Introduction

The tabanid genus “Dasybasis” Macquart is represented in southern Neotropical and Australasian/Oceanian regions (Daniels, 1989; Fairchild & Burger, 1994). The Neotropical region is distributed from Venezuela to southern South America (Chile and Argentina) (Coscarón & González, 1991), most of which are found in the Andean region, especially in the Subantarctic, Patagonia, and Central Chile subregions of Chile and Argentina, and in the Páramo Puneña subregion (Morrone, 2015). The tabanid genus Dasybasis Macquart, 1847, constitutes one of the most abundant and speciose components of the southern Neotropical fauna, with 70 taxa considered valid (Coscarón & Papavero 2009). “Dasybasis” also occurs in Australia and New Zealand, with 73 species described in two subgenera (Daniels, 1989): New Caledonia (Trojan, 1991) and the Fiji Archipelago (Burger, 2006). It is well represented in southern Chile and Argentina, with 34 and 47 species, respectively. It is part of the most basal group within the tribe Diachlorini, occurring predominantly in the colder zones of the Neotropics in specialized habitats (Mackerras, 1954; Fairchild, 1969).Coscarón & Philip (1967) defined “Dasybasis” using, among others, the following combination of characters: general color of the body grayish, medium size between 9.0 and 14.0 mm; eyes with sparsely pilose and without bands; frons wide, with frontal index rarely exceeding to 3.0, rarely convergent at the base; basal callus of similar width as frons and wider than taller, quadrangular. Ocelli and ocellar triangle variably developed; subcallus pilose laterally; maxillary palpi stout and short; scape variable in shape, pedicel with dorsal projection; first flagellomere slightly angulate and without dorsal projection; maxillary palpi short and stout, with pilosity of variable length. Mesonotum with longitudinal stripes; wing hyaline to smoky, often with clouds on veins, with appendix on R4. Abdomen with median longitudinal band or stripes delimiting short triangles; cerci subcircular, genital fork without basal branches.

Different “Dasybasis” species are polymorphic and show morphological variation in some of these characters. Some of these characters are represented in taxa other than “Dasybasis”, which might convert them into symplesiomorphic characters that could be used to support this genus classification. For example, ocular pilosity is also found in Eristalotabanus Kröber, Scaptia Walker, Protodasyapha Enderlein, basal callus as wide as the frons in Acanthocera (Polistimima) Fairchild, Dichelacera (Dichelacera) Macquart, and Stenotabanus (Stenotabanus) Lutz, and globose in Bolbodimyia Bigot and Querbetia Fairchild. Pedicel with dorsal prolongation occurs in Cryptotylus Lutz, Stibasoma Schiner, Phaeotabanus Lutz, first flagellomere slightly angulate in Pachyschelomyia Barreto, Erioneura Barreto, Stenotabanus Lutz, Leucotabanus Lutz, maxillary palpi short and stout as in Oopelma Enderlein, Stibasoma Schiner, Stenotabanus Lutz, mesonotum with longitudinal stripes as Haematopotina Coscarón & Philip, Eutabanus Kröber, and Diachlorus Osten Sacken. Wing hyaline and smoke-colored as in Stenotabanus Lutz, Agelanius Rondani, Dicladocera Lutz, appendix on R4 as in Phaetabanus Lutz, Dichelacera (Orthostyloceras) Lutz, Apatolestes Williston, abdomen with median longitudinal band as in Stenotabanus Lutz, Haematopotina Coscarón & Philip, and Nubiloides Coscarón & Philip.

The Neotropical species of “Dasybasis” were monographed by Coscarón & Philip (1967) who recognized five subgenera and 80 species: Dasybasis s.str. Agelanius Rondani, Haematopotina Coscarón & Philip, Nubiloides Coscarón & Philip and Scaptiodes Enderlein. Coscarón (1961, 1962a, 1962b, 1969, 1972, 1974, 1989) described additional species in Argentina and Chile. Recently, González (2000) described a new species in Chile. Additional species have been described by Rondani (1863), Surcouf (1919), Hine (1920), Enderlein (1925), and Kröber (1930), yielding a total number of 69 valid species (Fairchild and Burger 1994).

There are no other studies for “Dasybasis” in the countries where the genus also occurs, only lists of species. Bequaert & Renjifo (1946) listed Agelanius columbianus (Enderlein) (= D. montium (Surcouf)) for Colombia. Wilkerson (1979) listed only 2 species in his work from two Departments in Colombia. Wilkerson and Fairchild (1984) listed 20 species in the Tambopata Reservation in Perú. Fairchild and León (1986) listed five species in Ecuador. Coscarón and González (1991) listed 51 species in five subgenera in Chile. Finally, Chainey et al. (1994) listed nine species of “Dasybasis” in two subgenera for the Department of Santa Cruz, in Bolivia.

Kröber (1934) cataloged the species of “Dasybasis” for the first time as Tabanus L., subgenus Agelanius Rondani. Kröber (op. cit.) synonymized Archiplatius Enderlein with Agelanius. Kröber (1930), described some species of “Dasybasis” in Tabanus L., Stypommisa Enderlein, Therioplectes Zeller, and Agelanius Rondani. Fairchild (1971) cataloged the Neotropical species of “Dasybasis.” Fairchild and Burger (1994), in a new catalog for the Neotropical species of Tabanidae, proposed some taxonomic changes for the genus. Recently, González (1999) revised the taxon included as subgeneric units of “Dasybasis” by Coscarón and Philip (1967) and raised to generic status the taxon Agelanius Rondani, Haematopotina Coscarón & Philip, Nubiloides Coscarón & Philip and Scaptiodes Enderlein, based on their morphological differences from “Dasybasis”, s.str. Four species, formerly included in the genus Agelanius Rondani, were transferred to the genus Acellomyia González.

There are few published phylogenies of genera within the subfamilies of Tabanidae. Tian-qi (1988) presented a phylogenetic analysis of the subfamilies of Tabanidae. Fanq et al. (1999) presented a phylogeny of the family using the characteristics of mouthparts, and Morita (2008) presented the first comprehensive phylogenetic hypothesis for Philoliche and Tabanidae based on molecular data. Results of four analyses (Kluge and Farris Method, Nelson & Platnick method, Hennig Method and Farris-Wagner Method) and only analyzed 10 characters of external morphology of adults where after using Stratiomyiidae as the outgroup, he concluded that Pangoniinae plus Chrysopsinae should be treated as a new family, Pangoniidae. This is because categories within the family are not appropriate, leaving Tabanidae represented by only three subfamilies: Diachlorinae, Haematopotinae, and Tabaninae. Fang et al. (1999) presented a cladistic analysis using mouthpart characters derived from scanning electron microscope studies. More studies using molecular data have been recently published, and Weigmann et al. (2000) demonstrated the monophyly of the Tabanidae, with each subfamily recovering as monophyletic. Recently, Lessard et al. (2013) proposed the first phylogenetic hypothesis for the tribe Scionini and completed the systematic placement of all tribes in the subfamily Pangoniinae.

The monophyly of the family is not in doubt and has strong support based on morphological characters (Mackerras, 1954; Woodley, 1989; Yeates, 2002 and molecular evidence (Morita, 2008; Weigmann et al., 2000, 2003, 2011).Sinclair et al. (1994) checked male terminalia homologies in lower Brachycera and their implications in the phylogenetic relationships among these groups highlighting, also, the Athericidae + Tabanidae group monophyly, supported by the elongated gonocoxal apodeme and the fusion of the gonocoxites and the hypandrium.Yeates & Wiegmann (1999) stated that Tabanidae, Pelecorhynchidae, Rhagionidae, Athericidae, and Vermileonidae have been included in the Infraorder Tabanomorpha by the following characters: apomorphic presence of cephalic brush in the larval mandible, retractile larval head, and adults with bulbous and convex clypeus. Stuckenberg (2001) remarked that Tabanidae and Athericidae constitute a highly derived clade.

The relationships within the genus “Dasybasis”, as well as those “Dasybasis” relative to other genera, are unknown or has been only postulated (Coscarón & Philip 1967), but never subjected to a cladistic analysis. So, an analysis of the groupings within “Dasybasis” is presented. The goals of this study were to evaluate the monophyly of “Dasybasis”, to redefine this taxon, to establish major monophyletic groups within the genus “Dasybasis”, and to determine the phylogenetic relationships among those groups and propose changes to the existing classification of “Dasybasis” that more accurately reflect purported natural affinities.

Material and Methods

Material examined

Material from the following and individuals were examined: Museo de La Plata (MLP, La Plata, Argentina), Instituto de Entomología de Salta (IES, Salta, Argentina), Canadian National Collection (CNC, Ottawa, Canada), Museo Nacional de Historia Natural (MNHN, Santiago, Chile), Museo de Zoología (MZC, Concepción, Chile), Instituto de Agronomía, (IA, Arica, Chile), Instituto de Entomología, Universidad Metropolitana de Ciencias de la Educación (IEUMCE, Santiago, Chile), Colección Miguel Cerda (CMC, Santiago, Chile), Field Museum of Natural History (FMNH, Chicago, USA), Department of Zoology, University of New Hampshire (DZUNH, Durham, USA, Colection Dr. Jaime Buestán (Ecuador), Dr. Alejandro Vera (Chile).External morphology was studied from dry-pinned specimens, females, and males (when available) for character circumscription. Terminalia were macerated in 10% KOH at approx. 95°C for 6 h to remove soft tissue, then rinsed in distilled water and dilute glacial acetic acid, and dissected in water. Photographs of the flies were taken using a Nikon trinocular stereomicroscope SMZ 1500 and digital camera DS-Fi2. The depth of the field was enhanced using the NikonTD ACT-2U software by stacking multiple images.

Terminals

We used 86 species of “Dasybasis” (Neotropical and Australasian). As outgroups, we selected at least one species from Tabanus Linnaeus, Stenotabanus Lutz, Agelanius Rondani, Haematopotina Coscarón & Philip, and Acellomyia González, and the trees were rooted using Tabanus. The table with all species analyzed, additional material examined, and geographical distribution are shown in Appendix 1.

Morphological Characters

Traditional Morphology

Fifty-eight tradicional morphological external and female and male genitalia characters from the studied species were analyzed. Character definitions and morphological data matrices are available in Appendices 2 and 3, respectively. Most characters were treated as binary. and we considered multistate characters to be non-additive.

Wing Landmarks

We used 29 primary landmark points and a semi-landmark, considering vein junctions and insertion points (Torres & Miranda-Esquivel, 2016), SEE FIGURE 1.

Cladistic Analysis

The search for the most parsimonious trees was carried out using TNT 1.6 (Goloboff & Morales, 2023). We conducted cladistic analysis under homoplasy weight using implied weights (Goloboff, 1993). To evaluate the optimal concavity value, we used first the classical morphology matrix, and we performed a sensitivity analysis (sensu Wheeler, 1995). We conducted a Jacknife analysis using characte deletion with a fixed cut value of 33%. Following Goloboff (1997) and Ramirez (2003), a reference tree was utilized (for further details see, Goloboff et la 2008) [[command resample sibyl replic 1000]]. The tested k values ranged from 1 to 100. We used a fast search that guarantees the best fit, using the xmult comand with 10 replicates and 500 iterations of ratchet, followed by 500 adrtional iterations of ratchet [[ commnand xmult = rat 500;rat = iter 500]]. The optimal value was defined as the K value that recovered most groups after jackknife treatment (see Ramirez, 2003). Given the optimal value, the most comprehensive search was conducted using the xmult comand with 500 replicates, 1000 iterations of ratchet and tree-Drfiting [[command xmult = rep 500 rat 1000 drift 1000 ]] (Nixon, 1999; Goloboff & Farris, 2001).

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