

A new mid-Cretaceous cockroach of stem Nocticolidae and reestimating the age of Corydioidea (Dictyoptera: Blattodea)

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ABSTRACT

Nocticolidae are delicate cockroaches, characterized by simple but unique wing venation. They are included in Corydioidea with Corydiidae. No fossil of this family was reported. Here we describe a stem member of Nocticolidae, *Crenotricula burmanica* gen. et sp. nov., from mid-Cretaceous Burmese amber. Its morphology appears plesiomorphic for Nocticolidae, and exhibits transitional form between crown Nocticolidae and Latindiinae (in Corydiidae). Placing *Crenotricula* in stem Nocticolidae is confirmed by a preliminary morphological phylogeny based on 28 non-genital characters. We use *Crenotricula* and published fossils to calibrate dating analyses of Corydioidea under autocorrelated TK02 relaxed clock model in MrBayes, and the analyses in turn test the power of *Crenotricula* as a node calibration. The dataset comprises published DNA (12S, 16S, 18S and 28S) of 19 ingroup taxa of Corydioidea, and eight outgroup taxa including termites. As a result, *Crenotricula* is too young to be an effective calibration. It is suppressed by the oldest fossil of termites, which may also be crucial in previous studies provided that unjustified fossil calibrations (e.g. 'roachoids') are excluded. We compare two approaches to applying fossil calibrations: 1) in-analytical calibration, i.e. incorporating the fossil age in prior settings, and 2) post-analytical calibration, i.e. adjusting the fixed prior so that the estimated age does not conflict with the fossil age. In-analytical calibration may underestimate the age, whilst post-analytical calibration yields better estimates. Our dating analyses suggest that crown Corydioidea likely originated in the Late Triassic or Early Jurassic. Questionable genera in Nocticolidae are briefly discussed.

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1. Introduction

Nocticolidae are delicate, light-coloured cockroaches, they have membranous wings with reduced veins or do not have wings (Roth, 1988). Extant Nocticolidae are found in Africa, Australia, and Southeast Asia in the broadest sense (including southern China and Ryukyu) (Roth, 1988; Andersen and Kjærandsen, 1995; Trotter et al., 2017). Most of them live in caves, some in termite nets, and others in or under wet logs (Roth, 1988; Rentz, 2014; XRL, pers. obs.). In early taxonomic works, all cockroaches constituted a single family, Blattidae, in Orthoptera, and then nocticolid cockroaches were

Nocticolinae (Bolívar, 1892; but see Shelford, 1910a, Blattinae). In modern times, cockroaches are recognized as an order or suborder (Blattaria, Blattodea or other spellings), the Nocticolidae are among the families of cockroaches (from Bruner, 1915 to Beccaloni, 2014). Of many diagnostic characters of Nocticolidae suggested by Roth (1988), however, only few characters found in wing venation are decisive. Some characters of Nocticolidae are also present in other cockroaches and not useful alone. Nocticolidae are yet to be taxonomically revised: some genera may be synonyms of *Nocticola* (see Roth, 1988), and some are questionable in Nocticolidae (see section 4.1).

Recently, the phylogenetic position of Nocticolidae received much attention (e.g. Djernæs et al., 2015; Legendre et al., 2015; Wang et al., 2017). The male genitalia, which are essential in cockroach taxonomy, suggest close relationship between Nocticolidae and Corydiidae (Roth, 1988), which together constitute the Corydioidea. This was confirmed by recent molecular phylogenies

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(Djernæs et al., 2015; Legendre et al., 2015; Wang et al., 2017; Bourguignon et al., 2018; Evangelista et al., 2019), which recovered the following relationships: (Nocticolidae + Latindiinae) + Corydiidae excl. Latindiinae. The origin of crown Corydioidea was dated to the early half of Mesozoic (Djernæs et al., 2015; Legendre et al., 2015; Wang et al., 2017; Bourguignon et al., 2018; Evangelista et al., 2019); however, some cockroach fossils were used as dating calibrations before they are proven to be justified (Evangelista et al., 2017; Evangelista et al., 2019).

No fossil is recorded of Nocticolidae or of transitional forms between Nocticolidae and Latindiinae or other Corydiidae. Fossils are significant for tracing evolutionary history, estimating biodiversity, and calibrating dating. Here, we report a stem member of Nocticolidae from mid-Cretaceous Burmese ambers, and assess whether it is helpful for dating the Corydioidea.

2. Material and methods

2.1. Material and photo preparation

The ambers are from deposits in the Hukawng Valley of northern Myanmar (see Grimaldi et al., 2002, fig. 1). An amazing diversity of insects is preserved in Burmese ambers (Ross, 2019), of which the age is considered to be around the Albian-Cenomanian boundary (Ross et al., 2010; Shi et al., 2012; Rasnitsyn et al., 2016; Smith and Ross, 2018; Mao et al., 2018), likely latest Albian. We refer to the age as mid-Cretaceous until more precise data are available. Specimens are deposited at Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

Ambers were sanded with abrasive papers and polished with polishing powder. Photos were taken with a Zeiss AxioZoom V16 stereoscope and a Zeiss AXIO Imager Z2 microscope (green fluorescence); stacked using CombineZP (by Alan Hadley); and optimized using Photoshop CC 2015. The unit of measurements is millimetre.

2.2. Terminology and nomenclature

Morphological terminology largely follows Roth (2003); terms for wing venation follow Li et al. (2018). We use two names of taxa with autapomorphy-based definition: Dictyoptera *sensu* Ax (1999), = *sensu* Klass and Meier (2006), = *sensu* Inward et al. (2007); and Blattodea *sensu* Inward et al. (2007). Blattodea comprise monophyletic Isoptera, or termites, and paraphyletic Blattaria, or true cockroaches (Ax, 1999). This publication and nomenclatural acts herein were registered in ZooBank, and the LSID for this paper is urn:lsid:zoobank.org:pub:2373BD51-4E6E-40A6-8CE7-61F3C0C1CA20.

2.3. Phylogenetic inference

To examine the phylogenetic position of the new taxon, we perform parsimonious analysis and Bayesian inference. We select corydioid genera that have similar simple wing venation as the ingroup, including the new genus, all purported members of Nocticolidae, and six genera that were or are included in Latindiinae (Table 1). The composition of Latindiinae remains to be revised, but five genera are listed with confidence (Qiu et al., 2016; Lucañas, 2018): *Latindia* Stål, *Paralatinidia* de Saussure, *Sinolatindia* Qiu et al., *Gapudipentax* Lucañas, and *Austropolyphaga* Mackerras. Our taxaset does not include *Paralatinidia* due to lack of data. We include two genera whose subfamilial placement is unsettled: *Compsodes* Hebard, which was established upon former *Latindia*

Table 1 Genera included in morphological phylogenetic study and character score matrix.

Parent taxon	Genus/Char.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	Reference			
Nocticolidae	<i>Crenocicla</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	New genus	
Nocticolidae	<i>Nocticola</i>	1	1,2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	a; b; c; d	
Nocticolidae	<i>Alliuidellina</i>	1	1,2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	e; f; g	
Nocticolidae	<i>Cardacus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	f; h	
Nocticolidae	<i>Cardacopsis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	i	
Nocticolidae	<i>Metanocticola</i>	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	j	
? Nocticolidae	<i>Spelaeoblatta</i>	?	2	2	?	0,1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	k	
? Nocticolidae	<i>Helmhoblatta</i>	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	l	
? Nocticolidae	<i>Typhloblatta</i>	0	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	m; n	
? Nocticolidae	<i>Typhloblattodes</i>	?	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	o	
? Nocticolidae	<i>Pholeosiphia</i>	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	p
Corydiidae	<i>Homopteroidea</i>	1	1	1	1	1	1	1	1	1	1	1,2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	q; r; s	
Latindiinae	<i>Latindia</i>	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	q; r; s	
Latindiinae	<i>Sinolatindia</i>	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	q; r; s	
Corydiidae	<i>Compsodes</i>	1	1	2	?	0,1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	t; u
Latindiinae	<i>Austropolyphaga</i>	1	0	2	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	t; u; v; w
Latindiinae	<i>Gapudipentax</i>	1	1	2	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	x
Corydiidae	<i>Eucorydia</i>	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	y
Corydiidae	<i>Polyphaga</i>	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	z
Corydiidae	<i>Ergaula</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	za

References: a: Roth (1988); b: Roth and McGavin (1994); c: Andersen and Kjærandsen (1995); d: Trotter et al. (2017); e: Shelford (1910b); f: Gravely (1910); g: Chopard (1932); h: Shelford (1908); i: Kamy (1924); j: Roth (1999); k: Vidlicka et al. (2003); l: Vidlicka et al. (2017); m: Chopard (1924); n: Chopard (1946); o: Chopard (1958); q: photos from museums (see the text section 2); r: Roth (1995); s: Qiu et al. (2016); t: de Saussure (1870); u: de Saussure and Zehntner (1894); v: Hebard (1917); w: Gutiérrez (2012); x: Mackerras (1968); y: Lucañas (2018); z: Qiu et al. (2017); za: Qiu et al. (2018).

species (Hebard, 1917) and which is closely related to *Austropolyphaga* (Mackerras, 1968), and *Homopteroidea* Shelford, which shares many characters with *Latindia* and *Sinolatindia* (Qiu et al., 2016). According to previous studies (Djernæs et al., 2015; Legendre et al., 2015; Wang et al., 2017), three genera of Corydiinae are selected as outgroup (Table 1). The placement of some genera in Nocticolidae is debatable (see section 4.1), and those genera are marked with a question mark in Table 1.

Genital morphology is essential in phylogenetic studies of cockroaches (see McKittrick, 1964; Klass, 2001; Klass and Meier, 2006; Djernæs et al., 2015). However, few genital characters are available in fossils, and the documentation of the genitalia of Corydioidea is limited. Thorne and Carpenter (1992; see also Deitz et al., 2003) used many non-genital characters in the phylogenetic analysis of Dictyoptera, but most of the characters are either of order-level significance or unavailable in the present study. We use as many characters as available in the fossils and in the literature, and 12 out of 28 characters are of wings (Table 2). Please note that the wing-morph is not treated as a character (with macropterous, brachypterous and apterous as states), because it is potentially polymorphic and the polymorphism has been observed in many genera (for examples of *Nocticola* see Trotter et al., 2017; and also infraspecific polymorphism of *Alluaudellina cavernicola* in Chopard, 1932). Instead, when a certain wing-morph has not been observed, we treat corresponding characters as unknown rather than absent, and characters are scored a question mark. Morphological data are collected from previous studies (Table 1) or photos of the following specimens: *Latindia maurella* Stål, holotype, and *L. dohrniana* de Saussure and Zehntner in Swedish Museum of Natural History (Naturhistoriska riksmuseet), Stockholm (NRM),

and *Homopteroidea minor* Hanitsch in Oxford University Museum of Natural History (OUMNH).

Parsimonious analyses of the morphological phylogeny and of character change are performed in TNT 1.5 (Goloboff and Catalano, 2016), with collapsing rule set as “min length = 0” and searching algorithm as implicit enumeration. Bayesian inference of phylogeny is performed in MrBayes 3.2.6 (Ronquist et al., 2012). MCMC sampling stops when the average standard deviation of split frequencies between two independent runs is below 0.01; samples are taken every 1000 generations with 25% burn-in. We use Tracer 1.7.1 (Rambaut et al., 2018) to ensure sufficient samples. Topology is not constrained. We also use MrBayes to infer ancestral states of constrained nodes that are recovered from the previous analysis.

2.4. Divergence time estimation

The new taxon provides a chance to date Corydioidea, and the analyses in turn test the power of the new taxon as a node calibration. The analyses utilize published DNA sequences, which are downloaded from GenBank (Table 3). Eight outgroup species are selected from Blattoidea (Anaplectidae, Blattidae, Cryptocercidae, Lamproblattidae and Tryonicidae), Isoptera and Blaberoidea (Blaberidae and Ectobiidae). Of them, Blattoidea + Isoptera are sister to Corydioidea, and Blaberoidea are sister to Blattoidea + Isoptera + Corydioidea (Evangelista et al., 2019). Only four genes have good coverage of Corydioidea: mitochondrial 12S and 16S, and nuclear 18S and 28S; therefore we do not use other DNA fragments. Sequences are aligned using MUSCLE in MEGA7 with default settings (Kumar et al., 2016), and concatenated using Mesquite 3.51 (Maddison and Maddison, 2018). Data are divided into two partitions: mitochondrial rRNA

Table 2
Characters and scores for morphological phylogenetic study.

No.	Characters ^a with scores in parentheses
1	Head narrower [0] or wider than half the pronotum [1]
2 ^c	Ocular distance shorter [0] or longer [1] than that between antennal sockets, or eyes vestigial or absent [2]
3 ^c	Ocelli bulbous, bead-like [0]; vestigial, as fenestra or pale spots [1]; absent [2]
4	Clypeal suture developed, postclypeus larger than anteclypeus and usually swollen [0]; Clypeus simple, flat [1]
5	Pronotum length shorter [0] or longer [1] than 2/3 width
6	Pronotum densely pubescent [0] or not [1]
7	Pronotum with scattered long setae [1] or not [0]
8	Pronotum with tubercles [1] or not [0]
9	Pronotum with punctations [1] or not [0]
10	Pronotum with longitudinal median sulcation [1] or not [0]
11 ^c	Forewing at least partially heavily sclerotized, opaque to translucent [0]; modestly to weakly sclerotized, translucent to transparent [1]; almost membranous, transparent [2]
12 ^c	Fore- and hindwings with dense, curved longitudinal veins [0]; with modest longitudinal veins and cross veins, forming irregular network of cells [1]; with few essentially straight longitudinal veins [2]
13	Forewing humeral area broad and ScP often multi-branched [0]; narrow, ScP usually simple [1]
14	Forewing R with conspicuous pectinate branches [0] or not [1]
15	Forewing M and CuA have no much difference in branch number [0]; M simple or forked apically, i.e. has much fewer branches than CuA [1]
16	Forewing with [1] or without [0] diagonal channel
17 ^c	^b Typical number of veins that reach or almost reach the wing margin in the preclavus of the forewing: 8–12 [0]; 13–20 [1]; 21–30 [2]; 31–45 [3]; ≥46 [4]
18	Hindwing CuA with conspicuous pectinate branches [0] or not [1]
19	^b Hindwing vannus large, i.e. the span larger than half the length of vannal fold [0]; small [1]
20	Hindwing vannal veins branched [0]; simple [1]
21 ^c	^b Typical number of veins that reach or almost reach the wing margin in the prevannus of the hindwing: 8–12 [0]; 13–20 [1]; 21–30 [2]; 31–45 [3]; ≥46 [4]
22	Shape of reduced tegmen: oval, with attenuate base [0]; oval, with round base [1]; slightly angular and obliquely truncate, with blunt base [2]; hind margin sigmoid [3]
23	Plantulae absent [0]; present at four proximal tarsomeres [1]
24 ^c	Arolia absent [0]; tiny (shorter than basal width of the claws) [1]; small (longer than basal width of the claws and shorter than half length of the claws) [2]; modest (longer than half length of the claws and shorter than the claws) [3]; large (longer than the claws) [4]
25	Forefemur spination type CO [0]; C1 [1]; B [2]; A [3]
26	Hind tibiae except the distal end with many (≥16) spines [0]; fewer (≤12) spines [1]
27	Supra-anal plate nearly round rectangular, very short (usually shorter than half the width) [0]; nearly semicircular, triangular or nearly trapezoid (regardless of emargination) [1]
28	Male subgenital plate and styli symmetrical or nearly symmetrical [0]; more or less specialized [in different types 1,2,3...]

^a When inapplicable, characters are scored a question mark.

^b Applicable only to macropterous forms.

^c Ordered characters.

Table 3
Accession numbers of DNA sequences used for dating analyses.

Family: subfamily	Species with voucher or code ^a	12S	16S	18S	28S	Reference
Nocticolidae	<i>Nocticola australiensis</i> (IBE + DKE)	DQ874070	KF855864	DQ874158	DQ874234	Inward et al. (2007); Djernæs et al. (2015)
Nocticolidae	<i>Nocticola babindaensis</i> (DKE)	KF855785	KF855852		KF855819	Djernæs et al. (2015)
Nocticolidae	<i>Nocticola</i> sp. MNHN BL129		KP986313	KP986338	KP986373	Legendre et al. (2015)
Nocticolidae	<i>Nocticola</i> sp. NoctS01W01	MF286833			MF286962	Wang et al. (2017)
Nocticolidae	<i>Nocticola</i> sp. ZMUC:JD-1002		JN615302		JN615357	Djernæs et al. (2011)
Nocticolidae	<i>Nocticolidae</i> sp. BL131		EU253736	EU253695		Legendre et al. (2008)
Cor.: Latindiinae	<i>Latindia</i> sp. FL-2015	KP986263	KP986305	KP986332	KP986364	Legendre et al. (2015)
Cor.: Latindiinae	<i>Latindia</i> sp. MD-2014	KF855802			KF855822	Djernæs et al. (2015)
Cor.: Latindiinae	<i>Latindiinae</i> sp. MNHN BL128		KP986306	KP986333	KP986365	Legendre et al. (2015)
Cor.: Latindiinae	<i>Paralindia</i> sp. MD-2014	KF855803	KF855868		KF855823	Djernæs et al. (2015)
Cor.: Corydiinae	<i>Ergaula capucina</i> (IBE + DKE)	KF855789		DQ874130	DQ874214	Inward et al. (2007); Djernæs et al. (2015)
Cor.: Corydiinae	<i>Ergaula capucina</i> MNHN BL123	KP986254	KP986293		KP986384	Legendre et al. (2015)
Cor.: Corydiinae	<i>Ergaula</i> sp. ErgaS01E01	MF286823	MF286889		MF286955	Wang et al. (2017)
Cor.: Corydiinae	<i>Eucorydia purpuralis</i> EucoPurp01	MF286822	MF286888		MF286954	Wang et al. (2017)
Cor.: Corydiinae	<i>Eucorydia</i> sp. MNHN BL142		KP986294	KP986329	KP986355	Legendre et al. (2015)
Cor.: Corydiinae	<i>Polyphaga aegyptiaca</i> (IBE + DKE)	DQ874089	KF855871	DQ874177	DQ874248	Inward et al. (2007); Djernæs et al. (2015)
Cor.: Euthyrrhaphinae	<i>Euthyrrhapha pacifica</i> (IBE + DKE)	DQ874050	KF855861	DQ874137	DQ874218	Inward et al. (2007); Djernæs et al. (2015)
Cor.: Euthyrrhaphinae	<i>Holocompsa</i> sp. DJGI-2006	DQ874056	KF855862		DQ874223	Djernæs et al. (2015)
Cor.: Euthyrrhaphinae	<i>Tivia</i> sp. DJGI-2006	DQ874104	KF855874		DQ874259	Inward et al. (2007)
Cryptocercidae	<i>Cryptocercus kyebangensis</i> BL115	FJ805967	FJ806141	FJ806324	FJ806522	Svenson and Whiting (2009)
Cryptocercidae	<i>Cryptocercus</i> sp. BL120		FJ806143	FJ806326	FJ806524	Svenson and Whiting (2009)
Mastotermitidae	<i>Mastotermes darwiniensis</i> BYU IGC IS34	EU253710	EU253740	EU253778	EU253669	Legendre et al. (2008)
Rhinotermitidae	<i>Rhinotermes marginalis</i> BYU IGC IS61	EU253715	EU253754	EU253793	EU253674	Legendre et al. (2008)
Lamproblattidae	<i>Lamproblatta</i> sp. MNHN BL101	KP986262	KP986304	KP986331	KP986363	Legendre et al. (2015)
Blattidae	<i>Neostylopyga rhombifolia</i> MNHN BL105	KP986269	KP986312	KP986337	KP986245	Legendre et al. (2015)
Tryonicidae	<i>Tryonicus parvus</i> (DKE)	KF855799	KF855875	KF855844	KF855817	Djernæs et al. (2015)
Blaberidae	<i>Blaptica</i> sp. MNHN PG1	KP986251	KP986289	KP986326	KP986240	Legendre et al. (2015)

Cor. = Corydiidae.

^a The vouchers or codes were given in original text or GenBank; if not, we code the specimen with parenthesized acronym of the authors.

genes and nuclear rRNA genes. A better partition scheme is based on the secondary structure of RNA, which, however, is unavailable in the present study.

The analyses are performed in MrBayes. We do not use programs to select a 'best-fit' model, because the 'best-fit' is not necessarily the best or accurate (Kelchner and Thomas, 2007; Gatesy, 2007; Luo et al., 2010; Nascimento et al., 2017; Shepherd and Klaere, 2019). Instead, we choose the empirically generic model, GTR + I + G. Nodes of superfamilies, families and subfamilies are constrained according to previous studies (Djernæs et al., 2015; Legendre et al., 2015; Wang et al., 2017; Bourguignon et al., 2018; Evangelista et al., 2019); whenever the topologies are conflicting, we adopt the one inferred from the largest dataset.

Our taxaset contains many congeneric taxa and the families/subfamilies are closely related, therefore we choose the autocorrelated TK02 model (Thorne and Kishino, 2002; Ronquist et al., 2012) for the relaxed clock model. To explore the reasonable clock rate prior so as to avoid over-confident posterior estimates (dos Reis et al., 2014; Jin and Brown, 2018), we run a trial analysis in which we leave the rate prior default 'clockratepr = fixed(1.0)' and do not use calibrations. Then we obtain critical values of the clock rate by dividing the node height (the number of expected substitutions per site) by the age of fossils that are to calibrate those nodes. We use the new taxon to calibrate Nocticolidae + Latindiinae (100.5 Ma, see section 4.3 for details); the oldest termite, *Valditermes brenanae*, to Cryptocercidae + Isoptera (130.3 Ma, Wolfe et al., 2016); the oldest Euthyrrhaphinae, *Magniocula apiculata*, to Corydiinae + Euthyrrhaphinae (Qiu et al., 2019a; age as the new taxon). The log-normal rate prior is set so that: 1) probability of the interval from zero to the lowest of the three critical rates (obtained from *V. brenanae* in our case) is 95% (i.e. the 5% right tail starts from the lowest rate), and 2) the coefficient of variation is 20%.

In calibrated dating analyses, we use uniform priors for node age because the fossils are not informative about parameterization. All maximum bounds are set to 412 Ma, the oldest age of Rhynie Chert, as justified in Evangelista et al. (2019). The minimum bounds are set to the age (or minimum possible age when a precise age is unavailable) of the corresponding fossils (see above). For comparison, we also perform analyses with fixed rate prior by reference to the empirical estimations (Papadopoulou et al., 2010; Andújar et al., 2012). The rate varies due to different sampling of taxa and gene fragments and to other factors, therefore we explore a rate range. Since the estimated rate of ribosomal genes roughly ranges from 0.0006 to 0.006, and our dataset has a bias towards nuclear genes (particularly 18S which has very low K2P distance, 0.0597, compared with 12S: 0.4321, 16S: 0.4210, 28S: 0.1350), we perform analyses with every 0.0001 from 0.0001 to 0.0015. Finally, we arbitrarily choose a result, in which the posterior rate multipliers appear the most reasonable: excluding certain clades that evolve dramatically faster (Nocticolidae + Latindiinae in our case, see also Legendre et al., 2015; Bourguignon et al., 2018), the multipliers are neither too large nor too small (like 0.5–2), and the average of them approaches one.

The aforementioned procedure is typical of age estimation, termed in-analytical calibration, which incorporates the fossil age in prior settings. In-analytical calibration using MrBayes may yield biased results (see sections 3.3.1 and 4.4). Therefore, we perform additional analyses (on the contrary, post-analytical calibration) to explore more accurate estimates. The goal is that either the node of Cryptocercidae + Isoptera or its 95% CI is 'naturally' (in an uncalibrated analysis) older than *Valditermes brenanae*. We use fixed rate prior otherwise the posterior estimate of rate is always higher than the mean of prior distribution. We use fixed TK02 rate variance

prior to ensure reasonable rate multipliers, otherwise the posterior estimates of multipliers are always too large under the combination of estimated TK02 variance and low fixed rate.

Depending on the strategy of dating analysis, MCMC runs one million to five million iterations with 10% or 25% burn-in; samples are taken every 1000 iterations. We use Tracer 1.7.1 (Rambaut et al., 2018) to ensure sufficient samples. Results of the analyses are visualized using FigTree 1.4.3 (Andrew Rambaut, tree.bio.ed.ac.uk/software/figtree), and annotated using Adobe Illustrator CS6.

3. Results

3.1. Systematic palaeontology

Order Dictyoptera

Clade Blattodea

Suborder Blattaria

Family Nocticolidae Bolívar, 1892

Genus *Crenotricula* new genus

(LSID: urn:lsid:zoobank.org:act:1F84B82F-AC23-4F0F-BD69-A9F7E24240C8)

Type species: *Crenotricula burmanica* new species, original monotypy.

Etymology. *Cre.*, abbreviation for *Cretaceus*, namely Cretaceous; *nocticola*, the exact spelling of the type genus of Nocticolidae. Feminine.

Diagnosis (male only). Small, delicate, light-coloured. Head wider than half the width of pronotum; eyes moderate in size; ocellar fenestra cuneiform. Pronotum without protrusions or sharp angles, widest at posterior third; dorsad with scattered long setae. Wings membranous, minutely pubescent; veins few, essentially straight; more pubescent along veins; clavus and vannus small. Forefemur spination type C1. Middle and hind femora with two long distal spines: one anterodorsal, larger, the other anteroventral, smaller. Plantula and arolium absent; claws symmetrical, unspecialized. Cerci long, tapered. Subgenital plate symmetrical or nearly symmetrical, styli short, similar. Hook-like phallomere at left side, elongate, partially exposed; inner side of the hook with some long setae at the distal part of the shank and proximal part of the bend.

Taxonomic justification. The wing venation of *Crenotricula* gen. nov. is simple compared to most cockroaches. The forewings and hindwings are both membranous, the main veins are essentially straight and the clavus and vannus are small, these include *Crenotricula* into Nocticolidae, of which the unique, simple wing venation is largely used to define this family (Roth, 1988). The following characters are shared between *Nocticola* and the type species of *Crenotricula*: small body size, large head in relation to the pronotum, rounded pronotum, forefemoral spination of type C1, sparse tibial spines of all legs, absence of plantula and arolium, trapeziform supra-anal plate with emarginated hind margin, long cerci with tapered apex, and elongate hook-like phallomere with long setae on inner side (see Andersen and Kjærandsen, 1995; Trotter et al., 2017). These similarities, particularly in legs and genitalia, suggest a close relationship between *Nocticola* and *Crenotricula* gen. nov.

Crenotricula burmanica sp. nov. (Figs 1–3)

(LSID: urn:lsid:zoobank.org:act:75A17C6E-8792-4447-81BC-CB924291B53E)

Materials. Four male adults preserved in four ambers: holotype NIGP168931 (Fig. 1A–B); paratype NIGP168932 (Fig. 1C–D); paratype NIGP168933 (Fig. 1E–F); paratype NIGP170327 (Fig. 1G–H).

Etymology. Type locality, Myanmar, also known as Burma.

Description (male only). Body length 2.9–3.4, overall length including wings 4.0–4.5. Head (Fig. 2A): width including eyes 0.70–0.73, length from vertex to apex of mandible 0.80–0.81; ocular distance at vertex 0.43–0.45, antennal sockets distance 0.23–0.25; vertex convex, darker than frons; ocellar fenestrae conspicuous; antennae longer than the length from vertex to the tip of cercus; maxillary palpomere 1–5 lengths 0.04–0.05/0.09–0.10/0.19–0.23/0.16–0.22/0.18–0.23 (Fig. 2B). Pronotum (Fig. 2C,D): length 0.78 and width 0.99, ratio 1:1.27; almost flat, anterior margin and disc slightly convex; the long setae are denser along anterior and lateral margins than in the centre (some 24 setae around the promotal margin). Wings: shoulder width (between bases of forewings) 0.84–0.86; forewing length 3.0–3.7 and width 0.88, ratio 3.4–4.2, clavus length 1.05 (longitudinal projection 0.99) and width 0.27; ScP merging into costo-marginal vein (Fig. 3B); R/M/CuA with 8/3/3 terminal veinlets including intercalary veins, two more intercalary veins between R and M, and between M and CuA; CuP is the only observable vein in clavus; veins in the anterobasal part bear scattered setae. Hindwings exceeding (not necessarily longer than) forewings (Fig. 1); length 2.8–3.6, width of prevannus 0.9, length of vannal fold 1.2, width of vannus 0.5; ScP/RA/RP/M/CuA with 1/2/3–5/3/2 terminal veinlets including intercalary veins, two more intercalary veins between R and M, and between M and CuA (Fig. 3C–E); CuP unobservable or absent; Pcu(?) and V[1](?) simple. Venation pattern variable, even differs between the left and right wings of an individual (cp. Fig. 3A,B; cp. Fig. 3C–E). Leg segments length (femur/tibia/tarsomere 1/2/3/4/5): foreleg 0.88–1.08/0.57–0.77/0.38–0.50/0.11–0.15/0.08/0.06/0.11–0.12, midleg 0.95–1.13/0.84–1.08/0.55–0.73/0.14–0.18/0.08–0.10/0.05–0.06/0.10–0.15, hindleg 1.19–1.34/1.43–1.65/0.78–0.96/0.20–0.25/0.10–0.12/0.06–0.07/0.13–0.15. Anteroventral margin of femur with a row of spinules, terminating in one larger spine (Fig. 2E). Tibia with four distal long spines; additionally, foretibia with one outer (near apex) spine, midtibia with one anterior, two outer, and two posterior long spines (five spines arrange in three rows), hindtibia with one anterior, three outer, and three posterior long spines (seven spines arrange in three rows). Claws symmetrical, unspecialized (Fig. 2F). Terminalia: Supra-anal plate nearly trapezoid with round margin (Fig. 2G), exceeding subgenital plate; cerci length 0.98–1.20, tapered, with some ten segments (Fig. 1); subgenital plate with truncate hind margin, styli short, similar, far apart (Fig. 2H); hook-like phallomere long, partially exposed, the hook strongly bending backwards, with ten long setae sparsely aligned on the inner side of the distal part of the shank and proximal part of the bend (Fig. 2I).

Remarks. The interpretation of hindwing venation is provisional. According to Li et al. (2018), we identify a fusion of RP and M, because the anterior branch of this bifurcation extends to the anterior wing margin, and the posterior one to the wing apex, and also a short basal fusion of RP + M is sometimes found in cockroaches. This is likely the case, but requires evidence from extant Nocticolidae. We did not identify a CuP, and this vein may be absent or invisible due to preservation. Instead, we interpret a strong vein as Pcu, because this vein exhibits no connection with CuA, and Pcu is much stronger than CuP in relatively simple venation (see Li et al., 2018). We interpret a V[1] because it runs along the vannal fold. Identification with confidence requires an investigation of the wings of Nocticolidae, which is unavailable to us and not found in the literature. Characters regarding CuP, Pcu and V are not used in the phylogenetic inference. The infraspecific variation of wing venation pattern in Nocticolidae has been reported (Gravely, 1910; Andersen and Kjærandsen, 1995; Trotter et al., 2017), and the variation found in the present study is insufficient to recognize different species.

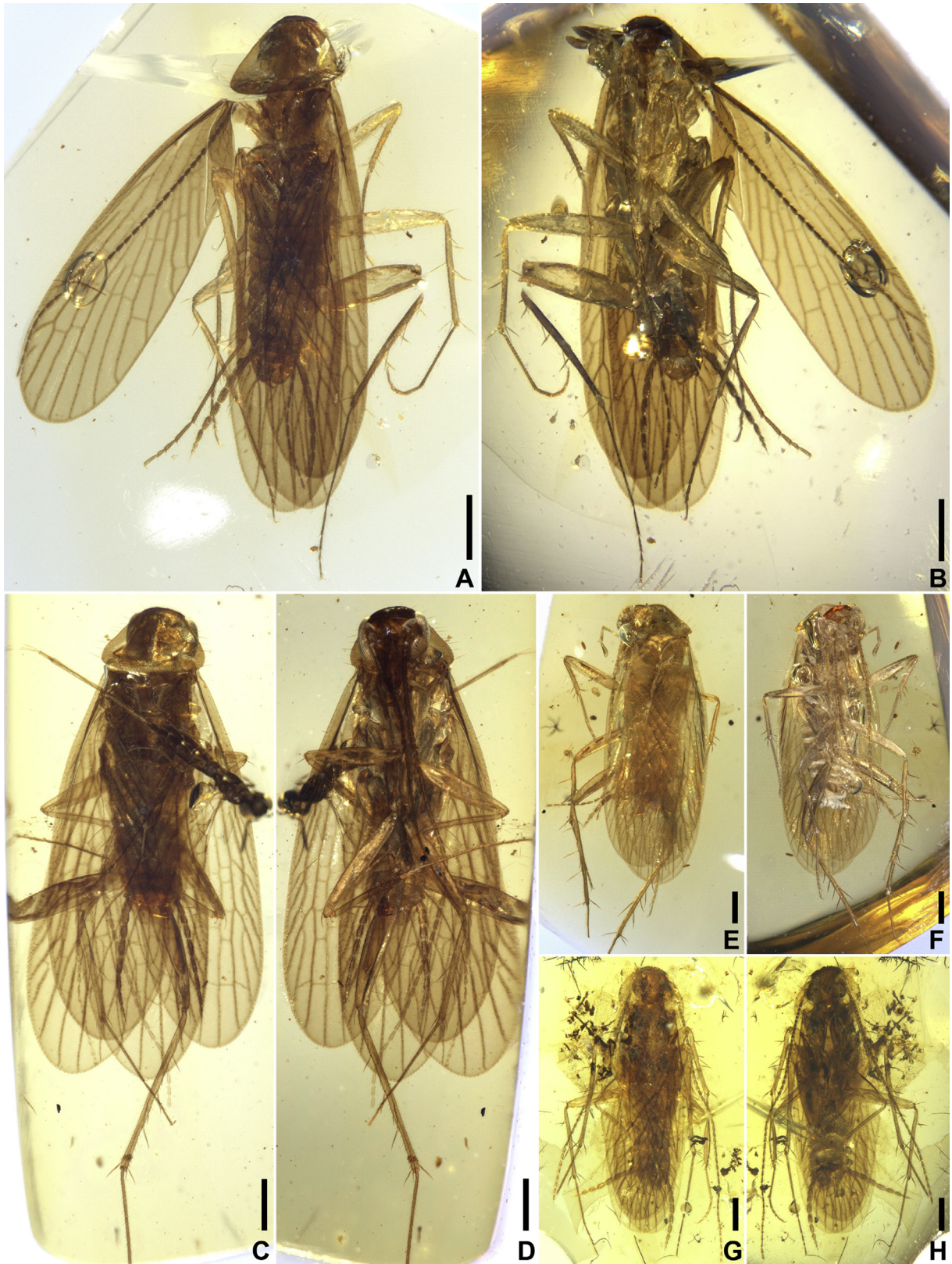


Fig. 1. *Crenotricula burmanica* gen. et sp. nov. A–B. Holotype NIGP168931. C–D. Paratype NIGP168932. E–F. Paratype NIGP168933. G–H. Paratype NIGP170327. Scale bars: 500 μ m.

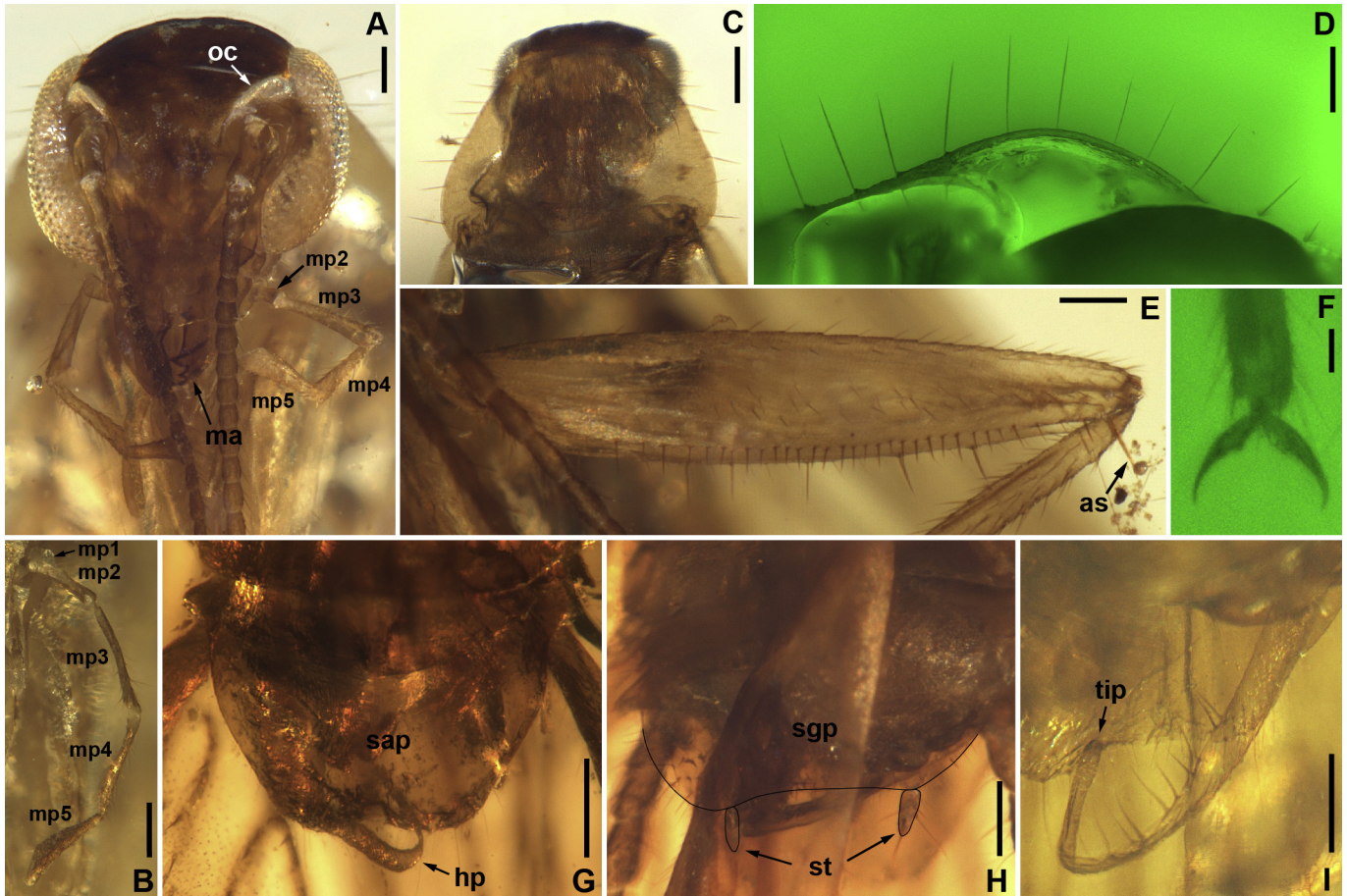


Fig. 2. Details of *Crenotricula burmanica* gen. et sp. nov. **A.** Head of paratype NIGP168932, note that the maxillary palpomeres are not in a plane and therefore the lengths (actually projection lengths) are incomparable. **B.** Maxillary palus of holotype NIGP168931, note that the first palpomere (mp1) is much thicker than the second (mp2). **C.** Pronotum of paratype NIGP168932. **D.** Pronotal setae (along anterior margin) of paratype NIGP168933, cephalic view. **E.** Forefemur of paratype NIGP168932, anterior view. **F.** Left midclaws of paratype NIGP168933. **G.** Supra-anal plate of holotype NIGP168931, dorsal view, with the exposed hook-like phallomere (hp). **H.** Subgenital plate of paratype NIGP168932, nearly ventral view, with emphasized outline of hind margin of subgenital plate and styli. **I.** Hook-like phallomere of paratype NIGP170327, ventral view. Abbreviations: as, apical spine; ce, cercus; hp, hook-like phallomere; ma, mandible; mp1–5, maxillary palpomere 1–5; oc, ocellus; sap, supra-anal plate; sgp, subgenital plate; st, styli. Scale bars: A,B,D,E,G,H,I, 100 μ m; C, 200 μ m; F, 20 μ m.

3.2. Phylogenetic inference

The analyses of the complete taxaset (20 genera) yielded implausible topology (Figs. S1 and S2); therefore we removed the five questionable genera purported to be Nocticolidae (see section 4.1), and re-performed the analyses. The parsimonious and Bayesian morphological phylogenies (Fig. 4) both recover the sister clades of *Crenotricula* and crown-Nocticolidae, i.e. a clade of Nocticolidae; this coincides with our taxonomic proposal. *Homopteroidea* is recovered as sister to Nocticolidae. Relationships among Latindiinae genera are not resolved. Reconstructions of character state changes suggest that the evolutionary history of Nocticolidae involves forewing thinning and severe reduction of wing veins.

3.3. Dating of Corydioidea

3.3.1. In-analytical calibration

In trial analysis, the minimum limit of substitution rate, 0.00125, resulted from the node of Cryptocercidae + Isoptera. Therefore the rate prior is set to 'lognormal (-7.0105, 0.1981)', of which the mean is 0.00092. The posterior estimate of the rate is 0.00133 (95% credibility interval 0.00106–0.00165), falling in the 5% tail of the prior; this suggests a statistical tendency towards higher rate. Of the

fixed rate analyses, we choose the one with rate prior 0.0008, of which the posterior rate multipliers appear most plausible and slightly larger than that in the log-normal rate prior analysis (Fig. 5). The posterior rate multipliers significantly increase as the fixed rate prior lowers. Two dating analyses, with log-normal rate prior and fixed rate prior, yield very close age estimates (Fig. 5), in which the 95% HPD of the Corydioidea age falls roughly in 115–140 Ma. Crown Nocticolidae + Latindiinae originated soon after crown Corydioidea, whilst crown Corydiinae + Euthyrrhaphinae are slightly younger. The node of Cryptocercidae + Isoptera has a very narrow credibility interval adjacent to the minimum bound, which indicates a conflict between the base substitution rate and the fossil age. The fossil calibration of this node, *Valditermes brenanae*, thus suppresses other two fossils, including *Crenotricula*.

3.3.2. Post-analytical calibration

In contrast to the results above, all credibility intervals in these analyses are of reasonable length and unbiased (Fig. 6). Therefore, the age estimates by post-analytical calibration are more reliable than that by in-analytical calibration. The estimated ages are much older. Crown Corydioidea are older than 170 Ma, and crown Nocticolidae + Latindiinae are older than crown

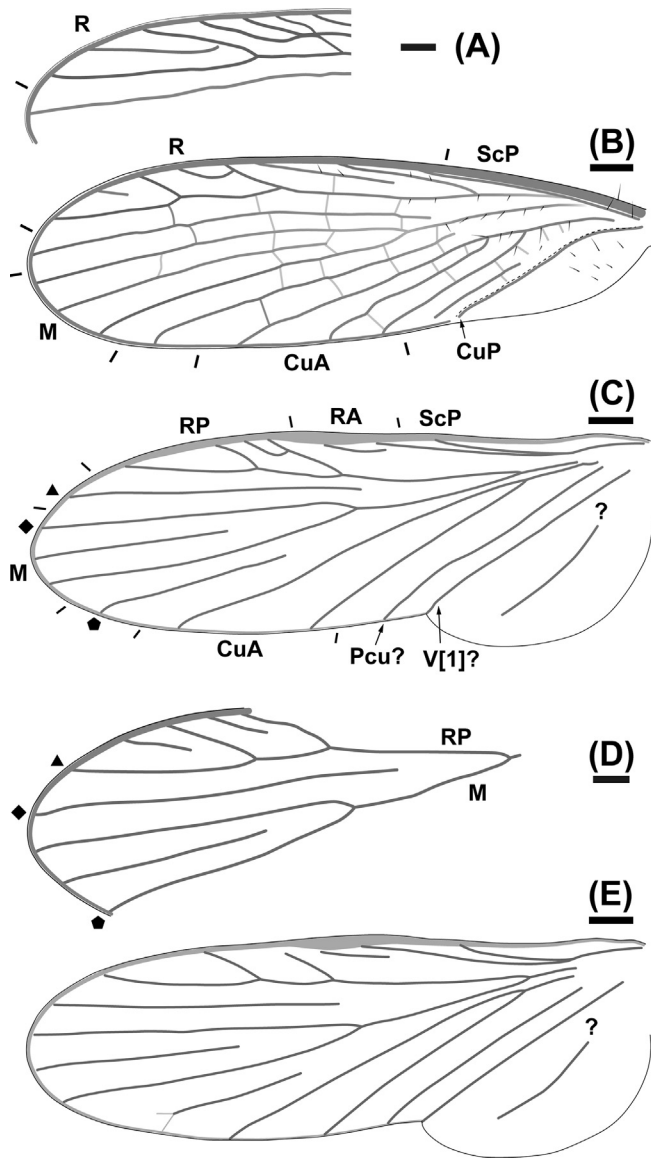


Fig. 3. Wings of *Crenocticola burmanica* gen. et sp. nov. **A.** Radial branches of the right forewing of paratype NIGP168932, ventral view, for comparison with **B.** Left forewing of holotype NIGP168931, dorsal view, minute pubescence omitted. **C.** Left hindwing of holotype NIGP168931, dorsal view. **D.** RP + M of left hindwing of paratype NIGP168932, dorsal view, for comparison with **C** and **E.** **E.** Right hindwing of holotype NIGP168931, ventral view. Question marks in **C** and **E** denote blurred basal connection of veins. Polygons in **C** and **D** indicate corresponding positions where the veins are of different identity: triangle, the intercalary vein between RP and M (**C**) or a branch of RP (**D**); diamond, a branch of M (**C**) or the intercalary vein between RP and M (**D**); pentagon, the intercalary vein between M and CuA (**C**) or a branch of M (**D**). The veins in **E** do not occur at the corresponding positions. Scale bars: 200 μ m.

Corydiinae + Euthyrrhaphinae. *Valditermes brenanae* still supresses other two fossil calibrations.

4. Discussion

4.1. Questionable genera in Nocticolidae

Some cockroaches, particularly cave dwellers, were included in Nocticolidae for delicate body, less pigmentation and reduced eyes. However, they differ from *Nocticola* (the type genus) in key characters and may be remote from Nocticolidae. These genera are: *Spelaeoblatta* Bolívar, *Typhloblatta* Chopard, *Typhloblattodes*

Chopard, *Pholeosilpha* Chopard, and *Helmablatta* Vidlička et al.. These genera were included in trials but excluded from formal analyses. We do not intend to clarify the phylogenetic position of these genera, because the actual position of them is likely outside the ingroup defined herein. Consequently, a phylogenetic analyses for these genera requires a large taxon sampling and redefining an outgroup; this is beyond the scope of the present paper and definitely needs the help of molecular data. Here we list some characters that may exclude these genera from Nocticolidae.

Spelaeoblatta (see Roth and McGavin, 1994; Vidlička et al., 2003): a pronotum with posterolateral extensions, a tegmen with relatively general venation pattern of cockroaches (instead of *Nocticola*-like), distinct forefemoral spination type (B1, instead of C1), and prickly legs.

Typhloblatta (see Chopard, 1921,1924): distinct forefemoral spination type (B2, instead of C1), and prickly tibiae.

Typhloblattodes (see Chopard, 1946): none.

Pholeosilpha (see Chopard, 1958): a tegmen with relatively general venation pattern of cockroaches (instead of *Nocticola*-like), distinct forefemoral spination type (B2, instead of C1), arolia present, and prickly legs.

Helmablatta (see Vidlička et al., 2017): a pronotum with posterolateral angles, a tegmen with broad humeral area (whilst no other veins than ScP were observed), and distinct forefemoral spination type (intermediate between A1 and B1, instead of C1).

Spelaeoblatta is relatively well described, its placement in Nocticolidae has not been doubted since Princis (1966) first listed it under Nocticolidae. However, the wing venation readily excludes this genus from Nocticolidae and Latindiinae. Besides, the forefemoral type B1 is unusual for Corydioidea. *Typhloblatta*, *Typhloblattodes* and *Pholeosilpha* were listed under Blattellidae (now Ectobiidae) by Princis (1969), and marked with a question mark by Roth (2003) though under Nocticolidae. Among the three, *Typhloblattodes* is poorly known and the taxonomic position remains uncertain; *Typhloblatta* and *Pholeosilpha* have distinct forefemoral spination type (B2) from Corydioidea (usually C1); the wing venation readily excludes *Pholeosilpha* from Nocticolidae and Latindiinae. The recently described *Helmablatta* appears a member of Nocticolidae, and the original authors (Vidlička et al., 2017) placed it in the family because of “small size, reduced coloration, reduced eyes and setation”, which, however, are not decisive characters for Nocticolidae. The broad humeral area of forewing and the alternate large and small spines of forefemoral spination are unusual for Nocticolidae. Vidlička et al. (2017) considered the phylogeny based on H3 gene as evidence of their taxonomic proposal. However, the DNA sequence used is too short (280 bases) and most of the top 20 BLAST results (on NCBI website) are not cockroaches, with virtually the same low identity, ca. 88%. The results comprise 14 Gastropoda (87.14%–88.36% identity), three Trichoptera (88.41% identity), one Coleoptera (88.52% identity), and two *Nocticola* (88.00%–88.36% identity). This DNA fragment is not informative for phylogenetic inference.

4.2. Phylogenetic relationships of *Crenocticola* and Nocticolidae

Nocticolidae are characterized by their unique wing venation. In the key to families in Roth (2003), Nocticolidae are differentiated from other cockroaches by a set of characters. Only those regarding wing and wing venation are decisive, and deemed to be autapomorphies among cockroaches, though Roth (2003) did not perform a computational phylogenetic analysis. Compared to modern macropterous Nocticolidae (Fig. 4; see also Gravely, 1910; Chopard, 1932), *Crenocticola* has more veins, the hindwing is more developed, and the vannus is larger. The comparatively developed wing venation excludes *Crenocticola* from crown Nocticolidae. On the

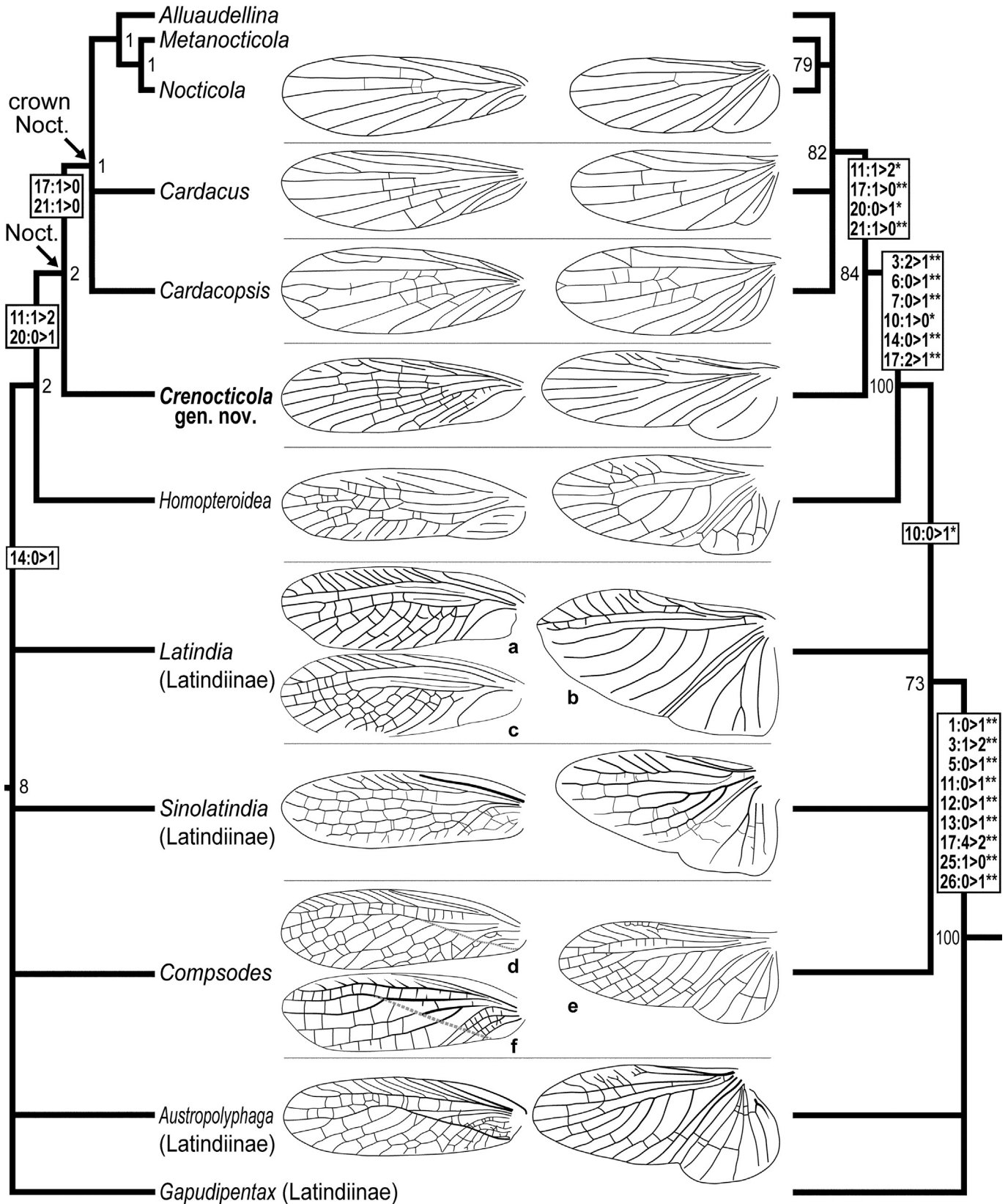


Fig. 4. Selected wing venation and phylograms with outgroup omitted. Left phylogram, strict consensus of five most parsimonious trees (49 steps), with Bremer support values to the right of nodes; right one, Bayesian inference, with posterior probabilities (percentage) to the left of nodes. The boxed are ancestral state changes, one asterisk—posterior probability larger than 0.8 at both nodes, two asterisks—posterior probability larger than 0.95 at both nodes. Wings to the left, forewings; wings to the right, hindwings. Wings from top to bottom: *Nocticola adebratti* Roth, 1994, modified from Roth and McGavin (1994); *Cardacus willeyi* (Shelford, 1908) modified from Gravely (1910); *Cardacopsis shelfordi* Karny, 1924, modified from Karny (1924); *Crenoticola burmanica* gen. et sp. nov. herein; *Homopteroidea nigra* Shelford, 1906, modified from Roth (1995); *Latindia dohrniana* de Saussure and Zehntner, 1894 (insets a, b), modified from de Saussure and Zehntner (1894); *Latindia pectinata* Rehn, 1937 (inset c), modified from Rehn (1937); *Sinolatindia petila* Qiu et al., 2016, modified from Qiu et al. (2016); *Compsodes mexicana* (de Saussure, 1868) (inset d, e), modified from de Saussure (1870); *Compsodes cucullata* (de Saussure and Zehntner, 1894) (inset f), modified from de Saussure and Zehntner (1894); and *Austropolyphaga perkinsi* Mackerras, 1968, modified from Mackerras (1968).

other hand, the wing venation of *Crenotricula* and suchlike forms are likely plesiomorphic for Nocticolidae, because Nocticolidae exhibit a tendency towards wing and wing vein reduction.

Previous molecular phylogenetic studies suggested that Nocticolidae are sister to Latindiinae, which were represented by *Latindia* and *Paralattindia* only (Djernæs et al., 2015; Legendre et al., 2015). *Crenotricula* gen. nov. supports this view because it exhibits transitional morphology between modern Nocticolidae and Latindiinae (and also Latindiinae-like genera) (Fig. 4). The morphological phylogenies (Fig. 4) suggest a closer relationship of Nocticolidae to *Homopteroidea* than to *Latindia*, *Sinolatindia* and *Compsodes*; *Austropolyphaga* and *Gapudipentax* are distant. This implies that *Homopteroidea* would be crucial in future phylogenetic studies of Latindiinae and Nocticolidae, and those studies would in turn better justify the calibration position of *Crenotricula*. In addition, the concept of Latindiinae remains vague and this subfamily needs a taxonomic revision.

4.3. *Crenotricula* as a fossil calibration

Crenotricula can serve as a fossil calibration in dating analyses (Figs 5, 6). Suitable fossil calibrations of cockroaches are rare, and the most common reason for ruling out a fossil as a calibration is poorly supported systematic placement (Evangelista et al., 2019). Evangelista et al. (2017) recommended four cockroach fossils for node calibration, whilst Evangelista et al. (2019) discarded one of them. *Crenotricula* can calibrate the node of Nocticolidae + sister group. We elucidate the adequacy of *Crenotricula* based on the five criteria suggested by Parham et al. (2011). (1) Type specimens of *Crenotricula burmanica* gen. & sp. nov. are kept at NIGP collection with accession numbers. (2) The phylogenetic placement of *Crenotricula* is clear: it possesses the autapomorphies of Nocticolidae and less derived than crown Nocticolidae, therefore it is a member of stem Nocticolidae (see above for details). (3) Molecular phylogenies agreed that the sister group of Nocticolidae is Latindiinae, no discrepant topologies inferred from various works or datasets are found. Given the insufficient sampling of Corydioidea, however, new data would probably reveal a closer sister group of Nocticolidae. Morphological phylogeny is lacking. The preliminary phylogenies herein cannot substitute for a phylogeny based on extensive genital characters. (4) & (5) Although there is uncertainty about the age of Burmese amber, the geological context is clear enough and allows a reliable calibration. The locality of Burmese amber is famous (see Grimaldi et al., 2002), and this guarantees that relevant data are readily accessible. Shi et al. (2012) dated Burmese amber at 98.79 ± 0.62 Ma based on zircon U–Pb SIMS. According to Mao et al. (2018), the zircon U–Pb SIMS age may be younger (possibly more than 1%) than the actual age due to methodological limits. Following Mao et al. (2018), we interpret the age as Early-Late Cretaceous boundary, namely 100.5 Ma, until more precise data are available. This age is also in accord with a synthesis of previous studies (Ross et al., 2010; Rasnitsyn et al., 2016; Smith and Ross, 2018). Besides, a difference of 1.7 Ma virtually has no impact on the dating of 100 Ma magnitude.

On the other hand, *Crenotricula* is too young to set the minimum bound of Nocticolidae + Latindiinae, provided the data are appropriately modelled herein. In our analyses (Fig. 6), *Crenotricula* is 60–70 Ma younger than the min of the 95% credibility interval of the node. Too young is the second cause of discarding a fossil calibration (Evangelista et al., 2019). Another example is *Proholocompsa fossilis* (Shelford, 1910) from Baltic amber. This fossil is well justified in Holocompsini (Gorokhov, 2007; but see Anisyutkin, 2008). Unfortunately, the age of Baltic amber is believed to be either middle Eocene (ca. 44.1 Ma, see Wappler, 2003) or late

Eocene (ca. 37.7 Ma, see Perkovsky et al., 2007), and thus too young to set the minimum bound of Holocompsini + sister.

Alternatively, *Crenotricula* may be used as a tip calibration, either in a morphological dating, or in a total evidence dating. Every informative fossil has the potential to be a competent tip calibration, e.g., *Paraeuthyrrhapha Anisyutkin*, 2008; *Nodosigalea Li and Huang*, 2018; and *Huablattula Qiu et al.*, 2019b, but such a dating analysis is not promising in the near future. One of the difficulties in using these fossil calibrations is the absence of adequate evolutionary models (Ronquist et al., 2016), and the other is the lacking in data of relevant living taxa.

4.4. Comparison between calibration strategies

In the in-analytical calibration analyses, crown Corydioidea originated in the Early Cretaceous (Fig. 5). Given the narrow credibility interval (CI), which is adjacent to the minimum bound, of the age of Cryptocercidae + Isoptera, Early Cretaceous is an underestimation, and the posterior substitution rate is overestimated. Besides, it is unrealistic that *Valditermes brenanae*, a termite with apomorphies of crown Isoptera, exists immediately after Isoptera and Cryptocercidae split. *Valditermes brenanae* also causes a narrow CI in dating analyses of insect orders (e.g. Misof et al., 2014) and of Dictyoptera (e.g. Evangelista et al., 2019). The issues in Misof et al. (2014) and our analyses (Fig. 5) are alike, but note that Evangelista et al. (2019) is not the case. The CI in Evangelista et al. (2019) is technically sound (MCMCtree prevents over-confident posterior estimates), but partially conflicts with the fossil age; although this is allowed by the soft bound, the effective CI that is compatible with *Valditermes brenanae* is only 16.7 Ma. A narrow CI can also result from other fossil calibrations, e.g. *Mylacris anthracophila* in Bourguignon et al. (2018). Using larger time unit (e.g. 10 Ma or 100 Ma, instead of 1 Ma as usual) in in-analytical calibration can relax the over-confident posterior estimates (narrow CIs). In this approach, however, the CIs are too wide (uncertainty is too high) to tolerate. 10 Ma appears to reach a compromise between a reasonable CI and the uncertainty, but age estimates are still biased (Fig. S3).

In the post-analytical calibration analyses, the issues above are corrected, and the abnormally narrow CI does not exist (Fig. 6). Although post-analytical calibration is more arbitrary, we consider the results more reliable. An alternative approach to post-analytical calibration is simply adjusting the time scale factor in tree visualizing software, e.g. FigTree, with an uncalibrated input tree. An analysis under default clock rate settings appears the easiest. However, the negative correlation between time unit and certainty is also an issue in post-analytical calibration. The time unit in default settings is the number of expected substitutions per site (see Command Reference for MrBayes); this is roughly 1000 Ma in our case, and results in very wide CIs. Using smaller time unit (e.g. 1 Ma) requires more sensitive fine-tuning of fixed rate prior and fixed TK02 rate variance prior, therefore our analyses are somewhat complicated. Nevertheless, one can save time on obtaining a desirable tree by tuning the time scale factor of a suboptimal tree, without running additional analyses. We did not go this efficient way simply because we prefer straightforward results.

4.5. The age of crown Corydioidea

Post-analytical calibration results suggest that crown Corydioidea are older than Middle Jurassic, and likely originated around the Triassic–Jurassic boundary (Fig. 6). The rate prior that yielded these results ranges from 0.0004 to 0.0005, which is reasonable given the empirical estimations (Papadopoulou et al.,

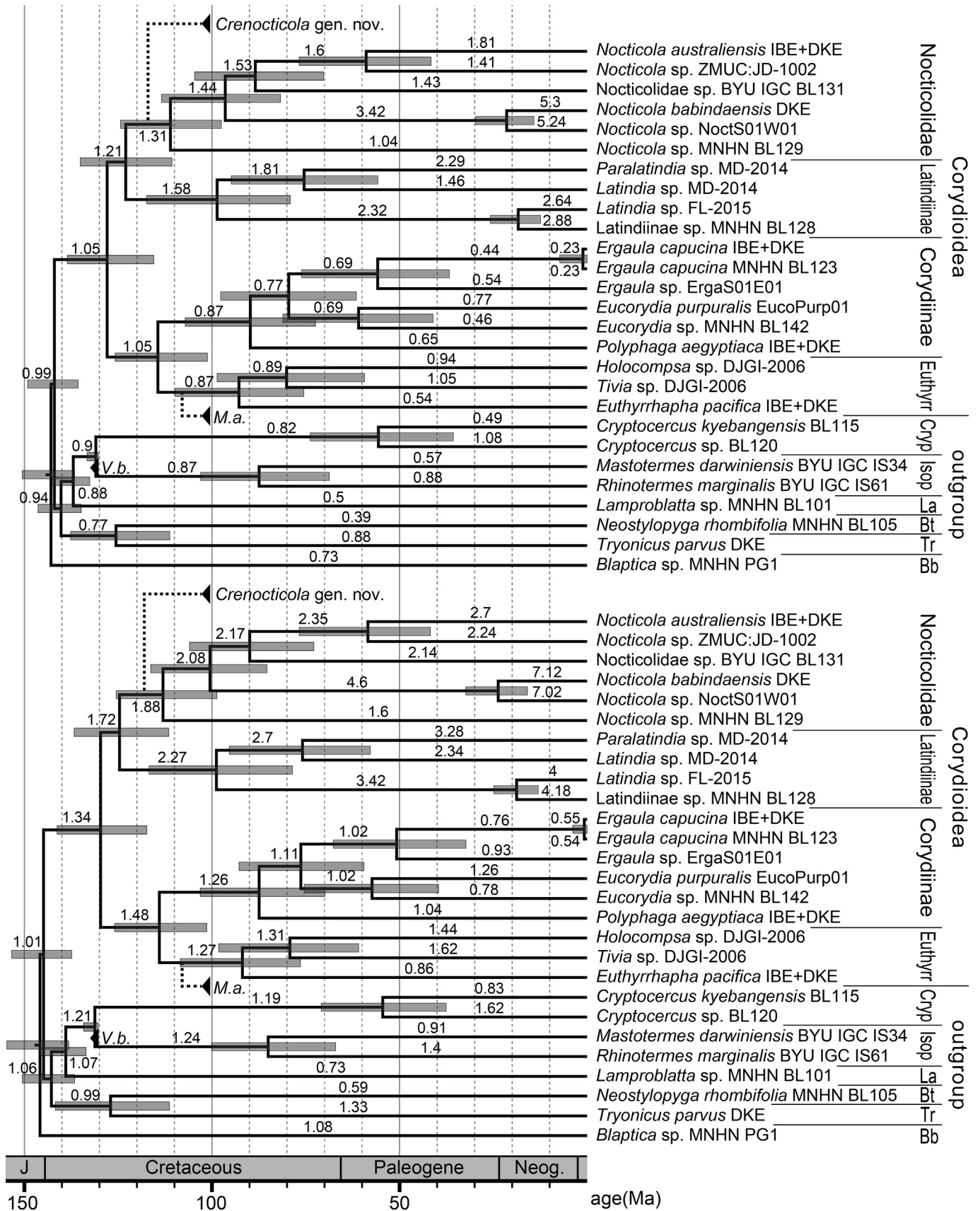


Fig. 5. In-analytical calibration dating of Corydioidea, calibrated by three fossils, under TK02 clock model in MrBayes. Top: rate prior set as lognormal (−7.0105, 0.1981), five million iterations with 10% burn-in; bottom: rate prior set as fixed (0.0008), two million iterations with 10% burn-in. Grey bars are 95% CI of the posterior estimates of node age (Ma). Numbers above or beside a branch are posterior rate multipliers. Triangle and dashed line indicate the position of fossils that are used for calibration: *M.a.* = *Magnicula apiculata*, *V.b.* = *Valditermes brenanae*. Abbreviations for taxa: Bb, Blaberidae; Bt, Blattidae; Cryp, Cryptocercidae; Euthyr, Euthyrhaphinae; Isop, Isoptera; La, Lamproblattidae; Tr, Tryonicidae.

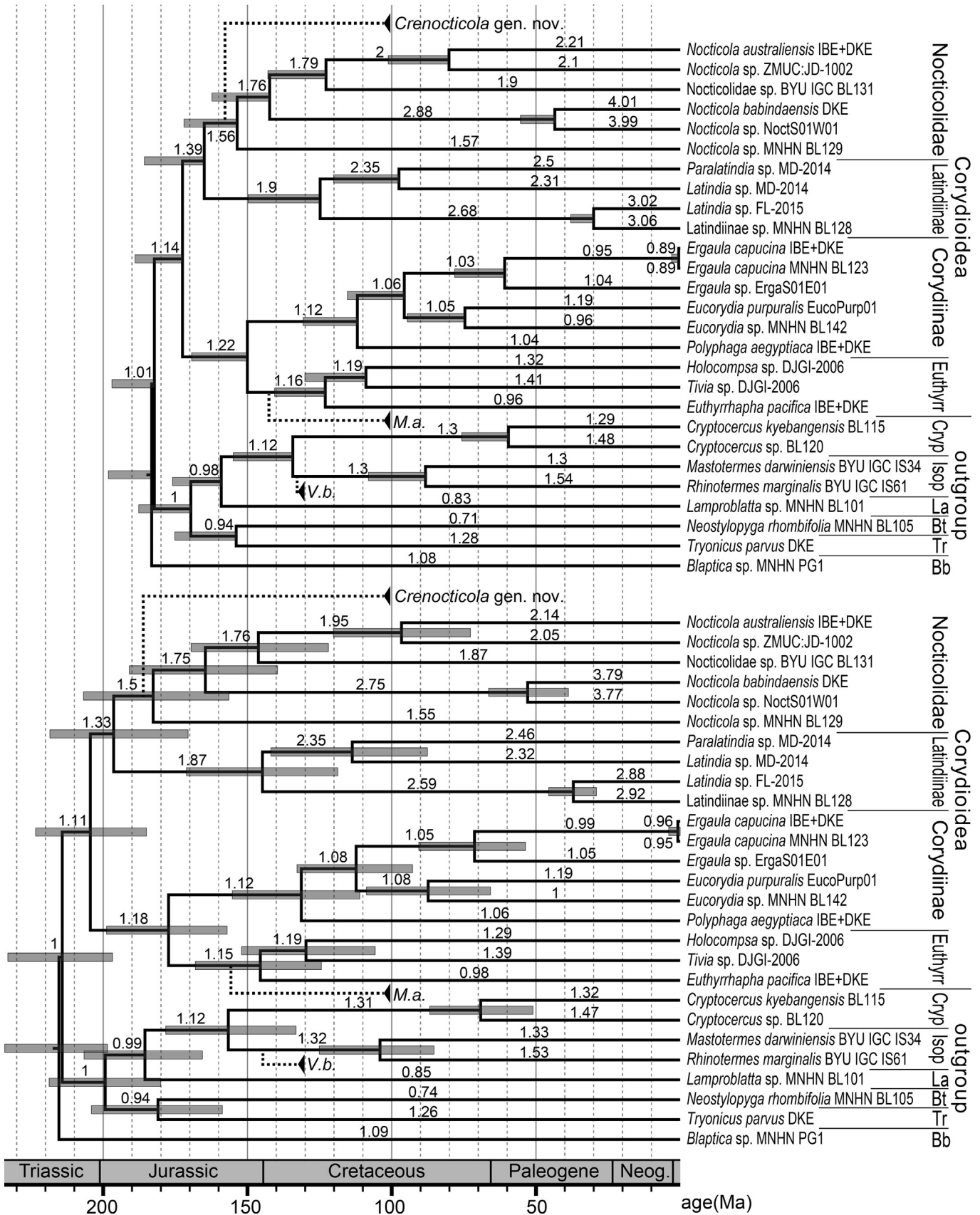


Fig. 6. Post-analytical calibration dating of Corydioidea, uncalibrated in running analyses, under TK02 clock model in MrBayes, one million iterations with 25% burn-in. Top: rate prior set as fixed (0.0005), TK02 variance as fixed (1.2). Grey bars are left half of 95% CI of the posterior estimates of node age (Ma); the right half conflicts with fossil records. Accordingly, nodes are at the minimum age estimates. Bottom: rate prior set as fixed (0.00041), TK02 variance as fixed (1). Grey bars are 95% CI of the posterior estimates of node age (Ma). Numbers above or aside a branch are posterior rate multipliers. Triangle and dashed line indicate the position of fossils that are used for comparing the node age (i.e. post-analytical calibration): *M.a.* = *Magnicocla apiculata*, *V.b.* = *Validitermes breanae*. Abbreviations for taxa: Bb, Blaberidae; Bt, Blattidae; Cryp, Cryptocercidae; Euthyr, Euthyrhaphinae; Isop, Isoptera; La, Lamproblattidae; Tr, Tryonicidae.

2010; Andújar et al., 2012) and our data bias towards nuclear genes. The age estimate is close to that in Wang et al. (2017), older than that in Evangelista et al. (2019, Middle-Late Jurassic), whereas younger than that in other studies (Djernæs et al., 2015: Middle Triassic; Bourguignon et al., 2018: Late Triassic). Legendre et al. (2015) did not explicitly provide an age estimate of crown Corydioidea, whilst the age, according to the figures, should be around the Early Triassic (note that the age and topology cited in Li and Huang, 2018 are incorrect). The difference is contributed by many factors, of which the fossil calibration is straightforward. Evangelista et al. (2019) extensively reviewed the fossil calibrations used in dating analyses of Dictyoptera (see also Evangelista et al., 2017) and justified the fossils they use, together with the large dataset, making their results the most robust ever. Even so, some fossils are still debatable. For example, Evangelista et al. (2019) considered *Cretaholocompsa montsecana* Martínez-Delclòs as stem-(Corydiinae + Euthyrrhaphinae) (but see Evangelista et al., 2017, as within crown clade) and calibrated the Corydioidea with this fossil. The tegminal venation of *C. montsecana* is indeed reminiscent of *Holocompsa* (see Martínez-Delclòs, 1993), however, the strong spines of forefemora readily excludes this species from Corydioidea (in contrast to Li and Huang, 2018). Using this fossil may not affect the age estimate, because it is too young (125.5 Ma as used in Evangelista et al.; see also Selden and Nudds, 2012, 130 Ma) to outperform *Valditermes brenanae*. The 'roachoid' species *Qilianiblattea namurensis* was used by Evangelista et al. (2019) to calibrate the node of Dictyoptera + sister. However, the view that 'roachoids' are all inside the total group Dictyoptera is frequently challenged, whether in the classic phylogenetic age (e.g. Hennig, 1969) or in current phylogenomic age (e.g. Kjer et al., 2015). We also consider that the phylogenetic position of 'roachoids' including *Q. namurensis* is too vague to use in a dating analysis. Bourguignon et al. (2018) also used a 'roachoid' species *Mylacris anthracophila*, which caused a narrow CI at the node of Dictyoptera + sister. Discarding this fossil makes the age estimates more plausible (e.g. fig. S12 in Bourguignon et al., 2018: the age of crown Corydioidea is Early-Middle Jurassic, but note that the narrow intervals occur at calibrated termite nodes instead). Li and Huang (2018) erroneously cited Evangelista et al. (2017) about the fossil calibrations used in Djernæs et al. (2015) and Wang et al. (2017): actually, Evangelista et al. (2017) did not cover the fossils in Djernæs et al. (2015), whilst the only fossil mentioned both in Wang et al. (2017) and Evangelista et al. (2017) was approved by the latter. Djernæs et al. (2015) used *Homocladus grandis* to calibrate crown Dictyoptera; this fossil has been proven unjustified (Evangelista et al., 2019 and references therein). The fossils used by Wang et al. (2017) are relatively young, and the likely crucial one is the termite *Baissatermes lapideus*, which was regarded as 137-Ma-old. Although the actual age of *Baissatermes lapideus* may be much younger (Wolfe et al., 2016), this fossil may play a role similar to *Valditermes brenanae*, and may contribute to the close age estimates of Wang et al. (2017) and of the present paper.

Current fossil records are not informative about the age of Corydioidea. One of the purported oldest corydioid fossils, *C. montsecana*, is unlikely a member of Corydioidea, as mentioned above. A contemporary genus, *Vitisma* Vršanský, though similar to extant *Euthyrrhapha*, could not be conclusively identified to Corydioidea due to insufficient characters preserved (see Vršanský, 1999). Consequently, unambiguous oldest fossils of Corydioidea are all from Burmese amber (Li and Huang, 2018; Qiu et al., 2019a; and the present paper). These fossils, however, are more or less derived, and suggest a much older age of crown Corydioidea.

So far, the fossil records and molecular dating analyses have not yet yielded very convincing age estimates of Corydioidea and of

other cockroaches. Nonetheless, we consider that crown Corydioidea likely originated in the Late Triassic or Early Jurassic.

5. Conclusions

Crenoticticola burmanica gen. et sp. nov., from mid-Cretaceous Burmese amber, is a stem member of Nocticolidae. It exhibits transitional morphology between crown Nocticolidae and Latindiinae. In view of clear phylogenetic position, *Crenoticticola* is a good fossil calibration, setting the minimum age bound of Nocticolidae + Latindiinae. However, it may be too young and other fossils may suppress its effectiveness as a calibration. This suggests that a good fossil is not necessarily a good calibration in a given analysis. In comparison, some fossils that are not good enough have been being used as calibrations; consequently, the age estimates would be questionable. We compared two approaches to applying fossil calibrations: 1) in-analytical calibration, i.e. incorporating the fossil age in prior settings, and 2) post-analytical calibration, i.e. adjusting the fixed prior so that the estimated age does not conflict with the fossil age. In-analytical calibration may underestimate the age, whilst post-analytical calibration yields better estimates. Our dating analyses suggest that crown Corydioidea likely originated in the Late Triassic or Early Jurassic.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2019.104202>.