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Insights on the evolution of Ululodini (Insecta: Neuroptera: Myrmeleontidae: Ascalaphinae), focusing on the systematics of the genus *Ascalorphne* Banks, 1915

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ABSTRACT

The tribe Ululodini is one of the most remarkable taxa of Neotropical Neuroptera, mainly due to its great flight ability, eyes divided into two lobes, and production of abortive eggs that act as a chemical barrier against predators. Nonetheless, Ululodini remains little studied. One genus of this tribe, *Ascalorphne* Banks 1915, currently comprises four valid species: *A. macrocerca* (Burmeister, 1839), *A. impavida* (Walker, 1853), *A. umbrina* (Gerstaecker, 1884), and *A. leisewitzi* (Navás, 1911). This study reviews the taxonomy of *Ascalorphne*, redescribing the external morphology and, for the first time, the male and female genitalia. Furthermore, *A. leisewitzi* is proposed as a new synonym of *A. umbrina*, an identification key is presented, and the geographic distribution of the genus is updated based on collected specimens and data available in the citizen science project iNaturalist. Also, the body and genital morphology of Ululodini were comparatively studied and analyzed in a phylogenetic context with all other Ascalaphinae tribes that occur in the Neotropics, allowing a better understanding of the evolution and biology of these insects. As a result, new synapomorphies for Ululodini are presented, *Albardia furcata* Oswald, 1903 is recovered as the sister taxon to the rest of the tribe, *Ameropterus* Esben-Petersen, 1922 was recovered as paraphyletic, and *Ascalorphne* was recovered as monophyletic in all analyses.

Introduction

Owlflies are some of the most beautiful and fascinating insects of the order Neuroptera, presenting a myriad of colors, shapes, and behaviors, but are still little studied, especially in the Neotropics. According to the current classification, proposed by Machado et al. (2019), the traditional family Ascalaphidae was classified as a subfamily of Myrmeleontidae and organized into six tribes: Dimarini, Palparini, Stilbopterygini, Ascalaphini, Ululodini and Haplogleniini, being the last three formerly included in Ascalaphidae, the true owlflies.

Worldwide, the owlflies (Ascalaphini + Ululodini + Haplogleniini) are represented by 438 valid species, and the Neotropical fauna currently comprises 89 species organized in ten genera (Machado et al., 2019). In the Neotropics, the Ululodini tribe is the most diverse group of Ascalaphinae, but paradoxically, it is the least studied (Ardila-Camacho et al., 2019).

Ululodini occurs throughout the New World and is composed of 61 valid species, classified into five genera: *Albardia* van der Weele, 1903 (1 sp., *A. furcata* van der Weele, 1903), *Ameropterus* Esben-Petersen, 1922 (21 spp.), *Ascalorphne* Banks, 1915 (4 spp.), *Cordulecerus* Rambur, 1842 (10 spp.) and *Ululodes* Smith, 1900 (25 spp.) (Ardila-Camacho et al., 2019; Machado et al., 2019).

Albardia furcata is one of the most striking species among Neotropical Neuroptera, due to the large number of autapomorphies exhibited by this species, which in the past led some authors to allocate it on its own subfamily (Albardiinae) (New, 1982; Penny, 1983). The study by Machado et al. (2019) classified this species as a member of Ululodini, sister to the rest of the tribe and, in addition, characters of the recently described larvae also support this relationship (Machado et al., 2021); however, Jones (2019) classified this species as a distinct group.

Adults of Ululodini are recognized by the long antennae (except *A. furcata*), hind wing with unforked CuA vein, production of repagula (abortive eggs with defense/feeding function) (New, 1971; Henry, 1972, 1978a, 1978b), transversely sulcated eyes (except *A. furcata*) and females with the eighth abdominal spiracle located in the pleura (not in the tergite, as in non-Ululodini Ascalaphinae).

Ascalorphne currently comprises four valid species: *A. macrocerca* (Burmeister, 1839) (Fig. 1A) and *A. impavida* (Walker, 1853) (Fig. 1B), known from Brazil, *A. umbrina* (Gerstaecker, 1894) with records from Bolivia and Paraguay and *A. leisewitzi* (Navás, 1911) recorded from Argentina, Paraguay and Bolivia.

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Figure 1 Adult males of *Ascalorphne macrocerca* (Burmeister, 1839) (A) and *Ascalorphne impavida* (B) (Myrmeleontidae: Ascalaphinae: Ululodini). Photos: Lucas Rubio.

All Ululodini genera lack modern taxonomic revision, presenting limited descriptions, outdated geographic distribution, uninformative illustrations, lost/destroyed type material, and lack of discussions of phylogenetic relevant characters. Furthermore, the genitalia of most species were never described, hindering the systematics of the group and the identification of the Ululodini species, as discussed by Ardila-Camacho et al. (2019).

The genus *Ascalorphne* fits into this context. The last revision of the group was carried out more than 100 years ago by Navás (1913). Only two identification keys have been proposed: the first by Navás (1912a), which was later reproduced without changes in Navás (1913), and the second by Heckman (2017), but based exclusively on literature compilation and not including *A. umbrina*.

Therefore, the main objective of this work is to review the taxonomy of *Ascalorphne*, redescribing the external morphology and, for the first time, the genitalia of both sexes, and evaluating the monophyly of the genus and the phylogenetic relationships between the genera of the Ululodini tribe. Additionally, this study sought to comparatively analyze the body and genital morphology of Ululodini in relation to all other tribes of neotropical Ascalaphinae, establishing new synapomorphies to the tribe.

Material and methods

Studied material

Ascalorphne specimens are rarely collected and, therefore, photographs or specimens were requested from several national and international institutions, including reference collections from most South American countries, but not all of them contained specimens of this genus. Therefore, the material analyzed in this study comes from the following institutions:

- APTA: Agência Paulista de Tecnologia dos Agronegócios - São Paulo, Brazil.
- NHMUK: Natural History Museum - Londres, England.
- CAS: California Academy of Sciences - São Francisco, United States of America.
- CEMT: Coleção Entomológica de Mato Grosso - Cuiabá, Brazil.
- CZMA: Coleção Zoológica do Maranhão - Caxias, Brazil
- DZUP: Coleção Entomológica Padre Jesus Santiago Moure – Curitiba, Brazil.
- FDACS: Florida Department of Agriculture and Consumer Services - Tallahassee, United States of America.
- FMNH: The Field Museum of Natural History - Chicago, United States of America.
- INPA: Instituto Nacional de Pesquisas da Amazônia - Manaus, Brazil.
- MCZ: Museum of Comparative Zoology, Harvard University - Cambridge, United States of America.
- MNHN: Muséum National d'Histoire Naturelle - Paris, France.
- MNHNP: Museo Nacional de Historia Natural del Paraguay - San Lorenzo, Paraguay.
- NHMD: Natural History Museum of Denmark - Copenhague, Denmark.
- NRM: Swedish Museum of Natural History - Estocolmo, Sweden.
- TAMUIC: Texas A&M University Insect Collection - College Station, United States of America.
- UFBA: Universidade Federal da Bahia - Salvador, Brazil.
- UFMG: Universidade Federal de Minas Gerais – Belo Horizonte, Brazil.
- USNM: Smithsonian Institution National Museum of Natural History -Washington, D.C., United States of America.
- ZIMUG: Zoologisches Institut und Museum, Universität Greifswald- Greifswald, Germany.
- ZSM: Zoologische Staatssammlung München – Munique, Germany.

The study of the type material was carried out through high resolution photographs taken from different angles. In total, 178 *Ascalorphne* specimens were personally analyzed (belonging to the following collections: CEMT, APTA, CZMA, DZUP, UFBA, UFMG, INPA, FDACS), in addition to 18 other specimens that were studied through images.

Taxonomic analysis

The wing venation terminology follows Breitkreuz et al. (2017) (Fig. S1), and the genital sclerites nomenclature was based on Aspöck and Aspöck (2008). Dissections, morphological studies, and phylogenetic analyses were based on 36 specimens representing 14 species (Table S1).

For the dissection of the genitalia, the last two abdominal segments were removed and cleared in a heated solution of 10% potassium hydroxide (Contreras-Ramos, 1999) for 25 minutes and cleaned with the aid of tweezers. The genitalia were preserved in microtubules containing glycerin and attached in association with the original specimens. The analyzed specimens are deposited at the DZUP or have been returned to the institution of origin with an identification label.

For the measurement of five males and five females of each species of *Ascalorphne*, an electronic caliper was used, taking the measurements of the body (length between forehead and abdomen apex), antennae (length between the antennae and the apex of the club), fore and hind wing (length between the base of the wing and its apex).

Abbreviations used in text and figures: AOS: anterior orbital sclerite, D: distivalve, E: ectoproct, GPC: gonarcus-paramere complex, GX: gonocoxite, GS: gonostyli, GP: gonapophysis, I: interdens, L: liguella, P: pelta, PU: pulvinus, R: repagula, S: sternite, T: tergite. New occurrence records are indicated by an asterisk (*) and a median point (•) separates collection campaigns within the same state.

Photos and maps

The photographs were taken with an Axiocam 305 color camera coupled to the Zeiss Discovery V20 stereomicroscope. The images were edited in Adobe Photoshop 2020.

The map was built using SimpleMappr (Shorthouse, 2022) and done by plotting the collection data present on the labels associated with each specimen. Additionally, it was included in the map occurrences of *Ascalorphne* submitted until 18.iii.2022 to the citizen science project iNaturalist (https://www.inaturalist.org) (Table S2).

Phylogenetic analyses

For phylogenetic analyses, the ingroup was composed of all species of *Ascalorphne* and the outgroup by representatives of all Ascalaphinae tribes that occur in the Neotropics: Ululodini (*Ululodes* sp.1 and sp.2; *Ameropterus dissimilis* (McLachlan, 1871), *Ameropterus* sp.1; *Cordulecerus alopecinus* (Burmeister, 1839), *Cordulecerus unicus* (Walker, 1860); *Albardia furcata*), Haplogleniini (*Haploglenius costatus* (Burmeister, 1839), *Amoea chlorops* (Blanchard, 1845)); and Ascalaphini (*Fillus amazonicus* Machado & Rafael, 2011). The resulting trees were rooted between *Dimares elegans* (Perty, 1833) (Dimarini) and all remaining species, because this species was recently recovered as the sister group to all the other Ascalaphinae (Machado et al., 2019).

A total of 35 morphological characters were obtained from all body regions and organized using the softwares Excel and Notepad. Maximum parsimony analyses were performed in TNT v.1.5 (Goloboff and Catalano, 2016) using the heuristic search method (TBR). As analysis parameters, it was adopted: memory configured for 1000 megabytes of RAM, random seed was set to 0, 1,000 replications, retention of 1,000 trees per replication. Characters were treated as discrete and unordered. Two types of analysis were performed: traditional search and implicit enumeration. In each type of analysis, equal weighting and implicit weighing were applied (using the standard value of TNT: K=3). Non-applicable characters were encoded with "-" and unknown/unobservable characters as "?". Winclada (Nixon, 2002) was used to edit the resulting trees and plot the character transformations onto them.

As support measures, we used relative Bremer support (Goloboff and Farris, 2001) calculated based on the TBR of existing trees and indicating the retention of trees with 1 to 5 extra steps, and Poisson bootstrap (Goloboff et al., 2003), both calculated in TNT.

Results

Redescription of the genus *Ascalorphne*
Family Myrmeleontidae Latreille, 1802

Subfamily Ascalaphinae Lefebvre, 1842
Tribe Ululodini Van der Weele, 1908

Genus *Ascalorphne* Banks, 1915

Diagnosis. Antennae long (reaching or extending beyond the apex of the forewing), wings long and narrow, petiolate and with a distinct projection (anal lobe) at the anal margin of the forewing, hind wing with CuP vein straight, males with expanded hind wing cubital area. Tibial spurs elongated, larger than the first four tarsomeres combined. Ectoproct oval, not elongated.

Distribution. Argentina, Bolivia, Brazil, Paraguay.

Type species. *Ascalaphus macrocerca* Burmeister, 1839.

Head: Labrum and clypeus brown, with a tuft of long setae on the dorsolateral region of the clypeus; mandible brown, concave and with inner margin strongly sclerotized, with three teeth; 5-segmented maxillary palp, hairy, except for the last two segments; labium yellowish, quadrangular and with tufts of black, long, falcated and thick setae that are restricted anterolaterally, ventrally labium with white, thin and long setae; labial palp with 3 palpomeres, with black setae on the second one, long, equal to or longer than the third segment, last palpomere brown/yellow with short setae; frons black; eye transversely sulcated, of variable color (yellowish, grayish or dark), in lateral view with a row of long white setae in the paraocular band of the ventral half of the eye; vertex brown and narrow; antennae long, with black rings, as long as/or longer than the forewing; scape and pedicel wider than long, scape covered by long setae (greater than basal four flagellomeres combined); 38-45 flagellomeres, longer than wide and with black and long setae at the apices, flagellomeres 8-23 with longer setae, in males these setae are specialized; fusiform/piriform antennal club composed of 10 flagellomeres, the distal one with a protuberance at the apex.

Thorax. Pleural region brown with yellow spots, mostly with long white setae and some black; pronotum narrow in dorsal view; prescutum frontally emarginated by long and dark setae; scutellum with two rounded and yellowish lateral maculae. **Leg**. Coxae and trochanter with long white setae; femur yellowish at the base and brown at the apex, with white long setae and some black; tibia brown or yellowish, with black long setae and some white; tibial spur brown, curved and long, larger than the four basal tarsomeres combined, in the fore and mid leg reaching the fourth tarsomere, but reaching the fifth in the hindleg; tarsomeres with short black setae, on the hindleg the tarsomere 1 is about twice as long as the others, except for tarsomere 5, which is about three times longer than tarsomere 1 of all legs, tarsomeres 2-4 with the same length; pretarsus with two claws, brown, curved and long, almost as long as tarsomere 5, planta with two long black setae.

Wings. Petiolate, membrane hyaline or pigmented, veins brown, pterostigma rhomboid, black or brown. **Forewing**. Presence of a distinct axillary lobe; apical area after fusion of Sc+R with 3-5 cell lines; RP with 4-5 bifurcations; MA long, without bifurcations and extending beyond the third bifurcation of RP; CuA+MP with 9-11 bifurcations; CuP straight and short, extending to the origin of RP; A1 extremely short, curving into the axillary lobe; cubital area with 3-4 cell lines. **Hind wing**. Shorter and narrower than forewing; males with an expanded cubital area; smaller pterostigma; MA straight and ending at or beyond the third RP fork; CuP straight, extending to the first RP fork; cubital area with 2-3 cell lines.

Abdomen. Shorter than wings, brown/yellowish; T1 yellowish with white short setae, and with a black macula; T2 with some long white setae; each side of the remaining tergites with two elongated black macula that become circular in tergites T7 and T8; S1-2 yellowish, other sternites brown with short black setae.

Terminalia and Genitalia. ♂**:** Ectoproct oval with black, strong and long setae; T9 not dorsally fused and as two triangular-shaped plates in lateral view; S9, in lateral view, concave and, in ventral view, spatula-shaped, with sclerotization on the edges and presence of black, short and long setae at the apex. **Gonarcus-paramere complex**. GX9 convergent, fusiform in lateral view, in ventral view oval, concave, and with apex sclerotized; GX11 membranous, concave and subtriangular in lateral view, with apex projecting over the apex of GX9; pelta broad, triangular, membranous, glabrous and located below the GX9; pulvinus not-everted, membranous, with short setae. ♀**:** Ectoproct oval in lateral view and full of black and long setae; T9 elongated, with anterior projection present, full of long black setae, longer and more abundant in the ventral portion; GX9 (distivalve) trapezoidal, with setae on the ventral margin; GP8 (linguella) membranous, subtriangular and with short setae; interdens sclerotized, small; GX8 (ventrovalvae) paired, membranous, concave, interiorized and glabrous.

Ascalorphne macrocerca (Burmeister, 1839)

Figs. 1A, 2, 3, 7B, 15J, 18C.

Ascalaphus macrocercus Burmeister, 1839:1000 (original description); Hagen, 1861:326 (list); Hagen, 1866:385 (cited); McLachlan, 1873:252 (taxonomy); van der Weele, 1908:139 (list); Navás, 1912b:80 (list); Banks, 1915:350 (taxonomy); Penny, 1977:11 (list); Penny, 1981b:404: (cited); Oswald and Penny, 1991:10 (list).

Orphne macrocerca (Burmeister, 1839): McLachlan, 1871:252, 401 (new combination/ distribution); van der Weele, 1908:139 (cited/ taxonomy/ redescription); Navás, 1912a:223 (key); Navás, 1912b:80 (key/ list/ taxonomy); Navás, 1913:64 (key).

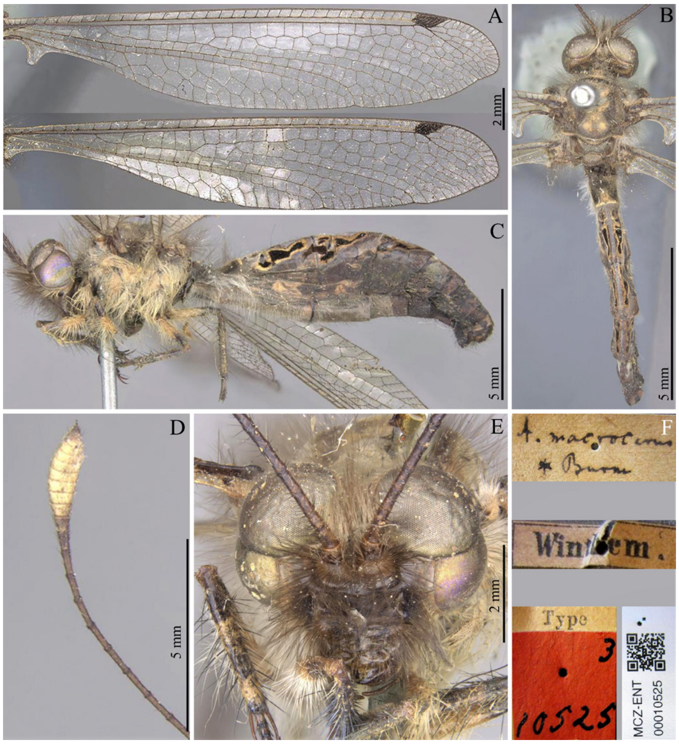

Figure 2 *Ascalaphus macrocercus* Burmeister, 1839 [= *Ascalorphne macrocerca* (Burmeister, 1839)], lectotype, female, MCZ. A) Fore and hind wing B) Body, dorsal; C) Body, lateral; D) Antennal club; E) Head, frontal; F) Labels.

Suhpalacsa macrocercus (Burmeister, 1839): Taschenberg, 1879:221 (redescription/ taxonomy/ distribution); Lefèbvre, 1842:7 (key); van der Weele, 1908:139 (cited); Penny, 1977:11 (list).

Suhpalacsa macroceras (Burmeister, 1839): Taschenberg, 1879:221 (redescription/ taxonomy/ distribution).

Colobopterus macrocercus (Burmeister, 1839): Hagen, 1866:399 (new combination).

Ascalorphne macrocerca (Burmeister, 1839): Banks, 1915:350 (new combination); Navás, 1920:37 (cited); Navás, 1928:109 (cited); Penny, 1977:11 (list/ distribution); Heckman, 2017:201 (key); Ardila-Camacho et al., 2019:3 (list); Oswald, 2022 (catalog); Schuster & Machado, 2021 (distribution); Machado & Martins, 2022 (catalog).

Diagnosis. Tuft of brown, long setae on the dorsolateral margin of clypeus. Males with short and thick setae, resembling spines, on the apices of flagellomeres 8-23. Fusiform antennal club, brown and with whitish/yellowish tip. Thorax with pleural region with conspicuous yellow spots and intense white pilosity. Coxae, trochanter and femur yellow, tibia with a variegated pattern of black and yellow. Ectoproct of both sexes with a wide sclerotized band.

Dimensions (mm). Body: ♀ 22.6 ± 3.06/ ♂ 23.9 ± 2.6; antennae: 31.2 ♀ ± 1.64/ ♂ 31.82 ± 2.53; forewing: ♀ 27.48 ± 1.35/ ♂ 26.08 ± 1.5; hind wing: ♀ 25.18 ± 2.01/ ♂ 24.38 ± 2.1.

Head (Figs. 2D, E). As in the description of the genus, but differing in the following characteristics: presence of tufts of brown and long setae on the dorsolateral margin of the clypeus; labial palp brown; antennae dark brown with black rings, with 44-45 flagellomeres, long, surpassing the apex of the forewing; in males the flagellomeres 8-23 have short and thick setae but in females these setae are simple and elongated, antennal club fusiform, dorsally brown and ventrally whitish/yellowish.

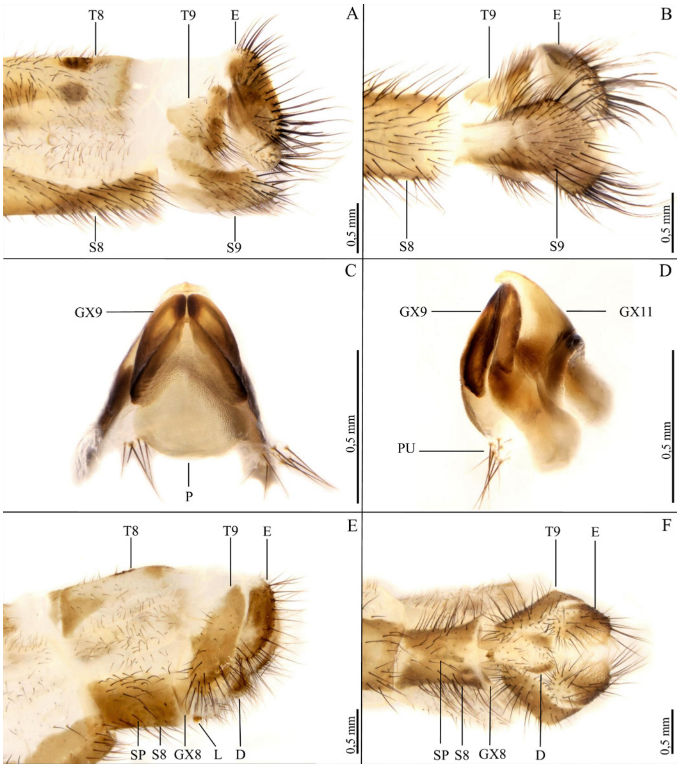

Figure 3 Terminalia /genitalia of *Ascalorphne macrocerca* (Burmeister, 1839). Male (A-D): A) Terminalia, lateral view; B) Idem, ventral view; C) Gonarcus-paramere complex, ventral view; D) Idem, lateral view. Female (E-F): E) Lateral view; F) Ventral view. D: distivalve, E: ectoproct, GX: gonocoxite, L: liguella, P: pelta, PU: pulvinus, S: sternite T: tergite, SP: spermatheca.

Thorax (Figs. 2B, C). Pleural region brown with yellow spots and with abundant long white setae and some black; brown/yellowish

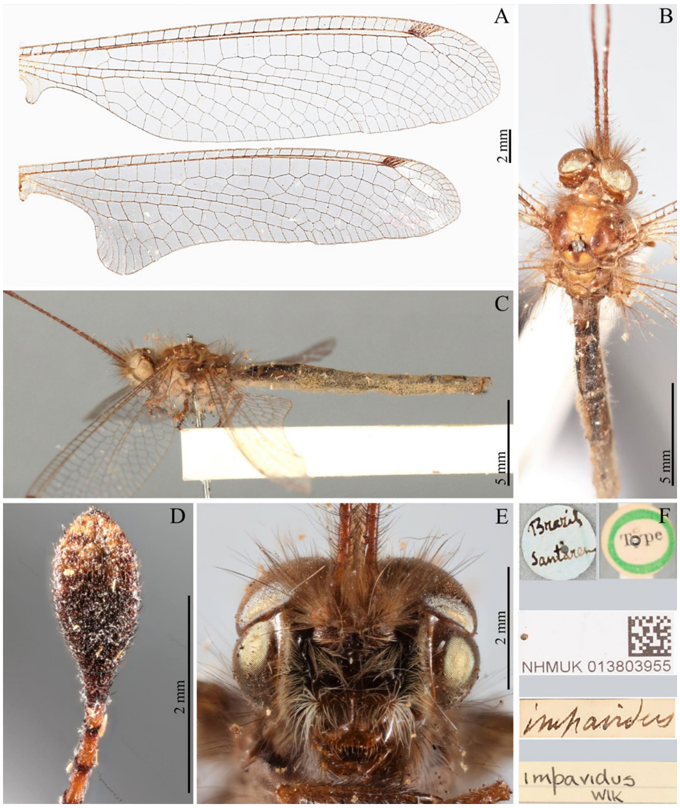

Figure 4 *Ascalaphus impavidus* Walker, 1853 (= *Ascalorphne impavida* (Walker, 1853)), holotype, male, NHMUK: A) Fore and hind wing; B) Body, dorsal; C) Body, lateral; D) Antennal club; E) Head, frontal; F) Labels.

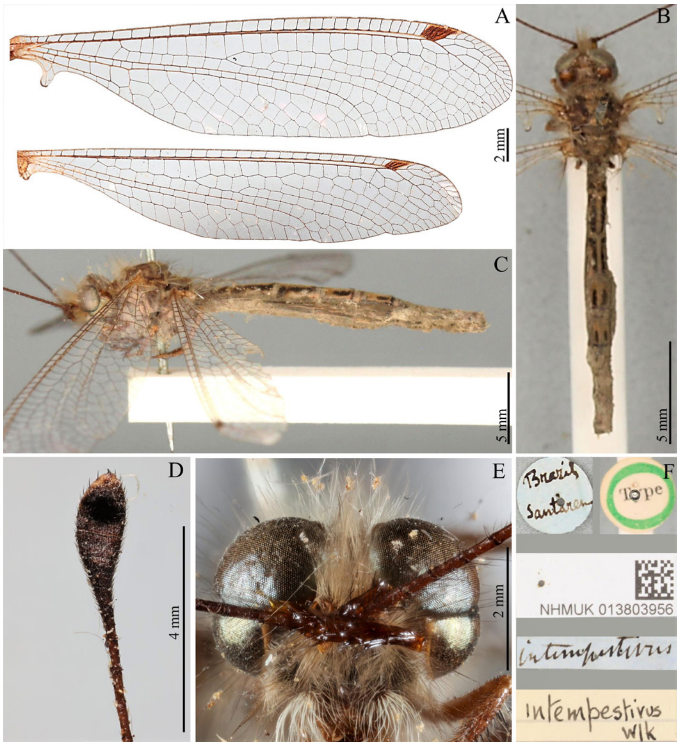

Figure 5 *Ascalaphus intempestivus* Walker, 1853 (= *Ascalorphne impavida* (Walker, 1853)), holotype, female, NHMUK: A) Fore and hind wing; B) Body, dorsal; C) Body, lateral; D) Antennal club; E) Head, frontal; F) Labels.

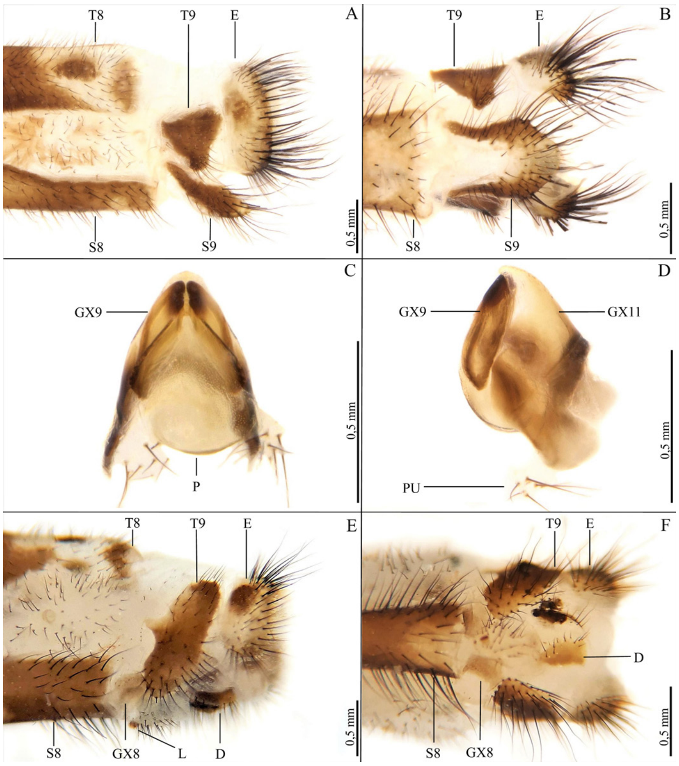

Figure 6 Terminalia/genitalia of *Ascalorphne impavida* (Walker, 1853). Male (A-D): A) Terminalia, lateral view; B) Idem, ventral view; C), Gonarcus-paramere complex, ventral view; D) Idem, lateral view. Female (E-F): E) Lateral view; F) Ventral view. D: distivalve, E: ectoproct, GX: gonocoxite, L: liguella, P: pelta, PU: pulvinus, S: sternite T: tergite.

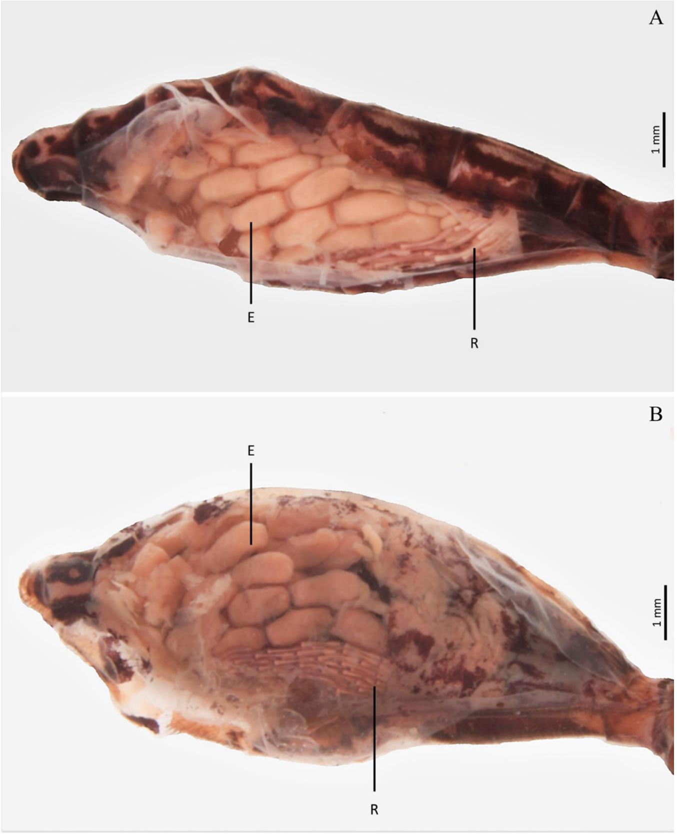

Figure 7 Abdomen of gravid females of A) *Ascalorphne impavida* (Walker, 1853); and B) *Ascalorphne macrocerca* (Burmeister, 1839), showing the fertilized eggs and the repagula. E: fertilized eggs, R: repagula.

pronotum with yellowish margin; prescutum yellowish; scutellum black. **Leg**. Coxae and trochanter yellowish, femur yellowish at the base and dark at the apex; tibia with a variegated pattern of black and yellow; tarsomeres yellowish with black apex and short black setae.

Forewing (Fig. 2A). Membrane usually hyaline, veins brown; pterostigma brown, with 6 crossveins; apical area, after fusion of Sc+R, with 3-5 cell lines; RP with 5 branches; MA long, without branches, extending beyond the third bifurcation of RP; CuA+MP with 11 branches; CuP straight and short, extending to the origin of RP; cubital area with 3-4 cell lines. **Hind wing** (Fig. 2A). Membrane and veins as above; pterostigma smaller, brown with 5 crossveins; MA straight, ending after the third RP branch; CuP straight, extending to the first RP branch; cubital area with 2-3 cell lines.

Abdomen (Figs. 2B, C). Shorter than wings, brown/yellowish. **Terminalia and genitalia** (Fig. 3). ♂: Ectoproct oval with a wide sclerotized band; T9 light brown, triangular, in lateral view, and with longer setae on the ventral portion; GPC, in lateral view, with GX11 wide and GX9, in dorsal view, narrow. ♀: Ectoproct with a wide sclerotized band.

Morphological variation. The pattern of macules in the eyes is highly variable. The general body coloration varies between light to dark brown; the pleural region can be brown and without distinct yellow spots, the pattern of spots on the dorsum of the thorax can be conspicuous or not, and the wing membrane can be pigmented (ambar/brownish) depending on the location or method of preservation.

Temporal distribution. Based on the dates on the labels of the analyzed specimens, adults of this species are usually collected between November and April, and are not observed between March and October.

Figure 8 *Orphne umbrina* Gerstaecker, 1894 [= *Ascalorphne umbrina* (Gerstaecker, 1894)], lectotype, male, ZIMUG. A) Fore and hind wing B) Body, dorsal; C) Body, lateral; D) Abdomen, lateral view; Antennal club; E) Head, frontal; F) Labels.

Geographic distribution (Fig. 12). Brazil: Bahia (Burmeister, 1839), Espírito Santo (van der Weele, 1908), Maranhão*, Minas Gerais*, Paraná

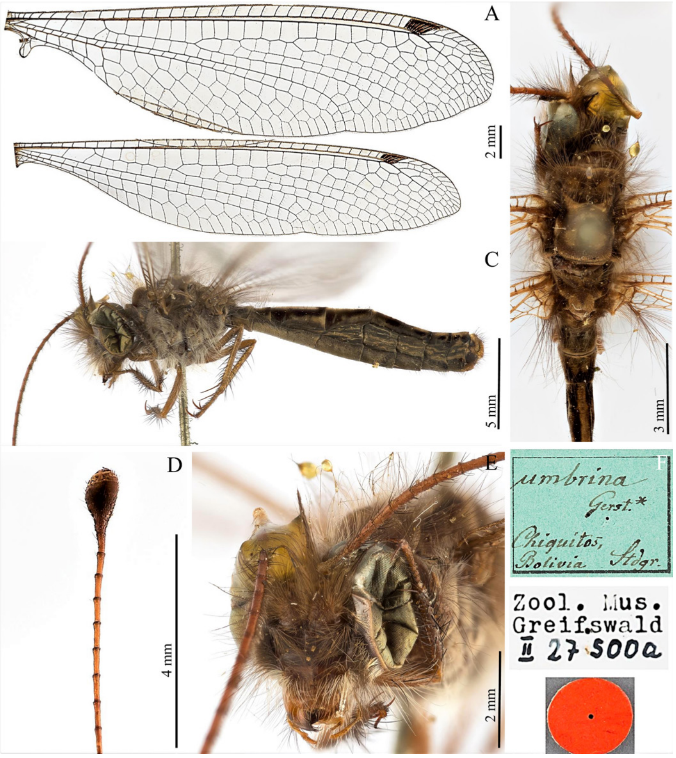

Figure 9 *Orphne umbrina* Gerstaecker, 1894 [= *Ascalorphne umbrina* (Gerstaecker, 1894)], paralectotype, female, ZIMUG. A) Fore and hind wing; B) Body, dorsal; C) Body, lateral; D) Antennal club; E) Head, frontal; F) Labels.

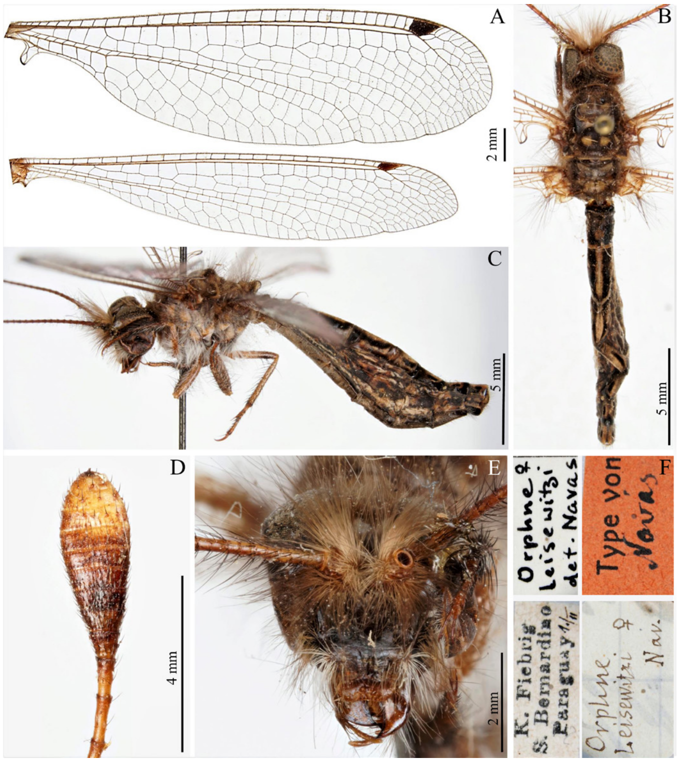

Figure 10 *Orphne leisewitzi* Navás, 1911 [= *Ascalorphne umbrina* (Gerstaecker, 1894)], holotype, female, ZSM. A) Fore and hind wing; B) Body, dorsal; C) Body, lateral; D) Antennal club; E) Head, frontal; F) Labels.

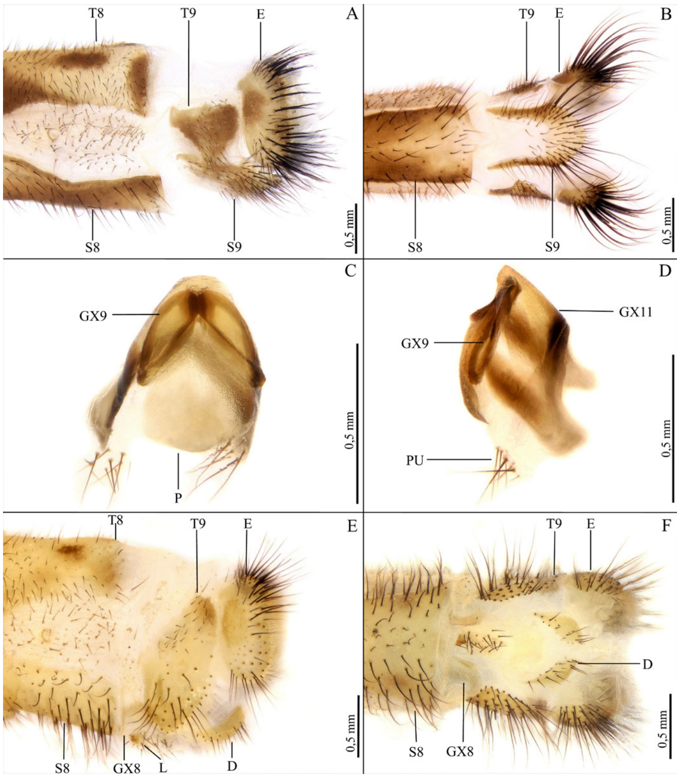

Figure 11 Terminalia/genitalia of *Ascalorphne umbrina* (Gerstaecker, 1894). Male (A-D): A) Terminalia, lateral view; B) Idem, ventral view; C) Gonarcus-paramere complex, ventral view; D) Idem, lateral view. Female (E-F): E) Lateral view; F) Ventral view. D: distivalve, E: ectoproct, GX: gonocoxite, L: li uella, P: pelta, PU: pulvinus, S: sternite T: tergite.

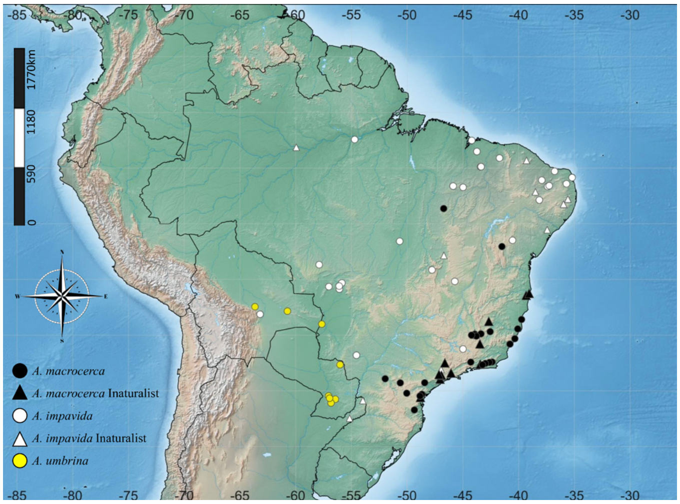

Figure 12 Distribution map of the genus *Ascalorphne* Banks, 1915 (Myrmeleontidae: Ascalaphinae: Ululodini).

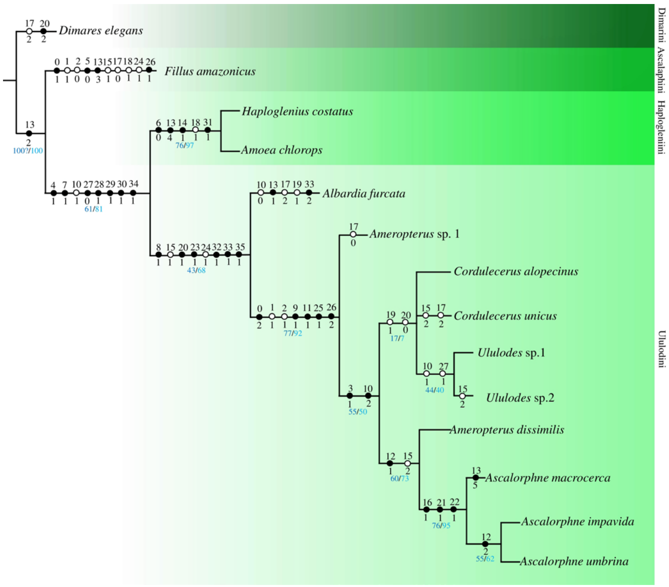

Figure 13 Phylogenetic tree of Neotropical Ascalaphinae. Most parsimonious and unique tree (number of steps=68, consistency index=69, retention index=79) obtained through the traditional search with implicit weighing (K=3). Numbers above the circles indicate the character and below, the state; unequivocal changes (black circles) and reversals or multiple changes (white circles); relative Bremer support (dark blue) and values of bootstrap with Poisson distribution (light blue).

(Schuster and Machado 2021), Rio de Janeiro (van der Weele, 1908), Santa Catarina (van der Weele, 1908), São Paulo*. **iNaturalist:** Brazil: Bahia, Minas Gerais*, Paraná, Rio de Janeiro, São Paulo*.

Primary types (Fig. 2). *Ascalaphus macrocercus*, 3 ♀, MCZ, high resolution images analyzed. **Lectotype** (here designated): ♀, type 3 (MCZ-ENT 0010525); **type locality**: Bahia; **labels**: 1) *A. macrocercus* *Burm., 2) Winthem, 3) Type 3 10525, 4) MCZ-ENT 0010525; **condition**: great.

Paralectotypes. 1 ♀, **labels**: 1) *A. macrocercus* *Burm., 2) Winthem, 3) Type 2 10525, 4) MCZ-ENT 00641047; **condition**: good, antennae missing / 1 ♀, **labels**: 1) *A. macrocercus* mihi *Burm. P.1000 NO: 3 Bahia, 2) Winthem, 3) Type 10525, 4) MCZ-ENT 00641048; **condition**: good, antennae missing.

Examined specimens. Brazil – **Espírito Santo**: • Conceição da Barra; 8.xi.1969; 1 ♂; C.T. & C. Elias • Iconha, Sítio Laranjeira; 20°'8'16.1318"S 40°'46'27.2834" W; 16.ix-14.x.2018; 1 ♂; Malaise; M.S. Lovali e equipe cols.; UFES160650 • Vitória, Jardim Penha Gomes; 10.xii.2000; I.T. col.; 1 ♀; UFESN54621. **Maranhão**: • Balsas, 525m; 8°'8'S46°'3'W; 15.ii.1999; 1♀; CZMA • Linhares, 20km, N. of Linhares, Forest. Reserv., 40 m; 19.iv.1992; 1 ♀; Edward S. Ross; CASENT8472563. **Minas Gerais**: • Belo Horizonte; 28.xi.1966; 1 ♀ e 1 ♂; O.H.H. Mielke Leg.; DZUP381249, DZUP381241 • Betim, Casa Amarela, Maloca, 795m; 20°00'2.3"S 44°13'18.7"W; 4.iii.2021; 1 ♂; puçá; A.R. Lima leg.; UFMG INE2200023 • Marliéria, Parque Estadual do Rio Doce; 19.xi.1980-26.xi.1980; 2 ♂ 6 ♀; M.A. Vulcano & F.S. Pereira et. al. leg.; UFMG INE2200007- 2200014 • idem, 13.xii.1978; 4 ♂ 3 ♀; UFMG INE220000-220006 • Ouro Preto, S. Bartolomeu, RPPN Quinta dos Cedros, 1035m; 20°17'38.4"S 43'34' 14.7"W; 17.iii.2013; 3 ♂ 1 ♀; lençol iluminado; P.G. Dias leg.; UFMG INE2200020, 2200021, 2200022 • idem, 01-3.iii.2013, 1 ♀; F. A. Silveira et al. leg. UFMG INE2200017 • S. Gonçalo do Rio Abaixo, E.A. Peti, CEMIG, 630m, 19°53′02"S;43°22′21″W; 8-15.iii.2013; 1 ♂; luminosa, A.R. Lima et al. leg.; UFMG INE2200016 • idem, 10-17.xii.2012; 1 ♂; UFMG INE2200018. **Paraná**: • Antonina, Reserva Sapitanduva; 25°28′00″S 048°50′00″W; 30.xii.1986, 31.i.1987, 32.i.1987, 26.ii.1987, 27.iii.1987, 28.iii.1987; 4 ♀ e 3 ♂; luminosa; R.C. Marinoni e R.R.C. Dutra leg.; PROFAUPAR; DZUP381644, DZUP381648, DZUP381652, DZUP381654-381656 • Antonina, RPPN Reserva Natural Guaricica (SPVS), alojamento Bom Jesus, 9 m. a. s. l; 25°18'42"S 48º40'18"W; 25-29.xi.2019; 2 ♂; pano branco; PPGEnto/Entomol. de Campo UFPR leg.; DZUP • Fênix, Reserva Estadual Vila Rica (ITCF); 23°54′51″S 051°57′45″W; 01.i.1987; 1 ♀ e 1 ♂; luminosa; R.C. Marinoni e R.R.C. Dutra leg.; PROFAUPAR; DZUP38164 • Ponta Grossa, Vila Velha, res. IAPAR BR 376; 25°13′02″S 050°02′14″W; 27.i.1987; 2 ♂; luminosa; R.C. Marinoni e R.R.C. Dutra leg.; PROFAUPAR; DZUP381649 • Morretes, IAPAR; 21.ii.1985; 2 ♀; luminosa; C.I.I.F; DZUP381211 • idem, 11.iii.1985; 2 ♀; DZUP381761 • idem, 06.iv.1985; 2 ♀; DZUP381209 • Telêmaco Borba, Reserva Biológica Klabin; 24°17′00″S 050°37′00″W; 26.ii.1987, 27.ii.1987, 28.ii.1987, 01.iii.1987, 27.iii.1987, 29.iii.1987; 6 ♀ e 1 ♂;

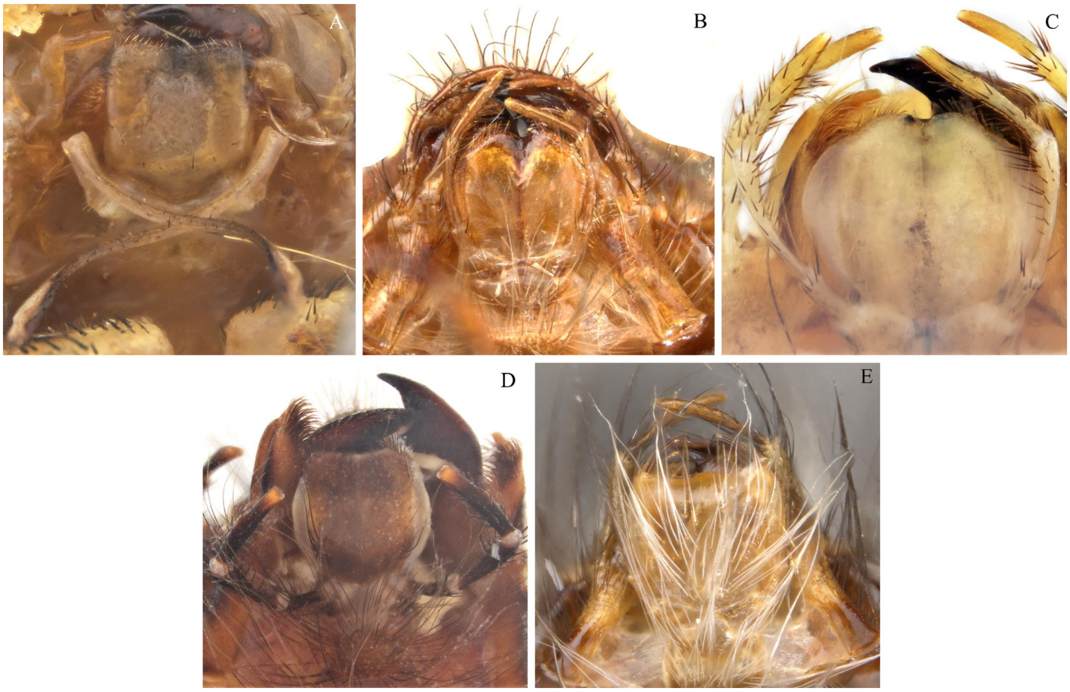

Figure 14 Labium and labial palps of the neotropical tribes of Ascalaphinae (Neuroptera: Myrmeleontidae). A) *Dimares elegans* (Perty, 1833); B) *Fillus amazonicus* (Machado & Rafael, 2011); C) *Haploglenius costatus* (Burmeister, 1839); D) *Albardia furcata* van der Weele, 1903; E) *Ascalorphne impavida* (Walker, 1853).

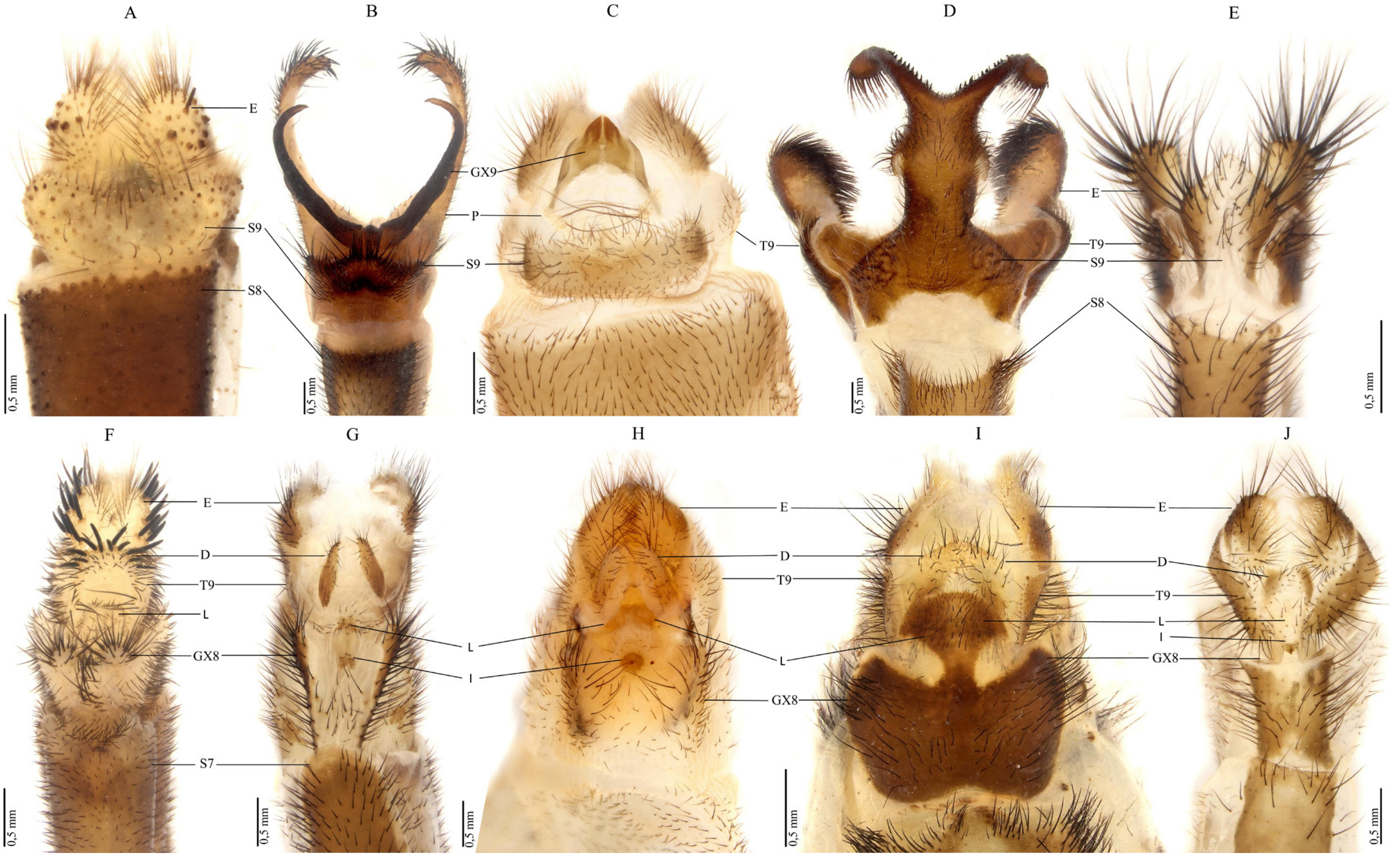

Figure 15 Ventral view of the male and female terminalia of neotropical tribes of Ascalaphinae (Neuroptera: Myrmeleontidae). Males terminalia (A-E): A) *Dimares elegans* (Perty, 1833), the gonarcus-paramere complex is removed; B) *Fillus amazonicus* Machado & Rafael, 2011; C) *Haploglenius costatus* (Burmeister, 1839); D) *Albardia furcata* van der Weele, 1903; E) *Ululodes* sp. Smith, 1900. Female terminalia (F-J). From left to right, in the same species order as above; except for J) *Ascalorphne macrocerca* (Burmeister, 1839). D: distivalve, E: ectoproct, GX: gonocoxite, I: interdens, L: liguella, P: pulvinus, S: sternite, T: tergite.

luminosa; R.C. Marinoni e R.R.C. Dutra leg.; PROFAUPAR; DZUP381646, DZUP381647, DZUP381650, DZUP381651, DZUP381653, DZUP381657.

Rio de Janeiro: • Cachoeiras de Macacu, CEDAE 550m; 18-21.i.1996; 1 ♀ e 3 ♂; O.C. Mielke & Mers leg.; DZUP381765 • Guapimirim; 1.iii.1970;

1 ♂; O.H.H. Mielke • Nova Friburgo, Lumiar, Sítio Kikiô, Rio Bonito el. 729m; 22º24’24”S 42º22’11”W; 29-31.xii.2017; 1 ♂; luminosa; A.P.M.S. & D.M.T.; DZUP • Duque de Caxias, Nova Campinas; 28.xi.2010; 1 ♀; Lopes, T.R.P.; UFBA#N350. • Porto Real; 1 ♀; Hardy de Dréneuf; Coll. V. D. Weele leg. 1907 n°6, Cat. n° 1; NBC. **São Paulo**: • Ribeirão Grande, Parque Estadual Intervales, ponto 5; 24°16’23”S 48°25’ 21.8”O; 21.ii.2011; 1 ♀; Malaise, ETOH 99,3 INPM; R.I.R. Lara e eq., cols. • idem, 24°16’27.7”S 48°25’19.3”O; 22.i.2010; 1 ♂. **Santa Catarina:** • Rio dos Cedros, 600m; 26°42 44.48S 49°20’57.95”W; 29.xii.2020-06.i.2021; 1 ♀; L. Queiros-Santos leg.; UFPR; DZUP.

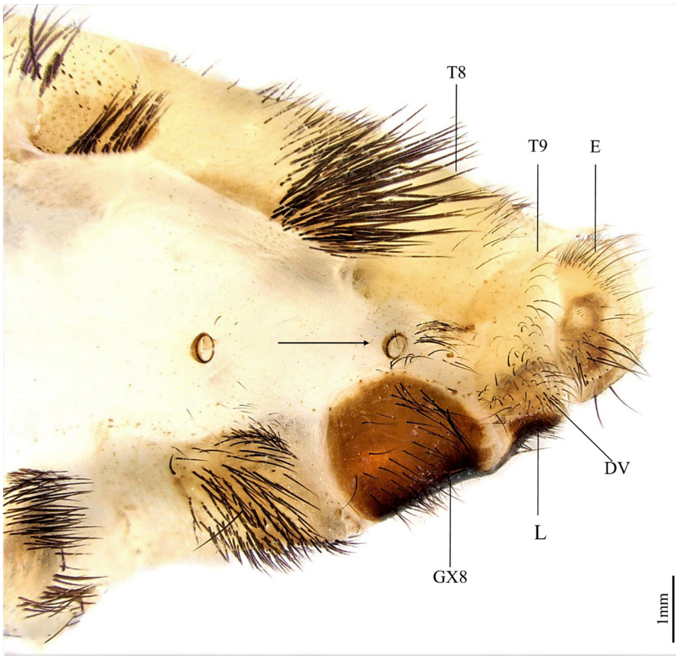

Figure 16 Position of the spiracle 8 in *Albardia furcata* van der Weele, 1903 female, lateral view. D: distivalve, E: ectoproct, GX: gonocoxite, L: liguella, T: tergite, Arrow: spiracle 8.

Comments. Almost nothing is known about the biology of this species, larvae are unknown. The most effective capture methods for adults are light traps and Malaise. This species occurs in the South, Southeast and Northeast geopolitical regions of Brazil. The presence of repagula is shown in this study for the first time (Fig. 7B).

Regarding the type series, McLachlan (1871) stated: “Burmeister’s examples were probably females, although he indicates that he had seen both sexes”. In fact, as verified in the type material deposited at the MCZ, Burmeister described this species based on three females, meaning that the distinct setae on the male’s antennae were only noticed by van der Weele (1908), but had never been properly described and illustrated in the literature, until now (Fig. 18C).

No specimen was indicated in the original publication as the holotype and therefore, according to the code 74.1 of the ICZN, the MCZ-ENT 0010525 specimen housed in the MCZ is herein designated as the lectotype, as it is the only one of the type series that has the antennae attached. Oswald (2022) cites the existence of a female syntype hosted at the Martin-Luther-Universität, Zoological Museum, Halle-Wittenberg, Sachsen-Anhalt, but it was not possible to analyze it.

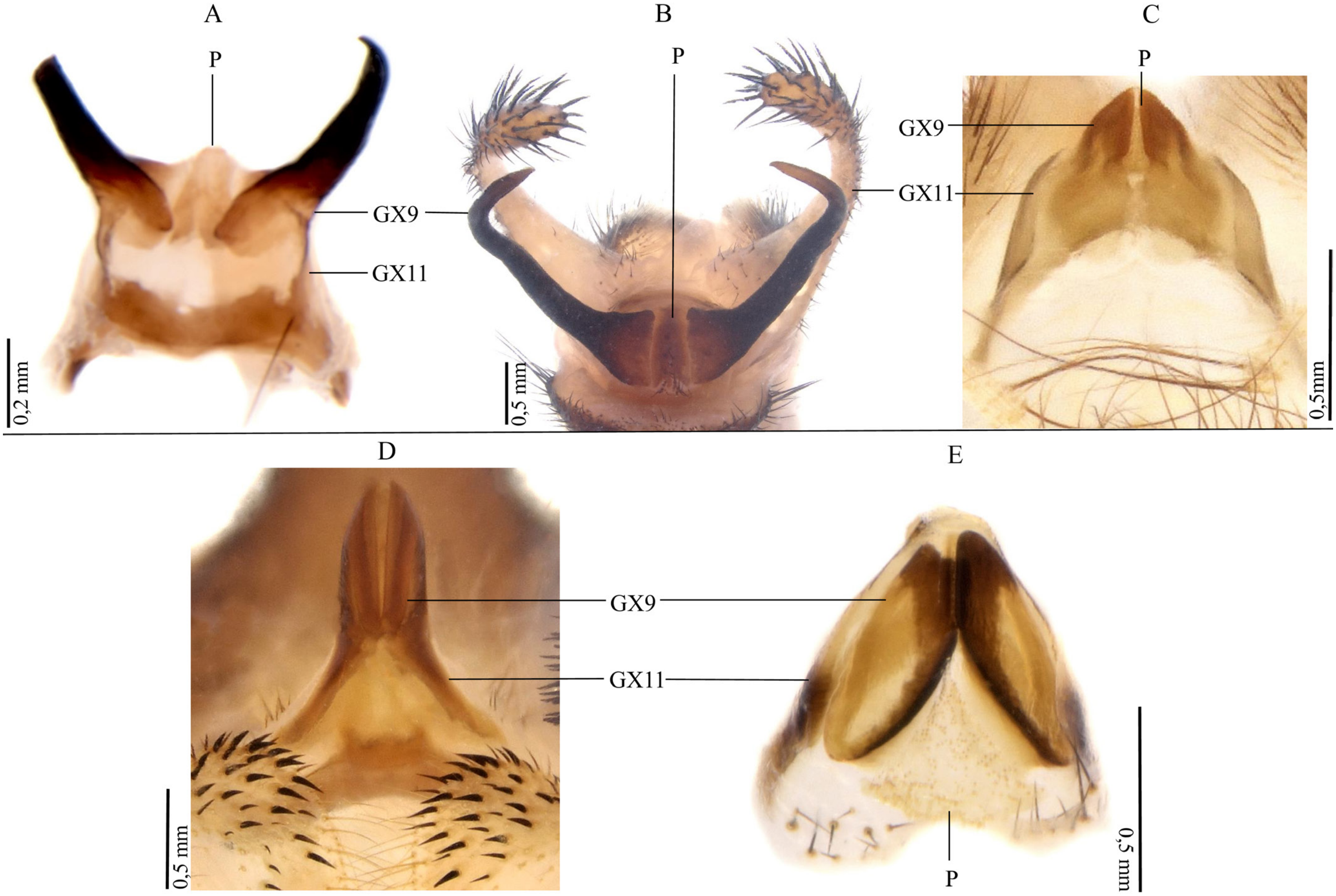

Figure 17 Gonarcus-paramere complex of the neotropical tribes of Ascalaphinae (Neuroptera: Myrmeleontidae), ventral view. A) *Dimares elegans* (Perty, 1833); B) *Fillus amazonicus* Machado & Rafael, 2011; C) *Haploglenius costatus* (Burmeister, 1839); D) *Albardia furcata* van der Weele, 1903; E) *Ululodes* sp. 1 Smith, 1900. GX: gonocoxite, P: pelta.

Another noteworthy observation is the presence of a specimen (CASENT 8472562) identified as *A. macrocerca* collected in Ecuador and housed at the CAS Entomology collection (https://www.gbif.org/occurrence/3080511303). The study of photographs of this specimen revealed that it is actually a male of *Ameropterus dissimilis,* the confusion was probably due to the thick setae on male's antennae of these two species (see the discussion of morphological characters below).

Ascalorphne impavida (Walker, 1853)

Figs. 1B, 4-6, 7A, 14D, 18A.

Ascalaphus impavidus Walker, 1853:443 (original description): Hagen, 1861:326 (list/ taxonomy); Hagen 1866:383 (cited); McLachlan, 1871:252 (synonym/ taxonomy); van der Weele, 1908:141 (redescription/ distribution); Navás 1912b:80 (list); Penny 1977:11 (list); Penny, 1981a:637 (taxonomy).

Orphne impavida (Walker, 1853): McLachlan, 1871:252,401 (new combination/ taxonomy); van der Weele, 1908:141 (cited); Penny 1977:11 (list); Navás, 1912 a:223 (key); Navás, 1912b:80 (key/ list); Navás, 1913:64 (key/ redescription).

Amoea impavida (Walker, 1853): Oswald, 2022 (cited).

Colobopterus impavidus (Walker, 1853): Hagen, 1866:399 (new combination).

Ascalorphne impavida (Walker, 1853): Banks, 1915:350 (new combination); Navás, 1920:37 (cited); Navás, 1928:109 (cited); New, 1971:75 (cited); Penny, 1977:11 (list); Penny, 1981a:637 (redescription); Whittington, 2002:377 (distribution); Ardila-Camacho et al., 2019:3 (list); Oswald, 2022 (catalog); Machado & Martins, 2022 (catalog).

Ascalaphus intempestivus Walker, 1853:444 (original description): Hagen, 1861:326 (list/ taxonomy); Hagen 1866:383 (cited) McLachlan, 1873:252 (synonym/ taxonomy); van der Weele, 1908:141 (cited); Penny 1977:11 (list); Penny, 1981a:637 (taxonomy).

Colobopterus intempestivus (Walker, 1853): Hagen, 1866:399 (new combination).

Diagnosis. Tuft of long white seta on the dorsolateral margin of the clypeus. Males with a thick row of short setae on the surface of flagellomeres 8-23. Piriform antennal club, brown with yellowish tip. Thorax brown, pleural region with white pilosity subtler than in *A. macrocerca*, and yellow spots in the pleural region may or may not be visible, if visible, less prominent than in *A. macrocerca*. Coxae, trochanter and femur brown and/or yellowish with dark apex, tibia uniformly brown. Ectoproct of both sexes with circular black macula. GPC smaller than in *A. macrocerca* and differing from *A. umbrina* mainly by the wide GX11 in lateral view and in dorsal view with the narrow GX9.

Dimensions (mm). Body: ♀ 21.08 ± 3.42/ ♂ 21.3 ± 2.32; antennae: ♀ 26.2 ± 0.88/ ♂ 25.38 ± 0.84; forewing: ♀ 24.8 ± 1.80/ ♂ 22.48 ± 1.07; hind wing: ♀ 22 ± 1.35/ ♂ 20.4 ± 1.01.

Head (Figs. 4, 5C-E). As in the description of the genus, but differing in the following characteristics: tufts of long white setae on the dorsolateral margin of the clypeus; yellowish-brown labial palp; antennae brown, with black rings,, 38-39 flagellomeres, long, reaching the apex of the forewing; in males flagellomeres 8-23 have a dense row of short setae, but in females these setae are simple and elongated; antennal club pyriform, dorsally brown and ventrally brown with yellowish-brown apex.

Thorax (Figs. 4, 5B, C). Pleural region brown with yellow macules and long white setae and some black; pronotum brown and medially with a light brown/yellowish macula; prescutum brown; scutum brown laterally and medially yellowish; scutellum brown with two yellowish maculae. **Leg**. Coxae and trochanter light brown and/or yellow; femur brown at the base and dark at the apex; tibia uniformly brown; tarsomeres brown with black apices or completely black and with short black setae.

Forewing (Figs. 4, 5A). Wing membrane hyaline, veins brown, pterostigma black, with 5 crossveins; apical area after fusion of Sc+R with 3-4 cell lines; RP with 4-5 branches; MA long, without branches, extending beyond the 3rd bifurcation of RP; CuA+MP with 9-10 branches;

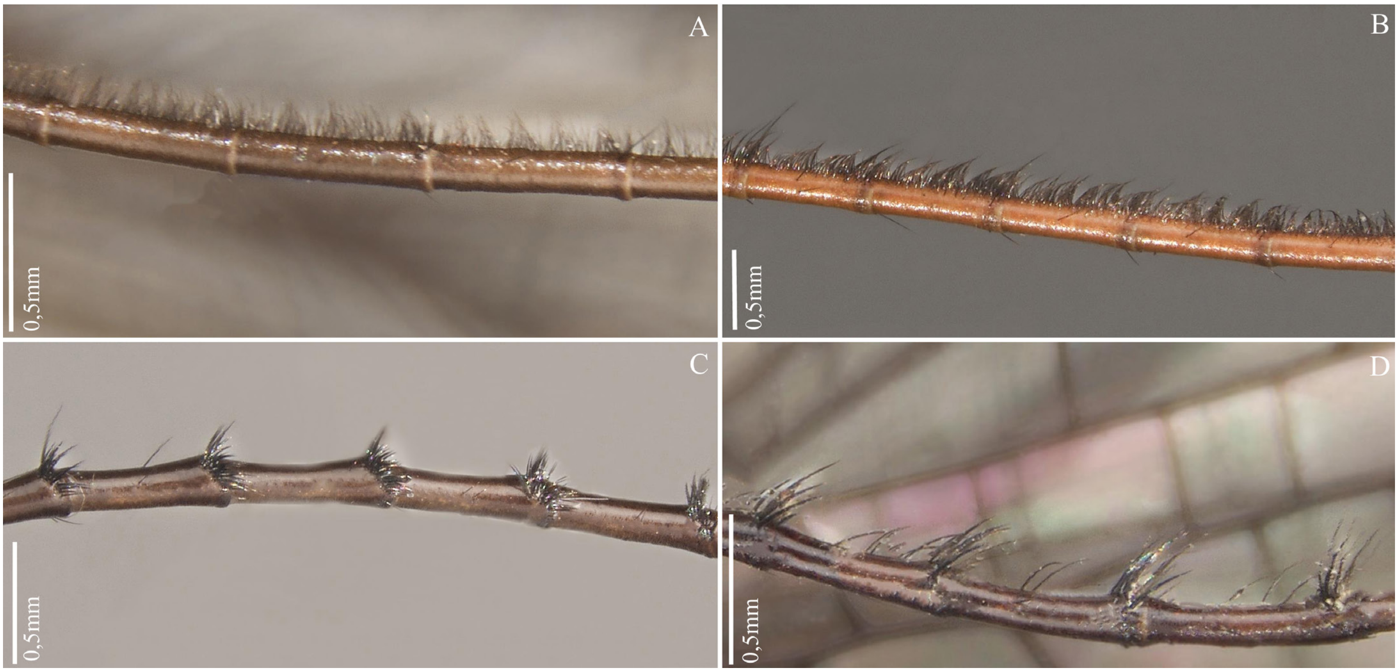

Figure 18 Antennal pilosity of males of *Ascalorphne* Banks, 1915 and *Ameropterus dissimilis* (McLachlan, 1871). A) *Ascalorphne impavida* (Walker, 1853); B) *Ascalorphne umbrina* (Gerstaecker, 1894); C) *Ascalorphne macrocerca* (Burmeister, 1839); D) *Ameropterus dissimilis.*

cubital area with 3-4 cell lines. **Hind wing** (Figs. 4, 5A). Membrane and veins as above; smaller pterostigma, black, with 4 crossveins; MA straight, ending at the 4th RP branch; CuP straight, extending to the first RP branch; cubital area with 2-3 cell lines.

Abdomen (Figs. 4, 5B, C). Shorter than wings, brown or dark brown. **Terminalia and genitalia** (Fig. 6). ♂: Ectoproct oval, with a circular macula; T9 brown, triangular, in lateral view, and with longer setae on the ventral portion; GPC with GX1, in lateral view, wide and GX9, in dorsal view, narrow. ♀: Ectoproct oval, with circular macula.

Morphological variation. The eye spots mentioned by Penny (1981a), may or may not be present, as in the other species. This species can present a great color variation, from dark brown to brown/yellowish individuals and with practically absent dorsal yellow spots or with conspicuous spots.

Temporal distribution. Based on dates on the labels of the analyzed specimens, *A. impavida* can be collected almost throughout the entire year, with a peak of occurrence between February and May, with the month of March presenting the largest number of individuals collected; Penny (1981a) indicated that in Maranhão (Brazil) the temporal distribution of adult's peaks around June, however he had few available specimens.

Geographic distribution (Fig. 12). Brazil: Bahia*, Espírito Santo*, Goiás*, Maranhão (Penny, 1981a), Mato Grosso do Sul*, Mato Grosso*, Minas Gerais*, Pará (Walker, 1853; Penny, 1981a), Pernambuco*, Piauí*, Rio de Janeiro*, Rio Grande do Norte*, Tocantins*. Bolivia: Santa Cruz*. Paraguay: Campito* (Háva, 2019). **iNaturalist.** Brasil: Amazonas*, Ceará*, Pernambuco*, Sergipe*, Tocantins*. Argentina*: Missiones*.

Primary type (Fig. 4). *Ascalaphus impavidus,* 1 ♂ NHMUK, high resolution images analyzed. **Holotype** (by monotypy): ♂ *A. impavidus*. 1 ♂ (NHMUK013803955); **type locality:** Santarém, Brasil; **labels:** 1) Brasil, Santarem, 2) *impavidus*, 3) *impavidus* Wlk, 4) NHMUK013803955; **condition**: excellent, abdomen slightly covered with fungus.

Primary type (Fig. 5). *Ascalaphus intempestivus,* 1 ♀ NHMUK, high resolution images analyzed. **Holotype** (by monotypy): ♀ *A. intempestivus*, **type locality:** Santarém, Brasil; l**abels**: 1) Brasil, Santarem, 2) *intempestivus*, 3) *intempestivus* Wlk, 4) NHMUK012803956; **condition**: excellent, abdomen covered with fungus.

Examined specimens. Brazil **– Bahia**: • Miguel Calmon, Mulungu do "chiola"; 9-16.vi.2021; 1 ♂; puçá; L. Tavares; UFBA#N610. **Distrito Federal:** 27.iii.1964; 1 ♀; C. E. & E. S. Ross; CASENT8472557. **Piauí**: • Piracuruca, Parque Nacional de Sete Cidades, Posto do ICMBIO; 04º05'57"S 41º42'34"W; 17-19.vii.2012; 2 ♀; luminosa; J.S. Pinto Junior & J.A. Rafael, cols. • idem, 1 ♂; 18-20.iv.2012; J.T. Camara & J.S. Pinto Junior cols. **Mato Grosso:** • Campo Novo do Parecis, BR 13; arbusto; 13.x.2017; 1 ♀; A.L. Klein.; DZUP • Cuiabá; 01.xii.1993; 1 ♀; C.T. Homes; UFMT • Chapada dos Guimarães, Rio Claro; 10.xii.1984; 1 ♀; Sebastião Marcolino; UFMT • Santo Antônio do Leverger, Fazendo Santa Maria; 09.iii.1992; 1 ♂; L. Moreira; UFMT • São Vicente; 19.X.1988; 1 ♀; D. Figueiredo; UFMT • Barra do Bugres, Reserva Araras; 22.ii.1987; 1 ♀; Y.O. Willis; UFMT. **Mato Grosso do Sul**: • "Corumbé"; 1.ii-8.iii.1966; 1 ♀; E. Golbach; FSCA00094852 • idem; ?. i.1971; 1 ♀; E. Golbach; FSCA00094861 • Rio Brilhante; 21-27. i.1971; 1 ♀; V. O. Becker leg.; DZUP. **Maranhão:** • Balsas 525m; 8°38'S 46°43'W; 15.II.99; 2 ♀ e 4 ♂; Coleção EMBRAPA; CPACNº13.776 • Caxias, Povoado Boa Vista; 20.v.2004; 1 ♀; F. Limeira-de-Oliveira et al. cols. • idem, Reserva Ecológica Inhamum; 21.iv.2005; 1 ♂; varredura; F. Limeira-de-Oliveira. • idem, Shalon; 30-31.iv.2004; lençol e luz mista; 1♀ e 1 ♂; F. Limeira-de Oliveira, col. • Mirador, Parque Estadual Mirador, Posto Avançado do Mel; 06°43'50"S 44°58'59"W; 01-10.iii.2014; luminosa; 1 ♀ e 2 ♂; F. Limeira-de-Oliveira, L. L. M. Santos & T. T. A. Silva • idem, Base da Geraldina; 06°37'25" S45°52'08"W; luminosa; 22.ii-01.iii.2009; 6 ♀ e 2 ♂; M.B. Aguiar-Neto & M.J.A, Holanda cols.; CZMA • idem, 29-31.i.2006; 1 ♀; F. Limeira-de-oliveira, col. • idem, 20-31.xii.2006, 1 ♂; F. Limeira-de-oliveira, col. • idem, 20-24.xii.2006; 1 ♂; R.O. Souza, J.C. Silva, et al. • idem, 17-21.ii.2007; 1 ♂; J.C Silva, M.J. Holanda. • idem, 20-23.iv.2007; 3 ♀ e 1 ♂; F. Limeira de Oliveira col. • idem, 20-23.ix.2007; 1 ♂; F. Limeira de Oliveira col. • idem, 08-13.iii.2008; 1 ♀; J.C. Silva & F. Limeira-de-Oliveira • idem, 07-14.v.2010; 1 ♀; J.S. Pinto Junior & M.M. Abreu. • idem, luminosa móvel; 07-15.?.2010; 1♀; L.L. Reis & L.M. Oliveira • idem, 07-14.iii.2013; 2 ♀ e 3 ♂; F. Limeira-de-Oliveira, A.A. Silva & C.F. Barros • idem, armadilha Malaise; 08-14.iii.2013; 1 ♂; F. Limeira-de-Oliveira, L.L.M. Santos & L.S. Santos • idem, Base do Mosquito; 04-08.ii.2011; 1 ♂; armadilha luminosa; F. Limeira-de-Oliveira • São Luís, APA Itapiracó; 28-31.v.2008; 1 ♂; luminosa; M.B. Aguiar-Neto, S.J.C. Silva. **Minas Gerais:** • Lavras, Bairro Centenário, dentro de casa 21°14'43.0"S 44°59'29.6"W; 28.ii.2014;1 ♂; ativa; P.G. Dias leg.; UFMG INE2200019. **Pernambuco:** • Triunfo, Canaã Recanto da Laje, 07°52'28.5"S 38°08'15.3"W; 02.v.2018; 1♀ e 1 ♂; bandeja; Cavalcante Pereira; UFBA#356 • idem, Riacho da Laje; 07°52'28.2"S 38° 08'13.6"W; 02.v.2019; 1 ♀; bandeja; Cavalcante Pereira; UFBA#N352. **Rio Grande do Norte**: • Alto dos Rodrigues, "abuaser", Arg.189; 17-18.vii.1996; B.L. equipe; 7-Margem de um declive rochoso; UFBA#N360 • Martins, Pousada Martinense; 04.v.2013; coleta manual; Ferreira, V.D.S; UFBA #N354 • Natal, Campus UFRN- CB; 13.v.2012; 1 ♂; Neto P.F.C., Dantas A.C.; UFBA#358 • idem, Capim Macio; 09.v.2012; 1 ♂; Salvino, S.C.A.; UFBA#355 • Serra de São Bento; 7.v.2006; 1 ♂; Freire, A.B.F.; UFBA#357 • Serra Negra do Norte, Servida, sede; iv.2005; 4 ♂ API; luz fluorescente; Varella, A.A.; UFBA#N351 • idem, ESEC Seridó, sede, ?.v. 2005; 1 ♀; sob luz florescente; UFBA#N353 • idem, 25.iv.2009; 1 ♂; API (noite); Varela-Freire; UFBA#N361 • idem, Açude Campos I, margem ocidental; 05-06.vi.1997; 1 ♂; B.L. Varela-Freire, A.A.; UFBA#359. **Tocantins:** • Santa Isabel do Morro, Ilha do Bananal; ?.vi.1961; FSCA00094864. Bolívia - **Santa Cruz:** • Buena vista, 380m; 17°27'69S,63°39'63"W; 20.ii.1999; 1 ♂; L. Stange; FSCA00094859.

Comments. The larvae are unknown and almost nothing is known about the biology of this species, including its feeding habits. Interestingly, Tjeder (1992) comments that, possibly, Ascalaphinae would not feed on Lepidoptera, due to the absence of scales in gut content. However, in two occasions during this work, collected specimens of *A. impavida* were observed firmly grasped and with the mandibles attached to disarticulated legs of a lepidopterans; it is possible, however, that this observation is an artifact, since the insect may have clung to another when captured in alcohol. Another specimen of *A. umbrina* was collected in the same situation, but clearly with the leg inside its mouth, reinforcing the hypothesis that butterflies/ moths might be an important dietary component of these owlflies. Also, the strong jaws of Ululodini indicate the ability to feed on hard-bodied prey, and by dissecting the crop of *A. impavida* it was observed a Coleoptera femur (Scarabaeoidea).

In the original description Walker (1853) described both sexes of *A. impavida* as two distinct species, which was later noticed and synonymized by McLachlan (1871). After reviewing the type material of *Ascalaphus impavidus* and *Ascalaphus intempestivus*, in addition to several specimens of both sexes of *A. impavida*, this synonymy is herein confirmed.

Through the work of Penny (1981a) *A. impavida* was the only species of the genus to receive an updated description, in addition to being the last taxonomic work containing *Ascalorphne*. The author also indicated that *A. impavida* would be confined to the southeastern region of the Amazon basin, but based on the data presented here it is evident that this is a widely distributed species (Fig. 12).

Also, it is interesting to note that the distribution of this species reaches the Bolivia–Brazil border (1 ♂, FSCA00094852 and 1 ♀, FSC 00094861, both collected in Corumbá, Mato Grosso do Sul) and a single individual was collected in Bolivia (1 ♂ FSCA 00094859, Santa Cruz), which led to the suspicion that it was, in fact, an *A. umbrina* specimen with a brown coloration, however the typical coloration of *A. impavida* and the narrow GX9 were observed in this specimen, indicating this overboard distribution.

According to van der Weele (1908) in *A. impavida* the veins of the wing apex are not as “dense” as in *A. macrocerca* and are rarely bifurcated, however, the number of vein bifurcations are interspecifically variable and cannot be used with confidence for species differentiation.

Another noteworthy comment is regarding the work by Háva (2019) which indicated a new of record of *Ameropterus selysi* (van der Weele, 1909) from Paraguay; however, the photo presented in the article belongs to a female *Ascalorphne*, probably *A. impavida* based on coloration.

***Ascalorphne umbrina* (Gerstaecker, 1884)**

Figs. 8-11, 18B.

Orphne umbrina Gerstaecker, 1884:107 (original description): Weele, 1908:142 (cited), Navás, 1912a:224 (key); Navás, 1912b:80 (key/list); Navás 1913:64 (key).

Ascalorphne umbrina (Gerstaecker, 1884): Banks 1915:350 (new combination); Navás 1920:37 (cited); Navás 1928:109 (cited); Penny 1977:11 (list); Heckman, 2017:201 (key); Ardila-Camacho et al., 2019:3 (list); Oswald, 2022 (catalog); Dobosz, 2021:26 (cited).

Orphne leisewitzi Navás, 1911:25 (original description): Navás, 1912a:224 (key); Navás, 1912b:80 (key/ list); Navás, 1913:64 (key) - **Syn. nov.**

Ascalorphne leisewitzi (Navás 1911): Banks, 1915:350 (new combination); Navás, 1920:37 (cited); Navás, 1928:109 (cited); Williner, 1945:436 (cited); Penny, 1977:11 (list); Heckman, 2017:201 (key); Ardila-Camacho et al., 2019:3 (list); Oswald, 2022 (catalog).

Diagnosis. Tuft of long white setae on the dorsolateral margin of the clypeus. Labial and maxillary palps yellow. Antennae reddish-brown. Males with a thick row of short setae on the surface of flagellomeres 8-23. Antennal club piriform, brown with yellowish tip. Thorax brown, with yellow spots, pleural region with white hairs. Coxae, trochanter and femur yellowish, tibia uniformly yellowish/brown. Wings hyaline or pigmented, subcostal area of wings with amber coloration. Ectoproct of both sexes with circular black maculae. This species is similar to *A. impavida*, but can be distinguished mainly by the narrow GX11 in lateral view and in dorsal view by the wide GX9.

Dimensions (mm). Body: ♀17.9 ± 0.47/ ♂ 19.34 ± 1.44; antennae: ♀ 25.48 ± 1.65/ ♂ 26.34 ± 1.36; forewing: ♀ 25.58 ± 1.09/ ♂ 23.7 ± 1.02; hind wing: ♀ 24.56 ± 4.7/ ♂ 21.06 ± 0.67.

Head (Figs. 8, 9, 10C-E). As in the description of the genus, but differing by the following characteristics: presence of tufts of white long setae on the dorsolateral margin of the clypeus; labial palps yellow; antennae reddish and yellowish, and brown at the apex, with black rings, 38-39 flagellomeres, long, reaching the apex of the forewing; in males flagellomeres 8-23 have a dense row of short setae, but in females these setae are simple and elongated, antennal club pyriform, dorsally brown and ventrally dark brown at the base and light brown at the apex.

Thorax (Figs. 8, 9, 10B, C). Pleural region brown with yellow spots and with long white setae and some black; pronotum brown, medially with a light-yellow macula; prescutum brown with yellow lateral macules; scutum brown laterally and medially yellowish; brown scutellum with two yellowish macules. **Leg**. Coxae and trochanter yellowish-brown; femur yellow at the base and dark at the apex; tibia uniformly yellowish-brown; tarsomeres dark yellow with black tips and short black setae.

Forewing (Figs. 8, 9, 10A). Females with wing membrane hyaline or slightly yellowish, males may have hyaline or pigmented wing membrane, veins brown but at the base of the wing it is yellowish, pterostigma brown with 6 crossveins; apical area after fusion of Sc+R with 3-4 cell lines; RP with 4-5 branches; CuA+MP with 9-10 branches; cubital area with 3-4 cell lines. **Hind wing** (Figs. 8-10A). Membrane as above, brown veins; pterostigma smaller, with 4 crossveins; MA straight, ending at the fourth RP branch; Cup straight and extending to the first RP branch; cubital area with 2-3 cell lines.

Abdomen (Figs. 8, 9, 10B, C). Shorter than wings, brown/yellowish. **Terminalia and genitalia** (Fig. 11). ♂: Ectoproct with a circular sclerotized macula in the upper portion; T9 brown, triangular, in lateral view, and with short setae on the ventral portion; GPC with GX11 (gonarcus), in lateral view, narrow and truncated, and GX9 in dorsal view broad; ♀: Ectoproct with circular sclerotized macula in the upper portion.

Morphological variation. The wings may be almost hyaline (especially in females) or pigmented (especially in males).

Temporal distribution. The insects analyzed in person or by photographs were collected on 12.vii and 03.vii, and there is no other source of data available for this species.

Geographic distribution (Fig. 12). **Bolivia**: Chiquitos, Buena Vista (Navás, 1928); Santa Cruz, Basílio. **Paraguay**: Sapucai; San. Bernadino (Navás, 1911), Villarrica, San Ignacio Missiones (Navás, 1920). **iNaturalist**. There are no records of this species.

Primary type (Figs. 8, 9). *Orphne umbrina*, 1 ♀ and 1 ♂, ZIMUG, high resolution images analyzed. **Lectotype** (here designated): ♂ *Orphne umbrina* (27500b); type locality: Chiquitos, Bolivia; **labels**: 1) Gerst Umbrina. * Chiquitos, Bolivia Hdgr, 2) Zoo. Mus Greifswald 27500b; **condition**: excellent, right antennae wrongly glued, belonging to a female. **Paralectotype**: 1 ♀, **label**: *umbrina* Gerst. * Chiquitos, Bolivia Hdgr., 2) Zoo. Mus Greifswald 27500a; **condition**: excellent, right antennae wrongly glued, belonging to a male.

Primary type (Fig. 10). *Orphne leisewitzi*, 1 ♀, ZSM, high resolution images analyzed. **Holotype** (by monotypy): ♀ *Orphne leisewitzi*; **type locality**: San Bernardino, Paraguay; **labels**: 1) Nav., 2) K. Fiebrig, S. Bernadino, Paraguay 1/ii, 3) Type von Navás, 4) *Orphne leisewitzi* ♀ det. Navás; **condition**: excellent, right antennae glued, abdomen and eye collapsed.

Examined specimens. Bolivia - **Santa Cruz**: • N. Basílio, 3km; 7.iii.1999; 1 ♀ e 5 ♂; Malaise; M.E. Irwin, F.D. Parker & L.A. Stange; FSCA 00094847, FSCA00094849, FSCA00094852, FSCA00094853, FSCA00094854, FSCA00094861, FSCA00094859, FSCA00094864, FSCA00094865 • **Idem,** 2 ♂; arm. Malaise; M.E. Irwin, F.D. Parker, L.A. Stange; TAMUICX0405250, X07405250 • idem; 1 ♀; USMBMB0253445. • Buena Vista, 380m; 17°27’69S 63°39’63”W; 20.ii.1999; 1 ♂; L.A. Stange; FSCA00094859. Paraguay: • 1 ♀; MNHN • **Cordillera**: • Piribebuy: Cruce Piribebuy; 2,25.377ºS 57.043ºW; 20.ii.2016; 1 ♀ B. & N. Garcete colls; MNHNP • **Paraguarí,** Parc. Nac. Ybycuí; 26.i.1982; 1 ♀ H. Ferreira C. Colr; MNHNP • idem; 6-9.iii.1984; 1 ♂; Colr. T. Bonace; MNHNP • **Sapucai**: 7.12.1904; 1 ♂; Coll. V.D. Weele leg.; NBCN°6 • **Villarrica**; 1 ♂; NHRS-JLKB000073614 • idem; 1 ♂; NHRS-JLKB 000073615 • Amambay, Parc. Nac. Cerro Corá; 7-21.ii.1982, 7-21.iii.1982; 2 ♂ H. Ferreira C. Col. MNHNP.

Comments. Nothing is known about the biology of this species and larvae are unknown. One specimen was collected with a Lepidoptera leg in its mouth indicating that butterflies/moths may be a food source for this genus (see *A. impavida* comments).

Ascalorphne umbrina was described by Gerstaecker (1884), based on specimens of both sexes from Bolivia; the author highlighted that this species would be smaller than the others and would be distinguished by the color of the wing, by the lighter color of antennae, yellowish mouthparts, yellowish legs and indicated that the male’s cubital lobe of hind wings would be shorter and with a different shape, and that in females the base of the hind wing would be a little wider than in *A. macrocerca*.

Later, Navás (1911) described *A. leisewitzi* from Paraguay and, despite mentioning male characteristics, the type material is composed by a single female. According to Navás, this species would be differentiated from *A. umbrina,* based on the hyaline wings with only the subcostal field slightly pigmented (wing entirely pigmented in *A. umbrina*), reddish antennae (brown in *A. umbrina*) (Navás, 1912a, 1912b). Navás (1928) expanded the distribution of *A. leisewitzi* to Bolivia, in the department of Santa Cruz, exactly the same location where the specimens housed at the FDASC were collected, and which were personally studied in the present work.

Previously, the deposit location of the type material of both species was unknown as mentioned in Oswald (2022). The types were herein located and their analysis reveals a single notable morphological difference: the wings of the female of *A. umbrina* are slightly pigmented while those of *A. leisewitzi* are completely hyaline. In addition, the reddish antennae of *A. leisewitzi* are very close to the reddish-brown coloration of the *A. umbrina* type. Furthermore, both species have overlapping distributions and variations in general body coloration are a common phenomenon within the genus (as observed in *A. impavida*, for example).

Also, according to the literature and research in databases, such as the Global Biodiversity Information Facility (GBIF), in addition to consultations in many institutions, only three specimens identified as *A. leisewitzi* was located (the holotype in the ZSM; another specimen cited for the first time by Navás (1920) and housed at the MNHN; and another one in the SMNH), all of them are females and were identified by the species author himself, Navás.

Thus, *A. leisewitzi* is herein indicated as a synonym of *A. umbrina*. Furthermore, no material was pointed as the holotype in the original publication of *A. umbrina* and therefore the male specimen (27500b) is herein designated as the lectotype.

It is important to mention that some specimens with strongly pigmented wings were located at the Museo Nacional de História Natural del Paraguay and Smithsonian Institution, National Museum of Natural History, but it was not possible to study those insects.

Identification key for the species of *Ascalorphne* Banks, 1915 (Neuroptera: Myrmeleontidae: Ascalaphinae)

1 Antennal club fusiform (Fig. 2D); tufts of brown dorsolateral setae on the clypeus (Fig. 2E); antennae uniformly dark brown, surpassing the apex of the forewing; males with tufts of thick setae at the apices of flagellomeres 8-23, similar to spines (Fig.18C); femur variegated in black and yellow; ectoproct with macula forming a broad band on the upper portion (Figs. 3A, E).... ....*A. macrocerca*

1' Antennal club piriform (Fig. 4D); tufts of white dorsolateral setae on the clypeus (Fig. 4E); antennae brown or reddish brown, reaching apex of forewing; males with thick row of setae along the flagellomeres 8-23 (Figs. 18A, B); femur uniformly brown/ yellow; ectoproct with circular-shaped macula (Figs. 6A, E)..........2

2 Male, in lateral view, with GX11 narrow and, in dorsal view, with GX9 wide (Figs. 11C, D); yellowish palps, reddish-brown antenna; coxae, trochanter and femur yellowish, tibia uniformly yellowish-brown; hyaline or pigmented wings (especially in males)................ ....*A. umbrina*

2' Male, in lateral view, with GX11 wide and, in dorsal view, with GX9 narrow (Figs. 6C, D); yellowish-brown palps, brown antennae; coxae, trochanter and femur yellowish-brown, tibia uniformly brown; hyaline wings...*A. impavida*

Character descriptions (data matrix: Table 1)

0. Anterior orbital sclerite (AOS), frontal view, shape: straight (0); slightly projected towards the eye (1); strongly projected towards the eye (2).

Comment. This character correlates to the level of ocular separation, being straight in insects with entire eyes (Dimarini and Haplogleniini), slightly projected in insects with inconspicuous eye division (*Fillus amazonicus*) and projected in insects with transversely sulcated eyes (Ululodini, except *A. furcata*).

1. Eye, sulcus: not transversely sulcated (0); transversely sulcated (1).

Comment. In Ascalaphinae the eyes can be entire (Dimarini, Palparini, Stilbopterygini and Haplogleniini) or dorsoventrally separated by a sulcus (Ascalaphini and Ululodini), with different levels of development in different taxa.

2. Sulcated eye, depth: eye entire (-); superficial sulcus, indistinct, as a slight medial depression (0); deep sulcus, distinct, medially separating the eye (1).

Comment. When present, the ocular division can be seen in two main forms: as a slight medial depression (*Fillus*) or as a deep sulcus (Ululodini, except *A. furcata*).

3. Paraocular band (PB), row of setae: absent (0); present (1).

Comment. At the PB, the lower half of the eye, there is a vertical row of setae, usually white and long, clearly visible in most Ululodini (except *A. furcata*), however, they may be absent or inconspicuous in some species of *Ameropterus*, but clearly present in others.

4. Clypeus, dorsolateral tufts of setae: absent or inconspicuous, with sparse setae not forming tufts (0); present and conspicuous (1).

Comment. Tufts of setae on the sides of the clypeus can be seen in some Ascalaphinae but not in others. They are distinct in Haplogleniini and Ululodini. They are completely absent in *D. elegans,* and in *Fillus* there are only a few long setae in this region, but they do not form a tuft.

5. Labrum, shape: trapezoidal (0); oval (1).

Comment. The labrum of *D. elegans* is oval and wide, as in Haplogleniini and Ululodini; *Fillus*, however, has a long, trapezoidal labrum.

6. Labium, proportion: wider than long (0); longer than wide (1).

Comment. *D. elegans* has a labium that is longer than wide, with the anterior margin lobed (with a median depression) and rounded. In *Fillus amazonicus* the labium is longer than wide, with the anterior margin slightly rounded. In Haplogleniini the labium is wider than long, round and the anterior margin is strongly bilobed. In Ululodini it is longer than wide, quadrangular. This feature appears to be associated with the character below, but they were separated in order to test the independence of characters.

7. Labium, setae on the anterior margin, length: short (0); long (1).

Comment. In *D. elegans* the setae are very short, similar to *F. amazonicus.* In Haplogleniini the setae are elongated, as in Ululodini, however, in the latter these setae are very long, thick and falcated at the apex (except in *A. furcata*).

8. Labium, setae distribution on the anterior margin: evenly distributed (0); lateralized in tufts of setae (1).

Comment. In *D. elegans* the setae are uniformly distributed along the entire anterior margin of the labium, as observed in *F. amazonicus* and in Haplogleniini. In Ululodini, however, these setae are completely displaced to the sides of the labium, forming tufts of elongated setae. This character is probably associated with character 7, in which the position and specialization of these setae accompany changes in the shape of the labium.

9. Labial palp, length of the setae on the second palpomere: less than half of the length of the third palpomere (0); longer than half of the length of the third palpomere (1).

Table 1
Species list and matrix of adult morphological characters of Neotropical Ascalaphinae (Neuroptera: Myrmeleontidae) utilized in the phylogenetic analysis. Unknown/unobservable characters (?), inapplicable characters (-).

Taxa	Characters and States																																			
	0					5					10					15					20					25					30					35
Dimares elegans (Perty, 1833)	0	0	-	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	-
Fillus amazonicus Machado & Rafael, 2011	1	1	1	0	0	0	1	0	0	0	0	0	0	3	0	1	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	-
Haploglenius costatus (Burmeister, 1839)	0	0	-	0	1	1	0	1	0	0	1	0	0	4	1	0	0	1	1	0	0	0	0	0	0	0	0	0	-	1	1	1	0	0	?	-
Amoea chlorops (Blanchard, 1845)	0	0	-	0	1	1	0	1	0	0	1	0	0	4	1	0	0	1	1	0	0	0	0	0	0	0	0	0	-	1	1	1	0	0	1	0
Albardia furcata van der Weele, 1903	0	0	-	0	1	1	1	1	1	0	0	0	0	1	0	1	0	2	0	1	1	0	0	1	1	-	0	0	-	1	1	0	1	2	1	1
Ameropterus sp. 1 Esben-Petersen, 1922	2	1	1	0	1	1	1	1	1	1	1	1	0	2	0	1	0	0	0	0	1	0	0	1	1	1	2	0	-	1	1	0	1	1	1	1
Ameropterus dissimilis (McLachlan, 1871)	2	1	1	1	1	1	1	1	1	1	2	1	1	2	0	2	0	1	0	0	1	0	0	1	1	1	2	0	-	1	1	0	1	1	1	1
Cordulecerus alopecinus (Burmeister, 1839)	2	1	1	1	1	1	1	1	1	1	2	1	0	2	0	1	0	1	0	1	0	0	0	1	1	1	2	0	-	1	1	0	1	1	1	1
Cordulecerus unicus (Walker, 1860)	2	1	1	1	1	1	1	1	1	1	2	1	0	2	0	2	0	2	0	1	0	0	0	1	1	1	2	0	-	1	1	0	1	1	1	1
Ululodes sp. 1 Smith, 1900	2	1	1	1	1	1	1	1	1	1	1	1	0	2	0	1	0	[01]	0	1	0	0	0	1	1	1	2	1	1	1	1	0	1	1	1	1
Ululodes sp. 2 Smith, 1900	2	1	1	1	1	1	1	1	1	1	1	1	0	2	0	2	0	1	0	1	0	0	0	1	1	1	2	1	1	1	1	0	1	1	1	1
Ascalorphne macrocerca (Burmeister, 1839)	2	1	1	1	1	1	1	1	1	1	2	1	1	5	0	2	1	1	0	0	1	1	1	1	1	1	2	0	-	1	1	0	1	1	1	1
Ascalorphne impavida (Walker, 1853)	2	1	1	1	1	1	1	1	1	1	2	1	2	2	0	2	1	1	0	0	1	1	1	1	1	1	2	0	-	1	1	0	1	1	1	1
Ascalorphne umbrina (Gerstaecker, 1894)	2	1	1	1	1	1	1	1	1	1	2	1	2	2	0	2	1	1	0	0	1	1	1	1	1	1	2	0	-	1	1	0	1	1	1	1

Comment. In *D. elegans* the labial palp is extremely elongated, with short and indistinct setae. In *F. amazonicus*, *A. furcata* and Haplogleniini these setae are short. Ululodini (except *A. furcata*) have long setae at the apex of the second palpomere, longer than half of the third one. It is important to note that the palpiger is not considered to be part of the labial palp.

10. Antennae, length: short, equal to or not reaching the first RP fork on the forewing (0); medium, reaching, at most, the third fork of RP (1); long, reaching or passing the fourth RP fork (2).

Comment. The antennae of most Ascalaphinae are quite elongated and end in a variably shaped club. *D. elegans* belongs to a group of Ascalaphinae that present some characteristics in their most plesiomorphic state, so the antennae in this species is short. In Haplogleniini the antennae always surpass the second RP branch and, according to Penny (1981a), the antenna usually reaches the second (*H. costatus*) or third RP fork, but in some species, they can extend to the fourth fork (Ardila-Camacho and Jones, 2012); *A. furcata* is different from the other Ululodini (and Ascalaphinae) because it has a shorter antenna, not even reaching the beginning of the RP vein. The *Fillus's* antennae is longer than *A. furcata*, but even so, it does not go beyond the first bifurcation of the RP. The rest of the Ululodini tribe have long antennae, especially *Ascalorphne* and *Ameropterus*.

11. Antennae, flagellomeres 1-6, pilosity: sparse, with few short setae (0); thick, with many long setae (1).

Comment. *D. elegans* has setae all over the antennae, but those are short and sparse. Penny (1981a) mentions that some Haplogleniini do not have setae on the antennae, however, they are present but are short. In general, the antennae of Ululodini (except *A. furcata*) are "hairier", having longer and more concentrated setae, especially in the first flagellomeres.

12. Antennae, male, specialized setae: absent (0); present, in the form of tufts of thick and short setae at the base of each flagellomere (1); present, in the form of a thick row of setae along the flagellomeres (2).

Comment. Present as tufts of thick, short setae in *A. macrocerca* and *A. dissimilis*, and present as a thick row of setae in *A. impavida* and *A. umbrina*. Other insects analyzed in this study do not have any form of specialization of the antennal pilosity.

13. Antennae, club shape: indistinct (0); subglobular (1); piriform (2); piriform curved (3); piriform elongated (4); fusiform (5).

Comment. The classification and nomenclature of the antennal-club shape is based on Tjeder (1992). The frequent collapse of the antennal-club in preserved specimens can make it difficult to distinguish between forms, and specimens stored in alcohol are generally more informative in this aspect. In *D. elegans* the antennae are similar to that found in Myrmeleontinae and do not form a distinct apical club (the apical flagellomeres gradually expand, without a conspicuous constriction at the base). *Fillus* species have a characteristic antennal club shape, similar to a golf club, named here as "piriform curved". In Haplogleniini the antennae are of the piriform elongated type, which are similar to the standard piriform shape, however, they are distinctly cylindrical. *A. furcata* has a subglobular antennal club, in this type the basal segments of the club expand abruptly so the club becomes enlarged very close to the base, giving it a rounded appearance. In the other Ululodini, all of the studied genera presented piriform club, except for *A. macrocerca,* in which the club is distinctly fusiform (tapered base and apex);

14. Pronotum, male, expanded pronotal lobe: absent (0); present (1).

Comment. A characteristic present only in some Neotropical Haplogleniini, such as *Haploglenius* Burmeister, 1839 (demonstrated for *H. luteus (*Walker, 1853*)*, *H. costatus* (this study) and *H. latoreticulatus* van der Weele, 1909) in which this lobe is developed and has a reflective pleural membrane; however, males of *A. chlorops* also have the membrane of this region expanded, forming a pronotal lobe, but it is less conspicuous when compared to that of Haploglenius, and the pleura is not white/reflective. Eisner and Adams (1975) indicate that the pronotal lobe is also present in *Ascalobyas* Penny, 1981, but the comparison with *Haploglenius* is difficult due to the lack of descriptions.

15. Middle leg, length of the tibial spur: short, reaching, at most, the second tarsomere (0); medium, reaching the third tarsomere (1); long, reaching or exceeding the fourth tarsomere (2).

Comment. In some cases, there may be small differences between the size of the tibial spur of the fore and hind legs and, therefore, in order to avoid difficulties in measuring this character, it was assumed that the best way is to observe the tibial spur of the middle leg. In *D. elegans* and Haplogleniini the tibial spur is short and in *F. amazonicus* reaches the third tarsomere. In Ululodini, the spurs are, generally, longer than in the other tribes: in *A. furcata*, they reach the third tarsomere; in *Ululodes* they can be short or medium; in *Am. dissimilis* it is long, but in *Ameropterus* sp. 1 is medium. *Ascalorphne* have particularly long tibial spurs, reaching the fourth tarsomere.

16. Forewing, axillary lobe: absent (0); present (1).

Comment. In Ululodini, the well-developed axillary lobe is considered a synapomorphy of the genus *Ascalorphne*, and is not present in the other analyzed group; It is important to note that different forms of projections off the anal area of the forewing are observed in various groups of Ascalaphinae worldwide (see the discussion section).

17. Forewing, MA vein length: short, reaching, at most, the second fork of RP (0); medium, reaching, at most, the third fork of RP (1); long, reaching/surpassing the fourth RP fork (2).

Comment. In the forewing of *D. elegans* the MA is very long, ending at the sixth fork of RP, close to the apex of the wing, as commonly observed in Myrmeleontinae. In *F. amazonicus* the MA is short, and in Haplogleniini it is medium. In Ululodini, only *A. furcata* has a long MA. In the other Ululodini the MA is medium, but in *Ameropterus* sp. 2 is short and, *Ululodes* sp. 1 males and females differ slightly in the size of this vein.

18. Hind wing, MP bifurcation: distinctly forked (0); without bifurcation (1).

Comment. Based on the analyzed material, the MP bifurcation of the hind wing can only be observed in *Fillus* and Haplogleniini.

19. Hind wing, CuA format: straight (0); sinuous (1).

Comment. According to McLachlan (1871) and van der Weele (1908) the sinuous form of CuA ("postcosta") is an important characteristic of Ululodini, however Stilbopteryginae also presents this characteristic, although it is subtler than that observed in *A. furcata*, for example. Despite being an important feature of the tribe, they do not occur in all members of the group, and their development is probably associated with the width of the wings, being sinuous in *A. furcata, Ululodes* and *Cordulecerus*, which have relatively wide wings, and straight in *Ameropterus* and *Ascalorphne*, which have a relatively narrow wing base.

20. Forewing, CuP vein, length: short, not reaching the origin of RP (0); medium, surpassing the origin of RP (1); long, surpassing the first fork of RP (2).

Comment. The size of the CuP varies between genera, but also between species of the same genus, however, some patterns can be observed. In *D. elegans*, the CuP vein is very long, extending beyond the middle of the wing; in *F. amazonicus* the vein is short, ending before the origin of RP; in *H. costatus* and *A. chlorops* it is short, approaching the origin of RP, a characteristic also observed in other Haplogleniini (Ardila-Camacho and Jones, 2012; Ábrahám, 2013). In *A. furcata* it is medium, and in *Ululodes* the CuP is short; in the analyzed species of *Ameropterus* the CuP is medium; in *Cordulecerus* it is short, and in *C. alopecinus* it reaches the origin of RP but does not go beyond it; in *Ascalorphne* this vein is medium, ending close to the first bifurcation of RP.

21. Hind wing, base width: wide (0); narrow (1).

Comment. *Ascalorphne*'s wings are remarkably narrow at the base, presenting a petiolate shape.

22. Hind wing, male, cubital area expanded in one lobe: absent (0); present (1).

Comment. A characteristic observed only in *Ascalorphne*. *Cordulecerus* and *Am. dissimilis* (specially in males) present this area relatively enlarged which gives a triangular appearance to the hind wings, but never forming a lobe.

23. Abdomen, male sternite 9 (S9), proportion: wider than long (0); longer than wide (1).

Comment. In *D. elegans*, *F. amazonicus* and Haplogleniini the S9 is wider than long, rectangular in ventral view; in Ululodini, however, this structure is longer than wide, spatula-shaped and with several long setae. *A. furcata* also shares that proportion however, in this species the S9 is extremely elongated, bifurcated and with short thick setae.

24. Abdomen, tergite 9 (T9) division: dorsally with inconspicuous separation, halves dorsally close (0); clearly divided dorsally, halves laterally segregated (1).

Comment. The T9 in Ascalaphinae is medially divided, forming two plates that can be dorsally close as in *D. elegans* and Haplogleniini, or clearly separated laterally (*Fillus* and Ululodini).

25. Genitalia, male, pelta position: between gonocoxites 9 (GX9) (0); below GX9 (1).

Comment. In *D. elegans*, *F. amazonicus* and Haplogleniini the pelta is located between GX9 and is relatively small compared to the Ululodini pelta, which is expanded and located below GX9 (except in *A. furcata,* where the pelta was not located, probably absent).

26. Genitalia, male, pelta shape: oval (0); rounded (1); triangular (2).

Comment. In Ascalaphinae, this structure can be found in different formats, which is probably related to the position of the GX9. In *D. elegans* the pelta is conspicuous and oval, similar to that observed in *F. amazonicus*, but in this species the pelta is rounded. In Haplogleniini the pelta is also oval, but inconspicuous. Except for *A. furcata*, in the rest of the Ululodini tribe this structure is expanded at the base and tapered at the apex, resulting in a triangular appearance.

27. Genitalia, male, pelta pilosity: inconspicuous (0); hairy (1).

Comment. Hairy pelta was observed only in *D. elegans*, *F. amazonicus* and *Ululodes* presenting differences in its length (see discussion below).

28. Genitalia, male, pelta, pilosity length: inconspicuous (-); conspicuous, long (0); conspicuous, short (1).

Comment. This character is related to the previous one, however, it is important to differentiate the types of pelta pilosity because, although probably homologous, they are quite different between groups. In *D. elegans* and *F. amazonicus*, the pelta has some elongated setae; this condition is radically different from that observed in *Ululodes*, which have a short and intense hairiness, a characteristic observed only in this genus.

29. Genitalia, male, GX9 (paramere), apex disposition: divergent (0); convergent (1).

Comment. The GX9 can be divergent, as seen in *D. elegans* and *F.* amazonicus, or convergent, as in Haplogleniini and Ululodini.

30. Genitalia, male, GX9 (paramere), length: long (0); short (1).

Comment. This character is probably related to the previous one: possibly, the divergent GX9 allowed the expressive development of this structure into elongated forms, as observed in *D. elegans* and *F. amazonicus*; in cases where the GX9 is convergent, and consequently more "compact", there is a limitation in the development of this structure, which consequently are short.

31. Genitalia, male, pulvinus, setae length: short (0); long (1).

Comment. In this study, long setae on the pulvinus were observed only in Haplogleniini.

32. Abdomen, female, spiracle eight, position: on the ventrolateral margin of T8 (0); in the pleural membrane of segment 8 (1).

Comment. In most Myrmeleontoidea, including Ascalaphinae, the eight abdominal spiracle is located on the ventrolateral margin of T8 (Jones, 2014). However, in Ululodini females, the opening of the spiracle occurs in the pleura. The first author to mention this characteristic was Tjeder (1977), indicating that this characteristic was perhaps "primitive". In males of all species analyzed, the spiracle is always at T8.

33. Genitalia, female, GX8 (ventrovalvae), disposition: paired, distinct, hairy (0); paired, indistinct, glabrous (1); fused and modified into a single sclerotized plaque (2).

Comment. The ventrovalvae is a plastic and important structure and should be considered more carefully in the systematics of Ascalaphinae. Three forms are here recognized: paired, distinct and hairy (Dimarini, Ascalaphini and Haplogleniini), as a single, sclerotized plaque (an autapomorphy of *A. furcata*), and paired, internalized, membranous and glabrous (other Ululodini).

34. Abdomen, female, repagula: absent (0); present (1).

Comment. The repagula of *Ululodes* sp., *Ameropterus* (*Colobopterus*) *dissimilis*, *C. alopecinus* and *A. impavida* were described in the studies of New (1971) and Henry (1972), while Ferreira and Yanega (1999) described the deposition of repagula *in A. furcata*. New (1971) also indicated that, in addition to Ululodini, the repagula is also present in some Haplogleniini, like *Amoea iniqua* (Walker, 1853) (in New as *Episperches aeruginosus* Walker, 1853) and *Ascalobyas* (as *Byas* sp. Walker, 1853), but they are less specialized than the repagula of Ululodini, both in shape and in function.

35. Repagula, morphology: similar to fertilized eggs (0); distinctive of fertilized eggs (1).

Comment. This character is contingent to character 34, so it was analyzed only in species in which the rapagula is present. It is likely that the little specialized repagula is also present in *Haploglenius*, however this characteristic was never mentioned in the literature for this genus and could not be analyzed in this study.

Phylogenetic relationships

Traditional search and implicit enumeration analyses with implicit weighting

In both analyses only one tree was obtained, with topologies identical to each other (Figs. 13, S2). *Fillus amazonicus* was indicated as a sister group to the remaining Ascalaphinae.

The tribe Haplogleniini formed a well-supported clade based on labium shape wider than long (6:0), antennal club piriform elongated (13:4), developed pronotal lobe (14:1) and elongated setae on the pulvinus (31:1). This clade was indicated as a sister group to Ululodini based on the following synapomorphies: the conspicuousness of the tufts of setae on the dorsolateral region of the clypeus (4:1); presence of long setae on the anterior labial margin (7:1); pelta pilosity inconspicuous when compared to *F. amazonicus* and *Ululodes* (28:1) (although usually present in many Ascalaphinae, these setae are frequently lost during the genitalia cleaning, however, this pilosity were not seem in Haplogleniini, probably because it was too small to see it just with an stereomicroscope); also, the GX9 is convergent (29:1) and short (30:1); and finally, production of repagula (34:1), although in Haplogleniini it is not as specialized as in Ululodini.

Ululodini formed a clade based on six synapomorphies: labium with lateralized tufts of setae (8:1), hind wing with medium CuP vein (20:1), male S9 longer than wide (23:1), abdominal spiracle 8 in the females located in the pleural membrane of segment 8 (32:1), GX8 paired, indistinct and glabrous (33:1) and production of specialized repagula (35:1). Additionally, two homoplasies were indicated at this branch: medium tibial spurs (15:1) and T9 divided (24:1) (see comments at character's description).

Albardia furcata was positioned as a member of Ululodini, sister to the other members of the tribe, but with relatively low values of Bremer and bootstrap support.

Ameropterus was indicated as paraphyletic, possibly due to similarities between *Am. dissimilis* and *As. macrocerca*; however, the removal of character 12 (specialized setae on male's antennae, a feature shared by these two species) resulted in a tree with a polytomy between *Ululodes*, *Cordulecerus* and *Ascalorphne* and a loss of resolution of the phylogenetic relationships within *Ascalorphne*.

The genera *Ululodes* and *Cordulecerus* formed a polytomy, with the latter being paraphyletic, possibly due to the great morphological diversity among species of this genus; *Ululodes* composed a clade based on two homoplasies: antennae reaching, at most, the third bifurcation of RP (10:1) and pilosity of the pelta present (27:1). This clade was recovered as sister to *Am. dissimilis* + *Ascalorphne,* based on two synapomorphies, the presence of a row of setae in the PB (3:1) and medium antennae (10:2).

In this study, *Am. dissimilis* was indicated, with high support values, as the sister group of the genus *Ascalorphne*, due to the presence of specialized setae on the male antennae (12:1) but also due to the longer tibial spurs (15:2), apparently a homoplasy.

Ascalorphne formed a clade in all analyses, with robust support, based on the following synapomorphies: axillary lobe present (16:1), petiolate hind wing (21:1) and male's hind wing with the cubital area expanded into a lobe (22:1). *Ascalorphne impavida* and *A. umbrina* are phylogenetically closer than *A. macrocerca*, based on the presence of a thick row of setae on the male's antennae (12:2).

Traditional search and implicit enumeration analyses, without implicit weighting

In both cases, three trees with similar topologies were obtained. In the first tree of both analyses (Figs. S3, S7) *Ameropterus* sp.1 was recovered as sister to *Am. dissimilis* plus *Ascalorphne* based on the homoplasies: hind wing with straight CuA (19:0) (in Ululodini this feature is shared only by these two genera) and hind wing with medium CuP vein (20:1) (however, this is a highly variable feature within *Ameropterus* (see comments on character list). The second tree obtained in the equal-weights analysis resulted in a tree with an identical topology to that of the implicit weighing analysis (Figs. S4, S8) The third tree (Figs. S5, S9) distinguishes from the others by the positioning of *Cordulecerus*, still paraphyletic, but no longer forming a polytomy with *Ululodes*. The consensus of those trees (Figs. S6, S10) differs from the implicit weighing analysis, mainly due to the formation of a polytomy that includes *Ameropterus* sp. 1, *Cordulecerus* and *Ululodes*.

Discussion

Taxonomy and distribution

The comparative analysis of the external morphology and genitalia of *Ascalorphne* did not indicate the occurrence of new species, although there is a significant color variation, especially in *A. impavida*. Redescriptions and descriptions of the genitalia of most Ululodini species will be extremely important to enable the understanding of the real diversity and evolutionary history of Ascalaphinae in the Neotropics.

According to Penny (2002) the terminalia of Ululodini specimens are extremely similar and practically useless in the species identification; indeed, only small morphological variations were observed in the genitalia of *Ascalorphne*, and the GPC is always very similar, however, some relevant features can be observed in the tribe, especially the ectoproct (color, shape), T9 (shape) and pelta pilosity; also, these characteristics greatly differ in the genera and species of Ululodini: *Ululodes*, for example, have an elongated ectoproct ("clasper-like", according to Shetlar, 1977; a feature unknow in any the other Ululodini genera, except for a undescribed species of *Ameropterus* from Brazil) and the S9 usually have a protuberant apex (Fig. 15E).

Penny (1981b) described *Ascalorphne* as "a small genus with restricted distribution". Although the genus, indeed, contains only a few species, its distribution proved to be wide, with species occurring in all regions of Brazil in addition to the distribution in other South American countries (Argentina, Bolivia and Paraguay). This genus possibly has a plastic biology, allowing it to occupy different biomes throughout its distribution; probably, forested areas with leaf litter accumulation are the ideal place for larvae development (and Ululodini larvae can be collected with Winkler extractor in this kind of habitat), while adults prefer open areas with short vegetation, suited for hunting.

Despite the wide distribution of *A. impavida* observed on iNaturalist (2022), the most frequently recorded species is *A. macrocerca* (74.3%), probably due to the distribution of this species and the concentration of users of the iNaturalist app in southern and southeastern regions of Brazil.

Phylogeny and morphology

The trees that best represent the results of this work were obtained through the analyses of TS and IE with implicit weighting (fewer polytomies, smaller steps numbers, higher values of consistency and retention, accordance with the most recent literature) and, therefore, we have selected the TS tree (Fig. 13) to guide the following discussion.

The tribe Haplogleniini was recovered as a monophyletic group in all phylogenetic analyses, and one of its synapomorphies is the development of the pronotal lobe, forming a flap that can be moved and which, at least in *Haploglenius*, are used for defense and/or intersexual communication (Eisner and Adams, 1975; Onore et al., 2014).

Currently, *Albardia furcata* is considered a member of the Ululodini tribe, as the sister taxon to the remaining genera (Machado et al., 2019). In this work, this hypothesis was corroborated in all analyses, in a relationship supported by six synapomorphies, as discussed below.

The chaetotaxy and labium shape were analyzed in a phylogenetic context for the first time for this group, and they were relevant in the classification of Ascalaphinae: in *D. elegans* (Dimarini) the labium is rectangular and the setae are very short, uniformly distributed along the entire anterior margin of the labium (Fig. 14A), similar to what was observed in *F. amazonicus* (Ascalaphini) (Fig. 14B). In Haplogleniini, the setae are elongated and also arranged along the labral margin, despite being separated medially by a groove (Fig. 14C).

One of the synapomorphies of the Ululodini tribe (including *A. furcata*) is the localization of these setae to the sides of the labrum, which is quadrangular, and the setae are elongated, thick and shaped like "hooks" at the apex (in *A. furcata*, however, these setae differ by being shorter and straight) (Figs. 14D, E). In Ululodini, these long setae probably optimize the ability to capture/manipulate prey, possibly acting as an extension of the labrum and/or acting in prey's chemical recognition.

Another feature with phylogenetic relevance is the shape of the male S9 in Ascalaphinae, with two main shapes observed: wider than long (Dimarini, Haplogleniini and Ascalaphini) (Figs. 15A-C) or longer than wide (Ululodini, in which this structure has a spatula-like shape; in *A. furcata* the S9 is longer than wide, but it is extremely elongated, bifurcated and with strong short setae, an autapomorphy) (Figs. 15D, E).

The female GX8 of Ululodini is radically different from the remaining Ascalaphinae: in *D. elegans* (Fig. 15F), it is short, membranous, with long setae and clearly visible; in *F. amazonicus* this structure is sclerotized and long (Fig. 15G) (Machado and Rafael, 2011; Ardila-Camacho et al., 2019), similar to what was observed in other Old World Ascalaphini, such as *Nousera* Navás, 1923 (Oriental) (long and sclerotized, with long setae at the apex), but may also be distinct in other genera of this tribe such as, for example, *Bubopsis* McLachlan, 1898 (Oriental) (short and membranous, but also with some short setae) (Yang et al., 2016); in *H. costatus* and *A. chlorops* (Haplogleniini) the GX8 is long, rectangular and with intense pilosity (Fig. 15H) but in other Haplogleniini, such as *Allocormodes* McLachlan, 1891 (Afrotropical) the GX8 is short, but it is also sclerotized and full of setae (Jones, 2014). In contrast, Ululodini is characterized by the GX8 being internalized, concave, rectangular, weakly sclerotized and glabrous (Fig. 15J).

Unlike other Ululodini, *A. furcata* has the GX8 as a single, sclerotized plate associated with gonapophysis 8 (liguella) (Fig. 15I) ("spatulate process" in New (1982)), a unique condition within Ascalaphinae, which is an autapomorphic and, probably, a plesiomorphic state. However, in some Old World Ascalaphinae (e.g., *Libelloides*) the GX8 is also partially or completely fused into a single plate (Aspöck and Aspöck, 2008), similar to the condition found in *A. furcata*. All other New World Ascalaphinae feature the GX8 as two completely separate plates.

As exposed, it is clear that the GX8 is an extremely plastic structure, however, it is still little explored in phylogenetic studies and should be considered more carefully in the systematics of Ascalaphinae.

Tjeder (1977) analyzed characteristics of the abdominal segments of several genera of Ascalaphinae and commented that *Ululodes* and *Cordulecerus* have a "possibly primitive condition of tergite 8 in females", in which the spiracle of eighth abdominal segment is located in the pleura and not on the ventrolateral margin of T8, as seen in most Myrmeleontiformia and Ascalaphinae (Jones, 2014). In this work, this feature was recovered as an important synapomorphy of the Ululodini and is evidenced for *A. furcata* for the first time (Fig. 16), corroborating the results of Machado et al. (2019). Another important synapomorphy of Ululodini is the production of specialized repagula, clearly distinct from fertilized eggs and covered with an ant-repellent secretion and distinct from the Haplogleniini repagula, which has a similar shape to that of the fertilized eggs and, apparently, acts only as food (and not as a chemical barrier) for the newly hatched larvae (New, 1971).

Other synapomorphies of Ululodini, except *A. furcata*, are: AOS strongly projected towards the eye (0:2), a feature related to the level of ocular division in each group; intense pilosity at the base of the flagellomeres (11:1), which, in this tribe are very conspicuous and long, and sometimes these setae are specialized in males (*Ascalorphne*, *Ameropterus dissimilis*) and the length of the setae of the second segment of the labial palp, that are longer than half of the third one (9:1) (Fig. 14E). The latter character is another synapomorphy of Ululodini recognized for the first time in this work. In *D. elegans* this character cannot be observed, since the labial palp is extremely elongated and the setae, therefore, are very short. In the other studied Ascalaphinae these setae are always short; short setae seem to be, indeed, a pattern for the tribe Haplogleniini, based on the illustration of *Neomelambrotus aurivilliusi* Van der Weele, 1909 (Afrotropical) (Tjeder, 1992). As a rule, Ululodini (except *A. furcata*) have some short setae and also long ones, usually longer than the fourth segment; however, in *Ameropterus* these setae may be a little shorter, but still longer than half of the next segment.

Regarding the male genitalia, both in Myrmeleontinae and Ascalaphinae, the GX11 and GX9 are associated forming the GPC (Aspöck and Aspöck, 2008). The pelta (which probably corresponds to the gonostyli 11) is located between these two sclerites; it can be more or less sclerotized in different groups, and may have a sensory function *in copula* for the positioning of the genitalia.

Badano et al. (2017) indicated that the paired projections of the genitalia of *D. elegans* represented the GS9, and that the base of these structures would correspond to the GX9 (maybe an editing mislabel). Based on Aspöck & Aspöck (2008) the GS9, actually, corresponds to the GX9; the pelta was not indicated in the figure by Badano et al. (2017), but is clearly visible between the GX9, and it is demonstrated in detail in the present work (Fig. 17B).

The pelta of the Ululodini tribe (except *A. furcata*) are distinguished for being distinctly expanded, triangular and membranous (26:2) and located below the GX9 (25:1) (Fig. 17E). In *A. furcata* there is only a membranous area where this sclerite is usually found (Fig. 17D), being inconspicuous or maybe absent in this species. In the other Neotropical Ascalaphinae groups, the pelta is lodged between GX9, and in *D. elegans* and *F. amazonicus* they have sparse and elongated setae.

In Ululodini, the pelta may have sparse or intense pilosity; importantly, the intense pilosity was found exclusively in the two studied species of *Ululodes* (Fig. 17E). Shetlar (1977) described and illustrated the genitalia of some Ululodes, and described it, for all species, as simply "triangular subpelta", except for *U. quadripunctatus* (Burmeister, 1839) which, according to the author, has the "subpelta triangular, covered with small spines" (but not shown in the illustration). The males of this species are very distinctive and, therefore, it is safe to say that at least this species also has hairy pelta.

Thus, it is currently not possible to indicate whether this feature is a synapomorphy for *Ululodes*, of just some species or a group of species. The identification of *Ululodes* species is complex (Ardila-Camacho et al., 2019) and this may be an important feature in the recognition of members of this genus.

Except for *Ameropterus* sp. 1, the other Ululodini were grouped based on the presence of a row of long setae in the PB (3:1) and also by the longer antennae (10:2). The presence of setae in PB is, probably, another synapomorphy of the Ululodini tribe, although in the phylogenetic analyses it was not recovered as such. This is because these setae may be absent and/or difficult to observe in some species of *Ameropterus* (*A.* sp. 1; *A. breviantennis*), but clearly present in others (*A. dissimilis*); but in other genera of Ululodini they are always conspicuous.

In addition to the observations in this work, Henry's (1978b) illustration of details of the head of an Ululodini (setae visible) and an Ascalaphini (not visible) reinforce the view of this character as a synapomorphy of Ululodini. In fact, apparently no Oriental (Hassan and Liu, 2021) or Palearctic (clearly absent in *Libelloides*, for example) genus has this feature, which possibly appeared only in Ululodini (except *A. furcata*).

Ameropterus dissimilis was recovered as a sister group of *Ascalorphne*, due to the presence of specialized setae on the male's antennae (12:1) (Fig. 18D). This is a distinct species among the other members of the genus, due to the triangular shape of the wings, especially in the males, and the condition of the antennal pilosity. Despite the strong influence that the characteristics of this species may have on the tree topology in this study, it is notable that the genus *Ameropterus* has been repeatedly indicated as paraphyletic, regardless of the species utilized or the type of analysis performed. For example, Jones (2019) used morphological and molecular data and included three genera of Ululodini (*Ascalorphne* absent); in the analyses based only on morphological data, the author obtained a polytomy for the entire Ululodini tribe, however, in the phylogenetic analyses based on molecular data and total-evidence *Ameropterus* was recovered as paraphyletic in relation to *Cordulecerus*, similar to the results obtained by Machado et al. (2019) based on genomic data.

Ameropterus is a diverse and taxonomically little-known group. Currently, the distinction of this taxon from the other Ululodini is based exclusively on the presence of a straight CuP vein and elongated antennae, as it is also observed in *Ascalorphne*, and differing from the latter only by the absence of an anal lobe; in addition, the presence of specialized setae on the male's antennae, fusiform club and elongated tibial spurs are also features observed in these two genera. Other authors that also indicated this relationship were van der Weele (1908), McLachlan (1871) and Penny (1981a). Only with the understanding of the relationships of the whole tribe it will be possible to understand the phylogenetic relevance of these features and it is likely that new taxa will have to be described in Ululodini with the revision of *Ameropterus*. The large amount of homoplasy is one of the challenges in the recovery of phylogenetic relationships in Ululodini. In addition, the lack of modern revisions of all genera, makes it difficult to understand the distribution of certain morphological traits in the tribe. In this sense the present work constitutes an initial effort in relation to the problematic taxonomy of this group, through the revision of the genus *Ascalorphne*.

In this study, *Ascalorphne* was recovered as monophyletic in all analyses. A notable structure of this genus is the development of the anal lobe in the forewings (16:1) and, indeed, this is a distinctive feature for the taxon within Ululodini. However, projections of the anal margin of the forewing are not exclusive to this genus and many other Ascalaphinae groups show a certain morphological diversity of these structures. For example, in *Tmesibasis lacerata* (Hagen, 1853) it is acuminated, and in *Balanopteryx locuples* Karsch, 1889 (Haplogleniini) it is tubular; the anal lobe may also present varying degrees of development: being slightly projected in *Nephoneura costalis* van der Weele, 1909 (Ascalaphini) or strongly projected in *Ascalorphne* (Ululodini).

The presence of these projections was noted by Tjeder (1992) who, studying the Afrotropical fauna of Ascalaphinae, reported specializations of microtrichia in the anal lobe of *T. lacerata*. Riek (1967) was another author who considered specializations of the anal region of the fore and hind wings in Neuropterida (and in other groups of insects), hypothesizing a stridulatory function between microtrichia in the anal lobe and a velvety area of the metascutum. Other possible adaptive functions of this type of wing projection may be related to wing attachment mechanisms or aerodynamics. No other work has further discussed this hypothesis, but these structures were clearly relevant in the evolutionary history of several groups within the subfamily.

Ascalorphne impavida and *A. umbrina* were recovered as phylogenetically closer than *A. macrocerca*, as previously suggested by van der Weele (1908), based on the presence of a thick row of setae on the male's antennae (12:2) (Figs. 18A-C). This sexual dimorphism probably maximizes male's perception of pheromones emitted by females. This feature seems to be exclusive to these two species, as it was not observed in any other Ascalaphinae analyzed or known in the literature.

The phylogenetic position of *A. macrocerca*, sister to the other species of the genus, is indicated by the shape of the antennal club, which is fusiform (13:5), a feature rarely found in Ululodini, and in fact, known only for *Ameropterus scutellaris* and *Am. versicolor* (Gerstaecker, 1894)

(Ardila-Camacho et al., 2019), probably a convergence. Furthermore, in males of *A. macrocerca*, the rows of setae are grouped in tufts of thick setae at the apices of the antennomeres, in a condition possibly apomorphic in relation to what is seen in *A. impavida* and *A. umbrina*. It is interesting to note that the presence of thick setae at the apex of flagellomeres seems to have been independently acquired by *Ascalorphne* and *Ameropterus*, as observed in *Am. dissimilis,* whose males also have thick tufts of setae (but less distinct than in *A. macrocerca*).

By reviewing one genus of Ululodini, comparing the morphology and evaluating the relationships between the members of this diverse Neotropical tribe, this study improved the understanding of the real diversity of this still little-known, but fascinating, group of Neuroptera.

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Conflicts of interest

The authors declare no conflicts of interest.

Author contribution statement

PAS formal analysis, text writing, review and editing, photographs and image editing. RJPM supervision, text writing and review.

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Supplementary material

The following online material is available for this article:

Table S1 - Ascalaphinae (Insecta: Neuroptera: Myrmeleontidae) specimens analyzed through genitalia dissections; S: sex; n= number of individuals.

Table S2 - *Ascalorphne* records submitted to the app Inaturalist (until 03/18/2022), utilized in the distribution map. S/D: State/Division; Mun. Municipality, S: Sex; n= number of individuals.

Figure S1 - Wings and veins interpretation of a male *Ascalorphne impavida* (Walker, 1853) (Myrmeleontidae: Ascalaphinae: Ululodini), following on Breitkreuz et al. (2017).

Figure S2 - Phylogenetic tree of Neotropical Ascalaphinae. Most parsimonious and unique tree (number of steps=68, consistency index=69, retention index=79) obtained through the implicit enumeration with implicit weighing (K=3). Numbers above the circles indicate the character and below, the state; unequivocal changes (black circles) and reversals or multiple changes (white circles); bootstrap with Poisson distribution (red). Due to an unknown error, it was not possible to calculate the Bremer support.

Figure S3 - Phylogenetic tree of Neotropical Ascalaphinae. Maximum parsimony phylogenetic tree 1/3, obtained through traditional search analysis without implicit weighting. Numbers above the circles indicate the character and below, the state; unequivocal changes (black circles) and reversals or multiple changes (white circles).

Figure S4 - Phylogenetic tree of Neotropical Ascalaphinae. Maximum parsimony phylogenetic tree 2/3, obtained through traditional search analysis without implicit weighting. Numbers above the circles indicate the character and below, the state; unequivocal changes (black circles) and reversals or multiple changes (white circles).

Figure S5 - Phylogenetic tree of Neotropical Ascalaphinae. Maximum parsimony phylogenetic tree 3/3, obtained through traditional search analysis without implicit weighting. Numbers above the circles indicate the character and below, the state; unequivocal changes (black circles) and reversals or multiple changes (white circles).

Figure S6 - Phylogenetic tree of Neotropical Ascalaphinae. Consensus from the maximum parsimony phylogenetic trees obtained through an equal-weights analysis with traditional search (number of steps=72, consistency index=65, retention index=75). Numbers above the circles indicate the character and below, the state; unequivocal changes (black circles) and reversals or multiple changes (white circles); relative Bremer support (blue) and values of bootstrap with Poisson distribution (red).

Figure S7 - Phylogenetic tree of Neotropical Ascalaphinae. Maximum parsimony phylogenetic tree 1/3, obtained through an equal-weights implicit enumeration analysis. Numbers above the circles indicate the character and below, the state; unequivocal changes (black circles) and reversals or multiple changes (white circles).

Figure S8 - Phylogenetic tree of Neotropical Ascalaphinae. Maximum parsimony phylogenetic tree 2/3, obtained through an equal-weights implicit enumeration analysis. Numbers above the circles indicate the character and below, the state; unequivocal changes (black circles) and reversals or multiple changes (white circles).

Figure S9 - Phylogenetic tree of Neotropical Ascalaphinae. Maximum parsimony phylogenetic tree 3/3, obtained through an equal-weights implicit enumeration analysis. Numbers above the circles indicate the character and below, the state; unequivocal changes (black circles) and reversals or multiple changes (white circles).

Figure S10 - Phylogenetic tree of Neotropical Ascalaphinae. Consensus from the maximum parsimony phylogenetic trees obtained through an equal-weights implicit enumeration analysis (number of steps=72, consistency index=65, retention index=75). Numbers above the circles indicate the character and below, the state; unequivocal changes (black circles) and reversals or multiple changes (white circles); relative Bremer support (blue) and values of bootstrap with Poisson distribution (red).