Taxonomic position of the cricket genus *Eneopteroides* Chopard, 1956 (Orthoptera : Grylloidea, Podoscirtidae), with descriptions of two new species

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Résumé – **Position taxonomique du genre *Eneopteroides* Chopard, 1956 (Orthoptera : Grylloidea, Podoscirtidae), et description de deux espèces nouvelles**. – Le genre *Eneopteroides* Chopard, 1956 est transféré de la famille des Eneopteridae à celle des Podoscirtidae sur la base de caractères présents dans la morphologie externe et les genitalia mâles. Une espèce décrite dans le genre *Aphonomorphus* Rehn, 1903, *A. bicolor* Hehard, 1928b, est replacée dans le genre *Eneopteroides* et deux espèces nouvelles originaires d'Amazonie occidentale sont décrites, *E. loretensis* n. sp. et *E. cordobensis* n. sp.

Abstract – The cricket genus *Eneopteroides* Chopard, 1956 is transferred from the Eneopteridae to the Podoscirtidae owing to characters in external morphology and male genitalia. One species initially described in the genus *Aphonomorphus* Rehn, 1903, *A. bicolor* Hebard, 1928b, is transferred to *Eneopteroides* and two new species from western Amazonia are described, *E. loretensis* n. sp. and *E. cordobensis* n. sp.

The genus *Eneopteroides* has been described by Chopard (1956) in the subfamily Eneopterinae (Eneopteridae). This subfamily is particularly interesting among the cricket clade, because of its diversified acoustic signals and behaviours. For example, slightly resonant calls have been documented in *Agnotecous* species (Desutter-Grandcolas 1997). Also, broad frequency modulations have been demonstrated in the advertisement calls of *Eneoptera* species (Desutter-Grandcolas 1998), while such a feature was considered improbable in cricket songs before because of the characteristics of their stridulatory apparatus (Fletcher 1992). In order to understand the evolution of calling songs in Eneopterinae, a phylogenetic analysis of the subfamily has been undertaken using both morpho-anatomical (Robillard & Desutter-Grandcolas, submit.) and molecular characters, thus resuming the phylogenetic studies previously achieved at the scale of neotropical taxa (Desutter 1990). In this context, it became evident that *Eneopteroides* does not belong to Eneopterinae. Desutter (1987) noted that this genus should be transferred to the Podoscirtinae (Podoscirtidae) subfamily, but gave no detailed arguments to justify this taxonomic decision at that time.

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Arguments to incorporate *Eneopteroides* in the podoscirtid tribe Aphonomorphini are consequently resumed here, taking into account both external morphology and male genitalic characters. Two new species of *Eneopteroides* are also described and one species presently classified in the genus *Aphonomorphus* Rehn, 1903 (Chopard 1968; Otte 1994) is transferred to *Eneopteroides*.

Material and methods

The present paper is based on material and types of the following institutions: ANSP, Academy of Natural Sciences of Philadelphia, Pennsylvania; MNHN, Muséum National d'Histoire Naturelle, Paris; NMNH, Smithsonian Institution, National Museum of Natural History, Washington.

In species description, the following measurements are indicated in millimeters (mean values in parentheses): Lpron, median length of pronotum; Wpron, posterior width of pronotum; Lteg, median length of tegmina; LFIII, length of hindfemora; LTIII, length of hindtibiae. Male genitalia are interpreted following Desutter (1987), modified in Desutter-Grandcolas (2003); membranous areas are figured with dots.

Abbreviations. *Male genitalia*: *E*, pseudepiphallic sclerite; *ec a*, ectophallic apodeme; *ec p*, ectophallic paramere; *en a*, endophallic apodeme; *en s*, endophallic sclerite; *ep p*, pseudepiphallic paramere; *l*, lophi; *r*, rami. – *Tibial spurs*: *A*, apical spurs; *SA*, subapical spurs. – *Tegminal venation*: *A1-3*, anal veins 1 to 3; *Cu A/ P*, anterior / posterior cubital vein.

Genus ***ENEOPTEROIDES*** Chopard, 1956

Eneopteroides Chopard, 1956: 278 (original description); Chopard 1968: 349; Desutter 1987: 235 (note); Otte 1994: 66.

Type species. *Eneopteroides flavifrons* Chopard, 1956, by original designation.

In his 1956 paper, Chopard separated Eneopteridae and Podoscirtidae (then considered two subfamilies of the family Eneopteridae) on the basis of the apical spurs of hindtibiae: in Eneopteridae, the apical spurs are long and the median is the longest on both sides; in Podoscirtidae, the outer spurs are short and almost equal in length, while the inner ones are long and very different in length with the upper the longest. This spur arrangement is actually a good character to distinguish Eneopteridae and Podoscirtidae. Yet, contrary to Chopard's key, and according to Chopard's own description, the spurs in *Eneopteroides* are podoscirtid-like (fig. 1) and not eneopterid-like. The structure of male genitalia further demonstrates the relationships of *Eneopteroides* with Podoscirtidae with the presence of a U-shaped endophallic sclerite bearing a high, crest-like endophallic apodeme (figs. 11-12); in Eneopteridae, the endophallic sclerite shows an additional median sclerotization and its apodeme is well shorter (Desutter 1987).

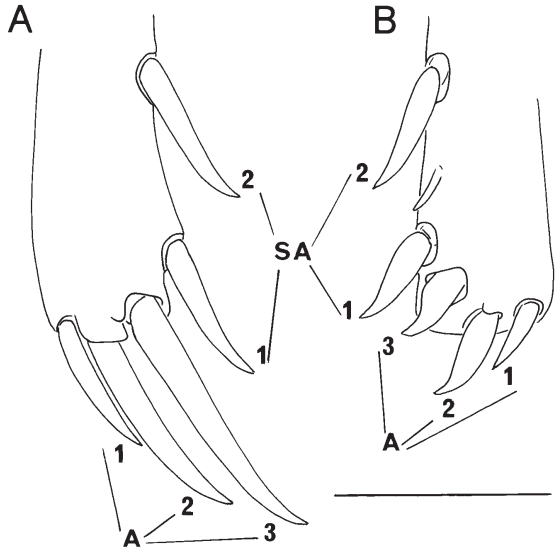


Figure 1
Eneopteroides flavifrons. Inner (A) and outer (B) spurs of hindtibia. Scale = 1 mm. Abbreviations: see material and methods.

Diagnosis – Among Podoscirtidae, *Eneopteroides* shares many characters with the taxa presently classified in the tribe Aphonomorphini (Desutter 1987; Otte 1994): all have a fusiform shape with well-developed wings and tegmina, 5 pairs of subapical spurs on hindtibiae, only one, inner, tibial tympana, ovoid in shape (except in *Paraphonus* Hebard, 1928a), an inflated foretibia at the level of the tympana and an elongate, furrowed subgenital plate in males; they also lack a stridulatory apparatus in males. Male genitalia are also similar in size, shape and structure: they are elongate and relatively flat, with correspondingly long ectophallic apodemes and endophallic sclerite; the pseudepiphallus bears two apical, simple lophi and two hook-like lateral parameres; the ectophallic fold is sclerotized apically, bearing two ectophallic parameres; the endophallus lacks a dorsal cavity; finally, the phallic complex is partly evaginable.

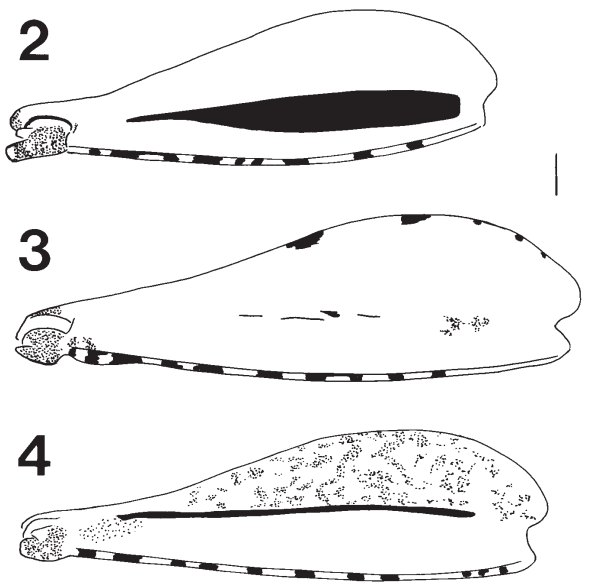
In the tribe Aphonomorphini, *Eneopteroides* is characterized by the small size and regular shape of its inner tympanum and the small inflation of the foretibiae at the level of the tympanum. By comparison, *Aphonomorphus* and *Euaphonus* Hebard, 1928a have a large inner tympanum and their foretibia is greatly enlarged; *Paraphonus* lacks tibial tympanum.

Male genitalia, which represent the only largely variable structures in Aphonomorphini (Desutter 1987), are very similar in *Eneopteroides* and *Paraphonus* (as defined by its type-species *P. cophus* Hebard, 1928a). Both taxa have a long, symmetrical pseudepiphallus, simple pseudepiphallic parameres and plate-like ectophallic parameres. They can however be easily distinguished by the size of the pseudepiphallic lophi (very small in *Eneopteroides*, largely separated from the pseudepiphallic sclerite in *Paraphonus*), the size of the pseudepiphallic parameres (much bigger in *Paraphonus*) and the shape of the ectophallic parameres (hook-like and narrower in *Paraphonus*).

Description – Species of medium size and fusiform shape. Head colouration distinctive, brown to dark brown, except for a transverse light-yellow band between the eyes, the epistemal suture and the ocelli; this band is prolonged on and behind the eyes, but becomes thinner and thinner and of a darker colour backwarks. Ocelli almost on a convex line, the transverse median ocellus smaller than the lateral ones, from which it is separated by a distance more or less equal to half its own width. Maxillary palpi very short, enlarged along their whole length. Scapes longer than wide, and as wide or slightly wider than the fastigium. Scapes and proximal parts of antennae light yellow.

Pronotum. Longer than wide, with well-developed lateral lobes. Margins of the dorsal disc slightly concave anteriorly, bisinuated posteriorly.

Legs. Foretibiae with an inner tympanum only, ovoid in shape; foretibiae only slightly inflated at the level of the tympanum. Tibiae I and II distinctly higher than wide in section and furrowed dorsally over their whole length (character not checked



Figures 2-4
Hindfemoral colouration of *Eneopteroides* species. – 2, *E. flavifrons*. – 3, *E. loretensis*. – 4, *E. cordobensis*. Scale = 1 mm.

in *E. bicolor* (Hebard, 1928b)). Hindfemora short and wide, with species-specific colour patterns; their ventral margin ringed ivory and black (figs. 2-4). Hindtibiae with 5 pairs of subapical spurs and 3 pairs of apical spurs; outer apical spurs very short, the median the longest; inner apical spurs long, the upper the longest. Hindtibiae dark brown ventrally and laterally, yellowish brown with oblique brown stripe dorsally (character not checked in *E. bicolor*).

Wings. Tegmina and wings well-developed, the wings longer than the tegmina. Tegmina brown to dark brown, the lateral field darker (except in *E. cordobensis* n. sp.). CuA yellowish over its anterior half and bordered laterally by a brown stripe. MA ringed ivory and black at midlength (figs. 5-7).

Male. Subgenital plate elongate, furrowed along its whole length. Stridulatory apparatus lacking; dorsal field of tegmina reticulated.

Male genitalia (figs. 10-12). Bilaterally symmetrical. Pseudepiphallic sclerite elongate, not transverse, equal in size or slightly longer than the rami. Pseudepiphallic lophi not widely separated the one from the other. Pseudepiphallic parameres small, comprising a basal plate and a spine-like processus. Ectophallic parameres having the shape of large, rounded plates. Ectophallic apodemes long and thin. Endophallic sclerite very long, prolonged internally by a moderately long endophallic apodeme.

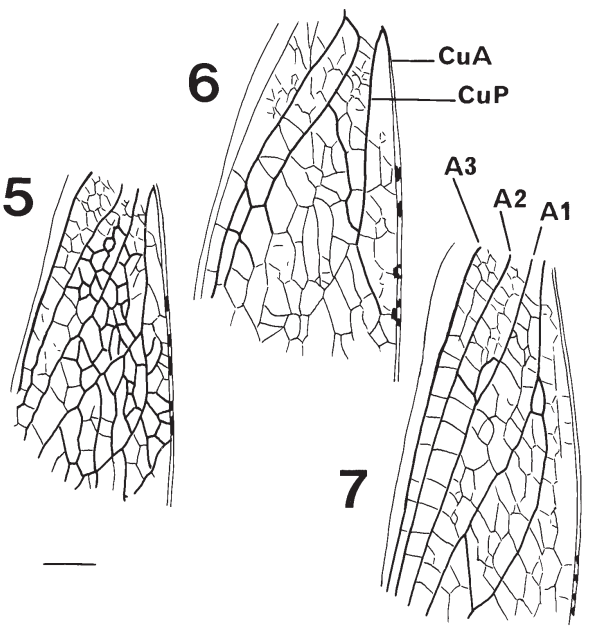
Female genitalia. Unknown.

The following species are included here in the genus *Eneopteroides*: *E. flavifrons* Chopard, 1956, *E. loretensis* n. sp., *E. bicolor* (Hebard, 1928b), *E. cordobensis* n. sp.

Hebard (1928b) mentioned that the head colouration described above is present also in *Aphonomorphus tenebrosus* Hebard, 1928b (known from one female from Panama, Gatun) and *A. flavifrons* (Saussure, 1897) from Mexico. Also both species resemble *Eneopteroides* by their foretibiae and *A. tenebrosus* shows the same tegminal colouration. Both differ, however, by the subapical spurs of their hindtibiae, having 4 (*A. flavifrons*) or 6 (*A. tenebrosus*) inner spurs according to original descriptions. The generic status of these species is yet uncertain.

Distribution – *Eneopteroides* is presently known from western Amazonia (Peru, Loreto and Ucayali regions), the lowlands of Panama and northwestern Colombia (Cordoba Department). Such an Amazonian and Panamanian distribution is characteristic of a forest-inhabiting taxon (Müller 1973, fig. 96); from a biogeographical point of view, it belongs to the Napo, Ucayali and Western Panamanian Isthmus provinces *sensu* Morrone (2001a, b).

The presence of *Eneopteroides* in the Cordoba Department, which has a more open and dry vegetation (Hüeck 1966; UNESCO 1981), is also coherent with Müller's (1973) definition of the Barranquilla centre (Morrone's (2001b) Maracaibo province p.p.) and its possible connection with other neotropical forested areas such as the Amazonian region. A similar distribution has been illustrated by Müller (1973, fig. 88) for the



Figures 5-7
Venation of tegminal dorsal field of *Eneopteroides* species: 5, *E. flavifrons*. – 6, *E. loretensis*. – 7, *E. cordobensis*. Scale = 1 mm. Abbreviations: see material and methods.

tamarin monkey (*Sanguinus* sp.), except that *Eneopteroides* has not been recorded yet in Guyanan and Para regions.

More generally, the Aphonomorphini tribe has been recorded mostly from the Amazonian and Guyanese regions and to a lesser extent from southern Central America (Panama, Costa Rica); it has not been mentioned yet from the Serra do Mar area (Desutter 1990 and pers. obs.), although this area is closely related to other humid forested areas of northwestern South America (Müller 1973; Cracraft & Prum 1988; Bates *et al.* 1998).

Eneopteroides flavifrons Chopard
(figs. 2, 5, 8)

Eneopteroides flavifrons Chopard, 1956: 278; Chopard 1968: 349; Desutter 1987: 235 (listed in Aphonomorphini); Otte 1994: 66.

Diagnosis – Species characterized by its colour pattern (hindfemora, tegmina), tegminal venation and to a lesser extent its size and male genitalia.

Description – Dorsal disc of the pronotum bordered laterally with a yellowish line. Foretibiae and forefemora black brown. Midfemora yellowish, except for their dark brown distal half. Midtibiae brown, their upper side yellowish proximad. Hindfemora with a wide longitudinal brown line on their outer sides, whitish spots on their inner sides, but no brown flecks on their dorsal sides (fig. 2). Tegmina brown, without whitish spots on the dorsal field; longitudinal and transverse veins all strong, the former somewhat stronger than the latter (fig. 5). Male subgenital plate dark brown ventrally and clear brown laterally. Male genitalia similar to those of *E. bicolor* (figs. 10-12), but the pseudepiphallic lophi oblique, the pseudepiphallic parameres shorter and the ectophallic parameres slightly curved apically (fig. 8).

Measurements. Lpron, 2.4 mm; Wpron, 4 mm; Lteg, 15.2 mm; LFIII, 11 mm; LTIII, 10.5 mm.

Material examined – Holotype ♂: Peru, Pucallpa, rio Ucayali, 9.XII.1947, J.M. Schunke (NMNH).

Eneopteroides loretensis n. sp.
(figs. 3, 6, 9)

Diagnosis – Species very similar to *E. flavifrons*, from which it can be distinguished mainly by its colour pattern (hindfemora, tegmina, subgenital plate), its tegminal venation and larger size, and to a lesser extent by its male genitalia.

Description – Dorsal disc of pronotum bordered with yellowish. Forefemora, foretibiae and midtibiae as in *E. flavifrons*. Midfemora yellowish, mottled with brown and with a distinct brown ring distad. Hindfemora yellowish, lacking a wide longitudinal brown line medially, but with several brown spots on their dorsal side (fig. 3). Tegmina darker brown than in *E. flavifrons*, and with weaker veins; cells delimited by longitudinal and transverse veins wider and more irregular than in *E. flavifrons* (fig. 6); dorsal field with 5 median groups of whitish cells distributed over its whole length. Subgenital plate entirely dark brown.

Male genitalia. Very similar to those of *E. flavifrons*, but ectophallic parameres more strongly curved at the apex and pseudepiphallic parameres shorter (fig. 9).

Measurements. Lpron, 2.8 mm; Wpron, 4.3 mm; Lteg, 18.6 mm; LFIII, 11.6 mm; LTIII, 10.8 mm.

Material examined – Holotype ♂: Peru, Loreto, Region de l'Ampiyacu, en aval du confluent des rios Zumun et Yahuasyacu, 3.XI.1985, L. Desutter (MNHN).

Eneopteroides bicolor (Hebard)
(figs. 10-12)

Aphonomorphus bicolor Hebard, 1928b: 279; Chopard 1968: 405; Otte 1994: 79.

Diagnosis – In the genus, species characterized by its large size, its colour pattern (pronotum, hindfemora, tegmina), tegminal venation and male genitalia (epiphallic lophi and parameres).

Description – Species large for the genus. Fastigium, occiput and pronotum black. Antennae brown, ringed with buff. Dorsal disc of pronotum without lateral yellowish line. Hindfemora buffy with a broad longitudinal median black band, which spreads on the distal half (Hebard, 1928b, pl. 14, fig. 7). Tegmina brown, except for the general colour pattern of the genus; vein pattern of the dorsal field not observed. Male genitalia (figs. 10-12) characterized by horizontal lophi, long pseudepiphallic parameres and apically flat ectophallic parameres.

Measurements (in Hebard, 1928b). Lpron, 3.8 mm; Wpron, 4 mm; Lteg, 17.8 mm; LFIII, 13.8 mm.

Material examined – Holotype ♂: Panama, Gatun, 17-23.VII.1916, D.E. Harrower (ANSP).

Eneopteroides cordobensis n. sp.
(figs. 4, 7, 13)

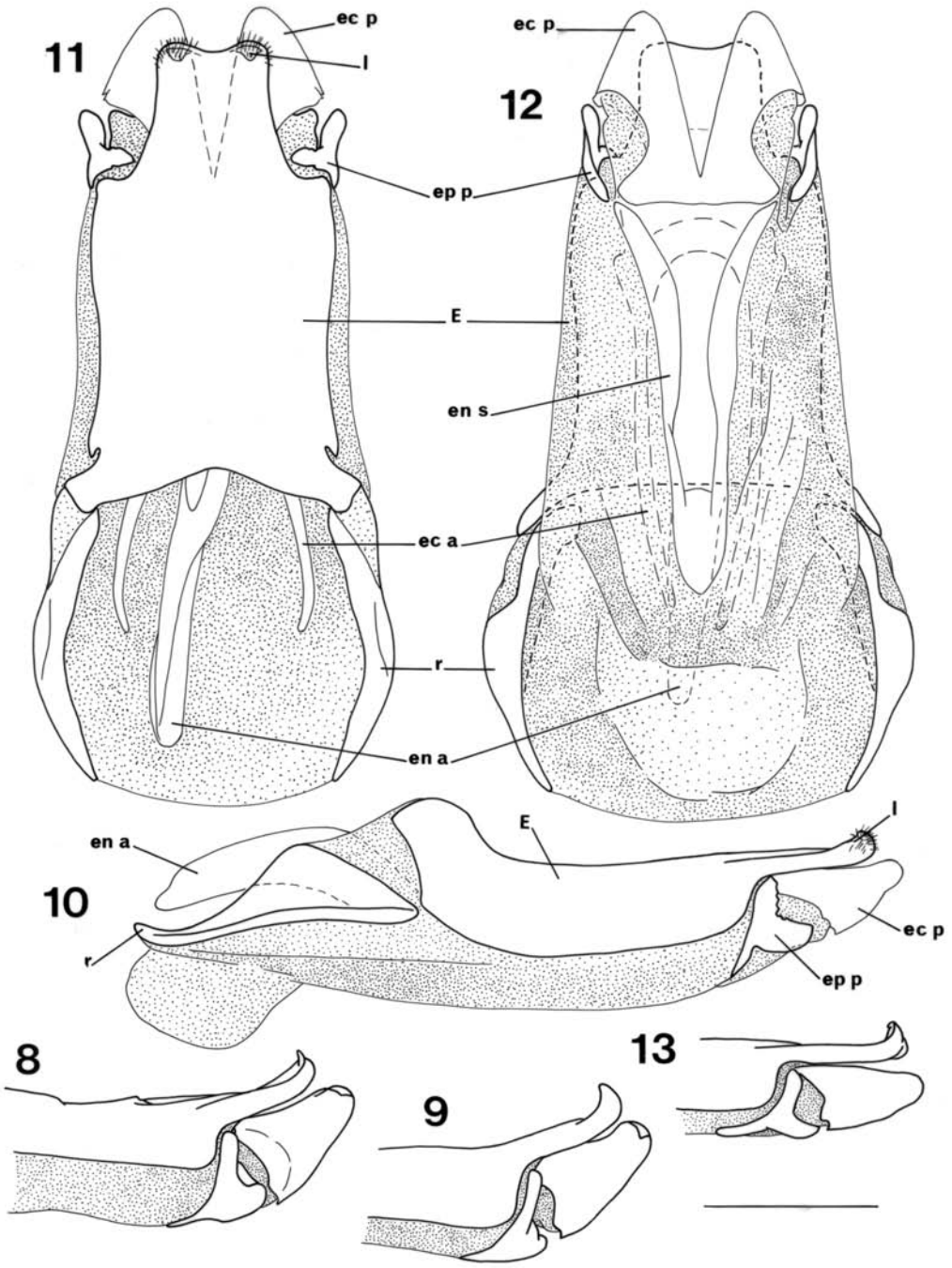
Diagnosis – Species very similar to *E. bicolor*, from which it can be distinguished by its abundant setae, hindtibial colouration, smaller size and male genitalia.

Description – Body densely covered with long setae, whitish on the pronotum, brown and white elsewhere. General colouration lighter than in the other species, especially on tegmina and legs.

Pronotum. Brown, the dorsal disc lighter but without a yellow lateral line.

Legs. Hindfemora light brown, darker on the inferior half of their outer side; a thin, median dark line along their whole length, somewhat spreading toward the knee (fig. 4); dorsal half of outer face mottled with brown and with many spots of white setae.

Subgenital plate light brown, with a dark brown line on both sides of the longitudinal furrow.



Figures 8-13
Male genitalia of *Eneopteroides* species in lateral (8-10, 13), dorsal (11) and ventral (12) views. – 8, *E. flavifrons*. – 9, *E. loretensis*. – 10-12, *E. bicolor*. – 13, *E. cordobensis*. Scale = 1 mm. Abbreviations: see material and methods.

Tegmina. Entirely light brown, the lateral field not darker than the dorsal field except for a thin brown line under the yellowish CuA. Longitudinal veins of dorsal field regularly arranged, almost parallel, the area between MP and A1 only slightly enlarged (fig. 7).

Male genitalia. Similar to those of *E. bicolor*, except for the shape of pseudepi- and ectophallic parameres (fig. 13).

Measurements. Lpron, 2.6; Wpron, 4; Lteg, 16; LFIII, 11.4; LTIII, 10.7.

Material examined – Holotype ♂: Colombia, dept. Cordoba, Tenerife (Monteria), 12.I.1968, M. Descamps (MNHN).

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