Preheterobathmia gen. nov. – a new non-glossatan taxon from Myanmar amber tentatively assigned to Heterobathmiidae (Insecta, Lepidoptera)

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Abstract. The description of a new fossil taxon *Preheterobathmia grimaldii* **gen. nov. et sp. nov.** is provided from Myanmar amber. The new taxon is tentatively assigned to the extant family Heterobathmiidae based on corresponding architecture of the female genitalia. It displays an interesting mixture of plesiomorphies and apomorphies, which are discussed in a comparison between *Preheterobathmia* **gen. nov.** and *Heterobathmia*. The fossil provides new information to the phylogeny and historical biogeography of ancestral Lepidoptera.

Introduction

Among extant Lepidoptera, species of the families Micropterigidae, Agathiphagidae and Heterobathmiidae are regarded and classified as the most ancestral taxa of the order. They are taxonomically not united into a single group but represent separate clades at the base of the Lepidoptera cladogram of phylogenetic relationships (Kristensen 1998; Grimaldi and Engel 2005; Regier et al. 2015). A common feature of these families is the non-glossatan nature of the mouthparts of the adults, which stands in contrast to the presence of a glossa, or proboscis, in all other families of Lepidoptera, notwithstanding cases of reduction and secondary loss.

Among these three families, Micropterigidae had been the only one to which fossil species had been ascribed over many years of palaeoentomological research. Today, the family is well represented by numerous taxa from localities in North America, Europe and Asia dating back to the Jurassic, Cretaceous and Tertiary (e. g. Cockerell 1919; Rebel 1936; Whalley 1978; Kozlov 1989; Skalski 1995; Ansorge 2002; Grimaldi and Engel 2005; Mey 2011, 2019; Zhang et al. 2017). A synopsis of Micropterigidae fossils described until 2012 is available from Sohn et al. (2012).

Recently, the first fossil species belonging to Agathiphagidae was discovered and described from inclusions in Myanmar amber (Mey et al. 2021). This type of amber is also referred to as Burmese or Kachin amber (Ross 2021).

The present article provides the description of a new fossil taxon from the Heterobathmiidae clade, again from Myanmar amber, thus completing records of all three extant, non-glossatan families as fossils of Cretaceous age, all from the same locality in Myanmar.

The known range of the extant Heterobathmiidae is confined to the southern part of South America, in Chile and Argentina, and the family was considered therefore as endemic to temperate South America (Nielsen 1985; Holloway and Nielsen 1998). The discovery of the family in Myanmar amber provides new information concerning phylogenetic history and issues of historical biogeography among ancestral Lepidoptera.

Material and methods

The studied amber material was collected by local people in the Hukawng Valley of northern Myanmar (Myitkyina District, Kachin State) and derives from an amber-bearing layer, which is not exposed at the surface, but extends to a depth of 2–15 m (Cruickshank and Ko 2003).

The age given by UPb dating of zircons from the volcanoclastic matrix of such amber is early Cenomanian (98.8 ± 0.6 million years) (Shi et al. 2012).

The fossil specimen is embedded in a small, flattened and polished amber piece cut out from a larger Myanmar amber block. Photos were taken using a Leica stereomicroscope M 420 Apozoom in combination with a Canon EOS 600D, EOS utility software and the Zerene Stacker software or were taken by the digital microscope Keyence VHX-900F.

The fossil was examined under incident and transmitted light using a stereomicroscope (Leica MZ125). Line drawings were produced with an attached drawing tube, and digitally processed using Adobe Photoshop CS4. Measurements were made with the ocular micrometer of the stereomicroscope.

The terminology used in the descriptions of the new taxa largely follows Kristensen (1984, 1998).

Systematic palaeontology

Order Lepidoptera Linnaeus, 1758
Suborder Heterobathmiina Kristensen & Nielsen, 1983
Superfamily Heterobathmioidea Nielsen, 1985
Family Heterobathmiidae Kristensen & Nielsen, 1983

Preheterobathmia gen. nov.

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Gender. feminine, type species: *P. grimaldii* sp. nov.

Etymology. composite noun, with the prefix “pre”, before, and the genus name *Heterobathmia*, referring to the more ancient status of the new genus.

Diagnosis. Head with ocelli and large labrum, epiphysis present, spur formula 0.4.4., wings densely covered by scales, forewing venation with SC apically forked, R1 simple, crossvein sc-r absent, pterostigma absent, radial branches from areole, M 3 branched, anal loop present; hindwing venation with median cell present; female genitalia without oviscapt, genital segment IX triangular, with genital orifice located in a depression on venter IX.

The new genus differs from *Heterobathmia* Kristensen & Nielsen, 1979 especially by the larger wing index, by two pairs of spurs of the mid-tibia versus only one pair in *Heterobathmia*, SC of forewing apically forked into SC1 and SC2 versus being un-forked apically and a lacking pterostigma. These characters, representing an ancestral state in *Preheterobathmia*, corroborate the notion of a more ancestral nature of the new genus in comparison with *Heterobathmia* (see Table 1).

Preheterobathmia gen. nov. is tentatively assigned to Heterobathmiidae mainly on the basis of the corresponding genitalia architecture of the female, which is unique for the family and very different from those of females in Micropterigidae, Agathiphagidae and basal Glossata as explained in detail by Kristensen (2003: 114).

Description. see description of *P. grimaldii* sp. nov. below.

Preheterobathmia grimaldii sp. nov.

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Figs 1a–d, 2–7

Material. ***Holotype***, female, Burmese Amber, deposited in NIGP – Nanjing Institute of Geology and Palaeontology, Nanjing, P. R. China; inventory number: NIGP 203445.

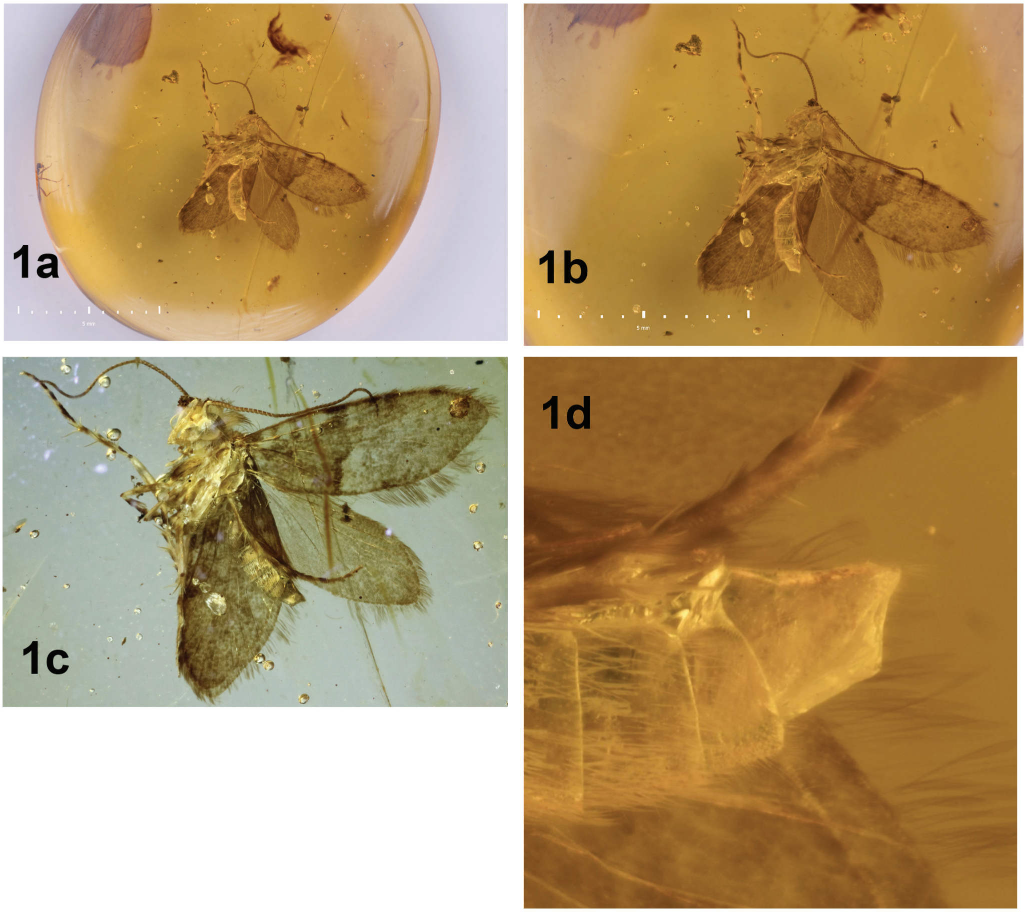
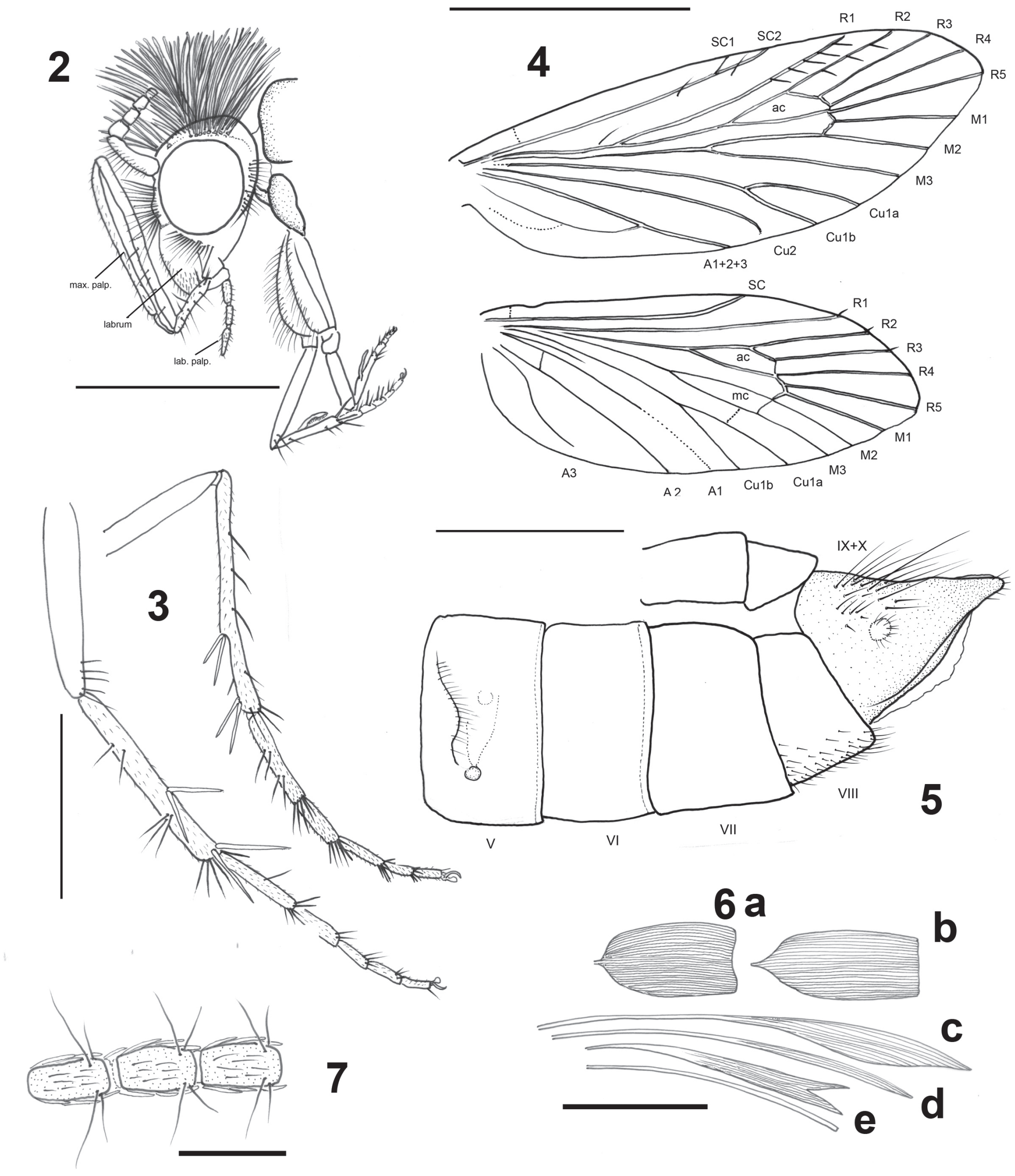


Figure 1. Female holotype of *Preheterobathmia grimaldii* sp. nov. **a.** Amber piece with inclusion of *Preheterobathmia* gen. nov.; **b, c.** Moth in lateral position under different illumination; **d.** Close-up of abdominal tip with female genitalia.



Figures 2–7. *Preheterobathmia grimaldii* sp. nov., female. **2.** Head; **3.** Middle and hind leg; **4.** Wings; **5.** Abdomen with genital segments in lateral view; **6.** Scales of forewing; **a, b.** At membrane; **c, d.** Termen margin; **e.** Costal fringe; **7.** Flagellomeres from the middle section of antenna, ventral view. Scale bars: 2 mm (**4**); 1 mm (**1**); 0.5 mm (**3, 5**); 0.1 mm (**7**); 0.05 mm (**6**).

Preservation. The fossil is embedded in a flattened, oval piece of amber (length: 17 mm) (Fig. 1a). This female is completely preserved, but in a position with the right wings overlapping and covering the body (Fig. 1b, c) on the side illustrated. Head, thorax and abdomen are only visible in lateral view. Small organic particles and several air bubbles are present in the amber matrix as well as close to the head and between the legs.

Etymology. The specific epithet is dedicated to D.A. Grimaldi for his important contributions to palaeoentomology.

Description. Female: Length of body 4.0 mm, forewings 4.2 mm; head vertex with tuft of erected, piliform scales directed dorsad and frontad; erected hairs on lateral sides of frons and subgenae below eyes; eyes rounded, hemispherical; ocelli very small; labrum large and broad, apical portion densely covered by small hairs; maxillary palpi of the micropterigid type, basal segment with long hairs, second and third segment of equal length, without intersegmental membrane, fourth segment longest, terminal segment short; labial palpi not reduced, three-segmented, final segment acute at apex; antenna long, ¾ of wing length, with 44 flagellomeres, dorsally covered by lamellar scales, ventral side with short hairs and at least one pair of long, spreading setae (Fig. 7); legs with spur formula 0.4.4.; forelegs with epiphysis, carrying a comb of small denticles at its ventral blade, spines of different strength present on tibia and tarsal segments of all leg pairs (Figs 2, 3).

Wings and venation (Fig. 4): Both wings broad, densely covered by overlapping scales, producing a pattern of darker and paler patches, scales on membrane sub-quadrangular and with apical margins obtuse (Fig. 6), without indentations, scales of wing margin elongate, club-shaped and acute at apex (unidentate), scattered piliform, erected scales present at veins and membrane on both wings; hindwing scaling similar to forewing; jugum in both wings apparently absent. Forewing C with long bristles at the basal lower surface, SC apically forked, R1 simple, cross-veins sc-r and r1-r2 absent, pterostigma absent, all radial veins free from accessory cell (= aureole), M 3-branched, Cu2 atrophied before wing margin, anal veins (A1+2+3) with long basal loop. Hindwing with SC and R1 unforked, without cross-veins, R branches not stalked, M with three branches emanating from long median cell, weak m-cu present, Cu2 present as short vein at the base, anal veins thin, A1 and A2 connected by cross-vein.

Abdomen with elongate scales in horizontal position on sternites (Fig. 1d), sternum V with small pad-like elevation and surface modification; segment VIII separated into sternum and tergum, the former slightly overlapping with the ventral part of segment IX in the female.

Female genitalia (Figs 1d, 5): Segment IX large, with triangular shape in lateral view, tapering distally to small lobes, not separated from segment IX, surface devoid of scales but vestiture of small and long setae present on dorsal, lateral and apical sides, in central position a small protuberance with short setae; gonopore and anus (or of a cloaca?) on ventral side of segment IX in a narrow, elongate depression laterally bordered by membranous walls.

Discussion

Phylogeny and systematics

When only the wings, head and legs of the given individual are available for study, which is often the case in the study of compression fossils, the species cannot be keyed out as belonging to Heterobathmiidae. Even when disregarding spur formulas, such species would run in the identification key of Carter and Kristensen (1998) and Zhang et al. (2013) to Micropterigidae. Only the visibility of the female genitalia revealed a genuine relationship of the present fossil with Heterobathmiidae.

Zhang et al. (2022) presented a cladogram of the phylogenetic relationships of basal Lepidoptera lineages. The extinct Jurassic families Ascololepidopterigidae, Eolepidopterigidae and Mesokristenseniidae were included and grouped together with Micropterigidae into a joint clade, with the remaining Lepidoptera as sister group. This is an interesting idea but has the disadvantage of not being supported by any synapomorphy indicated in the cladogram. The Jurassic families were established by characters of the wing venation, spur numbers of the legs and the presence of long apophyses in the female genitalia. The latter character is a very prominent feature clearly visible in the respective compression fossils. This character, however, has been considered as synapomorphy of the amphiesmenopteran clade (Kristensen 1984, 1998). Elongate apophyses in the female genitalia are absent in Heterobathmiidae.

The family Heterobathmiidae was established first as a subfamily in Micropterigidae (Kristensen and Nielsen 1979) and later, based on the study of immature stages, raised to a family of its own (Kristensen and Nielsen 1983). Five species have been described to date (Hünefeld and Kristensen 2012) and further five species await description (Humphries et al. 1986). The family was defined by 10 autapomorphies and 10 further characters of uncertain status. Most of these characters are unobservable in the amber inclusion containing *Preheterobathmia grimaldii* sp. nov. However, some of the external characters of the head, legs, wings, and abdomen (1–5) are clearly visible and can be compared with *Heterobathmia*. Further characters of the groundplan of Amphiesmenoptera (6–10) and Lepidoptera (11–13), or ones of ambiguous interpretation (14–17), can be added in a meaningful comparison of both genera (Table 1):

Table 1. Comparison of morphological characters visible from the amber individual of *Preheterobathmia* gen. nov. with *Heterobathmia pseuderiocrania* Kristensen & Nielsen, 1979.

character	*Heterobathmia*	*Preheterobathmia*
1. Forewing SC	simple	forked
2. Forewing R1 simple	simple	simple
3. Forewing sc-r absent	absent	absent
4. A1 with basal fork	present	absent
5. Female genitalia oviscapt	absent	absent
6. Forewing pterostigma	present	absent
7. Forewing median cell	present	absent
8. Forewing cu1-cu2	present	absent
9. Jugum	present	absent
10. Spurs	0.2.4	0.4.4
11. Scaling on fore- and hindwings	different	similar
12. Forewing M1 with angulate base	present	present
13. Labial palpi	reduced	long
14. Maxillary palpi	scaled	unscaled
15. Nr. of flagellomeres of antenna	26	44
16. R4 and R5 in both wings	forked	simple
17. Wing index (forewings/hindwing)	0.26/0.27	0.34/0.4

The new taxon thus displays an interesting mixture of plesiomorphies and apomorphies. Interestingly, extant *Heterobathmia* exhibits characters in the plesiomorphic state, which are apomorphic in *Preheterobathmia* gen. nov. These are the wing characters 6–9 in Table 1, which can be considered as autapomorphies of the new fossil taxon. The absence of the forewing pterostigma in *Preheterobathmia* gen. nov. and its presence in *Heterobathmia* is another notable observation. It does not support an interpretation of the pterostigma as an amphiesmenopteran or Lepidoptera ground-plan character, but seems instead to be a neoformation, which also occurs as a parallelism in some lower-grade Microlepidoptera families. As expected, the majority of characters for

Preheterobathmia listed in Table 1 represent the plesiomorphic state. Striking examples are the long labial palpi, the spur formula, the forked SC in the forewings, separate R4 and R5 veins in both wing pairs and the high number of flagellomeres. Another wing character that further corroborates the ancestry of the new genus is the wing index of Kristensen (1979) (No.17 in Table 1). The low index in *Heterobathmia* might be connected to the biology of its species as leaf-miners. From the primitive glossatan families, species of Acanthopteroctetidae are leaf-miners and have a similarly small wing index. There are many families with endophytic larvae mining in leaves, stems, twigs, etc. They are usually small-sized species with minute adults possessing narrow wings. If the small wing index of *Heterobathmia* is the apomorphic state, the broader wings of *Preheterobathmia* gen. nov. might be interpreted as a plesiomorphic character, that is perhaps not correlated with a leaf-mining habit. If this interpretation is correct, *Preheterobathmia* gen. nov. may have lived at a time (in the Middle Cretaceous) before the transition from a soil-dwelling to a leaf-mining lifestyle began.

Regarding the presence of apomorphic characters in *Preheterobathmia* gen. nov., which are in the plesiomorphic state in extant *Heterobathmia*, the latter cannot be derived from the former. The morphological differences of both genera are significant, but in my opinion not sufficiently divergent to establish a new family for the new fossil genus.

Historical biogeography

The presently known distribution of extant Heterobathmiidae lies at a latitude of between 39° and 43° south and an elevation of 600–1400 m on both sides of the Andes, in Chile and Argentina (Fig. 8). Their larvae develop as leaf miners on deciduous species of *Nothofagus* (Fagales), Southern Beeches. Since a related, deciduous *Nothofagus* species occurs in Tasmania, Kristensen and Nielsen (1983) discussed a possible occurrence of Heterobathmiidae in Tasmania. The family, however, was not recorded from there so far.

The discovery of the fossil *Preheterobathmia* gen. nov. from Myanmar amber is a somewhat unexpected finding. It may be evidence of a wider ancestral distribution of the family on the globe, challenging the Neotropical origin and status of the family as a Neotropical endemic. In the discussion on the historical biogeography of Agathiphagidae and Lophocoronidae, several hypotheses were provided as explanations for the disjunct distribution pattern (Mey et al. 2021). The present case is a similar example inasmuch as fossil and extant taxa need to be combined. However, perhaps it is not necessary to invoke moving continents, shifting terrane or long-distance dispersal. Molecular clock data indicate that the origin and first separation of basal clades in Lepidoptera occurred in the Late Triassic (Wahlberg et al. 2013) or much earlier in the Permian (Kawahara et al. 2019). However, inference of such an early origin long prior to their first appearance in the fossil record was questioned by Schachat et al. (2022). Pangaea began to separate at about 180 Ma ago (McIntyre et al. 2017), at a time, when the species of the basal-most clades of Lepidoptera must have already been dispersed across Pangaea. The worldwide distribution of extant Micropterigidae as observed today by taxa described from all continents (except Antarctica) and from continental terranes might be explained as an echo of this ancient, Pangaean range of the family. Regarding the locality of *Preheterobathmia* gen. nov. in Asia and the age of the group, a similar, Pangaean range could be envisaged for Heterobathmiidae too. Interestingly, the disjunct distribution pattern of Heterobathmiidae caused by integrating fossil and extant species, is paralleled by the range of the extant species of Neopseustidae (Fig. 9). At about 140 Ma, the estimated age of this homoneuran

Figure 8. Distribution of Heterobathmiidae, with the range of extant species in South America and the locality of fossil species in Myanmar in south-east Asia.

Figure 9. Distribution of Neopseustidae, with disjunct ranges in South America and Asia.

family is younger and has its origin in the Upper Jurassic (Wahlberg et al. 2013), after the breakup of Pangaea. Therefore, an ancient, Pangaean distribution cannot be ascribed to the family. Obviously, the formation of the disjunct, intercontinental range of Neopseustidae is the result of processes, which happened after the break-up of Pangaea. These processes almost certainly had an effect on the distribution of Heterobathmiidae as well, providing an alternative interpretation of the present-day range of Heterobathmiidae.

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