

# Mantids in the Mist – Taxonomy of the Andean genus *Pseudopogonogaster* Beier, 1942, a cloud forest specialist, with notes on its biogeography and ecology (Mantodea: Thespidae: Miopteryginae)

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## Abstract

The Neotropical lichen mimicking mantid genus *Pseudopogonogaster* Beier, 1942 is revisited and re-described. The examination of the type species, *P. mirabilis* Beier, 1942, the first described species of this lineage, allowed us to determine that those species currently included in *Pseudopogonogaster* and *Calopteromantis* Terra, 1982 are all congeneric. As a result, the genus *Calopteromantis* is now considered to be a junior synonym of *Pseudopogonogaster*. Accordingly, *Calopteromantis hebardii* Terra, 1982 and *Calopteromantis marulandae* Salazar, 2002 are transferred to *Pseudopogonogaster*. The species *Calopteromantis otongica* Lombardo & Ayala, 1998 from Ecuador was also found to be a synonym of *P. mirabilis*. In addition, a new species from northwestern Peru, *Pseudopogonogaster kanjaris*, is described herein, thus constituting a new genus and species record for this country. Analysis of the distribution of the six recognized species of *Pseudopogonogaster* suggests that this genus is endemic to the mountain forests of Colombia, Ecuador and northern Peru and its members are specialized inhabitants of epiphytic vegetation, exhibiting unique morphological and chromatic adaptations to these habitats. The newly available information on *Pseudopogonogaster* also allowed to determine that *Calopteromantis terrai* Jantsch, 1994, described from Mato Grosso, Brazil, is actually a member of the genus *Eumiopteryx* Giglio-Tos, 1915 (Thespidae: Pseudomiopteryginae) and, thus, is transferred to this genus as *E. terrai* (Jantsch, 1994) comb.n.

## Resumen

El género Neotropical de mantis liquen, *Pseudopogonogaster* Beier, 1942, es reanalizado y redescrito. El estudio de la especie tipo, *P. mirabilis* Beier, 1942, la primera especie de este linaje en ser descrita,

permitted to determine that those species included in *Pseudopogonogaster* and *Calopteromantis* Terra, 1982 are all cogenetic. As a result, the genus *Calopteromantis* is considered a new synonym of *Pseudopogonogaster*. In this way, *Calopteromantis hebardei* Terra, 1982 and *Calopteromantis marulandae* Salazar, 2002 are transferred to *Pseudopogonogaster*. The species *Calopteromantis otongica* Lombardo & Ayala, 1998 from Ecuador is also synonymized with *P. mirabilis*. In addition, a new species, *Pseudopogonogaster kanjaris* sp. n., from the northwest of Peru, is being described, constituting a new generic and specific record for this country. The analysis of the distribution of the six recognized species of *Pseudopogonogaster* suggests that this genus is endemic to the mountain forests of Colombia, Ecuador and northern Peru, and its members specialize in living on epiphytic vegetation, showing morphological and chromatic adaptations unique for this habitat. The new knowledge available permitted to determine that *Calopteromantis terrai* Jantsch, 1994, described from Mato Grosso, Brazil, is in reality a member of the genus *Eumiopteryx* Giglio-Tos, 1915 (Thespidae: Pseudomiopteriginae) for which it is transferred to this last genus as *Eumiopteryx terrai* (Jantsch, 1994) comb.n.

### Keywords

Neotropics, chromatic polymorphism, Huancabamba Depression, lichen mimicry, cloud forest, new species

### Introduction

Among the most impressive-looking mantids in terms of morphological adaptations are the members of *Pseudopogonogaster* Beier, 1942. These bizarre mantids live among lichen and other epiphytic vegetation that proliferate on tree bark in mountain rainforest (cloud forest) areas. The taxonomic history of this genus is complicated, mostly because of problems derived from misinterpretation of morphological characters attributable to their remarkable sexual dimorphism. The nomenclatural history of *Pseudopogonogaster* is closely linked to that of the genus *Calopteromantis* Terra, 1982, as both genera were independently described based on specimens of the opposite sex: *Pseudopogonogaster* was described based on a female specimen (Beier 1942), whereas *Calopteromantis* was described based on a male specimen (Terra 1982).

After careful literature review and examination of several specimens, including a new, undescribed species from northwestern Peru, we determine that *Calopteromantis* is a junior synonym of *Pseudopogonogaster*. In addition, we also take the opportunity to introduce modifications to the taxonomy of *Pseudopogonogaster* in the form of one new species level synonymy and a new morphological description for this genus. Finally, we provide additional notes on the ecology and biogeography of these mantids.

### Materials and Methods

The specimens studied belong to the following collections: Museo de Entomología Klaus Raven Büller, Universidad Nacional Agraria La Molina, Lima, Peru (UNALM) (five females and one male of *C. hebardei*; two females of *C. otongica*; two males and eight females of the new species herein described); Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland (MIZ) (holotype of *P. mirabilis*); Centro de Ornitología y Biodiversidad, Lima, Peru (CORBIDI) (one female paratype of the

new species described herein); and Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil (MCTP) (holotype of *Calopteromantis terrai*). Illustrations were made by using a binocular stereomicroscope (Wild M5) equipped with a camera lucida. Genitalia terminology follows Cerdá (1993), which is based on La Greca (1954). Measurements are given in mm. In order to avoid repetitive typing, we provide a spination formula for the fore legs, as first introduced by Rivera (2010a) and as in the following example: F=16IS/6ES/3DS (F=Femur; IS=Inner Spines; ES=External Spines; DS= Discoidal Spines; T=18IS/18–19ES (T=Tibia; IS=Inner Spines; ES=External Spines). The values indicate the corresponding number of spines for each series. The genicular spines of the femora and the apical spur of the tibia are not included in the spination formula, in congruence, for instance, with Kaltenbach (1996). The map of distribution shown in Fig. 27 was generated using Geographic Information System software with two overlapping layers: a Digital Elevation Model (DEM) with 90 meters of resolution and a map of the Terrestrial Ecoregions of the World according to Olson et al. (2001).

## Results

We present the taxonomic history of *Pseudopogonogaster* separately from that of *Calopteromantis*, making the timeline of taxonomic changes that led to their current organizations more transparent:

### *Taxonomic history of Pseudopogonogaster*

*Pseudopogonogaster* was described by Beier (1942) to accommodate his new species *P. mirabilis* Beier 1942, from Balzapamba, Ecuador. The description of this species was based on a single female now deposited at MIZ. Fifty years later, Terra (1995) listed *P. mirabilis* in his study on Neotropical mantids, but was unable to provide further information, as he had no specimens available for study. Shortly after, Salazar (2000) and Salazar & Carrejo (2002) described two new species from Colombia: *P. muscosa* Salazar, 2000 and *P. iguaquensis* Carrejo & Salazar, 2002. These two species were also described on the basis of single female specimens.

### *Taxonomic history of Calopteromantis*

Based on a single male specimen, Terra (1982), described a new genus, *Calopteromantis* Terra, 1982, to accommodate his new species, *C. hebardii* Terra, 1982 from Cerro de Bulán, Valle del Paute (i.e. Paute river valley), Ecuador. A second species, *C. terrai* Jantsch, 1994, was described based on a single male specimen collected in Mato Grosso, Brazil (Jantsch 1994). An important taxonomic paper was published later by Lombardo & Ayala (1998), in which the authors described a new species from Ecuador, *C. otongica* Lombardo & Ayala, 1998, and associated the alleged unknown female of *C. hebardii* to the conspecific male described by Terra (1982). In addition, Lombardo & Ayala, 1998 extended the distribution of *C. hebardii* to include Loja, Ecuador.

Finally, a fourth species, *C. marulandae* Salazar, 2002, was described from a single male specimen (Salazar 2002).

### *Pseudopogonogaster and Calopteromantis*

It appears to us that the dichotomy *Pseudopogonogaster*/*Calopteromantis* may have resulted from the historical analysis and subsequent description of specimens representing opposite sexes. Lombardo & Ayala (1998) represents the first study in which conspecific male and female specimens of *Calopteromantis* were correctly associated. However, the authors overlooked the similar morphology of female *Calopteromantis* and *Pseudopogonogaster*; thus, both genera remained valid until this current study (Lombardo & Agabiti 2001; Ehrmann 2002; Agudelo 2004; Otte & Spearman 2005; Agudelo et al. 2007; Battiston & Picciau 2008; Ehrmann & Koçak 2009). Unfortunately, such taxonomic errors are relatively common in mantid classification and largely attributable to the marked sexual dimorphism observed in certain lineages (Rivera 2010b).

We had the opportunity to examine multiple high quality digital images of the holotype of *P. mirabilis* (provided by MIZ). The type specimen (code MIZ-125726) is broken into two parts, with the pronotum/mesonotum articulation being the point of detachment (the abdomen, along with the meso- and metanotum all remain held in place on the pin by means of glue). Additionally, the abdominal foliaceous appendages are broken (except those on the distal-most tergite, Fig. 2), and most cursorial legs are missing or incomplete. Nevertheless, the head, pronotum and fore legs, where most relevant taxonomic features are found, were all preserved well enough to allow sufficient comparison with other specimens (Fig. 1). After the examination of the above-mentioned material, the original description of *P. mirabilis*, and other available material from Peru and Ecuador, we concluded that *Calopteromantis* and *Pseudopogonogaster* clearly represent the same genus. Accordingly, we establish *Calopteromantis* as a new junior synonym of *Pseudopogonogaster*.

In addition, comparison between the holotype of *P. mirabilis* and two topotypic females of *C. otongica* from La Otonga, Ecuador (deposited at UNALM) clearly indicate that *C. otongica*, described by Lombardo & Ayala (1998) and *P. mirabilis* are the same species. Despite minimal individual variation, the distinctive pronotal and fore leg proportions observed in *P. otongica* (Figs 3 and 4) correspond to those in *C. mirabilis* (Figs 5 and 6). Furthermore, the type (and only known) localities for each taxon (*P. mirabilis* from Balzapamba, in Bolivar province; *C. otongica*, from Otonga, in Cotopaxi province) both ecologically correspond to mountain rainforest, which in northwestern Ecuador once formed a continuous biogeographic unit prior to human disturbance within the past decades (see below). In fact, both localities are separated by as little as 170 km. Due to the morphological and biogeographical evidence, we establish *C. otongica* as a new junior synonym of *P. mirabilis*.

We provide a redescription of *Pseudopogonogaster* in order to unify the taxonomic knowledge amassed from this and other previously published studies on this genus and *Calopteromantis*.

## Systematics

### *Pseudopogonogaster* Beier, 1942

#### *Type species*

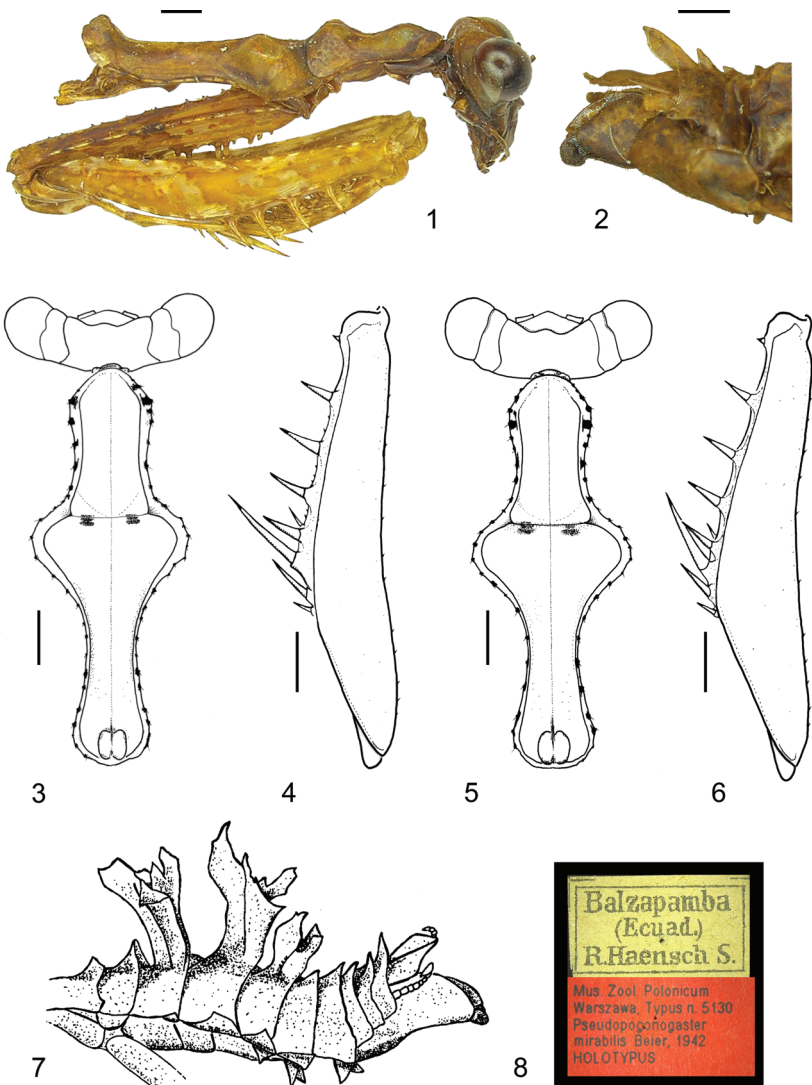
*Pseudopogonogaster mirabilis* Beier, 1942, by original designation.

*Pseudopogonogaster* Beier, 1942: 132–133 (original description); Terra, 1995: 51–52 (citation); Salazar, 2000: 32 (taxonomy); Ehrmann, 2002: 297 (redescription); Otte & Spearman, 2005: 377 (citation).

= *Calopteromantis* Terra, 1982: 330 (original description); Terra, 1995: 44 (redescription); Lombardo & Ayala, 1999: 107 (description of new species); Ehrmann, 2002: 87 (redescription); Otte & Spearman, 2005: 364 (citation) (syn.n.)

#### *Redescription*

Small mantids (body length, from vertex to tip of abdomen, 23–27 mm). Coloration intraspecifically highly variable, typically exhibiting characteristic patterns in green, grey, white, brown and/or black in different hues and combinations; exhibiting contrasting darker bands or spots on body and legs. Head with vertex poorly developed, straight and barely more elevated than the imaginary line connecting the top of the compound eyes; vertex concave in dorsal view; juxtaocular tubercles as elevated as the vertex. Frontal shield transverse, bearing a conspicuous and well-delimited protuberance along the lateral edges; clypeus with a medial tubercle. Pronotum with prozone and proximal section of metazone protuberant; metazone medially constricted and with distal tubercles well-developed and protuberant, often longitudinally cut by a deep depression (depression corresponding to the longitudinal carina of the pronotum, which in most species is vestigial). Lateral margins of pronotum often denticulated to various degrees, these denticles are minute (may be absent in males) and are basally surrounded by dark pigmentation. Supracoxal dilation well-developed. Forecoxa with anterior margin exhibiting minute denticles. Spination formula of forelegs: F=12IS/4ES/4DS; T=8-11IS/6ES. Meso- and metathoracic legs slender and long. Wings of male well-developed; mesothoracic wings slender and long, when folded, both meso- and metathoracic wings surpass the tip of the abdomen by as much as the length of the abdomen; surface of mesothoracic wings exhibiting multiple and contrasting dark spots. Females apterous. Meso- and metanotum of females with a recurved, distal projection. Abdomen of female dilated, each tergum exhibiting a foliaceous lobe of various sizes dorsomedially, those on terga 2–4 clearly more developed and with irregular dorsal margins, sometimes resembling secondary, smaller lobes. Lateroposterior angles of abdominal segments bearing small triangular lobes. Abdomen of males slender, lobed as in females but less conspicuously; dorsal lobes on terga 2–4 are present but atrophied, flattened and concealed by the wings (however, these lobes are distinct in the male nymphs). Supraanal plate tongue-like.



**Figs 1–8.** *Pseudopogonogaster mirabilis*. (1) Holotype, head and prothorax. (2) Holotype, distal abdominal segments. (3) Head and pronotum, dorsal view (specimen from La Otonga). (4) Fore left femur, lateral view (specimen from La Otonga). (5) Same as in Fig. 3 (holotype). (6) Same as in Fig. 4 (holotype). (7) Abdomen of female (fig. 4 from Ayala & Onore, 2001). (8) Holotype labels. Scale bar=1 mm (Fig. 7 originally without scale). This figure is published in colour in the online edition of this journal, which can be accessed [via http://www.brill.nl/ise](http://www.brill.nl/ise)

#### Locality of type species

Ecuador, Balsapamba (originally cited as Balzapamba, Fig. 8).

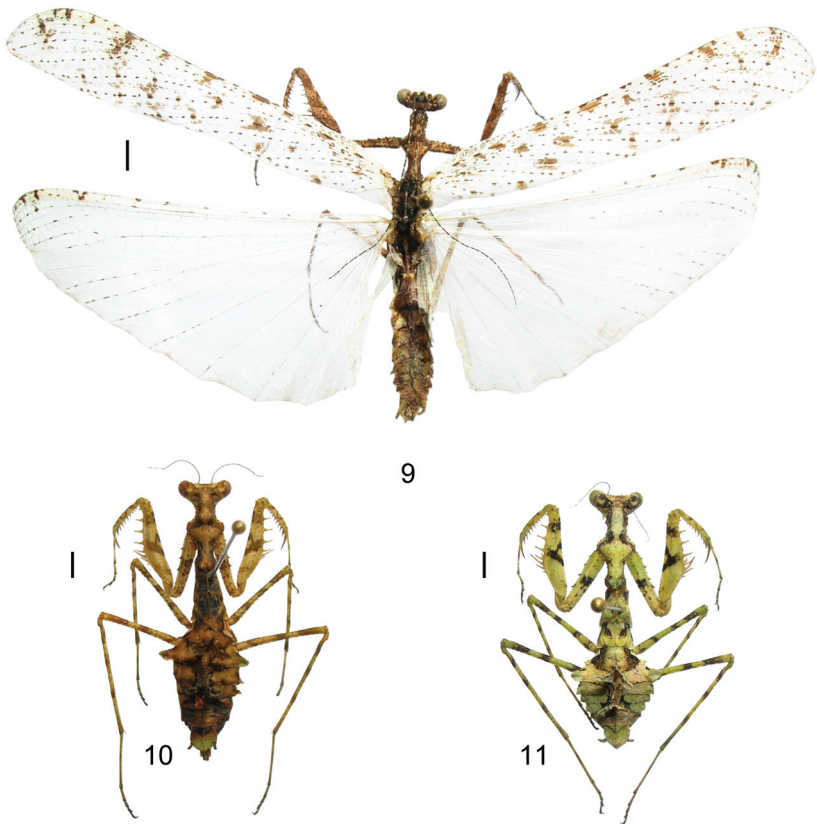
The following new combinations are now established: *P. hebardii* (Terra, 1982) comb.n. and *P. marulandae* (Salazar, 2002) comb.n.

Otte & Spearman (2005) listed the genus *Chersomantis* Gistel, 1856 as a synonym of *Pseudopogonogaster*. However, the authors did not specify the reasons for this. Interestingly, Caudell (1904) and Giglio-Tos (1927) had already referred to *Chersomantis* and indicated that its only species, *Chersomantis picta* Gistel, 1856, is only known from Egypt (its type locality). On the other hand, Ehrmann (2002) considered *Chersomantis* as a possible synonym of *Blepharopsis* Rehn, 1902, an old-world genus widespread across northern Africa and the Middle East to India (Battiston et al 2010). Whereas this latter question will require confirmation, it seems evident that *Chersomantis* does not refer to any particular Neotropical mantid lineage and, thus, cannot be considered a synonym of *Pseudopogonogaster*.

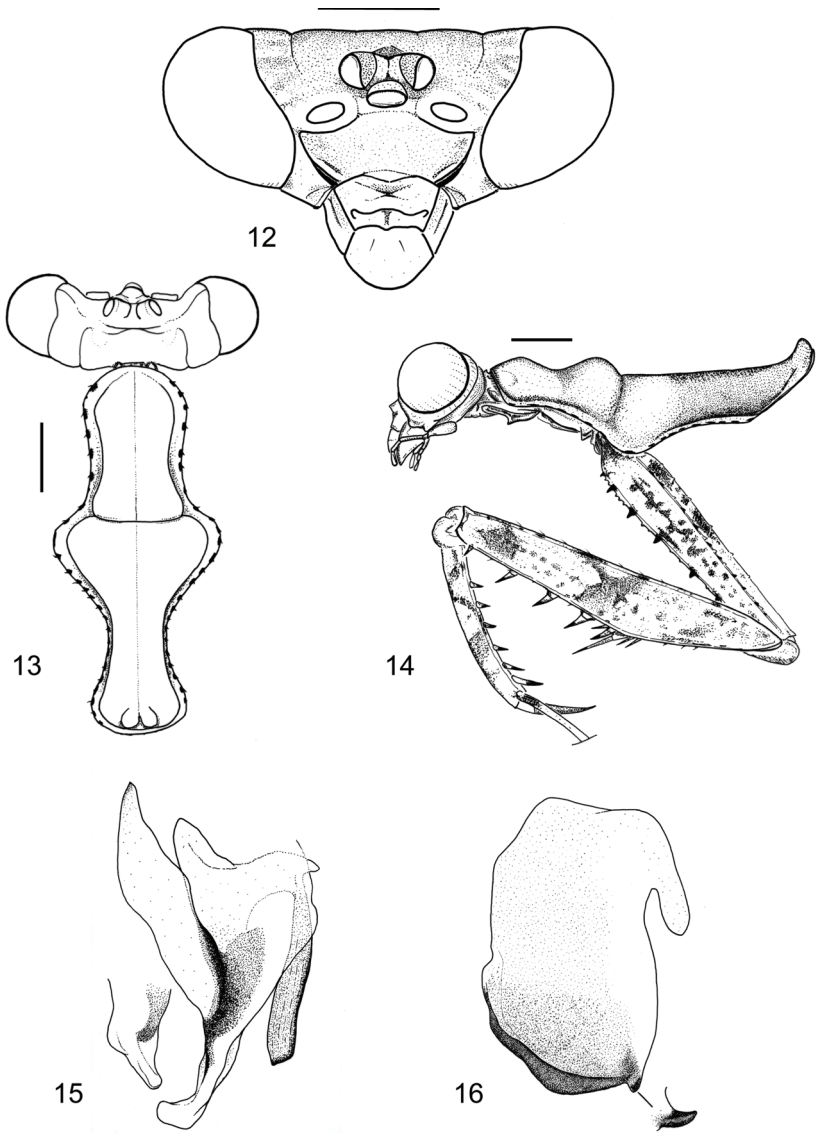
***Pseudopogonogaster kanjaris* Rivera & Yagui, sp.n.** (Figs 9–20, 24–29)

*Specimens*

Holotype male, eight female paratypes (one of which is a pre-adult juvenile) and one pre-adult male, collected at Peru, Lambayeque, Ferreñafe province, Kañaris district,



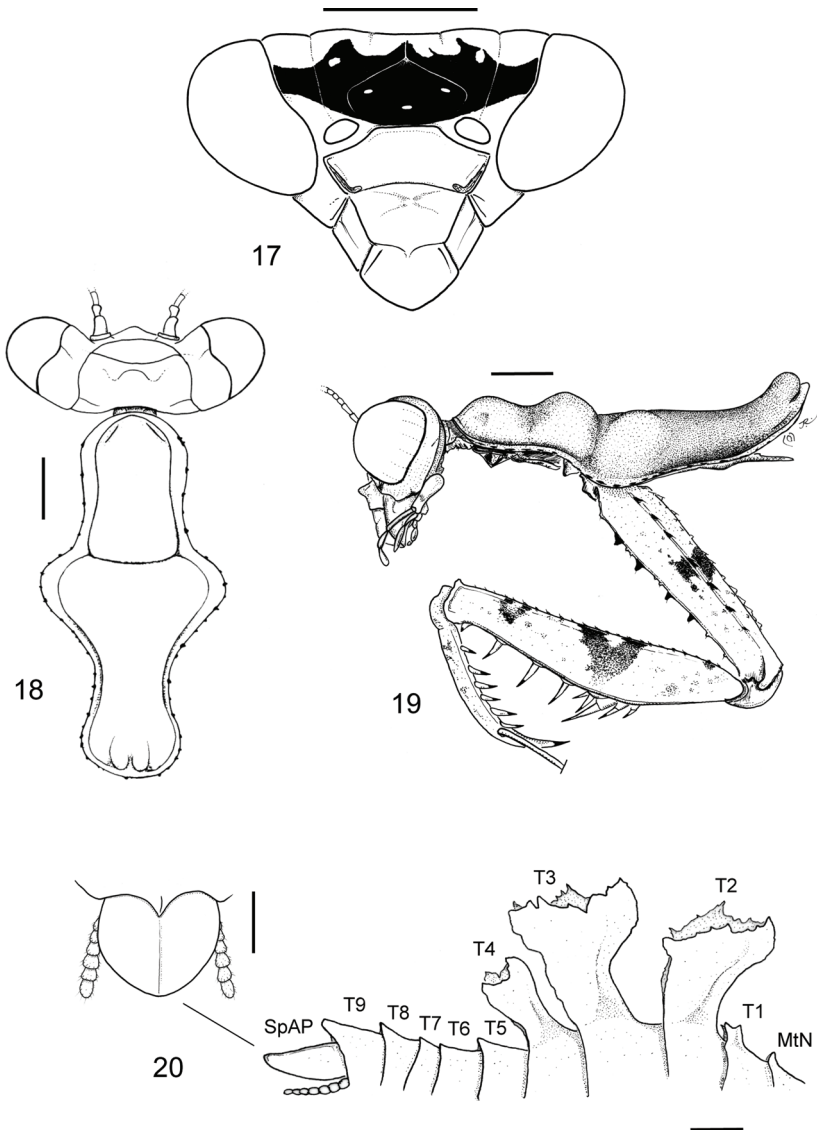
**Figs 9–11.** *Pseudopogonogaster kanjaris* sp.n. (9) Male holotype. (10, 11) Female paratypes. Scale bar=2 mm. This figure is published in colour in the online edition of this journal, which can be accessed via <http://www.brill.nl/ise>



**Figs 12–16.** *Pseudopogonogaster kanjaris* sp.n., male holotype. (12) Head, frontal view. (13) Head and pronotum, dorsal view. (14) Head and prothorax, lateral view. (15) Left dorsal phallomere (dorsal view), and a detail of distal process (in lateral view). (16) Ventral phallomere. Scale bar=1 mm.

Mountain Forest of Kañaris, 06°05'32.220" S, 79°16'0.234" W, 3000 m, 1.V.2010 (J. Rivera & E. Castro leg.). Specimens were collected on a fence made of tree bark planks invaded by local epiphytic vegetation at the Kañariaco Mining Project camp facility. All specimens are deposited at UNALM, except for one female paratype that is deposited at CORBIDI.

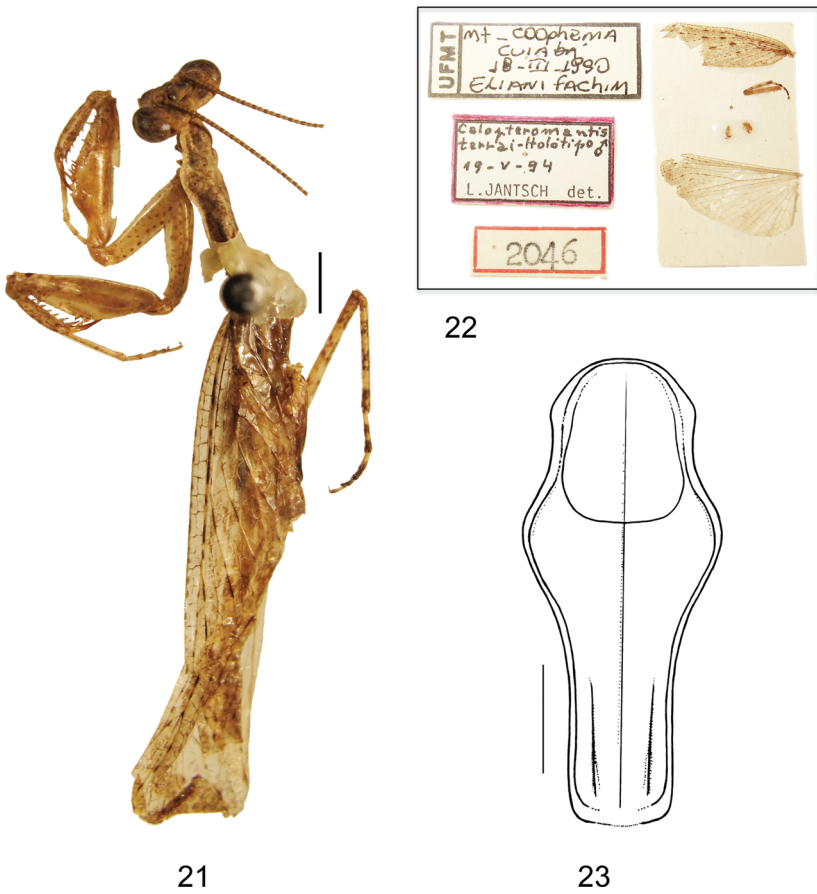




**Figs 17–20.** *Pseudopogonogaster kanjaris* sp.n., female. (17) Head, frontal view. (18) Head and pronotum, dorsal view. (19) Head and prothorax, lateral view. (20) Abdomen (lateral view) and detail of the supra-anal plate (dorsal view). Abbreviations: MtN, Metanotum; T, Tergum; SpAP, Supra-anal plate. Scale bar=1 mm.

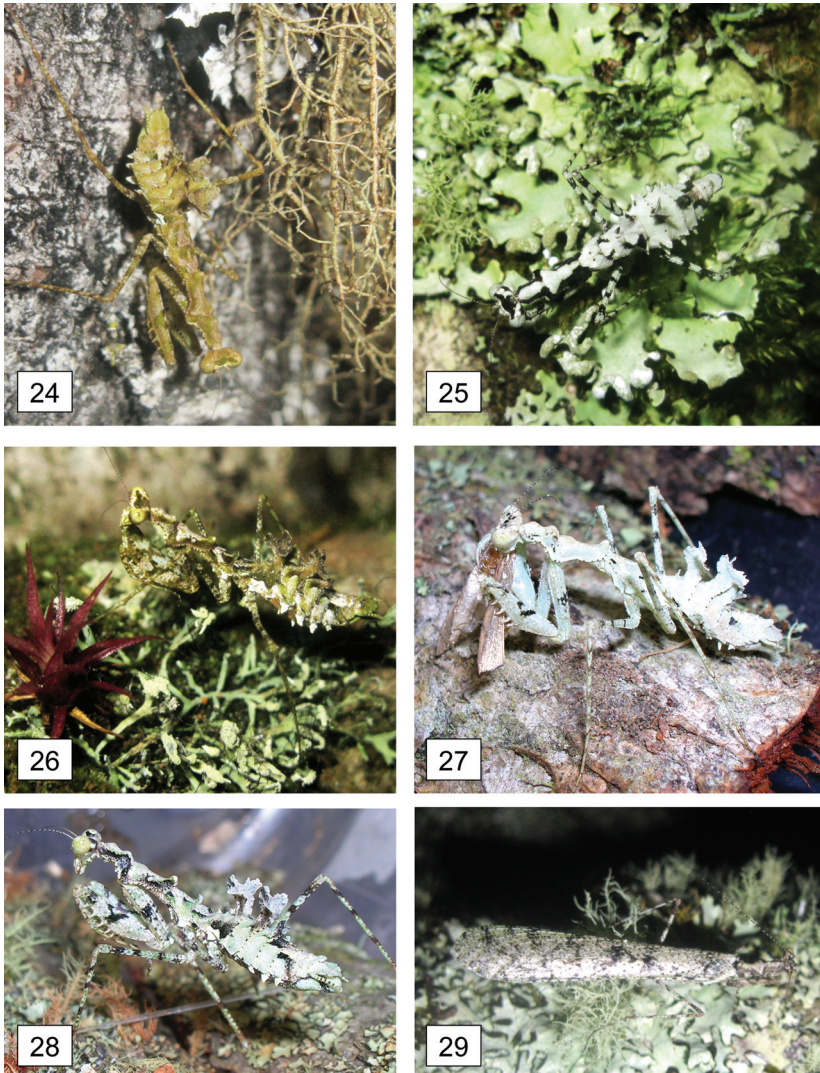
### Description

Male holotype (Fig. 9). General coloration of the body, greyish-brown with irregular black, brown and yellowish-white spots (Fig. 29). Measurements: length of body 23.5 mm, pronotum 5.3 mm, forecoxa 4.9 mm, forefemur 7.2 mm, foretibia 4 mm, mesothoracic coxa 2.5 mm, mesothoracic femur 7 mm, mesothoracic tibia 6.5 mm,



**Figs 21–23.** *Calopteromantis terrai*, male holotype. (21) Habitus, dorsal view (scale bar=2 mm). (22) Original labels and fragmented body parts on a piece of cardboard. (23) Pronotum, dorsal view (note: the proximal most section of the metazone is not accurately illustrated here because of the glue that conceals this particular area in the original specimen) (scale bar=1 mm). This figure is published in colour in the online edition of this journal, which can be accessed *via* <http://www.brill.nl/ise>

metathoracic coxa 2.8 mm, metathoracic femur 8.5 mm, metathoracic tibia 8 mm, mesothoracic wing 30.8 mm, metathoracic wing 28 mm. Head (Fig. 12): Triangular in shape, about 1.52 times as wide as the supracoxal dilation of pronotum; frontal shield transverse, hexagonal in shape and approximately 2.7-times as wide as long. Antennae elongate and filiform; scape, pedicel and the proximal four flagellomeres dark brown, then alternating with half white/half black flagellomeres up to the tip of the antennae where the white colour changes gradually to greenish white. The head with various dark spots while the vertex distinctly darker than remaining of head. Thorax: Pronotum (Fig. 13) short and stout, longer than wide, disc smooth; metazone/prozone ratio=0.73; lateral margins without denticles but with scattered, minute hairs located on dark spots. Supracoxal dilation well-developed, almost as wide as the vertex of head, with rounded margins. Prozone subdivided into two bulbous areas (clearly defined in the lateral view,



**Figs 24–29.** *Pseudopogonogaster kanjaris* sp.n., living specimens. (24–28) Female individuals: (24) Green and brown morph resting on bark next to a clump of lichen of the genus *Usnea* (Parmeliaceae). (25) Black and white morph on *Hypotrachyna* (Parmeliaceae). (26) Green and white morph on *Heterodermia* (Physciaceae). (27) Light green morph, captive individual. (28) Light green and black morph, captive individual. (29) Male holotype on *Hypotrachyna* and *Usnea*. This figure is published in colour in the online edition of this journal, which can be accessed via <http://www.brill.nl/ise>

Fig. 14), one near the anterior margin and the other, more developed one, just anterior to the supracoxal sulcus, the latter more developed and slightly subdivided by a medial carina. The metazone lacks medial carina (which is only indicated by a thin, brown longitudinal line); distal margin exhibiting two robust tubercles. Forelegs (Fig. 14) slender, with brown bands and scattered brownish black spots. Coxa bearing six black denticles on its anterior margin and 1–3 smaller, whitish denticles between the black

ones; posterior side of coxae bearing several black, very small denticles as well as scattered little hairs; inner distal lobes divergent. Spination formula: F=12IS/4ES/4DS and T=10IS/6ES; all spines of forefemora and tibiae with black tips. Foremetatarsi 1.08-times as long as remaining tarsomeres taken together. Mid and hind legs long and slender with small, scattered hairs; greenish white with brownish-black irregular bands. Mid and hind metatarsi respectively 1.2- and 1.4-times as long as remaining tarsomeres taken together, respectively. Wings well-developed, extending well beyond abdominal apex; mesothoracic wings hyaline with all veins light green; wing surface with numerous scattered and irregular blackish spots of various size. Metathoracic wings hyaline, costal area spotted as in the mesothoracic wings; remainder of the wings hyaline and colourless for the most part, except for some distal black spots on the longitudinal veins. Abdomen: Cylindrical and slender. Tergites 1–4 with flat, foliaceous extensions in the middle of their distal margin, those on the second and third tergites are more developed. Supra-anal plate tongue-like. Cerci slightly longer than the supra-anal plate. Male genitalia: left dorsal phallomere (Fig. 15) with the central region of dorsal plate heavily sclerotized, distal process slender, elongated and distally curved; phalloid apophysis long, heavily sclerotized and distally truncate, general surface exhibiting longitudinal striae. Ventral phallomere (Fig. 16) rectangular, heavily and conspicuously sclerotized, particularly on its distal portion (however, the right margin of this phallomere is less clearly sclerotized); right latero-distal corner with a conspicuous, well-sclerotized, short projection; right proximal corner with a conspicuous lateral process directed backwards.

Female (based on eight paratypes, two of which are shown in Figs 10 and 11). Coloration highly variable (see Figs 24–28). Measurements (adults only): length of body 19.2–22.9 mm, pronotum 5.8–6.2 mm, forecoxa 5.2–5.9 mm, forefemur 7.3–8 mm, foretibia 3.7–4 mm, mid coxa 1.7–2.3 mm, mid femur 6.5–7 mm, mid tibia 6.5–7.4 mm, hind coxa 2–2.3 mm, hind femur 7.5–9 mm, hind tibia 8.7–9.5 mm. Head (Fig. 17): triangular in shape, general shape as in the male but stouter, with reduced ocelli and shorter antennae; about 1.4–1.6-times as wide as the supracoxal dilation of the pronotum. Vertex exhibiting a transverse, darkened area (its coloration varies depending on the specimen's colour morph). Frontal shield as in the male, approximately 2.5–3-times as wide as long. Thorax: Pronotum (Fig. 18) as in the male but more robust; lateral margins with minute, black denticles, each bearing a very small hair; disc smooth. Supracoxal dilation as wide as vertex, with rounded margins. Prozone bulbous as in the male, but bulbs are more prominent (better seen in lateral view, Fig. 19); metazone/prozone ratio=0.73. Metazone with two well-developed distal tubercles. Meso- and metanotum with a recurved process on their distal margin, the one on the mesonotum about three times as large as that on the metanotum. Forelegs (Fig. 19) as in males but stouter. Forecoxae with 6–7 black denticles on the anterior edge with 1–3 white, smaller spines between them; posterior side with approximately 19–23 tiny denticles and several scattered small setae; a blackish spot is normally found in the middle of each coxa; inner distal lobes divergent. Forefemora with characteristic marking (regardless of colour morph): one V-shaped medial, dark spot in addition to another smaller and more distally located spot. Spination formula F=12IS/4ES/4DS and T=10–11IS/6ES. All femoral and tibial spines with black tips. Metatarsi 1.1–1.3

times as long as the remaining tarsomeres taken together. Mid and hind legs long and slender, exhibiting banded pattern and bearing very small, scattered setae. Mid and hind metatarsi 1.1–1.3 and 1.2–1.6 times, respectively, as long as the remaining tarsomeres taken together. Abdomen: Dilated, wider than in males. Latero-distal corners of tergites 2–6 with distinct lamellar extensions, those on the second and third tergites more developed (second larger than third). Tergum exhibiting foliaceous distal lobes of various sizes: first tergite with a rectangular lobe, slightly trilobated; terga 2–4 exhibiting much larger (somehow trilobate) foliaceous extensions (as shown in Fig. 20), all of them with irregular distal edges. Terga 5–7 each with a small distal process that decreases in size until almost disappearing in tergum 7, then becoming increasingly larger towards the ninth tergum. Supra-anal plate (tergum 10) tongue-like (Fig. 20), very wide and with a rounded margin. Cerci as in the male.

### Etymology

The specific epithet '*kanjaris*' derives from "Kañaris", the name under which the local indigenous people and their unique Quechua dialect became known. According to their traditions, the Kañaris are descendants of Inca clans that settled near the remote area where this species inhabits to escape Spanish domination.

### Diagnosis and Comments

*Pseudopogonogaster kanjaris* is a mid-sized species compared to other *Pseudopogonogaster* species; therefore, *P. kanjaris* can easily be separated from the larger and more slender *P. mirabilis* and the smaller but stouter *P. hebardii*. A character that distinguishes *P. kanjaris* from the other known species is the relative position of the supracoxal dilation, which is located at the middle of the pronotum; the same feature is located beyond the middle in the other known species. The males of *P. hebardii*, *P. mirabilis* and *P. kanjaris* can be further distinguished by comparing the morphology of their copulatory apparatus, with the most obvious differences being the slenderness of the distal process of the left dorsal phallomere and the shape of the ventral phallomere (see Figs 10–13 in Lombardo & Ayala 1998 for further comparisons). The original description of the male of *P. marulandae* makes excessive use of colour patterns, which in *Pseudopogonogaster* is of little use for comparative purposes because of extreme colour polymorphisms. However, Salazar (2002) does depict the pronotum of *P. marulandae*, which clearly shows the metazone to be more elongated than that of *P. kanjaris* but with a relatively shorter and stouter prozone. On the other hand, the females can be distinguished, among other characters, by the variability in the ornamentation of the abdominal tergites. *Pseudopogonogaster iguaquensis* is easily distinguished from *P. kanjaris* and the other known species based on its vestigial lobe on tergite 4, while the same lobe is well developed in all other known species of *Pseudopogonogaster*. On the other hand, *P. mirabilis* exhibits abdominal lobes (Fig. 7) that are longer and more slender than those of *P. kanjaris* and also exhibits filiform lobes on the distal tergites (Fig. 2), which are absent in *P. kanjaris*. However, such filiform lobes on the distal tergites are also present in *P. muscosa* (Salazar 2002a).

## Discussion

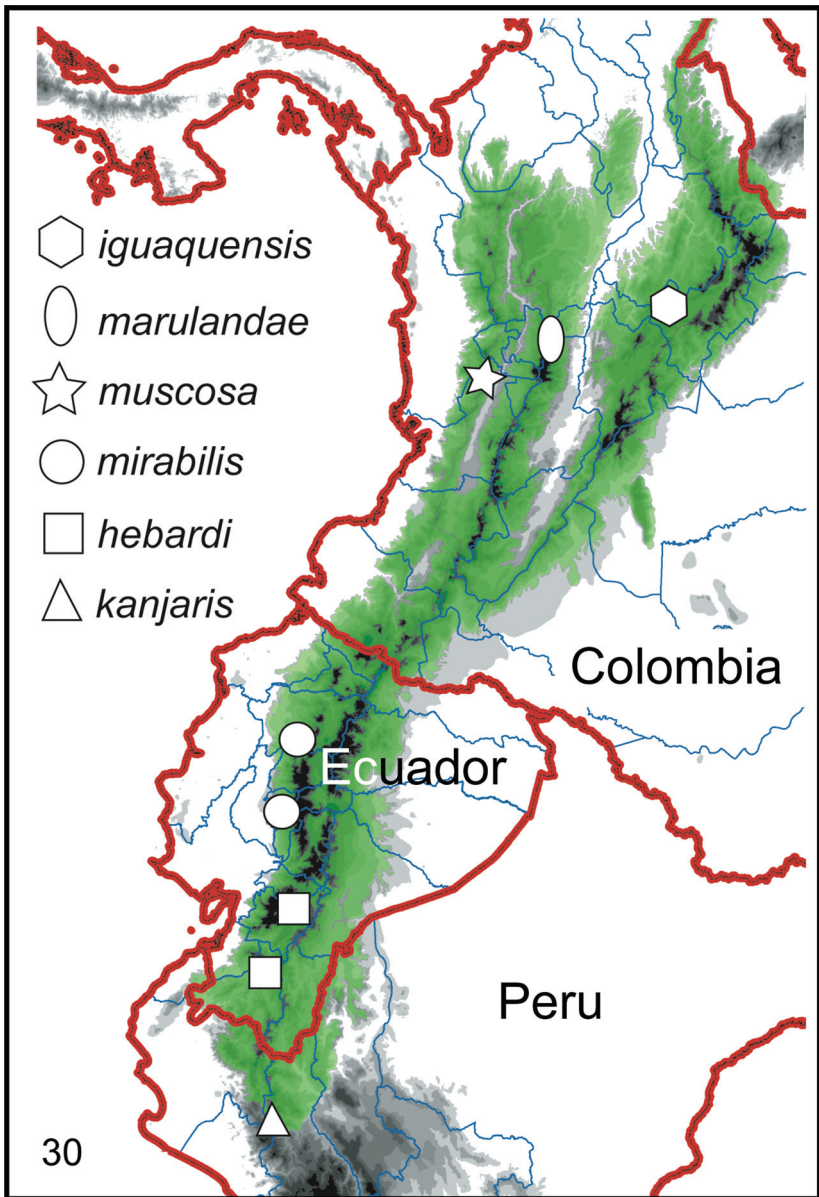
### *Biogeography of Pseudopogonogaster*

The distribution of *Pseudopogonogaster* (Fig. 30) suggests that this genus is endemic to mountain rainforest habitats along the Andean slopes of Colombia, Ecuador and northern Peru. These formations extend as a somewhat contiguous range between the Colombian Chocó and most of Ecuador (now highly disturbed in some areas). However, this habitat occurs in naturally disjunct patches in the southern-most limit of its range (i.e., southwestern Ecuador and northwestern Peru) (Weigend et al. 2005). According to the material studied by us in addition to other literature records, the various species of *Pseudopogonogaster* are found in mountain rainforest at elevations between 1500 and 3500 m. However, the type locality of *P. mirabilis*, Balsapamba, is located at 650 m, but it is likely that the type specimen was collected at a higher elevation in the vicinity of Balsapamba, which may merely be a referential location. Therefore, members of this genus arguably inhabit the highest elevations in the western hemisphere. In fact, the highest elevation collection record for any Neotropical mantid (3500 m) is that of a *P. hebardii* specimen (Lombardo & Ayala 1998).

A population of *P. kanjaris* was discovered in one of the few relicts of mountain rainforest that occurs as natural patches in northwestern Peru. This forest, known as 'Kañaris', is among the largest of its kind in northern Peru and remains understudied (Llatas-Quiroz & López-Mesones 2005). The Kañaris forest is located at the Huancabamba Depression, a major biogeographic feature in northern Peru, where the Andes mountains are partially interrupted (at the Cordillera Central and Cordillera Oriental) by the confluence of the Chamaya-Marañón Rivers; this is the lowest (2145 m) section of the Andes between Colombia and southern Chile (Duellman & Pramuk 1999). The Huancabamba Depression constitutes a barrier for dispersal of high-altitude taxa in the north–south direction (however, it allows dispersal along the Cordillera Occidental, which is not fully interrupted) as well as for amazonian taxa in the east–west direction (towards the Pacific lowlands) (O'Neill 1992). Due to its varied habitats and rich geological history, the Huancabamba Depression is considered to be a biodiversity hotspot with high levels of endemism (Young & Reynel 1997; Weigend 2002). The lowest elevation in this part of the Andes also allows moisture from the Atlantic to cross the Andes in the east–southeast direction, favoring precipitation in some areas before it reaches the western slope of the Andes, which remains relatively dry (Llatas-Quiroz & López-Mesones 2005). Thus, the Kañaris forest (Fig. 31) is very humid and often cold as it is almost permanently covered by clouds, and occurs at high elevation (1500–3000 m). *Pseudopogonogaster kanjaris* likely represents the southern-most limit of the range for this mantid lineage. Geographically, the nearest known species to *P. kanjaris* is *P. hebardii*, which is found ca. 250 km further north (Fig. 30).

### *Taxonomic status of Calopteromantis terrai Jantsch, 1994*

The distinctive distribution of *Pseudopogonogaster* in the Andean regions of Colombia, Ecuador and northern Peru further suggests that *Calopteromantis terrai*, described by



**Fig. 30.** Map showing the distribution of *Pseudopogonogaster* spp. The Andes are indicated in gray (darkest areas represent highest elevations), whereas green areas represent mountain forests. Most species are known only from their type locality. This figure is published in colour in the online edition of this journal, which can be accessed *via* <http://www.brill.nl/ise>

Jantsch (1994) from Coophema, Cuiabá, Mato Grosso, Brazil (approximate coordinates: 15°38'20" S, 56°3'42" W), is not a member of *Pseudopogonogaster*. This species is known only from a single male specimen, whose morphology clearly departs from that of *Pseudopogonogaster* in many respects, particularly regarding the structure of the



**Fig. 31.** Habitat of *Pseudopogonogaster kanjaris* in Kañaris, Lambayeque, Peru (as seen from the type locality). This figure is published in colour in the online edition of this journal, which can be accessed via <http://www.brill.nl/ise>

male genitalia (see Jantsch, 1994). In addition, Cuiabá is located in what ecologically corresponds to a lowland tropical savanna (Cerrado), clearly a radically different habitat compared to an Andean mountain forest where *Pseudopogonogaster* spp are found.

A preliminary assessment of the original description of *Calopteromantis terrai* and its accompanying figures suggested that this species might actually be a member of the Pseudomiopteriginae. Because of the actual identity of this species could not be determined with confidence based on Jantsch's description only, we examined the holotype deposited at MCTP. The holotype, shown in Fig. 21, is partially fragmented. The specimen remains fixed to the pin by glue and is missing both hind legs, whereas the meso- and metathoracic wings, the left mid leg and the genitalia, are all glued to a piece of cardboard associated to the specimen (Figs 21 and 22). There are three labels: (1) UFMT/MT-Coophema/Cuiabá/18-III-1990; (2) *Calopteromantis/terrai*-Holótipo male/19-V-94/L. Jantsch det.; (3) "2046". The illustration of the genitalia provided by Jantsch agrees in most respects with the actual structure, although it must be noticed here that Jantsch's designs of the holotype's genitalia also depicts some of the muscular tissue that is still attached to the preserved phallomeres, an uncommon (and potentially misleading) procedure when it comes to depict male genitalia.

The analysis of the holotype's external morphology revealed it to be a member of *Eumiopteryx* Giglio-Tos, 1915 (Thespidae: Pseudomiopteriginae). The pronotum,



an important character at the genus level, was not originally depicted by Jantsch (1994). The analyses of this structure in the holotype revealed the characteristic shape observed in *Eumiopteryx*, with well-developed anterolateral expansions on the prozone and one proximal laterodorsal carina on each side of the metazone (Fig. 23). Consequently, this species is now better referred to as *Eumiopteryx terrai* (Jantsch, 1994) comb.n. The little-studied genus *Eumiopteryx* now includes four species and the genus is in need of revision (Rivera 2010b). Whether *E. terrai* represents a valid species or is a synonym of a previously described one, still requires further investigation.

Finally, the records of *Calopteromantis hebardei* for Rio Grande do Sul, by Jantsch & Corseuil (1988) and Dorneles et al. (2005), almost certainly represent misidentifications, as this species seems to be restricted to the mountain forests of Southern Ecuador. Consequently, *C. hebardei* is here removed from the Brazilian mantid fauna. Further records of either *Calopteromantis* or *Pseudopogonogaster* occurring in southern Brazil must be dismissed.

### *Mantids in the mist*

The mountain forests of the tropical Andes are among the most species-rich ecosystems on earth (Myers et al. 2000). Such diversity is correlated with high levels of water input from precipitation and air moisture in the form of mist or fog, conditions that promote the proliferation of epiphytic flora, which constitutes a conspicuous component of these so-called cloud forests (Küper et al. 2004). For instance, more than a third of the plant species in the submontane and montane rainforests of Ecuador belong to the epiphytic or hemi-epiphytic community (Jørgensen & León-Yáñez 1999), which is typically composed of several types of non-vascular (moss, lichen) and vascular (pteridophyte, angiosperm) species. Given the dominance of epiphytic habitats and the diversification of their typical constituent members, it is not surprising that several organisms have evolved special adaptations for living among these plant communities. Clear examples of this are lichen-mimicry adaptations, which are common in many vertebrate and invertebrate animal taxa (Gerson 1973; Seaward 1988). Among insects, typical adaptations involve background matching and outline-breaking coloration, outgrowths and other lichen-like cuticular expansions on different parts of the body, stilt-like walking legs, and specialized behaviors (shade concealment, motionless postures, etc.).

### *Lichen-mimicry and colour polymorphism in Pseudopogonogaster*

The term ‘lichen mantids’ applies to various members of the order Mantodea with specialized morphology adapted for living among epiphytic vegetation. In the Neotropical region, lichen-mimicry and other similar adaptations (e.g., moss-mimicry) is known to have independently evolved in members of at least three different lineages: the genus *Pseudacanthops* Saussure, 1870 (Acanthopidae), the Thespidae genera *Pogonogaster* Rehn, 1918 and *Carrikerella* Hebard, 1921 (both of the subfamily Oligonicinae), and *Pseudopogonogaster* (Miopteryginae) (J.R. pers. obs.). Other old-world lineages with remarkably similar (but convergent) habitat adaptations include the genera *Haania*

Saussure, 1871 and *Astape* Stål, 1877 (Thespidae; Haaninae) (Liefstinck 1953), and *Calofulcinia* Giglio-Tos, 1915 (Mantidae: Nanomantinae) (F. Wieland, pers. commun.).

Epiphytic habitats consist of a mosaic of textures and colours that is generated by the various co-occurring species. A common occurrence among cryptically coloured organisms that tend to rest on such heterogeneous habitats is colour polymorphism. We had the opportunity to document this phenomenon in *Pseudopogonogaster kanjaris*, as we observed several female individuals exhibiting multiple colour patterns of green, brown, white, black and gray, in different hues and fixed combinations (Figs 24–28). On the other hand, little is known regarding the degree of variation among males, as this sex appears to be less abundant (and likely less sedentary) than females and, thus, hard to observe in their natural habitat (Fig. 29). Even though Ayala & Onore (2001) were the first in reporting such colour polymorphism in *P. mirabilis* (cited as *C. otongica*), Salazar (2005) was the first in photographically documenting such phenomenon in *P. iguaquensis* in Colombia. Although not yet documented, other *Pseudopogonogaster* species are likely to exhibit such variability as well. Similar adaptations, in terms of colour polymorphism, have also been observed in the Oriental mantid *Astape denticollis* Stål, 1877, a species that inhabits epiphytic lichens and mosses in the mountain forests of west Java, Indonesia (Liefstinck, 1953).

The phenomenon of colour polymorphism has been well studied and several mechanisms have been proposed to explain its occurrence (see Endler 1988; Ruxton et al. 2004). It is believed that colour polymorphism is the evolutionary result of the interaction between two separate mechanisms where visual predators (i.e., mantid's predators) act as the selective force: (i) frequency-dependent *apostatic selection*, in which predators, based on their experience and learning abilities, tend to attack the most abundant prey type more often, and (ii) *disruptive selection*, which favours those morphs that are more highly specialized in microhabitats within an heterogeneous environment, as less specialized morphs are selected against by predation (Endler 1988; Bond & Kamil 2006).

Such mechanisms seem plausible for explaining fixed colour patterns, whereas they do not explain ontogenetic changes in coloration. Certain species of mantids are known for being able to change their coloration among and within instars in response to various environmental cues (Edmunds & Brunner 1999). In fact, Ayala & Onore (2001) reported that immatures of *P. mirabilis* (cited as *C. otongica*) changed their coloration during development (i.e., across instars). We made a similar observation in one pre-adult female specimen of *P. kanjaris* that was kept in captivity after collection. This individual drastically changed its coloration from dark, brownish green to a black and white adult. There appear to be environmentally induced mechanisms that allow these mantids to change from one colour morph to another in order to match specific backgrounds during their development. Changes in size, vulnerability, reproductive status, habitat, seasonal weather conditions (e.g., light incidence, temperature, humidity) and metabolism are some of the environmental factors often suggested in promoting ontogenetic changes in coloration (Booth 2008). This interesting biological aspect of *Pseudopogonogaster* and the mechanisms behind it deserve further investigation.

### *Interspecific associations*

Ayala & Onore (2001) published some observations on the life history of *P. mirabilis* (as *C. otongica*) and provided a list of epiphytic species that constituted the habitat of this mantid in La Otonga Reserve, Northern Ecuador (for a complete list, see Ayala & Onore 2001), but they did not report on any lichen taxa. Salazar (2005) stated that in the region of Boyacá, Colombia, *P. iguaquensis* is associated with various non-vascular taxa such as epiphytic liverworts (Hepatophyta) of the genera *Bazzania* and *Plagiochila*, moss (Bryophyta) of the genus *Neckera*, and lichens of the genera *Parmelia*, *Parmotrema* and *Usnea* (all in the family Parmeliaceae). We found *P. kanjaris* living among lichen species of the genera *Usnea*, *Hypotrachina* and *Parmotrema* (all in Parmeliaceae), *Heterodermia* (Physciaceae), and *Lecanora* (Lecanoraceae). Interestingly, each chromatic form observed in *P. kanjaris* was best camouflaged against similarly coloured background (i.e., a particular species or combination of epiphytic species). For instance, the white and black morph (Fig. 25) seems to be better camouflaged among species of *Hypotrachina* and *Parmotrema*, which are rather common in cloud forest habitats. These lichen genera exhibit a black lower cortex that is often partially exposed among the broken edges of the lichen lobes, making a conspicuous contrast against the generally whitish, upper surface of the lichen. The black and white individuals show a remarkable resemblance to their model lichens, with their black marks enhancing the effect and disrupting the insect outline.

### Conclusions

As a result of the present study, we conclude that the genus *Pseudopogonogaster* comprises six species:

- Pseudopogonogaster hebaridi* (Terra, 1982), comb.n.  
= *Calopteromantis hebaridi* Terra, 1982
- Pseudopogonogaster iguaquensis* Carrejo & Salazar, 2002
- Pseudopogonogaster kanjaris* Rivera & Yagui, sp.n.
- Pseudopogonogaster marulandae* (Salazar, 2002), comb.n.  
= *Calopteromantis marulandae* Salazar, 2002
- Pseudopogonogaster mirabilis* Beier, 1942  
= *Calopteromantis otongica* Lombardo & Ayala, 1998, syn.n.
- Pseudopogonogaster muscosa* Salazar, 2000
- Species not included in *Pseudopogonogaster*  
*Eumiopteryx terrai* (Jantsch, 1994), comb.n.  
= *Calopteromantis terrai* Jantsch, 1994

Of these described species, only *P. mirabilis*, *P. hebaridi* and *P. kanjaris* are known from both sexes, including male genitalia (the male of *P. iguaquensis* was portrayed by Salazar (2005) but it has not yet been formally described). Conversely, *P. muscosa* and *P. marulandae* are known only from a single female and male specimen, respectively. Finally,

**Table 1.** List of species cited in the present study (as originally described), their type depository, sex of holotype and type locality.

Species	Depository	Holotype	Type locality
<i>Calopteromantis hebaridi</i>	ANSP	Male	Ecuador: Azuay (Cerro de Bulan, Valle del Paute). Other records: Ecuador: Loja (Saraguro, Taquil, Mamanuma)
<i>Calopteromantis marulandae</i>	MHN-UC	Male	Colombia: Caldas (Marulanda)
<i>Calopteromantis otongica</i>	DBUC	Male	Ecuador: Cotopaxi (San Francisco de las Pampas, Bosque Integral Otonga)
<i>Calopteromantis terrai</i>	MCTP	Male	Brazil: Mato Grosso (Cuiabá)
<i>Pseudopogonogaster kanjaris</i>	UNALM	Male	Peru: Lambayeque (Kañaris)
<i>Pseudopogonogaster iguaquensis</i>	UNIVALLE	Female	Colombia: Boyacá (Santuario de Flora y Fauna de Iguaque)
<i>Pseudopogonogaster mirabilis</i>	MIZ	Female	Ecuador: Bolivar (Balsapamba)
<i>Pseudopogonogaster muscosa</i>	UNIVALLE	Female	Colombia: Chocó (Cerro el Inglés)

Acronyms (not listed in Materials and Methods): ANSP, Academy of Natural Sciences (Philadelphia, PA, USA); DBUC, Dipartimento di Biologia Animale “Marcello La Greca”, Università di Catania (Catania, Italy); MHN-UC, Museo de Historia Natural, Universidad de Caldas (Manizales, Colombia); UNIVALLE, Museo de Entomología, Universidad del Valle (Cali, Colombia).

based on the evidence presented within this study, *Calopteromantis terrai* Jantsch, 1994 is now included within the genus *Eumiopteryx* (Thespidae: Pseudomiopteriginae). Table 1 summarizes the type depository, sex, type locality and additional distributional records (when known) of each of the species cited in this study for future references.

Because the distribution of *Pseudopogonogaster* is within remote and often inaccessible mountainous regions of the tropical Andes, it is likely that several other undescribed species (and even yet unknown genera) could be discovered. Within Peru, such populations might be found in other similar habitats known to exist in Lambayeque, Cajamarca and Piura departments, some of them now heavily disturbed (Weigend et al. 2005). Future descriptions of new species should include, whenever possible, both sexes to prevent further taxonomic confusions resulting from the marked sexual dimorphism within this genus.

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