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A diverse Cenozoic insect assemblage in Thailand

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ABSTRACT

In Western Thailand, Miocene shales from Wang Kaew, in the Mae Sot basin, have yielded a diverse insect assemblage comprising 115 articulated specimens. In this preliminary review, 15 subcomplete specimens are studied and referred to at least eight forms belonging to five orders (Coleoptera, Diptera, Hymenoptera, Orthoptera, and Hemiptera). Coleoptera are represented by very nicely preserved specimens of weevils (Curculionidae). Diptera are known by three different taxa referred to Bibionidae, Sciaridae and Brachycera. Hymenoptera are known by representatives of Vespidae and Formicidae. Orthoptera are represented by a single specimen of uncertain affinities and Hemiptera by one Gerrinae. This insect assemblage is the most complete ever reported in Southeast Asia during the Cenozoic.

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Fossil insects; Mae Sot Basin; Miocene; Thailand

Introduction

In Southeast Asia, the fossil insect record is mostly represented by Mesozoic forms. Exquisitely preserved insects are known from the famous Cretaceous Burmese ambers, in Northern Myanmar, with about 1,770 species reported or described, representing at least 28 orders, 455 families and 1,203 genera (Ross 2022). Fossil insects from the Cenozoic are much rarer, despite the tremendous diversity of living forms. In Indonesia, an exuvia of Hemiptera included in opal was recently reported from the Pliocene Genteng Formation (Chauviré et al. 2020) and the limoniid fly *Trentepohlia* (*Mongoma*) *pouilloni* Ngô-Muller et al. (2019) was described from amber of the Miocene South Sumatra Basin (Ngô-Muller et al. 2019). In Thailand, Brown et al. (1951) and Chaodumrong et al. (1983) reported undetermined insects remains from the Mae Sot series, in limestone beds tentatively dated as Pliocene (most of these beds are now considered Eocene-Miocene, e.g. Morley and Racey 2011). Vimuktanandana (1984) and Saengsrichan et al. (2009) also cited insect remains from the Mae Sot province. In 1966, Fujiyama (in Endo and Fujiyama 1966) ascribed a unique specimen from Wat Don Kaeo (Miocene, Mae Sot basin, western Thailand) to the aradid hemiptera *Neuroctenus* Fieber, 1860.

In 1982, a diverse fossil assemblage has been collected in Western Thailand, in the vicinity of Wang Kaew village, Mae Sot District, Tak Province, in shales putatively dated as middle-upper Miocene (Figure 1). This assemblage, reported and briefly described by Srisuk (2003, 2006), mostly consists of insects but reptiles (snakes), actinopterygians (cyprinids) and plants (dicotyledons) are also present. Insects are represented by 115 specimens, initially referred by Srisuk (2006) to Coleoptera, Diptera, Hymenoptera, Orthoptera, Hemiptera, Isoptera, Ephemeroptera, Mantoidea and possibly Culicidae, which constitutes the most diverse Cenozoic fossil insect assemblage in Southeast Asia. Several specimens are sufficiently preserved to be ascribed to an order, and sometimes to a family, but infrafamilial identifications are usually uncertain. In this new survey, 15 subcomplete or articulated specimens are described and are tentatively referred to Coleoptera, Diptera, Hymenoptera, Orthoptera and Hemiptera.

Geological settings

The specimens were collected by one of the authors (P.S.) in a road-cutting near the village of Wang Kaew, Tak Province (Western Thailand), in thinly laminated shales. The beds belong to the Mae Sot Basin, a large intermontane Cenozoic basin located between Thailand and Myanmar and formed by non-marine deposits which mostly consist of shale, oil shale, mudstone and marlstone (Gibling et al. 1985; Suwannathong and Sukhummongkol 2007). Three formations outcrop in the basin: the Palaeocene Mae Ramat Formation, deposited in alluvial plain and fans, and the younger Mae Pa and Mae Sot Formations, both corresponding to lacustrine and fluvio-lacustrine environments (Thanomsap and Sitahirun 1992; Suwannathong and Sukhummongkol 2007; Songtham and Chaodumrong 2014). The Wang Kaew outcrop is situated within the Mae Sot Formation and is probably middle-upper Miocene in age (ca. 16–5 Ma) (Watanasak 1989; Suwannathong and Sukhummongkol 2007). It is located in the vicinity of Wat Don Kaeo, where the Hemiptera *Neuroctenus* was reported by Fujiyama (in Endo and Fujiyama 1966).

Materials and methods

The Wang Kaew collection is represented by 115 insect specimens, initially housed in the Srisuk's House Museum under the acronym SHM-WK. They were later donated to the Palaeontological Research and Education Centre, Mahasarakham University, where they are currently stored under the acronym PRC. In order to ensure the traceability of the specimens, the older SHM-WK numbers, used in Srisuk (2003, 2006), are indicated between parentheses after the PRC numbers used herein.

All specimens consist of small articulated or slightly disarticulated flattened remains on shale slabs. From this collection, 15 specimens representing eight different taxa are studied herein. They were examined and measured using a stereomicroscope equipped with a micrometre. Photographs were taken with a Nikon D7500 digital camera coupled with Micro Nikkor

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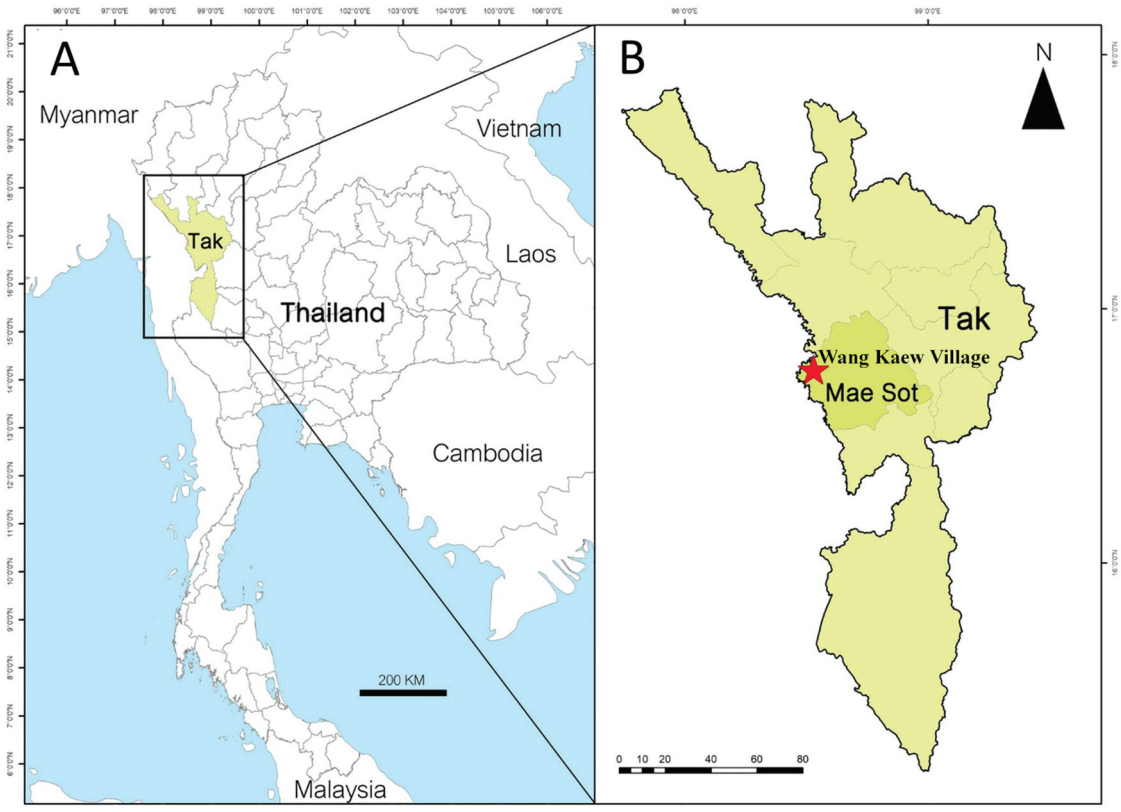

Figure 1. A, location of Tak province. B, location of Wang Kaew Village.

105 mm 1:2.8 D and Laowa 25 mm f/2.8 2.5–5x lenses. For each specimen, several pictures were taken at different focal points and assembled by focus stacking to increase the depth of field, using Adobe Photoshop or Helicon Focus.

Abbreviations

Anatomical abbreviations: A, Anal vein; **bM**, basal Medial; **C**, Costa; **Cu**, Cubitus; **CuA_1**, Cubitus anterior 1; **CuA_2**, Cubitus anterior 2; **M**, Media; **M_1**, Media 1; **M_2**, Media 2; **R**, Radius; **R_S**, Radius sector; **R_1**, Radius 1; **R_5**, Radius 5; **Sc**, Subcosta; **Sc_2**, Subcosta 2.

Institutional abbreviations: PRC, Palaeontological Research and Education Centre, Mahasarakham University, Thailand; **SHM-WK**, Srisuk's House Museum, Wang Kaew collection, Thailand.

Systematic palaeontology

Class Insecta Linnaeus 1758

Order Coleoptera Linnaeus 1758

Suborder Polyphaga Emery 1886

Family Curculionidae Latreille 1802a

Gen. et sp. indet.

Referred material. PRC 174 (SHM-WK 33 in Srisuk 2006)

?Additional materials. PRC 175 (SHM-WK 36), PRC 176 (SHM-WK 68), PRC 177 (SHM-WK 69), PRC 178 (SHM-WK 70), PRC 179 (SHM-WK 71), PRC 180 (SHM-WK 72), PRC 181 (SHM-WK 73)

Description

The description is based on PRC 174, which is the most complete specimen (Figure 2). Other specimens slightly differ from it and may correspond to another curculionid taxon (see Remarks).

Measurements. Body length without rostrum 3.2 mm, rostrum length 1.4 mm.

Body broadly stout, deep brown, distinctly ornamented.

Head oval, deeper than long, antennae not visible. Vertex relatively large and convex. Rostrum strongly curved, slender, relatively long and tapered at the apex. Eyes large oval.

Thorax with large pronotum, much wider than long, densely ornamented, approximately as wide as head. Mesepimeron, mesepisternum, metepimeron and metepisternum covered by elytra.

Wings: only forewings (elytra) visible, posterior part of elytra slightly disarticulated. Heavy vestiture. Nine elytral striae (counted from the right wing). All elytral striae distinctly straight, elytral stria 1 is the longest and nearly reaches the winged edge, elytral stria 3 jointing stria 6 distally, elytral stria 7 and 8 short and not reaching the edge. Interval striae distinct and relatively wide (Figure 2b). Elytra not abbreviated and covering the pygidium.

Legs: all visible legs folded, similar in size and showing a distinct ornamentation on the surface. Coxa not visible. All femurs relatively large and wide. Fore tibia not clearly visible. Uncus on the hind tibia distinct and small. Only four tarsi visible (pseudotetramerous). First, second and third tarsomeres round and short. Third tarsomere bilobed while fifth tarsomere elongated with no claws on the apex.

Remarks

The specimen PRC 174 is assigned to the superfamily Curculionoidea on the basis of the presence of the rostrum (Kuschel 2003; Marvaldi and Lanteri 2005; Gratshev and Legalov

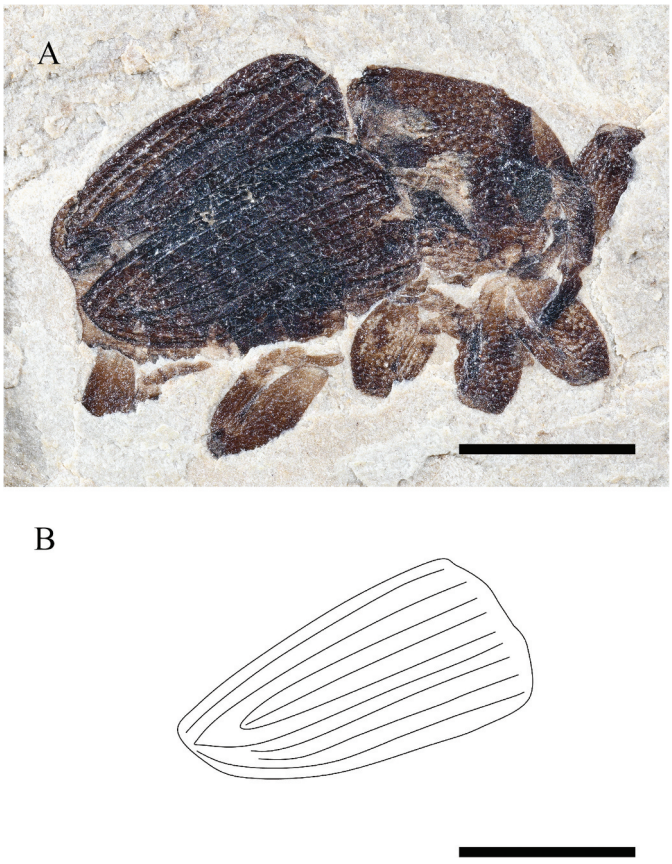

Figure 2. Curculionidae gen. et sp. indet. PRC 174. A, Photograph, dorsolateral view. B, outline of wing. Scale bar = 1 mm.

2014; Oberprieler et al. 2019). It differs from Brentidae s.l. by its non-elongated body (Legalov and Wappler 2021) and from Mesophyletidae, Nemonychidae and Belidae by the tibia with uncus (Legalov 2015; Clarke et al. 2019). This specimen is similar to Curculionidae by the tibia with uncus, which is a character retrieved in most subfamilies except Entiminae, as described by Legalov (2018). Within this family, it differs from Platypodinae, Scolytinae and Entiminae by the longer rostrum (Marvaldi and Lanteri 2005; Oberprieler et al. 2019). It shows many features of Curculioninae: small head subspherical; eye large, longitudinally oval and placed anteriorly; rostrum long and slender, longer than the head; prothorax wider than long; mesepimeron not visible in dorsal view; hind tibia with third tarsomere wider than second tarsomere; tibia with small uncus; fore and hind femurs similar in size and shape; pronotum wider than long; tibial spur absent (Legalov 2015). Other specimens from Wang Kaew (PRC 175–181, Figure 3) share several features with PRC 174, such as the long rostrum and the pronotum wider than long, which are diagnostic characters of Curculioninae (Legalov 2015). However, PRC 176, PRC 178 and PRC 179 differ by having longer and slender legs, PRC 180 by having relatively longer rostrum and PRC 181 by the elytra apparently abbreviated and not covering the pygidium. PRC 175 and PRC 177 are too incompletely preserved to be compared with the other specimens. As a result, all those additional specimens (PRC 175–181) are referred to curculionids but cannot be confidently considered conspecific with PRC 174.

Order Diptera Linnaeus 1758
Suborder Nematocera Latreille 1825
Family Bibionidae Fleming 1821
cf. *Plecia* Wiedemann, 1828

Referred material. PRC 182 (SHM-WK 88)

Description

Relative long and wide, pale brown specimen with slender legs preserved in lateral view (Figure 4).

Measurements. Body length 4.5 mm, abdomen length 4 mm, wing length 4 mm.

Body long and wide, compressed laterally.

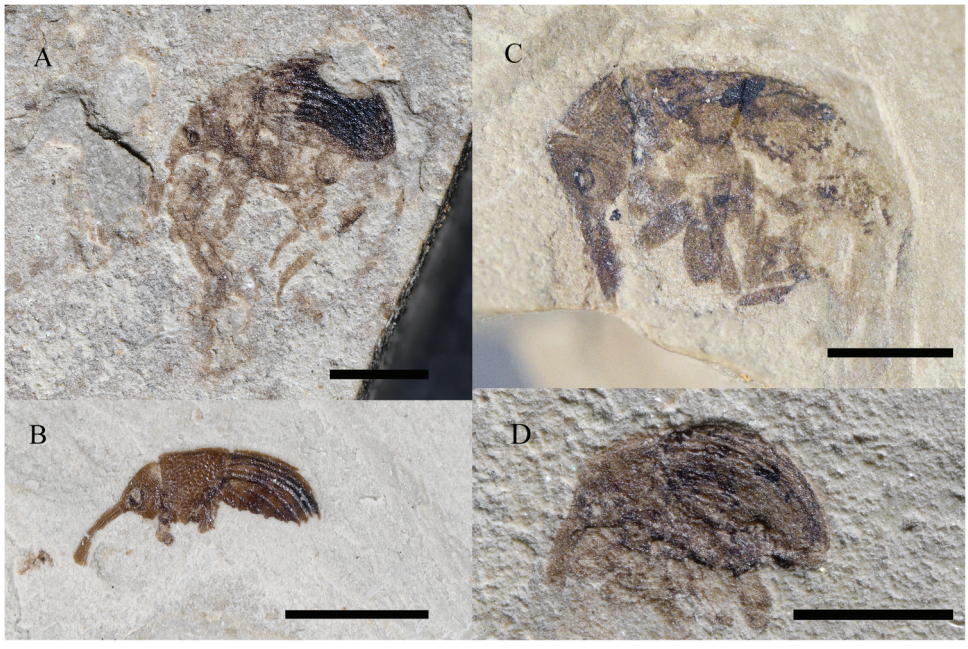

Figure 3. Curculionidae gen. et sp. indet. PRC 178. A, Photograph, dorsolateral view. PRC 180. B, Photograph, dorsolateral view. PRC 181. C, Photograph, dorsolateral view. PRC 175. D, Photograph, dorsolateral view.

Figure 4. Bibionidae gen. et sp. indet. PRC 182. Photograph, ventral view. Scale bar = 1 mm.

Head and thorax difficult to distinguish, both covered with setae, antennae relatively short.

Abdomen cylindrical, long and wide. More than seven abdominal segments can be counted. All segments nearly equal in size.

Wing large and wide, preserved only on the right side. Venation almost not visible, Costa (C) not distinct, subcostal (Sc) distinct, long and thick till the middle of costal margin.

Legs long and slender, densely covered with setae. Femur not visible. Tibia long and slender with no apical spine. Tarsomeres difficult to individualise, last segment long and distally widened.

Remarks

PRC 182 is reminiscent of the Bibionidae Pleciinae genus *Plecia* by the following features: relatively short antennae, wide cylindrical abdomen with at least seven abdominal segments, legs simple, slender and all similar in size, Sc four times shorter than C, and legs fully covered with setae (McAlpine et al. 1981; Skartveit and Nel 2017; Simov et al. 2021). This specimen is a female based on its wide abdomen (Collomb et al. 2008; Skartveit and Nel 2017). However, the wing venation is not sufficiently preserved to provide a specific determination.

Family Sciaridae Billberg 1820.

Gen. et sp. indet.

Referred material. PRC 183 (SHM-WK 81)

Description

Long and slender brown specimen with wing venation preserved in dorsolateral view (Figure 5).

Measurements. Body length 3.4 mm.

Body long, slender, brown and posteriorly tapered. Head and thorax not visible.

Abdomen long and slender, with approximately seven visible abdominal segments, gradually decreasing in size posteriorly. First segment is the largest, wider than long. Second segment is nearly as wide as first segment and larger than third, fourth and fifth segments. Segments are delimited by thick and distinct septa.

Wings poorly preserved, left-wing wider than long (Figure 5b). Veins are dark brown. C, R and bM are distinctly strong. C is extended on the wing apex. Sc is not visible. R is elongated, almost

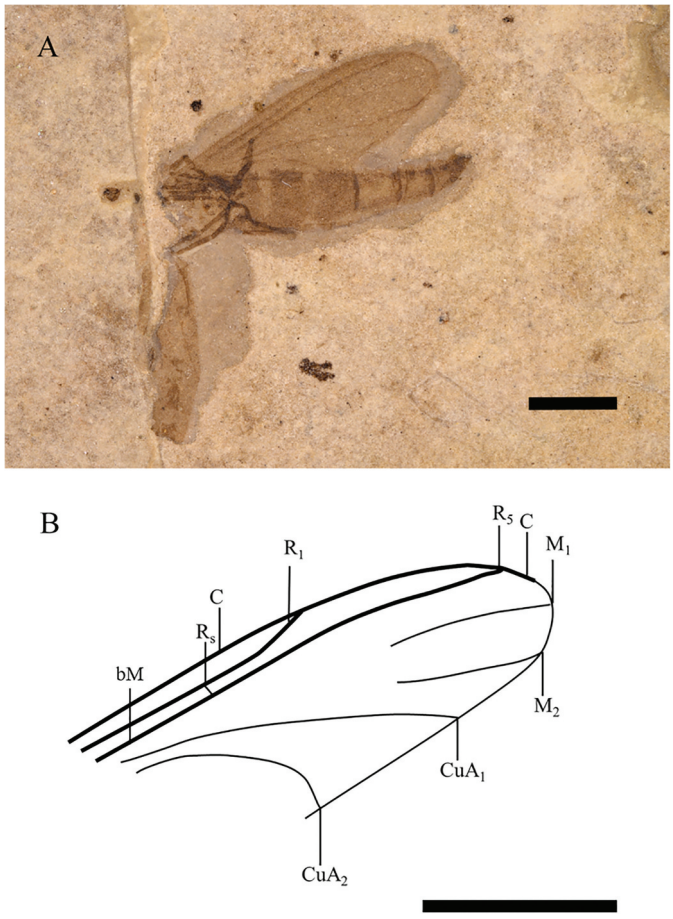

Figure 5. Sciaridae gen. et sp. indet. PRC 183. A, photograph, dorsolateral view. B, outline of wing venation. Scale bar = 1 mm. Abbreviations: C = Costa, R1 = Radius 1, RS = Radius sector, R5 = Radius 5, M1 = Media 1, M2 = Media 2 CuA1 = Cubitus anterior 1, CuA2 = Cubitus anterior 2.

half the length of C. Rs is short. bM is distinctly elongated, extended beyond the apex and divided into two branches. M and CuA are faded. M_1, M_2 and CuA_1 are long, CuA_2 is short and extended beyond the base of anal. On the right-wing, only C and R are visible.

Legs long, slender, black, with segments of comparable size.

Remarks

The specimen is assigned to the family Sciaridae (dark-winged fungus gnats) based on the following characters: long and slender body, slender legs, and especially wing venation pattern with C extending on the wing apex and ending beyond last branch of R and no more than two free branches of M (McAlpine et al. 1981; Menzel et al. 2003; Heller and Rulik 2016; Broadley et al. 2019). Moreover, this specimen is also similar to both fossil (Greenwalt et al. 2019) and living sciarids (Shin 2013; Menzel et al. 2020; Moravvej et al. 2022) in body shape and wing venation. However, the genus cannot be determined because the pattern of M_1 and M_2 is incompletely preserved.

Suborder Brachycera Zetterstedt 1842
Fam., gen. et sp. indet.

Referred material. PRC 184 (SHM-WK 56)

Description

Small stout brown specimen preserved in dorsolateral view (Figure 6).

Figure 6. Brachycera fam., gen. et sp. indet. PRC 184. Photograph, dorsolateral view. Scale bar = 1 mm.

Measurements. Body length 2.8 mm.

Body small and relatively long, brown to black.

Head wide, short and semicircular. Eyes very large and rounded, narrowly separated and largely covering the head.

Antennae very short in front of the head, with only one flagellomere on each side.

Thorax large and slightly convex.

Abdomen relatively large with six abdominal segments visible.

Wing: only right wing preserved, longer than thorax. Venation not visible.

Legs not preserved.

Remarks

PRC 184 is assigned to Brachycera by the following characters: reduced antennae with one flagellomere, oval body, wing longer than thorax, narrowly separated eyes (McAlpine et al. 1981; Yeates 2002). Although the specimen is incompletely preserved, precluding an in-depth identification, the overall body is roughly similar to Recent Muscomorpha described by McAlpine et al. (1981).

Order Hymenoptera Linnaeus 1758
Suborder Apocrita Gerstaecker 1867
?Family Vespidae Latreille, 1802b
?Subfamily Eumeninae Leach 1815

Gen. et sp. indet.

Referred material. PRC 185 (SHM-WK 19)

Description

Elongated and slender brown to black specimen preserved in lateral view (Figure 7).

Measurements. Body length 7.40 mm.

Body elongated, brown in lateral view.

Head relatively large and hypognathous. Eyes and antennae not visible.

Thorax with mesothorax relatively large, round and swollen.

Petiole node long and very robust.

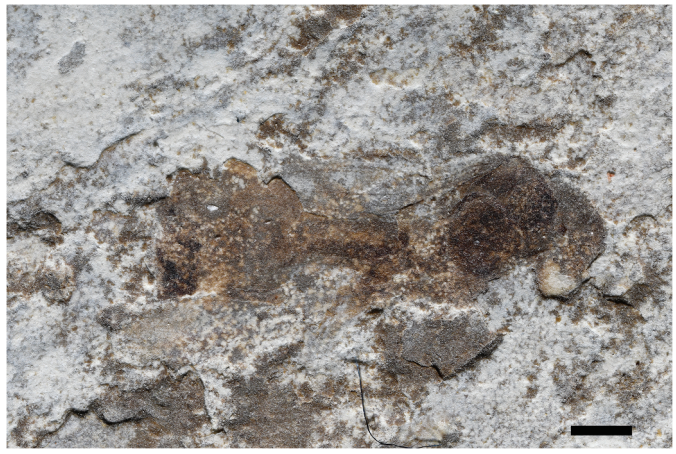

Figure 7. Eumeninae? gen et sp. indet. PRC 185. Photograph, dorsal view. Scale bar = 1 mm.

Abdomen relatively short and triangular. Remains of the first, second and third abdominal segments, all similar in size and shape.

Wings posteriorly directed, extended until the first abdominal segment. Venation not well preserved.

Remarks

This specimen is incompletely preserved but the long and broad petiole is reminiscent of the families Diapriidae (superfamily Diaprioidea), Roproniidae, Heloridae, Proctorenyxidae (Proctotrupoidea) and the potter wasps Eumeninae (Vespidae) (Goulet and Huber 1993; Nguyen 2015; Archibald et al. 2018). However, it differs from the four first families by the relatively broader petiole, thorax relatively short and triangular, and abdomen not flattened (Kim et al. 2016; Quadros and Brandão 2017; Archibald et al. 2018; Tymochko et al. 2021). It shares with Eumeninae a short and stout thorax, and relatively broader petiole (Nugroho et al. 2010; Thi and Nguyen 2015; JT et al. 2019).

Family Formicidae Latreille, 1809

Gen. et sp. indet

Referred material. PRC 186 (SHM-WK 59)

Description

Elongated black specimen preserved in lateral view. Antennae and legs not preserved (Figure 8).

Measurement. Body length 2.25 mm.

Body very tiny and relatively long, preserved in lateral view.

Head large, round and black. Eyes and antennae not visible.

Thorax not smooth, pronotum higher than long. Mesonotum and pronotum nearly equal in size. Propodeum relatively long and extended posteriorly. No trace of wings observed, suggesting a possible absence.

Petiole node single and convex dorsally.

Abdomen relatively enlarged, swollen and bulbous. Sting absent. Remains of third to fifth abdominal segments can be identified: third and fourth abdominal segments large, triangular and nearly equal in size, and fifth abdominal segment smaller.

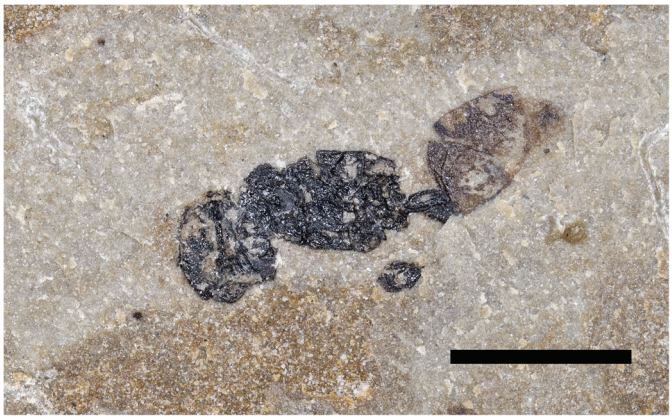

Figure 8. Formicidae gen et sp. indet. PRC 186. Photograph, lateral view. Scale bar = 1 mm.

Remarks

PRC 186 shows some traits of Formicidae such as the swollen and bulbous abdomen and the second abdominal segment (petiole). It is probably a worker because it apparently has a small and elongated body, a small abdomen and is wingless (Barden 2017). The single petiole and absence of sting are reminiscent of Formicinae Latreille, 1809 or Dolichoderinae Forel 1878; however, the long petiole suggests affinities with Dolichoderinae, compared with the shorter petiole of Formicinae (Collingwood et al. 2011).

Order Orthoptera? Olivier 1789
Suborder Ensifera Chopard 1920
Superfamily Grylloidea Laicharting 1781

Fam., gen. et sp. indet.

Referred material. PRC 187 (SHM-WK 16)

Description

Elongated brown specimen preserved in lateral view (Figure 9)

Measurement. Body length 7.35 mm.

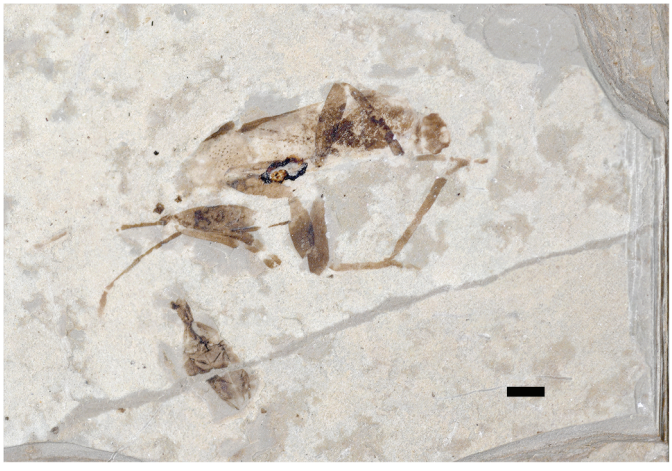

Figure 9. Ensifera? fam., gen. et sp. indet. PRC 187. Photograph, lateral view. Scale bar = 1 mm.

Body large and elongated.

Head hypognathous, relatively large and round. Eyes large and oval. Antennae not visible. Mouth wide.

Thorax triangular. Only the pronotum is visible and not enlarged.

Abdomen elongated, triangularly tapered posteriorly, abdominal segments not visible, ovipositor short.

Legs large and elongated, disarticulated from the body. Reversed fore leg, between thorax and abdomen with relatively large circular coxa. Femur long and wide, tibia long and slender, tarsus not visible. Middle leg with two relatively wide femurs under most of the abdomen. A large pair of legs or hind legs at the tip of abdomen with femurs very large and wide, tibiae very long and slender, tarsus not visible.

Wings not observed, possibly absent or not preserved.

Remarks

Although this specimen is incompletely preserved, it possesses the general appearance of Orthoptera with very enlarged hindlegs, hypognathous head and mandibulate mouth (Arillo and Ortuño 1997). Furthermore, it shows characters of Grylloidea such as a cylindrical body and very slender hind tibiae (Dawwrueng et al. 2017; Tan et al. 2019).

Order Hemiptera Linnaeus 1758
Suborder Heteroptera Latreille 1810
Family Gerridae Leach 1815
Subfamily Gerrinae Bianchi 1896

Gen. et sp. indet.

Referred material. PRC 188 (SHM-WK 34)

Description

Elongated brown macropterous specimen preserved in dorsal view (Figure 10).

Measurements. Body length 9.60 mm.

Body elongated, relatively wide and strong brown with long wings. Head and antennae not visible.

Thorax with pronotum relatively longer than wide, with a longitudinal stripe reaching the scutellum. Scutellum triangular, shorter than pronotum.

Wings: fore wings overlapping. Wings elongated and covering the entire abdomen. Their posterior tip is not preserved. Sc long and reaching the posterior wing edge. Sc_2 not visible. R and M half as long as subcostal. Cu half as long as R or M. R + M+ Cu meeting in the extension of Cu. A nearly as long as the M wing edge but branch not visible.

Legs: fore femur long, fore tibia only preserved as fragment and fore tarsomere not visible. Middle and hind femurs slender but disarticulated.

Remarks

This macropterous specimen is the unique representative of this taxon in the Wang Kaew collection. It is assigned to the subfamily Gerrinae on the basis of the pronotum with a median stripe (Zettel 2007). It could possibly be referred to the genera *Limnogonus* Stål, 1868 or *Limnometra* Mayr, 1865, which both bear the median stripe on the pronotum (Jehamalar and Chandra 2013). However, the absence of colour pattern of the stripes precludes a deeper identification.

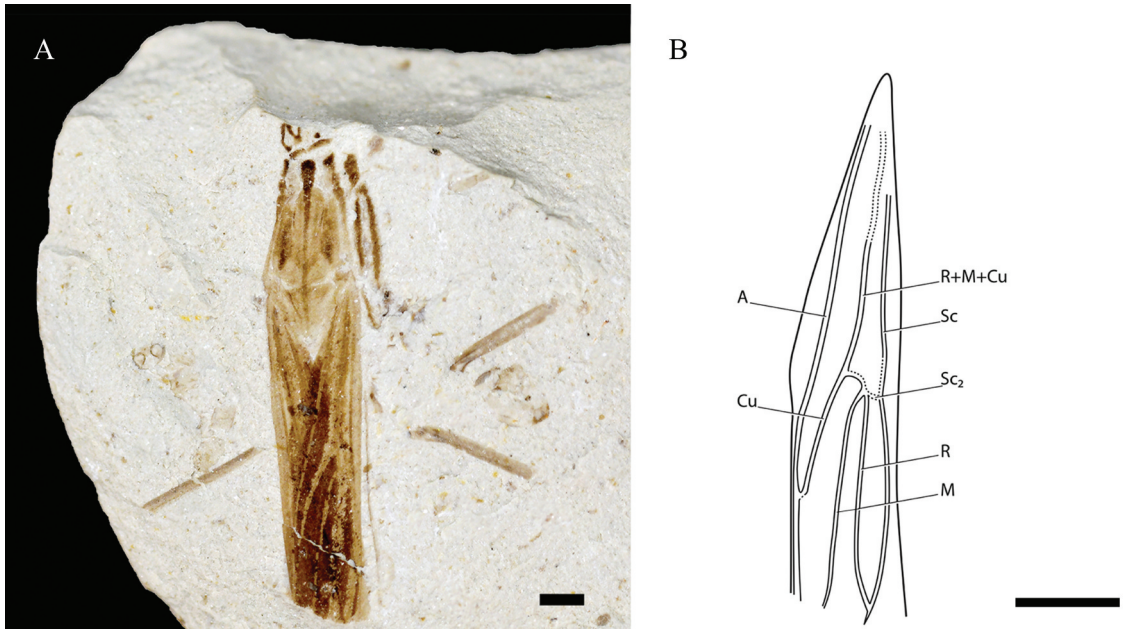

Figure 10. Gerrinae gen. et sp. indet. PRC 188. A, photograph, dorsal view. B, outline of wing venation. Scale bars = 1 mm. Abbreviations: Sc = Subcosta, Sc2 = Subcosta 2, R = Radius, M = Media, Cu = Cubitus, A = Anal vein.

Discussion

The Wang Kaew assemblage consists of herbivorous insects, such as curculionids, sciarids, bibionids and presumably grylloids, and predators and scavengers such as formicids, vespids and gerrids. All these taxa are currently widespread in Asia, where most of them are known since the Mesozoic (Ross 2022). However, as far as we know, this is their unique report in the Cenozoic fossil record from Thailand and more generally from Southeast Asia.

Mesozoic Curculionoidea are frequently reported from Central, Eastern and Southeast Asia, e.g. in Kazakhstan (Legalov 2014a), China (Davis et al. 2013; Lu et al. 2018), Myanmar (Davis and Engel 2014; Legalov and Poinar 2015; Clarke et al. 2019) and Mongolia (Legalov 2014b). A few remains are also known in Cenozoic deposits from India (Legalov 2015). Recent weevils are cosmopolitan including Thailand (Kojima et al. 2016), where they are often considered as a pest for agriculture (Jarruwat and Choomjaihan 2014).

Fossil Bibionidae are represented in Western Asia by late Oligocene occurrences of the genera *Bibio* Geoffroy, 1762 and *Penthetria* Meigen, 1803 from Turkey (Skartveit and Nel 2012) while the genus *Plecia* has been reported in East Asia from the middle Miocene of Japan (Fujiyama 1970). In Southeast Asia, several species of Bibionidae, including Plecinae, have been reported from the middle-late Cretaceous Burmese amber (Li et al. 2021) and the early Cretaceous of China (Ren et al. 1995). Recent species of *Plecia* are abundant in Indonesia, Malaysia, and Thailand (Hardy 1958) and are associated with a warm and tropical environment (Simov et al. 2021). This family is also widespread and very common in Oligocene-Miocene lacustrine deposits in Europe (Collomb et al. 2008), emphasising its cosmopolitan diversity, both in the fossil record and in the Recent forms.

The extant distribution of Sciaridae, dark-winged fungus gnats, is worldwide. Several fossil forms have been described from Baltic amber (Mohrig and Röschmann 1994; Hippa and Vilkamaa 2005). In Asia, they have been reported from the early Eocene of China (Wang et al. 2014) and the Pleistocene of Japan (Takahashi et al. 2017), and in Southeast Asia from the middle-late Cretaceous amber of Myanmar (Blagoderov and Grimaldi 2004). This family is currently well represented in Thailand (Vilkamaa and Hippa 1994) where they are usually associated with moist and shadow areas.

Fossil Brachycera are reported, among others, in Southeast Asia, from the middle-late Cretaceous of Myanmar (Grimaldi et al. 2011; Grimaldi 2016; Grimaldi and Barden 2016; Zhang et al. 2017; Ye et al. 2019; Liu et al. 2020). Nowadays, they also show a cosmopolitan distribution, including a great diversity in Thailand (Muenworn et al. 2010; Changbunjong et al. 2012).

Diapriidae, Roproniidae, Heloridae and Proctorenyxidae are parasitoid wasps (Goulet and Huber 1993; Archibald et al. 2018). Fossil diapriids and vespids are represented by several forms in the middle-late Cretaceous of Myanmar (Perrard et al. 2017; Jouault et al. 2020; Brazidec et al. 2021; Wu et al. 2021) while the Proctotrupoidea (Roproniidae, Heloridae and Proctorenyxidae) are frequently reported from the middle Jurassic and early Cretaceous of China (Shih et al. 2011; Shi et al. 2014; Longfeng et al. 2017). Among these families, only the diapriids and several members of the vespid subfamily Eumeninae are currently found in Thailand (Apiwathnasorn 2012; JT et al. 2019). However, Proctotrupoidea are nowadays represented in Thailand by the family Vanhorniidae (Timokhov and Belokobylskij 2020). Proctorenyxidae are distributed in Northern China, South Korea, and the southern Russian Far East (Kim et al. 2016), Heloridae are mostly found in the Northern hemisphere albeit a few forms are present in Indonesia (van Achterberg 2006), while Roproniidae are diverse in China (Chikun 1997).

In Asia, Mesozoic (late Cretaceous) ants are reported from Kazakhstan and Myanmar (Lapolla et al. 2013; Barden 2017) while Cenozoic ants are reported from India (early Eocene), Iran (Ataabadi et al. 2019) and China (early Eocene, early Miocene, middle Miocene) (Zhang 1989; Lapolla et al. 2013; Wang et al. 2021). Fossil Dolichoderinae are known from Myanmar (Perrichot 2019), and they are also distributed in Thailand nowadays (Jaitrong and Nabhitabhata 2005).

In Asia, fossil Orthoptera are reported from Iran (Oligocene) (Ataabadi et al. 2019), Kazakhstan (middle-late Jurassic), Japan (early Cretaceous) (Gu et al. 2010), China (Triassic, mid-late Jurassic) (Gorochov 2003; Gu et al. 2010; Xu et al. 2020) and South Korea (early Cretaceous) (Kim et al. 2021). In Southeast Asia, fossil Grylloidea are reported from Myanmar (middle-late Cretaceous) (Poinar et al. 2020; Yuan et al. 2022). Living Orthoptera, including Grylloidea, are very widespread in Thailand (Storozhenko and Dawwrueng 2015; Dawwrueng et al. 2017).

Water striders Gerrinae are quite rare in the fossil record. In Asia, they are reported from the Eocene to early Miocene of the Niubao Formation and Dingqing Formation in the Tibetan Plateau (Cai et al. 2019), which is probably the earliest unambiguous occurrence of gerrids in Asia. Nowadays, *Limnogonus* and *Limnometra* are found in Thailand (Ezra 2008; Jehamalar and Chandra 2013), both under tropical climate (Nummelin 1997; Damgaard et al. 2014).

Conclusion

The Wang Kaew insect assemblage is the most diverse Cenozoic entomofauna known so far in Thailand and Southeast Asia, with at least eight taxa reported herein. All these forms are referred to taxa currently represented in Thailand, indicating that they were already present during the Miocene. The diversity of diets, with herbivorous to predatory forms, also suggests a fertile paleoenvironment. According to the paleoenvironmental reconstructions based on palynology, the climate was subtropical to tropical in the Mae Sot basin during the Miocene (Songtham et al. 2003). A similar entomofauna with comparable environmental conditions highlights the stability of ecosystems in Thailand since the Neogene. Wang Kaew has a great potential for the study of the diversity of Cenozoic insects and the setting-up of Recent insect assemblages in Thailand and more generally in Southeast Asia.

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