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## Coniopterygidae (Neuroptera: Aleuropteryginae) in amber from the Eocene of India and the Miocene of Hispaniola

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### ABSTRACT

The genus *Spiloconis* Enderlein is comprised of six Recent Asian and Pacific species, ranging from Sri Lanka (and possibly Madagascar) in the west to eastern Australia and Fiji in the east. Two species previously described in Miocene amber from the Dominican Republic, *Spiloconis glaesaria* Meinander and *S. oediloma* Engel and Grimaldi, are redescribed for some details. *Spiloconis eominuta* Grimaldi and Engel, new species, is described in earliest Eocene Cambay amber from Gujarat, India, which has well-preserved male terminalia. *Neoconis paleo-caribis* Grimaldi and Engel, new species, is described from Dominican amber; this Recent genus is known from the southern United States and neotropics. The fossil *Spiloconis* may have significant biogeographic implications, but definitive determination of this requires a phylogenetic analysis of the 16 Recent genera in the monophyletic subfamily Aleuropteryginae. A Dominican amber–Australasian distribution pattern is known for 18 genera of insects in myriad orders (including *Spiloconis*), which are briefly reviewed.

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## INTRODUCTION

The Coniopterygidae is a family of approximately 560 described Recent species in 23 genera (Sziráki, 2011), comprised of diminutive lacewings that feed on small arthropods such as mites, aphids and scale insects. The family is definitively monophyletic, and the last major revisionary treatment was the monograph by Meinander (1972) on the world genera. Since then, there has been a world catalog of the species (Meinander, 1990; Sziráki, 2011), and various taxonomic treatments of particular faunas, the most notable being coverage of the Eurasian, North African, Arabian, and New Guinean faunas (e.g., Sziráki, 2004; Sziráki and van Harten, 2006). Unfortunately, as of yet there is no comprehensive phylogenetic treatment of the genera. The one molecular study utilized just a region of one gene with 15 exemplar species in nine genera (Wang and Liu, 2007). The fossil record of Coniopterygidae, in contrast, is well explored since these tiny lacewings are preserved in most major amber deposits from the Cretaceous and Tertiary periods.

Excluding species in copal (which are presumably Recent), some 21 fossil species in 13 genera are preserved in amber from eight localities, as follows: Lebanon (Hammana, Early Cretaceous, Neocomian: Whalley, 1980; Azar et al., 2000; Nel et al., 2005); France (Charante-Maritime, late Albian, Cretaceous: Nel et al., 2005); Myanmar (Kachin, Albian-Cenomanian boundary, Cretaceous: Engel, 2004); New Jersey (Raritan Formation, Turonian, Cretaceous: Grimaldi, 2000; Engel, 2002); Siberia (Taimyr Peninsula, Cretaceous: Santonian: Meinander, 1975); France (Oise, Les Quesnoys, Eocene: Nel et al., 2005); Baltic and the Ukraine (Eocene: Enderlein, 1910, 1930; Meinander, 1975; Dobosz and Krzemiński, 2000; Kupryjanowicz and Makarkin, 2008; Engel, 2010); and the Dominican Republic (Miocene: Meinander, 1998; Engel and Grimaldi, 2007). As yet, Coniopterygidae are unknown from amber of western Canada (Campanian: Late Cretaceous) or southern Mexico (Miocene). A summary of the fossil species in amber is provided in Engel and Grimaldi (2008), with additions by Kupryjanowicz and Makarkin (2008) and Engel (2010). There is a coniopterygid compression fossil from the Late Jurassic, *Juraconiopteryx zherichini* Meinander, but as described it is too poorly preserved for any meaningful interpretation (Meinander, 1975). It is interesting to note that most Cretaceous species, but not all, have three branches of the median vein in both wings, whereas all Tertiary and Recent species have two such branches in the forewing (*Archiconiocompsa prisca* Enderlein, 1910, in Baltic amber, has three *M* branches in the hind wing only). In lieu of a phylogenetic analysis, a three-branched vein *M* is probably plesiomorphic, and so many of these Cretaceous species are probably stem groups to Recent and Tertiary lineages.

The present report has primarily biogeographic significance. *Spiloconis* Enderlein today has six species, distributed according to Meinander (1990) in the Indo-Pacific Region from Sri Lanka in the west, east to eastern Australia and the Fijian archipelago, and also including Thailand, southern China, and the Philippines. Meinander (1972) also mentioned “possibly Madagascar” for the distribution of *Spiloconis*, in reference to the inadequate description of *Spiloconis nebulosa* Fraser, 1957, the type of which may be lost. Fossils of the genus in Miocene amber from the Dominican Republic (Meinander, 1998; Engel and Grimaldi, 2007) thus rep-

resent a dramatic range extension. Here we assess assignment of most of the Dominican species to *Spiloconis*, based on new specimens and restudy of the original specimens. According to Meinander (1998), *Spiloconis* is polyphyletic due to the dramatic differences in male genitalia, although phenetic disparity per se is not an index of relationships. This study was prompted by the discovery of two coniopterygids in a piece of amber from the Eocene of India, which also appear to be in *Spiloconis* or a related genus, and which are described here.

## MATERIAL AND METHODS

Dominican amber specimens, obtained from dealers, were originally excavated from mines just north of Santiago, Dominican Republic (reviewed in Grimaldi, 1995a). Age of the amber is Miocene, ca. 17–20 Ma (Iturralde-Vinent and MacPhee, 1996). Cambay amber from India was excavated directly by the authors from the Tadkeshwar lignite mines in Surat District, Gujarat state, India. Here, the amber is found in thick lignitic outcrops of the Cambay Shale Formation, dated as earliest Eocene, ca. 52 Ma. A review of the Cambay amber deposits and stratigraphy is provided by Rust et al. (2010). The Cambay amber is a dammar-type fossil resin, which is poorly cross-linked; most pieces, in fact, have interiors that are still tacky. Thus, it requires embedding in a high-quality synthetic resin to stabilize it and facilitate working with it. Embedding and preparation techniques followed that of Nascimbene and Silverstein (2000), with some modifications such as use of EpoTek-301 resin for the embedding. Material is deposited in the following repositories: **AMNH**, Division of Invertebrate Zoology, American Museum of Natural History, New York, New York, and **BSIP**, Birbal Sahni Institute of Palaeobotany, Lucknow, India. Those specimens from the large Cambay amber study (Rust et al., 2010) that derive from the Tadkeshwar mine have a database/collection number beginning with “Tad”; there are two such specimens in this study. Morphological terminology for the descriptive work follows that of Meinander (1972), and vein nomenclature is indicated in figure 5B.

## SYSTEMATIC PALEONTOLOGY

### Genus *Spiloconis* Enderlein

*Spiloconis* Enderlein, 1907: 6. Type species: *Spiloconis sexguttata* Enderlein, 1907, by original designation.

**DIAGNOSIS** (modified from Meinander, 1972): Frons largely membranous or faintly sclerotized, extending to clypeus. Antenna with 22–33 segments in Recent species, fossils with 17–24; scape large in Recent and some fossil species, length 3–4× width; pedicel large in Recent species, length 2.5–3× width. Forewing with 2 *M* setae; hind wing with basal fork of *Rs* in apical third of wing (vs. apical half), bases of *M* and *Cu* parallel and very close, separated by a distance approximately equal to diameter of vein. Male genitalia varied, stVIII (hypandrium) protruding apicad, scoop shaped in Recent species (see Meinander, 1972, for further description). Plicaturae on segments 2–7 in males, 2–6 in females.

*Spiloconis glaesaria* Meinander

Figures 1A, B; 2B; 4A

*Spiloconis glaesaria* Meinander, 1998: 33. Engel and Grimaldi, 2007: 19.

DIAGNOSIS: Oral margin in frontal view broad (width  $0.7\times$  the distance between compound eyes), much of frontal portion of head membranous/lightly sclerotized, most of it covered with fine setulae; dorsal margin of head barely protruding (cf. *Spiloconis oediloma* Engel and Grimaldi); wing with *r-rs* proximal to fork of  $R_{2+3}-R_{4+5}$  (i.e., *r-rs* connected to *Rs*); L/W basal discal cell 3.2; antenna with 21–22 flagellomeres (23–24 antennomeres), size of basal flagellomere nearly equal to that of other flagellomeres.

TYPE AND OTHER MATERIAL: Known only from Dominican amber. Holotype, AMNH DR14-1094, in clear yellow amber  $9 \times 4 \times 5$  mm in size, embedded in EpoTek 301 resin,  $12 \times 3 \times 5$  mm. The amber contains many bubbles, and the holotype is best observed ventrally. Meinander (1988) stated that the body of the specimen was covered with “wax” (a fine layer of which indeed coats most modern dustywings), but the fossil is actually covered with a milky froth, a preservational artifact common among inclusions in amber. Another specimen was reported (AMNH DR14-1094) with a photograph, in Engel and Grimaldi (2007). It is a well-preserved female in a small, clear yellow square of amber,  $4 \times 4 \times 1.5$  mm.

*Spiloconis oediloma* Engel and Grimaldi

Figures 1C; 2A; 3; 4B, C; 5A

*Spiloconis oediloma* Engel and Grimaldi, 2007: 19.

DIAGNOSIS: Distinguished from *S. glaesaria* by *S. oediloma* being slightly smaller species; oral margin in frontal view narrow ( $0.4\times$  width of distance between compound eyes); antenna with 20 flagellomeres, basal flagellomere significantly larger than distal ones; much of frontal portion of head membranous/lightly sclerotized, but with very sparse, fine setulae on only lower third of face; dorsal margin of head greatly protruding; wing with *r-rs* distal to fork of  $R_{2+3}-R_{4+5}$  (i.e., *r-rs* connected to  $R_{2+3}$ ), length of basal discal cell  $3.0-3.2\times$  of its greatest width.

DESCRIPTIVE NOTES: The forewing of DR15-421 (fig. 4C) is distinctive, having the base of *Rs* and the basal *rs-m* crossvein equal in length (i.e., the long stem of *Rs* is midway between *R* and *M*, forming a symmetrical V); also, *sc-r* and *r-rs* are in line and diagonal, not perpendicular to the longitudinal veins, and *m-cu* is diagonal to the adjoining longitudinal veins, not perpendicular. In DR14-1427 (fig. 5A), the wing has areas of infuscation that are darker and more extensive than in the other specimens, including a diffuse, longitudinal band in the distal discal cell. Also, the tips of the longitudinal veins are distinctly tapered before contacting the wing margin, and the anterior seta on *M* lies at the junction of the basal *rs-m* and *m-cu* (base of the forewing venation is unfortunately obscured). Other interesting details include the abdomen and appendages; abdominal segments 2–6 each with pair of plicaturae; plicature roughly tridentate in shape (fig. 3A); male genitalia (fig. 3B) relatively simple externally, with broad gonocoxae apparently fused to epandrium, aedeagus large and broad in lateral view, apically pointed; antenna with stout setae having blunt apices; tarsomere 4 much broader than other tarsomeres,



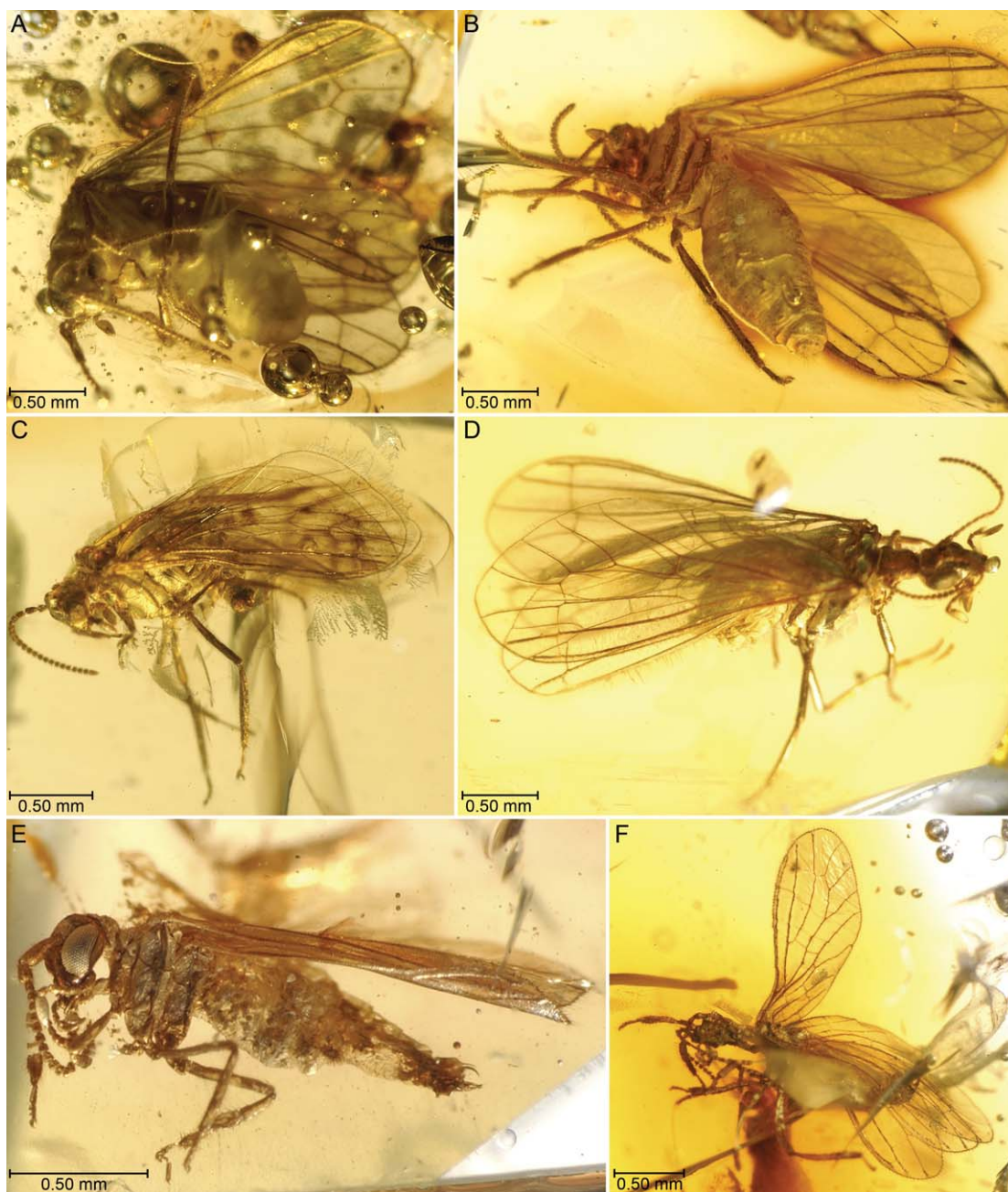


FIGURE 1. Photomicrographs of Aleuropteryginae in amber. **A–D:** In Miocene amber from the Dominican Republic. **A.** *Spiloconis glaesaria* Meinander, holotype, AMNH DR10-59. **B.** *S. glaesaria*, AMNH DR14-1094. **C.** *Spiloconis oediloma* Engel and Grimaldi, AMNH DR14-1427. **D.** *Neoconis paleocaribis* Grimaldi and Engel, new species, holotype, AMNH DR15-29. **E–F:** *Spiloconis eominuta* Grimaldi and Engel, new species, in Early Eocene Cambay amber from India; both are males. **E.** Holotype, BSIP Tad 316D. **F.** AMNH Tad 316B.

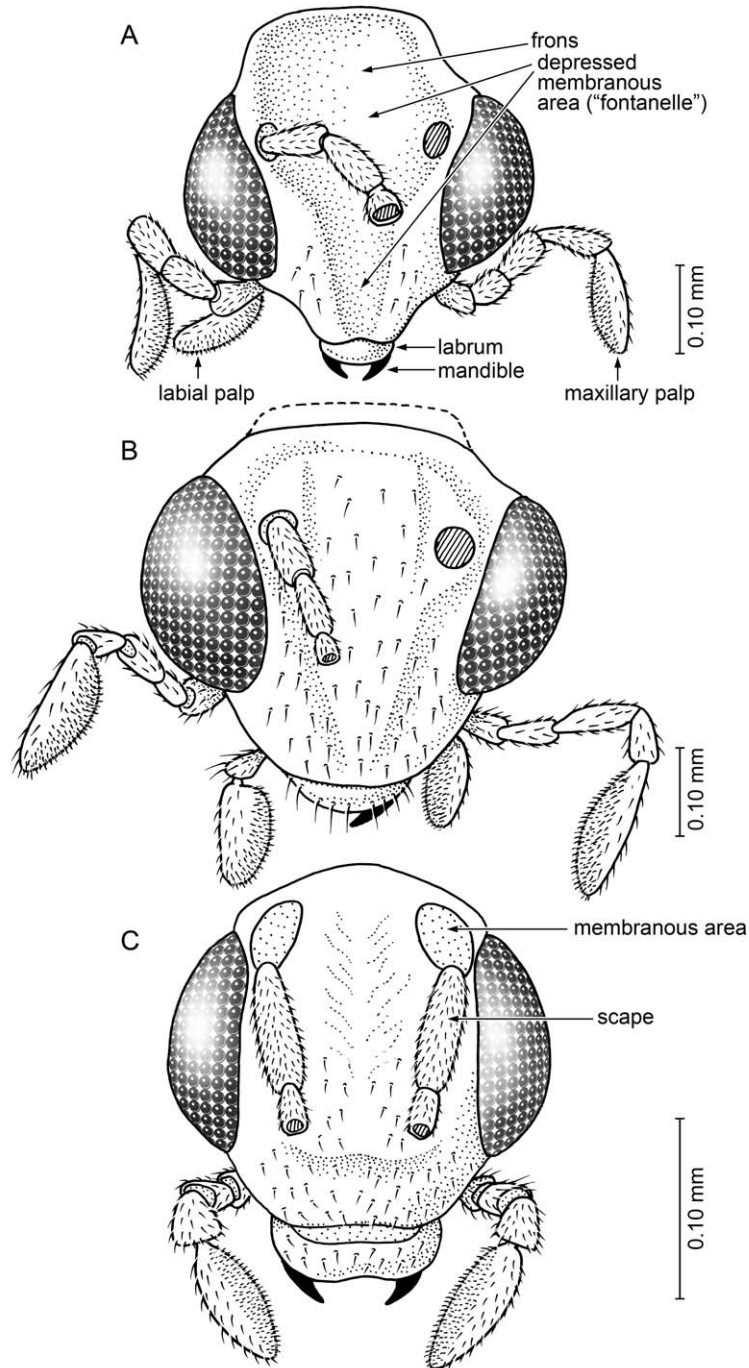


FIGURE 2. Frontal views of head of fossil species of *Spiloconis*. **A–B:** Dominican amber; **C:** Cambay amber. **A.** *Spiloconis oediloma* Engel and Grimaldi, AMNH DR15-421. **B.** *S. glaesaria* Meinander, holotype, AMNH DR10-59. Dashed line above head approximates dorsal margin. **C.** *S. eominuta* Grimaldi and Engel, new species, BSIP Tad 316D (reconstructed, based on right half of head). Note differences in scale between both A and B and C.

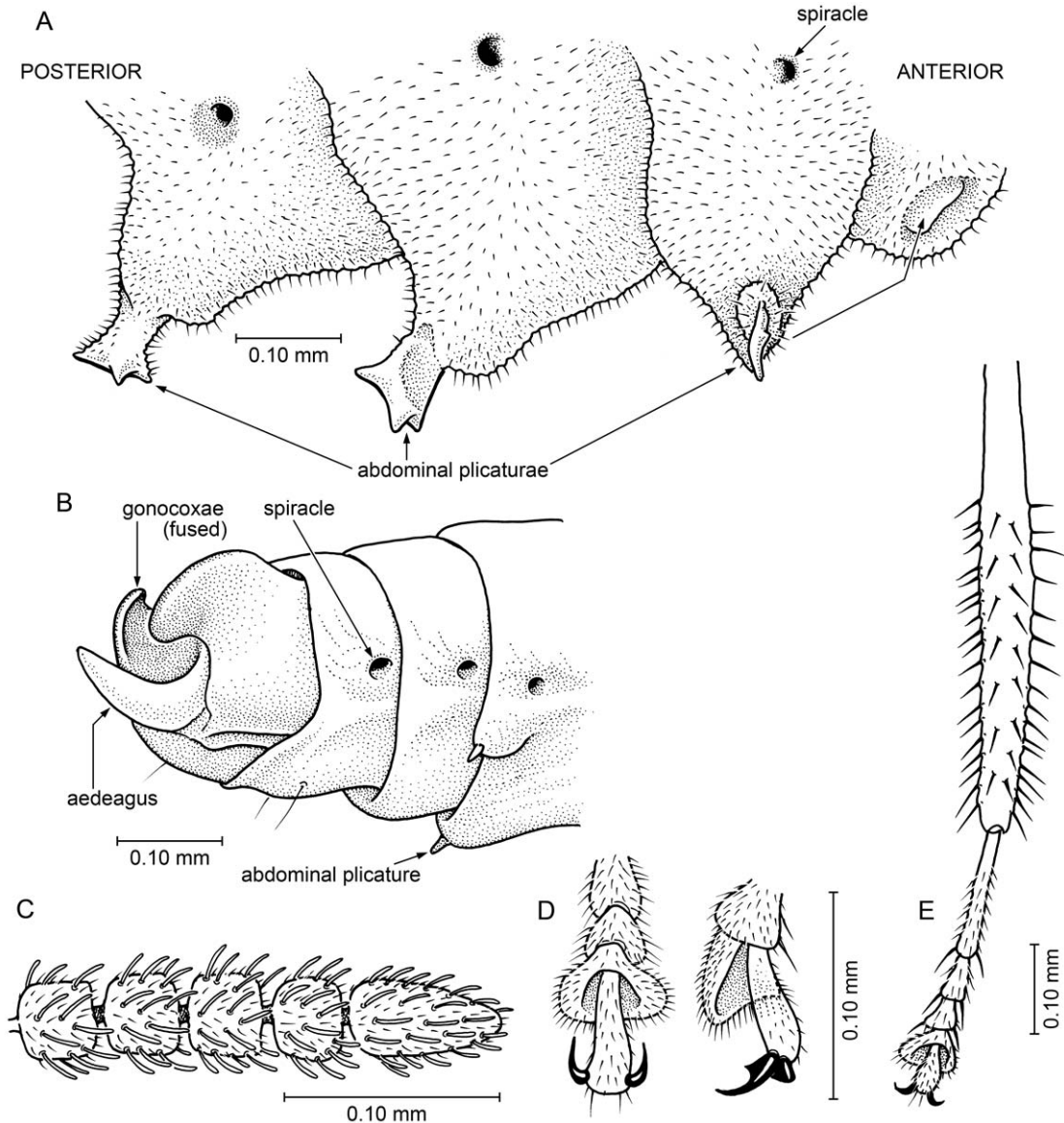


FIGURE 3. Features of *Spiloconis oediloma* Engel and Grimaldi in Dominican amber. A. Abdominal segments 2–5, AMNH DR14-1427. B. Male terminalia, AMNH DR15-421; oblique lateral view. C. Terminal five flagellomeres, AMNH DR14-1427. D. Detail of apical protarsomeres, AMNH DR14-1427; dorsal view and oblique lateral view. E. Mesotibia and mesotarsus, AMNH DR14-1427; dorsal view.

tarsomere 5 inserted into proximal end of tarsomere 4; tibiae with 4 longitudinal rows of stiff setae on dorsal and lateral surfaces, lengths of setae slightly less than width of tibia.

**TYPE AND OTHER MATERIAL:** Known only from Dominican amber. Holotype AMNH DR14-1097, in a clear, dark yellow amber  $2 \times 8 \times 10$  mm, filled with bubbles. Specimen is complete but partially obscured by some bubbles. Nontypes: Female, AMNH DR14-1427, a very well-preserved female in a small square ( $4 \times 3 \times 1.5$  mm) of clear yellow amber. Male,



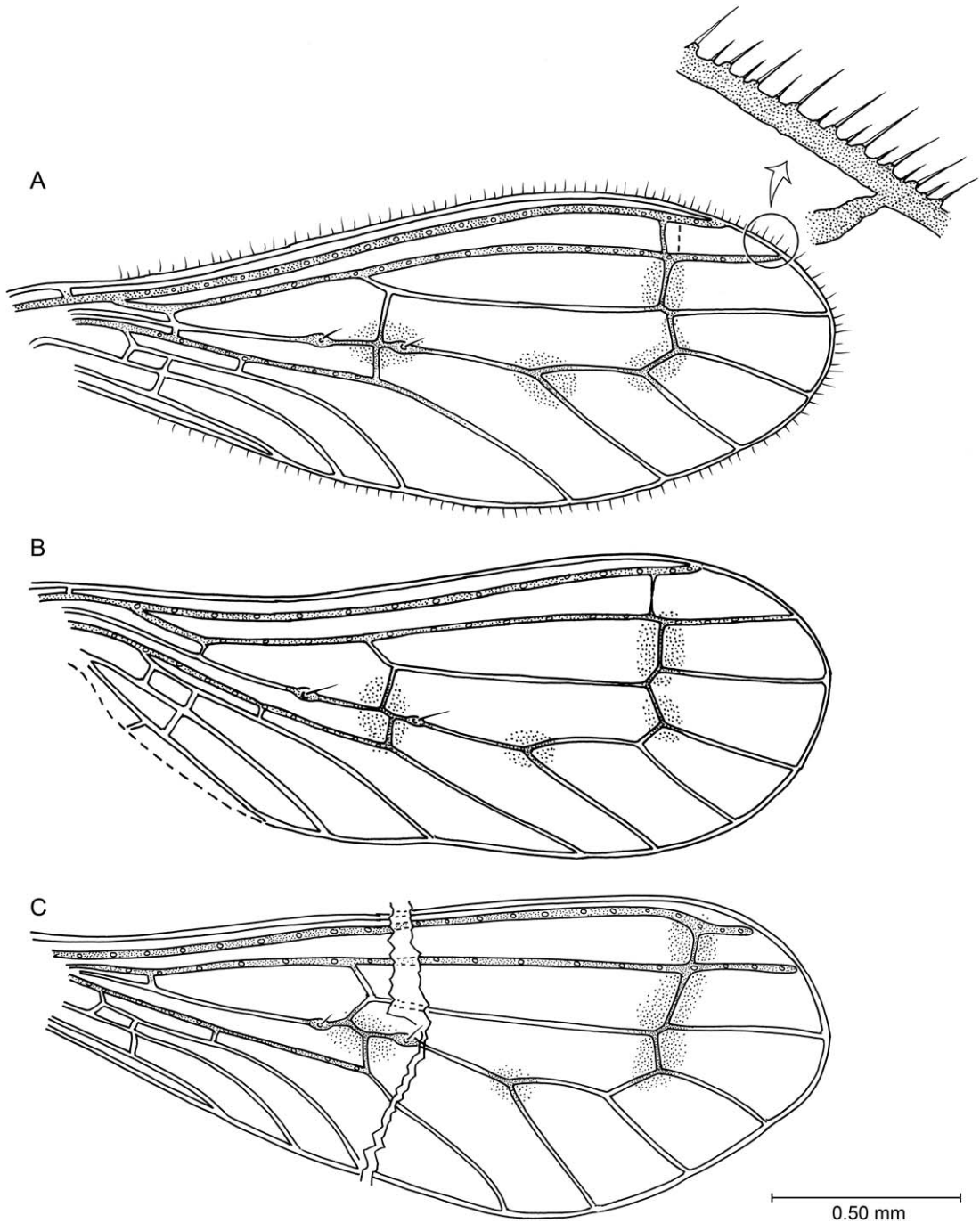


FIGURE 4. Forewings of fossil species of *Spiloconis* in Dominican amber. **A.** *Spiloconis glaesaria* Meinander, AMNH DR14-1094, also showing detail of costal setae. **B.** *S. oediloma* Engel and Grimaldi, holotype, AMNH DR14-1097. **C.** *S. oediloma*, AMNH DR15-421 (slightly reconstructed from fractured specimen). Costal setae omitted in B, C, and in figure 5.

AMNH DR15-421, well preserved but amber split in half, each half ca.  $8 \times 2 \times 2$  mm, one piece contains the body and basal portion of the wings, the other piece contains the apical half of the wings.

*Spiloconis eominuta* Grimaldi and Engel, new species

Figures 1E, F; 2C; 5C; 6

**DIAGNOSIS:** Known only from Eocene Cambay amber; very small species, forewing length 1.50 mm; front of head with cuticle weakly sclerotized, frons centrally with fine wrinkles (but not collapsed), oval membranous area just dorsal to antennal insertion; oral margin broad; scape large, antenna with 15 flagellomeres. Wing evenly fuscous, crossveins not clouded; with short basal cells (e.g., L/W of basal discal cell = 1.8); *M* with thickened, setigerous spot on each side of *1rs-m* and *m-cu* (*aMs*, *pMs* setae). Male genitalia as described and figured below.

**DESCRIPTION: Male.** Head: Narrow in lateral view, with long gena. Compound eye relatively large, length  $0.55\times$  that of head; compound eye L/W (in lateral view) ca. 1.8; posterior margin of compound eye slightly concave. Frons apparently not membranous but very weakly sclerotized, wrinkled medially; with sparse, fine setulae on ventral half of face and labrum; ovoid membranous areas dorsal to and contiguous with bases of scape (diameter of membranous areas slightly greater than that of scape). Scape large, length  $3\times$  greatest width, length ca.  $0.9\times$  depth of compound eye, expanded in width apicad (fig. 6A). Pedicel slightly larger than basal flagellomere. Antenna with 17 antennomeres (15 flagellomeres [only 13 visible in Tad-316D]); flagellomeres setulose, but without whorls; length and width of each flagellomere approximately equal. Maxillary palp with five palpomeres, apical palpomere large, slightly more than twice length of penultimate palpomere. Labial palps with three palpomeres, apical palpomere enlarged. Mesal surface of each apical palpomere with dense, short, fine mat of setulae. Labrum broad,  $0.70\times$  width between compound eyes (vs. ca. 0.50).

Thorax: Short, length in lateral view 0.35 mm, dorsally (with cervical and pronotal extension) 0.40 mm; mesopleuron largest segment, slightly thicker than pro- and metapleura. Legs: Femur and tibia of each leg approximately equal in length. Foreleg with tibia apically swollen (fig. 6B), having comb of fine, stiff, erect setae on ventral surface (some setae recurved); tarsomeres dorsally with dense, long setae (setal lengths approximately equal to diameter of tarsi); distal three tarsomeres with ventral mat of fine, dense setae; preapical tarsomere with expanded lateral lobes, cordate in shape.

Forewing: Length ca. 1.50 mm, width 0.60 mm (Tad-316B, fig. 5C), entirely fuscous, without any apparent clouds over crossveins. Crossvein *sc-r* slightly distal to *r-rs*; base of *Rs* and *1rs-m* approximately equal in length (fork symmetrical); basal discal cell very short, length  $2.0\times$  greatest width (vs.  $3.0\text{--}5.2$ ), basal medial cell concomitantly short, basal radial cell long (nearly equal in length to basal discal cell). Basal fork of *Sc-R* very distal to *h* crossvein, by  $5.5\times$  length of *h* (vs.  $1\text{--}2\times$ ); *m-cu* slightly proximal to *1rs-m* (vs. distal or opposite each other in other Tertiary and in Recent species); both *M* setae approximately equidistant from *1rs-m*; anterior cubital cell rather large, approximately equal in size to basal medial cell (vs.  $0.3\text{--}0.4\times$  the size).

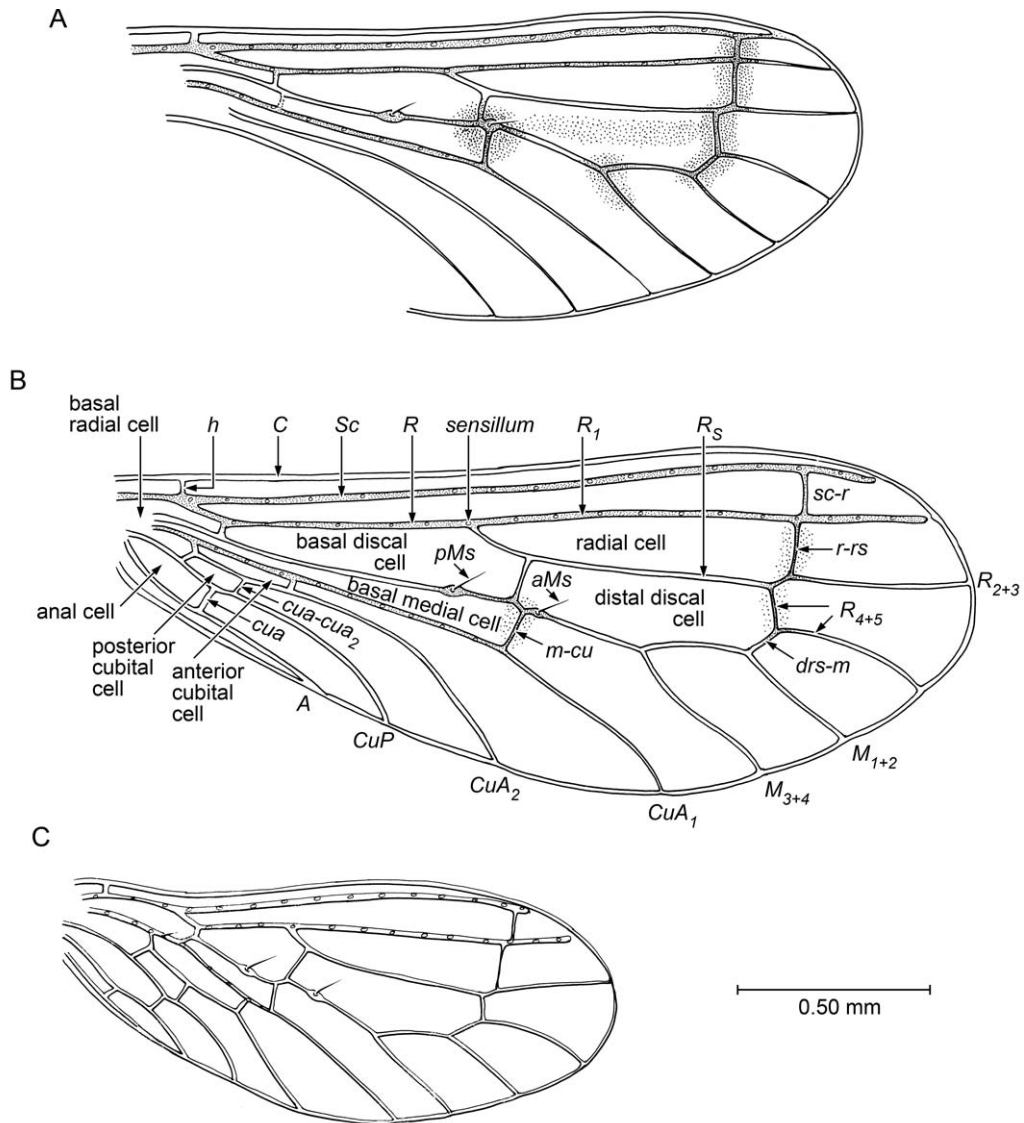


FIGURE 5. Forewings of fossil species of *Neoconis* and *Spiloconis* in Dominican (A, B) and Eocene Cambay amber (C). A. *Spiloconis oediloma* Engel and Grimaldi, AMNH DR14-1427, which shows extensive pigmentation. B. *Neoconis paleocaribis* Grimaldi and Engel, new species, holotype, AMNH DR15-29. C. *S. eominuta* Grimaldi and Engel, new species, paratype, AMNH Tad-316B.

Hindwing: Bases of veins *M* and *Cu* very close together and parallel, separated by distance approximately equal to diameter of either vein.

Abdomen: Number of pairs of abdominal plicaturae not entirely visible. Male terminalia well preserved, almost fully visible (fig. 6C, D). Male terminalia: Ventrally with very narrow, U-shaped hypandrium visible, posteriorly connected to pair of long, digitate parameres. Parameres with distinctive wartlike structures (possibly campaniform sensilla), each paramere with

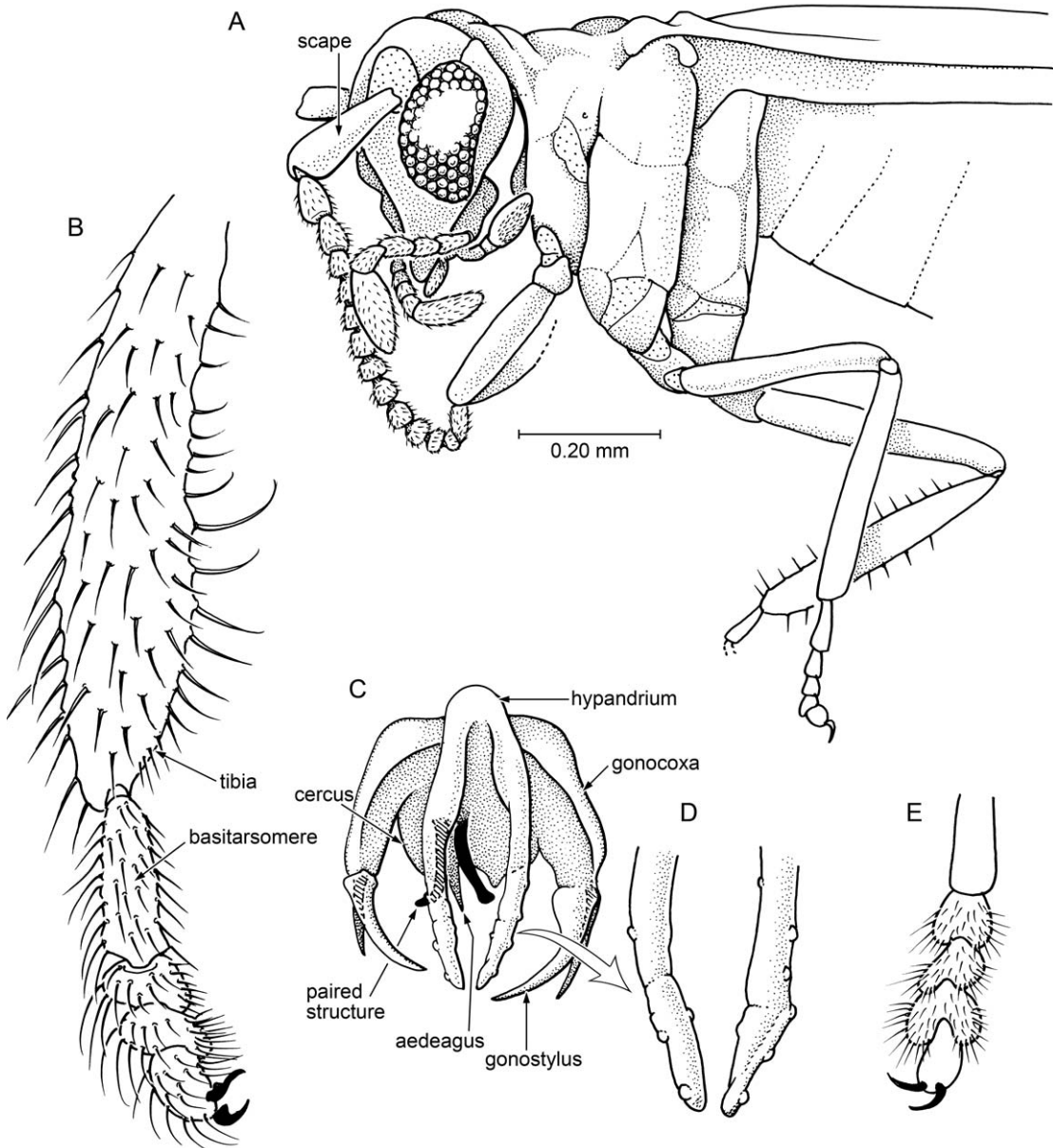


FIGURE 6. *Spiloconis eominuta* Grimaldi and Engel, new species, in Eocene Cambay amber. Holotype, BSIP Tad-316D. **A.** Left lateral view of anterior half of body. **B.** Lateral view of protibia and protarsus. **C.** Ventral view of male terminalia. **D.** Detail of parameres. **E.** Ventral view of mesotarsus.

faint transverse suture near midlength or distal third. Gonostyli fully articulated (not fused) to gonocoxae; gonostylus scimitar shaped, apically pointed; thin, pointed accessory lobe dorsal to each gonostylus, base of which articulates with gonocoxa. Aedeagus short, pointed, central structure (sclerotization difficult to discern), flanked by pair of clavate, sclerotized lobes approximately equal in length to aedeagus (the gonarcus, or styli, sensu Meinander, 1972).



**Female.** Unknown.

TYPE MATERIAL: Holotype, male, Tad-316D, in BSIP. Paratype, male, Tad-316B, in AMNH. Both specimens were in the same piece of turbid amber, but were embedded in EpoTek and the inclusions then separated. Tad-316D also contains a small beetle and midge, and occurs in an irregular piece of amber  $1 \times 2 \times 3$  mm; wings are mostly obscured, right side of the head is collapsed into the head capsule, and most of the abdomen is compressed; however, the thorax and terminalia are very well preserved, and the latter with its minute structures very well displayed (figs. 6B, C). Tad-316B is in a piece of amber  $1 \times 3 \times 6$  mm, with the wings and legs well displayed (fig. 1F, 5C), though basal portion of the venation required slight reconstruction; head and much of the body is compressed, and most of the genitalia is obscured.

ETYMOLOGY: The specific epithet is a combination of *eo*-, from “Eocene,” the geological epoch from which the amber derived, itself derived from the Greek *eos*, for “dawn” or “early,” and Latin *minutus*, in reference to the small body size.

**Genus *Neoconis* Enderlein**

*Neoconis* Enderlein, 1930: 112. Type species: *Helicoconis pistrinx* Enderlein, 1906, by original designation.

COMMENTS: The genus comprises 16 modern species occurring in the southern Nearctic southward to southern Brazil, Bolivia, and Paraguay and west to the Virgin Islands (Sziráki, 2011). The species geographically closest to *Hispaniola* are *Neoconis cubana* (Banks, 1938), which is recorded from Cuba and Dominica; *N. insulana* (Meinander, 1974) from Jamaica; and *Neoconis bispina* Meinander, 1972, from the Virgin Islands.

***Neoconis paleocaribis* Grimaldi and Engel, new species**

Figures 1D, 5B, 7

DIAGNOSIS: Larger than the other two Dominican amber aleuropterygines (forewing length 2.4 mm); distinguished by short scape and wing with long basal discal cell ( $L/W = 5.0$ , vs.  $3.2\text{--}4.1$ ). Distinguished from Recent species of the genus (all New World) based on following: 20 flagellomeres, basal 7–8 ones distinctly longer and thinner; dorsal half of frons membranous, ventral half with pair of lateral membranous lines only; forewing with two *M* setae on each side of basal *rs-m* and *m-cu* (vs. *pMs* on junction of *rs-m* and *M*); hind wing with bases of *CuA* and *M* separated by distance of  $3\text{--}4\times$  diameter of veins.

DESCRIPTION: **Female.** Largest fossil species in amber, wing length 2.4 mm. Head: Compound eye large and deep, depth more than  $2\times$  width,  $0.5\times$  depth of head. Frons entirely covered with fine, light setulae; depressed in large circular area between and surrounding antennae (apparently membranous, without any sclerotized spots in center); ventral to this area with pair of weak, membranous lines laterally, but area between lines not depressed or collapsed (either membranous or lightly sclerotized, not forming “tongue” of membrane

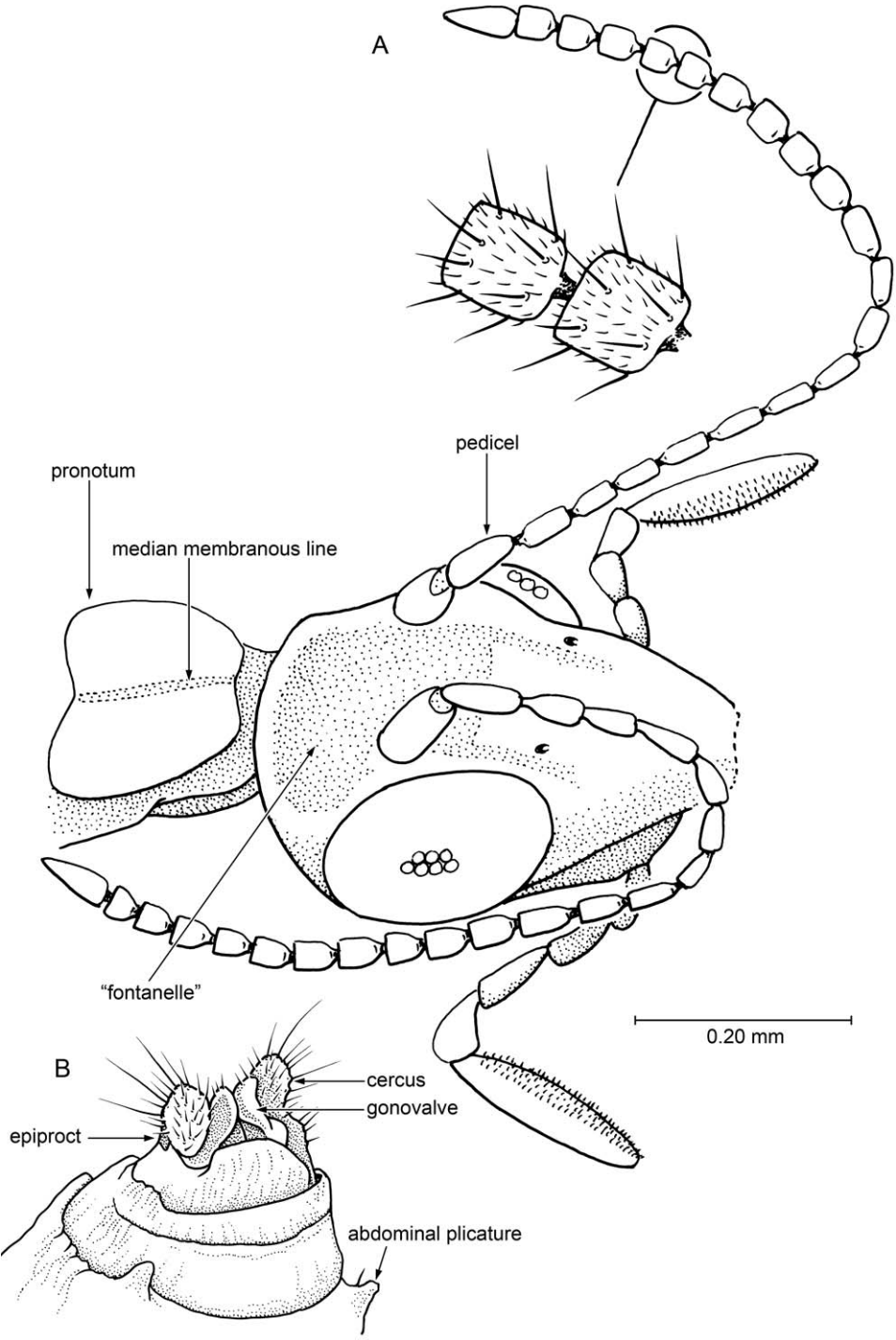


FIGURE 7. *Neoconis paleocaribis* Grimaldi and Engel, new species, in Dominican amber. Holotype, AMNH DR15-29. A. Head and pronotum, dorsolateral view. B. Female terminalia, oblique terminal view.

contacting clypeus). Membranous lines on frons do not extend to clypeus; anterior end of each line with well-defined anterior tentorial pit. Portion of head ventral to compound eyes deep, nearly equal in length to depth of compound eyes. Antenna with short, stout scape, length slightly greater than width; scape slightly wider than pedicel, lengths of both approximately equal and  $1.3\times$  longer than longest flagellomere. Antenna with 22 segments (20 flagellomeres), basal 7–8 flagellomeres distinctly longer and thinner than apical ones; preapical 11 flagellomeres approximately square in shape, apical flagellomere with tapered apex. Flagellomeres with very fine setulae only, not arranged in whorls. Maxillary palp with five segments; basal four segments small, apical segment large (length approximately equal to that of segments 2–4). Labrum narrow.

Thorax: Pronotum cordate, with slightly emarginate posterior margin; median line of pronotum membranous. Pleuron with sutures between thoracic segments arrayed at angle distinctly oblique to dorsal margin and parallel to each other. Legs slender, tibiae not swollen apically; apex of each tibia dorsally with thin, blackish, cuticular extension. Femora virtually bare; tibiae with faint longitudinal rows of light, short, sparse setae (setal lengths no more than  $0.6\text{--}0.7\times$  width of tibia). Tarsus: Basitarsomere slender, approximately equal in length to tarsomeres 2–5; distitarsomere (t-5) inserted into base of preapical tarsomere (t-4), not into apex; preapical tarsomere with two large lobes.

Forewing: Length 2.40 mm; nearly entirely hyaline, with extremely faint, small areas of infuscation over crossveins *sc-r*, *r-rs*, and *m-cu*. Crossvein *sc-r* slightly distal to *r-rs*; base of *Rs* slightly longer than *1rs-m* (= proximal *rs-m*), *1rs-m* nearly perpendicular to *Rs* (fork asymmetrical); basal discal cell long and slender, length  $4.6\times$  greatest width; basal medial cell extremely long and slender, length  $7.0\times$  greatest width, basal radial cell short ( $0.3\times$  length of basal discal cell). Basal fork of *Sc-R* slightly distal to level of *h* (humeral, or *c-sc*, crossvein); *m-cu* slightly distal to *1rs-m* (vs. distal or opposite each other); *aMs* (= apical *M* seta) approximately half distance from *1rs-m* than is *pMs* (= proximal *M* seta); anterior cubital cell narrow,  $0.3\times$  length of basal medial cell. Hindwing: Length of forked segments of *Rs* approx.  $0.3\times$  total length of *Rs*; bases of veins *M* and *Cu* not very close, separated by distance  $3\text{--}4\times$  diameter of either vein.

Abdomen: Five pairs of plicaturae in pleural membrane of segments 2–6; plicaturae on segments 3–6 flat and fan shaped, without pointed corners (cf. fig. 3C); plicaturae on segment 2 minute, budlike. Spiracles visible on segments 2–6. Female terminalia: Small, cerci small, ovoid, with apical setae longer than length of cercus; pair of small, scoop-shaped lobes medial to cerci (gonovalves); epiproct and hypoproct small, triangular sclerites.

**Male.** Unknown.

**HOLOTYPE:** Female (unique specimen), AMNH DR15-29, in an irregular piece of clear yellow amber  $7 \times 4 \times 2$  mm containing no other inclusions; from the Dominican Republic (specific provenance unknown). Deposited in AMNH.

**ETYMOLOGY:** The specific epithet is a combination of Greek *paleo*, for “ancient,” and Spanish *caribe*, in reference to the Caribbean (Hispaniolan) origin of the fossil.

## DISCUSSION

**Relationships.** All four species presented here clearly belong to the subfamily Aleuropteryginae (vs. Coniopteryginae), based on the following synapomorphic features: presence of abdominal plicaturae (found in both sexes on segments 2–6); two crossveins (vs. one) between veins *Rs* and *M* in the forewing; *M* with two fine, stiff setae, each with a socketed base situated in a thickened portion of the vein (these setae are lost in *Aleuropteryx* Löw). Zimmerman et al. (2009) hypothesized that the abdominal plicaturae are part of the ground plan of Coniopterygidae, and lost or highly reduced in Coniopteryginae. Other defining features of Aleuropteryginae cannot be observed in the fossils, namely, galea segmentation (three segments in Aleuropteryginae), and the number of pairs of abdominal spiracles (eight). A distinctive venational feature, where the bases of *M* and *Cu*<sub>1</sub> in the hind wing run very close to each other, cannot be observed in some of the Dominican amber specimens, but this feature definitely occurs in *S. eominuta*.

Unfortunately, discerning the relationships of the fossils to the Recent genera is compromised by a very modest understanding of relationships in the Coniopterygidae in general. Meinander's (1972) excellent monograph notwithstanding, his attempt at resolving relationships in the Aleuropteryginae (Meinander, 1979) was based on only 18 morphological characters for the 12 genera then recognized in the subfamily, at least eight characters of which autapomorphically define individual genera. Many of the characters are based on the complex male genitalia, which are mostly internal (and so are largely inaccessible in fossils), and individual genitalic structures are difficult to homologize as illustrated by Meinander (1972). Moreover, some of the characters are either homoplasious or improperly coded, such as the absence (putative loss) of the *M* setae and the nearly contiguous bases of veins *M* and *Cu* in the hind wing (occurring in the putative sister genera *Cryptosceneae* Enderlein and *Paraconis* Meinander and the unrelated genus *Aleuropteryx*). A distinctive feature, and one that pertains to the fossil taxa, is the presence of a large unsclerotized or membranous area on the frons that extends to the clypeus (the "fontanelle," not at all homologous with that in Isoptera and Zoraptera), which is convergently developed in the tribe Fontenelleini and in the genus *Spiloconis* according to Meinander (1972, 1979). A similar structure occurs in *Heteroconis* Enderlein, though in many species of this genus the "fontanelle" is also partly covered by a sclerotized flap. It is counter-intuitive to interpret such a distinctive character as the "fontanelle" as convergently developed.

These concerns in mind, the Cambay and two of the three Dominican amber Coniopterygidae appear most closely allied with *Spiloconis*, on the basis of a combination of distinctive features. First, the shape of the membranous "fontanelle" in the Dominican amber species is most like that of the Recent species of the genus, which includes a tongue of membranous area that extends to the clypeus. The size of the antennal scape and pedicel of the Dominican species, however, are relatively small for the Recent species of the genus. In this regard, the large scape of *S. eominuta* is very much like that of Recent *Spiloconis*, as is the closeness of hind wing veins *M* and *Cu*.



Two aspects of *Spiloconis eominuta* differ significantly with *Spiloconis*. First, the frons does not appear to be membranous, though the fine wrinkling of this area indicates a very weak sclerotization of the cuticle (also, the right half of the head is collapsed within the head capsule, making it difficult to observe a “fontanelle” with certainty). Second, the male genitalia—which are very well preserved and displayed in one specimen (probably from compression of the abdomen, causing eversion of terminal structures)—appear most similar to *Helicoconis capensis* Enderlein, 1914, as figured by Meinander (1972). *Helicoconis capensis* occurs in southern Africa. Male terminalia of *S. eominuta* and *H. capensis* both possess, for example, a thin, curved, pointed gonostylus flanked by an accessory lobe of similar shape (in *S. eominuta*, the accessory lobe articulates with the gonocoxa, in *H. capensis* it is attached to the base of the gonostylus); as well as possessing a short, pointed aedeagus flanked by a pair of sclerotized, clavate lobes. The two species differ most notably in that *H. capensis* has no *M* setae in the forewing. Also, the large, digitate parameres in *S. eominuta* are similar to those in *Vartiana necopinata* Aspöck and Aspöck, 1965, known from Central Asia.

There is little doubt that *N. paleocaribis* belongs to the Recent genus *Neoconis*, based on the proportions of scape and pedicel, the long basal-discal cell (a feature not mentioned by Meinander, 1972), and especially by the fact that some flagellomeres are significantly longer than wide. The gonovalves labeled in figure 7B probably are the pair of “free gonapophyses laterales” mentioned by Meinander (1972), which are apparently distinctive to the genus. The fossil lies within the present distribution of the genus, namely, from the southern United States (Texas, Arizona) in the north, through Central America and the Caribbean (Greater Antilles), and south to Peru.

**Biogeography.** The preponderance of taxa preserved in Dominican amber have their closest relatives in the Recent fauna of the West Indies and Central America, less so South America or southern portions of North America. There are, however, some relationships between the Dominican paleofauna and the Old World fauna. Surprisingly, most of these Old World connections involve Australia, Australasia, or the Indo-Pacific rather than the Palearctic or Ethiopian Regions. Examples include the stag beetle genus *Syndesus* MacLeay (Lucanidae), which today occurs in Australia (Woodruff, 2009). The fly family Valeseguuyidae is a relict sister group to the Scatopsoidea (which includes scavenger gnats, Scatopsidae, and their relatives), with one species in Dominican amber, one in Cretaceous amber from Myanmar, and one very rare species living in northern Australia (Grimaldi, 1991; Amorim and Grimaldi, 2005). This is a similar distribution to the scuttle fly genus *Abaristophora* Schmitz (Phoridae), the Dominican amber species of which most closely resembles species in New Zealand and Nepal (Brown, 1999).

Two genera of apterygote insects, which obviously have very limited vagility, show a similar distribution. The archaeognathan *Trinemurodes* Silvestri is represented by two species in Dominican amber and by two Recent species in the Malesian area (Sturm and Mendes, 1998). The silverfish genus *Hemitrinemura* Mendes occurs in the western Indo-Pacific and Dominican amber (Mendes and Poinar, 2004). Marine water striders of the genus *Halovelis* Bergroth (Veliidae), which presumably would have excellent dispersal ability, occur in the Indian Ocean to the southeastern Pacific; oddly, a species occurs in Dominican amber. Other Dominican amber–Old World affinities involve flies of the genus *Ogcodes* Latreille (Acroceridae) (Grimaldi,

1995b), some protopausine beetles (Carabidae) (Nagel, 1997), the oxyteline rove beetle *Dolichoxenus* Engel and Chatzimanolis (Staphylinidae) (Engel and Chatzimanolis, 2009), and the unusual, apterous wasp genus *Masona* van Achterberg (Braconidae), which has strikingly similar species in Dominican amber and from Queensland, Australia (van Achterberg, 2001).

At least four genera of ants show a Dominican–Old World connection. There are two fossil species of *Aphaenogaster* Mayr, one in Dominican amber the other in Mexican amber, whose closest living relatives occur in Madagascar, India, and southeast Asia (Andrade, 1995). Other genera include *Acropyga* Roger (LaPolla, 2005) and *Discothyrea* Roger (Andrade, 1998). Lastly, the genus of “spider ants,” *Leptomyrmex* Mayr, occurs in the Recent of eastern Australia, New Caledonia, and New Guinea, with one species in Dominican amber (Baroni-Urbani, 1980; Baroni-Urbani and Wilson, 1987) as well as a fossil species in Eocene Cambay amber from western India (Rust et al., 2010). Such a Recent and fossil distribution is quite similar to *Spiliconis*, described here, as well as to bugs of the subfamily Leptosaldinae (Rust et al., 2010). Naturally, intensive cladistic work is required in the Coniopterygidae to test relationships of the fossil and Recent species and fully assess their paleobiogeography.

The large, relict, basal genus of termite *Mastotermes* Froggat (Isoptera: Mastotermitidae) may provide a biogeographic model for the Dominican amber–Old World connection, including the co-occurrence of related taxa in Dominican and Cambay amber. There is one living species of *Mastotermes* (in northern Australia), and two fossil species very similar to it in Dominican amber and Mexican amber (e.g., Krishna and Grimaldi, 1991) (all three castes are known). In fact, beetles of the subfamily Trichopseniinae (Staphylinidae) that are inquilines of the living *Mastotermes* are also represented in Dominican amber (Kistner, 1998). Because of its large size, distinctive venation, and body proportions, *Mastotermes* has an excellent fossil record, as compression fossils as well as in amber. This genus and closely related, extinct genera occur throughout the Tertiary of South and Central America, North America, and Europe (summarized in Krishna et al. 2012). Although no *Mastotermes* occur in Cambay amber, such dramatic geographic extinction involving a Recent Australian relict suggests that an Australasian–Neotropical connection is likely due to dramatic contraction of the distribution, but why this distribution pattern seems not to involve Africa remains to be explained.

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