



Hymenoptera (wasps, bees and ants) in mid-Cretaceous Burmese amber: A review of the fauna

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ABSTRACT

The Burmese amber assemblage of Hymenoptera with its 47 constituent families is now the richest in Cretaceous. A collection of Burmite (Burmese amber) from the Hukawng Valley, Myanmar at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences was examined, revealing that Burmite inclusions contain a very highly diverse hymenopteran fauna with as many as ten families found new for the Burmese fossil assemblage. The mid-Cretaceous hymenopteran fauna of Burmese amber is revised at the family level. A high level of the first family occurrences and endemism is demonstrated suggestive of an insular syndrome affected the mid-Cretaceous Burmese biome, as well as somewhat contradictory features in composition of the hymenopteran families there.

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1. Introduction

Burmese amber has been long neglected (Rasnitsyn, 1996; Zherikhin and Ross, 2000) but now is one of the richest sources of knowledge about the past of insects and some other elements of the Cretaceous non-marine biosphere (Grimaldi et al., 2002; Ross et al., 2010; Rasnitsyn et al., 2016; Guo et al., 2017). By the end of 2013, the Burmese amber arthropod assemblage had already accounted for 252 families (Rasnitsyn et al., 2016). Until the end of April 2018, the number increased to 467 (Ross, 2018). Indeed, the Burmese amber assemblage is now the richest for Hymenoptera in the Cretaceous: the number of described species of Hymenoptera is 73 according to Guo et al. (2017), and soared to 104 by April 2018 (Ross, 2018).

The Hymenoptera represents a significant part of the world biodiversity at least since Cretaceous. For instance, Ross (2018) counts 49 families, that is, 10.5 per cent of the 467 total arthropod families in the Burmese amber. The present figure of 47 families (see below) is conservative because

identification of several groups, particularly among Aculeata, is problematic due to far insufficient knowledge. Additionally, our figure differs because of a somewhat different family concept in several cases (see below). Nevertheless, the present review of the family composition of Hymenoptera in the Burmese amber is worthwhile because it shows a considerable amount of novelty.

2. Material and methods

The present research is based on a collection of Burmese amber kept at the Nanjing Institute of Geology and Palaeontology, China Academy of Sciences (NIGPCAS). Ambers were collected from the amber mines sited in the Hukawng Valley of Kachin State, Myanmar. The rock containing the Burmese amber was radiometrically dated at 98.79 ± 0.62 Ma (Shi et al., 2012). Ross (2015), Smith and Ross (2018) show that some amber pieces display traces of marine transfer whilst the amber was fresh and soft inside suggesting its age to be the same as the enclosing rocks. Yet the re-deposition of amber can be never excluded, and given the above date being close to the boundary between the Albian and Cenomanian (100.5 Ma; International Commission on Stratigraphy, 2017), we prefer to refer to the amber age informally as mid-Cretaceous.

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There are about 12,800 insect amber pieces registered by our research team containing approximately 100,000 insects. The vast majority of insect amber came from the amber markets of Myanmar with no selection by researchers. We classify the amber at NIGPCAS by different insect orders according to the main well-preserved inclusions. Amber pieces containing Hymenoptera come in various shapes are often rounded to elliptic-oblong after the processing by sellers, mostly ranging from 1 to 3 cm in diameter. Totally, 1409 amber pieces containing Hymenoptera have been examined and 1775 specimens of Hymenoptera are recorded (Table 1).

The material was studied under Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnifications up to 800 $\times$ at the State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. In most instances,

incident and transmitted light were used simultaneously. Helicon Focus Pro was used to stack photos for better depth of field. The line drawings were prepared based on photographs using image-editing softwares (CorelDraw X7 and Adobe Photoshop CS6).

Table 1

Composition of Hymenoptera in the collection studied.

taxon	n	%
Anaxyelidae	7	0,4
Orussomorpha fam. nov.	1	0,1
Stephanidae	1	0,1
Myanmarinidae	6	0,3
Aptenoperissus	6	0,3
Praeaulacidae	26	1,5
Gasteruptiidae	50	2,8
Evaniidae	93	5,2
Megalyridae	57	3,2
Maimetshidae	20	1,1
Radiophronidae	1	0,1
Megaspilidae	6	0,3
Stigmaphronidae	6	0,3
Trigonalidae	1	0,1
Peleproctidae	5	0,3
Pelecinidae	1	0,1
Roproniidae	2	0,1
Austroniidae	1	0,1
Diapriidae	28	1,6
Spathiopterygidae	4	0,2
Scelionidae	285	16,1
Serphitidae	66	3,7
Gallorommatidae	6	0,3
Mymarommatidae	4	0,2
Mymarommatoidea fam.nov.?	2	0,1
Mymaridae	1	0,1
Ichneumonidae	6	0,3
Braconidae	43	2,4
Crabronidae	101	5,7
Scolecbythidae	13	0,7
Bethylidae	124	7,0
Falsifirmicidae	16	0,9
Chrysididae	204	11,5
Embolemyidae	8	0,5
Dryinidae	46	2,6
Sclerogibbidae	11	0,6
Angarosphecidae	3	0,2
Ampulicidae	86	4,9
Pompiloidea fam. nov.	10	0,6
Rhopalosomatidae	17	1,0
Tiphidae	21	1,2
Vespidae	38	2,1
Formicidae	162	9,1
Evanioidae? indet.	1	0,1
Evaniomorpha indet.	1	0,1
Mymarommatoidea indet.	1	0,1
Chalcidoidea indet.	12	0,7
Ichneumonoidea indet.	1	0,1
Parasitica indet.	1	0,1
Chrysidioidea indet.	3	0,2
Aculeata indet.	128	7,2
Apocrita indet.	26	1,5
Hymenoptera indet.	6	0,3
Total	1776	100,3



Fig. 1. Undescended Anaxyelidae (NIGP167956). Note the mesonotum lacking the transscutal suture and the forewing with 2r-m crossvein lost and 3r-m present.

3. Results

The results achieved are presented in Table 1. The data show a total of 47 hymenopteran families in the Burmese amber, which gives a considerable addition to those compiled by Rasnitsyn et al. (2016) who counted 30 families. Ross (2018) encompass as many as 49 families. However, several family records in Ross (2018) are either misinterpreted or unsupported in our opinion, and still others do not merit the family rank in our opinion.

Syspastoxyelidae (Engel et al., 2016a) in our understanding represent an aberrant group of Xyelidae, possibly only a separate tribe within subfamily Xyelinae.

Cretosapyga resincola Bennett and Engel was attributed to Sapygidae (Bennett and Engel, 2005). As described and figured, however, it displays no specific characters of the family. Instead, its very short propodeum suggests Vespidae which, however, contradicts to its apparently long pronotum with the hind margin weakly excised. It is necessary to restudy the holotype to reveal a correct taxonomic position of this interesting fossil. *Bryopompilus interfector* Engel and Grimaldi was described in Pompilidae (Engel and Grimaldi, 2006a), which was later reasonably questioned resulting in erection of the family Bryopompilidae without additional evidence (Rodriguez et al., 2016). At the same time a cursory study of the type by one of the present authors (APR) during his short visit to the American Museum of Natural History in 2017 suggests that the Bryopompilidae is a valid family apparently belonging to Vespoidea sensu Brothers (1975) and not related to Pompilidae.

Platygastridae are cited along with Scelionidae by mistake: the record is based on *Cascoscelio incassus* (Poinar and Buckley, 2011) which is a typical scelionid by its characters. Evidently Platygastridae sensu lato are meant there, that is, including Scelionidae.

Sphecidae are cited based on Antropov (2000) who followed an old usage of the name which is equivalent to the present Spheciformes (Apoidea): no Sphecidae s.str. is known in the Burmese amber as yet.

The references of Chalcididae and Sierolomorphidae are based on data by Poinar and Poinar (2008: 216, 217 respectively). However, these unsupported records can be taken at most as questionable: we disregard them for the aims of the present review.

Aulacidae in our eyes are only a subfamily of Gasteruptionidae and not a full family (Rasnitsyn, 2013).

The family status of Othniellithidae (Engel et al., 2016b) is debatable as opposed to its position of a subfamily of the predominantly Jurassic family Praeaulacidae (cf. Rasnitsyn, 1972; Zhang and Rasnitsyn, 2007, 2008). *Habraulacus* Li et al., 2015 with similar wing venation and particularly *Mesevania Basibuyuk* and Rasnitsyn, 2000 with similarly even if less radically modified head and inflated fore tibia suggestive of a hypertrophied vibration detector within (cf. Vilhelmsen, Turrissi, 2011) make it necessary to conduct a thorough consideration of that alternative. Othniellithidae are left tentatively in our list (Table 2).

A wealth of new even though badly incomplete information about inclusions in Burmese amber is recently provided by Zhang (2017), including Hymenoptera ascribed to families new to the Burmese biota. These deserve a more detail consideration, as follows.

Cephidae (Zhang, 2017: 526) looks like an ordinary Cephinae and represents a real addition to the fauna.

Unlike this, Xiphydriidae (Zhang, 2017: 526) show no diagnostic features of that family: the fossil looks similar to both Anaxyelidae and Sepulcidae, but the former identification is somewhat

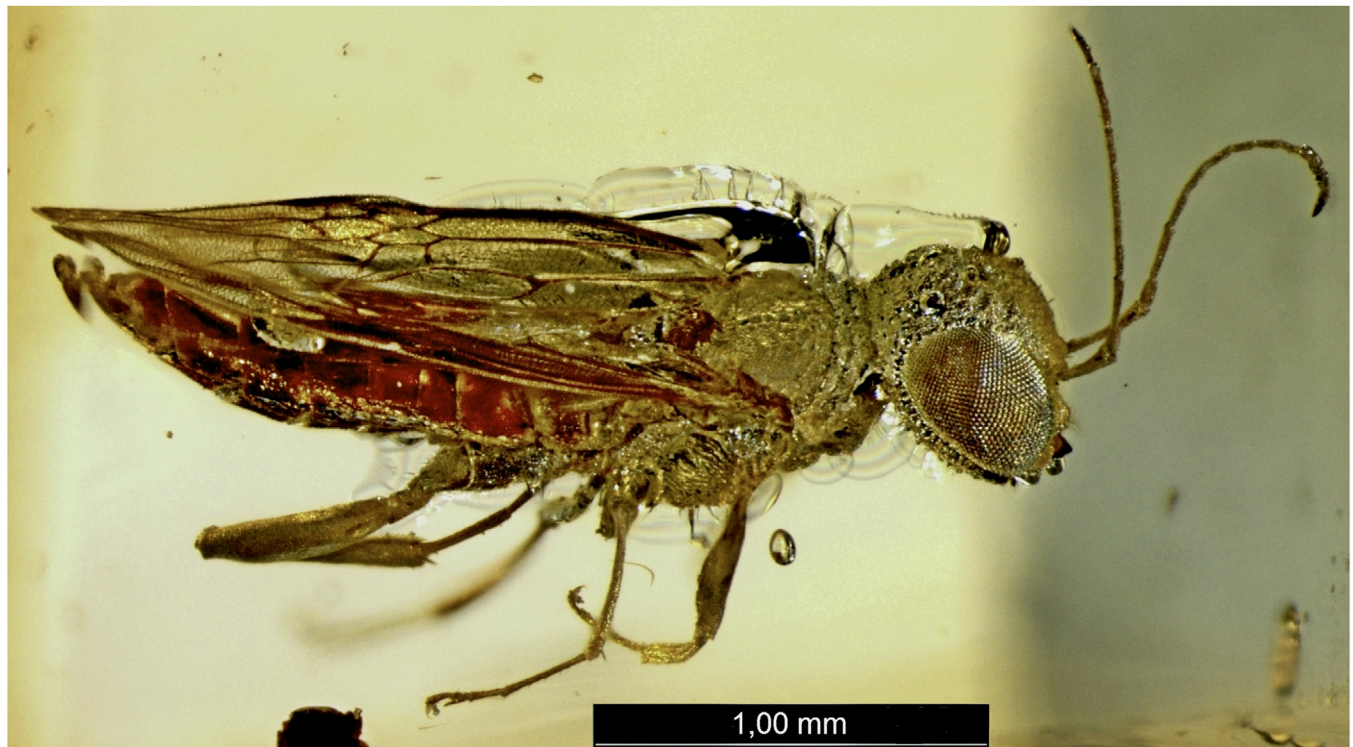


Fig. 2. New family of Orussomorpha (NIGP167698) (Zhang et al., 2018, under review). Note absence of any traces of the wasp waist and head with upper attachment of antennae and with crown of teeth.

preferable because of a long pronotum with central longitudinal line.

Identification of Siricidae (Zhang, 2017: 527) is probably incorrect as well: wing venation, even though being far from perfectly visible, shows short 1-RS which is not at all characteristic of Siricidae. We prefer to refer to it as Siricomorpha indet.

Sepulcidae (Zhang, 2017: 527) are misidentified: the specimens examined in the NIGPCAS belong to the same or related species (Fig. 1) and demonstrate similarity to Anaxyelidae: Syntexinae and particularly to *Cratoenigma* (Krogmann and Nel, 2012). The proposed similarity of *Cratoenigma* to Xiphydriidae and higher Hymenoptera (Suborder Vespina) in presence of transscutal suture (Krogmann and Nel, 2012) is based apparently on a misidentification: the structure indicated there (*op. cit.* Fig. 4, tsa) as that suture represents rather a crack. It meets mesoscutellum behind the apex of the latter and so cannot serve as a hinge which is the function of the real transscutal suture.

Megalyridae (Zhang, 2017: 528) is a misidentification because of the hind wing Cu aligned smoothly to M+Cu (never so in

Megalyridae, Trigonalidae and Ceraphronoidea s.str.). Identity of the insect needs study of the voucher specimen.

Evaniidae are either correctly identified (Zhang, 2017: 528, 530), or (Zhang, 2017: 529) represent Gasteruptionidae (Aulacinae).

Cynipoidea (Zhang, 2017: 531) is an undoubted misidentification, because the cell 3r (marginal) is not triangular, and flagellar segments lack long sensilla. Praeaulacidae could be an alternative, although a correct taxonomic position needs study of the fossil, particularly the wing venation and dorsal aspect of body. At the same time, Poinar and Poinar (2008: Plate 5B) provide a photo of an unquestionable Cynipoidea which closer identification needs a further study.

Mymaridae (Zhang, 2017: 531) are in fact Spathiopterygidae similar but not identical to described by Engel et al. (2015).

Identification of Serphitidae (Zhang, 2017: 532), Diapriidae (Zhang, 2017: 533) and Scelionidae (Zhang, 2017: 533–536, spelled Scclionidae) is correct. The same holds true for Pelecinidae (Zhang, 2017: 538–539) and Ichneumonidae (Zhang, 2017: 541).

The fossils identified as Heloridae (Zhang, 2017: 532) and Ceraphronidae (Zhang, 2017: 540) both represent Serphitidae, as their venation and thin and bisegmented petiole indicate. Those ascribed to Platygasteridae (Zhang, 2017: 536–538) are all belong to

Table 2

Families of Hymenoptera known in the Burmese amber.

Family	References and remarks
Xyelidae	for Syspastoxyelidae, see text
Cephidae	Zhang (2017)
Anaxyelidae	see text
Stephanidae	Engel et al. (2013)
New family of Orussomorpha	
Myanmarinidae	Zhang et al. (2018a)
Aptenoperissidae	Rasnitsyn, Öhm-Kühnle (2018)
Praeaulacidae	Li et al. (2015)
Othniodellithidae	Engel et al. (2016b)
Gasteruptionidae	Rasnitsyn, Ross (2000)
Evaniidae	Engel (2006)
Megalyridae	Grimaldi and Engel (2005)
Maimetshidae	Perrichot (2013)
Radiophronidae	see text
Megaspilidae	Rasnitsyn, Ross (2000)
Stigmaphronidae	Engel, Grimaldi (2009)
Trigonalidae?	see text
Peleserphidae	Zhang et al. (2018b)
Pelecinidae	Guo et al. (2016)
Ropronidae	see text
Austroniidae	see text
Diapriidae	Rasnitsyn, Ross (2000)
Spathiopterygidae	Engel et al. (2015)
Gallorommatidae	Engel, Grimaldi (2007)
Mymaromatidae	Engel, Grimaldi (2007)
New family of	see text
Mymarommatoidae	
Scelionidae	Rasnitsyn, Ross (2000)
Serphitidae	Rasnitsyn, Ross (2000)
Mymaridae	Huber, Poinar (2011)
Ichneumonidae	Li et al. (2016)
Braconidae	Engel et al. (2018)
Scolebythidae	Cockx and McKellar (2016)
Bethylidae	Rasnitsyn, Ross (2000)
Falsiformicidae	Perrichot et al. (2014)
Chrysididae	Lucena, Melo (2018)
Dryinidae	Olmi et al. (2014b)
Sclerogibbidae	see text
Embolemyidae	Olmi et al. (2014a)
Angarosphacidae	see text
Ampulicidae	Antropov (2000) as Ampulicinae
Crabronidae	Antropov (2000) as Sphecidae
Melittosphacidae	Poinar and Danforth (2006)
Burmusculidae	Zhang et al. (2018)
Rhopalosomatidae	Engel (2008)
Tiphidae	Engel et al. (2009)
Vespidae	Perrard et al. (2017)
Formicidae	Barden and Grimaldi (2016); Perrichot et al. (2016)



Fig. 3. Undescribed Radiophronidae (NIGP167957). Note the wide pre-radial space.

Scelionidae, as their developed wing venation indicates and antenna with more than 10 segments suggest.

Proctotrupoidea sp. (Zhang, 2017, p. 539) is an unmistakable male of Myanmarinidae (cf. Zhang et al., 2018a).

Megaspilidae (Zhang, 2017: 540) are probably a real addition to the fauna. Unfortunately the photograph is not sharp enough to permit reliable identification. Our material (Table 1) render a better evidence of presence of Megaspilidae in the Burmese fossil assemblage.

Identification of Braconidae is partially correct (Zhang, 2017: 542). Otherwise the respective fossils represents either Maimetshidae (Zhang, 2017: 541), or male Formicidae (Zhang, 2017: 543).

Identification of Dryinidae (Zhang, 2017: 543), Embolemidae (Zhang, 2017: 544) and some of Bethyidae (Zhang, 2017: 546 above, 548 below) raises no question. In contrast, other suggested Bethyidae represent in fact either Chrysididae (Zhang, 2017: 546 below, 547, 548 above) or Falsiformicidae (Zhang, 2017: 549).

Identification of Chrysididae (Zhang, 2017: 549–550) is correct.

Vespidae is referred to as Tiphidae (Zhang, 2017: 550).

Formicidae (Zhang, 2017: 551–559) are correctly identified.

Sphecidae (Zhang, 2017: 561) are taken in an old (wide) sense and represent Ampulicidae (above) and Crabronidae (below).

As a result, Zhang (2017) adds one families to the list of Hymenoptera in the Burmese fossil assemblage, the Cephiidae.

Our new additions to the family list of Hymenoptera in the Burmese amber are based on the materials kept at the Nanjing Institute of Geology and Paleontology (see above) which are either currently in their way to publication, or in preparation, or otherwise are directly supported with sufficiently informative photographs. These are as followed.

Anaxyelidae: Syntexinae near *Cratoenigma* Krogmann and Nel, 2012 (Fig. 1); see above for discussion. In preparation.

New family of Orussomorpha (Fig. 2) (Zhang et al., 2018, under review).

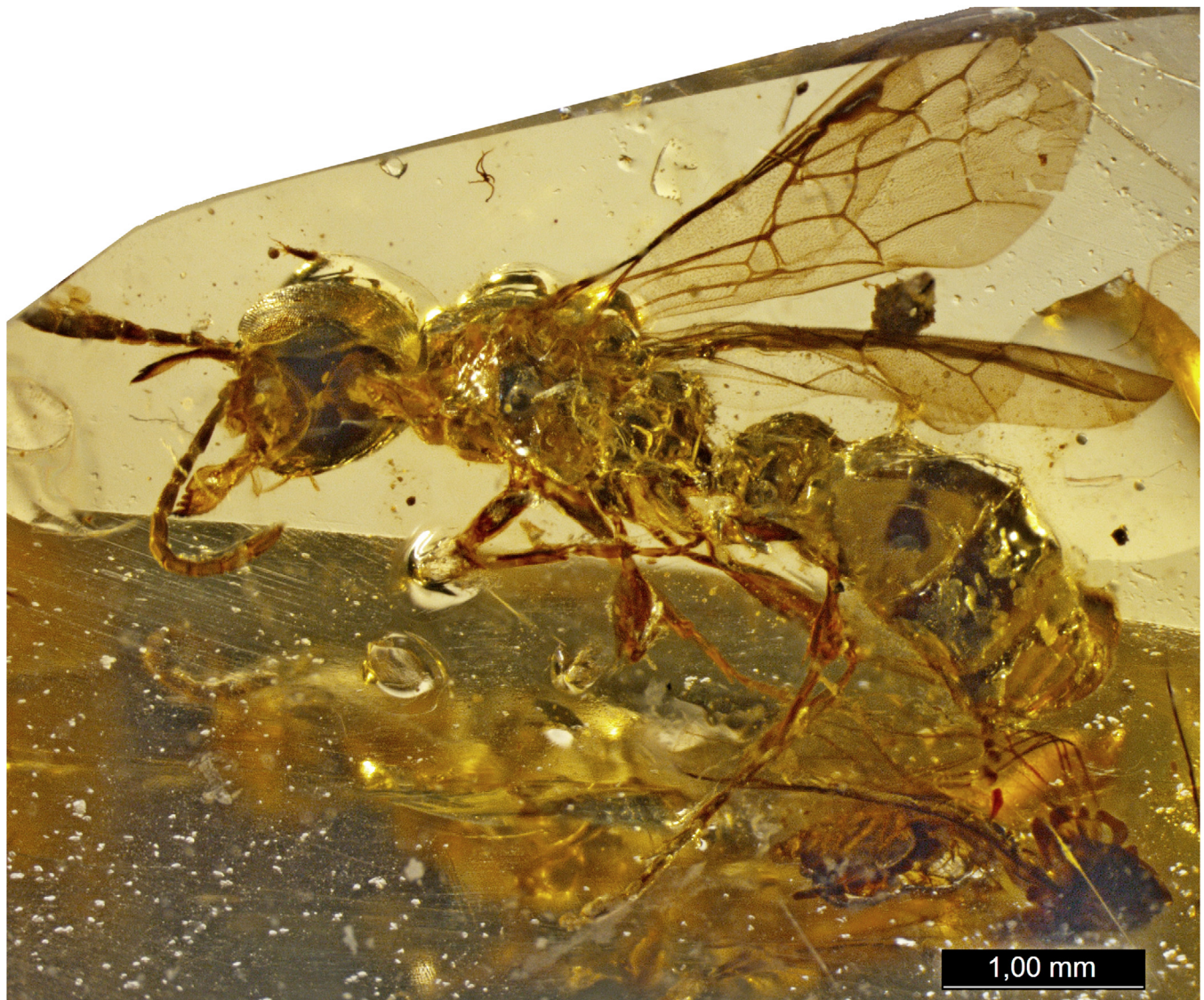


Fig. 4. Undescribed Trigonalidae (?) (NIGP167958). Note the hindwing with r-m and 1-M aligned, and free endings (distal of crossveins) of RS and Cu well developed but those of M and A lost.

Radiophronidae (Fig. 3): otherwise they are known from the Albian Spain amber (Ortega-Blanco et al., 2010) and earlier Early Cretaceous of Transbaikalia (Baissa) and Mongolia (Khotont) (APR, pers. observation).

Trigonalidae (?) (Fig. 4). The complete forewing venation of the fossil is equally characteristic of numerous non-chrysidoid aculeates. However, the hindwing with r-m and 1-M aligned and with free ends of M (distal of r-m) and A (distal of cu-a) both

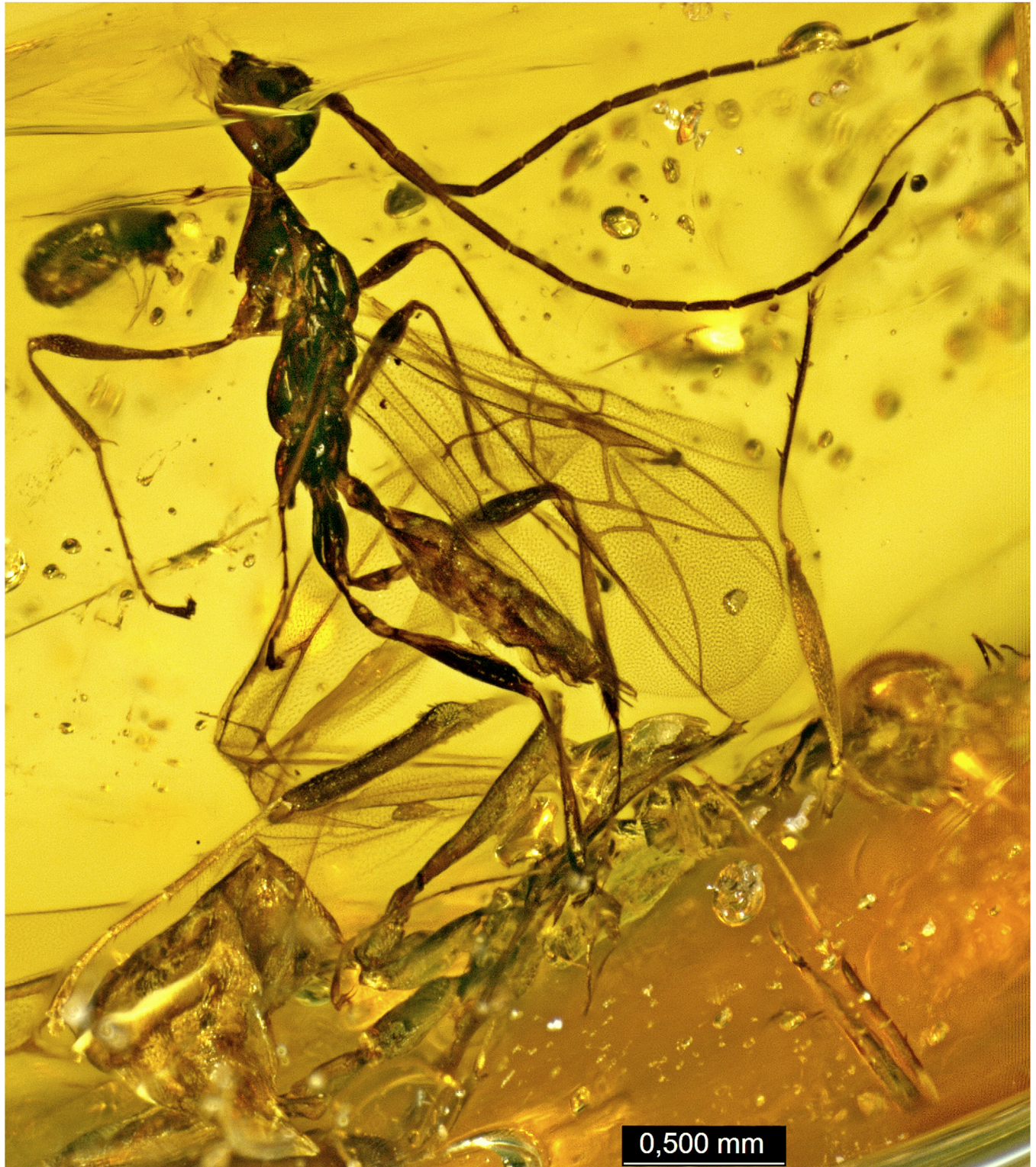


Fig. 5. Undescribed Roproniidae (NIGP167959). Note the tube-like first metasomal segment, the external ovipositor, and rectangular cell 1mcu.



Fig. 6. Undescribed Austroniidae of genus cf. *Trupochalcis* Kozlov, 1975 (NIGP167960).

rudimentary whilst those of RS and Cu well developed, and with the jugal lobe lost is characteristic of Trigonaliidae and unknown in Aculeata with a comparably complete wing venation (with the forewing 2cu-a crossvein developed as a tubular vein). The fossil under discussion differs from unquestionable (Cenozoic) Trigonaliidae in having antennae 12-segmented, mandibles elongate and symmetrical, and forewing crossvein cu-a antefurcal. However, these differences are not considered herein to prevent from the above attribution because the respective hiatuses do not look deep. In Trigonaliidae, the antenna is normally polymeric but sometimes 13-segmented, mandibles are rarely symmetrical even though short (Carmean and Kimsey, 2010), and the forewing crossvein cu-a is occasionally interstitial (*Teranishia glabrata* Chen et al., 2014: fig. 604). The only fossil available has a much distorted body which hinders comparison, but its absence of any traces of sting also agrees with Trigonaliidae rather than Aculeata. As a

result, attribution of the fossil to Trigonaliidae looks less controversial than in the case of *Albiogonaly* (Nel et al., 2003) which differs from Trigonaliidae in having a forewing with cell 2rm widely contacting with 1mcu, 3 rm long and cu-a interstitial, and a hindwing with r-m and 1-M not at all aligned and free M long. Stem Trigonaliidae looks as a possible attribution of this enigmatic insect.

Ropronidae (Fig. 5). The family is known since Jurassic (Rasnitsyn, 1990).

Austroniidae (Fig. 6). The family is known since earlier Early Cretaceous (Rasnitsyn, 2002: fig. 348).

New family of Mymarommatoidea (Fig. 7). Forewing structure is even more plesiomorphic than in Gallorommatoidea, and at the same time hind wing is totally lost. In preparation.

Sclerogibbidae (Fig. 8). The oldest fossil record is the Barremian Lebanese amber (Engel and Grimaldi, 2006b).

Angarosphecidae (Fig. 9). General appearance is similar to Ampulicidae but pronotum is movably attached to mesonotum unlike all other Apoidea. Similar construction of the pro- and mesonotal articulation is seen in unquestionable Angarosphecidae from the Aptian of Mongolia, such as *Cretosphecium* (Pulawski et al., 2000).

Burmusculidae (Fig. 10) (Zhang et al., 2018)

4. Discussion

The resulted list of families of Hymenoptera recorded in Burmese amber (Table 2) is unquestionably incomplete, as previous remarks suggest (e.g., about Zhang's (2017) 'Xiphidriidae', 'Cynipoidea' and Cynipoidea displayed by Poinar and Poinar, 2008), and particularly because the high diversity of aculeate wasps includes many fossils difficult to identify to family until special study (Table 1 shows as many as 128 wasps identified as Aculeata indet.). Nevertheless an analysis of the results may help to draw several non-trivial inferences.

The first inference is that the Burmese mid-Cretaceous fauna of Hymenoptera was unbelievably rich. Its diversity at the family rank level is seconds only to that of the Baltic amber (47 vs. 55 families; Archibald et al., 2018) in spite that the scientific study of the Baltic amber counts several centuries of history as compared with only two decades in the case of Burmese amber (Rasnitsyn, 1996; Ross and York, 2000).

Composition of families in the Hymenopteran fossil assemblage is also of interest. Table 2 shows eight families apparently meeting their first occurrence there in the fossil record (Stephanidae, Megaspilidae, Trigonaliidae?, Mymaridae, Falsificidae, Crabronidae, Rhopalosomatidae, Tiphidae). Two other family (Praeaulacidae, Radiophronidae) are found there for the last time in their fossil record, and eight others, a new family of Orussomorpha, Myanmarinidae, Aptenoperissidae, Othniodellitidae, Peleserphidae, new family of Mymarommatoidea, Melitosphecidae, Burmusculidae, are endemic, that is, known only from the Burmese amber.

The last category is particularly noteworthy. Eight endemic families of Hymenoptera is really an unprecedented figure for Cretaceous: even the Levantine amber, the only unquestionably Gondwanan Cretaceous amber, has yielded the only endemic family Archaeoserphitidae (Engel, 2015). The highest level of endemism implies an insular effect, a long isolation of the West Burma plate before it met S. Asia mainland (for detail cf. Rasnitsyn, Öhm-Kühnle, 2018).

The equally high number of the first occurrences of Hymenopteran families in Burmese amber is also important, even though this effect in a part could be a result of its better knowledge comparing other Cretaceous amber assemblages, which needs a special study.



Fig. 7. Undescribed new family of Mymarommatoidea (NIGP167961). Note the forewing with a moderately long marginal fringe lacking the elongate posterobasal seta, and the hindwing completely lost.



Fig. 8. Undescribed Sclerogibbidae (NIGP167962). Note the 15-segmented antenna attached to a shelf overhanging mouthparts.

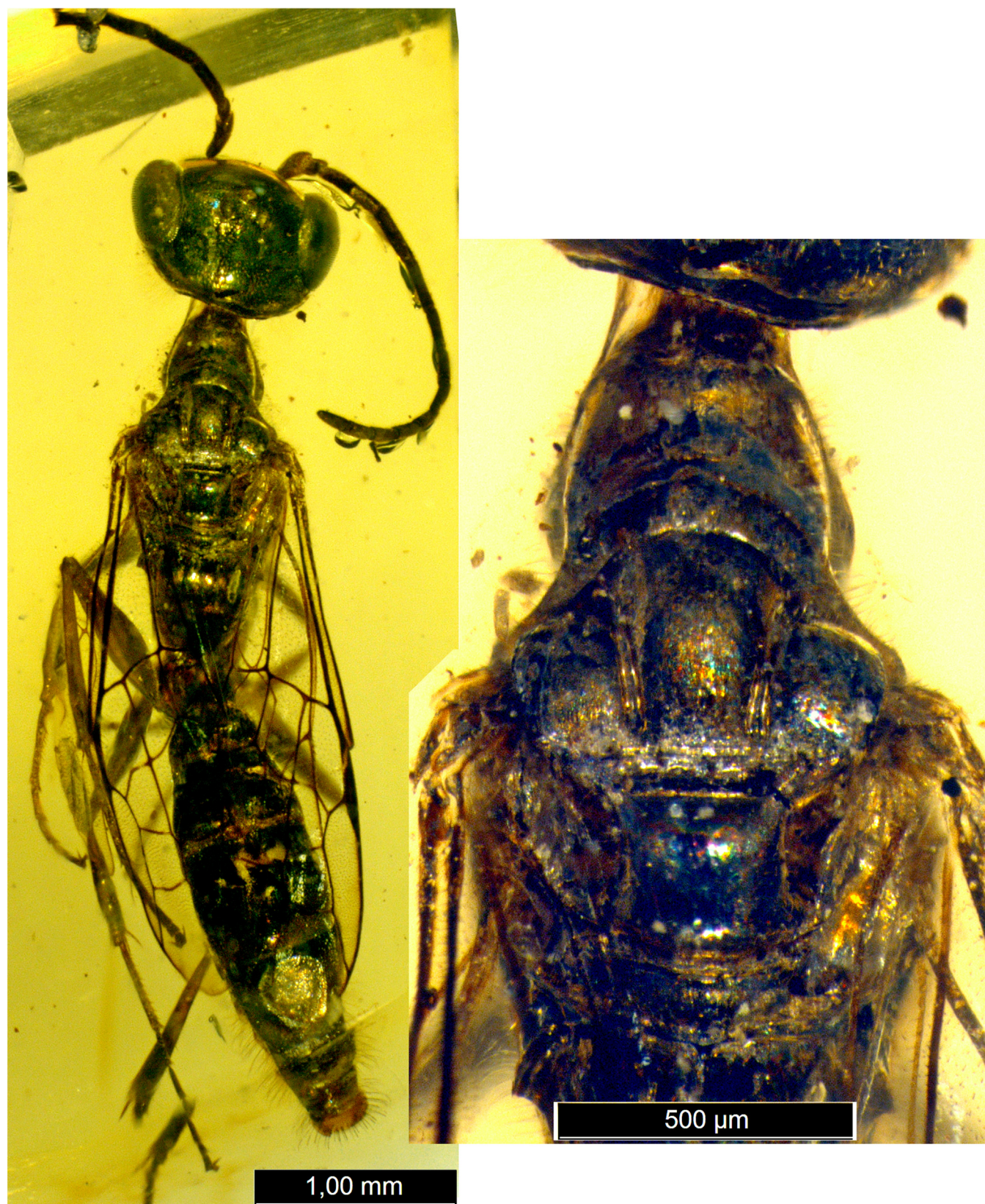


Fig. 9. Undescribed Angarospecidae (NIGP167963). General view and close-up of dorsal mesosoma showing the thin posterior margin of pronotum overlaying the smooth anterior mesoscutum.



Fig. 10. Burmusculidae (Zhang et al., 2018a). Note mesopleuron lacking oblique suture.

Ecological aspects of the fauna, including climatic, landscape and genetic relationships, are certainly of much interest but need more detailed study. For the present, based on the composition at family level, we would highlight only the presence of Cephidae of ordinary general appearance of Cephinae which are characteristic of temperate climate in sharp contrast to apparent thermophily of many other Burmese taxa, including Hymenoptera (Stephanidae, Scolebythidae, Sclerogibbidae, Ampulicidae, as well as rarity of Ichneumonidae as compared with Braconidae, cf. Li et al., 2016, and high diversity of ants). The case of Xyelidae is less indicative, because this generally temperate family is known there after an aberrant tribe Sysstoxylini which climatic attitude could be deviant as well.

5. Conclusion

The provided revision of Hymenoptera in the collection of Burmese amber kept at NIGPCAS presents new evidence on the incomparable richness of the source fauna as compared with other Cretaceous faunas, at least in terms of number of families (as many as 47). An unexpected aspect of this huge diversity is the wealth of endemic families found so far nowhere else in the world, which makes the source terrain suspicious in respect of its long-term isolation by the mid-Cretaceous. The above suspicion is additionally supported with the fact that a number of constituent families represent relicts of ancient lineages recorded in the Cretaceous and rooted well into the Jurassic. These are Myanmarinidae, Aptenopterissidae, Praeaulacidae, Othniodellithidae and Peleserphidae. We only hypothesize that the terrain might have been in isolation for millions of years.

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References

- Antropov, A.V., 2000. Digger wasps (Hymenoptera, Sphecidae) in Burmese amber. *Bulletin of the Natural History Museum, Geology Series* 56 (1), 59–77.
- Archibald, S.B., Rasnitsyn, A.P., Brothers, D.J., Mathewes, R.W., 2018. Modernisation of the Hymenoptera: ants, bees, wasps and sawflies of the early Eocene Okanagan Highlands. *Canadian Entomologist* 150, 205–257.
- Barden, P., Grimaldi, D., 2016. Adaptive radiation in socially advanced stem-group ants from the Cretaceous. *Current Biology* 26, 515–521.
- Basibuyuk, H.H., Rasnitsyn, A.P., 2000. Taxonomic names, in An archaic new genus of Evaniidae (Insecta: Hymenoptera) and implications for the biology of ancestral evanioids. *Bulletin of the Natural History Museum, Geology Series* 56, 54–56.
- Bennett, D.J., Engel, M.S., 2005. A primitive sapygid wasp in Burmese amber (Hymenoptera: Sapygidae). *Acta Zoologica Cracoviensia* 48B, 1–9.
- Brothers, D.J., 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. *University of Kansas Science Bulletin* 50, 483–648.
- Carmean, D., Kimsey, L., 2010. Phylogenetic revision of the parasitoid wasp family Trigonidae (Hymenoptera). *Systematic Entomology* 23, 35–76.
- Chen, Huayan, van Achterberg, C., He, Junhua, Xu, Zaifu, 2014. A revision of the Chinese Trigonidae (Hymenoptera, Trigonidae). *ZooKeys* 385, 1–207.
- Cockx, P.F.D., McKellar, R.C., 2016. First record of the family Scolebythidae (Hymenoptera) in mid-Cretaceous amber from Myanmar. *Cretaceous Research* 67, 133–139.
- Engel, M.S., 2006. Two ensign wasps in Cretaceous amber from New Jersey and Myanmar. *Polskie Pismo Entomologiczne* 75 (3), 443–454.
- Engel, M.S., 2008. The wasp family Rhopalosomatidae in Mid-Cretaceous amber from Myanmar (Hymenoptera: Vespidae). *Journal of the Kansas Entomological Society* 81 (3), 168–174.
- Engel, M.S., 2015. A new family of primitive serphitoid wasps in Lebanese amber (Hymenoptera, Serphitoidea). *Novitates Paleontologicae* No. 13, 1–22.
- Engel, M.S., Grimaldi, D.A., 2007. New false fairy wasps in Cretaceous amber from New Jersey and Myanmar (Hymenoptera: Mymarommatoidea). *Transactions of the Kansas Academy of Science* 110, 159–168.
- Engel, M.S., Grimaldi, D.A., 2009. Diversity and phylogeny of the Mesozoic wasp family Stigmaphronidae (Hymenoptera: Ceraphronidae). *Denisia* 26, 53–86.
- Engel, M.S., Grimaldi, D.A., 2006a. The first Cretaceous spider wasp (Hymenoptera: Pompilidae). *Journal of the Kansas Entomological Society* 79, 359–368.
- Engel, M.S., Grimaldi, D.A., 2006b. The first Cretaceous sclerogibbid wasp (Hymenoptera: Sclerogibbidae). *American Museum Novitates* 3515, 1–7.
- Engel, M.S., Ortega-Blanco, J., Bennett, D.J., 2009. A remarkable tiphiiform wasp in mid-Cretaceous amber from Myanmar (Hymenoptera: Tiphiidae). *Transactions of the Kansas Academy of Science* 112, 1–6.
- Engel, M.S., Grimaldi, D.A., Ortega-Blanco, J., 2013. A stephanid wasp in mid-Cretaceous Burmese amber (Hymenoptera: Stephanidae), with comments on the antiquity of the hymenopteran radiation. *Journal of the Kansas Entomological Society* 86 (3), 244–252.
- Engel, M.S., Huang, D., Azar, D., Nel, A., Davis, S.R., Alvarado, M., Breitkreuz, L.C.V., 2015. The wasp family Spathiopterygidae in mid-Cretaceous amber from Myanmar (Hymenoptera: Diapriidae). *Comptes Rendus Palevol* 14 (2), 95–100.
- Engel, M.S., Huang, D., Cai, C., Alqarni, A.S., 2018. A new lineage of braconid wasps in Burmese Cenomanian amber (Hymenoptera, Braconidae). *ZooKeys* 730, 73–84.
- Engel, M.S., Huang, D., Alqarni, A.S., Cai, C., 2016a. An unusual new lineage of sawflies (Hymenoptera) in Upper Cretaceous amber from northern Myanmar. *Cretaceous Research* 60, 281–286.
- Engel, M.S., Huang, D.Y., Alqarni, A.S., Cai, C.Y., 2016b. A remarkable evanioid wasp in mid-Cretaceous amber from northern Myanmar (Hymenoptera: Evanioidea). *Cretaceous Research* 60, 121–127.
- Engel, M.S., Nascimbene, P.C., 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates* 3361, 1–71.
- Grimaldi, D.A., Engel, M.S., 2005. *Evolution of Insects*. Cambridge University Press, New York, pp. 755.
- Guo, L., Shih, C., Li, L., Ren, D., 2016. New peleciniid wasps (Hymenoptera: Peleciniidae) from Upper Cretaceous Myanmar amber. *Cretaceous Research* 67, 84–90.
- Guo, M., Xing, L., Wang, B., Zhang, W., Wang, Sh., Shi, A., Bai, M., 2017. A catalogue of Burmite inclusions. *Zoological Systematics* 42 (3), 249–379.
- Huber, J.T., Poinar, G.Jr., 2011. A new genus of fossil Myrmecidae from Cretaceous amber and keys to Cretaceous myrmecid genera. *ZooKeys* 130, 461–472.
- International Commission on Stratigraphy, 2017. *International stratigraphic chart*, v2017/2.
- Kozlov, M.A., 1975. Taxonomy; Hymenoptera Apocrita of Mesozoic. *Transactions of the Palaeontological Institute Academy of Sciences of the USSR* 147, 1–134.
- Krogmann, L., Nel, A., 2012. On the edge of parasitoidism: a new Lower Cretaceous woodwasp forming the putative sister group of Xiphydriidae + Euhymenoptera. *Systematic Entomology* 37, 215–222.
- Li, L.F., Rasnitsyn, A.P., Shih, C.K., Ren, D., 2015. A new genus and species of Praeaulacidae (Hymenoptera: Evanioidea) from Upper Cretaceous Myanmar amber. *Cretaceous Research* 55, 19–24.
- Li, L.F., Kopylov, D.S., Shih, C., Ren, D., 2016. The first record of Ichneumonidae (Insecta: Hymenoptera) from the Upper Cretaceous of Myanmar. *Cretaceous Research* 70, 152–162.
- Lucena, D.A.A., Melo, G.A.R., 2018. Chrysidid wasps (Hymenoptera: Chrysididae) from Cretaceous Burmese amber: Phylogenetic affinities and classification. *Cretaceous Research* 89, 279–291.
- Nel, A., Perrichot, V., Néraudeau, D., 2003. The oldest trigonalid wasp in the Late Albian amber of Charente-Maritime (SW France) (Hymenoptera: Trigonidae). *Eclogae Geologicae Helvetiae* 96, 503–508.
- Olmi, M., Rasnitsyn, A.P., Brothers, D.J., Guglielmino, A., 2014a. The first fossil Embolemidae (Hymenoptera: Chrysoidea) from Burmese amber (Myanmar) and Orapa Kimberlitic deposits (Botswana) and their phylogenetic significance. *Journal of Systematic Palaeontology* 12 (6), 623–635 Corrigendum, p. 759.
- Olmi, M., Xu, Z., Guglielmino, A., 2014b. Descriptions of new fossil taxa of Dryinidae (Hymenoptera: Chrysoidea) from Burmese amber (Myanmar). *Acta Entomologica Musei Nationalis Pragae* 54 (2), 703–714.
- Ortega-Blanco, J., Rasnitsyn, A.P., Delclòs, X., 2010. A new family of ceraphronid wasps from Early Cretaceous Álava amber, Spain. *Acta Palaeontologica Polonica* 55 (2), 265–276.
- Perrard, A., Grimaldi, D., Carpenter, J.M., 2017. Early lineages of Vespidae (Hymenoptera) in Cretaceous amber. *Systematic Entomology* 42, 379–386.
- Perrichot, V., 2013. New maimetshid wasps in Cretaceous amber from Myanmar (Insecta: Hymenoptera). *Annales de Paléontologie* 99, 67–77.
- Perrichot, V., Engel, M.S., Nel, A., Ortega-Blanco, J., Delclòs, X., Soriano, C., Lohrmann, V., Tafforeau, P., 2014. "False Ants" from the Cretaceous (Hymenoptera: Chrysoidea: Falsiformicidae). *Mitteilungen des Entomologischen Vereins Stuttgart* 19 (1), 26.
- Perrichot, V., Wang, B., Engel, M.S., 2016. Extreme morphogenesis and ecological specialization among Cretaceous basal ants. *Current Biology* 26 (11), 1468–1472.
- Poinar, G., Buckley, R., 2011. Descriptions, in Predatory behaviour of the social orb-weaver spider, *Geratonephila burmanica* n. gen., n. sp. (Araneae: Nephilidae) with its wasp prey, *Cascolio incassus* n. gen., n. sp. (Hymenoptera: Platygasteridae) in Early Cretaceous Burmese amber. *Historical Biology* 24, 519–524.
- Poinar, G.O.Jr., Danforth, B.N., 2006. A fossil bee from Early Cretaceous Burmese amber. *Science* 314, 614.
- Poinar Jr., G.O., Poinar, R., 2008. *What bugged the dinosaurs?* Princeton University Press, Princeton, pp. 264.
- Pulawski, W.J., Rasnitsyn, A.P., Brothers, D.J., Archibald, S.B., 2000. New Genera of Angarosphecinae: *Cretospecium* from Early Cretaceous of Mongolia and

- Eosphecium* from Early Eocene of Canada (Hymenoptera: Sphecidae). Journal of Hymenopteran Research 9 (1), 34–40.
- Rasnitsyn, A.P., 1972. Late Jurassic hymenopterous insects (Preaulacidae) of Karatau. Paleontological Journal 6, 62–77.
- Rasnitsyn, A.P., 1990. Otryad Vespida. Pereponchatokrylye (Order Vespida. Hymenopterans). In Pozdnemeyozoiskie nasekomye Vostochnogo Zabaikalya (Late Mesozoic insects of eastern Transbaikalia). Rasnitsyn, A.P. (Ed.), Trudy Paleontologicheskogo instituta Akademii Nauk SSSR (Transactions of the Paleontological Institute of the Academy of Sciences of the Union of Soviet Socialist Republics) 239, 177–205 in Russian.
- Rasnitsyn, A.P., 1996. Burmese amber at the Natural History Museum. Wrosteck 23, 19–20.
- Rasnitsyn, A.P., 2002. Superorder Vespidea Laicharting, 1781. Order Hymenoptera Linné, 1758 (=Vespida Laicharting, 1781). In: Rasnitsyn, A.P., Quicke, D.L.J. (Eds.), History of Insects. Kluwer Academic Publishers, Dordrecht, pp. 242–254.
- Rasnitsyn, A.P., 2013. *Vectevania vetula* Cockerell, 1922 from the uppermost Eocene of Bembridge Marls, England, and the system of the family Gasteruptionidae s.l. [Vespida (= Hymenoptera), Evanioidea]. Proceedings of the Russian Entomological Society 84 (2), 98–106.
- Rasnitsyn, A., Öhm-Kühnle, Ch., 2018. Three new female *Aptenoperissus* from mid-Cretaceous Burmese amber (Hymenoptera, Stephanoidea, Aptenoperissidae): unexpected diversity of paradoxical wasps suggests insular features of source biome. Cretaceous Research 91, 168–175.
- Rasnitsyn, A.P., Ross, A.J., 2000. A preliminary list of arthropod families present in the Burmese amber collection at The Natural History Museum, London. Bulletin of the Natural History Museum, Geology Series 56 (1), 21–24.
- Rasnitsyn, A.P., Bashkuev, A.S., Kopylov, D.S., Lukashovich, E.D., Ponomarenko, A.G., Popov, Yu.A., Rasnitsyn, D.A., Ryzhkova, O.V., Sidorchuk, E.A., Sukatsheva, I.D., Vorontsov, D.D., 2016. Sequence and scale of changes in the terrestrial biota during the Cretaceous (based on materials from fossil resins). Cretaceous Research 61, 234–255.
- Rodriguez, J., Waichert, C., von Dohlen, C.D., Poinar, G.Jr., Pitts, J.P., 2016. Eocene and not Cretaceous origin of spider wasps: Fossil evidence from amber. Acta Palaeontologica Polonica 61 (1), 89–96.
- Ross, A., 2015. Insects in Burmese amber. Entomologentagung 02-05.03. Frankfurt/ M. Programm und Abstracts. Frankfurt/Main. p. 72. .
- Ross, A.J., 2018. Burmese (Myanmar) amber taxa, on-line checklist v.2018.1 96 pp. . <http://www.nms.ac.uk/explore/stories/natural-world/burmese-amber/>.
- Ross, A.J., York, P.V., 2000. A list of type and figured specimens of insects and other inclusions in Burmese amber. Bulletin of the Natural History Museum, Geology Series 56, 11–20.
- Ross, A., Mellish, C., York, P., Crighton, B., 2010. Burmese amber. In: Penney, D. (Ed.), Biodiversity of fossils in amber from the major world deposits. Siri Scientific Press, Manchester, pp. 208–235.
- Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Wang, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research 37, 155–163.
- Smith, R.D.A., Ross, A.J., 2018. Amberground pholadid bivalve borings and inclusions in Burmese amber: implications for proximity of resin-producing forests to brackish waters, and the age of the amber. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 107, 239–247.
- Vilhelmsen, L., Turrissi, G.F., 2011. Per arborem ad astra: Morphological adaptations to exploiting the woody habitat in the early evolution of Hymenoptera. Arthropod Structure and Development 40, 2–20.
- Zhang, W.W., 2017. Frozen dimensions of the fossil insects and other invertebrates in amber. Chongqing University Press 692 pp. (in Chinese).
- Zhang, H.C., Rasnitsyn, A.P., 2007. Nevaninae subfam. n., a new fossil taxon (Insecta: Hymenoptera: Evanioidea: Praeaulacidae) from the Middle Jurassic of Daohugou in Inner Mongolia, China. Insect Systematics and Evolution 38, 149–166.
- Zhang, H.C., Rasnitsyn, A.P., 2008. Middle Jurassic Praeaulacidae (Insecta: Hymenoptera: Evanioidea) of Inner Mongolia and Kazakhstan. Journal of Systematic Palaeontology 6, 463–487.
- Zhang, Q., Kopylov, D.S., Rasnitsyn, A.P., Wang, B., Zhang, H.C., 2018a. Burmorussidae, new Orussomorph wasps (Insecta: Hymenoptera) from mid-Cretaceous Burmese amber. Papers in Palaeontology. (under review).
- Zhang, Q., Alexandr, P.R., Zhang, H.C., 2018b. Burmusculidae, a new and basal family of pompiloid wasps from the Cretaceous of Eurasia (Hymenoptera: Pompiloidea). Cretaceous Research 91, 341–349.
- Zhang, Q., Rasnitsyn, A.P., Wang, B., Zhang, H.C., 2018c. Myanmarinidae, a new family of basal Apocrita (Hymenoptera: Stephanoidea) from upper-Cretaceous Burmese amber. Cretaceous Research 81, 86–92.
- Zhang, Q., Rasnitsyn, A.P., Wang, B., Zhang, H.C., 2018d. Peleserphidae, a new family of basal proctotrupomorphs (Hymenoptera: Proctotrupoidea) from mid-Cretaceous Burmese amber. Cretaceous Research 86, 66–72.
- Zherikhin, V.V., Ross, A.J., 2000. A review of the history, geology and age of Burmese amber (Burmite). Bulletin of the Natural History Museum, London (Geology) 56, 3–10.