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Including fossils in phylogeny: A glimpse into the evolution of the superfamily Evanioidea (Hymenoptera, Apocrita) under tip-dating and the fossilized birth-death process

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ABSTRACT

Using a fossilized birth-death model, a new phylogeny of the superfamily Evanioidea (including ensign wasps, nightshade wasps or hatchet wasps) is proposed with estimates of divergence times for its constitutive families, also corroborating the monophyly of Evanioidea. Additionally, our Bayesian analyses demonstrate the monophyly of †Anomopterellidae, †Othniodellithidae, †Andreneliidae, Aulacidae, Gasteruptiidae, and Evaniidae, while the †Praeaulacidae and †Baissidae appear to be paraphyletic lineages. *Vectevania vetula* and *Hyptiogastrites electrinus* are transferred in the Aulacidae. We estimate the divergence of Evanioidea in the Late Triassic (~203 Ma). Additionally, three new othniodellithid wasps are described and figured from mid-Cretaceous Burmese amber as *Keradellitha basilici* Jouault, Maréchal, Wang & Perrichot, **gen. et sp. nov.**, *Keradellitha anubis* Jouault, Maréchal, Wang & Perrichot, **sp. nov.**, and *Keradellitha kirina* Maréchal, Jouault & Perrichot **sp. nov.** We also document a temporal shift, in relative specific richness, between Ichneumonoidea and Evanioidea.

ADDITIONAL KEYWORDS: Bayesian inferences, fossilized birth-death, morphological phylogeny, time divergence, calibration

INTRODUCTION

Recent advances in phylogenomics have clarified relationships within the hymenopteran lineages and shown the monophyly of all superfamilies except Vespoidea (Sharkey *et al.*, 2012; Ronquist *et al.*, 2012a; Peters *et al.*, 2017; Sharanowski *et al.*, 2021). Nonetheless, the monophylies of these clades are not so clear-cut when fossils are considered. The most recent works have estimated robust time-calibrated phylogenies for Hymenoptera based on analyses of genomic data, and have found evidence that Evanioidea is the sister lineage of Stephanoidea (Peters *et al.*, 2017; Tang *et al.*, 2019). Additionally, molecular and morphological studies strongly support the monophyly of Evanioidea (Dowton & Austin, 1994; Dowton *et al.*, 1997; Vilhelmsen *et al.*, 2010; Heraty *et al.*, 2011; Sharkey *et al.*, 2012; Klopstein *et al.*, 2013; Payne *et al.*, 2013; Li *et al.*, 2018; Sharanowski *et al.*, 2018). The superfamily Evanioidea is currently composed of five fossil families (†Praeaulacidae, †Anomopterellidae, †Andreneliidae, †Baissidae, and †Othniodellithidae) that are widely represented in Mesozoic deposits, plus three extant families (Evaniidae, Aulacidae, Gasteruptiidae) with a rather extensive fossil record. The Evanioidea may have arisen during the Late Triassic (Sharkey *et al.*, 2012; Peters *et al.*, 2017; Tang *et al.*, 2019) but the evolutionary history and the molecular age estimates within the superfamily have not yet been studied, except for its extant families (Sharanowski *et al.*, 2018; Parslow *et al.*, 2020a).

Extant evanioid wasps are known from 310 aulacid, 580 evaniid, and about 500 gasteruptiid species (see details in Ramage & Jouault, 2020) but data on their biology are limited. Several studies report aulacid wasps as koinobiont endoparasitoids of wood-boring larvae of Hymenoptera Xiphydriidae and Coleoptera Cerambycidae and Buprestidae (e.g. Deyrup, 1984; Gauld & Hanson, 1995; Jennings & Austin, 2004; Kuroda *et al.*, 2020). Adults of gasteruptiids apparently feed on nectar and pollen (Jennings & Austin, 2004), while their larvae are predator-inquiline, feeding on larvae or larval food of solitary bees (Antophila of the families Apidae, Colletidae, Halictidae,

Megachilidae, and Stenotritidae) and of more inclusive apoid wasps (Crabronidae) (Malyshev, 1968; Jennings & Austin, 2004; Bogusch *et al.*, 2018; Perioto *et al.*, 2020; Parslow *et al.*, 2020b). Lastly, evaniid larvae are considered as predators of cockroach eggs in oothecae (Brown, 1973; Huben, 1995).

Recent efforts to reconstruct the phylogeny of Evanioidea took into account only molecular data and used fossils as calibration points, which may lead to under-integrations of the fossil lineages unearthed so far. This could induce conflicting interpretations of the phylogeny and the fossil record, and hinder a clear understanding of the evolutionary history of the superfamily Evanioidea. It is crucial to include the abundant evanioid fossil diversity in a phylogenetic framework, especially to study the origin and timing of diversification of their stem- and crown-groups. To incorporate extinct and extant taxa, the use of morphological-based matrix and total-evidence dating are required (e.g. Ronquist *et al.*, 2012a; Gavryushkina *et al.*, 2016; Pyron, 2017; Spasojevic *et al.*, 2020). The developments of the fossilized birth-death (FBD) (Heath *et al.*, 2014) model implemented in Bayesian inference allow integrating fossil species in a time-calibrated phylogeny, an approach also known as “tip-dating”. This approach has mostly been used for vertebrate clades (e.g. Zhang *et al.*, 2016; Gavryushkina *et al.*, 2016; Pyron, 2017) and remains little used for invertebrates (but see Ronquist *et al.*, 2012a; Vea & Grimaldi, 2016; Paterson *et al.*, 2019; Jouault *et al.*, 2021a). The tip-dating approach allows revisiting long-standing questions in macroevolution, such as the time of origin of a clade, its periods of diversification, or extinction events.

In the case of Evanioidea, uncertainty surrounds their timing of origin and diversification. Although incomplete, the fossil record suggests that the evanioid diversity was important during the Jurassic and decreased after the Cretaceous (Li *et al.*, 2018; Jouault *et al.*, 2021b). It is assumed that this change in diversification pattern was likely due to the diversification and expansion of a potentially competitive group, the Ichneumonoidea (Jouault *et al.*, 2021b). Both lineages show a shift in fossil abundance after the Cretaceous (Jouault *et al.*, 2021b). Ichneumonoidea and Evanioidea are

known from numerous specimens in the highly fossiliferous Burmese amber, representing respectively 2.4% and 5.2% of the valid species (Jouault *et al.*, 2021b). Thus it seems that the dominance of the ichneumonoids occurred during the middle to Late Cretaceous even if the evanioidea are already abundant during this period (Tabl. 1).

In this study we present and describe three new species of othniodellithid wasps belonging to a new genus. We also revise the fossil record of Evanioidea and propose a time-calibrated phylogeny for the group using a tip-dating approach. The analysis of the fossil record of the superfamilies Evanioidea and Ichneumonoidea is used to document the shift in specific richness between Evanioidea and Ichneumonoidea in the Cretaceous. We also discuss the record of two species belonging to a same genus but originating from two deposits of different ages.

MATERIAL AND METHODS

SPECIMEN SAMPLING AND MORPHOLOGICAL EXAMINATION

The two dark orange amber pieces containing *Keradellitha basilici* Jouault, Maréchal, Wang & Perrichot gen. et sp. nov. and *K. anubis* Jouault, Maréchal, Wang & Perrichot sp. nov. originate from the deposits of Noiye Bum in the Hukawng Valley (26° 29' N, 96° 35' E), Kachin State, Northern Myanmar (see Grimaldi & Ross, 2017: fig 2). Radiometric data established an early Cenomanian age (98.79 ± 0.62 Ma) for Kachin amber, based on zircons from volcanic clasts found within the amber-bearing sediments (Shi *et al.*, 2012). Some ammonites found in the amber-bearing bed and within amber corroborates a late Albian / early Cenomanian age (Cruickshank & Ko, 2003; Yu *et al.*, 2019). The amber piece, also dark orange, containing *Keradellitha kirina* Maréchal, Jouault & Perrichot sp. nov., originates from the Hkamti site (about 80 km southwest of the Angbamo site), Hkamti District, Sagaing Region, Myanmar; see detailed map in Zheng *et al.* (2018: supplementary figure 2) or in Xing & Qiu, (2020: fig 1). An early Albian age (109.7 ± 0.4 Ma) was established for Hkamti amber based on zircon U-Pb analyses of clastic sediments (Xing & Qiu, 2020).

The descriptions are based on complete and well-preserved individuals, except for *K. anubis* Jouault, Maréchal, Wang & Perrichot gen. et sp. nov. which is based on an individual missing the apices of legs and antennae. The type specimens from Kachin (Noije Bum) amber are housed in the collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science, China (NIGP), while the type specimen from Hkamti amber is housed in the amber collection of the Geological Department and Museum of the University of Rennes, France (IGR). The specimens were examined and photographed using a Leica MZ APO stereomicroscope equipped with a Canon EOS 5D Mark II camera. All images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus 6.7. Figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019. Wing venation terminology and description structures follow Engel (2017).

MORPHOLOGICAL DATA

The morphological data originated from Li *et al.* (2018) and were updated with the most recent taxonomic descriptions (Ronquist *et al.*, 1999; Jennings & Austin, 2000; Basibuyuk *et al.*, 2002; Turrisi *et al.*, 2009; Peñalver *et al.*, 2010; Rasnitsyn & Zhang, 2010; Sharkey *et al.*, 2012; Li *et al.*, 2013a,b; Li *et al.*, 2018; Turrisi & Ellenberger, 2019; Shih *et al.*, 2019; Poinar, 2020; Jouault & Nel, 2021). We used 81 adult characters (Appendix S1), coded for the 104 ingroup taxa and three outgroup taxa: *Orussus* sp., *Acephialtitia colossa* and *Praeproapocritus flexus*. All characters were treated as unordered and with equal weight. Inapplicable and unknown characters were coded with ‘–’ and ‘?’, respectively. The character matrix was established with Mesquite 3.61 (Maddison and Maddison, 2019). All consensus trees were visualized and drawn using FigTree 1.4.4 (Rambaut, 2009), and modified with Adobe Illustrator CC2019.

MAXIMUM PARSIMONY

Maximum parsimony (MP) analyses of the morphological dataset (Appendix S1) were conducted with PAUP 4.0a166 (Swofford, 2002). Outgroup taxa were treated as paraphyletic with respect to the ingroup. Tree searches were performed using a heuristic search method with the following options: maximum number of trees saved equal to 10,000, only optimal trees retained, collapse of zero-length branches, and a tree bisection and reconnection (TBR) swapping algorithm. When searches produced more than one optimal cladogram, a strict consensus was performed (Suppl. Fig. 1). To measure the robustness of the parsimony cladograms, bootstrap analyses (Felsenstein, 1985, Hillis & Bull, 1993) were executed using the full heuristic search option for 100 replicates. We considered values of bootstrap support (BS) equal or above 70 as strong node supports (Hillis & Bull, 1993).

BAYESIAN PHYLOGENETIC INFERENCE AND DIVERGENCE TIME ESTIMATES

We carried out Bayesian inferences (BI) using a relaxed clock model in MrBayes 3.2.7a (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003; Ronquist *et al.*, 2012b). We performed tip-dating analyses with a fossilized birth-death (FBD) model wherein fossil taxa are terminals. Analyses were computed with a Markov one parameter (Mkv) model (Lewis, 2001) with or without a gamma rate variation across characters and with the independent gamma relaxed clock model (Lepage *et al.*, 2007; *lset rates = invgamma*, *prset clockvarpr = igr*, *prset igrvarpr = exp(10)*; no rate variation was computed with *lset rates = equal*). Following Ronquist *et al.* (2012a), the prior used for the mean clock rate was gamma (2, 200), except in one analysis wherein we tested a normal but very flat prior (*prset clockratepr = normal(0.0025,1)*) and a flat uniform speciation prior (*prset speciationpr = uniform(0,10)*; Matzke & Wright, 2016). The proportion of extant taxa was set to 0.015 (21 extant species out of *ca.* 1,400 species). Sampling strategy of taxa was either set to diversity (*prset samplestrat = diversity* wherein fossils are sampled randomly and can be tips or ancestors), random (*prset samplestrat = random* wherein fossil can be tips or

ancestors) or fossil tip (*prset samplestrat = fossiltip* wherein fossil and taxa are assumed to be sampled randomly and fossil ancestor is not allowed). An exponential prior and a beta prior were used for the net speciation rate and the relative extinction rate using the following functions: *prset speciationpr = exp(100)*, and *prset extinctionpr = beta(1,1)*, respectively. In all our tip-dating analyses, the node age prior was set to ‘calibrated’. All analyses comprised two runs and four Markov chains Monte Carlo (MCMC), and were launched for 50 million generations. MCMC were sampled every 5000 generations and a burn-in fraction of 0.25 was used. Convergence diagnostics were checked for each analysis with the average standard deviation of split frequencies < 0.01, PRSF close to 1.0 in MrBayes outputs, and ESS > 200 in Tracer 1.7.1 (Rambaut *et al.*, 2018). We performed two tip-dating analyses: (1) we used extinct taxa calibrated with uniform distributions bounded according to the minimum and maximum ages of their deposits (Barido-Sottani *et al.*, 2019; Appendix S2), and (2) we used extinct taxa calibrated with fixed distributions bounded according to the minimum ages of their deposits. In the FBD model, all fossils were set as tips ($r = 1$). The prior probability distribution on branch lengths was set to *clock:fossilization*. Three nodes were assigned offset exponential priors: (1) the root of the tree (minimum age: 183 Ma, mean age: 245 Ma), (2) the clade Apocrita (183, 236 Ma), and (3) the ingroup (164 Ma, 178 Ma). Those ages were set according to the latest studies (Ronquist *et al.*, 2012a; Peters *et al.*, 2017; Tang *et al.*, 2019). All scripts are provided as Supporting Information.

Published work and nomenclatural acts are registered in ZooBank (<http://www.zoobank.org/>, last access: 15 March 2021), with the following LSID (reference):
urn:lsid:zoobank.org:pub:9E9E6EC8-29E8-488A-AF43-0619A1820A7A

SYSTEMATIC PALEONTOLOGY

CLASS INSECTA LINNAEUS, 1758

ORDER HYMENOPTERA LINNAEUS, 1758

SUBORDER APOCRITA GERSTAECKER, 1867

SUPERFAMILY EVANIOIDEA LATREILLE, 1802

FAMILY †OTHNIODELLITHIDAE ENGEL & HUANG, 2016

GENUS *KERADELLITHA* JOUAULT, MARECHAL, WANG & PERRICHOT, gen. nov.

urn:lsid:zoobank.org:act:1CFB1DFA-B7F1-4414-8CAD-67515F278530

Type species: *Keradellitha basilici* Jouault, Maréchal, Wang & Perrichot, sp. nov.

Other species included: *Keradellitha anubis* Jouault, Maréchal, Wang & Perrichot, sp. nov.; *Keradellitha kirina* Maréchal, Jouault & Perrichot sp. nov.

Etymology. The new generic name is a Latinised combination of the Greek words, *kéras* ('horn') and *dellithos* ('a kind of wasp'). The gender of the name is feminine.

Diagnosis. Head with vertex flat to slightly convex; cephalic horn without apical teeth, with two transverse and parallel ridges, anterior ridge being slightly wider than second but both similar in shape; compound eye ovoid, without circum-ocular carina, inner lateral margins slightly concave; toruli widely separated by cephalic horn, located on lateral surfaces, opening dorso-laterally; malar space shorter than width of mandibular base; mandible with apical teeth slightly pointing, not overlapping tooth of opposite mandible; gena shorter than compound eyes; antenna with 22 flagellomeres, flagellum gradually decreasing in length and slightly in width towards apex; pronotum extending forward as short neck; legs bearing tarsal plantulae; fore wing with lcu-a confluent to 1M; veins M+Cu et Cu aligned; 2m-cu tubular; 2cu-a and 2A present; hind wing with numerous hamuli (five or more).

KERADELLITHA BASILICI Jouault, Maréchal, Wang & Perrichot, sp. nov.

urn:lsid:zoobank.org:act:C67E5240-F1BC-4836-86F7-3B9D1D375AA8

(Figs. 1-2)

Holotype: NIGP174738, preserved in a rectangular piece of amber measuring $17 \times 10 \times 6$ mm.

Type locality and horizon: Noije Bum Hill, Hukawng Valley, Kachin State, Myanmar; upper Albian to lower Cenomanian, mid-Cretaceous.

Etymology. The specific epithet refers to a mythical beast (*Basiliscus*) that intermingled the traits of several animals, and is a general allusion to the fierce and enigmatic habitus of the species. The specific epithet is to be treated as a noun in a genitive case.

Diagnosis. Scape long, about 3,5 times longer than pedicel; outer (external) pretarsal claw of fore leg with two pre-apical teeth; fore wing vein $Rs+M$ as long as $2Rs$; third submarginal cell as long as second one; $1rs-m$ meeting Rs slightly before $r-rs$; $2rs-m$ tubular; second discal cell short (twice as long as wide); hind wing with six hamuli; gaster laterally compressed (as in Evaniidae), rounded-shape.

Description. Female. Total length as preserved 4.4 mm (excluding antennae and ovipositor); fore wing 2.7 mm long; integument dark brown except metasoma lighter; body largely glabrous except legs bearing short, thick setae; integument without pronounced sculpturing or punctation, largely finely imbricate; propodeum coarsely and strongly areolate; wings clear and hyaline, veins brown to light brown in preserved color.

Head slightly shorter than wide in frontal view, width 0.95 mm and length 0.87 mm; genal width 0.2 mm; compound eyes ovoid, without prominent circum-ocular carina, 0.51 mm long, 0.3 mm wide; ocelli present and situated in a small triangle on top of vertex above compound eyes and immediately behind facial prominence, ocelli separated by approximately their diameter and from posterior border of head by about twice their diameter. Prominent facial horn projecting to length of 0.37 mm in profile (from anterior toruli margin to apex of the horn). Antenna with scape about 3.5 times pedicel length, 0.43 mm long, 0.07 mm wide; pedicel more than twice as long as wide; flagellomeres each longer than wide except two apical most; flagellomere I the longest (0.31 mm long). Clypeal base indistinct from frons (epistomal sulcus lacking), with strong medial longitudinal ridge,

ridge extends posteriorly with a small sharp tooth and anteriorly projects as small triangular prominence between mandibles. Palp formula (maxillary-labial) at least 6-3. Mandible massive, square-shaped in frontal view, with straight outer and apical margins meeting in a rounded orthogonal angle; inner margin with ridges demarcating blunt 'teeth', apical tooth well projected without overlapping opposing mandible.

Mesosoma laterally compressed, longer than high, length 2.2 mm long, height 1.41 mm; pronotum prominent, with well-developed concave anterior surface, with poorly defined raised posterior surface, medially longer than wide, lateral surfaces large and slightly depressed; propleura long but not projecting anterior to pronotum; mesoscutum 0.53 mm long, notauli distinct; mesoscutellum convex in profile, 0.27 mm in its medial length; mesopleuron with small, oblique row of faint areolae demarcating border with pronotal lateral surface and more distinct, single row of areolae along border with metepisternum; propodeum weakly areolate, with prominent dorsal surface, dorsal length between metanotum and articulation with petiole equal to 0.3 mm. Legs long, with slender tarsi; meso- and meta-coxae closer to each other than to procoxa; metafemur 1.81 mm long, metatibia 1.71 mm long; metabasitarsus elongate but slightly shorter than combined lengths of remaining tarsomeres, metabasitarsus length 0.8 mm, lengths of remaining tarsomeres (from base to apex), 0.34 mm, 0.3 mm, 0.16 mm, and 0.23 mm. Tibial spurs formula 1-2-2. Apex of all tarsi with a plantula. Outer pretarsal claw of fore leg tridentate (bearing two small pre-apical teeth), all other claws bidentate (with a single pre-apical tooth).

Fore wing with costal space apically slightly broader than pterostigma; pterostigma longer than wide, tapering gradually in width to acute apex, margin inside marginal cell faintly convex; vein M+Cu forking after Sc+R mid-length; 1M straight, nearly aligned with and longer than 1Rs; 1Rs originating prior to pterostigma a distance inferior to its length; 1rs-m meeting Rs slightly before r-rs; 2Rs longer than 1Rs; 2M very small, meeting 1m-cu, then M abscissa extend toward wing apex; 2Rs slightly curved; r-rs originating from basal third of pterostigmal length, elongate, softly sinu-

ous, as long as 2Rs; marginal cell broad, three time as long as wide, greatest width near tangent of pterostigmal apex; 3Rs mostly straight for majority of marginal cell length; two rs-m crossveins present; second submarginal cell about as long as third, and slightly widening towards the wing margin; third submarginal cell slightly wider posteriorly than anteriorly; first discal cell almost forming strongly slanted rhomboid (not distinctly pentagonal owing to exceptionally short 2M); 1m-cu straight and sub-parallel to 1M; cu-a originating at M+Cu fork, nearly aligned with 1M; 2m-cu present but weaker than surrounding veins; A2 present and meeting Cu apically in a small 2cu-a vein (demarcating second sub-basal cell); vein 2A present. Hind wing with venation nearly complete, only lacking C; R with six distal hamuli and not meeting 2Rs apically; rs-m oblique, about twice as long as 1Rs, shorter than first free abscissa M; Cu+cu-a present, nearly orthogonal to M+Cu; apical abscissa Cu not visible if present; jugal lobe lacking.

Metasoma with first segment forming tubular petiole 0.57 mm long, tergum and sternum fused without apparent indication of individual sclerites; gaster 1.72 mm long, compressed laterally, ovoid in profile, obviously longer than high, maximum height 0.84 mm, widening to the third gastral segment and then narrowing toward apex; ovipositor exerted, at least 1 mm long (not totally visible), with five minute teeth present on apical declivitous face; sheaths slightly longer than ovipositor.

Male unknown.

KERADELLITHA ANUBIS Jouault, Maréchal, Wang & Perrichot sp. nov.

urn:lsid:zoobank.org:act:D217B456-4EEF-4EF7-87B9-A497EE9BCA66

(Figs 3-4)

Holotype: NIGP174739, preserved in a rectangular piece of amber measuring 5 × 5 × 4 mm.

Type locality and horizon: Noiye Bum Hill, Hukawng Valley, Kachin State, Myanmar; upper Albian to lower Cenomanian, mid-Cretaceous.

Etymology. Named in reference to the mythological Egyptian god Anubis, protector of graves and the deceased. The specific epithet 'anubis' is to be treated as a noun in apposition.

Diagnosis. Scape short, about twice as long as pedicel; pretarsal claws of all legs bidentate; Rs+M slightly longer than 2Rs; third submarginal cell longer than second one; 1rs-m aligned with r-rs; 2rs-m not fully tubular; second discal cell long, about three times as long as wide; hind wing with five hamuli; metasoma with cylindrical gaster.

Description. Male. Total length as preserved 4.06 mm (excluding antennae and ovipositor); fore wing length at least 2.2 mm; integument largely dark brown and largely glabrous; integument without pronounced sculpturing or punctation, only finely imbricate; propodeum coarsely and strongly areolate; wings clear and hyaline, veins brown to light brown in preserved color.

Head wider than long; clypeus and frons vertical and flat; genal width at about midlength 0.1 mm; compound eye 0.41 mm long, 0.27 mm wide; ocelli protruding, large, arranged in small triangle on top of vertex above compound eyes, separated by approximately their diameter and from posterior border of head by twice their diameter. Prominent facial horn projecting to length of 0.25 mm in profile (from anterior toruli margin to apex of horn); scape longer than wide, twice as long as pedicel, 0.2 mm long, 0.07 mm wide; pedicel more than twice as long as wide; flagellomere I the longest (about 0.25 mm long). Clypeal base indistinct from frons, without medial longitudinal ridge. Palpal formula at least 5-3. Mandible large, square in frontal view, with straight outer and apical margins, margins meeting at rounded obtuse outer angle; inner margin with four blunt teeth and with one stout and longer, pointed apical tooth.

Mesosoma laterally compressed, longer than high, 1.35 mm long, at least 0.8 mm high; pronotum well developed, with well-developed concave anterior surface, apparently slightly longer than wide, lateral surfaces large and slightly depressed; mesoscutum with weak notauli not meeting, mesoscutum 0.5 mm long; mesoscutellum well separated from mesoscutum, slightly convex in profile, 0.2 mm long; mesopleuron with oblique depression and small, single row of weak areolae demarcating

border with pronotal lateral surface, and even weaker row of areolae along border with metepisternum; propodeum coarsely and strongly areolate, dorsal length between metanotum and articulation with petiole equal to 0.23 mm. Legs not fully preserved except right hind legs; long, with meso- and meta-coxae closer than pro-coxa; hind femur medially swollen.

Fore wing with costal space apically about as broad as pterostigma; pterostigma much longer than wide, tapering gradually in width in apical half to acute apex; marginal cell narrow with vein 1Rs slightly convex; vein M+Cu forking distally to midlength of Sc+R; 1M slightly curved, forming faint angle at junction with 1Rs, 1M subequal to 1Rs; 1Rs originating basal to pterostigma at distance subequal to pterostigmal width; 1rs-m aligned with r-rs; Rs+M straight; 2Rs much longer than 2M but slightly shorter than Rs+M; 2M exceedingly short and directed posteriorly to meet lm-cu; 3M slightly convex basally then longitudinal; 2Rs slightly curved near Rs+M then almost straight; r-rs originating before pterostigmal midlength, weakly sinuous, elongate, slightly shorter than 2Rs; marginal cell damaged and partial; two rs-m crossveins present, second one distinctly weaker and thinner than surrounding veins (but not nebulous); second submarginal cell with posterior border 0.7 times shorter than posterior border of third one; third submarginal cell about 1.3 times longer than second; discal cell almost forming strongly slanted rhomboid (not distinctly pentagonal owing to exceptionally short 2M), lm-cu straight, 1.3 times longer than lCu; lCu-a slightly distal with 1M; 2m-cu conspicuous and tubular; 2cu-a present, enclosing subdiscal cell. Hind wing with venation nearly complete except lacking C; R with five distal hamuli, not meeting 2Rs apically; rs-m oblique, longer than 1Rs, about twice as short as first 1M; Cu present, virtually orthogonal to M+Cu; jugal lobe lacking.

Metasoma 2.0 mm long; first segment forming trapezoidal petiole, narrower basally, 0.44 mm long; tergum I and sternum I fused without apparent indication of individual sclerites; gaster compressed laterally, gradually and slightly tapering in height from mid-length to apical segment. Parameres directed backward, keel-shaped, protruding about 0.2 mm. Aedeagus not clearly visible.

Female unknown.

KERADELLITHA KIRINA Maréchal, Jouault & Perrichot sp. nov.

urn:lsid:zoobank.org:act:47865DDE-514F-4583-AB69-FF0D02A3BD5D

Holotype: IGR.BU-021, preserved in rectangular piece of amber measuring $9 \times 6 \times 3$ mm.

Type locality and horizon: Hkamti site, Hkamti District, Sagaing Region, Myanmar; early Albian (ca. 110 Ma), early Cretaceous.

Etymology. Named in reference to the fabulous animal from Chinese mythology: Qilin or Kirin that intermingled the traits of several animals, and is a general allusion to the fierce and enigmatic habits of the species. The specific epithet is to be treated as a noun in a genitive case.

Diagnosis. Scape short, about twice as long as pedicel; pretarsal claws of all legs bidentate; fore wing vein Rs+M longer than 2Rs; second and third submarginal cells equal in length; 1rs-m meeting Rs slightly after r-rs; 2rs-m complete and tubular; second discal cell short (about twice as long as wide); hind wing with five hamuli; metasoma with cylindrical gaster.

Description. Female. Total length as preserved 4.87 mm (excluding antennae and ovipositor); fore wing at least 2.35 mm long; hind wing ca. 1.5 mm long; integument largely dark brown or clear brown, glabrous mesosoma without pronounced sculpturing or punctation except on propodeum, which is coarsely and strongly areolate; wings clear and hyaline, veins brown to light brown.

Head wider than long, 0.64 mm wide; genal space about 0.2 mm; compound eye 0.42 mm long, 0.30 mm wide; three ocelli arranged in an equilateral triangle on vertex, about 0.05 mm in diameter each and distant from each other by 2.5 times their diameter; prominent facial horn projecting for 0.44 mm long (measured at apex); scape longer than wide, about 0.24 mm long; pedicel about 0.13 mm long, conical and shorter than flagellomere I; flagellomere I the longest, about 0.30 mm long; clypeal area partially hidden by debris within amber matrix; mandibles massive, rectangular, about

0.15 mm wide, the masticatory margin with large, blunt apical tooth followed by 2(?) blunt teeth; outer margin of mandible covered by setae; palp formula (maxillary-labial) at least 5-3.

Mesosoma laterally compressed, thinner than head, longer than high, 1.4 mm long, 0.94 mm high; pronotum well-developed, 0.28 mm in maximal length; mesoscutum 0.55 mm long, slightly arched anteriorly; notauli not visible due to preservation; mesopleuron wide, ca. 0.80 mm in maximal length, with small, oblique row of weak areolae along pronotal margin, and even weaker row of areolae along metepisternal margin; propodeum coarsely and strongly areolate, distinctly setose around petiolar insertion; length of propodeal dorsal surface between metanotum and articulation with metasomal petiole about 0.30 mm; legs long, thin, with five thin tarsomeres; meso- and metacoxae closer to each other than to procoxa; metacoxa 0.67 mm long, metatrochanter 0.29 mm long, metafemur 1.49 mm long, metatibia 1.29 mm long; metabasitarsus elongate, combined length of tarsomeres ca. 1.65 mm long; tibial spurs formula 1-2-2, protibial spur bifid; pretarsal claws ca. 0.05 mm long, each with a single pre-apical tooth situated at about 2/3 of claw length.

Fore wing with costal space apically about as broad as pterostigma; pterostigma much longer than wide, tapering gradually in width; marginal cell narrow, with vein 1Rs slightly convex; vein M+Cu forking distally of midlength of Sc+R; 1M straight to slightly curved, forming faint angle at junction with 1Rs; 1M shorter than 1Rs; 1Rs originating basal to pterostigma at distance subequal to pterostigmal width; 1rs-m meeting Rs slightly after r-rs; Rs+M nearly straight; 2Rs greatly longer than 2M but conspicuously shorter than Rs+M; 2M exceedingly short and directed posteriorly to meet lm-cu; r-rs originating slightly before pterostigmal midlength, elongate, longer than 2Rs; marginal cell long and wide; two rs-m crossveins present, both tubular; second submarginal cell with posterior border 0.66 times shorter than that of third submarginal cell; second and third submarginal cells subequal in length; discal cell almost forming strongly slanted rhomboid (not distinctly pentagonal owing to exceptionally short 2M); lm-cu slightly concave, slightly shorter than lCu; 2m-cu conspicuous and tubular; 2cu-a present, enclosing sub-basal cell. Hind wing with venation nearly

complete, only lacking C; R with five distal hamuli, not meeting 2Rs apically; rs-m oblique, longer than 1Rs; Cu orthogonal to M+Cu; jugal lobe absent.

Metasoma about 2.50 mm long; first metasomal segment forming a tubular petiole (0.66 mm long) slightly widening posteriorly, with tergum I and sternum I fused without apparent indication of individual sclerites; gaster slightly ovoid, elongate and laterally compressed (nearly flat, maybe due to conservation), broadest at about its midlength; six tergites visible, respectively 0.32 mm, 0.40 mm, 0.40 mm, 0.48 mm, 0.72 mm, and 0.16 mm long; ventral base of apical tergite covering ovipositor insertion; ovipositor exerted, moderately long, ca. 0.90 mm long (not totally visible), sheaths slightly longer than ovipositor.

Male unknown.

RESULTS

We summarized the fossil diversity of Evanioidea and Ichneumonoidea (Fig. 7) using the function count taxa in Paleobiology Database (<http://fossilworks.org>; last access November 25, 2020). Although diversity changes through time as estimated by this analysis are biased by the incompleteness of the fossil record, we could extract one general pattern showing that Evanioidea were already diversified in the Jurassic period with more than 70 species (Fig. 7), while the earliest record of Ichneumonoidea (*Cretobraconus maculatus* Rasnitsyn & Sharkey, 1988) was described from the Lower Cretaceous Ulugei Formation (Rasnitsyn & Sharkey, 1988; Kopylov *et al.*, 2020). Afterwards, the species number of Ichneumonoidea increased, until becoming almost equivalent to that of Evanioidea during the Early Cretaceous. After the Cretaceous, the number of species of Ichneumonoidea clearly exceeded the number of Evanioidea species with a peak during the Eocene (Fig. 7).

Adding 41 species to the morphological matrix has provided a relatively strong support for the monophyly of Evanioidea (PP = 1; BS = 63). The resulting phylogeny has also clarified the rela-

tionships among and between extant and extinct taxa (Fig. 8; Supplementary Fig. 1). We found the genus *Hyptiogastrites* as an early-diverging lineage within the Aulacidae, and *Vectevania vetula* Cockerell, 1922 among the Aulacidae as an early-diverging taxon relative to the crown-Aulacidae (*Aulacus* + *Pristaulacus*). Although weakly supported, the Nevaniinae were recovered as a monophyletic subfamily within the Praeaulacidae (PP = 0.61; BS = 68), and sister lineage of the genus *Eosaulacus* (PP = 0.13). The two species of *Keradellitha* gen. nov. coded in the matrix were found nested within the †Othniodellithidae in BI and MP, confirming our taxonomic attributions (Fig. 8; Supplementary Fig. 1). We summarized the phyletic states of each family in Tabl. 2.

In all our Bayesian analyses, Evanioidea, †Anomopterellidae (PP = 0.93; BS = 72), Gasteruptiidae (PP = 0.91; BS = 66), †Othniodellithidae (PP = 1; BS = 99), †Andreneliidae, Aulacidae (PP = 0.67), and Evaniidae (PP = 0.99; BS = 50) were recovered as monophyletic lineages, while †Praeaulacidae (PP = 0.24) and †Baissidae were recovered as paraphyletic. In the MP analysis, the family Aulacidae was polyphyletic (Tabl. 2; Supplementary Fig. 1). Based on these results, we proposed a new hierarchical suprageneric classification of Evanioidea (Tabl. 3).

Following our modified suprageneric classification of Evanioidea, the ‘protoevanioides’ clade (†Praeaulacidae + †Othniodellithidae) (PP = 0.24) corresponds to the earliest radiation of the evanioid wasps, characterized by their similarities shared with †Ephialtitidae. The second and main radiation of evanioid wasps, the ‘neoevanioides’ clade (PP = 0.95), comprises the families †Anomopterellidae, †Baissidae, Gasteruptiidae, †Andreneliidae, Aulacidae, and Evaniidae.

Besides the relationships of the new fossil taxa, we estimated divergence dates within Evanioidea (Fig. 8). Using tip-dating analyses (run with the Mkv+G, FBD model, uniform distribution, and *samplestrat* = *fossiltip*), we estimated the divergences of stem- and crown-Evanioidea to the Late Triassic and Early Jurassic: 203 Ma (95% HPD = 188–220 Ma) and 176 Ma (95% HPD = 159–194 Ma), respectively. The tip-dating analysis also indicated that the crown-protoevanioides originated around 201 Ma (95% HPD = 186–215 Ma). Among ‘protoevanioides’,

†Othniodellithidae were estimated to have diverged from their Praeaulacidae ancestor about 117 Ma (95% HPD = 110–127 Ma). The crown-‘neoevanioides’ was estimated at 190 Ma (95% HPD = 175–208 Ma). Among neoevanioides, we have also estimated the crown-euaulacides (Aulacidae + Gasteruptiidae) around 139 Ma (95% HPD = 121–158 Ma). Aulacidae were recovered as sister lineage to Gasteruptiidae and their crown-groups would date back to 68 Ma (95% HPD = 52–89 Ma) and 20 Ma (95% HPD = 6–36 Ma), respectively. Extant Evaniidae have a crown age at 58 Ma (95% HPD = 42–75 Ma), while their oldest relatives would date back to the Middle Jurassic (155 Ma, 95% HPD = 142–168 Ma). Divergence time estimates for the main evanioid lineages are summarized in Tabl. 4.

DISCUSSION

SYSTEMATIC PLACEMENT OF NEW TAXA

Our fossils present all the diagnostic characters of the family †Othniodellithidae as described by Engel *et al.* (2016a) and emended by Engel (2017), including the complete wing venation with two rs-m crossveins and 2m-cu usually present (see Engel *et al.*, 2016a: fig 3); vein M+Cu forking distad midlength of Sc+R; vein lcu-a confluent to slightly distal to 1M; marginal cell large, wide near tangent with apex of pterostigma and elongate, nearly reaching to wing apex. With a nearly complete hind wing venation, the fossils may be confused with †Praeaulacidae, except that othniodellithids are lacking the vein C and a jugal lobe. Also, our new taxa cannot be assigned to †Praeaulacidae as they have fewer antennomeres (22 vs. at least 31 in Praeaulacidae). Overall, they possess the typical horn of the †Othniodellithidae (synapomorphy); the same wing venation (with minor variations in the presence of vein 2m-cu or alignment of vein M+Cu and Cu); and the typical habitus of the family with well-developed pronotum and mesoscutum, and a metasoma separated from mesosoma with a petiole.

The new genus *Keradellitha* differs from all other othniodellithid genera by the antenna with 22 flagellomeres (vs. 20 or 21 in the other genera); the cephalic horn without apical teeth (vs. with apical teeth in *Othniodellitha mantichora*); the gena shorter than compound eyes (vs. wider than compound eyes in *O. mantichora*); the fore wing with M+Cu and Cu aligned (vs. non-aligned in *O. mantichora*), 2cu-a and 2m-cu present (vs. both veins absent in *O. mantichora*), 2rs-m tubular (vs. non tubular in the other genera), 2A present (vs. absent in *O. mantichora* and *Xenodellitha preta*); the hind wing with five or more hamuli (vs. three in *Xenodellitha*); and legs with tarsal plantulae present (vs. absent in the other genera, but maybe not mentioned).

KEY TO GENERA OF †OTHNIODELLITHIDAE:

1. Flagellum with 20 flagellomeres; hind wing with three hamuli *Xenodellitha* Engel, 2017
- Flagellum with more than 20 flagellomeres; hind wing with five or more hamuli 2
2. Flagellum with 21 flagellomeres; cephalic horn with apical teeth; fore wing with M+Cu not aligned with 1Cu, 2m-cu absent, 1M and 1cu-a not aligned, 2cu-a absent, 2A absent *Othniodellitha* Engel & Wang, 2016
1. - Flagellum with 22 flagellomeres; cephalic horn without apical teeth; fore wing with M+Cu aligned with 1Cu, 2m-cu present, 1M and 1cu-a aligned, 2cu-a present, 2A present *Keradellitha* Jouault, Maréchal, Wang & Perrichot gen. nov.

The three species of *Keradellitha* gen. nov. can be distinguished mainly by the characters given in the key below.

KEY TO SPECIES OF *KERADELLITHA* gen. nov.:

1. Scape short (about twice as long as pedicel); fore wing with Rs+M longer than 2Rs; hind wing with five hamuli; metasoma cylindrical 2

- Scape long (more than three times as long as pedicel); fore wing with Rs+M as long as 2Rs; hind wing with six hamuli; metasoma rounded *Keradellitha basilici* Jouault, Maréchal, Wang & Perrichot sp. nov.

2. Fore wing with third and second submarginal cells similar in length, second discal cell about twice as long as wide *Keradellitha kirina* Maréchal, Jouault & Perrichot sp. nov.

- Fore wing with third submarginal cell longer than second one, second discal cell conspicuously longer than wide (three times) *Keradellitha anubis* Jouault, Maréchal, Wang & Perrichot sp. nov.

Additionally, *K. anubis* differs from *K. basilici* Jouault, Maréchal, Wang & Perrichot gen. et sp. nov. by the antenna with a short scape (vs. long); the fore wing Rs+M longer than 2Rs (vs. equal), third submarginal cell longer than the second one (vs. equal), subdiscal cell long (vs. short and wide), 2rs-m incomplete (vs. complete and tubular); the hind wing with five hamuli (vs. six); and its metasoma cylindrical (vs. rounded). For additional comparisons, see the keys proposed above.

COMPARISONS OF DIVERGENCE TIME ESTIMATES FOR EVANIOIDEA

As previously mentioned, divergence time estimates have only been proposed for the superfamily Evanioidea, including the Aulacidae, Evaniidae, and Gasteruptidae. Our result from the tip-dating approach of the superfamily Evanioidea is congruent with previous studies (Ronquist *et al.*, 2012a; Peters *et al.*, 2017; Li *et al.*, 2018; Sharanowski *et al.*, 2018; Tang *et al.*, 2019), which estimated the origin of Evanioidea in the Middle Jurassic, or possibly the Late Triassic. A recent paper

has proposed the divergence of Evaniidae around 136.8 Ma (134.1–141.4 Ma, with lognormal prior) and around 151.5 Ma (135.9–166.7 Ma, with normal prior) (Sharanowski *et al.*, 2018). Our estimates are congruent with these results since our minimum and maximum time estimates range between 140 and 186 Ma. Based on our analyses, the first known diversification of the stem-Aulacidae is estimated during the Early Cretaceous (around 130 Ma, Fig. 8), which would be earlier than the first known diversification of the stem-Gasteruptiidae, estimated in the mid-Cretaceous (around 105 Ma, Tabl. 4, Fig. 8). Interestingly, the age of the first diversification of the Gasteruptiidae that we recovered corresponds to the oldest records of the Antophila that they predate (Debevec *et al.*, 2012; Cardinal *et al.*, 2018; Genise *et al.*, 2020). Sharanowski *et al.* (2018) proposed the divergence between Aulacidae and Gasteruptiidae around 111.6 Ma, which is likely underestimated because the earliest fossil record of aulacid wasp is dated from the mid-Cretaceous (Engel & Wang, 2016a). The most recent study investigating the Gasteruptiidae phylogeny estimated that the clade (Aulacidae + Gasteruptiidae) has diverged from Evaniidae *ca.* 151 Ma (Parslow *et al.*, 2020a). This is younger than our divergence estimate *ca.* 176 Ma, congruent with the numerous Evaniidae known from the Early Cretaceous Lebanese amber (Tabl. 1). According to Parslow *et al.* (2020a), the divergence between Aulacidae and Gasteruptiidae occurred *ca.* 83 Ma, which is highly incongruent with the oldest representatives of both families both known from mid-Cretaceous Burmese amber. However, they estimated the crown-Aulacidae to arise *ca.* 52 Ma, close to the 68 Ma estimate in our analysis. They proposed that the crown-gasteruptiids arose *ca.* 60 Ma while we only recover them *ca.* 20 Ma. This latter difference is directly influenced by the scarcity of the gasteruptiid fossil record. As for the estimate of crown-Aulacidae, Parslow *et al.* (2020a) may have slightly underestimated the age of stem-Evaniidae (*ca.* 137 Ma vs. 163 Ma in our analyses). Alternatively, analyses with the FBD process might, in certain circumstances that still need to be clearly identified, overestimate datings (Arcila *et al.*, 2015; O'Reilly & Donoghue, 2016; Matschiner, 2019).

REFINING STEM AND CROWN-AGES WITHIN EVANIOIDEA

Recently, a hierarchical, suprageneric classification of Evanioidea was proposed without reconstruction of a phylogenetic hypothesis to support this classification (Engel, 2017: tabl. 2). However, the former classification was almost similar to the one derived from our Bayesian analyses (Engel, 2017: tabl. 2). Therefore, we only slightly modified it to fit with our phylogenetic results (Tabl. 2).

Contrary to many other hymenopteran taxa, the Evanioidea had a greater diversity (in terms of family) in the deep past than today. This peculiar diversity pattern implies the extinctions or declines of several lineages. The study of this fossil record allows differentiating stem- from crown-groups, which is key to our understanding of how lineages waxed and waned (Budd & Mann, 2020). Since no phylogenetic analyses integrated both fossil and extant representatives in a time-calibrated phylogeny, the delimitation and age estimates of these groups were not clearly established in evanioids. Our study thus brings the first phylogeny-based attempt in this regard.

Among the ‘Neoevanioides’, the delineation of stem- and crown-groups has been challenged by the misplacement of controversial taxa, namely *Hyptiogastrites* Cockerell, 1917, *Vectevania* Cockerell, 1922, and †Andreneliidae. The monospecific genus *Hyptiogastrites* has been assigned to †Baissidae (Li *et al.*, 2018). However, following the description of a new male specimen (Turrisi & Ellenberger, 2019) and its coding in the current phylogenetic matrix, it is now recovered in the Aulacidae. This placement is congruent with a detailed morphological study and cladistic analysis (Jennings *et al.*, 2004) but also with the former suprageneric classification proposing *Hyptiogastrites* in an early-diverging position within Aulacidae (Engel, 2017). As a result, *Hyptiogastrites* should be transferred from †Baissidae to Aulacidae. Initially described from a single partially preserved specimen, from the latest Eocene Bembridge Marls in England (Cockerell, 1922), *Vectevania vetula* Cockerell, 1922 was formerly ascribed to the Evaniidae. Recently, its position was revised (Rasnitsyn, 2013), and *V. vetula* was placed among the ‘Aulacinae’ (= Aulacidae). The most recent

morphology-based phylogenetic analysis of the Evanioidea (Li *et al.*, 2018) has led its authors to erect a monogeneric family for this taxon. It seems, however, unlikely that *Vectevania* belongs to a family distinct from the other evanioid families because Vectevaniidae was not supported by any putative autapomorphic trait (Li *et al.*, 2018: fig 24). We recovered *Vectevania vetula* among the Aulacidae as an early-diverged taxon close to the extant genera (*Aulacus* + *Pristaulacus*).

The phylogenetic position of the family †Andreneliidae has long been controversial since Rasnitsyn (pers. comm. in Turrisi & Ellenberger, 2019) proposed the †Andreneliidae as an ‘intermediate’ clade between Evaniidae and (Aulacidae + Gasteruptiidae + †Baissidae) (Turrisi & Ellenberger, 2019). Here, the family †Andreneliidae occupies an early-diverging position relative to Evaniidae, consistent with the results of the recent morphology-based phylogeny (Li *et al.*, 2018). The challenging placement of the †Andreneliidae results from the poor preservation of the unique known andreneliid specimen, which does not allow confident discussion on its placement. In this way, we define the stem- and crown-groups of Gasteruptiidae, Aulacidae and Evaniidae as shown in Figure 8.

Therefore, we consider that the Evanioidea comprise eight families: †Andreneliidae, †Anomopterellidae, Aulacidae, †Baissidae, Evaniidae, Gasteruptiidae, †Othniodellithidae, and †Praeaulacidae.

OPPOSITE DIVERSITY PATTERN BETWEEN EVANIOIDEA AND ICHNEUMONOIDEA

A recent study provided new data about variations in the species richness of hymenopteran taxa, from the Early Cretaceous to present, and showed that the Evanioidea represented more than 20% of the hymenopteran species (at least 64 species) among non-aculeate apocritan wasps during the Early Cretaceous (Jouault *et al.*, 2021b: fig 6). Based on these previous results, it appears that a shift in relative proportions between Evanioidea and Ichneumonoidea occurred during the Cretaceous. The evanioids flourished during the Jurassic while no ichneumonoids are known during this

period. During the Early Cretaceous the proportion of evanioids and ichneumonoids varies and depends on the deposits: in the Khasurty deposits (Transbaikalian) the abundance of both superfamilies are similar (Kopylov *et al.*, 2020), while the evanioids prevail in the Gurvan-Eren Formation (western Mongolia: Rasnitsyn, 1990a). On the contrary the ichneumonoids are more diverse in the Bon-Tsagan deposits (Mongolia: Rasnitsyn, 1980b). The relative species richness of ichneumonoids and evanioids among non-aculeates shifted from *ca.* 25% during the middle to Late Cretaceous to more than 50% (for ichneumonoids) vs. less than 5% (for evanioids) after the early Late Cretaceous (Jouault *et al.*, 2021b: fig 6). This significant proportion of ichneumonoids almost invariably dominate the Late Cretaceous with an abundant ichneumonoid fauna described from the Yantardakh deposits (Taimyr) or from the Ola Formation (Rasnitsyn, 1980b). Similarly, they are abundant in the Late Cretaceous amber deposits (New Jersey and Canada ambers: see respectively (Grimaldi *et al.*, 2000; McKellar & Enel, 2012). The only exception is in Orapa, Botswana (Brothers & Rasnitsyn, 2003). It is possible that the shift in proportions between the two superfamilies' occurred earlier than the Cretaceous (see for instance dating estimates of Spasojevic *et al.*, 2021), although this hypothesis would need additional support as no ichneumonoid fossils are known from this period so far. In addition, these changes in diversity and abundance are not underestimated in the fossil record because the relative abundances of the ichneumonoid and evanioid wasps in the Burmese amber biota show that ichneumonoids were slightly less abundant than evanioids (Zhang *et al.*, 2018), while ichneumonoids are clearly more abundant than evanioids in the Cenozoic fossil record. However, data from the latest Cretaceous are too poor to be evaluated due to the lack of any deposits. Nowadays, Ichneumonoidea are hyper-diversified, hyper-abundant, and widespread with more than 44,000 known species, while Evanioidea are clearly less diversified with only *ca.* 1,400 species described (data compiled from <http://fossilworks.org/> and <https://hol.osu.edu/>; both accessed November 25, 2020).

Numerous hypotheses could be proposed to explain this shift. For instance, a host-related diversification may have contributed to this pattern, with a decrease in host abundance favourable to Evanioidea and an increase in those favourable to Ichneumonoidea. However, any hypothesis will be difficult to verify. It is also worth mentioning that the decline of evanioids (except the family Evaniidae) occurs in parallel with, and is probably correlated to, the diversification of the xylophilous ichneumonoids. In contrast, the rise of Evaniidae parallels that of the modern Dictyoptera that appeared temporally close to the Jurassic-Cretaceous boundary and diversified during Cretaceous and Cenozoic (Rasnitsyn & Quicke, 2002).

ONE GENUS & TWO DEPOSITS: A DIRECT EVIDENCE OF THE ISOLATION OF THE WEST BURMA BLOCK

The record of three new othniodellithid wasps from two different Cretaceous Burmese amber provides new clues to investigate the stability and the isolation of the West Burma Block (WBB). In fact, the WBB has experienced a tumultuous geological history with a long migration from Gondwana. During the Early Jurassic, the WBB was located near the Australian block in East Gondwana (Seton *et al.*, 2012; van Hinsbergen *et al.*, 2012) and was separated from East Laurasia (Asian region) by the Meso-Tethys Ocean. Numerous studies have investigated the break-up of the WBB + Indian block and they estimated that the break-up from the Gondwana + Australian block occurred between the Late Jurassic and the Early Cretaceous (Heine *et al.*, 2004; Heine and Müller, 2005). A recent study (Westerweel *et al.*, 2019) refined these estimates and agreed with previous works (Metcalf, 1990, 1996; Scotese, 2014), suggesting that the separation dated back *ca.* 125 Ma. They also assumed that the Terrane became an isolated island only after *ca.* 120 Ma. During the resin formation and production, both deposits (Hkamti and Noiye Bum) were isolated geographically and occupied an island position in the Tethys Ocean (Westerweel *et al.*, 2019), during more than 20 Ma (Heine *et al.*, 2004; Seton *et al.*, 2012; Licht *et al.*, 2020).

Interestingly, the geological history of the WBB and the othniodellithid fossil record confirm this isolation. In fact, the †Othniodellithidae are endemic to the Burmese amber biota and representatives of the family are now found in two Cretaceous Burmese deposits of different ages, respectively early Albian and Cenomanian. These records are direct evidence of the stability of the WBB biota during at least 10 Ma, which also supports the hypothesis of a long journey of the isolate plate through the Tethys Ocean from Gondwana to Asia. These new discoveries suggest that the WBB has remained isolated long enough for the development of a unique biota. If a part of Burmese amber biota shares affinities with the South Gondwana (e.g. de Sena Oliveira *et al.*, 2016; Poinar, 2018; Jouault and Nel, 2020) or Laurasia fauna (e.g. Gumovsky *et al.*, 2018; Martynova *et al.*, 2019; Jouault, 2021), an even larger part is endemic and results from the isolation of WBB for at least 10 to 20 Ma.

CONCLUSION

Our study presents the currently most complete phylogenetic hypothesis of Evanioidea, including most extinct genera, and provides divergence times for all known evanoid families. Bayesian inferences support the monophyly of the Evanioidea and of the families †Anomopterellidae, †Othniodellithidae, †Andreneliidae, Aulacidae, Gasteruptiidae, and Evaniidae. Praeaulacidae and †Baissidae appear to be paraphyletic. The Bayesian tree also allows the transfer of *Vectevania* and *Hyptiogastrites* among Aulacidae. The inferred divergence times of Evanioidea indicate that they have probably originated in the Late Triassic-Early Jurassic, which corroborates previous estimations. The evolutionary history of evanoid wasps seems to be a succession of appearances and extinctions of families, the most recent replacing the oldest in their ecological niches or conquering new ones thanks to clade-specific adaptations (viz. †Othniodellithidae). Additionally, the relative abundance and diversity of the evanoid and ichneumonoid wasps in the deep past seem to follow

an opposite pattern. However, further works are necessary to deepen our understanding of the various drivers of evanioid diversification, especially in relation to their competitors and hosts.

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REFERENCES

- Arcila D, Pyron A, Tyler JC, Ortí G, Betancur-R R. 2015.** An evaluation of fossil tip-dating versus node-age calibrations in tetraodontiform fishes (Teleostei: Percomorphaceae). *Molecular Phylogenetics and Evolution* **82**: 131–145. <https://doi.org/10.1016/j.ympev.2014.10.011>
- Barido-Sottani J, Aguirre-Fernández G, Hopkins MJ, Stadler T, Warnock R. 2019.** Ignoring stratigraphic age uncertainty leads to erroneous estimates of species divergence times under the fossilized birth–death process. *Proceedings of the Royal Society B* **286**: 20190685. <https://doi.org/10.1098/rspb.2019.0685>
- Basibuyuk HH, Fitton MG, Rasnitsyn AP. 2000.** Two new genera of the Evaniidae (Insecta: Hymenoptera) from Late Cretaceous New Jersey Amber. *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey* 313–325.
- Basibuyuk HH, Rasnitsyn AP, Fitton MG, Quicke DLJ. 2002.** The limits of the family Evaniidae (Insecta: Hymenoptera) and a new genus from Lebanese amber. *Insect Systematics & Evolution* **33**: 23–34. <https://doi.org/10.1163/187631202X00037>

- Behrensmeyer AK, Turner A. 2013.** Taxonomic occurrences of Evanioidea recorded in the Paleobiology Database. Fossilworks. <http://fossilworks.org>. (Last access 25/11/2020)
- Bogusch P, van Achterberg C, Šilhán K, Astapenková A, Heneberg P. 2018.** Description of mature larvae and ecological notes on *Gasteruption* Latreille (Hymenoptera, Evanioidea, Gasteruptionidae) parasitizing hymenopterans nesting in reed galls. *Journal of Hymenoptera Research* **65**: 1–21. <https://doi.org/10.3897/jhr.65.26645>
- Brothers DJ, Rasnitsyn AP. 2003.** Diversity of Hymenoptera and other insects in the Late Cretaceous (Turonian) deposits at Orapa, Botswana : a preliminary review. *African Entomology* **11**: 221–226. <https://hdl.handle.net/10520/EJC32559>
- Brown VK. 1973.** The biology and development of *Brachygaster minutus* Olivier (Hymenoptera: Evaniidae). a parasite of the oothecae of *Ectobius* spp. (Dictyoptera: Blattidae). *Journal of Natural History* **7**: 665–674. <https://doi.org/10.1080/00222937300770561>
- Brues CT. 1910.** The parasitic Hymenoptera of the Tertiary of Florissant, Colorado. *Bulletin of the Museum of Comparative Zoology at Harvard College* **54**: 1–125.
- Brues CT. 1933.** The parasitic Hymenoptera of the Baltic amber. *Bernstein-Forschungen* **3**: 4–178.
- Budd GE, Mann RP. 2020.** The dynamics of stem and crown groups. *Science Advances* **6**: eaaz1626. <https://doi.org/10.1126/sciadv.aaz1626>
- Cardinal S, Buchmann SL, Russell AL. 2018.** The evolution of floral sonication, a pollen foraging behavior used by bees (Anthophila). *Evolution*, **72**: 590–600. <https://doi.org/10.1111/evo.13446>
- Cockerell TDA. 1916.** Some American fossil insects. *Proceedings of the United States National Museum* **51**: 89–106.
- Cockerell TDA. 1917.** Fossil insects. *Annals of the Entomological Society of America* **10**: 1–22.
- Cockerell TDA. 1922.** Two families of insects new to British Tertiary strata. *Canadian Entomologist* **54**: 33–34. <https://doi.org/10.4039/Ent5433-2>

- Cruickshank RD, Ko K. 2003.** Geology of an amber locality in the Hukawng Valley, northern Myanmar. *Journal of Asian Earth Sciences* **21**: 441–455. [https://doi.org/10.1016/S1367-9120\(02\)00044-5](https://doi.org/10.1016/S1367-9120(02)00044-5)
- de Sena Oliveira IS, Bai M, Jahn H, Gross V, Martin C, Hammel JU, et al. 2016.** Earliest onychophoran in Amber Reveals Gondwanan Migration Patterns. *Current Biology* **26**: 2594–2601. <http://dx.doi.org/10.1016/j.cub.2016.07.023>.
- Deans AR. 2004.** Descriptions of two new Early Cretaceous (Hauterivian) ensign wasp genera (Hymenoptera: Evaniidae) from Lebanese amber. *Cretaceous Research* **25**: 509–516. <https://doi.org/10.1016/j.cretres.2004.04.003>
- Debevec AH, Cardinal S, Danforth BN. 2012.** Identifying the sister group to the bees: a molecular phylogeny of Aculeata with an emphasis on the superfamily Apoidea. *Zoologica Scripta* **41**: 527–535. <https://doi.org/10.1111/j.1463-6409.2012.00549.x>
- Deyrup MA. 1984.** A maple wood wasp, *Xiphydria maculata*, and its insect enemies (Hymenoptera: Xiphydriidae). *Great Lake Entomologist* **17**: 17–28. <https://scholar.valpo.edu/tgle/vol17/iss1/3>
- Dowton M, Austin A. 1994.** Molecular phylogeny of the insect order Hymenoptera: apocritan relationships. *Proceedings of the National Academy of Sciences of the USA* **91**: 9911–9915. <https://doi.org/10.1073/pnas.91.21.9911>
- Dowton M, Austin A, Dillon N, Bartowsky E. 1997.** Molecular phylogeny of the apocritan wasps: the Proctotrupomorpha and Evaniomorpha. *Systematic Entomology* **22**: 245–255. <https://doi.org/10.1046/j.1365-3113.1997.d01-42.x>
- EDNA 2015.** Fossil Insects Database. Palaeontological Association. Oxford University Press, New York, New York. URL <http://edna.palass-hosting.org>.
- Engel MS. 2006.** Two ensign wasps in Cretaceous amber from New Jersey and Myanmar (Hymenoptera: Evaniidae). *Polish Journal of Entomology* **75**: 443–454.

- Engel MS. 2013.** A new genus and species of Baissidae in Late Cretaceous amber from New Jersey (Hymenoptera: Evanioidea). *Novitates Paleontologicae* **3**: 1–8. <https://doi.org/10.17161/np.v0i3.4570>
- Engel MS. 2017.** New evanioid wasps from the Cenomanian of Myanmar (Hymenoptera: Othniellithidae, Aulacidae), with a summary of family-group names among Evanioidea. *American Museum Novitates* **3871**: 1–28. <https://doi.org/10.1206/3871.1>
- Engel MS, Huang D-Y, Alqarni AS, Cai C-Y. 2016a.** A remarkable evanioid wasp in mid-Cretaceous amber from northern Myanmar (Hymenoptera: Evanioidea). *Cretaceous Research* **60**: 121–127. <https://doi.org/10.1016/j.cretres.2015.11.012>
- Engel MS, Wang B. 2016a.** A plesiomorphic gasteruptiid wasp in Cenomanian amber from Myanmar (Hymenoptera: Gasteruptiidae). *Cretaceous Research* **63**: 177–182. <https://doi.org/10.1016/j.cretres.2016.03.011>
- Engel MS, Wang B. 2016b.** The first Oriental protorhyssaline wasp (Hymenoptera: Braconidae): A new genus and species in Upper Cretaceous amber from Myanmar. *Cretaceous Research* **63**: 28–32. <https://doi.org/10.1016/j.cretres.2016.02.012>
- Felsenstein J. 1985.** Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**: 783–391. <https://doi.org/10.1111/j.1558-5646.1985.tb00420.x>
- Gauld ID, Hanson B. 1995.** The evaniomorph parasitoid families. In: Hanson PE, Gauld ID. eds. *The Hymenoptera of Costa Rica*. Oxford: Oxford University Press 185–208.
- Gavryushkina A, Heath TA, Ksepka DT, Stadler T, Welch D, Drummond AJ. 2016.** Bayesian total-evidence dating reveals the recent crown radiation of penguins. *Systematic Biology* **66**: 57–73. <https://doi.org/10.1093/sysbio/syw060>
- Genise JF, Bellosi ES, Sarzetti LC, Krause JM, Dinghi PA, Sanchez MV, Umazano AM, Puerta P, Cantil LF, Jicha BR. 2020.** 100 Ma sweat bee nests: early and rapid codiversification of

crown bees and flowering plants. *Plos ONE* **15**: (e0227789) 1-20. <https://doi.org/10.1371/journal.pone.0227789>

Gerstaecker CEA. 1867. Über die Gattung *Oxybelus* Latr. und die bei Berlin vorkommenden Arten derselben. *Zeitschrift für die Gesamten Naturwissenschaft* **30**: 1–96.

Grimaldi D, Ross A. 2017. Extraordinary Lagerstätten in amber, with particular reference to the Cretaceous of Burma. In: Fraser NC, Sues H-D, eds. *Terrestrial conservation Lagerstätten: windows into the evolution of life on land*. Edinburgh: Dunedin Academic Press, 287–342.

Grimaldi D, Shedrinsky A, Wampler TP. 2000. A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey. In: Grimaldi D. ed., *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey*: 1–76. Leiden: Backhuys Publishers, 498 pp.

Gumovsky A, Perkovsky EE, Rasnitsyn AP. 2018. Laurasian ancestors and “Gondwanan” descendants of Rotoitidae (Hymenoptera: Chalcidoidea): what a review of Late Cretaceous Baeomorpha revealed. *Cretaceous Research* **84**: 286–322. <http://dx.doi.org/10.1016/j.cretres.2017.10.027>.

Heath TA, Huelsenbeck JP, Stadler T. 2014. The fossilized birth–death process for coherent calibration of divergence-time estimates. *Proceedings of the National Academy of Sciences of the USA* **111**: E2957–E2966. <https://doi.org/10.1073/pnas.1319091111>

Heine C, Müller RD. 2005. Late Jurassic rifting along the Australian North West Shelf: margin geometry and spreading ridge configuration. *Australian Journal of Earth Sciences* **52**: 27–39. <http://dx.doi.org/10.1080/08120090500100077> [39–27].

Heine C, Müller RD, Gaina C. 2004. Reconstructing the lost eastern Tethys ocean basin: convergence history of the SE Asian margin and marine gateways. *Geophysical Monograph Series* **149**: 1–18, <http://dx.doi.org/10.1029/149GM03>.

- Heraty JM, Ronquist F, Carpenter JM, Hawks D, Schulmeister S, Dowling AP, Murray D, Munro J, Wheeler WC, Schiff N, Sharkey MJ. 2011.** Evolution of the hymenopteran megara-diation. *Molecular Phylogenetics and Evolution* **60**: 73–88. <https://doi.org/10.1016/j.ympev.2011.04.003>
- Hillis DM, Bull JJ. 1993.** An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology* **42**: 182–192. <https://doi.org/10.1093/sysbio/42.2.182>
- Hong YC, Wang WL. 1990.** *Fossil insects from the Laiyang Basin, Shandong Province. Stratigraphy and Palaeontology of Laiyang Basin, Shandong Province.* Beijing: Dizhi Chuban She, 44–189.
- Huben M. 1995.** Evaniidae. In: Hanson PE, Gauld ID. eds. *The Hymenoptera of Costa Rica.* Oxford: Oxford University Press, 195–199.
- Huelsenbeck JP, Ronquist F. 2001.** MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* **17**: 754–755. <https://doi.org/10.1093/bioinformatics/17.8.754>
- Jell PA, Duncan PM. 1986.** Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. *Memoirs of the Association of Australasian Palaeontologists* **3**: 111–205.
- Jennings JT, Austin AD. 2000.** Higher-level phylogeny of the Aulacidae and Gasteruptiidae (Hymenoptera: Evanioidea). In: Austin AD, Downton M. ed. *The Hymenoptera: Evolution.* Melbourne: Biodiversity and Biological Control. C.S.I.R.O. Publishing, 154–164.
- Jennings JT, Austin AD. 2004.** Biology and host relationships of aulacid and gasteruptiid wasps (Hymenoptera: Evanioidea): a review. In: Rajmohana K, Sudheer K, Kumar G, Santhosh S. eds. *Perspectives on biosystematics and biodiversity.* Kerala: University of Calicut, 187–215.

- Jennings JT, Krogmann L. 2009.** A new species of *Pristaulacus* Kieffer (Hymenoptera: Aulacidae) from Baltic amber. *Insect Systematics & Evolution* **40**: 201–207. <https://doi.org/10.1163/187631209X440069>
- Jennings JT, Krogmann L, Mew SL. 2012.** *Hyptia deansi* sp. nov., the first record of Evaniidae (Hymenoptera) from Mexican amber. *Zootaxa* **3349**: 63–68. <https://doi.org/10.11646/zootaxa.3349.1.7>
- Jennings JT, Krogmann L, Mew SL. 2013.** *Cretevania bechlyi* sp. nov., from Cretaceous Burmese amber (Hymenoptera: Evaniidae). *Zootaxa* **3609**: 091–095. <https://doi.org/10.11646/zootaxa.3609.1.7>
- Jouault C. 2021.** Mid-Cretaceous Burmese amber peleciniid wasps (Hymenoptera, Peleciniidae) support the hypothesis of an Asian origin of the family. *Annales de Paléontologie* **107**: 102464. <https://doi.org/10.1016/j.annpal.2020.102464>
- Jouault C, Nel A. 2020.** The oldest record of window fly supports a Gondwanan origin of the family (Diptera: Scenopinidae). *Palaeoentomology* **3**: 483–491. <http://dx.doi.org/10.11646/palaeoentomology.3.5.6>.
- Jouault C, Nel A. 2021.** A new genus and species of Aulacidae (Hymenoptera: Evanioidea) from mid-Cretaceous Burmese amber. *Cretaceous Research* **104799**. <https://doi.org/10.1016/j.cretres.2021.104799>
- Jouault C, Nel A, Perrichot V. 2020.** New evanioid wasps (Hymenoptera: Praeaulacidae, Aulacidae) from Cenomanian Burmese amber. *Cretaceous Research* **110**: 104407. <https://doi.org/10.1016/j.cretres.2020.104407>
- Jouault C, Legendre F, Grandcolas P, Nel A. 2021a.** Revising dating estimates and the antiquity of eusociality in termites using the fossilized birth-death process. *Systematic Entomology* (in press)

- Jouault C, Rasnitsyn AP, Perrichot V. 2021b.** Ohlhoffiidae, a new Cretaceous family of basal parasitic wasps (Hymenoptera: Stephanoidea). *Cretaceous Research* **117**: 104635. <https://doi.org/10.1016/j.cretres.2020.104635>
- Kaddumi HF. 2007.** *Amber of Jordan*. The Oldest Prehistoric Insects in Fossilized Resin 1–298.
- Klopfstein S, Vilhelmsen L, Heraty JM, Sharkey M, Ronquist F. 2013.** The hymenopteran tree of life: evidence from protein-coding genes and objectively aligned ribosomal data. *PLoS One* **8**: e69344. <https://doi.org/10.1371/journal.pone.0069344>
- Kopylov DS, Rasnitsyn AP, Aristov DS, Bashkuev AS, Bazhenova NV, Dmitriev VY, Gorochov AV, Ignatov MS, Ivanov VD, Khramov AV, Legalov AA, Lukashevich ED, Mamontov YS, Melnitsky SI, Oglaza B, Ponomarenko AG, Prokin AA, Ryzhkova OV, Shmakov AS, Sinitshenkova ND, Solodovnikov AY, Strelnikova OD, Sukacheva ID, Uliakhin AV, Vasilenko DV, Wegierek P, Yan EV, Zmarzly M. 2020.** The Khasurty fossil insect lagerstätte. *Paleontological Journal* **54**: 1221–1394. <https://doi.org/10.1134/S0031030120110027>
- Kuroda K, Konishi K, Turrisi GF, Yamasako J. 2020.** A revisional study of the genus *Aulacus* Jurine (Hymenoptera: Aulacidae) of Japan. *Zootaxa* **4830**: 161–185. <https://doi-org.proxy.mnhn.-fr/10.3897/zookeys.587.7207>
- Latreille PA. 1802.** *Histoire Naturelle, Générale et Particulière des Crustacés et des Insectes, Tome Troisième* 1–467.
- Lepage T, Bryant D, Philippe H, Lartillot N. 2007.** A general comparison of relaxed molecular clock models. *Molecular Biology and Evolution* **24**: 2669–2680. <https://doi.org/10.1093/molbev/msm193>
- Lewis PO. 2001.** A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology* **50**: 913–925. <https://doi.org/10.1080/106351501753462876>

- Li LF, Rasnitsyn AP, Shih C, Labandeira CC, Buffington M, Li D, Ren D. 2018.** Phylogeny of Evanioidea (Hymenoptera, Apocrita), with descriptions of new Mesozoic species from China and Myanmar. *Systematic Entomology* **43**: 810–842. <https://doi.org/10.1111/syen.12315>
- Li LF, Rasnitsyn AP, Shih CK, Ren D. 2013a.** Anomopterellidae restored, with two new genera and its phylogeny in Evanioidea (Hymenoptera). *PLoS ONE* **8**: e82587. <https://doi.org/10.1371/journal.pone.0082587>
- Li, LF, Rasnitsyn AP, Shih CK, Ren D. 2015.** A new genus and species of Praeaulacidae (Hymenoptera: Evanioidea) from Upper Cretaceous Myanmar amber. *Cretaceous Research* **55**: 19–24. <https://doi.org/10.1016/j.cretres.2015.01.007>
- Li LF, Shih CK. 2015.** Two new fossil wasps (Insecta: Hymenoptera: Apocrita) from northeastern China. *Journal of Natural History* **49**: 829–840. <https://doi.org/10.1080/00222933.2014.953223>.
- Li LF, Shih CK, Li DQ, Ren D. 2019.** New fossil species of Ephialtitidae and Baissidae (Hymenoptera, Apocrita) from the mid-Mesozoic of northeastern China. *Alcheringa* **43**: 568–579. <https://doi.org/10.1080/03115518.2019.1601767>
- Li LF, Shih CK, Ren D. 2013b.** Two new species of *Nevania* (Hymenoptera: Evanioidea: Praeaulacidae: Nevaniinae) from the Middle Jurassic of China. *Alcheringa* **38**: 140–147. <https://doi.org/10.1080/03115518.2014.843376>
- Li LF, Shih CK, Ren D. 2014a.** New fossil Praeaulacinae wasps (Insecta: Hymenoptera: Evanioidea: Praeaulacidae) from the Middle Jurassic of China. *Zootaxa* **3814**: 432–442. <https://doi.org/10.11646/zootaxa.3814.3.10>
- Li LF, Shih CK, Ren D. 2014b.** Revision of *Anomopterella* Rasnitsyn, 1975 (Insecta, Hymenoptera, Anomopterellidae) with two new Middle Jurassic species from northeastern China. *Geologica Carpathica* **65**: 365–374. <https://doi.org/10.2478/geoca-2014-0025>

- Li LF, Shih CK, Ren D. 2014c.** New fossil evaniids (Hymenoptera, Evanioidea) from the Yixian Formation of western Liaoning, China. *Cretaceous Research* **47**: 48–55. <https://doi.org/10.1016/j.cretres.2013.10.006>
- Licht A, Win Z, Westerweel J, Cogné N, Morley CK, Chantraprasert S, Poblete F, Ugrai T, Nelson B, Wa Aung D, Dupont-Nivet G. 2020.** Magmatic history of central Myanmar and implications for the evolution of the Burma Terrane. *Gondwana Research* **87**: 303–319. <https://doi.org/10.1016/j.gr.2020.06.016>
- Lin QB. 1980.** *Fossil insects from the Mesozoic of Zhejiang and Anhui provinces*. In Nanjing Institute of Geology and Palaeontology ed. *Division and correlation of the Mesozoic volcano-sedimentary formations in the provinces of Zhejiang and Anhui*. Science Press, Beijing, 211–234. (In Chinese).
- Linnaeus C. 1758.** *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Editio Decima* **1**: 1–824.
- Maddison WP, Maddison DR. 2019.** Mesquite: a modular system for evolutionary analysis. Version 3.61. Available at: <http://www.mesquiteproject.org>
- Malyshev SI. 1968.** *Genesis of the Hymenoptera and the Phases of their Evolution*. Boston: Springer, 286.
- Martynova KV, Olmi M, Müller P, Perkovsky EE. 2019.** Description of the first sclerogibbid wasp (Hymenoptera: Sclerogibbidae) from Burmese (Myanmar) amber and its phylogenetic significance. *Journal of Systematic Paleontology* **17**: 1791–1803. <http://dx.doi.org/10.1080/14772019.2018.1551250>.
- Matschiner M. 2019.** Selective sampling of species and fossils influences age estimates under the Fossilized Birth–Death model. *Frontier in Genetics* **10**: 1064. <https://doi.org/10.3389/fgene.2019.01064>

- Matzke N, Wright A. 2016.** Inferring node dates from tip dates in fossil Canidae: the importance of tree priors. *Biology Letters* **12**: 20160328. <http://dx.doi.org/10.1098/rsbl.2016.0328>
- McKellar RC, Engel MS. 2012.** Hymenoptera in Canadian Cretaceous amber (Insecta). *Cretaceous Research* **35**: 258-279. <https://doi.org/10.1016/j.cretres.2011.12.009>
- Metcalf I. 1990.** Allochthonous terrane processes in Southeast Asia. *Philosophical Transactions of the Royal Society of London, A* **331**: 625–640. <http://dx.doi.org/10.1098/rsta.1990.0094>.
- Metcalf I. 1996.** Pre-cretaceous evolution of SE Asian terranes. In: Hall, R., Blundell, D. (Eds.), Tectonic evolution of Southeast Asia, 106. Geological Society Special Publication, pp. 122–197, <http://dx.doi.org/10.1144/GSL.SP.1996.106.01.09>.
- Nel A, Martínez-Delclòs X, Azar D. 2002.** A new ensign-fly from the Lower-Middle Miocene Dominican amber (Hymenoptera, Evaniidae). *Bulletin de la Société Entomologique de France* **107**: 217–221. www.persee.fr/doc/bsef_0037-928x_2002_num_107_3_16844
- Nel A, Waller, A, De Ploeg G. 2004.** An aulacid wasp in the Lowermost Eocene amber from the Paris Basin (Hymenoptera: Aulacidae). *Geologica Acta* **2**: 67–74. <https://doi.org/10.1344/105.000001636>
- Oberprieler SK, Rasnitsyn AP, Brothers DJ. 2012.** The first wasps from the Upper Jurassic of Australia (Hymenoptera: Evanioidea, Praeaulacidae). *Zootaxa* **3503**: 47–54. <https://doi.org/10.11646/zootaxa.3503.1.3>
- O'Reilly JE, Donoghue PCJ. 2016.** Tips and nodes are complementary not competing approaches to the calibration of molecular clocks. *Biology Letters* **12**: 20150975. <http://doi.org/10.1098/rsbl.2015.0975>
- Parslow BA, Jennings JT, Schwarz MP, Stevens MI. 2020a.** Phylogeny and divergence estimates for the gasteruptiid wasps (Hymenoptera: Evanioidea) reveals a correlation with hosts. *Invertebrate Systematics* **34**: 319–327. <https://doi.org/10.1071/IS19060>

- Parslow BA, Schwarz MP, Stevens MI. 2020b.** Review of the biology and host associations of the wasp genus *Gasteruption* (Evanioidea: Gasteruptionidae). *Zoological Journal of the Linnean Society* **189**: 1105–1122. <https://doi.org/10.1093/zoolinnean/zlaa005>
- Paterson JR, Edgecombe GD, Lee MSY. 2019.** Trilobite evolutionary rates constrain the duration of the Cambrian explosion. *Proceedings of the National Academy of Sciences of the USA* **116**: 4394–4399. <https://doi.org/10.1073/pnas.1819366116>
- Payne A, Barden PM, Wheeler WC, Carpenter JM. 2013.** Direct optimization, sensitivity analysis, and the evolution of the hymenopteran superfamilies. *American Museum Novitates* **3789**: 1–19. <https://doi.org/10.1206/3789.1>
- Peñalver E, Ortega-Blanco J, Nel A, Delclòs X. 2010.** Mesozoic Evaniidae (Insecta: Hymenoptera) in Spanish amber: reanalysis of the phylogeny of the Evanioidea. *Acta Geologica Sinica* **84**: 809–827. <https://doi.org/10.1111/j.1755-6724.2010.00257.x>
- Pérez-de la fuente R, Peñalver E, Ortega-Blanco J. 2012.** A new species of the diverse Cretaceous genus *Cretevania* Rasnitsyn, 1975 (Hymenoptera: Evaniidae) from Spanish amber. *Zootaxa* **3514**: 70–78. <https://doi.org/10.11646/zootaxa.3514.1.4>
- Perioto NW, Lara RIR, Macedo ACC. 2020.** Gasteruptionidae (Hymenoptera, Evanioidea) of three savannah phytogeographies of the Estação Ecológica do Jataí, in southeastern Brazil, under three sampling methods and a new record for *Gasteruption helenae* Macedo, 2011. *Anais da Academia Brasileira de Ciências* **92 (suppl. 2)**: 1–7. e20181073 DOI 10.1590/0001-3765202020181073
- Peters R, Krogmann L, Mayer C, Donath A, Gunkel S, Meusemann K, Kozlov A, Podsiadlowski L, Petersen M, Lanfear R, Diez P, Heraty J, Kjer K, Klopstein S, Meier R, Polidori C, Schmitt T, Liu S, Zhou X, Niehuis O. 2017.** Evolutionary history of the Hymenoptera. *Current Biology* **27**: 1013–1018. <http://dx.doi.org/10.1016/j.cub.2017.01.027>

- Poinar G. Jr. 2018.** Burmese amber: evidence of Gondwanan origin and Cretaceous dispersion. *Historical Biology* **31**: 1304–1309. <http://dx.doi.org/10.1080/08912963.2018.1446531>.
- Poinar G. Jr. 2019.** A new genus and species of wasp (Hymenoptera: Evanioidea: Praeaulacidae) associated with an angiosperm flower in Burmese amber. *Palaeoentomology* **2**: 474–481. <https://doi.org/10.11646/palaeoentomology.2.5.11>
- Poinar G. 2020.** Ensign wasps (Hymenoptera: Evaniidae) in Dominican and Mexican amber. *Historical Biology* <https://doi.org/10.1080/08912963.2020.1818075>
- Pyron RA. 2017.** Novel approaches for phylogenetic inference from morphological data and total-evidence dating in squamate reptiles (lizards, snakes, and amphisbaenians). *Systematic Biology* **66**: 38–56. <https://doi.org/10.1093/sysbio/syw068>
- Ramage T, Jouault C. 2020.** New species and records of Evanioidea and Stephanoidea from New Caledonia (Hymenoptera). *European Journal of Taxonomy* **723**: 1–32. <https://doi.org/10.5852/ejt.2020.723.1141>
- Rambaut A. 2009.** FigTree v1.4.4. Available via <http://tree.bio.ed.ac.uk/software/figtree/>. Accessed March 1, 2020.
- Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018.** Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* **67**: 901–904. <https://doi.org/10.1093/sysbio/syy032>
- Rasnitsyn AP. 1972.** Late Jurassic hymenopterous insects (Praeaulacidae) of Karatau. *Paleontological Journal* **6**: 62–77.
- Rasnitsyn AP. 1973.** *Praeaulacinus parvus* A. Rasnitsyn, n. nom. (Insecta, Hymenoptera). *Paleontological Journal* **7**: 116–116.
- Rasnitsyn AP. 1975.** Hymenoptera Apocrita of Mesozoic. *Transactions of the Palaeontological Institute Academy of Sciences of the USSR* **147**: 1–134.

- Rasnitsyn AP. 1980a.** K sisteme semeystva Aulacidae (Hymenoptera) v svyazi s novoy nakhodkoy v nizhnem Melu Manlya. Rannemelovoe Ozero Manlay. *Sovmestnaya Sovetsko-Mongol'skaya Paleontologicheskaya Ekspeditsiya Trudy* **13**: 65–67.
- Rasnitsyn AP. 1980b.** [Origin and evolution of Hymenoptera]. *Transactions of the Paleontological Institute, Academy of Sciences of the USSR* **174**: 1–192 [in Russian].
- Rasnitsyn AP. 1983.** New names for fossil insects. *Paleontological Journal* **17**: 99.
- Rasnitsyn AP. 1986.** Wasps. Vespida (= Hymenoptera), in Nasekomye v rannemelovykh ekosistemakh zapadnoy Mongolii. In Rasnitsyn AP. ed. *The Joint Soviet-Mongolian Palaeontological Expedition* **28**: 154–164.
- Rasnitsyn AP. 1990a.** New representatives of the hymenopterous family Praeaulacidae from Early Cretaceous Buryatia and Mongolia. *Vestnik Zoologii* **1990**: 27–31.
- Rasnitsyn AP. 1990b.** Hymenopterans, Vespida, in Pozdne-Mezozoyskie Nasekomye Vostochnogo Zabaykal'ya. In: Rasnitsyn AP.(ed.), Akademiya Nauk SSSR, *Trudy Paleontologicheskogo Instituta* **239**: 177–205.
- Rasnitsyn AP. 1991.** New hymenopterans of the genus *Baissa* (Gasteruptiidae s.l.) from Early Cretaceous Buryatia and Mongolia. *Vestnik Zoologii* **1991**: 78–79.
- Rasnitsyn AP. 2008.** Hymenopterous insects (Insecta: Vespida) in the Upper Jurassic deposits of Shar Teg, SW Mongolia. *Russian Entomological Journal* **17**: 299–310.
- Rasnitsyn AP. 2013.** *Vectevania vetula* Cockerell, 1922 from the uppermost Eocene of Bembridge Marls, England, and the system of the family Gasteruptiidae s.l. [(Vespida (=Hymenoptera), Evanioidea)]. *Proceedings of the Russian Entomological Society St. Petersburg* **84**: 98–106.
- Rasnitsyn AP, Brothers DJ. 2007.** Two new hymenopteran fossils from the mid-Cretaceous of southern Africa (Hymenoptera: Jurapriidae, Evaniidae). *African Invertebrates* **48**: 193–202.
- Rasnitsyn AP, Jarzembowski EA, Ross AJ. 1998.** Wasps (Insecta: Vespida = Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical

and palaeoenvironmental significance. *Cretaceous Research* **19**: 329–391. <https://doi.org/10.1006/cres.1997.0114>

Rasnitsyn AP, Martínez-Delclòs X. 2000. Wasps (Insecta: Vespida = Hymenoptera) from the Early Cretaceous of Spain. *Acta Geologica Hispanica* **35**: 65–95.

Rasnitsyn AP, Quicke DL. 2020. *History of insects*. Dordrecht: Netherlands Kluwer Academic Publisher.

Rasnitsyn AP, Sharkey M. 1988. New Eoichneumonidae from Early Cretaceous of Siberia and Mongolia (Hymenoptera: Ichneumonoidea). *Advances in Parasitic Hymenoptera Research* **1988**: 169–197.

Rasnitsyn AP, Zhang HC. 2010. Early evolution of Apocrita (Insect, Hymenoptera) as indicated by new findings in the Middle Jurassic of Daohugou, Northeast China. *Acta Geologica Sinica* **84**: 834–873. <https://doi.org/10.1111/j.1755-6724.2010.00254.x>

Ren D. 1995. *Insecta*. In: Ren D, Lu LW, Guo ZG, Ji SA. eds. *Faunae and stratigraphy of Jurassic-Cretaceous in Beijing and the adjacent areas*. Beijing: Seismic Publishing House 47–121.

Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574. <https://doi.org/10.1093/bioinformatics/btg180>

Ronquist F, Klopfstein S, Vilhelmsen L, Schulmeister S, Murray DL, Rasnitsyn AP. 2012a. A total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera. *Systematic Biology* **61**: 973–999. <https://doi.org/10.1093/sysbio/sys058>

Ronquist F, Rasnitsyn AP, Roy A, Eriksson K, Lindgren M. 1999. Phylogeny of the Hymenoptera: a cladistic reanalysis of Rasnitsyn's (1988) data. *Zoologica Scripta* **28**: 13–50. <https://doi.org/10.1046/j.1463-6409.1999.00023.x>

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012b. MRBAYES 3.2: Efficient Bayesian phylogenetic infer-

ence and model selection across a large model space. *Systematic Biology* **61**: 539–542. <https://doi.org/10.1093/sysbio/sys029>

Sawoniewicz J, Kupryjanowicz J. 2003. *Evaniella eocenica* sp. nov. from the Baltic amber (Hymenoptera: Evaniidae). *Acta Zoologica Cracoviensia* **46**: 267–270.

Scotese CR. 2014. Atlas of Early Cretaceous Paleogeographic Maps, PALEOMAP Atlas for ArcGIS, volume 2, The Cretaceous, Maps 23–31, Mollweide Projection, PALEOMAP Project, Evanston, Illinois.

Seton M, Müller RD, Zahirovic S, Gaina C, Torsvik T, Shepard G, Talsma A, Gurnis M, Turner M, Maus S, Chandler M. 2012. Global continental and ocean basin reconstructions since 200 Ma. *Earth-Science Review* **113**: 212–270. <http://dx.doi.org/10.1016/j.earscirev.2012.03.002>.

Sharanowski BJ, Peixoto L, Dal Molin A, Deans AR. 2018. Multi-gene phylogeny and divergence estimations for Evaniidae (Hymenoptera) *PeerJ* **7**: e6689. <https://doi.org/10.7717/peerj.6689>

Sharanowski BJ, Ridenbaugh RD, Piekarski PK, Broad GR, Burke GR, Deans AR, Lemmon AR, Lemmon ECM, Diehl GJ, Whitfield JB, Hines HM. 2021. Phylogenomics of Ichneumonoidea (Hymenoptera) and implications for evolution of mode of parasitism and viral endogenization. *Molecular Phylogenetics and Evolution* **156**: 107023. <https://doi.org/10.1016/j.ympev.2020.107023>

Sharkey MJ, Carpenter JM, Vilhelmsen L, Heraty J, Liljeblad J, Dowling AP, Schulmeister S, Murray D, Deans AR, Ronquist F, Krogmann L, Wheeler WC. 2012. Phylogenetic relationships among superfamilies of Hymenoptera. *Cladistics* **27**: 1–33. <https://doi.org/10.1111/j.1096-0031.2011.00366.x>

- Shi GH, Grimaldi DA, Harlow GE, Wang J, Wang J, Yang MC, Lei WY, Li QL, Li XH. 2012.** Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* **37**: 155–163. <https://doi.org/10.1016/j.cretres.2012.03.014>
- Shih PJM, Li L, Li D, Ren D. 2019.** Application of geometric morphometric analyses to confirm three new wasps of Evaniidae (Hymenoptera: Evanioidea) from mid-Cretaceous Myanmar amber. *Cretaceous Research* **109**: 104249. <https://doi.org/10.1016/j.cretres.2019.104249>
- Spasojevic T, Broad GR, Saaksjarvi IE, Schwarz M, Ito M, Korenko S, Klopstein S. 2020.** Mind the outgroup and bare branches in total-evidence dating: a case study of pimpliform Darwin wasps (Hymenoptera, Ichneumonidae). *Systematic Biology* syaa079. <https://doi.org/10.1093/sysbio/syaa079>
- Swofford DL. 2002.** PAUP: Phylogenetic Analysis Using Parsimony (and Other Methods), Version 4.0 Beta 10. Sinauer Associates, Sunderland.
- Tang P, Zhu JC, Zheng BY, Wei SJ, Sharkey M, Chen XX, Vogler AP. 2019.** Mitochondrial phylogenomics of the Hymenoptera. *Molecular Phylogenetics and Evolution* **131**: 8–18. <https://doi.org/10.1016/j.ympev.2018.10.040>
- Turrisi GF, Ellenberger S. 2019.** New aulacid wasps from the mid-Cretaceous of Myanmar (Hymenoptera: Evanioidea). *Cretaceous Research* **99**: 334–346. <https://doi.org/10.1016/j.cretres.2019.02.022>
- Turrisi GF, Jennings JT, Vilhelmsen L. 2009.** Phylogeny and generic concepts of the parasitoid wasp family Aulacidae (Hymenoptera: Evanioidea). *Invertebrate Systematics* **23**: 27–59. <https://doi.org/10.1071/IS08031>
- van Hinsbergen DJJ, Lippert PC, Dupont-Nivet G, McQuarrie N, Doubrovine PV, Spakman W, et al. 2012.** Greater India Basin hypothesis and a two-stage Cenozoic collision between India and Asia. *Proceedings of the National Academy of Sciences of the United States of America* **109**: 7659–7664. <http://dx.doi.org/10.1073/pnas.1117262109>.

- Vea IM, Grimaldi DA. 2016.** Putting scales into evolutionary time: the divergence of major scale insect lineages (Hemiptera) predates the radiation of modern angiosperm hosts. *Scientific Reports* **6**: 23487. <https://doi.org/10.1038/srep23487>
- Vilhelmsen L, Mikó I, Krogmann L. 2010.** Beyond the wasp waist: structural diversity and phylogenetic significance of the mesosoma in apocritan wasps (Insecta: Hymenoptera). *Zoological Journal of the Linnean Society* **159**: 22–194. <https://doi.org/10.1016/j.aspen.2013.01.007>
- Westerweel J, Roperch P, Licht A, Dupont-Nivet G, Win Z, Poblete F, et al. 2019.** Burma Terrane part of the Trans-Tethyan arc during collision with India according to palaeomagnetic data. *Nature Geoscience* **12**: 863–868. <http://dx.doi.org/10.1038/s41561-019-0443-2>.
- Xing L, Qiu L. 2020.** Zircon U–Pb age constraints on the mid-Cretaceous Hkamti amber biota in northern Myanmar. *Palaeogeography, Palaeoclimatology, Palaeoecology* **558**: 109960. <https://doi.org/10.1016/j.palaeo.2020.109960>
- Yu T, Kelly R, Mu L, Ross A, Kennedy J, Broly P, Xia F, Zhang H, Wang B, Dilcher D. 2019.** An ammonite trapped in Burmese amber. *Proceedings of the National Academy of Sciences of the USA* **116**: 11345–11350. <https://doi.org/10.1073/pnas.1821292116>
- Zhang C, Stadler T, Klopstein S, Heath TA, Ronquist F. 2016.** Total-evidence dating under the Fossilized Birth–Death Process. *Systematic Biology* **65**: 228–249. <https://doi.org/10.1093/sysbio/syv080>
- Zhang JF, Rasnitsyn AP, 2004.** Minute members of Baissinae (Insecta: Hymenoptera: Gasteruptionidae) from the upper Mesozoic of China and limits of the genus *Manlaya* Rasnitsyn, 1980. *Cretaceous Research* **25**: 797–805. <https://doi.org/10.1016/j.cretres.2004.08.001>
- Zhang HC, Rasnitsyn A.P. 2007.** Nevaniinae subfam. n, a new fossil taxon (Insecta: Hymenoptera: Evanioidea: Praeaulicidae) from the Middle Jurassic of Daohugou in Inner Mongolia, China. *Insect Systematics & Evolution* **38**: 149–166. <https://doi.org/10.1163/187631207788783987>

- Zhang HC, Rasnitsyn AP. 2008.** Middle Jurassic Praeaulacidae (Insecta: Hymenoptera: Evanioidea) of Inner Mongolia and Kazakhstan. *Journal of Systematic Palaeontology* **6**: 463–487. <https://doi.org/10.1017/S1477201907002428>
- Zhang Q, Rasnitsyn AP, Wang B, Zhang HC. 2018.** Hymenoptera (wasps, bees and ants) in mid-Cretaceous Burmese amber: A review of the fauna. *Proceedings of the Geologists' Association* **129**: 736–747. <https://doi.org/10.1016/j.pgeola.2018.06.004>
- Zhang HC, Rasnitsyn AP, Wang DJ, Zhang YT. 2007.** Some hatchet wasps (Hymenoptera, Evaniidae) from the Yixian Formation of western Liaoning, China. *Cretaceous Research* **28**: 310–316. <https://doi.org/10.1016/j.cretres.2006.05.003>
- Zhang HC, Zhang JF. 2000.** Discovery of Praeaulacidae (Insecta Hymenoptera) in China and its significance. *Acta Micropalaeontologica Sinica* **17**: 416–421.
- Zheng D, Chang S-C, Perrichot V, Dutta S, Rudra A, Mu L, Kelly RS, Li S, Zhang Q, Zhang Q, Wong J, Wang J, Wang H, Fang Y, Zhang H, Wang B. 2018.** A Late Cretaceous amber biota from central Myanmar. *Nature Communications* **9**: 3170. <https://doi.org/10.1038/s41467-018-05650-2>

Table and Figure captions

Table 1. Diversity and distribution of evanioid fossil genera.

Table 2. Comparison of results from maximum parsimony (MP) analysis and Bayesian analyses (BI).

Table 3. Hierarchical, and suprageneric classification of Evanioidea.

Table 4. Divergence time estimates of Evanioidea and its constitutive families under different models and priors.

Figure 1. *Keradellitha basilici* Jouault, Maréchal, Wang & Perrichot gen. et sp. nov., holotype NIG-P174738 (female) A: Habitus in right view. B: Habitus in left view. Scale bars: 0.5 mm

Figure 2. *Keradellitha basilici* Jouault, Maréchal, Wang & Perrichot gen. et sp. nov., holotype NIG-P174738 (female) A: Head in full-face view. B: Head in right profile view. C: Head in dorsal view. D: Wings. E: Line drawing of wing venation with nomenclature. Scale bars: 0.5 mm.

Figure 3. *Xenodellitha anubis* Jouault, Maréchal, Wang & Perrichot gen. et sp. nov., holotype NIG-P174739 (male) A: Habitus in right view. B: Head in right view. C: Head in frontal view. Scale bars: 0.5 mm.

Figure 4. *Xenodellitha anubis* Jouault, Maréchal, Wang & Perrichot gen. et sp. nov., holotype NIG-P174739 (male) A: Wing. B: Line drawing of wing venation with nomenclature. Scale bars: 0.5 mm.

Figure 5. *Xenodellitha kirina* Maréchal, Jouault & Perrichot gen. et sp. nov., holotype IGR.BU-021 (female) A: Habitus in left view. B: Head in right view. Scale bars: 1 mm.

Figure 6. *Xenodellitha kirina* Maréchal, Jouault & Perrichot gen. et sp. nov., holotype IGR.BU-021 (female) A: Head in left profile view. B: Head in full-face view. C: Wings. D: Line drawing of wing venation with nomenclature. Scale bars: 0.5 mm.

Figure 7. Fossil diversity (species) of Evanioidea and Ichneumonoidea during the mid-Mesozoic and Cenozoic (data from <http://fossilworks.org/>).

Figure 8. Bayesian time-calibrated tree of Evanioidea. This tree was recovered from a Mkv+G, FBD model, with uniform distribution, and *samplestrat = fossiltip*, combining extant and extinct species. Bars at each node represent 95% HPD in dating estimates. Dotted square represent crown-lineages. (L = Lower, Mid = Middle, Paleo = Paleocene, Oligo = Oligocene, PP = Pliocene + Pleistocene).

Supplementary files/figures:

Supplementary Figure 1. Strict cladogram generated from parsimony analysis. Tree length 829 steps; consistency index (CI) 0.1496; homoplasy index (HI) 0.8504; retention index (RI) 0.6597). Values above branches represent bootstrap percentages > 50% (majority-rule consensus).

Appendix S1: Nexus files + Trees + Summary post analyses

Appendix S2: Calibration and ages used in tip-dating analyses.

Table 1. Diversity and distribution of evanioid fossil genera.

Families/Subfamilies / Genera	Species	Distribution	Period	References
Praeaulacidae				
Cretocleistogastrinae				
<i>Cretocleistogaster</i> Rasnitsyn	3	Russia	Late Cretaceous	Rasnitsyn, 1975
<i>Miniwestratia</i> Rasnitsyn	1	Mongolia	Late Cretaceous	Rasnitsyn, 1990a
<i>Nanowestratia</i> Rasnitsyn	1	Russia	Late Cretaceous	Rasnitsyn, 1990a
<i>Sinowestratia</i> Zhang & Zhang	1	China	Late Cretaceous	Zhang & Zhang, 2000
<i>Westratia</i> Rasnitsyn	3	Russia	Late Cretaceous	Rasnitsyn, 1990a, 1990b
	4	Mongolia	Late Cretaceous	Rasnitsyn, 1990a
	1	Australia	Late Cretaceous	Jell & Duncan, 1986
Praeaulacinae				
<i>Archaulacus</i> Li, Shih & Ren	1	China	Middle Jurassic	Li et al., 2014a
<i>Aulacogastrinus</i> Rasnitsyn	1	Kazakhstan	Late Jurassic	Rasnitsyn, 1972, 1983
	3	China	Middle Jurassic	Zhang and Rasnitsyn, 2008
<i>Eonevania</i> Rasnitsyn & Zhang	1	China	Middle Jurassic	Rasnitsyn and Zhang, 2010
<i>Eosaulacus</i> Zhang & Rasnitsyn	1	China	Middle Jurassic	Zhang and Rasnitsyn, 2008
<i>Evanigaster</i> Rasnitsyn	1	Kazakhstan	Late Jurassic	Rasnitsyn, 1972
<i>Evaniops</i> Rasnitsyn	1	Kazakhstan	Late Jurassic	Rasnitsyn, 1972
<i>Gulgonga</i> Oberprieler, Rasnitsyn & Brothers	1	Australia	Late Jurassic	Oberprieler et al., 2012
<i>Habraulacus</i> Li, Rasnitsyn, Shih & Ren	1	Myanmar	Late Cretaceous	Li et al., 2015

Families/Subfamilies / Genera	Species	Distribution	Period	References
<i>Nevania</i> Zhang & Rasnitsyn	8	China	Middle Jurassic	Zhang and Rasnitsyn, 2007; Li et al., 2014b
	1	Kazakhstan	Late Jurassic	Zhang and Rasnitsyn, 2008
<i>Praeaulacinus</i> Rasnitsyn	3	Kazakhstan	Late Jurassic	Rasnitsyn, 1972, 1973
<i>Praeaulacites</i> Rasnitsyn	5	Kazakhstan	Late Jurassic	Rasnitsyn, 1972
<i>Praeaulacon</i> Rasnitsyn	4	Kazakhstan	Late Jurassic	Rasnitsyn, 1972
<i>Praeaulacops</i> Rasnitsyn	1	Kazakhstan	Late Jurassic	Rasnitsyn, 1972
<i>Praeaulacus</i> Rasnitsyn	6	Kazakhstan	Late Jurassic	Rasnitsyn, 1972
	2	Mongolia	Late Jurassic	Rasnitsyn, 2008
	9	China	Middle Jurassic	Zhang and Rasnitsyn, 2008; Li et al., 2014a, 2018; Li and Shih, 2015
<i>Paleosyncrasis</i> Poinar	1	Myanmar	Late Cretaceous	Poinar, 2019
<i>Rasnitsevania</i> Jouault, Nel & Perichot	1	Myanmar	Late Cretaceous	Jouault et al., 2020
Andreneliidae				
<i>Andrenelia</i> Rasnitsyn & Martínez-Delclòs	1	Spain	Early Cretaceous	Rasnitsyn & Martínez-Delclòs, 2000
Anomopterelidae				
<i>Anomopterella</i> Rasnitsyn	1	Kazakhstan	Middle Jurassic	Rasnitsyn, 1975
	1	Mongolia	Late Jurassic	Rasnitsyn, 2008

Families/Subfamilies / Genera	Species	Distribution	Period	References
	8	China	Middle Jurassic	Zhang & Rasnitsyn, 2008; Li et al. 2013b; Li et al. 2014b
<i>Choristopterella</i> Li et al.	1	Kazakhstan	Middle Jurassic	Rasnitsyn, 1975
<i>Synaphopterella</i> Li et al.	1	China	Middle Jurassic	Li et al. 2013a
Baissidae				
<i>Baissa</i> Rasnitsyn	2	Russia	Early Cretaceous	Rasnitsyn, 1975, 1991
	1	Mongolia	Early Cretaceous	Rasnitsyn, 1991
<i>Electrobaissa</i> Engel	1	USA	Late Cretaceous	Engel, 2013
<i>Heterobaissa</i> Li et al.	1	China	Early Cretaceous	Li et al. 2018
<i>Humiryssus</i> Lin	5	China	Early Cretaceous	Lin, 1980; Hong & Wang, 1990; Zhang and Rasnitsyn 2004
	1	United Kingdom	Early Cretaceous	Rasnitsyn et al., 1998
<i>Manlaya</i> Rasnitsyn	3	China	Early Cretaceous	Ren, 1995; Li et al., 2019
	8	Mongolia	Early Cretaceous	Rasnitsyn, 1980a; 1986
	2	Russia	Early Cretaceous	Rasnitsyn, 1980b
	2	Spain	Early Cretaceous	Rasnitsyn & Martínez-Delclòs, 2000
	3	United Kingdom	Early Cretaceous	Rasnitsyn et al., 1998
<i>Mesepipolaea</i> Zhang & Rasnitsyn	2	China	Early Cretaceous	Zhang & Rasnitsyn, 2004; Li et al., 2019
<i>Tillywhimia</i> Rasnitsyn & Jarzembowski	2	United Kingdom	Early Cretaceous	Rasnitsyn et al., 1998

Families/Subfamilies / Genera	Species	Distribution	Period	References
Othniodellithidae				
<i>Keradellitha</i> gen. nov. Jouault, Wang & Perrichot	2	Myanmar	Late Cretaceous	This study
	1	Myanmar	Early Cretaceous	This study
<i>Othniodellitha</i> Engel & Huang	1	Myanmar	Late Cretaceous	Engel et al., 2016a
<i>Xenodellitha</i> Engel	1	Myanmar	Late Cretaceous	Engel, 2017
Aulacidae				
<i>Paleoaulacus</i> Jouault & Nel	1	Myanmar	Late Cretaceous	Jouault & Nel, 2021
<i>Vectevania</i> Cockerell	1	United Kingdom	Eocene	Cockerell, 1922
Aulacinae				
<i>Aulacus</i> Jurine	1	France	Eocene	Nel et al., 2004
	2	Baltic amber	Eocene	Brues, 1933;
	1	USA	Oligocene	Brues, 1910
<i>Electrofeonia</i> Jouault et al.	1	Myanmar	Late Cretaceous	Jouault et al., 2020
<i>Electrofoenops</i> Engel	3	Myanmar	Late Cretaceous	Engel, 2017; Turrisi & Ellenberger, 2019
<i>Electrofoenus</i> Cockerell	1	Myanmar	Late Cretaceous	Cockerell, 1917
<i>Exilaulacus</i> Li et al.	2	Myanmar	Late Cretaceous	Li et al., 2018
<i>Pristaulacus</i> Kieffer	3	USA	Eocene	Brues, 1910; Cockerell, 1916
	3	Baltic amber	Eocene	Brues, 1933; Jennings & Krogmann, 2009
Hyptiogastritinae				

Families/Subfamilies / Genera	Species	Distribution	Period	References
<i>Archeofoenus</i> Engel	2	Myanmar	Late Cretaceous	Engel, 2017; Turrisi & Ellenberger, 2019
<i>Hyptiogastrites</i> Cockerell	1	Myanmar	Late Cretaceous	Cockerell, 1917
<i>Protofoenus</i> Cockerell	1	Myanmar	Late Cretaceous	Cockerell, 1917
Gasteruptiidae				
Hypselogastrinae				
<i>Hypselogastrion</i> Engel & Wang	1	Myanmar	Late Cretaceous	Engel & Wang, 2016
Kotujellitinae				
<i>Kotujellites</i> Rasnitsyn	1	Russia	Late Cretaceous	Rasnitsyn, 1975
<i>Kotujisca</i> Rasnitsyn	1	Mongolia	Late Cretaceous	Rasnitsyn, 1991
Evaniidae				
<i>Botstvania</i> Rasnitsyn & Brothers	1	South Africa	Late Cretaceous	Rasnitsyn & Brothers (2007)
<i>Brachygaster</i> Leach	1	Dominican Republic	Miocene	Nel et al., 2002
<i>Burmaevania</i> Shih et al.	2	Myanmar	Late Cretaceous	Shih et al., 2019
<i>Cretevania</i> Rasnitsyn	2	Russia	Late Cretaceous	Rasnitsyn, 1975
	1	Mongolia	Early Cretaceous	Rasnitsyn, 1991
	1	United Kingdom	Early Cretaceous	Rasnitsyn et al., 1998
	5	Spain	Early Cretaceous	Peñalver et al., 2010; Pérez-de la Fuente et al., 2012
	2	Myanmar	Late Cretaceous	Jennings et al., 2013; Li et al. 2018

Families/Subfamilies / Genera	Species	Distribution	Period	References
	4	China	Early Cretaceous	Zhang & Zhang, 2000; Zhang et al., 2007; Li et al. 2014c; Li et al. 2018
	1	Jordan	Early Cretaceous	Kaddumi, 2007
	1	Lebanon	Early Cretaceous	Deans, 2004
<i>Curtevania</i> Li et al.	1	Myanmar	Late Cretaceous	Li et al. 2018
<i>Eoevania</i> Nel et al.	1	France	Eocene	Nel et al., 2002
<i>Evaniella</i> Bradley	1	Baltic amber	Eocene	Sawoniewicz & Kupryjanowicz, 2003
	2	Dominican Republic	Miocene	Poinar, 2020
<i>Grimaldivania</i> Basibuyuk et al.	2	USA	Late Cretaceous	Basibuyuk et al., 2000
<i>Hyptia</i> Illiger	2	Mexico	Miocene	Jennings et al., 2012; Poinar, 2020
	1	Baltic amber	Eocene	Jennings et al., 2013
<i>Iberoevania</i> Peñalver et al.	1	Spain	Early Cretaceous	Peñalver et al., 2010
<i>Lebanevania</i> Basibuyuk & Rasnitsyn	1	Lebanon	Early Cretaceous	Basibuyuk et al., 2002
<i>Mesevania</i> Basibuyuk & Rasnitsyn	1	Myanmar	Late Cretaceous	Basibuyuk et al., 2000
<i>Newjersevania</i> Basibuyuk et al.	2	USA	Late Cretaceous	Basibuyuk et al. 2000
	3	Myanmar	Late Cretaceous	Li et al., 2018; Shih et al., 2019
<i>Praevania</i> Rasnitsyn	1	Mongolia	Early Cretaceous	Rasnitsyn, 1991
<i>Protoparevania</i> Deans	1	Lebanon	Early Cretaceous	Deans, 2004
<i>Semaeomyia</i> Bradley	1	Dominican Republic	Miocene	Poinar, 2020
<i>Sinuevania</i> Li et al.	1	Myanmar	Late Cretaceous	Li et al. 2018
<i>Sorellevania</i> Engel	1	Myanmar	Late Cretaceous	Engel, 2006

Table 2. Comparison of results from maximum parsimony (MP) analysis and Bayesian analyses (BI).

Taxa	MP analysis (from Li et al., 2018)	Bayesian analysis (from Li et al., 2018)	MP analysis (this study)	Fossilized Birth-Death process analyses (this study)
Evanioidea	Monophyly	Monophyly	Monophyly	Monophyly
Praeaulacidae	Paraphyly	Paraphyly	Paraphyly	Paraphyly
Anomopterellidae	Monophyly	Paraphyly	Monophyly	Monophyly
Aulacidae	Monophyly	Monophyly	Paraphyly	Monophyly
Baissidae	Monophyly	Paraphyly	Paraphyly	Paraphyly
Gasteruptiidae	Monophyly	Paraphyly	Monophyly	Monophyly
Othniodellithidae	Monophyly	Paraphyly	Monophyly	Monophyly
Andreneliidae	Monophyly	Paraphyly	Monophyly	Monophyly
Evaniidae	Monophyly	Paraphyly	Paraphyly	Monophyly

Table 3. Hierarchical, and suprageneric classification of Evanioidea.

Superfamily Evanioidea Latreille					
	Protoevanioides Jouault et al.				
				Family (f)Praeaulacidae Rasnitsyn	
					Subfamily (f)Praeaulacinae Rasnitsyn Subfamily (f)Cretocleistog astrinae Rasnitsyn Subfamily (f)Nevaniidae Zhang and Rasnitsyn
				Family (f)Othniodellith idae Engel and Huang	
	Neoevanioides Engel				
				Family (f)Anomopterel lidae Rasnitsyn	
		Aulaciformes Grimaldi and Engel			
				Family (f)Baissidae Rasnitsyn	
			Euaulacides Engel		
				Family Gasteruptiidae Ashmead	

Superfamily Evanoidea Latreille					
					Subfamily (f)Hypselogastrinae Engel Subfamily (f)Kotujellitinae Rasnitsyn Subfamily Hyptiogastrinae Crosskey Subfamily Gasteruptiinae Ashmead
				Family Aulacidae Shuckard	
					Subfamily fHyptiogastrinae Engel. Tribe (f)Archeofoenini, Engel. Tribe (f)Hyptiogastrini Engel Subfamily Aulacinae Shuckard Tribe (f)Electrofoenini Cockerell Tribe Aulacini Shuckard
		Evaniiformes Grimaldi and Engel			
				Family Evaniidae Latreille	
				Family (f)Andreneliidae Rasnitsyn and Martinez-Delclos	

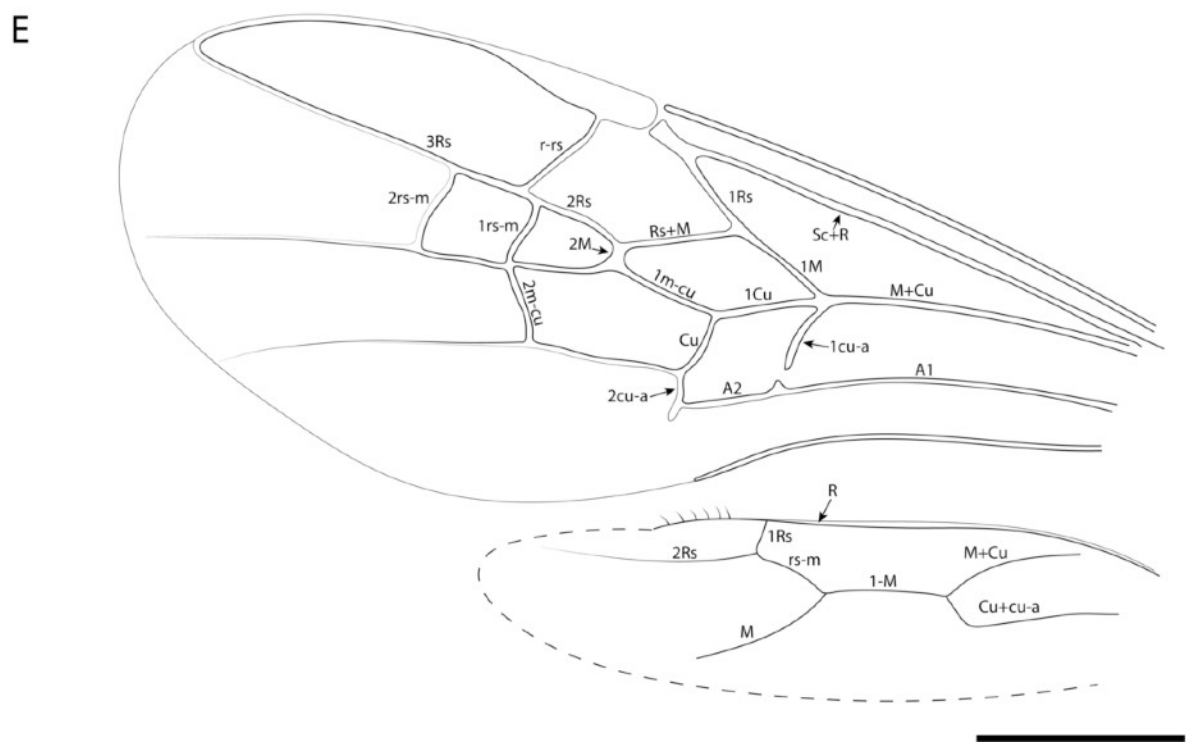
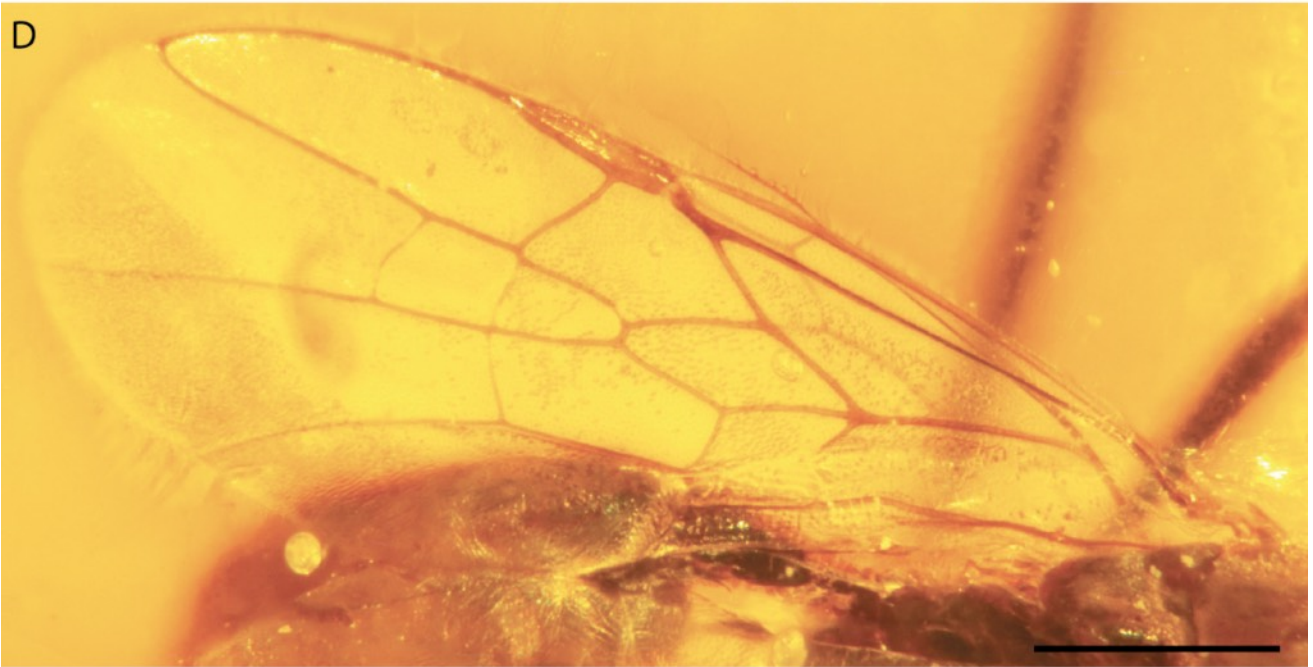
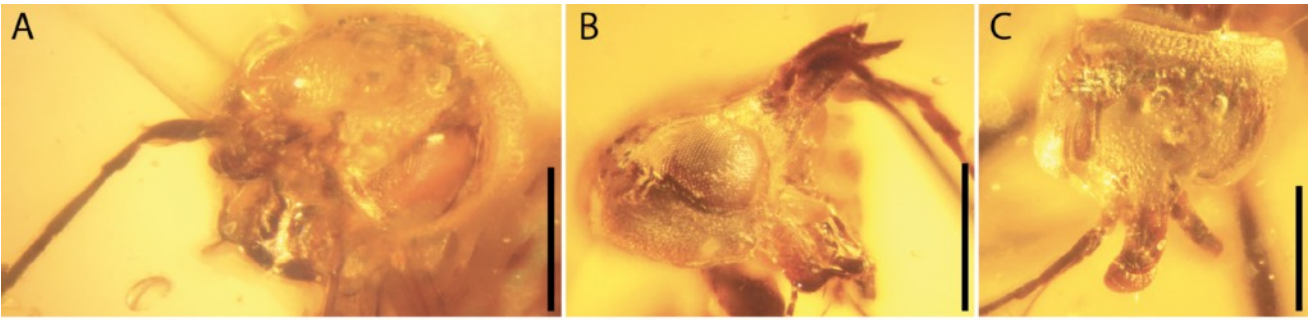
Table 4. Divergence time estimates of Evanioidea and its constitutive families under different models and priors.

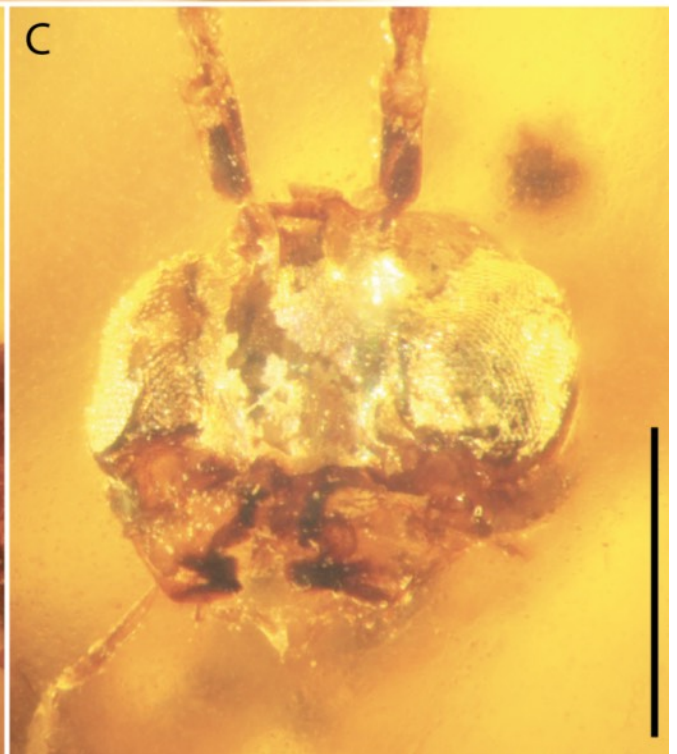
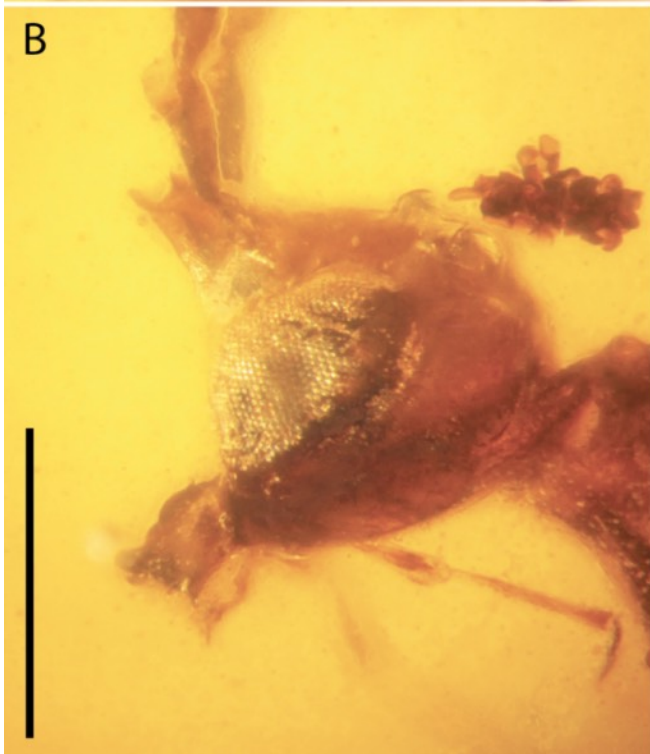
	MKv_-fixed_-Fossiltip		MKv_u-ni_fossiltip		MKvG_-fixed_-diversity		MKvG_-fixed_-Fossiltip		MKvG_-fixed_-random		MKv-G_uni_-diversity		MKv-G_uni_-flatprior		MKv-G_uni_-fossiltip		MKv-G_uni_-random	
	mean	95% HPD	mean	95% HPD	mean	95% HPD	mean	95% HPD	mean	95% HPD	mean	95% HPD	mean	95% HPD	mean	95% HPD	mean	95% HPD
Stem-Evanioidea	20.2	18.7-21.8	20.7	19.1-22.3	22.8	20.6-25.3	19.8	18.4-21.4	23.1	20.8-25.4	23.9	21.5-26.2	20.3	18.8-22.0	20.3	18.8-22.0	24.9	22.6-27.5
Crown-Evanioidea	17.5	16.0-19.2	17.8	16.1-19.6	19.7	17.8-21.9	17.3	15.6-18.9	19.9	18.0-22.1	20.6	18.6-22.7	17.6	16.0-19.4	17.6	15.9-19.4	21.4	19.3-23.8
Protoevanioidea	19.9	18.5-21.4	19.6	19.1-22.3	21.4	19.4-23.7	19.5	18.1-21.0	21.6	19.4-23.7	22.4	20.2-24.6	20.0	18.5-21.5	20.1	18.6-21.5	22.7	20.5-24.9
Praeaulacidae	19.9	18.5-21.4	19.6	19.1-22.3	21.4	19.4-23.7	19.5	18.1-21.0	21.6	19.4-23.7	22.4	20.2-24.6	20.0	18.5-21.5	20.1	18.6-21.5	22.7	20.5-24.9
Ottniodelliidae	11.6	11.0-12.6	11.7	10.9-12.7	11.7	11.0-12.7	11.6	11.0-12.5	11.8	11.0-12.8	12.0	11.1-13.0	11.7	11.0-12.7	11.7	11.0-12.7	12.3	11.3-13.5

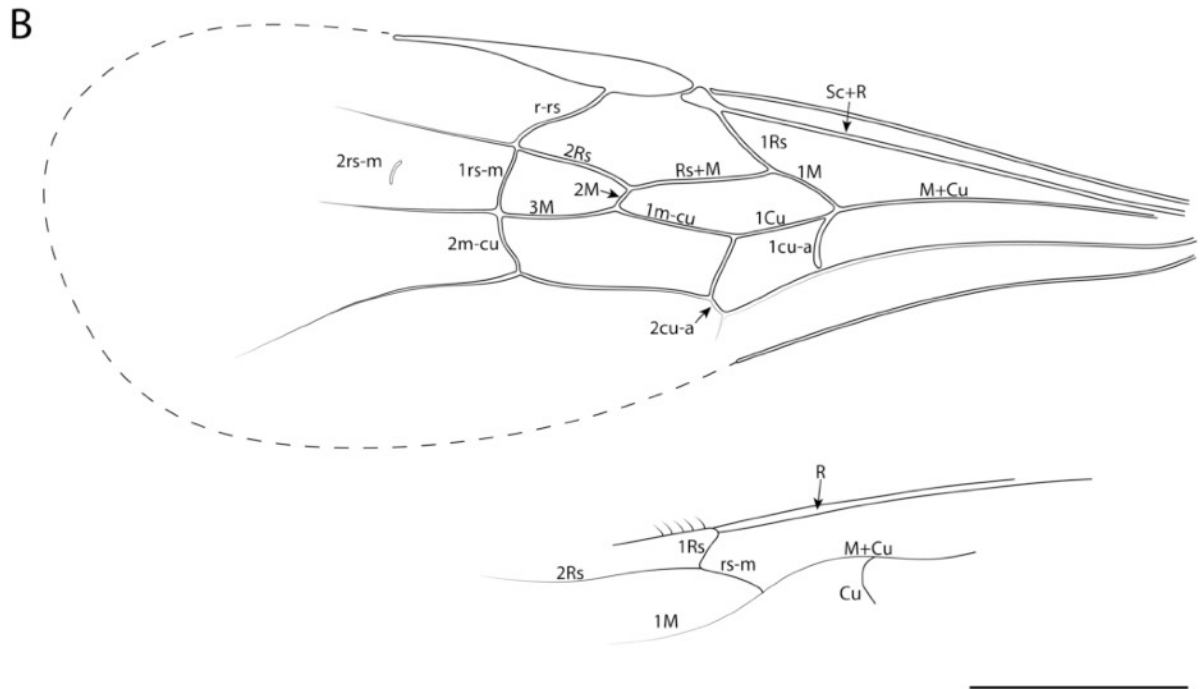
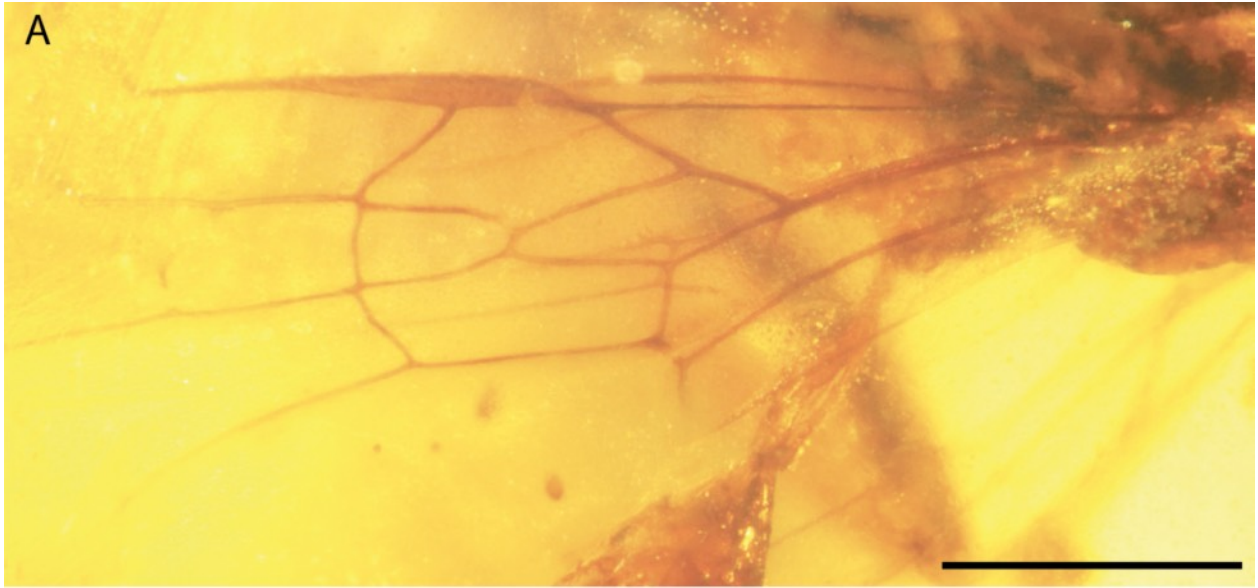
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	18 8	17 3- 20 4	19 2	17 6- 20 8	21 5	19 3- 23 8	18 6	17 1- 20 2	21 8	19 6- 24 1	22 5	20 3- 24 8	19 0	17 4- 20 7	19 0	17 5- 20 8	23 2	20 9- 25 8
Ne oe va ni oi de s	17 5	16 4- 18 7	17 9	16 8- 19 2	18 8	17 3- 20 5	17 3	16 3- 18 5	19 0	17 3- 20 7	19 6	17 9- 21 4	17 8	16 8- 19 0	17 8	16 8- 19 1	20 0	18 2- 21 9
An o m op ter elli da e	16 2	14 8- 17 7	16 5	15 0- 18 1	17 7	16 1- 19 6	16 0	14 6- 17 5	18 0	16 2- 19 7	17 0	16 7- 20 4	16 3	14 9- 18 0	16 4	14 8- 17 9	18 9	17 0- 21 0
An dr en elii da e	15 4	14 2- 16 6	15 6	14 4- 17 1	16 4	15 1- 17 9	15 2	14 0- 16 5	16 6	15 2- 18 1	16 4	15 7- 18 6	15 5	14 3- 16 9	15 5	14 2- 16 8	17 7	16 1- 19 4
St e m- Ev ani ida e	56	42 -7 3	59	43 -7 6	54	41 -9 9	54	40 -7 1	55	42 -7 0	59	44 -7 4	58	43 -7 5	58	42 -7 5	62	48 -7 9
Cr ow n- Ev ani ida e	15 9	14 4- 17 6	16 2	14 7- 18 0	15 8	14 3- 17 3	15 9	14 3- 17 4	16 0	14 4- 17 5	16 5	14 9- 18 1	16 2	14 7- 17 9	16 3	14 6- 17 9	17 0	15 4- 18 7
Ba iss ida e	10 4	98 -1 14	10 4	98 -1 15	10 4	98 -1 15	10 4	98 -1 14	10 5	98 -1 18	10 5	98 -1 17	10 5	98 -1 15	10 5	98 -1 16	10 5	98 -1 16
St e m- Ga st er up tii da e																		

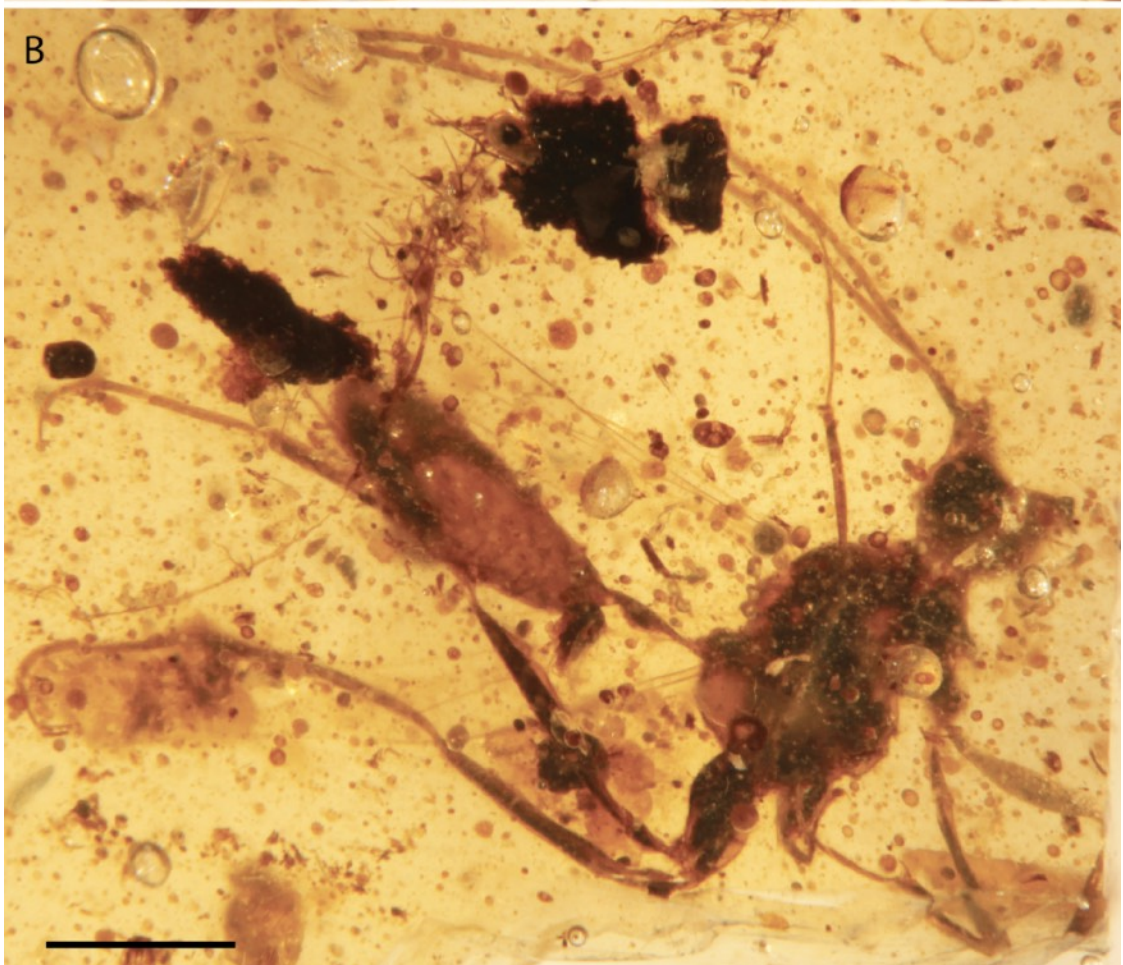
	MKv_- fixed_- Fossiltip		MKv_u- ni_fos- siltip		MKvG_- fixed_- diversity		MKvG_- fixed_- Fossiltip		MKvG_- fixed_- random		MKv- G_uni_- diversity		MKv- G_uni_- flatprior		MKv- G_uni_- fossiltip		MKv- G_uni_- random	
	21	6- 37	21	7- 38	15	7- 25	19	6- 35	15	6- 26	16	7- 27	20	6- 36	20	6- 36	20	7- 33
Cr ow - Ga st er up ti da e																		
St e m- Au lac ida e	12 7	11 5- 14 0	12 9	11 7- 14 3	13 6	12 2- 15 3	12 8	11 5- 14 4	13 7	12 2- 15 4	14 0	12 4- 15 7	12 9	11 6- 14 5	13 0	11 6- 15 8	14 3	12 6- 16 0
Cr ow n- Au lac ida e	69	51 -8 9	71	54 -9 3	59	49 -7 2	64	49 -8 4	60	49 -7 4	71	52 -8 0	68	52 -8 9	68	52 -8 9	69	54 -8 7

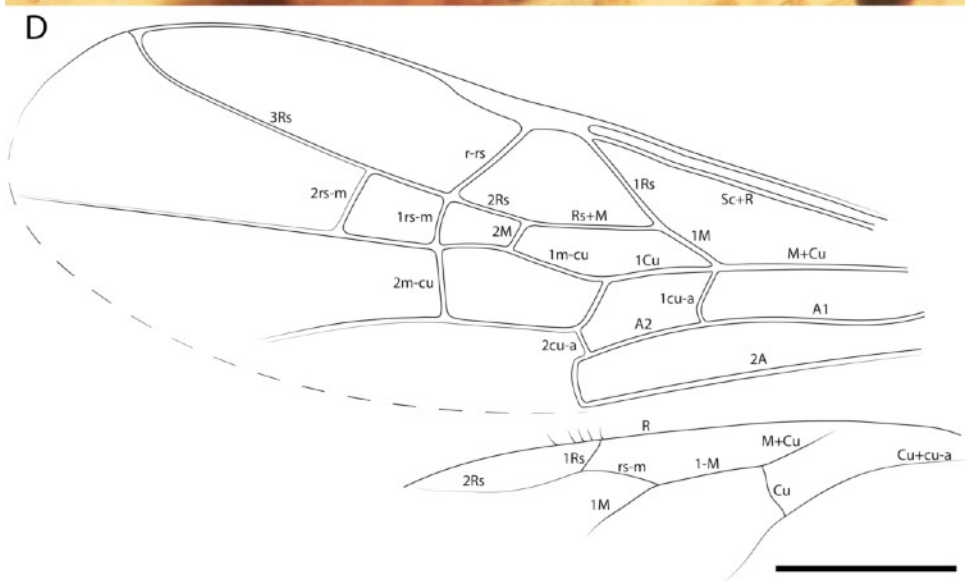
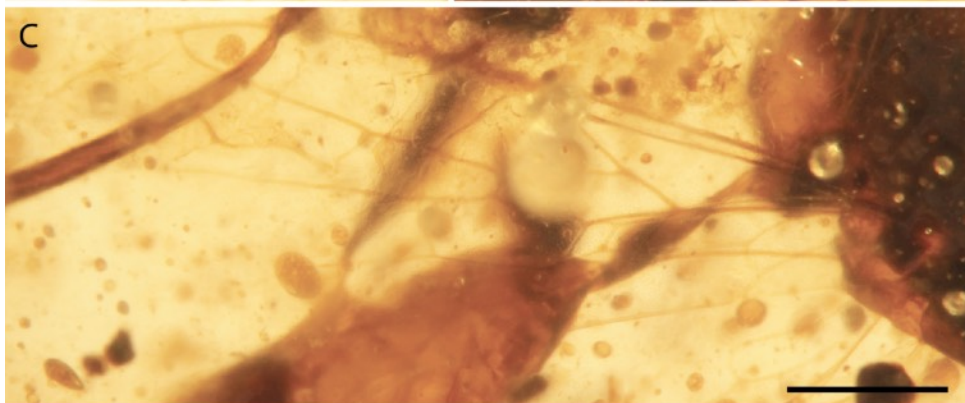
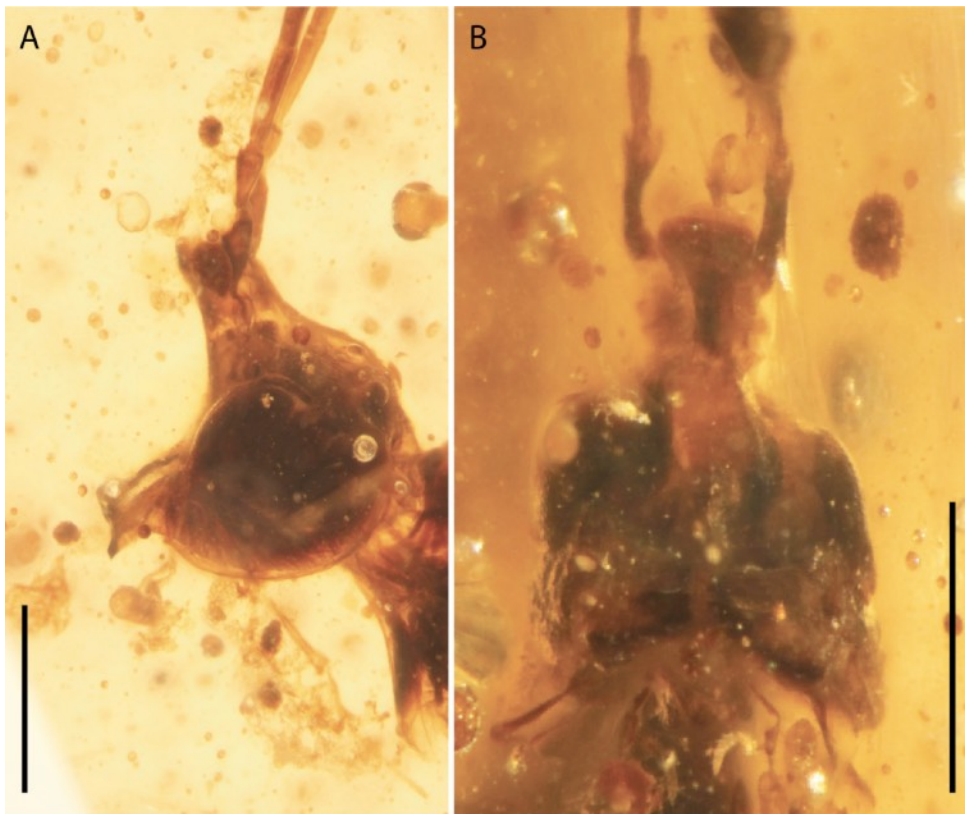


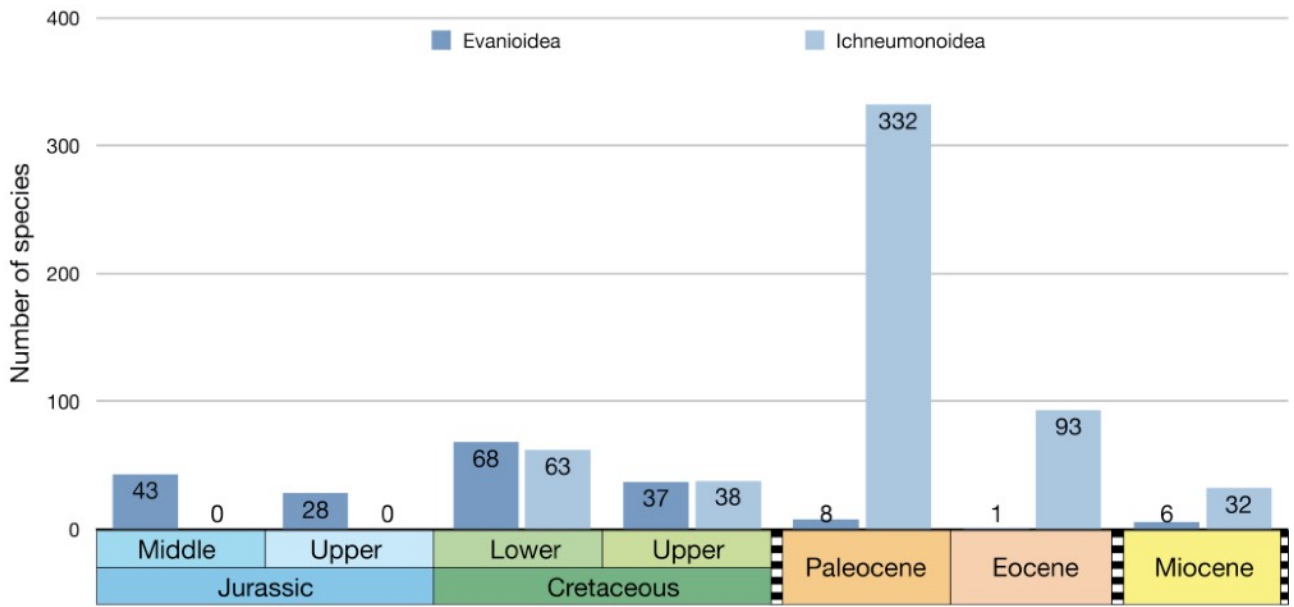












- Posterior Probabilities:
- 0.75–1
 - 0.5<0.75
 - 0<0.5
 - ★ Topology constraint

