First record of fossil 'rapismatid-like' Ithonidae (Insecta, Neuroptera) from the Lower Cretaceous Crato Formation of Brazil

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Abstract

A new genus and species, *Principiala incerta*, is described from the Nova Olinda Member of the Crato Formation (Aptian, Lower Cretaceous) in northeast Brazil. The systematic position of *Principiala* is discussed, and is interpreted to be most closely associated with "rapismatid-like" Ithonidae based on a set of head, thorax, and wing character states (i.e., very short antennae; large, shield-like pronotum; head almost entirely retracted under pronotum; dilated costal space basally, with numerous crossveins; numerous subcostal crossveins). The previously proposed synonymy of Ithonidae and Rapismatidae is discussed and provisionally confirmed.
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1. Introduction

The families Ithonidae and Rapismatidae appear to be the most "primitive" within Neuroptera, but hitherto had no fossil record. The extant genus *Rapisma* McLachlan (Rapismatidae) was erroneously placed in the Mesozoic Brongniartiellidae by Riek (1974), based on the assumption of a long geological history. Ithonidae were considered to be the sister group of the rest of the order (Tillyard, 1919; Withycombe, 1925). Their phylogenetic position was revised recently, and the taxon Ithonidae + Polystoechotidae is now treated as basal in the suborder Hemerobiiformia (Aspöck, 1992, 2001; Aspöck et al., 2001; Haring and Aspöck, 2004; Grimaldi and Engel, 2005).

The earliest occurrence (including stem-group) of the Ithonidae is estimated to be early Permian (Labandeira and Phillips, 1996). However, undescribed "ithonid-like" and "rapismatid-like" species are known only from the Middle

Jurassic of China (D. Ren, pers. comm. 2006). Ponomarenko (2002) implied that the Early Cretaceous *Mesomantispa siribica* Makarkin, 1997 could belong to the Ithonidae, but an additional, more complete specimen of this species confirms an affinity with the Mantispidae (Wedmann and Makarkin, 2007). In this paper we describe the new genus and species *Principiala incerta* based on two specimens from the Early Cretaceous Crato Formation of northeast Brazil, and interpret it as most closely associated with the Rapismatidae. This family is considered a synonym of the Ithonidae by many authors (e.g., Penny, 1996; Makarkin and Archibald, 2003; Grimaldi and Engel, 2005) and this view is supported here. We discuss this synonymy and the systematic position of *Principiala* within the Ithonidae.

2. Material and methods

The two specimens described here come from the Nova Olinda Member, which is the lowest member of the Crato Formation and consists of a succession of finely laminated limestones deposited in the bottom anoxic waters of a hypersaline lagoon during the late Aptian (Martill, 1993 and pers. comm.

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2006). The specimens examined are preserved in slabs of typical laminated limestone; they are housed in the palaeontology collections of the Staatlisches Museum für Naturkunde, Karlsruhe (SMNK) and the Staatliches Museum für Naturkunde, Stuttgart (SMNS) in Germany. Their exact provenance is unknown, but they were probably recovered from one of the stone quarries around the town of Nova Olinda (Ceará State). Preparation was carried out in the host museums. Photographs were taken with a D1X digital camera and drawings were produced using a camera lucida attached to an Olympus SZH Stereomicroscope. All wings in the drawings are shown with the apex to the right, as is standard. Two females of extant *Ithone fusca* Newman from Australia were examined for comparison. The terminology of male and female genital sclerites follows Adams (1969) and Oswald (1998) respectively. Wing nomenclature and abbreviations used in the text and figures are as follows: 1A–3A, anal veins; Cu, cubitus; CuA, anterior cubitus; CuP, posterior cubitus; f, frenulum; M, media; MA, anterior branch of media; MP, posterior branch of media; R, radius; R1, first branch of radius; Rs, radial sector; Sc, subcosta.

3. Systematic palaeontology

Order: Neuroptera Linnaeus, 1758
Family: Ithonidae Newman, 1853 (syn. Rapismatidae Krüger, 1922)
Genus *Principiala* gen. nov.

Derivation of name. After Prof. Dr. Maria Matilde Principi, eminent Italian entomologist, and Latin, *ala*, wing. Gender feminine.

Type species. *Principiala incerta* sp. nov.

Diagnosis. Antennae very short, 0.11–0.13 of forewing length (1). Forewing with regular complete costal gradate series of crossveins (2); subcostal crossveins numerous, not regularly spaced (3); R1 space very narrow in proximal portion, much narrower than subcostal space; most proximal branches of Rs fused with M (4); both branches of primary fork of MP analogous, i.e., with posteriorly directed pectination of anterior branch, and anteriorly directed pectination of posterior branch (5); CuA very stout in proximal part. Hindwing with basal crossvein r-m weakly developed, short (6); M simple, without primary fork (7); CuA with anteriorly directed pectinate branches (8).

Remarks. This genus is also noteworthy for characters other than those included in the diagnosis. Particularly, it is characterized by disproportionately stout veins: several longitudinal veins (especially Sc, MP and CuA) are very thick, while others (especially crossveins) are very thin. This condition is somewhat similar to that found in the Australian Ithonidae and Dilaridae (subfamily Dilarinae). Individual character states 2, 4, 7 and 8 are putative autapomorphies of *Principiala*; the structure of the forewing MP may also be considered an autapomorphic condition, but this is a complex character;

character state 6 is derived with regard to its plesiomorphic state, but is found in other families; the polarity of characters 1 and 3 is unclear (see below for a more detailed discussion).

Relative length of the antennae (character state 1). The antennae of *Principiala* seem to be the shortest among known Neuroptera, although they are only slightly shorter than those of species of *Rapisma* with the shortest antennae. This character varies considerably in different genera of extant Ithonidae. In the majority of species of *Rapisma* the antennae are of a variable length, but always very short: antenna length/forewing length ratio ranges from 0.18 (*R. viridipenne* Walker) to 0.39 (*R. corundum* Barnard), except for a group of closely related species of the *Rapisma malayanum*-complex, varying from 0.42 to 0.62 (estimated from data in Barnard, 1981; Barnard and New, 1985, 1986; New, 1985; Yang, 1993). Tillyard (1916, p. 274) mentioned in the definition of the Ithonidae (from which he excluded *Rapisma*) that they have "antennae of moderate length". Precise data on their relative length, however, in genera other than *Rapisma*, are scarce: e.g., 0.67 in *Ithone fulva* Tillyard (Tillyard, 1916); about 0.6 in *I. fusca* and about 0.4 in *Megalithone tillyardi* Riek (estimated from Riek, 1974, figs. 47, 48). Antennae in Polystoechotidae (the sister-group of Ithonidae) are also short, less than half the forewing length (Carpenter, 1940), but precise data are unavailable. Relatively short antennae also occur in systematically distant families, such as in the fossil *Tachinymphes* Ponomarenko (Mesochrysopidae) (Nel et al., 2005; the family treated here in the broad sense, as in Makarkin and Menon, 2005) and in the extant Myrmeleontidae, Psychopsidae and Mantispidae, while in most other families of the order they are of moderate length, usually 0.5–1.0 of forewing length, to very long, exceeding forewing length, as in Apochrysinae (Chrysopidae) (Brooks and Barnard, 1990).

Costal gradate series of crossveins (character state 2). Of all the species of Ithonidae, those belonging to *Rapisma* and *Varnia* possess numerous, irregularly spaced costal crossveins; the others have, at most, several occasional crossveins. In the Polystoechotidae the presence of costal crossveins is considered derived with regard to their absence, and probably homoplasious among these occurrences (Archibald and Makarkin, 2006). The same may be partially true for Ithonidae. The condition found in *Principiala*, however, may be treated as an autapomorphy of this genus, i.e., the regular costal gradate series of crossveins looking like a true longitudinal vein in the basal portion of the costal space.

Subcostal crossveins (character state 3). All species of some neuropteran families possess numerous crossveins in the forewing subcostal space (e.g., Panfiloviidae, Kalligrammatidae, Psychopsidae). In those families characterized by few subcostal crossveins, or only one, the condition of many subcostal crossveins may occur in some species or species groups (Archibald and Makarkin, 2006). In Ithonidae one basal and one (or a few) distal subcostal crossveins are characteristic of all genera, except for *Rapisma* (Barnard, 1981) and (to a lesser extent) *Varnia* (Riek, 1974). The condition of *Principiala* is most similar to that of *Rapisma*. The polarity of this character is not clear.

Fusion of proximal branches of Rs with M (character state 4). This feature is characteristic of the forewings of the majority of Chrysopidae, and possibly of the Upper Jurassic/Lower Cretaceous genus *Hongosmylites* Makarkin and Archibald, 2005. As these taxa are clearly distant from Ithonidae, the fusion of the most proximal branches of Rs with M found in *Principiala* may reasonably be considered independently derived, and consequently should be treated as autapomorphic, because this condition does not occur in other Ithonidae.

Structure of MP in the forewing (character state 5). The configuration of MP found in *Principiala* is unique in the order; it is a complex character that includes at least three individual character states: (1) basally, both branches of the primary fork of MP form an equal angle with the common stem of MP, so that it is impossible to deduce which branch is the continuation of the stem; (2) the anterior branch has posteriorly directed pectination; and (3) the posterior branch has anteriorly directed pectination. The generalized venation of the neuropteran forewing is characterized by primary branches (MA and MP) that are nearly parallel and not branched before their distal portions (Archibald and Makarkin, 2006).

Basal crossvein r-m in the hindwing (character state 6). Although this crossvein is poorly preserved (or weakly developed) in *Principiala*, it is certainly short, as seen from well-preserved adjacent venation. This character state is derived, with regard to the plesiomorphic condition of a long and sinuate crossvein (for further discussion, see below, section 4.2).

Structure of M in the hindwing (character state 7). The simple M in the hindwing of *Principiala* is almost unique to Neuroptera (it is also independently derived in some Coniopterygidae, the family characterized by very reduced venation), and should be considered an autapomorphy of this genus.

Pectination of CuA in the hindwing (character state 8). Similar one-sided, anteriorly directed pectination of various veins occurs in a number of other, mostly extinct, neuropteran taxa, for example MP in most Mesozoic Kalligrammatidae (e.g., Panfilov, 1968, figs. 3–8) and in the Upper Triassic osmylopsychopid *Petropsychops* Riek (Grimaldi and Engel, 2005, fig. 9.15) and Rs1 (= ORB1 of Oswald, 1993) in many extant and extinct genera of Hemerobiidae (Makarkin et al., 2003). All of these conditions are derived with regard to those of non-pectinate veins. Specifically, character state 8 does not occur in any other Ithonidae, and is undoubtedly an autapomorphy of *Principiala*.

Principiala incerta sp. nov.
Figs. 1–5

Derivation of name. Latin, *incertus*, uncertain, with reference to the uncertain taxonomic position of this genus and species within the family.

Material. Holotype SMNK PAL 5352, deposited in SMNK; a nearly complete, well-preserved specimen in dorsal aspect. Paratype SMNS 66000/255; an almost complete, but poorly preserved specimen exposed in ventral aspect, with wings overlapping considerably pair-wise at each side of the body. Both specimens collected in the vicinity of Nova Olinda, Chapada do Araripe, Ceará State, Brazil. Lower Cretaceous (Upper Aptian), Nova Olinda Member, Crato Formation.

Diagnosis. As for genus.

Description of holotype (Figs. 1–3). Head almost entirely retracted under pronotum, ca. 0.5 mm long in dorsal view. Left antenna complete, right one fragmented. Antennae short, much shorter than wings (ca. 2–2.5 mm long), probably moniliform. Thorax stout, apparently not hairy; pronotum very broad, shield-like, 2.5–3.0 mm long, ca. 4.0 mm wide; mesonotum 4.8 mm wide at forewing attachment; metanotum relatively
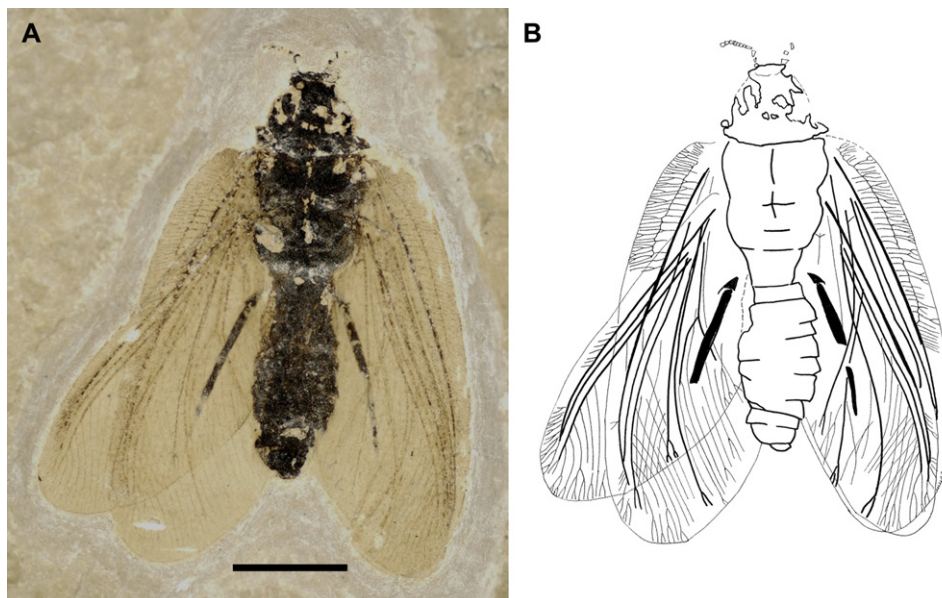

Fig. 1. *Principiala incerta* gen. et sp. nov., holotype SMNK PAL 5352. A, photograph, and B, drawing of the same specimen; scale bar represents 5 mm.

large. Fore and mid legs not preserved; hind legs incompletely preserved: coxae poorly preserved; trochanter 0.6 mm long, armed with spine-like structure on external surface; femur 5.5 mm long as preserved (left hind leg); tibia and tarsus poorly preserved (right hind leg). Abdomen 9 mm long, 3.7 mm in maximum width; apical portion somewhat narrowed, rounded, suggesting it is female.

Forewing broadly oval, with rounded apex, 19 mm long, 8 mm wide (estimated). Trichosors prominent, including those along costal wing margin. Nygmata not detected. Costal space strongly expanded basally (1.8 mm maximum width), narrowed apically. Humeral veinlet poorly determinable, represented either as vein continuing into costal gradate series of crossveins or as vein located posterior to this series (Figs. 2A, 3B). Costal gradate series of crossveins complete, appearing like a true longitudinal vein in its basal portion, running parallel to costal wing margin from wing base (alternatively, from humeral veinlet) to approximately mid-point of wing. Subcostal veinlets closely spaced, all forked once or twice anterior to costal gradate series, slightly bent towards apex in basal portion of costal space, more strongly bent in its apical portion. Sc very thick, appears to be fused with R1 basally (probably because they overlap), probably not fused with it distally: it is hard to distinguish in impression fossils whether condition of apparent distal fusion of Sc and R1 is caused by these veins being connected by distal crossvein or by Sc being fused with R1 at nearly a right angle. R1 entering margin well before wing apex. Subcostal space apparently narrowed basally, strongly dilated medially, narrowed apically; many closely spaced, irregular crossveins detected in basal half, one forked once; crossveins more widely spaced medially. Origin of Rs not discernible, probably close to wing base. R1 space very narrow basally, slightly expanded distally, much narrower than subcostal space in medial portion; a few crossveins detected in apical half of wing, others possible. Rs smooth, entirely lacking any zigzag features, entering margin before wing apex, with 13 branches (left forewing); proximal branches irregular, fused; distal branches more regular, mostly with one or two shallow marginal forks (except for two distalmost dichotomously forked branches), connected by few crossveins, not forming regular gradate series. Origin of M at wing base, probably not fused with R basally. M rather thick, dividing into MA and MP near wing base. MA simple with only marginal fork, reaching wing margin well after mid-point. MP rather thick proximal to primary fork, which has a peculiar configuration: both primary branches of MP equivalent, with posteriorly directed pectination of anterior branch, and anteriorly directed pectination of posterior branch. Several crossveins, simple or forked, between MA and MP. Cu forked near wing base, very thick. CuA very strong basally, as stout as basal portion of Sc, running very close, parallel to posterior branch of MP; probably not branched except for marginal fork (incompletely preserved). CuP thin, poorly preserved. 1A incompletely preserved, other anal veins and jugal lobe not preserved.

Hindwing broad, apparently widest in basal half (wings crumpled basally), with rounded apex; 17 mm long, 7 mm wide (at wing mid-point). Trichosors prominent, poorly

detected along costal wing margin. Nygmata not detected. Coupling apparatus well developed, probably with short frenulum (Fig. 2). Costal space wider basally (0.9 mm wide), slightly narrowed towards pterostigmal region. Subcostal veinlets mostly (or entirely) forked once, oblique with apices strongly bent towards apex. Sc very thick, not fused with R1 distally. R1 entering margin well before wing apex. Subcostal space narrow basally, slightly dilated medially, narrowing again before convergence of Sc and R1; 3−4 subcostal crossveins preserved before mid-point of wing, others possible. Origin of Rs at 2.1 mm from wing base. R1 space slightly narrower than subcostal space in medial portion, with two crossveins preserved in basal half of wing. Rs entering margin before wing apex, with >12 branches; of these, most proximal 2−3 branches very short, fused with M, next 3−4 branches fused with each other, others enter wing margin, forked once or twice distally. Basal crossvein between R and M very poorly preserved, weakly developed, of indeterminate course, but certainly short, as seen from well-preserved adjacent venation. Origin of M apparently not fused with R basally. M thin, nearly straight basally, very prominent distally, running smoothly, reaching margin well after wing mid-point, simple with one marginal fork. Cu dividing into CuA and CuP close to wing base. CuA stout, prominent for most of its length, with several anteriorly directed branches (at least five). Origin of CuP nearly at right angle to CuA, ca. 1.8 mm from wing
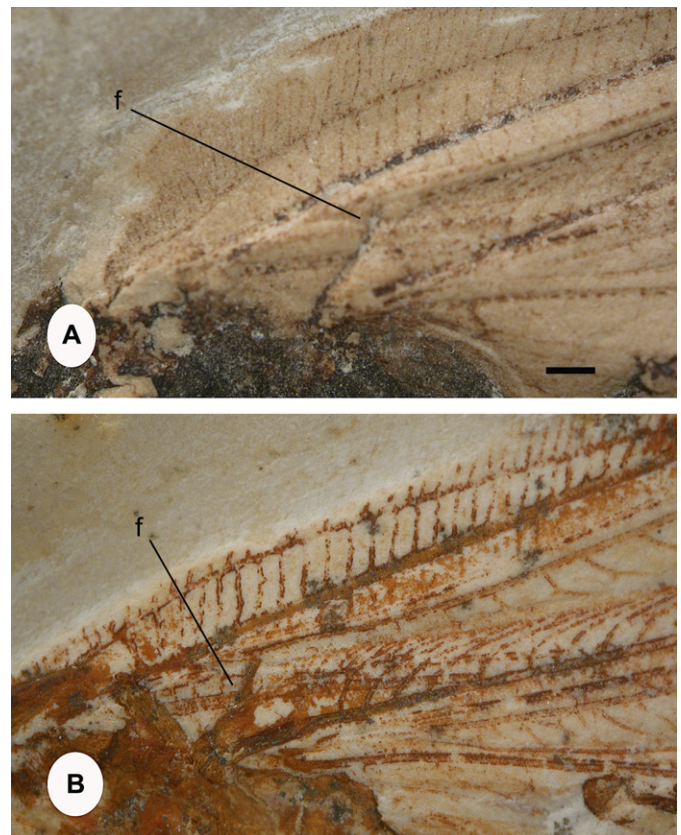

Fig. 2. *Principiala incerta* gen. et sp. nov., basal portion of right wings showing coupling apparatus in hindwing of A, the holotype SMNK PAL 5352 and B, paratype SMNS 66000/255; f, frenulum; scale bar represents 2 mm.
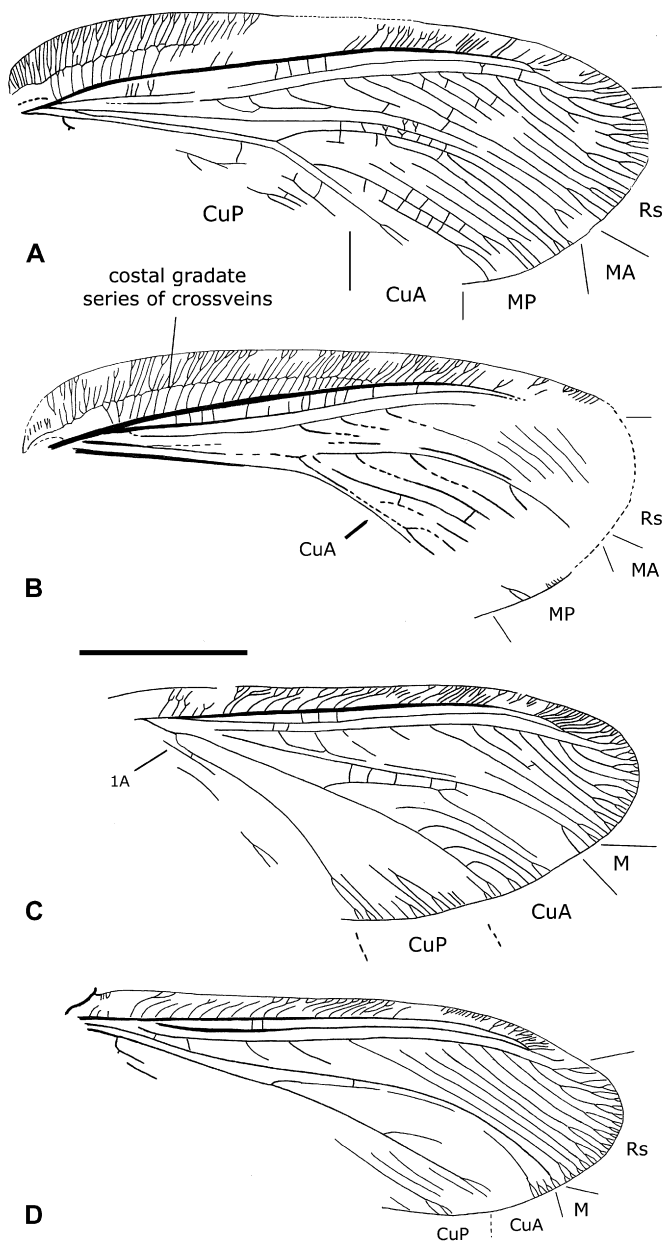
Fig. 3. *Principiala incerta* gen. et sp. nov., holotype SMNK PAL 5352. Drawings of A, left forewing, B, right forewing, C, left hindwing, and D, right hindwing; scale bar represents 5 mm.

base. CuP thinner than CuA, possibly with several anteriorly directed branches (alternatively, CuA with several posteriorly and anteriorly directed branches: intra-cubital space very poorly preserved). 1A incompletely preserved; 2A and 3A not preserved.

Description of paratype (Figs. 4, 5). Head rounded, 1.5 mm long, 2.5 mm wide, mostly retracted under pronotum; mouthparts and antennae not preserved; eyes visible mainly as impressions. Thorax unusually stout, 6 mm long, 6 mm wide (at level of attachment of forewings). Prothorax poorly visible. No legs preserved except for incomplete femora and

tibiae of hind pair; tibia 5 mm long, not armed with spines or setae. Abdomen relatively short (7.5 mm long), terminal segments enlarged, suggesting male specimen. Head, thorax and abdomen highly compressed; exoskeleton mostly not preserved.

Forewing: shape not determinable, apparently with rounded apex, ca. 17.5–18 mm long. Costal space apparently dilated basally (costal margin not preserved), slightly narrowed apically. Subcostal veinlets closely spaced, simple or forked once, bent towards apex. Costal gradate series of crossveins complete, accompanied by dark narrow streak. Sc thick, appears fused with R1 basally (probably because of overlap) and distally; distal fusion hardly determinable, at 2 mm from apex; possible Sc + R1 entering margin well before wing apex. Subcostal space very narrow basally, dilated medially, narrowed apically; several closely spaced crossveins detected in basal half. Origin of Rs very close to wing base. R1 space very narrow, much narrower than subcostal space medially, with a few crossveins perpendicular to R1 or oblique. Rs smooth, forked twice distally, entering margin before wing apex; with >13 branches, at least two most proximal branches appear fused with M, at least next three branches fused with each other; connected by a few crossveins in anterior portion of radial space. Origin of M not fused with R; M rather thick basally, its primary fork not preserved. Cu and CuA very stout basally. Several basal crossveins between M and Cu.

Hindwing: shape not detectable (partly crumpled), ca. 15.5–16 mm long, > 5 mm wide. Costal space wide basally (0.8 mm wide), slightly narrowed towards fusion, or close approach, of Sc and R1. Subcostal veinlets simple or forked once, oblique with apices strongly bent towards apex. Sc and R1 appear fused at 2.5 mm from wing apex: it cannot be determined whether they are connected by distal crossvein or Sc is fused with R1 at nearly a right angle. Possible Sc + R1 short, with three veinlets, entering margin well before wing apex. Subcostal space narrow basally, slightly dilated medially and before fusion (or approach) of Sc and R1; two subcostal crossveins detected at mid-point of wing. Rs originating ca. 2 mm from wing base. R1 space very narrow basally, slightly dilated apically, narrower than subcostal space medially, with a few crossveins oblique or perpendicular to R1. Rs forked distally, entering margin before wing apex, with ca. 14–15 branches, most proximal 3–4 branches very short, fused with M, next four branches fused with each other, others enter wing margin, forked once or twice distally; connected by a few randomly placed crossveins. Basal crossvein between R and M very poorly visible, weakly developed, short, possibly of longitudinal course. Origin of M not fused with R; M without apparent fork, thin basally (much thinner than basal Sc, R1, Rs and CuA), stouter and more prominent distally, running smoothly, reaching margin well after wing mid-point. Cu dividing into CuA and CuP very close to wing base. CuA very stout for most of length (as stout as Sc), with few anteriorly directed pectinate branches. Origin of CuP inclined at nearly a right angle to CuA; CuP thin. Crossveins between CuA and CuP thin, curved. Preserved 1A rather stout (as stout as origin of Rs); 2A and 3A not preserved.
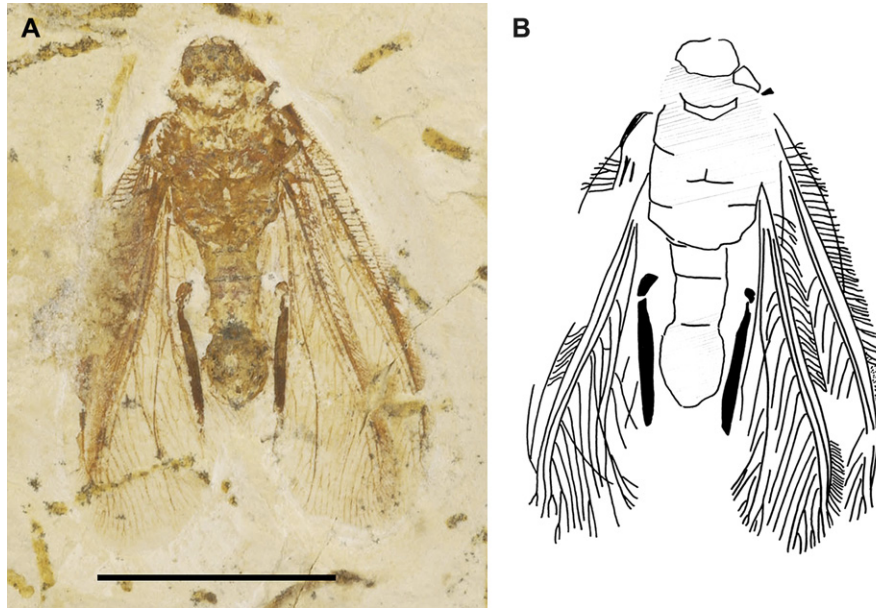
Fig. 4. *Principiala incerta* gen. et sp. nov., paratype SMNS 66000/255. A, photograph, and B, drawing of the same specimen; scale bar represents 10 mm.

Remarks. The holotype is generally well preserved; the majority of the exoskeleton is intact, displaying several details. The body is preserved in three-dimensions. The wing venation could be examined in detail despite the overlapping wings, especially the left ones. We interpret the spine-like structure on the external surface of the trochanter to be a strong hair (not a true spine), although the preservation of the leg portions does not support this conclusion.

The paratype is poorly preserved; the exoskeleton is mostly removed, and many body details are missing. Furthermore, the mineralization on the right wings and the partial overlap of the fore- and hindwings obscure the venation (especially that of the forewings). The state of preservation of this specimen poses limits to the description, especially of body parts and forewings. The interpretation of forewing venation is especially hard as the right wing is covered by mineralized matrix that could not be removed during preparation, and the left wing is mostly obscured by the overlapping hindwing.

4. Discussion

4.1. Determination of family affinity

The characters discussed above indicate that *Principiala* (excluding placement in a new family) could be referred to the Dilaridae, extinct Prohemerobiidae, Polystoechotidae, Ithonidae, or Rapismatidae. The genera of these families have much in common with this new genus in their general habitus, e.g., stout body (Ithonidae, Rapismatidae, some Polystoechotidae and Prohemerobiidae); head retracted under pronotum (Ithonidae, Rapismatidae and some Polystoechotidae); similar venation, including strongly irregular crossvenation (Dilaridae, Ithonidae and Rapismatidae). All other families are excluded with confidence.

The Dilaridae (consisting of two subfamilies, Dilarinae and Nallachiinae) is the least likely choice for *Principiala* because of the absence of a long ovipositor in the putative female of *Principiala* and pectinate longer antennae characteristic of all male dilarids, and is therefore excluded. This particularly applies to genera of the subfamily Nallachiinae, which differ
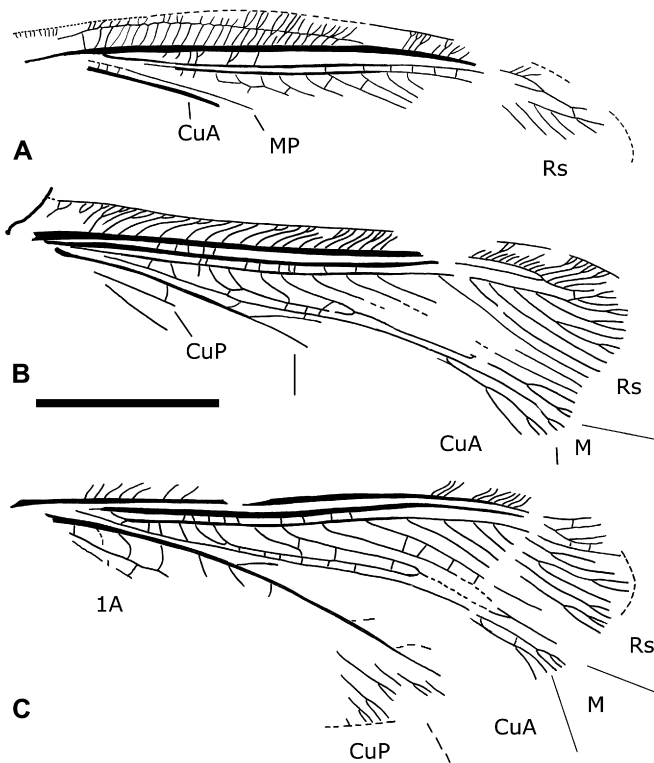

Fig. 5. *Principiala incerta* gen. et sp. nov., paratype SMNS 66000/255. Drawings of A, left forewing, B, left hindwing, and C, right hindwing; scale bar represents 5 mm.

greatly from *Principiala* in their small size and reduced venation (see, e.g., Adams, 1970). The subfamily Dilarinae could be suitable if only the size and general similarity in the venation are taken into account (venation of Dilarinae in Comstock, 1918, fig. 179; Monserrat, 1988, figs. 13–18; Makarkin, 1995, fig. 15.1).

The Prohemerobiidae require revision; they may be paraphyletic (Makarkin and Archibald, 2003; Wedmann and Makarkin, 2007). Some species, in which the body is preserved, are stout and moth-like, e.g., the Upper Liassic *Prohemerobius alysius* (Whalley) and *P. sexfasciatus* Bode (Whalley, 1988, fig. 2; Ponomarenko, 1996, fig. 15). The venation of these taxa resembles that of the type species of the family, *Prohemerobius dilaroides* Handlirsch, and to a lesser extent Dilaridae. Interestingly, prohemerobiids were treated by Navás (1913) only as a "tribe" of the Dilaridae. We exclude this family because these taxa with stout bodies are relatively small (forewing length 4.3–5.5 mm) and their venation is sufficiently different, although a close phylogenetic relationship of Dilaridae and some Prohemerobiidae (and possibly Ithonidae) is quite probable.

The family Polystoechotidae was recently reviewed in detail by Archibald and Makarkin (2006). Although some diagnostic character states of this family are shared with *Principiala* (i.e., forewing with recurrent and branched humeral veinlet, and a pectinately branched MP, if the anterior branch of MP in *Principiala* is treated as a continuation of its common stem; see Fig. 3A), the remaining characters are clearly distinctive or unknown. The extant *Platystoechotes*, which is the genus most distant from the other representatives of the family, is quite similar to *Principiala* (cf. Carpenter, 1940, fig. 71), in that, for example, Sc is not fused with R1, the body is stout, and the head is retracted under the pronotum. Its venation is otherwise very different from that of *Principiala*.

The combination of the character states of head, thorax and wings of *Principiala* indicates that this genus most probably belongs to an ithonid-like group, and seems to be most closely related to extant *Rapisma* McLachlan. These genera share the following character states: (1) very short antennae; (2) large, shield-like pronotum; (3) head almost entirely retracted under the pronotum; (4) dilated costal space basally, with numerous crossveins; (5) numerous subcostal crossveins. However, *Principiala* differs from *Rapisma* in many derived character states (see above and below).

4.2. Synonymy of Rapismatidae and Ithonidae

The extant representatives of these two families are distributed in southern Australia, Meso-America to southern North America (Ithonidae), and the Oriental Region (Rapismatidae). Typical Ithonidae occur in Australia, where 14 species of three genera (*Ithone* Newman, *Megalithone* Riek and *Varnia* Walker) are known (Tillyard, 1916, 1919; Riek, 1970, 1974; New, 1991). They were reviewed by Riek (1974), but this revision is unsatisfactory, and the family is in need of much more detailed treatment. In particular, the male internal genitalia are very poorly known; some information on single

species has been provided only by Carpenter (1951) and Acker (1960). Also, the female internal genitalia are known only for *Megalithone megacerca* (Tillyard) (Szíráki, 1996); the structure of the subgenitale is almost unknown (see below).

All other taxa from other regions of the world referred to Ithonidae might be considered (more or less) "atypical", and their assignment to this family requires confirmation.

Five to six species occur in the New World. These are restricted to southwest USA, Mexico, and Honduras. The ithonid affinity of *Oliarces clara* Banks was well-enough demonstrated by the examination of adults (Carpenter, 1951); however, the examination of larvae indicates that this affinity remains problematic, because the morphology of its first instar is more similar to that of Polystoechotidae than of *Ithone*, although clearly supporting a sister-group relationship of Polystoechotidae and Ithonidae (Grebennikov, 2004). This species is distributed in California and Arizona (Adams, 1950; Carpenter, 1951; Faulkner, 1990). Faulkner (1990) mentioned the presence of another, undescribed species of *Oliarces* in Baja California, Mexico.

Narodona mexicana Navás, originally described from Mexico and referred to the Osmylidae (Navás, 1930, p. 21, fig. 3), was tentatively transferred by Adams (1969, p. 2) to the Ithonidae, who wrote that this "is probably an ithonid, judging from the illustrations" (the type material is apparently lost; Penny, 1996). Navás (1930) created the monotypic "tribe" Narodonini to include only this genus. Judging from the original description and quite poor illustration (Navás, 1930, fig. 3), *Narodona* is apparently a true ithonid and probably not congeneric with the other two genera known from the region. It might be characterized by the hindwing character states: basal crossvein r-m straight (inclined in *Oliarces*); radial crossveins scarce; one basal and several distal subcostal crossveins; Sc rather short (long in *Adamsiana*); costal space dilated towards apex; two nygmata. Most of these states are shared with other American species.

Adamsiana curoei Penny, 1996 is the most completely described ithonid, known only from Honduras. It is noted for the aptery of the female, while wings of the male are normally developed (see below for discussion of other characters). Penny (1996, p. 86) also mentioned that in museums there are at least two other undescribed species of Ithonidae from Mexico and that the country "probably will eventually be recognized as a third center for ithonid/rapismatid distribution."

Rapismatidae comprise the single genus *Rapisma* McLachlan with 20 valid species, restricted to the mountains of the Oriental Region (Barnard, 1981; Oswald, 2003). The genus is considered by many authors to constitute a separate family (e.g., Krüger, 1922, 1923; Navás, 1929; Barnard, 1981; Barnard and New, 1985, 1986; New, 1985, 2002; Yang, 1993) or it is included in the Ithonidae (e.g., Comstock, 1918; Brues et al., 1954; Henry, 1982; Penny, 1996; Makarkin and Archibald, 2003; Grimaldi and Engel, 2005). Riek (1974) believed that *Rapisma* is the single extant representative of the otherwise extinct family Brongniartiellidae.

A synonymy of Rapismatidae and Ithonidae is mainly based on the presence in *Adamsiana curoei* of a mixture of character

states that are typical of the Ithonidae (i.e., the taxa occurring in Australia) and *Rapisma* (Penny, 1996). Based on the examination of this species, Penny (1996, p. 85) came to conclusion that "it is currently difficult to maintain the validity of the family name Rapismatidae." We find that the character states shared by all genera (including *Principiala*) in the body structure are as follows: (1) head retracted under pronotum, similar to that of extant *Platystoechotes lineatus* Carpenter and *Polystoechotes gazullai* Navás among Polystoechotidae (Carpenter, 1940; Oswald, 1998), but to a lesser extent; (2) pronotum large, mostly shield-like; (3) mesothorax very broad (or entire body stout), shared with some Prohemerobiidae (Whalley, 1988; Ponomarenko, 1996) and Polystoechotidae (however, the body in *Adamsiana curoei* is not especially stout). The generalized venation of Rapismatidae and Ithonidae is similar, although no synapomorphy was detected; it is not surprising that these (like any) "primitive" families lack clear venational autapomorphies. Barnard (1981) provided the following differences between these two families, which we consider, however, to be insufficient:

1. Tarsal claws broad, with a small projection in Rapismatidae, and elongate and simple in Ithonidae. *Adamsiana* has simple, elongate claws (Penny, 1996). Similar differences in the structure of claws occur within unquestionable monophyletic Chrysopidae (Brooks and Barnard, 1990, figs 11–12).

2. Legs densely hairy, without spurs in Rapismatidae, and spiny, with tibial spurs in Ithonidae. Spurs are also absent in *Adamsiana* (Penny, 1996). Within families of the Myrmeleontoidea these spurs are similarly varied; e.g., there are two groups of genera of Nymphidae, with and without two tibial spurs, which in the past were considered to be separate families: Nymphidae and Myiodactylidae (New, 1984).

3. One proximal nygma present on each wing in *Rapisma*, and two nygmata on the forewing and one on the hindwing in Ithonidae. In *Adamsiana* three nygmata are on the forewing and two on the hindwing (Penny, 1996). The presence of nygmata is a plesiomorphic feature; its variation in Ithonidae and Rapismatidae has been not studied. Oswald (1998) mentioned some variation in the presence or absence of nygmata in Polystoechotidae.

4. Trichosors very reduced in Rapismatidae, and well developed in Ithonidae; however, they are absent along the costal margin in the latter. The presence of trichosors is a plesiomorphic character.

5. "Base of MA [= basal crossvein r-m] usually "obsolete" in Rapismatidae, usually present in Ithonidae", according to Barnard (1981). A long, sinuous basal crossvein r-m is the plesiomorphic condition within the order, irrespective of its treatment as a basal part of MA or a true crossvein (e.g., Lambkin, 1986; Willmann, 1990). In all Australian genera this crossvein is usually very long and sinuous (but this condition is somewhat variable; Riek, 1974). The derived state of this crossvein is short and straight, as in *Rapisma* (Comstock, 1918, fig. 171; Yang, 1993, pl. 7, figs. X, Y, verified by our examination of the photographs

of *Rapisma veridipenne* Walker), *Adamsiana* (Penny, 1996, fig. 2), and *Narodona* (Navás, 1930, fig. 3). Its state in *Oliarces* is rather intermediate, slightly inclined (Carpenter, 1951, fig. 2). A similar situation occurs in Mantispidae, where both conditions are present in the different subfamilies (Lambkin, 1986).

6. Mandibles acute, long in Ithonidae (in fact, only in *Ithone*, *Megalithone* and *Varnia*), short and broad in Rapismatidae and *Adamsiana*. Male mandibles vary from relatively short in *Neoneuromus* van der Weele to disproportionately elongate in *Corydalus* Latreille and *Acanthacorydalis* van der Weele within the megalopteran family Corydalidae (e.g., Liu et al., 2005).

7. In the male, the gonarcus is complete, arched in Rapismatidae, and paired or triangular in Ithonidae, after Barnard (1981). In fact, those genera for which genitalia are described (*Rapisma*, *Adamsiana, Ithone* and *Oliarces*) appear to have been built rather similarly, consisting of gonarcus, paired gonocoxites and a small hypandrium internum (Acker, 1960; Barnard, 1981; Yang, 1993; Penny, 1996). The gonarcus is divided into two parts only in *Oliarces*. However, the internal genitalia of the males of most Australian species of Ithonidae and *Naradona* are unknown, and those of the remainder are in need of a more accurate description or detailed re-examination; hence, comparison of these structures is limited to this very short account.

8. Subgenitale of the female large in Rapismatidae, reduced in Ithonidae (Barnard, 1981). All that was known of the subgenitale of Australian Ithonidae was that "the eighth sternite is not visible externally" (Carpenter, 1951, p. 39) and the "subgenital plate [is] reduced" (Barnard, 1981, p. 123, referring to Riek, 1974); later this was repeated by Penny (1996, p. 85), although Riek (1974) wrote nothing on the subgenitale of any species. Moreover, the subgenitale of none of the species of this family is illustrated. Our examination of the female genitalia of *Ithone fusca* shows that its subgenitale is not visible in dried specimens, being located on the inside of ventral portions of elongate ninth tergites. The subgenitale is nearly as large as in *Rapisma*; its structure is, in general, similar in these two genera. It is rather more reduced in *Adamsiana* (Penny, 1996, fig. 7), but is still a considerable size. Thus, in all of the species of Ithonidae and Rapismatidae examined so far, the subgenitale is demonstrated to be not reduced. Within other neuropteran families, it may be present or absent, and the degree of its development is variable (e.g., very large in *Neuronema* McLachlan, and very small or absent in *Hemerobius* Linnaeus among Hemerobiidae).

9. Ninth sternite (= ninth gonocoxites) of the female unmodified in Rapismatidae, forms a psammarotrum in Ithonidae (Barnard, 1981). The ninth gonocoxites each have a short dorsal digitiform process in *Adamsiana* and *Oliarces*; with a paired ventral sclerotised "pseudostylus" of psammarotrum in the Australian genera (*Ithone, Megalithone* and *Varnia*), lacking any processes or with a small true stylus (*Rapisma*). The presence of a stylus in *Rapisma* was not

mentioned by Barnard (1981), Barnard and New (1985) and New (1985), but Yang (1993, figs. 1.3, 4.1) described a small stylus in the two Chinese species. The digitiform process of ninth gonocoxites in *Adamsiana* and *Oliarces* is probably homologous with the stylus of Osmylidae, Polystoechotidae and some Hemerobiidae, whereas the ''pseudostylus'' is probably not, because this is a simple projection of the ninth gonocoxite in a location different from that of the stylus. In Hemerobiidae nearly half of the genera possess a stylus; the others lack one (Oswald, 1993).

In summary, the majority of characters that have been analysed vary considerably within particular families of Neuropterida, and the differences between typical Ithonidae and Rapismatidae are not sufficient to support the family rank of the latter. Unfortunately, none of the characters can be considered as an obvious autapomorphy of Ithonidae as treated here to support the monophyly of this clade. The body structure and general venational pattern characteristic of this family are shared by some other groups. The head retracted under a large pronotum is apparently a single known imaginal synapomorphy of Ithonidae + Polystoechotidae. A sister-group relationship between these families is based primarily on the morphology of their larval head in connection with the hypothesis of phytosuccivory of larvae (Aspöck, 1992; Aspöck et al., 2001), a conclusion supported by the molecular analysis of Haring and Aspöck (2004). Generally, it is very hard to establish the monophyly of basal groups (to which the Ithonidae presumably belongs) because of the mainly plesiomorphic condition of their characters. Therefore, a synonymy of Ithonidae and Rapismatidae may be regarded as only tentatively supported by these data.

This is illustrated by the Hemerobiidae, whose monophyly appears to be unquestionable, and whose documented age is quite comparable to that of Ithonidae. The genera belonging to the Hemerobiidae are very different in size and venation (cf. large, rich-veined *Drepanepteryx* Leach and the small *Psectra* Hagen with reduced venation) and in the genitalia of both male and females (see, e.g., the very complicated male genitalia in *Notiobiella* Banks and the strongly reduced ones in *Psectra*; the presence of a large, structurally complicated subgenitale in the female of *Neuronema* McLachlan and its absence in some other genera, such as *Hemerobius*) (Oswald, 1993). The differences between genera within the Hemerobiidae are at least as great as between those of the Ithonidae and Rapismatidae. The Hemerobiidae have, however, retained in the extant fauna almost the entire spectrum of intermediate conditions between the extremes, whereas the Ithonidae have not. So, the question of synonymy of Ithonidae and Rapismatidae might be resolved unequivocally only when a sufficient variety of their fossil representatives has been found and described.

4.3. Systematic position of Principiala within Ithonidae

Supra-generic relationships within the Ithonidae remain unresolved. It is, therefore, impossible to assign *Principiala* to any of the subdivisions of the family. Below, we provide a short, preliminary essay on classification of Ithonidae based on all available data to determine the position of the new genus.

Of extant Ithonidae, the Australian genera *Ithone*, *Megalithone* and *Varnia* are certainly closely related, and seem to form the more derived group. Evidence in favour of this is the shared possession of a number of derived character states, which are mostly absent in other genera of the family, such as the tendency to develop long, acute mandibles (sometimes very long, comparable with head length), and to have more than one origin of Rs; the presence of a specialized psammarotrum; the absence of a true stylus in the female; and strong enlargement of the ectoprocts (= claspers of Riek, 1974) in the male. Some of these conditions may be treated as autapomorphies of this generic group (e.g., the presence of the psammarotrum). On the other hand, this group possesses such plesiomorphic character states at the order level (and probably at the family level) as: (1) a basal crossvein r-m in the hindwing that is usually very long and sinuate; and (2) a dilated proximal portion of the hindwing, resembling that of the Corydalidae (this state might, however, have appeared in these families independently, and may not be plesiomorphic).

Rapisma appears to be a rather isolated genus, possessing some character states not found in any other extant genera of Ithonidae (e.g., very short antennae that are sometimes serrated and numerous subcostal crossveins), together with some features shared with American genera (e.g., a straight basal crossvein r-m in the hindwing; a female ninth gonocoxites that is similar in structure; short, broad mandibles).

The placement of the American genera *Adamsiana* and *Oliarces* is difficult to assess. Their venation is similar to that of the Australian genera rather than to *Rapisma*, but the female and male genitalia are more similar to the latter (at least with respect to *Adamsiana*). In general, these genera have a set of character states intermediate between the Australian taxa and *Rapisma*, and may represent the oldest lineage of the family.

In summary, there appear to be three groups of extant ithonid genera: the presumably monophyletic *Ithone* group (*Ithone*, *Megalithone* and *Varnia*), the *Rapisma* group (*Rapisma*) and a possibly paraphyletic group consisting of *Narodona*, *Adamsiana* and *Oliarces*, whose relationships with other genera are not clear. *Principiala* strongly differs from the *Ithone* group, but might be associated with the *Rapisma* group based on the presence of the following derived character states: (1) very short antennae, (2) numerous subcostal crossveins, and (3) short basal crossvein r-m in the hindwing. However, such unusual venational characters as the structure of MP in the forewing, M in the hindwing, and the fusion of the proximal branches of Rs with M in both wings (see diagnosis above) are not characteristic of any of the ithonid genera. Interestingly, these characters are more derived in the Lower Cretaceous *Principiala* than that in extant *Rapisma*. Therefore, although *Principiala* is most similar to *Rapisma*, it may form its own suprageneric taxon, but until representatives of extant Ithonidae are revised, this is speculation. Future detailed

examination of the morphology of extant and fossil ithonids (including currently undescribed fossil taxa) should allow the evaluation of their phylogenetic relationships and the position of *Principiala*.

Prior to the discovery of *Principiala*, the opinion that " "rapismatids" are merely specialized, montane Ithonidae" (Grimaldi and Engel, 2005, p. 349) seemed to be valid. Now, this conclusion is not so well supported. The habitat of *Principiala* probably differed from that of *Rapisma*: *Principiala* is considered to have lived in the warm, humid tropical forest surrounding the Crato lagoon, whereas species of *Rapisma* live in the forests of southeast Asia at moderately high altitudes (900–2595 m) (Barnard, 1981; Yang, 1993). *Adamsiana* inhabits primary mixed tropical cloud forest at an elevation of 1900 m in the Cordillera del Merendón Range of northwest Honduras (Penny, 1996). On the other hand, *Oliarces* and *Ithone* occur predominantly in the desert and sandy coastal areas of Australia and the southwestern USA (Tillyard, 1919; Faulkner, 1990; New, 1991).

Acknowledgements

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