

Early evolution of Nemopteridae illuminated with the first and oldest thread-winged lacewing in Cretaceous amber

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Abstract. Nemopteridae are a charismatic family of lacewings distinguished by specialization of morphology in both larvae and adults as well as in their biology and behaviour. The evolutionary history of Nemopteridae is largely unknown due to the scarcity of fossil records. Here we report a new genus and species of Nemopteridae (*Cretocroce xiai* **gen. et sp.n.**) based on an exquisitely preserved adult specimen in mid-Cretaceous Burmese amber. We place the new genus in the subfamily Crocinae, which is characterized by filamentous hindwings with a sensory function as an adaptation to their cavernicolous habitats. The new genus represents the first nemopterid in amber and the oldest crocine known to date. The new fossil crocine is nearly morphologically unchanged over 99 Ma compared with its modern counterparts. Moreover, it is estimated to be closely related to some extant crocines endemic to South America based on morphological phylogenetic analysis. The new finding provides direct evidence to demonstrate the antiquity of Crocinae morphological innovation and related biology, such as pollenophagous habits, and further corroborates Gondwanan origin of the subfamily.

The published work has been registered on ZooBank: <http://zoobank.org/urn:lsid:zoobank.org:pub:3D29DE48-DBD8-4614-8387-D9FCF90B0640>.

Introduction

Nemopteridae are an enigmatic family of lacewings distinguished by elongated ribbon- or thread-like hindwings as well as frequently specialized mouthparts with long rostrum for pollen collection. Extant Nemopteridae comprise two subfamilies: Crocinae (thread-wings) and Nemopterinae (spoon- and ribbon-wings). Currently, there are 142 valid species worldwide, including 43 species of Crocinae and 99 species of Nemopterinae (Sole *et al.*, 2013). The extant fauna of family is distributed in all zoogeographical regions except the Nearctic. However, the major species diversity of Nemopteridae

is confined to southern Africa where 72 species (48% of the world fauna) occur (Mansell, 1996; Sole *et al.*, 2013). Moreover, 57 species (38% of the world fauna) are endemic to the Western and Northern Cape Provinces of South Africa (mostly Nemopterinae), indicating a possible radiation that coevolved with rich Cape flora (Mansell, 1996) as these species are pollen feeders of certain indigenous plants (Picker, 1987).

Nemopteridae belong to the superfamily Myrmeleontoidea, which also include Nymphidae, Myrmeleontidae, Ascalaphidae and two extinct families Babinskaiidae and Rafaelianidae (Engel *et al.*, 2018). The sister-group relationship between Nemopteridae and Myrmeleontidae + Ascalaphidae was repeatedly recovered in several recent studies on molecular phylogenetics of Neuroptera (Winterton *et al.*, 2010, 2018; Michel *et al.*, 2017; Wang *et al.*, 2017), although some phylogenetic studies based on morphological data assigned Nemopteridae as the sister group of a lineage including Nymphidae, Myrmeleontidae and

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Table 1. Known fossils of Nemopteridae.

No.	Species	Subfamily	Age	Locality
1	<i>Roesleriana exotica</i> (Martins-Neto & Vulcano, 1989)	Roeslerianinae	Lower Cretaceous (Aptian)	Crato Formation, Nova Olinda Member, Brazil
2	<i>Cratonemopteryx audax</i> (Martins-Neto & Vulcano, 1989)	Incertae sedis	Lower Cretaceous (Aptian)	Crato Formation, Nova Olinda Member, Brazil
3	<i>Cratonemopteryx robusta</i> (Martins-Neto & Vulcano, 1989)	Incertae sedis	Lower Cretaceous (Aptian)	Crato Formation, Nova Olinda Member, Brazil
4	<i>Cratonemopteryx speciosa</i> Martins-Neto & Vulcano, 1997	Incertae sedis	Lower Cretaceous (Aptian)	Crato Formation, Nova Olinda Member, Brazil
5	<i>Krika pilosa</i> Martins-Neto, 1992	Incertae sedis	Lower Cretaceous (Aptian)	Crato Formation, Nova Olinda Member, Brazil
6	<i>Cretocroce xiai</i> gen. et sp.n.	Crocinae	Upper Cretaceous (Cenomanian)	Tanai, Myitkyina, Kachin, Myanmar
7	<i>Marquettia americana</i> (Cockerell, 1907)	Nemopterinae	Eocene (Priabonian)	Florissant Formation, Colorado, USA
8	<i>Marquettia metzeli</i> (Pierce & Kirkby, 1959)	Nemopterinae	Oligocene	Renova Formation, Montana, USA
9	Undetermined genus and species (Nel, 1990)	Nemopterinae	Oligocene	Alsace potash field, Anna pit, France

Ascalaphidae (Mansell, 1992; Beutel *et al.*, 2010; Randolph *et al.*, 2014; Badano *et al.*, 2017).

Molecular dating indicates that Nemopteridae diverged during the Middle Jurassic (Winterton *et al.*, 2010, 2018; Michel *et al.*, 2017; Wang *et al.*, 2017). However, fossils of Nemopteridae are extremely rare (Table 1). The oldest of these are known from the Lower Cretaceous of Brazil (Crato Formation). This palaeofauna of Nemopteridae comprises three genera and five species (Martins-Neto, 2000). Among them, *Roesleriana* Martins-Neto & Vulcano is placed in the extinct subfamily Roeslerianinae, while the remaining genera (*Krika* Martins-Neto and *Cratonemopteryx* Martins-Neto) have uncertain subfamilial placement (Martins-Neto, 1992, 2002; Oswald, 2018). Besides these Cretaceous nemopterids, two Tertiary fossil species are known from the Eocene and Oligocene of western U.S.A., namely *Marquettia americana* (Cockerell) and *Marquettia metzeli* (Pierce & Kirkby), respectively, both of which belong to Nemopterinae. Hitherto, no fossils of Crocinae have been reported.

Here we report a new genus and species of Nemopteridae from the mid-Cretaceous of Myanmar based on an exquisitely preserved male specimen in Burmese amber. It represents the first nemopterid species discovered in amber. Morphological data suggest that the new genus belongs to the subfamily Crocinae, which is characterized by filamentous hindwings and long rostrum in adults. The present finding provides significant evidence for understanding the early evolution of Crocinae as well as Nemopteridae and their morphological specialization.

Material and methods

Specimen preparation

The Burmese amber sample under present study is from the Hukawng Valley in Tanai Township, Myitkyina District of Kachin State, Myanmar (see Kania *et al.*, 2015: Fig. 1). The age of the Burmese amber deposit has been dated to ~99 Ma (earliest

Cenomanian) by U-Pb dating of zircons from the volcaniclastic matrix of the amber (Shi *et al.*, 2012). The specimen is deposited in the Entomological Museum of China Agricultural University (CAU), Beijing, China. Photographs and drawings were taken using a Zeiss SteREO Discovery V12 stereomicroscope system (Germany). Figures were prepared with Adobe PHOTOSHOP CS4. The terminology of wing venation generally follows Aspöck *et al.* (1980) and Kukalová-Peck & Lawrence (2004). Abbreviations of wing venation are as follows: A, anal vein; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; MA, media anterior; MP, media posterior; RA, radius anterior; RP, radius posterior; ScP, subcosta posterior; ps, presectorial crossvein. Terminology of male genitalia follows Aspöck & Aspöck (2008) with exception of gonostyli 11 that are herein interpreted as gonocoxites 10. In the description we add alternative terms (e.g. paramere, mediuncus, and gonarcus) in parenthesis for the 'gonocoxites' of genitalia, as this terminology was often used in the literature on Nemopteridae (Tjeder, 1967; Hölzel, 1975).

Phylogenetic analysis

We included all extant genera of Crocinae and the new genus as the ingroup taxa. Three fossil genera of Nemopteridae from the Lower Cretaceous of Brazil were also included to assess their phylogenetic status. We used *Nymphes* Leach (Nymphidae) and *Derhynchia* Tjeder (Nemopteridae: Nemopterinae) as outgroup taxa. Morphological characters used in analysis comprise 29 adult characters and four larval characters, most of which are referenced from Hölzel (1975) and Mansell (1986) (see Appendix). Unknown characters were coded as '?'. The data matrix is given in File S1. All characters were treated as unordered and with equal weight. Analyses were performed using a heuristic search with multiple tree-bisection-reconnection (TBR) in NONA ver. 2.0 (Goloboff, 1993). Maximum trees to keep were set to 10 000 and the number of replications to 100. Bootstrap values were calculated with the number of replications set to 10 000 and the number of search replications set to 10. Character states



Fig. 1. *Cretocroce xiai* gen. et sp.n., holotype, CAU-BA-XF-18001. Photograph of habitus, lateral view. Scale bar, 1.0 mm. [Colour figure can be viewed at wileyonlinelibrary.com].

were mapped on the strict consensus tree using WINCLADA ver. 1.00.08 (Nixon, 2002), showing only unambiguous changes.

Taxonomy

Family Nemopteridae Burmeister.

Subfamily Crocinae Navás.

Cretocroce gen.n.

(Figs 1–5)

<http://zoobank.org/urn:lsid:zoobank.org:act:30173C76-09E6-4052-82A9-0300B8BDCD0F>

Type species: *Cretocroce xiai* sp.n.

Diagnosis. Head with relatively short, narrow rostrum, nearly equal in length to inner margin of compound eye; vertex with a slightly domed area. Antenna filiform, about a quarter as long as forewing, slightly widened towards apex, with regular short setae. Pronotum longer than wide, with a transverse furrow across anterior portion. Legs short, slender; procoxa much longer than meso- and metacoxa; tibial spurs absent; arolium absent. Forewing ovoid, with greatly narrowed base,

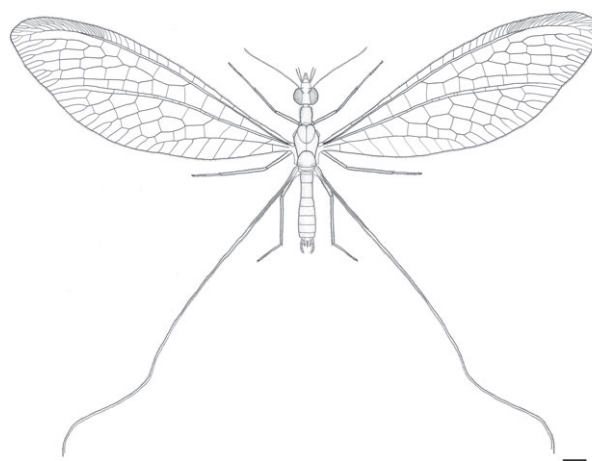


Fig. 2. Habitus reconstruction of *Cretocroce xiai* gen. et sp.n., male, dorsal view. Scale bar, 1.0 mm.

apex slightly tapered. Pterostigma present along proximal half of hypostigmal cell. Hypostigmal cell $\sim 6.0\times$ as long as wide. Bulla absent. RP + MA diverging approximately from proximal third of wing; RP with six primary branches, which are barely curved posteriad, some of these branches distally forked. Three presectorial crossveins present. Four crossveins present in RA space. MP1 simple. MP2 + CuA with six primary branches. CuP diverging near wing base, proximally fused with A1, distally terminating at proximal third of wing. Hindwing greatly narrowed, thread-like along entire length. Venation distinct only within proximal part of wing, consisting of strong C, R and ambient vein, but a weak Sc. Abdomen slender, nearly as long as thorax. Male genitalia: Tergum 9 much shorter than tergum 8, in lateral view subtriangular, probably splitting into two halves. Sternum 9 posteriorly with strongly elongate, digitiform projection. Gonocoxites 9 (= parameres) present as a pair of long, digitiform processes. Ectoprocts paired, distally with long, digitiform process distally. Putative gonocoxites 10 (= mediuncus) present as singular, attenuate sclerite, strongly narrowed into a digitiform process distally.

Etymology. The generic name is a combination of ‘Cret-’ (Cretaceous) and ‘Croce’ (means cross in reference to the forewing crossveins, being used as the genus-name of the type genus of Crocinae). Gender: Feminine.

Remarks. The new genus belongs to the subfamily Crocinae based on the procoxa that is longer than meso- and metacoxa (procoxa are nearly equal in length to meso- and metacoxa in Nemopterinae), the absence of forewing A3 (forewing A3 present in Nemopterinae), the hindwing with largely reduced venation (hindwing with more veins in Nemopterinae), and the male gonocoxites 9 not fused with each other distally (male gonocoxites 9 distally fused with each other in Nemopterinae).

Within Crocinae the new genus can be distinguished from all the other genera of this subfamily by forewing venation with the RP + MA that is separated from R at the proximal

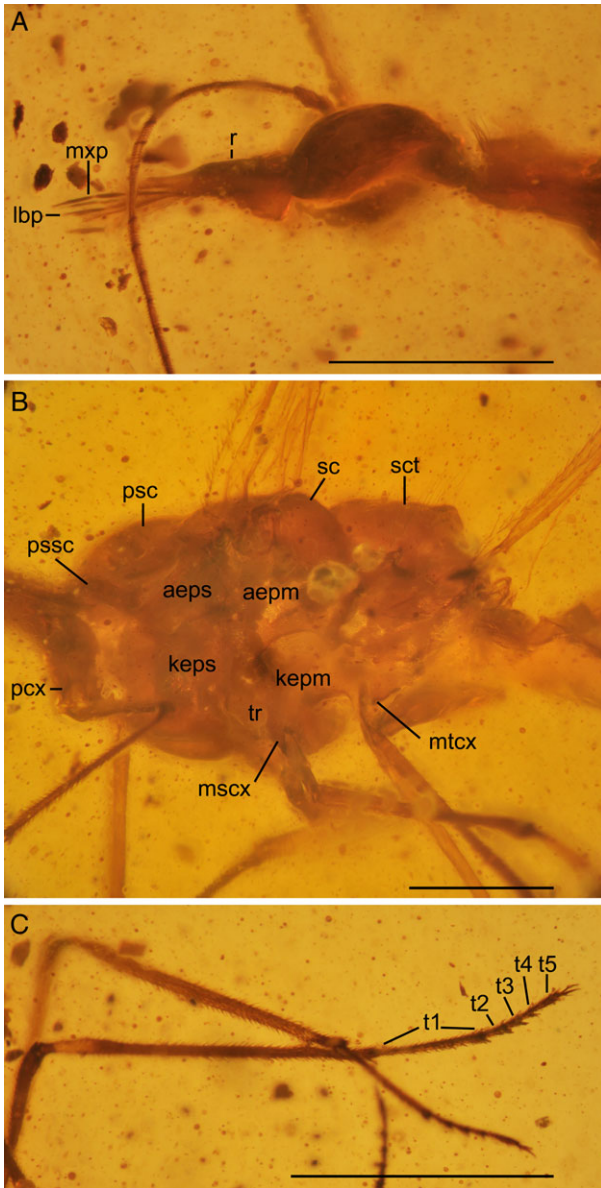


Fig. 3. *Cretochrome xiai* gen. et sp.n., holotype, CAU-BA-XF-18001. (A) Photograph of head, lateral view; (B) photograph of meso- and metathorax, lateral view; (C) photograph of hind legs. mxp, maxillary palp; lbp, labial palp; r, rostrum; spsc, spiracular sclerite; psc, prescutum; sc, scutum; sct, scutellum; aeps, antepisternum; keps, katepisternum; aepm, antepimeron; kepm, katenpimeron; tr, trochantin; psc, procoxa; msxc, mesocoxa; mtcx, metacoxa; t, tarsus. Scale bar, 1.0 mm. [Colour figure can be viewed at wileyonlinelibrary.com].

third of wing. In all extant genera of Crocinae the forewing RP+MA is separated from R at the proximal quarter of wing or even near base. Moreover, the new genus differs from most crocine genera except *Pastranaia* Orfila by the forewing RP branches mostly forked and weakly curved posteriad (in most crocine genera except *Pastranaia* the forewing RP branches are mostly simple and distinctly curved posteriad, especially the distal branches). Therefore, *Cretochrome* gen.n. appears to

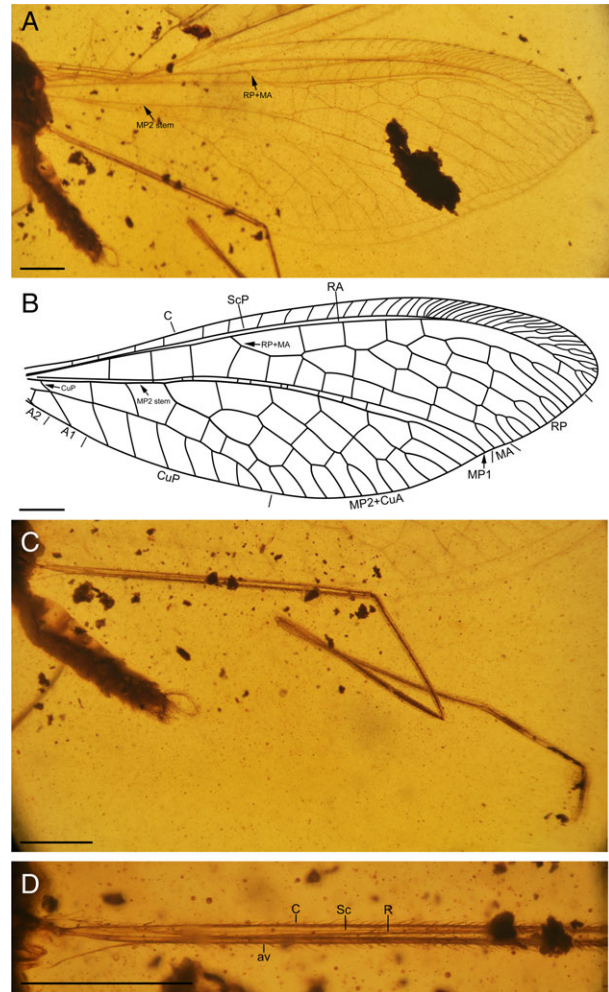


Fig. 4. *Cretochrome xiai* gen. et sp.n., holotype, CAU-BA-XF-18001. (A, B) Photograph (A) and drawing (B) of left forewing; (C) photograph of left hindwing; (D) photograph of proximal part of left hindwing. Av, ambient vein. Scale bar = 1.0 mm. [Colour figure can be viewed at wileyonlinelibrary.com].

be closely related to *Pastranaia* (an extant genus endemic to Argentina) in having similar forewing RP+MA and RP that has several distally forked branches and is not distinctly curved posteriad. Furthermore, these two genera also share long digitiform ectoprocts in the male genitalia. However, the new genus can be distinguished from *Pastranaia* by the forewing RP+MA separated from R at the proximal third of wing (forewing RP+MA separated from R at proximal quarter of wing in *Pastranaia*), fusion of forewing CuP and A1 (these two veins not fused proximally in *Pastranaia*), relatively short forewing CuP ending in the proximal third of wing (forewing CuP ending approximately at midpoint of wing in *Pastranaia*), and male sternum 9 with a long digitiform median projection (male sternum 9 lacking median projection in *Pastranaia*).

Among Mesozoic nemopterids, the new genus differs from *Roesleriana* (Roeslerianinae) and *Krika* (subfamily incertae sedis), both known from the Lower Cretaceous of Brazil,

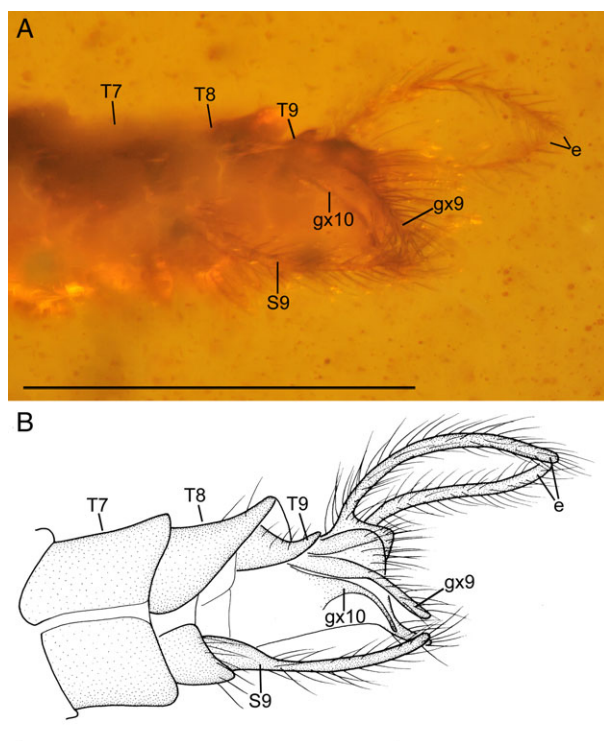


Fig. 5. *Creto Croce xiai* gen. et sp.n., holotype, CAU-BA-XF-18001. (A, B) Photograph (A) and drawing (B) of male genitalia, ventrolateral view. T, tergum; S, sternum; gx, gonocoxites; e, ectoproct. Scale bar, 1.0 mm. [Colour figure can be viewed at wileyonlinelibrary.com].

by having simple forewing costal crossveins (several forked forewing costal crossveins present in the latter two genera) and simple branches of forewing CuP (forewing CuP with several branches secondarily forked in the latter two genera); it is distinguished from *Cratonemopteryx* (subfamily incertae sedis), also from the Lower Cretaceous of Brazil, by three forewing presectorial crossveins (one or two ps in *Cratonemopteryx*), fusion of forewing CuP and A1 (separated in *Cratonemopteryx*), and reduction of hindwing venation (many distinct longitudinal veins and crossveins present in hindwings of *Cratonemopteryx*).

Creto Croce xiai sp.n.

(Figs 1–5)

<http://zoobank.org/urn:lsid:zoobank.org:act:AD05CBCA-6A05-49C3-A70E-E70043AE5853>

Diagnosis. Same as for the genus.

Description. Body 7.52 mm long; integument of body in general pale brown, with ventral portions of thorax and abdomen yellow. Head 1.25 mm long and 0.91 mm wide, with relatively short, narrow rostrum, nearly equal in length to inner margin of compound eye; vertex with slightly domed area; cephalic sutures and anterior tentorial pits invisible. Compound eyes large, semi-ellipsoidal, widely separated, distance between them nearly as long as transverse diameter of eye, length of

inner margin 0.79 mm. Antenna filiform, 3.30 mm long, about a quarter as long as forewing, slightly inflated towards apex (inflated part 0.40 mm long), with regular short setae; terminal flagellomere acutely pointed. Clypeus and labrum short and slightly narrowed anteriorly, nearly equal in length with each other. Maxillae long, distinctly extending beyond apex of labrum; maxillary palp 0.39 mm long, four-segmented, terminal palpomere acutely pointed distad. Labium with only labial palp discernible, 0.27 mm long, three-segmented, proximal two palpomeres subequal in length, terminal palpomere about two-thirds length of palpomere 2 and acutely pointed distad.

Pronotum longer than wide, 0.74 mm long and 0.31 mm wide, with a transverse furrow across anterior portion, moderately setose along lateral portions. Mesonotum large, 1.75 mm long; spiracle sclerite short and narrow; prescutum long, heart-shaped, with a distinct longitudinal suture; scutum slightly longer than prescutum in lateral view; scutellum nearly as long as prescutum, with strongly arcuate anterior margin, posterior margin nearly truncate, setose posterolaterally; anepisternum sub-oblong, nearly twice as long as wide; katepisternum broad, $\sim 2.0\times$ width of anepisternum; trochantin nearly rhombic; antepimeron broad, nearly equal in width to episternum; katepimeron slightly smaller than trochantin. Metathorax small, 0.31 mm long, almost one-third the length of mesothorax. Legs short and slender, with dense short setae; total length of foreleg 2.1 mm, procoxa 0.16 mm, protrochanter 0.02 mm, profemur 0.30 mm, protibia 0.72 mm, protarsus 0.90 mm; total length of midleg 2.98 mm, mesocoxa 0.08 mm, mesotrochanter 0.01 mm, mesofemur 0.82 mm, mesotibia 1.11 mm, mesotarsus 0.96 mm; total length of hind leg 3.95 mm, metacoxa 0.08 mm, metatrochanter 0.01 mm, metafemur 0.98 mm, metatibia 1.76 mm, metatarsus 1.12 mm; tibial spurs absent; tarsomere 1 nearly as long as tarsomeres 2–5 together, each tarsomere with some stiff setae on apex; pretarsal claws feebly curved; arolium absent.

Forewing 13.58 mm long and 4.33 mm wide, hyaline, immaculate, ovoid, with strongly narrowed base, wing apex slightly tapered; wing margins and veins densely setose. Pterostigma present along proximal half of hypostigmal cell. Hypostigmal cell $\sim 6.0\times$ as long as wide. No bulla present at hind margin. Costal space narrow, slightly widened distad, with 23 simple costal crossveins. Most veinlets of ScP + RA deeply forked. RP + MA diverging approximately from proximal third of wing; RP with six primary branches, barely curved posteriorly, posterior three of them forked near wing margin; MA forked near wing margin. Three ps present. Four crossveins present in RA space. Ten crossveins present among branches of RP + MA and distal branches of RP. MP1 simple. Oblique vein (stem of MP2) rather short. Nine short crossveins present between MP1 and MP2 + CuA. MP2 + CuA with six primary branches, posterior-most branch deeply bifurcated into two main subbranches, each forked near wing margin; other primary branches, except for distal-most two, forked near wing margin. Eleven crossveins present among branches of MP2 + CuA. CuP diverging near wing base, proximally fused with A1, distally terminating at proximal third of wing, CuP + A1 with eight short simple branches. Six crossveins present between

MP2 + CuA and CuP + A1. A2 weak, simple, connecting to A1 by a crossvein.

Hindwing with preserved part strongly narrowed throughout, slightly longer than forewing, 18.05 mm long and 0.11 mm wide; wing margins and veins densely setose. Venation distinct only within proximal part of wing, consisting of strong C, R and ambient vein, as well as a weak Sc.

Abdomen slender, 3.15 mm long and 0.55 mm wide. Pleuriticocavae absent. Male genitalia covered with long setae. Tergum 9 much shorter than tergum 8, in lateral view subtriangular, probably splitting into two halves. Sternum 9 widely apart from tergum 9, posteriorly with a strongly elongate, digitiform projection. Gonocoxites 9 (= parameres) present as a pair of long, digitiform processes that are slightly incurved. Ectoprocts paired, with base sub-quadrangle, distally with a long, digitiform process (0.67 mm long) that is slightly curved inward and ventrad; callus cerci invisible. Putative gonocoxites 10 (= mediuncus) present as a singular, attenuate sclerite, distally strongly narrowed into a digitiform process. Fused gonocoxites 11 (= gonarcus) invisible.

Type material. Holotype: CAU-BA-XF-18001: amber piece preserving an almost complete adult male of *C. xiai*; it is polished in the form of a flattened ellipsoid cabochon, transparent, with length \times width about 27.5 \times 18.0 mm, height about 5.7 mm.

Etymology. The new species is dedicated to Mr Fangyuan Xia who kindly provided the specimen of the new species for our study.

Phylogenetic analysis

The heuristic search in NONA yielded four MPTs (length = 66, consistency index = 57, retention index = 76). Among the four MPTs, the major topological differences refer to the phylogenetic relationships between the nemopterine genus *Derhynchia* and the three fossil genera, i.e. *Roesleriana*, *Krika* and *Cratonemopteryx* (see File S2). Missing data on the genitalia and larvae of these fossil genera limited further inference of the phylogenetic status of these taxa. Additionally, *Cretocroce gen.n.* was assigned to be either the sister group of the South American genus *Pastranaia* or the sister group of the clade including most extant crocine genera except *Pastranaia*. The strict consensus tree is shown in Fig. 6. All crocine genera formed a monophyletic group, with three synapomorphic characters, i.e. the absence of forewing A3 (char. 9:1), the reduction of veins in hindwing (char. 13:1), and the procoxa longer than meso- and metacoxa (char. 28:1). All crocine genera except *Cretocroce gen.n.* and *Pastranaia* were assigned to be monophyletic based on the forewing RP distinctly curved posteriad (char. 3:1) and with all branches simple (char. 4:1). Within this group, the South American genus *Veurise* Navás was assigned a sister group position. The remaining genera formed a monophyletic subgroup, which splits into three clades, based on the long forewing CuP (char. 7:1) and the male gonocoxites 9 with inflated apex (char. 23:1). Clade I includes *Concroce* Tjeder, *Austrocroce* Tjeder, *Carnarviana* Mansell, *Josandrevia* Navás

and *Croce* McLachlan. The close relationship among these genera is consistent with the hypothesis in Mansell (1986), although it is weakly supported only by the presence of pseudo-teeth on larval jaws (char. 31:1). Clade II is composed of three southern African genera, i.e. *Tjederia* Mansell, *Thysanocroce* Withycombe and *Laurhervasia* Navás. Monophyly of clade II is well supported by a number of synapomorphies, such as the unpaired male tergum 9 that is strongly extending ventrad (chars. 16:1, 17:1), presence of gonosaccus on male gonocoxites 9 (char. 20:1), and fusion between female gonocoxites 8 and 9 (char. 26:2). Clade III comprises the remaining genera, which are mostly from southern Europe, northern Africa, the Middle East and India, with the exception of *Amerocroce* Mansell and *Moranida* Mansell, both from South America. Synapomorphies of clade III are the forewing RP that approximates RA with many closely spaced radial crossveins (char. 2:1) and the vertically curved male gonocoxites 9 (char. 22:1). The sister-group relationship between clades II and III was recovered by two larval character states, i.e. larval head narrowed posteriad (char. 30:1) and strongly elongated cervix (char. 33:1).

Discussion

Habitat of Cretocroce gen.n.

Extant species of Crocinae generally inhabit arid and semiarid areas. The habitats of crocine larvae are mainly confined to dusty recesses under rock overhangs, small caves and completely sheltered microhabitats (Sole *et al.*, 2013). Interestingly, some crocine larvae were reported to inhabit structures constructed by humans, such as rock tombs, ceilings of houses and cavities in buildings (Mansell, 1996). They can also occupy cavities amongst the tree roots and holes in sandy areas as well as plant and animal detritus in small caves and rock crevices (Mansell, 1996). The adults of a few crocine species [e.g. *Croce filipennis* (Westwood) and *Josandrevia sazi* Navás] live indoors, such as the rooms of bungalows, outhouses, etc., but also occur in the close vicinity of their larval habitats (Tjeder, 1967). Their thread-like hindwings have sensory and stabilization function, enabling them to fly in limited spaces such as those in rock crevices and holes (Mansell, 1996). However, South African Crocinae are not cavernicolous in the adult stage; instead they are crepuscular or nocturnal and can be attracted to light (Tjeder, 1967).

The holotype of *C. xiai sp.n.* is the only nemopterid adult specimen from hundreds of Burmese amber samples with neuropteran inclusions that we examined, suggesting that the adults of *C. xiai sp.n.* probably inhabited sheltered habitats similar to those of extant crocines, resulting in a few individuals becoming mired in the tree resin. Interestingly, compared with the rarity of nemopterid adults from Burmese amber, larvae of Nemopteridae are easily found from this deposit (see Xia *et al.*, 2015; Zhang, 2017). Their larval morphology resembles larvae of some extant Crocinae, having a strongly elongated cervix. However, all of these larvae possess a row of teeth on their jaws, while no larvae of extant Crocinae have such teeth. Accordingly, Makarkin *et al.* (2017) considered these crocine-like larvae

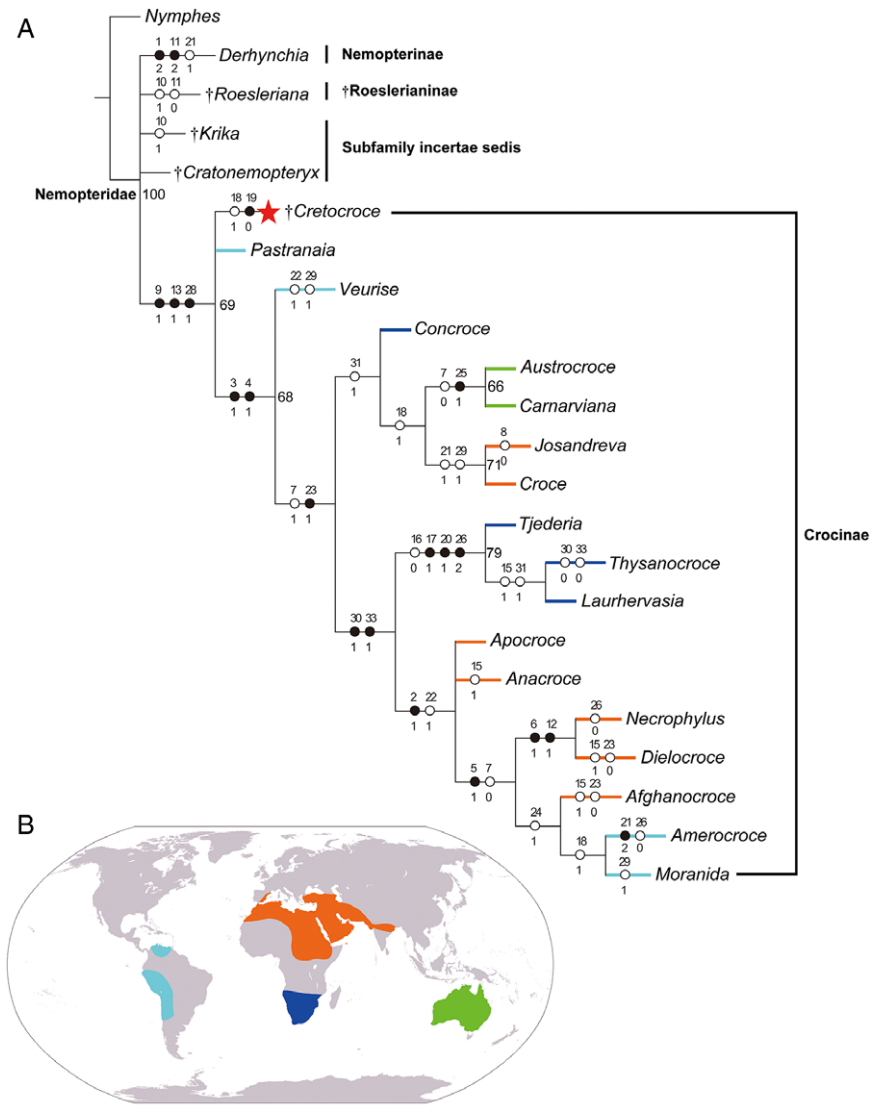


Fig. 6. Phylogenetic relationships among genera of Crocinae. (A) Strict consensus tree of the four most parsimonious trees herein generated. Unambiguous morphological character state changes are shown on the tree with a black circle as the homologous state and a white circle as the homoplasious state. Bootstrap values (≥ 50) are shown next to relevant nodes. The branch colour refers to the distribution area of each genus shown in panel (B). (B) Geographical distribution of Crocinae. Distribution records mainly follow Hölzel (1975) and Oswald (2018). The red star indicates the genus from the Burmese amber. [Colour figure can be viewed at wileyonlinelibrary.com].

as belonging to the antlion subfamily Araripeneurinae, but provided no supportive argument. The discovery of this adult crocine from Burmese amber provides direct evidence for the existence of Nemopteridae from the mid-Cretaceous of Myanmar. Thus, the possibility of crocine affinity for the aforementioned larvae cannot be excluded.

As mentioned earlier, extant Crocinae could be an indicator of arid or semiarid environment. However, the mid-Cretaceous palaeoenvironment of Myanmar is considered to be tropical with an average temperature range of 32–55°C (Grimaldi *et al.*, 2002), and rainforest is thought to be the dominant vegetation type in this area (Poinar & Poinar, 2008). It is noteworthy that several neuropterid families, e.g. Sialidae (Megaloptera)

and Nevrothidae (Neuroptera), with exclusive aquatic larvae are recorded from the Burmese amber (Liu *et al.*, 2017; Lu *et al.*, 2018). It indicates that the palaeoenvironment of mid-Cretaceous of Myanmar was unlikely to be arid or semi-arid, but warm and humid instead. As such, a dramatic habitat shift can be inferred between the new crocine genus from the mid-Cretaceous of Myanmar and its modern counterparts.

Feeding habits of Cretocroce gen.n.

Crocine larvae are predatory, and their prey are composed of psocids and dermestid larvae in natural conditions (Tjeder, 1967). Possessing a long rostrum indicates that crocine adults

are a kind of flower-visiting insect, similar to the adults of Nemopterinae. Their food is almost exclusively pollen, based on examination of gut contents (Tjeder, 1967; Monserrat, 1983). However, the plant species that serve as food resources for crocine adults are completely unknown. In the detailed ecological notes for southern African crocine species (Tjeder, 1967), adult specimens of different species were collected from various habitats, including dry area with scrub and bush, open woodland, sandy ground close to luxuriant riverine forest, and rocky mountain area with Cape alpine flora. Plants in the collecting sites mentioned by Tjeder (1967) comprise *Acacia*, *Prosopis* and Mopane trees, as well as *Euphorbia* and sedges. In addition, a South American species (*Moranida manselli* Miller & Stange) was reported to inhabit rocky limestone outcrops on top of mountains with xeric vegetation of cacti, agaves, etc., while pungent blooming agaves were noted as the only flowers around the area where adults were collected (Miller & Stange, 1989).

Compared with modern crocines, the adult mouthparts of *Cretocroce* **gen.n.** show little change in general morphology, having prolonged labrum, maxillae, and labium, associated with elongated clypeus into a rostrum. Nevertheless, the length of the rostrum in *Cretocroce* **gen.n.** is relatively short compared with most extant crocines, but similar to that of *Josandrewa* (see Monserrat *et al.*, 2012). In fact, the modifications of adult mouthparts between extant Crocinae and Nemopterinae are also generally similar (Tjeder, 1967), indicating possible analogous feeding behaviour. Nemopterinae are better documented for their flower-visiting behaviour than Crocinae, which lack direct evidence of flower-visiting (Monserrat, 1996; Krenn *et al.*, 2008). However, the similar mouthpart structures and detection of pollen in the gut content in both Crocinae and Nemopterinae suggest that crocine adults are also flower visitors. Thus, the present finding of Cretaceous Crocinae demonstrates that evolution of such insect–plant association predates the Cenomanian. *Cretocroce* **gen.n.** was most likely a pollinator of gymnosperms or angiosperms like its extant counterpart (Wardhaugh, 2015). Together with other mid-Cretaceous flower-visiting insects, including flies, thrips, scorpion flies, kalligrammatid lacewings, and beetles (Labandeira, 2010; Peris *et al.*, 2017), these insects may have played an important role in the terrestrial ecosystem.

Phylogenetic position of Cretocroce gen.n.

Our phylogenetic analysis corroborates the placement of *Cretocroce* **gen.n.** in Crocinae. The autapomorphies of *Cretocroce* **gen.n.** comprise male sternum 9 with strongly elongated projection and setose male gonocoxites 9. The setose male gonocoxites 9, however, are attributed to a plesiomorphic condition in our opinion, as it is present in Raphidioptera and some earlier diverged lacewing families, such as Nevrothidae (Aspöck & Aspöck, 2008). In extant Myrmeleontoidea, the male gonocoxites 9 usually lack setation (Aspöck & Aspöck, 2008). On one hand, if glabrous male gonocoxites 9 are also present in ancient Mesozoic Myrmeleontoidea, the setose condition in *Cretocroce* **gen.n.** could be considered an autapomorphy (unique derived character). On the other hand, the

setose condition in *Cretocroce* **gen.n.** could be plesiomorphic if it was widely present in Mesozoic Nemopteridae or other Myrmeleontoidea. In some Burmese amber Psychopsoidea, which is the sister group of Myrmeleontoidea, the male gonocoxites 9 are also setose and even present as a pair of external sclerites in some basal groups of Neuropterida (Lu *et al.*, 2016).

Within Crocinae, the new genus was recovered to be an earlier diverged group compared with the rest of the subfamily, but being either the sister group of the extant genus *Pastranaia* from South America or the sister group of the most extant crocine genera except *Pastranaia*. Morphology supporting the sister-group relationship between *Cretocroce* **gen.n.** and *Pastranaia* refers to long, digitiform male ectoprocts. Nevertheless, this character state is also shared by three other genera, i.e. *Afghanocroce* Hölzel, *Amerocroce*, and *Moranida*, all belonging to the crown lineage of Crocinae. The other possible phylogenetic position of *Cretocroce* **gen.n.** mentioned earlier, is supported only by the fusion of forewing CuP and A1. However, this character state can be also found in most Myrmeleontidae and Ascalaphidae.

Larval characters, particularly those of head and prothorax, are important for phylogenetic inference of Crocinae. Unfortunately, the larvae of *Cretocroce* **gen.n.**, as well as some extant genera, such as *Pastranaia*, are unknown. Thus, we must be cautious to interpret the phylogenetic position of *Cretocroce* **gen.n.** and relationships among the extant crocine genera based on the present result from limited morphological data. Nevertheless, the result is largely consistent with the hypothesis proposed by Mansell (1986). Future study on Burmese amber nemopterid larvae and molecular phylogenetics of extant Crocinae will develop further understanding on the phylogeny and evolution of this subfamily.

Biogeographical implications

Mansell (1986) proposed a Gondwanan origin of Crocinae based on their current distribution pattern. The present result of phylogenetic analysis seems to support this hypothesis, because most extant genera from southern Africa, Australia, and South America are assigned to more basal lineages, while all genera from the northern hemisphere appear to be more derived. The discovery of Crocinae from the mid-Cretaceous of Myanmar provides important evidence for understanding the biogeography of this subfamily. Morphological similarity and a possible close relationship between *Cretocroce* **gen.n.** and *Pastranaia* endemic to Argentina stand as an example showing that the organisms in Burmese amber have their closest extant relatives sharing a Gondwanan distribution (see Grimaldi *et al.*, 2002 and Poinar, 2018 for more examples). In Neuropterida, a similar faunal connection was reported in both Sialidae and Rhachiberthidae (Grimaldi *et al.*, 2002; Huang *et al.*, 2016). However, occurrence of these species from Burmese amber is also explained by formerly widespread distributions of 'austral' taxa followed by extensive extinction, rather than by indication of Gondwanan origin (Grimaldi *et al.*, 2002; Grimaldi & Engel, 2005; Huang *et al.*, 2016).

The estimated timing of lacewing diversification in a recent phylogenomic study (Winterton *et al.*, 2018) suggested that Crocinae and Nemopterinae might have diverged in the Early Cretaceous (~115 Ma). In this work, divergence time estimates among four crocine genera were presented, i.e. *Pastranaia*, *Austrocroce*, *Concroce* and *Necrophylus* Roux (Winterton *et al.*, 2018). Notably, *Pastranaia* was estimated to have diverged from the remaining genera at the end of Cretaceous (~65 Ma) (Winterton *et al.*, 2018). It is noteworthy that the estimated origin of Crocinae is contemporary with major rifting between Laurasia and Gondwana (Seton *et al.*, 2012). Thus, it suggests that a Pangaeian distribution of Crocinae is unlikely. So far, fossils of Crocinae as well as other nemopterids have not yet been found from any deposits of the Lower Cretaceous in the northern hemisphere, which indicates that Crocinae, perhaps even Nemopteridae, might have originated in Gondwana.

In light of Gondwanan origin of Crocinae in the Early Cretaceous, it is intriguing to consider the palaeofaunal relevance of the Burmese amber crocine. The mines of Burmese amber are on the West Burma Block (Cruickshank & Ko, 2003; Metcalfe, 2017), which was originally attached to Gondwana (Heine & Müller, 2005; Seton *et al.*, 2012). The West Burma Block was proposed to have initiated rifting from the northwestern margin of Australia in the Late Jurassic (~156 Ma) to reach its present location in Southeast Asia in the Late Cretaceous (~80 Ma) (Heine & Müller, 2005; Seton *et al.*, 2012). However, Metcalfe (2013) proposed that the West Burma Block would have been separated from Gondwana as far back as the Devonian and collided with Eurasia in the Triassic.

Based on any one of these two scenarios, the occurrence of Burmese amber Crocinae requires Early Cretaceous migration of this group from Gondwana, where it originated, to Laurasia. A Eurogondwanan migration proposed by Ezcurra & Agnolín (2012) may explain this palaeobiogeographical pattern. Similar migration was also reported to infer historical biogeography of Burmese amber velvet worms (Onychophora: Peripatidae) (Oliveira *et al.*, 2016). However, two issues should draw attention. First, the Eurogondwanan migration was estimated to take place during the earliest Cretaceous (Berriasian-Hauterivian, c. 145.5–130 Ma), which is slightly earlier than the origin of Crocinae (~115 Ma) estimated based on molecular data (Winterton *et al.*, 2018). Second, following the scenario of continental drift proposed by Seton *et al.* (2012), the West Burma Block was close to but had not collided with Eurasia by the mid-Cretaceous (~100 Ma). Thus, the colonization of Crocinae from Eurasia to the West Burma Block after the Eurogondwanan migration requires across-sea dispersal, which seems unlikely for the thread-winged lacewings as they are poor flyers.

Alternatively, an Early Cretaceous origin of Crocinae, as well as phylogenetic relationships between Burmese amber Crocinae and their extant austral relatives, match well a recently proposed hypothesis that the West Burma Block could not have rafted from Gondwana to Southeast Asia before the Early Cretaceous based on angiosperm and insect evidence (see Poinar, 2018). However, this scenario lacks sufficient geological evidence and needs further testing.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

File S1. Data matrix.

File S2. Four most parsimonious trees herein generated.

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Appendix. List of the characters coded for the phylogenetic analysis

Forewing:

- 1 RP+MA: (0) diverging from R near wing base, at most at proximal quarter of wing; (1) diverging from R at proximal third of wing; (2) diverging from R nearly at midpoint of wing.
 - 2 RP: (0) not approximating RA; (1) distinctly approximating RA, with several closely spaced radial crossveins.
 - 3 RP: (0) feebly curved posteriad; (1) distinctly curved posteriad.
 - 4 RP: (0) with some branches distally forked; (1) with all branches simple.
 - 5 MA: (0) initially branched near wing margin; (1) initially branched proximad its midpoint.
 - 6 CuA2: (0) longer than other branches of CuA; (1) distinctly shortened.
 - 7 CuP: (0) short, ending to wing margin approximately at proximal third of wing or more proximad; (1) long, ending to wing margin approximately at midpoint of wing.
 - 8 CuP and A1: (0) not fused; (1) proximally fused into CuP + A1.
 - 9 A3: (0) present; (1) absent
 - 10 Costal crossveins: (0) simple; (1) with some forked ones proximad pterostigma.
 - 11 Presectorial crossveins: (0) absent; (1) present, two or three; (2) present, more than five.
 - 12 Bulla: (0) absent; (1) present.
- Hindwing:
- 13 Venation: (0) not reduced distally; (1) largely reduced distally.
 - 14 Shape: (0) similar to that of forewing; (1) strongly narrowed and elongated.
 - 15 Bulla: (0) absent; (1) present.
- Male genitalia:
- 16 Tergum 9: (0) not paired; (1) paired due to dorsal incision.
 - 17 Tergum 9: (0) not strongly extending ventrad; (1) strongly extending ventrad.
 - 18 Sternum 9: (0) moderately convex posteriad; (1) strongly produced posteriad.
 - 19 Gonocoxites 9: (0) with many long setae; (1) hairless.
 - 20 Gonocoxites 9: (0) without gonosaccus; (1) medially with a gonosaccus.
 - 21 Gonocoxites 9: (0) not fused distally; (1) fused distally, but lacking a median large lobe; (2) fused distally by a large median lobe.
 - 22 Gonocoxites 9: (0) not vertically curved medially; (1) vertically curved medially.
 - 23 Gonocoxites 9: (0) with apex not inflated; (1) with inflated apex.
 - 24 Ectoproct: (0) short and valvate; (1) strongly elongated, digitiform.
 - 25 Gonocoxites 11: (0) not broadened laterally; (1) distinctly broadened laterally.
- Female genitalia:
- 26 Gonocoxites 8: (0) present, separated from gonocoxites 9; (1) absent; (2) present, fused with gonocoxites 9.
- Other characters:
- 27 Head: (0) without a long rostrum; (1) with a long rostrum.
 - 28 Procoxa: (0) nearly equal in length to meso- and metacoxa; (1) longer than meso- and metacoxa.
 - 29 Pleuritocavae: (0) absent; (1) present.
- Larva:
- 30 Head: (0) subquadrate; (1) nearly triangular due to vertex posteriorly narrowed.
 - 31 Pseudoteeth on jaws: (0) absent; (1) present.
 - 32 Prothorax: (0) not elongated. (1) elongated.
 - 33 Cervix: (0) not or feebly elongated; (1) strongly elongated, ~1.5× as long as prothorax; (2) strongly elongated, ~3.0× as long as prothorax.