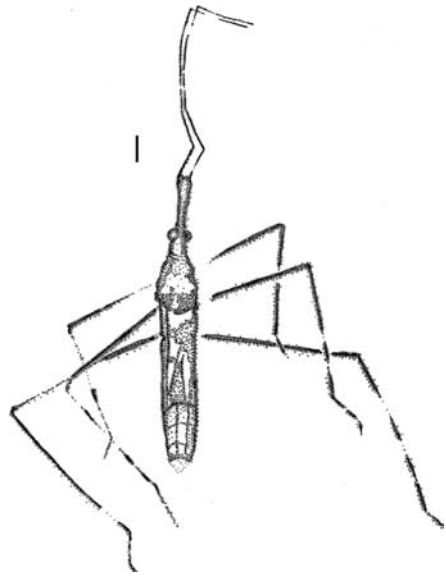

Fig. 11.58. Crato Formation Hydrometridae: *Incertametra santanensis* Goodwyn, 2002, holotype SMNS 64652; scale bar, 1 mm. After Goodwyn (2002).

Cretaceous of Central Mongolia (Aptian, Bon-Tsagan) Popov, 1986, and from the Late Cretaceous of north-east Siberia (Santonian, Magadan district). The Cydnoidea (Figure 11.56c) have already been discussed above. Unfortunately, a great number of terrestrial bugs from the Crato Formation have yet to be evaluated.

11.16 Neuropterida: snakeflies, dobsonflies and lacewings

Rafael G. Martins-Neto, Sam W. Heads and Günter Bechly

The Neuropterida, instantly recognizable by their proportionally large, hyaline wings and net-like venation, are one of the most basal groups of Holometabola and comprise the Raphidioptera (snakeflies), Megaloptera (dobsonflies and alderflies) and Neuroptera (lacewings and antlions). Aside from their typically busy venation, the Neuropterida are characterized by the fusion of the gonoplacs in the ovipositor, a medially divided metapostnotum, a proventriculus with an unpaired diverticulum and the first abdominal tergum having a caudally bifid longitudinal sulcus (Kristensen, 1991; Grimaldi and Engel, 2005). Although neuropterid monophyly is well established, the internal relationships of the group have proved difficult to resolve and remain controversial (Grimaldi and Engel, 2005). All three orders are represented in the Crato Formation, although many of the taxa (particularly the

Neuroptera) require extensive revision and re-description as undoubted synonymies exist.

Recently, the extraordinary new family Rafaelidae was described by Nel *et al*. (2005) with two new species *Rafaelia maxima* (Plate 14a) and *Rafaelia minima*. This family was only tentatively attributed to the neuripterid clade because the veins RP and MA have independent stems in Rafaelidae, but are fused in all known Neuropterida. Also, the other characters do not allow attribution to any of the neuropterid orders nor any other known insect order. The large compound eyes (head similar to libellulid Odonata), the distinct ovipositor and unusual wing venation (particularly the structure of Subcosta, Radius and Media) are unique characters within Neuropterida. Consequently, this family has to be considered as a new insect order, which we here give the new name Schwickertoptera Bechly, ordo. nov. (Plate 14a), in honour of Mr Michael Schwickert (Sulzbachtal, Germany) in recognition of his generous and ongoing support of numerous scientists and public natural history museums around the world.

Raphidioptera: snakeflies

Characterized by their elongate prothorax, the snake-like 'neck' from which the group takes its vernacular name, distinct venation and prominent ovipositor in females, the snakeflies constitute one of the least diverse holometabolous orders (Figures 11.59a–c and 11.69a, Plate 14e). Although monophyly of the order is not in doubt, compelling autapomorphies have never been immediately obvious. Traditionally the group has been characterized by the absence of a pretarsal arolium, the termination of Sc into the anterior wing margin and the bilobed third tarsomere (Kristensen, 1991; Grimaldi and Engel, 2005). In a recent reassessment Aspöck and Aspöck (2004: 16) added two further, apparently strong autapomorphies for the order; amalgamation of tergite and sternite of the ninth segment in the male to form a ring, and elongation of the ovipositor of the female. Interestingly, the ovipositor was discussed by Kristensen (1991) but was regarded as plesiomorphic following Mickoleit (1973). Following the classification of Engel (2002) the order is currently subdivided into two suborders: Priscaenigmatomorpha, including the single extinct family Priscaenigmatidae; and Raphidiomorpha, including the extinct families Baissopteridae, Mesoraphidiidae and Alloraphidiidae along with the two living families, Raphidiidae and Inocellidae.

In the Crato Formation, snakeflies are represented by four species in three genera that have undergone recent revisions by Willmann (1994) and Engel (2002) and represent the only Southern-Hemisphere occurrence of the order. Among the Baissopteridae, the genus *Austroraphidia* was erected by Willmann (1994) to accommodate *Raphidia brasiliensis* (Nel, Séméria and Martins-Neto, 1990). In addition,

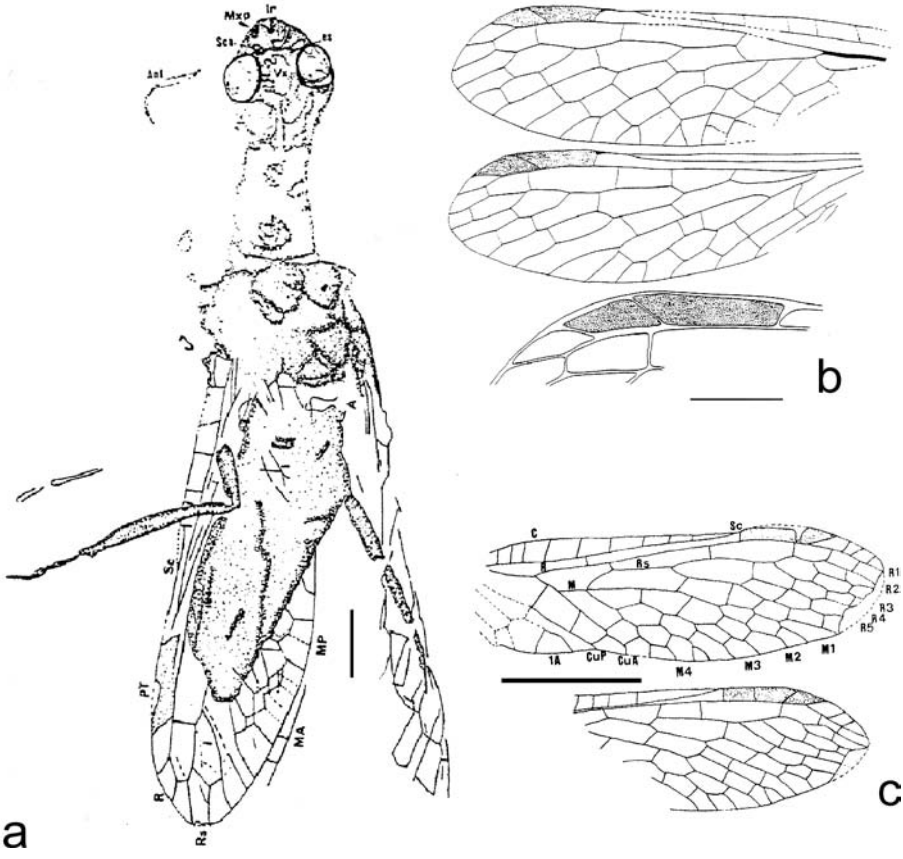

Fig. 11.59. Crato Formation Raphidioptera: (a) *Arariperaphidia rochai* Martins-Neto and Vulcano, 1990, holotype, CV-5010; (b) *Raphidia brasiliensis* Nel, Séméria and Martins-Neto, 1990, holotype MNHN IPM-R54102, forewing (above), hind wing (centre), detail of pterostigma; (c) *Cratoraphidia pulchra* Martins-Neto and Nel, 1993, holotype, GP/IT-1673, forewing (above), hind wing (below). Scale bars, 1 mm. (a) After Martins-Neto and Vulcano (1990); (b) after Nel, Séméria and Martins-Neto (1990); (c) after Martins-Neto and Nel (1993).

Cratoraphidia pulchra (Martins-Neto and Nel, 1992) was moved to the genus *Baissoptera* by Engel (2002). A second species, *B. brasiliensis* Oswald, 1990 is also known from the Crato Formation. In his catalogue, Engel (2002: 15) suggests that *Austroraphidia* may be a junior synonym of *Baissoptera* but notes several characters supporting a separate generic assignment. The monotypic *Arariperaphidia rochai* Martins-Neto and Vulcano, 1989a was the first snakefly to be reported from the Crato Formation, and in fact the first from South America, and was retained in Engel's (2002) catalogue as Raphidioptera *incertae sedis*.

Megaloptera: dobsonflies and alderflies

The Megaloptera (Figures 11.69b and c and 11.90f) are typically large insects that resemble Neuroptera but retain a broad anal region in the hind wing. The larvae are aquatic with lateral gills and lack the sucking mouthparts typical of neuropterans (Grimaldi and Engel, 2005). Like the Raphidioptera, compelling evidence for megalopteran monophyly is sparse and the order has been considered by some to be paraphyletic with respect to snakeflies (Achtelig, 1967; Afzelius and Dallai, 1988). Although traditionally considered a primitive trait, some authors now consider the aquatic lifestyle of megalopteran larvae as independently derived from that of basal Neuroptera. For example, Grimaldi and Engel (2005) suggest that an aquatic lifestyle and lateral gills in the larvae may be potential autapomorphies for the order. This, along with some evidence from molecular studies (Wheeler *et al*., 2001), supports monophyly of the group. The order is currently subdivided into two families: Corydalidae, the dobsonflies; and Sailidae, the alderflies. Two extinct families have been described: the Parasailidae from the Permian of Russia (Ponomarenko, 1977, 2000); and the Euchauliodidae from the Triassic of South Africa (Riek, 1974). Although there have been no formal descriptions of Megaloptera from the Crato Formation, an adult specimen in a private collection was mentioned by Martins-Neto (1999a). In addition, several undescribed adult specimens in the collections at SMNS probably represent a new taxon. The fossil record of the order was recently reviewed by Grimaldi and Engel (2005) and although their rarity in the Crato Formation might seem surprising considering the aquatic lifestyle of their larvae, fossil Megaloptera are also rare elsewhere.

Neuroptera: lacewings and antlions

The predatory Neuroptera (Figures 11.60–11.68, 11.69d–i and 11.70) are among the most ancient members of the Holometabola and comprise the familiar lacewings and antlions. Readily identified by their complex venation the order is defined by the association of the ninth gonocoxites with the gonarcus and the unusual larval mouthparts in which the maxillae and mandibles form a sucking tube for liquid feeding (Aspöck *et al*., 2001; Grimaldi and Engel, 2005). Although the internal phylogeny of the order is largely unresolved, most recent accounts recognize three distinct subgroups: the basal Nevrorthiformia, comprising the single Recent family Nevrorthidae; and the more diverse Myrmeleontiformia and Hemerobiiformia. Only the latter two groups have been recorded from the Crato Formation and have been documented extensively by Martins-Neto and Vulcano (1989b,c, 1990a,b, 1997) and Martins-Neto (1998b, 1990b, 1991d, 1992b, 1994, 1997a, 1998d, 2000, 2002a, 2005). Martins-Neto (2000) provided a key to all 11 families, 28 genera

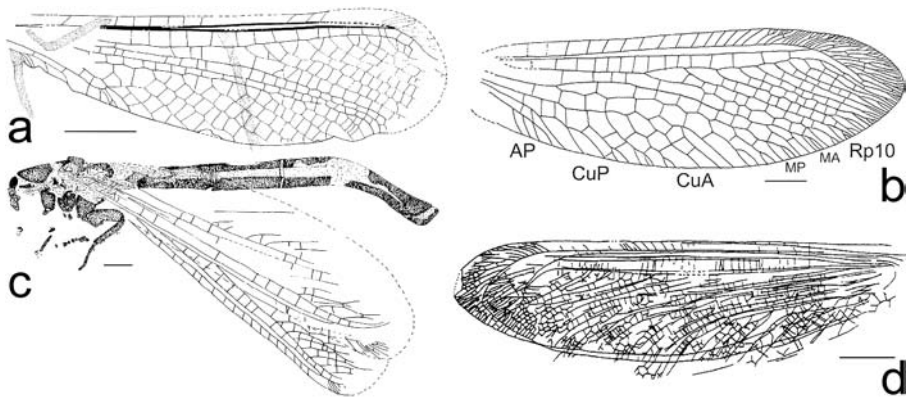

Fig. 11.60. Crato Formation Neuroptera: (a) *Cratoscalpha electroneura* Martins-Neto and Vulcano, 1997, holotype CV-2711, forewing venation; (b) *Olindanymphes makarkini* Martins-Neto, 2005, holotype forewing, MPFT-1–030; (c) *Neurastenyx gigas* Martins-Neto and Vulcano, 1997, holotype CV-2836; (d) *Neurastenyx polyhymnia* Martins-Neto, 1997, holotype AMNH 44412, forewing venation. Scale bars, 5 mm, except (b) 2 mm. (a) After Martins-Neto and Vulcano (1997); (b) after Martins-Neto (2005); d, after Martins-Neto (1997).

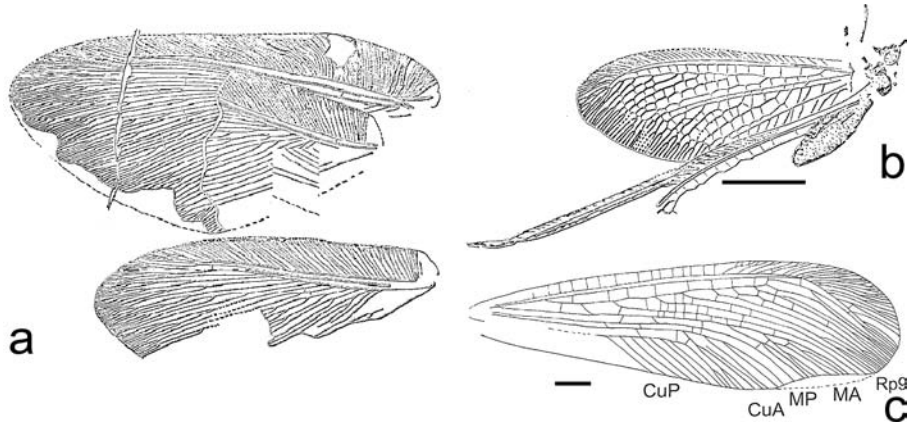

Fig. 11.61. Crato Formation Neuroptera: (a) *Pulchroptilonia espatiafata* Martins-Neto, 1997, holotype RGMN-T110, forewing (above) and hind wing (below); (b) *Roesleriana exotica* Martins-Neto and Vulcano, 1989, habitus; scale bar, 10 mm; (c) *Santananymphes ponomarenkoi* Martins-Neto, 2005, holotype MPFT-1-031, forewing, scale bar, 2 mm. (a) After Martins-Neto (1997); (b) after Martins-Neto and Vulcano (1989); (c) after Martins-Neto (2005).

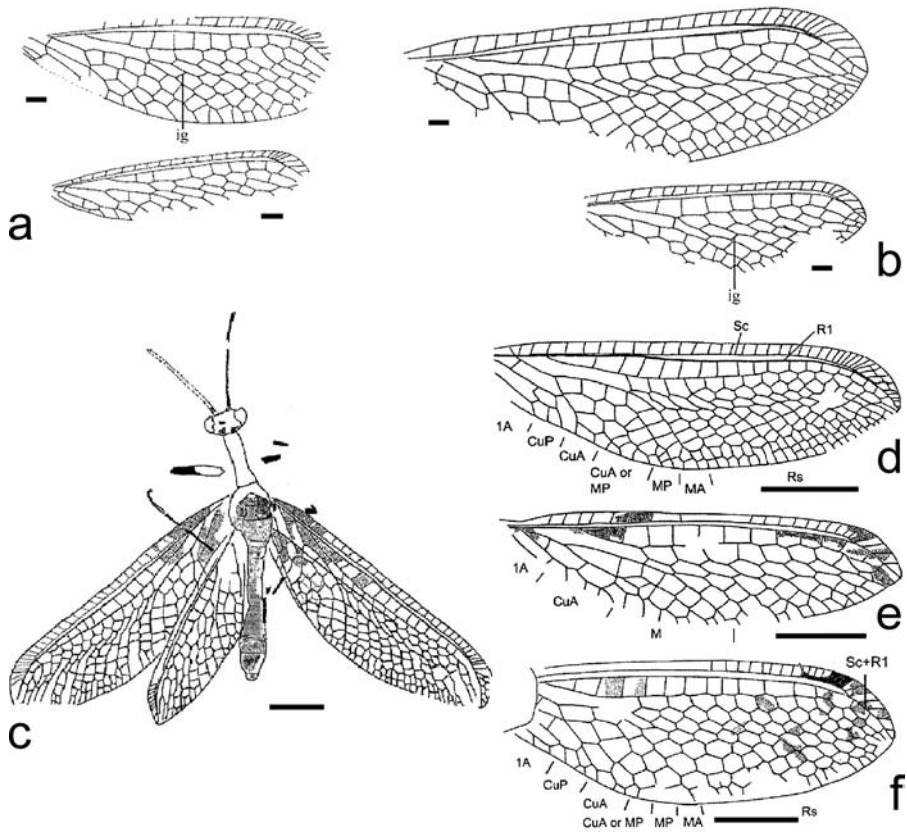

Fig. 11.62. Crato Formation Neuroptera: (a) *Armandochrysopa borschukewitzi* Nel, Delclo's and Hutin, 2005, forewing (above) and hind wing (below), holotype MNHN DHT-R55201, scale bar, 1 mm; (b) *Karenina breviptera* Martins-Neto, 1997, forewing (above) and hind wing (below); scale bars, 1 mm; (c–e) *Karenina longicollis* Makarkin and Menon, 2005, holotype, SMNS 65505; (c) complete specimen; (d) right forewing; (e) hind wing; (f) *Karenina leilana* Makarkin and Menon, 2005, holotype SMNS 66506, forewing. Scale bars: a, 1 mm; b–e, 5 mm. (a–b) After Nel and (2005); (c–f) after Makarkin and Menon (2005).

and 50 species of fossil Neuroptera described from the Crato Formation until then. Despite this, however, most forms described from the Crato Formation require re-description and a comprehensive revision of the fauna is still lacking. A complete list of the species and their current familial assignments is provided in the appendix.

Myrmeleontiformia

The Myrmeleontiformia includes some of the biggest and most impressive Neuroptera and comprises five Recent families: Psychopsidae (silky lacewings), Nemopteridae (spoon-winged and thread-winged lacewings; Plates 14c and d), Ascalaphidae (owlflies), Nymphidae (split-footed lacewings) and Myrmeleontidae

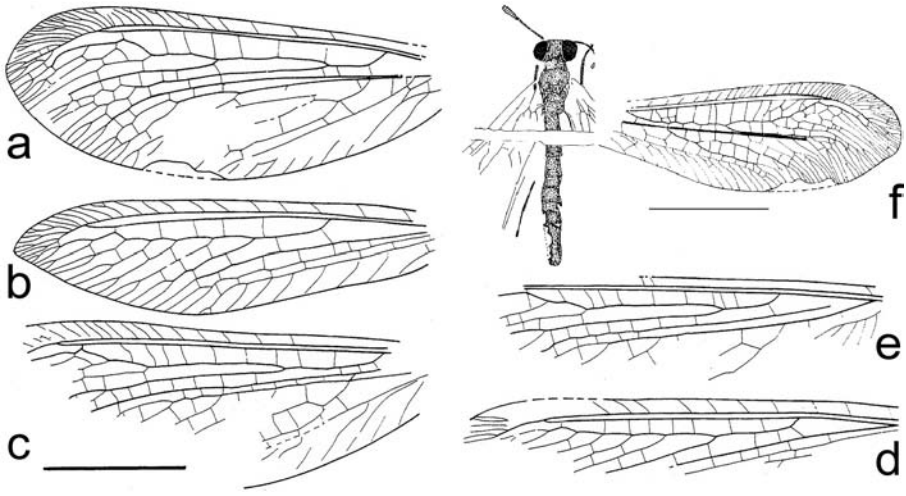

Fig. 11.63. Crato Formation Neuroptera: (a–b) *Caririneura regia* Martins-Neto and Vulcano, 1997, wing venation; (a) forewing; (b) hind wing; (c) *Caririneura crassatella* Martins-Neto and Vulcano, 1997, forewing of paratype, CV-995; (d, e) *Caririneura damianii* Martins-Neto, 1992, wing venation; (e) forewing; (d) hind wing; (f) *Paracaririneura priscila* Martins-Neto and Vulcano, 1997, holotype CV-6110. Scale bars, 5 mm. All figures after Martins-Neto and Vulcano (1997).

(antlions; Figure 11.69h). Of these, all but Psychopsidae are known from the Crato Formation, along with various extinct stem group 'myrmeleontoids' including Palaeoleontidae (Figure 11.69f, Plates 2e and 14b), Nymphitidae, Araripeneuridae, Babinskaiidae, Makarkiniidae, Brogniartiellidae and Kalligrammatidae. The assignment of *Pulchroptilonia espatifata* Martins-Neto, 1997a to Psychopsidae has to be reconsidered. Some 'families' described from the Crato Formation may be junior synonyms of crown group taxa (e.g. Roeslerianidae are without doubt plesiomorphic Nemopteridae and should at best be considered a subfamily of the latter) while others, such as Kalligrammatidae and Brogniartiellidae, likely represent stem groups to the Psychopsidae–Nemopteridae clade (Andersen, 2001; Grimaldi and Engel, 2005). The relationships of other groups are less clear. Palaeoleontidae are clearly 'myrmeleontoid' in general appearance (Heads *et al*., 2005) and may be a subgroup of Myrmeleontidae or a paraphyletic stem group. Araripeneuridae and Babinskaiidae likely represent stem groups to the entire Nymphidae–Myrmeleontidae–Ascalaphidae clade. A single myrmeleontoid larva of the antlion-type is known from the Crato Formation (Figure 11.69d).

Hemerobiiformia

The Hemerobiiformia is the most diverse group of Neuroptera and comprises 11 Recent families: Polystoechotidae (giant lacewings), Ithonidae (moth lacewings),

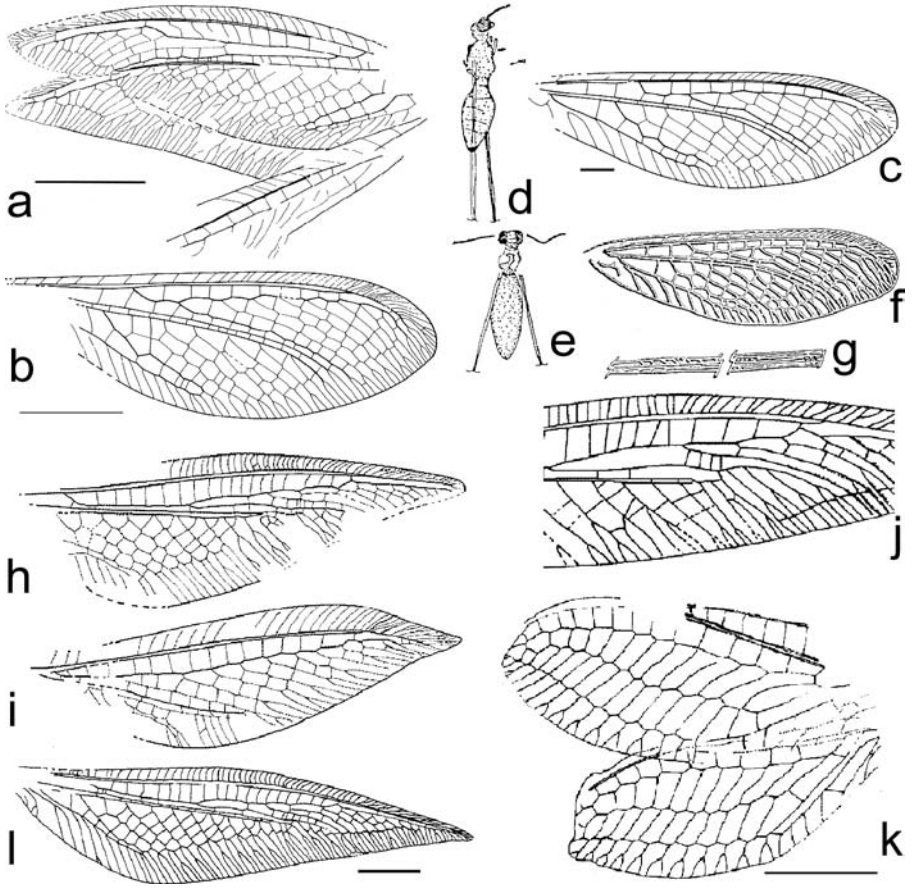

Fig. 11.64. Crato Formation Neuroptera: (a) *Cratoalloneura acuminata* Martins-Neto, 1992, CV-2712 fore- and hind wings; (b) *Cratonemopteryx speciosa* Martins-Neto and Vulcano, 1997, forewing; (c, d) *Cratonemopteryx audax* Martins-Neto, 1992, forewing and body respectively; (e–g) *Cratonemopteryx robusta* Martins-Neto, 1992, holotype, body, portion of forewing, portion of hind wing respectively; (h, i) *Cratoneura dividens* Martins-Neto, 1994 fore- and hind wings respectively; (j) *Cratoneura longissima* Martins-Neto, 1992; (k) *Mesypchrysa criptovenata* Martins-Neto, 1992, RGMN-T008, fore- and hind wings; (l) *Cratoneura dividens* Martins-Neto, 1994, forewing. (a–c, h–l) After Martins-Neto (1997); (d–f) after Martins-Neto (2000).

Osmylidae (osmylids), Chrysopidae (green lacewings), Hemerobiidae (brown lacewings), Coniopterygidae (dusty lacewings), Sisyridae (spongillaflies), Dilaridae (pleasing lacewings), Mantispidae (mantispids), Rachiberothidae (thorny lacewings) and Berothidae (beaded lacewings). Of the Recent hemerobiiforms, Osmylidae, Chrysopidae (Figure 11.69i), Hemerobiidae (Figure 11.70a), ?Sisyridae, Ithonidae (Figure 11.70b) and Berothidae are recorded from the Crato

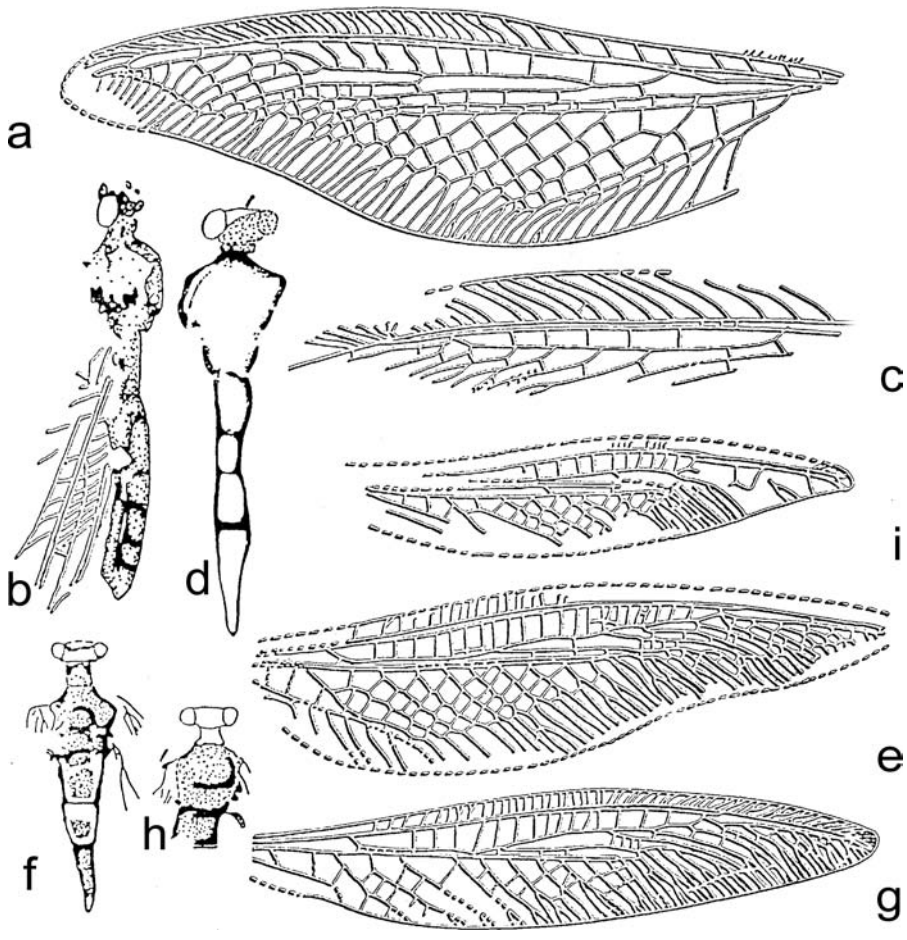

Fig. 11.65. Crato Formation Neuroptera: (a) *Cratoalloneura acuminata* Martins-Neto, 1992, forewing; (b) *Cratoalloneura acuminata* detail of body; (c) *Cratoalloneura acuminata* hind wing; (d) *Catoneura dividens* Martins-Neto, 1994, holotype body; (e) *Catoneura dividens* holotype forewing; (f) *Cratoneura longissima* Martins-Neto, 1992, holotype body; (g) *Cratoneura longissima* holotype forewing; (h) *Cratoneura pulchella* Martins-Neto, 1992, body of holotype; (i) *Cratoneura pulchella*, forewing of holotype. Based on Martins-Neto (2000).

Formation, along with the extinct chrysopoid families Mesochrysopidae (Figure 11.70c, Plate 15a), Limaiidae and Allopteridae (Figures 11.69e and g). Grimaldi and Engel (2005: 353) noted that *Cratosisyrops gonzagi* (Figure 11.66c), even though described by Martins-Neto (1997a) as earliest Sisyridae, has to be considered as *incertae sedis*. The Crato fauna is dominated by Chrysopoidea which have recently been revised by Nel *et al*. (2005).

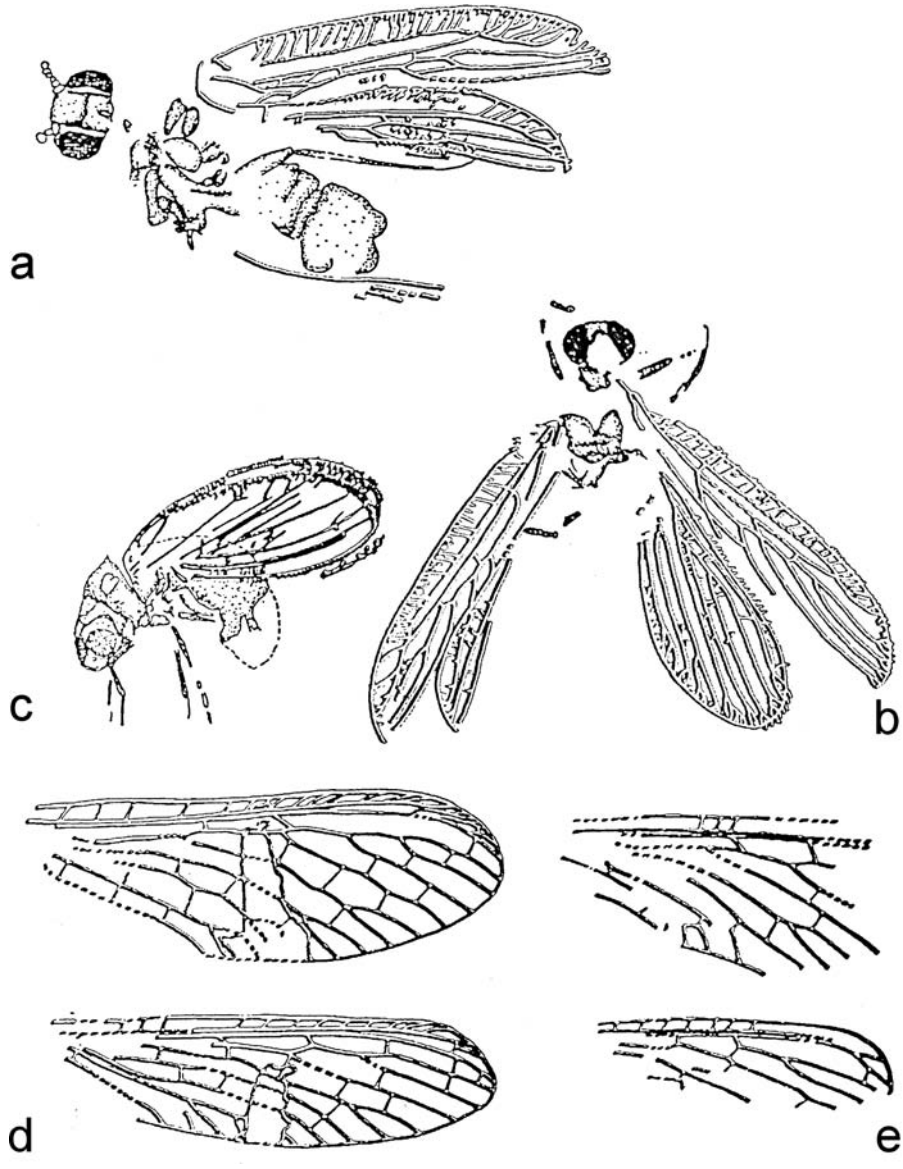

Fig. 11.66. Crato Formation Neuroptera: (a) *Caririberotha martinsi* Martins-Neto and Vulcano, 1990, holotype; (b) *Araripeberotha fairchildi* Martins-Neto and Vulcano, 1990, holotype; (c) *Cratosisyrops gonzagi* Martins-Neto, 1997, holotype, CV-1356; (d) *Cratochrysa wilmanni* Martins-Neto, 1997, forewing (above) and hind wing (below); (e) *Cratochrysa sublapsa* Martins-Neto, 1997, forewing (above) and hind wing (below). Figures based on Martins-Neto (2000).

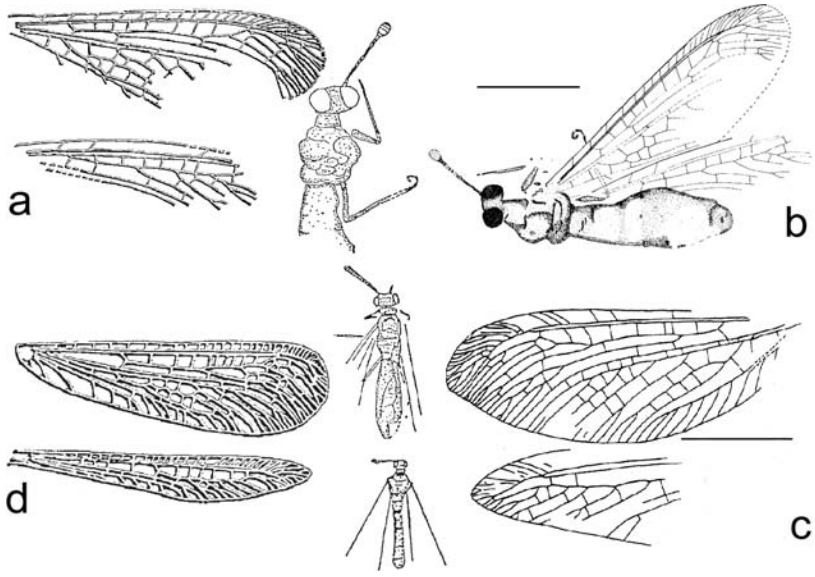

Fig. 11.67. Crato Formation Neuroptera: (a) *Caririneura crassatella* Martins-Neto and Vulcano, 1997, forewing (above), hind wing and body; (b) *Caririneura crassatella* Martins-Neto and Vulcano, 1997, holotype, CV-2461; scale bar, 5 mm; (c) *Caririneura damianii* Martins-Neto, 1992, forewing (above), hind wing and body, AMNH 43289; scale bar, 5 mm; (d) *Caririneura microcephala* Martins-Neto and Vulcano, 1989, forewing (above), hind wing and body. After Martins-Neto (2000) and Martins-Neto and Vulcano (1997).

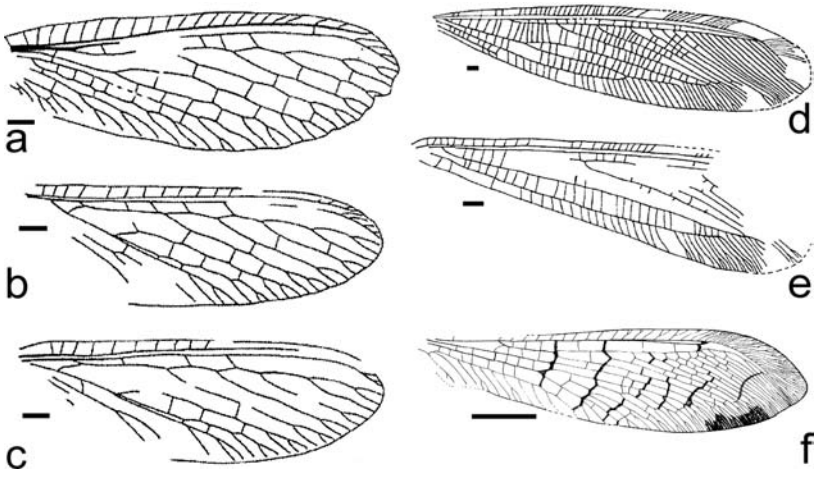

Fig. 11.68. Crato Formation Neuroptera: (a–c) Familia *incertae sedis*, *Cratochrysa martinsnetoi* Nel, Delclō's and Hutin, 2005; (a) holotype right forewing; (b) holotype right hind wing; (c) holotype left hind wing (reversed), MNHN-DHT R55224; (d, e) *Araripenymphes seldeni* Menon, Martins-Neto and Martill, 2005; (d), right forewing; (e) left hind wing (reversed); (f) *Blittersdorffia pulcherrina* Martins-Neto and Vulcano, 1997, holotype, coll. Vulcano no. CV-2080 m. Scale bars: a–e, 1 mm, f, 5 mm. (a–c) After Nel *et al.* (2005); (d,e) after Menon *et al.* (2005); (f) after Martins-Neto and Vulcano (1997).

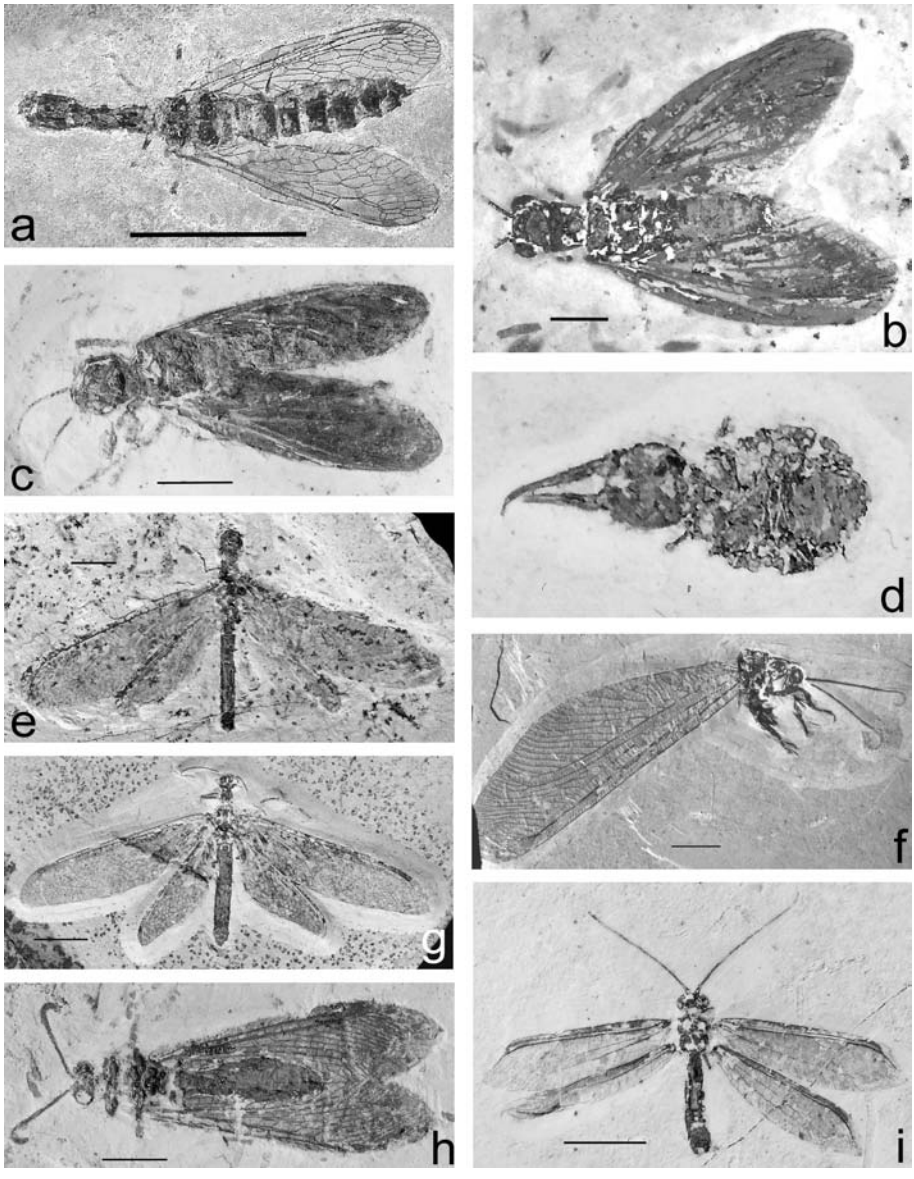

Fig. 11.69. Crato Formation Neuropterida: (a) Raphidioptera, Baissopteridae, *Baissoptera* sp.; scale bar, 10 mm; (b) Megaloptera gen. et sp. nov.; scale bar, 5 mm; (c) Megaloptera gen. et sp. nov.; scale bar, 5 mm; (d) Neuroptera, Myrmeleontiformia, Myrmeleontidae?, larva, MB coll.; (e) Neuroptera, Hemerobiiformia, Allopteridae, *Triangulochrysopa formosa*, SMNS coll.; (f) Neuroptera, Myrmeleontiformia, Palaeoleontidae, *Parapalaeoleon magnus*, holotype SMNS 66000-268; (g) Neuroptera, Hemerobiiformia, Allopteridae, *Triangulochrysopa formosa*, holotype SMNS 66000-271; (h) Neuroptera, Myrmeleontiformia, Myrmeleontidae, SMNS coll.; (i) Neuroptera, Hemerobiiformia, Chrysopidae, SMNS coll. Scale bars: b,c,e,h,i, 5 mm; a,f,g, 10 mm.

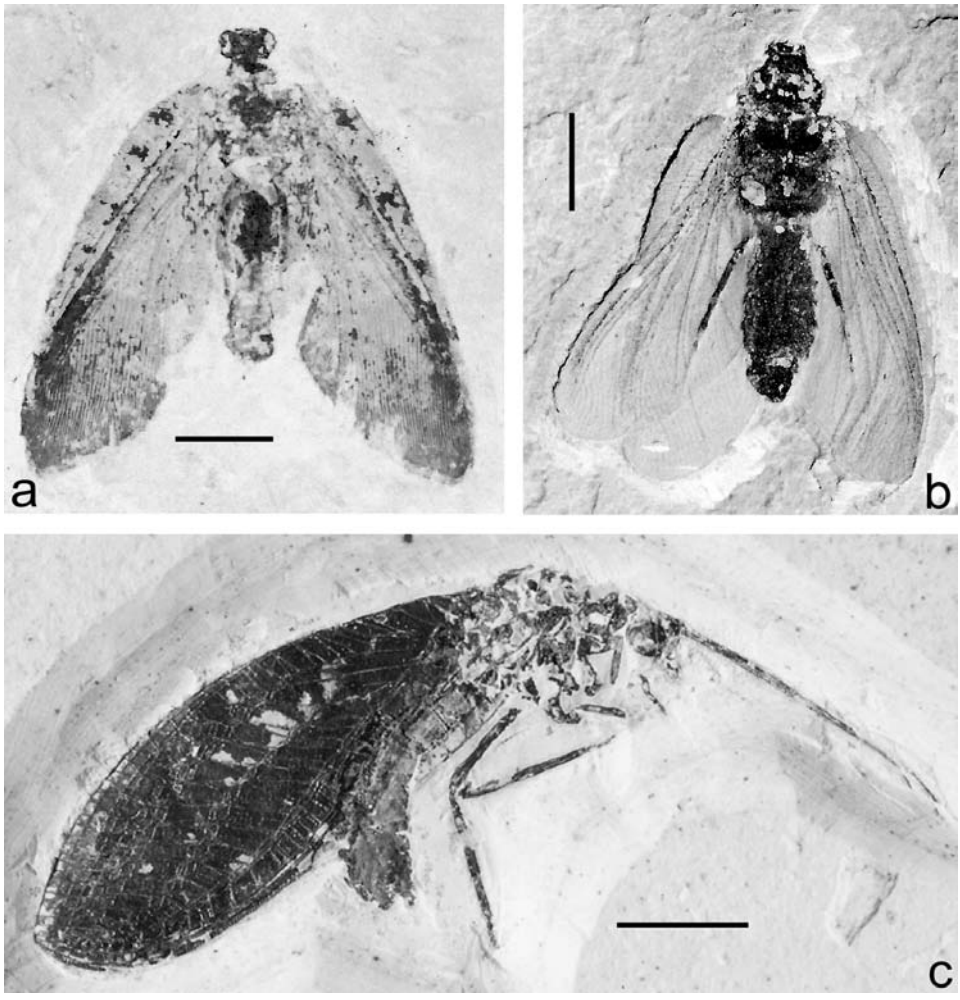

Fig. 11.70. Crato Formation Neuroptera, Hemerobiiformia: (a) Hemerobiidae gen et sp. undetermined, SMNS coll.; (b) Ithonidae *Principalia incerta* Makarkin and Menon, 2007, SMNK PAL 5352; (c) Mesochrysopidae undetermined, SMNS SMNK coll. Scale bars: a, 15 mm; b,c, 5 mm.

11.17 Coleoptera: beetles

Karin Wolf-Schwenninger and Wolfgang Schawaller

The Recent Coleoptera, with four suborders and 166 families (Lawrence and Newton, 1995), are probably the taxon with the highest number of species, not only among insects but also all other animals in general. Early estimates placed the figure at about 500,000 different species worldwide, but more recent studies on

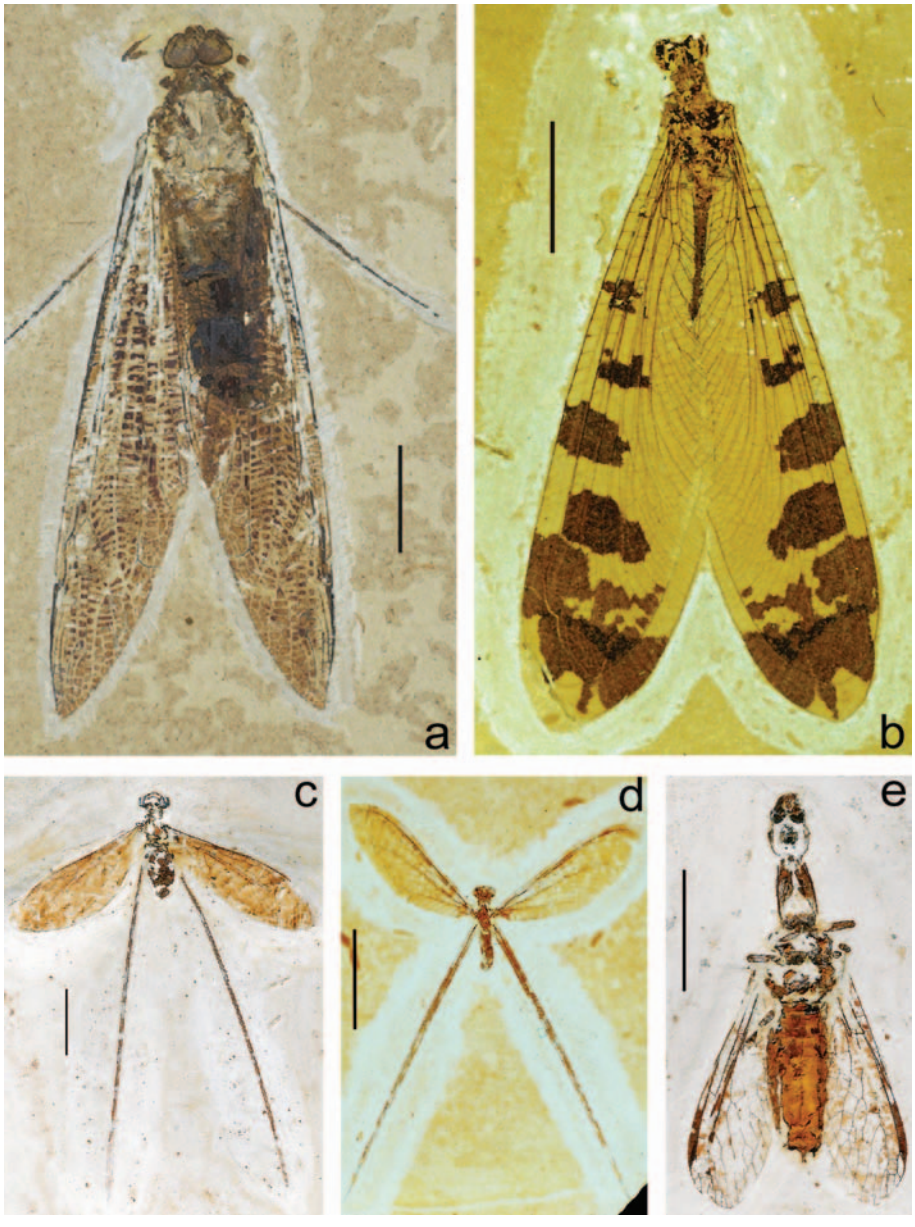

Plate 14. Crato Neuropterida: (a) Schwickertoptera Bechly ord. nov., *Rafaelia maxima* Nel *et al*. 2005, SMNS coll.; (b) Myrmeleontiformia, Palaeoleontidae, SMNS coll.; (c) Myrmeleontiformia, Nemopteridae sp. 2, SMNS 66000/260; (d) Myrmeleontiformia, Nemopteridae sp. 1, priv. coll.; (e) Raphidioptera, *Baissoptera* sp. Scale bars, 10 mm, except (e), 5 mm.

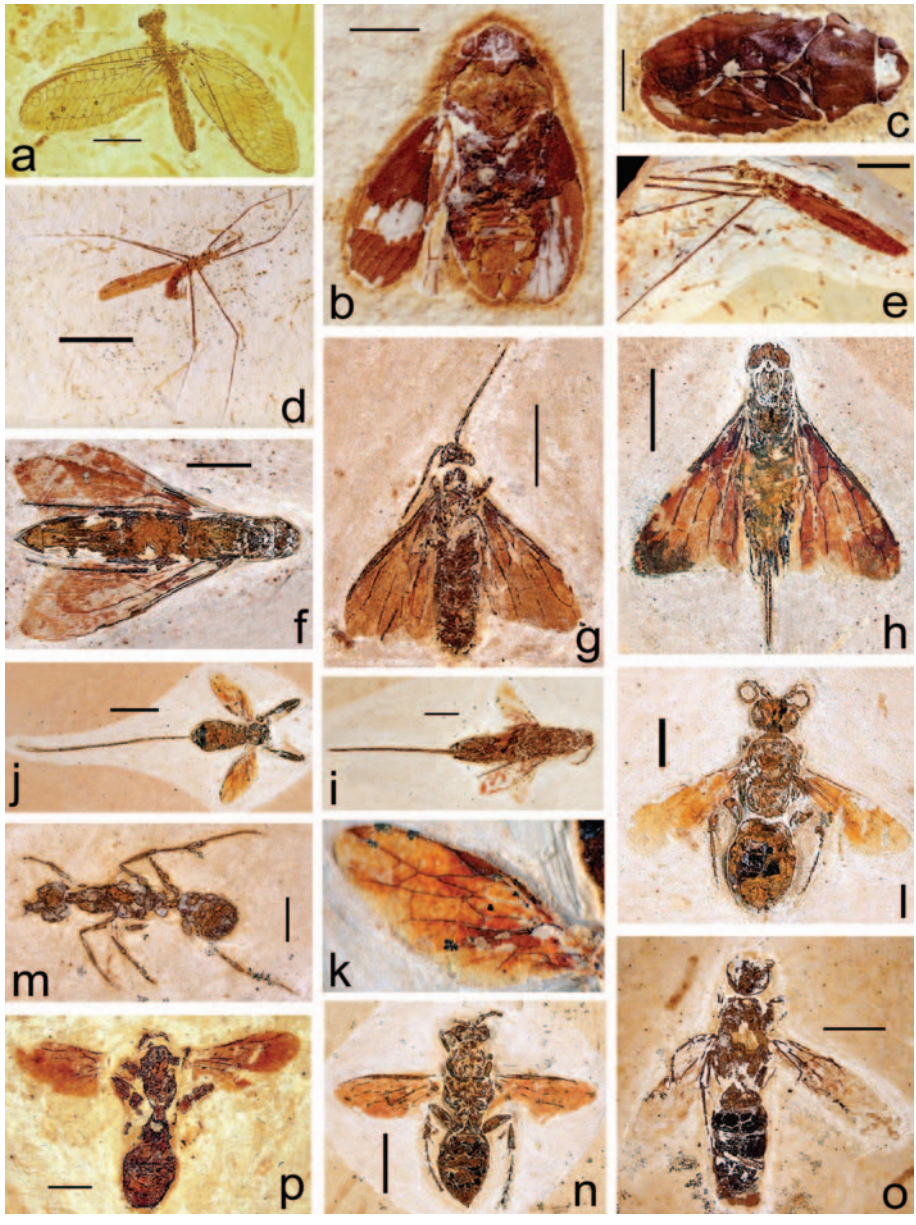

Plate 15. Crato insects: (a) Neuroptera, Hemerobiiformia, Mesochrysopidae gen. et sp. nov., priv. coll.; scale bar, 5 mm; (b) Coleorrhyncha, Progonocimidae gen. et sp. nov. SMNS 66423; scale bar, 2 mm; (c) Coleorrhyncha, Progonocimidae gen. et sp. nov. SMNS 66431; scale bar, 2 mm; (d) Chresmododea, Chresmodidae, *Chresmoda* sp. nov., SMNS prelim. no. 0134 (old no. H56), scale bar = 20 mm; (e) Chresmododea, Chresmodidae, *Chresmoda* sp. nov., ex MSF coll G88; scale bar, 10 mm; (f) Hymenoptera, Anaxyelidae, MURJ without number; scale bar, 5 mm; (g) Anaxyelidae, *Protsyntexis* sp., SMNS 66304; scale bar, 5 mm; (h) Siricidae, MURJ without number; scale bar, 5 mm; (i)?Ichneumonoidea, MURJ without number; scale bar, 5 mm; (j) Ephialtitidae, *Cretephialtites kourios*, MURJ without number; scale bar, 5 mm; (k) Ephialtitidae, *Cretephialtites kourios*, right wings, MURJ without number, without scale; (l) ?Pompilidae, MURJ without number; scale bar, 2 mm; (m) Formicidae, Myrmeciinae, *Cariridris bipetiolata*, SMNS 66565; scale bar, 2 mm; (n) Tiphiidae, *Architiphia rasnitsyni*, MURJ without number; scale bar, 5 mm; (o) Tiphiidae,?Myzininae, SMNS 66303; scale bar, 5 mm; (p) Vespidae, ?Eumeninae, SMNS 66295; scale bar, 2 mm.