Figure 1. Author collecting at Grande Sertão Veredas National Park, at the border of Minas Gerais and Bahia (Brazil).

Morphology in the era of phylogenomics: **a case for Dexiinae (Tachinidae) phylogeny**

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The subfamily Dexiinae is a large and morphologically diverse group, with larvae that parasitize mainly immatures of Coleoptera and Lepidoptera. The subfamily is distributed worldwide (Guimarães 1971, Crosskey 1976, Cantrell & Crosskey 1989, Herting & Dely-Draskovits 1993, O'Hara & Wood 2004, O'Hara & Cerretti, 2016, O'Hara *et al*., 2019) and contains 1375 species in 287 genera. Dexiinae have had a problematic history regarding their systematic position relative to the other tachinid subfamilies. The subfamily has been regarded as close to Tachininae (Herting 1983), Voriinae (Dexiinae, in part) (Mesnil 1966, Richter 1987), Dufouriinae (Dexiinae, in part), and Phasiinae (Shima 1989). Shima's (1989) proposition was partially recovered by Cerretti *et al*. (2014), because Dexiinae were considered as close to Phasiinae, but as paraphyletic with it. However, in the last phylogenetic hypothesis of Tachinidae, Stireman *et al*. (2019) considered it as monophyletic. Today Dexiinae appears to be established as having a sister group relationship with Phasiinae.

For a long time the Dexiinae were thought to be supported as a subfamily of Tachinidae by a putative synapomorphy in the male terminalia, that being a membranous and flexible connection between the basiphallus and distiphallus. However, this traditional putative synapomorphy was not confirmed by Cerretti *et al*. (2014). Instead, this character state was interpreted as having undergone a reversal, being secondarily lost in most Phasiinae. In contrast to previously hypotheses, this character state of a dexiine-type phallus was a synapomorphy of the clade Dexiinae + Phasiinae. The Dexiinae were paraphyletic in this reconstruction because the Dufouriini were not monophyletic and were more closely related to the Phasiinae than to the rest of Dexiinae. Santis (submitted) also found the Dexiinae to be paraphyletic in relation to Phasiinae, with evidence supporting a likely new subfamily, Dufouriinae (with Dufouriini and Freraeini), formerly in Dexiinae, as the sister group to Phasiinae.

Cerretti *et al* (2014) discussed three tribes of Dexiinae: Dexiini, Dufouriini and Voriini. Of these, only Dexiini was regarded as monophyletic. As more tribes and genera were sampled, Stireman *et al*. (2019) recovered some tribes as polyphyletic, leading the authors to suggest that the tribal classification is likely to need a major revision. For instance, Voriini and Dexiini were recovered as polyphyletic groups, the former appearing in five distinct places in the Dexiinae clade and having one genus in the Tachininae (*Microchaetina* van der Wulp), and the latter appearing in three places in the Dexiinae clade as well as having one genus in the Tachininae (*Eulasiona* Townsend). Both *Microchaetina* and *Eulasiona* were singled out as possibly misplaced in the Dexiinae.

The checklist of Tachinidae of O'Hara *et al*. (2019) was compiled on a world basis and followed some of the better-supported changes suggested by the recently published phylogenies (i.e., Cerretti *et al*. 2014, Blaschke *et al*. 2018, Stireman *et al*. 2019). Therefore it can be cited here for comparative purposes. In it, the Dexiinae are composed of 13 tribes: Dexiini, Doleschallini, Dufouriini, Epigrimyiini, Eutherini, Freraeini, Imitomyiini, Parerigonini, Rutiliini, Sophiini Telothyriini, Uramyini and Voriini. One of these, the tribe Imitomyiini, is an ambiguous taxon, being considered as Phasiinae in Cerretti *et al*. (2014) and Blaschke *et al*. (2018), but as Dexiinae in Stireman *et al*. (2019). The checklist also reflects a big change in the interpretation of the Voriini, suppressing into it the former tribes Thelairini, Camplylochetini and Wagneriini. My study is favoring a different tribal composition within the Dexiinae, namely the following nine tribes: Dexiini, Doleschallini, Epigrimyiini, Eutherini, Rutiliini, Sophiini, Telothyriini, Uramyini and Voriini (along with tribes that were considered as Dufouriinae by Santis (submitted): Dufouriini, Freraeini and the currently invalid Oestrophasiini).

Certainly, Dexiinae systematics has recently undergone improvements in its knowledge and understanding. However, the Neotropical dexiines are still in great need of taxonomic and phylogenetic work. The Neotropical Region is recognized for its rich and diverse fauna and flora and different ecoregions. For instance, the Cerrado is the largest savanna formation in South America and is characterized by a ground layer of grasses and a mixture of small palms, shrubs, and trees (Fig. 2).

Figure 2. The Cerrado, a vast and heterogeneous savanna covering much of southcentral Brazil.

Regarding tachinids, the Neotropical Region is noteworthy for its high rates of endemic species. Of the 1073 species of Tachinidae in the world that are endemic to one region, 608 (57%) of them are in the Neotropics (O'Hara & Henderson 2018). But, at the same time, this highly endemic fauna holds serious taxonomic problems. These problems can be related to two issues: an excessive number of genera (many originally described without illustrations or with characters that currently do not aid in their recognition) and by the high number of undescribed species. The identification of Neotropical material requires cross-checking among existing identification keys and other resources, often prepared for other regions (e.g., Wood & Zumbado 2010) to reach an approximation of a particular group to which a taxon may belong. Even with the great contributions of authors like J.H. Guimarães (mainly Brazilian taxa), R. Cortés (Chile and Argentina), J.M. Aldrich (particularly Patagonia), W.R. Thompson (Trinidad), H.J. Reinhard, D.M. Wood and J.E. O'Hara, the progress has been small in relation to the immensity of the taxonomic problems still unresolved. In the Dexiinae for instance, of the 288 genera in the world, 162 occur in the Neotropics and of these 85 (or 52%) are monotypic. The main keys to these genera are still those in Townsend's (1934–1942) Manual of Myiology

The early 21th Century marked a new generation of tachinidologists, for instance, the revisions and new species of dexiine genera from Area de Conservación Guanacaste in northwestern Costa Rica by Fleming and coauthors (e.g., Fleming *et al*. 2015, 2017), and by Brazilian workers dealing with Neotropical taxa (e.g., Toma 2001, Nihei & Pansonato 2006, Santis 2018, Dios & Santis 2019). Only recently has all the Neotropical taxa of Dexiinae and the rest of Tachinidae been assembled together into a checklist of world Tachinidae (O'Hara *et al*., 2019). While this is clearly an advance in comparison to Guimarães (1971), as a checklist it does not have descriptions or keys to genera or species and therefore does not help with the identification of the difficult Neotropical fauna of tachinids.

Given these problems with Neotropical Tachinidae, there is always room for more work and much that can be added. My Ph.D. project is being done at the Laboratório de Sistemática e Biogeografia de Insecta at the Universidade de São Paulo (Brazil) under the supervision of Dr. Silvio Shigueo Nihei. The general objective of this study is to propose a natural classification (i.e., containing only monophyletic groups) which represents the phylogeny of Dexiinae, based on adult and immature (egg and larval) stages, and with an emphasis on Neotropical taxa. With the resulting phylogenetic tree, I hope to determine if Phasiinae are the sister group of Dexiinae, and if Dexiinae are monophyletic or paraphyletic. My more specific objectives are to delimit the following ambiguous tribes in order to propose for each of them a well-supported systematic placement at the subfamily and tribal level:

1) are the Eutherini a clade of Dexiinae?
2) are the Imitomyini a clade of Phasiinae?
3) are tribes Thelairini, Campylochetini and Wagneriini of Crosskey (1976) invalid and best placed within a large Voriini?
4) are the tribes Zeliini and Trichodurini of Townsend (1934–1942) invalid and best placed within Dexiini?
5) are the subtribes Rhamphinina, Stominina, Phyllomyina and Eriothrixina of Mesnil (1966) invalid and best placed within Voriini?

To answer the above questions in my Ph.D., I intend to include all the valid and invalid tribes of Dexiinae, and possible Dexiinae, from all over the world. I am trying to sample the greatest number of genera of Neotropical Dexiinae as possible, and by doing so I hope to understand the morphological disparity of this group. This will help with the identification and placement of long unrecognized taxa; e.g., *Tyreomma muscinum* van der Wulp, 1896 (Fig. 3).

It soon became clear that taxonomic revisions are needed, and some are being prepared. For example, the Dexiini with spine-like setae on the abdomen, like *Hystrichodexia insolita* (Walker, 1853) (Fig. 4). I am expanding my knowledge and sampling of Dexiinae by studying the collection of the Natural History Museum (London, England). At this museum I have been able to study the type material described by van der Wulp, Bigot and Walker, authors who famously described species using poorly defined characters and some trivial ones. Visiting this collection has also allowed me to include more terminal taxa in the analysis. My preliminary analyses recovered a tree for the Dexiinae that again is paraphyletic andthe results are different from those proposed before. They are, however, preliminary and some changes will occur once more taxa are added to

the analysis. I expect to recognize synapomorphies for most or all of the tribes and for the subfamily itself, as well as discuss and try to interpret some important Dexiinae traits.

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Figures 3-4. Type specimens of Dexiinae in the Natural History Museum, London. **3**. *Tyreomma muscinum* van der Wulp (female). **4**. *Hystrichodexia insolita* (Walker) (female).

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