



## A new genus and first Cenozoic fossil record of moth lacewings (Neuroptera: Ithonidae) from the Early Eocene of North America

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### Abstract

A new genus and species *Allorapisma chuorum* **gen. sp. nov.** is described from the Early Eocene locality at Republic, Washington, U.S.A. The forewing venation of *Allorapisma* is most similar to that of the genus *Principiala* Makarkin & Menon from the Early Cretaceous of Brazil and Britain. A new, informal suprageneric taxon consisting of these genera is proposed, the *Principiala* group. The habitats of extant and fossil Ithonidae are briefly discussed.

**Key words:** Ithonidae, Eocene, Okanagan Highlands

### Introduction

The family Ithonidae is traditionally considered to be among the most primitive within the order. Today, it consists of 35 named species in seven genera (Tillyard 1919; Riek 1974; Barnard 1981; Yang 1993; Penny 1996), discontinuously distributed globally (Fig. 1). Their larvae are thought to be saprophagous or phytophagous-succivorous (Gallard 1932; Faulkner 1990a, b; Oswald *et al.* 2002), whereas those of other neuropterans are known to be predaceous, with the possible exception of Polystoechotidae. It has been suspected that the family is relictual, although the first fossil ithonid was only recently described, *Principiala incerta* Makarkin & Menon from the Early Cretaceous of the Crato Formation of Brazil (Makarkin & Menon 2007). Some features of wing venation found in *P. incerta* are quite different from those of extant taxa, however, it is confidently placed in the family based on a set of distinctive head and thorax characters (*e.g.*, very short antennae; large, shield-like pronotum; head almost entirely retracted under pronotum), together with other wing character states. Another species of *Principiala* was recently discovered in the British Early Cretaceous Upper Weald Clays (Jepson *et al.*, submitted). The discovery reported here of two specimens from the Early Eocene of North America (Republic, Washington, U.S.A.) with venation similar to that of *Principiala* is noteworthy. Below, we describe a new genus and species based on these specimens, and discuss its systematic position within the family and the habitats of ithonids (extant and fossil).

### Material and methods

The specimens described here are from exposures of the Tom Thumb Tuff Member of the Klondike Mountain Formation in town of Republic, Ferry County, in northeastern Washington (USA), assigned a date of  $49.42 \pm 0.54$  Ma, *i.e.*, Early Eocene (Ypresian) (Greenwood *et al.* 2005; Moss *et al.* 2005).

We follow the traditional (*sensu* Wootton 2003) venational terminology of Comstock (1918) in the recent interpretation of Oswald (1993), Makarkin & Menon (2005), Archibald & Makarkin (2006), and Wedmann &

Makarkin (2007). Venation abbreviations: 1A–3A, anal veins; C, costa; CuA, anterior cubitus; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media (M); R1, first branch of radius (R); Rs, radial sector; Rs1, most proximal branch of Rs; Sc, subcosta.

Institutional abbreviations: SRIC, Stonerose Interpretive Center, Republic, Washington (U.S.A.).



**FIGURE 1.** Distribution of extant and fossil Ithonidae. Circles indicate extant genera: A, *Adamsiana*; O, *Oliarces*; N, *Narodona*; ?, unknown genus; R, *Rapisma*; I, *Ithone*; V, *Varnia*; M, *Megalithone*; squares indicate fossil genera: A, *Allorapisma* (Early Eocene); P, *Principiala* (Early Cretaceous).

## Systematic paleontology

### Insecta Linnaeus, 1758

### Neuroptera Linnaeus, 1758

### Ithonidae Newman, 1853

### Genus *Allorapisma* gen. nov.

**Etymology.** Allo- (from the Greek *allo*, other) + *-rapisma* (from *Rapisma*, a genus-group name), in reference to its venational similarity to the genus *Rapisma* Navás. Gender neuter.

**Type species.** *Allorapisma chuorum* sp. nov.

**Included species.** The type species only.

**Diagnosis.** Forewing separable from those of all other ithonid genera except *Principiala* by proximal branches of Rs short, appear fused with MA; from *Principiala* by R1 space (between R1, Rs), much wider than subcostal space [contrary in *Principiala*] and costal gradate series of crossveins represented by few basal crossveins located near costal margin [extended to at least mid-point of costal space, located far from costal margin in *Principiala*].

**Remarks.** Some character states found in *Allorapisma* are of considerable interest.

The proximal branches of Rs are short and appear to fuse with MA. Within the family, this has been previously only found in the Cretaceous genus *Principiala* Makarkin & Menon (Makarkin & Menon 2007:

Fig. 5A). This feature is also found in the vast majority of Chrysopidae (*i.e.*, all Chrysopinae, Apochrysininae, and some Nothochrysininae, but absent in Mesozoic Lamiinae), and possibly in the psychopoid genus *Hongosmylites* Makarkin & Archibald, 2005. It appears clear that this condition is convergent among these three phylogenetically distant taxa, *i.e.*, Ithonidae, Chrysopidae, and Psychopsoidea.

MA and MP are completely separated, with MA originating from R. This condition has been reported to occur very rarely within the order, and it is currently unclear if any of these cases may withstand close scrutiny. Makarkin and Menon (2007) considered M to be divided into MA and MP near the forewing base in *Principiala incerta*. Here we revise this interpretation. *P. incerta* is known from two specimens; in both, this region is somewhat obscured by the frenulum of the hind wing. Despite this, it can be confidently determined that in the forewing of the holotype of *P. incerta*, MA and MP indeed approach each other toward the wing base and it's possible that they might have a common stem of M. In the paratype, however, MA appears to originate from R, *i.e.*, MA is separated from MP (Makarkin & Menon 2007: as seen in the photograph of basal portions of the wings in Makarkin & Menon 2007: Fig. 2B; the forewing was incompletely drawn in Makarkin & Menon 2007: Fig. 5A). Therefore, it should be considered that this character state may be variable in this species. Most Australian Ithonidae and some Eurasian Dilaridae (*i.e.*, the majority of species of *Dilar* Rambur) possess a superficially similar vein configuration in this area. In these taxa, one to three branches of what might appear to be MA also originate from R basal to the origin of Rs; here, we interpret these confidently as branches of Rs, as indicated of the location of the distal nygma, which in these families is always situated between the two most proximal branches of Rs (*e.g.*, New 1991: Fig. 34.7A, for Ithonidae; Monserrat 1988: Fig. 13–17, for Dilaridae).

The basal fusion of MP and Cu is unique within the Neuroptera. If this is a consistent character state within the species and not an individual anomaly of the holotype (this part of the wing is missing from the paratype), it is unquestionably a significant autapomorphy.

The strong concavity of MA is unusual in hemerobiiform Neuroptera; it is a condition more characteristic of psychopoids (*e.g.*, Kalligrammatidae, Osmylopsychopidae) and myrmelentoids (*e.g.*, Palaeoleontidae) (Menon & Makarkin 2008).

### ***Allorapisma chuorum* sp. nov.**

Figs. 2–3

**Etymology.** The specific epithet is formed from the surname of the Chu family of Kirkland, Washington (see Acknowledgements), the collectors of the holotype, in recognition of their generous contribution to science in the donation of this specimen.

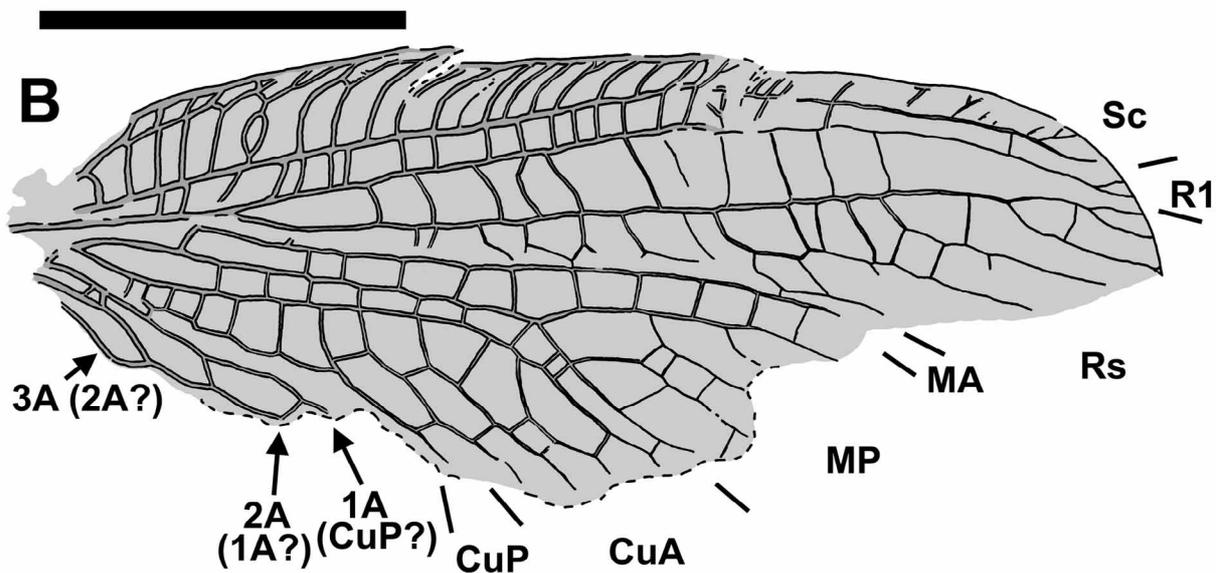
**Holotype.** Specimen SR 08-14-01 (part only), collected on June 23, 2007 by the Chu family at the Boot Hill exposure B4131, and deposited in SRIC. A nearly complete, beautifully preserved forewing (probably left).

**Paratype.** Specimen SRUI 08-04-01 (part only), collected on July 15, 2007 by Karl Volkman at the Corner Lot exposure A0307, and deposited in SRIC. A nearly complete, beautifully preserved forewing (probably right).

**Type locality and horizon.** Tom Thumb Tuff Member of the Klondike Mountain Formation, Republic, Washington, U.S.A.; Early Eocene.

**Diagnosis.** As for genus.

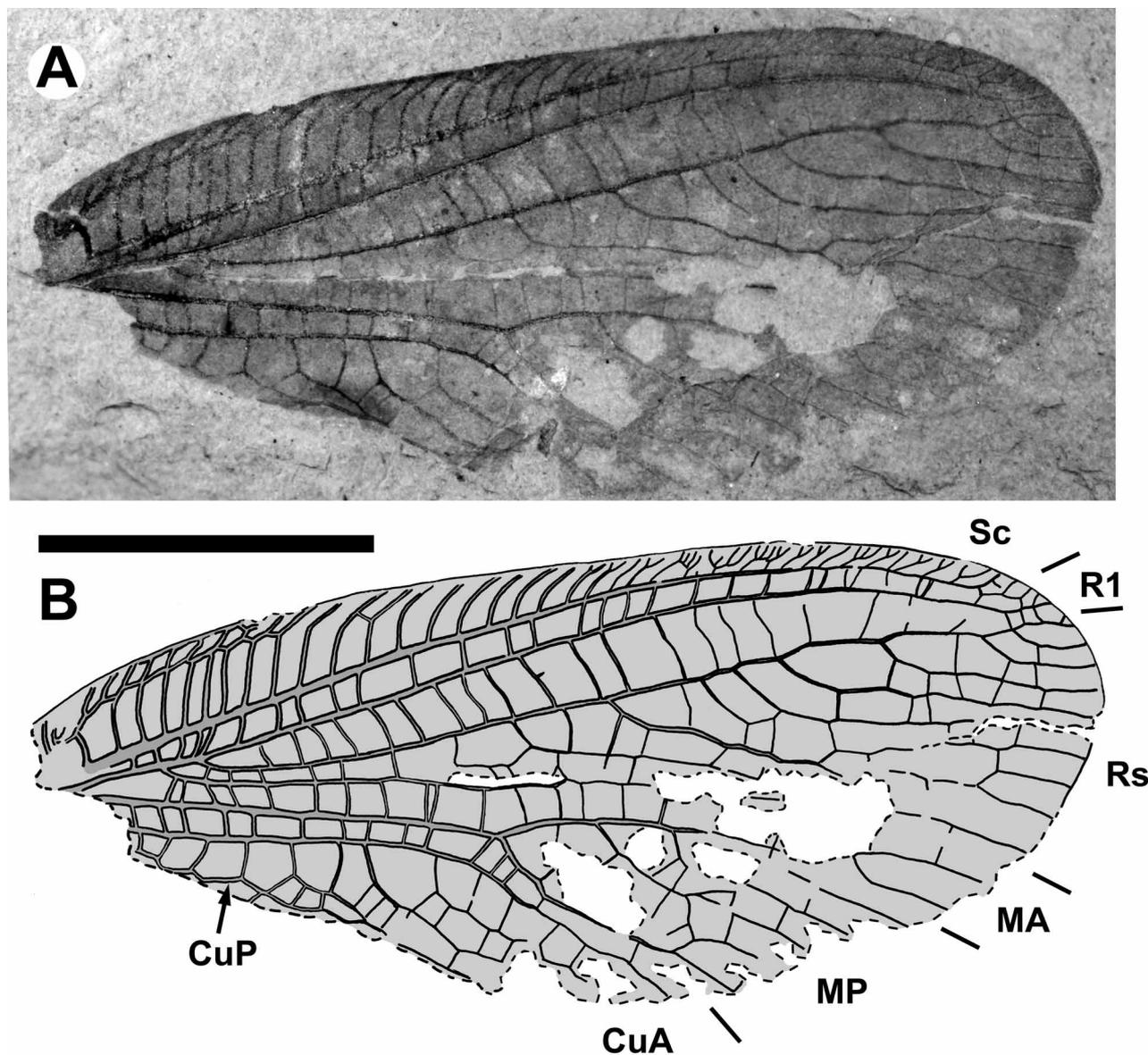
**Description of the holotype.** Forewing oval, with rounded apex, approximately 16 mm long, 6.2–6.3 mm wide. Trichosors, nygmata not detected. Costal space moderately expanded basally (1.3 mm maximum width), narrowed apically. Subcostal veinlets closely spaced, mostly simple proximally (one anomalous, with loop-like doubling), forked distally; slightly oblique, strongly bent towards apex near C in basal portion of costal space, more strongly oblique in its apical portion. Humeral veinlet well-developed, incompletely preserved. Costal gradate series represented by few crossveins in basal part of wing, parallel with, close to



**FIGURE 2.** *Allorapisma chuorum* gen. et sp. nov., holotype specimen SR 08-14-01. **A**, photograph. **B**, drawing of the forewing. Scale bar = 5 mm.

costal wing margin. Sc thick in proximal half, not fused with R1 distally. R1 with marginal fork only, entering margin before wing apex. Subcostal space rather broad for entire length except basally; numerous (approximately 22 as preserved), more or less regularly spaced crossveins. R1 space (between R1, Rs) very broad medially, maximum width approximately as broad as basal portion of costal space (1.1–1.2 mm); several crossveins, mainly in medial portion. Rs originating at acute angle relatively far from wing base, smooth, not zigzagged for almost entire length, only slightly zigzagged in distal portion, entering margin before wing apex; proximal branches short, irregular, fused with MA; four distal branches free, connected by few crossveins. MA, MP separated. MA fused with R basally, strongly concave, originating near origin of Rs, entering wing margin well distad mid-point. Oblique, strongly concave crossvein (basal part of MA?) between MA, MP. MP basally not fused with R, stout, with peculiar configuration distally: both branches of primary fork at equal angle to stem; anterior branch with posteriorly directed pectination, posterior branch with anteriorly directed pectination. MP, Cu convergent towards wing base, appear fused. CuA stout in proximal half, running nearly parallel to MP for most part, then to posterior branch of MP, with four pectinate branches connected by several crossveins. Origin of CuP poorly visible as preserved; CuP poorly developed, much thinner than CuA, connected with it by five crossveins, fused distally with most proximal branch of CuA

[alternatively, apparent 'CuP' a false vein formed by several aligned crossveins between branches of CuA (if so, short, fused with CuP)]. Several crossveins between MA, MP; MP, CuA. 1A [alternatively, CuP] long, with few branches. 2A [alternatively, 1A] rather short, simple, connected with 1A [alternatively, CuP] by two short crossvein basally, by long oblique crossvein distally. 3A [alternatively, 2A] simple, appears fused distally with 2A [alternatively, connected by long oblique crossvein]. Jugal lobe not detected as preserved. Wing membrane tinged with brown to dark brown.



**FIGURE 3.** *Allorapisma chuorum* gen. et sp. nov., paratype specimen SRUI 08-04-01. **A**, photograph. **B**, drawing of the forewing. Scale bar = 5 mm.

**Description of the paratype.** Forewing oval, with rounded apex, approximately 16.5 mm long, 6.3 mm wide (hind wing margin poorly preserved). Trichosors, nygmata not detected. Costal space moderately expanded basally (1.3 mm maximum width), narrowed apically. Subcostal veinlets closely spaced, simple proximally, forked distally; slightly oblique, strongly bent towards apex near C in basal portion of costal space, apical portion more strongly oblique. Humeral veinlet well-developed, with three branches. Costal gradate series represented by few crossveins in basal part of wing; running parallel, close to costal wing margin. Sc thick in proximal 1/3, not fused with R1 distally. R1 with shallow marginal fork, short distal forked

branch, terminating on margin before wing apex. Subcostal space rather broad for entire length except basally; numerous (approximately 30), more or less regularly spaced crossveins. R1 space very broad medially, maximum width approximately as broad as basal portion of costal space (1.1 mm); many crossveins in proximal half, lesser crossveins in distal half. Rs originating at acute angle relatively far from wing base, smooth, lacking any zigzag features for almost entire length, entering margin before wing apex. Six proximal branches [alternatively, crossveins] short, fused with MA; next two branches much longer, sinuate, fused with MA; distal seven branches free, irregular, simple (except for one branch with deep branching, another represented only as basal portion), connected by crossveins, not forming regular gradate series. M represented by separate MA, MP. MA fused with R basally, strongly concave, simple, reaching wing margin well after mid-point. MP not fused with R basally, peculiarly configured distally: both branches of primary fork at equal angle to stem; anterior branch with posteriorly directed pectination, posterior branch with anteriorly directed branch (incompletely preserved). Fork of Cu not preserved. CuA stout proximally, running nearly parallel to MP, then posterior branch of MP, with three pectinate branches connecting with several irregularly arranged crossveins. Several crossveins between MA, MP; MP, CuA. CuP, anal veins, jugal lobe not detected as preserved. Wing membrane tinged with dark brown.

**Remarks.** The apparent absence of trichosors and nygmata in this species is possibly an artefact. In the forewing of extant *Rapisma* species, these characters are poorly developed and often not clearly discernible.

## Discussion

### Systematic position of *Allorapisma*

Makarkin and Menon (2007) discussed the relationships of extant genera within the Ithonidae, establishing three groups: (1) the presumably monophyletic *Ithone* group (*Ithone* Newman, *Megalithone* Riek and *Varnia* Walker), (2) the *Rapisma* group (*Rapisma*) and (3) a possibly paraphyletic group consisting of *Narodona* Navás, *Adamsiana* Penny and *Oliarces* Banks, whose relationship with other genera is not clear. The forewing venation of *Allorapisma* is most similar to that of another fossil genus, *Principiala* Makarkin & Menon, particularly in the following shared features: the proximal branches of Rs are fused with MA; MA is simple; the peculiar configuration of MP (anteriorly curved at its primary fork, so that both branches of the primary fork of MP appear running at an equal angle to the proximal stem of MP); and CuA running close and parallel to MP and the most proximal branch of MP. These features suggest the establishment of a new informal suprageneric taxon, the *Principiala* group, consisting of *Principiala* and *Allorapisma*. The *Principiala* group seems most closely related to the *Rapisma* group by the following shared venational characters, distinctive within the Ithonidae: numerous subcostal crossveins and more or less regular costal gradate series of crossveins.

### The habitat of extant and fossil Ithonidae

Extant ithonids inhabit regions with a wide variety of climates. They may be generally divided into forest and arid region genera. The Australian *Ithone*, *Varnia*, and the southwestern North American *Oliarces* occur predominantly in arid, sandy areas (Tillyard 1919, 1922; Riek 1974; Faulkner 1990a; New 1991). *Megalithone* occurs mainly in high altitude areas of Queensland and New South Wales (New 1991), but its precise habitat is unknown. The forest-dwelling genera *Rapisma*, *Adamsiana*, and *Narodona* occur mainly in subtropical and tropical mountains. Species of *Rapisma* live in moderately high altitude (900–2595 m) forests of the Oriental Region (Barnard 1981; Barnard & New 1985, 1986; New 1985; Yang 1993). The single known species of *Adamsiana* has been found in the primary mixed tropical cloud forest at an elevation of 1900 m in the Cordillera del Merendo'n Range of Honduras (Penny 1996); this species (or an undescribed related species) has been collected in Guatemala (environment not reported) (Oswald *et al.* 2002). *Narodona* is known from a single specimen collected in a forested mountain region of Pacific coastal Mexico at Colima (Navás 1930). Another possible Mexican species is known only from larvae reared from the eggs collected in

Chiapas. These eggs were laid on the fronds of the palm genus *Chamaeodora*, growing mainly in the rainforest understory (Faulkner 1990a; O. Flint, pers. comm.; this larva was described by Grebennikov 2004 as “Polystoechotidae sp.”).

Fossil Ithonidae appear to be found in subsets of this broad climatic range. Paleoclimate modelling for the Early Cretaceous (Bareman) habitat of the Wealden *Principiala* sp. indicates seasonal temperatures there similar to that found in parts of the modern southern Mediterranean, and likely high, year round precipitation (Haywood *et al.* 2004). The overall insect assemblage is consistent with this characterization, and also with a wetland habitat surrounded by woods and glades (Jarzembowski 1995).

Equatorial regions were drier during the Cretaceous, likely with xeromorphic vegetation and patchy forests (Crane & Lidgard 1989, Wing *et al.* 1992; Spicer *et al.* 1993). The habitat of the Early Cretaceous (Aptian) Brazilian species *Principiala incerta* was assumed by Makarkin & Menon (2007) to have been a warm, humid tropical forest surrounding the Crato lagoon/lake based on the habitats of the nearest living relatives of some insects found there. However, other elements of the arthropod assemblage of the Crato Formation (Martins-Neto 2006; Menon 2007; Martill *et al.* 2008) indicate a dry, open environment. Various indicators suggest aridity for at least part of the surrounding region, or for some portion of Crato time (da Silva 1986; Grimaldi & Maisey 1990; Batten 2008).

The Early Eocene Republic environment of *A. chuorum* was an upland forest similar in ways to the modern North American eastern deciduous zone, with a climate suggested by paleobotanical indicators to have been mesic and cool, yet with mild winters (Greenwood *et al.* 2005). Insects and plants associated today with cool higher latitudes coexisted there with warm low latitude taxa, which were presumably not excluded by the severe winters; this biotic mixture may be found today in tropical uplands, *e.g.*, mountainous regions of tropical Mexico (Archibald & Farrell 2003; Greenwood *et al.* 2005; Moss *et al.* 2005; references therein).

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