Cretaceous Research 84 (2018) 600–621

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

A systematic reappraisal of Araripeneuridae (Neuroptera: Myrmeleontoidea), with description of new species from the Lower Cretaceous Crato Formation of Brazil

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ARTICLE INFO

Article history:
Received 25 October 2017
Received in revised form
20 December 2017
Accepted in revised form 31 December 2017
Available online 4 January 2018

Keywords:
Myrmeleontoidea
Araripeneuridae
Nemopteridae
Crato Formation
Bon-Tsagaan

ABSTRACT

Two new species of the extinct family Araripeneuridae are described from the Lower Cretaceous Crato Formation of Brazil: *Caririneura macrothoracica* sp. nov. and *Cratoneura minor* sp. nov. *Caririneura damianii* Martins-Neto, 1992a and *C. crassatella* Martins-Neto and Vulcano, 1997 are transferred to the genus *Araripeneura* Martins-Neto and Vulcano, 1989a. The genera *Blittersdorffia* Martins-Neto and Vulcano, 1989a, *Pseudonymphes* Martins-Neto and Vulcano, 1989a and *Burmaneura* Huang et al., 2016 are removed from Araripeneuridae. These genera, together with *Choromyrmeleon* Ren and Guo, 1996, constitute the perhaps paraphyletic “Pseudonymphidae”, which may be a stem group of Myrmeleontidae + Ascalaphidae. *Pseudonymphes* is a most primitive genus of Myrmeleontoidae, having trichosors at the wing apex. The family Araripeneuridae as restricted herein, is considered to comprise 15–17 Early Cretaceous species in 7–9 genera. Due to the lack of distinguishing characters, the two subfamilies Cratoalloneurinae and Cratopteryxinae are synonymised with Araripeneuridae. The forewing venation of Araripeneuridae is most similar to that of Nemopteridae, and these families might be closely related, constituting a nemopterid lineage.

1. Introduction

The myrmeleontoid family Araripeneuridae is known only from the Cretaceous, currently comprising 13 genera and 28 species. The vast majority of them have been described from the late Aptian Crato Formation of Brazil (Martins-Neto and Vulcano, 1989a,b, 1997; Martins-Neto, 1990, 1992a,b, 1994, 1997, 1998, 2003; Martins-Neto and Rodrigues, 2010). Two monotypic genera are known from Asia: *Paracroce* Ponomarenko, 1992 from the Barremian/Aptian of Bon-Tsagan, Mongolia (Makarkin et al., 2012), and *Burmaneura* Huang et al., 2016 from the latest Albian/earliest Cenomanian Burmese amber (Huang et al., 2016). Additionally, the genus *Choromyrmeleon* Ren and Guo, 1996 from the Barremian/Aptian Yixian Formation of China was preliminarily referred to this family by Makarkin et al. (2012).

The taxon was established as a subfamily of Myrmeleontidae (see Martins-Neto and Vulcano, 1989a), and some authors continue to consider it as such (e.g., Stange, 2004; Engel and Grimaldi, 2007; Huang et al., 2016). Since 2003, however, this taxon has also been treated as a distinct family (i.e., Martins-Neto, 2003; Martins-Neto et al., 2007; Martill et al., 2007; Makarkin et al., 2013). Here, we treat the Araripeneuridae as a valid family although no unequivocal autapomorphies of the family were found (see below).

The taxonomy of Araripeneuridae is poorly understood. In fact, all our knowledge about the Crato Formation Araripeneuridae was limited to descriptions and drawings of Rafael Martins-Neto and his co-authors, which were often incomplete and at least partially inadequate. The photographs in these publications are mostly not detailed and provide little additional information. Unfortunately, types of most these species are currently not accessible for study. No species of this family were hitherto adequately and completely described. Therefore, it is time to begin to revise the family.

Recently, the first species of Araripeneuridae was described from the mid-Cretaceous Burmese amber, *Burmaneura minuta*

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https://doi.org/10.1016/j.cretres.2017.12.018

Huang et al., 2016, but we here remove it from the family and treat as belonging to the stem group "Pseudonymphidae" which is likely paraphyletic.

In this paper, we study some genera of Araripeneuridae, which provide a better understanding of their relationships with other myrmeleontoid families: an oldest known genus (*Paracroce*), some genera from the Crato Formation including the type genus *Araripeneura* Martins-Neto and Vulcano, 1989a, and the genus *Pseudonymphes* Martins-Neto and Vulcano, 1989a, which is rather closely related to a genus occurring in Burmese amber (i.e., *Burmaneura*).

2. Material and methods

This study is based on 10 specimens from the Lower Cretaceous Crato Formation (Brazil) and the Bon-Tsagaan locality (Mongolia) housed in different collections. The Crato Formation is a well-known Lagerstätte famous for its Early Cretaceous biota located in north-eastern Brazil (see more details in Makarkin et al., 2017). The Bon-Tsagaan [=Bon-Tsagan] locality is located in several kilometers south of Bon Tsagaan Nuur [=Bööntsagaan Nuur] Lake (Fig. 1B). The Khurilt Sequence to which these deposits belong is considered to be Barremian/Aptian (Rasnitsyn and Zherikhin, 2002).

The photographs of *Paracroce altaica* Ponomarenko, 1992 were taken by Alexander Khramov (PIN) using a Leica M165 stereomicroscope with an attached Leica DFC 425 digital camera; of specimens from SMNS by SW using a Leica M165 stereomicroscope with an attached Leica DFC 495 digital camera and a Leica MZ12.5 stereomicroscope with an attached Nikon D300 camera, and by Federica Menon using Nikon D1X and Sony DCS-717 digital cameras, and of specimens from INHSP by M. Jared Thomas (INHSP) using a Canon 5D Mark III DSLR camera with Canon MP-E 65 mm 1–5x macro lens mounted on a Cognisys StackShot automated focus stacking rail. The photomicrograph shown in figure 9B was produced by Jared Thomas using a Zeiss SteREO Discovery.V20 zoom stereomicroscope with a Plan-Apochromat S 0.63x f/Reo WD = 81 mm objective. Line drawings were prepared by VM using Adobe Photoshop CS3.

Venation terminology generally follows Kukalová-Peck and Lawrence (2004) as modified by Yang et al. (2012, 2014). Terminology of wing spaces and details of venation (e.g., veinlets, traces) follows Oswald (1993). The posteriorly directed branches of pectinately-branched veins (i.e., RP, MP+CuA (or MP and CuA) and CuP in the forewing; RP, MP and CuA in the hind wing) are designated successively from the anterior traces of those veins, starting from the wing base: e.g., vein RP1 is the proximal-most branch of the anterior trace of RP; vein RP2 is the second branch of the anterior trace of RP; vein CuA1 is the proximal-most branch of the anterior trace of CuA; vein (MP+CuA)1 is the proximal-most branch of the anterior trace of MP+CuA.

All taxonomic acts established in the present work have been registered in ZooBank LSID (see below), together with the electronic publication purn: lsid:zoobank.org:pub:EA022353-082A-4A93-829B-8D145AD44DE4.

AbbreviationsAA1–AA3, first to third branches of the anterior Analis; CuA, anterior Cubitus; CuA1, proximal-most branch of CuA; CuP,posterior Cubitus; *irc*, proximal intraradial cell; MA and MP, anterior and posterior branches of the Media; MA1, MP1, proximal-most branches of MA and MP, respectively; RA, anterior Radius; RP, posterior Radius; RP1, proximal-most branch of RP; ScP, posterior Subcosta.

Institutional abbreviations: INHSP, Illinois Natural History Survey Paleontology Collection, Urbana-Champaign, U.S.A.; PIN, Paleontological Institute of the Russian Academy of Science, Moscow, Russia; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

3. Systematic palaeontology

Class Insecta Linnaeus, 1758
Order Neuroptera Linnaeus, 1758
Superfamily Myrmeleontoidea Latreille, 1802

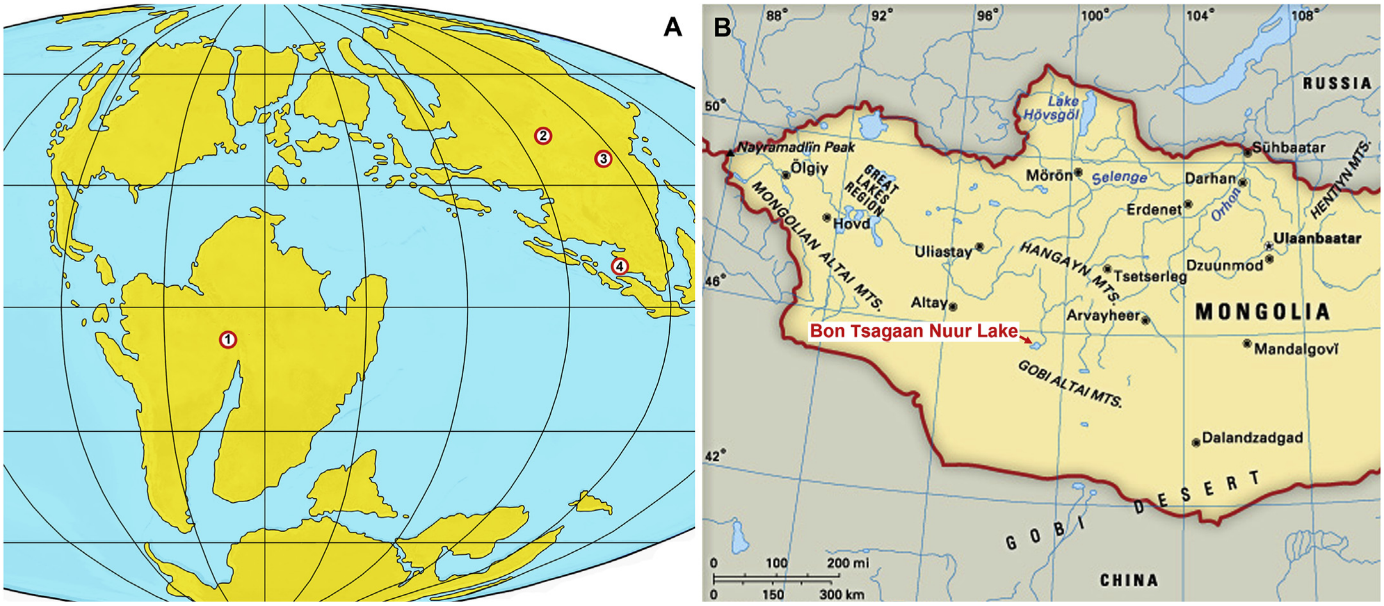

Fig. 1. A, Paleogeographic map of the Early Cretaceous (Aptian, 120 Ma) showing localities of Araripeneuridae and "Pseudonymphidae" (the map is simplified from http://jan.ucc.nau.edu/rcb7/120moll.jpg). 1, Crato Formation, Brazil (maps in Bechly and Makarkin, 2016, fig. 1); 2, Bon-Tsagaan, Mongolia (approximate coordinates 45°27′57.13″N 99°8′4.90″E); 3, Yixian Formation, China (see details in Makarkin et al., 2012; map in Yang et al., 2015, fig. 1); 4, Burmese amber (see details Makarkin et al., 2017). B, Modern map of Mongolia showing location of the Bon Tsagann Nuur [=Bööntsagaan Nuur] Lake.

Epifamily Myrmeleontoidae Latreille, 1802

Diagnosis. Myrmeleontoids with trichosors entirely absent or present only at tips of wings; MP crossvein-like, then fused with CuA in forewing (except for a few species, see below).

Families included. †“Palaeoleontidae” (paraphyletic?), †“Pseudonymphidae” (paraphyletic ?), †Araripeneuridae, Nemopteridae, Ascalaphidae, and Myrmeleontidae.

Remarks. The diagnosis of the superfamily Myrmeleontoidea was provided previously (Makarkin et al., 2017). We found that one genus of Myrmeleontoidae (i.e., *Pseudonymphes* considered up to now within Araripeneuridae) possesses character states not characteristic of this epifamily, i.e., vestigial trichosors are present and the forewing MP is sometimes not fused with CuA. This genus is here removed from Araripeneuridae and considered a most primitive representative of Myrmeleontoidae, in the likely paraphyletic stem group “Pseudonymphidae” (see below for details).

Family Araripeneuridae Martins-Neto and Vulcano, 1989a

1989a Araripeneurinae Martins-Neto and Vulcano, p. 371 [as a subfamily of Myrmeleontidae];
1989a Alloneurinae Martins-Neto and Vulcano, p. 385 [nom. praeocc.; as a subfamily of Nymphidae];
1990 Cratoalloneurinae Martins-Neto, p. 7 [nom. nov. pro Alloneurinae], syn. nov.;
2010 Cratopteryxinae [sic] Martins-Neto and Rodrigues, p. 4 [as a subfamily of Araripeneuridae], syn. nov.

Revised diagnosis. Moderately-sized myrmeleontoids (forewings 12.5–37.0 mm long) with the following combination of character states: antennae short, weakly clavate. Abdomen markedly shorter than forewing. In forewing, presectoral crossveins absent (present probably apomorphically in some species); RP originates relatively close to moderately far from wing base (at 0.14–0.26 of wing length); RP1 dichotomously branched; anterior and posterior Banksian lines absent; MP crossvein-like, then fused with CuA proximad proximal fork of MP+CuA; M/MA running relatively close to CuA/anterior trace of MP+CuA; MP+CuA forked proximad origin of RP or slightly distad this, with long branches; (MP+CuA)1 deeply forked in most genera (this bifurcation may be false, see Discussion), shallowly forked in few species; CuP strongly pectinate, not fused with AA1; AA1 deeply forked. In hind wing, MP with few pectinate branches (except *Caririneura* Martins-Neto and Vulcano, 1989a); CuA strongly pectinate; CuP short, simple or (possibly) few branched.

Genera included. Paracroce Ponomarenko, 1992 (Barremian/Aptian of Mongolia); *Araripeneura* Martins-Neto and Vulcano, 1989a; *Caririneura*; *Cratoneura* Martins-Neto, 1992b; *Cratoalloneura* Martins-Neto, 1992a; *Cratopteryx* Martins-Neto and Vulcano, 1989a; *Paracaririneura* Martins-Neto and Vulcano, 1997; ?*Caldasia* Martins-Neto and Vulcano, 1989a; ?*Bleyeria* Martins-Neto, 1992a (all from the late Aptian Crato Formation of Brazil).

Remarks. Two subfamilies were established within the family: Cratoalloneurinae Martins-Neto, 1990 and Cratopteryginae Martins-Neto and Rodrigues, 2010 (originally misspelled as Cratopteryxinae [sic]). Here these two subfamilies are synonymized with Araripeneuridae because no characters can be found to define and demarcate them reliably, as explained below.

The subfamily Cratoalloneurinae (established as Alloneurinae Martins-Neto and Vulcano, 1989a, preoccupied name) was defined by possessing of a number of subcostal crossveins in *Cratoalloneura acuminata* (Martins-Neto and Vulcano, 1989a), a single species in the subfamily in that time (Martins-Neto, 1990). Indeed, this condition occurs rarely in Myrmeleontoidae. However, a species of the genus described later (i.e., *Cratoalloneura verdandia* Martins-Neto, 2003) lacks these crossveins (see Martins-Neto, 2003, fig. 2D). Therefore, the presence of such crossveins in *C. acuminata* is probably a species autapomorphy. Interestingly, these crossveins were not mentioned when the author compared these two species (see Martins-Neto, 2003). Therefore, these crossveins may theoretically be an artefact. In other characters, this genus is very similar to *Cratoneura*, which does not possess subcostal crossveins (probably except for a basal crossvein).

The subfamily Cratopteryginae was established by Martins-Neto and Rodrigues (2010) and included two genera, *Cratopteryx* and *Diegopteryx* Martins-Neto in Martins-Neto and Rodrigues, 2010. The author defined the subfamily by a relatively small intraradial cell and “a notably long antenna” (p. 5). However, the first character state is plesiomorphic, and also present in *Caririneura* and *Paracroce*.

Cratopteryx is represented by two species, *Cratopteryx robertosantosi* Martins-Neto and Vulcano, 1989a and *C. nemopteroides* Martins-Neto, 2003. The type species *C. robertosantosi* is represented by a very poorly-preserved holotype (see Martins-Neto and Vulcano, 1989a, figs. 7, 21). It has been long assigned to Ascalaphidae due to the presence of long and clavate antennae (see Martins-Neto and Vulcano, 1989a, 1997; Martins-Neto, 1990, 1992b, 1994, 1997). However, if we compare the photo and drawing, their form appears to be incorrectly interpreted; at least, the ‘ascalaphid’ shape of the antennae needs confirmation. The venation of the holotype is incomplete, but allows assignment of the genus to Araripeneuridae. The venation of *C. nemopteroides* is more complete, including that of the hind wing (antennae are not preserved), but its generic affinity requires confirmation because of strong differences between these two species (see also below remarks on genus *Caririneura*). In general, both species are typical Araripeneuridae, and there is no basis to treat them in a separate subfamily. Judging from the drawings of the holotype (see Martins-Neto and Rodrigues, 2010, fig. 4), *Diegopteryx raptorius* Martins-Neto in Martins-Neto and Rodrigues, 2010 was described inadequately and requires re-examination. This species is probably most similar to *Blittersdorffia* and therefore, does not belong to Araripeneuridae.

The monotypic genera *Caldasia* and *Bleyeria*, which are only represented by incomplete holotypes, are tentatively considered as members of this family. *Caldasia cretacea* Martins-Neto and Vulcano, 1989a is very poorly preserved, and its generic status requires confirmation (see Martins-Neto and Vulcano, 1989a, fig. 5A, B; 1989b, fig. 4A). The forewing venation of *Bleyeria nordestina* Martins-Neto, 1992a differs rather strongly from that of other genera, e.g., the presumed (MP+CuA)1 originates far distad the origin of RP (see Martins-Neto, 1992a, fig. 8). These genera need a more accurate examination based on new materials, and are not considered in detail below.

The following genera are removed from the family: *Blittersdorffia* Martins-Neto and Vulcano, 1989a, *Pseudonymphes*, and *Burmaneura* (see below for details).

Genus ***Paracroce*** Ponomarenko, 1992

1992 *Paracroce* Ponomarenko, p. 110.

Type and only species. *Paracroce altaica* Ponomarenko, 1992, by original designation.

Revised diagnosis. In forewing (12.7 mm long), RA space gradually narrowed towards wing apex; *irc* relatively short and broad; (MP+CuA)1 and (MP+CuA)2 nearly parallel (its distal part is not preserved).

Remarks. Originally, the genus was not assigned to a family, only to the superfamily Myrmeleontoidea (Ponomarenko, 1992). According to Ponomarenko, it is distinguished from other myrmeleontoids (except Nymphidae) by the presence of trichosors. The examination of the holotype, however, shows that trichosors are absent in the preserved part of the forewing (but its apical part is not preserved). Makarkin et al. (2012) assumed that the venation of *Paracroce* is similar to that of Araripeneuridae (treated then as a subfamily of Myrmeleontidae). In this study, we confirm its araripeneurid attribution, as its oldest known genus.

Paracroce altaica Ponomarenko, 1992
Fig. 2

1992 *Paracroce altaica* Ponomarenko, p. 110, fig. 8; pl. 29, fig. 3.

Material. Holotype PIN 3559/5962. A proximal part of a forewing.
Type locality and horizon. Mongolia: Bayankhongor Aymag: Bon-Tsagaan [=Bon-Tsagan] locality several kilometers south of Bon Tsagaan Nuur [=Bööntsagaan Nuur] Lake. Early Cretaceous (Barremian/Aptian); Khurilt Sequence.
Description. Forewing 12.7 mm long as preserved (estimated complete length ca. 16 mm), 4.4 mm wide as preserved (estimated complete width ca. 5 mm) (length/width ratio ca. 3.2). Costal space relatively broad, slightly dilated towards apex. Subcostal veinlets simple, widely spaced becoming increasingly more closely spaced towards pterostigmal region. Subcostal space narrow; no crossveins detected. RA space only slightly narrowed distally, with six widely-spaced crossveins detected. Basal 1r-m oblique, apparently bifurcated. No presectoral crossveins. RP originates moderately far from wing base (at 0.21 of estimated wing length), with four preserved branches. RP1 originates far from origin of RP. Crossveins between branches of RP relatively scarce, regularly arranged; *irc* relatively short, broad. Four crossveins between stem of RP and MA. M not fused basally with R; forked slightly proximad (MP+CuA)1. MA nearly straight, rather close and parallel to anterior trace of MP+CuA; nine crossveins between them detected. MP basally appears as oblique crossvein then fused with CuA. Basal 1m-cu oblique, aligned with 1r-m. Cu dividing into CuA and CuP rather close to wing base. MP+CuA with five preserved pectinate branches, which are not deeply forked (their distal parts not preserved); (MP+CuA)1 originates remarkably distad origin of RP. Crossveins between branches of CuA scarce, regularly spaced. Five crossveins detected in intracubital space: three connecting CuA, CuP, and two connecting CuA1, CuP. CuP nearly parallel to posterior margin, strongly pectinate, with six preserved, nearly straight, long branches. Three crossveins between Cu/CuP, AA1: basal crossvein long, connecting Cu, AA1; second crossvein very short, connecting CuP, AA1; distal crossvein short, connecting CuP and anterior branch of AA1. AA1 relatively long, deeply forked. AA2 relatively long, probably simple. AA3 not preserved.

Genus ***Araripeneura*** Martins-Neto and Vulcano, 1989a

1989a *Araripeneura* Martins-Neto and Vulcano, p. 371.

Type species. *Araripeneura regia* Martins-Neto and Vulcano, 1989a, by original designation.
Revised diagnosis. Forewing ovate, with rounded apex (13–19 mm long); presectoral crossveins absent; RA space abruptly narrowed distally; *irc* very long and narrow; (MP+CuA)1 deeply forked; branches of CuP sigmoidly curved basally. Hind wing broad proximally with acute apex; shorter than forewing; presectoral crossveins absent; CuA long.
Species included. *Araripeneura regia*, *A. gracilis* Martins-Neto and Vulcano, 1989a, *A. damianii* (Martins-Neto, 1992a), comb. nov., *A. crassatella* (Martins-Neto and Vulcano, 1997), comb. nov., and *A. urda* Martins-Neto, 2003 from the late Aptian Crato Formation of Brazil.
Remarks. *Caririneura damianii* and *C. crassatella* are here moved to the genus *Araripeneura* as these species possess all characteristic features of the latter genus. The other species of *Caririneura* easily differ from those of *Araripeneura* by many character states, especially in the hind wing (see their diagnoses).

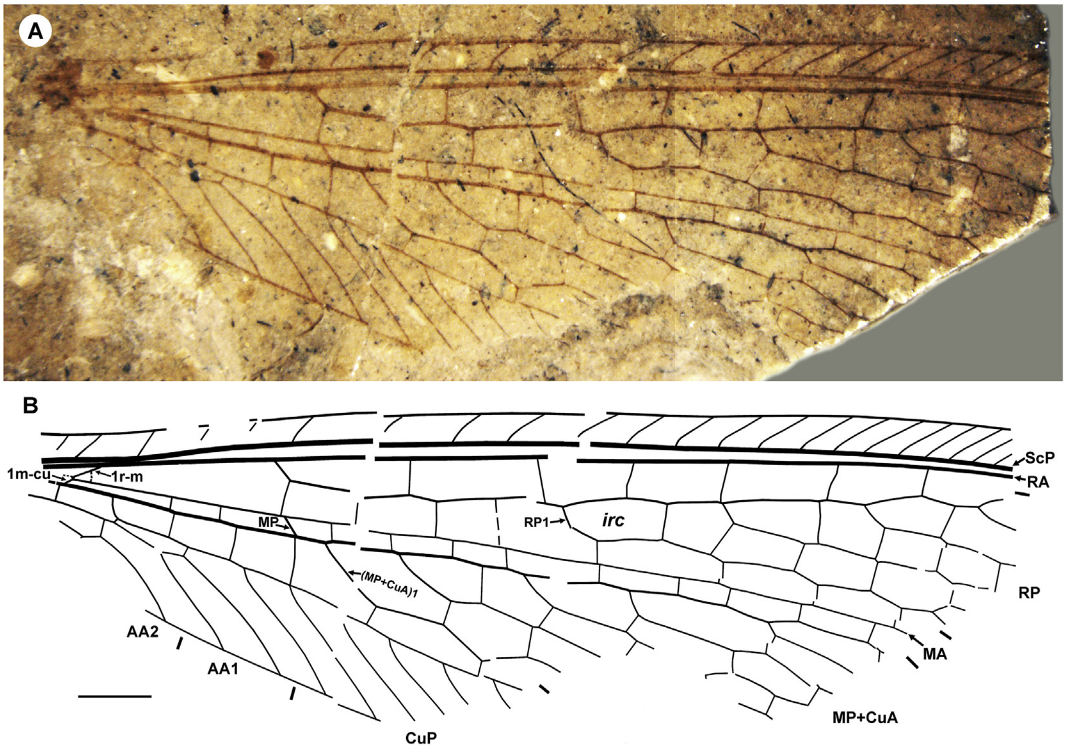

Fig. 2. *Paracroce altaica* Ponomarenko, 1992, holotype PIN 3559/5962. A, Specimen as preserved (part). B, Forewing venation. Scale bar represents 1 mm (both to scale).

The venation of all the species of *Araripeneura* are similar to each other; some of the species are possibly junior synonyms. All the species are poorly defined, so it is hard to assign new specimens to a species without examination of their types. We studied three specimens which were assigned to two species.

Araripeneura regia Martins-Neto and Vulcano, 1989a Figs. 3–5

1989a *Araripeneura regia* Martins-Neto and Vulcano, p. 371, figs. 1, 15.

Material. Specimen SMNS 66000/259, a nearly complete specimen in lateral aspect, with all wings incompletely preserved. Specimen INHSP 1763, an incomplete specimen in lateral view, with left forewing nearly complete, left hind wing incomplete, and right wings fragmentarily preserved.

Locality and horizon. Northeastern Brazil: Chapada do Araripe (precise locality unknown). Lower Cretaceous: upper Aptian (Crato Formation: Nova Olinda Member).

Diagnosis. Forewing elongate-oval with obtuse apex [forewing elongate with rounded apex in *A. crassatella*, *A. gracilis*].

Description. Specimen SMNS 66000/259 (Figs. 3, 4). Head visible in lateral view; antennae short (less than 4 mm), clavate; diameter of eye 1 mm; no details of mouthparts recognizable. Thorax ca. 5 mm long; pronotum short. Left hind-leg: Femur 2.3 mm long, 0.4 mm wide; tibia 2.2 mm long, 0.2 mm wide; tarsus 3 mm long, 0.1 mm wide. Abdomen short (less than 8 mm long), rather stout; terminal segments without projections.

Forewing elongate-oval with obtuse apex, ca. 18 mm long (estimated), 5.7 mm wide (length/width ratio 3.16). Costal space narrow, dilated towards apex. Subcostal veinlets simple (except one distal), widely spaced becoming increasingly more closely spaced to pterostigmal region. ScP, RA fused far from wing apex. Pterostigma indistinctly preserved, small. ScP+RA entering margin well after wing apex. Veinlets of ScP+RA long, one to three times forked distally; some veinlets connected with each other by short crossveins (five in left wing) forming one gradate series. Subcostal space narrow; no crossveins detected. RA space moderately broad proximally, strongly narrowed at distal-most (short) crossvein before fusion of last ScP and RA; moderately narrow after this crossvein; with eight crossveins proximad fusion of ScP and RA (four longest crossveins curved or sinuous); two crossveins thereafter. Hypostigmal cell long. No presectoral crossveins detected. RP originates moderately far from wing base (at ca. 0.26 of estimated wing length), with five branches. RP1 originates relatively close to origin of RP, profusely branched (generally pectinate, with proximal branch twice forked); RP2 distant from RP1, once forked; RP3–RP5 close to each other, simple. Crossveins between branches of RP numerous between RP1, RP2; scarce between other branches; outer gradate series present, consisting of 5–6 crossveins; *irc* long, narrow. Two crossveins between stem of RP, MA. M probably forked slightly proximad (MP+CuA)1 (incompletely preserved). MA rather close and parallel to anterior trace of MP+CuA, deeply forked distally. MP basally appears as oblique crossvein (incompletely preserved) then fused with CuA. Anterior trace of MP+CuA deeply forked distally, with five pectinate branches. (MP+CuA)1 originates slightly proximad origin of RP, deeply forked; (MP+CuA)2 to (MP+CuA)5 once to twice rather deeply forked. Crossveins between branches of CuA relatively numerous, regularly spaced. Many crossveins detected in intracubital space: one distal connecting CuA, CuP, and eight connecting CuA1, CuP. CuP even inclined to posterior margin, strongly pectinate; with eight long simple branches, proximal of which sinuous basally. Only anterior branch of AA1 partially preserved.

Hind wing distinctly narrower than forewing, slightly falcate, with acute apex, ca. 16.5 mm long (estimated), 4.3 mm wide (estimated). Costal space slightly broader than in forewing, dilated towards apex. Subcostal veinlets simple, widely spaced becoming increasingly more closely spaced to pterostigmal region. ScP, RA fused relatively close to wing apex. Pterostigma indistinctly preserved. ScP+RA entering margin well after wing apex. Veinlets of ScP+RA once forked; no crossveins between them. Subcostal space narrow; no crossveins detected. RA space moderately broad proximally, strongly narrowed at distal-most (short) crossvein before fusion of last ScP, RA; moderately narrow after this crossvein; with up to seven crossveins proximad fusion of ScP, RA; one short crossvein thereafter. Hypostigmal cell long. RP originates far from wing base, with six branches. RP1 originates rather far from origin of RP, twice forked; other branches once to twice forked, except distal-most, which is simple. Three crossveins between RP1, RP2; two between RP2, RP3; one between RP3, RP4 and RP4, RP5. Two crossveins between stem of RP, MA. M probably forked near wing base (incompletely preserved); MA once forked, MP twice forked distally. Intramedial space rather broad, with at least six crossveins. CuA pectinately branched, with six simple, moderately long preserved branches. Mediocubital space clearly narrower than intramedial space. CuP, anal veins not preserved.

Specimen INHSP 1763 (Fig. 5). Head visible in latero-ventral view; antennae short (ca. 4.4 mm long), clavate. Thorax, abdomen poorly preserved. Pronotum probably short. Abdomen short, ca. 7.2 mm long; terminal segments without projections. Legs not preserved.

Forewing elongate-oval with obtuse apex, slightly falcate, ca. 16 mm long, 5.1 mm wide (length/width ratio 3.14). Costal space narrow, dilated towards apex. Subcostal veinlets simple, widely spaced becoming increasingly more closely spaced to pterostigmal region. ScP, RA fused far from wing apex. Pterostigma dark, relatively short, located in area of fusion of ScP, RA. ScP+RA enters margin well after wing apex. Veinlets of ScP+RA long, one to three times forked distally; some veinlets connected with each other by short crossveins (four detected) forming one gradate series. Subcostal space narrow; no crossveins detected. RA space moderately broad proximally, strongly narrowed at distal-most crossvein before fusion of last ScP, RA; moderately narrow after this crossvein; with eight crossveins proximad fusion of ScP, RA (three longest crossveins curved or sinuous), two short crossveins

Fig. 3. *Araripeneura regia* Martins-Neto and Vulcano, 1989a, specimen SMNS 66000/259. Scale bar represents 5 mm.

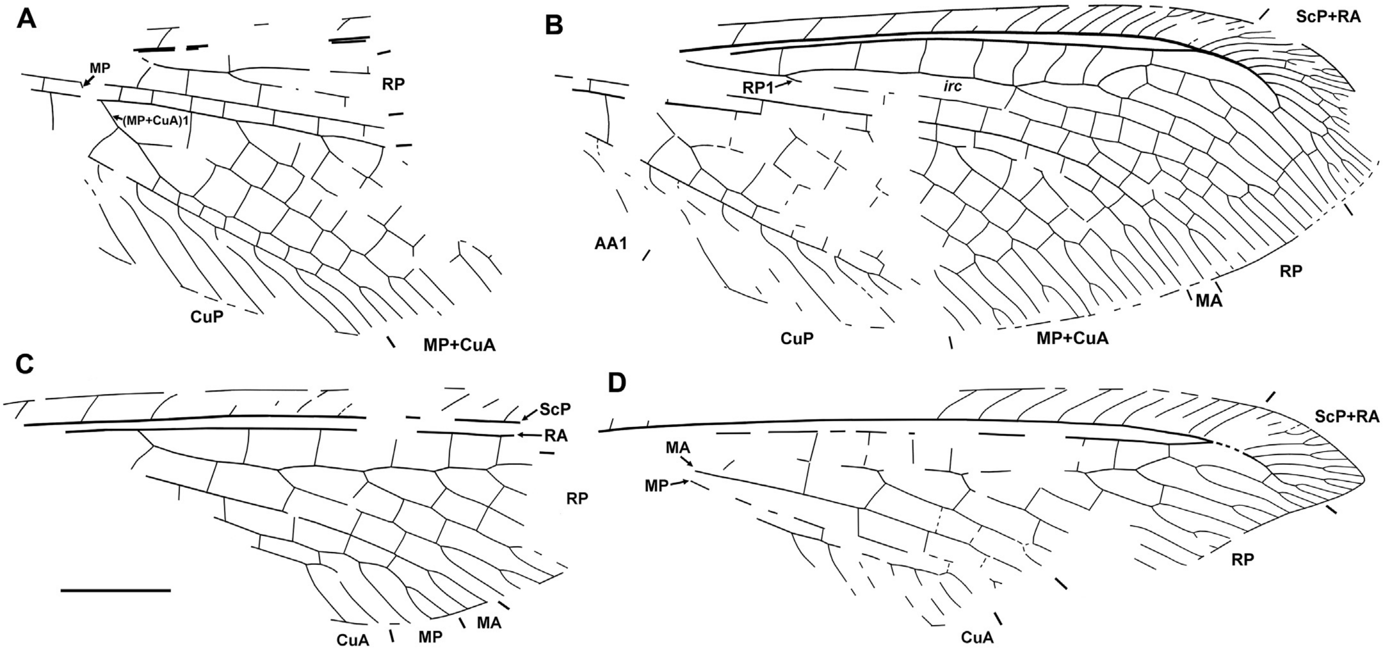

Fig. 4. Wing venation of *Araripeneura regia* Martins-Neto and Vulcano, 1989a, specimen SMNS 66000/259. A, Right forewing. B, Left forewing. C, Right hind wing. D, Left hind wing (all converted to right dorsal view). Scale bar represents 2 mm (all to scale).

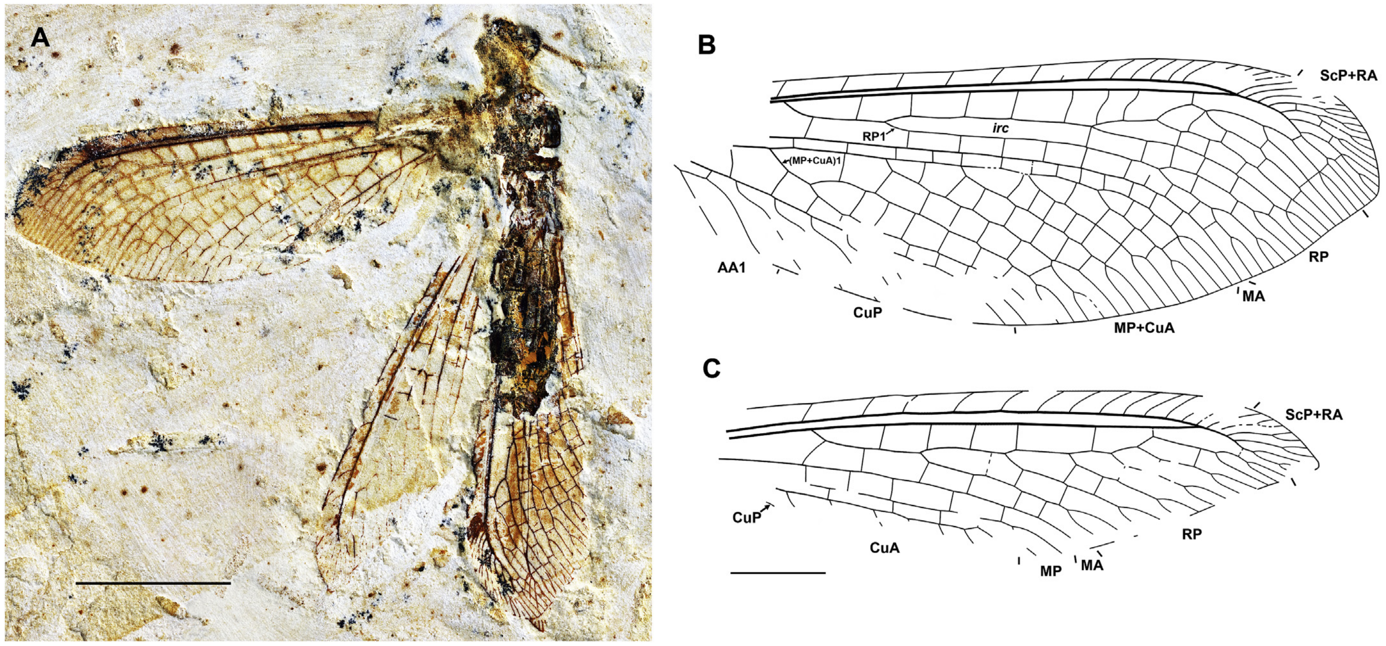

Fig. 5. *Araripeneura ?regia* Martins-Neto and Vulcano, 1989a, INHSP 1763. A, Specimen as preserved. B, Left forewing. C, Left hind wing (both converted to right dorsal view). Scale bars represent 5 mm (A), 2 mm (B, C).

thereafter. Hypostigmal cell long. No presectoral crossveins detected. RP originates moderately far from wing base (at ca. 0.26 of estimated wing length), with six branches. RP1 originates relatively close to origin of RP, profusely dichotomously branched; RP2 distant from RP1, once forked; RP3–RP6 close to each other, simple. Crossveins between branches of RP rather numerous, irregularly spaced; outer gradate series of crossveins distinct consisting of six crossveins; *irc* long, narrow. One crossvein detected between stem of RP, MA; then between RP1. MA. MA simple, rather close and parallel to anterior trace of MP+CuA. Anterior trace of MP+CuA deeply forked distally, with five pectinate branches. (MP+CuA)1 originates slightly proximad origin of RP, deeply forked; other branches once or twice rather deeply forked. Crossveins between MA, anterior trace of MP+CuA numerous. Crossveins between branches of CuA numerous, rather regularly spaced. Seven crossveins detected in intracubital space: one connecting CuA/MP+CuA, CuP, and six (probably seven when restored) connecting (MP+CuA)1, CuP. CuP even inclined to posterior margin, strongly pectinate;

with more than five long simple branches, four of which sinuous basally. AA1 deeply forked. One distal crossvein connecting CuP, AA1 detected.

Hind wing distinctly narrower than forewing, with acute apex, ca. 14.0 mm long, ca. 3.6 mm wide (estimated). Trichosors not detected. Costal space slightly broader than in forewing, dilated towards apex. Subcostal veinlets simple, widely spaced becoming increasingly more closely spaced to pterostigmal region. ScP, RA fused relatively close to wing apex. Pterostigma not detected. ScP+RA enters margin well after wing apex. Veinlets of ScP+RA once forked; no crossvein between them detected. Subcostal space moderately broad for entire length; no crossveins detected. RA space moderately broad proximally, strongly narrowed at distal-most crossvein before fusion of last ScP, RA; moderately narrow after this crossvein; with six-seven crossveins proximad fusion of ScP, RA; one crossvein thereafter. Hypostigmal cell rather long. RP originates rather far from wing base, with seven branches. RP1 originates far from origin of RP (at ca. 0.28 of estimated wing length); all branches once forked, except distal-most, which is simple. Crossveins between branches scarce (three between RP1, RP2; two between RP2, RP3; one between each RP3, RP4; RP4, RP5, and RP5, stem of RP). Two crossveins between stem of RP, MA; four between RP1, MA. MA probably simple, MP forked distally. Intramedial space rather broad, with at least five crossveins. CuA pectinately branched, with six branches (incompletely preserved). Mediocubital space clearly narrower than intramedial space. CuP fragmentary. Anal veins not preserved.

Remarks. Three species of *Araripeneura* are very similar to each other judging from their original descriptions (i.e., *A. regia*, *A. damianii*, and *A. urda*). Until their types are reexamined it is hard to decide whether they really constitute three different species or are conspecific. However, the wing shape and venation of two examined specimens (SMNS 66000/259 and INHSP 1763) are well concordant with those of the earliest described species (*A. regia*), so we assigned them to this species.

Four specimens were assigned to *A. regia* until now. The holotype was inadequately figured (see Martins-Neto and Vulcano, 1989a, figs. 1, 15), but these deficiencies were corrected in drawings of additional specimens (see Martins-Neto and Vulcano, 1997, fig. 1A, B; Martins-Neto, 2003, figs. 1C–E, pl. 1B).

The venation of specimen SMNS 66000/262 from an unknown locality of the Nova Olinda Member of the Crato Formation is poorly preserved, but generally similar to that of *A. regia* as well as its wing shape. Its colour pattern, however, is remarkable (Fig. 6). It is unknown if this is the original wing pattern or a secondary colouration due to taphonomic processes. If this colour pattern is original then this specimen may represent a species other than *A. regia*.

Araripeneura ?crassatella (Martins-Neto and Vulcano, 1997), comb. nov.

Fig. 7

1997 *Caririneura crassatella* Martins-Neto and Vulcano, p. 65, figs. 1C, 3, 9.

Material. Specimen INHSP 1506. An incomplete specimen in lateral aspect, with two left wings incompletely preserved.

Locality and horizon. Northeastern Brazil: Chapada do Araripe (precise locality unknown). Lower Cretaceous: upper Aptian (Crato Formation: Nova Olinda Member).

Diagnosis. Forewing elongate, with rounded apex [elongate-oval with obtuse apex in *A. regia*].

Description of INHSP 1506. Head transverse (in dorsal view), with rather large eyes; antennae short (apices not preserved). Prothorax short. Only one fore leg incompletely preserved: tibia slender, slightly swollen medially, short (ca. 0.5 mm). Abdomen short (ca. 7 mm), mostly pale with very dark terminal segments, which lack projections and clear appendages.

Forewing elongate, with rounded apex, 14.3 mm long, ca. 3.5 mm wide as preserved. Costal space very narrow basally, dilated towards apex. Subcostal veinlets simple, widely spaced becoming increasingly more closely spaced toward pterostigmal region. ScP, RA fused far from wing apex. ScP+RA enters margin after wing apex. Veinlets of ScP+RA long, at least once forked; some veinlets connected with each other by short crossveins (three detected) forming one gradate series. Subcostal space narrow; no crossveins detected. RA space moderately broad proximally, strongly narrowed at distal-most (short) crossvein before fusion of last ScP, RA; narrowed after this crossvein; with eight crossveins proximad fusion of ScP, RA (three longest crossveins

Fig. 6. *Araripeneura* sp., specimen SMNS 66000/262. Scale bar represents 5 mm.

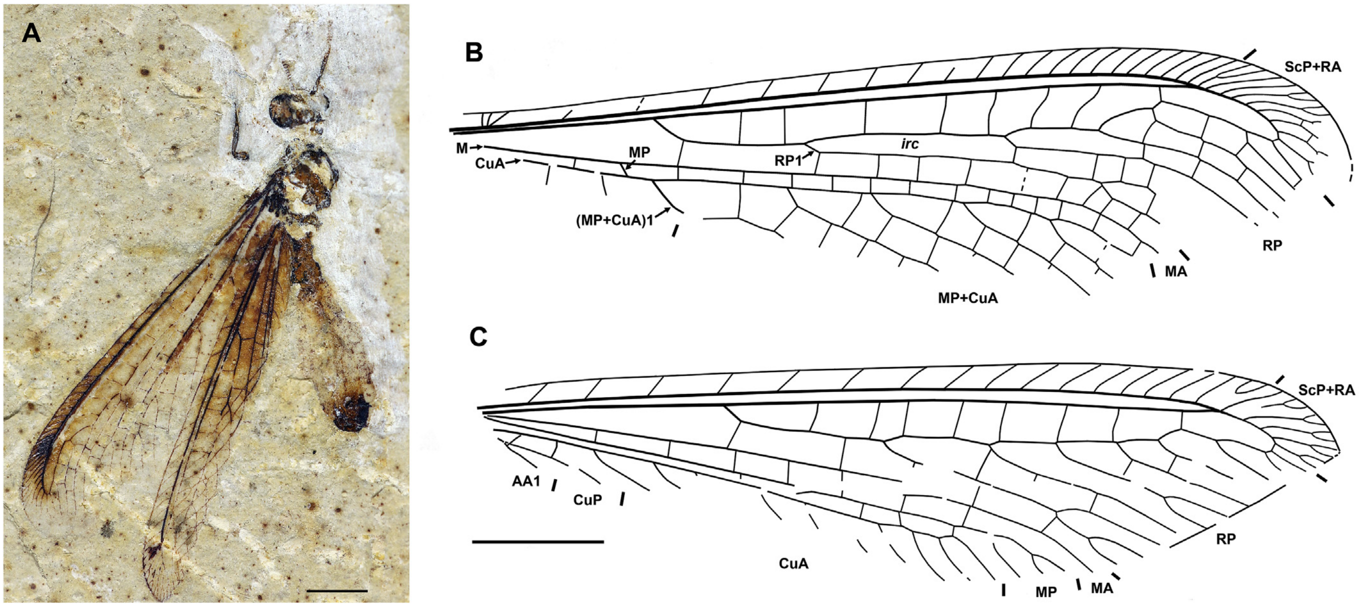

Fig. 7. *Araripeneura ?crassatella* (Martins-Neto and Vulcano, 1997), INHSP 1506. A, Specimen as preserved; B, Left forewing; C, Left hind wing. Scale bar represents 2 mm.

sinuous); one short crossveins detected thereafter. Hypostigmal cell long. No presectoral crossveins detected. RP originates moderately far from wing base (at 0.26 of wing length), with five branches. RP1 originates far from origin of RP, probably profusely branched (incompletely preserved); other branches apparently simple (their terminations not preserved). Crossveins between branches of RP not numerous, irregularly arranged; four detected between RP1, RP2; one to three between other branches; *irc* long, narrow. One crossvein between stem of RP, MA. M probably forked slightly proximad (MP+CuA)1 (poorly preserved). MA running parallel to anterior trace of MP+CuA. MP basally appears as oblique crossvein (poorly preserved) then fused with CuA. Anterior trace of MP+CuA with five pectinate preserved branches. (MP+CuA)1 originates opposite origin of RP, deeply forked. Crossveins between branches of CuA relatively numerous, regularly spaced. In intracubital space, two crossveins connecting CuA, CuP detected. CuP, AA1 not preserved.

Hind wing apparently with acute apex, ca. 14 mm long, ca. 3.4 mm wide (estimated). Costal space markedly broader than in forewing, dilated towards apex. Subcostal veinlets simple, widely spaced becoming increasingly more closely spaced to pterostigmal region. ScP, RA fused relatively far from wing apex. ScP+RA probably enters margin after wing apex. Veinlets of ScP+RA (except one) once forked; no crossvein between them. Subcostal space narrow; no crossveins detected. RA space moderately broad proximally, strongly narrowed at distal-most (short) crossvein before fusion of last ScP, RA; slightly narrower after this crossvein; with eight crossveins proximad fusion of ScP, RA; one crossvein thereafter. Hypostigmal cell elongate. RP originates far from wing base (at ca. 0.36 of wing length), with six branches. RP1 originates far from origin of RP, twice forked; other branches simple (except one which is once forked). Three crossveins between RP1, RP2; one between RP3, RP4 and RP4, RP5. Two crossveins between stem of RP, MA. M probably forked near wing base (incompletely preserved); MA simple, MP twice forked distally. Intramedial space rather broad, with at least seven crossveins. CuA strongly pectinate, with nineteen simple, moderately long branches. Mediocubital space clearly narrower than intramedial space, with several crossveins. Distal parts of CuP, AA1 simple.

Remarks. This specimen is assigned to *Araripeneura crassatella* due to the strong similarity of its venation to that of the holotype (see Martins-Neto and Vulcano, 1997, fig. 3). Particularly, the forewing of both specimens appears to be more elongate and has a more rounded apex than in *A. regia*, *A. damianii* and *A. urda*. The venation of *A. crassatella* is similar to that of *A. gracilis* (cf. Martins-Neto and Vulcano, 1989a, fig. 2). However, we cannot assign INHSP 1506 to *A. gracilis* as the configuration of its RA space differs somewhat from that of *A. crassatella*. In any case, the species attribution of this specimen is tentative.

Genus ***Caririneura*** Martins-Neto and Vulcano, 1989a

1989a *Caririneura* Martins-Neto and Vulcano, p. 378.

Type species. *Caririneura microcephala* Martins-Neto and Vulcano, 1989a, by original designation.

Revised diagnosis. Forewing oblanceolate (12.5–15.0 mm long); presectoral crossveins sometimes present; RA space strongly narrowed distally; *irc* short; (MP+CuA)1 deeply forked. Hind wing slightly longer than forewing; very slender proximally with acute apex; more than two presectoral crossveins; RP originating very far from wing base (at 0.40–0.50 of wing length); MP long, strongly pectinate; CuA short (terminated on hind margin far proximad origin of RP), pectinate.

Species included. C. microcephala and *C. macrothoracica* sp. nov. from the late Aptian Crato Formation of Brazil.

Remarks. The hind wing venation of *Caririneura* is very similar to that of *Cratopteryx nemopteroides* Martins-Neto, 2003: (1) all these species have a short CuA (long in other Araripeneuridae when CuA is preserved); (2) they possess presectoral crossveins (absent in other Araripeneuridae except apparently *Cratoneura dividens* Martins-Neto, 1994); (3) their hind wing is slightly longer than the forewing (shorter in other Araripeneuridae when the hind wing is complete). All these character states are certainly apomorphic at the family level. Therefore, it is probable that *Cratopteryx nemopteroides* belongs to *Caririneura*. However, the reexamination the type species of *Cratopteryx* (i.e., *C. robertosantosi*) is needed to decide whether or not these two genera are synonyms.

Caririneura macrothoracica sp. nov.
(urn:lsid:zoobank.org:act:5298ECCC-90DF-47E6-B7C6-EB3900F298E9)
Figs. 8, 9

Derivation of name. From the Greek *macros* [μακρος], long, and *thorax* [θώραξ], thorax, referring to long prothorax of the holotype.

Material. Holotype INHSP 1525. A nearly complete specimen in dorsal aspect, with all wings incompletely preserved and crumpled.

Type locality and horizon. Northeastern Brazil: Chapada do Araripe (precise locality unknown). Lower Cretaceous: upper Aptian (Crato Formation: Nova Olinda Member).

Diagnosis. Prothorax elongate [short in *C. microcephala*]. Forewing with proximal intraradial cell short, broad (triangular) [elongate, narrow in *C. microcephala*]; one–two presectoral crossveins [absent/not detected *C. microcephala*]; RP originating proximad origin of (MP+CuA)1. Hind wing with two–three presectoral crossveins [six in *C. microcephala*]; RP originates at 0.40 of wing length [at 0.50 in *C. microcephala*].

Description. Head poorly preserved, with only eyes visible, transverse in dorsal view; right antenna incompletely preserved (without apex). Prothorax elongate (ca. 1 mm long); rather broad in dorsal view, but markedly narrower than head. Legs relatively long, but lengths of their femora and tibiae impossible to measure due to preservation; tarsi not preserved. Abdomen slender (ca. 6 mm long), with most segments elongated; terminal segments without projections.

Forewing elongate-ovate or oblanceolate (crumpled), 12.2 mm long (as preserved; estimated complete length ca. 12.5 mm), 3.3 mm wide (as preserved; estimated complete width ca. 3.5 mm). Costal space narrow, apically wider. Subcostal veinlets simple, widely spaced. Subcostal space very narrow. Veinlets of ScP+RA rather dense, long. RA space wide for most length, strongly narrowed distally; with eight crossveins proximad fusion ScP, RA; hypostigmal cell long. Basal crossvein 1r-m oblique. One long presectoral crossvein in both wings; other short (more basal) crossvein in left wing. RP originates far from wing base (at 0.23 of estimated wing

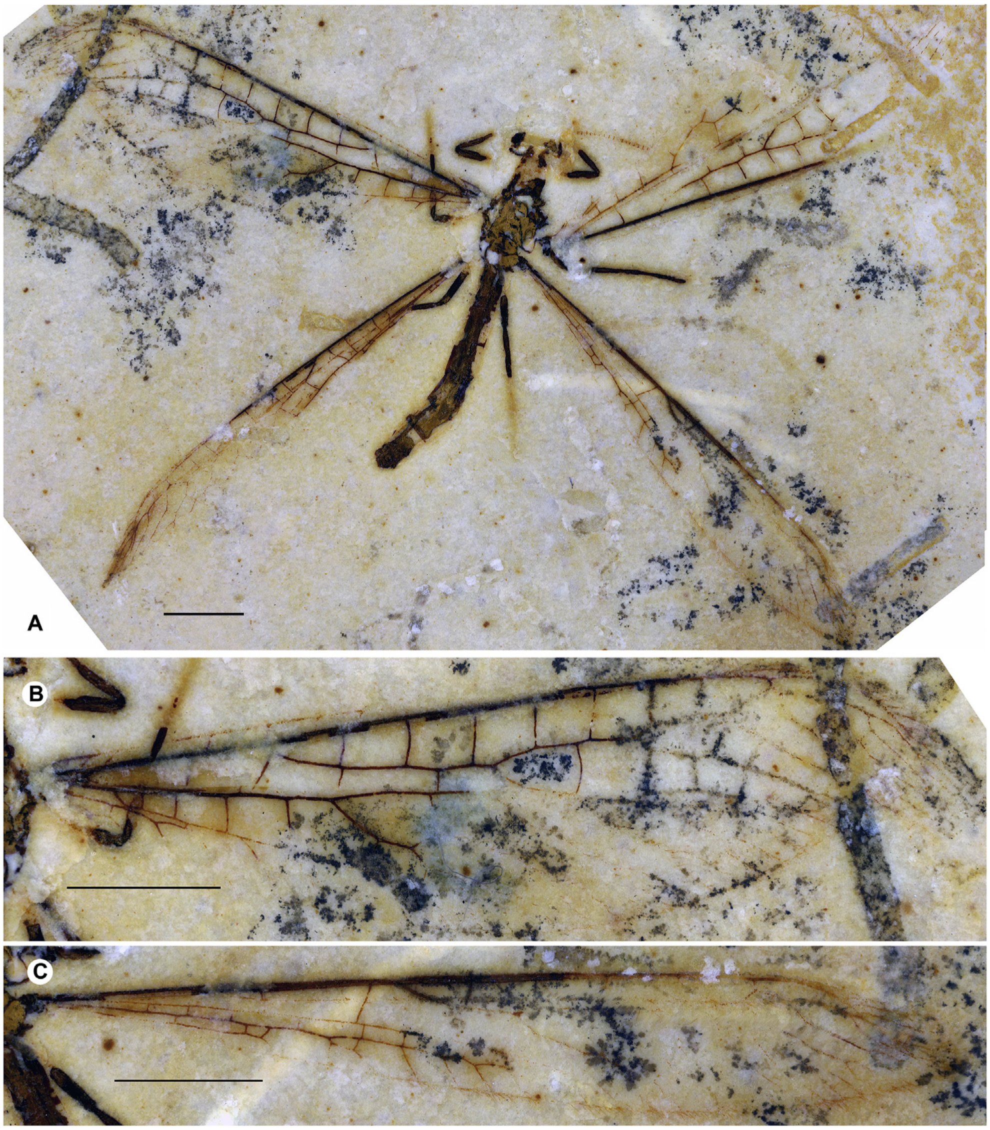

Fig. 8. *Caririneura macrothoracica* sp. nov., holotype INHSP 1525. A, Specimen as preserved (dorsal view). B, Left forewing (converted to right dorsal view). C, Right hind wing. Scale bars represent 2 mm.

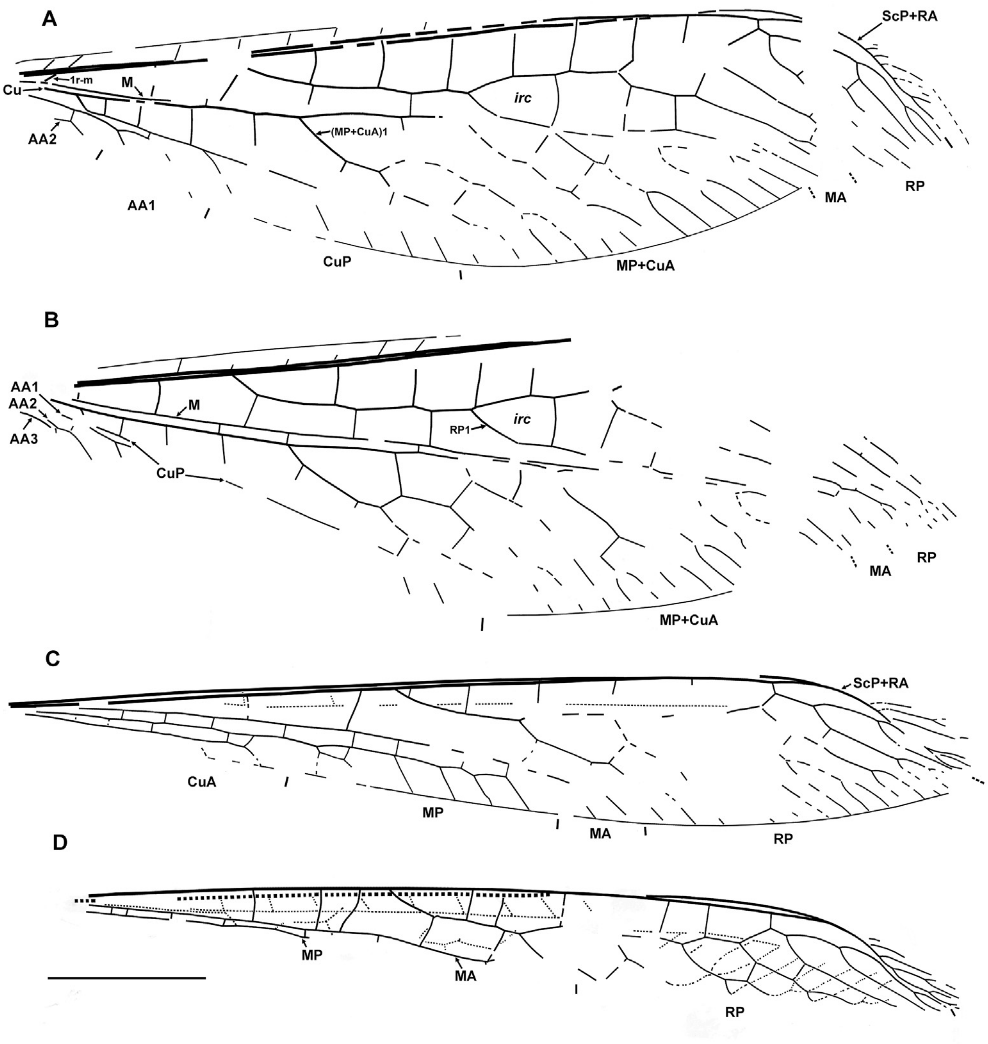

Fig. 9. Wing venation of *Caririneura macrothoracica* sp. nov., holotype INHSP 1525. A, Right forewing. B, Left forewing. C, Right hind wing. D, Left hind wing. Scale bar represents 2 mm (all to scale).

length), with seven branches. RP1 originates far from origin of RP. Crossveins between branches of RP poorly preserved, apparently not numerous; *irc* short, nearly triangular. Three crossveins between stem of RP, MA. M not fused basally with R; its fork not detected. M (then MA) running close to CuA (then anterior trace of MP+CuA); crossveins short, scarcely arranged, perpendicular to both veins. Cu dividing into CuA, CuP relatively close to wing base. MP+CuA with 5–6 pectinate branches; (MP+CuA)1 long, twice deeply forked; (MP+CuA)2 twice forked; (MP+CuA)3 to (MP+CuA) 5 once forked. One to two crossveins connect branches of MP+CuA. Six crossveins between CuP, CuA/(MP+CuA)1. CuP straight, probably with six simple pectinate branches. AA1 rather long, deeply forked. Between CuP, AA1 one crossvein detected, connecting CuP, anterior branch of AA1. Crossvein between AA1, AA2 long. AA2, AA3 probably simple; crossvein between these short.

Hind wing narrow, oblanceolate, ca. 12.6 mm long, ca. 2.2 wide. Costal space narrow basally, markedly wider apically. Preserved subcostal veinlets simple, widely spaced. Veinlets of ScP+RA rather dense, long, mostly apically forked. Subcostal space very narrow. RA space wide for most of length, strongly narrowed distally; with 6–7 crossveins proximad fusion ScP, RA; hypostigmal cell long. Two (right wing) or three (left wing) preserved presectoral crossveins. RP originates very far from wing base (at 0.40 of estimated wing length), with seven branches. RP1 originates rather far from origin of RP; all branches except distal-most once to twice rather deeply forked. Apparently one crossvein between proximal five/six branches of RP (three crossveins preserved in both hind wings). Two crossveins between stem of RP, MA. M forked very close to wing base (common stem not detected). MA apparently with two simple pectinate branches. MP pectinate, with 4–5 simple branches (right wing). Intramedial space narrow, with several widely spaces crossveins (eight detected in right wing). Five crossveins between MP, CuA. CuA running close and parallel to posterior margin; probably pectinate. CuP, anal veins not detected.

Remarks. The new species is similar to *Caririneura microcephala*, but clearly distinguished from it by the characters provided in the diagnosis. The holotype of *C. microcephala* is slightly larger than the holotype of *C. macrothoracica* (the forewing is 15 mm long, and the hind wing is 15.5 mm long), and its prothorax is much longer judging from the photograph (Martins-Neto and Vulcano, 1989a, fig. 20) and the drawing (Martins-Neto, 1992a, fig. 15D).

Genus ***Cratoneura*** Martins-Neto, 1992b

1992b *Cratoneura* Martins-Neto, p. 808.

Type species: *Cratoneura longissima* Martins-Neto, 1992b, by original designation.

Revised diagnosis. Forewing elongate (24–38 mm long), widest proximally or medially with narrow to strongly narrow distal part; presectoral crossveins absent; RA space abruptly narrowed distally; *irc* very long, narrow; (MP+CuA)1 deeply forked; branches of CuP sigmoidly curved basally. Hind wing broad proximally with acute apex; shorter than forewing; presectoral crossveins sometimes apparently present; CuA long, with long branches.

Species included. Cratoneura longissima, *C. pulchella* Martins-Neto, 1992b, *C. dividens*, and *C. minor* sp. nov. from the Crato Formation.

Remarks. The wing shape, size and venation of *Cratoneura* are very similar to those of *Cratoalloneura*, which is known from two species from the Crato Formation. The latter was created (as *Alloneura* Martins-Neto and Vulcano, 1989a, preoccupied name) for *Alloneura acuminata* represented by the holotype (CV-1181) and the paratype (CV-1182), of which only the holotype was figured (the body and the 'forewing': Martins-Neto and Vulcano, 1989a, figs. 5C, G). The 'forewing' is in fact a hind wing, while only a short basal part of the proper forewing is preserved. Later, Martins-Neto (1992b: 806) "amended" the diagnosis of the genus and described and figured a new specimen (UnG/1T-08) of *Cratoalloneura acuminata*, whose hind wing venation, however, is mostly unclear due to poor preservation. Subsequently, drawings of this specimen were erroneously indicated as drawn from the holotype (see Martins-Neto, 2000, figs. 6A, B). Later, three additional specimens were reported, all probably *sensu* Martins-Neto (1992b), without any description or figures of the hind wing venation: CV-2712 (Martins-Neto and Vulcano, 1997, figs. 2, 13), and MPFT-I-011, MPFT-I-012 (Martins-Neto, 2003, pl. II, figs, D, E). Thus, *Cratoalloneura acuminata sensu* Martins-Neto and Vulcano (1989a) and *C. acuminata sensu* Martins-Neto (1992b) may theoretically belong to two different taxa.

The genera *Cratoneura* and *Cratoalloneura* appear to be closely related or even synonyms. They differ from each other principally by the distance between origins of RP and RP1: RP1 originates far from the origin of RP in *Cratoneura* and close to it in *Cratoalloneura.*

Cratoneura dividens Martins-Neto, 1994

Fig. 10

1994 *Cratoneura dividens* Martins-Neto, p. 275, figs. 3A, D, 5; pl. I, fig. A.

Material examined: Holotype INHSP 1522. An incomplete specimen in lateral aspect, with all wings incompletely preserved; hind wings crumpled.

Diagnosis. Most similar to *C. minor* sp. nov., but distinctly larger (forewing 34–38 mm long); posterior margin of forewing distinctly concave [only slightly concave distally in *C. minor* sp. nov.]; medial subcostal veinlets of forewing strongly curved [slightly curved in *C. minor* sp. nov.,].

Description of specimen INHSP-1522. Head and thorax poorly preserved; details not visible. Hind-legs relatively long: femur moderately stout, ca. 4 mm; tibia slender, slightly swollen medially, >4 mm long. Abdomen ca. 13 mm long; terminal segments lacking any special prolongations, appendages or projections.

Forewing 32 mm long as preserved (estimated complete length ca. 33.5–34 mm), 8.0 mm wide at maximal curvature of posterior margin (length/width ratio 4.19–4.25); strongly dilated in proximal one-quarter (maximal curvature of posterior margin at 0.26–0.27 of estimated wing length), narrowed toward apex. Costal space very narrow basally, dilated towards mid-point, and then slightly narrowed towards distal crossvein between ScP+RA, RP. Subcostal veinlets simple, relatively closely spaced except basally; strongly curved slightly distad most dilated part of costal space. ScP, RA fused far from wing apex. Pterostigma not detected. ScP+RA enters margin well after wing apex. Veinlets of ScP+RA long, strongly bent, mostly once forked distally, except three distal veinlets, which are parallel to costal margin and profusely branched; three-four most distal veinlets connected with each other by short crossvein (twp-three detected) forming one gradate series. Subcostal space narrow; no crossveins detected. RA space broad in proximal two-thirds, strongly narrowed in distal one-thirds; with 19 crossveins proximad fusion of ScP, RA, two short crossveins thereafter. Hypostigmal cell very long, narrow. No presectoral crossveins detected. RP originates relatively close to wing base (at 0.14–0.16 of estimated wing length), with 13–14 branches. RP1 originates very far from origin of RP, pectinately branched, with three long branches (of these, one-two deeply forked); RP2–RP8, RP10 once deeply forked; RP9, RP11–13 simple (left wing). Crossveins between branches of RP rather numerous, irregularly spaced; outer gradate series of crossveins distinct, consisting of ten crossveins (left wing); *irc* long, narrow. Three crossveins detected between stem of RP, MA; seven between RP1, MA. M dividing into MA, MP proximad (MP+CuA)1. Anterior trace of MA very close and parallel to anterior trace of MP+CuA; deeply forked distally, with two pectinate branches (one of them deeply forked). Crossveins between MA, anterior trace of MP+CuA numerous, very short. Basal part of MP crossvein-like, distinctly oblique. Anterior trace of MP+CuA with nine pectinate branches. (MP+CuA)1 originates slightly proximad origin of RP, very deeply forked; other branches mainly once rather deeply forked. Crossveins between branches of MP+CuA rather regularly, widely spaced. Seven crossveins detected in intracubital space: two connecting CuA, CuP, and five-six connecting (MP+CuA)1, CuP. CuP parallel to posterior margin for most length, strongly pectinate; with six long simple branches, four of which sinuous basally. AA1 deeply forked. One distal crossvein connecting CuP, anterior branch of AA1 detected.

Hind wings strongly crumpled.

Remarks. The forewing venation, shape and size of the specimen INHSP-1522 is similar to those of others specimens from the Nova Olinda Member of the Crato Formation assigned to this species (including the holotype) whose forewings are 37–38 mm long (see Martins-Neto, 1994, 1997, 2003). The specimen SMNS 66000/265 (forewing is 38 mm long), also from the Nova Olinda Member, certainly belongs to this species. Therefore, *Cratoneura dividens* is rather common in this member.

Cratoneura minor sp. nov.

(urn:lsid:zoobank.org:act:2384E836-892B-48A4-B906-567A662B40C5)

Fig. 11

Derivation of name. From the Latin *parvus* [-a, -um] (comparative *minor*), small (smaller), in the reference to smaller size in comparison to that of closely related *Cratoneura dividens*.

Material examined: Holotype INHSP 1523. A very incomplete specimen in dorsal aspect, with head, thorax and two outspread forewings preserved.

Diagnosis. Most similar to *C. dividens*, but distinctly smaller (forewing 24.5 mm long); posterior margin of forewing only slightly concave distally [distinctly concave in *C. dividens*]; medial subcostal veinlets of forewing slightly curved [strongly curved in *C. dividens*].

Description of specimen INHSP-1523. Head transverse in dorsal view. Prothorax appears short, narrow. Mesothorax moderately large.

Forewing 24.5 mm long, 6.5 mm wide at maximal curvature of posterior margin (length/width ratio 3.77); rather strongly dilated in proximal one-third (maximal curvature of posterior margin at 0.35 of wing length), narrowed toward apex. Costal space narrow

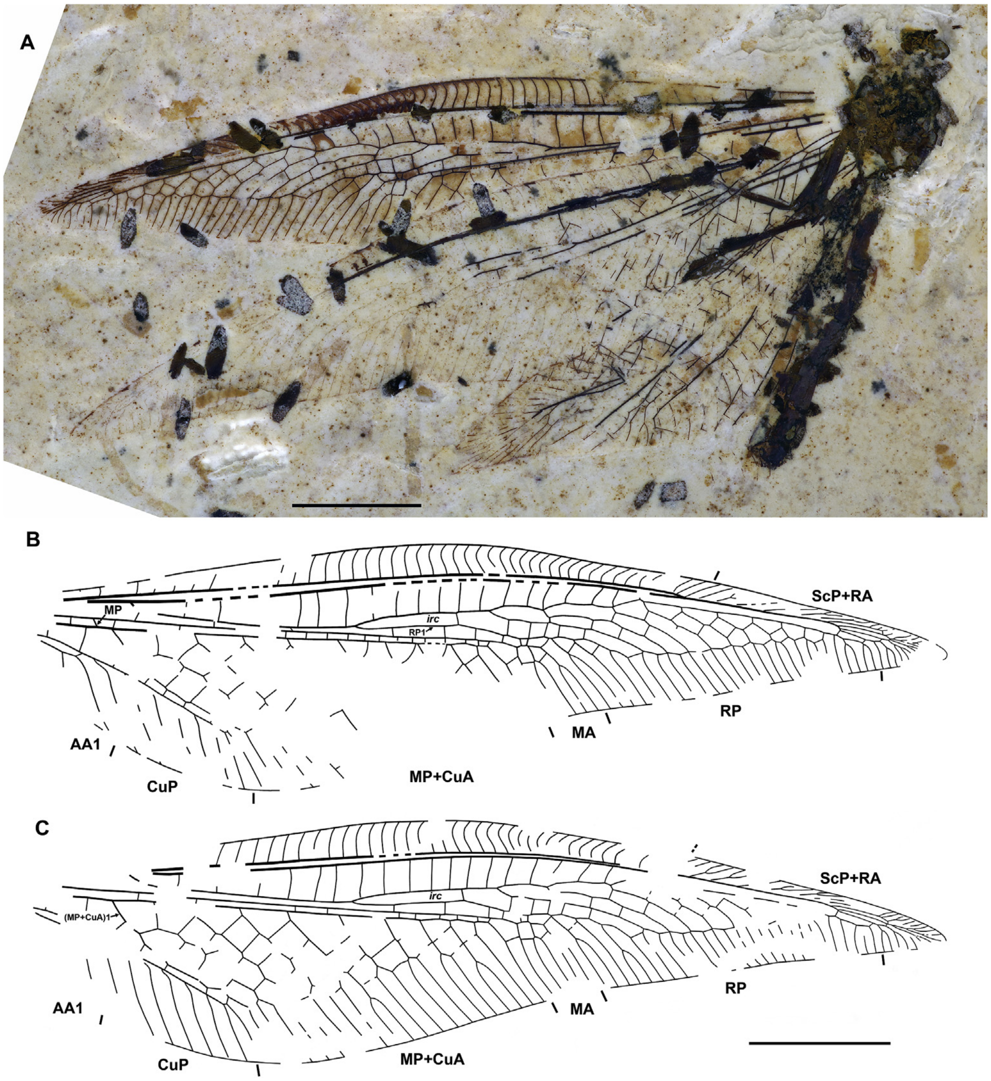

Fig. 10. *Cratoneura dividens* Martins-Neto, 1994, INHSP 1522. A, Specimen as preserved. B, Left forewing. C, Right forewing. Both converted to right dorsal view. Scale bars represent 5 mm (B, C to scale).

basally, yet narrowed towards origin of RP, then dilated towards mid-point, and then slightly narrowed after this maximum width; equally moderately broad in distal part. Subcostal veinlets simple, relatively closely spaced except basally; slightly curved in most dilated part of costal space. ScP, RA fused far from wing apex. Pterostigma not detected. ScP+RA enters margin well after wing apex. Veinlets of ScP+RA long, strongly bent, mostly simple, except three-four distal veinlets, which are parallel to costal margin and deeply forked or profusely branched; four most distal veinlets connected with each other by short crossvein (three detected in left wing) forming one gradate series. Subcostal space narrow; no crossveins detected. RA space broad in proximal 3/4, strongly narrowed in distal one-fourth; with 16 crossveins proximad fusion of ScP, RA, two short crossveins thereafter. Hypostigmal cell long, narrow. No presectoral crossveins detected. RP originates moderately far from wing base (at 0.20 of wing length), with eleven branches. RP1 originates very far from origin of RP, pectinately branched, with two-three long branches (of these, one deeply forked in each wing); other branches mainly simple (two (right wing) and three (left wing) forked)). Crossveins between branches of RP irregularly spaced; outer gradate series of crossveins consists of eight crossveins (left wing), arranged irregularly; *irc* elongate. Two crossveins detected between stem of RP, MA; five–six between RP1, MA. M dividing into MA, MP proximad (MP+CuA)1. Anterior trace of MA very close and parallel to anterior trace of MP+CuA; deeply forked distally, with two deeply forked pectinate branches (one simple in right wing). Crossveins between MA, anterior trace of MP+CuA numerous, very short. Basal part of MP crossvein-like, distinctly oblique. MP+CuA with eight pectinate branches; (MP+CuA)1 originates slightly proximad origin of RP, very deeply forked; other branches (except distal-most) once rather deeply forked. Crossveins between branches of MP+CuA rather regularly, widely spaced. Six crossveins detected in intracubital space: two connecting CuA and CuP, and four connecting (MP+CuA)1 and CuP. CuP parallel to posterior margin for most length, strongly pectinate; with six long simple branches. AA1 deeply forked.

Remarks. Both species have rather similar forewing shape, but they are distinguished from each other as indicated in the diagnoses. The other two species of the genus (i.e., *Cratoneura longissima* and *C. pulchella*) have relatively narrow forewings, at least not distinctly dilated either basally or medially.

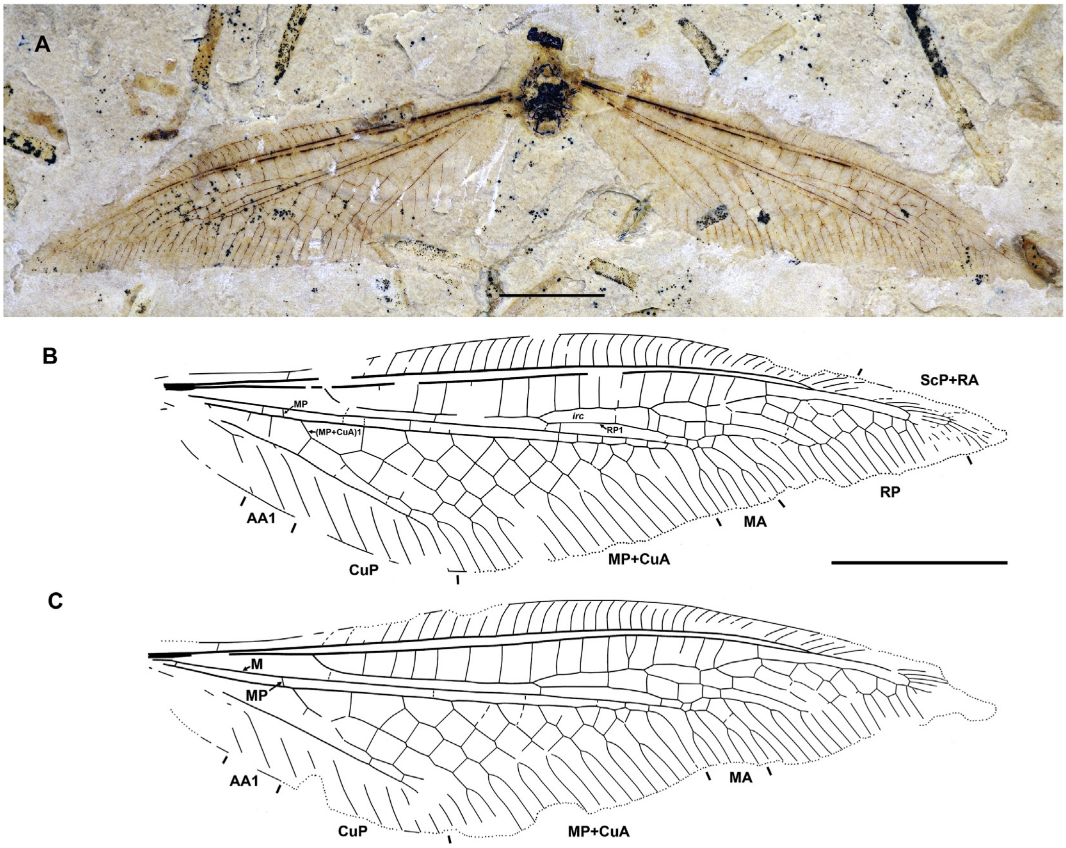

Fig. 11. *Cratoneura minor* sp. nov., holotype INHSP 1523. A, Specimen as preserved. B, Left forewing (converted to right dorsal view). C, Right forewing. Scale bars represent 5 mm (B, C to scale).

The Myrmeleontoidae stem group "Pseudonymphidae" Martins-Neto, 1990

Diagnosis. May be characterized by the following character states: *icr* short; MP forked distad or at origin of CuA1, and far distad origin of RP; M/MA runs clearly more distant from CuA/anterior trace of MP+CuA than in Araripeneuridae; origin of CuA1 located far distad origin of RP; MP+CuA space relatively narrow; AA1 simple (unknown in *Pseudonymphes*).

Genera included. Choromyrmeleon (Barremian/Aptian Yixian Formation of China), *Blittersdorffia*, *Pseudonymphes* (both from the late Aptian Crato Formation of Brazil) and *Burmaneura* (mid-Cretaceous Burmese amber).

Remarks. These four Cretaceous genera belong to neither Araripeneuridae nor "Palaeoleontidae," but are more similar to the latter. In particular, the forewing venation of *Blittersdorffia dicotomica* Martins-Neto, 1990 is especially similar to that of some "Palaeoleontidae" (see Martins-Neto, 1990, fig. 1C). So, this species requires re-examination as it perhaps belongs to the latter family.

The taxonomic status of this group remains uncertain. It has some common features in the venation (see diagnosis) which may theoretically support its monophyly. On the other hands, the genera *Choromyrmeleon* and *Pseudonymphes* are different enough to believe that this taxon is paraphyletic. Here, it is called the Myrmeleontoidae stem group "Pseudonymphidae" pending further taxonomic examination. "Pseudonymphidae" seems to be a stem group of Myrmeleontidae + Ascalaphidae.

Genus ***Pseudonymphes*** Martins-Neto and Vulcano, 1989a

1989a *Pseudonymphes* Martins-Neto and Vulcano, p. 376.

Type species. *Pseudonymphes araripensis* Martins-Neto and Vulcano, 1989a, by original designation.

Revised diagnosis. Forewing elongate (14–15 mm long), M forked far distad origin of RP; MP fused with CuA for short distance or not fused (connected by crossvein); trichosors present along apical margin before apex in fore- and hind wings. Hind wing: MP pectinate, with several branches; CuA strongly pectinate; CuP probably simple or few branched.

Species included. Pseudonymphes araripensis, *P. ponomarenkoi* Martins-Neto, 1992a, *P. brunherottae* Martins-Neto, 1994, and ? *P. zambonii* Martins-Neto, 1998 from the Crato Formation.

Remarks. The three former species are surely closely related, and may in principle belong to one species, if its venation is variable. The holotypes of all these species require reexamination.

P. zambonii is distantly related to the others (its forewing is 6 mm). This species probably belongs to a distinct genus, and its character states are not included in the diagnosis of *Pseudonymphes*.

Pseudonymphes ?araripensis Martins-Neto and Vulcano, 1989a
Figs. 12, 13

1989a *Pseudonymphes araripensis* Martins-Neto and Vulcano, p. 376, figs. 4, 18.

Material. Specimen INHSP 1526. An incomplete specimen preserved in lateral aspect, with left and right wings partially overlapping pairwise.

Locality and horizon. Northeastern Brazil: Chapada do Araripe (precise locality unknown). Lower Cretaceous: upper Aptian (Crato Formation: Nova Olinda Member).

Diagnosis. Forewing MP fused with CuA for a short distance.

Fig. 12. *Pseudonymphes ?araripensis* Martins-Neto and Vulcano, 1989a, INHSP 1526. A, Specimen as preserved. B, Presumable trichosors (tr) along apical margin of right forewing. Scale bars represent 2 mm (A), 0.5 mm (B).

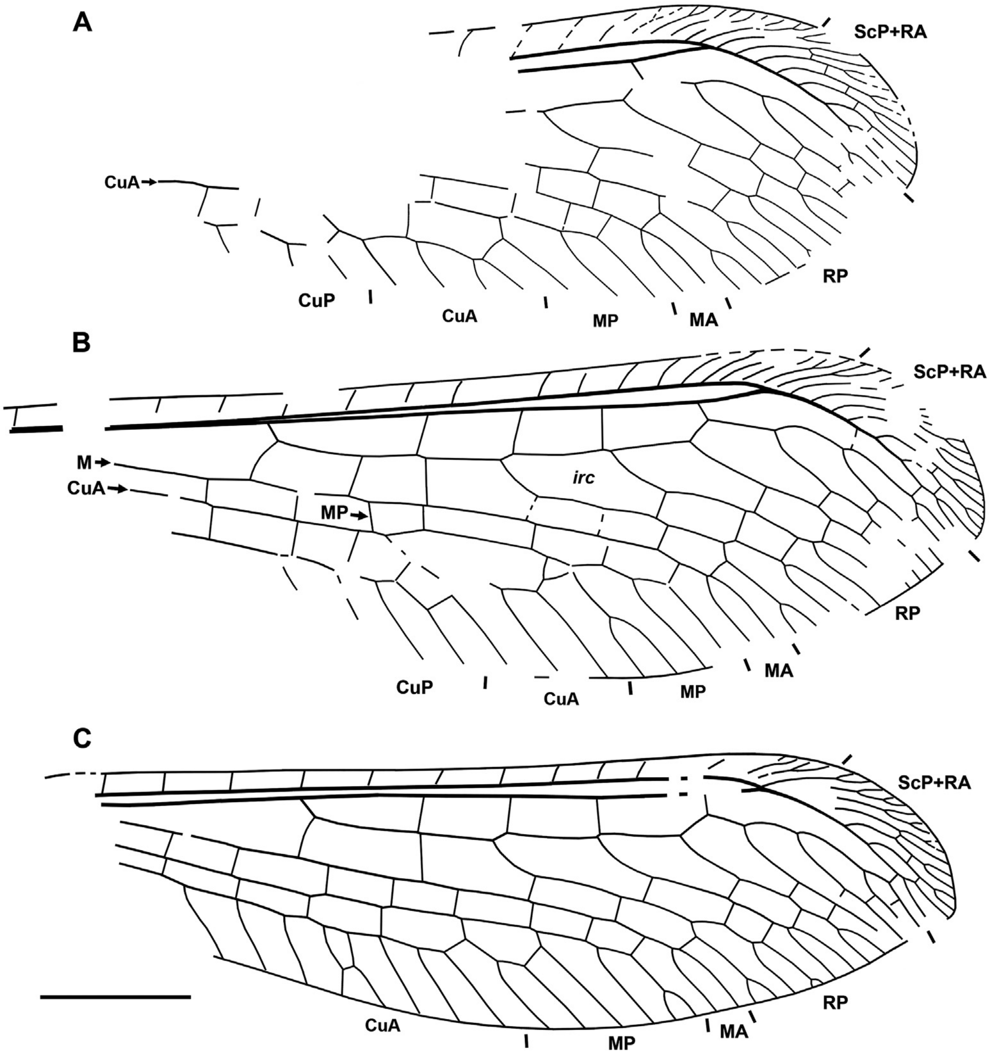

Fig. 13. Wing venation of *Pseudonymphes ?araripensis* Martins-Neto and Vulcano, 1989a, INHSP 1526. A, Left forewing (converted to right dorsal view). B, Right forewing. C, Right hind wing. Scale bar represents 2 mm.

Description. Body poorly preserved; details not visible. Antennae, legs not preserved.

Forewing elongate, ca. 14 mm long, 4.1 mm wide (length/width ratio 3.42). Trichosors detected along apical margin (before apex) in right forewing (Fig. 11B). Costal space narrow, wider apically. Subcostal veinlets simple widely spaced, becoming increasingly more closely spaced to pterostigmal region; forked in pterostigmal area. ScP, RA fused far from wing apex. ScP+RA enters margin slightly after wing apex. Subcostal space appears narrow proximally, moderately broad distally. Pterostigma dark, rounded, relatively small, located in area of fusion of ScP, RA. Veinlets of ScP+RA rather dense, long, once forked; distal veinlets connected by crossveins forming one gradate series (five crossveins preserved in right forewing). RA space moderately wide proximally, slightly narrowed distally; with four crossveins proximad fusion ScP, RA, two poorly-preserved crossveins distad fusion in right forewing; hypostigmal cell long. No presectoral crossveins detected. RP originates far from wing base (at ca. 0.32 of estimated wing length), with six branches. RP1 originates far from origin of RP; dichotomously branched distally; RP2, RP3 once rather deeply forked; RP4–RP6 simple. Crossveins between branches of RP scarce: three between RP1, RP2; two between RP2 to RP5; one between RP5, RP6; *irc* pentagonal. Three crossveins between stem of RP, MA; four between RP1, MA. M forked far distad origin of RP. MA once deeply forked terminally. M (then MA) running rather distant from CuA (then anterior trace of MP). MP basally looks as long crossvein then fused for short distance with CuA; distally with two pectinate long branches (proximal branch deeply-forked in right forewing). Four crossveins in intramedial space. Crossveins between M, CuA, and MA, anterior trace of MP relatively long, scarcely arranged, nearly perpendicular to both veins. Anterior trace of CuA bent porteriorly after fusion with MP; with two simple (right forewing) or three (left forewing) pectinate branches. Between MP, CuA two crossveins (distal crossvein in right forewing abnormally bifurcated near MP). Five preserved crossveins between CuP, CuA. CuP pectinately branched, with three preserved branches. Anal veins not preserved.

Hind wing elongate, ca. 13.0 mm long, 3.5 mm wide. Costal space similar to that of forewing, but slightly narrower. Subcostal veinlets simple, widely spaced. ScP, RA fused far from wing apex. ScP+RA enters margin distinctly after wing apex. Veinlets of ScP+RA rather dense, long, once to twice forked. Subcostal space narrow; moderately broad distally. RA space similar to that of forewing; with four crossveins proximad fusion ScP, RA, one distad fusion; hypostigmal cell very long. No presectoral crossveins. RP originates very far from wing base (at ca. 0.33 of estimated wing length), with six branches. RP1 originates rather far from origin of RP, dichotomously branched; RP2, RP3 once forked; other branches simple. Crossveins between branches of RP rather scarce (ten in total): three between RP1, RP2; two between RP2 to RP4; one between RP4 to stem of RP. Two crossveins between stem of RP, MA; three between RP1, MA. Fork of M not preserved. MA once rather deeply forked terminally. Anterior trace of MP terminally forked, pectinate with three branches (proximal branch deeply forked, other branches simple); one crossvein connects anterior branch of MP1, MP2. Intramedial space with several widely spaced crossveins (eight detected in right wing). Five crossveins between MP, CuA; distal-most crossvein connects MP1, CuA. CuA parallel to posterior margin; strongly pectinate, with seven simple, rather long branches; one crossvein between branches of CuA, probably representing aberration. CuP, anal veins not preserved.

Remarks. The specimen INHSP 1526 is assigned to *Pseudonymphes araripensis* based on close concordance with the specimen CV-1501, which is treated as *P. araripensis* nov. *sensu* Martins-Neto (1992a, fig. 11C). Probably, the forewing of the holotype was inadequately figured (see Martins-Neto and Vulcano, 1989a, fig. 4). This assignment is preliminary.

Pseudonymphes ?brunherottae Martins-Neto, 1994

Fig. 14

1994 *Pseudonymphes brunherottae* Martins-Neto, p. 274, figs. 2B, C; pl. II, fig. C.

Material. Specimen SMNS 66000/256. A nearly complete specimen preserved in dorso-ventral aspect, with left and right wings nearly fully overlapping pairwise.

Locality and horizon. Northeastern Brazil: Chapada do Araripe (precise locality unknown). Lower Cretaceous: upper Aptian (Crato Formation: Nova Olinda Member).

Diagnosis. Forewing MP not fused with CuA, connected via short crossvein.

Description. Head transverse-oval in dorsal view; antennae strongly clavate, ca. 4.5 mm long. Prothorax very short. Mesothorax rather large. Legs not preserved. Abdomen short (ca. 5.5 mm long), rather stout dorsally; apex rounded; terminal segments lacking any appendages, projections.

Forewing elongate, slightly falcate, ca. 14.2 mm long, ca. 4.2 mm wide (length/width ratio 3.38). Costal space narrow, wider apically. Subcostal veinlets simple widely spaced, becoming increasingly more closely spaced to pterostigmal region. ScP, RA fused far from wing apex. ScP+RA enters margin well after wing apex. Pterostigma dark, large. Subcostal space appears narrow proximally, moderately broad distally. Veinlets of ScP+RA rather dense, long (poorly-preserved); no crossveins between these detected. RA space moderately wide proximally, slightly narrowed distally; with five crossveins proximad fusion ScP, RA, one poorly-preserved crossveins distad fusion in right wing; hypostigmal cell very long. No presectoral crossveins detected. RP originates far from wing base (at ca. 0.28 of estimated wing length), with five branches. RP1 originates far from origin of RP; dichotomously branched distally; RP2–RP4 once forked; RP5 simple. Crossveins between branches of RP: three between RP1, RP2; one preserved between RP2, RP3; two between RP3, RP4; one between RP4, RP5; *irc* pentagonal. Three crossveins between stem of RP, MA; four between RP1, MA. M forked far distad origin of RP. MA once deeply forked terminally. MP not fused with CuA, basally connected with this by short crossvein; distally with two pectinate long branches. Four crossveins in intramedial space. Anterior trace of CuA bent porteriorly after proximal crossvein connecting MP, CuA, shallowly forked terminally; with three simple pectinate branches. Between MP, CuA three crossveins; distal crossvein in right wing connects MP1, CuA. Six preserved crossveins between CuP, CuA. CuP with five pectinately branches. Anal veins poorly preserved with no details recognizable.

Hind wing elongate, slightly falcate, ca. 13.3 mm long, 3.7 mm wide. Poorly-preserved trichosors detected along apical margin (before apex), similar to those in forewing of *Pseudonymphes ?araripensis*. Costal space similar to that of forewing, but slightly narrower. Subcostal veinlets simple, widely spaced. ScP, RA fused far from wing apex. ScP+RA enters margin well after wing apex. Pterostigma dark, large. Veinlets of ScP+RA rather dense, long, once to twice forked. Subcostal space narrow; moderately broad distally. RA space similar to that of forewing; with four crossveins proximad fusion ScP, RA, one distad fusion; hypostigmal cell very long. No presectoral crossveins. RP originates far from wing base (at ca. 0.29 of estimated wing length), with five branches. RP1 originates rather far from origin of RP, dichotomously branched; others once forked, except one in each wing (RP4 in left wing; RP5 in right wing). Crossveins between branches of RP rather scarce (nine to ten in total): three (left wing), four (right wing) between RP1, RP2; two

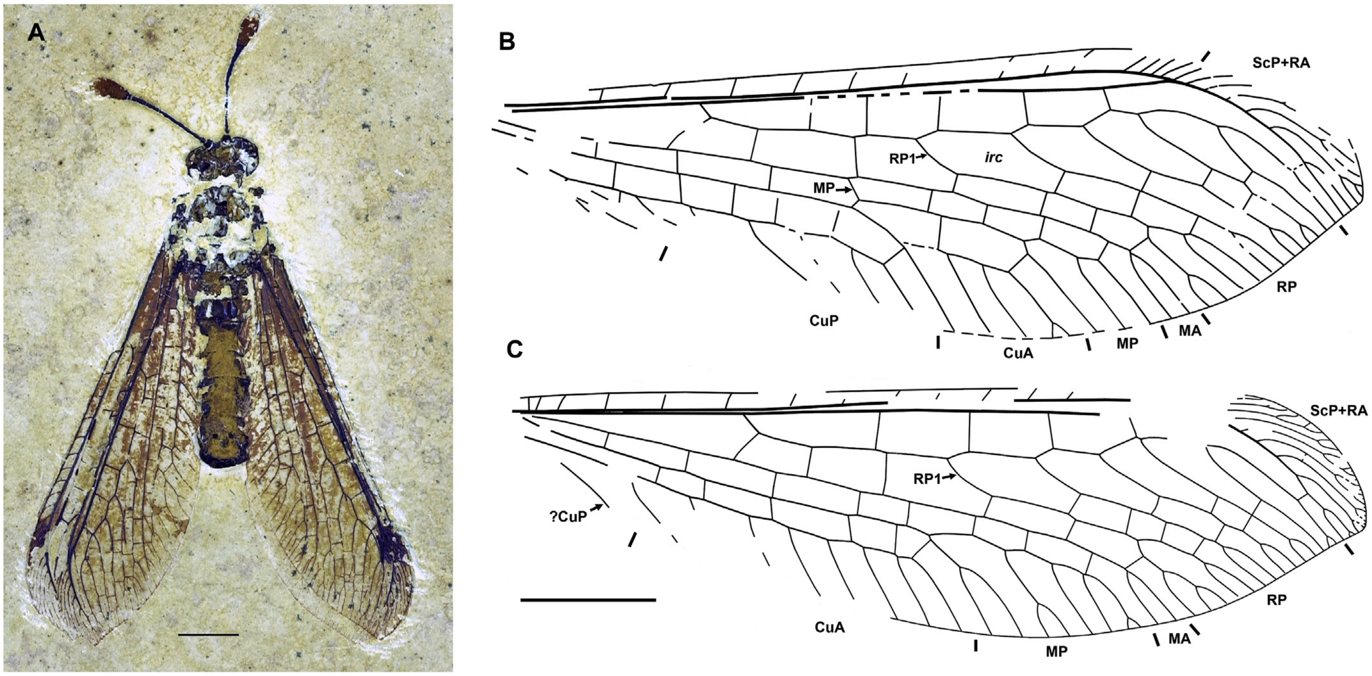

Fig. 14. *Pseudonymphes ?brunherottae* Martins-Neto, 1994, SMNS 66000/256. A, Specimen as preserved. B, Right forewing. C, Right hind wing. Scale bars represent 2 mm.

between RP2, RP3 and RP3, RP4; one between RP4, RP5, and RP5, stem of RP in left wing. Three crossveins between stem of RP, MA; three between RP1, MA. M forked near wing base, common stem not detected. MA once rather deeply forked terminally. Anterior trace of MP terminally shallowly forked, pectinate with four (right wing) or three branches (left wing); MP1 deeply forked (right wing), dichotomously forked (left wing); MP2 once forked; other branches simple; one crossvein connecting MP1, MP2 in left wing. Intramedial space with eight widely spaced crossveins (right wing). At least six crossveins between MP, CuA; distal-most crossvein connects MP1, CuA. CuA parallel to posterior margin; strongly pectinate, with seven simple, rather long branches. CuP incomplete (one branch preserved). Anal veins not preserved.

Remarks. The holotype is a single specimen, which is very poorly preserved. The assignment of specimen SMNS 66000/256 is based on MP not being fused with CuA (see Martins-Neto, 1994, fig. 2C). Nevertheless, this assignment is preliminary.

4. Discussion

4.1. Diagnostic characters of Araripeneuridae

The Araripeneuridae in its current composition is obviously a heterogeneous taxon. In this paper, the family is restricted to only those genera which may theoretically constitute a monophyletic taxon. The above diagnosis of the family pertains to this set of genera. The following genera are removed from the family: *Blittersdorffia*, *Pseudonymphes*, and *Burmaneura* (considered separately below).

The genital segments of Araripeneuridae (especially 9th tergite, ectoproct, 9th sternite, gonocoxite 9) are generalized (plesiomorphic), i.e., lacking special prolongations, appendages, projections, etc. So, it is often hard to understand to which sex each specimen belongs, because boundaries of genital segments are usually poorly discernible. The structure of these abdominal segments can help little in understanding the affinities of the family.

An analysis of the characters of *Paracroce*, the oldest known araripeneurid genus, is important. Its venation is in general typical for the family, but many character states are plesiomorphic at family level, e.g., the proximal intraradial cell is short, RP originates relatively close to the wing base; the branches (MP+CuA)1 and (MP+CuA)2 are nearly parallel (i.e., the false or real deep bifurcation of (MP+CuA)1 is absent, see below). The fork of M in this genus may be easily determined by the presence of the well-preserved ‘oblique vein’. The fusion of the distal part of MP (i.e., distad ‘oblique vein’) and CuA is complete. It means that this fusion in this lineage has occurred before the Barremian/Aptian.

No venational autapomorphy of the family is found. Nevertheless, the characteristic venation pattern of all included species strongly suggests their forming a distinct family. Below, several character states found in Araripeneuridae which are most important for the diagnosis of the family are analyzed.

4.1.1. Presectoral crossveins

Among Myrmeleontoidae, the presence of presectoral crossveins (i.e., between R and M/MA proximad the origin of RP and distad the basal crossvein 1r-m) is characteristic of all taxa of Myrmeleontidae, Ascalaphidae and Nemopteridae, and clearly apomorphic. At least in Myrmeleontidae, the number of these crossveins is of taxonomic value (see e.g., Stange, 1994). However, presectoral crossveins are absent in most Araripeneuridae (except for a few species), all “Palaeoleontidae” and “Pseudonymphidae”.

In Araripeneuridae, both species of *Caririneura* possess three-six presectoral crossveins in the hind wing, and *C. macrothoracica* sp. nov. one presectoral crossvein in the forewing. Besides this genus, one presectoral crossvein was reported in the forewing of *Cratoalloneura verdandia* (see Martins-Neto, 2003, fig. 2D), one in the hind wing of *Cratoneura dividens* (see Martins-Neto, 1994, fig. 2E), and three in the hind wing of *Cratopteryx nemopteroides* (see Martins-Neto, 2003, fig 1B). We have assumed above that *C. nemopteroides* may belong to *Caririneura*. Therefore, presectoral crossveins are present only in genera with more specialized venation and wing shape, i.e., *Caririneura* (strongly narrowed and elongated hind wings), *Cratoalloneura* and *Cratoneura* (peculiar shape of the forewing). We may reasonably assume that presectoral crossveins might have evolved independently several times within the family Araripeneuridae. Their absence in genera with more generalized venation (e.g., *Paracroce* and *Araripeneura*), as well as in most other Cretaceous Myrmeleontoidae, probably indicates that this condition is plesiomorphic for Araripeneuridae (see also Makarkin et al., 2017).

4.1.2. Interrelation between MP and CuA in the forewing

In all Araripeneuridae, in which the forewing is well preserved, the basal part of MP is oblique and crossvein-like, then entirely fused with CuA. This basal part of MP is most clearly visible in *Paracroce altaica* (see Fig. 1). In a few species, MP cannot be confidently identified (see e.g., Fig. 8B). The fusion of MP and CuA in all Araripeneuridae (as well as in all Nemopteridae) is shifted proximad the proximal-most branches of the apparent MP+CuA; the latter (i.e., (MP+CuA)1) is obviously homologous with CuA1 in those taxa where the fusion of MP and CuA is shifted distad the first branch of CuA (e.g., in the vast majority of Myrmeleontidae).

In general, all families of Myrmeleontoidae are characterized by the fusion of MP and CuA in the forewing (except for some *Pseudonymphes* and possibly *Burmaneura*). Early stages of this fusion are detected in some Early Cretaceous palaeoleontid genera (e.g., *Parapalaeoleon* Menon and Makarkin, 2008 and *Guyiling* Shi et al., 2012), where MP is fused with CuA only for a short distance. *Guyiling jianboni* Shi et al., 2012 is the only known species within Myrmeleontoidae where both the branched CuA1 and the distal part of CuA are well preserved (see Shi et al., 2012, fig. 2C, D). In *Parapalaeoleon*, it is unclear if a profusely branched vein (the proximal branch of MP+CuA in Menon and Makarkin, 2008, fig. 4B) represents CuA1 or the whole CuA. In *Choromyrmeleon*, this fusion is at a more advanced stage, where MP is completely fused with CuA, but the branched CuA1 is still existing (Ren and Guo, 1996, fig. 9; Ren and Engel, 2008, fig. 4). This condition is retained in some Myrmeleontidae, both fossil (Makarkin, 2017, fig. 5) and extant (e.g. Stange, 1994, fig. 15).

Araripeneuridae belong to a group where this fusion is complete and in which CuA1 is not heavy branched, at most once deeply forked (see also below). Besides this family, this state occurs in Nemopteridae, Ascalaphidae, and some Myrmeleontidae.

4.1.3. Proximal-most branch of MP+CuA in the forewing

The apparent (MP+CuA)1 is deeply forked and each branch is usually shallowly forked once in most genera of Araripeneuridae (see Figs. 3A, B; 4B; 8A, B; 9C; 10B, C). Such a condition of the apparent (MP+CuA)1 is also characteristic of most Nemopteridae. However in *Paracroce altaica* and *Cratopteryx nemopteroides*, the deep fork of (MP+CuA)1 is absent and this branch is nearly parallel to (MP+CuA)2 (Fig. 2B; Martins-Neto, 2003, fig 1B). In some extant Nemopteridae, the deep fork of (MP+CuA)1 is also indistinct (e.g., Tjeder, 1967, fig. 1922) or absent (e.g., Tjeder, 1967, figs. 2136, 2139). It is unclear yet if this deep bifurcation of (MP+CuA)1 is primarily in both families or is a result of strong transformation of the two proximal branches of MP+CuA to form a false deep bifurcation of the apparent branch (MP+CuA)1. If the first, then the deep bifurcation of (MP+CuA)1 is an important synapomorphy of Araripeneuridae and Nemopteridae. The second scenario may be hypothesized as follows: (MP+CuA)2 is basally directed towards (MP+CuA)1 and touched the proximal crossvein between (MP+CuA)1 and (MP+CuA)2 which is directed to the wing apex, and (MP+CuA)1 is slightly curved distad that crossvein. This may be supported by the fact that the deep bifurcation of (MP+CuA) in the majority of Nemopteridae from the Crato Formation is indistinct or absent (e.g., Martins-Neto and Vlucano, 1989a, fig. 10A; Martins-Neto et al., 2007, figs. 11.64c, f). In this case, the condition of (MP+CuA)1 found in *Paracroce altaica*, *Cratopteryx nemopteroides* and the majority of the Crato Formation Nemopteridae is plesiomorphic, and its false deep bifurcation is the result of convergent evolution in these families.

4.1.4. AA1 and CuP in the forewing

The forewing AA1 of Araripeneuridae (visible only when the basal portion of the wing is well preserved) is not fused with CuP (Figs. 2B, 9B). This state is plesiomorphic and also occurs in “Palaeoleontidae”, *Burmaneura*, and most Nemopteridae except the derived Crocini.

The forewing AA1 and CuP are fused for most of their length in Myrmeleontidae (except most Palparinae) and Ascalaphidae (e.g., Tjeder, 1992, figs. 36, 38; Stange, 1994, fig. 15).

4.1.5. Anal veins in the forewing

The anal veins of Araripeneuridae appear to be similarly configured within the family: AA1 is deeply forked, and AA2 and AA3 are simple. Such a configuration of anal veins is also found in most Nemopteridae (Fig. 15B, C).

In “Palaeoleontidae”, all anal veins in the forewing are simple (e.g., Menon and Makarkin, 2008, fig. 4B; Myskowiak and Nel, 2016, figs. 4, 5), or AA1 is shallowly forked (e.g., Martins-Neto, 1998, fig. 1A). In *Burmaneura*, all anal veins are also simple (Huang et al., 2016, fig. 4A); these veins are poorly preserved in other “Pseudonymphidae”.

In Myrmeleontidae, the configuration of anal veins varies. In most Palparinae (in which AA1 is not fused with CuP), all three anal veins are usually branched (see e.g., Kimmins, 1952, fig, 1; Markl, 1954, fig. 62; Mansell, 1990, figs. 1, 15, 32; Ábrahám, 2010, fig. 2). In the Myrmeleontidae in which AA1 is fused with CuP, AA2 and AA3 is variously configured, from simple to few branched; but remarkably that AA3 in most of these Myrmeleontidae is shallowly forked (see e.g., Riek, 1967, figs. 5B, F). AA2 and AA3 are partially fused (or connected by a very short crossvein) in some Myrmeleontidae and Ascalaphidae (see Riek, 1967, figs. 5E, 6B, E, F; Tjeder, 1992, figs. 196, 197).

4.2. Why is Araripeneuridae not a subfamily of Myrmeleontidae?

The taxon Araripeneuridae was established as a subfamily of Myrmeleontidae (Martins-Neto and Vulcano, 1989a), and some authors consider it in such status (e.g., Stange, 2004; Engel and Grimaldi, 2007; Huang et al., 2016). Indeed, Araripeneuridae superficially resemble Myrmeleontidae in general appearance and by their short, apically dilated antennae. We believe however that the similarity of Araripeneuridae with Myrmeleontidae is convergent. The wings of Araripeneuridae are entirely dissimilar to those of Myrmeleontidae in which the forewing CuP is not fused with AA1 (a plesiomorphic condition shared by both families), and superficially resemble only certain Myrmeleontinae in which the forewing CuP is short and then fused with AA1.

The absence of presectoral crossveins in those genera of Araripeneuridae which we consider having most generalized venation is also important. All Myrmeleontidae (including most primitive taxa) possess these crossveins. Further, the configuration of anal veins in all Myrmeleontidae strongly differs from those of Araripeneuridae (see above).

The following character in the venation appears to be most important: The fork of M is located proximad the origin of the proximal-most branch of CuA (formally, of MP+CuA) in Araripeneuridae (state 1), but distad the origin of CuA in almost all Myrmeleontidae, including most Palparinae (state 2). The exception are

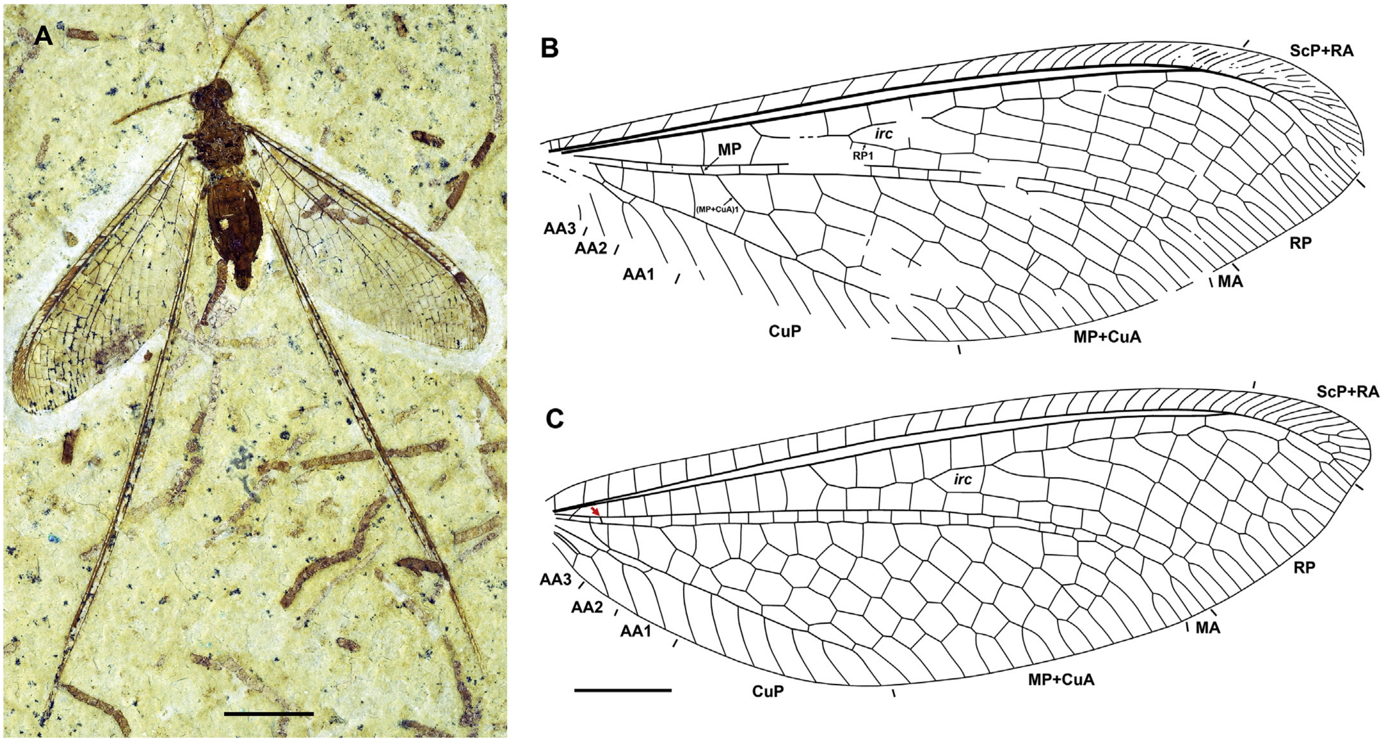

Fig. 15. Representatives of Nemopteridae. A, The Early Cretaceous *Cratonemopteryx speciosa* Martins-Neto and Vulcano, 1997 from the Crato Formation, specimen SMNS 66000/260b as preserved. B, Right forewing venation of specimen SMNS 66000/260b. C, Forewing venation of extant *Nemopterella* sp. from South Africa based on photographs (figs. 2394–2402) and the drawing of the basal wing part (fig. 1930) in Tjeder (1967). The basal part of MP is shown by red arrow. Scale bars represent 5 mm (A), 2 mm (B); no scale (C). (For interpretation of the references to color/colour in this figure legend, the reader is referred to the Web version of this article.)

two genera of Palparinae with few species: *Dimares* Hagen, 1866 (see Markl, 1954, fig. 65) and *Pseudimares* Kimmins, 1933 (see Kimmins, 1933, pl. 6; Aspöck and Aspöck, 2009, fig. 8). However, in *Dimares*, as in other genera of the tribe Dimarini, CuP is short and then fused with AA1 like in Myrmeleontinae, and dissimilar in that with Araripeneuridae. But in *Pseudimares* (which constitutes the tribe Pseudimarini) these veins are separate like in most other Palparinae (i.e., Palparini and Palparidiini). So, *Pseudimares* is the only genus of Myrmeleontidae in which these two character states are similar to those of Araripeneuridae. However, the proximal fork of M (i.e., distad or at the origin of CuA1) occurs in all Cretaceous “Palaeoleontidae” whose venation is rather similar to primitive Palparinae (see e.g., Menon and Makarkin, 2008, fig. 4B; Shi et al., 2012, fig. 2C, D). The hind wing venation of *Dimares* and *Pseudimares* is generally similar to that of *Choromyrmeleon* (“Pseudonymphidae”), in which the forewing M is forked slightly proximad or at the origin of CuA1 (i.e., state 1). Therefore, state 1 is probably plesiomorphic, so that *Pseudimares* is similar to Araripeneuridae only by plesiomorphic conditions. The general venation of *Dimares* and *Pseudimares* is evidently more similar to *Choromyrmeleon*, *Blittersdorffia* and some “Palaeoleontidae” than to Araripeneuridae. This scattered distribution of characters leads to the conclusion of convergent evolution.

Finally, the pilula axillaris (=Eltringham's organ of Elofsson and Löfqvist, 1974) is present in the base of hind wings in males of the majority of the genera of Myrmeleontidae, including Palparini, Palparidiini and Dimarini (Stange, 1994), but not detected in Araripeneuridae. This organ is odoriferous in function, functionally connected with a pit on the first abdominal tergite where a gland is open (Elofsson and Löfqvist, 1974). It is considered an important autapomorphy of the family Myrmeleontidae (including Stilbopteryginae) (Stange, 1994).

4.3. Araripeneuridae and Nemopteridae

The forewing venation of typical Araripeneuridae (i.e., taxa similar to the type genus) is most similar to that of those Nemopteridae that possess generalized venation at the family level, i.e., all nemopterids from the Cretaceous Crato Formation; the majority of genera of Nemopterinae; and *Pastranaia* Orfila, 1955, which represents a single genus of the tribe Pastranaiini (Crocinae) (see Fig. 15; Orfila, 1955, fig. 2; Tjeder, 1967, fig. 1930; Riek, 1967, fig. 3E). These families share many important character states, e.g., MP is fused with CuA proximad the proximal branch of MP+CuA; M/MA is running close to CuA/anterior trace of MP+CuA; the MP+CuA space is broad; the proximal branch of MP+CuA is deeply forked (or there is the false bifurcation of (MP+CuA)1, see above) in the majority of species; there are three fully-separated similarly configured anal veins; AA1 is deeply forked; AA2 and AA3 are short, simple and closely spaced at a crossvein between AA2 and AA3.

The forewing venation in other Nemopteridae is more specialized. In some Nemopterinae, AA2 and AA3 are fused one with the other, only distally (see Tjeder, 1967, fig. 1922) or wholly (see Tjeder, 1967, fig. 1925). In Crocini, there is only one fully-separate simple anal vein (AA2 or the fused AA2 and AA3), and AA1 is distally fused with CuP, except for *Josandreva* Navás, 1906, in which these veins are fully separate (see Hölzel, 1975, figs. 11–13).

All Nemopteridae are characterized by thread-like or ribbon-like hind wings, which are much longer than the forewings (the hind wing of Nemopterinae is often distally dilated). This transformation of the hind wings is a clear autapomorphy of the family. The hind wings of the late Aptian Crato Formation genera do not principally differ from those of some extant genera of Nemopterinae whose apical parts are not dilated, e.g., *Nemopterella* Banks, 1910 (see Tjeder, 1992, figs. 2356–2359).

In addition to hind wing shape, there are two main differences between Araripeneuridae and Nemopteridae. (1) Antennae in Nemopteridae are filiform and elongate, although these are rather short in some species, particularly in the Cretaceous taxa (see Fig. 15A). But the antennae in some genera of extant Myrmeleontidae are also elongate and lack terminal dilation (i.e., not clavate), especially in *Cymothales* Gerstaecker (see Mansell, 1987, figs. 41, 53, 97), and weakly clavate in some other genera (see e.g., Stange, 2002, fig. 610). It is unclear yet if a filiform and elongate antenna in Nemopteridae is a plesiomorphic condition or secondary simplification.

(2) The forewing RP1 is simple or only once forked distally in all Nemopteridae, while it is dichotomously (often profusely) branched in all Araripeneuridae. However, the latter condition is clearly plesiomorphic in Myrmeleontoidae as it occurs in all "Palaeoleontidae" and Ascalaphidae, and many Myrmeleontidae (especially Palparinae). Given that Nemopteridae represent a more specialized group relative to Araripeneuridae, the presence of this apomorphic condition of RP1 is fully understandable.

The great similarity of the forewing venation of these families allows assuming a close phylogenetic relationship between Araripeneuridae and Nemopteridae. The similar configuration of (MP+CuA)1 may represent their only venational synapomorphy (see above).

Among Araripeneuridae, the genus *Caririneura* is most similar to Nemopteridae with generalized venation. In this genus, the hind wings are narrow and slightly longer than forewings. This is especially important as the hind wings of Nemopteridae are much longer than forewings. The shape of the forewing intraradial cell, the presence of the forewing presectoral crossveins, and the configuration of the forewing anal veins in *Caririneura macrothoracica* sp. nov. are very similar to those of all or most species of Nemopteridae. In fact, the forewing venation of *C. macrothoracica* sp. nov. differs from that of Nemopteridae only in small details (e.g., RA space in *C. macrothoracica* sp. nov. is abruptly narrowed at the distal-most crossvein before the fusion of ScP and RA; that in Nemopteridae is gradually narrowed for entire length).

Michel et al. (2017) also suggested close phylogenetic relationship of Araripeneuridae and Nemopteridae: the former taxon "is composed, at least in part, of remote stem-Nemopteridae" (p. 109).

4.4. *Taxonomic affinity of the genus Burmaneura*

Burmaneura minuta is the only species in this genus represented by the very small holotype (the hind wing is ca. 9 mm long) from mid-Cretaceous Burmese amber. The venation and strongly clavate antennae indicate that this genus belongs to Myrmeleontoidae. The forewing is proximally narrow, with the venation very dissimilar to that of any Araripeneuridae: the apparent M runs distantly from CuA; 'oblique vein' (basal MP) is not observable; all branches of CuA (or possibly of MP+CuA; including CuA1) are simple; the origin of CuA1 is far distad the origin of RP; the presumed MP+CuA space is relatively narrow; AA1 is simple. Its hind wing venation, however, is similar to that of some Araripeneuridae, especially *Caririneura* in having the very short CuA and the presence of one presectoral crossvein. Note however, that the hind wing venation of *Pseudonymphes* is also similar to that of Araripeneuridae.

Huang et al. (2016) wrote that "*Burmaneura* differ greatly from all Araripeneurinae [treating as a subfamily of Myrmeleontidae], except *Blittersdorffia volkheimeri* Martins-Neto and Vulcano, 1989a" (p. 6). We want to stress also that the forewing venation of *Burmaneura* is similar to that of *Pseudonymphes*. Therefore, we remove here this genus from the family as restricted in this paper. More likely it belongs to the possibly paraphyletic "Pseudonymphidae" (see below) as its forewing venation is generally similar to that of *Pseudonymphes* and *Blittersdorffia*.

4.5. *Taxonomic affinity of the genera Blittersdorffia and Choromyrmeleon*

The venation of *Blittersdorffia* is very similar to that of the Barremian/Aptian genus *Choromyrmeleon* from the Yixian Formation of China, differing from it only in some details. *Choromyrmeleon aspoeckorum* Ren and Engel, 2008 from the Yixian Formation and *Blittersdorffia pulcherrima* Martins-Neto, 1997 from the Crato Formation are so similar that it is hard to find any generic differences between them. These genera are possibly synonyms.

The genus *Choromyrmeleon* is usually considered as belonging to Myrmeleontidae of uncertain affinity (e.g., Stange, 2004; Ren and Engel, 2008; Huang et al., 2016). Makarkin et al. (2012) preliminarily referred it to Araripeneuridae due to the absence of presectoral crossveins.

The forewing venation of both genera is indeed similar to that of some Myrmeleontidae: MP is forked distad or at CuA1; M/MA is more distant from CuA/anterior trace of MP+CuA than in Araripeneuridae; the origin of CuA1 is located far distad the origin of RP; CuA1 is branched. But these genera have no presectoral crossveins which are present in all Myrmeleontidae. Also, these genera do not belong to Araripeneuridae with certainty, as their venation is very dissimilar to that family. We preliminary assigned these to "Pseudonymphidae" because of their general similarity in the venation.

4.6. *Taxonomic affinity of the genus Pseudonymphes*

The forewing venation of this genus is very dissimilar to that of Araripeneuridae: M and CuA are forked distally, much distad the origin of RP; MP and CuA are fused only for a short distance or connected by a crossvein; M and CuA are more distant; trichosors are present along the wing tip.

The hind wing venation of *Pseudonymphes* is in general similar to that of Araripeneuridae, but its MP is pectinate with several branches (few-branched in the majority of Araripeneuridae). This venation (as well as of Araripeneuridae and *Choromyrmeleon*) is also similar to a few extant representatives of various Myrmeleontidae in respect to the long straight CuA, reaching at least mid-wing, and the absence of a clear triangle of MP formed by its distal part, MP1 and the posterior margin of the wing. These myrmeleontids are for example *Isonemurus longipalpis* Esben-Petersen, 1928 (Myrmeleontinae: Maulini); species of *Maracandula* Currie, 1901 (Myrmeleontinae: Gnopholeontini) and *Pseudimares* (Palpirinae: Pseudimarini) (see Esben-Petersen, 1928, fig. 1; Aspöck and Aspöck, 2009, fig. 8; Miller and Stange, 2009, figs. 1, 9). We may assume that these conditions (i.e., the long CuA and the absence of a MP triangle) are plesiomorphic as similar condition is present in other "Pseudonymphidae" and most Araripeneuridae and "Palaeoleontidae" (i.e., in the majority of Cretaceous Myrmeleontoidae except Nemopteridae).

The genus *Pseudonymphes* appears to be most primitive among Myrmeleontoidae by the presence of trichosors (although restricted to a very small area) and MP not fused with CuA in some species (or specimens). On the other hand, its antennal club is similar to that of Myrmeleontidae and stronger developed than that of most Araripeneuridae.

Pseudonymphes is the type of Pseudonymphinae. The latter was created as a subfamily of Myrmeleontidae, and treated to comprise only the type genus *Pseudonymphes* (Martins-Neto, 1990, 1992a, 1994, 1997, 1998). Later however, its status was elevated to family (i.e., Pseudonymphidae) based on "a phylogenetic approach", to include three genera from the Crato Formation (i.e., *Pseudonymphes*, *Blittersdorffia*, and *Bleyeria*) and "other

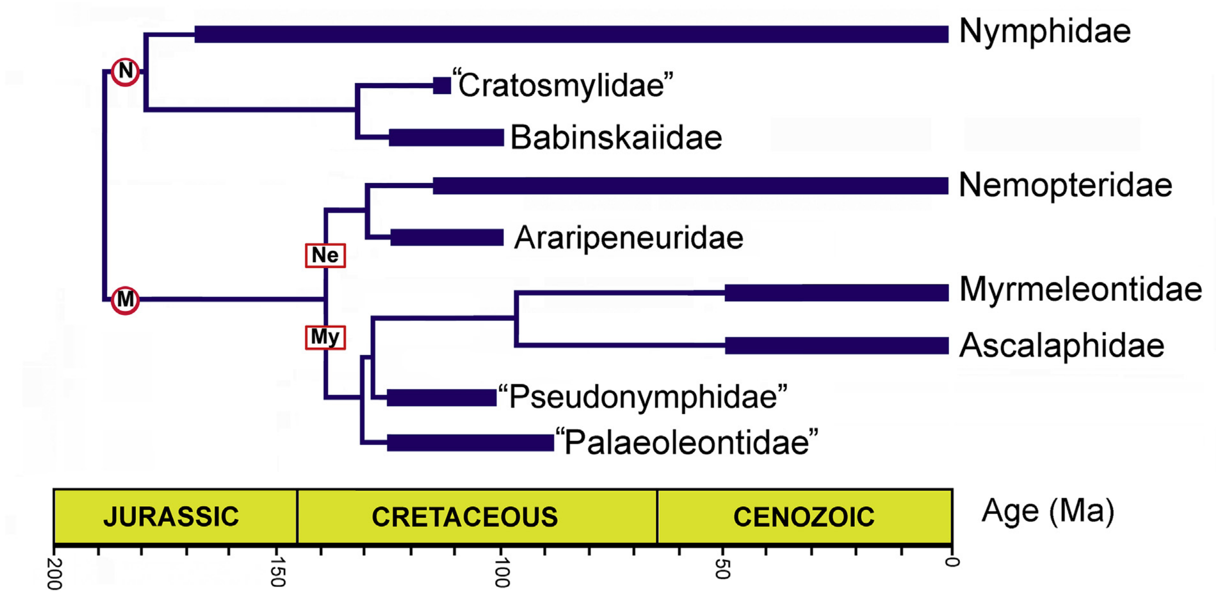

Fig. 16. Probable phylogenetic relationships within the superfamily Myrmeleontoidea. M, the epifamily Myrmeleontoidea; My, the myrmeleontid lineage; N, the epifamily Nymphoidea; Ne, the nemopterid lineage. The perhaps paraphyletic families and stem groups are in quotes.

genera described for the Asiatic Lower Cretaceous" (Martins-Neto, 2003, p. 55). It is very probable that one of these Asiatic genera is *Choromyrmeleon*. We consider here "Pseudonymphidae" to be the stem group within Myrmeleontoidae, which needs further taxonomic study (see above).

4.7. *Possible relationships within Myrmeleontoidae*

The extant Myrmeleontoidae (i.e., Nemopteridae, Myrmeleontidae and Ascalaphidae) are considered to constitute a monophyletic clade by nearly all of authors (e.g., Haring and Aspöck, 2004; Winterton et al., 2010; Wang et al., 2017). Based on molecular data, Michel et al. (2017) estimated that Nemopteridae originated in Berriasian (141.1 Ma ago), Myrmeleontidae diversified in Valanginian (138.2 Ma ago), and Ascalaphidae appeared in Aptian (119.8 Ma ago); i.e., all these taxa originated in Early Cretaceous. This scheme is in general concordant with phylogenetic relationships between these families by Wang et al. (2017) based also on molecular data, although Nemopteridae estimated as originated in Late Jurassic. Sometimes, Myrmeleontidae are recovered paraphyletic with respect to Ascalaphidae (e.g., Winterton et al., 2010, 2017)

The available material on Cretaceous myrmeleontoids allows hypothesizing on two distinct lineages within Myrmeleontoidae. One lineage includes a number of the Cretaceous genera, which are now considered in the possibly paraphyletic "Palaeoleontidae" and the stem group "Pseudonymphidae", and the Myrmeleontidae and Ascalaphidae recorded only from the Cenozoic (a myrmeleontid lineage). The second lineage includes Araripeneuridae and Nemopteridae (a nemopterid lineage) (see Fig. 16).

A main problem is the absence of fossils in the myrmeleontid lineage between the mid-Cretaceous and the early Eocene when the principal processes of the evolution of Myrmeleontidae and Ascalaphidae took place. Nevertheless, the venation and general habitus of some genera of "Palaeoleontidae" (e.g., *Parapalaeoleon*) and "Pseudonymphidae" (e.g., *Choromyrmeleon*, *Blittersdorffia*) resemble primitive Myrmeleontidae, and these are apparently similar to ancestors of Myrmeleontidae + Ascalaphidae. However, the majority of the known Early Cretaceous genera in this lineage appear to belong to extinct (dead-ended) branches.

Among the nemopterid lineage, *Paracroce* is the oldest known genus (Barremian/Aptian); the others are from the late Aptian Crato Formation. As shown above, Araripeneuridae and Nemopteridae are more closely related to each other than to other Myrmeleontoidae, but interrelations between these families are unclear. In general, Nemopteridae seem certainly more derived than Araripeneuridae. Given that the presence of presectoral crossveins is a derived character state which appeared later within Myrmeleontoidae, the Nemopteridae might have evolved as a side branch of the Araripeneuridae, which would render Araripeneuridae paraphyletic. In this case, *Paracroce* may belong to the stem group of this lineage (i.e., Araripeneuridae + Nemopteridae), not Araripeneuridae. Unfortunately, the scarcity of fossils belonging to this lineage from horizons older than the Aptian presents a significant problem in resolving this issue.

The oldest known members of these two lineages occur in the Barremian/Aptian, i.e., the myrmeleontid lineage's *Choromyrmeleon* and *Guyiling* from the Yixian Formation of China, and the nemopterid lineage's *Paracroce* from Mongolia. Therefore, the Myrmeleontoidae certainly split into these lineages earlier. In general, these data support estimated divergence times of Michel et al. (2017), Wang et al. (2017) and Winterton et al. (2017).

5. Conclusions

We argue here that the Araripeneuridae is an extinct branch of Myrmeleontoidea, and that Araripeneuridae may be most closely related to Nemopteridae with both families together constituting the nemopterid lineage. Another lineage of Cretaceous Myrmeleontoidea probably leads to the extant Myrmeleontidae and Ascalaphidae. However, there are many questions concerning their systematic relationships which are currently impossible to answer due to the scarcity of Early Cretaceous myrmeleontoid fossils. The resolution of these problems lies in the future.

Acknowledgements

We thank M. Jared Thomas for help with photography of several specimens from the INHSP collection; Alexander V.

Khramov (PIN) for photographs of the holotype of *Paracroce altaica*; Günter Schweigert for the loan of several specimens from the SMNS collection, Federica Menon for some photographs from that collection; and anonymous reviewers for providing valuable suggestions to improve this manuscript. The study is supported by Grant No. 16-04-00053 of the Russian Foundation for Basic Research.

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