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Phylogeny of *Anisepyris* Kieffer (Hymenoptera: Bethylidae: E pyrinae), with investigation of diagnostic features

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Abstract

A cladistic analysis based on 120 morphological characters and 72 OTUs was conducted for the flat wasp genus *Anisepyris* Kieffer. The genus is mainly Neotropical region with few Nearctic species. The analysis retrieved well-supported relationships among the *Anisepyris* species and exposed the distribution of synapomorphies among the lineages, particularly concerning the mandible shape, dorsal pronotal area sulcus, and mesopleural foveae. The main diagnostic characters, described by Barbosa and Azevedo (2018) for the 13 species-groups of *Anisepyris*, were scrutinized. Transformation series and evolutionary hypotheses were also discussed. This discussion elucidates the importance of each character in the evolution and diversification along the different lineages. A discussion on the species-groups distribution is proposed, in relation to their diagnostic features. A hypothesis about the original distribution and the subsequent diversifications was also discussed. In conclusion, due to a possible recent origin for *Anisepyris* species, the dispersion could be related primarily to dense forest areas; and the retrieved synapomorphies could be related to posterior distributions of the species in disparate areas from their original environment.

Key words

character evolution, cladistic analysis, morphological characters, historical distribution, Neotropical region.

1. Introduction

Anisepyris was described by Kieffer (1906). After him, Evans (1965, 1966) proposed a cluster of characters to separate its species and species-groups. These characters concerned: metallic body reflection, eye pilosity, number of mandibular teeth, shape of first antennal flagellomere, presence of antennal foramen carina, and presences vs. absences of dorsal pronotal area carinae, of mesopleural foveae, and of a mesotibial spine. However, Barbosa and Azevedo (2018) revealed that these characters as insufficient for accurate identifications of the *Anisepyris* species-groups.

For a genus with 254 described species (and huge potential for additional new species), "functional" subdivisions of the genus are necessary. Therefore, the "species-group" concept, even if it is not a formalized taxonomic category by the International Code of Zoological Nomenclature (ICZN), is a useful tool to for the recognition and comparison of species for alpha-taxonomic stud-

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ies. Evans (1965, 1966) defined 10 species-groups for *Anisepyris*, later refined by Barbosa and Azevedo (2018).

These last authors revised and described the morphological characteristics to recognize the *Anisepyris* species and species-groups. But no phylogenetic analysis was done to verify the monophyly, the relationships, and the evolutionary history of these "groups". Here I propose the first phylogenetic hypothesis on the basis of morphological characters.

The goal is to describe the evolutionary history of the characters of *Anisepyris* and, when possible, to compare extant and fossil species, and host choice data. Furthermore, I evaluate the species-groups definitions, and discuss their relationships and the historical distribution of species.

2. Methods

2.1. Terminology

The terms applied to the structures follow Kawada et al. (2015), Barbosa and Azevedo (2018), Lanes et al. (2020), and Barbosa et al. (2021). Those related to the integument follow Harris (1979).

2.2. Taxon selection

Seventy two species were selected to compose the ingroup (Table 1). The species were selected to cover the maximum possible morphological diversity attributed to each species-group and to facilitate the analysis of the evolutionary history of the characteristics.

The analyses were based on both females and males because the species have marked sexual dimorphism. An analysis based on only one sex could not give an accurate evolutionary history for *Anisepyris* species. Therefore, the selection of OTUs was further narrowed down to those species known from both sexes. The choice of outgroups is justified as follows: Waichert and Azevedo (2009); and Alencar & Azevedo (2013).

2.3. Characters list

A total of 120 characters (Supplementary file 1) were extracted and analyzed from Barbosa and Azevedo (2018). This work compiled all the characteristics described by Evans (1965, 1966) and some features introduced by Barbosa and Azevedo (2018).

2.4. Character matrix

The character matrix (Supplementary file 2) was produced using DELTA software (Dallwitz et al. 1993). Binary and multistate characters were treated as unordered. Inapplicable characters were treated as "?".

2.5. Cladistic analysis

The searches for the most parsimonious trees were carried out with the software TNT ver. 1.1 (Goloboff et al. 2008b), using the New Technology algorithms. Parameters were as follows: collapsing rules selected for TBR; random seed set to 0; Sectorial Search (Goloboff 1999) in default mode; the ratchet with 200 iterations, and perturbation phase with eight up-weighting probability and eight down –weighting probability (Nixon 1999); 40 cycles for Drift (Goloboff 1999); 10 rounds for Tree Fusing (Goloboff 1999). The data matrices were submitted to the "Traditional Search" algorithm for the search of the "Wagner trees". This protocol is used to determine the number of analyses and replications.

It has been argued that results based on properly weighted characters are preferable to those with all characters with the same weights (Goloboff 1993; Goloboff et al. 2008a). Implied weighting is the most widely used method for attributing different weights during tree search, because it is independent of previous analyses and weights, unlike, for example, successive weighting. The weighting strength against homoplasy under implied weighting is related to a constant k – the lower the value of k, the higher the strength against homoplasy. Goloboff et al. (2008b) suggested that the concavity value k should be calculated as a function of N, which is the ratio of a single extra step to the cost of the most homoplastic character. In this paper, the TNT script setk.run, written by Salvador Arias (Instituto Miguel Lillo, San Miguel de Tucuman, Argentina), was used to calculate the appropriate value of k. The script returned a value of $k = 12.153320$ for our data set.

2.6. Distribution maps

The maps of distribution for each species-group were produced using the software QGIS Desktop v.3.16.0. The shapefile was based on the geographical sub-regions proposed for the Neotropical region and described by Morrone (2013), as follows: Mesoamerica, Antilles, North-western South America, Northern Amazonia, South-eastern Amazonia, South-western Amazonia, Chaco, Parana, Nearctic, Andean, Mexican transition zone, and South America transition zone.

2.7. Illustrations

All figures were edited in GNU Image Manipulation Program (GIMP) v.2.10.18. The phylogenetic characters were extracted from Barbosa and Azevedo (2018). Readers are referred to this publication for character illustrations.

Table 1. Outgroup and ingroup species list.

Taxon	Species group	Collection
Outgroup	—	-
Chlorepyris sp. 1	—	UFES
Laelius sp. 1	—	UFES
Laelius sp. 2	—	UFES
Ingroup	—	—
A. aeneus Kieffer, 1906	*aeneus*	CASC
A. bradely (Evans, 1959)	*aeneus*	CNCI
A. tlaloc Evans, 1966	*aeneus*	MCZH
A. amrasis Barbosa & Azevedo, 2018	*aeneus*	UFES
A. barahiris Barbosa & Azevedo, 2018	*aeneus*	UFES
A. aurichalceus (Westwood, 1874)	*aeneus*	OXUM
A. portoricensis Evans, 1966	*aeneus*	USNM
A. wolcotti Evans, 1959	*aeneus*	USNM
A. amazonicus (Westwood, 1874)	*amazonicus*	OXUM
A. bakeri Evans, 1966	*amazonicus*	USNM
A. bregolasi Barbosa & Azevedo, 2018	*amazonicus*	UFES
A. darlingtoni Evans, 1959	*amazonicus*	MCZH
A. dominicanus Evans, 1966	*amazonicus*	USNM
A. excisus Evans, 1959	*amazonicus*	MCZH
A. jocundus Evans, 1966	*amazonicus*	MCZH
A. ramosus Santos & Azevedo, 2008	*bifidus*	UFES
A. trinitatis Evans, 1966	*bifidus*	MCZH
A. bogotensis (Kieffer, 1910)	*bogotensis*	ZMBH
A. borlachi Barbosa & Azevedo, 2018	*bogotensis*	UFES
A. columbianus (Ashmead, 1893)	*columbianus*	UFES
A. grandis (Ashmead, 1887)	*columbianus*	AMNH
A. nigripes Evans, 1966	*columbianus*	MCZH
A. williansi Evans, 1959	*columbianus*	CASC
A. arizonicus Evans, 1959	*columbianus*	USNM
A. albistigmus Evans, 1966	*columbianus*	USNM
A. alienus Evans, 1966	*columbianus*	MCZH
A. peruvianus (Kieffer, 1910)	*columbianus*	ZMBH
A. insularis (Ashmead, 1894)	*columbianus*	USNM
A. interruptus Santos and Azevedo, 2000	*columbianus*	INPA
A. penai Evans, 1966	*columbianus*	MCZH
A. similis Santos and Azevedo, 2000	*columbianus*	MPEG
A. westwoodi (Cameron, 1888)	*columbianus*	BMNH
A. analis (Cresson, 1872)	*cupreolus*	USNM
A. bregoi Barbosa and Azevedo, 2018	*cupreolus*	OSUC
A. ecuadiroanus Evans, 1966	cupreolus	BPBM
A. cupreolus (Evans, 1965)	*cupreolus*	MCZH
A. iridescens (Evans, 1965)	*cupreolus*	MCZH
A. superpilosus (Azevedo, 1993)	cupreolus	UFES
A. indivisus Santos and Azevedo, 2000	*dietrichorum*	UFES
A. triangulatus Moreira and Azevedo, 2003	*dietrichorum*	UFES
A. annaeli Barbosa and Azevedo, 2018	*dietrichorum*	UFES
A. eoli Barbosa and Azevedo, 2018	*dietrichorum*	MPEG
A. anduzei Evans, 1966	*franciscanus*	MCZH

Taxon	Species group	Collection
A. brasilienses Evans, 1966	*franciscanus*	USNM
A. elegantulus Evans, 1966	*franciscanus*	BPBM
A. franciscanus Evans, 1966	*franciscanus*	BPBM
A. cepus Santos and Azevedo, 2008	*guianae*	UFES
A. guianae Evans, 1966	*guianae*	BPBM
A. carolinianus (Evans, 1965)	*megacephalus*	UFES
A. megacephalus (Ashmead, 1893)	*megacephalus*	USNM
A. texanus (Evans, 1965)	*megacephalus*	MCZH
A. werneri (Evans, 1965)	*megacephalus*	USNM
A. amlachi Barbosa and Azevedo, 2018	*megacephalus*	UFES
A. delicatus Evans, 1966	*megacephalus*	MCZH
A. finduilasi Barbosa and Azevedo, 2018	*megacephalus*	CNCI
A. fuinuri Barbosa and Azevedo, 2018	*megacephalus*	SEAN
A. pulchripennis (Evans, 1965)	*megacephalus*	USNM
A. proteus Evans, 1966	*proteus*	MCZH
A. pollicis Santos and Azevedo, 2000	*strictus*	IBGE
A. rectus Santos and Azevedo, 2000	*strictus*	IBGE
A. strictus Santos and Azevedo, 2000	*strictus*	INPA
A. tuberosus Santos and Azevedo, 2000	*strictus*	CNCI
A. wilsoni Evans, 1966	*strictus*	MCZH
A. eganellus (Westwood, 1874)	*venustus*	BMNH
A. rotundus Santos, 2002	*venustus*	UFES
A. smithanus (Westwood, 1874)	*venustus*	BMNH
A. lobatus Santos and Azevedo, 2000	*venustus*	UFES
A. venustus Evans, 1964	*venustus*	MCZH
A. attenuatus Santos, 2002	*venustus*	UFES

2.8. Depositories

AMNH – American Museum of Natural History, U.S.A. (James Carpenter); BPBM – Bernice Pauahi Bishop Museum, U.S.A. (James Boone); CASC – California Academy of Sciences, San Francisco, U.S.A. (Robert Zuparko); CNCI – Canadian National Collection of Insects, Ottawa, Canada (John Huber); IBGE – Instituto Brasileiro de Geografia e Estatística, Brazil (Braulio Dias, Mauro César); INPA – Instituto Nacional de Pesquisas da Amazônia, Brazil (José A. Rafael); MCZH – Museum of Comparative Zoology, U.S.A. (Stefan Cover, Phillip Perkins); MPEG – Museu Paraense Emílio Goeldi, Brazil (Orlando Tobias); NHM – The Natural History Museum, London, England (David Notton); OSUC – Ohio State University Collection, U.S.A. (Norman Johnson); OXUM – Oxford University Museum of Natural History, England (James Hogan); SEAN – Museo Entomológico de Léon, Nicaragua (Jean–Michel Maes); UFES – Universidade Federal do Espírito Santo, Vitória, Brazil (Marcelo Tavares); USNM – National Museum of Natural History, Washington D.C., U.S.A. (David Furth); ZMBH – Museum für Naturkunde, Berlin, Germany (Frank Koch).

3. Results

3.1. Phylogenetic results

The implied weighting analyses retrieved one most parsimonious cladogram with k = 12.153320; best score = 33.69644; steps = 928; consistency index (CI) = 0.15; and retention index (RI) = 0.47) (Fig. 1). The monophyly of *Anisepyris*, previously retrieved previously by Waichert and Azevedo (2009) and Alencar and Azevedo (2013), is also found in this analysis.

The analyses under equal weight retrieved one most parsimonious cladogram. However, the phylogenetic inferences using parsimony are best achieved when carried out under differential weighting schemes (Hermes et al., 2014). For arguments on the advantages of character weighting of morphological data sets, see Goloboff et al. (2008a).

Eleven character states were retrieved as synapomorphies for *Anisepyris*, eight of them were exclusive to the genus: presence of eye pilosity (#16:1) (Barbosa and Azevedo 2018: fig. 1B); notauli complete (#24:0); first inner metapostnotal carina incomplete (#28:0); presence of male eye pilosity (#77:1) (Barbosa and Azevedo 2018: fig. 1B); presence of anterior sulcus of dorsal pronotal

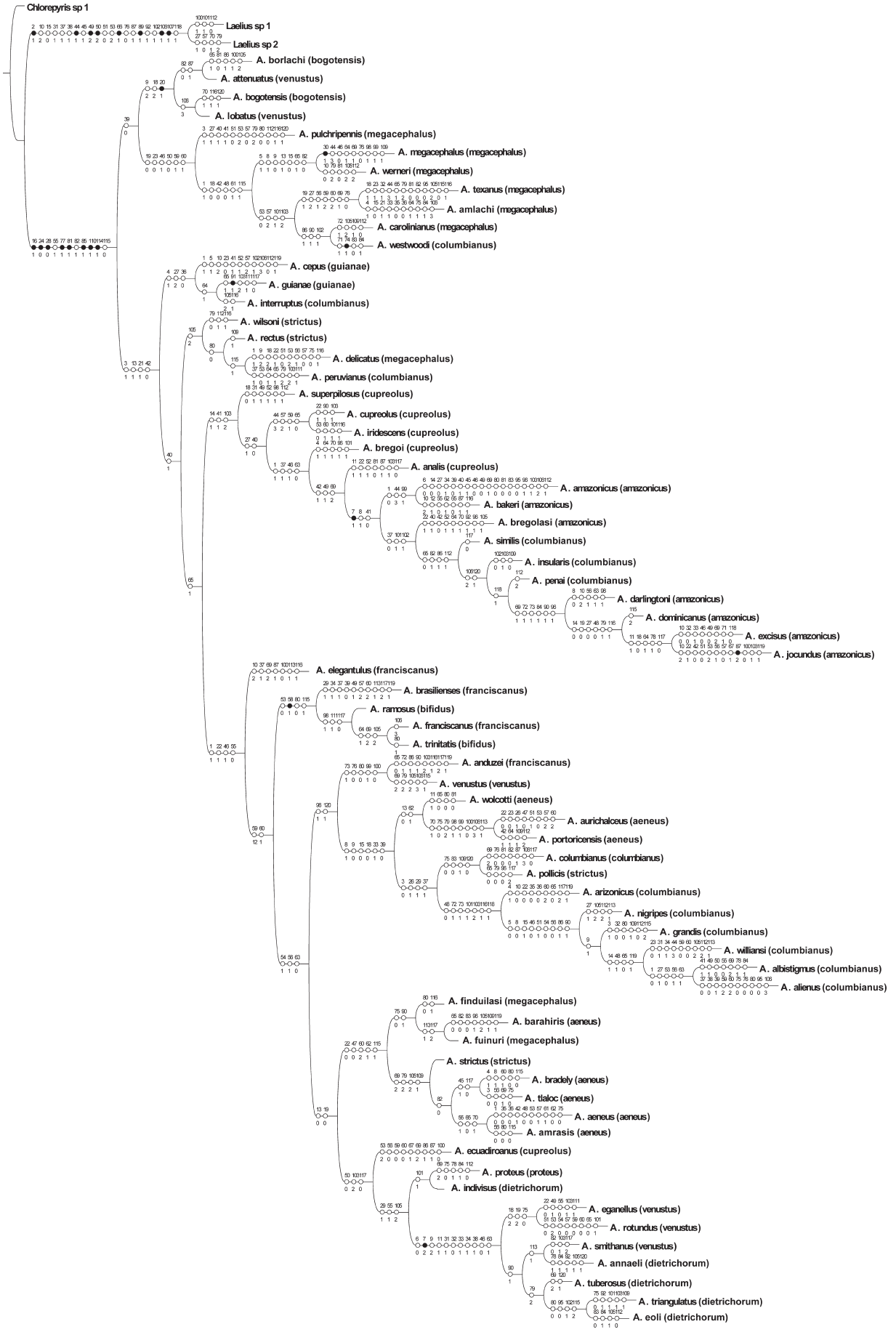


Figure 1. Cladogram of most parsimonious tree under implied weight, for species represented by female and male specimens. *k* = 12.153320, best score = 33,69644, steps = 928, (CI) = 0.15, (RI) = 0.47. Abbreviations: constant *k* (*k*), consistency index (CI), retention index (RI).

Table 2. *Anisepyris* species-groups distribution A. Nearctic region; B. Me×ican Transition Zone; C. Mesoamerica; D. Antilles; E. north-western South America; F. northern Amazonia; G. south-eastern Amazonia; H. south-western Amazonia; I. Chaco; J. Paraná; K. South American Transition Zone; L. Andean region.

	A	B	C	D	E	F	G	H	I	J	K	L
Aeneus	×		×	×	×				×	×		
Amazonicus	×	×	×	×	×	×	×	×	×	×		
Bifidus			×		×					×		
Bogotensis					×	×				×		
Columbianus	×	×	×	×	×	×	×	×	×	×		
Cupreolus		×	×		×	×	×		×	×		
Dietrichorum						×	×	×		×		
Franciscanus			×		×	×	×	×	×	×		
Guianae						×	×			×		
Megacephalus	×	×	×	×	×	×	×		×	×		
Proteus					×	×	×	×	×	×		
Strictus			×		×	×	×	×	×	×		
Venustus			×	×	×	×	×	×	×	×		

area (#81:1) Barbosa and Azevedo 2018: fig. 1K); male notauli complete (#85:1); dorsal position of basiparamere (#110:1); and bifid cuspis (#114:1).

Three others character states were not retrieved exclusively for *Anisepyris*, but are important to define the genus: genitalia with T9 with very swollen apex (#55:1) (Barbosa and Azevedo 2018: fig. 30); presence of lateral sulcus of dorsal pronotal area (#82:1) (Barbosa and Azevedo 2018: fig. 1K); and short length of cuspis arm (#115:0).

From the *Anisepyris* synapomorphies in Waichert and Azevedo (2009), just the presence of eye pilosity (#16:1) and the presence anterior sulcus of dorsal pronotal area (#81:1) were retrieved in this work. The synapomorphies retrieved for *Anisepyris* in Alencar and Azevedo (2013) were not retrieved in this paper; however, all of them were retrieved as synapomorphies for the clade ((*Anisepyris* + *Laelius*) + *Chlorepyris*) in this work. Thus, they occurred as non-informative characters. From the 18 diagnostic features of *Anisepyris* proposed in Azevedo et al. (2018), just three were retrieved in our work as synapomorphies: presence of eye pilosity (#16:1), presence of anterior sulcus of dorsal pronotal area (#81:1), bifid cuspis (#114:1); 12 characteristics were retrieved as synapomorphies for the clade ((*Anisepyris* + *Laelius*) + *Chlorepyris*); and the other three characters were retrieved among various *Anisepyris* lineages.

The sub-clades in our analysis are in general agreement to the species-groups proposed by Barbosa and Azevedo (2018). However, some of the species-groups were not retrieved as monophyletic. The genus has 254 described species and only one third of these are known from both sexes. Thus, only species with both sexes described were selected. The reduced representation of the species diversity could have interfered with the monophyly of some species-groups.

3.2. Distribution and Geographic results

The geographic distribution is illustrated and summarized below (Table 2 and Figs 2–8).

Anisepyris species are unknown from the South America transitional zone or Andean region. All species-groups were recognized in the Atlantic forest (Paraná region). The *amazonicus* and *columbianus* species-groups were registered for all other regions. The *megacephalus* species-group had the same distribution, except for its absence from the south-western Amazonia region. The *bifidus*, *cupreolus*, *dietrichorum*, *franciscanus*, *guianae*, *proteus*, and *strictus* species-groups were not registered from the Antilles region. And the *bifidus*, *bogotensis*, *dietrichorum*, and *guianae* species-groups were not found in the Chaco region.

4. Discussion

Among 11 synapomorphies of *Anisepyris*, only one was retrieved in correspondence with Waichert and Azevedo (2009) and Alencar and Azevedo (2013), viz., the presence of eye pilosity 19:1/18:1 (female/male). The previous works were not able to retrieve the 12 other characters. However, the scope of their project was to solve the phylogeny of Epyrinae at the tribe-level; thus, just a few informative characters were selected for each genus of Epyrinae. Based on 120 characters and 72 species, this sample provided an opportunity to define new synapomorphies for *Anisepyris*. The monophyly of *Anisepyris* is not disputed. Moreover, my discussion focuses on describing the evolutionary history of the main characters of the species-groups defined by Barbosa and Azevedo (2018), and their biogeographic implications.

4.1. Body surface with metallic reflections

(Barbosa and Azevedo 2018: figs 1A, C)

According to Michelson (1911), metallic reflections and colors are caused by the opacity of substances of the integument, in which the impossibility of entering the substance causes reflection of light; causing light reflection to reveal brilliant metallic colors (for more detailed description of these mechanisms see Doucet and Meadows 2009; Seago et al. 2009).

The genus has 35 species without metallic reflection on the body surface (Barbosa and Azevedo 2018: fig. 1C); all others species have metallic reflection (Barbosa and Azevedo 2018: fig. 1A). The metallic reflection for these species is not restricted to green, but ranges from golden to blue reflection.

Apidae have huge species diversity in the Neotropical region, represented by 5016 species (Moure et al. 2012); many of these have iridescence, e.g., Augochlorini and Caenohalictina (Halictinae), and Euglossini (Apinae). This iridescence is generally green or blue, and in some cases, gold.

Wallace (1877) described four kinds of relationships between the connection between colors and behavior of species living in dense forests, as follow: protective, warning, sexual, and typical colors. According to this author, green metallic reflection is protective for insects that inhabit tropical forests. For *Anisepyris*, this could be corroborated because the species are mainly recorded from tropical forests in Neotropical regions.

The Epyrinae are the second most diverse subfamily within Bethylidae. Within the subfamily, just like *Anisepyris*, the genera *Bakeriella*, *Chlorepyris*, and *Laelius* have species with body surface iridescent; but for *Bakeriella* and *Laelius*, most species lack metallic coloration. In *Anisepyris* and *Chlorepyris*, the majority of species have metallic coloration.

For the above mentioned Apidae, and also for *Anisepyris*, species diversity is related to the presence of integumental iridescence, mainly green to blue. This exemplifies the importance of the relationship between the green to blue iridescence and the forest habitat. From this scenario, the importance of the metallic coloration of the body surface for *Anisepyris* is clear, and is a main distinction from the other epyrine genera.

4.2. Eye pilosity

For the bethylid genera, the hairy eye is not a common character. Few inconspicuous setae are present in some species, but these do not constitute a hairy eye. The bethylid genera that have this character are the pristocerine *Caloapenesia*, *Protisobrachium*, and *Pseudisobrachium* (Terayama 1999), and all the genera of Mesitiinae (Barbosa and Azevedo 2011b). Within Epyrinae, only the *Anisepyris* spp. show an "eye pilosity" (Barbosa and Azevedo 2018, fig. 1B, C); this character being a synapomorphy of the genus.

Sorg (1988) described *Anisepyris gradatus*, a fossil species from the Dominican Republic Miocene amber. All the *Anisepyris* diagnostic features were observed in this species, and Sorg indicated that "the head is clearly sculptured coarsely punctured, granulated and densely hairy. Likewise, long hair located on the compound eyes". Thus *A. gradatus* can be accurately considered as an *Anisepyris*.

When comparing the species distributions of *Laelius* Ashmead, with those of the *Anisepyris* species, *Laelius* species have a cosmopolitan distribution (Barbosa and Azevedo 2011); and *Anisepyris* species are restricted to the Neotropical region and to a restricted portion of the Nearctic region. However, *Anisepyris* species diversity (254 described species) is larger than *Laelius* (61 described species). Therefore, the character "presence of eye pilosity" could be correlated to the *Anisepyris* stem group.

4.3. Mandible teeth number

Anisepyris and *Laelius* were retrieved as sister-groups by Waichert and Azevedo (2009), Alencar and Azevedo (2013), and also in our work. Based on this hypothesis, it is possible to propose a transformation series of the characters "Mandible distal teeth number" (#6) and "Development of mandible distal teeth" (#7).

All species described from *Laelius* have the mandible with five distal teeth; for majority of these species, the teeth have the same width, but in some species the two most inferior teeth (in frontal view) are wider than others. For *Anisepyris* species the same condition is observed for all males and the majority of female specimens.

The species *Anisepyris bakeri* Evans, 1966 and *A. bregolasi* Barbosa and Azevedo, 2018, have the mandible with five distal teeth differently developed (different width among them). However, the distinction between the two superior distal teeth is observed only as an inconspicuous suture. Females specimens of the *venustus* and *amazonicus* species-groups have the mandible with four distal teeth (#6:0), all these species have the mandible with the distal teeth differently developed on their width (#7:1/2) (Barbosa and Azevedo 2018: figs 1F, H); this is probably due to the fusion of the two superior distal teeth. The loss of the most superior distal tooth likely occurred by fusion with its immediately inferior distal tooth. Therefore, the differences in tooth development are related to the presence of a wider superior distal tooth, which could be formed by the previous fusion of the two superior distal teeth.

The mandible distal teeth configuration, recorded here as "differently developed" (#7:1) (Barbosa and Azevedo 2018: fig. 1H), is not found in any other bethylid genera and was retrieved only in the *amazonicus* species-group. Also, this mandible distal tooth pattern can be found in other Aculeata species, e.g., *Polistes* (Vespidae, Polistinae) and some species of Formicidae. These wasp and ant species are characterized by having their mandibles adapted for better manipulation of food resources, larvae, and

building nests. Thus, the species of the *amazonicus* species-group may have developed this mandibular conformation for better manipulation of prey or food resources.

The mandible distal tooth configuration, recorded here as "curved upward" (#7:2) (Barbosa and Azevedo 2018: fig. 1F), is also not found in any other Bethylidae genera and was retrieved only for the *venustus* species-group. This same mandible distal teeth pattern can be found in Coleoptera species from the genus *Acalolepta* Pascoe, 1858 (Cerambycidae, Lamiinae). The main character of this mandible pattern is the "superior blade" (the most superior tooth forming a blade). The *Acalolepta* species slice and eat wood in forests; thus, the mandible with "superior blades" are adapted to cutting and manipulating wood. Based on this similarity, we hypothesize that the species of the *venustus* group also use their mandibles to cut wood; probably to find hosts living in tree trunks (Evans 1959, 1965, 1966). Additionally, species from the *venustus* group have the median lobe of the clypeus flattened. This clypeus configuration is also recorded for *Acalolepta* species, as their common name suggests: "flat-faced longhorn beetle". This adaptation could provide more space for mandible cutting action.

For *Anisepyris*, the hypothesis of the "loss of superior mandible distal tooth" by the fusion between two superior distal teeth constitutes an apomorphic transformation within the genus. Hence, this could indicate that the male specimens retain the plesiomorphic characteristic, viz. "mandible with five distal teeth". Additionally, this transformation could have arisen twice independently, in the *amazonicus* and *venustus* species-groups; and these transformations could be related with two distinct behaviors, as described above.

4.4. Presence of the Anterior and lateral sulcus of dorsal pronotal area

(Barbosa and Azevedo 2018: fig. 1K)

The anterior sulcus of the dorsal pronotal area is recorded in few other Bethylidae genera: *Bakeriella*, *Holepyris*, and *Parascleroderma.* However, the lateral sulcus of the dorsal pronotal area is recorded only for *Anisepyris* species.

Sorg (1988) described the fossil species *Anisepyris gradatus* as having the dorsal pronotal area with anterior and lateral sulci; the author stated: "The pronotum has a cross-bar as well as two lateral longitudinal strips in the edge region of the strips". Although recognized in this fossil species, these characteristics were not retrieved as synapomorphies for *Anisepyris*, unlike those proposed by Waichert and Azevedo (2009) and Alencar and Azevedo (2013). However, in this work these characteristics were retrieved within *Anisepyris* as synapomorphies for some species-groups.

According to Mikó et al. (2007) the muscle t1-ph1 arises from the anteromedian region of the pronotum and inserts at first phragma (at the anteromesoscutum); specifically, it arises from the anterior corner of pronotum, between the anterior (pronotal collar) and dorsal regions (dorsal pronotal area) of the pronotum. Species of Bethylidae have an articulation between the pronotum and the mesoscutum, making it possible for the pronotum to slide over the mesoscutum; this movement is aided by contraction of the muscle t1-ph1.

The presence of an external sulcus on a sclerite indicates the presence of an internal apodeme. Therefore, the apodemes represented by the anterior and lateral sulcus of the dorsal pronotal area could increase mobility between the pronotum and mesoscutum, allowing a greater range of movement in the mesosoma.

4.5. Mesopleural foveae

Waichert and Azevedo (2009) and Alencar and Azevedo (2013) suggested that having the mesopleuron subdivided by foveae could be a synapomorphy for Epyrinae. This work supports that hypothesis; based on this and previous works, which tried to identify the evolutionary transformation series of the characters, related to mesopleuron subdivision among *Anisepyris* lineages.

The phylogenetic signal for the characters of the mesopleural foveae was not retrieved in the topologies, because low consistence indices were retrieved for these characters, ci = 0.09–0.33. Therefore, it was more parsimonious to infer independent origins for the four characters dealing with the mesopleural foveae subdivisions (characters 35–38:1, and 99–102:1). These four characters were analyzed individually to explain their evolutionary transformations hypothesis.

Closed anterior mesopleural and mesopleural fovea
(character 35–36:1 and 99–100:1/2)

(Barbosa and Azevedo 2018: figs 2C, D)

This character was observed in almost all species of *Anisepyris* and *Laelius*. Possibly, this character arose from the common ancestor of these two genera and is as synapomorphy for the clade (*Anisepyris* + *Laelius*).

Closed lower mesopleural fovea
(character 37:1 and 101:1)

(Barbosa and Azevedo 2018: fig. 2D)

According to Evans (1966), this is the main characteristic to identify the *amazonicus* and *columbianus* species-groups. However, it was not retrieved as a synapomorphy for these species-groups. This characteristic was retrieved independently as a synapomorphy for the *columbianus* species-group, for species *A. amazonicus*, and for a few other species belonging to other *Anisepyris* species-groups.

Unfortunately, it was not possible to accurately define this transformation, because the characteristic was retrieved arising independently among different branches of the topology. However, *columbianus* species-group is the only one with the "closed lower mesopleural fovea" as a synapomorphy. Thus, I hypothesize that the "closed lower mesopleural fovea" represents an apomorphic character state in relation to the "opened lower mesopleural fovea".

Presence of Posterior mesopleural fovea
(character 38:1 and 102:1)

(Barbosa and Azevedo 2018: fig. 2E)

Evans (1966) described this character state as "divided lower fovea" and identified it as a diagnostic character for the *columbianus* species-group. Barbosa and Azevedo (2009) identified these foveae as distinct from each other and described them as "lower fovea" and "posterior fovea". Waichert and Azevedo (2009) treated this fovea as "episternal groove". Alencar and Azevedo (2013) classified this fovea just as a division of "lower fovea", as suggested by Evans (1966). The primary homology hypothesis proposed here was: posterior mesopleural fovea: (0) absent; (1) present.

Contrary to the suggestion by Evans (1966), this characteristic was also observed for species belonging to the *venustus* species-group. Apparently, this characteristic arose independently in the *columbianus* and *venustus* species-groups. Moreover, the shape and placement of the posterior mesopleural fovea differs between these two groups.

The "presence of posterior mesopleural fovea" is a common characteristic for *Laelius* species, the sister-group of *Anisepyris*. According to the definition of deep homology by Shubin et al. (2009), the "structures arose by the modification of pre-existing genetic regulatory circuits established in early metazoans". Thus, because these two genera are sister groups, the "presence of posterior mesopleural fovea" could likely correspond to a case of deep homology.

Additionally, Shubin (2009) indicated that "the deep homology of generative processes and cell-type specification mechanisms in animal development has provided the foundation for the independent evolution of a great variety of structures". Thus, from this affirmation it was understood that the differences between "posterior mesopleural fovea" of the *columbianus* and *venustus* species-groups could be worthy of investigation for deep homology.

Unfortunately, no additional information about muscle insertions at the mesopleural foveae is available; this could give more accurate information about the evolutionary history of these foveae. The possibility to resolve the mesopleural foveae issue depends on the investigation of the transformation series among Epyrinae genera, and then to apply these to *Anisepyris* species evolution. This investigation could target the subdivision of mesopleural foveae, as discussed above.

4.6. Female sting characters

(Barbosa and Azevedo 2018: fig. 30)

As stated by Ernst et al. (2013), "since traditionally used morphological characters have been phylogenetically inconsistent the utilization of unexplored character systems, such as the male and female terminalia might offer additional data relevant to more robustly estimate the phylogenetic history of this group". Thus, some characters of female sting were selected for cladistic analyses of the *Anisepyris* species. Therefore, 13 characters of the female sting were delimited for this analysis (chars #51-63).

A large number of independent origins were retrieved within the trees. However, all these characters had substantial importance for identification and diagnosis of *Anisepyris* species. The use of these characters for alpha-taxonomic analyses will be useful and will contribute to taxonomy of the female specimens of *Anisepyris* species. The female sting characters will be more accurate after deep analyses of their features (movement, muscle, and behavior adaptation). These analyses could start firstly at higher taxonomic levels, in view to establish a hypothesis of transformations and ordination of their character states, as accomplished by Ernst et al. (2013).

4.7. Potential phylogenetic signals

Evans (1965, 1966) proposed characters to define ten species-groups within *Anisepyris*, as follows: (females) #13:1, presence of torular carina (Barbosa and Azevedo 2018: fig. 1A); #15:1, small size of eye; #37:0/1, opened/closed lower mesopleural fovea; #38:1, presence of posterior mesopleural fovea; #41:1, bi-banded forewing; #46:1, presence of spine of mesotibia; #48:0/1, bifid/trifid tarsal claw; (males) #70:1, elongate antennal length; #73:1, ring shape of first flagellomere (Barbosa and Azevedo 2018: fig. 1E); #75:1, presence of torular carina (Barbosa and Azevedo 2018: fig. 1B); #101:0/1, opened/closed lower mesopleural fovea; #102:1, presence of posterior mesopleural fovea. Unfortunately, none of these characteristics were retrieved as synapomorphies for these species-groups.

Evans (1965, 1966) established these characters based on *Anisepyris* species mainly from the Nearctic region, with just a few representatives from the Neotropical region. Currently, it is known that species diversity of the genus in the Neotropical region is substantial, and the Nearctic region is comparatively species-poor. Therefore, is not possible to establish the diagnostic characters of all the species-groups of *Anisepyris* without accessing the majority of species diversity.

These characteristics (defined by Evans 1965, 1966) were retrieved as synapomorphies for small clades within the species-groups. Additionally, some of these clades are restricted to sub-regions in the Neotropical and Nearctic regions, as defined by Morrone (2003). This is an interesting issue, which could indicate patterns of distribution of *Anisepyris* species.

According to Azevedo and Azar (2012), the minimum age of Bethylidae is about 125 Ma, represented by *Lancepyris opertus* Azevedo and Azar (2012) from Barremian Cretaceous amber. According Sorg (1988) the minimum age of *Anisepyris* is about 16 Ma, based on a record from Dominican Miocene amber. Indicating that *Anisepyris* could be a comparatively young genus within the family. Thus, the set of characters discussed above could be considered "potential phylogenetic signals"; and a hypothesis that analyzing these characters could resolve evolving lineages within the genus.

4.8. Speculation about the distribution of Anisepyris species

As discussed by Gonçalves (2015) for *Ceratalictus* Moure (Apidae, Halictinae), biogeographical reconstruction for *Anisepyris* is difficult due the over estimation of the role of some areas; additionally, the phylogenetic reconstruction had some difficulties due the underrepresentation of species known from both sexes. Therefore, the distributional history of *Anisepyris* is discussed in six different topics.

Diversity and relationship to species distribution

To understand species irradiation and distribution of *Anisepyris*, this analysis was based on the division in sub-regions proposed by Morrone (2013). This division proposal tried to explain the dispersal and distribution patterns of the biota into the Neotropical and Nearctic regions.

Evans (1966) proposed that *Anisepyris* had its "dispersal center" in the Nearctic region, more specifically in Southern North America, this region also matches what Morrone (2013) defined as Nearctic region. Evans's proposal was based on the fact what *Anisepyris megacephalus*, *A. apache*, and some species of the *aeneus* and *proteus* species-groups are distributed throughout southwestern of United States; and that some apotypic species ranged into the West Indies. His argument was not well supported, and the diagram proposed by him did not clearly explain the hypothesis.

Evans (1966) cited: "There are undoubtedly new species to be discovered, especially in South America, and there may even be undiscovered species-groups on that continent". This citation was completely corroborated by Barbosa and Azevedo (2008), however, the distribution of the new species described by them contradicts the hypothesized dispersal center proposed by Evans (1966) for *Anisepyris*. The author (Evans, 1966) did not have access to expressive samples of *Anisepyris* specimens from many regions below the Equator; hence, the diversity of the genus was inadequately sampled in his revision.

Accessing a higher diversity of the genus from the revision by Barbosa and Azevedo (2018), was able to reach a different distribution pattern hypothesis. Based on the divergence of characters and distribution of the species and species-groups, the hypothesis is: *Anisepyris* has a

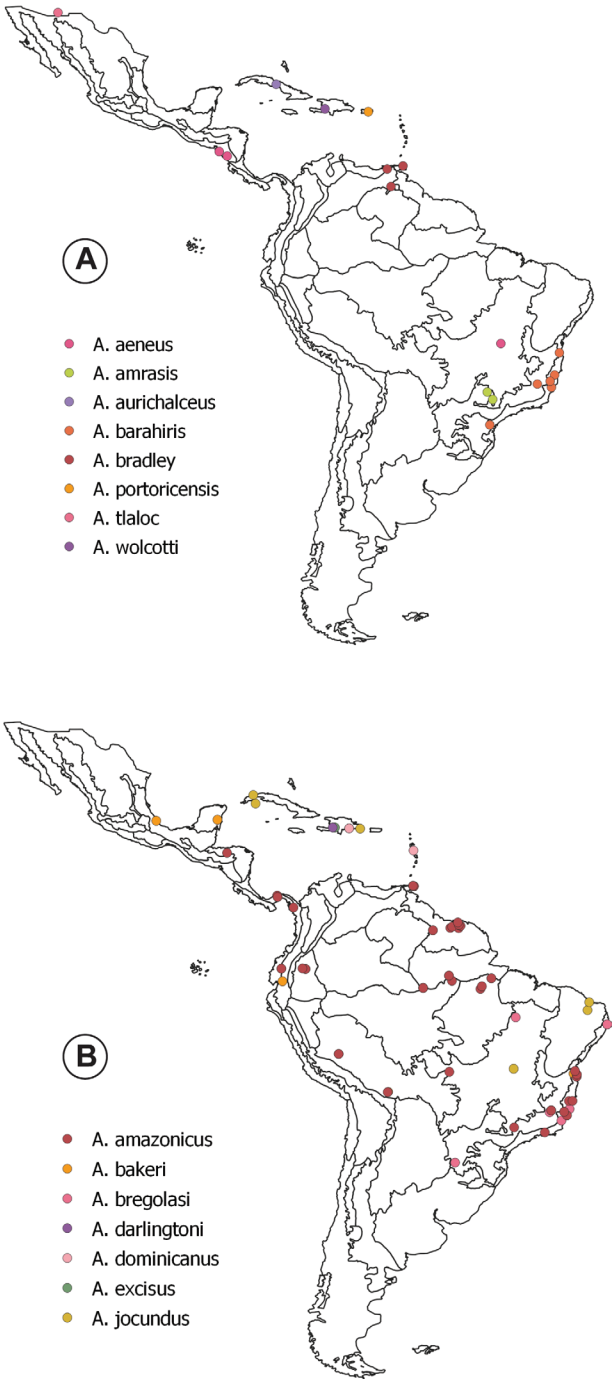


Figure 2. Geographical distribution of species-group. **A** *aeneus* **B** *amazonicus*.

probable original distribution in the Neotropical region with subsequent distribution into the Nearctic region. This hypothesis is based on the discrepancy of morphological characteristics of species, and the diversity assigned to each sub-region defined by Morrone (2013). This relationship for *Anisepyris* species occurs because when a sub-region is more diverse, there are narrower morphological discrepancies between species and when the sub-region is less diverse, there are larger morphological discrepancies between species.

From this, and based on the former premises above, I identify the Northern Amazonia and Paraná regions as having the highest diversity and narrowest morphological

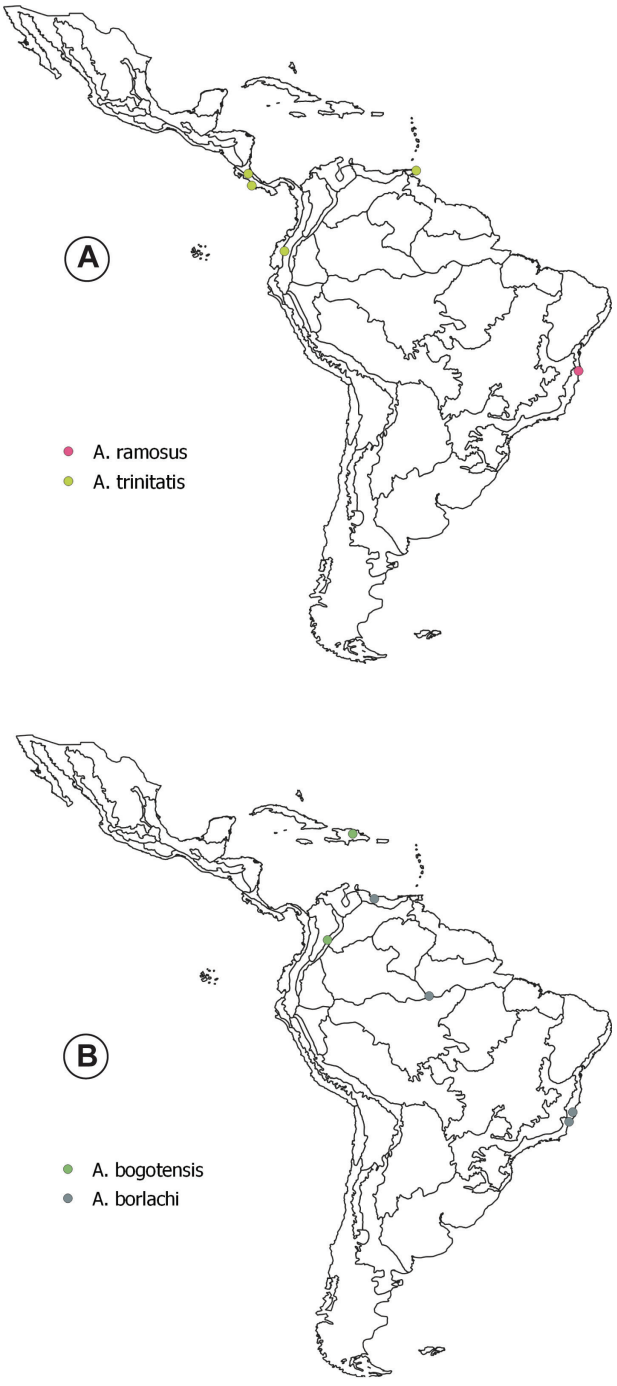


Figure 3. Geographical distribution of species-group. **A** *bifidus* **B** *bogotensis*.

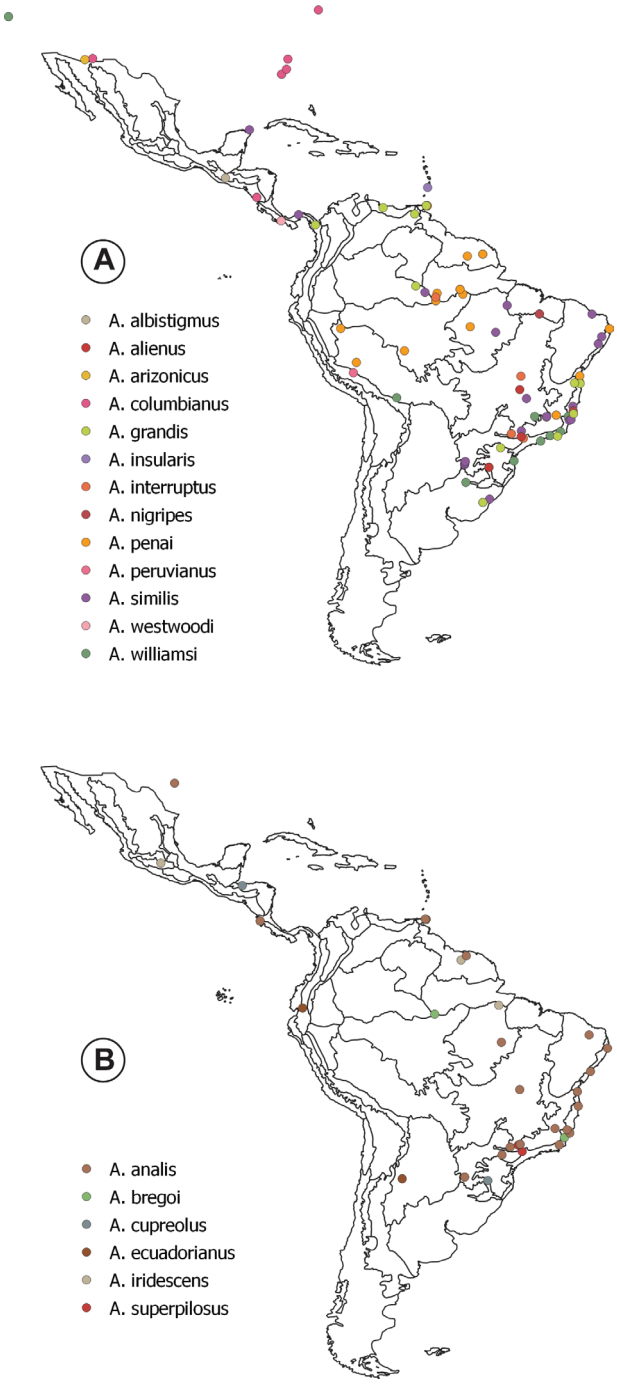
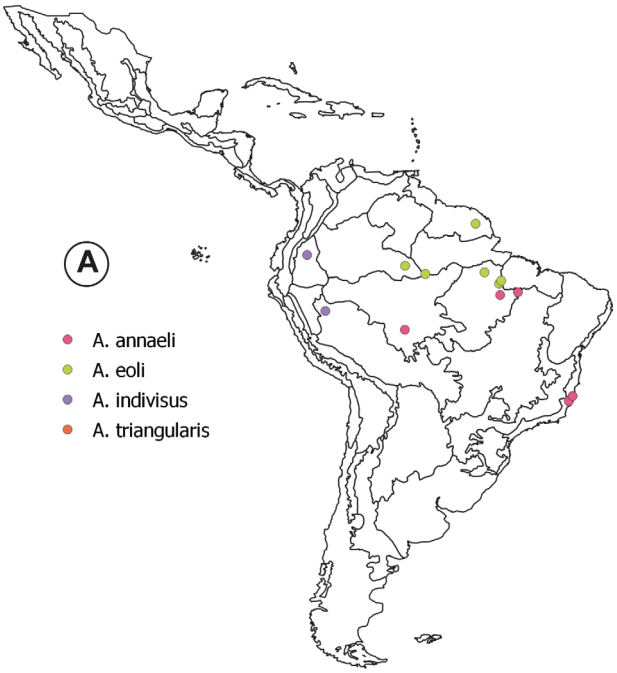


Figure 4. Geographical distribution of species-group. **A** *columbianus* **B** *cupreolus*.

discrepancies among *Anisepyris* species; thus, was could propose an original distribution hypothesis to the genus. Probably, when the genus emerged in a specific area, the tendency was that diversity increased and, consequently, the character discrepancy narrowed; because, these species likely had similar niche opportunities, in view that the group persisted in these areas for a long time period. Thus, when this area does not bore adaptive niche, dispersal events were possible, the groups gained access to areas with greater opportunities, and there underwent rapid speciation, as cited by Cox and Moore (2000). This event could explain the higher character discrepancy between species that occur farther away from these original regions, like the southern Chaco region, Antilles region, and Nearctic region.

In short, new niches imply the selection of new features and increased competition, which justifies the lower diversity; hence the more peculiar characteristics, and limited distribution of *Anisepyris* species in regions farther away from the hypothesized original distribution area (see Cox and Moore 2000).

Additionally, it was observed that even the species-groups with restricted distribution, like *bifidus*, *bogotensis*, and *dietrichorum,* are recorded from Northern Amazonia and the Paraná region. The Paraná region, specifically, is unique in including species from all spe-



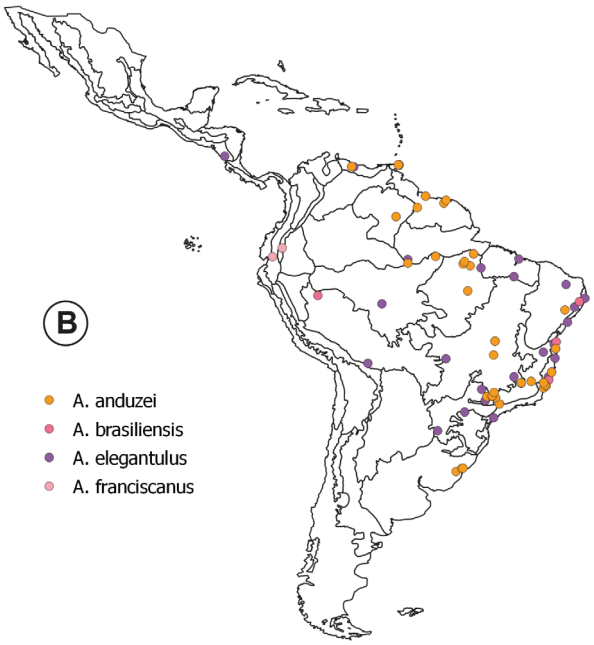


Figure 5. Geographical distribution of species-group. **A** *dietrichorum* **B** *franciscanus*.

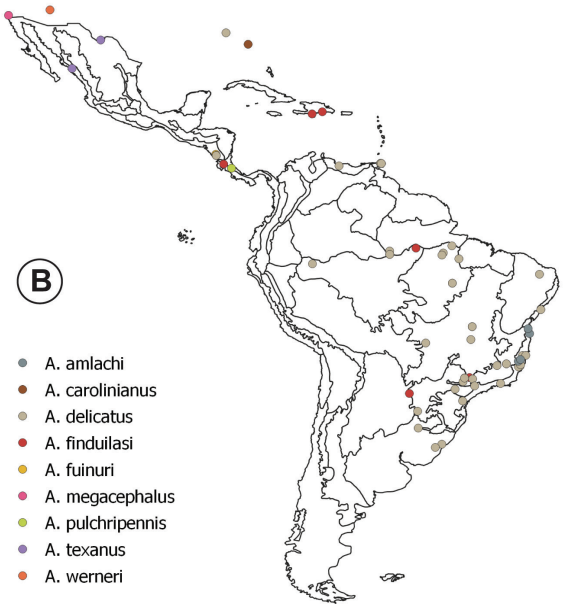


Figure 6. Geographical distribution of species-group. **A** *guianae* **B** *megacephalus*.

cies-groups. This further supports the hypothesis that the Northern Amazonia or Paraná region could be the original distribution area for *Anisepyris* species; moreover, these areas are often recognized as important areas of endemism (see Nihei and Carvalho 2007).

This also indicates a close relationship between the Northern Amazonia and Paraná regions, in concordance with Pires and Marinoni (2010). The concordance with Pires and Marinoni (2010) is explained because both groups (*Anisepyris* and Sciomyzidae, Diptera) are dominant in wet forest (Amazonia and Atlantic) areas with fewer records from open areas (Cerrado), indicating the influence of open areas on posterior diversification.

Moreover, the discussion about the species with metallic reflection on the body surface further supports the hypothesis of the original distribution area, because these are covered by dense forests.

Andean Amazonia distribution

An interesting feature of *Anisepyris* distribution is the absence of species from the South American Transition Zone and Andean regions. All species registered from the Andes were related to a continuous of Amazonia forest, from the Northern Amazonia region.

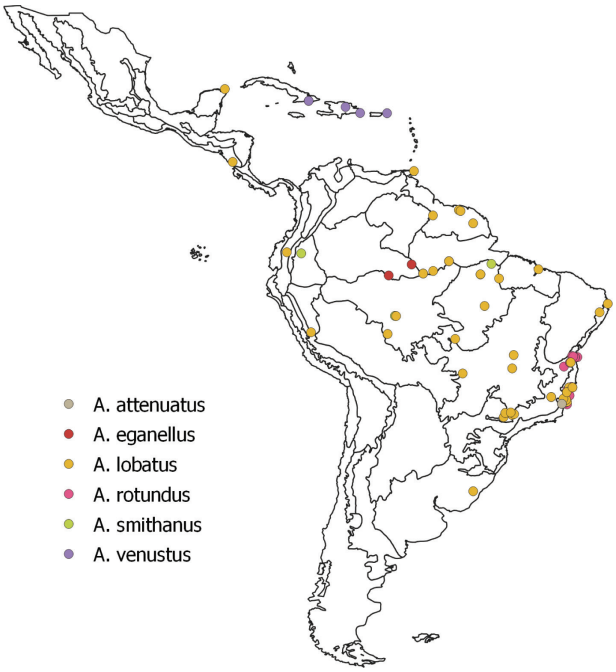


Figure 8. Geographical distribution of *venustus* species-group.

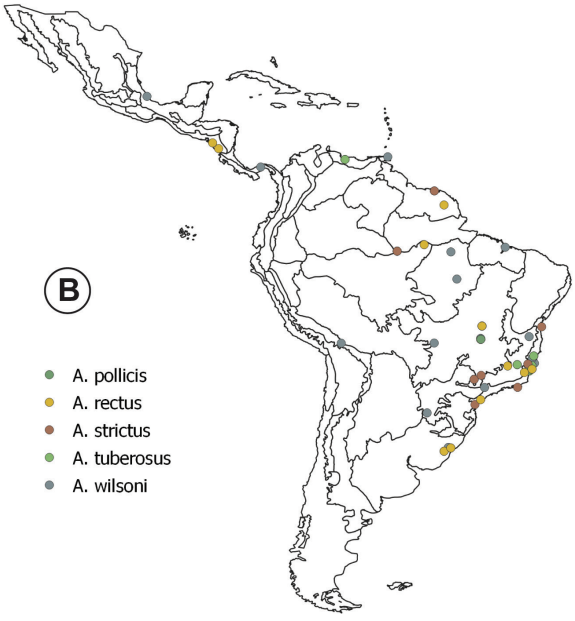


Figure 7. Geographical distribution of species-group. **A** *proteus* **B** *strictus*.

The Andes mountain range had its formation about 66 million years ago, which occurred previous to the apparent origin of the *Anisepyris* stem group. This conformation could explain the absence of species registers in the South American Transition Zone and Andean regions, and corroborate the Northern Amazonia or Paraná regions as the original distribution area for *Anisepyris* species.

The historical connection between the Northern Amazonia and Paraná regions was frequently reported and described (see Pennington et al. 2010); this connection was lost in Pleistocene glacial cycles due to retraction of forest habitats and the expansion of open xerophilous vegetation. Camargo and Pedro (2003) discussed that faunal exchanges were observed to the north of the Andes and Mérida (Venezuela), but with no relation to the fauna of the south-western America region. For Meliponini (Apidae, Apinae), such an overlap could be attributed to the recent Quaternary, in groups related to the Guianas Brazil craton (northern Amazonia region), and could extend to Panama. From this, the hypothesis that the original distribution area for *Anisepyris* was the northern Amazonian region or Paraná regions, and dispersal to the North-western American region occurred subsequently is plausible.

Distant distributions and autapomorphies

The species-groups *aeneus*, *amazonicus*, *columbianus*, *megacephalus*, *proteus*, and *venustus* have greater diversity than the other groups. Hence, their distributions extend to the Antilles, Mesoamerica, and Nearctic regions; except the *amazonicus* species-group that was not registered from the Nearctic region, and the *proteus* species-group that was not registered from the Antilles.

From the topology retrieved (Fig. 1), some autapomorphic characteristics were observed, as follow: complete extension of metapostnotal-propodeal suture – fused with posterior carina (#30:1, for *A. megacephalus*); long setae of flagellomeral pubescence (#74:1, for *A. westwoodi*); longer than wide length of metapectal-propodeal complex (#87:2, for *A. jocundus*). Some other exclusive characteristics were described for *Anisepyris* species by Barbosa and Azevedo (2018), and almost all of them are for species included in the species-groups cited above.

It is interesting that these species with distribution distant from the hypothesized original distribution are have discrepant characteristics; the same was observed for species of the *bogotensis* species-group, related to their distribution at Antilles region. The prevalence of autapomorphies in species from outlying distributions could further

support the hypothesis of the Amazonia or Paraná regions as the original distribution area for the genus.

Chaco distribution

Some *Anisepyris* species have their body surface without metallic reflection. The species with this characteristic were registered from the Nearctic region and Chaco region. Both regions are characterized by forests with less density, unlike the dense Amazonia and Atlantic forests. From the previous discussion about metallic reflection, insights can be gained regarding the subsequent dispersal of *Anisepyris* species from original distribution areas to the Chaco regions, based on the absence of metallic reflection in species registered from the Chaco region.

This scenario could be explained based on data from Pires and Marinoni (2010) (also in Ramos and Melo 2010), since the authors postulated that the species in the Chaco region could have originated from an enclave of humid forest previously present in this region, which had its origin from the Pleistocene contraction of the Amazonia and Atlantic forests. According to Costa (2003), the central Brazilian areas could play an important role as both present and past habitats for rain forest species. As corroborated by Pires and Marinoni (2010), and in this work, *Anisepyris* species are prevalent in gallery forests found along rivers, emphasizing the importance of savanna biomes in the investigation of the history of humid environments. Thus, the Chaco region could have influenced the evolutionary history of species in the Amazonia and Paraná regions.

Therefore, the reduced records of *Anisepyris* species from the Chaco region and lack of metallic reflection could be related to subsequent dispersal of these species from Amazonia and Paraná regions to Chaco region, and their consequent adaptation to niches related to lower forest density.

Probable dispersal routes

From the scenarios exposed above and the related geographic and morphological character distributions of *Anisepyris* species, the following probable ancient dispersal routes for species is proposed:

– Northern Amazonia > Paraná;
– Paraná > Northern Amazonia;
– Northern Amazonia > Chaco;
– Paraná > Chaco;
– Northern Amazonia > Antilles
– Paraná > Northern Amazonia > Antilles;
– Northern Amazonia > north-western South America > Mesoamerica > Nearctic;
– Paraná > Northern Amazonia > north-western South America > Mesoamerica > Nearctic.

Discrepant distribution patterns

Besides the hypothesis of original distribution area, and the distribution and dispersal patterns discussed above, two species-groups have discrepancies in relationship to all other groups. The *bifidus* species-group has its distribution recorded only from the Paraná region; and the *proteus* species-group, one of most diverse, has no distributions registered from the Antilles and Mesoamerica regions.

For the *bifidus* species-group, this could be explained based on a possible recent origin of this group. The species-group has an exclusive characteristic in comparison to the other *Anisepyris* species-groups; in all species the male genitalia have the paramere bifid. No other species-group shares this characteristic, which could indicate this monophyletic lineage arose recently (Fig. 1) within the genus. This recent origin could explain the restricted distribution of this species-group.

For the *proteus* species-group, the explanation could be more complex, in view that this group has huge species diversity and wide distribution across the sub-regions of the Neotropical region. Despite the high species diversity, there is not a high diversity of morphological characteristics; contrary to that observed in other species-groups with high species diversity. Thus, it is probable that the proteus species-group's evolutionary lineage was restricted to fewer niches, in comparison to the other species-groups. Therefore, its diversification could have favored sympatric speciation that restricted the group's dispersal to other sub-regions, such as the Antilles and Mesoamerica regions.

5. Conclusions

Anisepyris is doubtlessly a monophyletic group, corroborating all previous works cited. Moreover, its synapomorphies were here reestablished based on a large set of species; thus, a more accurate definition for this genus was suggested.

The characteristics analyzed for the *Anisepyris* species-groups indicated some derived characteristics, in relation to the other Epyrinae (Bethylidae) genera. And their relationship with the distributional registers turned up some hypothesis for species distribution among the Neotropical sub-regions.

Furthermore, the transformations of the characteristics observed along the topologies could elucidate some transformation series not just for the genus, but also for the subfamily Epyrinae.

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Supplementary material

File 1

Authors: Barbosa DN (2021)
Data type: .doc
Explanation note: Characters of females – Characters not applicable to taxa for which only male specimens are available.
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File 2

Authors: Barbosa DN (2021)
Data type: .xlsx
Explanation note: Data matrix of morphological characters.
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