm. This estimated error accounts for error in judging the positions of the measurement points, and the accuracy of the reading. It is considered constant (*i.e.*, does not vary with wing size). Width of the area between M and CuPaa, opposite the free part of CuA (diverging from M + CuA, before its fusion with CuPaa), was measured under a microscope equipped with a graticule. A positive figure represents a free CuA, while a negative one indicates (1) that a M + CuA + CuPaa fusion occurs (*i.e.*, there is no free part of CuA: *e.g.*, Fig. 8E, G), and (2) the length of this fusion. This approach was prompted by the fact that the series of states ranging from 'long free part of CuA' to 'long M + CuA + CuPaa' form a continuum (Fig. 13M-Q) better appreciated by a single measurement.

Comparative analysis

The rationale of such analysis is clarified in Béthoux (2012: 44). In summary, conjectures of topological homology (=THCs) are established so that the amount of transformation that has to be assumed to explain differences between patterns is minimized. Ideally, sets of THCs (=STHCs) can be compared based on the total amount of transformation assumed by each STHC. However the methodology for this step is still little developed. In the following competing STHCs (see Fig. 10; 'classical' STHC including Fig. 10E-H; alternative STHC including Fig. 10I-N) will be compared based on the occurrence (or lack thereof) of predicted intermediate patterns, and their consistence with respect to observed variants. This approach is grounded in that any given STHC can be challenged by a new, more performing one.

The wing venation of *cf. mexicanus* de Saussure, 1859: 209, *laudatum* Johns, 1997, *ornata* Willemse, 1963, *cf. bicornis* Karny, 1929a, *pinguipes*? Rentz in Morton & Rentz, 1983, *pinguipes* Rentz in Morton & Rentz, 1983, sp. undet., *punctipennis* Walker, 1869, and *rufovaria* Kirby, 1888, will be compared successively in the following. These species were selected based on their position as putative intermediates (*i.e.*, exhibiting a unique pattern), reliable determination at the species level, and/or abundance of specimens available to the author. Variations observed in several aspects of wing venation are summarized in Appendix 4.

The fossil species †uralica Sharov, 1968 (Fig. 1) was selected to represent the presumed plesiotypic 'oedischoid' forewing morphology. As with most other Permian stem-orthopterans and Carboniferous relatives (Béthoux *et al.* 2012), †uralica possesses a common stem composed of M (green) and CuA (orange), a branched M (into MA and MP), a distinct free part of CuA, and CuP (purple) giving rise to CuPa (purple) and CuPb, a CuPa giving rise to CuPaa (blue) and CuPaβ (red), and a fusion of CuA with CuPaa resulting into a composite stem. Béthoux (2007d) suggested that CuA is simple in oedischoids and groups that derived from them. A simple CuA is conjectured for †uralica and in the following.

Species cf. *mexicanus*

A single specimen of cf. *mexicanus* was investigated (Fig. 2). Comparison with wing morphology of *laudatum* (Fig. 3) suggests that cf. *mexicanus* possesses abbreviated wings. In forewings, traits allowing this species to be distinguished from *†uralica* are: first branch of ScP reaching ScA; M + CuA and R coalescing near wing base (variable; Fig. 2G-H); RA simple; MA simple; CuA + CuPaa with two branches (i.e., CuPaa simple; in the right forewing CuPaa is probably forked with the two resulting branches re-uniting into a single stem); CuA, CuPaa, CuPaβ, and AA1 and other anal veins reaching wing margin in a very distal position; intercalary veins occur in areas between CuPaβ and CuPb, CuPb and AA1, and between anal veins. Otherwise, as in *†uralica*, a distinct free part of CuA (emerging from M + CuA, before fusing with CuPaa) occurs. It must be indicated that it could easily be confused with surrounding cross-veins, which are comparatively strong. Minor variation is exhibited by this specimen: RP is 2- and 3-branched in the left and right forewing, respectively.

The hind wing morphology of cf. *mexicanus* poses an issue relevant to the whole comparative analysis of hind wing venation. Unlike Palaeozoic stem-orthopterans (see Sharov 1968, 1971: figs 8C, E, 11C), the free part of CuPaa fusing with CuA was not detected. Although the basal stem of CuP can be identified from the wing base (it gives rise to CuPaβ and CuPb, and is located anterior to AA1; Fig. 2I,J), the area between M + CuA and CuPaβ is filled with regular cross-vein-like structures (Fig. 2I,J). Three conjectures are equally likely: (1) CuPaa is fused with M + CuA from the wing base (i.e., CuPaa is translocated onto M + CuA; if so 'M + CuA' and 'CuP' on Fig. 2I should read 'M + CuA + CuPaa' and 'CuPaβ + CuPb', respectively); (2) CuPaa fuses with M + CuA at the narrowing of the area between M + CuA and CuP; (3) CuPaa was reduced to a cross-vein (i.e., is inconspicuous) but actually fuses with CuA distal to its divergence from M + CuA. Translocations have been documented in several cases (Béthoux 2007d, Béthoux *et al.* 2010, Béthoux & Wieland 2009), making the conjecture (1) possible. However, it will be demonstrated below that the free part of CuA (emerging from M + CuA, basal to its fusion with CuPaa) can turn into a rather inconspicuous cross-vein-like structure, rendering (3) equally plausible. This issue is left unresolved.

Apart from this aspect, traits allowing the hind wing of cf. *mexicanus* to be distinguished from that of Palaeozoic stem-orthopterans are: RA simple (possibly a consequence of abbreviation); lack of strong inflexion point of the wing outline opposite the end of CuPb; CuA + CuPaa fusing with CuPaβ (near posterior wing margin). Notice the occurrence of a single intercalary vein between MP and CuA + CuPaa + CuPaβ.

Species *laudatum*

Wing venation of *laudatum* was investigated based on a larger sample. The usual forewing venation of the species is represented on Figs 3C,L, 4C (and see Appendix 4), and is characterized by: veinlet(s) from ScP reaching ScA; RA anteriorly pectinate; RP 2-branched; near wing base, occurrence of a convex intercalary vein between M + CuA and CuPa (covering hind wing base at rest); MA distinct from R; MP distinct from CuA / CuA + CuPaa; short free part of CuA; CuA and CuPaa diverging distally, both simple.

Various deviations from this pattern were observed. In a few cases no genuine ScP veinlets reaches ScA (compare Figs 3A,J, 4A to Figs 3B,K, 4B, same individual). Regarding this trait, some conditions are ambiguous even (see Fig. 3H,Q), with a structure that could equally

be a ScP veinlet, or a strong cross-vein. The length of the free part of M (between the divergence point of CuA and the branching of MP) varies, although it is usually short. The length of the free part of CuA varies moderately (Table 1), with one specimen exhibiting a short M + CuA + CuPaa stem (Figs 3E,N, 4E). Among the whole set of surveyed material, two forewings exhibit a connection of RA with ScP (one of them reproduced on Fig. 3E,N); a single forewing exhibits a fusion of MA with R (Figs 3G,P, 4F); one forewing exhibits a pectinate fusion of RP with RA (i.e., anterior branch of RP translocated onto RA, with successive origin of RP branches; Fig. 3H,Q; and see the *ornata* case); one forewing lacks the usual free part of CuPaa (diverging from CuPa), indicative of a translocation of CuPaa onto M + CuA (Figs 3I,R, 4G). Other cases observed in single forewings but not illustrated are: RP 3-branched; RP simple; MP branched (MA branch translocated onto MP?), with anterior branch vanishing; MA fused with RP at wing base.

Hind wings of *laudatum* (Fig. 5) differ from those of cf. *mexicanus* (and all other surveyed extant species) chiefly by the occurrence of a RP + MA fusion, of somewhat variable length (Fig. 5A,B,D,E; the hind wing reproduced on Fig. 5E is about 1.14 longer than that represented on Fig. 5A-B). Other notable traits are: occurrence of a single intercalary vein between MP and CuA + CuPaa + CuPaβ, and area between AA1 and the first AA2 vein filled with strongly sigmoidal cross-veins. RP is usually 2-branched, but the two hind wings of one of the 6 prepared specimens have a 3-branched RP (Fig. 5E).

Species *ornata*

This species proved to have forewings often exhibiting rare and unusual traits, to the point that a usual condition was impossible to delimit based on the available material. The most noticeable aspect regards the organization of RP. As observed on forewing represented on Fig. 6A,B,D,E,F,H, the stem of R emits several posterior stems earlier to the usual RA anterior branches, and sometimes additional posterior stem(s) distal to the first anterior ones. These successive posterior stems are interpreted as RP branches. In other words, it is assumed that a pectinate fusion of RP with RA occurs. An alternative conjecture would be that the first posterior branch is MA, but this option is easily discarded: (1) as in *†uralica*, cf. *mexicanus*, and *laudatum*, the stem of M near the origin of CuA is forked into two simple branches, therefore the anterior stem of M observed in *ornata* is likely the genuine MA, and (2) the left forewing of the specimen ANIC IWC OB 16 (Fig. 6C,G) has a MA actually translocated onto R (demonstrated by the basal origin of this stem, and the simple free part of M, hence composed of MP alone), yet it possesses 'successive posterior branches of R [indeed RP]'. The organization resulting from the pectinate fusion is variable: points of divergence of the successive RP branches, and the number of their own branches, vary widely. As a consequence apical branches are not always evident to assign either to RA or RP, and the range of RP branches is difficult to delimit (ca 4-6).

In this species it is nearly equally common that CuA diverges distal to the MA / MP fork (Fig. 6A,E; i.e., CuA is fused with MP for a short distance before diverging), basal to the MA / MP fork (as in species surveyed above), or that CuA is not distinguishable from surrounding cross-veins (Fig. 6D,H). The branching pattern of CuA + CuPaa is also variable: usually its two components diverge distally (Fig. 6A,E), but can keep fused (Fig. 6C,G; Appendix 4). Intermediate conditions occur, either with CuA (Fig. 6D,H) or CuPaa vanishing. A rare and informative case was observed in the right forewing of the specimen ANIC IWC OB 15 (Fig. 6B,F). At the first glance,

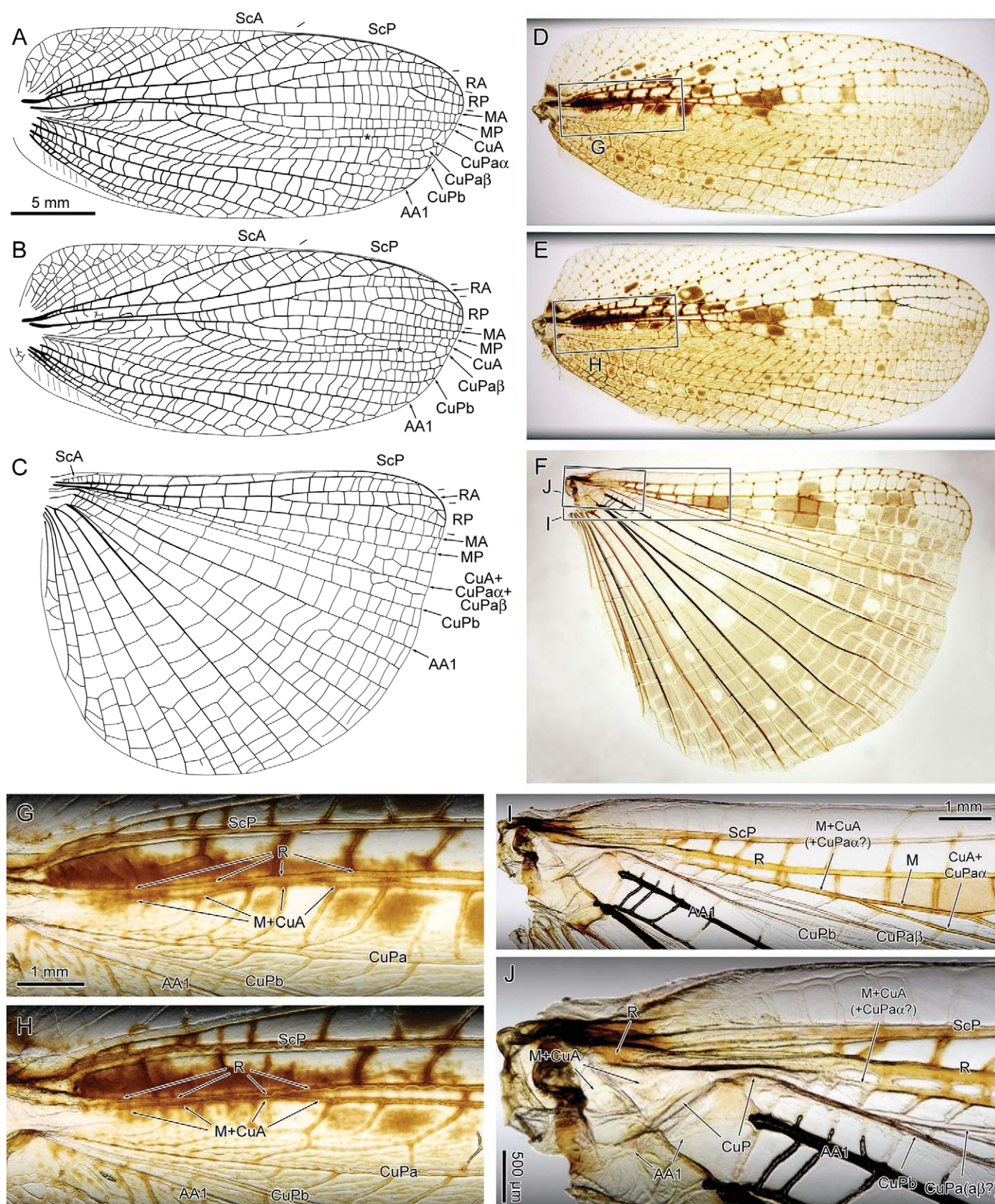


Fig. 2. Species cf. *mexicanus* de Saussure, 1859: 209, specimen ANIC IWC OB 26 (♀; A-F at the same scale; G-H at the same scale; A, * indicates CuPa α); A, D, drawing and photograph of the left forewing; B, E, drawing and photograph of the right forewing; C, F, drawing and photograph of the left hind wing; G, detail of the left forewing, as located on D; H, detail of the left forewing, as located on E; I, J, detail of the left forewing, as located on D.

Fig. 3. Continued: F-G, O-P, specimen ANIC IWC OB 8 (♀); F, O, drawing and photograph of the right forewing; G, P, drawing and photograph of the left forewing; H, Q, specimen QM (♂), drawing and photograph of the left forewing; I, R, specimen ANIC IWC OB 9 (♂), drawing and photograph of the left forewing.



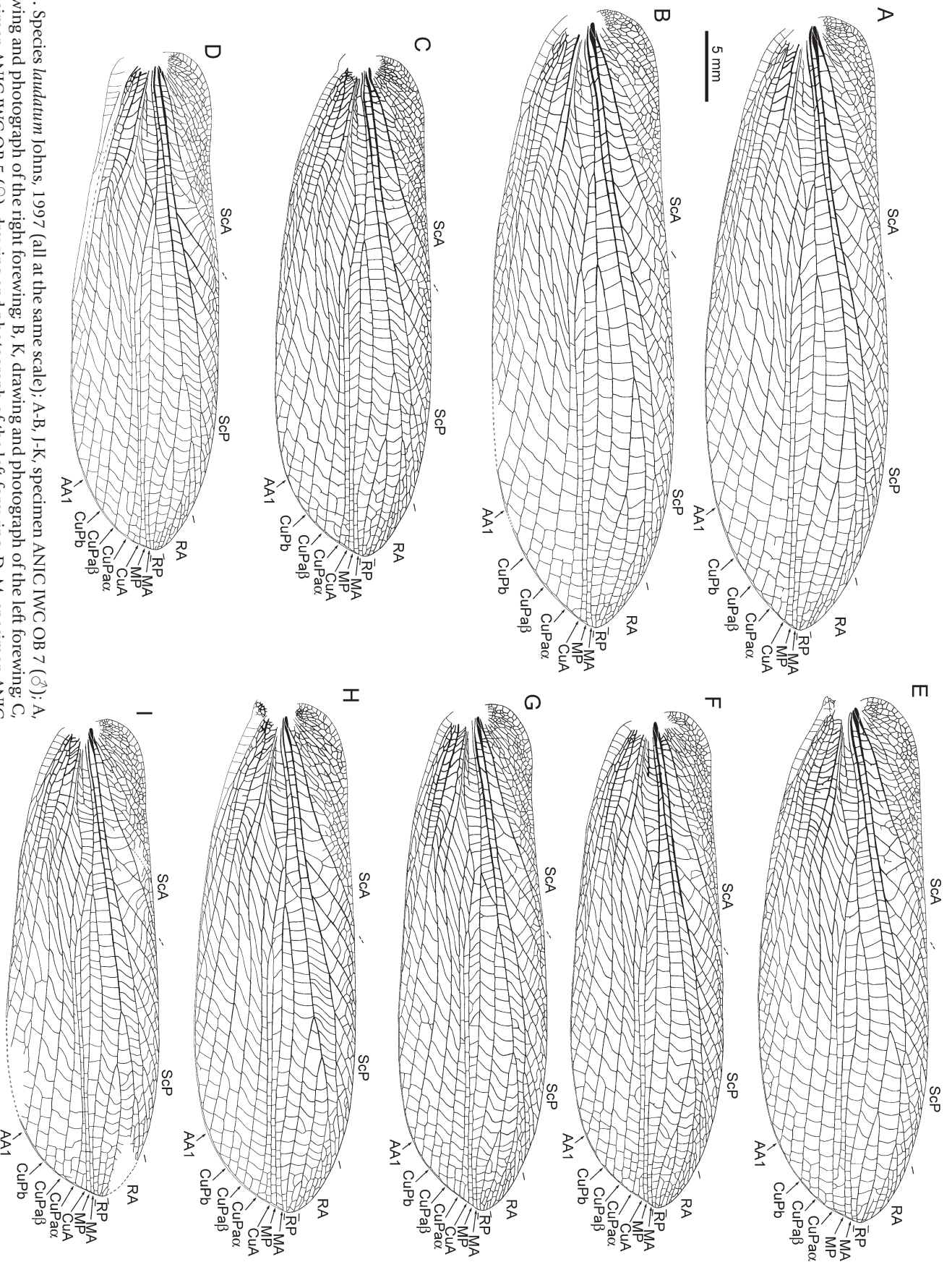


Fig. 3. Species *laudatum* Johns, 1997 (all at the same scale): A-B, J-K, specimen ANIC IWC OB 7 (♂); A, J, drawing and photograph of the right forewing; B, K, drawing and photograph of the left forewing; C, L, specimen ANIC IWC OB 5 (♀); drawing and photograph of the left forewing; D, M, specimen ANIC IWC OB 6 (♀); drawing and photograph of the left forewing; E, N, specimen ANIC IWC OB 10 (♂); drawing and photograph of the left forewing.

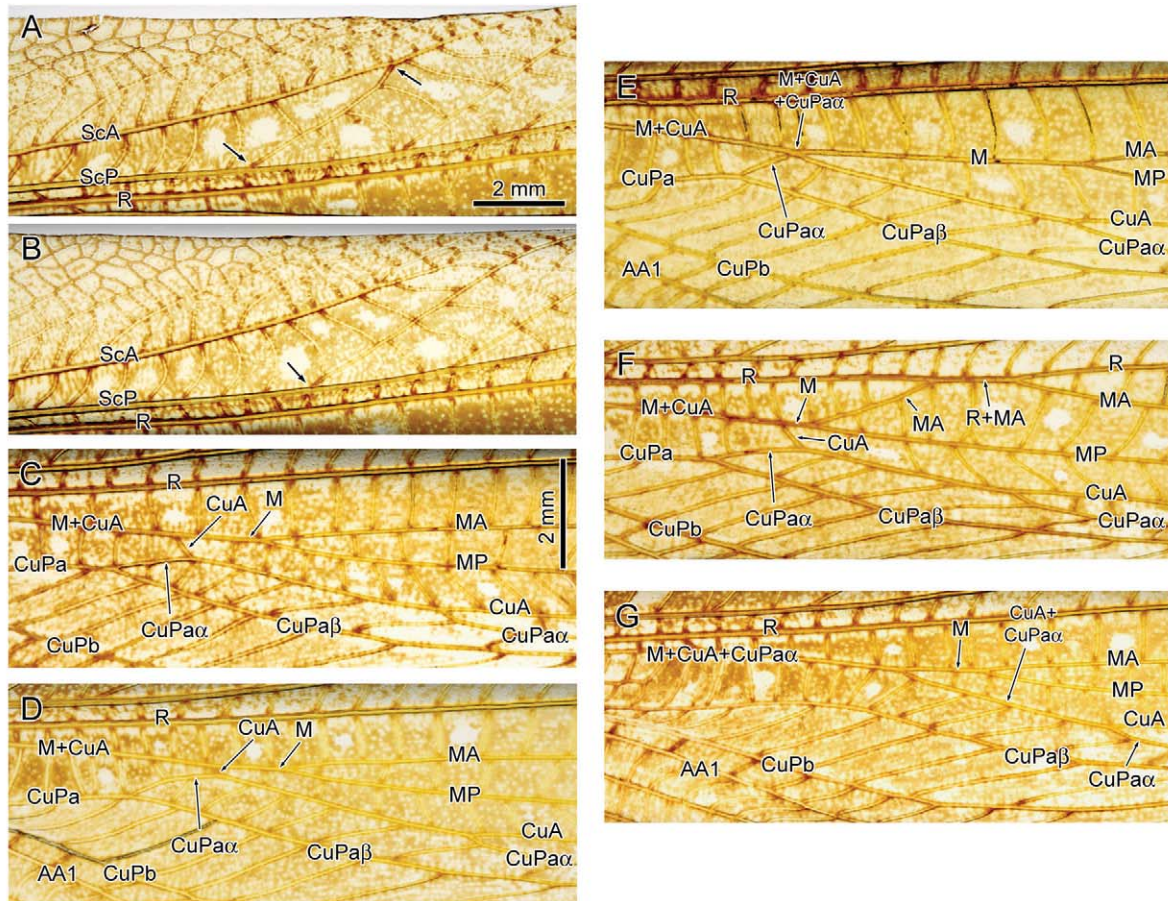


Fig. 4. Species *laudatum* Johns, 1997, details as located on Fig. 2; A-B, specimen ANIC IWC OB 7 (♂), detail of costal area; A, right forewing, arrows indicate the first ScP branch (reaching ScA); B, left forewing, arrow indicates the origin of the first ScP branch (reaching anterior wing margin); C-G, detail of medio-cubital area; C, specimen ANIC IWC OB 5 (♀), left forewing; D, specimen ANIC IWC OB 6 (♀), left forewing; E, specimen ANIC IWC OB 10 (♂), left forewing; F, specimen ANIC OWC OB 8 (♀), left forewing; G, specimen ANIC IWC OB 9 (♂), left forewing.

a 'vein-like portion' (indicated as ° on Fig. 6B) could have been considered as homologous to the basal section of CuPα, as usual, and as observed in the other wing of the same individual (° on Fig. 6A). However, this conjecture must be discarded: in this particular forewing the portion of CuPα distal to the origin of CuA (indicated as * on Fig. 6B) diverges from CuPa, *i.e.*, is not fused with CuA. As a consequence the structure indicated as ° on Fig. 6B is a 'phantom CuPα', *i.e.*, a remnant of the usual course of CuPα. This is possibly a case of 'tracheal un-capture' (see Béthoux 2012 for this transformation type).

Hind wings of *ornata* lack the pectinate fusion of RP with RA, and lack the RP + MA fusion observed in *laudatum*. The number of branches of RP varies between 3 and 4 (based on two hind wing pairs). A single intercalary vein occurs between MP and CuA + CuPα + CuPβ. A noticeable trait is the very basal origin of RP.

Species cf. *bicornis*

Illustrations of parts of the wing venation of *bicornis* are available from Karny (1929a: fig. 29). A more comprehensive treatment will prove necessary. Owing to their comparatively long ScA and short ScP, forewings of cf. *bicornis* might be abbreviated.

The usual organization of the connection of CuA with CuPα is represented on Fig. 8C,I (and see Appendix 4). It involves a short CuA diverging from M near the point of divergence of MA

and MP, and fusing with CuPα. However, a M + CuA + CuPα fusion (therefore without free part of CuA) was observed in 6 cases (4 of them composing 2 forewing pairs of single individuals; Fig. 8D-E,J-L). The standard deviation of the width of the 'CuA area / length of M + CuA + CuPα' is higher than in other species (Table 1), indicating an unusual variability of this character in cf. *bicornis*. Notice that standard deviation falls down to 0.44 if forewings of the specimen ANIC IWC OB 12 (the one with the two longest MP + CuA + CuPα fusions observed; Fig. 8E-F,K-L) is removed. Yet it is higher than in the other surveyed species.

In addition, the free part of CuA was observed to diverge distal to the MA / MP fork (*i.e.*, CuA is briefly fused with MP) in 6 cases (Fig. 8A,G). Also, MP was observed to diverge from CuA + CuPα (is re-routed along the free part of CuA) in 2 cases (Fig. 8B,H).

Except from the area involving the free part of CuA (or the lack thereof), the forewing venation of this species is comparatively stable. Veinlets of ScP rarely reach ScA (Appendix 4), RP is usually simple (20 cases), sometimes forked (13 cases; including 3 presumed cases of 'RA + RP pectinate fusion').

The hind wing morphology of cf. *bicornis* is unusual in that M + CuA and CuPa are very inconspicuous, and fuse near the wing base (Fig. 9). Although inconspicuous, a CuPβ distinct from CuA + CuPα was observed, as in species surveyed above (both veins fuse before reaching the wing margin). Another noticeable aspect is the occurrence of strong ScP branches. Such organization is common in

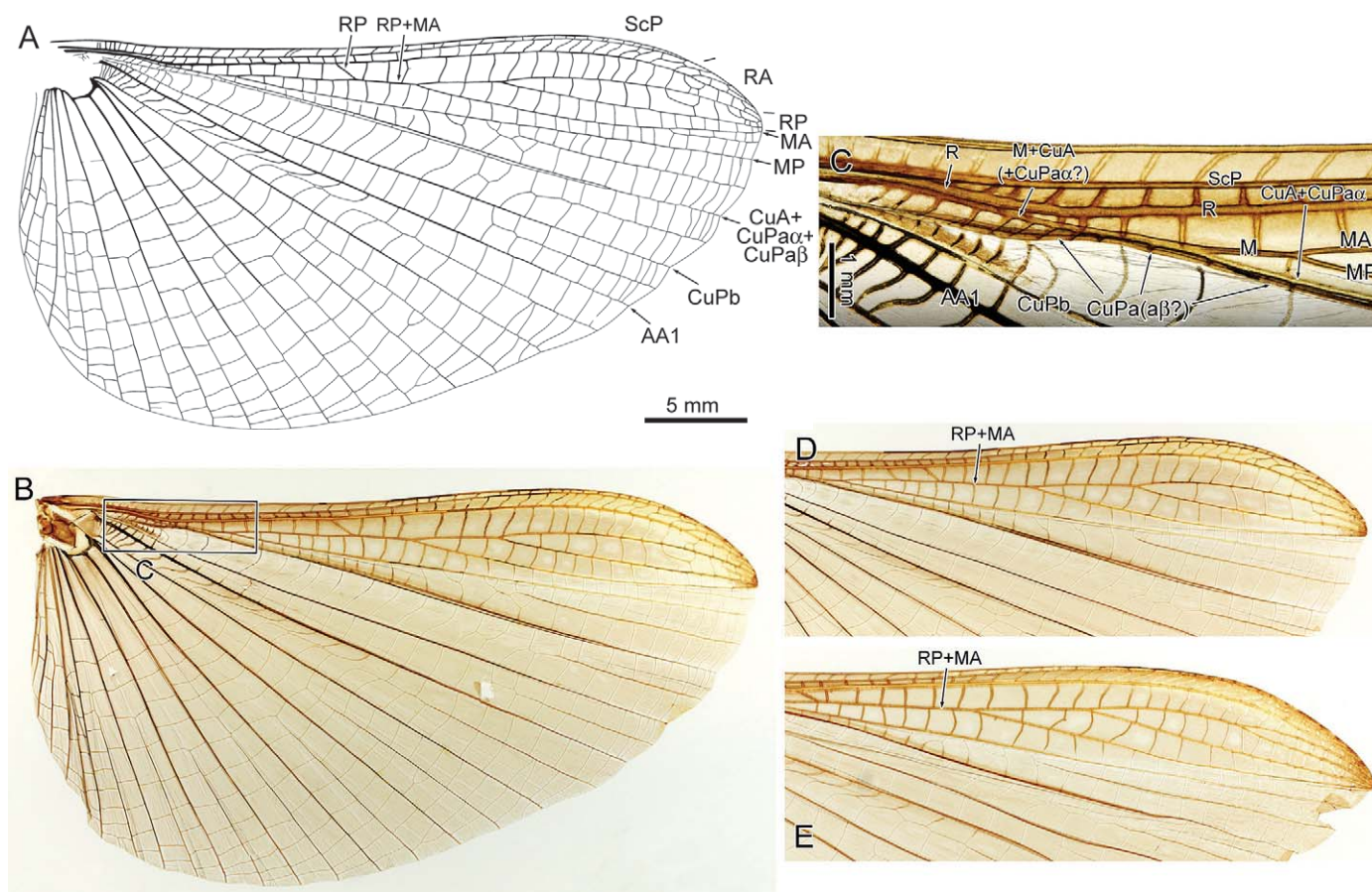


Fig. 5. Species *laudatum* Johns, 1997 (A-B, D-E at the same scale); A-D, specimen ANIC IWC OB 10 (♂); A-B, left hind wing, drawing and photograph; C, detail as located on B; D, portion of right hind wing, photograph; E, specimen ANIC IWC OB 7 (♂), portion of left hind wing, photograph.

forewings of orthopterans, but its occurrence in hind wings seems unique (at least among species considered herein).

Species *pinguipes*?

The corresponding specimen is essential to the establishment of forewing venation homologies of the species surveyed thereafter. Two possible transformation series are summarized on Fig. 10. They concern topological homologies of the medio-cubital area in forewings [according to Béthoux & Nel's (2001) conjecture and nomenclature for the whole orthopterans; correspondence with the Zeuner's (1939), Sharov's (1968, 1971), and Ragge's (1955) conjectures, under which the structure indicated as * is MP, is indicated by annotations in gray; annotations in light gray follow Karny's (1928b) conjecture, under which the structure indicated as * is a cross-vein].

The plesiotypic condition observed in †*uralica* (see Fig. 1) is schematized on Fig. 10A, and two patterns observed in *pinguipes* and closely related species are schematized on Fig. 10B,C. The aim of this section is to interpret these two patterns according to the conjecture of topological homologies posited for †*uralica*. Fig. 10F represents a conjecture proposed by Sharov (1968, 1971: fig. 27.B; see also Karny 1928b: figs 2, 9), assuming a simple M (Sharov's 'MA'), and a 3-branched CuA + CuPαα (Sharov's 'MP + CuA1'). According to this author, his 'MA' is branched in †*uralica*, so the implied transformation is M becoming simple. Another needed transformation involves the branching pattern of his 'MP + CuA1'

(here CuA + CuPαα), splitting into a simple 'MP' (here CuA) and a forked 'CuA1' (here CuPαα).

Fig. 10G represents the conjecture for the pattern reproduced on Fig. 10C according to Zeuner (1939: pl. 2, upper figure). This conjecture assumes a simple M (Zeuner's 'MA') and a 2-branched CuA + CuPαα (Zeuner's 'MP + CuA'). Provided that Zeuner assumes a forewing venation ground plan of orthopterans with a branched 'MA' (Zeuner 1939: pl. 9, upper figure), this author assumes the same transformation as Sharov (1968, 1971), viz. M (or 'MA') becoming simple in *pinguipes* and closely related species.

Two patterns can bridge those represented on Fig. 10A and Fig. 10F. One of them is represented on Fig. 10E, and assumes that the branching pattern of CuA + CuPαα was modified first. The other one (not represented) assumes that M becomes simple first. The most critical aspects of the argument being made here is that neither of these two patterns has ever been observed in actual specimens.

To date, another transformation series has never been considered. Starting from Fig. 10A, it assumes that CuPαα becomes simple (Fig. 10I). The corresponding pattern fits that observed in cf. *mexicanus*, *laudatum*, *ornata*, cf. *bicornis*, and was observed in the left forewing of the specimen ANIC IWC OB 24 (Fig. 11A,C,E,G). In the last case, this morphology is unusual for the species.

Then (Fig. 10J) MP is assumed to be re-routed together with the free part of CuA; the composite stem fuses with CuPαα; MP and CuA + CuPαα diverge distally; CuA and CuPαα diverge distally. Such a re-routing of MP was documented by Sharov (1968, 1971) in the *Gigantitanidae* (and see Béthoux 2007d: fig. 1D). This transformation was also documented in cf. *bicornis* (rare occurrences), and is

Fig. 6. Species *ornata* Willemse, 1963 (all ♂; all at the same scale; * indicates the portion of CuPaα distal to its divergence from CuA; ° indicates the portion of CuPaα basal to its fusion with CuA, or its 'phantom'; × indicates RA + RP *partim* stems); A-B, E-F, specimen ANIC IWC OB 15; A, E, left forewing, drawing and photograph; B, F, right forewing, drawing and photograph; C-D, G-H, specimen ANIC IWC OB 16; C, G, left forewing, drawing and photograph; D, H, right forewing, drawing and photograph.

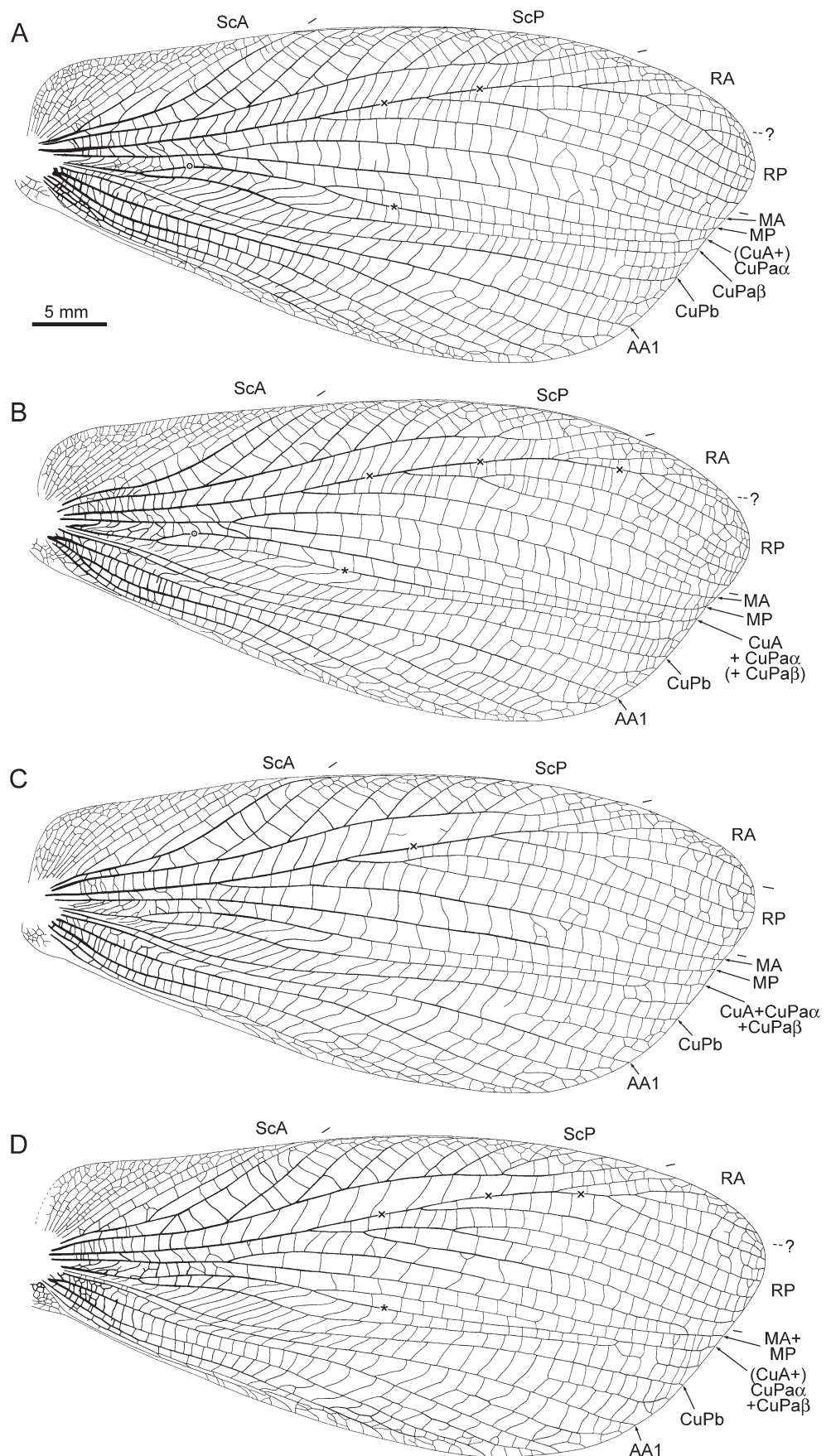
therefore highly plausible.

This alternative transformation series supposes the occurrence of a common stem MP + CuA. Direct evidence for this common stem is provided by the right forewing of the specimen ANIC IWC OB 24 (Fig. 11B,D,E,H). Exceptionally enough, this wing lacks the fusion of CuA (or MP + CuA) with CuPaα, present in all orthopterans since the Late Carboniferous (at least). Homologies in the right forewing are readily established based on the left one (compare Fig. 11E and F): the distal portions match, with a two-branched M, and simple CuA, CuPaα, and CuPaβ. Tracing MP and CuA backwards in the right forewing reveals that they form the common stem MP + CuA, as predicted.

This specimen indicates that the most plausible interpretation of the pattern represented on Fig. 10B is provided on Fig. 10J. From this step, interpretation of the pattern represented on Fig. 10C is straightforward: CuA and CuPaα keep being fused up to the posterior wing margin (Fig. 10K).

Species *pinguipes*

Forewing THC in this species are mainly established based on the previous case, but an additional specimen belonging to *pinguipes* supports the 'MP + CuA' conjecture (schematized on Fig. 10I-K). Forewings of this specimen are represented on Fig. 12. In both forewings M + CuA (presumably) separates into MA and MP + CuA, but MP diverges from MP + CuA and re-unites with MA, 're-forming' the M stem observed in previous species. Another interesting aspect of this specimen regards CuA



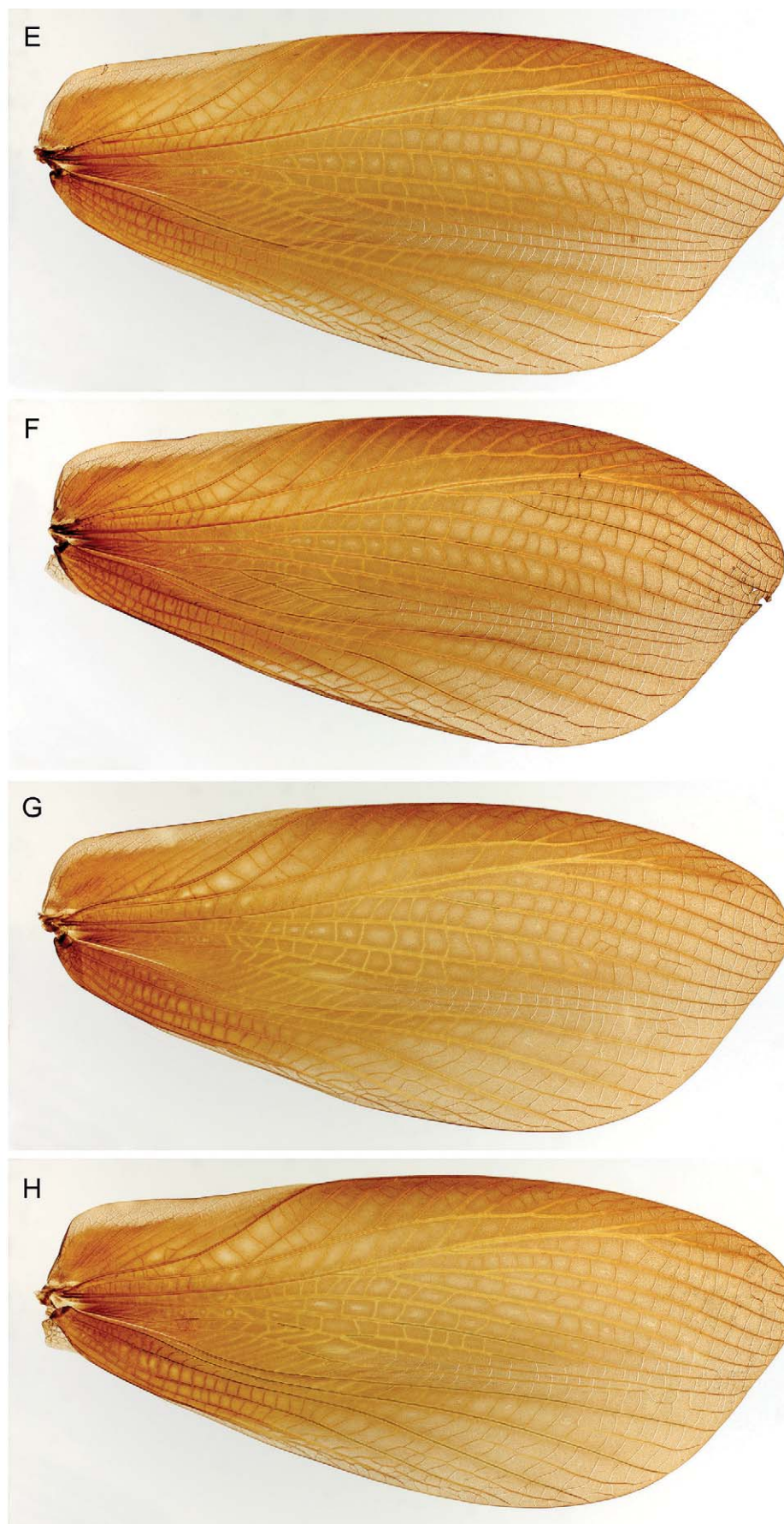


Fig. 6. Continued.

+ CuPaa. This stem is easily identified in both wings as being located posterior to MP, and anterior to CuPa β (itself easily located based on the location of its point of origin, similar in both wings). The point is that CuA + CuPaa is forked in the left forewing (Fig. 12A,C) and simple in the right one (Fig. 12B,D). The former case is uncommon in this species and was observed in females only (Table 1). This specimen validates the transformation assumed to have occurred between patterns represented on Fig. 10B and Fig. 10C (namely, CuA + CuPaa becoming simple): apart from the brief MA – MP reunification, its left and right forewings are schematized in Fig. 10J and Fig. 10K, respectively.

The species could be surveyed based on a large sample (Appendix 4), a selection of which is represented in Figs 13-14. A trait that significantly varies is the connection of CuA with CuPaa. The usual organization is represented on Fig. 13G,I, with a short free part of CuA. A complete series ranging from a long free CuA (Fig. 13A,D,M) to a long M + CuA + CuPaa fusion (longest fusion represented on Fig. 13I,L,Q) was documented in both males and females (Fig. 13; Appendix 4).

Unusual morphologies are documented in Fig. 14. Although the right forewing of the specimen ANIC IWC OB 20 possesses the usual CuPaa stem fusing with CuA (emerging from M + CuA; Fig. 13A,D,M), its left forewing has no such free CuPaa stem (Fig. 14A-B,K). Therefore it is assumed that CuPaa is translocated onto M + CuA. The left forewing of the specimen ANIC IWC OB 17 (Fig. 14D,E,L) has a MA fused with R opposite the fusion of MP and CuA with CuPaa. The fusion of MA with the radial system continues on along RP; at some point MA diverges from RP, shortly fuses with MP, and recovers its usual route. The right forewing of the same specimen (Fig. 14C,E) has the usual MA distinct from R and RP. Finally, the specimen ANIC IWC OB 21 has both forewings with a branched CuA + CuPaa (Fig. 14G-J; already observed in the specimen ANIC IWC OB 19, Fig. 12A,C), and the left forewing has a short RP + MA fusion (Fig. 14H,I).

Instead of having a stem of R straight, as in species surveyed above, the hind wings of *pinguipes* possess a R stem posteriorly bent basal to the point of divergence of RP (Fig. 15). Another peculiar aspect regards M. A fusion of a 'median element' with RP is evident (Fig. 15C). Posterior to this

Fig. 7. Species *ornata* Willemse, 1963, specimen ANIC IWC OB 15 (♂), left hind wing; A, B, drawing and photograph (same scale); C, detail as located on B.

'median element' occurs the genuine $\text{CuA} + \text{CuPa}\alpha$, identified based on its distal fusion with $\text{CuPa}\beta$. Whether the 'median element' is MA, or M, will be demonstrated based on the next case. Suffices to notice that (1) the free part of the 'median element' is simple (genuine RP branches are located very distally from its origin), and that (2) two intercalary veins occur between the free part of the 'median element' and $\text{CuA} + \text{CuPa}\alpha + \text{CuPa}\beta$ (unlike in previous species, in which a single intercalary vein occurs). Therefore two plausible options are to be considered: (a) a fusion of M with RP occurs (*i.e.*, MA and MP stay fused); or (b) a fusion of RP with MA occurs, and MP runs together with $\text{CuA} + \text{CuPa}\alpha$, as in forewings (but does not diverge distally).

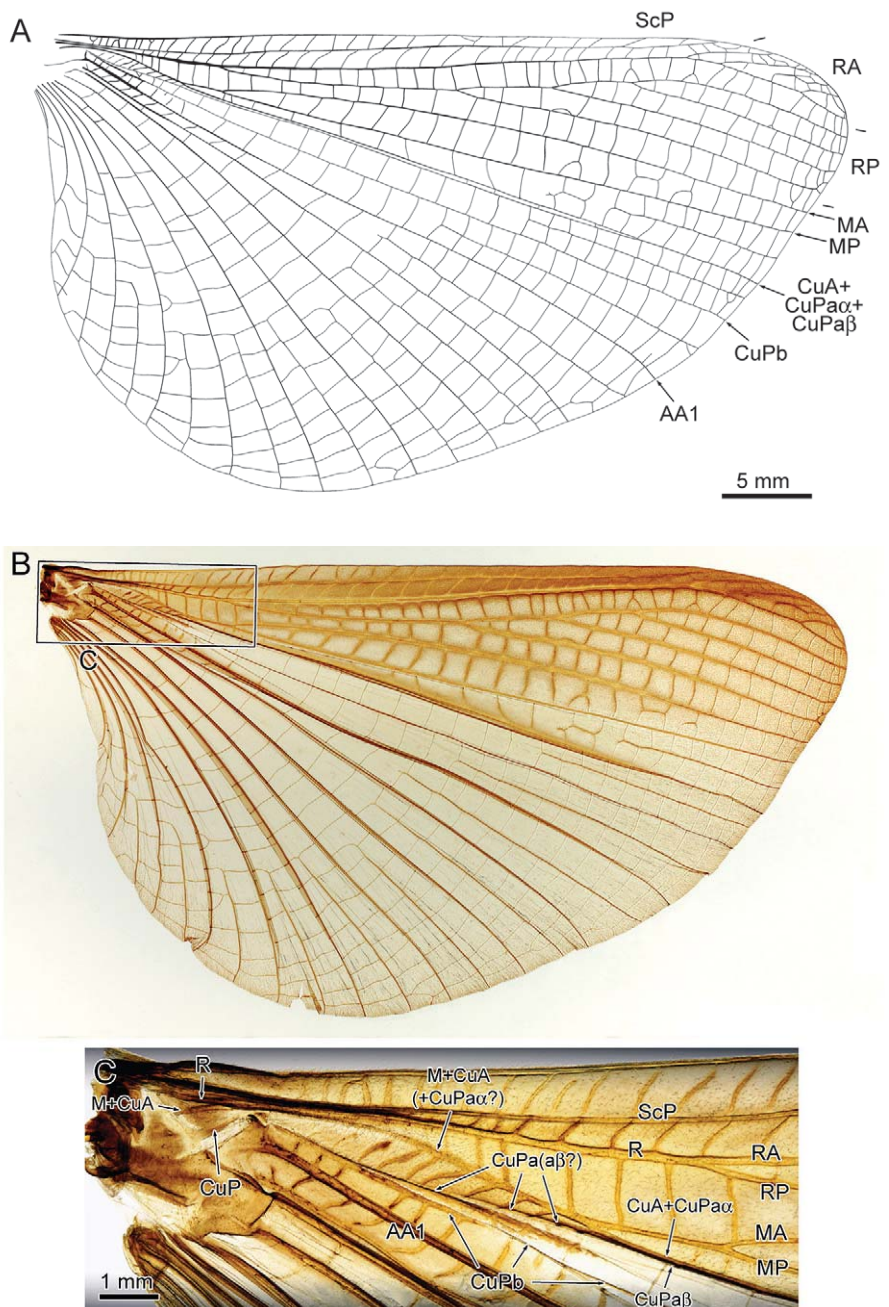
With respect to previous species, a peculiar trait is the organization of RA branches: in both fore- and hind wings, they arise basal to the first RP fork, and run parallel and close to the main RA stem for some distance.

Species undetermined

The corresponding single specimen was selected for differences observed among forewings, and for hind wing venation, allowing that observed in *pinguipes* to be interpreted. Both species are closely related, owing to the occurrence of a $\text{MP} + \text{CuA} + \text{CuPa}\alpha$ stem, of a simple $\text{CuA} + \text{CuPa}\alpha$ in forewings, and to the organization of RA branches in both wing pairs (*viz.* delimiting very narrow areas).

Although the right forewing possesses a usual free part of $\text{CuPa}\alpha$ fusing with $\text{M} + \text{CuA}$ (Fig. 16A,D,G), this portion does not occur in the left forewing (Fig. 16B,E,H). It is assumed that $\text{CuPa}\alpha$ is translocated onto $\text{M} + \text{CuA}$ from the wing base, a transformation already conjectured in a specimen of *pinguipes* (Fig. 14A-B,K).

Regarding hind wings, as in *pinguipes*, a fusion of a 'median element' with RP was observed (Fig. 14C,E,I). In addition, as in *pinguipes*, two intercalary veins occur between the first posterior branch of this composite stem and $\text{CuA} + \text{CuPa}\alpha$ (itself identified based on its distal fusion with $\text{CuPa}\beta$). However, unlike in *pinguipes*, two 'median elements' diverge posteriorly basal to genuine RP branches (themselves arising distally). These two 'elements' are likely to be MA and MP. Therefore MA and MP are located between RP and its branches, and an area with two intercalary veins. Applied to *pinguipes*, it implies that the simple 'median element' is an undivided M [*i.e.*, the above-cited conjecture (a) is correct]. It is not excluded that the morphology observed in the specimens ANIC IWC OB 25 is unusual for the corresponding species.



Species punctipennis

The usual organization of M, CuA, and of branches of CuPa in forewings of *punctipennis* is represented on Fig. 17A,E, and is schematized on Fig. 10D. As aptly recognized by Karny (1910), Zeuner (1939), and Ragge (1955), MA ('M' of previous authors) is fused with R at the wing base (Fig. 10H,L-N). It is the most plausible conjecture for the occurrence of a single stem basal to the RA / RP fork. Although tracheae were uneasy to observe in material of *punctipennis*, the stem of 'R' is provided with two evident tracheae in forewings of *rufovaria* (Fig. 19E), *viz.* R and MA.

Several conjectures are possible for the remaining medio-cubital elements. According to Ragge (1955: fig. 54), M is simple and no fusion of 'MP' (here CuA) occurs, and 'Cu_{1a}' (here CuPaα) and 'Cu_{1b}' (here CuPaβ) diverge distally. However, this option is balanced in the text (pp. 76-77), in which this author suggested that 'MP' (CuA)

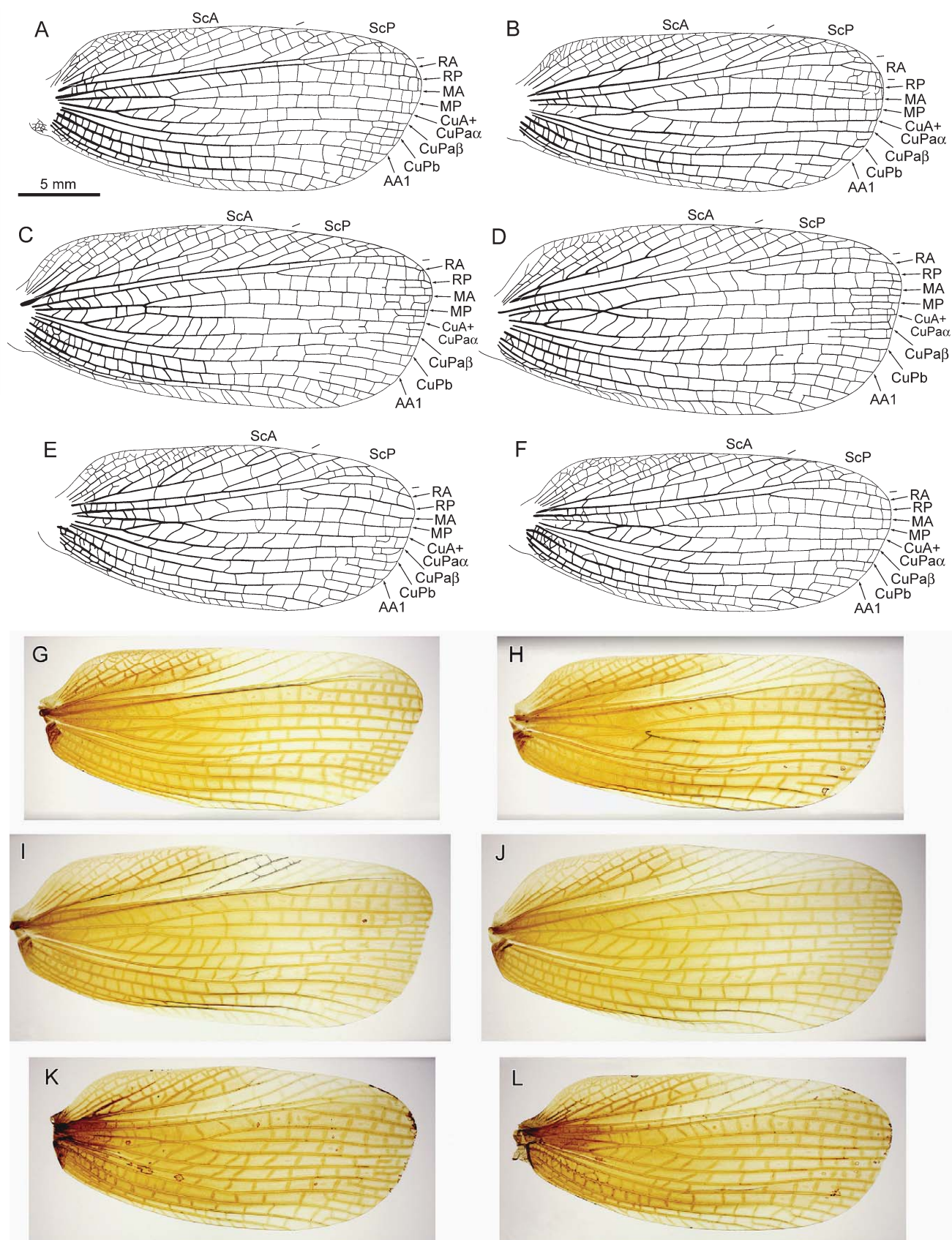


Fig. 8. Species cf. *bicornis* Karny, 1929a (all ♀; all at the same scale); A, G, specimen ANIC IWC OB 13, right forewing, drawing and photograph; B, H, specimen ANIC IWC OB 11, left forewing, drawing and photograph; C-D, I-J, specimen ANIC IWC OB 14; C, I, left forewing, drawing and photograph; D, J, right forewing, drawing and photograph; E-F, K-L, specimen ANIC IWC OB 12; E, K, left forewing, drawing and photograph; F, L, right forewing, drawing and photograph.

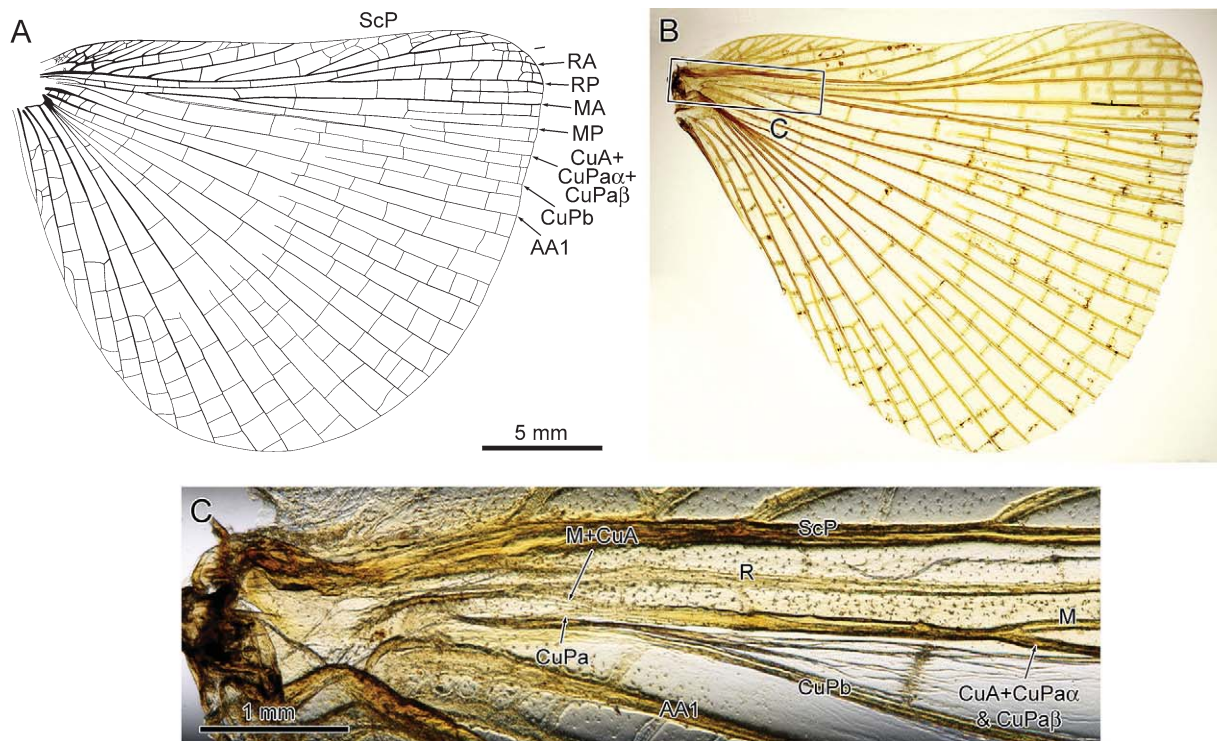


Fig. 9. Species cf. *bicornis* Karny, 1929a, specimen ANIC IWC OB 11 (♀), right hind wing; A, B, drawing and photograph (same scale); C, detail as located on B.

could be fused with 'Cu₁' (CuPa). This option is schematized on Fig. 10H. An issue with this interpretation is that it can hardly account for the occurrence of the pattern observed in the left forewing of the specimen ANIC IWC OB 37 (Fig. 17B,F; schematized on Fig. 10L): it would necessitate a branched 'Cu_{1b}' (here CuPaβ) (but this vein is simple in all orthopterans), or a translocation of 'Cu_{1a}' (here CuPaα) onto 'Cu_{1b}' (here CuPaβ). A more plausible option is based on one of the THC proposed for *pinguipes* and schematized on Fig. 10K), implying the occurrence of a common stem MP + CuA + CuPaα which splits into MP and a simple CuA + CuPaα. Applying this pattern to the left forewing of the specimen ANIC IWC OB 37 (Fig. 17B, F) leads to the interpretation schematized on Fig. 10L: in both cases (Fig. 10K, L), posterior to MA successively occur the simple MP, then the composite (and simple) CuA + CuPaα stem, and then CuPaβ. On Fig. 10L, if traced backwards, the course of these elements reveals a composite stem CuA + CuPaα + CuPaβ, and a more basal composite stem MP + CuA + CuPa (CuPa or CuPaα + CuPaβ). No evidence was found for a 'composite anterior stem' [i.e., composed of MP and other 'elements', as suggested by Ragge (1955)]. Therefore it is assumed that in the usual forewing morphology of *punctipennis* MP + CuA + CuPa / CuPaα + CuPaβ divides into MP and a simple CuA + CuPa / CuPaα + CuPaβ (Fig. 10M). Among specimens of *punctipennis*, a single forewing was observed with an undivided composite MP + CuA + CuPa / CuPaα + CuPaβ stem (Fig. 17D,H), but it is not uncommon to observe the first fork of MP + CuA + CuPa / CuPaα + CuPaβ in a distal position (Fig. 17C,G). One specimen was observed with MP diverging from MA (hence M; Appendix 4). Very probably CuPa does not actually forks into CuPaα and CuPaβ in the usual morphology.

Limited variation was observed in the number of RP branches (♂, 11 forewings with 2-branched RP, 7 with 3-branched RP; ♀, 4 forewings with 2-branched RP, 8 with 3-branched RP). The organization of ScA is peculiar in that branches of the main stem originate at

the wing base, resulting in a seemingly simple ScA complemented by branches of another vein / vein sector anterior to it. However, all these branches clearly belong to ScA.

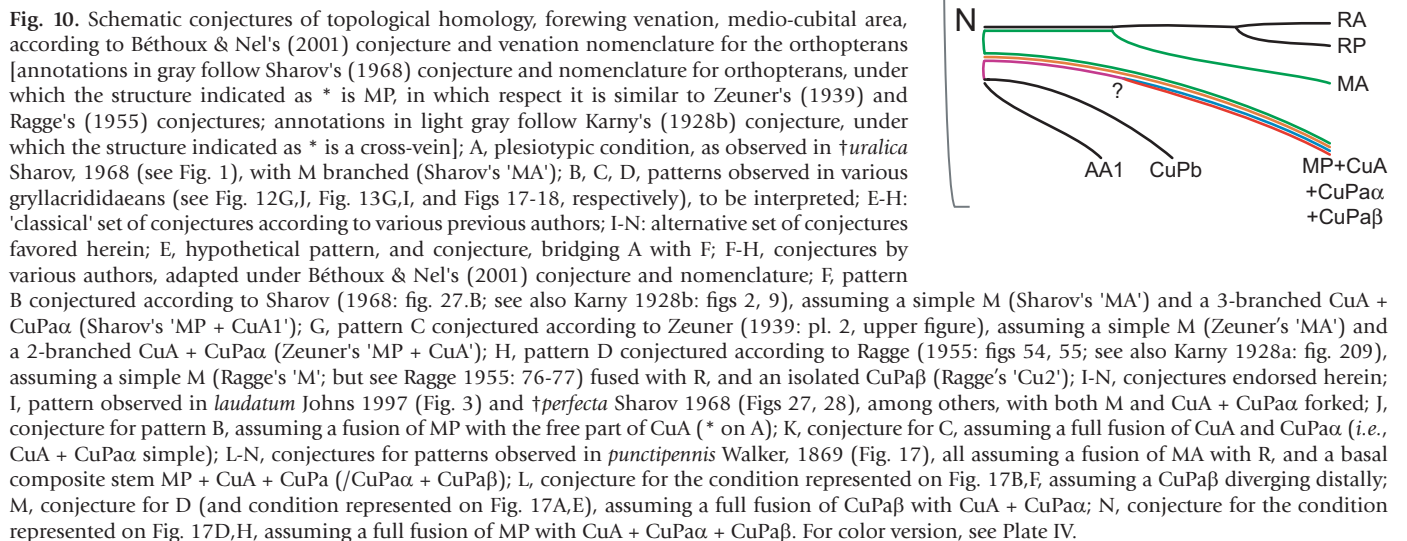
As for hind wings, a fusion of M with R (instead of with RP as in *pinguipes*) occurs near the base in *punctipennis* (Figs 17I, 18). Then M diverges from R but usually re-fuses with RP, near the origin of the latter, for some distance (Fig. 18B-D). This second fusion is very variable, ranging from 'fusion absent' (Fig. 18A) to a full fusion of M with R and RP, with a distal free part of M only (Fig. 18E-F). The length of the M + RP fusion itself varies widely (Fig. 18B-D).

Species *rufovaria*

Wing venation of this species (Fig. 19) is very similar to that of *punctipennis*. It was investigated primarily because tracheation was well-discernible in the available material. In forewings the MA trachea running 'inside' the radial vein is evident (Fig. 19E). Interestingly R and MA tracheae are entwined, with MA taking an anterior position with respect to RP for some distance. Another interesting aspect regards MP + CuA + CuPa / CuPaα + CuPaβ. This structure, genuinely composite, is provided with a single trachea.

Summary and comment

The comparative analysis demonstrates that the 'classical' STHC (Fig. 10E-H), which basically assumes a simple M (starting from the pattern represented on Fig. 10F), does not fit the data as well as the alternative one (Fig. 10I-N). In particular, the pattern represented on Fig. 10E, which is needed to complete the 'classical' series, has never been actually observed. In addition the alternative STHC accommodates more satisfactorily the observed variants, such as those represented on Figs 11, 12, 17B,F. In particular the wing venation pattern represented on Fig. 17B,F (and schematized on Fig. 10L)



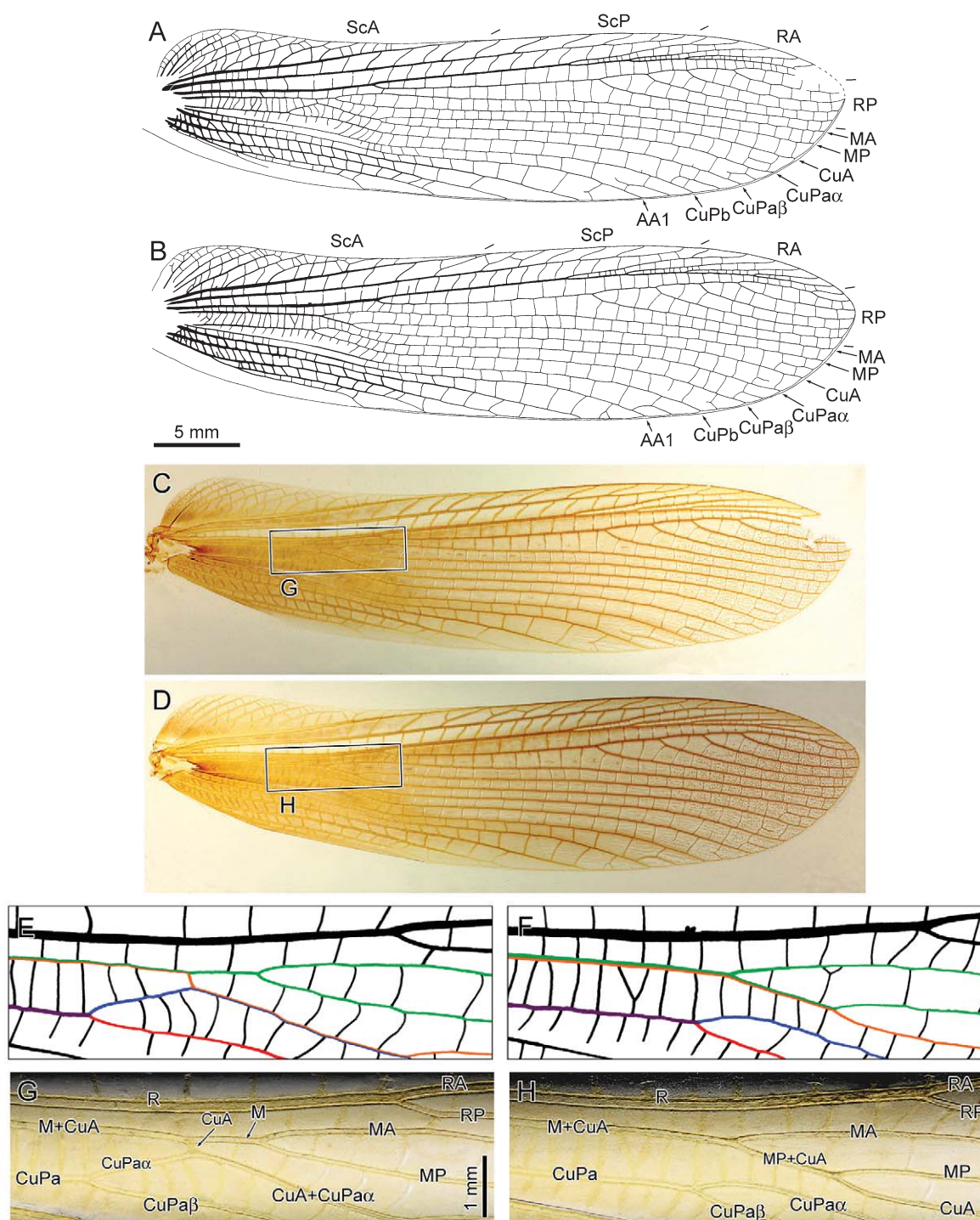


Fig. 11. Species *pinguipes*? Rentz in Morton & Rentz, 1983, specimen ANIC IWC OB 24 (♂; A-D at the same scale; E-H at the same scale); A, C, left forewing, drawing and photograph; B, D, right forewing drawing and photograph; E-H, details of medio-cubital area (see text for color-coding); E, G, interpretation and photograph, as located on C; F, H, interpretation and photograph, as located on D. For color version, see Plate V.

cannot be satisfactorily explained if one assumes a simple M. In order to facilitate comparison with actual material, the favored THCs are summarized on Fig. 20 (including interpretation for *†perfecta* Sharov, 1968; see below).

An oblique and comparatively strong cross-vein-like structure was observed between R and M + CuA in various specimens (* on Figs 12G, 14K, 19E). It has never been observed in Palaeozoic orthopterans and therefore is supernumerary. Its nature is unknown.

Taxonomic and nomenclatural implications

Taxonomy and nomenclature of several fossil species and taxa only remotely related to extant king crickets, raspy crickets & weta are considered first. It can be mentioned here that material yielded by the Dzaylyaucho locality [Madygen Formation, Kyrgyzstan; Ladinian/Carnian, late Middle to early Late Triassic, according to Dobruskina (1995)] was deformed during fossilization (Rasnitsyn 1982; Sharov 1968, 1971; Figs 21, 27C,I). Based on preliminary investigations on

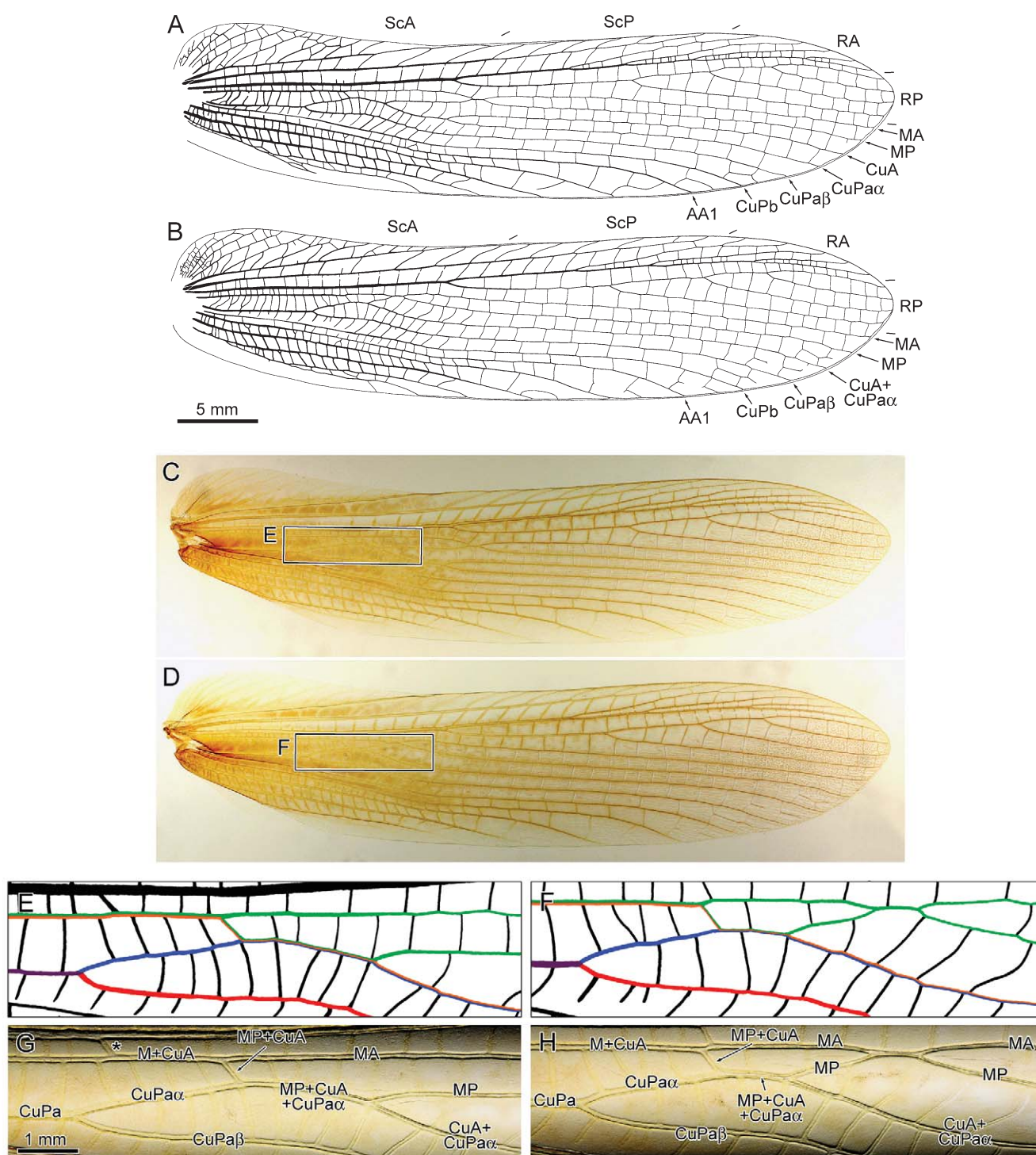


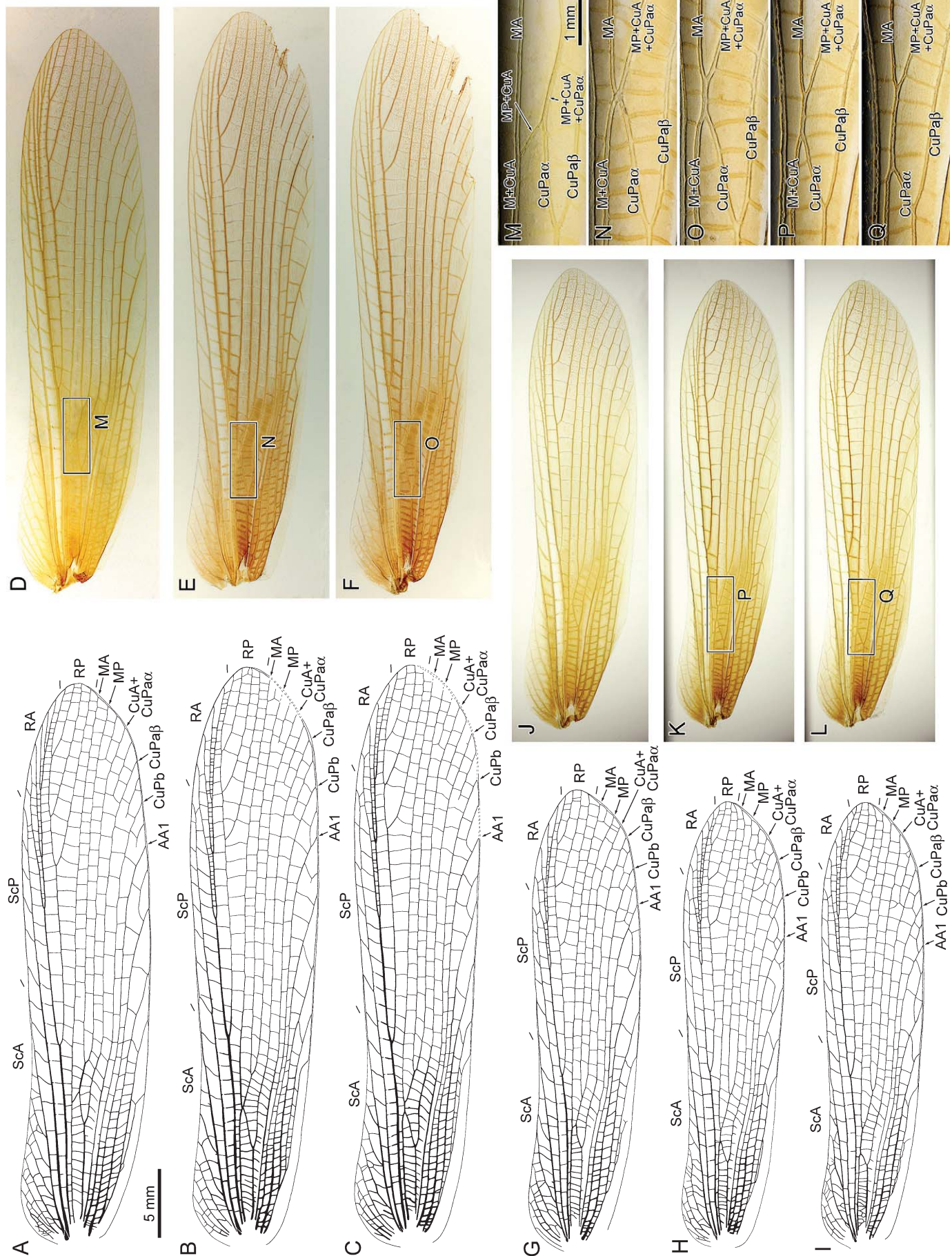
Fig. 12. Species *pinguipes* Rentz in Morton & Rentz, 1983, specimen ANIC IWC OB 19 (♀, A-D at the same scale; E-H at the same scale); A, C, left forewing, drawing and photograph; B, D, right forewing drawing and photograph; E-H, details of medio-cubital area (see text for color-coding); E, G, interpretation and photograph, as located on C; F, H, interpretation and photograph, as located on D. For color version, see Plate VI.

material from this locality (in prep.), a plastic elongation of 150% best explains the observed aspect ratios. Species involved by such deformation are †*abscissa* Gorochov, 1987a, †*triassica* Sharov, 1968: 168, †*perfecta*, and †*orientalis* Sharov, 1968 (and species considered as junior synonyms of these in the following).

**Taxon *Archaeorthoptera* nom. Béthoux & Nel, 2002a,
dis.-typ. Béthoux, 2007d**

**Species †*abscissa* Gorochov, 1987a
Fig. 22**

Discussion.—This species is assigned by Gorochov (1987a) to his preparagryllacridinaean assemblage, to which belongs †*perfecta*,



revised below. The species †*abscissa* is treated separately from members of the taxon *Agryllacris* (as defined below, and including †*perfecta*) due to the following. It is based on single, fragmentary, and only moderately well-preserved specimen (Fig. 22). Differences with †*perfecta* (and presumed closely related species) are substantial: according to Gorochov (1987a), it can be characterized by (1) small size, (2) ScP ending not far from wing apex, (3) RA 2-branched, (4) CuA + CuPaa 3-branched (instead of 2 in proparagryllacridinaean), (5) loss of veins 'parallelization'. Regarding the character state (4), it must be mentioned that the wing base is not preserved, therefore it cannot be excluded that CuA + CuPaa was provided with more than 3 branches.

It is unclear why Gorochov (1987a) considers this species as closely related to †*perfecta*. Several hagloideaean species collected from the same locality possess a simple MA (Gorochov 1986: figs 16, 19-23, 25-27, 29, 32-33, 36-38, 43-44), and although males of this assemblage do have MA and MP strongly bent in their proximal part (unlike in †*abscissa*), females do not (Sharov 1968: fig. 20B, D; Gorochov 1986: figs 32-34; see also Jurassic material illustrated by Sharov 1968). Assignment of the holotype of †*abscissa* to a female of one of the hagloideaean species reported from Madygen is consistent with the characters listed above: for example, the holotype of *saussurei* Gorochov 1986 (Gorochov 1986: fig. 21) has a width similar to that of †*abscissa* (about 9.0 mm in the former, 7.1 mm in the latter) (1), ScP ending close to wing apex (2), RA with 2 to 3 branches (3), CuA + CuPaa with more than 2 branches (4), and non-parallel main veins (5). In addition, although the comparatively poor preservation does not allow a conclusive statement, the holotype of †*abscissa* exhibits 'ScP veins' that can be interpreted as secondary intercalary veins instead (* on Fig. 22), a trait proper to stem-hagloideaans (Béthoux & Nel 2002a, Béthoux *et al.* 2002). In conclusion, †*abscissa* is better considered as a female of one of the numerous hagloideaean species already described from the same locality. It will not be considered further.

**Taxon †Bintoniellidae nom. Handlirsch, 1938,
dis. Sharov, 1968, typ. nov.**

Definition.—Species that evolved from the metapopulation lineage in which the character state 'in forewing, no distinct base of CuPaa diverging from CuPa (and fusing with CuA or M + CuA)', as exhibited by †*triassica* Sharov, 1968: 168 and †*brodiei* Handlirsch, 1938, has been acquired.

Cladotypes.—Specimen PIN 2069/2320 (holotype of †*triassica*; Fig. 23A-B; Dzaylyaucho; Madygen Formation, Kyrgyzstan; Ladinian/Carnian, late Middle to early Late Triassic), and NHM I.6784 [collected from the same locality as the holotype of †*brodiei* and assigned

by Whalley (1982) to this species; Fig. 24C-E; Binton, Warwickshire, UK; Lower Jurassic].

Composition.—Cladotypic species; and †*crassa* Gorochov, 1987a, †*oblonga* Gorochov, 1987a, and †*angusta* Gorochov, 1987a, if considered as valid species (but see below).

Discussion.—The antonym of the defining character state is 'in forewing, CuPaa with a distinct base diverging from CuPa, distal to the wing base (and fusing with CuA or M + CuA)'. This state is most likely plesiomorphic as it is exhibited by the vast majority of Palaeozoic *Archaeorthoptera* and saltatorians (Béthoux *et al.* 2012; Béthoux & Nel 2003, 2005a, b; Sharov 1968, 1971; among others). The corresponding taxon name was erected by Handlirsch (1938) for the species †*brodiei* only, known from abundant material (Figs 24-25). Later on Sharov (1968, 1971) assigned the species †*triassica* to this taxon. According to this author "the differences [of bintoniellidaeans with respect to vitimiidaeans] are only that the base of CuA1 [CuPaa] disappeared [...] and became a crossvein so that the stem of MP + CuA1 [CuA + CuPaa] branches from M". Rather than assuming a 'cross-vein-like' transformation of CuPaa, I assume that this stem is translocated onto M + CuA, *i.e.*, is fused with M + CuA from the wing base. Whether Sharov (1968) should be granted for associating a single diagnostic character state with the taxon name 'Bintoniellidae' is an interesting case. The formulation of the defining character state I propose leaves both options open (*viz.* cross-vein-like transformation *vs* translocation). It does not assume any particular transformation, and instead focuses on the condition observed in †*triassica* and †*brodiei*. The statement by Sharov (1968, 1971) is both a plain description of the observed condition, and a hypothesis on the transformation responsible for this condition. Provided that his statement fits, in part, the chosen character state formulation, I propose to grant Sharov for recognizing the defining character state of the taxon. Under cladotypic nomenclature, this makes the name 'Bintoniellidae' preoccupied (*i.e.*, it has been previously associated with a single character state – presumably derived).

According to the provisional delimitation of †*triassica* (see below), the second available specimen of this species exhibits the antonym of the defining character state (Fig. 23C-D). However, I assume that this case accounts for the rare occurrence of a plesiomorphic condition, fitting within the range of usual intra-specific variability (see below).

Species †*triassica* Sharov, 1968: 168

Fig. 23

Species †*triassica* Sharov, 1968, p. 168, fig. 16B; holotype PIN 2069/2320 (Fig. 23A,B).

Species †*primaria* Sharov, 1968, p. 168, fig. 16A; holotype PIN 2240/1865 (Fig. 28C,F), *syn. nov.*

Discussion.—The forewing of the holotype of †*triassica* lacks a distinct origin of CuPaa from CuPa (*i.e.*, it exhibits a M + CuA + CuPaa basal stem; Fig. 23A-B). Such configuration was documented by Gorochov (1987a) in the species †*crassa* Gorochov, 1987a, †*oblonga* Gorochov, 1987a, and †*angusta* Gorochov, 1987a. All were collected from the same locality as the holotype of †*triassica*, and each is documented after a single specimen. These specimens were available to Sharov, who probably assigned them to 'his' †*triassica* [17 forewing imprints are reported by Sharov (1968, 1971) but without indication of specimen numbers]. The additional species erected by Gorochov (1987a) differ from †*triassica* by a few traits.

Fig. 13. (Preceding page) Species *pinguipes* Rentz in Morton & Rentz, 1983 (A-E, M-O, ♀; G-L, P-Q, ♂; A-L at the same scale; M-Q at the same scale); A, D, M, specimen ANIC IWC OB 20, right forewing, drawing, photograph, and detail of medio-cubital area as located on D; B-C, E-F, N-O, specimen ANIC IWC OB 18; B, E, N, right forewing, drawing, photograph, and detail of medio-cubital area as located on E; C, E, O, left forewing, drawing, photograph, and detail of medio-cubital area as located on F; G, J, specimen ANIC IWC OB 23, right forewing, drawing and photograph; H-I, K-L, P-Q, specimens ANIC IWC OB 22; H, K, P, left forewing, drawing, photograph, and detail of medio-cubital area as located on P; I, L, Q, left forewing, drawing, photograph, and detail of medio-cubital area as located on Q.



Fig. 15. Species *pinguipes* Rentz in Morton & Rentz, 1983, specimen ANIC IWC OB 18 (♀), left hind wing; A, B, drawing and photograph (same scale); C, detail as located on B.

Revision of the corresponding material was not carried out, and proper data is lacking to allow Gorochov's (1987a) delimitation to be debated. On the other hand, grounds for Gorochov's (1987a) delimitation was never made explicit. I provisionally and informally consider these species as junior synonyms of †*triassica*.

The holotype of the species †*primaria* differs from material mentioned above by the occurrence of a distinct CuPaa stem diverging from CuPa distal to the wing base (a plesiomorphic condition; Fig. 23C-D). The survey of extant material carried out above demonstrates that the rare occurrence of a plesiomorphic condition is a common case at the species level. Therefore, assuming that †*triassica* is recorded thanks to four specimens exhibiting the derived condition (*viz.* the holotypes of †*triassica*, †*crassa*, †*oblonga*, and †*angusta*), it is reasonable to assume that the condition exhibited by this specimen merely accounts for intra-specific variation in †*triassica*. After all, it can merely be considered as an atavism. Observations made in *laudatum* and *pinguipes* of rare occurrence of a M + CuA + CuPaa (Fig. 3I,R, and Fig. 14A,B, respectively) mirror the assumption of a rare occurrence of the ancestral condition in †*triassica* (inclusive of †*primaria*).

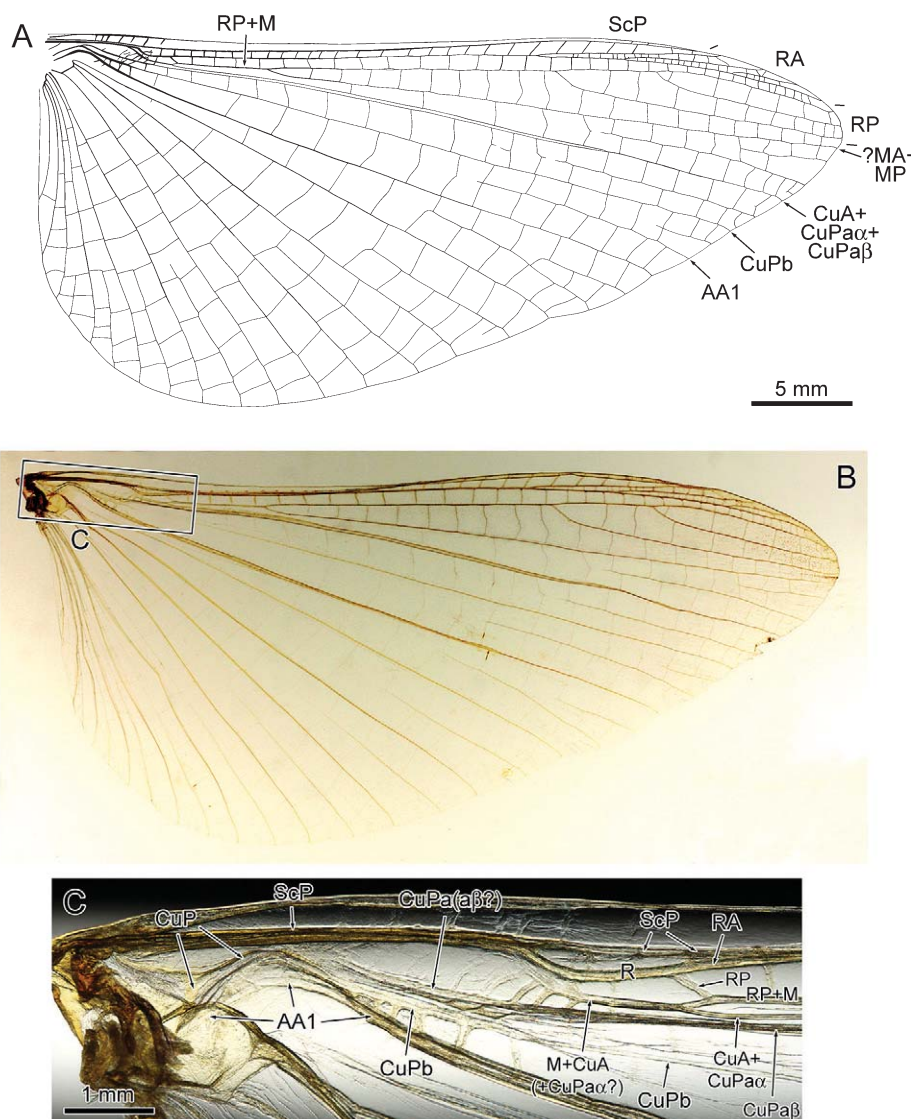
Sharov (1968: 168; and Sharov 1971: 172) indicates that, in addition to the distinct CuPaa base, †*primaria* differs from †*triassica* by a "curved CuA2 [CuPaβ]". However no difference was noted in that respect (Fig. 23). Provided that no other traits allows †*primaria* to be distinguished from †*triassica* (chiefly because of the very fragmentary state of the holotype of the former), I consider the former as a junior synonym of the latter.

Taxon *Agryllacris* nom.-dis.-typ. nov.

Etymology.—Part of '*Tagryllacris*' (see below).

Definition.—Species that evolved from the metapopulation lineage in which the character state 'in forewing, CuA + CuPaa with two distal branches only', as exhibited by *laudatum* Johns, 1997 and *carli* Griffini, 1911a, has been acquired.

Fig. 14. (Preceding page) Species *pinguipes* Rentz in Morton & Rentz, 1983 (A-J at the same scale; K-L at the same scale); A-B, K, specimen ANIC IWC OB 20 (♀), left forewing, drawing, photograph, and detail of medio-cubital area as located on B; C-E, L, specimen ANIC IWC OB 17 (♂); C, E, right forewing, drawing and photograph; D, F, L, left forewing, drawing, photograph, and detail of medio-cubital area; G-J, specimen ANIC IWC OB 21 (♀); G, I, right forewing; H, J, left forewing.



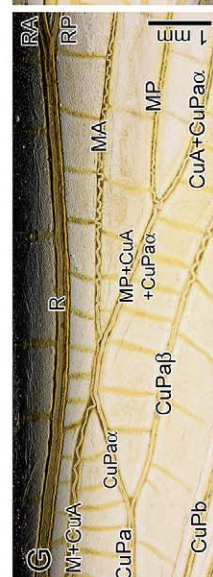
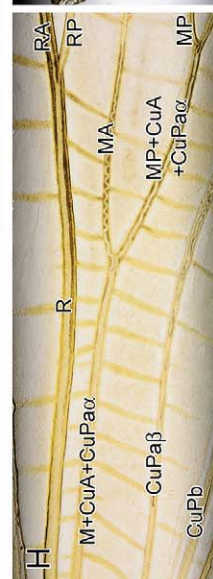
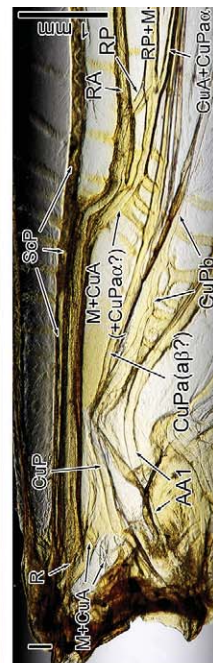
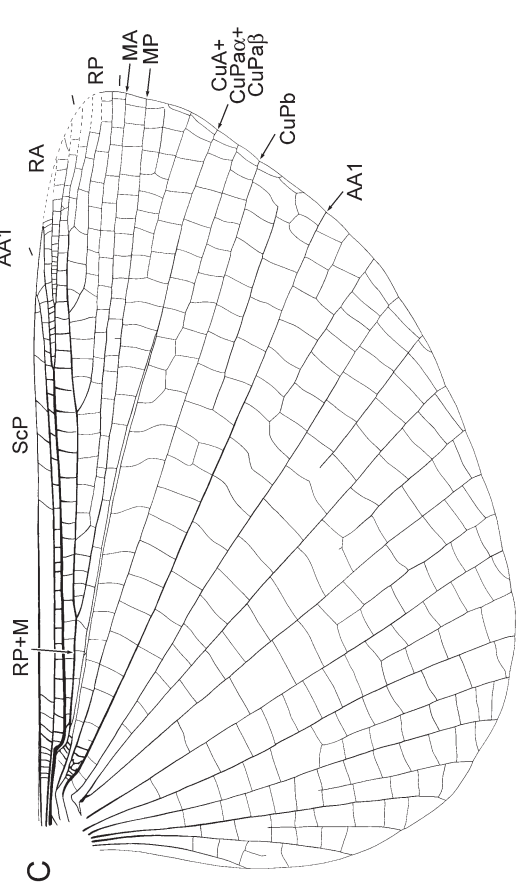
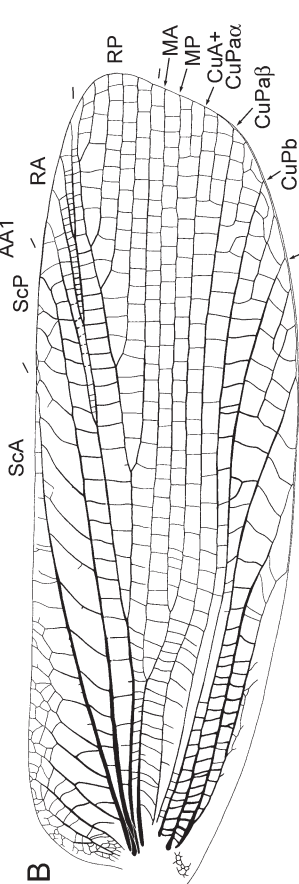
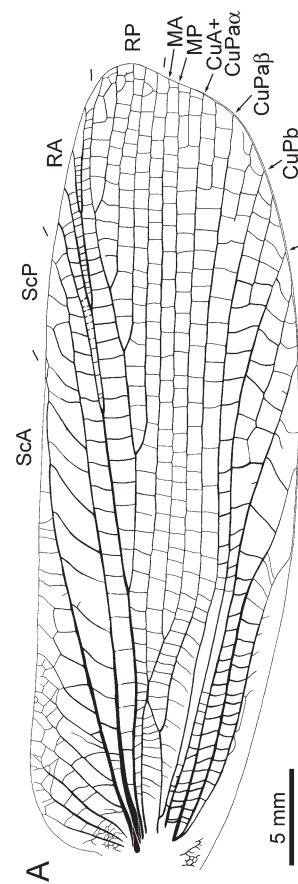
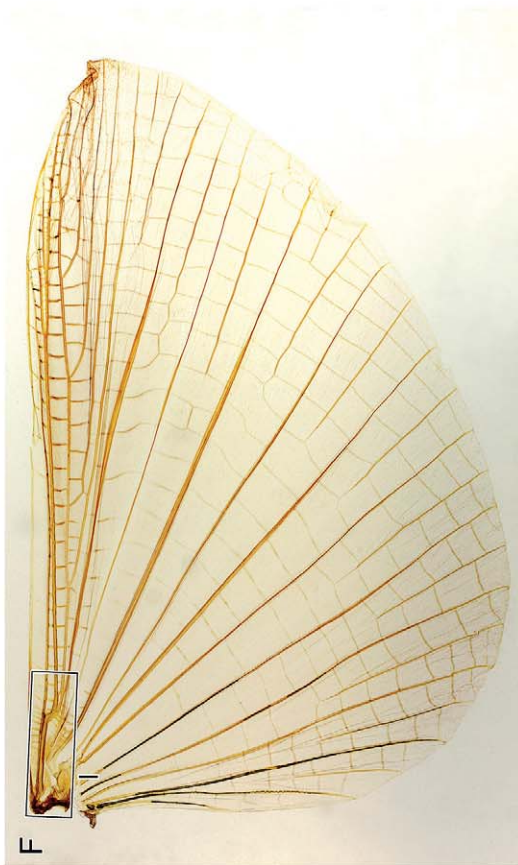
Cladotypes.—Holotype of *laudatum* Johns, 1997 (housed at the QM), and holotype of *carli* Griffini, 1911a (housed at the MNHG; Fig. 26A,B).

Composition.—See Fig. 30 and Appendix 3.

Discussion.—The antonym of the defining character state is 'CuA + CuPaa with more, or less, than two distal branches'. The putative plesiomorphic condition is 'CuA + CuPaa with more than two distal branches': it is exhibited by the vast majority of Palaeozoic *Archaeoptera* and saltatorians (Béthoux & Nel 2002b, 2005a, b; Sharov 1968, 1971; among others, and Fig. 1). The two distal branches of CuA + CuPaa are conjectured as being CuA, and CuPaa, respectively. If so, and if assuming a simple CuA in †*uralica*, the character state 'CuPaa simple' (as opposed to 'CuPaa branched') is a synonym of the defining character state.

The morphology of *carli* Griffini, 1911a was investigated based on photographs of the holotype (Fig. 26A,B). Another specimen housed at Institute of Zoology, Chinese Academy of Sciences (Beijing, P.R. of China; specimen number IOZ(E) 1343118), determined as *carli*, was observed. It exhibits the defining character state.

The possible importance of the defining character state to the systematics of the gryllacrididaeans seems to have been ignored by



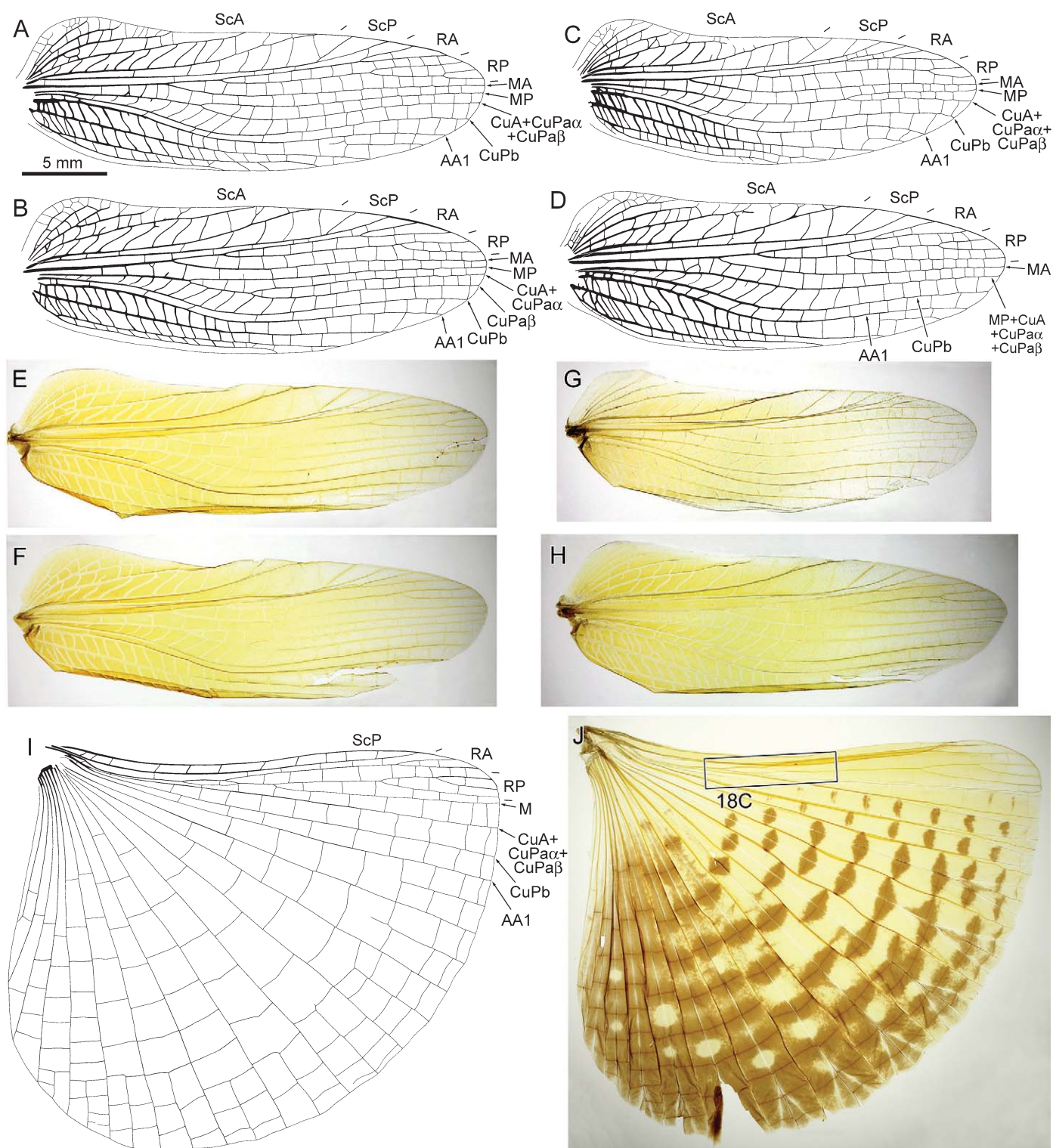


Fig. 17. Species *punctipennis* Walker, 1869 (all same scale); A-B, E-F, specimen ANIC IWC OB 37 (♂); A, E, right forewing, drawing and photograph; B, F, left forewing, drawing and photograph; C, G, specimen ANIC IWC OB 36 (♀), right forewing, drawing and photograph; D, H, specimen ANIC IWC OB 38 (♂), left forewing, drawing and photograph; I-J, specimen ANIC IWC OB 37 (♂), left hind wing, drawing and photograph.

Fig. 16. (Preceding page) Species undetermined, specimen ANIC IWC OB 25 (♂; A-F at the same scale; G-H at the same scale); A, D, G, right forewing, drawing, photograph, and detail of medio-cubital area as located on D; B, E, H, left forewing, drawing, photograph, and detail of medio-cubital area as located on E; C, E, I, left hind wing drawing, photograph, and detail as located on E.

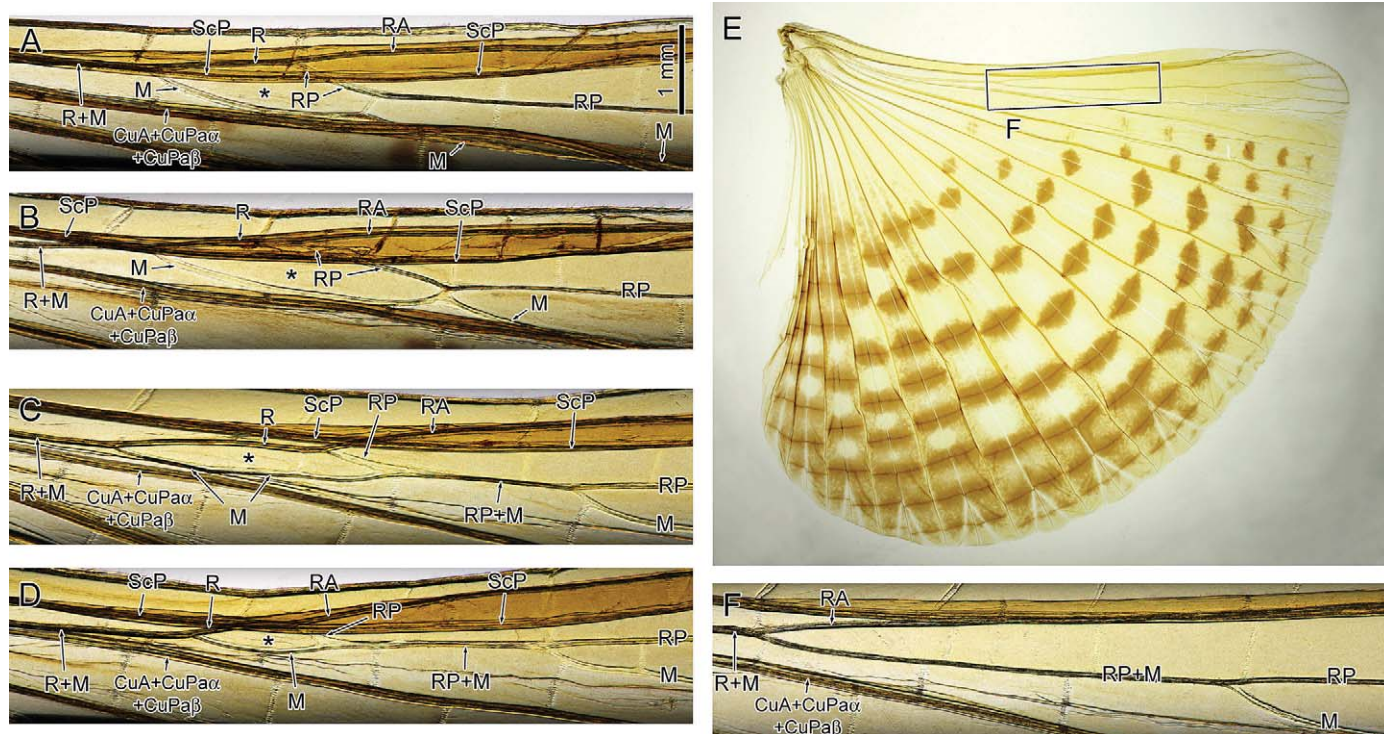


Fig. 18. Species *punctipennis* Walker, 1869; A-D, E, details of the connection between RP and M, hind wing (all at the same scale; * indicates the cell delimited by R, RP, and M); A-B, specimen ANIC IWC OB 36 (♀); A, right hind wing; B, left hind wing; C-D, specimen ANIC IWC OB 37 (♂); C, left hind wing, detail as located on Fig. 17J; D, right hind wing; E-F, specimen ANIC IWC OB 38 (♂), right hind wing; E, photograph; F, detail as located on E.

previous authors, in connection with the improper identification of fossil species. It must be acknowledged that this condition was most likely acquired convergently in elcanid orthopterans, and in *†brodiei* (see below), at least. A preliminary composition of *Agryllacris* is provided in Appendix 3, but several cases require a detailed discussion.

The species *†perfecta* is herein assigned to *Agryllacris* because it exhibits the defining character state of this taxon (Figs 20A,B, 27, 28). This view contrasts with that of Sharov (1968: 82-84; and Sharov 1971: 83-84) who excludes direct relationships of this species (and other proparagryllacrididaeans) with gryllacrididaeans, and instead considers the species as 'Ensifera incertae sedis' [Gorochov (1995a) assigns the corresponding species to his paraphyletic Palaeozoic and Triassic assemblage 'Oedischioida']. Sharov (1968, 1971) argues that the five-segmented tarsus provided with an arolium which he describes for *†perfecta* (fig. 33D; and see Fig. 29A) excludes relationships with the gryllacrididaeans, possessing a 4-segmented tarsus without a broad arolium. However photographic data indicate that an alternative interpretation of the corresponding (moderately well preserved) specimen is equally plausible (Fig. 29B). Firstly, it is not evident that the arolium is preserved (or broad). Secondly, Sharov's (1968, 1971) 4th tarsal segment is not evident. Additionally, even if one adopts Sharov's (1968, 1971) interpretation, the states assumed by this author are plesiomorphic at the level of *Archaeorthoptera* [see Béthoux (2009a); and see Sharov (1968, 1971: figs 11D, 12E), representing 5-segmented tarsi in stem-orthopterans]. In other words, the hypothesis that *†perfecta* is a stem-gryllacrididaean is not contradicted by Sharov's (1968, 1971) interpretation.

Based on fossil imprints only, Sharov (1968, 1971) argues that "the wings formed a sheath around the body at rest" in *†perfecta*, and that the species "resemble in this respect the Triassic Phasmatodea on one hand and the Gryllacrididae on the other; however, it is also

unjustified to place them into any of these two groups because of the method of wing folding". However, how wing folding in *†perfecta* and gryllacrididaeans is similar but dissimilar is as obscure as the way to determine wing folding at rest based on fossil imprints of mostly isolated wings. Sharov (1968, 1971) further argues that, in *†perfecta*, "the costa [ScA] has displaced the proximal branches of Sc [ScP], but it does not cross them, retaining the same position as in the Oedischiidae [...]". A wide range of variation of this character was documented among the surveyed extant species, in particular at the intra-specific level. And indeed the condition formulated by Sharov (1968, 1971) was observed in *ornata* and *rufovaria*, among others. What Sharov (1968, 1971) means by "displacement of the beginning of CuA [CuPa?] almost to the middle of CuP [CuPb]", assumed to be absent in gryllacrididaeans but present in *†perfecta* according to him, is obscure to me.

In summary Sharov's (1968, 1971) argument does not allow the hypothesis that *†perfecta* is a stem-gryllacrididaean to be discarded. It must be noticed that the defining character state of *Agryllacris* has been subjected to iterative acquisitions (see below). However, assignment of *†perfecta* to this taxon is also supported by the very long CuPb, reaching the posterior wing margin distal to the second third of wing length, which is a putative apomorphy. I found no character that could reject the hypothesis that *†perfecta* belongs to *Agryllacris*.

Data on a single forewing of the Triassic species *†giganteus* Riek, 1955 is available (Riek 1955: fig. 31). This species has forked M and CuA + CuPaa, as in *†perfecta*. Similarities between the two species extend to the wing shape and size too. Based on this evidence I propose to assign *†giganteus* to *Agryllacris*. This proposition complies with Riek (1955), who considered the corresponding species as a gryllacrididaean.

The species *†orientalis* Sharov, 1968 is also assigned to *Agryllacris*

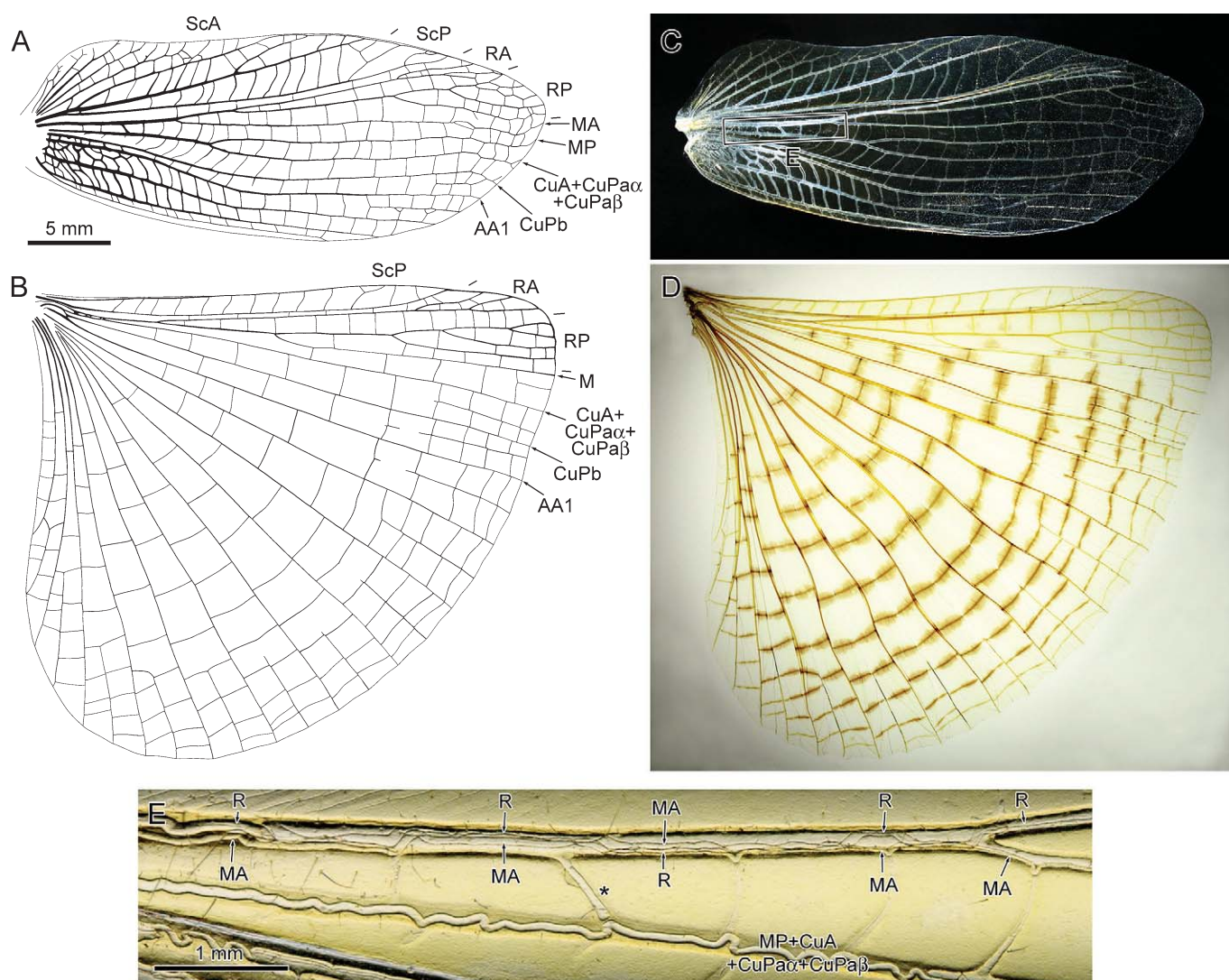


Fig. 19. Species *rufovaria* Kirby, 1888, specimen ANIC IWC OB 27 (♂; A-D at the same scale); A, C, right forewing, drawing and photograph; B, D, right hind wing, drawing and photograph; E, detail of the R + MA fusion, as located on C (* indicates a strong cross-vein free of trachea).

because it exhibits the defining character state of this taxon (Sharov 1968, 1971: fig. 18C). This species, assigned to the genus '*Madygenia*' by Sharov (1968, 1971), is considered as a 'stem-tettigonid' by this author, but this option is discarded by Gorochov (1995a, b), who considers it as closely related to †*perfecta* (i.e., as a stem-orthopteran). I concur because (1) in addition to the defining character state of *Agryllacris*, †*orientalis* also has a simple MA, and (2) ground for Sharov's (1968, 1971) hypothesis is virtually non-existent. This author (p. 47, p. 45, respectively) argues that "other characters of the venation show that *Madygenia* deviates from the line of evolution to the Tettigoniidae: RS [RP] has lost its pectinate form, MP + CuA1 [CuA + CuPaa] has retained only two long veins; the base of CuA [CuPa] has been lost in the hind wings, while CuA2 [CuPab] became fused with MP + CuA1 [CuA + CuPaa], forming a single vein". However (1) Sharov (1968, 1971) illustrates tettigonids with a pectinate RP in forewing (fig. 19E,H); (2) CuA + CuPaa is two branched in forewings of †*perfecta*, †*giganteus*, and †*laudatum* (among others), and Sharov (1968, 1971) illustrates a tettigonid with a CuA + CuPaa with more than 2 branches in forewing (fig. 19E); (3) above I discuss the case of CuPa in hind wings of surveyed extant species and demonstrate that it conforms to the statement made by Sharov

(1968, 1971). Finally, Sharov (1968, 1971) advocates the occurrence of a secondary archedictyon. However the tettigonid archedictyon is made of very small cells, themselves composing larger cells delimited by stronger cross-veins, while cells in †*orientalis* are larger and do not compose larger cells. It suggests that these 'archedictyons' are not homologous.

Gorochov (1987a) erected a number of species assumed to be closely related to †*orientalis*, based on material collected from the same locality as †*orientalis*. These species are †*extremalis* Gorochov, 1987a, †*ovalis* Gorochov, 1987a, †*longissima* Gorochov, 1987a, and †*grandis* Gorochov, 1987a. As for †*triassica*-like species, each is documented after a single specimen, belonging to the set of specimens available to Sharov, and that this author probably assigned to †*orientalis* [39 imprints are reported by Sharov (1968, 1971) but without indication of specimen numbers]. The additional species differ from †*orientalis* by a few traits which could fit within an intra-specific range of variation. Revision of the corresponding material was not carried out, therefore I consider these species as junior synonyms of †*orientalis* on a provisional and informal ground.

A number of poorly documented fossil species have been considered at some point as gryllacrididaeans. Zeuner (1939), fol-

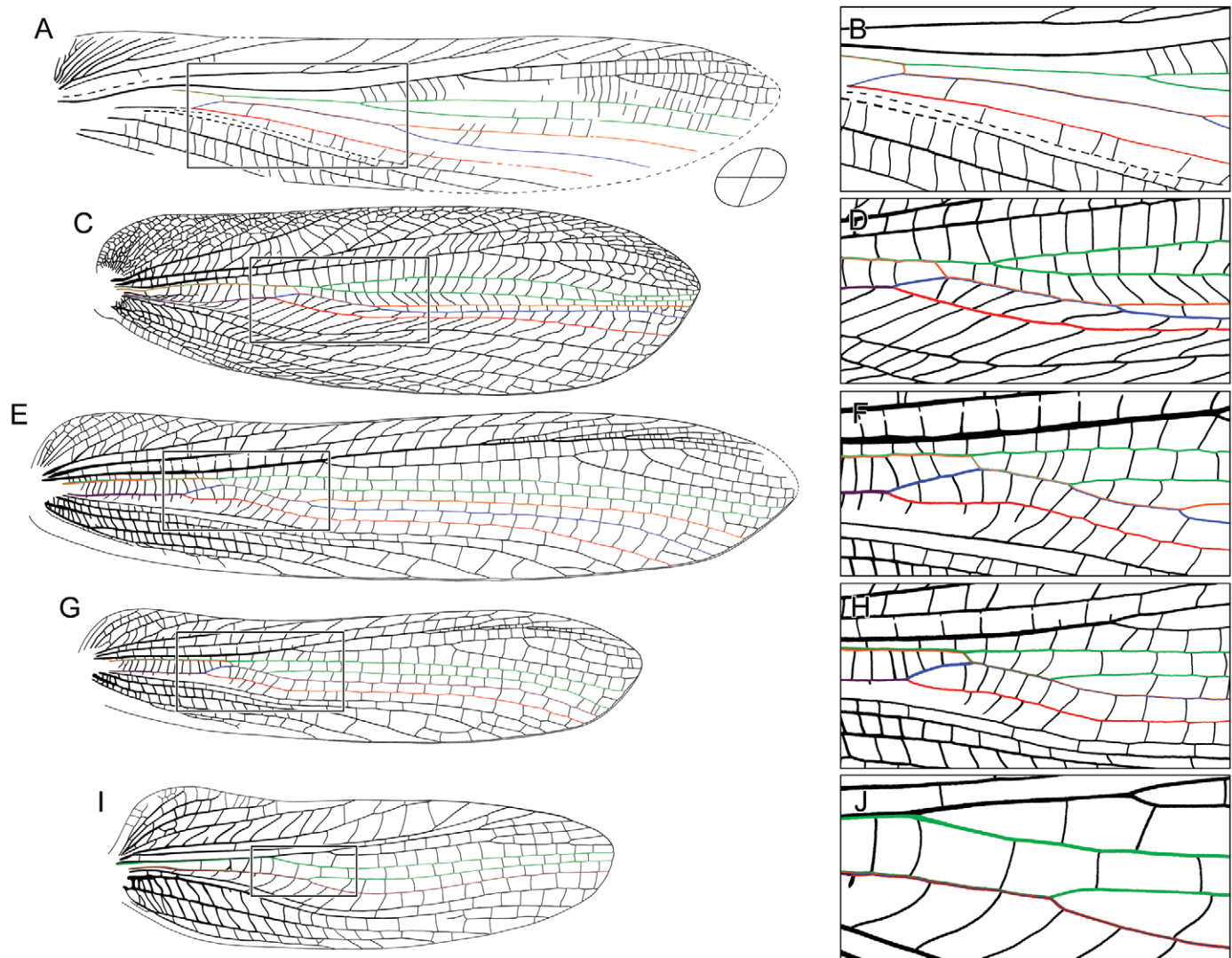


Fig. 20. Summary of topological homologies in *Tagryllacris* nom.-dis.-typ. nov. (compare to Fig. 1); A-B, species *laudatum* Johns, 1997; C-D, species *†perfecta* Sharov, 1968; E-H, species *pinguipes* Rentz in Morton & Rentz 1983; I-J, species *punctipennis* Walker, 1869. For color version, see Plate VII.

lowed by Sharov (1968, 1971), considers *scotica* Zeuner, 1939 as a gryllacrididae [and Gorochov (1995a) as a stenopelmatoidean]. However, the only available forewing of this species exhibits a ScA that seemingly crosses ScP branches (Zeuner 1939: pl. 72, fig. 5; Sharov 1968, 1971: fig. 27A; *contra* Zeuner 1939: pl. 46, fig. 5), a trait diagnostic of prophalangopsidae and absent in gryllacrididae (at least all those I surveyed; *contra* Sharov 1968, 1971). Also a CuA + CuPau with more than 2 branches does not occur in gryllacrididae, but is a usual condition in prophalangopsidae. Indeed comparison with the forewing of the presumed female of *obscura* Walker, 1869 (Liu *et al.* 2009: fig. 1) strongly suggests that *scotica* is not a gryllacrididae but a female of a prophalangopsidae. The same applies to the species *maculata* Cockerell, 1908, considered by Zeuner (1939) as a gryllacrididae (data on the species are minimal due to the very fragmentary state of the only available specimen).

I concur with Gorochov (1995a) and consider *gryllacroides* Zeuner, 1937 as a hagloidean *incertae sedis*. A revision of the material of *ungeri* Heer, 1849 would be needed before it could be conclusively assigned to *Agryllacris*, because the available illustrations (*e.g.*, in Zeuner 1937) are insufficient. The assignment of *†crassifemur* Riek, 1956 to the gryllacrididae by Riek (1956) must also be discussed

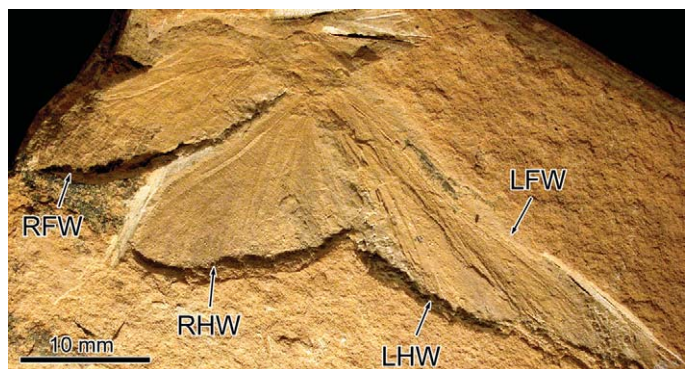


Fig. 21. Species *†reducta* Sharov, 1968, specimen PIN 2555/1445 (holotype; Madygen Formation, Kyrgyzstan; Ladinian/Carnian, late Middle to early Late Triassic), photograph (negative imprint, light-mirrored), witnessing deformation experienced by material from the Dzaylyaucho locality.

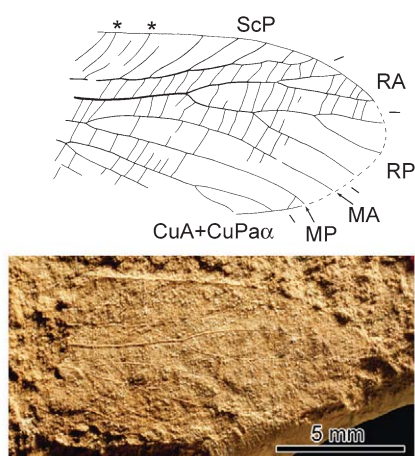


Fig. 22. Species *†abscissa* Gorochov, 1987a, specimen PIN 2069/2240 (holotype; Madygen Formation, Kyrgyzstan; Ladinian/Carnian, late Middle to early Late Triassic), drawing (* indicate presumed intercalary veins) and photograph (left forewing, positive imprint, flipped horizontally).

[the species is considered as a proparagryllacrididae by Sharov (1968, 1971)]. The wing venation interpretation proposed by Riek (1956: fig. 2) is problematic: if one wants to make Riek's drawing fit a typical *Agryllacris* wing venation, 'Sc' should be the stem of R (Gorochov 1995a: fig. 222). However, 'Sc' / ScP and R are strongly concave, and convex, respectively, in all *Archaeorthoptera*, and can hardly be mistaken. Due to this inconsistency, and to the fragmentary state of the corresponding material, I provisionally exclude *†crassifemur* from *Agryllacris*.

Except for a single specimen (Fig. 24N-P), forewings of the species *†brodiei* exhibit the defining character state of *Agryllacris* (Figs 24, 25A). In addition, as in *Agryllacris*, MA and MP are both simple. However *†brodiei* (1) has a short ScA (it is comparatively longer in *Agryllacris*), (2) a constant width of the area between CuPb and AA1 (it is broadened distally in *Agryllacris*), (3) and CuPb reaching the posterior wing margin opposite wing mid-length (distal to the second third in *Agryllacris*). In addition *†brodiei* shares with *†triassica* (4) a CuPaa translocated onto M + CuA, and (5) a pterostigma-like structure in fore- and hind wings (Figs 23, 25; lacking in *Agryllacris*), indicating close relationships of these two species. Provided that *†triassica* has a multi-branched MA and CuA + CuPaa, the simple MA and the 2-branched CuA + CuPaa observed in *†brodiei* is considered as acquired independently from *Agryllacris*.

Species *†perfecta* Sharov, 1968

Figs 20A,B, 27-29

Species *†perfecta* Sharov, 1968, p. 185, fig. 33, pl. 6 fig. 4; holotype PIN 2240/4132 (Fig. 27A, G), paratypes PIN 2555/1237 (Fig. 27B, H), PIN 2555/1200 (Fig. 28A, D), PIN 2240/1865 (Fig. 28B, E).

Species *†perfecta* Sharov, 1971, p. 191, fig. 33, pl. 6 fig. 4.

Species *†megaptera* Gorochov, 1987a, p. 25, fig. 5; holotype PIN 2240/1865 (Fig. 28C, F), syn. nov.

Species *†simplicis* Gorochov, 1987a, p. 25, fig. 6; holotype PIN

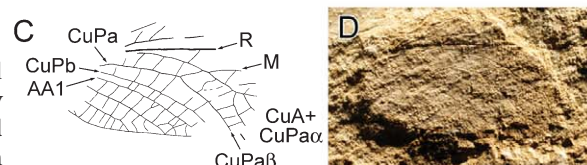
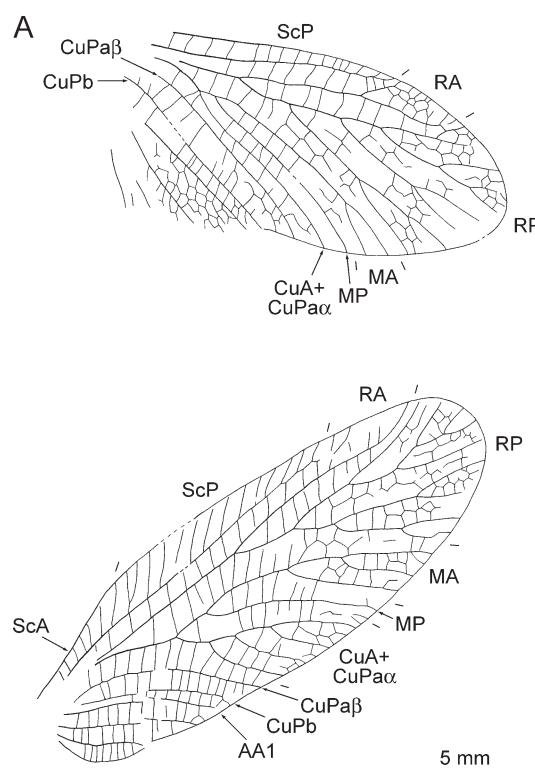


Fig. 23. Species *†triassica* Sharov, 1968: 168 (all the same scale; all Madygen Formation, Kyrgyzstan; Ladinian/Carnian, late Middle to early Late Triassic); A-B, specimen PIN 2069/2320 (holotype; right fore- and hind wing), drawing and photograph (positive imprint); C-D, specimen PIN 2240/4312 (holotype of primaria Sharov, 1968; right forewing), drawing and photograph (negative imprint; flipped horizontally).

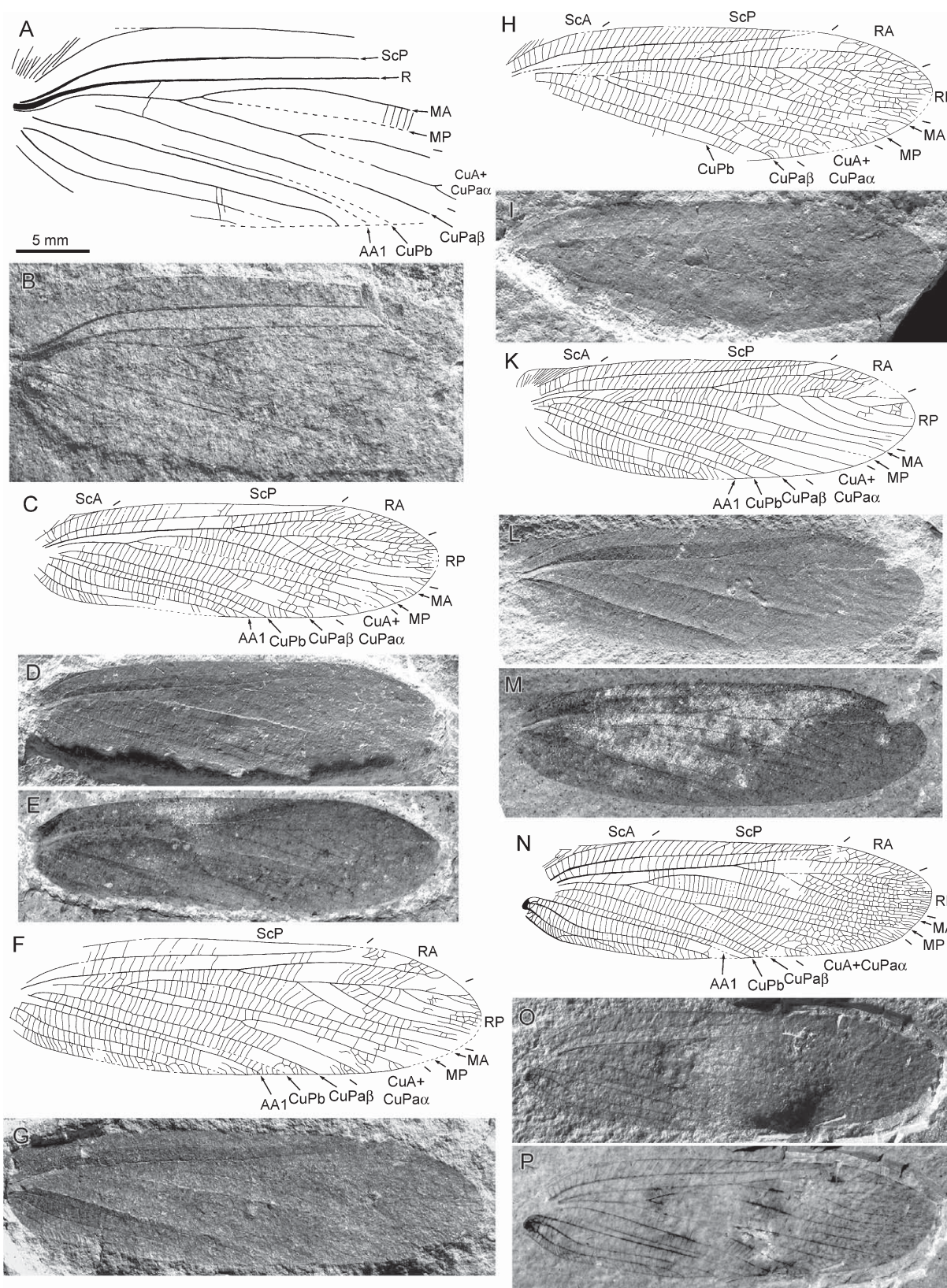


Fig. 24. Species †*brodiei* Handlirsch, 1938, forewings (all the same scale; except for NHM I. 6790 (K-M), Binton, Warwickshire, UK; all Lower Jurassic); A-B, presumed ♀; C-P presumed ♂; A-B, specimen NHM I.10463 (holotype; left forewing), drawing and photograph (positive imprint, flipped horizontally); C-E, specimen NHM I.6784 (right forewing), drawing and photographs (positive imprint; light mirrored, and under ethanol); F-G, specimen NHM I.10464 (right forewing), drawing and photograph (negative imprint; flipped horizontally); H-I, specimen NHM I.3383 (right forewing), drawing and photograph (positive imprint); K-M, specimen NHM I.6790 (right forewing; 'climbers', Warwickshire?, UK), drawing and photographs (positive imprint; light mirrored, and under ethanol); N-P, specimen NHM I.6656 (right forewing), drawing and photographs (positive imprint; dry, and under ethanol).

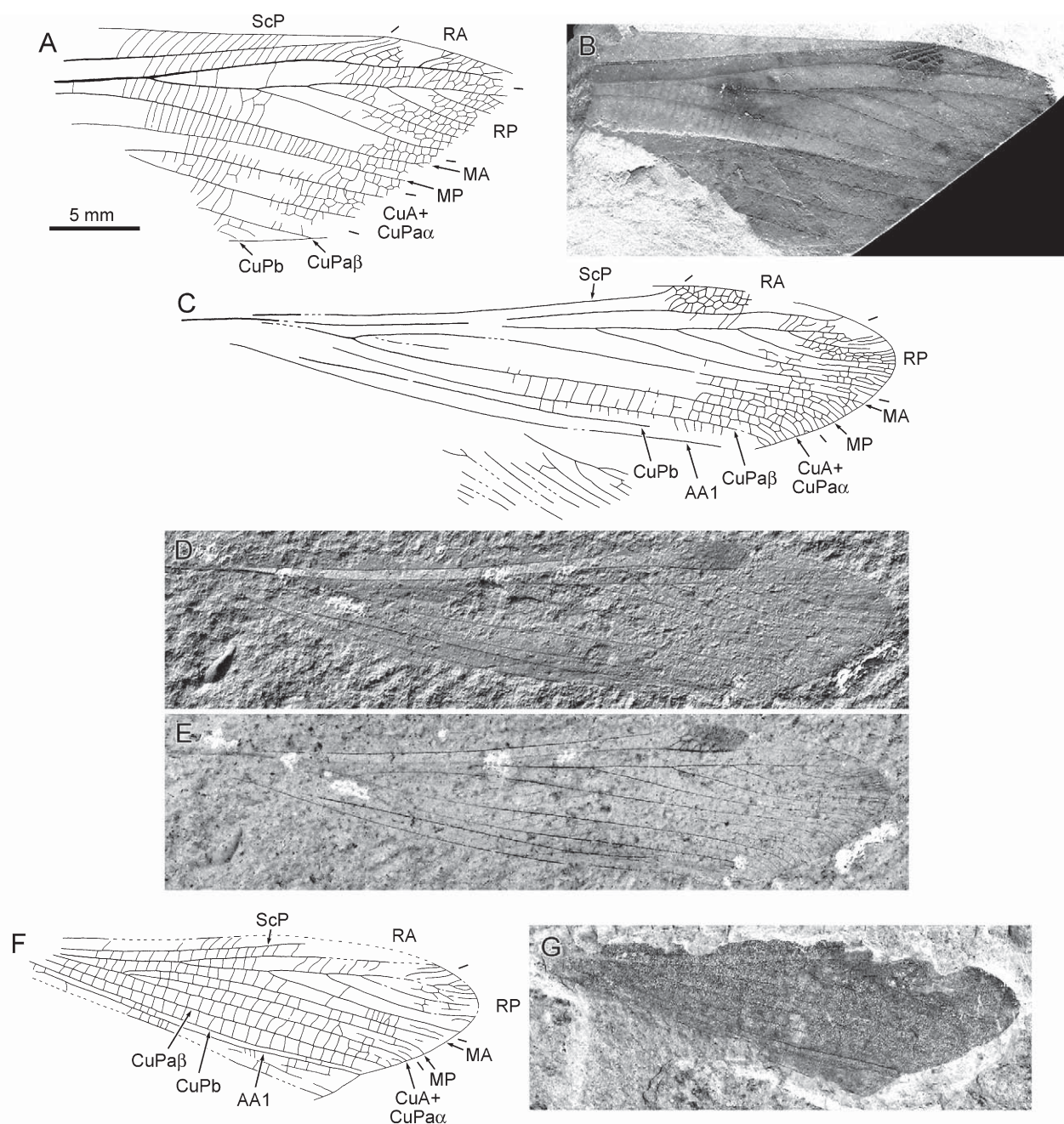


Fig. 25. Species *†brodiei* Handlirsch, 1938 (all the same scale; all Binton, Warwickshire, UK; Lower Jurassic); A-B, presumed ♀; C-G, hind wings, presumed ♂; A-B, specimen NHM I. 10668 (right forewing), drawing and photograph (negative imprint, flipped horizontally); C-E, specimen NHM I. 10536 (left hind wing), drawing and photographs (negative imprint, light-mirrored; dry, and under ethanol); F-G, specimen NHM I. 6779 (left hind wing), drawing and photograph (positive imprint, flipped horizontally; under ethanol).

2240/4123 (Fig. 27G, M), syn. nov.

Species *†elongata* Gorochov, 1987a, p. 25, fig. 7; holotype PIN

2240/4159 (Fig. 27D, J), syn. nov.

Species *†madygenioides* Gorochov, 1987a, p. 25, fig. 8; holotype PIN

2240/4113 (Fig. 27C, I), syn. nov.

Species *†perlonga* Gorochov, 1987a, p. 26, fig. 9; holotype PIN

2240/4120 (Fig. 27E, L), syn. nov.

Species *†devexa* Gorochov, 1987a, p. 26, fig. 10; holotype PIN

2240/4124 (Fig. 27E, K), syn. nov.

Discussion. — Among species listed by Gorochov (1987b) as belonging to the subfamily 'Proparagryllacridinae', the species listed above, in addition to *†abscissa* Gorochov, 1987, were all collected from

the Dzaylyauch locality. Each of the species erected by Gorochov (1987b) is documented based on a single specimen. Data collected from fossil and extant material will be used to reconsider Gorochov's (1987b) species delimitations.

Gorochov (1987b) assigned the species *†megaptera* Gorochov, 1987b to the monotypic genus '*†Batkenella*' Gorochov, 1987b. This author does not provide a differential diagnosis of *†megaptera*, but of '*†Batkenella*'. According to this diagnosis, the species *†megaptera* can be differentiated from other proparagryllacridinaeans after (1) a broad forewing, (2) a broad area between anterior wing margin and ScP, (3) long RA / RP and MA / MP areas, and (4) a basal position of the point of divergence of MA and MP. However the width of *†megaptera* forewing (Fig. 28C,F) does not differ significantly from

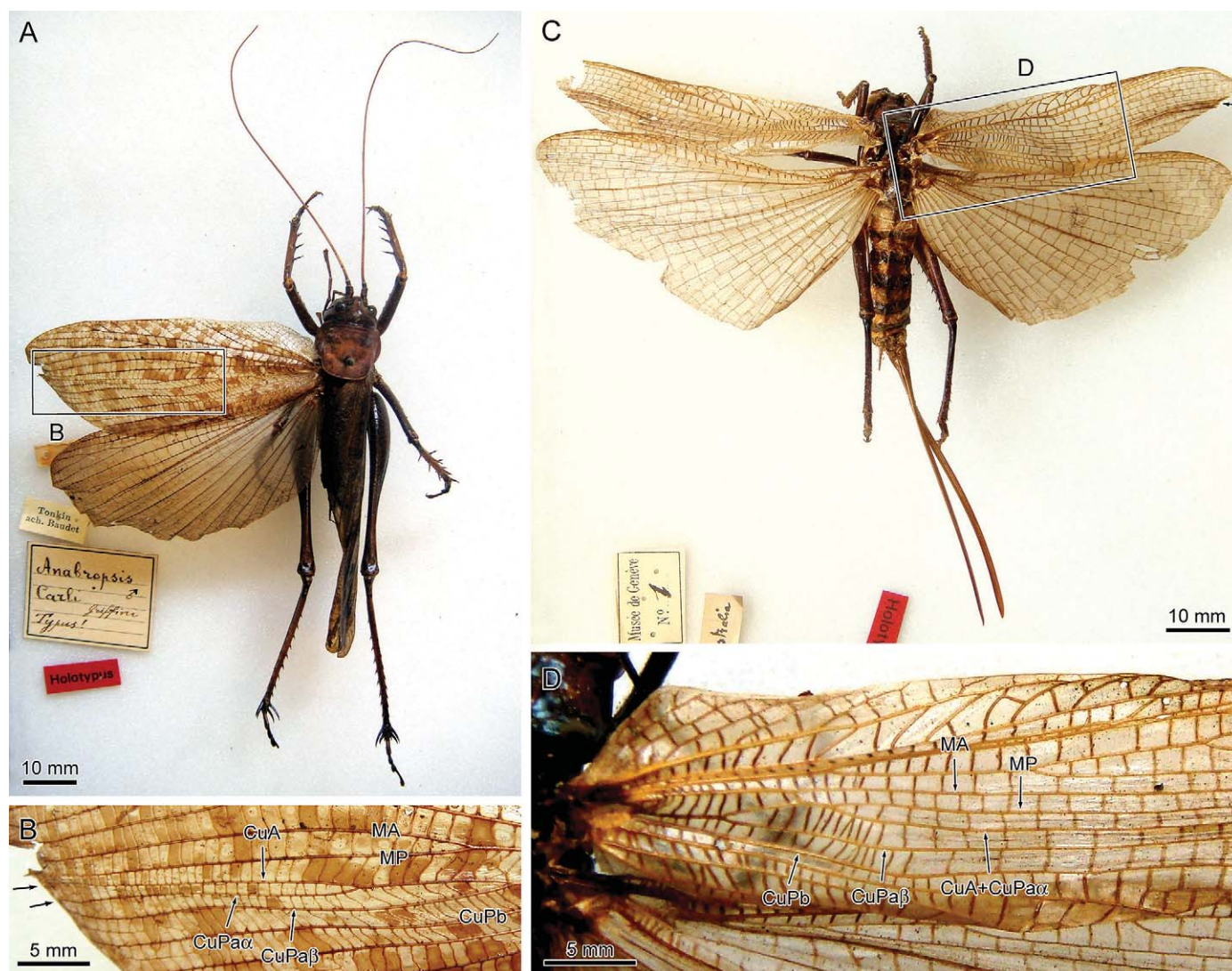


Fig. 26. Selected cladotypes housed at the MHNG (photographs courtesy of P. Schwendinger); A-B, species *carli* Griffini, 1911a, holotype; A, habitus; B, detail of left forewing venation, as located on A (arrows without labels indicate the endings of CuA and CuPa α); C-D, species *magnifica* Brunner von Wattenwyl, 1888, holotype; C, habitus (arrow indicates the end of CuA + CuPa α); D, detail of right forewing venation, as located on C.

that of the specimen PIN 2240/4112 (Fig. 28B,E), paratype of \dagger *perfecta*. Provided a possible width alteration of 150% due to a plastic deformation during fossilization, the width of the area between the anterior wing margin and ScP is to be considered as similar to that exhibited by the specimen PIN 2240/4132 (Fig. 27A,G), holotype of \dagger *perfecta*. The RA / RP area actually is shorter in \dagger *megaptera* than in the specimen PIN 2240/4112 (Fig. 28B,E). The length of the MA / MP area relates to the point of divergence of MA and MP, supposedly comparatively basal. However the length of M (from the divergence of CuA to its first fork) represents 41.2% of the distance between the point of divergence of CuA and the point of origin of RP in \dagger *megaptera*, while is represents 43.9% in the holotype of \dagger *perfecta* (Fig. 27A, G). Such difference is to be considered as insignificant, as demonstrated by the variation of this trait documented in *laudatum* (Fig. 3). The forewing pair of the specimen PIN 2240/4113 [holotype of \dagger *madygenioides* Gorochov, 1987a, below considered as a junior synonym of \dagger *perfecta*] also demonstrates that the character is variable in this (set of) species: in this specimen the left forewing has a comparatively basal point of divergence of MA / MP, but this

point is located distal to the origin of RP in the right forewing.

According to Gorochov (1987b) the species \dagger *simplicis* Gorochov, 1987b is characterized by (1) a short forewing, (2) a short ScA, (3) a broad area between anterior wing margin and ScP, and (4) CuP and AA branches forming an angle with the wing longitudinal axis. The forewing length of the holotype of \dagger *simplicis* (Fig. 27G,M) represents about 83% of that of the holotype of \dagger *perfecta* (Fig. 27A,G) (length of about 30.2 mm, and 36.6 mm, respectively). This ratio falls within the intra-specific variation observed in extant species (Appendix 4; not even taking sexual dimorphism and deformation into consideration). The vein ScA reaches the anterior wing margin about 11.4 mm distal to wing base in the holotype of \dagger *perfecta*, 10.7 mm in \dagger *simplicis*. Reported to the wing length, ScA is comparatively longer in \dagger *simplicis* (about 35.4%) than in \dagger *perfecta* (about 32.8%), contradicting Gorochov's (1987b) 2nd character (state). In \dagger *perfecta* the width of the area between the anterior wing margin and ScP represents about 23.9% of wing width, about 23.8% in \dagger *simplicis*. What Gorochov (1987b) refers to as a comparatively 'broad area between anterior wing margin and ScP' (3) is therefore unclear.

Explanation is provided by Gorochov (1987b) regarding the character (4) (p. 25): "in *G. perfecta* CuP and A [AA] are located almost parallel to the wing longitudinal axis". Therefore one must be able to distinguish veins forming 'an undetermined angle with wing longitudinal axis' from 'veins almost parallel to wing longitudinal axis' in order to diagnose †*simplicis*. Unfortunately this does not fall within the range of my capacities [and see below; in addition a wing elongated along its longitudinal axis (e.g., Figs 27B-C, E, H-I, L) will exhibit veins forming a comparatively lower angle with the longitudinal axis].

According to Gorochov (1987b) the species †*elongata* Gorochov, 1987b is characterized by (1) a narrow inter-radial (RA / RP?) area, (2) the position of MP close to the branching point of CuA + CuPaa, (3) numerous branches of RA, (4) narrow area between anterior wing margin and ScA, (5) long ScA, and (6) orientation of CuP and AA branches intermediate between †*perfecta* and †*simplicis*. However, the width of the RA / RP area represents about 12.3% of wing width in the holotype of *perfecta* (Fig. 27A, G), 12.9% in the holotype of †*simplicis* (Fig. 27D, I) (measurements taken at the mid-length of RP from its origin to its first fork). These ratios, independent of possible deformation, indicate that the character (1) is not species relevant. Variation in the proximity of MP and CuA near their point of divergence (from M, and from CuA + CuPaa, respectively; 2) was observed as intra-individual variation in the specimen ANIC IWC OB 26 (Fig. 2A-B, D-E; with an actual short fusion of MP with CuA). In addition, in the specimen ANIC IWC OB 24, MP is distinct from CuA in the left forewing (Fig. 11A, C, E, G), but fuses with it for a short distance in the right forewing (Fig. 11B, D, E, H). This represents a variation as substantial as that observed in †*simplicis* as compared to †*perfecta*. The formulation of the character (3) (viz. 'numerous branches of RA') is enigmatic, because †*simplicis* has 2 branches of RA, and the holotype of †*perfecta* 3. The correct formulation was probably 'fewer branches of RA' rather than 'numerous branches of RA'. However, a variation of 2 to 3 branches was observed within the forewing pair of a single specimen of cf. *mexicanus* (ANIC IWC OB 26; Fig. 2A-B, D-E), and similar range of variation (4 to 5) was documented in material of *pinguipes* (Fig. 14) (among others). The character state (4) is impossible to appreciate simply because the corresponding area is not preserved on the holotype (Gorochov 1987b: fig. 7; Fig. 27J). Similarly, the length of ScA (5) is difficult to appreciate in this context, because ScA forms a very narrow angle with the anterior wing margin near its end. Without proper preservation of the area between the anterior wing margin and ScA, the length of the latter is therefore impossible to measure with accuracy. It has been mentioned above that the orientation of CuP and AA branches with respect to the wing longitudinal axis was impossible to distinguish between †*perfecta* and †*similis*. That †*elongata* is supposed to exhibit an intermediate condition reinforces the opinion that this character is not useful for discriminating the different species recognized by Gorochov (1987b).

According to Gorochov (1987b) the species †*madygenioides* Gorochov, 1987b is characterized by (1) the location of the bases of RP, MP, and the branching point of CuA + CuPaa, as in †*perfecta* and †*simplicis* but different from that observed in †*elongata*, and (2) CuPaa fused with M + CuA (as a consequence, basal to the divergence of CuA from M + CuA). Apparently this diagnosis is only based on the left forewing of the holotype of †*madygenioides* (Gorochov 1987b: fig. 8; to be compared with Fig. 27C, I). It is quite unfortunate that the right forewing was not given full consideration by Gorochov (1987b) because it shows that the location of the base of MP is variable in this individual: indeed it is located distal to the origin of RP in this wing. Therefore the holotype of †*madygenioides* shows

that the character (1) varies more widely within a single individual than among species as delimited by Gorochov (1987b). Regarding the fusion of CuPaa with CuA vs M + CuA, both states were documented in *laudatum* (Fig. 4), cf. *bicornis* (Fig. 8), and *pinguipes* (Fig. 13).

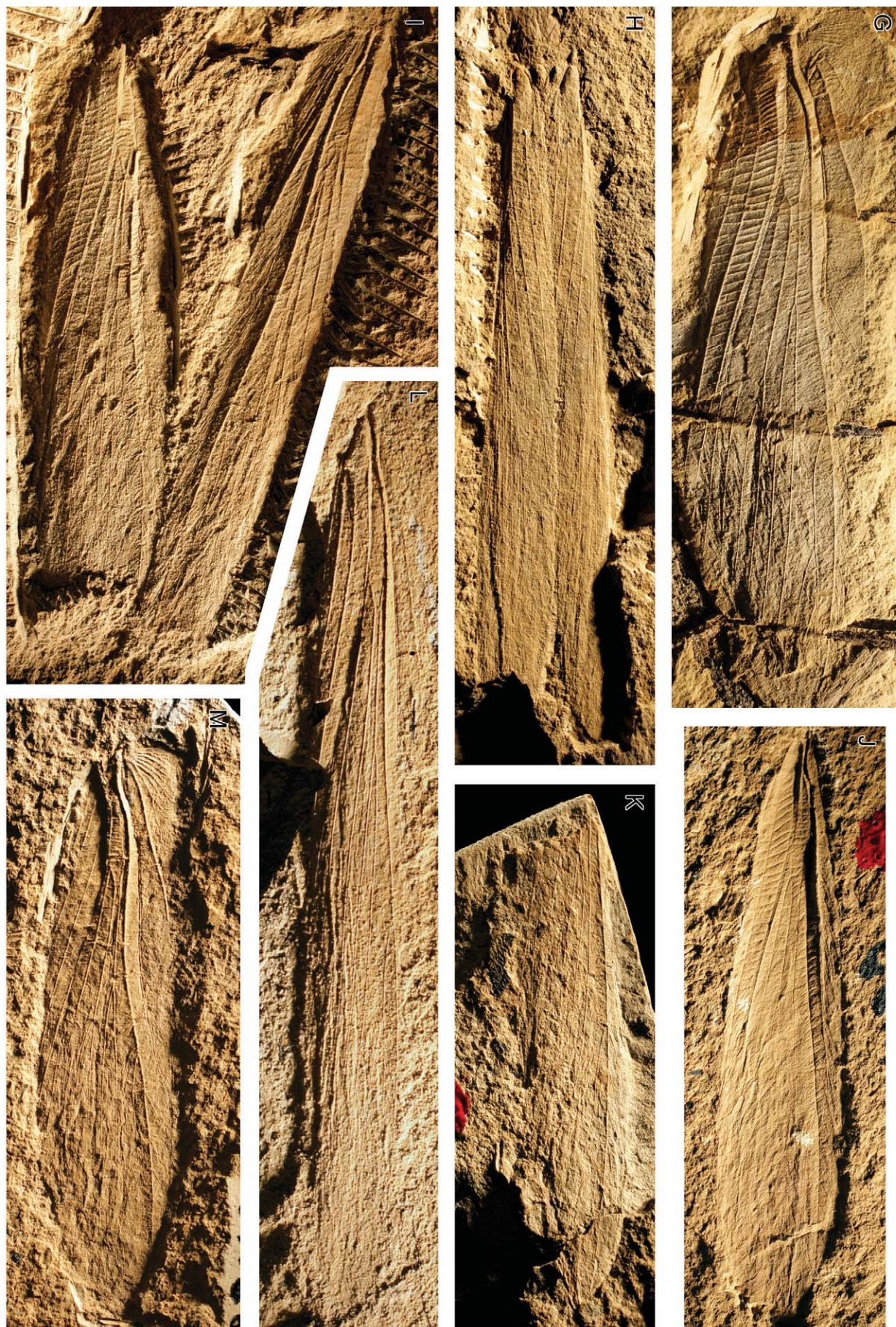
Gorochov (1987b) assigned the species †*perlonga* Gorochov, 1987b to the monotypic genus †*Dolichobatkenella* Gorochov, 1987b. This author does not provide a differential diagnosis of †*perlonga*, but of †*Dolichobatkenella*. According to this diagnosis, †*perlonga* can be differentiated from other proparagryllacridinaean taxa after (1) narrow and elongated forewing, and (2) CuPaa translocated onto CuPaß. As mentioned above characters relating to wing aspect ratios (1) are better ignored for material provided by the Dzayly-auch locality, because of plastic deformation that affected the material. Regarding the character (2), unusual translocations were documented in *laudatum* (translocation of the anterior branch of RP onto RA, see Fig. 3H, Q; translocation of CuPaa onto M + CuA, see Fig. 3I, R), *ornata* (in particular branches of RP onto RA, see Fig. 6), and *pinguipes* (translocation of CuPaa onto M + CuA, Fig. 14A, B, K). Therefore it cannot be excluded that †*perlonga* is merely a variant of †*perfecta*.

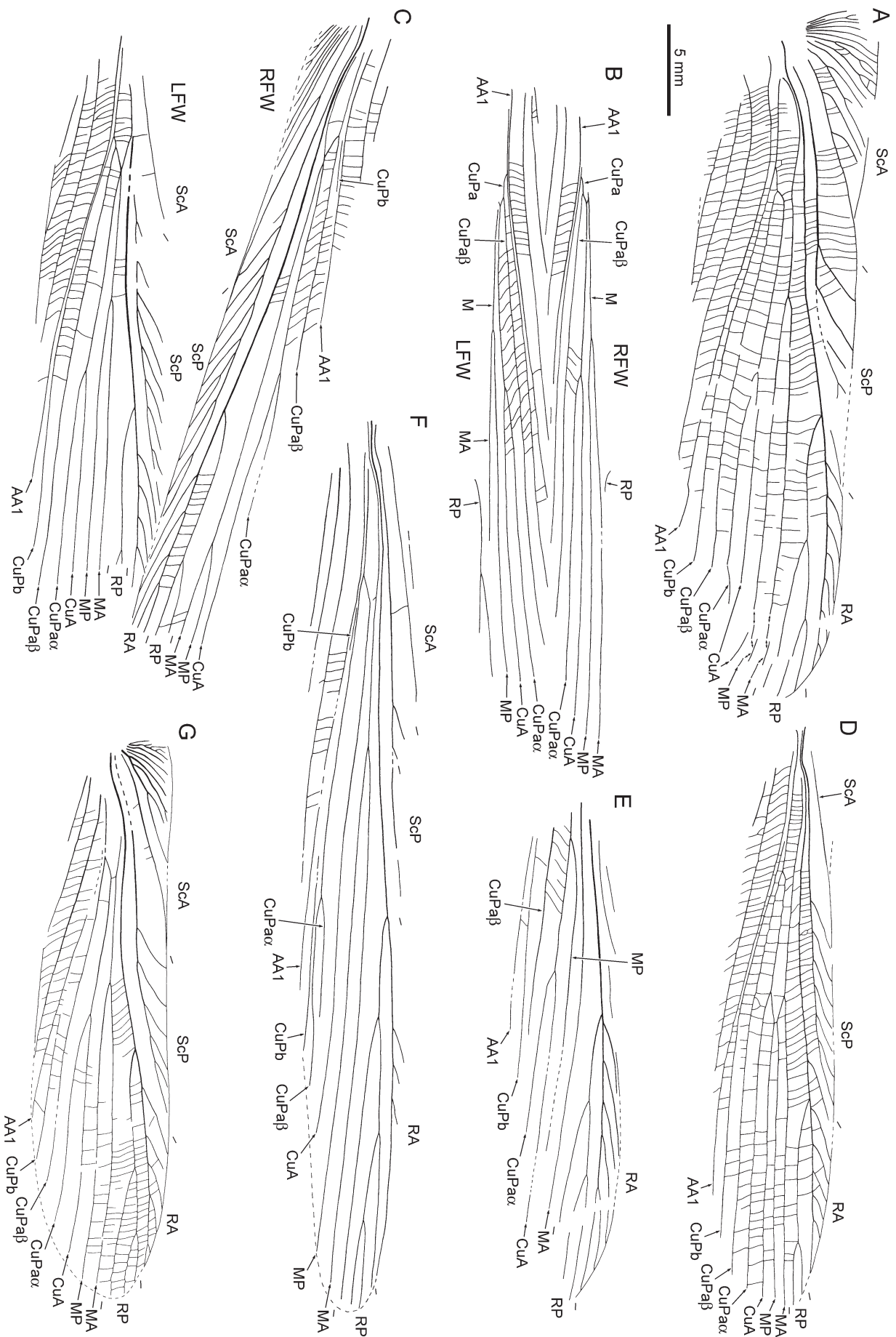
Gorochov (1987b) assigned the species †*devexa* Gorochov, 1987b to the monotypic genus †*Eubatkenella* Gorochov, 1987b. This author does not provide a differential diagnosis of †*devexa*, but of †*Eubatkenella*. According to this diagnosis, †*devexa* can be differentiated from other proparagryllacridinaean taxa after (1) oblique branches of ScP, and (2) translocation of MP onto CuA + CuPaa. Regarding the character state (1), the corresponding area is so poorly preserved (Fig. 27K; if preserved at all) that the character cannot be properly appreciated. Regarding the character state (2), such rare translocations are considered trivial for delimiting orthopteran species, because they occur repeatedly as rare variations in extant species (see above).

Data on fossil and extant material indicate that characters used by Gorochov (1987b) to delimit a number of species from the same locality as †*perfecta* could not be observed on the actual specimens, fall within the range of intra-specific variability, and/or likely are the consequence of deformation that affected the fossil material. In summary the corresponding species are to be considered as junior synonyms of †*perfecta*.

At this step it must be noticed that Sharov (1968, 1971) reports "7 imprints of body with wings, 65 imprints of wings of males, 12 imprints of fore wings of females and one imprint of a hind wing from the same locality". Unfortunately, apart from specimens used for his restoration (fig. 33), specimen numbers were not provided. However, the first part of PIN numbers refers to specific collections,

Fig. 27. (Following 2 pages) Species †*perfecta* Sharov, 1968, presumed ♂ (all at the same scale; all Madygen Formation, Kyrgyzstan; Ladinian/Carnian, late Middle to early Late Triassic); A, G, specimen PIN 2240/4132 (holotype; left forewing), drawing and photograph (positive imprint, flipped horizontally); B, H, specimen PIN 2555/1237 (right and left forewings), drawing and photograph (positive imprint); C, I, specimen PIN 2240/4113 (right and left forewings), drawing and photograph (positive imprint, flipped horizontally); D, J, specimen PIN 2240/4159 (right forewing), drawing and photograph (negative imprint, flipped horizontally); E, K, specimen PIN 2240/4124 (right forewing), drawing and photograph (positive imprint); F, L, specimen PIN 2240/4120 (left forewing), drawing and photograph (positive imprint, flipped horizontally); G, M, specimen PIN 2240/4123 (right forewing), drawing and photograph (positive imprint).





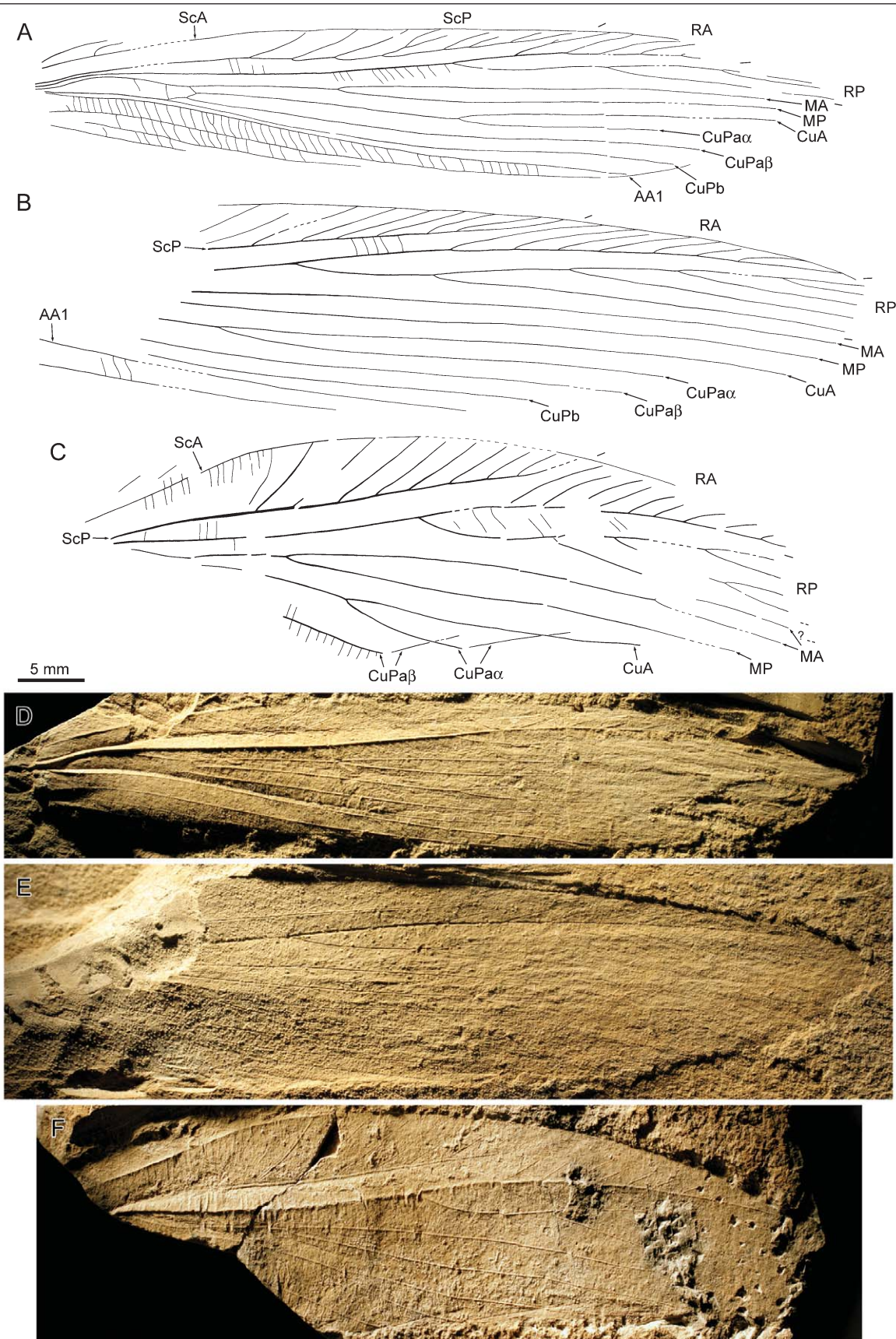


Fig. 28. Species *†perfecta* Sharov, 1968, presumed ♀ (all at the same scale; all Madygen Formation, Kyrgyzstan; Ladinian/Carnian, late Middle to early Late Triassic); A, D, specimen PIN 2555/1200 (right forewing), drawing and photograph (positive imprint); B, E, specimen PIN 2240/4112 (left forewing), drawing and photograph (negative imprint); C, F, specimen PIN 2240/1865 (right forewing), drawing and photograph (positive imprint).

and the numbers 2240 and 2555 indicate collections supervised by Sharov himself in 1964 and 1965, respectively (Shcherbakov 2008, and A.P. Rasnitsyn, pers. com. to OB, 2011). Therefore all specimens used by Gorochov (1987b) to erect '*†perfecta*-like' species were available to Sharov in 1968, and there is little doubt that they belong to the set of specimens determined as *†perfecta* by himself. If so I concur with Sharov's (1968, 1971) species delimitation.

Taxon *Tagryllacris* nom.-dis.-typ. nov.

Etymology.—Part of '*Etagryllacris*' (see below).

Definition.—Species that evolved from the metapopulation lineage in which the character state 'in forewing, M + CuA splits into MA and MP + CuA', as exhibited by *pinguipes* Rentz in Morton & Rentz, 1983 and *magnifica* Brunner von Wattenwyl, 1888, has been acquired.

Cladotypes.—Paratype of *pinguipes* Rentz in Morton & Rentz 1983 (ANIC ethanol collection; label reading: 26.00S 131.25E, 26km WSW. of Milga Park, H.S., N.T., 18.i.1982), and holotype of *magnifica* Brunner von Wattenwyl, 1888 (housed at the MNHG; Fig. 26C,D).

Composition.—See Fig. 30 and Appendix 3.

Discussion.—The antonym of the defining character state is 'in forewing, M + CuA splits into M and CuA'. This condition was documented in several species of the taxon *Agryllacris* (Figs 2-4, 6), and occurs in all Palaeozoic saltatorians (Béthoux & Nel 2002b, Carpenter 1992, Sharov 1968, Sharov 1971, among others). Therefore the defining character state of *Etagryllacris* likely is derived.

The same character state defines the *Gigatitanidae* nom. Sharov 1968, dis.-typ. Béthoux 2007d. The two taxa can be distinguished based on numerous apomorphies, on each side. It is not questionable that the same defining character state was acquired independently in *Tagryllacris* and *Gigatitanidae* (i.e., is a parallelism s.l. as defined below).

The morphology of *magnifica* was investigated based on pho-

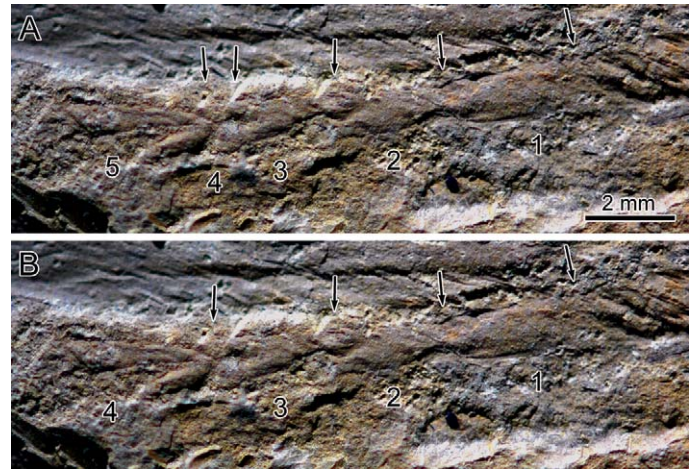


Fig. 29. Species *†perfecta* Sharov, 1968, specimen PIN 2240/4112 (Madygen Formation, Kyrgyzstan; Ladinian/Carnian, late Middle to early Late Triassic), detail of the tarsus (photograph courtesy of A.P. Rasnitsyn); arrows and numbers indicate tarsus segmentation; A, Sharov's (1968) interpretation; B, alternative interpretation.

tographs of the holotype (Fig. 26C,D), and photographs of ANIC (drawers containing) dry specimens of this species, and of closely related ones. The usual organization of the median and cubital systems in forewings conforms to that observed in the forewings of the holotype specimen, viz. exhibits a MP fused with the free part of CuA and with CuA + CuPa α (and then diverging), and a CuA + CuPa α being simple.

Taxon *Etagryllacris* nom.-dis.-typ. nov.

Etymology.—Part of '*Metagryllacris*' (see below).

Definition.—Species that evolved from the metapopulation lineage in which the character state 'in forewing, CuA + CuPa α keep fused', as

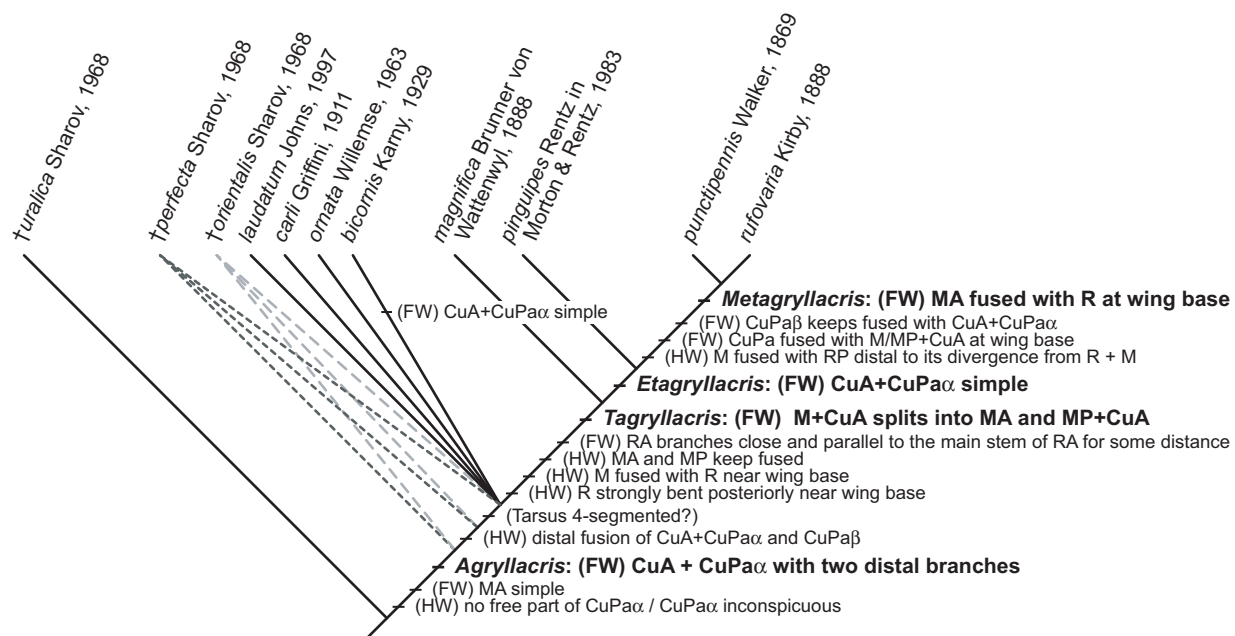


Fig. 30. Hypothetical phylogenetic relationships (based on the favored conjectures, and summarizing the presumed sequence of character state acquisitions), and nomenclatural treatment (with relevant character states).

exhibited by *pinguipes* Rentz in Morton & Rentz, 1983 and *magnifica* Brunner von Wattenwyl, 1888, has been acquired.

Cladotypes.—Paratype of *pinguipes* Rentz in Morton & Rentz, 1983 (ANIC ethanol collection; label reading: 26.00S 131.25E, 26km WSW. of Milga Park, H.S., N.T., 18.i.1982), and holotype of *magnifica* Brunner von Wattenwyl, 1888 (housed at the MNHG; Fig. 26C,D).

Composition.—See Fig. 30 and Appendix 3.

Discussion.—A synonym of the defining character state is 'CuA + CuPaa simple'. The antonym of the defining character state is 'in forewing, CuA and CuPaa diverge distally'. Distal divergence of CuA and CuPaa was documented in other species of the taxon *Agryllacris* (Figs 2-4, 6), and in all Palaeozoic saltatorians (Béthoux & Nel 2002b, Carpenter 1992, Sharov 1968, Sharov 1971, among others). Therefore the defining character state of *Etagryllacris* likely is derived. A branched CuA + CuPaa occurs only rarely in *pinguipes* (Appendix 4).

The species *bicornis* exhibits the defining character state of *Etagryllacris* (Fig. 8). However I propose to exclude this species from this taxon primarily because it lacks several character states shared by *Tagryllacris* species (Fig. 30). In other words, I consider the occurrence of a simple CuA + CuPaa in *bicornis* as the result of homoplastic evolution. Note that *bicornis* is not to be automatically assigned to *Etagryllacris* because it exhibits the defining character state of this taxon: *Etagryllacris* is the lineage in which the defining character as observed in *pinguipes* and *punctipennis* was acquired and, according to the proposed phylogenetic scheme, *bicornis* did not derive from this lineage.

Taxon *Metagryllacris* nom. nov., dis. Zeuner, 1939, typ. nov.

Etymology.—From 'meta', change, transition, in Greek, and 'Gryllacris', a taxon name commonly used under the Linnaean procedure; the name '*Metagryllacris*' accounts for the adaptation of 'Gryllacris' under the cladotypic procedure.

Definition.—Species that evolved from the metapopulation lineage in which the character state 'in forewing, MA fused with R at wing base', as exhibited by *punctipennis* Walker 1869, and *rufovaria* Kirby, 1888, has been acquired.

Cladotypes.—Specimen ANIC IWC OB 37, male of *punctipennis* Walker, 1869 (see Fig. 17A,B), and specimen ANIC IWC OB 27, male of *rufovaria* Kirby, 1888 (see Fig. 19A).

Composition.—See Fig. 30 and Appendix 3.

Discussion.—The defining character state was first outlined by Karny (1910: 38; Karny's 'M' is MA; and see Karny 1930) as typical of his 'Typus IV' (also present in his 'Typus V', presumable derived from 'Typus IV'). However he also listed "Radius sector [RP] less developed than in Type I, obviously reduced" in addition to the defining character state of *Metagryllacris*. Zeuner (1939: 60), acknowledging Karny, recognized the same character as the single trait proper to a single group, referred to as 'B' in his determination key (and including Karny's Types IV and V). Based on his examination of an undetermined species of the genus 'Gryllacris', Ragge (1955) also recognizes this trait as proper to (a subset of) gryllacridids. It turns out that Zeuner (1939) is the first author to associate the defining character state only with a single lineage ('B'), and his therefore

granted priority for the characterization of the group.

Adaptation of the taxon name '*Gryllacris*', which is commonly used under the Linnaean procedure, could have appeared as a suitable option for this taxon. However several '*Gryllacris*' species were assigned by Karny (1930) to 'Types' other than IV and V. In contrast this taxon name has a more restricted composition nowadays, excluding some species belonging to the taxon *Metagryllacris* (Eades *et al.* 2012). The taxon name '*Gryllacris*' is therefore highly polysemic under the Linnaean procedure, and therefore was avoided. With this provision I propose to coin the new taxon name *Metagryllacris*.

Discussion

Origin and evolution.—According to Dobruskina (1995; followed by Shcherbakov 2008), the Dzaylyauch locality, from which the material of †*perfecta* and †*orientalis* (and '†*orientalis*-like' species) has been unearthed, is Ladinian-Carnian in age (late Middle to early Late Triassic). Therefore the assignment of these species to the taxon *Agryllacris* implies that this lineage diverged *ca* 235 million years ago (mya) at least. This is in sharp contrast with the prevalent view (Heads & Leuzinger 2011), predicting a divergence of king crickets, raspy crickets & weta (forming a monophyletic group, or not) *ca* 65 mya (at best).

The new proposition has direct implications on scenarios regarding the lack of the *Grylloptera* stridulatory apparatus in extant king crickets, raspy crickets & weta. The earliest species showing such a stridulatory apparatus were collected from the same locality as †*perfecta* and †*orientalis* (Béthoux 2012; Gorochoff, 1986; Sharov 1968, 1971). According to Béthoux (2012) the file, typical of this apparatus, was acquired once. The point is to determine whether *Agryllacris* belongs to *Grylloptera* (i.e., if *Agryllacris* derived from a lineage possessing the *Grylloptera* file), or not (if *Agryllacris* does not derive from a lineage possessing the *Grylloptera* file).

Different degrees of complexity in stridulatory apparatuses are documented in *Grylloptera* from Dzaylyauch (Béthoux 2012; Gorochoff 1986; Sharov 1968, 1971). In other words, by the time of existence of †*perfecta* and †*orientalis*, the *Grylloptera* stridulatory apparatus was undergoing its early evolution. Therefore it is unparsimonious to assume that †*perfecta* and †*orientalis* could have already gained and lost the corresponding organization. Indeed Gorochoff (1995a, b) roots †*perfecta* and †*orientalis* in the 'oedischoid wastebasket', composed of stem-orthopterans that never gained the *Grylloptera* stridulatory apparatus. I concur with this view: indeed the 'oedischoid' †*buttsi* Béthoux & Beckemeyer, 2007 and †*noblensis* Béthoux & Beckemeyer, 2007, possessing forewings with a low number of MA and CuA + CuPaa branches, and lacking the *Grylloptera* file, could well form the Early Permian 'oedischoid' stock from which *Agryllacris* derived.

Particular aspects of wing venation evolution.—In forewing, species of the taxon *Metagryllacris* exhibit a ScA with a long posterior stem, often simple, and separated from other ScA branches by broad area filled with strong cross-veins (Figs 17, 19). This single stem cannot be mistaken with ScP because it is strongly convex (additionally the genuine ScP is evident). In contrast, in other species of the taxon *Agryllacris*, ScA is composed of a single main stem regularly emitting anterior branches, more or less all similar. Without proper phylogenetic scheme, the anterior area in forewing of *Metagryllacris* species could have been interpreted as composed of a simple ScA, and of a CP area anterior to it. The occurrence of a Costal system to which CP would belong is hypothesized by Kukalová-Peck (1991; and references therein) in her insect ground plan. However observations

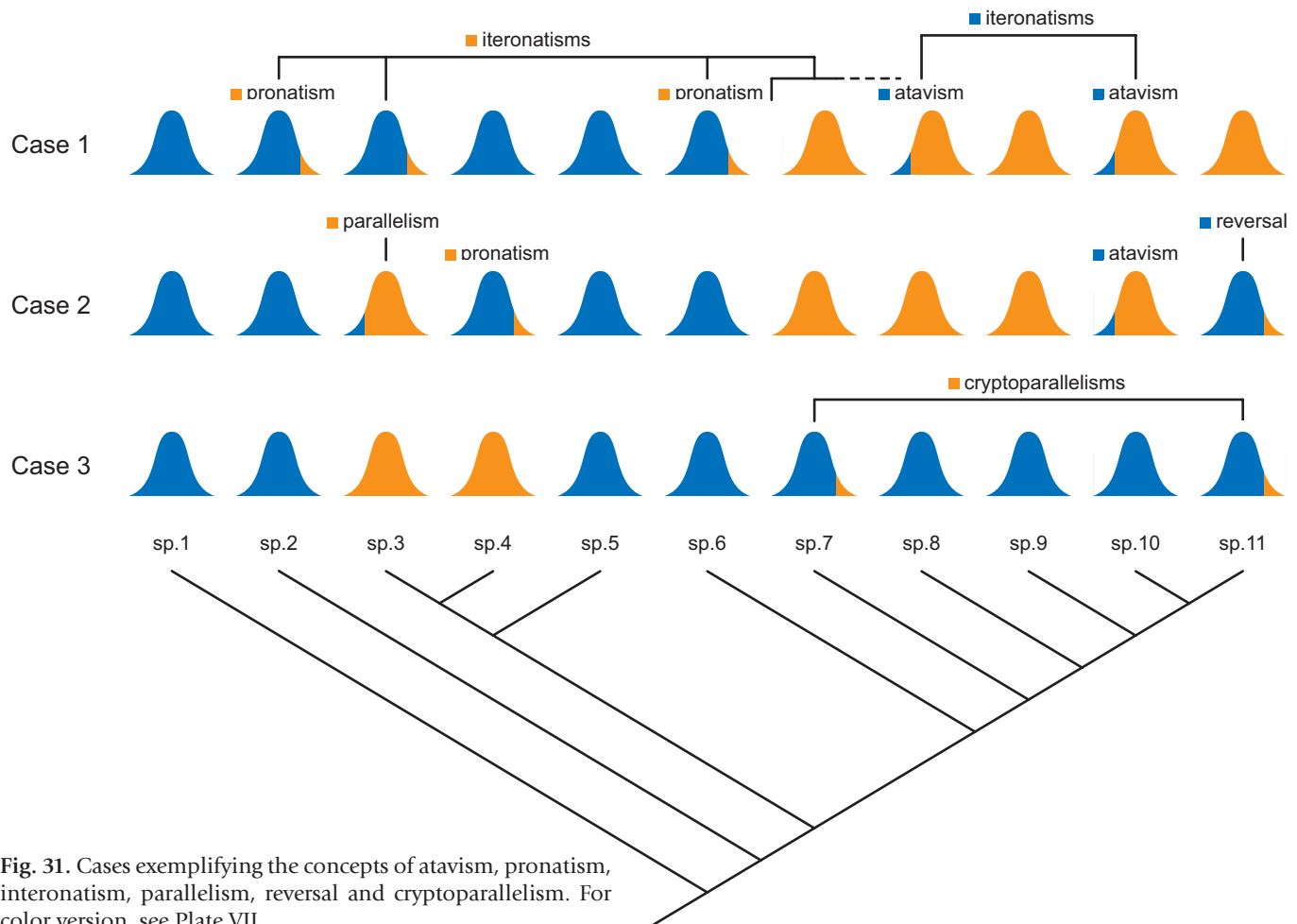


Fig. 31. Cases exemplifying the concepts of atavism, pronatism, iteronatism, parallelism, reversal and cryptoparallelism. For color version, see Plate VII.

by this author have been questioned. In particular the presumably plesiomorphic occurrence of a CP area in stem-Amphiesmenoptera, observed by Kukalová-Peck & Willmann (1990), was later discarded by Willmann (1997). Elcanid orthopterans provide the only convincing support for a presumed CP area: in the most recent representatives (see Sharov 1968, 1971: fig. 14H), three veins occur anterior to RA, which could be interpreted as ScP (Sharov's 'Sc'), ScA (Sharov's 'C'), and CP (not labelled by Sharov) (notice that Carpenter dealt with this case by hypothesizing a bifid ScP; Carpenter 1992: fig. 99.7). However observations in *Metagrallacris* match the interpretation by Sharov (1968, 1971) of the elcanid pattern, with the anterior area being filled with a ScA provided with a simple and long posterior stem, and with another anterior stem. In other words no hypothetical CP occurs. These observations suggest that the occurrence of a Costal system in insect wings might have to be reconsidered.

The actual course and organization of tracheae within wing veins have long been recognized as a potential source of inference for establishing conjectures of topological homologies (Comstock & Needham 1898, 1899). Typically, the observation of a pair of tracheae running in a single 'vein' is indicative of a composite stem, such as R and MA in *rufovaria*, each represented by a trachea within the 'R vein' (Fig. 19E). However, the same material demonstrates that the corollary, namely that a single trachea is indicative a single vein, is not supported: the eminently composite stem MP + CuA + CuPa / CuPaa + CuPaβ is provided with a single trachea (Fig. 19E) in the same species. It implies that vein fusion is probably 'completed' by tracheal fusion at some point.

Variation, variability, and iterative evolution.—Variation in the variability of wing venation has been seldom investigated (but see Ross 2012; and references therein). The available data on *Agrallacris* demonstrate that the range of variation varies among the surveyed species (Tab. 1). For example, although the number of branches of CuA + CuPaa was found to be very stable in *laudatum* and *bicornis*, it varies within a limited range in *pinquipes* and *punctipennis*, and more widely in *ornata*. The character 'width of the area with the free part of CuA / length of the M + CuA + CuPaa common stem' is comparatively stable, and variable, in *laudatum* and *pinquipes*, respectively (Appendix 4).

The connection (or the lack thereof) of MP with CuA and CuA + CuPaa is also a relevant case. A connection is consistently absent in *laudatum* and *ornata*, while species of the taxon *Tagryllacris* usually exhibit a fusion of MP with CuA and CuA + CuPaa (as a consequence, there is not free stem of M). However, the left forewing of the specimen ANIC IWC OB 24 (Fig. 11A,C,E,G), itself belonging to the taxon *Tagryllacris*, exhibits the condition observed in *laudatum* and *ornata*. In addition a peculiar intermediate condition was observed in a single *pinquipes* specimen: the actual fusion of MP with CuA and CuA + CuPaa occurs, but MP further re-unites with MA (Fig. 12), reforming the stem of M observed in the earlier lineages. The fusion of MP with CuA and CuA + CuPaa occurs more consistently in species of the taxon *Metagrallacris*, without intermediate condition being observed. These examples indicate that variability possibly varies according to the phylogenetic position of a given species. Note that a similar variation in variability has been documented in the fusion of a branch of RP with RA in mantodeans (Béthoux

& Wieland 2009), with occurrence of intermediate conditions in variable species.

Based on these examples, variation in character states distribution can be encompassed by three cases (Fig. 31). First, within a species exhibiting an apomorphic condition, rare variants exhibit the condition usually present in successive stem-lineages. This is the case of CuA + CuPaa being forked in *pinguipes* and *punctipennis* (Appendix 4), for example. These are atavisms, *viz.* the rare occurrence of a plesiomorphic condition. Although this concept usually applies to species only remotely related to the corresponding stem-lineages, it seems appropriate to use it even in species closely related to these (Fig. 31, sp. 8 in case 1): it can be argued that atavism borders on intra-specific variability indeed. The connection between atavism and reversal (or taxic atavism) is evident (Hall 2003; Stiassny 1992): both are the consequence of the persistence of functional genetic modules responsible for plesiomorphic states. The term 'atavism' refers to low frequency of occurrence of the plesiomorphic state in a given species (Fig. 31, sp. 10 in case 2), while reversal is characterized by a high frequency of occurrence (Fig. 31, sp. 11 in case 2).

The complementary configuration, *viz.* the rare occurrence of an apomorphic condition in a species usually exhibiting the plesiomorphic one, is equally plausible. Examples were documented above, such as the pectinate fusion of RP with RA, usually observed in *ornata*, and found to occur rarely in *laudatum* (Fig. 3H,Q; and see Béthoux & Wieland 2009: fig. 13C-D). I failed to find the proper counterpart to the term 'atavism' for such case, therefore I propose to coin the term 'pronatism' ('pro-' = before; 'natus' = born). It is proposed to apply this concept only to lineages which derived directly from the corresponding stem-lineage (such as spp. 2 and 6 in case 1 on Fig. 31; see below for sp. 3; referred to as direct relative in the following). As for atavism, it is assumed that pronatism is based on a genetic organization similar to that underlying the high-frequency condition (but see below for a broader sense). And as for atavism and reversal, an evident connection exists between pronatism and parallelism (*sensu* Hall 2003): assuming similar genetic ground, the former is characterized by low frequency, the latter high frequency. And as for atavism, pronatism borders on intra-specific variability.

At this step confusion between parallelism on one hand, and atavism, reversal, and pronatism on the other, is possible. Hall (2003: tab. 2) defines parallelism as follows: "a feature present in closely related organisms but not present continuously in all members of the lineage" and which development is based on "normally similar developmental pathways". However, this definition applies to atavism and reversal as well, because they are the re-expression of a genetic organization inherited from the same stem-lineage (therefore arguably similar), and of course to pronatism as defined above. I propose to give a narrower sense to parallelism, restricted to the repeated acquisition of a derived condition at high frequency, due to similar genetic ground. Atavism and reversal apply to expression of a plesiomorphic conditions.

We are left with a final case involving (1) a derived condition occurring at high frequency in a lineage, and (2) the same derived condition occurring at low frequency within a lineage which is not a direct relative of the former (Fig. 31, case 3, spp. 3 and 4 on one hand, and 7 and 11 on the other; and sp. 3 as opposed to spp. 7-11 in case 1). The translocation of CuPaa onto M + CuA fits this case: it occurs at low frequency in *laudatum* (Fig. 3I, R), *pinguipes* (Fig. 14A-B, K), and in one wing of the specimen ANIC IWC OB 25 (Fig. 16B,E,H), but at high frequency in *†brodiei* (Fig. 24), which is only remotely related to species of the taxon *Agryllacris*. Assuming similar genetic ground, the observed rare occurrences do not qualify for pronatism: they do not predate the expression of the

corresponding derived condition at high frequency. This case better fits with parallelism as outlined above, except for the occurrence frequency. I propose to refer to the low frequency occurrences as 'cryptoparallelisms'.

At this stage I propose to coin the term 'iteronatism' ('intero-' = repeated) to encompass the concepts of atavism, reversal, cryptoparallelism, pronatism, and parallelism altogether. All have in common the repeated occurrence of a condition (either plesiomorphic or apomorphic) due to a similar underlying genetic organization. Defined on this ground, an iteronatism differs from a convergence in that the latter is due to a different underlying genetic organization (Hall 2003; and references therein).

Finally, I propose to extend the concept of iteronatism beyond repeated appearances due to similar underlying genetic organization. Given an initial pattern (*i.e.*, the orthopteran forewing venation pattern) and a transformation type commonly observed (*i.e.* vein translocation), one can predict iterative appearances of the very same derived condition (*i.e.* CuPaa diverging from M + CuA as a consequence of a translocation) in various lineages, regardless of the adaptative significance of the transformation. In other words, provided an initial morphological context, exhaustion of morphological character states (*sensu* Wagner 2000), due to a limited number of transformation types, is likely to occur. A similar genetic organization is not necessarily underlying these iterative appearances, but a propensity of the condition to appear can be advocated. This broader perspective applies to all cases of iteronatism detailed above, and to the actual cases investigated herein. The concepts elaborated above are summarized as follows:

Iteronatism: repeated occurrence of a condition of any polarity, and at any species-level frequency, due to a similar underlying genetic organization (*s.str.*) / to a shared propensity of the condition to appear, provided the ancestral context (*s.l.*).

Atavism: occurrence of a plesiomorphic condition at low species-level frequency, due to the persistence and re-expression of an ancestral genetic organization; can repeat.

Reversal: occurrence of a plesiomorphic condition at high species-level frequency, due to the persistence and re-expression of an ancestral genetic organization; can repeat.

Cryptoparallelism: repeated occurrence of an apomorphic condition at low species-level frequency, due to a similar underlying genetic organization (*s.str.*) / to a shared propensity of the condition to appear, provided the ancestral context (*s.l.*).

Pronatism: appearance of an apomorphic condition at low species-level frequency, predating its expression at high frequency in a direct relative, due to a similar underlying genetic organization (*s.str.*) / to a shared propensity of the condition to appear, provided the ancestral context (*s.l.*); can repeat.

Parallelism: repeated occurrence of an apomorphic condition at high species-level frequency, due to a similar underlying genetic organization (*s.str.*) / to a shared propensity of the condition to appear, provided the ancestral context (*s.l.*).

Conclusion

This contribution exemplifies the importance of giving full consideration to intra-specific variation for establishing conjectures of topological homology. Indeed within-species variants can serve as Remane's (1952) intermediates and fill a gap in a transformation series otherwise incomplete. In that respect within-specimen variation taking place in symmetrical and/or serially arranged organs, such as wings, is a pinnacle. The most illuminating encountered case regards the specimen ANIC IWC OB 24 (Fig. 11), which right forewing exhibits an extremely rare configuration providing logical evidence in favor of a new STHC.

There is an unfortunate tendency of palaeoentomologists to erect new species without giving proper consideration to intra-specific variation (Béthoux 2009b). The current contribution exemplifies this issue, with six species, erected by a single author, demonstrated to be synonyms of a junior one, thanks to data on extant material. Where this trend is dramatic is that demonstrating junior synonymy is much more labor-intensive than erection of doubtful species, and can be achieved only when appropriate extant material is available (e.g., Schneider 1977, 1978), and/or on the basis of exceptional sample of fossil material (e.g., Cui *et al.* 2011). The routine erection of new species based on any observed difference is fundamentally flawed in that it neglects the fact that biological evolution could not take place without intra-specific variability.

A consequence of the assignment of †*perfecta* to *Agryllacris* is that this group stems in the Triassic, at least, in other words *ca* 170 my earlier than previously assumed. A loss of the complex gryllopteran stridulatory apparatus is no longer needed to account for the morphology of king crickets, raspy crickets and weta forewing.

Only a subset of recognized transformations was used to develop a new nomenclatural scheme (Fig. 30). The surveyed material was insufficient to allow relative timing of acquisition of the corresponding character states, and to define corresponding lineages. It is anticipated that this comparative analysis will allow wing venation homologies to be assessed in additional species, and the longest branches in the proposed transformation series to be split according to the sequence of character states acquisition.

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Appendix 1. Names and classification of species surveyed in the comparative analysis and indicated on Fig. 30 according to the current traditional nomenclature (Eades *et al.* 2012), and approximate correspondence with current cladotypic nomenclature.

	<i>Archaeorthoptera</i>
Orthoptera ¹	
Ensifera ²	
†Oedischiidea Sharov, 1968 ³	
†Pruvostitidae Zalesky, 1929 ⁴	
† <i>Sylvoedischia</i> Sharov, 1968	
† <i>Sylvoedischia uralica</i> Sharov, 1968	† <i>uralica</i> Sharov, 1968
	<i>Agryllacris</i>
†Proparagryllacrididae Riek, 1956 ⁵	
†Proparagryllacridinae Riek, 1956	
† <i>Gryllacrimima</i> Sharov, 1968	
† <i>Gryllacrimima perfecta</i>	† <i>perfecta</i> Sharov, 1968
†Madygeniinae Gorochoy, 1987b	
† <i>Madygenia</i> Sharov, 1968	
† <i>Madygenia orientalis</i>	† <i>orientalis</i> Sharov, 1968
Stenopelmatoidea Burmeister, 1838 ⁶	
Anastostomatidae de Saussure, 1869	
Subfamily incertae sedis	
<i>Transaevum</i> Johns, 1997 ⁷	
<i>Transaevum laudatum</i>	<i>laudatum</i> Johns, 1997
Anabropsinae Rentz & Weissman, 1973	
<i>Anabropsis</i> Rehn, 1901	
<i>Anabropsis mexicana</i>	cf. <i>mexicanus</i> de Saussure, 1859: 209
<i>Paterdecolyus</i> Griffini, 1913	
<i>Paterdecolyus carli</i>	<i>carli</i> Griffini, 1911a
<i>Exogryllacris</i> Willemse, 1963	
<i>Exogryllacris ornata</i>	<i>ornata</i> Willemse, 1963
Anastostomatinae de Saussure, 1869	
<i>Gryllotaurus</i> Karny, 1929a	
<i>Gryllotaurus bicornis</i>	cf. <i>bicornis</i> Karny, 1929a
	<i>Tagryllacris</i>
Gryllacrididae Blanchard, 1845	
Gryllacridinae Blanchard, 1845	
<i>Hadrogryllacris</i> Karny, 1937	
<i>Hadrogryllacris magnifica</i>	<i>magnifica</i> Brunner von Wattenwyl, 1888
	<i>Etagryllacris</i>
<i>Bothriogryllacris</i> Rentz, 1983	
<i>Bothriogryllacris pinguipes</i>	<i>pinguipes</i> Rentz in Morton & Rentz, 1983
	<i>Metagryllacris</i>
<i>Xanthogryllacris</i> Karny, 1937	
<i>Xanthogryllacris punctipennis</i>	<i>punctipennis</i> Walker, 1869
<i>Gryllacris</i> Audinet-Serville, 1831	
<i>Gryllacris rufovaria</i>	<i>rufovaria</i> Kirby, 1888

¹understood as crown-group; if understood as total-group (*i.e.*, including all species more closely related to extant orthopterans than to any other extant group of insects), it includes *Archaeorthoptera*.

²understood as composition-based name in its current usage, *viz.* Orthoptera excluding Caelifera; however the name itself refers to the sword-shaped ovipositor, occurring in Carboniferous *Archaeorthoptera* (pers. obs.), so 'Ensifera' understood as 'possessing a sword-shaped ovipositor' includes all extant Orthoptera, and *Archaeorthoptera*.

³a paraphyletic assemblage; if considered as including the common ancestor of its included species, and all descendants of this common ancestor, its composition roughly equates that of Orthoptera.

⁴monophyly not demonstrated, considered as synonym of Oedischiidae by Sharov (1968).

⁵according to the current analysis, monophyly not demonstrated.

⁶monophyly uncertain according to Legendre *et al.* (2010).

⁷according to Gorochoy (2001: 8) the position of this genus at the familial level is unclear.

Appendix 2. Nomenclatural treatment in accordance to the ICZN

Genus †*Probintoniella* Sharov, 1968

†*Probintoniella* Sharov, 1968, p. 168

†*Oshiellana* Gorochov, 1994, p. 54, syn. nov.

Discussion.— The type-species of the genus †*Oshiellana* Gorochov, 1994 is considered as a junior synonym of the type-species of the genus †*Probintoniella* Sharov, 1968, therefore the former is a junior synonym of the latter.

†*Probintoniella triassica* Sharov, 1968

Fig. 23.

†*Probintoniella triassica* Sharov, 1968, p. 168, fig. 16B; holotype PIN 2069/2320 (Fig. 23A,B)

†*Probintoniella primaria* Sharov, 1968, p. 168, fig. 16A; holotype PIN 2240/4312 (Fig. 23C,D), syn. nov.

†*Oshiellana primaria* (Sharov, 1968) Gorochov, 1994, p. 54, syn. nov.

Discussion.— See main text for discussion on proposed synonymy.

Genus †*Gryllacrimima* Sharov, 1968

†*Gryllacrimima* Sharov, 1968, p. 185

†*Batkenella* Gorochov, 1987a, p. 25, syn. nov.

†*Dolichobatkenella* Gorochov, 1987a, p. 26, syn. nov.

†*Eubatkenella* Gorochov, 1987a, p. 26, syn. nov.

†*Brevibatkenella* Gorochov, 1987a, p. 26, syn. nov.

Discussion.— All type-species of listed genera are considered as junior synonyms of *Gryllacrimima perfecta* Sharov, 1968 (see below), therefore the corresponding genera are junior synonyms of *Gryllacrimima* Sharov, 1968.

†*Gryllacrimima perfecta* Sharov, 1968

Figs 20A,B, 27-29

†*Gryllacrimima perfecta* Sharov 1968, p. 185, fig. 33, pl. 6 fig. 4

†*Gryllacrimima perfecta* Sharov 1971, p. 191, fig. 33, pl. 6 fig. 4

†*Batkenella megaptera* Gorochov 1987a, p. 25, fig. 5; holotype PIN 2240/1865 (Fig. 28C,F), syn. nov.

†*Gryllacrimima simplicis* Gorochov 1987a, p. 25, fig. 6; holotype PIN 2240/4123 (Fig. 27G,M), syn. nov.

†*Gryllacrimima elongata* Gorochov 1987a, p. 25, fig. 7; holotype PIN 2240/4159 (Fig. 27D,I), syn. nov.

†*Gryllacrimima madygenoides* Gorochov 1987a, p. 25, fig. 8; holotype PIN 2240/4113 (Fig. 27C,I), syn. nov.

†*Dolichobatkenella perlonga* Gorochov 1987a, p. 26, fig. 9; holotype PIN 2240/4120 (Fig. 27E,L), syn. nov.

†*Eubatkenella devexa* Gorochov 1987a, p. 26, fig. 10; holotype PIN 2240/4124 (Fig. 27E,K), syn. nov.

Discussion.— See main text for discussion on proposed synonymies.

Appendix 3. Provisional composition of the taxon *Agryllacris* nom.-dis.-typ. nov., mainly based on photographs available from Eades et al. (2012) (and few direct observations, and literature data) allowing conclusive assignment.

†*perfecta* Sharov, 1968
 †*giganteus* Riek, 1955
 †*orientalis* Sharov, 1968
carli Griffini, 1911a
bicornis Karny, 1929a
laudatum Johns, 1997
ornata Willemse, 1963
Tagryllacris nom.-dis.-typ. nov.
 magnifica Brunner von Wattenwyl, 1888
 magna Brunner von Wattenwyl, 1888
 shelfordi Griffini, 1909
Etagryllacris nom.-dis.-typ. nov.
 pinguipes Rentz in Morton & Rentz, 1983
 nigriceps Karsch, 1891
 fruhstorferi Griffini, 1908
 humberti Griffini, 1915
 nigrivertex Karny, 1926
 podocausta de Haan, 1842 *mutabilis* Pictet & de Saussure, 1893
 aequalis Walker, 1859
 trinotata Walker, 1870
 singaporeae Karny, 1923
 signatifrons de Haan, 1842 *raapi* Griffini, 1908
 dimidiata Brunner von Wattenwyl, 1888
 dyscrita Karny, 1928c
 ligata Brunner von Wattenwyl, 1888: 359
 combusta Gerstaecker, 1860
Metagryllacris nom. nov., dis. Zeuner, 1939, typ. nov.
 punctipennis Walker 1869
 rufovaria Kirby 1888
 braueri Griffini, 1911b
 athleta Brunner von Wattenwyl, 1888
 excelsa Brunner von Wattenwyl, 1888
 appendiculata Brunner von Wattenwyl, 1888
 contracta Walker, 1869: 169
 discoidalis Walker, 1869: 174
 nigrilabris Gerstaecker, 1860
 peracca Karny, 1923
 vittata Walker, 1869
 bodenklossi Karny, 1926
 robinsoni Karny, 1926
 atriceps Brunner von Wattenwyl, 1888
 multicolor Karny, 1928
 personata Audinet-Serville, 1831
 urania Griffini, 1911c

Appendix 4. Variations observed in various characters in forewings of *laudatum* Johns, 1997, *ornata* Willemse, 1963, *bicornis* Karny, 1929a, *pinguipes* Rentz in Morton & Rentz, 1983, *punctipennis* Walker, 1869, and *rufovaria* Kirby, 1888; °, °°, °°°, not applicable/observable in 1, 2, 3 cases, respectively; *, ***, ***, based on n-1, n-4, n-6, respectively.

		Branches of ScP reaching ScA			MA with respect to R/RP			Width of area with free part of CuA (+) / length of M+CuA+CuPaa common stem (-)		MP with respect to CuA/CuA+CuPaa			
		n	yes	no	MA distinct from R/RP	MA connected with RP at wing midlength	MA fused with R at wing base or midlength	min/average/max	standard deviation	MP distinct from CuA/CuA+CuPaa	MP fused with CuA/CuA+CuPaa(α)		
											MP diverges distally		MP keeps fused with CuA+CuPa
											then reunited shortly with MA	then distinct from MA	
Species <i>laudatum</i> Johns, 1997	♀	49	43	6	49	1	0	0.15/0.54/0.61°°	0.09	49	0	0	0
	♂	39	37	2	39	0	1	-0.17/0.42/0.62°	0.14	39	0	0	0
Species <i>ornata</i> Willemse, 1963	♀	21	12	9	21	0	0	0.83/1.07/1.24	0.11	21	0	0	0
	♂	19	12	7	17	0	2	0.59/0.89/1.11°	0.13	18°	0	0	0
Species <i>bicornis</i> Karny, 1929	♀	29	6	23	29	0	0	-2.01/0.21/0.83	0.68	26	0	3	0
	♂	4	0	4	4	0	0	0.45/0.6/0.77	0.2	3	0	1	0
Species <i>pinguipes</i> Rentz in Morton & Rentz, 1983	♀	58	n/a	n/a	55	3	0	-0.70/0.17/0.57	0.22	0	5	53	0
	♂	38	n/a	n/a	37	0	1	-0.90/0.02/0.47	0.41	0	1	37	0
Species <i>punctipennis</i> Walker, 1869	♀	12	n/a	n/a	0	0	12	n/a	n/a	0	0	12	0
	♂	18	n/a	n/a	0	0	18	n/a	n/a	1	0	16	1
Species <i>rufovaria</i> Kirby, 1888	♂ + ♀	10	0	10	0	0	10	n/a	n/a	0	0	10	0

		CuPaa diverges from M+CuA (<i>i.e.</i> , translocated to M+CuA)			CuA and CuPaa		At wing base, CuPa with respect to M+CuA		Forewing total length	
		n	no	yes	diverge distally	keep fused	distinct	CuPa fused with M+CuA	min/average/max	standard deviation
Species <i>laudatum</i> Johns, 1997	♀	49	47	2	49	0	49	0	34.0/38.6/44.6*****	3.7
	♂	39	38	1	39	0	39	0	32.7/39.5/51.5****	3.6
Species <i>ornata</i> Willemse, 1963	♀	21	21	0	14	7	21	0	51.4/52.9/56.4*	2.0
	♂	19	19	0	14°°°	2	19	0	42.0/47.0/50.0*	2.4
Species <i>bicornis</i> Karny, 1929	♀	29	29	0	0	29	29	0	18.9/21.5/25.5	1.6
	♂	4	4	0	0	4	4	0	21.1/23.2/25.2	2.2
Species <i>pinguipes</i> Rentz in Morton & Rentz, 1983	♀	58	57	1	8	50	58	0	37.0/42.4/47.4	2.9
	♂	38	38	0	0	38	38	0	29.9/34.9/39.7	2.9
Species <i>punctipennis</i> Walker, 1869	♀	12	n/a	n/a	0	12	0	12	22.3/24.6/27.5	1.7
	♂	18	n/a	n/a	1	17	0	18	18.6/23.8/27.1	2.7
Species <i>rufovaria</i> Kirby, 1888	♂ + ♀	10	n/a	n/a	0	10	0	10	23.4/26.9/31.1	2.7