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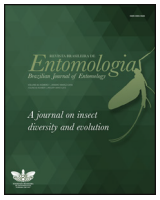

Antlions of formerly recognized tribe Gnopholeontini (Neuroptera: Myrmeleontidae: Brachynemurini) from Peninsula of Baja California, with a new species of *Tyttholeon* Adams

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ABSTRACT

A new antlion species, *Tyttholeon froehlichi* Tavares, Marquez and Contreras **sp. n.**, is described from the Baja California Peninsula, Mexico, an area biogeographically significant for its high number of endemic species. Previously monotypic, *Tyttholeon* Adams now comprises two Nearctic species. Three of the four genera within the formerly recognized tribe Gnopholeontini and their respective species, all present in the Peninsula of Baja California (*Gnopholeon barberi* Currie, *G. delicatulus* Currie, *G. zapotecus* Stange, *Menkeleon bellulus* Banks, and *Tyttholeon puerilis* Adams), are herein diagnosed, illustrated, and have their distribution updated and analyzed. A taxonomic key is provided for *Tyttholeon*.

Introduction

The Baja California peninsula is located in northwestern Mexico and includes the states of Baja California and Baja California Sur. It currently contains 19 Natural Protected Areas and is recognized for its high number of endemic species (González-Abraham et al., 2010; Morrone, 2021). A large number of recorded endemics is partly due to the complexity of the region's relief, the flow between island and continental species, as well as a long geological history with periods of submergence and tectonic uplift; therefore, the Peninsula of Baja California is an important area of conservation (Grismer, 2000; González-Abraham et al., 2010). The Baja California peninsula belongs to the Western Subregion of the Nearctic Region and has its own regionalization (Escalante et al., 2021), which consists of three biogeographic provinces, each with its own biogeographic districts defined by the presence of different vegetation types and diverse environmental conditions. The dominant vegetation in Baja California is xerophilous scrub, with small portions of tropical dry forest and temperate forest (CONANP, 2003; Rzedowski, 2006).

The Myrmeleontidae, largest family of Neuroptera with 2118 valid extant species around the world (Oswald, 2023), are known to be adapted to a large number of habitats but are frequently associated with arid and semiarid environments (Oswald and Machado, 2018). In Mexico, there are little over 100 recorded species of antlions, of which about 50 have been recorded from the Baja California peninsula, with 24 placed in the tribe Brachynemurini (Contreras-Ramos and Rosas, 2014; Oswald, 2023). These records come mostly from species descriptions, checklists, and taxonomic reviews, as only recently has survey work in the Peninsula started through a project led by one of us (ACR).

Brachynemurini are endemic to the Americas, especially abundant in arid areas (Mansell, 1999). This tribe is diagnosed by a postventral lobe in the male ectoproct, and the hinged parameres in the male genitalia (Adams, 1956; Stange, 1970, 1994; Tavares et al., 2023). Previously, Brachynemurini was divided into three different tribes (Brachynemurini, Gnopholeontini, and Lemolemini), based on larval morphology (Stange, 1994, 2004). Posteriorly, Machado et al. (2019) merged Gnopholeontini and Lemolemini under Brachynemurini, because Gnopholeontini was recovered nested deeply into Brachynemurini in a phylogenomic analysis. Although Lemolemini was not included in that analysis, it was deemed

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as enough evidence to predict this tribe would be recovered inside Brachynemurini as well, based on shared morphological characters between the three groups.

Despite the many similarities between the Gnopholeontini (*sensu* Stange, 1994) and the remaining Brachynemurini, the genera comprised by the former bear impressive morphological specializations and are apparently rarely collected (Fig. 1) (Stange, 1970, 1994). These genera, *Gnopholeon* Stange, 1970 (three species), *Maracandula* Currie, 1901 (five species), *Menkeleon* Stange, 1970 (one species) and *Tyttholeon* Adams, 1956 (one species), comprise generally very small insects lacking tibial spurs (except for *Gnopholeon*), bearing wings with a simple venation and very characteristic chaetotaxy. They may be identified with the key proposed by Miller and Stange (2009). Despite their importance as an endemic and rare fauna, these genera have a poor representation in literature, including morphological and molecular phylogenetic treatments. Besides its preliminary revision (Stange, 1970) and a morphological analysis that established the former Gnopholeontini (Stange, 1994), which included all four genera (analyzed at the genus level), only two species have been used in subsequent phylogenies, with *Menkeleon* represented once in a morphological analysis (Badano et al., 2018) and *Gnopholeon delicatulus* (Currie, 1903) used twice in phylogenomic analyses (Winterton et al., 2018; Machado et al., 2019). *Maracandula* has been revised recently (Miller and Stange, 2009), yet additional citations for the remaining genera are limited to inventories of scientific collections (Penny, 1977; Penny et al., 1997; Flint Júnior, 2002). Furthermore, apart from *Maracandula*, all genera and species formerly included in Gnopholeontini lack comprehensive images, and the existing illustrations are representative of only a few species, referring to specific characters such as tarsomeres, male ectoprocts and genitalia (Banks, 1942; Adams, 1956; Stange, 1970, 1994). We herein provide diagnoses and illustrations for the species formerly comprised in Gnopholeontini that have been recorded from Baja California.

We gladly dedicate this contribution to Prof. Dr. Claudio Gilberto Froehlich, with our admiration for his bright and extensive career in invertebrate zoology, insect morphology, as well as aquatic insect ecology and systematics in the Neotropics. He has been an inspiration to generations of entomologists and students, including CCM, who had the great opportunity to study in the same department of the Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto - USP, where Dr. Claudio taught and worked for many years.

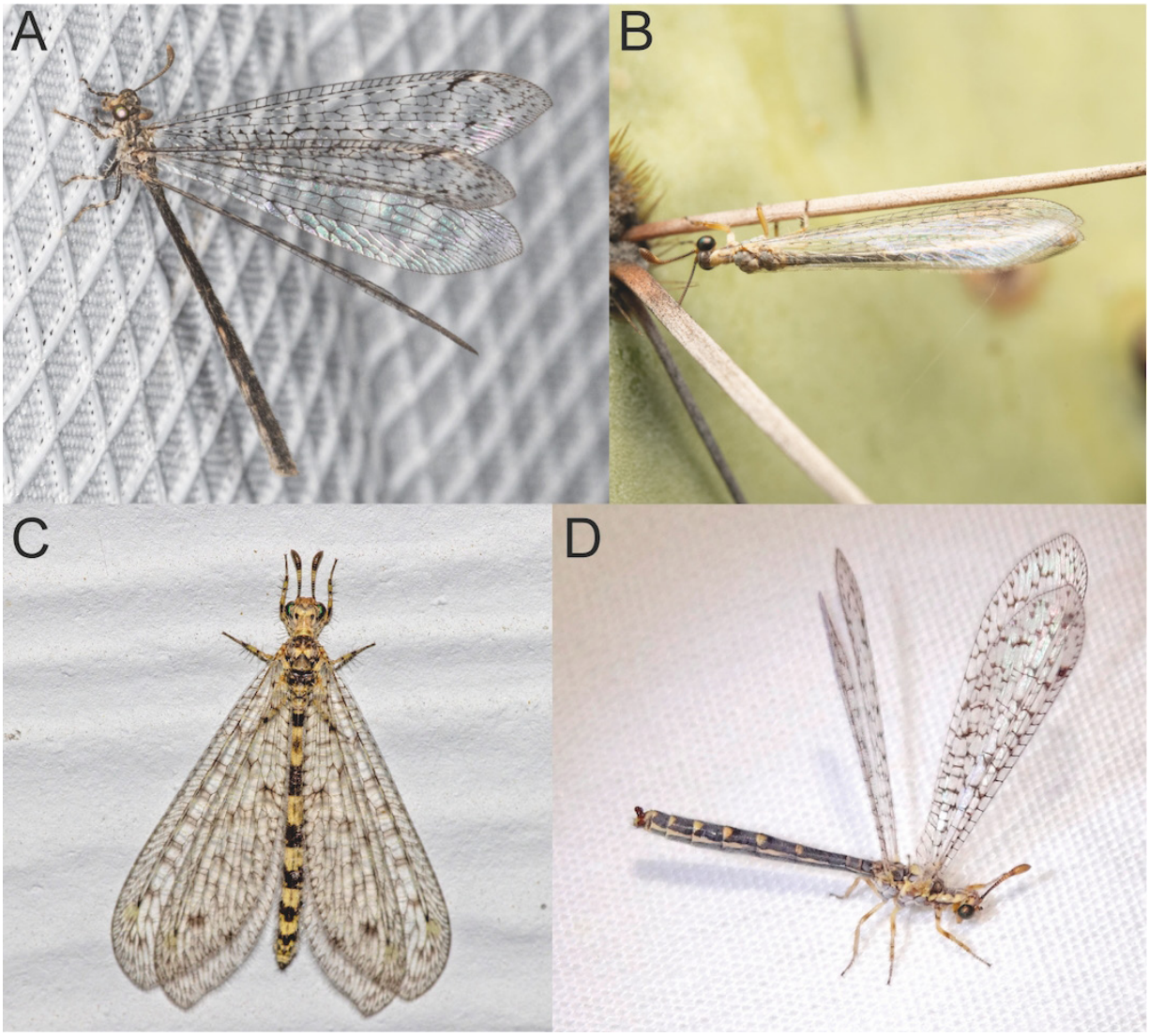

Figure 1 Live specimens of species comprised in the former Gnopholeontini: A) *Gnopholeon barberi* (Currie, 1903), by BJ Stacey. B) *Gnopholeon delicatulus* (Currie, 1903), by CD Martinez. C) *Menkeleon bellulus* (Banks, 1905), by Sean Werle. D) *Tyttholeon puerilis* Adams, 1957, by BJ Stacey.

Materials & methods

A total of 54 adult specimens were examined, all of them collected in many prior events and, especially, 47 from two field trips to Baja California Peninsula carried out between 2021 and 2022 at six different localities distributed along the Baja California Peninsula. The remaining seven specimens were from different collection events in Mexico and the United States. The myrmeleontids were sampled in mercury, metallic additive and UV light traps, held between 6:00 and 11:00 pm. All specimens collected in field trips were stored pinned or in alcohol and deposited at Colección Nacional de Insectos (CNIN) of the Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM). The holotype of *Tyttholeon puerilis* Banks, 1956 is stored at the California Academy of Sciences (CAS) and was analyzed through high quality photographs; holotype of *Gnopholeon zapotecus* Stange, 1970 is deposited at Bohart Museum of Entomology, University of California-Davis (UCDC). The specimens were identified to genus using the Gnopholeontini key of Miller and Stange (2009), and to species using the key in Stange (1970), as well as by comparison with original descriptions.

For the study of genital structures, the last four abdominal segments were removed and cleared with a 10% potassium hydroxide (KOH) solution; washed with distilled water, 10% acetic acid, and 70% ethyl alcohol, following the protocol of Cummings (1992). Cleared abdomens were stored in microvials with glycerine and kept together with the respective adult specimen. Series of high-resolution photographs were taken using a Carl Zeiss Discovery V8 stereomicroscope or a Carl Zeiss AxioZoom V16 with an AxioCam 305 camera, both stereomicroscopes with stacking system. Final images and plates were edited using Adobe Photoshop 2021.

General and genital morphological terminology follows Stange (1994), Miller and Stange (2017), and Tavares et al. (2023), while wing venation terminology follows Breitkreuz et al. (2017), considering that MA and RP are not fused, with the hindwing sigmoidal vein (or vein 'b') interpreted as 1r-m and not the basal part of MA. Distribution maps were made in QGIS software version 3.30.3 with the ecoregion maps of Mexico corresponding to those published in the CONABIO Geoportal and district maps of the Baja California peninsula corresponding to González-Abraham et al. (2010). Maps were constructed with original data from specimens from the two field trips to the Peninsula and specimens deposited at CNIN and CAS. Distribution data published in GBIF were also downloaded, for a more complete treatment of known distribution information of the species. The GBIF data were downloaded and mapped with the GBIF (2023) occurrences download plug-in and they are indicated with circles in the maps (Figs. 14-15). States in bold denote new distribution record.

Abbreviations for USA states are Arizona (AZ), California (CA), New Mexico (NM), Nevada (NV), Texas (TX), and Utah (UT), while abbreviations for Mexican states are Baja California (BC), Baja California Sur (BCS), Chihuahua (CHIH), Morelos (MOR), Oaxaca (OAX), Sinaloa (SIN), Sonora (SON), and Veracruz (VC), following Oswald et al. (2002).

Results

Among the analyzed specimens, six species in three genera were identified, including a new species of *Tyttholeon*. The most abundant species was *Gnopholeon barberi* (Currie, 1903), with 44 specimens.

Taxonomy

Gnopholeon Stange, 1970

Figs. 1A, B, 2–7

Gnopholeon Stange, 1970: 148 [Type species: *Gnopholeon zapotecus* Stange, by original designation]. – Penny, 1977: 54 [distribution]. – Stange, 1994: 90 [taxonomy, redescription, phylogeny]. – Penny et al., 1997: 85 [distribution]. – Stange, 2004: 249 [taxonomy, types, distribution]. – Machado et al., 2019: 441 [list of genera].

Distribution. USA, Mexico.

Included species. *G. barberi* (Currie, 1903), *G. delicatulus* (Currie, 1903), *G. zapotecus* Stange, 1970 (Key to species in Stange (1970)).

Larvae known. *G. barberi*.

Diagnosis. Adults. Antenna with 25-34 flagellomeres, flagellomere 1 longer than wide; vertex well developed and dorsally projected; frons without setae; ocular rim with or without setae that projects over eye; greatest ocular width about half interocular distance; labial palpi with distal palpomere greatly swollen; pronotum longer than wide or as wide as long; legs short, profemur about 1.5 times longer than procoxa, not swollen; hind leg longer than foreleg which is almost the same size as midleg; profemur with or without clavate setae, if present, then clustered or almost in a row; profemur with or without elongated white bristles; profemural sense hair shorter than profemur length, and mesofemoral sense hair shorter than profemoral sense hair; tibial spurs well developed, at least as long as first three tarsomeres together; pretarsal claws large, slightly shorter than distal tarsomere; basitarsus very short, half the length of distal tarsomere at most; wings narrow; hypostigmatic cell without crossveins; both wings with an apical streak formed by infuscations on hypostigmatic cell and pterostigma; banksian lines absent; hind wing posterior area narrow, with cells delimited by crossveins that are longer than wide; CuA bends to hind margin before MP fork; pilula axillaris small, moderately well developed with setae concentrated toward distal margin of knob; abdomen shorter than wings in rest; male genitalia in folded position when in rest; male ectoproct with or without a postventral lobe, if present shorter than ectoproct height; male genitalia with an arched gonarcus dorsal to the parameres; mediuncus present, narrow, projecting posterodorsally, curved and sclerotized apically, with transversal grooves; parameres free, hinged; paramere plates dorsoventrally short; male ectoproct postventral lobe very short; female ectoproct with or without digging setae; female posterior gonapophysis swollen, thumb-like; lateral gonapophysis not fused; pregenital plate narrow with a median tooth, gonapophyseal plate large, with many long, hairlike setae.

Larvae. In Stange (1994).

Remarks. This genus has a few recognizable characteristics among the Brachynemurini. The enlarged tibial spurs and pretarsal claws, along with the evidently short basitarsus is only seen in *Dejuna* Navás, 1924 and *Peruveleon* Miller and Stange, 2011 yet both lack *Gnopholeon* genitalia general shape. The presence of clavate setae on profemur is also seen in *Chaetoleon* Banks, 1920 and *Peruveleon*, but with far less density of setae. The ocular rim setae are also present in *Chaetoleon, Peruveleon,* and *Menkeleon*. More importantly, *Gnopholeon* larval morphology is extremely different from every known Brachynemurini larvae up to date (Stange, 1994); it is ascalaphid-like with long thoracic and abdominal scoli, the mandible bases are very close together and the head capsule is conspicuously wide (Stange, 1994).

Stange (1994) discusses the possibility of paraphyly for this genus because of chaetotaxy differences between *G. delicatulus* and the remaining two species, however an overall reduction of leg setae, tibial spurs and pretarsal claws is present in other Brachynemurini genera, such as *Ameromyia* Banks, 1913, *Scotoleon* Banks, 1913 and *Brachynemurus* Hagen, 1888 (Stange, 1970, 1994; Tavares et al., 2023), so monophyly of *Gnopholeon* has support but should be further tested.

Gnopholeon barberi (Currie, 1903)

Figs. 1A, 2–3

Brachynemurus barberi Currie, 1903: 282 [Holotype female, Hot Springs (USNM)]. – Banks, 1907: 31 [species list]. – Banks, 1913: 65 [species list].

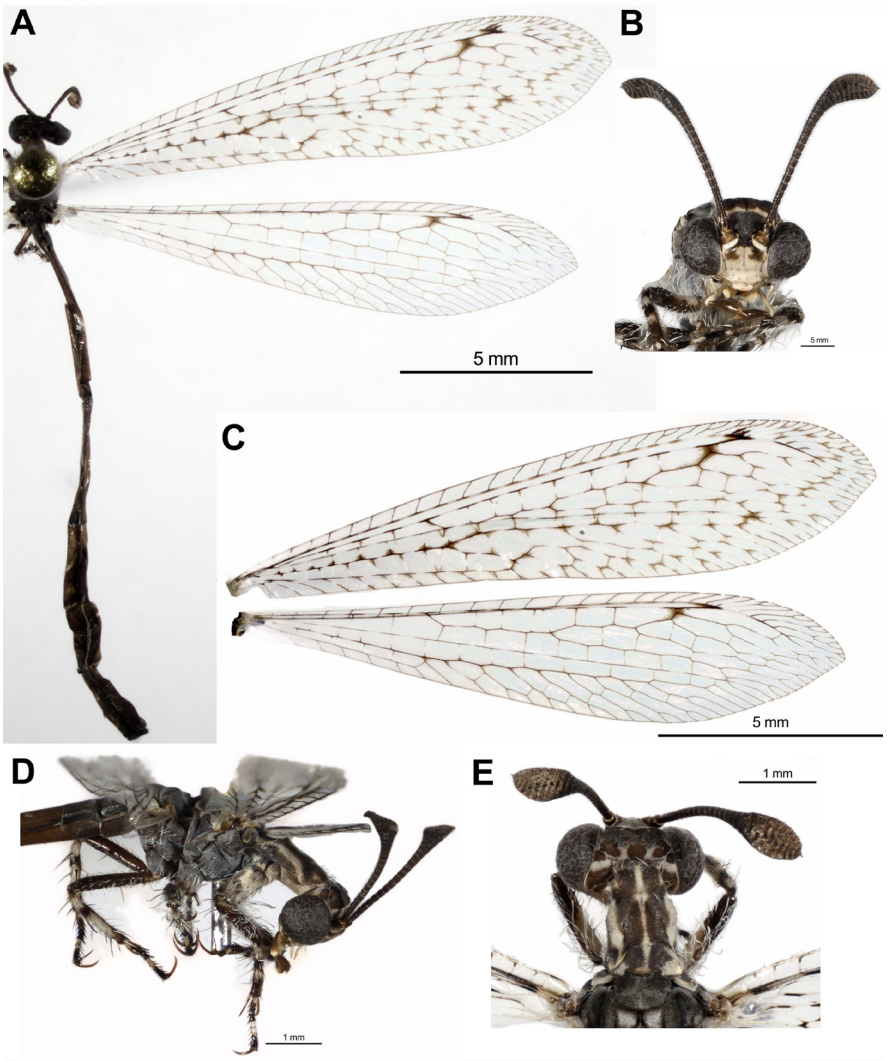

Figure 2 *Gnopholeon barberi* (Currie, 1903), male specimen. A) habitus, dorsal. B) head, frontal view. C) fore and hind wings. D) head, thorax and legs, lateral view. E) head and prothorax, dorsal view.

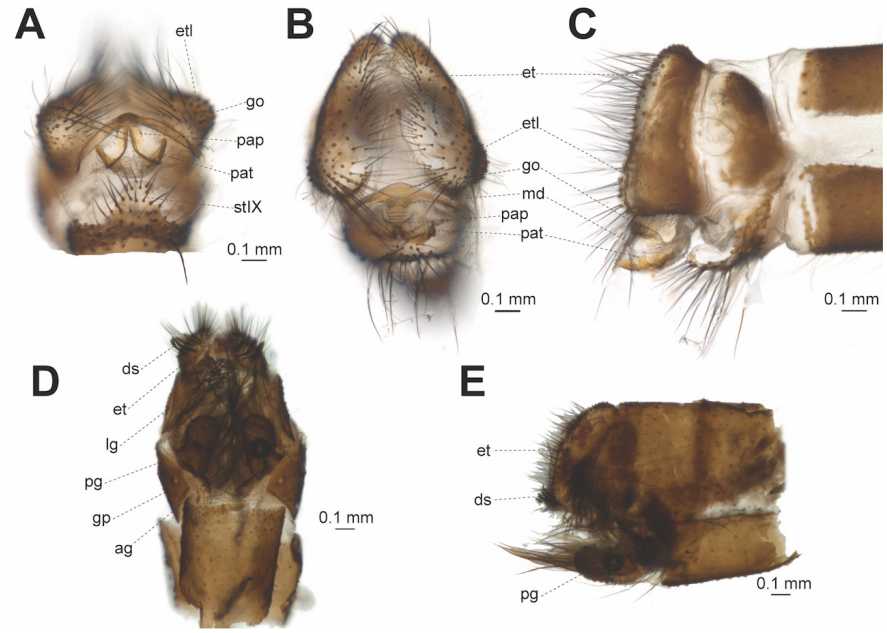

Figure 3 *Gnopholeon barberi* (Currie, 1903), male and female terminalia. A) male terminalia, posterior view. B) male terminalia, posterior view. C) male terminalia, lateral view. D) female terminalia, ventral view. E) female terminalia, lateral view. — Abbreviations: ag: anterior gonapophysis; ds: digging setae; et: ectoproct; etl: ectoproct postventral lobe; go: gonarcus; gp: gonapophyseal plate; lg: lateral gonapophysis; md: mediuncus; pap: paramere plates; pat: paramere tooth; pg: posterior gonapophysis; pgp: pregenital plate; stIX: sternite IX.

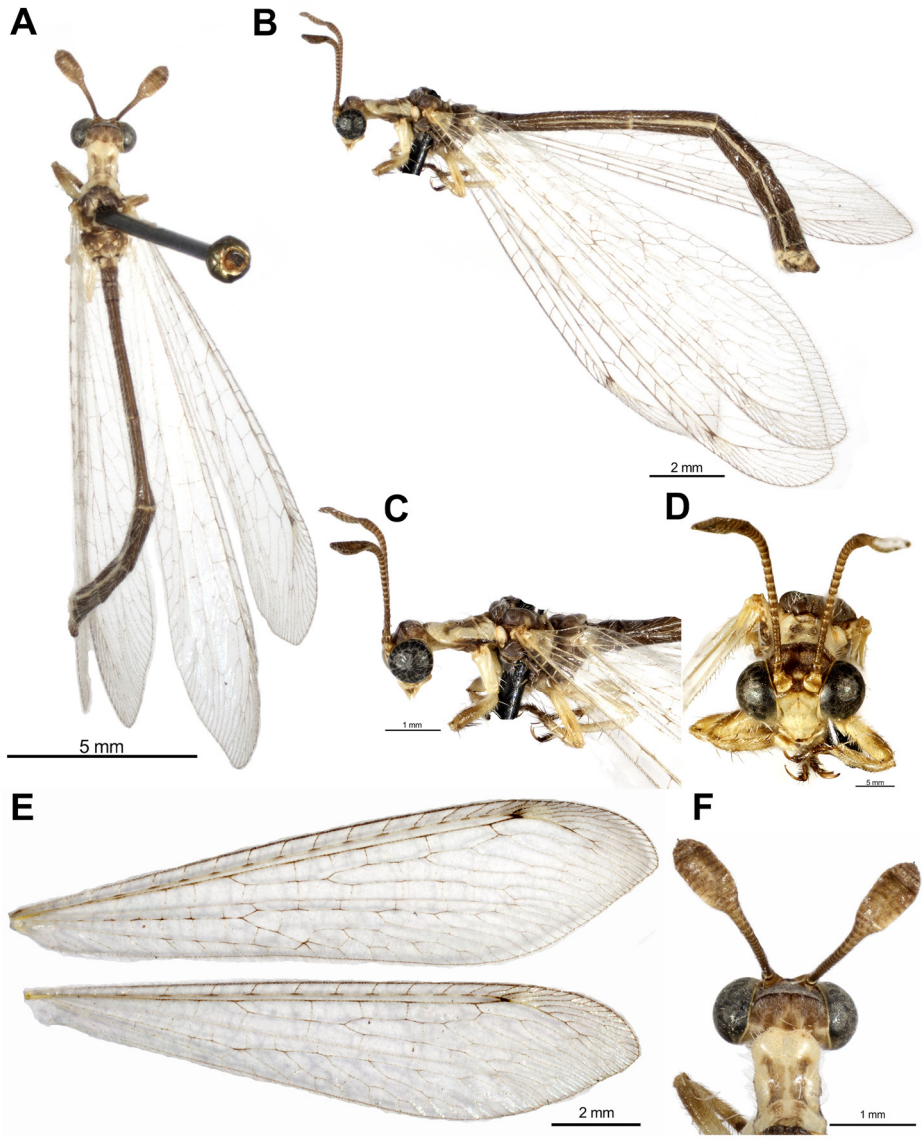

Figure 4 *Gnopholeon delicatulus* (Currie, 1903), female specimen. A) habitus, dorsal view. B) habitus, lateral view. C) head, thorax and legs, lateral view. D) head, frontal view. E) fore and hind wings. F) head and prothorax, dorsal view.

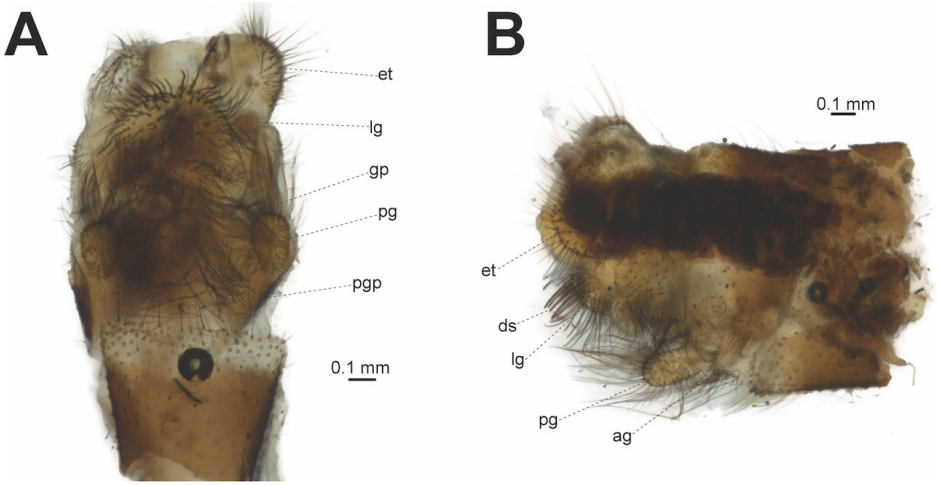

Figure 5 *Gnopholeon delicatulus* (Currie, 1903), female terminalia. A) ventral view. B) lateral view. — Abbreviations: ag: anterior gonapophysis; ds: digging setae; et: ectoproct; gp: gonapophyseal plate; lg: lateral gonapophysis; pg: posterior gonapophysis; pgp: pregenital plate.

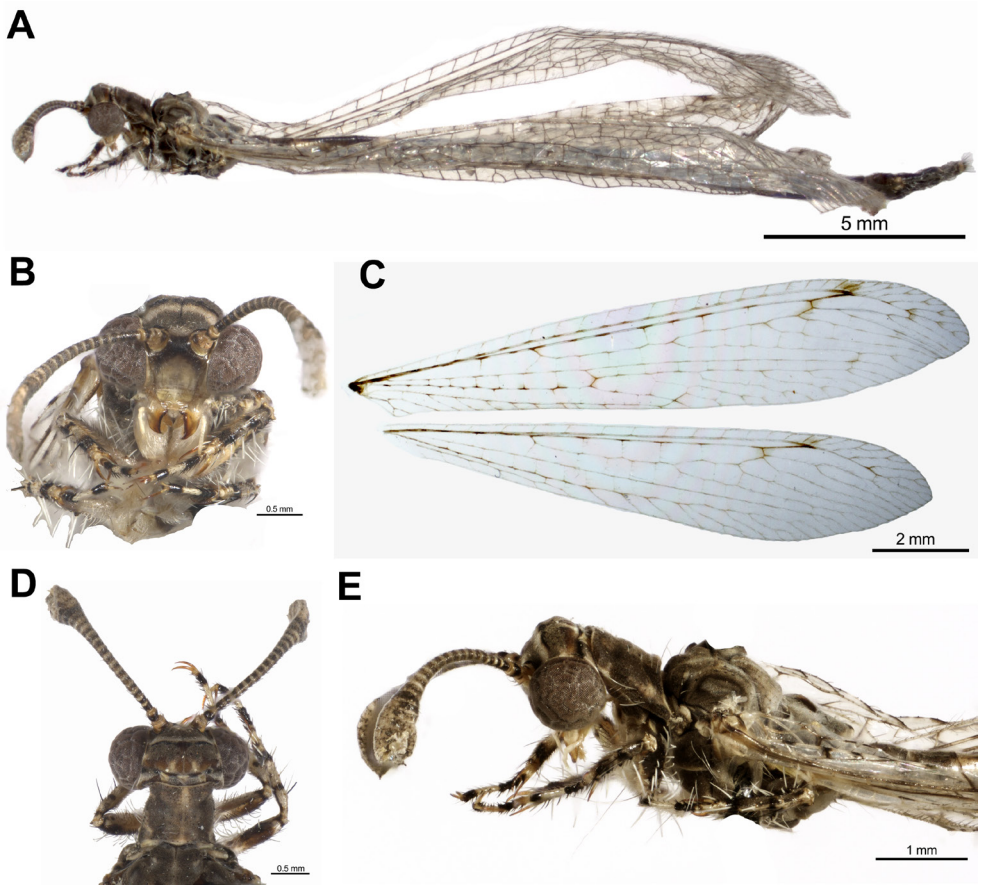

Figure 6 *Gnopholeon zapotecus* Stange, 1970, male specimen. A) habitus, lateral view. B) head and legs, frontal view. C) fore and hind wings. D) head and prothorax, dorsal view. E) head, thorax and legs, lateral view.

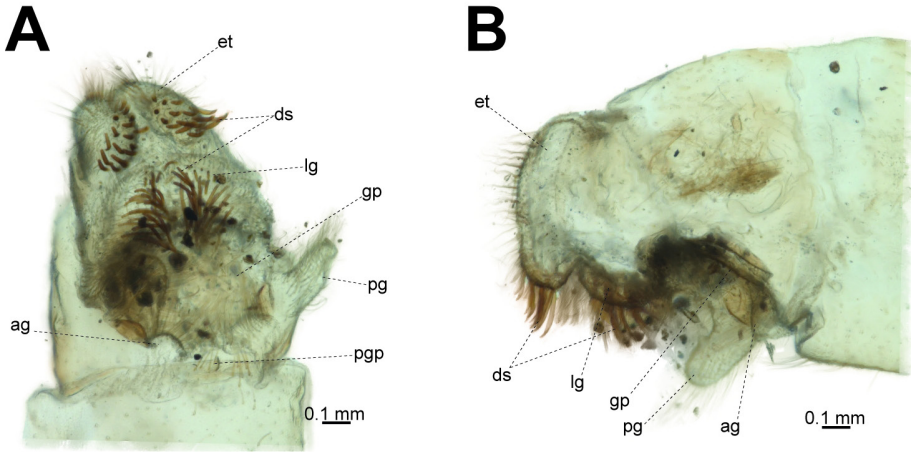

Figure 7 *Gnopholeon zapotecus* Stange, 1970, female terminalia. A) ventral view. B) lateral view. — Abbreviations: ag: anterior gonapophysis; ds: digging setae; et: ectoproct; gp: gonapophyseal plate; lg: lateral gonapophysis; pg: posterior gonapophysis; pgp: pregenital plate.

= *Scotoleon barberi* (Currie, 1903). – Banks, 1913: 65 [new combination].

= *Austroleon barberi* (Currie, 1903). – Banks, 1927: 55 [new combination, redescription, taxonomy, distribution, illustration]. – Banks, 1942: 143 [redescription, taxonomy, distribution, illustration].

= *Gnopholeon barberi* (Currie, 1903). – Stange, 1970: 149, 150, 173, 192 [new combination, redescription, taxonomy, distribution, illustrations, key]. – Penny, 1977: 45 [distribution]. – Miller, 1990: 173 [larva photograph]. – Stange, 1994: 90, 117 [species list, larvae photograph]. – Penny et al., 1997: 85 [taxonomy, distribution]. – Flint Júnior, 2002: 96 [type]. – Oswald et al., 2002: 581 [distribution]. – Stange, 2004: 250 [taxonomy, types, distribution].

Distribution. USA (AZ, CA), Mexico (BC, **BCS**, SIN).

Diagnosis. Adults. General coloration dark; ocular rim with short setae projecting over the eye; labial palpi with distal palpomere greatly swollen; procoxae and profemur with many clavate, clustered white setae; male ectoproct with a very short, almost unnoticeable postventral lobe; gonarcus narrow, slightly twisted on lateral margins; paramere plates sclerotized ventrally; paramere teeth basally not expanded; paramere

teeth slender, elongated, slightly curved and pointing posterodorsally; female ectoproct with short digging setae; lateral gonapophysis small, with short digging setae; posterior gonapophysis greatly swollen, with many long hairlike setae; anterior gonapophysis plate-like, with many long hairlike setae; pregenital plate membranous.

Remarks. At first look, *G. barberi* resembles a dark species of *Chaetoleon*, however it may be readily diagnosed by its large and well-developed tarsal claws and tibial spurs, as well as a swollen distal labial palpomere. It may be further identified by the large number of clustered clavate setae on the profemur, a unique trait among all Brachynemurini. This species was already recorded from Baja California (Stange, 1970), yet this is the first record of the species for Baja California Sur.

Material examined. (27♂, 17♀) Mexico – Baja California: Ensenada, Humedal, 500 m SE Hotel Misión Cataviñá, Carr[etera] 1, 521 m; 29º43.494'N, 114º43.016'W; 04.vii.2022; 1♂; trampa de luz UV, vapor de mercurio, aditivos metálicos; A. Contreras, A. Gómez, Y. Marquez, A. Ramírez, M. Ramírez; CNIN NEU:MYR:4093 • Ensenada, Hotel Misión Cataviñá, Carr[etera] 1, palapas, 558 m; 29º43.626'N, 114º43.194'W; 03.vii.2022; 1 ♀; trampa de luz UV, vapor de mercurio, aditivos metálicos; A. Contreras, A. Gómez, Y. Marquez, A. Ramírez, M. Ramírez; CNIN NEU:MYR:4097 • Baja California Sur: Loreto, Misión San Fco. Javier de Viggé-Biaundó, Arroyo San Javier (pozas), 393 m; 25°51.347'N, 111°33.005'W; 07.vii.2022; 1♂, 3♀; trampa de luz UV, vapor de mercurio, aditivos metálicos; A. Contreras, A. Gómez, Y. Marquez, A. Ramírez, M. Ramírez; CNIN NEU:MYR:4092 • same as preceding, 3♀; CNIN NEU:MYR:4099 • same as preceding, 12♂, 3♀; CNIN NEU:MYR:4100 • Los Cabos, Sierra de La Laguna, Rancho Ecológico Sol de Mayo, Cañon de la Zorra, pozas sur de la cascada, 232 m; 23º29.829'N, 109º47.592'W; 12.vii.2022; 2♀; trampa de luz UV, vapor de mercurio, aditivos metálicos; A. Contreras, A. Gómez, Y. Marquez, A. Ramírez, M. Ramírez; CNIN NEU:MYR:4094 • same as preceding, 10♂, 2♀; CNIN NEU:MYR:4095 • same as preceding, 3♂, 1♀; CNIN NEU:MYR:4096 • same as preceding, 1♀; CNIN NEU:MYR:4098 • Golfo de California, Isla San José, Punta NW; 17.viii.1986; 1 ♀; F. Arias; CNIN.

Gnopholeon delicatulus (Currie, 1903)

Figs. 1B, 4–5

Brachynemurus delicatulus Currie, 1903: 279 [Holotype male, Phoenix (USNM)]. – Banks, 1907: 31 [species list]. – Banks, 1913: 65 [species list].

= *Scotoleon delicatulus* (Currie, 1903). – Banks, 1913: 65 [new combination].

= *Clathroneuria delicatulus* (Currie, 1903). – Banks, 1927: 52 [new combination, redescription, taxonomy, distribution]. – Banks, 1938: 419, 421 [redescription, distribution, illustrations].

= *Gnopholeon delicatulus* (Currie, 1903). – Stange, 1970: 38, 50, 111, 112, 149, 151, 156, 173, 192 [new combination, redescription, taxonomy, distribution, illustrations, key]. – Penny et al., 1997: 85 [taxonomy, distribution]. – Flint Júnior, 2002: 96 [type]. – Winterton et al., 2018: 8 [phylogeny]. – Machado et al., 2019: 7 [phylogeny].

Distribution. USA (AZ, CA, NV, TX), Mexico (BC).

Diagnosis. Adults. General coloration pale and reddish brown; ocular rim setae absent; labial palpi distal palpomere swollen; legs without clavate setae; female ectoproct without digging setae; lateral gonapophysis digging setae long and slender; posterior gonapophysis swollen, with many hairlike setae; anterior gonapophysis unnoticeable, pregenital plate reduced.

Remarks. This species was reported from Baja California in Oswald et al. (2002), but the specific locality is unclear. This species clearly stands out when compared to the other two *Gnopholeon* species. Superficially, *G. delicatulus* resembles a *Tyttholeon* species because its pale coloration and reduction of body setae, but the large pretarsal claws, tibial spurs, and tarsomere size and proportion are all diagnostic to *Gnopholeon*. Stange (1970) describes the male genitalia of *G. delicatulus* as about the same as *G. zapotecus*. No male specimens were analyzed during this work, and thus the detailed morphology of the male genitalia of *G. delicatulus* remains unknown in the literature.

Material examined. (1♀) United States – Arizona: Tucson; 28.vi.1968; 1♀; F. D. Parker, L. A. Stange; CNIN NEU:MYR:2636.

Gnopholeon zapotecus Stange, 1970

Figs. 6–7

Gnopholeon zapotecus Stange, 1970: 150 [Holotype male, 23 miles South Matías Romero, Oaxaca, Mexico (UCDC)]. – Penny, 1977: 45 [distribution]. – Oswald et al., 2002: 581 [distribution]. – Stange, 2004: 250 [taxonomy, types, distribution].

Distribution. Mexico (MOR, OAX, **VC**).

Diagnosis. Adults. General coloration dark; ocular rim with short setae projecting over the eye; labial palpi with distal palpomere greatly swollen; procoxae and profemur with clavate white setae, slightly rowed; male ectoproct with a very short postventral lobe; gonarcus narrow, slightly twisted on lateral margins; paramere plates sclerotized ventrally; paramere teeth basally not expanded, slender, elongated, slightly curved and pointing posterodorsally; female ectoproct with large digging setae; lateral gonapophysis with large digging setae; posterior gonapophysis swollen, with many long hairlike setae; anterior gonapophysis short, convex, with many long hairlike setae; pregenital plate membranous.

Remarks. This species is very similar to *G. barberi*. A key difference is present in the profemur clavate setae density, which is noticeably lower, with setae not as clustered in *G. zapotecus*. Also, *G. zapotecus* is restricted to southern Mexico, while *G. barberi* occurs on northwestern Mexico and southwestern United States. This is the first record of the species from the state of Veracruz. Although this species does not occur in Baja California, we included it here for comparison with the other species of *Gnopholeon*.

Material examined. (1♂, 2♀) Mexico – Morelos: 2.5 km N y 4 km al W Huautla, Estación CEAMISH, 940 m; 18°27.671'N, 99º02.475'W; 10-15.v.1996; 1♀; trampa Malaise 4; S. Zaragoza, F. Noguera, E. González, E. Ramírez; CNIN NEU:MYR:2535 • same as preceding, 09-14.v.1996; 1♂; CNIN NEU:MYR:2447 • Veracruz: Zapotal de Zaragoza, 10 km Sur de Tuxpan; 17.v.2012; 1 ♀; H. Brailovsky, E. Barrera; CNIN NEU:MYR:2635.

Menkeleon Stange, 1970

Figs. 1C, 8–9

Menkeleon Stange, 1970: 154 [Type species: *Maracandula bellula* Banks, by original designation and monotypy]. – Penny, 1977: 45 [distribution]. – Penny et al., 1997: 85 [taxonomy, distribution]. – Stange, 1994: 92, 112, 117 [larvae description, illustrations, larvae photograph]. – Oswald et al., 2002 [distribution]. – Stange, 2004: 251 [taxonomy, types, distribution] – Machado et al., 2019: 441 [list of genera].

Distribution. MX, US.

Included species. *M. bellulus* (Banks, 1905).

Larvae known. *M. bellulus*.

Diagnosis. Adults. Antenna with 20-29 flagellomeres, flagellomere 1 longer than wide; vertex well developed and dorsally projected; frons without setae; ocular rim with white setae that projects over eye; greatest ocular width about half of interocular distance; labial palpi with distal palpomere not swollen; pronotum longer than wide; legs short, profemur about 1.5 times longer than procoxa, not swollen; hindleg longer than foreleg which is almost the same size as midleg; profemur without clavate setae; procoxae and all femora with elongated white bristles; two femoral sense hairs on pro and meso femur; profemoral sense hairs shorter than profemur length, and

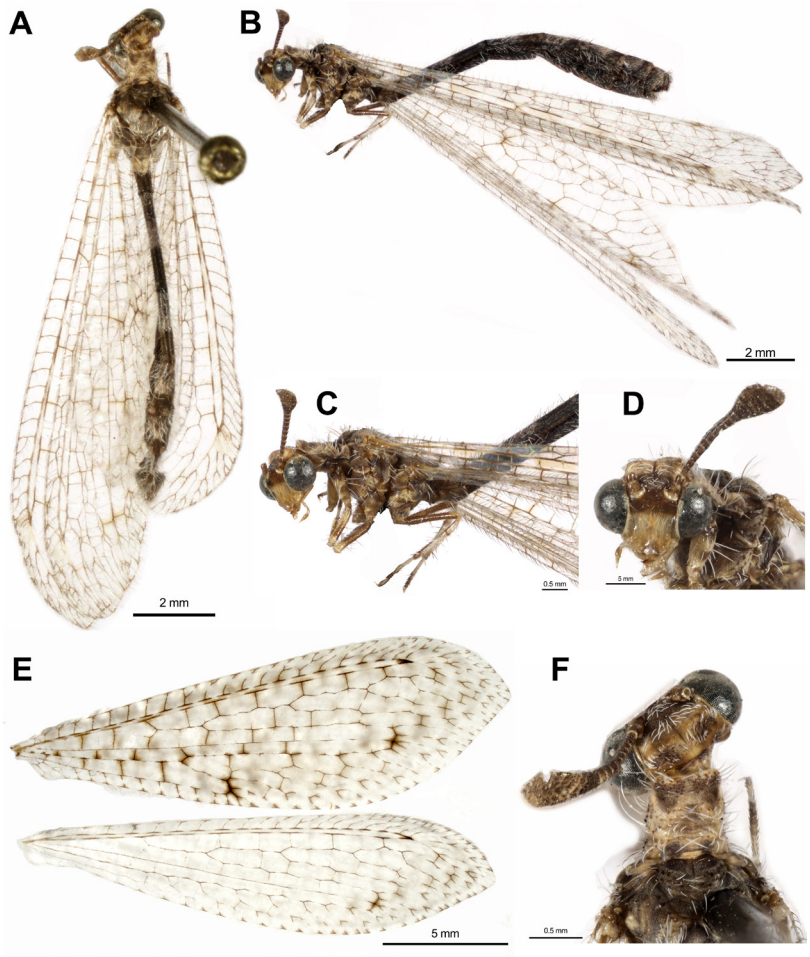

Figure 8 *Menkeleon bellulus* (Banks, 1905), female specimen. A) habitus, dorsal view. B) habitus, lateral view. C) head, thorax and legs, lateral view. D) head, frontal view. E) fore and hind wings. F) head and thorax, dorsal view.

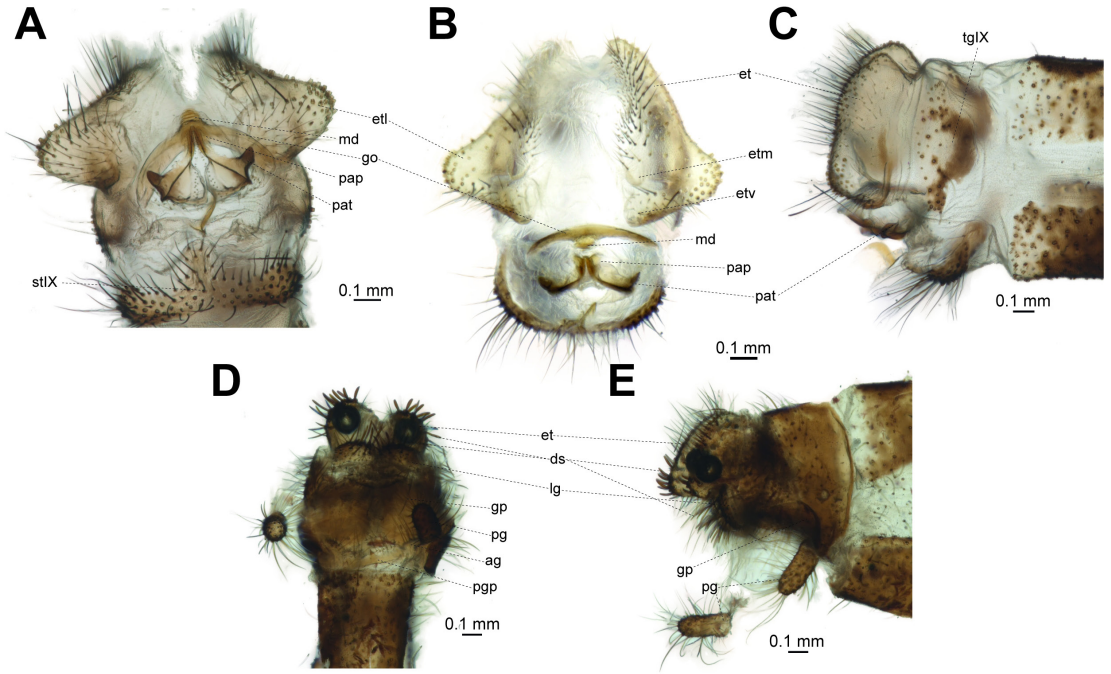

Figure 9 *Menkeleon bellulus* (Banks, 1905), male and female terminalia. A) male terminalia, ventral view. B) male terminalia, posterior view. C) male terminalia, lateral view. D) female terminalia, ventral view. E) female terminalia, lateral view. — Abbreviations: ag: anterior gonapophysis; ds: digging setae; et: ectoproct; etl: ectoproct postventral lobe; etm: ectoproct median process; etv: ectoproct ventral process; go: gonarcus; gp: gonapophyseal plate; lg: lateral gonapophysis; md: mediuncus; pap: paramere plates; pat: paramere tooth; pg: posterior gonapophysis; pgp: pregenital plate; stlX: sternite IX; tglX: tergite IX.

mesofemoral sense hairs approximately the same size as profemoral sense hair; tibial spurs absent; pretarsal claws short, much shorter than distal tarsomere; basitarsi elongated, hindleg basitarsus very long, longer than distal tarsomere; wings relatively broad with dense venation; wing veins with many long erect white and/or dark bristles; hypostigmatic cell without crossveins; banksian lines absent; hind wing posterior area narrow, with cells delimited by crossveins that are longer than wide; CuA bends to hind margin before MP fork; pilula axillaris small, with setae concentrated toward distal margin of knob; abdomen shorter than wings in rest; male ectoproct with a very short postventral lobe; male ectoproct internal face with a small median projection, which is basal to a strong convex fold; male genitalia with an arched gonarcus dorsal to the parameres; mediuncus present, narrow, projecting posterodorsally and curved and more sclerotized apically, with transversal grooves; parameres free, hinged; paramere plates dorsoventrally short, and broadening anteriorly; female ectoproct with digging setae; female posterior gonapophysis cylindrical, slightly swollen; lateral gonapophysis not fused; pregenital plate narrow with a median tooth, gonapophyseal plate large.

Larvae. In Stange (1994).

Remarks. A monotypic genus, *Menkeleon* is somewhat similar to all other genera previously included in the Gnopholeontini (Stange, 1970, 1994). The male genitalia with an anterior broadening of the parameres, broad wings and the body with many white bristles relate it to *Maracandula*, but the male ectoprocts are quite similar to *Tyttholeon*, while the female genitalia resemble *Gnopholeon*. Nonetheless, the double femoral sense hairs and the bristled wing veins are seemingly diagnostic traits for *Menkeleon*.

Menkeleon bellulus (Banks, 1905)

Figs. 1C, 8–9

Maracandula bellula Banks, 1905: 7 [Lectotype female, Three Rivers, California (MCZ), designated by Stange, 1970: 155]. – Baker, 1905: 90 [distribution]. – Banks, 1907: 32 [species list]. – Banks 1927: 59 [redescription, taxonomy, distribution]. – Markl, 1954: 224 [illustration of wings]. – Adams, 1956: 93 [genitalia illustration].

= *Maracandula minima* Banks, 1942: 140 [Holotype male, San Miguel, Lower California, 03.vii.1938, M & R (CAS)]. – Banks, 1942 [illustrations]. – Stange, 1970: 155 [synonymy].

= *Menkeleon bellulus* (Banks, 1905). – Stange, 1970: 155 [new combination, redescription, taxonomy, distribution]. – Penny, 1977: 45 [distribution]. – Penny et al., 1997: 85 [taxonomy, distribution]. – Stange, 1994: 92, 112, 117 [larvae description, illustration, larvae photograph]. – Stange, 2004: 251 [taxonomy, types, distribution]. – Badano et al., 2018: 936, 937 [phylogeny].

Distribution. US (AZ, CA, NM, TX, UT), Mexico (BC, CHIH, SON).

Diagnosis. Adults. Abdomen banded with pale and dark brown; wings in rest in a moth-like position; male gonarcus broad, not twisted laterally; paramere plates sclerotized ventrally; paramere teeth basally expanded, broad, slightly curved and pointing posterodorsally; female lateral gonapophysis with long digging setae; posterior gonapophysis cylindrical, with hairlike setae.

Remarks. This species was first recorded from Mexico (and Baja California) by Stange (1970). The general pale and dark coloration with a banded abdomen and setose body are very characteristic for this species. Additionally, when perched, *M. bellulus* individulas rest their wings in a characteristic moth-like position (Fig. 1C), a behavior also seen in *Chaetoleon tripunctatus* (Banks, 1922), *C. variabilis* Banks, 1942 and in a few Brachynemurini formerly included in the Lemolemini.

Material examined. (1♂, 2♀) México – Baja California: Ensenada, Rancho Mike's Sky, Hotel, 1205 m; 31°06.569'N, 115º38.199'W; 01.vii.2022; 1 ♀; colecta manual; A. Contreras, A. Gómez, Y. Marquez, A. Ramírez, M. Ramírez; CNIN NEU:MYR:4008 • Sierra Juarez, 1.1 km N Rancho El Piedra, ca. 15 km S Parque Nacional Constitución de 1857, 1512 m; 31°53.832'N, 115º57.936'W; 29.vi.2022; 1♂; trampa de luz UV, vapor de mercurio, aditivos metálicos; A. Contreras, A. Gómez, Y. Marquez, A. Ramírez, M. Ramírez; CNIN NEU:MYR:4091. Sonora: La Aduana; 22.v.1062; 1 ♀; F. D. Parker, L. A. Stange; CNIN NEU:MYR:2637.

Tyttholeon Adams, 1956

Figs. 1D, 10–13

Tyttholeon Adams, 1956: 106 [Type species: *Tyttholeon puerilis* Adams, 1956, by original designation and monotypy]. – Stange, 1970: 50, 157, 180, 183 [redescription, taxonomy, distribution, illustrations]. – Stange and Miller 1990: 159 [larva head photo]. – Stange, 1994: 92 [taxonomy, description, phylogeny]. – Penny et al., 1997: 86 [taxonomy, distribution]. – Stange, 2004: 251 [taxonomy, type, distribution]. – Machado et al., 2019: 441 [list of genera].

Distribution. Southwestern USA, Northwestern MX.

Included species. *Tyttholeon puerilis* Adams, 1956; *Tyttholeon froehlichi* **n. sp.**

Larvae known. *T. puerilis*.

Diagnosis. Adults. Diminutive size, 10-15 mm in both sexes; antenna with 20-25 flagellomeres, flagellomere 1 longer than wide; vertex well developed and dorsally projected; frons without setae; ocular rim setae absent; greatest ocular width about half interocular distance; labial palpi with distal palpomere slightly swollen; pronotum as wide as long; legs short, profemur about 1.5 times longer than procoxa, not swollen; hindleg longer than foreleg, which is almost the same size as midleg; profemur without clavate setae; profemur without elongated white bristles; profemural sense hair shorter than half profemur length, and mesofemoral sense hair equal or shorter than profemoral sense hair; tibial spurs absent; pretarsal claw short, shorter than hind basitarsus, which is either longer or shorter than distal tarsomere; narrow wings; hypostigmatic cell without crossveins; banksian lines absent; hind wing posterior area narrow, with cells delimited by crossveins that are longer than wide; CuA bends to hind margin before MP fork; pilula axillaris small, moderately well developed with setae concentrated toward distal margin of knob; abdomen shorter than wings in rest; male ectoproct with postventral lobe absent, if present very short; male genitalia in unfolded position when in rest; male genitalia with an arched gonarcus dorsal to the parameres; mediuncus present, narrow, projecting dorsoposteriorly and curved and more sclerotized apically, with transversal grooves; parameres free, hinged; paramere plates dorsoventrally short; paramere teeth bilobed; male ectoproct with a ventral process, with or without a postventral lobe (if present very short); female posterior gonapophysis subcylindrical, lateral gonapophysis not fused; gonapophyseal plate large; pregenital plate greatly enlarged with a prominent median process posteriorly.

Larvae. In Stange (1994).

Etymology. *Tyttho* is greek to "small, young", an allusion to the diminutive size of the *Tyttholeon* specimens.

Remarks. Previously monotypic, *Tyttholeon* was originally described by Adams (1956) as a genus related to *Maracandula*, but with simpler and different wing venation, fewer setae, and simpler male genitalia. Stange (1970) redescribed *Tyttholeon* to include terminalia characters, such as a highly modified female pregenital plate and a male ectoproct "produced mesally below". The same characters were mentioned later as being autapomorphic to the genus, adding the ectoproct as not bearing postventral lobes (Stange, 1994). Herein, we update *Tyttholeon* diagnosis, as the male of the new species does bear ventral processes on ectoprocts, as well as a very short postventral lobe. The mesofemoral sense hair size is also updated to reflect the new species.

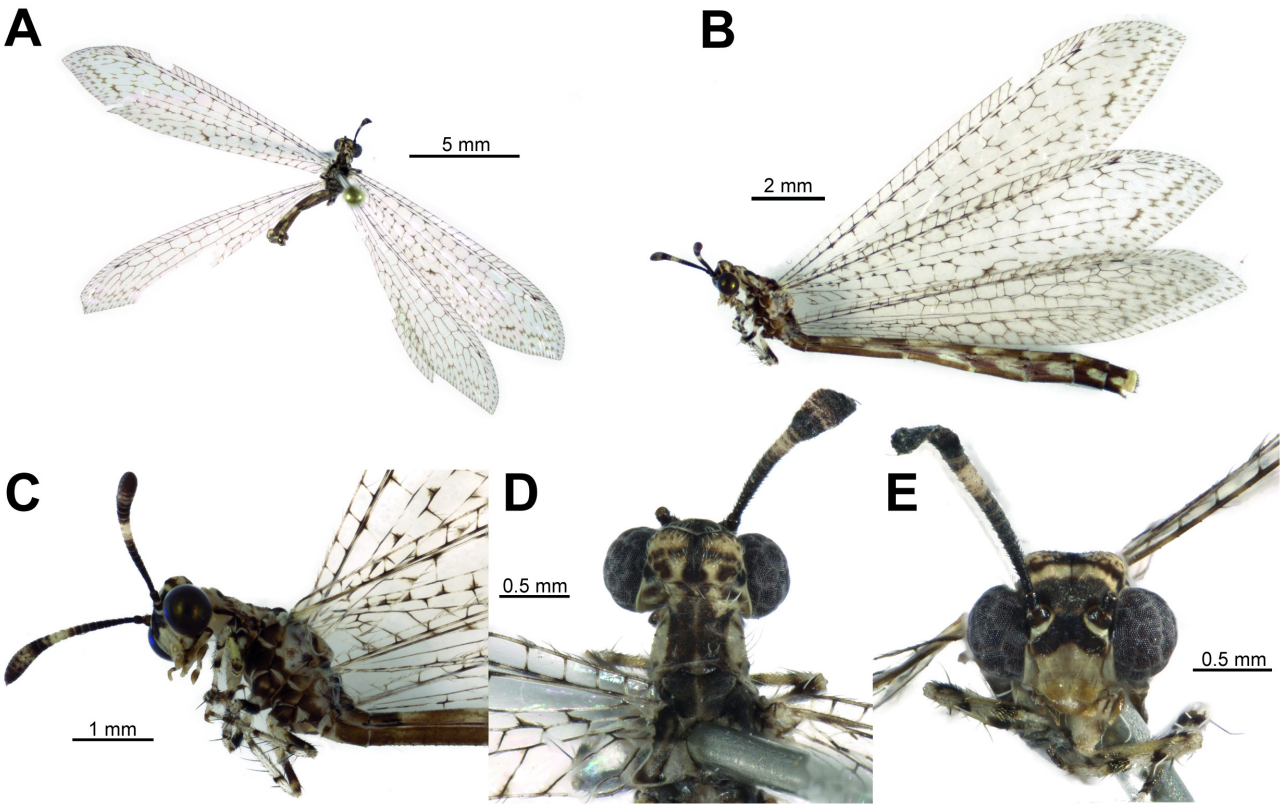

Figure 10 *Tyttholeon froehlichi* **sp. nov.**, holotype. A) habitus, dorsal view. B) habitus, lateral view. C) head, thorax and legs, lateral view. D) head and thorax, dorsal view. E) head and forelegs, frontal view.

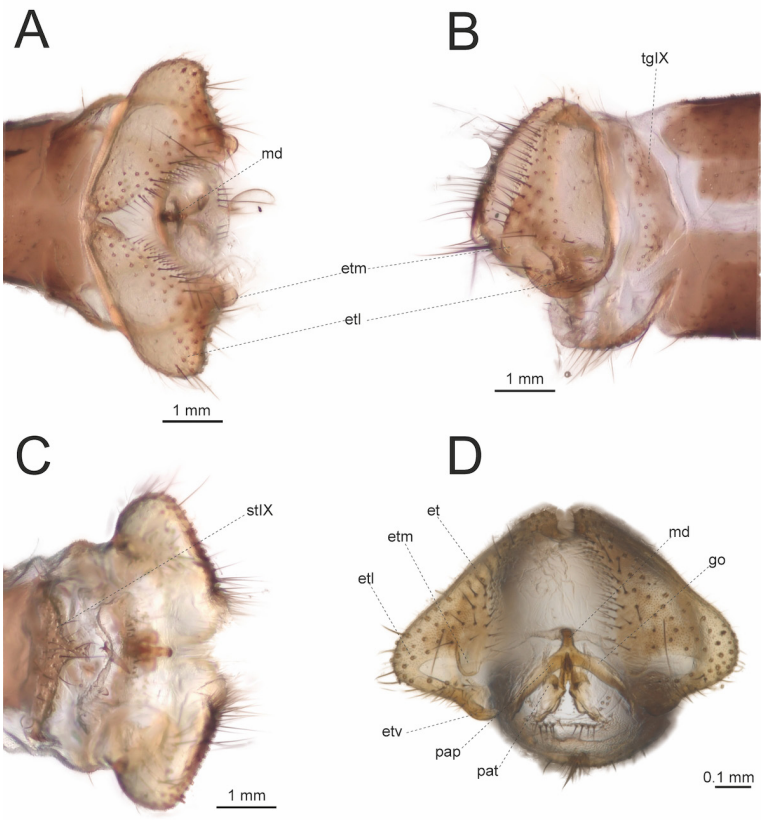

Figure 11 *Tyttholeon froehlichi* **sp. nov.**, holotype male terminalia. A) dorsal view. B) lateral view. C) ventral view. D) posterior view, gonarcus complex in ventral view. — Abbreviations: et: ectoproct; etl: ectoproct postventral lobe; etm: ectoproct median process; etv: ectoproct ventral process; go: gonarcus; md: mediuncus; pap: paramere plates; pat: paramere tooth; stIX: sternite IX; tgIX: tergite IX.

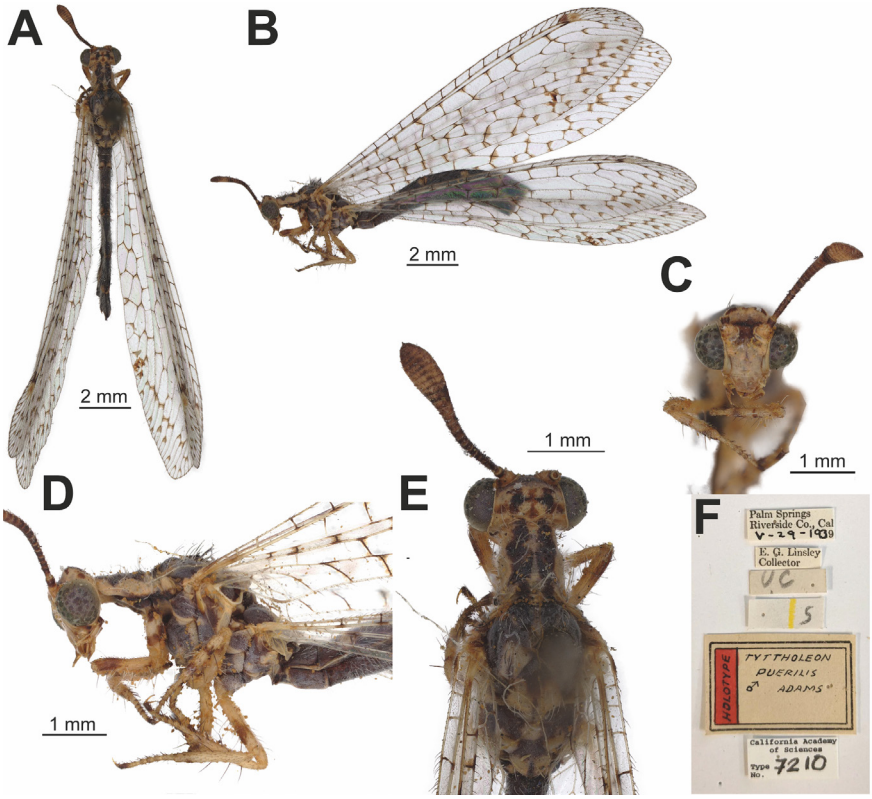

Figure 12 *Tyttholeon puerilis* Adams, 1956, holotype. A) habitus, dorsal view. B) habitus, lateral view. C) head and forelegs, frontal view. D) head, thorax and legs, lateral view. E) head and thorax, dorsal view. F) type labels. Photographs by Rachel Diaz-Bastin (CAS).

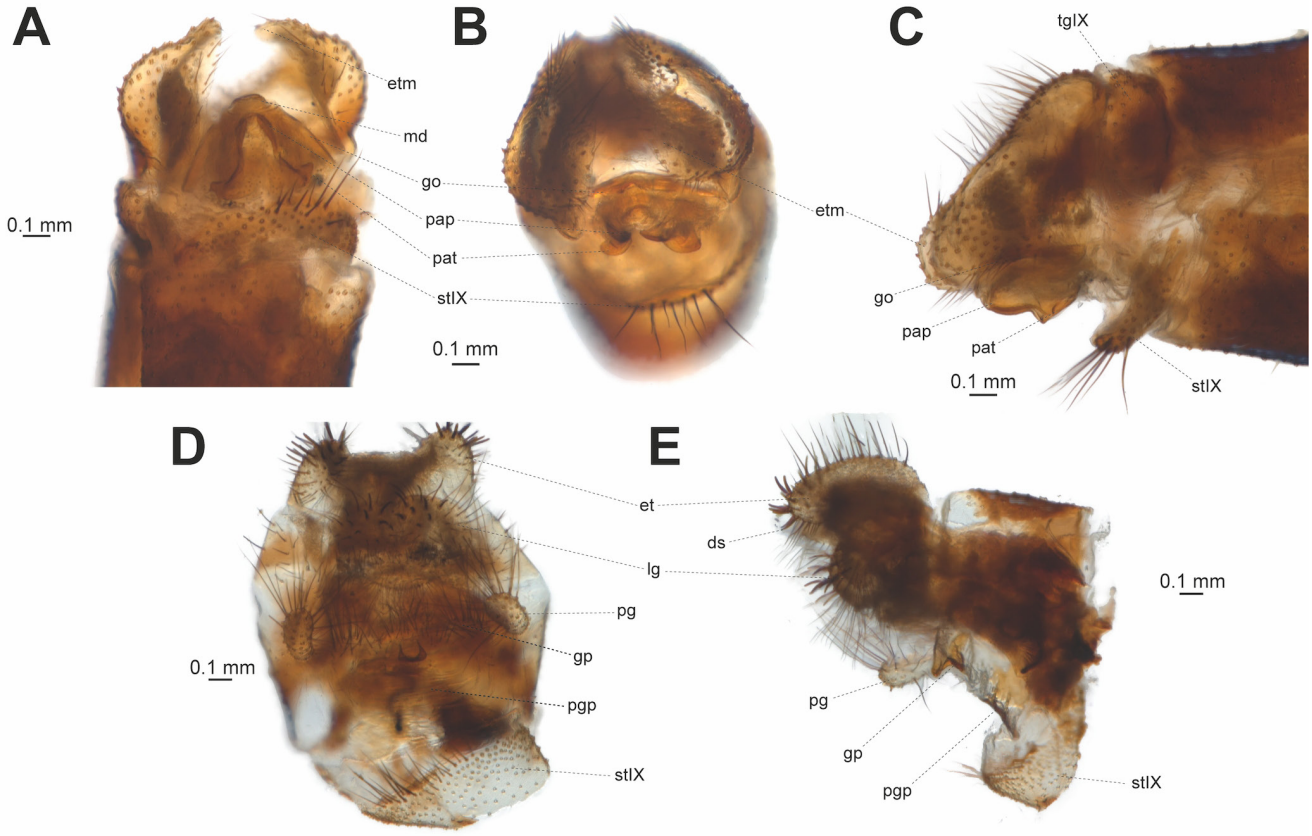

Figure 13 *Tyttholeon puerilis* Adams, 1956, male and female terminalia. A) male terminalia, ventral view, B) posterior view and C) lateral view. D) female terminalia, ventral view and E) lateral view. — Abbreviations: ds: digging setae; et: ectoproct; etm: ectoproct median process; go: gonarcus; gp: gonapophyseal plate; lg: lateral gonapophysis; md: mediuncus; pap: paramere plates; pat: paramere tooth; pg: posterior gonapophysis; pgp: pregenital plate; stIX: sternite IX; tgIX: tergite IX.

Martins Neto and Vulcano (1989) illustrated the forewing of *T. puerilis* together with the description of several fossil species of Neuroptera and stated that the wing venation of the antlion species from the Crato formation were most similar to *Tyttholeon*, but did not explain why. This similarity was presumably due to the reduced venation of *Tyttholeon*, and the fewer RP veins in the fossil species, although the less dense wing venation of *T. puerilis* might be correlated to its diminutive size.

Key to species of *Tyttholeon* Adams

urn:lsid:zoobank.org:pub:5978D8C0-E25F-452A-A526-C37F5EDC1D2B

1 Clypeolabrum height less than half eye width; hindleg basitarsus longer than distal tarsomere; male ectoproct with a postventral lobe in addition to the median process (Figs. 10–11) … ***Tyttholeon froehlichi*, sp. n.**

1' Clypeolabrum height more than half eye width; hindleg basitarsus shorter than distal tarsomere; male ectoproct with a median process and no postventral lobe (Figs. 12–13) …… ***Tyttholeon puerilis* Adams, 1956**

***Tyttholeon froehlichi* Tavares, Marquez, and Contreras, new species**

Figs. 10–11

Diagnosis. Clypeolabrum height less than half the eye width; wings narrow; hindleg basitarsus longer than distal tarsomere; male ectoproct with very short postventral lobes; gonarcus slightly twisted on lateral margins; paramere teeth basally not expanded; paramere teeth broad, short, oblong, straight and pointing posterodorsally, very proximad to paramere plates.

Description. Adult. Head: Antennae clubbed with 22 flagellomeres. Scape and pedicel dark brown. Flagellum dark brown, except for flagellomeres IX-XI and XV-XVI which are pale brown. Vertex well raised, pale, with a longitudinal dark brown band, dark brown transversal lines on anterior and middle rows, and four dark brown spots on posterior row, with two small grey spots between each dark brown spot on each side of posterior row. Vertex with a few scattered dark decumbent setae, and white decumbent setae mostly laterally and anteriorly of anterior row. Epicranial mark dark brown, with white decumbent setae. Interantennal mark dark brown, with a tenuous pale brown area between epicranial mark. Frons dark brown on posterior half, with a sinuous, emarginate margin between the anterior half, which is pale brown. Frons with very few scattered and short dark decumbent setae, and a long erect dark seta near each clypeal lateral margins. Clypeus pale brown, slightly darker than frons. Labrum brown, with a row of long brown setae on anterior margin. Clypeolabrum height less than half eye height. Mandible dark brown. Labial palpi brown, distal palpomere slightly enlarged and dark brown.

Thorax: Thorax dark and pale brown. Pronotum as broad as long at middle diameter, pale brown, with two large longitudinal dark brown bands at middle, two large longitudinal, slightly concave dark brown bands submedially, and two small, slightly convex dark brown lines at lateral margins near furrow. Pronotum with a few scattered white bristles dorsally, many white and dark anteriorly oriented setae on anterior and lateral margins, and two or three anteriorly oriented outstanding white bristles on lateral margins. Mesothoracic prescutum dark brown with a thin longitudinal pale line at the middle, not raised, bean-shaped, with two posteriorly oriented small white bristles laterally on each side. Mesoscutum laterally dark brown, with two triangular-shaped pale brown marks at middle, and one oblique pale brown line submedially on each side. Mesoscutellum pale brown, with a triangular dark brown patch on anterior margin and a longitudinal dark brown band medially, forming an "arrow-shaped" pattern. Metathoracic prescutum inconspicuous, pale brown, dark brown laterally. Metascutum dark brown, pale brown medially. Metascutellum pale brown, with dark brown margins. Meso and metathorax laterally dark brown, with pale maculation around sutures.

Wings: Wings lanceolate. Venation relatively simple. Fore and hind wing veins with dashed dark brown and pale brown pattern. Wing veins and crossveins with many spaced, dark and short setae. Wing membrane mostly hyaline, with dark brown infuscation around crossveins intersections on forewing veins RA, RP, CuA, on rhegmal area, at wing posterior margin and gradates. Costal area with simple crossveins anterior to pterostigma. Pterostigma inconspicuous, with a small dark brown patch encompassing two crossveins at the end of subcostal area on forewing and encompassing a single crossvein on hind wing. Base of male forewing with posterior vein darkened and slightly swollen.

Legs: Coxae dark brown, except for procoxae which is pale, with a small dark patch at the base, and a transversal dark brown band medially on external face. Coxae with few white bristles ventrally oriented, and forecoxae with one or two outstanding white bristles. Femora dark brown on exterior face, and pale on interior face, except for hind femur which is pale basally. Femora with many dark decumbent setae, a few white bristles apically and subapically on exterior face, and a few white bristles along interior face. Profemural sense hair very short, much less than half of profemur length, and mesofemoral sense hair shorter than that of profemur. Tibiae pale, with sub basal and subapical dark brown bands. Tibiae with many dark decumbent setae, a row of outstanding dark bristles on exterior face, and a pair of dark setae on tibial spurs placement. Pro and mesotibiae with many white bristles. Basitarsus pale, tarsomere II and distal tarsomeres basally pale and apically dark brown, and tarsomeres III and IV dark brown. Basitarsus of fore and mid legs subequal in size to distal tarsomere. Basitarsus of hindleg longer than distal tarsomere, more than three times its middle diameter. Tarsal claws short, roughly half the size of distal tarsomere. Tarsomeres with many decumbent short dark setae.

Abdomen: Abdomen banded, pale and dark brown. Tergites I, II and VIII dark brown, tergite III dark brown with a pale brown band medially, remaining tergites basally pale and distally dark brown, pale areas frequently with a thin, longitudinal brown line medially. Abdomen chaetotaxy. Tergites with many short setae, dark on dark half, and white on pale half, which are longer near terminalia. Sternites dark brown, pale brown on posterior margin. Sternites with many short white setae, and a few scattered dark setae. Male tergite IX very narrow, pale with some dark brown patches, with mostly white setae and few dark setae. Male sternite IX triangular on ventral view, with a narrow posterior projection medially, with many posteriorly oriented dark setae. Male ectoproct pale, with many long, posteriorly oriented dark and white setae on posterior face. Male ectoproct subtriangular on posterior view, with a very short postventral lobe. Male ectoproct internal face with a small ventral projection, which is basad to a strong convex fold. gonarcus narrow, slightly twisted on lateral margins; mediuncus elongated, very narrow, paramere plates sclerotized ventrally; paramere teeth basally not expanded; paramere teeth broad, short, oblong, straight and pointing posterodorsally, proximal to paramere plates.

Larva. Unknown.

Holotype. Male (CNIN), CNIN:NEU:MYR:4090, Mexico: Baja California Sur, Los Cabos, Sierra de la Laguna, Rancho Ecológico Sol de Mayo, Cañón de la Zorra, pozas sur de la cascada; 23°29.829' N, 109°47.592' W, 232 m; 12.vii.2022, trampa de luz UV, vapor de mercurio, aditivos metálicos; A. Contreras, A. Gómez, Y. Marquez, A. Ramírez, M. Ramírez.

Etymology. This species is named after Prof. Dr. Claudio Gilberto Froehlich, as an homage to his many contributions to South American entomology, particularly on aquatic insects.

Distribution. Mexico (BCS).

Remarks. The sampling site for this new species is located within the Biosphere Reserve of Sierra de la Laguna, which is an important mountain range that divides the dry tropical and desert environments of the Peninsula in the southern part (González-Abraham et al., 2010). *Tyttholeon froehlichi* **n. sp.** is the second species described in the previously monotypic genus *Tyttholeon*. It is very similar to its congener *T. puerilis*. Notable differences are in the wing venation, which is denser than in *T. puerilis*, although not as dense as in other Brachynemurini; the hindleg basitarsus which is longer than the distal tarsomere, the clypeolabral height which is evidently shorter than in *T. puerilis*, the presence of a postventral lobe on the male ectoproct, and the male genitalia in which the mediuncus is narrower and the paramere teeth are more posteriorly oriented.

Stange (1994) mentioned an undescribed species from southern Baja California, but it is unclear whether it is the same species described here, or if it is another *Tyttholeon* species altogether. The metathoracic leg basitarsus size in his updated description for the genus fits that of our new species, but the absence of an ectoproct postventral lobe and the mesofemoral sense hair does not, which raises the possibility of a third, undescribed *Tyttholeon* species occurring in Baja California.

Tyttholeon puerilis Adams, 1956

Figs. 1D, 12–13

Tyttholeon puerilis Adams, 1956: 107 [Holotype male, Palm Springs, Riverside County, California, 27.vi.1939, E. Linsley Coll., Type Nº 7210 (CAS)]. – Stange, 1970: 50, 157, 180, 183 [redescription, taxonomy, distribution, illustrations]. – Martins Neto and Vulcano, 1989: 379 [forewing illustration]. – Stange and Miller 1990: 159 [larva head photograph]. – Stange, 1994: 111, 113, 114, 117 [illustrations, larva photograph]. – Penny et al., 1997: 86 [taxonomy, distribution]. – Oswald et al., 2002: 581 [distribution]. – Stange, 2004: 252 [taxonomy, type, distribution].

Distribution. Mexico (BC), USA (AZ, CA, NV).

Diagnosis. Clypeolabrum height more than half eye width; narrow wings with sparse wing venation; hind basitarsus shorter than distal tarsomere; male ectoproct without postventral lobes; paramere teeth broad, short, oblong, straight and pointing posterodorsally, very basad to paramere plates; lateral gonapophysis with short digging setae; posterior gonapophysis with long hairlike setae.

Larvae. In Stange (1994).

Remarks. This species was firstly registered from Baja California by Oswald et al. (2002). It can be readily differentiated from *T. froehlichi* **n. sp.** by the sparser wing venation, the male ectoproct without postventral lobes and the hindleg basitarsus shorter than the distal tarsomere. The type specimen is covered in pollen (Fig. 12), which is interesting as the gut content of this species was previously reported as containing solely aphids (Stange, 1970).

Material examined. (1♂, 1♀) United States – California: Lassen Co.,11 km N Doyle on Hackstaff Rd; 0º06'59.4"N, 120º07'20.1"W, 1266 m; 08-24.vii.2019; 1♂, 1♀; Malaise with *Artimesia tridentata* on sand; ME Irwin, GR Ballmer (CNIN).

Discussion

The species studied here have a Nearctic affinity, with records from the United States and Mexico. Three biogeographic provinces are recognized in the Baja California Peninsula, which are different in terms of floristic composition and relief (Fig. 14) (González-Abraham et al., 2010; Morrone, 2021). Most of the territory of the Peninsula corresponds to the Baja Californian province, which is made up of eight districts and

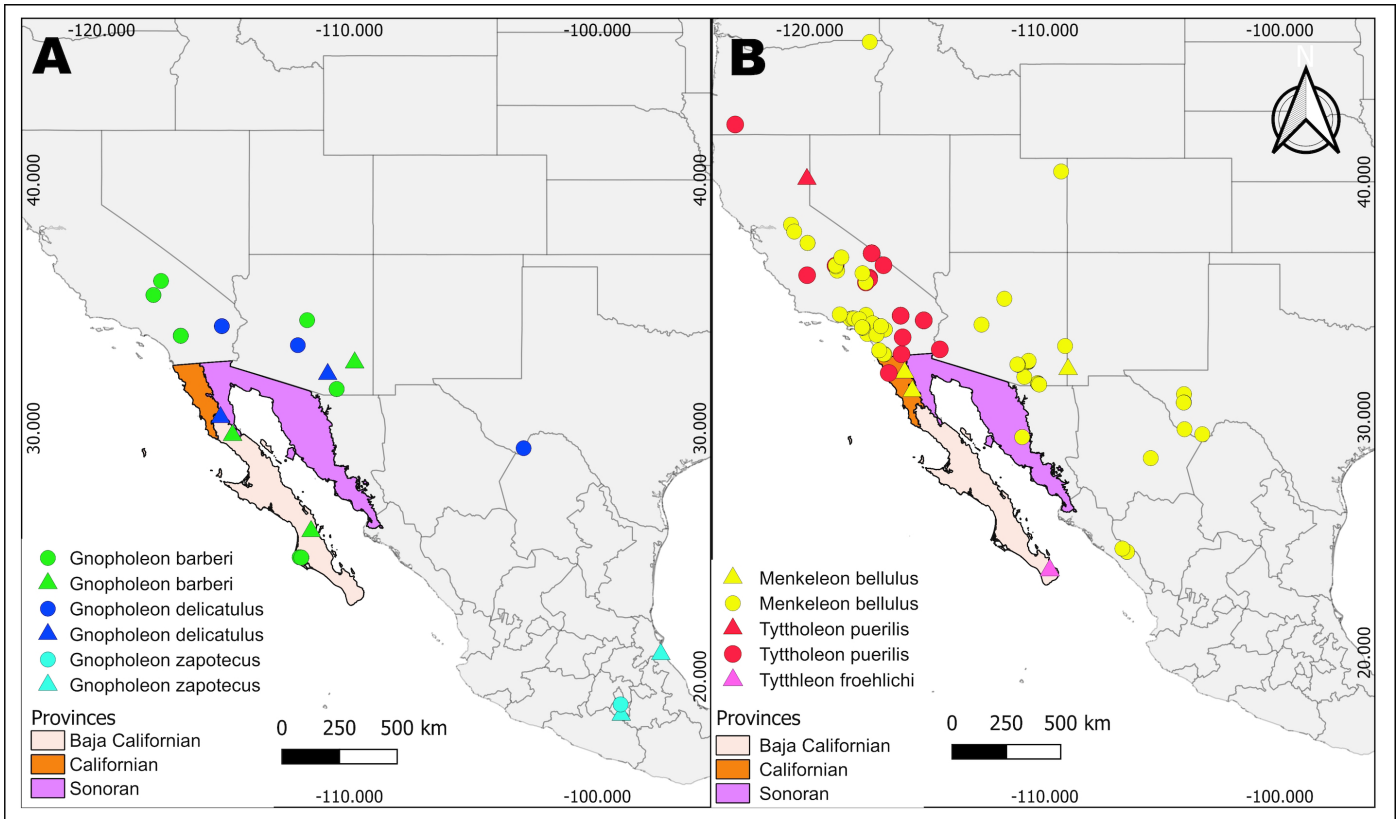

Figure 14 Known distribution of the species of the formerly recognized tribe Gnopholeontini with the three biogeographic provinces from the Baja California Peninsula highlighted. A) *Gnopholeon* Stange, 1970. B) *Menkeleon* Stange, 1970 and *Tyttholeon* Adams, 1956. Circles indicate records from GBIF database and triangles indicate original records.

where the species *Gnopholeon barberi*, *G. delicatulus* and *Tyttholeon froehlichi* **n. sp.** are distributed (Fig. 15A) (González-Abraham et al., 2010; Morrone, 2021).

Gnopholeon delicatulus is distributed only in the Central Desert District, where the physiography is dominated by sarcocaulescent plants, mainly *Fouquieria columnaris* (Fig 15A). For *G. barberi*, the most recorded species in this province, is distributed in the Central Desert, Sierra de la Giganta and Magdalena Plains districts (Fig. 15A). The Sierra de la Giganta District is characterized by the presence of mountainous areas located in the southern portion of the Baja California Peninsula, the physiography is governed by some leguminous tree species, with few cacti representatives and in the oasis zone by palms (Fig. 15B). The Magdalena Plains District is occupied by arboreal shrubs (e.g., *Prosopis glandulosa*) and giant columnar cacti (e.g., *Pachycereus pringlei*, *Stenocereus gummosus*).

Tyttholeon puerilis is recorded for the Baja California province and two of their four districts, which are the Sierra de Juárez and San Pedro Mártir and Coast Scrub. (Fig. 14, 15). The Sierra de Juárez and San Pedro Mártir are two mountain ranges that are connected with the mountains of southern California. Sierra de Juárez and San Pedro Mártir, together with Sierra de la Laguna, are the only two districts that have forest cover, with the former one dominated by *Pinus*, *Abies* and *Quercus* (González-Abraham et al., 2010).

Tyttholeon froehlichi **n. sp.** was collected in Sierra de la Laguna district, located at more than 1000 m of altitude, dominated by different types of forest, corresponding to a tropical area of the Baja California Peninsula (Fig. 15B) (González-Abraham et al., 2010). This is an important district because its high degree of endemism due to isolation caused by the mountains' height (González-Abraham et al., 2010).

The Californian Province is smaller compared to the Baja California Province and has four districts: Sierra de Juárez, Chaparral, Coastal Scrub, and Coastal Rosetophytic Scrub (Figs. 14, 15). So far, only two of them have records for *Menkeleon bellulus* (Fig. 14B). In the Chaparral District, which is characterized by dense shrub strata of no more than 3 m in height with coarse-textured soils, and the Coastal Scrub District, which has a less dense shrub stratum in addition to an herbaceous stratum that generally does not exceed 1.5 m in height and is commonly associated with coastal hills and low slopes (Fig. 15B).

The Sonoran province comprises approximately half of the territory of the state of Sonora and a small part of the northeastern portion of the Peninsula, in which only one district can be identified, corresponding to the San Felipe Desert, where the species *Menkeleon bellulus* is recorded, but until now only in the part of the state of Sonora (Fig.14B).

Regarding *Tyttholeon*, the new species fits the general diagnosis of this previously monotypic genus, which further supports its taxonomic validity. Stange mentions a male ectoproct "produced mesally below" in *Tyttholeon* as diagnostic (1970) and autapomorphic (1994). In *T. puerilis*, the male ectoproct is produced ventrally, rather than posteriorly as lobes, as more commonly seen in other Brachynemurini (Fig. 13). In *T. froehlichi* **n. sp.**, the male ectoproct indeed bears a short postventral lobe in addition to the ventral process (Fig. 11). This is very much akin to the male ectoprocts of *Chaetoleon*, *Clathroneuria* Banks, 1913 and *Mexoleon* Stange, 1994, in which they also bear a ventral projection. However, in these genera this morphological feature is described as "somewhat produced ventrally" (in *Chaetoleon*), "produced ventrally into a process" (in *Mexoleon*), and in *Clathroneuria*, the ventral process is described as a median lobe and as part of the postventral lobe rather than belonging to the ectoproct (Stange, 1970, 1994). It is unclear why these structures were

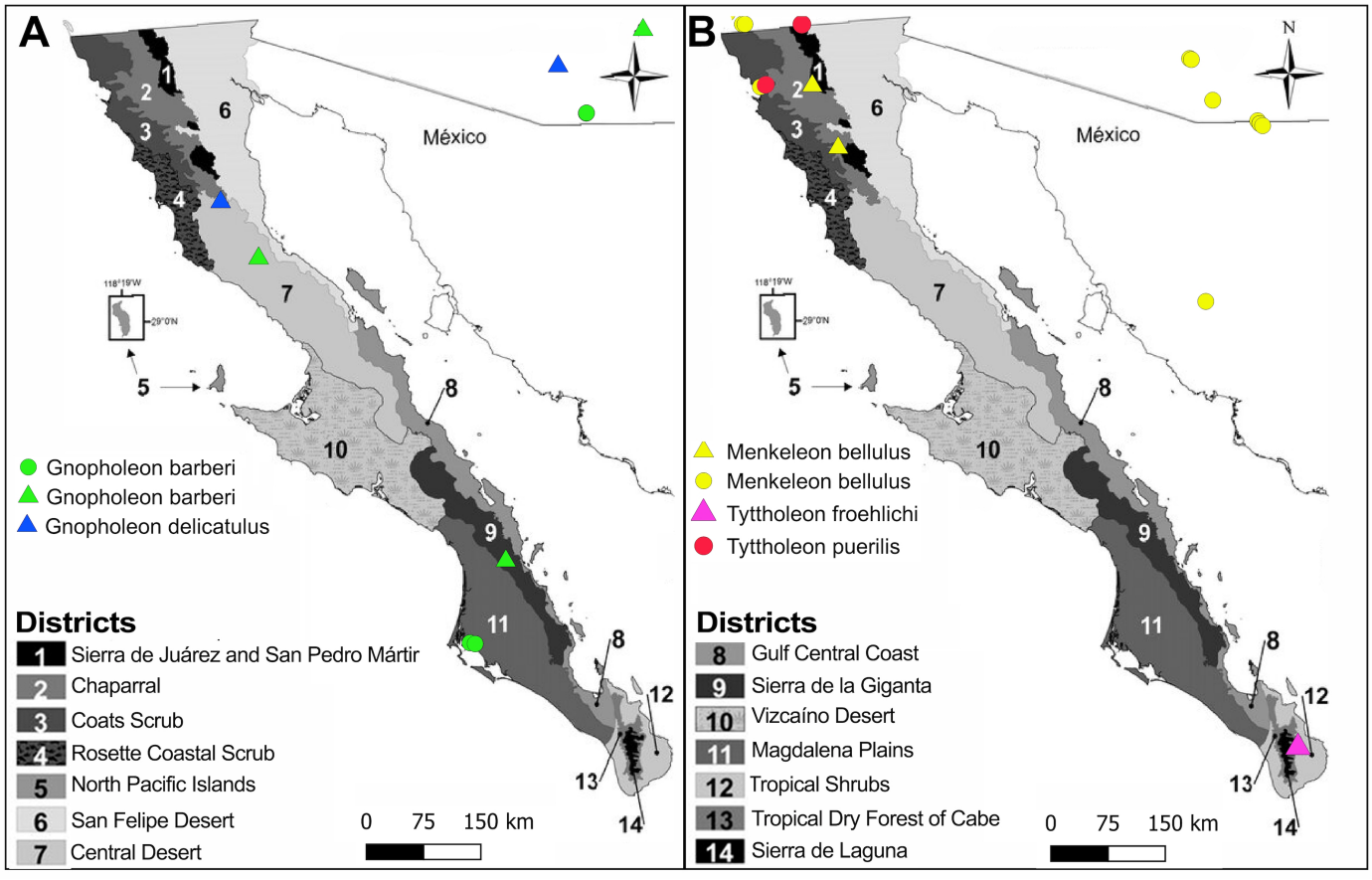

Figure 15 Distribution of the species of the formerly recognized tribe Gnopholeontini in the biogeographic districts of the Baja California Peninsula according to González-Abraham et al. (2010). A) *Gnopholeon* Stange, 1970. B) *Menkeleon* Stange, 1970 and *Tyttholeon* Adams, 1956. Circles indicate records from GBIF database and triangles indicate original records.

described so differently as they are extremely similar in their morphology and are apparently homologous. All these genera (and *Menkeleon*) also bear a "median process" at the male ectoproct internal face, as well as a strong invagination of the ectoproct (Figs. 09, 11). Additionally, these three genera were also recovered as somewhat closely related to each other by Machado et al (2019) (with *Clathroneuria* paraphyletic in relation to *Mexoleon*) at the "base" of the clade composed by the North American Brachynemurini, a region of the tree where the sole representative of the former Gnopholeontini, *G. delicatulus,* was also recovered.

Stange (1994) did a cladistic analysis of the Brachynemurini and split the tribe into Brachynemurini *s.s.*, Gnopholeontini and Lemolemini, mostly based on larval morphology (for the Gnopholeontini) and female terminalia (for the Lemolemini). This classification was followed by posterior publications (Stange, 2004), until the phylogenomic study published by Machado et al. (2019), who proposed a new classification for the family, including the return of Brachynemurini to its anterior topology, containing Gnopholeontini and Lemolemini.

For the former Gnopholeontini, there is much taxonomic background supporting its return to the Brachynemurini former arrangement. The known larvae of *Gnopholeon*, *Menkeleon* and *Tyttholeon* characteristically bear the mandible bases very close together and the labium is very narrow, however, these genera (and also *Maracandula*) also possess all other synapomorphies and diagnostic characters of the Brachynemurini, and more importantly, they bear hinged male parameres which are exclusive of this tribe (Figs. 3, 9, 11, 13) (Adams, 1956; Stange, 1970, 1994; Tavares et al., 2023), in addition to molecular data that supports Gnopholeontini within Brachynemurini (Machado et al., 2019). All four genera were previously coded as having non-hinged male parameres (Stange, 1994), but upon a closer look those are evidently hinged and have the general morphology and shape very much akin to other North American Brachynemurini. Upon further analysis of the specimens in this work, as well as Brachynemurini specimens from many other genera, it came to light that all the male genitalia previously illustrated and photographed as in a "posterior view" (Adams, 1956; Miller, 2008, 2016; Stange, 1970, 1994; Miller and Stange, 2009, 2017), are in fact in a ventral view (as in Figs. 03A, 09A, 11D).

Other recovered synapomorphies for the Gnopholeontini (Stange, 1994) may be discussed as plastic characters among the tribe, such as the absence (or presence, but very short) of male ectoproct postventral lobes (also absent in *Austroleon* Banks and *Chaetoleon* Banks), the large female gonapophyseal plate and the lack of tibial spurs (variable in the tribe, even among congeners), and the male abdomen that is shorter or barely longer than wings at rest (also present in *Ameromyia* Banks, *Austroleon*, and *Scotoleon*).

The taxonomic situation of the former Lemolemini remains confusing, as the species formerly included in this tribe are divided into seven genera and information about them in literature is scarce. These species have never received proper taxonomic treatment besides their original descriptions (Stange, 2004) and have not been included in a phylogenetic study (Machado et al., 2019). Only two species have the male genitalia illustrated in the literature: *Galapagoleon darwini* (Stange, 1989) and *Ecualeon ovispargus* Stange, 1994. The first species clearly bears hinged male parameres, supporting its placement in the current configuration of Brachynemurini, but in *E. ovispargus* the male genitalia show an unusual morphology for the tribe (Stange 1994), and a more detailed study is required to truly determine its placement. Furthermore, the lack or reduction of digging setae on the female ectoproct described by Stange (1994) as a diagnostic character to the former tribe is also an unreliable character, as it is heavily influenced by the female oviposition behavior (Miller, 1990), and other genera which do not lay eggs in the sand, such as *Gnopholeon* (Figs. 03, 05, 07) and *Navasoleon* Banks, 1943, also bear this character (Stange, 1994; Stange and Miller, 2018).

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Conflicts of interest

The authors declare no conflicts of interest.

Author contribution statement

LGMT conceptualization-equal, investigation-equal, methodology-equal, visualization-equal, writing – original draft, writing – review & editing-equal. YML investigation-equal, methodology-equal, validation-equal, visualization-equal, writing – review & editing-equal. RJPM investigation-equal, methodology-equal, validation-equal, visualization-equal, writing – review & editing-equal. CCM investigation-equal, methodology-equal, validation-equal, visualization-equal, writing – review & editing-equal. ACR funding acquisition-equal, supervision-equal, validation-equal, writing – review & editing-equal.

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