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RESEARCH ARTICLE

Bayesian and parsimony analyses based on morphological data reveal a new genus of spilomenine wasps (Hymenoptera: Crabronidae: Pemphredoninae) from Australia

Brunno B. Rosa[1,2], **Gabriel A.R. Melo**[2]

[1]*Laboratório de Biologia Comparada e Abelhas, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo. 14040-901 Ribeirão Preto, SP, Brazil.*
[2]*Laboratório de Biologia Comparada de Hymenoptera, Departamento de Zoologia, Universidade Federal do Paraná. Caixa Postal 19020, 81530-980 Curitiba, PR, Brazil.*
Corresponding author: Brunno B. Rosa (brunnobueno27@gmail.com)

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ABSTRACT. Pemphredoninae are a very large lineage of crabronid wasps with more than a thousand species. In this lineage, the subtribe Spilomenina stand out for containing the smallest apoid wasps and by exhibiting relatively complex social behavior such as female nest-sharing and even eusocial colonies. One of the most conspicuous features of this subtribe, and which seems to be associated with its social behavior, is the presence of silk spinnerets that are used for lining and nest building. In the present study, we conducted Bayesian inference and parsimony analyses with a subset of a previously established morphological data matrix of Pemphredoninae. Our phylogenetic results indicate that *Spilomena subterranea* McCoquodale & Naumann, 1988, an Australian spilomenine species that presents nest-sharing behavior but lacking silk apparatus represents an independent lineage, recognized here in a new genus, *Australomena* **gen. nov.** Our results indicate that *Australomena* **gen. nov.** is sister group of the remaining Spilomenina (*Arpactophilus*, *Microstigmus*, *Spilomena* and *Xysma*). The females of *Australomena* **gen. nov.** shows clear adaptations for ground nesting, such as a pygidial plate and basitibial plates on the hind legs, that means that nest-sharing behavior arose very early in Spilomenina evolution, apparently long before the emergence of the silk apparatus.

KEY WORDS. Crabronidae, *Spilomena*, apoid wasps, eusociality, partitioning, homoplasy criterion, social behavior, silk spinnerets.

INTRODUCTION

Pemphredonine wasps are a lineage of crabronid, a group of predatory wasps with 1,035 living species worldwide (Pulawski 2022). Together with the families Ampulicidae, Heterogynaidae, Sphecidae and bees (Apidae sensu lato) they comprise the superfamily Apoidea, one of the most important clades of Hymenoptera with more than 30,000 living described species (Ascher and Pickering 2023, Pulawski 2022). Although the monophyly of these four families seems stable, the relationships of the crabronid lineages remain under discussion (Melo 1999, Sann et al. 2018, Pulawski 2022). In the main hypotheses, the crabronid lineage forms a monophyletic group closely related to bees (Crabronidae + Apidae) (Melo 1999); or the crabronids are paraphyletic relative to bees (Alexander 1992, Debevec et al. 2012, Branstetter et al. 2017, Peters et al. 2017, Sann et al. 2018).

Pemphredonines are often abundant, but smaller forms are usually overlooked by collectors (Bohart and Menke 1976). The females provision their nests with Hemiptera or in few cases with Thysanoptera or Collembola (Bohart and Menke 1976, Melo 2000). The subfamily is usually split in two tribes, that can be easily distinguished by the presence of three submarginal cells in Psenini and no more than two in the Pemphredonini (Bohart and Menke 1976). Traditionally, Pemphredonini is composed of three subtribes: Ammoplanina, Pemphredonina and Stigmina (Bohart and Menke 1976). However, phylogenetic results based on morphological and genomic data show that the Ammoplanina do not belong to this lineage (Melo 1999, Sann et al. 2018). Morphological data support evidence that this lineage belongs to the Astatinae (Melo 1999), while genomic data suggest that this group may be related to bees (Sann et al. 2018). Furthermore, Stigmina was redefined by Menke (1989) separating the group into two subtribes: Spilomenina and Stigmina. This redefinition is very strongly supported by phylogenetic analyses based on morphological data (Melo 1999).

Spilomenina contains the smallest apoid wasps, with body length of 1.8 to 5.0 mm, and many of the species exhibiting social behavior in the form of female nest-sharing and even eusocial colonies (Matthews 1968, Melo and Campos 1993, Melo 2000, 2020). The subtribe comprises about 202 living species in four genera (Menke 1989, Melo 1999, Pulawski 2022). *Arpactophilus* has an Australasian distribution and contains approximately 74 species (Menke 1989, Pulawski 2022). *Microstigmus* has about 29 species very well distributed throughout the Neotropical region, while *Xysma* has three described species found in the USA, West Indies and Panama (Pulawski 2022), in addition to a few undescribed species (GAR Melo, unpubl. data). Unlike the other genera, *Spilomena* is found in all biogeographic regions and are relatively abundant, also presenting the greatest diversity of the subtribe, with about 95 living species (Pulawski 2022).

The monophyly of Spilomenina is strongly supported by the morphological evidence (Melo 1999). The most conspicuous synapomorphy of this clade is the presence of silk spinnerets associated with the 6th metasomal tergum of the female (Melo 1997, 1999). From these spinnerets, silk is secreted and used in lining and building nests (Naumann 1988, Melo 1997, 2000, 2020). As far as known, all pemphredonine species that shows social behavior also have a silk apparatus (Melo 2000, 2020). Conversely, a peculiar Australian species, *Spilomena subterranea* McCoquodale & Naumann, 1988 is an exception which, despite not having silk spinnerets, also exhibits nest-sharing behavior (Matthews and Naumann 1989, Matthews 1991). The combination between this distinct morphology and remarkable behavior seem to indicate an independent lineage in Spilomenina (Melo 1997, 1999). In this work we evaluate the phylogenetic position of *S. subterranea* and propose the recognition of this lineage as a new genus based on a subset of morphological characters presented by Melo (1999), and analyzed under parsimony and Bayesian inference.

MATERIAL AND METHODS

Examined material and morphological dataset

We examined 10 females and one male of *Spilomena subterranea* from Brisbane Water National Park (33°28'S; 151°21'E), New South Wales, Australia, deposited in the Coleção Entomológica Pe. Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brazil. Its external morphology was studied from pinned specimens and the internal morphology was studied from complete dissection of a female. The dissection protocols followed Melo (1999). The dataset used for the phylogenetic analyses comprises a subset from the morphological matrix presented in Melo (1999) and in Rosa and Melo (2023). Some characters have been simplified by reducing the number of states. The matrix and the character list are available as Supplementary Materials S1 and S2, respectively. The terminals used in the analyses were the same as those used in Melo (1999), comprising species of Spilomenina, Stigmina and Pemphredonina, namely: *Arpactophilus steindachneri* Kohl, 1884, *Spilomena catamarca* Antropov, 1992, *Parastigmus huecuvus* Finnamore, 1995, *Stigmus temporalis* Kohl, 1892, *Diodontus rugosus* Fox, 1892, *Passaloecus areolatus* Vincent, 1979, and *Pemphredon inornata* Say, 1824. Rooting of the trees was placed in the branch leading to *Mimesa cressonii* Packard. In total, the dataset used corresponds to nine terminals and 64 characters. The terminology and classification used follow Melo (1999).

Parsimony analyses

Parsimony analyses was conducted in TNT version 1.5 (Goloboff et al. 2008, Goloboff and Catalano 2016), with all characters treated as unordered. Characters for which no information was available were coded as missing data using "?" and characters for which encoding did not apply were marked as "*". Analyses were conducted with equal weights and under implied weighting. For implied weighing, the software default (k = 3) was used. For the two analyses cited, a traditional heuristic search for the most parsimonious cladograms was used, with the following commands: Traditional search; hold1000; multi*1000; hold/10; and multiple TBR+TBR. The resulting cladograms were visualized in Winclada software version 1.0.8 (Nixon 2002), with only unambiguous optimizations being plotted. The ancestor state reconstruction of the silk apparatus and the nest-sharing behavior was conducted in Mesquite v. 2.75 (Maddison and Maddison 2014). Both characters were treated as unordered in the parsimony optimization.

Bayesian inference

The matrix was partitioned according to the homoplasy criterion proposed by Rosa et al. (2019). Under this criterion, the characters are partitioned according to their homoplasy values, therefore, the characters are organized in partitions corresponding to these values (Table 1). We measured the homoplasy values using the TNT (Goloboff et al. 2008) through an implied weighing analysis, with the default concavity parameter (k = 3). The values are normalized between 0 and 1, with the lowest value corresponding to no homoplasy. The values indicated as "–" correspond to non-informative characters. The model fit was adjusted according to suggestions by Rosa et al. (2019), as follow: ascertainment bias as variable, branch lengths linked among-partition rate variation, equal rates among-character rate variation, and the branch length prior equal to 10. We compare two partitioning models: one where non-informative characters are left in an independent partition, and another where these same characters are placed in the same partition containing the characters with zero homoplasy.

Table 1. Characters contained in each partition with their respective homoplasy values.

Homoplasy values	Characters
Partition 1 = 0	9, 10, 14, 15, 17, 18, 23, 28, 33, 37, 42, 47, 51, 54-58, 63, 64
Partition 2 = 0.25	2, 6, 19, 21, 24, 26, 30-32, 35, 36, 41, 45, 48, 49, 52
Partition 3 = 0.4	25, 29, 38, 61, 62
Partition 4 = –	1, 3-5, 7, 8, 11-13, 16, 20, 22, 27, 34, 39, 40, 43, 44, 46, 50, 53, 59, 60

Bayesian inference was carried out in MrBayes 3.2.7 (Ronquist et al. 2012), using runs of 1×10^6 generations, two independent runs (four chains each) and 25% of initial burnin. The convergence and performance of the runs were evaluated according to the average standard deviation of divided frequencies (ADSSF), less than 0.01; potential scale reduction factor (PSRF) equal or very close to 1.00; and the estimated sample size (ESS) for each parameter above 200. For generating the trees, we applied the 50% majority rule consensus (Contype = Halfcompat) and the majority rule consensus with all-compatible groups added (Contype = allcompat). For both consensuses, the posterior probability was used as branch support. The two partitioning models were compared using Bayes factors and interpreted according to Kass and Raftery (1995). Marginal likelihood was calculated using the stepping stone method in MrBayes software (Xie et al. 2011). Fifty steps were applied to estimate the marginal likelihood with 5 x 10^6 generations at a sampling frequency of 5000 units and a burnin of 25%.

RESULTS

Phylogenetic results

The partitioning schemes evaluated showed distinct marginal likelihoods. Model 1, containing the non-informative characters in their own partition, presented a marginal likelihood equal to -327.58, while model 2, where these characters were included in the partition of characters with zero homoplasy, presented -330.36 marginal likelihood units. According to the values presented in Kass and Raftery (1995), the final bayes factor between the models indicates "positive evidence" against H_0, that is, model 1 is considerably better than model 2. The MCMC analysis conducted with four partitions did not present difficulties in their convergence and the resulting topology is shown in Fig. 1A and 1B.

The parsimony analyses under equal or implied weighting showed significantly similar topology, with the only difference being a polytomy between the relationships involving the Pemphredonina in the unweighted tree. The analysis under implied weighting resulted in a single tree with a length of 109 steps, a consistency index of 74 and a retention rate of 64. The analysis under equal weights resulted in two equally parsimonious trees with a length of 107 steps, a consistency index of 75 and a retention index of 66. These two topologies are shown in Fig. 1C and 1D, respectively.

TAXONOMY

Pemphredonini Dahlbom, 1835

Spilomenina Menke, 1989

Australomena gen. nov.

Fig. 2

https://zoobank.org/B6469B91-6868-47A8-900A-069FC9CCC5FB

Type species: *Spilomena subterranea* McCoquodale & Naumann, 1988. Holotype: ♀, Australia: New South Wales: Brisbane Water National Park (Australian National Insect Collection, Commonwealth Scientific and Industrial Research Organization, Canberra, ACT, Australia).

Diagnosis. *Australomena* gen. nov. can be easily recognized by palpal formula 6-4, fore tarsus of female rather expanded apically, hind leg with a basitibial plate, T6 of female lacking silk spinnerets, pygidial plate present on female, hind tibia and T6 of female and T7 and S8 of male with stout spiniform setae, and T5-T7 of male with medial dorsal groove.

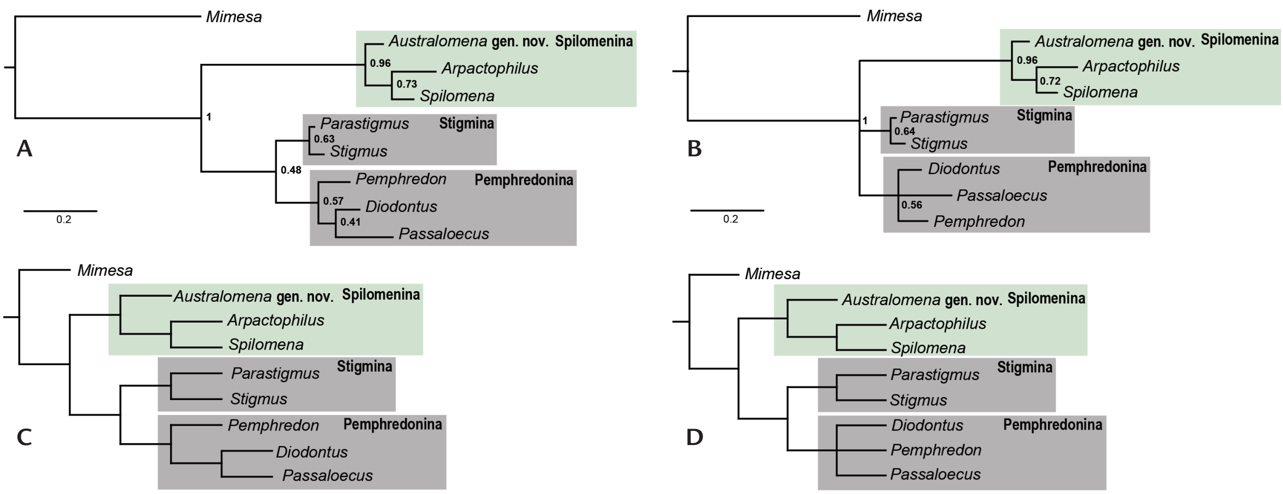


Figure 1. Phylogenetic hypotheses of Pemphredonini based on morphological data: (A) Bayesian inference tree with majority rule consensus with all-compatible groups added. Posterior probability as branch support. (B) Bayesian inference tree with 50% majority rule consensus. Posterior probability as branch support. (D) Parsimony tree under implied weighting. (C) Strict consensus under equal weights.

Description. Head: In frontal view wider than long; labrum small and bilobed; palpal formula 6-4; mandible with one dorsal subapical tooth, inner and outer surfaces of mandible evenly curved; clypeus with short, weak, longitudinal carina, lower margin of female clypeus with medial, narrow, U-shaped emargination, V-shaped in male; apical inflection of clypeus joining mesal to tentorial pit; epistomal suture extending above tangent to upper rim of antennal sockets; tentorial pit above tangent to lower rim of antennal sockets; antennal socket in contact with clypeus, their distance nil; antenna with scape and flagellomeres stout, scape as long as F1-F7; inner orbits of eye convex and diverging below; hypostomal carina sinuate; occipital carina interrupted ventrally. Mesosoma: pronotal collar delimited with transverse carina; mesoscutum convex; admedian line and parapsidial lines distinct; notauli indicated by shallow sulci anteriorly; mesepisternal sulcus restricted to lateral portion of mesepisternum (absent ventrally); omaular sulcus and carina present; fore basitarsus broad, mid and hind basitarsus slender; dorsoapical margins of tarsomeres not bilobed; hind tibia with basitibial plate; hind tibia with row of stout spiniform setae; triangular posterior extension of metapostnotum flat. Wings: fore wing with two submarginal cells and marginal cell distally acute; hind wing M vein diverging from CuA at cu-a. Metasoma: anterior portion of T1 not forming petiole; T1 of female with anteromedian groove; T5-T7 of male with medial longitudinal groove; S2 of female with deep and transverse slope; T6 of female dorsally flattened with narrow pygidial plate; S8 of male posteromedial broadly produced posterolateral acutely; T6 of female and T7 and S8 of males with stout spiniform setae.

Remarks. The new genus is currently known only from Australia. In addition to the type species, there are several undescribed species (see McCorquodale and Naumann 1988: 228).

DISCUSSION

The application of Bayesian methods in morphological data has been increasingly frequent in phylogenetic studies (Clarke and Middleton 2008, Lee et al. 2013, 2014, Tarasov and Génier 2015, Lee and Palci 2015, Rosa et al. 2019, Porto et al. 2021, Casali et al. 2022, Gonçalves et al. 2022). One of the aspects that has been heavily investigated in these approaches is the partitioning of morphological data (Clarke and Middleton 2008, Tarasov and Génier 2015, Rosa et al. 2019). The homoplasy partitioning criterion is the most efficient way of partitioning morphological data and its biggest advantage is that it requires a very simplified model fit (Rosa et al. 2019). The homoplasy value of each character works as a proxy for morphological evolution rates which guarantees their better accommodation in a given model (Rosa et al. 2019). Currently, it has been argued that non-informative characters should be part of the category (partition) of

Figure 2. *Australomena subterranean*: (A) female frontal head; (B) female lateral habitus; (C) male frontal head view; (D) male lateral habitus. Scale bars: A, C = 0.2 mm, B, D = 1 mm.

non-homoplastic characters rather than a category itself. This adjustment increased the marginal likelihood between competing models, and therefore was considered as a relevant adjustment to the models (Rosa et al. 2019, Casali et al. 2022, Gonçalves et al. 2022).

Our results point to the opposite, where the model with an independent partition for the non-informative characters had a considerably increased marginal likelihood compared to the other evaluated model. This increase seems to be related to the size of this partition. In our dataset, the number of non-informative characters is greater than the non-homoplastic character set, 23 and 20 characters, respectively. This considerable difference in marginal likelihood seems to indicate that reducing a partition of this size did not efficiently accommodate the heterogeneity of rates. However, even if these results are of interest in understanding the functioning of the homoplasy criterion, matrices with a high number of non-informative characters are uncommon, and therefore, including the non-informative characters in the same partition as the non-homoplastic ones still seems the best procedure.

The Bayesian inference analysis with four partitions, as well as the results of the parsimony analysis, point to the recognition of three lineages in Pemphredonini: Spilomenina, Sitgmina and Pemphredonina (Fig. 1). Additionally, most of our results seem to indicate two major clades in Pemphredonini, one composed by Spilomenina and the other by Stigmina + Pemphredonina (Fig. 1A, 1C and 1D). These results corroborate those presented in Melo (1999) and as indicated by this author, the Stigmina + Pemphredonina clade is supported by few but strong synapomorphies (Fig. 3).

The monophyly of Spilomenina is very well supported in our results, with at least nine transformations (Fig. 3). The main transformations of this clade are the posterior wall of pharynx not expanded (9:0) and the upper part forming a pair of elongate diverticula (10:1), the apical inflection of clypeus joining considerably mesal to tentorial pit (15:1), the forewing M + CuA longer than cu-a (47:1) and the triangular posterior extension of metapostnotum flat (51:0) (Fig. 3). Spilomenina is defined here to include the genera *Arpactophilus*, *Microstigmus*, *Spilomena*, *Xysma* and *Australomena* gen. nov. These results corroborate those already presented by Melo (1999).

The clade represented here by *Arpactophilus* and *Spilomena*, but which also includes *Microstigmus* and *Xysma*, has three unique transformations: the socket of foreleg spur narrowly connected to basitarsal socket and away from tibial apex (28:1), silk glands associated with spinnerets in the female T6 (55:1) and loss of the pygidial plate (56:1). In this clade, the modifications of the female 6th tergum as a silk apparatus are directly associated with the nesting habits, that is use of pre-existing cavities or digging of nest tunnels in very friable substrates (Matthews 1968, Matthews and Naumann 1989, Matthews 1991, Melo 2000, Matthews and Naumann 2002). Also, the silk secreted by spinnerets is used in covering and building these nests (Melo 2000). In addition, several species of *Arpactophilus*, *Spilomena* and *Microstigmus* exhibit social behavior in the form of female nest-sharing and even eusocial colonies (Matthews 1968, Melo and Campos 1993, Melo 2000, 2020).

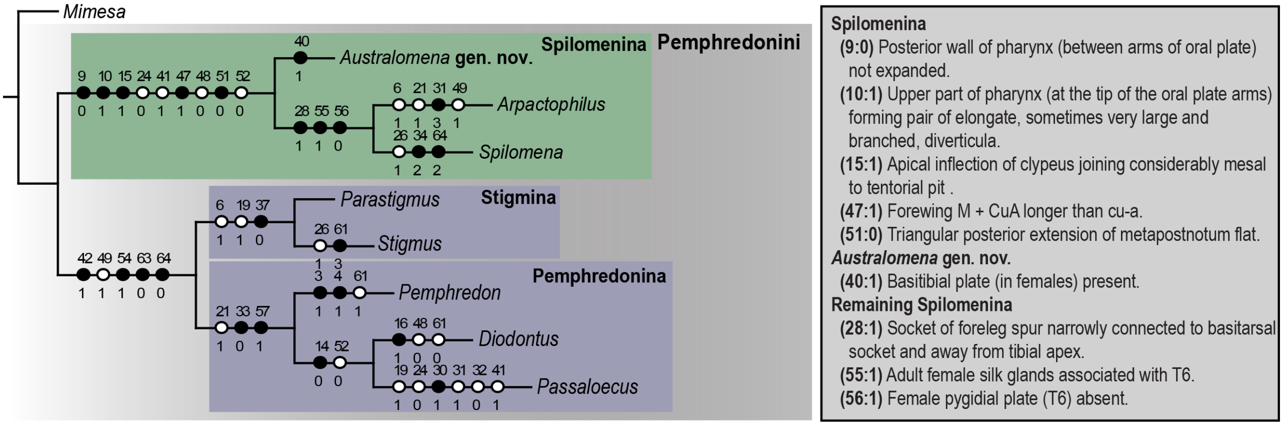
Nest-sharing is particularly interesting because the most complex societies found in Hymenoptera are composed of females specialized in the care of offspring and nest maintenance, and a single or few fertile females specialized in egg production (Melo 2000, 2020). *Australomena* gen. nov. also exhibits nest-sharing behavior, commonly with 2-4 females per nest, but unlike other Spilomenina it has strong adaptations for digging nests in relatively compact soils (McCorquodale and Naumann 1988). Also, the females have a well-defined basitibial plate on the hind leg (40:1; see figures 17 and 18 in McCorquodale and Naumann 1988) that probably are pressed against the nest walls to hold the females in place. Possession of a pygidial plate, spiniform setae and expanded tarsi assist females in digging their nests, as do other apoid wasps (Bohart and Menke 1976, McCorquodale and Naumann 1988).

This combination of features in *Australomena* gen. nov. suggests that the nest-sharing behavior arose early in the Spilomenina lineage, long before the evolution of silk glands and spinnerets (Fig. 4). Our phylogenetic results support this hypothesis since *Australomena* gen. nov. is consistently positioned as a sister group to the other genera of the subtribe (Figs 1 and 4). Finally, another interesting issue of the emergence of silk spinners is that apparently the production of silk allowed the evolution of nests with relatively complex architecture in some lineages of Spilomenina, especially in *Microstigmus* (Melo 2000, 2020). Future work linking all these aspects with more detailed investigation and a broader species representation in a phylogenetic framework will be pivotal for fully understanding the factors underlying the evolution of silk spinnerets in Pemphredoninae.

Concluding remarks

Phylogenetic approaches are fundamental to the recognition new taxa in modern classifications. Using both parsimony and Bayesian inference has shown a powerful combination to test evolutionary relationships using morphological data. In a phylogenetic Bayesian perspective, the homoplasy partitioning criterion is strongly effective even in small datasets. Also, model tests are decisive in choosing different partitioning schemes even when applying a single partitioning criterion. Other comparative methods, in this case the reconstruction of ancestral characters, were also fundamental for understanding the evolutionary phenomena involved in the present study.

Australomena gen. nov. belongs to the Spilomenina clade and is consistently positioned as sister group to the other genera of the subtribe. The combination of presence of nest-sharing and the absence of spinnerets in the T6 suggests that silk production arose long after the emergence of social behavior in Spilomenina. Even if the appearance of the silk apparatus came late in Spilomenina, this may have been a turning point in the emergence of complex behaviors, especially related to nest building. Recognition of this new lineage sheds light on the evolution of pemphredonine wasps and expands our knowledge of the evolution of social behavior in Apoidea. Finally, additional new species of *Australomena* gen. nov. are known, but describing them goes beyond the scope of the present study and will be dealt with in future contributions.



Spilomenina
(9:0) Posterior wall of pharynx (between arms of oral plate) not expanded.
(10:1) Upper part of pharynx (at the tip of the oral plate arms) forming pair of elongate, sometimes very large and branched, diverticula.
(15:1) Apical inflection of clypeus joining considerably mesal to tentorial pit .
(47:1) Forewing M + CuA longer than cu-a.
(51:0) Triangular posterior extension of metapostnotum flat.
***Australomena* gen. nov.**
(40:1) Basitibial plate (in females) present.
Remaining Spilomenina
(28:1) Socket of foreleg spur narrowly connected to basitarsal socket and away from tibial apex.
(55:1) Adult female silk glands associated with T6.
(56:1) Female pygidial plate (T6) absent.

Figure 3. Parsimony tree with implicit weighting and unambiguous transformations.

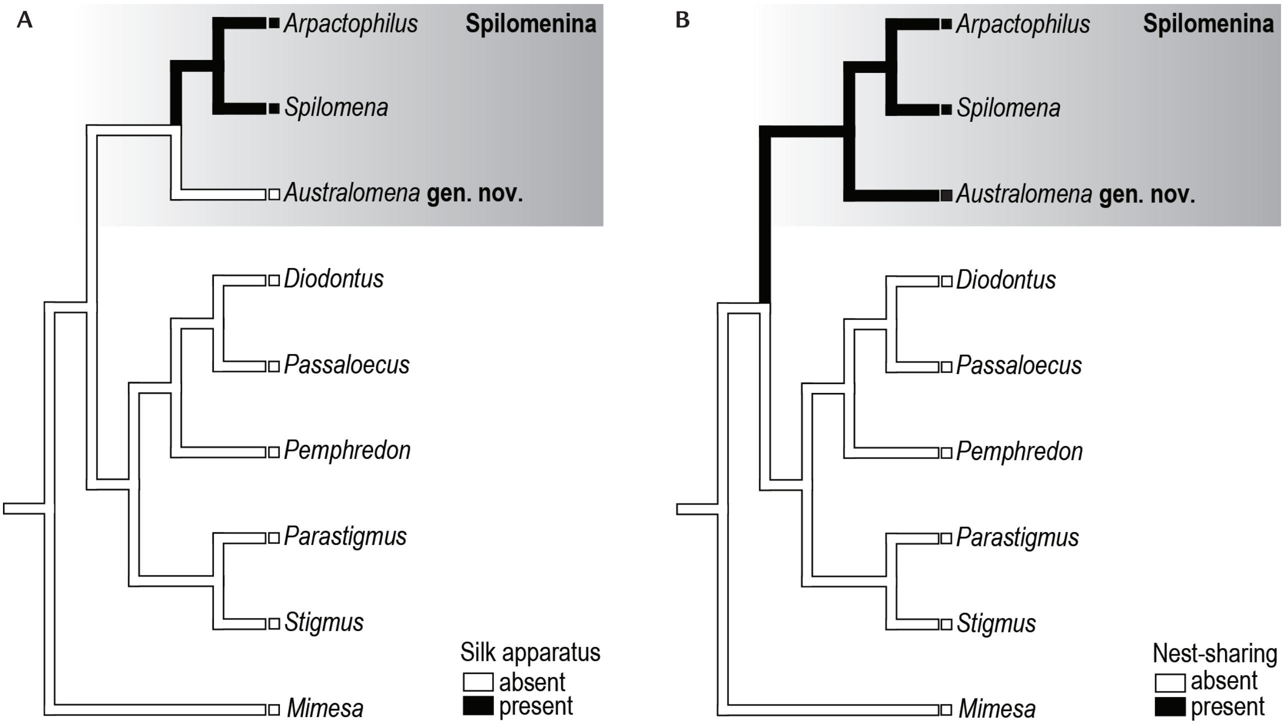


Figure 4. Ancestral character state reconstruction (parsimony optimization) for two features found in Spilomenina: (A) Silk apparatus; (B) Nest-sharing behavior.

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Supplementary material S1

Supplementary S1. List of phylogenetic characters.
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Supplementary material S2

Supplementary S2. Phylogenetic matrix.
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