



CAROLINA DE ALMEIDA GARCIA

**Systematics of the porricondylines
(Diptera, Cecidomyiidae) with
particular emphasis on the Brazilian
Fauna**

Single Volume

SÃO PAULO

2023

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**Sistemática dos porricondilíneos (Diptera, Cecidomyiidae) com
ênfase na fauna Brasileira**

Single Volume

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RESUMO

Os porricondilíneos incluem 880 espécies de mosquitos fungívoros incluídas em 118 gêneros distribuídos em duas subfamílias, Porricondylinae e Winnertziinae. As espécies conhecidas estão distribuídas principalmente na região Paleártica, constituindo 75% de sua distribuição global. Dentro da região Neotropical, 48 espécies de 15 gêneros de porricondilíneos contribuem para essa diversidade. O Brasil abriga espécies de apenas cinco gêneros: *Bryocrypta*, *Cassidoidea*, *Claspettomyia*, *Porricondyla* e *Haplusia*. Apesar da aparente prevalência do grupo na região Paleártica, a região Neotropical carece de mais pesquisas e especialistas em cecidomiídeos não-galhadores, gerando incertezas sobre a abrangência da distribuição desse grupo. As larvas dos porricondilíneos são conhecidas por seus hábitos saproxílicos ou oligófagos, prosperando em diversos ambientes. Já os adultos exibem comportamentos distintos, alguns empoleiram em teias de aranha, outros habitam folhas caídas ou formam enxames próximos ao solo. Um total de 116 espécimes machos pertencentes às subfamílias Porricondylinae e Winnertziinae foram obtidos de amostras de insetos coletadas em armadilhas Malaise armazenadas nas coleções de Diptera do Museu de Zoologia e da Faculdade de Filosofia de Ribeirão Preto, ambas unidades da Universidade de São Paulo, e da Universidade Federal de Goiás. As amostras abrangem cinco países da Região Neotropical: Brasil, Colômbia, Chile, Peru e Paraguai. No caso do Brasil, 19 estados foram amostrados. Visando o posicionamento dos novos táxons, uma análise cladística baseada na morfologia dos machos foi conduzida. Um total de 97 caracteres discretos foram levantados. Além disso, uma classificação previamente aceita de Porricondylinae e Winnertziinae foi reexaminada neste estudo, revelando que a composição dessas subfamílias, conforme atualmente consideradas na literatura, é não monofilética. A análise propõe uma reclassificação, resultando em quatro subfamílias distintas: Heteropezinae, Diallactiinae, Winnertziinae e Porricondylinae, apoiadas por altos valores do índice de Bremer Relativo (89, 60, 47 e 74, respectivamente). Este estudo, também corrobora Cecidomyiinae como o grupo-irmão de uma tribo de Porricondylinae, evidenciando a necessidade de continuar a investigar as relações destas duas subfamílias. Os resultados da análise cladística mostraram que todos os espécimes no estudo pertencem a 72 novas espécies e 30 novos gêneros. Dentre eles, 36 espécies estão classificadas em nove gêneros previamente conhecidos. Esta pesquisa contribui para o entendimento da diversidade dos porricondilíneos no Brasil, lançando luz sobre sua distribuição e suas relações evolutivas.

Palavras-chave: Biodiversidade. Análise Cladística. Fungívoros. Região Neotropical.
Porricondylinae. Reclassificação Taxonômica. Winnertziinae.

ABSTRACT

The porricondyline species include 880 fungivore species into 118 genera distributed in two subfamilies, Porricondylinae and Winnertziinae. The known species are primarily distributed in the Palearctic region, constituting 75% of their global distribution. Within the Neotropical region, 48 species from 15 genera of porricondyline species contribute to this diversity. Brazil hosts species from only five genera: *Bryocrypta*, *Cassidoidea*, *Claspetomyia*, *Porricondyla*, and *Haplusia*. Despite their prevalence in the Palearctic region, the Neotropical region lacks comprehensive research and experts in non-gall midges, leading to uncertainties about their distribution. The larvae of this group are known for their saproxylic or oligophagous mycelium-feeding habits and thrive in diverse environments. Adult porricondyline species exhibit distinctive behaviors, including roosting in spider webs, inhabiting leaf litter, and forming swarms near the ground. A total of 116 male specimens belonging to the subfamilies Porricondylinae and Winnertziinae were obtained from insect samples collected in Malaise traps that are stored in the Diptera collections of the Museu de Zoologia and Faculdade de Filosofia de Ribeirão Preto, both belonging to the Universidade de São Paulo, and the Universidade Federal de Goiás. The samples comprise five countries of the Neotropical Region: Brazil, Colombia, Chile, Peru, and Paraguay. In the case of Brazil, 19 States were covered. To place the new taxa a cladistic analysis based on the male morphology was conducted. The sampling resulted in 97 discrete characters for analysis. Additionally, a previously accepted classification of Porricondylinae and Winnertziinae was reexamined in this study, revealing that the composition of these subfamilies, as they are currently considered in the literature, is non-monophyletic. The analysis proposes a reclassification, resulting in four distinct subfamilies: Heteropezinae, Diallactiinae, Winnertziinae, and Porricondylinae, supported by high Relative Bremer values (89, 60, 47, and 74, respectively). This study also corroborates Cecidomyiinae as the sister group of a tribe of Porricondylinae, highlighting the need to continue investigating the relationship of these two subfamilies. The results of the phylogenetic analysis showed that all the specimens in the study belong to 72 new species and 30 new genera. Among them, 36 species are classified into nine genera that were previously known. This research contributes to understanding the diversity of the porricondyline species in Brazil, shedding light on their distribution and evolutionary relationships.

Keywords: Biodiversity. Cladistic Analysis. Fungivores. Neotropical Region. Porricondylinae. Taxonomic Reclassification. Winnertziinae.

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1. INTRODUCTION

Cecidomyiidae is a group of small flies commonly known as gall midges. The family is classified within the Order Diptera, Infraorder Bibionomorpha, Superfamily Sciaroidea, and it is one of the most diverse family of Diptera encompassing more than 6,600 documented species distributed across 812 genera worldwide (Dorchin et al., 2017, Gagné & Jaschhof, 2021). The synapomorphies of the family Cecidomyiidae are the absence of tibial spurs, reduced larval cephalic capsule with elongated and styliform mandibles, and presence of larval prothoracic spatula (Gagné & Jaschhof, 2021).

Adults are generally characterized by body size ranging from 1 to 10 mm, usually light to dark brown, orange, or yellow. Head with holoptic eyes, ocelli absent (excepted in Lestremiinae and Micromyinae), antennae usually with 10–14 flagellomeres, that may range from fewer than 10 to 67, each ornamented with circumfila or other translucent sensilla. Wing venation reduced to R1, R4+5 and M4 + CuA veins, legs long with first tarsomere shortened, male terminalia diverse, and female ovipositor usually long and protrusible (Dorchin et al., 2017).

Six subfamilies are currently recognized in the literature: Catotrichinae (not reported in Europe), Lestremiinae, Micromyinae, Porricondylinae, Winnertziinae, and Cecidomyiinae. Although the majority of the species exhibit a galling habit, accounting for 75% of the species richness, the first five subfamilies mentioned above, along with two supertribes within Cecidomyiinae (Brachineuridi and Stomatosematidi), still possess the mycophagous feeding behavior (Gagné & Jaschhof, 2021).

Porricondylinae and Winnertziinae (*sensu* Jaschhof & Jaschhof, 2013), collectively referred to here as porricondylines, consist of approximately 880 species of fungivores, distributed into 118 extant genera, 6 tribes, and 88 fossils at present. The three tribes exhibiting the highest levels of diversity are: Porricondylini, comprising a total of 328 species; Winnertziini with 171 species; and Asynaptini, comprising 164 species (Table 1). The Palearctic region accounts for 75% of the total distribution of these species (Gagné & Jaschhof, 2021).

Within the Neotropical region, 48 species belonging to 15 genera constitute a portion of the overall species diversity (see Appendix A – Table 1). Two genera, namely *Feltomyia* Alexander, 1936 and *Zadbimyia* Jaschhof & Jaschhof, 2014 (22 spp.) (Gagné & Jaschhof,

2021), are exclusive to this region. Porricondylinae (*sensu* Jaschhof & Jaschhof, 2013) comprises 11 species and four genera in Brazil, namely *Bryocrypta* Kieffer, 1896, *Cassidoidea* Mamaev, 1960, *Claspettomyia* Grover, 1964, and *Porricondyla* Rondani, 1840 (Garcia et al., 2023a, Garcia et al., 2023b, Garcia et al., 2023c, Garcia et al., 2023d). In Winnertziinae, seven genera occur in the Neotropical region: *Gynapteromyia* Mamaev, 1965, *Haplusia* Karsh, 1877, *Jhonsonomyia* Felt, 1908, *Loboplusia* Jaschhof, 2016, *Makrostyles* Jaschhof, 2016, and *Winnertzia* Rondani, 1860. Only the monotypic genus *Makrostyles* is exclusive to this region (Gagné & Jaschhof, 2021). For the time being, *Haplusia plumipes* Karsh, 1877 and *H. braziliensis* Felt, 1915, are the only species reported in Brazil (Gagné & Jaschhof, 2021).

Table 1. Number of species within each tribe belonging to the subfamilies Porricondylinae and Winnertziinae (*sensu* Jaschhof & Jaschhof, 2013).

Subfamilies	Tribes	Total number of species	Number of species in Brazil	Number of species in the Neotropical Region
Winnertziinae	Heteropezini	46 sp. (9 genera)	_____	_____
	Diallactini	46 sp. (13 genera)	2 sp. (1 genus)	5 sp. (4 genera)
	Winnertziini	171 sp. (7 genera)	_____	2 sp. (1 genus)
	Unplaced	2 sp. (2 genera)	_____	_____
Porricondylinae	Dicerurini	84 sp. (16 genera)	_____	_____
	Porricondylini	328 sp. (50 genera)	11 sp. (4 genera)	1 sp. (1 genus)
	Asynaptini	164 sp. (14 genera)	_____	27 sp. (4 genera)
	Unplaced	10 sp. (8 genera)	_____	_____

The Palearctic region stands out for the remarkable richness and abundance of non-gall midges, a notable contrast when measured against the comparatively lower numbers found in the Neotropics. The lack of research and experts on this group has probably obscured their occurrence in the region. Evidence for this is the porricondylines described to Costa Rica (Jaschhof & Jaschhof, 2014), which indicate a significant richness in the Neotropical region. This emphasizes the necessity to undertake similar studies in other regions. Carmo-Neto et. al (2019) have resumed the studies of the subfamily Lestremiinae to Brazil. The authors have

been reporting the occurrence of dozens of new species (Carmo-Neto unpublished doctoral thesis, Carmo-Neto et. al, 2021). This work aims to contribute to the beginning of the studies of the porricondyline of Brazil and the progress of the knowledge of this still so-neglected group.

1.1. Biology of the porricondyline

The literature on the biology of this group is notably limited and it generally focuses on the morphological description of immature stages. Plakidas (2018) exemplifies this with a comprehensive work on larval morphology and an illustrated identification key for Porricondyline in Pennsylvania, USA. However, despite these efforts, there is a noticeable scarcity of information regarding the overall biology of this group.

Larvae of Porricondyline species are known for their saproxylic or oligophagous mycelium-feeding habits, and they inhabit various environments. These include decaying wood surroundings, spaces beneath tree bark, and in some cases, they can even be found in association with cones and cacti (Foote, 1956, Hedlin & Johnson, 1968, Jaschhof & Jaschhof, 2013). Larvae of the genus *Dicerura* Kieffer, 1899 and those in the tribe Asynaptini have been found in the cavities of living plants, probably feeding mainly on the mycelia growing in these hollows (Spungis, 1987, Jaschhof & Jaschhof, 2013).

A little more is known about the biology of Heteropezini species. Wyatt (1967) investigated the immature stages of Cecidomyiidae, shedding light on the unique life cycle of Heteropezini. His research unveiled that Heteropezini larvae exhibit paedogenesis, a phenomenon in which certain insects can reproduce while still in the larval stage. The larvae of the genus *Miastor* Meinert, 1864, produce eggs from ovarioles distributed throughout the larval fat body. In cases where food is scarce, the developing embryos obtain nutrients from the mother's fat body. After hatching, the larvae begin to feed on the mother's internal organs, initiating another cycle of paedogenesis immediately after emerging from the cuticle (Klowden & Palli, 2022).

Adult porricondyline display distinct behaviors, such as roosting in spider webs or inhabiting leaf litter, some close to living plants, or forming swarms near the ground (Jaschhof & Jaschhof, 2013). Intriguingly, this behavior bears a resemblance to species found in the subfamilies Lestremiinae (*Anarete* Haliday, 1833 and *Conarete* Pritchard, 1951) and

Micromyinae (*Micromyia* Rondani, 1840), hinting at potential ecological connections among these groups (Jaschhof & Jaschhof, 2013).

1.2. Classification of the porricondyline

The classification of the porricondyline has been a subject of historical debate among cecidomyiologists, particularly the controversial placement of the Heteropezini within the evolutionary history of the aforementioned group.

In 1868, Schiner initially established Heteropezinae as a subfamily of Cecidomyiidae, along Lestremiinae and Cecidomyiinae. In 1913, Kieffer assigned the subgroup Porricondylariae to the subfamily Cecidomyiinae. Enderlein (1936) subdivided Porricondylinae into three families: Camplomyzidae, Heteropezidae, and Cecidomyiidae (Jaschhof & Jaschhof, 2013). Möhn (1955) reclassified the tribe Porricondylini as an independent family and Heteropezinae as a subfamily, based on analyses of larval morphology.

Panelius (1965) revised the European porricondyline and, following Möhn (1965) clarified that Porricondylinae constituted a paraphyletic group. According to his dendrogram (Figure 1), Porricondylinae is the sister group of Cecidomyiinae (former Itonidinae) and comprises five tribes: Leptosynini, Winnertziini, Diallactini, Porricondylini, and Asynaptini. Panelius (1965) also indicated that Diallactini is a paraphyletic group that originated from the lineage leading to the sister-group Asynaptini + Porricondylini.

Wyatt (1967) established the tribe Heteropezini under Porricondylinae based on studies of larval paedogenesis. He proposed that paedogenesis occurred independently two times in Cecidomyiidae: first in the subfamily Lestremiinae, and then once more in the former Heteropezinae Shiner, 1868. (Parnell, 1971, Jaschhof & Jaschhof, 2013). Mamaev (1968) classified Heteropezini and Porricondylini as two tribes within the subfamily Cecidomyiinae.

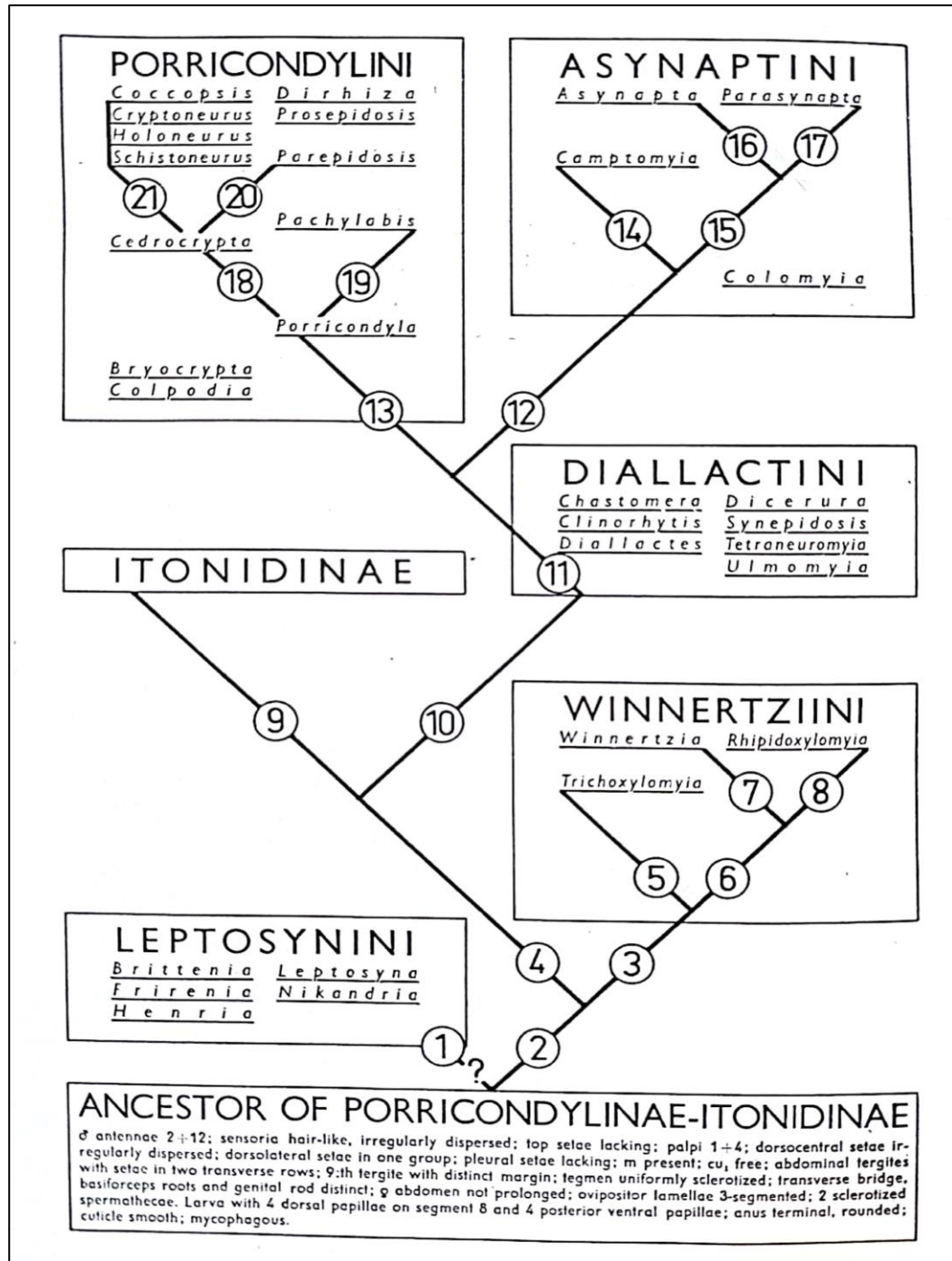


Figure 1. Dendrogram of the evolutionary history of Porricondylinae proposed by Panelius (1965). 1. Antennae with 11 flagellomeres, dorsocentral setae reduced, pleural setae present, wing veins reduced, paedogenesis; 2. Larval anus split-shaped; 3. M vein reduced, female abdomen prolonged, larval cuticle striated; 4. Ring-shaped sensilla, top setae present, pleural setae present; 5. Antennae with 11 flagellomeres; 6. Sensilla present medially and laterally; 7. Two sensillas; 8. Four sensillas; 9. Wing veins reduced, terminalia specialized, larva with two dorsal and two ventral papillae on segment 8; 10. Antennae with 14 flagellomeres, dorsocentral setae in row, dorsolateral setae in two groups; 11. M vein reduced, tegmen not sclerotized, female cerci bi-segmented; 12. Antennae with more than 14 flagellomeres, tergite setae in four groups, abdomen prolonged; 13. Cu forked; 14. Cu forked, terminalia with lateral hooks; 15. Dorsolateral setae only anteriorly, apodemes of tergite 9, aedeagus and gonocoxites recuded. 16. Spermatheca; 17. Cu forked; 18. Transverse bridge reduced; 19. Transverse bridge posteriorly, gonostylus club-shaped; 20. Margin of tegmen strongly sclerotized; 21. CuA reduced.

Tastás-Duque in his unpublished PhD thesis (Department of Zoology, Stockholm University, 2001), studied the ultrastructure of female abdomen, male terminalia, and the head of 3rd instar larva of 33 terminal taxa of Cecidomyiidae, including Sciaridae and Mycetophilidae as outgroup. Through a cladistic analysis he classified the subfamily into four distinct subfamilies, Heteropezinae, Diallactinae, Winnertziinae, and Porricondyliinae (Fig. 2). The distinguishing characteristics supporting Heteropezinae were: absence of ocelli, reduced wing venation, non-sclerotized spermatheca, unseparated gonocoxites, and legs with fewer than five tarsomeres. Diallactinae exhibited synapomorphies such as furcation of the M vein, five tarsomeres, significantly shorter first tarsomere compared to the others, a single sclerotized spermatheca, and unseparated gonocoxites. The adult features supporting Winnertziinae included the presence of simple circumfila and three-segmented female cerci. Porricondyliinae, on the other hand, was distinguished by the presence of circumfila and bi-segmented female cerci.

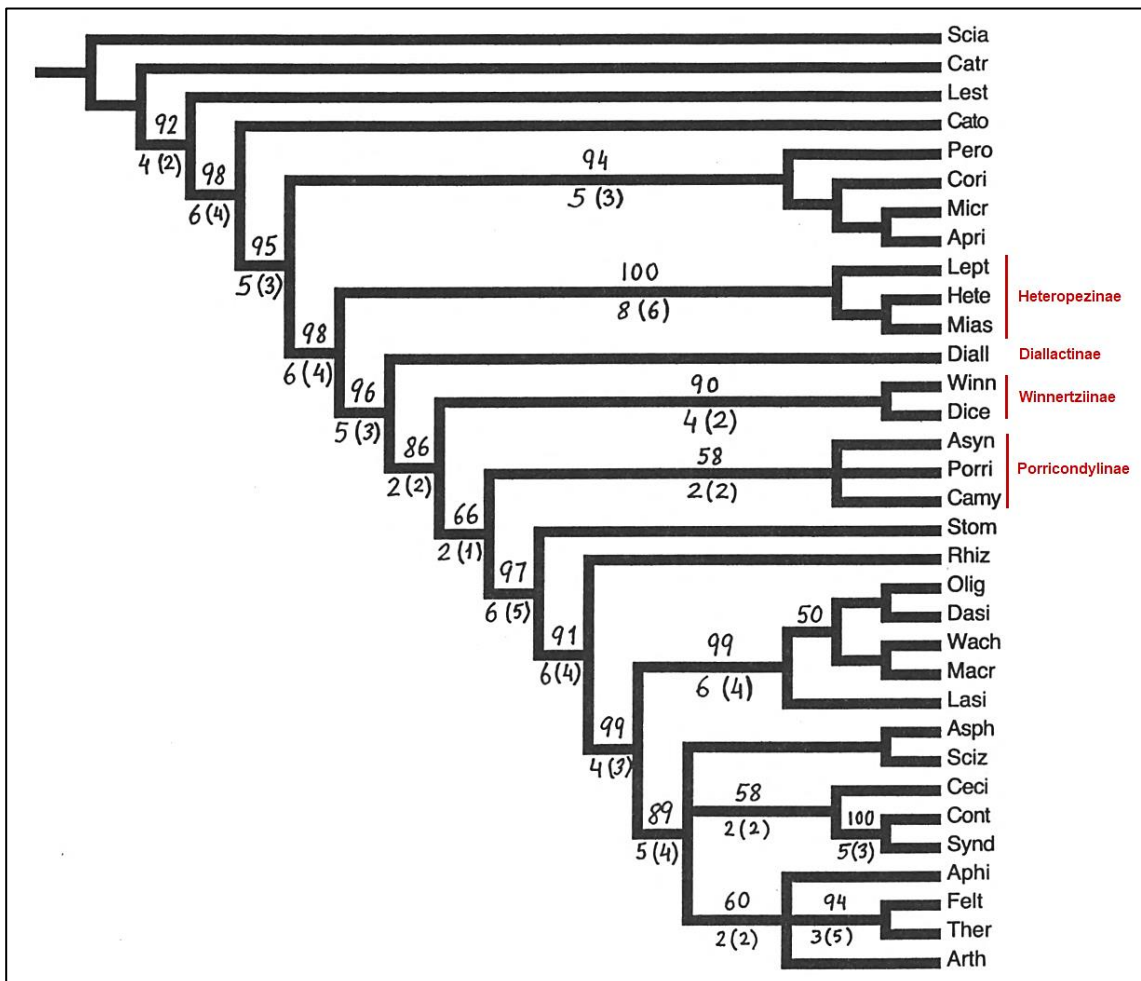


Figure 2. Consensus tree of the cladistic analysis of Cecidomyiidae by Tastás-Duque (2001, unpublished PhD thesis). Modified from Tastás-Duque (2001, unpublished PhD thesis).

Fedotova & Perkovsky (2009) proposed a different classification for Cecidomyiidae, arranging it into three subfamilies: Lasiopterinae, Porricondylinae, and Cecidomyiinae. Some Porricondylinae were distributed among the remaining subfamilies, and Heteropezidi was designated as a monophyletic supertribe within Lasiopterinae.

Jaschhof & Jaschhof (2013) revised the traditional Porricondylinae and reclassified the group into two subfamilies: Porricondylinae, consisting of three tribes (Dicerurini, Porricondylini, and Asynaptini), and Winnertziinae, which includes three other tribes (Heteropezini, Diallactini, and Winnertziini). Winnertziinae had previously been considered by earlier authors as a group of the Porricondylinae (Gagné & Jaschhof, 2021). Jaschhof & Jaschhof (2013) also present generic subdivisions for some genera/tribes within the subfamilies. The genus *Winnertzia*, for example, is subdivided into five groups. Likewise, the genus *Porricondyla* is divided into three distinct groups based on the type of gonostylus claws. The tribe Porricondylini is categorized into four generic groups based on the number of flagellomeres and basitarsal spines. Despite Jaschhof & Jaschhof's (2013) classification being widely accepted (Fig. 3), it has a weak point that can be criticized, namely the fact it was based on intuitive assumptions rather than a robust cladistic analysis. Additionally, some of the considered tribes lack synapomorphies to support their clades (see Fig. 3).

Jaschhof & Jaschhof's (2013) classification is based on the presence or absence of "true circumfila" (Fig. 6H–I). They proposed that the presence of this character is a shared derived trait of Porricondylinae + Cecidomyiinae. The "true circumfila" is absent in species of Winnertziinae and other primitive subfamilies. However, an important question that requires further clarification is the resemblance between the circumfila and the translucent sensilla (Fig. 6B–G) found in the Winnertziini tribe. Tastás-Duque hypothesized that the sensilla and the "true circumfila" are homologous. He referred to the ribbon-shaped circumfila in the Winnertziinae as "simple circumfila", which differs from the complete whorl formation seen in Cecidomyiinae. Panelius (1965) previously recognized the ring-shaped circumfila as a derived character, whereas the original type comprised irregularly scattered sensory hairs present in some Winnertziinae.

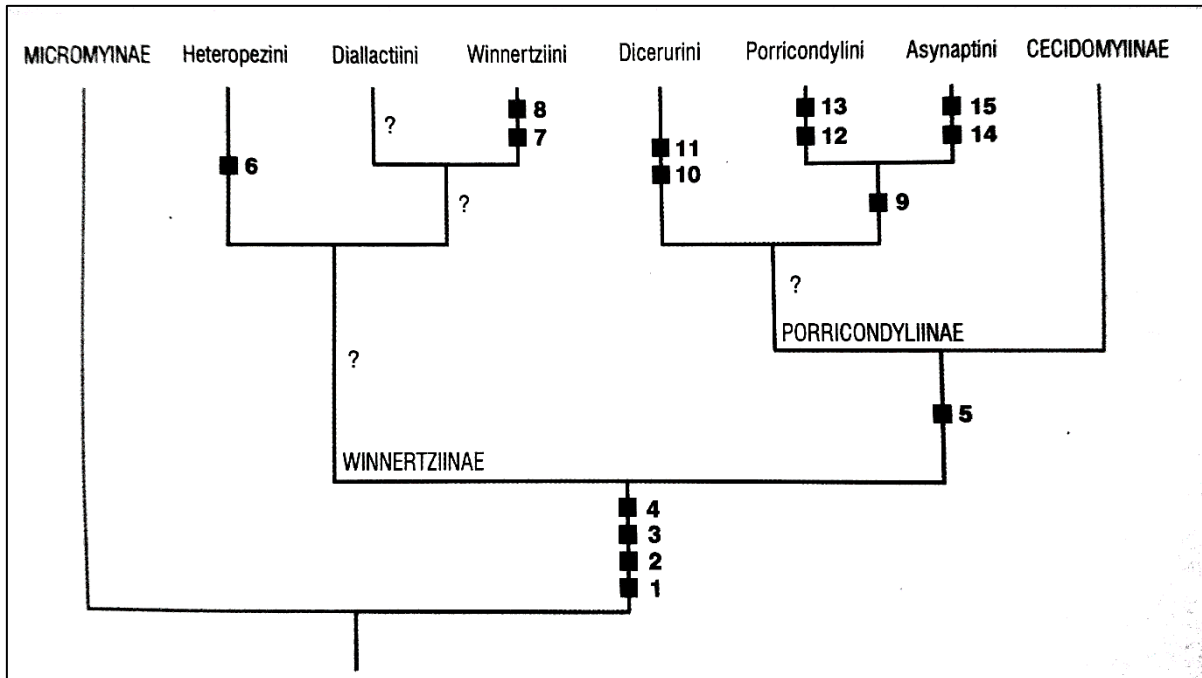


Figure 3. Intuitive classification of Porricondyliinae and Winnertziinae proposed by Jaschhof & Jaschhof (2013). 1. Ocelli absent; 2. Basitarsi shorter than second tarsomeres; 3. C and R5 confluent; 4. Wing membrane setae reflexed; 5. Circumfila present; 6. Fewer than 5 tarsomeres; 7. Aedeagus bulge present; 8. Ovipositor strongly prolonged; 9. Dorsal ovipositor lamellae 2-segmented; 10. Male circumfila with long extensions; 11. Parameral apodemes prolonged and curved; 12. Female with fewer than 14 flagellomeres; 13. Female ninth tergite enlarged; 14. More than 14 flagellomeres; 15. Abdominal sclerites are divided into 2 or 4.

Sikora et al. (2019) conducted a molecular analysis (Fig. 4) and found that all tribes of Cecidomyiidae, except Diallactiini (Winnertziinae) and Dicerurini (Porricondyliinae), form monophyletic groups. The authors argued that the paraphyly of Winnertziinae, based on the absence of circumfila, challenges the proposal made by Jaschhof & Jaschhof (2013) which, according to them, is difficult to defend.

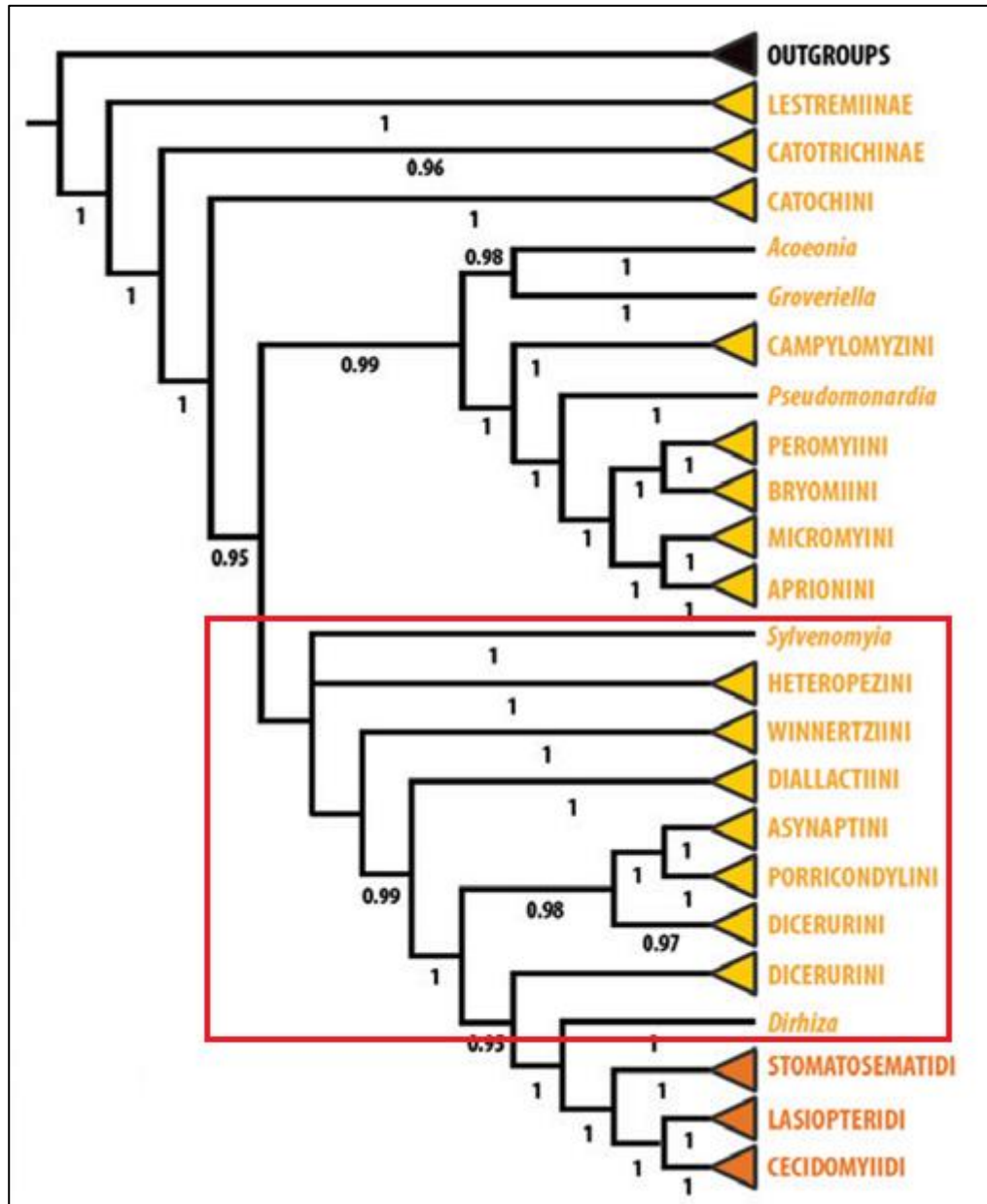


Figure 4. Simplified Bayesian cladogram of Cecidomyiidae proposed by Sikora et al. (2019). The taxa within the red rectangle belong to the subfamilies Porricondylinae and Winnertziinae. Modified from Sikora et al. (2019).

1.3. Adult morphology of the porricondylines

In broad terms, the porricondylines are delicate midges with legs that are much longer than their bodies, resembling those of Lestremiinae. The body size ranges from 1 to 7 mm. Specimens of the porricondylines are orange or yellow, elongated, and slender, with long antennae, and hairy wings. Winnertziinae can be characterized by their brown color, short and robust bodies, short antennae, and scale-covered wings.

The description provided below for the porricondyline is for males and it is primarily based on the works of Panelius (1965) and Jaschhof & Jaschhof (2013).

Head. Ocelli absent. The head capsule is subglobular (Fig. 5A), and the maxillary may be protuberant (Fig. 5B–C), aetose and membranous. The antennae vary in length between 9–63 flagellomeres and the flagellomeres are gradually shortened toward apex. The scape is usually cylindrical, the pedicel is rounded, and the nodes contain translucent sensillas (Fig. 6). The sensillas vary in size and shape, and are divided into two groups, multiporous (filiform, U- or Y-shaped, and circumfila) and uniporous (filiform). In Dicerurini, the circumfila has posteriorly extensions. In Diallactiini, the flagellomere nodes have a crenulated whorl of hooded alveoli. The postfron is bilobed and aetose, the prefrons are large, and the labrum is elongated. Palpus usually with 4 segments, but it may range from 1 to 4 segments, gradually longer and covered by microtrichia and setae. In Diallactiini, the segments bear translucent sensilla.

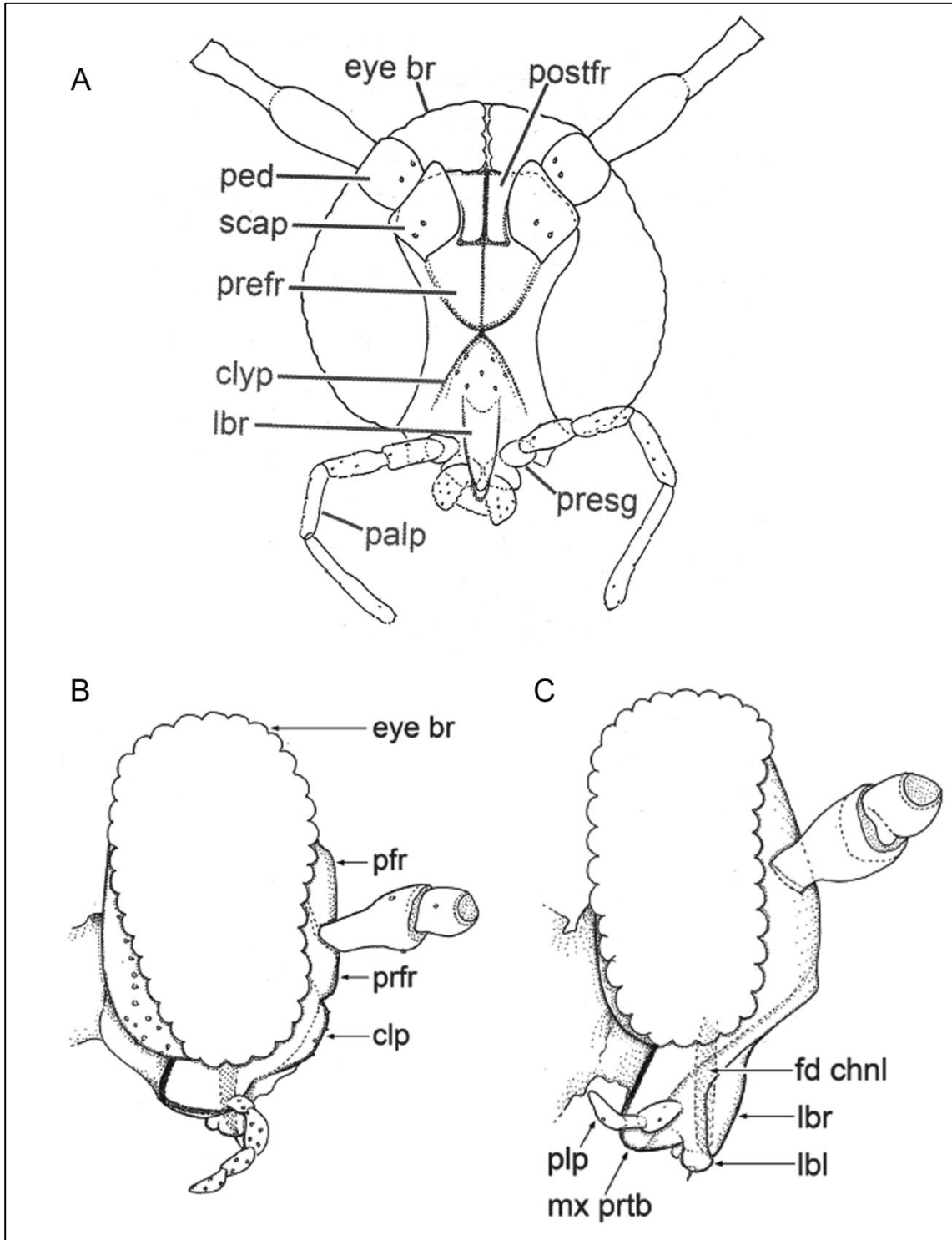


Figure 5. Head morphology of the porricondylines. A. *Diallyctia crocea* (Kieffer, 1894); B. *Zadbimya anniae* Jaschhof & Jaschhof, 2014; C. *Zadbimya spinapiscis* Jaschhof & Jaschhof, 2014. Without scale. clp = clypeus, eye br = eye bridge, fd chnl = food channel, lbl = labellum, lbr = labrum, mx prt = maxillary protuberance, ped = pedicel, pfr/postfr = postfrons, plp/palp = palpus, prfr/prefr = prefrons, presg = presegment, scap = scape. Modified from Jaschhof & Jaschhof (2013, 2014).

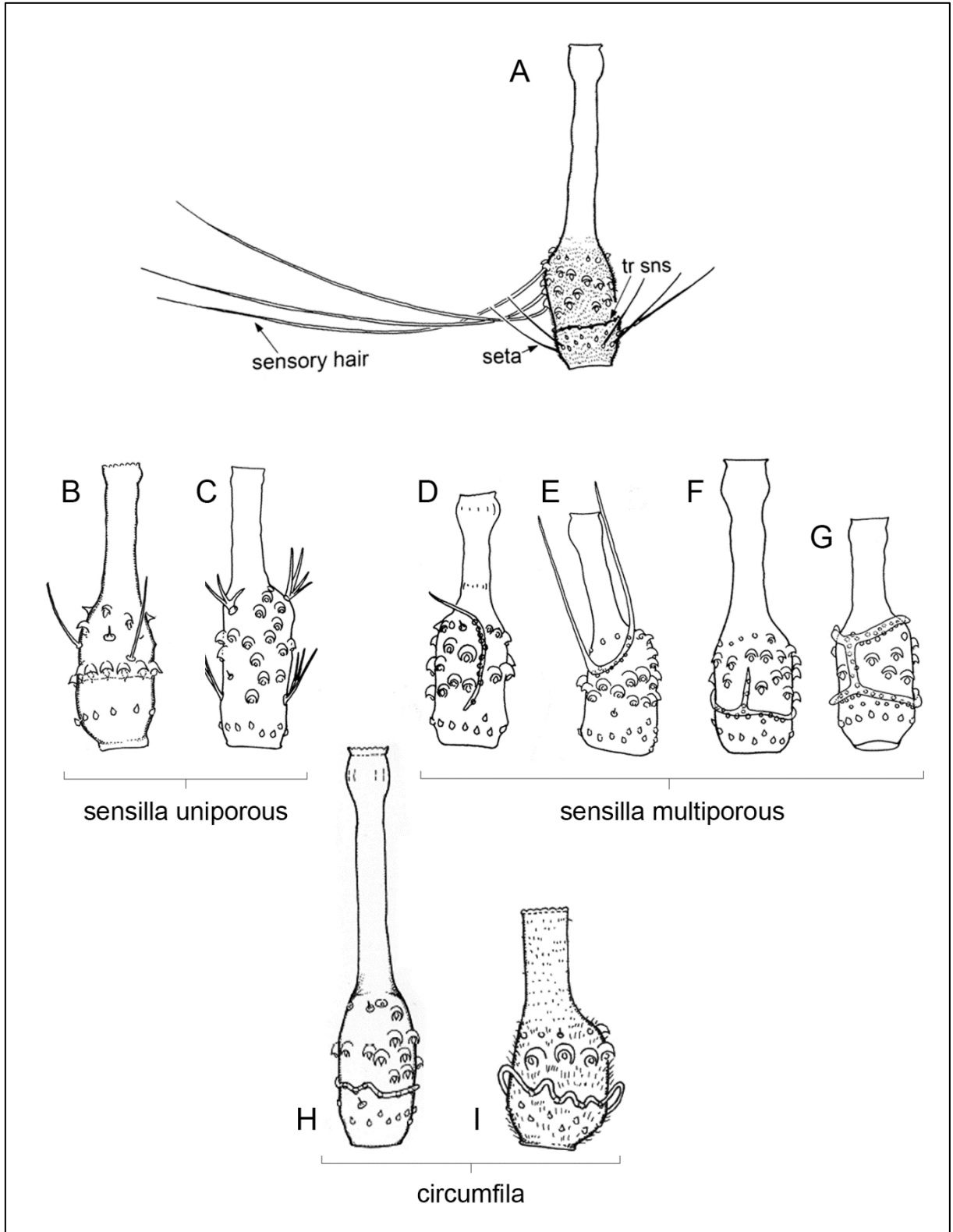


Figure 6. Sensillas of the porricondyline. A. *Porricondyla fulvescens* Panelius, 1965; B. *Gynapteromyia costaricensis* Jaschhof, 2016; C. *Rhipidoxylomyia excavata* Mamaev, 1964; D. *Winnertzia xylostei* Mamaev, 1963; E. *Winnertzia tridens* Panelius, 1965; F-G. *Dicerura mixta* Spungis, 1987; H. *Porricondyla diversicornis* Jaschhof, 2020; I. *Zadbimya costaricensis* Jaschhof & Jaschhof, 2014. Modified from Jaschhof & Jaschhof (2013, 2014, 2016, 2020).

Thorax. The mesothoracic pleurites are usually setose (Fig. 7A), being absent in Winnertziini. In some Porricondylini, the thorax has membranous windows, one anterior of the parapsidal suture and the other anterior of the scutellum. The wings are longer than the body. The veins pattern is: C and R4+5 confluent, Rs distinct, following the same direction of R1 or R4+5 or, as observed in Winnertziini, forming an angle with these two veins, M may be absent or weak, CuA reaching wing base, M4 may be present or absent (Fig. 7B). Wing venation is markedly reduced in Heteropezini.

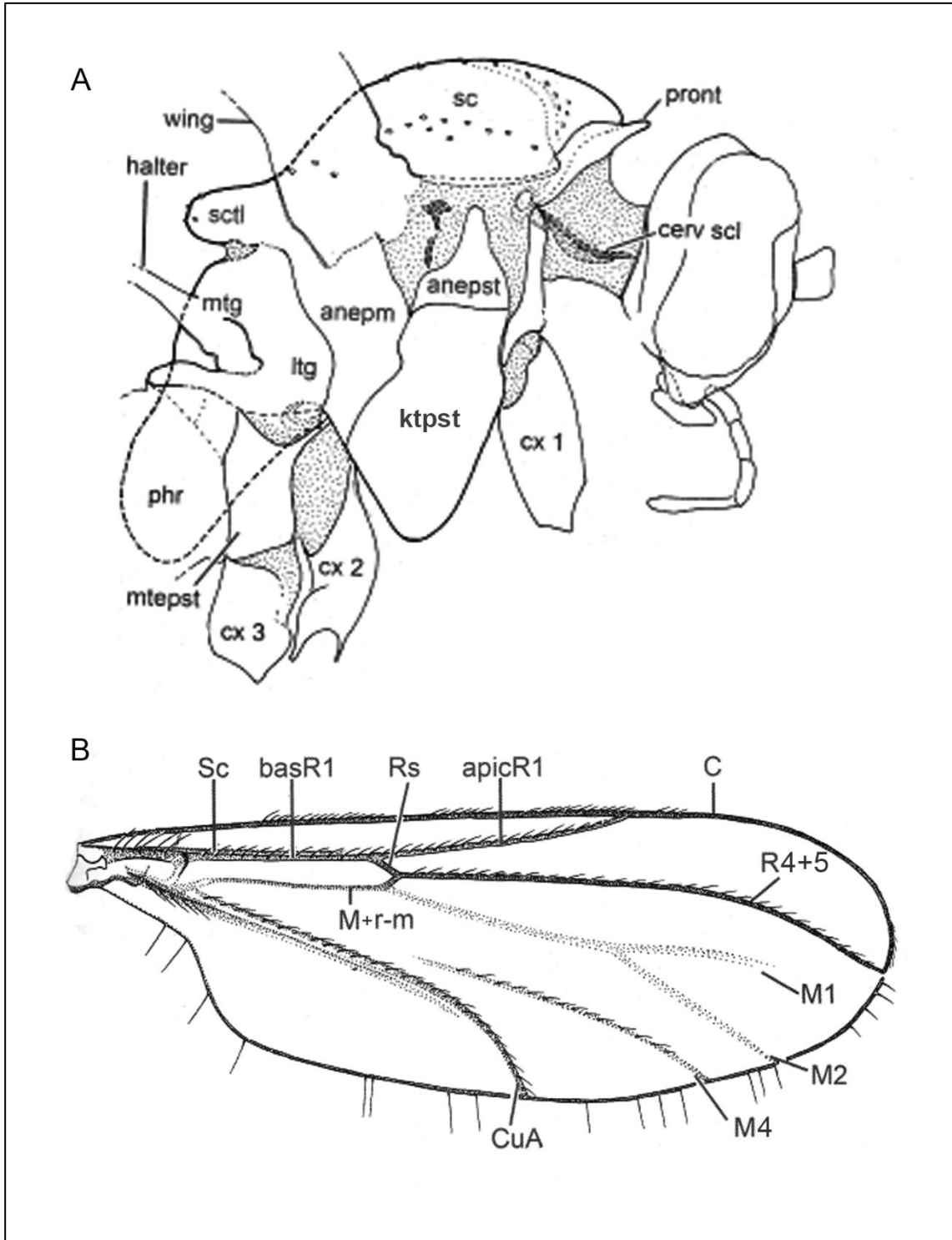


Figure 7. Thorax and wing morphology of the porricondyline. A. *Diallactia crocea* (Kieffer, 1894); **B.** *Wyattella* sp. Mamaev, 1964. Without scale. anepm = anepimeron, anepst = anepisternum, cerv scl = cervical sclerite, cx = coxa, ktpst = katepisternum, lrg = laterotergite, mtepst = metepisternum, mtg = medio tergite, phr = phragma, preepst = preepisternum, proepst = proepisternum, pront = pronotum, sc = scutum, scti = scutellum. Modified from Jaschhof & Jaschhof (2013).

Legs. The legs are two or three times longer than the body and covered by setae. The first tarsomere is shorter than the second, and the basitarsi are prolonged ventroapically to form a microtrichose projection or a short spine (Fig. 8B–C). The claws are curved, simple, or toothed, and the empodia is shorter than claws or rudimentary (Fig. 8D–F).

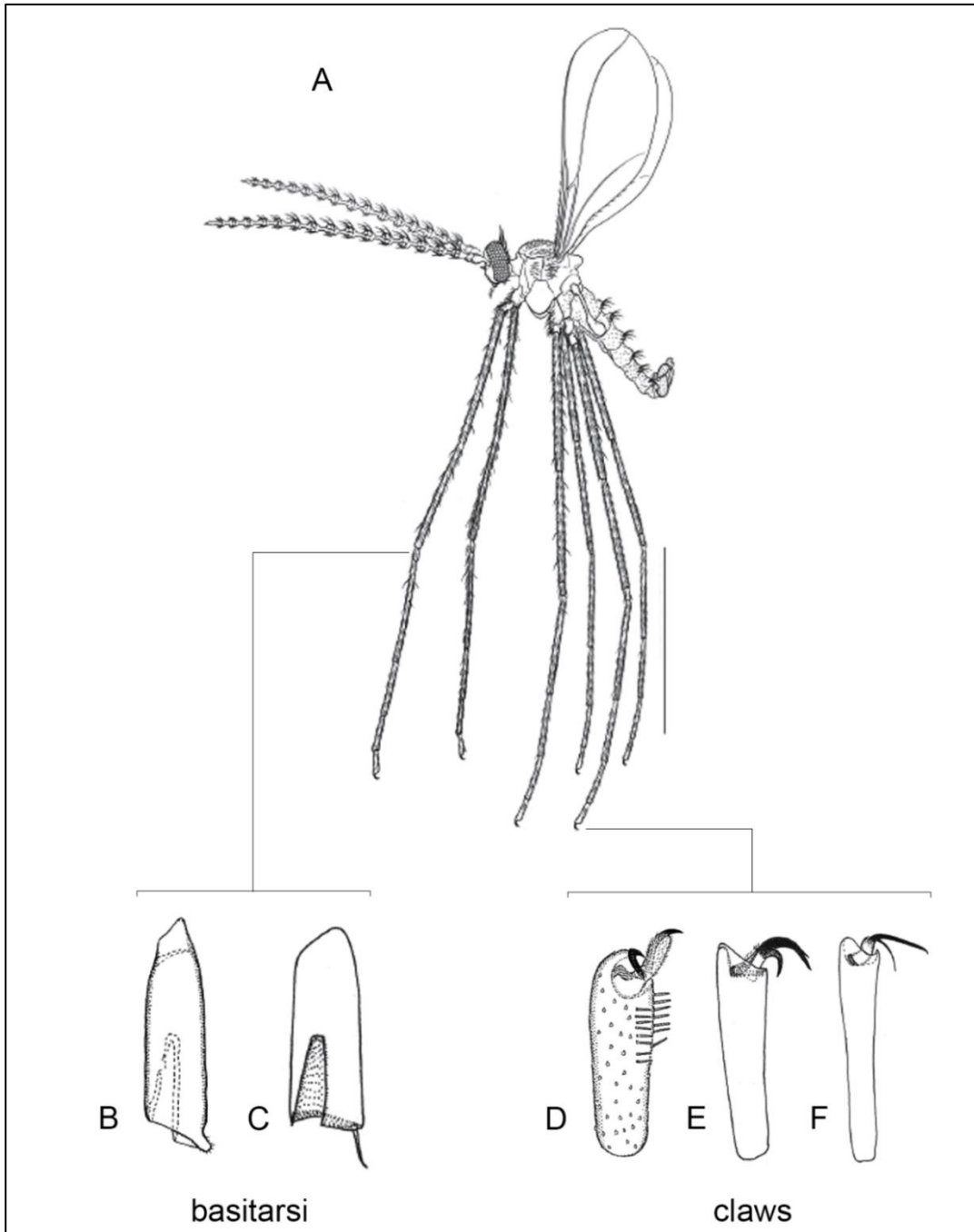


Figure 8. Legs of the porricondylines. A. *Zadbimya* sp. Scale 1.0 mm; B. *Glemparon warra* Jaschhof, 2018; C. *Zadbimya browni* J Jaschhof & Jaschhof, 2014; D. *Gardenforsia oelandica* Jaschhof, 2019; E. *Zadbimya browni* Jaschhof & Jaschhof, 2014; F. *Zadbimya aberrans* Jaschhof & Jaschhof, 2014. Modified from Jaschhof & Jaschhof (2014, 2018, 2019).

Terminalia (Fig. 9A–B). The gonocoxites are interconnected by a ventral and a dorsal bridge. Gonocoxal processes are present on each side of the ventral emargination, they vary in size, sclerotization, and shape. The gonostyli may bear microtrichia (Fig. 10A), strong setae apically (Fig. 10B), or different types of claws such as pectinate (Fig. 10C–D), toothed (Fig. 10E), or plaque-like (Fig. 10F). The parameres are strongly sclerotized, bifid or single in most Porricondylinae (*sensu* Jaschhof & Jaschhof, 2013) or fused forming a membranous tegmen in Winnertziinae. The aedeagal apodeme is rodlike or tubelike. The hypoproct may be single and conical or bilobed, and bears 1–2 pairs of apical setae. The cerci are bilobed, wider and more setose than hypoproct. Tergite 9 is usually emarginated, subrectangular to subtrapezoid with scattered setae (Jaschhof & Jaschhof, 2013).

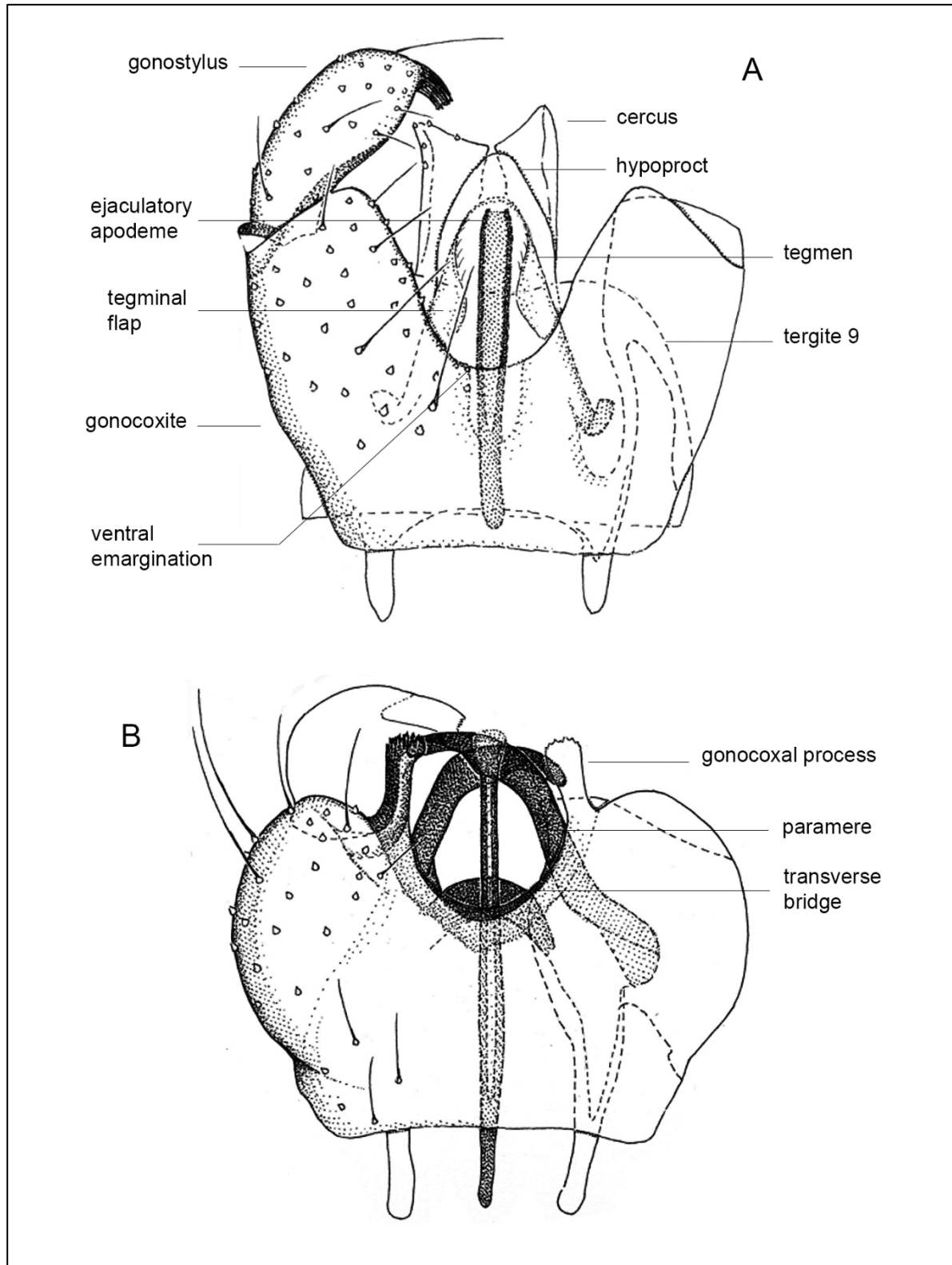


Figure 9. Morphology of the male terminalia of the porricondyline. **A.** *Winnertzia ekdalensis* Jaschhof & Jaschhof, 2020; **B.** *Porricondyla nigripennis* Jaschhof, 2013. Without scale. Modified from Jaschhof & Jaschhof (2020a).

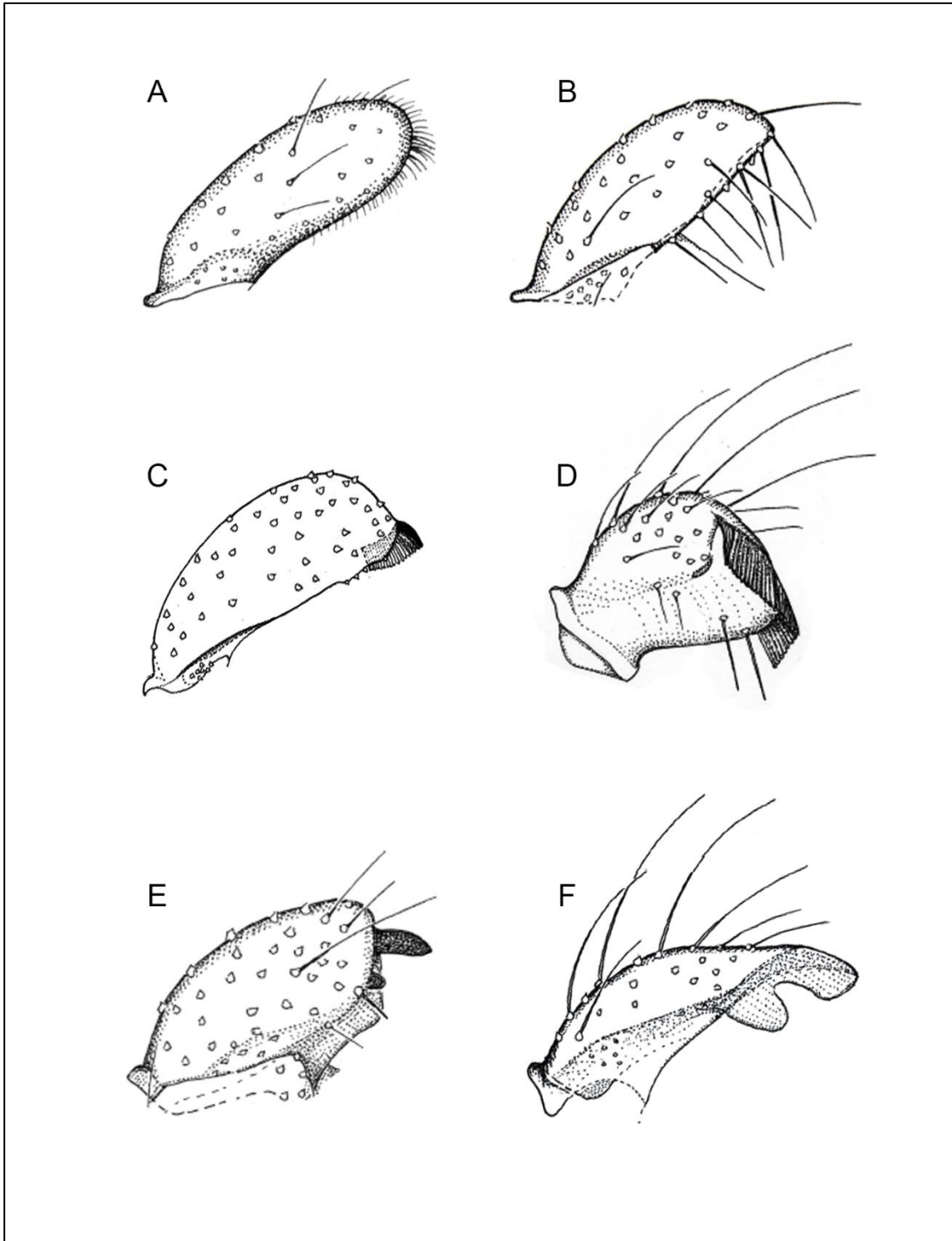


Figure 10. Types of gonostylar claws of the porricondylines. **A.** Microtrichia of *Winnertzia angustistylus* Jaschhof, 2020a; **B.** Clawless gonostyli with strong setae apically of *Rhipidoxylomyia excavata* Mamaev, 1964; **C.** Pectinate claw of *Winnertzia bulbifera* Mamaev, 1963; **D.** Pectinate claw of *Porricondyla gemina* Jaschhof, 2020b; **E.** Teeth of *Porricondyla bidentula* Jaschhof, 2020b; **F.** Plaque-like claw of *Monepidosis sceptroides* Jaschhof, 2016. Without scale. Modified from Jaschhof & Jaschhof (2013, 2016, 2020a, 2020b).

6. CONCLUDING REMARKS

- The classification of Porricondylinae and Winnertziinae, as proposed by Jaschhof & Jaschhof (2013), has undergone a comprehensive re-evaluation. A new classification system, based on a rigorous cladistic analysis, has been introduced.
- Porricondylinae and Winnertziinae (*sensu* Jaschhof & Jaschhof, 2013) have been divided into four distinct subfamilies: Heteropezinae, Diallactiinae, Winnertziinae and Porricondylinae. This reclassification is in line with earlier findings presented in Tastás-Duque's unpublished PhD thesis (2001).
- This rigorous and detailed study has enriched the Neotropical fauna with 72 new species and the introduction of 30 new genera to be published. This represents an increase of almost 10% in the richness of this fauna.
- After this study, the porricondyline of the Neotropical fauna represent 10% of the diversity of this group, which corresponds to the representativeness average of this fauna in the world.
- The vastly neglected group of fungivorous midges is highlighted here, revealing their remarkable diversity. It is therefore imperative that future research efforts continue to be undertaken to further explore and understand the inner relationships of these groups, the limits, and geographic realms of the supraspecific taxa.
- All the material studied was already collected and deposited in different collections housed in Brazilian and foreign institutions. The Natural History Museums, such as the MZUSP, where the study was carried out, play a fundamental role in the safeguard of such testimonies of biodiversity.

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